

*NORTH
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ANADROMOUS
FISH
COMMISSION*



BULLETIN NUMBER 1

Assessment and Status of Pacific Rim Salmonid Stocks



Edited by: David W. Welch, Douglas M. Eggers,
Kiyoshi Wakabayashi, and Vladimir I. Karpenko

Technical Editors: Hisashi Endo and David W. Welch

VANCOUVER, CANADA, 1998

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The elegant illustration on the cover of this Bulletin is the work of Marijke Nap, a Dutch artist who lives in Canada. Marijke was born in Telémaco Borba, Brazil. After moving to Canada she studied art at Capilano College, Vancouver, and is presently a member of the Print Making Art Institute at Capilano College. She was a member of the INPFC Secretariat Staff from 1988-1992, and then worked again for the NPAFC Secretariat from 1995-1997.

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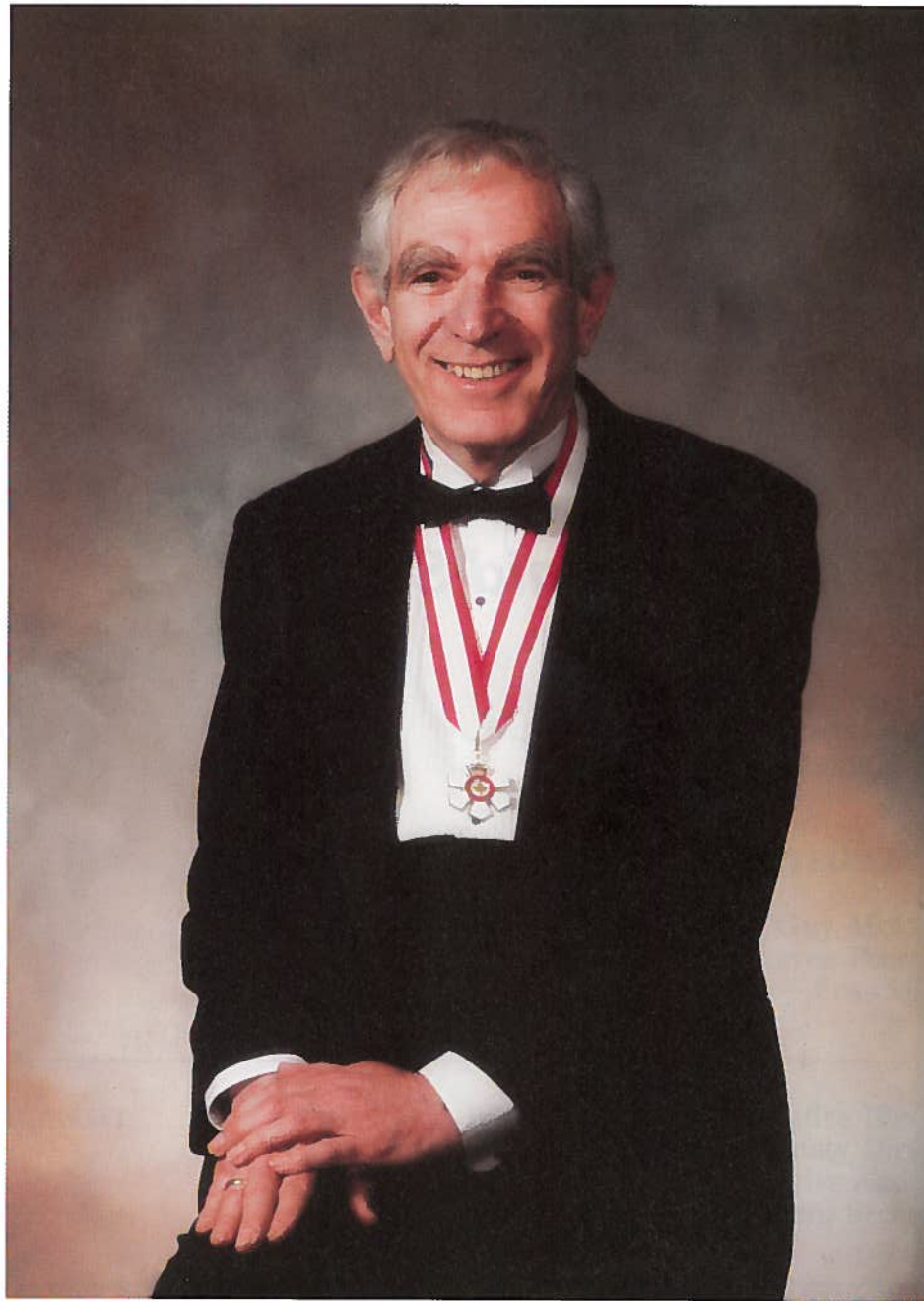
Assessment and Status of Pacific Rim Salmonid Stocks

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In Memoriam
Leo Margolis, O.C., Ph.D., F.R.S.C
1927-1997



This first Bulletin of the North Pacific Anadromous Fish Commission is dedicated to the memory of Dr. Leo Margolis (1927-1997), a friend and mentor to many of the scientists from around the Pacific Rim attending this Symposium.

I. Preface

This Bulletin is a compilation of papers presented at an International Symposium on Assessment and Status of Pacific Rim Salmonid Stocks, held in Sapporo, Japan, October 28-29, 1996, under the auspices of the North Pacific Anadromous Fish Commission. The Symposium, hosted by the Government of Japan, was the first scientific symposium held by the Commission.

The symposium was organized by the Symposium Steering Committee, which was composed of scientists from the Parties for the Commission. The members were:

Akira Taniguchi (Chairman)
Tohoku University
Sendai, Japan

Douglas Eggers
Alaska Department of Fish and Game
Juneau, Alaska, U.S.A.

Osamu Hiroi
National Salmon Hatchery
Fisheries Agency of Japan
Sapporo, Japan

Donald Noakes
Pacific Biological Station
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Nanaimo, British Columbia, Canada

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Kamchatka Fisheries and Oceanography Research
Institute (KamchatNIRO), Kamchatka, Russia

Kiyoshi Wakabayashi
National Research Institute of Far Seas Fisheries
Fisheries Agency of Japan
Shimizu, Japan

Local arrangements were made by a local organizing committee established by the host country, Japan.

Research papers were presented by scientists of the Parties (Canada, Japan, Russia, and the United States)

and by the Republic of Korea. Scientific papers were submitted at the symposium. The papers were peer reviewed and revised by the authors before final review and acceptance by the Editors before publication.

I wish to thank the other members of the Editorial Committee, Douglas Eggers (Alaska Department of Fish and Game, U.S.A.), Vladimir Karpenko (Kamchatka Fisheries and Oceanography Research Institute, Russia), and Kiyoshi Wakabayashi (National Research Institute of Far Seas Fisheries, Japan) and the many other scientists of the Parties who participated in the technical reviews of the manuscripts.

The publication of this Bulletin marks two milestones in the distinguished history of INPFC and its successor, the NPAFC. The completion of this, the first Bulletin of NPAFC, was completed in the exceptional period of only 1 year and 3 months from the ending of the Symposium to completion of the bound Proceedings—a record not previously matched by any INPFC bulletin nor (to my knowledge) any other organization in the North Pacific. I would like to express my sincere thanks to the Director of the NPAFC, Dr Irina Shestakova, and her staff, Ms Wakako Morris and Ms Denise McGrann, for their skill and assistance in organizing and executing the Symposium, and in preparing all of the documents for publication in camera-ready format. I also wish to thank Mr Hisashi Endo of the Secretariat of the Commission for his substantial contribution to the publication as technical editor and a member of the Secretariat until his return to Japan at the end of his term as Deputy Director, in June 1997. The Secretariat was also ably assisted by Dr Clif Forrester in the editing of several manuscripts after Mr Endo's return to Japan. The Secretariat's exemplary performance in completing this Symposium sets a high standard for future Symposia to aspire to.

Approval for publication by the Commission does not necessarily constitute endorsement of the views of the authors.

David W. Welch
Chairman
Editorial Committee



Participants: (from left to right, from back to front row)

(back row) Kate Myers, Michael Henderson, Terry Beacham, Jack Helle, Leo Margolis, Vladimir Karpenko, Kazuhiko Utsumi, Koji Imamura, Brian Bue, Bill Heard, Toshio Hidejima, Ibrahim Fares, Richard Wilmot, Paul Niemeier, Leon D. Khorevin, Vladimir Radchenko, Oleg Gritsenko, Vladimir Tsiger, Conrad Mahnken, David Welch, Paul Ryall, Kazuya Nagasawa, Ole Mathisen, Hal Geiger, Hisashi Endo, Jiro Seki, Masa-aki Fukuwaka, Alexander Kaev, Hiroyasu Hasegawa, Kinya Nishimura, Nobuhisa Koide, Toshiya Suzuki. (second from back row) Chong Guk Park, Houji Okada, Toyohiko Hikita, Kazuzki Naito, Skip McKinnell, Hiroshi Ueda, Michael Dahlberg, Don Noakes, Jim Seeb, Robert Kope, Akihiko Hara, Doug Eggers, Dale Kolody, Tony Gharrett, David Meerburg, Shigehiko Urawa, Robert Walker, Shigeo Hayase, Toshimasa Ban. (second from front row) Loh-Lee Low, Jessica Gharrett, Hiroyuki Sakano, Taiki Asami, Soto-o Ito, Shogo Takagi, Bruce Finney, Dick Beamish, Natalya Varnavskaya, Gary Winans, Sharon Hawkins, Ken-ichi Hayashizaki, Yutaka Nagata, Masahide Kaeriyama, Sergei Sinyakov, Kazuma Ohkuma, Wakako Morris, Nancy Davis. (front row) Tatsuya Takami, Steven Fried, Hiroshi Kojima, Akira Taniguchi, Hiroshi Kawamura, Ki Baik Seong, Ulrich Reinhardt, Irina Shestakova, Kiyoshi Wakabayashi, Kohei Yamauchi, Hiroshi Mayama, Yukimasa Ishida, Morihiko Kawana.

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III. Opening Remarks

Welcome to the first science symposium of the North Pacific Anadromous Fish Commission -- an international symposium on salmon. There have been many similar salmon symposia before, but this one is special to the Commission because it brings together significant numbers of salmon experts from the four major salmon producing countries of the North Pacific Rim and experts from other countries to advance salmon science for the Commission. After all, salmon is still the most important fisheries resource in the North Pacific Ocean. It certainly has the richest legacy of all the fisheries in the North Pacific Ocean.

Hokkaido is certainly the ideal spot to hold such a symposium. Salmon is important to the Japanese

people and Hokkaido is where salmon are mostly produced in Japan. The organizing committee of the symposium and the local organizing committee of this event have done an excellent job of setting up the agenda and the venue for us to indulge in the intricacies of salmon issues.

Over the next few days, we'll be reviewing and learning of new research on the biology of Pacific salmon, their history, their wide geographical distribution, and their interacting dynamics with their ecosystems. We will learn about enhancement of salmon runs and become cognizant of their success and impacts on natural runs and the carrying capacity of the ecosystem. Let us begin.

Loh-Lee Low
Chairman
Committee on Scientific Research and Statistics
1996-1997

IV. Introductory Remarks

"Ohayo-gozaïmasu (Good morning)," ladies and gentlemen.

It is a great honor for me to make the introductory remarks at this very first symposium of the North Pacific Anadromous Fish Commission (NPAFC), entitled "Assessment and Status of Pacific Rim Salmonid Stocks," here in Sapporo, Japan. My major field is planktology, not the biology of salmon. Therefore, some of you may wonder why I have been given the chairmanship of this symposium. Let me explain. Although I am not a salmon biologist, I am not a complete layman in the field either. Since relationships between plankton and salmon are very close in natural systems, plankton biologists and salmon biologists are also closely connected.

It was the famous planktologist, the late Professor Sigeru Motoda of the Faculty of Fisheries of Hokkaido University (FFHU), who repeatedly emphasized the importance of the systematic and quantitative investigation of the plankton communities in the subarctic Pacific. This is because the subarctic Pacific nurtures rich populations of commercially important fish, including Pacific salmon (cf. Taniguchi 1995). During his time at Hokkaido University, Dr. Motoda was always the leader of the long-term plankton investigation, starting from the inception in the 1950s (Motoda and Minoda 1974). He always encouraged FFHU people to continue this investigation. Such investigations were not easy in Japan in the years shortly after World War II. Because the fisheries harvesting salmon and many other species of fish were of particular economic importance in Japan, most people tended to quickly promote technical and practical work to increase the catch, rather than investigating the environmental factors that control fish production in natural systems. However, after much effort Dr. Motoda finally got agreement from the staff of FFHU and was able to draw financial support from the Fisheries Agency of Japan (JFA). Every year since then, the JFA has supported such plankton investigations as part of the ocean surveys of Pacific salmon, which were originally carried out by the FFHU's Training Ship *Oshoro Maru*, and later also by the *T/S Hokusei Maru*. The data obtained by these surveys have been regularly published in the Data Record of the Oceanographic Investigations and Exploratory Fishing, which has been published annually since 1957 by FFHU.

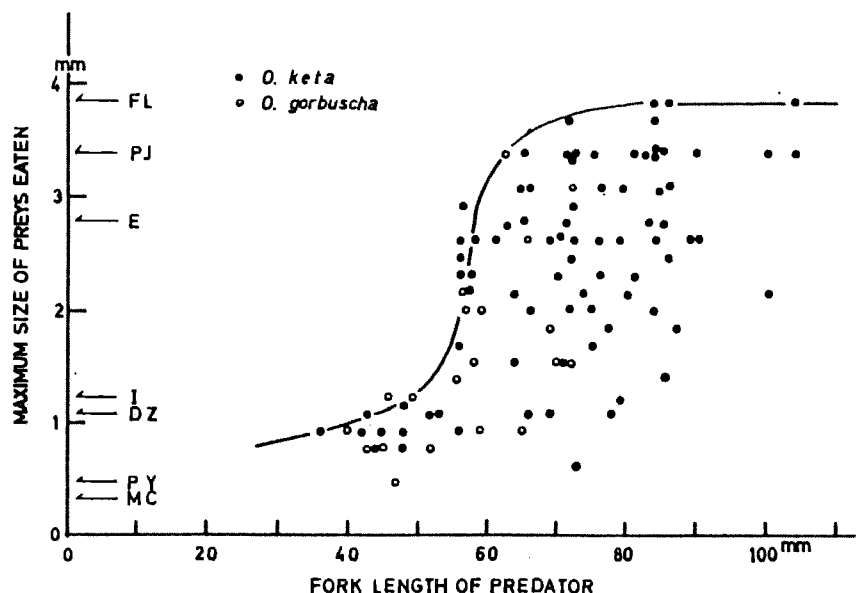
The accumulated data, begun under Dr. Motoda's leadership in the 1950s and continuing today, are now recognized as one of the longest ongoing studies of the biomass of summer zooplankton in the subarctic Pacific Ocean. This data set is now a shared treasure

among the Pacific Rim countries, and is frequently quoted in modern analyses of the long-term trend of plankton productivity (e.g. Brodeur and Ware 1992). I am very proud of my own contribution, though very small, to this data set which I made when I was a student of Professor Motoda. It is very regrettable that he passed away last year, on 24th September, 1995. If he were alive, he would be here and make us enjoy his invaluable, although sometimes dry and acerbic, comments on the salmonid studies of today.

Just after I "hatched out" of his supervision, I did an investigation of the gut contents of the salmonid fry inhabiting the inshore water of southern Hokkaido, Japan (Okada and Taniguchi 1971). Fig. 1 is the main conclusion of that work, indicating that the feeding capability of salmonid fry suddenly increases during their life in inshore waters. Development of their feeding capability is not a simple linear function of their body size. This trend was clear when their prey size was expressed in body width, instead of body length, which may explain the relative difficulty for the fry to bite their prey organisms. In other words, the predatory capacity of salmon fry may not be determined only by the swimming or escaping ability of the prey organisms, which is related as a linear function of their body length. Instead, the development of predation capability of the salmon fry may be much more important. This capacity may follow discrete stages, or steps, as a result of a possible stepwise development in the function of feeding organs like the mouth and eyes, as well as their swimming ability.

Lying in the background to this symposium is the question of the future of the Pacific salmonid populations, and the uncertainty concerning the healthiness of these rapidly growing populations. Although an increase in stock size is basically welcomed, concurrent declines in body size and increasing age at maturity, plus the slump in the market value resulting from increased catches are causing anxiety about the future. To resolve this issue, it is necessary to determine and monitor the size and status of the salmonid stocks. Therefore, the subject of this symposium is quite suitable for the first NPAFC symposium. I sincerely hope for all participants that this symposium will be a forum leading to continual cooperative international investigations on Pacific Rim salmonid populations. Of course, planktologists will also contribute to these investigations in various aspects. For example, I expect that planktologists may predict changes in the taxonomic composition of the subarctic zooplankton community under increasing predation pressure by salmonid populations.

Fig. 1 Prey-predator relationship in size between chum and pink salmon fry and food organisms observed in inshore waters of southern Hokkaido, Japan. Sigmoid curve traces size of the largest prey ingested by fry of various fork lengths. Arrows indicate the maximum size (measured as body width) of common prey organisms: micro-copepods (MC), young *Parathemisto* spp. (PY), decapod zoea (DZ), insects (I), adult euphausiids (E), adult *Parathemisto japonica* (PJ), and fish larvae (FL). (After Okada and Taniguchi, 1971).



In the subarctic Pacific, nutrients are hardly depleted by primary producers even in summer (Anderson et al. 1969; Taniguchi 1972; Shiimoto 1994; Saito 1996; Kasai et al. 1997). The stock of nutrients in summer is quite large compared to those of phytoplankton and net zooplankton (Table 1), except in the Oyashio region where intensive diatom blooms occur in April/May (Kasai et al. 1997). This indicates that the primary production in summer in these sea areas is controlled by other factors than nutrient limitation. Zooplankton grazing is the most probable factor (e.g. Frost 1983, 1991; Shiimoto et al. 1997). It was recently reported that microzooplankton are major grazers in the Gulf of Alaska (Miller et al. 1991; also cf. Banse 1995; Landry et al. 1997), where net zooplankton biomass is particularly low among the subarctic Pacific sea areas (Table 1). Grazing pressure by net zooplankton alone is not large enough to control the phytoplankton growth there (Miller and Nielsen 1988: cited from Miller et al. 1991). On the other hand, there have been some indications that the daily food requirement of net zooplankton is relatively large compared to daily primary production in the Oyashio region and the Bering Sea (cf. Taniguchi 1973; Ikeda and Motoda 1978a,b). If the latter is the case, net zooplankton control the primary production in these sea areas. This seems to be supported by the fact that net zooplankton biomass is apparently large in the Bering Sea and Oyashio region (Table 1). Dominant herbivorous zooplankters in these areas are not microzooplankton (Taniguchi, 1984), but large-sized

crustaceans such as *Calanus* spp., amphipods and euphausiids.

When the increasing salmon populations feed on these crustaceans, phytoplankton released from the grazing pressure can increase by taking advantage of the rich nutrients (Cooney 1988; Shiimoto et al. 1997). In such a situation, it can be possible that the production of zooplankton increase again. This is analogous to the cattle-farming technique that thins out excess cattle from a limited area of the grazing land. In nutrient rich areas like the subarctic Pacific, the thinning-out process of net zooplankton (in this case by increasing salmon predation) may enhance total plankton production (Taniguchi 1992). In other words, it is not impossible that the increasing salmonid biomass can expand the carrying capacity of their own habitat. However, this does not necessarily mean that the increased plankton production expands in a directly-proportional manner with the carrying capacity. Again the relationship between these two may be non-linear.

Zooplankton populations which emerge after intensification of salmonid predation would not be exactly the same as those before the predation. *Calanus*, amphipods, and euphausiids possess a life span of one year or more and usually spawn at depth in cold seasons. Although their young are abundant in the surface layer in spring and early summer, they all descend to depth well below the surface layer by late summer (e.g. Heinrich 1957; Ponomareva 1963; Fulton 1973; Miller et al. 1984). Therefore, if predation removes them from the surface layer during

Table 1. Average values of stocks of nitrate-nitrogen, phytoplankton chlorophyll *a* and net zooplankton wet weight (>330 μ m) in surface layer of different open sea areas of the subarctic Pacific in summer. Equivalent carbon weight of each stock is also given.

Sea area (Reference)	NO ₃ -N ^{a)}		Phytoplankton ^{b)}		Net zooplankton ^{c)}	
	(μ M)	(mgC m ⁻³)	(μ gChl l ⁻¹)	(mgC m ⁻³)	(mgWW m ⁻³)	(mgC m ⁻³)
Bering Basin (3, 5)	15	1193	0.9	45	450	22.5
South of Aleutian (2, 5)	13	1034	0.3	15	200	10.0
Gulf of Alaska (1)	11	875	0.3	15	100	5.0
Oyashio Region (2, 4, 5)	2	159	0.5	25	340	17.0

Conversion factors to carbon weight: ^{a)} 12×10^{16} , ^{b)} 50, ^{c)} 0.05

Reference: 1 Frost (1983), 2 Kasai et al. (1997), 3 Motoda and Minoda (1974),
4 Saito (1996), 5 Taniguchi (1972)

warm seasons, their population cannot recover until the next winter/spring. Opportunistic zooplankters which can increase during warm seasons should be those which possess shorter life spans and rapid growth rates. Apart from the microzooplankters, which have been confirmed to predominate in the Gulf of Alaska (loc.cit.), small-sized copepods, for example, *Acartia*, *Oithona*, *Pseudocalanus*, and most gelatinous zooplankters, such as hydromedusae and salps, are the most probable components of the latter type of zooplankton (Fig. 2). Lower abundance of large-sized copepods in the years when abundance of pink salmon is high is actually found south of the Aleutians (Shiomoto et al. 1997). This shift in zooplankton species composition should alter its value as food stock for different salmonid species. Such an alteration then will change the carrying capacity in a

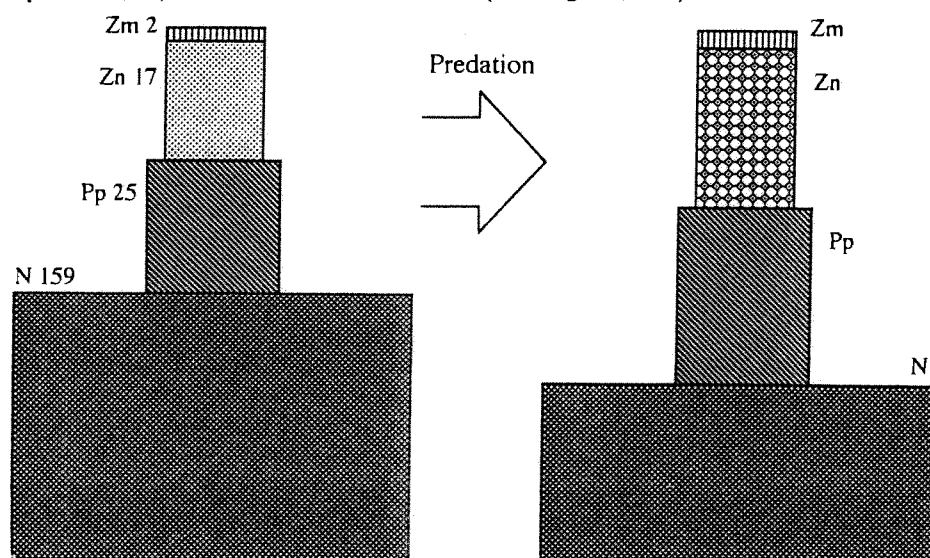
species-specific manner, and in the final analysis, change the salmonid populations' species composition.

The Steering Committee has accepted 71 papers from six countries for presentation: Canada, Japan, Korea, Russia, the U.K., and the U.S.A. Twenty-four of the 71 papers will be presented orally and the remaining 47 will be presented at the poster session. We hope this symposium will lead all participants to fruitful discussions and the consolidation of future cooperative research and management of our Pacific salmonid stocks.

Thank you very much.

Akira Taniguchi
Chairman
Steering Committee

Fig. 2. Diagram illustrating a potential alteration in species composition of net zooplankton after intensified predation by salmon in the nutrient-rich subarctic Pacific in summer/fall. Dominant species of net zooplankton would change from larger crustaceans such as *Calanus*, amphipods, and euphausiids to small-sized copepods and gelatinous plankters such as hydromedusae and salps. For standing stocks before predation, average values in Oyashio region (listed in Table 1) are adapted to nutrient (N), phytoplankton (Pp) and net zooplankton (Zn). Biomass of microzooplankton (Zm) is assumed to be ca. 10% of Zn (cf. Taniguchi, 1984).



ACKNOWLEDGEMENT

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Trends in the Status of Pacific Salmon Populations in Washington, Oregon, California, and Idaho

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Kope, R. and T. Wainwright. 1998. Trends in the status of Pacific salmon populations in Washington, Oregon, California, and Idaho. N. Pac. Anadr. Fish Comm. Bull. No. 1: 1-12

Over the past 3 years, the National Marine Fisheries Service, Northwest Fisheries Science Center has conducted coastwide status reviews of Pacific salmon in Washington, Oregon, California, and Idaho. Patterns of stock health have emerged that relate to life history, and freshwater and marine distribution. For most species, the health of natural populations declines from north to south. The health of natural populations also declines from west to east as the length of freshwater migration increases. Across species and life history strategies, declines in natural populations generally increase with the length of freshwater residence. Populations of pink salmon and chum salmon are doing relatively well, while populations of chinook, coho, and sockeye salmon have experienced greater declines. Trends in the abundance of natural populations of steelhead, and chinook and coho salmon are obscured to some degree by extensive hatchery programs. These patterns implicate the availability and quality of freshwater habitat as a primary factor in observed declines in abundance.



INTRODUCTION

The National Marine Fisheries Service (NMFS) has responsibility for administering the United States Endangered Species Act (ESA) for marine and anadromous species. The ESA recognizes the importance of variability within vertebrate species by allowing the listing of "distinct population segments". NMFS has adopted a policy defining distinct population segments as evolutionarily significant units (ESU), then further defining ESUs (Waples 1991).

After receiving several petitions to list individual runs of Pacific salmon as endangered species, the NMFS initiated coastwide status reviews for all species of Pacific salmon. Status reviews have been completed for coho salmon (Weitkamp et al. 1995), pink salmon (Hard et al. 1995), and steelhead trout (Busby et al. 1996), and status reviews for chum salmon, sockeye salmon, chinook salmon, and cutthroat trout are in various stages of completion. Because the ESA is concerned specifically with the health of natural populations and the ecosystems they depend on, these status reviews have focused on natural populations and have included consideration of the demographic and genetic impacts of artificial propagation on natural production.

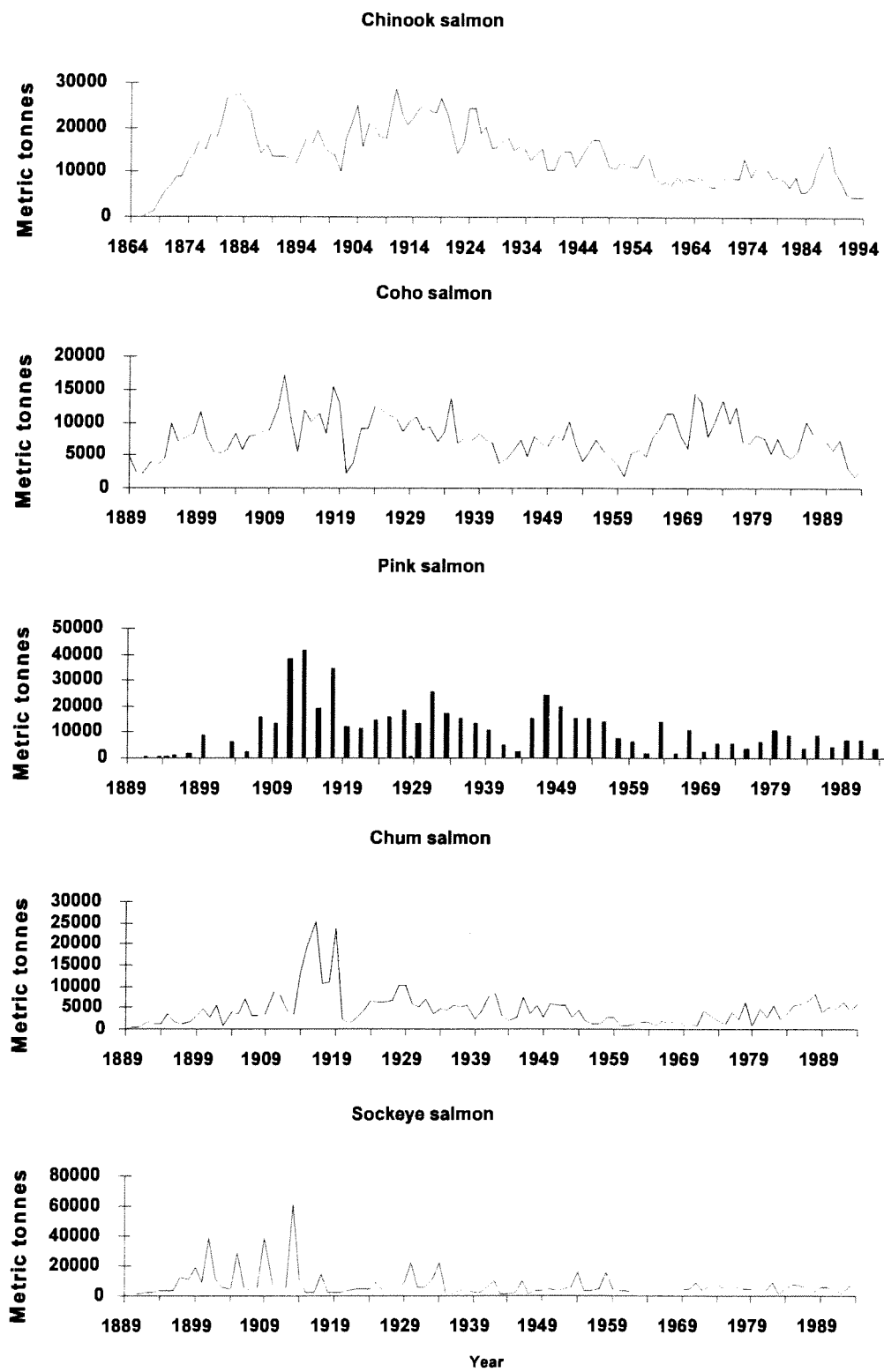
The process that NMFS has adopted for status reviews consists of two steps; the first is defining the ESUs comprising a biological species, and the second

is evaluating the risk of extinction faced by each ESU. These evaluations are carried out by a team of knowledgeable scientists after considering a variety of information. Factors considered in defining ESUs include: genetic similarity, life history patterns, freshwater and marine distribution, behavior, ecology, habitat types, and biogeography. Factors considered in evaluating the risk of extinction include: total abundance, current abundance relative to historic abundance, trends in abundance, demographic and genetic effects of artificial propagation, habitat condition, harvest, and other risk factors. Not all of these status reviews have been concluded, so rather than trying to summarize conclusions of the status reviews, we will summarize some of the information considered by the review team. Information summarized here will be limited to harvest, previous status reviews, and spawning escapement, and limited in geographic scope to Washington, Oregon, California and Idaho.

TOTAL HARVEST

Perhaps the most readily available measure of stock health is landed commercial catch (Fig. 1). Landings of most species peaked prior to 1920, and landings of chinook, coho, and pink salmon have varied considerably, but declined since then. Landings of sockeye salmon have varied widely, but

Fig. 1 Total commercial landings of salmon from California, Oregon, and Washington in metric tonnes.



have not had any clear trend since the 1920s, and chum salmon landings declined sharply until the late 1950s and have been increasing since then.

There are several reasons why landings for all species do not accurately reflect stock health. Harvest of chinook and coho salmon initially occurred in freshwater where only mature fish were taken. Most harvest of these species now occurs at sea where immature fish are taken, so numbers of fish harvested have not declined to the extent that the weight of landings has. Much of the harvest of Washington and Oregon stocks of these two species occurs in Canadian and Alaskan waters. This harvest is not included in domestic landings. In addition, much of the natural production reflected in the early landings has been replaced by hatchery production.

Most harvest of pink, chum, and sockeye salmon occurs in Puget Sound, but the landed catch of pink and sockeye salmon is dominated by Canadian stocks returning to the Fraser River. The declines in chum salmon landings in the early part of the century reflect the loss of many large stocks of chum salmon in the Columbia River and large declines in coastal Oregon stocks. The increase in landings since about 1960 is due to increases in the abundance of Puget Sound stocks.

PREVIOUS STATUS REVIEWS

Among the data considered in the course of the status reviews were prior population status assessments. Several reviews of stock status have recently been conducted. Nehlsen et al. (1991) examined a wide variety of risk factors and compiled a list of stocks from California, Oregon, Washington, and Idaho that they considered at risk of extinction. They classified stocks as extinct, possibly extinct, at high risk of extinction, at moderate risk of extinction, and of special concern. The categories of high and moderate risk of extinction were intended to roughly correspond to ESA categories of endangered and threatened respectively. Higgins et al. (1992) considered stocks on a finer scale than Nehlsen et al. (1991) and compiled a more detailed list for northern California.

Because Nehlsen et al. (1991) only considered stocks at risk, Huntington et al. (1996) compiled a coastwide list of healthy native stocks to complement Nehlsen et al. (1991). Again a wide variety of risk factors were considered, but their final criteria were based on abundance. They considered stocks to be healthy (Level II) if recent abundance was between 1/3 and 2/3 of what they estimated it would be in the absence of human impacts, and healthy (Level I) if recent abundance was at least 2/3 of what it would be in the absence of human impacts.

Status reviews analogous to Nehlsen et al. (1991)

and Huntington et al. (1996) have also been compiled for British Columbia (Slaney et al. 1996) and southeast Alaska (Baker et al. 1996), but they are outside the geographic scope of this summary.

Stock inventories were also compiled for salmonid stocks in Washington state (WDF et al. 1993), and for coastal basins in Oregon (Nickelson et al. 1992). WDF et al. (1993) evaluated stock status, but the criteria used depended primarily on level of recent production relative to the current potential. They did not consider the effects of hatchery production and stock transfers on the health of natural, native populations. Nickelson et al. (1992) did consider the effect of hatchery production and hatchery stock origin, but used numeric criteria that are not consistent with the other reviews.

Because only Nehlsen et al. (1991), and Huntington et al. (1996) applied uniform standards of stock status to the entire coast, only the lists they developed are summarized below. It should be noted that these lists are not comprehensive. There are many stocks that fail to meet the criteria for healthy stocks or for stocks at risk. The majority of stocks probably fall somewhere between these two broad categories.

When all stocks are considered, there is a tendency for a higher proportion of stocks in the extinct and high risk categories to occur in species with greater dependence on freshwater habitat as measured by the fraction of their lives spent in freshwater (Fig. 2, Appendix Table 1). Sockeye salmon have the greatest proportion of stocks in the extinct category, and pink and chum salmon have the highest proportion in the healthy categories. Steelhead are an exception to this pattern, with a higher proportion of stocks in lower risk categories than coho salmon or chinook salmon. This may be because they are more opportunistic, and their iteroparous life history and ability to residualize in freshwater may serve as a buffer against poor environmental conditions.

Confounding the relationship between degree of risk and life history is a tendency for more extinctions and greater risk for stocks with longer spawning migrations (Fig. 3, Appendix Table 1). Stocks with the longest migration corridors also have the greatest opportunity to encounter impassible dams and be excluded from their historic spawning habitat. In general, chinook, inland steelhead, and sockeye salmon have the longest spawning migrations.

When only coastal populations are considered, there is also a clear tendency for northern stocks to be in better health than southern stocks (Fig. 3, Appendix Table 1). Again, this pattern is confounded somewhat by the species composition in individual states. Only steelhead, chinook and coho salmon occur in all three states. Extant sockeye salmon populations only occur in Washington, and Idaho, pink salmon only occur in

Fig. 2 Proportion of stocks in each risk category from Nehlsen et al. (1991) and Huntington et al. (1996) by species. Species are arranged from front to back in decreasing order of the proportion of total life history spent in freshwater.

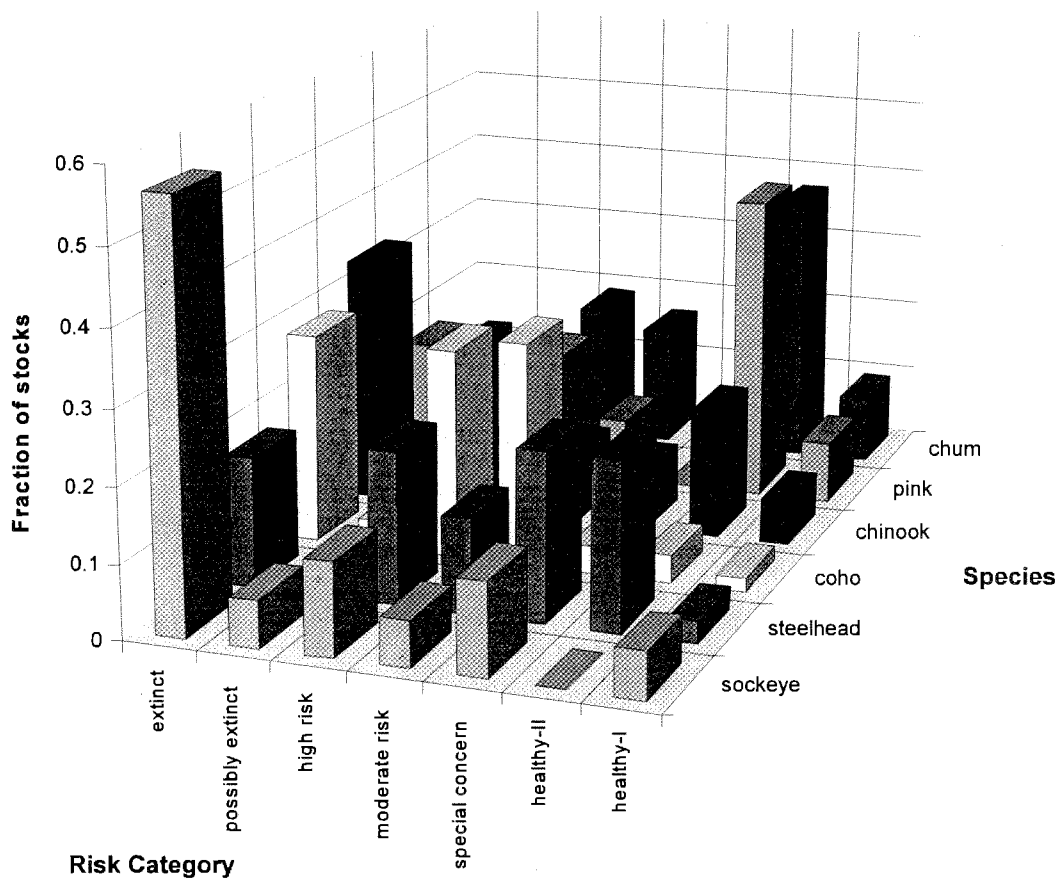
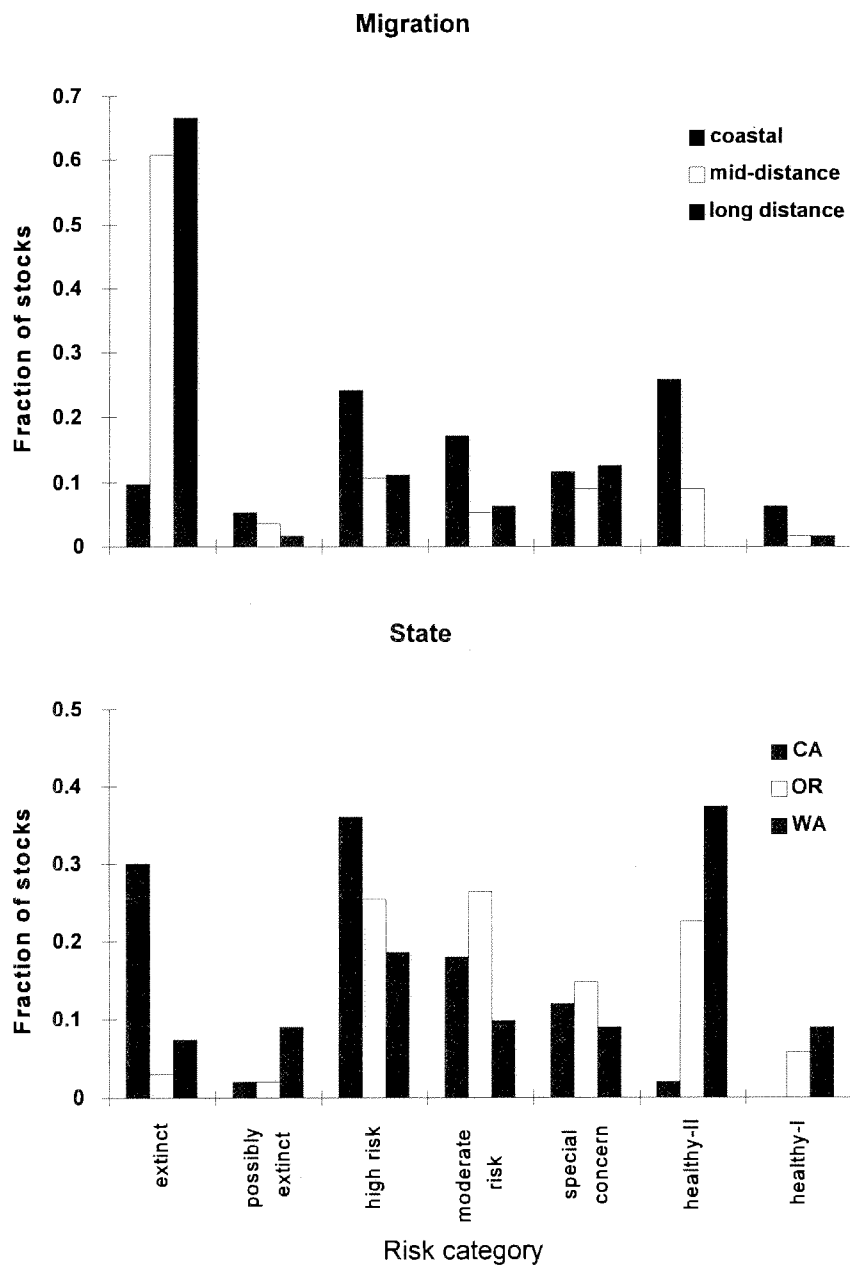


Fig. 3 Proportion of stocks in each risk category from Nehlsen et al. (1991) and Huntington et al. (1996) by migration distance (upper panel) and by state for coastal stocks (lower panel). Long distance migrations includes stocks from rivers draining the west slope of the Rocky Mountains. Mid-distance migrations include stock from rivers draining the east slope of the Cascade Mountains or basins east of the crest of the Coast Range in California and Oregon. All stocks from rivers draining the west slope of the Cascade Mountains or Coast Range were classified as coastal.



Washington, and chum salmon occur primarily in Washington with a few populations in coastal Oregon. If coastal stocks of the three species with coastwide distributions are considered individually (Fig. 4, Appendix Table 1), the same general pattern persists, though it is somewhat obscured by small sample sizes.

ESCAPEMENT TRENDS

Another primary data type considered by NMFS in the status reviews was abundance of natural stocks. The most readily available stock-specific information is spawning escapement. The availability, type, and quality of escapement data vary depending on locality and species, and range from fishway counts at dams to carcass estimates for index areas. Escapement data summarized here are compiled in the NMFS database of salmon catch, escapement, and historical abundance (available from the Pacific States Marine Fisheries Commission, 2501 SW First Ave., Suite 200, Portland, OR 97201, USA). For some species in some locations, total escapement estimates and harvest rate information can be used to calculate recruitment and estimate stock productivity. However, escapement data often only encompass a portion of the stock and cannot be used to estimate total spawning escapement, much less total stock production. In order to provide the broadest and most consistent geographic coverage, we have only summarized escapement trend data here. Exponential trends were fitted to spawning escapement or escapement index data wherever such data were available. The trends summarized here were fitted to entire time series of escapement data.

In general, trends in escapement data show patterns similar to those for the risk categories of Nehlsen et al. (1991) and Huntington et al. (1996). Though the majority of trends in escapement are small in magnitude, there is a tendency for a higher proportion of negative trends for species spending a greater proportion of their lives in freshwater (Fig. 5, Appendix Table 2). There is also a tendency for the proportion of negative trends to increase from north to south, and as the length of the spawning migration increases (Fig. 6, Appendix Table 2).

DISCUSSION AND CONCLUSIONS

In the course of reviewing a variety of salmon stock information, patterns of abundance and stock health have emerged. Abundance of all species harvested commercially, as measured by total landings, has declined since the early part of the century. Declines for chinook and coho salmon have occurred despite large hatchery programs intended to mitigate losses of freshwater habitat and enhance fisheries. More integrated measures of stock health demonstrate patterns relative to the latitudinal distribution of stocks, the distance of spawning migration, and the degree of dependence on freshwater habitat. In general, the health of salmonid stocks in California, Oregon, Washington, and Idaho declines from north to south, with the length of the spawning migration, and with the proportion of life history spent in freshwater.

In recent years much attention has focused on the relationship between marine climatic regimes and abundance of salmon in the eastern north Pacific and the Gulf of Alaska (Beamish and Bouillon 1993; Lawson 1993; Francis and Hare 1994; Hare and Francis 1995). Climatic regime shifts apparently occurred in the late 1940s and late 1970s. The change that occurred in the late 1970s was associated with an increase in abundance of stocks that rear primarily in the Gulf of Alaska (Beamish and Bouillon 1993; Hare and Francis 1995) and a decrease in abundance of stocks that reside off the coast of California, Oregon, Washington, and British Columbia (Lawson 1993). While it might be expected that stocks with similar freshwater origins would be subject to similar marine conditions, different species have very different marine distributions and life-histories (Beamish and Bouillon 1993; Groot and Margolis 1991). Similarly, conspecific stocks with proximate freshwater habitats can have different life-histories and marine distributions (Weitkamp et al. 1995; Nicholas and Hankin 1988). Though ocean conditions clearly affect marine growth and survival, the consistency of relationships between stock health and freshwater life history argue that freshwater conditions are a primary causal factor in current trends stock status.

Fig. 4 Proportion of coastal stocks in each risk category from Nehlsen et al. (1991) and Huntington et al. (1996) plotted by state for each of the three species with coastwide distributions.

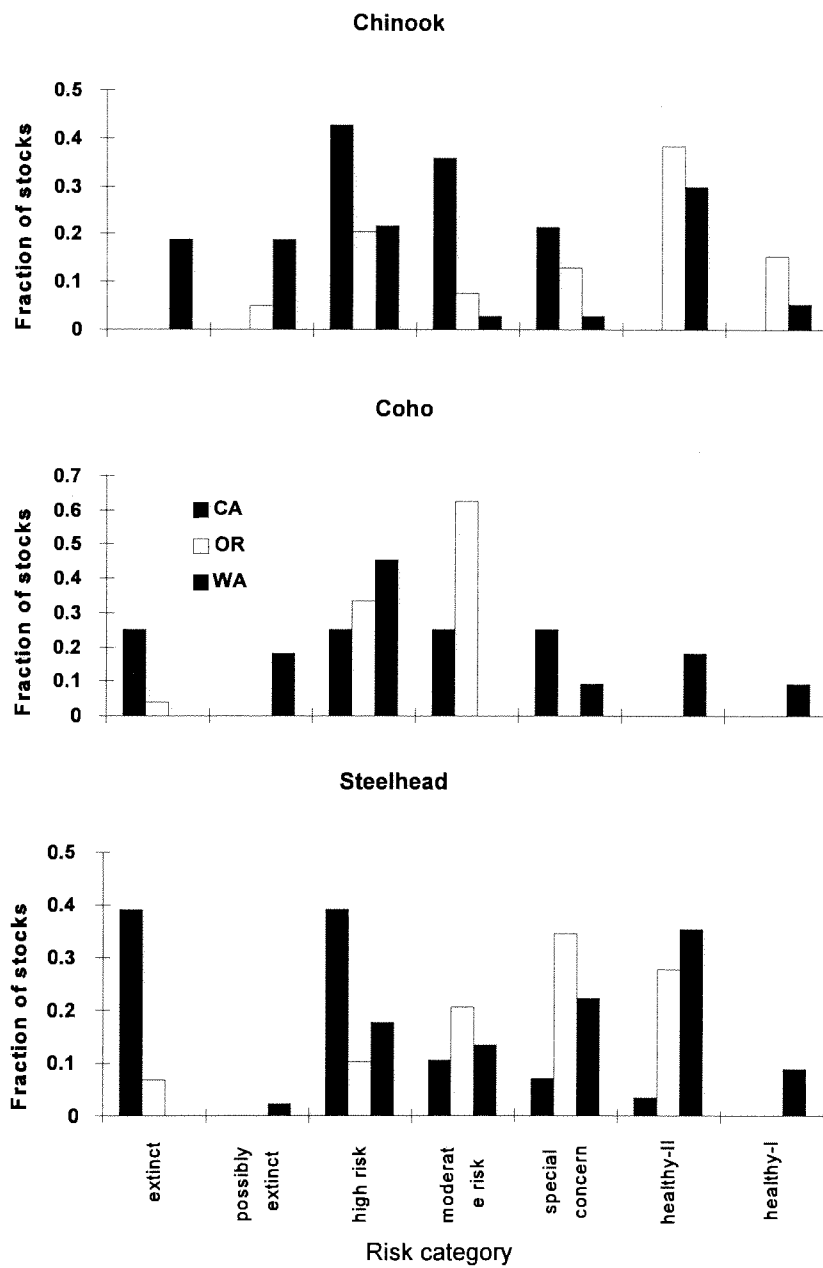


Fig. 5 Distribution of trends in spawning escapement for each species. Species are arranged from front to back in order of decreasing proportion of life history spent in freshwater. Trends were calculated as exponential trends fitted to the entire data series. Series length, data types, and data quality vary.

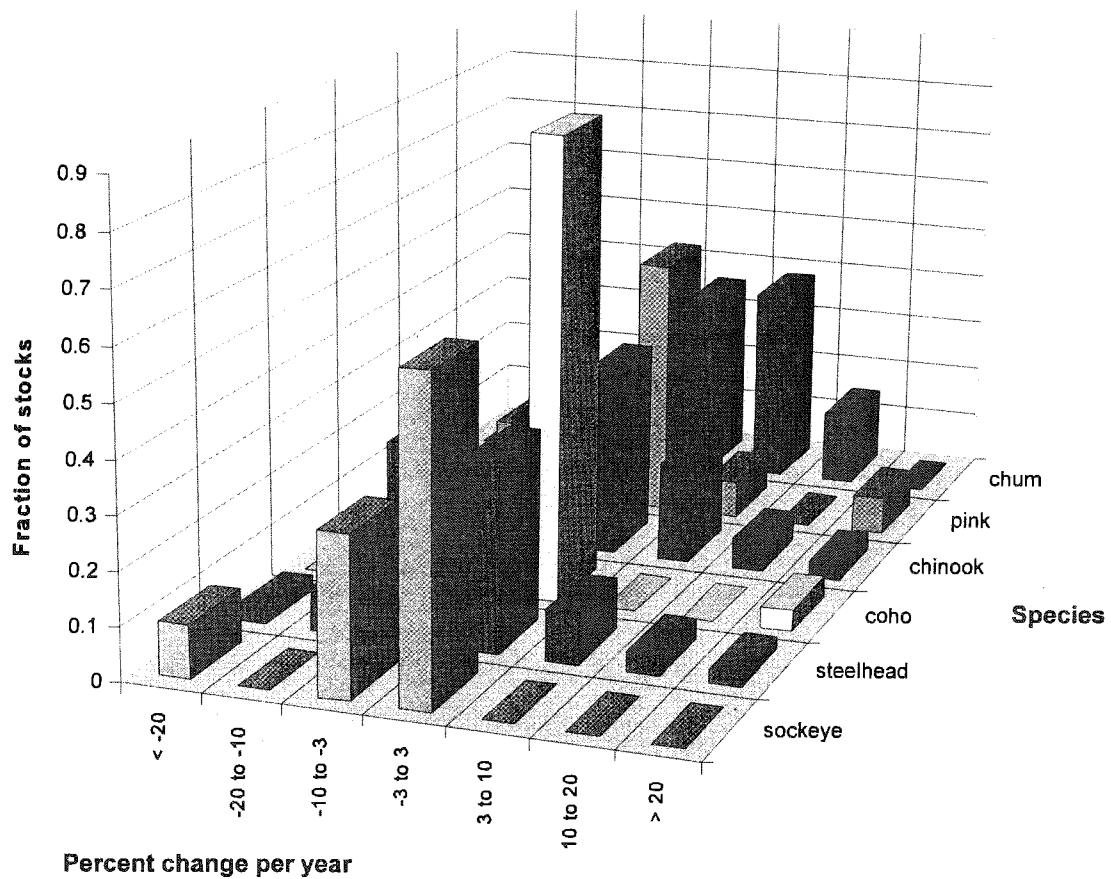
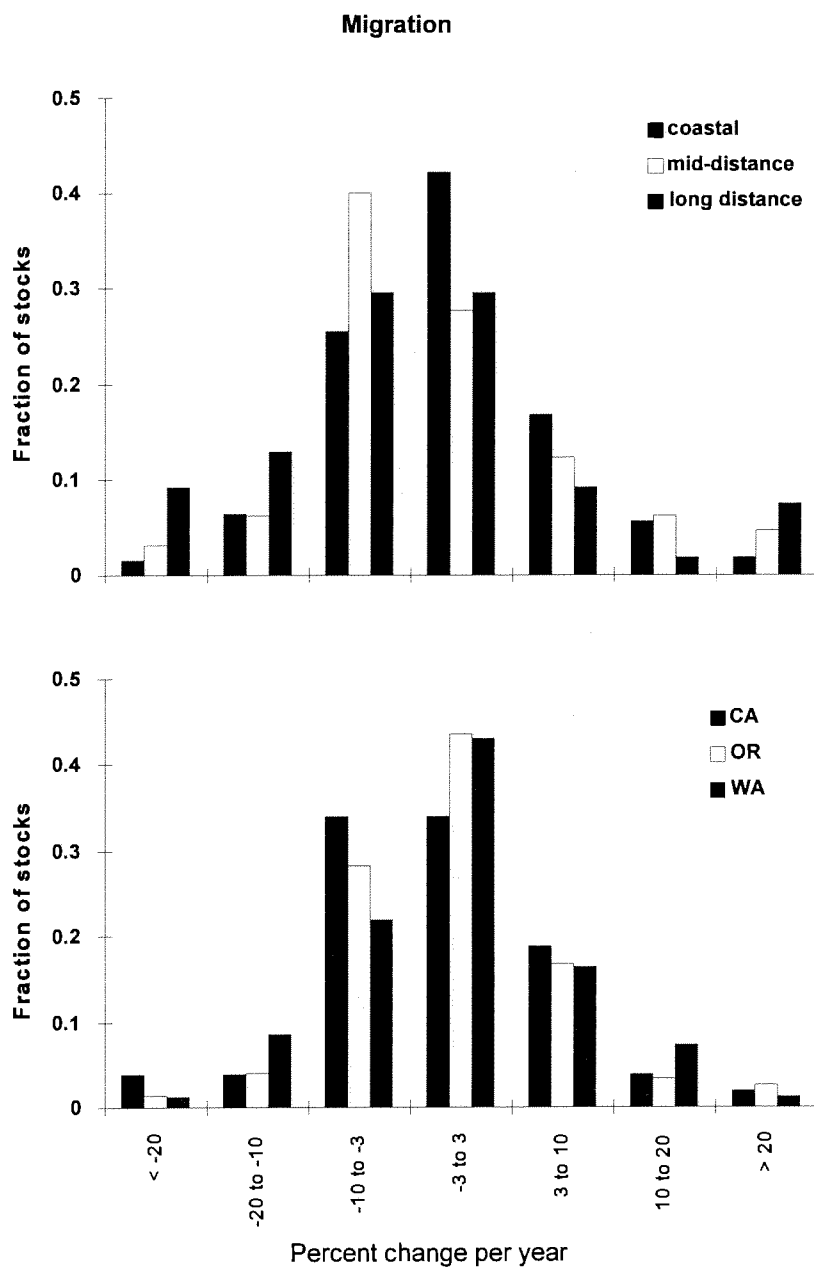


Fig. 6 Distribution of trends in spawning escapement by length of freshwater spawning migration (upper panel), and by state for coastal stocks (lower panel).



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Appendix

Table 1. Number of stocks assigned to each risk category by Nehlson et al. (1991), and Huntington et al. (1996).

		Risk category*						Total
		X	A+	A	B	C	H-II	
Species								
chum		5	3	8	7	0	16	43
pink		2	1	2	1	0	5	12
chinook		50	10	28	14	12	26	149
coho		15	2	15	16	2	2	53
steelhead		23	1	27	17	30	30	132
sockeye		16	1	2	1	2	0	23
Total		111	18	82	56	46	79	412
Freshwater spawning migration								
coastal		28	15	69	49	33	74	286
mid-distance		34	2	6	3	5	5	56
long distance		49	1	7	4	8	0	70
Total		111	18	82	56	46	79	412
Stocks with coastal freshwater spawning migrations								
Species	State							
chinook	CA	0.00	0	6	5	3	0	14
	OR	0	2	8	3	5	15	39
	WA	7	7	8	1	1	11	37
coho	CA	1	0	1	1	1	0	4
	OR	1	0	8	15	0	0	24
	WA	0	2	5	0	1	2	11
steelhead	CA	11	0	11	3	2	1	28
	OR	2	0	3	6	10	8	29
	WA	0	1	8	6	10	16	45
All species	CA	15	1	18	9	6	1	50
	OR	3	2	26	27	15	23	102
	WA	10	12	25	13	12	50	134
Total		28	15	69	49	33	74	286

* Risk categories: X, extinct; A+, possibly extinct; A, high risk; B, moderate risk; C, special concern; H-II, between 1/3 and 2/3 of pristine abundance; H-I greater than 2/3 pristine abundance.

Appendix (continued)

Table 2. Stocks grouped by the annual rate of change in abundance. Annual rates of change were estimated as geometric trends by linear regression of the log transforms of non-zero values of abundance indices against year.

		Annual percent change in abundance							Total
Species		< -20	-20 to -10	-10 to -3	-3 to 3	3 to 10	10 to 20	> 20	
chum		0	1	4	15	16	6	0	42
pink		0	2	3	7	1	0	1	14
chinook		7	19	64	92	49	15	8	254
coho		0	0	2	22	0	0	1	25
steelhead		6	17	77	75	20	8	5	208
sockeye		1	0	3	6	0	0	0	10
Total		14	39	153	217	86	29	15	553
Migration	State								
coastal	CA	2	2	18	18	10	2	1	53
	OR	2	6	42	65	25	5	4	149
	WA	3	20	51	100	38	17	3	232
coastal total		7	28	111	183	73	24	8	434
mid distance total		2	4	26	18	8	4	3	65
long distance total		5	7	16	16	5	1	4	54
Grand Total		14	39	153	217	86	29	15	553

History and Status of Pacific Salmon in British Columbia

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Henderson, M.A., and C.C. Graham. History and current status of Pacific salmon in British Columbia.
N. Pac. Anadr. Fish Comm. Bull. No. 1: 13-22

Pacific salmon colonized the west coast of Canada following the last ice age (Groot and Margolis 1991) and are now found throughout British Columbia. British Columbia salmon have been harvested by members of the aboriginal community for several thousand years (Kew and Griggs 1991). More recently however, particularly over the last 125 years, salmon have also become the focus of intense commercial and recreational fisheries (Shephard et al. 1985). This paper reviews the history and status of the five major species of Pacific salmon in this century, and provides a brief summary of the major factors currently thought to affect the status of each stock.



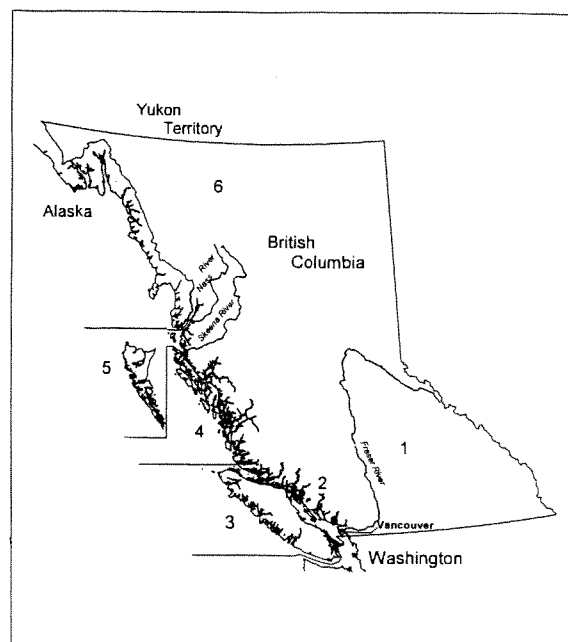
INTRODUCTION

The purpose of this paper is to provide a summary of the history and current status of salmon in British Columbia. More specifically, we provide a description of the general distribution of sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), and chinook salmon (*O. tshawytscha*) in British Columbia, describe historical trends in catch and spawning escapement, and summarize the current status of each species. We also identify those factors that have contributed the most to the current status of the species, and provide an overview of the contribution of the Pacific salmon catch in British Columbia to total Pacific Rim production.

Distribution Of Pacific Salmon Production Systems In British Columbia

Populations of all five species of Pacific salmon considered in this paper can be found throughout the Province of British Columbia, which is 623,000 square kilometers in size and has 2,700 km of coastline. There are approximately 10,000 unique salmon spawning locations in the Province. Although found throughout British Columbia, the relative magnitude of production of each species varies by location along the coast. Generally, the coast of British Columbia can be separated into six production zones; northern British Columbia, north coast, central coast, west coast of Vancouver Island, south coast and the Fraser River (Fig. 1).

Fig. 1. Major Pacific salmon production zones in British Columbia (1-Fraser River; 2-South Coast; 3-west coast of Vancouver Island; 4-central coast; 5-north coast; 6-northern British Columbia and the Yukon Territory).



The total annual return of salmon to the coast of British Columbia is dominated by production originating from the Fraser River and the Skeena River, the two largest river systems on the coast of British Columbia. The Fraser River alone accounts, on average, for over 50% of all British Columbia salmon production and has been described as the

largest single salmon production system in the world (Northcote and Larkin 1989).

Sockeye

Sockeye is the second most abundant species of salmon in British Columbia and is composed of about 900 unique stocks. The distribution of spawning stocks is the consequence of the unique specialization of the species. Sockeye salmon usually spawn in areas associated with lakes, where the juveniles rear before they migrate to sea. Although sockeye production occurs throughout the coast, over 80% of sockeye production comes from two primary systems, the Fraser and Skeena rivers, and four secondary systems, the Nass River on the north coast, Rivers Inlet, and Smith Inlet on the central coast, and Barkley Sound on Vancouver Island. Spawning locations are located throughout the watershed of most large river systems.

The Fraser River is the largest sockeye production system in British Columbia and usually accounts for over half the total production of this species. The major sockeye stock complexes in the Fraser River include early and late Stuart, Chilko, Adams, Horsefly, Quesnel, Fraser, Bowron, Harrison, and Weaver. In addition, there at least 80 smaller sockeye production systems ranging in size from several tens of thousands of spawners to a few hundred. Returns of sockeye to several of the major systems on the Fraser are characterized by a distinct four year cycle. In general, there is one year with very high production followed by a year with intermediate production followed in turn by two years of very low production. This cyclic pattern in abundance accounts in a large part for the fluctuations in catch and spawning escapement. In excess of 95% of the sockeye returning to the Fraser River are four years of age. In contrast, other major production systems consist on average of approximately even numbers of four and five year old fish.

The Skeena River system is the second largest sockeye production system in British Columbia. Babine Lake and its tributary streams and lakes are the major production area. The sockeye spawning areas have been supplemented by spawning channels at Fulton River and Pinkut Creek.

Pink

Pink salmon is numerically the most abundant salmon species in British Columbia and consists of about 2200 unique stocks. Pink salmon are distinguished from other Pacific salmon by having a fixed, two-year life span. This has resulted in the development of even and odd year stocks that are reproductively isolated and developed into genetically different lines. In some systems like the Fraser River,

only the odd-year line exists in fishable numbers. In other river systems, both even and odd-year lines exist.

Pink salmon production is more dispersed along the coast of British Columbia than is observed in sockeye salmon. Returns to the Fraser and Skeena rivers constitute a significant part of the total annual return but there are other production areas of equal importance. Foremost among these are the central coast and the southwest mainland of British Columbia (excluding the Fraser River) where there are over 600 pink salmon spawning locations. In all areas, pink salmon spawning locations are usually concentrated in the lower portions of watersheds, particularly in the larger river systems.

Chum

Chum salmon have the widest geographic distribution of all Pacific salmon species. They spawn in streams of various sizes. Spawning locations for most chum stocks are in the lower areas of river systems and fry migrate directly to the sea soon after emergence.

There are approximately 1600 chum stocks in British Columbia. These stocks are widely dispersed with major production areas in the Nass River, the central coast, the Fraser River and the east and west coasts of Vancouver Island. A large component of the total chum production, particularly in southern British Columbia, derives from enhanced stocks. Most chum stocks can be identified as either summer or fall runs. The former dominate in northern British Columbia while the latter are more common in southern British Columbia.

Chinook

Chinook salmon originate from approximately 850 stocks in a geographically and physically diverse array of river systems throughout the coast of British Columbia. Unlike pink, chum and coho salmon where production is concentrated in small rivers or the lower portions of larger rivers, chinook spawning stocks can be found from the mouths through to the headwaters of large river systems. Particularly important production areas include the Fraser and Skeena rivers, the east and west coasts of Vancouver Island, and the central coast. The Harrison River chinook stock, located in the lower portion of the Fraser River is the largest single chinook stock in British Columbia and possibly the world.

Coho

Coho salmon are widely dispersed throughout British Columbia and make up about 2600 unique

stocks. In most areas, coho occur in small numbers compared to other species of Pacific salmon. In the larger river systems, including the Fraser, Skeena, Bella-Coola, Nass, and Taku rivers, they migrate some distance inland to spawn in smaller tributaries. Significant production also occurs in individual river systems in the Queen Charlotte Islands, the north and central coast, and both the east and west coasts of Vancouver Island.

HISTORICAL TRENDS IN SALMON PRODUCTION IN BRITISH COLUMBIA

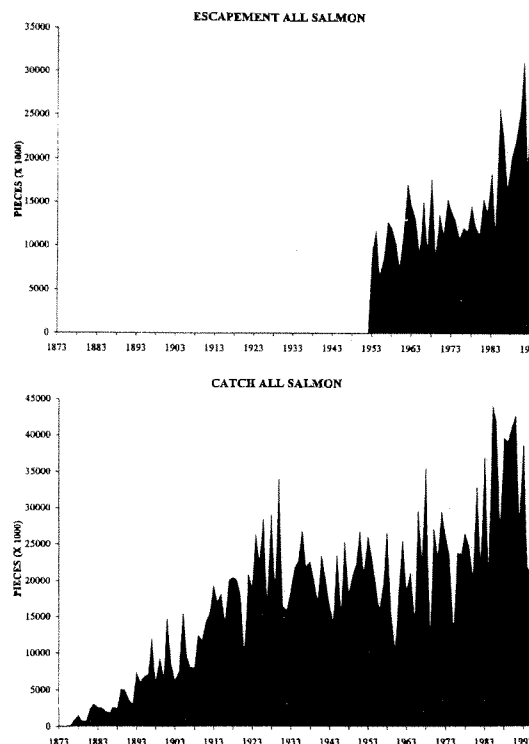
Inferences can be made about historical trends in British Columbia salmon production from catch and spawning escapement data sets. The catch data set provides estimates of the total annual British Columbia salmon catch by species from 1873 to the present. Estimates of catch from 1873 to 1950 are taken from Shepard et al. (1985). More recent catch estimates come from the catch monitoring program of the Canadian Department of Fisheries and Oceans (CDFO). Catch estimates provide an index of salmon abundance (Beamish and Bouillon 1993) from which one can discern periods of major change in fish production.

The spawning escapement data set provides estimates of total annual salmon spawning escapement by species from 1951 to the present and were obtained from the salmon escapement data base of CDFO. There are no reliable estimates of coast-wide spawning escapement or total production (i.e. catch plus escapement) prior to 1951. Catch and spawning escapement data sets, when examined together, provide more complete and detailed information on the status of the species than can be inferred from a catch time series alone.

All Species

The large scale harvest of salmon in British Columbia commenced with the introduction of commercial fish canning operations in the latter part of the 1860s. The all species salmon catch increased discontinuously from that time, peaking in the late 1920s and early 1930s with catches in the range of approximately 25 to 30 million pieces (Fig. 2). Catch subsequently declined to relatively low levels in the 1950s and 1960s. The all species salmon catch has shown a discontinuous increase from the early 1970s through 1995 with the catches in the late 1980s and early 1990s exceeding 40 million fish, greater than the historical high levels observed in the earlier part of the century. The higher levels of catch observed in recent years are the result of increases in spawning escapement and improved marine survival conditions.

Fig. 2. Total annual catch (1873 to 1995) and spawning escapement (1951 to 1994) for all species (sockeye, pink, chum, coho, chinook) of British Columbia salmon.



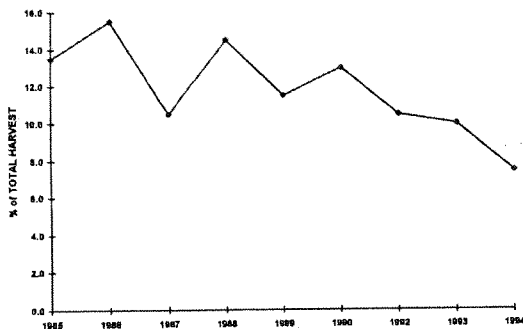
The overall trend in salmon catch throughout the time series is determined primarily by pink and sockeye, the two most abundant salmon species in British Columbia. Despite the increase in recent time, the contribution of British Columbia Pacific salmon production to total Pacific Rim production has declined from approximately 14% in the mid 1980s to 8% in 1994 (Fig. 3). The decline reflects, in part, the rapid increase in wild sockeye and hatchery chum production in Alaska and Japan respectively, and the increasing importance of farmed chinook and coho salmon, particularly in Chile.

The combined spawning escapement of all species of Pacific salmon increased gradually from the early 1950s through the late 1970s. Over the last 1½ decades, escapement levels have increased more rapidly reflecting, in part, an intentional effort to increase the size of many salmon stocks in British Columbia by increasing the number of fish on the spawning grounds. The recent estimates of all species salmon escapement have surpassed 35 million fish.

Sockeye Salmon

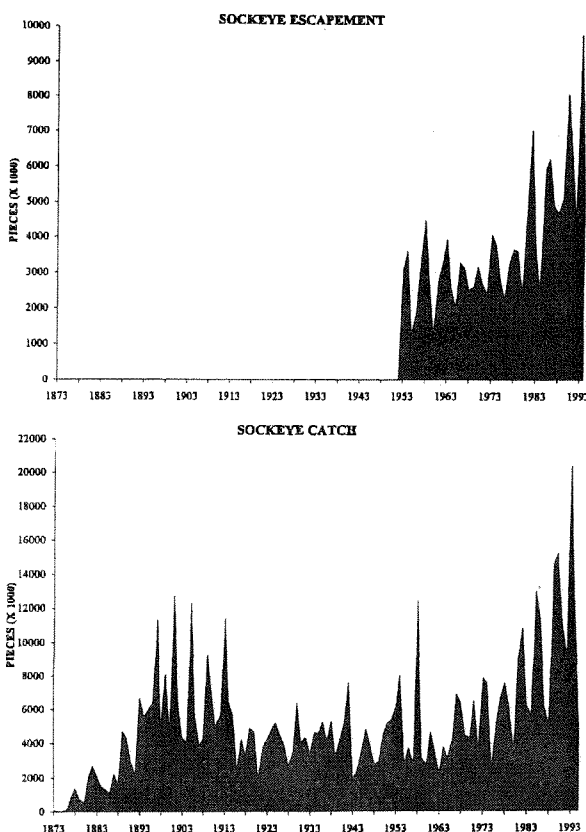
On average, 60% of the total catch originates from the Fraser River. Several of the larger Fraser River sockeye stocks exhibit a distinct four year cycle

Fig. 3. Percent of the total world Pacific salmon production (wild and farmed) contributed by British Columbia from 1985 to 1994.



in abundance; a dominant year with very large returns, followed by a sub-dominant year with approximately half the production observed in the dominant year, followed in turn by two years of low returns. This cyclic pattern in abundance for some of the large Fraser River sockeye stocks accounts, in large part, for the regular fluctuations in catch and spawning escapement (Fig. 4).

Fig. 4. Total annual catch (1873 to 1995) and spawning escapement (1951 to 1994) of British Columbia sockeye salmon.



Sockeye salmon was the initial focus of the commercial canning industry in British Columbia. Sockeye catches increased rapidly in the late 19th century and the early part of the 20th century. Peak catches during this period were approximately 10 to 12 million fish. There was a precipitous decline in the coast-wide sockeye catch beginning in 1917 to levels of four to five million fish. The reduction in catch was the result of a rock slide in the Hell's Gate area of the lower Fraser River. The slide blocked much of the cross-section of the river and, as a consequence, few sockeye were able to reach their spawning grounds in 1913 and 1914. Passage conditions were dramatically improved following the removal of the obstruction caused by the rock slide and the construction of fishways. However it required several decades to rebuild Fraser River sockeye spawning stocks to their former level.

Catches of British Columbia sockeye salmon remained low through the late 1960s. They began to increase in an exponential fashion beginning in the early 1970s through to the present. Recent catches have been greater than those of the previous peak at the turn of the century with one total annual catch in excess of 20 million fish. The recent increase in the sockeye catch can be attributed to a deliberate attempt to increase the number of fish reaching the spawning grounds, particularly in the Fraser River, in conjunction with the above average marine survival in the 1980s. The increase in sockeye catches was also aided by the development of spawning channels in the Skeena River in the mid 1960s which increased adult returns nearly four-fold (West and Mason 1987).

Coast-wide sockeye spawning escapement has followed a similar trend to that exhibited by catch since 1951 (Fig. 4). Escapements for the period from the mid 1950s through the late 1970s were generally between three and four million fish. More recently however, annual spawning escapement has risen rapidly to levels exceeding 10 million fish.

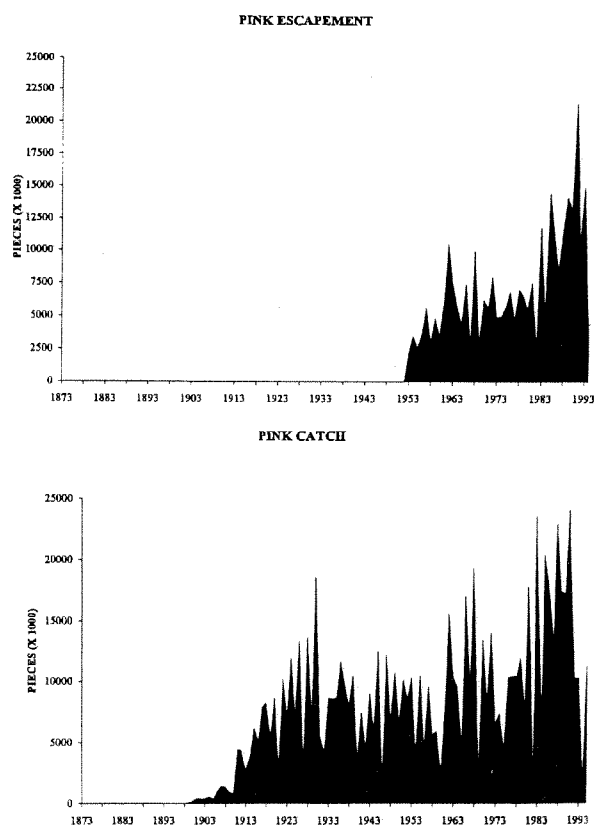
The high levels of sockeye production are the result of efforts to increase spawning escapement to major stocks over the last 30 years combined with a period of high marine survival, particularly in the 1980s. Marine survival appeared to decline in the early 1990s but subsequently increased for the dominate brood years of the 1996 adult returns (1991 and 1992). Alterations to the freshwater habitat of sockeye have been relatively minor and had little effect on sockeye production.

Pink Salmon

Pink is numerically the most abundant salmon species in British Columbia. Large pink salmon fisheries developed two to three decades after the advent of major sockeye fisheries with the first

significant catches occurring in the early part of the 20th century (Fig. 5). The Fraser River is a major contributor to total British Columbia pink salmon production, although to a lesser extent than is the case for sockeye. Fraser River pink production is dominated by a unique "on - off" cycle with large numbers of fish, sometimes in excess of 20 million, returning in odd numbered years and very small numbers, usually a few thousand fish, returning in even numbered years. This feature of the Fraser River pink salmon returns is reflected in the highly discontinuous nature of the total British Columbia catch and spawning escapement time series (Fig. 5).

Fig. 5. Total annual catch (1873 to 1995) and spawning escapement (1951 to 1994) of British Columbia pink salmon.



British Columbia pink salmon catch increased rapidly in the early part of the 20th century, reaching a peak of approximately 19 million fish in 1929. The Hell's Gate slide on the Fraser River, referred to above, had less effect on pink returns and catch as much of the pink production from this system originates from the lower river below the location of the slide. British Columbia pink salmon catches declined to lower levels in the 1930s through the 1950s and then subsequently increased through the late 1980s when catches exceeded 20 million fish. The catches of pink salmon have declined in the early

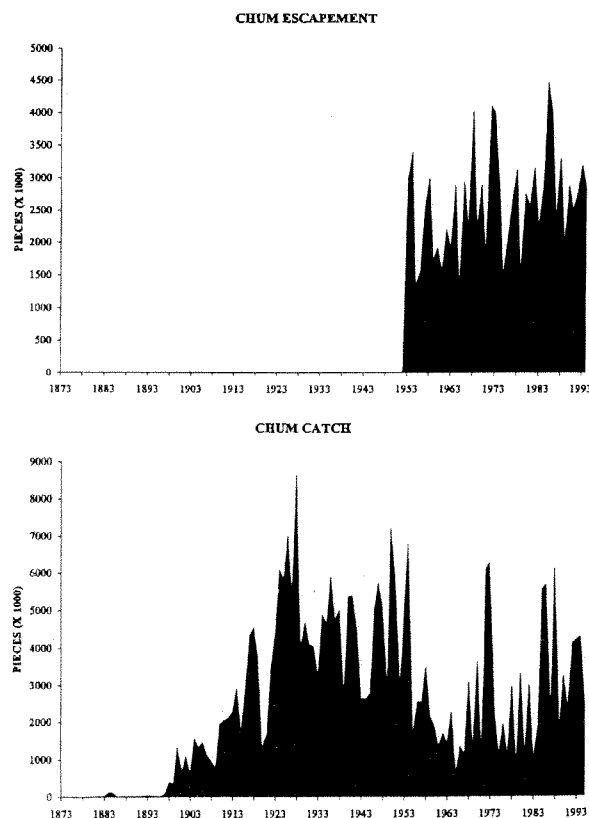
1990s.

Annual pink salmon spawning escapement gradually increased from the early 1950s through the late 1970s and averaged approximately six million fish. Escapements increased rapidly beginning in the early 1980s and peaked in 1991 at over 20 million fish. The relationship between the spawning escapement of pink salmon and subsequent adult returns from the brood year are much more ephemeral than observed in other salmon species. Variations in the rate of marine survival are likely the primary determinate of total pink salmon returns. The significant effect of periodic winter flood conditions in freshwater systems also serves to obscure the relationship between the number of spawners and subsequent returns.

Chum Salmon

Chum salmon is the least abundant of the three salmon species (i.e. sockeye, pink, and chum) of primary interest to the commercial fishing industry in British Columbia. The total catch of chum salmon in British Columbia increased for the early part of the present century through the mid 1920s when the catch peaked in excess of eight million fish (Fig. 6).

Fig. 6. Total annual catch (1873 to 1995) and spawning escapement (1951 to 1994) of British Columbia chum salmon.



Annual catches then declined discontinuously through the early 1960s to levels generally in the range of one to two million fish. There was no trend in annual catches, although there was significant interannual variation, from the mid 1960s to the mid 1980s. Over the last decade, catches have again increased and have ranged from two to six million fish.

Estimates of total spawning escapement of British Columbia chum salmon have increased slowly and discontinuously since the early 1950s. Typical levels of spawning escapement in recent years are in the range of 2.5 to 3 million fish compared to estimates from the 1950s and 1960 which generally ranged from 1.5 to 2.5 million fish. The decline in chum salmon catches through the 1950s and 1960s was probably the result of excessive harvest and poor marine survival while the more recent improvement can be attributed to the reversal of these two conditions.

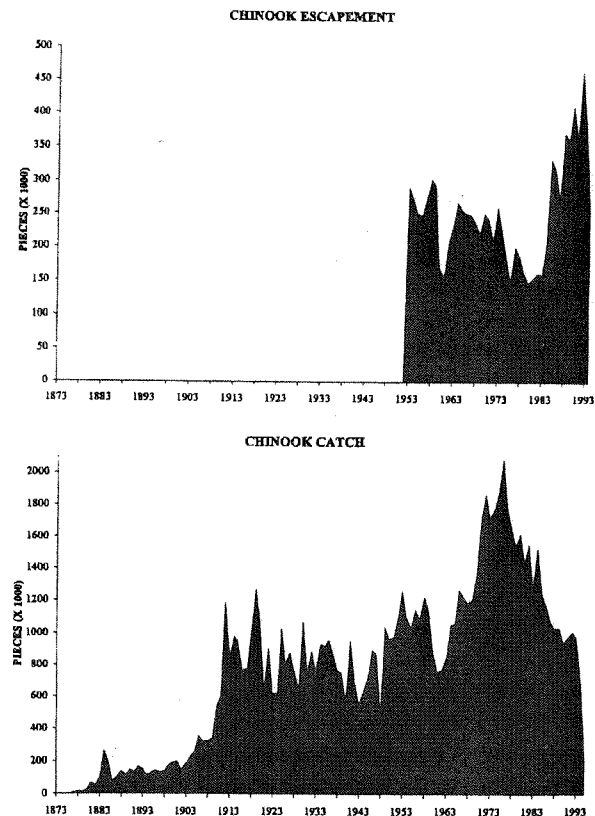
Chinook Salmon

Chinook is the least abundant of the five British Columbia salmon species considered in this paper. During the early part of its exploitation history, chinook salmon was primarily the target of commercial fisheries as was the case for pink, sockeye and chum salmon. However, over the last several decades, an increasingly significant component of the total annual catch has been taken by recreational fishers.

The catch of chinook salmon in British Columbia increased rapidly from the late 19th century through the early part of the 20th century peaking at approximately 1.2 million fish in the early 1920s (Fig. 7). Total annual catches from the mid 1920s to the mid 1960s were relatively stable and generally ranged from 700,000 to 1.3 million. Catches of chinook salmon again increased rapidly from the mid 1960s through the late 1970s and exceeded two million fish in one year. This second period of rapidly increasing chinook catch was primarily the result of an expanding recreational fishery, particularly in southern British Columbia. The annual chinook catch declined discontinuously from the peak catches of the late 1970s to present levels of approximately one million fish.

Estimates of the level of chinook salmon spawning escapement declined from the early 1950s through the mid 1980s, overlapping the period of time when catches were increasing rapidly. The harvest rate exerted on some chinook stocks during this time was too high and led to a subsequent decline in overall chinook production. Beginning in 1985, a salmon treaty between Canada and the United States

Fig. 7. Total annual catch (1873 to 1995) and spawning escapement (1951 to 1994) of British Columbia chinook salmon.



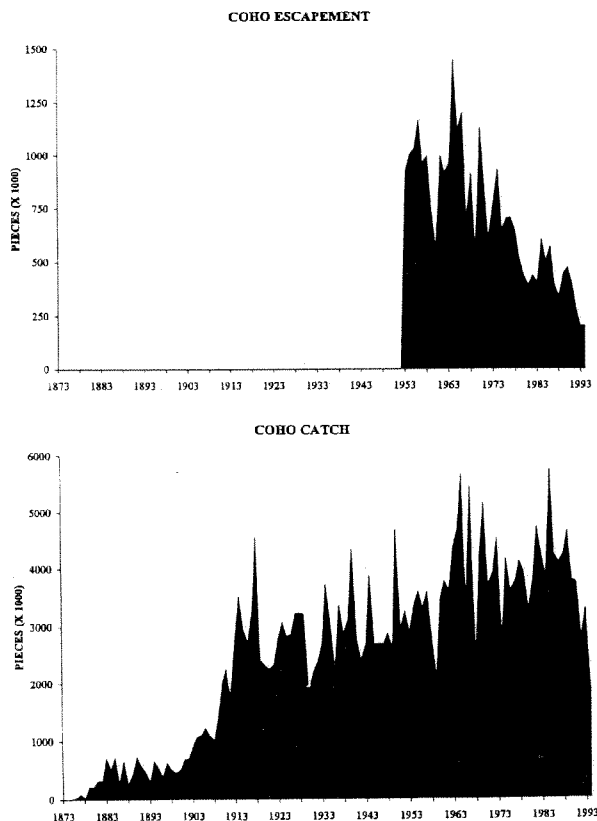
took effect and dealt, in part, with the management and rebuilding of North American chinook stocks. One aspect of the treaty placed reduced limits on the harvest of chinook in different locations along the coast. As a consequence of the treaty, and as a result of management actions in Canada, estimates of annual spawning escapement of chinook salmon have increased from pre-treaty levels of 150,000 to 200,000 to close to 500,000 in recent times. The increase in spawning escapement is resulting in an increase in total chinook abundance in British Columbia.

Coho Salmon

The abundance of coho salmon in British Columbia is much less than observed for pink and sockeye but similar to the abundance of chum. Coho salmon, like chinook, has changed from a species that was primarily harvested by commercial fishers to one where a major component of the total annual harvest is taken by recreational fishers.

Coho catches increased rapidly from the latter part of the 19th century through the early part of the 20th century and peaked at a level in excess of four million fish in 1916 (Fig. 8). There was an abrupt

Fig. 8. Total annual catch (1873 to 1996) and spawning escapement (1951 to 1994) or British Columbia coho salmon.



decline in coho catch over the next few years and then a gradual, discontinuous increase in coho harvest through the mid 1960s when the total catch exceeded five million fish. The annual catch from the mid 1960s through the mid-1980s was relatively stable and generally fluctuated between three and five million fish. Over the last decade however, the total coho salmon catch has declined steadily to levels in some years of less than three million fish.

Estimates of the spawning escapement of coho salmon in British Columbia should be treated as indices of escapement rather than absolute estimates. Coho are the last of the five species of salmon to enter rivers and spawn in British Columbia. Often early winter weather conditions, freshets, and ice formation in rivers precludes obtaining complete estimates of the number of spawners.

Although there were wide fluctuations, estimates of coho spawning escapement were relatively stable between the mid 1950s and the mid 1960s (Fig. 8). However, estimates of spawning escapement declined discontinuously but rapidly from in excess of one million fish in the mid 1960s to 200,000 to 300,000 in recent years. The appearance of a relatively stable catch from the mid 1960s through mid 1980s in the

presence of declining spawning escapement indicates that the status of British Columbia coho salmon has been declining in recent time.

Factors leading to the decline in coho abundance over the last thirty years are numerous and complex. Of greatest concern is the alteration of freshwater spawning and rearing habitat. Most coho production in British Columbia originates from small, low gradient river systems. Many of these systems, particularly in southern British Columbia, have been impacted by the process of urbanization and include the effects of channelization, installation of culverts, siltation, and various agricultural and forestry practices that reduce the quality of the freshwater aquatic environment. Further, because coho production originates from a large number of small systems, most fisheries are of a mixed stock nature which tends to over-harvest the less productive stocks. This, combined with the rapid development of the recreational fishery in southern British Columbia in the last thirty years, has resulted in excessive harvest for some stocks. Finally, recent changes in the ocean environment, and particularly in the Strait of Georgia, have resulted in a reduction in marine survival.

CURRENT STATUS OF SALMON SPECIES IN BRITISH COLUMBIA

The above summary of historical trends in salmon catch and escapement provides temporal information on a decadal scale. More current information on species status however is available from assessment work produced over the last five years. Inferences regarding current status are presented first on a coast-wide basis. This is followed by comments on individual stocks or stock groups that exhibit exceptions to the current coast-wide trend. Also identified is the major factor accounting for the current status of a species. All three major factors, marine environment, freshwater environment, and spawning escapement effect total production but in most cases one of these is dominant.

Sockeye Salmon

The current coast-wide status of sockeye salmon is good with catch and spawning escapement stable to increasing and at historical highs (Table 1). The primary causative factor underlying this good sockeye production is a high level of spawning escapement in recent years. Contributing factors include the recent return to favourable marine survival conditions, and maintenance of critical freshwater habitat. Marine survival of sockeye was very high in the 1980s but declined in the early 1990s. Adult sockeye returns were significantly above forecast in 1996 and apparently associated with a return to above average

Table 1. Summary of the current status of salmon species in British Columbia and the major factors effecting current status.

	Status (Trend/Spawning Escapement)	Major Factors Effecting Current Species Status		
		Marine Environment	Freshwater Environment	Spawning Escapement
Sockeye	Stable to Increasing/High			X
Pink	Stable to Increasing/High	X		
Chum	Stable/Medium	X		
Chinook	Increasing/Low-Medium			X
Coho	Decreasing/Medium-Low	X	X	

marine survival. Most of the freshwater habitat concerns for British Columbia sockeye have been mitigated by the remote location of spawning and rearing areas utilized by juvenile sockeye, and the introduction of strict forestry practices designed to protect fish habitat.

Although the coast-wide status of sockeye salmon is good with both catch and spawning escapement at historical highs, there remains some areas of concern. The large, productive stocks in the Fraser and Skeena rivers have responded rapidly to increases in spawning escapement over the last several decades. This is not the situation however for some of the small, less productive stocks. Sockeye stocks from major river systems, such as the Fraser and Skeena, tend to co-migrate through fishing areas in the coastal waters of British Columbia on their return to the spawning grounds as adults. In the past, harvest rates have been set at levels appropriate for the larger, more productive stocks. As a consequence, some of the less productive stocks have been over-harvested and spawning escapement has remained low. We have also observed the continuation of a long-term trend toward less than expected production from three of the secondary sockeye production systems in British Columbia; Rivers Inlet and Smith Inlet on the central coast, and Barkley Sound on the west coast of Vancouver Island. In each case the stocks have not responded to significant increases in spawning escapement and there are no apparent problems associated with freshwater survival conditions or by-catch in fisheries that do not target these stocks.

Pink Salmon

The current coast-wide status of pink salmon is good (Table 1). Both catch and spawning escapement have been high through most of the 1990s although total production has declined somewhat over the last two years. The cause of the decline is not the result of a reduction in spawning escapement that produced adult returns over the last two years but is probably

associated with a decrease in marine survival of juvenile pink salmon. In general, freshwater habitat required by pink salmon is in good condition.

Pink salmon are continuing to recolonize those areas of the Fraser River above Hells Gate where stocks were eliminated or severely reduced in size as a result of the rock slide in 1913 (Ricker 1989). This is, in part, a result of the decline in the number of fisheries that harvest Fraser River pink salmon as a by-catch and an overall reduction in the harvest rate on these stocks groups. Pink salmon originating from the central coast of British Columbia and the west coast of Vancouver Island however continue to produce at less than expected levels. In both cases, a decline in spawning escapement appears to be the primary cause although the reason for the decline is unknown.

Chum Salmon

The total abundance and spawning escapement of British Columbia chum salmon is stable (Table 1) at the present time but less than observed during the earlier part of the century.

Chinook

From a coast-wide perspective, chinook salmon are rebuilding from the very low levels observed in the mid-1980s. Total returns continue to gradually increase and the level of spawning escapement in many stocks is also increasing from low levels, in part as the result of major reductions in catch (Table 1). An increase in spawning escapement is the primary causative factor contributing to the current status of the species.

There remains concern however for several chinook stock complexes, particularly in southern British Columbia. The El Niño events off the west coast of Vancouver Island in 1992 and 1993 resulted in very high mortality on juvenile chinook from approximately 30 stocks that would return as adults in

1995, 1996, and 1997. Although fishing effort on west coast of Vancouver Island stocks has been dramatically reduced in recent years as a result, in some cases almost to zero, spawning escapement remains low and rebuilding these stocks will require several years. The returns for most chinook stocks on the east side of Vancouver Island and the mainland of south western British Columbia are increasing although there are several notable and unexplained exceptions. Foremost among these are the recent low returns to the Campbell River and Harrison River stocks.

Alteration of the freshwater environment is a major concern for chinook production. Chinook generally spend 3 months to a year as juveniles in freshwater and as a result, habitat alteration in urban areas of southern British Columbia can potentially reduce the survival of juvenile chinook. Mitigating against this concern to some extent is the concentration of relatively large chinook stocks in the upper reaches, and less developed areas of some river systems.

Coho Salmon

The abundance of coho salmon in British Columbia continues to decline and the spawning escapement for most stocks is in the medium to low range (Table 1). Of greatest concern are several small coho stocks situated around the Strait of Georgia and the west coast of Vancouver Island in southern British Columbia. These are the stocks that, as described above, are most susceptible to the effects of urbanization.

CURRENT CHALLENGES IN THE ASSESSMENT AND MANAGEMENT OF BRITISH COLUMBIA SALMON

Ensuring the conservation and sustainable use of the Pacific salmon resource of British Columbia requires accurate and timely stock assessment information that incorporates the appropriate elements of uncertainty into the assessments. It also requires that fisheries managers understand the limitations and uncertainty associated with the stock assessment information and, based on that understanding, develop suitably risk averse fishing strategies.

Several changes made to the stock assessment process in recent years have improved the quality of assessment information. These include more accurate estimates of spawning escapement based on the use of fences, and hydroacoustic and mark-recapture studies, improvements in the quality control procedures for catch estimation, and the development of new stock identification techniques, particularly electrophoretic and DNA based, for apportioning catch to stock.

These improvements combined with new analytical techniques allow for a greater degree of certainty in stock assessment information. However our incomplete understanding of the biological processes governing salmon production, particularly as they relate to the ocean environment, combined with the uncertainty in estimates of catch and escapement, imply that fisheries management decisions will always be made in the context of some degree of uncertainty. As a consequence, fishery managers must make explicit decisions about the level of risk they are willing to accept with regard to meeting their objectives (e.g. a spawning escapement target) in the context of developing fishing plans. Those responsible for performing stock assessments must ensure the estimates they generate contain an adequate description of the associated uncertainty.

Future fisheries management strategies must address the complex problem of mixed species and stock fisheries. Fishing regimes must be developed using a more precautionary approach to the pre-season design and in-season implementation so spawning escapement goals or harvest rate guidelines are achieved and not exceeded. Development of new fishery management regimes for salmon will include:

- the use of significant time and area closures to control harvest rates and reduce the potential impact of any single fishery to over-harvest the resource;
- reducing harvest rates in key interception fisheries where greater uncertainty exists regarding the run size and stock composition of the returns; and,
- encouraging development of species selective harvest techniques to reduce the impact of fisheries on non-target species that co-migrate with the target stocks.

Canada has also embarked on a significant program to reduce the harvesting capacity of the commercial fishing fleet in British Columbia in order to improve the management of the fishery and improve the economic returns to individual fishers.

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Historical Trends of Salmon Fisheries and Stock Conditions in Japan

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Artificial salmon hatchery operation in Japan can be described from various aspects such as salmon resources, resources management, economic effects, and future prospects. Almost all the salmon resources in Japan have been supported by artificial propagation. Recent annual total salmon catch increased to about 300 thousand tons, in which the coastal catch accounted for over 80 percent. With regard to the species composition of commercial catch, the chum catch is the largest, about 230 thousand tons (about 80 percent). Resource management coupled with active propagation made the set net fishery for chum and pink salmon stable. Economic returns from harvesting (about 50-80 billion yen) in the coastal fishery vis-a-vis expenses (about 10-14 billion yen) for artificial propagation of salmon is about 5-8 times.



INTRODUCTION

Almost all the salmon resources in Japan have been supported by artificial propagation. Species subject to artificial propagation programmes in Japan are: chum salmon (*Oncorhynchus keta*), pink salmon (*O. gorbuscha*), masu salmon (*O. masou*) and kokanee salmon (*O. nerka*). Smolt cultured from the lake-living kokanee, a land-locked sockeye salmon, have been released on a pilot basis in natural rivers with a view to developing sockeye resources. Only a limited number of chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*) and sockeye salmon (*O. nerka*) are caught in the coastal sea or the North Pacific Ocean. Coho salmon are becoming cultured in cages or in freshwater ponds. To promote efficient artificial propagation of salmon, it is important to make a model of some aspects of behaviour in the life cycle of the fish, especially those concerned with spawning migration, spawning, breeding, development, smoltification, downstream migration and feeding migration.

to 1982, and increased to over 170 thousand tons since 1983, reaching about 303 thousand tons in 1995 in spite of a gradual decrease in the distant water catches, from 120 to 12 thousand tons, following to the cease of salmon fisheries among open areas of the North Pacific Ocean since 1990. Almost all the coastal catch comes from artificial propagation in Japan. The percentage of coastal catch has increased to over 60 percent since 1979 and over 80 percent since 1986. Since 1981, the total annual commercial catch has been 112-231 thousand tons (73-85 percent) for chum, 12-35 thousand tons (5-16 percent) for pink, 2.5-4.0 thousand tons (0.9-2.5 percent) for masu, 0.5-7.8 thousand tons (0.2-3.3 percent) for sockeye, 3.2-26.0 thousand tons (1.9-12.1 percent) for coho and 0.3-1.4 thousand tons (0.1-0.9 percent) for chinook. Recently, production of pen-cultured coho salmon has increased to 25 thousand tons in 1991-2 (see Table 1).

Annual Adult Returns and Return Percentage for Salmon Released from Japan

EFFECTS ON RESOURCES

Annual Catches of the Japanese Salmon Fisheries

Annual catches of the Japanese salmon fishery are shown in Table 1. Total catches of salmon fluctuated between 100-160 thousand tons from 1965

Annual adult returns for chum released from Hokkaido and Honshu Islands are shown in Table 2 and Figure 1. The numbers of chum fry released from both Hokkaido and Honshu Islands, have increased to 1900 from 470 million fish, from 1965 to 1981, and have stabilized at about 2000 million fish since 1982. Adult returns to rivers and coastal

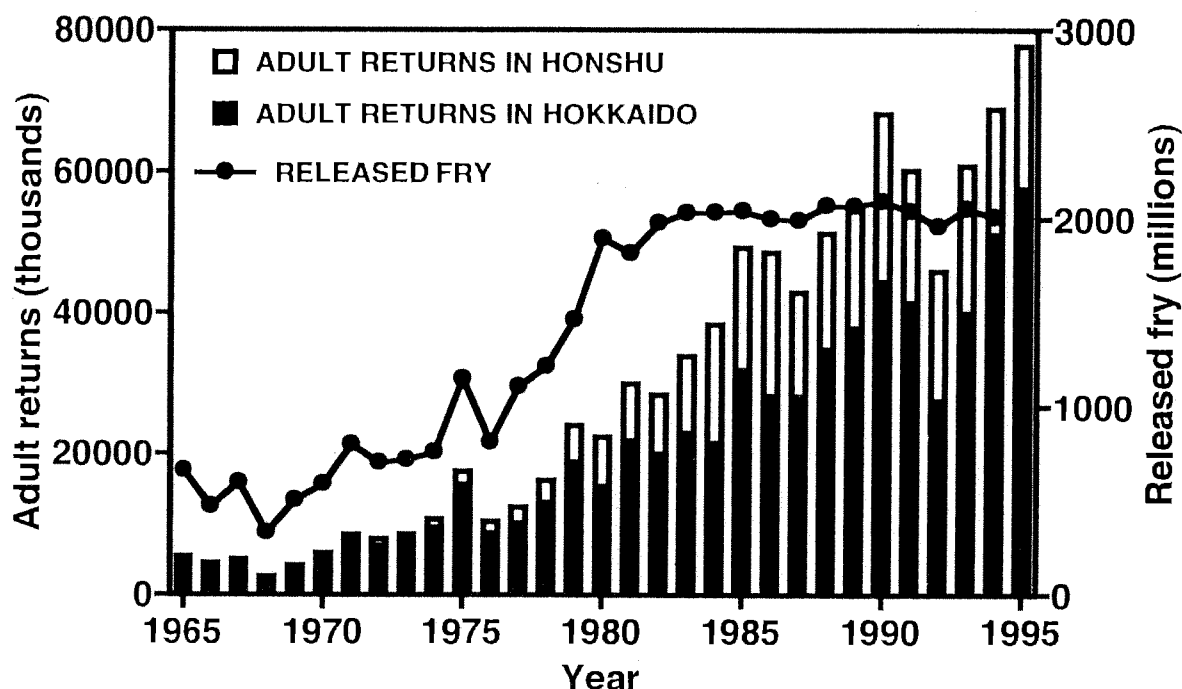
Table 1. Annual catches in the Japanese salmon fishery.

Year	Far-seas catch (thousand tons)	Coastal Sea catch (thousand tons)	Freshwater catch (thousand tons)	Total (thousand tons)	Percentage of coastal catch	Pen-culture coho (thousand tons)
1965	126.8	18.8	3.6	149.2	12.6	
1966	110.1	16.5	2.2	128.8	12.8	
1967	128.3	20.1	3.0	151.4	13.3	
1968	102.2	11.6	1.4	115.2	10.1	
1969	122.1	19.2	2.0	143.3	13.4	
1970	95.8	22.1	1.9	119.8	18.4	
1971	102.3	37.0	2.6	141.9	26.1	
1972	92.6	27.0	2.0	121.6	22.2	
1973	97.2	38.8	3.0	139.0	27.9	
1974	88.5	44.0	2.9	135.4	32.5	-
1975	92.8	66.5	7.0	166.3	40.0	-
1976	84.4	41.7	3.9	130.0	32.1	-
1977	64.3	52.2	3.7	120.2	43.4	-
1978	42.7	60.1	4.1	106.9	56.2	0.1
1979	43.5	87.5	6.5	137.5	63.6	0.4
1980	43.4	79.1	9.4	131.9	60.0	1.9
1981	43.2	106.6	8.9	158.7	67.2	1.2
1982	43.6	92.7	9.3	145.6	63.7	2.1
1983	43.3	117.8	9.0	170.1	69.3	2.8
1984	36.4	120.9	9.0	166.3	72.7	5.0
1985	35.5	167.6	11.4	214.5	78.1	7.0
1986	20.9	146.5	10.0	177.4	82.6	7.5
1987	20.5	140.2	8.6	169.3	82.8	12.2
1988	15.5	151.8	10.8	178.1	85.2	16.5
1989	18.4	173.7	13.3	205.4	84.6	19.8
1990	11.9	211.3	15.9	239.1	88.4	23.6
1991	16.5	198.2	13.4	228.1	86.9	25.7
1992	23.4	155.9	10.2	189.5	82.3	25.5
1993	26.1	204.0	14.4	244.5	83.4	21.1
1994	23.8	216.1	21.1	261.0	82.8	22.8
1995	33.0	251.0	19.3	303.3	82.8	15.0

Table 2. Annual chum salmon runs (thousands) to Hokkaido and Honshu.

Year	Hokkaido			Honshu			Total		
	Coastal Sea	Rivers	Total	Coastal Sea	Rivers	Total	Coastal Sea	Rivers	Total
1966	3408	396	3804	451	187	638	3859	583	4442
1967	3908	592	4500	370	142	512	4278	734	5012
1968	1902	236	2138	260	115	375	2162	351	2513
1969	3595	578	4173	313	134	447	3908	712	4620
1970	4651	627	5278	424	149	573	5075	776	5851
1971	6806	845	7651	652	245	897	7458	1090	8548
1972	6343	614	6957	698	229	927	7041	843	7884
1973	7724	597	8321	616	238	854	8340	835	9175
1974	9026	601	9627	901	224	1125	9927	825	10752
1975	14217	1557	15774	1463	362	1825	15680	1919	17599
1976	8342	463	8805	1361	271	1632	9703	734	10437
1977	9466	742	10208	1873	374	2247	11339	1116	12455
1978	12284	863	13147	2667	394	3061	14951	1257	16208
1979	17751	1151	18902	4518	608	5126	22269	1759	24028
1980	13786	1660	15446	5873	1099	6972	19659	2759	22418
1981	20296	1630	21926	7251	727	7978	27547	2357	29904
1982	18270	1770	20040	7448	894	8342	25718	2664	28382
1983	21235	1778	23013	10052	776	10828	31287	2554	33841
1984	19741	1831	21572	15880	895	16775	35621	2726	38347
1985	29461	2413	31874	16559	888	17447	46020	3301	49321
1986	26218	1999	28217	19206	1201	20407	45424	3200	48624
1987	26560	1567	28127	13937	837	14774	40497	2404	42901
1988	32514	2315	34829	15489	968	16457	48003	3283	51286
1989	34973	2903	37876	15722	991	16713	50695	3894	54589
1990	41210	3264	44474	22171	1539	23710	63381	4083	68184
1991	39071	2390	41461	17346	1353	18699	56417	3743	60160
1992	26014	1534	27548	17180	1164	18344	43194	2698	45892
1993	37220	2789	40009	19407	1357	20764	56627	4146	60773
1994	46986	4204	51190	16211	1468	17679	63197	5672	68869
1995	53793	3899	57692	18395	1690	20085	72188	5589	77777

Fig. 1 Annual changes in adult returns and released fry for chum salmon from Japan, 1965-1995.



seas totalled over 10 million fish 1974, over 20 million fish since 1979, over 30 million fish since 1983, over 40 million fish since 1985, over 50 million fish since 1988 and over 60 million fish since 1990 (except 1992). The largest return, about 78 million fish, was seen in 1995. Over 70 million fish are also expected in 1996. Annual chum fry to adult return rate by brood year for chum released from Hokkaido and Honshu Islands are shown in Table 3. The adult return rate has stabilized at over 2 percent since 1968, over 3 percent since 1984 and over 4 percent since 1987 except 1988 in Hokkaido, and between 1.6-2.5 percent since 1975 in Honshu. Recently, the largest return rate in Japan has been estimated at about 3.8 percent in 1991. In one local stock of Hokkaido, a return rate over 13 percent was recorded. The recent rapid increase in adult returns and return rates are due not only to an increase in the number of fry released by expansion and improvement of hatchery facilities, but also to effective use of spring waters and full protection of river fish from coastal fishing, and prolonged feeding periods (two to five months) prior to release.

Annual changes in adult returns and the return rates of pink salmon from Hokkaido are shown in Table 4 and Figure 2. The numbers of released pink fry have fluctuated between 16 to 150 million fish from 1969 to 1986, and have been regulated at

120-150 million fish since 1987. The adult returns to rivers and coastal seas fluctuated between 0.4-2.7 million fish with a clear trend of increasing in odd years and of decreasing in even years from 1969 to 1986. Without a difference in odd years and even years, they increased to over 3.8 million fish since 1987 except 1990 and over 8 million fish since 1991. The largest return, about 17 million fish, was seen in 1994. In 1996, they expect over 19 million fish. The adult return rate for pink fry released from Hokkaido has stabilized at over 5 percent since 1989. The largest return rate, about 12 percent, was seen in the 1992 brood.

For the masu salmon in Hokkaido, since 1986, 3.1-8.0 million fry or smolts have been liberated and 264-869 thousand adults have been caught in the coastal seas near the home stream, corresponding to a return rate of 8-28 percent.

For the sockeye salmon, since 1982, 31-2015 thousand fry or smolts have been liberated and 0.4-8.2 thousand adults have been caught in the coastal seas near the home stream, corresponding to a roughly return rate of 0.1-2.5 percent.

RESOURCE MANAGEMENT

To promote an effective use and adequate control of salmon resources maintained by artificial production, it is necessary to keep an appropriate

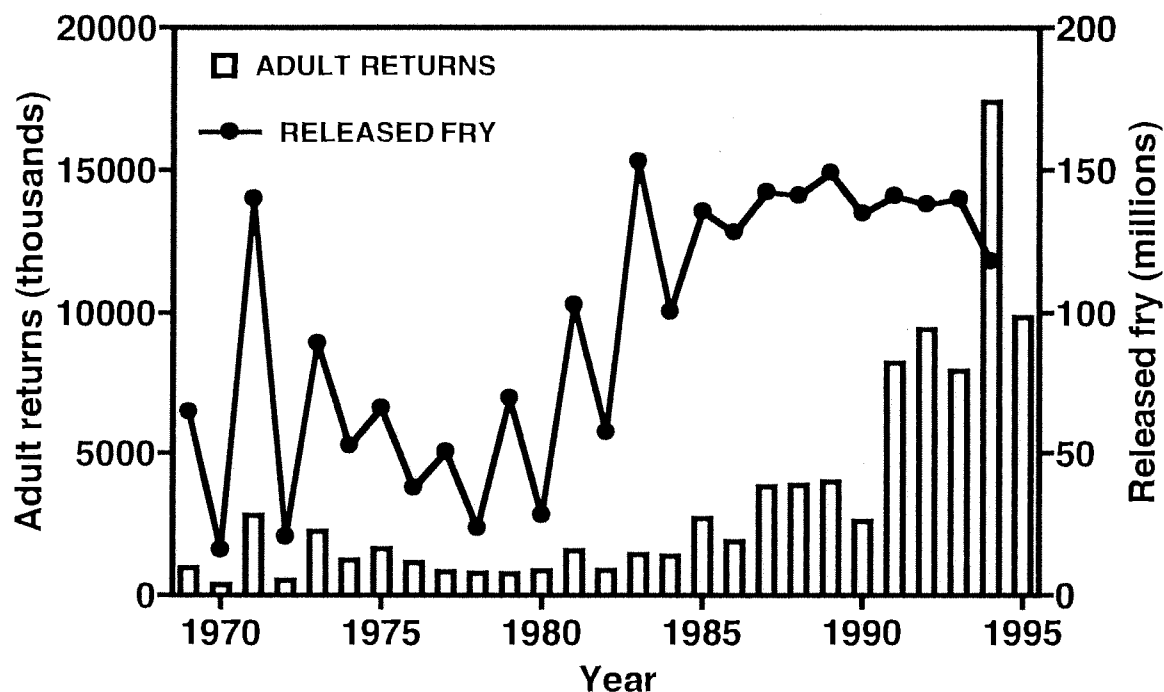
Table 3. Annual chum fry to adult return rates by brood year. Figures in brackets indicate number or rate of adult returns after four years.

Year	Hokkaido			Honshu		
	Liberated Fry (thousands)	Adult Returns (thousands)	Return Rates (%)	Liberated Fry (thousands)	Adult Returns (thousands)	Return Rates (%)
1962	280743	3025	1.08	138267	(718)	(0.52)
1963	272106	4983	1.83	116476	(572)	(0.49)
1964	334463	2119	0.63	139575	(415)	(0.30)
1965	549278	2572	0.47	109836	(497)	(0.45)
1966	272036	5943	2.18	196469	(653)	(0.33)
1967	434729	8110	1.87	161240	(987)	(0.61)
1968	207438	4881	2.35	121193	(1017)	(0.84)
1969	361571	8737	2.42	139536	(1004)	(0.72)
1970	442101	10110	2.29	144673	(1275)	(0.88)
1971	575986	12913	2.24	222516	1351	0.61
1972	475805	11909	2.50	224946	1898	0.84
1973	445510	9036	2.03	271223	2588	0.95
1974	484849	11342	2.34	271708	2414	0.89
1975	801991	21322	2.66	343988	5546	1.61
1976	523221	13092	2.50	287133	6889	2.40
1977	693222	20872	3.01	412625	7422	1.80
1978	779269	23917	3.07	433177	8341	1.93
1979	873489	18809	2.15	589905	10174	1.72
1980	1146346	26810	2.34	750113	(17085)	(2.28)
1981	1079708	31919	2.96	738055	(17693)	(2.40)
1982	1145880	28326	2.47	864601	(20393)	(2.36)
1983	1146763	28330	2.47	885534	(14769)	(1.67)
1984	1139496	35154	3.09	895018	(16448)	(1.84)
1985	1131739	41855	3.70	910476	(16709)	(1.84)
1986	1072605	39864	3.72	927853	(23247)	(2.51)
1987	1054616	43283	4.10	937447	(19044)	(2.03)
1988	1097165	31753	2.89	972496	(18646)	(1.92)
1989	1122345	46438	4.14	945954	(20652)	(2.18)
1990	1100957	(50705)	(4.61)	993257	(18164)	(1.83)
1991	1051520	(57277)	(5.45)	989287	(20501)	(2.07)
1992	1008750			950878		
1993	1083954			968786		
1994	1053813			955940		

Table 4. Annual adult returns and the return rates for pink salmon from Hokkaido. Figure in bracket indicates a number reported en route.

Year	Liberated Fry (thousands)	Adult returns (thousands)			Return rate (%)
		Coastal Sea	Rivers	Total	
1969	64556	858	103	961	4.35
1970	15873	329	43	372	3.28
1971	139687	2535	274	2809	1.61
1972	20390	470	51	521	6.07
1973	89091	2048	202	2250	1.83
1974	52460	1115	122	1237	2.18
1975	65864	1484	147	1631	1.25
1976	37558	1054	88	1142	2.04
1977	50390	710	116	826	1.49
1978	23398	719	47	766	3.69
1979	69433	597	153	750	2.25
1980	27918	796	68	864	3.16
1981	102703	1370	193	1563	1.39
1982	57277	762	120	882	2.40
1983	152790	1051	378	1429	1.77
1984	100290	1110	266	1376	1.89
1985	135414	2116	590	2706	2.83
1986	127998	1499	396	1895	3.02
1987	142085	2987	841	3828	2.81
1988	140968	3320	544	3864	1.84
1989	148953	3386	600	3986	5.52
1990	134598	2222	375	2597	7.00
1991	140824	7041	1174	8215	5.63
1992	137847	8469	950	9419	12.61
1993	139821	7543	387	7930	7.05
1994	117920	15481	1907	17388	(16.24)
1995		9035	820	9855	
1996		(17004)	(2143)	(19147)	

Fig. 2 Annual changes in adult returns and released fry for pink salmon from Japan, 1969-1996.



management of coastal commercial catches to ensure that the adequate stock size returns to rivers. Coastal maturing salmon migrating near home streams are caught by several kinds of fishery, set net and drift net, etc. Recently, the share of set net fishery is the largest of those in coastal commercial catches. Set net fishery for chum and/or pink has increased both in number of licenses issued and in earnings, coupled with the rapid increase of resources. In Hokkaido, to accomplish the adequate size of salmon runs to secure the proper production capacity of the resources, the Government has stipulated various regulation such as fishery-term and distance from shore for the chum and pink set net fishery for each of the respective districts. These regulations are subjected to review every five years. In each year, moreover, temporary removals of set net during the fishery season have been required in cases where the level of spawning run has been considered to be inadequate. The adequate levels are estimated for respective districts by resources analyses, on the basis of the presumed number of adult returns to both rivers and coastal seas. Thus, the set net fishery for chum and pink, recently, became stable thanks to resource management with active propagations.

ECONOMIC EFFECTS

Expenses for the artificial propagation of migrating salmon in Japan are Y 10-14 billion, while harvests from the coastal catch of the adult return are worth Y 50-90 billion, more than five times the expense since 1985.

FUTURE EFFECTS

With regard to chum and pink salmon, resources have reached a stable level by artificial propagation, efforts to select adults with a long freshwater life during anadromous migration are now being paid for. These fish take premium prices because of the silvery body colour observed in coastal seas near home streams. On the other hand, further efforts are needed to increase resources for the districts or prefectures with low level production and to secure higher return rates.

With regard to masu and sockeye which are among the most valuable species in the salmon family, it is important to accomplish most rapidly the artificial propagation technique by using the smolt-release methods, to increase resources, and to raise return rates.

Historical Trends of Fisheries and Stock Condition of Pacific Salmon in Russia

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At the present time, the main pink salmon and sockeye salmon stocks are in good condition on the Russian far east. However, pink stocks have tended to decrease in recent years. Wild stocks of chum salmon are currently in poor condition in many far-eastern regions, except for those of the north Okhotsk Sea coast and Okhotsk region. We do not expect a noticeable increase in the near future.

There are abundant Pacific salmon stocks that are under intensive exploitation on the whole coast of Russian far east. In the long-term, the dynamics of these stocks are mainly determined by variability of global environmental conditions. Climate and related oceanographical effects determine general trends in Pacific salmon catches, although the trend can be strengthened or slowed by management of harvest and the releases of hatchery fry. At present, only the dynamics of the catch of salmon can be used as a quantitative indicator of long-term salmon stock conditions. Sometimes the coincidence of catch and salmon stock condition may not be exact.



INTRODUCTION

Salmon together with walleye pollock and crab are the three most important fisheries in the Russian Far East. During the 1990s, the salmon catch varied in the range of 120-250 thousand tons. Salmon contribute 4-6% of the total fisheries harvest of the region by weight, and have a high market value as a food product. These factors determine the exceptional significance of Pacific salmon for Russian Fisheries Branch. Since 1992, the Pacific salmon catch became the highest of the pelagic fish species harvested in Russia, surpassing the Pacific herring and saury catch. Commercial fisheries for Pacific salmon fisheries are developed on the entire Russian far eastern coast: from the Anadyr River to the southern Primorie (Figure 1). Chum salmon are the primary species harvested in the far northern and far southern regions. Pacific salmon catches reported here include the catch from the Japanese concessional fishery in the Russian EEZ that occurred from 1915 - 1943 (Chigirinsky 1994) as well as the catches from the inshore Russian fishery

North Pacific Ocean (Shuntov 1994). Among Pacific salmon species, pink salmon has the second highest biomass behind chum salmon and constitutes about 25% of the total (Konovalov 1986). In the 1990's the pink salmon constitutes 72-86% of the Russian salmon catch in odd years and 68-74% of the Russian catch in even years.

The condition of pink salmon stocks in the Russian Far East has significantly fluctuated during the long-term period of fisheries exploitation, similar to the stocks of other salmon species. Unfortunately, it is only at the present time that the dynamics of salmon harvest value can be used as a quantitative parameter of salmon stocks' condition, and in long-term series sometimes the coincidence of catch and stock condition may not be exact. Some figures relating to this question will be represented below.

In the beginning of the Russian Pacific salmon fishery a approximate 15-year period of gradual increasing catch occurred (Figure 2). This gradual increase in catch occurred as the fishery was developed with increasing effort and market formation. It is significant that inter-annual variability in catch between even and odd years was not observed at this time. Substantial inter-annual variability in catch is characteristic of the subsequent 80 years of the fishery, with comparatively larger catches occurring in one year followed by lower catches in the following year.

PINK SALMON

Pink salmon is the most abundant salmonid species of the Russian Far Eastern Coast, and contributes about 40% of total salmon catch in the

Fig. 1 Main regions of Pacific salmon coastal fisheries in the Russian far east.

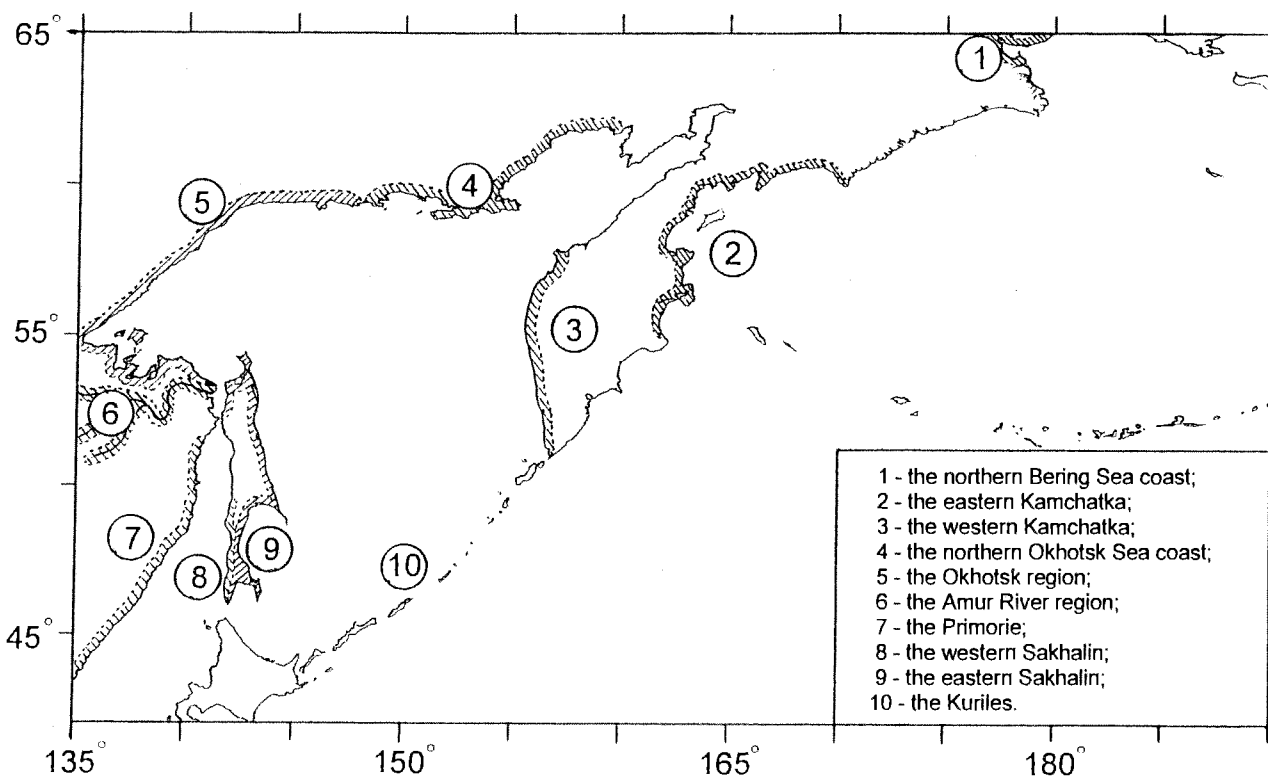
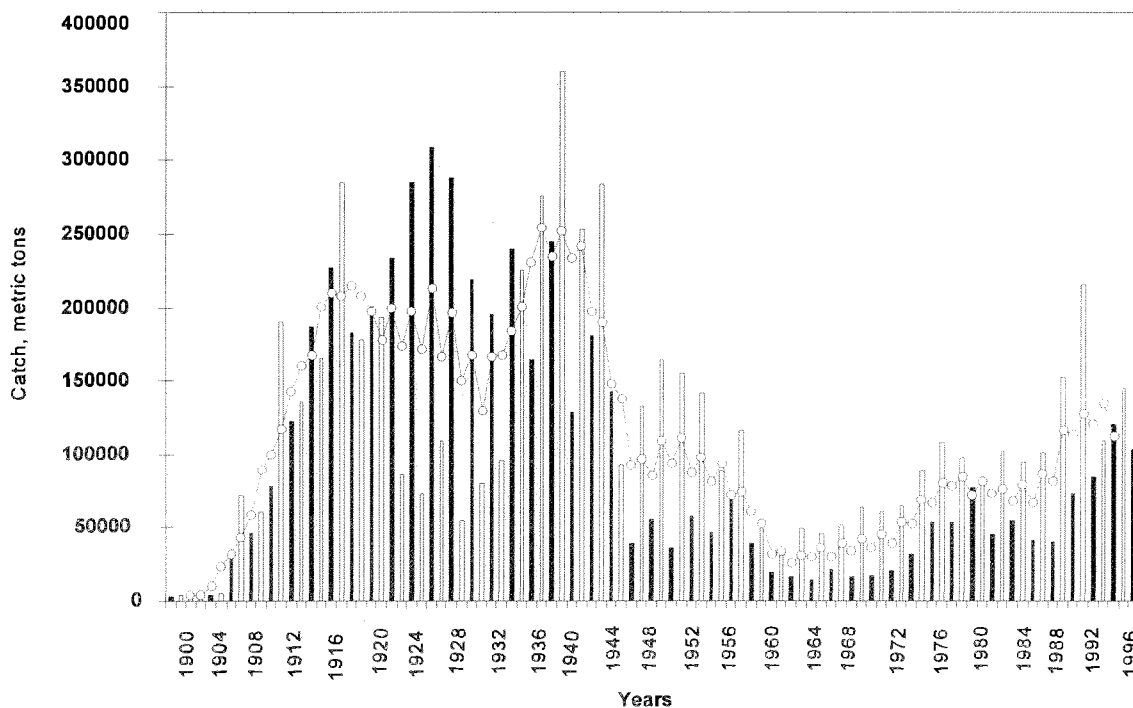
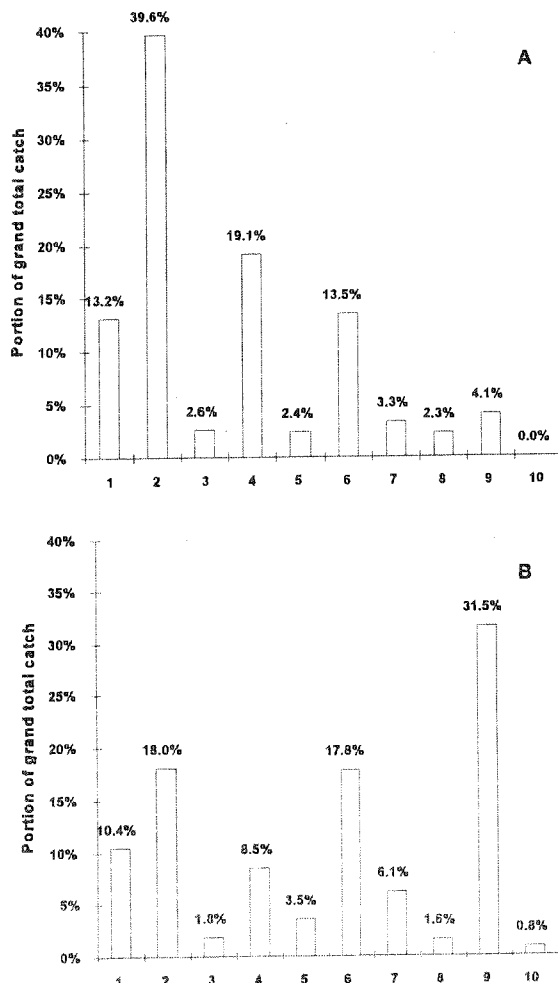


Fig. 2 Total Russian catch of pink salmon with 5-year moving average (solid line). Dark bars-even years, light bars-odd years.



By 1915 the annual pink salmon catch attained a level of 200 - 215 thousand tons. We consider this catch was sustainable and corresponded to a healthy stock condition. This level of harvest was maintained until 1922. In 1923 a sharp decline of harvest occurred during the odd years on the Kamchatka Peninsula. At that time, the Kamchatka Peninsula was the main region of salmon fisheries development in Russia. Later, a salmon fisheries infra-structure based on pink salmon was developed on Sakhalin Island too (Figure 3).

Fig. 3 Regional distribution of grand total catch of pink (A) and chum (B) salmon, 1900-1996. Regions: 1 - eastern Kamchatka; 2 - western Kamchatka; 3 - northern Okhotsk Sea coast; 4 - eastern Sakhalin; 5 - western Sakhalin; 6 - Kuriles; 7 - Okhotsk region; 8 - Primorie; 9 - Amur River; 10 - northern Bering Sea coast.



During odd-years of 1923 - 1933 the total Russian catch of pink salmon fell to 33 - 42 thousand tons. During this time the foreign catch also fell with a total odd year catch of 56 - 118 thousand tons. In contrast, the even-year catch of pink salmon increased and exceeded 300 thousand tons in 1926.

During the decade (1934-1944) odd-year catches increased and even-year catches decreased with catches remaining relatively stable in the range of 240-260 thousand tons. The development of the pink salmon fisheries on Sakhalin Island, where the odd-year populations dominate, contributed to the increase in odd-year catches. The odd-year dominance of inter-annual catch structure formed during the 1930's has been maintained to the present time. Note that low catches during the period 1945 - 1947 were due to political reasons (i.e., foreign fisheries were not conducted in Russian waters). In 1939 the historical high pink salmon catch was achieved - 360.3 thousand tons (Chigirinsky 1994). A total of 379.9 million fish, or 531.7 thousand tons of Asian pink salmon, were harvested including the Japanese driftnet fishery in the high-sea zone.

The Russian pink salmon catch has been decreasing from the early 1940's to the early 1960's. This decrease may have corresponded to a general decline in the health of pink stocks. It is believed that the main trends of pink salmon stock dynamics are the consequences of local or global environmental conditions and not related to harvest effort. We can relate many of the observed trends in catch with global climate variability over the North Pacific. Briefly, the intensity of water circulation in the Subarctic macro-gyre slackens during the periods of positive anomalies in reiteration of meridional form M-1 (Girs 1971) of atmospheric circulation. The Subarctic Front shifts northwards in these years, and subtropical waters spread northwards too. Therefore, the area suitable for pink salmon feeding in the Pacific ocean narrows and feeding conditions worsen.

The basis of the northward shift of main fronts and currents in North Pacific since 1957 has been described by Tully et al. (1960). During that period, the salmon production and catches declined on the both the Asian and American coasts of the Pacific Ocean (see Beamish and Bouillon 1993; Chigirinsky 1993). In contrast, in the south-western Pacific Ocean, the Japanese catch of subtropical fishes and squids (Japanese anchovy, Japanese common squid) increased to a level 4-5 times that of the period 1910-1950 (Davydov 1986). In the second half of 1970s another decrease of catch of subtropical species appeared, and conditions of salmon feeding may have improved. The return rate of chum to the Japanese hatcheries did not exceed 2% prior to 1976, and afterwards (1977-1986) it grew up to 3% even though no changes in chum hatchery technology occurred (Klyashtorin and Smirnov 1992). A gradual increase in Russian salmon catches, in particular those of pink salmon, was observed after the mid 1970's. The timing of these changes in salmon productivity coincides well with years of environmental regime shifts that were identified by many authors to have

occurred during the early 1950s and mid 1970s (Hare and Francis 1995).

Presently, the runs of pink salmon to the Russian far east coastal areas are in relatively good condition. The rate of increase in odd-year runs since the 1970's was similar to that for even-year runs although the catch in odd-year runs was greater. There appears to be some changes in stock structure, with the distribution of catches among western Kamchatka river systems variable over the period 1981 - 1986 (Figure 4). Catches were concentrated in the most southern group (from the Kihchik to the Opala Rivers) before 1985. A similar situation has occurred in eastern Kamchatka rivers (Figure 5).

In the 1990's, it appears that dynamics of climatic processes over the North Pacific appear to have become unfavorable for salmon production (Beamish and Bouillon 1993; Chigirinsky 1993). However, pink salmon is the most difficult of salmon species to forecast future runs. Currently, the even-year stocks are very productive in Western Kamchatka and in the Southern Kurile Islands. If this situation continues, a return comparable to the high harvest levels of 1920 - 1930 may occur. Furthermore, the environmental conditions in mid 1990s are rather different from those in early 1950s, where the salmon productivity declined. At that time the growth of biomass of

Japanese common squid and Japanese anchovy took place simultaneously with the high level and actual increase of Asian pink salmon productivity.

CHUM SALMON

The Russian year-to year catch of chum salmon has been more stable than the catch of pink salmon (Figure 6). Initially, the chum salmon fishery developed very rapidly. The rapid development was due in part to the fact that the early fisheries occurred in rivers, primarily in the Amur River reservoir. Fishing in rivers is logistically simpler than in marine coastal areas. In the early years, 60-75% of total Russian chum salmon catch was from the early ("summer") race, harvested primarily in the Amur region. In 1910 the chum catch reached the historical high of 138 thousand tons. This initial period of high harvest was short-lived, and by 1916 the chum salmon catch declined to 21.7 thousand tons, of which only 5 thousand tons were caught in the Amur region. Researchers have cited over-harvest as a possible reason for the collapse of the summer-run stocks. However, other natural causes may also have contributed to the decline as a simultaneous decrease of chum salmon stocks also appeared on the whole Russian coast.

Fig. 4 Ratio of pink salmon catch between river groups (from north to south) in western Kamchatka, 1980-1986. Row 1 - from the Lesnaya to Utkholok River; 2 - from the Kovran to Sopoch'naya River; 3 - from the Saychek to Kolpakova River; 4 - from the Brjumska to Pymta River; 5 - from the Kihchik to Opala River; 6 - from the Opala to Kamalnaya River.

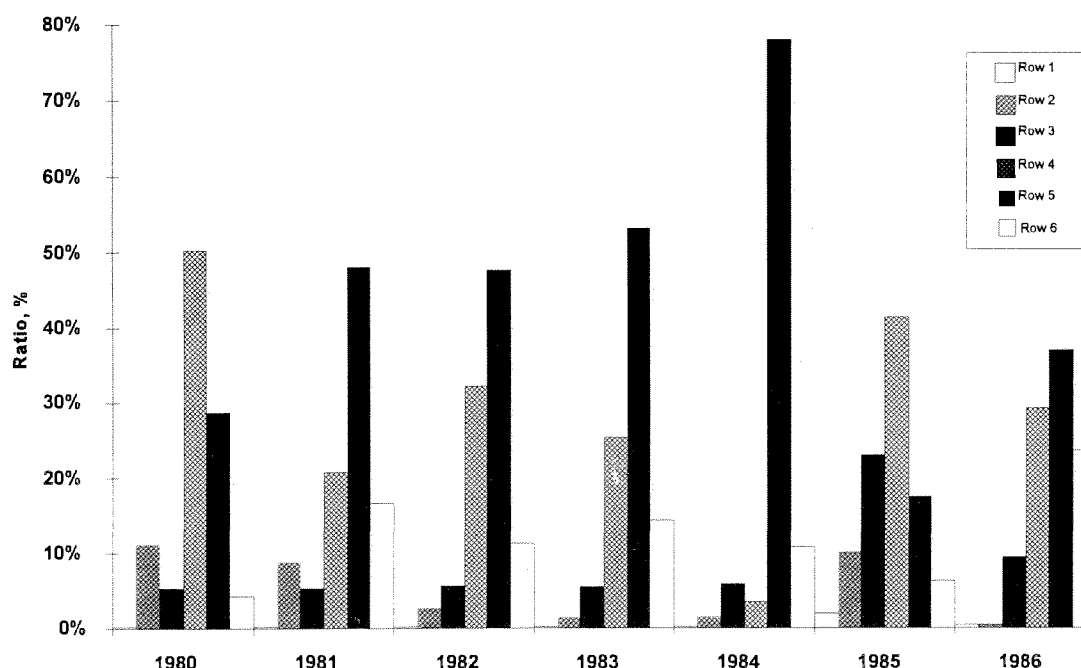


Fig. 5 Ratio of pink salmon catch between river groups (from south to north) in eastern Kamchatka, 1980-1986. Row 1 - from the Khodutka to Bearezovaya River; 2 - the Kamchatka River; 3 - from the Ucka to Drapka River; 4 - from the Kikmavayam to Tymlat River; 5 - from the Packlavayam to Anapka River; 6 - from the Lylangvayam to Kultushnaya River; 7 - from the Impucka to Apucka River.

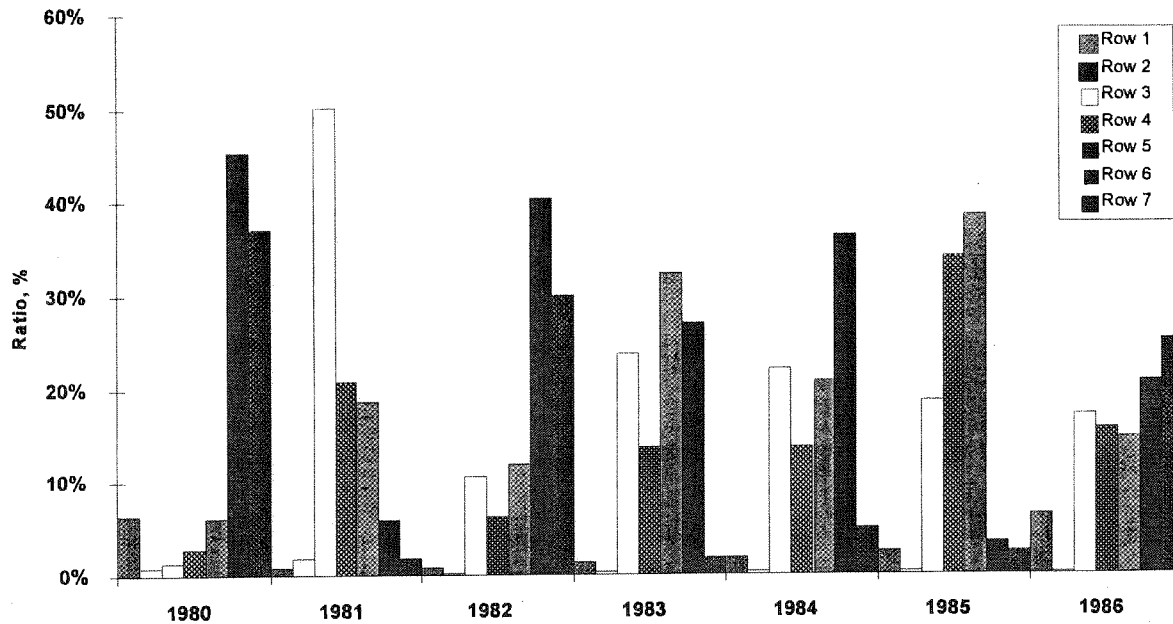
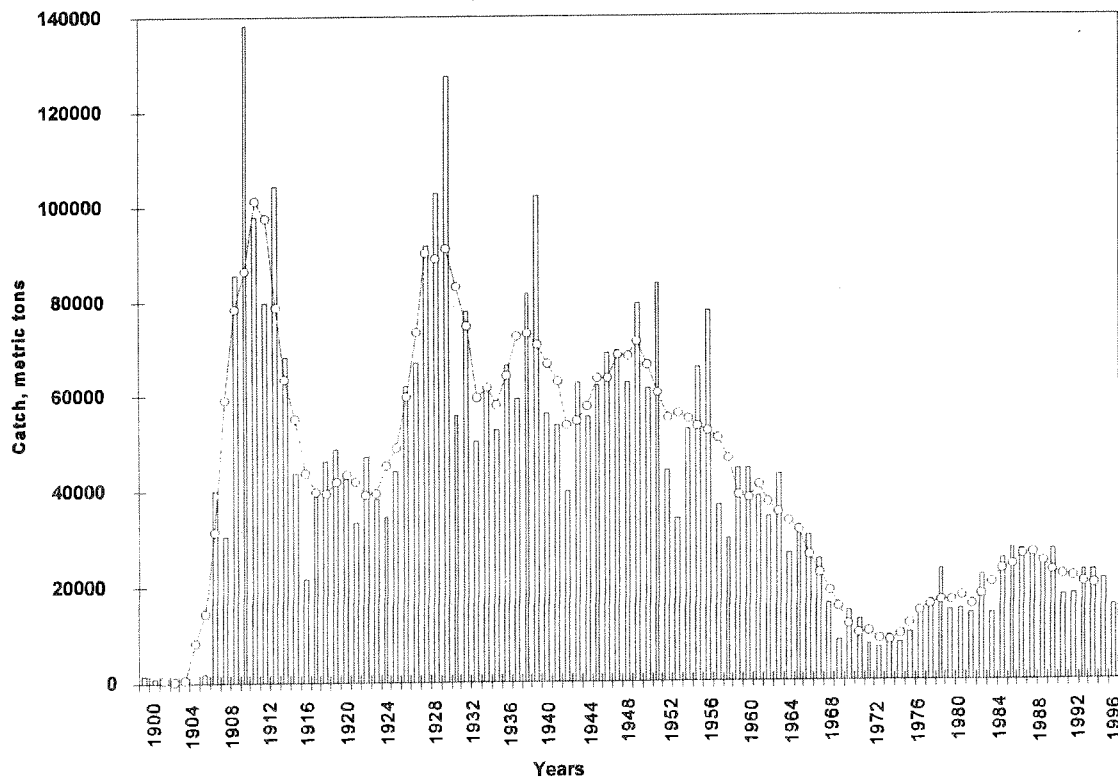


Fig. 6 Total Russian catch of chum salmon with 5-year moving average (solid line).



In 1929-1930 the harvest of chum salmon increased to comparatively high values. This increase was due to development of fisheries for chum salmon outside the Amur Region which contributed no more than 17-19% of the total catch. During that period, the western Kamchatka stocks were the largest component of the Russian chum fisheries, contributing 47.7 - 48.4% of the total. In the 1930s - 1940s, the harvest of chum salmon was relatively stable. Annual catch varied in three year cycles within the range of 52 - 79 thousand tons. According to classical theory, these stable cycles may have been related to over-seeding of the spawning grounds. It is well known that three-year-olds contribute a substantial component of spawners in these Russian stocks, especially in years of high population numbers.

From the early 1950s to the mid 1970s the Russian harvest of chum salmon again decreased. This decrease was gradual but rather significant and was undoubtedly connected to the depleted condition of Russian chum salmon stocks. The decline occurred in all Russian regions (Figure 3). The eastern Kamchatka annual catch value fell from 10-11 tons down to 0.7 - 1.2 thousand tons; the western Kamchatka annual catch fell from 15-23 to 0.2 - 0.3 thousand tons; the Sakhalin and Kuriles annual catches fell from 7-10 thousand tons to 1.8 - 1.9 thousand tons; the Okhotsk Sea coast annual catches fell from 11-19 thousand tons to 0.2 - 0.3 thousand tons; the Amur region annual catch fell from 11-13 thousand tons to 2.6 - 3 thousand tons; the Primorje region annual catch fell from 2.5 - 4 thousand tons to 0. The

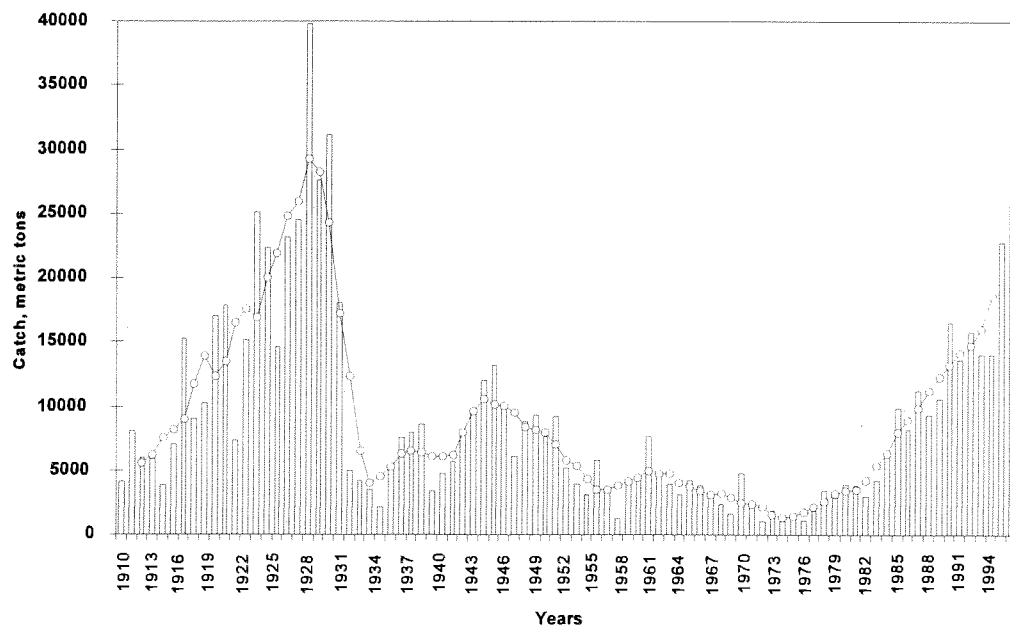
southern stocks of chum salmon have not recovered to this time. In the Amur and Primorje regions, the anthropogenic influence on spawning habitat impacted chum stock restoration. On Sakhalin and Iturup Island, depleted chum stocks are too weak to be commercially fished. On the northern Okhotsk Sea coast and eastern Kamchatka, a slow recovery of chum stocks has occurred after 1975, but during the 1990s these stocks began to decrease again.

It is believed that competition with the chum juveniles of Japanese hatchery origin during the marine rearing phase has prevented recovery of the wild Russian chum stocks to some degree. More than 2 billion chum smolts are released annually from the Hokkaido and Honshu hatcheries. These hatchery releases resulted in a 12-fold increase in the Japanese catch of chum salmon since the mid 1970s. Chum salmon of all Asian and American stocks spend their feeding period in the Bering Sea and adjacent Pacific waters during the warm seasons. This is a relatively limited area, and the concentration of fish increases the competition for food. It is possible that the decreasing trend in catch of wild stocks of chum salmon will continue in the near future, given expected unfavorable climatic conditions mentioned above.

SOCKEYE SALMON

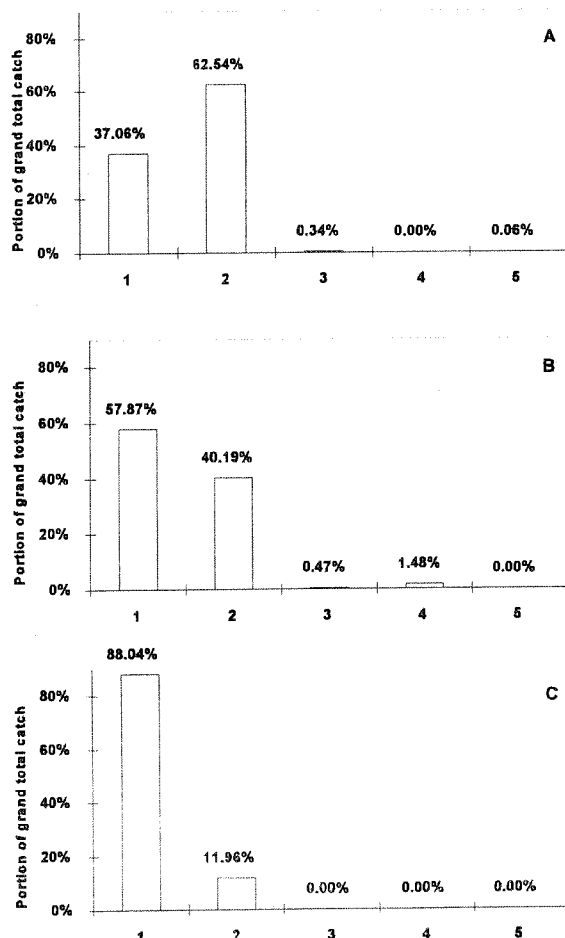
In contrast to chum salmon, the Asian stocks of sockeye salmon are currently in good condition (Figure 7). These stocks are almost completely

Fig. 7 Total Russian catch of sockeye salmon with 5-year moving average (solid line).



concentrated on the Kamchatka Peninsula in the lake systems of the Ozernaya and Kamchatka Rivers (see Figure 8 for distribution of regional catch). Since sockeye salmon always had the highest market value, stock condition has been well reflected by cyclic trends of its harvest. Furthermore, the increasing harvests of sockeye salmon in recent years suggests that stocks are rebuilding from the depressed levels of the early 1970's. At the beginning of sockeye fisheries, the annual catch increased with the development of the fishery. In 1928 the historical peak of sockeye salmon catch, 39.7 thousand tons, occurred (Figure 7).

Fig. 8 Regional distribution of grand total catch of sockeye (A), coho (B) and chinook (C) salmon, 1900-1996. Regions: 1 - eastern Kamchatka; 2 - western Kamchatka; 3 - northern Okhotsk Sea coast; 4 - Okhotsk region; 5 - northern Bering Sea coast.



In the 1930's, a sharp decline in catches occurred, followed by a long period of low stock levels. Interceptions by Japanese driftnet fishery near the Kamchatka coast (Harris 1989) which developed during this period, may have contributed to the low stock levels of Asian sockeye stocks during the 1950's

to the late 1970's. However, the driftnet fishery may not be the only reason for the sharp decline in catch. Unfavorable climatic conditions may have contributed additionally to detrimental effects of the driftnet fishery in 1950s - 1970s. For example, after the very cold winters of 1968 - 1970, the sockeye salmon catch reached its lowest level of 1.0 thousand tons in 1972. Chum catch also declined to a minimal level of ~0.7 thousand tons in this year.

Like other salmon species, the stock condition and catches of sockeye salmon increased after the mid 1970s. In 1995, the total harvest (including the catch of Russian and foreign driftnet fleet within the limits of the Russian Economic Exclusive Zone) of sockeye salmon exceeded 20 thousand tons for the first time since the 1930's. The cessation of high seas driftnet fishery has promoted the growth of sockeye catch in the Russian EEZ. It appeared in accordance with the international convention under the aegis of NPAFC.

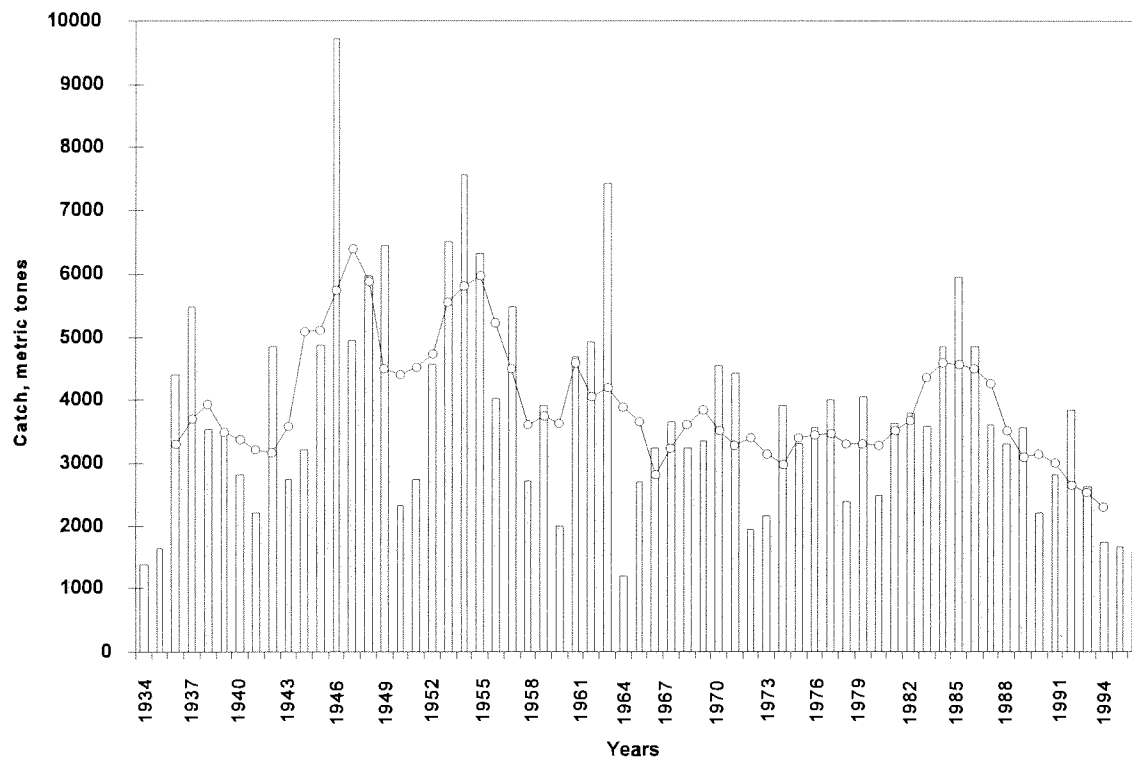
Prior to 1926, the proportion of western Kamchatka sockeye salmon stocks in the Russian catch was noticeably higher than that of eastern Kamchatka. During the period 1926 - 1929 the sockeye catches in eastern Kamchatka increased sharply, surpassing those of western Kamchatka by 1.2 - 1.5 times. During the period of low catches there were no consistent differences in the proportion of sockeye salmon catches among eastern and western Kamchatka. Since 1985, the catches from western Kamchatka region have been higher than eastern Kamchatka and this dominance has been gradually increasing. During the period 1910-1996, the proportion of sockeye catches from western Kamchatka has averaged 62.6%, while that of eastern Kamchatka was 37% (Figure 8).

CHINOOK AND COHO SALMON

Catches of chinook and coho salmon were lower than those of the other species of Pacific salmon. Relatively abundant populations of coho salmon spawn on the Kamchatka Peninsula and northern Okhotsk Sea coast (Figure 9). Coho salmon catch statistics exist since 1934. The five-year moving average was relatively stable in the range of 3.0 - 4.7 thousand tons (Figure 9). In recent years catches of coho salmon have been declining. It is believed that this decrease in stock condition has been related to increased poaching (illegal fishery) of coho salmon on the spawning grounds.

The Russian catch of chinook salmon consists mainly of one stock, the Kamchatka River, which has contributed more than 85% of the catch during 1934-1996. The remainder of the catch was from the Bolshaya River on the western Kamchatka peninsula. There exist several stocks of chinook salmon in western Kamchatka that are currently unexploited. It

Fig. 9 Total Russian catch of coho salmon with 5-year moving average (solid line).



is believed that these small stocks would allow an additional catch of about 100 tons of chinook salmon annually, if exploited. Dynamics of the Kamchatka River stock were characterized by increasing catches during the period 1969 - 1988 (Figure 10). Catches have been decreasing since 1977, when the peak catch of 3.1 thousand tons was achieved.

FUTURE OUTLOOK

It is believed that there is a significant potential for increasing the yield from salmon fisheries in some regions of the Russian far east by improving fishing methods and gears. More than 90% of the total salmon catch in the Russian EEZ is obtained by beach and river seines that are operated by small vessels. This fleet of small vessels sometimes finds it difficult to conduct fishing operations even during modest storms that are common during the fishing season. Thus, the large and modern motherships (where salmon are processed) must often stand idle because of stormy weather. This is especially true for western Kamchatka region where because of the exposed coast line it is difficult to conduct beach seining operations. In western Kamchatka a much lower proportion of the run is harvested relative to other areas (Figure 11). This is especially so during years of high pink abundance. In some areas logistical problems with the salmon processing industry has resulted in limited

utilization of salmon runs.

Since 1991, the TINRO-Center had the opportunity to conduct large-scale complex sea expeditions during the Pacific salmon anadromous run. The number and biomass of maturing salmon were assessed by trawl surveys in the main regions of the Russian EEZ. In the near future, such expeditions may provide us with more correct information on the condition of Pacific salmon stocks, in particular pink salmon, in the Russian Far East.

Pacific salmon hatcheries are developing on the Russian far east in the main regions of salmon fisheries. The volume of enhanced Pacific salmon production is about 500-550 million fry released annually, with pink salmon comprising approximately 53% and chum salmon 48% of the fry released. The primary locations of salmon hatcheries are in the Sakhalin and Iturup Islands. The contribution of enhanced salmon production to the total Russian catch can not be clearly assessed. Some specialists consider that hatcheries had an important role in increasing pink salmon returning to the eastern Sakhalin coast during 1994 - 1995. This was due to the improving technology of the new hatcheries, built in the framework of a Russian - Japanese cooperative project. However, this view cannot be substantiated based on the estimated low proportion of hatchery fry (15%) of the total salmon fry produced.

Fig. 10 Total Russian catch of chinook salmon with 5-year moving average (solid line).

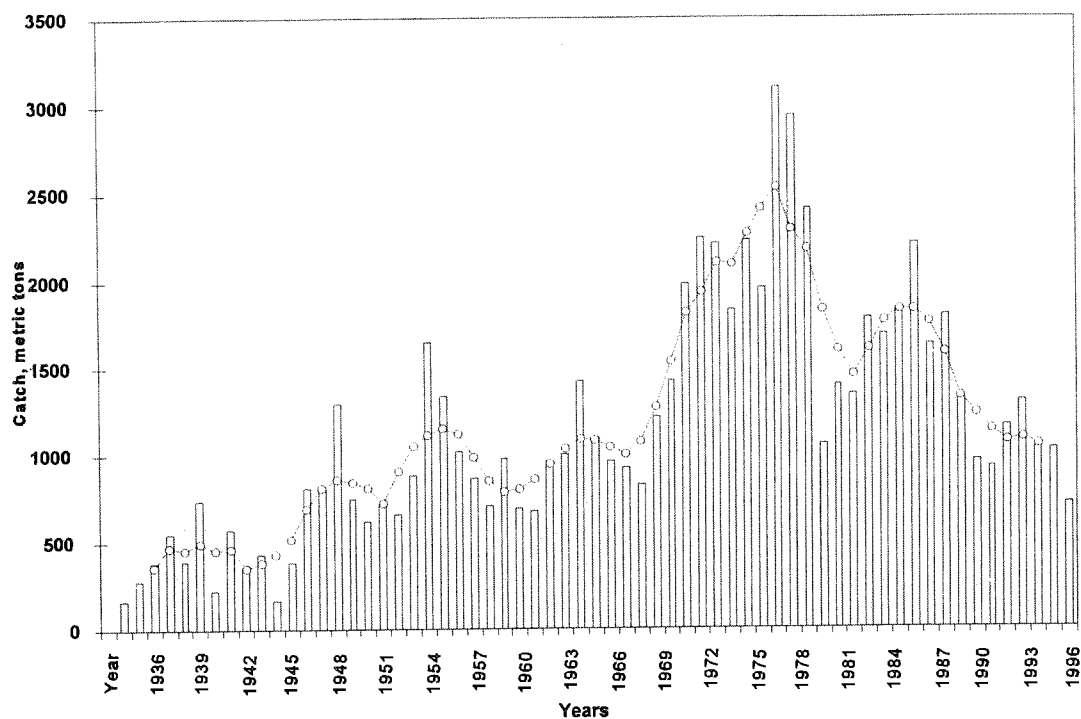
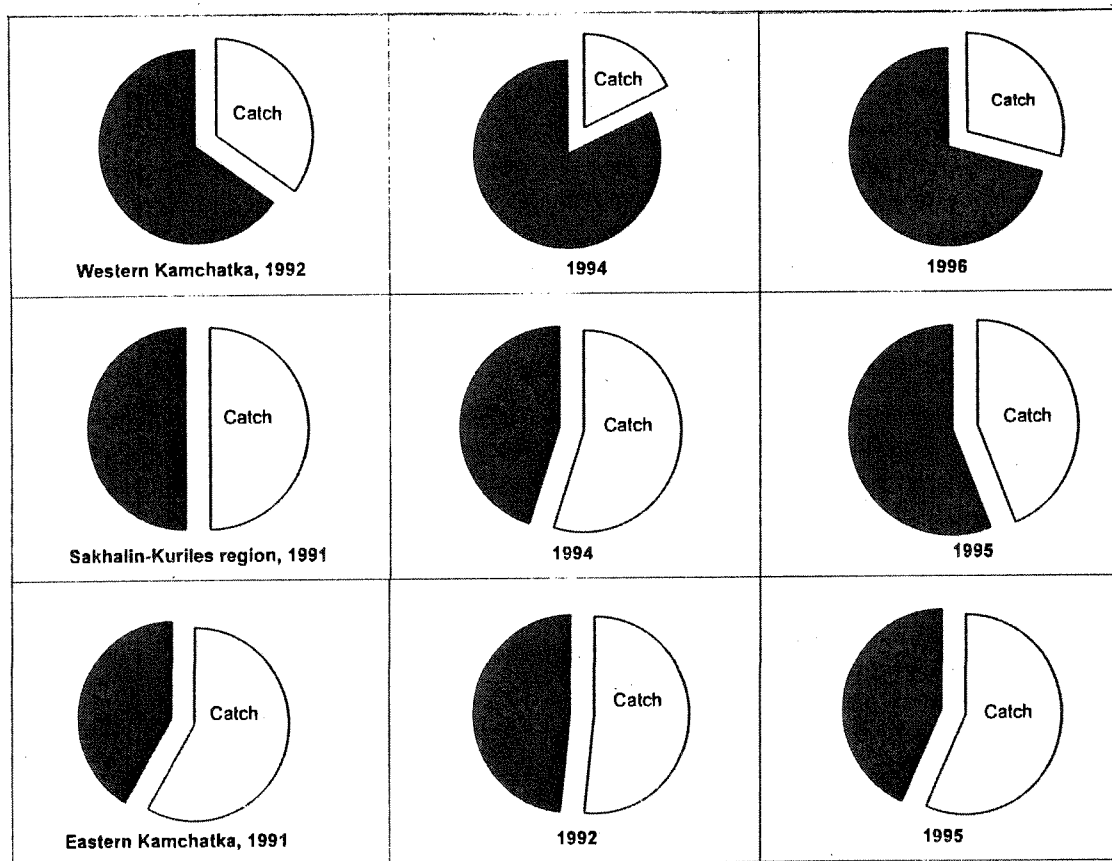


Fig. 11 Relative magnitude of pink salmon catch (open) and escapement (shade), by region, during 1990's.



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A Historical Perspective on Salmonid Production from Pacific Rim Hatcheries

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Annual hatchery production rates of chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*), masu (*O. masu*) salmon, and steelhead trout (*O. mykiss*) were obtained from published and unpublished sources and compiled as a computer database. Pacific Rim hatchery production trends for the 40-year period from 1950-1992 were analyzed for all species from four geographic areas: Pacific Northwest (Washington, Oregon, Idaho, and California), Canada (British Columbia), Alaska, and Japan (Honshu and Hokkaido). Production of chum, sockeye, and pink salmon has increased dramatically in Japan, Canada, and Alaska in the past 20 years. Chinook, coho, steelhead, and masu have also experienced moderate increases in the same time period; however, production of coho, chinook and steelhead has declined since 1985. Trends in survival of hatchery fish over the period 1970-90 are demonstrated where data were available. We noted that survival of coho salmon was greatest for releases into large estuaries, such as southeast Alaska, Georgia Strait, and Puget Sound, than into drainages discharging directly into the Eastern Pacific Ocean. A negative cline in survival of coho salmon was observed moving both north and south from the center of the distribution of the species in British Columbia. Survival trends for fall chinook released north of Puget Sound tended to be the opposite of those released to the south. Survival of Japanese chum salmon released into the North Pacific Ocean has increased steadily from the mid-1960's to the present.



INTRODUCTION

Development of the North Pacific salmonid hatchery system began in the late 19th century and has played a prominent role in enhancement of the salmonid resource in Pacific Rim nations since the 1950s. Until recently, the artificial propagation approach to enhancement of fisheries has not been seriously questioned, but the recent alarming declines in wild spawning stocks have forced a re-evaluation of industrial-scale hatchery production of north Pacific salmonids. Declines have been observed in chinook, coho, and sockeye salmon stocks in the Pacific Northwest; high harvest rates of wild fish in fisheries targeted on the more abundant hatchery stocks have continued, and high production of hatchery chum salmon in Japan and both pinks and chum salmon in

Alaska, declining fish size and altered return timing and age at maturity, have raised concerns over limits on ocean carrying capacity.

In the Pacific Northwest, recent Endangered Species Act listings of Redfish Lake sockeye in the Stanley Basin of Idaho, Sacramento River winter chinook in California, and fall, summer, and spring runs of chinook in the Snake River Basin of Idaho and Oregon have focused attention not only on habitat loss and fishery-related impacts on the wild stocks but on the genetic and demographic consequences of uncontrolled expansion of hatcheries as well (Meffe 1992; Nehlsen et al. 1991). Proposed recovery plans for listed Snake River chinooks and sockeye call for a limit on annual releases from Columbia Basin hatcheries to 1994 levels (Schmitt et al. 1995).

In Alaska, the hatchery successes that were hailed

in the mid 1980s are being assailed in the 1990s. The return of record numbers of hatchery pink and chum salmon and high abundance of natural fish in the North Pacific has led to record high catches and record low revenues to fishermen, and has brought forward new criticism of hatchery management strategies. Concerns over decreasing fish size in the hatchery-based fishery for chum salmon in northern Japan has led to a decision by the Japanese government to reduce hatchery releases. Similar concerns for declining size and increasing age at maturity observed in North Pacific stocks of five salmon species suggests that large-scale hatchery production is resulting in density-dependant growth reduction (Kaeriyama and Urawa 1992; Bigler et al. 1996).

This report provides managers with an historical data set of hatchery releases from Pacific Rim nations, excluding Russia, for the six Pacific salmon species and steelhead through 1992. In addition, an analysis of survival trends for hatchery coho and fall chinook from the eastern Pacific and chum from Japan are presented.

METHODS

Release Data

Annual production rates from Pacific Rim hatcheries were obtained for six species of Pacific salmon: chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye, (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*), masu (*O. masu*), and steelhead trout (*O. mykiss*). We compiled this information from published and unpublished sources and organized it in a computer database. Production trends for the 40-year period from 1950-1990 were analyzed for all species from four geographic areas: Pacific Northwest (Washington, Oregon, Idaho, and California), Canada (British Columbia), Alaska, and Japan (Honshu and Hokkaido). Data from Russia and Korea were unavailable as a continuous historical series, however discontinuous data were available from three sources and were used to estimate total present Pacific Rim output (Heard 1995; Mahnken et al. 1983; Kononov 1980).

Release data from Alaska for chum, pink, coho, sockeye, and chinook salmon were obtained through Alaska Department of Fish and Game annual reports (McNair 1996). Alaska steelhead releases were supplied by Alaska Department of Fish and Game (Marianne McNair, Alaska Department of Fish and Game, P.O. Box 25526 Juneau Alaska, Pers. commun., Oct., 1996). Release data for all species from British Columbia were provided by Canadian Fisheries and Oceans (Ted Perry, Canadian Fisheries

and Oceans, 555 West Hastings Street, Vancouver, B.C., Pers. commun., Oct. 1996). Japanese release information on chum and pink salmon was supplied by the Hokkaido Salmon Hatchery (Masahide Kaeriyama and Shigihiko Urawa, Hokkaido Salmon Hatchery, 2-2 Nakanoshima, Toyohira-ku, Sapporo 062, Japan, Pers. commun., Oct., 1996).

Until recently, a consolidated data set for hatchery production has been unavailable for the western United States (Wahle and Smith 1979; Mahnken et al. 1983; Isaksson 1988). We compiled a comprehensive historical data set from previously unreported raw data forms archived by fishery agencies, annual reports of hatcheries, and electronic databases. We obtained earlier salmon release records from Oregon and Idaho and steelhead from Washington which were previously not available.

Survival Data

Survival information for coho and chinook salmon was obtained from coded wire tag (CWT) data bases maintained by the Pacific States Marine Fisheries Commission. The historical CWT data set was assembled by Maria Claribel Coronado-Hernandez (1995) and is contained in her doctoral dissertation. This seminal work synthesizes and analyzes, for the first time, spatial and temporal factors affecting survival of hatchery-reared chinook and coho salmon and steelhead in western North America over the time period for which coded wire tag recoveries are available (1971-1989). Release-recovery information is presented in the form of expanded CWT recoveries using only non-experimental production groups. Recoveries were standardized to the most common age at return using virtual population analysis (Coronado-Hernandez 1995).

We computed mean survival rates from this data set and used two-way analysis of variance to make statistical comparisons of mean survival values over time. We chose coho and fall chinook salmon for analysis of temporal and geographic variation because of the large data sets available for these species. Pairwise comparisons between sampling dates were made using the Fishers PLSD test. All statements about statistical comparisons are based on the $P < 0.05$ significance level.

Survival data for Japanese chum salmon was provided by the Hokkaido Salmon Hatchery (Masahide Kaeriyama and Shigihiko Urawa, Hokkaido Salmon Hatchery, 2-2 Nakanoshima, Toyohira-ku, Sapporo 062, Japan, Pers. commun., Oct., 1996). These data were compiled through records of fishery catch and hatchery escapement to the Japanese coastal net fishery and to Hokkaido and Honshu hatcheries, respectively.

RESULTS - HISTORICAL PRODUCTION OF PACIFIC SALMON AT PACIFIC RIM HATCHERIES

Coho Salmon

Coho salmon are among the most successful of hatchery-cultivated species in the Pacific Northwest and Canada. Coho salmon hatcheries were highly successful in returning adults to the fisheries in the 1970s, when record smolt-to-adult survivals were recorded in the British Columbia and Puget Sound regions.

Coho salmon production in western North America grew slowly from its inception at the turn of the century, and before 1940 the output from hatcheries never exceeded about 25 million fish annually (Fig. 1A). The slow rate of growth can be attributed to failure of hatcheries to contribute to expansion of the fishery (McNeil and Bailey 1975). Following a period of reduced production during World War II, coho salmon hatcheries entered an industrial phase of expansion that lasted through the 1970s.

In the 1950s and 1960s, advances in the knowledge of feeds, diseases, and the early life history culture requirements of coho salmon led to improved post-release survival of hatchery fish (Lichatowich and McIntyre 1987). Coho salmon are released either as fry or as yearling smolts (25-30 g) and size at release had also been increased over the years and contributed to improved adult survival (Wahle and Smith 1979). These achievements were even more important in that they coincided with a period of rapid deterioration of freshwater habitat and blockage of major migratory pathways by hydroelectric dams. Given these successes, fishery managers came to believe that hatcheries were a means by which the Pacific Northwest could continue to develop its water resources for power, irrigation, and industrial or domestic use and at the same time, maintain fisheries at historic levels (Lichatowich and McIntyre 1987). Increased reliance on hatchery coho salmon led to the rapid expansion of production through the 1970s. In the late 1970s and early 1980s, private sea ranches added 9.3 million smolts per year to Oregon coastal production (Fig. 1A) and helped lead to a record production of 198 million hatchery coho salmon in 1981. In the years that followed however, coho salmon production in the Pacific Northwest stabilized and began to decline (Fig. 1A).

Beginning in 1989, a period of declining production began in most sectors of the coho salmon hatchery system. The decline in overall production from the contiguous western United States was partially offset by the added production of 40 million hatchery fish from Alaska and British Columbia. This

decline can be attributed to various factors: Survival of adult hatchery fish declined following the oceanic regime shift in 1976 and a series of El Niños events in the late 1970s and early 1980s. These conditions resulted in reduced escapement, and hatcheries were unable to meet egg needs for full production. More restrictive inter-basin egg transfer policies were introduced to protect remaining wild populations, and reduced operating budgets at some hatcheries further reduced coho salmon production.

Chinook salmon

Like coho salmon, chinook salmon are released either as fry or as yearling smolts. Chinook salmon were the first salmon species to be artificially propagated in western north America and are artificially propagated in hatcheries along the eastern Pacific seaboard from California to Alaska. More chinook salmon have been produced from hatcheries than any other species in the Pacific Northwest. The first effort to artificially propagate chinook salmon in North America was at the Baird Fish Hatchery on the McCloud River in California in 1872. This hatchery was established to obtain chinook salmon eggs for transport to Atlantic Ocean tributaries to replace depleted Atlantic salmon (*Salmo salar*) runs. Today, the center of hatchery production is the Columbia River Basin where approximately 27% of world chinook salmon is produced.

Fall chinook are the most commonly cultured life history type in both British Columbia and the Pacific Northwest. Also known as "ocean-type" (Healey 1991), fall chinook salmon most frequently inhabit coastal rivers, although ocean-type fish are cultured in the Columbia River as far upstream as the Methow River. Fall chinook salmon are sometimes released as fry but are more commonly reared for three months and released at hatcheries in the spring at approximately 7-10 g. To improve survival, some hatchery populations of fall chinook are reared to yearling size and generally released in the spring at 25-30 g as age-1 smolts (Wahle and Smith 1979).

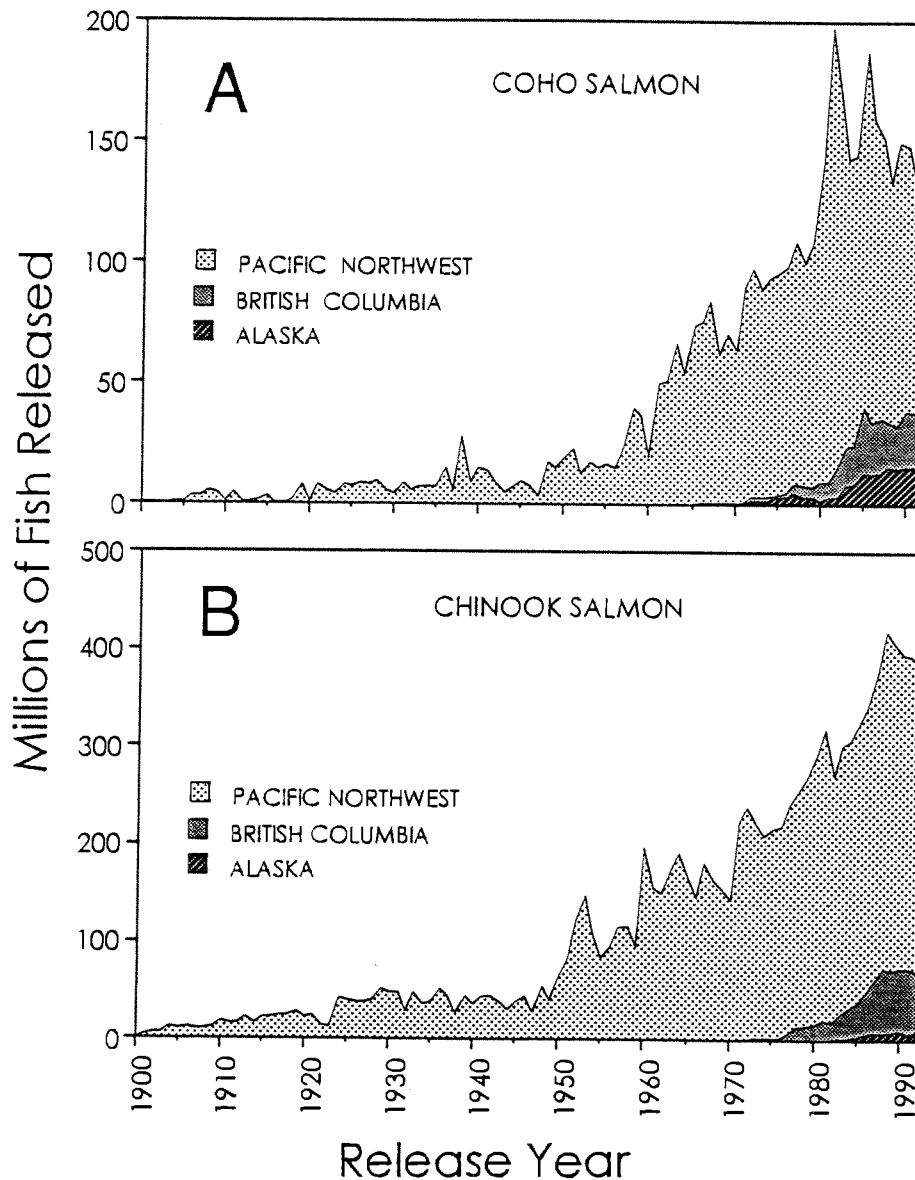
Spring and summer chinook salmon, or "stream-type" life history stocks (Healey 1991), are produced at hatcheries located primarily on large river systems of the Pacific Northwest, British Columbia, and Alaska. Spring chinook salmon are the predominant stocks produced in Alaskan hatcheries. Spring and summer stocks of chinook salmon are seldom released as underyearlings and are grown in hatcheries to the largest size, often over 100 g average, of any of the Pacific salmon species (NRC, 1995). Underyearling releases have been attempted at hatcheries where high rearing water temperatures result in accelerated growth, but survival to adult from releases of these intermediate sized fish is generally lower than those of

larger yearling fish (Zaugg et al. 1985, 1986).

Hatchery production of chinook salmon began in Washington State in 1895 at the Kalama hatchery on the Columbia River, and production grew slowly to around 50 million fish released until the late 1930's (Fig. 1B). Production dropped slightly during World War II, then accelerated following improvements in culture technology and construction of new hatcheries. The decade of 1950-1960 began the industrial phase of chinook salmon hatchery production, as development in the Pacific Northwest resulted in loss of freshwater habitat. Growth of the fisheries also added pressure to the hatchery system to increase production. New hatcheries on the middle Columbia River were constructed to mitigate for lost habitat above Grand

Coulee dam and other mid-Columbia hydroelectric projects. Between 1960 and 1976, 30 hatcheries and 12 rearing ponds raised anadromous salmonids in this region (Wahle and Smith 1979). Another surge in production occurred in Puget Sound hatcheries in Washington State during the 1960s. New lower Columbia River hatcheries and growing production in other sectors of the Pacific Northwest drove annual releases to more than 300 million chinook salmon smolts by the early 1980s. Production increases from British Columbia and Alaska hatcheries in the 1980s added another 100 million fish annually. By 1988, when production peaked, more than 420 million fry, fingerling, and smolts were being released from eastern Pacific hatcheries, a seven-fold increase from the base level of 59 million fish released in 1949.

Fig. 1 Hatchery production of (A) coho salmon and (B) chinook salmon juveniles from Pacific Northwest, British Columbia, and Alaska hatcheries, 1990-1992.



Chinook salmon hatchery production began to decline in the late 1980s for the same reasons that coho salmon production is now falling.

Chum salmon

From the late 1880s until the recent expansion of chum salmon ranching in Japan, hatcheries released fry from rearing ponds to the stream soon after yolk sac absorption. Egg and fry development was accelerated in Hokkaido through the use of constant, 8°C ground water. These conditions favored releases from early to mid-February when fry were sometimes subjected to severe conditions in the streams and coastal marine waters. With temperatures as low as 0-5°C during February and March, survival was minimal. In 1962, production-scale hatchery experiments were undertaken to delay release to a time of more favorable sea temperatures. These experiments involved feeding up to 300 million fry for short periods (Mayama 1985) and demonstrated that dry diets could increase body weight from 0.6 to 1.0 g in about one month. Fry fed on these diets could be released from Hokkaido hatcheries in May, when coastal water temperatures exceeded 10°C. These fry are usually released 50 d before average sea surface temperature reaches 15°C. Larger fish of 2-3 g average weight released to coastal waters during spring periods of high primary and secondary productivity survived at a much higher rate than smaller ones. Adult returns from unfed fry released in 1950-60 averaged 1.2%; returns improved to 2.3% after 1966 as the percentage of fed fish increased (Isaksson 1988).

Japanese chum salmon catch was high prior to World War II, but dropped during the war years. Following the war, catch increased for a few years, then decreased as stocks were overexploited. Beginning in the 1970s, catch of Asian chum salmon rose again, primarily as a result of massive Japanese hatchery releases. From 1950 until 1970 Japanese hatchery production rose from 260 million fish released to around 580 million (Fig. 2A). Following improvements in adult contribution through the release of fed fry, and the loss of foreign fishing grounds to exclusive economic zones (EEZs), the Japanese chum salmon hatchery system entered a phase of rapid industrialization. Production rose from 260 million fry released in 1970 to 2 billion released in 1981. After the early 1980s, Japanese production of chum salmon leveled off.

The Japanese hatchery system is the largest in the world in terms of fish released and returned 78 million adult fish to the Japanese coastal fisheries in 1995 (H. Urawa, pers. commun.). The Japanese land-based fishery is almost entirely hatchery-dependant; wild stocks are virtually non-existent in northern

Japan. Another interesting feature of the Japanese hatchery system is that it has reduced reliance on high-seas fisheries. The imposition of foreign EEZs has restricted the Japanese high-seas fishery on chum salmon destined for Russia and North America, but the loss to the national fishery has been more than replaced by hatcheries.

In North America, enhancement efforts for chum salmon also accelerated in the 1970s, primarily in Alaska and British Columbia (Fig. 2A), adding an additional 850 million fry to the already impressive releases by Japan for a total Pacific Rim production of nearly three billion chum salmon fry (exclusive of Russian hatchery releases).

Pink salmon

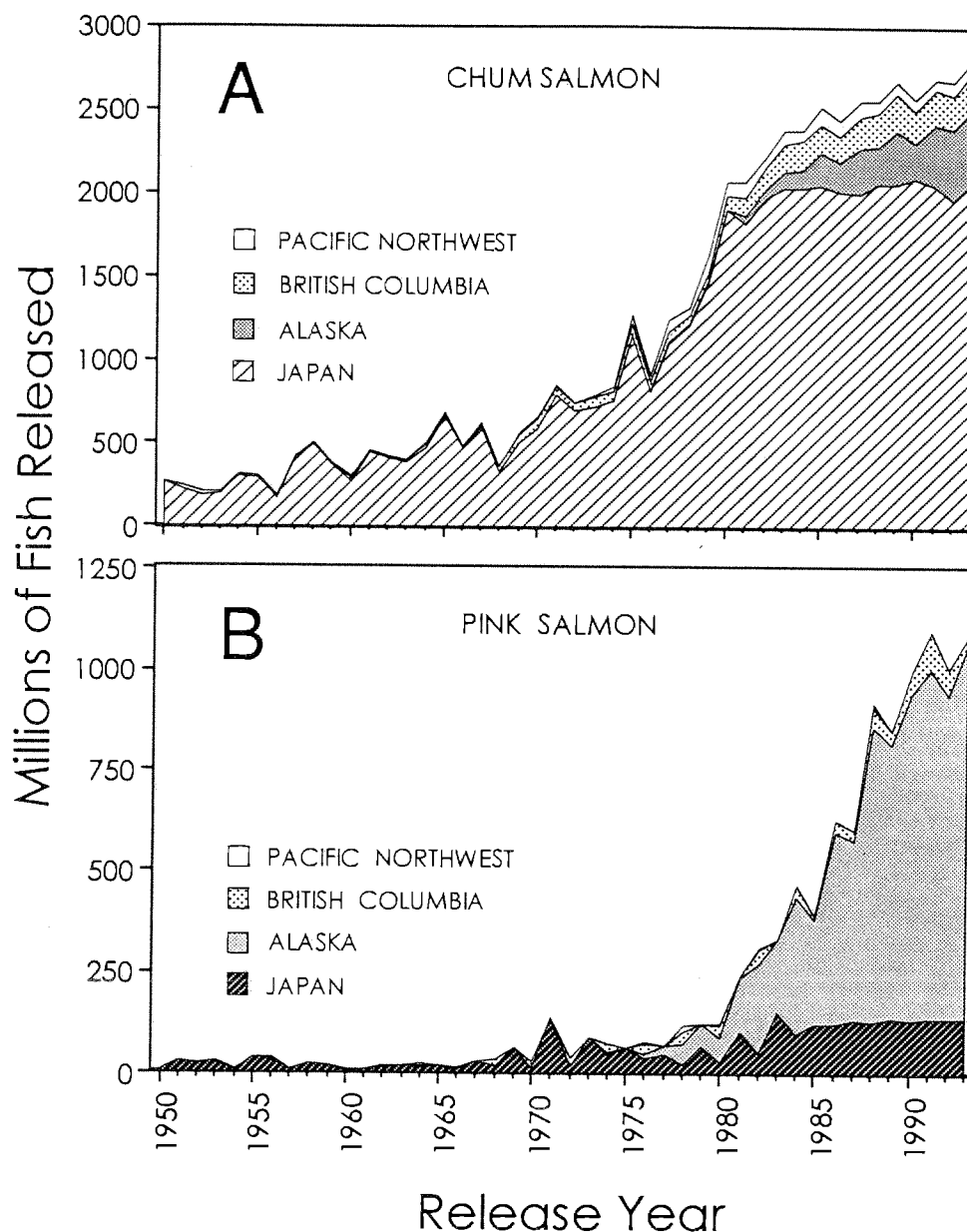
Pink salmon are second to chum salmon in the numbers of juveniles released into the North Pacific Ocean; accounting for 29% of the total reported in 1992 (Heard 1995). Pink salmon are released from most hatcheries at 0.5-2.0 g size (Isaksson 1988). Alaska is the largest producer of pink salmon and released more than 800 million juveniles in 1992 (Heard 1995; McNair 1996). Heard (1995) also notes that Russia is the second largest producer of hatchery pinks; with 584 million juveniles released in 1992.

Pink salmon releases remained low (less than 100 million) until the early 1980s, when an industrialization period began in Alaska, and numbers of released fish from North America increased tenfold to a total of 1.006 billion in 1992 (Fig. 2B). When added to Russian production, total world production of pink salmon was 1.590 billion produced in 1992. Pink salmon is the most recent of the Pacific salmon species to be industrially produced.

Sockeye salmon

Sockeye salmon were propagated in Alaska before the turn of the century to enhance existing runs, and millions of eggs were sent to the Atlantic coast in an attempt to establish runs there (Roppel 1982). However, initial culture efforts in Alaska were unsuccessful, and sockeye salmon programs were discontinued early in the 20th century (Allee 1990). Similarly, 11 sockeye salmon hatcheries built in British Columbia before 1917 produced no consistent benefits, and production ceased soon thereafter (Foerster 1968). In Washington, artificial propagation of sockeye salmon began in 1896 at the Baker Lake Station in the Skagit River basin and continued until this facility was closed in 1933. In addition to supplementing the run of sockeye salmon to Baker Lake, this facility was the source for the sockeye salmon introduced into Lake Washington where a strong run was eventually established (Kemmerich 1945).

Fig. 2 Hatchery production of (A) chum salmon and (B) pink salmon juveniles from Pacific Northwest, British Columbia, Alaska, and Japanese hatcheries, 1950-1993.



Sockeye salmon culture began in the Columbia River in the 1940s at the Leavenworth Hatchery in eastern Washington state. This production effort attempted to mitigate for losses of sockeye due to construction of hydroelectric dams on the middle Columbia River (Mullan 1986). Smolts were produced for a period of about 20 years, but disease and low returns forced abandonment of the program by the 1960s. Small smolt and fry-release programs still exist for sockeye in Puget Sound and on the Washington coast, but by and large, sockeye salmon culture in the Pacific Northwest is insignificant. Along with pink salmon, sockeye salmon production constitutes one of the smallest artificial propagation

programs for any species in the Pacific Northwest. Recent attempts to reinvigorate sockeye salmon culture program in the Pacific Northwest include a combined hatchery and net-pen culture system operated by the State of Washington in Lake Wenatchee and a recovery program for the endangered Redfish Lake sockeye salmon in Idaho's Stanley Basin (Flagg et al. 1991, 1995).

British Columbia is now by far the largest producer of artificially propagated sockeye salmon, producing more than 290 million fry in 1993 (Fig. 3A). Fry are produced in spawning channels containing gravel substrates, where returning adults spawn naturally. Fry are allowed to migrate

volitionally out of the channels upon swimup, usually into a lake. Spawning-channel culture of sockeye salmon in British Columbia constitutes the least invasive culture technique used to mass culture Pacific salmon. These extensive artificial propagation techniques require no feed, use natural spawning substrates, and require no handling of either juveniles or adults during rearing. Although spawning-channel culture of sockeye was initiated prior to the 1950s, the program did not accelerate until the 1960s when output increased from 2 million fry in 1960 to 258 million in 1980 (Fig. 3A).

The Alaskan hatchery system is now the major producer of sockeye smolts in North America, and although a recent entrant (1974) into large-scale sockeye production, has grown rapidly and produced

75 million smolts in 1994, or 21% of total North American production (Fig. 3A). Alaska also releases age-0 sockeye after brief holding in sea-pens.

Steelhead and masu salmon

Hatchery steelhead are produced entirely in North America (Fig. 3B), while masu salmon are only produced in significant numbers in Japan (Fig. 4). In terms of total production, steelhead and masu salmon are minor species, but in terms of their contribution to regional fisheries, steelhead programs are important and produced an estimated 738,000 adults annually from 1978 to 1987 (Light 1989). Like coho salmon and chinook salmon, steelhead coho salmon and chinook salmon, steelhead coho salmon and chinook

Fig. 3 Hatchery production of (A) sockeye salmon and (B) steelhead salmon juveniles from Pacific Northwest, British Columbia, and Alaska hatcheries and spawning channels, 1900-1992.

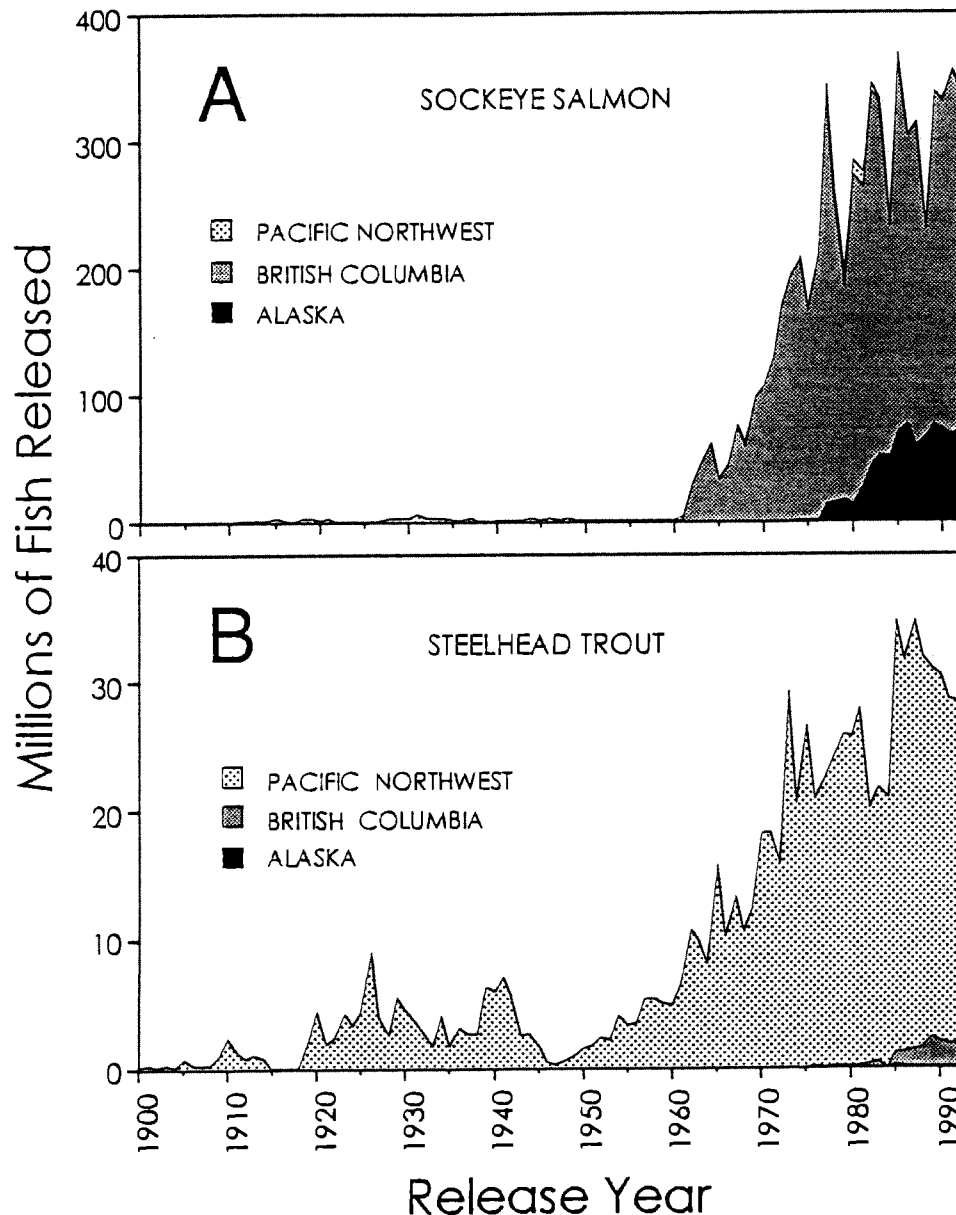
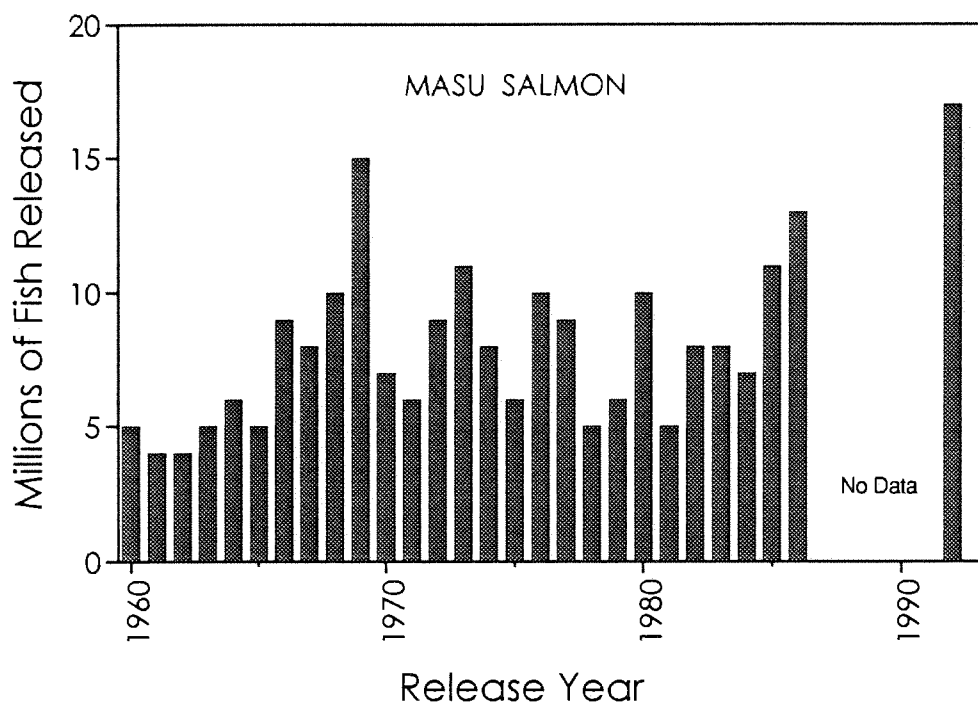


Fig. 4 Production of masu salmon juveniles from Japanese hatcheries, 1960-1992.



salmon, steelhead populations in Washington, Oregon, Idaho and California have experienced steep declines in abundance in recent years.

Artificial propagation programs for steelhead first appeared in the late 1800s and are presently operating throughout the Pacific coast region from Alaska to California. Coastwide releases did not exceed 5 million fish for most of the first half of the century. Releases declined during the war years but increased rapidly from 1960 to a peak production of 35 million fish released in 1985-87. There was a steep reduction in steelhead production in Washington state (Fig. 3B) following the 1977 U.S. vs. Washington court decision that established tribal treaty fishing rights, but the state resumed former levels of production in 1984. Steelhead production dropped by about 20% from 1989-1992. In 1992, more than 90% of total steelhead production was from hatcheries in the Pacific Northwest.

Unlike chum salmon in Japan, masu salmon production has actually decreased in the last two decades (Ohkuma and Nomura 1991). Masu salmon, which are highly dependent on the riverine environment for up to two years prior to outmigration to the sea and upon their early return as adults, have suffered due to degraded freshwater habitats. Channelization of stream banks with concrete and the construction of dams have damaged freshwater spawning and rearing habitat, and the practice of intercepting returning adults at the mouths of rivers for hatchery propagation has reduced the number of

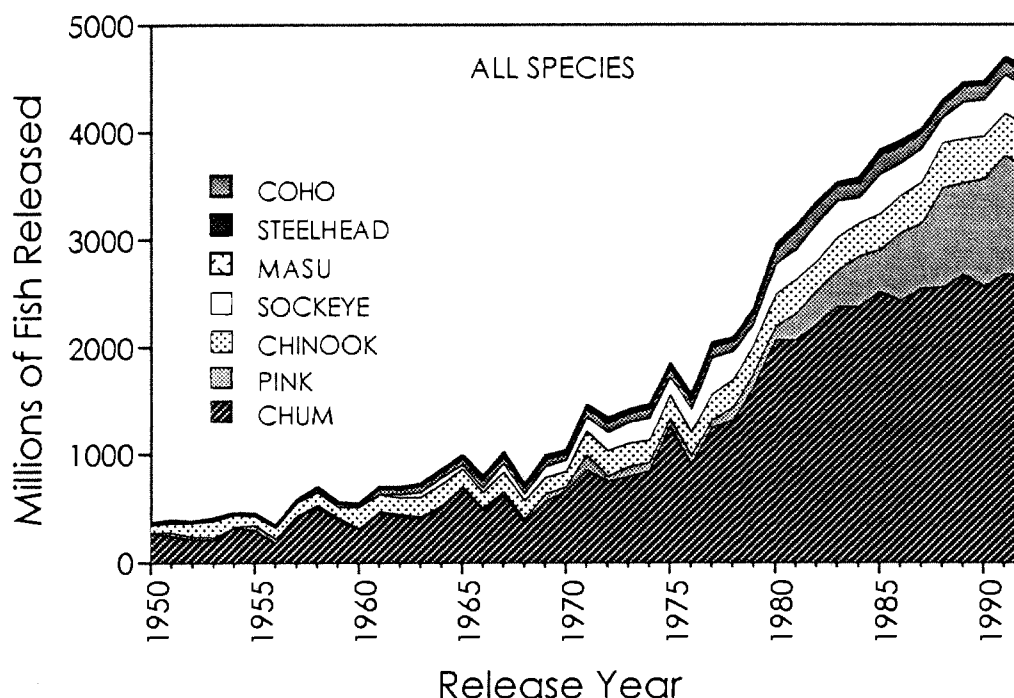
naturally spawning adults (Ohkuma and Nomura 1991).

No dramatic rise in production releases have occurred in the years since 1960 for which data is available. Less than 10 million fish have been released annually (Fig. 4).

Total Pacific Rim Production

Total Pacific Rim production for all species combined, excluding Russia, is given in Figure 5. Four phases in the development of the Pacific Rim hatchery system are evident: 1) a developmental period beginning in the late 1800s and ending around 1970, during which a rudimentary hatchery husbandry was developed; 2) a period from 1970 to 1980, during which significant technological improvements in feed and disease control were made and new hatcheries were constructed; 3) an industrialization period from 1980 to 1990 when intense fishing, loss of freshwater habitat, and declining ocean productivity accentuated the construction of more mitigation and enhancement hatcheries and accelerated production; and 4) a post-industrialization hatchery period where survival declined, hatchery escapement goals for adult spawners were not reached, and reduced operating budgets resulted in a decline in production of chinook and coho salmon and steelhead in the Pacific Northwest and Canada while high production in the north Pacific for chum and pink salmon reduced north Pacific for chum and pink salmon reduced

Fig. 5 Total hatchery production of coho, steelhead, masu, sockeye, chinook, pink, and chum salmon juveniles from the Pacific Northwest, British Columbia, Alaska, and Japan, 1950-1992.



revenues to the fishermen and resulted in a leveling off or reduction of hatchery releases for chum and pink salmon. Total Pacific Rim production for all species in 1992 stood at more than 5.5 billion fry, fingerlings, and smolts released (Heard 1995).

RESULTS - TRENDS IN SURVIVAL OF HATCHERY FISH

Coho salmon

Regular CWT sampling of Alaskan coho salmon stocks began in the early 1970s. Short- and long-term trends in mean survival of hatchery coho salmon were evident for both southeast Alaska and the more northerly coastal regions. Survival of southeast Alaska hatchery stocks was much higher than that of fish from the coastal regions to the north. Southeast Alaska stocks showed two peaks in adult return: one in 1982 and another in 1988-89. Variance was highest during these peak years when mean survival exceeded 10%.

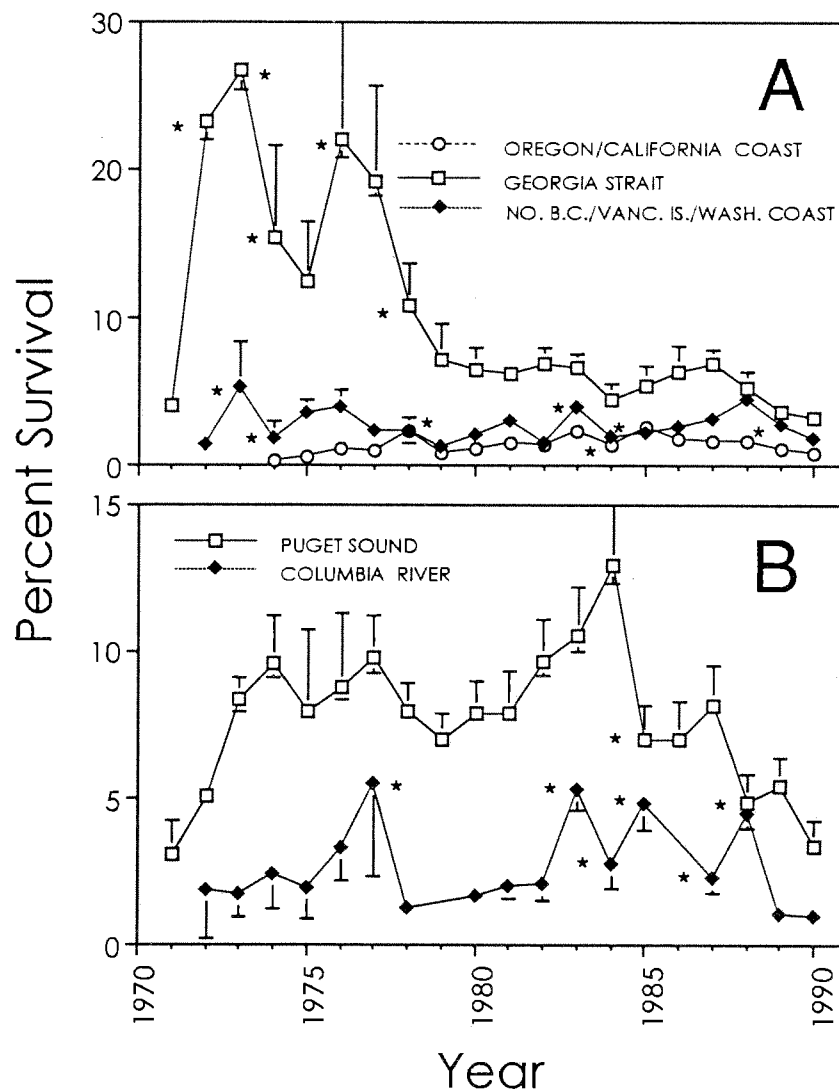
Mean survivals of hatchery coho salmon released into tributaries of British Columbia's Strait of Georgia peaked in the early 1970s; these were the highest mean survivals (> 25%) recorded for any location within the North American range of the species (Fig. 6A). As in southeastern Alaska, variance was highest in years of high survival. Survival dropped from an average of around 20% in 1972-76 to less than 7% in the 1980s. The trend in survival since 1980 has

continued downward, reaching record lows of less than 2% in 1990. Fraser River hatchery stocks, which also enter the waters of Georgia Strait after release, showed a similar declining trend and comparable low survivals in the 1980s.

A comparison of Puget Sound and Columbia River coho salmon stocks showed a similar trend of higher survival for those stocks released into coastal estuaries than those released into coastal oceanic environments (Fig. 6B). Puget Sound stocks exhibit consistently high mean survivals (7-13%) from the early 1970s through the mid 1980s, with notable declines following the 1977 and 1983 El Niños. The decline associated with the 1983 El Niño continued at least through 1990. Again, variation was highest during years of highest survival. On the other hand, Columbia River hatchery stocks exhibited mean survivals of generally less than 5% from 1972-90. Like Puget Sound stocks, declines in survival of Columbia River stocks occurred after the El Niños of 1977 and 1983, but unlike Puget Sound stocks, the general downward trend was not evident after 1983.

We noted a striking difference in survival between hatchery coho salmon stocks released into the larger, protected coastal estuaries along the eastern Pacific seaboard (southeastern Alaska, Strait of Georgia, Puget Sound) and those released directly to the ocean. Figure 6A compares survival trends in a typical estuary, for example the Strait of Georgia, with those of all coastal stocks north of the Columbia River and south of the Columbia River. Although Georgia Strait

Fig. 6 Mean survival (coded-wire tags) of coho salmon released from Pacific coast hatcheries 1970-1990. (A) Georgia Strait estuary, coastal regions of north British Columbia/outer Vancouver Island/Washington, and coastal regions of Oregon/California. (B) Puget Sound and the Columbia River. Error bars are 1 standard error. Asterisks denote differences ($P < 0.05$) ANOVA, Fisher PLSD between successive means.



stock survivals fluctuate widely and exhibit a severe decline in the 1980s, they remained more than twice as productive (approximately 5%) as the coastal stocks (approximately 2%) until 1987. After 1987, all stocks declined to survivals around 2%.

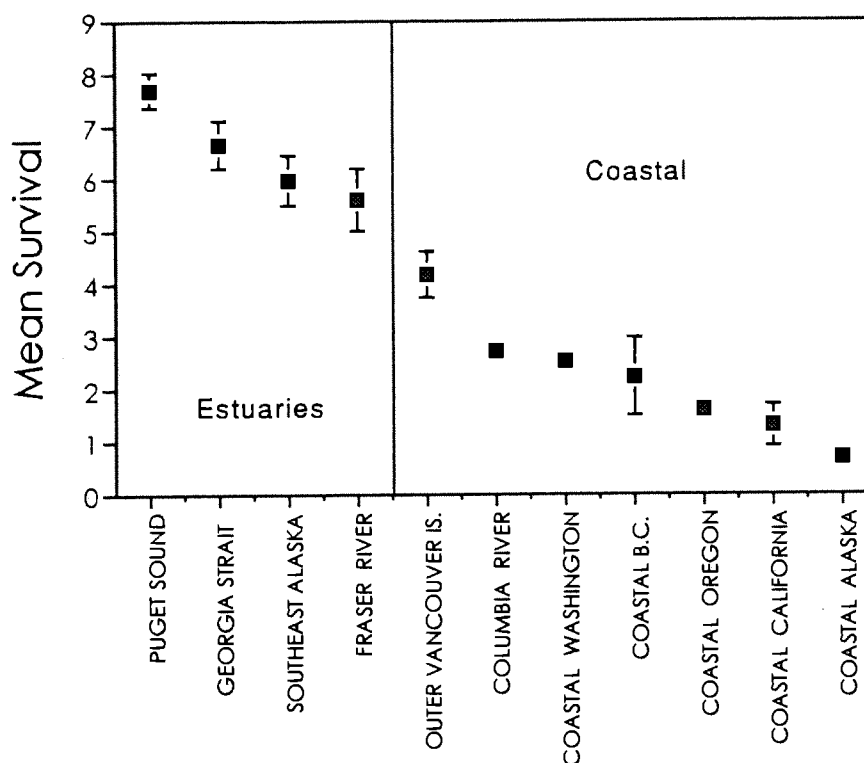
A comparison of bi-decadal mean survival by region revealed another interesting feature of hatchery coho salmon releases from 1970-90 (Fig. 7). When arranged in order of declining survival, general latitudinal clines appeared among the coastal stocks, both north and south from the center of the geographic distribution of the species, at about the latitude of Vancouver Island. This region had the highest survival (4%), with coastal California and coastal Alaska (at either end of the geographic range) having the lowest survivals, at 1-1.5%. Latitudinal anomalies were observed in large coastal estuaries such as the

Strait of Georgia, Puget Sound, and southeast Alaska. These areas are known to be excellent areas for juvenile rearing and for survival of salmonids (Healey, 1980; Simenstead et al., 1982), with relatively high survivals of 5.5-7.5% during this period.

Fall chinook salmon

Fall chinook salmon exhibit quite different survival characteristics from coho salmon. Because of smaller size at release, survival of hatchery fall chinook salmon is less than that of coho salmon. Furthermore, survivals and trends in survival are distinctly different between fall chinook salmon hatchery stocks north of Puget Sound and those to the south (Fig. 8). Survivals peaked in Puget Sound, Strait of Georgia and outer Vancouver Island in the

Fig. 7 Mean survival of hatchery coho salmon by region, 1970-1990.



mid-1970s at between 3-4%, then declined sharply to less than 2% in the 1980s following the El Niño of 1977 (Fig. 8A). A further decline to about 0.5% survival followed the 1983 El Niño and survival has continued downward since. Stocks south of Puget Sound showed the opposite trend, with survival rates of less than 1% through 1982 rising to around 2% following the 1983 El Niño (Fig. 8B). It appears that the 1983 El Niño acted to enhance survival of southern fall chinook salmon in the mid-1980s rather than to decrease survival. However, mean survival of fall chinook salmon, aggregated by region, failed to show the same geographic cline as that of coho salmon.

Chum salmon

Survival of chum salmon released from Hokkaido hatcheries has followed a trend that appears to be less influenced by ocean conditions and more by improvements in hatchery technology (Figure 9). Survival of Hokkaido chum salmon has risen uniformly from 2.5 to 4% from 1965-1988, a period in which production increased from 550 to 970 million fry released. The number of juveniles released and their survival both increased with time. This apparent inverse density-dependant survival has been noted by McNeil (1991) who suggests that the relationship may be an artifact of improved hatchery technology, or

satiation of predators at higher levels of juvenile production. However, Kaeriyama (1996) presented evidence that other life history characteristics of enhanced chum salmon, namely decreased body size and an increase of age-at-maturity may indicate the beginning of a density-dependant effect of continued large-scale releases from Japanese hatcheries.

DISCUSSION

Researchers from North America and Japan have noted the dramatic decline in salmon stock abundance and body size in the southern portion of the species range in North America. These declines have been especially apparent over the past two decades (Nehlsen et al. 1991; Bigler et al. 1996; Ricker 1981). However, while the abundance of stocks in the Pacific Northwest has declined, the abundance of populations to the north, both in Asia and North America, remain healthy and some have reached historical highs (Heard 1995; Kaeriyama and Urawa 1992; Burger and Wertheimer 1995; Zorpette 1995). Attempts have been made to assess the cause of these declines based on changes in freshwater conditions, fishing, or on variations in the marine environment (Beamish and Bouillon 1993; Cooper and Johnson 1992; Johnson 1984; Lawson 1993; Lichatowich 1993; Nickelson 1986; Northcote and Atagi 1994; Pearcy 1992; Richards and Olsen 1993; Olsen and Richards 1994;

Fig. 8 Mean survival (coded-wire tags) of fall chinook salmon released from Pacific coast hatcheries 1970-1990. (A) Puget Sound, Strait of Georgia, and outer Vancouver Island regions. (B) upper and lower Columbia River, and Washington and Oregon coastal regions. Error bars are omitted for simplicity. Asterisks denote differences ($P < 0.05$) ANOVA, Fisher PLSD between successive means.

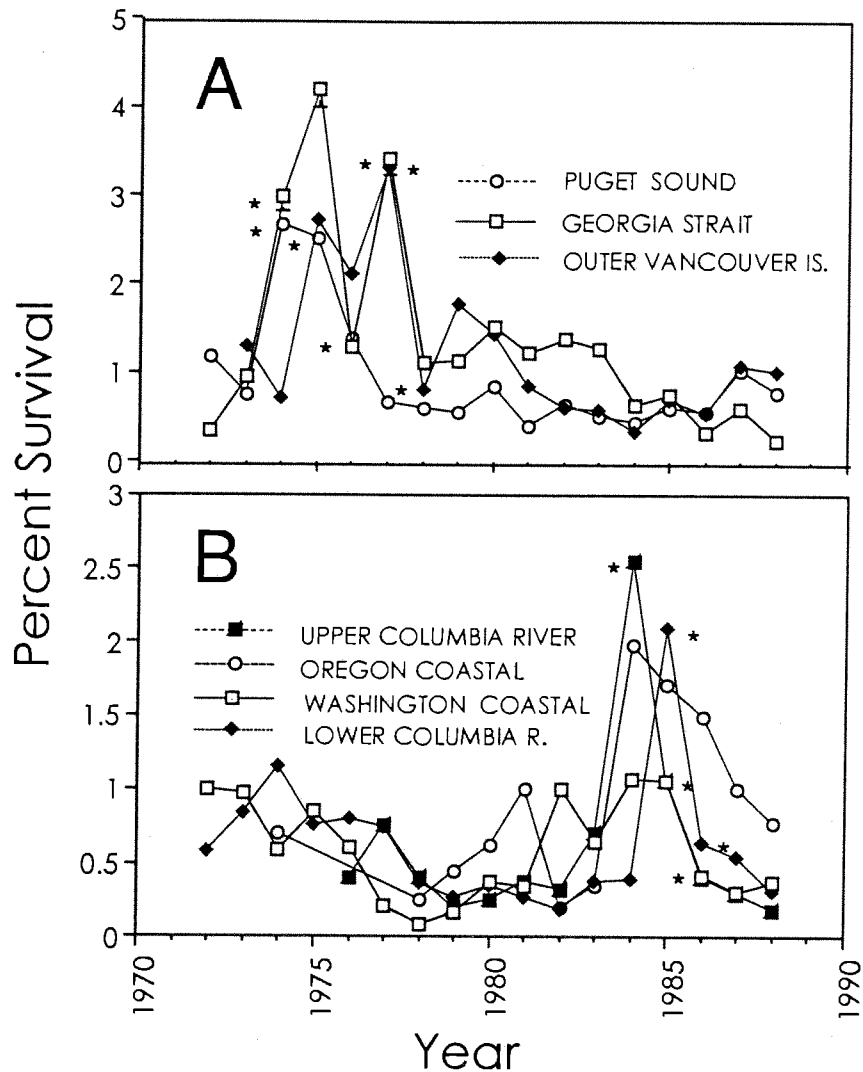
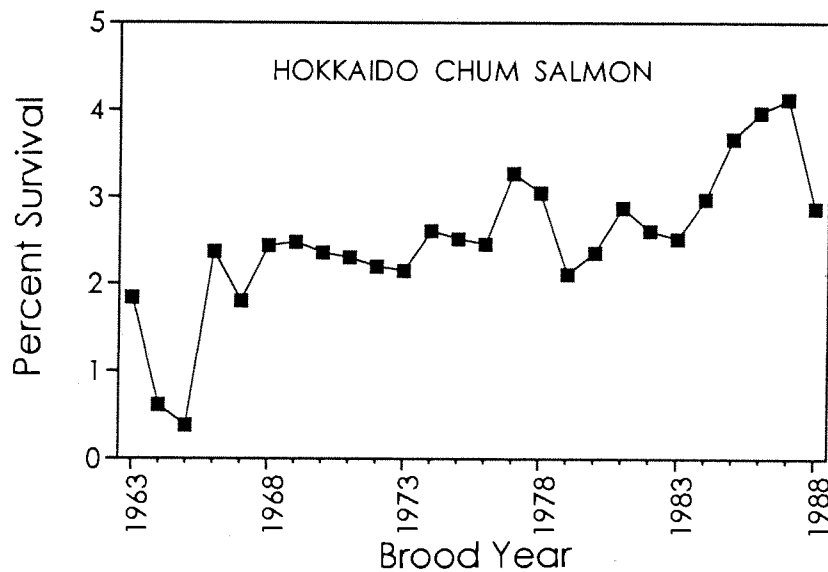


Fig. 9 Mean survival of chum salmon released from Japanese hatcheries in Hokkaido, 1963-1988.



Francis and Sibley 1991; Kaeriyama 1996). Most researchers have concluded that, whatever the major factor(s) affecting survival of Pacific salmonids, they are most likely to occur in the ocean environment.

Cooper and Johnson (1992), compared trends in abundance of Washington, Oregon, and British Columbia steelhead and concluded that there were similarities in trends over the entire geographic range that indicated common factors were responsible for the observed changes in survival. Because freshwater, estuarine, and nearshore conditions differ considerably from year to year within this region, they concluded that these factors alone could not explain the similarities in steelhead survivals. They suggested that similarities in steelhead abundance trends in widely separated geographical regions indicated that common factors were responsible for the observed declines, and that oceanic conditions were responsible. Olsen and Richards (1994) came to a similar conclusion while working with aggregated coastwide chinook salmon production data, namely that similar chinook salmon run-size trends can be observed between several west coast river basins, and that the data support the hypothesis that ocean conditions have had a marked and uniform impact on chinook salmon production in the Pacific Northwest. Lichatowich (1993) has pointed out that the magnitude of oceanic environmental changes and their impacts on salmon survival may be so large as to mask changes that occur in the freshwater habitat. He cautioned that this may cause managers to falsely attribute increased ocean survival to restoration effects in freshwater. Hilborn et al. (1993) further emphasizes the same point by stating that attempts to understand the impact of in-river (Columbia River) actions on survival will be confounded by changes in ocean conditions.

Coded-wire tag data shows that for the period 1970-1990, coho salmon adult survival was highest for stocks released into large coastal estuaries. Survival in these estuaries is typified by widely fluctuating mean survivals. Conversely, survival of hatchery coho salmon released into coastal regions that lack protective coastal estuaries is typified by lower, more constant survival. However, differences in survival between estuarine and coastal releases of fall chinook salmon are not as dramatic, with regions like outer Vancouver Island and coastal Oregon performing as well or better than Puget Sound and the Strait of Georgia. It is possible that such factors as size and time of entry to seawater, location and length of time in estuaries prior to outmigration, and predation may influence differences in absolute survival and temporal trends between the species.

Coho salmon survivals were depressed following the unusually strong El Niño events of the past two decades (Fig. 6) and continued to decline throughout the 1980s. Depressed survival associated with El

Niño events is most evident in regions where survival has been historically high (southeast Alaska and Georgia Strait following the 1982-83 El Niño, Puget Sound following the 1976-77 El Niño). In the past 40 years, nine El Niños have affected the coastal regions of the eastern Pacific. In the 1970s and 1980s, the coastal regions of the Pacific Northwest and Canada have been beset by a series of four moderate-to-strong El Niño events, most notably the 1982-83 El Niño, which by many measures was the strongest this century. Since 1970, El Niños have occurred in 1972-73, 1976-77, 1982-83, and 1987-88.

A strong negative cline in survival of coho salmon is observed moving both north and south from the center of the species distribution in British Columbia, with stocks in western Alaska and California exhibiting the lowest survival. Fall chinook salmon, on the other hand, do not show the same strong latitudinal cline.

Fall chinook salmon survival, although apparently also affected by El Niño events, seems directed by other external factors. Stock survival north of the Columbia River peaked in the mid 1970s, while survival for regions south of the river peaked in the mid-1980s. Furthermore, mean survival of fall chinook salmon aggregated by region failed to show the same geographic cline as coho salmon. The Strait of Georgia estuary produced highest survivals, but Puget Sound fall chinook salmon did not produce higher survivals than Coastal Oregon, and produced only slightly better survival than outer Vancouver Island or coastal California. This is surprising, given the well-documented importance of estuaries for growth and survival of juvenile chinook salmon (Healey 1991; McCabe et al. 1986). Nevertheless, there is some indication that hatchery fall chinook salmon juveniles spend less time in estuaries than wild juveniles which may reduce the benefits of such areas to artificially propagated fish (Levings et al. 1986). It may be that the overall lower survival of fall chinook salmon masks regional geographic differences so evident with coho salmon.

It is tempting to postulate a cause and effect relationship between the occurrence of El Niño events and declines in survival of hatchery fish in the eastern Pacific, but no convincing ecological relationship exists. Climate conditions are known to have changed recently in the Pacific Northwest. Most Pacific salmonid stocks south of British Columbia have been affected by changes in ocean production that occurred during the 1970s. Percy (1992) and Lawson (1993) attribute this decline largely to ocean factors, but do not identify specific effects. However, given the increased frequency of El Niño events in the past two decades, and large-scale secular warming of the region (Freeland 1990), it is certainly plausible that there is at least some response to El Niño events in the form

of reduced survival of the species.

Survival of coho and chinook salmon in the southern regions may be driven by an entirely different set of regional ocean/climate conditions than those governing survival of chum, pink, and sockeye salmon; the most abundant species in the northerly regions. Two forms of decline were evident in coho salmon survival curves: sharp, short-term declines associated with El Niño events, and a more prolonged long-term decline, typical of the late 1980s, that may be related to general warming trends in Pacific waters along the eastern Pacific seaboard (Freeland 1990; Welch et al. 1995; Beamish and Bouillon 1993). Stocks released from southern regions are believed to migrate in a narrow coastal corridor that is characterized by highly variable interannual changes in flow, temperature, and current (Pearcy, 1992). Those species and stocks released into the more northerly regions enter a much larger area of acceptable ocean conditions that is greatly influenced by the Aleutian low pressure system (Beamish and Bouillon 1993).

Hatcheries have played a major role in supplying salmon and trout to the common property fishery in the Pacific Northwest. But with the near catastrophic decline in the population of southern stocks and overabundance of the northern stocks, we have entered a new era in the operation of hatcheries that cannot help but impact the traditional users of hatchery fish. The two-pronged dilemma is, how can we institute hatchery reform to both protect and recover wild/natural stocks and at the same time maintain some reasonable level of harvest for the fishers?

The present hatchery system was developed to produce an increasing supply of hatchery fish into a constant oceanic ecosystem believed to be nearly limitless in its capacity to accommodate juvenile salmonids. Until recently, these oceanic ecosystems were believed to be stable, internally regulated, and to behave in a deterministic manner. The more current view is of an open system in near constant flux--a system without long-term stability and one that is often under the influence of stochastic factors, many originating outside the ecosystem itself (Mangel et al. 1996). The modern view of the ecosystem is one characterized by ecological uncertainty. Lack of understanding of this principle and its impact on interannual variability of salmonid abundance and survival has acted against wild fish populations through unregulated propagation and harvests of hatchery fish. Perhaps it is time for fishery managers to regulate hatchery releases to accommodate decadal-scale variation in ocean productivity.

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Growth Studies from 1956-95 Collections of Pink and Chum Salmon Scales in the Central North Pacific Ocean

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This study was initiated to investigate whether long-term collections of scale samples could provide further information on recent observations related to ocean growth and abundance of Pacific salmon (*Oncorhynchus* spp.): size-at-return of salmon of several stocks has decreased in recent years; and oceanographic conditions changed around 1976-1977, possibly affecting abundance and growth of salmon. We examined growth patterns on scales of pink (*O. gorbuscha*) and chum (*O. keta*) salmon to determine if there were differences in growth between the periods before and after the oceanographic change and if changes in relative abundances of the two species were correlated with any changes in growth. The scales were collected by the Fisheries Research Institute of the University of Washington (1956-91), the U.S. Bureau of Commercial Fisheries (1967-71), and the Fisheries Agency of Japan (1981-95). Scales collected in late June from adult age 0.1 pink salmon and primarily immature age 0.2 chum salmon were measured. The scales were from fish caught in the North Pacific Ocean south of Adak Island in the central Aleutians. Measurements were made of each circulus in the last year of ocean residence and to the edge of each preceding annular mark. Chum salmon caught in this area in 1983-95 had significant decreases in fork length and in growth at the edge of the scale compared to those caught in earlier years (1956-70). Pink salmon showed fewer differences in growth between periods, although odd-year pinks were smaller in 1983-95 than in 1959-67. Scale-edge growth of chum salmon was negatively correlated with Asian pink and chum salmon abundance. Adult pink salmon abundance may exert an influence on the third-year growth of chum salmon in this area.



INTRODUCTION

In 1976 or 1977 a major oceanographic and climatologic change occurred which seems to be correlated with changes in abundance of Pacific salmon (*Oncorhynchus* spp.; Trenberth 1990; Beamish and Bouillion 1993; Hare and Francis 1995). Features of the change included cooler sea surface temperatures and a deeper winter-spring mixed layer depth in the central North Pacific, a shallower mixed-layer depth in the Gulf of Alaska, and warmer surface temperatures in the extreme eastern North Pacific (Francis and Hare 1996; Mantua et al. 1997). Winter and spring climate has been warmer in the Bering Sea and Gulf of Alaska. In North America, the pre-1977 period favored the abundance of more

southerly salmon stocks of the west coast, while the current post-1977 period favors Alaskan stocks. Coinciding with this change, a significant decrease has been noted in recent years in the size of returning adult fish of various runs of salmon in the North Pacific Ocean (Kaeriyama 1989 1996a,b; Ishida et al. 1993; Rogers and Ruggerone 1993; Thomas and Mathisen 1993; Helle and Hoffman 1995; Bigler et al. 1996). This decrease has occurred in a period when overall abundance of salmon has been high and hatchery production has increased and leads to questions such as whether the size decrease is a result of density-dependent intra- and inter-specific competition and whether there is a correlation with changes in oceanic conditions.

A number of recent papers have speculated on

interactions affecting growth between and within species (Ishida et al. 1993; Welch and Morris 1994; McKinnell 1995; Ishida and Ito 1995; Bugaev et al. 1996). Salo (1991) noted that pink salmon (*O. gorbuscha*) may cause changes in behavior, age at maturity, size, marine survival, and abundance of chum salmon (*O. keta*), and Tadokoro et al. (1996) have hypothesized that when pink salmon are abundant, chum salmon may change their diet to less nutritious prey items, which may indicate limitations in available prey resources for Pacific salmon.

Several researchers have examined patterns of growth on salmon scales in attempts to understand whether there are indications of long-term trends in growth, whether interactions affecting growth occur between salmonid species, and at what life history stage growth differences are apparent. Ogura et al. (1991) saw no trend in size of second ocean year growth of western North Pacific coho salmon (*O. kisutch*) caught in 1975-87, but second year growth was smaller in odd years and was negatively correlated with the catch-per-unit-effort (CPUE) of pink salmon. Myers (1994) found that pink salmon caught near the central Aleutian Islands had more coastal growth and better winter growth in a period of higher abundance (1977-78) compared with a period of lower abundance (1970-75). However, odd-year fish in the period of high abundance had lower summer growth and circulus counts, especially in the second ocean year. Similarly, Ishida et al. (1995) found that second ocean year growth of odd-year pink salmon from the western North Pacific (1972-95) was negatively correlated with pink salmon CPUE. In a study of British Columbia sockeye (*O. nerka*) and pink salmon, sockeye showed no trend in offshore marine growth, but a trend of decreasing growth from the 1950s to the 1990s in the more coastal first and last marine years (Welch 1994). Pink salmon showed little or no trend in their "coastal" (first ocean year) growth.

This study was undertaken to investigate if there have been detectable changes over time in growth of salmon at a particular location in the North Pacific, as reflected in patterns on scales, and if changes are correlated between different species. Our hypothesis is that growth may have been different before and after the major oceanographic event occurring around 1976-1977. Over forty years of high seas salmon field studies by the United States, Japan, Russia, and Canada have yielded a large archive of scale samples spanning several decades and covering, in patches, large parts of the North Pacific Ocean and Bering Sea. For pink salmon, these collections represent one of the few long-term series of scale samples, as inshore agencies rarely collect pink salmon for ageing and management purposes.

Studies from inshore scale samples have a disadvantage in that the area of the ocean where growth took place is not known with much precision. Of special interest in marine growth studies are the questions of where and when oceanographic and inter-specific effects on growth are occurring. By studying recent growth of fish at particular times and places, we hope to answer whether interactions are, or are not, occurring in those specific time-area strata. The area studied here is a crossroads for salmon from Asia and North America. Pink salmon are on homeward migrations to Asia and western Alaska, while immature chum salmon from nearly all Pacific Rim production areas are intermingling in feeding migrations. Because the origin and prior travels of fish caught on the high seas are unknown, attention was focused on growth at the edge of the scale, which most likely reflects response to conditions near the point of capture. We expect to extend the study to other species in the same region of the ocean and other geographic regions in the North Pacific.

MATERIALS AND METHODS

Sample Sources and Study Area

The Fisheries Research Institute (FRI) of the University of Washington retains samples collected during FRI and joint FRI-Russian tagging cruises from 1956-1991, as well as collections from the U.S. Bureau of Commercial Fisheries (BCF; the predecessor of the current U.S. National Marine Fisheries Service) cruises (1955-1972) and copies of scales from various Fisheries Agency of Japan (FAJ) research cruises (1980-1996). Samples taken by FRI and joint Russian-FRI tagging cruises were collected from fish caught by purse seine (732 m long, 40 m deep). BCF and FAJ samples were collected from fish caught by varied mesh (non-selective) gillnet (BCF: primarily 51, 64, 83, 98, 114, and 133 mm; FAJ 48, 55, 63, 72, 82, 93, 106, 121, 121, 138, and 157 mm mesh). A few FAJ scale samples were taken from longline-caught fish.

The study was initiated with measurements of chum and pink salmon scales from fish caught in an area south of the central Aleutian Islands (roughly 175°E to 170°W, between 46°N and 52°N) in and around the last 10 days of June, 1956-95. This time-area stratum contains adequate sample sizes for chum salmon from 19 years and for pink salmon from 14 years (Table 1). The majority of the samples were collected between 180° and 175°W, 50°N to 52°N.

The central Aleutians are a region of mixing of salmon from Asia and North America. Tag recoveries indicate that chum salmon stocks in this

Table 1. Scale samples measured for growth studies. Scales were collected south of the central Aleutian Islands, between 175°E and 170°W, and between 46°N and 52°N in and around the last 10 days of June, 1956-95. Sources of the samples were research cruises by the Fisheries Research Institute (F; in conjunction with Russia in 1983 and 1989), U.S. Bureau of Commercial Fisheries (B), and the Fisheries Agency of Japan (J).

U.S. Bureau of Commercial Fisheries (B), and the Fisheries Agency of Japan (J).					
Year	Source	N	Dates		Areas ¹
			Begin	End	
<u>Chum:</u>					
1956	F	129	6/23	6/30	W7550, W8050
1957	F	19	6/21	6/26	W8050, E7550
1958	F	106	6/25	6/30	W8050
1959	F	67	6/22	6/29	W8050
1960	F	27	6/21	6/27	W8050
1961	F	88	6/22	6/27	W8050
1962	F	120	6/22	6/30	W8050
1963	F	43	6/21	6/30	W8050
1964	F	110	6/21	6/29	W8050
1965	F	100	6/25	6/29	W7550, W8050
1966	F,B	102	6/23	6/30	W8050
1967	F,B	100	6/26	6/29	W8050, W8048
1970	F	98	6/30	6/30	W8050
1983	F	56	6/19	6/27	E7548
1991	J	110	6/21	6/27	W8046, W8048, W8050
1992	J	38	6/25	6/30	W8046, W8048, W8050
1993	J	102	6/29	6/30	W8048
1994	J	98	6/28	6/30	W8048, W8050
1995	J	40	6/26	6/30	W8046, W8048, W8050
Total Chum		1,553			
Year	Source	N	Dates		Areas ¹
			Begin	End	
<u>Pink:</u>					
1959	F	102	6/22	6/29	W8050
1960	F	29	6/19	6/27	E7550, W8050
1961	F	100	6/22	6/27	W8050
1963	F	65	6/21	6/30	W8050
1964	F	63	6/19	6/29	W8050
1965	F	100	6/25	6/30	W7550, W8050
1966	F,B	65	6/23	7/1	W8050
1967	F,B	100	6/25	6/29	W8050
1983	F	106	6/21	6/27	E7548
1989	F,J	46	6/21	6/27	W8046, E7548, W8048, W7550
1991	J	21	6/21	6/22	W8046
1993	J	57	6/27	6/30	W8046, W8048
1994	J	87	6/28	7/1	W8046, W8048, W8050
1995	J	57	6/26	7/1	W8046, W8048, W8050
Total Pink		998			

¹ Areas are 5° longitude by 2° latitude statistical areas, where the initial letter indicates the hemisphere, first two digits represent westernmost degree of longitude minus 100°, and last two digits represent southernmost degree of latitude.

area are predominantly Asian (from Japan, Sakhalin and Kuril Islands, northern Okhotsk Sea coast, and eastern and western Kamchatka) and western Alaskan. Nearly all recoveries of pink salmon tagged in this area come from eastern Kamchatka and western Alaska. Eastern Kamchatkan pink salmon stocks are dominant in odd-year cycles, and the less abundant western Alaskan stocks are more abundant in even years.

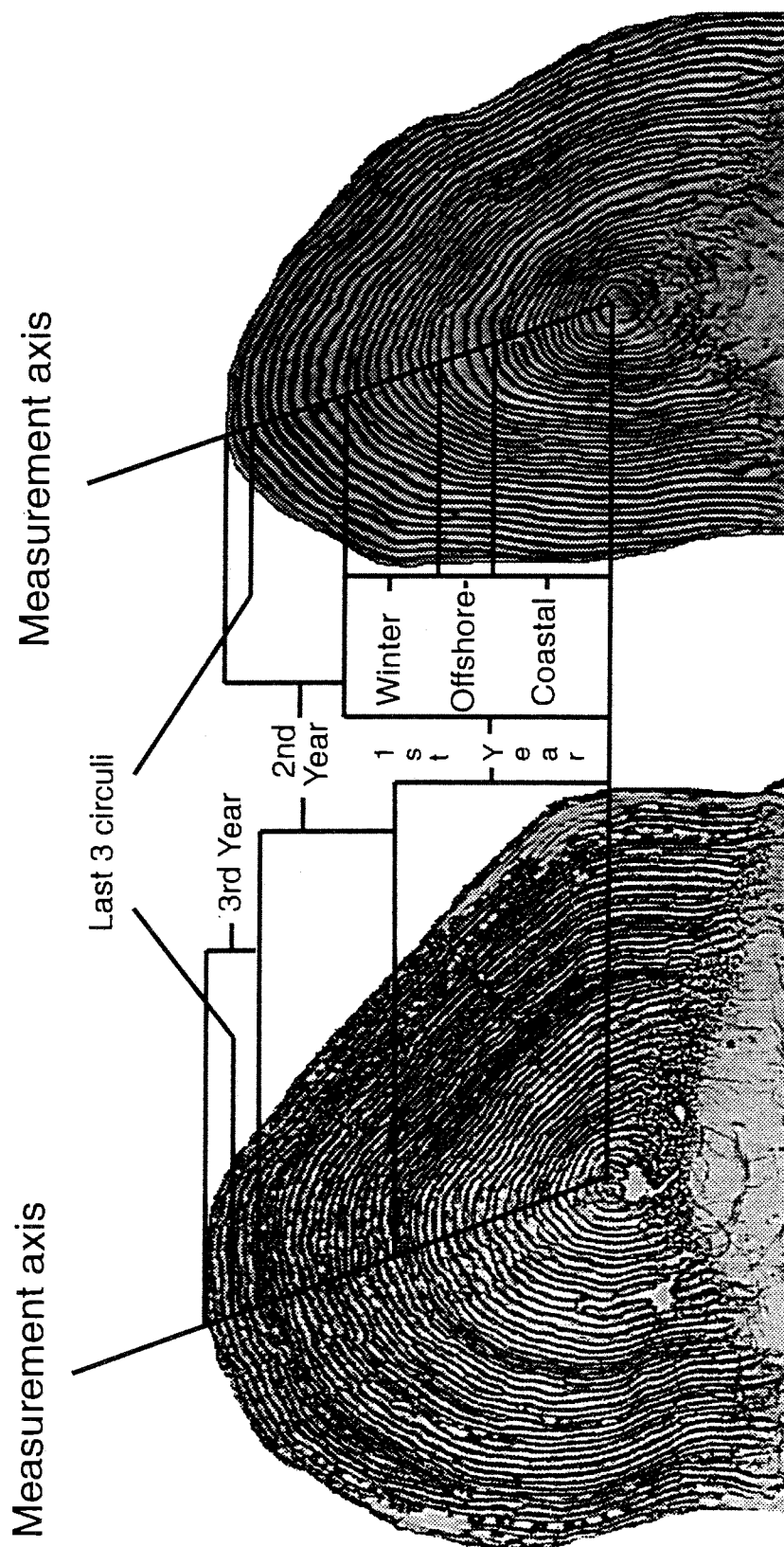
Scale Selection and Measurement

All non-regenerated scales with clean measurement axes from fish caught between June 21 and June 30 were measured, up to 100 scales per

year. In some cases, additional scales were measured to ensure a final sample of 100. In other cases, scales from fish caught one or two days prior to or after the target sampling period were measured to increase sample sizes. When samples were available from more than one day or fishing operation, scales were apportioned evenly between days and operations.

Scales were measured along the longest anterior-posterior axis. Measurements of chum salmon were made on age 0.2 scales (primarily immature fish) to the ends of the first and second ocean zones and to every circulus thereafter (in the third ocean zone) to the edge of the scale (Fig. 1). Measurements of pink salmon scales were made to the outer edges of initial

Fig. 1 Scales of chum (left) and pink salmon (right) showing axis and measurements used in growth analysis. Scale images are at different magnifications.



coastal growth (if any), offshore first ocean summer, ocean winter, and second ocean summer (edge of scale; Fig. 1). Measurements were also made to each circulus on the scale. Life history zones were identified visually, based primarily on the appearance of circulus spacing. Closely spaced circuli immediately following the focus at the center of the scale were identified as "coastal" growth. More widely spaced circuli beyond the coastal growth, or following the focus if coastal growth was not present, were identified as "offshore" growth in the first ocean summer. Narrowly spaced circuli following the offshore summer growth were identified as "winter" growth, the annulus of the scale. All scales were measured by one person using Optical Pattern Recognition System (OPRS; BioSonics, Inc.) image analysis software (chum at 113X magnification and pink at 151X), and measurements were converted to microns.

Scale Variables

Variables used included length of fish (tip of snout to fork of tail), scale edge measurements, and early scale growth measurements. Scale edge measurements consisted of size (radial distance) of the last (third ocean summer in chum, second ocean summer in pink) ocean zone, number of circuli in last ocean zone, average spacing of circuli in last ocean zone, and size of last three circuli at the edge of the scale (if fewer than three circuli were present between the last annulus and edge on chum scales, this measurement was to the annulus and might include two, one, or no circuli; all pink scales had at least three circuli in the last ocean zone). Early scale growth measurements consisted of size of first and second ocean years in chum salmon, and size, number of circuli, and average circulus spacing of the first ocean year in pink salmon.

Statistical Analyses

Scale data were divided into pre-1977 and post-1977 climate regime groups. Our samples from the post-1977 period are mainly from the 1990s. Trenberth and Hoar (1996) have characterized 1990-95 as the longest El Niño-Southern Oscillation (ENSO) event on record, and a part of the pattern for more frequent ENSO events since 1976. Thus the years of collection of our samples, while perhaps not representative of the entire post-1977 period, are nonetheless within the overall character of the period.

Unpaired t-tests (2-tailed, $\alpha=0.01$, assuming unequal variances) were used to test the hypothesis that there was no difference between growth in the two regimes. Because many scale characters were significantly correlated with overall length of the fish,

t-tests were also run on variables that were proportions of the length (scale distance divided by length).

Because there is substantial year-to-year variability in growth and in scale characters, additional analyses were performed to test for differences due to regime and to year. Data were selected so that equal numbers of years were represented in each regime and all cells contained the same number of measurements (regimes represented by 100 fish/cell for chum, from each of three years [pre-1977: 1965, 1966, 1967; post-1977: 1991, 1993, 1994], and 50 fish/cell for pink [pre-1977: 1959, 1965, 1967; post-1977: 1983, 1993, 1995]). These data subsets were tested using analysis of variance (ANOVA), with years nested within regimes.

Growth variables were tested for correlations with abundance of pink and chum salmon for indications of density-dependent effects on growth. Run size data were taken from an unpublished compilation taken from International North Pacific Fisheries Commission statistics and other data, maintained by D.E. Rogers at FRI (Rogers 1996). Pearson r statistics were used to test mean annual values of scale growth variables and length in each regime for correlations with annual run sizes of major regional runs of pink and chum salmon. Pink salmon growth data were compared with pink abundance in the same year and with chum in the same year, except for measurements of the first ocean zone, which were tested against chum abundance two years later, the same year-class as pink salmon in their first ocean year. Because most age 0.2 chum salmon are immature, chum growth variables were tested against chum salmon runs in the following year. Early (first- and second-year) ocean growth of chum scales was tested against pink salmon abundance in the previous year, while edge growth (third-ocean year) and length were tested against pink salmon abundance in the same year.

RESULTS

Differences between Regimes

All measures of growth at the edge of age 0.2 chum salmon scales showed marked differences between the pre-1977 and post-1977 groups (Table 2). Pre-1977 scales had substantially larger third ocean year summer zones, with more circuli, which were more widely spaced. This was true for absolute measurements and for measurements scaled to the length of the fish. Pre-1977 fish were also larger. These differences held for both even- and odd-year fish.

Pink salmon scales showed no overall significant differences between pre- and post-1977 regime groups

Table 2. Results of unpaired t-tests on fish length and scale variables calculated from long-axis scale measurements and circulus counts of age 0.2 chum salmon caught south of the central Aleutian Islands, between 175°E and 170°W, and between 46°N and 52°N in and around the last 10 days of June, 1956-95. All scale measurements are in microns.

Chum salmon	1956-70	1983-95	Prob. (2-tail)
<u>All Years</u>			
N	1109	444	
Size - 1st ocean year	1225.42	1258.20	9.6X10 ⁻⁶ *
Size - 2nd ocean year	661.21	631.29	2.6X10 ⁻⁷ *
Edge			
Size - 3rd ocean summer	241.95	193.17	3.9X10 ⁻²³ *
No. circuli - 3rd ocean	5.37	4.74	9.5X10 ⁻¹¹ *
Circ. spacing - 3rd ocean	44.04	39.32	7.0X10 ⁻¹⁶ *
Spacing - last 3 edge circuli [†]	130.47	112.90	9.0X10 ⁻²⁵ *
Length of fish (mm)	435.91	427.57	1.5X10 ⁻⁷ *
<u>Odd Years</u>			
N	417	308	
Size - 1st ocean year	1224.94	1264.98	5.6X10 ⁻⁵ *
Size - 2nd ocean year	636.00	621.45	0.071
Edge			
Size - 3rd ocean summer	237.58	196.31	4.4X10 ⁻¹⁰ *
No. circuli - 3rd ocean	5.24	4.80	0.0004
Circ. spacing - 3rd ocean	44.30	39.42	8.6X10 ⁻⁹ *
Spacing - last 3 edge circuli [†]	130.36	114.02	2.9X10 ⁻¹³ *
Length of fish (mm)	432.60	429.08	0.107
<u>Even Years</u>			
N	692	136	
Size - 1st ocean year	1225.70	1243.12	0.163
Size - 2nd ocean year	676.41	653.57	0.007 *
Edge			
Size - 3rd ocean summer	244.58	186.04	1.2X10 ⁻¹² *
No. circuli - 3rd ocean	5.44	4.60	1.3X10 ⁻⁶ *
Circ. spacing - 3rd ocean	43.88	39.10	1.9X10 ⁻⁹ *
Spacing - last 3 edge circuli [†]	130.53	110.35	7.8X10 ⁻¹² *
Length of fish (mm)	437.91	424.15	4.4X10 ⁻⁹ *

* = statistically significant difference ($\alpha = 0.01$)[†] = distance from scale edge inward to third circulus from edge (or distance to second or first circulus, or no measurement, if there were not three circuli present between last annulus and edge)

in size, circulus count, or spacing of the first and second ocean years, or in length or scaled-to-length variables (Table 3). The average spacing of the last three circuli at the edge of the scale was slightly smaller ($p=0.048$) in the earlier regime. When samples were stratified by even and odd years, a few differences emerged between the two periods. Note, however, that even years in the post-1977 period were represented by samples from only one year. Lengths were greater for pre-1977 period fish in odd years, and less in even years. In odd years, the spacing of circuli in the second ocean year was greater in the pre-1977 regime. In even years, the size of and number of circuli in the first ocean zone and spacing of the last three circuli at the edge of the scale was smaller in the pre-1977 period.

Results of nested ANOVA tests showed that there were significant between-year effects for both chum and pink scale variables (Tables 4 and 5). However, all significant between-regime effects for chum scale growth that were detected by t-tests in the full data set were also significant in the nested ANOVA tests on the reduced, balanced data set. For pink salmon, there was one difference: in the reduced data set (containing only odd years), spacing of circuli in the second ocean year was not significantly different between regimes.

Correlations with Run Sizes

Edge growth of chum salmon showed negative correlations (Pearson r greater than 0.5) with Asian pink salmon run sizes, although the correlation was stronger in the pre-1977 regime (Table 6). Edge growth and length showed positive correlations with Japanese chum run sizes in the pre-1977 period when runs were low, but the correlations were weakly negative in the later regime. Edge growth and length showed negative correlations with Russian chum run sizes in both the pre- and post-1977 regimes. Russian runs were of the same magnitude in both periods, but were larger than Japanese runs in the pre-1977 period and substantially smaller in the later period.

Size of the second (last) year of ocean growth of pink salmon showed negative correlations with Asian pink salmon run sizes before 1977, but a positive correlation after 1977 (Table 7). Correlations of edge growth with Russian and western Alaskan chum runs were also negative in the pre-1977 period. First year ocean growth and overall length both were positively correlated with Asian pink and Japanese chum run sizes in the post-1977 regime.

Table 3. Results of unpaired t-tests on fish length and scale variables calculated from long-axis scale measurements and circulus counts of pink salmon caught south of the central Aleutian Islands, between 175°E and 170°W, and between 46°N and 52°N in and around the last 10 days of June, 1959-95. All scale measurements are in microns.

Pink salmon	1959-67	1983-95	Prob. (2-tail)
<u>All Years</u>			
N	624	374	
Size - 1st ocean year	944.70	941.84	0.682
No. circuli - 1st ocean	21.57	21.67	0.472
Circ. spacing - 1st ocean	43.89	43.89	0.162
<u>Edge</u>			
Size - 2nd ocean summer	529.207	521.36	0.252
No. circuli - 2nd ocean summer	10.70	10.70	0.960
Circ. spacing - 2nd ocean summer	49.71	49.00	0.048
Spacing - last 3 edge circuli	50.39	51.82	0.039
Length of fish (mm)	447.21	446.26	0.593
<u>Odd Years</u>			
N	467	287	
Size - 1st ocean year	945.39	931.80	0.088
No. circuli - 1st ocean	21.51	21.39	0.495
Circ. spacing - 1st ocean	44.05	43.69	0.169
<u>Edge</u>			
Size - 2nd ocean summer	515.79	514.21	0.844
No. circuli - 2nd ocean summer	10.38	10.58	0.206
Circ. spacing - 2nd ocean summer	50.00	48.85	0.006 *
Spacing - last 3 edge circuli	50.82	51.15	0.678
Length of fish (mm)	448.09	439.77	2.3x10 ⁻⁶ *
<u>Even Years</u>			
N	157	87	
Size - 1st ocean year	942.65	974.98	0.023
No. circuli - 1st ocean	21.75	22.61	0.002 *
Circ. spacing - 1st ocean	43.44	43.18	0.604
<u>Edge</u>			
Size - 2nd ocean summer	569.38	544.93	0.055
No. circuli - 2nd ocean summer	11.66	11.07	0.013
Circ. spacing - 2nd ocean summer	48.86	49.49	0.385
Spacing - last 3 edge circuli	49.11	54.06	0.0006 *
Length of fish (mm)	444.60	467.68	8.7x10 ⁻¹² *

* = statistically significant difference ($\alpha = 0.01$)

Table 4. Results of nested analyses of variance (ANOVAs) on fish length and scale variables calculated from long-axis scale measurements and circulus counts of age 0.2 chum salmon caught south of the central Aleutian Islands the last 10 days of June. Regimes represented by 100 fish from each of three years (pre-1977: 1965, 1966, 1967; post-1977: 1991, 1993, 1994). Years nested within regime. All scale measurements are in microns.

Chum salmon	Source	df	F-value	P
Size - 1st ocean year	Regime	1	18.968	0.0001 *
	Year	4	1.481	0.2063
Size - 2nd ocean year	Regime	1	34.592	0.0001 *
	Year	4	24.324	0.0001 *
<u>Edge</u>				
Size - 3rd ocean summer	Regime	1	162.717	0.0001 *
	Year	4	12.982	0.0001 *
No. circuli - 3rd ocean summer	Regime	1	64.153	0.0001 *
	Year	4	11.914	0.0001 *
Circ. spacing - 3rd ocean summer	Regime	1	131.625	0.0001 *
	Year	4	5.368	0.0003 *
Spacing - last 3 edge circuli ¹	Regime	1	71.601	0.0001 *
	Year	4	9.825	0.0001 *
Length of fish (mm)	Regime	1	74.320	0.0001 *
	Year	4	14.905	0.0001 *

* = statistically significant difference ($\alpha = 0.01$) (small values may be rounded up to 0.0001)

¹ = distance from scale edge inward to third circulus from edge (or distance to second or first circulus, if there were not three circuli present between last annulus and edge)

Table 5. Results of nested analyses of variance (ANOVAs) on fish length and scale variables calculated from long-axis scale measurements and circulus counts of pink salmon caught south of the central Aleutian Islands the last 10 days of June. Regimes represented by 50 fish from each of three years (pre-1977: 1959, 1965, 1967; post-1977: 1983, 1993, 1995). Years nested within regime. All scale measurements are in microns.

Pink salmon	Source	df	F-value	P
Size - 1st ocean year	Regime	1	0.342	0.5589
	Year	4	8.268	0.0001 *
	Regime	1	2.576	0.1096
	Year	4	8.182	0.0001 *
	Regime	1	1.542	0.2153
	Year	4	1.634	0.1657
No. circuli - 1st ocean	Regime	1	0.007	0.9337
	Year	4	10.103	0.0001 *
	Regime	1	0.106	0.7447
	Year	4	16.196	0.0001 *
	Regime	1	0.080	0.7780
	Year	4	5.534	0.0003 *
Circ. spacing - 1st ocean	Regime	1	3.832	0.0512
	Year	4	12.295	0.0001 *
	Regime	1	5.694	0.0177
	Year	4	27.537	0.0001 *
	Regime	1	0.007	0.9337
	Year	4	10.103	0.0001 *
Edge	Regime	1	0.106	0.7447
	Year	4	16.196	0.0001 *
	Regime	1	0.080	0.7780
	Year	4	5.534	0.0003 *
	Regime	1	3.832	0.0512
	Year	4	12.295	0.0001 *
Spacing - last 3 edge circuli	Regime	1	5.694	0.0177
	Year	4	27.537	0.0001 *
	Regime	1	0.007	0.9337
	Year	4	10.103	0.0001 *
	Regime	1	0.106	0.7447
	Year	4	16.196	0.0001 *
Length of fish (mm)	Regime	1	0.080	0.7780
	Year	4	5.534	0.0003 *
	Regime	1	3.832	0.0512
	Year	4	12.295	0.0001 *
	Regime	1	5.694	0.0177
	Year	4	27.537	0.0001 *

* = statistically significant difference ($\alpha = 0.01$) (small values may be rounded up to 0.0001)

Table 6. Correlations (Pearson r) between annual means of fish length and scale variables of chum salmon (caught south of the central Aleutian Islands, between 175°E and 170°W, and between 46°N and 52°N in and around the last 10 days of June, 1959-95) and annual regional run sizes of pink and chum salmon. Average run sizes for years of scale samples, in millions of fish, included for comparison between periods.

Chum salmon	Pink abundance ¹		Chum abundance ²		
	Asia	W. Alaska	Japan	Russia	W. Alaska
<u>1956-70</u>					
Mean run sizes x 10 ⁶	92	1	5	17	4
1st Ocean	0.17	-0.17	0.46	-0.41	0.01
2nd Ocean	-0.003	0.59	0.44	-0.32	-0.29
Edge:					
3rd Ocean	-0.56	0.05	0.79	-0.76	-0.19
3rd Ocean spacing	-0.61	-0.09	0.71	-0.60	-0.20
Last 3 circuli ³	-0.65	-0.03	0.74	-0.63	-0.16
Length	-0.73	0.14	0.52	-0.46	0.04
<u>1983-95</u>					
Run sizes x 10 ⁶	208	1	55	15	8
1st Ocean	-0.26	0.18	0.14	0.16	-0.01
2nd Ocean	0.76	0.36	0.09	-0.02	-0.28
Edge:					
3rd Ocean	-0.63	-0.42	-0.06	0.18	-0.15
3rd Ocean spacing	-0.29	-0.22	-0.38	-0.60	0.56
Last 3 circuli ³	-0.26	-0.29	-0.31	-0.49	0.52
Length	0.01	-0.33	-0.67	-0.65	0.46

¹ = pink salmon abundances were lagged by one year for comparisons with first and second ocean zones (e.g., first and second ocean zone measurements from chum caught in 1956 were compared with returning pink salmon abundance in 1955)

² = chum salmon abundances were advanced by one year for comparisons with all scale measurements (e.g., measurements from chum caught in 1956 were compared with returning chum salmon abundance in 1957)

³ = distance from scale edge inward to third circulus from edge (or distance to second or first circulus, or no measurement, if there were not three circuli present between last annulus and edge)

Table 7. Correlations (Pearson r) between annual means of fish length and scale variables of pink salmon (caught south of the central Aleutian Islands, between 175°E and 170°W, and between 46°N and 52°N in and around the last 10 days of June, 1959-95) and annual regional run sizes of pink and chum salmon. Average run sizes for years of scale samples, in millions of fish, included for comparison between periods.

Pink salmon	Pink abundance		Chum abundance ¹		
	Asia	W. Alaska	Japan	Russia	W. Alaska
<u>1959-67</u>					
Run sizes x 10 ⁶	88	1	5	19	4
1st Ocean	0.09	0.02	-0.30	-0.07	-0.78
Edge:					
2nd Ocean	-0.57	0.70	0.59	-0.61	-0.41
2nd Ocean spacing	0.12	-0.14	0.25	-0.14	-0.51
Last 3 circuli	0.14	0.14	-0.21	0.21	-0.27
Length	0.08	-0.01	0.55	-0.51	-0.42
<u>1983-95</u>					
Run sizes x 10 ⁶	213	1	55	14	8
1st Ocean	0.75	0.32	0.40	0.64	-0.88
Edge:					
2nd Ocean	0.59	0.12	0.42	-0.27	0.32
2nd Ocean spacing	-0.44	0.34	-0.30	0.07	0.32
Last 3 circuli	0.07	0.56	-0.06	-0.12	0.59
Length	0.76	0.70	0.65	0.10	0.31

¹= chum salmon abundances were advanced by two years for comparisons with first ocean zones (e.g., first ocean zone measurements from pink caught in 1959 were compared with returning chum salmon abundance in 1961)

DISCUSSION

It seems clear that a major oceanographic change about 1976-77 has had a positive effect on abundance of northern Pacific salmon stocks. There has also been a concomitant decrease in growth and size in a number of stocks, due either directly to the oceanographic change or as a density-dependent result of the increase in abundance. Age 0.2 chum salmon in the area south of the central Aleutians clearly demonstrate reduced growth and size in the post-1977 regime. This period has seen an overall increase in abundance of salmon migrating in the region, particularly of Asian pink and Japanese chum. Chum salmon growth seems to be negatively correlated with both Asian pink and chum salmon abundance.

Ishida et al. (1993) also noted decreases in weight and third-ocean year scale growth of Japanese and Russian stocks since 1970. They found about 35% in the decline in weight could be attributed to intra-specific density-dependent effects (as determined by correlations with central North Pacific CPUE of chum salmon). They speculated that the remainder of the decline could be due to changes in ocean temperature and density-dependent effects of other species of salmon. Such inter-specific effects have been detected by several authors. Maturing Ozernaya River sockeye were shorter and weighed less when marine abundance of pink salmon was higher (Krogius 1960; Bugaev et

al. 1996). Ogura et al. (1991) found that the second (final) year of marine growth of coho salmon in the western North Pacific was less in odd years when Asia pink salmon abundances were high.

Pink salmon show fewer differences between the two regimes. Their growth also seems less clearly correlated with run sizes of pink or chum. Myers (1994) also found no significant length differences between pink salmon in periods of low (1970-75) and high (1977-78) abundance in this same ocean area; pink salmon from this region had better winter growth in the later regime, but second-year growth was less for odd-year stocks. Those samples were collected in July, and the number of years analyzed was limited. Several workers (Welch and Morris 1994; Ishida and Ito 1995; Ishida et al. 1995) have found intra-specific density-dependent effects on growth and overall size of pink salmon. Perhaps we did not find a similar negative relationship between edge growth and pink salmon abundance because such effects occur at a later stage in pink salmon homeward migration as fish become more concentrated in coastal and near-offshore waters. Rogers (1980) has proposed that density-dependent growth occurs in maturing Bristol Bay sockeye salmon when they are concentrated north of the Alaska Peninsula during their final weeks at sea. For fish from the time-area stratum we studied, this may be in July, in the Bering Sea, or in more coastal waters of eastern Kamchatka and western

Alaska. In addition, the measurement axis we used is more sensitive to increases in length than to increases in weight. Much of the final growth of maturing pink salmon is in weight, not length (e.g. Ricker 1964). In any case, it is interesting that no strong density-dependent effect is obvious at this point in the growth in length of the fish in this area.

It seems clear that there are significant intra-specific density-dependent effects on growth and size in sockeye salmon. An inverse relationships between abundance and size at maturity of Bristol Bay sockeye salmon was demonstrated by Rogers (1980), and Peterman (1984) found negative correlations in the size of British Columbia and Bristol Bay sockeye with abundance of sockeye in the Gulf of Alaska (combined stocks). McKinnell (1995) substantiated this effect with British Columbia sockeye which had spent three years at sea and were perhaps more likely than two-ocean fish to have migrated further offshore where interaction with Bristol Bay stocks was more probable. In addition to the strong effect of pink salmon abundance on returning size of Ozernaya River sockeye, Bugaev et al. (1996) also found a lesser negative effect when Kamchatka sockeye were abundant.

Pink salmon abundance seems to exert an influence on chum salmon growth, especially in their third ocean summer, while pink salmon growth shows less correlation to changes in chum salmon abundance. In addition, intra-specific competition between pink salmon does not seem to be as strong as the effect on chum salmon. In western Kamchatka, the central North Pacific, and the Bering Sea, Andrievskaya (1966) and Tadokoro et al. (1996) noted that the two species had similar diets when pink salmon were less abundant, but that chum salmon fed on prey of lower nutritional quality when pink salmon were abundant. Salo (1991) has provided a good summary of the findings of the interactions between pink and chum salmon. He suggests that chum salmon are more plastic and adapt around the inflexibly structured life history of pink salmon.

Positive associations of first-year ocean growth for pink salmon with Asian pink and Japanese chum runs indicates that conditions which favor early survival of these species also favor early growth of pink salmon. Myers (1994) found better coastal and winter growth in pink salmon in years of high abundance, and Welch (1994) noted that early marine growth of two stocks of British Columbia pink salmon showed little or no trend from the 1950s to the 1980s, which suggested that pink salmon smolts were not food limited in that period. Ishida et al. (1995) also found no correlation between early marine growth and abundance (CPUE) of pink salmon caught in the western North Pacific, but did find negative correlations in those caught in the Bering Sea. They

attributed this difference to higher zooplankton density in the Okhotsk Sea rearing areas of western North Pacific pink salmon, compared to lower zooplankton density in the coastal waters of eastern Kamchatka. Studies of early marine intra-specific density effects in sockeye salmon are also conflicting; Peterman (1984) thought that density-dependent effects operated at early ocean life history stages of British Columbia sockeye salmon, while McKinnell's (1995) study of scale growth did not demonstrate an early ocean effect.

The interaction between juvenile pink and chum at this life history stage is not clear. We did not find strong positive or negative correlations of chum salmon first-year growth with lagged abundances of pink salmon. However, Salo (1991) cites studies finding lower feeding rates of juveniles of both species when juveniles were abundant, larger Strait of Georgia chum fry when pink salmon were not present, better survival of Fraser River and Hood Canal chum in years when pink salmon were not abundant, and studies which considered the most important site of Puget Sound pink-chum salmon competition to be the early marine environment. Azuma (1996) has postulated different growth and energy storage strategies for juvenile pink and chum salmon during their early marine growth in waters north and east of Japan but did not make any comparison with abundance. Chum salmon grew more quickly and stored less energy in their earliest stages, but switched this pattern as they grew, while young pink salmon had low growth and energy storage rates which both gradually increased as they grew.

An overall picture of recent changes in Pacific salmon abundance and growth has begun to emerge from the many studies cited here, and our findings are not the first to make these points. Some current views of recent ocean events and interactions between species might be summarized as follows:

- (a) A change in oceanographic and climatologic conditions occurred about 1977. The change is associated with an increase in abundance of many northern stocks. Other factors influencing salmon abundance in this period include increases in hatchery production, declines of offshore fisheries and marine mammal populations, and changes in freshwater habitat.
- (b) Conditions favoring increased abundance may also favor increased early marine growth. Faster growth is probably an important factor in survival and thus in determining higher abundance. The evidence for intra- or inter-specific density-dependent effects or food limitation in the first, more coastal, year of ocean growth is mixed. Predation and abiotic factors may be more important at this point.
- (c) When salmon are in higher abundance, density-

dependent effects on growth and final size may be seen later in life either when fish are immatures (e.g., age 0.2 chum salmon) or in maturing fish as they become more concentrated in their homeward migrations (pink and sockeye salmon). Pink salmon may exert stronger effects on other species than vice-versa.

CONCLUSIONS

We have linked edge-of-scale growth information for chum and pink salmon to a specific time and area in the North Pacific. In this region, age 0.2 chum salmon have grown less than in the pre-1977 regime, and their growth may respond to abundance of pink salmon. Pink salmon, on the other hand, show little evidence of growth differences between the regimes in this time-area stratum. We intend to continue to look at growth of these species in other time periods and areas and extend the study to sockeye and coho salmon. One hypothesis we wish to investigate is that there are inter-specific effects on growth of sockeye and chum salmon in this area. We also plan to link scale growth measurements to data on stomach contents and level of insulin-like growth factor collected from the same fish. New data sets from recent cruises will allow us to examine associations between growth and oceanographic conditions and to compare growth with abundance of each species in the specific time-area stratum as measured by a standardized CPUE. Recent cruises have given indications that temperatures may be warming again in the central North Pacific and cooling in the Gulf of Alaska. We hope to assess any effect of future oceanographic shifts on growth with samples from coming cruises.

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Seasonal Growth Patterns of Pacific Salmon (*Oncorhynchus* spp.) in Offshore Waters of the North Pacific Ocean

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Seasonal growth patterns of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean were explored using biological data collections from the Japanese salmon research programs. Seasonal change in fork length and body weight was similar between sockeye and chum salmon, and between pink and coho salmon. Seasonal change in condition factors was very similar among the five species, that is, condition factors increased in spring, peaked in summer, decreased in fall, and were lowest in winter. Average growth rate in weight during maturing stage was significantly higher than that in immature stage for sockeye, pink, and coho salmon. For chum salmon, there was no significant difference in growth rate between immature and maturing fish, but the growth rate of immature fish was higher than those of other species, especially at age 0.2. Growth rates during life stages when density-dependent growth may occur are higher than those in other life stages. We can hypothesize that higher growth rates require greater demands for food intake, which may lead to density-dependent growth during these rapid-growth seasons if prey resources are limited.



INTRODUCTION

There is a great deal of evidence that the sizes of Pacific salmon caught in commercial fisheries have varied from year to year in the North Pacific Ocean (Ricker 1995; Helle and Hoffman 1995; Bigler et al. 1996). To explain these changes in body size, several hypotheses - such as density-dependent growth, selection by size selective fisheries or artificial enhancement, and changes in ocean conditions - were suggested for some species and stocks (Ricker 1981; Kaeriyama 1989; Ishida et al. 1993, 1995). In general, most fish continue to grow throughout their lives (Moyle and Cech 1988). For Pacific salmon, there is substantial information on body size of out migrating juveniles and returning adults for many stocks. However, the growth of Pacific salmon during the marine rearing phase has not been defined precisely because of very limited ocean sampling, especially in winter (LeBrasseur and Parker 1964; Lander and Tanonaka 1964; Lander et al. 1966; LaLanne 1971). Three methods have been used to estimate marine growth of Pacific salmon: (1) seasonal changes in the average sizes of fish sampled at frequent intervals at sea, (2) tag-recovery data, and (3) fish lengths back-calculated from scales (Birman 1951; Taguchi 1961; Ricker 1964; LaLanne 1971;

Kaeriyama 1996). Japanese scientists have conducted salmon research in offshore waters since 1953. Biological data collected during this research was used to estimate marine growth of Pacific salmon.

The purposes of this study were to provide a basic description of the marine growth of five species of Pacific salmon, to compare these results with those from previous studies, and to discuss the relationship between seasonal growth pattern and density-dependent growth.

MATERIALS AND METHODS

Data (Appendix Tables 1 - 8) used for this study were collected by the following three salmon research programs: (1) the Spring and Summer Salmon Research Program, (2) the Winter Salmon Research Program, and (3) the Juvenile Salmon Research Program. In the Spring and Summer Salmon Research Program, fish were caught by non-selective drift gillnets (C nets with 10 different mesh sizes from 48 to 157 mm; Takagi 1975), special mesh drift gillnets (F nets with mesh sizes less than 48mm and greater than 157 mm), commercial drift gillnets (Nets with mesh sizes from 112 to 130 mm), and surface longlines on Japanese salmon research vessels from 1972 through 1995 in the North Pacific Ocean,

Okhotsk Sea, Bering Sea, and Gulf of Alaska. In this study, biological data collected by C and F nets were used. In the Winter Salmon Research Program, drift gillnets and surface longlines were used in the North Pacific Ocean in the winters of 1968 and 1969, and a trawl net was used in the North Pacific Ocean and Gulf of Alaska in the winters of 1992 and 1996. In the Juvenile Salmon Research Program, purse seines, small mesh gillnets (22 to 63 mm), and trawl nets were used in the western North Pacific Ocean and Okhotsk Sea in June-October of 1988-1995.

Fish were processed by recording fork length, body weight, sex, and gonad weight. A scale for age determination was removed from the standard International North Pacific Fisheries Commission (INPFC) preferred area of the body of each fish, if scales were present. Age was determined in the laboratory by visual examination of scale samples. Maturity was determined from gonad weights (Takagi 1961; Ito et al. 1974). In this study, average fork length (FL) in mm, body weight (BW) in g, and condition factor ($10^7 \times BW/FL^3$) were calculated by species, maturity, ocean age, and month. Growth rates are defined as increments in fork length or body weight per month (mm/mo or g/mo). Average growth rates are calculated by immature and maturing fish including negative values. All freshwater age groups, sexes, years, and gear types were combined. Data points calculated from less than 10 fish were excluded from the analysis. We did not analyze data by geographic area and stock, so growth patterns in this study are not for specific stocks, but for several stocks combined.

RESULTS

Fork Length

Seasonal change in fork length was similar between sockeye and chum salmon, and between pink and coho salmon. Juvenile sockeye salmon were about 210 mm in fork length in August and grew to 270 mm by the end of the first year. For immature sockeye salmon, the average fork length in July was 350 mm, 480 mm, and 540 mm for the second to the fourth year, respectively. For maturing sockeye salmon, the average fork length in July was 390 mm, 550 mm, 610 mm, and 620 mm from the second to the fifth year, respectively (Fig. 1). The average growth rate was 10 mm/mo for immature sockeye salmon, and 14 mm/mo for maturing sockeye salmon, but these differences were not significant (t-test, $P < 0.05$) (Table 1).

Juvenile chum salmon were about 150 mm in fork length in July and grew to 240 mm at the end of the first year (Fig. 1). For immature chum salmon, the average fork length in July was 340 mm, 460 mm,

520 mm, and 560 mm from the second to the fifth year, respectively. For maturing chum salmon, the average fork length in July was 400 mm, 520 mm, 590 mm, 620 mm, and 630 mm from the second to the sixth year, respectively (Fig. 1). The average growth rates were 14 mm/mo for both immature and maturing chum salmon but these differences were not significant (t-test, $P < 0.05$) (Table 1).

Pink and coho salmon grew linearly, although the growth slowed from October to January. The average fork lengths of pink and coho salmon were 250 mm and 340 mm at the end of the first year, respectively, and 500 mm and 620 mm in September of the second year, respectively (Fig. 1). There was no significant difference between the growth rates of immature and maturing fish for both species (t-test, $P < 0.05$) (Table 1). Chinook salmon appeared to have a linear growth pattern, although data were not sufficient to estimate growth rates (Fig. 1).

Body Weight

Seasonal changes in body weight were similar to those in fork length, but much more drastic, especially during the season of rapid growth. Juvenile sockeye salmon were about 100 g in body weight in August and grew to 230 g by the end of the first year. For immature sockeye salmon, the average body weight in July was 470 g, 1280 g, and 1950 g from the second to the fourth year, respectively. The average body weight of maturing sockeye salmon in July was 740 g, 2230 g, 3060 g, and 3280 g from the second to the fifth year, respectively (Fig. 2). The average growth rate of maturing sockeye salmon was significantly higher than that of immature sockeye salmon (t-test, $P < 0.05$) (Table 1). The body weight growth rates of maturing sockeye salmon at ocean age .2 and .3 were higher than those of other ages.

Juvenile chum salmon were about 40 g in body weight in July and grew to 140 g at the end of the first year. For immature chum salmon, the average body weight in July was 440 g, 1160 g, 1770 g, and 2170 g from the second to the fifth year, respectively. The average body weight of maturing chum salmon in July was 780 g, 1890 g, 2790 g, and 3260 g from the second to the sixth year, respectively (Fig. 2). The average body weights of immature chum salmon decreased during winter. The average growth rates of immature and maturing chum salmon were high and not statistically different (t-test, $P < 0.05$) (Table 1). The body weight growth rate of immature chum salmon at age 0.2 and 0.3 were higher than those of other ages.

The average body weights for pink and coho salmon were 170 and 480 g in December of the first year, respectively, and 1520 g and 3440 g in September of the second year, respectively (Fig. 2).

Fig. 1 Average fork lengths of Pacific salmon taken at sea by month. Open circles indicate immature fish and closed circles indicate maturing fish.

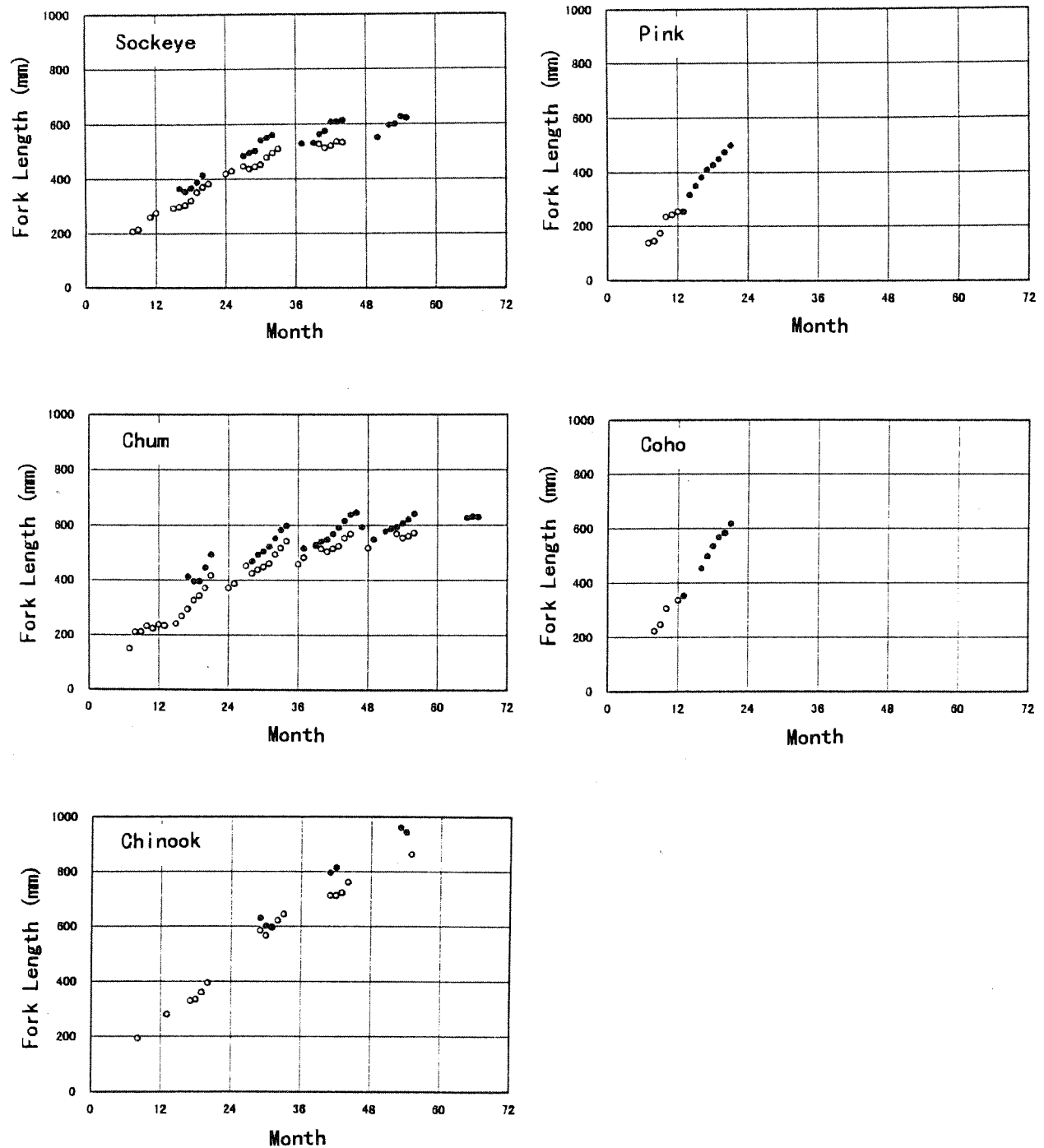
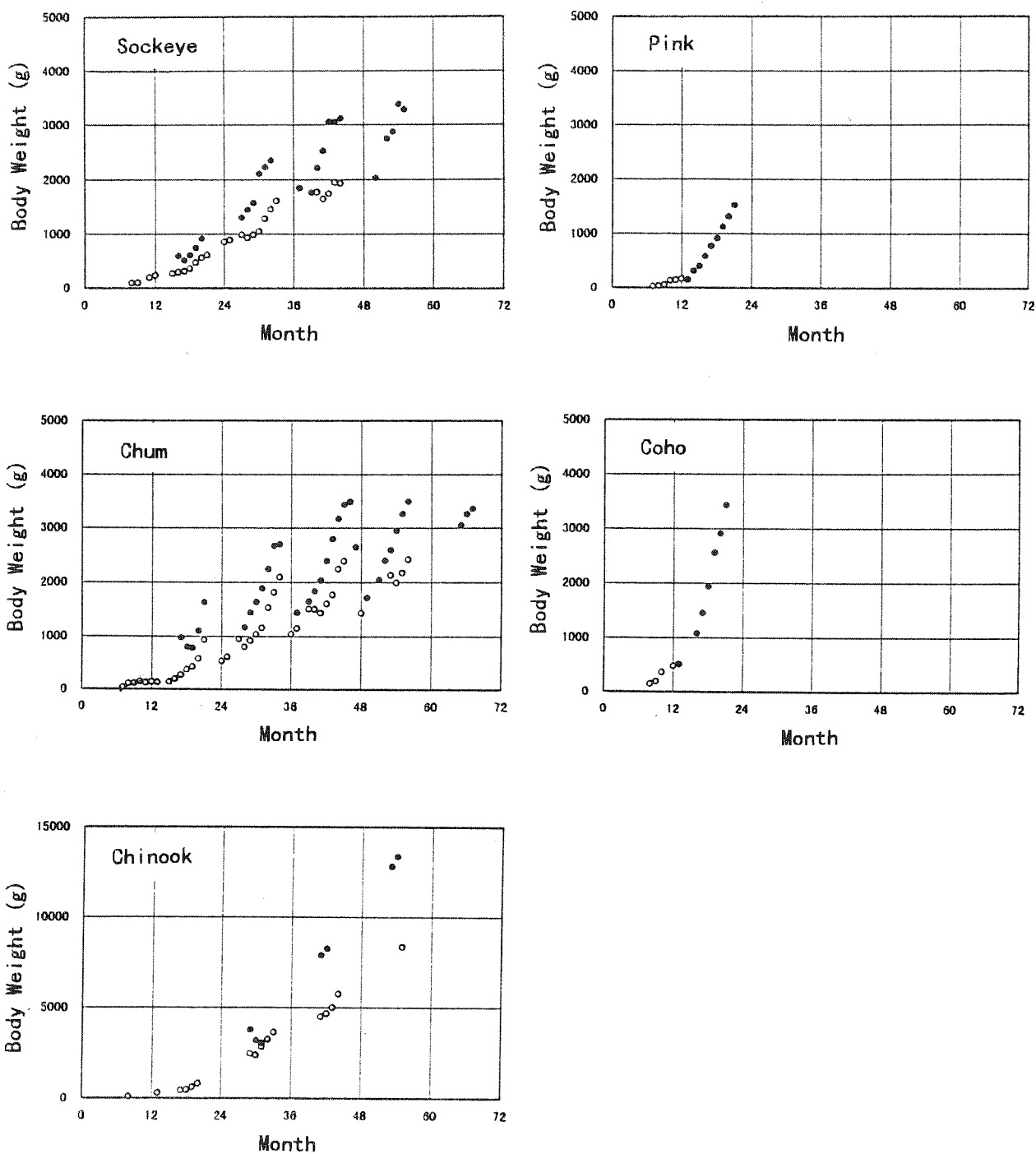


Table 1. Growth rate in fork length and body weight by species, maturity, and ocean age.

Species Ocean Age	FL/mo		BW/mo	
	Immature	Maturing	Immature	Maturing
Sockeye				
Age .0	11.5±6.0		20.5±26.8	
Age .1	15.0±9.4	12.5±16.6	57.5±35.7	80.3±114.5
Age .2	10.5±10.8	15.2±13.5	94.5±98.3	209.7±184.3
Age .3	1.7±13.0	16.7±15.1	39.5±145.1	273.1±239.4
Age .4		8.6±15.4		178.4±308.4
Mean±S.D.	10.2±10.9	13.8±13.9	63.5±88.6	192.4±206.1
Chum				
Age .0	17.4±26.3		20.8±38.7	
Age .1	24.4±15.3	20.1±33.9	111.6±117.0	163.6±321.6
Age .2	13.1±18.2	21.8±7.5	152.6±159.8	254.6±136.0
Age .3	9.7±15.5	8.0±25.9	140.1±171.6	124.3±408.0
Age .4	0.9±14.3	12.8±5.1	95.6±206.8	288.5±71.2
Age .5		2.1±3.8		153.2±75.9
Mean±S.D.	14.4±18.4	13.8±20.0	112.4±142.7	197.0±266.7
Pink				
Age .0	23.1±22.7		28.2±30.5	
Age .1		27.2±16.6		150.0±73.1
Mean±S.D.	23.1±22.7	27.2±16.6	28.2±30.5	150.0±73.1
Coho				
Age .0	41.7±25.6		105.5±88.3	
Age .1		39.9±11.7		398.2±204.8
Mean±S.D.	41.7±25.6	39.9±11.7	105.5±88.3	398.2±204.8

Fig. 2 Average body weights of Pacific salmon taken at sea by month. Open circles indicate immature fish and closed circles indicate maturing fish.



For both species, the average growth rate of maturing fish was significantly higher than that of immature fish (t-test, $P < 0.05$) (Table 1).

Condition Factor

Seasonal change in condition factors was very similar among the five species, that is, condition factors increased in spring, peaked in summer, decreased in fall, and were lowest in winter (Fig. 3). In addition to seasonal changes, condition factors of sockeye and chinook salmon showed increasing trends in peak and low values as ocean age increased. In contrast, the peak and low values of condition factors of chum salmon were stable regardless of ocean age (about 130 and 100, respectively). The condition factors of coho salmon were higher than those of pink salmon in all seasons.

DISCUSSION

Comparison with Other Studies

For sockeye salmon, we obtained a growth pattern similar to that presented by French et al. (1976) based on the seasonal size of fish sampled in the North Pacific Ocean and Bering Sea. In both areas, the growth of sockeye salmon was positive for most of the year. Continuous growth for sockeye salmon was also observed by Bilton and Ludwig (1966) using scale examination.

For chum salmon, the present estimates of body size for each age group were smaller than those provided in previous studies (Birman 1951; Kaeriyama 1996). The body size of chum salmon at the end of the first year was 240 mm in the present study, but 260-300 mm and 350-370 mm in the previous studies based on scale measurements. There are three possible explanations for this difference. Firstly, these differences may be stock specific as Birman (1951) examined a wild stock in the Amur River, and Kaeriyama (1996) examined a hatchery stock in Japan. In general, body sizes of out migrating juveniles of hatchery stocks are larger than those of wild stocks, because hatchery fish are fed artificially before release. The chum salmon in the present study are mixed stocks, so the difference in body size may be partly due to the difference of stocks or stock composition. Secondly, these differences may be temporal. Kaeriyama (1996) indicated that the average sizes of chum salmon in 1985-1992 were smaller than those in 1976-1980, and that this difference in growth was due to the changes in fish density. Most of the juveniles in the present study were collected after 1985. Therefore, the differences in sizes of juvenile chum salmon may be partly explained by differences in growth conditions due to fish density. Lastly, these

differences may be related to differences in methodology. Birman (1951) and Kaeriyama (1996) measured the widths between annuli on scales and estimated fork length by back-calculation using an estimated scale-length relationship. This relationship was developed using mature adults, and it has not yet been validated with juvenile fish.

For pink salmon, the present growth pattern is within the range of those provide by Ricker (1964), LeBrasseur and Parker (1964), and Takagi et al. (1981). There is a season of slow growth from October to January in the present growth pattern. A similar slow-growth season was also found by Ricker (1964). This slow-growth season for pink salmon corresponds to the time of annulus formation in December or January (Birman 1960; Bilton and Ludwig 1966). Average fork length at the time of annulus formation was estimated to be 28 cm by back-calculation (Birman 1960), while the average fork length in the present study was 25 cm in January.

Growth Rate and Density-Dependent Growth

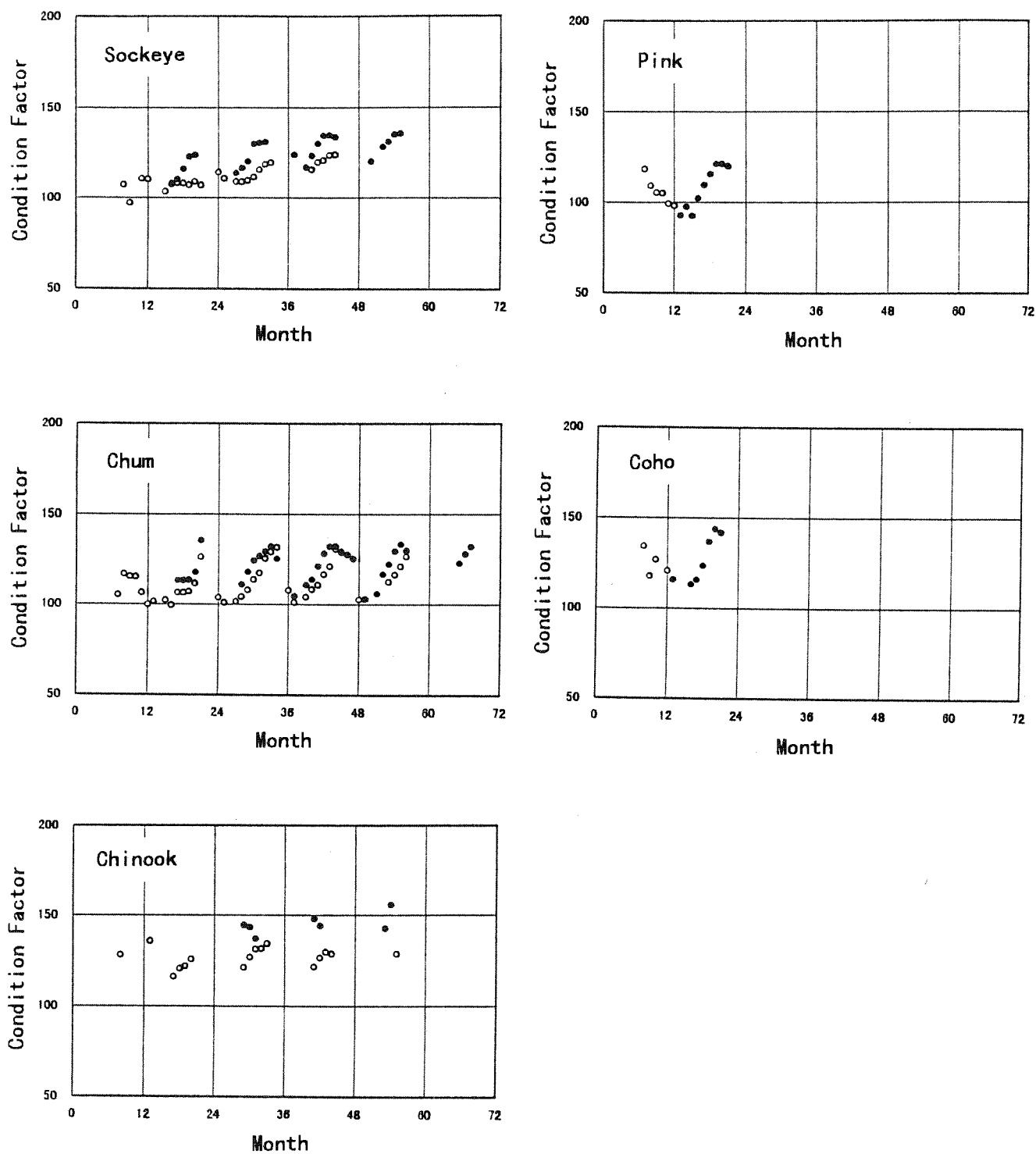
Average growth rate in weight during maturing stage was significantly higher than that in immature stage for sockeye, pink, and coho salmon. For chum salmon, there was no significant difference between immature and maturing fish, but the growth rate of immature fish was higher than those other species, especially at age 0.2.

It is reported that density-dependent growth in salmon occurs at a specific life history stage in the North Pacific Ocean. For sockeye salmon, density-dependent growth occurs in maturing fish in the last few months at sea (Rogers and Ruggerone 1993). For chum salmon, density-dependent growth occurs in the first through the fourth year, especially in the third year (Ishida et al. 1993; Kaeriyama 1996). For pink and coho salmon, growth variation in the second year at sea is related to abundance of pink salmon (Ogura et al. 1991, Ishida et al. 1995). Growth rates during life stages when density-dependent growth may occur are higher than those in other life stages. We can hypothesize that higher growth rates require greater demands for food intake, which may lead to density-dependent growth during these rapid-growth seasons if prey resources are limited.

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Fig. 3 Average condition factors of Pacific salmon taken at sea by month. Open circles indicate immature fish and closed circles indicate maturing fish.



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Appendix

Table 1. Fork length, body weight, and condition factor of immature sockeye salmon.

TABLE 1. Fork length, body weight, and condition factor of winter flounder stocks, 1980-1990.													
Ocean Age	Month	Fork Length				Body Weight				Condition Factor			
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.0	1												
	2												
	3												
	4												
	5												
	6												
	7												
	8	375	207.1	±	15.7		96.2	±	22.9		107.2	±	10.9
	9	19	214.3	±	13.7	7.2	97.8	±	25.8	1.6	97.2	±	10.8
	10												
	11	21	258.9	±	14.0		193.2	±	33.1		110.6	±	7.0
	12	17	274.7	±	22.1	15.8	232.8	±	62.3	39.5	110.3	±	6.9
.1	1												
	2												
	3	53	291.9	±	31.9		265.3	±	86.9		103.5	±	10.7
	4	449	296.8	±	33.6	4.9	290.4	±	113.5	25.1	107.4	±	14.2
	5	1907	303.0	±	31.1	6.2	309.2	±	101.2	18.8	108.2	±	14.2
	6	6181	320.0	±	31.8	17.0	362.6	±	121.9	53.4	108.1	±	13.8
	7	12827	350.4	±	33.6	30.4	472.7	±	144.9	110.1	107.1	±	11.6
	8	3831	369.1	±	33.9	18.7	561.2	±	167.2	88.5	109.0	±	12.3
	9	313	381.9	±	33.7	12.8	610.5	±	190.2	49.3	106.9	±	12.0
	10												
	11												
	12	73	418.8	±	30.2		852.8	±	209.7		114.2	±	8.1
.2	1	30	428.7	±	33.9	9.9	889.0	±	209.6	36.2	110.7	±	5.7
	2												
	3	151	446.1	±	28.4		981.8	±	203.7		109.1	±	6.4
	4	558	436.7	±	34.3	-9.5	923.5	±	238.6	-58.3	108.8	±	7.9
	5	2627	444.9	±	31.9	8.2	980.9	±	232.4	57.3	109.7	±	9.5
	6	5708	452.2	±	30.7	7.4	1047.1	±	245.6	66.2	111.5	±	10.3
	7	16394	477.7	±	32.7	25.5	1280.9	±	302.4	233.8	115.6	±	10.8
	8	2897	494.7	±	33.6	17.0	1455.4	±	322.9	174.5	118.6	±	12.3
	9	271	509.9	±	32.0	15.2	1607.2	±	344.6	151.8	119.6	±	9.9
	10												
	11												
	12												
.3	1												
	2												
	3												
	4	22	527.2	±	53.1		1770.0	±	599.1		115.6	±	8.3
	5	117	512.8	±	36.2	-14.5	1641.4	±	4161.1	-128.6	119.7	±	12.8
	6	322	520.9	±	37.1	8.1	1739.1	±	455.1	97.8	120.8	±	12.4
	7	538	536.4	±	40.7	15.5	1946.4	±	501.3	207.2	123.5	±	12.4
	8	73	533.9	±	43.3	-2.5	1928.1	±	508.1	-18.3	123.8	±	9.0
	9												
	10												
	11												
	12												

Appendix (continued)

Table 2. Fork length, body weight, and condition factor of maturing sockeye salmon.

Ocean Age	Month	Fork Length					Body Weight				Condition Factor		
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.1	1												
	2												
	3												
	4	20	363.6	±	70.2		592.0	±	388.0		108.0	±	9.6
	5	106	352.4	±	39.8	-11.2	506.2	±	187.6	-85.8	110.2	±	15.0
	6	326	367.0	±	44.1	14.5	606.5	±	319.3	100.3	116.0	±	15.8
	7	414	386.7	±	40.7	19.7	740.8	±	294.6	134.2	122.9	±	13.9
	8	183	413.8	±	42.6	27.1	913.1	±	398.9	172.3	123.8	±	13.2
	9												
	10												
	11												
	12												
.2	1												
	2												
	3	136	484.5	±	20.9		1299.9	±	184.5		113.6	±	5.6
	4	845	496.2	±	30.4	11.7	1442.8	±	303.1	142.9	116.5	±	9.4
	5	3187	503.0	±	40.6	6.8	1571.0	±	457.6	128.2	120.1	±	12.6
	6	6331	542.1	±	40.3	39.2	2109.9	±	516.2	538.9	129.8	±	13.2
	7	6710	550.9	±	42.5	8.8	2229.4	±	568.9	119.5	130.5	±	13.8
	8	370	560.4	±	38.4	9.5	2348.3	±	553.4	118.9	131.0	±	12.7
	9												
	10												
	11												
	12												
.3	1	14	528.9	±	20.5		1838.6	±	212.6		123.9	±	6.0
	2												
	3	36	530.9	±	23.4		1755.3	±	229.9		116.8	±	6.5
	4	435	562.4	±	32.9	31.5	2214.5	±	413.2	459.2	123.2	±	8.8
	5	2677	575.3	±	39.0	12.9	2518.5	±	598.3	304.0	130.0	±	11.5
	6	7277	608.5	±	36.8	33.2	3061.3	±	592.9	542.9	134.5	±	12.0
	7	5738	608.3	±	33.7	-0.2	3056.8	±	563.3	-4.5	134.7	±	12.7
	8	279	614.4	±	29.9	6.1	3120.6	±	522.4	63.8	133.6	±	10.4
	9												
	10												
	11												
	12												
.4	1												
	2	20	551.1	±	29.3		2029.5	±	383.1		120.1	±	8.8
	3												
	4	15	595.8	±	34.4		2745.3	±	542.1		128.3	±	8.7
	5	72	600.7	±	33.8	4.9	2870.4	±	555.5	125.1	131.1	±	12.0
	6	122	626.3	±	45.6	25.6	3380.4	±	757.5	510.0	135.3	±	12.0
	7	96	621.6	±	34.1	-4.7	3280.5	±	586.8	-99.9	135.7	±	13.2
	8												
	9												
	10												
	11												
	12												

Appendix (continued)

Table 3. Fork length, body weight, and condition factor of immature chum salmon.

Ocean Age	Month	Fork Length				Body Weight				Condition Factor			
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.0	1												
	2												
	3												
	4												
	5												
	6												
	7	33	150.6	±	23.0		37.9	±	17.1		105.3	±	13.7
	8	88	209.9	±	32.4	59.3	113.1	±	45.3	75.2	116.9	±	17.4
	9	144	211.6	±	24.5	1.7	113.4	±	41.0	0.4	115.5	±	11.1
	10	416	232.2	±	21.1	20.6	148.1	±	44.7	34.7	115.3	±	8.7
	11	295	222.2	±	21.2	-10.0	119.6	±	33.5	28.6	106.6	±	7.9
	12	18	237.5	±	36.8	15.4	141.7	±	73.2	22.1	99.9	±	8.4
.1	1	215	233.3	±	18.8	-4.2	131.6	±	35.9	-10.1	101.4	±	7.0
	2												
	3	41	241.1	±	15.0		144.4	±	28.2		102.3	±	7.5
	4	302	268.4	±	22.6	27.3	194.2	±	54.5	49.8	99.3	±	13.9
	5	553	294.1	±	19.8	25.8	274.3	±	67.2	80.2	106.5	±	14.2
	6	4990	326.3	±	24.5	32.2	375.9	±	107.5	101.5	106.4	±	12.7
	7	23542	342.3	±	25.0	15.9	436.4	±	113.8	60.5	107.1	±	11.6
	8	5688	370.7	±	27.9	28.5	581.9	±	182.7	145.6	111.5	±	13.1
	9	236	415.8	±	31.6	45.0	935.7	±	275.5	353.8	126.4	±	15.8
	10												
	11												
	12	147	370.9	±	25.5		534.1	±	105.3		103.8	±	7.2
.2	1	75	386.0	±	43.9	15.1	612.6	±	259.2	78.5	100.9	±	9.4
	2												
	3	13	451.1	±	30.5		953.1	±	244.7		101.7	±	9.8
	4	478	423.3	±	32.2	-27.7	806.9	±	212.5	-146.2	104.2	±	8.6
	5	1367	436.5	±	32.9	13.2	918.8	±	253.0	111.9	108.1	±	10.4
	6	8612	447.6	±	32.5	11.1	1042.1	±	277.0	123.3	113.9	±	11.7
	7	25045	459.3	±	33.8	11.7	1163.2	±	311.7	121.1	117.6	±	13.4
	8	4921	492.3	±	38.0	33.0	1535.0	±	433.1	371.8	125.7	±	12.9
	9	440	515.4	±	39.9	23.1	1813.1	±	505.7	278.1	129.3	±	12.5
	10	22	541.0	±	20.1	25.6	2095.0	±	327.0	281.9	131.8	±	15.5
	11												
	12	76	457.2	±	29.4	457.2	1045.3	±	234.7	1045.3	107.9	±	11.5
.3	1	42	418.9	±	42.2	24.7	1152.1	±	306.7	106.8	101.0	±	9.9
	2												
	3	22	524.9	±	28.4	524.9	1512.3	±	223.9	1512.3	104.0	±	5.1
	4	182	513.6	±	42.6	-11.3	1509.1	±	461.3	-3.2	108.3	±	10.7
	5	696	503.5	±	34.5	-10.1	1440.2	±	360.9	-68.8	111.0	±	12.2
	6	3465	514.1	±	34.7	10.6	1607.9	±	367.0	167.7	116.8	±	12.2
	7	8355	523.9	±	35.4	9.8	1771.9	±	442.9	164.0	121.2	±	14.0
	8	970	552.4	±	37.9	28.5	2243.6	±	554.2	471.7	130.9	±	14.4
	9	79	568.3	±	30.0	15.9	2386.1	±	420.8	142.5	129.0	±	11.4
	10												
	11												
	12	19	517.0	±	35.4	517.0	1436.7	±	334.5	1436.7	102.8	±	12.4
.4	1												
	2												
	3												
	4												
	5	26	568.5	±	43.9	568.5	2132.7	±	687.7	2132.7	122.6	±	11.3
	6	142	553.0	±	41.2	-15.5	1992.7	±	461.8	-140.0	116.6	±	12.4
	7	335	560.2	±	42.0	7.2	2172.6	±	593.2	180.0	121.4	±	15.1
	8	23	571.2	±	51.3	11.0	2419.6	±	691.5	246.9	126.8	±	19.6
	9												
	10												
	11												
	12												

Appendix (continued)

Table 4. Fork length, body weight, and condition factor of maturing chum salmon.

Ocean Age	Month	Fork Length				Body Weight				Condition Factor			
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.1	1												
	2												
	3												
	4												
	5	19	412.5	±	94.8		981.1	±	905.6		113.3	±	13.8
	6	107	394.9	±	76.2	-17.6	806.7	±	618.5	-174.4	113.2	±	14.9
	7	181	395.4	±	62.5	-0.5	781.6	±	542.5	-25.1	113.7	±	18.4
	8	51	445.0	±	56.3	49.7	1104.5	±	472.6	323.0	117.9	±	12.4
	9	16	492.8	±	37.5	47.7	1635.6	±	406.6	531.1	135.7	±	21.9
	10												
	11												
	12												
.2	1												
	2												
	3												
	4	245	468.0	±	41.0		1169.5	±	347.6		111.2	±	12.2
	5	915	492.0	±	38.2	24.1	1444.7	±	412.9	275.2	118.2	±	12.4
	6	2892	503.9	±	42.2	11.9	1640.7	±	500.2	196.1	124.5	±	15.4
	7	3691	522.7	±	49.2	18.8	1890.9	±	658.6	250.1	127.1	±	16.1
	8	790	551.7	±	49.4	29.0	2244.6	±	681.2	353.8	129.6	±	15.1
	9	97	582.7	±	42.5	31.0	2667.4	±	666.3	422.8	132.4	±	11.1
	10	37	598.9	±	35.0	16.1	2697.3	±	463.5	29.9	125.4	±	18.1
	11												
	12												
.3	1	51	515.0	±	38.0		1446.8	±	309.9		104.6	±	10.2
	2												
	3	115	528.8	±	26.9		1653.1	±	297.1		111.0	±	10.1
	4	2418	541.5	±	34.2	12.7	1835.4	±	416.8	182.2	114.0	±	11.1
	5	9329	549.1	±	35.0	7.6	2037.7	±	468.8	202.3	121.3	±	12.6
	6	19734	568.6	±	36.7	19.5	2394.1	±	542.4	356.5	128.5	±	14.0
	7	16745	591.3	±	42.5	22.8	2792.8	±	726.2	398.7	132.3	±	15.5
	8	1650	617.0	±	46.1	25.6	3170.3	±	823.1	377.5	132.5	±	15.9
	9	166	639.0	±	45.9	22.1	3435.4	±	837.7	265.0	129.5	±	13.3
	10	108	646.7	±	47.0	7.1	3492.1	±	766.2	56.8	127.7	±	11.5
	11	23	593.0	±	41.4	-53.7	2647.8	±	562.2	-844.3	125.5	±	9.4
	12												
.4	1	14	548.9	±	33.4		1720.4	±	313.2		103.1	±	8.5
	2												
	3	50	577.6	±	25.6		2047.0	±	290.2		105.9	±	9.6
	4	494	587.2	±	36.8	9.6	2396.9	±	533.8	349.9	116.9	±	12.0
	5	2246	593.8	±	36.2	6.7	2593.6	±	564.7	196.7	122.4	±	12.4
	6	5691	608.1	±	37.2	14.2	2948.2	±	615.2	354.6	129.8	±	13.5
	7	5216	621.7	±	40.8	13.6	3258.2	±	760.8	310.0	133.5	±	14.7
	8	281	641.8	±	46.5	20.2	3489.7	±	823.2	231.5	130.1	±	13.5
	9												
	10												
	11												
	12												
.5	1												
	2												
	3												
	4												
	5	44	626.5	±	28.1		3052.1	±	536.0		123.2	±	12.5
	6	134	631.3	±	36.4	4.8	3258.9	±	686.8	206.8	128.2	±	13.6
	7	163	630.7	±	45.5	-0.6	3358.4	±	790.1	99.5	132.1	±	14.6
	8												
	9												
	10												
	11												
	12												

Appendix (continued)

Table 5. Fork length, body weight, and condition factor of pink salmon.

Ocean Age	Month	Fork Length					Body Weight				Condition Factor		
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.0	1												
	2												
	3												
	4												
	5												
	6												
	7	56	138.7	±	9.1		31.8	±	5.8		118.5	±	11.3
	8	17	146.0	±	27.1	7.3	39.5	±	27.5	7.7	109.2	±	12.5
	9	90	173.7	±	18.0	27.7	58.1	±	25.5	18.6	105.4	±	12.4
	10	937	234.7	±	17.8	61.0	138.7	±	40.7	80.6	105.1	±	7.7
	11	707	243.1	±	38.5	8.4	145.7	±	38.5	6.9	99.2	±	8.4
	12	275	254.2	±	33.1	11.1	172.9	±	81.4	27.2	98.1	±	8.8
.1	1	215	254.2	±	18.7	0.0	154.9	±	36.7	-18.0	92.7	±	5.6
	2	239	316.9	±	28.6	62.7	318.5	±	93.0	163.7	97.6	±	7.9
	3	111	348.7	±	36.6	31.8	408.3	±	153.7	89.8	92.6	±	7.5
	4	12494	381.6	±	35.5	32.9	584.5	±	184.8	176.2	102.2	±	11.7
	5	50466	410.4	±	33.4	28.9	777.6	±	232.3	193.0	109.6	±	12.7
	6	129518	426.7	±	32.3	16.3	919.0	±	252.3	141.5	115.8	±	12.6
	7	126480	449.5	±	35.1	22.7	1128.9	±	322.5	209.9	121.3	±	13.0
	8	5884	474.7	±	32.4	25.2	1320.6	±	336.6	191.7	121.2	±	13.8
	9	1163	499.0	±	35.8	24.3	1523.1	±	397.6	202.6	120.1	±	13.5
	10												
	11												
	12												

Table 6. Fork length, body weight, and condition factor of coho salmon.

Ocean Age	Month	Fork Length				Body Weight				Condition Factor			
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.0	1												
	2												
	3												
	4												
	5												
	6												
	7												
	8	540	222.5	±	26.2		153.5	±	62.3		134.4	±	13.4
	9	27	246.1	±	43.9	23.6	196.6	±	129.4	43.1	117.9	±	16.4
	10	28	305.9	±	16.8	59.8	364.6	±	55.6	168.0	127.0	±	10.5
	11												
	12	68	336.9	±	38.3		480.0	±	171.4		120.9	±	9.8
.1	1	57	352.9	±	34.1	16.0	513.9	±	158.2	33.9	116.1	±	15.7
	2												
	3												
	4	228	453.6	±	38.9		1080.7	±	288.3		113.3	±	12.0
	5	625	497.2	±	39.7	43.6	1450.4	±	358.0	369.7	115.9	±	10.6
	6	6439	534.9	±	43.0	37.7	1937.0	±	539.6	486.6	123.7	±	13.6
	7	15250	567.5	±	45.8	32.6	2557.8	±	690.1	620.7	136.9	±	15.8
	8	3802	582.8	±	47.5	15.2	2909.0	±	759.3	351.2	143.8	±	13.8
	9	76	617.1	±	54.4	34.3	3436.1	±	995.3	527.1	141.8	±	16.1
	10												
	11												
	12												

Appendix (continued)

Table 7. Fork length, body weight, and condition factor of immature chinook salmon.

Ocean Age	Month	Fork Length				Body Weight				Condition Factor			
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.0	1												
	2												
	3												
	4												
	5												
	6												
	7												
	8	50	193.6	±	11.0		94.0	±	17.3		128.5	±	9.4
	9												
	10												
	11												
	12												
.1	1	29	281.0	±	14.6		304.3	±	52.2		135.9	±	6.4
	2												
	3												
	4												
	5	14	330.2	±	40.5		438.6	±	181.5		116.4	±	17.0
	6	323	334.9	±	42.7	4.6	478.7	±	278.7	40.1	120.7	±	12.9
	7	504	359.9	±	49.9	25.1	612.4	±	428.0	133.7	122.1	±	13.0
	8	71	394.9	±	46.7	35.0	816.3	±	371.0	204.0	125.8	±	9.7
	9												
	10												
	11												
	12												
.2	1												
	2												
	3												
	4												
	5	88	584.5	±	52.9		2471.9	±	636.0		121.3	±	12.1
	6	534	565.8	±	58.5	-18.7	2377.5	±	764.8	-94.4	127.0	±	12.3
	7	1275	595.2	±	55.5	29.4	2853.6	±	838.5	476.1	131.4	±	13.2
	8	145	622.6	±	50.7	27.4	3265.3	±	904.8	411.7	131.8	±	12.0
	9	23	645.6	±	33.7	22.9	3648.3	±	649.2	383.0	134.6	±	9.1
	10												
	11												
	12												
.3	1												
	2												
	3												
	4												
	5	91	712.5	±	53.2		4510.8	±	1302.4		121.6	±	11.6
	6	192	713.1	±	59.7	0.6	4690.9	±	1303.6	180.2	126.7	±	15.8
	7	239	722.9	±	60.6	9.8	5021.8	±	1431.6	330.8	129.9	±	13.0
	8	16	760.8	±	47.4	37.9	5763.1	±	1327.3	741.4	128.7	±	7.9
	9												
	10												
	11												
	12												
.4	1												
	2												
	3												
	4												
	5												
	6												
	7	10	862.4	±	47.9		8351.0	±	1505.6	8351.0	128.8	±	6.4
	8												
	9												
	10												
	11												
	12												

Appendix (continued)

Table 8. Fork length, body weight, and condition factor of maturing chinook salmon.

Table 8. Fork length, body weight, and condition factor of maturing chinook salmon.													
Ocean Age	Month	Fork Length				Body Weight				Condition Factor			
		No	Mean	±	S.D.	FL/dt	Mean	±	S.D.	BW/dt	Mean	±	S.D.
.2	1												
	2												
	3												
	4												
	5	33	631.0	±	66.3		3780.3	±	1452.5		144.6	±	16.6
	6	53	601.9	±	52.0	-29.1	3204.0	±	911.5	-576.3	143.4	±	11.9
	7	27	598.5	±	65.7	-3.4	3038.5	±	961.3	-165.4	137.2	±	17.0
	8												
	9												
	10												
	11												
	12												
.3	1												
	2												
	3												
	4												
	5	22	795.6	±	107.4		7894.1	±	3455.9		147.9	±	17.3
	6	40	813.9	±	105.7	18.4	8264.5	±	3498.1	370.4	144.2	±	14.4
	7												
	8												
	9												
	10												
	11												
	12												
.4	1												
	2												
	3												
	4												
	5	21	960.9	±	70.5		12819.5	±	2836.9		142.8	±	11.5
	6	32	943.8	±	81.1	-17.1	13378.1	±	3830.7	558.6	155.6	±	21.9
	7												
	8												
	9												
	10												
	11												
	12												

Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus keta*) before and after a major regime shift in the North Pacific Ocean

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Helle, J.H., and M.S. Hoffman. 1998. Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus keta*) before and after a major regime shift in the North Pacific Ocean. N. Pac. Anadr. Fish Comm. Bull. No. 1: 81-89

Changes in size and age at maturity of chum salmon (*Oncorhynchus keta*) were monitored for two locations in North America. Chum salmon spawners returning to Fish Creek, southeastern Alaska, were sampled yearly from 1972 through 1996. Spawners returning to the Quilcene National Fish Hatchery in Hood Canal, Washington, were sampled yearly from 1973 through 1996. Size at maturity of both populations declined significantly from about 1980 to the mid-1990s. Age at maturity increased during this time. These changes were associated with a major ocean climate regime shift in the North Pacific Ocean that occurred in 1976–77. Population abundance of chum salmon increased greatly after the regime shift, especially in Asia. Similar changes in size and age at maturity occurred in Asian chum salmon; because the range of North American and Asian chum salmon overlaps on the high seas, these changes are discussed in relation to possible density-dependent population factors. Since the mid-1990s, size at maturity and population abundance have increased, possibly indicating another climate change in the North Pacific Ocean.



INTRODUCTION

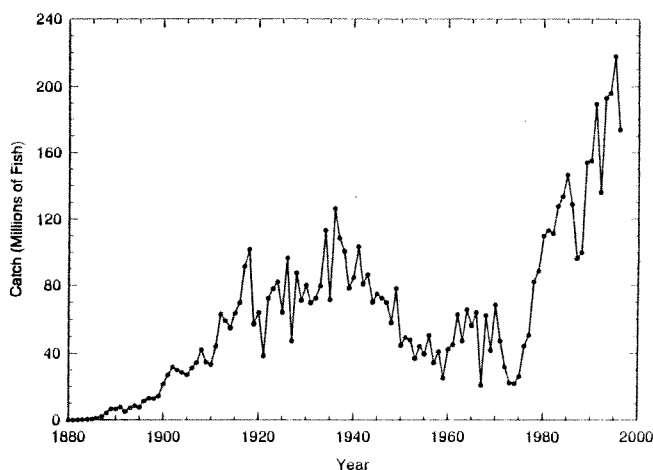
A major change in ocean climate (regime shift) occurred in the North Pacific Ocean during 1976–77 and has persisted into the mid-1990s (Graham 1994; McLain 1984; Miller et al. 1994; Trenberth 1990; Trenberth and Hurrell 1994). Salmon abundance in Alaska increased greatly after the regime shift (Fig. 1). However, mean size declined and the age at maturity increased in most populations of salmon in North America after the regime shift (Bigler et al. 1996; Helle and Hoffman 1995).

Helle and Hoffman (1995) monitored changes in size and age at maturity of chum salmon (*Oncorhynchus keta*) from two locations in North America between 1972 and 1992, before and after the regime shift. One population spawned in Fish Creek, a tributary of the Salmon River, which enters the ocean at the head of Portland Canal in southern southeast Alaska. The other population returned to the Quilcene National Fish Hatchery, in western Washington near Quilcene. Both populations declined significantly in size at maturity starting about 1980. Four-year-old males declined in weight by about 46% between the early 1970s and the early 1990s. As growth decreased during these years, mean age at

maturity increased. This information was reported for the years 1972–92 (Helle and Hoffman 1995).

We have collected four more years (1993–96) of data on age and size of maturity of these two populations. These data have been added to the 1972–92 data base and are discussed in this paper.

Fig. 1 Catch of all species of salmon in Alaska from 1880 through 1996. (Data from Alaska Department of Fish and Game).



STUDY AREA

Fish Creek

Fish Creek flows into the Salmon River near Hyder, Alaska, about 5 km upstream from the ocean (Portland Canal) in southern southeast Alaska (Fig. 2). The creek produces very large chum salmon (Helle 1984). A detailed description of the area is in Helle and Hoffman (1995).

Quilcene National Fish Hatchery

Quilcene National Fish Hatchery is next to the Quilcene River about 5 km from the ocean (Hood Canal) near Quilcene, Washington (Fig. 2). This salmon hatchery is operated by the U.S. Fish and Wildlife Service, Department of the Interior.

METHODS

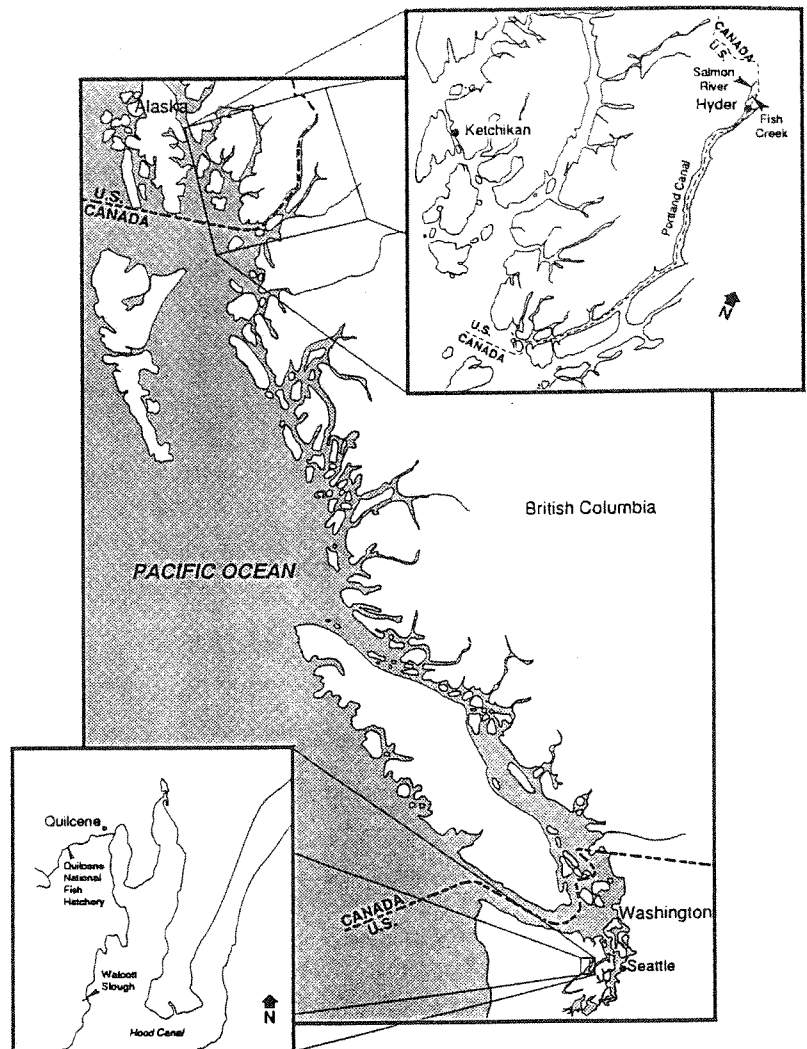
Fish Creek

Spawning chum salmon were counted several times during each spawning season by observers walking along the stream bank. Most of the counts were made by the senior author. Spawners were also estimated periodically during the season by Alaska Department of Fish and Game (ADF&G) biologists from low-flying fixed-wing aircraft. A counting fence (weir) was also operated at the mouth of Fish Creek between 1991 and 1995 by ADF&G personnel.

Scales and length measurements were taken from spawned dead chum salmon. Scales from chum salmon do not usually show excessive resorption on the edge and can be used for ageing (Helle 1979; Oakley 1966). The age composition of chum salmon changes during the season (Helle 1979). Therefore, to make consistent age-specific comparisons between years, samples were taken during the approximate peak of the spawning run—mid to late August (Table 1). The target sample size was a minimum of 100 males and 100 females, which was attained in most years.

One scale was removed from the left side of each fish with a forceps and placed onto a gummed card. The scale was taken from the area about four rows above the lateral line immediately below the posterior insertion of the dorsal fin. Later, a plastic impression of the gummed card was made in the laboratory

Fig. 2 Location of Fish Creek at the head of Portland Canal, near Hyder, Alaska, and of Quilcene National Fish Hatchery and Walcott Slough, near Quilcene, Washington.



(Arnold 1951). Age was determined from a projected image of the scale impression magnified 80 diameters. All fish were aged by the senior author. Age designation is by the method of Gilbert and Rich (1927) minus the subscript, which is always 1 in chum salmon.

Length of each fish was measured with a caliper to the nearest 1 mm with the fish flat on the ground. Length was measured from the middle of the eye to the end of the hypural plate. All lengths were measured by the senior author for continuity from year to year.

Mean lengths of 4-year-old chum salmon are plotted with 95% confidence intervals. Small, non-overlapping confidence intervals of the means between years usually indicate significant differences (Simpson et al. 1960).

A more detailed description of the sampling

Table 1. Number of chum salmon by date and sex, sampled at Fish Creek and Quilcene National Fish Hatchery 1972-96. Dash indicates no data.

Year	Fish Creek			Quilcene		
	Date	Males (no.)	Females (no.)	Date	Males (no.)	Females (no.)
1972	Aug. 17	90	100	—	—	—
1973	Aug. 16	108	89	Dec. 10	78	69
1974	Aug. 22	127	105	Dec. 9	110	124
1975	Aug. 20	100	99	Dec. 10	129	79
1976	Aug. 24	163	181	Dec. 8	150	109
1977	Aug. 24	99	103	Dec. 9	108	90
1978	Aug. 29	117	109	Dec. 11	118	103
1979	Aug. 29	131	133	Dec. 10	80	46
1980	Sep. 7	112	117	Dec. 15, 17	53	152
1981	Aug. 26	103	127	Dec. 8, 10	71	134
1982	Aug. 24	150	150	Dec. 6	106	98
1983	Aug. 9, 10	94	103	Dec. 19	132	154
1984	Aug. 23	146	178	Dec. 10	139	139
1985	Aug. 27	167	130	Dec. 10	124	82
1986	Aug. 14, 15	134	145	Dec. 10	168	196
1987	Aug. 27	160	152	Dec. 10	75	150
1988	Aug. 29	206	190	Dec. 5	152	154
1989	Aug. 26	152	160	Dec. 4	88	51
1990	Aug. 19	115	128	Dec. 5	184	89
1991	Aug. 23-29	47	45	Dec. 16	30	25
1992	Aug. 25	158	125	Dec. 7	99	36
1993	Aug. 17	144	135	Dec. 7	155	128
1994	Aug. 9	162	148	Dec. 15	160	121
1995	Aug. 1, 17	237	235	Dec. 12	138	156
1996	Aug. 15	67	126	Dec. 10	144	144

methods is in Helle and Hoffman (1995).

Quilcene National Fish Hatchery

Chum salmon were captured in a weir-trap as they returned to the hatchery facilities. Before 1985, fry were released at Walcott Slough, a small, spring-fed intertidal stream near Brinnon, about 16 km south of the hatchery. Adults returned to Walcott Slough. In the early 1980s, fry were also released at the hatchery on the Quilcene River and in 1985 no more fry were released at Walcott Slough, due to a change in fishery management plans (see Helle and Hoffman 1995).

Scale samples and length measurements were taken from chum salmon used for gametes for the hatchery. Sample sizes, scale samples, and length measurements were collected as described for Fish Creek. Except for 1973, all fish were measured by the senior author for year-to-year continuity. All fish were aged by the senior author. Detailed descriptions of the sampling methods are in Helle and Hoffman (1995).

RESULTS

Abundance of Spawners

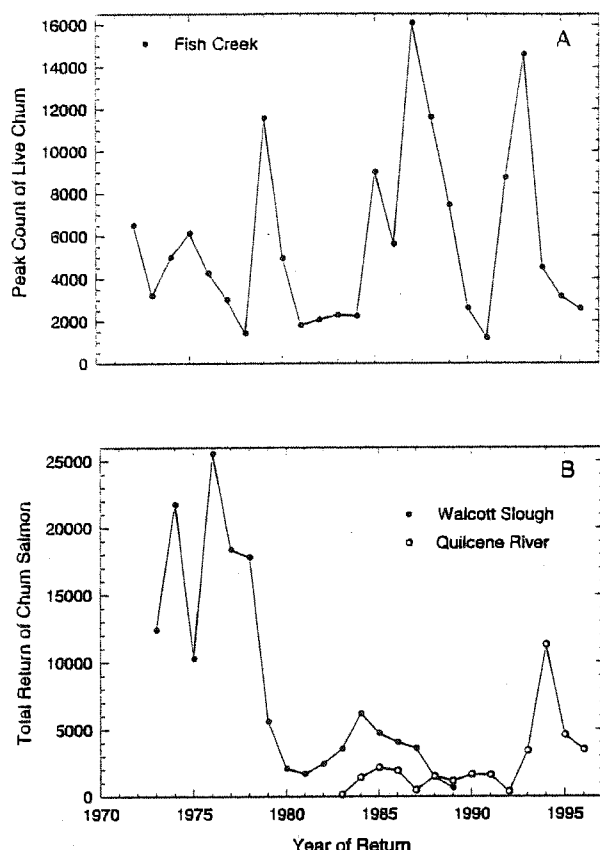
Chum salmon return from the ocean to spawn in Fish Creek from late June to November. Peak numbers of fish are usually in the stream during mid- to late August. Yearly peak counts of chum salmon spawners in Fish Creek vary greatly (Fig. 3a).

From 1991 through 1995, ADF&G operated a weir near the mouth of Fish Creek to obtain a total count of the chum salmon entering the stream. A comparison of the weir counts with foot-survey counts during the 5 years shows a significant positive relationship (Fig. 4).

Chum salmon return from the ocean to the Quilcene National Fish Hatchery facilities from late November through December. A remnant summer run also returns to spawn in the Quilcene River in August. Only the late chum salmon were sampled for abundance, age, and size in this study.

A planned reduction in the number of releases and eventual cessation of chum salmon fry released at Walcott Slough is evident from the declining adult returns from 1979 through 1989 (Fig. 3b). Returns to the hatchery on the Quilcene River have been increasing slowly in recent years since consolidating fry releases at the hatchery on the Quilcene River.

Fig. 3 Changes in the peak count of live chum salmon spawners in Fish Creek, 1972-96, and the total return of chum salmon spawners to Quilcene National Fish Hatchery facilities at Walcott Slough and Quilcene River, 1973-96.



Age of Spawners

Age-4 chum salmon are the most abundant age group in most years at Fish Creek; however, age-5 fish have generally been increasing in abundance since the mid-1980s (Fig. 5). Age-6 fish were absent in the early years of this study, but they have been increasing in frequency in recent years.

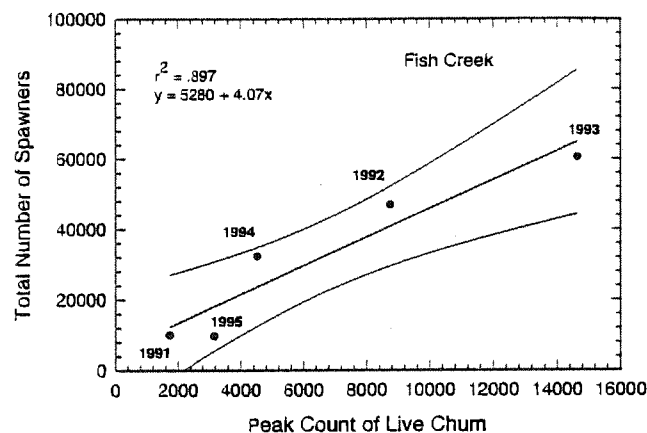
At Quilcene National Fish Hatchery, age-4 and -3 fish are the predominant age groups (Fig. 5). However, in general the fish have become older since the mid-1980s.

Size of Spawners

Generally, at both Fish Creek and Quilcene older fish are longer in any given year (Fig. 6). Age-4 and -5 fish are the dominant age groups at Fish Creek and generally decreased in length from 1980 through 1994. In the same year, Quilcene age-4 fish are longer than age-3 fish. Age-5 fish were abundant at Quilcene only in later years.

Age-4 chum salmon were usually the most

Fig. 4 Comparison of the relation between the peak count of live spawners and the total number (weir count) of chum salmon spawners in Fish Creek, 1991-95. Weir count data from J. Koerner and B. van Alen, Alaska Department of Fish and Game, Juneau.



abundant age group during the study. At Fish Creek the mean length of age-4 fish declined from about 1983 through 1987 (Fig. 7). Mean length increased significantly (in males) in 1988, then declined again through 1994. In 1995 and 1996, mean length increased significantly at Fish Creek for both sexes. Mean length of age-4 Quilcene chum salmon generally declined from the mid-1980s through 1993, then increased in 1994, 1995, and 1996.

DISCUSSION

Chum salmon returning to Fish Creek are intercepted in commercial fisheries in southern southeast Alaska and northern British Columbia. Some of these fisheries target chum salmon, but most of the fisheries in both areas target pink (*O. gorbuscha*) or sockeye (*O. nerka*) salmon, and chum salmon are captured incidentally. Catches of chum salmon (and pink and sockeye salmon) have generally increased in southern southeast Alaska since the early 1980s (Fig. 8). Catches of chum and sockeye salmon in northern British Columbia have also been large in recent years. Catches of chum salmon in Puget Sound, Washington, have generally increased since the early 1980s (Fig. 9).

Exploitation rates of chum salmon returning to Fish Creek and Quilcene National Fish Hatchery are not known precisely and certainly vary from year to year (see Helle and Hoffman 1995). Therefore, the escapements in each year may not reflect the same proportion of the actual total production of chum salmon in each year. Escapement of chum salmon in Fish Creek varied greatly during this study. However, some large escapements have occurred between 1979 and 1993 (Fig. 3); the largest had a

Fig. 5 Percent age composition in year of return of age-3, -4, -5, and -6 male and female chum salmon at Fish Creek and age-3, -4, and -5 at Quilcene National Fish Hatchery. Data for ages 3, 4, and 5 smoothed by a 3-year moving average with equal weights.

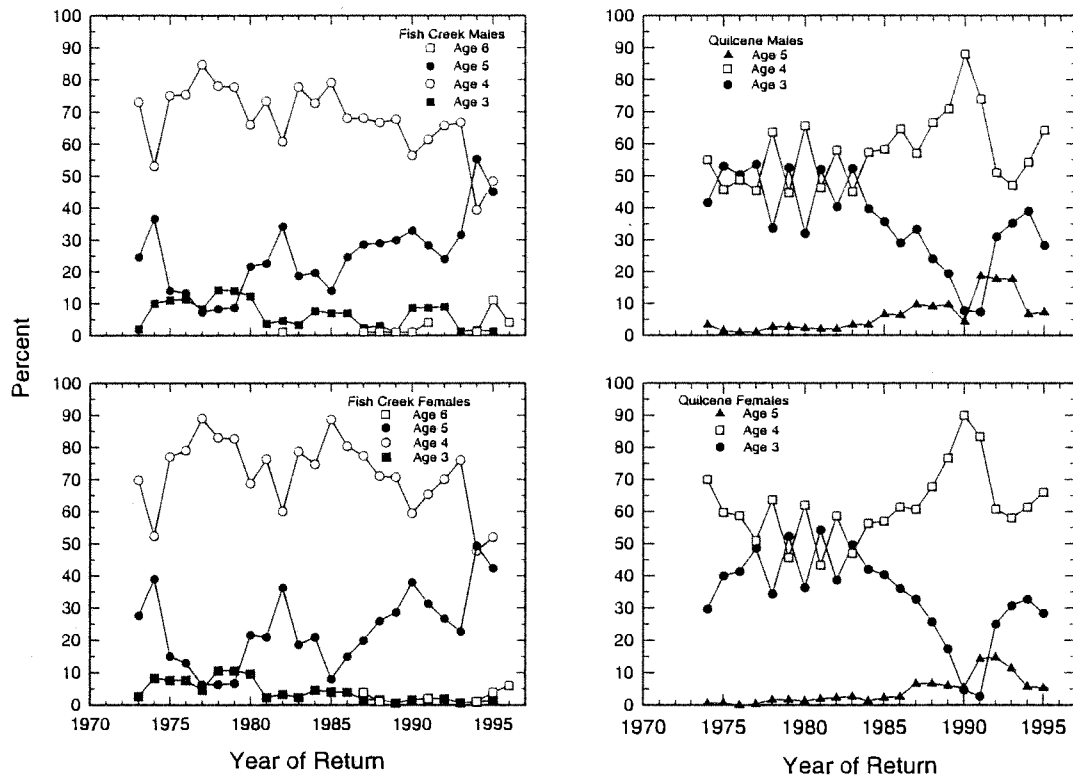


Fig. 6 Mean length of age-3, -4, and -5 chum salmon spawners at Fish Creek, and age-3 and -4 spawners at Quilcene National Fish Hatchery. Means were not calculated for sample sizes fewer than four fish. Dotted lines connect means when data for intervening years are based on $N < 4$.

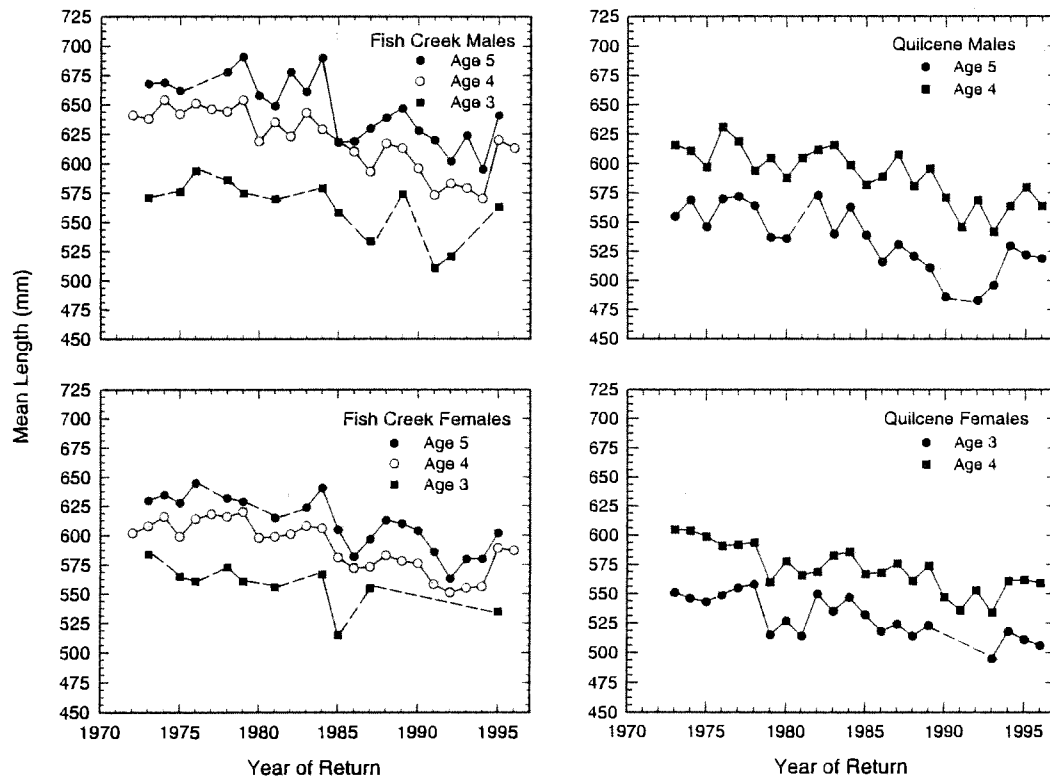


Fig. 7 Mean length and 95% confidence interval for age-4 male and female chum salmon spawners at Fish Creek, 1972-96, and at Quilcene National Fish Hatchery, 1973-96.

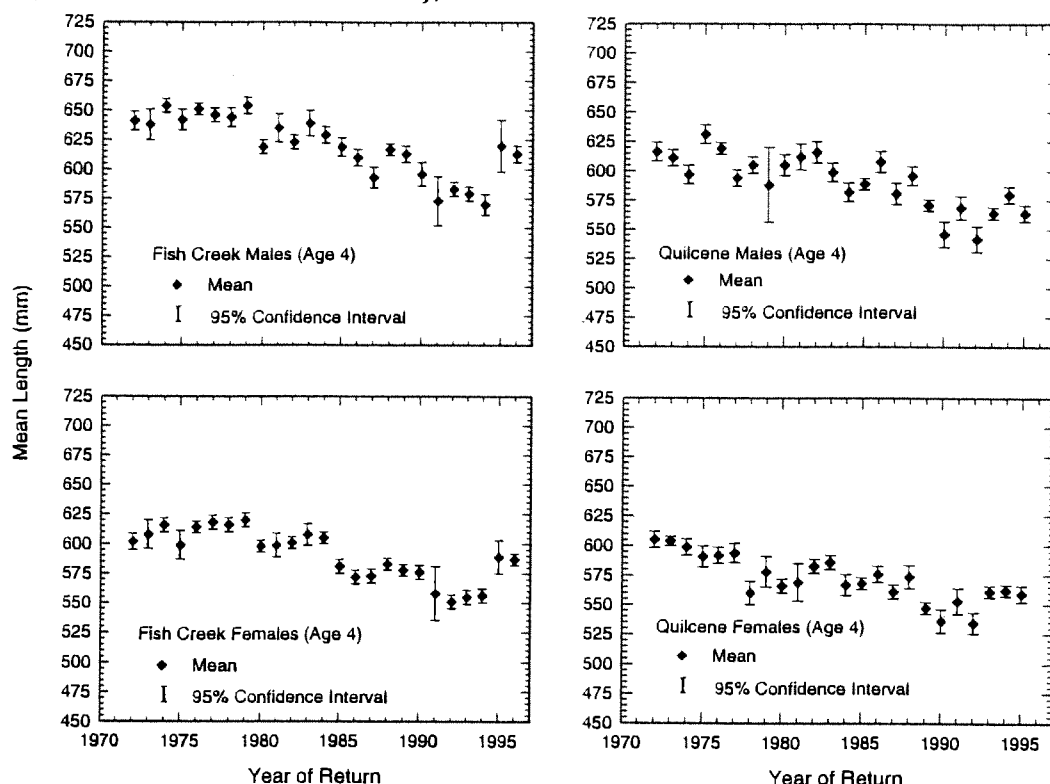


Fig. 8 Commercial catch of pink, sockeye, and chum salmon in southern southeast Alaska and northern British Columbia, 1972-96. Data from Northern Boundary Technical Committee (1997).

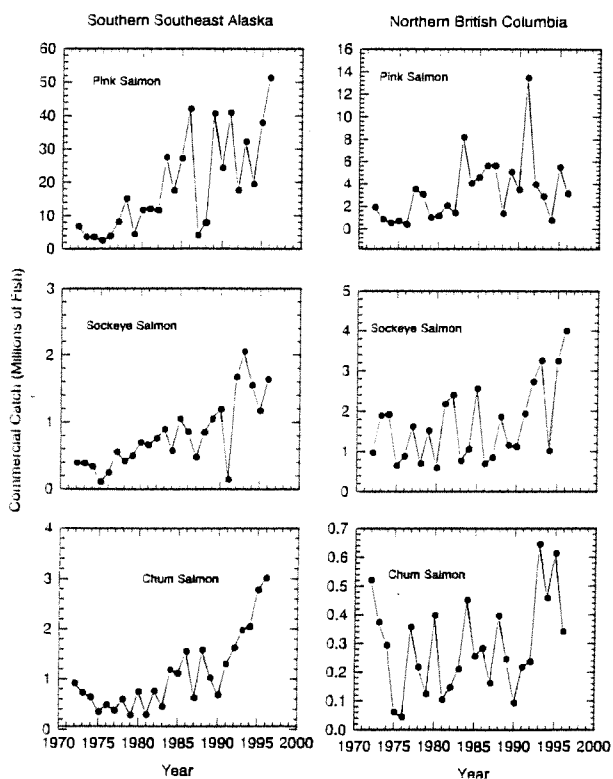
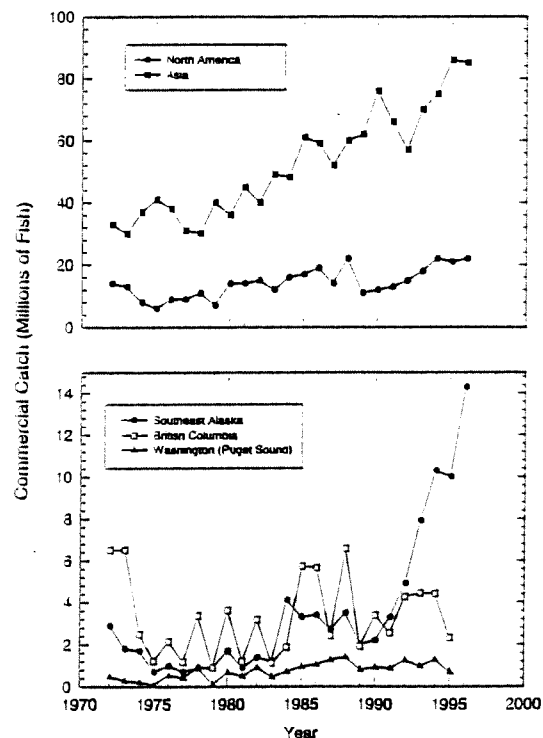


Fig. 9 Commercial catch of chum salmon in North America and Asia, southeastern Alaska, British Columbia, and Washington (Puget Sound). Data from D. Rogers, Fisheries Research Institute, University of Washington, Seattle; B. Snyder, Canada Department of Fisheries and Oceans, Vancouver; and J. Ames, Washington Department of Fisheries, Olympia.



peak live count of about 16,000 spawners in 1987. Using the inverse regression method (Fig. 4), the total escapement of chum salmon in 1987 was estimated to be about 70,700 fish (see Aitchison and Dunsmore, 1975). Considering the variation within the data, this method lets us estimate the relation between peak live counts and the total escapement for each year at Fish Creek. The returns of chum salmon to the Quilcene National Fish Hatchery do not reflect the abundance of chum salmon returning to Puget Sound (Figs. 3, 9). Hatchery output was modified due to fishery management concerns (Helle and Hoffman 1995). Escapements to Fish Creek and Quilcene National Fish Hatchery vary greatly; nevertheless, the overall abundance of chum salmon in North America, as reflected in the catches, has generally increased during the past 15 years (Fig. 9).

Anomalous cold winters in the North Pacific Ocean (1971–75) preceded the regime shift in 1976–77 (McLain and Favorite 1976). Salmon catches in Alaska declined immediately after these cold winters, followed by a generally increasing trend in catches from the late 1970s into the late 1990s (Fig. 1). The regime shift resulted in climate and oceanographic conditions that were highly favorable for salmon survival (Freeland 1990; McLain 1984; Miller et al. 1994; Pearcy 1992; Tabata 1984, 1989). Increasing catches of chum salmon in both North America and Asia (Fig. 9) and general increases in most other species of salmon in northern British Columbia and Alaska occurred after the regime shift in the North Pacific Ocean in 1976–77 (Beamish 1993; Beamish and Bouillon 1993; Hare and Francis 1995).

Along with the general increases in abundance, age at maturity has generally increased (Fig. 5) and the length at age has decreased (Fig. 6) at both Fish Creek and Quilcene National Fish Hatchery through the early 1990s (Helle and Hoffman 1995). These same trends in abundance, age at maturity, and size of chum salmon in North America have also been described in Asia. Kaeriyama (1989, 1996) and Ishida et al. (1993) report these age and size changes in Asian chum salmon stocks and suggest these changes may be due to density-dependent population factors in the ocean. Asian catches of chum salmon have increased since the late 1970s (Fig. 9). These increasing catches in Asia are predominately from artificial production facilities in Japan (see Pearcy 1992).

The distribution of both North American and Asian chum salmon overlaps extensively on the high seas (Manzer et al. 1965; Myers et al. 1996; Neave et al. 1976; Ogura and Ito 1994; Salo 1991). This overlap in forage range and the increased abundance, decline in size, and older age at maturity of chum salmon from both sides of the Pacific Ocean suggest that density-dependent population factors may be

affecting both North American and Asian stocks of chum salmon.

Size-dependent and density-dependent effects on growth and survival of salmon are not understood clearly (Peterman 1978, 1987; Peterman and Wong 1984; Ricker 1962, 1976). Evidence for density-dependent population effects on growth of salmon in the ocean has been accumulating in recent years (e.g., Bigler et al. 1996; Helle and Hoffman 1995; Ishida et al. 1993; Kaeriyama 1996; Peterman 1984; Rogers 1980). Also, size of parents may influence the survival of their offspring (Forbes and Peterman 1994; Helle 1989; Vladimirov 1973). Clearly, the ocean regime change of 1976–77 influenced the abundance and size of salmon populations in the North Pacific Ocean (Figs. 1, 7–9). Most species of salmon in the North Pacific Ocean declined in length soon after the abundance started increasing, about 1980, through the early 1990s (Bigler et al. 1996; Helle and Hoffman 1995; Ishida et al. 1993; Kaeriyama 1989, 1996; Ricker 1995).

Mean size at maturity at Fish Creek remained small in 1993 and 1994; however, in 1995 and 1996 mean length increased significantly. At Quilcene River the mean length of chum salmon dropped in 1993, but increased significantly in 1994, 1995, and 1996. If density-dependent population factors were influencing size at maturity in 1995 and 1996, the mean length should have continued to decrease because catches in southeastern Alaska and Asia increased (Fig. 9). Instead, mean length increased significantly.

Chum salmon may be indicators of ocean carrying capacity because they respond to competition by changing their size and age at maturity (Salo 1988). We suggest that size at maturity of chum salmon may be a surrogate for ocean conditions. Increases in size at maturity seen in 1995 and 1996 may signal another ocean regime shift and a change in the steep declines in length that started about 1980.

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The many people that assisted in collecting samples and counting spawners during 1972–92 were acknowledged in Helle and Hoffman (1995). During the 1993–96 seasons the following assistance is gratefully acknowledged: Steven Hoffman, Jerrold Koerner, and Kathleen Wendt from the Alaska Department of Fish and Game, Ketchikan; Jerome Pella, Auke Bay Laboratory, helped with the field studies at Fish Creek and gave advice on the use of regression analyses; Ellen Martinson, Auke Bay Laboratory, helped in scale preparations; and Larry Telles and Ron Wong, U.S. Fish and Wildlife Service, provided data on chum salmon returns to the Quilcene National Fish Hatchery.

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Dynamics of Chum Salmon, *Oncorhynchus keta*, Populations Released from Hokkaido, Japan

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Kaeriyama, M. 1998. Dynamics of chum salmon, *Oncorhynchus keta*, populations released from Hokkaido, Japan. N. Pac. Anadr. Fish Comm. Bull. No. 1: 90-102

Body size of Hokkaido chum salmon (*Oncorhynchus keta*) at maturity showed a significant decreasing trend from the late 1970s to the early 1980s and has remained relatively constant since the late 1980s. A significant negative relationship between population abundance and fork length was observed. In Hokkaido chum salmon population, average age at maturity in cohorts increased from 3.7 years in the 1972 cohort to over 4 years in cohorts after 1980. A significant positive relationship between population abundance and average age at maturity of cohorts was observed in the Hokkaido chum salmon population. Growth analysis back-calculated from scales showed that a growth reduction occurred after the second year, especially in the third year of oceanic life of Hokkaido chum salmon. The synchronous decreasing body size and increasing age at maturity of Hokkaido chum salmon occurred in face of rising marine survival rates and ocean conditions favorable for growth. This suggested that reduced growth and increasing age at maturity was due to density dependent intraspecific competition and high abundance of chum salmon on the North Pacific Ocean.



INTRODUCTION

In the last two decades, the population size of chum salmon (*O. keta*) released from Japan has increased significantly (Kaeriyama 1989). Since the 1980s, the biomass of Pacific salmon has been increasing throughout the North Pacific Ocean. According to FAO fisheries statistics the annual catch of Pacific salmon in the area averaged 0.72 million tons during 1981-1993, and in 1995 exceeded 0.95 million tons, which surpassed the previous historical high. Biomass of chum, sockeye (*O. nerka*), and pink salmon (*O. gorbuscha*) is increasing in the North Pacific Ocean (Fig. 1). This increase is thought to have coincided with favorable oceanic conditions and successful artificial enhancement programs (Beamish and Bouillon 1993; Brodeur and Ware 1992; Kaeriyama 1996; Pearcy 1992).

However, with this increase in population abundance, individual growth reduction has been observed for many Pacific salmon populations, such as Bristol Bay sockeye (Rogers and Ruggerone 1993), Japanese chum (Kaeriyama 1989, 1996; Ishida et al. 1993), and North American pink salmon (Bigler et al. 1996). These findings suggest that salmon research from a view point of population ecology is very important in order to carry out the stock management and effective artificial enhancement program of

Pacific salmon.

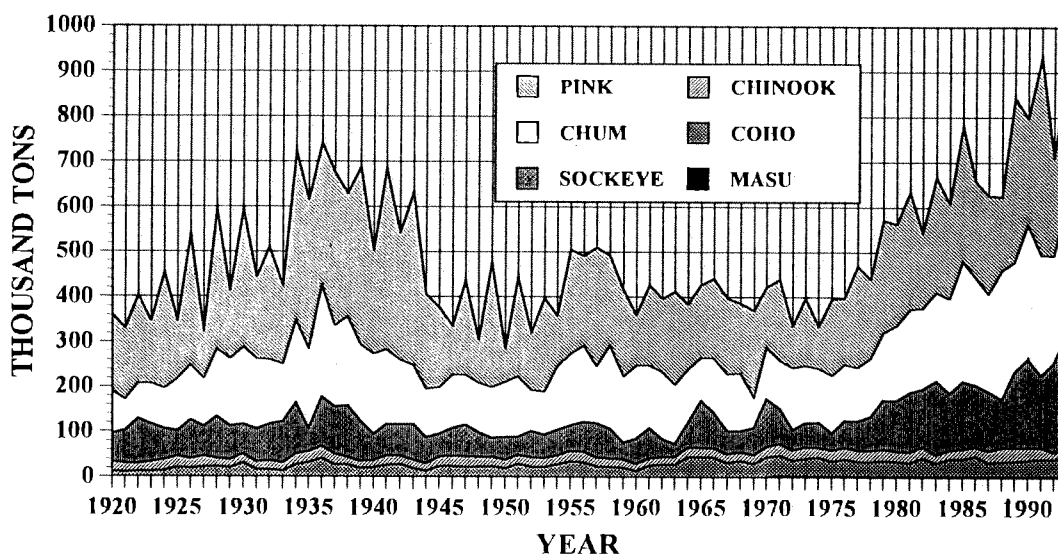
The purpose of this paper is to examine changes in body size, age at maturity, and growth pattern, and to clarify population-density-dependent effects as intraspecific competition on Hokkaido chum salmon for the elucidation of factors affecting the biological characteristics of Pacific salmon populations.

MATERIALS AND METHODS

Fork length data of female adults returning to 11 rivers in Hokkaido from 1953 to 1995 were used to quantify change in body size at maturity of chum salmon. Condition factors (CF) were calculated from fork length (L, cm) and body weight (W, g) of male adult chum salmon returning to Ishikari River; $CF = W/L^3 \times 1000$. These sample sizes per age were more than 10 individuals by sex in each river population. Especially, the sample size for age 4 was more than 60 individuals. The following data were excepted from analysis: (1) cohorts which sample size was less than 10 individuals, and (2) cohorts indicating more than 10 % in coefficient of variations of fork length and body weight.

Scales of chum salmon collected in Ishikari River during 1976-1995 were measured with a scale image processor (Ratoc System Engineering Co.) to provide an index of growth during each year at sea. Distances

Fig. 1 Change in annual catch of Pacific salmon in the North Pacific Ocean during 1920-1993 (from FAO Fisheries Statistics). Statistics for mariculture and aquaculture production are excepted.



and number of circuli from the focus to the inner edges of individual annuli of approximately 100 scales from each age group by year were measured to the nearest one micrometer along the longest axis.

Fecundity and egg size of age-4 female chum salmon (78 individuals) were examined in the Ishikari River from 1986 to 1995. Fecundity was counted as total number of eggs per female, and egg size was determined from volume of water-hardened eggs with excess surface moisture removed as follows: $D = 20(4V/(3\pi N))^{1/3}$, where D is egg diameter (mm), V and N are volume (ml) and number of total alive water-hardened eggs, respectively (Watanabe 1955).

Data on sea surface temperature (SST) were provided as the monthly mean global sea surface temperature data of two by two degree grid by marine division of Japan Meteorological Agency. SSTs were examined in western (48-50°N, 164-166°E), central (48-50°N, 179°E-179°W), and eastern (Gulf of Alaska; 48-50°N, 144-146°W) areas of the Subarctic North Pacific Ocean during salmon growth period (from May to October).

Exponential smoothing analysis (SPSS Inc.) was used to estimate the trend of annual change in fork length of Ishikari River adult chum salmon. Alpha values were 0.4 in age-3, 0.5 in age-4, and 0.4 in age-5. Analysis of variance (ANOVA) and nonparametric Mann-Whitney test were used to compare slopes in regression lines between population size and fork length among age groups and breeding characters of age-4 female between 1940-1943 and 1986-1995 in Ishikari River adult chum salmon respectively.

RESULTS

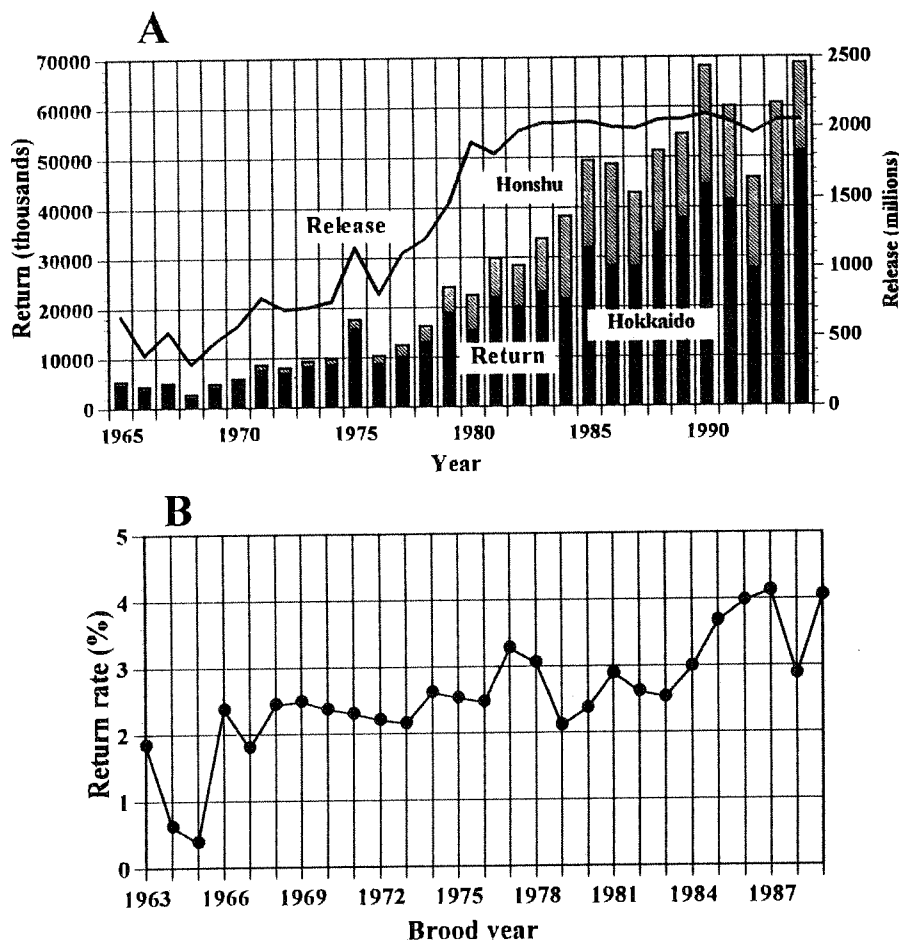
1. Changes in production trends and return rate of chum salmon in Japan

The number of adult chum salmon returning to Japan from 1900 through 1970 averaged about 3 million individuals, ranging from 1 to 5 million individuals. Since the late 1970s, adult returns have increased to more than 50 million individuals until the late 1980s, and reached 77 million individuals (57 million individuals in Hokkaido and 20 million individuals in Honshu) in 1995 (Fig. 2A). This population size accounted for 70-80% to all chum salmon catch in the North Pacific Ocean. The number of juveniles released increased from 800 million individuals in the early 1970s to 2 billion individuals in 1982, and has been limited to about 2 billion individuals since the early 1980s (Fig. 2A).

In the Hokkaido chum salmon population, return rate (adult returns as a percentage of juveniles released) for a brood-year population had fluctuated around 1% until 1965. The return rate has increased to above 2% after 1966, attained more than 3% after 1984, and has tended to increase (Fig. 2B). Therefore, the considerable increase in adult return since the 1980s was due to increase in survival of released juveniles.

The rise in the return rate was the effect of successful artificial enhancement programs such as the technology of release after feeding (Kobayashi 1980; Mayama 1985; Kaeriyama 1989) as well as influence of favorable oceanic conditions in the North Pacific Ocean. For instance, significant positive relationship between the proportion of reared fish to

Fig. 2 Annual changes in numbers of adult returns, juvenile releases (A), and return rate (B) of chum salmon in Japan during 1965-1995.



total juvenile released and the return rate was observed in the Hokkaido salmon population ($r=0.799$, $P<0.001$; Fig. 3A). Change in return rate was similar to that in average body weight of juvenile released ($r=0.665$, $P<0.05$; Fig. 3B).

2. Body size and average age at maturity of Hokkaido chum salmon

Figure 4 illustrates annual changes in mean fork length at maturity of age-3, 4, and 5 female chum salmon returning to the Ishikari River in 1953-1995. A decrease in body size of age 3-5 chum salmon occurred after the late 1970s coincident with increases in abundance. The mean fork length of age 3-5 female chum salmon decreased from 1979 to 1984. For instance, the average fork length of age-4 female declined by about 9 % from the late 1970s (687 mm) to the early 1980s (638 mm). Exponential smoothing analysis demonstrates that fork length has remained stable and small size since the late 1980s (Fig. 4).

A significant negative relationship between

population size of Hokkaido chum salmon and mean fork length of adult chum salmon returning to Ishikari River was observed ($r<-0.6$, $P<0.001$; Fig. 5). Negative linear relationships between population size and fork length were observed in all river populations examined in Hokkaido (Table 1). Averages and standard deviations of slopes (b) in regression lines indicated -1.08 ± 0.28 mm / age-3 million fish, -1.53 ± 0.25 mm / age-4 million fish, and -1.54 ± 0.28 mm / age-5 million fish. Slopes for age-4 and -5 were significantly more negative than that of age-3 fish (t-test; $P<0.001$).

Condition factor of male adult chum salmon returning to the Ishikari River did not change annually after the 1970s, although it fluctuated in the 1950s and the 1960s (Fig. 6). If condition factor is used as indicator of fatness, health or well-being of a population (Cone 1989), then the stable condition factor observed for Hokkaido chum salmon since the 1980s indicates healthiness of the population.

The age composition of a brood-year population

Fig. 3 Relationships between rearing rate (A) or body size (B) of juvenile released and return rate in Hokkaido chum salmon population. Rearing rate indicates percentage of reared fish to total juvenile released. Return rate is the percentage of adult returns to juveniles released.

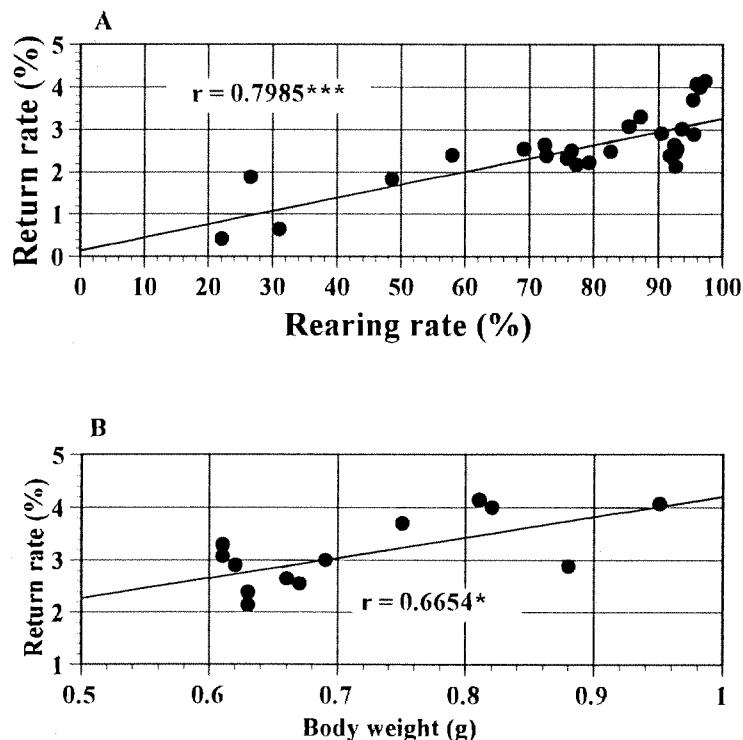


Fig. 4 Annual change in average fork length of female adult chum salmon returning to the Ishikari River in 1953-1995. Lines indicate result of exponential smoothing analysis. Alpha values were 0.4 in age -3, 0.5 in age -4, and 0.4 in age -5.

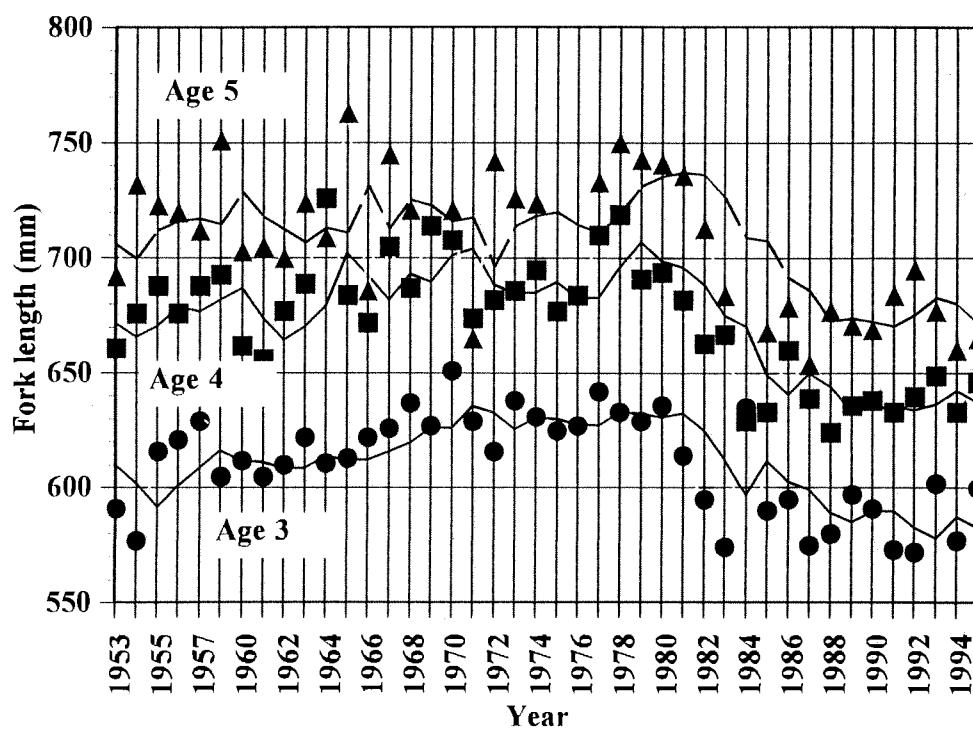


Fig. 5 Relationship between population size of Hokkaido chum salmon and average fork length of female adult chum salmon returning to the Ishikari River in 1953-1995. Age -3: $r = -0.5700$ ($P < 0.001$), Age -4: $r = -0.7145$ ($P < 0.001$), Age -5: $r = -0.6682$ ($P < 0.001$).

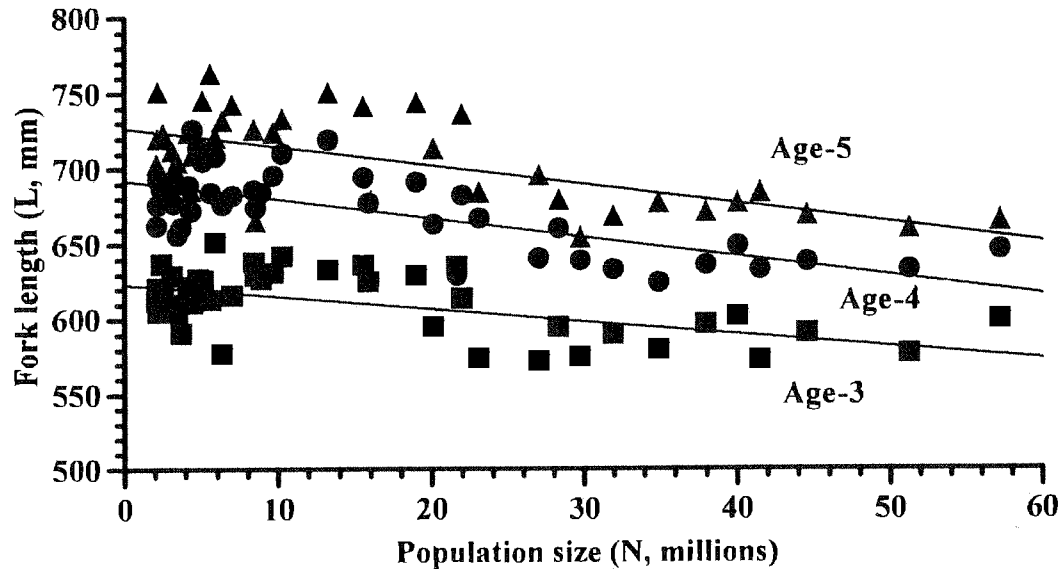
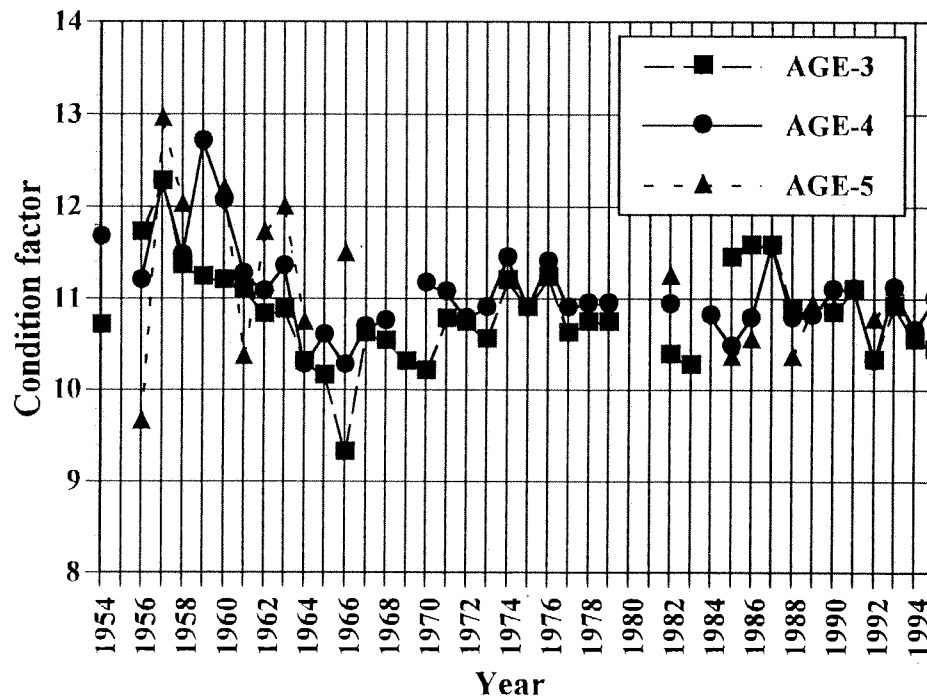


Table 1. Relationships between population size and average fork length of Hokkaido chum salmon populations. n = number of years of data, a = constant, b = slope, r = the correlation coefficient, and P = the probability that b=0 (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).

Area*	River	Age	n	a	b	r	P
OKS	Abashiri	3	32	620	-0.755	-0.4194	*
		4	32	689	-1.406	-0.7133	***
		5	31	715	-0.970	-0.4132	***
	Shari	3	21	632	-1.369	-0.6693	***
		4	21	707	-1.829	-0.8234	***
		5	19	744	-1.798	-0.7730	***
NMS	Shibetsu	3	25	643	-1.524	-0.6911	***
		4	25	703	-1.922	-0.8811	***
		5	23	741	-1.996	-0.8811	***
	Nishibetsu	3	30	644	-1.459	-0.7771	***
		4	36	706	-1.617	-0.8131	***
		5	36	743	-1.626	-0.7376	***
NEP	Tokachi	3	37	636	-0.755	-0.4157	*
		4	37	711	-1.204	-0.5504	***
		5	35	770	-1.740	-0.8359	***
	Kushiro	3	32	635	-1.006	-0.5506	***
		4	34	709	-1.475	-0.7583	***
		5	34	755	-1.649	-0.7456	***
NWP	Shizunai	3	30	629	-0.829	-0.4829	**
		4	34	709	-1.168	-0.6538	***
		5	32	752	-1.380	-0.6344	***
	Yurappu	3	31	653	-0.982	-0.4854	**
		4	31	736	-1.488	-0.7702	***
		5	30	773	-1.287	-0.6051	***
	Shiriuchi	3	31	659	-1.018	-0.6732	***
		4	31	733	-1.723	-0.8011	***
		5	31	772	-1.763	-0.8081	***
NJS	Ishikari	3	40	623	-0.822	-0.570	***
		4	42	693	-1.257	-0.7145	***
		5	40	728	-1.289	-0.6682	***
	Teshio	3	32	636	-1.313	-0.6097	***
		4	34	699	-1.761	-0.8022	***
		5	32	727	-1.471	-0.6242	***

*OKS: Okhotsk Sea area, NMS: Nemuro Strate area, NEP: Northeastern Pacific Ocean area, NWP: Northwestern Pacific Ocean area, NJS: North Japan Sea area.

Fig 6. Annual change in condition factor of male adult chum salmon returning to Ishikari River in 1954-1995.



has changed with recent large returns of Hokkaido chum salmon. The average age at maturity of a brood-year population was about 3.7 years until 1972, then increased gradually and exceeded 4 years since 1980 (Fig. 7A). A significant positive relationship between population size and average age of a population at maturity was observed ($r=0.909$, $P<0.001$; Fig. 7B). The increase in age at maturity was synchronous with the decrease in body size until the 1980 brood year. The Hokkaido chum salmon population continues to increase in age at return after 1980 although the fork length has remained stable at small size.

3. Changes in growth of body and scale

Figure 8 demonstrates normal and narrow types of scales from age-4 chum salmon returning to Hokkaido in 1993. Scale width in the third-year zone of narrow type is evidently smaller than those in other zones. Recently, narrow-type scales have been frequently observed in adult chum salmon returning to Japan. Changes in mean scale width by each year zone of age-4 adult female chum salmon returning to the Ishikari River (Fig. 9) indicated that 1) scale width of first-year zone remained stable (about 1.3 mm), 2) scale widths of second- and third-year zones were decreasing, 3) scale width of fourth-year zone

was increasing rather than stable since 1993.

Annual growth in fork length of Ishikari River adult chum salmon from 1976 to 1995 was estimated by back-calculation, estimating fork length as scale radius (S , μm) and fork length (L , mm): $L=0.0358(S-114)^{1.2406}+40$ (Fig. 10; $r^2=0.990$, $P<0.001$), where values "114" and "40" estimate focus radius (Fukuwaka and Kaeriyama, 1994) and fork length at squamation (Kaeriyama and Bunya, 1982). Growth differences between 1976-1980 (large-size period) and 1985-1995 (small-size period) adults showed (Table 2);

- 1) growth reduction in the third year was considerably higher than those in the other years,
- 2) growth reduction in the first year increased with increasing age, and
- 3) growth in the second year of age 4 fish and in the fourth year of age 5 fish was reduced 14.7 % and 18.2 % respectively.

These findings suggest that the growth reduction of Hokkaido chum salmon occurs after the second year of oceanic life, especially in the third year when they extend their migration to the eastern North Pacific Ocean and the Bering Sea (Ogura and Ito 1994).

Fig 7. Annual changes in population size and average age (A), and relationship between population size and average age (B) at maturity of Hokkaido chum salmon population during the brood years of 1963-1989

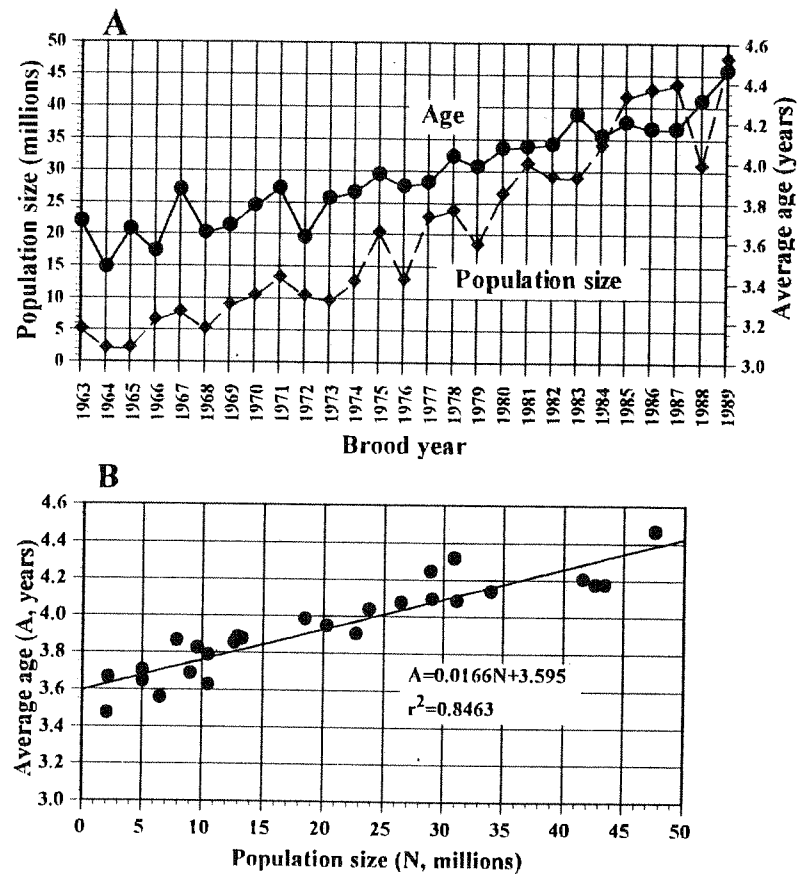


Fig 8. Photographs of normal (A) and narrow (B) types of scale from age-4 chum salmon returning to Hokkaido in 1993.



Fig. 9 Annual changes in mean scale width by each year zone of age-4 female adult chum salmon returning to Ishikari River in 1979-1995. W1: width of first year zone, W2: width of second year zone, W3: width of third year zone, W4: width of fourth year zone.

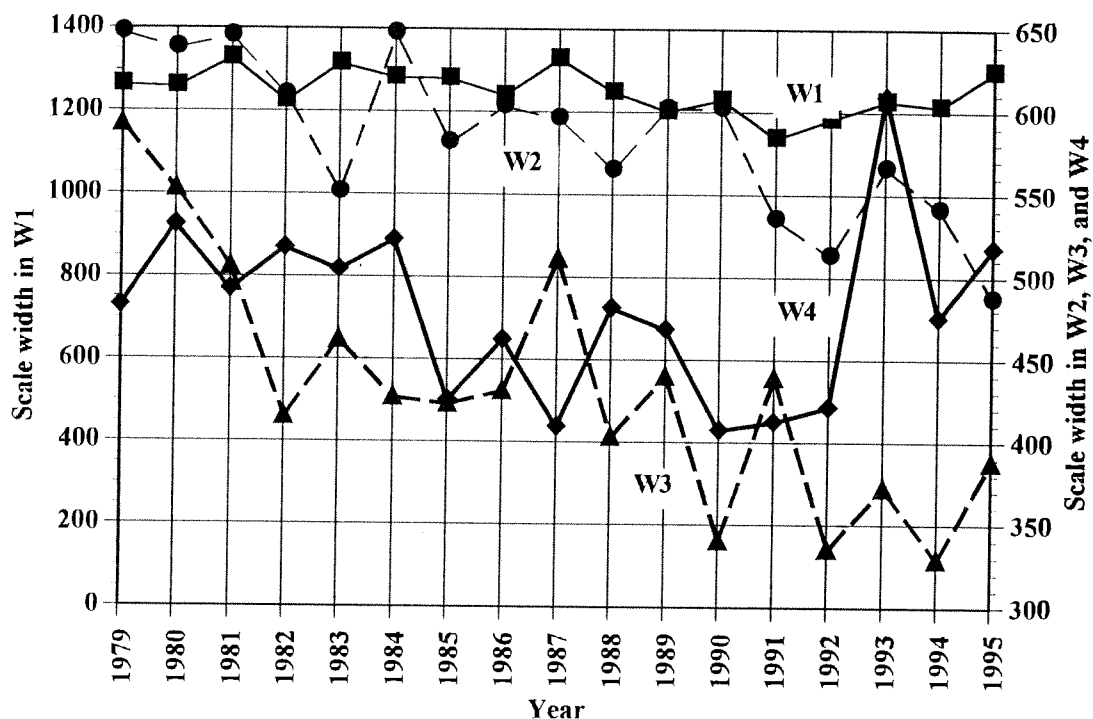
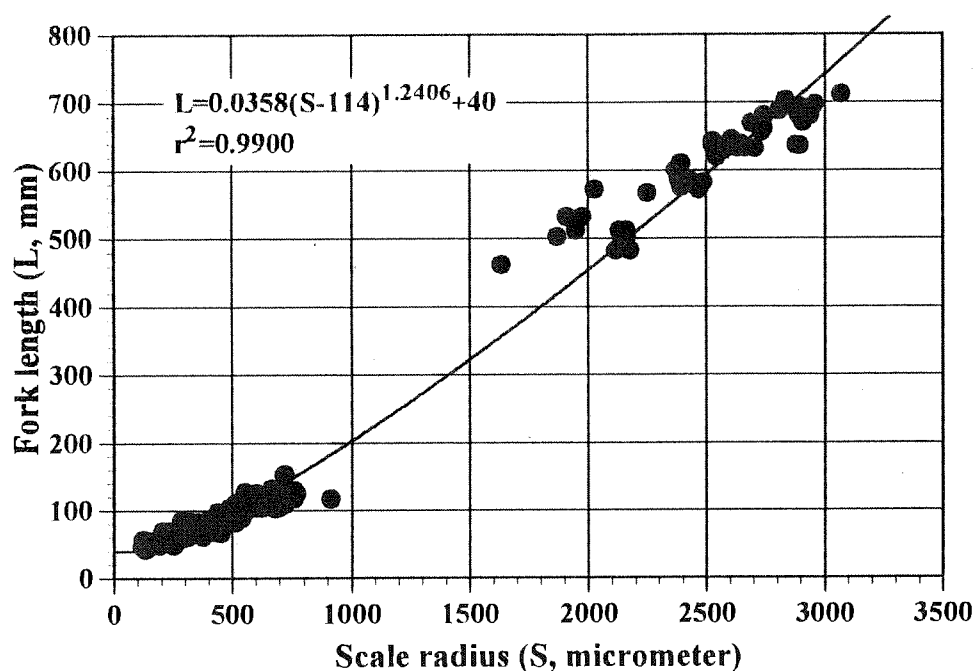


Table 2. Calculative growth reduction of adult chum salmon returning to the Ishikari River from 1976 to 1995. Annual growth is estimated from the back calculation in allometry formula between the scale radius (S , μm) and fork length (L , mm): $L = 0.0358 (S - 114)^{1.2406} + 40$.

Age class	Ocean life period	Annual mean growth (mm)		Growth reduction	
		1976-1980	1985-1995	mm	(%)
3	1st year	267	264	3	(1.2)
	2nd year	171	158	14	(8.0)
	3rd year	168	146	22	(13.0)
	Total	606	568	39	(6.3)
4	1st year	268	256	12	(4.3)
	2nd year	165	141	24	(14.7)
	3rd year	147	108	39	(26.4)
	4th year	152	132	20	(13.3)
	Total	732	637	95	(13.0)
5	1st year	276	249	26	(9.6)
	2nd year	140	135	5	(3.7)
	3rd year	131	92	39	(29.9)
	4th year	128	105	23	(18.2)
	5th year	106	116	-10	(9.5)
	Total	781	697	83	(10.6)

Fig. 10 Relationship between scale length and fork length of chum salmon.



4. Changes in reproduction characters of adult chum salmon

Fecundity of Pacific salmon varies with body size, and is influenced by environmental factors. Although their egg size is affected by both environmental and genetic factors, it remains constant within a cohort (Kaeriyama et al. 1995).

Figure 11 illustrates comparison of body size (body weight), fecundity, and egg size of Ishikari River age-4 female chum salmon between 1940-1943 (from Watanabe 1955) and 1986-1995. Body weight in 1986-1995 was significantly smaller than that in 1940-1943 (U-test, $P < 0.01$), and no differences were observed in fecundity and egg size (U-test, $P > 0.05$). This result indicates that recent growth reduction had no significant effect on fecundity and egg size of Hokkaido chum salmon.

5. Relation between SST anomaly and change in growth

Climate of the Subarctic North Pacific Ocean changed during the late 1970s. Temperature anomalies in the Gulf of Alaska and Bering Sea illustrate a relative warm period in the late 1950s, followed by cooling especially in the early 1970s and a rapid temperature increase in the latter part of that decade (U. S. GLOBEC 1995). Beginning in the 1980s, sea surface temperature (SST) during the growth period of salmon (May to October) in the western and eastern Gulf of Alaska was generally

higher than normal, although in the eastern and central areas of the Subarctic North Pacific Ocean SST fluctuated normally (Fig. 12).

A significant positive relationship between mean SST anomaly during the ocean life period and the population size of Hokkaido chum salmon was observed in the Gulf of Alaska ($r^2 = 0.318$, $P < 0.001$). Body size of adult chum salmon in Ishikari River was negatively related to the mean SST anomaly in Gulf of Alaska ($r^2 > 0.239$, $P < 0.01$). However, there was no significant correlation between SST anomaly and population size or body size in other areas of Subarctic North Pacific Ocean (Tables 3, 4).

DISCUSSION

The Aleutian Low intensified after the late 1970s (Trenberth and Hurrell 1994). SST rose rapidly by several degrees in Gulf of Alaska (Rogers and Ruggerone 1993). Zooplankton biomass and catches of epipelagic nekton increased after the mid 1970s in the Northeast Pacific Ocean (Brodeur and Ware 1992, 1995). Salmon catches from the North Pacific increased sharply in the late 1970s, and exceeded historical levels in the early 1990s (Fig. 1).

Three factors have been suggested for decrease in size at maturity: 1) effect of changes in the ocean environment (Killick and Clements 1963; Rogers

Fig. 11 Comparison of body weight (BW), fecundity (Fec), and egg sizes (ES) of age-4 adult chum salmon returning to Ishikari River between 1940-1943 and 1986-1995. Bars represent standard deviation.

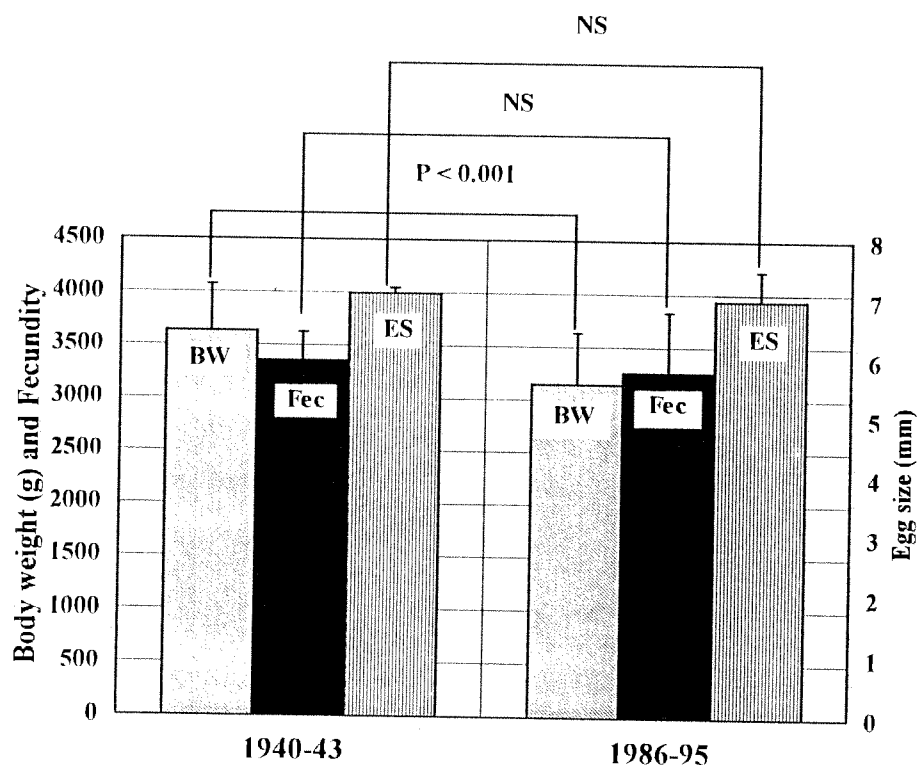


Fig. 12 Annual changes in sea surface temperature (SST) anomalies in western (48-50°N, 164-166°E), central (48-50°N, 179°E-179°W), and eastern (Gulf of Alaska; 48-50°N, 144-146°W) areas of Subarctic North Pacific Ocean during 1946-1995.

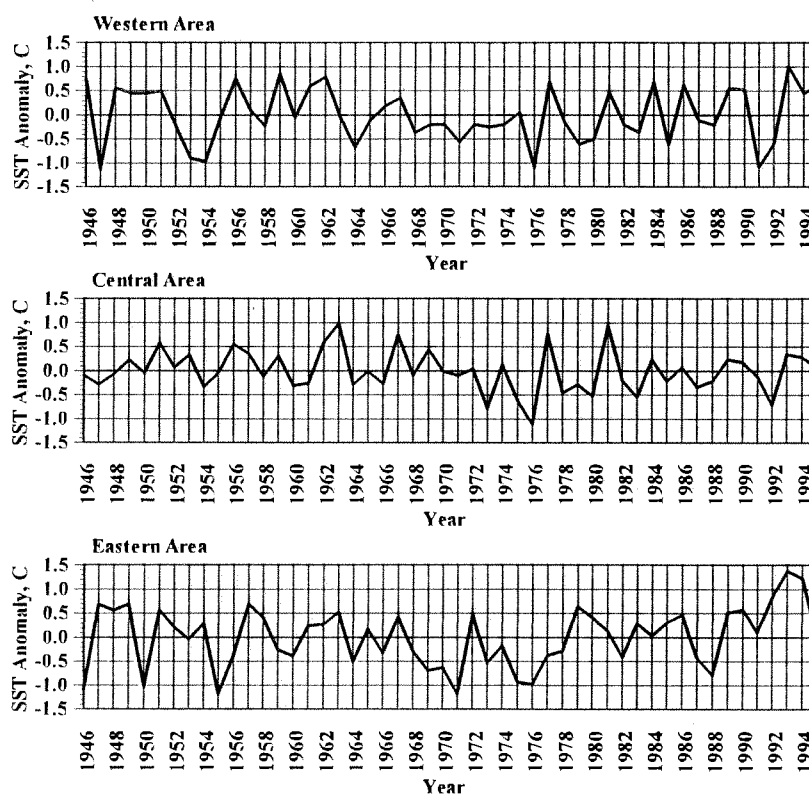


Table 3. Relationship between SST anomaly in the North Pacific Ocean and population size of Hokkaido chum salmon. n = number of years of data, a = constant, b = slope, r^2 = the coefficient of determination, and P = the probability that $b=0$ (NS: $P>0.05$, *: $P<0.001$).**

Location	Western Area 48-50N164-166E	Central Area 48-50N179E-179W	Eastern Area 48-50N144-146W
n	42	42	42
a	17,029	14,961	17,979
b	11,409	-24,936	23,638
r^2	0.1761	0.3153	0.5639
P	NS	Ns	***

Table 4. Relationship between SST anomaly in the Subarctic North Pacific Ocean and fork length of Ishikari River adult chum salmon. n = number of years of data, a = constant, b = slope, r^2 = the coefficient of determination, and P = the probability that $b=0$ (NS: $P>0.05$, **: $P<0.01$, *: $P<0.001$).**

Location	Western Area 48-50N164-166E			Central Area 48-50N179E-179W			Eastern Area 48-50N144-146W		
Age	3	4	5	3	4	5	3	4	5
n	42	42	38	42	42	38	42	42	38
a	609	670	704	609	673	706	608	669	701
b	-8.92	-23.90	-48.20	-4.73	18.11	-4.88	-30.30	-36.10	-60.90
r^2	0.112 7	0.2083	0.3300	0.050 0	0.130 0	0.003 0	0.559 5	0.4887	0.5966
P	NS	NS	NS	NS	NS	NS	***	**	***

and Ruggerone 1993; Ishida et al. 1995), 2) selection and cumulative genetic effect by fishing gear (Ricker 1981), and 3) population-density effects such as those shown for sockeye (Rogers 1980; Peterman 1984; Kaeriyama 1991; Rogers and Ruggerone 1993) and chum salmon (Kaeriyama 1989, 1992, 1996; Ishida et al. 1993).

The results of the present study show that significant negative relationships between population size and body size was observed for Hokkaido chum salmon population (Fig. 5, Table 1), and that the body size of Ishikari River adult chum salmon was negatively related to the mean SST anomaly during salmon growth period in Gulf of Alaska while those relationships were not observed in other areas of the Subarctic North Pacific Ocean (Table 3, 4). Rogers and Ruggerone (1993) noted that the size of adult sockeye salmon in Bristol Bay was inversely related to the Bristol Bay sockeye population size and positively related to SST during winter and spring. Ishida et al. (1995) reported that growth of salmon was positively correlated with spring SST in the central North Pacific, and stated that growth reduction caused by decreasing SST and increasing

population-density. For the Hokkaido chum salmon population, however, the present result of a negative relationship between SST anomaly during the growth period in the ocean and body size at maturity suggests that growth reduction may be affected by their population size rather than change in the SST.

Response of body size to selection by fisheries and hatchery practices may not be the main factor affecting the recent growth reduction because there has been a synchronous increase in age at maturity (Fig. 7). Therefore, population-density effect appears to have a great potential for explaining the cause of the individual growth reduction and the increase in age of Hokkaido chum salmon population.

For the Hokkaido chum salmon population, the recent individual growth reduction has not brought about detectable changes in fecundity and egg size (Fig. 11). Condition factor has been stable since the 1970s (Fig. 6). These results indicate that adult chum salmon returning to Hokkaido are reproductively fit. Return rate, which is survival rate from release to return, continues to rise (Fig. 2B). Several tests of population-density-dependent effects

such as Morris and Varley-Gradwell methods shows that density-dependent mortality has not occurred in Hokkaido chum salmon population (Kaeriyama 1992).

On the other hand, body size has remained stable at small size despite the increases in population size and age since the late 1980s (Fig. 4, 7A). Scale analyses show that growth reduction of Hokkaido chum salmon occurs after the second year of ocean life, especially in the third year (Table 2). The possible causes responsible for these are; 1) Japanese adult chum salmon has already attained a biological minimum size at maturity. In age-4, only individuals which grow extremely rapidly at 4 year will be able to mature and to return; 2) profitable ocean environment may restrain the population-density effect. However, aging is now in progress; and 3) carrying capacity of Hokkaido chum salmon population has increased in the North Pacific Ocean.

If adults have attained the biological minimum size at maturity, the population-density effect may progress to the next step from the individual growth reduction in Japanese chum salmon population.

In conclusion, the synchronous decreasing body size and increasing age at maturity of Hokkaido chum salmon was caused due to intraspecific competition and high abundance of chum salmon on the North Pacific Ocean. In future, therefore, it is extremely important issue for the salmon enhancement program to establish an optimum population system by clarifying the mechanism of population regulation such as population-density-dependent effect, and by monitoring biological characters of population such as migration pattern, body size, age composition, fecundity, and egg size.

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Biochemical Approach to Assessing Growth Characteristics in Salmonids

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Growth characteristics were examined for pink, *Oncorhynchus gorbusha*, chum, *O. keta*, and sockeye salmon, *O. nerka*, caught in the Okhotsk Sea, North Pacific, and the Bering Sea from biochemical aspects. Adult pink, chum, and sockeye salmon had higher condition factor, protein content, and RNA:DNA and protein:DNA ratios than the juveniles. In adult fishes, while both RNA:DNA and protein:DNA ratios increased with condition factor commonly in the three species, positive correlations of both RNA:DNA and protein:DNA with fork length were seen only in chum salmon. In contrast with adults, juvenile chum salmon exhibited negative correlations of both RNA:DNA and RNA:protein ratios with fork length, and the RNA:DNA ratio decreases with triacylglycerol content. These correlations suggest that juvenile chum salmon build up lipid reserves at the expense of protein synthesis just prior to the onset of winter. However, in juvenile pink salmon alternative strategy was shown in which continued rapid growth is favored. These results suggest that Pacific salmon adopt species-specific strategies for allocating resources for somatic growth, and hence exhibit varying growth characteristics as measured by biochemical parameters that depend on species and life history stage during their years at sea.



INTRODUCTION

In the 1990's sockeye, *Oncorhynchus nerka*, chum, *O. keta*, and pink salmon, *O. gorbusha* in the North Pacific have been at high levels of abundance due a combination of environmental changes favorable to salmon (Beamish and Bouillon 1993; Miller et al. 1994; Francis and Hare 1994), and an increase in hatchery production by Pacific Rim countries. However, these increases have been accompanied by increases in age of maturation and decreases in size at age, especially for chum salmon originating from Japan and Russia (Ishida et al. 1993; Ida and Hayashizaki 1994). These trends suggest that density dependent decreases in growth rate and an overall decline in nutrition may be taking place in the North

Pacific. Additionally, since the different species of Pacific salmon are known to frequently occupy common feeding areas (Mishima et al 1966; Mishima and Shimazaki 1969; Takagi 1971 and 1996; Brodeur 1989; Azuma 1991; Perry et al. 1996), interspecific relationships associated with their growth condition also deserve further investigation. It is important, therefore, to clarify species specific growth and physiological condition, so that we can have an improved qualitative assessment of the salmon stocks.

Biochemical approaches for estimating growth characteristics have been adopted for many fish species including salmonids since the 1980's (Nakano et al. 1985; Fukuda et al. 1986; Houlihan et al. 1993; Shearer et al. 1994). However, for Pacific salmon in the marine stages of their life history, the biochemical

parameters associated with growth are poorly understood. The purpose of this study is to assess the growth characteristics of Pacific salmon through examining triacylglycerol and protein content, and nucleic acid ratios.

MATERIALS AND METHODS

A total of 653 salmon (363 pink, 227 chum, and 63 sockeye) were examined in this study. They were caught using gillnets and surface trawls in the Okhotsk Sea and the eastern North Pacific Ocean in the fall of 1993 by the *Wakashio maru* and the *Kaiyo maru*, gillnets and longlines in the Bering Sea in the summer of 1994 by the *Wakatake maru*, and gillnets in the central North Pacific Ocean in the summers of 1994 and 1995 by the *Hokko maru* and the *Wakatake maru*.

In this study, pink, chum, and sockeye salmon caught from the Okhotsk Sea and western North Pacific in the fall are defined as juveniles, while those from the Bering Sea and central North Pacific in the summer of 1994 and 1995 are called adults.

Processing of salmon at sea included measurement of fork length, body weight, gonad weight, identification of sex, and collection of scale samples. Whole fish were frozen at -40°C immediately following ship board processing and stored at -80°C in the laboratory until analysis.

Using white muscle tissue taken from the lateral part just beneath the dorsal fin of each fish, we measured triacylglycerol, protein, RNA and DNA contents, and then calculated RNA:DNA, RNA:protein, and protein:DNA ratios individually. Triacylglycerol was extracted from the muscle with ethanol-ether solution (3:1, v/v) and estimated by the GPO-p-chlorophenol method using Wako's kit which includes standard solution (Triglyceride G-Test Wako, Wako Ltd). Protein content was determined by the method of Lowry et al. (1951) on a white muscle

homogenate buffered in a 0.25 M sucrose -20mM Tris -HCl -1mM EDTA solution at 7.5 pH, using bovine serum albumin as a standard. RNA and DNA were extracted from the same buffered homogenate and determined spectrophotometrically by the Schmit-Thanhauser-Schneider method, as modified by Nakano (1988), using both ibonucleic acid from yeast and deoxyribonucleic acid extracted from salmon sperm as standards. Nucleic acid contents published by Azuma (1995) for juvenile salmon collected from Okhotsk Sea in 1993 were re-estimated according to the renewed assay system. Determinations of triacylglycerol and protein contents were expressed as μg per mg of wet weight of white muscle tissue.

Data were grouped by species and by the life history stage mentioned above. Statistically significant differences for biological and biochemical parameters among seasonal and life history groups within each species were determined with the Student's t-test for unequal sample size; and statistically significant correlations between biochemical parameters, and both fork length, and condition factor (CF, $\text{CF} = \text{BW}(\text{g}) \cdot \text{FL}(\text{mm})^{-3} \cdot 10^6$) were determined with the F-test. When there was ten percent or higher coefficient of determination in significant correlation between any two parameters, the regression line was drawn with a solid line in the relevant figure. When significant correlations with coefficient of determination was less than 10 %, the regression line was expressed with a broken line.

RESULTS

Pink Salmon

Juveniles captured in November were larger ($P < 0.05$) but thinner ($P < 0.05$) than those in October (Table 1). November - caught fish also exhibited much higher values in protein content ($P < 0.0001$)

Table 1. Biological characteristics of pink, chum, and sockeye salmon examined. The values indicate the mean and (in brackets) one standard error.

Species	Stage	Location	Date	Number of Fish	Fork Length (mm)	Body Weight (g)	Condition Factor
Pink Salmon	Juvenile	Okhotsk & Western North Pacific	Oct., 1993	135	239(1.3)	142(2.7)	10.25(0.06)
			Nov., 1993	172	244(1.3)	149(2.7)	10.07(0.06)
	Adult	Bering Sea & North Pacific	June & July in 1994 & 1995	56	468(4.1)	1297(38.8)	12.51(0.15)
Chum Salmon	Juvenile	Okhotsk & Western North Pacific	Aug. & Sep., 1993	25	215(5.0)	119(9.0)	11.42(0.18)
			Oct., 1993	79	245(3.1)	172(6.6)	11.23(0.08)
			Nov., 1993	70	234(2.4)	136(4.2)	10.40(0.09)
	Adult	Bering Sea & North Pacific	June & July in 1994 & 1995	53	524(8.2)	1866(85.7)	12.39(0.16)
Sockeye Salmon	Juvenile	Okhotsk & Western North Pacific	Oct. & Nov., 1993	17	262(7.8)	224(25.1)	11.87(0.21)
	Adult	Bering Sea & North Pacific	June & July in 1994 & 1995	46	501(8.5)	1633(105.0)	12.34(0.19)

and protein:DNA ratio ($P < 0.0001$), while exhibited much lower values in RNA:protein ratio ($P < 0.0001$) and triacylglycerol content ($P < 0.001$) than those in October (Table 2). Adult pink showed even higher values in condition factor ($P < 0.0001$), triacylglycerol content ($P < 0.005$), protein content ($P < 0.0001$), RNA:DNA ratio ($P < 0.0001$), and protein:DNA ratio ($P < 0.005$) compared with juveniles (Tables 1 and 2). The RNA:protein ratio of adult pink was intermediate between the two juvenile groups (Table 2).

Chum Salmon

Juveniles captured in November were smaller than those in October ($P < 0.005$ in fork length and $P < 0.0001$ in body weight), although they were larger than those captured in late August to early September ($P < 0.005$), although the latter had the highest CF of the three juvenile groups (Table 1). Condition factor

of adult chum was higher than for juveniles, similar pink salmon ($P < 0.0005$). Triacylglycerol content of juveniles in October was highest but did not differ from that of adult chum significantly (Table 2). Protein content of juveniles decreased with season but again rose in adult stage ($P < 0.0001$) (Table 2). RNA:DNA ratio was highest in adult chum, while RNA:protein ratio was highest in juveniles captured in early fall (Table 2). Protein:DNA was higher in adults than in any juvenile groups ($P < 0.001$).

Sockeye Salmon

No significant difference was shown in condition factor between juveniles and adults (Table 1). Triacylglycerol and protein contents, RNA:DNA and protein:DNA ratios were much higher in adults than juveniles, while RNA:protein ratio was higher in juveniles than adults ($P < 0.005$) (Table 2).

Table 2. Biochemical characteristics of dorsal white muscle of pink, chum, and sockeye salmon examined (means and, in parentheses, standard errors).

Species	Stage	Location	Date	Number of Fish	Triacylglycerol (%)	Protein(%)	RNA:DNA	(RNA:Protein) $\times 10^3$	Protein:DNA
Pink Salmon	Juvenile	Okhotsk & Western North Pacific	Oct., 1993	135	**0.75(0.05)	*13.6(0.18)	4.84(0.09)	*29.9(0.65)	*174.8(5.4)
			Nov., 1993	172	0.51(0.03)	15.6(0.07)	4.84(0.08)	21.5(0.19)	226.6(3.4)
	Adult	Bering Sea & North Pacific	June & July in 1994 & 1995	56	0.96(0.10)	16.3(0.16)	6.16(0.20)	24.8(0.43)	249.9(7.9)
Chum Salmon	Juvenile	Okhotsk & Western North Pacific	Aug. & Sep., 1993	25	0.88(0.11)	16.1(0.29)	4.93(0.13)	30.3(0.73)	164.0(4.6)
			Oct., 1993	79	1.67(0.17)	15.5(0.20)	3.75(0.06)	17.6(0.48)	221.2(5.3)
			Nov., 1993	70	***0.85(0.09)	14.9(0.19)	3.63(0.09)	19.7(0.60)	187.9(3.5)
	Adult	Bering Sea & North Pacific	June & July in 1994 & 1995	53	1.25(0.15)	16.1(0.16)	5.18(0.15)	20.3(0.40)	262.1(10.1)
Sockeye Salmon	Juvenile	Okhotsk & Western North Pacific	Oct. & Nov., 1993	17	0.30(0.04)	14.7(0.19)	3.96(0.17)	20.0(0.47)	197.8(6.7)
	Adult	Bering Sea & North Pacific	June & July in 1994 & 1995	46	1.63(0.17)	16.9(0.23)	5.27(0.18)	17.7(0.41)	305.5(12.8)

+N=133, ++N=130, +++N=69

Relationships Among Biochemical and Biological Characteristics

Positive relationships between triacylglycerol content and fork length was seen only in juvenile chum and in adult sockeye (Fig. 1). Significant regressions between triacylglycerol content and condition factor were observed in juvenile pink and chum salmon and adult pink and sockeye salmon, but the coefficient of determinations were low, particularly in juvenile pink (Fig 1).

Protein content increased with both fork length and condition factor in juvenile pink and chum but not sockeye, although the coefficient of determinations were low in pink and chum salmon (Fig. 2). Positive relationships were observed only between protein content and fork length in adult chum and sockeye salmon (Fig. 2).

RNA:DNA ratio increased with condition factor except for juvenile sockeye (Fig. 3). Although significant relationships between RNA:DNA ratio and fork length were shown in chum salmon, the slope of regression lines was negative in juveniles and positive in adults (Fig. 3).

Negative correlations were observed between RNA:protein ratio and fork length for juvenile chum and pink, although the correlation was very weak in pink (Fig. 4). Between RNA:protein and condition factor, only adult pink exhibited a positive correlation (Fig. 4).

Protein:DNA ratio increased with fork length in juvenile pink and both juvenile and adult chum salmon (Fig. 5). Protein:DNA ratios increased with condition factor in all cases except juvenile sockeye (Fig. 5).

Only juvenile chum exhibited negative correlations of triacylglycerol content with both RNA:DNA ratio and RNA:protein ratios, although the coefficient of determination was below 10% in the former case (Figs. 6 and 7).

DISCUSSION

In the present study, we examined triacylglycerol and protein contents and RNA:DNA, RNA:protein, and protein:DNA ratios in white muscle tissue to assess the growth characteristics of salmonids. Triacylglycerol is the major constituent of neutral fat, which is the primary material for energy storage. Protein is directly related to somatic body construction and can be viewed as a measure of growth condition. Both RNA:DNA and RNA:protein ratios reflect protein synthetic rates (Foster et al. 1993; Houlihan et al. 1993). Since the former is standardized by DNA, the value is affected by the change of cell size in contrast with the RNA:protein ratio. Protein:DNA ratio reflects relative cell size (Bulow, 1987), and muscle development can be evaluated from it. The

Fig. 1 Relationship of triacylglycerol content of white muscle with fork length and condition factor by species and by life history stage.

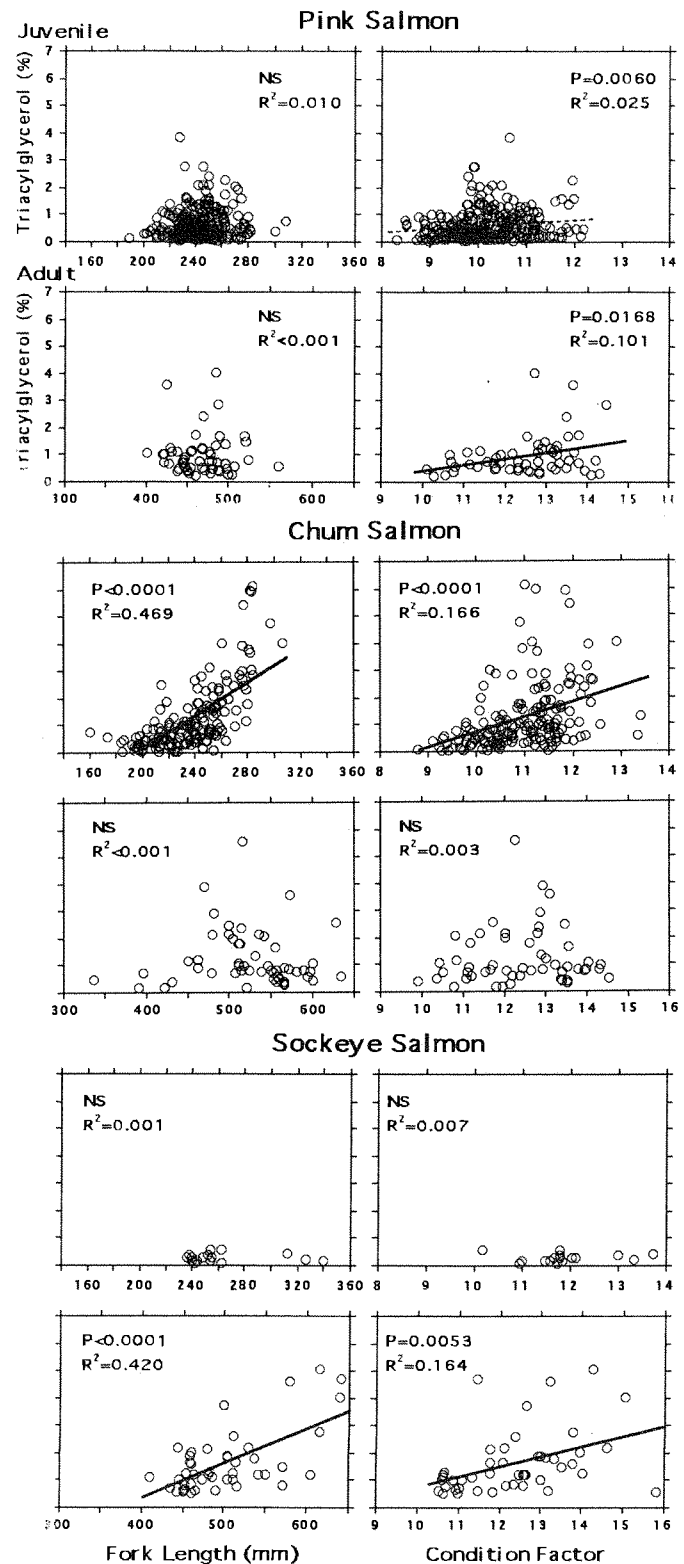


Fig. 2 Relationship of protein content of white muscle with fork length and condition factor by species and by life history stage.

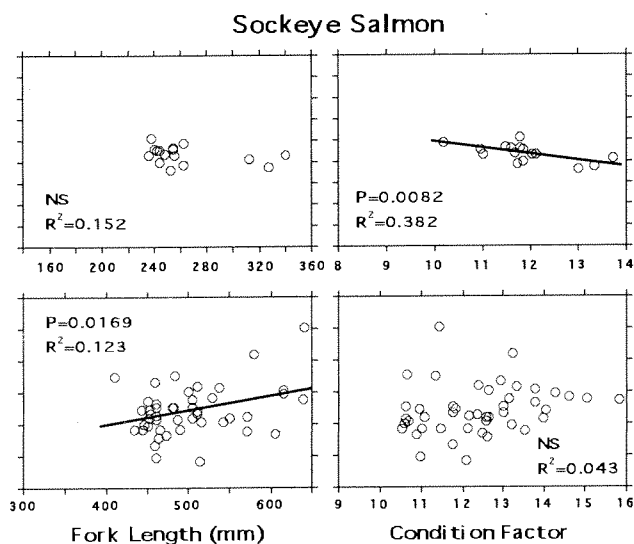
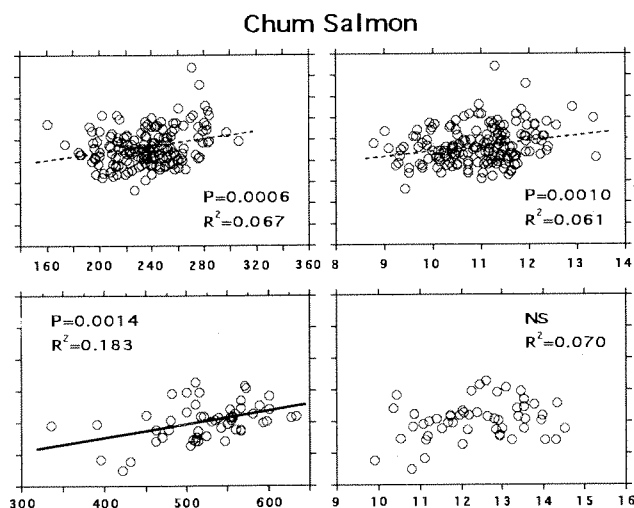
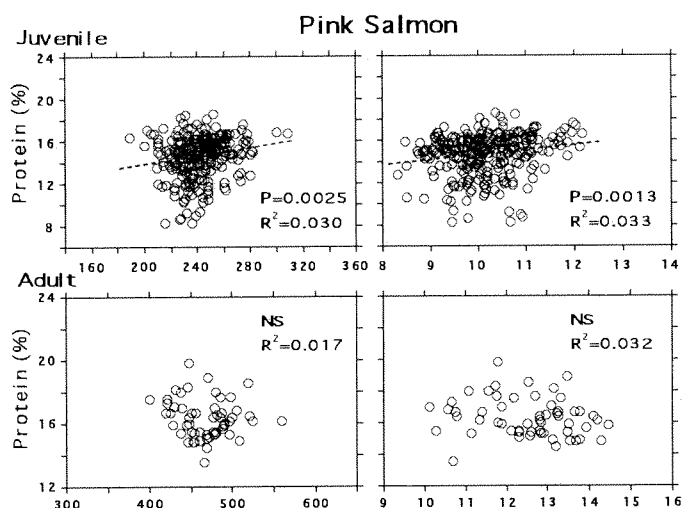


Fig. 3 Relationship of RNA:DNA ratio of white muscle with fork length and condition factor by species and by life history stage.

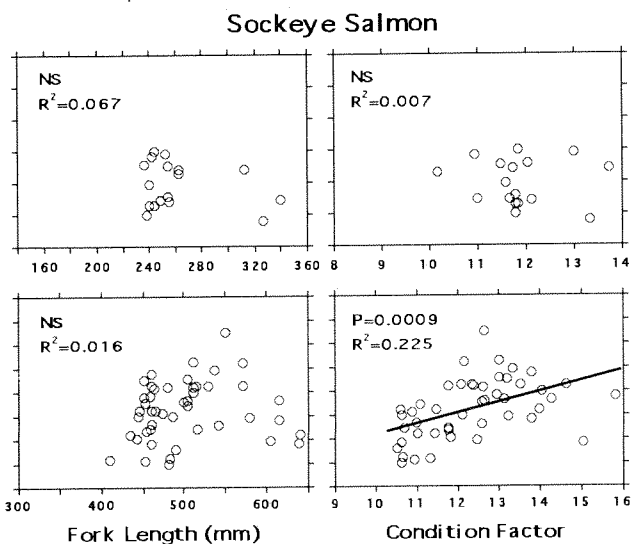
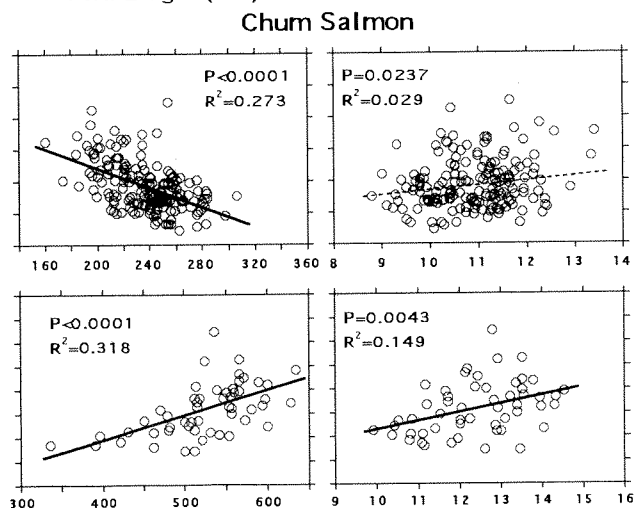
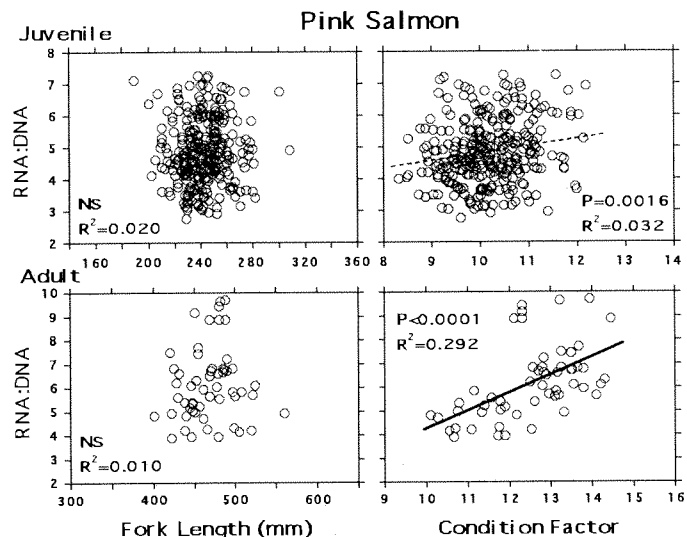


Fig. 4 Relationship of RNA:protein ratio of white muscle with fork length and condition factor by species and by life history stage.

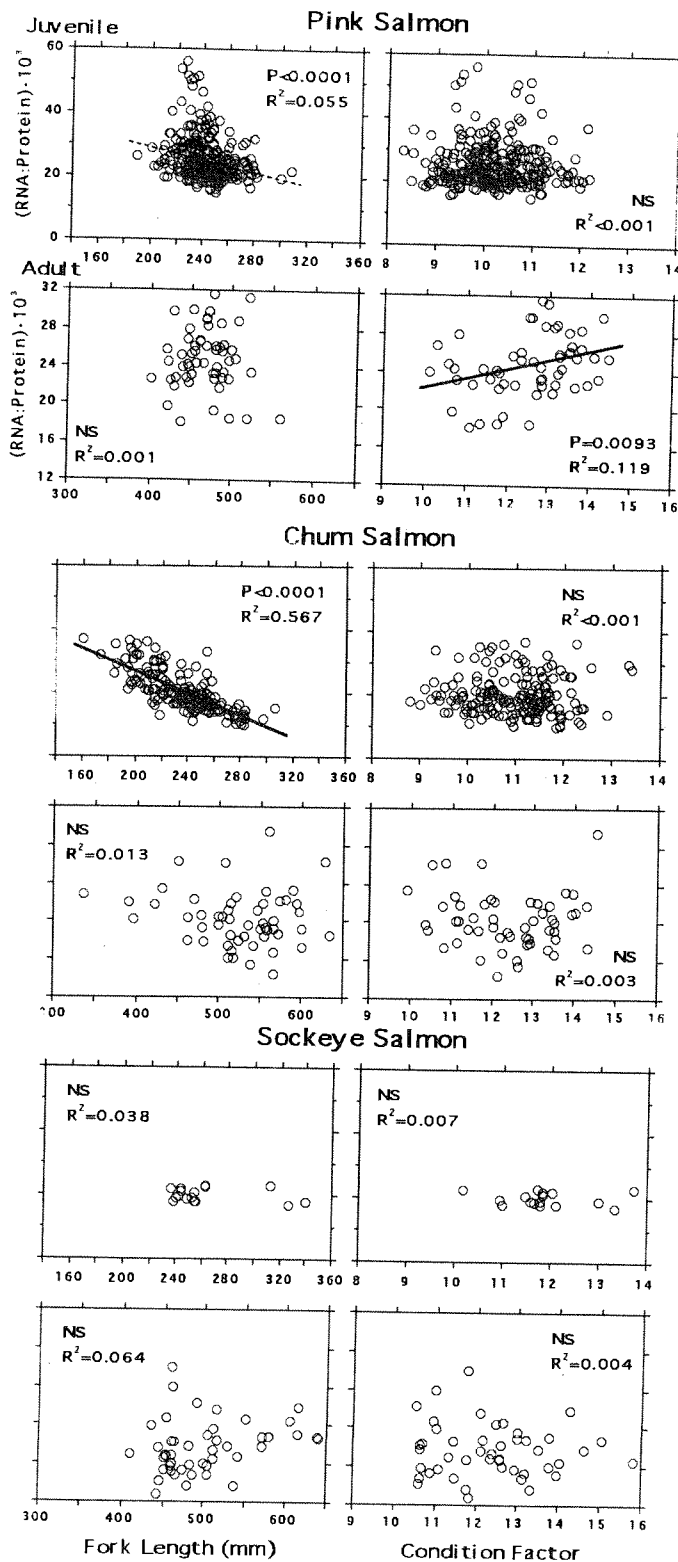


Fig. 5 Relationships of protein:DNA ratio of white muscle with fork length and condition factor by species and by life history stage.

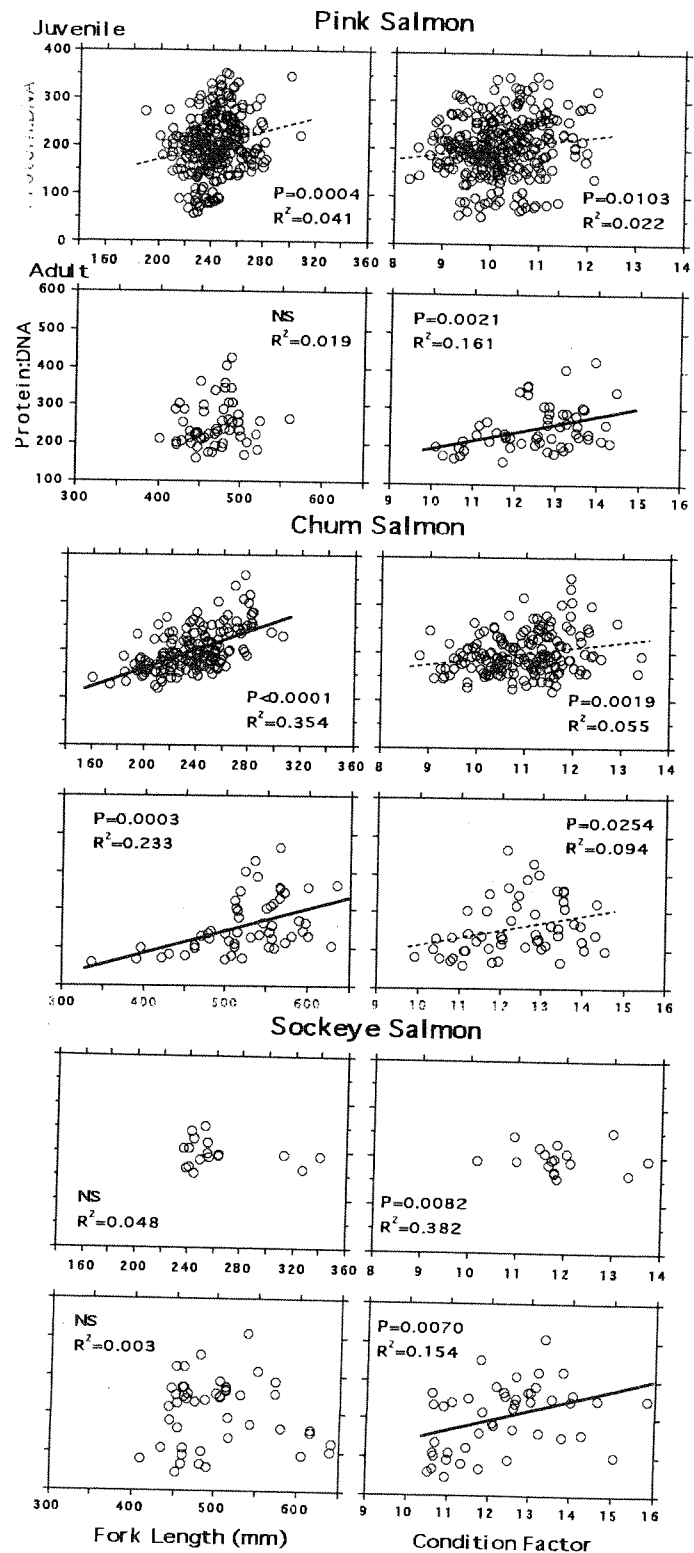
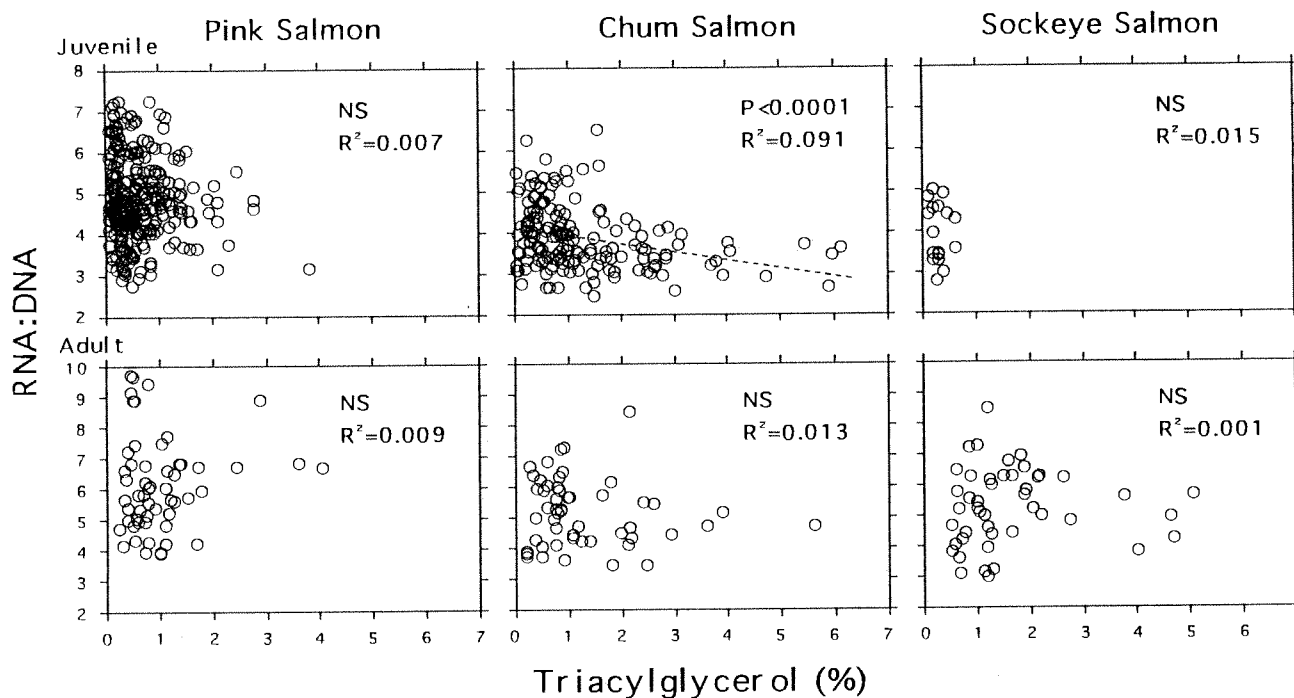
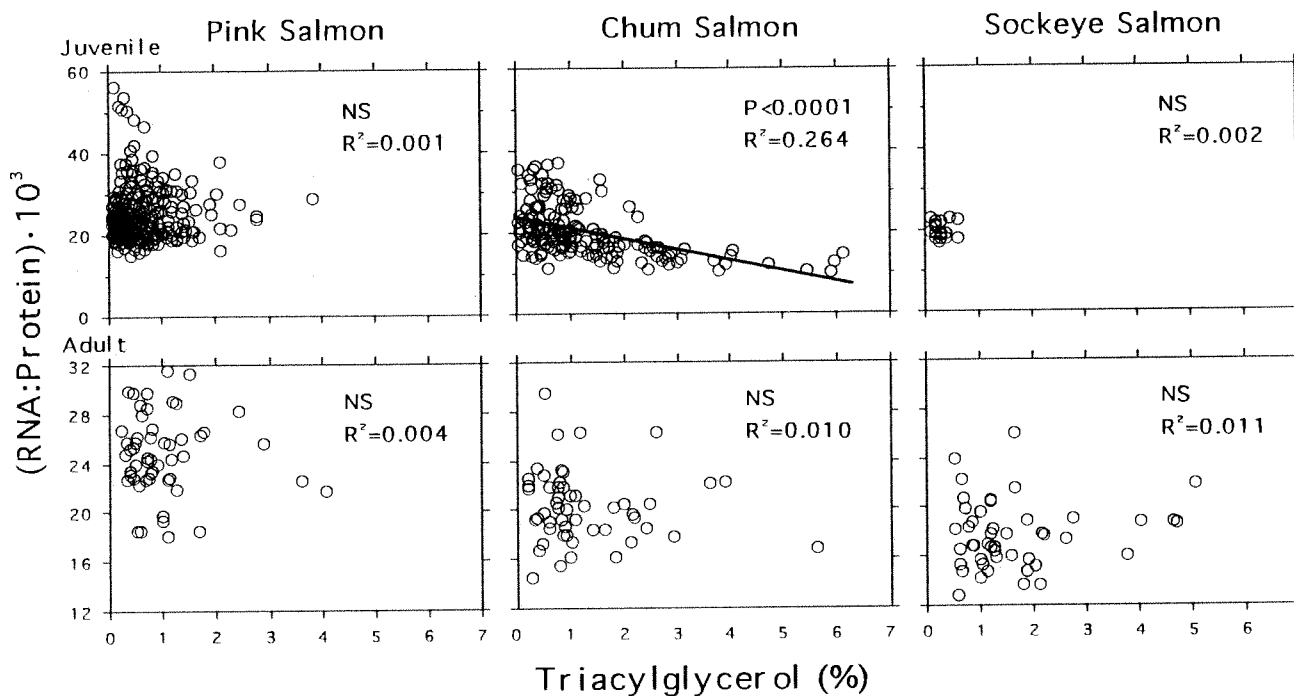


Fig. 6 Relationship of RNA:DNA ratio with triacylglycerol content of white muscle by species and by life history stage.**Fig. 7 Relationship of RNA:protein ratio with triacylglycerol content of white muscle by species and by life history stage.**

RNA:DNA and RNA:protein ratios in white muscle have been demonstrated to be positively correlated with specific growth rate in salmonids (Thorpe et al. 1982; Wilder and Stanley 1983; Miglavs and Jobling

1989; Ferguson and Dazmann 1990; Varnavskiy et al. 1991; Wang et al. 1993; Grant 1996). These parameters are therefore supposed to indicate the growth potential of fish. In practice, white muscle

comprises most of the body mass (Grant 1996), and Houlihan et al. (1993) reported that the protein synthesis in white muscle is more strongly correlated with somatic growth rate than other tissues.

In adult salmonids, we found that condition factor is positively correlated with RNA:DNA and protein:DNA ratios in all three species. This indicates that condition factor generally reflect growth potential expressed as protein synthetic rate per unit DNA content, and cell development in white muscle. However, it was found that relationships of either triacylglycerol content, protein content, or RNA:protein with condition factor differ from species to species. Correlations of biochemical parameters with body size seem to reflect species-specific growth characteristics. A positive correlation between triacylglycerol content and body size was seen in sockeye alone, and correlations of RNA:DNA ratio and protein:DNA ratio with body size were seen in chum.

Biological and biochemical characteristics of juvenile pink salmon indicate that development of skeletal muscle through the fall was supported by hypertrophy of muscle at the expense of energy reserves, because the protein:DNA ratio increased and triacylglycerol content decreased from October to November. However, since the correlation between protein:DNA and fork length was not strong, it cannot be clearly said that somatic growth is associated with cell enlargement of white muscle during the juvenile stage. Comparing juvenile chum and sockeye salmon, juvenile pink exhibited larger variation in protein and nucleic acid contents. This might be due to the broader distribution and wider range of water temperatures at which pink salmon were caught (National Research Institute of Far Seas Fisheries, 1993), and higher variability of such components due to temperature (Ferguson and Danzmann 1990; Houlihan et al. 1993). Judging from their biochemistry, juvenile pink appear to adopt a strategy of not storing the energy but maintaining a high somatic growth rate instead. The higher growth potentials also seen in adult stage is consistent with their faster growth rate during the oceanic period of their life history.

Juvenile chum salmon, in contrast with juvenile pink, clearly deposit much greater energy reserves inside the white muscle as they grow. Although cell enlargement of white muscle was presumed to happen through growth, judging from the relationship between the protein:DNA ratio and fork length, the rate of protein synthesis unit per DNA decreased with body size. These results indicate that the decrease in the ribosomal capacity for protein synthesis was more significant during the juvenile stage in chum salmon entering winter. The negative correlation of triacylglycerol content with RNA:DNA and

RNA:protein ratios demonstrates that juvenile chum slow down their growth rate to maintain their energy reserve. This may be a suitable strategy for chum salmon which do not exhibit as fast a growth rate as pink salmon when winter zooplankton abundance will be low. These results are consistent with the finding that juvenile pink migrating northward on the west coast of Vancouver Island exhibit higher potential growth rates than do co-migrating juvenile chum (Perry et al. 1996).

No strategy was evident for juvenile sockeye salmon, probably because of small sample sizes.

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Correlations Between Homing, Migration, and Reproduction of Chum Salmon

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The onset of gonadal maturation which is regulated by the endocrinological functions is considered to play leading roles in making salmon migrate a long distance from the ocean to their natal streams for spawning. Both cytological profiles of salmon gonadotropin-releasing hormone (sGnRH) neurons and serum gonadal steroid hormone profiles are investigated in chum salmon (*Oncorhynchus keta*) during the homing migration. Cytophysiological differences were observed between sGnRH neurons in the olfactory nerve and those in the preoptic area before and after upstream migration; the former could possibly be involved in the olfactory functions, and the latter would appear to be involved in gonadal maturation. Changes in serum steroid hormone levels were measured during the homing migration from the North Pacific Ocean to the spawning grounds, and the results revealed good correlations between estradiol-17 β and vitellogenesis, 11-ketotestosterone and spermatogenesis, and 17 α ,20 β -dihydroxy-4-pregnen-3-one and final gonadal maturation in both sexes, but the roles of testosterone in gonadal development in both sexes were still obscure. These findings are discussed in relation to homing migration and gonadal maturation of chum salmon.



INTRODUCTION

Salmon have the ability to migrate thousands of kilometers from the ocean to their natal streams for spawning after a few years of feeding migration (Smith 1985). Although the shift from feeding migration to homing migration has been thought to coincide with the onset of gonadal maturation (Ueda and Yamauchi 1995), the mechanisms controlling this shift are still unknown. Since the gonadal maturation is mainly regulated by the hypothalamo-pituitary-gonadal axis (Fink 1988), it is highly important to investigate endocrinological changes of various hormone profiles in salmon during homing migration.

Anadromous chum salmon (*Oncorhynchus keta*) migrating from the North Pacific Ocean to natal streams in Japan are a good model for studying the correlations between homing migration and reproduction, because mature chum salmon of both sexes return to the natal area with high accuracy. The present paper reviews the endocrinological functions of chum salmon during the homing migration with special reference to cytophysiological profiles of salmon type gonadotropin-releasing hormone

(sGnRH) as well as serum gonadal steroid hormone profiles.

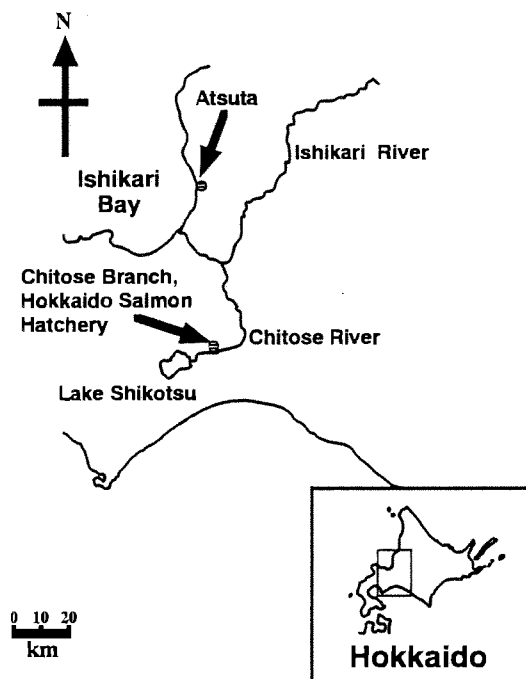
MATERIALS AND METHODS

Salmon Gonadotropin-Releasing Hormone (sGnRH)

Ten male and ten female four year old adult chum salmon were captured at two locations during their homing migration. Fish at an early phase of the homing migration were captured in the coastal sea near the maternal river, Atsuta, Hokkaido, Japan on October, 1992, and those at the time of spawning on the spawning ground itself in the maternal river were obtained just after the completion of upstream migration at the Chitose Branch, Hokkaido Salmon Hatchery on October, 1992 (Fig. 1). Fish were deeply anesthetized, and the forebrain (olfactory nerve, olfactory bulb, telencephalon, and preoptic area) were isolated.

The procedures of immunocytochemistry using the antiserum to sGnRH (Okuzawa et al. 1990) and in situ hybridization using the oligonucleotide for pro-sGnRH mRNA probe (Suzuki et al. 1992) were described previously (Kudo et al. 1996).

Fig. 1 Map of the coastal sea and the Ishikari and Chitose Rivers showing the sampling areas for chum salmon.



Serum steroid Hormones

Fourteen male and female adult chum salmon of age 3 to 5 years were caught at 14 sampling points from 41.30°N-156.30°E to 45.32°N-173.31°E in the north Pacific Ocean in May and June, 1982. Thirty male and twenty-three female were captured in the coastal sea near the maternal river, Atsuta and at the Chitose Branch, Hokkaido Salmon Hatchery on October, 1982.

Serum levels of various steroid hormones (estradiol-17b, testosterone, 11-ketotestosterone, and 17 α ,20 β -dihydroxy-4-pregnen-3-one) were measured by radioimmunoassay methods specific to each steroid (Kagawa et al. 1982; Ueda et al. 1991a; Ueda et al. 1985; Young et al. 1983).

Statistics

Significance of differences were determined by use of Student's test or Student-Newman-Keuls' multiple range test.

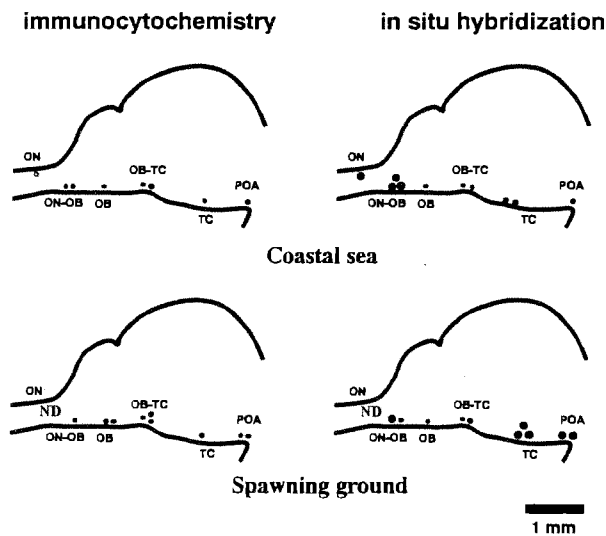
RESULTS

Salmon Gonadotropin-Releasing Hormone (sGnRH)

Cytophysiological changes of sGnRH producing neurons in chum salmon were examined during

homing migration by immunocytochemistry with a specific antiserum to sGnRH and *in situ* hybridization with an oligonucleotide encoding the sGnRH precursor. In the forebrain (olfactory nerve, ON; olfactory bulb, OB; telencephalon, TC; preoptic area, POA), sGnRH immunoreactive neurons and neurons showing signals for pro-sGnRH mRNA were compared between fish in the coastal sea and those on the spawning ground. Neurons in the ON and between the ON and OB (ON-OB) exhibited strong sGnRH immunoreactivity and strong hybridization signals in fish in the coastal sea, whereas these activities and signals disappeared or decreased in animals on the spawning ground. In contrast, neurons in the TC and POA showed sGnRH immunoreactivity and hybridization signals of sGnRH during homing migration, and the hybridization signals of sGnRH in the TC and POA were stronger in fish on the spawning ground than those in the coastal sea (Fig. 2).

Fig. 2 Distribution of neurons showing sGnRH immunoreactivity and hybridization signals for pro-sGnRH mRNA in the forebrain of chum salmon during homing migration. Small and large circles indicate weak and strong hybridization signals, respectively. ND, non-detectable.

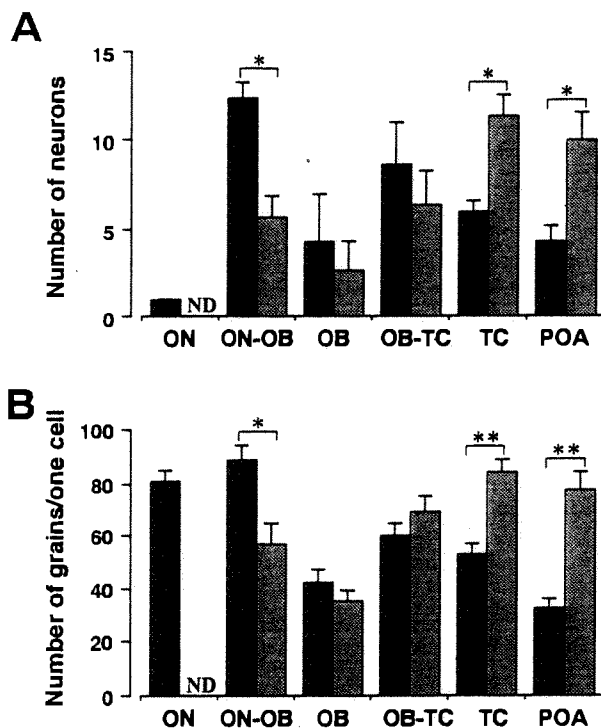


Both the number of neurons and the intensity of signals for pro-sGnRH mRNA between the ON-OB were significantly greater in fish in the coastal sea than those on the spawning ground. However, neurons showing signals for pro-sGnRH mRNA in the TC and POA increased significantly in number and in intensity in fish on the spawning ground (Fig. 3).

Serum Steroid Hormones

Changes in serum steroid hormones were measured during spawning migration from the North Pacific Ocean to the spawning ground of chum

Fig. 3 Changes in the number of neurons showing signals for pro-sGnRH mRNA (A) and the intensity of pro-sGnRH mRNA levels in sGnRH neurons (B) in chum salmon from the coastal sea (darker stippled bars) and from the spawning ground (Lighter stippled bars). Vertical bars represent the mean + SE. Significant differences at 5% (*) and 0.1% (**) levels are indicated.



salmon (Ueda et al. 1984a; 1991a; 1991b). In females, serum estradiol-17 β (E_2) levels increased sharply during seawater migration, but were followed by a sharp drop during upstream migration. Serum 17 α ,20 β -dihydroxy-4-pregnen-3-one (DHP) levels were very low collected from the North Pacific Ocean to the river at the pre-spawning period, and increased dramatically at the spawning ground (Fig. 4).

In males, serum 11-ketotestosterone (11KT) and testosterone (T) levels increased sharply and gradually from the North Pacific Ocean to the coastal sea and to the river at the pre-spawning period, respectively. Levels of both androgens in serum decreased at the spawning period when serum DHP level rapidly increased (Fig. 5).

DISCUSSION

Salmonid homing migration is considered to be closely related with the gonadal maturation which is regulated by the endocrinological functions, mainly by the hypothalamo-pituitary-gonadal axis. Briefly, GnRH controls gonadotropin (GtH) release from the pituitary gland, GtHs induce steroidogenesis in the gonads, and steroid hormones stimulate gameto-

Fig. 4 Changes in serum estradiol-17 β (E_2) and 17 α ,20 β -dihydroxy-4-pregnen-3-one (DHP) levels during the spawning migration of female chum salmon. The vertical bars represent the means $\pm$ SE.

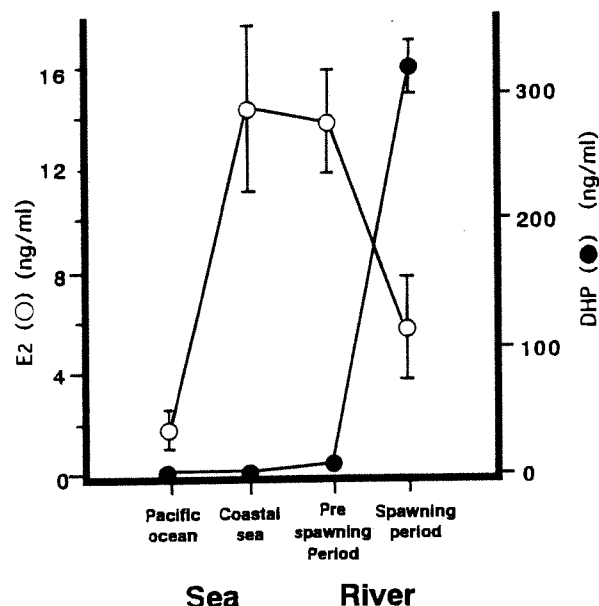
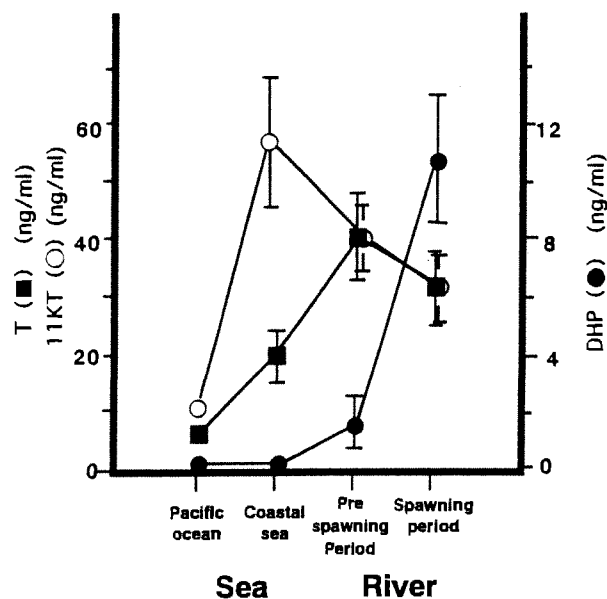


Fig. 5 Changes in serum testosterone (T), 11-ketotestosterone (11-KT) and 17 α ,20 β -dihydroxy-4-pregnen-3-one (DHP) levels during the spawning migration of male chum salmon. The vertical bars represent the means $\pm$ SE.



genesis and final gameto-maturation. The present review focuses on the homing migration of chum salmon in connection with cytophysiological profiles of sGnRH producing neurons as well as serum steroid hormone profiles.

sGnRH neurons in the ON showed distinct cytophysiological changes; both immunoreactivity of sGnRH and strong hybridization signals for pro-sGnRH mRNA were observed in fish at the early phase of the upstream migration, but were rare in fish at the time of the spawning period. These somata were still observed by counterstaining with cresyl violet, but the sGnRH immunoreactivity was lacking and the hybridization signals were hardly detectable, suggesting that the ON neurons had stopped production of sGnRH on the spawning ground. Both the number of somata and the intensity of the signals of sGnRH neurons in the ON-OB also decreased during upstream migration. On the contrary, sGnRH neurons in the TC and POA showed a different cytophysiological pattern from those in the olfactory system. sGnRH-immunoreactive neurons were more abundant in the TC and POA in fish on the spawning ground, and the signals for pro-sGnRH mRNA were stronger than those in fish in the coastal sea. These findings suggest that sGnRH neurons in the ON and ON-OB have different pattern of sGnRH production from those in the TC and POA in the chum salmon during the homing migration.

Involvement of sGnRH in olfactory functions of masu salmon (*O. masou*) was also examined by means of immunocytochemical technique. sGnRH immunoreactive bipolar neuron, which might be related to the terminal nerve, is located in dorsal portion of the olfactory nerve in masu salmon as in chum salmon. Immunoelectron microscopy reveals the presence of sGnRH immunoreactive electron-dense granule-like structure of 50 nm in fibers of the olfactory nerve close to both the olfactory epithelium and to the olfactory bulb (Kudo et al. 1994). These findings suggest that sGnRH in the olfactory system might participate in neurotransmission and/or neuromodulation, and might have important roles in olfactory recognitions since the coastal sea stage is the most important time for discriminations of the natal stream odorants. In contrast, sGnRH in the TC and POA is considered to be participated in gonadal maturation, mainly in the stimulation of gonadotropin(s) release from the pituitary gonadotrophs.

It is now widely accepted that the functional roles of gonadal steroid hormones in salmonid gametogenesis are E_2 in vitellogenesis, 11KT in spermatogenesis, and DHP in final gameto-

maturation (Nagahama 1994). The shifts from E_2 to DHP in females and 11KT to DHP during homing migration as the predominant steroid in serum are also found in other salmonid species (Ueda and Yamauchi 1995). Although the roles of T in gamatogenesis have not been clarified yet, high serum levels of T are detected in many salmonid fishes of both sexes during the spawning period (Lou et al. 1986; Fitzpatrick et al. 1986; Mayer et al. 1992), and T was considered to be a substrate for E_2 and 11KT biosyntheses (Kagawa et al. 1982; Ueda et al. 1984b). During spawning migration of salmonids, serum T levels maintained high and declined after spawning (Truscott et al. 1986; Slater et al. 1994). The peak of plasma T levels in land-locked sockeye salmon of both sexes was observed at the time when they gathered at the mouth of natal stream in Lake Chuzenji (Ikuta 1996).

Recently, homing behavior of lacustrine sockeye salmon (*O. nerka*) in Lake Shikotsu has been studied in connection with changes in serum gonadal steroid hormone (Unpublished data). In males, the shortening of homing duration coincided with the increase of serum T and 11KT levels, and the reduction of homing percentage is associated with the decrease of serum T levels and the increase of serum DHP levels. In females, the shortening of homing duration corresponds with the elevation of serum T and DHP levels, and the drop of serum E_2 levels. Moreover, GnRH analog (GnRHa) implantation is highly efficient in shortening of homing duration, especially in females. The GnRHa treatment causes dramatical increase of serum DHP levels in both sexes on average, but early returned GnRHa-treated males show higher serum T levels and lower serum DHP levels than late returned ones. These results indicate that homing behaviors of lacustrine sockeye salmon are sexually different, and these differences may be reflected by changes in serum steroid hormone levels, particularly of T.

CONCLUSION

The present paper reviews several previous findings on the relations between homing migration and reproduction in chum salmon. Each salmonid species should have different strategies of homing migration using different sensory abilities which could be directly affected by hormone states. Further behavioral and molecular biological analyses using other salmonid species will help to clarify the mechanisms of homing migration and gonadal maturation as well as to evaluate the status of salmonid stocks.

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Numerical Simulations of Fraser River Sockeye Salmon Homing Migration Routes in a Dynamic Marine Environment

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A spatially-explicit individual-based model was used to simulate adult sockeye salmon return migration routes from the Gulf of Alaska to the Fraser River through temporally variable, spatially-explicit environmental fields. We wanted to examine whether coastal migration route variability could be explained by the interactions between simple behavior rules and a dynamic ocean environment described by historical temperature observations and estimated surface currents. Assuming that sockeye were broadly distributed throughout the central Gulf of Alaska prior to homeward migration, and that during homeward migration they oriented on a fixed compass bearing, the following mechanisms were invoked to produce migration route variations among years: 1) the distribution prior to homing was constrained by thermal limits, 2) sockeye were advected by surface currents during open ocean migration, and 3) sockeye tended to avoid high water temperatures. The behavioural component of the model was numerically optimized to maximize the fit between simulated and observed coastal migration routes, while maintaining swimming speeds and migratory timing consistent with the literature. The optimized model suggested that southern thermal limits and current advection could not explain much of the observed coastal migration route variability. The tendency to avoid high temperatures explained about 33% of the variation and suggested that coastal processes may be more important than offshore.



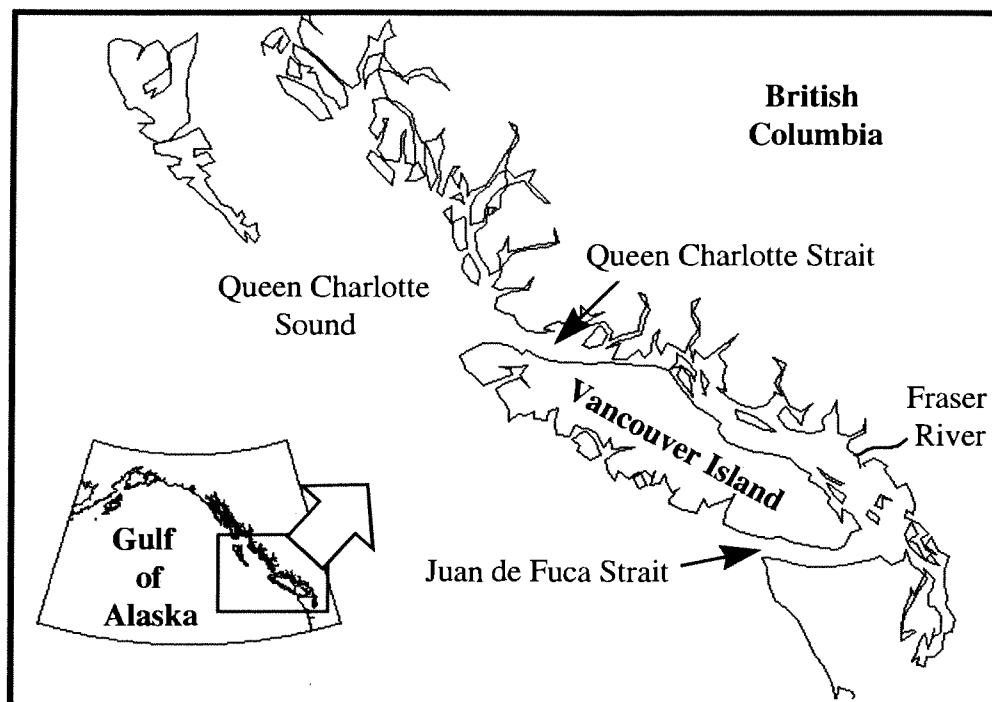
INTRODUCTION

Adult sockeye salmon (*Oncorhynchus nerka*) can return from the Gulf of Alaska to the Fraser River by migrating around either the north or south end of Vancouver Island (Fig. 1). The proportion of fish using the northern route (northern diversion rate) varies considerably among years, and it is not known what factors cause this variation. This variability is of theoretical interest to behavioural ecologists studying the mechanisms of salmon migration, but also has practical implications for fisheries managers attempting to meet complex harvest allocation and escapement objectives.

A number of studies have looked for an association between diversion rate variability and oceanographic variability. The most common oceanographic factors explored have included: 1) sea surface temperatures (SST) offshore or in coastal waters near the north end of Vancouver Island (Groot and Quinn 1987, Hamilton 1985, Hsieh et al. 1991, Royal and Tully 1961, Tully et al. 1960, Xie and Hsieh 1989), 2) coastal salinity patterns and the

volume of Fraser River discharge (Favorite 1961, Groot and Quinn 1987, Hamilton 1985, Xie and Hsieh 1989), or 3) currents (Groot and Quinn 1987, Hsieh et al. 1991, Thomson et al. 1992). These studies have generally involved either regressing the northern diversion rate time series onto various environmental indices, or describing contrast in oceanographic conditions associated with specific high and low diversion years. None of these published relationships has been shown to be consistent for the entire duration of the historical record. The proposed biological and oceanographic interactions were often either poorly defined, or the physical data were indexed at points in time and space where the proposed interaction could not have been direct. Continued use of this approach is not likely to substantially improve our understanding of the underlying mechanisms, because there is a high probability of describing spurious relationships (e.g. Walters and Collie 1989), and the appropriate scale of interaction cannot be defined when temporally and spatially variable environmental factors are condensed into a single annual index.

Fig. 1 Map of the coastal approaches to the Fraser River showing important locations referred to in the text.



As an alternative investigative approach, we used a process-based model to explore explicit, testable hypotheses about the effects of oceanic conditions on Fraser sockeye coastal migration routes on temporal and spatial scales relevant to the decision processes of individuals. Specifically, we chose to explore how sockeye migration routes could be affected by 1) the initial distribution in the NE Pacific Ocean, 2) advection by open ocean surface currents, and 3) SST preference behaviours. Marine distributions and migration routes of sockeye salmon are not well known, but there is empirical evidence suggesting that temperatures and currents may affect the sockeye distribution prior to and during the homing migration. Mark and recapture studies have suggested that during the year prior to homing, Fraser sockeye are located throughout the Gulf of Alaska (French et al. 1976). Welch et al. (1995) observed that the southern limit of the offshore sockeye distribution is associated with SST. It is not known what effect SST has during the marine phase of the homing migration, but high river temperatures can delay salmon migration into and within rivers (e.g. Major and Mighell 1966, Alabaster 1990). Presumably, avoidance of high temperature could also result in deflected trajectories of sockeye in marine areas. Similarly, Thomson et al. (1992) have shown that ocean currents in the Gulf of Alaska are strong enough and variable enough to have a substantial effect on the latitude at which homing

sockeye reach the coast. The two years which they examined, 1982 and 1983, corresponded to low and high diversion years, respectively. A small sample of Fraser River sockeye tagged on the north coast of British Columbia during these years also suggested that the Fraser sockeye were less abundant in northern coastal waters in 1982 relative to 1983 (Groot and Quinn 1987). We used a spatially-explicit, individual-based model to explore the potential effects of these three factors on coastal migration routes. Numerical optimization of behavioural parameters was used to maximize the fit between modelled and observed diversion rate time series, subject to external constraints which were imposed to maintain consistency with other biological observations. The potential importance of individual and combined mechanisms is examined.

METHODS

Northern Diversion Rate Time Series

The Fraser River sockeye salmon northern diversion rate is estimated annually from commercial fisheries catch data and in-river escapement monitoring, but the estimation methodology has never been published (Jim Woodey, Pacific Salmon Commission, 600 - 1155 Robson St., Vancouver, B.C., Canada, pers. comm.). There has not been any formal attempt to quantify diversion rate

variability within years or among stocks. However, there is no pattern in the time series to suggest that diversion variability is related to the 4 year cycles of abundance characteristic of Fraser sockeye. While there is an unknown amount of estimation error in the time series, it is certain that the extreme high and low events, that we are most interested in, are not the result of estimation errors.

Numerical Representation of the Physical Oceanography of the NE Pacific Ocean

The model domain covered the NE Pacific Ocean from 44-61°N and 123-160°W and incorporated temporal and spatial variability of observed SST and estimated surface currents in the open ocean region. The land mask was approximated on a 0.18 × 0.18 degree grid corresponding to the SST grid resolution, and the coastal region was defined as all areas within approximately 50 km of the land mask.

Gulf of Alaska SST was described by weekly Advanced Very High Resolution Radiometry (AVHRR) images (1982-94), obtained from the Physical Oceanography Distributed Active Archive Center at Jet Propulsion Laboratory/California Institute of Technology. Calibration and image processing details are provided at the web site http://podaac.jpl.nasa.gov:2031/DATASET_DOCS/avhrr_wkly_mcsst.html#17 (3 Oct 1997). Images were archived on an equal-angle grid with spatial resolution of approximately 0.18 × 0.18 degrees (19.5 × 19.5 km on the equator). Each weekly (approximately) image was a composite of numerous images produced during a week, and often considerable spatial interpolation was required to estimate temperatures beneath cloud cover. In our model, linear interpolation was used to estimate SST between the available image dates.

Surface currents within the model were approximated by hindcast output from the Ocean Surface Current Simulations (OSCURS) model described by Ingraham and Miyahara (1988, 1989). OSCURS currents are calculated as the vector sum of long term mean baroclinic geostrophic flow and daily wind driven surface flow. Sea level pressure fields are used to generate the wind driven current estimates over a rectangular grid of approximately 90 km resolution across the north Pacific Ocean. To reduce data storage requirements for our individual-based model, daily hindcast current observations (1982-94) were converted to monthly averages and interpolated onto a 1 degree grid. During simulations, bilinear spatial interpolation and linear temporal interpolation were used to estimate currents at specific points in time and space. Currents were reduced to 0 in coastal areas, because OSCURS does

not account for coastal geometry or tidal effects. There is at present no satisfactory means of hindcasting British Columbia coastal currents for the period of interest.

Numerical Representation of Sockeye Salmon Homing Migration Behaviour

Sockeye salmon homing migrations were simulated from the central Gulf of Alaska to the coastal approaches of the Fraser River. Fish that arrived at Queen Charlotte Strait or Juan de Fuca Strait were removed from the model and committed to either the northern or southern migration routes respectively. Fish which wandered out of the model domain or failed to reach Queen Charlotte Strait or Juan de Fuca Strait by the end of the simulation were not included in annual diversion rate calculations, but were recorded for homing success rate calculations. A complete run of the model involved simulating homing trajectories for years 1982-94 and calculating time series of annual diversion rates and homing success rates.

The model required a large number of parameters to describe behavioural interactions with the ocean environment and ensure reasonably successful homing rates (Table 1). These parameters contributed to one of the following roles: 1) establishing the initial sockeye distribution, 2) defining general orientation behaviour, 3) helping to avoid trapping in complex coastal geometry, or 4) describing interactions between sockeye and local SST.

The initial Fraser River sockeye distribution in the NE Pacific Ocean was described by the latitude, longitude and spread of the distribution. We assumed that the distribution was of uniform density and circular, roughly covering the central Gulf of Alaska as indicated by the French et al. (1976) summary of tagging studies. During the optimization procedure, the parameters describing the location and spread of the initial distribution were not constrained. However, one model scenario involved using seasonally-varying thermal limits to constrain the initial distribution. We assumed a simplified version of the seasonal thermal limits defined by Welch et al. (in press). Prior to Day-Of-Year (DOY) 170, the limit was 8°C, between DOY 170 - 190, the limit increased linearly to 12°C, and between DOY 190 and 250, the limit remained at 12°C. In the thermal limit scenario, fish were established according to the location and spread parameters, but as each simulation year was initialized, fish located in regions with SST exceeding the thermal limit were eliminated. The initial temperatures and thermal limits were averaged over the preceding 21 days under the assumption that fish take some time to

Table 1. Range of valid parameter values in the spatially-explicit individual-based migration model.

Parameter	min.	max.
latitude of initial distribution centre	48	55°N
longitude of initial distribution centre	140	150°W
radius of distribution	0	1000 km
initiation date for homing migration	150	190 DOY
swimming speed	20	60 km/d
open ocean compass bearing	0	360°
coastal compass bearing	0	360°
(inertial/compass) open ocean directional weighting	0	100
(inertial/compass) coastal directional weighting	0	100
open ocean directional precision	0	1
coastal directional precision	0	1
probability of reorienting to the compass (per timestep)	0	1
SST difference detection threshold	0	5°C
SST preference random factor	0	10°C
thermal limit adjustment factor	-4	4°C

react to changing temperatures and redistribute themselves.

During a simulated homeward migration, all sockeye used the same fixed compass bearing (which differed between open ocean and coastal regions) as the primary direction finding mechanism. Swim speeds were confined to limits suggested by tagging studies (French et al. 1976, Quinn 1988) and migration initiation dates were determined by the requirement for sockeye to return to the Fraser River during the interval DOY 170-250 (Killick and Clemens 1963).

A number of parameters were invoked largely to help fish migrate through complex coastal geometry that would trap individuals if they migrated on a compass bearing with perfect accuracy. These included: 1) a probability of reorienting to the compass bearing during a given time step, 2) an inertial directional component, which describes the tendency to keep migrating in the same direction, and 3) a coefficient of directedness, describing directional precision. These parameters provided a stochastic element to the orientation similar to those invoked by Pascual and Quinn (1991).

The interactions between fish and local SST consisted of a simple decision; whether or not to enter an adjacent SST box (0.18×0.18 degree AVHRR SST grid unit). On any given timestep, the fish had an initial migration direction. If the fish reached the border with an adjacent SST box, it either entered the box and continued swimming in the same direction, or it rebounded off the adjacent box like an elastic particle (if the fish struck land it always rebounded). The decision to enter or rebound was based on the relative difference in preference values between adjacent boxes. If the fish was moving from a lower preference value to a higher preference value it would always proceed, however,

if it was moving from higher to lower preference, the fish may have rebounded, depending on whether the magnitude of the difference exceeded a minimum detection threshold plus a stochastic decision element. All temperatures below the seasonally-varying thermal limit threshold were considered to be of equally high baseline preference value. Preference values for temperatures exceeding the thermal limit were lower than the baseline value by a factor proportional to the squared difference between the local SST and the thermal limit. The direct biological interpretation of this decision process was: fish detected physical conditions where they were at any given time, and could remember physical conditions experienced an average of ~10 km prior. The fish assessed water quality only in water masses that it directly experienced, and could only distinguish gradients over distances of ~18 km or less, and then only if a minimum detection threshold difference was exceeded. In this way, net migration from lower to higher preference water masses resulted from reactive movement away from undesirable areas, rather than a proactive movement into favourable areas.

Numerical Optimization with a Floating Point Genetic Algorithm

The migration model required many parameters, most of which could not be directly quantified from the literature. Therefore an objective optimization scheme was needed to test parameter combinations that potentially included all reasonable values. We used a floating point genetic algorithm (e.g. Michalewicz 1992) as a computationally intensive numerical method of fitting simulated and observed time series. This technique is merely an optimization tool, and we are not using it to imply anything about

salmon genetics or evolution. However, the floating point genetic algorithm is most easily described by functional analogy with genetic evolution. A single parameter is analogous to a gene, a complete set of model parameters is analogous to a genotype, and the superset of all genotypes can be thought of as the genepool. Genotype fitness in this case was calculated as the goodness of fit (R^2 , coefficient of determination) between modelled and observed coastal migration routes described below. The genetic algorithm calculated a fitness value for all genotypes from an initial arbitrary genepool, and then selected genotypes with highest fitness for the next generation, while low fitness genotypes were removed from the genepool. The genotypes in the new generation were subjected to random perturbations of parameters (mutations) and switching of groups of parameters (crossovers). Fitness values of the new genotypes were then calculated and the whole process was repeated until maximum fitness values no longer increased from one generation to the next.

Genotype fitness was calculated as the goodness of fit between modelled and observed coastal migration routes, subject to the following constraints: 1) swimming speeds had to be consistent with tagging studies, 2) arrival timing in coastal fisheries had to fall within the period from late June to early September, and 3) homing success rates had to exceed 70%. While there is no way of knowing what the actual homing success rate is, a navigational failure rate of 30% is probably much too high. However, without introducing more complex navigational behaviour, we were not able to produce both consistently high success rates, and substantial interannual migration route variation. We felt that a 70% success rate represented a trade-off between describing trajectories of the majority of the fish, and allowing us to explore potential effects of interannual oceanographic variations by not overly constraining the initial positions and orientation behaviour of the fish.

The coefficient of determination (R^2), was used as a comparative index of the goodness of fit between simulated and observed migration route time series:

$$R^2 = 1 - \text{ESS} / \text{TSS}$$

where:

ESS = Error Sums of Squares

$$= \sum_{i=1982}^{1994} (\hat{y}_i - y_i)^2,$$

TSS = corrected Total Sums of Squares

$$= \sum_{i=1982}^{1994} (y_i - \bar{y})^2,$$

$\hat{y}_i$ = simulated northern diversion rate in year i ,

y_i = observed northern diversion rate in year i , and

$\bar{y}$ = mean observed northern diversion rate 1982-94.

This value is equal to the familiar R^2 in least squares linear regression. However, in this case, predicted and observed values of y are not related by a least squares linear regression fit, so the properties of R^2 are slightly different. $R^2 = 1$ indicates that the modelled and observed time series are identical, $0 < R^2 \leq 1$ indicates that some of the variation around the mean diversion rate can be explained by the model, and $R^2 < 0$ indicates that the mean diversion rate is a better fit to the time series than the model result. The coefficient of determination was used as a relative measure to evaluate and compare alternative models, but we did not attempt to assess the statistical significance of these models.

The genetic algorithm may not find a global optimum solution, because parameter combinations may become trapped in local optima, and the stochastic behaviour of the fish may obscure the true optimum. However, this method should identify solutions that are reasonably close to the global optimum if it exists over a reasonably large parameter space. Substantially different parameter combinations may yield similar goodness of fit values because two parameters may have offsetting effects. For example, a late initiation date and fast swimming speed may yield essentially the same result as an early initiation date and a slow swimming speed. In this study, the role of the numerical optimization was to quantify (approximately) how much coastal migration route variability could be explained by each behavioural/oceanographic mechanism. Thus, the relative explanatory power of each mechanism is of primary importance, while the actual parameter values are of secondary interest and not reported.

This method of optimization raises two important concerns: 1) because there are so many parameters in the model, the genetic algorithm may be able to produce good, but spurious, coherence between modelled and observed coastal migration routes using any mechanism, or conversely 2) the genetic algorithm may not be able to optimize the model adequately, so that the explanatory power of one or more mechanisms could be severely underestimated. If the first situation occurred, it would be obvious. If the second situation occurred, it would not be detectable, and the apparent effects of the different mechanisms would be the result of random events during optimization. We attempted to address this concern by using the migration model as a reference model. An arbitrary set of parameters was selected to produce a time series of coastal migration routes

with substantial interannual variability. Then the genetic algorithm was used to optimize the model from random initial conditions. This process was repeated a number of times and we found that the optimized model could consistently explain a substantial amount of the migration route variability ($0.75 < R^2 < 0.97$). Individual parameters often varied substantially between the reference model and the optimized model, but the relative contribution of the different mechanisms changed relatively little. This gives us some confidence that the optimization procedure performs as we hoped, but we cannot be certain that it is effective in all situations.

Stepwise Assessment of Mechanisms Potentially Affecting Coastal Migration Routes

The effects of three mechanisms on coastal migration route variability were explored:

- 1) the Fraser sockeye distribution prior to migrating is constrained by thermal limits
- 2) sockeye salmon are advected by offshore surface currents in the Gulf of Alaska
- 3) sockeye tend to avoid water temperatures that are bioenergetically unfavourable.

The model was optimized several times, first to examine the effects of each mechanism independently, and then to examine the mechanisms in combination. The SST constraints and high SST avoidance behaviours were removed to optimize the model for current variability alone. To optimize the model for either SST constraints or high SST avoidance alone, year-specific monthly currents were replaced by monthly mean currents averaged over the years 1982-94.

RESULTS

Sockeye orientation in the optimized models always included a somewhat eastward directional preference in offshore waters, and a south-eastward directional preference in coastal waters. Thus, successful sockeye always arrived at the coast somewhere north of Juan de Fuca Strait and then followed the coast south.

Effects of Thermal Constraints on the Sockeye Distribution Prior to Homing

Thermal constraints on the sockeye initial distribution did not explain very much of the northern diversion rate variability ($R^2 = 0.07$). In the optimized model, thermal limit constraints had the greatest effect on the initial distribution in 1983, and no effect in several other years (Fig. 2). In a

few years, the distributions were marginally affected on the southern and eastern boundaries, while northern and western boundaries were always unaffected.

The model is not able to produce both high and low diversions with a single parameter combination because constraints essentially affect only the south-east boundary. As the distribution contracts along this boundary, the number of southern migrants decreases, resulting in an increase in the proportion of northern migrants. As the boundary extends southward, the number of southern migrants increases, but the number of northern migrants remains the same. Without a concurrent decrease in the number of northern migrants, the northern diversion rate cannot reach very low values. Of course, the northern diversion rate could take very low values if the preferred compass bearing was shifted to the south, but then the problem would be reversed and very high diversion rates would not be attainable.

Effects of Current Advection

Current advection in the offshore oceanic region did not explain any of the observed coastal migration route variability ($R^2 = 0$). Mean migration trajectories of salmon in offshore waters (Fig. 3) indicate that currents do not produce large route deviations relative to the width of the optimized initial distribution. Since offshore currents are the only mechanism introducing variability in this case, variability in the latitude of arrival in coastal waters determines the diversion rate. All fish are affected by interannual current variation, but when the initial distribution is broad, only a small proportion are positioned so that the current displacement causes them to switch between northern and southern routes. If the initial distribution is very narrow, then the proportion of fish which change routes may be much greater. However, the genetic algorithm could not identify any broad or narrow initial distributions that would indicate that current variability was consistent with the diversion rate time series.

Effects of a Behavioural Tendency to Avoid High SST During Homing Migration

The behavioural tendency to avoid high SST explained the most northern diversion rate variability ($R^2 = 0.33$). The optimal parameter set was unexpected in that the initial distribution was essentially a point source (20 km diameter) and open ocean migration precision was essentially perfect (coefficient of directedness = 0.98). This resulted in a single mass of fish arriving simultaneously in the coastal waters north of Vancouver Island (Fig. 4).

Fig. 2 Range of sockeye salmon initial distributions that resulted when the migration model was optimized with thermal limit constraints on the initial distribution. 1983 demonstrated the most restricted distribution, while 1987 (and some other years) were not affected by thermal limits.

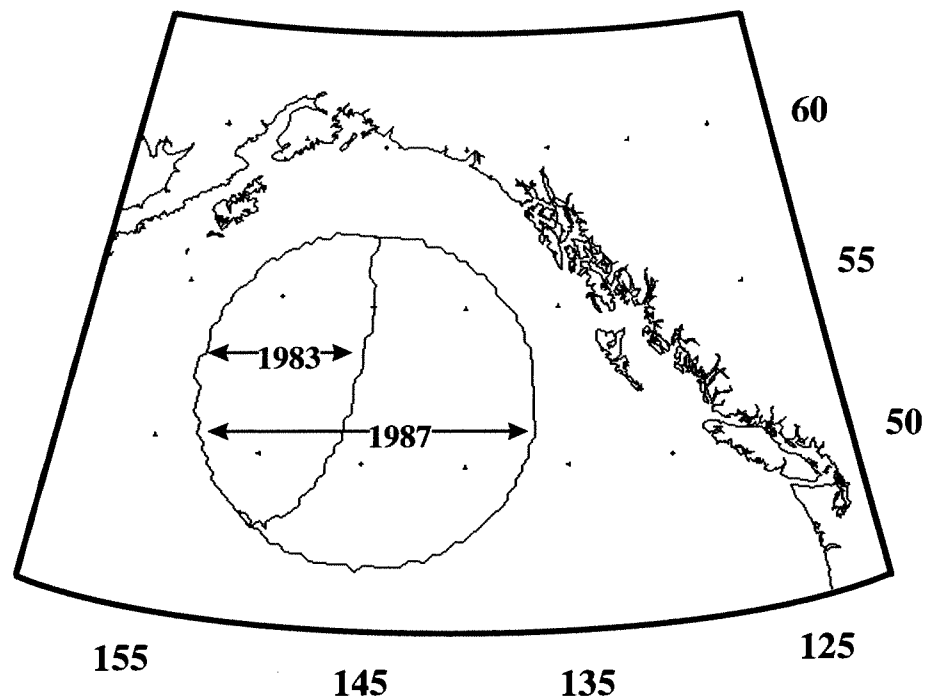


Fig. 3 Initial distribution and mean migration trajectories that resulted when the model was optimized with offshore current variability. The large circle outlines the initial distribution; each line connecting the distribution centre to the coast represents the mean open ocean trajectory of all individuals from a single year (1982-94).

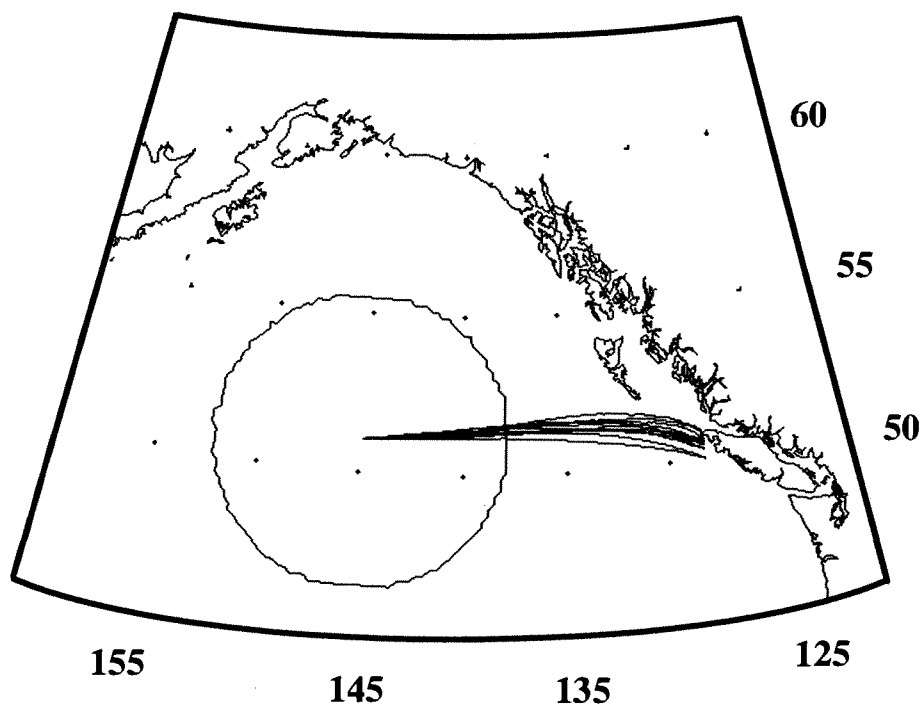
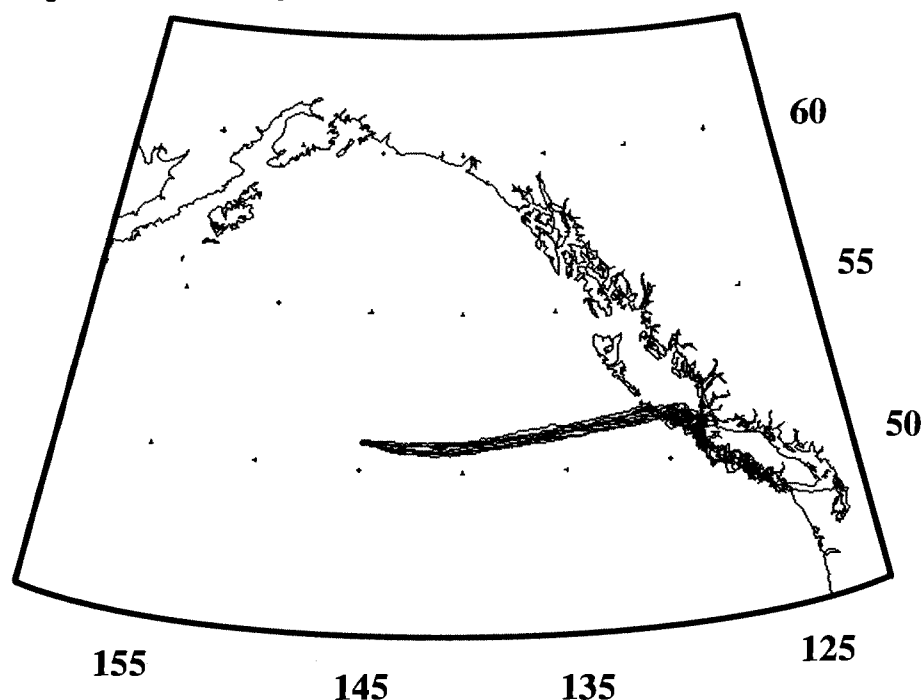


Fig. 4 Typical trajectories that resulted when the model was optimized with a behavioural tendency to avoid high SST. Ten trajectories from 1982 are shown, and are representative of the precise open ocean migration and more dispersed coastal migration observed in all years. The initial distribution was essentially a point source.



The open ocean trajectories did not differ much among years, and the fish rapidly dispersed in coastal waters (only 10 trajectories from a single year are shown because the overlapping paths are confusing and uninformative). The comparison of modelled and observed diversion rates (Fig. 5) indicates that the model did not produce much diversion variability.

The model did simulate higher than average diversions in the four high diversion years (1983, 1992-94), but not nearly as high as observed. Only 1990 appeared as a very low diversion year in the simulations, similar to the observed value. The highest and lowest diversion years in the simulations (1983 and 1990 respectively), were also two of the warmest years along the British Columbia coast. This demonstrates that the high SST avoidance behaviour can result in both high and low diversions depending on the fine scale SST spatial distribution. Thus, defining the appropriate scale of interaction between salmon and SST may be critical for understanding migration routes.

We also optimized this model with the additional constraint that the initial distribution had to be greater than 500 km in diameter, but in this case, much less diversion rate variability could be explained ($R^2 = 0.12$).

Effects of Combined Mechanisms

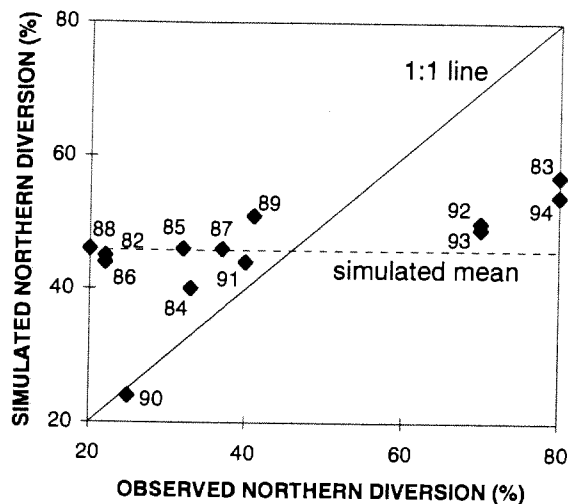
The northern diversion rate variability explained

by individual and combined mechanisms is summarized in Table 2. Combined mechanisms did not result in any increased explanatory power. When high SST avoidance and thermal limit constraints were combined, the thermal limits did not actually have any effect in the optimized models because the initial distribution was essentially a point source as described above. The slight decrease in explained variation resulting from the addition of currents to thermal limits or high SST avoidance further suggests that current variability does not covary with diversion rates, but may also indicate imperfect optimization.

Table 2. Goodness of fit between modelled and observed Fraser River sockeye salmon coastal migration routes (1982-94). Behavioural parameters were optimized independently for each individual mechanism and each combination of mechanisms.

Mechanism	$R^2 \times 100$
(1) thermal limit constraints on the initial distribution	7
(2) offshore current advection	0
(3) behavioural avoidance of high SST	33
(1) & (2)	5
(1) & (3)	33
(2) & (3)	29
(1) & (2) & (3)	29

Fig. 5 Comparison of simulated and observed annual northern diversion rates (1982-94) generated when the model was optimized with a behavioural tendency to avoid high SST. Individual years are labeled.



DISCUSSION

Our model was unable to reproduce the Fraser sockeye northern diversion rate time series well enough to demonstrate the viability of a causal hypothesis, or to be a useful predictive tool for fisheries management. The failure of the model to explain more of the northern diversion rate variability was most likely due to two main factors: 1) inappropriate representation of salmon behaviour, and 2) inappropriate representation of the NE Pacific oceanography. Incomplete optimization and errors in the observed northern diversion rate time series are probably of lesser importance. However, the model has provided insight into the workings of the system and the results suggest directions for additional modelling and field studies.

Our representation of salmon behaviour was obviously simplistic. We ignored interactions between behaviour and all environmental stimuli except for SST (and the static stimuli required for salmon to distinguish open ocean and coastal regions, land, and compass directions). Our representation of navigation behaviour was the simplest that we could conceive of, such that fish could reach the coastal approaches to the Fraser River from vastly different initial positions. However, the low homing success rates attained in some years (approaching 70 %), suggests that additional behaviours are likely important. Some kind of longer term memory could help fish avoid becoming trapped in coastal geometry or prevent substantial delays in regions of high water temperature which could be handled most efficiently with more directed swimming. With simple compass navigation, fish may bypass their coastal target, and fail to return

home because there is no provision for turning around (but we do not know if this is a problem in reality). The assumptions that the initial distribution was uniform, and that all stocks began migrating at the same time is also likely unrealistic. Different coastal migratory timing observed for different stocks (Clemens and Killick 1963) suggests that either the stocks occupy different areas of the ocean, they start migrating at different times, they swim at different rates or they follow different routes. The model would have to be optimized separately for each stock to account for this variability, but the biological data are not sufficient to describe stock-specific variations in any of these features.

Our results suggested that the offshore processes that we defined could not explain as much northern diversion rate variability as coastal processes. If all salmon orient on a similar compass bearing, and offshore distributions are as broad as field studies have suggested (French et al. 1976, Welch et al. 1995), then it is unlikely that thermal limits and offshore currents could produce both very high and very low diversion rates. Broad initial distributions also prevented SST avoidance behaviour from reproducing observed diversion rates, but we did not explore whether this behaviour was capable of producing arbitrarily high and low diversions. However, if all fish arrive north of Vancouver Island in a tight spatial distribution and narrow time window, then SST preference behaviours can reproduce a substantial amount of northern diversion rate variability. This supports the notion that initial conditions prior to migrating do not necessarily influence diversion rates. If the migration route decision is made at essentially the same coastal location by all fish, then offshore processes may be largely irrelevant. For this to occur, there would have to be some mechanism aggregating the fish. The most obvious aggregation occurs as sockeye swim eastward and 'pile up' on the coast. If the majority of the fish arrive on the coast north of Vancouver Island, they will all migrate through a relatively narrow corridor in the Queen Charlotte Sound area, although the timing will not be synchronous. Thus the coastal migration route decision process could be determined in a very confined area despite a broad and variable open ocean distribution.

We did not expect to explain much coastal migration route variability with coastal processes because the model timestep and physical oceanographic representation were more appropriate for open ocean processes. The AVHRR SST images probably provided adequate resolution in time and space for the offshore processes that we were describing. These images do not resolve mesoscale SST variability very well, and this is probably a more serious problem in coastal areas. Relative to offshore

waters, British Columbia coastal oceanography is characterized by steep SST gradients, and complex tidal, wind driven, and buoyancy-driven currents. This coastal heterogeneity was not well represented in our model, so we cannot confidently describe the potential interactions between salmon and oceanographic variability in the region north of Vancouver Island. Our model results demonstrated that high SST avoidance behaviours could explain some of the interannual migration route variability, and suggested that the system might be very sensitive to the scale of interaction. High annual temperatures could produce both high and low diversions, depending on the SST spatial distribution. If the important temporal and spatial patterns are not described with the appropriate resolution, substantial errors will likely eventually result from any predictive model, even if the underlying processes are essentially understood. In this system, predictive correlation models based on annual indices and vague understanding of important processes are probably doomed to predictive failure.

Our results suggest that further research into the mechanisms driving migration route variability should be focused on the coastal region, particularly around the north end of Vancouver Island. Seemingly small interannual variations in coastal SST distributions or Fraser River northward flow patterns may have a large effect on coastal migration routes. Simulation modelling of fine scale interactions between coastal oceanographic variability and fish behaviour may help to further define critical decision points in the migration route, however, the mechanisms that drive migration route variability will never be adequately described without additional field studies. Detailed observations of sockeye migration trajectories may help to quantify the important behaviours. It may be informative to observe how trajectories of individuals around the north end of Vancouver Island relate to mesoscale oceanographic variability, especially SST and salinity gradients. Although if the important factors are difficult to measure (e.g. Fraser River odours), individual trajectories may not be informative. If consistent behaviours could be identified, and quantitatively described, we could work toward understanding the spatial and temporal scales of interaction, and modify our migration models accordingly.

CONCLUSIONS

- 1) Seasonally-varying thermal limits constraining the sockeye distribution in the Gulf of Alaska are not likely to be a sufficient mechanism to explain Fraser sockeye coastal migration route variability.
- 2) Offshore currents in the Gulf of Alaska do not appear to be sufficient to explain Fraser sockeye

coastal migration route variability.

- 3) A behavioural tendency for sockeye to avoid high SST while migrating could explain a substantial amount of Fraser sockeye coastal migration route variability, and it appears that this behaviour may be most important in the coastal region north of Vancouver Island.

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We thank David Welch and an anonymous reviewer for helpful suggestions, Leonardo Huato for his plotting code, Jim Ingraham for providing us with OSCURS current vectors, and James Scandol and Emily Walter for condensing the current vectors. This work was funded by an NSERC strategic grant to MH.

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Blood Plasma Levels of Insulin-Like Growth Factor-I in Pacific Salmon in Offshore Waters in Winter

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This paper reports on the first study of blood plasma levels of insulin-like growth factor-I (IGF-I) in Pacific salmon (*Oncorhynchus* spp.) in offshore waters of the North Pacific Ocean. Environmental and physiological regulation of salmon growth in offshore waters is poorly understood. Physiological indices of growth are needed to better understand the factors that affect ocean production of salmon. IGF-I is an important regulator of growth and development in teleosts. Previous research has shown that seasonal increases in IGF-I in salmon precede rapid growth, and may be associated with environmental cues (water temperature, photoperiod). We collected blood samples from salmon caught by research trawl in three regions of the North Pacific Ocean (western, central, eastern) during an offshore survey in January 1996. Plasma IGF-I levels were determined by radioimmunoassay. All of the samples were analyzed by the same assay so that inter-and intra-specific comparisons could be made. Mean IGF-I levels were significantly different among the five species sampled: pink (*O. gorbuscha*; mean = 28 ng/ml, n = 14), chum (*O. keta*; mean = 33 ng/ml, n=28), chinook (*O. tshawytscha*; mean = 48 ng/ml, n = 15), sockeye (*O. nerka*; mean = 84 ng/ml, n = 13), and coho (*O. kisutch*; mean = 120 ng/ml, n =26) salmon. High levels of IGF-I in coho salmon correlates with high growth rates in this species found in other studies. There were significant positive correlations between body weight, liver weight, and IGF-I levels in all species except pink salmon. Samples were not collected at enough stations to adequately evaluate correlations between IGF-I and environmental factors. There were significant intra-specific differences in mean IGF-I levels by ocean age and region. Size of age .1 pink salmon was not significantly different by ocean region, but mean IGF-I levels in pink salmon were significantly higher in the eastern North Pacific than in the western region, which may indicate earlier resumption of rapid spring growth in the Gulf of Alaska. Similarly, body size and IGF-I levels in age .1 coho salmon were significantly higher in the eastern North Pacific, than in the central region. We conclude that IGF-I may be a useful measure of ocean growth rates of salmon in the North Pacific Ocean, but additional data on the significance of high or low levels of IGF-I are needed.



INTRODUCTION

Environmental and physiological regulation of growth of Pacific salmon (*Oncorhynchus* spp.) in offshore waters is poorly understood. Physiological indices of growth are needed to better understand the

factors that affect ocean production of salmon. Insulin-like growth factor-I (IGF-I), a 70-amino-acid polypeptide, is an important regulator of growth and development in mammals, birds, and teleosts (e.g., Bern et al. 1991; Kikuchi et al. 1991; Cohick and Clemmons 1993; Duan et al. 1994, 1995). In yearling

coho salmon (*O. kisutch*) held in seawater net pens, seasonal (springtime) increases in IGF-I precede rapid growth, and are associated with environmental (photoperiod, water temperature, food availability) cues (Duan et al. 1995).

Factors affecting changes in the ocean growth of salmon were identified by the North Pacific Anadromous Fish Commission as a critical issue for research (NPAFC 1996). In January 1996, we initiated a cooperative Japan-U.S. study of blood plasma levels of IGF-I in salmon caught during a trans-Pacific survey (Ueno et al. 1996). In this paper, we present the first information on plasma levels of IGF-I in salmon caught in offshore waters. We evaluate inter- and intra-specific differences in IGF-I by sex, age, and ocean region (western, central, and eastern North Pacific) and correlations between IGF-I levels and various biological and environmental factors.

METHODS

Study Area and Biological and Oceanographic Sampling

Samples were collected aboard a Fisheries Agency of Japan (FAJ) research vessel, R/V *Kaiyo maru*, during a cooperative NPAFC-related trans-Pacific salmon survey in January 1996 (Ueno et al. 1996). A large surface rope trawl (208-m long, 63.2-m headrope, and 400-m warp) was used to catch salmon in three offshore regions (western, central, and

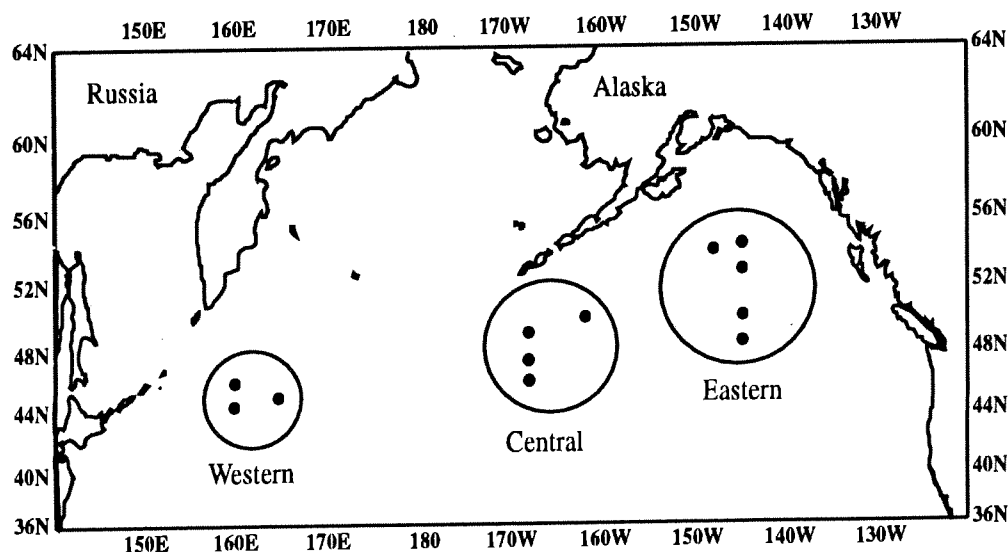
eastern North Pacific Ocean; Fig. 1). A CTD was used to collect data on conductivity, temperature, depth, and dissolved oxygen before or after trawl operations. Seawater was collected by a bucket at the surface and by a CTD rosette sampling system. Seawater nutrients (nitrite-nitrate, silicate, phosphate) and chlorophyll-a were determined from seawater samples within a day of sampling.

Biological Data and Ocean Age Determination

After the net was hauled, salmon in the catch were immediately sorted to species, scales were collected for age determination, the fish were measured (fork length and body weight), blood samples were taken, and the fish were frozen whole (-40°C). After the R/V *Kaiyo maru* returned to Japan, the frozen fish samples were transferred to the National Research Institute of Far Seas Fisheries, FAJ, where additional biological data (sex, gonad weight, liver weight, and stomach content weight) were collected.

Ocean ages of salmon were determined by scientists at the Fisheries Research Institute, University of Washington, from counts of annuli on acetate impressions of scale samples. Ocean age is designated by the European method (a period followed by a number, which is the number of ocean annuli or winters in the ocean). By convention, all salmon caught on the high seas after 1 January are one year older, even if an annulus has not yet formed at the edge of the scale.

Fig. 1 Map showing locations where salmon were sampled for blood during the January 1996 salmon research cruise of R/V *Kaiyo maru* in the western, central, and eastern regions of the North Pacific Ocean.



Blood Sampling and Measurement of IGF-I

We attempted to collect blood samples from at least 15 fish per species over the entire survey area (Fig. 1). Blood samples were drawn from the caudal veins of fish (within approximately 1/2 hr after landing) using 10-ml vacuum tubes and holders or syringes fitted with 19-gauge needles. Plasma was separated by centrifugation at 3000 rpm for 15 min. The plasma was auto-pipetted into 1.5-ml cryo-tubes (approximately 1.0 ml of plasma), and stored in a shipboard freezer (-70°C). During the U.S. port call of the R/V *Kaiyo maru*, the frozen plasma samples were transferred to a freezer (-80°C) at the Northwest Fisheries Science Center, National Marine Fisheries Service. Plasma levels of IGF-I in the samples were measured by a homologous radioimmunoassay (RIA; Moriyama et al. 1994). All of the samples were analyzed by the same RIA so that inter- and intra-specific comparisons could be made. Samples with plasma IGF-I levels outside of the area of sensitivity of the RIA were not included in the statistical analyses.

Statistical Analyses

The purposes of our statistical analyses were to evaluate: (1) if the fish in the IGF-I samples were representative of the entire catch, (2) inter-specific differences in plasma IGF-I levels, (3) correlations between IGF-I levels and various biological and environmental variables, and (4) inter- and intra-specific differences in IGF-I levels by sex, age, and ocean region. To evaluate whether fish in the IGF-I samples were representative of the entire catch, body weights of the fish in the IGF-I and non-IGF-I (those fish not sampled for IGF-I) samples were compared by analysis of variance (ANOVA; Super-ANOVA, Abacus Concepts, Berkeley, CA). Inter- and intra-specific differences in plasma IGF-I levels were assessed by ANOVA and Tukey multiple comparisons tests. Plasma IGF-I levels and other biological variables (length, body weight, liver weight, gonad weight, stomach content weight, stomach content index [$100 \times \text{stomach content weight/body weight}$], and condition factor [$\text{body weight (g)/fork length (mm)}^3 \times 10^3$]) were tested for correlations (Pearson r statistics, significance tested by Fisher's r to z transformation; StatView, Abacus Concepts, Berkeley, CA). Mean plasma IGF-I levels and environmental data collected at each station (sea surface temperature, surface salinity, surface dissolved oxygen, surface chlorophyll- a , surface nutrients: silicate, phosphate, and nitrate+nitrite) were also tested for correlations. Statistical differences at the $p < 0.05$ level were considered to be significant.

RESULTS

Samples from 98 fish were analyzed by RIA for plasma IGF-I levels: 13 sockeye (*O. nerka*), 29 chum (*O. keta*), 15 pink (*O. gorbuscha*), 26 coho, and 15 chinook (*O. tshawytscha*) salmon. One pink salmon and one chum salmon had IGF-I levels outside of the range of sensitivity of the RIA, and were not included in the statistical analyses. The mean body weights of sockeye and chum salmon in the IGF-I samples were significantly larger than in the non-IGF-I samples (sockeye: $p = 0.03$; chum: $p < 0.01$). There were no significant differences in mean body weights between samples for the other species (pink: $p = 0.08$; coho: $p = 0.20$; and chinook: $p = 0.99$). In the central and eastern regions, the mean body weights of sockeye and chum salmon in the IGF-I samples were larger than those in the entire catch. The mean weights of all species except pink salmon in both the IGF-I samples and in the entire catch increased from west to east across the North Pacific in January (Fig. 2a, b).

For samples pooled over all sex, size, and age groups and ocean regions, mean IGF-I levels were significantly different among the five species sampled: pink (mean = 28 ng/ml, $n = 14$), chum (mean = 33 ng/ml, $n = 28$), chinook (mean = 48 ng/ml, $n = 15$), sockeye (mean = 84 ng/ml, $n = 13$), and coho (mean = 120 ng/ml, $n = 26$) salmon ($p < 0.01$, Table 1). A multiple comparisons test indicated that plasma IGF-I levels in pink, chum, and chinook salmon were not significantly different; levels in pink and chum salmon were significantly different than in sockeye and coho salmon; levels in chinook salmon were significantly different than in coho salmon, but not in sockeye salmon; and levels in sockeye and coho salmon were not significantly different.

Correlations between IGF-I and the biological and environmental variables varied among the species (Table 2). For all species except pink salmon, fork length, body weight, and liver weight were positively correlated with IGF-I levels, and condition factor was negatively correlated with IGF-I levels (Fig. 3, Table 2). Pink salmon IGF-I levels were not correlated with any of the biological variables. Because IGF-I samples from sockeye and pink salmon were collected at only three stations, they were not analyzed for correlations with the environmental data. For chum, chinook, and coho salmon, none of the correlations between mean IGF-I and the environmental data were statistically significant (Table 3).

The species and age composition of fish in the R/V *Kaiyo maru* catches and IGF-I samples varied considerably by ocean region (Ueno et al. 1996; Table 1, Fig. 2). All of the chum, pink, and chinook salmon caught in the western North Pacific were age .1. No sockeye or coho salmon were caught in the western

Fig. 2 Mean body weights and plasma IGF-I levels in five species of salmon by region of the North Pacific Ocean in January 1996. (a) Mean body weight of salmon in IGF-I sample; (b) mean body weight of salmon in the January 1996 *Kaiyo maru* catch; (c) mean levels of plasma IGF-I. Values are mean + SEM. The numbers over the SEM bars in (a) and (b) are sample size.

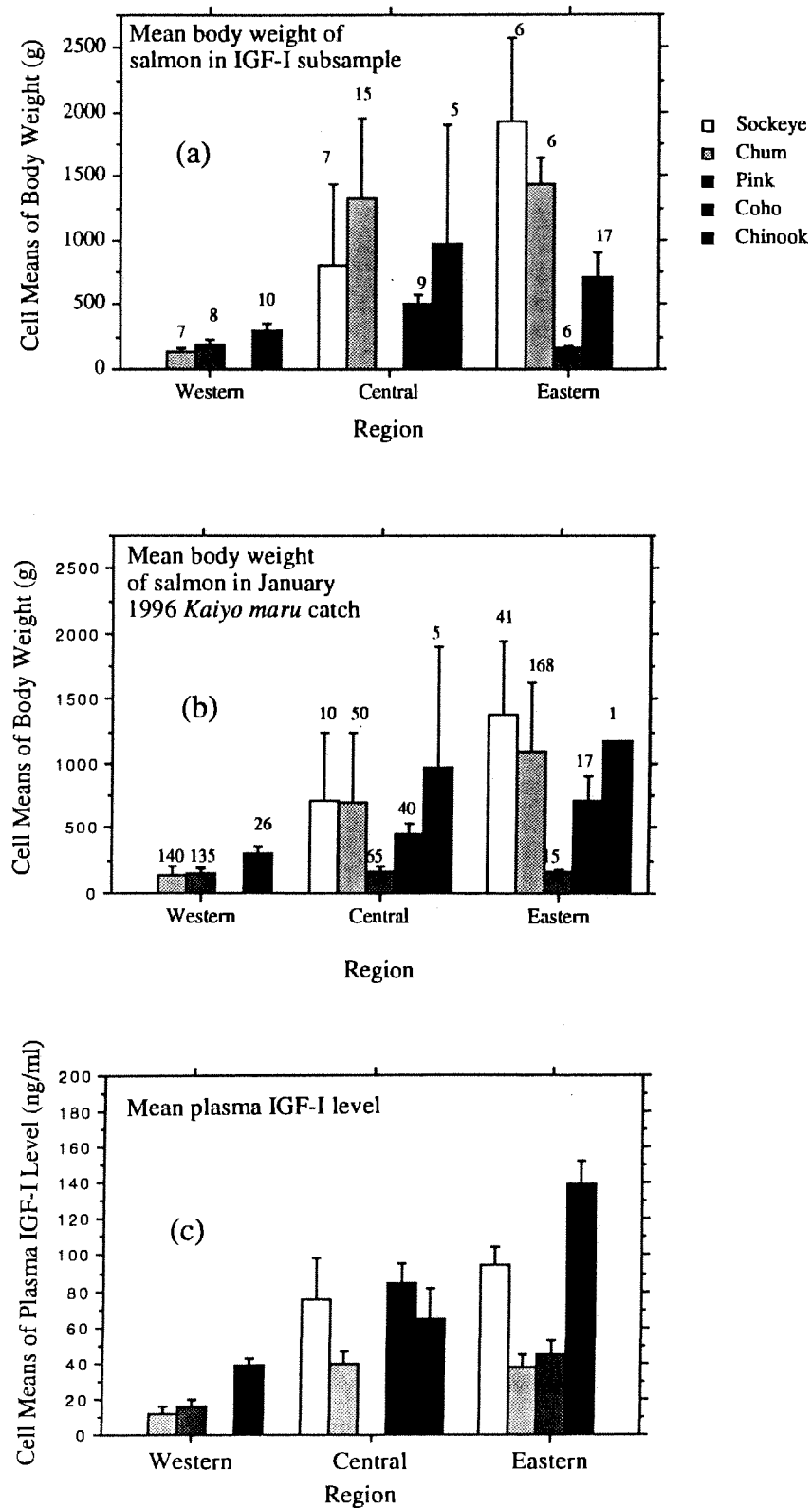


Table 1. Sample size (n) by species, ocean region, and age group, and mean and standard deviation (S.D.) of plasma IGF-I levels.

Species	Region	Age .1			Age .2			Age .3			Age .4			Total		
		n	mean	S.D.	n	mean	S.D.	n	mean	S.D.	n	mean	S.D.	n	mean	S.D.
Sockeye	Western															
	Central	1	44.3		5	54.5	9.8	1	211.4					7	75.5	60.6
	Eastern				1	101.9		5	92.8	27.3				6	94.3	24.7
	Total	1	44.3		6	62.4	21.3	6	112.6	54.2				13	84.2	46.8
Chum	Western	7	12.3	9.9										7	12.3	9.9
	Central				6	16.5	7.3	4	65.2	16.4	5	48.2	26.4	15	40.0	26.8
	Eastern				1	61.9		5	33.0	14.2				6	37.8	17.3
	Total	7	12.3	9.9	7	22.9	18.4	9	47.3	22.1	5	48.2	26.4	28	32.6	24.4
Pink	Western	8	16.1	9.7										8	16.1	9.7
	Central															
	Eastern	6	44.5	20.3										6	44.5	20.3
	Total	14	28.3	20.6										14	28.3	20.6
Coho	Western															
	Central	9	84.5	33.1										9	84.5	33.1
	Eastern	17	138.9	55.3										17	138.9	55.3
	Total	26	120.1	54.8										26	120.1	54.8
Chinook	Western	10	38.8	14.0										10	38.8	14.0
	Central	3	59.6	41.7	2	73.5	39.2							5	65.2	36.2
	Eastern															
	Total	13	43.6	22.8	2	73.5	39.2							15	47.6	25.8
Total n		61			15			15			5			96		
% of total		63.5			15.6			15.6			5.2					

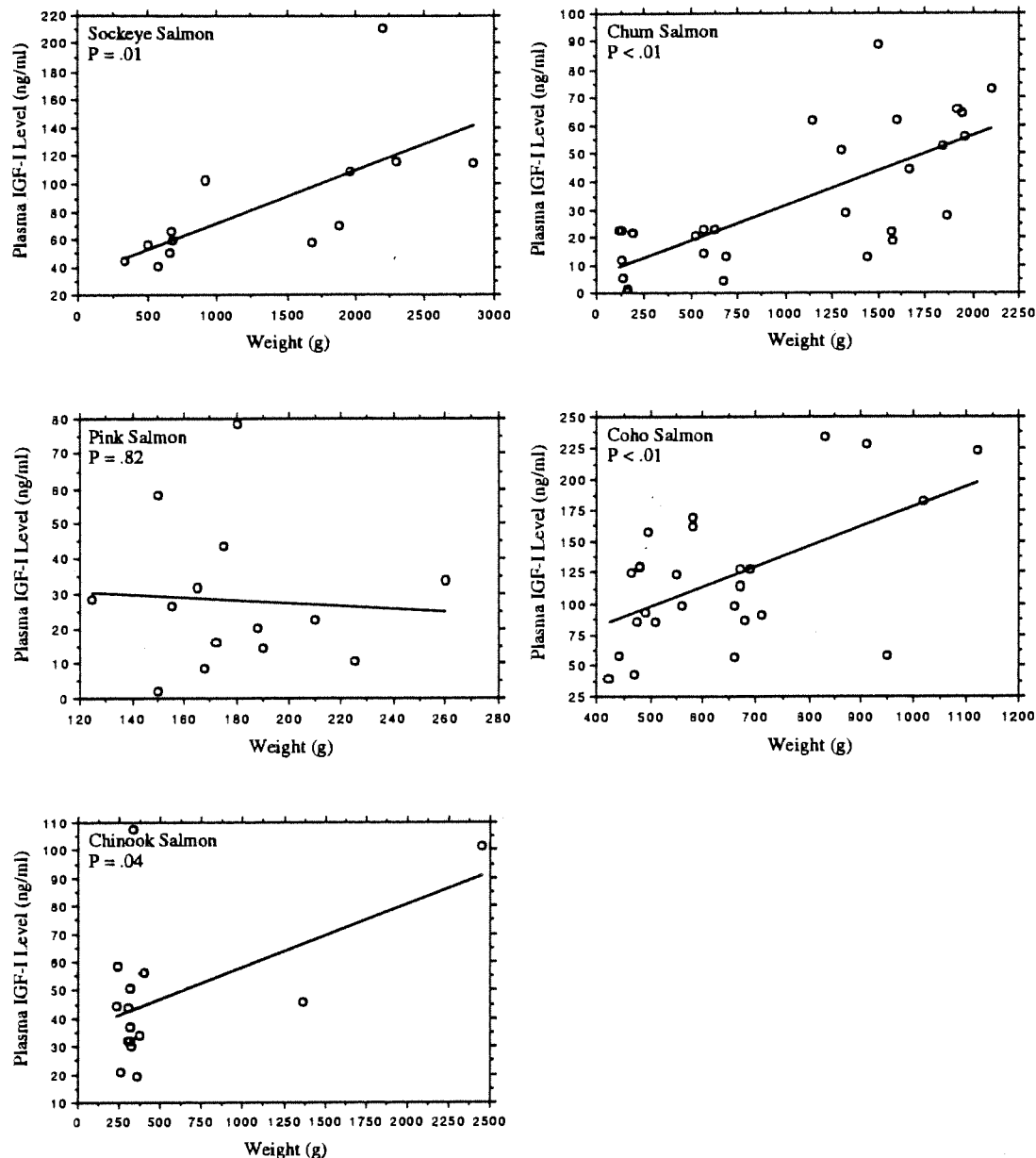
Table 2. Correlations (Pearson r) between plasma IGF-I levels and other biological variables by species. * = statistically significant.

Variables	Sockeye		Chum		Pink		Coho		Chinook	
	r	P-value	r	P-value	r	P-value	r	P-value	r	P-value
Fork length	0.699	0.0062 *	0.654	<0.0001 *	0.008	0.9779	0.538	0.0039 *	0.490	0.0632
Body weight	0.682	0.0084 *	0.723	<0.0001 *	-0.068	0.8225	0.557	0.0026 *	0.524	0.0439 *
Liver weight	0.588	0.0327 *	0.651	0.0001 *	0.376	0.1903	0.519	0.0058 *	0.582	0.0212 *
Gonad weight	0.512	0.0738	0.069	0.7305	0.065	0.8282	-0.216	0.2933	0.580	0.0218 *
Stomach content weight	0.321	0.2919	0.443	0.0172 *	-0.179	0.5495	-0.093	0.6553	-0.100	0.7278
Stomach content index	0.213	0.4939	-0.109	0.5847	-0.241	0.4142	0.254	0.2138	-0.299	0.2853
Condition factor	-0.632	0.0186 *	-0.583	0.0009 *	0.095	0.7520	-0.545	0.0034 *	-0.418	0.1231
Number of observations	13		28		14		26		15	

Table 3. Correlations (Pearson r) between mean plasma IGF-I levels and environmental variables by species. None of the correlations were statistically significant.

Variables	Chum		Coho		Chinook	
	r	P-value	r	P-value	r	P-value
Sea temperature	-0.141	0.7764	0.288	0.6751	0.450	0.4927
Salinity	-0.599	0.1669	-0.386	0.5653	-0.763	0.1555
Dissolved oxygen	0.253	0.6048	-0.023	0.9739	-0.125	0.8594
Chlorophyll-a	-0.577	0.1884	-0.047	0.9467	-0.416	0.5316
Silicate	0.629	0.1392	-0.075	0.9153	0.744	0.1750
Phosphate	-0.404	0.3911	0.385	0.5654	-0.659	0.2630
Nitrite-Nitrate	-0.119	0.8109	0.205	0.7685	-0.582	0.3465
Number of observations	7		5		5	

Fig. 3 Scatter plots showing correlations (Pearsons r) between plasma IGF-I levels and body weight in five species of salmon sampled in the North Pacific Ocean in January 1996. Regression lines are also plotted.



North Pacific. All of the pink and coho salmon in the catches were age .1 (first winter in the ocean). Pink salmon were caught in all regions, but they were not sampled for IGF-I in the central region. The ages of sockeye, chum, and chinook salmon increased from west to east across the North Pacific. Only one chinook salmon was caught in the eastern region, and was not sampled for IGF-I. For samples pooled over all regions, there were no significant differences in mean IGF-I levels by sex for pooled ages .2 and .3 sockeye ($p = 0.75$), age .1 pink ($p = 0.97$), age .1 coho ($p = 0.09$), age .1 chinook ($p = 0.90$), and

ocean ages .1 ($p = 0.47$), .2 ($p = 0.19$), and .3 ($p = 0.28$) chum salmon. Only one female age .4 chum salmon was sampled.

There were significant inter- and intra-specific differences in mean IGF-I levels by age group and by region (Table 1). In general, mean IGF-I levels in all species increased from west to east across the North Pacific Ocean in January (Fig. 2c). The mean IGF-I levels of age .1 chum, pink, and chinook salmon in the western North Pacific were significantly different ($p < 0.01$). A multiple comparisons test indicated that the mean IGF-I in age .1 chinook salmon was

significantly higher than in age .1 pink and chum salmon in the western North Pacific, and levels in pink and chum salmon were not significantly different. The mean IGF-I of age .1 pink salmon was significantly higher in the eastern than in the western region ($p < 0.01$). The mean IGF-I of coho salmon was significantly higher in the eastern than in the central region ($p = 0.01$). For samples pooled over both the central and eastern North Pacific regions, age .3 sockeye salmon had significantly higher IGF-I levels than age .2 fish ($p < 0.01$).

For chum salmon samples pooled over all regions, there were significant differences ($p = 0.01$) in mean IGF-I levels by ocean age group. A multiple comparisons test indicated that mean IGF-I levels were significantly higher for older (ocean ages .3 and .4) than for younger (ocean ages .1 and .2) chum salmon, but differences between ages .1 and .2 fish and between ages .3 and .4 fish were not significant. Samples were generally not sufficient to make comparisons for the differences in IGF-I levels of the four age groups of chum salmon within and between regions, but mean IGF-I levels of age .3 chum salmon were significantly higher ($p = 0.02$) in the central than in the eastern region. In the central region, mean IGF-I levels of ages .2, .3, and .4 chum salmon were significantly different ($p < 0.01$), and a multiple comparisons test indicated that levels in younger (age .2) chum salmon were significantly lower than older (ages .3 and .4) fish. The IGF-I levels in older chum salmon in the central region were not significantly different from each other.

DISCUSSION

In this paper, we used a new physiological approach to investigate the growth of salmon in offshore waters. We selected serum IGF-I levels as a growth index because a previous study showed that IGF-I was significantly correlated with specific growth rates for coho salmon held in seawater net pens (Duan et al. 1995). In salmon, the liver is the major site of IGF-I synthesis, and growth hormone (GH) is the primary positive regulator of IGF-I synthesis (Duan et al. 1994). Insulin and thyroid hormone also stimulate IGF-I expression (e.g., Duan et al. 1992; Duguay et al. 1994; Plisetskaya and Duan 1994). Through a negative feedback loop, IGF-I inhibits synthesis, secretion, and release of GH (Tannenbaum et al. 1983; Yamashita and Melmed 1986; Perez-Sanchez et al. 1993). Duan et al. (1995) hypothesized that elevated GH levels in stunted coho salmon are due to low plasma IGF-I, which results in reduced negative feedback on GH production. Studies on seasonal and developmental (during the parr-smolt transformation and sexual maturation periods) changes of plasma-circulating IGF-I in salmonid fish are in progress

(Moriyama, Duan, Dickhoff, Larsen, Beckman, Swanson, and Plisetskaya, unpublished, cited by Duan et al. 1995). There were no previous data, however, on plasma IGF-I levels for salmon in offshore waters. Our study was limited to a relatively small number of samples collected in the North Pacific Ocean in January 1996. Additional samples from broader times and areas are needed to better understand the role of IGF-I in growth of salmon in offshore waters.

The quality of blood samples from trawl-caught salmon for RIA was excellent (only 2% of the samples were unusable). However, the samples of chum and sockeye salmon from the central and eastern regions were not representative of the entire catch (significantly larger body weights, Fig. 2a, b). Because plasma IGF-I levels are correlated with body size of fish in most species (Fig. 3), future high-seas samples should be stratified by body size of fish if possible. In reality, because many variables and factors are involved (e.g., origin, season, race, sex, maturity, age, gear selectivity, and variations between years, areas, and conditions), random sampling of salmon in offshore waters is difficult, and there is never certainty that samples are unbiased (Takagi et al. 1981). In addition, we encourage the collection of samples from as many different stations as possible. In our study, the number of stations sampled for each species was not sufficient to evaluate correlations between mean IGF-I levels and environmental factors.

The inter-specific differences in IGF-I levels in our samples probably reflect differences in growth rates among species of salmon in the North Pacific Ocean, but we need more information on the significance of high and low levels of IGF-I. According to Ishida et al. (1998), data on monthly changes in average fork length, body weight, and condition factor of salmonids caught in offshore waters of the North Pacific Ocean indicates that pink, coho, and sockeye salmon continue to grow throughout the winter; coho salmon, which had the highest levels of IGF-I in our study, grow faster in winter than any of the other species; sockeye and chinook salmon, which did not have significantly different levels of IGF-I, may have similar winter growth patterns; and chum salmon, which had low levels of IGF-I, apparently do not grow during winter months. IGF-I levels might be expected to be lower in pink salmon than in coho salmon, because pink salmon apparently grow more slowly than coho salmon (Ishida et al. 1998). But if pink salmon continue to grow throughout the winter and chum salmon do not, we do not understand why IGF-I levels in pink and chum salmon caught in the western region were not significantly different.

In all of the species except pink salmon, IGF-I levels were positively correlated with fork length, body weight, and liver weight, and negatively

correlated with condition factor (Table 2, Fig. 3). Perhaps pink salmon IGF-I levels were not correlated with any of the biological variables because there was less variation in the size of pink salmon than there was in the other species. The significant negative correlations between IGF-I and condition factor in sockeye, chum, and coho salmon are interesting. In the North Pacific Ocean, condition factors in all species of salmon are lowest in winter (Ishida et al. 1998). Perhaps the inverse relation between condition factor and IGF-I may be due to IGF-I having a greater effect on growth in length than weight.

That there are significant intra-specific differences in the ocean growth of salmon by sex, age, origin, maturity group, ocean region, and many other factors is well known (e.g., Takagi et al. 1981). Ueno et al. (1996) hypothesized that in the western North Pacific Ocean young (age .1) pink and chum salmon move offshore from coastal waters in January, and immature (including young) sockeye and chum salmon migrate eastward from the northwestern Pacific to the central North Pacific in winter. Because salmon make rapid and extensive migrations in offshore waters, their plasma IGF-I levels may not be directly related to local environmental conditions. Some of the intra-specific differences in IGF-I levels that we observed could be stock-specific, but origins of fish in our samples were not known. Significantly higher mean IGF-I levels in pink salmon in the eastern than in the western North Pacific, may indicate the earlier resumption of rapid growth in pink salmon in the Gulf of Alaska.

North Pacific researchers have used stomach content data as an indicator of how well fish are feeding and growing (e.g., Ishida et al. 1996). In all but one case, IGF-I levels were not significantly correlated with stomach content variables (chum salmon stomach content weight, Table 2). Duan et al. (1995) cautioned that poor growth in salmon may sometimes be linked to GH resistance and reduced IGF-I production rather than to fasting or starvation. In their study, stunted fish fed actively and most had full stomachs, but they had significantly lower IGF-I levels, growth rates, body weights, lengths, and condition factors than normally growing fish. We think that IGF-I levels may provide a useful tool for detecting poorly growing fish in high-seas samples.

CONCLUSIONS

Additional data on the significance of high or low levels of IGF-I in salmon are needed. The most straight-forward interpretation of our results is that high IGF-I levels correlate with high growth rates. However, there may be some exceptions that we do not know about. Cooperative Japan-U.S. investigations of IGF-I in North Pacific salmon are

continuing. Salmon blood samples were collected in June-July 1996 aboard the Japanese vessels R/V *Wakatake maru* and T/S *Oshoro maru* in the central North Pacific, Bering Sea, and Gulf of Alaska (Davis et al. 1996; Myers et al. 1996). These samples will be evaluated with respect to biological and environmental factors and scale-pattern measures of growth (Walker et al. 1998). We also hope to incorporate information on growth rates from IGF-I into species-, region-, and stock-specific bioenergetic models being developed for salmon in offshore waters (Davis et al. 1998).

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Variation in Prey Size Selectivity of Fingerling Chum Salmon (*Oncorhynchus keta*) in Sea Life: Effects of Stomach Fullness and Prey Abundance

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Prey size selection by fingerling chum salmon (*Oncorhynchus keta*) was studied with respect to variations in the stomach fullness of fish and their estimated prey abundance in the coastal waters of the Japan Sea off northern Honshu, Japan. Fingerlings mainly fed on zooplankton, and their diets consisted of two size groups of major prey taxa. Fingerlings showed two behavioral patterns: selective foraging for the larger prey and non-selective foraging. The effects of prey abundance on the selectivity of fish were different between the size groups. Fingerlings intensified their foraging selectivity with an increase in the abundance of larger prey. On the contrary, the abundance of smaller prey did not influence the prey size selectivity. The stomach fullness of fish was also positively correlated with the prey size selectivity. Since the abundance of larger prey and the stomach fullness of fish varied independently of each other, both are considered to be important factors affecting the prey size selection and diet composition of fingerling chum salmon in the sea.



INTRODUCTION

Changes in prey selectivity of predators in relation to status of prey and (or) predator are well known in various taxa of animal (see Stephens and Krebs 1986). For teleost fish, prey selection has been studied intensively on visual and particulate feeders, which feed on planktonic or epibenthic prey one at a time or no more than a few at a time (see Durbin 1979; Ringler 1979a; Sawara 1987; Gerking 1994). Previous studies pointed out factors affecting prey selection, such as size and abundance of prey (e.g., Ivlev 1965; Werner and Hall 1974; O'Brien et al. 1976) and size (or developmental stage) and stomach fullness of fish (e.g. Ivlev 1965; Hart and Ison 1991; Hart and Gill 1992).

Salmonids are recognized as visual and particulate feeders (see Gerking 1994), and juvenile chum salmon (*Oncorhynchus keta*) feed on zooplankton in their sea life (Salo 1991; Higgs et al. 1995). Juvenile chum salmon feed opportunistically on most prey species (LeBrasseur 1996; Peterson et al. 1982; Brodeur and Percy 1990), but selectively on larger prey (LeBrasseur 1969; Bailey et al. 1975; Healey 1980, 1991; Simenstad and Salo 1982; Cordell 1986). On the other hand, temporal and geographical variations in the size of dominant prey have been observed for juvenile chum salmon (Manzer 1969; Kaeriyama 1986), which suggests that the prey size selectivity of

juvenile chum salmon is variable. Nevertheless, little information is available on variation in the prey size selectivity of juvenile chum salmon, except for the ontogenetic change with development from the fry stage to the fingerling stage (Suzuki et al. 1994).

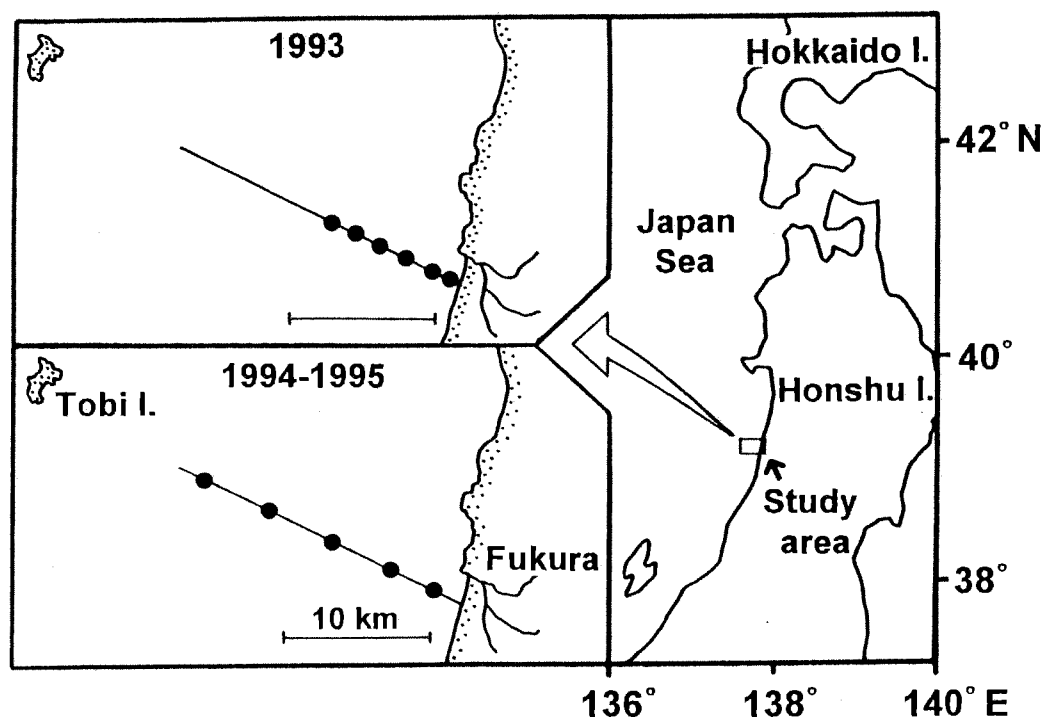
This paper examines variations in prey size selection of fingerling chum salmon with respect to their stomach fullness and prey abundance using data collected from fingerling chum salmon inhabiting the coastal waters of the Japan Sea off northern Honshu Island.

MATERIALS AND METHODS

Study Area

This study was conducted in the Japan Sea off the coast of Fukura, northern Honshu Island, Japan, during March and May in 1993-1995 (Fig. 1). Six stations were located along a southeast-to-northwest transect in the area in 1993. The distances from the shore line to each station ranged from 1 km to 10 km. In 1994 and 1995, five stations (2-20 km offshore) were located on the transect. The depth at the stations ranged from 12 m to 120 m. Temperature and salinity of surface water measured at each stations varied between 8.5-14.3°C and 18.5-34.1‰ in the sampling period during the 3 years.

Fig. 1 Location of the study area and the sampling stations (dots) in 1993 and 1994-1995 in the coastal waters of the Japan Sea off Fukura, northern Honshu Island, Japan



Juvenile Chum Salmon

Juvenile chum salmon were collected with a surface trawl net, which was operated by two vessels. The net was 8 m wide and 4 m deep at the mouth and equipped with 25-34 mm (stretched) mesh in the body and 7.5 mm mesh in the cod end. The net was towed parallel to the shore line at a speed of 4 km/h. The net was towed for thirty minutes at each station in 1993. Three sets of 15 minute tows at each station were carried out in 1994 and 1995. Most collections were made in the morning. Catches were anaesthetized in MS-222 and preserved in buffered 10% formalin-seawater solution aboard, following which samples were transferred to 70% ethanol solution in 1994 and 1995.

Fishes were sorted to species, measured FL (fork length) and wet weight recorded (nearest 0.1 mm and 0.01 g, respectively). We selected juvenile chum salmon larger than 50 mm FL (the size chum salmon change their developmental stage from fry to fingerling (Kaeriyama 1986)) for our analyses. Young chum salmon (larger than 120 mm FL) were not caught in this study.

Zooplankton

Zooplankton samples were collected using a Norpac net (0.45 m diameter, 0.33 mm mesh size)

twice (before and after the fish collection) in 1993 and 3 times (after fish collection) in 1994 and 1995 at each station. The Norpac net was towed vertically from 20 m to the surface. At the stations where depth was less than 20 m, the net was towed from the bottom. Filtered water volume was measured using a flow meter (Rigoshia Co. Ltd., Japan). The samples were fixed in 10% buffered formalin-seawater solution.

Zooplankton samples were sorted to the lowest possible taxonomic level and life history stage and the number of each taxon was recorded. Abundance of zooplankton was defined as density per cubic meter. The percent composition and abundance of zooplankton at each station were expressed as the mean value of the sets within a station. Body length and body width of zooplankton were measured to the nearest 0.01 mm on a random sample of 50 individuals in each taxon. Assuming that the form of zooplankton was a cylinder, we calculated a volume of zooplankton as a size index of each taxon.

We estimated a food environment of fingerlings from daytime zooplankton collections. However, juvenile salmon generally start feeding at dawn (Bailey et al. 1975; Godin 1981; Kaeriyama 1986) and diel vertical migration of zooplankton is common (see Raymont 1983), suggesting that the food environment would change temporally. Thus, to compare abundance of prey between dawn and day, we collected zooplankton at dawn at some stations in

1995. The abundance of two prey groups (described in the next section) did not differ significantly by time of collection except for a single case (Table 1), suggesting that our estimation is reliable.

Diet Analyses

Stomach contents from up to 30 specimens were analyzed for each station; Obrebski and Sibert (1977) suggested that the full range of dietary organisms is usually found in a sample of 30 fish.

Stomachs were opened and the entire contents were weighed (wet weight) to the nearest 1mg. A relative stomach weight (SCI) was used for an index of the stomach fullness of fingerlings: $SCI = 100 \times SCW / (BW - SCW)$; where SCW and BW are the weight of stomach contents and fish body weight, respectively.

Food items were identified to the lowest possible taxonomic level and life history stage, and the number of each taxon was recorded. Diet composition was expressed as percent number at each station. Only

prey taxa contributing more than 5% to the diet composition at a station were used in our prey selectivity analysis. However, fish larvae and an amphipod, *Themisto japonica*, were omitted because they were not collected by the Norpac net. Accordingly, we excluded three stations where fish larvae and *Themisto japonica* were dominant (> 50%) in the diet composition.

Prey taxa were divided into two size groups according to their mean sizes (Fig. 2). The smaller taxa, such as *Evadne nordmanni*, *Podon leuckarti*, euphausiid calyptopis larvae, and *Oikopleura* spp. are called small prey. The larger taxa, such as euphausiid furcilia larvae, polychaetes, *Calanus sinicus*, and *Neocalanus plumchrus* copepodid V stage (*Neocalanus plumchrus* CV) were classified as large prey.

Selectivity for the prey groups by fingerlings was measured by the Rank Preference Index (Johnson 1980) for each station. Following this method, we compared differences in selectivity among food items without influence of inclusion or exclusion of a specific food item.

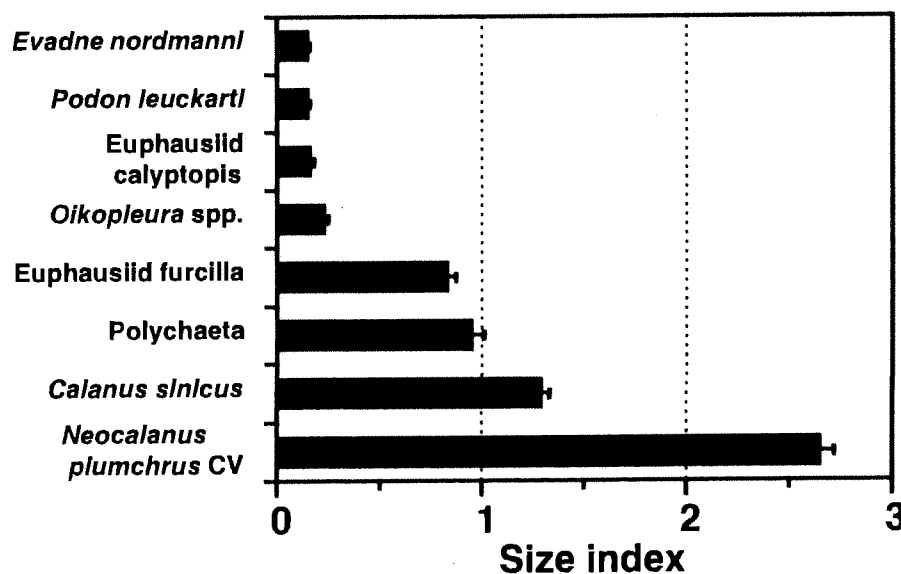
Table 1. Comparisons between abundance of prey (average $\pm$ S.E., N=3) collected at dawn and that collected in day at each station by one-way ANOVA. The values of abundance were log-transformed.

Date	Station ^a	Large prey			Small prey		
		Dawn	Day	p	Dawn	Day	p
Apr. 12, 1995	10	4.13 $\pm$ 0.17	3.27 $\pm$ 0.26	*	6.05 $\pm$ 0.21	5.94 $\pm$ 0.29	NS
Apr. 28, 1995	10	2.36 $\pm$ 0.47	3.34 $\pm$ 0.12	NS	5.58 $\pm$ 0.60	6.59 $\pm$ 0.36	NS
Apr. 28, 1995	20	4.65 $\pm$ 1.22	6.04 $\pm$ 1.15	NS	7.38 $\pm$ 1.05	5.84 $\pm$ 0.61	NS
May 09, 1995	10	2.00 $\pm$ 0.34	1.14 $\pm$ 0.29	NS	6.73 $\pm$ 0.23	6.75 $\pm$ 0.41	NS
May 10, 1995	20	1.95 $\pm$ 0.09	2.50 $\pm$ 0.39	NS	6.07 $\pm$ 0.29	6.74 $\pm$ 0.26	NS

^a: The numbers indicate distance (km) from the shore to the stations.

*: $p < 0.05$, NS: $p \geq 0.05$

Fig. 2 Average body size of the major prey taxa of fingerling chum salmon. The horizontal lines indicate standard errors. The size index is indicated as volume of prey, whose shape is assumed to be a cylinder.



RESULTS

Factors Affecting the Prey Size Selection

Prey Size Selection

Fingerling chum salmon showed two behavioral patterns: selective foraging for larger prey and non-selective foraging. The large prey were ranked higher in selectivity than the small prey in 17 of the stations (Table 2); in seven other stations, the ranks of selectivity were tied or not significantly different ($F_{1,2}=2.00$, $p=0.293$). These variations in the prey size selectivity of fingerlings did not depend on relative abundance of prey, because the ranks of the small prey in zooplankton composition were consistently higher than those of the large prey.

In the following analyses, the rank of selectivity for the small prey was used for an index of prey size selectivity of fingerlings, since the rank of the large prey was constant as rank 1 among stations; the rank 1 and the rank 2 indicated non-selective and selective foraging, respectively.

We used three factors i.e., the abundance of the large prey, that of the small prey, and the stomach fullness of fingerlings (SCI) to evaluate effects on the variation in the prey size selectivity of fingerling chum salmon. These three factors varied independently from one another in this study (Table 3). A significant positive relationship between the rank of selectivity for the small prey and the abundance of the large prey indicated that fingerling chum salmon intensified foraging selectivity with an increase in the availability of the large prey ($r_s=0.616$, $p<0.001$, Fig. 3). On the contrary, the abundance of the small prey was not related to the variation in the selectivity of the small prey ($r_s=-0.331$, $p>0.05$, Fig. 4). The SCI was positively correlated with the rank of selectivity for the smaller prey ($r_s=0.556$, $p<0.01$, Fig. 5), showing a tendency for fingerlings to forage selectively as they became satiated.

Table 2. Ranks of the large prey (LP) and the small prey (SP) in the zooplankton compositions (percent by number), in the diet compositions (percent by number), and in selectivity of fingerling chum salmon at each sampling station.

Year	Date	Station ^a	Zooplankton composition		Diet composition ^b		Selectivity ^c		N ^d
			LP	SP	LP	SP	LP	SP	
1993	Apr. 28	1	2	1	1.4	1.6	1	2	7
1993	Apr. 28	2	2	1	1.0	2.0	1	2	28
1993	Apr. 28	4	2	1	1.0	2.0	1	2	4
1993	Apr. 28	8	2	1	1.0	2.0	1	2	30
1993	May 18	2	2	1	2.0	1.0	1	1	3
1993	May 18	6	2	1	2.0	1.0	1	1	3
1994	Mar. 22	2	2	1	2.0	1.0	1	1	3
1994	Apr. 7	2	2	1	1.8	1.2	1	2	28
1994	Apr. 7	5	2	1	1.0	2.0	1	2	4
1994	Apr. 21	2	2	1	2.0	1.0	1	1	15
1994	Apr. 21	5	2	1	2.0	1.0	1	1	15
1994	Apr. 21	10	2	1	1.8	1.2	1	2	26
1994	Apr. 21	15	2	1	1.0	2.0	1	2	6
1994	Apr. 21	20	2	1	1.0	2.0	1	2	5
1995	Apr. 12	2	2	1	1.0	2.0	1	2	12
1995	Apr. 12	10	2	1	1.0	2.0	1	2	2
1995	Apr. 28	2	2	1	1.0	2.0	1	2	22
1995	Apr. 28	10	2	1	1.3	1.8	1	2	4
1995	Apr. 29	15	2	1	2.0	1.0	1	1	3
1995	May 9	10	2	1	1.5	1.5	1*	2*	2
1995	May 9	15	2	1	1.0	2.0	1	2	11
1995	May 9	20	2	1	1.0	2.0	1	2	30
1995	May 10	2	2	1	1.1	1.9	1	2	8
1995	May 10	5	2	1	1.1	1.9	1	2	27

^a: The numbers indicate distance (km) from the shore to the stations.

^b: The rank of prey item is indicated by mean value of fingerlings at each station.

^c: The rank of selectivity is indicated by the Rank Preference Index (Johnson 1980).

^d: The number of fish examined at each station.

*: Ranks are not significantly different using ANOVA ($p>0.05$).

Table 3. Relationship between the abundance of the large prey (LP), that of the small prey (SP), and the stomach fullness (SCI) of fingerling chum salmon among the sampling stations (N=24). The values of abundance were log-transformed.

Variables		r	P
LP	SP	-0.083	0.702
LP	SCI	0.150	0.485
SP	SCI	0.248	0.243

Fig. 3 Relationship between abundance of the large prey and the rank preference index of the small prey. r_s indicates Spearman's rank correlation coefficient. ***: $p < 0.001$.

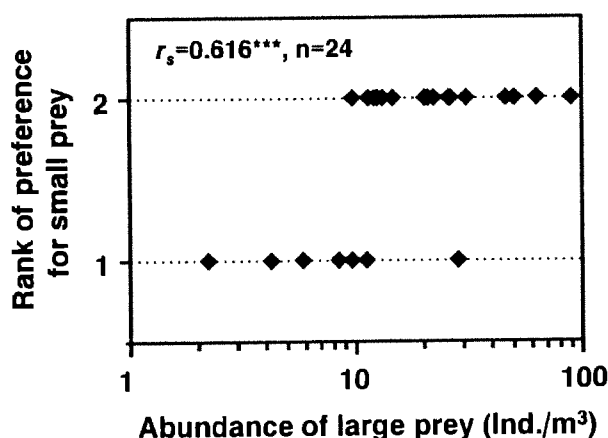


Fig. 4 Relationship between abundance of the small prey and the rank preference index of the small prey. r_s indicates Spearman's rank correlation coefficient. NS: $p > 0.05$.

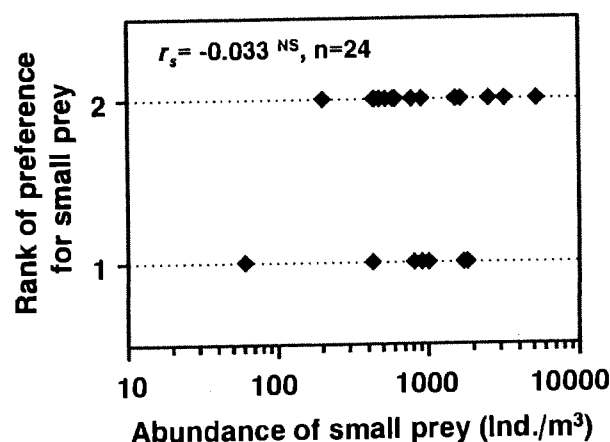
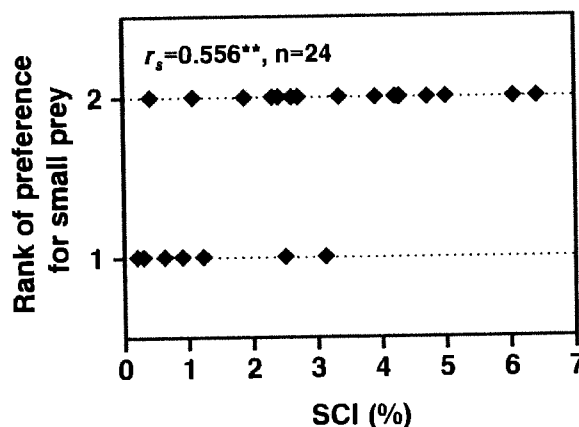


Fig. 5 Relationship between stomach fullness of fingerling chum salmon and the rank preference index of the small prey. The stomach fullness is indicated by SCI (relative weight of stomach contents per body weight). r_s indicates Spearman's rank correlation coefficient. **: $p < 0.01$.



DISCUSSION

Estimation of Prey Abundance

We assumed that fingerling chum salmon inhabit near-surface waters shallower than 20 m in depth. However, there has been little research directed at determining vertical distribution of juvenile salmon at sea. Burgner (1991) concluded that salmon generally occur in near-surface waters by reviewing research and commercial high-seas salmon fisheries information. For chum salmon, both young and adult fish mostly swam above the 20-24m layer in the North Pacific Ocean from spring to autumn (Manzer 1964; Machidori 1967; French et al. 1971; Ogura and Ishida 1995).

The prey abundance was not significantly different between dawn and day at most stations. This result was supported by previous studies on the diel vertical distribution of major prey taxa found in this study. Euphausiid calyptopis larvae do not show diel vertical migration (Iguchi 1995). *Evadne nordmanni* and *Podon leuckarti* inhabited near-surface water throughout the day (Onbe 1974). This distribution pattern is also observed with *Neocalanus plumchrus* CV in the spring (Fulton 1973; Taka et al. 1982). *Calanus sinicus* and euphausiid furilia larvae migrate down below the range of our zooplankton sampling, but they descend to this habitat before dawn (Hirakawa et al. 1990; Uye et al. 1990; Taki et al. 1996). For *Oikopleura* spp., there is little information of diel vertical migration; however, Shiga (1985) reported that their vertical distribution is governed by hydrographic conditions and that they are

homogeneously distributed when the water column is vertically mixed. Since the water column had not yet stratified throughout this study period (Suzuki and Fukuwaka, unpublished data), the vertical distribution of *Oikopleura* spp. would not change greatly on a daily basis.

Factors Affecting Prey Size Selectivity

Fingerling chum salmon showed two behavioral patterns: selective foraging for large prey and non-selective foraging. Selection for a larger prey has been previously observed in various particulate planktivore fishes, including chum salmon (see Sawara 1987; Salo 1991; Gerking 1994; Higgs et al. 1995). Size is recognized as one of the most important characteristics of prey affecting selection in particulate planktivores (Kislalioglu and Gibson 1976). It has been suggested that selection for larger prey can be attributed to their higher visibility (Ware 1972; Confer and Blades 1975) and a higher rate of energy intake per prey item (Werner and Hall 1974; Ringler 1979b).

Fingerlings foraged selectively for large prey with increasing abundance of the large prey, irrespective of the abundance of the small prey. Indices for measurement of foraging selectivity, in general, can vary depending on the relative abundance of prey items in the environment and on the relative number of prey in the diet. In this study, however, the relative abundance of prey in the environment was not related to the variation in prey size selectivity, because small prey were consistently more abundant than large prey in the environment. Selective foraging for large prey resulted when fingerlings fed more on large prey than small prey. Consequently, the observed variation in prey size selection by fingerling chum salmon reflects a foraging behaviour of particulate planktivore fishes where frequency of predation on small prey was higher when large prey were relatively rare irrespective of the abundance of small prey (Sunaga 1970, 1971; Eggers 1982).

Selective foraging was indicated by fingerling chum salmon that contained a relatively large amount of food in their stomachs. Ivlev (1965), Hart and Ison (1991), and Hart and Gill (1992) examined the effect of stomach fullness on prey selection of particulate feeding fishes by observing their foraging behaviour directly until fish reach satiation. They demonstrated that as fish approached satiation, they became highly selective and ate only preferred prey. Although we could not clarify the level of hunger when the fingerlings started feeding, previous studies suggest that the rate of preferred prey in diet would increase with an increase of stomach fullness.

Sawara (1987) suggested that a change in prey selection with prey abundance may only reflect the change with fish stomach fullness, since he speculated

that the best index that fish can use to evaluate prey abundance would be their stomach fullness and that feeding intensity in general would relate positively to prey availability. Contrary to this hypothesis, we demonstrated that prey abundance and stomach fullness independently affect prey selection, which is consistent with the experimental study by Hart and Ison (1991).

Although we could not clarify a ecological and physiological explanation for the variation in prey size selectivity of fingerling chum salmon from this empirical study, some quantitative experiments have succeeded in explaining the prey selection of particulate planktivore fishes functionally or causally (e.g., Werner and Hall 1974; O'Brien et al. 1976; Ringler 1979b; Hart and Gill 1992). Such a study is needed to further understanding of prey selection by fingerling chum salmon.

CONCLUSIONS

The present study indicated that prey size selectivity by fingerling chum salmon in sea life is variable. We pointed out both extrinsic and intrinsic factors, such as abundance of a larger prey and stomach fullness of fish as important factors affecting the variation. These two factors were positively related to the selectivity for a larger prey.

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Caloric Value of High-Seas Salmon Prey Organisms and Simulated Salmon Ocean Growth and Prey Consumption

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To investigate the relationship between salmon prey consumption and growth, this study used recent field data on salmon food habits and growth, experimental caloric determinations of salmon and salmon prey organisms, and a published bioenergetics model. Salmon and their prey were collected at sea, and caloric density determined by bomb calorimetry. Calorimetry results indicated that small medusae had low caloric density. Copepods, euphausiids, hyperiid amphipods, pteropods, and appendicularians had values in the middle range for caloric density, and squid and fish were calorically dense. Whole-body caloric values of high-seas caught immature sockeye salmon and maturing pink and coho salmon were higher than for immature chum salmon.

Bioenergetic models were used to estimate growth and daily ration for common age and maturity groups of sockeye, chum, pink, and coho salmon caught in the central North Pacific Ocean and Bering Sea in summer. Assuming a constant daily ration for 60 days in June and July and a temperature of 5-9°C, an immature ocean age .1 sockeye salmon (361-568 g) required a daily ration of 3.6-4.1% wet body weight (bw)/day, an immature ocean age .2 chum salmon (1042-1547 g) required 3.3-3.9% bw/day, and a maturing ocean age .1 pink salmon (912-1313 g) required 2.7-3.1% bw/day. A maturing ocean age .1 coho salmon (1909-2975 g) required 2.6-2.9% bw/day at 9-11°C. Model simulations indicate that salmon are feeding at a rate close to their physiological maximum. Therefore, any decrease in daily ration could cause significant decreases in growth over a time period as short as two months. We suggest that when prey is abundant, conditions favorable to salmon growth may be bounded at high temperatures by metabolic rates and at low temperatures by consumption rates.



INTRODUCTION

A climatic regime shift that occurred in 1976-77 may have led to favorable environmental conditions for northern salmon stocks and an increase in the abundance of sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon (Trenberth 1990; Beamish and Bouillon 1993; Miller et al. 1994; Hare and Francis 1995). In the last decade, researchers have documented a gradual decrease in size of Asian and North American stocks of chum and pink salmon (Kaeriyama 1989; Kaeriyama and Urawa 1992; Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996).

Investigations of the relationship between the increase in salmon abundance and the decrease in body size throughout the North Pacific have led scientists to hypothesize that salmon may be showing evidence of density-dependent growth. The feeding efficiency of salmon in the ocean has a major effect on salmon production. For example, the biomass of returning sockeye salmon adults can be almost 25 times greater than the biomass of out-migrating smolts (Brett 1986).

Food habits of immature and maturing salmon in offshore waters have been investigated in the Gulf of Alaska (LeBrasseur 1966; Manzer 1968; Pearcy et al. 1988; Walker 1993; Myers et al. 1996), the

Bering Sea (Nishiyama 1970, 1977; Kanno and Hamai 1972; Davis et al. 1996), the North Pacific Ocean (Allen and Aron 1958; Andrievskaya 1957, 1966; Ito 1964; Takeuchi 1972; Sobolevskii and Senchenko 1996; Tadokoro et al. 1996), and the Okhotsk Sea (Gorbatenko and Chuchukalo 1989). Brodeur (1990) summarized marine food habits and feeding ecology of salmon by species and life-history type, and concluded that, despite differences in prey organisms, salmon may be non-selective feeders within a preferred prey size range. Studies have indicated that the prey composition of chum salmon can change in response to the abundance of pink salmon (Andrievskaya 1966, 1970; Shuntov et al. 1993; Tadokoro et al. 1996). Tadokoro et al. (1996) observed that when pink salmon abundance was low, chum salmon fed on a diet similar to the prey ingested by sockeye and pink salmon, but when pink salmon abundance was high, chum salmon increased the proportion of gelatinous zooplankton and reduced the proportion of crustacean prey in their diet.

Bioenergetic models are useful tools for extrapolating from stomach contents data to estimate prey consumption through time. Two researchers used bioenergetics to investigate the prey rations of adult salmon in offshore waters. Nishiyama (1970, 1977) examined the bioenergetics of maturing sockeye salmon in the Bering Sea as they migrate into Bristol Bay on their spawning run, and estimated that the daily ration required for a 2211-g female was 39 kcal/kg/day and for a 2546-g male was 54 kcal/kg/day. Brett (1983, 1986) developed a bioenergetics model of the life history of Babine Lake sockeye salmon, and estimated the average daily ration for maturing fish was 41.4 kcal/kg/day. He suggested the ocean growth of salmon was maximal and could exceed those observed under laboratory conditions (Brett 1983).

In this study, we use field observations on sea surface temperatures and salmon food habits in summer in the central North Pacific Ocean and Bering Sea, data on caloric density of salmon and salmon prey determined from bomb calorimetry, and a published fish bioenergetics model to simulate salmon growth and estimate prey consumption over a 60-day period. Growth estimates from the model were compared with summer monthly mean weights of high-seas caught salmon to evaluate daily ration. Gross conversion efficiency (growth/consumption), mean consumption rate (g prey/day), total consumption by prey category (g), and total energy consumed (kcal) were estimated at the end of the 60-day simulated period.

MATERIALS AND METHODS

Bomb Calorimetry

Common salmon prey, including medusae, copepods, hyperiid amphipods, euphausiids, pteropods, cephalopods, urochordates, and fish were collected from net tows and salmon stomachs during high-seas salmon research cruises in the central North Pacific Ocean, Bering Sea, and Gulf of Alaska in 1992-1995. Immature sockeye and chum, and immature and maturing pink and coho salmon were collected in the North Pacific and Gulf of Alaska. These samples were frozen at sea (approximately -20°C), then thawed and blotted to determine wet weights in the laboratory. When body size was small, i.e., amphipods, copepods, and euphausiids, prey organisms were whole-body samples of numerous individuals. When body size was large, i.e., squid and fish, prey were whole-body samples of single individuals. Wet weight sample sizes ranged from approximately 5 to 150 g. Salmon were ground and homogenized whole, from which subsamples of approximately 50 to 80 g wet weight were collected. Samples were freeze-dried in a Virtis freeze drier (Freeze Mobile 6, Gardiner, NY) for three to four days. The dried samples were ground to a powder. Approximately 1 g of powder was pressed into pellets (to increase the likelihood of complete burning of the sample) and used to determine the gross energy content. One sample per organism was burned at 30 atm of oxygen in a Parr oxygen bomb calorimeter (Model 1341, Moline, IL). Formation of acids following combustion under pressure in the calorimeter produces heat, but acid correction of the bomb washings was not included because of the small degree of error expected for marine animal species ($<2\%$; Paine 1964, 1971).

The proportion of prey energy content that was indigestible by salmon was calculated based on proximate and moisture content from other studies of the same or closely related prey species. The gross energy content and the digestible energy content of each prey species were calculated. The gross energy values for protein (5640 cal/g on a dry weight basis[dwb]), lipid (8700 cal/g dwb), and carbohydrates (4111 cal/g dwb; Higgs et al. 1995) was multiplied by the proximate composition determined by other authors (McBride et al. 1959; Ikeda 1972; Nishiyama 1977; Higgs et al. 1995). To determine the digestible energy content, the energy digestible by salmon of protein (5091 cal/g dwb), lipid (8508 cal/g dwb) and carbohydrate (3800 cal/g dwb; Higgs et al. 1995) was multiplied by the proximate composition particular to each prey species. Dividing the digestible energy content by

the gross energy content gave the proportion of digestible energy available in each prey organism. The proportion of indigestible energy was calculated by subtracting the proportion of digestible energy from one.

Bioenergetics Modeling

Growth and prey consumption were calculated using the fish bioenergetics Model 2 (Hewett and Johnson 1992). Model 2 uses a balanced energy equation where energy consumed in the diet equals energy expended for metabolism, waste elimination, and fish growth. Factors that affect the energy budget are water temperature, fish size, predator and prey energy density, and prey availability. Model 2 input and output values are on a wet weight basis (wwb), computations are specific rates (per unit body weight), and fish weight and consumption are computed on a daily basis in the simulation. Consumption is estimated from an allometric weight function giving the maximum specific consumption rate, modified by a proportionality constant representing prey availability and a temperature function (Appendix 1). The temperature algorithm is the product of two curves: the first curve is the relationship whereby consumption increases with increasing temperature up to a cut-off temperature, and the second is the relationship whereby consumption decreases above the cut-off temperature. This consumption algorithm simulates cold-water fish at low temperatures (Thornton and Lessem 1978). Respiration is determined by calculating the standard (resting) metabolism from an allometric weight function and modifying it for the effect of temperature, an activity factor, and specific dynamic action (metabolic heat loss from digestion of food; Appendix 1). Egestion is a function of temperature and ration and includes a correction factor for the indigestible portion of each prey category. Excretion is a function of temperature, ration, and a proportion of consumption minus egestion (Appendix 1).

The physiological parameter values provided with Model 2 software included values for pink and sockeye salmon (identical values), and coho salmon (Appendix Table 1). Because there were no parameter values given for chum salmon, we used the same parameter values given for pink and sockeye salmon and made a modification to the CA parameter (intercept for weight dependence of maximum consumption). The CA parameter was increased from 0.303 to 0.394 (30%) because preliminary simulations indicated the consumption estimates were too low for chum salmon. This modification of the CA parameter was justified because the specific size of chum stomachs is larger

than other salmon, enabling them to have a higher consumption rate (Azuma 1995; Welch 1997).

Pacific salmon are not equally abundant in all areas of the Subarctic North Pacific Ocean (Pearcy 1992). Summertime gillnet and longline salmon catches in the central Bering Sea are dominated by sockeye, chum, and, in odd-years, pink salmon (Davis et al. 1996). We attempted to model growth and consumption for sockeye, chum, and pink salmon in conditions that closely resemble the central Bering Sea (52°-58°N, 180° and 177°E to 177°W) in summertime. Seawater temperatures frequently encountered in surface waters (0 to 30 m) in the Bering Sea range from 5° to 9°C. For coho salmon, we modeled summertime conditions in the central North Pacific Ocean (44°-47°N, 180°) because coho salmon are abundant in catches in this area (Davis et al. 1996). Seawater temperatures in the surface waters (0 to 40 m) of the central North Pacific frequently range from 7° to 11°C. Details of how salmon move within these regions and change their thermal habitat on a monthly basis have not yet been determined. Therefore, temperature was held constant for each 60-day simulation and separate simulations were run for each 1°C interval across the range of temperatures (Table 1).

To determine the salmon prey composition for use in the bioenergetics model, salmon stomach contents from salmon caught in the central North Pacific Ocean and Bering Sea were used (Davis et al. 1996). Sockeye and pink salmon in the central Bering Sea have similar prey organisms found in their stomach contents including euphausiids, copepods, amphipods, squid, pteropods, and fish. The difference between sockeye and pink salmon stomach contents is that sockeye salmon contain more copepods and hyperiid amphipods while pink salmon contain more squid and fish (Davis et al. 1996). Chum salmon caught in the Bering Sea commonly feed on many of the same prey as sockeye and pink salmon, including euphausiids, amphipods, pteropods, and fish, but chum salmon have a broader assortment of prey organisms found in their stomachs because they also feed on medusae and appendicularians (Davis et al. 1996; Tadokoro et al. 1996). Coho salmon in the central North Pacific Ocean feed primarily on squid and secondarily on hyperiid amphipods (Davis et al. 1996). The prey composition used for the bioenergetics model was the mean percent composition of the common prey categories observed from 1991 to 1996 for sockeye, chum, and pink salmon caught in the Bering Sea, and coho salmon caught in the central North Pacific Ocean normalized to equal 100% (Table 1; Davis et al. 1996).

The caloric value for medusae used in the

Table 1. Environmental temperatures, salmon, and prey characteristics used as input values to simulate conditions in the central North Pacific Ocean and the Bering Sea. Grams are expressed on a wet weight basis. Prey caloric density is the gross energy content, and the mean prey caloric density is weighted by the prey composition.

Salmon Predator	Predator Caloric Density (cal/g)	Region	Temperature Range (°C)	Prey Category	Prey Composition	Prey Caloric Density (cal/g)	Proportion Indigestible
Sockeye	1633-1665*	Bering Sea	5° to 9°	Euphausiids	0.14	743	0.1035
				Copepods	0.13	627	0.0904
				Amphipods	0.24	589	0.1299
				Squid	0.25	732	0.0891
				Pteropods	0.08	624	0.0907
				Fish	0.16	1185	0.0898
				mean		749	
Chum	1376	Bering Sea	5° to 9°	Euphausiids	0.26	743	0.1035
				Amphipods	0.12	589	0.1299
				Pteropods	0.11	624	0.0907
				Fish	0.12	1185	0.0898
				Medusae	0.27	169	0.1125
				Appendicularians	0.12	759	0.0926
Pink	1702-1752*	Bering Sea	5° to 9°	mean		611	
				Euphausiids	0.15	743	0.1035
				Copepods	0.08	627	0.0904
				Amphipods	0.09	589	0.1299
				Squid	0.30	732	0.0891
				Pteropods	0.04	624	0.0907
				Fish	0.34	1185	0.0898
Coho	2083	Central North Pacific	7° to 11°	mean		862	
				Squid	0.83	1550	0.0775
				Amphipods	0.17	589	0.1299
				mean		1387	

* predator energy density is a linear function of body weight.

bioenergetics model was the average of the values determined in our study and the caloric value for *Aglantha digitale* collected in the Bering Sea by Ikeda (1972; Table 2). The squid (unidentified spp.) eaten by pink and sockeye salmon in the Bering Sea were not well represented by the squid collected in our study of caloric value, because our squid samples were collected from stomachs of coho salmon caught south of the Aleutian Islands. Therefore, we used the published caloric value for squid eaten by sockeye salmon caught in Bristol Bay (Table 2; Nishiyama 1977). The caloric value used for the squid prey category of coho salmon was based on that of *Berryteuthis* spp. determined by calorimetry in this study. The caloric values for copepods, euphausiids, hyperiid amphipods, pteropods, and appendicularians used in the model were determined in our study (Table 1). The fish prey category used for simulations of the sockeye, chum, and pink salmon was the mean value for juvenile *Hemilepidotus* spp. and Atka mackerel (*Pleurogrammus monopterygius*), both commonly

found in salmon stomachs in the Bering Sea. The predator energy density for pink and sockeye salmon was defined to be a function of weight (following Hewitt and Johnson 1992), and values of 1375 cal/g ww and 2083 cal/g ww were used for chum and coho salmon (Table 1).

The life history stages we selected for the simulations represent common ages and maturity stages of salmon caught in the Bering Sea and central North Pacific Ocean during recent summertime cruises of the *Wakatake maru* (Davis et al. 1996). Bering Sea salmon catches were primarily composed of sockeye, chum, and pink salmon, and immature ocean age .1 sockeye and ocean age .2 chum salmon were selected because these life history groups were common. All pink and coho salmon caught by the *Wakatake maru* are maturing ocean age .1s, the life-history stage for our simulations. Individual salmon weights used in the simulations were the mean weights for June through July (60 days) for immature ocean age .1 sockeye (growing from 361 to 568 g), immature

Table 2. Gross caloric density (cal/g wet weight) for high-seas salmon prey organisms, and the estimated proportion of prey that is indigestible for salmon.

Organism or Group	cal/g Wet Weight	Proportion Indigestible	Reference
Cnidaria			
<i>Aglantha digitale</i>	202	0.1125	Ikeda 1972
Copepoda			
<i>Neocalanus cristatus</i>	717	0.0886	Nishiyama 1977
<i>N. cristatus</i>	910	0.1094	Ikeda 1972
Copepods	1104	0.0731	Higgs et al. 1995
Euphausiacea			
<i>Thysanoessa raschii</i>	928	0.1103	Ikeda 1972
<i>Thysanoessa</i> spp.	1117	0.0966	Nishiyama 1977
<i>Euphausia pacifica</i>	1107	0.1018	Nishiyama 1977
Euphausiacea	1130	0.1053	Higgs et al. 1995
Amphipoda			
<i>Parathemisto pacifica</i>	665	0.1151	Nishiyama 1977
<i>P. libellula</i>	716	0.1204	Nishiyama 1977
<i>P. libellula</i>	975	0.1541	Ikeda 1972
Gastropoda			
<i>Limacina helicina</i>	636	0.0850	Nishiyama 1977
<i>Clione limacina</i>	563	0.0744	Nishiyama 1977
<i>C. limacina</i>	520	0.1127	Ikeda 1972
Cephalopoda			
Squid	732	0.0891	Nishiyama 1977
Squid	1134	0.0659	Higgs et al. 1995
Teleostei			
<i>Clupea harengus pallasii</i>	2341	0.0774	McBride et al. 1959
<i>Mallotus villosus</i>	1179	0.0945	Higgs et al. 1995
<i>Tarletonbeania</i>	1060	0.1029	Nishiyama 1977
<i>crenularis</i>	1633	0.0844	Higgs et al. 1995
Unidentified Fish			

ocean age .2 chum (growing from 1042 to 1547 g), and maturing pink (growing from 912 to 1313 g) and coho salmon (growing from 1909 to 2975 g) calculated from data collected aboard Japanese research vessels operating in the North Pacific and Bering Sea (1972-1995). These weights are an approximation of what the specific age and maturity groups might gain over the summer. The true initial weight and growth of an individual salmon from the Bering Sea and central North Pacific Ocean might be different from these values because the mean values are pooled over a large geographical area and from different salmon stocks. It is possible that an individual salmon feeding and residing in different oceanographic habitats would have significantly different growth rates than the

average values used in these simulations.

Daily ration levels used in the simulations included daily maintenance (daily ration resulting in zero growth), daily percent of body weight (1%, 2%, 3%, 4% of wet body weight [bw]), and the physiological maximum ration. The physiological maximum is calculated daily and is expressed as a percentage of body weight, decreasing as the fish grows. Over the 60-day period, net production (g), gross conversion efficiency (%; cumulative growth [g]/cumulative consumption [g]), and average consumption rate (total prey consumed g/60 days) were calculated. Prey consumption was summarized by total weight (g) of each prey category consumed and the total energy consumed (kcal) over the 60-day period.

RESULTS

Caloric Determinations

Calorimetric determinations of salmon prey organisms indicated that small medusae had a low energy content and a high water content (136 cal/g ww; 94% water; Table 3). Copepods (627 cal/g ww), euphausiids (743 cal/g ww), hyperiid amphipods (589 cal/g ww), pteropods (624 cal/g ww), and appendicularians (759 cal/g ww) had

values in the middle range for caloric density (Table 3). Squid and fish were calorically dense prey groups, in the range of 896-2041 cal/g ww (Table 3). The caloric value of *Beryteuthis* spp. squid increased with size from 978 (28 to 38 mm mantle length) to 1550 cal/g ww (66-100 mm mantle length; Table 3). Small threespine sticklebacks (*Gasterosteus aculeatus*, <45 mm standard length [sl]), capelin (*Mallotus villosus*), Atka mackerel, blue lanternfish (*Tarletonbeania crenularis*, 65-75 mm sl), and walleye pollock (*Theragra chalcogramma*)

Table 3. Gross energy values of salmon and common prey organisms determined by bomb calorimetry. Caloric values for each prey category are determined from a single 1-g sample combustion. Size (mm): mxl=maximum length, shl=shell length, ml=mantle length, sl=standard length, fl=fork length, bw=body weight (g). Sex: F=female, M=male, imm=immature, mat=mature, gw=gonad weight. Sample area: GOA=Gulf of Alaska, NPO=North Pacific Ocean, BS=Bering Sea, Aleut=Aleutian Islands.

Organism or Group	cal/g Wet Weight	cal/g Dry Weight	% Water	Size, Sex, or Maturity	Month	Sample Area
Cnidaria small medusae	136	2231	93.9	whole; mxl=10-13	June-July	NPO and BS
Copepoda <i>Neocalanus cristatus</i>	627	5504	88.6	whole; mxl=7-8	June-July	NPO and BS
Euphausiacea <i>Thysanoessa</i> spp.	743	4675	84.1	whole; mxl=11-26	June-July	NPO and BS
Amphipoda Hyperiid amphipods	589	3952	85.1	whole; mxl=3-6	July	BS
Gastropoda <i>Limacina</i> spp.	624	3547	82.4	whole; shl=3	June-July	NPO, BS, GOA
Cephalopoda <i>Beryteuthis</i> spp.	978	5147	81.0	whole; ml=28-38	June-July	NPO and BS
<i>Beryteuthis</i> spp.	1550	5983	74.1	whole; ml=66-100	June-July	NPO and GOA
<i>Gonatopsis borealis</i>	1125	5259	78.6	whole; ml=42-59	June-July	NPO and BS
<i>G. borealis</i>	1155	5224	77.9	whole; ml=62	Nov-Dec	NPO
<i>Gonatus</i> spp.	1877	6680	71.9	whole; ml=57-71	June-July	BS
<i>Onychoteuthis borealijaponica</i>	1201	5046	76.2	whole; ml=45-61	June, Nov, Dec	NPO
Urochordata Appendicularians	759	4414	82.8	whole	June	NPO
Teleostei (non-salmonids)						
<i>Bathymasteridae</i>	1153	4487	74.3	whole; sl=42-48	July	BS
<i>Clupea harengus pallasii</i>	1914	5907	67.6	whole; sl=97-104	October	GOA
<i>Cololabis saira</i>	1536	5224	70.6	whole; sl=177	October	GOA
<i>Gasterosteus aculeatus</i>	1166	4049	71.2	whole; sl=32-44	October	GOA
<i>G. aculeatus</i>	1533	4367	64.9	whole; sl=56-62	October	GOA
<i>Hemilepidotus</i> sp.	1184	4520	73.8	whole; sl=18-31	July	Aleut Is and BS
<i>Mallotus villosus</i>	1277	5277	75.8	whole; sl=63-71	October	GOA
<i>Pleurogrammus monopterygius</i>	1186	4841	75.5	whole; sl=42-70	June-July	NPO, BS, GOA
<i>Stenobrachius leucopsarus</i>	2041	6398	68.1	whole; sl=32-90	June-July	NPO and BS
<i>Tarletonbeania crenularis</i>	896	4435	79.8	whole; sl=24-50	June	NPO
<i>T. crenularis</i>	1283	4771	73.1	whole; sl=65-75	June	NPO
<i>Theragra chalcogramma</i>	1101	4554	77.8	whole; sl=75-95	October	GOA
Teleostei (salmonids)						
<i>Oncorhynchus nerka</i>	1342	5326	74.8	fl=413; bw=693; F; imm; gw=5	Nov-Dec	NPO
<i>O. nerka</i>	1920	5926	67.6	fl=426; bw=854; M; imm; gw=1	Nov-Dec	NPO
<i>O. nerka</i>	2331	6420	63.7	fl=500; bw=1366; F; imm; gw=6	Nov-Dec	NPO
<i>O. keta</i>	1212	5203	76.7	fl=217; bw=112; F; imm; gw=1	January	NPO
<i>O. keta</i>	1188	5186	77.1	fl=355; bw=362; F; imm; gw=2	Nov-Dec	NPO
<i>O. keta</i>	1854	6100	69.6	fl=420; bw=701; F; imm; gw=3	Nov-Dec	NPO
<i>O. keta</i>	1249	5205	76.0	fl=513; bw=1215; M; imm; gw=1	Nov-Dec	NPO
<i>O. gorbuscha</i>	1300	5307	75.5	fl=242; bw=137; F; imm; gw=2	January	NPO
<i>O. gorbuscha</i>	1796	5986	70.0	fl=473; bw=1122; M; mat; gw=4	July	GOA
<i>O. gorbuscha</i>	1785	5833	69.4	fl=532; bw=1838; F; mat; gw=144	July	GOA
<i>O. kisutch</i>	2083	5917	64.8	fl=548; bw=2656; M; mat; gw=85	July	GOA
<i>O. kisutch</i>	1287	5046	74.5	fl=630; bw=2134; M; mat; gw=13	July	GOA

juveniles ranged from 1000 to 1300 cal/g ww. Larger sticklebacks (>50mm sl) and Pacific saury (*Cololabis saira*) were approximately 1530 cal/g ww, and herring (*Clupea harengus pallasi*) and northern lampfish (*Stenobrachius leucopsarus*) were the most calorically dense fish prey category (>1900 cal/g ww; Table 3).

The mean whole body caloric value for immature chum salmon was generally lower than for the other salmon species examined (mean=1375 cal/g ww; Table 3). Caloric density was higher for immature sockeye and maturing pink salmon (mean=1864 and 1790; Table 3). The two estimates for coho salmon were widely separated, from 1287 to 2083 cal/g ww (Table 3). The wide disparity between these values

for coho salmon could have occurred because the higher caloric value came from a mature fish with a significantly higher gonad weight, and, therefore may have contained a higher lipid content, or as the result of using a non-representative subsample of the whole body for bomb calorimetry.

Bioenergetics Modeling

Sockeye salmon

The estimated maintenance ration for an immature ocean age .1 sockeye in the Bering Sea in June and July ranged from 0.8 to 1.3% bw/day at 5-9°C (Table 4). The maintenance ration increased

Table 4. Estimated sockeye salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 immature sockeye salmon in the Bering Sea in June and July and an initial weight of 361 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, EU=euphausiids, CO=copepods, AM=hyperiid amphipods, SQ=squid, PT=pteropods, FI=fish.

Sockeye Salmon													
Temp (°C)	Daily Ration (% BW/day)	Final Wt (g)	Net Production (g)	Gross Conversion Efficiency	Consump- tion Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	CO	AM	SQ	PT	FI	Total	
5	maint (0.8%)	361	0	0.0	3.0	25	23	43	44	14	28	177	133
	1.0% BW	372	11	5.0	3.7	31	29	53	55	18	35	221	165
	2.0% BW	439	78	16.4	8.0	67	62	115	119	38	76	477	358
	3.0% BW	518	157	20.1	13.0	109	101	187	195	62	125	779	585
	3.57% BW	568	207 *	21.2	16.2	136	127	234	244	78	156	975	731
	max (3.6-4.1%)	589	228	21.5	17.7	148	138	254	265	85	170	1060	794
6	maint (0.9%)	361	0	0.0	3.3	28	26	48	50	16	32	200	149
	1.0% BW	366	5	2.2	3.6	31	28	52	55	17	35	218	163
	2.0% BW	432	71	15.0	7.9	66	62	114	118	38	76	474	355
	3.0% BW	509	148	19.1	12.9	108	101	186	193	62	124	774	580
	3.68% BW	568	207 *	20.6	16.8	141	131	241	251	80	161	1005	753
	max (3.8-4.3%)	602	241	21.1	19.0	159	148	273	285	91	182	1138	853
7	maint (1.0%)	361	0	0.0	3.7	31	29	54	56	18	36	224	167
	2.0% BW	424	63	13.4	7.8	66	61	113	117	38	75	470	352
	3.0% BW	499	138	18.1	12.8	107	100	184	191	61	122	765	574
	3.8% BW	568	207 *	20.0	17.3	145	135	249	260	83	166	1038	778
	4.0% BW	587	226	20.3	18.5	156	145	267	278	89	178	1113	833
	max (4.0-4.6%)	611	250	20.7	20.2	169	157	290	302	97	193	1208	906
8	maint (1.2%)	361	0	0.0	4.2	35	33	60	63	20	40	251	189
	2.0% BW	415	54	11.6	7.7	65	60	111	116	37	74	463	348
	3.0% BW	488	127	16.8	12.6	106	98	182	189	61	121	757	567
	3.94% BW	568	207 *	19.3	17.9	151	140	258	269	86	172	1076	807
	4.0% BW	574	213	19.4	18.3	154	143	264	275	88	176	1100	823
	max (4.1-4.8%)	616	255	20.1	21.2	178	165	305	318	102	203	1271	953
9	maint (1.3%)	361	0	0.0	4.7	40	37	68	71	23	45	284	213
	2.0% BW	405	44	9.5	7.6	64	60	110	115	37	73	459	344
	3.0% BW	476	115	15.4	12.5	105	97	179	187	60	120	748	560
	4.0% BW	560	199	18.3	18.1	152	141	260	271	87	173	1084	812
	4.09% BW	567	206 *	18.5	18.6	156	145	268	279	89	179	1116	837
	max (4.3-5.0%)	618	257	19.4	22.1	185	172	318	331	106	212	1324	992

* net production estimated for June through July from Japanese research vessel data.

with temperature as the energetic costs of metabolism increased. Likewise, the physiological maximum ration increased from 3.6 to 5.0% bw/day over the 5-9°C temperature range considered. Net production at each ration level decreased as the temperature increased. For example, at a constant ration of 2% bw/day, the net production decreased by 43% between 5-9°C (Table 4). Gross conversion efficiency was highest at the maximum ration and the lowest temperature (21.5%, 5°C; Table 4). An ocean age .1 sockeye growing from 361 to 568 g would therefore consume an average of 16-19 g of prey/day, the equivalent of 3.57 to 4.09% bw/day (27-31 cal/g-predator/day), depending on temperature. To achieve this net production (207 g), the sockeye would have

to feed at 88 to 93% of its physiological maximum rate. Over two months, the total prey consumption was estimated as 0.975-1.116 kg, the equivalent of 731-837 kcal (Table 4).

Chum salmon

The estimated maintenance ration for an immature ocean age .2 chum salmon in the Bering Sea ranged from 0.9 to 1.4% bw/day and the maximum ration ranged from 3.5 to 4.8% bw/day at 5-9°C (Table 5). At a daily ration of 2% bw/day, net production decreased by 52% from 5° to 9°C. To grow from 1042 to 1547 g, a mean ration of 3.28-3.86% bw/day (20-24 cal/g-predator/day) was

Table 5. Estimated chum salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .2 immature chum salmon in the Bering Sea in June and July and an initial weight of 1042 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, EU=euphausiids, AM=hyperiid amphipods, PT=pteropods, FI=fish, GE=medusae, AP=appendicularians.

Chum Salmon

Temp (°C)	Daily Ration (% BW/day)	Final Wt (g)	Net Pro- duction (g)	Gross Con- version Effi- ciency	Cons- ump- tion Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	AM	PT	FI	GE	AP	Total	
5	maint (0.9%)	1042	0	0.0	9.2	144	66	61	66	149	66	552	338
	1% BW	1061	19	3.0	10.5	164	76	69	76	170	76	631	386
	2% BW	1252	210	15.3	22.8	356	164	151	164	370	164	1369	838
	3% BW	1477	435	19.4	37.3	581	268	246	268	604	268	2235	1367
	3.28% BW	1546	504 *	20.1	41.7	651	301	276	301	676	301	2506	1531
	max (3.5-3.9%)	1659	617	21.0	49.0	764	353	323	353	794	353	2940	1798
6	maint (1%)	1042	0	0.0	10.4	162	75	68	75	168	75	623	381
	2% BW	1229	187	13.8	22.6	353	163	149	163	366	162	1356	830
	3% BW	1449	407	18.4	36.9	576	266	244	266	598	266	2216	1354
	3.4% BW	1548	506 *	19.5	43.3	675	312	286	312	701	312	2598	1588
	max (3.7-4.2%)	1690	648	20.5	52.6	820	379	347	379	852	379	3156	1929
7	maint (1.1%)	1042	0	0.0	11.7	183	84	77	84	190	84	702	430
	2% BW	1203	161	12.0	22.4	349	161	148	161	363	161	1343	821
	3% BW	1418	376	17.2	36.5	569	263	241	263	591	263	2190	1339
	3.53% BW	1547	505 *	18.7	44.9	701	324	297	324	728	324	2698	1648
	max (3.9-4.4%)	1712	670	20.0	55.8	871	402	368	402	904	402	3349	2047
8	maint (1.3%)	1042	0	0.0	13.2	207	95	87	95	215	95	794	486
	2% BW	1174	132	10.0	22.1	345	159	146	159	358	159	1326	811
	3% BW	1383	341	15.8	36.0	562	259	238	259	584	259	2161	1322
	3.68% BW	1546	504 *	17.9	46.8	731	337	309	337	759	337	2810	1718
	4.0% BW	1629	587	18.7	52.3	816	377	345	377	848	377	3140	1919
	max (4.1-4.7%)	1722	680	19.4	58.6	914	422	387	422	949	422	3516	2149
9	maint (1.4%)	1042	0	0.0	15.0	234	108	99	108	243	108	900	551
	2% BW	1142	100	7.7	21.8	340	157	144	157	353	157	1308	800
	3% BW	1345	303	14.2	35.5	554	256	234	256	575	256	2131	1303
	3.86% BW	1547	505 *	17.1	49.1	767	354	324	354	796	354	2949	1803
	4.0% BW	1583	541	17.5	51.5	804	371	340	371	835	371	3092	1890
	max (4.2-4.8%)	1721	679	18.6	60.9	810	374	343	374	842	374	3117	1906

* net production estimated for June through July from Japanese research vessel data.

required, which was a daily consumption rate of 42 to 49 g-prey/day, or 85 to 89% of its physiological maximum consumption rate per day, depending on temperature. Estimated chum salmon cumulative consumption was 2.506-2.949 kg or 1531-1803 kcal (Table 5).

Pink salmon

The estimated maintenance ration for a maturing ocean age .1 pink salmon in the Bering Sea ranged from 0.6 to 1.0% bw/day, and the physiological

maximum ration ranged from 2.8 to 3.9% bw/day at 5-9°C (Table 6). At a daily ration of 2% bw/day, net production decreased by 31% from 5° to 9°C. If a maturing pink salmon grew from 912 to 1313 g, the required ration was estimated as 2.73-3.14% bw/day (24-27 cal/g-predator/day) and a daily prey consumption of 30-35 g/day, or 86 to 94% of its physiological maximum consumption rate per day, depending on temperature. Over 60 days, 1.800-2.068 kg of prey, or 1552-1783 kcal were estimated to be consumed (Table 6).

Table 6. Estimated pink salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 maturing pink salmon in the Bering Sea in June and July and an initial weight of 912 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, EU=euphausiids, CO=copepods, AM=hyperiid amphipods, SQ=squid, PT=pteropods, FI=fish.

Pink Salmon

Temp (°C)	Daily Ration (% BW/day)	Final Wt (g)	Net Pro- duction (g)	Gross Con- version Effi- ciency	Cons ump- tion Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	CO	AM	SQ	PT	FI	Total	
5	maint (0.6%)	912	0	0.0	5.7	52	28	31	103	14	117	345	296
	1.0% BW	974	62	10.9	9.4	85	45	51	170	23	192	566	487
	2.0% BW	1160	248	20.1	20.6	185	99	111	371	49	420	1235	1065
	2.73% BW	1314	402 *	22.3	30.0	270	144	162	540	72	612	1800	1552
	max (2.8-3.0%)	1363	451	22.7	33.1	298	159	179	595	79	674	1984	1710
6	maint (0.7%)	912	0	0.0	6.5	58	31	35	116	15	132	387	334
	1.0% BW	960	48	8.6	9.4	84	45	51	168	22	191	561	484
	2.0% BW	1144	232	18.9	20.4	184	98	110	368	49	417	1226	1057
	2.81% BW	1313	401 *	21.7	30.9	278	148	167	556	74	630	1853	1597
	3.0% BW	1356	444	22.1	33.5	302	161	181	603	80	684	2011	1734
7	max (3.0-3.4%)	1394	482	22.3	33.9	323	172	194	647	86	733	2155	1858
	maint (0.8%)	912	0	0.0	7.3	66	35	39	131	17	149	437	377
	1.0% BW	945	33	5.9	9.3	84	45	50	167	22	189	557	480
	2.0% BW	1125	213	17.6	20.3	182	97	109	365	49	413	1215	1048
	2.91% BW	1314	402 *	21.0	32.0	288	153	173	576	77	652	1919	1654
8	3.0% BW	1334	422	21.2	33.2	299	159	179	598	80	678	1993	1719
	max (3.1-3.5%)	1410	498	21.8	38.1	343	183	206	686	91	777	2286	1971
	maint (0.9%)	912	0	0.0	8.2	74	40	44	148	20	168	494	426
	1.0% BW	928	16	2.8	9.2	83	44	50	166	22	188	553	476
	2.0% BW	1105	193	16.0	20.1	181	96	108	361	48	410	1204	1039
9	3.0% BW	1310	398	20.1	32.9	296	158	178	592	79	671	1974	1702
	3.02% BW	1314	402 *	20.2	33.2	299	159	179	597	80	677	1991	1716
	max (3.3-3.7%)	1420	508	21.2	40.0	360	192	216	720	96	816	2401	2070
	maint (1.0%)	912	0	0.0	9.3	84	45	50	168	22	190	559	482
	2.0% BW	1082	170	14.3	19.9	179	95	107	358	48	405	1192	1027
9	3.0% BW	1282	370	19.0	32.5	293	156	176	586	78	664	1953	1683
	3.14% BW	1313	401 *	19.4	34.5	310	165	186	621	83	703	2068	1783
	max (3.4-3.9%)	1423	511	20.4	41.6	375	200	225	750	100	850	2500	2154

* net production estimated for June through July from Japanese research vessel data.

Coho salmon

The estimated maintenance ration for a maturing ocean age .1 coho salmon in the central North Pacific Ocean ranged between 0.7 and 1.1% bw/day, and the physiological maximum consumption ranged from 2.0 to 3.4% bw/day at 7-11°C (Table 7). At a daily ration of 2% bw/day, net production decreased by 33% from 7° to 11°C. A maturing coho salmon growing from 1909 to 2975 g would consume 2.64-2.86% bw/day (37-40 cal/g-predator/day) and a daily prey consumption of 63-68 g-prey/day at 9° to 11°C, or 91 to 96% of its physiological maximum consumption rate. Over two months, 3.785-4.105 kg of prey, or 5248-5693 kcal of energy would be consumed (Table 7).

DISCUSSION

The specific energy requirements for the smaller (361-568 g) immature sockeye salmon found in this study were lower (27-31 cal/g-predator/day) than the ration required for large (2211 and 2546 g) maturing sockeye returning to Bristol Bay reported by Nishiyama (1970; 39 cal/g-predator/day for females; 54 cal/g-predator/day for males). This is reasonable because of the large difference in weight, maturity, and age of the sockeye salmon investigated. The specific consumption increases and the ration as a percentage of body weight gradually decreases as the fish grow. Sockeye salmon gross conversion efficiency in this study was estimated at 18.5-21.2%, slightly less than the lifetime conversion efficiency

Table 7. Estimated coho salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 maturing coho salmon in the central North Pacific Ocean in June and July and an initial weight of 1909 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, SQ=squid, AM=hyperiid amphipods.

Coho Salmon									
Temp (°C)	Daily Ration (%BW/day)	Final Wt (g)	Net Pro- duction (g)	Gross Con- version Effi- ciency	Con- sump- tion Rate (g/day)	Total Prey Consumption (g)			Total kcal
						SQ	AM	Total	
7	maint (0.7%)	1909	0	0.0	13.2	657	135	792	1098
	1.0% BW	2064	155	13.0	19.8	988	202	1190	1650
	2.0% BW	2652	743	27.5	45.1	2244	460	2704	3749
	max (2.0-2.2%)	2715	806	28.1	47.8	2381	488	2869	3977
8	maint (0.8%)	1909	0	0.0	14.6	728	149	877	1217
	1.0% BW	2024	115	9.7	19.6	978	200	1178	1635
	2.0% BW	2599	690	25.8	44.6	2221	455	2676	3710
	max (2.3-2.6%)	2905	996	28.7	57.9	2881	590	3471	4813
9	maint (0.9%)	1909	0	0.0	16.3	810	166	976	1354
	1.0% BW	1980	71	6.1	19.4	968	198	1166	1617
	2.0% BW	2541	632	23.9	44.1	2195	450	2645	3667
	2.64%BW	2976	1067 *	28.2	63.1	3142	643	3785	5248
	max (2.6-2.9%)	3055	1146	28.7	66.6	3319	680	3999	5545
10	maint (1.0%)	1909	0	0.0	18.2	904	185	1089	1511
	1.0% BW	1932	23	2.0	19.2	956	196	1152	1598
	2.0% BW	2477	568	21.8	43.5	2166	444	2610	3619
	2.74% BW	2975	1066 *	27.1	65.5	3264	669	3933	5453
	max (2.8-3.0%)	3126	1217	28.1	72.3	3599	737	4336	6013
11	maint (1.1%)	1909	0	0.0	20.3	1011	207	1218	1689
	2.0% BW	2407	498	19.4	42.9	2135	437	2572	3567
	2.86% BW	2976	1067 *	26.0	68.4	3407	698	4105	5693
	3.0% BW	3080	1171	26.7	73.1	3638	745	4383	6078
	max (2.9-3.4%)	3197	1288	27.3	78.5	3911	801	4712	6533

* net production estimated for June through July from Japanese research vessel data.

(26%) estimated for Babine Lake sockeye salmon (Table 4; Brett 1986). The conversion efficiency will likely be higher for older, larger fish, thereby raising the lifetime efficiency for sockeye with two to three years at sea above that determined for the ocean age .1 sockeye salmon in this study. Brett (1983, 1986) hypothesized that high conversion efficiencies such as these are the result of a strategy whereby juvenile sockeye salmon feed heavily in coastal areas, quickly attaining a large size and reducing size-dependent mortality, and that sockeye sustain a high growth rate throughout their ocean residence until they move into freshwater for spawning. In comparisons of our results with those of other studies, it must be taken into consideration that our growth data are pooled and are not from a single stock or ocean production area. There may be considerable variation in growth rates among stocks and oceanic production areas (Brett 1986).

Our estimates of daily ration for an immature ocean age .2 chum salmon (3.3-3.9% bw; 20-24 cal/g-predator/day) and a maturing pink salmon (2.7-3.1% bw; 24-27 cal/g-predator/day; Tables 5, 6) in the Bering Sea were smaller than the estimates of daily ration that Gorbatenko and Chuchukalo (1989) obtained for pre-spawning adult chum (7% bw) and pink salmon (5.8-6.4%) caught on the West Kamchatka shelf in summer. They estimated ration from the amount of food consumed and the digestion rate. Perhaps our estimates of daily ration were lower because we assumed a higher prey caloric density and prey digestibility than Gorbatenko and Chuchukalo (1989).

Our estimate of 2.6-2.9% bw (37-40 cal/g-predator/day) daily ration for maturing coho salmon is the first published for adult coho in offshore marine habitats (Table 7). Brodeur and Pearcy (1987) determined daily ration for juvenile coho at 2.4-3.7% bw for temperatures slightly warmer than those used in this study. At 7° and 8°C, our coho salmon simulations were not able to attain the 1066 g net production indicated from the mean monthly values from the high-seas salmon research vessel data. This indicates either that the model consumption parameters were too low for a maturing offshore coho salmon, or that the mean monthly size values were too large. Consumption would have to increase by 18% (increase CA from 0.303 to 0.359; Appendix Table 1) in order for simulated net production to equal 1066 g under conditions of a constant 7° or 8° C thermal habitat. Coho salmon have been caught at 7° and 8° C, so it is not likely that the thermal conditions were unrealistic. Examination of coho salmon stock- and location-specific ocean growth deserves further study.

Chum salmon feed upon a wide range of prey organisms. In addition to the prey organisms

(euphausiids, amphipods, and fish) commonly eaten by sockeye, pink, and chum salmon, chum salmon also can eat gelatinous zooplankton (cnidarians, ctenophores, and salps) not common in the stomachs of other salmon (Andrievskaya 1957, 1966; Ito 1964; Brodeur 1990; Davis et al. 1996; Tadokoro et al. 1996). By utilizing gelatinous zooplankton in their diet, chum salmon may reduce direct trophic competition with other salmon (Welch and Parsons 1993). Chum salmon have been shown to have higher stomach acidity and larger stomach capacity as a proportion of body size than other salmon (Azuma 1995; Welch 1997). The esophageal villi and extensive vascularization in the stomach wall observed by Welch (1997) may increase surface area and perhaps speed digestion of prey. This could be particularly helpful for efficient digestion of prey, such as gelatinous zooplankton, that contain a large amount of water (Table 3). However, it is unlikely that chum salmon could grow, particularly at summertime temperatures, on a diet composed mostly of gelatinous zooplankton because the caloric value of gelatinous prey is too low (approximately 20% of the caloric value of crustaceans; Table 3). When chum or pink salmon abundance is high and chum salmon increase the portion of gelatinous zooplankton in their diet, the results may be a reduction or cessation of growth as observed on chum salmon scales by Ishida et al. (1993).

Tadokoro et al. (1996) suggested that micro-nekton, such as fish and squid, were the most efficient prey group for salmon to feed upon because of their relatively large size when compared to the small-sized crustaceans such as amphipods and copepods frequently found in salmon stomach contents. Fish and squid were the most calorically dense salmon prey organisms among those we analyzed (Table 3). Micro-nekton are active swimmers making them more demanding for salmon to catch, but the energetic cost of pursuing and capturing fish and squid is probably offset by the consumption of this energy-rich prey. However, when fish and squid abundance is low, and the time and energy required to search for and capture these prey increases, a smaller proportion of ingested energy is available for salmon growth.

The balance between growth and metabolism is affected by temperature (Jobling 1994). As temperature increases, prey consumption and metabolism increase, but the energetic requirements of metabolism increase faster than the energy gained through increasing consumption, and this reduces growth (Brett et al. 1969). Assuming prey is abundant and that salmon reside in summertime temperatures similar to those used in our simulations (5-9°C in the Bering Sea and 7-11°C in the central North Pacific Ocean), we speculate that as the energy requirements of metabolism increase with temperature, prey

consumption increases and provides sufficient energy for substantial growth. In this temperature range, prey availability rather than metabolic efficiency governs how much the salmon will grow. Welch et al. (1995) observed a step-function response in salmon catch data to upper sea surface temperatures in the northeastern Pacific Ocean in the spring. Perhaps the upper thermal limits Welch et al. (1995) described represent the temperature where energy demands of metabolism begin to rapidly exceed the energy supplied by consumption, even when prey is readily available and consumption rate is at a maximum. We suggest that there may be lower thermal limits below which, although the energy conversion efficiency for salmon is high because metabolic demands are low, consumption rates are also low, and therefore growth is reduced. For example, hydroacoustic data from a winter trans-Pacific survey showed that salmon were not in sub-surface waters colder than 4°C (Sakai et al. 1996). If true, when salmon prey is abundant, an upper thermal limit favorable for salmon growth may be bounded by metabolic requirements, and a lower limit may be bounded by the capacity for prey consumption at low temperatures. The three dimensional aspect of ocean salmon thermal habitat is difficult to characterize. Movements of salmon during their summer ocean residence have been detected using transmitters mounted on salmon and used in conjunction with oceanographic temperature probes to provide a detailed record of individual salmon movements (Ogura and Ishida 1992, 1995; Ogura 1994). However, these data have not been analyzed with respect to salmon feeding habits and bioenergetics. Changes in temperatures can have a large effect on the conversion efficiencies and therefore growth of salmon. Clarification of changes in ocean salmon thermal habitats and changes in diurnal feeding are an important area of continuing research.

CONCLUSIONS

If our estimates of monthly growth during June and July are reasonable, then our simulations indicate that salmon are feeding at a rate close to their physiological maximum (85 to 93% of the maximum for immature sockeye and chum, and 86 to 96% of the maximum for maturing pink and coho salmon). In addition, our estimates indicate that small decreases in the daily ration can cause significant decreases in growth over a time as short as two months during the summer when feeding and growth opportunities are generally thought to be at a maximum. The growth estimates used in these simulations are from pooled data which may not represent growth rates of a particular stock or growth

conditions in a specific ocean production area. Therefore, stock- and ocean region-specific growth data for particular stocks and time periods are needed for further bioenergetics modeling and to evaluate the recently observed decrease in fish size observed in many Pacific Rim salmon stocks.

The bioenergetics approach was helpful in making estimates of consumption and growth using ship-board observations on salmon feeding habits and environmental conditions. The bioenergetics Model 2 developed by Hewitt and Johnson (1992) has been used in previous studies to estimate consumption by juvenile sockeye and coho in freshwater and juvenile coho and chinook in coastal waters, and in those cases, the model was in close agreement with laboratory experiments (Beauchamp et al. 1989; Brodeur et al. 1992; Ruggerone and Rogers 1992). Because the model is constrained by the balanced energy equation, it limits error propagation from the numerous parameters used in the model (Hansen et al. 1993). Model parameter estimates could be improved by additional laboratory experiments measuring the metabolic cost of activity at several levels of swimming effort. Additional observations from field studies of salmon thermal habitats would be useful improvements to model parameters. These data may be easier to measure *in situ* with recent advances in more economical archival tags capable of recording temperature profiles as the fish moves through its ocean habitat.

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Appendix

Appendix 1. Equations used to calculate consumption, respiration, egestion, and excretion rates of salmon. Symbols and equations are those of Hewett and Johnson (1992).

(1) Consumption

$$C = CA * W^{CB} * P * f(T)$$

where

$$f(T) = K_A * K_B$$

$$K_A = (CK1 * L1) / (1 + CK1 * (L1 - 1))$$

$$L1 = e^{(G1 * (T - CQ))}$$

$$G1 = (1 / (CTO - CQ)) * \ln((0.98 * (1 - CK1)) / (CK1 * 0.02))$$

$$K_B = (CK4 * L2) / (1 + CK4 * (L2 - 1))$$

$$L2 = e^{(G2 * (CTL - T))}$$

$$G2 = (1 / (CTL - CTM)) * \ln((0.98 * (1 - CK4)) / (CK4 * 0.02))$$

(2) Respiration

$$R = (RA * W^{RB} * f(T) * \text{Activity}) + (SDA * (C - F))$$

where

$$f(T) = e^{(RQ * T)}$$

$$\text{Activity} = e^{((RTO - (RTM * T)) * VEL)}$$

$$VEL = ACT * e^{(BACT * T)} * W^{(RK4)}$$

when temperature is $\leq 25^\circ\text{C}$

(3) Egestion

$$F = PF * C$$

where

$$PF = ((PE - 0.1) / (1 - 0.1)) * (1 - PFF) + PFF$$

$$PE = FA * T^{FB} * e^{(FG * P)}$$

$$PFF = \sum (\text{PREYK}[n] * \text{DIET}[n], \text{ for } n = 1 \text{ to number of prey categories})$$

$$\text{PREYK}[n] = \text{indigestible proportion of the } n\text{th prey category}$$

$$\text{DIET}[n] = \text{proportion of } n\text{th prey category in the diet}$$

(4) Excretion

$$U = UA * T^{(UB)} * e^{(UG * P)} * (C - F)$$

Appendix (continued)

Appendix Table 1. Fish bioenergetics Model 2 parameter values used to estimate growth and prey consumption by sockeye, chum, pink, and coho salmon given a constant daily food ration (Hewett and Johnson 1992).

Symbol	Physiological Parameter Value	Nominal Value		
		Pink/Sockeye	Chum	Coho
CONSUMPTION (CON)				
C	Specific feeding rate (g/g/day)			
P	Constant proportion of maximum feeding rate			
W	Fish weight (g)			
CA	Intercept for weight dependence of CON	0.303	0.394	0.303
CB	Slope for weight dependence is CON	-0.275	-0.275	-0.275
CQ	Lower temperature where dependence is CK1	3	3	5
CTO	Higher temperature where dependence is 0.98 of max	20	20	15
CTM	Temp _≥ CTO where dependence is still .98 of max	20	20	18
CTL	Temperature where dependence is CK4	24	24	24
CK1	Temperature dependence at CQ	0.58	0.58	0.36
CK4	Temperature dependence at CTL	0.50	0.50	0.01
RESPIRATION (RES)				
R	Specific rate of respiration (g-O2/g/day)			
RA	Intercept for std. metabolism vs weight, temperature, and swimming speed	0.00143	0.00143	0.00264
RB	Slope for weight dependence of standard metabolism	-0.209	-0.209	-0.217
RQ	Coefficient for temperature dependence of metabolism	0.086	0.086	0.06818
RTO	Coefficient for swimming speed dependence of metabolism	0.0234	0.0234	0.0234
RTM	Coefficient for swim speed dependence of temperature	0	0	0
RTL	Cut-off temp	25	25	25
RK1	Intercept for weight dependence of swimming speed when temperatures >RTL	1	1	1
RK4	Slope for weight dependence of swimming speed at all temperatures	0.13	0.13	0.13
ACT	Intercept for swimming speed vs temperature and weight (cm/sec/1-g fish at 0°), when temperature <RTL	9.9	9.9	9.7
BAC	Coefficient for temperature dependence of swimming speed when temperature <RTL	0.0405	0.0405	0.0405
T	Proportion of assimilated energy lost to specific dynamic action	0.172	0.172	0.172
SDA				
EGESTION (EGES)				
F	Specific rate of egestion (g/g/day)			
FA	Intercept for proportion of consumption EGES vs temperature and ration	0.212	0.212	0.212
FB	Slope for temperature dependence of EGES	-0.222	-0.222	-0.222
FG	Coefficient for feeding level dependence of EGES	0.631	0.631	0.631
EXCRETION (EXCR)				
UA	Intercept for proportion of assimilated consumption EXCR vs temperature and ration	0.0314	0.0314	0.0314
UB	Slope for temperature dependence of EXCR	0.58	0.58	0.58
UG	Coefficient for feeding level dependence of EXCR	-0.299	-0.299	-0.299

Life History Strategy and Migration Pattern of Juvenile Sockeye (*Oncorhynchus nerka*) and Chum Salmon (*O. keta*) in Japan: a Review

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Life histories of sockeye (*Oncorhynchus nerka*) and chum salmon (*O. keta*) show a conditional strategy which have two tactics of residence and migration. They remain in lakes and rivers if they can obtain sufficient resources such as food and habitat, or migrate seaward when they do not have enough resources to satisfy their energy metabolism. Their migration pattern, controlled by effects of "prior residence" and "precedent migration", may be influenced by trade off between the profitability of resource acquisition and risks such as osmoregulation, energetic demands of swimming, exposure to predators, and mobilization to non-adaptable habitat by water current. The life history strategy and migration pattern of the genus *Oncorhynchus* reflect an evolution of anadromous fish by which they have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in freshwater.



INTRODUCTION

The migrations of fishes are generally classed biologically as "alimential" for food procurement, "climatic" for reaching a region of better climate, "gametic" for reproduction (Harden-Jones 1968), and oceanographically as "mobilization" by water current (McKeown 1984). For diadromous fishes, alimential and gametic migrations influence their adaptation and differentiation through intraspecific competition.

McDowall (1987) estimated the total number of fish species as about 20,000 and considered that 162 (0.8%) of these are diadromous. Of these species, 87 (54%) are anadromous, 41 (25%) catadromous, and 34 (21%) amphidromous. Baker (1978) showed that anadromy and catadromy are the most in polar-temperate and tropical environments, respectively. Anadromous species have evolved when food resources in the sea exceed those in fresh water, and catadromous species have evolved when freshwater food resources exceed those in the sea (Gross 1987). Pacific salmon (*Oncorhynchus spp.*) would have obtained the ability of homing migration for maximizing reproductive success in fresh water.

The purpose of this paper is to review the migration of Japanese Pacific salmon by focusing on variation in the life history strategy of sockeye salmon (*O. nerka*), which have a diverse pattern of the life history, and chum salmon (*O. keta*), which migrate seaward immediately after emergence, but may reside for a short period of time in freshwater.

OCEAN DISTRIBUTION AND BIOMASS OF PACIFIC SALMON

Of the six species of Pacific salmon, masu salmon (*O. masou*) have the most limited distribution and the least abundance. They occur only in areas of the Far East. Coho (*O. kisutch*), chinook (*O. tshawytscha*), and sockeye salmon have the relatively wide distribution in the North Pacific Ocean. Chum and pink salmon (*O. gorbuscha*) have the widest distribution in the North Pacific Ocean. Pink salmon also have the most abundant among Pacific salmon. In general, the more abundant species of Pacific salmon have the wider ocean distribution in the North Pacific Ocean (Fig. 1).

The six species of Pacific salmon vary widely in

Fig. 1 Relationship between the ocean distribution index and the biomass in Pacific salmon. The ocean distribution index indicates matrix numbers of $2^{\circ} \times 5^{\circ}$ area where salmon were caught until 1985. The biomass shows an average total catch by species in 1952-1975 (Kaeriyama 1985).

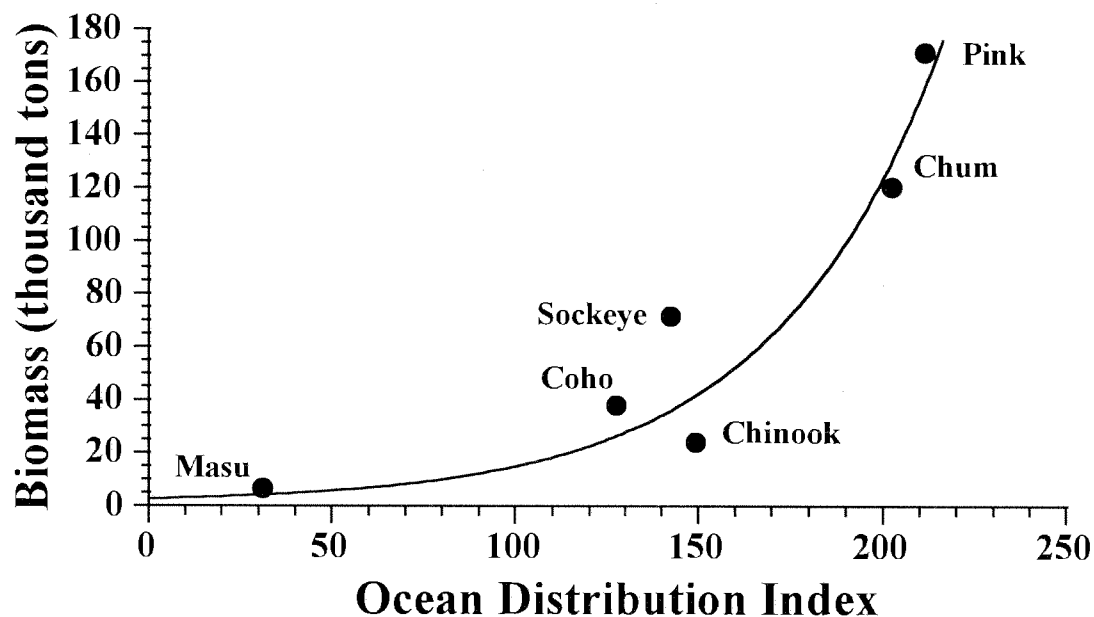


Fig. 2 Area of the downstream migration at the underyearling stage in species of Pacific Salmon.

Species	Fresh Water (River or Lake)	Sea	
		Estuary	Coast
Masu			
Coho			
Chinook			
Sockeye			
Chum	 		
Pink			

their freshwater residence and migration pattern (Fig. 2). Masu and coho salmon reside in freshwater for at least one or two years before migrating seaward as smolt. Most individuals of chinook and sockeye salmon rear in freshwater for one or more years before seaward migration. A portion of them, however, enter the sea at the underyearling stage, known as ocean-type or sea-type stocks (Clarke et al. 1989; Wood et al. 1987). Numerous chum salmon fry migrate seaward immediately after emergence. Only a few juveniles reside in the river for up to several months (Kaeriyama 1986). All pink salmon enter the sea as fry immediately after the emergence (Heard 1991).

In Pacific salmon, the species that migrate seaward at an earlier developmental stage and rear in the sea may have greater abundance and a wider area of ocean distribution than the species that rear extensively in freshwater (Kaeriyama 1985).

MIGRATION AND FRESHWATER RESIDENCE OF SOCKEYE SALMON

Sockeye and chinook salmon exhibit the most diverse life histories among Pacific salmon. For instance, adult sockeye salmon have the largest number of common age-groups (Table 1). Although sockeye are primarily anadromous, there are distinct populations of "residual" sockeye and kokanee salmon (Ricker 1940). Residual sockeye are, at least in part, progeny of anadromous parents (Burgner 1991). A part of them, however, juveniles remain in fresh water to mature and reproduce. The residual population tends to have a higher growth rate and to mature at an earlier age than the anadromous population (Ricker 1938; Simirnov 1959). The kokanee, on the other hand, have fully adapted to a freshwater existence and presumably diverted from a common anadromous stock in recent geological times (Ricker 1940). However, the process of evolution is not clear (Burgner, 1991). In anadromous sockeye salmon, juvenile typically rear in lakes for one or more years before the seaward migration (lake type),

but, particularly in northern populations, some individuals go to the sea immediately after their emergence (sea type) or inhabit river channels for at least one year (river type) (Wood et al. 1987).

Lacustrine sockeye salmon are fully reproduced by artificial enhancement program within Lake Shikotsu. They were originally transplanted from the residual population in Lake Akan, Hokkaido Island, in 1893 and from the anadromous population in Lake Urumobetsu, Iturup Island, during 1925-1940. They produce smolts regardless of being geographically landlocked over 15 generations in the lake (Kaeriyama 1991). Those smolts ascended the other river, where they were artificially released, as anadromous sockeye salmon after 0-3 years of marine life. Most of the smolts, 3 years old (age-2.0), migrated downstream between late June and early July. The age and timing at seaward migration of Lake Shikotsu smolts corresponded with those of sockeye salmon smolt in Lake Urumobetsu, although the limnological environments of Lake Shikotsu differ much from those of Lake Urumobetsu. On the other hand, progeny of sockeye introduced to Lake Shikotsu led more diverse life history patterns including precocity (precocious male returning the river several months after marine life; 200 mm in mean fork length), lacustrine (250 mm in mean fork length), and anadromy (400 mm, 520 mm, and 590 mm in mean fork lengths of age- .1, .2, and .3) (Kaeriyama et al. 1992; Kaeriyama 1994).

Of the same population (age-2.0) in Lake Shikotsu, smolts captured in outlet of the lake by set nets were smaller than residual fish taken in the center of the lake by gill nets (Fig. 3). Based on the allometry between fork length and body weight (Fig. 4), Lake Shikotsu sockeye salmon smolts are more slender in body shape than residuals. Fig. 5 shows a relationship between the population size and smolt rate (number of smolts / population size) of Lake Shikotsu sockeye salmon. In 1984-1986, smolts (145 ± 4 mm) were significantly smaller ($P < 0.001$) in fork length and smolt rate was significantly higher ($P < 0.001$) than those in other

Table 1. The most common age groups of genus *Oncorhynchus* by species based on Major et al. (1978), Healey (1986), Burgner (1991), Salo (1991), Healey (1991), and Sandercock (1991)

Species	Age-groups	Numbers
Pink Salmon	0.1*	(1)
Chum salmon	0.1*, 0.2*, 0.3*, 0.4*, 0.5*	(5)
Sockeye salmon	0.2, 0.3, 0.4, 0.5, 1.0*, 1.1*, 1.2*, 1.3*, 1.4, 2.1*, 2.2*, 2.3, 2.4, 3.1, 3.2, 3.3, 3.4, 4.1, 4.2, 4.3	(20)
Chinook salmon	0.1, 0.2, 0.3, 0.4, 0.5, 1.1, 1.2, 1.3, 1.4, 1.5, 1.6, 2.1, 2.2, 2.3, 2.4, 2.5	(16)
Coho salmon	1.0, 1.1, 2.1, 3.1, 4.1	(5)
Masu salmon	1.1*, 2.1*	(2)

* Common age-groups in Japan.

Fig. 3 Frequency distribution of body weight of residual and smolt sockeye salmon collected in Lake Shikotsu on July 15, 1987.

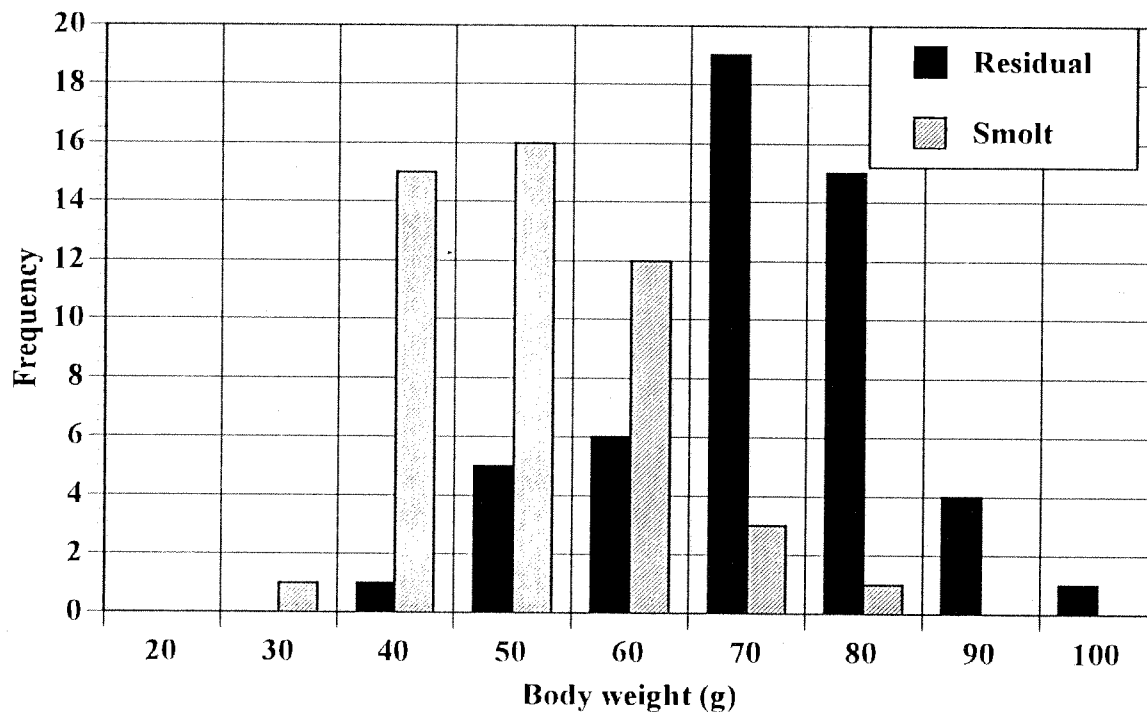


Fig. 4 Relationships between fork length and body weight of residual and smolt sockeye salmon collected in Lake Shikotsu on July 13, 1987.

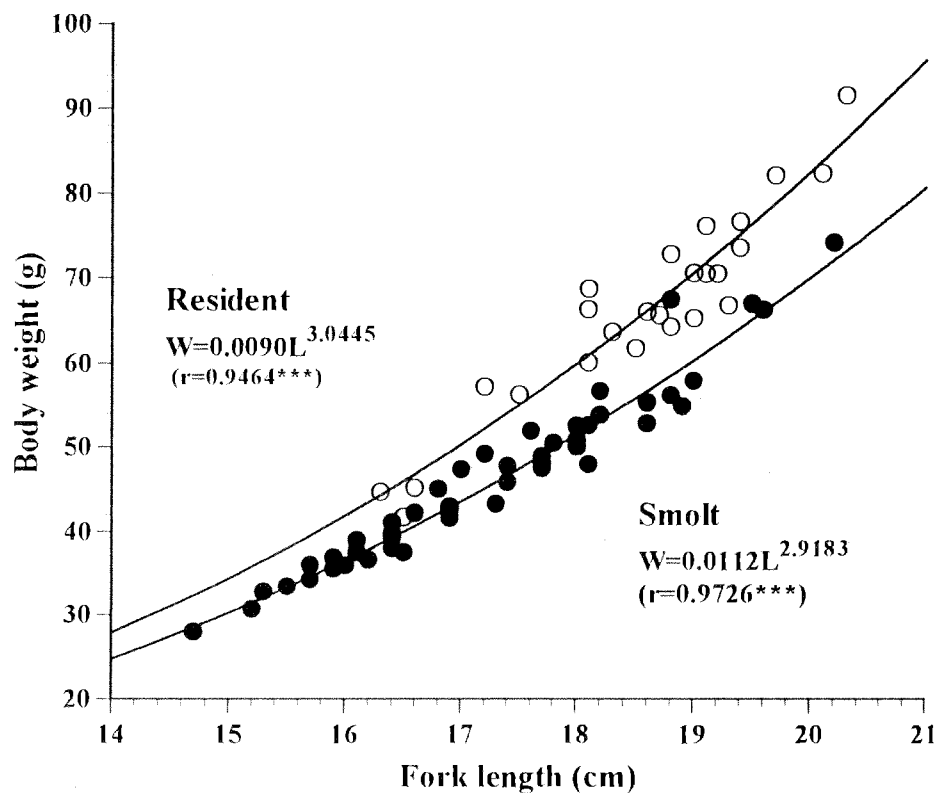
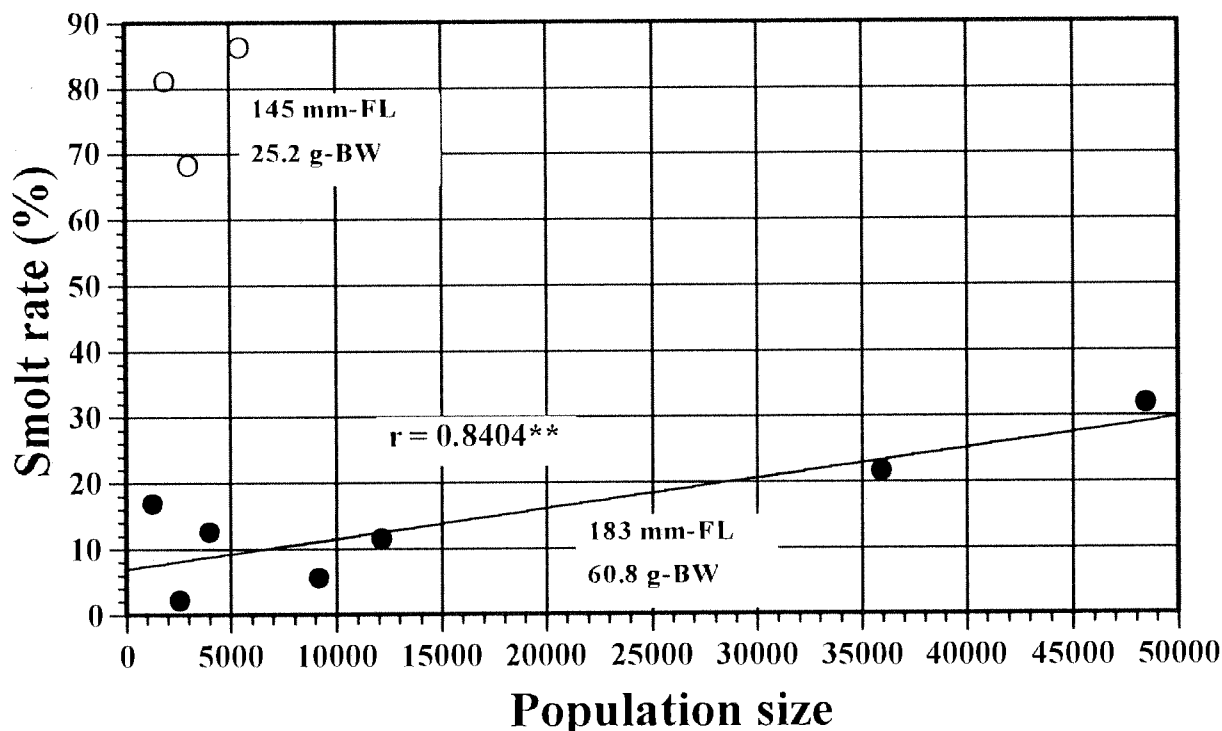


Fig. 5 Relationship between population size (P) and smolt rate (S) of lacustrine sockeye salmon in Lake Shikotsu: $S = 0.0000045P + 0.0699$ ($r = 0.8404^{**}$). The population size shows total numbers of smolt and adult, and the smolt rate represents the number of smolt per population size in a population. Fork lengths of smolt population are 183 ± 15 mm in 1978-1983 and 1987-1988, and 145 ± 4 mm in 1984-1986. Data are obtained from Kaeriyama (1991).



years (183 ± 15 mm). A significant positive relationship between population size and smolt rate was observed except for the 1984-1986 populations ($r = 0.8404$, $P < 0.01$). These results indicate that (1) their residence or seaward migration may be affected by both the population density and the resource condition, which reflects their growth, in the lake, and that (2) they may migrate seaward when they do not fully benefit from the resources in the lake.

These results also suggest that the life history of sockeye salmon may be a conditional strategy that has two tactics of residence and migration. Lake Shikotsu sockeye salmon remain in the lake as a residual type if they can obtain sufficient resources such as food and habitat, whereas a part of the population migrates seaward as smolts after one or two years in the lake when they do not have enough resources to satisfy their energy metabolism. These smolts grow to the anadromous type larger than the residual type.

MIGRATION PATTERN OF JUVENILE CHUM SALMON

For juvenile chum salmon, the migration pattern is controlled by effects of "prior residence" in spawning areas and "precedent migration" in rivers

and at sea (Kaeriyama 1986). Juvenile chum salmon migrate to the sea from late winter to early summer in Japan. Kaeriyama (1986) divided the migrating juvenile into three groups: (1) the "river" type, which remain in the river until early summer; (2) the "foraging migration" type, which migrate to the coastal area where they forage until the Oyashiko Current approaches; and (3) the "escape migration" type, which remain in the coastal area until early summer.

The small percentage of fry that emerge from spawning redds in early spring and remain in rivers for several months are characterized by low specific growth rate. These early emerging individuals tend to dominate over numerous late emerging individuals in the river (Kaeriyama 1996). Their migration behaviors has been sometimes observed as the delayed seaward migration (Mason 1974). Most of wild juveniles migrate downstream immediately after the emergence. Most of enhanced juveniles migrate seaward from rivers at the fry stage (fork length < 50 mm) less than 10 days after release because of high population density (Kaeriyama and Sato 1979; Mayama et al. 1982). There is a significant difference ($P < 10^{-9}$) in fork length during the seaward migration between the wild population (54 ± 7 mm)

staying during long period in the Bibi River at low density (less than a million juveniles) and enhanced juveniles (40 ± 6 mm) migrating seaward immediately after the release at high density (more than 50 million juveniles) in the Tokachi River (Fig. 6).

Because the chum salmon spawn in areas of upwelling groundwater, there may be little changes of the water temperature and a few prey around the spawning area. Early emerging individuals, therefore, have a low growth rate (Specific growth rate; $SGR < 0.006$). On the other hand, numerous juvenile migrating downstream temporarily stay in the estuary, where increased food abundance and higher temperatures are available for growth. They rapidly grow in the estuary ($SGR > 0.01$). Namely, growth inversion occurs between a few prior-resident and numerous migrating juveniles (Fig. 7).

Juvenile chum salmon remain in the coastal sea for a time and migrate offshore at post-fingerling stage in Japan. This offshore migration is usually preceded by larger individuals (the "foraging migration" type; 120 mm in mean fork length), which have the higher growth rate and forage more actively

on prey than others (the "escape migration" type; 80 mm in mean fork length), which passively escape from unsuitable environmental conditions such as higher temperature (Kaeriyama 1986; Salo 1991). For instance, larger marked juveniles released into the Kitakami River in the spring of 1983 began to migrate offshore and to feed on pelagic organisms earlier than the others. Juveniles caught offshore preyed on pelagic organisms such as *Themisto japonica* and *Euphausia pacifica*. They showed much better growth than those from neritic and inshore waters, which fed on coastal zooplankton and terrestrial insects, respectively (Kaeriyama 1986). On the other hand, a significant multiple regression plane indicates that the specific growth rate of marked juvenile chum salmon is a function of days after release and distance from the released river (Fig. 8). These results suggest that larger juveniles which have a higher growth rate migrate more rapidly and farther away from release river. Namely, larger juveniles which have the higher energy metabolism and growth rate migrate more rapidly than others in chum salmon as well as in sockeye salmon.

Fig. 6 Frequency distribution of fork length of juvenile chum salmon from the Tokachi (enhanced) and Bibi (wild) rivers.

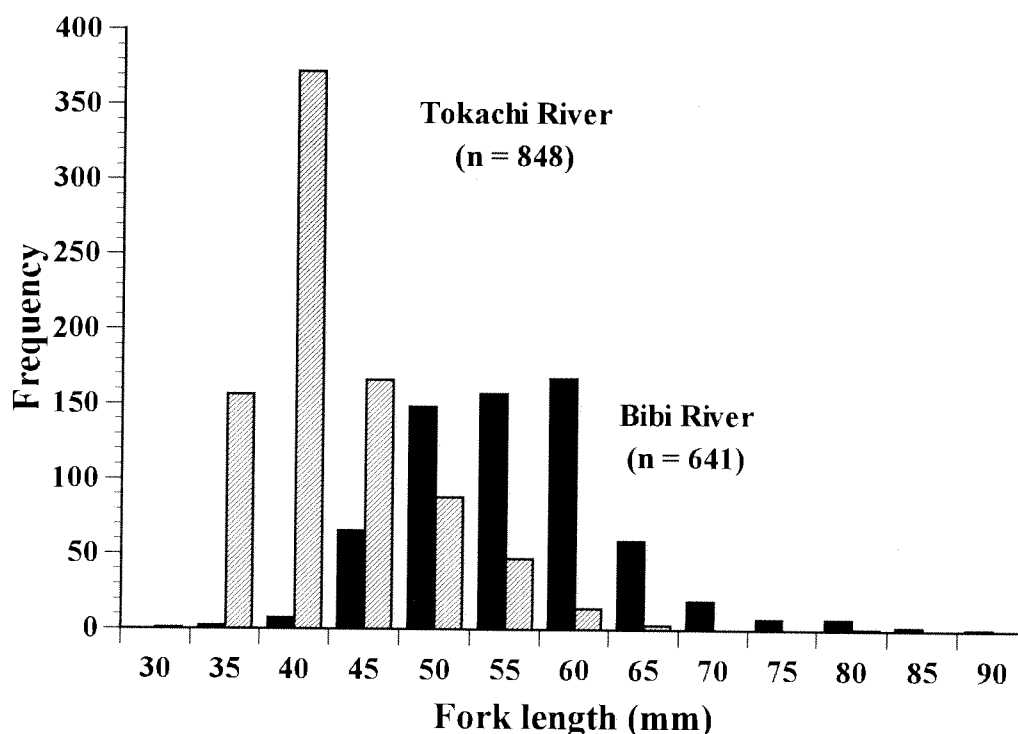


Fig. 7 A model of growth inversion between a few prior-resident (SGR=0.006) and numerous migrating juveniles chum salmon (SGR=0.010) in the river and at the coastal sea. The SGR shows a specific growth rate.

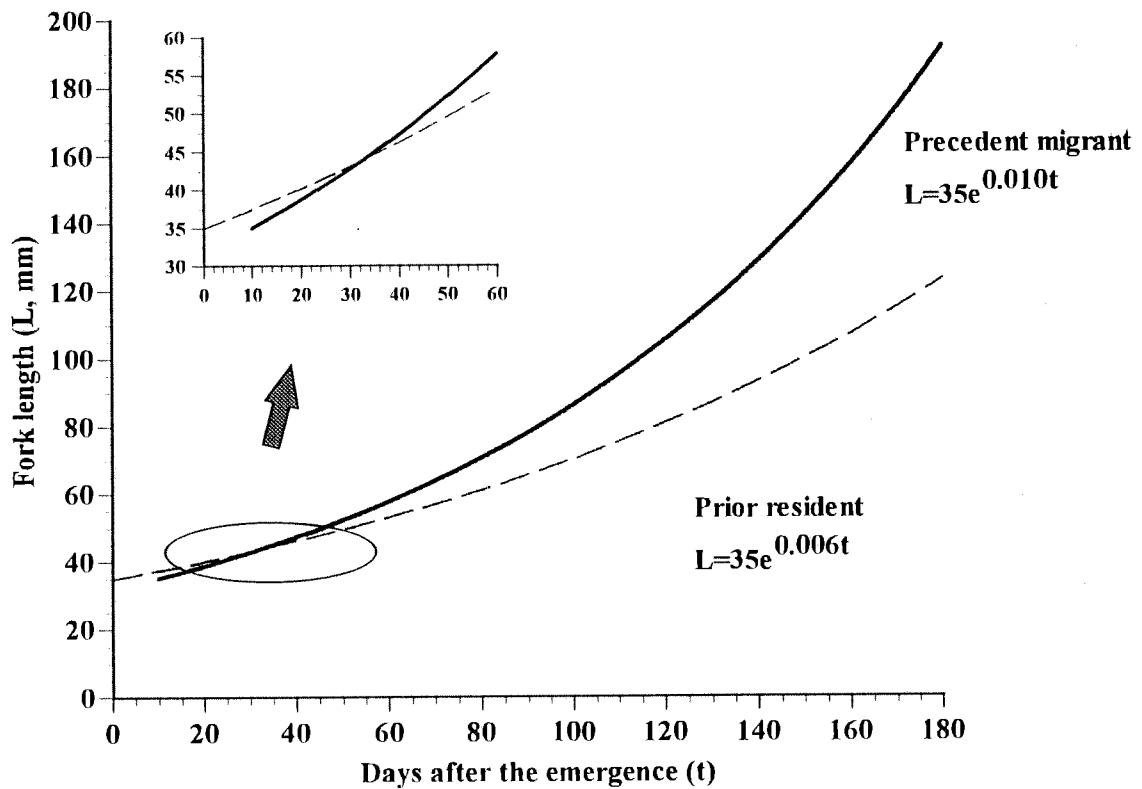
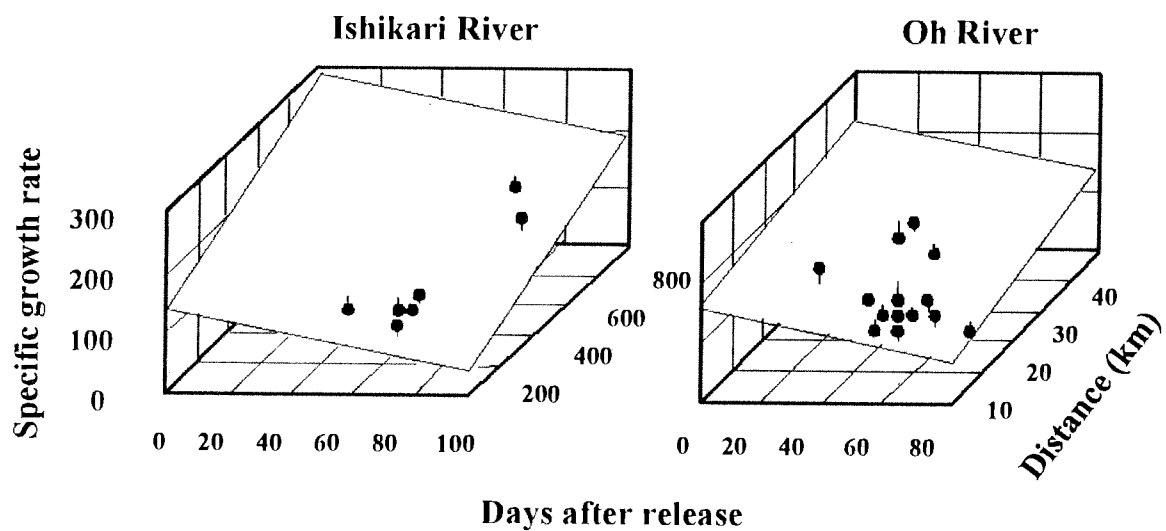


Fig. 8 Multiple regression analysis in specific growth rate (G) of marked juveniles on days after release (t) and distance from release river (k: km) in chum salmon population released from Oh and Ishikari rivers (Modified from Kaeriyama 1986). Oh River: $G = -1.450t + 1.953k + 163$, Ishikari River: $G = -1.010t + 0.147k + 140$.



CONCLUSIONS

The life history strategy of chum salmon may correspond with the conditional strategy of sockeye salmon. The prior-resident individuals may result from a phenotype of resident tactics in the conditional strategy. Their migration pattern indicates the precedent migration of large juveniles. This life history strategy is also known for masu salmon, which is supposed the most primitive species in Pacific salmon. Early emerging juveniles reside dominantly in upper rivers to mature and reproduce as parr. Late emerging juveniles migrate downstream, spend one or two years in middle- or lower-rivers, and migrate seaward as smolts (Kubo, 1980; Mayama, 1992). The conditional strategy and the precedent migration pattern, therefore, may apply to all species of Pacific salmon.

Expanding the habitat area, therefore, Pacific salmon are able to get more resources. In contrast, they incur many risks such as osmoregulation, energetic demands of swimming, exposure to predators, mobilization to non-adaptable habitat by water current through migration. Therefore, the benefits of their migration may involve a trade-off between the profitability of resource acquisition and risks associated with migration. The life history strategy and migration pattern of the genus *Oncorhynchus* evidently reflect an evolution of anadromous fish that have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in the freshwater.

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Age Determination and Growth of Lacustrine Sockeye Salmon, *Oncorhynchus nerka*, in Lake Toya

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Sockeye salmon (*Oncorhynchus nerka*) inhabiting Lake Toya are considered to have a lacustrine (lake resident) type of life history. Although life history studies of anadromous sockeye salmon are numerous, there are few studies of lacustrine sockeye salmon. The present study was conducted to develop an age-determination method using scales and to determine factors responsible for growth variation of different year classes of lacustrine sockeye salmon in Lake Toya. In Lake Toya, annuli formation of scales of lacustrine sockeye salmon did not occur regularly. Age determination was conducted as follows; when the number of circuli between two checks was high, an annulus wasn't formed. When the number of circuli between two checks was low, a false annulus was formed. So age determination was done after discriminating false annuli and missing annuli from true annuli by the number of circuli between checks. Seasonal changes in growth rate calculated from growth curves showed that the growth difference from age 0* to 1* caused much of the growth variation between year classes. Makino and Ban (personal communication) observed annual changes of zooplankton biomass which corresponded to the growth rate of lacustrine sockeye salmon. In Lake Toya, the growth variation between year classes may be caused by zooplankton biomass fluctuations.



INTRODUCTION

Sockeye salmon (*Oncorhynchus nerka*) are classified into three types by the life history of this species; anadromous, lake resident, and kokanee (Ricker 1940). Anadromous sockeye migrate to sea after living in fresh water from 1 to 3 years. Kokanee live in fresh water habitat all of their life. The lake resident sockeye are a form that originates from the anadromous type and most of their individuals stay in lakes with migration of relatively few individuals. The hime masu of Japan was thought to be lacustrine sockeye salmon (Kaeriyama 1991).

Most studies of salmonids, including sockeye salmon, focused on population dynamics in the marine life stage and life history characters like return size and age. The growth of sockeye salmon in the marine life stage was thought to be affected by density-

dependent factors (Rogers 1980; Peterman 1982), and the growth difference of sockeye salmon was thought to be because competition for prey was the result of not only intra-population but also inter-population competition between fish that originated from different rivers (Peterman 1984). In coho salmon (*O. kisutch*), the growth in early marine life stage was correlated with number of coho salmon (Mathews 1980), and the number of maturing fish was negatively correlated with weight (McGie 1984). Ricker (1981) suggested that increment of growth rate in sockeye salmon in British Columbia was affected by gradual cooling of the ocean.

A relationship between annulus formation and growth was observed for lacustrine sockeye salmon by analyzing growth patterns resulting from age determination using scales (Kurohagi and Sasaki 1964; Kurohagi 1965; Tokui 1988). A relationship between

growth, age of maturity, and egg size was also reported (Kato 1978, 1980). In Lake Shikotsu, the number of returns of lacustrine sockeye salmon was negatively correlated with size, and a density-dependent mechanism was observed in Lake Shikotsu (Kaeriyama 1991). Rieman and Myers (1992) suggested that there was a negative correlation between age specific size and lake productivity, and also that density-dependent mechanism was higher in low-productivity lakes than in high-productivity lakes, for oligotrophic lakes where kokanee were found. Compared with anadromous sockeye salmon, few attempts have been made to study the basic and ecology of lacustrine sockeye salmon, and in particular to test the use of scales for age determination and growth variation. Furthermore, only fragmentary research was conducted on lacustrine sockeye salmon since they were stocked in Lake Toya in 1893. Over the past few decades no studies have been made on lacustrine sockeye salmon in Lake Toya since those of Oono and Ando (1932), Takayasu and Kondo (1934), Tanakadate (1940) and Watanabe (1960). Most lacustrine sockeye salmon die after spawning, however, individuals of each life history stage can be sampled throughout the year in Lake Toya. Therefore, we were able to investigate the effects of the limnological environment and prey abundance in the lake on stock abundance of lacustrine sockeye salmon, along with growth variations in each life history stage and age determination in different cohorts.

The purpose of this paper is to test the accuracy of scale characteristics for age determination by comparing scales of marked fish and to understand differences in growth patterns in different cohorts of lacustrine sockeye salmon in Lake Toya. From these data we establish an age determination method and discuss various mechanisms of growth for these fish in the lake.

MATERIALS AND METHODS

Study site

This study was carried out in Lake Toya, which is a large oligotrophic lake located in a caldera in the central area of Hokkaido, Northern Japan, at an elevation of 84 m. The lake has a surface area of 70.44 km², a maximum depth of 179 m, and an average depth of 116.3 m (Fig.1). Starting from 1939, the pH has gradually decreased due to the inflow of Osaru River which contains acid mine waste. The lowest level (pH 5.0) occurred in 1970. In 1972, neutralization was started and the pH rapidly increased. The pH is now about 7.0 (Imada et al., 1988). Mt. Usu, located near the lakeside, erupted in August 7, 1977. So much volcanic ash fell into the

lake that the transparency decreased to about 1 m temporarily, but recovery began after October, 1977.

The most common commercial fish species in the lake were lacustrine sockeye salmon, Japanese pond smelt (*Hypomesus transpacificus nipponensis*), and masu salmon (*O. masou*). These species were introduced by fisherman. Lacustrine sockeye salmon were introduced from Lake Akan in 1893, and the catch (tonne) has been totaled from 1930 by the Toya Lake Fisherman's Association (Fig.2a). The catch of lacustrine sockeye salmon has fluctuated; it was about 25 tonnes in the 1930's, increased to about 100 tonnes in the 1950's, rapidly decreased following lake acidification, and showed no increase since the 1960's. Japanese pond smelt catches varied between 10 and 20 tonnes till 1966, when the catch increased to about 50 tonnes in 1986 (Fig. 2b). Masu salmon catch was low, although the Toya Lake Fisherman's Association did not record catch. However, in recent years, the number of returns of masu salmon has increased (Fig. 2c).

Surface water temperatures were as low as -0.3 ~ -0.9 °C during winter and as high as 20.0 ~ 23.3 °C during summer (Fig. 3). Average water temperature was high in 1990 and 1991, and was low in 1993.

Fish Sampling

Lacustrine sockeye salmon were sampled from May 1991 to October 1995. Sampling was conducted with gillnets and a beach seine in front of the Toya Lake Station for Environmental Biology. Additional samples were collected from June 1995 to August 1995 by the Toya Lake Fisherman's Association.

We used commercial gillnets with stretched mesh of 15, 24, 57, and 63 mm from May 1991 to September 1994, and two sets of research gillnets that have a stretched mesh of 19, 21, 24, 27, 33, 37, 42, 48, 54, 63, 72, and 82 mm from October 1994 to October 1995. It was thought that the research gillnets were non-selective (Takagi 1993). Gillnet sampling was conducted weekly each month, with nets set overnight and retrieved the next day. Spawners were collected by beach seine near the station. The number of lacustrine sockeye salmon caught by Toya Lake Station was around 3,059 and by Toya Lake Fisherman's Association was 196.

50,000 individuals of the 1991 brood were marked by cutting adipose fin and were released at about 1 g in Lake Toya.

Measurement of Fish

The samples from the station were measured to the nearest 1 mm for length and weight to the nearest 0.01 g fresh weight. Standard length was transformed to fork length by following formula,

Fig. 1 Map of sampling sites in Lake Toya.

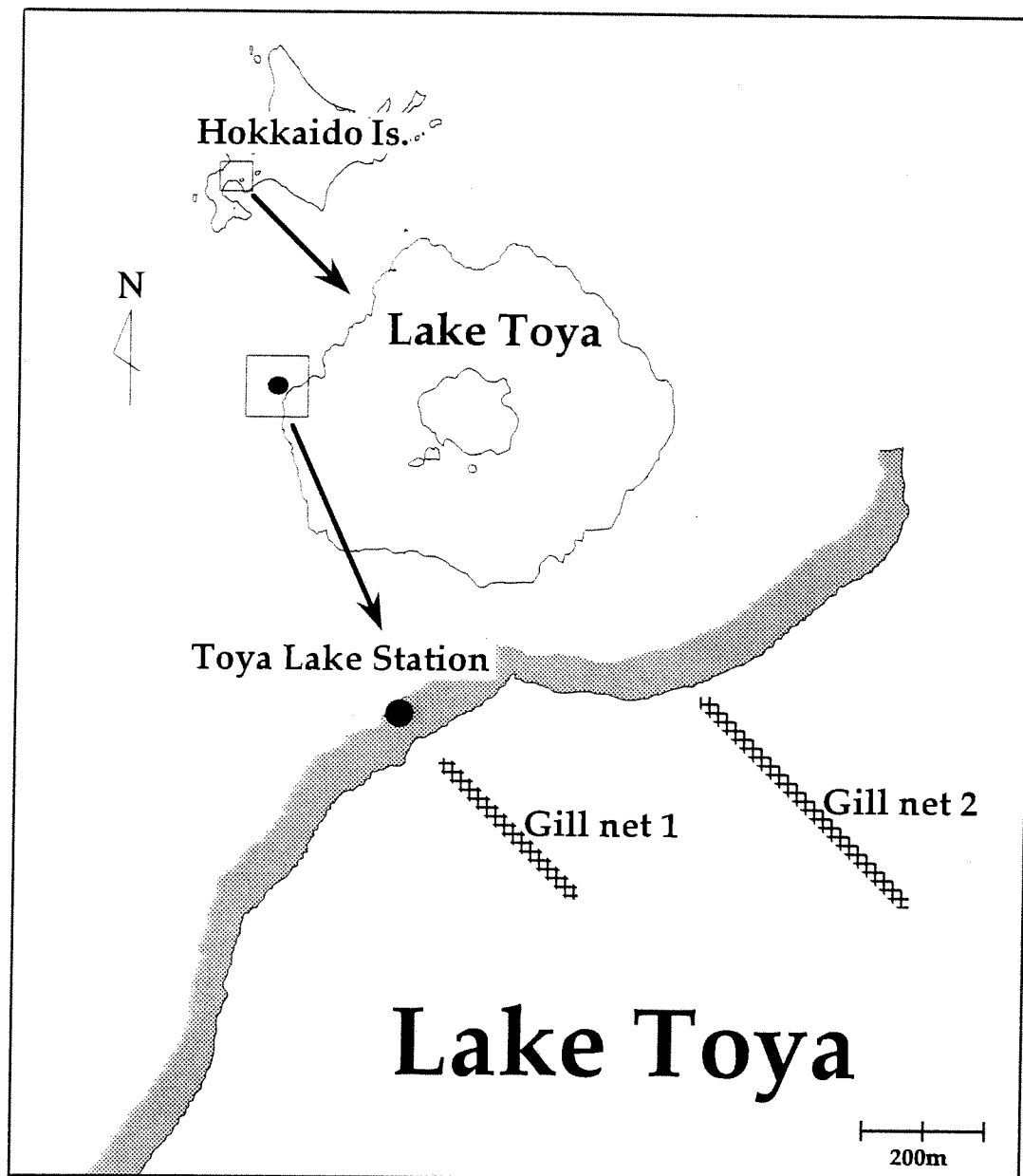


Fig. 2 Annual changes in catch weight (tonnes) and number released (thousands) from 1930 to 1994. Solid bar and line indicate catch weight and number released for (Top) lacustrine sockeye salmon (thousands) and (Middle) pond smelt (millions), respectively. The sockeye salmon population collapsed in 1966. (Bottom) Annual changes in number of masu salmon returns from 1992 to 1995.

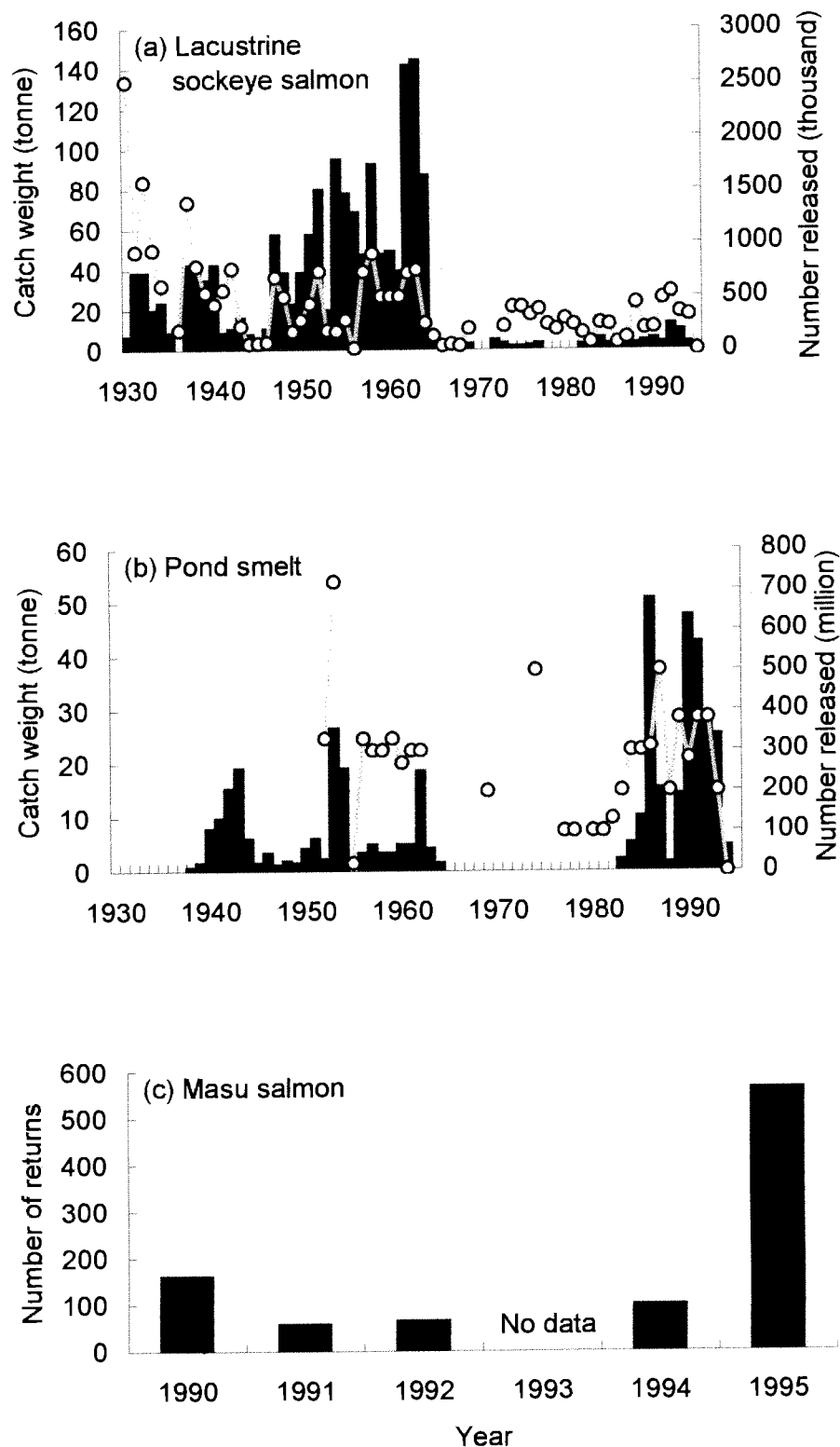
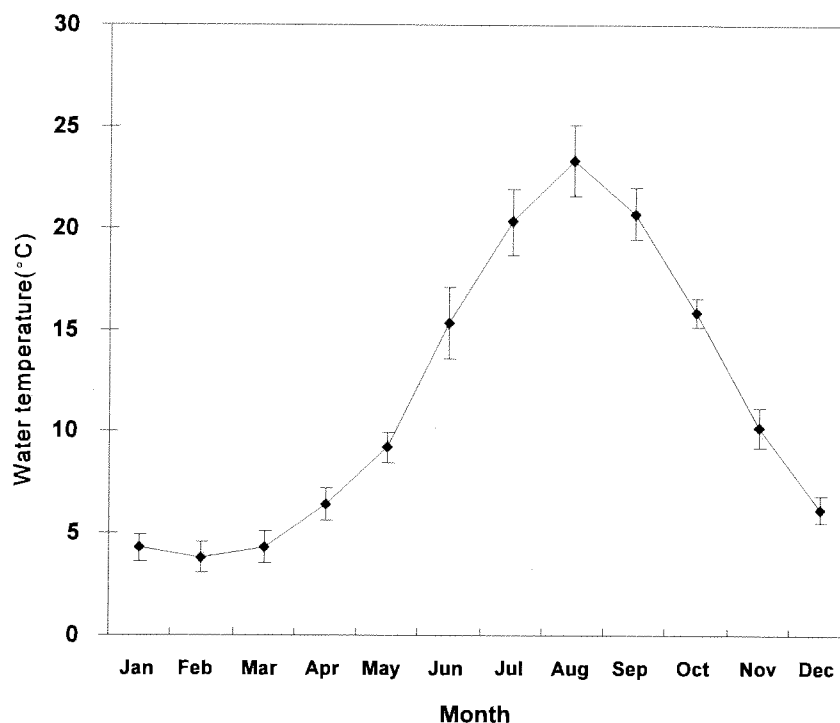


Fig. 3 Seasonal changes in average and standard deviation of surface water temperature in Lake Toya from 1988 to 1994.



Fork length = $1.081 \times \text{Standard length} + 1.079$

($r = 0.97$, $p < 0.01$, $n = 71$).

Additional samples from the Toya Lake Fisherman's Association were measured to the nearest 1 mm and weight to the nearest 5g fresh weight.

Scales were taken for age determination ($n = 2,432$) from an area between the dorsal fin and the lateral line and were pressed in plastic plates following Koo (1955).

Scale Analysis and Age Determination

We used a projector to magnify each scale one hundred times, and measured the number of checks, circuli, and the lengths of the scale (Fig. 4). The lengths of 295 scales were measured along the long axis from the focus to each check on scale and to the edge of the scale. A check was identified in areas where the circuli interval was narrow or discontinuous. In marked fish, the annulus was a check which formed regularly, while false annuli were checks which formed irregularly. Annuli formation of the non-marked fish was identified by comparing the number of circuli in the last growth zone in the season that marked fish annuli was formed. Then we assumed that if the number of circuli was more, the scale had not formed an annulus, and if the number of circuli was fewer, the scale had formed a false annulus.

Finally, age determination was conducted by

analyzing the number of annuli, the number of circuli between checks, and the fork length distribution. Age was designated by an Arabic numeral and a plus sign (+): 0⁺ young of the year; 1⁺ in second year; 2⁺ in third year; and so on.

Back Calculation

Fork length (cm) at earlier ages was back-calculated from the relationship between fork length and number of circuli. Fukuwaka and Kaeriyama (1994) suggested that back-calculation should be conducted from relationship between fork length and scale radius. However, since significant correlations exist between scale radius, number of circuli, and fork length, we calculated fork length from the relationship between fork length and number of circuli when the annuli were formed. Geometric mean regression (GMR; Ricker 1973) was used to calculate the relationship between fork length and number of circuli using the Fraser-Lee method as described by Ricker (1992). We assumed that the fork length was 4 cm when the scale was formed, following the result for sockeye salmon in Bristol Bay reported by Koo (1955) and for lacustrine sockeye in our experimental result (unpublished data).

Data Analysis

Correlation coefficients were used to analyze the

Fig. 4 Photograph of scale of marked lacustrine sockeye salmon (age 3⁺) in Lake Toya. This fork length and scale radius was 29.9 cm and 1.650 mm, respectively.



relationships between fork length and number of circuli, and between scale radius and number of circuli. We used the Mann-Whitney U test to compare fork length between males and females. Estimation of the parameters of von Bertalanffy's growth curve was conducted by non-linear regression, using the simplex search method. AIC (Akaike's Information Criteria) was calculated from residual sum of squares.

RESULTS

Establishment of Age Determination Method

Checks were observed in 1,899 of 2,432 scale samples. Checks were not observed in 509 scales, and in 24 scales the check wasn't observed because of maturation or scale regeneration.

From the circuli distribution of the last growth zone (LGZ) on each check of marked fishes stocked in spring 1992, the relationship between checks and age was analyzed (Fig. 5). The mode of circuli in LGZ increased with month. In September 1992, only one scale had formed a check. From May to July 1993, a check formed on most scales, but scales with unformed checks were still found in May (1 of 17 fishes), June (3 of 34 fishes) and July (1 of 59 fishes).

To differentiate between irregular and regular formed check marks, the number and frequency distribution of circuli to the time of check formation was examined (Fig. 6). The number of circuli of the single fish with a check mark was 14 in September 1992, similar to the numbers observed of these fish with no checks. The number of circuli increased between September and the following May. Many fish with an unformed check in September increased

Fig. 5 Frequency distribution of number of circuli classified by presence of annuli for marked lacustrine sockeye salmon released in June, 1992 into Lake Toya. Open and solid bars indicate zero and one check on scale, respectively.

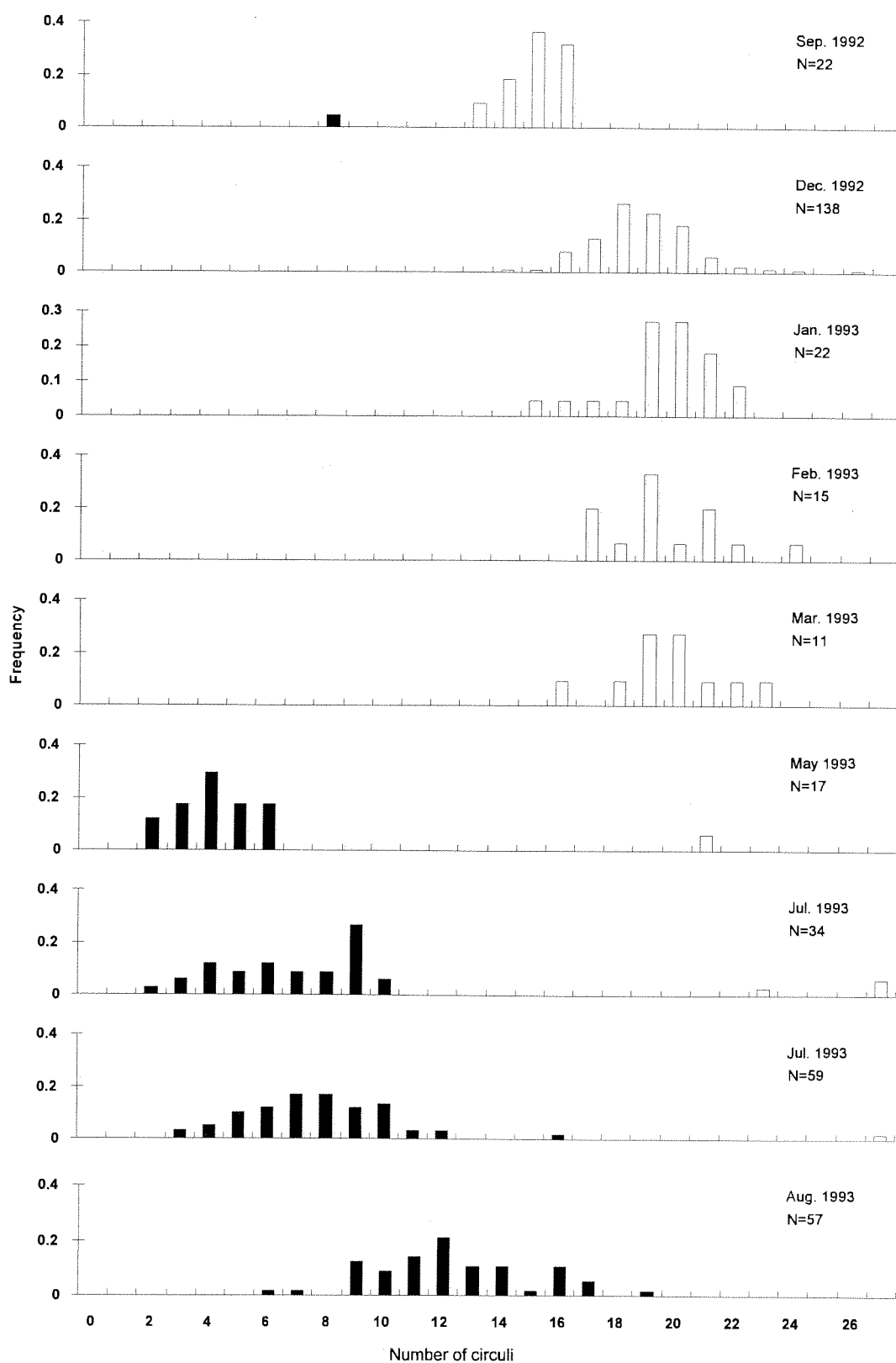
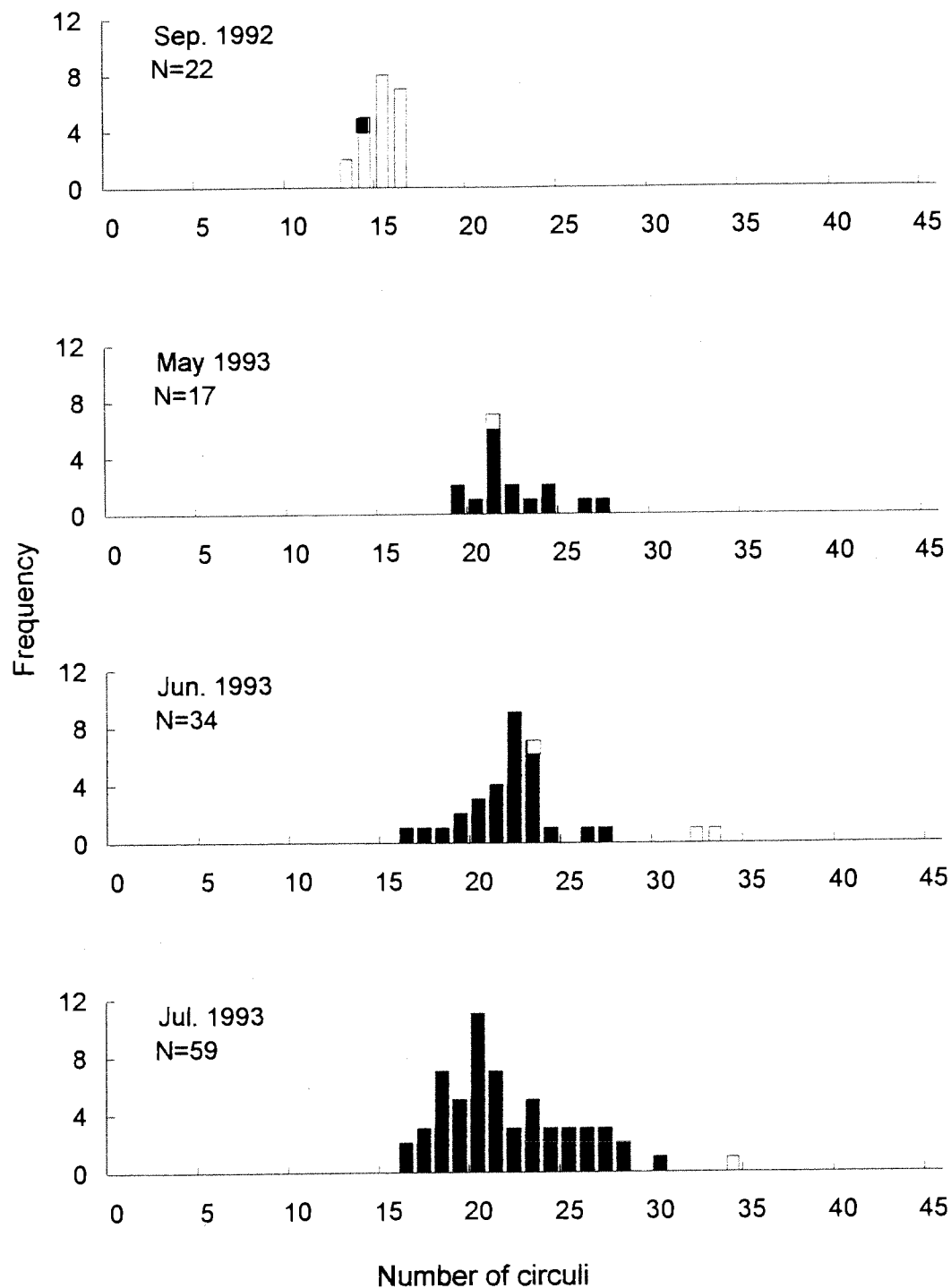


Fig. 6 Frequency distribution of number of circuli to first check of marked lacustrine sockeye salmon in 1991 cohort captured in Lake Toya. Open and shaded bars indicate zero and one check on scale, respectively.



the number of circuli to the first check and the first formed annulus in May 1993. Fish without checks in May, June, and July 1993 were of two types; the first type was fish with no difference in the number or distribution of circuli from fish with a check, and second type was fish that had more frequent numbers of circuli than those with a formed check (Fig. 6).

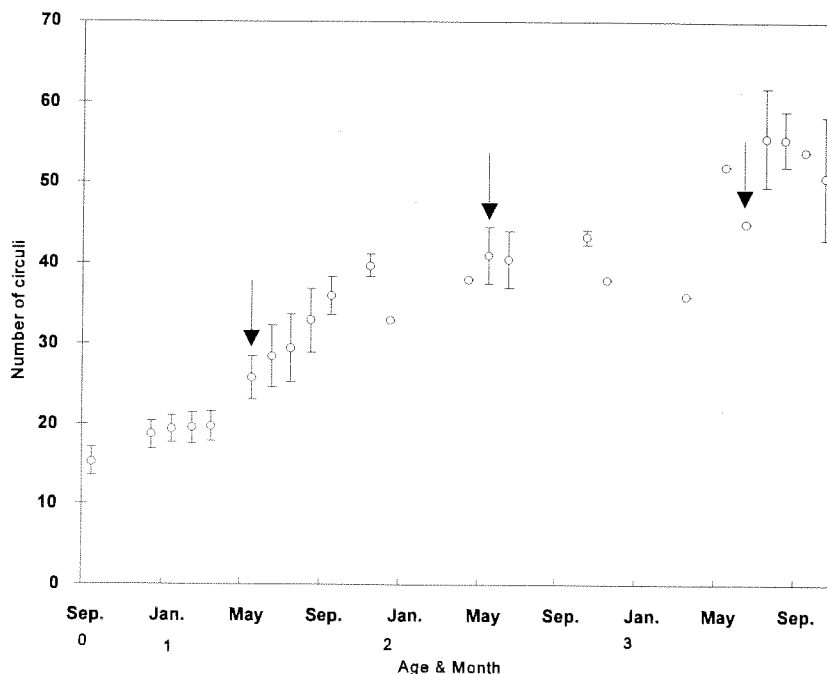
Fig. 7 shows the seasonal changes in number of circuli and clarifies when the circuli number increased and when the first check was formed. Most of the first check marks were formed during the period between May and June. In winter (from December to March), the number of circuli did not change and the check tended to be formed at the beginning of the period when the number of circuli began to increase again. Most marked fish formed a check around May which is defined as a true "annulus".

To estimate the period when checks formed on unmarked fish, seasonal changes in frequency distribution of number of circuli in last growth zone (LGZ) was examined (Table 1). Assuming that the month when the check was formed was the month when the number of circuli in the LGZ was low, the month when a check formed varied between years.

For fish captured in 1991, it was thought that the second and third checks were formed about July. For fish captured in 1992, it was thought that each check was formed in May, while frequency distributions of number of circuli in LGZ indicated bimodality and variation for fish captured in 1993, 1994 and 1995. In June 1993, there was marked bimodality in frequency distribution of number of circuli in the second check, and many fish were judged to have formed a check from April to June.

For reasons mentioned above, age determination in lacustrine sockeye salmon in Lake Toya was conducted using the following procedure. From the number of circuli counted between two checks in scales of marked fish (mean and standard deviation: 21.0 and 2.8, max=30, min=14, n=198), we classified fish that had many circuli (>31) as fish that had not formed an annulus and those with few circuli (<14) as fish that had formed a false annulus. The true age was estimated by adding one to the age of fish without an annulus and by deducting one from the age of fish that had formed a false annulus. Furthermore, we excluded fishes that did not fit the expected age-specific fork length distribution.

Fig. 7 Seasonal changes in average and standard deviation (bars) of number of circuli of marked lacustrine sockeye salmon in 1991 cohort captured in Lake Toya. Arrows indicate times of annulus formation.



(a) 1991

(b) 1992

Table 1. (continued)

(c) 1993																												
Number of circuli																												
Month	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	+
Check number = 1																												
Apr.								1																				
May			2	3	5	3	3																					
Jun.	1		3	9	6	10	8	5	5	12	3								1	2	1	1	2	1				
Jul.			2	10	14	12	21	19	18	10	13	2	4	1		1												
Check number =2																												
Apr.	1	2		1	1																							
May		2	1	8	14	13	6																					
Jun.				1	1	3	1																					
Jul.					3	7		4	1	1	1	4	1															
Check number =3																												
Apr.	19	1			1	1		1																				
May	1	3	2	3	3	1			1			1																
Jun.							1																					
(d) 1994																												
Number of circuli																												
Month	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	+
Check number=1																												
Apr.																												
May																												
Jun.	1															1	4	2	6	2								
Jul.			1											1		1	2	6	3		1		1	1				
Check number=2																												
Apr.																												
May	2																											
Jun.	1									1	1	3	2	3	1													
Jul.																												
Check number=3																												
May			1																									
Jun.							1																					

(e) 1995

[illegible]

Patterns of Scale Growth

To compare the number of circuli in each cohort, seasonal changes in the number of circuli in the 1990 and 1991 cohort were examined (Fig. 8). The number of circuli on scales of each cohort did not increase during the winter and increased only during summer, but the number of circuli was not stable. The increment of circuli in the 1990 cohort was large in age 1⁺ and few in age 3⁺, while the increment of circuli in 1991 cohort was low in age 1⁺ and large in age 3⁺.

Fig. 9 shows the number of circuli between annuli in two cohorts. The number of circuli in the 1990 cohort was largest at age 0⁺ and 1⁺, and decreased at age 2⁺. Conversely, the number of circuli in the 1991 cohort changed very little with age.

These result show that the growth of the scale was minimal during winter and that the number of circuli differed over time and with age.

Growth Variation among Cohorts

Before turning to an examination of growth variation, we compared growth of males and females, by comparing fork lengths of males and females at ages 0⁺, 1⁺ and 2⁺. No significant differences between males and females was found in except for age 0⁺ fish captured in August 1993 (Mann Whitney

U-test, $p < 0.05$). As the difference in fork length between males and females in each age was small, the growth analysis described next was therefore conducted by pooling males and females.

The von Bertalanffy growth curves were fitted to 1990 and 1991 cohorts to compare growth patterns. The growth of the 1990 cohort was rapid at age 0⁺, but the 1991 cohort was lower. Both the growth pattern and the parameter of the growth curve differed between cohorts (1990: $L_{\max} = 30.3$, $K = 0.143$, $R^2 = 0.99$, $n = 357$, $AIC = 2,699$, 1991: $L_{\max} = 44.0$, $K = 0.023$, $R^2 = 0.98$, $n = 1,465$, $AIC = 13,334$). The growth coefficient, K , of the 1990 cohort was larger than that of 1991, and $L_{\max}$ of the 1990 cohort was less than that of the 1991 cohort.

Changes in Growth Rate with Time

Fig. 10 shows the estimated changes in growth rate over time from the von Bertalanffy growth curves fitted to each cohort to clarify differences in growth pattern of each cohort. The growth rate of the 1991 cohort was initially lower than that of the 1990 cohort at young ages but declined more slowly, so that the growth rate of 1991 cohort was higher than that of 1990 cohort at ages > 3 years. The major difference in growth pattern between the 1990 and 1991 cohorts was caused the difference in growth rates at age 0⁺ and 1⁺.

Fig. 8 Seasonal changes in average and standard deviation (bars) of number of circuli for 1990 and 1991 cohort of lacustrine sockeye salmon in Lake Toya. Solid horizontal bars indicate winter periods.

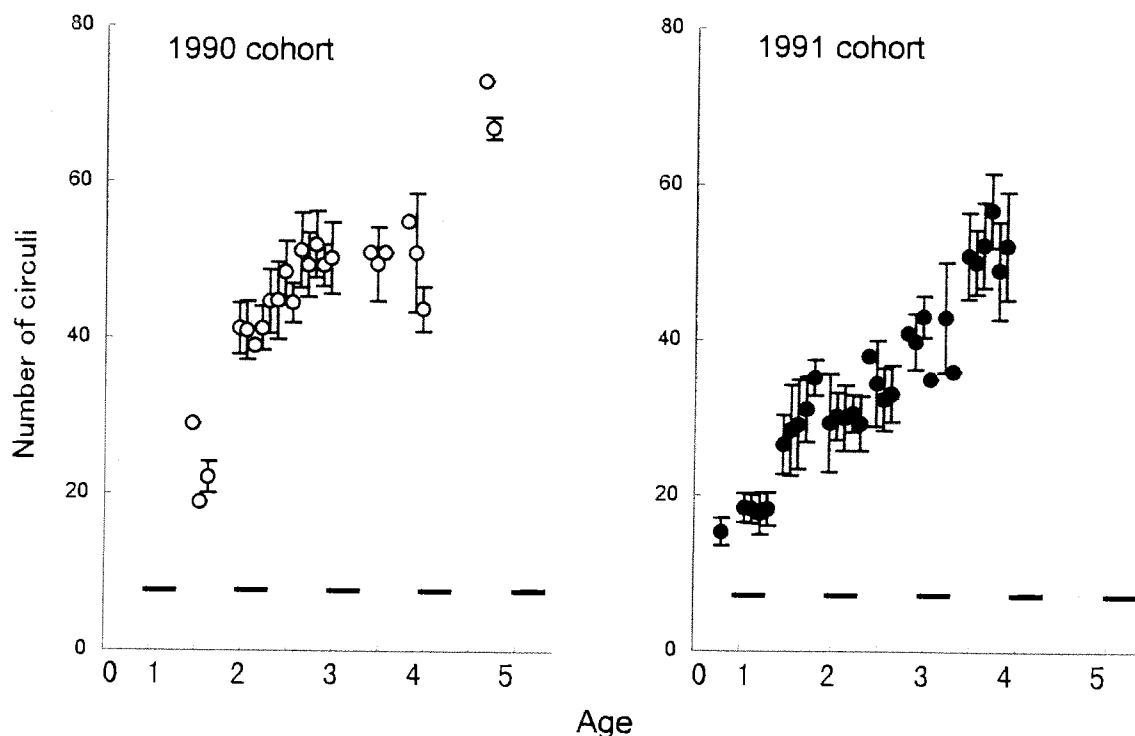


Fig. 9 Annual changes in average and standard deviation (bars) of circuli increments on scales of lacustrine sockeye salmon from 1990 and 1991 cohorts in Lake Toya. Parentheses show sample size.

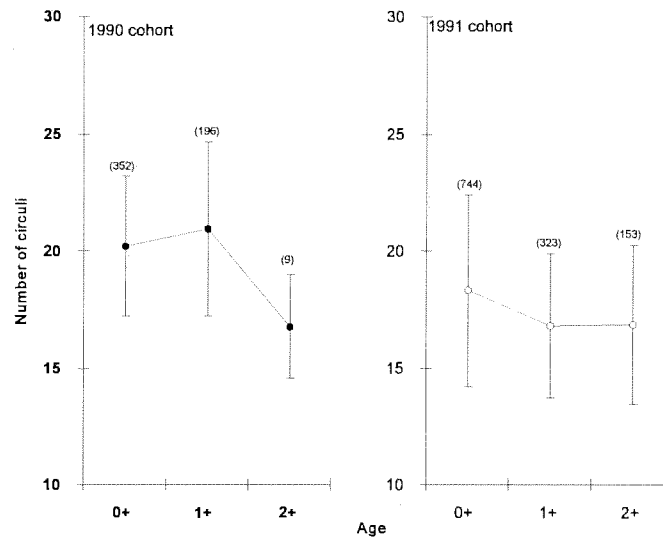
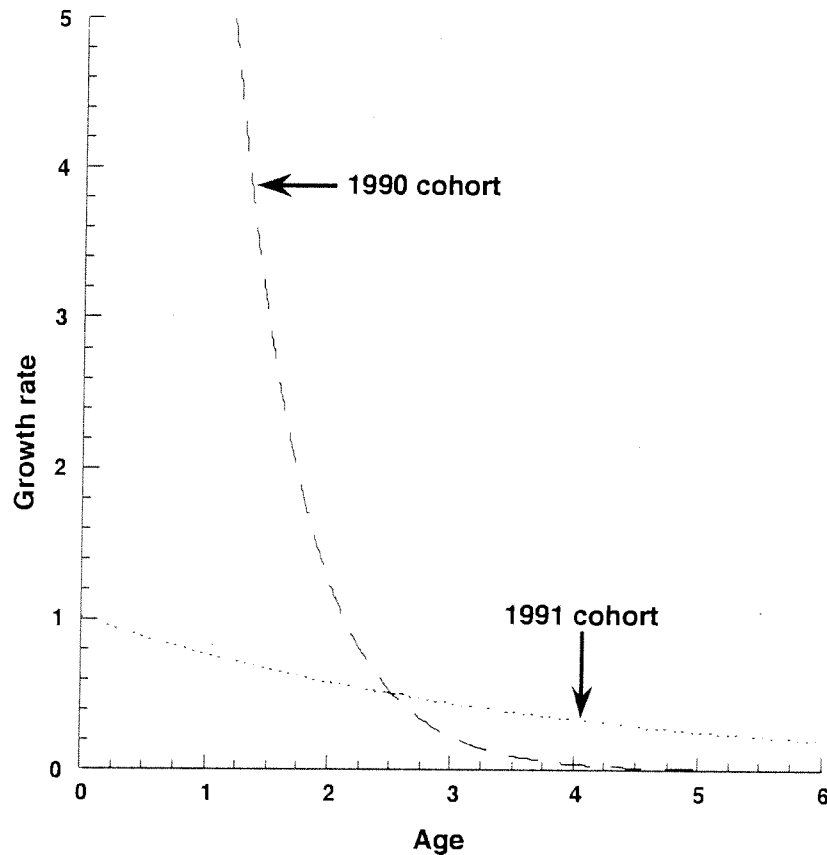


Fig. 10 Changes in growth rate of lacustrine sockeye salmon with time calculated from the fitted von Bertalanffy growth functions for the 1990 and 1991 cohorts.



We will expand this result for two cohorts to many, by comparing the growth coefficient back-calculated from fork length, to clarify at what ages most of the growth variation occur. We calculated the geometric mean regression equation by estimating relationship between fork length and number of circuli:

$$C = -3.89 + 1.97L \quad (r^2=0.92)$$

where C is number of circuli and L is fork length (cm). The coordinates (Cs, Ls) of the standard point in the Fraser-Lee method is (4, 4.001), and back-calculated fork length at earlier sizes was calculated from the Fraser-Lee equation. The growth coefficient calculated from back-calculated fork length was compared between each cohorts (Fig. 11). The

growth coefficient of the 1990 cohort is higher than that of the 1991 from age 0⁺ to age 1⁺, and lower than that of the 1991 for age 2⁺ and 3⁺, consistent with our previous analysis. The growth coefficients by age classes of all cohorts was highest in the age 0⁺ period. The growth coefficients then decreased with age but varied by cohorts. These results showed that growth coefficients (or growth rates) might vary markedly between early life (e.g. age 0⁺, and 1⁺).

Fig. 12 shows the relationship between the growth coefficient and summer surface water temperature from 1990 to 1994. The growth coefficient does not relate to summer surface water temperature (Spearman's rank correlation, water temperature VS 0⁺ growth rate; $p=0.40$, water temperature VS 1⁺ growth rate; $p=0.30$, water temperature VS 2⁺ growth rate; $p=0.16$).

Fig. 11 Comparison of specific growth rate (SGR) with (a) age 0⁺, (b) 1⁺ and (c) age 2⁺ for 1989 to 1993 cohorts of lacustrine sockeye salmon captured in Lake Toya. Bars represent standard deviation.

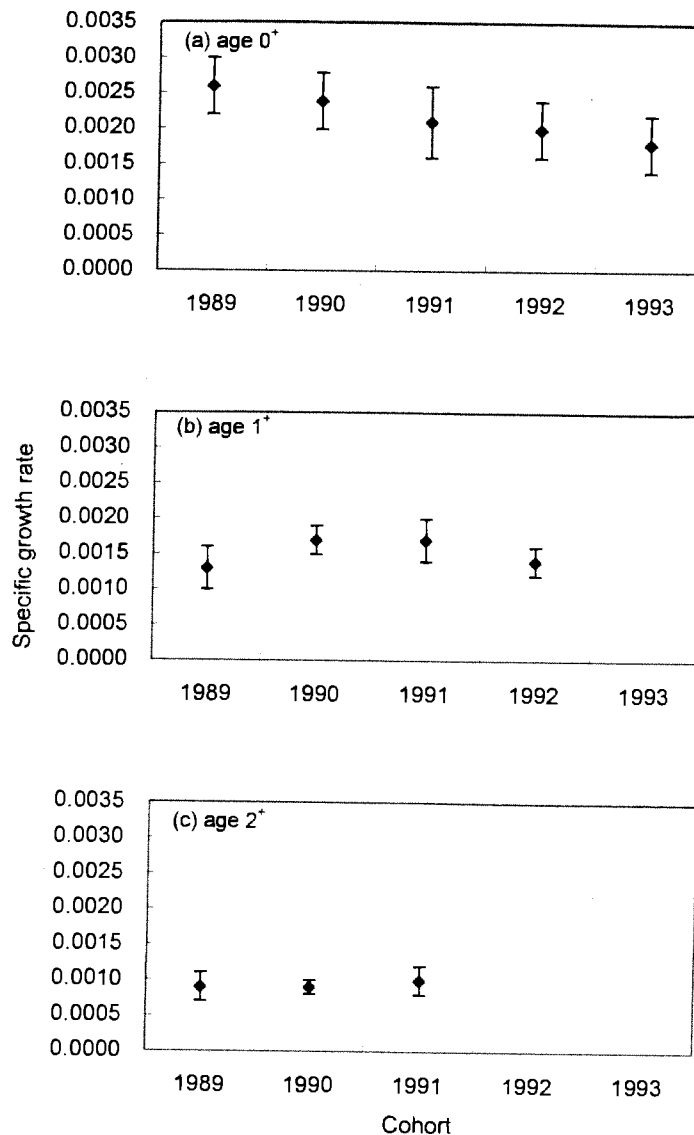
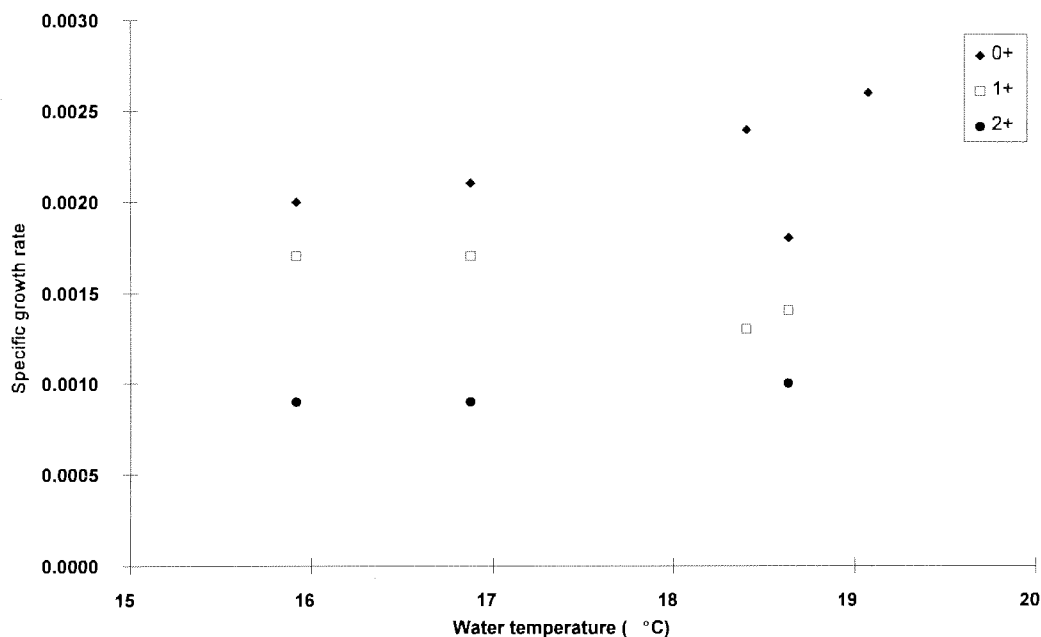


Fig. 12 Relationships between summer surface water temperature and specific growth rate at age 0⁺, 1⁺ and 2⁺.

DISCUSSION

From analysis of number of circuli in the last growth zone, it was clear that most of the marked fish in Lake Toya formed a check during the period of increasing circuli from April to June. We therefore defined a check formed in this period as the annulus. However, there were a few marked fish that formed a false annulus or failed to form an annulus during the growing season. The number of circuli to a false annulus was fewer than in fishes that formed a true annulus. Furthermore, the number of circuli in fish that failed to form an annulus was higher than in fish forming a true annulus. From observation of seasonal changes in the number of circuli, the annulus formation period for unmarked fish was from April to June, but the scale formation period differed each year.

Several articles have been reported on studies of age in lacustrine sockeye salmon, focusing on how and when annulus formation occurs. Kurohagi and Sasaki (1964) reported that the period of annulus formation in Lake Shikotsu lacustrine sockeye salmon was related to their body growth, and that the third annulus was formed between January to May. In contrast, Tokui (1985, 1988) reported that the annulus formed before the start of body growth, and that annuli were formed from May to August in Lake Shikotsu and about May in Lake Kuttara. These estimates of the time of annulus formation in lacustrine sockeye salmon differ

between lakes and years. In this study, it was clear that the period of annulus formation occurred between April to June and that the annulus formed during periods of body growth. The period of annulus formation in unmarked fish was from April to June, but the possibility of variability in the time of annulus formation was noted by Kurohagi and Sasaki (1964) and was similar to results of previous studies. Bilton and Robins (1971) reported that change in even one factor was enough to affect check formation on scales of sockeye salmon (e.g., food). Based upon this study, Suzuki and Kaeriyama (1990) suggested that the width of circuli on scales of juvenile sockeye salmon was affected by the feeding level and that a check might be formed by increasing growth rate. The present results suggest that a false annulus was formed by increasing growth rate except in the period from April to June (i.e., just after release), and that fish showing no increased growth rate from April to June might not form an annulus. Therefore, in this paper, we distinguished fish with false annuli and without annuli from with true annuli by the number of circuli between checks.

The number of circuli on scales of juvenile sockeye salmon is related to scale increment and body growth (Fukuwaka 1995), and fish with a large number of circuli between two checks might indicate a large increment of body growth between the two checks. In marked fishes, it is clear that fish that had not formed an annulus had a large number of circuli

between checks, while those which had formed a false annulus had fewer. Therefore, in unmarked fishes, it was thought that fish which had not formed an annulus likely had a greater number of circuli between two checks. Therefore, annulus discrimination should be conducted using the number of circuli between checks.

Generally, age determination using scale and otolith measurements requires corresponding data on fork length and number of rings, a stable time of ring formation, and known time interval of ring formation (Tanaka 1985). In lacustrine sockeye salmon in Lake Toya, regularity of annulus formation was not always observed, so it is important to distinguish fish that formed a false annulus and those without an annulus, and to consider the effect of the growing season on age determination. In this study, the errors of age determination were probably few, because only two fishes differed from the others in age specific fork length distribution.

The present results suggested that scale growth differ between cohorts. The von Bertalanffy growth curves of the 1990 and 1991 cohorts differed primarily because of differences in growth rates at age 0⁺ and 1⁺. Furthermore, in cohorts without measured growth curves, differences in growth rates between annuli were also observed. Annual variation in the number of circuli was observed in sockeye salmon in Lake Azabach'e, Kamchatka River, and this phenomenon might be related to food supply, water temperature and population density (Bugaev et al. 1994). It should be concluded, from the previous reference and the present results, that the differences in growth pattern between 1990 and 1991 cohorts in lacustrine sockeye salmon in Lake Toya might be influenced by biotic factor in the lake. Makino and Ban (personal communication) observed annual changes of zooplankton biomass from 1992 to 1995. On the other hand, the growth rates of lacustrine sockeye salmon does not relate to summer surface water temperature. However, summer surface water temperature seems to relate to the growth rate of lacustrine sockeye salmon (Fig. 11). Brett et al. (1969) reported that water temperature also affected growth rate of fingerling sockeye salmon. Zooplankton biomass fluctuations and annual water temperature changes may affect the growth rate of lacustrine sockeye salmon in Lake Toya.

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Scale and Otolith Patterns Prove Growth History of Pacific Salmon

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Scale and otolith patterns are frequently used for age determination, growth estimation, and stock identification of Pacific salmon. However, little information is available about their formation mechanism such as circulus, check in the scale, and growth increment in the otolith. I clarified the formation mechanisms of scale and otolith patterns by rearing experiments using juvenile sockeye and chum salmon. Circulus spacing was positively correlated with somatic growth in juvenile chum salmon. A check was formed soon after release from a hatchery in juvenile chum salmon and at the time of tagging in juvenile sockeye salmon. Growth increments were produced in otolith on a daily basis. An allometric equation was fitted to the relationship between fish length and otolith length. These results indicate that growth history of individual fish can be back-calculated from scale and otolith patterns. Circulus spacing is also useful as an indicator of somatic growth. Scale and otolith patterns are influenced by somatic growth rate and by environmental conditions. From this, scale and otolith patterns are useful for the estimation of fish growth through the life history.



INTRODUCTION

The assessment of growth condition provides valuable information for monitoring salmonid stocks. Ocean growth is a determinant of the biomass of salmonid stocks inhabiting Pacific Ocean. Somatic growth would also influence the population dynamics of Pacific salmon. Mortality of slower growing fish is generally higher than for faster growing fish (Healey 1982; Holtby et al. 1990). Density-dependent growth reduction was suggested in some populations of chum salmon (Ishida et al. 1993). Somatic growth rate is strongly influenced by environmental conditions (see Brett 1979). Growth estimation may also provide information on the environmental condition of salmonid stocks.

Growth estimation has been performed by sequential sampling, mark-recapture, scale and otolith readings in fisheries studies (Ricker 1976). Especially, scale or otolith readings have been routinely performed during age determination. Age determination and growth estimation have been performed using annual rings or growth checks in scales or otoliths. Back-calculation technique has been used in growth estimation from otoliths or scales. It is necessary in back-calculation to validate the formation periodicity of growth check and to establish the relationship between scale/otolith size and fish size (Campana and Neilson 1985). However, little information is available for formation mechanism of

scale and otolith characteristics.

Scales of teleost fish are calcified tissues formed of calcium phosphate, and are embedded in the connective tissue of the skin (Yamada and Mugiya 1988). The upper surface of the scale is characterized by a series of ridges. Scale formation by the osteoblasts proceeds around the periphery of the scale. The scale ridge grows in the intercellular space formed by two overlapping osteoblasts on the scale surface (Yamada 1971). The overlapping of the osteoblasts is brought about in the course of transformation of marginal round osteoblasts into inner flattened ones. The concentric scale ridges form the surface structure of scale, which are called the circuli. The annulus or growth check on salmonid scale are observed as the band of narrowly spaced circuli and/or the discontinuously formed circulus (Kobayashi 1961). Many investigators have considered that the annulus forms in the winter, when the fish experiences low growth rate in cold water.

Otoliths are crystalline (calcium carbonate) structures within the inner ear of teleost fish. They are acellular and grow in a manner similar to molluscan shell formation rather than by ossification that occurs in the scale and other hard parts of fish. Microstructure of otoliths consist of translucent incremental and opaque discontinuous zones (Campana and Neilson 1985). An incremental and a discontinuous zone is usually formed over 24 hours (Campana and Neilson 1985). The formation

periodicity of growth increment consisting of two zones has been validated by rearing and sequential sacrifice, otolith marking experiments, estimation of hatching dates, and so on (Geffen 1987).

To assess usefulness of scale and otolith patterns for growth estimation, I examined the formation mechanisms of scale and otolith increments by rearing experiments using chum and sockeye salmon.

MATERIALS AND METHODS

Rearing Experiments in Different Environmental Conditions

In the fall of 1993, eggs and sperm were stripped from chum salmon returning to the Chitose River. Eggs fertilized by the dry method were incubated in about 8°C water. From emergence to reaching about 0.5g in body weight, juveniles were reared in tanks and fed dry pellets in 8°C water for one or two weeks. Six hundred juveniles were sacrificed and their body weight were measured to calculate feeding rates. Six sets of 30 juveniles were measured for fork length and observed as to whether scales were formed. Another 6 sets of 200 juveniles were reared for 2 weeks in different sets of environmental conditions: 8, 10°C in water temperature × 70, 85, 100% of the maximum feeding rate for a given water temperature and fish size (Suzuki et al. 1994). At the end of the rearing period, 30 juveniles were measured for fork length, and scales were collected from the body area near the lateral line between dorsal and anal fins.

The number of scale circuli, scale radius to the outermost circulus of the scale, and scale radius of the focus were counted and measured along the longest axis. Average circulus spacing was estimated by the equation:

$$\text{circulus spacing } (\mu\text{m}) = \{ \text{scale radius to the outermost circulus } (\mu\text{m}) - \text{scale radius of the focus } (\mu\text{m}) \} / (\text{number of circuli} - 1).$$

Somatic growth was calculated as the difference between initial mean fork length in each subgroup and individual fork length at the end of rearing period, because initial individual fork length was not available in this analysis. The analysis of variance (ANOVA) was used to detect the effects of water temperature and feeding rate on somatic growth. The analysis of covariance (ANCOVA) was used to detect the effects of two variables on circulus spacing.

Field Mark-Recapture Experiment

Juvenile chum salmon were marked by clipping both ventral fins from March 24 to April 5, 1993. Marked juveniles were collected on March 29 and

April 5 in Shou River Hatchery in Shou River which discharges into Toyama Bay in Japan Sea. Juveniles were released from the hatchery on April 5, 1993. These fish were recaptured in coastal waters off northern Honshu in Japan Sea. After fixation in 10% formalin, I measured fork length and collected scales.

Radii and circulus spacings of scales mounted in glycerin-gelatin were measured along the longest axis. The change in circulus spacing was analyzed by determining the correlation between circulus spacing and circulus number from the center of the scale focus to each circulus. To detect the check, circulus spacings were smoothed by calculating a moving average.

Individual Tagging Experiment

In the fall of 1991, eggs and sperm were stripped from anadromous sockeye salmon returning to the Bibi River and from nonanadromous sockeye in Lake Shikotsu. Eggs fertilized by the dry method were incubated in about 8°C water. After emergence, juveniles were reared in tanks and fed dry pellets. For measurement of individual growth, Passive Integrated Transponder (PIT) tags were injected into the peritoneal cavities of 152 juveniles after measurement of fork length on October 8, 1992. These juveniles were transported to Chitose Hatchery and reared in a circular tank for 214 days under a natural photoperiod.

On May 10, 1993, juveniles were measured (fork length in millimeters), and their scales were collected. Collected scales were mounted on a glass slide in glycerin-gelatin. Scale radius and circulus spacing were measured in micrometers along the longest axis of scale. A check was found by calculating the moving average of circulus spacing (Fukuwaka and Kaeriyama 1994). Scale radius at check formation was equal to the sum of the circulus spacing from the center of the focus to the check. In this paper, I considered the check as a very narrowly spaced and/or discontinuously formed circulus.

For the relationship between fork length and scale characters since scale formation, we observed early growth of scale in 43 juvenile collected at Lake Shikotsu Hatchery on May 17, 26, and June 24, 1994. To use in back-calculation, I measured scale radius and fork length for 5 juveniles (age 0.0) with no circuli evident, collected at Lake Shikotsu Hatchery. To estimate individual fork length at the check formation, I used the biological intercept back-calculation (Belding, 1934; Campana, 1990; Ricker, 1992):

$$(S_E - S_0) / (L_E - L_0) = (S_C - S_0) / (L_C - L_0)$$

where S_E , S_0 , and S_C were scale radii at the end of the experiment, at squamation, and at check formation,

respectively, and L_E , L_0 , and L_C were fork lengths at the end of the experiment, at squamation, and at check formation, respectively.

Otolith Marking Experiment

On October 25, 1993, chum salmon eggs were stripped and fertilized and then incubated in 8°C water. Twenty embryos, alevins, or fry were collected at 0, 10, 20, 30, 60, 90, 120, and 150 days after fertilization. The fish were fixed in 10% buffered formalin for one day and then stained with alizarin red S so that their otoliths could be easily observed. For the otolith growth of successive stages, chum salmon juveniles were also collected off Yamagata, Japan Sea in March 22, April 7 and 21, 1994. These fish were fixed in 10% buffered formalin for 3 or 4 days and then preserved in 70% ethanol. Total or fork lengths taken on the fish were in millimeters. Sagittae were dissected from all specimens under a stereo microscope. The long axis of each sagitta was measured in millimeters. To describe the relative growth of otolith, I used an allometric equation:

$$O = O_0 + a \cdot (L - L_0)^b$$

where O is sagitta length (mm); L is body length (mm); O_0 is sagitta length at hatching; L_0 is body length at hatching; a and b are constants.

To investigate increment periodicity, a mark was

induced on the otoliths of 40 juvenile chum salmon by immersing the fish in 10 ppm alizarin complexone (ALC) for one day on May 17, 1994 (Tsukamoto 1988). Each fish was also marked a second time; ten were marked 7 days after receiving their first exposure to ALC, and other sets of ten fish were marked at 14, 21, and 28 days. Seven days after the fish had been marked for the second time, they were sacrificed and fixed in 70% ethanol. Sagittae from each fish were ground and polished to produce thin sections for microscopic observation. A fluorescent microscope was used to count the number of growth increments between the two ALC marks.

RESULTS

Scale Growth in Chum Salmon Juveniles

Mean fork lengths at the start of rearing period were not significantly different among 6 sets of juveniles (ANOVA, $P > 0.05$; Table 1). Fourteen juveniles did not form the second circulus in their scales at the end of rearing period, so that they were rejected in these analyses. Somatic growth of chum salmon juveniles was affected by rearing water temperature but not by feeding level (Table 2). Circulus spacing was positively correlated with

Table 1. Mean fork lengths at the start and end of the experiment and scale measurements of juvenile chum salmon reared in different 6 conditions of water temperature and feeding level. Numbers in parentheses indicate standard deviations.

Water temp. (°C)	Feeding level (%)	Fork length at the start (mm)	F. L. at the end (mm)	Scale radius (μm)	Number of circuli	Circulus spacing (μm)	<i>n</i>
8	70	43.0 (1.91)	48.2 (2.30)	170 (20.7)	2.28 (0.458)	40.6 (9.06)	25
8	85	42.9 (1.98)	48.3 (2.25)	164 (23.8)	2.29 (0.460)	41.6 (8.62)	28
8	100	41.7 (2.61)	47.4 (2.71)	159 (19.0)	2.08 (0.277)	36.3 (5.50)	25
10	70	42.9 (1.85)	49.6 (2.37)	183 (20.5)	2.80 (0.484)	41.3 (5.64)	30
10	85	41.8 (2.50)	48.5 (2.78)	180 (26.9)	2.60 (0.563)	40.4 (8.69)	30
10	100	41.7 (3.08)	49.5 (2.83)	187 (22.6)	2.57 (0.504)	38.5 (6.94)	28

Table 2. ANOVA table of somatic growth on water temperature and feeding level in the rearing experiment of juvenile chum salmon.

Source of variation	<i>df</i>	<i>SS</i>	<i>F</i> -ratio	<i>P</i>
Water temperature	1	158	24.3	<0.001
Feeding level	2	1.80	0.138	0.871
Water temperature by feeding level	2	28.1	2.15	0.120
Error	3	1044		

somatic growth ($r = 0.244$, $P < 0.01$; Fig. 1). Circulus spacing was affected by feeding level from ANCOVA with somatic growth as the covariate (Table 3).

Fig. 1 Relationship between somatic growth and circulus spacing of juvenile chum salmon. The line indicates the regression equation: circulus spacing (μm) = $0.683 \cdot \text{somatic growth (mm)} + 35.6$ ($r = 0.244$, $n = 166$, $P < 0.01$).

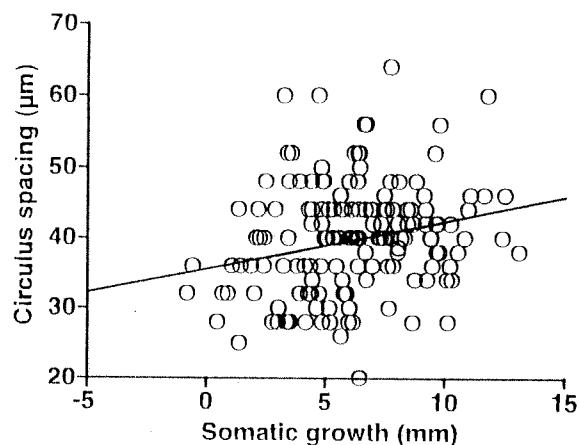


Fig. 2 Circulus spacings of juvenile chum salmon reared in the Shou River Hatchery (from Fukuwaka and Kaeriyama 1994). Vertical bars indicate 95% confidence limits.

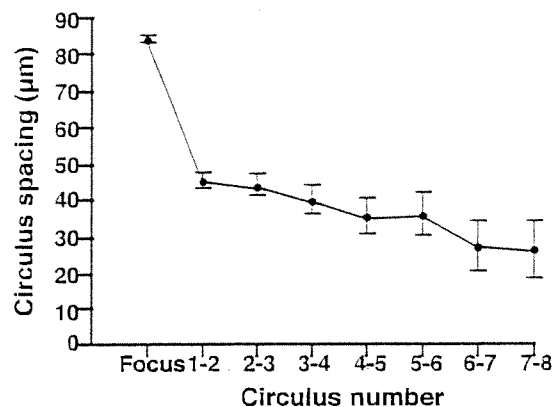
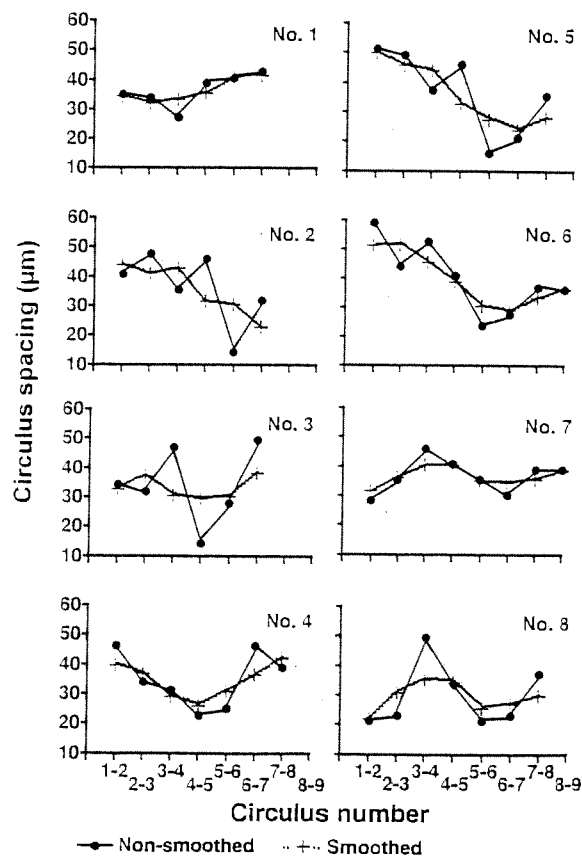


Fig. 3 Changes in circulus spacings of 8 juvenile chum salmon recaptured in coastal waters (from Fukuwaka and Kaeriyama 1994). Solid and broken lines indicate non-smoothed and smoothed (by moving average) circulus spacings, respectively.



Check Formation in Chum Salmon Juvenile

Circulus number of chum salmon juvenile ranged from 3 to 8 at the date of release from Shou River Hatchery. Circulus spacings of juveniles decreased simply as circulus number increased during the rearing period in the hatchery (Fig. 2). Eight fishes were recaptured in coastal waters after more than 14 days after release. A check was observed in each of their scales (Fig. 3).

Table 3. ANCOVA table of circulus spacing on water temperature and feeding level with somatic growth as the covariate.

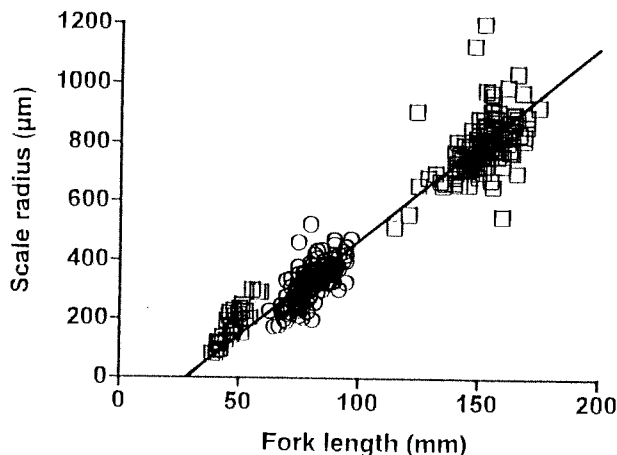
Source of variation	df	SS	F-ratio	P
Somatic growth	1	600	11.2	0.001
Water temperature	1	31.9	0.595	0.442
Feeding level	2	501	4.67	0.011
Water temperature by feeding level	2	32.0	0.299	0.742
Error	159	8523		

The number of circuli from the focus to the check (3 - 7) was consistent with the number of circuli at release (3 - 8). The scales of these fish showed the following pattern: circulus spacing decreased continuously during the rearing period in the hatchery, the check was formed immediately after release, and circulus spacing increased in the early ocean life period (Fig. 3).

Check Formation in Sockeye Salmon Juvenile

A common relationship between fork length and scale radius at check formation (the mid-sized group in Fig. 4) and the relationship between fork length and scale radius (the small and large fishes in Fig. 4) is evident. Back-calculated fork length at check

Fig. 4 Relationships between fork length and scale radius ($\square$), and between fork length at tagging and scale radius at check formation ($\circ$) in PIT-tagged juvenile sockeye salmon. The line indicates the common regression equation: scale radius (μm) = $6.51 \cdot$ fork length (mm) - 192 ($r = 0.968$, $n = 347$, $P < 0.001$).



formation was consistent with fork length at tagging (Fig. 5). The regression equation was fork length at check formation (mm) = $1.04 \cdot$ fork length at tagging (mm) - 5.89 ($r = 0.759$, $n = 152$, $P < 0.001$).

Otolith Growth in Chum Salmon Juvenile

Sagittae were first observed in developing chum salmon 60 days after fertilization (at hatching). At this time the mean total body length was 19.5 mm (0.75 SD) and the sagitta had a mean longitudinal length of 0.312 mm (0.0256 SD). The allometric equation:

$$\text{sagitta length (mm)} = 0.312 + 0.0359 \times \{\text{body length (mm)} - 19.5\}^{0.790}$$

was fitted the relationship between body length and sagitta length (Fig. 6).

Fig. 5 Relationship between fork length at tagging and back-calculated fork length at check formation. The line indicates the regression equation: back-calculated fork length at check formation (mm) = $1.04 \cdot$ fork length at tagging (mm) - 5.89 ($r = 0.758$, $n = 152$, $P < 0.001$). Upper and lower curves indicate 95% confidence limits of the regression line.

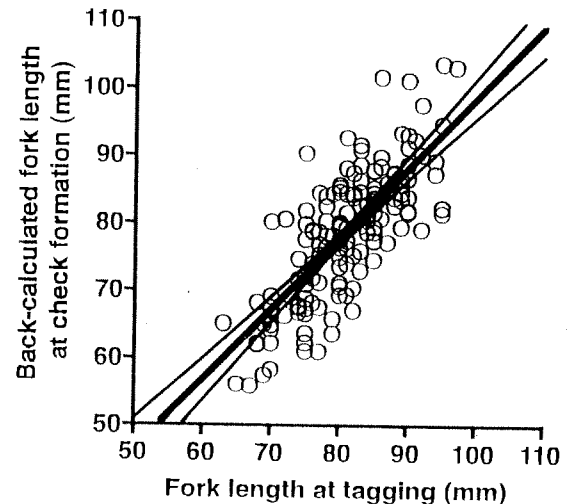
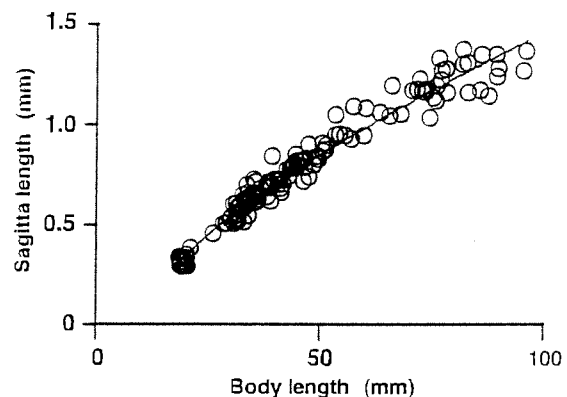


Fig. 6 Relationship between body length and sagitta length of juvenile chum salmon during early life (from Fukuwaka 1996). Curve indicates the allometric equation: sagitta length (mm) = $0.312 + 0.0359 \cdot \{\text{body length (mm)} - 19.5\}^{0.790}$.

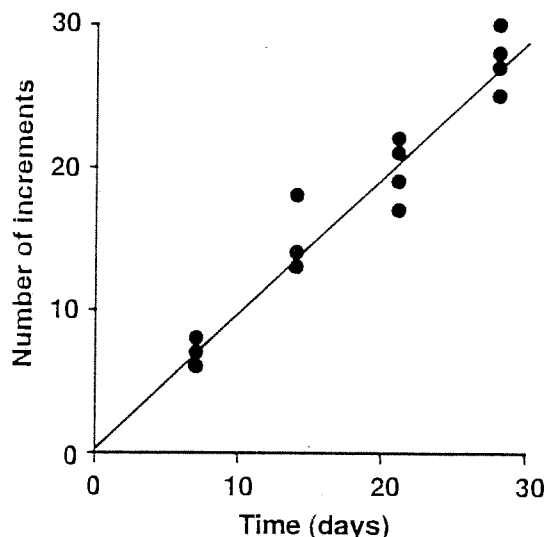


A regression analysis on increment number and time in days between ALC marking episodes produced the following equation (Fig. 7):

$$\text{number of increments} = 0.962 \cdot \text{time (days)} + 0.0556.$$

The correlation coefficient (r) for this equation equaled 0.932 and n was 40. A t -test ($0.2 < P < 0.5$) disclosed that the regression coefficient was not different from unity, and thus growth increments were produced in the sagittae on a daily basis.

Fig. 7 Relationship between time in days and number of formed increments between two fluorescent markings in juvenile chum salmon otolith (from Fukuwaka 1996). The line indicates the regression equation: number of increments = $0.962 \cdot \text{time (days)} + 0.0556$ ($r = 0.932$, $n = 40$, $P < 0.001$).



DISCUSSION

Somatic Growth and Scale Circulus Spacing

The relationship between somatic growth and circulus spacing is positive but weak in Pacific salmon (Fig. 1; Fisher and Pearcy 1990; Fukuwaka and Kaeriyama 1997). A linear relationship between circulus spacing and somatic growth rate was useful in estimating individual growth rate in an experimental population of tilapia (Doyle et al. 1987), but in coho salmon it was useful only for comparing somatic growth rate between groups of juveniles (Fisher and Pearcy 1990). Healey (1982) suggested the size-selective mortality of chum salmon juvenile from the scale analysis. Fukuwaka and Kaeriyama (1997) indicated that circulus spacing was useful for comparing mean growths among groups of juvenile sockeye salmon, but less useful to estimate individual growth. Circulus spacing was also influenced by environmental conditions (Table 3). Circulus spacing may be used as an indicator of mean growths in the same condition of environmental factors, but cannot be used in the calculation of individual growth.

Scale Annulus Formation

The annulus is observed in salmonid scales as a

band of closely spaced circuli and/or discontinuously formed circuli (Kobayashi 1961). The narrowly spaced and discontinuously formed circuli is considered as the check in this paper. A check was formed at release in chum salmon juveniles (Fig. 3) and at tagging in sockeye salmon juveniles (Fig. 4 and 5). The check of tagged sockeye salmon juvenile is likely formed as a result of the stress of tagging and transporting procedures and the change in growth rate in the different rearing conditions. The check of recaptured chum salmon juvenile is likely formed as a result of large changes in growth rate induced by the drastic change of their environment. Marked juveniles migrating into the sea immediately after release encounter changes in the environment from the hatchery to the sea. The check on the scales of marked juveniles would be formed immediately after their release. The check formation was not affected by additional handling at fin-clipping because release checks were also observed on the scales of non-marked juveniles caught in the coastal waters.

A check is likely formed at the time of large and discontinuous changes of somatic growth rate and environmental factors. Bilton (1975) suggested from rearing experiments for sockeye salmon that the check formed as a result of increased growth. He stated that the checks were formed as a result of changes in physical and non-physical factors affecting circulus formation, such as water temperature, food, and light. Suzuki and Kaeriyama (1990) also indicated that a check formed at the time when the feeding level increased.

Circuli spacing was positively correlated with somatic growth, and the band of closely spaced and continuously formed circulus appears to be formed during the period of slow growth (Fig. 1; Bilton 1975; Fukuwaka and Kaeriyama 1997). Scale growth would be stopped when fish growth is stopped. Suzuki and Kaeriyama (1990) observed that scale growth was stopped during the starvation period in their rearing experiment of sockeye salmon.

Thus an annulus defined as the band of closely spaced circuli and/or discontinuously formed circulus should be formed during the period of slow growth occurring before or after the period of stopped growth in winter, and would be completed in the short duration at the start of growing period from spring to fall. Bilton and Ludwig (1965) concluded from the observation of scales from fishes collected in winter that the annulus was formed in January in sockeye, in late December in pink, and in February or March in chum salmon. However, Vedensky (1954) stated that in pink salmon a band of narrowly spaced circuli was formed in early spring when the fish had low assimilation rates and low feeding rates after and before the no-growth period in winter. He also suggested that the annulus would be formed in early

spring after the period of stopped growth in winter.

Back-calculation using the scale annuli would be an evaluation of fish sizes in winter and early spring. Ricker (1976) pointed out that a weakness of back-calculation method for Pacific salmon was that the information on the timing of annulus formation was scanty and contradictory between different authors. A comparison of field observations between the timing of annulus formation and the seasonal growth pattern would be necessary for the assessment of somatic growth of Pacific salmon in the ocean by means of back-calculation to be fully satisfactory.

Somatic Growth and Otolith Growth

Daily growth increment of otolith has been used to estimate fish growth by back-calculation (for example, Wilson and Larkin 1982). The formation periodicity of growth increment was validated in the otolith of chum salmon juvenile. Volk et al. (1984) also observed the production of daily increments in chum salmon juveniles when they were held in sea water tanks. However, non-daily increment production was observed in juvenile pink salmon that had been freely migrating and feeding in an Alaskan estuary (Volk et al. 1995). Consequently, when studies are undertaken to evaluate early marine growth of chum salmon or other juvenile salmonids it will be necessary to conduct field evaluations of increment production by using otolith marking and recapture experiments.

The relationship between otolith length and fish length was found to be allometric during the alevin and juvenile stages in chum salmon. Hence it is not possible to simply use a proportional back-calculation method to predict fish size based on otolith size. Fitzhugh and Rice (1995) described the relationship between otolith size and fish size by an allometric equation. Other non-linear relationships between otolith length and fish length are often observed during early life in many fishes. For example, otolith - fish size relationship have been described by using a polynomial equation (Mugiya and Tanaka 1992). Moreover, this relationship appears to change with ontogenetic stages in early life (Hare and Cowen 1995). In their review, for instance, Campana and Neilson (1985) state that a curvilinear relationship is characteristic during larval phases and this usually changes into a linear one during later juvenile stages.

Allometric back-calculation may be used to estimate somatic growth rate of chum salmon juvenile. However, it is necessary in back-calculation to validate the formation periodicity of growth increment and to establish the relationship between otolith size and fish size (Campana and Neilson 1985). I validated the daily growth increment and established the relationship between otolith size and fish size of juvenile chum salmon. Volk et al. (1984) used another

method to estimate somatic growth of chum salmon. They found that the width of daily growth increment was positively correlated with the instantaneous growth rate in body weight (Volk et al. 1984).

CONCLUSIONS

Scale patterns formed by circuli, growth checks, and annuli are related to somatic growth of chum and sockeye salmon. Circulus spacing was positively correlated with somatic growth, and might be useful as an indicator of somatic growth. A check was formed after the time of large change in somatic growth. Therefore, an annulus would be formed in a short duration of slow growth after the period of stopped growth. Scale radius at annulus formation would indicate fish size at winter or early spring when the fish began to grow in the ocean. Otolith pattern formed by growth increment also shows somatic growth of juvenile chum salmon. Somatic growth of juvenile chum salmon would be estimated by the back-calculation technique or the regression analysis using the width of otolith daily growth increment.

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Stock Identification of Chinook Salmon (*Oncorhynchus tshawytscha*) in the North Pacific Ocean and Bering Sea by Parasite Tags

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The continental origins of chinook salmon (*Oncorhynchus tshawytscha*) in the North Pacific Ocean and Bering Sea were estimated by using two freshwater parasites (*Myxobolus arcticus* and *M. kisutchi*) as biological tags. The parasite survey of adult chinook salmon from major spawning rivers in North America and Kamchatka indicated that *M. arcticus* was commonly found in Asian chinook stocks (prevalence=57-94%), while rarely among most North American stocks except for those from Vancouver Island, B. C. The unweighted overall sample prevalence of *M. arcticus* was 67.7% and 2.3% in Asian and North American stocks, respectively. *Myxobolus kisutchi* was found only in chinook salmon from the Columbia River (prevalence=8-11% and 43-65% in fall and spring adult stocks, respectively) and its vicinities. The prevalence of *M. arcticus* in high-seas samples of chinook salmon showed a distinct longitudinal cline in the North Pacific Ocean: the overall prevalence was 92% west of 160°E, 81% between 160°E and 170°E, 58% between 170°E and 180°, and 38% between 150°W and 160°W, whereas it was only 0-3% in the central Bering Sea. These results suggest that Asian chinook salmon are widely distributed in the North Pacific Ocean, occurring possibly as far east as 150°W, and are probably predominant in the waters west of 180°. The extreme low prevalence of *M. arcticus* in central Bering Sea chinook salmon suggests that up to 98% of chinook salmon caught in this area are of North American origin. One chinook salmon infected with *M. kisutchi* was found in the Gulf of Alaska, suggesting the presence of Columbia River chinook salmon in this area.



INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) are widely distributed along the Pacific coast of North America and Asia, although they are the least abundant of five major species of high-seas Pacific salmon. In North America, chinook salmon spawn in rivers from California to western Alaska. Asian spawning grounds range from the Anadyr River to the

Amur River in Russia, but most Asian chinook salmon spawn in rivers of the Kamchatka Peninsula (Major et al. 1978). Chinook salmon spawn in many streams, but their spawning is concentrated in larger river systems. Chinook salmon have two life history patterns designated "stream type" and "ocean type"

† This paper was completed after the sudden passing of our dear friend Leo Margolis. We shall miss his warm personality and his outstanding scientific contributions.

(Healey 1983). Stream type (spring) chinook salmon are typical in Asian and northern North American populations and spend one or more years in fresh water before migrating to the sea. Ocean-type (fall) chinook salmon are typical of populations on the North American coast south of 56°N, and migrate to the sea after a few days to a few months of freshwater residence.

Chinook salmon occur broadly in the North Pacific Ocean, Bering Sea and the adjacent waters, but oceanic distribution patterns of individual stocks are not well known yet. Four methods may be applied for the stock identification of high-seas chinook salmon: tagging, scale pattern analysis, genetic analysis, and use of parasites as biological tags. However, low abundance of chinook salmon makes it difficult to determine the status of individual stocks by tagging (Harris 1988). While about 3,000 chinook salmon were tagged and released on the high seas over the last three decades, only 14 have been recovered in coastal areas (Myers et al. 1993). Several scale pattern studies were conducted to determine the origin of high-seas chinook salmon (Ito et al. 1985, 1986; Myers et al. 1987, 1993), but were not conclusive due to discrepancies in the results (see Healey 1991). Recently developed genetic techniques may be useful to determine stock origins of high-seas chinook salmon, but the coast-wide genetic baseline covering the Pacific rims, especially Asian area, has not been completed.

It has been well recognized that naturally occurring parasites may be used for stock

identification of anadromous salmon (Margolis 1963, 1965, 1982, 1984, 1985; Konovalov 1975; Urawa 1989; Moles et al. 1990; Awakura et al. 1995). In this study, we tried to estimate the marine distribution of Asian and North American chinook salmon on the high seas of the North Pacific Ocean and Bering Sea by using parasites as biological tags.

SELECTION OF PARASITES

The following five conditions must be met to evaluate the usefulness of a parasite as biological tag for stock identification of anadromous salmonids (modified from Margolis 1984):

1. The parasite must be present in one stock or group of stocks and absent or rare in others.
2. The parasite infection should occur within a limited area and time before the stocks become mixed in the ocean. Thus, parasites of freshwater origin are particularly good tags for anadromous salmonids.
3. The parasite must have a long life span, preferably as long as that of its fish host, or at least as long as that period of the host's life over which observations on the stock are being made.
4. The parasite should have no marked effect on survival and behaviour of the fish if the parasite is to be used to estimate proportions of stock in a mixed stock sample.
5. The parasite should be easily detected and identified.

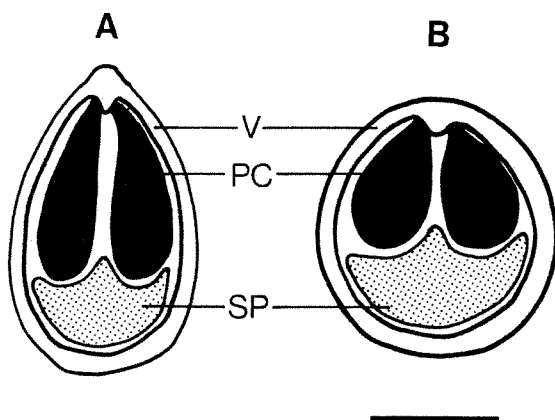
Table 1. Parasites recovered from chinook salmon caught on the high seas of the North Pacific Ocean and Bering Sea.

Parasite species	Site of infection	Origin*
Protozoa (Myxozoa: Myxosporaea)		
<i>Myxobolus arcticus</i>	brain and spinal cord	FW
<i>M. kisutchi</i>	brain and spinal cord	FW
Trematoda (Digenea) - adults		
<i>Hemiurus levinseni</i>	stomach and intestine	M
Cestoda - adults		
<i>Eubothrium crassum</i>	pyloric caeca and intestine	M
Cestoda - metacestode stage		
<i>Diphylobothrium</i> sp. plerocercoid	liver	FW
<i>Nybelinia surmenicola</i> plerocercoid	body cavity	M
<i>Phyllobothrium caudatum</i> plerocercoid	intestine	M
Nematoda		
<i>Anisakis simplex</i> larvae	somatic musculature	M
? <i>Contracaecum osculatum</i> larvae	intestine	M
Acanthocephala		
<i>Bolbosoma caenoforme</i> juvenile	intestine	M
Copepoda		
<i>Lepeophtheirus salmonis</i> adult	external body surface	M

* FW, acquired in fresh water; M, acquired in the marine environment.

Preliminary samples of chinook salmon caught in the central Bering Sea (55°N, 175-177°W, n=20) and western North Pacific Ocean (41-46°N, 166-177°E, n=13) were examined for parasites (Nagasawa and Urawa 1987). Ten species of parasites were recovered from these chinook salmon (Table 1): 1 Protozoa (Myxozoa: Myxosporea); 1 Trematoda (Digenea); 4 Cestoda; 2 Nematoda; 1 Acanthocephala; and 1 Copepoda. In addition, another myxosporean *Myxobolus kisutchi* was found in a chinook salmon captured in the Gulf of Alaska (Urawa and Nagasawa 1995, as *M. neurobius*).

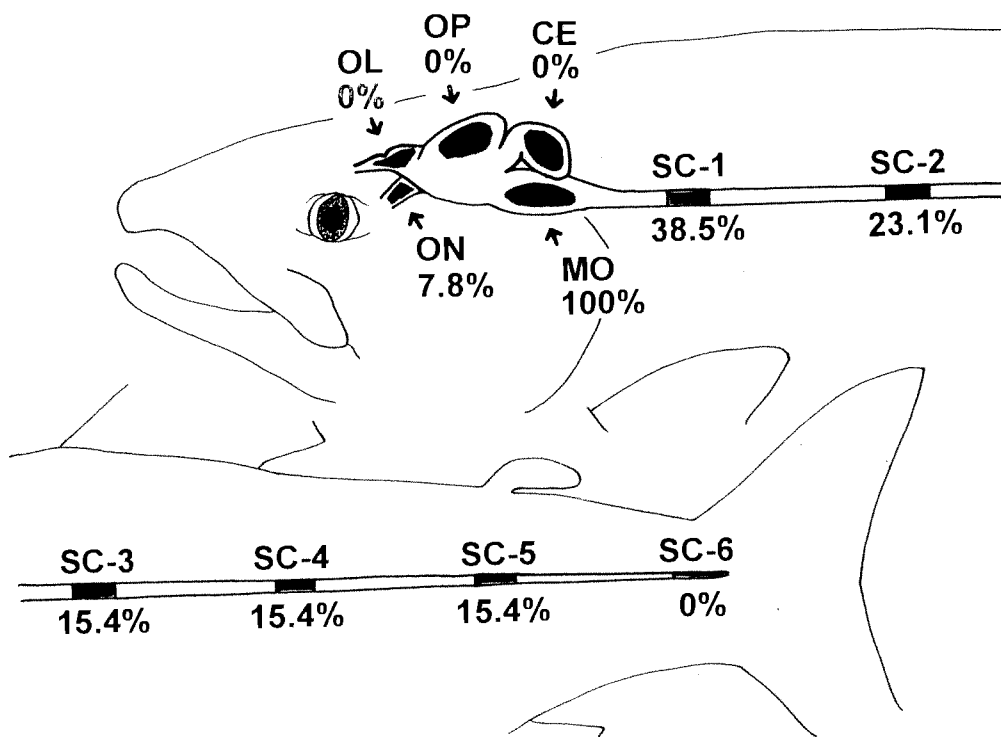
Fig. 1 Spores of *Myxobolus arcticus* (A) and *M. kisutchi* (B) from the brain of chinook salmon. V, valve; PC, polar capsule; SP, sporoplasm. Scale bar indicates 5 μ m.



Of these, most species (8/11) were acquired at sea, but only three species, *M. arcticus*, *M. kisutchi*, and *Diphyllobothrium* sp. in fresh water. The myxosporean parasites *M. arcticus* and *M. kisutchi* were found in the central nerve tissues, and plerocercoids of the cestode *Diphyllobothrium* sp. in the liver. *Diphyllobothrium* sp. was present across the geographical area, but prevalence of *M. arcticus* and *M. kisutchi* in chinook salmon showed regional differences.

Myxobolus arcticus and *M. kisutchi* are easily differentiated by the spore shapes (Fig. 1). The spore of *M. arcticus* is pyriform in front view (Urawa and Nagasawa 1995), while that of *M. kisutchi* is oval or round (Urawa et al. 1997). The alternate hosts of *M. arcticus* are freshwater oligochaetes (Kent et al. 1993; Urawa and Awakura 1994). The parasites infect juvenile salmon in fresh water before they migrate to the sea, and the myxosporean spores remain in the central nerve tissues throughout the freshwater and marine life of anadromous hosts (Urawa and Awakura 1994). The life cycle of *M. kisutchi* is unknown, but may be similar with that of *M. arcticus*. The parasite spores are easily detected in the medulla oblongata (Fig. 2). There is no record that the parasites cause the host mortality. Thus, two species of freshwater myxosporeans, *M. arcticus* and *M. kisutchi* were candidate for biological tags to identify the origin of high-seas chinook salmon.

Fig. 2 Spatial distribution of *Myxobolus arcticus* spores in the nerve tissues of chinook salmon (n=13). Numerals indicate prevalence (%) of the parasite in each nerve tissue. CE, cerebellum; MO, medulla oblongata; OL, olfactory lobe; ON, optic nerves; OP, optic lobe; SC, spinal cord.



BASELINE OF PARASITES

In order to evaluate usefulness of *Myxobolus* as a tag, 5,691 chinook adults returning to major spawning rivers in Kamchatka and North America were examined for parasites (Urawa and Nagasawa 1989, 1991; Urawa et al. 1990). In Asia, more than 75% of Asian chinook salmon spawn in two rivers: the Kamchatka River on the east coast of the Kamchatka Peninsula, and the Bolshaya River on the west coast. Prevalence of *M. arcticus* in adult chinooks was 57% in the Kamchatka River, and 94% in the Bolshaya River. In North America, we examined adult chinooks from 39 spawning rivers and 4 regions from the Sacramento River in California to the Yukon River in western Alaska, which accounted for more than 70% of North American chinook populations (according to spawning estimates by Wahle and Pearson 1987). However, *M. arcticus* rarely occurred among North American stocks except for Vancouver Island, B. C., where it was found in 7 of 9 stocks sampled, with prevalence of 2-56%. The overall prevalence of parasite was 19.5% in Vancouver Island chinook stocks, but only 4.7% in the entire chinook stocks in British Columbia when prevalence was weighted in proportion of number of spawners in each river. The Asian origin chinook salmon are stream-type, whereas the Vancouver Island chinook salmon stocks are almost entirely ocean-type (Healey 1991). Thus, *M. arcticus* infected chinook salmon from Asia can be distinguished from those from Vancouver Island on the basis of freshwater age.

Myxobolus kisutchi has been found only in the Columbia River and its vicinities (the Minter Creek

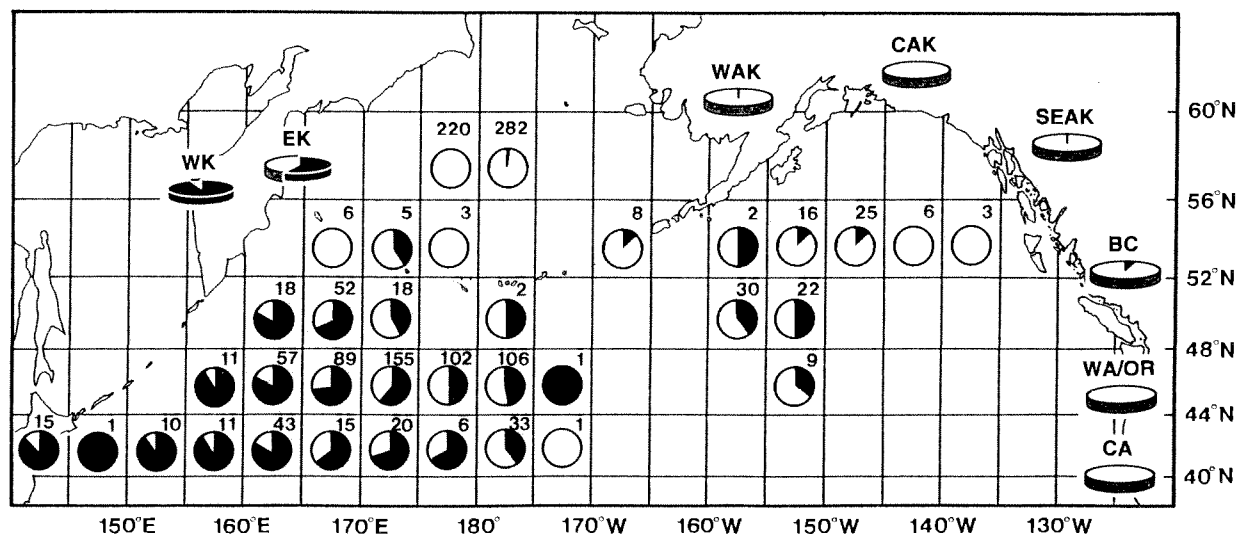
and Shehalus River in Washington)(Yasutake and Wood 1957; Urawa and Nagasawa 1991; Urawa et al. 1997). In the Columbia River, the prevalence was 43-65% in spring chinook salmon, but only 8-11% in fall chinooks (Urawa and Nagasawa 1991). This might be attributable to differences in a period of freshwater residence between spring and fall chinook smolts.

We concluded that *M. arcticus* is useful as an indicator of Asian origin chinook salmon, and *M. kisutchi* is a good indicator of chinook salmon originating from the Columbia River and its vicinities. The baseline prevalence of *M. arcticus* (Fig. 3) was 94% in western Kamchatka, 57% in eastern Kamchatka, and almost 0% in North American stocks except for British Columbia, where it was 4.7%.

OCCURRENCE OF PARASITES IN MARINE CHINOOK SALMON

We examined 1,403 chinook salmon captured in the North Pacific Ocean and central Bering Sea in the summers of 1988, 1989, and 1990 (Urawa and Nagasawa 1991). Ocean-type chinook salmon (freshwater age 0) were not found among these samples. The prevalence of *M. arcticus* was extremely low (less than 2%) in chinook salmon captured in the central Bering Sea, while in the North Pacific Ocean caught in the waters east of 145°W (Fig. 3). The parasite prevalence showed a longitudinal cline in three years, averaging 92% west of 160°E, 81% between 160°E and 170°E, 58% between 170°E and 180°, 38% between 150°W and 160°W, but less than 10% in waters east of 150°W. Another parasite survey for chinook salmon captured in offshore waters

Fig. 3 Prevalence (indicated by black shading in pie chart) of *Myxobolus arcticus* in chinook salmon in the North Pacific Ocean and Bering Sea by 4° x 5° area in the summers of 1988-1990. Numerals within area indicate the number of fish examined. Three-dimensional pie charts indicate the baseline prevalences of the parasite in western Kamchatka (WK), eastern Kamchatka (EK), western Alaska (WAK), central Alaska (CAK), southeastern Alaska (SEAK), British Columbia (BC), Washington and Oregon (WA/OR), and California (CA) chinook stocks.



10% in waters east of 150°W. Another parasite survey for chinook salmon captured in offshore waters along the Alaska Peninsula and Aleutian Islands in August 1996 indicated that prevalence of *M. arcticus* was 9.6% in eastern waters (55-56°N, 156°W, n=52) and 15.4% in central waters (51-52°N, 176°W, n=13).

As for *M. kisutchi*, only one chinook salmon infected with this parasite was found in the Gulf of Alaska in 1987, suggesting the presence of Columbia River chinook salmon in this area (Urawa and Nagasawa 1995).

MARINE DISTRIBUTION OF CHINOOK SALMON

The occurrence of *M. arcticus* suggests that Asian chinook salmon are widely distributed in the North Pacific Ocean west of 150°W, which is beyond the eastern limit of 175°W previously estimated by a tag recovery. Our results suggest that Asian chinook salmon are the predominant stocks in the western waters of the North Pacific Ocean but are rarely found in the Bering Sea. In contrast, North American chinook salmon appear to be the predominant stocks in the Bering Sea but may be largely absent in the western North Pacific Ocean. Tagging and scale pattern studies suggested that western Alaska chinook salmon are predominant in the Bering Sea (Myers et al. 1987, 1993). The other North American chinook stocks may be distributed mainly in the North American coastal waters (Healey 1983). It is an amazing result that Asian chinook salmon are widely distributed in the North Pacific Ocean, despite their relatively low abundance comparing with North American stocks. Further studies are requested to clarify factors determining the ocean distribution of chinook salmon.

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Are Naturally-Occurring Parasite "Tags" Stable? An Appraisal from Four Case Histories Involving Pacific Salmonids

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This paper summarizes the biological characteristics of naturally acquired parasites that serve as "tags" for anadromous salmonid stocks, and reviews the advantages of parasite "tags" over traditional methods of tagging or marking. Four case histories of Canadian studies on the use of freshwater parasites in Pacific salmonid stock identification are examined with respect to the annual stability of the parasite "tags." Two of these studies involve the use of parasites to determine the ocean distribution of stock groups of sockeye salmon (*Oncorhynchus nerka*) and steelhead trout (*O. mykiss*), one relates to seaward migration routes of mainly Fraser River (British Columbia) juvenile sockeye salmon, and the fourth concerns quantitative estimates of the stock composition in a mixed stock sockeye salmon fishery on the west coast of Vancouver Island, British Columbia. The conclusions reached are: (1) Where stock identification is based on the unique presence of certain heteroxenous helminth parasites, the use of such parasite "tags" usually provides a stable basis for qualitative stock identification. In these instances the presence of the parasite "tag" in a salmonid stock is dependent on the co-existence of the salmonid and one of the other essential hosts in the life cycle of the parasite; (2) where parasites are used for quantitative estimates of stock composition, baseline data may have to be re-established annually to take into account annual variations in parasite prevalence (% of stock with the parasite) and intensity (numbers of parasites in each host) among the stocks to be distinguished; and (3) some quantitative parasite differences among salmonid stocks may appear to be stable for periods up to 10 or more years, but may show marked changes over the longer term.



INTRODUCTION

The potential for using naturally-occurring parasites as "tags" or markers in Pacific salmonid stock identification was initially explored some forty years ago within the research program conducted under the auspices of the International North Pacific Fisheries Commission. The research by Canadian scientists culminated in the successful application of this technique for describing the ocean distribution of western Alaskan and Kamchatkan sockeye salmon (*Oncorhynchus nerka*) stocks (Margolis 1963). In subsequent years scientists of all four member parties of the North Pacific Anadromous Fish Commission (NPAFC) engaged in salmonid stock identification studies using parasite "tags" either alone or in combination with other stock-distinguishing characteristics. Both local and intercontinental stock differentiation problems were successfully investigated

(Konovalov 1971; Awakura et al. 1982, 1995; Bugaev 1982, 1986; Butorina and Shedko 1985; Awakura 1989; Dalton 1989a, 1989b, 1991; Urawa 1989; Moles et al. 1990; Myers et al. 1991; Urawa and Nagasawa 1991, 1995; and Canadian references listed below).

Canadian research, the focus of this paper, concentrated on four studies involving sockeye salmon and steelhead trout (*Oncorhynchus mykiss*) (Margolis 1963, 1982, 1984, 1985, 1990; Quinn et al. 1987; Bailey et al. 1988, 1989; Groot et al. 1989; Beacham et al. 1997).

In the NPAFC Science Plan for 1995-96 (Anonymous, 1996), one of the questions raised concerning stock identification was: "Are baseline data (genetic, parasite, etc.) stable?"

The purpose of the present paper is to examine available data pertaining to this question with respect to the four Canadian studies.

Before examining these four case histories and the stability of the parasite tags used therein, as background it seems appropriate to list the important

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conditions that must be met to ensure the usefulness of a parasite as a tag for fish population studies, and to review the advantages of parasite tags over conventional tagging and marking methods that generally have been used in such studies.

There are at least three general conditions that must be met to ensure the usefulness of a parasite as a population tag. These are:

1. The parasite must be present in one stock or group of stocks, and absent or rare in others from which it is to be distinguished, or it must occur in markedly different numbers in the stocks to be distinguished;
2. It is essential that the parasite have a long life span, preferably as long as that of its host, or at least as long as that period of the host's life over which observations on the stock are being made; and
3. The parasite should have a negligible effect on survival and behaviour of the host.

For anadromous salmonids, the important criteria may be listed as follows:

1. The parasite should have a freshwater life cycle, with no transmission or inter-host transfer at sea;
2. A restricted freshwater distribution within the range of the salmonid host; and
3. A long life span, including survival during all or part of the marine life of the salmonid host.

Advantages of parasite tags are:

1. A much larger proportion (sometimes all) of the stock may be marked naturally by a particular parasite than is usually possible when applying artificial tags or marks, at least for wild fish populations;
2. The fish do not have to be handled to apply the tag or mark, thus eliminating so-called "tagging" or "marking" mortality and possible influences on migratory or other behaviour; and
3. The fish need only be caught once to derive information about its origins, migrations, or stock affinities, whereas in conventional tagging and marking the fish must be caught to be tagged or marked, returned to the water, and recaptured a second time.

Although these advantages of parasite tags are evident, it is clear that parasites are not a panacea for solving all stock identification problems, but when appropriate differences exist, this technique can be a powerful tool in stock identification.

Comparison of the parasite-tag method of stock identification with that of the newer genetic techniques is discussed in Beacham et al. (1998) in this volume.

CASE HISTORIES

Case History 1

The first case history to be discussed is that in which two freshwater parasites were used to define the ocean distribution of North American and Asian sockeye salmon (Margolis 1963). In this study, the occurrence of the plerocercoid (or juvenile) stage of the tapeworm *Triaenophorus crassus* in the somatic musculature and the presence of the nematode *Truttaedacnitis truttae* in the intestine were used to identify the ocean distribution of western Alaskan (essentially Bristol Bay) and Kamchatkan sockeye salmon, respectively (Fig. 1). Both parasites are acquired in fresh water and apparently survive throughout the marine life of sockeye salmon.

The obligatory definitive host of *T. crassus* is the northern pike, *Esox lucius*. Sockeye salmon become infected with the juvenile tapeworm only in lakes where pike and sockeye salmon are sympatric, such as occurs in western Alaska. Therefore, as a tag identifying the western Alaskan origin of sockeye salmon, *T. crassus* would be stable unless pike carrying the adult tapeworm were to be introduced into other watersheds where sockeye salmon occur.

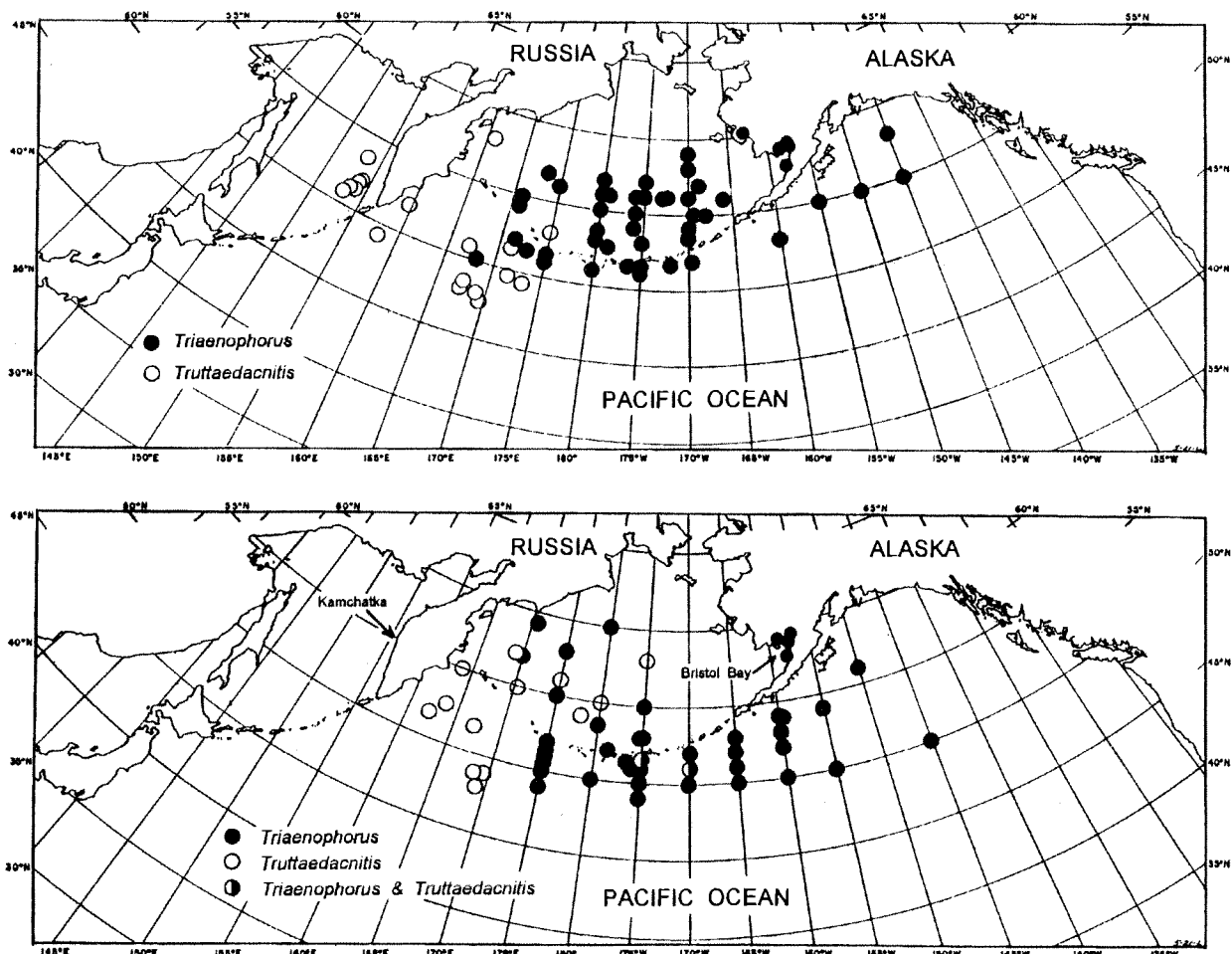
It has been proposed that the prevalence of *T. crassus* can be used to estimate proportions of Bristol Bay sockeye salmon in offshore samples (Margolis 1963). However, the prevalence of the plerocercoids in Bristol Bay sockeye salmon is highly variable annually (Table 1), requiring that the baseline data be re-established annually. In this sense, for quantitative estimates of stock composition, *T. crassus* is clearly unstable.

Table 1. Estimated prevalence of *Triaenophorus crassus* plerocercoids in Bristol Bay adult sockeye salmon (*Oncorhynchus nerka*), 1957-1959 (from Margolis, 1963).

Year	Prevalence (%)
1957	3.2
1958	22.0
1959	10.6-13.3

The life history of *T. truttae* remains unclear but it is apparently a stream rather than lacustrine parasite and hence would only occur in sockeye salmon stocks that rear in streams. Insufficient knowledge about the biology of *T. truttae* in Kamchatka precludes commenting definitively on the stability of this nematode as a tag. All that can be said is that it has not been reported from North American sockeye salmon, suggesting that it is a stable qualitative tag for Kamchatkan sockeye salmon.

Fig. 1. Ocean distribution of western Alaskan and Kamchatkan sockeye salmon (*Oncorhynchus nerka*) as determined by the occurrence of *Trienophorus crassus* and *Truttaedacnitis truttae*, respectively, in samples from the North Pacific Ocean and adjacent seas, 1955-1959. Upper chart, maturing fish; lower chart, immature fish. (Adapted from Margolis, 1963.)



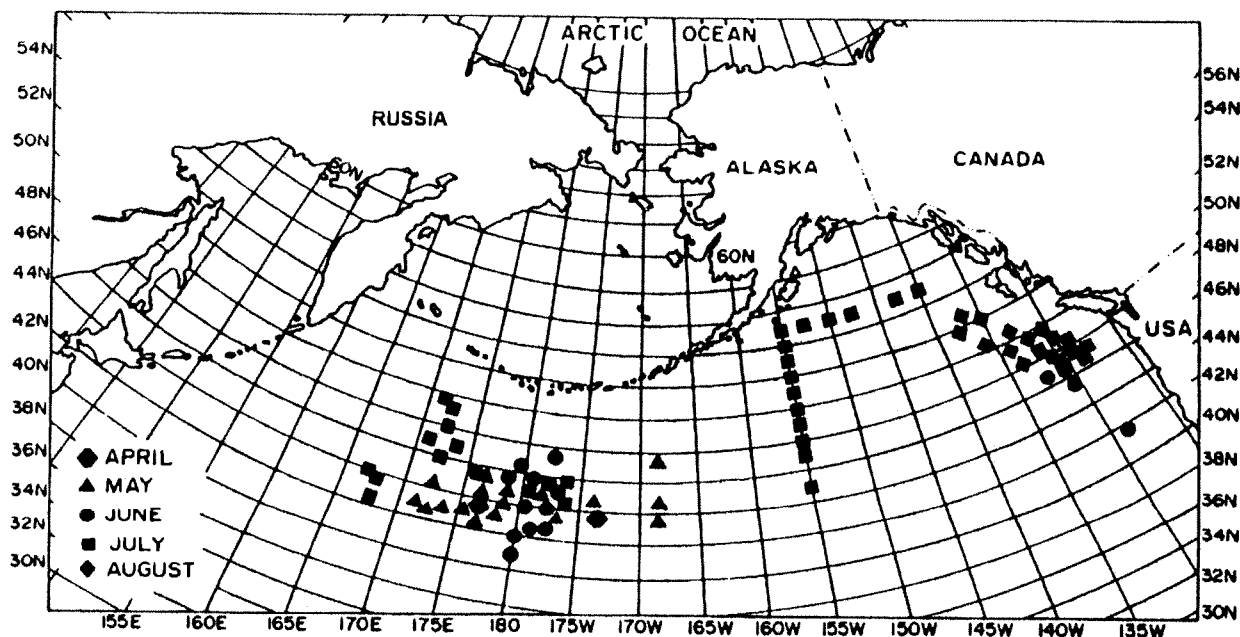
Case History 2

The second case history revolved around the use of two freshwater trematode parasites (*Nanophyetus salmincola* and *Plagioporus shawi*) to identify the ocean range (Fig. 2) of steelhead trout originating from the northwestern part of the United States, from northern California to northern Washington and including Idaho (Margolis 1984, 1985, 1990; Dalton 1989a, 1989b; Burgner et al. 1992). *Nanophyetus salmincola* occurs as a juvenile or metacercaria encysted in various tissues or organs, particularly the kidney, and *P. shawi* occurs as an adult in the intestine. Both parasites are acquired in fresh water and apparently many, if not all, *N. salmincola* survive through the marine life of the anadromous host. An undetermined proportion of *P. shawi* seem to perish at sea.

The freshwater distribution of these two parasites is governed by the distribution of their obligatory first intermediate snail hosts, *Juga* spp. for *N. salmincola* and *Fluminicola virens* for *P. shawi*. Steelhead trout and these snail hosts are sympatric only in the U.S. northwestern states previously mentioned, accounting for the restricted freshwater distribution of infected steelhead trout. The other hosts in the life cycle (Margolis 1984, 1985, 1990) are not specific and hence are not limiting factors in the freshwater distribution of these parasites.

The possibility of using prevalence data on *N. salmincola* and *P. shawi* to estimate proportions of U.S. Pacific Northwest steelhead trout in high-seas samples was first recognized by Margolis (1984, 1985) and pursued by Dalton (1989a, 1991) using data on *N. salmincola* only. However, annual changes in prevalence of *N. salmincola* and in the relative

Fig. 2. Ocean distribution of U.S. Pacific Northwest steelhead trout (*Oncorhynchus mykiss*) as determined by the presence of *Nanophyetus salmincola* and/or *Plagioporus shawi* in samples from the North Pacific Ocean, 1983-1987. (Adapted from Margolis, 1982.)



abundance of the many steelhead trout stocks complicated this attempt to quantify the representation of steelhead trout from the *N. salmincola*-endemic area in high-seas samples.

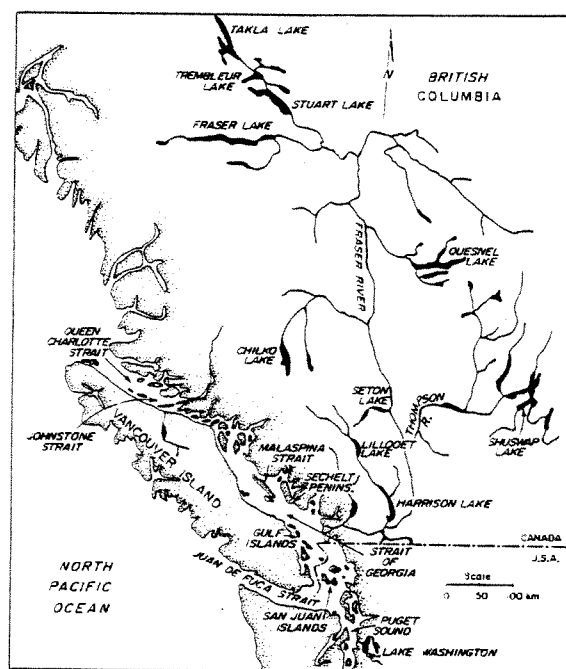
Like the previous case on sockeye salmon, for qualitative description of the oceanic range of U.S. Pacific Northwest steelhead trout, the two trematode tags may be considered stable, unless the distributions of the obligatory snail hosts are expanded beyond the U.S. Pacific Northwest through human activities. For quantitative estimates of stock composition, the parasites must be classified as unstable because of annual changes in prevalence.

Case History 3

In this case history, stock differences in an assemblage of 12 freshwater parasites were used to estimate the stock composition of juvenile sockeye salmon migrating seaward through the Strait of Georgia, British Columbia (Bailey et al. 1988; Groot et al. 1989). These sockeye salmon originate primarily from various tributaries of the Fraser River and from Lake Washington (Fig. 3).

The data on differences in parasite prevalence, intensity, or abundance (see Margolis et al. 1982 for definitions) were analyzed using the maximum-likelihood mixture model (Fournier et al. 1984; Wood et al. 1987). Although this approach proved to

Fig. 3. Principal sockeye salmon (*Oncorhynchus nerka*) lakes of the Fraser River system, British Columbia, and Puget Sound, Washington. (From Groot et al., 1989.)

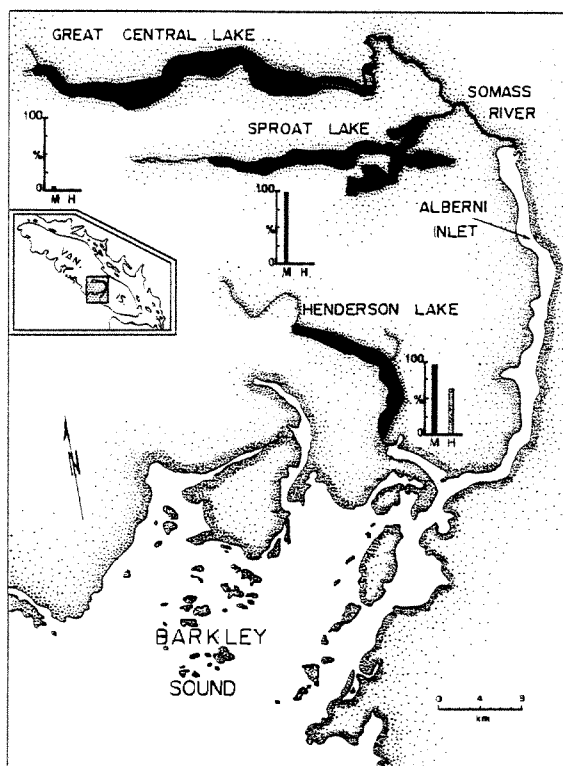


be an effective method of stock identification it was clear that in the three years of study, 1982-1984, the abundance of many of the parasites used in the analysis varied markedly by year, requiring the baseline data to be re-established annually, again indicating quantitative instability in the parasite tags.

Case History 4

Case history 4 is perhaps the most interesting of all from the point of view of stability of parasite tags. In this example, three sockeye salmon stocks in Barkley Sound (west coast of Vancouver Island, British Columbia) are the subject of a mixed stock fishery. The three stocks are associated with Great Central Lake, Sproat Lake, and Henderson Lake (Fig. 4).

Fig. 4 Barkley Sound, Vancouver Island, area, showing the three sockeye salmon (*Oncorhynchus nerka*) producing lakes and prevalences of *Myxobolus arcticus* and *Henneguya salminicola*.



To avoid overexploitation of individual stocks in the fishery, knowledge is required of the stock composition throughout the fishing season. During the late 1970s and in the 1980s, this was successfully accomplished by distinguishing the stocks on the basis of unique parasite characteristics in each stock (Margolis 1982). The differences involved two myxosporeans, one (*Myxobolus arcticus*) occurring in

the brain, and the other (*Henneguya salminicola*) located in macroscopic "cysts" in the somatic musculature.

During the years 1977-1984, sampling of smolts and returning adults to each of the lake systems demonstrated considerable stability in the occurrence of each of the parasites in each of the stocks: Great Central Lake sockeye salmon were characterized by low prevalence of *M. arcticus* (mean <5%) and *H. salminicola* (<1%); Sproat Lake sockeye salmon were characterized by almost 100% prevalence of *M. arcticus* and absence of *H. salminicola*; Henderson Lake sockeye salmon were characterized by almost 100% prevalence of *M. arcticus* and 55-76% (mean 66%) prevalence of *H. salminicola* (Fig. 5). These stock characteristics were stable for approximately 10 or more years and permitted accurate estimates of the stock composition in the Barkley Sound fishery and in weekly pre-fishery forecasts.

However, baseline sampling of the three constituent stocks from 1993-1995 indicated a major change had taken place in the prevalence of both parasites in Great Central Lake sockeye salmon (Table 2), which greatly reduced the reliability of these parasites for determining stock composition of the mixed sockeye salmon population in Barkley Sound. No change in Henderson Lake sockeye salmon and minimal change of *H. salminicola* in Sproat Lake sockeye salmon occurred during this period.

This example indicates that parasite tags may be stable for a decade or more, only to undergo major changes subsequently. It is imperative, therefore, to check baseline data periodically when using parasites to estimate stock composition in mixed stock fisheries.

CONCLUSIONS

1. Where stock identification is based on the unique presence of certain heteroxenous helminth parasites, the use of such parasite "tags" usually provides a stable basis for qualitative stock identification. In these instances the presence of the parasite "tag" in a salmonid stock is dependent on the sympatric occurrence of the salmonid and one of the other essential hosts in the life cycle of the parasite.
2. When parasites are used for quantitative estimates of stock composition, baseline data may have to be re-established annually to take into account annual variations in parasite prevalence (% of stock with the parasite) and intensity (numbers of parasites in each host) among the stocks to be distinguished.
3. Some quantitative parasite differences among salmonid stocks may appear to be stable for periods up to 10 or more years, but may show marked changes over the longer term.

Fig. 5 Prevalence of *Myxobolus arcticus* and *Henneguya salminicola* in adult sockeye salmon (*Oncorhynchus nerka*) stocks from the Barkley Sound area, Vancouver Island, British Columbia, 1977-1984 combined.

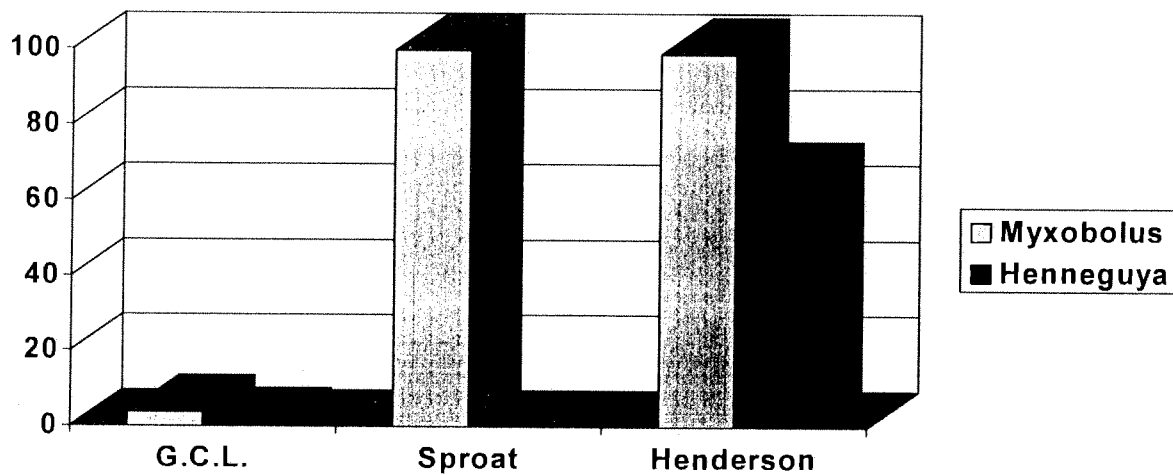


Table 2. Prevalence of *Myxobolus arcticus* (M) and *Henneguya salminicola* (H) in adult sockeye salmon (*Oncorhynchus nerka*) stocks from Barkley Sound, B.C., 1993-1995.

Year	Great Central		Sproat		Henderson	
	M	H	M	H	M	H
1993	52.4	18.7	99.7	0.0	-	-
1994	69.4	23.4	99.6	2.0	-	-
1995	75.5	19.0	100.0	0.0	100	75

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Simulations of the Even-Year Asian Pink Salmon (*Oncorhynchus gorbuscha*) Genetic Baseline to Determine Accuracy and Precision of Stock Composition Estimates

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Electrophoretic analysis of Asian even brood-year pink salmon stocks has shown regional heterogeneity (Noll et al. in review). Hypothetical mixed fisheries were created using data from 24 variable loci from Noll et al. in review. The mixture was analyzed to test the accuracy and precision of this baseline data for potential use in mixed fishery analyses. Thirteen stocks were separated into four management regions: Japan, Sakhalin, eastern Kamchatka, and western Kamchatka. Simulations were varied in sample size, number of loci, and percent regional contribution. The simulated mixtures were analyzed using the Conditional Maximum Likelihood Estimate (MLE). The mean estimate, standard deviation, and coefficient of variation were calculated for standardized comparison by both stock and region. Computed MLEs showed that estimates for the Noll et al. baseline improved in accuracy and precision with increased sample size and retention of important loci. When 24 loci and a minimum of 200 samples in a mixture were used, the baseline was approximately 80% accurate in its ability to distinguish regions from a mixture.



INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) are distributed around the North Pacific Rim from Japan to northern California, extending into the northernmost reaches of Asia and North America. It is the most abundant salmon species in the North Pacific Ocean (Heard 1991) as well as one of the most abundantly harvested. The commercial importance of this species to coastal countries of the North Pacific is verified by a catch rate of approximately 300,000 metric tons annually. Annual odd-year catch rates are typically larger, on the order of 350,000 metric tons, compared to the average even year rate of 250,000 metric tons (Fishery Statistics, 1995). The value of

the fishery often causes conflict when neighboring nations are unable to satisfactorily divide the catch. The complexity of mixed fishery dispute increases where transboundary rivers exist, or migration routes pass through open waters of neighboring countries.

This study examines the feasibility of using the even-year pink salmon genetic baseline (Noll et al. in review) as a tool in assessing stock composition in mixed-stock fisheries. Stock composition estimates from simulated samples of various mixtures can be used to describe the potential utility of the baseline for estimating the composition of real mixtures.

Because gene flow in pink salmon occurs only between generations spawning biennially, significant genetic divergence has occurred between the even-

and odd-year lines (Salmenkova et al. 1981; Beacham et al. 1985, 1988; Gagalchy 1986; Efremov 1991; Makoyedov et al. 1993) and are separate entities for genetic analyses and management purposes. The scope of this paper will discuss only the even brood-year line.

METHODS

Data were selected from the even-year pink salmon baseline (Noll et al. in review) which included thirteen 1990 collections: two stocks from river systems on Hokkaido Island, Japan, four from southern Sakhalin Island, five from the western Kamchatkan peninsula, and two from the eastern Kamchatkan peninsula, Russia.

Mixtures were simulated from the baseline allele frequencies using the program SIMULATR developed at the Auke Bay Laboratory (Pella et al. 1996). The program generated series of random samples from the baseline data using the bootstrap procedure, and created mixture samples of specified size and expected stock composition. SIMULATR computed the conditional maximum likelihood estimate (MLE) (Pella and Milner 1987) for each set of baseline and mixture samples it generated. To begin the search for an MLE, the 13 baseline stocks were assumed to contribute equally to each mixture. The program searched until at least 95% of the maximum of the likelihood function was attained.

Sample Size

SIMULATR created mixture samples from 24 variable loci in the 36 loci baseline whereby each region, (Japan, Sakhalin, West Kamchatka, and East Kamchatka) was comprised of equal portions of the stocks within that region. One thousand sets of baseline and mixture samples were generated from each region, with a mixture sample size of 50. The simulation was repeated varying the mixture sample size from 50 to 1000, for a total of fifteen mixture series for each region. MLEs were computed for each of the 60,000 sets of samples (15 mixtures x 4 regions x 1000 bootstrap samples). The coefficient of variation was calculated and plotted against the sample size for standardized comparison to describe the effect of sample size on the analysis (Marlowe and Busack 1995).

Important Loci

The five most distinguishing loci, *GR-I**, *sAAT-3**, *PEP-B1**, *PGDH**, and *PEP-D2** were determined by gene diversity analysis (Noll et al. in review). The earlier series of simulations was modified and repeated with these five most distinct

loci omitted and the remaining 19 loci included. The number of sets of baseline and mixture samples generated per experimental combination was reduced to 100 from 1000 in order to limit computation time. Mixture sample size was limited to 200. MLEs, confidence intervals, and coefficients of variation were calculated to compare the 19- and 24-loci analyses. Additional mixtures were created and MLEs computed for a variety of combinations of loci to determine which set of loci produced best accuracy and precision.

Precision and Accuracy

Finally, 40 hypothetical mixtures were created in which the percent contribution from each region was varied. MLEs were computed for the series of simulated mixtures using 24 loci, a mixture sample size of 200, and 100 bootstrap samples. An additional four series of mixtures (11 mixtures in each series) were created for which the percent contribution of each region varied from 0% to 100% in increments of 10%. The mean, standard deviation, confidence interval, and coefficient of variation were calculated to describe the accuracy and precision of stock composition estimation from the baseline.

RESULTS AND DISCUSSION

The simulations and maximum likelihood estimates (MLEs) were used to examine the utility of the Asian pink salmon baseline (Noll et al. in review) for mixed-stock analyses and related applications.

Estimated composition of a mixture improved in accuracy and precision with increased sample size (Table 1), however, significant bias remained in that all stocks were underestimated. The relationship between the coefficient of variation and the mixture sample size showed that a minimum sample size of approximately 200 was necessary for a stock composition estimate with an average standard error of less than 20% (Fig. 1). Rate of change of increased accuracy and precision diminished above $N=200$. Estimates obtained from sample sizes less than 200 were of questionable value because the standard error exceeded the actual composition.

MLE's of mixture samples composed of 100% of each of four regions with stocks in equal portions from that region, using 100 bootstrap samples, 24 loci, and a mixture sample size of 200, produced mean estimates (with standard deviations) as follows: Sakhalin - 86% (0.09), Japan - 68% (0.14), West Kamchatka - 84% (0.06), and East Kamchatka - 80% (0.08) (Table 2). True mixtures of multiple stocks will generally yield a more accurate estimate because the MLE was constrained between 0 and 100% and therefore simulated mixtures with contributions

Table 1. Sample size (N), Estimated Mean, Standard Deviation (S.D.), and Coefficient of Variation (C.V.) where each region comprises 100% of the mixture, using 24 loci.

N	Japan			Sakhalin			W. Kamchatka			E. Kamchatka		
	Mean	S.D.	C.V.	Mean	S.D.	C.V.	Mean	S.D.	C.V.	Mean	S.D.	C.V.
50	.589	.226	.384	.794	.164	.207	.800	.129	.161	.737	.145	.197
100	.635	.182	.286	.842	.130	.155	.824	.097	.117	.766	.111	.144
150	.667	.153	.230	.859	.100	.117	.833	.087	.105	.778	.098	.126
200	.672	.143	.213	.869	.095	.109	.838	.072	.086	.789	.089	.113
250	.682	.129	.190	.880	.083	.094	.837	.072	.086	.786	.086	.109
300	.687	.119	.174	.886	.073	.083	.841	.067	.080	.790	.082	.104
350	.689	.118	.171	.887	.073	.083	.843	.065	.077	.791	.082	.103
400	.690	.108	.157	.890	.072	.081	.845	.061	.072	.793	.078	.099
450	.692	.110	.159	.895	.067	.075	.842	.063	.074	.790	.079	.100
500	.694	.106	.153	.901	.063	.069	.844	.057	.068	.792	.076	.096
600	.687	.104	.151	.903	.057	.063	.849	.058	.069	.793	.073	.092
700	.695	.100	.143	.906	.060	.066	.850	.054	.064	.794	.070	.088
800	.698	.098	.140	.907	.054	.060	.848	.054	.063	.796	.070	.088
900	.697	.100	.144	.908	.054	.059	.847	.055	.065	.799	.068	.085
1000	.698	.095	.135	.908	.053	.058	.852	.051	.060	.797	.067	.084

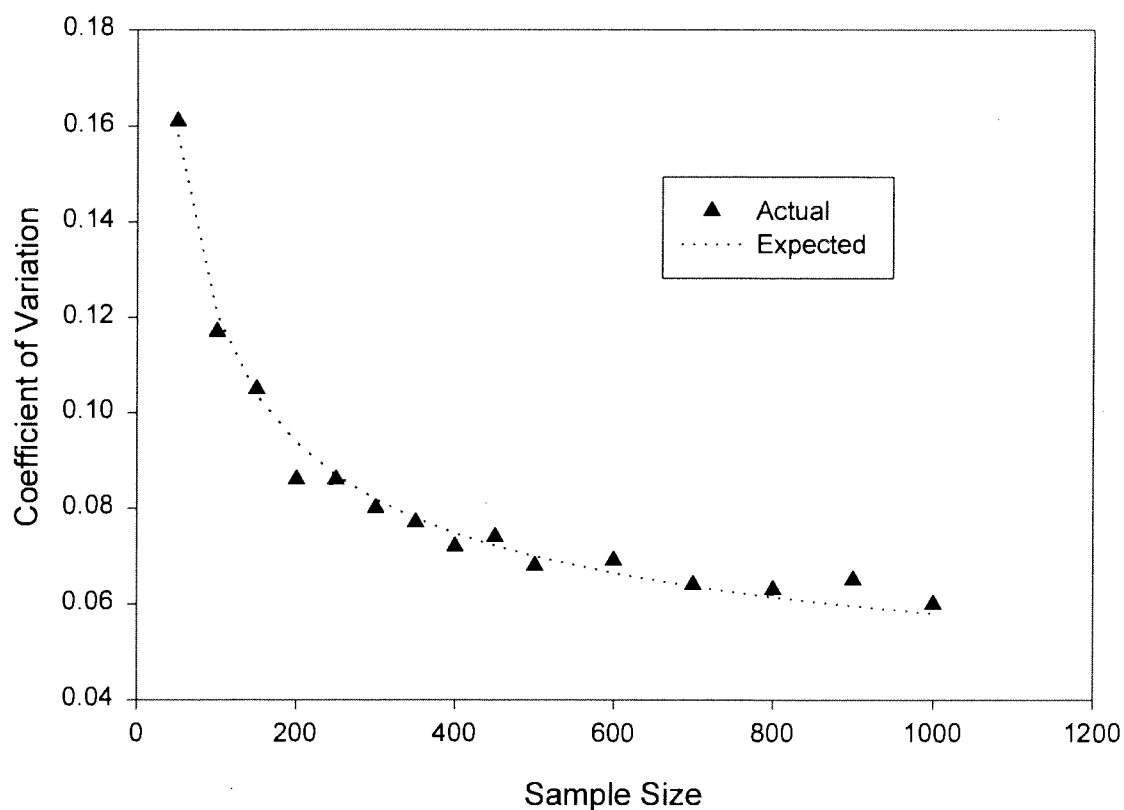
Fig. 1 Curve describing the relationship between sample size and the coefficient of variation. The curve represents a mixture comprising a 100% contribution of the western Kamchatka region and 1000 bootstrap resamplings of the baseline for 24 loci.

Table 2. For the 19 loci analysis, sAAT-3*, GR-1*, PEP-B1*, PGDH, and PEP-D2* were eliminated; for the 18 loci analysis, an additional discriminating locus was removed: FDHG* from Japan, TPI-4* from Sakhalin, GPI-A* from W. Kamchatka, and mIDHP-1* from E. Kamchatka. Each region consists of 100% of the mixture; the sample size 200.

# Loci	Japan			Sakhalin			W. Kam			E. Kam		
	Mean	S. D.	C.V.	Mean	S. D.	C.V.	Mean	S. D.	C.V.	Mean	S. D.	C.V.
24	.679	.143	.211	.858	.098	.114	.839	.065	.077	.802	.080	.099
19	.532	.192	.361	.800	.141	.176	.659	.161	.244	.657	.159	.242
18	.474	.200	.422	.763	.153	.201	.548	.152	.277	.627	.126	.203

approaching these limits deviate from the actual contribution (Fig. 2). Pella and Milner (1987) noted abundant stocks will be underestimated, and rare stocks, overestimated.

Simulated mixtures of 100% composition of each region produced an overall average maximum likelihood estimate of 80%, with 10% standard deviation, whereas the chum salmon (*O. keta*) baseline (Seeb et al. 1995; Wilmot et al. 1995), and chinook salmon (*O. tshawytscha*) baseline (Marshall et al. 1990; Marlow and Busack 1990) yield estimates of 95% and greater for similar pure (100%) regional

mixtures. Misallocation occurs because stocks are genetically similar.

In mixtures comprised of all four regions, contributions for Sakhalin were overestimated, whereas they were underestimated for Japan, East Kamchatka, and, to a much lesser extent, West Kamchatka. Most of the misallocation went to Sakhalin (Fig. 3), most likely because its populations are the most similar genetically to eastern Kamchatka and Japan (Noll et al. in review). The Japanese region had the largest bias between the actual and the estimated contribution, indicating a lack of

Fig. 2 Estimated versus true proportions of each region. Estimates are the mean of 100 bootstrap resamplings, and error bars are one standard deviation around the mean.

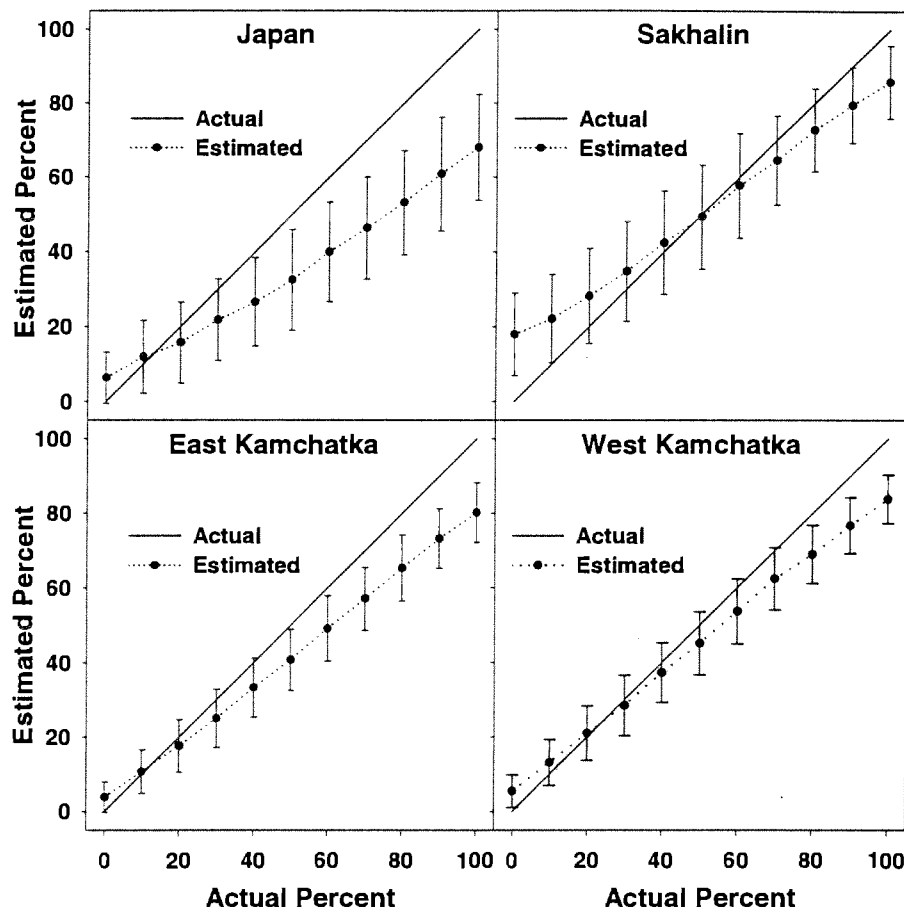
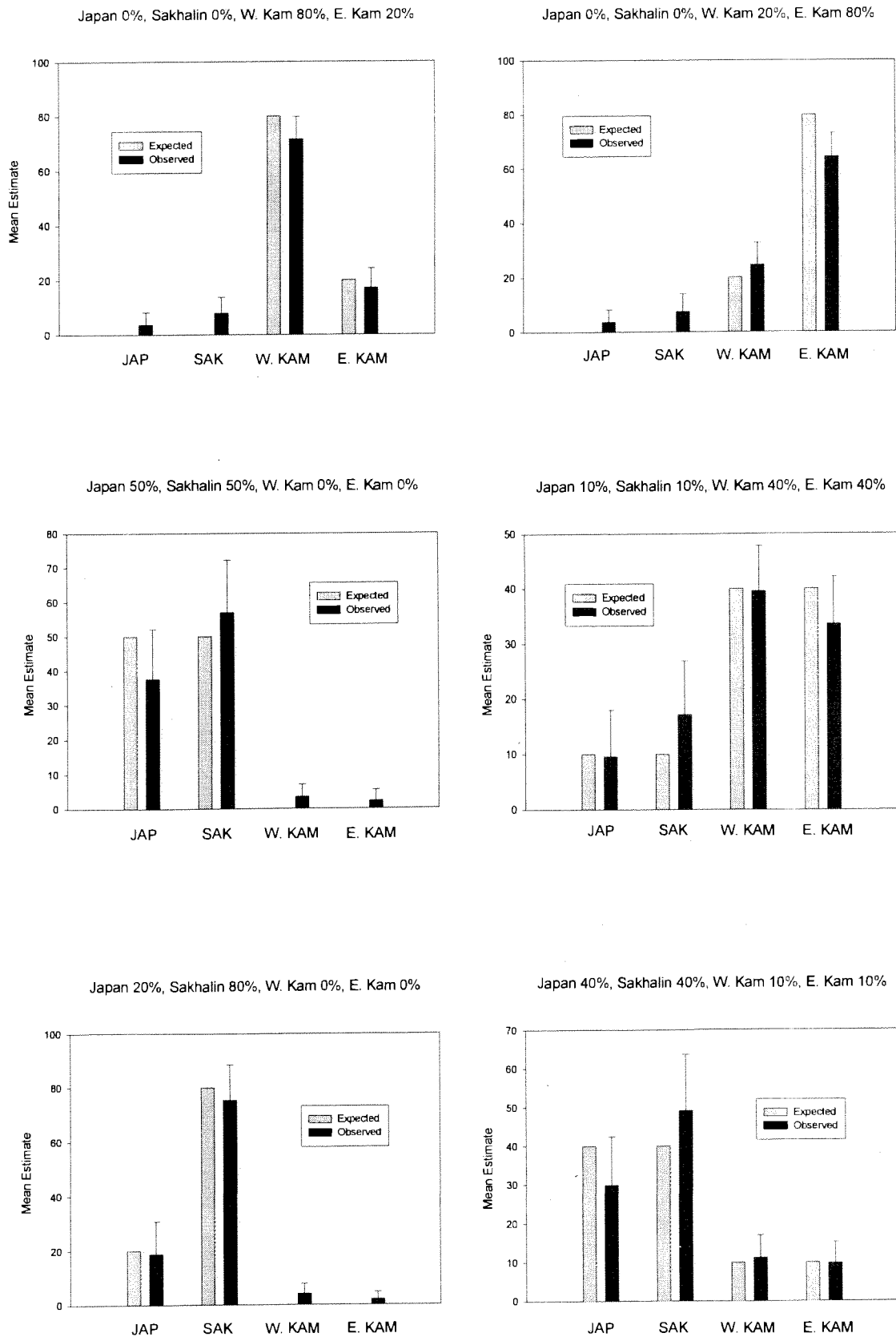


Fig. 3 Expected versus observed mean estimates with one standard deviation around the mean for simulated mixtures, using 100 bootstrap resamplings and 24 loci.



differentiating genetic markers. This is confirmed by Noll et al. (In review). The two Japanese populations, Tokushibetsu (northern Hokkaido) and Kushiro (southeastern Hokkaido), are separated by the Kuril Islands and flow into different seas: the Tokushibetsu into the Sea of Okhotsk, and Kushiro into the North Pacific Ocean. They differ genetically (Noll et al., in review.), and need to be considered as separate regions for mixed-stock analysis. While the goal to determine the regional or country of origin of mixtures may be to resolve mixed fishery disputes, Sakhalin Island, Russia and Tokushibetsu, Japan, are genetically one region (Noll et al. in review), making separation difficult with current information.

An increased number of loci might demonstrate greater genetic heterogeneity among regions. The earliest protein studies of Asian pink salmon resolved only 5-6 loci (Zhitovitsky et al. 1989) and indicated that no heterogeneity existed among regions. With data from new loci, heterogeneity among populations has been detected (Noll et al. in review). Gene diversity analysis for 24 loci (Noll et al. in review) show the five loci with the highest level of regional heterogeneity are *AAT-3**, *GR-1**, *PEPB-1**, *PGDH**, and *PEPD-2**. When these five loci were eliminated from the analyses, precision and accuracy decreased substantially for every region. For example, the coefficient of variation for western Kamchatka increased from 7.7% with 24 loci, to 24.4% with 19 loci (Table 3). In addition, *FDHG** was important in determining the accuracy of the estimate for Japan, *TPI-4** for Sakhalin, *IDHP-1** for eastern Kamchatka, *GPI-A** and, to a lesser extent *TPI-4** and *IDHP-1**, for western Kamchatka. The omission of six important loci increased the coefficient of variation from 21.1% with 24 loci to 42.2% with 18 loci for Japan (Table 2). Loss of discriminating loci degraded accuracy and precision of composition estimation.

The degradation of proteins in tissue samples of poor quality can result in loss of important loci for composition estimation. Because several loci showing significant regional heterogeneity are expressed in highly labile proteins, sample quality is critical for genetic stock separation. Data for the baseline (Noll et al. in review) included 36 loci out of a potential 69 loci for pink salmon.

CONCLUSIONS

Each genetic baseline must be evaluated individually for reliability for mixed stock fishery analysis. Conclusions in this manuscript can only be applied to the Noll et al. (in review) baseline.

Precision and accuracy of regional composition improved substantially for mixture sample sizes of about 200. Mixture samples less than 200 were

unsatisfactory because the standard error of the estimates exceeded known contributions.

Maximum likelihood estimates of the Noll et al. (in review) genetic baseline data produced a mean estimate of $80\% \pm 10\%$, with a mixture sample size of 200. Precision may not be accurate enough to estimate regional contributions to mixed stock fisheries. However, it may be the most accurate and cost effective method currently available. Improved sample quality might produce additional distinct loci and improve accuracy and precision of stock contribution estimates.

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Genetic Stock Identification of Chum Salmon in Highseas Test Fisheries in the Western North Pacific Ocean and Bering Sea.

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Substantial genetic variability among populations of chum salmon (*Oncorhynchus keta*) around the Pacific Rim make it possible to estimate the stock composition of complex mixed-stock fisheries using genetic stock identification (GSI) techniques. We briefly discuss the history of the use of portions or all of the Asian-North American baseline for protein genetic characters to resolve mixtures of chum salmon. We use the species-wide genetic database to analyze test fishery samples taken aboard Japanese research cruises in 1991-1992 in the Kuril Islands (145° E), the western North Pacific Ocean (165° E), and the North Pacific Ocean and Bering Sea at 179° 30' W. Mixture samples from the Kuril Islands and western North Pacific Ocean were dominated (>75%) by single stock groups, i.e., Japanese and Russian stocks, respectively. At 179° 30' W, the stock profile in the Bering Sea was 45% Japanese, 38% Russian, and 15% Alaskan and differed considerably from the samples (1991-1992) taken in the North Pacific Ocean (15% Japanese, 62% Russian, and 22% Alaskan). This protein genetic dataset has been standardized across international agencies and can be used across the species' distribution for accurate mixed-stock fishery analyses. Results from genetic stock identification can and are being used fisheries management and applied to biological models of stock distributions of salmon in the North Pacific Ocean.



INTRODUCTION

A genetic dataset for protein genetic (allozyme) characters exists for chum salmon populations throughout its distribution. The baseline dataset extends from Japan and Russia (Winans et al. 1994) eastward through western and southeast Alaska (Wilmot et al. 1994; Kondzela 1994; Seeb et al. 1995) to southern British Columbia and Washington (Phelps et al. 1994). The level and patterns of regional differentiation have been explored in the above studies and applied to questions of zoogeography, speciation, and fishery management.

Regional segments of this species-wide dataset have been used in several instances for coastal or

nearshore mixed-stock fishery analyses. Canadian biologists have used genetic stock identification to estimate the proportional contribution of Canadian and US stocks of chum salmon and for in season monitoring of Canadian stocks in several southern BC fisheries (Hop Wo et al. 1992). Their 41 stock/7 locus baseline is primarily BC stocks with representative Washington stocks. Since 1991, a 39 stock/30 locus baseline is being used in Washington by state and tribal agencies to monitor the timing and abundance of stocks in Puget Sound (NWIFC 1995). Stock composition estimates collected on a weekly basis through a portion of the fishery have been applied along with catch-per-unit effort for in-season and post-season models for management and

conservation of chum salmon (NWIFC 1995).

The species-wide dataset has been used to assess complex, international mixed-stock fisheries in two instances. Seeb et al (1995) estimated stock composition of chum salmon caught incidentally in sockeye salmon (*O. nerka*) fisheries in two areas of southern Alaska Peninsula in 1993 and 1994. Using available genetic data from Asia and North America, they constructed a 69 stock group/20 locus dataset. Wilmot et al (1995) added several Asian stocks to this baseline (77 stock groups total) and estimated the stock composition of chum salmon caught incidentally in Bering Sea trawl fisheries for walleye pollock (*Theragra chalcogramma*). Analyses of simulated high-seas mixtures indicate accurate estimates can be made to stock groups using slightly different versions of the species-wide baseline (Winans et al. 1994; Seeb et al 1995; Wilmot et al. 1995).

In this report we use the newly-assembled genetic baseline to describe test fisheries of chum salmon caught during several research cruises in the west Pacific Ocean, north Pacific Ocean, and Bering Sea.

MATERIALS AND METHODS

Tissues were collected from fish caught by longline or gillnet on high seas research vessels from 1991 to 1992 (Table 1). Samples of muscle, heart, liver, and retinal tissue were frozen and held onboard at approximately -20°C until transported to -80°C freezers, and ultimately shipped to the Northwest Fisheries Science Center, Seattle for processing and analysis.

Samples were examined for protein electrophoretic variation on horizontal starch gels using standard procedures described by Aebersold et al. (1987) and Winans et al. (1994). Standard nomenclature for loci and alleles was used as outlined in Shaklee et al. (1990). Alleles were compared and

standardized for 20 polymorphic loci (Seeb et al. 1995).

Baseline Data

Data are available for approximately 200 stocks species-wide. We used the simplified baseline dataset formulated in Seeb et al. (1995) for 69 stock groups that was augmented by Wilmot et al. (1995) to a 77 stock group/20 locus dataset. Seeb et al. (1995) simplified the entire Pacific Rim baseline by selecting representative stocks from southeast Alaska, British Columbia, and Washington and by pooling statistically nonsignificant regional stock pairs or groups for a total of 69 stock groups. Wilmot et al. (1995) added two stocks from China and six stocks from Russia for a total of 77 stock groups. Mixed-stock fishery results were no more precise when assessing contributions by geographic region when additional populations from southeast Alaska, British Columbia, and Washington were added for a total of 190 stocks (R. Wilmot, pers. comm., National Marine Fisheries Service). Our analyses were based on a 19-locus baseline; we dropped *PEPA* from our analyses because it was frequently missed in the electrophoretic screening of mixture samples. Because of the low level of *PEPA* variation, its exclusion from the mixture analyses had minimal to no effect on results reported herein. The 19 loci are: *sAAT-1,2*, *mA-3*, *mAAT-1*, *ALAT*, *ESTD*, *G3PDH-2*, *GPI-A*, *GPI-B1,2*, *mIDHP-1*, *sIDHP-2*, *LDH-A1*, *LDH-B2*, *PEPB-1*, *sMDH-A1*, *sMDH-B1,2*, *sMEP-1*, *mMEP-2*, *MPI*, and *PGDH*. Allele frequencies for the isoloci were computed over both loci and treated as a single locus.

For a multilocus estimate of population differentiation, Cavalli-Sforza and Edwards' chord distances (1967) and Nei's unbiased genetic distance values (Nei 1978) were calculated for all pair-wise comparisons of populations with the computer program BIOSYS (Swofford and Selander 1981), and

Table 1. Summary of research cruises with test fisheries of chum salmon for which tissues were available for genetic analysis. Number of fish refers to number of fish successfully processed for protein genetic data.

Research Cruise	Date	Latitude	Longitude	No. of fish	Gear	Reference
<i>Wakatake maru</i> 1991: Bering Sea	7/2-7/9	56-57 N ^{\$}	179 W-178 30 W	155	longline & gillnet	Ishida et al. 1991
<i>Wakatake maru</i> 1992: Bering Sea	7/5-7/6	56-58 N	179 30 W	196	longline & gillnet	Ishida et al. 1992
<i>Wakatake maru</i> 1992: N. Pac. Ocean	6/25-6/27	46-48 N	179 30 W	102	longline & gillnet	Ishida et al. 1992
<i>Hokuho maru</i> 1992 (Kuril Islands)	9/13-10/5	42-50 N	145-160 E	234	longline	Ishida et al. 1994
<i>Hokko maru</i> 1992	7/3-7/13	42-50 N	165 E	207	gillnet	Azuma & Yoshida 1992

^{\$} stations 20 and 27 only.

genetic relationships among populations were depicted in three-dimensional space with a multidimensional scaling (MDS) technique using the NTSYS-pc program (Rohlf 1994).

Mixed-stock Analysis

Estimates of stock contributions were made with a conditional maximum likelihood algorithm (Pella and Milner 1987) using the GIRLSEM program of Masuda et al. (1991). Precision of the composition estimates was calculated by bootstrap resampling (Efron 1981). Estimates were computed repeatedly from resampled observations of the baseline and mixture samples (Pella and Milner 1987). Standard deviations of estimates were calculated after 500 bootstrap resamplings. Estimates were made to individual stocks and then pooled to regional stock groups used by Seeb et al. (1995) and Wilmot et al. (1995). The regional stock groups are Japan, Russia, Western Alaska (summer run stocks), Yukon River (fall run stocks), Alaska Peninsula/Kodiak, SE Alaska and Prince William Sound, British Columbia, and Washington. Simulation studies of Wilmot et al. (1995) indicated that when true group contributions were 100%, average estimates were greater than 80% accurate for each of the eight groups.

RESULTS

The genetic relationships among the 77 stock groups are depicted in Figure 1. As seen previously (Seeb et al. 1995; Wilmot et al. 1995), regional groups of stocks are genetically similar. For example, the western Alaskan stocks cluster together, as do the Washington, Yukon, and Japan stocks. Although the majority of the Russian and Alaskan Peninsula stocks form distinctive, separate clusters, outliers are seen in

both of these groups. A similar pattern of genetic differentiation was obtained with Nei's genetic distance values (results not shown).

Estimates for the mixed stock fisheries are summarized in Table 2. As expected, estimated stock contributions differed among the test fishery locales. The Bering Sea samples from the *Wakatake maru* cruises in early July for 1991 and 1992 were a mix of Japanese and Russian chum salmon, and differed considerably from the mixture samples taken approximately two weeks earlier from the North Pacific Ocean which were predominantly Russian-origin chum salmon. The three predominant stock groups in the Bering Sea over the two sampling periods were Japan (34-56%), Russia (32-44%), and Alaska (11-20%). The Alaska Peninsula/Kodiak Island or Western Alaska stock group constituted approximately half of the Alaskan contributions in the Bering Sea samples in 1991 and 1992, respectively (Table 2).

The North Pacific Ocean mixture from the *Wakatake maru* cruise in 1992 was 62% Russian stocks. Alaskan stocks made up 22.3% and Japanese stocks constituted 14.9% of the mixture. At 14.3%, the Alaska Peninsula/Kodiak Island stock group was the largest Alaska stock group.

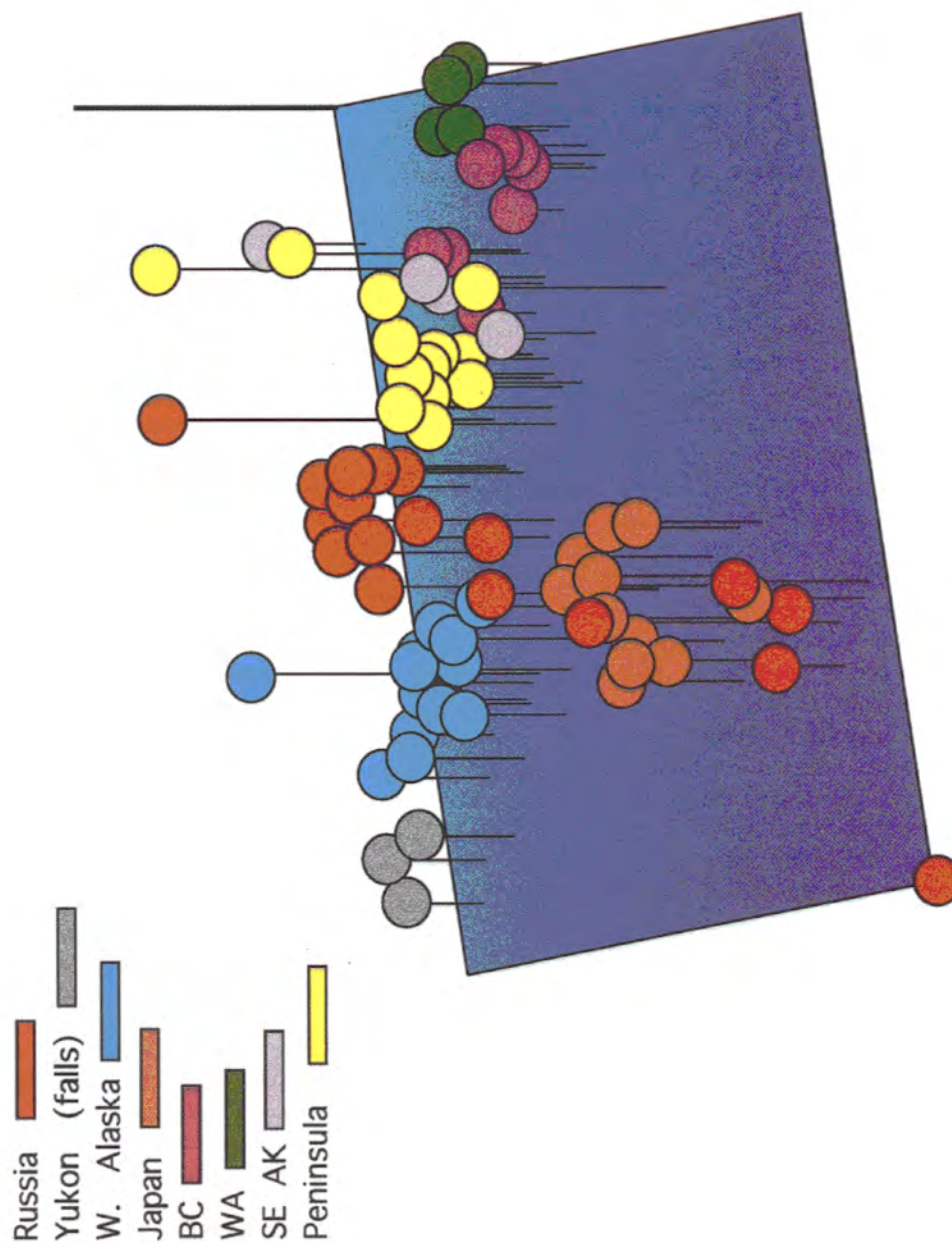
The two mixtures in the western North Pacific were each dominated by one stock group. The *Hokuho maru* 1992 mixture was 78% Japanese stocks, with smaller contributions from Russia (15.9%) and Alaska (5.5%). The *Hokko maru* 1992 was 86% Russian stocks, with lesser contributions from Alaska (10.9%) and Japan (1.9%).

Contributions from southern North American stocks were minimal in these test fisheries. The largest estimated contributions from the Southeast Alaska/Prince William Sound stock group was approximately 3.5% in both 1992 *Wakatake maru*

Table 2. Estimates of percent stock composition by region in test fisheries of chum salmon. The regional groups are: Japan, Russia, Alaska total, Western Alaska (summer run stocks), Yukon River (fall run stocks), Alaska Peninsula/Kodiak, Southeast Alaska/Prince William Sound, British Columbia, and Washington. Standard deviations, in parentheses, were calculated from 500 bootstrap samples of the baseline and mixture samples.

Research Cruise	Japan	Russia	Alaska total	Pen/Kodiak	W. Alaska	Yukon Fall	SE/PWS	BC	WA
<i>Wakatake maru</i> 1991/Bering Sea	56.0 (6.6)	32.4 (7.3)	11.4 (5.8)	5.6 (4.4)	4.0 (3.2)	0.2 (0.5)	1.6 (2.2)	0	0
<i>Wakatake maru</i> 1992/Bering Sea	34.4 (6.1)	43.9 (7.7)	19.7 (6.8)	5.9 (3.5)	10.3 (5.7)	0	3.5 (2.4)	1.9 (1.7)	0.1 (0.4)
<i>Wakatake maru</i> 1992/N. Pac. Ocean	14.9 (6.9)	62.1 (8.3)	22.3 (7.8)	14.3 (6.8)	4.3 (3.8)	0	3.8 (4.2)	0.6 (1.4)	0
<i>Hokuho maru</i> 1992 (Kurils)	78.0 (4.7)	15.9 (4.1)	5.5 (3.1)	2.0 (1.9)	3.5 (2.5)	0	0	0.5 (0.8)	0
<i>Hokko maru</i> 1992	1.9 (2.4)	86.1 (5.7)	10.9 (5.2)	4.9 (3.7)	5.6 (3.7)	0.1 (0.3)	0.2 (0.5)	1.0 (1.0)	0

Fig. 1 Multidimensional scaling (MDS) plot of Cavalli-Sforza and Edwards' chord distances among 77 stock groups of chum salmon based on allele frequencies at 19 loci. Stock groups are: Russia, Yukon River (fall run stocks), Western Alaska (summer run stocks), Japan, British Columbia, Washington, SE Alaska and Prince William Sound, and Alaska Peninsula/Kodiak.



mixtures. British Columbia stock contributions were all 1.9% or less. Estimates of contributions for Washington stocks were essentially 0; only one estimate was actually non-zero (0.1% in the *Wakatake maru* Bering Sea mixture, 1992).

The reported standard deviations for estimates > 10% were small (Table 2). In general, the 95% confidence intervals for these estimates were approximately 1-2% around each estimate, e.g., for *Hokko maru* 1992, the confidence intervals of the estimates were 85.6%-86.6% Russian, 10.4-11.3% Alaskan, and 1.7-2.2% Japanese. On the other hand, estimates of < 10% had relatively greater standard deviations, as is frequently seen (Pella and Milner 1987).

DISCUSSION

The observed level of genetic differentiation among groups of chum salmon across the species distribution permits accurate mixed-stock fishery estimates with protein genetic markers. The use of regional genetic baselines for stock identification has been demonstrated in British Columbia (Hop Wo et al. 1992) and in the United States and Canada (NWIFC 1995) in efforts to monitor the composition of near-shore fisheries of chum salmon. Determining stock compositions of more complex fisheries has been demonstrated in the Bering Sea and the Alaska Peninsula (Wilmot et al. 1995; Seeb et al. 1995) using a species-wide baseline.

We used the a 19-locus version of the 20-locus species-wide baseline established recently by Seeb et al. (1995), as augmented by Wilmot et al. (1995). This baseline represents our current best possible genetic profile for the major contributing stocks across the species' distribution. We recognize, however, that it is subject to refinement, with the addition of more polymorphic, stock-discriminating loci (protein or DNA-based), and more representative stocks. For more localized management applications (Hop Wo et al. 1992; NWIFC 1995), additions of regionally-important stocks and deletions of geographically-distant stocks groups are warranted. For example, for future analyses of mixtures from the Sea of Okhotsk, additional baseline samples from Sakhalin Island and Japan need to be evaluated and considered for a more precise mixed-stock fishery application (S. Urawa, unpublished data).

Mixture samples from the western portion of the north Pacific Ocean were dominated by single stock groups. The *Hokko maru* mixtures (1992 and 1995) were primarily Russian stocks (86-87%), with approximately 10% Alaskan and 2% Japanese stocks. On the other hand, the sample from the Kuril Islands (*Hokuho maru* 1992) was primarily Japanese stocks (78%) with approximately 16% Russian stocks and

6% Alaskan stocks. Stocks from British Columbia were detected in 6 of the 8 mixtures at a level of $\leq$ 1.9%. Washington stocks were essentially absent in these samples.

After two years of sampling at 179° 30'W in early July, we have evidence of a broad difference in the relative abundance of the three primary stock groups between the Bering Sea and North Pacific Ocean. The stock profile for Japanese/Russian/Alaskan stocks in the Bering Sea was approximately 45:38:15% and differed substantially from the data available from the same cruise survey at 179° 30'W in the North Pacific Ocean. The approximate profile for Japanese/Russian/Alaskan stocks in the North Pacific Ocean was 15:62:22%. This trend is also apparent in 1995 data (S. Urawa, unpublished data). Similarly, the *Hokko maru* sample which was primarily Russian chum salmon in 1992 was predominantly Russian stocks in 1995 (S. Urawa, unpublished data). These suggestions of stock abundance trends for specific time and places will be examined in future studies.

These broad differences presumably represent distributional patterns inherent to the stocks at a particular life history stage in a particular water mass. Therefore stock composition estimates will vary with water mass characteristics, stock age, stock maturity, etc. This study demonstrates that protein genetic markers can be used to accurately identify the composition of mixtures to a regional level. We recognize that the same biotic and abiotic conditions in the ocean that establish these broad differences may also be responsible for the between-year difference within one area, e.g., compare 1991 and 1992 results in the Bering Sea (Table 2). As more information on water mass characteristics (e.g., Davis et al. 1996) are collected, further canonical comparisons will add information about stock abundance variables.

Other genetic markers may someday augment or replace these protein genetic markers. Some of the leading contenders are DNA-based characters (Park and Moran 1994) that can be derived, in theory, from fins, scales, and tissues preserved with alcohol--thus, eliminating the need for ultracold preservation of the four tissues required here. In light of these potential developments, protein genetic profiles are available now across the species' distribution and can be implemented in accurate mixed-stock fishery analyses. Protein genetic characters are available species wide, are economically processed in the laboratory, and have been standardized across international agencies. Results like those reported here can be used in programs of highseas stock assessment.

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A Comparison of Methods of Stock Identification for Sockeye Salmon (*Oncorhynchus nerka*) in Barkley Sound, British Columbia

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Sockeye salmon (*Oncorhynchus nerka*) returning to Barkley Sound on the west coast of Vancouver Island originate from three stocks: Sproat Lake, Great Central Lake, and Henderson Lake. Evaluations of four methods of stock identification were conducted, with the annual stability of the stock-discriminating markers also examined. Variation observed in parasite infection rates, at protein electrophoretic loci, minisatellite DNA loci, and microsatellite DNA loci was used to assess the accuracy and precision of estimates of stock composition for these three stocks. Significant annual variability in parasite infection rates was observed in two of six comparisons for the stocks sampled annually during 1977-84, and in two of four comparisons for two stocks sampled annually during 1993-95. No significant annual variability in allele frequencies was observed at three electrophoretic loci (two stocks sampled in two years, 1983 and 1990) or four microsatellite DNA loci examined (three stocks each sampled for three years during 1987-95 for two loci, two stocks sampled for two years, 1990 and 1992, for two loci). Highest accuracy and greatest precision of estimated stock compositions were observed using the prevalences of two myxosporean parasites (*Myxobolus arcticus* and *Henneguya salminicola*) observed in the stocks during 1977-84. However, changes in the prevalence of both parasites in Great Central Lake sockeye salmon during 1993-95 substantially reduced the precision of the estimates. The use of variation at four microsatellite loci (Ots3, Ots100, Ots103, and Omy77) resulted in the accuracy and precision of the stock composition estimates similar to that observed with parasites during 1977-84, but greater than that obtained during 1993-95. Stock composition analysis utilizing variation at minisatellite loci was less reliable than analysis based upon microsatellite loci, with minisatellite allele frequencies determined using three probes (Ssa1, Ssa-A34, and OtsPBS-1). Protein electrophoresis (variation at three polymorphic loci used: PGM-1, PGM-2, and PGDH) provided the least reliable estimates of the four methods evaluated, although data for all loci known to be polymorphic in sockeye salmon were not available for the Barkley Sound stocks.



INTRODUCTION

Sockeye salmon (*Oncorhynchus nerka*) returning to Barkley Sound on the west coast of Vancouver Island originate from three stocks: Sproat Lake, Great Central Lake, and Henderson Lake, and these stocks are exploited in a mixed-stock commercial fishery. The early development of this fishery, prior to 1940, could be characterized as largely a terminal beach

seine and gillnet fishery that provided annual catches as high as 125,000 fish (Hyatt and Steer 1987), and because of its terminal nature, there was little requirement to determine the stock composition of the catch. During 1940-71, the fishery was characterized by a more diffuse gillnet fishery with an annual catch of up to 76,000 fish (Hyatt and Steer 1987). Since 1972, the fishery has been conducted by both gillnetters and purse seiners over a wide area in Barkley Sound and Alberni Inlet, and the annual catch has been highly variable, ranging from no catch

† deceased

(fishery closed) to about 1.2 million fish. Sockeye salmon from Sproat Lake and Great Central Lake have dominated the catch since 1980, comprising over 95% of the landings (Hyatt and Steer 1987). To prevent overexploitation of each of the component stocks, effective management of the current fishery, given its mixed-stock nature, requires accurate and precise estimates of stock composition to be available.

Lake fertilization has been used as a method to enhance the production of Barkley Sound sockeye salmon (LeBrasseur et al. 1978; Hyatt and Stockner 1985). Great Central Lake was fertilized annually from 1970-1973, and from 1977 to the present. Henderson Lake has been fertilized from 1976 to the present, and Sproat Lake from 1985-1987. The assessment of net changes in adult sockeye salmon production resulting from fertilization of nursery lakes is an integral part of evaluation of the utility of enhancing sockeye salmon production by this method (Hyatt and Stockner 1985).

Management of the Barkley Sound sockeye salmon fishery, as well as assessing the effects of longer-term fertilization of Great Central and Henderson lakes, required that reliable estimates of stock composition of the catch be determined. A survey of frequency of occurrence of two myxosporean parasites, *Myxobolus arcticus* (formerly identified as *M. neurobius*: see McDonald and Margolis (1995)) in the brain and *Henneguya salminicola* in the muscle, indicated that there were very substantial differences in the prevalence of these parasites among sockeye salmon in the three lakes during 1977-1984 (Quinn et al. 1987). These differences in prevalence were used to provide estimates of stock composition during this period (Steer et al. 1986, 1988). However, in the 1990s, it was observed that the prevalences of the parasites in Great Central Lake sockeye salmon changed substantially, with a marked decline in the ability to discriminate among stocks. Other methods of stock identification were required to provide effective management and assessment advice. In the present study, we evaluate four methods of stock identification of Barkley Sound sockeye salmon: prevalence of *Myxobolus* and *Henneguya* during 1977-84 and 1993-95, and three methods incorporating genetic variation, using allele frequency differences at protein electrophoretic, minisatellite DNA, and microsatellite DNA loci. Accuracy and precision of estimated stock compositions are evaluated, as well as temporal stability of either the parasite prevalences or allele frequencies.

MATERIALS AND METHODS

Samples and Laboratory Procedures

Parasites

Adult sockeye salmon were examined for the presence of two myxosporean parasites. *Myxobolus arcticus* was detectable in the brain as spores following digestion of the brain in a pepsin-hydrochloric acid solution, centrifugation, and microscopic examination of the resultant sediment. *Henneguya salminicola* was visually detectable in the musculature as macroscopic cysts (Boyce et al. 1985). The proportion of adults infected with *Myxobolus arcticus* was determined annually between 1977-1984 and between 1993-1995 for Sproat Lake and Great Central Lake sockeye salmon, and between 1978-1984 and in 1995 for Henderson Lake sockeye salmon (Fig. 1). *Henneguya salminicola* infection rates were recorded between 1979-1981 and 1993-1995 for Sproat and Great Central Lake sockeye salmon, and between 1978-1984 and in 1995 for Henderson Lake sockeye salmon.

Protein Electrophoresis

Heart, liver, muscle, and eye tissues were collected from all three stocks in 1983, and from Sproat Lake and Great Central Lake stocks in 1990. Samples were frozen, and variation at 35 protein-coding loci examined by starch gel electrophoresis (Aebersold et al. 1987). Levels of polymorphism at only 3 loci (PGM-1, PGM-2, and PGDH) were large enough to be evaluated for their utility in stock identification. Additional laboratory procedures have been outlined by Wood et al. (1994).

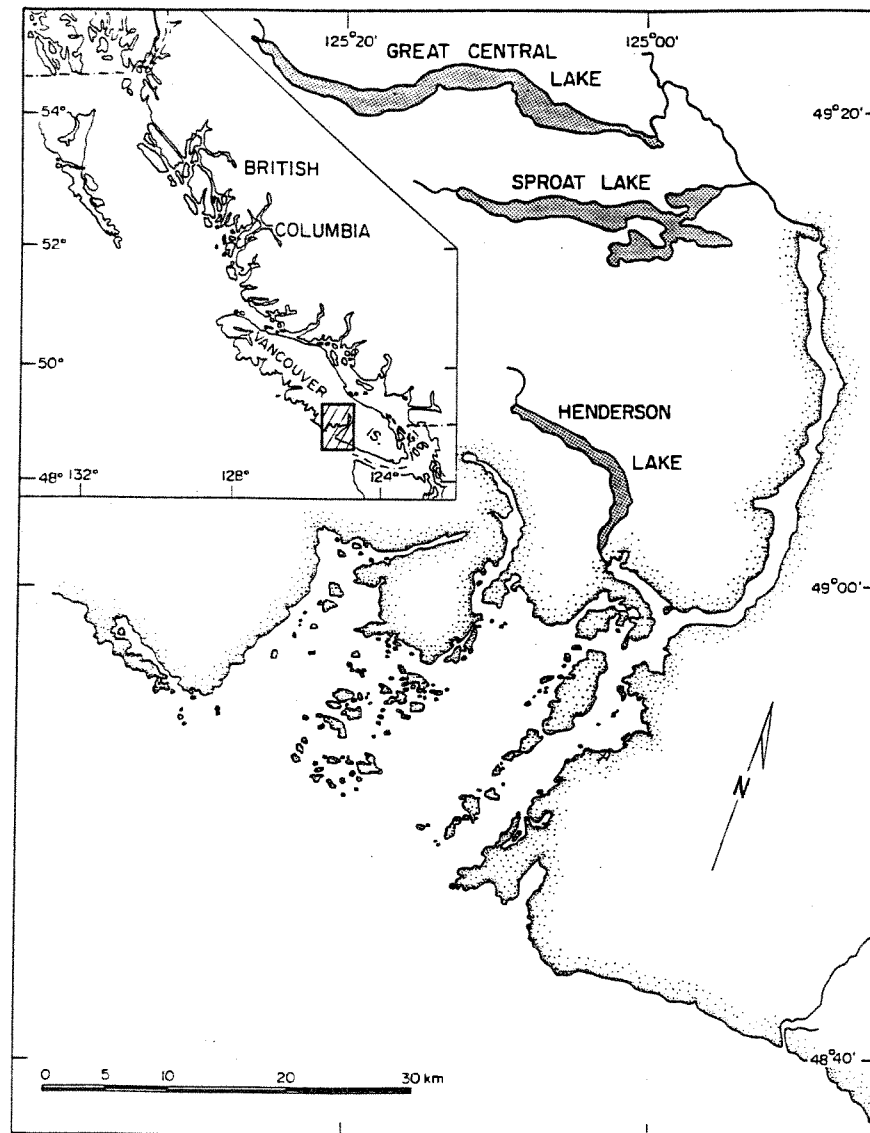
Minisatellite DNA Variation

Variation at minisatellite loci was examined with two single-locus (Ssa-1 and Ssa-A34) and one multi-locus (OtsPBS-1) probes for Sproat Lake and Great Central Lake sockeye salmon sampled in 1992. Genomic DNA was restricted with either AluI or HaeIII, loaded on to an agarose gel where it was size fractionated by electrophoresis, transferred to a nylon membrane, denatured, and hybridized with the appropriate denatured probe. A more complete description of laboratory procedures was outlined by Beacham et al. (1995).

Microsatellite DNA Variation

Variation at four microsatellite loci was examined via the polymerase chain reaction (PCR) with the

Fig. 1 Location of study area, including Barkley Sound, Alberni Inlet, Great Central Lake, Sproat Lake, and Henderson Lake on Vancouver Island, British Columbia, Canada.



primer sets Omy77 (Morris et al. 1996), Ots100 (Nelson and Beacham in prep.), Ots3 (Olsen et al. 1996), and Ots103. The Ots103 locus has not been described previously. Summarized briefly, a tetranucleotide GACA repeat was observed at the locus. The sequence of the primers which were used to amplify Ots103 were: forward, 5'-AGGCTCTGGGTCCGTG-3' and reverse, 5'-TGATATGGTGTGATAGCTGG-3'. Samples were analyzed for Sproat Lake and Great Central Lake sockeye salmon sampled in 1987, 1990, and 1992, and Henderson Lake sockeye salmon sampled in 1988, 1993, and 1995. Genomic DNA was derived from either scales or liver tissue samples, the locus amplified via PCR using the appropriate primers, the

amplified products loaded on to an acrylamide gel for size fractionation by electrophoresis, and allele size estimated. A more complete description of the laboratory analysis, primer development for Ots100, and estimation of allele size was provided by Nelson and Beacham (in prep.).

Data Analysis

Annual variation in parasite prevalence or allele frequencies at protein electrophoretic or microsatellite DNA loci was examined with the χ^2 test with 1,000 simulations conducted to determine the significance of the variability (Roff and Bentzen 1989). Significance levels were adjusted to account for the number of

multiple comparisons conducted (ie. $0.05/N$, where N is the number of tests conducted) (Lessios 1992). Differences in parasite prevalence or allele frequencies were used to calculate a generalized distance (D), where $D^2 = \sum (X_A - X_B)^2$ (Pimentel 1979). This distance was calculated between each pair of stocks with sampling years combined, and a pairwise distance was calculated between all sampling years within each stock. Data on parasite prevalence was analyzed as two separate blocks, with the years 1977-84 as one block, and 1993-95 as the second block.

Estimation of Stock Composition

In order to estimate the stock composition of a mixture using the maximum likelihood method of Fournier et al. (1984), it is first necessary to determine the distributions of characters discriminating the stocks contributing to the mixture. For *Myxobolus* and *Henneguya*, the observed numbers of fish infected or not infected with each parasite in each stock were determined, and the resultant matrix (two rows by two columns for each stock) used to characterize the stocks in each of the two time blocks. Genotypic frequencies at each of three polymorphic protein-coding loci (PGM-1, PGM-2, PGDH) were determined from the reported allelic frequencies by assuming that the stocks were in Hardy-Weinberg equilibrium, as was reported by Wood et al. (1994). Three genotypes were possible at each locus, so each stock was characterized by a 3X3 matrix containing expected genotypic frequencies. The general procedures used to incorporate minisatellite DNA variation to characterize the baseline stocks have been outlined by Beacham et al. (1995). Summarized briefly, allele counts at the Ssa1 locus (nine variables) and Ssa-A34 locus (two variables) and band counts observed with OtsPBS-1 (22 variables) were combined for each fish, and principal component analysis on the correlation matrix of the 33 variables was conducted to obtain uncorrelated variables or principal components. The continuous distributions of the principal component scores were summarized as 12-bin histograms, and 25 principal components were used in the analysis, so each stock was characterized by a matrix of 25 rows and 12 columns. Microsatellite DNA variation was incorporated as follows. Variation was scored at 10 alleles but subsequently condensed and summarized by eight alleles (36 genotypes) at the Omy77 locus, initially by 17 alleles and condensed to nine alleles (45 genotypes) at the Ots100 locus, initially by 16 alleles and condensed to 8 alleles (36 genotypes) at the Ots3 locus, and initially by 21 alleles and condensed to 10 alleles (55 genotypes) at the Ots103 locus. For example, 10 alleles at Omy77 were

initially identified as follows: 91-93 bp (1), 94-96 bp (2), 97-99 bp (3), 100-102 bp (4), 103-106 bp (5), 107-109 bp (6), 110-112 bp (7), 113-115 bp (8), 116-118 bp (9), 119-121 bp (10). However, given the low observed frequency of allele 1 in any stock (<0.02), it was combined with allele 2, and alleles 9 and 10 were also combined, resulting in eight alleles used in determination of genotypic frequencies. Combining low frequency adjacent alleles in this example reduced the number of genotypic frequencies to be estimated with the available samples from 55 genotypes to 36 genotypes, with little or no loss in the ability to discriminate among stocks. Each locus was considered to be in Hardy-Weinberg equilibrium, and expected genotypic frequencies were determined from the observed allele frequencies. Each stock was characterized by an input of four rows, with the first row containing counts for 36 genotypes, the second row counts for 45 genotypes, the third row counts for 36 genotypes, and the fourth row counts for 55 genotypes. For all four methods, each baseline stock was resampled with replacement in order to simulate random variation involved in the collection of the baseline samples during the estimation of stock composition of each mixture.

Hypothetical fishery samples of 200 fish were generated by randomly resampling with replacement the three baseline stocks, and adding the appropriate number of fish from each stock to the mixture. Estimated stock composition of the mixture was then determined using the method of Fournier et al. (1984), with the whole process repeated 50 times to estimate the mean and standard deviation of the individual stock composition estimates.

RESULTS

Parasites

Substantial differences in the prevalence of *Myxobolus* were observed among Sproat Lake and Great Central Lake sockeye salmon sampled during 1977-84 (Table 1). Even though both lakes are part of the Somass River drainage, virtually all sockeye salmon in Sproat Lake were infected with *Myxobolus*, whereas an average of only 5% of Great Central Lake sockeye salmon were infected. Virtually all Henderson Lake sockeye salmon were infected, and small but statistically significant annual variation was observed ($P < 0.001$). The high rates of prevalence limited the utility of this parasite in differentiating between the Sproat Lake and Henderson Lake stocks. Significant annual variation in the prevalence of *Myxobolus* in Great Central Lake was observed ($P < 0.001$), but the prevalence of infection never reached 9% in any year during 1977-84 (Table 1). A

marked change in *Myxobolus* prevalence was observed in Great Central Lake sockeye salmon sampled during 1993-95, with an average 63% of fish sampled infected with the parasite. The parasite prevalence increased significantly in each of the three years sampled ($P < 0.001$), with about 75% of the fish sampled in 1995 infected. If present trends continue, virtually all of Great Central Lake sockeye salmon may be infected by 1997, rendering *Myxobolus* prevalence of no value in discriminating among the three stocks.

Henneguya was virtually absent from Sproat Lake and Great Central Lake sockeye salmon sampled during 1977-84, but present in an average of 66% of Henderson Lake fish (Table 1). Significant annual variation was observed in *Henneguya* prevalence in Henderson Lake fish during 1977-84 ($P < 0.001$), with from 55 to 75% of the fish examined infected. During 1993-95, the prevalence of *Henneguya* in Great Central Lake sockeye salmon was significantly higher (21%) than observed during 1977-84 ($< 1\%$), but prevalence in the other two lakes was within the range observed in the earlier years. The prevalence in 1994 (2%) in Sproat Lake sockeye salmon was significantly higher ($P < 0.001$) than in other years,

when it was 0%.

During 1977-84, the mean distance between Sproat Lake and Great Central Lake Sockeye salmon, both stocks originating from the same drainage and dominating the catch in the fishery, was 0.99.

The mean pairwise distance between all three stocks was 0.95 (range 0.66-1.19). During 1993-95, the change in prevalence of both parasites in Great Central Lake sockeye salmon reduced the previous differentiation observed among the three stocks (Table 1). The mean pairwise distance declined to 0.61 (range 0.42 to 0.74), with the distance between the Sproat Lake and Great Central Lake stocks being 0.42.

Protein Electrophoresis

Although 35 loci were screened, only three loci were found where the frequency of a variant allele was > 0.05 . The greatest differentiation among stocks was observed at the PGM-1 locus, and the least differentiation at PGDH, but all differences were significant ($P < 0.001$). Allele frequencies of Sproat Lake and Great Central Lake sockeye salmon were more similar to each other than to Henderson Lake

Table 1. Prevalence of the brain parasite *Myxobolus arcticus* and the muscle parasite *Henneguya salminicola* in three stocks of sockeye salmon from Barkley Sound, 1977-95. Results for 1977-84 have been adapted from Quinn et al. (1987). N is the number of fish sampled in each year.

Year	Sproat		Great Central		Henderson	
	N	%	N	%	N	%
<i>Myxobolus</i>						
1977	15	100.0	15	0.0	0	-
1978	175	99.4	245	0.8	150	97.3
1979	760	99.6	900	2.7	211	98.1
1980	1330	99.9	1179	5.6	200	100.0
1981	1181	99.9	1337	8.4	300	98.3
1982	843	99.9	679	7.8	300	98.7
1983	1127	99.7	1034	2.4	299	100.0
1984	781	99.9	851	3.8	201	99.0
1977-84	6212	99.8	6240	5.0	1661	99.9
1993	650	99.7	632	52.4	0	-
1994	450	99.6	545	69.4	0	-
1995	225	100.0	274	75.5	100	100.0
1993-95	1325	99.7	1451	63.1	100	100.0
<i>Henneguya</i>						
1978	0	-	0	-	188	54.8
1979	175	0.0	174	0.6	211	75.8
1980	1330	0.0	1165	0.6	200	71.5
1981	1181	0.0	1336	0.5	300	72.7
1982	0	-	0	-	300	63.3
1983	0	-	0	-	299	58.5
1984	0	-	0	-	201	65.7
1978-84	2686	0.0	2675	0.6	1699	66.0
1993	650	0.0	632	18.7	0	-
1994	450	2.0	545	23.4	0	-
1995	225	0.0	274	19.0	100	75.0
1993-95	1325	0.7	1451	20.6	100	75.0

sockeye salmon (Table 2). No significant annual variability in allele frequency was observed at any locus. The mean pairwise distance between stocks was 0.28 (range 0.17 to 0.42), and the distance between Sproat Lake and Great Central Lake stocks was 0.17.

Minisatellite DNA

Although three probes were used to examine variation at minisatellite DNA in Sproat and Great Central Lake sockeye salmon, a significant difference between stocks was observed only with AluI-

restricted genomic DNA hybridized with Ssa1 (Table 3). The distance between these two stocks was 0.50.

Microsatellite DNA

Marked differences in allele frequencies were observed among stocks at the Omy77 locus ($P < 0.001$), with the frequency of allele 1 ranging from 0.490 in Sproat Lake sockeye salmon to 0.008 in Henderson Lake sockeye salmon (Table 4). Conversely, the frequency of allele 4 was 0.223 in Sproat Lake sockeye salmon, but 0.556 in Henderson

Table 2 Allele frequencies of the 100 allele at the PGM-1, PGM-2, and PGDH loci for Barkley Sound sockeye salmon. Results have been adapted from Wood et al. (1994). N is the number of fish sampled.

Year	Sproat Lake		Great Central Lake		Henderson Lake	
	N	Freq.	N	Freq.	N	Freq.
PGM-1						
1983	132	0.617	111	0.761	138	0.964
1990	50	0.570	99	0.747	0	-
1983-90	82	0.605	210	0.752	138	0.964
PGM-2						
1983	182	0.799	136	0.879	149	0.977
1990	650	0.840	99	0.383	0	-
1983-90	232	0.808	235	0.862	149	0.977
PGDH						
1983	183	0.850	136	0.915	104	1.00
1990	50	0.880	100	0.900	0	-
1983-90	233	0.856	236	0.909	104	1.00

Table 3 Allele frequencies at the Ssa1 and Ssa-A34 loci and mean band counts at 12 DNA fragment intervals for the probe OtsPBS-1 for Sproat Lake and Great Central Lake sockeye salmon. Results have been adapted from Beacham et al. (1995). Genomic DNA was restricted with either AluI or HaeIII before hybridization with Ssa1. Sample sizes range from 34-37 fish sampled for Sproat Lake and 41-46 fish for Great Central Lake.

Allele/Band	Sproat Lake	Great Central Lake
Ssa1 (AluI)		
1	0.632	0.370
2	0.132	0.315
3	0.235	0.315
Ssa1 (HaeIII)		
1	0.786	0.707
2	0.186	0.283
3	0.028	0.010
Ssa-A34		
1	0.500	0.565
OtsPBS-1		
1	0.00	0.05
2	0.14	0.41
3	0.30	0.29
4	0.03	0.02
5	0.05	0.12
6	0.03	0.00
7	0.00	0.12
8	0.05	0.05
9	0.08	0.05
10	0.03	0.05
11	0.84	0.68
12	0.05	0.10

Table 4 Allele frequencies at the Omy77, Ots100, Ots3, and Ots103 microsatellite loci for Barkley Sound sockeye salmon. Results for Omy77 and Ots100 have been adapted from Nelson and Beacham (in prep.). Allele sizes at Omy77 were: 91-96 bp (1), 97-99 bp (2), 100-102 bp (3), 103-106 bp (4), 107-109 bp (5), 110-112 bp (6), 113-115 bp (7), and 116-121 bp (8). Allele sizes at Ots100 were: 129-152 bp (1), 153-156 bp (2), 157-161 bp (3), 162-166 bp (4), 167-179 bp (5), 180-184 bp (6), 185-187 bp (7), 188-191 bp (8), and 192-205 bp (9). Allele sizes at Ots3 were: 74-75 bp (1), 76-87 bp (2), 88-90 bp (3), 91-92 bp (4), 93-94 bp (5), 95-98 bp (6), 99-100 bp (7), and 101-106 bp (8). Allele sizes at Ots103 were: 130-167 bp (1), 168-171 bp (2), 172-175 bp (3), 176-179 bp (4), 180-183 bp (5), 184-187 bp (6), 188-191 bp (7), 192-195 bp (8), 196-199 bp (9), and 200-227 bp (10). N is the number of fish sampled.

Stock	Year	N	1	2	3	4	5	6	7	8	9	10
<u>Omy77</u>												
Sproat Lake	1987	78	0.481	0.013	0.128	0.224	0.058	0.064	0.000	0.032		
	1990	91	0.467	0.016	0.143	0.231	0.022	0.060	0.011	0.049		
	1992	95	0.522	0.011	0.121	0.216	0.042	0.037	0.000	0.052		
	1987-92	264	0.490	0.013	0.131	0.223	0.040	0.053	0.004	0.046		
Great Central Lake	1987	89	0.197	0.000	0.247	0.371	0.000	0.017	0.135	0.034		
	1990	98	0.168	0.020	0.240	0.372	0.010	0.077	0.077	0.036		
	1992	116	0.215	0.000	0.224	0.375	0.004	0.065	0.065	0.052		
	1987-92	303	0.194	0.007	0.236	0.373	0.005	0.054	0.089	0.041		
Henderson Lake	1988	97	0.005	0.000	0.289	0.567	0.000	0.134	0.000	0.005		
	1993	94	0.016	0.000	0.330	0.569	0.000	0.074	0.011	0.000		
	1995	114	0.004	0.000	0.298	0.561	0.004	0.096	0.013	0.022		
	1988-95	305	0.008	0.000	0.305	0.566	0.002	0.102	0.008	0.010		
<u>Ots100</u>												
Sproat Lake	1987	51	0.078	0.020	0.284	0.176	0.020	0.343	0.059	0.000	0.020	
	1990	76	0.047	0.013	0.283	0.178	0.033	0.408	0.020	0.007	0.013	
	1992	87	0.086	0.011	0.322	0.155	0.023	0.328	0.040	0.011	0.022	
	1987-92	214	0.069	0.014	0.299	0.168	0.025	0.360	0.037	0.007	0.019	
Great Central lake	1987	91	0.011	0.055	0.341	0.077	0.060	0.225	0.088	0.049	0.093	
	1990	99	0.010	0.020	0.343	0.071	0.071	0.242	0.076	0.056	0.111	
	1992	118	0.012	0.025	0.403	0.059	0.047	0.237	0.047	0.021	0.148	
	1987-92	308	0.011	0.032	0.365	0.068	0.058	0.235	0.068	0.041	0.120	
Henderson Lake	1988	93	0.016	0.032	0.548	0.145	0.049	0.145	0.022	0.027	0.016	
	1993	70	0.000	0.007	0.479	0.136	0.100	0.236	0.021	0.029	0.007	
	1995	118	0.000	0.013	0.504	0.157	0.055	0.237	0.013	0.008	0.012	
	1988-95	281	0.006	0.018	0.512	0.148	0.064	0.206	0.018	0.020	0.012	
<u>Ots3</u>												
Sproat Lake	1990	44	0.114	0.011	0.568	0.000	0.239	0.011	0.057	0.000		
	1992	46	0.109	0.000	0.587	0.011	0.272	0.000	0.043	0.000		
	1990-92	90	0.111	0.006	0.578	0.006	0.256	0.006	0.050	0.000		
Great Central Lake	1990	87	0.121	0.006	0.391	0.029	0.362	0.011	0.080	0.000		
	1992	48	0.135	0.010	0.333	0.010	0.469	0.000	0.031	0.001		
	1990-92	135	0.126	0.007	0.370	0.022	0.400	0.007	0.063	0.004		
Henderson Lake	1995	94	0.112	0.026	0.080	0.000	0.527	0.027	0.229	0.000		
<u>Ots103</u>												
Sproat Lake	1990	43	0.197	0.012	0.000	0.023	0.012	0.035	0.058	0.302	0.256	0.105
	1992	48	0.136	0.010	0.021	0.010	0.042	0.021	0.073	0.271	0.313	0.104
	1990-92	91	0.164	0.011	0.011	0.016	0.027	0.027	0.066	0.286	0.286	0.104
Great Central lake	1990	92	0.092	0.005	0.043	0.027	0.082	0.076	0.168	0.255	0.158	0.092
	1992	48	0.061	0.042	0.000	0.021	0.021	0.125	0.125	0.250	0.167	0.146
	1990-92	140	0.081	0.018	0.029	0.025	0.031	0.093	0.154	0.254	0.161	0.129
Henderson Lake	1995	96	0.031	0.000	0.016	0.042	0.078	0.052	0.063	0.359	0.224	0.145

Lake sockeye salmon, the dominant allele in the stock. Initially, for the three stocks, a significant annual difference in allele frequencies was observed for Great Central Lake sockeye salmon ($P=0.02$), but after correction of the significance level to account for the number of simultaneous tests

($0.05/10=0.005$), the difference was not significant. Significant differences in allele frequencies among stocks were also observed at the Ots100 locus ($P<0.001$) (Table 4). No significant annual variation in allele frequencies, even before correction of the significance level, was observed at the Ots100 locus

for any stock. There were marked differences among stocks in the allele frequencies at the Ots3 locus, with the frequency of allele 3 ranging from 0.58 to 0.08 among stocks (Table 4). No significant annual variability in allele frequencies was observed. Finally, at the Ots103 locus, substantial variation in allele frequencies among stocks was observed ($P < 0.001$) (Table 4). Initial significant annual variability was observed in Great Central Lake sockeye salmon ($P = 0.02$), but as with Omy77 locus, the difference was not significant after consideration of the number of tests conducted. The mean pairwise distance between stocks was 0.66 (range 0.53-0.92). Analysis of microsatellite DNA variation indicated that there was substantial differentiation of allele frequencies among stocks relative to the annual variability within stocks.

Variation Among and Within Stocks

In order to compare the relative variation among and within stocks, we used the distance metric previously outlined for two sets of comparisons. Pairwise distances between stocks were determined, as were pairwise differences between sampling years within stocks. The mean pairwise distance within each stock was calculated. As the utility of a particular set of characteristics for stock identification is a function of both the differentiation among and within stocks, we compared the distance between a pair of stocks with the larger within-stock distance of the pair. The first set of comparisons involved comparing the differences between and within Sproat Lake and Great Central Lake stocks. The second set involved determining the minimum pairwise distance among the three stocks, and comparing it with the larger within-stock distance of the pair. The greatest separation between Sproat Lake and Great Central Lake stocks was obtained with parasite prevalences observed during 1977-84, with microsatellite DNA variation next in separation (Table 5). Although significant annual variation was observed in the prevalence of *Myxobolus* in Great Central Lake

during this period, the magnitude of the difference between the two stocks was about 33 times greater than the within-stock variation of the more variable stock, which suggests that in this case the annual variation was of no practical significance. Conversely, although there was no significant annual variation in allele frequency at the protein-coding loci, there was also little differentiation between the two stocks, so that stock separation was only 2.4 times greater than annual separation (Table 5). The ranking of the different techniques (relative to among- and within-stock separation) indicated that parasite prevalence during 1977-84 resulted in the greatest relative differentiation, and protein electrophoresis resulted in the least relative differentiation.

Estimation of Stock Composition

Three different mixtures were simulated, in which either Sproat Lake, Great Central Lake, or Henderson Lake sockeye salmon predominated in the mixture. The simulations indicated that parasite prevalence during 1977-84 was a very effective method of stock identification, with the estimates of the Great Central Lake component accurate to a mean error of 0.2% and a coefficient of variation (CV) less than 5% (Table 6). The precision of the Sproat Lake and Henderson Lake components was less than that of the Great Central component, primarily due to the inability to distinguish between Henderson Lake sockeye salmon not infected with *Henneguya* and Sproat Lake sockeye salmon. However, parasite prevalences observed during 1977-84 provided the most accurate and precise estimates of stock composition for all techniques investigated (Table 7).

The change in the parasite prevalence of Great Central Lake sockeye salmon observed during 1993-95 resulted in a substantial decline in the precision of the estimated stock compositions (Tables 6, 7). For example, the use of parasite prevalences during 1977-84 to estimate a true contribution of 20% Great Central Lake resulted in estimates with a CV of about 4%, whereas parasite prevalences during 1993-95 resulted in a CV of 28%. The greater uncertainty and increased bias in the estimated stock compositions, particularly when Great Central Lake sockeye salmon predominated in the mixture (Table 6), reduced the effectiveness of parasite prevalence in management of the fishery in the 1990s.

Variation at microsatellite loci provided the most accurate and precise estimates of stock composition of the three methods examined utilizing genetic variation.

The separation observed between Great Central Lake and Sproat Lake sockeye salmon was $D = 0.53$, between Sproat Lake and Henderson Lake fish $D = 0.92$, and between Great Central Lake and Henderson Lake sockeye salmon $D = 0.54$, similar to

Table.5 Mean generalized distance (D) between Sproat Lake and Great Central Lake sockeye salmon stocks, the mean distance among years within stocks, and the ratio of the two distances for three methods of stock identification are indicated.

Method	Between	Within	Ratio
Parasites 1977-84	0.993	0.030	33.10
1993-95	0.417	0.161	2.59
Electrophoresis	0.165	0.069	2.39
Microsatellite DNA	0.528	0.108	4.89

Table 6. Estimated percentage composition of three mixtures of Barkley Sound sockeye salmon for five methods of stock identification. Each mixture of 200 fish was generated 50 times with replacement, and stock compositions of the mixtures estimated by resampling each baseline stock with replacement to obtain a new distribution of parasite prevalence or allele frequencies, with the same sample size in the new distribution as in the original one. For the minisatellite DNA analysis, mixtures evaluated were: (1) 75% Sproat, 25% Great Central, and (2) 25% Sproat, 75% Great Central as data for Henderson Lake sockeye salmon were not available. Standard deviation is in parenthesis.

Method	Sproat	Great Central	Henderson
True %	75.0	20.0	5.0
Parasites 1977-84	75.4 (1.8)	19.8 (0.8)	4.7 (1.4)
1993-95	74.4 (5.6)	18.5 (5.1)	7.2 (2.9)
Electrophoresis	84.3 (12.5)	15.4 (12.7)	0.3 (1.1)
Minisatellite DNA	67.8 (5.4)	32.2 (5.4)	-
Microsatellite DNA	71.6 (3.8)	23.9 (4.5)	4.5 (1.7)
True %	20.0	75.0	5.0
Parasites 1977-84	19.1 (2.0)	75.3 (1.4)	5.6 (1.2)
993-95	13.6 (9.3)	73.2 (11.1)	13.2 (4.4)
Electrophoresis	28.6 (21.9)	71.4 (21.9)	0.0 (-)
Minisatellite DNA	30.2 (6.0)	69.8 (6.0)	-
Microsatellite DNA	19.9 (3.6)	74.7 (4.8)	5.5 (2.2)
True %	10.0	10.0	80.0
Parasites 1977-84	10.6 (3.8)	9.8 (0.5)	79.6 (3.8)
1993-95	9.5 (4.3)	10.7 (7.1)	79.8 (6.4)
Electrophoresis	23.3 (6.9)	2.3 (3.4)	74.4 (5.4)
Microsatellite DNA	9.5 (2.0)	12.4 (3.4)	78.2 (2.8)

Table 7. Mean bias over all simulated mixtures of Barkley Sound sockeye salmon from Table 6 and mean coefficient of variation (CV) for stocks comprising 5, 10, 20, 75, and 80% mixtures.

	Mean Bias	Mean CV for stock at (%)				
		5	10	20	75	80
Parasites 1977-84	0.4	26.0	21.5	7.0	2.2	4.8
1993-95	2.5	73.0	57.0	36.0	11.2	8.0
Electrophoresis	7.0	22.0	51.5	86.5	23.0	6.8
Minisatellite DNA	6.2	-	-	25.8*	7.7	-
Microsatellite DNA	1.5	39.0	24.2	18.4	5.9	3.6

* CV at 25% of total mixture.

the magnitude of the difference between Great Central Lake and Sproat Lake fish. Accordingly, estimation of the Henderson Lake component of the simulated mixtures was the most precise with the least amount of bias (Table 6). The mean CV of a stock comprising 20% of the mixture was about 20% using microsatellite loci variation, greater than 7% observed with parasite prevalence during 1977-84, but less than all other techniques evaluated (Table 7).

Variation at minisatellite loci was available only for Sproat Lake and Great Central Lake sockeye salmon. Separation between these stocks was sufficient to provide estimates of similar precision to those observed with microsatellite loci, but accuracy was lower (Table 7). A characterization of variation for Henderson Lake sockeye salmon is required before more definitive conclusions concerning the utility of minisatellite DNA variation can be made.

Although significant differences in allele frequencies were observed among the three stocks for three protein-coding loci, and no significant differences were observed between sampling years within stocks, the level of differentiation observed

among the three stocks was insufficient to provide reliable estimates of stock composition. Stocks comprising 20% or less of the mixture could not be reliably identified as being present (Table 6). The high levels of uncertainty associated with the estimated stock compositions, coupled with the bias observed in the compositions, precluded the use of protein electrophoresis as a viable method of estimating stock compositions of Barkley Sound sockeye salmon.

DISCUSSION

Parasites have been demonstrated to be quite useful in studies of population structure in marine fish (Kabata 1963; MacKenzie 1983; Williams et al. 1992), and in their application to Pacific salmon stock identification and migration (Margolis 1963; Bailey et al. 1988; Groot et al. 1989; Wood et al. 1989). Application to stock composition of adult salmon is necessarily restricted to those parasite species that are long lived, which in the case of sockeye salmon would be up to five yr. If differences in prevalence of

parasites can be found among local stocks of sockeye salmon, Konovalov (1995) suggested that there was hardly a more efficient or inexpensive method of stock identification. However, the application in the Barkley Sound fishery indicated that parasite prevalence worked very well for about 10 yr, but a subsequent change in the parasite prevalence resulted in the application becoming less reliable. Temporal changes in parasite prevalences have been recorded in marine fish (MacKenzie, 1987), some over a period of less than five yr (Nagasawa et al., 1988). The results of our study indicated that there was statistically significant but limited annual variation in the prevalence of both parasites during 1977-84, but marked annual variation in the prevalence of *Myxobolus* in Great Central Lake sockeye salmon in the 1990s.

Management of the fishery in Barkley Sound required that an accurate and precise method of stock identification of the catch be available, and the prevalence of the parasites *M. arcticus* and *H. salminicola* provided an effective method of stock identification in the late 1970s and the 1980s (Steer et al. 1986, 1988). Unfortunately, the change in the prevalence of these two parasites in Great Central Lake in the 1990s resulted in poorer discrimination among the stocks, with the resultant uncertainty in the estimates large enough to result in the cessation of the use of parasite prevalence as a method of stock identification in this fishery. The causes of the change in parasite prevalence in Great Central Lake sockeye salmon are uncertain, but may include an increase in abundance of the oligochaete alternate hosts of the myxosporeans (*Stylodrilus heringianus* in the case of *M. arcticus*; Kent et al. 1993) as a result of long-term fertilization of the lake; an increase in spawning escapements of sockeye salmon, and possibly other salmonids, resulting in progressively increasing abundance of the myxosporean spores in the lake; or an increased infection of sockeye salmon smolts in the Somass River after emigration from Great Central Lake (see Quinn et al. 1987), resulting in returns to Great Central Lake of progressively increasing numbers of *M. arcticus*-infected adult sockeye salmon over time. It is clear that in applications where parasites have been used to estimate stock compositions in Pacific salmon, periodic sampling of the baseline stocks should be conducted to confirm the utility of the technique.

Microsatellite DNA consists of tandemly arrayed repeated nucleotide sequences of two, three, or four nucleotides, flanked by regions of non-repetitive DNA (Tautz 1989, Weber and May 1989). Microsatellites have a number of attributes that are useful in studies of population structure and stock identification, including their high levels of variation, alleles show codominant Mendelian inheritance, and only small

amounts of tissue (such as scales) are required for analysis (O'Reilly and Wright 1995). Microsatellite loci have been shown to be quite useful in determination of population structure of salmonids (Angers et al. 1995; McConnell et al. 1995). The four microsatellite loci examined in our study showed significant differentiation among stocks, but no significant annual variation in allele frequencies, with samples spanning a range of six to eight yr. The two features of substantial variation in allele frequencies among populations and annual stability of allele frequencies resulted in the highest levels of accuracy and precision of estimated stock compositions of the three genetic methods evaluated.

Minisatellite DNA is similar to microsatellite DNA in that it consists of tandemly arrayed repeated nucleotide sequences, but the repeated sequences are longer, perhaps up to 75 nucleotides (Jarman and Wells 1989), with the alleles consequently larger in size than at microsatellite loci. Substantial differentiation at minisatellite loci has been observed among salmonid stocks, and application of variation at these loci can be an effective method of salmonid stock identification (Miller et al. 1996; Beacham et al. 1996). However, the larger allele size at minisatellite loci usually requires that variation be analyzed by Southern blotting techniques, whereas variation at microsatellite loci is analyzed via the polymerase chain reaction, which can be substantially faster and cheaper than Southern blotting. In our study, variation at minisatellite loci for Henderson Lake sockeye would have to be analyzed before the utility of applying variation at minisatellite loci for stock identification of Barkley Sound sockeye salmon could be fully evaluated.

There have been many applications of using protein electrophoresis for stock identification of Pacific salmon (eg. Utter et al. 1987), and specifically for sockeye salmon (Wood et al. 1989). Although 35 loci were screened for the Barkley Sound stocks, there was sufficient variation at only three loci to be of use in stock differentiation and identification. However, not all loci that are known to be polymorphic in sockeye salmon have been analyzed in our study, as they have not been analyzed for Barkley Sound sockeye salmon stocks. However, the low level of differentiation observed at protein-coding loci that have been analyzed for the Barkley Sound stocks indicated that protein electrophoresis was unlikely to be a viable method of stock identification for this fishery.

Two alternate methods of stock identification of Barkley Sound sockeye salmon have been explored. Scale pattern analysis has been reported to be an effective method of stock identification of some sockeye salmon stocks (Cook and Lord 1978; Marshall et al. 1987). However, the annual variability

in the characters used in stock discrimination usually requires that samples from contributing stocks be collected and analyzed annually (Wood et al. 1989), with age-specific functions usually employed (Bilton and Messinger 1975). An analysis of scale pattern variation in Barkley Sound sockeye salmon did not reveal variation that could be consistently used to provide reliable discrimination among the stocks (K. D. Hyatt, Pac. Biol. Stat., Nanaimo, pers. comm.). Another stock identification method involved an examination of variation in mitochondrial (mtDNA) DNA, as the cytochrome b sequence in mtDNA has been reported to differ among sockeye salmon populations (Bickham et al. 1995). For both Sproat Lake and Great Central Lake sockeye salmon, the cytochrome b and ND1 regions of mtDNA were amplified via the polymerase chain reaction (PCR), the amplified products restricted with *ApaI*, *BfaI*, *BseEII*, and *RsaI*, and the DNA fragments were separated electrophoretically. The observed frequency of the haplotypes did not differ for Sproat Lake and Great Central Lake sockeye salmon (C. C. Wood, Pac. Biol. Stat., Nanaimo, pers. comm.), rendering variation at these segments of mtDNA of little value in applications to stock identification of Barkley Sound sockeye salmon.

The choice of a particular stock identification method is dependent upon the stock resolution required in the application, the accuracy and precision that is required of the estimates, technical capability of laboratory procedures, and cost of the analysis. For Barkley Sound sockeye salmon, the cost of obtaining samples from the commercial fishery would be highest for the parasite and electrophoretic applications, as whole fish would be required to be purchased, compared with minimal scale, blood, or fin samples required for minisatellite or microsatellite analysis. However, the laboratory procedures for parasite and electrophoretic applications are less complex (and hence less expensive and require less technical training) than for the DNA applications, particularly the Southern blotting approach generally used to survey variation at minisatellite loci. For applications that are currently available to managers of the Barkley Sound sockeye salmon fishery, microsatellite DNA would be the preferred choice, given the minimal additional costs of obtaining samples, the reliability of the estimates, and the relative ease and cost of laboratory analysis.

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Estimating Salmon Escapement using Area-Under-the-Curve, Aerial Observer Efficiency, and Stream-Life Estimates: The Prince William Sound Pink Salmon Example

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Accurate estimates of Pacific salmon spawners are needed to set spawning escapement goals and regulate harvests. Estimating the number of pink salmon *Oncorhynchus gorbuscha* spawning in Prince William Sound, Alaska, is difficult since annual runs have ranged between 2.2 million and 19.6 million and spawning occurs in over one thousand individual freshwater systems. Escapement monitoring is accomplished by surveying a collection of 208 index creeks several times over a period of weeks from fixed wing aircraft. Unadjusted survey counts are used to monitor escapements during the commercial fishing season, while estimates of the total number of spawners are calculated after the season using area-under-the-curve methods. We examined the accuracy of area-under-the-curve estimates by using information obtained on creeks with intertidal weirs: 3 creeks in 1990, 8 creeks in 1991, and 7 creeks in 1992. Aerial observer efficiency and stream-life values, calculated for each study creek each year of the study, used in conjunction with aerial observations, produced pink salmon escapement estimates that were on average within 10% of weir counts for these same creeks. Currently used methods, using only the area-under-the-curve and a constant stream life of 17.5 days, produced escapement estimates that were on average less than 50% of the corresponding weir counts. The use of a correction for aerial observer efficiency provided the greatest improvement in escapement estimates, although, the adjustment for stream life also provided substantial improvement. An investigation of the effect of survey frequency on area-under-the-curve estimates indicated that accuracy deteriorated when the survey interval exceeded 7 days.



INTRODUCTION

The annual wild pink salmon *Oncorhynchus gorbuscha* run to Prince William Sound, Alaska, has ranged between 2.2 million and 19.6 million since 1977 (Morstad et al. 1996). These salmon are harvested within nine commercial fishing districts and spawn in over one thousand freshwater systems within Prince William Sound. To ensure the continued viability of the run, district spawning goals have been set and spawning populations have been monitored by aerial surveyors in a collection of 208 index creeks (Fried 1994). Although unadjusted survey counts are used to monitor spawning escapements during the fishing season, estimates of the total number of spawners within each surveyed creek are calculated after the season using area-under-the-curve calculations (e.g. English, Bocking, and

Irvine 1992; Johnson and Barrett 1988; Pirtle 1977).

The accuracy of total escapement estimates based on aerial surveys depends upon the number of observations made and their distribution throughout the run, the accuracy of counts (observer efficiency), and the amount of time salmon entering the survey area were visible to observers (stream life). In this paper, we report results of studies conducted in 1990-1992 on 10 creeks with intertidal weirs. Our results indicate that survey frequency was adequate, that aerial observers tend to undercount, and that stream life, while quite variable, appears to be less than the 17.5 day estimate currently used for Prince William Sound. These findings show that current methods used to estimate pink salmon spawning populations in Prince William Sound provide values that are biased low.

MATERIALS AND METHODS

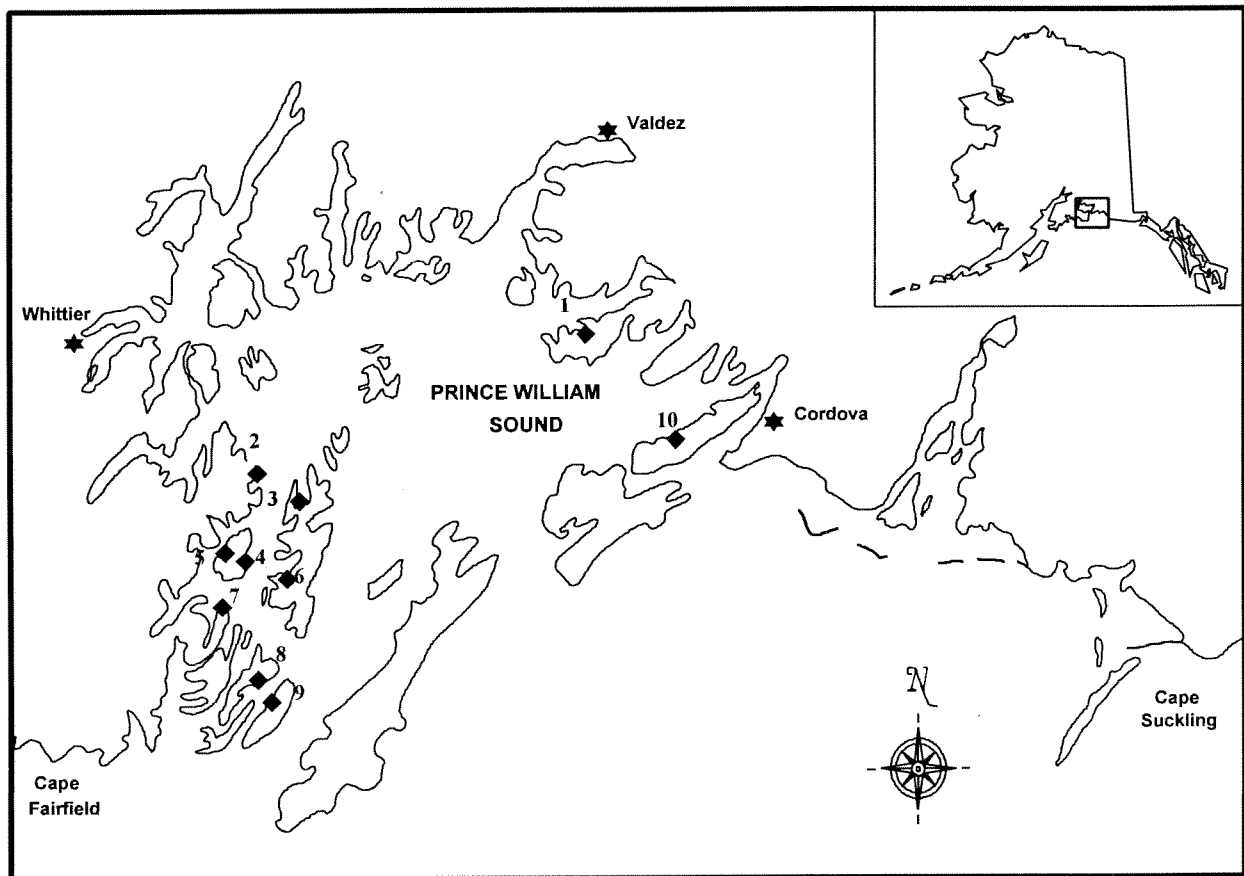
Weir Operation

Weirs were installed on pink salmon creeks in Prince William Sound during 1990-1992 to enumerate spawning escapement. All weirs were installed in the intertidal zone because approximately 75% of Prince William Sound pink salmon spawn within this area (Helle et al. 1964). This appears to have been the first time that intertidal weirs were used in Alaska. Four weirs were used in 1990, while 10 were used in 1991 and 1992 (Fig. 1). The study creeks included two moderate sized creeks in the eastern Sound (Irish and Hawkins creeks) and eight small to medium creeks in western Prince William Sound (Loomis, Totemoff, Chenega, Point Countess, O'Brien, Hayden, Herring, and Cathead creeks). Salmon were visually counted as they swam upstream through a

small opening in the weir made by raising a few pickets. No live boxes were used. Salmon were passed through the weir several times each day in response to tides and salmon movement patterns. Total escapement into each creek was defined as the sum of daily counts of pink salmon passed upstream through the weir.

Daily ground surveys were made above each weir to enumerate pink salmon that had recently died. The tail was removed from each dead salmon, and its carcass was thrown onto the streambank to avoid counting an individual salmon more than once. The combination of total weir live counts and total ground survey dead counts by day allowed the number of live pink salmon in the creek to be estimated on a daily basis. We estimated the number alive ($\hat{L}_j$) for day j of the run by,

Fig. 1 Location of creeks (filled diamonds) used to examine pink salmon aerial escapement estimation methodology, Prince William Sound, Alaska, 1990-1992. Stream identifiers are (1) Irish Creek, (2) Loomis Creek, (3) Herring Creek, (4) Chenega Creek, (5) Totemoff Creek, (6) Cathead Creek, (7) Point Countess Creek, (8) O'Brien Creek, (9) Hayden Creek, (10) Hawkins Creek.



$$\hat{L}_j = \sum_{k=1}^j (W_k - D_k), \quad (1)$$

where W_k was the number of live pink salmon counted through the weir and D_k was the number of newly dead pink salmon on day k . Counts of live pink salmon were also made during ground surveys.

During periods of high creek flows, caused by heavy rains, weir pickets had to be raised to avoid weir destruction, and ground surveys often could not be conducted. In these instances, missing weir ($\hat{W}$) and ground survey dead ($\hat{D}$) counts were estimated by,

$$\hat{W}_j = [(G_j - G_{(j-1)}) / O] + D_j, \text{ and} \quad (2)$$

$$\hat{D}_j = D_{next} / m, \quad (3)$$

where G_j was the number of live pink salmon counted during the ground survey on day j ; O was the slope of the linear regression, fitted through the origin, of the estimated number alive ($\hat{L}_j$) during ground survey counts for each day of the season prior to the day of the first missing count; D_{next} was the first daily dead count after the period to be interpolated; and m was the number of consecutive days of missed observations.

In designing the project, we assumed that (1) errors made in estimating pink salmon past the weirs due to breaches in the weir or errors in counting were small, and (2) errors made in counting dead salmon above weirs due to removals by predators or errors in counting were also small. If both assumptions were valid, we expected the total weir count of live pink salmon to equal the total ground survey count of dead pink salmon within each creek. If the ratio of weir live to ground survey dead counts was not close to one, we assumed that at least one of these assumptions had been violated and that stream life and aerial observer efficiency estimates based on these data were not accurate.

Aerial surveys were flown at least weekly, weather permitting, from mid-June to mid-September by biologists stationed in Cordova. Four observers were used each year.

Escapement Estimation

Three components are required to estimate salmon escapements using visual counts: (1) counts collected systematically throughout the time salmon are present in the study area; (2) an estimate of observer efficiency; and (3) an estimate of the average time an individual salmon remains in the

survey area, commonly called stream life. The area-under-the-curve is a commonly applied method of estimating salmon escapement (E) when periodic visual counts are used (e.g. English, Bocking, and Irvine 1992, Johnson and Barrett 1988),

$$\hat{E} = \frac{\hat{A}}{\hat{S}\hat{B}}, \quad (4)$$

where $\hat{A}$ is an estimate of the area under the escapement curve, $\hat{S}$ is an estimate of stream life, and $\hat{B}$ is an estimate of observer efficiency.

Area-under-the-curve (A) was estimated using a trapezoidal approximation procedure similar to that described in English, Bocking, and Irvine (1992),

$$\hat{A} = \sum_{i=2}^n \frac{(t_i - t_{i-1})(c_i + c_{i-1})}{2}, \quad (5)$$

where t_i was the date and c_i was the number of salmon observed for the i^{th} survey. Attempts were made to initiate surveys prior to the presence of pink salmon in the creek. When pink salmon were present for the first survey, the parameter A prior to the first survey was estimated as,

$$\hat{A}_{first} = \frac{c_1 \hat{S}}{2}. \quad (6)$$

We also made an effort to continue surveys until all pink salmon had died. When this was not possible, we estimated A after the final survey as,

$$\hat{A}_{last} = \frac{c_1 \hat{S}}{2}. \quad (7)$$

Stream life (S), the residence time or survey life of pink salmon within each creek, was estimated as the mean number of days which elapsed between creek entry and post-spawning death,

$$\hat{S} = \frac{\sum_{j=1}^n \hat{L}_j}{\sum_{j=1}^n W_j}. \quad (8)$$

Calibration regression was used to estimate observer efficiency (Neter, Wasserman, and Kutner 1990). We assumed that (1) the relationship between the estimated number of live pink salmon in a creek (independent variable) and survey counts (dependent variable) was linear, and (2) aerial observers would

not see salmon in a creek when none were present (i.e. the fitted line passed through the origin). Observer efficiency (B) was estimated by the slope of the linear fit, constrained to pass through the origin, of survey counts regressed against daily estimates ($\hat{L}_j$).

Evaluation of Survey Frequency

An evaluation of the effect of survey frequency on area-under-the-curve estimates was undertaken using a simple systematic simulation and our estimates of the number of live salmon above the weirs ($\hat{L}_j$; equation 1). The simulation assumed (1) the number of live salmon above the weir was known and (2) the first survey occurred during the first week salmon were in the creek. The simulation was initiated by selecting a survey frequency (F) and a day during the first week salmon were present in the creek (j_1 , where j_1 was in the range of 1 to 7). The second day (j_2) was selected by

$$j_2 = j_1 + F, \quad (9)$$

and all remaining days were selected at intervals of F . The number of live salmon above the weir ($\hat{L}_j$) for each selected j was then used to estimate area-under-the-curve using equations 5, 6, and 7. Seven simulations were performed for each $F \geq 0$, one simulation for each day of the first week that salmon were present in the stream. The number of

simulations for $F < 7$ was equal to F . Average area-under-the-curve for a survey frequency (F) was estimated as the mean of the simulated estimates.

Comparison of Historic Escapement Estimates to Revised Estimates

Total spawning escapement estimates from currently applied methods for each study creek were compared to estimates using the new information obtained from our study. Currently, area-under-the-curve is estimated using the trapezoidal approximation method described previously, and total escapement estimates are made using a stream life of 17.5 days and no observer efficiency adjustment. We used the same method to estimate area-under-the-curve, but used our estimates of creek-specific stream life and observer efficiency to estimate escapements. Escapement estimates were expressed as a percent of the corresponding weir count to determine the incremental effect of each modification.

RESULTS

Weir Operation

While 24 creek-year data sets were obtained from 10 different creeks over the three years of the study, we chose to use only 18 data sets from 9 different creeks (Table 1). Three data sets were not used because the total number of dead pink salmon far

Table 1. Aerial observer, stream life, and observer efficiency data collected for spawning pink salmon in study creeks with weirs and daily ground surveys, Prince William Sound, Alaska, 1990-1992.

weirs and daily ground surveys, Prince William Sound, Alaska, 1990-1992.									
	Total Weir	W/D	Number of	Days Between Surveys				Observer Efficiency	
Stream Name	Count	Ratio ^a	Surveys	Average	Min	Max	A ^b	Stream Life	b ^c
<u>1990</u>									
Irish Creek	44,900	0.97	18	4.7	2	7	474,010	18.1	0.499
Herring Creek	4,927	0.97	12	6.0	3	9	43,896	11.4	0.888
Cathead Creek	7,971	1.01	12	5.1	2	9	58,305	9.8	0.825
<u>1991</u>									
Irish Creek	95,034	1.00	17	5.1	1	16	397,733	16.0	0.177
Loomis Creek	20,315	1.08	10	5.3	3	8	51,741	6.8	0.322
Chenega Creek	49,769	0.96	5	8.0	5	10	140,680	10.2	0.234
Pt. Countess Creek	15,028	1.06	10	5.3	3	8	61,192	9.7	0.456
Hayden Creek	18,372	1.12	10	5.3	2	8	73,947	11.7	0.485
Herring Creek	13,022	0.95	10	5.3	2	8	72,337	11.8	0.371
Cathead Creek	9,629	1.10	10	5.3	2	8	23,007	11.0	0.246
Hawkins Creek	40,433	0.95	9	8.8	4	14	236,768	15.6	0.406
<u>1992</u>									
Irish Creek	8,208	0.94	14	5.2	2	9	117,169	21.5	0.554
Loomis Creek	3,845	1.21	10	7.4	1	15	5,939	9.6	0.177
Totemoff Creek	8,428	1.09	9	7.4	6	9	61,675	14.7	0.535
Chenega Creek	10,658	1.21	6	7.6	5	11	38,722	14.2	0.245
Hayden Creek	2,708	1.08	9	7.1	6	8	8,337	9.0	0.359
Herring Creek	911	1.24	9	7.4	1	11	5,625	13.7	0.388
Cathead Creek	3,937	1.22	9	7.4	1	11	27,450	11.9	0.685

^a W/D ratio is the ratio of total weir count to total dead count.

^b Area-under-the-curve estimate.

^c Slope of the regression of aerial counts on estimated number of salmon above the weir.

exceeded the total number of live pink salmon counted through weirs (Totemoff Creek, 1990; Totemoff and O'Brien Creeks, 1992). Three other data sets were excluded because large amounts of weir and ground survey data were missing due to several high creek flow events (O'Brien, Point Countess, and Hawkins Creeks, 1992).

For the 18 creek-year data sets used in our study, escapements ranged from 95,034 (Irish Creek, 1991) to 911 (Herring Creek, 1992) pink salmon (Table 1). The ratio of weir live to ground survey dead counts ranged from 0.94 (Irish Creek, 1992) to 1.24 (Herring Creek, 1992). Odd-year escapements in 1991 were greater than even-year escapements in 1990 and 1992 for all creeks retained in the data set for two (Loomis, Chenega, and Hayden Creeks) or three (Irish, Herring, and Cathead Creeks) years. For example, the Irish Creek 1991 escapement of 95,034 pink salmon was more than two times greater than the 1990 escapement of 44,900 pink salmon, and more than 11 times greater than the 1992 escapement of 8,208 pink salmon.

Escapement Estimation

Aerial survey frequency declined from an average of 5 days between surveys in 1990, to 6 days in 1991,

and to 7 days in 1992 (Table 1). Area-under-the-curve estimates, unadjusted for either observer efficiency or stream life, did not always show trends similar to those of weir counts for all study streams. For example, total weir counts for Irish Creek in 1990 and 1991, and Cathead Creek in 1990, 1991, and 1992 increased while area-under-the-curve estimates decreased.

Our simulation results on the effect of survey frequency on area-under-the-curve estimates indicated that accuracy and precision decreased as surveys became less frequent (Table 2; Fig. 2). It appears that a survey frequency of 5-7 days would provide the best allocation of survey effort for Prince William Sound pink salmon.

Stream-life estimates for the 18 creek-year combinations ranged from 6.8 days (Loomis Creek, 1991) to 21.5 days (Irish Creek, 1992; Table 1 and Fig. 3). The median stream-life value for all 18 data sets was 11.6 and the mean was 12.6 days. While pink salmon stream life was shorter in 1991 than 1992 for five (Irish, Herring, Cathead, Loomis, Chenega, and Herring Creeks) of the six creeks retained in the data set both these years, only one (Irish Creek) of the three creeks retained in the data set all three years had a shorter stream life in 1991 than in either 1990 or 1992.

Table 2. Average error in area-under-the-curve estimates for simulated systematic pink salmon escapement surveys.

Stream Name	Average Error ^a in Area-Under-The-Curve Estimates ^b												
	Number of Days Between Surveys												
	2	3	4	5	6	7	8	9	10	11	12	13	14
1990													
Irish Creek	0.00	0.00	0.00	0.00	0.00	-0.01	-0.01	-0.02	-0.02	-0.01	-0.06	0.10	0.01
Herring Creek	0.00	-0.02	-0.01	-0.01	0.06	0.00	0.06	0.14	0.19	0.38	-0.13	0.29	0.74
Cathead Creek	0.00	-0.01	-0.02	-0.04	-0.04	-0.07	-0.07	-0.08	-0.01	-0.14	-0.18	0.06	0.13
1991													
Irish Creek	0.00	0.00	0.00	0.00	-0.01	-0.01	0.02	0.02	0.00	0.03	-0.03	-0.01	0.06
Loomis Creek	-0.04	-0.05	-0.04	0.02	-0.05	0.04	0.17	0.25	-0.30	0.07	0.38	-0.51	-0.40
Chenega Creek	0.00	-0.01	-0.01	-0.02	0.11	0.09	0.24	0.39	0.26	0.09	0.32	0.31	-0.25
Pt. Countess Creek	-0.02	-0.02	-0.01	-0.02	0.01	0.03	0.24	0.38	0.26	0.10	0.31	-0.25	-0.11
Hayden Creek	0.00	-0.01	-0.01	-0.02	-0.02	-0.08	-0.09	-0.12	-0.06	-0.11	-0.12	0.04	0.01
Herring Creek	0.00	0.00	-0.02	-0.02	-0.02	-0.02	-0.02	0.17	0.03	-0.02	0.19	0.29	0.26
Cathead Creek	-0.03	-0.05	-0.04	-0.07	-0.09	-0.09	-0.08	0.14	-0.06	0.09	0.08	0.04	-0.34
Hawkins Creek	0.00	0.00	-0.01	-0.01	0.00	0.00	0.00	0.03	-0.01	0.14	0.04	0.05	0.16
1992													
Irish Creek	0.00	0.00	0.00	0.00	-0.01	-0.01	0.04	0.08	-0.05	0.07	0.37	0.23	0.09
Loomis Creek	-0.01	-0.03	-0.07	-0.06	-0.14	-0.07	-0.01	-0.10	0.14	0.05	-0.40	-0.22	-0.02
Totemoff Creek	-0.01	0.00	-0.02	-0.04	-0.04	-0.03	-0.03	-0.06	-0.10	-0.04	-0.12	-0.06	-0.19
Chenega Creek	-0.02	-0.03	-0.06	-0.09	-0.12	-0.11	-0.12	-0.14	0.04	-0.05	-0.04	0.07	0.03
Hayden Creek	-0.02	-0.03	-0.05	-0.07	-0.05	0.02	0.06	-0.08	0.11	-0.34	-0.07	0.15	-0.43
Herring Creek	0.00	-0.01	-0.06	-0.09	-0.06	-0.01	0.02	-0.09	0.04	-0.10	-0.02	0.00	-0.42
Cathead Creek	0.04	0.04	0.07	0.09	0.05	0.08	0.04	-0.05	-0.16	-0.11	-0.19	-0.11	-0.08

^a Average Error is defined as $(\bar{A} - A)/A$ where A is the true area and $\bar{A}$ is the average area from simulations.

^b Underestimate is indicated by a negative sign; all errors greater than or equal to 0.10 are underlined and bold.

Fig. 2 Number of salmon present by day and the results of a systematic simulation of area-under-the-curve estimates for Irish Creek (A and B) and Herring Creek (C and D) in 1990, Prince William Sound, Alaska. Large solid dots indicate the mean of the simulations while the short lines indicate individual simulations.

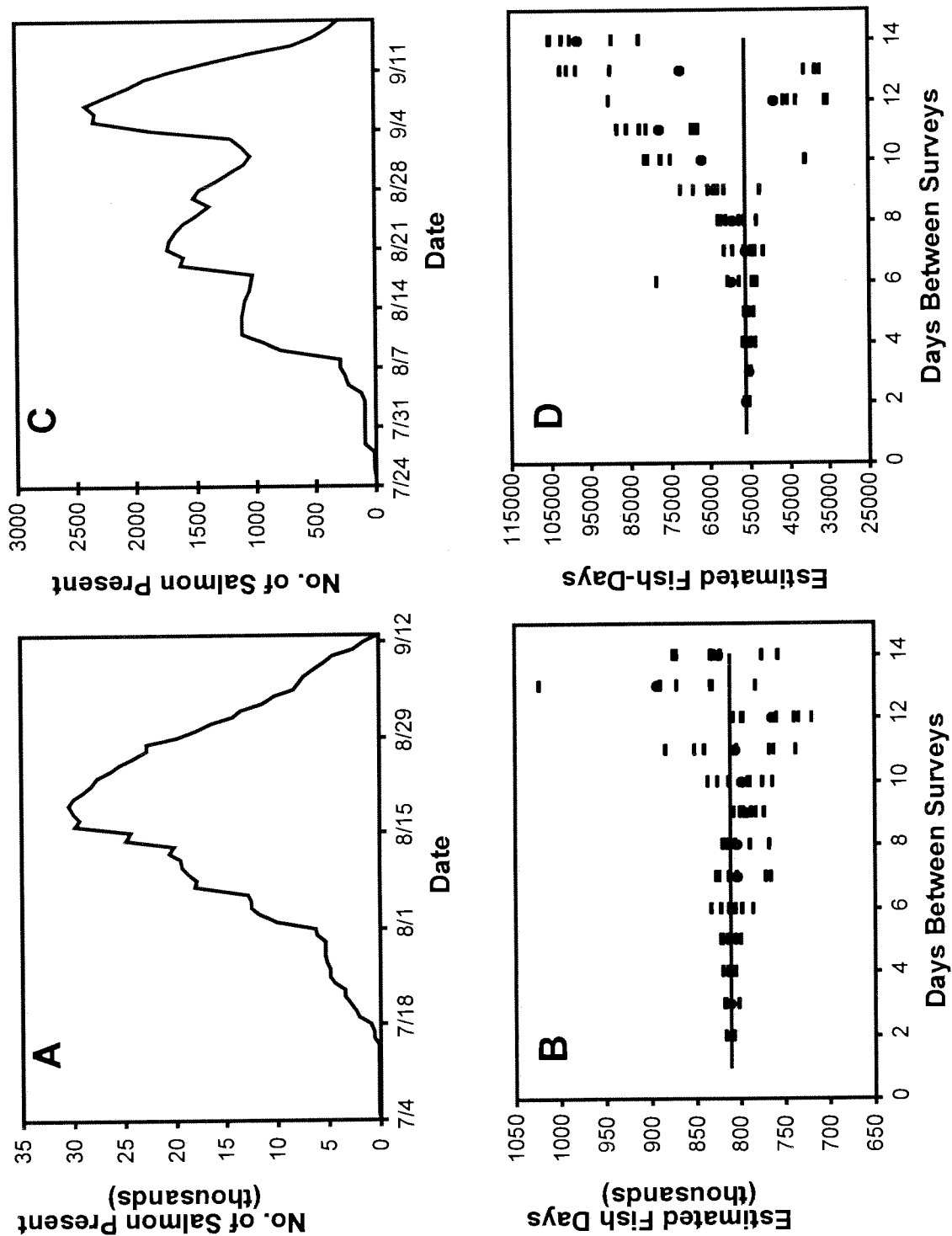
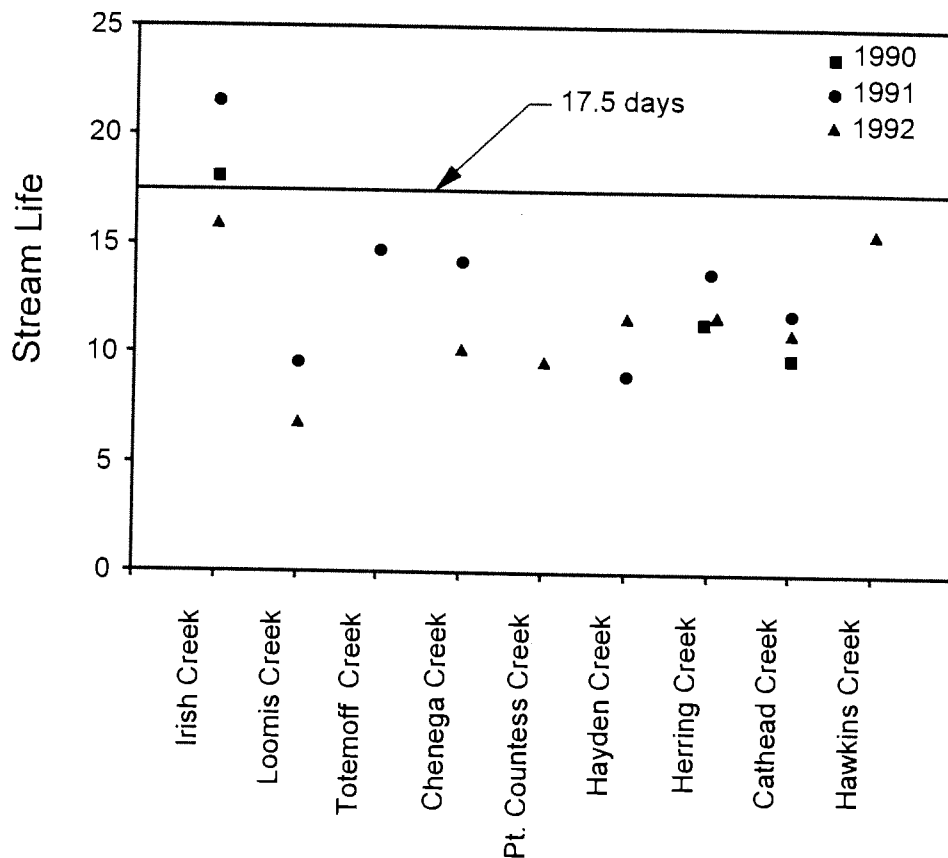


Fig. 3 Estimated stream life for selected study creeks in Prince William Sound, Alaska, 1990-1992.



Stream-life values were generally much shorter than the 17.5 day value currently used to estimate total pink salmon escapement into Prince William Sound spawning creeks (Table 1 and Fig. 3). Only Irish and Hawkins Creek pink salmon had stream-life values similar to (16.0 days, Irish Creek, 1991; 15.6 days, Hawkins Creek, 1991) or greater than (18.1 days, Irish Creek, 1990; 21.5 days, Irish Creek, 1992) the 17.5 day stream-life value. Pink salmon in all other study creeks had stream-life values that ranged from 1.9 (Hawkins Creek, 1991) to 10.7 (Loomis Creek, 1991) days shorter than the currently used 17.5 day value.

Individual creeks were surveyed five to 18 times during the course of each season (Table 1). Aerial observer efficiency estimates ranged from 0.177 (Irish Creek, 1991; Loomis Creek, 1992) to 0.888 (Herring Creek, 1990). This meant that aerial observers generally were able to count from 17.7% to 88.8% of the live pink salmon present. The median observer efficiency value for all 18 data sets was 0.406, while the mean value was 0.436. There appeared to be a trend in aerial observer efficiency between odd- and even-year escapements. Values were lower in 1991 than in 1992 for three (Irish, Chenega, and Cathead Creeks) of the six creeks retained in the data set both these years, and values were lower in 1991 than in

both 1990 and 1992 for the three creeks (Irish, Herring, and Cathead Creeks) retained all three years. Overall, aerial observers tended to under-count the actual number of pink salmon available, and this trend appeared to be accentuated in odd-years as well as when the number of pink salmon available to observers increased (Fig. 4).

Comparison of Historic Escapement Estimates to Revised Estimates

Total escapement estimates based on currently applied methods accounted for, on average, 51%, 22%, and 35% of the total weir counts in 1990, 1991, and 1992, respectively (Table 3; Fig. 5). These estimates improved when the appropriate stream-life value was used in place of the currently used 17.5 day value. On average, total escapement estimates based on appropriate stream-life values accounted for 70%, 34%, and 42% of the total weir counts in 1990, 1991, and 1992, respectively. A greater improvement in estimates was obtained when observer efficiency was taken into account, even when a 17.5 day stream-life value was used for all study creeks. On average, total escapement estimates which had been adjusted for observer efficiency accounted for 76%, 71%, and 80% of the total weir counts in 1990, 1991, and

Fig. 4 Observer efficiency relationships used for Irish Creek, Prince William Sound, Alaska for 1990 (A), and 1992 (B). Solid line is the regression fit while the dashed line represents the 1:1 line.

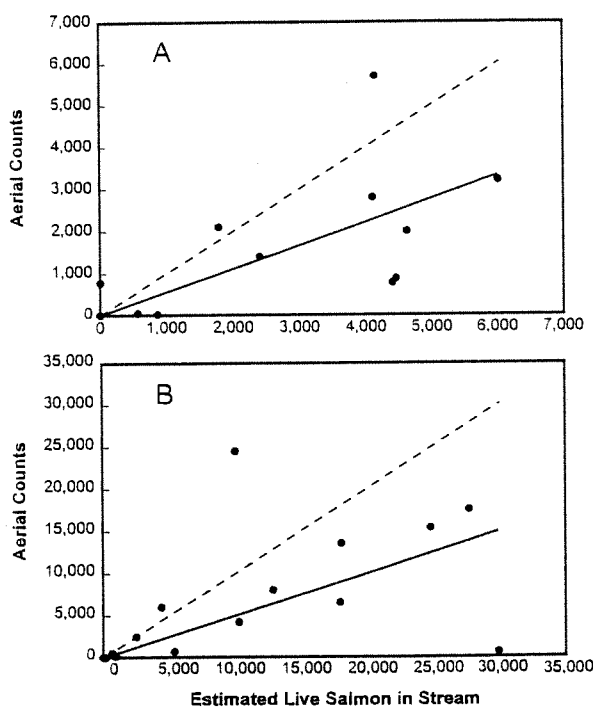


Table 3. Escapement estimates obtained using current and adjusted methods for spawning pink salmon in study creeks with weirs and daily ground surveys, Prince William Sound, Alaska, 1990-1992.

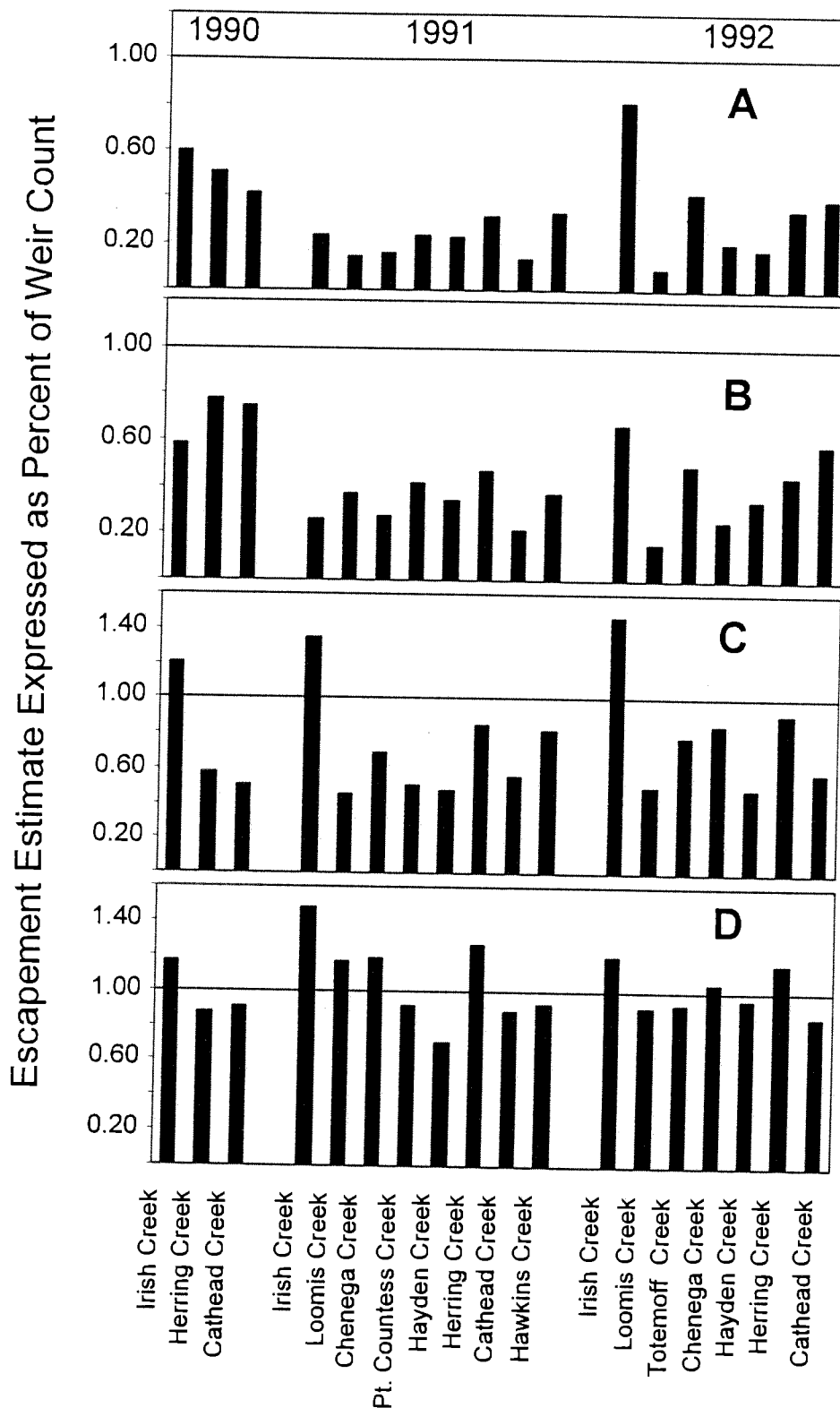
Estimates from Aerial Surveys					
Stream	Total Weir Count	Current Method ^a		Adjusted ^b	
		Estimate	% ^c	Estimate	% ^c
<u>1990</u>					
Irish Creek	44,900	27,086	60	52,482	117
Herring Creek	4,927	2,508	51	4,336	88
Cathead Creek	7,971	3,332	42	7,212	90
Average			51		98
<u>1991</u>					
Irish Creek	95,034	22,728	24	140,442	148
Loomis Creek	20,315	2,957	15	23,630	116
Chenega Creek	49,769	8,039	16	58,941	118
Pt. Countess Creek	15,028	3,497	23	13,834	92
Hayden Creek	18,372	4,226	23	13,031	71
Herring Creek	13,022	4,134	32	16,524	127
Cathead Creek	9,629	1,315	14	8,502	88
Hawkins Creek	40,433	13,530	33	37,383	92
Average			22		107
<u>1992</u>					
Irish Creek	8,208	6,695	82	9,837	120
Loomis Creek	3,845	339	9	3,495	91
Totemoff Creek	8,428	3,524	42	7,842	93
Chenega Creek	10,658	2,213	21	11,130	104
Hayden Creek	2,708	476	18	2,580	95
Herring Creek	911	321	35	1,058	116
Cathead Creek	3,937	1,569	40	3,367	86
Average			35		101

^a Constant 17.5 day stream life and no observer efficiency adjustment.

^b Creek-specific stream life and observer adjustment.

^c Percent of total weir count.

Fig. 5 Escapement estimates expressed as a percent of the weir count for the currently used method (A: 17.5 day stream life, no correction for observer efficiency), adjusted for stream life only (B: stream-specific stream life used, no correction for observer), adjusted for observer efficiency only (C: stream-specific observer correction with 17.5 day stream life), and adjusted for stream life and observer efficiency combined (D: stream-specific stream life and observer efficiency corrections). The solid line at 1.00 in each plot indicates the weir count.



1992, respectively. When both appropriate stream-life and observer efficiency values were used, total escapement estimates accounted for, on average, 98%, 107% and 101% of the total weir counts in 1990, 1991, and 1992, respectively (Fig. 5). This provided total escapement estimates that were within 20% of the total weir count in 15 of the 18 cases examined (Table 3).

DISCUSSION

This study shows that aerial surveys can be used to estimate pink salmon escapement if survey frequency is maintained at 5-7 day intervals throughout the run and reasonable estimates of stream life and observer efficiency are available. One could argue that an unbiased evaluation of the methodology was not performed because total weir counts were used to estimate stream life and observer efficiency as well as measure total escapement. However, we obtained strong evidence that escapement estimates based on appropriate stream-life and observer efficiency values were more accurate than those based on the currently used 17.5 day stream-life value and no adjustment for observer efficiency. This is best evidenced by Irish and Cathead Creeks in 1990 and 1991 where estimates based on the currently used method declined while corresponding total weir counts increased. The most dramatic example can be seen at Irish Creek in 1991, when the total weir count was more than double the estimate based on the currently used method. Although escapement estimates to Irish and Cathead Creeks using appropriate stream-life and observer efficiency values were not always very accurate (48% over-estimate for Irish Creek in 1991), they at least trended in the correct direction and were closer to the total weir count than estimates based on currently used methods.

Some of the error presently associated with estimating pink salmon escapements in Prince William Sound from aerial survey data is due to use of a stream life of 17.5 days for all creeks. This value was based on Helle et al. (1964) study of the pink salmon run to the middle portion of Olsen Creek in eastern Prince William Sound. Results of studies by McCurdy (1984) suggested that stream life varies among Prince William Sound pink salmon spawning systems and that the 17.5 day estimate used to calculate total escapement may be too large, especially for smaller streams. Our studies confirm McCurdy's (1984) findings. Most stream-life values for pink salmon in our study creeks were shorter than 17.5 days. However, pink salmon spawning in Irish Creek, a large system more similar to Olsen Creek, had annual stream-life values similar to 17.5 days.

Another, and possibly greater, source of error in

estimating pink salmon spawning escapements is due to aerial observer efficiency. Our study indicates that aerial observers tend to under-count pink salmon in Prince William Sound spawning systems. Great differences can exist among different observers, and we assume that each observer's efficiency changes in response to both viewing conditions and learning.

Great fluctuations in water level and velocity due to heavy rain, effects of which were magnified by steep gradients and loose gravel substrate, all contributed to problems in maintaining weirs in the various creeks used in this study. Not only did these high water flow events make it necessary to remove weir pickets and miss counts, but they also caused gaps at the bottom of weirs which sometimes went unnoticed and allowed salmon to pass uncaptured. We caution that weirs will provide accurate counts of spawning salmon only if efforts are made to carefully maintain their integrity. The use of properly designed ground surveys to count dead salmon can provide a valuable independent check on weir counts.

Finally, our results suggest that use of appropriate stream-life and aerial observer efficiency values will provide more accurate aerial estimates of salmon spawning populations. We caution, however, that treating stream life and aerial observer efficiency as constants will continue to introduce unknown errors into annual spawning population numbers. We recommend that weirs be maintained on a subset of the 208 index creeks both to calibrate aerial observers and to track changes in stream life more closely. Such projects need not be done every year, but particular care should be taken when changes in aerial observers occur.

ACKNOWLEDGEMENTS

We would like to thank the Division of Commercial Fisheries Management and Development staff that spent many long, often uncomfortable hours, peering out the windows of small single-engine planes while counting pink salmon. This work would also not have been possible without the hard work and dedication of the many seasonal employees that operated and maintained weir sites and conducted ground surveys to count pink salmon. This study was partly financed by the Exxon Valdez Oil Spill Trustee Council under State/Federal Natural Resource Damage Assessment Investigations. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or positions of the Trustee Council. Contribution PP-141 of the Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Juneau.

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Ocean Mortality of Northeast Kamchatka Pink Salmon and Influencing Factors

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Conditions affecting abundance and production of Karaginskii district pink salmon have been studied for a period of 20 years. Main ecological factors limiting productivity of generations at early stages of ontogenesis have been identified and estimated. The ocean mortality of seven broods of pink salmon was estimated - in coastal waters estimates range from 53.1% to 94.4% in the first weeks (40 - 45 days) and from 55.4% to 95.8% in the last period of ocean life (about 360 days).



INTRODUCTION

The mortality rate of salmon at different periods of life in the sea varies. According to Godfrey (1958) the abundance of pink salmon in the ocean and the final rate of return are determined at an early stage of sealife. This period of the juvenile's life is critical in the productivity of Pacific salmon generations (Royal 1962). A number of scientists think that the sooner pink and chum fry migrate to the sea and the shorter their period of stay in coastal waters, the higher their survival rate and larger their average size as mature fish (Vernon 1958; Skud 1959; Hunter 1959). That is why even in one area of salmon's reproduction where environmental factors influencing productivity of individual broods show considerable interannual differences, that influence can change at some stage. In such a case it is difficult to identify the main limiting factors (Iwamoto and Salo 1977), because in nature their influence is complex and scientists may observe only the final result.

This paper is dedicated to analysis of some environmental factors influencing survival of pink salmon in the Karaginskii district (North-East Kamchatka) and to determination of the rate of influence of some of the factors in abnormal situations. The main focus of the work is estimation of pink salmon mortality at different stages of their life cycle.

MATERIALS AND METHODS

Materials for this paper are observations of the conditions that affect productivity of 20 pink salmon

broods of the Karaginskii district at different stages of the life cycle. The most detailed data have been gathered in the most important of the generations' survival period, i.e. downstream migration of fry and entering to the sea. For this purpose a complex survey of the coastal districts has been made. While making the survey hydrological, hydrobiological, ichthyological and other data has been gathered and later worked up with standard and original methods.

Pink salmon mortality estimation has been made on the basis of direct calculation of the generations' abundance in different periods of life. The main materials for computations are:

1. - total abundance of spawners as estimated from helicopter surveys (E) and abundance of mature fish taken by fishing (Y);
2. - counts of fry at traps (M) in the Khailyulya and Kichiga rivers and purse seine catches of juveniles at standard stations (K) in Lithke Strait at the end of July - beginning of August. In the last case abundance of pink salmon juveniles in Lithke Strait was estimated by the squares method, based on the distribution of catches (Maisky 1940; Aksyutina 1968). In this method, the squares with equal catches were used.

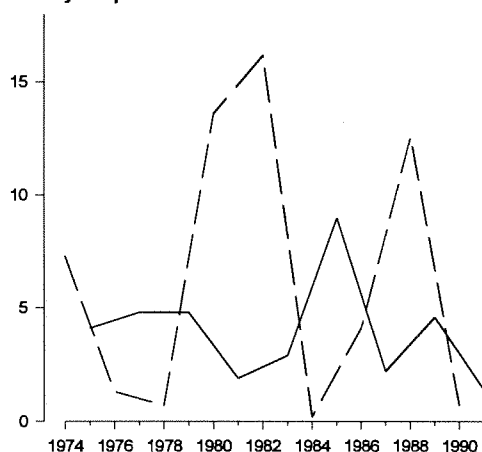
RESULTS AND DISCUSSION

When defining a generations' survival rate the most convenient species of Pacific salmon is pink. The easiest way of estimating salmon mortality in fresh and sea waters is by calculation of separate generations' survival measure (R/E), which is the correlation of the progeny's abundance to the parents'

abundance for the corresponding generation. Defining pink salmon R/E is an easy task as the fish of each generation stay in the sea only one winter and completely return for spawning the next year.

The survival measure of 18 pink salmon broods of Karaginskii district changed from 0.2 to 16.2 (Fig. 1), which is indicative of the great variability of conditions of the fry's life in freshwater and early marine periods. Variability of pink salmon survival as a measure of high abundance (odd-year) broods is less - from 0.9 to 9.0 (average 3.96) than of low abundance (even-year) broods - from 0.2 to 16.2 (average 6.3).

Fig. 1 Survival measure (R/E) of odd year and even year pink salmon broods.



This is natural, for abundant broods downstream migration is longer and the lower proportion of the fry are unfavorably influenced by the limiting factors as they get to the sea in relatively different feeding conditions. Low broods undergo more elimination, if the downstream migration occurs during a relatively short period of unfavorable environmental conditions. Their abundance can be limited by any of the natural factors - temperature, salinity, food, predators, diseases, etc.

Mortality of salmon juveniles in the early marine period of life in Karaginskii Bay is determined mostly by the influence of the coastal water's hydrological conditions, food resources and loss to predators. In recent years (from 1987) parasitic diseases of the fry have been noted. Their influence can easily be traced on survival of pink and chum salmon that migrate to the sea only at the age of 0+ (underyearling).

In the last few years (1980's-1990's) variations of North-East Kamchatka pink salmon abundance and values of parameters that indicate the fry's life conditions in coastal waters have varied widely. This caused considerable variability of the runs in even and odd years and allowed a determination of the influence of separate environmental factors on each

generations' survival, particularly in cases of abnormal deviations.

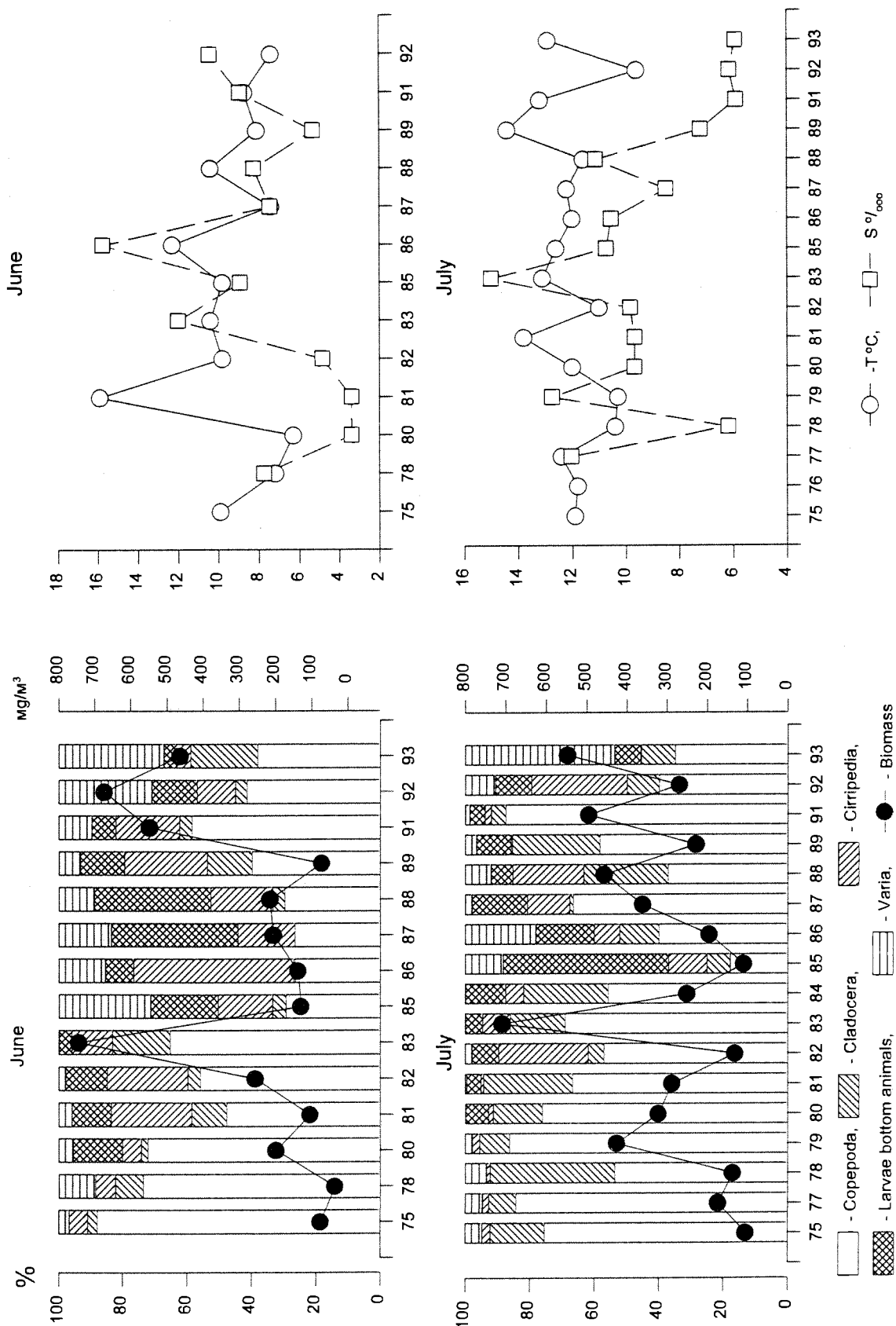
For estimation of the influence of hydrological conditions on salmon fry survival scientists use mainly the correlation between the temperature or salinity in zones inhabited by the fry and the rate of productive return of the corresponding salmon broods. A negative correlation between the surface water temperature in the Strait of Georgia and pink salmon catches in the next year ($r = -0.86$) was for the first time noticed by Vernon (1966). A correlation but with a contrary sign has been found by us for Karaginskii district pink salmon. Close values of the correlation coefficient have been obtained between brood survival and the coastal water ($r = 0.68$) and seaward water temperatures ($r = 0.70$) in July, and between brood survival and average air temperature ($r = 0.82$) in May - July, at Uka station. Most pink salmon fry of Karaginskii district migrate to Uka Bay at the end of July - August period. The contrary signs of the correlation coefficients for North American and North Kamchatkan pink salmon are reflection of the differences in the thermal conditions of those regions. So, for North American waters, early warm up is typical and higher survival rate of pink salmon fry is noted for early downstream migration to waters with lower temperature. In Kamchatkan waters a contrary phenomenon is observed - survival of the fry migrating faster is lower.

Dependence between abundance and hydrological conditions in coastal waters was determined for pink salmon of Kodiak Island (Donnelly 1983), and chum of the Anadyr river (Putivkin 1988), Iturup Island (Kaye 1983) and South East Sakhalin (Shershnev 1975).

In the coastal waters of Kamchatka the water temperature in summer is notable for small variability. Usually from June to July it rises 2-4° C, though in some years (1981 and 1986) maximum coastal waters heating was noted in June (Fig. 2) (Karpenko 1994a). Low temperatures causing pink salmon fry mortality were noted only four times during the observation period - in 1977, 1980, 1987, and 1990 when a long ice delay at the coasts was observed. This caused both a direct influence of the low temperature on salmon fry and a delay of development of food crustacea.

From many years' investigations it was determined that favorable conditions in the coastal waters of Karaginskii Bay were formed when ice was carried from Lithka Strait by the end of the first ten days of June, and by the end of the month the water temperature exceeds 8°C and salinity in the estuaries of the rivers was not more than 6-8‰. Later in July the water temperature rises 4-5°C and salinity not more than 2‰ (Fig. 2). With other changes of

Fig. 2 Composition and biomass mesoplankton, average temperature and salinity in littoral zone of Karaginski Bay



these parameters conditions for zooplankton production worsen and the food supply for salmon juveniles is lower. Better juvenile survival was observed in years when the spring flood in the rivers happens in the middle-to-end of June period and the coastal waters are of low salinity. If salinity declines in the middle-to-end of July a considerable percentage of the migrants appears to be eliminated due to stress situations - big gradients are formed in the estuaries earlier. This is promoted by both the negative influence of low temperature and high salinity of the coastal waters lowering the fish's swimming abilities.

The influence of water temperature and salinity on juvenile salmon survival is more often displayed by means of development of food organisms. In the years of delay of the biological spring the biomass of plankton animals is low and does not satisfy food demands of the fry. With early migration of fry and lack of coincidence with mass development of zooplankton a high mortality of fish due to food lack has been observed and noted for pink salmon generations of 1976, 1978 and 1984 (Karpenko 1994a). The delay of the biological spring in 1975, 1978, 1981, 1985 and 1989 was reflected in the general biomass of mesoplankton in whose structure there were few of the younger stages of Copepoda. In those years larval stages of bottom animals also appeared in the plankton later than usual (Fig.2). That is why with unfavorable hydrological processes negative consequences of development of the food reserve of salmon fry are revealed abnormally strongly and lead to extremely low survival, for example the pink salmon generation 1984 - $R/E=0.2$ (Karpenko 1994a).

The influence of provision of food on survival of a pink salmon generations is illustrated by the following: at high biomass of zooplankton in 1979 (424.2 mg/m^3) and in 1983 (708.2 mg/m^3) a high return of pink salmon in 1980 and 1984 was to be expected. Nevertheless, in 1980 as a result of an

early migration of the fry and late development of zooplankton the pink salmon return was low - $R/E=0.7$. In 1983 the course of the two processes coincided and pink salmon return was very high - $R/E=16.2$ in 1984. The two processes favorable coincidence influenced formation of the most productive pink salmon generation of 1987 while a relatively low food reserve and low fry growth rate in 1988 resulted in a good return in 1989 - $R/E=2.2$ (Table 1).

The main food objects of the salmon fry after migration to sea are copepods and pelagic larvae of the bottom animals. As a rule, because of rise in the water temperature and mass development of copepods, predominating both in number and biomass (up to 80%), the total biomass of mesoplankton increases from June to July. If its quantity reaches 200 mg/m^3 in June and 400 mg/m^3 in July, feeding conditions and juvenile survival may be considered favorable. At low water temperature (ice delay) the biological spring is late and biomass of zooplankton is low (down to 70 mg/m^3) in June, and that leads to a considerable part of fry mortality from lack of food. A similar situation is possible also in a later period in July. Between the number of copepods and pink salmon juvenile there is a steady negative connection ($r=-0.58$) most strongly pronounced in the years of high abundance of juveniles, that is evidence of their being prey for certain predators in even years.

In some years the leading cause in salmon fry mortality is predatory fish. It is easy to single this factor out of the complex of others, if one succeeds in defining the rate of the predation on a particular generation of one of the Pacific salmon species. However, as predation on salmon fry is not always the regulating factor and more often appears episodically, the rates of damage differ considerably in the years even in one and the same region or estuary of a particular river.

The predatory fish's effect on salmon fry depends

Table 1. Feeding conditions of pink salmon juveniles in southern Karaginskii Bay

Index	1987	1988
Number of fry (10^6)	33,5	4104,0
Average length in July, mm	26,5	33,1
Average weight in July, g	0,178	0,231
Daily linear growth rate, mm	1,8	1,3
Daily weight growth rate, g	0,192	0,140
Coefficient of variation in length, %	5,4	11,3
Coefficient of variation in weight, %	16,7	33,3
Stomach fullness, ‰	227,8	109,9
Biomass of mesoplankton, mg/m^3	360,0	456,0
Food supply index*	5,31	0,19
Return, mln	5,5	62,5
Survival measure	4,1	2,2

* Relative quantity of food per one fish (sum of number of pink and chum fry)

mainly on the density and power of migrants (Gorshkov et al. 1989) as well as on the coincidence of the fry's migration out from rivers with predators migration in the sea (Karpenko 1994a, b). In river estuaries and in coastal waters accumulations of fry usually happen because of high gradients of temperature and salinity, for migration through which a period of adaptation is necessary.

Pink salmon fry were found in stomachs of 10 species of fish but the main predators were Arctic char (*Salvelinus alpinus*), Asian smelt (*Osmerus mordax dentex*) and Siberian char (*Salvelinus leucomaenis*). Considerable damage to salmon populations can be caused by Arctic char and smelt only because of relatively high numbers in coastal waters. In even years, even at a high number of migrants (1982, 1984, 1988) predation on pink salmon was low (1988) or not evident (1982, 1984) (Table 2). In years of low abundance of pink salmon (odd years) the migration period was usually short, high density of the migrants was observed in coastal waters, which promoted predation on fry. That is why in 1985 and 1987 even at low numbers of the main predator - Arctic char (0.2 - 0.35 fish per catch) predation on fry reached 17.4% and 21.3% of the generation (Table 3).

Within the period of 18 years of observations there was a considerable rate of predation on pink salmon fry but not consistently each year and not occurring everywhere. We have tried to evaluate the regional differences of the rate of damage caused to populations of the fry by predators as well as interannual changes of the main predators' needs during a season, assuming maximum terms for rates of predators and prey contacts in estuaries of rivers. The highest number of estuaries where pink salmon fry were observed was noted in 1978, when the predators Arctic char and smelt exterminated 18% of the pink salmon generation (Table 3).

The main predation on fry was noted in 10 estuaries and lasted from 13 to 32 days. Smelt ate pink salmon fry for a longer period. Out of 373 million pink salmon fry migrating from those rivers predators exterminated more than 54 million of the fry, which is about 15% of the generation (Table 4). Out of this number smelt exterminated 91.7% and Arctic char 8.3% of the fry. A considerable predation on pink salmon fry was observed both in strongly stratified (1st type) estuaries of the Virovayam and Belaya-Kichiga rivers and mixed (2nd type) - the Makarovka-Kayum, Anapka, Ossora rivers. Mass predation on pink salmon occurred only in the feeding period of Arctic char and smelt near the rivers' estuaries and in each case the rate of damage caused by predators depended on the conditions forming in the estuaries. Thus, in estuaries of the first type with

sharp gradients of temperature and salinity, conditions heightening concentrations of fry, predation was two-three times more than in that of the second type, where salmon fry did not encounter such stress inducing situations during migration to the sea.

Based on daily food intake by predators and the period when fry were found in predators' stomachs, the highest number of pink salmon fry eaten by Arctic char per season was observed in 1987 - 230 fishes, and by smelt in 1978 - 85 fishes (Karpenko 1994a). Considering the number of predators the maximum predation on pink salmon by Arctic char was noted in 1980 - 20.11 million fishes, and by smelt in 1978 - 63.78 million fishes; the total number of pink salmon fry eaten during the 18 years was 115.4 million fishes, and of this amount 65.9% was taken by smelts.

In the coastal waters of North-East Kamchatka predation on salmon fry by three bird species has been noted: arctic (*Sterna hirundo*) and common (*S. paradisaea*) terns and kittiwake (*Rissa tridactyle*). However, we believe the rate of damage caused by them to populations of pink salmon fry is not large.

In recent years one of the important factors that influenced North East Kamchatkan salmon fry's survival, became parasitization with larvae of trematodes (*Cryptocotyle sp.*). Mass parasitization of pink and chum fry was first noted in the summer-fall period of 1987 in some districts of Karaginskii Bay, mostly in the Bays of Uala and Anapka and also in Lozhnykh Vestei Bay. In 1988 besides the above mentioned districts parasitized fish were seen in Gek Bay and in the Makarovka river estuary. These districts remain the basic places of salmon fry parasitization at present. The maximum number of trematode larvae reached 163 in one pink salmon sample. Fish with high intensity of parasitism showed tail stem destruction up to atrophy as well as damage to thoracic and abdominal fins. Mass parasitization of salmon fry with *Cryptocotyle sp.* raises the natural mortality rate of the fish of this generation (Karpenko 1994a, b) which in some districts may increase by 10% for this reason.

Besides the survival measure that is evidence of the general mortality of a generation during a pink salmon life cycle, precise evaluation of the mortality rate may be obtained on the basis of calculation of fish numbers at different stages of their seaward migration: in the river, in coastal waters, in open sea waters and in the places of wintering. To calculate the number of fish in all the above mentioned places for one generation is a very difficult and often impractical task both from the point of view of technics and methods. First, to provide such research with research vessels is very expensive. Second, with fish of separate populations moving from coastal

Table 2. Frequency of salmon juveniles in predator's food, %.

Species	1975	1976	1978	1979	1980	1981	1983	1985	1986	1987	1988	1989	1991
	VI	VIII	VI	VII	VI	VII	VI	VI	VII	VI	VII	VI	VI
Pink	-	-	17.5 (58.7)	6.8 (28.0)*	-	13.2	2.9	-	2.1	-	6.3	1.3	6.3
Chum	5.9	-	-	-	25.0	-	37.5	-	-	49.0	5.0	-	(22.6)
Sockeye	-	-	-	-	-	-	12.5	6.3	-	2.0	-	-	-
													27.3
Pink	-	-	-	-	-	-	10.0	-	2.2	-	4.0	-	-
Chum	-	-	-	-	-	-	-	-	24.0	-	-	-	2.4
Sockeye	-	-	-	-	-	-	-	16.0	1.2	-	-	-	4.8
													28.6
Pink	-	51.5 (66.2)	-	18.6	-	40.0	-	-	-	-	-	-	8.3
Chum	-	-	-	7.0	-	10.0	11.1	-	25.7	-	-	16.1	16.6
Sockeye	-	-	-	-	-	16.7	-	-	11.1	-	-	-	-

* In brackets - a portion from food mass, %

Table 3. Salmon juveniles eaten by Arctic char and Asian smelt in a season (millions).

Species	1975	1978	1980	1981	1983	1985	1987	1989
<u>Arctic char</u>								
Pink	-	3,54(1,0)*	20,11(17,9)	-	-	3,49(17,4)	7,46(21,3)	-
Chum	2,50	-	-	12,48	-	-	5,80(16,8)	-
Sockeye	-	-	-	0,84	-	0,59	0,06	-
<u>Asian smelt</u>								
Pink	-	63,78(17,0)	12,28(10,9)	-	-	-	-	4,74(11,2)
Chum	-	6,92	4,61(11,0)	-	13,90	0,36(1,8)	-	4,68(2,1)
Sockeye	-	-	1,09	-	1,25	0,06	-	-

Table 4. Number of pink salmon juveniles eaten by predators in the estuaries of some rivers of the Karaginskii district in 1978.

River	Fry abundance , mln	Catch per haul.		Vulnerable period, day s		No. of Pink eaten					
		Ar. char	smelt	Ar. char	smelt	mln			% of migrants		
						Ar. char	smelt	total	Ar. char	smelt	total
Anapka	65,0	0,75	1,10	23	25	3,18	10,20	13,38	4,9	15,7	20,6
Virovayam	0,13	0,15	0,85	22	16	0,01	0,07	0,08	7,7	53,8	61,5
Belaya-Kichiga	58,5	0,13	80,60	25	18	0,04	25,66	25,70	0,1	43,8	43,9
Ossora	2,0	0,62	0,13	17	13	0,11	0,02	0,13	5,5	1,0	6,5
Makarovka-Kayum	56,6	0,05	5,09	18	22	0,07	12,36	12,43	0,1	21,9	22,0
Dranka	52,0	1,60	-	27	-	0,62	-	0,62	1,1	-	1,1
Rusakova	13,0	0,07	0,87	30	32	0,01	0,25	0,26	0,1	1,9	2,00
Khailyula	97,5	0,30	2,00	22	23	0,03	0,28	0,31	0,03	0,29	0,32
river Karaginskii Island	28,4	0,50	0,96	21	18	0,49	1,15	1,64	1,7	4,0	5,7
All rivers	373,1	-	-	-	-	4,56	49,99	54,55	1,2	13,4	14,6

waters and schools mixing demands either mass marking of each of them or at least working out efficient methods for their differentiation in the sea. The solution to this problem is complicated, which is why scientists in most cases have data for small populations of fish only and limited periods of the fish mortality estimation.

Salmon fry counts in two rivers of the Karaginskii district - the Khailyulya and Kichiga - were done during 15 and 10 year periods respectively; the numbers estimated in the coastal waters - over a 18 year period and, further to the sea, salmon fry catch was begun from 1987 after developing and mastering the use of a purse seine for this purpose. Trawls were used to calculate abundance of salmon fry from 1981(but not for all years) and, in some years, the time and methods were not standardized. For these reasons, reliable estimation of pink salmon's mortality rate has been obtained for only seven generations and singling out just two periods of their life cycle: 1- first 40 - 45 days of their stay in the coastal waters and 2 - in the last period of ocean life - about 360 days (Karpenko 1995).

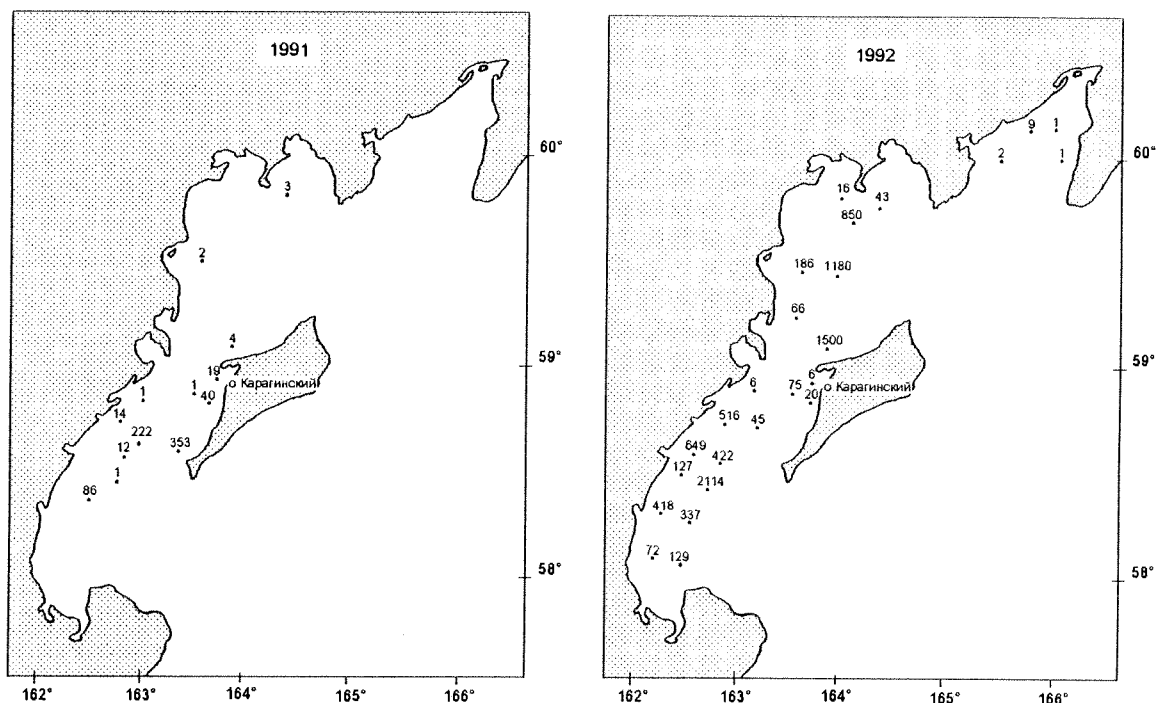
Catches and number of pink salmon fry in Lithka

Strait changed considerably, especially in the years of high abundance of juveniles (Table 5 and Fig.3). However, if the number of fry changed more than 100 times, the numbers of juveniles in Lithka Strait and the returns of mature fish were considerably less which is evidence of the powerful natural mechanism regulating pink salmon numbers. Compared with other salmon species the maximum mortality of pink salmon occurs right after their entering the sea, and this natural mechanism's highest influence is displayed exactly in the early marine period of life.

Mortality in coastal waters of low generations (even years) is usually lower than that of high (odd years) and, also, lower than in the high seas (Table 5). Both cases of estimation of pink salmon mortality in the early marine period of life and the last periods of oceanic life have shown contrary results. Mortality of the most numerous generation of 1987 was the highest just in the early marine period - 94.4% when the fry after migration to sea were feeding in coastal waters for a long time. In contrast, with the generation of 1991 which migrated early to Lithka Strait the mortality rate was higher in the last period of life - 90.3%. The latter is connected with the fact that in 1992 in the open part of Lithka Strait

Table 5. Ocean mortality of Karaginskii district pink salmon.

Brood	Abundance (millions of fish)				Mortality, %		
	Spawners	Fry	Juveniles	Run Size	Coastal	Offshore	Total
1986	1,34	33,5	12,33	5,5	63,2	55,4	83,6
1987	28,5	4104,0	231,7	62,5	94,4	73,0	98,7
1988	1,83	295,5	99,55	21,3	66,3	78,6	92,8
1989	18,9	1631,3	-	86,7	-	-	94,7
1990	8,8	328,2	153,8	6,4	53,1	95,8	98,0
1991	29,3	2105,2	432,6	41,8	79,5	90,3	98,0
1992	1,98	-	82,51	9,4	-	88,6	-

Fig. 3 Catch of pink salmon juveniles by purse seine in the Lithke Strait, Karaginskii Bay (July-August)

feeding conditions did not adequately provide for fry survival due to their great numbers. This was proved by biological and biochemical indices of the juveniles which were lower than those of the other productive generations (Karpenko et al. 1994).

The results have shown a high pink salmon mortality in the sea in both periods of life. In first 40 - 45 days it ranged from 53.1% to 94.4% and in the last period - from 55.4% to 95.8%, and on the whole - from 83.6% to 98.7% (Table 5). Using the method of two-stepped marking of fry and juveniles similar indices of mortality have been obtained by Parker (1962, 1968) for three generations of pink salmon of the Bella Coola river. They were, in the first 40 days 59 - 77% of the initial number of fry and in the last 410 days - 78 - 95% of the initial number of juveniles going to the high seas. Taylor (1980) reported that

the survival rate of hatched pink salmon depends on the time of release to the sea: an early release leads to higher mortality of the fry - 99.83% in comparison with a late release mortality of 98.54%.

Knowing the mortality rate of separate generations of fry and factors that cause that condition allows a correct evaluation of the potential spawning and a determination of the degree of commercial catch. Obtaining data on fish numbers at different stages of the life cycle allows one to understand the dynamics of the decrease in fish, to uncover the reasons and to foresee possible rapid changes in the number of productive returns of separate stocks and populations. For the comparatively isolated stocks of Karaginskii district this method has been used during the last 12 years. The results of the juvenile numbers estimated and

Table 6. Main coefficient correlation return pink salmon Karaginskii region with some environmental factors.

1. R-E=0.70(15)-3	2. R-K=0.67(15)-3	3. R-M=0.73(12)-3	4. R-L=-0.51(14)-2
Inner relationships			
5. E-K=0.77(15)-3	6. E-M=0.86(12)-3	7. K-L=-0.57(14)-2	8. K-M=0.84(12)-3
9. R/E-T=0.62(11)-2	10. R/E-T=0.70(15)-3	11. R/E-T=0.68(14)-3	12. R/E-T=0.82(13)-3
13. L-T=0.63(10)-2	14. L-S=0.85(9)-3	15. L-S=0.62(11)-2	16. B-B=0.84(11)-3
17. B-S=0.85(10)-3	18. B-S=0.63(12)-2	19. T-T=0.70(11)-2	20. T-T=0.66(11)-2
21. T-T=0.73(9)-2	22. T-S=0.58(13)-2	23. S-T=0.60(10)-1	24. S-S=0.58(10)-1
25. S-T=0.52(11)-1	26. T-T=0.75(9)-2	27. E-L=0.49(14)-1	28. L-T=0.71(10)-2

Parameters: R - return, mln; E - escapement, mln; K - juvenile abundance in coastal waters, smpl; M - fry from Khailjula River, mln; L - average length of juveniles in coastal waters in July, cm; R/E - survival measure; T - water temperature 0-10m in June; T - water temperature 0-10m in July; T - water temperature in littoral zone 0m in June; T - water temperature in littoral zone 0m in July; T - average air temperature in May-July in Uka station; S - salinity in 15-mile zone in June; S - salinity in 15-mile zone in July; S - salinity in littoral zone in June; S - salinity in littoral zone in July; B - zooplankton biomass in June; B - zooplankton biomass in July;

In bracket - number of years investigations;

Significance level: 1 - 0.90; 2 - 0.95 and 3 - 0.99.

feeding conditions in the coastal waters are formulated in regression equations for pink salmon generations of different productivity. For this purpose an analysis of the meaningfulness in rate of separate environmental factors in forming pink salmon generations numbers of the last twenty years has been done. A regression analysis of 16 parameters that are indicative of conditions that influence generations' numbers has been done and a study made of the significance to total return of each of those parameters (Table 6). It was determined that the basic influences on the rate of return of pink salmon are conditioned by the number of parents, fry and feeding conditions after downstream migration. Based on this, equations of dependence have been calculated, which are:

$$1. R = aE + bK \text{ and}$$

$$2. R = aE + bK + c, \text{ where:}$$

R - total return of brood, millions of fishes;

E - escapement, millions of fishes;

K - number of juveniles in coastal waters, based on average catch per haul;

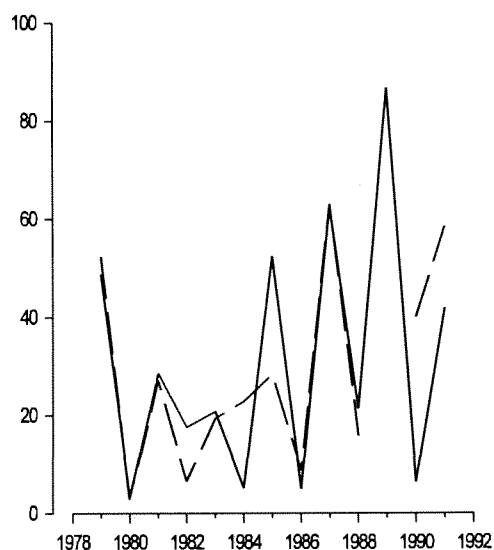
a, b and c - coefficients which had different values depending on the duration of observation used. In the 1990s the equations looked like this:

$$1. R = 1.72E + 10.18K \text{ and}$$

$$2. R = 1.29E + 8.03K + 9.18, \text{ where the difference between the equations depends on whether or not the intercept is assumed to be zero.}$$

Traditionally the salmon return prognosis was done two years in advance and in practice only the abundance of spawners was used to forecast the tendencies for change in salmon broods and the catch statistics. Using equations (1) and (2) calculation of

the pink salmon productive return rate of 13 generations was made one year in advance. With no abnormal deviations of the environmental factors which determine the fry's survival, a more precise definition of the pink salmon forecast gave a positive result. Thus, from six high pink salmon broods only for the generation of 1985 did the actual return deviate substantially (46.2%) from the forecast. In the other cases the deviation did not exceed 10% (Fig. 4). For seven low broods the precision of the forecast evaluation was usually lower, particularly in cases with abnormal deviations of feeding conditions for the juveniles: the generations of 1984 and 1990

Fig. 4 Actual and predicted pink salmon returns the results of the juvenile calculation in coastal waters for Karaginskii area.

experienced unfavorable environmental factors and their survival was much lower than expected. The generations of 1980, 1982 and 1988 on the contrary were in favorable conditions after migration to sea and their return was high. That is why the sign of deviation of the prognosis rate may be defined using an expert evaluation of the juvenile feeding conditions in coastal waters (Karpenko 1989, 1994a, b).

Similar methods of correction of salmon returns are used comparatively seldom. A high correlation has been determined between scale growth, including the first weeks in the sea (growth of the first three circuli) and the rate of return of pink salmon of the northern part of south-east Alaska ($r=0.57 - 0.79$), which is used for forecasting abundance of adult fish (Jaenicke et al. 1994). Data about the nature of juvenile growth in coastal waters has been used for forecasting chum salmon of Iturup Island (Kayevev 1979, 1983), and juvenile abundance in coastal waters was used by E.T.Nikolayeva (personal communication) for calculating the rate of return of North East Kamchatka chum.

The early marine period of Pacific salmon therefore plays a special role in forming productivity of generations. For the main species of Asian salmon - pink and chum, the fry's survival rate during this period determines not only the number but also the production (biomass) of generations. Determining and estimating the main factors limiting those indices is the major task at working out measures of rational exploitation in each particular region.

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Migration Timing, a Life History Trait Important in the Genetic Structure of Pink Salmon

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Anadr. Fish Comm. Bull. No. 1: 262-273

Timings of migration are critical events in salmon life history. The physical conditions of the stream (e.g. temperature and water flow) determine spawning success and estuarine conditions markedly influence emigrant survival. Previous studies that demonstrated the contribution of genetic components to timing related polygenic traits such as migration timing and rate of embryo development suggest that with sufficient statistical power, genetic divergence related to timing should be detectable in biochemical genetic traits in pink salmon. Here we analyzed allozyme data from pink salmon in Auke Creek and other streams near Juneau, Alaska to examine the influences of return timing, spawning site, stream, and sample year on genetic structure. Log-linear modeling and heterogeneity G-tests indicated that return timing (early or late), year of return, and stream all influenced structure. Site within stream (upstream or intertidal) had no effect. For odd-brood-year Auke Creek collections, timing had a stronger influence than year. For 1979 collections from streams in the Juneau area, timing and stream both influenced structure and timing had a stronger influence. For even-brood-year collections, timing, stream, and year influenced structure, but we could not differentiate the extent of their influence. A similar study of data from Iterup Island (Kuril Islands in Asia) pink salmon revealed only an effect of year, but the analysis was weak because data from few loci were available. Detection of biochemical genetic variation correlated to life history characters demonstrates the importance of such characteristics in determining the population structure and basis for productivity of salmon populations.



INTRODUCTION

The time during the spawning season at which salmon return to a stream to spawn is clearly important to their survival and productivity. Because water flows and temperatures vary seasonally, the fish must time their return for when the stream provides satisfactory spawning conditions and, subsequently, water flows and temperatures favorable for incubation, development, and timely emergence of deposited embryos. The importance of timing has been documented in a variety of experiments from broad geographic scales to local. At the scale of species range, salmon spawning migrations generally occur

earlier in northern regions and later in southern regions. For example, most chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) spawning in systems draining into the Bering Sea return during July and August; whereas in the Pacific Northwest and Japan, those species return from between September and January (Heard 1991; Salo 1991). In both instances, the fish return when stream and incubation conditions are generally favorable. Evidence for the importance of timing also exists at the regional level. The Fraser River system has several different lake systems that support sockeye salmon populations. The mean incubation temperature varies among those systems from a little over 2° to more than 8°C.

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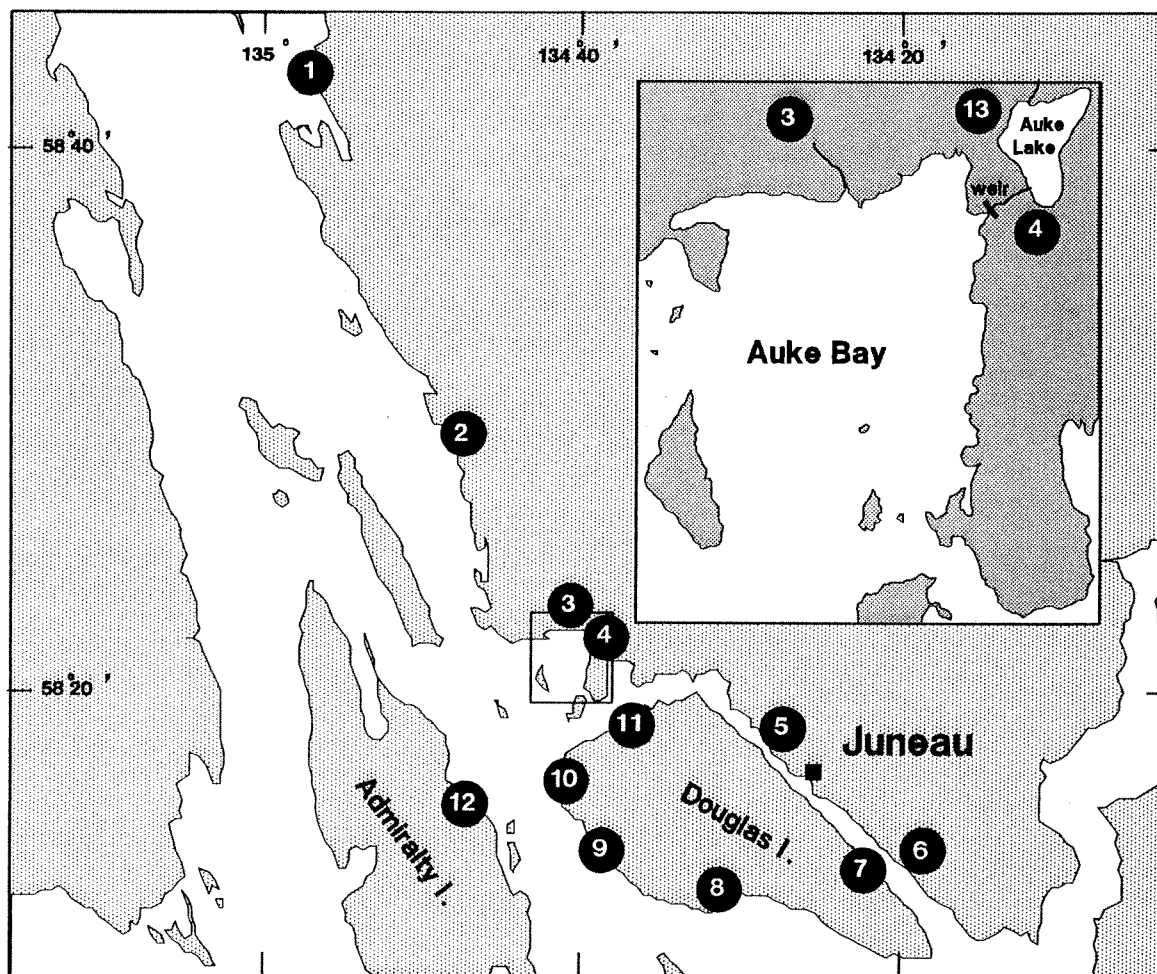
Spawning timing of populations returning to a lake is strongly correlated with the temperature of the system, populations returning to colder lakes return earlier, presumably to allow more time for embryonic development (Brannon 1987).

Genetically based temporal structure also exists within streams, even very small streams. Pink salmon in Auke Creek, 18 km north of Juneau, Alaska have been intensively studied using markers, genetic marking, and quantitative genetic analysis. Auke Creek flows approximately 350 m from Auke Lake into Auke Bay (Figure 1). The National Marine Fisheries Service operates a weir just above tidewater that enumerates returning adult salmon and emigrant fry and a small hatchery that is used for cooperative interagency research programs. The stream has natural runs of both even- and odd-year pink salmon. Fin-marking studies identified both temporal and spatial structure of the pink salmon returning (Taylor 1980); four components within Auke Creek are early-

run intertidal (below the weir), early run upstream (above the weir), late run intertidal, and late run upstream. The early run returns from late July to August; the late run returns during September. The late run is ordinarily preceded by reduced returns of early-run fish and indicated by incompletely mature, "sea-bright" fish.

The temporal structure of pink salmon returns in Auke Creek were more thoroughly examined by genetically marking the latter half of the late upstream component. In 1979, the frequencies of allozyme alleles were altered in that component by screening adults for and breeding in the hatchery only individuals possessing *MDH-3,4*70** and not *MDH-3,4*130** alleles (Lane 1984; Lane et al. 1990). These fish returned in 1981 and interbred with naturally produced fish, genetically marking the run. From samples taken throughout the run it was observed that the marked component of the run remained in the late portion of the late upstream

Fig. 1 Map of the locations of Alaskan pink salmon streams studied. An inset shows Auke Bay and the Auke Lake drainage. Streams are: 1 Sawmill Creek, 2 Peterson Creek (mainland), 3 Waydelich Creek, 4 Auke Creek, 5 Salmon Creek, 6 Sheep Creek, 7 Ready Bullion Creek, 8 Hilda Creek, 9 Middle Point Creek, 10 Peterson Creek (Douglas Island), 11 Fish Creek, 12 Bear Creek, and 13 Lake Creek.



component for several generations (Gharrett et al. in prep.). Additional evidence that timing is an important component of population structure is that emigrant fry produced by the late-run component emigrated later (on average) than fry produced by earlier returning parents (Gharrett and Smoker 1993).

The genetic marking experiment provided compelling evidence that timing was an important component of population structure and probably had a genetic basis, because the marked component produced offspring that had the same timing. For confirmation, Smoker et al. (in prep) conducted breeding experiments in both early-run and late-run Auke Creek fish and demonstrated a significant heritable component (sire effect) in return timing, not just for return to early or late run, but for timing of return within each period. This experiment shows that a fish tends to return to spawn at the same time during a run that its parents did.

With abundant evidence for the role of timing in population structure, and specific evidence that at least partial reproductive isolation exists among components of Auke Creek pink salmon, we would expect some divergence in molecular markers of those components. Temporal structure does not preclude gene flow; however, significant divergence can be detected in the presence of gene flow if sufficient power is used to detect it (Gharrett 1994).

Between 1978 and 1984, we conducted allozyme surveys of the spatial-temporal components of Auke Creek and of other systems near Juneau, Alaska (including McGregor 1983; Lane 1984). Here we analyze those data to test for heterogeneity among collections in frequencies of allozyme alleles and determine which factors have significant effects on allele frequencies. The factors we examine are timing of spawning (early versus late), site of spawning (intertidal versus upstream), the spawning stream, and the year in which data were collected (Appendix). Where sufficient data were available, we also estimated gene flow in numbers of individuals per generation.

MATERIALS AND METHODS

Protein electrophoresis

Protein electrophoresis (Aebersold et al. 1987) was used to estimate allozyme frequencies in collections of pink salmon from streams near Juneau, Alaska. Tissues sampled were kept at -20 °C until analysis. Loci (Shaklee et al. 1990) examined were aconitate hydratase (*mAH-3** and *mAH-4**), adenosine deaminase (*ADA-2**), aspartate amino transferase (*sAAT-3**), glycerol-3-phosphate dehydrogenase (*G3PDH-1**), isocitrate dehydrogenase (*sIDH-1*), leucyl-glycyl-glycine peptidase (*PEPB-1**), malate

dehydrogenase (*sMDH-B1,2**), malic enzyme (*mMEP-1**), mannose-6-phosphate isomerase (*PMI**), phenylalanyl-proline peptidase (*PEPD-2**), phosphoglucomutase (*PGM-2**), 6-phosphoglucose isomerase (*GPIA** and *GPI-B1,2**), and 6-phosphogluconate dehydrogenase (*PGDH**). Tissue specificities and buffer conditions were described previously (Gharrett and Thomason 1987) except for *sIDH-1* which we resolved in liver on a pH 7.0 tris-citrate buffer (Shaw and Prasad 1970).

Analysis

Allele frequency analyses were made with log-likelihood ratios (Sokol and Rohlf 1995). Analyses for effects on allele frequencies were conducted using log-linear modeling which is the categorical data analog to analysis of variance. In our analyses, only models that involved interactions between effects and allele frequencies were examined because we were looking for effects of factors on allele frequencies. Without allele frequency in the model, the factors test only sample size differences among collections, which are of no interest. Log linear models generate log-likelihood ratios (*G*-statistics) for effects and interactions of effects. Balanced data of allele frequencies of odd-year pink salmon sampled from early intertidal, early upstream, late intertidal, and late upstream components of Auke Creek in each of 1979, 1981, and 1983, were analyzed using a saturated model for interactions of effects with allele frequency:

$$\ln f_{ijkl} = A_i * T_i + A_i * S_j + A_i * Y_k + A_i * T_i * S_j + A_i * T_i * Y_k + A_i * S_j * Y_k + A_i * T_i * S_j * Y_k$$

where T_i is the effect of timing (early or late run), S_j is the effect of spawning site (intertidal or upstream), and Y_k is the effect of year (1979, 1981, and 1983). A_i is allele frequency, and is tacitly assumed in subsequent models and table headings. Because *sMDH-B1,2** was involved in the genetic mark of a component of Auke Creek, it was omitted from the analysis. Also, because an (unsuccessful) attempt was made to mark the even-year brood line with a *G3PDH-1** allele, *G3PDH-1** data were omitted from potentially affected Auke Creek components (1982 and 1984 late-run). Of interest in this analysis were not only the factors that significantly influenced allele frequency, but also the relative effect of some pairs of factors. Such ranking was done with an *F*-statistic estimated as:

$$F_{df(i), df(j)} = [G_i / df(i)] / [G_j / df(j)]$$

where G_i and G_j are the log-likelihood ratios for factors i and j , and $df(i)$ and $df(j)$ are their degrees of freedom.

Other data sets were unbalanced and a saturated model could not be analyzed. Therefore, we estimated first order effects on allele frequency but not higher level interactions. We used only data for which there averaged at least one allele of each type per collection used in the analysis. Because infrequent observations may occasionally produce G -statistics that are not asymptotic to the χ^2 -distribution and exaggerate departure from expectations, the significance of all "significant" single factor tests were confirmed by comparison of the test statistic to a distribution of 2000 statistics generated by Monte-Carlo resampling assuming the null hypothesis, homogeneity. All results of this compared well with significance deduced from the χ^2 -distribution.

When the structural hierarchy of populations had been determined, we used analysis of variance of allele frequencies (assuming Hardy-Weinberg equilibrium) to estimate components of variation attributable to each factor in the hierarchy (Weir and Cockerham 1984; Weir 1996). These components are analogous to estimates of gene diversity (Nei 1973; Chakraborty and Leimar 1987) and can be used to estimate the number of immigrants ($N_e m$) per generation from:

$$\theta = \{4N_e m [n / (n-1)]^2 + 1\}^{-1}$$

where θ is the component of variance estimated from the analysis of variance, m is the rate of immigration into a component of the population structure, N_e is the effective size of the component ($N_e m$ is the number of individuals), and n is the number of components in a particular level of the hierarchical model. For example, if one considers timing to be either early or late, there are only 2 components, so the $[n/(n-1)]^2$ term is 4, whereas if one considers that there are a large number of streams in the area (n is large), even though we only sampled a subset of the total, $(n/(n-1))^2$ approaches 1 (Zhivotovsky et al. 1994).

RESULTS

We approached our questions about the hierarchical structure of pink salmon populations by starting at the finest scale, the within population structure of Auke Creek. Results obtained at the finest level should be pertinent to coarser scales, but the reverse may not be true. Data for odd-year Auke Creek pink salmon were available for three brood years, 1979, 1981, and 1983. For each year we had data from samples of all four Auke Creek spatially and temporally defined components for nearly every allozyme locus we examined. These data permitted us to examine the effects of **timing**, **site**, and **year** on allele frequency using a saturated model for these factors and their interactions (Table 1). The question

posed here involves the combined analysis of several loci to detect influences on the overall genetic structure of populations. The power in the analysis comes from the number of loci involved; significant divergence at particular loci is of lesser interest, especially if divergence is attributed to isolation and is random. In this analysis both **timing** ($P < 0.001$) and **year** ($P < 0.01$) significantly affected allele frequencies, whereas spawning **site** did not. Comparisons of the variability due to **timing** with that due to spawning **site** indicates that **timing** is more important than **site** ($P < 0.01$). Similarly, although both **timing** and **year** affect frequencies, **timing** appears to be a stronger influence.

From these results, we can deduce that population structure within Auke Creek can be conceptually structured as spawning **site** nested within **timing**. In this hierarchy, we consider **year** as replication of a particular spawning time and place within Auke Creek. Presumably returns to a time and place in Auke Creek derive primarily from parents spawning at the same place during the same time of the spawning season the previous generation. We used that hierarchy as the basis of an analysis of variance to partition genetic variation into components attributable to each level of hierarchy, analogous to gene diversity analysis. Although the components were small relative to the within-collection genetic variation, those attributable to differences in run timing and to differences between sites within run timing were much larger than their standard errors. Estimates (95% confidence interval) of gene flow ($N_e m$) were between 11 and 37.4 for the effective number of fish moving between early and late run times within Auke Creek and 41.7 to 165.8 for the number moving between intertidal and upstream components within a run time.

We extended our analysis of the genetic structure of odd-year pink salmon to additional streams in the area. Because **year** had a significant effect on allele frequencies and not all streams were sampled in every year, we restricted this analysis to collections sampled in 1979, before any genetically marked fish returned. Not all streams had both intertidal and upstream components, and we did not obtain samples for both early- and late-run fish for every stream. Therefore, it was not possible to analyze the complete model for all possible effects and interactions of effects on allele frequency. Our analysis examined the primary factors **timing**, **site**, and **stream** (Table 2). Both **timing** ($P < 0.001$) and **stream** ($P < 0.01$) significantly influenced allele frequencies; **timing** had a larger effect than either **stream** ($P < 0.001$) or **site** ($P < 0.05$).

We nested stream within run time and used analysis of variance to partition the genetic variation. The result was small components for both variation due to differences in run timing and to differences in

Table 1. A. Analysis of within stream population structure of odd-year pink salmon for Auke Creek, Alaska. Contingency analyses (log-linear modeling) partitioned the effects of spawning location (upstream or intertidal), spawning time (early or late), and year (1979, 1981, 1983) on allozyme variation. Tabled are G-statistics and degrees of freedom for each effect and interaction of effects. B. Gene flow (N_m) between components of odd-year pink salmon in Auke Creek, Alaska. Gene diversity was estimated using ANOVA of allele frequencies (Weir 1996). The population's structural hierarchy is spawning site (upstream or intertidal) within spawning time (early or late); years (1979, 1981, 1983) are replicates within sites. Estimates were based on 14 variable allozyme loci. * $P < 0.05$; ^a $P < 0.01$; ^c $P < 0.001$; ^d $P < 0.001$.

Locus	Time	Site	Year	T*S	T*Y	S*Y	T*S*Y	Total for locus
mAH-3*	31.33 ^d	1	4.36	0.87	1	4.93	2	47.39 ^d
mAH-4*	13.89 ^c	1	12.1	2.63	1	14.94 ^c	2	47.86 ^d
SAAT-3*	0.08	1	6.55*	2	0.05	2.20	2	18.84
PGDH*	0.22	1	0.65	0.36	1	2.01	2	9.21
GPIA*	0.01	1	3.62	0.34	1	1.18	2	15.12
PEPD-2*	8.04*	2	6.15	1.25	2	2.47	4	24.96
PGM-2*	7.86 ^b	1	3.84	4.09*	1	0.01	2	23.98*
G3PDH-1*	4.66*	1	0.05	1.13	1	2.08	2	9.64
mMEP-1*	0.16	1	6.11*	2	0.62	2.40	2	20.21*
MPI*	0.30	1	3.68	1.09	1	1.93	2	12.88
sIDHP-1*	11.03 ^c	1	0.33	3.37	1	2.09	2	22.65*
ADA-2*	0.14	1	4.92	1.00	1	1.28	2	7.74
Total	77.70 ^d	13	52.36*	20.01	13	34.33	26	260.48 ^d

F-test for run timing (Time) versus spawning location (Site): $F_{1,13} = 4.70$; $P < 0.01$.

F-test for run timing (Time) versus brood year spawning location (Year): $F_{13,28} = 2.97$; $P < 0.05$.

B.

Source	Parameter	Value $\pm$ S.E.	N_m (95% C.I.)
Total for collections	θ_{ss}	0.00504 $\pm$ 0.00071	
Among years within sites	$\theta_{ss} - \theta_s$	0.00042 $\pm$ 0.00060	includes ∞
Between sites within run time	$\theta_s - \theta_p$	0.00096 $\pm$ 0.00030	41.7 - 165.8
Between run times	θ_p	0.00367 $\pm$ 0.00102	11.0 - 37.4

Table 2. A. Analysis of population structure of odd-year pink salmon streams near Juneau, Alaska. Contingency analyses partitioned the effects of spawning time (early or late), site (upstream or intertidal), and stream (12 local streams) on allozyme variation of 1979 returns. Tabled are G-statistics and degrees of freedom for each effect. Data are unbalanced, so no interactions were estimated. B. Gene flow ($N_e m$) between components of odd-year pink salmon near Juneau, Alaska. Gene diversity was estimated using ANOVA of allele frequencies (Weir 1996). The population's structural hierarchy is stream within spawning time (early or late). Estimates were based on 16 variable allozyme loci. * $P < 0.05$; ^b $P < 0.01$; ^c $P < 0.001$; ^d $P < 0.001$.

A. Locus	Stream		Timing		Site	
SAAT-3*	18.88	11	0.32	1	0.01	1
PGDH*	20.33*	11	5.87*	1	0.51	1
mAH-3*	12.09	11	17.66 ^c	1	1.59	1
G3PDH-1*	9.83	11	1.12	1	0.00	1
GPIA*	15.05	11	0.22	1	0.35	1
PEPD-2*	28.22	22	0.29	2	0.39	2
PGM-2*	11.73	11	12.46 ^c	1	4.68*	1
mMEP-1*	11.04	11	0.02	1	7.29 ^b	1
MPI*	18.99	11	0.00	1	0.34	1
sIDHP-1*	15.64	10	3.84*	1	1.10	1
ADA-2*	17.22	11	15.39 ^d	1	0.32	1
Total for factor	179.02 ^b	131	57.19 ^d	12	16.58	12

F-test for run timing (Timing) versus stream (Stream): $F_{12,131} = 3.48$; $P < 0.001$

F-test for run timing (Timing) versus stream (Site): $F_{12,12} = 3.45$; $P < 0.05$

B. Source	Parameter	Value $\pm$ S.E.	$N_e m$ (95% C.I.)
Total for collections	θ_s	0.00286 $\pm$ 0.00062	
Among streams for a run time	$\theta_s - \theta_p$	0.00193 $\pm$ 0.00055	83.1 -292.5
Between run times	θ_p	0.00086 $\pm$ 0.00017	41.0 -182.7

stream. Estimates of gene flow ($N_e m$) were 41.0 to 182.7 (95% confidence interval) as the effective number of fish moving between early and late runs and between 83.1 to 292.5 fish immigrating into each stream from the combination of other streams.

Data from even-year pink salmon in the area were not as abundant and many of the systems were not sampled. Combining all the even-year data permitted us to examine the effect of single factors on allele frequencies, but not interactions of more than one factor. In this analysis, **timing** ($P < 0.001$), **stream** ($P < 0.001$), and **year** ($P < 0.001$) significantly influenced allele frequency, but **site** ($P > 0.05$) did not (Table 3). Comparisons of the effect of **timing** to the effects of **site**, **year**, and **stream** were not significant, which means that it is not possible to infer a hierarchy of effects, although it is probably safe to conclude that site is at the bottom of the hierarchy. Because the data were sparse and a clear hierarchy could not be deduced, no further analysis was conducted on these data.

In a parallel experiment conducted in the same years, Zhivotovsky et al. (1989) sampled streams on Iterup Island in the Kuril Islands throughout the spawning period. We analyzed the effects of **stream** and **timing** on allele frequencies of even-year collections made in 1982 and of **stream**, **timing**, and **year** on frequencies in collections taken in 1979, 1981, and 1983 (Table 4). Of these effects, only **year**

had a significant influence on allele frequencies, and that factor was examined only for odd-year samples. These analyses had relatively little power; data from only 3 loci were available for even-year collections, and data from 4 loci were available from odd-year collections.

DISCUSSION

Spawning time was previously demonstrated in several ways as an important component of population structure. Our prediction was that, **with sufficient statistical power**, we should be able to detect the influence of spawning time on allele frequencies. Results presented herein demonstrate those effects on different components of Auke Creek odd-year pink salmon returns. We also observed spawning timing effects on allele frequencies of both odd-year and even-year pink salmon in streams near Juneau, Alaska. For odd-year pink salmon we also detected a significant influence of year of return within Auke Creek and for stream in the survey of 1979 returns. In both analyses, spawning time had a stronger effect. Spawning site within the stream had no significant influence. The even-year pink salmon returns to the Juneau area were not as completely sampled (and therefore a weaker test), but exhibited effects of spawning time, year of return, and stream on allele frequencies. In that experiment, spawning time was

Table 3. Analysis of population structure of even-year pink salmon streams near Juneau, Alaska. Contingency analyses partitioned the effects of spawning time (early or late), site (upstream or intertidal), stream (6 local streams), and year (1978, 1980, 1982, and 1984) of sample on allozyme variation. Tabled are G-statistics and degrees of freedom for each effect. Data are unbalanced, no interactions were estimated. ^a $P < 0.05$; ^b $P < 0.01$; ^c $P < 0.001$; ^d $P < 0.001$.

Locus	Timing		Site		Year		Stream	
SAAT-3*	5.08 ^a	1	6.07 ^a	1	0.38	2	3.33	5
PGDH*	0.44	1	5.26 ^a	1	8.92 ^a	3	18.99 ^b	5
mAH-4*	0.37	1	0.58	1	7.31	3	5.74	4
G3PDH-1*	0.25	1	0.07	1	5.36	3	28.26 ^d	5
PEPD-2*	8.03 ^a	2	0.76	2	14.86 ^a	6	27.52	10
PGM-2*	8.70 ^b	1	0.75	1	0.74	3	12.57	5
PEPB-1*	0.31	2	2.60	2	0.51	2	18.30	10
sMDH-B2*	1.40	2	1.94	2	19.61 ^b	6	14.07	10
mMEP-1*	4.45 ^a	1	2.10	1	8.18 ^b	3	6.45	5
ADA-2*	5.76	2	0.84	2	6.93	4	5.12	10
sIDHP-1*	2.42	1	1.45	1	1.04	1	8.29	4
Total	37.21 ^d	15	22.42	15	73.84 ^c	36	148.64 ^d	73

F-test for Timing versus Site: $F_{15,15} = 1.66$; $P > 0.05$

F-test for Timing versus Year: $F_{15,36} = 1.21$; $P > 0.05$

F-test for Timing versus Stream: $F_{15,73} = 1.22$; $P > 0.05$

Table 4. Analysis of genetic structure of Iterup Island (Kuril) pink salmon. Log-likelihood ratios partitioned the effects of spawning time (early or late) and stream on allozyme variation. These are 1979, 1981, 1982, and 1983 returns. Tabled are G-statistics and degrees of freedom for each effect. Estimates of interactions of effects were confounded by the unbalanced data, but all were very small. ^a $P < 0.05$; ^b $P < 0.01$.

Even year return (1982)				
Locus	Stream		Timing	
G3PDH-1*	1.16	4	0.07	1
PGDH*	1.95	8	0.00	2
sMDH-B1,2*	7.56	4	0.80	1
Total	10.67	16	0.87	4

F-test for Stream versus Timing: $F_{16,4} = 1.50$; $P > 0.05$.

Odd year returns (1979, 1981, 1983)

Locus	Stream		Timing		Year	
G3PDH-1*	7.63	8	0.01	1	1.74	2
PGDH*	23.04	16	1.42	2	5.17	4
sMDH-B1,2*	13.92	8	1.31	1	10.59 ^a	2
PGM-2*	9.23	8	0.06	1	6.84 ^a	2
Total	53.82	40	2.80	5	24.34 ^b	10

F-test for Stream versus Timing: $F_{10,5} = 4.35$; $P > 0.05$

F-test for Stream versus Year: $F_{10,40} = 1.81$; $P > 0.05$

not a significantly stronger influence than year of return, spawning site, or stream. Tests of the effect of spawning time on Kuril Island pink salmon returns were quite weak because they involved only 3 or 4 loci. Only an effect of year of return was detected.

Failure to detect an effect or to be able to determine a hierarchy of effects in the latter analyses does not necessarily mean that there is no effect or hierarchy. Failure could also mean that with the number of loci, collections, and sample sizes used (i.e. the statistical power) the effects and structure could not be resolved, taking us back to our original prediction which required **sufficient power**. We are aware of two other studies that attempted to resolve an effect of return timing on allele frequencies. Whereas nine collections of even-year pink salmon from the Znamenka River and six collections from the

Ochepucha River on Sakhalin Island revealed no heterogeneity (Noll et al. In prep.), more powerful tests involving pools of collections indicated temporal structure of both even- and odd-year pink salmon returns to the Poronaisk River and odd-year returns to the Firsovka and Lesnaya rivers on Sakhalin Island (Altukhov et al. 1983).

In our interpretation of the results, we must consider the possibility that our marking experiments of 1979 and 1980 influenced our results. In order to minimize any influence we removed *sMDH-B1,2** entirely from the analysis of odd-year fish and removed *G3PDH-1** data from 1982 and 1984 late-run collections which might have been influenced by the less successful even-year marking experiment. It should be noted that the 1978, 1979, and 1980 brood years could not have been influenced by the

experiments, and most of the 1981 and 1982 Auke Creek returns revealed no effect. The number of parents used as breeders for the marked fish was large (about 200 males and 200 females) and their returns contributed at most one-half of the late returns. We detected no gametic disequilibrium in returning genetically marked fish (identified by a fin mark) and saw heterogeneity between years only at the *PEPD-2** locus of 1979 and 1981 late returns. *PEPD-2** does not contribute to the significance of interannual variability in analyses of odd-year collections. Finally, and most compelling, the analysis of the 1979 data for streams near Juneau, Alaska produced similar results.

The basis of the influences of spawning timing and site on genetic composition are easy to understand; interannual variation is not as straightforward. An obvious explanation is that differences between generations reflect random genetic drift, errors in sampling gametes from a finite population. An alternative explanation is that the difference attributed to year results in part from the spawning time effect. Most collections of samples were made on one or a few days during the early or the late returns, not throughout the run. Because return timing has a heritable component, temporal genetic structure exists beyond "early-" and "late-run" (Smoker et al. in prep.). Our inability to sample exactly the same portion of the run in several years may mean that some of the statistical effect of year of return reflects temporal genetic structure within a return.

For two of our odd-year analyses of Auke Creek and Juneau-area pink salmon, we estimated average gene flow between levels of hierarchy in genetically effective fish per generation ($N_e m$). Within odd-year Auke Creek returns, we estimated that 11.0 to 37.4 fish moved between spawning times and 41.7 to 165.8 moved between intertidal and upstream spawning areas. The size of both these estimates seems reasonable. Early and late runs have overlapping tails which might make the estimated number of migrants seem small; however, heritable adaptive differences (e.g. Hebert et al. accepted) between the runs may reduce fitness of hybrids and there is some evidence that fish spawning during the overlap of early and late returns have lower survivals (Joyce 1986). In Auke Creek, gene flow between intertidal and upstream spawners is enhanced by the weir which does not allow fish that move past it to return down stream. In light of this and the extensive movements in which pink salmon engage prior to spawning (Jones and Thomason 1984; Thrower 1988), it is surprising that the number is not larger.

Among odd-year populations in the Juneau area, we estimated that 41.0 to 182.7 fish moved between spawning times and that each stream received between

83.1 and 292.5 immigrants from other local systems in each of the early and late run components. The size of these estimates appears reasonable. But, intuitively, the estimate of movement between early and late components seems low whereas the movement among streams seems high based on our study of genetically marked Auke Creek pink salmon (Gharrett et al. in prep.).

It is important to realize that the model used to estimate $N_e m$ assumes no selection and that equilibrium has obtained (Zhivotovsky et al. 1994). Moreover, these estimates reflect long-term averages, not necessarily constant generation by generation movements. If equilibrium has not obtained or there is convergent (homogenizing) selection, the estimates of gene flow will be high. If there is divergent (heterogeneous) selection and equilibrium has obtained, the estimates of gene flow will be low (e.g. Gharrett 1994). Although equilibrium for gene diversity estimates (F_{ST} , G_{ST} , and θ_s) is relatively rapid on an evolutionary time scale (Chakraborty and Leimar 1987), the key phrase is **evolutionary time** which is measured in hundreds or more of generations. Much of the habitat pink salmon occupy is more transient than that. Watershed altering cataclysms such as land and snow slides and earthquakes occur frequently. In Southeast Alaska, many new streams appeared (and are still appearing) in recent centuries following glacial recession which began about 10,000 years ago and continues today. What is surprising is that given the dynamic nature of their habitat and of necessity the populations, there is any detectable structure. Our ability to attribute that structure to spawning time and stream suggest that both are critical components in the genetic structure of pink salmon populations and critical elements in their productivity. Although there is gene flow among population components, the estimates are relatively small, such numbers would be inadequate to ensure short-term maintenance of productivity if some of the components in the system were severely depleted. Over long time periods, however, the movements should be sufficient to colonize (or restore) available habitat. The question we can not address using molecular markers alone is the extent of divergence among population components that is adaptively important and that may be necessary for restoration after a natural or anthropogenic cataclysm.

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Appendix

Frequencies of allozyme alleles in collections of pink salmon near Juneau, Alaska. E designates early run, L late run, I intertidal spawners, and U upstream spawners. Common allele frequencies (100%) are omitted.

Creek	Year	Date	Time	Site	SAAT-3*		PGDH*		MAH-4*		Ada-2*		
					n	85*	n	90*	n	85* &115*	n	87* 113*	
Odd brood-year													
1	Sawmill	1979	12/VIII	E	I	98	0.21	100	0.02	101	0	101	0.05
2	Peterson (mainland)	1979	14/VIII	E	U	49	0.18	48	0.06	48	0	48	0.03
3a	Waydelich	1979	14/VIII-29/VIII	E	I&U	43	0.27	43	0.02	43	0	43	0.08
b		1979	12/IX	L	I&U	31	0.31	31	0	31	0	31	0.13
4a	Auke	1979	15/VIII-27/VIII	E	I	91	0.24	89	0.01	90	0.02	90	0.07
b		1979	27/VIII-30/VIII	E	U	80	0.18	80	0.01	80	0	81	0.08
c		1979	19/IX-27/IX	L	I	97	0.24	100	0.02	100	0	100	0.08
d		1979	5/IX-9/X	L	U	454	0.24	506	0.01	460	0	456	0.09
e		1981	13/VIII-1/IX	E	I	99	0.23	100	0.02	100	0.02	100	0.13
f		1981	13/VIII-25/VIII	E	U	101	0.24	101	0.02	101	0.02	101	0.07
g		1981	1/IX-18/IX	L	I	98	0.29	98	0.02	98	0	98	0.10
h		1981	15/IX-28/IX	L	U	101	0.23	99	0.01	102	0.01	102	0.12
i		1983	14/VIII	E	I	32	0.25	33	0.02	33	0	0	
j		1983	12/VIII	E	U	62	0.22	94	0.02	65	0.03	28	0.05
k		1983	1/IX-15/IX	L	I	71	0.23	88	0	88	0	0	
l		1983	14/IX	L	U	126	0.14	154	0.02	154	0.01	114	0.07
5	Salmon	1979	20/VIII	E	I&U	89	0.25	45	0.01	45	0	45	0.02
6	Sheep	1979	20/VIII-27/VIII	E	I	102	0.25	43	0.01	43	0	43	0.06
7	Bullion	1979	16/VIII-22/VIII	E	I	63	0.21	63	0.02	63	0.01	63	0.04
8a	Hilda	1979	19/VIII	E	I	30	0.32	33	0.02	33	0.02	32	0.06
b		1979	7/XI	L	I	58	0.21	44	0	44	0.01	44	0.13
9a	Middle Point	1979	19/VIII	E	I	47	0.26	54	0.02	54	0.01	54	0.04
b		1979	7/IX	L	I	76	0.20	67	0	76	0.01	75	0.11
10a	Peterson (Douglas I.)	1979	20/VIII	E	I	41	0.24	40	0.03	40	0	40	0.08
b		1979	29/VIII	E	U	41	0.26	42	0.04	42	0	42	0.07
c		1979	14/IX-18/IX	L	I	52	0.28	51	0.02	51	0	51	0.08
11a	Fish	1979	7/VIII-13/VIII	E	I	83	0.23	83	0.05	83	0.01	83	0.06
b		1979	13/VIII	E	U	87	0.34	87	0.03	87	0.01	66	0.04
c		1979	18/IX-21/IX	L	I	88	0.29	89	0.02	89	0.01	89	0.10
12	Bear	1979	25/VIII	E	I&U	80	0.16	80	0.01	80	0.01	79	0.07
Even brood-year													
2a	Peterson (mainland)	1978	25/VIII	E	U	0		41	0.06	0		0	
b		1978	13/IX	L	U	0		45	0.04	0		0	
c		1982	3/IX-5/IX	E	U	85	0.31	97	0.04	50	0.03	97	0.05 0.03
3a	Waydelich	1980	20/VIII-25/VIII	E	I&U	100	0.27	104	0.04	103	0.04	103	0.05 0.02
b		1980	8/IX-19/IX	L	I&U	100	0.31	78	0.04	102	0.03	102	0.01 0.01
c		1982	2/IX	E	I&U	95	0.23	100	0.07	100	0.04	100	0.05 0.03
d		1982	24/IX	L	I&U	98	0.28	100	0.04	101	0.01	101	0.07 0.02
e		1984	28/VIII	E	I&U	71	0.25	78	0	78	0.04	40	0.11 0.04
f		1984	19/IX-26/IX	L	I&U	28	0.29	28	0.05	26	0.08	28	0.07 0.04
4a	Auke	1978	22/VIII-3/IX	E	U	0		128	0.06	64	0.06	0	
b		1978	9/X	L	I	0		63	0.08	15	0.17	0	
c		1978	5/IX-9/X	L	U	0		133	0.04	33	0.06	0	
d		1980	24/VIII	E	I	88	0.22	87	0.07	98	0.04	98	0.07 0.01
e		1980	24/VIII	E	U	92	0.26	90	0.04	103	0.03	103	0.11 0.01
f		1980	6/IX-28/IX	L	U	173	0.30	206	0.06	214	0.05	98	0.04 0.01
g		1982	pre 6/IX	E	I	63	0.27	67	0.05	67	0.05	67	0.05 0.04
h		1982	1/IX	E	U	100	0.29	100	0.06	100	0.03	100	0.02 0.01
i		1982	12/IX-26/IX	L	U	115	0.26	119	0.05	119	0.04	119	0.05 0.03
j		1984	30/VIII-6/IV	E	I	80	0.19	80	0.03	80	0.06	80	0.06 0.04
k		1984	9/IX-22/IX	E	U	89	0.30	90	0.04	90	0.07	0	
l		1984	18/IX-19/IX	L	I	80	0.29	80	0.07	80	0.06	80	0.04 0.01
m		1984	21/VIII-25/VIII	L	U	90	0.32	90	0.04	90	0.06	0	
5	Salmon	1982	7/IX	E	I&U	49	0.21	50	0.03	0		50	0.05 0.01
10	Peterson (Douglas I.)	1982	14/IX	L	I&U	100	0.25	100	0.03	100	0.07	50	0.04 0.01
11a	Fish	1978	27/VIII-31/VIII	E	I	0		183	0.09	120	0.05	0	
b		1978	27/VIII-31/VIII	E	U	0		78	0.06	51	0.04	0	
c		1982	12/IX	L	I&U	82	0.28	80	0.08	100	0.05	100	0.04 0.02

Appendix (continued)

Creek	G3PDH-1*		PEPD-2*		PGM-2*		mMEP-1*		siDHP-1*		mAH-3*		GP/A*		MPI*		
	n	200*	n	109*	93*	n	150*	n	130*	n	120*	n	78*	n	90*	n	85*
	& others										& 130*				110*		115*
Odd brood-year																	
1	101	0.12	101	0.21	0.14	101	0.06	100	0.03	101	0.59	101	0.01	101	0.01	101	0
2	47	0.06	48	0.17	0.10	48	0.04	48	0.02	47	0.78	48	0	48	0.01	48	0.02
3a	43	0.12	43	0.17	0.09	43	0.05	43	0.03	43	0.66	43	0.02	43	0	43	0
b	3	0.06	31	0.19	0.10	31	0.06	31	0.02	31	0.71	30	0	31	0	31	0
4a	90	0.11	88	0.21	0.11	90	0.05	90	0.04	86	0.77	90	0.01	90	0	90	0.01
b	81	0.07	81	0.20	0.14	81	0.07	81	0.05	80	0.62	80	0.03	81	0	81	0.01
c	100	0.09	100	0.21	0.11	100	0.06	100	0.03	85	0.59	100	0	100	0.01	100	0.01
d	460	0.12	459	0.21	0.10	460	0.03	461	0.06	90	0.62	460	0.00	459	0.00	457	0.00
e	100	0.09	99	0.24	0.11	100	0.06	100	0.05	100	0.72	100	0.01	100	0.01	98	0.02
f	101	0.10	101	0.24	0.10	101	0.05	101	0.06	98	0.68	101	0.04	101	0.02	100	0.01
g	98	0.13	97	0.21	0.11	98	0.05	98	0.06	95	0.62	98	0	98	0.01	98	0.01
h	102	0.13	102	0.14	0.08	102	0.01	102	0.03	101	0.62	102	0.01	102	0	101	0.01
i	33	0.13	33	0.24	0.17	33	0.09	33	0.02	33	0.65	33	0.03	33	0	33	0
j	572	0.10	423	0.20	0.13	507	0.05	158	0.09	65	0.67	65	0.02	539	0.00	159	0
k	88	0.13	83	0.20	0.11	88	0.07	68	0.09	86	0.63	88	0	88	0.01	88	0
l	154	0.11	0			154	0.04	120	0.06	53	0.63	154	0	154	0.01	153	0.01
5	45	0.17	45	0.27	0.02	45	0.06	45	0.06	45	0.66	45	0.02	45	0	45	0
6	43	0.09	43	0.22	0.13	43	0.07	43	0.06	43	0.69	43	0.03	43	0	43	0
7	63	0.12	63	0.18	0.14	63	0.09	63	0.06	0		63	0.01	63	0	63	0.02
8a	33	0.11	33	0.24	0.09	33	0.06	33	0.03	32	0.53	33	0	33	0	33	0.01
b	44	0.10	44	0.14	0.13	44	0.03	44	0.02	0		44	0.01	44	0	44	0
9a	54	0.13	54	0.20	0.06	54	0.06	54	0.04	51	0.66	54	0.02	54	0	54	0.02
b	76	0.13	76	0.16	0.11	76	0.08	76	0.02	70	0.67	76	0.01	76	0.01	76	0.01
10a	40	0.13	40	0.20	0.13	40	0.10	40	0.04	40	0.66	40	0	40	0	40	0
b	42	0.18	42	0.15	0.12	42	0.08	42	0.06	40	0.65	42	0.01	42	0.01	42	0
c	51	0.09	51	0.18	0.20	51	0.01	51	0.03	51	0.60	51	0.01	51	0	51	0.02
11a	83	0.07	82	0.16	0.07	83	0.05	83	0.04	83	0.66	83	0.03	83	0	83	0
b	87	0.07	62	0.14	0.15	87	0.06	86	0.05	85	0.71	87	0.01	87	0	64	0
c	89	0.13	89	0.20	0.11	89	0.04	89	0.02	89	0.61	89	0	89	0	89	0.01
12	80	0.09	79	0.19	0.13	80	0.06	80	0.03	80	0.65	80	0.04	80	0	80	0
Creek	G3PDH-1*		PEPD-2*		PGM-2*		mMEP-1*		siDHP-1*		PEPB-1*		MDH-B1,2*				
	n	200*	n	109*	93*	n	150*	n	130*	n	120*	n	130*	140*	n	130*	70*
	& others										& 130*						
Even brood-year																	
2a	47	0.20	36	0.24	0.22	47	0	43	0.19	0		0		47	0.01	0	
b	46	0.17	37	0.23	0.20	45	0	38	0.21	0		0		46	0	0	
c	96	0.15	97	0.22	0.21	97	0	77	0.19	0		95	0.17	0.01	97	0	0
3a	104	0.13	104	0.24	0.21	104	0.01	104	0.27	0		0		104	0.00	0	
b	102	0.19	102	0.19	0.25	102	0.00	102	0.26	0		0		102	0.01	0.02	
c	100	0.14	98	0.22	0.22	100	0	99	0.19	98	0.37	100	0.15	0.01	100	0.02	0.01
d	100	0.18	97	0.19	0.23	101	0.03	101	0.23	84	0.27	50	0.10	0	101	0.02	0
e	78	0.13	78	0.21	0.16	78	0	78	0.24	78	0.35	78	0.12	0.01	78	0.01	0.02
f	28	0.18	28	0.29	0.30	28	0	27	0.28	23	0.33	28	0.14	0.02	28	0	0
4a	132	0.22	74	0.22	0.28	131	0.01	123	0.22	0	0			133	0.02	0.00	
b	64	0.17	58	0.16	0.33	64	0.02	61	0.29	0		0		64	0	0	
c	244	0.19	31	0.23	0.26	220	0.01	236	0.26	0		0		235	0.01	0.00	
d	98	0.22	98	0.18	0.27	98	0	98	0.24	0		0		98	0	0	
e	104	0.21	103	0.16	0.26	102	0.01	104	0.25	0		0		104	0.00	0.00	
f	214	0.17	214	0.14	0.32	214	0.01	213	0.21	0		0		214	0.01	0	
g	67	0.13	67	0.19	0.28	67	0	67	0.26	51	0.25	67	0.09	0.02	67	0	0
h	99	0.31	98	0.14	0.22	100	0	99	0.18	100	0.25	90	0.11	0.03	100	0	0
i	0		118	0.20	0.27	119	0	119	0.19	103	0.25	119	0.11	0.03	119	0	0
j	80	0.17	80	0.19	0.23	80	0	80	0.21	78	0.35	80	0.14	0.03	80	0.02	0.01
k	703	0.19	763	0.22	0.27	90	0	753	0.19	0		90	0.09	0.02	90	0.03	0
l	0		80	0.15	0.35	80	0.01	80	0.21	79	0.25	80	0.12	0.05	80	0.03	0
m	0		90	0.20	0.31	90	0.02	90	0.23	0		90	0.07	0.01	90	0.00	0.04
5	50	0.15	50	0.22	0.27	50	0	48	0.22	45	0.29	48	0.07	0.01	50	0.01	0.01
10	100	0.27	100	0.22	0.27	100	0.02	100	0.23	100	0.34	99	0.11	0.02	100	0.02	0.00
11a	195	0.23	154	0.23	0.19	187	0	162	0.20	0		0		194	0.01	0	
b	79	0.25	57	0.19	0.25	76	0.01	62	0.15	0		0		79	0.01	0	
c	100	0.24	97	0.20	0.25	100	0	99	0.22	86	0.28	99	0.09	0.03	100	0.02	0.01

Determining Area of Origin of Pink Salmon Juveniles on Their Catadromous Migration in the Okhotsk Sea in 1995 Using Genetic Stock Identification Techniques.

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The purpose of this study was to reveal distribution patterns and density of even-year pink salmon juveniles in the eastern Okhotsk Sea, to identify the origin of juveniles caught in mixed stock fisheries in the Okhotsk Sea, and to estimate their relative abundance and migration routes. Trawls at 45 stations in the eastern Okhotsk Sea, from September 10th to October 9th, 1995, yielded a total catch of 3,241 pink salmon juveniles. Of those, 775 were measured and weighed, and 200 were analyzed by protein starch gel electrophoresis.

Allelic frequencies in juveniles collected at eight stations showed significant heterogeneity ($P < 0.01$) at four loci - sAAT-3*, GR*, PEPB-1*, and PGDH*. The genetic baseline used for mixed-stock identification analysis included allelic frequencies at 31 polymorphic loci in 18 stocks from rivers of the Pacific Ocean coast, studied in 1990, 1992, and 1994. The analysis of simulated mixtures which were composed of 100% of fish from one region showed sufficient ability of the baseline to identify stocks from a mixture.

Mean estimates calculated from Maximum Likelihood Estimate (MLE) analysis showed regional contributions from the simulated mixtures of: western Kamchatka - 39.1%, northwestern Kamchatka - 30.3%, Magadan 0.3%, Sakhalin - 4.3%, southern Kuril Islands - 10.9%, Hokkaido 10.7%, and unknown - 4.4%. In two large regional groups, the estimates were: southern Okhotsk coast - $25.9 \pm 7.5\%$, northern Okhotsk coast - $69.7 \pm 7.5\%$, and unknown - 4.4%. Weighted by the actual abundance of juveniles in the sea, the regional ratio became: western Kamchatka - 57.0%, northwestern Kamchatka - 29.1%, Magadan - 1.6%, Sakhalin - 2.4%, southern Kuril Islands - 3.5%, Hokkaido - 1.9%, and unknown 4.7%; southern Okhotsk coast - 7.8%, northern Okhotsk coast 87.7%, and unknown - 4.7%. Juveniles from Hokkaido and Iturup rivers were found at latitude 55 N, and juveniles from the southwestern Kamchatka rivers were found at latitude 58 N, which indicates that juveniles migrate north after entering the sea. The migration routes of juveniles from the southern Okhotsk coast, Kamchatka and Magadan are discussed.



INTRODUCTION

Pacific salmon spend significant portion of their life cycle in the Pacific Ocean and its attached seas. Pink salmon, *Oncorhynchus gorbuscha* (Walbaum), juveniles migrate to the sea the same spring they emerge from their redds (Gritzenko et al. 1987), and some still have residual yolk upon entering salt water (Kinas 1988). Because of such an early migration, the mortality of pink salmon may be the highest at this period of their life cycle (Karpenko 1996a,b). Estimation of the survival rate of pink salmon in this period is important in forecasting the abundance of returning adults (Karpenko et al. 1993). The most reliable way for such estimations is to survey the

density of juveniles in the sea, and to calculate approximate abundance after the period of adaptation to sea water when juveniles have moved away off the shore. Such survey studies were performed in the Okhotsk (Shuntov 1989a) and Bering sea (Shuntov 1989b; Erokhin 1990). During the life in the Okhotsk Sea and the Pacific Ocean the survival rates of pink salmon are usually more constant and easier to forecast (Karpenko 1996a). Therefore, the juvenile survey data in the Okhotsk Sea could be very useful in fisheries management.

Pink salmon juveniles stay in the Okhotsk Sea in summer to feed before migrating to the Pacific Ocean in September-November. The Okhotsk Sea is a mixing ground for juveniles from three main natal

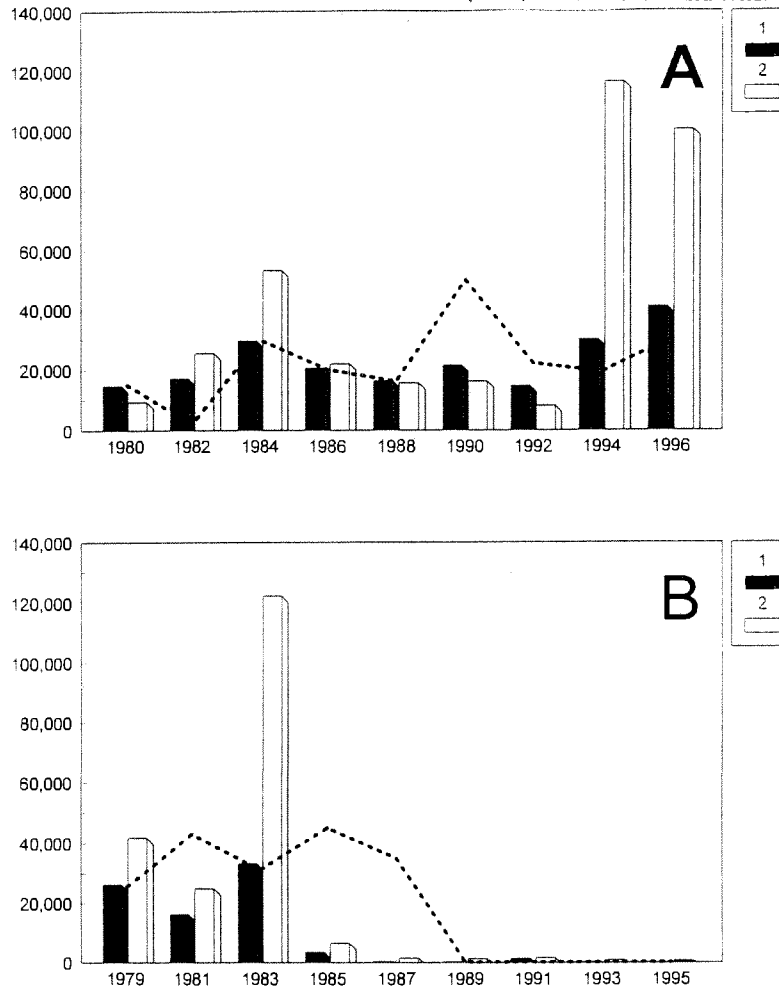
regions: West Kamchatka, East Sakhalin Island, and the northern Okhotsk Sea coast (Magadan Coast).

Pink are the most abundant of Pacific salmon, and they are of significant commercial importance for many Pacific rim countries. They spend approximately a year in freshwater, and a year in the ocean. Their life cycle consists of exactly two years between spawning of consequent generations (Shuntov et al. 1993a,b). Generations spawning in odd years never interbreed with generations spawning in even years. Thus, the species is divided into two genetically different broodlines (Salmenkova et al. 1981; Beacham et al. 1985, 1988; Gagalchy 1986; Jivotovsky et al. 1989; Efremov 1991; Makoyedov et al. 1993), which must be treated separately for research and management purposes. Both even-year and odd-year broodlines experience great fluctuations in abundance (Varnavskaya et al. 1995), making forecasting difficult. Previous miscalculations in forecasting were made in 1985 and 1987 when a great decline in odd-year pink salmon abundance occurred in southwestern Kamchatka rivers (Fig. 1).

In 1983 approximately 100 million of pink salmon spawned in this area; consequently managers expected

a similar return in 1985. Instead, an extremely low return of pink salmon occurred in 1985. Overcrowding on the spawning grounds in 1983, resulting in low survival of eggs and fry, is considered the main cause for the decline. A low return of pink salmon in 1985 was expected to produce a low return in 1987. However, an autumn 1986 survey of juveniles in the Okhotsk Sea revealed a high abundance of pink juveniles on the Kamchatka shelf, and the inference was made that fry survival was high and resulted in a high forecast for the 1987 return (Fig. 1). The expected return did not occur, and led us to believe that Kamchatkan juvenile pink salmon share the Kamchatka shelf with juveniles from other spawning areas, such as those from Magadan or Sakhalin. The main problem was to identify the juveniles from different areas and to estimate their relative abundance on Kamchatka shelf. Such information could be useful for estimations of survival rates of juveniles from different areas, and to reveal the migration routes of juveniles in Okhotsk Sea. The only way to collect such information was to identify genetic markers suitable for mixed-stock identification of juveniles from different spawning areas.

Fig. 1 Catches (1), forecast (---), and spawners (2) of pink salmon of even (A) and odd (B) year broodlines from the rivers of Okhotsk Sea coast of Kamchatka in 1979-1996. X-axis – years, Y-axis – thousand tons.



An Asian pink salmon genetic baseline was developed in a cooperative study by American, Canadian, Japanese, and Russian scientists, from 1988 to 1994. (Varnavskaya and Beacham 1992; Varnavskaya 1992; Shaklee and Varnavskaya 1994; Noll et al. 1995; Noll et al. in press).

The purpose of the present study is to determine the distribution and density of even-year pink salmon juveniles in the eastern Okhotsk Sea, to identify the juveniles originating from different spawning areas of the Okhotsk Sea coast in mixed-stock fisheries, and to estimate their relative abundance and migration routes.

MATERIAL AND METHODS

Juvenile pink salmon were caught by trawling at 45 stations in the eastern Okhotsk Sea (Fig. 2, Table 1) from September 10th until October 9th, 1995. Trawling was conducted from south to north

between latitudes 51°N - 58°N, and from east to west and back between longitudes 148°E - 156°E (Fig. 2). Surface water temperatures were measured at each station. A total of 3,241 juveniles were caught, 775 were measured and weighed, 200 of these were analyzed by protein starch gel electrophoresis. (Table 1, Fig. 2). Four tissues (skeletal muscle, heart muscle, liver, and eye retina) were sampled from each freshly caught fish and preserved at -20°C. Long-term storage was in liquid nitrogen. The analysis was conducted at Auke Bay Laboratory by horizontal starch gel electrophoresis (Aebersold et al. 1987). The tissue samples were homogenized in a mixture containing reagents to break down mitochondria, so as to incorporate in the analysis enzymes fixed on the mitochondrial membrane (Aebersold et al. 1987). The proteins were fractionated by starch gel electrophoresis using six buffer systems (Table 2). The active enzyme zones on the gel were revealed by

Table 1. Average body lengths and weights of pink salmon juveniles sampled from mixed-stock catches in Okhotsk Sea in 1995.

Area of Okhotsk Sea	Body length (cm)		Body mass (g)		Number of fish
	Average	Min-Max	Average	Min-Max	
South-West	18.6	15.5-25.5	94.7	34-170	208
South-East	18.9	12.6-25.0	68.7	15-160	197
West, central part	22.2	18.0-25.0	118.3	55-175	134
East, central part	20.4	14.3-25.3	88.8	27-165	94
North-West	18.1	17.2-20.2	67.3	53-95	19
North-East	19.1	13.9-28.0	69.7	22-28	113

Fig. 2 Trawl stations and average water surface temperatures in eastern Okhotsk Sea in September-October, 1995. Stars designated with numbers - the trawl stations where fish were sampled for electrophoretic analysis.

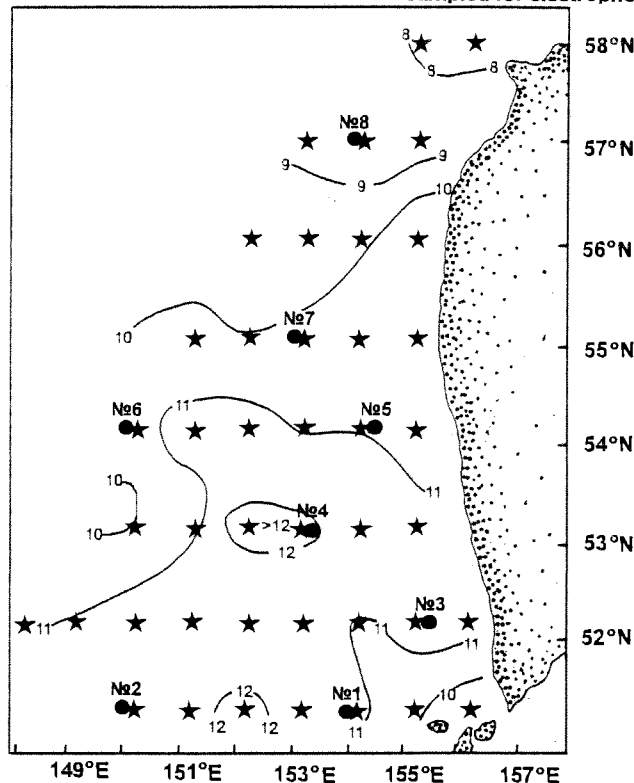


Table 2. Enzyme and loci, screened in even-year broodline pink salmon juveniles from mixed-stock catches in Okhotsk Sea in 1995.

Enzyme	Subunit structure	IUBNC number	Loci	BS	Tissue
Aspartate aminotransferase	dimer	2.6.1.1	<i>sAAT1,2</i>	2,3,4	MH
			<i>mAAT1</i>	2,3,4	MH
			<i>mAAT2</i>	2,3,4	L
Adenosine deaminase	monomer	3.5.4.4	<i>ADA-2</i>	3	MH
Creatine kinase	dimer	2.7.3.2	<i>CKA1</i>	3	M
			<i>CKA2</i>	3	M
Formaldehyde dehydrogenase	dimer	1.2.1.1	<i>FGDH</i>	4	MH
Glycerol-3-phosphate dehydrogenase	dimer	1.1.1.8	<i>G3PDH1</i>	6	M
Glucose-6-phosphate isomerase	dimer	5.3.1.9	<i>GPIA</i>	3	MH
Isocitrate dehydrogenase	dimer		<i>mIDHP1</i>	4	M
Lactate dehydrogenase	tetramer	1.1.1.14	<i>LDHA1</i>	2,3	M
			<i>LDHA2</i>	2,3	M
			<i>LDHB1</i>	2,3	MHE
			<i>LDHB2</i>	2,3	MLE
			<i>LDHC</i>	2,3	E
Malate dehydrogenase NAD	dimer	1.1.1.37	<i>sMDHA1,2</i>	4,6	LHE
			<i>sMDHB1,2</i>	4,6	M
Malate dehydrogenase NADP	tetramer	1.1.1.40	<i>mMEP1</i>	1	MH
Mannosephosphate isomerase	monomer	5.3.1.8	<i>MPI</i>	2	H
Peptidases		3.4.*.*			
Glycyl-leucine(GL, DPEP)	dimer		<i>PEPA</i>	2	M
Leucyl-glycyl-glycine(LGG, TAPEP)	dimer		<i>PEPB1</i>	2	MLE
Phenylalanine-proline(PP, PDPEP)	dimer		<i>PEPD1</i>	2,4	MH
			<i>PEPD2</i>		MH
6-Phosphogluconate dehydrogenase	dimer	1.1.1.44	<i>PGDH</i>	4	MHLE
Phosphoglucomutase	monomer	5.4.2.2	<i>PGM2</i>	4	MHLE
Pyruvate kinase		2.7.1.40	<i>PK2</i>	4	MHE
Triosephosphate isomerase	dimer	5.3.1.1	<i>TPI1</i>	2,3	MHE
			<i>TPI2</i>	2,3	MHE
			<i>TPI3</i>	2,3	MHE
			<i>TPI4</i>	2,3	mHE

BS – buffer system: 1 - TRIS - citrate buffer, pH 5.8 (TC-4) (Dreyfus and Alexander 1972), 2 - TRIS-EDTA-borate buffer, pH 8.5 (TBE) (Boyer et al. 1963), 3 - TRIS-citrate-lithium-borate buffer, pH 8.0 (TBCL) (Ridgway et al. 1970), 4 - N-(3-aminopropyle)-morpholine-citrate-EDTA buffer, pH 6.1 (ACE) (Clayton and Tretiak 1972), 5 - TRIS-Glycine buffer, pH 8.9 (0.04M TRIS, 0.12M glycine for gel and electrode buffer), 6 - N-(3-aminopropyle)-morpholine-citrate buffer (AC) (Dreyfus and Alexander 1972). Tissue designation: M - muscle, H - heart, E - eye, L - liver.

standard stain procedure with agar cover (Aebersold et al., 1987). The enzyme coding loci and alleles were designated using current nomenclature (Shaklee et al. 1990).

The list of analyzed enzymes and laboratory conditions for each are presented in Table 2. Genetic interpretation of screened allozyme variation was made according to previous studies (Beacham et al. 1985, 1988; Gharrett et al. 1988; Shaklee et al. 1991).

Statistical analysis of the resulting data was performed using BIOSYS (Swofford and Selander 1981) and NTSYS (Rohlf 1992) computer programs. The significance of departures from Hardy-Weinberg-Castle equilibrium was estimated using a chi-square goodness-fit test. We used likelihood ratio analysis (G-test; Sokal and Rohlf 1981) to test for heterogeneity in allelic frequencies among samples of juveniles collected at different times and locations in

the Okhotsk Sea.

Conditional Maximum Likelihood estimates (MLE) were calculated from the mixed fisheries using GIRLS program (Pella and Milner 1987; Masuda et al. 1991). This approach had already been used to determine the origin of mixed-stock fisheries of adult pink salmon in the Okhotsk Sea in August, 1994 (Varnavskaya and Davydenko 1995).

The baseline with which the juvenile mixture was compared for stock identification was selected from the even-year pink salmon baseline collected in 1988-1994 (Noll et al. 1995, in press, plus our unpublished data). It included allelic frequencies at 31 variable loci from 18 pink salmon populations from the Okhotsk Sea coast (Tables 2,3). The genetic frequencies from geographically close and genetically similar populations were pooled to increase the number of loci for better accuracy and precision. For the MLE-analysis the populations were combined in regional groups: Hokkaido (Japan), eastern Sakhalin, Iturup (southern Kuril Islands), north-western Kamchatka, south-western Kamchatka, and Magadan (northern coast of the Okhotsk Sea).

A series of mixtures were simulated from the baseline using the program SIMULATR (Masuda et al. 1991). SIMULATR generates random samples from the baseline data, and creates mixtures of specified size and composition. Each simulated mixture was then analyzed using the Conditional Maximum Likelihood Estimate (MLE). Simulated mixtures were created in two ways: an equal

percentage of abundance from each of the 18 populations and a percentage of 100% of each regional group of populations (total of 8 mixtures). In simulation 2 the actual contribution approaches the limit of the MLE, 0 or 100%. Results are presented as average estimates.

RESULTS

Water surface temperatures at examined stations in the Okhotsk sea (Fig. 2) averaged 10°C in September and October 1995. Regionally, northern Okhotsk Sea stations averaged 8.5°C, and southern stations averaged approximately 11°C. Central stations were the warmest, with surface temperatures averaging 12°C. This central, warmer area exhibited the greatest abundance (Fig. 3) and largest average body size (Table 1) of pink salmon juveniles. Other large schools of pink salmon juveniles were found in the northern part of the Okhotsk Sea, but no juveniles were found near shore to Western Kamchatka in September and October.

Allelic frequencies in juveniles collected at eight stations (Fig. 4) were significantly heterogeneous at four loci — sAAT-3*, GR*, PEP-B1*, and PGDH*. The total for all loci was $P < 0.01$. This suggests that juveniles caught in different locations of the Okhotsk Sea originated from genetically different populations.

Before analyzing mixed-stock juvenile fisheries, simulations, each composed of 100% of fish from a single region, were run to estimate the accuracy and

Table 3. Populations of even-year broodline pink salmon included in database (31 variable loci) for identification in mixed-stock catches of juveniles in Okhotsk Sea in 1995.

Region	N	Population	Number of collections	Number of fish	Years
Japan	1	Kushiro River	1	100	1988
	2	Tokadzu River	1	100	1988
	3	Yurappu	1	100	1988
Sakhalin	4	Monetka	2	200	1990
	5	Znamenka	2	200	1990
	6	Lutoga	3	300	1990,92
	7	Pugachevka	2	200	1990,92
	8	Dolinka	2	100	1990,92
	9	South-Eastern rivers	9	900	1992
Kuril Islands	10	Rivers of Iturup Island	3	240	1994
West Kamchatka	11	Kik-Chik	1	80	1990
	12	Utka	2	160	1990,92
	13	Kol	3	240	1990,92
	14	Homutina	2	160	1990,92
	15	Pymta	2	160	1990,92
North-West Kamchatka	16	Hairusova, Kovran	4	200	1990,94
Magadan Coast of Okhotsk Sea	17	Uglekank	1	80	1990
	18	Tau	1	80	1990
Total			42	3600	1988,90,92,94

Table 4. Log-likelihood analysis (G-test) of genetic heterogeneity among collections of juveniles from Okhotsk Sea in 1995.

Loci	Number of fish	q	G-test	IDF	P
<i>sAAT1,2</i>	199	0.992	5.9	7	non
<i>sAAT-3</i>	180	0.969	21.9	7	<0.01
<i>mAAT-4</i>	139	0.525	1.4	6	non
<i>ADA-2</i>	188	0.952	15.5	14	non
<i>FGDH</i>	172	0.994	8.0	14	non
<i>FH</i>	170	0.977	18.5	14	non
<i>G3PDH1</i>	199	0.915	6.1	7	non
<i>GDA</i>	194	0.474	13.8	14	non
<i>GR</i>	197	0.926	18.3	7	<0.01
<i>mMEP1</i>	196	0.806	7.1	7	non
<i>PEPB1</i>	186	0.852	33.3	7	<0.001
<i>PEPD2</i>	195	0.618	5.1	14	non
<i>PGDH</i>	196	0.834	17.1	7	<0.05
Total	-	-	180.9	132	<0.01

precision of the baseline for stock identification analysis. The results of the simulations showed that with our baseline data we were able to reveal in the mixture the portion mainly not less than 5-10%.

To determine the distribution of juveniles from different natal rivers in the eastern Okhotsk Sea in September and October, MLE analysis was used to calculate percent composition for each mixed-stock collection (Fig. 4). Off the southwestern end of Kamchatka (stations 1, 2 and 3, Fig. 4), juveniles from Sakhalin comprised about 16, 18 and 6%, from Hokkaido - 9, 23 and 6%, and from Iturup - 4, 2 and 26%. Juveniles from the southern Okhotsk Sea Coast (Sakhalin, southern Kuril Islands, and Japan) comprised nearly 50% over these three collections (Fig. 4). A collection from the station 7 was of a similar composition. At all four above mentioned stations (1, 2, 3, and 7) the juveniles were of the lowest abundance (25 fish per trawl) (Fig. 3). At all other stations fish from Kamchatka predominated (up to 95%). At stations 4 (300 fish per trawl), 5 (100 fish per trawl), and 8 (100 fish per trawl) juveniles were very abundant (Fig. 3), and fish from the southwestern Kamchatka rivers predominated in collections (Fig. 4).

Estimates of percent origin of juvenile pink salmon in the Sea of Okhotsk were made based on average of individual station percent origins weighted by the number of fish per trawl. The results were: south-western Kamchatka - 57.0%, northwestern Kamchatka - 29.1%, the Magadan coast - 1.6%, Sakhalin - 2.4%, southern Kuril Islands - 3.5%, Hokkaido - 1.9% and unknown 4.7%. For the total, the southern Okhotsk Coast aggregate comprised 7.8%, the northern Okhotsk Coast aggregate comprised 87.7%, and unknown - 4.7%

DISCUSSION

Pink salmon juveniles from Hokkaido and Iturup rivers were found at latitude 55°N and those from South-Western Kamchatka rivers were found at latitude 58°N. This indicates that pink salmon juveniles are migrating far north of their natal rivers using ocean currents which flow north along the Kuril and Kamchatka shelf (Davydov 1975). Kuril and Hokkaido pink salmon juveniles migrate north along the Kuril and Kamchatka shelf, turn to the south somewhere at 53-55°N latitude, and then head to the south (Fig 5). Having already covered a significant distance through rich feeding grounds, they grow to 21-24 cm while traveling north, and gain larger size on their way south. Migrating simultaneously in the same currents are small southwestern Kamchatkan juveniles (Fig. 5). These juveniles continue the northerly migration to Shelekhov Bay and Gijiga Inlet after the southern juveniles turn south around 55°N. In Shelekhov Bay, two currents meet and mix, providing ample nutrients and propitious feeding and growth for juveniles (Davydov 1975). Kamchatkan juveniles probably remain in Shelekhov Bay for a substantial period of time (Erokhin 1990). This is confirmed by the fact that the stock composition of juveniles in this zone (Fig. 4) resembled the actual ratio of abundance of northern and southern Kamchatkan even-year pink salmon stocks (Varnavskaya et al. 1995). Juveniles from Magadan Coast may also migrate in the northeastern direction to Shelekhov Bay and mix with juveniles from Kamchatka. Determining an accurate estimate of Magadan region juveniles in a mixture is difficult because the rivers of that region yield a low

Fig. 3 The density of schools of juveniles in eastern Okhotsk Sea in September-October, 1995. Numbers represent the quantity of fish caught in one trawl.

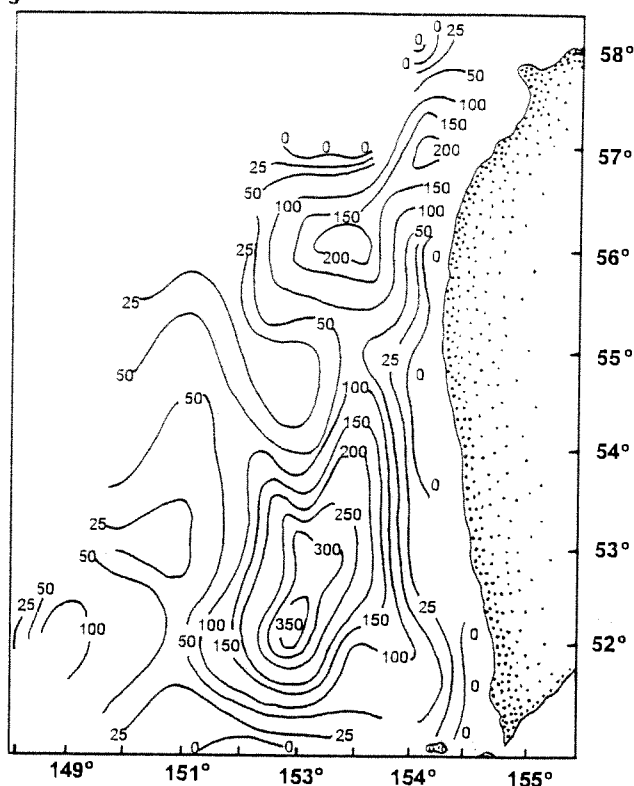


Fig. 4 The percentage of juveniles from six spawning regions in mixed samples calculated by MLE-analysis based on allelic variation at 31 loci in eastern Okhotsk Sea in September-October, 1995.

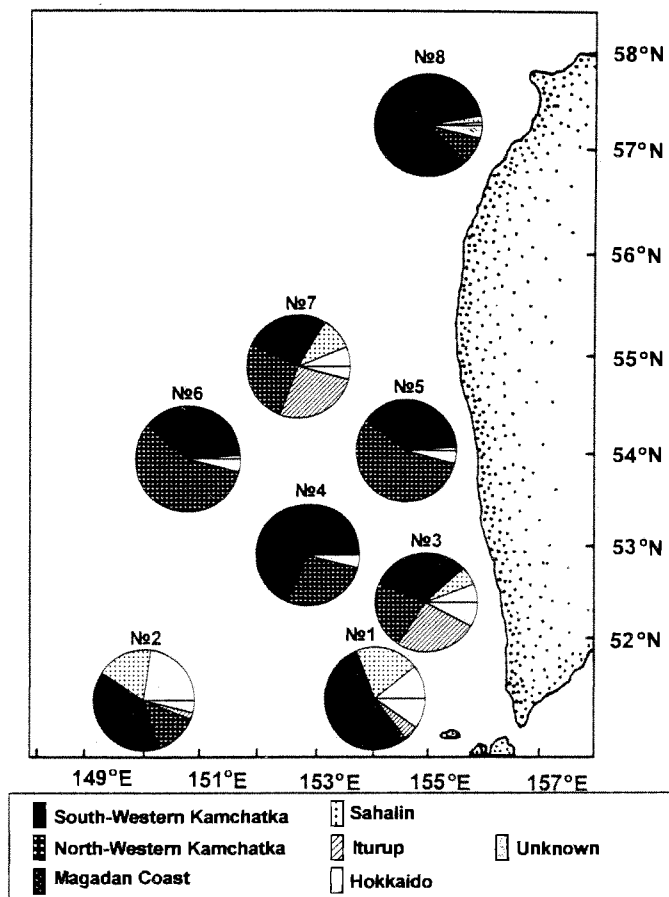
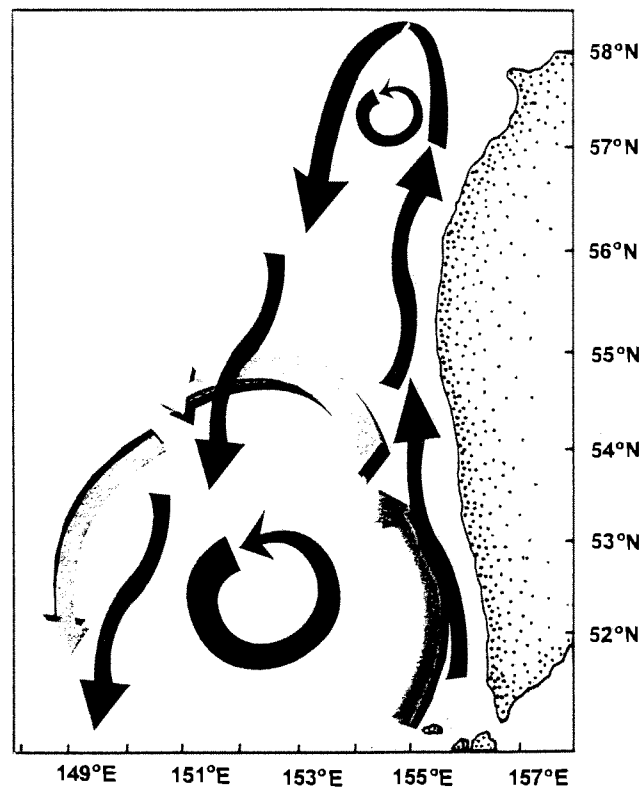


Fig. 5 The scheme of migration routes of pink salmon juveniles in eastern Okhotsk Sea in September-October, 1995. Light arrows - southern Okhotsk Sea group (Hokkaido, Sakhalin, Iturup), dark arrows - northern Okhotsk Sea group (Magadan and Kamchatka coast).



abundance of pink salmon in the even year. The largest portion of Magadan juveniles (4%) was found at station 8, located near the feeding area in Shelekhov Bay (Fig. 4). After a prolonged stay in Shelekhov Bay, the juveniles migrate south, using a route further offshore than the Kamchatka coastline route.

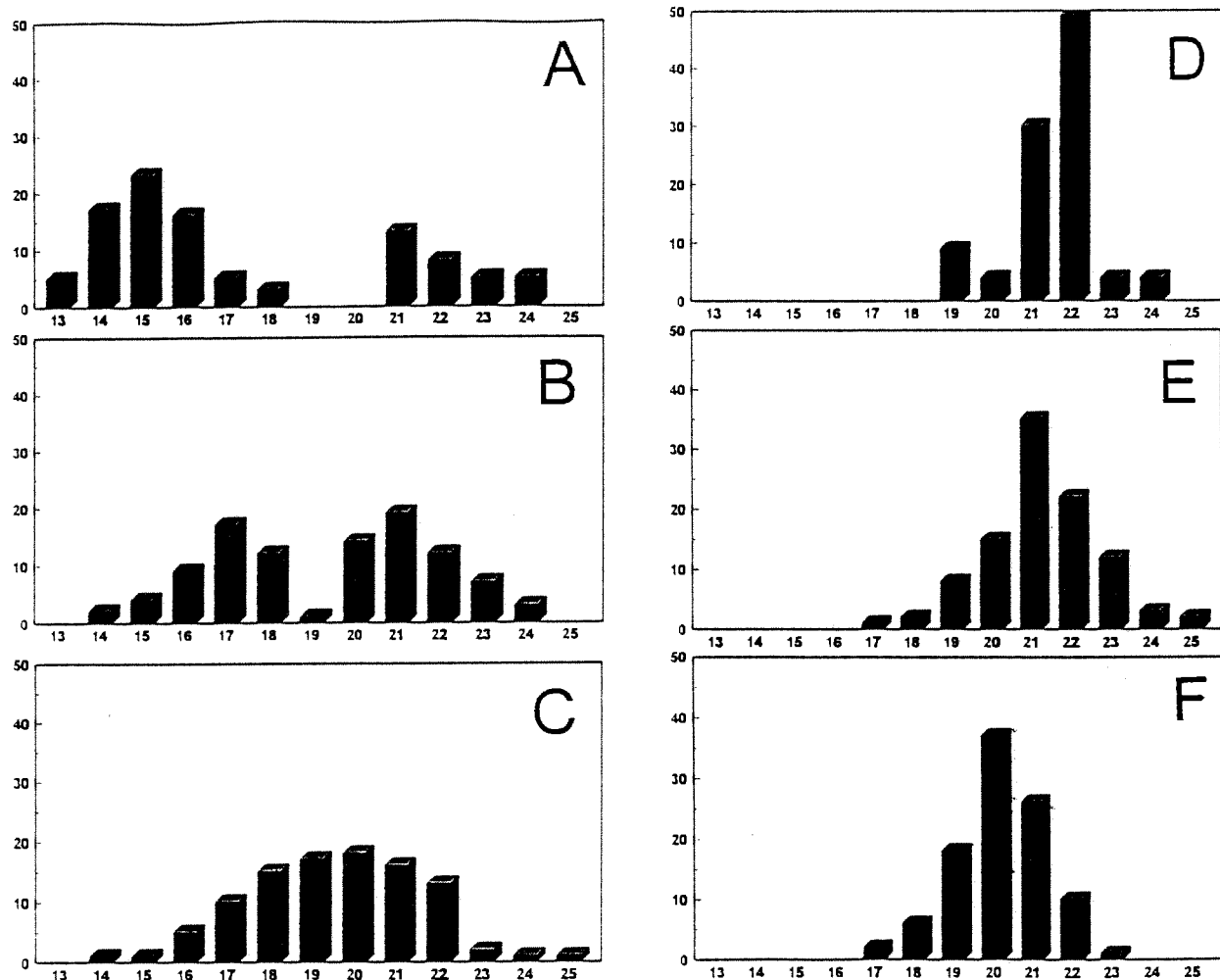
In the central part of the Okhotsk Sea there is a zone of higher temperatures (Figs. 3, 5). Both southern and northern migrations of juveniles are likely to use this area for an extended time. The stock composition in this area is similar to the average estimates for the entire Okhotsk Sea in 1995. Though the sample size was small which resulted in big standard error for each collection, the data still allowed us to reveal the migration routes of pink salmon in the Okhotsk Sea (Figs. 4, 5).

The scheme of migration routes of juveniles in the eastern Okhotsk Sea (Fig. 5), constructed from the stock identification results (Fig. 4), is supported confirmed by the analysis of body length and weight distribution of juveniles caught along latitude 52°N. Six collections of juveniles were analyzed for body length and weight (A, B, C, D, E, and F), caught near 155°E, 153°E, 152°E, 151°E, 150°E, and 149°E, respectively (Fig. 6). Collection A, at 155°E near the south-western coast of Kamchatka, presented two

distributions for body length: 13-18 cm., and 21-24 cm. This confirmed the hypothesis that two populations of juveniles existed in this area; small Kamchatka juveniles, and larger Hokkaido-Kuril-Sakhalin juveniles. The Hokkaido-Kuril-Sakhalin juveniles are believed to be almost twice the size of the Kamchatka juveniles because they have been at sea for a longer time as inferred from the migration time necessary to arrive in the southeastern Sea of Okhotsk. The Kamchatkan juveniles have just recently entered the sea from West Kamchatka rivers. The group of large bodied fish represented approximately 35% of the collection. The stock composition estimate of juveniles from this area (station 3), showed an approximate 38% representation of southern (Hokkaido, Kuril, and Sakhalin) juveniles (Fig. 4).

At 153E and 152E (Fig. 6, B, C) in the central warmer zone the body length distributions were flat and had a negative excess, which indicated, that there was a mixture of all juveniles of all body sizes, as it was supposed to be according to our conclusion of juveniles mixing over there and staying for feeding and growth. At 151°E, 150°E, and 149°E (Fig. 6, D, E, F) the body length distributions looked normal, or had a positive excess, and indicated the presence of larger fish, which were, according to our conclusion,

Fig. 6 Body length distributions in collections of pink salmon juveniles caught along 52°N (A - 155°E, B - 153°E, C - 152°E, D - 151°E, E - 150°E, F - 149°E). X-axis – body length (cm), Y-axis – percentage of fish.



on their southward migration out of the Okhotsk Sea.

Though juvenile pink salmon from Sakhalin were detected in mixtures in the eastern Okhotsk Sea, the percentage does not account for the total abundance of Sakhalin juveniles. We conclude that perhaps only the juveniles from Aniva Bay, and, maybe, partly Terpenie Bay (southern Okhotsk coast of Sakhalin), migrate north together with juveniles from Hokkaido and Iturup along Kuril shelf to Kamchatka shelf, and the remaining portion of the Sakhalin fish migrate north along the Siberian coastline, joining schools of juveniles from the Amur River and rivers of the western Okhotsk coast. To reveal their migration routes we need sampling in the western Okhotsk Sea.

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Genetic Stock Identification of Chum Salmon Harvested Incidentally in the 1994 and 1995 Bering Sea Trawl Fishery

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In some years, the Bering Sea trawl fishery incidentally harvests (bycatch) large numbers of chum salmon. Because chum salmon were declining in some western Alaska areas, the origins of the chum salmon bycatch were important. Tagging studies have shown that chum salmon originating in Asia and North America migrate through the eastern Bering Sea. Genetic stock identification (GSI), a method of estimating stock composition in mixed-stock fisheries, has helped in evaluating stock contributions to salmon fisheries on the western coast of North America. Through cooperative efforts between state and federal agencies, a comprehensive genetic baseline for Pacific Rim chum salmon stocks has been developed, which enables GSI in fisheries such as the Bering Sea trawl fishery.

In 1994, the National Marine Fisheries Service, Auke Bay Laboratory, initiated a feasibility study of GSI in determining the origins of the chum salmon bycatch in the Bering Sea trawl fishery. Sampling in 1995 was intensified and resulted in samples covering the entire fishing season, representing nearly 11% of the total chum salmon bycatch.

Estimates for our 1994 fishery samples over three period were 39-55% Asian stocks, 20-35% western Alaska stocks, and 21-29% southeastern Alaska, British Columbia, or Washington stocks. One small sample (N = 47) of maturing fish showed a surprisingly large contribution of British Columbia stocks (53%). Estimates for our 1995 samples over seven time periods were 13-51% Asian stocks, 33-53% western Alaska stocks, and 9-46% southeastern Alaska, British Columbia, or Washington stocks. As in 1994, the sample of maturing fish (N = 277) showed a large contribution of British Columbia stocks (49%) and Washington stocks (25%).



INTRODUCTION

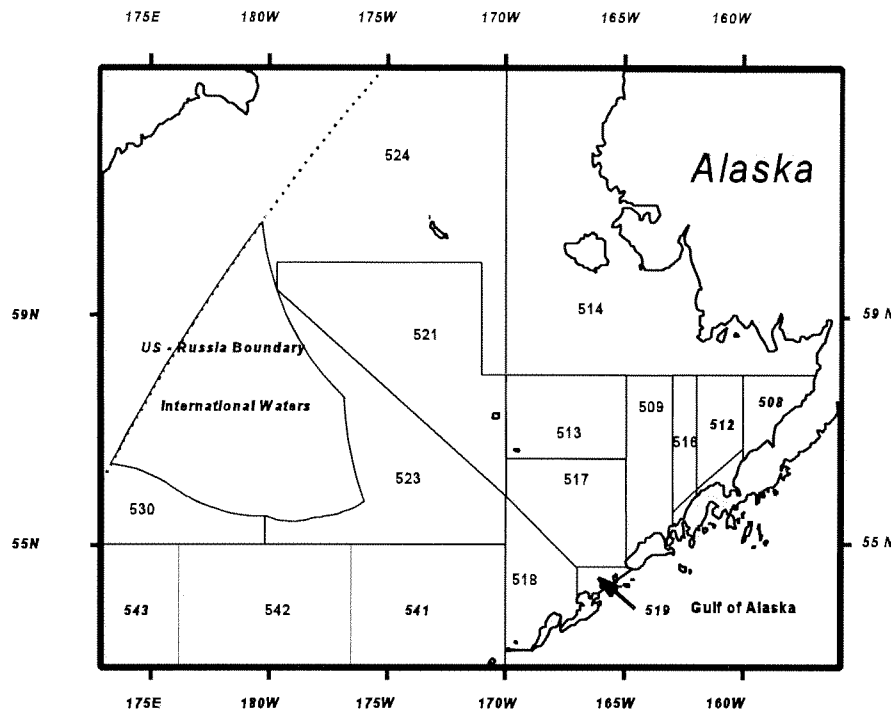
In some years, the Bering Sea trawl fishery for walleye pollock (*Theragra chalcogramma*) incidentally harvests (bycatch) large numbers of chum salmon (*Oncorhynchus keta*). The fishery takes place north of the Alaska Peninsula (Fig. 1) from January to March (the "A" fishery) and from late August to mid-October (the "B" fishery). Most of the chum salmon bycatch is taken in the "B" fishery. The incidental harvest of chum salmon became of concern when spawning escapements of chum salmon to several western Alaska areas declined below historic levels (Eggers 1995), and the stock origins of the bycatch were seen as important to evaluating this fishery's effect on those stocks. The terms stock and population will be used interchangeably and refer to "fish spawning in a particular lake or stream (or portion of) at a particular season, which fish to a substantial degree do not

interbreed with any group spawning in a different place, or in the same place at a different season" (Ricker 1972, p. 28).

Tagging studies have shown that chum salmon originating in Asia and North America migrate through the eastern Bering Sea (Aro 1972; Aro et al. 1971; Brannian 1984; Eggers 1992; Eggers et al. 1991; Meyer 1983). Although tagging studies demonstrated the presence of many stocks in the fishery, estimates of the contributions of these stocks from tagging would be unreliable, given the low level of tagging and the disproportionate tag recovery effort among stocks.

Genetic stock identification (GSI), a method for estimating stock composition in mixed-stock fisheries, was developed in the 1970s and has been used to evaluate stock contributions to salmon fisheries on the western coast of North America (Grant et al. 1980; Milner et al. 1981; Okazaki 1981; Seeb et al. 1986,

Fig. 1 Statistical Reporting Areas of the Bering Sea/Aleutian Islands



1990, 1995; Shaklee et al. 1991; Utter et al. 1974; Wilmot et al. 1992; Winans et al. 1989; Wishard 1980). The method relies on genetic differences among stocks in relative frequencies of protein-coding genes detected by allozyme electrophoresis. The preferred statistical method for computing the stock composition is conditional maximum likelihood (Fournier et al. 1984; Millar 1987; Milner et al. 1981; Pella and Milner 1987; Pella et al. 1996; Smouse et al. 1990). GSI can be used to assess the stock composition of the Bering Sea trawl fishery bycatch of chum salmon.

However, before GSI could be applied, a genetic baseline from potentially contributing chum salmon stocks was needed. Various state and federal agencies cooperated to create this data base (Kondzela et al. 1994; Phelps et al. 1994; Seeb et al. 1995; Wilmot et al. 1994; Winans et al. 1994), which contains information for more than 200 populations of chum salmon throughout the Pacific Rim. Some collections have data on more than 60 loci; however, data for the complete range of chum salmon are currently limited to 20 loci.

Previous studies found geographic differentiation of allozyme frequencies among chum salmon stocks that should provide good estimates of regional contributions to mixed-stock fisheries. Seeb et al. (1995) recently estimated contributions from chum salmon stocks of major regions (Japan; Russia; western Alaska; fall Yukon; Alaska Peninsula,

Kodiak, and Chignik [AP/K/C]; Prince William Sound and southeastern Alaska [PWS/SEA]; British Columbia [BC]; and Washington [WA]) to incidental catches in the South Unimak, Alaska, sockeye salmon fishery.

In 1994, the National Marine Fisheries Service (NMFS) Auke Bay Laboratory (ABL) was assigned the task of determining the feasibility of using GSI to estimate the regional stock contributions to samples from the chum salmon bycatch taken in the 1994 Bering Sea "B" season trawl fishery. The first year, we determined the feasibility of using the existing NMFS Observer Program to collect samples; the second year, the observers took enough samples for statistically valid estimates of stock contributions.

MATERIALS AND METHODS

Baseline Data

The baseline included the 69 populations used by the Alaska Department of Fish and Game (ADF&G) (Seeb et al. 1995) from data provided by various agencies: NMFS (Kondzela et al. 1994; Winans et al. 1994), Washington Department of Fish and Wildlife (Phelps et al. 1995), and the U.S. Fish and Wildlife Service (Wilmot et al. 1994). In addition, eight populations from two new areas in Asia, two from China and six from Russia (Appendix I), were added, for a 77-population baseline. Twenty loci were

available for each population. The rationale behind the construction of the Pacific Rim chum salmon baseline was discussed thoroughly in Seeb et al. (1995).

The baseline samples from China came from the Heilong (Amur) River (fall run) and the Suifen River and were collected by personnel from the Heilongjiang Fisheries Research Institute, Chinese Academy of Fisheries Science, Harbin, People's Republic of China. The Heilong River is the Chinese name for their portion of the river called the Amur River in Russia. The Suifen River flows south from China to the Pacific Ocean just south of Vladivostok, Russia. The baseline samples from Russia were taken by personnel from the Institute of Marine Biology, Far East Branch of the Russian Academy of Science in Vladivostok. Three were from the southern end of Sakhalin Island (Naiba, Udarnitsa, and Kalinka Rivers), and three were from the Premor'ye region near Vladivostok (Avakumovka, Narva, and Ryzanovka Rivers). Tissue samples from Russia and China (eye, heart, liver, and muscle) were taken from each fish, frozen and delivered to ABL for electrophoretic analysis.

Bycatch Sampling

Chum salmon bycatch samples from the Bering Sea "B" fishery were collected by personnel of the NMFS Observer Program. Whole heads were removed so that muscle tissue, heart, and liver remained with the head. The heads were packaged individually with catch information, frozen, and shipped to ABL. Tissue samples were taken from the heads, placed in individual tubes, and frozen at -80°C until electrophoretic analysis.

A total of 457 chum salmon were sampled in 1994 from Aug. 29 to Oct. 8 (Figs. 1, 2) from five statistical areas in the Bering Sea [Areas 509 (N = 8), 513 (N = 24), 517 (N = 316), 521 (N = 91), and 541 (N = 13)]; 410 were immature fish, and 47 were maturing fish that were expected to spawn in the fall of 1994. Maturity was determined by the size of the fish and the condition of the gonads. Four kinds of stock composition comparisons were performed: mature versus immature; east versus west; time periods; and specific areas. Only areas 517 and 521 had sufficient numbers of samples for independent analysis. Areas 521 and 541 were pooled (N = 104) and areas 509, 513, and 517 were pooled (N = 348) for an east-versus west comparison. The samples were stratified by three periods: Aug. 29 to Sept. 5 (N = 319), Sept. 6 to 9 (N = 51), and Sept. 11 to Oct 8 (N = 82).

In 1995, 1,853 chum salmon were sampled from Aug. 14 to Oct. 1 (Fig. 2), and represented nearly 11% of the total chum salmon bycatch (Fig. 3). Due

Fig. 2 Number of chum salmon sampled by the NMFS Observer Program from the 1994 and 1995 Bering Sea trawl "B" season by day.

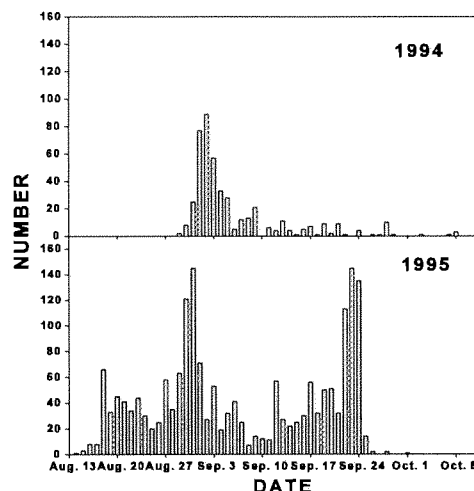
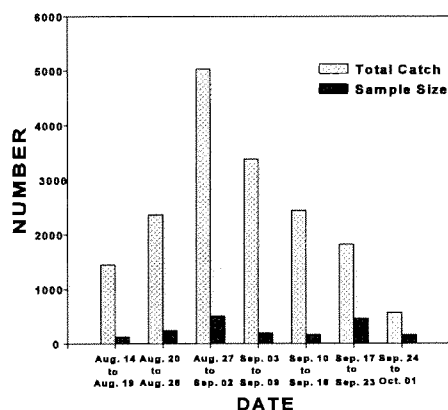


Fig. 3 Total chum bycatch in the 1995 Bering Sea trawl "B" season fishery by week compared with the sample size.



to the reporting procedure in 1995, it was impossible to assign the catch by area. The boats crossed back and forth between areas, and catch records did not indicate which fish were actually caught in which area. All samples appeared to have been harvested in one of four areas: 509, 517, 518, or 519. The stage of maturity was identified by examination of the gonads for 1,650 fish: 1,373 immature and 277 maturing fish. The samples were stratified into seven periods matching the bycatch harvest reporting periods used by the NMFS, Alaska Regional Office: Aug. 14-19 (N = 118), Aug. 20-26 (N = 237), Aug. 27 to Sept. 2 (N = 500), Sept. 3-9 (N = 191), Sept. 10-16 (N = 160), Sept. 17-23 (N = 456), and Sept. 24 to Oct. 1 (N = 153).

Electrophoretic analysis followed procedures described by Aebersold et al. (1987) and Harris and Hopkinson (1976), and results are reported using the genetic nomenclature of the American Fisheries

Society (Shaklee et al., 1990). A total of 62 loci were resolved, of which 20 can be used in the current Pacific Rim baseline. Details for standardizing allele mobility and allele pooling are in Seeb et al. (1995).

Statistical Procedures

The genetic structure of the baseline populations was described by a dendrogram constructed from Cavalli-Sforza and Edwards (1967) chord distances among all 77 populations, using the Unweighted Pair-Group Method with arithmetic averages (UPGMA) (Sneath and Sokal 1973).

Conditional maximum likelihood estimates (MLE) of stock composition of the mixed fishery samples were calculated using the GIRLS program of Masuda et al. (1991). Standard errors of stock composition estimates were determined by 500 bootstrap resamplings of baseline and mixture samples (Efron and Tibshirani 1986).

Simulation studies were conducted to evaluate the reliability of stock composition estimates:

- 1) Simulated baseline samples of sizes equal to actual baseline samples were generated by resampling. Mixture samples composed of 100% of stocks from a given region in equal proportions were simulated from baseline allele frequencies. Genotypes of individuals in these hypothetical mixtures of known composition were generated from baseline allele frequencies assuming independence of loci and Hardy-Weinberg equilibrium. The GIRLS program calculated the MLE of stock composition for each simulated set of baseline and mixture samples, and the average MLEs of regional composition were compared with the true contribution.

- 2) We added incremental numbers of simulated fish from a region to a real catch sample to determine how accurately the average composition estimates could track the changing composition of the altered sample. Genotypes of the simulated fish were generated from the baseline in the same manner as described for the simulation studies.

RESULTS

Baseline Data

The addition of the eight new populations from China and Russia to the UPGMA dendrogram (Fig. 4) had little effect on the basic geographic structure displayed in the dendrogram in Seeb et al. (1995). The populations from Sakhalin Island and Premor'ye clustered with the Japanese stocks. A group of outlier observations from Wallace H. Noerenberg (WHN) Hatchery, Prince William Sound; Peterson Lagoon, Alaska Peninsula; and Big Sukhoi Creek and Sturgeon River, Kodiak, Alaska, was shown in Seeb et al.

(1995). Two of the eight additional populations joined these outliers: the Heilong River, China, and the Kalininka River, Sakhalin Island.

Mixture Analysis

Regional stock groups for reporting estimates were the same as ADF&G used for the South Unimak fishery (Seeb et al., 1995): Japan, Russia, western Alaska (summer run), Yukon River (fall run), AP/K/C, PWS/SEA, BC, and WA. In simulation studies where the true regional contributions were 100%, the MLE average estimates were >80% accurate. Estimates for the PWS/SEA region were least accurate (82%), and the estimate for the Yukon River fall run the most accurate (96%) (Table 1).

1994 bycatch

Estimates of the origins of immature and maturing fish were substantially different (Table 2). The Asian component (Japan and Russia) in the immature fish was estimated at 51% versus 32% (no Russian-origin fish) of maturing fish; western Alaska (including western Alaska summer run, fall Yukon, and AP/K/C), 29% versus 12%; and PWS/SEA/BC/WA, 20% versus 56% (BC = 53% of the 56%).

Of the three periods, the first (Aug. 29 to Sept. 5) consisted of approximately 44% Asian, 35% western Alaska, and 21% PWS/SEA/BC/WA fish. The second period (Sept. 6-9) consisted of 39% Asian, 32% western Alaska, and 28% PWS/SEA/BC/WA fish. In the third period (Sept. 11 to Oct. 8), the Asian component increased to 55%, the western Alaska component declined to 20%, and the PWS/SEA/BC/WA component stayed relatively constant at 24%.

Area 517 consisted of 43% Asian, 28% western Alaska, and 30% PWS/SEA/BC/WA fish. Area 521 consisted of 58% Asian, 30% western Alaska, and 12% PWS/SEA/BC/WA fish. Areas 513 and 517 were combined to form an eastern Bering Sea group, close to the Alaska Peninsula and the mouth of Bristol Bay. This group consisted of 42% Asian, 29% western Alaska, and 27% PWS/SEA/BC/WA fish. Areas 521 and 541 were combined to form a western Bering Sea group, which consisted of 66% Asian, 23% western Alaska, and 11% PWS/SEA/BC/WA fish.

The MLEs accurately tracked known additions to an actual mixture sample (Fig. 5). We used the maturing fish mixture sample (Table 2) because the MLE estimates indicated a high percentage of British Columbia fish. Known numbers of simulated British Columbia fish were added to the observed mixture sample (equivalent to altering BC percentages from 53% to 88%), and known numbers of simulated

Fig. 4 UPGMA clustering of Cavalli-Sforza and Edwards (1967) chord distance among 77 populations of Pacific Rim chum salmon.

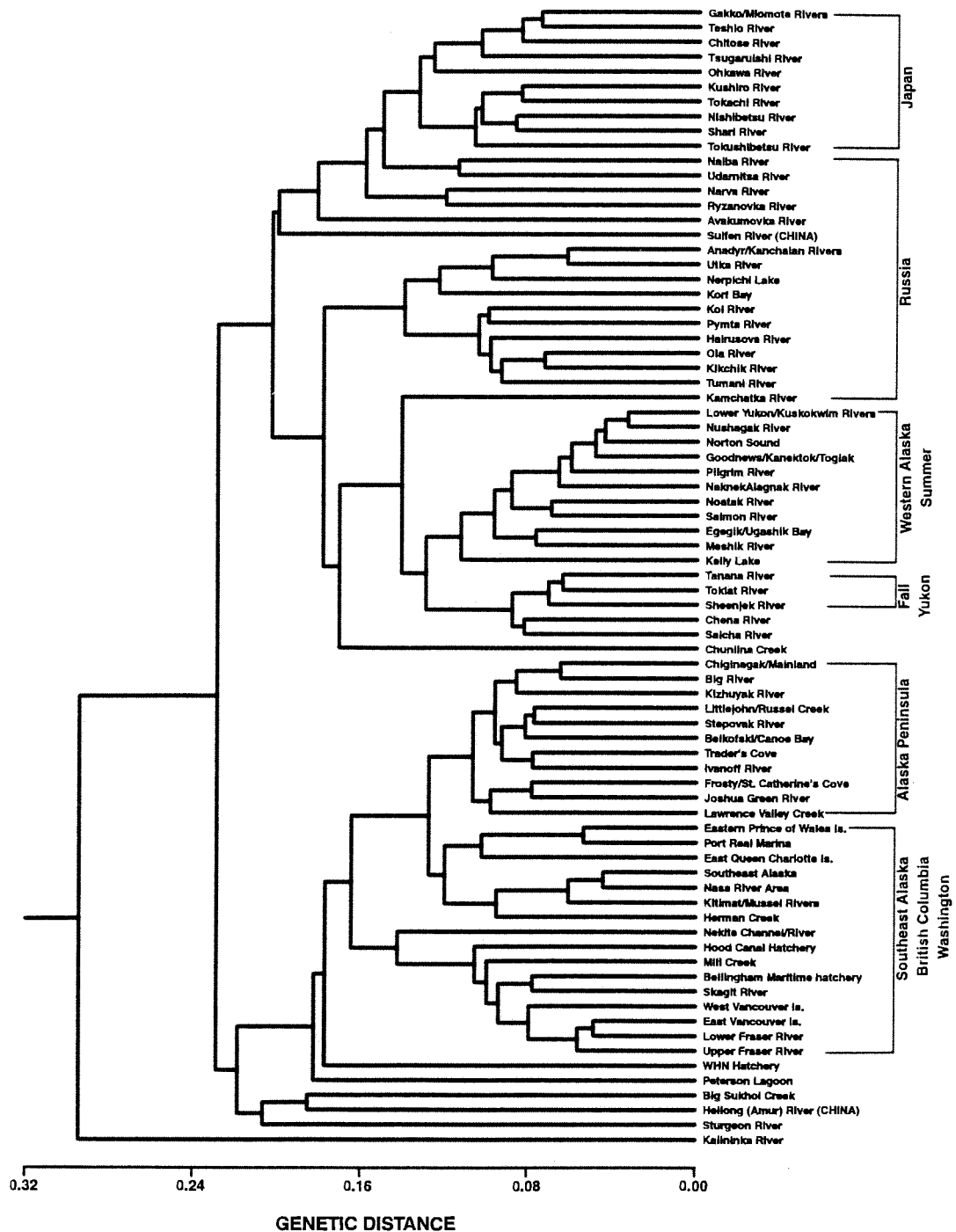


Table 1. Mean estimated proportion for 500 simulations where each region comprises 100% of the mixture (N=300). Cells with asterisks are the correct allocation and should equal 1.000.

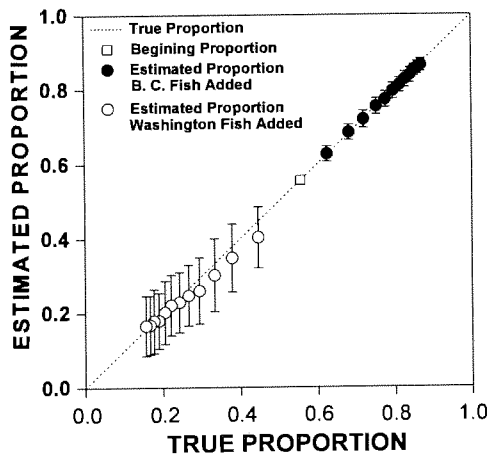
Estimated Region	100% Simulations							
	Japan	Russia	Western Alaska (Summer run)	Fall Yukon	Peninsula/Kodiak/Chignik	SE Alaska/PWS	British Columbia	Washington
Japan	0.9446*	0.0337	0.0082	0.0010	0.0056	0.0032	0.0017	0.0002
Russia	0.0266	0.8921*	0.0265	0.0031	0.0254	0.0237	0.0107	0.0023
Western Alaska (Summer run)	0.0143	0.0376	0.9205*	0.0374	0.0062	0.0052	0.0017	0.0001
Fall Yukon	0.0035	0.9205*	0.0368	0.9573*	0.0013	0.0011	0.0005	0.0000
Peninsula/Kodiak/Chignik	0.0080	0.0242	0.0066	0.0007	0.9348*	0.0233	0.0255	0.0020
SE Alaska/PWS	0.0014	0.0048	0.0006	0.0002	0.0122	0.8211*	0.0575	0.0033
British Columbia	0.0011	0.0043	0.0004	0.0002	0.0123	0.0748	0.8517*	0.0522
Washington	0.0004	0.0009	0.0002	0.0001	0.0022	0.0176	0.0506	0.9399*

Table 2. Estimated regional proportions of Pacific Rim chum salmon in the 1994 Bering Sea trawl fishery. Standard deviations (S.D.) were calculated from 500 bootstraps of the mixture and baseline samples.

Sample	N	Japan		Russia		Western Alaska		Fall Yukon	
		Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Immature	410	0.2593	0.0361	0.2485	0.0453	0.2260	0.0502	0.0301	0.0279
Maturing	47	0.3245	0.0932	0.0000	0.0450	0.0630	0.0518	0.0567	0.0546
Aug 29 - Sep 05	319	0.2545	0.0403	0.1806	0.0452	0.2617	0.0526	0.0192	0.0257
Sep 06 - Sep 09	51	0.1511	0.0767	0.2428	0.1082	0.2648	0.1035	0.0251	0.0658
Sep 11 - Oct 08	82	0.3092	0.0754	0.2452	0.0830	0.0929	0.0738	0.1104	0.0522
Area 517	316	0.2421	0.0403	0.1844	0.0491	0.2358	0.0487	0.0146	0.0250
Area 521	91	0.3668	0.0807	0.2101	0.0769	0.2258	0.0862	0.0472	0.0486
Areas 521/541	104	0.4021	0.0710	0.2597	0.0768	0.1686	0.0791	0.0393	0.0412
Areas 509/513/517	348	0.2324	0.0376	0.1882	0.0452	0.2224	0.0521	0.0372	0.0300

Sample	N	Alaska Peninsula, Kodiak and Chignik		Southeast AK/PWS		British Columbia		Washington	
		Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Immature	410	0.0322	0.0255	0.0545	0.0320	0.1034	0.0362	0.0462	0.0288
Maturing	47	0.0000	0.0247	0.000	0.0044	0.5324	0.1369	0.0234	0.1084
Aug 29 - Sep 05	319	0.0717	0.0328	0.0212	0.0317	0.1671	0.0413	0.0240	0.0294
Sep 06 - Sep 09	51	0.0312	0.0695	0.0538	0.0722	0.1179	0.0895	0.1132	0.0700
Sep 11 - Oct 08	82	0.0000	0.0195	0.0000	0.0344	0.1051	0.0579	0.1373	0.0618
Area 517	316	0.0277	0.0288	0.0594	0.0381	0.1601	0.0503	0.0759	0.0446
Area 521	91	0.0265	0.0365	0.0006	0.0245	0.1079	0.0444	0.0151	0.0185
Areas 521/541	104	0.0207	0.0308	0.0012	0.0220	0.0960	0.0387	0.0124	0.0167
Areas 509/513/517	348	0.0268	0.0267	0.0547	0.0364	0.1502	0.0489	0.0880	0.0447

Fig. 5 Results of simulation tests to determine the accuracy of the conditional maximum likelihood estimates (MLEs) to follow additions of known numbers of British Columbia fish to an actual mixture sample. The 45 dotted line represents 100% accuracy; the black circles represent the calculated proportion when British Columbia fish are added, and the open circles represent the calculated portion when Washington fish are added. Error bars are one standard deviation derived from 100 bootstrap resamplings.



Washington fish (equivalent to altering BC percentages from 53% to 16%). Estimated proportions were plotted against the known, altered proportion (Fig. 5). Average MLEs were within 1% of the true proportions when British Columbia fish were added, and within 5% when Washington fish were added.

1995 bycatch

Estimates of the origins of immature and maturing fish in 1995 again differed substantially (Table 3). The Asian component (Japan and Russia) of the immature fish group was estimated at 43% versus 12% of the maturing fish, western Alaska (including western Alaska summer run, fall Yukon, and AP/K/C) at 45% versus 14%, and PWS/SEA/BC/WA at 13% versus 74% (BC = 49% and WA = 25% of the maturing fish).

During the seven periods, the Asian component ranged from 13% to 51% and, in general, increased as the season progressed (Table 3). Russian-origin fish were 2-4 times more abundant than Japanese fish. The western Alaska component (including western Alaska summer run, fall Yukon, and AP/K/C) ranged from 33% to 53%, with the largest proportion showing in late August and early September. Two periods (Sept. 3-9 and Sept. 24 to Oct. 1) showed large proportions of fall Yukon River fish (14% and 16%, respectively). The PWS/SEA/BC/WA

component ranged from 9% to 46% over the fishing season, most occurring early in the season. British Columbia fish made up the largest proportion, followed by Washington fish; PWS/SEA fish did not contribute more than 8%.

We applied the weekly stock composition estimates to the weekly bycatch figures from the NMFS-Alaska Regional Office to arrive at numbers harvested by origin and time period (Table 4). Salmon bycatch figures are reported as chinook salmon or "other" salmon. In the fall fishery, "other" salmon are considered to be almost totally chum salmon. Estimated contributions by regions for all periods were approximately 5,500 Asian; 7,500 western Alaska summer run, fall Yukon, and AP/K/C; and 4,100 PWS/SEA/BC/WA fish.

DISCUSSION

Geographic differentiation among Pacific Rim chum salmon made accurate stock identification at the regional level feasible as a management tool. This genetic differentiation has been amply described by Kondzela et al. (1994), Phelps et al. (1994), Wilmot et al. (1994), and Winans et al. (1994) and summarized in Seeb et al. (1995). Below the regional level, estimates must be viewed cautiously. The fall run of chum salmon into the Yukon River is an exception because of their substantial genetic separation. The addition of eight new populations to the baseline had little effect on the population geographic structure shown in Seeb et al. (1995) for 69 populations. As expected, six of these populations clustered between the Japanese and northern Russian populations: Sakhalin Island and Premor'ye are near Japan, and represented an area where summer-run chum salmon typical of northern Russia overlap with fall-run chum salmon typical of Japan. Two of the eight stocks were outliers: Kalininka River on Sakhalin Island and the Heilong River. According to our Russian source (Dr. Vladimir Efremov, Institute of Marine Biology, Far East Branch Russian Academy of Sciences, Valdivostok), Kalininka chum salmon originated from hatchery operations that started with a small number of fish that probably changed gene frequencies substantially from those of the original wild stock. The samples from those of the original wild stock. The samples from the Heilong River came from a spawning area nearly 1,000 km upstream from the mouth. The genetic differences of these fish may be analogous to the situation in the Yukon River where upriver spawners differ substantially from lower river spawners (Wilmot et al. 1994).

Regional compositions of these Bering Sea chum salmon samples differed substantially from that found by Seeb et al. (1995) for the chum salmon bycatch in the South Unimak sockeye salmon fishery in 1993 and

Table 3. Estimated regional proportions of Pacific Rim chum salmon in the 1995 Bering Sea trawl fishery bycatch. Standard deviations (S.D.) were calculated from 500 bootstraps of the mixture and baseline samples.

Sample	N	Japan		Russia		Western Alaska		Fall Yukon	
		Estimate	S. D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Immature	1373	0.1051	0.0176	0.3220	0.0272	0.3420	0.0322	0.0818	0.0214
Maturing	277	0.0717	0.0218	0.0521	0.0339	0.0521	0.0231	0.0051	0.0051
Aug 14 - Aug 19	118	0.0367	0.0344	0.0901	0.0512	0.3156	0.0801	0.0463	0.0519
Aug 20 - Aug 26	237	0.1116	0.0389	0.2224	0.0598	0.3022	0.0645	0.0466	0.0256
Aug 27- Sep 2	500	0.0508	0.0206	0.2440	0.0402	0.3696	0.0525	0.0654	0.0364
Sep 3 - Sep 9	191	0.0706	0.0331	0.2173	0.0581	0.2777	0.0600	0.1431	0.0412
Sep 10 - Sep 16	160	0.0830	0.0422	0.2846	0.0618	0.2702	0.0605	0.0641	0.0309
Sep 17 - Sep 23	456	0.1201	0.0298	0.3850	0.0486	0.2473	0.0509	0.0637	0.0300
Sep 24 - Oct 1	153	0.1651	0.0527	0.2759	0.0654	0.2182	0.0831	0.1567	0.0534

Sample	N	Alaska Peninsula, Kodiak and Chignik		SE Alaska/PWS		British Columbia		Washington	
		Estimate	S. D.	Estimate	S. D.	Estimate	S. D.	Estimate	S.D.
Immature	1373	0.0240	0.0139	0.0615	0.0184	0.0279	0.0144	0.0357	0.0123
Maturing	277	0.0806	0.0388	0.0000	0.0107	0.4928	0.0655	0.2455	0.0704
Aug 14 - Aug 19	118	0.0557	0.0424	0.0482	0.0505	0.3939	0.0690	0.0136	0.0462
Aug 20 - Aug 26	237	0.0340	0.0309	0.0808	0.0438	0.1756	0.0543	0.0269	0.0399
Aug 27 - Sep 2	500	0.0394	0.0226	0.0236	0.0223	0.1245	0.0308	0.0826	0.0271
Sep 3 - Sep 9	191	0.1081	0.0405	0.0408	0.0306	0.0343	0.0405	0.1079	0.0445
Sep 10 - Sep 16	160	0.0000	0.0220	0.0253	0.0231	0.1244	0.0513	0.1485	0.0562
Sep 17 - Sep 23	456	0.0898	0.0321	0.0098	0.0227	0.0368	0.0261	0.0476	0.0228
Sep 24 - Oct 1	153	0.0222	0.0258	0.0392	0.0330	0.1167	0.0430	0.0061	0.0302

Table 4. Estimated number of Pacific Rim chum salmon harvested in the 1995 Bering Sea trawl fishery by area. Standard deviations (S.D.) were calculated from 500 bootstraps of the mixture and baseline samples.

Sample	N	Japan		Russia		Western Alaska		Fall Yukon	
		Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Aug 14 - Aug 19	1448	53	50	130	74	457	116	67	75
Aug 20 - Aug 26	2360	263	92	525	141	713	152	110	60
Aug 27 - Sep 2	5029	256	104	1227	202	1859	264	329	183
Sep 3 - Sep 9	3379	239	112	734	196	939	203	484	139
Sep 10 - Sep 16	2439	202	103	694	151	659	148	156	75
Sep 17 - Sep 23	1817	218	54	700	88	449	92	116	55
Sep 24 - Oct 1	565	93	30	156	37	123	47	89	30
Total	17039	1324	545	4166	890	5199	1022	1351	618

Sample	N	Alaska Peninsula Kodiak and Chignik		Southeast AK/PWS		British Columbia		Washington	
		Estimate	S.D.	Estimate	S.D.	Estimate	S.D.	Estimate	S.D.
Aug 14 - Aug 19	1448	81	61	70	73	570	100	20	67
Aug 20 - Aug 26	2360	80	73	191	103	414	128	63	94
Aug 27 - Sep 2	5029	198	114	119	112	626	155	415	136
Sep 3 - Sep 9	3379	365	137	138	103	116	137	365	150
Sep 10 - Sep 16	2439	0	54	62	56	303	125	362	137
Sep 17 - Sep 23	1817	163	58	18	41	67	47	86	41
Sep 24 - Oct 1	565	13	15	22	19	66	24	3	17
Total	17039	900	511	620	508	2162	717	1314	643

1994. They found western Alaska (including fall run Yukon River and AP/K/C) stocks dominated the catch, 59-83%; Asian stocks, 15% to 32%; and PWS/SEA/BC/WA stocks, 2-11%. In contrast, over the total fishing season our samples consisted of 20-35% western Alaska stocks in 1994 and 33-53% in 1995, 39-55% Asian stocks in 1994 and 13-51% in 1995, and 21-29% (excluding the exclusively maturing fish group) PWS/SEA/BC/WA stocks in 1994 and 9-46% in 1995. The large contribution in both 1994 and 1995 (53% [S.E. = 14%] and 49% [S.E. = 7%], respectively) of British Columbia stocks to the maturing fish group was unexpected. Given the small mixture sample in 1994 ($N = 47$), these results should be regarded with caution. However, the 1995 sample was sufficiently large ($N = 277$) for much greater confidence in the stock composition estimates. The simulation studies showed that the contribution of the British Columbia stock group could be estimated reliably when the mixture sample size was increased by the addition of BC fish so that the composition was altered.

Differences in composition between the South Unimak fishery and the Bering Sea trawl fishery could have resulted from both seasonal migratory timing and geography. The South Unimak fishery occurs in June south of the Alaska Peninsula. The Bering Sea trawl fishery occurs from late August to early October north of the Alaska Peninsula, when most western Alaska chum salmon spawners would be in the rivers.

Tagging information supports the presence of British Columbia fish in the Bering Sea trawl fishery area. Four coded-wire tagged chum salmon from British Columbia have been caught in this fishery since 1986 (Dahlberg et al. 1994), and estimated annual return to southern British Columbia over recent years has exceeded five million chum salmon per year (Pacific Salmon Commission 1994). Maturing fish from British Columbia would have to migrate approximately 3,000 km to their spawning rivers. Hartt (1966) estimated ocean migration speeds of chum salmon at about 40 km/day, and this rate increased with proximity to their spawning rivers. Many British Columbia chum salmon spawn in November and December and would have sufficient time to migrate from the Bering Sea in August and September to their spawning rivers in southern British Columbia in November and December (approximately 75 days).

The preliminary study showed that the collection methods used by the NMFS Observer Program could provide high quality samples suitable for allozyme and GSI analysis. Although sampling in the 1994 fishery was minimal and not designed to be representative of the total chum salmon bycatch, the 1995 sampling effort does reflect the total bycatch. Shaklee (1991), in studies of the Columbia River spring chinook

salmon baseline, recommends a mixture sample size of at least 180 individuals. Marlowe and Busack (1995) conducted studies on the chinook salmon baseline from California to southern British Columbia, and mixed fishery samples from the Washington Coast and Strait of Juan de Fuca troll fisheries. Their results showed that for stocks that contribute at least 5-6%, 200 samples are probably sufficient. Stocks or stock groupings that contribute 2% or less to the fishery require 800 samples or more. Sampling in 1995 allowed us to analyze mixed fishery samples of at least 118 fish (first period) and the remainder of our mixed fishery sample groups were greater than 150 fish (153-1,373 fish).

Exploratory studies on the Bering Sea trawl chum salmon bycatch samples used a 190-population baseline. The increase from the 77-population baseline used in the current analysis came from additional populations from SEA/BC/WA. This expanded baseline had little effect on composition estimates for the Asian and western Alaska components of the mixture samples. It did, however, affect the composition distribution among SEA, BC, and WA. In most samples, the MLEs for British Columbia declined, and increased for southeastern Alaska and Washington. However, the change was slight, and accuracy did not improve.

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Appendix

Allelic frequencies at 20 loci for populations of chum salmon from China and Russia. Alleles are designated by their mobility relative to the most common allele (100).

		sAAT-1,2*				mAAT-1*			
Population	N	100	120	65	95	N	-100	-120	-70
CHINA									
Heilong River (Amur)	46	0.962	0.039	0.000	0.000	46	0.924	0.000	0.076
Suifen River	25	0.980	0.020	0.000	0.000	25	1.000	0.000	0.000
RUSSIA - PREMOR'YE									
Avakumovka River	35	0.964	0.007	0.000	0.029	35	1.000	0.000	0.000
Narva River	18	0.958	0.042	0.000	0.000	18	1.000	0.000	0.000
Ryzanovka River	51	0.990	0.010	0.000	0.000	51	1.000	0.000	0.000
RUSSIA - SAKHALIN ISLAND									
Kalininka River	49	0.954	0.046	0.000	0.000	49	1.000	0.000	0.000
Naiba River	61	0.934	0.066	0.000	0.000	61	0.975	0.016	0.008
Udarnitsa River	98	0.944	0.056	0.000	0.000	98	0.985	0.000	0.015

		mAH-3*		ALAT*			
Population	N	100	124	N	100	93	78
CHINA							
Heilong River (Amur)	43	0.907	0.093	39	0.500	0.500	0.000
Suifen River	23	0.587	0.413	24	1.000	0.000	0.000
RUSSIA - PREMOR'YE							
Avakumovka River	23	0.457	0.544	34	0.838	0.162	0.000
Narva River	17	0.206	0.794	18	0.750	0.250	0.000
Ryzanovka River	28	0.411	0.589	50	0.750	0.250	0.000
RUSSIA - SAKHALIN ISLAND							
Kalininka River	35	0.571	0.429	48	0.521	0.479	0.000
Naiba River	30	0.717	0.283	60	0.750	0.233	0.017
Udarnitsa River	42	0.595	0.405	96	0.672	0.328	0.000

		ESTD*			G3PDH-2*		
Population	N	100	91	110	N	100	90
CHINA							
Heilong River (Amur)	46	0.989	0.011	0.000	44	0.761	0.239
Suifen River	25	0.860	0.140	0.000	23	0.848	0.152
RUSSIA - PREMOR'YE							
Avakumovka River	35	0.729	0.271	0.000	34	0.868	0.132
Narva River	18	0.472	0.528	0.000	18	0.972	0.028
Ryzanovka River	51	0.657	0.343	0.000	50	0.940	0.060
RUSSIA - SAKHALIN ISLAND							
Kalininka River	49	0.153	0.847	0.000	49	0.786	0.214
Naiba River	61	0.762	0.238	0.000	61	0.820	0.180
Udarnitsa River	98	0.551	0.449	0.000	98	0.903	0.097

Appendix (continued)

Population	N	GPI-B1,2*			N	GPI-A*		
		100	145	40		100	95	105
CHINA								
Heilong River (Amur)	40	1.000	0.000	0.000	46	1.000	0.000	0.000
Suifen River	24	1.000	0.000	0.000	25	1.000	0.000	0.000
RUSSIA - PREMOR'YE								
Avakumovka River	35	0.993	0.007	0.000	34	1.000	0.000	0.000
Narva River	18	1.000	0.000	0.000	18	0.972	0.028	0.000
Ryzanovka River	51	0.995	0.005	0.000	51	0.971	0.029	0.000
RUSSIA - SAKHALIN ISLAND								
Kalininka River	49	1.000	0.000	0.000	49	1.000	0.000	0.000
Naiba River	55	1.000	0.000	0.000	61	1.000	0.000	0.000
Udarnitsa River	98	1.000	0.000	0.000	97	1.000	0.000	0.000

		mIDHP-1*				
Population	N	100	60	140	20	85
CHINA						
Heilong River (Amur)	40	0.675	0.325	0.000	0.000	0.000
Suifen River	24	0.813	0.188	0.000	0.000	0.000
RUSSIA - PREMOR'YE						
Avakumovka River	35	0.871	0.129	0.000	0.000	0.000
Narva River	18	0.917	0.083	0.000	0.000	0.000
Ryzanovka River	51	0.882	0.118	0.000	0.000	0.000
RUSSIA - SAKHALIN ISLAND						
Kalininka River	48	0.875	0.125	0.000	0.000	0.000
Naiba River	60	0.875	0.125	0.000	0.000	0.000
Udarnitsa River	96	0.839	0.162	0.000	0.000	0.000

		sIDHP-2*							
Population	N	100	35	85	25	20	110	28	45
CHINA									
Heilong River (Amur)	47	0.457	0.404	0.085	0.053	0.000	0.000	0.000	0.000
Suifen River	24	0.688	0.313	0.000	0.000	0.000	0.000	0.000	0.000
RUSSIA - PREMOR'YE									
Avakumovka River	30	0.583	0.183	0.000	0.000	0.000	0.233	0.000	0.000
Narva River	18	0.528	0.389	0.000	0.056	0.000	0.028	0.000	0.000
Ryzanovka River	47	0.553	0.245	0.000	0.138	0.000	0.064	0.000	0.000
RUSSIA - SAKHALIN ISLAND									
Kalininka River	27	0.593	0.296	0.000	0.037	0.000	0.074	0.000	0.000
Naiba River	20	0.650	0.250	0.075	0.000	0.000	0.025	0.000	0.000
Udarnitsa River	53	0.585	0.255	0.047	0.066	0.000	0.047	0.000	0.000

Appendix (continued)

Population	N	LDH-A1*			N	LDH-B2*			
		100	50	110		100	120	60	
CHINA									
Heilong River (Amur)	38	1.000	0.000	0.000	48	1.000	0.000	0.000	
Suifen River	24	0.917	0.021	0.063	25	1.000	0.000	0.000	
RUSSIA - PREMOR'YE									
Avakumovka River	35	0.871	0.071	0.057	35	1.000	0.000	0.000	
Narva River	18	0.972	0.028	0.000	18	1.000	0.000	0.000	
Ryzanovka River	50	0.930	0.040	0.030	51	1.000	0.000	0.000	
RUSSIA - SAKHALIN ISLAND									
Kalininka River	48	0.969	0.031	0.000	49	1.000	0.000	0.000	
Naiba River	61	0.943	0.057	0.000	61	1.000	0.000	0.000	
Udarnitsa River	98	0.954	0.046	0.000	98	1.000	0.000	0.000	
Population	N	sMDH-A1*			N	sMDH-B1,2*			
		100	200	400		100	72	50	130
CHINA									
Heilong River (Amur)	48	0.906	0.094	0.000	46	1.000	0.000	0.000	0.000
Suifen River	24	0.750	0.250	0.000	25	1.000	0.000	0.000	0.000
RUSSIA - PREMOR'YE									
Avakumovka River	35	0.871	0.129	0.000	35	0.957	0.014	0.000	0.029
Narva River	18	0.889	0.111	0.000	18	0.958	0.028	0.014	0.000
Ryzanovka River	50	0.750	0.250	0.000	51	0.990	0.010	0.000	0.000
RUSSIA - SAKHALIN ISLAND									
Kalininka River	49	1.000	0.000	0.000	49	0.857	0.015	0.122	0.005
Naiba River	35	0.929	0.071	0.000	61	0.967	0.004	0.004	0.025
Udarnitsa River	95	0.916	0.084	0.000	98	0.929	0.010	0.046	0.015
Population	N	mMEP-2*			N	sMEP-1*			
		100	122	100		90			
CHINA									
Heilong River (Amur)	40	0.950	0.050	40.000	1.000	0.000			
Suifen River	24	0.833	0.167	24.000	1.000	0.000			
RUSSIA - PREMOR'YE									
Avakumovka River	35	0.857	0.143	35.000	1.000	0.000			
Narva River	18	0.889	0.111	18.000	1.000	0.000			
Ryzanovka River	51	0.922	0.078	51.000	0.990	0.010			
RUSSIA - SAKHALIN ISLAND									
Kalininka River	48	0.896	0.104	48.000	1.000	0.000			
Naiba River	60	0.825	0.175	60.000	1.000	0.000			
Udarnitsa River	97	0.881	0.119	98.000	1.000	0.000			

Appendix (continued)

MPI*						PEPA*			
Population	N	100	94	110	80	N	100	90	113
CHINA									
Heilong River (Amur)	44	0.875	0.125	0.000	0.000	44	1.000	0.000	0.000
Suifen River	23	1.000	0.000	0.000	0.000	23	1.000	0.000	0.000
RUSSIA - PREMOR'YE									
Avakumovka River	34	0.941	0.059	0.000	0.000	34	1.000	0.000	0.000
Narva River	18	1.000	0.000	0.000	0.000	18	1.000	0.000	0.000
Ryzanovka River	49	1.000	0.000	0.000	0.000	50	1.000	0.000	0.000
RUSSIA - SAKHALIN ISLAND									
Kalininka River	49	1.000	0.000	0.000	0.000	49	1.000	0.000	0.000
Naiba River	61	0.975	0.025	0.000	0.000	61	1.000	0.000	0.000
Udarnitsa River	98	0.980	0.020	0.000	0.000	98	1.000	0.000	0.000

Population	N	PEP-B1*				
		-100	-146	-126	-127	-72
CHINA						
Heilong River (Amur)	47	0.968	0.032	0.000	0.000	0.000
Suifen River	24	0.854	0.000	0.146	0.000	0.000
RUSSIA - PREMOR'YE						
Avakumovka River	34	0.750	0.044	0.206	0.000	0.000
Narva River	18	0.861	0.000	0.139	0.000	0.000
Ryzanovka River	51	0.745	0.020	0.235	0.000	0.000
RUSSIA - SAKHALIN ISLAND						
Kalininka River	49	0.469	0.092	0.439	0.000	0.000
Naiba River	61	0.795	0.025	0.180	0.000	0.000
Udarnitsa River	96	0.719	0.057	0.224	0.000	0.000

Population	N	PGDH*			
		100	88	106	95
CHINA					
Heilong River (Amur)	48	0.969	0.031	0.000	0.000
Suifen River	25	1.000	0.000	0.000	0.000
RUSSIA - PREMOR'YE					
Avakumovka River	35	0.986	0.014	0.000	0.000
Narva River	18	0.972	0.028	0.000	0.000
Ryzanovka River	51	0.961	0.039	0.000	0.000
RUSSIA - SAKHALIN ISLAND					
Kalininka River	49	1.000	0.000	0.000	0.000
Naiba River	61	0.967	0.033	0.000	0.000
Udarnitsa River	98	0.995	0.005	0.000	0.000

Allozyme, mtDNA, and microsatellite variants describe structure of populations of pink and sockeye salmon in Alaska

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We are interested in applying knowledge of population genetics to the sustained management of salmonids of commercial importance. Some populations in Alaska have been adversely affected by climactic or anthropogenic events, and fishery closures to protect these depleted stocks can lead to underutilization of other healthy stocks when both occur in mixed-stock fisheries. A vast array of contemporary gene-detection techniques might identify stocks in a timely manner and thereby improve management. We are currently applying data collected from allozyme electrophoresis and from analysis of restriction fragment length polymorphism of mitochondrial DNA (mtDNA) to solve questions of population structure. We also report pilot studies to collect data on length polymorphisms observed in microsatellite DNA and sequence polymorphisms observed in mtDNA loci and other nuclear DNA (nDNA) loci, testing for site-specific variants that may be assayed using a simple mismatch analysis probe. We focus on results obtained from using these approaches in an array of studies of the structure of commercially important pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) populations affected by the 41 million liter *Exxon Valdez* oil spill of 1989. In the case of sockeye salmon, the allozyme data was used to guide harvest in-season in order to conserve depleted populations. While we focus our discussion of molecular markers on studies of pink and sockeye salmon in Alaska, similar applications are clearly possible for other salmonids over their entire range.



INTRODUCTION

Describing the genetic structure of populations of Pacific salmon became a central focus of research and management as anthropogenic factors, including overharvest, habitat destruction, and adverse effects on wild populations from hatchery propagation, eroded components of the productivity of the billion-dollar fishery in the North Pacific Ocean (e.g., see reviews in Ryman and Utter 1987; Carvalho and Pitcher 1994). The primary question asked by fisheries managers that seek genetic solutions often is

"how can we partition the annual harvest among genetically discrete components of the species in such a way to maximize long-term productivity?" (e.g., Lincoln 1994). Several categories of molecular techniques emerged during the last three decades that may potentially provide answers to this sometimes daunting challenge (see reviews in Park et al. 1994; Ferguson et al. 1995).

Gharrett and Smoker (1994) graph the increasing importance of genetic study as a component of the fish biology literature. Adapting this approach, we demonstrate the relative increased importance of the

four basic types of molecular approaches used in the genetic study of salmonids today (Fig. 1A). Advantages of these different approaches include such factors as relative cost and difficulty of field sampling

and laboratory analysis (Table 1). One of these molecular approaches, minisatellite analysis, is not pursued by many laboratories because of difficulties in standardizing and interpreting the multi-locus fragment

Table 1. Relative attributes of four molecular techniques for study of population genetics of Pacific salmon.

Technique	Cost	Number of Loci	Resolving Power	Throughput	Existing Baseline	Lethal Sampling	Cryo-preservation	Development Needed
Allozymes	low	many	variable	rapid	extensive	usually	yes	very little
mtDNA	medium	one	variable	slow	some	no	no	little
Microsatellite	high	many	variable	slow	little	no	no	new primers
Minisatellite	high	many	variable	slow	little	no	no	low priority

data. Of the remaining categories of molecular markers, allozymes and mitochondrial DNA (mtDNA) were used most frequently to define population structure of salmonids. Allozyme analysis remains the preferred approach for study of population genetics for many species of salmonids because of its power to resolve populations of many species in the family by assaying many nuclear loci rapidly and inexpensively (Allendorf 1994). Additional advantages of allozymes include the fact that many laboratories cooperate on inter-institutional examinations of salmonids using allozymes, providing a support structure including a wealth of compatible data for comparison among Pacific Rim populations (e.g., for pink salmon *Oncorhynchus gorbuscha* see Shaklee et al. 1991; White and Shaklee 1991; Shaklee and Varnavskaya 1994; Seeb et al. 1996b).

The utility of mtDNA approaches to study genetic diversity of salmonid populations is controversial because of relatively high cost and slow throughput (Allendorf 1994). Additionally, sometimes mtDNA data reveal less diversity than do allozyme data because mtDNA cannot recombine and is maternally inherited as a single locus so that the variation is absolutely linked (Smouse et al. 1994; contrast the lack of geographic resolution observed for mtDNA data for populations of chum salmon in Park et al. (1993) with the geographic resolution apparent for similar populations in Winans et al. (1994)). One advantage of screening for genetic variation in mtDNA can be that the mitochondrial genome experiences an elevated rate of nucleotide substitution over that of nuclear DNA (nDNA; Lynch 1996). The fidelity of DNA replication in the mitochondria is also reduced, and mtDNA repair systems are less stringent (Alberts et al. 1994). Lynch (1996) not only confirmed that mtDNA accumulates mutations much faster than nDNA, but also showed that even deleterious mutations may become fixed due to the relaxed control over DNA repair and replication. For these reasons, the use of both nDNA and mtDNA

approaches sometimes provides complementary information for the resolution of population structure.

In some cases, the disadvantages of allozymes and mtDNA make either technique unsuitable for a particular application. Some species exhibit low or no variation at allozyme loci, making estimates of between population diversity difficult to obtain (e.g., Milner 1993). mtDNA sometimes provides useful insights into microgeographic structure, but relationships on a macrogeographic scale may become obscured because of convergent evolution (cf., Adams et al. 1994). Thus, additional approaches to genetic analysis focusing upon sequence variants in nDNA emerged in recent years to address these limitations (see Fig. 1A, 1B). Of these, the most useful appear to be the techniques that rely on polymerase chain reaction (PCR) amplification of DNA template for further analyses of fragment or sequence variation (e.g., for microsatellites see Estoup et al. 1993; Angers et al. 1995; Morris et al. 1996). Further, the application of a rapid assay to detect site-specific single nucleotide (nt) substitutions for study of fish genetics was promoted by Park and Moran (1994). The use of allele-specific PCR using 3'-primer mismatch analysis (MMA) was shown to be a rapid and sensitive technique for identification of single nt substitutions in rainbow trout (Bailey et al. 1996), and the advent of automated DNA sequencing strategies elevates the opportunity for observing site-specific mutations appropriate for such study.

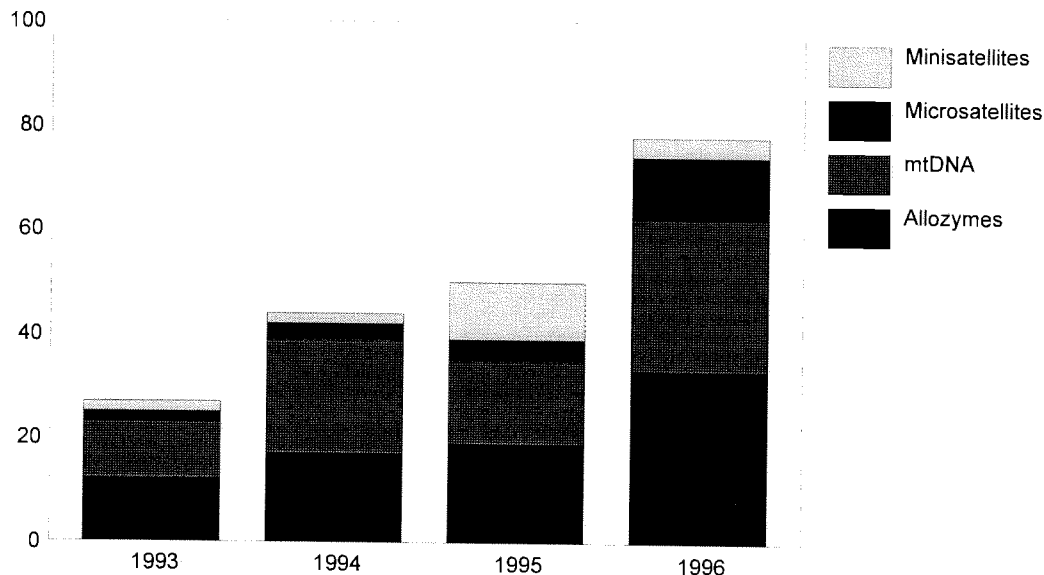
In this paper we review our studies of genetic variation in pink and sockeye salmon *O. nerka* in order to provide an overview of the utility of allozymes, mtDNA, microsatellites, and potentially MMA for detecting genetic differences that distinguish Pacific salmon populations. These studies were initiated in response to the Exxon Valdez oil spill. On March 24, 1989, the supertanker Exxon Valdez ran aground on Bligh Reef in Prince William Sound (PWS), Alaska, spilling approximately 41 million liters of crude oil. The oil slick, pushed by winds and

currents, moved through western PWS and southern Cook Inlet, depositing toxic polycyclic aromatic hydrocarbons onto spawning gravels and into the

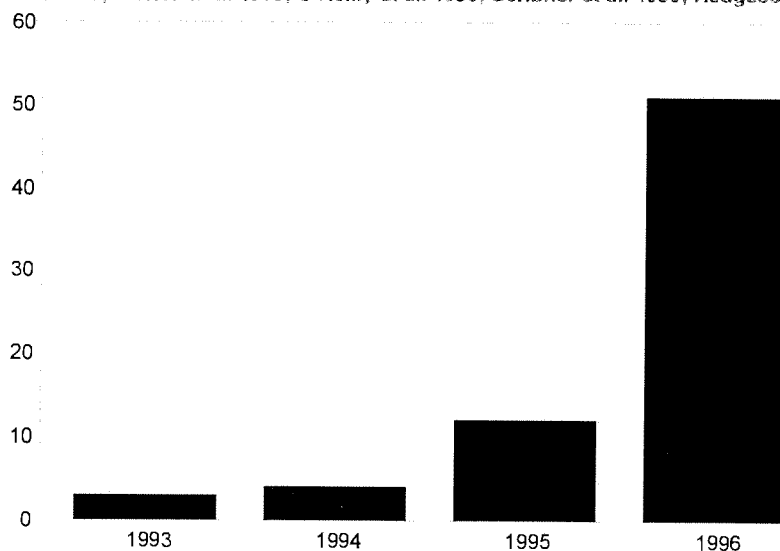
salmonid food chain. Subsurface oil remained in some of the beaches for years in spite of the multi-billion dollar clean-up and restoration effort (Wolfe et

Fig. 1

A. Number of citations listed in Current Contents™ on various techniques used to study genetics of salmonid populations from 1993-1996.



B. Cumulative number of microsatellite primer sets developed in salmonids that were published or are in press since 1993 (adapted from Olsen et al. 1996; please see Estoup et al. 1993; Sakamoto et al. 1994; Angers et al. 1995; McConnell et al. 1995; Morris et al. 1995; O'Reilly et al. 1996; Scribner et al. 1996; Hedgecock et al. in press).



al. 1994), and populations of some species of salmonids may not be fully recovered (Bue et al. 1996). Of the salmonids inhabiting the spill zone, populations of pink and sockeye salmon were the most adversely impacted.

PINK SALMON STUDIES

Pink salmon is the most abundant North American species of the Pacific salmon (Heard 1991), making it an ecological cornerstone in biological communities of

the Pacific Rim and an economic mainstay for many coastal communities. Pink salmon are both anadromous and semelparous: in their natural range, they make long oceanic migrations, home to their natal streams to spawn, and die at age two. Annual catches of pink salmon ranged from 46 to 128 million fish in Alaska alone during the period from 1985-1995. Many hundreds of streams drain into PWS, and most provide a freshwater home to spawning pink salmon each summer. Little is known about the structure of populations inhabiting PWS or of the

genetic relationships of these populations to other populations inhabiting the region. Pink salmon spawn in the intertidal portions of most streams in PWS; some larger rivers host large aggregations of spawners in upstream areas as well. Temporal isolation occurs between aggregations that spawn in mid summer and those that spawn in the fall. Combining this life history evidence with observations of other physiographic and climactic variables in PWS led us to suggest that population substructuring was present. Our objective was to test for both temporal and geographical structuring among even- and odd-year classes by examining genetic differences between early- and late-season spawners, upstream and intertidal spawners, and stream of spawning within each. Additionally, genetic positioning of the local hatchery populations within this structure was of interest because the extensive releases of pink salmon fry in PWS in recent decades may have affected the partitioning of naturally occurring genetic diversity. Important to this study was the fact that even- and odd-year classes have independent population structures because of the rigid two-year life cycle of pink salmon. For example, climactic, tectonic or other such events (such as the major 1964 earthquake (Roys 1971) or the 1989 oil spill) may affect the population structure of one year class, cycle through subsequent generations, and leave the alternate cycle of year-classes relatively unchanged. Therefore, population structure and conservation strategies must be independently assessed for the even- and odd-year classes.

Our primary focus was to screen allozymes and mtDNA for variation that would address the objectives above. Allozymes were selected because extensive baseline data exist for pink salmon (see references above) including a pre-oilspill data set from PWS (Seeb and Wishard 1977). Mitochondrial DNA was selected to add complementary data because we know from other allozyme study that adjacent pink salmon populations can be very closely related (Gharrett et al. 1988).

We also chose to conduct a preliminary screen for microsatellite variation and variation detected at the DNA sequence level. These latter studies were initiated originally to screen for elevated rates of mutation that may have resulted from exposure of individuals to the genotoxic hydrocarbons present due to the oil spill (cf., Bailey et al. 1996). We also wanted to conduct a pilot study to test the viability of these methods to detect genetic variation in pink salmon populations.

Allozyme and Mitochondrial DNA Analyses

To begin the study in 1994, tissues were collected

from 92 - 100 individuals from each of 25 spawning aggregations from wild-stock streams and two hatcheries. PWS was historically divided into subdivisions for management and conservation purposes according to biological, geographical, and geological factors (i.e., see Rugolo 1984), and we distributed sampling effort among the current harvest management zones. Sampling was done to include at least one collection from each of the five major subdivisions (Southeast, East, North, Southwest, Montague; Fig. 2A). Although a majority of pink salmon spawning in PWS occurs in areas of tidal influence, some larger tributaries also possess somewhat discrete aggregations that spawn in upstream areas above the influence of tides. Samples were collected from both tidal and upstream sites in five of these creeks.

Our allozyme screen of 77 loci yielded 38 loci that were polymorphic (frequency of common allele less than 0.99; Seeb et al. 1996b). Cavalli-Sforza and Edwards (1967) chord distances were calculated to evaluate genetic relationships and were used as input into a non-metric multidimensional scaling analysis (MDS; Lessa 1990) using functions in *S-Plus* (Mathsoft, Inc., Seattle, WA).

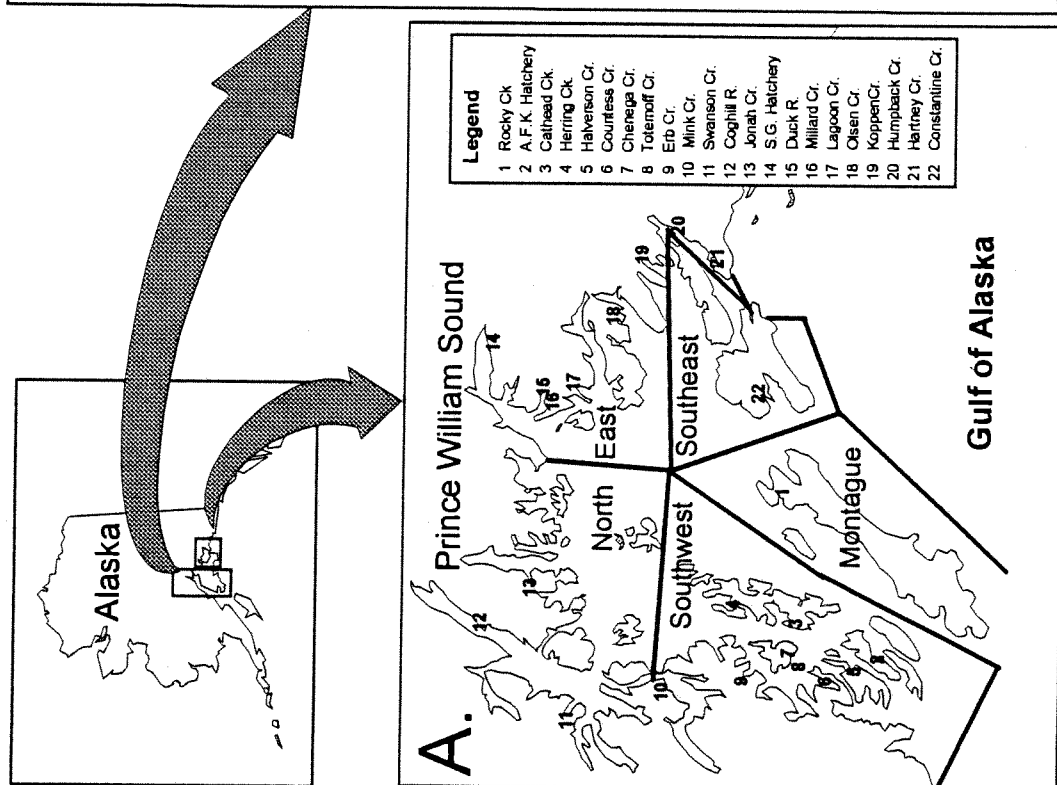
A subset of 40 individuals from each of the 27 collections was assayed for restriction fragment length polymorphism (RFLP) at sites previously identified in the ND5/ND6 region (Fetzner et al. *in prep.*). After extraction, DNA was amplified using PCR. Amplified DNA was cut with the six restriction enzymes found to detect haplotype polymorphisms (of the 30 screened in Fetzner et al. (*in prep.*), *Apa I*, *BstU I*, *EcoR V*, *Hinf I*, *Rsa I*, *Xba I*) and electrophoresed on agarose gels. Fragments were visualized under UV light, and the restriction sites detected for each enzyme were pooled as composite haplotypes for the statistical analyses.

We tested for genetic structure in three steps. First we used a hierarchical log likelihood analysis (allozymes) and Monte Carlo simulations (mtDNA; Roff and Bentzen 1989) to investigate heterogeneity (1) among wild collections from different elevations (tidal and upstream), (2) among management regions within elevation, and (3) among collections within regions within elevation. Second, we performed pairwise tests within streams where we had both tidal and upstream collections. Third, we performed a gene-diversity analysis to partition variation into hierarchical levels stratified by site, region, and elevation.

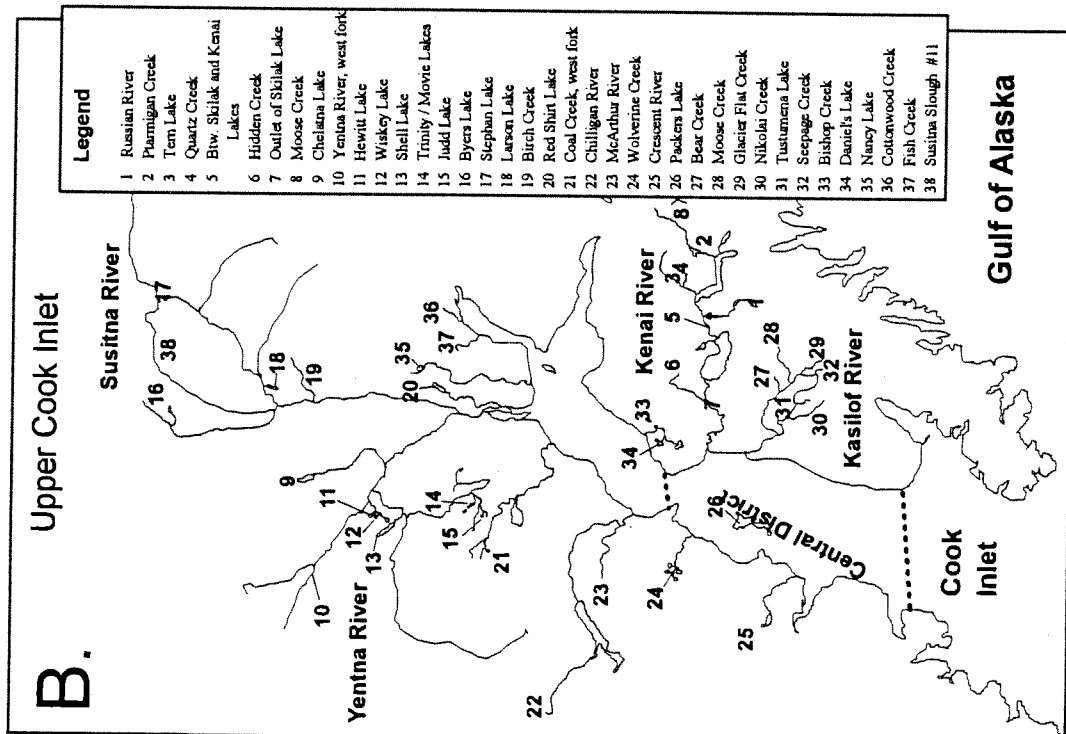
Significant differences between overall upstream and tidal collections were detected. Further examination with paired tests revealed that both Lagoon Creek (allozymes) and Koppen Creek (mtDNA) tidal and upstream collections were

Fig. 2

A. Sample collection locations for spawning aggregates of pink salmon scattered among the five major management districts within Prince William Sound used to define population structure.



B. Sample collection locations for spawning aggregates of sockeye salmon in Upper Cook Inlet used to develop a baseline for in-season mixed-stock identification of fish caught in the Central District fishery.



significantly different (Table 2). Significant regional heterogeneity was detected within upstream (allozymes and mtDNA) and tidal (allozymes) collections. Pairwise log-likelihood tests between pooled

populations within regions were significantly different from the two regions containing the most collections (Southwest and East).

Table 2. Heterogeneity between paired tidal and upstream collections for allozyme and haplotype frequencies. Log-likelihood tests were performed to test homogeneity of allozyme frequencies. Homogeneity of mtDNA was tested using 10,000 Monte Carlo simulations (Roff and Bentzen 1989); probabilities of exceeding the original χ^2 by chance alone are given.

Stream	Allozyme			mtDNA	
	Log-likelihood	df	P	χ^2	P
Olsen Creek	51.8	47	0.292	2.2	0.905
Mink Creek	58.73	47	0.117	3.94	0.599
Lagoon Creek	115.73	43	0.000 *	6.9	0.022
Koppen Creek	56.97	46	0.129	13.56	0.002 *
Constantine Creek	63.07	1	0.120	1.17	0.738

* Significant differences using an initial sequential Bonferroni adjustment of $\alpha=0.01$ within each laboratory method

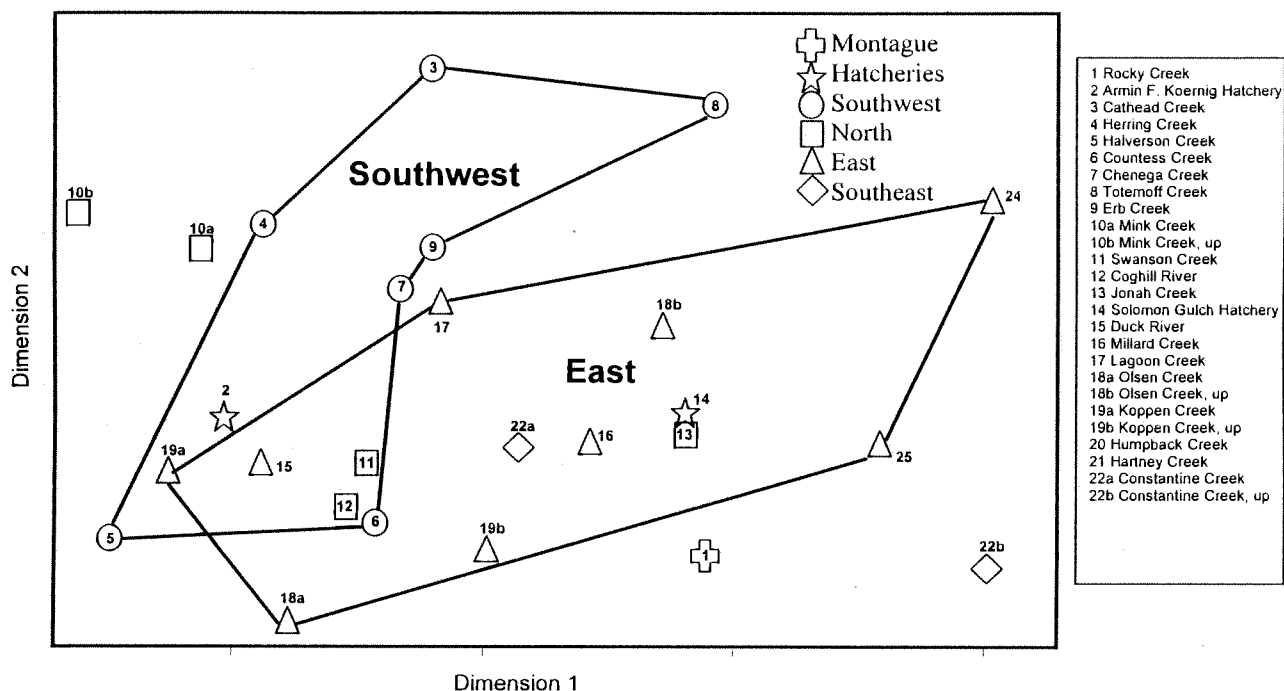
The hierarchical gene-diversity analysis was performed using 30 polymorphic allozyme loci (isoloci were excluded; Table 3). By far the majority of the variation (99.3%) occurred within collections. The remaining heterogeneity was divided among collections within regions (0.5%), among regions within elevation (0.2%), and between elevations (0.1%). A similar analysis of the distribution of molecular variance was made using AMOVA

(Excoffier et al. 1992) and utilizing a matrix of Euclidean distances between haplotypes (Table 3). Pairwise Euclidean distances were calculated as the total number of site changes between haplotypes. The AMOVA analysis allows for only a two-level hierarchy, so we were unable to partition regions within elevations as in the preceding analyses; distribution of variation varied little between the two data sets.

Table 3. Gene diversity analyses. Estimated gene diversity for allozymes were calculated following Nei (1973); estimates for mtDNA were calculated using AMOVA (Excoffier et al. 1992).

Technique	Source	Relative Gene Diversity
PINK SALMON		
Allozyme	Within sites	0.993
	Among sites within regions	0.005
	Among regions within elevations	0.002
	Among elevations	0.001
mtDNA	Within sites	0.984
	Among sites within elevations	0.010
	Among elevations	0.006
SOCKEYE SALMON		
Allozyme	Within sites	0.878
	Among sites within nurseries	0.004
	Among nurseries within regions	0.078
	Among regions	0.041
mtDNA	Within sites	0.669
	Among sites within regions	0.186
	Among regions	0.148

Fig. 3 Multidimensional scaling analysis (Lessa 1990) based on Cavalli-Sforza and Edwards (1967) chord distances generated from allozyme data from pink salmon collections taken from Prince William Sound spawners during 1994 (excluding the upstream collection from Lagoon Creek). Location numbers match those in Fig. 2A with collections containing tidal and upstream locations followed by "a" and "b", respectively.



An initial MDS performed with the allozyme data with all collections demonstrated the uniqueness of the upstream Lagoon Creek collection. To visualize the relationships among the other collections better, a second MDS was generated excluding the Lagoon Creek upstream collection (Fig. 3). Some regional structuring is apparent from the plot. The Southwest collections tend to occupy the left and upper portions of the plot; the East collections occupy a lower area that extends to the extreme right of the plot. Some overlap between the Southwest and East regions occurs. The North collections tend to occupy space across both the Southwest and East regions. The hatchery collections both occur in the central positions of their respective regions, and Armin F. Koernig (AFK) Hatchery is located near the area of overlap between the Southwest and East collections.

The position of the upstream collections is particularly interesting. Upstream collections from Olsen and Koppen Creeks, both in the East region, occupy space within the area bounded by East collections. However, upstream collections from both Mink Creek and Constantine Creek are outliers at the extreme edge of the plot. Interestingly, the tidal collection from Mink Creek is intermediate between the upstream Mink Creek collection and other tidal collections from the North region. As mentioned earlier, Lagoon Creek upstream was not included in this plot because of its highly distant position.

We also examined the relationship between the hatchery and wild collections. Armin F. Koernig Hatchery was not different from any of the regions for tidal collections but was significantly different from all upstream collections. Solomon Gulch Hatchery, located in the East region, was different from all but the East region. These hatchery results follow expectations based on the hatchery locations, original brood stock sources, and annual brood stock acquisition methods (e.g., see below). Although both hatcheries cluster into their respective regions in the MDS plot, AFK Hatchery clusters near the area overlapped by the East region collections (Fig. 3). Armin F. Koernig Hatchery also clustered closely with Duck River, an eastern PWS site from which gametes were collected to establish the even-year hatchery population in 1976.

Implications for Harvest Management

Understanding genetic structure of Pacific salmon populations is critical to their management and conservation. Managing on too fine a scale may adversely affect the fishing industry and waste management resources, while managing on too large a scale may result in loss of genetic adaptations and diversity.

Inferences from studies showing genetic homogeneity for allozymes over vast geographic

distances (e.g., Shaklee and Varnavskaya 1994) led some to suggest that pink salmon populations within PWS, spanning only 100 kilometers, should be genetically homogenous. In contrast, implications from other allozyme studies (Lane et al. 1990) suggest that pink salmon populations in PWS might be substantially heterogenous. Our objective was to generate molecular genetic data to support or reject these alternatives.

Our analysis of the 1994 collections showed significant substructuring of pink salmon in PWS based upon both allozyme and mtDNA data sets. The heterogeneity analysis, a very conservative analysis because all alleles observed are assumed to exist in all collections thereby inflating the degrees of freedom, showed significant allele frequency differences occurring between stream elevations and among and within regions. Further pairwise analyses indicate that, for tidal spawning aggregates, the Southwest and East regions are distinct from each other. For upstream spawners, pairwise comparisons show genetic differences occurring among all regions where upstream spawners were sampled.

These data provided insight not only into the structure of the wild fish within PWS, but also into the genetic relationships between hatchery fish and these wild fish. Armin F. Koernig Hatchery could not be distinguished from any of the regions when tidal fish within region were pooled. The even-year lineage for AFK Hatchery was founded originally with more than one stock that included gametes from Duck River, a site across PWS in the East region. Annual propagation at the hatchery comes from brood stock seined from fish milling in front of the hatchery, and evidence from coded-wire-tag recoveries suggests these milling fish include some wild fish headed for other areas (Sharr et al. 1995). Armin F. Koernig Hatchery is located adjacent to the strait through which most pink salmon enter PWS on their spawning immigration (Templin et al. 1996); consequently hatchery brood stock may include stocks from throughout PWS. Therefore, inability to distinguish the AFK Hatchery brood stock mixture from stocks from other regions is not surprising. Conversely, Solomon Gulch Hatchery is located at the end on the Valdez Arm in eastern PWS. Few pink salmon bound for other regions of PWS are likely to be milling near this hatchery when the brood stock are seined. In addition, the original brood stock for this hatchery was locally obtained. As might be expected, the Solomon Gulch Hatchery collection was not different from other East collections but was different from collections from every other region.

Our preliminary analyses clearly show that significant genetic heterogeneity exists among pink salmon spawning aggregates in both nuclear and mtDNA markers, indicating that pink salmon in PWS

do not form a single panmictic unit. We recognize, however, that the data show the even-year lineage to have a shallow genetic structure (in contrast to the structure of sockeye salmon populations from a similar geographic range in Cook Inlet, Alaska; see below), and population differences are not great enough to identify the components of population mixtures during harvest. Yet population structure and barriers to gene flow exist for these fish, and these data confirm that harvest- and hatchery-management decisions made for conservation purposes should best be made on a population-specific rather than species-specific basis. Expansion of this study to include odd-year and additional even-year collections is continuing; the analysis of data from multiple year classes will allow us to test the appropriateness of current management regions more rigorously.

Microsatellite Variation in Pink Salmon

We conducted a pilot study to test the ability of variation detected at microsatellite loci to discriminate structure of pink salmon populations by looking at three populations in PWS. We selected five prospective loci from those developed in other species based upon criteria reported from an earlier screening of 35 microsatellite primer pairs in five species of Pacific salmon (Olsen et al. 1996): *One μ 3* (developed in sockeye salmon; Scribner et al. 1996), *Ots1* (chinook salmon *O. tshawytscha*; Hedgecock et al. *in press*), *μ Sat60* (brown trout *Salmo trutta*; Estoup et al. 1993), and *Ssa 85* and *Ssa197* (Atlantic salmon *S. salar*; McConnell et al. 1995, O'Reilly et al. 1996). For this pilot study, we compared one even-year population collected in 1994 (Koppen Creek late/tidal) and two odd-year populations collected in 1995 (AFK Hatchery, and Koppen Creek late/tidal).

All loci were polymorphic in all populations. Tests to confirm Mendelian inheritance were performed on all loci using full-sib pink salmon families. The results of these tests confirmed Mendelian segregation at all loci and also revealed the presence of a "null" (non-amplifying) allele(s) at locus *Ssa197*, thus explaining a significant heterozygote deficiency (see below). Rather than attempt a redesign of primers, we chose to exclude *Ssa197* from subsequent statistical analysis of these three populations.

The range of detectable variation was considerable (Table 4). Numbers of alleles per locus ranged from 2 (*One μ 3*) to 47 (*Ssa85*), and the allele distribution varied from 12 nucleotides (nt) (*One μ 3*) to 116nt (*Ssa85*). Frequency of the most common allele varied from 9% (*Ssa85*) to 91% (*μ Sat60*). Observed heterozygosity ranged from 0.18 to 0.93 for microsatellites *One μ 3*, *Ots1* and *μ Sat60*. The mean heterozygosity for all loci (excluding *Ssa197*) was

0.65 for AFK Hatchery, 0.70 for Koppen Creek (1995) and 0.58 for Koppen Creek (1994). A test of Hardy-Weinberg equilibrium (HWE) revealed no significant differences between observed versus expected heterozygosities within each population at One μ 3, Ots1 and μ Sat60 (following sequential Bonferroni adjustment using an initial α of 0.0125;

Rice 1989). However, observed heterozygosity did differ significantly from expected for microsatellite Ssa197 ($P < 0.0125$).

We found significant differences in allele frequencies ($p < 0.0011$, $SE < 0.0001$) for all populations at microsatellite μ Sat60 and Ssa85 using GENEPOP computer program (Raymond and Rousset

Table 4. Allelic variability at four microsatellite loci in two odd- and one even-year pink salmon populations from Prince William Sound, Alaska. Samples were from Armin F. Koernig Hatchery (AFK) and from Koppen Creek late intertidal spawners. Sample size (N), number of alleles (A), allele range (R) in nucleotide bases, maximum allele frequency and size of the most frequent allele (M), and observed heterozygosity (H_o) are reported for each population and locus.

Population		One μ 3	Ots1	μ Sat60	Ssa85	Ssa197*	Avg.
AFK Hatchery (1995)	N	52	52	52	52	47	
	A	3	17	4	30	17	14
	R	156 - 168	216 - 268	109 - 121	157-247	128 - 196	
	M	0.61(162)	0.28(232)	0.73(109)	0.11(201)	0.12(160)	
Koppen Creek (1995)	H_o	0.48	0.85	0.35	0.90	0.55*	0.65
	N	44	44	44	44	40	
	A	2	17	5	29	15	13
	R	162 - 168	220 - 260	107 - 117	153-253	132 - 192	
Koppen Creek (1994)	M	0.61(162)	0.24(232)	0.67(109)	0.09(197)	0.18(144)	
	H_o	0.50	0.93	0.48	0.89	0.60*	0.70
	N	40	40	40	40	40	
	A	2	13	2	35	17	13
All pops.	R	162 - 168	220 - 248	109 - 113	137-245	124 - 204	
	M	0.51(168)	0.24(228)	0.91(109)	0.09(191)	0.10(144)	
	H_o	0.38	0.90	0.18	0.85	0.85	0.58
	N	136	136	136	136	127	
	A	3	21	6	47	20	19
	R	156 - 168	216 - 268	107 - 121	137-253	124-204	
	M	0.57(162)	0.25(232)	0.76(109)	0.09(197)	0.12(144)	
	H_o	0.45	0.89	0.34	0.88	0.67	0.64

* Ssa197 exhibited 3 alleles of equal frequency in the 1994 sample from Koppen Creek.

1995) to estimate the probability of independence from an exact Fisher test on multiple RxC contingency tables. Further, a pairwise comparison of all populations showed significant differences ($P > 0.0125$) in allele frequencies at μ Sat60 and Ssa85 when each odd-year population was compared with the Koppen Creek even-year population. An estimate of the F_{ST} analog (θ) (Weir and Cockerham 1984) was made for each locus and revealed slight genetic differentiation; values ranged from -0.004 to 0.0350. For all loci combined θ was estimated at 0.006 with a 95% bootstrap confidence interval of -0.006 to 0.030. This value is of a similar magnitude to those observed for allozymes and mtDNA for the larger group of populations (Table 3).

DNA Sequencing and Site-Specific Mutations

We initially chose to screen tumor suppressor gene *p53* and the mtDNA gene cytochrome *b* as potential sentinel loci for detecting differences in

mutation rates between embryos incubated in oiled and unoiled gravel in the laboratory. It was our hope that we might develop methods to detect site-specific mutations that would provide insight into both genetic damage as a response to genotoxic challenge and into the population structure of damaged populations (Bue et al. 1996).

Tumor suppressor gene *p53* was selected because research establishing a molecular link between pollution and the onset of tumors has been active; much is known about mutations in *p53* and PCR primers are available to amplify it. Mutations within certain 'hot-spot' regions of *p53* are associated with about 50% of all human cancers (Harris 1993). Most mutations are found clustered in exons 5-8 of this gene, allowing efficient screening for DNA sequence alterations. Intense work sequencing this gene from many tumors has now identified more than 5000 cases of nucleotide substitutions (Hollstein et al. 1996). Finally, naturally occurring variation in *p53* exons 7-10 is observed in chinook salmon *O. tshawytscha*

populations (Park et al. 1996), making the locus attractive for population screening in pink salmon.

We chose to screen cytochrome *b* for site-specific mutations for two reasons. Cytochrome *b* has been shown to be a diagnostic, mutationally active gene for studies of molecular evolution of salmonids (Shedlock et al. 1992; Palsson and Arnason 1994; Patarnello et al. 1994; Bernatchez and Osinov 1995). Further, Baker et al. (1996) found that the base-pair substitution rates for the cytochrome *b* gene in voles living near the Chernobyl nuclear reactor were hundreds of times greater than is typically found for vertebrates, evidence for a lack of stringent DNA-repair.

A 1066nt region composing exons 7-10 of *p53* was PCR amplified and sequenced (Seeb et al. 1996a). Primers used were:

p53-7F1 5' CAG GTG GGA TCA GAG
TGT ACC 3' (Park et al. 1996) and
p53-10R1 5' AGC GTC GGC AAC AGG
CAC CAA CTC 3'.

The second primer was developed by selecting a conserved region found through comparison of exon 10 sequence of chinook salmon (Park et al. 1996) with that of rainbow trout (de Fromental et al. 1992). We developed additional primers to subdivide the 1066nt template by selecting optimal 20mers about 400nt towards the center of the template from the two ends:

p53-8R1 5' CCG ACC CAG GCG CTG CCC
3',
p53-9R1 5' GAG GGG CAG GCA GGG
AGG CC 3', and
p53-9F1 5' GGC CTC CCT GCC TGC CCC
TC 3'.

We found no evidence of mutations in response to oil and little variation in our initial screen of the *p53* gene in several dozen individuals originating from two Alaskan populations, including embryos from one population maintained in oiled substrate (Seeb et al. 1996a). However, both populations were polymorphic at the base pair corresponding to nt 1,054 of *p53* in rainbow trout copy DNA (cDNA; de Fromental et al. 1992), and two heterozygote x homozygote matings demonstrated codominant segregation (data not shown).

A 795nt segment of cytochrome *b* region of mtDNA was PCR amplified and sequenced (Seeb et al. 1996a) using primers:

LGL-765 5' GAA AAA CCA YCG TTG
TWA TTC AAC T 3' (Cronin et al.
1993),

H15498 5' GGA ATA AGT TAT CTG GGT
CTC 3' (Kocher et al. 1989).

Unexpectedly little variation was found in the DNA sequence in our preliminary screen of 20 pink salmon from PWS. Nucleotide 486 in codon 162 was an "A" in all individuals except one female that was a "G".

Both of these polymorphisms in *p53* and cytochrome *b* are candidates for allele-specific PCR assays. At this writing we are optimizing PCR conditions for 24nt primers for cytochrome *b* that contain the polymorphic base at the three prime end (5'-TATGTGGGCGGCGCCCTAGTACAG-3', or 5'-23mer-A-3'). One can determine the genotype of an individual by using these primers jointly in paired assays by doing the PCR amplification only; no sequence analysis would be required. Similar primers will be developed for the *p53* polymorphism at nt 1,054.

SOCKEYE SALMON STUDIES

Commercial fisheries on sockeye salmon in Cook Inlet have occurred since the late 1800s and represent a significant economic resource to southcentral Alaska. Harvest levels have ranged from 95,000 to 9.5 million fish (Rigby et al. 1991; Ruesch and Fox 1994), and in the last 10 years the total value of the fishery reached \$111.1 million (Ruesch and Fox 1994). In July of 1989, however, fishing time in the Cook Inlet area was greatly reduced due to the presence of oil from the *Exxon Valdez* spill.

As a direct result of the reduced exploitation, sockeye salmon spawning in the Kenai River system exceeded optimal escapement goals by three times. Extremely high escapements can produce enough fry to deplete zooplankton prey populations, causing high fry mortality, and can alter the species composition and productivity of prey populations for several years (Schmidt et al. 1995). In response to a potential decline in the fishery, efforts began in 1992 to refine population identification and management techniques and to increase knowledge of the diversity and abundance of sockeye salmon in Cook Inlet.

Most of the sockeye salmon production in Upper Cook Inlet (UCI) comes from four major river systems. The largest sockeye salmon producer (2.8 million fish annually) is the Kenai River which drains the Kenai Peninsula on the east side of UCI (Fig. 2B). Next are the Kasilof and Susitna River systems which each produce approximately 700,000 sockeye salmon annually followed by the Crescent River drainage (200,000 fish). The Kenai, Kasilof and Crescent River systems are characterized by large, central glacial lakes fed by numerous smaller tributaries. The Susitna River system has many smaller lakes, each of

which empties into the mainstem through smaller, separate streams. The remainder of the sockeye salmon production in UCI is composed of many minor populations (Ruesch and Fox 1994).

Cook Inlet sockeye salmon have been the focus of a number of population identification studies. Extensive efforts were made to delineate populations through scale pattern analyses (Marshall et al. 1987) and parasites (Waltemeyer et al. 1993). Neither technique proved adequate. Significant temporal and sexual variability within populations exists with scale pattern analyses (Waltemeyer et al. 1996), and it is difficult to obtain population-specific scales on an in-season basis. Similarly, temporal instability eroded the usefulness of parasite data. Grant et al. (1980) found considerable heterogeneity among populations inhabiting the region using allozymes. In evaluations of their resulting mixed-population model, Grant et al. (1980) demonstrated a high degree of success using three loci to classify populations from the Kasilof River and Susitna River drainages, but incomplete baseline data was thought to confound the Kenai River classifications. Additional data from the Russian River, one of the Kenai River drainages, was presented by Wilmot and Burger (1985) who found significant differences between early and late runs from the Russian River. However, no comprehensive genetic survey of Cook Inlet has been undertaken since the 1970s. In this paper, we review the genetic data that were collected to aid in the population identification and restoration of Kenai River sockeye salmon.

Allozyme and Mitochondrial DNA Analyses

Tissue samples from 100 spawning individuals were collected from all major sockeye salmon-producing systems of UCI. Approximately 7,000 individual sockeye salmon were sampled (Fig. 2B). Mixed-population collections originating from Cook Inlet fisheries (Central District; Fig. 2B) were collected in a similar manner to that of spawning samples. Samples of muscle, liver, retinal tissue, and heart were dissected from freshly killed individuals. Individual sample numbers were assigned to uniquely identify all genetic samples. Allozyme techniques followed those of Aebersold et al. (1987); nomenclature followed the American Fisheries Society standard (Shaklee et al. 1990). A total of 68 allozyme loci were resolved (Seeb et al. 1995; Seeb et al. *in press*).

A subset of 25 populations was surveyed for RFLP variation at mtDNA. Whole DNA was extracted from liver or heart tissue, purified, quantitated, and diluted (100ng/ μ l) for PCR amplification. The primers of Cronin et al. (1993) and Park et al. (1993) were used to amplify the

mitochondrial NADH dehydrogenase subunits 5 and 6 (ND5/ND6) using PCR. Amplified DNA was cut with six restriction enzymes (*Apa* I, *Hha* I, *Hinf* I, *Kpn* I, *Stu* I, and *Taq* I).

Populations were grouped *a priori* into seven regions: Kenai River, Kasilof River, Susitna River, Yentna River, Northeast Cook Inlet, Knik Arm, and West Cook Inlet. To describe the subdivision of genetic diversity further, a hierarchical gene diversity analysis (Nei 1973; Excoffier et al. 1992) was conducted. The allozyme data was organized to test for the distribution of variability among sites within nursery lakes, among nursery lakes within regions, and among regions. Because fewer samples were analyzed for mtDNA variation, the hierarchy tested for those data were limited to among sites within regions and among regions.

Population contributions to the mixture samples were estimated via maximum likelihood (MLE; Pella and Milner 1987) using a conjugate gradient searching algorithm with square root transformations (Pella et al. 1996) and the computer program SPAM (ADFG 1997); the precision (standard error) of the population composition was estimated by an infinitesimal jackknife procedure (Millar 1987). Individual population estimates were first calculated, then summed into regional groupings (allocate-sum procedure, Wood et al. 1987). Simulated mixtures were used to evaluate the accuracy of the population composition estimates from reporting regions. These hypothetical mixtures ($n = 400$) were generated from the baseline allele frequencies assuming Hardy-Weinberg equilibrium, and the precision of the simulated mixtures was estimated by a parametric bootstrap (Efron and Tibshirani 1986). One hundred bootstrap iterations were performed, and a series of 100% simulations for the seven reporting regions (hypothetical mixtures composed entirely of populations from the individual region). In order to maintain confidence in the estimates, fishery managers desired reporting regions that showed at least 90% allocation to the region of origin.

Heterogeneity Within and Among Regions

A high level of gene diversity revealed by allozymes was found within some regions. Two lineages of related populations were evident based upon overall similarity: Mainstem Kenai River populations and a second cluster of populations composed of the Tustumena Lake populations from the Kasilof drainage. The Northeastern Cook Inlet and Knik Arm populations also demonstrate regional affinities, but little regional structuring is apparent in the remaining populations. The Russian River, within the Kenai River, was particularly divergent.

A total of 10 composite mtDNA haplotypes was

revealed with the six restriction enzymes. Two composite haplotypes representing variation in the *Apa I* enzyme were encountered most frequently (i.e., in 78% of the samples) in Cook Inlet. The distributions of these two haplotypes appear to correlate with geography; haplotype I was present at a high frequency in the Kenai (56.2%) and Kasilof (30.0%) River samples, whereas haplotype II was present at high frequencies in the Kink Arm (55.4%), Susitna River (57.5%), Yentna River (55.4%), and Western Cook Inlet (61.9%) samples. The Northeastern Cook Inlet samples were fixed for haplotype II.

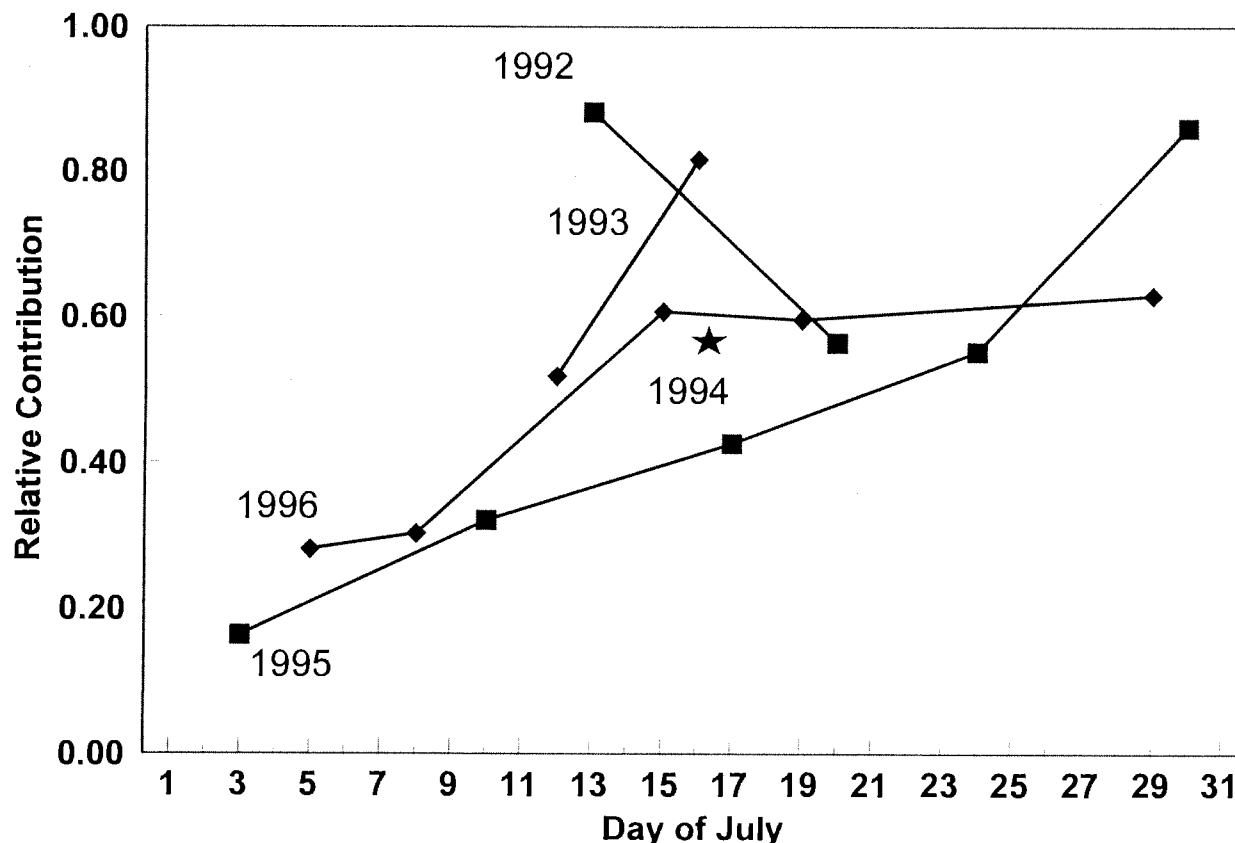
A hierarchical gene diversity analysis stratified variation by site, nursery lake, and region. The greatest amount of variation (87.8%) occurred within sites. Relatively little variability was detected among sites within nursery lakes (0.4%; Table 3). However, considerable heterogeneity (7.8%) existed among nursery lakes within regions with the remaining 4.1% of the variability allocated to the among-regions component. An AMOVA analysis similar to the pink salmon analysis was also conducted with the mtDNA; however, only two hierarchical levels, site and region,

were analyzed (Seeb et al. 1995).

Mixed-Population Analyses

Clearly there is far greater among-population diversity in sockeye salmon from Cook Inlet than in pink salmon from PWS (Table 3). This diversity allows for the use of Mixed Stock Analysis (MSA) analyses in Cook Inlet, whereas MSA is probably not possible for routine applications for pink salmon in PWS. The performance of the MSA model for Cook Inlet sockeye salmon was investigated through simulations. Fishery managers set an *a priori* goal of 90% accuracy for analysis of simulated mixtures prior to accepting MSA for management purposes. The Kenai River region, the group of greatest concern, showed 91% classification in these simulations; Northeastern Cook Inlet, Kasilof River and Knik Arm also were above or close to the goal (99%, 92% and 88% respectively). Although the Yentna River at 88% was near the goal, the Susitna River misclassified to both the Yentna River and Western Cook Inlet, resulting in a correct classification of only 77%; when

Fig. 4 Relative contribution of Kenai River populations of sockeye salmon to the Cook Inlet drift fisheries in the Central District during the month of July, 1992-1996.



the Susitna and Yentna regions were combined, the allocation rose to 87%. Western Cook Inlet, a heterogeneous grouping based on geographic proximity, performed at 86%.

Maximum likelihood estimates were calculated for all samples collected from the Central District drift gillnet fisheries. These estimates were then summed by region for use in management. In 1992, 1993, and 1994, few samples were taken, and estimated contributions shed little light on the interactions of regions within the fishery (Fig. 4). In 1995 and 1996, five collections were taken from that portion of the season coinciding with the expected presence of Kenai River sockeye salmon (Fig. 4). These collections showed an increase through July of Kenai River sockeye salmon in the drift gillnet fishery over the period examined.

Finer scale estimation was also possible for some populations within some river drainages. A 100% simulation was conducted on the upper Russian River populations. The simulation result was 99.4% (SD = 0.5%), indicating that the upper Russian River could be identified in mixtures of Cook Inlet populations with a high degree of accuracy and precision. The proportion of upper Russian River populations in admixtures within the Kenai River have been estimated during the last several years. The results suggested a pulse of early-run fish, a lull, and then a large pulse of late-run fish.

The mtDNA data was tested for its ability to improve allozyme-based MSA estimates within Cook Inlet (results not shown). This testing procedure involved running two sets of simulations. The first set of simulations used allozyme data only from the same subset of populations that were analyzed for mtDNA variation. For all simulations, the region being tested composed 100% of the mixture ($N = 400$), and 100 bootstrap resamplings were conducted. In general, the mtDNA data somewhat improved the accuracy of the estimates. The standard deviations of the mean estimated allocations to the correct regions showed a similar decreasing trend with the addition of mtDNA data, indicating an improvement in precision. However, the small improvements do not warrant the additional costs and substantial additional time required to add mtDNA data into the in-season analysis at this time.

Management Implications

The results of the maximum likelihood estimates indicated that Kenai River populations can be identified in mixtures of Cook Inlet sockeye salmon with a level of precision, accuracy, and timeliness useful for fisheries management. The genetics estimates were first incorporated into in-season fishery

management in 1995; to date results have been reported for Kenai River/non-Kenai River components only. In future years it is likely that additional reporting groups will be added to the analysis.

Application of genetic data to population identification in fishery management has several advantages over other methods, including stability of allele frequencies over time, ability to process large number of samples rapidly (allozyme data), and reasonable cost (allozyme data). The accuracy and precision of the estimates can likely be further improved as additional genetic markers become available and processing costs and times of DNA methods decline. These applications are currently underway in Cook Inlet to aid in management and conservation.

Microsatellite Variation in Sockeye Salmon

We also conducted a small-scale pilot study to measure microsatellite variation in sockeye salmon by looking at four Cook Inlet populations. Fifteen microsatellite primer pairs were screened to assess quality of amplified PCR product, optimize PCR conditions, and assess their potential for measuring genetic population structure (see Olsen et al. 1996). Of the 15 primer pairs, 5 were chosen for the population screen including *One μ 1*, *One μ 2*, *One μ 11*, and *One μ 14*, developed from sockeye salmon (Scribner et al. 1996), and *Ssa293*, developed from Atlantic salmon (McConnell et al. 1995). The populations surveyed included the Russian River (late run) and Skilak Lake outlet (Kenai River drainage), Moose Creek (Kasilof River drainage), and the Yentna River (Susitna River drainage).

The range of variation was considerable. All loci were polymorphic, and all but *One μ 1* were polymorphic in all populations. Numbers of alleles per locus ranged from 3-13 (Table 5). Observed heterozygosity ranged from 0.00 to 0.90 for microsatellites *One μ 1*, *One μ 2*, *One μ 11* and *One μ 14*. A test of Hardy-Weinberg equilibrium (HWE) revealed no significant differences between observed versus expected heterozygosities within each population at these four loci ($P > 0.08$). However, observed heterozygosity was significantly below that expected for microsatellite *Ssa293* ($P < 0.001$). In fact, some samples failed to exhibit any *Ssa293* alleles. We believe the lack of heterozygotes and lack of expression observed at the *Ssa293* locus is due to one or more null alleles as observed in the pink salmon data set above. Null alleles have been described previously for human microsatellites (Callen et al. 1993) and are more likely to occur when using primers developed in related species (Forbes et al. 1995). We chose to exclude *Ssa293* from subsequent

Table 5. Sample size (N), number of alleles (A), and observed heterozygosity (H_o) at five microsatellite loci in Cook Inlet sockeye salmon. The Avg. column includes averages from all loci except Ssa293.

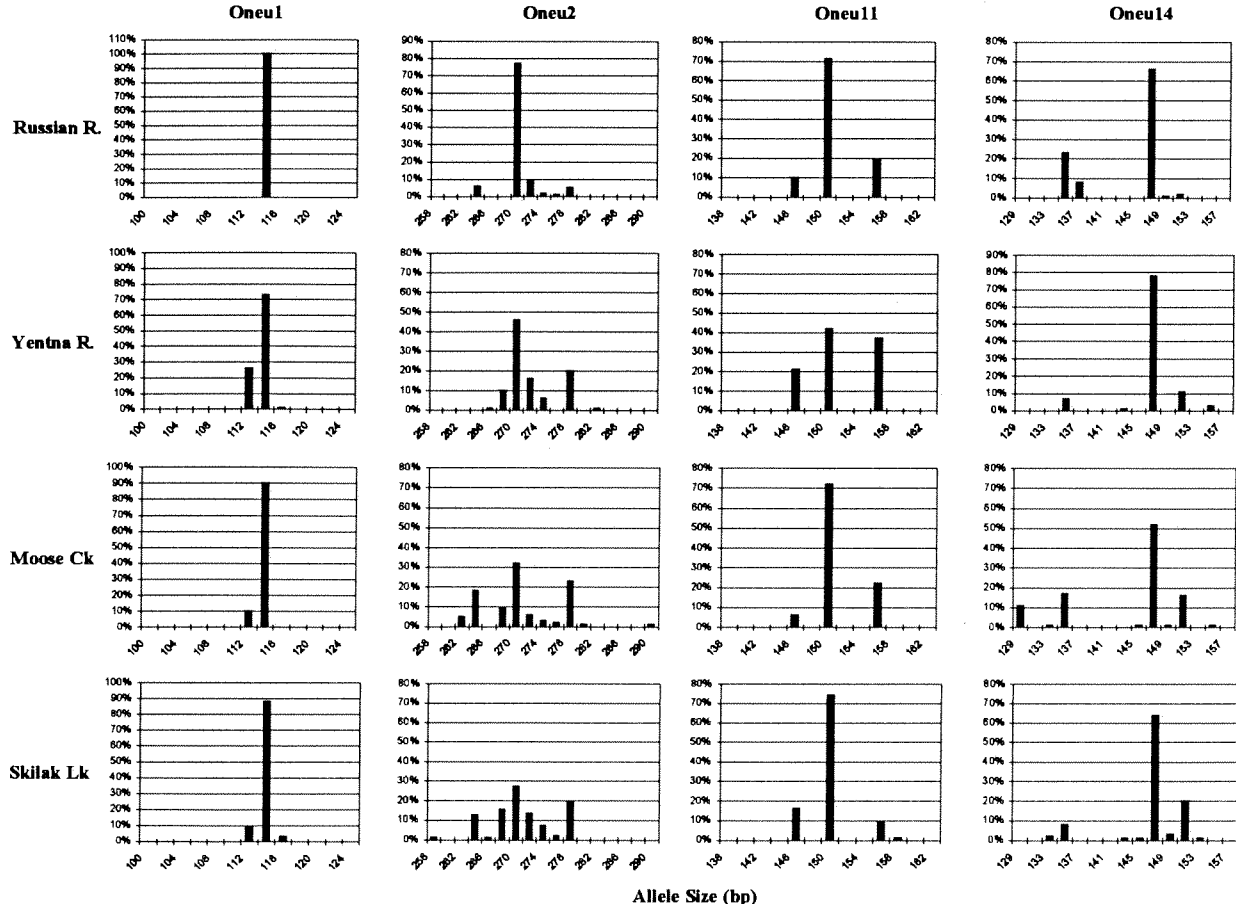
Population		One μ 1	One μ 2	One μ 11	One μ 14	Ssa293	Avg.
Moose Creek	N	50	50	50	50	43	
	A	2	10	3	8	4	5.8
	H_o	0.20	0.76	0.46	0.64	0.28*	0.52
Russian River	N	50	50	50	50	41	
	A	1	6	3	5	5	3.8
	H_o	0.00	0.38	0.36	0.52	0.10*	0.32
Skilak Lake	N	50	48	50	50	40	
	A	3	9	4	8	9	6.0
	H_o	0.24	0.90	0.42	0.54	0.25*	0.52
Yentna River	N	50	50	50	50	41	
	A	3	7	3	5	8	4.5
	H_o	0.38	0.68	0.58	0.38	0.34*	0.51
All pops	N	200	198	200	200	165	
	A	3	13	4	10	10	8.0
	H_o	0.21	0.68	0.46	0.52	0.24	0.42

* Significant differences between observed and expected heterozygosity for each population were determined using a Bonferroni adjustment (initial $\alpha = 0.0125$) and are indexed with an asterisk (*).

statistical analysis because verification of the null allele hypothesis requires redesigning the primers and conducting inheritance studies-- beyond the scope of this pilot study at this writing.

The mean heterozygosity for the four One μ loci was approximately 0.50 for Moose Creek, Skilak Lake, and Yentna River. The Russian River exhibited

the lowest degree of variability with a mean heterozygosity of 0.32. Allele frequencies differed among all populations and ranged from 1 to 100% (Fig. 5). No clear pattern was evident in the shapes of the allele distributions across populations. For each locus the same allele was most frequent in all populations: One μ 1(114), One μ 2(270), One μ 11(150),

Fig. 5 Allele frequency distributions for four microsatellite loci in four populations of sockeye salmon from Cook Inlet, Alaska.

One μ 14(147). At three of the four loci at least one population-unique allele was present. Notably, the 129 and 137 alleles at One μ 14 had frequencies of about 11% and 8%, respectively, in Moose Creek and Russian River. Additional screening is needed to determine if these alleles are present in other populations.

Significant differences in allele frequencies ($p < 0.0001$, $SE < 0.0001$) were shown for all populations using the Markov chain algorithm in GENEPOP. Further, a pairwise comparison of all populations using the same algorithm showed significant differences (following sequential Bonferroni adjustment using an initial α of 0.0125) in allele frequencies at most loci. The exceptions were: Moose Creek and Skilak Lake at One μ 1 and One μ 2, Moose Creek and Russian River at One μ 11, Russian River and Skilak Lake at One μ 11, and Skilak Lake and Yentna River at One μ 14. Finally, an estimate of the F_{ST} analog (θ) (Weir and Cockerham 1984) was made for each locus and revealed moderate genetic differentiation. Values ranged from 0.042-0.100. For all loci combined θ was estimated at 0.071, the 95% bootstrap confidence interval being 0.049-0.092. The θ value for the same group of populations and individuals for 13 allozyme loci was 0.198, greater than that detected through microsatellites.

CONCLUSIONS

Our goals were to use proven genetic techniques to define population structure and thus determine the useful scope of management based upon genetic data; where practicable, collect genetic data on fishery mixtures, in-season, to identify populations intercepted; and explore the utility of new DNA markers for defining population structure for population management.

An array of conservation and restoration alternatives are often proposed for "species" suffering impacts from habitat loss, over fishing, or impacts such as the *Exxon Valdez* oil spill. However, species-based proposals often do not provide the resolution needed to sustain conservation of genetically diverse aggregates of salmon populations. It is essential to manage and restore depleted salmon resources on a population basis in order to conserve between-population diversity and long-term viability.

In this paper we apply allozyme analyses and RFLP analyses of mtDNA to identify Alaskan populations; we further review our development of polymorphism screens using microsatellite analysis, sequencing of the nuclear gene *p53*, and sequencing the cytochrome *b* region of mtDNA. At this time the allozyme and RFLP analyses appear to provide the most useful results in terms of relative cost, throughput, and discriminating power. The relative

ability of these two techniques to delineate populations appears to be a matter of scale. Allozymes often discriminate populations on a large scale where mtDNA data may lack resolving power due to probable convergence of haplotype frequencies (cf., Adams et al. 1994; Fetzner et al. *in prep.*). Mitochondrial DNA may sometimes provide improved resolving power on finer-scale study of population structure. These two approaches provided complementary resolving power on fine-scale study of pink and sockeye salmon structure reported here. Of all of these techniques, in our hands allozymes is the only one that currently provides the resolution and speed necessary to provide in-season fishery estimates. Yet allozymes do not always provide the resolution necessary to define the relationships of intra-specific populations. Because of this, additional techniques of DNA analysis are being developed (e.g., Fig. 1), and we conducted pilot studies of microsatellite and DNA sequence variation.

Of the new techniques, microsatellite analysis has probably received the most emphasis recently (Fig. 1B). We found population subdivision using microsatellite analysis, but the between-population diversity detected was not remarkably different from that observed using other techniques. The apparent common occurrence of null alleles may confound the interpretation of variation at some loci. The observed heterozygosity was remarkably high, however, and this in itself may provide advantages to microsatellites in some cases. Our observation is that the slow relative throughput and high relative expense of microsatellite analysis will limit its utility to the study of populations that otherwise cannot be resolved using allozymes or in which lethal sampling is not possible, and we would not expect this approach to have utility for in-season estimates in the near future.

We also report DNA sequence polymorphism detected in our study of potential genetic damage in pink salmon. We are interested in these data for population genetic study in as much as others suggest that allele-specific PCR could provide a rapid-throughput approach for the collection of genetic data. One of the primary reasons that DNA data is not used for stock assessment of harvest mixtures in real-time management is that a comparatively long time is required for data collection. Electrophoretic data from RFLP analyses, let alone DNA sequencing, does not provide data rapidly enough for use in harvest-management decision making. Allele-specific PCR of single nucleotide substitutions detected by either sequencing or RFLP assays should provide more rapid results because genotypes are determined directly from the PCR reaction without the need for additional electrophoretic separation of the DNA products.

While the potential for stock assessment using some of the newly developed DNA techniques is

great, substantial development and testing remains to be done with many species. Fisheries managers sometimes accuse geneticists of prematurely promoting newly developed but unproven approaches to stock assessment (e.g., see Lincoln 1994). We recommend continued implementation of successful approaches such as allozyme electrophoresis for harvest management; however, we recognize the value of pursuing research into additional genetic technologies that may improve existing assessment capabilities.

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Identification of Long and Short-Term Reared Masu Salmon with Quantified Scale Characteristics

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Masu salmon (*Oncorhynchus masou*) are important to coastal commercial fisheries in northern Japan. Enhancement programs include a combination of release of fry in the spring (short-term rearing: ST) and release as juveniles in the fall, or as smolts the following spring (both long-term rearing: LT). In recent years, the number of LT fish released has increased and it has been practically and financially difficult to mark all of the releases. A simple and accurate method is needed to identify LT and ST fish in the overall numbers of returning adult masu salmon, to evaluate the success of alternative rearing and release strategies. Accordingly, a modification of the assignment rule developed to identify wild and hatchery steelhead stocks in Lake Michigan was applied to masu salmon. Scales of 1,129 adult masu salmon, which returned to the Shiribetsu River in 1989, were examined and various numerical scale characteristics were compared between the LT and ST fish groups. Significant differences in scale characteristics were found between LT and ST fish groups. Two scale variables were found that provided an acceptable level of discrimination. However, the fish could not be discriminated individually, due to an overlap in the distribution of scale variables. Accordingly, further examination is still required to find an effective scale characteristic that can detect individual differences.



INTRODUCTION

Masu salmon (*Oncorhynchus masou*) spend one year in the ocean following seaward migration of juveniles from natal rearing habitat and migrate back to their natal river in the succeeding spring (Machidori and Kato 1984; Kato 1991). Natural production of masu salmon is limited due to shortage of suitable spawning and rearing habitat. To increase production of masu salmon the national and prefectural governments have been carrying out programs of enhancement. These programs consist of either short-term (ST) rearing of fry that are released in the spring or longer-term (LT) strategies involving rearing of juveniles for release before winter or for release as smolts in the succeeding spring (Mayama 1991, 1992; Ohkuma and Nomura 1991). Releasing fry in the spring was the most common approach prior to introduction of the LT methods. In recent years releases of LT fish have become so large that it has been practically and financially difficult to mark all of these fish. A simple and accurate method is needed to identify LT and ST fish among the returning adult masu salmon so fishery contributions can be estimated to evaluate release strategy. Accordingly, I attempted

to apply and modify the assignment rule developed by Seelbach and Whelan (1988) to identify wild and hatchery steelhead stocks in Lake Michigan.

MATERIALS AND METHODS

Scales were collected from 3,209 fish out of the 3,731 adult masu salmon that returned to the Mena River, a branch of the Shiribetsu River, in 1989 (Fig. 1). The 1989 return was larger than the 1988 or 1990 return. Scales were removed from the preferred location on the body, a few rows above the lateral line between adipose fin and posterior end of dorsal fin. Scale measurements were taken using vinyl acetate plate impressions magnified 100 times under micro projector. Regenerated scales and age 2.1 fish were excluded and 1,129 age 1.1 fish were examined. Among the scales examined, 701 were from fish (marked: MK) that had been marked and released as 0+ juveniles (right ventral fin clip) in autumn of 1987, or marked and released as 1+ smolts (left ventral fin clip, both LT fish) in the spring of 1988 (Table 1). 428 scales (no-marked: NM) were from unmarked survivors of the 827,000 fry released in the spring of 1987 (ST).

Fig. 1 Locations of the hatchery and trapping site, from which masu salmon were obtained, on the Mena River.

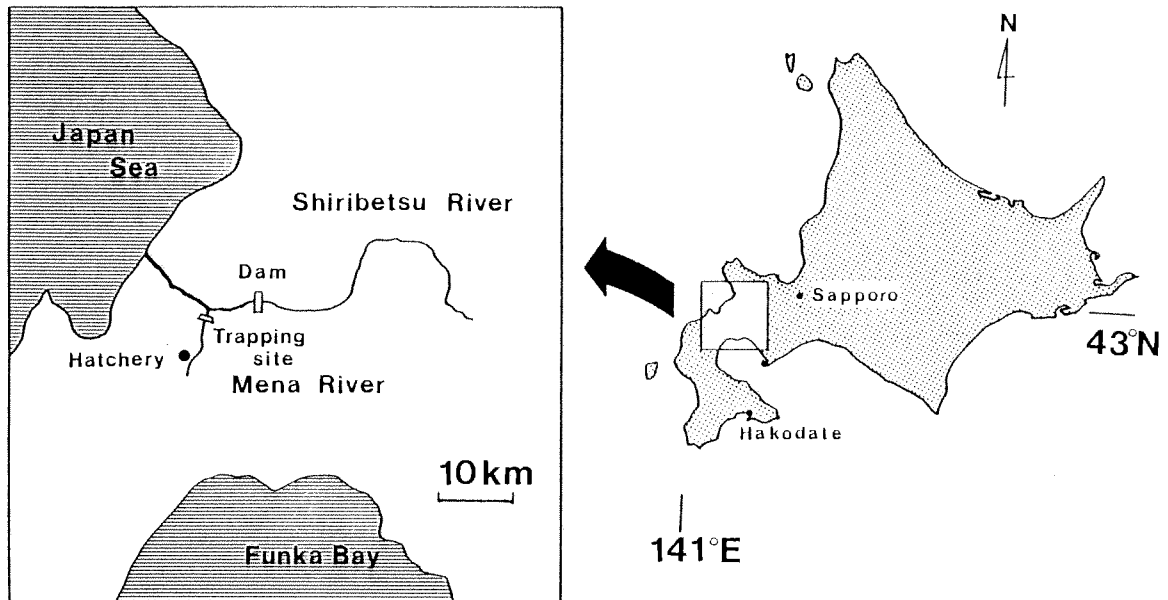


Table 1. Rearing and release history of adult masu salmon returned in 1989 as age 1.1 fish.

Year & Season	1986 brood year group		
1985 Autumn	Fertilization		
1986 Spring			
Autumn			
1987 Spring	release 827,000		
Autumn	F	release 97,000 0+ J (Rv cut)	release 158,000 1+ S (Lv cut: 143,000)
1988 Spring			
Autumn			
1989 Spring			
Autumn			
		return as age 1.1 fish	

F: fry, J: juvenile, S: smolt, Lv: left ventral fin, Rv: right ventral fin

The stock of masu salmon in this Mena River system is maintained primarily by artificial propagation. The fish that escape through the weir may spawn; however, there were few fry from natural spawning found in sampling in the river prior to the fry release in the spring of 1987. Therefore, almost all NM fish examined in this study were considered to be ST fish. After reviewing the records from the 1987 release of age 1+ smolts, it was determined that 15,000 out of 158,000 LT smolts released were not marked.

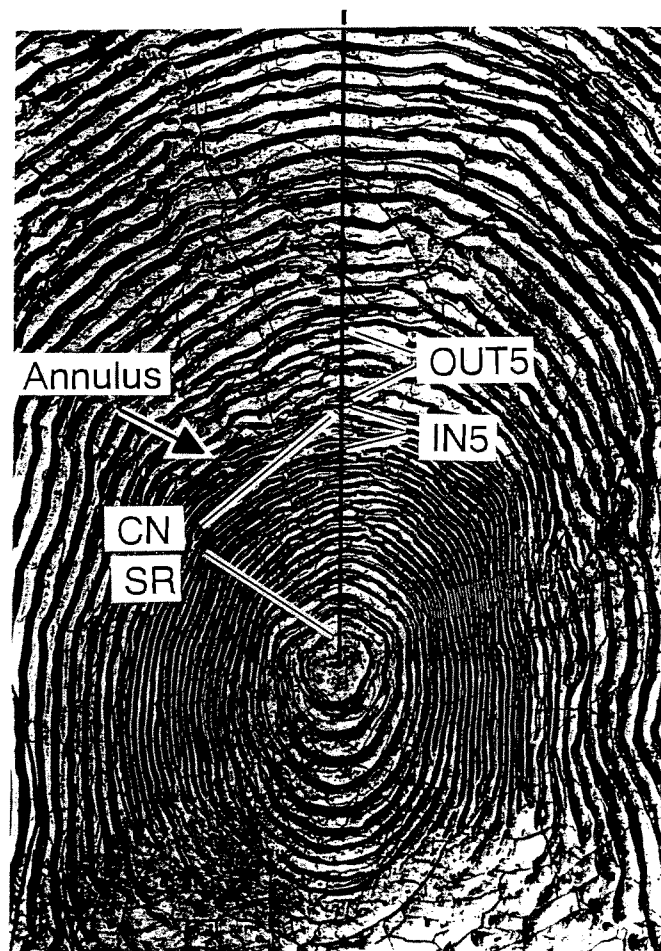
The following five scale characteristics were measured or counted along the longest axis of freshwater growth zone (Fig. 2): scale radius (SR) from the first circuli to the freshwater annulus, number of circuli (CN) in the extent within the width of five intercirculus spaces inside and outside annulus (IN5 and OUT5, respectively), and ratio between IN5 and OUT5 expressed as OUT5/IN5 (R5). The ratio R5 was a reciprocal number described as band 23 in Seelbach and Whelan (1988).

Statistical significance was examined using 2 tailed t-test for difference between female and male

fish, and Mann-Whitney U-test and Smirnov-Kolmogorov 2-sample test were used to examine the difference between NM and MK fish groups.

For identifying LT and ST fish using R5 value solely, two different threshold levels were selected and calculated. The first value was calculated from the average value of R5 of NM and MK fish in 1989, expressed as the point midway between each average (rule A). The other level was also expressed as the midpoint midway of each average of NM and MK fish, but the source for calculation includes fish sampled in 1980-1982, 1988, and 1989 (rule B). Total number of samples used to calculate the threshold value of rule B was 1,334 NM and 1,064 MK fish. A discriminant function analysis using SR and R5 variables was used as rule C (Arima and Ishimura 1987). Measurements of SR and R5 from 1,129 samples collected in 1989 were used for estimating the discriminant function used in this study. In addition, identification using visual examination of scales with aid of a micro projector (rule D) was included in a comparison of accuracy among the different rules. Each scale sample was read three to

Fig. 2 Measured and counted scale characteristics for analysis in this study.



five times. Scale samples were read in random order in an attempt to avoid biasing classification between readings. Scales were classified to either ST or LT groups based on results from three out of five readings. Accuracy was calculated by fish groups (i.e. NM and MK), respectively, and expressed as error rate (%) as follows:

$$\text{Error rate} = \text{Nf/Nt} \times 100$$

where Nf is number of misidentified fish, and Nt is number of fish belonging to each group.

RESULTS

No significant differences were found in the five scale variables between female and male MK fish, but OUT5 and R5 showed significant difference for NM fish at $P < 0.05$ and $p < 0.01$ (Table 2). In contrast, all five variables showed highly significant difference between NM and MK fish ($p < 0.001$) when sexes were combined.

The distribution of R5 for MK fish is peaked and skewed to the right while the distribution of NM fish is more evenly distributed (Figure 3). Error rate by the rule A shows 25.5% and 16.1% for NM(ST) fish and MK (=LT) fish, respectively. Rule B shows similar results to rule A with slightly lower rate for MK and higher rate for NM fish. Rule C, using a linear discriminant function combining SR and R5

showed lower rate than rule A and B, and error rate by scale reading by eye shows lowest result in all rules for MK fish though the rate for NM fish is almost same as rule C. The tendency of higher error rates on NM(ST) fish using all rules was observed. This might be due to 15,000 LT juvenile released without marking (Table 1). Distribution patterns of R5 of MK fish, and of NM fish, identified as LT or ST fish by scale reading are shown in Figure 4 and 5, respectively. Though the fish identified as ST of MK fish were very rare, R5 of the fish identified as LT of NM fish were mainly distributed in lower range. Figure 6 shows the distribution pattern of R5 of NM-ST and MK-LT fish excluding mis-read samples. To reduce the effect of not marked LT juvenile from the error rates listed in Table 3, number of LT fish among no mark fish (Na) were estimated from Table 1 and the following equation:

$$\text{Na} = 607 \times (158,000 - 143,000) / 143,000,$$

where 607 is the number of Lv-cut LT fish among total of 701 LT fish specimen. The rest of 94 fish were Rv-cut LT fish. Then, Na was estimated as 64. This means 64 fish among 428 NM fish are LT, but no-mark fish. The revised rates are listed in Table 4, and these rates in NM fish by derived from rule A and B decreased to almost half. Also those rates by rule C and D decreased to one-third to one-fourth, though that of MK fish did not show clear decrease.

Table 2. Averages and the results of statistical examination of the scale characteristics of masu salmon. Scale characteristics are described in figure 2. NS denotes no significance ($p > 0.05$); asterisks denote significance at $p \leq 0.05^*$, $p \leq 0.01^{**}$, or $p \leq 0.001^{***}$. Standard deviations are listed in parentheses.

p = 0.001, p = 0.001, p = 0.001, p = 0.001. Standard deviations are listed in parentheses.							
Group	N	Scale characteristics					Test
		CN	SR (mm)	IN5 (mm)	OUT5 (mm)	R5	
NM fish							
Female	322	15.14 (3.035)	0.355 (0.077)	0.097 (0.018)	0.188 (0.031)	1.991 (0.426)	A
Male	106	15.34 (3.101)	0.361 (0.077)	0.099 (0.017)	0.180 (0.030)	1.863 (0.393)	
Result		NS	NS	NS	*	**	
MK fish							
Female	526	16.00 (2.408)	0.438 (0.075)	0.124 (0.017)	0.172 (0.031)	1.406 (0.287)	A
Male	175	16.18 (2.050)	0.438 (0.063)	0.125 (0.019)	0.168 (0.031)	1.378 (0.320)	
Result		NS	NS	NS	NS	NS	
							B
NM fish	428	15.19 (3.049)	0.356 (0.077)	0.098 (0.017)	0.186 (0.031)	1.959 (0.421)	
MK fish	701	16.04 (2.324)	0.438 (0.073)	0.124 (0.018)	0.171 (0.031)	1.399 (0.296)	
Result		***	***	***	***	***	

A: two-tailed t—test

B: Mann-Whitney's U—test and Kolmogorov—Smirnov's 2—sample test.

Fig. 3 Frequency distribution of R5 of NM and MK masu salmon returned in 1989.

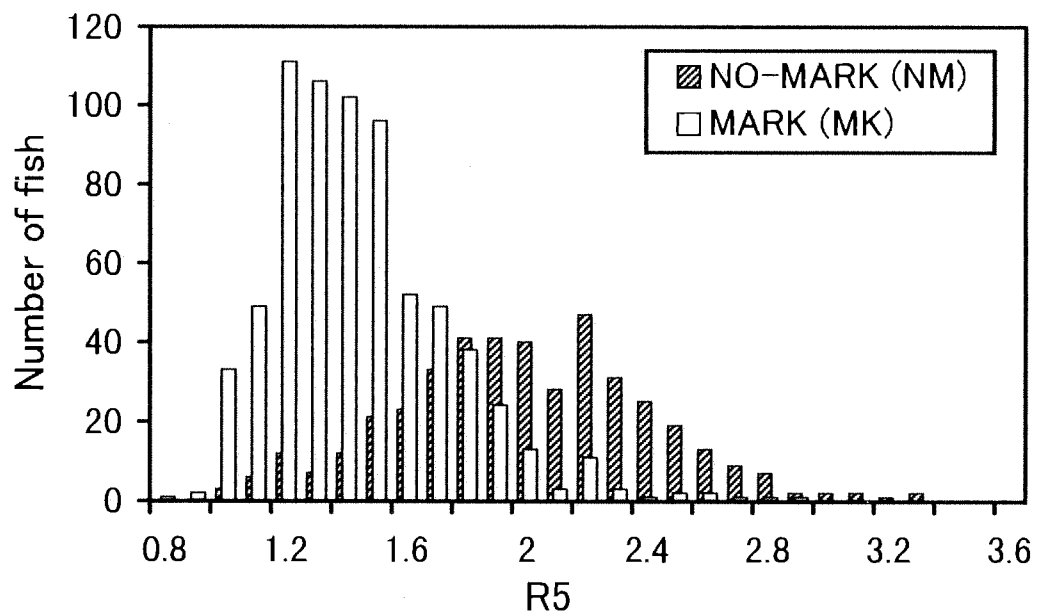


Fig. 4 Frequency distribution of R5 of MK fish identified as ST or LT by scale reading.

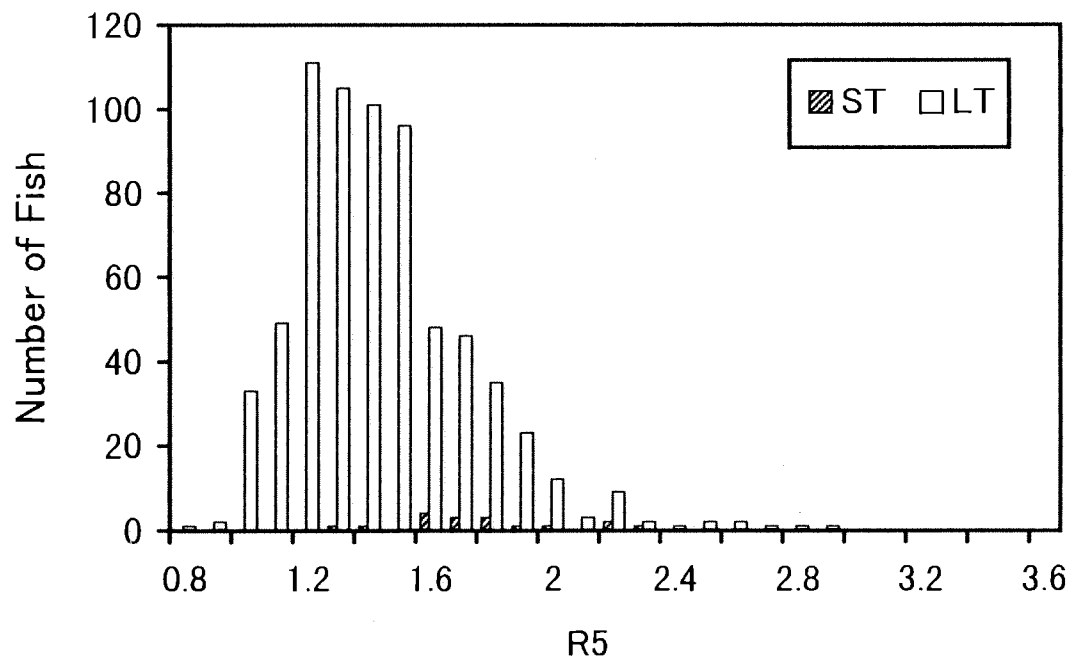


Fig. 5 Frequency distribution of R5 of NM fish identified as LT or ST by scale reading.

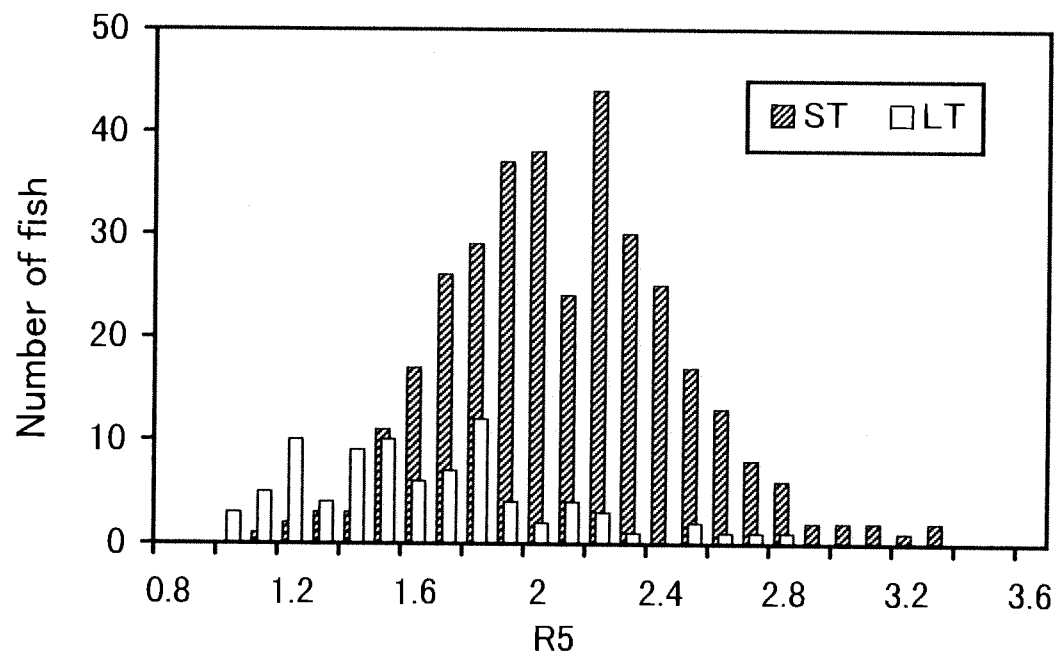


Fig. 6 Distribution of R5 of NM fish identified as ST, and MK fish identified as LT.

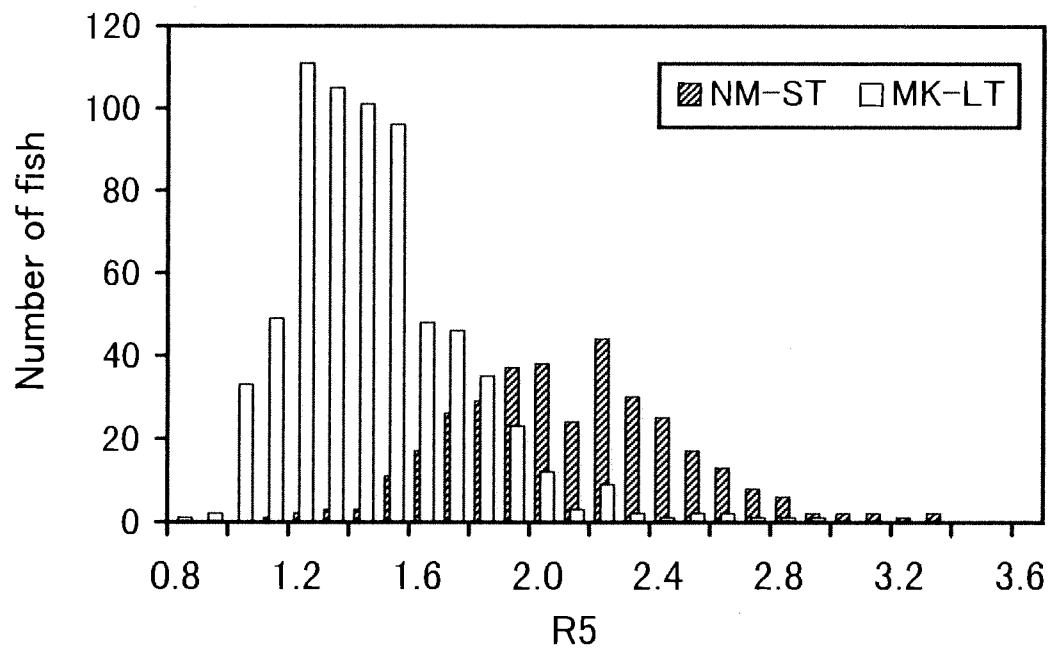


Table 3. Comparison of the error rates of identification of masu adults returned in 1989, using various decision rules.

	NM(ST)	MK	mean %	Decision rule
Error rate %				
	25.5	16.1	20.8	A)
	28.0	13.8	20.9	B)
	19.2	13.4	16.3	C)
	19.9	2.4	11.2	D)
Number of fish	428	701	-	

A) identified using midpoint of average R5 of NM (ST) and MK (LT) fish of the year (threshold value $t=1.6786$)

B) identified using midpoint of average R5 of 1,334 NM (ST) and 1,064 MK (LT) fish. ($t=1.7080$)

C) identified using the following discriminant calculated with SR and R5 of 1,129 age 1.1 fish returned in 1989:
discriminant: $14.467 \text{ SR} - 4.521 \text{ R5} + 1.845 > 0$ defined as LT fish
 $14.467 \text{ SR} - 4.521 \text{ R5} + 1.845 < 0$ defined as ST fish

D) results from scale reading by eye.

Error rate (%) was calculated with following formula: $N_f/N_t \times 100$,

for marked (MK) fish,

N_f : number of MK fish defined as ST fish,

N_t : number of MK fish,

for no-mark (NM) fish,

N_f : number of NM fish defined as LT fish,

N_t : number of NM fish

Table 4. Revised error rates of identification. Initial rates are listed in table 3.

Rule	Revised error rate %			
	NM(ST)	MK	Mean	Total
A)	12.4	14.8	13.6	
B)	15.3	12.7	14.0	
C)	4.9	12.2	8.6	
D)	5.8	2.2	4.0	
Initial N	428	701		1,129
Revised N	364	765		1,129

DISCUSSION

Seelbach and Whelan (1988) stated that scale variables that are utilized must have following criteria: 1) be stable through years, 2) show clear difference between ST and LT fish, and 3) show little difference among neighboring rivers. The ratio (R5) between five intercirculus spaces inside and outside annulus met these criteria. In addition, it is necessary for accurate classification that scale variables have low standard deviation and wide differences in means between the two fish groups (i.e. ST and LT). Though all five characteristics examined in this study showed significant difference between NM and MK fish at $p < 0.001$, both CN and OUT5 were not satisfactory for utilization due to their smaller difference in means and large standard deviations. The ratio between the remainder of averages and the mean of the standard deviation showed that the ratio of R5 ranked as top at 1.56, followed by IN5 at 1.49, and SR at 1.09. Those of CN and OUT5 were less than 0.5. From these reasons, it was ascertained that

R5 was a satisfactory characteristics for discrimination, as Seelbach and Whelan (1988) stated.

It is necessary to calculate a threshold value for separating two groups using R5. In this study, a point midway between the averages was chosen as the value for rule A and B. As the threshold value for rule A was calculated from the data obtained in 1989 only, the results were considered to be biased due to the presence of un-marked LT fish in ST fish group. Thus, the alternate value was calculated using data obtained in 1980-82, 1988, and 1989. LT fish were not present in the 1980 and 1981 samples. Though the sampled fish in 1982 included LT and ST, the LT fish of the year were fully marked and thus they could be classified completely. The fish in 1988 contained no-marked LT fish, as in 1989. As the threshold value for separation calculated using these data were slightly larger than that of rule A, the results of rule A and B were somewhat different in each group, but showed scarce difference in the mean value.

The author tried to improve the accuracy of identification using two variables in a discriminant function analysis. Discriminant analysis requires that variables are not correlated. Because the variables R5, IN5 and OUT5 were highly correlated because they were derived from OUT5/IN5, their use was not appropriate. Out of the two remaining characteristics, CN was omitted due to its low difference between groups and high standard deviation. Thus, the discriminant function was calculated with R5 and SR using the data of 1989. Although this method showed high accuracy, results might be affected by variable growth of fish rearing in natural conditions. Though it might be possible to control fish growth in artificial rearing conditions, it is quite reasonable that fish

growth under natural river conditions may vary among years, contributing to high variability in scale growth increments (i.e., the scale radius from focus to freshwater annulus) (Ohkuma 1988). These classification rules were calculated based on standards collected in the same year the mixed stock samples were collected. Differences in scale measurements between years could bias ST and LT classifications in other years. The possibility of using scale measurements from smolts to classify fish as adults might be investigated.

Lastly, identification by scale reading (rule D) was compared with these objective methods based on the quantified scale data, shown above. The accuracy by rule D was nearly 100% for MK fish, and close to the accuracy for NM fish using rule C. Thus, scale reading by trained observers can be used to discriminate fish with unexpectedly high accuracy.

The error rates of NM fish were higher than that of MK fish (Table 3) for all classification rules examined. These differences were thought to be due to the 15,000 no-marked LT smolts among total of 158,000 released 1+ LT smolts, as stated before. The error rates were revised assuming some unmarked fish in the LT group, and those error rates of the NM fish decreased nearly to those of MK fish except for rule C (Table 4). The mean of the revised error rates were comparable to those observed by Seelbach and Whelan (1988). For scale patterns to be viable, the accuracy should be the same as that by scale reading. For such improvement, other techniques using other scale characteristics, such as identification from classifying patterns of changes of intercirculus width by circulus, or measuring and counting scale characteristics along another axis, should be developed. However, with progress on the techniques for producing smolts under artificial condition, more natural-like smolt might be produced in the near future. If that is the case, the methods for identification examined and discussed in this report might be abandoned at that time.

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On the Possibility of Using the Pink Salmon Survival Measure (R/E) in the Forecast of Chum Salmon Returns in North-East Kamchatka

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The time of downstream migration and body size of pink and chum salmon juveniles are very similar in north-east Kamchatka. The supposition that environmental factors, such as hydrometeorological conditions, predation, availability of feeding resource etc., have a similar effect on the yearlings of both species on their way downstream toward sea was examined. The ratio R/E as a measure of survival of a salmon generation during their life time was calculated for pink and chum salmon. A correlation between survival measures of both species was shown. Survival of pink salmon may be used as a good predictor for forecasting chum salmon returns in north-east Kamchatka.



INTRODUCTION

A number of ecological similarities in chum and pink salmon species have served as premises for the evaluation approach described here.

The juveniles of both species migrate to sea in the late spring of the year following spawning, and the downstream migration timing and body sizes are similar in north-eastern Kamchatka. According to Karpenko (1996, 1998), in the period from 1978 through 1992, over 80% of chum and pink salmon juveniles migrated to sea between June 10 and 30. The body length of pink salmon juveniles averaged 3.07 - 3.29 cm, while that of chum salmon was 3.58 - 3.76 cm. This allows the supposition that environmental factors such as hydrological and meteorological conditions, predation, availability of food resources (for a certain period), may have a similar effect on the yearlings of both species migrating to sea.

The mortality level is at its highest among the species in the period of downstream migration, as compared with the rest of their life cycle. Therefore, it is during this period that the environmental conditions should be considered as the most critical for survival of the generation. If that inference is true, then logically it will appear that the similarity in environmental effects during the downstream migration can be manifested in similar survival results in both species, as expressed by the survival measure

(return/escapement ratio, R/E) and dynamics. If common survival results are manifested and can be expressed quantitatively, then these can be applied to forecasting the chum salmon return, as it happens 1 to 3 years following that of pink salmon. This research was dedicated to examine the above supposition.

Attempts to evaluate chum salmon returns while forecasting that of pink salmon were made earlier by Nickolayeva (1988) for the Kamchatka River, based on the idea of the possible relationships between chum and pink salmon generations. She indicated that the average age at maturity and survival measure of chum salmon generations of the Kamchatka River were related to pink salmon abundance in north-eastern Kamchatka.

MATERIALS AND METHODS

Data on landed catches and number of chum and pink salmon spawners in north-eastern Kamchatka from 1957 to 1995 (KamchatNIRO Archives), material on pink and chum salmon juveniles migrating downstream in the Khailyulya River from 1978 to 1992 (Karpenko 1996), as well as the data on age composition of the Khailyulya River parent chum salmon stock during 1973 - 1995 (E.T.Nickolayeva and L.O.Zavarina) were kindly provided by L.O.Zavarina. These were used as the initial basis for this research.

Reliable data on the abundance of 37 pink salmon

broods and their respective survival measure values (K_{Pink}), are available for north-eastern Kamchatka. It is not possible to determine chum salmon survival measures, based only upon the data on returns and number of spawners, because chum salmon have a longer life cycle, as well as a more complex age composition. We used only the data on age compositions and abundance of 17 chum salmon generations, for the brood years 1973 - 1989. The reliable chum salmon survival measure, determined via consideration of the age composition, will be referred to as the true survival measure (K_{True}).

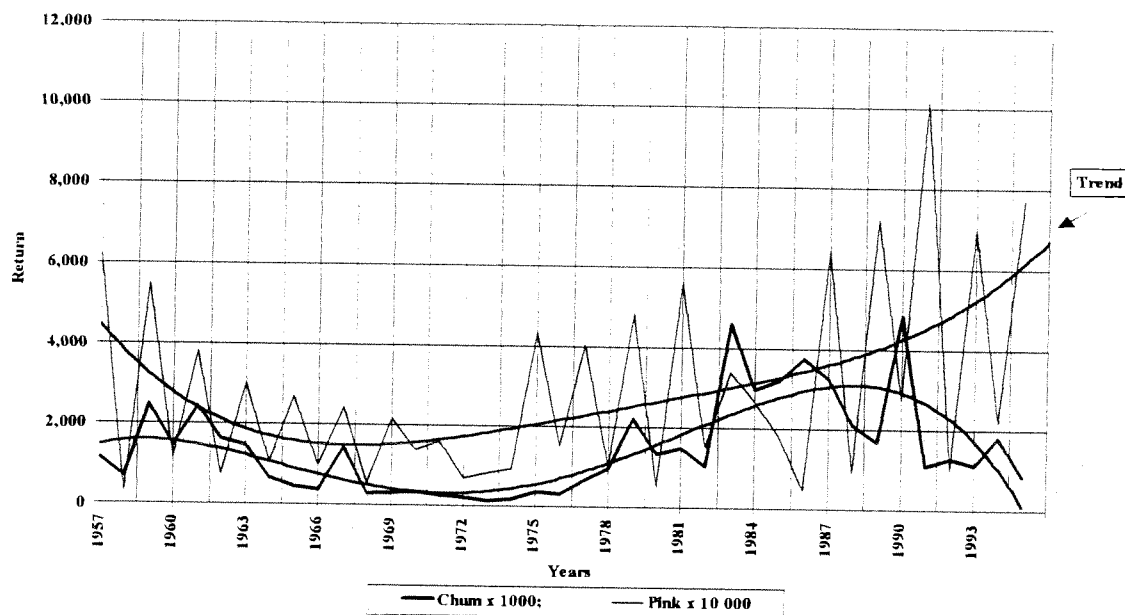
RESULTS AND DISCUSSION

The fluctuations in pink and chum salmon returns

are shown in Figure 1. Pink salmon register a ten- to hundredfold higher abundance than chums, as well as greater amplitude and frequency of fluctuations, which relates to this species' life cycle. A decline in abundance of both species was observed during the late 1950s to mid 1970s. After the mid 1970s, there was a steady increase in both species, but a decline for chum salmon in the late 1980s. Pink salmon abundance remained steadily high to 1995. Figure 1 suggests there may be a certain similarity in environmental factors influencing chum and pink salmon returns, although it is also evident that direct comparison of return dynamics yields little promise for forecast adjustments.

Figure 2 shows fluctuations in pink and chum salmon survival measures. Figure 2, more distinctly

Fig. 1 Dynamics of pink salmon and chum salmon return.

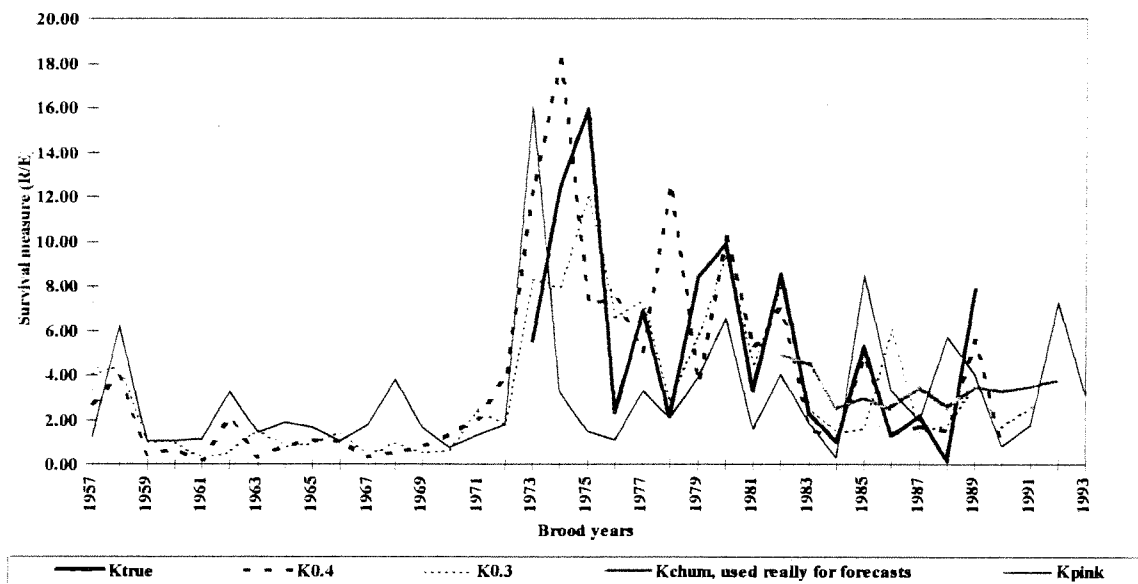


than Figure 1, shows the similarity in survival trends. The K_{True} dynamics closely match with the K_{Pink} fluctuations from 1975 to 1986, excluding 1973 to 1975. The highest recorded survival for pink salmon reached its peak value in the brood year 1973 and in 1975 for chum. Possibly, either the peaks themselves or their apparent delays resulted from extremely low spawning runs during the specified periods, a mere tens of thousands for chum, and about three million for pink salmon, i.e. about tenfold below average. Also, one should bear in mind that the measurement error ratio may increase as a species' return declines dramatically. A more realistic explanation can be given only upon a closer consideration of conditions during spawning, migrating, and marine periods.

Conspicuously in counterphase are the survival measures for the brood year 1988. A change in the long-term tendency of the chum salmon abundance dynamics, compared to those of pink salmon, was a possible cause for the differences. Resumption of driftnet fishing was possibly another factor, where chum salmon were landed in much greater quantity than pink salmon, and results of which were not included in the overall return evaluation in the last years. However, in general, Figure 2 demonstrates that the survival measure fluctuations are synchronous for the periods of concurring abundance fluctuations.

The short observation series for chum salmon survival measure values, covering only 17 brood years, does not allow for a statistically correct and

Fig. 2 Dynamics of survival measures of pink salmon and chum salmon.



well-grounded conclusion. In order to mitigate this basic data deficiency, we made a number of assumptions.

According to the data on parent salmon age composition it is known that the core of the returning chum salmon stock, 90%, is made up of 0.3 and 0.4 year-olds in north-eastern Kamchatka. The share of each age group can vary between 10% and 90%, however through 17 years the 0.3 year-olds averaged 48% and 0.4 year-olds 44% of the total. The remainder is split approximately equally among the 2+ and 5+ year-olds. The 6+ year-olds account for less than 1% of the total run in each year. Based on the above figures, one can assume that should one divide, for example the 1990 return figure by the 1985 spawner. A definite value should be attained statistically related to K_{True} . It will characterize the share of the 0.4 year-olds in 1985 contributing to the return in 1990. This value will be referred to as the conditional survival measure (K0.4). The K0.3 conditional survival measure is defined the same way. Quite naturally, this type of approach is not applicable to 2+ and 5+ year-olds, which do not belong with the core age groups. The legitimacy of this approach can be judged by examining Figure 2, that shows the proximity of K0.4 and K0.3 values and dynamics with those of K_{True} . The correlation coefficient between K0.4 and K_{True} equals 0.53 ($P < 0.05$), and between

K0.3 and K_{True} equals 0.77.

Table 1. Statistical characteristics of K_{True} , K0.4, K0.3, and K_{Pink}

	K_{True}	K0.4	K0.3	K_{Pink}
Average	5.62	3.85	3.36	3.37
Minimum	0.17	0.22	0.27	0.29
Maximum	15.94	18.14	12.01	22.7
Standard deviation	4.59	4.28	3.11	3.87

According to Table 1, the average K_{True} is slightly higher than K0.4 and K0.3. However, based on Figures 1 and 2, one can assume that this is because the observation period when the average K_{True} was produced coincided with the highest survival period of chum salmon during the return increase, and, incidentally, the real average for a period since 1957 cannot be adequately expressed by K_{True} . The statistical data on K0.4, K0.3, and K_{Pink} are very close. This is a formal proof that these can be applied for juxtaposition purposes, in respect to the conditions affecting the survival and dynamics of pink and chum salmon populations.

Attention was also paid to density dependencies between spawners and progeny of pink and chum

salmon, as well as interdependence of spawners in both species. Figures 3 and 4 show the spawner-to-progeny density dependencies, founded on the true survival measures for pink and chum salmon. These are approximated via exponential functions shown on Figures 3 and 4. It is clear that the exponents are practically the same for pink and chum salmon. It can be seen from Figures 5 and 6, that similar dependencies, produced for $K_{0.4}$ and $K_{0.3}$, are close

to those for K_{True} . Figures 3 to 6 show the decline in survival measure with the increase in spawners while Figure 7 shows no dependence of the chum salmon survival measure upon the abundance of pink salmon spawners simultaneously returning to the spawning grounds.

The ultimate output of the calculation is presented in Figure 8. It can be seen therefrom that the curve for the better part corresponds to actual abundance

Fig. 3 Dependence of survival measures of chum salmon on the number of spawners.

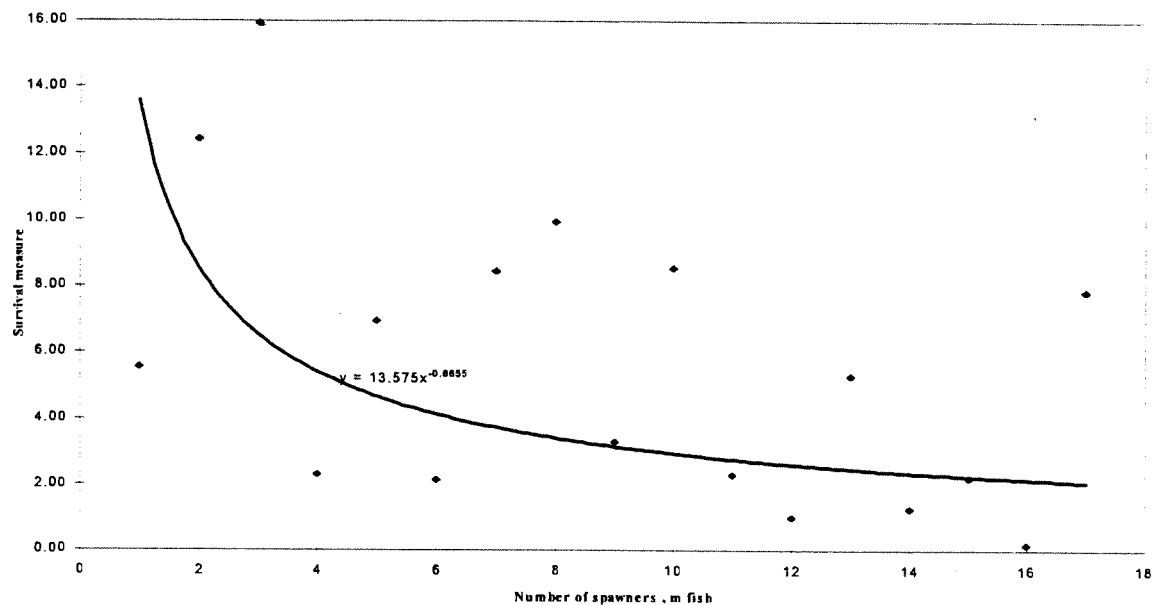


Fig. 4 Dependence of survival measure of pink salmon on number of spawners.

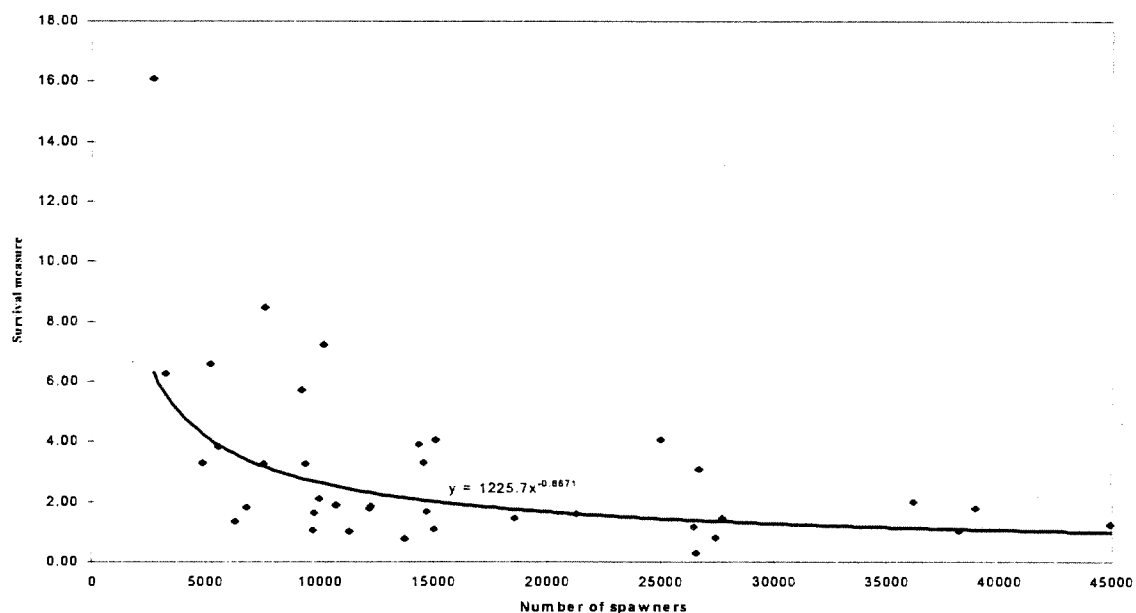


Fig. 5 Dependence of conditional survival measure (K0.4) of chum salmon on the number of spawners.

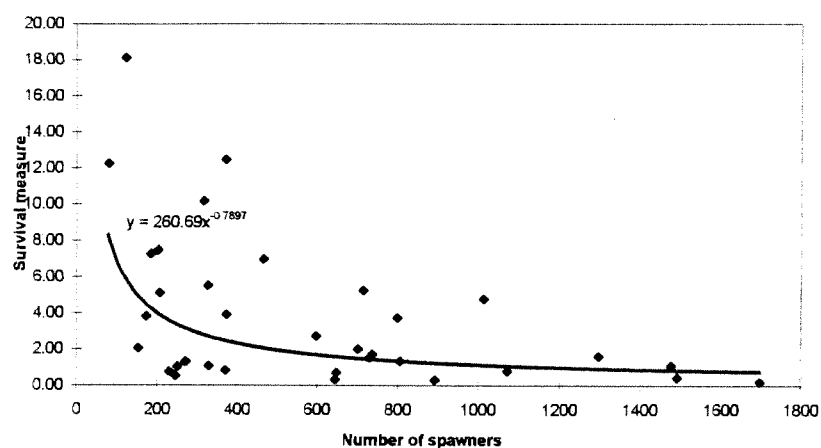


Fig. 6 Dependence of conditional survival measure (K0.3) of chum salmon on number of spawners.

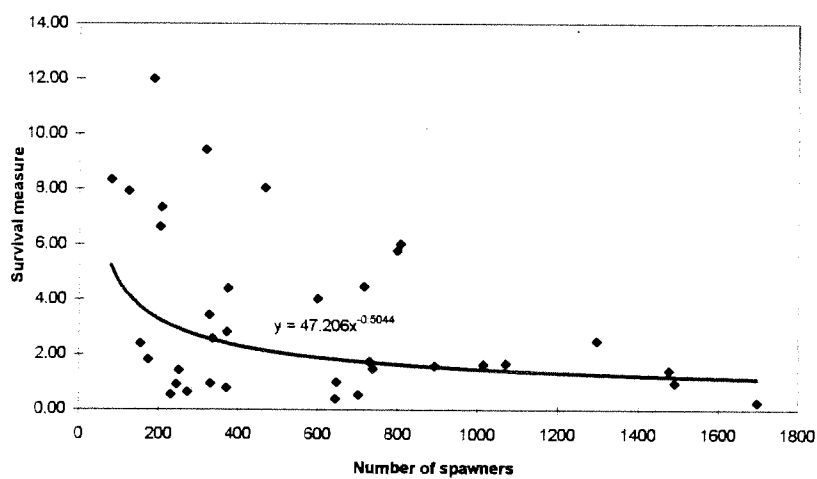
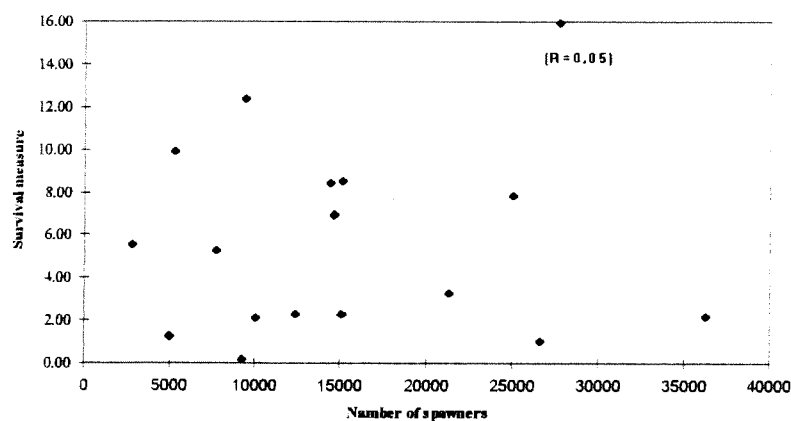
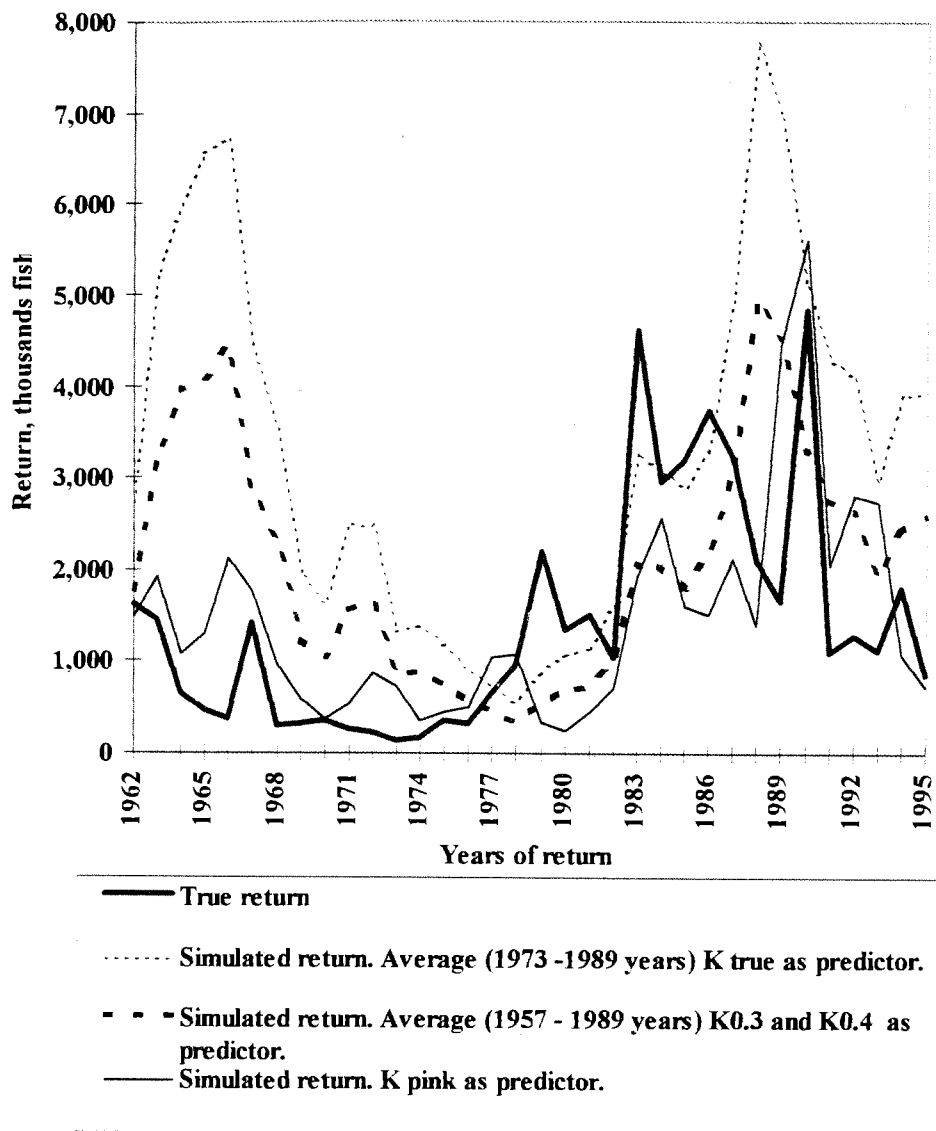
Fig. 7 Dependence of K_{True} of chum salmon on number of pink salmon spawners.

Fig. 8 Dynamics of true and simulated return of chum salmon in northeast Kamchatka.



dynamics. The maximum error did not exceed the one present in the real forecasts.

Comparing Figures 3 - 6 with Figure 7 one can conclude that, in respect to pink and chum salmon in north-eastern Kamchatka, interspecific density regulation is manifested to a much lower degree than is intraspecific regulation. Small ($r=0.44$; $r=0.37$) but significant ($P<0.05$) correlation coefficients between $K_{0.4}$ and K_{pink} , and $K_{0.3}$ and K_{pink} , accordingly, can be treated as additional support of this conclusion.

Generally, the data shown above lead to the conclusion that the environmental factors during the spawning, downstream migration, and marine periods affect pink and chum salmon yearlings in much the same fashion. This influence is much stronger than that of the interspecific regulation. To prove the

above, the assessment of chum salmon returns was undertaken during an observation period, using the abundance of chum salmon 0.4 and 0.3 year-old spawners as predictors, assuming that the contributions of 0.3 and 0.4 year-old spawners were equal. The other predictor was during that period K_{pink} . The return was calculated using the following formula:

$$N = 0.5 \cdot (E_{0.3}) \cdot K_{pink}(3) + 0.5 \cdot (E_{0.4}) \cdot K_{pink}(4)$$

where N - chum salmon return;

$E_{0.3}$ and $E_{0.4}$ - chum salmon 0.3 and 0.4 year-old spawners;

$K_{pink}(3)$ and $K_{pink}(4)$ - pink salmon survival measures for corresponding broods.

For juxtaposition purposes, a similar calculation was made, where pink salmon survival measure dynamics were not presented. Instead, the average K_{True} , in one case, and the average $K_{0.4}$ and $K_{0.3}$, in the other, were used as applied to the whole observation period. As seen from Figure 8, the calculation output is much less reflective of the real chum salmon abundance dynamics, than is the case with K_{Pink} . The average standard deviation of the assessed chum salmon return against the actual value (for the series presented on Fig. 8) is as follows: 1133 - when using K_{Pink} as predictor, 2782 - when using the average K_{True} for a period from 1973 through 1989, and 1714 - when using the average $K_{0.3}$ and $K_{0.4}$ for a period from 1957 through 1995.

Based on Figure 8, one can conclude that using the average K_{True} for the period from 1973 to 1989 as predictor in a return forecast could yield good results only if applied to a narrow time span (1976 - 1987), when chum salmon return experienced a considerable upsurge. If applied to the period from 1962 through 1975 this given survival measure will appear quite exaggerated.

The major elements of the chum salmon return forecast include the estimation of the survival measure per brood year, and evaluation of which part of each brood matures at age 0.3 or 0.4, respectively. As predictors, the data on abundance dynamics, qualitative fish indicators, as well as hydrological and meteorological information for the period between spawning and migrating to sea were used. Each of these influences expresses itself indirectly and cannot be exactly measured. The calculations are mostly of a statistical character, and are based on a relatively short observation series. We can compare chum salmon survival measures used for forecasts ($K_{forecast}$) and K_{True} , evaluated for forecasting, beginning from 1982 (Fig. 2). $K_{forecast}$ appears, in a number of cases, at great variance with K_{True} . The average standard deviation of $K_{forecast}$ from K_{True} equals 3.24 (the average standard deviation of K_{Pink} from K_{True} in respective years equals 3.04).

The official forecast of chum salmon returns is prepared 2 years in advance. i.e., the forecast for 1998 is made in 1996. The core of the 1998 return will be made of 0.3 and 0.4 year-olds, i.e. the brood year 1993 and 1994. Survival measures for pink salmon broods 1993 and 1994 were already known in 1996. As indicated above, survival measures for pink and chum salmon are statistically interconnected. Therefore, if the spawning and migrating conditions had been favorable for pink salmon broods of 1993 and 1994, they would have been as much so for chum salmon. Of importance is that 2 to 3 years prior to

chum salmon returns there is the possibility to evaluate more accurately than by any other method (except for direct enumeration) the conditions in the most critical period for salmon stock development.

CONCLUSIONS

The environmental factors have similar effects on chum and pink salmon during spawning and downstream migration periods. This similarity is strong enough in the majority of cases that possible differences in the rearing conditions during the ocean life do not smooth over those effects. This confirms that the downstream migration and coastal periods are crucial for salmon stock development.

The similarity in chum and pink salmon return/escapement dynamics can be expressed quantitatively and applied to chum salmon return forecasting. For example, it is absolutely true that the lower than forecast chum salmon return in 1995 resulted not from the erroneous age composition prediction, but from the high mortality rate during the spawning, migrating, and coastal periods, and, consequently, from the low return/escapement ratio. The low return/escapement ratio for pink salmon brood year 1990 is a testimony to the aforesaid and its consideration was instrumental in producing a more accurate chum salmon forecast.

Of course, the similarity of survival dynamics can hardly be idealized. It does not insure against errors, and is not suggested as an alternative to already existing forecasting methods, although it can be employed as an additional predictor. Thus, in some cases, considerable forecast refinements may be attained. This suggested approach should be further proved for its applicability for other regions, with priority given to western Kamchatka, and possibly for other salmon species.

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Salmon Abundance in Offshore Waters of the North Pacific Ocean and Its Relationship to Coastal Salmon Returns

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Ishida, Y., and S. Ito. 1998. Salmon abundance in offshore waters of the North Pacific Ocean and its relationship to coastal salmon returns. N. Pac. Anadr. Fish Comm. Bull. No. 1: 334-339

Catch-per-unit-effort (CPUE: fish/tan caught by commercial-type gillnet with mesh sizes from 112 to 130 mm) was calculated using the data collected on board Japanese salmon research vessels in offshore waters of the North Pacific Ocean from 1972 to 1995. These data were stratified by month, 2 degree latitude by 5 degree longitude areas (2x5 areas), species, and maturity, and related to the returns of Japanese chum salmon and Bristol Bay sockeye salmon. Significant correlations and high average CPUEs (sockeye > 0.1 and chum > 0.3 fish/tan) were found in several areas. There were significant correlations between the abundance of immature chum salmon occurring in areas south of the Aleutian Islands in June ($r=0.55^*$ to 0.79^{**}) and the central Bering Sea in July ($r=0.51^*$ to 0.63^*) and the return of Japanese chum salmon the following year. There were also significant correlations between CPUE of maturing chum salmon in areas south of the Aleutian Islands in June ($r=0.57^*$ to 0.85^{**}) and central Bering Sea in June ($r=0.68^*$ to 0.79^{**}) and July ($r=0.46^*$ to 0.74^{**}) and the current year return of Japanese chum salmon. The abundance of immature fish in areas south of the Aleutian Islands ($r=0.47^*$ to 0.65^{**}) and central Bering Sea ($r=0.48^*$ to 0.64^*) in July was significantly correlated with the returns of Bristol Bay sockeye salmon the following year. There were also significant correlations between the abundance of maturing sockeye in areas south of the Aleutian Islands in June ($r=0.65^{**}$ to 0.86^{**}) and July ($r=0.69^{**}$) and the current year return of Bristol Bay sockeye salmon. These correlations suggest that abundance of salmon in offshore areas based on CPUE of commercial-type gillnet operations could be used to develop pre-season forecasts of Japanese chum salmon and Bristol Bay sockeye returns.



INTRODUCTION

Accurate forecasts of salmon returns to coastal areas are used for more effective coastal and inshore fisheries management and particularly useful to managers and fishers for harvest planning decisions relating efficient use of their resources. Pre-season forecasts have been conducted based on the level of parent escapement, numbers of juvenile fish migrating to the ocean, information from the fisheries in offshore waters, and environmental indices such as sea surface temperature (Henderson et al. 1987; Eggers et al. 1983). Data on catch-per-unit-effort (CPUE) obtained from the Japanese salmon research vessels on the high seas had been used to forecast sockeye salmon returning to Bristol Bay (Fried et al. 1987; Ishida et al. 1989).

The objectives of this study were to examine the possibility of forecasting salmon returns of Japanese chum and Bristol Bay sockeye salmon based on CPUE data obtained from gillnet operations of the Japanese

salmon research vessels which have been conducted for many years and to make recommendations to improve the accuracy of this method.

MATERIALS AND METHODS

Salmon research vessels have used research-type gillnets (containing 10 different mesh sizes ranging from 48 to 157 mm), commercial-type gillnets with mesh sizes ranging from 112 to 130 mm, and longlines. We used data obtained by commercial-type gillnets because this gear was most efficient at capturing maturing fish returning in the present year (t) and immature fish returning in the following year ($t+1$). Maturity was determined from gonad weights (Takagi 1961).

Catch-per-unit-effort (CPUE: fish/tan caught by commercial-type gillnets) was calculated using the data collected on board Japanese salmon research vessels in offshore waters of the North Pacific Ocean from 1972 to 1995. These data were stratified by

month, 2 degree latitude by 5 degree longitude areas (2x5 areas), species, and maturity, and related with the returns of Japanese chum salmon and Bristol Bay sockeye salmon (Kaeriyama 1996; ADF&GD 1997). We calculated the correlation between CPUE value of maturing fish at each area in year t and number of fish returning to the coastal area in year t , and the correlation between CPUE values of immature fish in year t and the number of fish returning to coastal area in year $t+1$. Strata used for forecasting were selected from strata with high average CPUE (sockeye >0.1 and chum >0.3 fish/tan), 10 or more years of data, and significant correlation coefficient ($P < 0.05$). For each strata selected, a regression of number of salmon returning to coastal areas and CPUE was calculated. These were used to predict the number of salmon returning to coastal areas in 1996 and 1997

from CPUE values of maturing and immature fish in July, 1996.

RESULTS

Japanese Chum Salmon

There were significant correlations between the return of Japanese chum and immature chum salmon occurring in several areas south of the Aleutian Islands in June ($r=0.55^*$ to 0.79^{**}) and central Bering Sea in July ($r=0.51^*$ to 0.63^*). Significant correlations with maturing fish were also found in areas south of the Aleutian Islands in June ($r=0.57^*$ to 0.85^{**}) and central Bering Sea in June ($r=0.68^*$ to 0.79^{**}) and July ($r=0.46^*$ to 0.74^{**}) (Fig. 1 and Fig. 2).

Fig. 1 Correlation coefficients between CPUE of immature chum salmon in $2^\circ \times 5^\circ$ area in June and July of year t and return of Japanese chum salmon in year $t+1$. Shaded areas indicate higher average CPUE (immature >0.3 fish/tan) and significant correlation coefficient ($P < 0.05$).

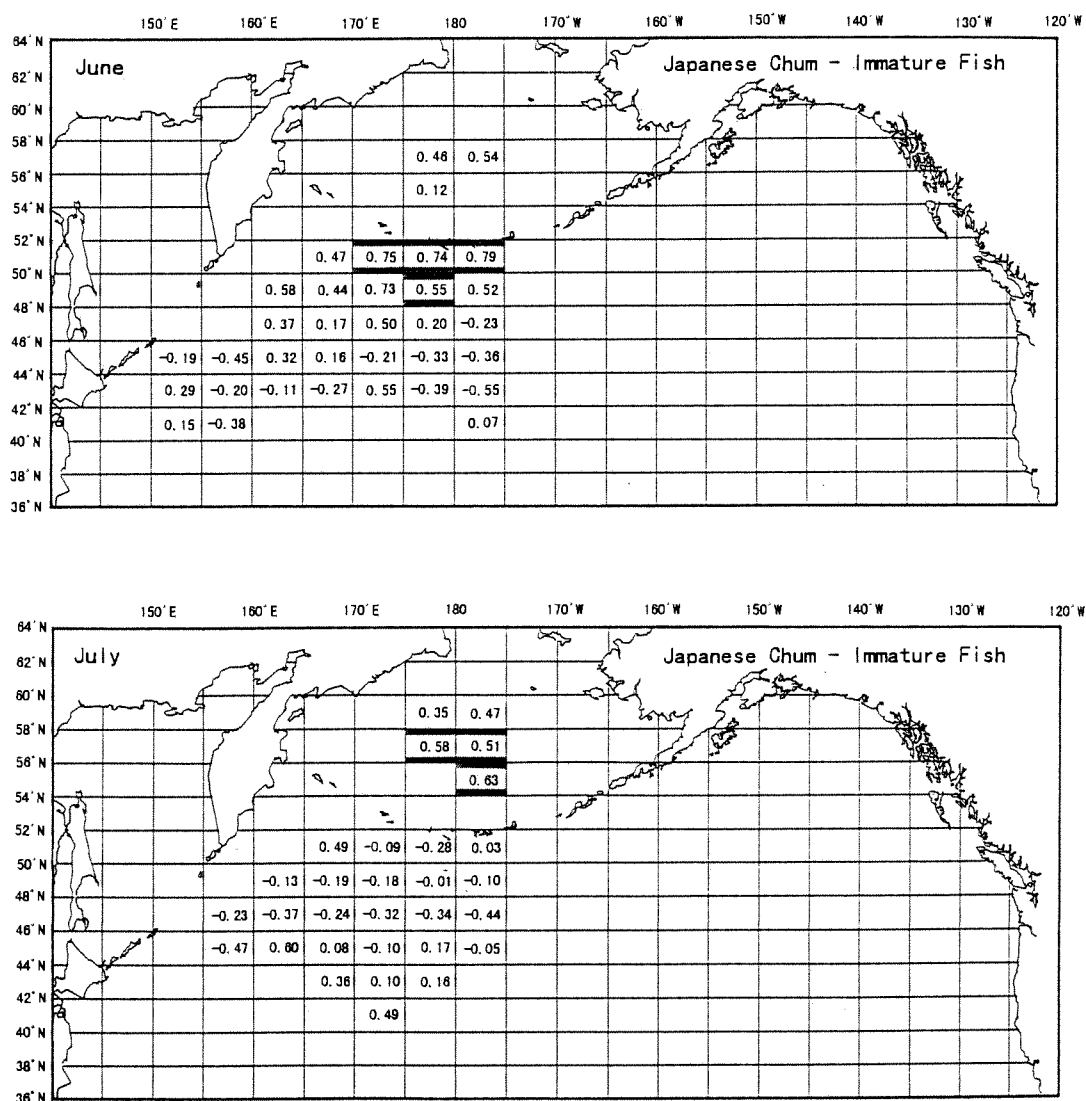
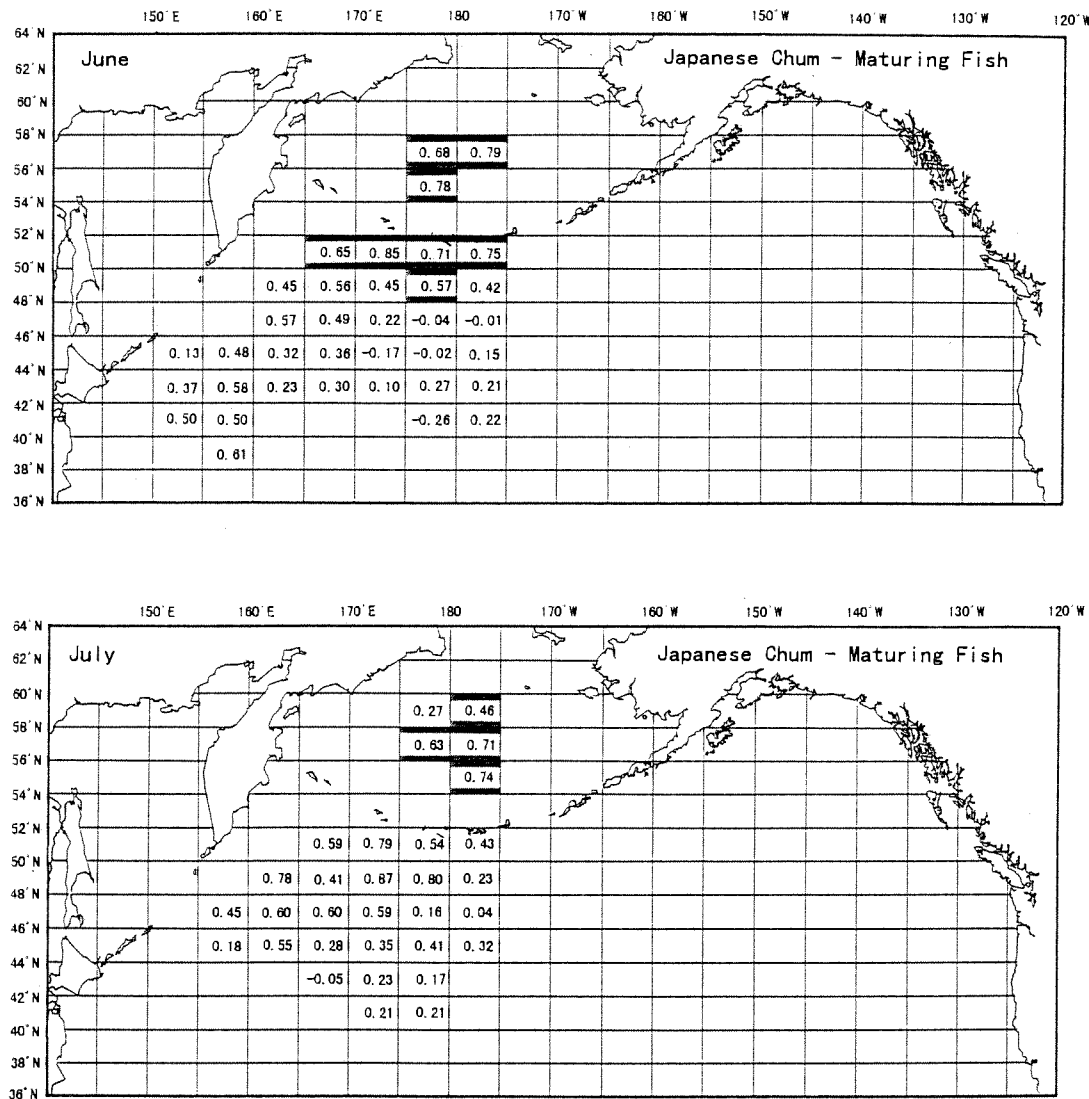


Fig. 2 Correlation coefficients between CPUE of maturing chum salmon in $2^\circ \times 5^\circ$ area in June and July of year t and return of Japanese chum salmon in year t . Shaded areas indicate higher average CPUE (maturing >0.3 fish/tan) and significant correlation coefficient ($P<0.05$).



The number of fish returning to coastal area in 1996 was estimated to be 41-59 million fish (mean 47 million fish, S.D. 8 million fish) from CPUE value (1.56-6.10 fish per tan) of maturing fish in the Bering Sea in July, 1996. The number of fish returning to coastal area in 1997 was estimated to be 40 -52 million fish (mean 45 million fish, S.D. 6 million fish) from CPUE value (0.91-3.32 fish per tan) of immature fish in 1996 (Table 1).

Bristol Bay Sockeye Salmon

For Bristol Bay sockeye salmon, the abundance of immature fish in areas south of the Aleutian Islands and central Bering Sea in July was significantly correlated with their returns ($r=0.47^*$ to 0.65^{**} and

$r=0.48^*$ to 0.64^* , respectively). There were also significant correlations of returning fish to those maturing in areas south of the Aleutian Islands in June ($r=0.65^{**}$ to 0.86^{**}) and July ($r=0.69^{**}$). Strong correlations found in these time and area strata are useful for pre-season forecasts of these salmonids (Fig.3 and Fig.4).

The number of fish returning to coastal area in 1996 was estimated to be 67 million fish from CPUE value (1.88 fish per tan) of maturing fish in July, 1996. The number of fish returning to coastal area in 1997 was estimated to be 29-60 million fish (mean 41 million fish, S.D. 12 million fish) from CPUE value (0.29-3.11 fish per tan) of immature fish in 1996 (Table 1).

DISCUSSION

The significant correlations between CPUE of maturing and immature chum and sockeye salmon in Japanese research vessel surveys of offshore waters and respective inshore runs suggests the use of this information to develop preseason forecasts of Japanese chum salmon and Bristol Bay sockeye salmon runs. The areas and times where strong correlations were found corresponded to areas and times where these major stocks of salmon are known to occur, based on tag recovery data. Japanese chum salmon are distributed in the Gulf of Alaska, central and western North Pacific, and are concentrated in the Bering Sea, during July. Bristol Bay sockeye salmon are distributed in the Gulf of Alaska, waters of south of Aleutian Islands, and the Bering Sea (Myers et al. 1990).

However, there were large discrepancies between the 1996 forecast and the actual run both in Japanese chum salmon and Bristol sockeye salmon. For example, 1996 forecast of Japanese chum was 47

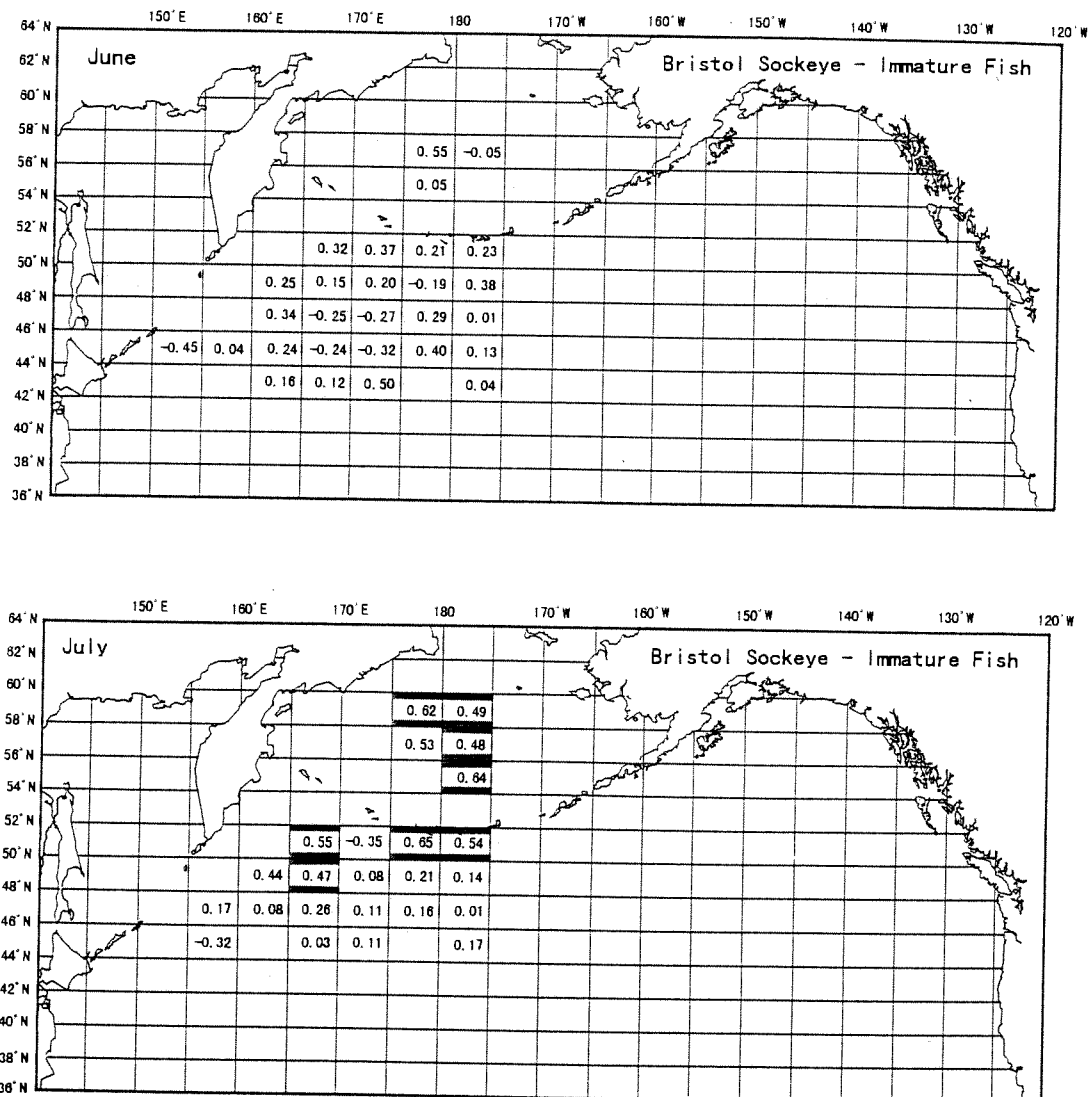
million fish and far below the actual return of 80 million. For Bristol Bay sockeye salmon, 1996 forecast was 67 million and far exceeded the actual run of 38 million.

In order to improve the present forecasting models, additional variables should be examined in the future analysis. Since the ocean age composition of the inshore Bristol Bay return is quite variable and potential exists for differential vulnerability of salmon ocean age classes to gillnet operations, catches should be stratified by ocean age and forecasts developed for returns of respective ocean age classes. Sampling date and sea surface temperature should be considered as an indicator of the survey timing relative to migratory timing of the stocks forecasted in the area of the survey. Body size should be considered because it may relate to the catch efficiency of gillnet operations and to fish density (Ishida et al. 1993). Total CPUE including other salmon species should also be considered as an indicator of whether gear saturation or interspecific interaction is occurring when other species of fish are abundant.

Table 1. Relationship between CPUE (X) and return (Y). Estimates were made based on CPUE data collected in July, 1996. IM-CPUE was CPUE of immature fish, and MT-CPUE was CPUE of maturing fish.

Stock	Month	Area	Relationship	r	n	X	Y
						1996 MT-CPUE	1996 Forecast
Japanese Chum	July	5875W	Y = 3.09 X + 25.55	r=0.46*	n=21	6.10	44.39
		5675E	Y = 10.55 X + 24.14	r=0.63*	n=15	1.56	40.59
		5675W	Y = 10.08 X + 17.99	r=0.71**	n=21	2.50	43.18
		5475W	Y = 15.34 X + 16.91	r=0.74**	n=14	2.72	58.64
						Mean	46.70
						S.D.	8.12
						1996 IM-CPUE	1997 Forecast
Japanese Chum	July	5675E	Y = 6.17 X + 34.67	r=0.58*	n=14	0.91	40.28
		5675W	Y = 5.78 X + 32.65	r=0.51*	n=20	3.32	51.85
		5475W	Y = 5.41 X + 30.79	r=0.63*	n=13	2.23	42.84
						Mean	44.99
						S.D.	6.07
						1996 MT-CPUE	1996 Forecast
Bristol Bay Sockeye	July	5065E	Y = 25.89 X + 18.31	r=0.69**	n=17	1.88	66.99
						1996 IM-CPUE	1997 Forecast
Bristol Bay Sockeye	July	5875W	Y = 8.16 X + 30.75	r=0.49*	n=20	0.54	35.16
		5675W	Y = 11.00 X + 29.39	r=0.48*	n=20	1.50	45.90
		5475W	Y = 12.49 X + 29.35	r=0.64*	n=13	0.37	33.97
		5065E	Y = 14.13 X + 16.13	r=0.55*	n=16	3.11	60.07
		4865E	Y = 18.14 X + 23.91	r=0.48*	n=20	0.29	29.17
						Mean	40.85
						S.D.	12.36

Fig. 3 Correlation coefficients between CPUE of immature sockeye salmon in $2^\circ \times 5^\circ$ area in June and July of year t and return of Bristol Bay sockeye salmon in year $t+1$. Shaded areas indicate higher average CPUE (immature >0.1 fish/tan) and significant correlation coefficient ($P<0.05$).



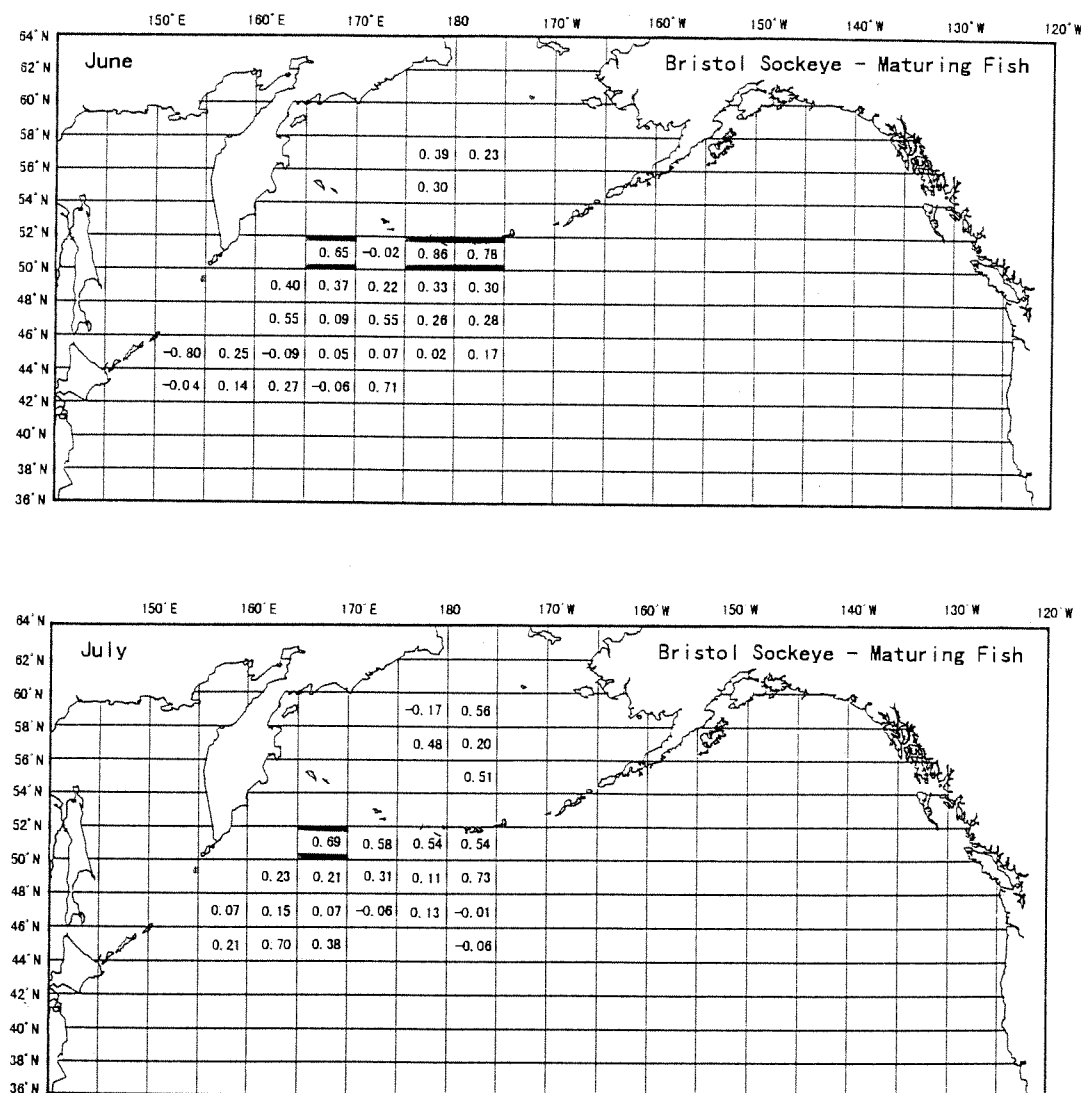
ACKNOWLEDGEMENTS

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Fig. 4 Correlation coefficients between CPUE of maturing sockeye salmon in $2^\circ \times 5^\circ$ area in June and July of year t and return of Bristol Bay sockeye salmon in year t . Shaded areas indicate higher average CPUE (maturing >0.1 fish/tan) and significant correlation coefficient ($P<0.05$).



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Review of the Stock Condition and Fishery of Masu and Pink Salmon of the Sea of Japan

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Tsiger, V.V., and V.G. Markovtsev. 1998. Review of the stock condition and fishery of masu and pink salmon of the Sea of Japan. N. Pac. Anadr. Fish Comm. Bull. No. 1: 340-351

Information on the masu and pink salmon fishery in the Sea of Japan is discussed. Salmon catch, species composition by month and year, stock origins, seasonal changes of fishing grounds, and catch per gillnet are analyzed. Calculations were made from data obtained from Japanese gillnet surveys conducted in 1970-1991 in the Sea of Japan. In the beginning of the season in offshore waters of Japan the masu salmon is the main target species of the fishery. Chum salmon are only occasionally caught in the Sea of Japan in spring, and not in every year. This indicates that chum salmon originating from rivers draining into the Sea of Japan usually do not spend the winter in the Sea of Japan, but probably migrate to the Pacific Ocean and to the Okhotsk Sea. In March and April pink and masu salmon did not form concentrations in the 200-mile economic zone of Russia in the Sea of Japan. A decreasing trend in masu salmon catch and catch per gillnet is clear, and indicates a reduction in masu salmon abundance over the entire area of its distribution. Pink salmon abundance also declined to a low level. Information about the origin of pink and masu salmon in the Sea of Japan indicates that almost all pink salmon and part of the masu salmon in the commercial catches of Japanese and Korean fishermen are of Russian origin. In consideration of the decreasing abundance of masu and pink salmon in the Sea of Japan, co-operation between countries of the Sea of Japan (Russia, Japan, South and North Korea) is needed to conserve and restore the stocks that maintain these fisheries.



INTRODUCTION

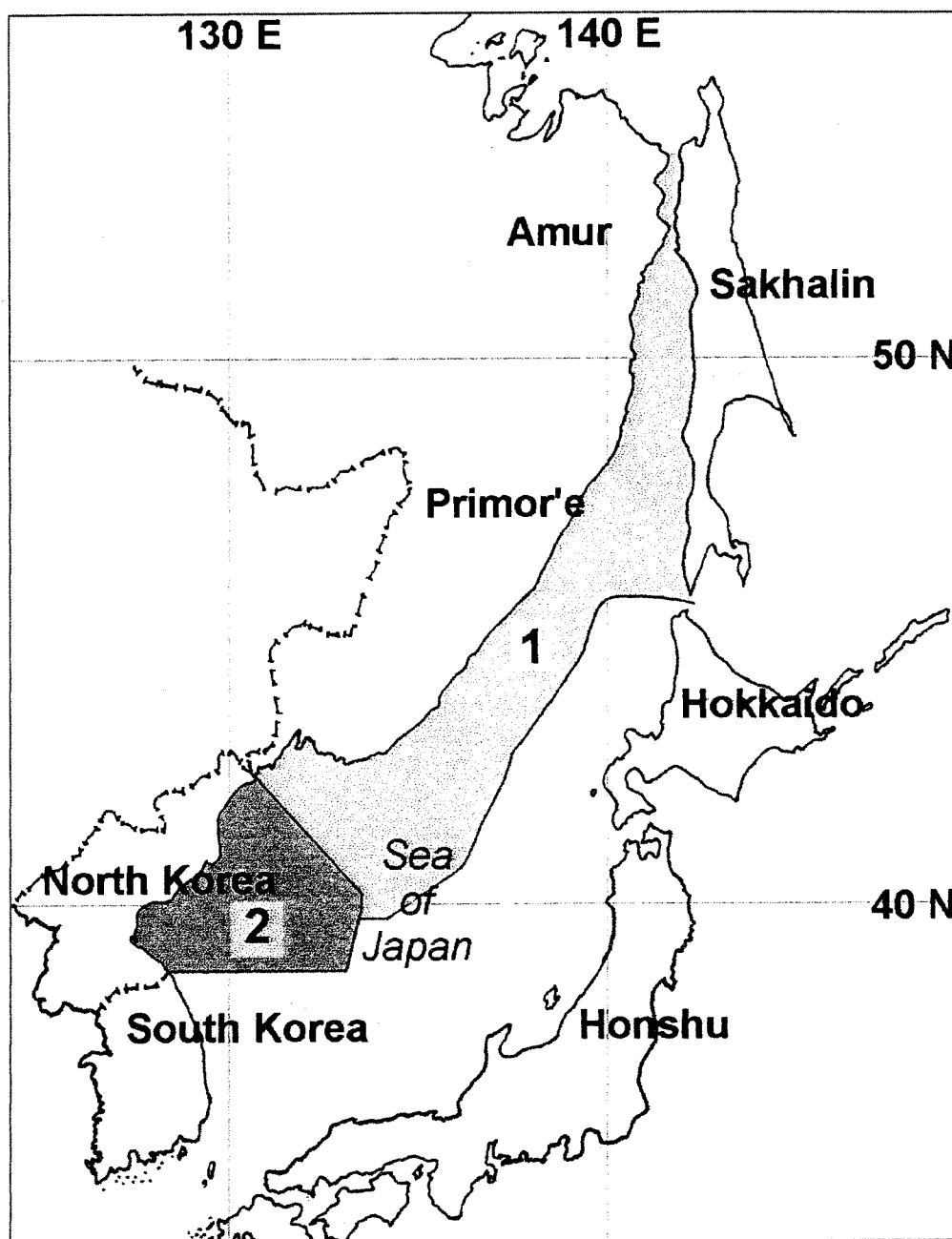
Pink, masu, and chum salmon are the most abundant Pacific salmon in the Sea of Japan. Although their abundance in this area is not as high as in other areas of the North Pacific, all these species are important fishery targets in countries adjacent to the Sea of Japan: Russia, Japan, South and North Korea (Fig. 1). Unlike pink and masu salmon, chum salmon rarely occur in the southern part of Japan Sea in spring. Therefore, in spring only pink and masu salmon are fishery targets. Because pink salmon abundance significantly exceeds the abundance of masu salmon, it is the main fishery target during this season. However, masu salmon is the more valuable fish because of its larger size and higher palatability.

There has been little salmon research conducted in the Sea of Japan by Russian scientists (Darda 1968; Birman 1972; Gavrilov Pushkaryova 1984, 1994), while Japanese scientists have collected a lot of material in this area. Samples collected by Russian scientists were rather small until 1995 (hundreds of

masu and pink), while Japanese research vessels over about a 40-year period (from middle 1950's) have collected tens of thousands of masu and hundreds of thousands of pink salmon. Data on masu salmon were summarized and published by Tanaka (1965) for 1954-1961, and by Machidori and Kato (1984) and Kato (1991) for 1962-1972. There is no similar report on Sea of Japan pink salmon, with the exception of tagging and other information summarized by Takagi et al. (1981). Therefore we used results of salmon surveys which were published in the prefectural stations' Bulletins. Those data were used for summarising information on shifts in the fishing grounds and CPUE (Reports of Japanese prefectural Fisheries experimental stations of Ishikawa, Toyama, Niigata, Yamagata, Aomori and Akita Prefectures on gillnet salmon research, conducted in 1970-1991 in the Sea of Japan¹ (1972-1993)).

¹Further Cited as "Reports"

Fig. 1 Countries of the Sea of Japan: Russia (Primor'e, Amur, Sakhalin), Japan (Hokkaido, Honshu), North Korea and South Korea. 1 - economic zone of Russia in the Sea of Japan, 2 - economic zone of North Korea.



MARINE PINK AND MASU SALMON FISHERY IN THE SEA OF JAPAN

In Japan, the salmon fishery is separated into coastal and offshore fisheries. The offshore fishery in the Sea of Japan starts in March. Fishing grounds during this period are located near Sado Island and westward to Korean Bay, mainly between 37° and 39°N. In winter and spring salmon distribute over wide water temperatures, but the main concentrations are found in rather warm waters with surface

temperature about 8-10°C (Tanaka 1965; Birman 1972; Machidori and Kato 1984).

Pink salmon is the main target of fishery and the most abundant species. However in March body size of pink is small. Due to this, masu salmon are more valuable and many vessels fish mainly for masu. The appropriate area for masu is the smallest in the beginning of season. Due to their concentration, fish density and CPUE were highest in that period (Tanaka 1965; Machidori and Kato 1984; Reports, 1972-1993).

With warming surface waters, fishing grounds

shift northward, reaching 40°N in April. For just a few years only some vessels conducted operations more northward than 40°N at this time. Large-scale gillnet fishery has been conducted in the Sea of Japan from the 1950s. Over this time fishermen have become experienced in searching for appropriate fishing grounds. Therefore, data on the shift of fishing grounds reflect shifts in salmon distribution. Until 200-mile economic zones (EZ) were established in 1977 nothing prohibited Japanese fishermen from entering Primor'e waters, which are located now inside EZ of Russia (Fig. 1). However before establishment of EZs Japanese never conducted fishing operations in March and April in the area of the present Russian EZ (Reports, 1972-1979).

This is explained by the fact that the Primor'e area is influenced by the cold Primor'e Current, and until May it is too cool for salmon. Due to this, in winter and spring masu and pink salmon inhabit waters influenced by the warm Tsushima Current. This is correct for present days also. In 1994 in southern part of Russian EZ in the Sea of Japan, a salmon survey has been conducted from April 11 to April 26. Surface water temperature varied from 2 to 5 °C. In total during the whole research 5920 tans of gillnets were set, but total salmon catch was only 114

fishes. So, catch per tan of gillnet (CPUE) was only 0.02. A survey conducted by three Japanese salmon fishery vessels in 1995 the same area also indicated that in late April and early May masu and pink salmon did not form fishable concentrations in the area adjacent to Primor'e waters due to low surface water temperature (less than 5 °C).

Historically, forty to eighty percent of the total masu salmon catch in Japan was taken in coastal waters (Machidori and Kato 1984). At the present time about 90% of marine catch is taken by coastal fishery according to official statistics (Fisheries Agency of Japan 1993-1996). In the case of pink salmon, the main catch is taken by the offshore fishery. But the proportion of the catch taken offshore in 1970-1994 varied substantially from year to year: from 0.1% to 42.4% (averaging 9.8%; Table 1). Most (about 90%) of masu and pink salmon are caught from March to June; however these species were caught by coastal fishery through the whole year.

Before 1981 pink and masu salmon catch of the Republic of Korea was less than 1000 tons. From 1981 its catch sharply increased due to increased effort, and exceeded 2700 tons (INPFC 1996). After that, until 1994, on average annual catch consisted 1674 tons (varied from 666 to 2767) (Table 1, Fig. 2).

Table 1. Catch of the Sea of Japan pink salmon by regions and countries in metric tons.

Year	Amur ¹	N-W Sakhalin ²	Primor'e ³	South Korea ⁴	Japan offshore ⁵	Hokkaido coastal	Honshu coastal	Total
1970	340	100	470	89 ⁶	5558	2135	497	9189
1971	2000	1020	3850	89	5815	81	119	12974
1972	250	510	130	382	4998	13	13	6296
1973	2910	690	3000	400	5616	17	117	12750
1974	500	310	140	206	5198	53	22	6429
1975	2000	500	1800	131	5476	406	402	10715
1976	2000	440	950	53	5026	92	91	8652
1977	1530	180	1630	80	3684	123	494	7721
1978	3410	440	2760	59	3954	13	141	10777
1979	1000	260	1410	65	3830	6	60	6631
1980	3451	1150	650	128	3815	44	10	9248
1981	2400	960	1260	2727	3869	6	15	11237
1982	3200	120	870	1107	3771	6	16	9090
1983	3600	1380	970	2122	3754	31	4	11861
1984	4330	392	620	2605	3501	20	78	11546
1985	3900	1234	1750	2353	3975	36	95	13343
1986	3200	610	700	2767	2549	380	636	10842
1987	2150	2120	3190	1372	2206	384	688	12110
1988	1650	220	340	1533	2179	227	399	6548
1989	877	657	4700	1197	1853	507	617	10408
1990	1476	843	640	666	1420	395	652	6092
1991	140	141	5250	1074	1234	2	1	7842
1992	2363	710	1830	1505	1252	59	15	7734
1993	118	123	3970	1269	1207	2	0	6689
1994	525	769	850	1144	1352	8	0	4648
1995	189	883	460		1467	1	1	3001

¹Data from "Pacific salmon catches (1989)" and Khabarovsk Branch of TINRO.

²Data on Rybnovskiy area in North-Western Sakhalin from "Pacific salmon catches (1989)" and Khabarovsk Branch of TINRO.

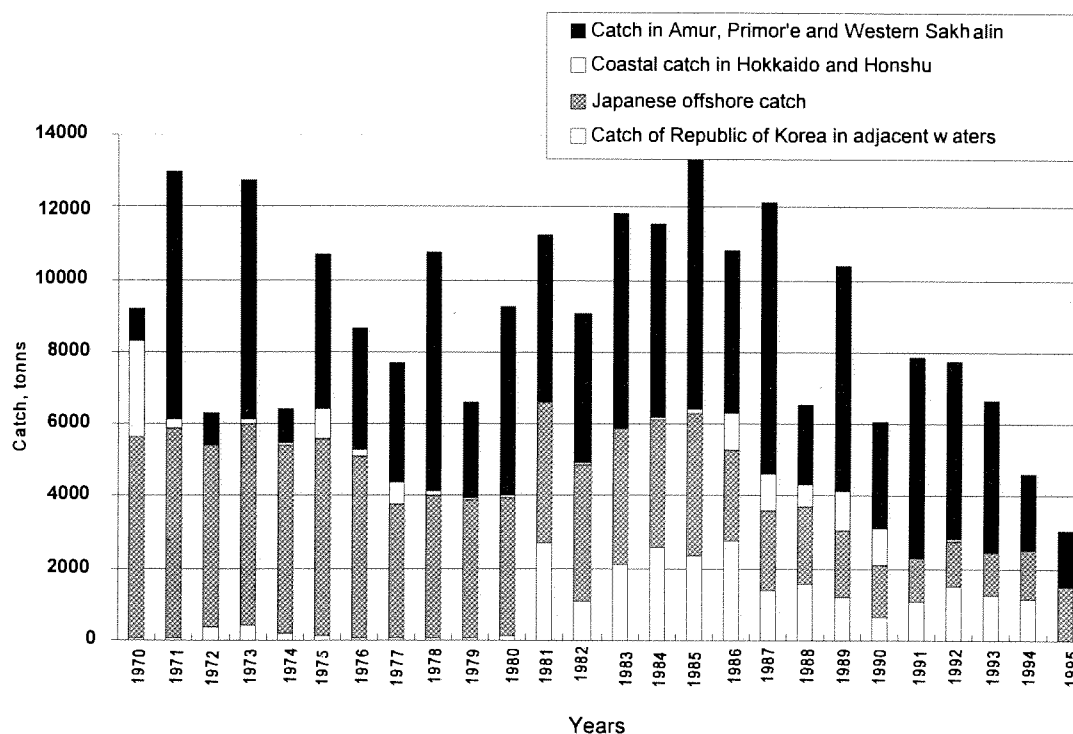
³Data of Khabarovsk Branch of TINRO.

⁴INPFC (1987-1996).

⁵From "Pacific salmon catches (1989)", INPFC (1987-1996) and Fisheries Agency of Japan (1993-1996).

⁶Averaged data for 1961-1971.

Fig. 2 Pink salmon catch in tons in the Sea of Japan, Amur, Primor'e and North-Western Sakhalin (Catch of South Korea for 1995 is not included).



Before 1981 more than 90% of pink salmon in the Sea of Japan were caught by Japanese fishermen. But from 1981 the percentage of pink salmon caught by Korean fishermen significantly increased (Fig. 2). Data on the percentage of pink and masu salmon are not given in the INPFC document, only that the species taken are mainly pink salmon with some masu.

Fishing also occurs in the Sea of Japan in the waters of North Korea (Gavrilov and Pushkaryova, 1994). However there is no information available on the catch. Masu salmon are caught in trapnets from February to June (Tanaka 1965). Beside Korean vessels, Japanese vessels also conducted salmon fishing in EZ of North Korea (Valencia 1989, 1992). Russian fishermen do not fish offshore in the Sea of Japan, but harvest salmon in rivers and along adjacent coasts.

SPECIES COMPOSITION OF SALMON CATCH DURING SPRING IN THE SEA OF JAPAN

Pink salmon is the dominant species in the salmon catch in the Sea of Japan in spring. In the 1960s and early 1970s, the percentage of pink salmon in the catch usually exceeded 90% (Fukataki and Kato 1974). From 1970 to 1991 pink salmon percentage in total catch ($N=284,291$) of prefectural research vessels was 79.9% (masu was 20.1%). Occasionally

chum salmon also were caught, consisting of 0.06% of the total catch. The percentage of masu significantly varies during this season. Masu salmon were the main part of the salmon catch early in the season; the percentage of masu salmon in the catch from 1970 to 1991 averaged 67% in March (varying from 8 to 99%), to 32% in April (varying from 4 to 87%), to 9% in May (0-40%), and to 0.6% in June (0-2.5%) (Table 2; calculated from data in Reports, 1972-1993).

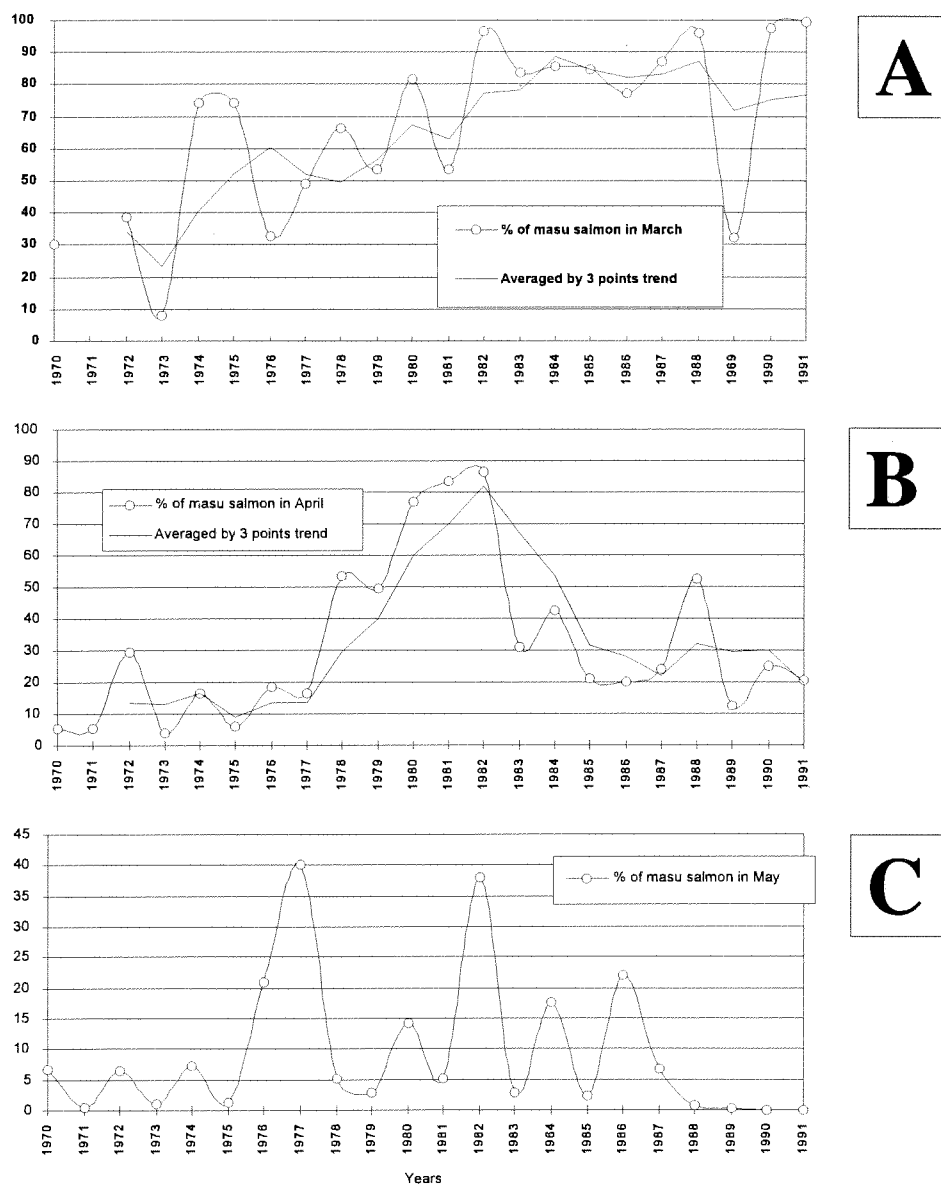
In recent years, when Japan Sea's pink abundance decreased, percentage of masu had a tendency to increase in the beginning of the season (Fig. 3A). In April a decreasing trend is observed (Fig. 3B), and in May there are cyclic fluctuations influenced by the abundance of pink salmon (Fig. 3C). In years of low pink abundance masu percentage significantly increased, reaching 40% in May.

Chum salmon were not observed every year and the percentage in the catch was always very low. Usually chum salmon were caught in the Sea of Japan northward of 40°N (about 60% from all chum). However, some fish were caught near 38°N. The occasional occurrence of only a low percentage of chum salmon in the catch indicates that chum salmon spawning in rivers draining into the Sea of Japan winter mainly outside the Sea of Japan, migrating probably to the Pacific Ocean and Sea of Okhotsk.

Table 2. Species composition (%) of salmon catch and CPUE (fish per tan) in the Sea of Japan by months and years. All calculations are done from "Report" (1972-1993). N - number of summarized reports, N fish - sample size, N tan - amount of tans used.

Year	N	percent			N fish	N tan	CPUE		N	percent			N fish	N tan	CPUE	
		masu	pink	chum			masu	pink		masu	pink	chum			masu	pink
M a r c h									A p r i l							
1970	1	30.0	70.0	0.00	337	540	0.19	0.44	1	5.6	94.4	0.00	1441	1195	0.07	1.14
1972	1	38.8	61.2	0.00	508	659	0.30	0.47	1	5.4	94.6	0.00	4069	1217	0.18	3.16
1973	1	8.0	92.0	0.00	267	375	0.05	0.58	2	29.4	70.6	0.00	2040	1948	0.31	0.74
1974	2	74.2	25.8	0.00	330	1329	0.18	0.06	4	4.0	96.0	0.00	7438	2884	0.10	2.48
1975	3	74.1	25.9	0.00	2537	4453	0.42	0.15	2	16.5	83.5	0.00	5653	4735	0.20	1.00
1976	3	32.7	67.3	0.00	8605	5601	0.50	1.03	6	5.9	94.1	0.00	18582	8244	0.13	2.12
1977	3	48.8	51.2	0.00	907	3428	0.13	0.14	4	18.7	81.3	0.01	9272	7510	0.23	1.00
1978	2	66.6	32.9	0.49	2058	3943	0.35	0.17	4	16.6	83.4	0.00	2776	4678	0.10	0.50
1979	3	53.5	46.2	0.34	5654	4351	0.70	0.60	5	53.7	45.1	1.24	1052	5271	0.11	0.09
1980	4	81.8	18.2	0.01	7517	5851	1.05	0.23	5	49.6	50.4	0.00	389	4722	0.04	0.04
1981	4	53.5	46.3	0.18	7913	7681	0.55	0.48	5	76.8	23.1	0.14	1461	7795	0.14	0.04
1982	3	96.8	3.2	0.07	4351	5796	0.73	0.02	4	83.3	16.7	0.00	1878	7090	0.22	0.04
1983	4	83.8	16.2	0.03	3982	7572	0.44	0.09	4	86.6	13.2	0.15	1375	9531	0.13	0.02
1984	2	85.4	14.6	0.00	803	3642	0.19	0.03	5	30.8	69.2	0.00	1507	8134	0.06	0.13
1985	3	84.4	15.5	0.12	3369	5620	0.51	0.09	4	42.5	57.5	0.03	2972	8674	0.15	0.20
1986	3	77.3	22.7	0.00	1163	4303	0.21	0.06	3	21.2	78.7	0.07	2740	6441	0.09	0.34
1987	3	87.2	12.8	0.00	2537	6112	0.36	0.05	3	20.2	79.7	0.11	3786	4709	0.16	0.64
1988	3	96.3	3.7	0.00	1016	3419	0.29	0.01	3	24.1	75.8	0.08	1247	4669	0.06	0.20
1989	2	32.4	67.3	0.31	324	2348	0.05	0.09	3	52.3	47.5	0.21	480	5105	0.05	0.05
1990	2	97.7	2.3	0.00	478	2380	0.20	0.01	3	12.5	87.4	0.07	1505	4541	0.04	0.29
1991	1	99.5	0.5	0.00	212	1455	0.15	0.00	3	24.9	75.1	0.00	2966	5246	0.14	0.43
1991	1	99.5	0.5	0.00	212	1455	0.15	0.00	3	20.5	79.4	0.06	3556	5527	0.13	0.51
Total					54838	80858						76744	118670			
Average		66.8	33.1	0.07			0.36	0.23	31.9 68.0 0.10					0.13	0.69	
Min		8.0	0.5	0.00			0.05	0.00	4.0 13.2 0.00					0.04	0.02	
Max		99.5	92.0	0.49			1.05	1.03	86.6 96.0 1.24					0.31	3.16	
M a y									J u n e							
1970	1	6.7	93.3	0.00	2998	1212	0.17	2.31	1	2.2	97.8	0.00	847	1060	0.02	0.78
1971	1	0.4	99.6	0.00	10525	1877	0.02	5.59	1	0.0	100.0	0.00	4738	360	0.01	13.16
1972	2	6.5	93.5	0.00	817	2189	0.02	0.35								
1973	2	1.0	99.0	0.00	8109	3981	0.02	2.02	1	0.1	99.9	0.00	4098	741	0.01	5.53
1974	4	7.4	92.6	0.00	10161	9249	0.08	1.02	4	0.5	99.5	0.00	4020	3614	0.01	1.11
1975	6	1.2	98.8	0.01	33182	10163	0.04	3.23	4	0.0	100.0	0.02	9249	3391	0.00	2.73
1976	4	20.9	78.9	0.19	6675	7038	0.20	0.75	3	0.1	99.9	0.03	7068	4374	0.00	1.61
1977	2	40.1	60.0	0.00	412	892	0.19	0.28								
1978	3	5.3	94.6	0.13	9407	5979	0.08	1.49	1	0.1	99.9	0.00	2185	925	0.00	2.36
1979	3	2.9	97.0	0.18	16190	7427	0.06	2.11	1	0.2	99.7	0.16	1245	1870	0.00	0.66
1980	3	14.3	85.6	0.08	1292	5632	0.03	0.20	2	0.5	98.9	0.63	2077	2236	0.00	0.92
1981	3	5.1	94.8	0.03	3931	5920	0.03	0.63	1	2.5	92.4	5.06	79	848	0.00	0.09
1982	4	38.0	62.0	0.00	748	6139	0.05	0.08								
1983	3	2.8	97.2	0.05	2053	5656	0.01	0.35								
1984	2	17.7	82.2	0.07	1373	3527	0.07	0.32								
1985	2	2.3	97.5	0.18	3299	3700	0.02	0.87								
1986	1	22.0	78.0	0.00	214	2052	0.02	0.08								
1987	2	6.6	93.3	0.08	1282	2989	0.03	0.40								
1988	1	0.8	99.2	0.00	258	871	0.00	0.29								
1989	1	0.2	99.8	0.00	492	1182	0.00	0.42								
1990	1	0.0	100.0	0.00	874	1465	0.00	0.60								
1991	1	0.0	100.0	0.00	1370	1068	0.00	1.28								
Total					115662	90208						35606	19419			
Average		9.2	90.8	0.05			0.05	1.12	0.6 98.8 0.59					0.00	2.89	
Min		0.0	60.0	0.00			0.00	0.08	0.0 92.4 0.00					0.00	0.09	
Max		40.1	100.0	0.19			0.20	5.59	2.5 100.0 5.06					0.02	13.16	

Fig. 3 Proportion of masu salmon (as % total number salmon caught) in Japanese gillnet catch in March (A), April (B) and May (C) in the Sea of Japan.



CATCH OF MASU AND PINK SALMON PER GILLNET (CPUE)

Catch per unit gillnet (CPUE) of masu salmon was highest in March and decreased during the season (Fig. 4A). In March CPUE of masu was 0.36 fish per tan in April, 0.13; and in May, 0.05 (Table 2). Unlike masu salmon, CPUE values for pink salmon increased from March to June (Fig. 4B). Beginning in the 1980s, a trend of decreasing CPUE for masu salmon is observed in March. CPUE of masu salmon also declined slightly in April and May, excluding some increases in 1990-91 in April.

In March CPUE of pink salmon was 0.23 fish per tan, in April - 0.69, in May - 1.12 and in June - 2.89. From 1982 to 1991 in March CPUE of pink did not exceed 0.1 (Table 2) It was also low in other months, with two slight peaks in the middle 1980s and in the beginning of the 1990s (Fig. 4B).

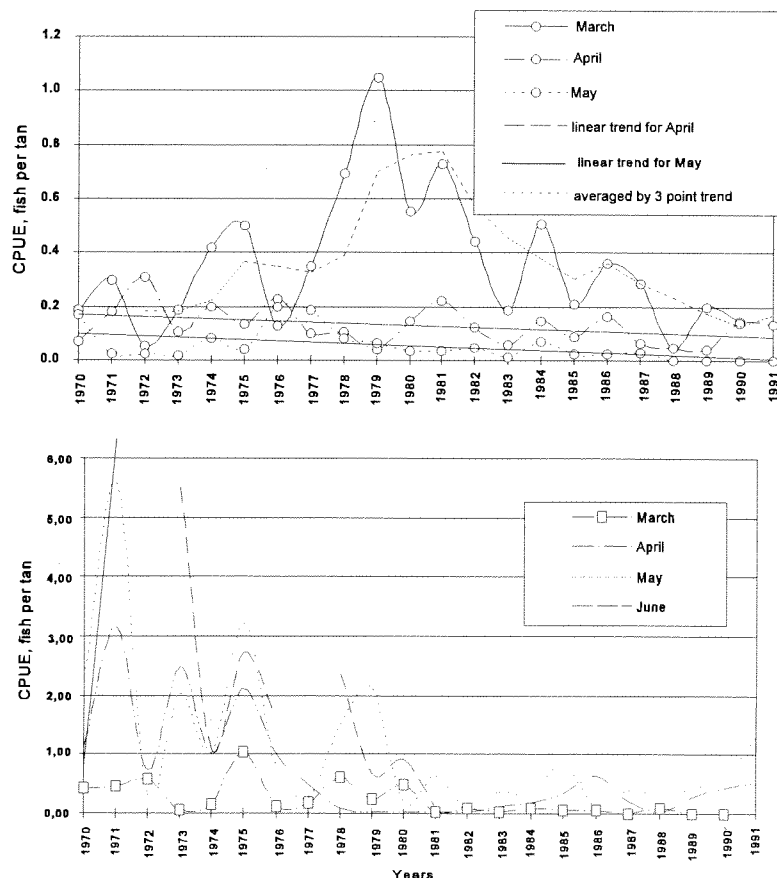
ORIGIN OF PINK AND MASU SALMON FROM CATCH IN ZONES OF JAPAN AND COUNTRIES OF KOREAN PENINSULA

For determination of origin of pink salmon, wintering in the Sea of Japan, Japanese scientists

during many years conducted tagging operations in spring sampling. From 1956 to 1971 in the Sea of Japan 6921 fish of .1 age were released with attached tags. Of these fish, 78 fish were recovered in Primor'e, 13 fish in Amur, 59 fish along the west coast of Sakhalin, 15 along the east coast of Sakhalin and one pink salmon along the northern coast of Okhotsk Sea (Fukataki and Kato 1974; Takagi et al. 1981). Earlier experiments (before 1949) sampling pink salmon in the Sea of Japan and near west coast of Sakhalin (Hirano 1953; cited by Takagi et al. 1981) revealed that pink salmon recovered in west Sakhalin can migrate to rivers of Primor'e, Amur, rivers of east coast of Sakhalin and north coast of Okhotsk Sea.

While tagging experiments revealed that pink salmon wintering in the Sea of Japan spawn mainly in Primor'e, Amur and western Sakhalin, fish from eastern Sakhalin, Kuril Islands and northern coast of Sea of Okhotsk are also present here. There were no recoveries of pink salmon tagged in the Sea of Japan in rivers of Hokkaido, and there are no pink salmon spawning stocks on Honshu. On the continental side, North Korea is the southern limit of pink salmon's spawning, but significant stocks occurred northward only from middle Primor'e of Russia. Therefore, pink salmon distributed in the Sea of Japan originate

Fig.4 Masu salmon (A) and pink salmon (B) catch per gillnet (CPUE) in the Sea of Japan in different months by year.



almost exclusively from Russian rivers.

Masu salmon inhabiting the Sea of Japan also originated from different regions. Information on tagging experiments of masu salmon is limited in comparison to pink salmon. Masu salmon tagged in central part of Japan Sea were recovered in rivers of Primor'e, and in coastal waters of Sakhalin, coastal waters and rivers of Japan (Fukataki 1970; Machidori and Kato 1984). The fact that some fish tagged in zone of Japan were recovered in rivers of Russia proved that some masu salmon from the catch of Japanese fishermen originated from Russia. This fact was also confirmed by biological information (Tsiger 1993, 1994; Kurmazov and Tsygir 1993).

A significant part of fish from central part of Japan Sea moves to Primor'e when water temperature increases in spring (Tanaka 1965; Machidori and Kato 1984; Reports of Ishikawa and Yamagata, 1973-79). This also suggests that those fish originated from Primor'e rivers. Many fish caught near Western Kamchatka had hooks in their mouths which were used in longline fishery in the Sea of Japan, evidence that the longline fishery is harvesting masu salmon from Western Kamchatka wintering in the Japan Sea (Shimazaki 1971). Freshwater age of masu salmon is shorter on average in southern rivers than in northern ones. About 90-95% of sea-run adults from rivers of Japanese Islands are fish which spent 1 year in rivers. Masu salmon collected in waters near Hokkaido included many fish which had spent 2 winters in rivers (Okazaki 1989). Consequently, many fish migrating near the Japanese Islands did not originate from rivers of Japan.

Percentage of males in sea-run stocks of masu salmon varies from 0% in the southern regions to more than 40% in the northern populations. Therefore, high percentage of males in waters near Honshu in area of 38-39°N in early March is evidence of the presence of fish from northern spawning populations (Machidori and Kato 1984). In the co-operative Japanese-Russian research cruises conducted in 1993 and 1994 in 200-mile economic zone of Japan, scale samples of masu salmon were collected and age determinations were made for 33 fish. Of these, 33% were fish with freshwater age of 2 years. This is higher than the usual ratio for Japanese rivers. The percentage of males (39%) was also higher than is observed in Japanese rivers. Therefore it's reasonable to suggest that some fish originated from rivers of Russia.

Masu salmon from Russian rivers are caught not only in offshore waters in the Sea of Japan, but also in coastal waters on Sea of Japan side and Pacific Ocean side, based on age and sex composition as well as allele frequency from both sides of Japanese Islands (Okazaki 1989). The presence in coastal catch from the Pacific side of masu salmon with freshwater

age 3., also indicated that some fish from Western Kamchatka spent winter there.²

Masu salmon caught in Ishikawa Prefecture (Honshu) in March consist mainly of fish of Russian origin (Kimoto et al. 1994). The size of catch depends on the influence of Tsushima warm current, because in cold years masu salmon spent more time in coastal waters where they are susceptible to the coastal fishery. In coastal waters of Niigata Prefecture, the main part of masu salmon caught are fish from more northern regions, including rivers of Russia (Shinji 1989).

Unlike masu salmon, pink salmon do not spawn in rivers of Korean Peninsula. Consequently masu salmon of Korean origin are present in marine salmon catch from the coastal waters of Korean Peninsula. However, abundance of masu in North Korea is significantly lower than in Russia. In the case of South Korea abundance of masu was very low 30 years ago when only 100-200 fish entered a few rivers (Machidori and Kato 1984). Because there was no mention of masu salmon in later listings of anadromous fish (cited by Valencia 1989) it can be concluded that reproduction of sea-run form of masu is virtually non-existent in South Korea. On this basis, it can be assumed that the majority of masu salmon taken in Korean waters consists of fish from Russian rivers.

Because masu salmon from all countries adjacent to the Sea of Japan are concentrated in the coastal zones of Japan and Korea during the winter and spring season, and the main spawning rivers for masu salmon are located in Russia, part of the masu salmon caught in the zones of these countries are fish originating from Russia. Stock differentiation research is necessary for estimation of the exact share.

STOCK CONDITION OF SEA OF JAPAN'S SALMONS AND NECESSITY OF INTERNATIONAL CO-OPERATION FOR THEIR RATIONAL USAGE

Historical data on pink salmon catch in the main reproduction areas of the Sea of Japan (Primor'e and Amur) are presented in Fig. 5. Statistics on north-western Sakhalin (Rybnovskiy region) are also included because fish caught there originated mainly from the Amur area. Statistics on other parts of Sakhalin were not included because it was impossible to differentiate Sea of Japan from Pacific Ocean stocks.³ These data show that abundance and catch Sea of Japan's pink salmon significantly varied within

² Masu salmon with freshwater age 3 are known from Western Kamchatka only.

³ Sea of Japan's stocks spend winter in the Sea of Japan, Pacific Ocean's stocks in the Pacific Ocean.

Fig. 5-A Historical catch of pink salmon in Amur, Rybnovskiy (North-Western Sakhalin), and Primor'e area of Russia in odd years of current century, tons.

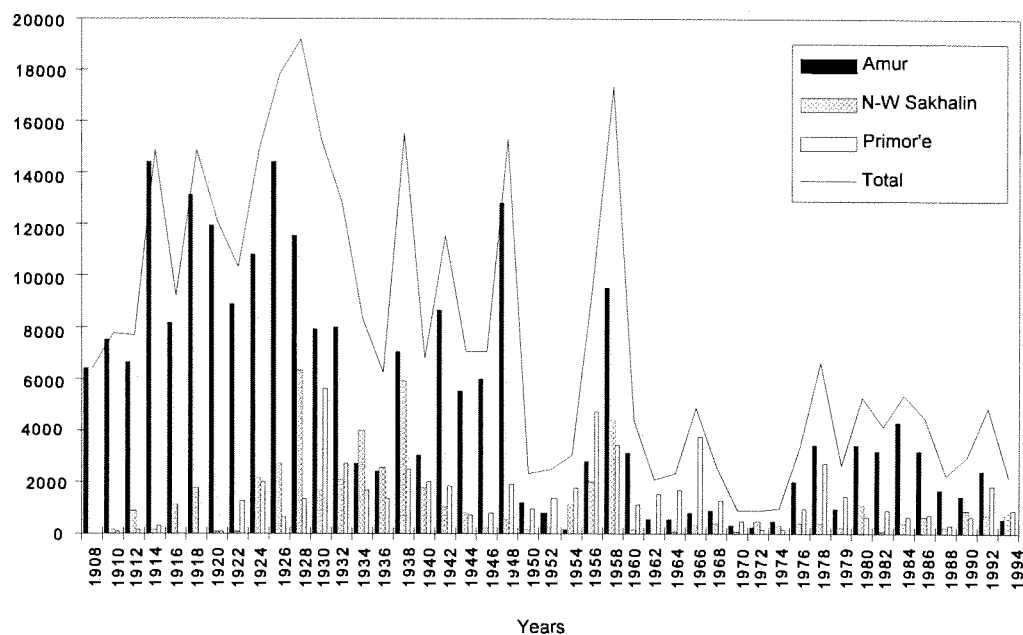
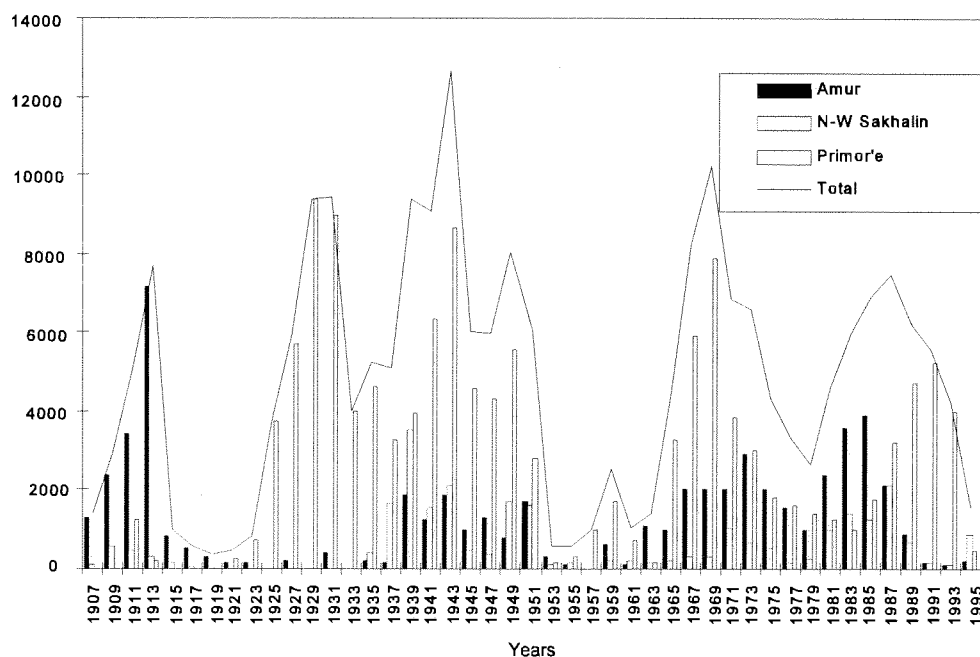


Fig. 5-B Historical catch of pink salmon in Amur, Rybnovskiy (North-Western Sakhalin), and Primor'e area of Russia in even years of current century, tons.



areas in odd and even years as well as between areas in the same year. Despite this great variation total catches were highest in the first half of century both for odd and even years, reaching a maximum about 20,000 metric tons in even years and about 13,000 in odd ones. In odd years, generally, Amur pink salmon were more abundant, while in even years Primor'e pink salmon were more abundant. There were exceptions to these generalizations for both generations. However, stock abundance is presently low in Primor'e and Amur for both generations (Fig. 5A,B). The low abundance has been attributed to the deficiency of spawners in rivers (Pushkaryova 1975, 1981), which is strongly influenced by marine fishery (Gavrilov and Pushkaryova 1984, 1994).

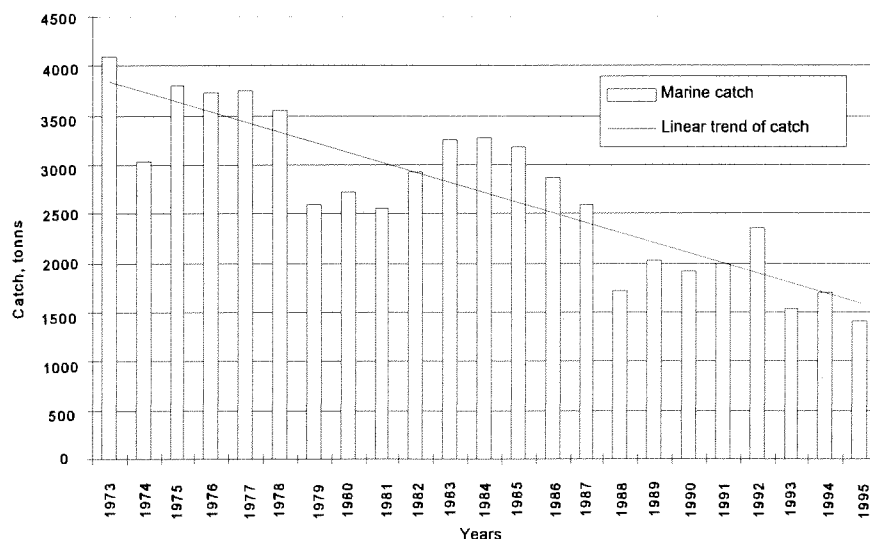
Before World War II, abundance of masu salmon was much higher than now in Russia (Semenchenko 1989) and in Japan (Machidori and Kato 1984; Nagasawa and Torisawa 1991). Masu salmon stocks of middle and northern Primor'e were the most abundant through whole area. Some years the catch of masu exceeded the catch of pink salmon in weight. In northern Primor'e in 1928-1943 annual catch of masu varied from 600 to 1200 tons (on average 770 tons). Masu salmon were also at relatively high abundance in the Amur River where annual catch was 830 tons (Semenchenko 1989). Over the past 50 years, the abundance of masu salmon strongly decreased in Russia (Semenchenko 1989). At the same time stock reduction took place in rivers of Hokkaido (Nagasawa and Torisawa 1991). Undoubtedly, the development of Japanese fishery in the Sea of Japan was one of the reasons for the decline. In 1957 due to reduction of stock size, fishing for masu salmon has been prohibited in Primor'e. However abundance of masu has remained at a low level.

For the present time only Japanese fishery statistics on masu salmon are available. Until 1973 the catch of masu was not separated from catch of pink. From 1973 the number of pink and masu salmon caught is calculated separately when possible and data on both species was reported to FAO (Machidori and Kato 1984). According to these data the catch of masu salmon in 1973-1994 was from 1,403 to 4,100 (on average 2,723) thousand tons (FAO 1977-1992; Fisheries Agency of Japan 1994, 1995). According to these data annual marine catch by Japan has tended to decline (Fig. 6) despite a lot of effort in the artificial reproduction of masu salmon in Japan.

The number of Japanese fishing vessels also declined significantly in the Sea of Japan. In the beginning of the 1970s there were more than 700 fishery vessels. In the mid 1970s, their number was reduced to 500 (Pacific Salmon Catch, 1989). In 1995 only 30 Japanese vessels fished in the Sea of Japan. Taking into account the trend of decreasing marine catch of masu salmon, and the decreasing catch per gillnet, we conclude that masu salmon abundance has declined in the Sea of Japan.

From the beginning of the 1970s until the present, a declining trend in the marine catch of pink salmon has also been observed in the Sea of Japan (Fig. 2). However, the level of reproduction of Japan's pink salmon is low during the present period. Russia and Japan achieved agreement for gillnet and longline fisheries of pink salmon in the 200-mile economic zone of Japan. A quota is set by Russia and the fishery stops when the permitted amount of salmon are caught. But salmon fishing in zones of Korean countries is not restricted, and size of catch is not controlled. Because of the decreasing abundance of

Fig. 6 Marine masu salmon catch by Japan (FAO 1977-92 and Fisheries Agency of Japan 1993-96).



salmon and the existing uncontrolled marine fishery of salmon of Russian origin, international agreement is necessary between the four countries of the Sea of Japan (Russia, Japan, Southern and Northern Korea). The aims of such agreement should be regulation of the salmon fisheries in the Sea of Japan and co-ordination of scientific research. Fishermen from these countries should be interested in the conservation and restoration of Sea of Japan's salmon stocks, because continued reduction of Russian salmon's stocks will result in continuing declines in their catches.

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Abundance and Biology of Kamchatkan Salmon During the Initial Year of Ocean Residence

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Represented in this paper are results of a 15-year research study on juvenile biology of five Pacific salmon species, conducted during the fall period in Kamchatkan coastal waters of the Sea of Okhotsk and western Bering Sea. The variation in distribution, migration, feeding, and growth of juvenile salmonids was described in relation to hydrological conditions and juvenile abundance. Assessments of juvenile pink salmon abundance were used to forecast runs of pink salmon the following year.



INTRODUCTION

Regular studies of Pacific salmon species in their ocean life periods have been conducted in Kamchatka for 40 years. The biology of juvenile salmonids in Kamchatka coastal waters of the Sea of Okhotsk and Bering Sea have been subject of intensive research during the most recent 25 years (Birman 1985; Karpenko 1992). Initially, juvenile sampling was done using passive fishing gear like drift nets; however, because of its selectivity, sampling was not thought to be representative of salmon abundance or their biological characteristics. During the mid 1970's, Kamchatkan scientists introduced active fishing gear such as beach seines, purse seines, and pelagic trawls for sampling purposes. These gears, because of their higher efficiency and effectiveness in capturing smaller individuals, provided a versatile and more quantitative sampling method for salmon populations at various life history stages in marine waters. Beach and purse seines were the main fishing gear deployed for juvenile salmon sampling in Kamchatkan coastal waters and trawls were the main fishing gears deployed in Kamchatkan offshore waters (Karpenko 1992).

The period when juvenile salmon reside in coastal waters, following seaward migration, is of great importance to salmon stock formation and reproduction. During this period, the mortality of pink and chum salmon, the most numerous salmon species in the Russian Far East, exceeds 2/3 of the total cohort entering the ocean. Mortality rates of other salmon species, was estimated to exceed one

half of the total cohort entering the ocean. Knowledge of conditions during the first year of marine residence is very important for evaluation of salmon stocks returns. Kamchatka scientists monitor the ocean abundance of the largest salmon stocks in western and north-eastern Kamchatka for the purpose of forecasting runs enabling more rational management of salmon fisheries on these stocks.

The results of research on juvenile salmon ecology of five species - pink, chum, sockeye, coho, and chinook - in Kamchatka coastal waters of the Sea of Okhotsk and Bering Sea during the most recent 15-year period (1981-1995) and evaluation of pink salmon run forecast based on marine abundance juvenile salmon during fall season is presented.

MATERIALS AND METHODS

The data presented in this paper were collected on annual cruises of research vessels to the eastern Sea of Okhotsk and the south-western Bering Sea during summer and fall of 1981-1995. Sampling was conducted based on a standard station grid and was timed to occur after juvenile migration into the survey area was completed. Juvenile salmon sampling, since 1985, was done using adjustable depth wire trawl 54.4/192 meters, equipped with dally insert (cell size 12 mm), 3.3 m² boards, and hydrodynamic device. Duration of survey trawling was set at 1 hour after net deployment was completed, with an average trawling speed of 4.5 knots. Sampling was conducted in the 0-35 m depth interval which are the limits of juvenile salmon daily vertical migration.

The survey area was divided into sectors and estimates of salmon abundance were made, by sector, based on expansion of trawl catches by the ratio of the sector area and the estimated area swept of the trawl. The trawling area was calculated assuming a distance of 50 meters between the trawl wings.

Also, we used three biological characteristics for juveniles:

- 1 - Fulton's index - $F = W \cdot 100 / L^3$;
- 2 - Clark's index - $C = W1 \cdot 100 / L^3$, where
W - total weight, g,
W1 - weight without internal organs, g,
L - fork length, cm; and
- 3 - Stomach fullness which changed from 0 to 4.

Data collection and data processing were conducted using standard methods, established in TINRO (Pacific Research Institute for Fisheries and Oceanography). It was not possible to determine age composition due to descaling of juvenile salmon due to trawling operations.

In addition to data collected during the fall juvenile salmon investigations, the data on spring-summer juvenile salmon investigations were used to forecast adult pink salmon runs (Karpenko 1992, 1994). Besides, annual studies of early marine period life of juvenile salmon have been carried out in the south-western Bering Sea since 1975, some results of which have been included in one of the reports of the present Symposium (Karpenko 1996). These data were used to describe the ecology of Kamchatka salmon and variation in stock reproduction.

RESULTS

Juvenile Salmon Biology

The Sea of Okhotsk

Pink Salmon. Seaward migration of pink salmon in western Kamchatka rivers occurred in late May through July. The peak of the migration occurred during the first part of June. Pink salmon moved rapidly through the narrow coastal desalinated zone, and then resided in coastal waters. Initially, due to their small sizes, juvenile salmon moved with strong oceanic currents in a northerly direction. In September, pink salmon juveniles occurred throughout the eastern Sea of Okhotsk. The highest density shoals were observed in the area 52°-56°N, 151°-154°E (See Fig.1). Later in the season, these Kamchatkan coastal shoals migrated in a southerly direction, and overwintered in the southern Sea of Okhotsk.

The western Kamchatka shelf and the central Sea of Okhotsk were important rearing and feeding areas for the juvenile salmon that originated from the Gulf

of Shelekhova, Kamchatka West Coast. and Sakhalin East coast. The largest runs occur to the rivers of West Kamchatka and East Sakhalin. The abundance of these stocks fluctuates in asynchronous cycles with odd-year runs dominant in east Sakhalin and even-year runs dominant in west Kamchatka. Indeed, over the period 1985-1993 the odd-year total runs in the West Kamchatka rivers averaged 20 thousand t, and over the period 1986-1992 the even-year runs averaged 140 thousand t; in contrast for the same period the odd-year total runs in the East Sakhalin rivers averaged 550 thousand t, and even-year runs averaged 160 thousand t (Varnavskaya et al. 1995).

In common case, migratory patterns of most juvenile salmon out of rivers draining in the northern Sea of Okhotsk have directional tendencies such as follow: (a) in odd years they move **west** (exploitation of Western Kamchatka Shelf) - **south-west** (the central Sea of Okhotsk) - **south** (the southern Sea of Okhotsk) - **east** (entrance to the Pacific Ocean); (b) in even years they direct **north-east** - **east** - **south-west** - **south-east**. This migration cycle period covers five months at least, from August till December, according to V.P. Shuntov (1989a). The vanguard of migrating pink salmon is made of larger fish of earlier migrants.

The trawling survey in the Sea of Okhotsk provided aggregate stock abundance estimates in Kamchatkan coastal waters, although the lack of stock identification methods prevented quantitative determination of contribution made by each salmon stock to populations in the Sea of Okhotsk. Analysis of coastal runs suggested that three types of geographical distribution of pink salmon occur near the Kamchatka coast (Erokhin, press):

- 1- *Aboriginal* - when these waters are mostly inhabited by western Kamchatka pink salmon;
- 2- *Immigratory* - western Kamchatkan pink stock abundance is very low, under 10%;
- 3- *Intermediate* - most frequent type, where pink juveniles of Kamchatka origin rear jointly with visitor stocks in the eastern Sea of Okhotsk;

In September-early October, more than half of all pink salmon in Kamchatka coastal waters in the Sea of Okhotsk had average length 21-23 cm, and average weight 100-170 g (Table 1). The length of juvenile pink salmon north of 54°N was 1.5-2 cm less than the length of pink salmon in the southern areas. A decrease in Fulton's index (1.26 to 0.92) was also observed from the southern to northern areas of the Sea of Okhotsk. Juvenile pink salmon in southern areas tended to have a greater weight than juvenile pink salmon of the same size in the northern areas.

Fig. 1 Distribution of pink salmon sample juveniles in the Sea of Okhotsk (fish/trawl): A - September-October 1990; B - September-October 1991.

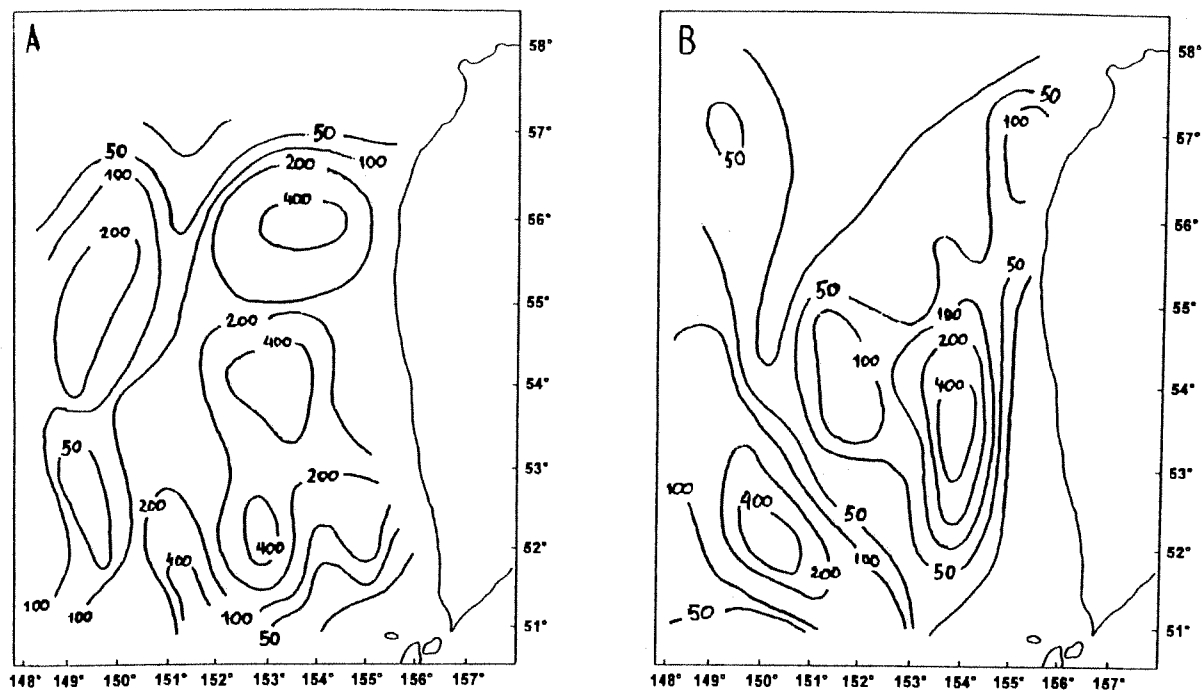


Table 1. Average length (cm) and weight (g) of juvenile salmon in Kamchatka coastal waters of the Sea of Okhotsk and Bering Sea during fall seasons of 1981-95.

Year	Pink		Chum		Sockeye		Coho		Chinook	
	l, cm	m, g	l, cm	m, g	l, cm	m, g	l, cm	m, g	l, cm	m, g
Sea of Okhotsk										
1981	19.3	77.2	20.2	88.6	21.7	117.7	28.5	310.0	22.8	157.5
1982	18.7	66.1	18.3	68.1	22.5	134.0	26.6	243.0	21.2	142.4
1986	20.7	97.3	21.9	112.6	23.0	140.7	29.7	378.4	23.1	174.0
1987	20.4	87.3	23.0	141.1	-	-	28.7	326.9	24.1	190.0
1989	22.0	122.7	22.7	143.4	23.0	162.7	30.3	396.6	24.5	210.8
1990	21.0	107.1	22.7	138.6	22.0	122.6	28.7	308.1	22.4	172.6
1991	22.1	114.3	22.1	121.0	22.9	138.2	28.1	306.4	22.5	168.1
1995	19.5	87.1	21.3	111.9	20.8	103.6	27.9	318.2	24.8	195.2
Bering Sea										
1981	18.0	62.1	21.5	73.3	18.2	66.5	30.4	145.2	22.7	173.2
1982	15.7	36.6	15.4	36.6	20.8	103.7	27.1	267.7	21.9	135.9
1984*	12.8	19.3	13.4	25.5	18.8	74.8	21.9	132.6	16.9	60.0
1986	19.0	72.1	18.1	65.6	21.4	118.0	28.3	310.4	23.0	163.1
1987	19.4	85.7	18.6	74.0	21.5	114.8	27.0	235.7	21.6	130.2
1988	19.5	71.5	19.5	83.3	23.9	153.1	26.7	232.6	20.8	111.0
1989	20.4	82.4	18.5	69.4	23.5	145.0	27.7	280.0	20.4	120.0
1990	18.9	69.1	18.7	73.6	22.7	144.2	26.5	236.4	21.6	126.9
1991	20.0	80.0	20.0	91.4	17.6	73.1	25.5	255.4	19.4	110.0
1992	18.5	55.5	17.4	51.6	20.8	113.7	24.7	165.0	22.5	104.7
1994	17.8	55.5	21.4	120.2	-	-	-	-	-	-

● - August

Growth rates of pink salmon in the eastern Sea of Okhotsk were higher than those in the other parts. The juveniles reached 20 cm in length after 3-3.5 months of rearing. Daily growth rate during September were 1.5-2.8 mm/day and 3-4.2 g/day south of 55°N, and 2 mm/day and 2.9 g/day north of 55°N (Table 2). Growth rate of pink salmon during winters were low, 0.7 mm/day and 1.31 g/day from October through March, 1985-1986 (Erokhin 1990).

Biological indicators of pink juveniles varied, depending on distribution type. During the years with *immigratory* and *intermediary* distributions (1986, 1989-91) pink salmon were larger with 60-90% of length 21-23 cm and of weight 80-120 g. In years with *aboriginal* distribution (1982, 1995) pink salmon were smaller with 70% of fish of length 17-22 cm and weight less than 70 g. During years with *aboriginal* distribution, 50% of fish were of length less than 18.5 cm, while years with *immigratory* and *intermediary* distributions, only 14% of fish were of length less than 18.5 cm.

Pink salmon feeding intensity was high in fall, especially in the evening. In 1995, stomach fullness averaged 2.1-2.53 at various locations, with no empty stomachs occurring. The major prey for pink salmon were *hyperiid*s and *euphausiid*s.

Chum Salmon. The seaward migration of Sea of Okhotsk chum salmon was coincident with that of pink salmon, although the downstream migration was more protracted (Maksimenkov and Tokranov 1994), and the residence period in coastal brackish waters was longer than that of pink salmon. In the fall season, chum salmon occurred throughout the area off west Kamchatka, and mostly in the area bounded by 51°-56°N and 151°-155°E. The area of chum salmon concentration was between areas of pink salmon concentration on the west, and sockeye,

chinook, and coho salmon concentration on the east (Fig. 2). In September and October, the number of chum salmon juveniles south of 53°N were 2-3 times the number of those north of 53°N in Kamchatka coastal waters. The rearing of chum salmon to the south of 53°N continued into November.

Kamchatka chum salmon shoals were a mixture of chum salmon from west Kamchatka and from the northern parts of the Sea of Okhotsk. The abundance of chum salmon in the area between 56°-57°N increased rapidly from late September through mid-October due to influx of the juveniles from the northern parts of the Sea of Okhotsk.

In September, over 60% of chum salmon were of length 21-24 cm and weight 100-120 g, with larger fish occurring in the south (Table 1). Smaller fish, 12-19 cm, occurred within the 20-50 mile coastal zone in the north-east of the area. Chum salmon growth rates in September were relatively stable, although lower than those of pink salmon. Growth rates, 1989-91 were estimated to be 1.4-1.7 mm/day and 2.2-3.8 g/day. Feeding intensity of chum salmon was similar to pink salmon; however, the diet was different. Fulton's index for juvenile chum salmon ranged from 1.06 to 1.20, and was higher in coastal locations.

Sockeye Salmon. The seaward migration of Sea of Okhotsk sockeye salmon juveniles occurred over a protracted period from May to August (Bugayev 1995). During September - October, sockeye salmon formed two aggregations between 51°-58°N and 152°E-off the Kamchatka Coast (Fig. 2). Abundance in the southern aggregation was usually higher and accounted for 92%, 78%, 63%, and 46% of total juvenile sockeye abundance in 1986, 1989, 1990, and 1991, respectively.

Table 2. Growth rate of juvenile salmon in Kamchatka coastal waters of the Sea of Okhotsk and Bering Sea.

Species	Daily linear growth rate, mm	Daily weight growth rate, g
Sea of Okhotsk		
Pink	0.51-2.85	1.43-4.28
Chum	1.40-1.73	2.21-3.76
Sockeye	1.53-3.16	1.57-2.74
Coho	1.30-5.50	4.57-18.7
Chinook	0.70-1.50	1.14-3.48
Bering Sea		
Pink	1.1-1.8	1.7-2.8
Chum	1.8-2.3	1.3-1.6
Sockeye	1.8-2.2	1.3-1.8
Coho	2.0-2.7	3.0-4.0
Chinook	1.5	3.5

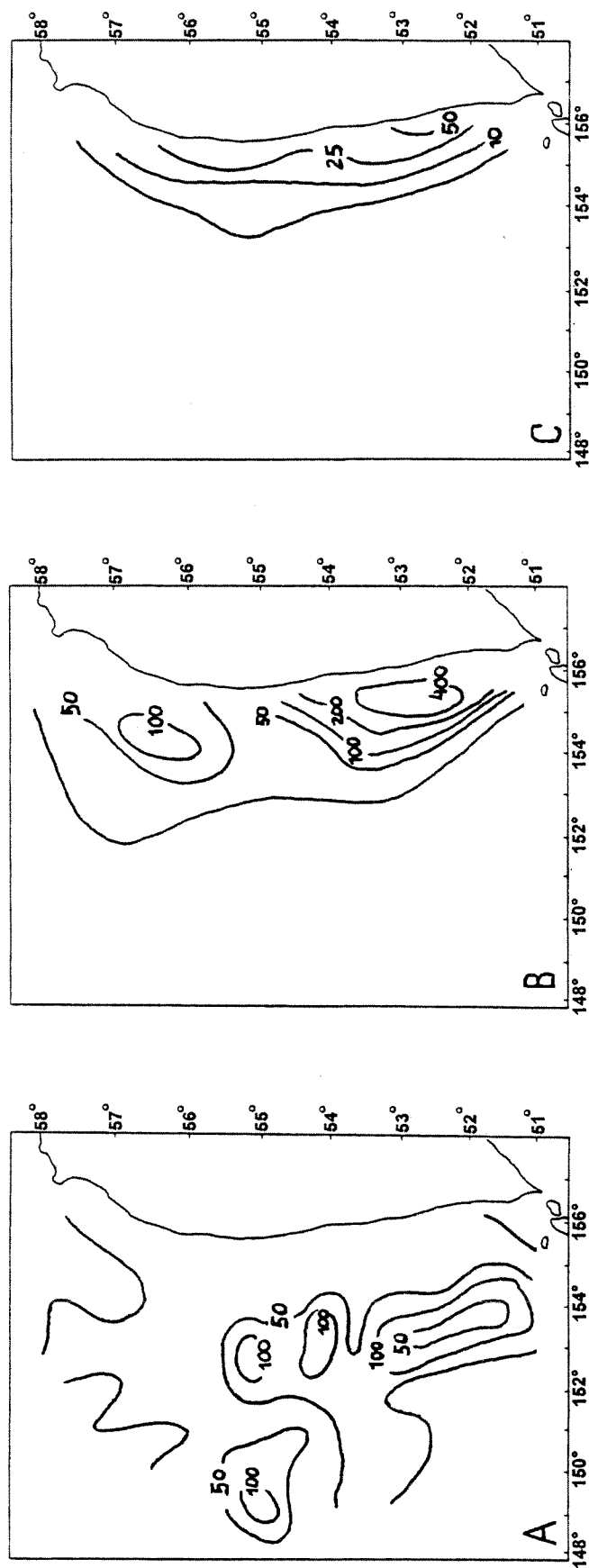


Fig. 2 Typical distributions of chum (A), sockeye (B), and chinook (C) juveniles in September-October in the Sea of Okhotsk, fish/trawl.

As is the case with other salmon species, juvenile sockeye migratory patterns during the marine rearing period were highly dependent on directions of oceanic currents in the eastern part of the Sea of Okhotsk, particularly that of the Western Kamchatka Stream. Since 90% of sockeye in this region originated from Kuril Lake, it was easy to determine the direction of migration of sockeye juveniles in Kamchatka coastal waters. On entering the ocean, most juveniles were carried westward along Kamchatka's west coast by the western Kamchatka stream (Fig. 3).

A large shoal of sockeye, originating from Kuril Lake and Bolshaya River, forms in September. It was believed that a portion of Kuril Lake and Bolshaya River sockeye migrated northward and intermingle with sockeye that originated from rivers of northwestern Kamchatka. The second shoal was formed in northern area and persisted until October. The northern aggregation migrated southward, and during the third week in September joined the southern aggregation. By mid-October, sockeye salmon did not occur north of 55°N.

The length and weight of sockeye during the fall season ranged from 15 to 30 cm, and from 50 to 295 g, respectively. Most fish were of length 21-24 cm and weight, 100-200 g. There occurred a longitudinal gradient in fish size with larger fish occurring offshore. The longitudinal size gradient was greater than the latitudinal gradient in length. The growth rates of sockeye were high and similar to pink salmon. In 1986-91, daily growth rate was estimated to be 1.5-3.2 mm/day and 1.57-2.74 g/day. Fulton's index ranged between 1.00 and 1.19. The major prey for sockeye were larger crustaceans and fish fry.

Coho Salmon. The seaward migration of coho salmon occurred at the time as sockeye salmon. Coho salmon formed 2 aggregations. During September-October a northwestern group was located north of 54°N and west of 153°E, and a southeastern group was located south of 54°N and east of 153°E (see Fig.4). The northwestern aggregation formed earlier, during August-early September however, a migration occurred from the northwestern group to the southeastern group and by the second half of September only 30% of the total coho population remained in the northern area.

Coho salmon migration from the Sea of Okhotsk to Pacific Ocean began in mid September. By early November coho shoals left the Sea of Okhotsk. It appeared that migration was initiated when temperature decreases to 8°C (Erokhin 1987).

Coho salmon in western Kamchatka rivers migrated to the sea at age 1+ or 2+. Scale samples of rearing coho salmon (143 fish) collected in 1986

from the area to the south of 55°N were 40.6% age 1+ and 59.4% age 2+, with younger fish occurring closer to shore. Based on samples averaged over all years, the length of juvenile coho salmon during September-October ranged from 21-35 cm, with 60% of fish 28-30 cm and 17% less than 28 cm. Average length and weight during September ranged from 28.1 cm and 306.4 g in 1989 to 30.3 cm and 396.6 g in 1991. September growth rate of coho salmon ranged from 1.3 to 5.5 mm/day and 5 and 18.7 g/day. Coho salmon growth rates were the highest observed among the Pacific salmon genus. Growth rates for age 1+ coho salmon during the August - September period were believed to be higher than those for age 2+ coho, based on greater number of circuli observed for the initial year of marine growth.

Coho salmon juveniles fed actively, consuming mostly pollock fry (up to 95% of total prey). Fulton's index ranged from 1.34 to 1.49, and Clark's index from 1.19 to 1.34.

Chinook salmon. Chinook salmon reared in the eastern Sea of Okhotsk for an average of two weeks longer than coho salmon and were generally located east of 153°E. Chinook started moving from the areas located to the north of 55°N in the second part of September after water temperature decreased to 7-7.5°C. Chinook salmon did not occur north of 55°N in the Sea of Okhotsk after mid or late October (see Fig. 2). The exact timing of departure of chinook salmon from the Sea of Okhotsk to the Pacific Ocean is uncertain, but based on low catches in early November, chinook salmon probably left by late November.

In September, the majority of chinook juveniles were of length 22-25 cm and weight 150-220 g (Table 1). Growth rate during the fall was increasing but low relative to other species and ranged from 0.7-1.5 mm/day and 1.14-3.48 g/day. Feeding intensity of chinook salmon was lower than that of coho salmon, with the diet in 1986 consisting mainly of sandfish (62%). Fulton's index ranged from 1.34 and 1.47, and Clark's index ranged from 1.17 and 1.29.

The Bering Sea

Pink Salmon. The seaward migration of pink salmon in north-eastern Kamchatkan rivers occurred during June through the first half of July, with the peak of the migration occurring in the second half of June. During the early period of marine residence pink salmon occurred in nearshore areas as well as Lithke Strait. By late August pink salmon moved to offshore areas in the Bering Sea. The major concentrations of pink salmon juveniles at the time of offshore migration from the Lithke Strait occurred in

Fig. 3 Juvenile sockeye migrations in the eastern Sea of Okhotsk: A - (July) August, B - September, C - October. Arrows - migratory patterns; bold arrows - stable shoals without migratory manifestations; shaded areas- areas occupied by juvenile sockeye.

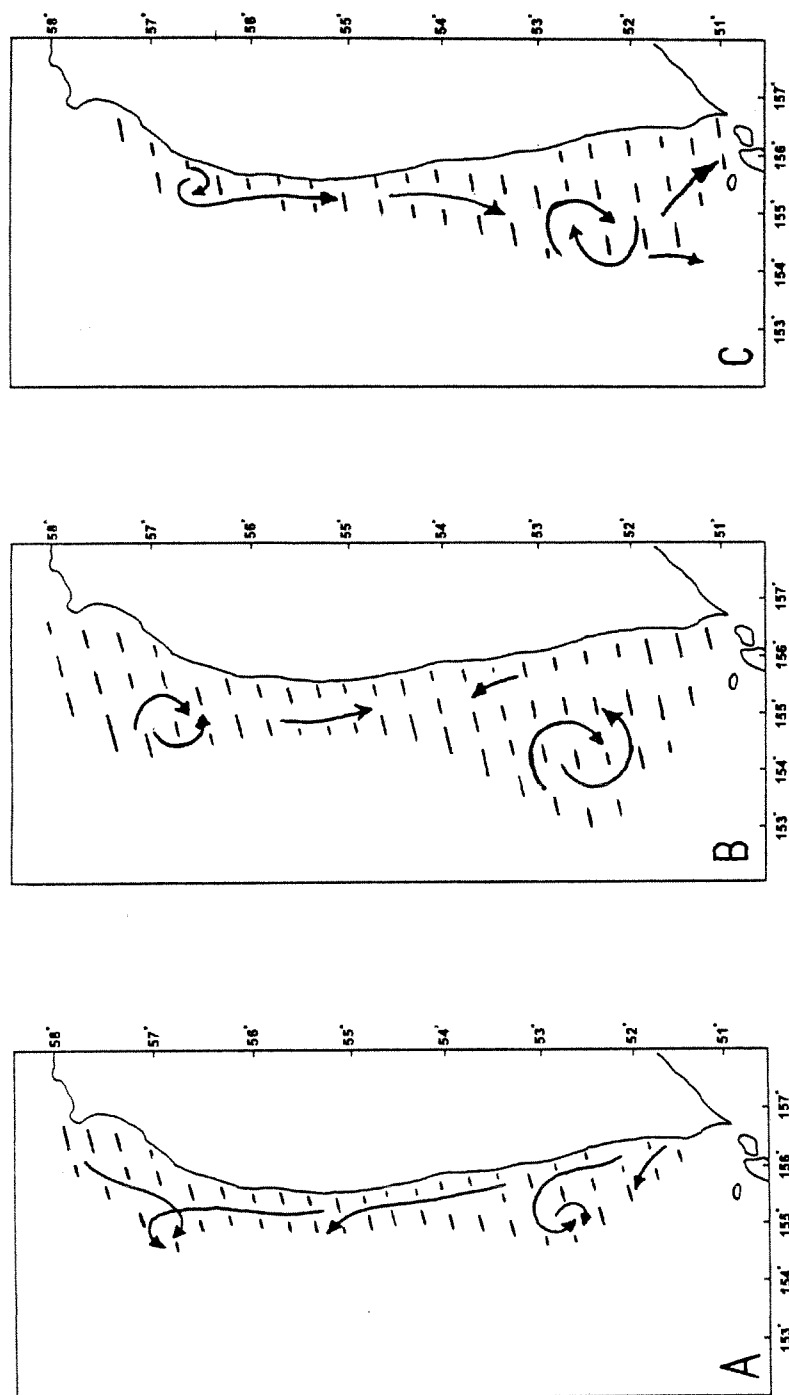
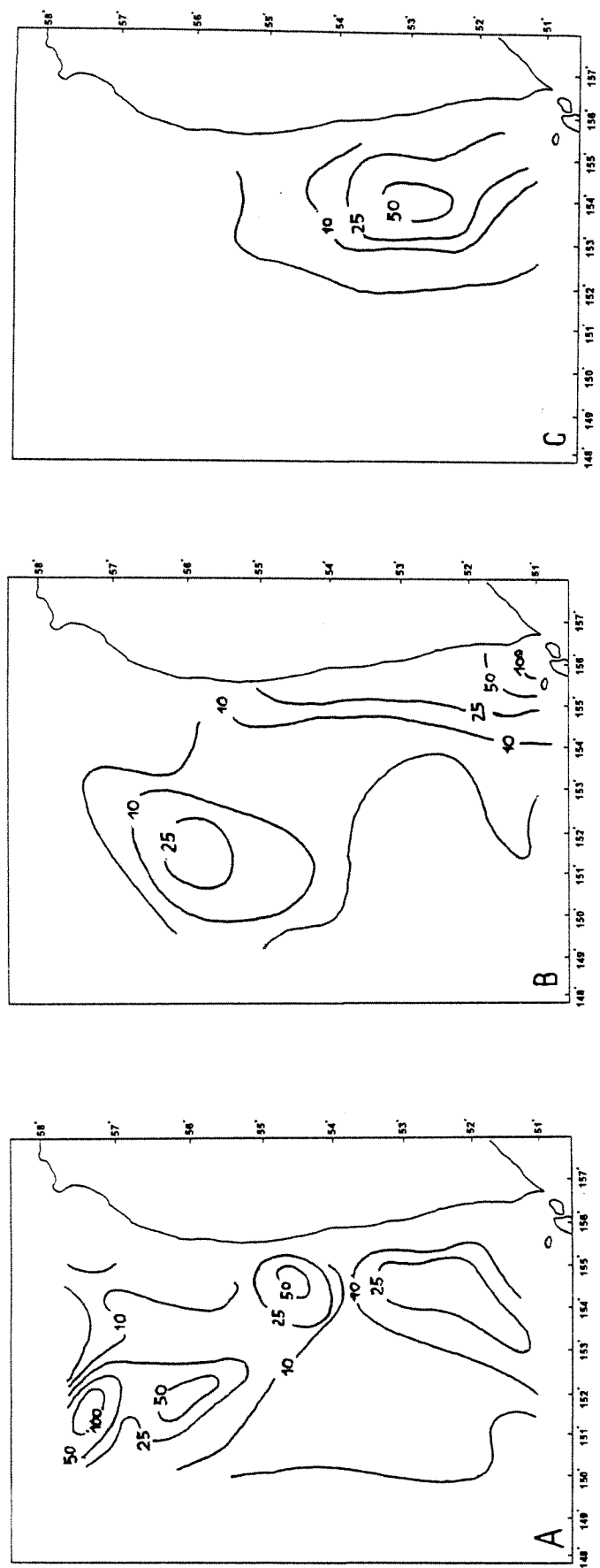


Fig. 4 Distribution of juvenile coho in the eastern Sea of Okhotsk, fish/rawl: A - late August-early September 1986; B - September-early October 1989; C - late September-first half of October 1991.



areas of active mixing at the boundary of sea currents in the vicinity of capes in the southern part of Karaginskii Bay. Later, the offshore distribution of pink salmon juveniles was determined by water temperature conditions and thickness of the surface mixed layer in the south-western Bering Sea (Fig. 5). Pink salmon migrated along isotherms and was southbound in years when isotherms had a north-south orientation and eastbound when isotherms had an east-west orientation (Karpenko et al. 1993). In September, pink juveniles were fully recruited to the rearing areas surveyed.

The length and weight of pink salmon juveniles were in the range 17-22 cm and 60-100 g, respectively (Table 1). The size of pink salmon juveniles varied among brood years, with fish of smaller and more variable size occurring in years of high pink salmon abundance. The highest growth rates (2.3-2.6 mm/day and 1.4-1.8 g/day) of pink salmon juveniles were observed in August in the Karaginskii Bay. During the period of offshore residence, pink salmon growth rates decreased to 1.1 to 1.8 mm/day and 1.7 to 2.8 g/day. Fulton's index ranged from 1.0 to 1.2. Growth rates and Fulton's indices were lower than those observed for pink salmon in the Sea of Okhotsk. These differences were due to diet and the length of the offshore rearing period. Thus, juvenile pink of the Bering Sea reared less in offshore waters and longer in coastal waters. Bering Sea pink salmon fed mostly on euphausiids while Sea of Okhotsk pink salmon fed on hyperiids and fish larvae of various species.

Chum Salmon. The seaward migration of western Bering Sea chum salmon was later than pink salmon, with the peak of the migration occurring in July. Chum salmon juvenile aggregations occurred closer to shore relative to pink salmon (Fig. 5), and presumably due to their later seaward migration and delayed offshore migration. Although chum salmon had a later migration, the distribution and migration routes were similar to those of pink salmon (Birman 1985). In September, chum salmon shoals seemed to be located on the peripheries of the most dense shoals of pink salmon. However, because of greater pink salmon abundance in this region, catches of chum salmon were lower and more dispersed.

In September, the length of chum salmon juveniles ranged from 17 to 21 cm and weight ranged from 50 to 100 g (Table 1). The average size of juvenile chum salmon was generally smaller than that of pink salmon, due to later entry to marine rearing areas and to lower growth rate. In September, average daily growth rates ranged from 1.8 to 2.3 mm/day and 1.3 to 1.6 g/day. The maximum growth rates observed for chum salmon occurred 10 to 15

days later than those of pink salmon. Fulton's index ranged between 1.15 and 1.22.

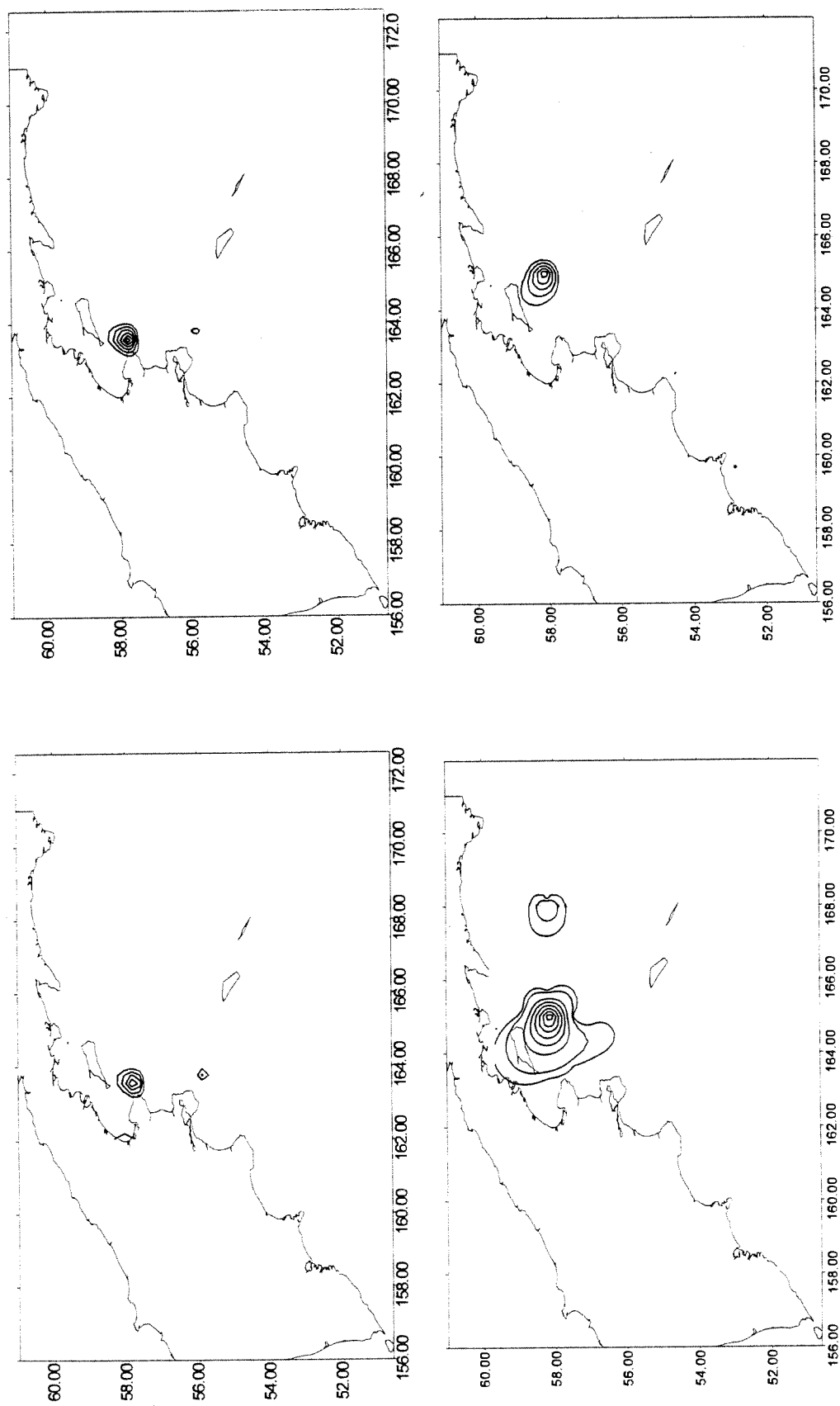
Because of the limited rearing areas and high density of competitors in the south-western Bering Sea, there was a potential for strong competition among pink and chum salmon. In years of high abundance for pink salmon, a decreasing similarity in diet occurred between these species. During periods of high pink salmon abundance, the chum salmon diet included lower energy prey such as tunicates, polychaete larvae, and fish larvae.

Sockeye Salmon. The peak of sockeye salmon seaward migration in north-eastern Kamchatkan rivers was similar to that in Kuril Lake, but was less protracted. The relative magnitude of the three freshwater age classes of sockeye juveniles in coastal waters was 67.4% age 0+, 30.2% age 1+, and 2.4% age 2+. During September, in high seas areas of the Bering Sea ages 1+ and 2+ predominated, and age 0+ sockeye salmon juveniles were rare due to their later timing of seaward migration. By mid September, the major juvenile sockeye shoals were located offshore, 80 - 120 miles south-east of Karaginskii Island. Juvenile sockeye (0 ocean age) were caught together with 1 and 2 ocean age fish which were often more abundant than juvenile sockeye. Sockeye juveniles occurred in this region until mid-October and then migrated offshore after water temperature decreased to 6-7°C.

The length of sockeye salmon juveniles ranged from 12 to 22 cm and weight ranged from 70 to 120 g (Table 1). In general, older, larger fish tended to be farther offshore. There was little difference in mean size of juvenile sockeye between years, with observed differences due to variability in timing of survey and migration timing. The highest juvenile sockeye salmon growth rates were observed in September, and ranged from 1.8 to 2.2 mm/day and 1.3 to 1.8 g/day. Growth rates in coastal waters were generally lower and averaged 1.5 mm/day and 0.5 g/day. Fulton's index ranged 1.20 to 1.32. In the Bering Sea high seas' area the juvenile sockeye salmon diet consisted of euphausiids, crab and hyperiid larvae. In Bering Sea coastal waters the sockeye salmon diet consisted of small copepodes and fish larvae.

Coho Salmon. The seaward migration of coho salmon in eastern Kamchatkan rivers was similar to that of chum salmon, with the peak of the migration occurring in July. The relative magnitude of the four freshwater age classes of coho salmon juveniles in coastal waters was 3.0% age 0+, 50.8% age 1+, 44.9% age 2+, and 1.3% age 3+. In offshore Bering Sea areas freshwater age 1+ and 2+ were

Fig. 5 Distribution of pink (left) and chum (right) juveniles in the south-western Bering Sea. Above - 1989, and Below - 1991.



predominant. Distribution of coho salmon is relatively even, although it may be higher in the south of the region, which may be associated with the common migratory pattern of all salmon species. Coho salmon are primarily concentrated around junctions of oceanic currents (commonly in the peripheral zones of shoals of other salmon juveniles), the venue for the major prey of coho salmon, fry of sandfish, pollock and other fish species. The coho salmon diet consisted of pollock and sandfish larvae, crab larvae and zooplankton (euphausiids, hyperiids and copepods).

In September, the length of most coho salmon juveniles was in the range 23 to 27 cm and weight in the range 150 to 200 g. Older and larger fish generally occurred offshore in the southern areas of the survey area, and younger coho occurred closer to shore. Like coho salmon of the Sea of Okhotsk, coho juveniles of the Bering Sea had higher growth rates than juveniles of other salmon species, and in September, ranged from 2-2.7 mm/day and 3-4 g/day. Growth rates were similar among freshwater age groups. Fulton's index of juvenile coho salmon in coastal areas ranged from 1.30 to 1.40, and in offshore areas ranged from 1.45 to 1.58.

Chinook Salmon. The seaward migration of chinook salmon occurred later than other salmon species, with the peak of the migration occurring in July-August. The relative magnitude of the three freshwater age classes of chinook salmon juveniles in coastal waters was 3.5% age 0+, 71.9% age 1+, and 24.6% age 2+. In the western Bering Sea, chinook salmon spent longer periods in coastal waters than other species, and were found within 20-50 miles of river estuaries in mid October. It is believed that juvenile chinook migrated from coastal waters to the offshore areas of the south-western Bering Sea in late October when water temperature decreased to 6.2-6.5°C.

In September, the length of chinook juveniles ranged from 18 to 23 cm and weight ranged from 70 to 160 (Table 1). The growth rate was low relative to other species and was estimated to be 1.5 mm/day and 3.5 g/day (or 3-4% per day). The maximum growth rate occurred in the mid August and averaged 1.84 mm/day and 2.32 g/day (or 6-7 % per day), and is conditioned by the shift to rapacious feeding among chinook juveniles, which prevails thereafter. The diet of juvenile chinook salmon included juveniles of smelt, herring, pollock, and sandfish, with minor occurrence of larger crustaceans. Fulton's index of chinook salmon in coastal waters ranged from 1.15 to 1.25, and in offshore areas ranged from 1.23 to 1.35.

FORECASTS OF PINK SALMON RUNS BASED ON JUVENILE ABUNDANCE DURING THE FALL PERIOD OF OCEAN RESIDENCE

The highest mortality of salmon juveniles occurs during the first months of ocean residence. By fall, Kamchatkan scientists believe that abundance in ocean rearing areas has stabilized and further mortality occurs at a constant rate that varies little among years. Because of this, a method of forecasting future runs of salmon was developed based on estimation of juvenile salmon abundance in the fall following migration to ocean rearing areas. Estimates of juvenile abundance were based on trawling with standardized methods on a standard station grid covering Kamchatkan coastal waters of the Sea of Okhotsk and Bering Sea. In fall, abundance of salmon juveniles of all species varied considerably in both the Sea of Okhotsk and Bering Sea survey areas. In the eastern Sea of Okhotsk, salmon abundance fluctuated between 150 and 300 million individuals, and in the western Bering Sea between 70 and 150 million individuals. Pink salmon constitute the majority of the catches in both areas, and abundance estimation is believed to be of great importance in preseason forecasting of adult salmon runs.

The trawl survey was carried out over a considerable area in a relatively short time and therefore is believed to provide a quantitative evaluation of juvenile salmon distribution and abundance (Shuntov et al. 1986; Shuntov 1989a,b; Kislyakov 1990; Erokhin et al. 1990). In two weeks, two research vessel covered with a grid of 100-120 survey stations, an area of over 600,000 km² in the Kamchatkan coastal waters of the Sea of Okhotsk and in the Bering Sea. The optimum period for conducting the survey was September through the first 10 days of October, after juvenile fish of Kamchatkan salmon stocks had completed their migration from coastal waters to the offshore waters.

In the western Bering Sea, the accuracy of preseason forecasts based on the juvenile salmon survey depended on strict observance of standard surveying methods and whether the survey covered the marine distribution of juvenile salmon. The origin of juvenile salmon in the western Bering Sea, in contrast to the eastern Sea of Okhotsk, is from northeastern Kamchatkan rivers. Results of pink salmon run forecasts for north-eastern Kamchatka are presented in Table 3. Note that preseason run forecasts were made for 1986 to 1992 and used survey data collected with the 54.4/192 m special trawl that was first deployed in the 1985 survey. Forecasts with satisfactory accuracy (% deviation of adjusted forecast and actual run less than 25%)

Table 3. Juvenile pink salmon abundance and runs to the Kamchatka northeastern rivers, million fish.

Survey Periods	Juvenile Abundance	Runs Forecast		Actual Runs
		preliminary, 2 yr advance	adjusted, based on trawling survey results	
1981 26.08-09.09	2.6	6.6	n/a	15.1
1982 optimum	45.2	46.0	n/a	40.5
1983 -	n/a	13.0	-	24.5
1984 09-27.08	7.05	30.2	n/a	22.0
1985 -	n/a	14.0	-	4.3
1986 optimum	40.0	26.1	46.0	54.8
1987 optimum	1.2	8.3	2.0	9.1
1988 optimum	7.5	42.1	65.0	67.0
1989 optimum	26.7	12.6	21.2	27.1
1990 optimum	87.0	54.4	70.0	99.2
1991 optimum	26.9	10.0	10.5	9.8
1992 03-14.10	-	41.3	41.3	65.0

occurred for 67% of years where juvenile surveys were conducted (1986-91), 75% for brood years of high abundance (see Fig.6).

The accuracy of the preseason forecasts were poor for some years, due to the following conditions:

- 1- In years when juvenile abundance was low (less 10 million), the relative error in surveys of juvenile abundance is high, e.g. in 1981 and 1987.
- 2- For certain years (i.e., 1981 and 1984), the survey occurred prior to the time that migration from coastal rearing areas was complete.
- 3- Standard sampling methods were not observed during the 1988 survey. In 1988 the ship was equipped with larger trawl doors instead of standard doors (4.2 m² instead of 3.3 m²). This slowed the trawling speed and decreased the distance between the vessel and the trawl so that the net could not be deployed near surface.

Similar problems may have occurred in the trawl surveys in the Sea of Okhotsk; however, the accuracy of forecasts of western Kamchatkan salmon runs based on juvenile abundance was mainly affected by the presence of juvenile salmon from Sakhalin, the Amur River, and northern coast of the Sea of Okhotsk. Because stock identification methods were not available, it was not possible to sort out the presence of juveniles originating from rivers outside western Kamchatka. Therefore the survey results give only the data on overall juvenile pink abundance rearing in Kamchatkan coastal waters of the Sea of Okhotsk. Evaluation of juvenile pink originating in Kamchatka rivers and lakes is made depending on the type of pink salmon distributed, as specified above.

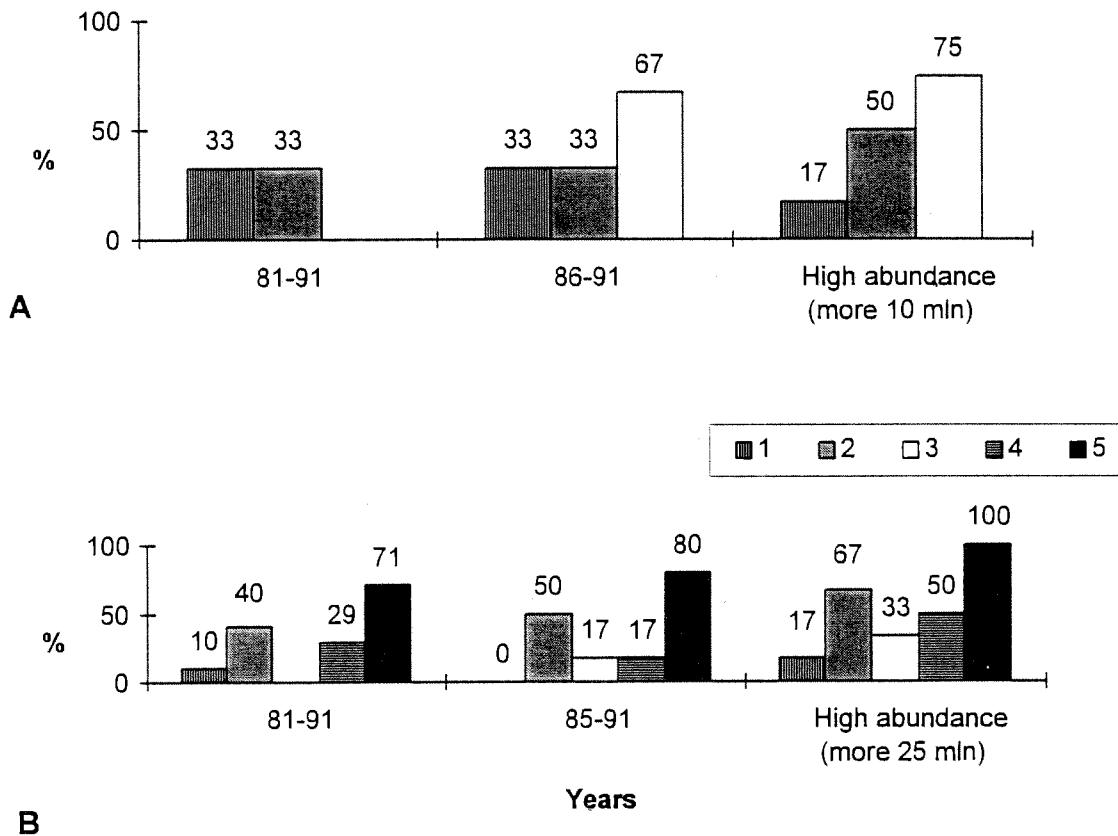
Accordingly, the *aboriginal* type of pink juveniles distributed in the East part of the Sea of

Okhotsk were identified by the following criteria: 1 - high return of spawners to the rivers of the West Kamchatka; 2 - small average size of juveniles (length 17-22 cm, weight less then 70 g); 3 - high variability of body size: from 11 to 30 cm; 4 - significant number of individuals smaller then 18-19 cm (>50%); 5 - the size of juveniles increased from the shore of Kamchatka to the offshore.

The *immigratory* and *intermediate* types were identified by the following criteria: 1 - low return of spawners to the rivers of the West Kamchatka; 2 - large average size of juveniles (length 21-23 cm, weight 80-120 g); 3 - low variability of body size: from 15 to 28 cm; 4 - number of individuals smaller than 18-19 cm, less than 50 % of total abundance; 5 - the size of juveniles decreased from the shore of Kamchatka to the offshore. Criteria 2-5 were thought to be caused by differential migration of early emerging and larger sized individuals from the east Sakhalin rivers to the west Kamchatkan shelf.

For years of *aboriginal* distribution (i.e., 1982 and, partially, 1983), the eastern Sea of Okhotsk was primarily occupied by western Kamchatka origin pink salmon. Thus, in fall 1982, 128.5 million juvenile pink salmon were estimated ($K_{catch}=1$), while total return of adult pink salmon to western Kamchatka 1983 was 141.3 million. For years of *immigratory* distribution (i.e., 1984, 1986, 1990), the Sea of Okhotsk was primarily occupied by juvenile pink salmon that originated outside of western Kamchatka. In fall 1990, 92.7 million juvenile pink salmon were estimated, while the total run of adult pink salmon to western Kamchatka in 1991, was 2.0 million fish. In 1991, the run of pink salmon to the rivers draining into the northern Sea of Okhotsk and Sakhalin Island and excluding the Amur River, was 150 million fish. So assuming perfect assessment of abundance, negligible overwinter mortality, and no contribution

Fig. 6 Frequency of satisfactory forecasts for pink salmon in northeastern (A) and western (B) Kamchatka: 1 - traditional forecast; 2 - forecast based on the trawling survey; 3 - adjusted forecast; 4 - forecast based on the linear growth rate analysis; 5 - forecast based on body length analysis.



of Amur River pink salmon, 60% of juveniles from non western-Kamchatkan rivers reared in Kamchatkan coastal waters the previous year, while juveniles from western Kamchatkan rivers accounted for 5%. For years of mixed or intermediate distribution (i.e., 1981, 1985, 1987, 1989, 1991, 1995) it is necessary to sort out pink salmon of western Kamchatka origin.

Table 4 presents the evaluation of the preseason forecasts of western Kamchatka pink salmon runs based on the previous fall juvenile abundance. There were significant errors in the forecast using the aggregate juvenile abundance during years with *immigratory* and *intermediate* distribution of pink salmon stocks. We attempted to sort out western Kamchatka pink salmon assuming that smaller pink salmon within 60 miles of the coast were of western Kamchatka origin and those outside of 60 miles were mixtures of stock. The proportion of Western Kamchatka pink salmon was estimated as the proportion of smaller sized fish in the aggregate stock size distribution.

Satisfactory accuracy (percent deviation less than

25%) of the adjusted forecast based on the trawl surveys occurred in 17% of years where trawl survey was used (Table 4) and represented a slight improvement over that observed for traditional forecasting. Satisfactory accuracy for brood years of high abundance was 33% using the adjusted trawl survey forecast and 67% using traditional forecast method (see Fig.6).

Fish growth rates and size have been observed to be an indicator of run strength and used to forecast pink salmon runs in the Karaginskii area of northeastern Kamchatka (Karpenko 1985) and for pink and chum salmon runs in Iturup Island (Kaev and Chupakhin 1986). An attempt was made to apply this method to western Kamchatka pink salmon. It was believed that pink salmon in the area adjacent to the Kamchatka Peninsula, 52-55°N and 152-155°E, were likely to be of western Kamchatka origin. Pink salmon growth rates during September in this area varied between 1.28 and 2.51 mm/day, and average length varied between 20 and 25 cm. Regressions of daily growth rate and length and western Alaska pink

Table 4. Juvenile pink salmon abundance and runs to the Kamchatka western rivers, million fish.

Survey Periods	Juvenile Abundance		Runs Forecast		Actual Runs
	east of 150°E	Western Kamchatka	preliminary, 2 yr advance	adjusted, based on trawling survey results	
1981 optimum	15.5	15.5	28.0	n/a	37.3
1982 26.09-15.10	128.5	128.5	55.0	n/a	141.3
1983 optimum	11.0	11.0	41.6	n/a	87.0
1984 optimum	17.7	17.7	17.0	90.0	7.6
1985 optimum	9.2	9.2	89.0	35.0	36.6
1986 optimum	50.3	15.0	15.9	15.0	1.7
1987 optimum	24.7	24.7	37.7	37.7	26.0
1989 optimum	165.1	24.8	48.1	80.0	26.3
1990 optimum	92.7	19.4	6.0	6.0	2.0
1991 optimum	36.3	28.9	30.0	30.0	15.9

salmon abundance were developed:

$$N = 66.27 - 26.92l$$

and

$$N = 245.66 - 9.75L, \text{ where}$$

N - salmon return, millions;

l - daily linear growth rate, mm;

L - average length in September, cm.

The above equations were used to forecast abundance and improved the accuracy of western Kamchatka pink salmon forecasts considerably (Fig. 6).

CONCLUSIONS

Forecasts of pink salmon runs based on trawl surveys of juvenile abundance the previous fall are more accurate than traditional forecasts based on brood year returns. This method provide an adjustment to traditional forecasts 8 to 9 months in advance of the run and has potential for application to other species' forecasts. Trawling survey have been successfully applied in identifying salmon natal migration routes (Shuntov et al. 1993a,b). The criteria for optimum trawling conditions for surveys of juvenile salmon abundance during the fall season included:

1. Survey conducted from September 1 through October 10.
2. Trawl towed between 4 to 5 knots;
3. The distance between vessel and trawl mouth be maintained at 200 m;
4. The upper rope of the trawl must emerge from the water surface.

The juvenile salmon abundance should be considered with auxiliary biological data on juvenile salmon, presence of stocks in the survey area from other areas in Sea of Okhotsk, and in the Bering Sea very weak brood year runs.

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Incidental By-catch of Pacific Salmon During Russian Bottom Trawl Surveys in the Bering Sea and Some Remarks on its Ecology

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Radchenko, V.I., I.I. Glebov. 1998. Incidental by-catch of Pacific salmon during Russian bottom trawl surveys in the Bering Sea and some remarks on its ecology. N. Pac. Anadr. Fish Comm. Bull. No. 1: 367-374

The data on Pacific salmon by-catch in bottom trawl surveys of the Bering Sea are regarded. During 1974-1991 260 salmonids, mostly chinook and chum salmon, were collected. Chinook and chum salmon vertical distribution were discussed in relation to features of their feeding habits.



INTRODUCTION

It is traditionally considered that the Pacific salmon dwells the upper pelagic layer, mainly during the sea-run phase of its life (Machidori 1966; Birman 1985). However, salmon are by-caught frequently during the groundfish trawl fisheries, particularly the walleye pollock fishery. Since the early 1970s, the Bering Sea has become the chief region of the walleye pollock fishery and has been the major fishery until the early 1990s (Shuntov et al. 1993). Rather comprehensive statistics exist on Pacific salmon by-catch on the eastern Bering Sea shelf and continental slope (Low and Berger 1994). In some years the salmon by-catch reached 120 thousand fish, or about 0,3 thousand tons. In Russian waters such information is missing due to the limited monitoring of groundfish fishery.

To a certain extent, the data from scientific surveys mitigates the information deficit on Pacific salmon by-catch in bottom trawl fisheries. Since 1974, the Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO) has conducted more than 110 scientific and research cruises in the Bering Sea. Data from these cruises are kept in the TINRO-center archive. Until the early 1990s, the bottom trawl survey was one of the main methods of scientific and fisheries information collection. In the 1970s and 1980s such information was collected no less than in 60% of all expeditions. Our report is devoted to analysis of this archival information.

MATERIALS AND METHODS

Examination of the data from bottom trawl surveys made during the 1970s and 1980s shows that information on by-catch species appears to be both scarce and approximate. In addition, in some cases the Pacific salmon were not recorded in catches due to fear of penalties for unsanctioned by-catch. For this reason, information from only those bottom trawl surveys where salmon by-catch data were taken was used for the analysis.

The information file contained data from 21 cruises from 1974 to 1991 which encompassed the entire period: 5 cruises in 1974-1980, 9 - in 1981-1985, 7 - in 1986-1991. To a great degree the data reflected the intensity of research activity in the Bering Sea region, rather than the salmon stock dynamics. In these expeditions 2,880 bottom and 469 near-bottom (in contact with the ground) trawl operations were executed. Salmonid fishes were captured in 133 cases (4.0%). The bottom trawl operations with salmon by-catch were conducted at a depth range of 20-1,100 m, with most above 350 m. Near-bottom trawls were made at depths of 40-360 m, with depth recorded as that of the upper trawl panel position. In some cases trawling was conducted at several tow depths, and it was assumed that salmon were caught at the upper-most depth. The duration of trawl towing varied from 0.5 to 4.25 hours.

During surveys, the whole size spectrum of

trawls were used. Bottom trawls had vertical openings from 3 to 8 m, and horizontal openings from 20 to 30 m. Pelagic trawls had vertical openings in near-bottom operations from 20 to 30 m, and horizontal openings from 35 to 80 m. On the whole, 256 salmon specimens and 4 chars were collected, 97 from near-bottom trawl operations.

RESULTS

Among the salmon by-catch, 113 specimens (44.9%) were identified as chinook, 100 (39.1%) as chum, 6 (2.3%) as pink, and 3 (1.2%) as coho. Thirty-three fish (12.9%) were identified as sockeye, but we considered the identification to be doubtful. Most of the sockeye identifications (31 fish) were specified for the central Anadyr Gulf and were made by the same collector during one cruise. Chum salmon were the principal species found in the by-catch of other vessels operating in the same location at the same time. Besides, sockeye do not occur on the northern Bering Sea shelf even in pelagic layers (Shuntov 1989; Radchenko and Chigirinsky 1995). This is likely related to the sockeye adherence to the thermocline layer in the deep-sea zone (Radchenko 1994). The occurrence of 2 sockeye specimens on the south-eastern slope seems more possible. Furthermore, the same occurrences were considered in Low and Berger (1994). The coho salmon occurrences on the western Bering Sea shelf (south of the Navarin Cape) seem doubtful to us as well. As indicated by salmon body length (up to 78 cm), these specimens should probably be classified as chinook. In addition to the species mentioned above, an unclassified juvenile salmon with body length 17 cm and weight 100 g was also caught in one case. The by-catch of chars were identified to species as Dolly varden (2 specimens), in one case and to genera (*Salvelinus*) in another.

Areas with Pacific salmon by-catch have been localized in the Anadyr Gulf, on the shelf and upper continental slope of the Oljutorsky-Navarinsky region (Fig. 1- 4). Outside of this area, in summer of 1984 seven chum specimens were caught in southern Karaginsky Bay (Fig. 2) and in autumn and winter 2 chinook were caught in the Oljutorsky Bay (Fig. 3, 4). Single salmon catches (chinook in 7 of 9 cases) were found along the 200-meter contour on the whole eastern Bering Sea shelf in winter (Fig. 4).

As a whole, 68 of 71 salmon specimens caught in winter (95.8%) were chinook. Also 32 chinook specimens were caught in an area not further than 100 miles from the Navarin Cape during the fall, and an additional 14 salmon were caught in summer and 2 in the spring. Almost all chum, and both pink

salmon were caught in summer and fall - from July to October inclusively. In July, chum were encountered in the Karaginsky Bay and a few were by-caught more generally in the northern Bering Sea (a distance of up to 200 miles from the continental coast). In August, chum occurred mainly in catches in the near-shore zone. In September, chum were chiefly concentrated in the western Anadyr Gulf (opposite the Anadyr River estuary) and in October were found near the Navarin Cape and southwards along the shelf edge. Pink salmon by-catch occurred in July of 1974 in the Navarin region and in September of 1989 in the Shirshov Ridge area.

Chinook by-catch specimens ranged in body length from 21 to 130 cm, with a modal group of 60-80 cm representing 67.6% of the total number (Fig. 5). Chum salmon were mostly represented by large maturing specimens with body lengths ranging from 25 to 78 cm and a modal length of 60 to 65 cm (34%). Fish with a body length above 60 cm comprised more than three-quarters of the chum number. A dependence of the frequency of salmon occurrence by time of day was not evident. Possibly, some part of the salmon stock occupies the near-bottom layers throughout the day.

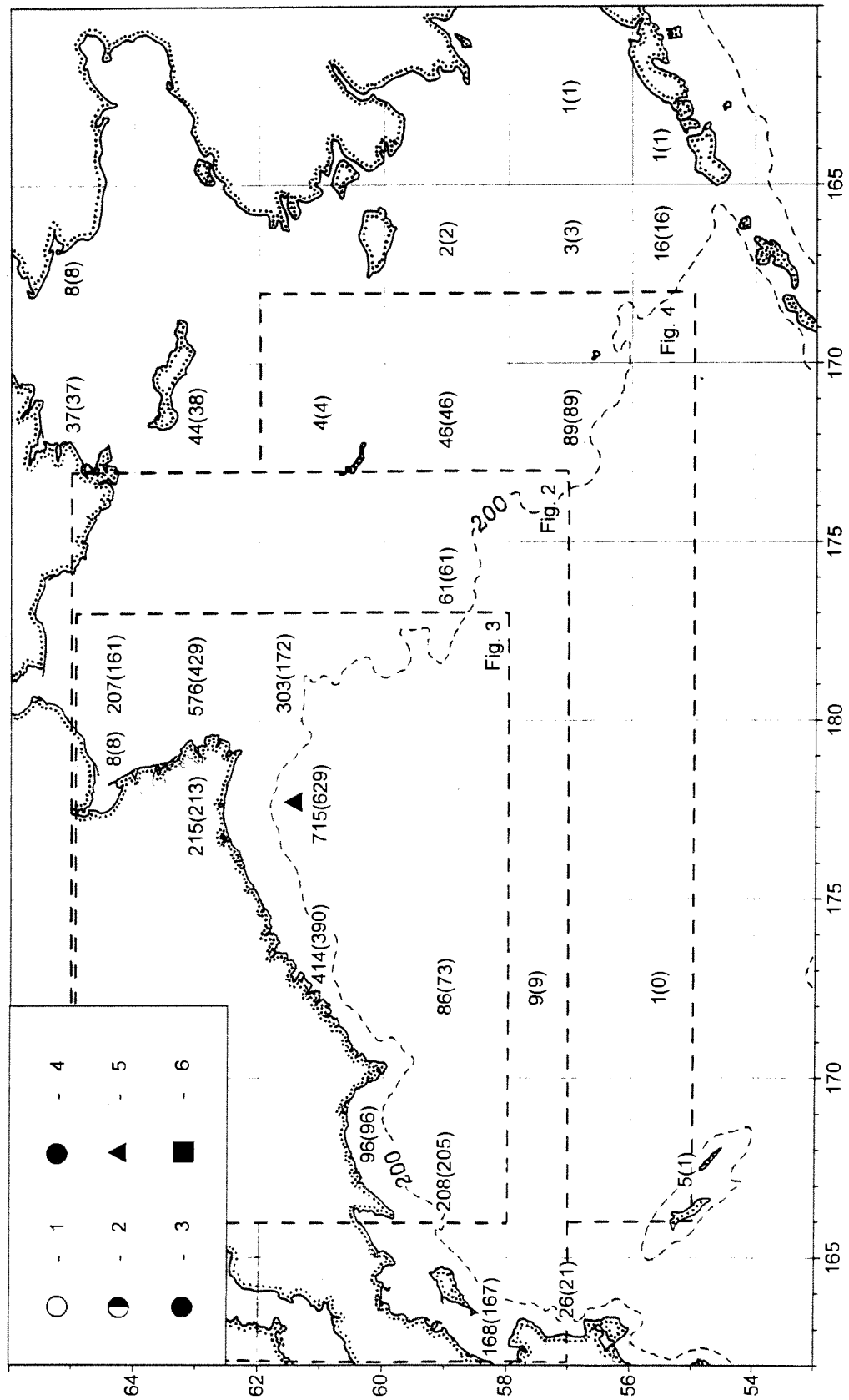
DISCUSSION

Because of the small vertical opening of a bottom trawl, it is unlikely that salmon are by-caught during the trawl retrieval operation in large numbers. Besides, chinook salmon generally occur in the near-bottom zone (up to 110 m) (Healey 1991).

The number of immature chinook of ocean age 2 or older are likely significantly underestimated during the pelagic trawl surveys. For instance, in autumn 1987 the calculated number of chinook with a body length above 40 cm contributed 9.0%, and above 50 cm 2.3% of the total numbers. Later in the year, chinook salmon begin to leave the Russian exclusive economic zone and the portion of larger sized specimens increases with the oceanward migrations of smaller individuals. In late October - November of 1990 the portion of chinook above 50 cm contributed 17.0% of the total species number, and in November - December of 1988 31.6% of the total. Therefore, part of the chinook stock likely spends winter in near-bottom layers of the northern Bering Sea.

A synthetic curve combining data from the length distribution of chinook salmon in the western and central Bering Sea pelagic zone throughout the year but seasons mainly summer and autumn has only one well-expressed peak. It coincides to the number of chinook specimens spending their second marine year in the pelagic zone (Fig. 5). On the contrary, larger chinook aged 1.2 - 2.2 mainly appear

Fig. 1 Distribution of the groundfish survey efforts in the Bering Sea, 1974-1991. Ciphers show the total number of bottom and near-bottom trawl hauls in rectangles 2°N per 5°E and W, in brackets-bottom hauls only. Triangle shows single salmon catch in spring. Position of areas with salmon catches in other seasons are given. The symbols for Fig. 1-4 are following: 1 - first month of season; 2 - second month; 3 - third month; 4 - Chum; 5 - Chinook; 6 - Pink.



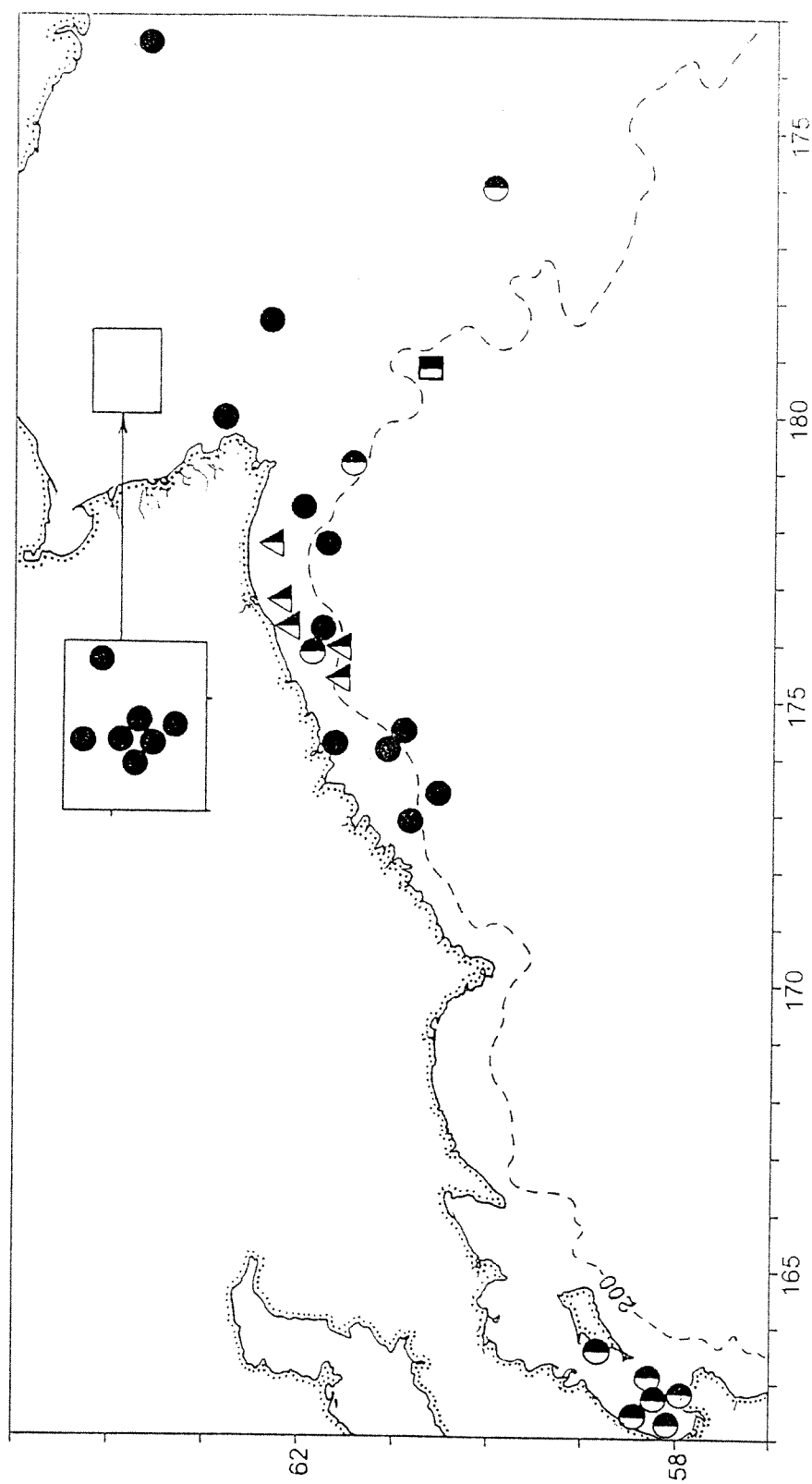
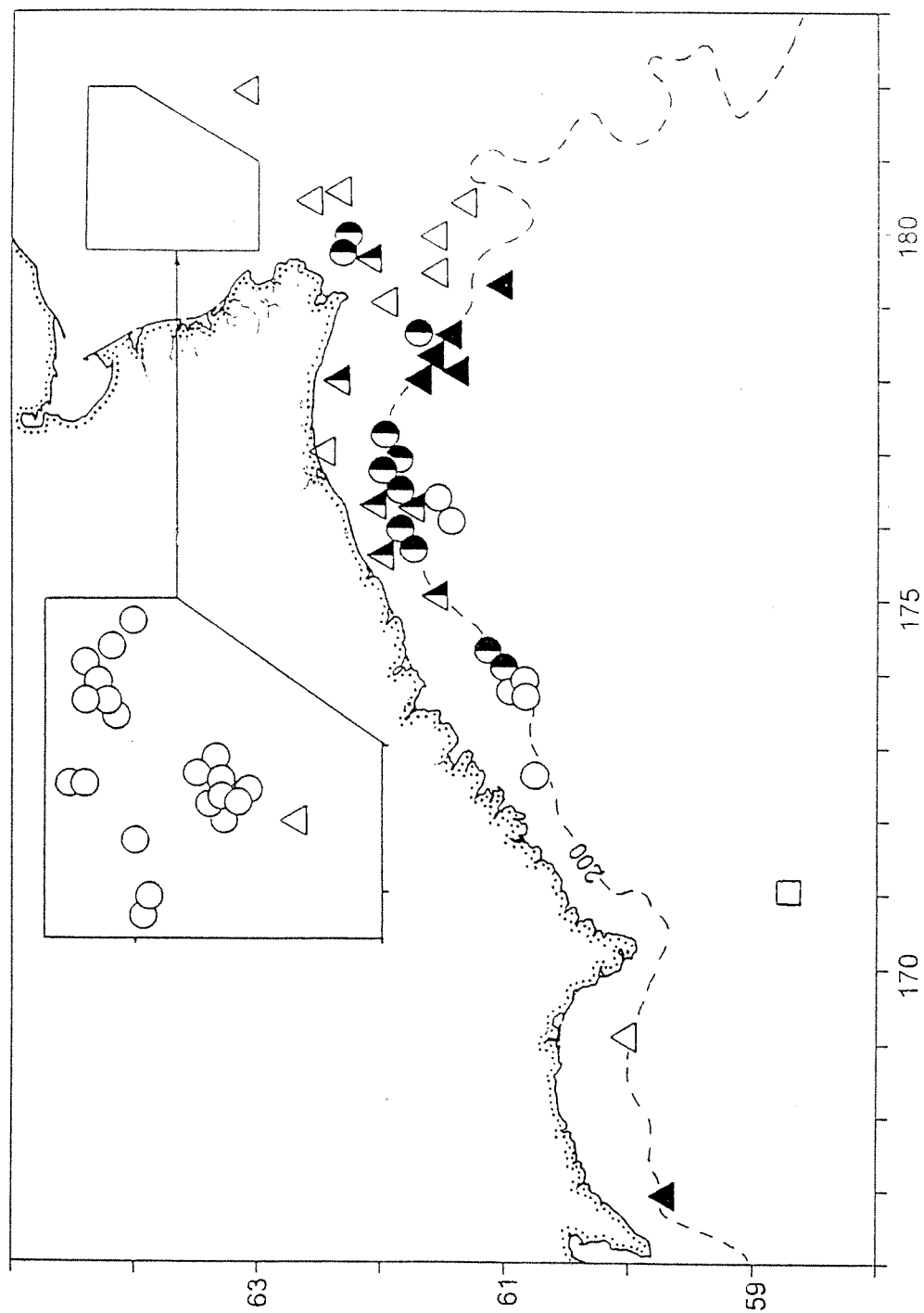


Fig. 2 Pacific salmon catch distribution during the groundfish surveys in the Bering Sea in summer. Legends as on Fig. 1.

Fig. 3 Pacific salmon catch distribution during the groundfish surveys in the Bering Sea in autumn.
Legends as on Fig. 1.



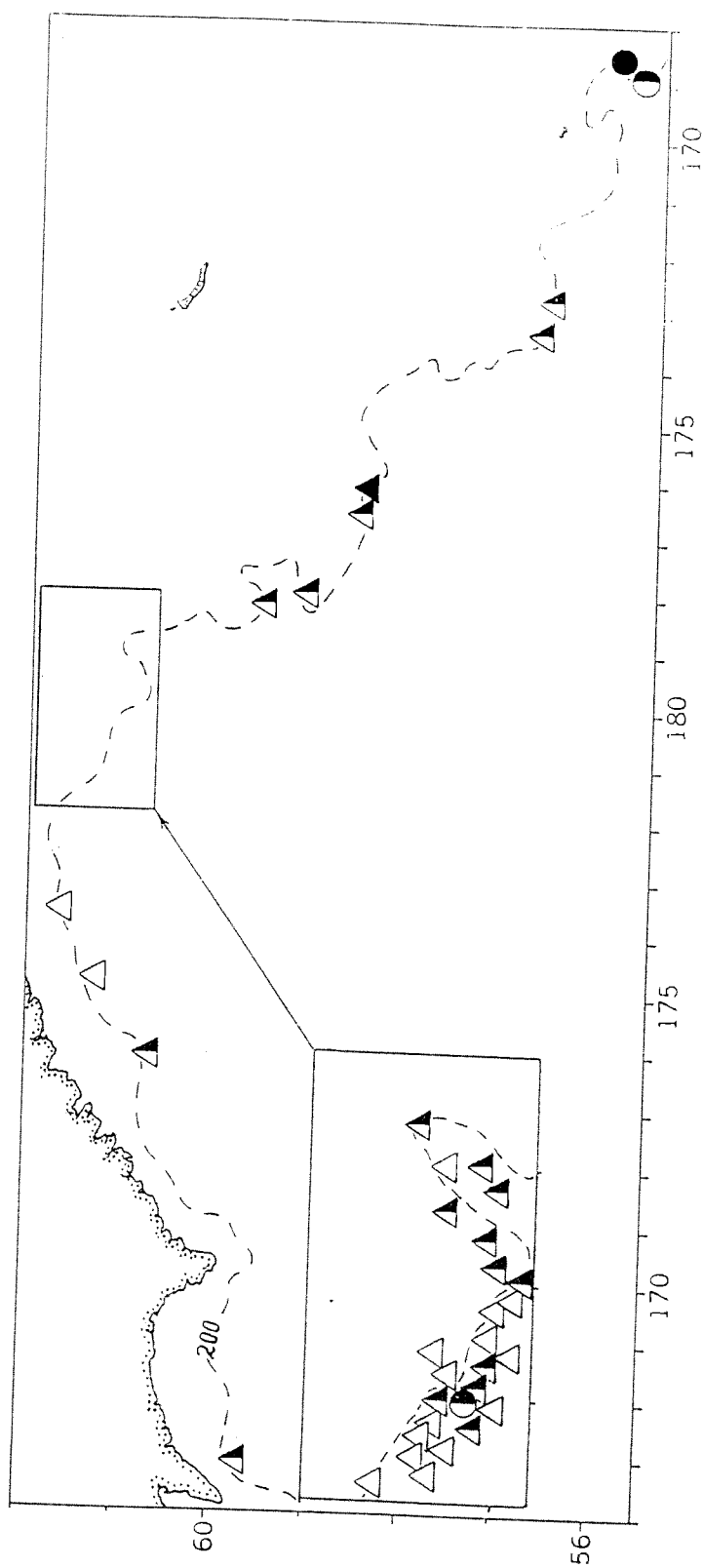
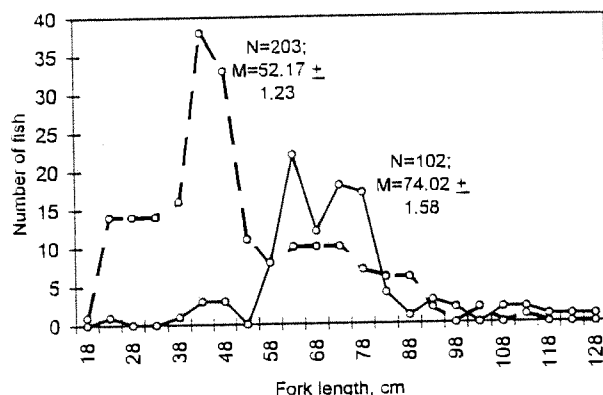


Fig. 4 Pacific salmon catch distribution during the groundfish surveys in the Bering Sea in winter. Legends as on Fig. 1.

Fig. 5 Length distribution of chinook salmon from the bottom (solid line) and pelagic (dotted line) trawl catches, 1974-1993.



in the bottom and near-bottom trawl catches. After their third year at sea, chinook salmon in the Bering Sea usually mature and this is reflected by the decreasing occurrence of larger fish in trawl catches (Fig. 5).

The organisms at near-bottom layers of the outer shelf, in particular adult squid *Berryteuthis magister*, predominate in the chinook diet composition (Radchenko and Chigirinsky, 1995). At the same time, juvenile squid dwell chiefly in pelagic deep-sea regions (Radchenko 1992) and constitute the main part of chinook diet during the second marine year. Also euphausiids are an important component of chinook diet in pelagic deep-sea regions (Chuchukalo et al. 1994). Thus, features of chinook distribution coincide well with the distribution of their primary food organisms.

Large, mostly maturing chum salmon occur in near-bottom layers. It is interesting that during pelagic trawl surveys the largest chum specimens are caught in the near-shore zone. Chum salmon of 0.2 age occur over the outer shelf and continental slope and yearlings in the offshore Bering Sea (Sobolevsky et al. 1994). During May-June in the Gulf of Alaska, chum prefer the 53-65 m layer (Manzer 1964). During the May-June period 80-100% of the chum salmon were maturing. Then, in late June to early July, the percentage of immature chum increased to 50-58.3% and during day-light hours, a portion of the chum stock was found in a layer from 0 to 26 m and another layer (likely maturing specimens) below 53 m (Manzer 1964). It must be noted that the food spectra differ noticeably between immature and maturing chum (Gorbatenko and Chuchukalo 1989).

Chum adherence to deeper sea layers in warm seasons may be connected to the dynamics of salmon maturation in the relatively cold temperatures of near-bottom water. The increase of efficiency of consumed food utilization is known for fish at low

positive water temperatures in comparison with higher ones (Smith et al. 1986). It is possible that the change-over between somatic and gonadal growth appears in such conditions for maturing chum. In any case, the metabolic costs are noticeably reduced for salmon in conditions of low oxygen concentrations and temperatures of 3-5°C (Hoar et al. 1979). This is reflected in the lowest values of the maintaining ration in such conditions (Brett et al. 1969) cited after Hoar et al., 1979.

Existing data on the intensity of walleye pollock fishing in the Navarin region in 1980s - 1990s allow us to estimate the value of Pacific salmon by-catch. In 1979 - 1988 the walleye pollock catch varied in the Navarin region from 218 to 855x10³ tons, until in 1995 declined to 135x10³ tons (Wespestad 1995). The long-term average was 379x10³ tons. Average catch per unit effort for large-tonnage vessels was 19.1 tons for 1979 - 1988. Thus, no less than 19.9 thousand trawl operations have been conducted annually for the determination of the mean value of walleye pollock catch. Since the walleye pollock fishery is usually conducted by pelagic trawls in the near-bottom layer, the annual Pacific salmon by-catch can be estimated at approximately 4.1 thousand fish (chinook and chum), or a salmon biomass estimate of roughly 12.2x10³ tons based on the mean weight of salmon specimens for the south-eastern Bering Sea shelf (Low and Berger 1994). This value is insignificant in comparison with either natural salmon mortality or commercial catches. The groundfish trawl fisheries in other regions of the western Bering Sea shelf and on other species are characterized by significantly lower fisheries effort.

CONCLUSIONS

The groundfish trawl fisheries in the shelf and continental slope zones of the Bering Sea do not appear to measurably affect the stock conditions of salmon feeding in this region. However, observations of the cases of salmon by-catch suggest some interesting features of chinook and chum salmon ecology. Salmon vertical distribution in the ocean varies among species and among age chum within species as well. These differences are perhaps related to differences in trophic linkages and metabolism and among chum age groups within species as well.

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Artificial Propagation of Chum Salmon (*Oncorhynchus keta*) in Korea

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Seong, K.B. 1998. Artificial propagation of chum salmon (*Oncorhynchus keta*) in Korea. N. Pac. Anadr. Fish Comm. Bull. No. 1: 375-379

The artificial propagation of salmon in Korea began in 1913. Since 1984, the survival rate and number of juvenile fish released has increased as a result of research and innovations in fish culture methods. As a result, the annual in-river harvest of salmon increased to about 35,000 fish in 1995. In 1996, 16 million juvenile chum salmon (*Oncorhynchus keta*) were released from Korean hatcheries. From 1984 to the present, chum salmon adults have been captured in the Namdae River, Yangyang, Kangwondo. Through this period the captured fish were examined to determine: age, length, weight, sex, and run timing. The study was conducted at the Yangyang Inland Fisheries Research Institute.



INTRODUCTION

Chum salmon are found in streams of the North Pacific and the Arctic Ocean (Chyung 1977). Though both chum and cherry salmon (*Oncorhynchus masou*) occur in Korean waters, chum salmon are the most common salmon homing to the east coast of Korea (Seong et al. 1992 and 1995). Salmon are considered an important marine resource in many countries adjoining the North Pacific. Fishery scientists in these countries have conducted research into large-scale hatchery production of these fish. The first salmon hatchery in Korea was built in Kowon, Hamkyungnamdo in 1913. Modern fish culture in Korea began when hatcheries were established on the Milyang River of Kyungsangnamdo and on the Osip River in Samchuk City in 1967. The Yangyang Inland Fisheries Research Institute was established in 1984. Hatchery-produced chum salmon are released in 12 streams on the east coast of Korea. Through the period from 1970 to 1995, the number of juvenile chum salmon released from hatchery programs increased from 8,000 to 16,000,000. Through this period the rate of survival of juvenile chum salmon at release to adult has ranged from 0.3% to 1.5% (Seong et al. 1992, 1994 and 1995).

Because of recent advances in fish culture technology in Korea, the number of chum salmon harvested in freshwater has increased from 410 in 1970 to 35,000 in 1995. An average total of 120,000 chum salmon have been harvested in Korean waters

annually since 1990, when set nets were first deployed in marine waters to harvest these fish.

The following is a report on chum salmon characteristics, harvest and hatchery performance in the Namdae River, Yangyang, Kangwondo, which has the greatest return of chum salmon among the 12 streams where chum salmon are harvested. The work has been done in an effort to improve the survival rate of juveniles to adult and thereby expand the scale of the project.

MATERIALS AND METHODS

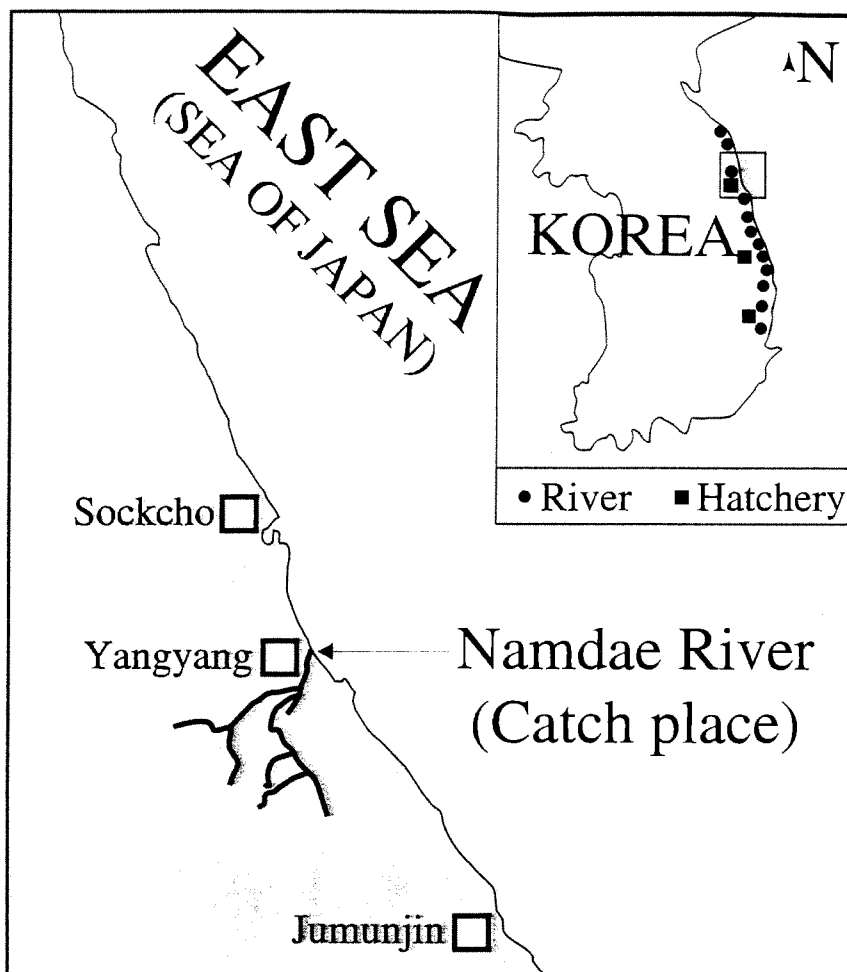
Adult Salmon Capture and Measurement

Adult salmon for the study were captured in river-blocking nets deployed 1.5 km away from the mouth of Namdae River (Fig. 1) as well as in other rivers on the east coast of Korea. Adult chum salmon were captured from mid-September through mid-December of each year from 1984 through 1995. After capture, male and female fish were sorted and sacrificed with a blow to the head. We then determined the fork length (nearest 0.1 cm) and body weight (nearest 0.1 g) of each fish.

Assessment of Age

Scales were collected from each fish to assess their age. In order to more easily determine age, the scales were magnified 20 times on a profile projector and the number of annuli counted.

Fig. 1 A map showing the catch and releasing places in the river of Korea. Solid circles represent the locations of catching place and solid squares indicate hatchery place.



Egg Stripping and Fertilization

One person held the fish while a second person opened the female by incision and removed the eggs. Conspicuously dead eggs were removed and discarded. Sperm from one or two males was added to the eggs from three or four females. The eggs and sperm were gently mixed prior to adding water. The fertilized eggs were then gently rinsed to remove excess sperm and any other contaminants. The eggs were then placed in an egg washing tank (55x80x63 cm) and exposed to gently flowing water for one hour, after which they are considered water hardened. At this point fertilized eggs are ready for transport to the hatchery. The eggs were removed from the water and placed in wooden boxes with about 10% additional pressure to reduce the impact during transport. The wooden boxes of eggs were then moved to the hatchery in the Yangyang Inland Fisheries Research Institute.

Incubation and fry emergence

When the eggs arrived at the hatchery they were disinfected with iodine (1/200 dilution) for 15 minutes and placed in incubators.

Adkins type incubators (295x35x30 cm), cylinder type (66x30 cm), and boxes (55x80x63 cm) are used for incubation. Incubators were loaded with 300,000 eggs for Adkins-type, 90,000 for cylinders and from 400,000 to 500,000 per box-type incubator.

Well water was used for incubation. Incubation water was first passed through high-pressure filters and then depurated with an ultraviolet running water sterilizer. A flow rate of from 20 to 30 liters per minute was used for each incubator. The eggs were bathed in malachite green (3 ppm) at three day intervals to control the growth of fungus on dead eggs (Leitritz and Lewis 1980). Since the fertilized eggs are easily killed by even moderate shock, malachite green was used until the eggs were eyed

and the dead eggs could be physically removed. Live eggs were sorted from the dead eggs with an automatic egg sorter when they had accumulated 420 C temperature units and were strongly eyed. Eggs that died after sorting were removed from the incubators using tweezers.

At about three days before hatching, the eyed eggs were disinfected with iodine and moved from incubators to the indoor pebbly breeding pond. The eggs were placed on hatch nets in a single or double layer at a density of approximately 15,000 eggs per m². After hatching sac fry swam down through the hatching net and into the spaces between the pebbles until later emergence. When hatching was complete, at from 480 to 520 C temperature units, the nets were removed. Water flow was maintained at about 1 to 2 centimeters per second through the pebbly pond.

Rearing

Sac fry finished absorbing their yolks at from 820 to 900 C temperature units. At this point the fry emerged and were free swimming and needed to be fed. Fry were initially started on feed with rainbow trout mash. As the fry grew the size of the mash and pellets was increased up to No. 2 pellets. We used the following schedule for change in feed size: fry below 0.3g were fed mash; from 0.3 to 0.5 g, No. 1 pellets; and, from 0.5 g until release at about 1 g, No. 2 pellets. The fry were fed a measured amount of feed, 3% to 5% of the average body weight per day (Hashimoto 1982-a).

The commercial feed used for rearing contained 2% fat. Feed oil was added to the commercial feed to increase the fat content to 10%. The intent of the added fat was to increase the growth rate. In addition, a variety of vitamins (2% to 3% of the feed) and antibiotics were added with the fat. The fingerlings were kept free of external parasites and bacteria by treating them with formalin.

Fry were fed about 10 times each day while they were on mash. Once they were on pellets, the number of feedings was reduced to 5 times each day. Generally rearing took place from January until the fish were released.

In order to assess growth, 40 fry were drawn at random, anesthetized with MS 222 (0.1 g per liter of water) and measured to determine fork length (nearest 0.1 cm) and weighed (nearest 0.1g).

Transport and release

The juveniles were released between mid-February and March as they reached about 1 g in weight. We released some juveniles into the Namdae River through the fishway linking the institute to the

river, while others were transported to other rivers for release. All juveniles were judged in good condition before they were released.

Determining survival from juveniles at release to returning adult

The annual survival rate for returning adult salmon was determined by dividing the number of returning adults in any year by the number of juveniles released three years before.

RESULTS

Juveniles were from 4.7 to 5.6 cm long and weighed from 0.6 to 1.2 g at release from mid-February through March. Various patterns of fin clipping were used to mark and later identify the fish (Table 1). The number of juveniles released has increased annually and a total of 147,270,000 fish have been released in the program through 1995. Survival from juvenile to returning adult has ranged from 0.3% to 1.5% (Fig. 2).

The return of adult chum salmon (Fig. 3) occurred from mid-September through mid-December with 0.1% returning in September, 36.2% in October, 62.5% in November and 1.2% in December. November was the peak period of upstream migration; 34.9% of the upstream movement took place in the first several days of the month. The sex ratio of the returning adults captured in the river was 42.7% female.

The length of adult salmon varied by age and sex. The fork length of males ranged from 42 to 88 cm and that of females from 46.5 to 83.8 cm. Most males measured from 55 to 60 cm; females from 65 to 70 cm. The weight of males ranged from 0.5 to 6.8 kg; female weight ranged from 0.7 to 5.2 kg.

Most of the returning adult fish were 3 and 4 years old; 64.5% of the males were 3 years old and 56.9% of the females were 4 years old. The 2 and 5-year-old salmon respectively represented only 1.25% and 0.4% of the adults. Average fork length and weight of male adults according to age (Fig. 4) was: 49.4 cm and 1.235 kg at 2 years; 58.1 cm and 1.952 kg at 3 years; 64.7 cm and 2.739 kg at 4 years; and, 73.1 and 3.981 kg at 5 years of age. The average fork length and weight of females at age was: 53.9 cm and 1.465 kg at 2 years; 60.1 cm and 2.240 kg at 3 years; 65.1 cm and 2.786 kg at 4 years; and, 68.8 cm and 3.381 kg at 5 years of age.

SUMMARY

1. The length of juveniles at release (mid February through March) was from 4.7 to 5.6 cm and the

Table 1. Release of marked chum salmon by year.

Year	Cutting of left ventral fin	Cutting of right ventral fin	Cutting of left ventral fin and adipose fin	Cutting of right ventral fin and adipose fin
Total	210,000	210,000	150,000	200,000
1985	100,000	100,000		
1986	50,000	50,000		
1987	20,000	20,000		
1988	20,000	20,000		
1989	20,000	20,000		
1990				50,000
1991			50,000	
1992				50,000
1993			50,000	
1994				50,000
1995			50,000	
1996				50,000

Fig. 2 Numbers of juveniles released and annual changes in return rates of chum salmon in Korea, during 1985-1996.

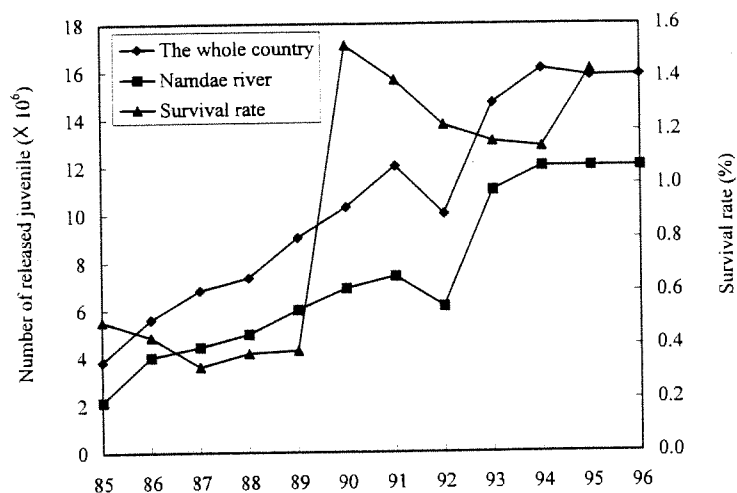


Fig. 3 Numbers of adult chum salmon returning to Korea, during 1984 to 1995.

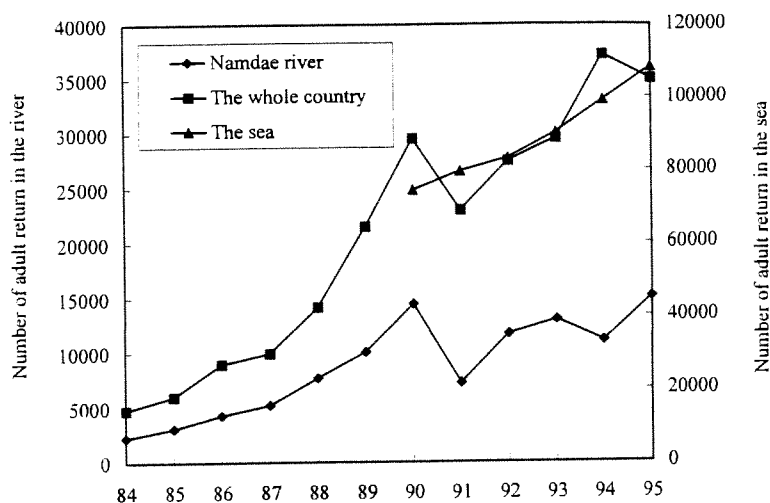
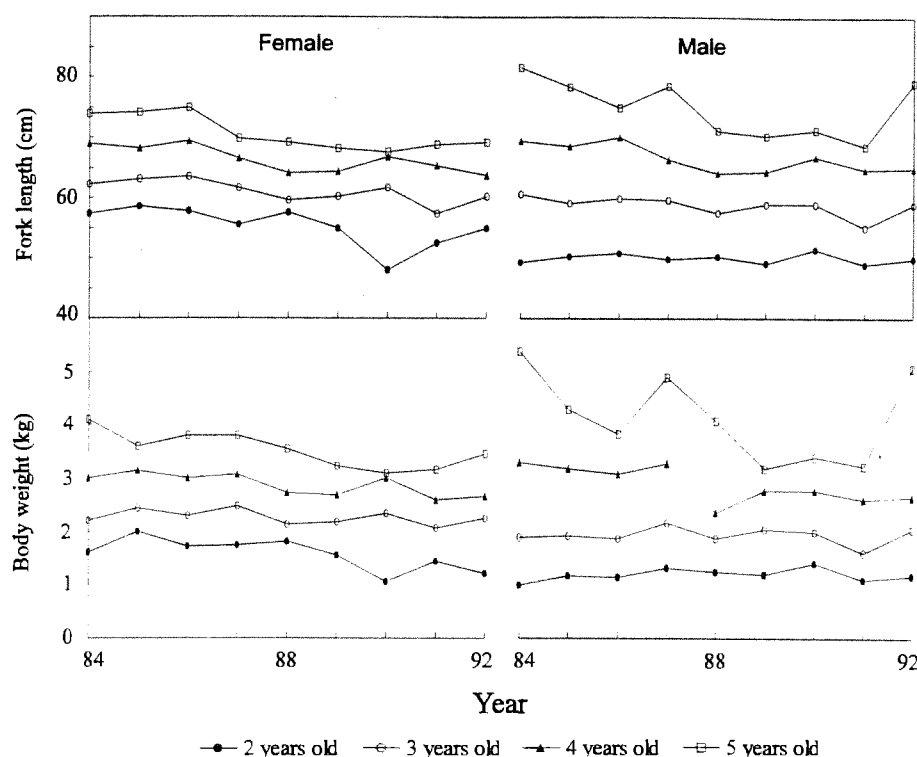


Fig. 4 Annual changes of fork lengths and body weight of adult chum salmon returning to Namdae river in 1984-1992.



- weight of the same juveniles was from 0.6 to 1.2 g.
2. The survival rate for juvenile fish to adult ranged from 0.3% to 1.5%.
 3. Adult upstream migration occurs from mid-September to mid-December with the peak of migration into freshwater in early November.
 4. The run in freshwater was composed of 42.7% female fish.
 5. Most adult females captured in the river were from 65 to 70 cm long (fork length) while most males were from 55 to 60 cm long (fork length).
 6. The age of returning adults was from 2 to 5 years; females were predominantly 4 years old and males 3 years old.

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Evaluation of the Reliability of In-Season Run Size Estimation Techniques Used For Southern British Columbia Chum Salmon (*Oncorhynchus keta*) Runs

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A number of models were examined for their ability to estimate in-season the run size of chum salmon stocks returning to Johnstone Strait to the Fraser River area in southern British Columbia. The in-season run size techniques rely upon two basic data sources for the independent variable; test fisheries and commercial fisheries in Johnstone Strait. Both of these fisheries occur in the ocean migration pathway. The dependent variable run size is determined from the combination of all catch (commercial, sport, aboriginal, etc.) and escapement to the spawning grounds. Regression models are developed utilizing various combinations of catch, effort and catch per effort in order to predict total returning run size. The different models were evaluated based upon the criteria of minimizing the residual mean square. Estimates from the individual models were pooled using an inverse weighting technique. Pooled estimates generally resulted in more accurate forecasts of the returning run strength than those produced by individual models. Also the models tended to under-estimate the run size early in the season. This reversed to an over-estimate of true run size by the end of the season. Implications to fishery management are discussed.



INTRODUCTION

One of the most important components of an in-season salmon fishery management system is the estimate of returning run size. This figure then determines the total number of salmon available for harvest. Managers rely upon these figures to schedule fishery openings, to ensure that catch is allocated among various user groups and to meet specified harvest rate targets or escapement goals. Errors in the process of estimating the run size can trigger or postpone commercial openings, which may lead to under or over-escapement to spawning grounds and/or subsequent fisheries. Pre-season forecasts and in-season run size estimates are also used by fishermen to make decisions regarding how they will allocate their effort among various fishing opportunities.

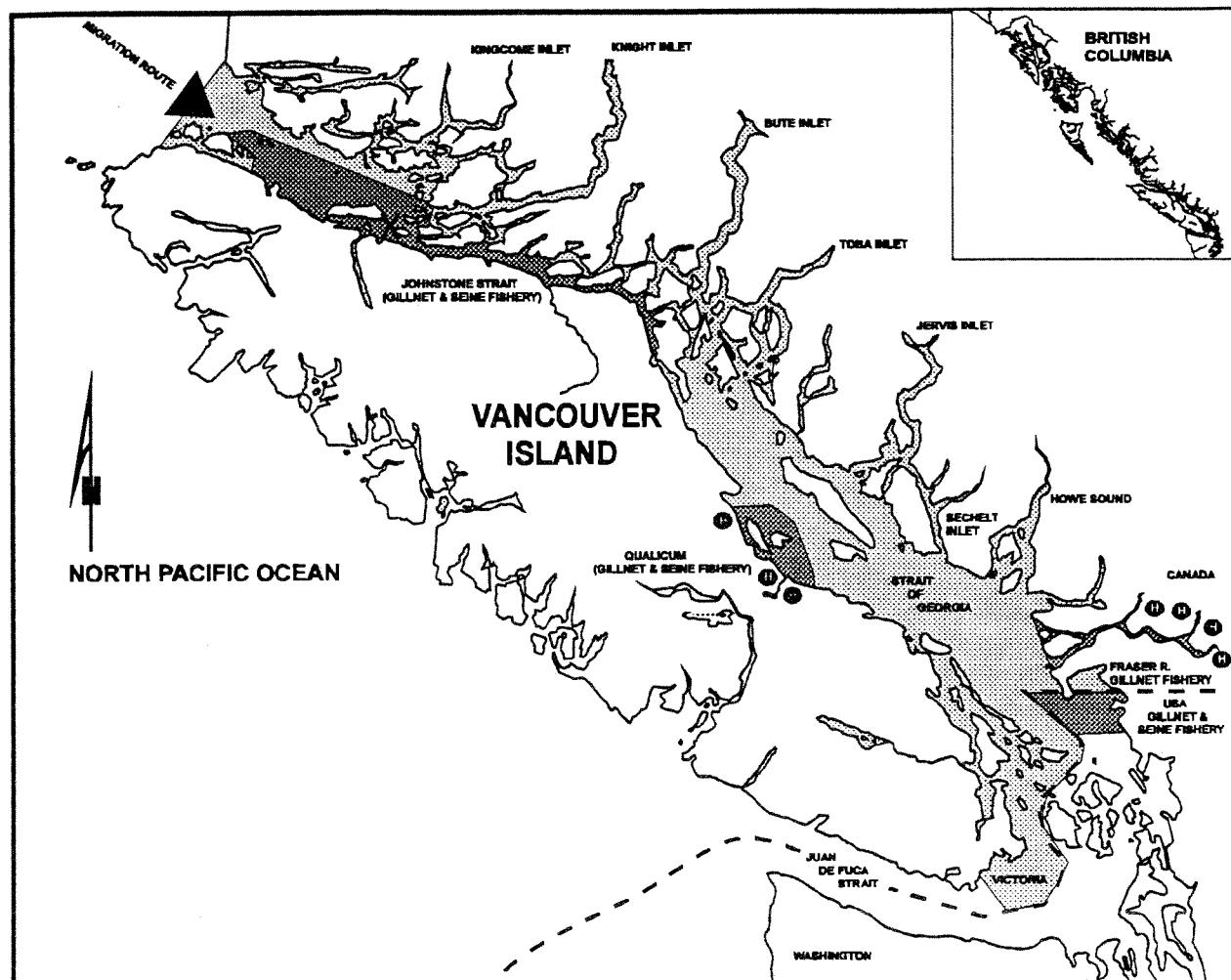
Many models have been developed for estimating returning run abundance. Run size estimates can be obtained from pre-season forecasts, commercial fisheries (catch and catch per unit effort (CPE)), test fisheries and spawning escapement monitoring. The process of estimating run strength occurs over the length of migration producing an array of run size estimates. The manager must then combine these estimates to produce a "best" estimate. Managers

generally consider in-season estimates more reliable than pre-season estimates (Walters and Buckingham 1975). A number of authors (Fried and Hilborn 1988; Fried and Yuen 1987; Henderson et al. 1987) have proposed and evaluated various techniques to both estimate run size and how to combine several independent indicators of run strength.

The purpose of this report is to:

1. Describe the models currently used for assessing the returning strength of chum salmon to the inside waters of southern British Columbia (Fig. 1).
2. Determine whether one model performs with more consistent accuracy than any of the others.
3. Finally to determine whether run size estimation can be improved by pooling results from independent models.

Fig. 1 Map of 'Study Area' chum salmon stocks and vicinity. X denotes the location of the Johnstone Strait test fishery; ① are locations of major enhancement facilities; and ■ are locations of major commercial fisheries on the 'Study Area' chum salmon stock.



METHODS

'Study Area' Chum Salmon Stocks

The region from Johnstone Strait to and including the Fraser River is called the 'Study Area' in terms of DFO chum management (Fig. 1). After an ocean residence of 3 to 5 years chum salmon from the 'Study Area' return, mainly through Johnstone Strait to spawn. Numerous stocks with a wide range of productivity's contribute to this migration; with the largest contributor the Fraser River system. In addition to the many other river systems contributing wild stocks (Mainland Inlets, east coast of Vancouver Island and Puget Sound) there is a significant enhanced component of about 25% of the total returning run size (Gould et al. 1991). The enhanced component is mainly produced at seven major facilities; four in the Fraser River and three on the

east coast of Vancouver Island. The main migration route for these chum salmon stocks is through Johnstone Strait and then into the Strait of Georgia (Anderson and Beacham 1983). Along this pathway the chum salmon are potentially harvested by three major Canadian fisheries and one American fishery. The first fishery and single largest producer is a commercial fishery in Johnstone Strait. Both purse seine and gill net gear have participated, with purse seine gear harvesting the largest share (about 80%). This fishery harvests chum stock from the entire 'Study Area' (wild and enhanced). An other major fishery, focuses upon the enhanced returns to mid-Vancouver Island. This fishery was developed to harvest surplus production from hatcheries and spawning channels in the area. Next, there is the Fraser River fishery focusing upon returning Fraser River chum stocks (wild and enhanced). This a gill net only fishery. Then there is a American fishery

near the mouth of the Fraser River which harvests mainly Fraser River chum stocks. Finally, there are a number of terminal single stock fisheries that occur when abundance exceeds escapement requirements.

The management strategy governing 'Study Area' chum stocks is known locally as the 'Clockwork'. It was so named due to a set of rules dictating management of the 'Study Area' chum salmon. The Clockwork management plan (Hilborn and Luedke 1987), which was introduced in 1983, outlined the objectives and strategy by which the Johnstone Strait and other chum fisheries in the 'Study Area' would be managed. The main objectives of the strategy are to: (1) achieve a wild escapement of 2.5 million chum in 3 to 4 cycles; (2) allow fishing at low stock sizes; (3) stabilize the annual catch; and (4) learn about the stock productivity by allowing for escapements above 2.5 million in years when stock sizes permitted.

In order to achieve the above objectives, commercial fishing is limited to a variable harvest rate, set according to the magnitude of the returning chum run. Currently there are four steps starting at a 10% harvest rate for run sizes under 3.0 million, increasing to 20% for run sizes between 3.0 million and 3.9 million, 30% for run sizes between 3.9 million and 5.3 million and finally a 40% harvest rate for run sizes greater than 5.3 million.

Data Sources

Data used in the following analyses are estimates of catch, escapement, fishing effort and age structure. Commercial catch statistics are derived from DFO and Washington Department of Fish and Wildlife sale slips records. Aboriginal catches are also included in the total run estimate and these are obtained from a variety of sources including Bijsterveld and James (1986) and MacDonald (1987). Escapement estimates are obtained from more than 175 streams within the 'Study Area' (Fig. 1). Of these 175 streams, only 36 streams have consistently had more than 5,000 wild spawners. There is also an enhanced component from seven major facilities; three on Vancouver Island and four in the lower Fraser River (Fig. 1). The majority of the escapement estimates are visual estimates provided by stream walks, aerial or float surveys. Escapement into enhanced systems are generally determined with much greater accuracy and are obtained from fence counts and occasionally mark-recapture studies. Fish scales used to determine age structure are derived from catch (commercial and test fisheries) and escapement samples. Fish age was determined from annular ring counts. For example a chum salmon scale with three annular rings would be classified as a 4-year old fish. In the European system this fish would be designated as a 0.3.

Effort information is recorded as boat days for

commercial fisheries and number of sets for the test fisheries. Effort counts were obtained visually via overflights during the operation of the commercial fishery.

The final primary source of data used in this report was obtained from two seine vessels operating under charter to DFO within Johnstone Strait (Fig. 1). The program was initiated in 1965, primarily in years of low expected abundance. Starting in the late 1970's the program has begun in late September and continued through until early November. Each vessel is required to make six test sets per day among 40 possible locations within Johnstone Strait. Full descriptions of this operation can be found in HopWo et al. (1993) and are not repeated here.

Model

Six models, one pre-season and five in-season, were constructed to forecast total stock size. The pre-season wild stock prediction for each year i from 1988 to 1994 was calculated by determining the average proportion of 3-, 4- and 5-year olds in the returning stock over the period 1980 to 1994. These proportions were based upon chum salmon scales collected from test and commercial fisheries in Johnstone Strait and the Fraser River. Next, the expected total return from years $i-3$, $i-4$ and $i-5$ was calculated by taking the product of the escapement and the return rate per spawner. The average proportion of age 3, 4 and 5's in the recent 15 years has been 19%, 70% and 11%, respectively. The average return per spawner over the same 15 years was 2.1:1.0. Finally, returns from each brood year were summed to produce the predicted wild run size for year i . For the enhanced component contribution to the total returning run size, run size was estimated by applying survival rates for each type of enhancement facility and the average return by age group, to the number of fry released by the facilities. The total return was then the sum of the wild and enhanced components.

The five in-season models all had the same structure of the form:

$$\hat{\text{LN}}(Y)_{i,j} = \text{LN}\alpha + \beta \text{LN}(X)_{i,j}$$

where $\hat{Y}_{i,j}$ equals the predicted total run size estimated from data source i and time j , α = the y-axis intercept, β = slope of the regression line, and $X_{i,j}$ = data from data source i for time period j . The five data sources for the in-season model are: (1) test fishing CPE by week or cumulative CPE; (2) total commercial catch (seine and gill net) in a Johnstone Strait fishery; (3) commercial seine gear catch in a Johnstone Strait fishery; (4) commercial seine gear CPE; (5) pooled

estimate combining a test fishery estimate with one of the other model estimates. Pooling was based upon the residual mean square error (RMS) (Hilborn and Walters 1992).

$$\bar{R}_j = \sum_{i=1}^2 [R_{i,j} \times (1/\text{RMS}_{i,j})] / \sum_{i=1}^2 (1/\text{RMS}_{i,j})$$

where $\bar{R}_j$ = weighted mean run size for time j ;

$R_{i,j}$ = estimated run size for time j and method i ;

and $\text{RMS}_{i,j}$ residual mean square error from the linear regressions for time j and method i derived in equation (1).

A hindcasting procedure was used to examine the predictive capabilities of the various models. Only data prior to the year of interest was used to calculate the predictive equations. Simulations were conducted for the years 1988 to 1994. Run size estimates are classified into pre- and early-season, mid-season and final. The pre- and early season includes the pre-season forecast, test fishing results in the fourth week of September (9/4) and a commercial fishery held the same week. Mid-season includes cumulative test fishing CPE from the fourth week of September to the second week of October (10/2) and any commercial fisheries held during the second week of October. The final estimate is derived from cumulative test fishing CPE from the fourth week of September up to and including the third week of October (10/3) and any commercial fisheries held after the second week of October. Predictive regressions were only used if

F-tests for the model were significant at the 95% level.

Three methods of comparing run size estimates were used: (1) annual percent error, (2) mean percent error (MPE); and (3) mean absolute percent error (MAPE). Annual percent error was calculated as:

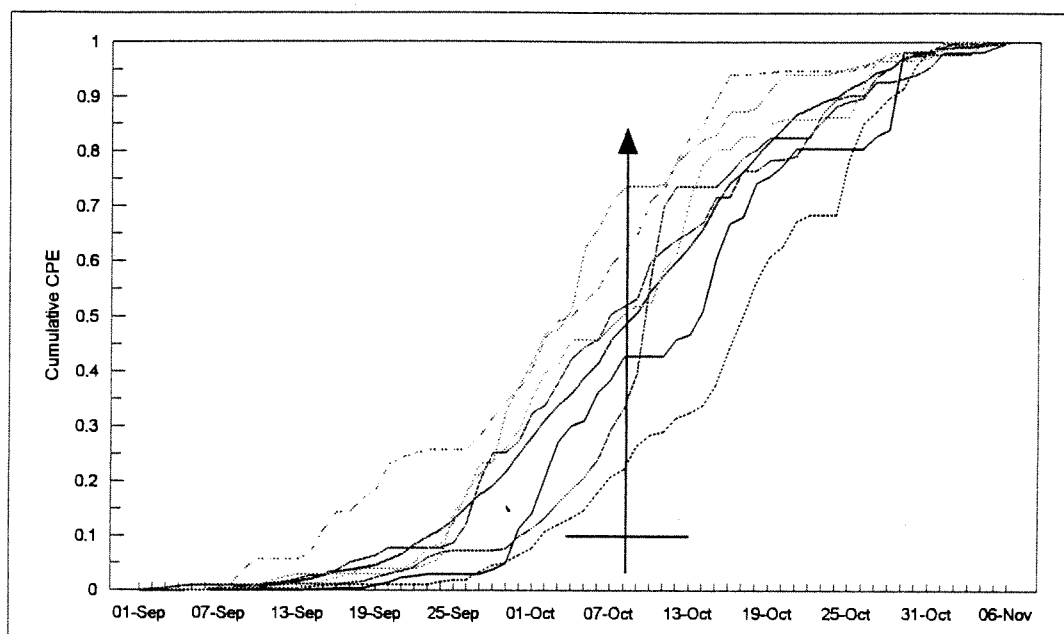
$$[-(A_k - R_{i,j,k}) / A_k] \times 100$$

where A_k = actual run size in year k and $R_{i,j,k}$ = predicted run size for time i with model j and in year k . MPE provides for a measure of bias in any of the methods used; examining for persistent over- or under-estimates of run size. To assist in examination of the range and distribution of underforecasting (negative MPE) and overforecasting (positive MPE) bar charts were constructed. MAPE yields a measure of overall model performance with over- and under-estimates in run size treated equally.

RESULTS

The size of the chum salmon run varied from a low of 1,815,000 in 1989 to a high of 4,377,000 in 1992. Escapement did not vary as much, ranging from a low of 1,023,000 in 1989 to over 1,931,000 wild spawners in 1994. The run timing as measured by cumulative test fishing CPE in Johnstone Strait varied considerably among years, with the 1989 run arriving the earliest and 1994 the latest (Fig. 2). The actual dates when 50% of the run passed the Johnstone Strait test fishery ranged from October 4 in 1989 to October 17 in 1993.

Fig. 2 'Study Area' chum salmon run timing through Johnstone Strait calculated from cumulative CPE test fishing catch and effort data; years 1988-94. Arrow marks the 50% date and the horizontal line is the 95% confidence interval.



Pre- and Early Season

The accuracy of the various models tested (Pre-season, Test Fishing CPE, Total Catch, Seine Catch and Seine CPE) varied greatly both among and within years (Fig. 3). The Pre-Season forecast had the largest deviation from the true run size during the Pre- and Early Season time frame. Both the Pre-Season and Test Fishing CPE model's produced the largest errors from the true run size; accounting for six out of the seven years between them. There was an overall tendency for the Test Fishing CPE, Total Catch, and Seine CPE models to under-estimate the true run size. With respect to overall model performance there was no single model that outperformed all the others. The MAPE's for all models ranged from a low of 21.3% for the Total Catch model to a high of 28.5% for the Test fishing CPE model. Finally, though, the weighted model estimates were always more accurate than the least accurate of its components.

Mid-Season

Overall, the individual models improved in their forecasting ability from the earlier time frame as evidenced by a reduction in their MAPE values. This improvement in forecasting ability was evidenced by large decreases in the RMS over the course of the season (Fig. 4). There was also a reversal from earlier in the season when the commercial models (Total Catch, Seine Catch and Seine CPE) tended to under-estimate the true run size to a significant over-estimate later in the season as evidenced by their positive MPE values. The Test Fishing CPE model did not exhibit any consistent bias with equal number of under- and over-estimates of run size. As in the Pre- and Early Season time frame the weighted models were always more accurate than its individual components.

End of season

Once again no single model performed consistently better than any of the others. Overall though, the weighted estimates performed better than their individual components. In addition, there was a reduction in MAPE values from the Pre-, Early- and Mid-Season time frames. Also though there was a tendency for the MPE values to be positive (though slightly larger in magnitude from the Mid-season values) indicating a tendency to over-estimate the returning run size by the commercial models (Total Catch, Seine Catch and Seine CPE). The Total Catch model had five out of six years and both the Seine Catch and CPE model's had four out of six years that over-estimated the true run size.

DISCUSSION

The present paper describes the current technique used to estimate the run strength of chum salmon returning to the 'Study Area'. The results show that no one single model examined in this paper outperformed any of the others. It did show though, that pooling of the individual estimates generally improved the overall accuracy and reduced the bias (as measured by MPE) of the run size estimates produced. This result is in agreement with results of Fried and Yuen (1987) who examined a similar pooling methodology for forecasting the returning sockeye salmon run strength to Bristol Bay, Alaska. Fried and Hilborn (1988) also examined Bayesian probability theory to produce in-season estimates for sockeye salmon returning to Bristol Bay, Alaska. They also found that while the Bayesian method was not always more accurate than the most accurate individual method, it was always more accurate than the least accurate individual method.

A number of findings in the present study have some results of interest to management of the 'Study Area' chum salmon fishery. Firstly, there was the noted result of early in the season to under-estimate the actual size of the returning chum salmon run size. This has the effect of delaying any additional harvest until more information from test fishing becomes available. The net result is to reduce the risk of over-harvesting the "Study Area" chum salmon stocks. However, this tendency is actually reversed later in the season when the models tend to over-estimate the run size. This is particularly noticeable in 1989 when the run timing 50% date was October 4 (Fig. 2). The mean 50% date is about October 8 (95% C.L. of 4.6 days). While this explains the initial over-estimation early in the season it does not explain the continuing over-estimation of run size throughout the fishing season. The second important finding from this analysis is that while the amount of error averaged 15-20% by the end of the season there was still 1 year out 7 that over-estimated the run size by 50-60% (1989). Due to the harvest management regime in place for the 'Study Area' chum salmon that places a ceiling upon the harvest rate; this tendency to over-estimate the run size may be ameliorated.

All the models examined in the present study require estimates of catch and escapement. Naturally the reliability of these models will depend upon the quality of these data. While the catch statistics are reasonably easy and consistently collected, the same cannot be said for the escapement data. As pointed out earlier there are a large number of streams contributing to the 'Study Area' chum salmon and a wide variety of escapement methodologies applied.

Fig. 3. Percent error of various models used to predict total run size of 'Study Area' chum salmon. TF CPE9/4 = hindcasting based upon test fishery CPE from week 9/4; Total Catch = Hindcasts based upon total commercial catch (purse seine and gill net gear); Seine Catch = hindcasts based upon total purseseine catch; Seine CPE = hindcasts based upon purse seine CPE; Wt. Mean = estimated based upon models pooled together by their individuals RMS.

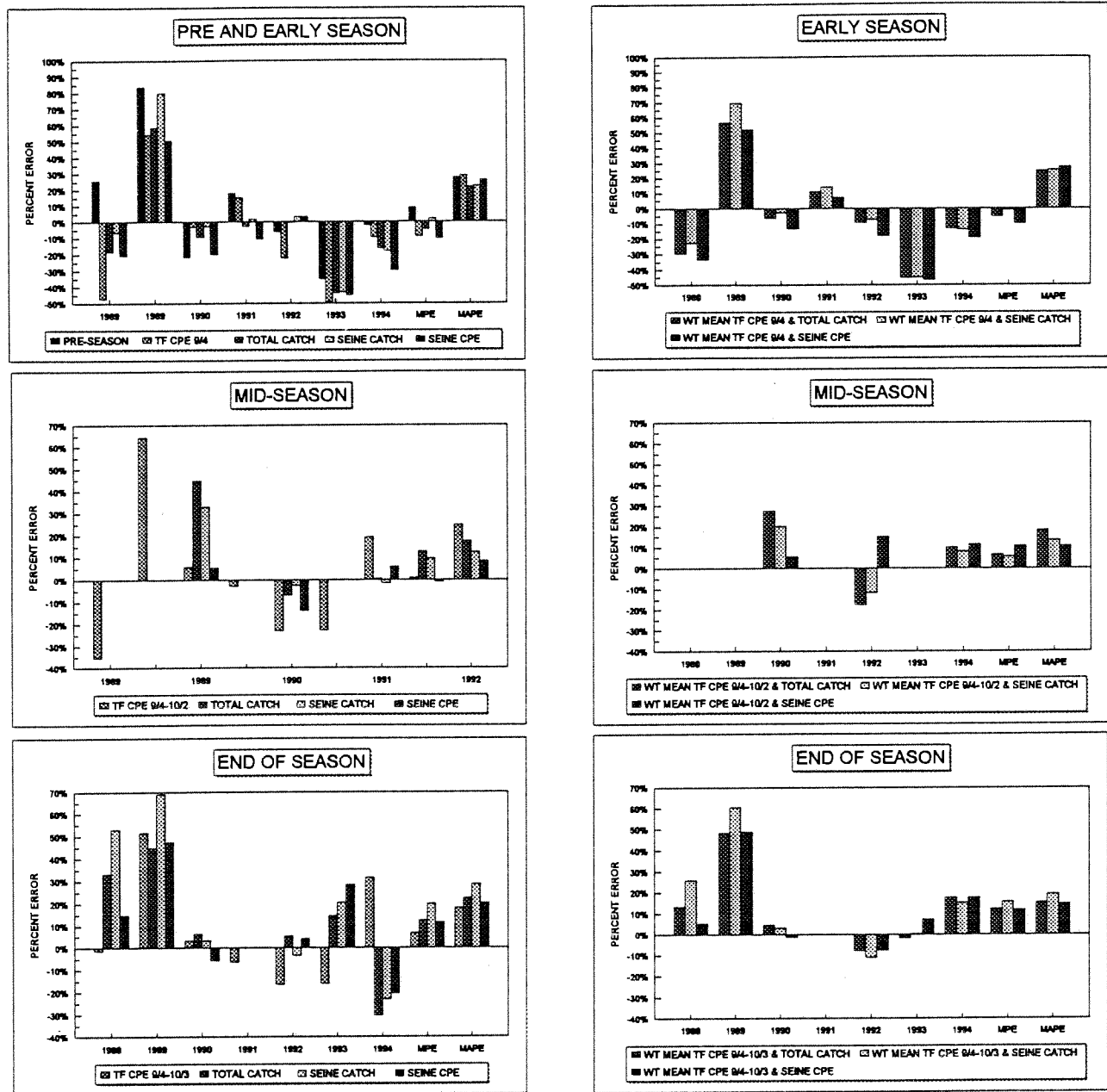
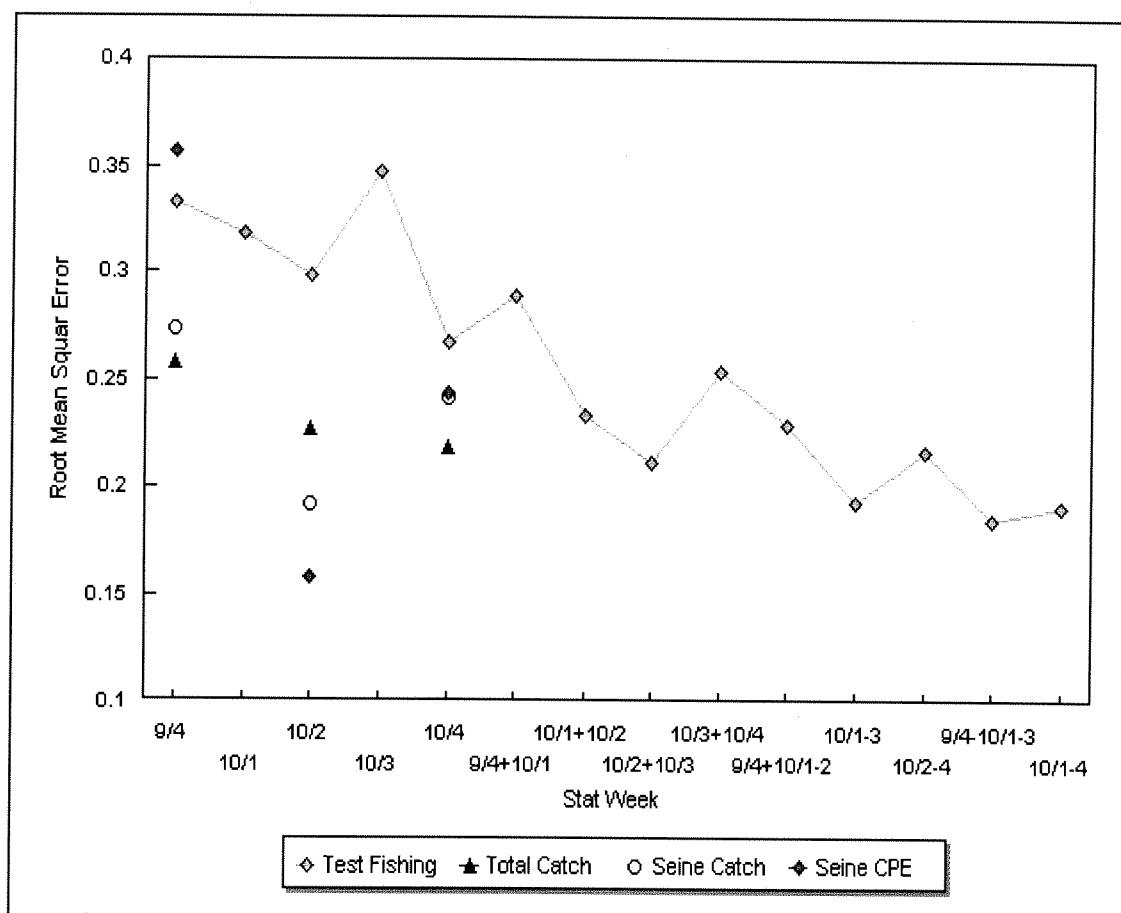


Fig. 4 Residual mean square error associated with four of the models used to predict run size estimates in-season. Test fishing RMS is shown for individual weeks and various cumulative weeks' CPE models.



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I would like to thank all the staff of DFO that have participated in collecting and compiling the data over the years which made this analysis possible. Special note is made to Don Anderson, Leroy Hop Wo, Al Gould, Wilf Luedke, Carmen McConnell, Sue DeNovo and Alf Stephenson who spent many hours acquiring, analyzing, compiling and conducting test fisheries upon which this work is based. Finally I wish to acknowledge the work of S. Fried, R. Hilborn and H. Yuen on Bristol Bay sockeye run size estimation.

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Long-Term Variability of Alaskan Sockeye Salmon Abundance Determined by Analysis of Sediment Cores

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Records of prehistoric variations in salmon abundance are reconstructed from analysis of stable nitrogen isotopes in sediment cores. This new application of N isotopes is based on the observation that Pacific salmon supply nutrients into freshwater systems when they return to spawn. Nitrogen derived from adult salmon is enriched in ^{15}N relative to terrestrially-derived N. Thus input of salmon-derived N can be quantified by analysis of ^{15}N . Changes in the number of returning adult salmon will be reflected by downcore changes in sedimentary $\delta^{15}\text{N}$. Sedimentary $\delta^{15}\text{N}$ has been analyzed in two cores from Karluk Lake, Kodiak Island, Alaska. The record spans the past approximately 500 years and shows large changes in $\delta^{15}\text{N}$ and thus inferred escapement. Significant minima occurred during the mid to late 1900s, the early 1800s, the early 1700s and the mid 1500s. Relatively high values are observed from the mid 1800s to the early 1900s, the late 1700s, around 1700, the early to mid 1600s, the late 1500s, and the early 1500s. The record is not well correlated with estimates of Gulf of Alaska sea surface temperature (SST) determined from coastal tree ring records. Low salmon abundance during the early 1800s corresponds with a prolonged period of anomalously cold SST throughout a large region of the North Pacific. However, the period of high estimated abundance in the late 1800s and early 1900s was also a period of lower than average temperatures in the Gulf of Alaska. If variations in the abundance of Karluk Lake sockeye are influenced by ocean conditions, the differing responses during periods of cool temperature may indicate that different circulation patterns in the North Pacific may result in cool temperatures in the Gulf of Alaska, and impact biological systems differently. The decline in $\delta^{15}\text{N}$ that began in the mid 1900s is the most extreme in the record. However, tree ring based temperature trends suggest that conditions similar to the mid 1900s occurred several other times during the last few hundred years. Commercial harvest may have influenced the recent decline in $\delta^{15}\text{N}$ and salmon abundance at Karluk Lake, through impacts on freshwater nutrient input.



INTRODUCTION

Information on past changes in North Pacific salmon abundance prior to those reflected by catch data would provide valuable insight into the relationships between climate and salmon abundance. Such long-term data would provide a perspective on variability prior to anthropogenic influences, such as harvest, habitat alteration, hatchery production and greenhouse gas buildup, on biological and physical systems. In addition, longer time-series are required to detect responses to lower frequency changes, such as the 50 to 75 year period in temperature suggested by some records (Ware 1995). Finally, long-term data allow for testing of hypotheses regarding the response of salmon to changes in ocean/climate state.

This paper focuses on recent research aimed at

reconstructing past changes in the abundance of Pacific salmon. The first part of this paper will describe the methodology used to reconstruct past changes in salmon abundance from sediment core analysis. In the second part, this methodology will be used to estimate variations in sockeye salmon abundance in Karluk Lake on Kodiak Island, Alaska over the past 500 years. This record will be compared to paleoclimatic data to explore relationships between salmon abundance and climate change.

Physical and limnological characteristics of Karluk Lake, which has been studied for more than 70 years, are shown in Table 1. Relative to other sockeye nursery lakes, the lake is very productive in terms of adult fish production per lake size (Burgner 1991), though the lake has suffered a long-term decline in production (Barnaby 1944; Koenings and

Table 1. Physical and limnological characteristics of Karluk Lake, Alaska.

Surface Area	39.5 km ²
Volume	1,920 m ³ x 10 ⁶
Elevation	106 m
Mean depth	48.6 m
Annual precipitation	172 cm
Water residence time	4.8 yr
Light compensation point	23 m
Total phosphorus (May-October)	7.8 µg/L
Total nitrogen (May-October)	121.3 µg/L
Chlorophyll a (May-October)	2.5 µg/L
Sockeye escapement (mean 1922-1995)	646,000 fish

From Koenings and Burkett (1987 a,b).

Burkett 1987a; Schmidt et al. 1997). The timing of the sockeye spawning has been described as having a bimodal distribution; spawning by the early (spring) run generally peaks in early to mid-July, and spawning by the late (fall) run peaks in September (Koenings and Burkett 1987a). Numerous spawning streams are distributed around the lake (Juday et al. 1932, Baranaby 1944). In general, the early spawning fish favor streams, while the late run fish utilize lake beaches in addition to streams (Koenings and Burkett 1987a). The lake is estimated to have produced returns greater than 5 million fish before its decline (Koenings and Burkett 1987a). Weir-based escapement data has been collected since 1922 (Fig. 1). Escapements averaged more than 1 million fish from the beginning of the record until the late 1930s, declining to an average of 300,000 to 400,000 fish in the 1960s and 1970s. Escapements generally increased in the 1980s and 1990s, but the lake remains below historical high production levels (Koenings and Burkett 1987a; Schmidt et al. 1997).

METHODS

Sediment cores were obtained using a hand operated gravity core with a messenger activated valve. This type of corer has been designed to take samples without disturbing the sediment-water interface, and inspection of the cores after recovery indicated that the core tops were well preserved. Core 2, 17 cm long, was recovered in Oct. 1994, and Core 3, 43 cm long, was recovered in Aug. 1995. Both cores were taken in the main basin of the lake near Station 3 of Juday et al (1932) and the Alaska Department of Fish and Game (57°25' N, 154°5' W, 52 meters water depth). The cores were continuously sampled at 0.5 cm increments shortly after recovery using an extruding device. Each sample was measured for wet and dry (85°C) weight, and magnetic susceptibility. Nitrogen isotopes were

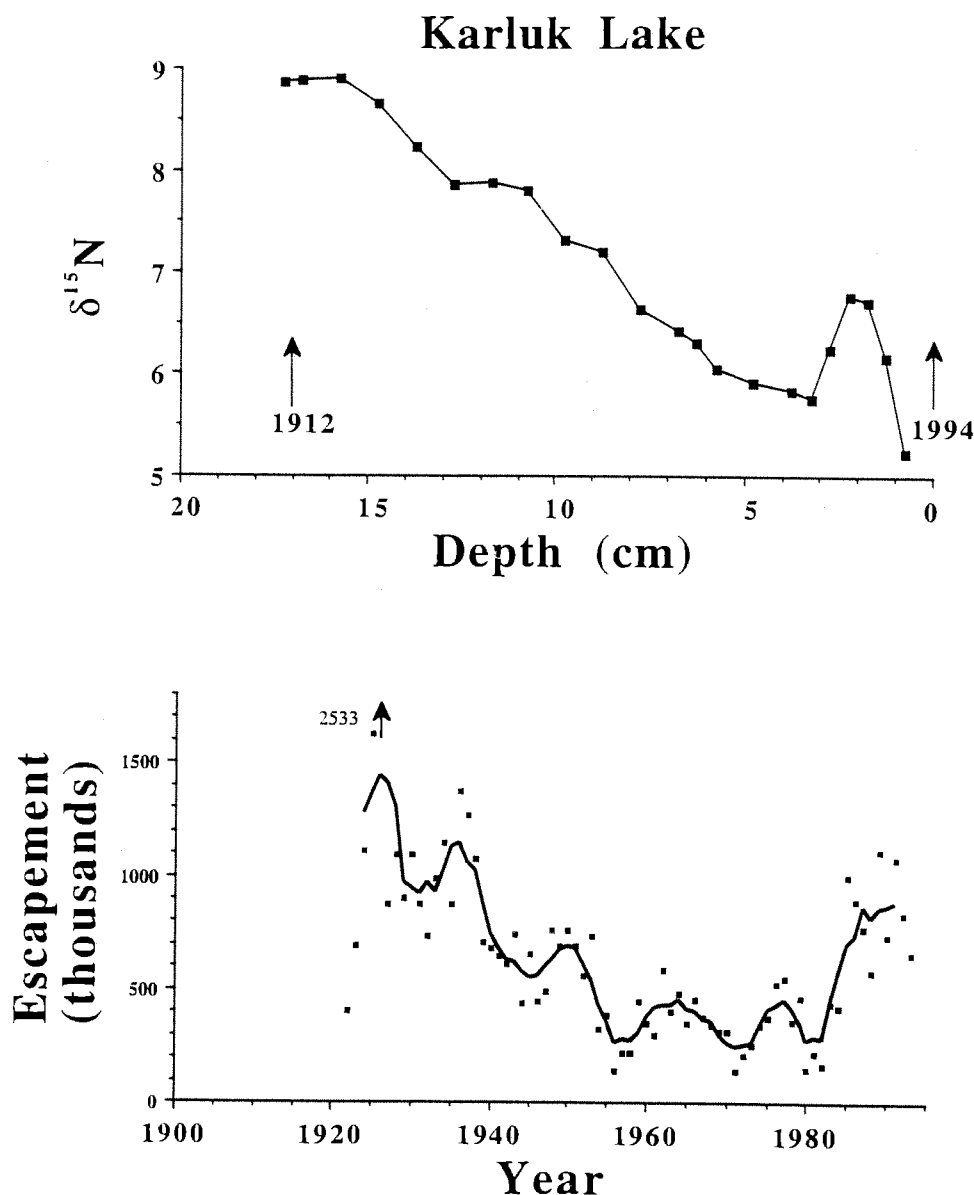
measured on bulk samples using a Europa Scientific 20/20 mass spectrometer equipped with a Roboprep combustion device. The isotopic analyses are reported in the standard δ notation relative to atmospheric N₂. Analytical precision is better than ± 0.2 ‰.

Age control is based on identification of ash layers, and by ²¹⁰Pb dating. Ash layers were identified by the presence of peaks in magnetic susceptibility, and were confirmed by microscopic observation. The Katmai 1912 ash was identified by comparing the chemical composition of glass shards, determined by microprobe analysis, to that of glass of known Katmai 1912 origin (Beget et al. 1994). Both cores contain the Katmai 1912 ash, and the longer Core 3 has an older ash fall event that occurred c.a. 1720. The age of 1912 was assigned to the depth of the peak in magnetic susceptibility associated with the Katmai event for each core. Age estimates are determined by assuming a constant sediment accumulation rate on a dry mass basis, using the rate determined during the period from 1912 to the time of core collection (13.7 mg/cm²/yr). The rate based on the ²¹⁰Pb data (14.0 mg/cm²/yr) is in close agreement with this accumulation rate estimate. The error of age estimates, particularly in the older sections, is difficult to assess. The character of the sediments is uniform throughout, suggesting no major changes in depositional processes.

Reconstructing Salmon Escapement

The method I have employed to estimate past changes in salmon escapement is based on downcore measurements of $\delta^{15}\text{N}$ in sediments. This new application of N stable isotopes is based on several observations determined from previous research. Adult salmon transport significant quantities of marine-derived nutrients (MDN) into some

Fig. 1. Upper figure shows downcore plot of sedimentary $\delta^{15}\text{N}$ in Karluk Lake Core 2. The location of the Katmai 1912 ash is indicated. Lower figure shows the weir based sockeye salmon escapement history for Karluk Lake. The bold line is a 5 year running mean.



freshwater systems when they return to spawn and subsequently die and decompose (Koenings and Burkett 1987a; Kline et al. 1993). In some systems, salmon may be the largest source of N and P annually (Koenings and Burkett 1987a; Stockner 1987). In Karluk Lake, for example, 1 million sockeye bring in more N (64,100 kg/yr) than that supplied by rivers (estimated to be 43,200 kg/yr when the effects of spawning salmon are excluded) and rain (800 kg/yr). N fixation is assumed to be low as blue green algae are a minor component of the phytoplankton assemblage (Juday et al. 1932). The $\delta^{15}\text{N}$ of adult sockeye averages about 11 to 12 (Kline

et al. 1993; Welch and Parsons 1993) as they feed at an elevated trophic level in the ocean. The other main source of N into freshwater systems is much lower in ^{15}N as it is derived from atmospheric N ($\delta^{15}\text{N} = 0$). This large difference in $\delta^{15}\text{N}$ of nitrogen sources allows salmon-derived N to be traced and quantified into freshwater environments.

I hypothesize that past changes in abundance of adult salmon returning to freshwater will be recorded by downcore changes in sedimentary $\delta^{15}\text{N}$. Periods of high abundance will result in high loadings of salmon-derived N into freshwater systems, and thus high sedimentary $\delta^{15}\text{N}$. Conversely, periods of low

abundance will result in deposition of sediments with low $\delta^{15}\text{N}$. Initial studies have focused on sockeye salmon because they generally require a lake for rearing. Many studies have shown that lake sediments are often well suited for high-resolution paleoenvironmental analysis due to relatively fast sedimentation, low bioturbation, and continuous deposition (e.g., Schelske 1991; Charles et al. 1991).

To test this hypothesis, I sampled a suite of 12 Alaskan sockeye lakes over a large region of the northern Gulf of Alaska. The average sedimentary $\delta^{15}\text{N}$ in these lakes is positively correlated ($R^2 = 0.88$) with the ratio of salmon escapement (in numbers) divided by the lake surface area, which is a measure of the relative input of salmon-derived N (Finney unpublished data). This indicates that the $\delta^{15}\text{N}$ recorded by sediments is reflecting input of MDN and hence escapement. The salmon/sediment $\delta^{15}\text{N}$ hypothesis can also be evaluated by comparing temporal trends in sedimentary $\delta^{15}\text{N}$ with historical counts of salmon escapement. In Frazer Lake, Kodiak Island, a sharp increase in sediment $\delta^{15}\text{N}$ closely matches the time when salmon were introduced into this system (McNeil 1997). For Karluk Lake the trend in sediment $\delta^{15}\text{N}$ closely follows the 75 year historical escapement record (Fig. 1). In fact, the strong positive relationship

between the decadal averages of $\delta^{15}\text{N}$ and escapement ($R^2 = 0.85$) establishes a calibration to hindcast past escapement in Karluk Lake (Fig. 2). These lines of evidence offer support for the use of sedimentary $\delta^{15}\text{N}$ to reconstruct possible changes in sockeye salmon abundance.

RESULTS

Sediment $\delta^{15}\text{N}$ profiles for the two cores from Karluk Lake show high overall values (averaging about 8‰) compared to many sockeye and non-sockeye lake sediments (Fig. 3). There is a large range in $\delta^{15}\text{N}$ of about 4‰, with values ranging from about 5.5‰ to 9.5‰. The $\delta^{15}\text{N}$ records in both cores are very similar in the overlapping portion indicating that the sedimentary $\delta^{15}\text{N}$ trends are reproducible. Prominent minima in $\delta^{15}\text{N}$ are observed in the mid to late 1900s, the early 1800s, the early 1700s, and the mid 1500s. Periods with relatively high values in $\delta^{15}\text{N}$ occurred in the mid 1800s to the early 1900s, the late 1700s, around 1700, the early to mid 1600s, the late 1500s and the early 1500s. The data suggest that major periods of escapement variation occurred over time scales of 50 to 100 years before the onset of commercial fishing (c.a., 1890; Koenings and Burkett 1987a).

Fig. 2. Relationship between sedimentary $\delta^{15}\text{N}$ in Core 2 and sockeye escapement in Karluk Lake for the period since 1921 (decadal averages). An exponential curve fit ($R^2=0.85$) excludes the uppermost point (open square), which may be low due to recent additions of fertilizer with $\delta^{15}\text{N}=0$ into the lake. The nonlinear relationship is expected because as escapement increases, the relative contribution of salmon-derived N decreases (see Finney and McNeil, in review, for more details).

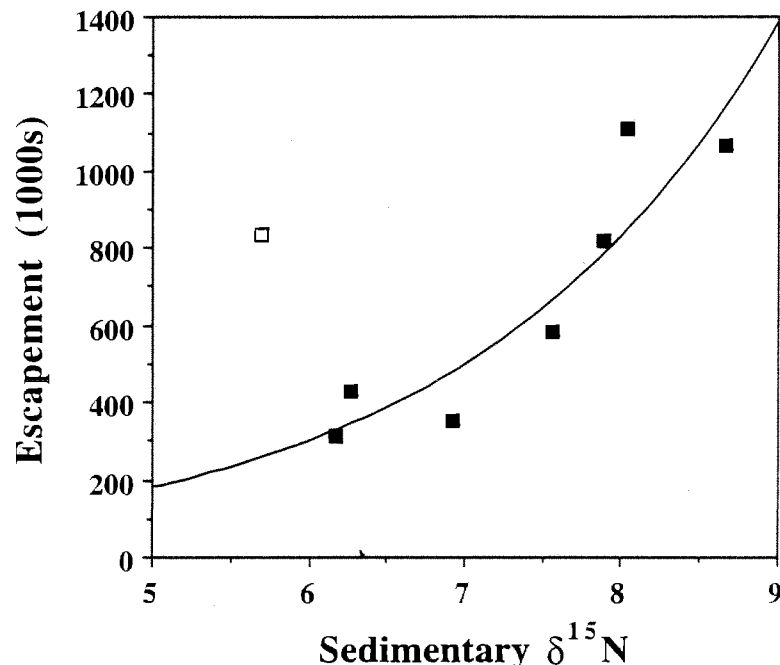
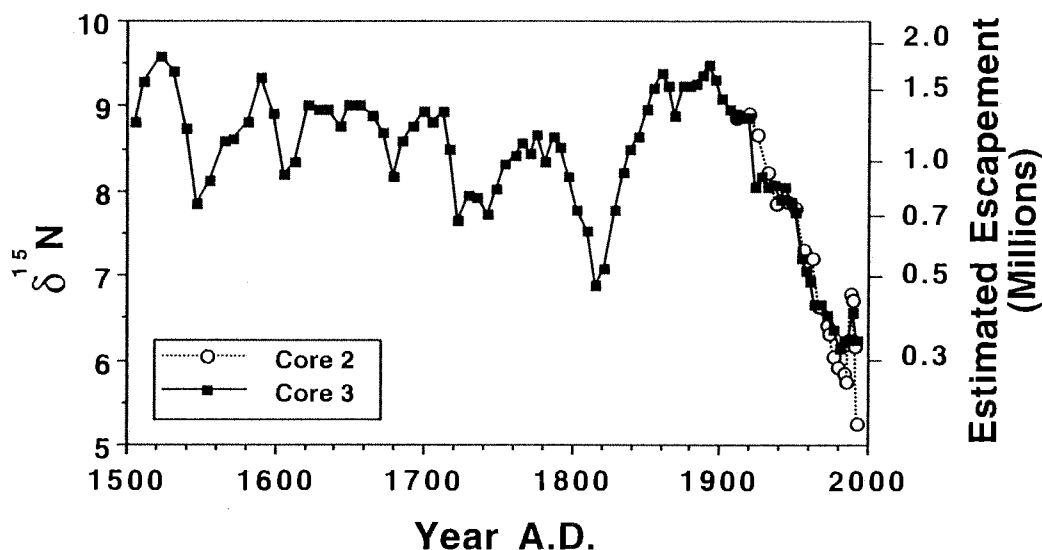


Fig. 3. Karluk Lake sediment $\delta^{15}\text{N}$ variations since about 1500. Note the similar trends in Cores 2 and 3 over the overlapping period. Estimated escapement is based on the equation from the exponential fit shown in Figure 2.



The estimated escapement values are based on the calibration shown in Figure 2. These estimates assume that there has been no significant change in sockeye size or their $\delta^{15}\text{N}$ values over this period. The rate of input and isotopic content of N from non-salmon sources is also assumed to remain constant. The estimates probably reflect averages for 5 to 10 year periods as the sampling increment averages several years of deposition. Bioturbation may also smooth the $\delta^{15}\text{N}$ profile. In addition, some dampening of changes in the lakes N budget due to escapement would be due to water residence time effects, which is 4.8 years in Karluk Lake (Koenings and Burkett 1987a). The average estimated escapement has ranged from about 300,000 to 2 million fish/year over the past 500 years. The average estimated escapement prior to commercial exploitation was on the order of 1 million fish/year.

DISCUSSION

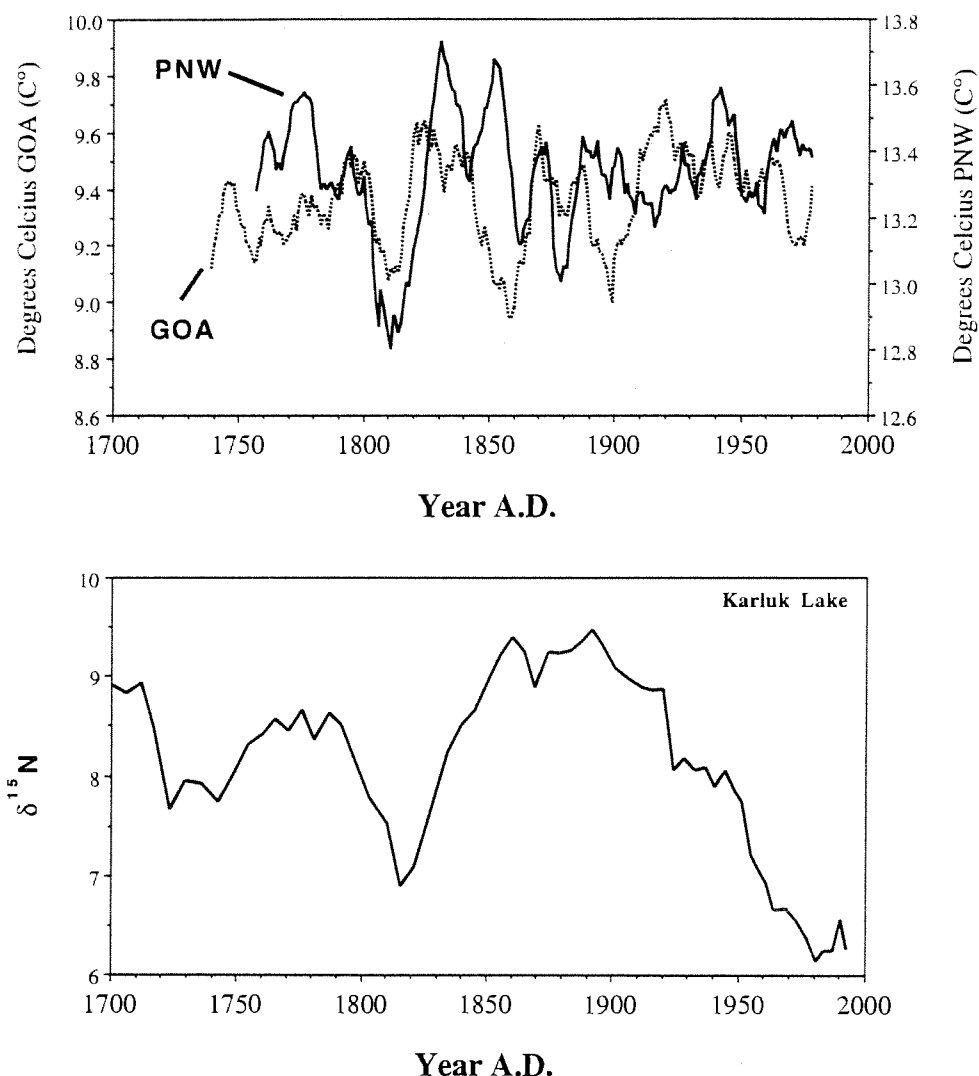
Evaluation of potential mechanisms to explain the long-term changes in Karluk Lake sockeye abundance is challenging because detailed information on concurrent climate, oceanic and lacustrine conditions is sparse. Sockeye production is influenced by conditions in both the oceanic and freshwater phases (e.g., Burgner 1991). In addition, both physical (e.g. water mass structure, temperature, nutrient flux) and biological (e.g. prey and predator abundance) factors are likely to be important in regulating salmon populations.

Reconstructions of variation in coastal temperatures derived from tree ring records along the northeast Pacific coast are the most suitable currently

available paleoclimatic data to compare with the $\delta^{15}\text{N}$ trends. Wiles et al. (1996) have recently published tree ring based reconstructions of spring and summer coastal land temperatures for sites along the northern Gulf of Alaska and the Pacific Northwest coast (Fig. 4). These coastal air temperature reconstructions are positively correlated with sea surface temperatures (SSTs) over a large region of the adjacent ocean during the period the records overlap (44 years, Wiles et al. 1996). Though the exact mechanism is unclear, changes in historical production of Alaskan salmon appear to have followed large scale changes in temperature during the 20th century. Periods of high salmon production, including those for Kodiak Island sockeye, tend to be associated with warm regimes in the Gulf of Alaska (Francis and Hare 1994). Changes in the strength of the Aleutian Low have been suggested as one possible mechanism. During periods of a more intense low, productivity and hence prey abundance is increased, and warmer SSTs are observed in the Gulf of Alaska (Beamish and Bouillon 1993).

A comparison of the Karluk Lake $\delta^{15}\text{N}$ record with the tree ring temperature reconstruction (Figs. 3 and 4) shows higher frequency variability in the temperature reconstruction. This would be expected due to the averaging effects in the sediment record discussed above. In using the $\delta^{15}\text{N}$ data to evaluate hypotheses regarding the influence of climate on salmon abundance, it is assumed that the interpretation of the sedimentary $\delta^{15}\text{N}$ data is correct, and that sockeye populations at Karluk Lake are representative of a larger region. Based on the discussion above, positive relationships between $\delta^{15}\text{N}$ and temperature might be expected. However, there

Fig. 4. Reconstructions of the northeast Pacific coastal temperatures since about 1750 from tree ring records (upper panel; from Wiles et al., 1996). The Gulf of Alaska (GOA) record is based on Alaskan trees from the northern GOA coast, and the Pacific Northwest (PNW) record is based on coastal trees in the Puget Sound region. The data represent warm season temperatures (May-October) and are plotted as 10 year running means. For comparison, the Karluk Lake sediment $\delta^{15}\text{N}$ record for this same period is shown in the lower panel.



are both similarities and differences in the temperature and $\delta^{15}\text{N}$ records. Intervals of low $\delta^{15}\text{N}$ appear to correspond with negative temperature anomalies during some periods, such as the mid 1900s and the early 1800s. In contrast, the period of high $\delta^{15}\text{N}$ during the late 1800s/early 1900s appears to coincide with relatively cool temperatures.

It is informative to compare the reconstructed temperature trends from the two widespread regions (Fig. 4). The Pacific Northwest sites are near the transition zone between the subarctic gyre and the California Current system, as opposed to the Gulf of Alaska sites which are solidly in the gyre system. Not all intervals with cool temperature anomalies in the Gulf of Alaska correspond with cool temperatures in the Pacific Northwest. For example, inferred temperatures during the early 1800s were cool in

both regions, but cool periods in the Gulf of Alaska around 1850 and 1890 coincided with relatively warm temperature anomalies in the Pacific Northwest. This indicates that different circulation patterns may result in cool temperatures in the Gulf of Alaska. If this is the case, then the different circulation patterns may also result in different oceanographic conditions such as nutrient flux, productivity and prey abundance. Thus depending on the resultant physical and biological conditions, salmon populations may respond differently to cooler conditions. Coupled physical/biological models for the North Pacific are needed to study these processes.

The Karluk Lake sediment record has the lowest $\delta^{15}\text{N}$ values during the mid to late 1900s (Figs. 1 and 3). The reconstructed temperatures during this

period, however, are moderate relative to other cool periods. Furthermore, according to the tree ring reconstructions, several periods with similar temperature patterns occurred during the last few hundred years without being accompanied by the low $\delta^{15}\text{N}$ values that are observed during this century. Thus the Karluk Lake sediment $\delta^{15}\text{N}$ data may show a significant impact on salmon production by commercial fishing, as has been suggested by other workers (see Koenings and Burkett 1987a).

The long-term data from Karluk Lake also provide a view on variations in the carrying capacity of the system prior to commercial harvest that is useful for management. The data indicate that escapement fluctuated around an average of about 1 million fish/year for about 400 years prior to commercial exploitation. Such levels are not predicted from analysis of recent zooplankton stocks (Schmidt et al. 1997). This discrepancy points to the possible role of escapement in influencing the carrying capacity of the lake through nutrient input. A positive feedback may result from higher escapements through increased nutrient input, and subsequently higher production of nursery lake prey. The significant role of sockeye carcasses in the budgets of phosphorus (Koenings and Burkett 1987a) and nitrogen (this work), and the correspondence between escapement and sedimentary $\delta^{15}\text{N}$, suggest this feedback process may be important.

CONCLUSIONS

1. Sediment $\delta^{15}\text{N}$ appears to be a useful tool for reconstructing past changes in salmon abundance. In Karluk Lake, Kodiak Island, Alaska, sedimentary $\delta^{15}\text{N}$ tracks the historical record of escapement over the past 75 years.
2. The pattern in $\delta^{15}\text{N}$ and thus inferred sockeye escapement in Karluk Lake shows significant variation over the past 500 years. Significant changes in $\delta^{15}\text{N}$ occur over periods of 50 to 100 years. Prominent minima in $\delta^{15}\text{N}$ are observed in the mid to late 1900s, the early 1800s, the early 1700s, and the mid 1500s. Periods with relatively high $\delta^{15}\text{N}$ values occurred during the mid 1800s to the early 1900s, the late 1700s, around 1700, the early to mid 1600s, the late 1500s and the early 1500s. Estimated escapement was larger on average prior to commercial exploitation of the system.
3. There is no simple relationship between Karluk Lake sediment $\delta^{15}\text{N}$ and coastal temperature records reconstructed from tree rings. Some, but not all, periods of lower $\delta^{15}\text{N}$ correspond with negative temperature anomalies. If variations in the abundance of Karluk Lake sockeye are influenced by ocean conditions, the

differing responses during cool periods may indicate that very different oceanic conditions can result when the Gulf of Alaska experiences cool temperatures. There may be more than one mode or pattern of circulation in the North Pacific that results in relatively cool temperatures in the Gulf of Alaska, and thus the impacts on biological processes and hence salmon may be different. Further work on validating salmon abundance and temperature trends is clearly needed to support the preliminary ideas presented here. However, long-term data on salmon abundance and concurrent climatic and oceanic conditions, may provide insight to better understand how salmon production may respond to future climatic changes.

ACKNOWLEDGEMENTS

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Thermal Limits On The Ocean Distribution Of Steelhead Trout (*Oncorhynchus mykiss*)

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We describe sharp thermal limits to the ocean distribution of steelhead trout (*Oncorhynchus mykiss*) which restrict the distribution of steelhead to only a small fraction of the area of the North Pacific otherwise available for grazing. Maximum likelihood estimates indicate that: (1) steelhead exhibit a strong response to temperature in all regions of the North Pacific ocean and in all seasons of the year; (2) both upper and lower thermal thresholds exist; (3) although the thermal limits have been largely stable over the last 40 years, the temperature defining the southern edge of the steelhead distribution exhibits statistically significant fine-scale differences between regions ($<2^{\circ}\text{C}$) and between decades ($<0.5^{\circ}\text{C}$). As a result of this strong thermal control, steelhead are distributed in a narrow north-south band stretching across much of the width of the Pacific. Projections of the degree of ocean warming resulting from greenhouse gas induced climate change suggest that the ocean distribution of steelhead may shift far enough north under a $2\times\text{CO}_2$ climate that large areas of currently occupied ocean habitat could lie outside the range of these thermal limits by the middle of the next century.



INTRODUCTION

Steelhead trout (*Oncorhynchus mykiss*) are the most primitive North American member of the genus *Oncorhynchus* (Stearley and Smith 1993). The biology of steelhead has recently been reviewed by Burgner et al. (1992). Compared with the other members of the genus, steelhead possess a number of unusual characteristics, including the ability of a significant fraction of some populations to survive spawning, and then to return to the ocean for one or more years before returning to spawn again. Steelhead are also unusual in their migration timing, with many races returning to freshwater in the fall or early winter, and then overwintering in their natal streams before spawning in the spring.

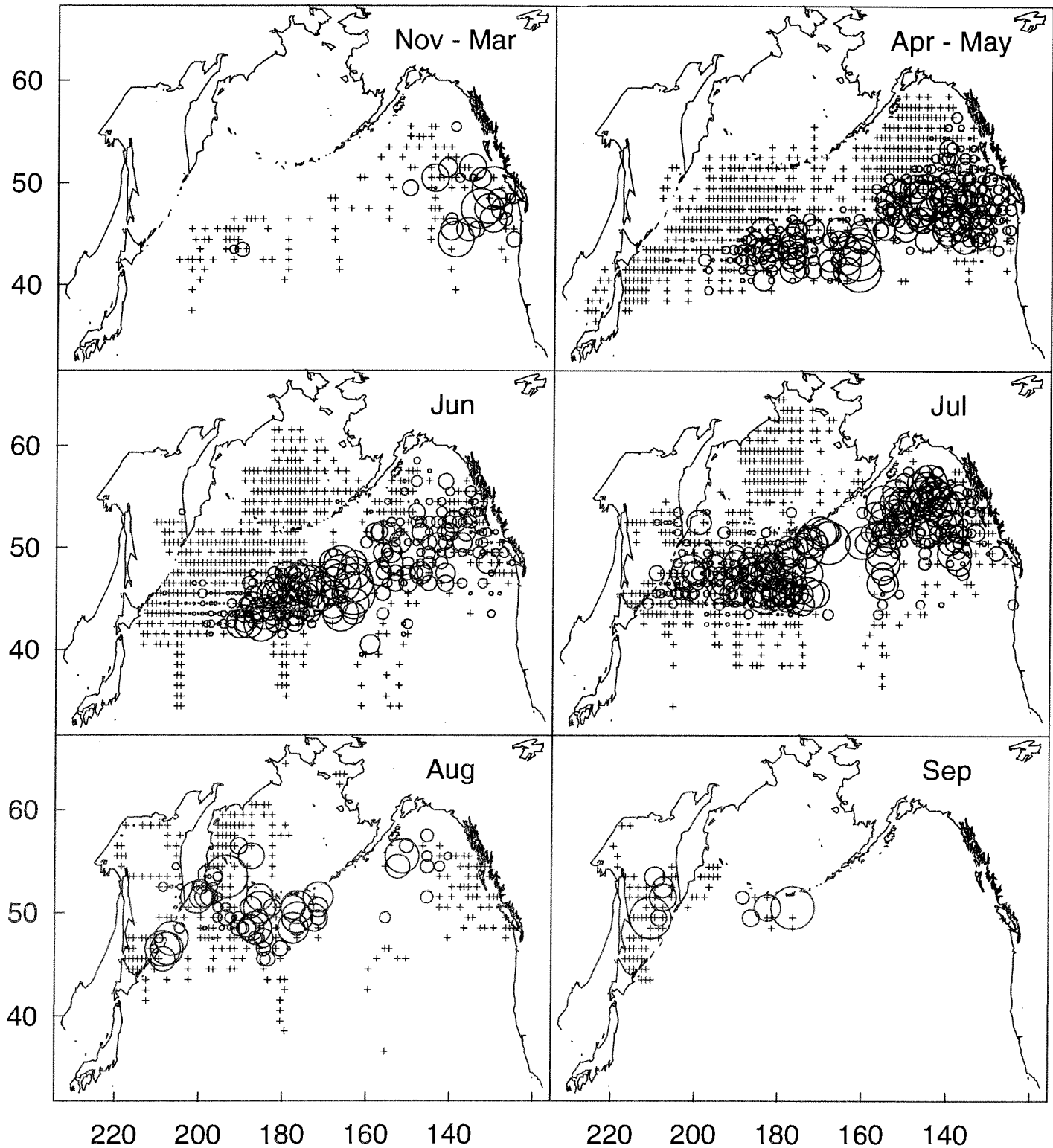
The unusual strategy of overwintering in freshwater prior to spawning may also be reflected in aspects of their marine distribution. In this paper, we report on an extensive analysis based on essentially all

available survey data useful for describing the ocean distribution and relative abundance of Pacific salmon since 1956. This data set has been used previously (Welch et al. 1998) to describe the ocean distribution and thermal limits of sockeye salmon (*O. nerka*). In this paper, we use the same data set to describe a very different but equally sharp relationship between the distribution of ocean temperatures and the marine distribution of steelhead trout.

MATERIALS AND METHODS

The steelhead analysis reported here is based on the extensive collection of ocean salmon survey data on the marine distribution of sockeye salmon (*Oncorhynchus nerka*) described in Welch et al. (1998). Briefly, these data comprise all available Canadian longline observations (and some similar American sampling) from studies in the Gulf of Alaska in the 1950s and 1960s (reported in Turner and

Fig. 1 Distribution of available observations, 1956-1996 (N=20,397) in winter (Nov-March), spring (April-May), and summer months. The panels show the relative abundance of steelhead averaged over all available data for 1° x 1° ocean regions. Individual observations were first normalized by dividing by the annual average catch for each sampling gear in order to remove effects due to interannual variations in abundance and gear type. A "+" indicates no catch, and an open circle is used to indicate relative abundance; circle radius is proportional to $\log_{10}(\text{CPUE})$. Although sampling in warmer (southern) regions of the North Pacific is relatively sparse throughout the year, steelhead are clearly distributed in a relatively narrow band across the North Pacific, with greatest abundance in southern and eastern regions of the subarctic North Pacific.



Aro 1968), results from Canadian high seas gillnet surveys for the 1950s and 1960s (found in archives of the Pacific Biological Station), and all Canadian high seas survey results for the 1980s and 1990s. These data were combined with the results from Japanese high seas salmon surveys for the period 1972-1996. Japanese data for earlier periods were not in a consistent format amenable to computer analysis.

In order for comparisons between time periods and areas to be made on a consistent basis, longline, gillnet, and trawl catch data were standardized to a common unit of effort by dividing by the number of hachi of longline (1 hachi=138m of longline) and tans of gillnet (1 tan=50m of gillnet). Annual mean catches by gear type were calculated and the CPUE data normalized by this value in order to reduce the effects of differences in gear efficiency and inter-annual variation in steelhead abundance on the analysis; however, the general findings we report are not dependent on this manipulation.

RESULTS

General Distribution

The general ocean distribution of steelhead trout is similar to that reported in Burgner *et al.* (1992), with clearly defined northern and southern limits resulting in a band-like distribution across the North Pacific (Fig. 1). Although the sporadic distribution of sampling effort in the winter limits interpretation, the highest steelhead densities are found close to the North American coast. In spring (April-May) and early summer (June), the ocean distribution shifts southward and extends westward, with the greatest southern extent achieved in spring and highest densities observed in the central North Pacific and southern Gulf of Alaska. By late summer (July-August), the distribution shifts north again so that steelhead appear to be distributed in a band just south of the Aleutian archipelago, although the absence of sampling in the North Pacific from 160-180°W in August limits this interpretation; however, despite extensive sampling in June and July, steelhead were only sporadically found in the Bering Sea.

Relationship to Temperature

The band-like structure to the distribution raises the twin questions of what determines these geographic limits, and why steelhead are not found in regions to the north where other salmonids are. A comparison with sea surface temperature (SST) shows a relatively well-defined upper and lower thermal limit to the distribution in most months (Fig. 2), with the temperatures determining both the upper and lower thermal limits increasing into summer. Breaking the

data into three regions shows that different regions have slightly different upper thermal limits for the same month, and that the distribution of steelhead relative to SST is consequently sharper than when the data are aggregated.

By splitting the data into regions and by decades an even sharper relationship is evident between temperature and steelhead distribution. Comparing the data for July, when the greatest number of observations is available (Fig. 3), a nearly knife-edge relationship defining the southern limit to the steelhead distribution is evident in most possible comparisons. The northern limit also appears to be sharply defined, but here the relationship is ambiguous because there are few observations within the North Pacific taken at water temperatures low enough to clearly establish that steelhead are absent from lower temperature areas. In essence the data are confounded because steelhead are found in almost all regions of the central and western North Pacific up to the Bering Sea; their absence from the colder waters of the Bering Sea raises the question of whether steelhead avoid the temperatures found in the Bering Sea or the region itself.

The 1970s and 1980s data for the central North Pacific suggest that it is the lower temperatures that are being avoided, because the abundance of steelhead appears to decline at temperatures just above the minimum observed temperatures (Fig. 3); if correct, then steelhead are limited to the north by SST rather than by the presence of the Aleutian archipelago. (Data for the eastern North Pacific is uninformative, because observed SSTs were always higher than the apparent thermal limit for regions to the west). However, if the data for June, when the northern limit of the distribution clearly occurs to the south of the Aleutians (Fig. 1), are divided as in Fig. 3 then a sharp northern limit defined by temperature, not the position of the Aleutian archipelago, is evident.

A quantitative estimate of the temperature defining the upper thermal limit and its associated uncertainty can be obtained by fitting a curve through the CPUE observations (Welch *et al.* 1995). In this approach, each fish in the population is assumed to have a specific individual temperature which it will not exceed, and the response observed is the fraction of the population remaining at each temperature. Assuming that the variability in the response of individual steelhead to temperature is Gaussian, then the CPUE at the observed temperature for the i th observation, $n(T_i)$, is

$$n(T_i) = \mu_i [1 - \Phi(T_i | T_{crit}, \sigma_T)]$$

where $\Phi(T_i | T_{crit}, \sigma_T)$ is the value of the cumulative normal probability distribution with parameters T_{crit} and σ_T , and observed temperature at the i -th location,

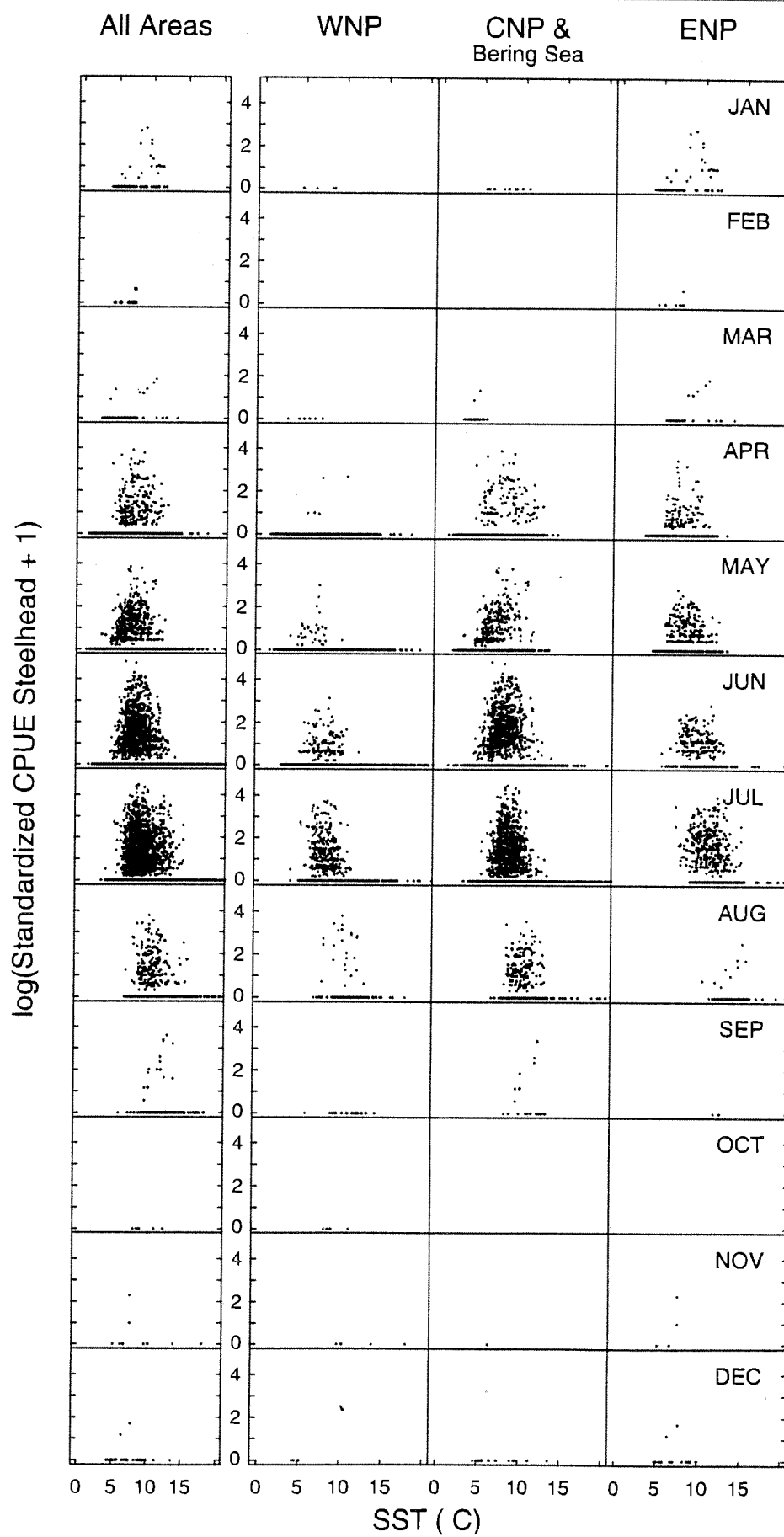


Fig. 2 Monthly comparison of log (Standardized CPUE Steelhead + 1) vs temperature for all areas and decades combined, and for 3 separate areas of the North Pacific. The North Pacific has been split into three different regions using the definition (ENP < 165° E, 140° E < WNP < 160° W, and 165° E < CNP < 160° W). Under this transformation observations of zero catch remain as zero. Sharp upper and lower thermal bounds on the steelhead distribution are evident. Note that the temperature defining the upper thermal limit increases into the summer in all areas.

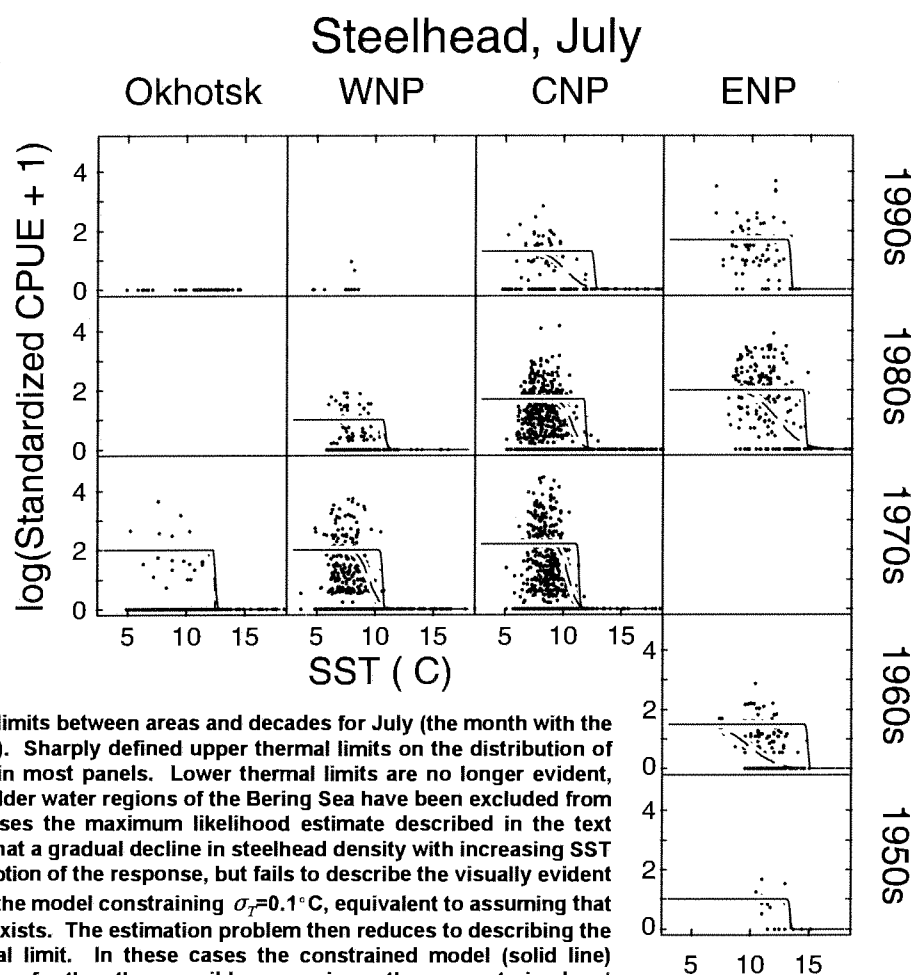


Fig. 3 Comparison of thermal limits between areas and decades for July (the month with the greatest available data). Sharply defined upper thermal limits on the distribution of steelhead are evident in most panels. Lower thermal limits are no longer evident, because data for the colder water regions of the Bering Sea have been excluded from the plots. In some cases the maximum likelihood estimate described in the text (dashed line) indicates that a gradual decline in steelhead density with increasing SST provides the best description of the response, but fails to describe the visually evident thermal edge. We refit the model constraining $\sigma_T=0.1^\circ\text{C}$, equivalent to assuming that a sharp step-function exists. The estimation problem then reduces to describing the position of the thermal limit. In these cases the constrained model (solid line) captured the thermal edge; for the other possible comparisons the unconstrained and constrained estimates of the shape of the response are nearly identical. Results for other months are similar.

T_i . The parameters T_i and σ_T represent, respectively, the critical temperature at which the steelhead density falls to 50% of the value in the interior of the distribution (i.e. the mid-point of the southern edge), and the rate at which abundance changes around this temperature. The mean steelhead density in the interior of the geographic distribution, as measured with each of the $j=1, \dots, 3$ possible gears is defined as μ_j . In this model, we assume that the measured response of abundance to temperature is the same for all sampling gears, and that the only difference between gears is in their average CPUE.

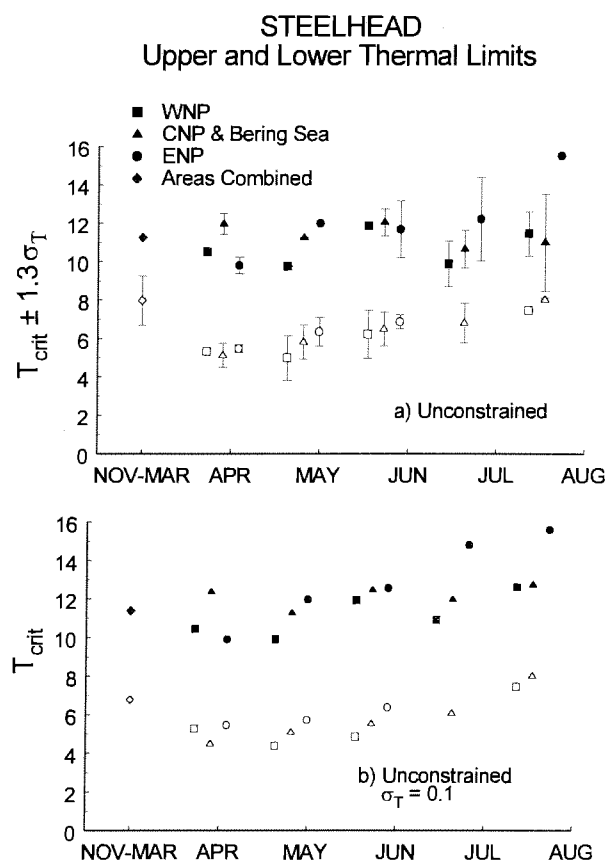
Fig. 4 shows the monthly changes in the maximum likelihood estimates of T_{crit} and σ_T , plotted as $T_{crit} \pm 1.3 \sigma_T$; over this estimated temperature range abundance declines by an order of magnitude. For winter through early summer months the upper thermal limit occurs at ca. 11°C , and then increases to $12\text{--}15.5^\circ\text{C}$ by August, depending on area. In general, the coldest thermal limits for a given month are found in the western North Pacific and the warmest limits are found in the eastern North Pacific. In most possible comparisons the southern edge of the

distribution is extremely sharply defined, with abundance dropping by an order of magnitude in 1°C or less. Given that the monthly estimates of the thermal range over which abundance declines are based on data from all decades, and that variation between decades in the position of the thermal limits (see below) will blur these edges, the sharpness of the edge is remarkable.

In most cases, fits of this model provided a realistic description of the sharp thermal limit evident in the data. However, in some cases the fitted model indicated that abundance decreased steadily with increasing SST over a broad range of temperatures, but failed to describe the visually evident edge (Fig. 3). We therefore refit the model after constraining $\sigma_T=0.1^\circ\text{C}$, which is equivalent to assuming that a sharp edge to the distribution exists, and then estimating the temperature at which the edge is located. The constrained estimates of the critical upper and lower temperature defining the distribution were identical to the unconstrained fits in most cases (Fig. 4).

The upper thermal limit tends to occur at higher

Fig. 4 (Upper Panel) Estimated critical temperatures defining the upper and lower thermal limits to the steelhead distribution, T_{crit} , and the estimated temperature range over which the abundance drops by a factor of ten, $T_{crit} \pm 1.3\sigma_T$. The estimated range is smaller than the size of the symbol when vertical bars are not evident. (Lower Panel) Estimated critical temperatures for the constrained model, assuming $\sigma_T = 0.1^\circ\text{C}$. The upper thermal limit occurs at approximately 11°C in winter, and then increases slightly to $12\text{--}15^\circ\text{C}$ in late summer, depending on region. Some change in the lower thermal limit is also evident. Lower thermal limits were estimated in a similar manner to the upper thermal limits (Welch et al 1995).

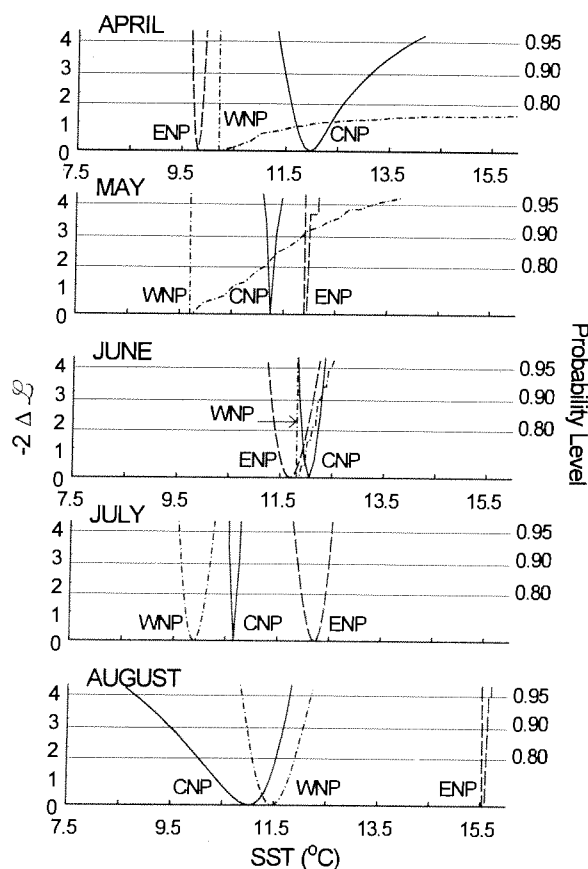


temperatures later in the summer or in progressively more eastern regions of the North Pacific (Figs. 2 and 4). An evaluation of the statistical significance of these differences can be made by comparing the likelihood profiles for individual estimates of T_{crit} . A likelihood profile is defined by taking twice the difference in log-likelihoods from the maximum likelihood estimate $\mathcal{L}^*(T_{crit}^*, \sigma_T^*, \mu_{j=1,\dots,3}^*)$ or $-2\Delta\mathcal{L} = -(\mathcal{L}_{alt} - \mathcal{L}^*)$, fixing T_{crit} at possible alternative temperatures T_{alt} and finding the likelihood $\mathcal{L}_{alt}(T_{alt}, \sigma_T^*, \mu_{j=1,\dots,3}^*)$ associated with the new constrained maximum likelihood estimates for σ_T and steelhead density under this alternative assumption about the temperature defining the edge. This value is

approximately distributed as $X^2_{1df, 1-\alpha}$ so an approximate 95% confidence interval on an estimated parameter can be defined by finding the temperature bounds at which $-2\Delta\mathcal{L} = X^2_{1,0.95} = 3.81$.

For a given region, comparison of the likelihood profiles of the estimated temperature defining the upper thermal limit shows that the temperature defining the southern edge to the distribution generally increases in the late summer (Fig. 5) and that the

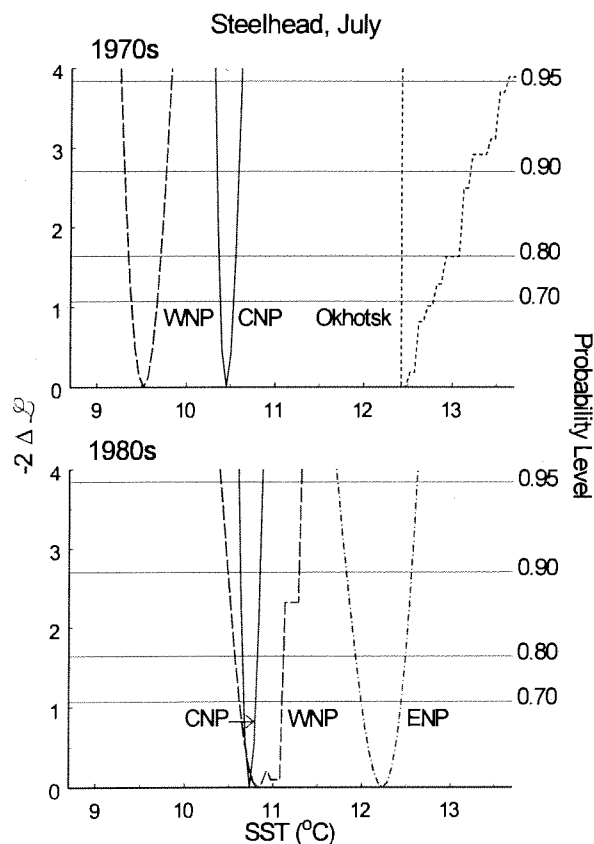
Fig. 5 Comparison of the monthly change from April to August in the temperature defining the upper thermal limit (southern boundary) of the steelhead distribution. Unlike Fig. 4, these figures show the statistical uncertainty (as the likelihood profile) in the estimate of the critical temperature defining the southern edge to the distribution; they do not indicate the relative sharpness of the edge in different area or months. The upper thermal limit for steelhead was generally highest in the Gulf of Alaska. In all areas there is a general increasing trend with time in the temperature at which the thermal boundary is expressed. Likelihood profiles are based on calculating twice the difference in log-likelihoods for a given temperature from the unconstrained maximum likelihood estimate of T_{crit} , which occurs at $-2\Delta\mathcal{L} = 0$, allowing all other parameters to vary freely. Probability levels are based on a chi-squared distribution with one degree of freedom, appropriate for testing differences in one parameter. The width of the profile at a given probability level defines the confidence interval on the estimated temperature describing the upper thermal limit.



differences between months for a given region only become statistically significant in the late summer, supporting the impression from Fig. 4. Fig. 5 also demonstrates that the differences in the thermal location of the southern boundary in different regions of the Pacific are also significant in most possible comparisons, although the between-region differences are generally smaller than the differences between months.

Rather large differences in the temperature at which the upper thermal limit is expressed occurred between regions during the 1970s and 1980s (Fig. 6),

Fig. 6 Comparison of the change between areas in the 1970s and 1980s for the unconstrained estimates of the July upper thermal limits. The upper thermal limit was higher in the 1980s than the 1970s, and also higher in the Okhotsk Sea and Gulf of Alaska (ENP). Ocean productivity was likely higher in the 1980s than the 1970s because of more intense meteorological conditions (Beamish and Bouillon 1993), and also higher in the Gulf of Alaska and Okhotsk Sea than the central and western North Pacific because of enhanced nutrient availability from upwelling and estuarine recirculation processes (Tully and Barber 1960).

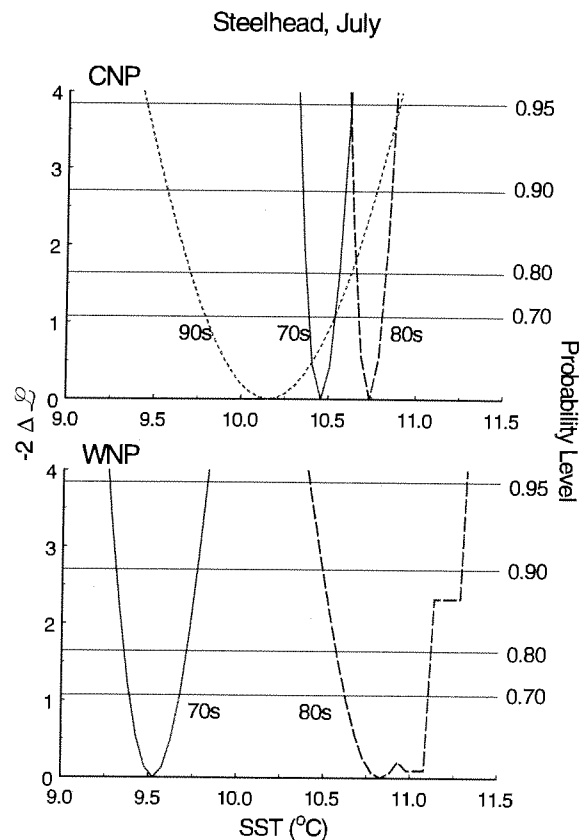


although these differences are smaller than the seasonal changes. In general, the thermal limit for a given region was found at higher temperatures in the 1980s than in the 1970s. (Owing to limited catches in

the 1990s, a regional comparison of the thermal limits in the 1990s is not possible; cf. Fig. 3). The differences are generally consistent with the hypothesis that higher thermal limits are found in regions of enhanced productivity due either to increased nutrient input from estuarine recycling (the Okhotsk Sea) or upwelling (the eastern North Pacific; Tully and Barber 1960).

Further support for this reasoning can be found in the fine scale thermal differences ($<0.5^{\circ}\text{C}$) in the position of the southern limit evident between decades (Fig. 7). Estimating the position of the upper thermal

Fig. 7 Likelihood profiles comparing the changes in the unconstrained estimates of the critical temperature defining the July upper thermal limit for the central and western North Pacific. In both areas, thermal limits were greatest in the 1980s. The limited data for the 1990s is ambiguous, but suggests that productivity may have declined from the level of the 1980s in the central North Pacific.



limits indicates that in both the central and western North Pacific the upper thermal limit was found at slightly higher temperatures in the 1980s than the 1970s. A similar comparison for the eastern North Pacific is unfortunately not possible, because 1990 surveys in the Gulf of Alaska did not extend sufficiently far south into waters above the thermal limit for steelhead (cf. Fig. 3).

Although the differences are generally consistent

with the inter-regional pattern found for sockeye salmon (Welch et al., 1998), the thermal limits in the eastern North Pacific appear to be higher than in the Okhotsk sea, which was the reverse of that found by Welch et al. for sockeye. However, the more limited catches of steelhead trout prevent a fully consistent comparison, as the between-region differences in steelhead thermal limits are also confounded with decadal differences.

A potential projection of changes in the ocean range of steelhead trout can be made by examining the predicted position of the winter and summer isotherms limiting the distribution of steelhead trout under current and future climates. Using the Canadian Climate Center's coupled atmosphere-ocean model (Boer et al. 1992; McFarlane et al. 1992) to make this projection indicates that a doubling of atmospheric CO_2 concentration is likely to shift both the upper and

lower isotherms defining the steelhead distribution well to the north, significantly changing the marine distribution of steelhead trout (Fig. 8), and potentially disrupting aspects of their marine life history.

DISCUSSION

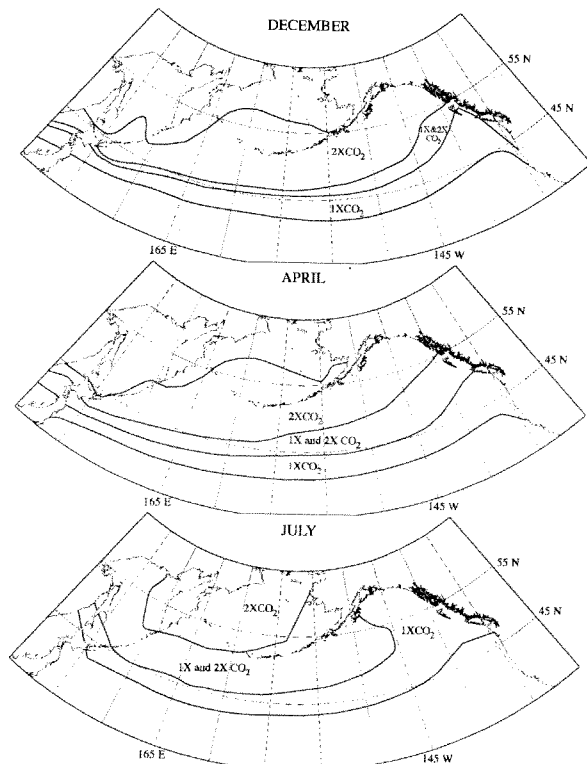
A particularly interesting issue in assessing the potential impact of climate warming on steelhead trout is raised by the intersection of the upper and lower thermal limits determining the ocean distribution of steelhead with the North American coast. In both winter and spring the location of these thermal limits under the current ($1\times\text{CO}_2$) climate roughly matches the observed freshwater spawning distribution of steelhead in North America (Burgner et al. 1992). This raises the fascinating question of whether the observed spawning distribution primarily reflects the needs of the smolts in freshwater, or whether the thermal requirements of steelhead after entering the ocean are shaping the distribution of steelhead spawning populations on the continent. If the latter influence is of importance then the projected shift northwards in the ocean distribution of the isotherms defining the marine distribution of steelhead with climatic warming could be large enough to no longer overlap with the area currently defining where the bulk of North American steelhead populations are found.

Although forecasts of future ocean climate under increased levels of greenhouse gas concentration are still speculative, it is generally accepted that significant warming in northern latitudes will occur as a result of continuing greenhouse gas emissions (IPCC 1996). The sensitivity of the ocean distribution of steelhead trout to ocean temperatures raises the important question of what underlying mechanism causes such sharp thermal avoidance behaviour to be expressed, and what impact future changes in climate may have on their productivity.

The distributional controls for steelhead trout we describe are qualitatively and quantitatively different from those for sockeye salmon, where the large amplitude of the annual cycle in temperatures defining the upper thermal boundary results in substantial geographic movement of sockeye over the year (Welch et al. 1998). Steelhead are largely absent from colder (northern) regions of the North Pacific occupied by the other species of Pacific salmon, particularly in winter and spring, and the upper thermal limit is therefore amongst the warmest observed for much of the year. As a result, the oceanic distribution that results is a long thin band stretching across much of the North Pacific ocean. This band overlaps very little with much of the marine habitat exploited by other species of Pacific salmon.

Our findings are similar to the general

Fig. 8 Comparison of the projected steelhead salmon distribution under current and future climates (Albers equal area projection). Under a doubling of atmospheric CO_2 the location of acceptable thermal habitat in the North Pacific is predicted to change significantly. For these projections the thermal limits have been taken to be the constrained estimates shown in Fig. 4. Note that the intersection of the upper and lower thermal limits with the North American coast in winter and spring closely matches the freshwater spawning distribution of North American steelhead. The projected intersection of the same thermal limits with the North American coast under a doubling of atmospheric CO_2 shows little overlap with the current spawning distribution.



distributional response to temperature for steelhead trout reported by Burgner et al. (1992). Our results differ in demonstrating that the overall marine distribution of steelhead is much more strongly determined by temperature than previously thought, and in showing that fine scale regional and decadal scale differences in upper thermal limits exist. The latter are consistent with the theory that the upper thermal boundary exists as a result of balancing energy gain from foraging with energy loss due to metabolic rate processes, the major conclusion of Welch et al. (1998).

The different characteristics of the steelhead trout distribution suggest that the evolutionary factors shaping the ocean distribution of steelhead are significantly different from the more evolutionarily advanced members of the genus. One unusual point in the biology of steelhead is the migration of maturing individuals into freshwater in the summer or fall, several months prior to spawning in the spring.

By overwintering in freshwater sexually mature steelhead effectively move into the lower temperature regimes sought out by sockeye in winter, but do so in a way that minimizes distributional overlap with other species of salmon. While a simple explanation for the different winter thermal limits observed for steelhead and sockeye in the ocean, the explanation is not fully satisfactory because steelhead spend several winters in the ocean prior to maturation without apparently moving to the much colder waters characteristic of sockeye.

We have suggested elsewhere that the sharpness of the response observed at the upper thermal limit in sockeye salmon is most consistent with avoidance of thermal environments where basal metabolic rates exceed the energy gained from feeding (Welch et al. 1998). The movement of both steelhead and sockeye into warmer regions by late summer, when prey levels are probably highest, is consistent with this observation, as are the regional and decadal scale differences. However, it is unclear whether the clear evidence for expression of a lower thermal limit in steelhead is also consistent with this mechanism. A better appreciation of the biological basis underlying the expression of this behaviour would contribute significantly to our understanding of the ocean migrations and general evolutionary biology of salmon during the marine phase of their life history.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge our many colleagues and predecessors who contributed to the

collection of the data analyzed here over the past 40 years, and to the many ship's crews who supported this work. The existence of the widespread and remarkably sharp thermal limits which we report here would not have been possible without the dedicated efforts of a wide range of professionals. We dedicate this paper to their contributions.

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Do Hatchery Salmon Affect the North Pacific Ocean Ecosystem?

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Releases of hatchery-reared anadromous salmon into the North Pacific Ocean are currently estimated between 5 and 6 billion juveniles per year. Wild spawning salmon may produce an additional 4 to 5 times this number of juveniles. With as many as 25 billion juvenile Pacific salmon annually entering the ocean and currently producing over 1.0 million mt of returning adults, salmon survival and production in the North Pacific Ocean is currently at historically high levels in spite of depressed runs and endangered stocks in some regions. Biological changes in size and age at maturity of some stocks have raised questions on the density effects of high abundance, and on the long-term well being and health of salmon stocks. Changes in size and age notwithstanding, favorable ocean conditions for survival and growth, even growth at reduced levels, have produced historic numbers and biomass of salmon suggesting the evidence for limitations in the carrying capacity for these fishes is inconclusive. Important studies are underway in several countries to better understand the effects of hatchery-wild stock interactions on the spawning grounds but little attention has been directed toward this issue in the ocean. New mass marking and identification technologies for both hatchery and wild fish provide mechanisms for investigating the interactions of salmon in the open ocean. Given biological concerns about ocean carrying capacity and socio-economic issues associated with record runs, should NPAFC member countries consider cooperative quotas to limit production of salmon around the North Pacific Rim? If implemented, each country could determine what portion of its quota would be derived from wild and hatchery production.



INTRODUCTION

North Pacific Rim countries with significant runs of anadromous salmon utilize hatcheries or other types of enhancement for some portion of current stock abundance. The portion of salmon abundance dependant on hatchery production, however, varies considerably among countries and across regions within countries. Although the present level of salmon abundance is at or near historic highs, some regions still have depressed runs of specific stocks. For example, both Alaska and Japan recorded all time record commercial harvest of salmon in 1995 reaching 477 and 246 thousand metric tons (mt) respectively in those regions. Preliminary estimates indicate capture fisheries for salmon throughout the Pacific Rim in 1995, not including sport fisheries, exceeded one million mt, probably an all time record. At the same time the depressed status of some stocks in Pacific Northwest states of Washington, Oregon, Idaho, and California has necessitated additional listings under the Endangered Species Act (ESA) of the United States.

Concomitant with record-level runs of adult salmon are record releases of juveniles from hatcheries. Estimates of the total numbers of juvenile salmon released from Pacific Rim hatcheries have

increased from 2.6 billion in 1976 (McNeil 1979) to 4.4 billion in 1985 (McNeil 1988) to 5.5 billion in 1992 (Heard 1995). Much of the recent increase has occurred in Alaska where releases have grown from 6 million juveniles in 1976 to 1.3 billion in 1992 (Table 1). Zorpette (1995) suggested the number of juvenile salmon entering the ocean from wild spawners each year is perhaps 20 billion individuals.

With roughly 25 billion juvenile salmon entering the North Pacific Ocean each year, production of adults originating from wild spawning parents and hatchery programs varies greatly among regions. In the United States for example, the principal source of salmon caught in capture fisheries is in Alaska. Hatchery fish have accounted for 16-30 percent of the Alaskan harvest in recent years (Heard 1996). Within Alaska, however, hatcheries make no contribution to fisheries in some areas (Bristol Bay) and over 70 percent in others (Prince William Sound). Contributions from hatcheries now account for over half of the salmon produced in the Pacific Northwest (NRCC 1996). Production from hatcheries comprises almost all of the salmon caught in Japan and in Russia hatcheries are major contributors to salmon production in the Sakhalin-Kurile Islands region.

Table 1. Estimates for numbers of juvenile salmon released into the North Pacific Ocean and adjacent seas in 1992 by hatcheries, enhancement and ocean ranching programs, in millions of fish (from Heard 1995).

Country/Region	Species						Totals
	Pink	Chum	Sockeye	Coho	Chinook	Masu	
Canada ¹	64.7	200.4	286.3	23.5	58.8	---	633.7
China ²	---	1.0	---	---	---	---	1.0
Japan ³							
Hokkaido	140.8	1,053.9	2.9	---	---	13.5	1,211.1
Honshu	---	987.7	---	---	---	3.4	991.1
Korea ²	---	10.0	---	---	---	---	10.0
Russia ⁴							
Sakhalin/Kuriles	584.5	206.8	---	---	---	---	791.3
Other	11.7	67.7	0.2	0.1	0.1	---	79.8
United States							
Alaska ⁵	802.8	436.4	75.3	20.7	10.9	---	1,346.1
Other ⁶	2.4	66.1	0.2	112.5	267.0	---	448.2
Totals	1,606.9	3,030.0	364.9	156.8	336.8	16.9	5,512.3

¹ Data from E.A. Perry, SEP, Canada DFO.² Data from China and Korea provided by H. Kawamura, Hokkaido Fish Hatchery.³ NPAFC DOC. 40.⁴ Data from F. Rukhlov, Sakhalin Branch, TINRO.⁵ Data from NPAFC, Doc. 33; W.R. Heard, NMFS; S. Leask, Metlakatla Indian Community.⁶ Data from K. Johnson, PSMFC; I. Blanketship, WDF&W; C. Corrarino, ODF&W; and F. Fisher, CDFG.

ABUNDANCE-RELATED BIOLOGICAL ISSUES

During the past 15-20 years record levels of salmon production throughout much of the Pacific Rim have occurred simultaneously with significant biological changes in many stocks. Decline in average size of returning adults and increase in average age at maturity for some stocks pose important questions about relationships between levels of abundance, climatic factors, and capacity of the North Pacific Ocean to produce salmon (Ishida et al. 1993; Rogers and Ruggerone 1993; Kaeriyama 1996; Bigler et al. 1996). Paramount among these questions is the extent to which recent record levels of hatchery production may have influenced these biological changes.

There is no doubt that ocean survivals for many stocks of Pacific Rim salmon have been high in recent years. One can surmise, therefore, given the high levels of juveniles entering the ocean, both from hatchery and wild stocks, that survival is not negatively correlated with abundance, at least under current conditions. Favorable oceanographic and climatic factors throughout much of the Pacific Rim marine environment are likely responsible for current high survivals (Brodeur and Ware 1992; Beamish and Bouillon 1993; Klyashtorin and Smirnov 1995) irrespective of the numbers of salmon in the ocean.

Density-dependent effects of decreased size and increased age at maturity in certain salmon stocks may be associated with specific time-area phenomena. Rogers and Ruggerone (1993) suggested carrying capacity limitations for Bristol Bay sockeye salmon may be... "on migratory routes of returning adults when the fish are most concentrated and their growth

most limited by their food supply". Ishida et al. (1993) found that, after 1970, significant decreases in body weight, scale radius, and width of the third-year growth zones of scales occurred in age 4 Japanese and Russian chum salmon. They attributed the cause to increasing abundance of Japanese stocks and to overlapping ocean distribution patterns of immature chum salmon from the two countries. While evidence of density-dependent effects on growth of many salmon stocks during some portion of their life history at sea seems unequivocal, there is little cogent evidence of density-dependent marine mortality or that any reduction in overall production of salmon has occurred under recent oceanographic conditions.

HATCHERY-WILD STOCK INTERACTIONS

Many recent conferences, symposia, and workshops have addressed the issue of hatchery-wild stock interactions in salmonids. Most of this attention has been directed at interactions in freshwater spawning and rearing habitats or on harvest management strategies in coastal or riverine fisheries. Biological concerns in freshwater include potential adverse impacts on wild stocks through genetic interactions including loss of diversity and fitness through interbreeding with domesticated hatchery fish (Waples et al. 1990; Hinder et al. 1991; Waples 1991). Other concerns involve depletion of wild stock spawners through egg collections for hatcheries, or over harvesting weak wild stocks in fisheries targeted on more abundant hatchery fish (Walters 1988; Hilborn 1992).

These and other related issues have spawned a

plethora of continuing, sometimes heated, discussions in North America over the pros and cons of Pacific salmon hatcheries and of the future role of hatcheries in salmon management (Hilborn and Winton 1993; Winton and Hilborn 1994; Thomas and Mathisen 1993; Martin et al. 1992; Daley 1993; Incerpi 1996). Although habitat losses due to human activities in the Pacific Northwest have been major contributors to the extinction, threatened, or endangered status of many salmon runs in that region, the past extensive use and management practices of hatcheries is now thought also to have had serious adverse effects on natural populations (NRCC 1996).

Only recently have hatchery-wild stock concerns been expanded to include the ocean environment. While there are many issues associated with these concerns they, at least partly, are reflected in the following question. Do large numbers of hatchery salmon influence the ecology of the North Pacific Ocean; specifically do hatcheries affect the carrying capacity of the ocean environment to produce salmon?

Using a simple carrying capacity simulation model and assuming that salmon out-compete other potential predators for their prey, Honkalehto (1984) estimated that Pacific salmon.... "consume less than 0.5% of the available zooplankton biomass and less than 5.0% of the available larval fish biomass". In another study also using an ecosystem simulation model, Favorite and Laevastu (1979) postulated the apparent North Pacific Ocean carrying capacity..... "in respect to salmon can easily sustain ten times higher standing stock of salmon than at present (provided that salmon is very competitive for food and predation on salmon is not a limiting factor)".

It has been suggested (Bigler et al. 1996) that expansion of Pacific Rim enhancement programs in the 1980s and early 1990s is a probable factor in the ocean-wide reduced size of salmon. These authors also argue the inverse relationship between the current high abundance and reduced size of salmon indicates there is a limitation to the salmon-sustaining resources of the ocean. There are ultimate limitations for any biological ecosystem, however, it can also be argued, given current record levels of abundance, that recent oceanic conditions around the Pacific Rim have provided very favorable resources for sustaining salmon. Reduced size notwithstanding, favorable ocean conditions for survival and growth, even growth at reduced levels, have produced record historic levels of salmon abundance and biomass. Pearcy (1992) felt that growth rates were more sensitive than survival rates and that growth would provide the best evidence for density dependence. He found, however, that evidence was inconclusive for limitations in the carrying capacity of salmonids in the North Pacific.

Beamish and Bouillon (1993) concluded that recent trends in salmon abundance were not primarily

a result of fishing effort, management actions, or artificial rearing, but rather were strongly linked to climatic factors and a favorable ocean environment. In another report Beamish (1993) found that sudden physical changes in marine environments dramatically affects population dynamics of many fishes, almost simultaneously over vast ocean areas. Density-dependent effects resulting in reduced size may reflect limited time-area food or space resource bottlenecks along ocean migration pathways. Overall survival, however, may be more reflective of the integrated, collective influences of marine environments for salmon production. It seems, therefore, that a concept of ocean carrying capacity for salmon (or any other group of organisms) is not a fixed or static situation and precise definitions are difficult, even evasive. Ocean carrying capacity is a highly dynamic ecosystem principle that fluctuates often, perhaps in a cyclic manner, and is strongly influenced by a plethora of ecological variables, and, generally, is poorly understood.

OCEAN TRACKING HATCHERY-ORIGIN AND WILD-ORIGIN SALMON

Recent developments in stock identification and in mass marking technologies provide avenues for examining interactions of hatchery and wild salmon in the open ocean environment. Coded wire tags (cwt) are used extensively in North America for research and management of both hatchery and wild salmon. This technology, used principally on chinook and coho salmon, requires placing tags in individual fish and is more widely used on hatchery fish than on wild fish. Nevertheless, around 40 million cwt marked juvenile salmon are released into the ocean each year (Johnson and Longwill 1993) and this technology has provided much of the knowledge currently used in scientific management of many coast wide stocks and fisheries.

The use of controlled thermal events in hatcheries allows development of specific recognizable banding patterns on otolith structures of embryonic salmonids (Volk et al. 1990; Schroder et al. 1996). Banding patterns developed on embryos remain identifiable throughout subsequent life stages. This technology is developing rapidly and now provides the potential to use bar code symbology to identify point sources, and even differential treatments within groups of fish from the same hatchery. Fishery science now has the ability to otolith mark every hatchery salmon released into the North Pacific Ocean (Volk et al. 1994). Otolith marks on hatchery-origin salmon are now used as a real-time decision tool for management of some North American commercial fisheries and in monitoring homing and straying patterns of hatchery fish.

In 1996 the estimated number of otolith marked

salmon released from North American hatcheries was 870 million fish (Table 2). Expanding otolith thermal banding to other North American and to Asian hatcheries, perhaps with some form of an oversight role by North Pacific Anadromous Fish Commission (NPAFC), would provide a powerful research potential to more fully understand distribution, migration and behavior patterns, throughout the Pacific Rim, of hatchery-origin salmon in the ocean environment. Some recent projects examining otolith patterns of ocean-caught juvenile and immature salmon, including those caught as unintended bycatch in non-salmon fisheries, are just beginning to realize some of this potential (Ignell et al. 1997).

Wild stocks of salmon can be identified in the ocean at differing levels of resolution with a variety of procedures including scale pattern analyses (Major et al. 1978; Myers et al. 1987), genetic stock identification (gsi) techniques (Beacham et al. 1987; Utter 1989; Wilmot et al. 1992), parasite markers (Margolis 1963; Urawa et al. in press), and applications of DNA technology (Park et al. 1994). Species-wide protein electrophoreses baselines now provide a basis for estimating the regional origins of complex mixtures of salmon sampled in the open ocean (Winans et al. in press; Hawkins et al. in press).

Another procedure for identifying wild stocks of salmon in the open ocean involves spectrographic analysis of trace elements found in the composition of primal bone structures. The procedure, laser ablation inductively coupled plasma mass spectroscopy (LA-ICPMS), analyzes micro vaporized portions of otolith or scale nuclei to detect differences in elemental composition that reflects uniqueness of the hydro geochemistry of natal waters. Using discriminant function analysis this concept has been successfully used to identify separate stocks of steelhead trout (*O. mykiss*) in the Skeena River watershed of British Columbia (Robert Brown, Elemental Research Inc., personal communication) and Atlantic cod (*Gadus morhua*) from different spawning grounds in the northwest Atlantic (Campana et al. 1994).

The idea of an elemental fingerprint within the

scale nucleus of individual stocks of salmon is an exciting concept that should be closely examined as a tool to identify wild stocks in the ocean. This principle likely holds the most promise for species with sufficient residence time to firmly establish a fingerprint in freshwater habitats. Furthermore, extensive scale collections by researchers around the Pacific Rim could provide a readily available database for many stocks.

DISCUSSION

There are many unanswered questions about salmon ecology in the North Pacific Ocean (Pearcy 1992), and more specifically about how hatchery and wild fish may or may not interact in the marine environment. Are ocean distribution patterns similar for wild and hatchery salmon from the same region or river system? When young fish leave riverine and near shore coastal regions, do wild and hatchery salmon from the same areas mingle together or remain in relatively discrete groups? Are there differences in dietary preferences of the two groups? Specific answers to these and other similar questions are limited, hence a definitive answer to the question title of this paper, "Do hatchery salmon affect the North Pacific Ocean ecosystem?" is equivocal.

With few exceptions there is lack of cogent evidence that hatchery salmon have any direct effect on the North Pacific Ocean ecosystem. One exception noted by Ogura and Ito (1994) documented a change in the known ocean distribution of chum salmon. These authors concluded an enlargement in ocean distribution of Japanese chum salmon was associated with dramatic increases in numbers of chum salmon produced by Japanese hatcheries. Ocean research in other regions should determine if large hatchery releases of juvenile salmon are also affecting ocean migration and distribution patterns. Increased otolith marking of hatchery juveniles and expanded use of available tools for identifying wild stocks, coordinated with an effective ocean sampling program, can provide new insight into these and related issues.

Table 2. Estimated number of otolith marked juvenile salmon released from North American hatcheries in 1996 (in millions).

Area	Species					Total
	Pink	Chum	Sockeye	Chinook	Coho	
Washington	----	----	9.0	13.0	----	22.0
British Columbia	----	18.0	----	22.0	----	40.0
Alaska						
Southeast	9.0	146.0	4.1	0.6	1.0	160.7
Prince William Sound	645.0	----	----	----	----	645.0
Cook Inlet	----	----	2.7	----	----	2.7
Totals	654.0	164.0	15.8	35.6	1.0	870.4

Based on the current high survival rates of wild and hatchery fish reflected in record runs in many Asian and North American stocks, there is little evidence the overall carrying capacity of the North Pacific Ocean for salmon production has been exceeded or diminished. Helle (1989) found a strong positive correlation between body size of chum salmon spawners at Olsen Creek, Alaska and subsequent life history survival of their progeny (cumulative survival for freshwater, marine, and coastal fishery periods). It follows, given this parent progeny relationship and the density-dependent effects of decreased body size in many stocks, that present survival rates should be diminishing or trending downward. In general, however, this has not happened and overall cumulative survivals are currently at record high levels.

Although strong evidence is lacking for limitations in ocean carrying capacity, record runs of Pacific salmon both in Asia and North America have severely depressed prices paid to fishermen (Kaeriyama and Urawa 1993; Heard 1996). In some instances surplus runs of salmon have gone unharvested due to lack of price or demand. Continued world-wide growth of farmed salmon also directly affects both price and demand of anadromous species. The current levels of salmon abundance have created socio-economic concerns over the long-term status and well being of capture fisheries in many areas. Given these concerns along with the many biological questions about carrying capacity of the North Pacific Ocean, perhaps NPAFC member countries should consider a concept of cooperative quotas or a partitioning system to limit production of Pacific Rim salmon. Such a system could allow each country to decide what portion of its quota would be derived from wild and hatchery fish.

The idea of a quota or partitioning of Pacific salmon production among countries is not new. Joyner (1975) outlined a system of using the seas as a range or cropland including a concept of North Pacific Ocean grazing rights for salmon production. Bigler et al. (1996) suggested that allocation of ocean resources may need to be considered for.... "optimal common management of salmon".

In terms of current hatchery programs, Japan has had a self-imposed quota or cap on the number of juvenile chum salmon released from hatcheries for over a decade. Since about 1982 the numbers of juvenile salmon released in Japan has been fixed at about 2 billion fry per year (Kaeriyama 1989; Kaeriyama and Urawa 1993). Japanese fry releases of chum salmon during this period have been divided about equally between Hokkaido and Honshu. Dramatic increases in numbers of adult chum salmon produced from Japanese hatcheries have been solely the result of continued increases in ocean survival unrelated to any increased output of hatchery fry.

Variability in marine survival clearly illustrates only one of the many issues that would need to be addressed in a Pacific Rim quota system for limiting or allocating production. Predicting survival by brood year of either wild or hatchery salmon would become a key element in any quota program. In turn this would require a more comprehensive understanding of the dynamics of ocean ecology and the role of salmon in the North Pacific Ocean ecosystem.

Even without a cooperative effort toward a concept of quotas, understanding interannual variations in ocean survival of salmon is a worthy goal. The issue of survival along with many other aspects of marine ecology of salmon, including better knowledge of hatchery-wild stock interactions, is sufficient reason to continue and expand joint oceanic research by NPAFC member countries around the Pacific Rim.

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Interaction Between Chum Salmon and Fat Greenling Juveniles in the Coastal Sea of Japan off Northern Hokkaido

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We examined potential interactions between chum salmon (*Oncorhynchus keta*) and fat greenling (*Hexagrammos otakii*) juveniles in terms of their distribution, abundance, growth and food habit in the Sea of Japan along the Mashike coast in northern Hokkaido. We captured the juveniles by a Sayori tow net from mid-April to mid-June in 1995. To compare the distribution patterns of both species, we calculated the point correlation coefficient (PCC, Dagneli's Φ) and Morisita's C_h . We used Kimoto's C_m as a similarity index of a stomach content composition between the two species, and SCI (Stomach Content Index, %). Although chum salmon juveniles were collected from mid-April to mid-June, fat greenling continued to inhabit till early May. Both species showed the highest abundance in early May and their distributions were restricted to inshore waters except for mid-April. There was a significant correlation of PCC in mid-April ($PCC=0.75$, $\chi^2=6.857$, $p<0.01$), however, Morisita's C_h remained at low levels (0.2~0.28) during the same period. Although there was significant difference in mean fork length between the two species in this period (t-test, $P<0.05$), frequency distributions of fork length were very similar. The mean values of SCI in mid-April ranged from 0.6% to 1.1% for chum salmon and from 0.8% to 1.8% for fat greenling among the sampling sites. The same food organisms, *Tortanus discaudatus* and *Themisto japonica*, were found in the stomachs of both species. Kimoto's C_m showed high values ranging from 0.34 to 0.58 in mid-April. It is suggested that there is potential competition between chum and fat greenling juveniles in terms of the food and habitat requirements during the early ocean life of chum salmon juveniles.



INTRODUCTION

It is hypothesized that the survival of salmon juveniles may be controlled by the competition for food and the predation during the early ocean life (Parker 1968; Healey 1982; Pearcy 1992).

Chum salmon (*Oncorhynchus keta*) stocks in Japan have been increasing, however, chum salmon stock along the coast of the Sea of Japan is smaller than those along the Pacific Ocean and the Sea of Okhotsk coasts in Hokkaido. It is considered that the lower level of chum salmon stock of the Sea of Japan is affected by the strength of Tsushima warm current

in spring when chum salmon juveniles migrate to the sea and inhabit inshore waters. For the juveniles, Tsushima warm current brings about a higher water temperature for the residence and a change in zooplankton composition for their food (Seki et al. 1984; Kaeriyama 1989; Irie 1990).

However, little is known about the relation between chum salmon juveniles and other marine fish in terms of prey organism and distribution in inshore waters of the Sea of Japan. We hypothesized that chum salmon juveniles of the coastal Sea of Japan were more restricted to their resident time inshore for growth than those of the Pacific Ocean and the Sea of

Okhotsk coasts, and that timing of abundance of food organisms and competition with other fishes with a similar life strategy in feeding behavior were important for growth within a restricted time period.

The objective of this study was to clarify the relation between chum salmon and fat greenling (*Hexagrammos otakii*) juveniles in terms of their distribution, abundance, growth and food habit. Fat greenling juveniles are a common species that inhabits coastal waters of the Sea of Japan in spring (Sato 1991).

MATERIALS AND METHODS

Sampling Sites and Gear

We established fifteen sampling stations in the Mashike coastal area in the Sea of Japan of Hokkaido (Fig. 1). We captured the juveniles with a Sayori tow net at a speed of approximately two knots for thirty minutes at seven to ten stations, which were located with Global Positioning System, six times from mid-May to mid-June in 1995. Sayori tow net had a mouth that was eight meters wide, five meters deep and eighteen meters long with wing nets seven meters long, and towed by two fishing boats.

Stomach Content Analysis

Sampled fishes were fixed in five percent neutral

formalin solution for several hours and then moved to seventy percent ethanol. In the laboratory, we measured fork length (FL) to the nearest 0.1 mm, body weight (BW) to the nearest 1mg and stomach content weight (SCW) to the nearest 1mg, and calculated stomach content index (SCI) as $SCI = ((SCW/(BW-SCW)) \cdot 100$.

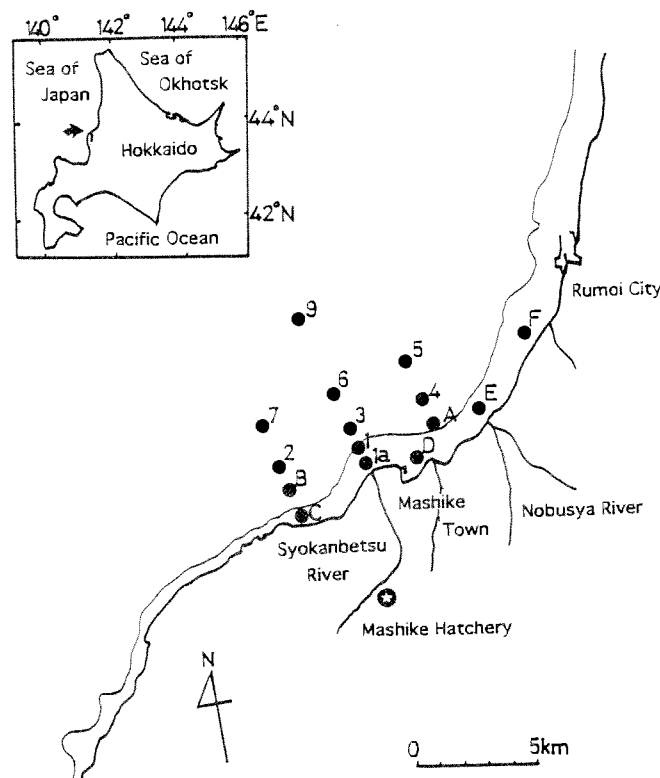
Prey items in each stomach were counted and identified to species whenever possible. A similarity index of stomach content composition was examined using Kimoto's $C\pi$ (Kimoto 1967).

$$C\pi = \frac{2 \sum_{i=1}^s n_{1i} n_{2i}}{(\sum_{i=1}^s \pi_i^2 + \sum_{i=1}^s \pi_i^2) N_1 N_2}, \quad \sum_{i=1}^s \pi_i^2 = \frac{\sum_{i=1}^s n_{1i}^2}{N_1^2},$$

$$\sum_{i=1}^s \pi_i^2 = \frac{\sum_{i=1}^s n_{2i}^2}{N_2^2}$$

where n_{1i} and n_{2i} are the number of a given prey species in the stomach content of fish group n1 and group n2, respectively, and N_1 and N_2 are the total of every prey species in the diet of fish group n1 and group n2, respectively. This results in an index ranging from 0 to +1, with 0 indicating no selection.

Fig. 1 Map showing the sampling stations along the Mashike coast of the Sea of Japan off Hokkaido, Japan.



Distributional Pattern Analysis

We examined an interspecific association between chum salmon and fat greenling juveniles with Dagnelie's ϕ (Dagnelie 1962), that is Point Correlation Coefficient and a distributional overlap with Morisita's C_s (Morisita 1959).

$$\text{Dagnelie's } \phi \text{ (PCC)} = \frac{ad - bc}{\sqrt{(a+b)(a+c)(b+d)(c+d)}}$$

where a, b, c and d show four categories; a is the number of the sampling site where both chum and fat greenling are found, b or c is that collecting site where either chum or fat greenling occur and d is the number of sites where both species are absent. This correlation coefficient ranges from -1 to +1, with +1 showing preference for the same environment. Morisita's C_s is written:

$$C_s = \frac{2\sum n_1 n_2}{(\delta_1 + \delta_2) M_1 M_2}$$

where n_1 and n_2 are the number of a given species at every sampling site and δ_1 and δ_2 show unbiased inference values of Simpson's λ (Simpson, 1949). M_1 and M_2 indicate a total number at every sampling site. This results in an index ranging from 0 to +1, with 0 indicating no distributional overlap.

RESULT

Abundance and distribution of sampled fishes

We captured nine species of fish by a Sayori tow net from mid-April to mid-June (Table 1). Chum salmon juveniles were numerically predominant through the survey period except for late-April. A lot of fat greenling juveniles were captured from mid-April to early-May except for late-April, when only few chum and fat greenling juveniles were caught. The other species, masu salmon (*O. masou*) juveniles, walleye pollock (*Theragra chalcogramma*)

larvae, threespine stickleback (*Gasterosteus aculeatus*), Japanese needlefish (*Hemiramphus sajori*), needlefish (*Strongylura anastomella*), Temmink's surfperch (*Ditrema temnincki*) adults and Pacific sand lance (*Ammodytes personatus*) juveniles, were caught in few numbers from mid-April to mid-June.

Chum salmon juveniles distributed to inshore waters within one kilometer from the Mashike coast line except for mid-April, when the juveniles extend their distribution farther offshore. Also, the distribution of fat greenling juveniles spread to farther offshore waters in mid-April, however, they distributed to inshore waters in early-May. It seemed that both species of juveniles showed similar distributions. So, we analyzed interspecific association and degree of distributional overlap between chum and fat greenling juveniles with Dagnelie's ϕ and Morisita's C_s , respectively.

Dagnelie's ϕ value was significantly high in mid-April (Table 2). Although Dagnelie's ϕ in mid-April was 0.75 (Chi square: 6.875, $P > 0.01$), the values in late-April and early-May showed low levels (0.4 and 0.41), showing that chum and fat greenling juveniles preferred similar environments in mid-April. On the other hand, Morisita's C_s values were low, ranging from 0.2 to 0.283 (Table 2), suggesting that every species of juvenile may have fine-scale habitat segregations.

Growth

We captured chum salmon juveniles in fork length ranging from 39 mm to 59 mm and fat greenling juveniles ranging from 30 mm to 55 mm in mid-April. The average fork length of chum and fat greenling juveniles in mid-April was 47 mm (N:244, SD: 4 mm) and 44 mm (N:101, SD: 6 mm), respectively. Although, there was significant difference of mean fork length between both juveniles (t-test, $P > 0.05$), the frequency distributions in fork length of both juveniles were similar except for the class of small size in fat greenling (30~38 mm).

Table 1. Fish species and individual numbers captured with a Sayori tow net.

Species	April 14	April 25	May 9	May 16	May 31	June 13	Total
<i>Oncorhynchus keta</i>	244	5	3,356	1,061	112	22	4,800
<i>Oncorhynchus masou</i>				2	6		8
<i>Hexagrammos otakii</i>	103	8	236				377
<i>Theragra chalcogramma</i>		5					5
<i>Gasterosteus aculeatus</i>	6	2	9	2			18
<i>Hemiramphus sajori</i>			5				5
<i>Strongylura anastomella</i>					1		1
<i>Ditrema temnincki</i>			1				1
<i>Ammodytes personatus</i>			61				61

Table 2. Interspecific association and distributional overlap between chum salmon and fat greenling juveniles in the Mashike coast.

	April 14	April 25	May 9
No. of stations	9	10	8
C_h	0.283	0.2	0.275
ϕ	0.75	0.4	0.41
χ^2	6.857	1.12	1.667
	$p < 0.01$	ns	ns

C_h from Morisita (1959) and ϕ from Dagnelie (1962).

Stomach Content Analysis

Stomach Content Index (SCI)

We compared the SCI of chum salmon with that of fat greenling in mid-April when both juveniles preferred similar environments. The mean values of SCI in mid-April ranged from 0.6% to 1.1% for chum salmon and from 0.8% to 1.8% for fat greenling among sampling sites (Table 3). At three sites where two species juveniles distributed sympatrically, there was no significant difference of mean SCI between the two species except for station B (t-test, $P > 0.05$). Although SCI of fat greenling at station B showed a higher value than that of chum salmon, that may be caused by a higher prey catchability of the larger size juvenile than those of the other sites. This is supported by a higher value of SCI at station 6, where fat greenling juvenile were larger than at most other sampling sites (Table 3).

Stomach Content Composition

Table 4 represents the results of stomach content analysis and the numbers of prey item per fish at three stations where two species of juveniles were distributed sympatrically in mid-April. Although fat greenling juveniles preferred *Pseudocalanus minutus* and *Metridia* sp. (Copepodid), several prey items, such as *Tortanus discaudatus*, *Harpacticus* sp., *Themisto japonica* and fish larvae were found in stomachs of chum salmon and fat greenling juveniles. Only at station B, zoea of *Anomura* occupied chum and fat greenling stomachs. It was evident that the

same prey organisms were available for food of chum salmon and fat greenling juveniles.

Consequently, we calculated Kimoto's C_π as a similarity index of stomach content composition, comparing the individual size, because fish size may effect feeding behavior between individuals of different sizes. Kimoto's values showed higher levels ranging from 0.34 to 0.58 between the two species for similar body sizes (Table 5). However, Kimoto's value for individuals of different size showed a lower level (0.04). It was evident that there is potential competition for prey organisms between chum salmon and fat greenling juveniles of similar body size.

DISCUSSION

Our study showed that chum and fat greenling juveniles preferred similar environments, and that they might show fine-scale segregation in coastal waters of the Sea of Japan in mid-April. Moreover, it was observed from the analysis of their stomach content composition that several prey organisms were available for their food. There have been a number of reports on food habits of juvenile chum salmon during early ocean life (Kaczynski et al. 1973; Mason 1974; Healey 1979; Sibert 1979; Kaeriyama 1986; Irie 1990; Suzuki et al. 1994). Although Wissmart and Simenstad (1988) surmised that a balance between growth of juvenile chum salmon and abundance of prey organism could be evaluated with some growth efficiency level in an estuary, this is a possible food limitation in the early ocean life of growth of salmon juveniles.

Table 3. Comparison of stomach content index between chum salmon and fat greenling on April 14.

Station	<i>Oncorhynchus keta</i>			<i>Hexagrammos otakii</i>		
	N	FL(mm)	SCI(%)	N	FL(mm)	SCI(%)
St 1	99	45.3±3.4	0.60±0.71	12	38.6±4.2	0.91±0.62
St 3	62	46.0±3.3	0.29±0.54	-		
St 4	24	48.1±2.7	1.09±0.77	-		
St 6	-			45	46.5±4.3	1.57±0.88
St A	11	48.3±5.5	0.97±1.23	33	42.3±5.2	0.82±0.49
St B	45	51.7±4.1	*0.87±0.79	7	46.8±3.1	*1.78±0.821

Mean±SD

* : Student's t test ($p < 0.05$)

Table 4. Comparison of stomach content composition of chum salmon and fat greenling juveniles off the Mashike coast in mid-April, 1995.

Station	St 1	St 1	St 1	St A	St A	St B	St B
Predator Species	*1 O. k	*2 O. k	H. o	O. k	H. o	O. k	H. o
Annelida				0.1			
Mollusca						0.5	
Arthropoda		0.2	0.8				0.1
		0.1					
							0.1
					0.1	0.1	
			0.3	0.1	0.5		3.6
		0.1	0.9		1.7		2.7
	5.1	13.2	0.9	0.8	0.3	1.1	0.4
	0.9	0.8	2.2		0.6	0.7	1.6
		0.1					
	3.4	0.1		1.2	0.3	0.5	3.3
	0.1					0.1	
	0.1	0.1				0.2	
						0.1	
	0.3						
	0.6	0.1	0.2	2.1	3.3	0.4	
			0.1			4.9	4.7
					0.2	0.1	
							0.1
					0.1		
	0.4						
Prochordata	0.1				0.2		
Vertebrate	0.2	0.2		0.4	0.2	9.0	1.1

*1 shows larger size chum salmon (FL>50mm) and *2 indicates smaller size one (FL<40mm). The numbers of prey item represent individuals per fish.

Table 5. Comparison of Kimoto's C_{π} as a similarity index of stomach content composition between chum salmon and fat greenling juveniles in the Mashike coast in mid-April, 1995.

Species	size	H. otakii middle	H. otakii small
O. keta	large	0.58(St A) 0.42(St 1)	0.04(St 1)
O. keta	middle	0.41(St B)	
O. keta	small		0.34(St 1)

Large, middle, and small chum salmon had mean fork lengths of, 58mm, 48mm and 41mm, respectively.

Middle and small fat greenling were 47mm and 39mm in mean fork length, respectively.

In this study, the size of chum salmon juveniles was similar to that of fat greenling and Kimoto's C_{π} , as a similarity index of stomach content composition, was highest between the two species when fished similar size were compared. However, severe competition for food did not occur, since there was no significant difference of stomach content index between both species. These results suggest that prey resources may be sufficient in the surveyed sites, however, a potential for competition may exist between the two species when prey are scarce.

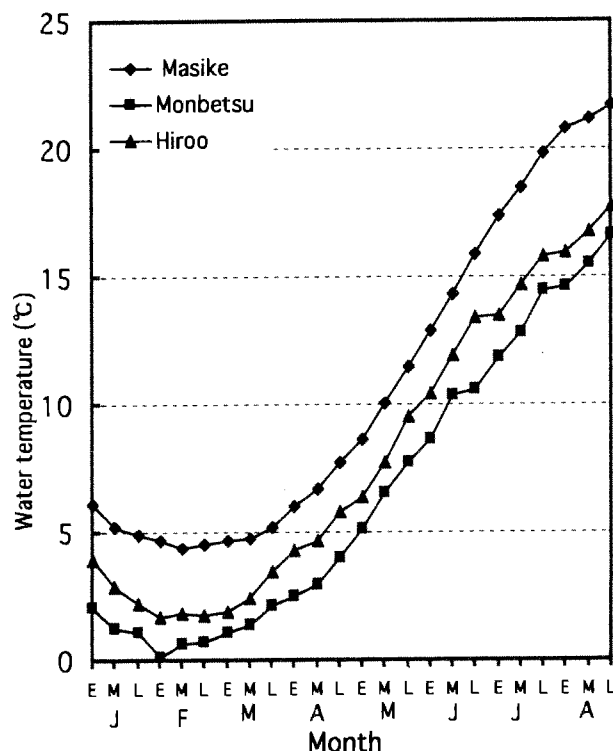
On the other hand, it was observed that chum and

fat greenling juveniles were distributed in narrow areas inshore along the Mashike coast. Distribution pattern of chum salmon in the Mashike coast was different from that of north American region, where juvenile chum salmon inhabit the marsh or estuary during a restricted time after the seaward migration (Kaczynski et al. 1973; Mason 1974; Healey 1979; Congleton et al. 1981; Percy et al. 1989). Although there has been a number of reports on the factors affecting the distribution in inshore waters of chum salmon, such as temperature, salinity, flow, prey abundance and predators (Bax 1981; Congleton et al. 1981; Kaeriyama 1989; Percy et al. 1989; Irie 1990), we consider that prey abundance and ocean condition are more important for the survival of juvenile chum salmon in the inshore waters of Mashike. Since it has been represented that juvenile chum salmon migrate offshore at a constant body size (approximately 70 mm in fork length), and that they are forced to move offshore at more than about 13°C of seawater temperature (Irie 1985, 1990; Kaeriyama 1989), chum salmon need to grow to a constant body size within a restricted time for survival. Growth of salmon juveniles is influenced by prey abundance, ocean condition and social interaction, such as competition and density-dependent effect (Percy 1992).

Strength of Tsushima warm current (TWC) implicates in a resident time of juvenile chum salmon inshore waters of the Sea of Japan, particularly through a higher temperature. Based on changes in surface temperatures of the three coastal regions of Hokkaido, the temperature of Mashike coast begins to increase earliest during the early spring (Fig. 2). As a result, juvenile chum salmon along the Mashike coast have to grow most quickly to reach an offshore migrating size among the three coastal regions. We observed, furthermore, that prey resources of Mashike coast were affected by the development of TWC, and that the change in ocean condition brought a decrease in stomach content (Kawamura and Hirano, unpublished data).

Consequently, it is important for survival that juvenile chum salmon have available good prey resources and grow to a offshore migrating size within a restricted time under a favorable coastal condition, such as lower temperature ranging 6°C to 12°C and lower salinity, before the development of TWC. Also, the interaction between chum salmon and fat greenling juveniles is thought to be important for our understanding the fluctuations in chum salmon stock of the Sea of Japan, because of their similar prey availability and habitat.

Fig. 2 Fluctuations in average surface water temperatures (1990-1996) of Masike, Monbetsu and Hiroo from January to August. Masike, Monbetsu and Hiroo are located along the coasts of the Sea of Japan, the Okhotsk Sea and the Pacific Ocean of Hokkaido, respectively.



CONCLUSIONS

We examined potential interactions between chum salmon and fat greenling juveniles in terms of their distribution, abundance, growth and food habit along the Mashike coast of the Sea of Japan off northern Hokkaido. In mid-April, chum and fat greenling juveniles preferred similar environments. Moreover, similar prey organisms were available for both chum and fat greenling juveniles' food. On the other hand, their distributions inshore were restricted to within one kilometer from the Mashike coast line except for mid-April. As a result, it is suggested that there is a potential for competition between chum and fat greenling juveniles for food and habitat requirements during the early ocean life of chum salmon juveniles.

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Predation by Salmon Sharks (*Lamna ditropis*) on Pacific Salmon (*Oncorhynchus* spp.) in the North Pacific Ocean

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Nagasawa, K. 1998. Predation by salmon sharks (*Lamna ditropis*) on Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. N. Pac. Anadr. Fish Comm. Bull. No. 1: 419-433

This paper reviews the biology of salmon sharks (*Lamna ditropis*) and evaluates their current status as predators of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. Salmon sharks are widely distributed in subarctic and northern temperate waters. They segregate in distribution by size and sex and conduct seasonal migrations. Larger (older) salmon sharks go to more northern waters. In the western North Pacific, salmon sharks migrate from Japanese waters to the Okhotsk Sea and the western Bering Sea. They copulate in autumn and females bear young in spring. Salmon sharks are long-lived (over 20 years). They are opportunistic feeders but occupy the highest trophic level in the food web of subarctic waters. Salmonids are the major prey item in subarctic waters. Although the importance of each species of Pacific salmon eaten varies among regions, sockeye salmon (*O. nerka*) are most frequently fed on, followed by chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon. The estimated abundance of salmon sharks was at least about 2 million fish for 1989. Of these fish, age_≥5 salmon sharks (595×10^3 fish) occurring in subarctic waters appear to have consumed $73\text{--}146 \times 10^6$ salmonids ($113\text{--}226 \times 10^3$ metric tons) from spring to autumn in 1989, which corresponded to 12.6–25.2% of the total annual run of Pacific salmon for that year. I therefore suggest that the predation by salmon sharks highly causes the ocean mortality of Pacific salmon.



INTRODUCTION

Fish ocean mortality includes deaths due to fisheries and natural causes (i.e., predation and diseases). Since North Pacific high-seas salmon fisheries were banned in 1992, natural mortality appears to be the current most important factor to reduce salmonid abundance in the North Pacific Ocean. Pacific salmon (*Oncorhynchus* spp.) are subjected to various types of predators (elasmobranchs, teleosts, seabirds, and marine mammals) in both coastal and offshore waters of the North Pacific Ocean. The degree of predation by these animals on salmonids is different by area and season.

The salmon shark, *Lamna ditropis* Hubbs and Follett, 1947, is a relatively large species (up to over 3 m) occurring in a wide area of the northern North Pacific and adjacent seas. In the late 1950's and early 1960's, this species was studied by Sano (1959a, b, 1960, 1962) in terms of predation on Pacific salmon and it has been regarded as one of the most important predators of salmonids in offshore waters. However, its importance as a predator has never been discussed since, except for brief notes by Tanaka (1980) and

Paust and Smith (1989). In this paper, I review various aspects of the biology of the salmon shark and then evaluate its current status as a predator of Pacific salmon.

BIOLOGY OF SALMON SHARKS

Taxonomy and Morphology

The salmon shark was described as a new species by Hubbs and Follett (1947) from a male adult specimen collected off La Jolla, California. This species is placed in the family Lamnidae of the order Lamniformes (Compagno 1984). The genus *Lamna* is one of three genera of the family. There are only two species in the genus: the salmon shark *L. ditropis* and the porbeagle *L. nanus* (Bonnaterre 1788).

Although the original description of *L. ditropis* was very short, Nakaya (1971) and Tanaka (1980) gave a detailed description of its morphology. This species has a heavy spindle-shaped body with large first dorsal fin and small second dorsal and anal fins; the snout is short and conical; there are strong keels on the caudal peduncle and short secondary keels on the caudal base; the caudal fin is crescentic; the mouth

is broadly rounded; the upper jaw has 28-30 teeth and the lower jaw 26-27; the teeth are awl-like with smooth edges and basal denticles; the vertebrates are 170-181 (mostly 173) for males and 171-184 (mostly 176-177) for females; the color is dark bluish gray to bluish black above, changing to snow white on the ventral surface with dark blotches.

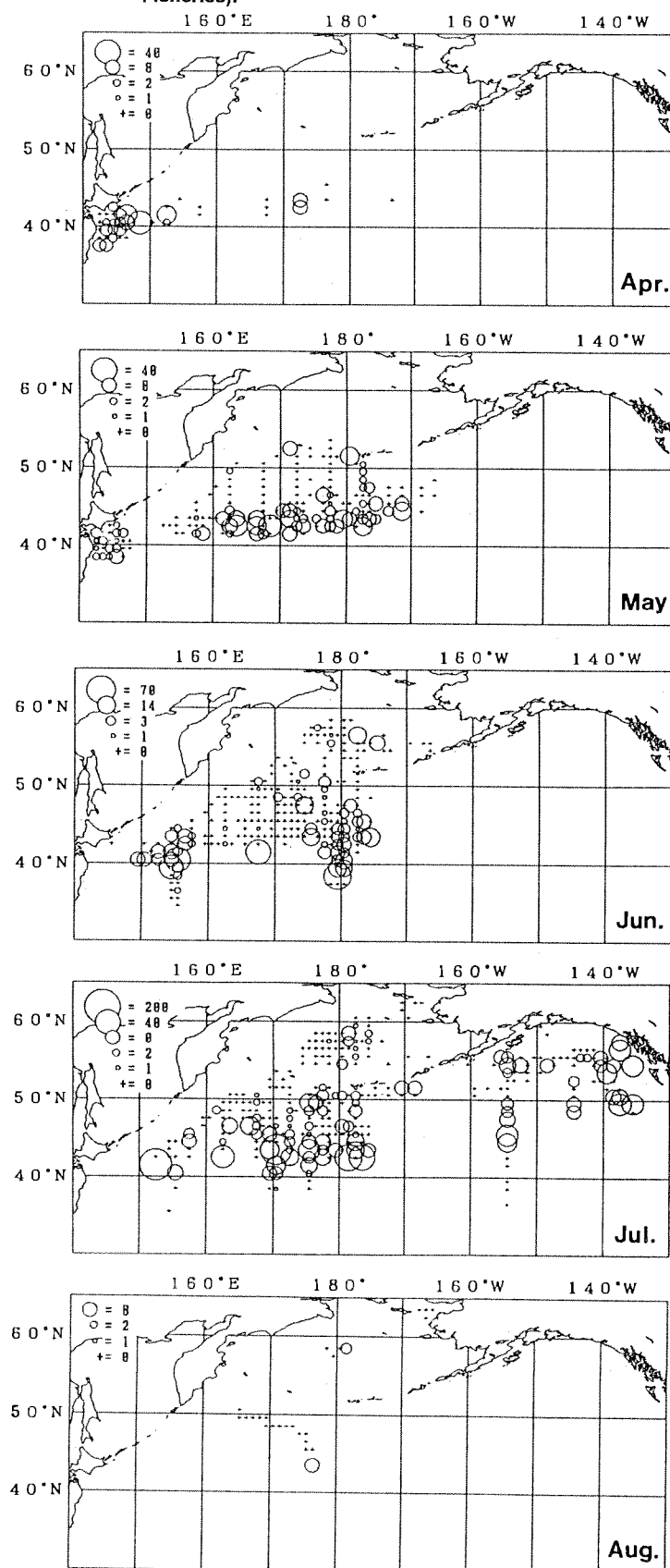
Distribution

The salmon shark is widely distributed in subarctic and northern temperate waters (usually north of 35°N) of the North Pacific Ocean, including the Bering Sea, Okhotsk Sea, and Japan Sea (Strasburg 1958; Parin 1966; Tanaka 1980; Compagno 1984; Brodeur 1988). In the Bering Sea, this species occurs as far north as 67°N in the Gulf of Anadyr (Blagoderov 1993). The southernmost catch records are from 23°N in the western North Pacific (Tanaka 1980) and from 0° to 10°N in the eastern North Pacific (Sivasubramaniam 1963). This species is also found near the Bonin Islands (27°N) in winter (Tanaka 1986). In the central North Pacific, it occurs mostly north of 35°N (Strasburg 1958). Although Compagno (1984, map figure on p.247) shows this species as occurring in the East China Sea and Yellow Sea, there have been no records from these seas (Yamada et al. 1985; Dr. M. Tokimura, Seikai National Fisheries Research Institute, Nagasaki 850, Japan, per. comm.).

In the western North Pacific, salmon sharks are concentrated in Japanese coastal waters in winter but extend eastward to offshore waters in spring (Blagoderov 1993). In summer, many salmon sharks are found off the east coast of Hokkaido and the southern Kuril Islands. A similar distributional pattern is found in autumn but salmon sharks are caught in the widest area in this season, some reaching the northernmost part of the Okhotsk Sea and the Gulf of Anadyr (Bering Sea) (Blagoderov 1993). In waters off northern Honshu, salmon sharks are concentrated around the Oyashio Front (Kawasaki et al. 1962).

Monthly variations in offshore distribution of salmon sharks, based on incidental catch data from Japanese high seas salmon surveys, are shown in Fig. 1. In May, high catches are recorded from a broad latitudinal band at 41°-43°N. In June and July, areas of high catches are slightly

Fig. 1 Monthly variation in distribution of salmon sharks in the North Pacific Ocean (from Nakano and Nagasawa 1996, with permission of the Japanese Society of Scientific Fisheries).



scattered and extend to the north. There are also consistent catches off the east coast of northern Japan in April and May. In the Gulf of Alaska, salmon sharks occur farther north than in the western and central North Pacific (Nakano and Nagasawa 1994, 1996).

Salmon sharks occur over a wide range of sea surface temperature (SST) and salinity (Naito et al. 1977; Brodeur 1988; Nakano and Nagasawa 1996). They have been collected between 3.5° and 22.5°C with highest catch at 14°C (Nakano and Nagasawa 1996) and between 31.00 and 34.60 psu with two peaks at 31.50 and 34.25 psu (Nagasawa unpublished). Although the SST range of salmon shark catches overlaps with that of salmonids (Fig. 2), the subarctic boundary, which corresponds to the 34.0 psu isohaline, is known as the southern limit of salmonid distribution in the oceanic North Pacific. Nevertheless, there is no clear relation between the distribution of salmon shark and the subarctic boundary.

There is a regional difference in distribution and abundance by size and sex of salmon sharks (Sano 1962; Tanaka 1980). Large sharks predominate in waters north of 47°N and east of 155°E, whereas small- or medium-sized sharks are abundant in southwestern waters (Fig. 3). The percentage of males occurring in samples of salmon sharks increases with increasing latitude (Fig. 4). These results suggest that the distributional and migratory patterns of salmon sharks differ with sex and size or age.

Stocks

The stock structure of salmon sharks are poorly understood. Sano (1959a, 1960) first thought that small sharks occurring off Japan and the southern Kuril Islands formed a different stock from large sharks caught near the Aleutian Islands and in the western and central Bering Sea. Sano (1962) later amended his earlier idea, stating that these sharks are segregated by maturity (size) and could not be divided into different stocks. A similar suggestion was made by Blagoderov (1993), who stated that salmon sharks spend winter in Japanese coastal waters and migrate north to the Okhotsk Sea and western Bering Sea from spring through autumn. Tanaka (1980) reported that large salmon sharks migrate from Japanese waters to the central North Pacific (east of 155°E). These suggestions imply that salmon sharks constitute a single stock in the western and central North Pacific, including the Okhotsk Sea and western Bering Sea.

For salmon sharks found in the eastern North Pacific and Japan Sea, no information is available on their stock structure.

Migration

The salmon shark is definitely a seasonal migrant. This species overwinters and reproduces in northern temperate waters and migrates to more northerly subarctic waters in other seasons. As early as 1939, Iino first suggested a seasonal northward (spring-

Fig. 2 Sea surface temperature for entire range of capture (open boxes) and range of highest catches (shaded boxes) for salmonids and salmon sharks, for all gear types and areas combined (modified from Brodeur 1988).

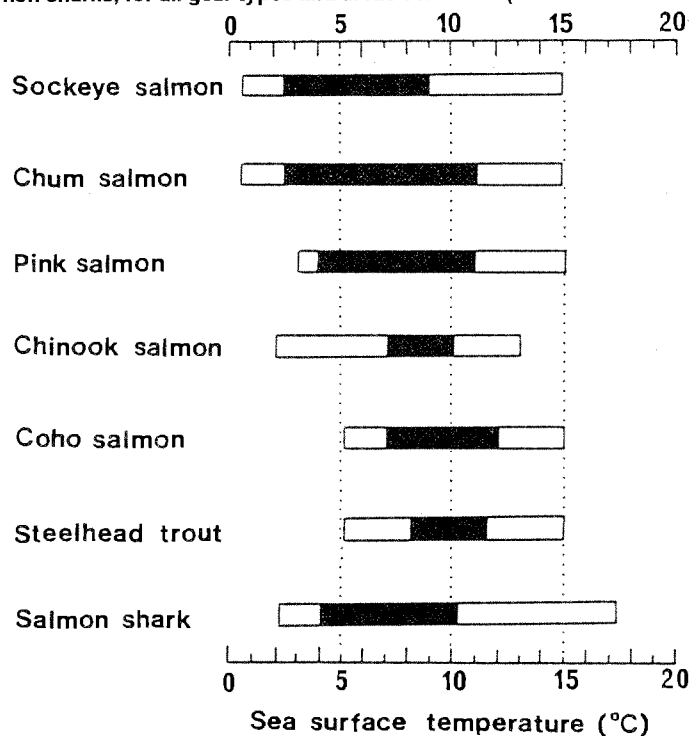


Fig. 3 Latitudinal changes in frequency distribution of body weight for female (closed bars) and male (open bars) salmon sharks in the North Pacific (modified from Sano 1962).

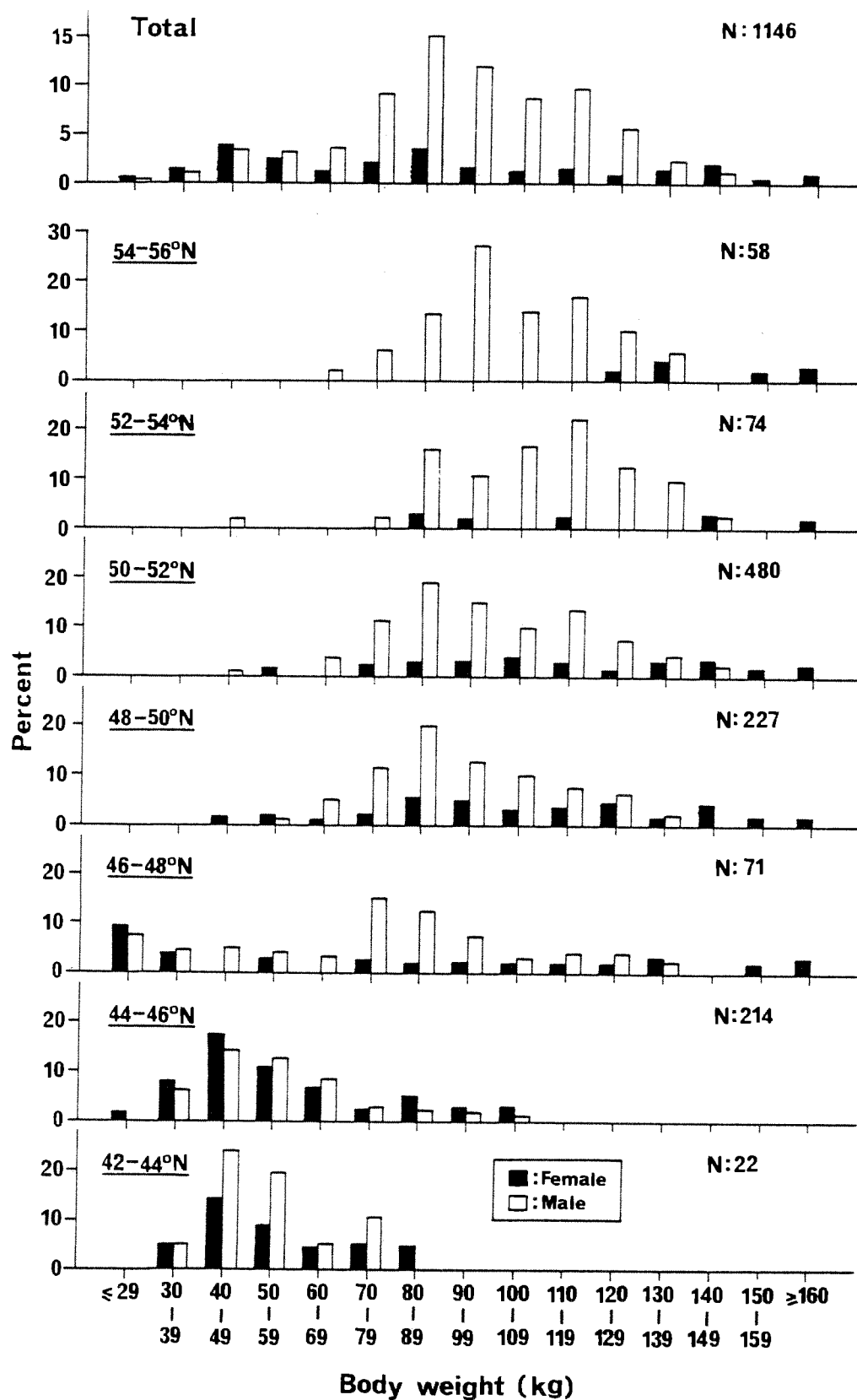
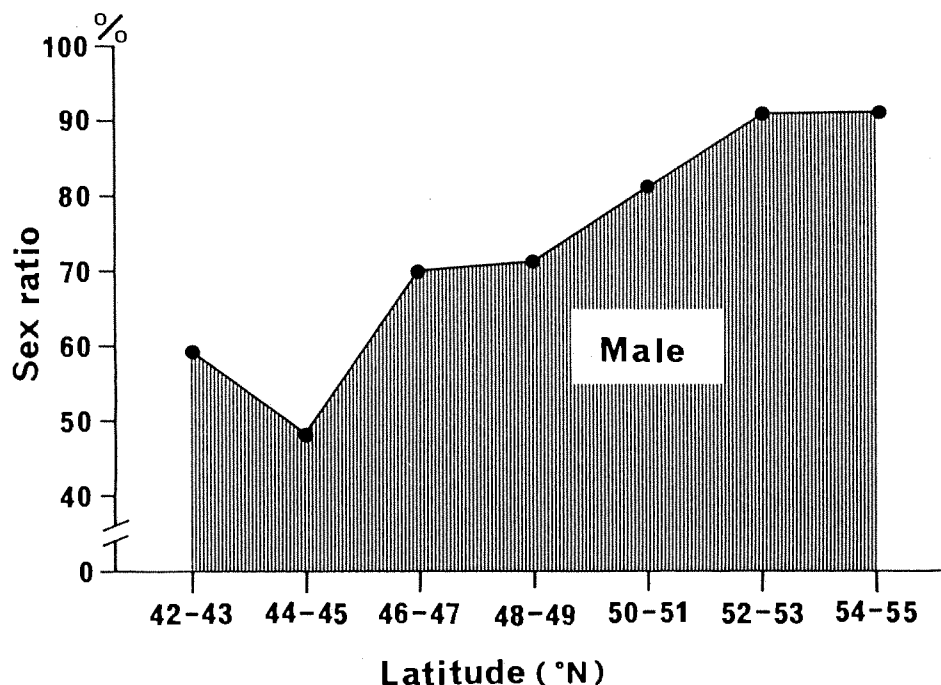


Fig. 4 Latitudinal changes in sex ratio of salmon sharks in the North Pacific Ocean (based on raw data from Sano 1962).



summer) and southward (autumn-winter) migration of the species in waters off the Pacific coast of Japan. Subsequently, based on detailed analyses of monthly longline catch data, Tanaka (1980) made a similar suggestion that in the western and central North Pacific salmon sharks migrate north in spring and south in autumn. Relative to medium-sized sharks (100-150 cm precaudal length [PCL]), which occurred mainly in waters west of 155°E, large sharks (> 150 cm PCL) migrate farther, reaching the central North Pacific and waters north of 46°N. Blagoderov (1993) also suggested that salmon sharks migrate from Japanese coastal waters as far north as the northern Okhotsk Sea and Bering Sea. Gorbatenko and Cheblukova (1990) stated that salmon sharks are abundant in summer in the Okhotsk Sea off southeast Sakhalin. In the Japan Sea salmon sharks appear to conduct a seasonal migration (Kosugi and Tsuchisaki, 1950).

Salmon sharks seem to conduct seasonal migrations in the Japan Sea as well (Blagoderov 1993). In the Gulf of Alaska, there is no obvious seasonal change in distribution of salmon sharks, although they are more frequently caught in late summer than in spring and early summer (Neave and Hanavan 1960).

Tagging experiments were conducted by the Japan Marine Fishery Resource Research Center in 1979 and 1980 (Makihara et al. 1980b; Yamaki and Maruyama 1981). A total of 134 salmon sharks was tagged and released in the western North Pacific. One shark (91 cm PCL) released at 40°21'N, 145°28'E on

December 29, 1979, was recaptured at 41°01'N, 144°55'E on May 24, 1980. There was a 5-cm growth in PCL during this five month period.

Reproduction and Nursery

Male and female salmon sharks mature, respectively, at 140 cm PCL and between 170 and 180 cm PCL (Tanaka 1980, 1986). The age at maturity is 5 years for males and 8-10 years for females. Copulation occurs in autumn, and the females are ovoviparous. In the parent's uterus young eat eggs ovulated from the ovary (Tanaka 1986). Adult females bear 4-5 young in spring (March-May). At birth young are between 60 and 65 cm PCL. Assuming that this species has an annual reproductive cycle, it is estimated that a female salmon shark makes parturition 15-16 times and bears about 70 young during her life.

Little information is available about the parturition ground of salmon sharks. However, mature adults and newly born young are found off northeastern Honshu and the southern Kuril Islands and also in offshore waters of the North Pacific. It is thus likely that these areas are parturition grounds for salmon sharks (Tanaka 1980; Blagoderov 1993).

Small salmon sharks, 70-110 cm PCL, are abundant in waters north of the subarctic boundary, which are thought to be their nursery ground. In this area, there are two advantages for the survival and growth of small sharks. i.e., they can avoid predation by large sharks, including adult salmon sharks and

blue sharks (*Prionace glauca*) which inhabit more northern and southern areas, and they also can utilize the high production of subarctic waters by preying on abundant squids and fishes (Nakano and Nagasawa 1996).

Age and Growth

Ages of salmon sharks can be determined by reading the rings of vertebral centra (Tanaka 1980). Two types of rings, formed in June-August and September-May, are observed in the vertebral centrum. One type of the rings is easily stained with hematoxylin and can be regarded as the annulus. The 65th vertebral centrum is well developed and the best for age determination. Because young taken from the uterus of adult sharks caught in March have one ring that can be well stained, such a ring should be excluded from counting for age determination. The maximum number of annular rings is 25 for males and 17 for females, indicating that the longevity of salmon sharks is long.

The maximum length recorded is 190 cm for males and 214 cm for females (Tanaka 1980), although there are reports that they grow up to about 305 cm in total length (Compagno 1984). According to Paust (1987), unofficial reports suggest that they may reach lengths in excess of 3.7 m and weights of 454 kg or more.

Young salmon sharks, 60-65 cm PCL, are born in spring and grow to 90-105 cm PCL by the next spring (Tanaka 1980). Subsequent annual growth is 10-15 cm up to age-4 fish. For age ≥ 5 fish, females grow better than males, attaining 173 and 163 cm PCL at age 10, respectively. The fit of the von Bertalanffy growth equation for each sex of western North Pacific salmon sharks is:

$$L_t = 180.3 \{1 - \exp[-0.1708 (t + 3.628)]\} \text{ for males}$$

$L_t = 203.8 \{1 - \exp[-0.1358 (t + 3.946)]\}$ for females
where L_t is PCL in cm at age t and t is the age in years. Although the estimated maximum lengths are smaller than the actually recorded lengths, this may be due to the small sample size of large old sharks.

The body length-body weight relationship for each sex is shown as follows:

$$W = 1.170 \times 10^{-4} L^{2.652} \text{ for males}$$

$$W = 1.039 \times 10^{-4} L^{2.679} \text{ for females}$$

where W is the body weight in kg and L is the PCL in cm. There are statistically significant differences in regression coefficients between sexes (Tanaka 1980).

The age composition of salmon sharks caught off the Pacific coast of northern Honshu was examined by Tanaka (1980). Age-4 males and age-3 females were predominant. Age-2 to age-4 sharks accounted for about 60% of the total for both sexes, and all were immature. The predominance of young salmon sharks in this area is because large old sharks migrate to

offshore waters and are thus not fished as frequently.

Abundance

Based on the catch data from the Japanese squid driftnet fishery, large-mesh driftnet fishery, salmon gillnet fishery, and tuna longline fishery, the minimum stock size of salmon sharks in the North Pacific Ocean was estimated to be $1.66\text{--}2.19 \times 10^6$ (mean: 1.92×10^6) fish in 1989 (Shimada and Nakano, unpublished manuscript). Large (age ≥ 5) salmon sharks occurring in subarctic waters account for 27-36% of this total (Shimada and Nakano unpublished manuscript), or $490\text{--}710 \times 10^3$ (mean: 595×10^3) fish.

The regional biomass of salmon sharks was estimated from Russian trawl surveys to total 9.7×10^3 metric tons in the Gulf of Anadyr and Navarin'skiy regions (September 1986), 12.6×10^3 metric tons in the western Bering Sea (June-July 1991), and 14.7×10^3 metric tons in the southern Okhotsk Sea (July-August 1991; Shuntov et al. 1993a, b; Blagoderov 1993). These estimates are equivalent to about 94×10^3 , 122×10^3 , and 153×10^3 salmon sharks in individual regions, respectively, assuming mean body weights of 103, 103, and 96 kg in these regions, based on the reported mean body lengths (178, 178, and 169 cm) in Blagoderov (1993).

It is difficult at present to assess long-term changes in salmon shark abundance in the North Pacific Ocean. Based on landing data for at Kesennuma Port, northern Honshu, Takahashi and Taniuchi (1996) stated that the population of salmon sharks appears to have been fairly stable in the western North Pacific from 1985 to 1995.

Swimming Depths and Schooling

Salmon sharks generally swim in the surface layer of cold subarctic waters but occur in deep waters in southern warm regions. In subarctic and northern temperate waters, they are usually caught with surface gillnets and longlines, but there is also a catch record from a depth of 40 m in the Gulf of Alaska (Smith and Rhodes 1983). In California, Hubbs and Follett (1947) collected this species at depth of 92-107 m. Compagno (1984) stated that salmon sharks are found at depths from the surface to at least 152 m.

Salmon sharks are solitary, at least when caught in surface gillnets in northern subarctic waters. In the former offshore salmon fishery, only 1-6 salmon sharks were captured per fishing operation using 10-15 km long salmon gillnets, but over 10 sharks (up to 40 sharks) were occasionally caught in waters near the Aleutian Islands (Sano 1960). In southern regions, gravid females are also believed to be solitary (Tanaka 1980). However, salmon sharks have been occasionally observed to form schools of 30-40

individuals (Castro 1983; Compagno 1984). According to Blagoderov (1993), salmon sharks aggregate when they feed on schooling Japanese sardines (*Sardinops melanostictus*).

Parasites

Salmon sharks carry various types of parasites. A tetrahymin cestode *Nybelinia surmenicola* is found in the digestive tract, mainly stomach, of the salmon shark (Shimazu 1975). Fishes and squids serve as paratenic hosts of this parasite and salmon sharks acquire infection by preying on these animals (Shimazu 1975; Nagasawa 1993). The ascarid nematode *Anisakis simplex* larvae (= *Anisakis* larvae type I) are found in the musculature of salmon sharks (Suzuki and Ishida 1982). Nine human cases of infection with *A. simplex* caused by eating the raw flesh of salmon sharks have been reported from northern Japan (Suzuki and Ishida 1982). Like *N. surmenicola*, salmon sharks possibly get infected with *A. simplex* by feeding on fishes and squids harboring its larvae. Siphonotomoid copepods (*Anthosoma crassum*, *Echthrogaleus coleoptaratus*, *Dinemoura latifolia* [= *Dinematura latifolia*] and *Dinemoura affinis* [= *Dinematura affinis*]) are known to occur on salmon sharks as ectoparasites in coastal waters of northern Japan (Yamaguti 1936; Shiino 1955, 1957; Izawa 1994). The possibility of using parasites as biological tags to identify stocks of salmon sharks has not been examined.

Fisheries and Fishing

Salmon sharks are caught by shark longlines in the western North Pacific (Tanaka 1980). Previously they were captured as a by-catch in surface gillnets for salmonids in subarctic waters (Sano 1959a, 1960, 1962). Salmon sharks were also incidentally caught in driftnets for neon flying squid (*Ommastrephes bartrami*), tunas and billfishes (Yatsu et al. 1993; Nakano et al. 1993; Bonfil 1994). From 1978 to 1981, the Japan Marine Fishery Resource Research Center conducted extensive surveys of salmon sharks to examine their abundance and distribution in the North Pacific Ocean (Makihara et al. 1980a, b; Yamaki and Maruyama 1981; Yatsu et al. 1984). Recently, a commercial fishery for salmon sharks has developed in the Gulf of Alaska (Paust 1987; Paust and Smith, 1989).

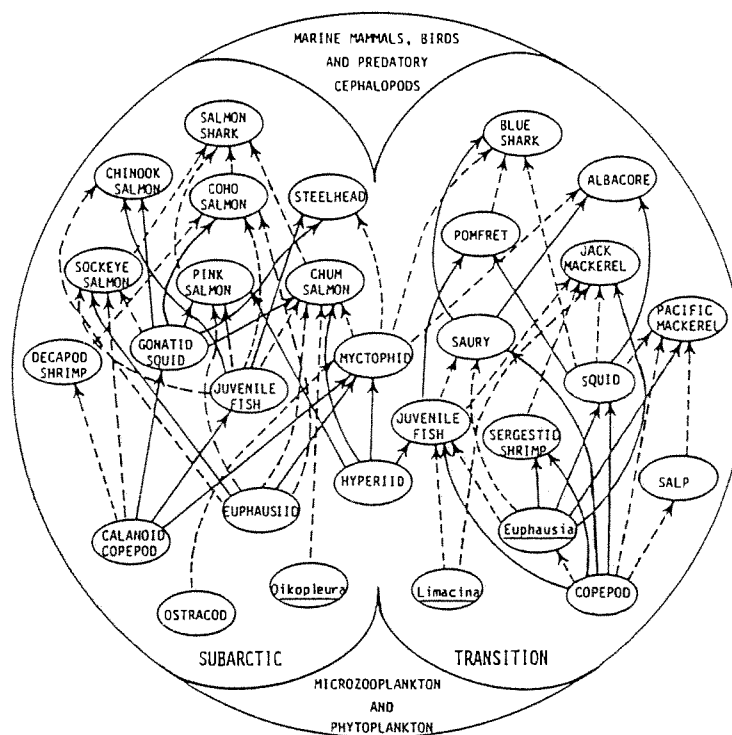
Salmon sharks are not gamefish. However, sports fishermen fish them in parts of the Strait of Georgia using surface and bottom baits (Castro 1983).

SALMON SHARKS AS PREDATORS OF SALMONIDS

General Feeding Habits

Salmon sharks occupy the highest trophic level in the food web of subarctic waters along marine mammals and seabirds (Brodeur 1988; Fig. 5). They are principally piscivorous but opportunistic feeders.

Fig. 5 Food web for the subarctic (left) and transition (right) zones showing major (solid lines) and minor (dashed lines) trophic linkage (Brodeur 1988). Food web is arranged from top to bottom by decreasing trophic levels.



They prey on a variety of epipelagic fishes and squids (Sano 1960, 1962), although they have been reported to feed on benthic crustaceans, such as tanner crabs (*Chionoecetes* sp.) and shrimps, in the Bering Sea (Okada and Kobayashi 1968).

There are marked variations in stomach contents between areas and seasons (Sano 1960, 1962; Kawasaki et al. 1962; Tanaka 1980, 1986; Blagoderov 1993). In subarctic waters, salmon sharks feed mainly on Pacific salmon (*Oncorhynchus* spp.) in spring and summer, whereas in southern waters they prey on other fishes and squids.

Non-salmonids recorded from the stomachs of salmon sharks sampled in subarctic waters include squids, daggettooth (*Anotopterus pharao*), longnose lancetfish (*Alepisaurus ferox*), Atka mackerel (*Pleurogrammus monopterygius*), Pacific spiny lumpstickers (*Eumicrotremus orbis*)*, walleye pollock (*Theragra chalcogramma*), Pacific sauries (*Cololabis saira*), spiny dogfish (*Squalus acanthias*), lanternfishes (Myctophidae), Pacific pomfret (*Brama japonica*), and chub mackerel (*Scomber japonicus*). Of these animals, squids are most frequently eaten. The first five teleosts are eaten in northern subarctic waters but the remaining teleosts are preyed on in southern subarctic waters.

* This identification may be wrong and it is possible that it is the smooth lumpstickers (*Aptocyclus ventriosus*) which was actually fed on by the salmon shark from the Bering Sea (Okada and Kobayashi 1968; Nagasawa unpublished observation). The smooth lumpstickers is common in the epipelagic layer of the Bering Sea.

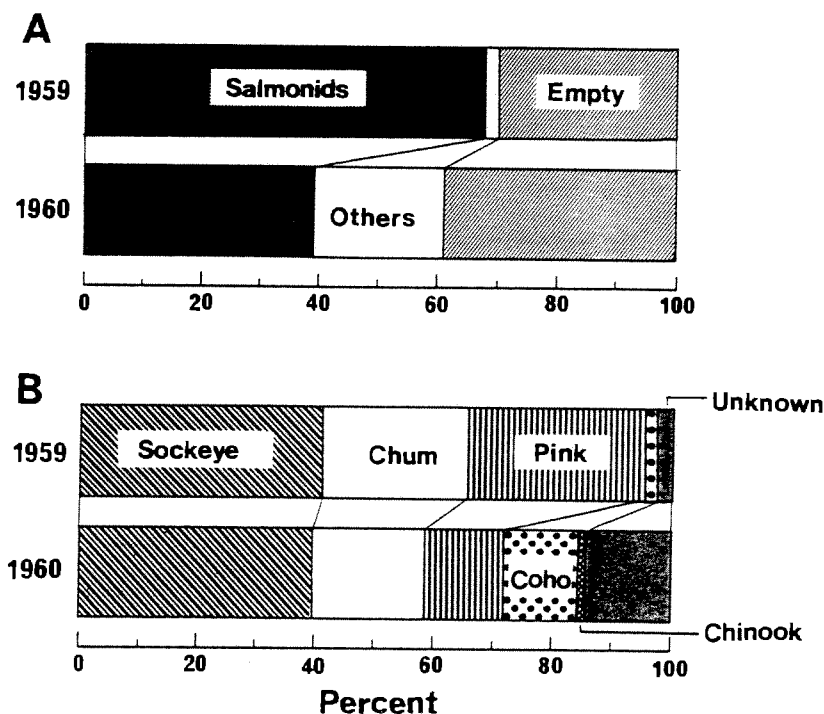
Salmonids Eaten and Their Frequency and Amount in the Stomachs of Salmon Sharks in Subarctic Waters

The salmonid species eaten by salmon sharks are sockeye salmon (*O. nerka*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), and chinook salmon (*O. tshawytscha*) (Sano 1960, 1962). There was no record of steelhead trout (*O. mykiss*).

Of 859 and 176 salmon sharks caught in the western North Pacific and Bering Sea from late May to early August in 1959 and 1960, 68 and 39% (mean 63% for both years combined) were found to have salmonids in their stomachs (Sano 1960, 1962; Fig. 6A). Other fishes and squids were found in 2 and 27% (mean 7%) of the stomachs. Empty stomachs were often observed in both years (30 and 34% [mean 31%]). There was a trend towards a higher frequency of occurrence of salmonids in salmon shark stomachs in waters of high salmonid abundance.

Sockeye salmon were most frequently eaten, followed by chum or pink, coho, and chinook salmon (Sano 1960, 1962). Sockeye salmon accounted for 42 and 40% of the records in 1959 and 1960 (Fig. 6B). A single salmonid was found most often (80.1%). The largest number of salmonids found in a single stomach was three. Only 16.6 and 3.3% stomachs were found to contain two and three salmonids, respectively. The mean number of salmonids found in a stomach was 1.23.

Fig. 6 (A) Stomach contents and (B) salmonid species composition for salmon sharks caught in the North Pacific Ocean in 1959 and 1960 (based on raw data from Sano 1960, 1962).



There are regional differences in species composition of salmonids fed on by salmon sharks (Fig. 7). In the western North Pacific, salmon sharks preyed largely on pink salmon but they fed mainly on sockeye and chum salmon in the central North Pacific and Bering Sea. In the waters between 160°E and 173°E, salmon sharks consumed various salmonids including coho salmon. These differences are probably caused by different distributional patterns for each species of Pacific salmon.

Preyed salmonids were found in all stages of digestion in the stomachs of salmon sharks (Sano 1960). When two or three salmonids were found in a single stomach, one was usually fresh and the other(s) well digested. These observations suggest that feeding is not continuous but intermittent.

The recorded stomach content weight ranged from 0.1 to 4.7 kg with a mean of 1.68 kg. The size of preyed salmonids was the same as that of commercially caught fish (=immature and maturing fish).

Occurrence and Migration of Salmon Sharks in Salmon Fishing Grounds

An interesting relationship between the daily catch rate of salmonids and salmon sharks was recorded from a salmon fishing ground off southeast Kamchatka in the summer of 1958 (Sano 1959a). Changes in daily catch of salmon sharks were nearly synchronized with those of salmonids (Fig. 8), with high catches of salmon sharks on days of high salmonid catches and vice versa. As these data were recorded under conditions of constant fishing effort in a confined area (Fig. 8), the observed changes were determined by the recruitment of both salmonids and salmon sharks to the fishing ground and their movements to other areas. Thus, salmon sharks migrate together with migrating salmonids.

Salmon sharks also appear to migrate to areas of high salmonid abundance. In waters south of 48°N, large numbers of salmon sharks were captured in late April and early May but catches abruptly decreased in mid-May and thereafter remained at a low level (Fig. 9). In more northern waters catches increased in early June, peaked in mid-June, and then declined. These trends are presumably the result of the northward migration of salmon sharks following salmonids which move from southern to northern waters from spring to summer.

Biomass of Salmonids Eaten by Salmon Sharks

For the following estimation, I used the number of salmon sharks estimated for 1989 by Shimada and Nakano (unpublished manuscript). I then assumed that only older (age ≥ 5) salmon sharks (i.e., 595×10^3

fish) feed on salmonids from spring to autumn (for 244 days from April to November), because they occur in subarctic waters in this period but migrate to northern temperate waters for overwintering. Younger salmon sharks inhabit southern waters where salmonids are not distributed. In addition, since salmon sharks are opportunistic feeders, all salmon sharks are not thought to constantly eat salmonids.

The number (N) of salmonids eaten by salmon sharks in 1989 was calculated as:

$$N = S \times D \times F$$

where S is the estimated number of salmon sharks ($= 595 \times 10^3$ fish), D is the number of days for which salmon sharks can feed on salmonids (=244 days), and F is the number of salmonids consumed by a salmon shark per day. F equals $BW_1 \times DR \times P / BW_2$, where BW_1 is the average body weight of salmon sharks (=86.5 kg, based on Sano [1962, table 8]), DR is the daily ration (expressed as a percentage body weight of a salmon shark), P is the proportion of non-empty stomachs containing salmonids ($= 63 / [63 + 7] = 0.9$, see previous section), and BW_2 is the average body weight of salmonids caught offshore in spring and summer, 1989 (=1.547 kg, Dr. Y. Ishida, National Research Institute of Far Seas Fisheries, Shimizu 424, Japan, per. comm.). Since data on daily ration are not available for salmon sharks, I used 1 or 2% body weight per day as approximations, because published estimates of daily ration for sharks range from 0.4 to 3.2% body weight per day (Wetherbee et al. 1990). As a result, the number (F) of salmonids consumed daily by a salmon shark was estimated as 0.50 or 1.01 fish (0.78 or 1.56 kg). Therefore, salmon sharks consumed an estimated 73.0×10^6 or 146.0×10^6 fish (113×10^3 or 226×10^3 metric tons) in 1989.

The total annual run of Pacific salmon was 580×10^6 fish in 1989 (sockeye: 95×10^6 , chum: 87×10^6 , pink: 373×10^6 , coho: 19.2×10^6 , chinook: 5.5×10^6) (Rogers, unpublished manuscript). Thus, the estimated number of salmonids eaten by salmon sharks in 1989 corresponds to 12.6 or 25.2% of the annual salmonid run for that year.

Multiple Teeth Marks on Preyed Salmonids

There is some need to describe the different types of teeth marks found on preyed salmonids, in relation to the striking, slash marks which are often observed on one side (only) of salmonids (Gilhausen 1989; Welch et al. 1991). Sano (1959b, 1960) thought that a slash mark was formed when a salmonid escaped from an attacking salmon shark, but was wounded by the protruding teeth. He regarded slash marks as the lacerations caused by salmon shark attacks. However, Welch et al. (1991) provided the first direct evidence, differing from Sano's view, for the cause of slash

Fig. 7 Regional variation in species composition of salmonids found in the stomachs of salmon sharks from the North Pacific Ocean in 1960 (top: modified from Sano 1962, bottom: based on raw data from Sano 1962).

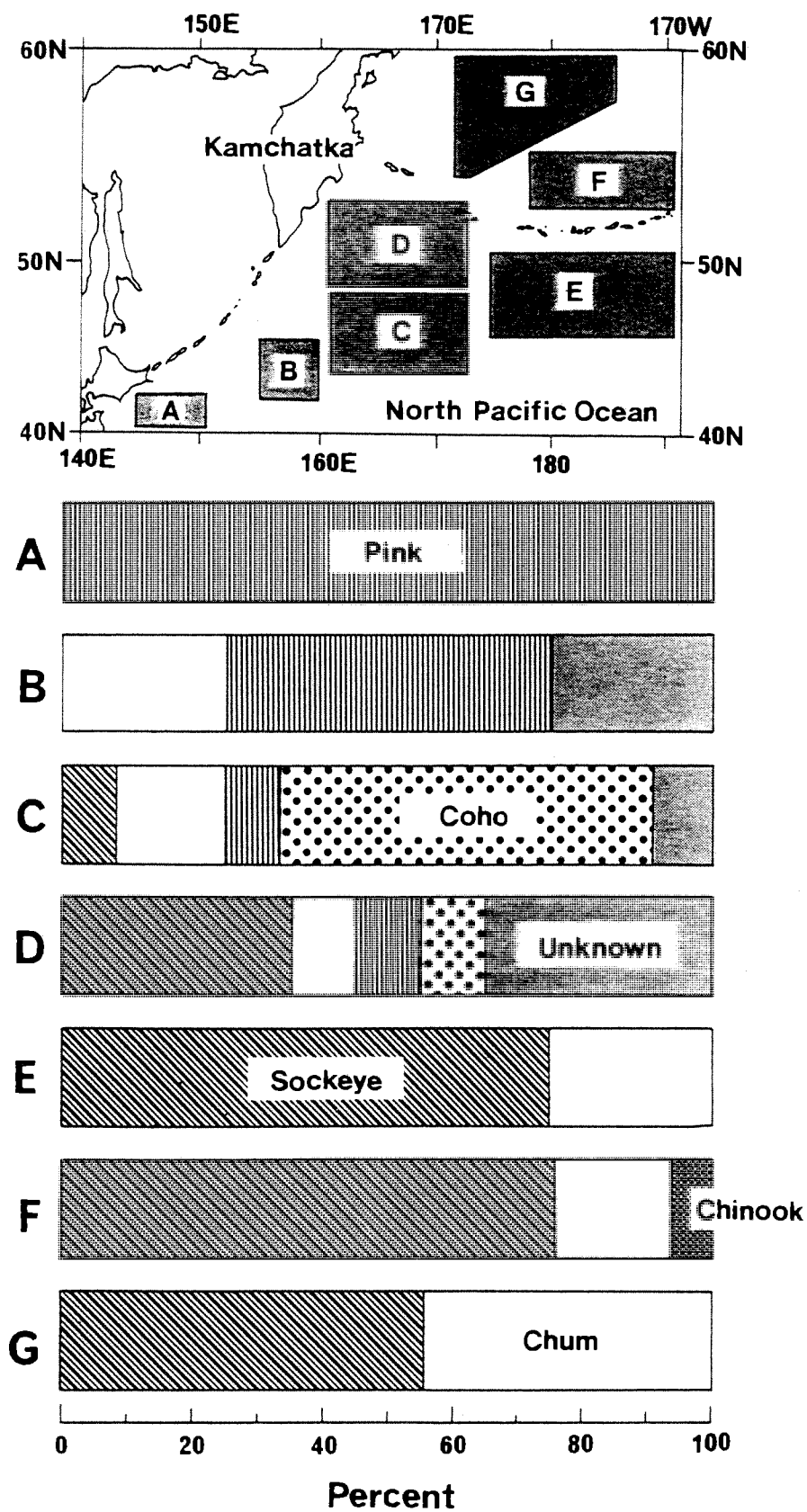


Fig. 8 Daily changes in catch of salmonids (open circles) and salmon sharks (filled circles) by one fleet of the mothership fishery in the fishing ground (stippled area) of the western North Pacific Ocean in the summer of 1958 (modified from Sano 1959a).

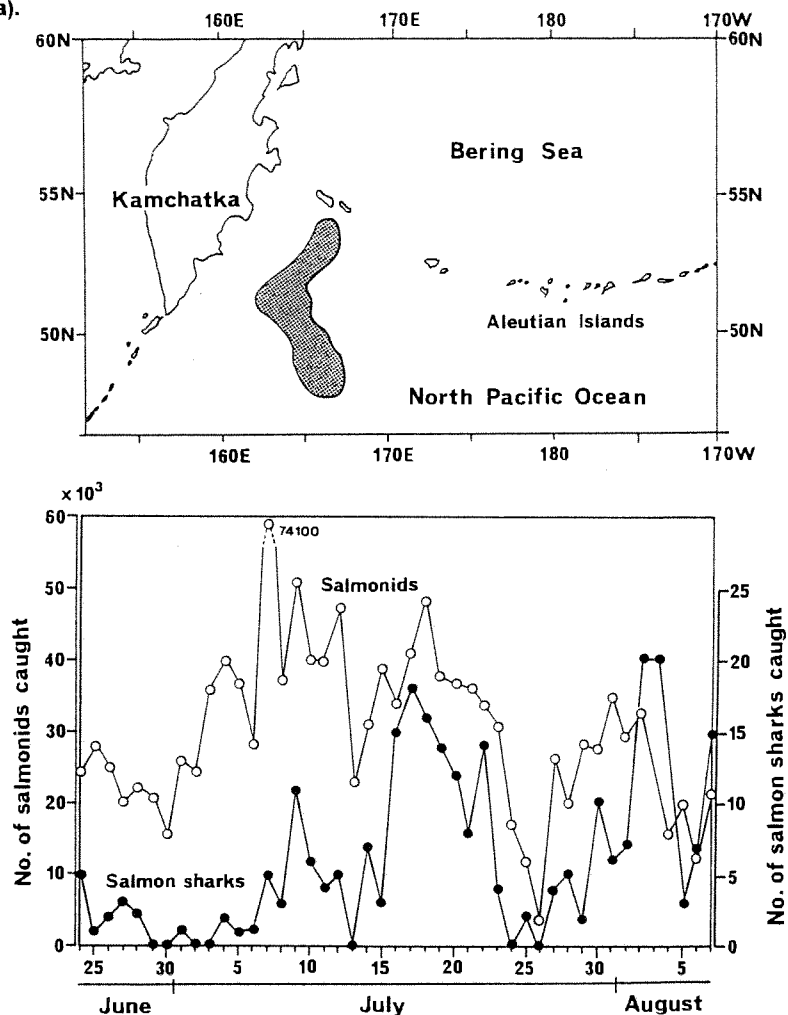
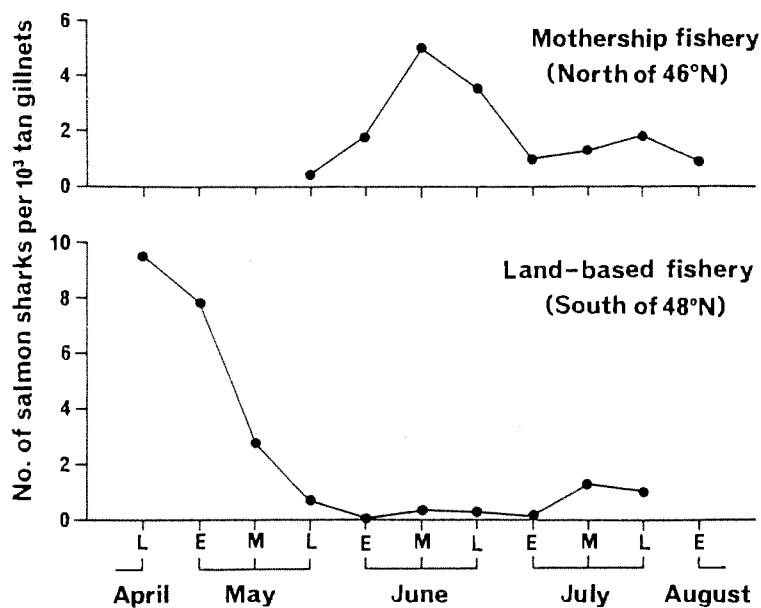


Fig. 9 Changes in catch of salmon sharks by the land-based (bottom) and mothership (top) fisheries in the summer of 1958, by ten-day intervals (based on raw data from Sano 1962). Tan is a unit of gillnets, approximately 50m in length.



marks. They recovered a jaw fragment of a daggertooth from the wound of a slash-marked sockeye salmon and stated that slash marks are caused by the attacks of daggertooth, not salmon sharks.

When we carefully look at the photographs of preyed salmonids shown by Sano (1960), there are often two types of wounds on the side of the salmonid body, i.e., typical diagonal slash marks (Sano 1960; figs. 1a, 1b, 5) and multiple teeth marks (Sano 1960; figs. 3a, 3b, 7). Sano (1960) thought that both types of wounds resulted from salmon shark attacks, but only the latter teeth marks are likely due to salmon shark predation (Fig. 10). One reason why slash-marked salmonids are found in salmon shark stomachs is that such fish may be weakened and thus easily preyed on.

CONCLUSIONS

Salmon sharks occupy the highest trophic level in the food web of subarctic waters. Although their prey also include various fishes and squids in subarctic waters, there is no doubt that salmonids are the major

food item. The estimated number of salmonids eaten by salmon sharks in 1989 is $73\text{--}146 \times 10^6$ fish ($113\text{--}226 \times 10^3$ metric tons), which is equivalent to 12.6–25.2% of the total annual salmonid run from the North Pacific for that year. It is thus concluded that predation by salmon sharks is a significant contributor to the ocean mortality of Pacific salmon in offshore waters of the North Pacific Ocean.

ACKNOWLEDGEMENTS

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Fig. 10 Sockeye salmon found in the stomach of a salmon shark from the Bering Sea (from Shimazu 1975, with permission of the Japanese Society of Scientific Fisheries). Note the multiple teeth marks on the body. Scale bar: 10cm.



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Ecological Functioning of Lake Kuril Relative to Sockeye Salmon Production

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Lake Kuril is the hatchery and nursery area for the largest Asian stock of sockeye salmon (*Oncorhynchus nerka*) within the Ozernaya River watershed. The average annual return for the last decade was 6.3 million sockeye and the range was 3.7 to 10.4 million. Trophic data for Lake Kuril such as water temperature, phosphorus input, phytoplankton and zooplankton densities, size and abundance of smolts, and the number of returning sockeye are available for 30-50 years and were examined relative to sockeye production. Ecosystem dynamics of Lake Kuril indicated the presence of a density-dependent regulating system for sockeye salmon. Smolt size was dependent on zooplankton biomass, and smolt weight was strongly correlated ($R^2 = 0.73$) with adult survival. The estimate of optimum escapement based on stock-recruitment analysis and size of spawning area is 1.5 million; however, when the zooplankton forage base is considered the estimate of optimum escapement can drastically vary. Our work demonstrates the need to consider the current limnological conditions in a lake to assess escapement goals and emphasizes the need to collect limnological and freshwater fisheries data to effectively manage sockeye stocks.



INTRODUCTION

Lake Kuril serves as the major hatchery and rearing area for the largest sockeye salmon population within the Ozernaya River watershed. This sockeye stock is currently managed for an optimum escapement (1.5 million) based on stock-recruitment analyses and the spawning area (Selifonov 1988). However, it is well known that the freshwater rearing environment effects juvenile sockeye growth and can even limit sockeye production (Koenings and Burkett 1987; Kyle et al. 1988). Thus, a density-dependent regulating function can occur in sockeye lakes whereby the biomass of juvenile sockeye is dependent on zooplankton biomass (Brocksen et al. 1970; Kyle et al. 1988; Koenings and Kyle 1997).

A long-term collection of fisheries and limnological data is available to evaluate the ecosystem of Lake Kuril relative to sockeye production and in particular to assess if a density regulating mechanism is evident. This type of controlling function in lakes has been thoroughly documented and is quite characteristic for sockeye nursery lakes (Krogus 1961; Burgner 1964; Mathisen and Kerns 1964; Mathisen 1969; Goodlad et al. 1974; Bugaev 1983; Kyle et al. 1988; Eggers and Rogers 1987). Based on controlling freshwater conditions the rearing capacity of lakes can be over- or under-estimated when using

only spawning area or stock-recruitment analyses. The objective of this paper is to show the influence of Lake Kuril's ecosystem in controlling sockeye production, and to incorporate the rearing capacity (forage base) in the assessment of the optimum escapement in order to maximize return and harvest.

METHODS

Study Site Description

Lake Kuril is located in southern Kamchatka and drains into the Ozernaya River. The lake has a watershed area of 392 km², a surface area of 77.1 km², and a volume of 14.6 km³ (Resursy..., 1966). The maximum and mean depths are 316 and 180 m, respectively, and the water residence time is 17.4 years. Lake Kuril is basically an oligotrophic lake (Table 1) but demonstrates mesotrophic features in some years. Phytoplankton in Lake Kuril is dominated by diatoms (mainly *Melosira*, *Stephanodiscus*, *Cyclotella*, and *Synedra* (E. V. Lepskaya, personal communication). *Melosira italica* is the major phytoplankton species and the main food source for zooplankton. The average density of *M. italica*, depending on phosphorus levels, is 0.25 to 11753 million cells m⁻³. Zooplankton in Lake Kuril comprises of two

Table 1. Limnological features of Lake Kurilskoye

Variable	Range	Average
Euphotic Zone depth (May-October), m	13.8 - 18.3	15.5
Average annual precipitation, mm	471 - 1220	776
Average annual water temperature in the outlet, °C	2.3 - 4.9	3.6
Average annual water temperature in the lake at depth 0 - 100 m (dwelling zone of sockeye salmon fry), °C	2.4 - 4.2	3.5
Degree days with average water temperature at a depth of 0 - 100 m that is 4°C or greater (Period of active sockeye fry growth), °C - day	259 - 1190	712
Average annual contribution of phosphorus released from sockeye carcasses, tons	0.91 - 22.39	4.8
Chlorophyll, mg/m ³	0.2 - 6.8	1

copepods (*Cyclops scutifer* and *Acanthocyclops gigas*), two cladocerans (*Daphnia longiremis* and *Bosmina longirostris*), and nine Rotifer species. *Cyclops scutifer* and *Daphnia longiremis* are main prey of sockeye salmon fry in Lake Kuril. The average density of *Cyclops* ranged from 0.6 to 21.9 thousand m⁻³, that for *Daphnia* ranged from 0.1 to 0.7 thousand m⁻³, and Rotifers ranged in density from 3.6 to 49.8 thousand m⁻³. Average annual biomass of all zooplankton ranged from 15.5 to 242.0 mg m⁻³. The abundance of sockeye salmon in Lake Kuril has ranged from 0.26 million during depressed years to 6 million in peak years. The average spawner abundance is 1.6 million (Selifonov 1988). Spawning area of this lake comprises just over 1 million m² (Ostroumov 1970), and the substrate consists of massive layers of pumice sand lying above bedrock (Brajtseva et al. 1965). The mild climate in southern Kamchatka and the thick snow cover during the winter prevents the spawning area from freezing. The lake was fertilized in 1981, 1982, 1985, 1987, and 1989 in an attempt to increase the zooplankton forage base, and ultimately to benefit rearing sockeye fry.

Physical Features and Phosphorus

Annual water and air temperatures (at the outlet of Lake Kuril), as well as precipitation and water levels are available since 1942 (data of KamchatNIRO). Average annual input of phosphorus was calculated after Dillon (1975), and the phosphorus retention coefficient was calculated after Ostrofsky (1978). The contribution of phosphorus from salmon carcasses was based on Kizzevetter (1942) estimate of 0.28% P₂O₅ per sockeye salmon, and expressed as total phosphorus. In this paper we consider the major sources of phosphorus input to Kuril Lake are

salmon carcasses and fertilizers.

Plankton

Phytoplankton (*Melosira*) density and biomass data were available since 1972. This time period was sufficient to track the influence exerted by phosphorus input on *Melosira* biomass, as this period encompassed a period of minimum and maximum phosphorus input to the lake. Zooplankton data (density and biomass) were available since 1950. Net samples (collected from the entire water column) were taken at established stations once or twice per month depending on season, and analyzed for species composition, density, fecundity, and age/life stage.

Juvenile and Adult Sockeye

Sockeye egg to emergent fry survival was determined by standardized digging of the spawning redds in the lake, tributaries, and lake outlet. Egg to emergent fry survival data were available since 1941. Smolt weight data (available since 1942) were collected with the use of a trap placed in the face of the weir at the lake's outlet. The abundance of smolts was estimated from the number of spawners expressed by the relationship:

$$1) \text{ SN} = 28.48 + 0.0188\text{E} \quad (r = 0.66; p < 0.001)$$

where SN = the number of smolts (millions) and E = the escapement (thousands). Sockeye spawner data (size, weight, sex, age, and fecundity) were collected by use of a weir in the lake's outlet, and were available since 1940.

RESULTS AND DISCUSSION

An excess in Kuril Lake sockeye escapement occurred in 1943, 1947, 1949, 1951, 1952, 1959,

and 1961 before the very large escapements starting in the 1980s (Fig. 1). During 1962-1977, sockeye escapements were below the optimum of 1.5 million. The highest spawner deficiency occurred from 1969 through 1976. Beginning in the early 1980s, the sockeye escapement reached historical high levels. Correspondingly, the annual input of phosphorus (from fish carcasses and fertilizers) was also the highest in the 1980s (Fig. 1). The amount of total phosphorus contribution from fertilizers was 7.38 tons in 1981, 19.10 tons in 1982, 8.48 tons in 1985, 3.1 tons in 1987, and 4.63 tons in 1989.

The annual biomass of *Melosira* corresponded with the increase in phosphorus as in the early 1970s the biomass was at minimum levels and during the 1980-1990s the biomass reached maximum levels. The first major peak of *Melosira* occurred in 1986, and in 1990 *Melosira* biomass was the highest. In 1986, 1990 and 1991 *Melosira* biomass in Lake Kuril passed the lower limit defined for mesotrophic lakes (100-300 mg C m⁻³). Between the major peaks of *Melosira*, there

were 2- and 3-year long periods of depressed levels. Apparently, following periods of high biomass, *Melosira* settles to the bottom depositions, and in subsequent years, under low water temperature conditions the release of phosphorus sets the stage for another peak in *Melosira*. As phosphorus declines, *Melosira* again decreases in biomass. In the late 1980s and early 1990s energy transformation in Lake Kuril followed this cycle as the ecosystem was a detrital type; a very small amount of phytoplankton was consumed by zooplankton.

Temperature, precipitation, and sockeye egg survival for Lake Kuril are plotted in (Fig. 2). There was no dependency between egg survival, substrate type, freezing of substrate, presence or absence of ice, and water temperature (Selifonov 1975). Egg survival depends to a high degree on precipitation, and to a lower degree on spawner abundance. The relationship of survival to precipitation and spawner abundance is expressed by:

Fig. 1 Summary of sockeye escapement, annual phosphorus input and *Melosira* concentration in Lake Kuril.

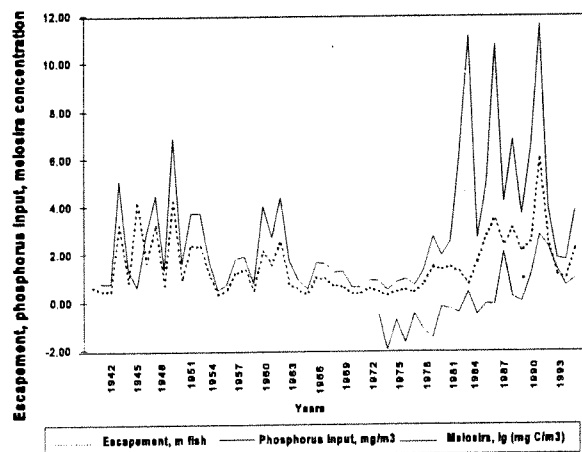
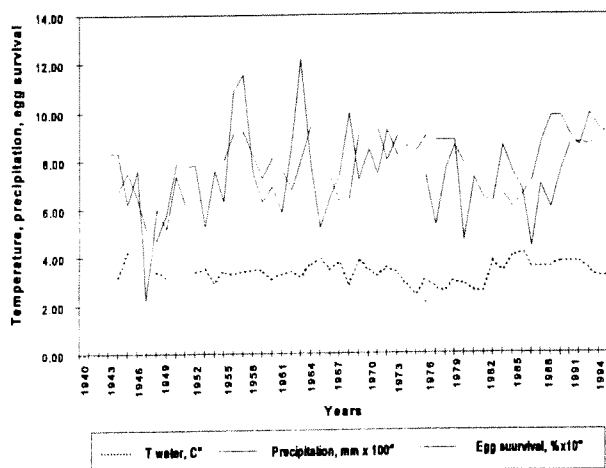


Fig. 2 Summary of annual water temperature (0-100m), precipitation, and sockeye egg survival in Lake Kuril.



$$2) ES = 39.175 + 0.05817P - 0.00643SA$$

$$(R^2 = 0.70; p < 0.05)$$

where ES = egg survival (%), P = average annual precipitation (mm), and SA = spawner abundance (thousands).

The historical trend in zooplankton biomass shows a steady increase from the 1950s to the mid 1970s, followed by a decline from the mid 1970s to 1980 (Fig. 3). During the 1980s zooplankton biomass was at high levels, peaked in 1986, and was followed by another decline through the early 1990s to the lowest recorded levels.

From the mid 1950s through the mid 1970s the sockeye escapement and phosphorus input decreased (Fig. 1), and most assuredly the number of rearing juveniles decreased. In contrast, during this period the zooplankton biomass increased (Fig. 3). In addition, the highest zooplankton biomass (since the early 1970s) was observed in the years with the lowest biomass of *Melosira* (Fig. 1). The influence of *Melosira* biomass on zooplankton biomass was insignificant (r was ~ 0). This suggests that *Melosira* biomass provided for a near maximum feeding ration for zooplankton. Therefore, a minimum content of *Melosira* was sufficient for meeting the nutritional needs of zooplankton, such that the *Melosira* biomass could increase. The rapid decline of

zooplankton biomass in the late 1970s cannot be explained by the low *Melosira* biomass, but rather by the growing abundance of rearing sockeye juveniles.

The increase of zooplankton biomass in the 1980s is influenced by the increase in average water temperature (Fig. 2) along with a sufficient abundance of *Melosira*. The zooplankton biomass increase occurred initially despite an increase in the abundance and biomass of rearing sockeye juveniles; however, consecutive years of high escapements appeared to over-crop the zooplankton forage base as the lowest zooplankton biomass was observed in the early 1990s.

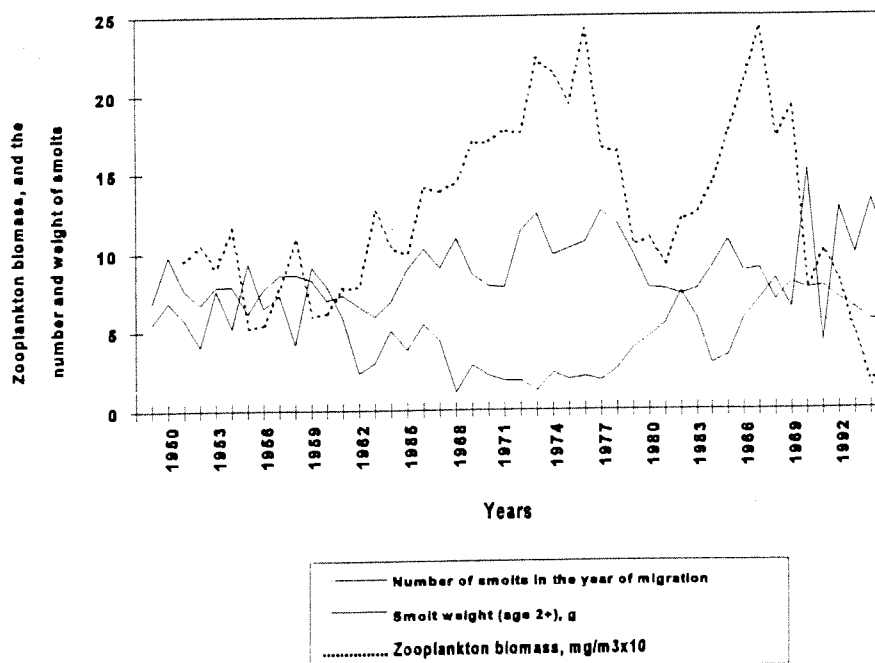
The dramatic decline in zooplankton biomass also occurred when the annual water temperature dropped (from 3.0° C in 1990 to 2.4° C in 1994). Zooplankton biomass was found to be associated with the biomass of rearing juvenile sockeye (as indexed by escapements) and average annual water temperature (at 0-100 m), and is represented by a multiple regressive equation:

$$3) ZB = 1276.87 - 0.986JB - 577.66T + 0.000039JB^2 + 72.64T^2 + 0.259JB \cdot T$$

$$(R^2 = 0.55; p < 0.01)$$

where ZB = zooplankton biomass (mg m⁻³), JB = juvenile sockeye biomass (tons), T = water temperature at 0-100 m (°C).

Fig. 3 Dynamics of zooplankton biomass, number of 2+ smolt and weight in Lake Kuril.



When sockeye escapement into Lake Kuril is low (up to 1 million), the smolt number fluctuates primarily between 20 and 50 million (Fig. 4). At an average escapement (1.6 million), the smolt number ranges from 30 to 80 million, and with larger escapements the smolt number increases with a higher dispersion of points.

In our assessment of rearing capacity we considered a zooplankton biomass level of 100 mg m^{-3} and a smolt production of 60 million (<300 tons in biomass) as low, a zooplankton range of $100\text{--}150 \text{ mg m}^{-3}$ and a smolt production of 40–60 million (300–500 tons) as medium, and a zooplankton biomass over 150 mg m^{-3} and a smolt production >60 million (>500 tons) as high. During the 1970s, when the smolt number and biomass were lowest and water temperatures were cooler a high zooplankton biomass was observed. During the 1980s, when the smolt number and biomass were high and water temperatures were warmer a high zooplankton biomass was also observed. In the early 1990s, when the water temperature decreased but the smolt number and biomass was high the zooplankton biomass was low. Thus, a high zooplankton biomass in Lake Kuril is possible under conditions of cooler water temperatures ($2.4^{\circ}\text{--}3.3^{\circ}\text{C}$) providing that the biomass of juvenile sockeye remains in the medium range. However, if smolt number and biomass are high, a high level of zooplankton biomass is possible only for a short period of time (initial years) and only if the average annual temperature is warmer ($3.6^{\circ}\text{--}4.2^{\circ}\text{C}$) and *Melosira* biomass remains adequate. These conditions are necessary to ensure zooplankton regeneration.

An additional assessment of the rearing

capacity was the weight of the major (87% by composition) age class (2+) of smolts in Kuril Lake. During the 42-year observation period, age 2+ smolts ranged from 5.6 to 12.6 g, and averaged 8.4 g. The weight of smolts, even during periods of high juvenile abundance, was far greater than the threshold value of 2 g (Koenings and Burkett 1987). The largest smolts were observed during the period of low juvenile abundance and high zooplankton biomass (1970s and mid 1980s). In contrast, the smallest smolts were observed in the early 1990s when juvenile abundance was high and the zooplankton biomass was at record lows. Smolt weight was dependent upon the preceding year's zooplankton biomass as well as smolt number, and is represented by a multiple regression equation:

$$4) \text{ SW} = 5.95809 - 0.01812\text{SN} + 0.04063\text{ZB} + 0.00014\text{SN}^2 - 0.00006\text{ZB}^2 - 0.00018\text{SN}*\text{ZB} \quad (R^2 = 0.53; p < 0.001)$$

where SW = smolt weight of age 2+ (g), SN = number of smolts (millions), and ZB = zooplankton biomass.

From this relationship, an average smolt weight (8.4 g) is produced if zooplankton biomass is over 125 mg m^{-3} and smolt production is 50 million. A larger smolt ($>10.4 \text{ g}$) is possible if zooplankton biomass is over 150 mg m^{-3} and the number of smolts does not exceed 40 million. Thus, smolt weight is equally dependent on smolt number (fry rearing abundance) and zooplankton biomass during the first and second year of rearing (Fig. 5). Also, from (Fig. 5) one can conclude that at low and medium zooplankton biomass, this dependency is expressed more distinctly.

Fig. 4 Relationship between adult sockeye spawners and number of 2+ smolts in Lake Kuril.

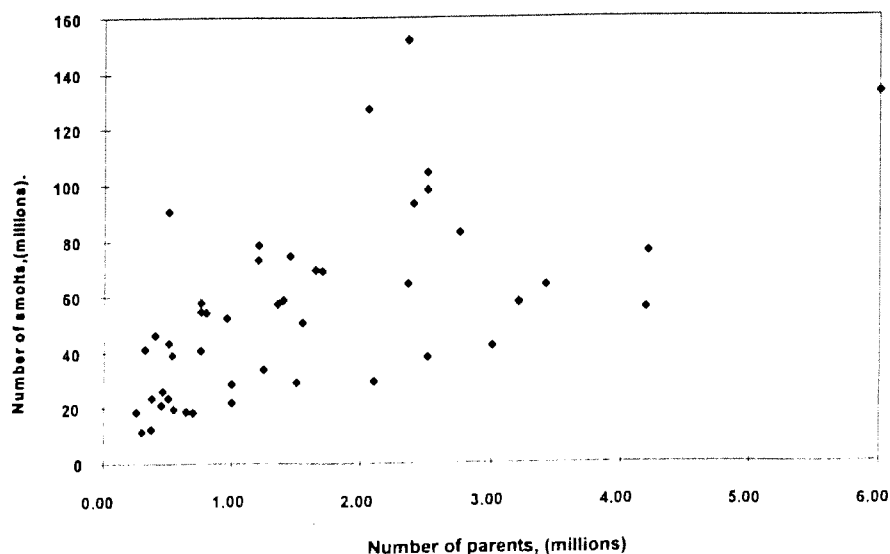
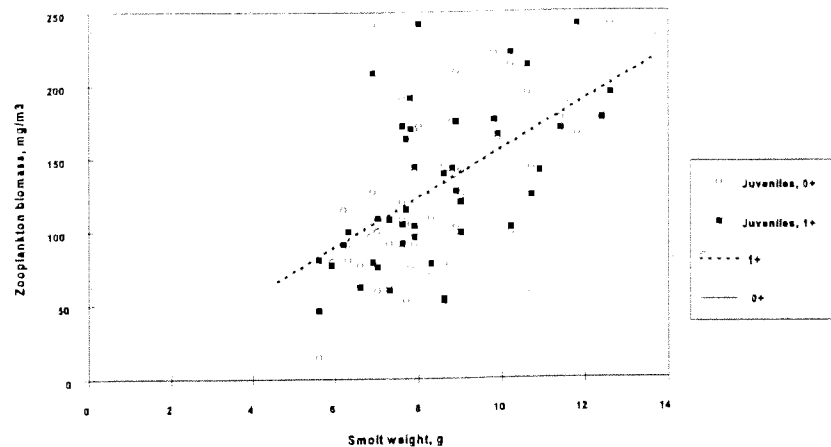


Fig. 5 Dependence of smolt 2+ weight on zooplankton biomass during the first and second rearing year, Kuril Lake.



Chronology of Trophic Level Changes in Lake Kuril

The ecosystem of Lake Kuril relative to sockeye salmon production from 1940 through 1994 has undergone some major changes that need to be considered in order to assess the escapement goal and rearing capacity. Since 1950s, sockeye escapements gradually declined and reached a low from 1970 to 1974. At the same time, the smolt number decreased, smolt weight increased, and zooplankton biomass increased to a maximum in the mid 1970s. The increase in zooplankton biomass resulted from a low forage pressure by juvenile sockeye and excellent trophic conditions in the lake - mainly due to a period of high precipitation that increased allochthonous nutrient input. Thus, the years 1970 to 1974 were a critical point of change in the ecosystem of Lake Kuril relative to sockeye production, and were characterized by low sockeye escapements, a high level of precipitation (watershed nutrient input), low smolt numbers of large size, and a high forage base (zooplankton biomass). The sockeye of Lake Kuril began to restore in the early 1980s as larger escapements were achieved and lake fertilization was implemented. However, a gradual increase in smolt number (rearing juveniles) had a negative effect on the forage base and resulted in smaller smolts. The decline in the average smolt weight was presumably due to intraspecific competition and as such the increase in forage pressure had more of a negative effect on the zooplankton community than fertilization exerted as a positive effect on the zooplankton community. The latest period (1990-1994) was a crucial change in the lake's ecosystem as the number of spawners was very high, and the precipitation level, egg

survival, and smolt number were at their maximum for the 55-year period. The record number of rearing juveniles (as indexed from the escapements) had a severe effect on the zooplankton community as zooplankton biomass was at unprecedented low levels.

Management Implications

If only the spawning ground area and stock-recruitment analysis are used to assess the optimum escapement for Lake Kuril the estimate is 1.5 million sockeye. However, these analyses are limited and based on the premise that freshwater conditions do not change. As the above chronology portrayed, Lake Kuril has undergone some dynamic changes in trophic level production, and in order to better manage this system trophic interactions need to be considered:

1) Lake Kuril spawning grounds possess unique ambient characteristics and provide for a consistently high egg survival; thus, a close relationship exists between the number of spawners and smolts ($r = 0.66$), which allows modeling of abundance;

2) Smolt number influences zooplankton biomass and at low water temperatures zooplankton development is further hindered. Zooplankton biomass affects smolt weight (see Fig. 3 and Fig. 5). The dependence between zooplankton biomass, smolt biomass, and temperature is related (see equation 3). By knowing the temperature, zooplankton biomass, and taking into account responses on juvenile sockeye, it is possible to evaluate rearing conditions in the lake. This can be used to evaluate current rearing capacity and to forecast responses to existing limnological conditions in the lake.

3) There is a strong dependence ($R^2 = 0.73$; $p = 0.01$) between smolt weight and survival (Fig. 6 & 7). These figures show data since 1964 when such data were available. Consequently, future survival can be predicted, and this relationship serves as a decision-making basis for management of future runs.

Using the empirical data from Lake Kuril to define relationships dealing with trophic level responses to various limnological conditions and escapements, a table can be formulated to assess sockeye production (Table 2). This table can assist in assessing escapement goals and in making management decisions using data pertinent to the current state of the rearing environment. For example, this can be demonstrated in reference to a situation for Lake Kuril in 1996. Let us assume that a decision was made to allow 2 million sockeye to escape into the lake in 1995. However, in 1996 the zooplankton biomass was extremely low ($\sim 35 \text{ mg m}^{-3}$), and as such the rearing juveniles reared under an impoverished forage base and were relatively small. If the smolt weight of these fry is less than 6.6 g, their survival factor would be 1.5 for a total return of 3 million sockeye salmon (Table 2). Now, let's assume it was decided to allow only 1 million spawners

instead of 2 million under the same condition of low zooplankton biomass.

According to (Table 2), a higher survival factor would result (1.7) because there would be less intraspecific competition for food. In this case, the forecast return will amount to about 1.7 million sockeye. The escapement of 2 million spawners resulted in a return of 1.3 million more sockeye than the escapement of 1 million; however, to accomplish this 1 million more fish had to be taken from the catch and the consequences of putting more fish into a depressed rearing environment need to be considered. That is, the recovery time for the zooplankton community and the low adult returns during the restorative years would most likely be more costly than the short-term benefits of a higher catch in one year.

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We are grateful Dr. V. Dubinin who provided unpublished data on juvenile sockeye salmon and Dr. I. Tiller for help. We would like to especially thank Dr. G.B. Kyle (Alaska Department of Fish and Game) for reviewing and editing early version of this paper.

Fig. 6 Smolt 2+ weight dynamics and survival measure for sockeye generations, corresponding to smolt brood years, Kuril Lake.

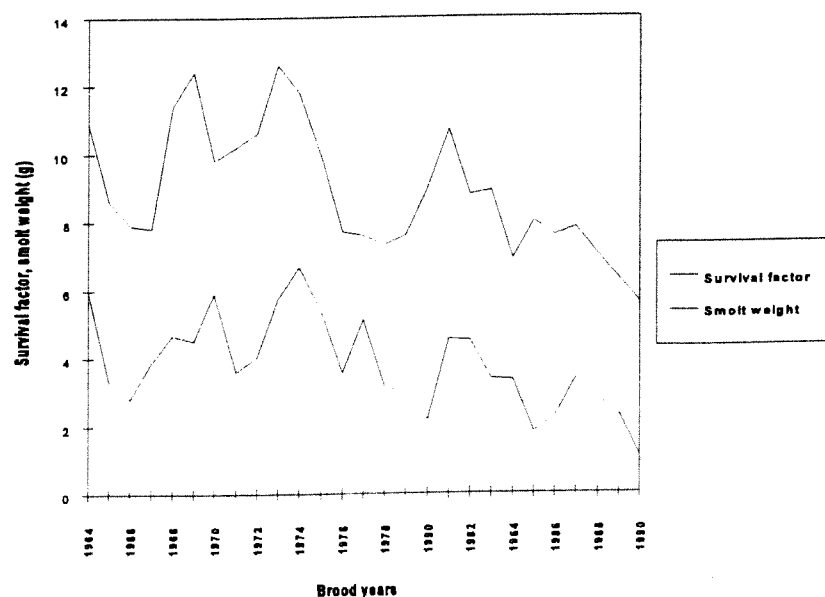


Fig. 7 Relation between survival factor and smolt 2+ weight for Lake Kuril sockeye salmon.

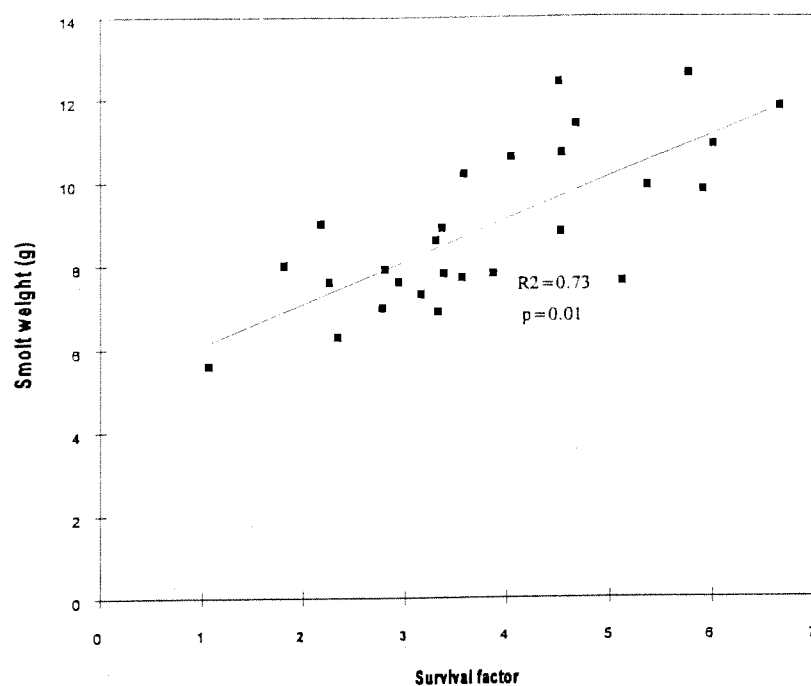


Table 2. Approximate weight of smolts and survival factors of Lake Kuril sockeye at various spawner and zooplankton concentrations.

Relative Conditions	Zooplankton concentration, mg/m ³	Forecast range of smolt weight, (g)	Forecast survival factor
Escapement of 1 M spawners (47 M smolts)			
Below medium	under 50	=< 6.9	=< 1.7
Below medium	50-100	6.8-8.0 (7.4)	2.5
Medium	100-150	8-9 (8.5)	3.2
High	150-200	9-9.5 (9.2)	4.0
High	over 200	over 9.5	>= 4.5
Escapement of 2 M spawners (66 M smolts)			
Below medium	under 50	under 6.6	under 1.5
Below medium	50-100	6.6-7.5 (7.0)	2.0
Medium	100-150	7.5-8.2 (7.8)	2.6
High	150-200	8.2-8.7 (8.4)	3.2
High	over 200	8.5-8.9 (8.7)	3.5
Escapement of 3 M spawners (85 M smolts)			
Below medium	under 50	under 6.4	under 1.4
Below medium	50-100	6.4-7.2 (6.8)	1.6
Medium	100-150	7.2-7.8 (7.5)	2.4
High	150-200	7.8	2.6
High	over 200	7.9-8.1 (8.0)	2.8

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Recent Changes in the Marine Distribution of Juvenile Chum Salmon off Canada

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Beamish, R.J., and M. Folkes. 1998. Recent changes in the marine distribution of juvenile chum salmon off Canada. *N. Pac. Anadr. Fish Comm. Bull. No. 1*: 443-453

In 1995, abundance surveys for juvenile Pacific salmon were carried out in the Strait of Georgia using either rope trawls or beam trawls. All five species of salmon were captured and in this paper we report the preliminary results of the distribution and abundance of chum salmon. Chum were not caught in the earliest survey and were not abundant in the samples until late May. Once chum were abundant in the catches, they were distributed throughout the Strait, including the Gulf Islands area. By mid-November, chum were still abundant and had a mean size of 22 cm and ranged from 16-28 cm. A swept volume estimate of abundance indicated there could be approximately 1.3 million juveniles at this time. Depending on the amount of marine mortality that had occurred by November, the juveniles that remained in this relatively small marine ecosystem could contribute significantly to the future catch and escapement. It appears that the occurrence of such large numbers of juveniles in the Strait of Georgia, so late in the year, is a recent phenomena that may be related to natural changes in the Strait of Georgia ecosystem that, in turn, are linked to large scale climate-ocean events in the North Pacific.



INTRODUCTION

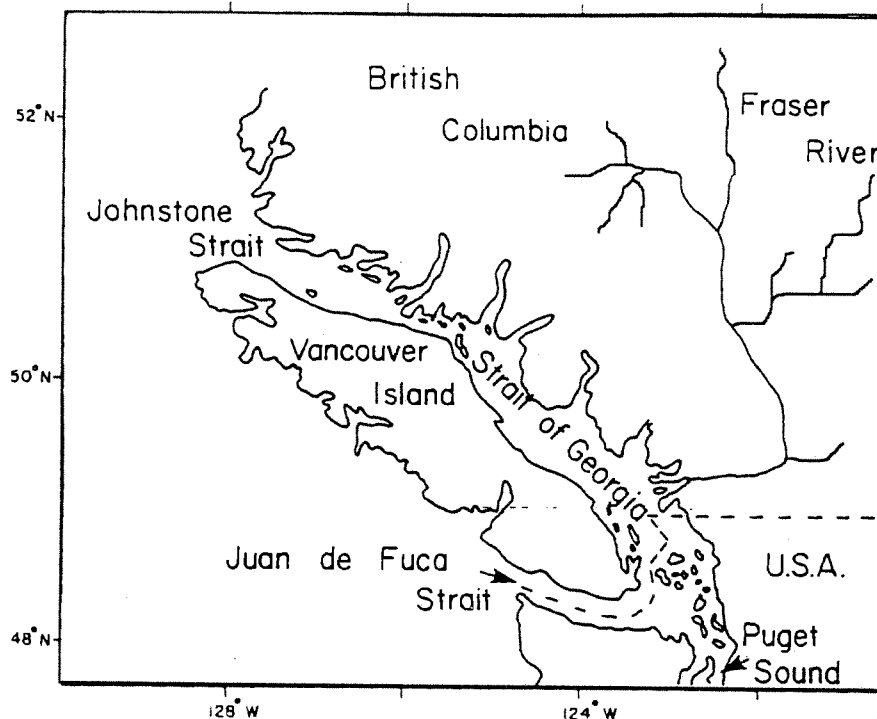
The Strait of Georgia (Fig. 1) is a small marine ecosystem located between Vancouver Island and the mainland British Columbia, Canada. It is the most important juvenile rearing salmon area on Canada's west coast and possibly one of the most important salmon rearing areas in the North Pacific. Historically, Fraser River salmon stocks accounted for 35-40% of the total Canadian catch of Pacific salmon. Thus, large numbers of pink, chum, sockeye, coho, and chinook salmon enter the Strait early in the year from the Fraser River. In addition to the wild stocks from the Fraser River and other smaller rivers that flow into the Strait, large numbers of hatchery-reared salmon are presently released into the Strait. In general, more than one half of Canada's one half billion artificially enhanced Pacific salmon are released into the Strait of Georgia (Dept. of Fisheries and Oceans 1996). These releases are mostly chinook and coho from Canadian hatcheries, but hatchery released salmon from United States hatcheries in Puget Sound, and a few wild salmon also feed for varying lengths of time in the Strait of Georgia. Beamish et al. (1995A,B) and Beamish (1996) showed that the number of hatchery-reared chinook and coho either are equal to or exceed the

number of wild juveniles from Canadian rivers and that the combined number represents a substantial increase in total smolt abundance compared to earlier years when there was mostly wild production.

Throughout the range in the distribution of chum salmon, there is a general tendency for the average time of ocean entry to be later with increasing latitude (Godin 1982), with the latest migrants entering salt water by the end of June (Salo 1991). In British Columbia, chum salmon commonly migrate into salt water from February to May. Migration from the shoreline and shallow nearshore areas occurs for most North Pacific stocks after a few weeks and is believed to be related to food abundance (Whitmus 1985, Bax 1983). Movement into the deeper waters in the Strait of Georgia was reported by Healey (1980) to occur in June at an average size of 80-100 mm. Movement out of the Strait of Georgia occurred in July, with movements possibly related to foraging success (Healey 1980).

We show that relatively large numbers of chum salmon are presently remaining in the Strait of Georgia until late in the year and that this behaviour is different than observed during the studies of Healey and others in the 1960s and 1970s. The reasons for the change in behaviour are unknown, but may be associated with a change in the Strait of Georgia

Fig. 1 Study area showing the Strait of Georgia, Puget Sound and the Fraser River.



ecosystem that was associated with basin wide changes in climate in the North Pacific. Our study is continuing and the results reported here should be considered as preliminary observations of work in progress.

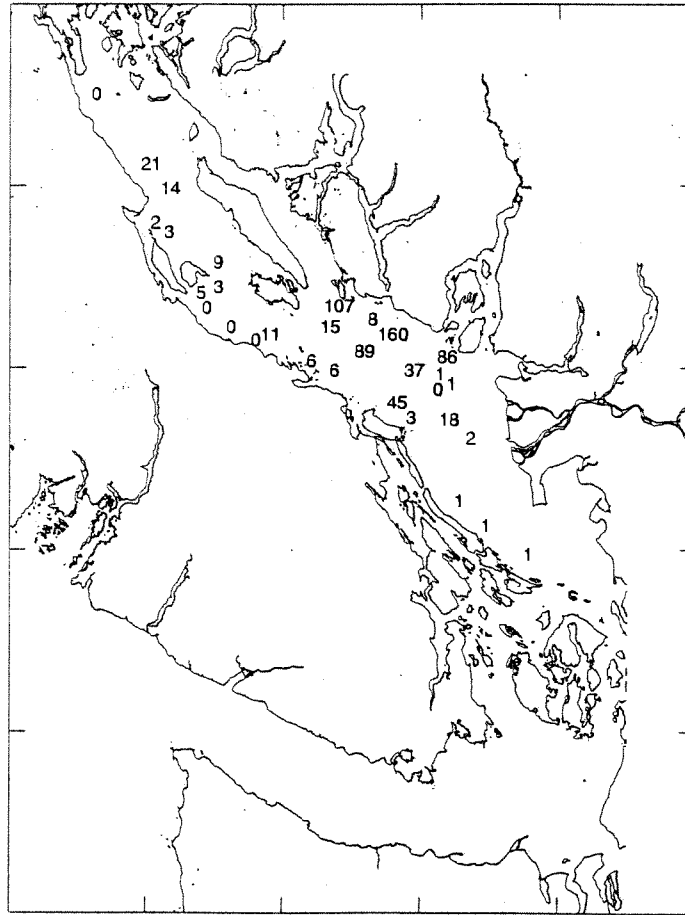
METHODS

Surveys of juvenile salmon abundance were made in the Strait of Georgia, throughout 1995. Initially, samples were collected with a beam trawl, but the catches reported here were made with a rope trawl that was fished at different depths and towed at speeds averaging from 4 to 5.2 knots. When fishing to design specifications the rope trawl will fish 21.3 m deep and 63.5 m wide. The first 54.3 m of the net, or the front end, consists of large rope meshes that can range from a minimum of less than 2 m in width to over 3.8 m. The intermediate portion has meshes ranging from 1.6 m to 20 cm. The cod end has 10 cm meshes with a 1 cm liner in the last 7.6 m of the net. The net is held open with USA Jet Doors Model P that can be hooked up to fish at the surface or any depth. The specified bridle length is 61 m, but we used 30.5 m to fish the net at the surface. This shorter bridle length reduced the opening of the net to approximately 14 m deep by 28 m wide, but the size and shape of the opening varied according to tides and sea conditions. When the doors were at the surface, the head rope was between the surface and

3.5 m. A Simrad TS3300 net sounder was attached near the head rope and provided a continuous image of the net opening, large schools of fish that were entering the net, and a continuous indication of head rope depth. The survey design represented a series of sets along track lines that were distributed within the Strait of Georgia (Fig. 2) so that juvenile salmon were collected from areas of known abundance, as well as sampling in the centre and both sides of the Strait. All rope trawls were made during daylight hours because the large net could readily be fished at all depths. The amount of daily effort was limited to 12 hours because of controls on the hours that the crew could work.

The abundance was estimated using the average area of the mouth of the net as determined from a net sounder attached to the head rope. The distance fished was the distance traveled during the set which was usually 1 hour. The efficiency of the net was assumed to be between 1 and 0.5 (i.e., the net caught everything in its path or 50% of the fish in its path). The habitat depth was determined from preliminary surveys in which 90-95% of chum caught were in the top 30 m. The habitat area was considered to be the surface area of the Strait of Georgia minus the island areas. The abundance, therefore, was the total catch at depths from the surface to 30 m x Strait of Georgia volume to 30 m / swept volume of the trawl net. One method of estimating the accuracy of the swept volume estimates of chum salmon was to compare

Fig. 2 Catches of ocean age 0 chum salmon in the Strait of Georgia, in November 1995. The tows were approximately one hour, and the catches indicated have been standardized to one hour. Standardized catches are identified for all fishing depths.



swept volume abundance estimates of coho in November 1995 with the total abundance of coho as determined from sport and commercial catches and from estimates of escapements. The abundances for coho for past years was known and if the swept volume estimates of coho from the November 1995 sample were consistent with the known abundance it would indicate that the estimate of chum abundance probably was a reasonable approximation of the true abundance.

We compared our catches of chum salmon with catches of chum salmon from other, earlier studies of juvenile chum salmon in the Strait of Georgia. We were able to identify 79 separate cruises or distinct sampling efforts from 1965 to the present. In addition to 20 surveys in our study, there were 59 other studies. However, 11 occurred from September 1st to December 31st and were directed at salmon life history, movement, and diet. Those past collections were typically summarized in federal technical and data reports available at the Pacific Biological Station library. The samples from other surveys were collected using a variety of gear including small mesh

purse seines, surface trawls, and two boat trawls. We standardized catches by comparing the ratio of chum catches to the combined chinook and coho catches. This was necessary because the various studies used different sampling gear. We used this method of comparing abundances because our surveys showed that coho and chinook also remained in the Strait of Georgia later until late in the year. We believe this method of comparing chum abundances is conservative because the abundance of coho and chinook juveniles actually increased in the 1990s compared to the 1970s as mentioned earlier, and this would bias the abundance estimate in favour of a lower estimate of chum abundance.

The Strait of Georgia (Fig. 1) has a water surface area of 6320 km² and an average depth of 155 m. The flushing time of the basin ranges from 50-75 days in the summer to 100-200 days in the winter (Thomson 1994). The flushing time and the circulation in and out of the Strait is related primarily to the flows of the Fraser River drainage, which accounts for approximately 80% of the land runoff area. The circulation is the typical estuarine

circulation which brings in offshore bottom water to compensate for the movement of surface low salinity water that moves out of the Strait through Johnstone Strait as a result of the discharge from the Fraser River (Thomson 1981). The estuarine circulation is also the major supplier of nitrates to the Strait, accounting for approximately 5 times the amount contributed by other sources (Yin et al. 1995).

RESULTS

The comparison of survey catches in the present study with earlier studies, indicates that there has been an increase in chum abundance (Fig. 3). The abundance of chum salmon in the Strait of Georgia after September 1 is about 4 times higher in the 1990s than in the past. We have five observations in the 1990s and there is considerable variation. The lowest catch ratio, or the lowest abundance of chum, in the 1990s was in 1993, a year in which large numbers of coho did not move offshore (Fig. 4). There is less variation in the catch ratio in the early 1970s, with 6 of the 7 surveys finding relatively small abundances of chum relative to the combined abundance of chinook and coho. There has been an increase in hatchery produced chum salmon in the 1980s and 1990s (Fig. 5), however, hatcheries were also producing relatively large numbers of chum at the

time of the surveys in the 1970s.

In 1995, there were 6 cruises, (Table 1). In April, no chum were caught. The first and largest catches were in late May when chum had an average length of 8 cm. By mid-November, chum had an average length of 22 cm. In 1995, the estimated abundance of chum using a net efficiency of 100% in September was 1,797,000 and 1,314,000 in

The estimated abundance of coho salmon in November 1995, using a net efficiency of 100% was 563,000 (Table 2). This compares to an average commercial and sport catch in the Strait of Georgia in the 1990s (1990-1994) of approximately 650,000 (Fig. 6). A difficulty with this calibration is the tendency for coho to move out of the Strait in the 1990s (Fig. 4). The estimates in Fig. 6 are for commercial and sport catches, while our estimates are for juveniles before they enter the fishery and before all the coho moved offshore. In 1994, the catches of coho in the Strait of Georgia were 352,000 and 74% of the Strait of Georgia coho were offshore for a total catch of 1.35 million. Assuming escapements were approximately 25% of the total (75% harvest rate), the total catch and escapement was 1.8 million fish. In November, 1995 the estimate of 563,000 coho represents about one third of the total catch and escapement in 1994.

The estimate of 1,314,000 ocean age 0 chum in

Fig. 3 Comparison of chum catches in this study with catches from other, earlier studies. The catch ratio is the ratio of the catch of chum divided by the combined catch of coho and chinook. Each value represents the average catch ratio from one study.

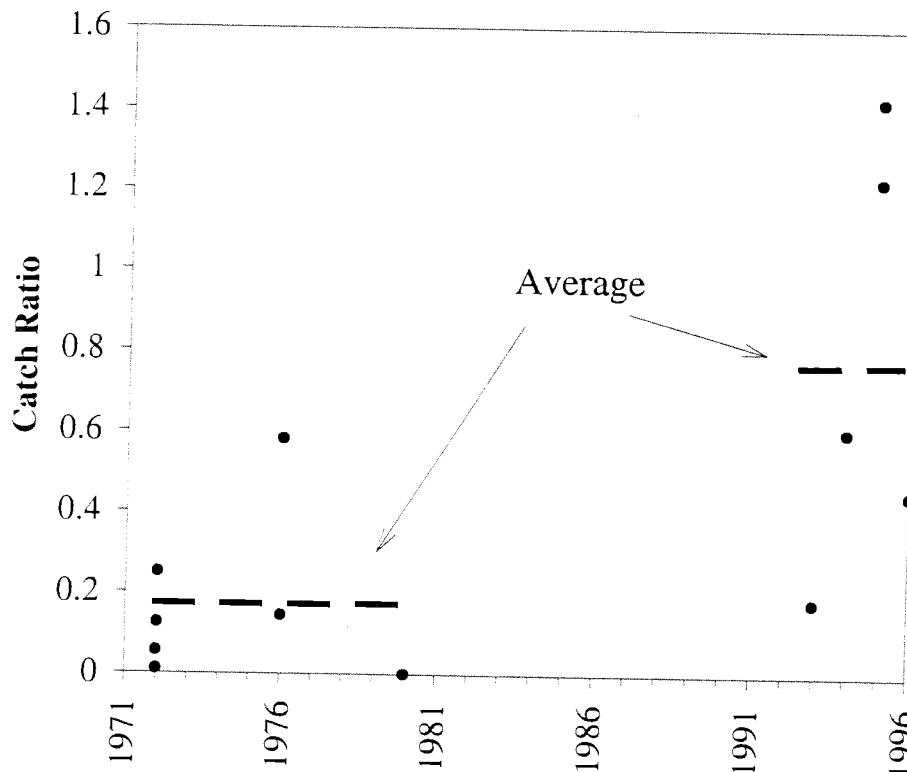


Fig. 4 The percentage of coho that were caught in offshore fisheries showing that in recent years more coho move out of the Strait of Georgia. Data labels indicate catch year which is one year later than the year coho enter the ocean (x axis). The 1997 catch is an estimate based on catches as of July 30, 1997.

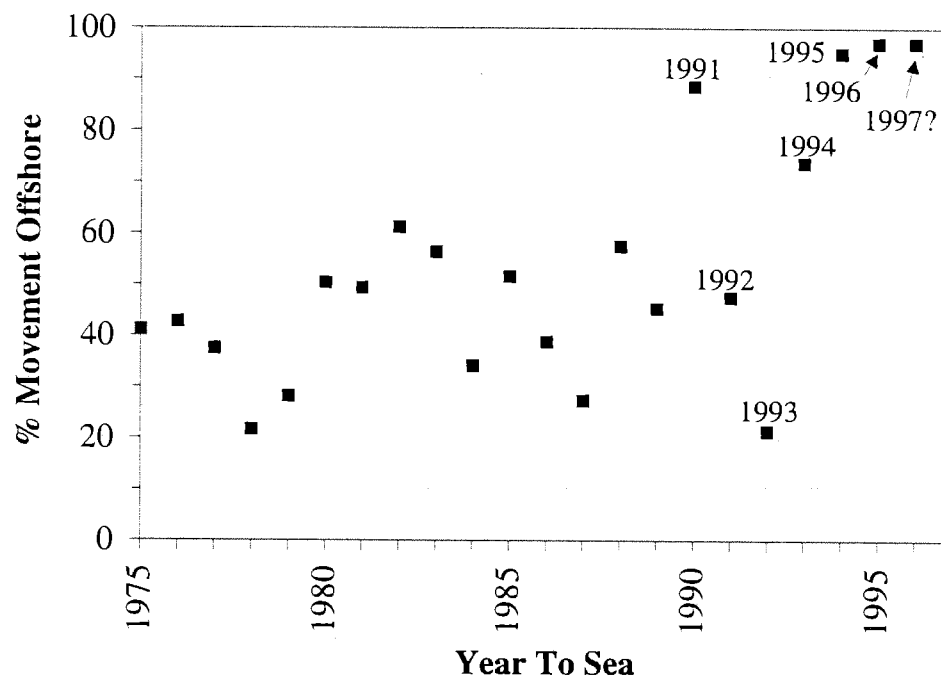


Fig. 5 Numbers of chum salmon reared in hatcheries and released into the Strait of Georgia or in Puget Sound.

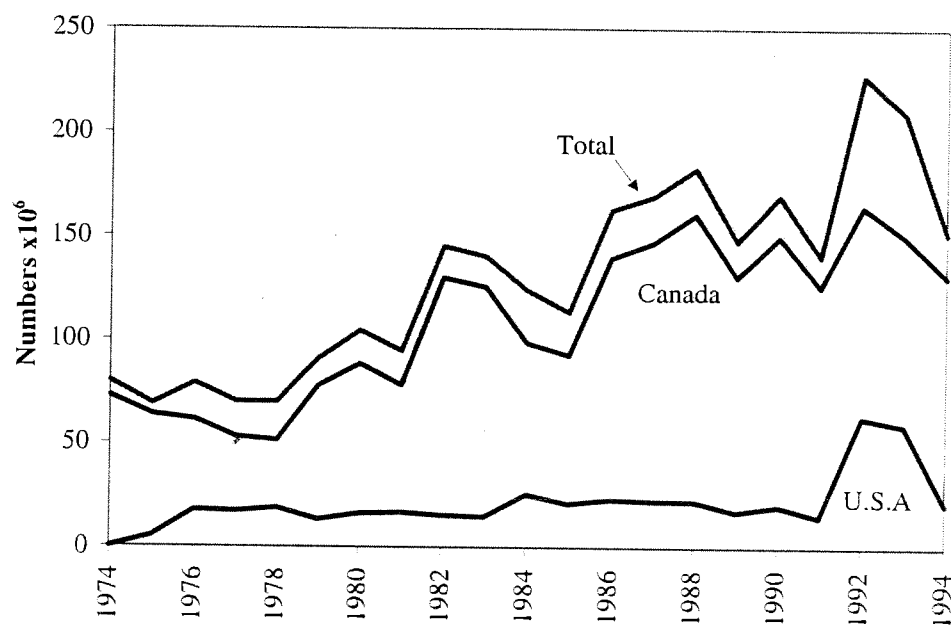


Table 1. Catches of Chum salmon from the cruises in the Strait of Georgia in 1995.

Date	Number of Sets	Gear	Catch	Average Length (cm)
April 21-27	33	Rope Trawl	0	
May 23-30	120	Beam Trawl	10,177	8
June 19-26	109	Beam Trawl	4,987	10
July 6-21	44	Beam Trawl	1,799	10
Sept. 11-24	138	Beam Trawl/ Rope Trawl	577	16
Nov.6-18	40	Rope Trawl	657	22

Table 2. Swept volume abundance estimates, using a 100% net efficiency and 50% net efficiency. The habitat depth was 30m. The estimates of coho abundance are included.

	Species	N	Estimated abundance using a Net Efficiency of:	
			100	50%
September 11-24, 1995	Chum	145	1,797,000	3,594,000
November 7-17, 1995	Chum	657	1,314,000	2,628,000
November 7-17, 1995	Coho	305	563,000	1,126,000

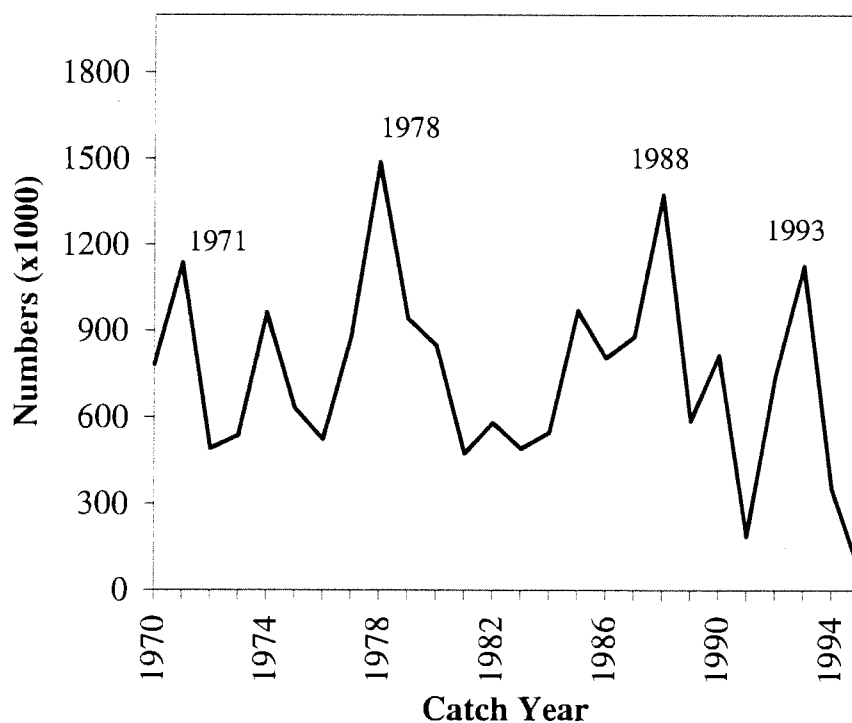
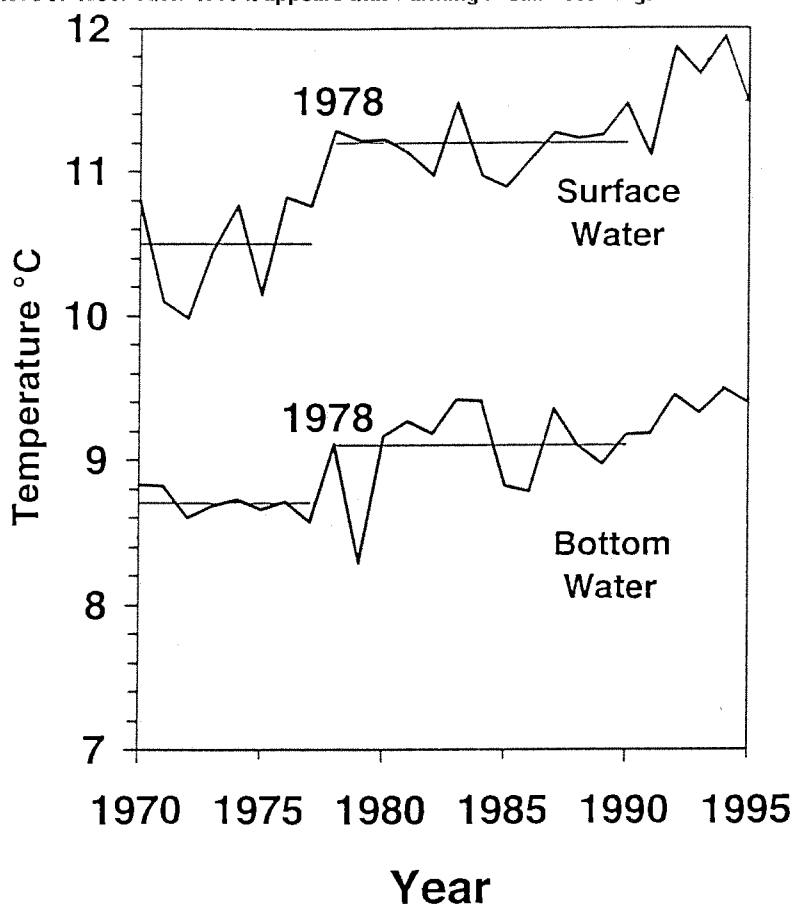
Fig. 6 Commercial & sport catch of coho salmon in the Strait of Georgia.

Fig. 7 Strait of Georgia temperatures, sampled at the Nanoose site. The Strait lines are the average temperatures from 1970 to 1977 and 1978 to 1990. After 1990 it appears that warming is still occurring.



November 1995 was converted to catch using an average harvest rate of 35% and assuming that the November 1995 abundance is what remained after 95% of the total 98% expected marine mortality had occurred. The resulting calculated future catch of 184,000 (Table 3) compares to average catches of 465,000 in the Strait from 1992-1995 (Table 4) or 2,384,000 for the entire southern catch, including catches outside of the Strait. If the catch in the Strait of Georgia in 1995 of 66,000 fish or 610,000 for all southern stocks, is an indication of continued low catches, then the potential catch from the ocean age 0 chum in the Strait of Georgia in November 1995 could represent 3 times the total catch within the Strait and approximately 1/3 of the total southern catch if the total returns (catch and escapement) from these fish are similar to the 1995 total returns.

The importance of the Strait of Georgia as a juvenile salmon rearing area is illustrated by the mid-September 1996 survey catches (Table 5). All five species of Pacific salmon were present in the catches including pink, chum, and sockeye. Using a net efficiency of 100%, abundance per km² of surface area was 793 for sockeye, 499 for chum,

334 for chinook, and 265 for pink, and 192 for coho.

Beginning in the late 1970s, the temperatures in the Strait of Georgia increased (Fig. 7) as a result of the Pacific basin wide changes that occurred with the 1976-1977 regime shift (Beamish et al. 1995A). In the 1990s, it appears that there may be a continued trend of increasing temperatures (Fig. 7), although there has been cooling in 1995. Associated with the warmer water, there has been a decline in the Fraser River flows that also started with the 1976-1977 regime shift (Fig. 8). Since the late 1980s, there has been earlier spring freshets as indicated by the larger April flows (Fig. 9). These earlier flows indicate an earlier melting of the snow pack, which would occur if the air temperatures were warmer. There was a change in the intensity of the Aleutian Low (Fig. 10) beginning in the late 1980s which would result in less intense winter winds as well as a change in the dominant direction of the winter winds. We included the 1997 winter anomaly to show the extreme change from 1996. The less intense low, means that high pressures were more common.

Table 3. The November 1995 abundance estimates of juvenile chum salmon, and the estimated catch when adults return.

	Net Efficiency	Net Efficiency
	100%	50%
November Abundance	1,314,000	2,628,000
Estimated adult catch from the juveniles in the Strait of Georgia in 1995 ¹	184,000	368,000

¹ The estimated future catch was made by assuming that 95% marine mortality had occurred before the November survey and the total marine mortality would be 98%. The harvest rate of the remaining chum was assumed to be 35%.

Table 4. Catches of chum salmon in the Strait of Georgia and southern British Columbia and the estimated total adult returns (catch plus escapement).

	Southern British Columbia	Strait of Georgia
1995 chum catch	610,000	66,000
1995 total chum returns assuming 35% harvest rate.	1,743,000	189,000
1992-1995 average chum catch	2,384,000	465,000
1992-1995 average chum returns assuming 35% harvest rate	6,811,000	1,329,000

Table 5. Catches of ocean age 0 Pacific salmon from 62 sets in the Strait of Georgia September 9-20, 1996. The abundance estimate was made assuming a net efficiency of 100% and a habitat depth of 30m.

Species	Catch	Total Abundance Estimate	Numbers per km ²
Chum	2,121	2,496,000	499
Pink	1,125	1,324,000	265
Coho	814	958,000	192
Sockeye	3,370	3,965,000	793
Chinook	1,824	2,146,000	334

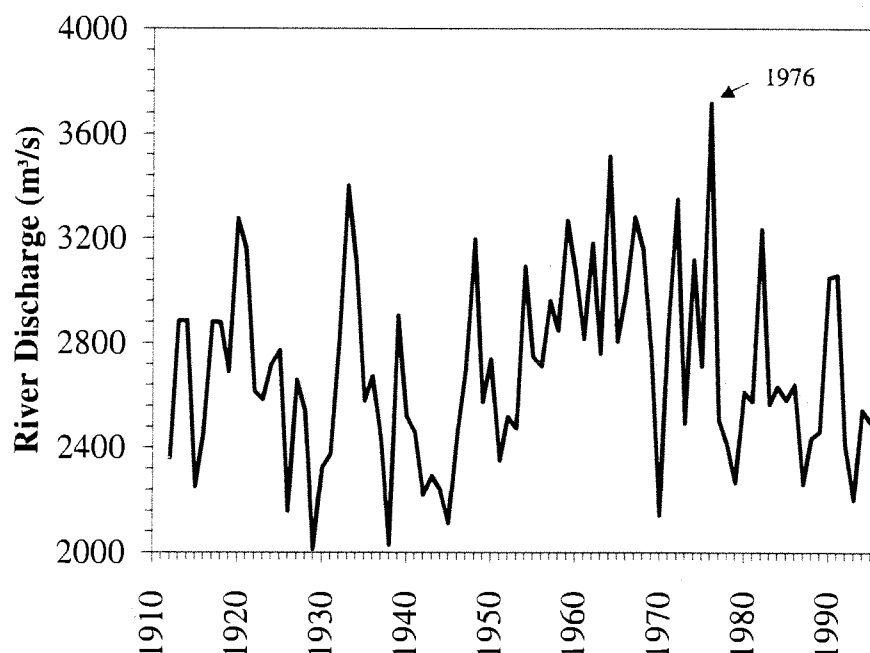
Fig. 8 The trend in the annual Fraser River total from the discharge. Since 1976, there has been a decreasing trend.

Fig. 9 The daily discharge in April (m^3/sec). Beginning in the late 1980s, the flows in April increased. The individual graphs show the daily values for the entire month.

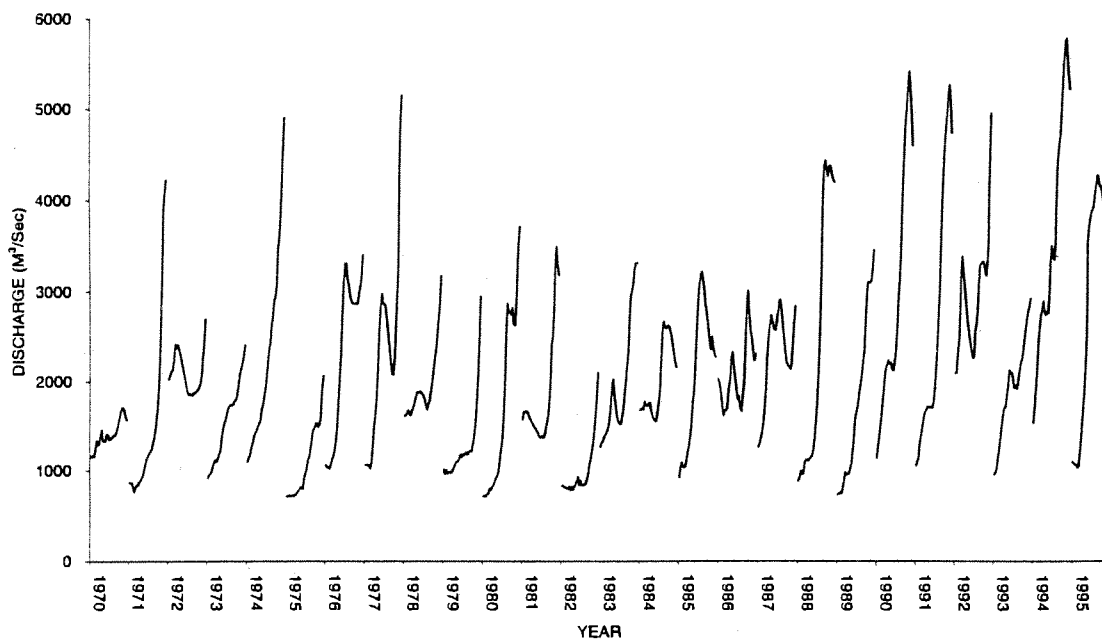
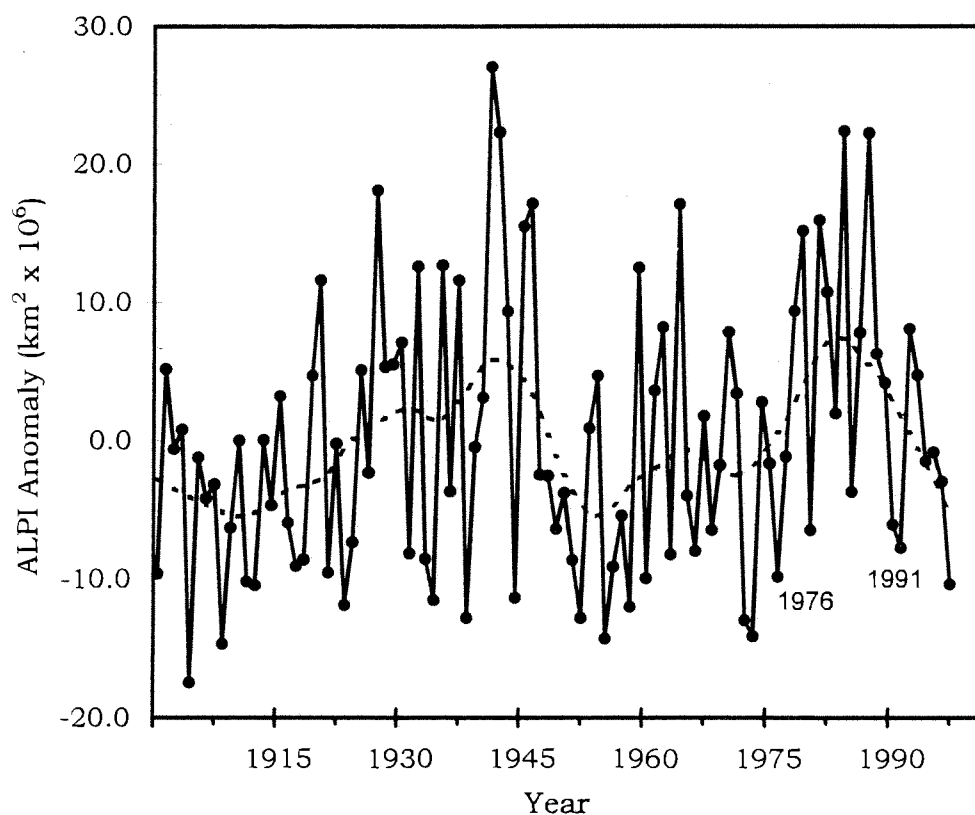


Fig. 10 The Aleutian Low Pressure Index (ALPI) (Beamish et al. 1997) showing the period of intensification after 1976 and the period of weak lows in the 1990s.



DISCUSSION

The largest abundance of chum salmon in British Columbia is produced in the Fraser River and it is these chum stocks plus the stocks in other rivers flowing into the Strait of Georgia that rear in the Strait of Georgia. The early studies of Healey (1982) indicated that these chum juveniles gradually leave the Strait during the summer months. The observation in our study that large numbers of chum salmon remained in the Strait of Georgia as late as November, indicate that the behaviour of chum has changed. A difficulty with our method of comparison of our catches with chum catches in other studies is the changing abundance of chinook and coho. It is true that catches of chinook were higher in the 1970s than in the 1990s, but Beamish et al. (1995 A) have shown that there actually was an increase in chinook smolt production relative to the 1970 levels as a consequence of hatchery production. Beamish et al. (1995 B) showed that increases also occurred for coho. However, these increases for both chinook and coho were associated with higher marine mortality rates. Despite the difficulties in quantifying the abundance changes, the results of the comparisons of catches of chum juveniles relative to the combined coho and chinook catches and the earlier observations of Healey (1980) of few chum late in year, indicate that relatively large numbers of chum are remaining longer in the Strait of Georgia than in the past. As we do not have observations in the 1980s, it is not possible to determine when chum salmon started to remain longer in the Strait of Georgia, thus it is possible that more chum remain in the Strait because of the increased releases of hatchery-reared chum salmon. However, except for 1992 and 1994, the total releases from Canada have not changed since the late 1980s, and as other species such as pink and sockeye are also found later in the year (Table 5) it is probable that the behaviour change is real.

The numbers estimated from the swept volume method are preliminary estimates as the accuracy of the determination is unknown. However, the abundance estimate may be conservative because it is unlikely that the net catches 100% of the fish in front of the net. There are other difficulties with the estimate that are associated with the patchiness of the distributions of chum and the estimated habitat depth of 30 m. We examined the accuracy of our swept-volume abundance estimates by comparing similar estimates for coho with total catch and escapements of coho from previous years. The November estimates of 563,000 coho is approximately 1/3 of the total catch and escapements

reported in 1994. As a high percentage of coho caught in 1995 were outside of the Strait of Georgia it is possible coho were moving out of the Strait in the late fall and early winter. Our estimate of 563,000 coho or about 1/3 of the 1994 catch and escapement, therefore, is within an expected range of abundances. We suggest that this indicates that the abundance estimates for chum juveniles, also, are within the range of the actual abundances.

Our estimate of the contribution of the juveniles to future catch and escapement was based on an assumption that by November, 95% of the marine mortality had occurred and the total marine mortality would be 98%. When the total returns become known in 1998, we will be able to determine the validity of these assumptions. If we compare the estimated future catch of chum in the Strait of Georgia of 184,000 to previous Strait of Georgia catches of 446,000, it is apparent that a significant number of juvenile chum are remaining longer in the Strait. If only the 1995 catches were compared to the estimated future returns, then the catch of juveniles in the Strait of Georgia in 1995 when they eventually are fished could represent 3 times the catches in 1995. We assumed that the marine mortality prior to the November survey was 95%. The basis for this assumption was the common assumption that most marine mortality occurs shortly after salmon enter the ocean. Even if we were to use an estimate of 50% marine mortality by the November sampling period, the abundance of chum salmon would still equate to a high percentage of the subsequent catch if the future catches remain about the level of the 1995 catch. The numbers of chum estimated to remain in the Strait, therefore, appear large relative to the previous catches and escapements.

The reason for the change in behaviour is unknown, however it coincides with a change in the ALPI index about 1989-1990. Another change at about the same time was the earlier beginning of the increased Fraser River flows and a general increase in sea surface temperatures. We speculate that the longer residence time is related to these physical changes which may have improved feeding conditions.

An important observation from this study is that the behaviour of chum salmon changed. If it is valid to assume that the change in chum salmon behaviour results from changes in the ecosystem, then we need to look at ways of detecting when ecosystems change. We also need to recognize that multi-year behaviour trends can change. Decadal-scale variability, therefore, may be an important component of salmon population dynamics.

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On the Coherence of Salmon Abundance Trends and Environmental Factors

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Salmon catches from Pacific rim countries have shown a high degree of consistency in trend over time. This pattern is exhibited over wide spatial and temporal scales suggesting a significant influence of the marine environment. The relationships among all-nation catches of sockeye, pink and chum salmon and three indices of atmospheric conditions are considered in this paper. Time series models are employed to remove the trend component of the data as well as any autocorrelation. Cross-correlation analyses of the residuals from each of the models are used to identify plausible links between salmon catches and the various climate indices. Significant relationships were observed between the all-nation salmon catch time series and each of the climate indices. The Atmospheric Circulation Index (ACI) exhibited a downward change around 1990 and if the relationship holds, this may indicate all-nation salmon production could be reduced in the near future.



INTRODUCTION

There is clear and mounting evidence that variations in the size and distribution of marine fish stocks are related to changes in the marine environment (see for example Beamish 1995; Beamish and Bouillon 1991, 1993; Beamish et al. 1997b; Hare and Francis 1995; Steele 1996). In general, traditional stock assessment methods do not adequately incorporate (either explicitly or implicitly) environmental change in population models and this does not usually pose a serious problem provided environmental conditions are relatively stable or change slowly over a reasonable time scale. Abrupt shifts in the ecosystem as characterized by dramatic changes in the population dynamics of fish stocks often result in spectacular failures of assessment models and sub-optimal management decisions that could have serious consequences for fish stocks in both the short and long term. Incorporation of key environmental signals into assessment models or at

least the development of environmental indices that mimic or predict general trends in fish production would be helpful to individuals wishing to adopt a risk adverse approach to fisheries management.

In this paper, we statistically examine three climate indices for the north Pacific Ocean to determine if they are related to trends in the production of Pacific salmon (Beamish et al. 1997a). The models employed are necessarily simplistic and do not attempt to account for the different life strategies of the various salmon species and the consequences of variable management regimes employed in each region in the Pacific rim. Time series models are employed to remove the trend component for each of the data series as well as to model any observed autocorrelation. Cross-correlation analyses of the residuals from each of the models are used to identify plausible links between salmon production and each of the climate indices. Finally, transfer function models incorporating both all nation salmon catch and environmental data are developed.

MATERIALS AND METHODS

Salmon Data

All nation catches of sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon are used to represent salmon production trends in the north Pacific Ocean. The catch of these three species represents about 90 percent of the total salmon catch in the north Pacific and exploitation rates for these species are relatively and consistently high (40 to 80 percent) over time. While total production requires catch and escapement estimates for each stock, these data are not generally available and are of quite variable quality. For these reasons, total catch is viewed as a reasonable surrogate of salmon production trends and the use of such data is consistent with approaches used in previous studies (Beamish and Bouillon 1993).

Climate Indices

Three climate indices are used in this study. The Aleutian Low Pressure Index (ALPI) was developed by Beamish and Bouillon (1991, 1993) and represents the area of the low pressure region less than or equal to 100.5 kPa averaged over the period from December to May. The ALPI used in this study is the modified index described in Beamish et al. (1997a). It can be considered as a measure of the mid-ocean upwelling in the north Pacific that influences plankton production in that area. Periods of intense Aleutian lows generally result in increased primary production and in turn lead to increases in salmon production in subsequent years (Beamish and Bouillon 1993).

The second climate index employed was developed by Trenberth and Hurrell (1995). Their North Pacific Index (NPI) represents the deviation from the long-term mean sea level pressure over a fixed area in the north Pacific Ocean that generally includes the area occupied by the Aleutian low. Like the ALPI, trends in the NPI may represent trends in primary productivity resulting from changes in upwelling or other biological or physical processes. While one could argue the use of a fairly large fixed geographic area provides a more inclusive picture of the climate in the north Pacific, the NPI may also be less informative than ALPI which varies in size and shape annually.

The last climate index used in this study is an Atmospheric Circulation Index (ACI) (Beamish et al. 1997a). The ACI represents the intensity of the prevailing climate pattern over the upper northern hemisphere in a particular year. Daily weather patterns are categorized as one of three general types

and the dominant pattern for the year becomes the climate type for that year. The number of days for the dominant pattern in the year determines the intensity of the index for that year. As with the other indices, the ACI is viewed as a surrogate measure of the complex biological and physical process that influence primary production in the ocean and subsequently fish production (Beamish et al. 1997a). The ACI is a more general index than either the ALPI or the NPI since climatic conditions in the Northern Hemisphere are considered simultaneously.

Statistical Models and Procedures

Time series models (Box and Jenkins 1976) were used to remove trends as well as to model any autocorrelation in each of the catch and climate data series. Where appropriate, the time series models incorporated autoregressive or moving average components or both. In an autoregressive process, the catch at time t , C_t , is related in a linear fashion to previous catches (say to lag p) such that

$$(C_t - \mu) = \phi_1(C_{t-1} - \mu) + \phi_2(C_{t-2} - \mu) + \dots + \phi_p(C_{t-p} - \mu) + a_t$$

where μ is the mean catch, ϕ_i , $i = 1, 2, \dots, p$ are the p autoregressive parameters for the model, and a_t is an error term assumed to be normally and independently distributed with mean 0 and constant variance σ_a^2 . In a moving average process, the catch at time t , C_t , is linearly related to past errors (say to lag q), a_{t-j} , $j = 1, 2, \dots, q$, such that

$$(C_t - \mu) = a_t + \theta_1 a_{t-1} + \theta_2 a_{t-2} + \dots + \theta_q a_{t-q}$$

where θ_j , $j = 1, 2, \dots, q$ are the q moving average parameters. Combining both autoregressive and moving average components in the model provides a robust approach to modelling autocorrelated time series and this family of models has been shown to be useful in fisheries (see for example Campbell et al. 1991; Fogarty 1988; Hare and Francis 1995) as well as economics (Makridakis et al. 1982; Granger and Newbold 1977) and environmental science (Hipel and McLeod 1994).

To identify models that incorporate both salmon catch and climatic indices, cross-correlations were calculated using the model residuals from each time series (Haugh 1976; Haugh and Box 1977; Hipel et al. 1982, 1985). Employing model residuals instead of the raw data minimizes the chances of obtaining spurious correlations. Once tentative models and

appropriate lags have been identified, transfer function models linking salmon catch to climate indices were developed such that

$$(C_t - \mu) = \omega_0 X_t + \omega_1 X_{t-1} + \dots + \omega_v X_{t-v} + N$$

where X_t is the climate index ω_k , $k = 1, 2, \dots, v$ are the parameters associated with the transfer function component of the model, and N is the stochastic noise component of the model which includes the appropriate autoregressive and moving average terms as well as the random error term, a_t .

RESULTS

Salmon Data Models

All nation sockeye, pink, and chum salmon catch data are available for the period 1926-95 inclusive (Fig. 1a). Catches were in the 700,000 t range from 1926 until about 1940, decreased to about 350,000 t between 1940 and the mid-1970s, and have increased steadily since the mid-1970s to their current level of approximately 875,000 t in 1995. In spite of the obvious year to year variability, there are strong and persistent trends in the data. The persistence in the time series may indicate a high degree of autocorrelation in the data and it may be possible to account for the trends using an autoregressive model. However, it may also be necessary to remove the trends as part of the overall model. One common approach to removing trends is to difference the data and fit a model to the differenced time series, D_t , such that

$$D_t = C_t - C_{t-1}$$

where D_t is the difference between successive observations. For the salmon catch data, the differenced log transformed data (Fig. 1b) show no residual trend.

A number of potential models were considered and the residuals from each model were examined to ensure key statistical assumptions were satisfied. In each case, the data were log transformed to provide a closer approximation to normality. The best two or three models (one model included differencing the data) were all quite similar and included a single moving average component at lag one and significant weight being given to catches two years previous (indicative of the important role pink salmon plays in the total catch). The general overall model for catch is given as

$$\ln(C_t) = \phi_2 \ln(C_{t-2}) + a_t + \theta_1 a_{t-1} + \text{constant}$$

where C_t and C_{t-1} are catch at time t and $t-1$, a_t and a_{t-1} are the error terms at time t and $t-1$, ϕ_2 ($= 0.9$) and θ_1 ($= 0.4$) are the autoregressive and moving average parameters, respectively, and the constant is the weighted mean of the log transformed catch data $[(1 - \phi_2) \mu = 0.6]$. Overall, this model (and other similar candidate models) accounted for approximately 80 % of the variance of the raw data.

Climate Index Models

NPI data were only available for the period 1926 - 1994. No significant autocorrelation was detected for either the ALPI (Fig. 2) or the NPI (Fig. 3) so the best predictor of each is the series mean. Given the similar basis for the ALPI and NPI, a significant linear relationship ($R^2 = 0.74$) exists between ALPI and NPI (Fig. 4).

Like the all nation catch of sockeye, pink, and chum salmon, the ACI time series exhibited distinct trends over time (Fig. 5). Differencing was required to remove the trend (Fig. 6a, b) before various combinations of autoregressive and moving average models were fitted to the differenced data. The best model was of the form

$$ACI_t = \phi_1 ACI_{t-1} + \phi_3 ACI_{t-3} + a_t$$

where the autoregressive parameters, ϕ_1 and ϕ_3 , were 1.5 and -0.5, respectively.

Transfer Function Models

The model residuals from the catch and climate time series were used to calculate cross-correlations for both positive and negative lags to identify plausible links between all nation sockeye, pink, and chum catch and the three climate indices. These analyses indicated possible links between catch and both ALPI and NPI at a lag of three years. That is, ALPI and NPI may be useful in predicting catch up to three years in advance. Similar analysis, indicated ACI may be useful in predicting catch one year in advance. Transfer function models were fitted to the data and in all cases the parameter linking the climate index and catch was significant at the 5 % level. All transfer function models provided modest improvements in fit over using catch data alone. Of all the indices, the ACI appears to track salmon catch reasonably well (Fig. 7). The relationship between all nation sockeye, pink, and chum salmon catch and

Fig. 1a All nation catch of sockeye, pink and chum salmon (solid line) from 1926-1995. The trend line (dashed) is a loess smooth of the data.

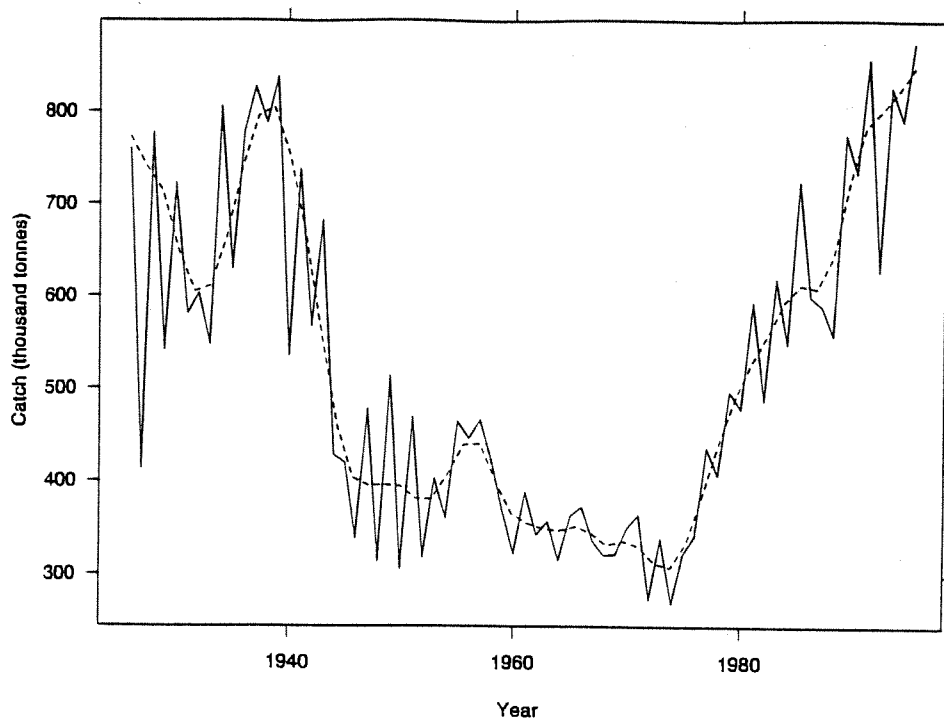


Fig. 1b Differenced and log transformed all nation catch of sockeye, pink, and chum salmon from 1926-1995.

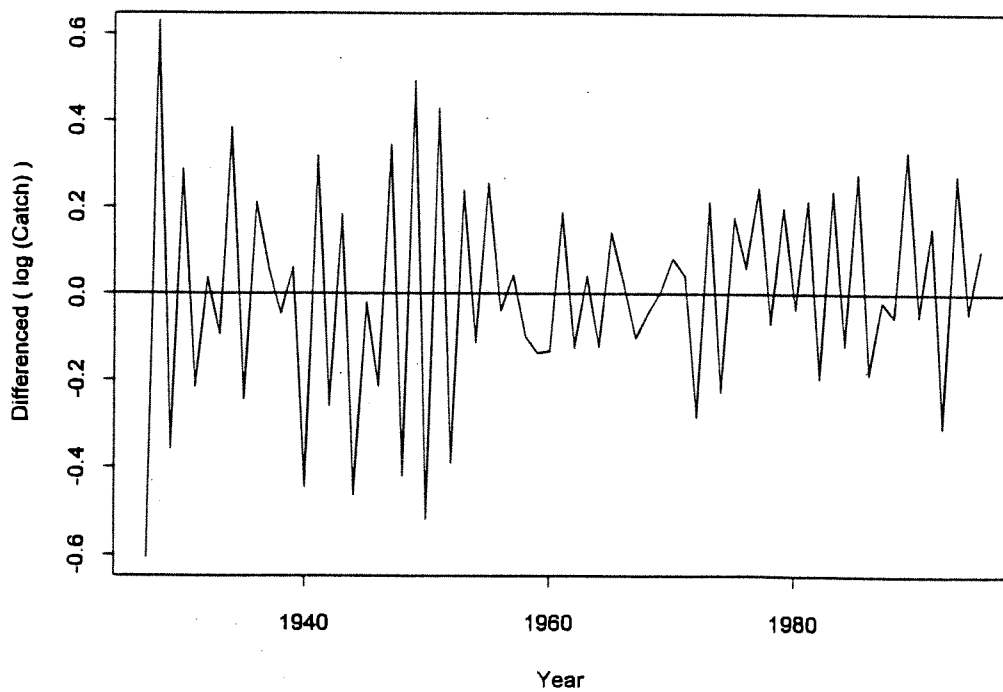


Fig. 2 December - May Aleutian Low Pressure Index (ALPI) from 1926-1995.

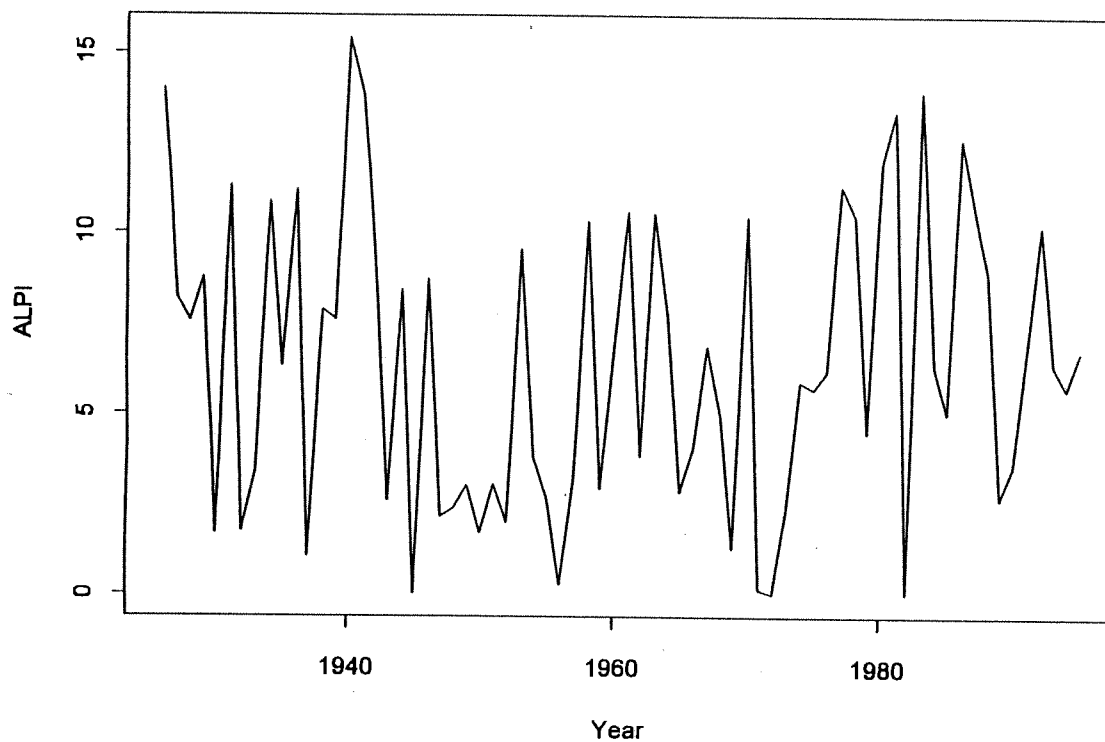


Fig. 3 North Pacific Index (NPI) from 1926-1994.

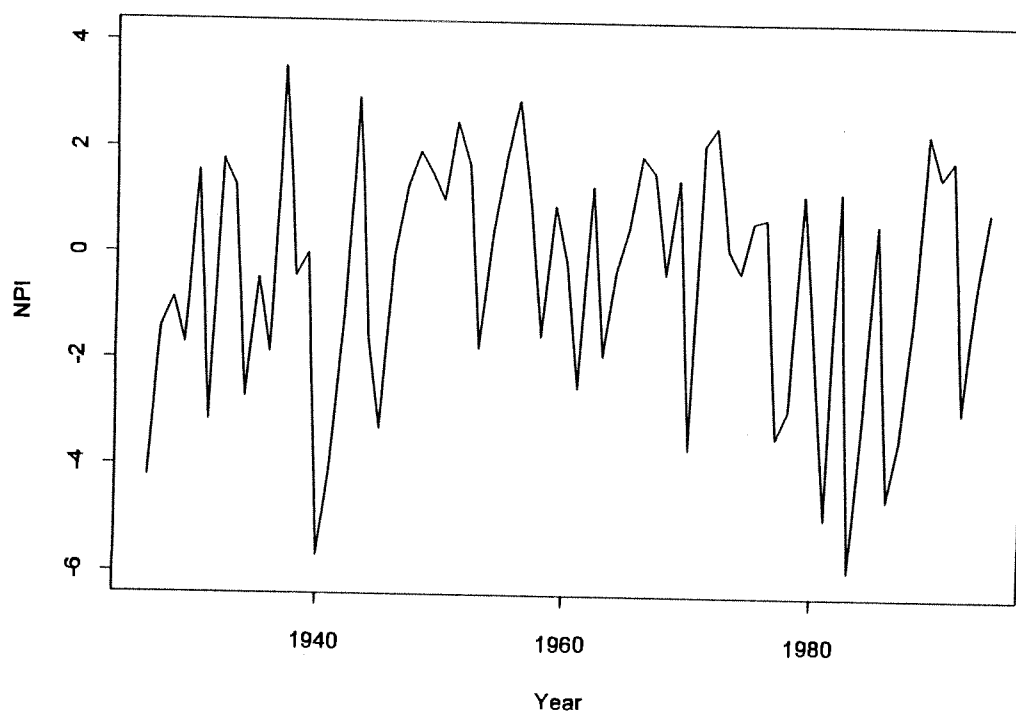


Fig. 4 Relationship between ALPI and NPI, 1926-1994.

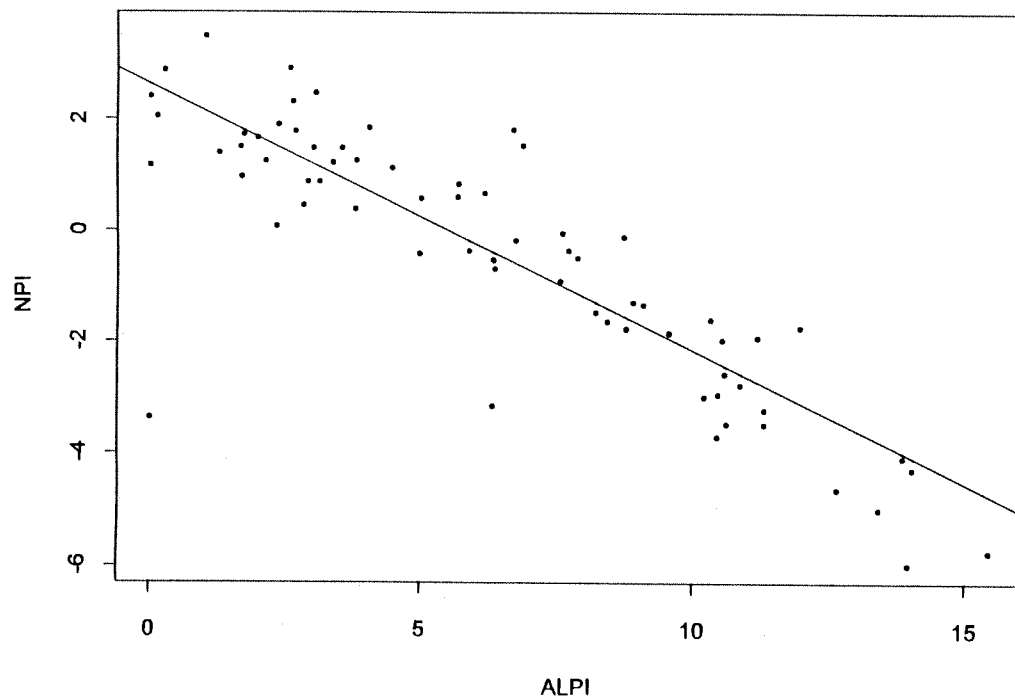


Fig. 5 Atmospheric Circulation Index (ACI) from 1926-1995

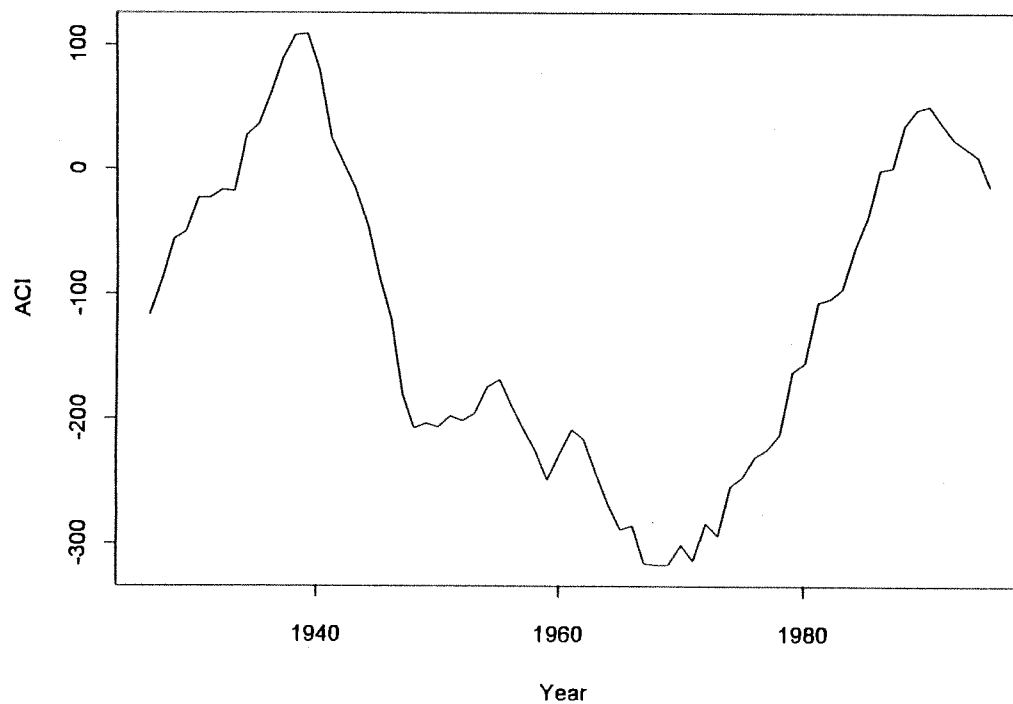


Fig. 6a First order differencing of ACI.

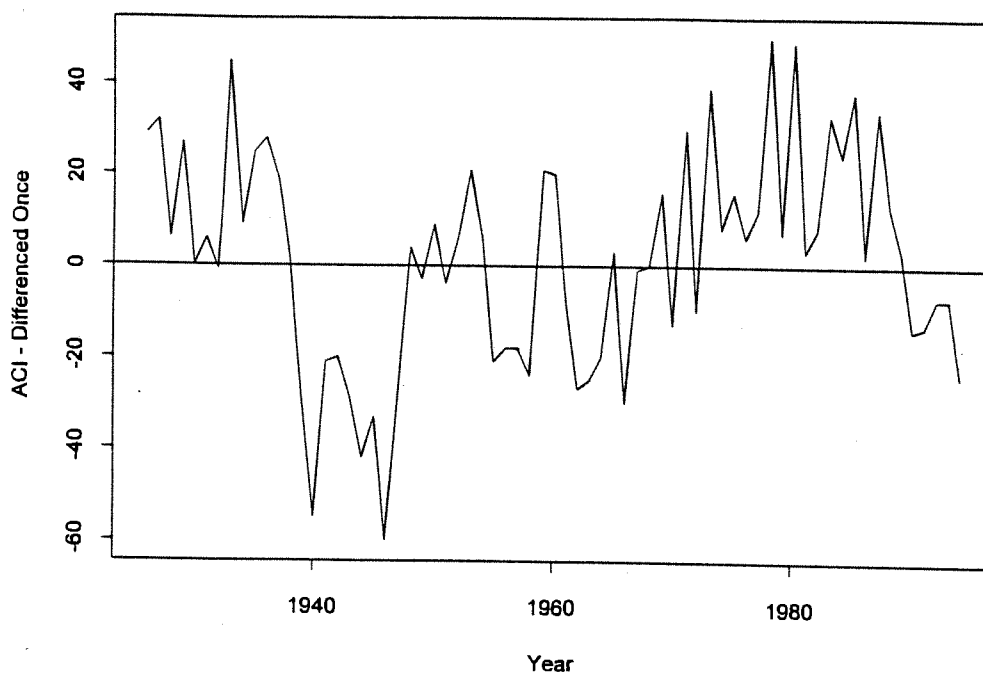


Fig. 6b Second order differencing of ACI.

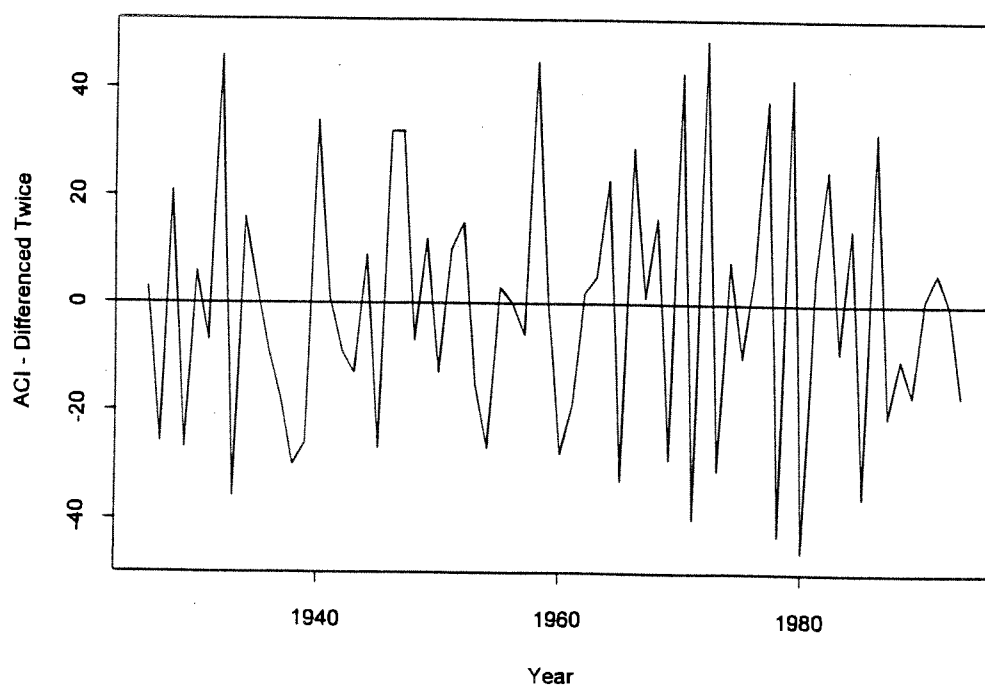
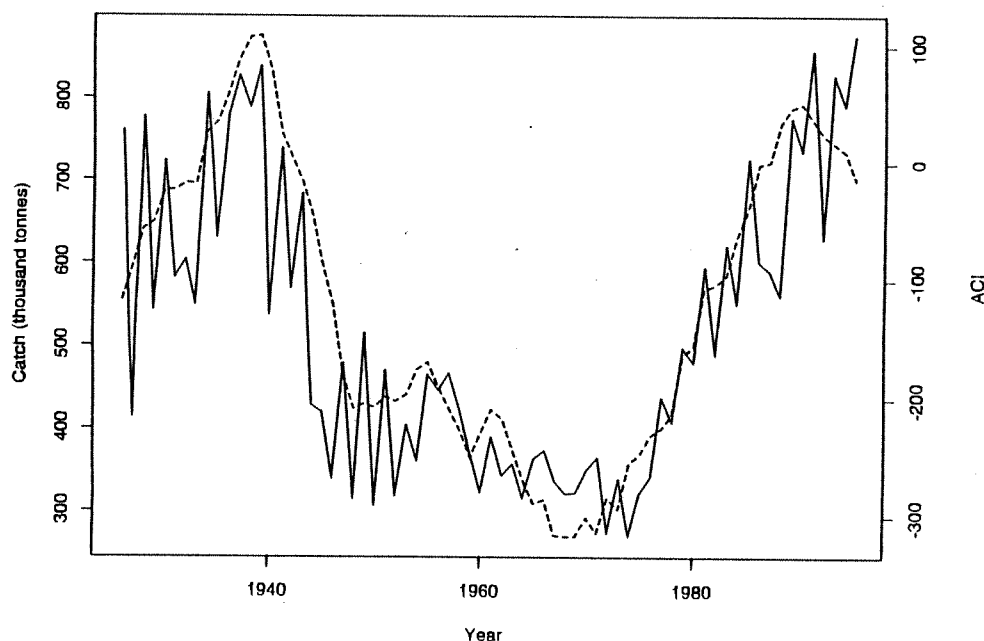


Fig. 7 All nation catch of sockeye, pink and chum salmon (solid line) and ACI (dashed line) for the period 1926-1995.



the ACI also appears to be well approximated by a linear function (Fig. 8).

DISCUSSION AND CONCLUSIONS

The marine environment clearly has a significant influence on fish stocks and this study provides additional evidence to support that thesis. Statistically significant linear relationships were found between all of the climate indices employed in this study and all nation sockeye, pink and chum salmon catch. The inclusion of these climate data provided modest improvements in fit compared to models developed using catch data alone and each index acted as a leading indicator of catch. Of the three indices examined, the ACI appears (visually) to track all nation salmon catch reasonably well and the relationship between catch and ACI appears to be approximately linear (Fig. 8).

There have been significant salmon enhancement activities in the Pacific rim over the last twenty years and there is no doubt these activities have impacted (at least locally) the dynamics of some salmon populations. Recent changes in the size of returning salmon (Ricker 1995) and the leveling off of salmon catches in recent years may indicate the ocean ecosystem is reaching the practical carrying capacity for some salmon species in some areas of the ocean. If true, it may be possible to detect and quantify changes in the marine environment and to relate these shifts to changes in fish population. Beamish et al.

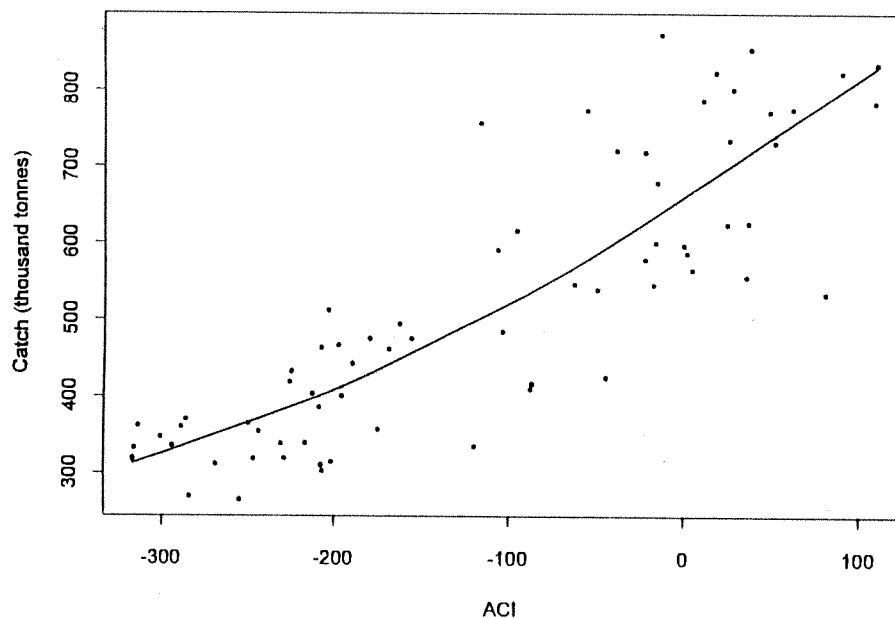
(1997a) showed there was an obvious change (from an increasing to a decreasing trend) in the climate around 1990 and this may indicate a change in ocean conditions to what would be expected to be a less productive state in terms of salmon production. So far, all nation catch has not dropped significantly but the rate of growth in catch has clearly decreased. It may also be possible that these shifts may only impact some populations. Certainly, some salmon populations in Washington, Oregon and British Columbia have not returned at expected levels in the early 1990s and this trend appears to be due to decreased marine survival since smolt and fry production has generally remain stable or increased during the same period.

The models employed in this paper are necessarily simplistic because we have neither the understanding of the biological or physical processes nor the necessary data to construct more comprehensive and complex models at this time. Our retrospective analysis suggest we might expect a modest increase in our ability to predict future catches by including these climate indices in our models.

ACKNOWLEDGEMENT

Models presented in this paper were fit using the McLeod Hipel (Hipel and McLeod, 1994) time series package. Partial support for travel was provided by the Professional Partnerships Program.

Fig. 8 Relationship (solid line is a loess smooth) between all nation catch of sockeye, pink, and chum salmon and the ACI for the period 1926-1995.



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Long-term Climate Change and Pink Salmon Stock Fluctuations

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Northern Hemisphere surface air temperature anomaly (dT) and Aleutian Low Pressure Index (ALPI) are highly variable and have not reliable correlation with Pacific salmon and Pink salmon abundance for the period 1920-1995. Atmospheric Circulation Index (ACI) by G. Wangengeim method correlate closely with Pacific salmon, Pink salmon and a number of Pacific commercial stock dynamics (Japanese, Californian and Peruvian sardine, Alaska Pollock and others).

This allows us to suppose a principal cause of long-term fluctuations in Pacific salmon and pink salmon abundance is oceanic climate conditions. The close relationship was observed between high- and low abundant pink salmon generation in Asian and not American stock. The new approach is proposed on this basis to forecast inter-annual pink salmon stock fluctuations for Kamchatka and Sakhalin regions and for Asian pink salmon as whole.



INTRODUCTION

Pacific salmon catches fluctuated throughout this century with highest catches registered in the late 1930s and early 1990s and lowest ones in the period from 1950-60s. At the same time there were large changes in abundance in three sardine populations in the Northern and Southern Pacific oceans (Kawasaki 1992 a,b, 1994). Recent studies (Beamish & Bouillon 1993; Francis & Hare 1994; Klyashtorin & Smirnov 1995) have shown that fluctuations of Pacific salmon stocks correspond to long-term change in Global Climate. Following Beamish and Bouillon (1993) we believe that salmon catch statistics in vast region reflects, in general, salmon stock dynamics. An important problem still remains to be answered, however, which is to find a relative method of predicting long term changes in the stock dynamics of Pacific salmon in general and pink salmon in particular. For pink salmon, sharp inter-annual variations in catches are well known feature of its stock dynamics (Heard 1991).

The purposes of the study therefore are the following: 1. To identify climatic variables that can

be reliably correlated with long-term salmon stock dynamics. 2. To demonstrate a way to predict long-term fluctuations of total Pacific salmon and pink salmon stocks. 3. To outline new approaches for prediction of inter-annual changes in pink salmon abundance.

DATA AND METHODS

Reliable commercial statistics for Pacific region are available since 1920s. Main sources of statistical data used in this paper are: F.A.O. Yearbook of Statistics (1957-1994), Statistical collected volume (1989), and Klyashtorin & Smirnov (1992). Global data on air surface temperature anomaly (dT) were taken from (Halpert et al. (ed.) 1994). Aleutian Low Pressure Index (ALPI) is used as a characteristic of historical weather over the North Pacific Ocean. ALPI is calculated as the area (mln. of square kilometres) of the North Pacific Ocean covered by Aleutian Low Pressure system enclosed by the isobar of 100.5 kPa. Annual values of ALPI since 1900 were taken from Beamish & Bouillon (1993). The index of the general circulation of the westerly winds, or the Atmospheric

Circulation Index (ACI) in the Atlantic-Eurasian region was determined by the method of Wangengeim-Girs method (Girs 1971). The indices of temperature anomaly (ΔT) and Aleutian Low (ALPI) are quite common climatologic characteristics, but the ACI is less well-known one.

The founder of the ACI -- George Wangengeim is a well-known climatologist in Russia. The so-called Wangengeim-Girs classification of atmospheric circulation is a basic idea in the modern school of Russian climatology (Girs 1971). According to this method, all patterns of westerley winds in the Northern Hemisphere are combined in 3 main forms: Western (W), Eastern (E) and Meridional (C). Each day the analysis of atmospheric pressure charts of the Northern Atlantic-Eurasian region identified the dominant form. The number of days of each circulation form observed (W, E or C) is expressed as "days" for a year and the dominant form for the year results in the year being classified as that type. Annual sum of days of all forms is obvious to be equal to 365. The observation series for the atmospheric circulation forms have been maintained continuously since 1891.

The forms of the atmospheric circulation can be conveniently displayed in the form of anomalies (deviations from time series average for each form) rather than plain "days". It is even more informative to present data as consequent summation of anomalies. The resulting integral curve demonstrate the long-term trend of Atmospheric Circulation change for each

circulation form: W, E or C (Girs 1971). The integral of the sum of (W+E) or the ACI exhibits long-term (about 30-years) regular oscillations, called "circulation epochs". The epoch of meridional (C) circulation dominated in the periods 1890-1920 and 1950-1980. The epoch of combined (W+E) circulation dominated in the periods 1920-1950 and 1980-1990s (Girs 1971). Current (W+E) epoch is not completed yet. The recent pattern is similar to the climatic phase of 1940-50s and probably will close in the first decade of next century.

The ACI for 1900-1995 were kindly placed in our disposal by directorate of Russian Federation Arctic and Antarctic Institute (AARI) in St. Petersburg. The full catalogue of the forms of atmospheric circulation has been maintained by the staff of this institute since 1891.

RESULTS AND DISCUSSION

The fluctuations of Pacific salmon and pink salmon total catches (Fig. 1) are in phase. The maximum catch occurred in late 1930s, followed by depression in 1950-1960s and recent maximum in the early 1990s; the trends are tightly correlated ($r=0.89$, $p<0.001$).

The similar long-term catch dynamics was observed for a range other major commercial species in the Pacific Ocean. Catches of Japanese and Californian sardine (Fig.2) fluctuated in phase with Pacific salmon maximum in late 1930s, followed by

Fig. 1 Total Pacific salmon and pink salmon catch 1920-1994. Correlation coefficient between total and pink salmon catch is: 0.89, $p<0.001$.

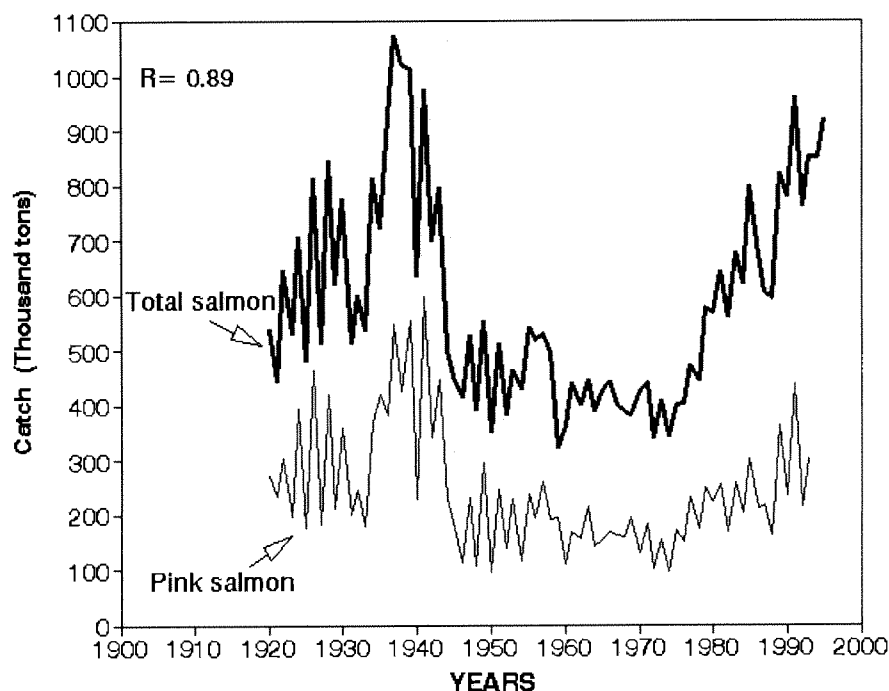
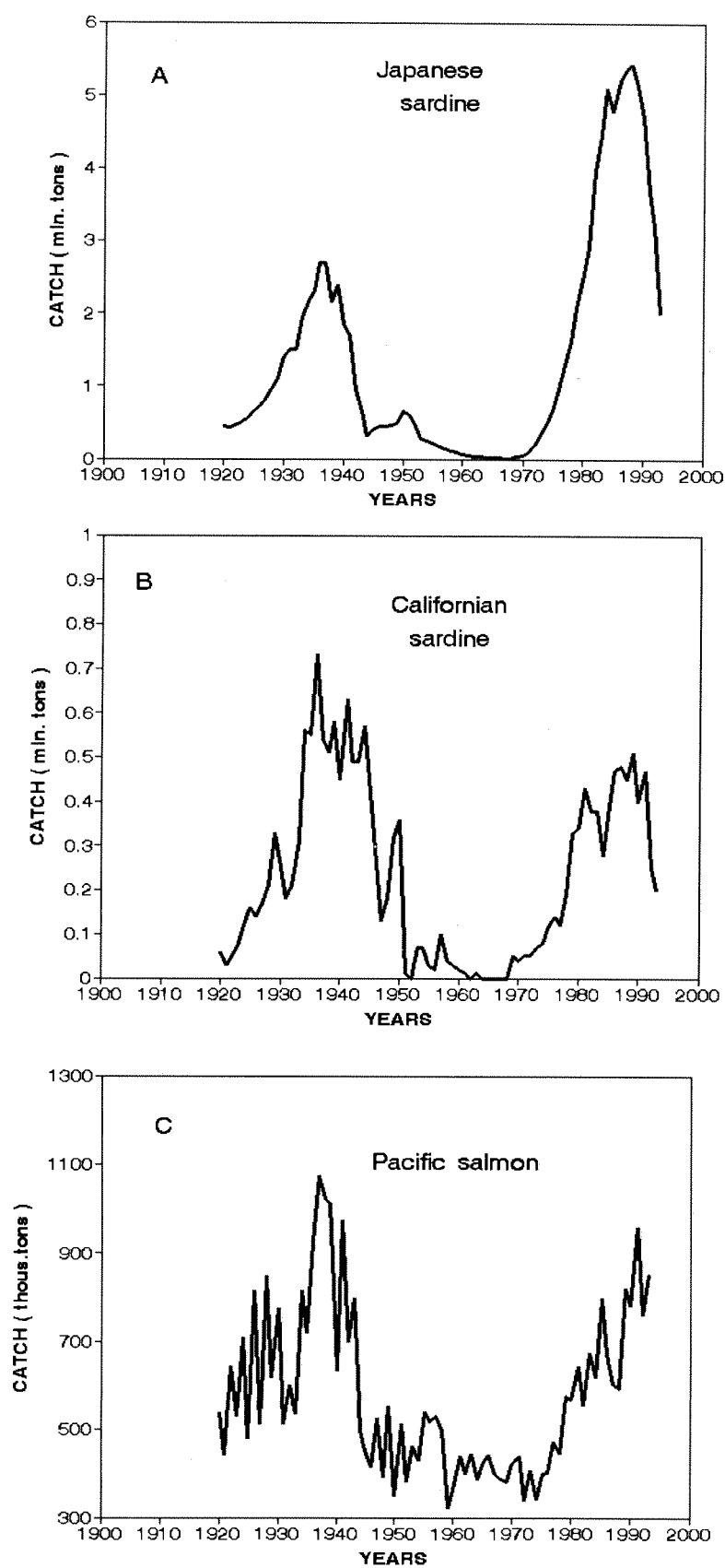


Fig. 2 Total catch of Japanese sardine (A), Californian sardine (B), and total Pacific salmon (C), 1920-1994.

the depressions in 1950-1960s and maximum in late 1980s-early 1990s. The synchronous fluctuations of Japanese and Californian sardines and Pacific salmon are likely caused by long-term Global Climate changes (Klyashtorin & Smirnov 1995).

If there is a common factor affecting the abundance fluctuations of Pacific salmon and sardines which climatic index corresponds to the catch trends best and which can be used to predict the simultaneous fluctuations of above mentioned species abundance?

The trends of dT and ALPI are highly variable and this indices hardly satisfy F-criterion of statistical significance (Fig. 3). The 13-year smoothed curves of dT and the ALPI can demonstrate general direction of the climatic changes; however, they are less reliable forecasting tools because of the large variance.

In contrast, ACI variability is substantially less and the ACI trend is in a good agreement with smoothed trends of dT (global climatic characteristic) (Fig. 4) and the ALPI (main climate forcing factor of the Northern Pacific (Fig. 5).

General curves for dT, ALPI and ACI have rather similar general shape: a maximum in the 1930s, minimum in the 1950-1960s and a new maximum about 1990.

The ACI curve correlates tightly with long-term dynamics of other important commercial species in the Pacific such as: Japanese, Californian and Peruvian sardine, Alaska pollock, Chilean jack mackerel and others. It is believed that ACI long-term dynamics, although measured in Atlantic - Euro-Asiatic region, reflects Global climate changes (Klyashtorin & Sidorenkov 1996).

A good correlation is observed between ACI and total Pacific salmon catch ($r = 0.81$, $p < 0.001$) (Fig. 6). The curve for Pacific salmon catch dynamics has a "saw-like" form because of the interannual alternations of pink salmon abundance. Smoothing of curve of pink salmon catches with 3-year averaging increases the correlation coefficient to 0.92 (Fig 7).

The correlation coefficient (r) between pink salmon catch (unsmoothed) and ACI is rather moderate ($r=0.64$) because of natural inter-annual stock fluctuations (Fig 8). To improve the relationship the pink salmon catch was smoothed by 3 year running averaging. Even such slight smoothing results in significant increase of correlation coefficient to 0.84 ($p < 0.001$) (Fig. 9)

Variation of Pacific salmon harvest throughout this century can be defined as two sequential natural climate-governed production cycles with large catches in the late of 1930-s and early 90s. The latter (current) cycle is not completed yet but is going into final descending phase (late 1990s-early 2000s), that corresponds to the one of 1940-1950s and associated with similar climatic phase.

Total stock of pink and Pacific salmon are now at

their highest levels. However, we expect gradual decrease of their stocks as early as late 90s, in accordance with the descending ACI trend. Similar fluctuations in stock dynamics have been observed for more climate sensitive species: Japanese, Californian, and Peruvian sardine (Kawasaki 1992 a, b).

The similar stock dynamics of ecologically different species (including Pacific salmon), suggests that the similar climate-governed oceanic mechanisms can be responsible for the long-term fluctuations of total productivity over the whole Pacific (Klyashtorin & Sidorenkov 1996). Mechanisms of climate impacts on the marine ecosystems productivity are not clear yet. Some authors suppose that the most probable reason is the changes in the character of the global atmospheric and water mass transportation (Bakun 1990, Kawasaki 1992, 1994, Hsieh & Boer 1992, Ware & Thompson 1991, Ware 1995).

The stock fluctuations of main species of pelagic fish in the Pacific can be considered in its turn as a sensitive indicator of oncoming climate change. "In many instances biological organisms are integrators of environmental variables and may be more sensitive to low frequency climate events than physical time series" (Polovina et al. 1994).

It is commonly accepted in North America that pink salmon abundance fluctuates between odd and even runs, however the persistence of these fluctuations can be questioned if the observations are extended over a number of years. The magnitude and regularity of the odd-even year alternation of high and low abundant generations differ in various regions (Heard 1991).

For example, catches of pink salmon from North America (Fig. 10) do not exhibit annual alternation. Since 1920 the reverse of "odd-even" generation dominance has been observed 31 times for 74 years period (Fig. 11). Ricker (1962) suggesting that dominance exist when one generation line is at least twice the size of the other, and this condition persist for at least four generations. In this respect the phenomenon of even-odd catch alternating is questionable for "Total American" pink salmon.

The reversal of the dominance has occurred much less in the Asian pink salmon population (Fig. 12). In contrast to "American" pink salmon, "Asian" pink salmon catch exhibits clear and regular inter-annual alterations. A characteristic feature of "Asian" pink salmon dynamics is rare occurrence of dominance change: regular odd-even alternation was broken only once in 74 years (Fig. 13).

Let us follow the history of high- and low abundant pink salmon generations separately. Figure 14 demonstrates that the curves of high- and low abundant generations of Asian pink salmon have a similar shape and correlate rather tightly ($r=0.76$, $p < 0.001$). "American" high- and low abundant lines

Fig. 3 The run of climatic index curves 1900-1994. A. Global air surface Temperature Anomaly (ΔT); B. Aleutian Low Pressure Index (ALPI) (thin line — annual fluctuations, thick line — smoothed by 13-years averaging); C. Atmospheric Circulation Index (ACI) — integral curve of combined (W+E) circulation form (unsmoothed).

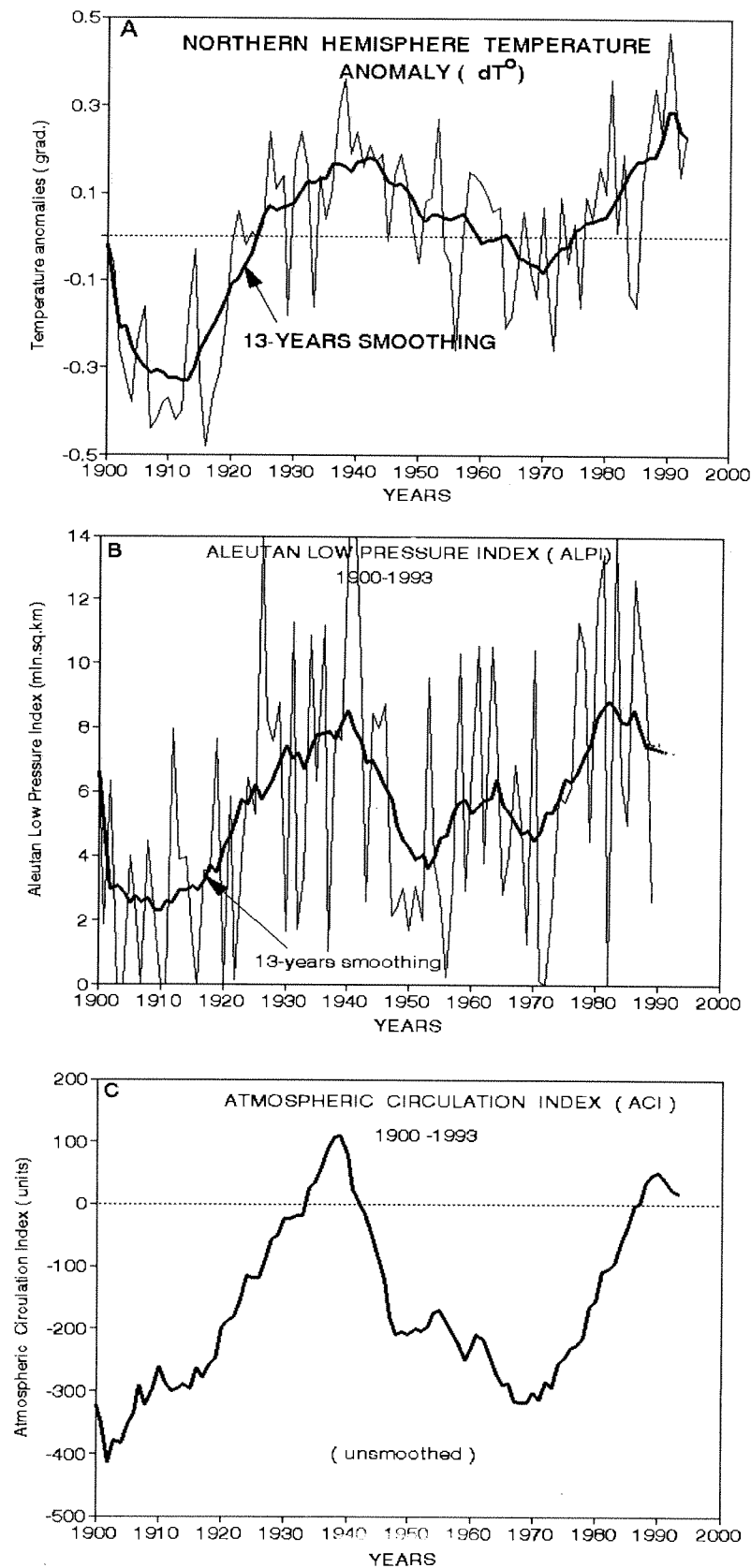


Fig. 4 Long-term run of temperature anomaly (dT) and Atmospheric Circulation (ACI) curves 1900-1994. Thin line — ACI (unsmoothed), thick line — dT (smoothed by 13-years averaging).

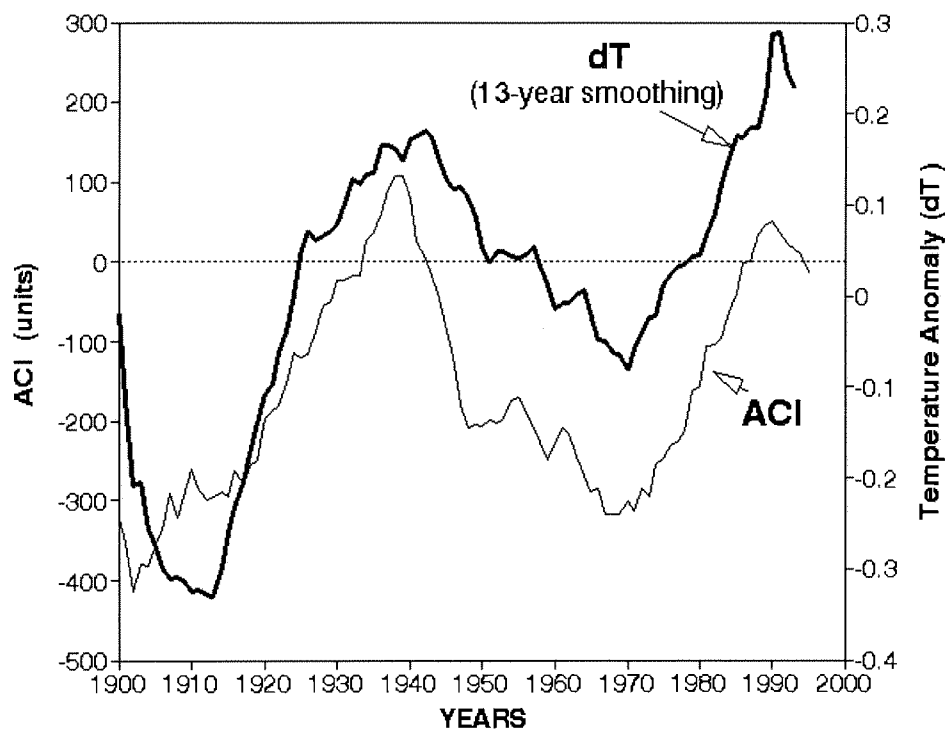


Fig. 5 Long-term run of Atmospheric Circulation Index (ACI) and Aleutian Low Pressure Index (ALPI).

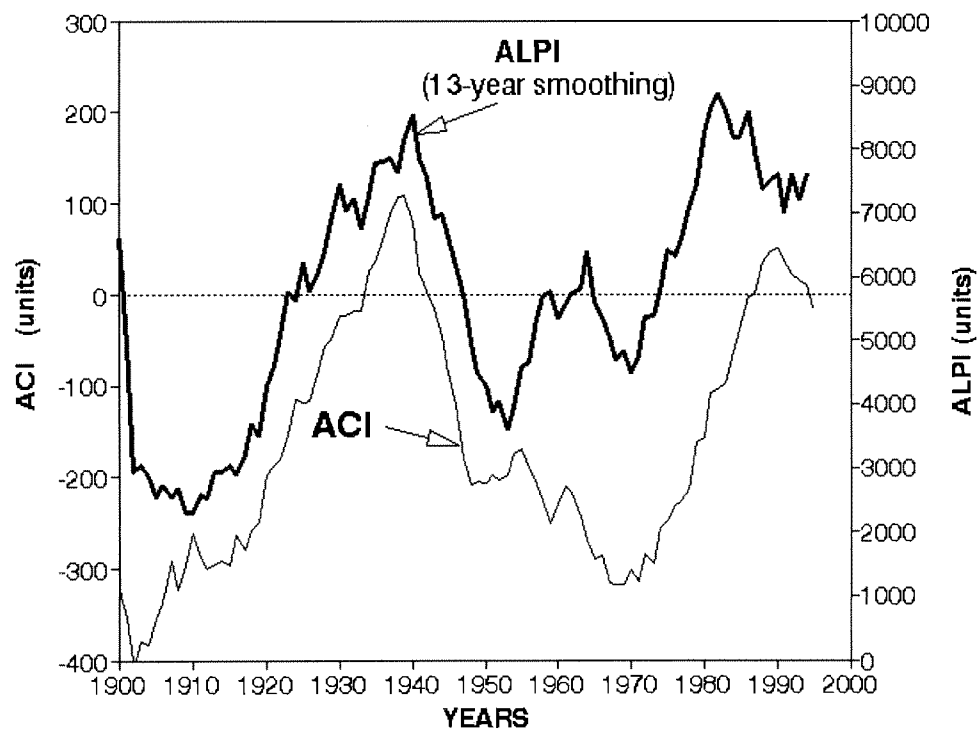


Fig. 6 Total unsmoothed Pacific salmon catch and Atmospheric Circulation Index (ACI) 1900-1994. Correlation coefficient between ACI and catch curves is: 0.81, $p < 0.001$.

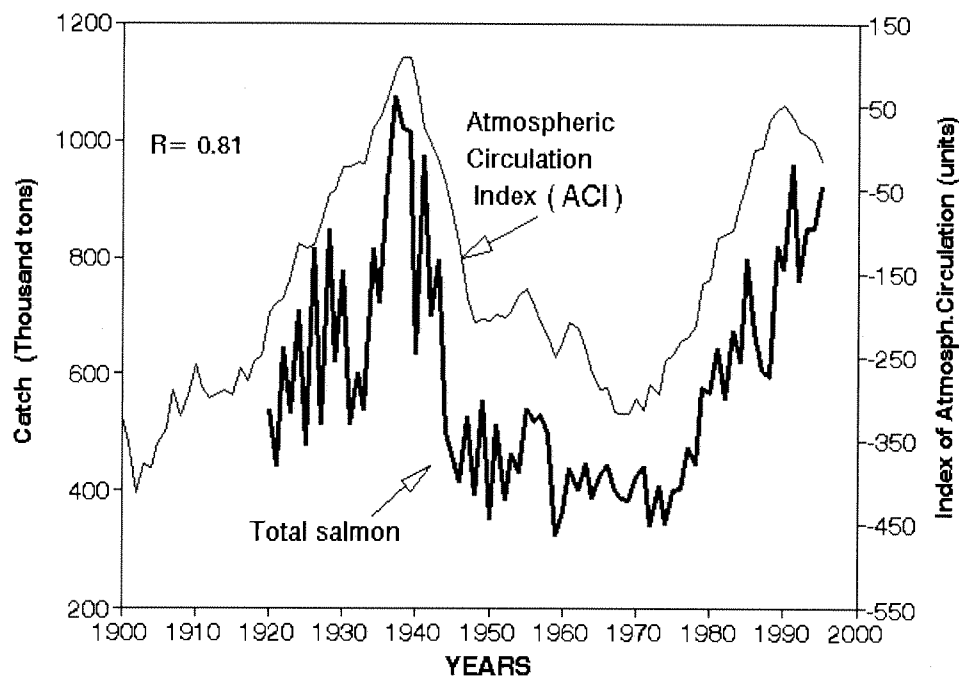


Fig. 7 Total 3-year smoothed Pacific salmon catch and Atmospheric Circulation Index (ACI) 1920-1994. Correlation coefficient between ACI and the smoothed catch is: 0.92, $p < 0.001$.

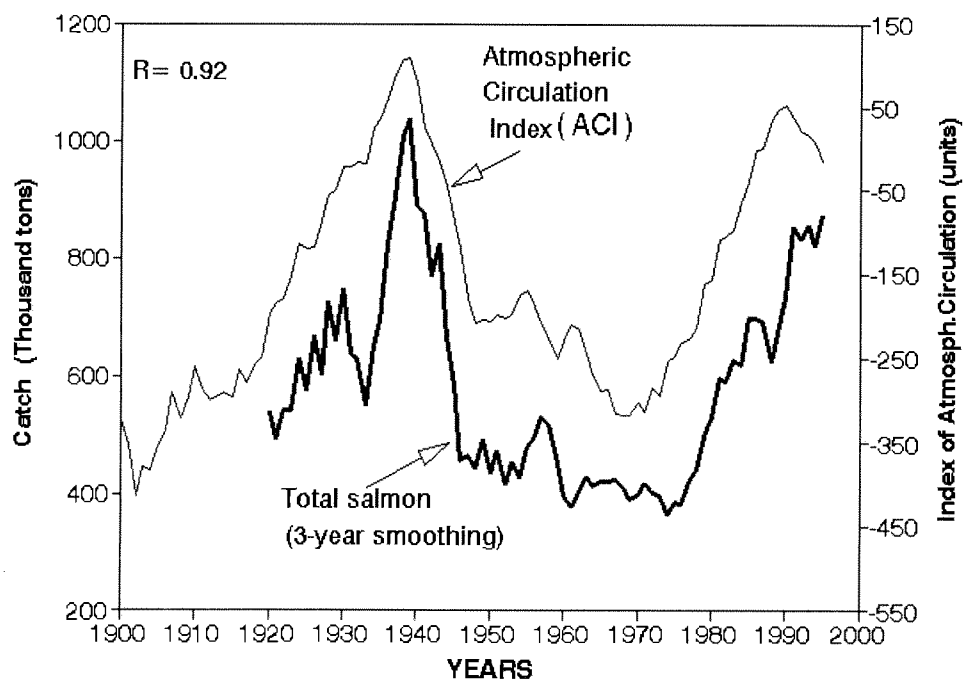


Fig. 8 Total unsmoothed pink salmon catch and Atmospheric Circulation Index (ACI) 1920-1994. Correlation coefficient between ACI and the catch is: 0.64, $p < 0.001$.

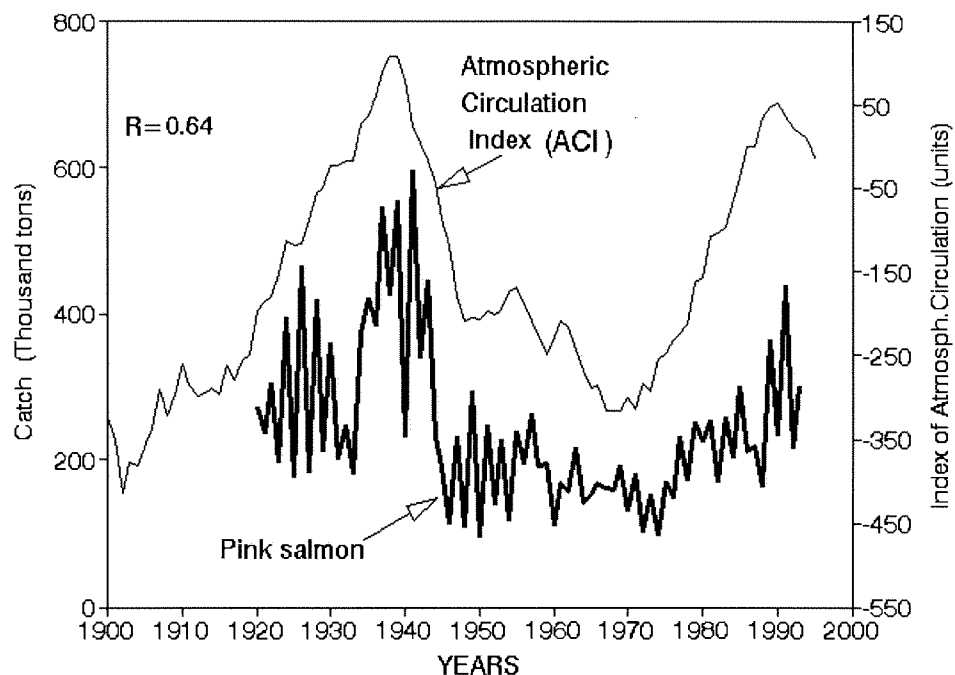


Fig. 9 Total 3-year smoothed pink salmon catch and Atmospheric Circulation Index (ACI) 1920-1994. Correlation coefficient between ACI and the smoothed catch is: 0.84, $p < 0.001$.

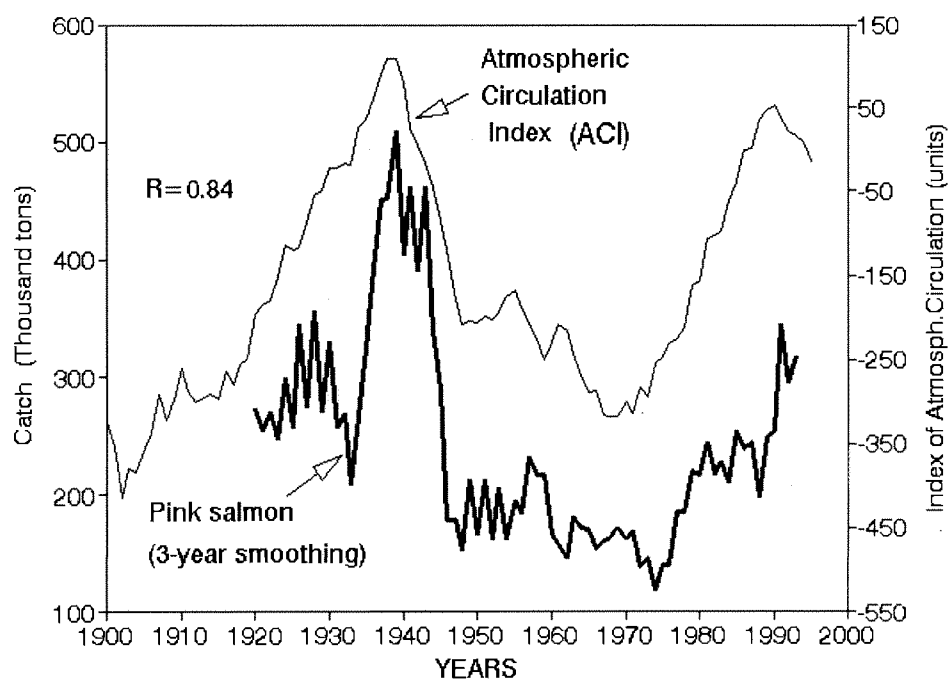


Fig. 10 Total American pink salmon catch, 1920-1994.

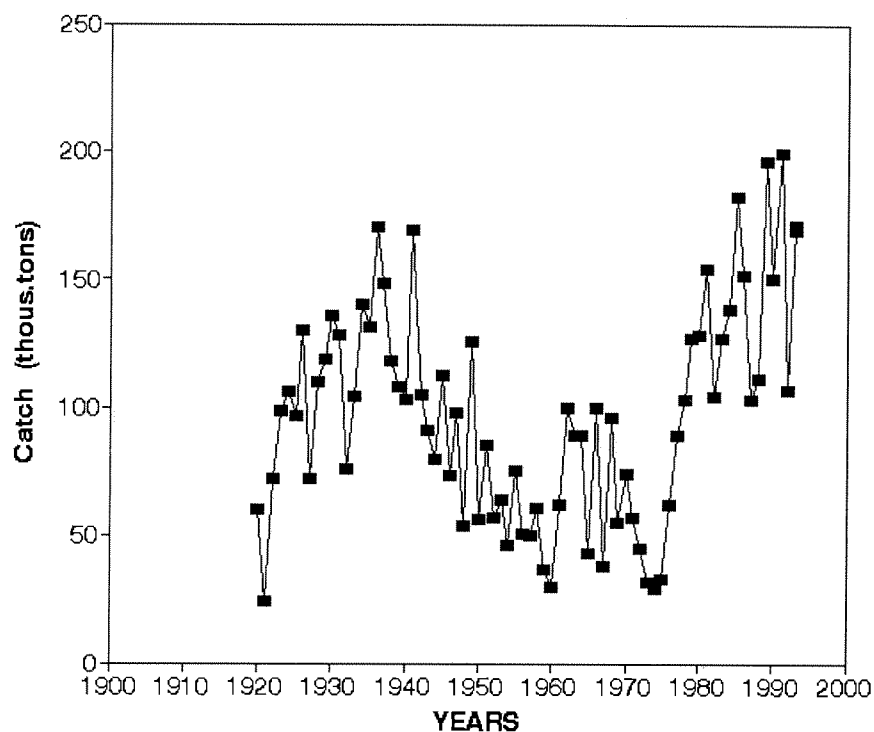


Fig. 11 American pink salmon of even- and odd year catch 1920-1994. Bars indicate the year of dominance change.

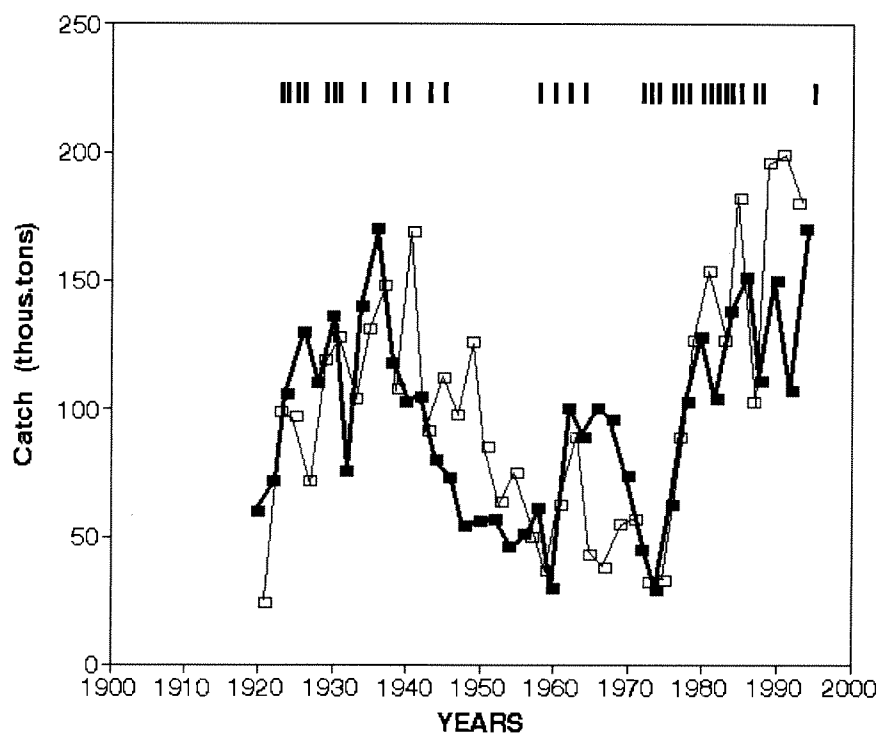


Fig. 12 Total Asian pink salmon catch, 1920-1994.

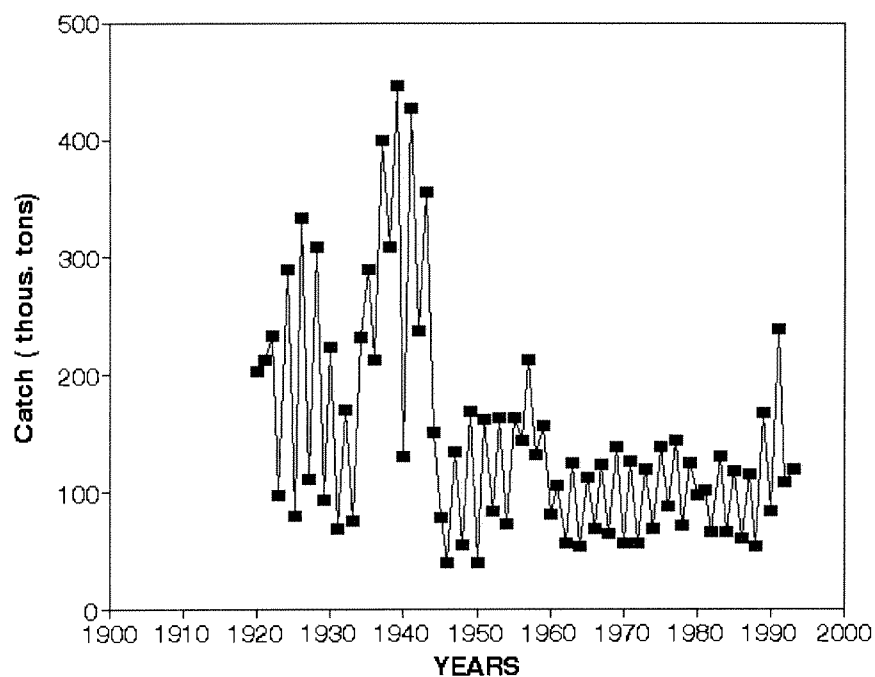


Fig. 13 Asian pink salmon of even- and odd year catch. Bold line — even year generations, thin line — odd year generation. Bars indicate the year of dominance change.

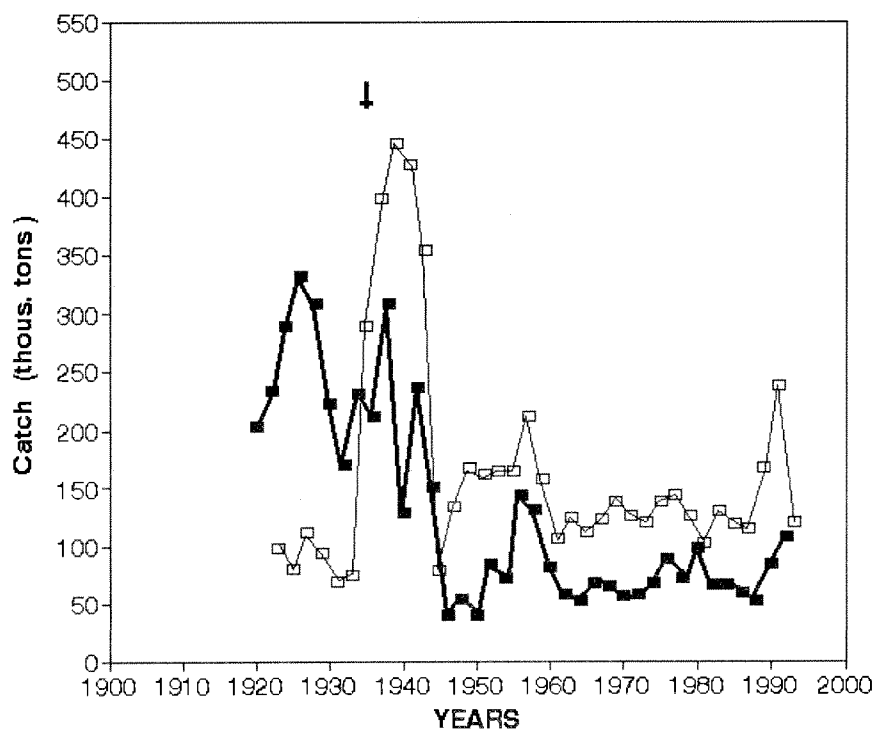
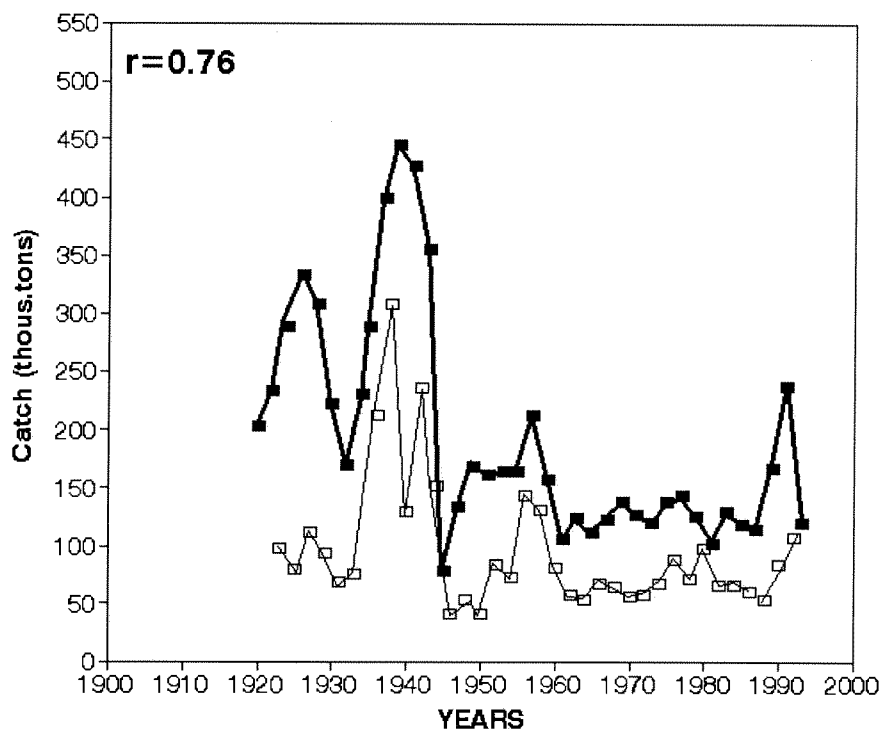


Fig. 14 Asian pink salmon high- and low abundant generations. Bold line — high abundant generations, thin line — low abundant generations. Correlation coefficient between high- and low abundant lines is: 0.76, $p < 0.001$.



also exhibit similar dynamics (Fig. 15), but it is difficult to calculate correlation between these two lines because of a numerous "intermediate" catch points. It is interesting to note that the "intermediate" pink salmon catches demonstrate similar dynamics to the catches of high and low abundant lines.

Impressive results were obtained in Kamchatka and Sakhalin regions. In Kamchatka strong inter-annual alteration was observed for pink salmon catches (Fig. 16). The change of the dominance was observed only three times for the 74-year period 1920-1994 (Fig. 17). Close correlation ($r=0.92$, $p < 0.001$) was revealed between dynamics of high- and low abundant generations of Kamchatka pink salmon (Fig. 18).

Fig. 19 illustrate the dynamics of Sakhalin pink salmon catch. The change in dominance for Sakhalin pink generations was observed 8 times during 74 year period 1920-1994 (Fig. 20). The correlation between high- and low-abundant generation trends (Fig. 21) is rather moderate ($r=0.70$, $p < 0.001$). Nevertheless the general dynamics of Sakhalin pink salmon catch were similar to ones observed over Kamchatka and Asian region on the whole.

It is significant that both high- and low abundant pink salmon generations demonstrate similar long-term dynamics closely related to the ACI trend. At the same time, the dynamics of high and low abundant

pink generation is in general agreement with dT and ALPI dynamics. This suggests that climate change influence high and low abundant pink salmon stocks in the same way.

The close correlation between the trends of high and low abundant pink generations makes it possible to calculate roughly the abundance of next year populations based on previous one. This procedure can be applied to Asian pink salmon populations only, since the latter exhibit more or less regular alternation of even-odd generations. The long-term change of both lines of pink salmon stock correspond to long-term trends of global and hemisphere climatic indices, first of all to ACI dynamics.

The proposed approach is under way now and preliminary results are hopeful.

CONCLUSIONS

There is a close association between the dynamics of some global climatic indices (dT, ALPI, ACI) and long-term fluctuations of Pacific salmon and pink salmon abundance.

ACI is the most reliable climatic index of all indices analyzed. Close agreement in long-term stock dynamics of Pacific salmon, Japanese, Californian and Peruvian sardines and a range of other Pacific commercial species suggest that some climate-

Fig. 15 American pink salmon high- and low abundant generations. Bold line — high abundant generations, thin line — low abundant generations.

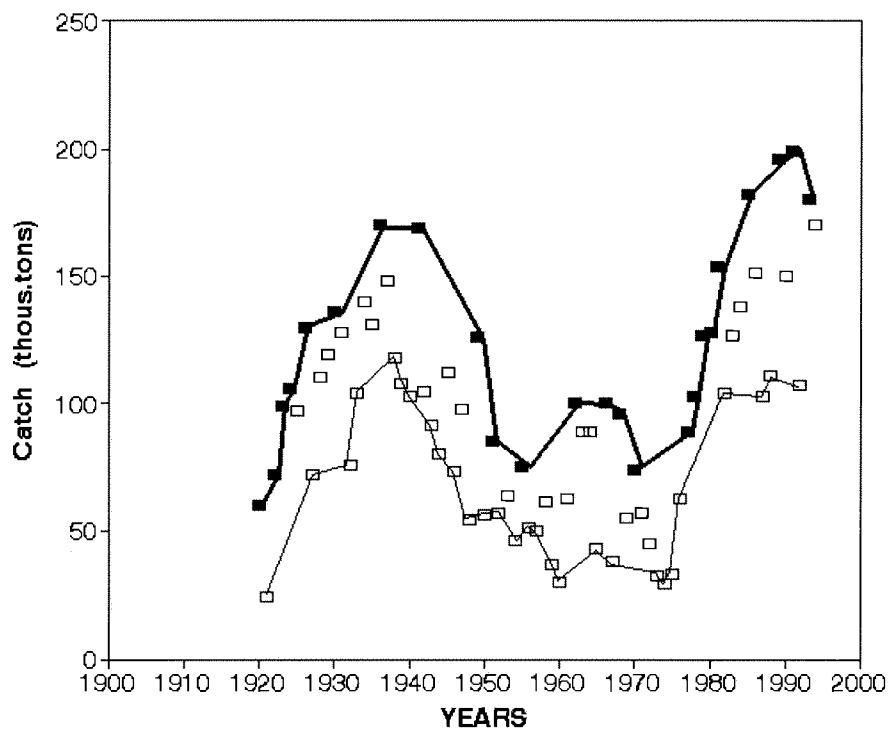


Fig. 16 Kamchatka pink salmon catch, 1920 - 1994.

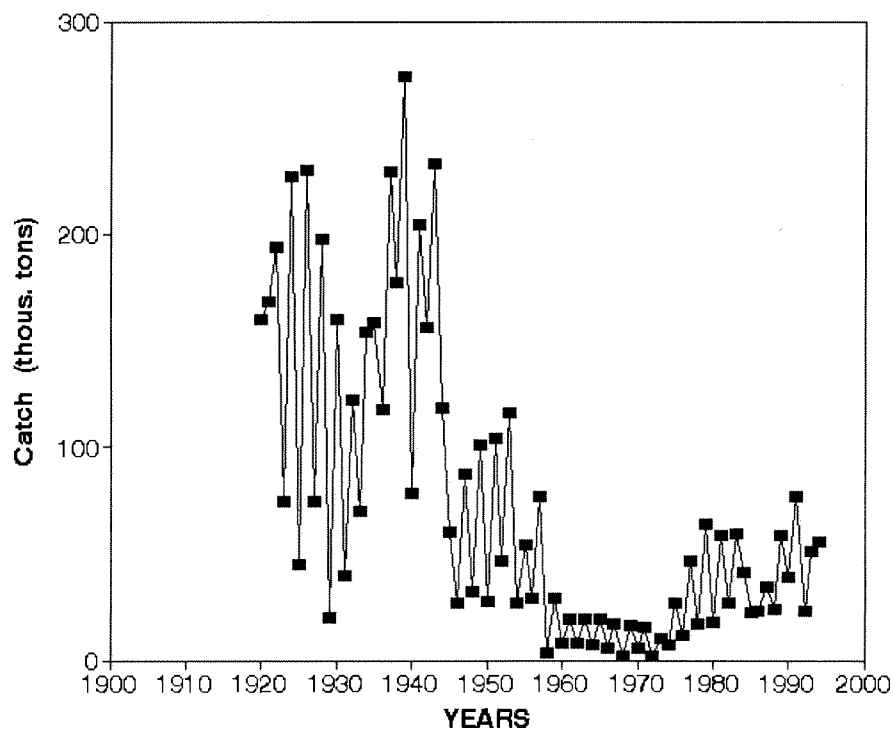


Fig. 17 Kamchatka pink salmon of even- and odd year catch. Bold line — even year generations, thin line — odd year generations. Bars indicate the year of the dominance change.

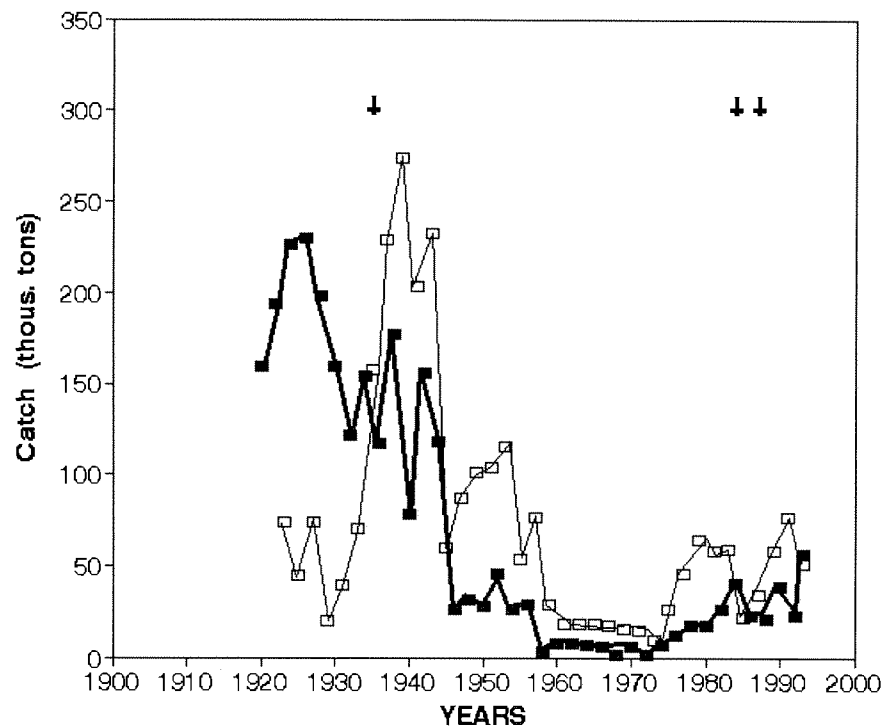


Fig. 18 Kamchatka pink salmon high- and low abundant generations. Bold line — high abundant generations, thin line — low abundant generations; correlation coefficient between high and low abundant lines is: 0.92, $p < 0.001$.

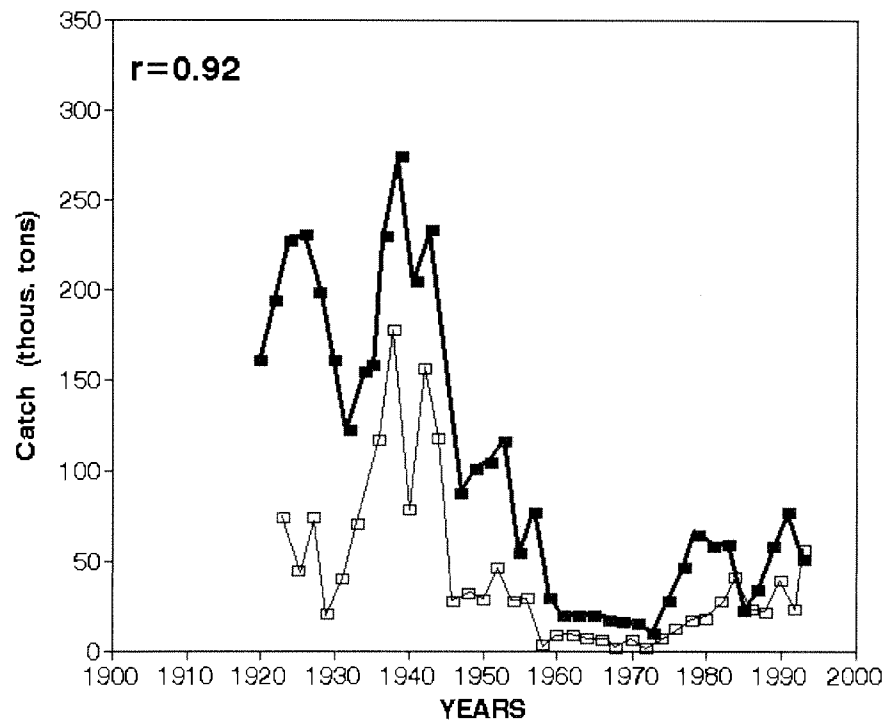


Fig. 19 Sakhalin pink salmon catch, 1920-1994.

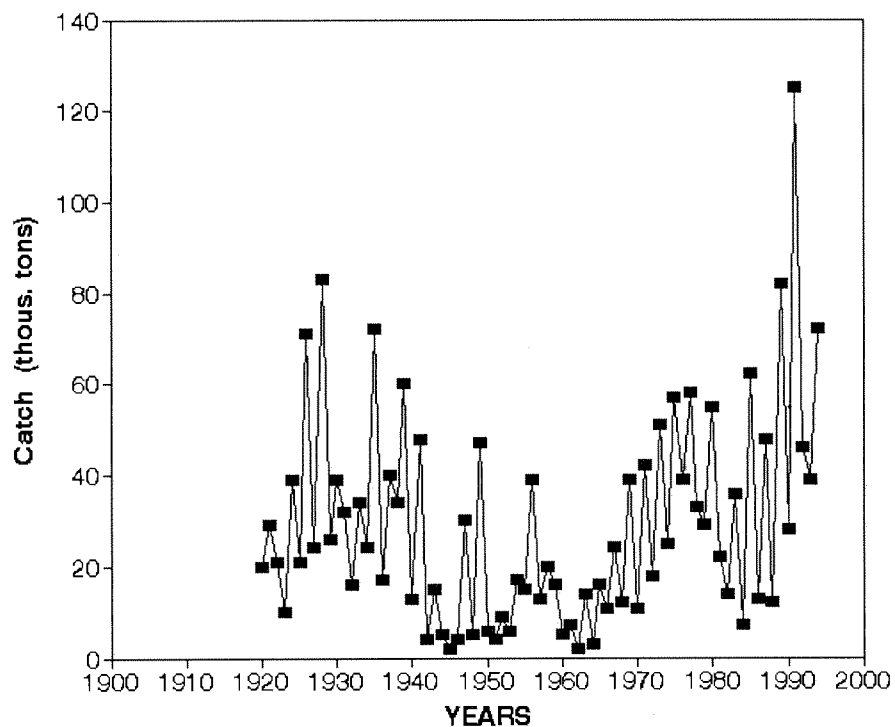


Fig. 20 Sakhalin pink salmon of even- and odd year catch. Bold line — even year generations, thin line — odd year generations; bars indicate point the year of the dominance change.

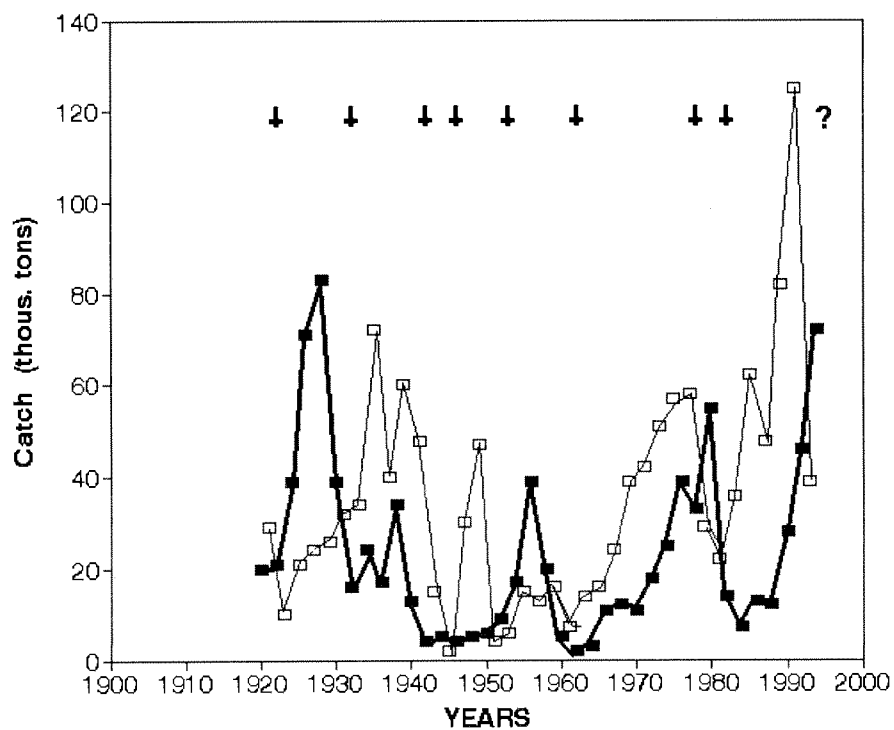
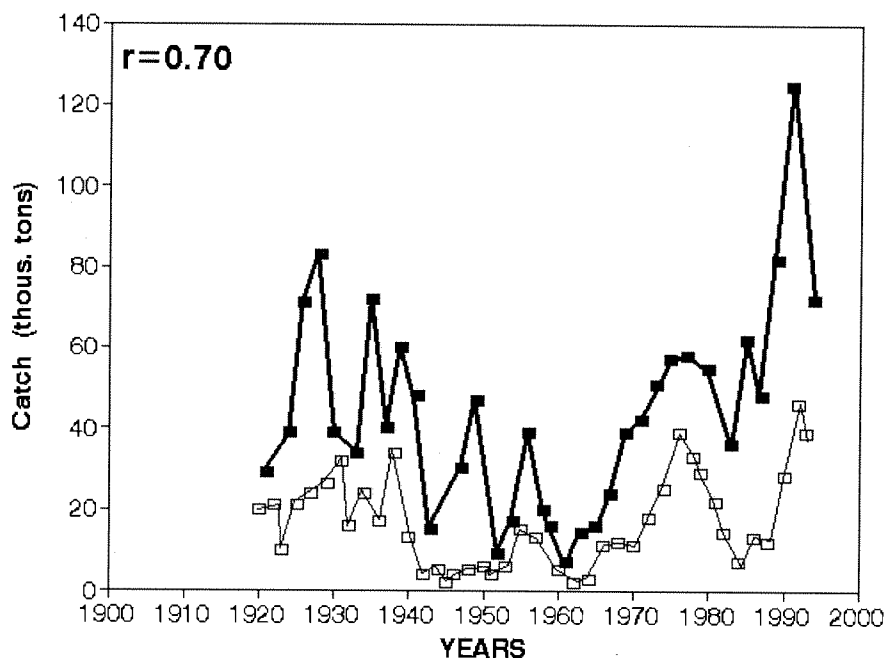


Fig. 21 Sakhalin pink salmon high- and low abundant generations. Bold line — high abundant generations, thin line — low abundant generations; correlation coefficient between high and low abundant lines is 0.70, $p < 0.001$.



governed oceanic factors are first responsible for long-term fluctuation of Pacific salmon and pink salmon stocks.

As for the long -period inter-annual dynamics of pink salmon population, general curves of high- and low abundant generations of Asian pink salmon are similar in shape and demonstrate a tight correlation.

A new approach can be outlined on this basis to forecast Asian pink salmon abundance one year ahead.

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Fish and Seabird Predation on Juvenile Chum Salmon (*Oncorhynchus keta*) in Japanese Coastal Waters, and an Evaluation of the Impact

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This paper examines the available literature on the fauna and diets of fishes and seabirds in coastal waters of northern Japan from spring to summer, and discusses the impact of fish and seabird predation on chum salmon (*Oncorhynchus keta*) populations in Japan. Although over 90 fish species have been reported to occur with chum salmon juveniles, fishes recorded as predators in river-mouth areas and at sea are the following nine species: Japanese dace (*Tribolodon hakonensis*), Far Eastern dace (*T. brandti*), white-spotted charr (*Salvelinus leucomaenis*), Japanese halibut (*Paralichthys olivaceus*), Japanese sea perch (*Lateolabrax japonicus*), spiny dogfish (*Squalus acanthias*), arabesque greenling (*Pleurogrammus azonus*), pink salmon (*O. gorbuscha*) and masu salmon (*O. masou*). Fish predation may cause substantial loss of chum salmon juveniles in localities where these predatory fishes, especially Japanese dace and arabesque greenling, are abundant. However, there is no evidence that fish predation has much impact on the number of returning adult chum salmon in Japan. The release of large hatchery-reared juveniles possibly reduces mortality due to fish predation. Rhinoceros auklets (*Cerorhinca monocerata*) and black-tailed gulls (*Larus crassirostris*) have been recorded as predators of juvenile chum salmon. These seabirds abundantly breed in northern Japan, and the impact of their predation on Japanese chum salmon populations may be significant.



INTRODUCTION

Because of the success of stock enhancement program, the population size of chum salmon (*Oncorhynchus keta*) has increased greatly in Japan since the mid-1970's (Kaeriyama 1989, 1994). In 1995, over 70 million adult chum salmon returned to Japan. The major factors contributing to this success are both feeding juveniles after the emergence and release of fed fish at a proper season (Kobayashi 1980; Mayama 1985). According to Kobayashi (1980) and Shirahata (1985), the rate of adult chum salmon returning to Japan increased proportionally with the percentage of fed juveniles increased. Compared with such an emphasis on the techniques which might have enhanced the survival rate of juveniles, little is known about natural mortality of released juveniles in rivers and coastal waters of Japan. Since only 2-3% of 2 billion annually released juveniles return to Japan as adults (Kaeriyama 1989, 1994), 97-98% (more than 1.9 billion fish) still die from either fishing or natural mortality. Because of the recent ban on the offshore salmon fishery, natural mortality appears to be more important in controlling

the salmonid abundance than fishing mortality.

Predation has been suggested to be a major source of natural mortality for juvenile salmonids during their early marine life (Parker 1968, 1971; Mace 1983; Bayer 1985; Hargreaves 1988; Beamish et al. 1992). Nagasawa and Kaeriyama (1995) previously provided a review on the predation by fishes and seabirds on Japanese chum salmon juveniles in their early ocean life but the literature they cited was incomplete. In this paper, I compile information on the fauna and diets of fishes and seabirds in coastal waters of northern Japan in spring and summer based on various literature sources, and discuss the impact of predation by fishes and seabirds on Japanese populations of chum salmon.

DATA SOURCES

Fishes

The data used are mainly from the reports of "A General Study on the Development of Mass Production of Anadromous Salmonids". This study was conducted with the financial support of the

Japanese Government for five years (1977-1981) by seven national research fisheries institutes, 16 prefectural fisheries experimental stations, and three universities. The study included ecological research of chum salmon juveniles, such as distribution, food and growth, and the reports often provided data on fishes which were caught together with juvenile chum salmon. The present paper analyzes such data on the fauna and stomach contents of the fishes. In addition, some other survey reports on Japanese chum and masu salmon enhancement programs in various prefectures are also referred to.

The survey area was mainly the coastal waters of Hokkaido, including the Japan Sea, Okhotsk Sea, and North Pacific Ocean (Fig. 1). Some surveys were also conducted off the Pacific and Japan Sea coasts of northern Honshu, off the Pacific and Okhotsk coasts of the south Kuril Islands, and off the southeast coast of Sakhalin. Various types of fishing gear, such as purse seine, small-mesh gillnets, larval fish net, dip net, and beach seine, were employed to catch salmonid juveniles and other fishes, but purse seines and gillnets were commonly used. The survey season ranged from February to August (mainly May-July) when chum salmon juveniles migrate along the coasts of northern Japan (Fig. 1).

Seabirds

Information on the fauna and feeding habits of seabirds in northern Japan is obtained from various papers and reports in scientific journals and books. The reports of "A General Study on the Development of Mass Production of Anadromous Salmonids" were also examined.

FISH PREDATION ON CHUM SALMON JUVENILES

Fish Fauna

Over 90 fish species have been recorded to occur with chum salmon juveniles in Japanese coastal waters (Appendix table 1). These fish species belong to 14 orders and 41 families. The species that were most abundantly caught with chum salmon juveniles in Hokkaido waters were arabesque greenling (*Pleurogrammus azonus*) in the gillnet catch and Japanese sand lance (*Ammodytes personatus*) in the purse seine catch (Mishima et al. 1982a, b).

Predators of Chum Salmon Juveniles

Despite the fact that many species are known to occur with chum salmon juveniles, there are only nine species that have been reported to be predators of

juvenile chum salmon in river-mouth areas and at sea: Japanese dace (*Tribolodon hakonensis*), Far Eastern dace (*Tridolodon brandti*), white-spotted charr (*Salvelinus leucomaenis*), Japanese halibut (*Paralichthys olivaceus*), Japanese sea perch (*Lateolabrax japonicus*), spiny dogfish (*Squalus acanthias*), arabesque greenling, pink salmon (*Oncorhynchus gorbuscha*), and masu salmon (*Oncorhynchus masou*).

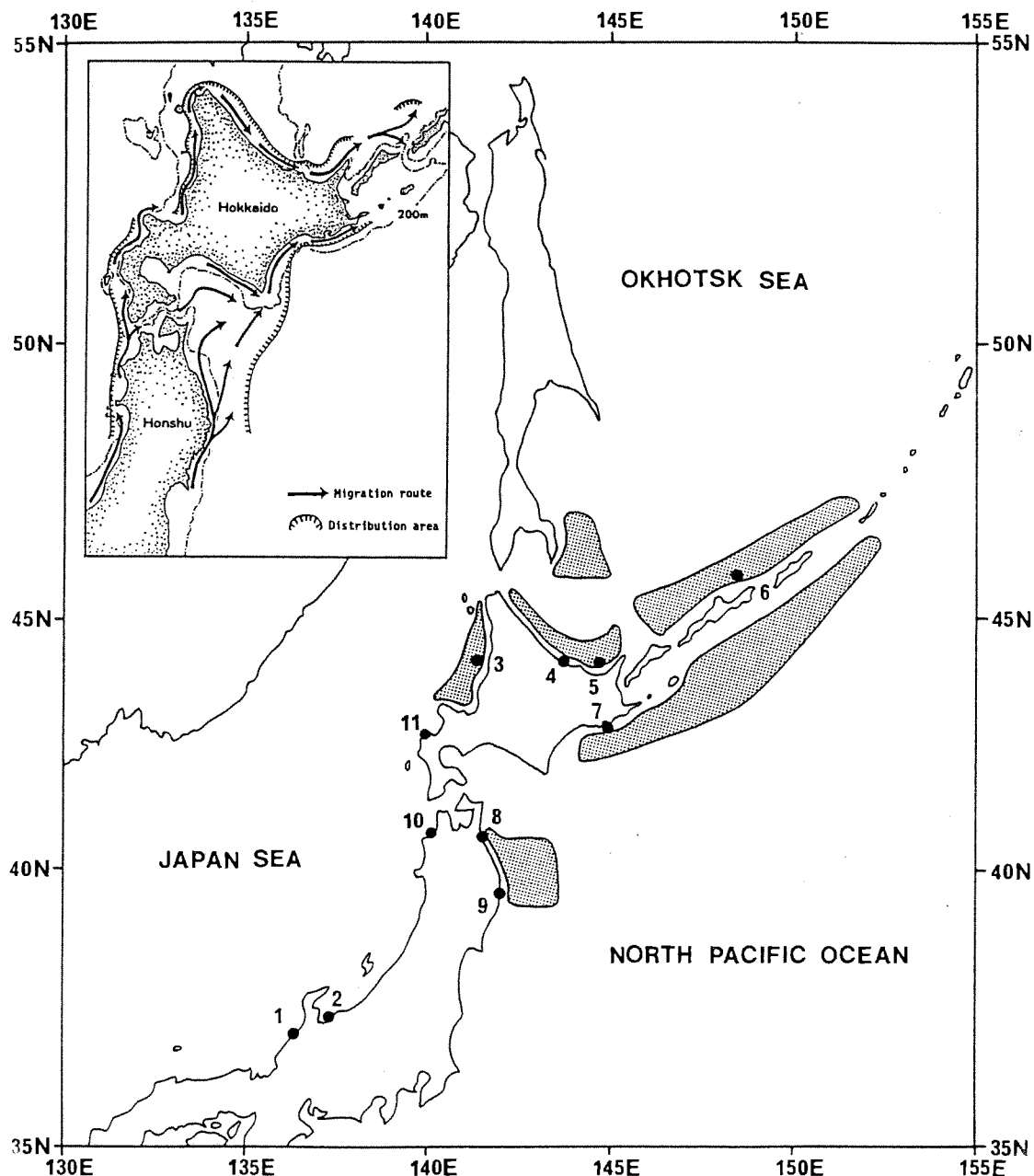
Although juvenile chum salmon were found in the stomach of yellowtail (*Seriola quinqueradiata*) captured in a setnet in the Japan Sea (Anonymous 1993), this paper does not include the latter species as a predator, because it is unknown whether the juveniles were preyed on before or after the yellowtail entered the net. In addition, Shirahata and Sakaguchi (1981) suggested that fish vertebrae found in the stomach of rainbow smelt (*Osmerus eperlanus mordax*) from a brackish-water lagoon, Lake Saroma (Fig. 1), in Hokkaido were those of chum salmon juveniles, but their identification was uncertain: thus the rainbow smelt is not included here as a predator of chum salmon juveniles.

Japanese dace

The Japanese dace, although it belongs to the family Cyprinidae, occurs in both fresh and marine waters (Nakamura 1969). This species is found abundantly in brackish waters such as estuaries, inlets, and river mouths of northern Japan. There are reports that Japanese dace consumed chum salmon juveniles at the estuary of the Tedoru River (Fig. 1, Anonymous 1980b, 1981). Eight to 28% of Japanese dace examined on various occasions from mid-February to mid-March in 1979 were found to have ingested up to 19 juveniles (Anonymous 1980b). The Japanese dace that consumed the juveniles ranged from 19.8 to 23.1 cm fork length (FL). Similar predation by Japanese dace was observed in 1980 as well, and many Japanese dace were removed from the Tedoru River in order to reduce the predation mortality of chum salmon juveniles (Anonymous 1981).

Based on a laboratory feeding study, Yasunaga et al. (1980) found that Japanese dace of 20 and 30 cm total length (TL) eat about 8 and 17 chum salmon juveniles per day, respectively. These authors estimated that 148×10^3 (=77.4 kg) chum salmon juveniles (0.5 g body weight) are consumed by one metric ton of Japanese dace (31 cm TL) for three months (March-May). These results suggest that predation on juvenile chum salmon by Japanese dace is significant in localities where the latter fish are abundant, but it is not clear how much such predation has any impact on local chum salmon populations in Japan.

Fig. 1 A map of Japan showing the survey locations for chum salmon juveniles and seabirds (modified from Nagasawa and Kaeriyama, 1995, with permission of the Hokkaido Salmon Hatchery). Stippled areas show those where juvenile chum salmon and other fishes were collected. Numerals represent the study sites mentioned in the text. 1. Tedomi River; 2. Toyama Bay; 3. Teuri Island; 4. Lake Saroma; 5. Abashiri Bay; 6. off Iturup Island; 7. Daikoku Island; 8. Kabu Island; 9. Otsuchi River; 10. Akaiashi River; 11. Tomari River. Insert map: migration route and distribution of chum salmon juveniles along the coast of northern Japan (Irie 1990).



Far Eastern Dace

Far Eastern dace usually inhabit coastal marine waters and ascend rivers only for spawning (Nakamura 1969). One of six Far Eastern dace (23.2–33.7 cm FL) collected in early April from the coastal Japan Sea was found to have a juvenile chum salmon in the stomach (Anonymous 1994a). The dace,

30.4cm FL, consumed crustaceans as well as the juvenile. No further information is available.

White-spotted charr

In the coastal Japan Sea along the southwest coast of Hokkaido, white-spotted charr go to the sea in December or April and stay at sea before they ascend

rivers in June (Takami 1995). Takami and Aoyama (1997) examined the stomach contents of white-spotted charr (34.7-63.8 cm FL) collected at sea near the mouth of the Tomari River (Fig. 1) in April and May 1996 in order to assess the role of this species as a predator. These authors found that the charr consumed mostly Japanese sand lance but also fed on juvenile chum salmon. A total of 99 juveniles was found in 109 charr stomachs examined. The highest number of juveniles found in a single stomach was 27. Predation by white-spotted charr was remarkable two days after the release of chum salmon juveniles from a hatchery on the Tomari River: 12 (23.1%) of 52 charr were found to have 79 (mean 6.6) juveniles in the stomachs. Takami and Aoyama (1997) suggested that white-spotted charr serve as important predators of chum salmon juveniles in river-mouth areas of southwestern Hokkaido. In the Bol'shaya River estuary, Kamchatka, white-spotted charr are known to feed on pink salmon juveniles (Tokranov and Maksimenkov 1995).

Japanese halibut

Wakabayashi (1995) made an experiment on Japanese halibut predation on chum salmon juveniles in captivity. Although all juveniles smaller than 40 mm FL were preyed on, predation mortality decreased with increasing size and the survival rate of juveniles larger than 91 mm FL reached 100%. Larger halibut (19.0-23.4 cm FL) fed more heavily on juveniles than smaller halibut (14.5-16.9 cm FL). Since the distribution of Japanese halibut of these sizes overlaps with that of chum salmon juveniles in shallow waters, Wakabayashi (1995) suggested that small-sized chum salmon juveniles are easily fed on by Japanese halibut.

Four chum salmon juveniles (72-77 mm FL) were actually found in one of three stomachs from Japanese halibut (20.2-23.3 cm FL) captured at a depth of 7 m in mid-May from the coastal Japan Sea (Sato et al. 1995).

Japanese sea perch

There are two reports on the predation by Japanese sea perch on chum salmon juveniles (Anonymous 1994b, 1995a). One Japanese sea perch (41.0 cm TL) caught off the mouth of the Akaishi River (Japan Sea, Fig. 1) in mid-May was found to have as many as 24 chum salmon juveniles in the stomach (Anonymous 1995a). The body weight of the ingested juveniles ranged from 1.5 to 2.0 g. Another case was reported from the Japan Sea coast of Yamagata, where one Japanese sea perch (37.7 cm FL) consumed two chum salmon juveniles (Anonymous 1994b).

Spiny dogfish

Spiny dogfish undergo seasonal migrations along the coast of Hokkaido (Sato 1935). This species has been reported to eat juvenile chum salmon off Akkeshi on the Pacific coast of Hokkaido during the early summer eastward migration (Sato 1935). The chum juveniles found were about 10.0 cm BL. Spiny dogfish are known to serve as predators of salmonid juveniles in coastal waters of Vancouver Island, Canada, as well (Beamish et al. 1992).

Arabesque greenling

Mishima et al. (1982b) found two chum salmon juveniles in two of 30 stomachs from arabesque greenling captured from Abashiri Bay (Okhotsk Sea, Fig. 1). The juveniles found were relatively small (4.8 and 4.9 cm FL). The authors also found six juveniles from a single arabesque greenling stomach taken in the Japan Sea off the west coast of Hokkaido, and suggested that predation by arabesque greenling on chum salmon juveniles is significant in waters with large populations of the former species. Predation by arabesque greenling on juvenile chum salmon was also recorded from off the mouth of the Akaishi River (Anonymous 1995a). Yori (1980) pointed out a possibility that with an increased population of arabesque greenling, predation by this species may have caused a reduction of the number of adult salmon returning to the Japan Sea coast of northern Honshu.

Pink salmon

Ueno et al. (1992) found one juvenile chum salmon in the stomach of adult pink salmon caught off Iturup Island (Fig. 1). Information on this case of predation, however, is very limited because these authors examined only five pink salmon for stomach contents (Dr. Y. Ueno, National Research Institute of Far Seas Fisheries, Shimizu 424, Japan, per. comm.).

Masu salmon

In Japan, masu salmon enter the sea as juveniles after their residence in fresh waters for one or two years (Kato 1991). It has been reported that those sea-inhabiting juvenile masu salmon prey on chum salmon juveniles at various localities of northern Japan (e.g., Hokkaido [Asami and Hayano 1995], Aomori [Harako 1996], Iwate [Miyazawa et al. 1986], Yamagata [Anonymous 1994b], Niigata [Kato 1983; Kaneko et al. 1988], Toyama [Sumi 1982], see Nagasawa and Mayama 1997). The importance of chum salmon juveniles as prey differs among locations (Nagasawa and Mayama 1997). In the coastal Japan Sea off

Niigata, chum salmon juveniles were heavily fed on (Kaneko et al. 1988), whereas in the coastal Pacific Ocean off Iwate, juveniles were rarely preyed on (Miyazawa et al. 1986). In Niigata, most of consumed juveniles were less than 1 g body weight and 1-5 juveniles were found in a masu salmon stomach (Kaneko et al. 1988). According to Miyazawa et al. (1986), immature masu salmon that spent one winter at sea occasionally feed on chum salmon juveniles off the Pacific coast of Iwate.

Other fishes

Some scientists examined the foods of teleosts from various localities of northern Japan, but predation on chum salmon juveniles by such fishes could not be demonstrated. For example, Oike and Ikehara (1979) examined 25 species of carnivorous fishes (1 Salmonidae, 1 Cyprinidae, 1 Lophiidae, 1 Sphyraenidae, 1 Sillaginidae, 1 Sciaenidae, 2 Carangidae, 1 Sparidae, 1 Uranoscopidae, 2 Percichthidae, 1 Oplegnathidae, 1 Scombridae, 3 Scorpaenidae, 2 Hexagrammidae, 2 Triglidae, 1 Paralichthyidae, 2 Pleuronectidae, 1 Tetraodontidae) from Toyama Bay (Japan Sea, Fig. 1) without detecting any juvenile chum salmon. Shirahata and Sakaguchi (1981) also found no salmonid juveniles in the stomachs of 10 fish species (2 Osmeridae, 1 Gadidae, 2 Stichaeidae, 1 Zoarcidae, 2 Scorpaenidae, 1 Cottidae, 1 Pleuronectidae) from Lake Saroma (Fig. 1) on the Okhotsk coast of Hokkaido. Similar results were obtained in some other localities (e.g., Aomori [Sato et al. 1995], Niigata [Anonymous 1995b]).

SEABIRD PREDATION ON CHUM SALMON JUVENILES

Various species of seabirds are found in inshore and offshore waters of northern Japan. According to Hotta et al. (1961), eight families and 26 species of seabirds have been recorded from the North Pacific Ocean off northern Honshu (Table 1). Gulls (family Laridae) and shearwaters (family Procellariidae) are dominant in inshore and offshore waters, respectively. Watanuki et al. (1988) also recognized five families and 13 species as seabirds breeding in Hokkaido (Table 2) and found that Leach's storm-petrels (*Oceanodroma leucorhoa*), rhinoceros auklets (*Cerorhinca monocerata*), slaty-backed gulls (*Larus schistisagus*), and black-tailed gulls (*Larus crassirostris*) are the most abundant among them.

The seabirds which have so far been recognized as predators of chum salmon juveniles in Japan are rhinoceros auklets and black-tailed gulls.

Rhinoceros auklets

Watanuki (1990) demonstrated that breeding rhinoceros auklets feed chicks small pelagic fishes including chum salmon juveniles on both Teuri Island (Fig. 1) in the Japan Sea and Daikoku Island (Fig. 1) in the North Pacific. The main diets of chicks were Japanese sand lance, hexagrammids (*Hexagrammos* sp.) or Japanese anchovies (*Engraulis japonicus*), but the percentage occurrence of chum salmon juveniles in the food of chicks ranged from 3.6% on Teuri Island to a high of 16.1% on Daikoku Island. Salmonid juveniles have been reported to be the prey of rhinoceros auklets in other regions as well (e.g., Bertram and Kaiser 1993; Burger et al. 1993).

Among seabirds breeding in Hokkaido, rhinoceros auklets are the second most abundant species with about 180×10^3 pairs nesting a year in the 1980's (Watanuki et al. 1988). This species breeds on five islands in Hokkaido. The breeding season ranges from early April to early August (Watanuki 1987).

Black-tailed gulls

On the basis of radiological surveys near the mouth of the Otsuchi River (Fig. 1), Hiyama et al. (1972a) indicated that black-tailed gulls are important predators of chum salmon juveniles. They marked chum salmon fry with ^{32}P before release and traced the radioactivity of ^{32}P in various fishes and birds which were taken in river-mouth areas. As a result, they detected the radioactivity in the feces of black-tailed gulls and therefore demonstrated that these birds took up ^{32}P originally administered to the juveniles. However, they could not clarify whether the uptake of radioactivity is due to direct predation on juveniles by these birds or to indirect transfer by eating predatory fishes of chum salmon.

Although quantitative data are unavailable, Hashiba and his coworkers (Hashiba and Yasui 1980; Hashiba et al. 1981, 1982; Hashiba and Otaki 1982) observed that black-tailed gulls preyed on chum salmon juveniles in coastal waters of Sanriku, northern Honshu. They found that the distribution of black-tailed gulls off the Pacific coast of Sanriku is in accordance with that of juvenile chum salmon (Figs. 2-3) and strongly suggested that seabirds, particularly black-tailed gulls, are predators of the juveniles. Hashiba and Yasui (1980) actually discovered remains of juvenile chum salmon on Kabu Island (Fig. 1), at which one of the largest colonies in Japan of black-tailed gulls is located.

Black-tailed gulls are widely distributed in Japan, with breeding colonies found from Hokkaido to Kyushu. They are one of the most common seabirds

Table 1. Seabirds found in the western North Pacific Ocean off northern Honshu and Hokkaido (Hotta et al. 1961).

Family	English name	Scientific name
Diomedelidae	Laysan albatross	<i>Diomedea immutabilis</i>
	Black-footed albatross	<i>Diomedea nigripes</i>
Procellariidae	Northern fulmar	<i>Fulmarus glacialis</i>
	Streaked shearwater	<i>Calonectris leucomelas</i>
	Flesh-footed shearwater	<i>Puffinus carneipes</i>
	Sooty shearwater	<i>Puffinus griseus</i>
	Short-tailed shearwater	<i>Puffinus tenuirostris</i>
Oceanitidae	Madeiran storm-petrel	<i>Oceanodroma castro</i>
	Leach's storm-petrel	<i>Oceanodroma leucorhoa</i>
	Trisram's storm-petrel	<i>Oceanodroma tristrami</i>
	Fork-tailed storm-petrel	<i>Oceanodroma furcata</i>
Sulidae	Brown booby	<i>Sula leucogaster</i>
Phalaropodidae	Red phalarope	<i>Phalaropus fulicarius</i>
Stercorariidae	Great skua	<i>Catharacta skua</i>
	Pomarine skua	<i>Stercorarius pomarinus</i>
	Long-tailed skua	<i>Stercorarius longicaudus</i>
Laridae	Black-tailed gull	<i>Larus crassirostris</i>
	Common gull	<i>Larus canus</i>
	Herring gull	<i>Larus argentatus</i>
	Slaty-backed gull	<i>Larus schistisagus</i>
	Black-headed gull	<i>Larus ridibundus</i>
	Black-legged kittiwake	<i>Larus tridactyla</i>
Alcidae	Thick-billed murre	<i>Uria lomvia</i>
	Common murre	<i>Uria aalge</i>
	Rhinoceros auklet	<i>Cerorhinca monocerata</i>
	Tufted puffin	<i>Lunda cirrhata</i>

Table 2. Seabirds breeding in Hokkaido and numbers of their breeding pairs in the 1980's (Watanuki et al. 1988).

Family	English name	Scientific name	No. of breeding pairs ($\times 10^3$)
Procellariidae	Streaked shearwater	<i>Calonectris leucomelas</i>	+
Oceanitidae	Leach's storm-petrel	<i>Oceanodroma leucorhoa</i>	500
Phalacrocoracidae	Japanese cormorant	<i>Phalacrocorax filamentosus</i>	1.9
	Pelagic cormorant	<i>Phalacrocorax pelagicus</i>	0.01
	Red-faced cormorant	<i>Phalacrocorax urile</i>	0.00-0.01
Laridae	Slaty-backed gull	<i>Larus schistisagus</i>	9.6-10.0
	Black-tailed gull	<i>Larus crassirostris</i>	36.0-40.0
Alcidae	Thin-billed murre	<i>Uria aalge</i>	0.03-0.06
	Spectacled guillemot	<i>Cephus carbo</i>	400 adults
	Ancient murrelet	<i>Synthliboramphus antiquus</i>	0.1?
	Marbled murrelet	<i>Brachyramphus marmoratus</i>	+
	Rhinoceros auklet	<i>Cerorhinca monocerata</i>	180
	Tufted puffin	<i>Lunda cirrhata</i>	20 adults

* The breeding of these species was confirmed in Hokkaido.

Fig. 2 Distribution of chum salmon juveniles (top) and seabirds (mainly black-tailed gulls) (bottom) in the western North Pacific Ocean off Sanriku, northern Honshu, from May 29 to June 5, 1979 (Nagasawa and Kaeriyama, 1995, with permission of the Hokkaido Salmon Hatchery). Juveniles were caught with dip nets by three crew persons for 20 min., and seabirds were observed during these juvenile chum salmon collections.

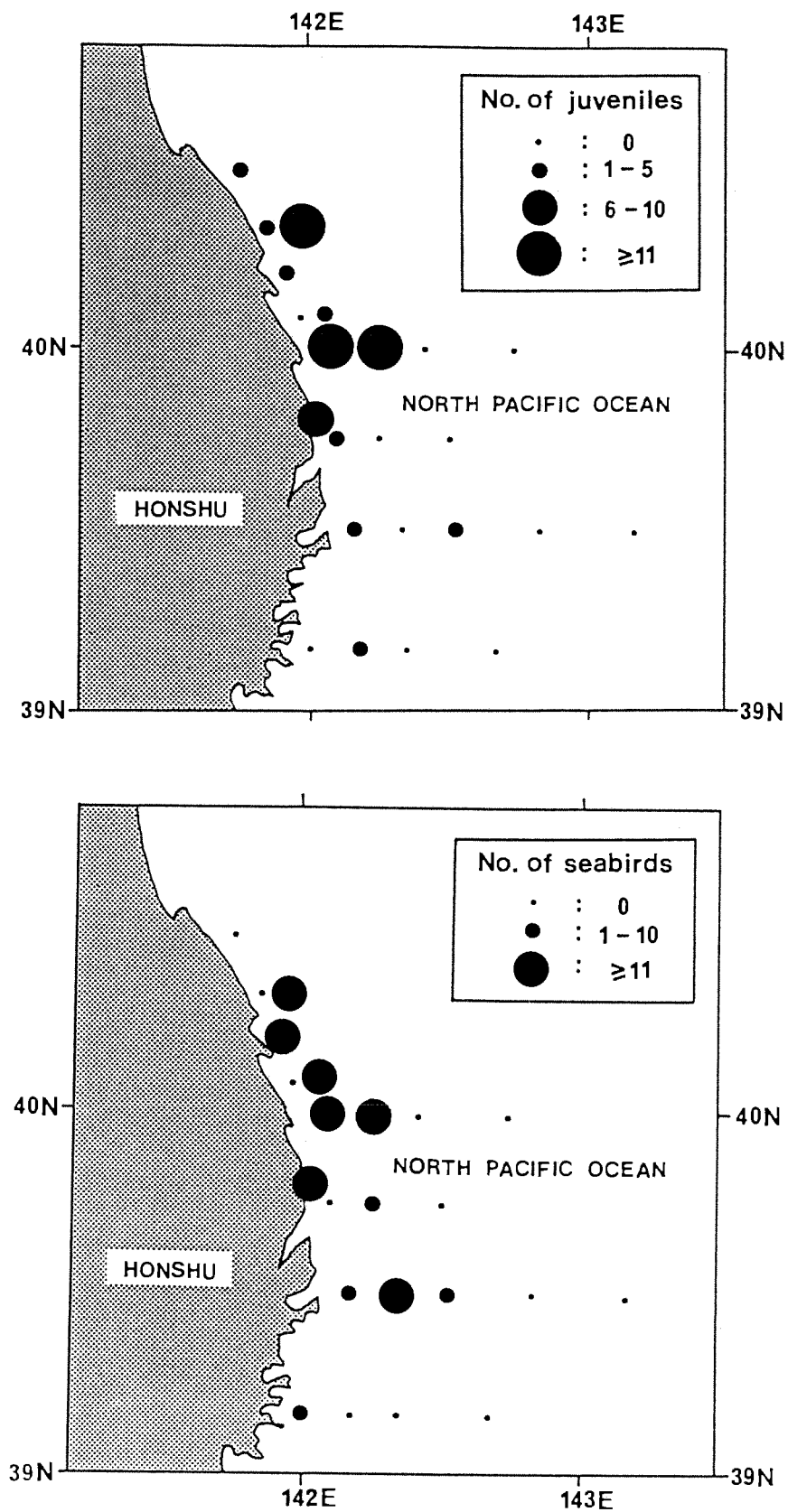
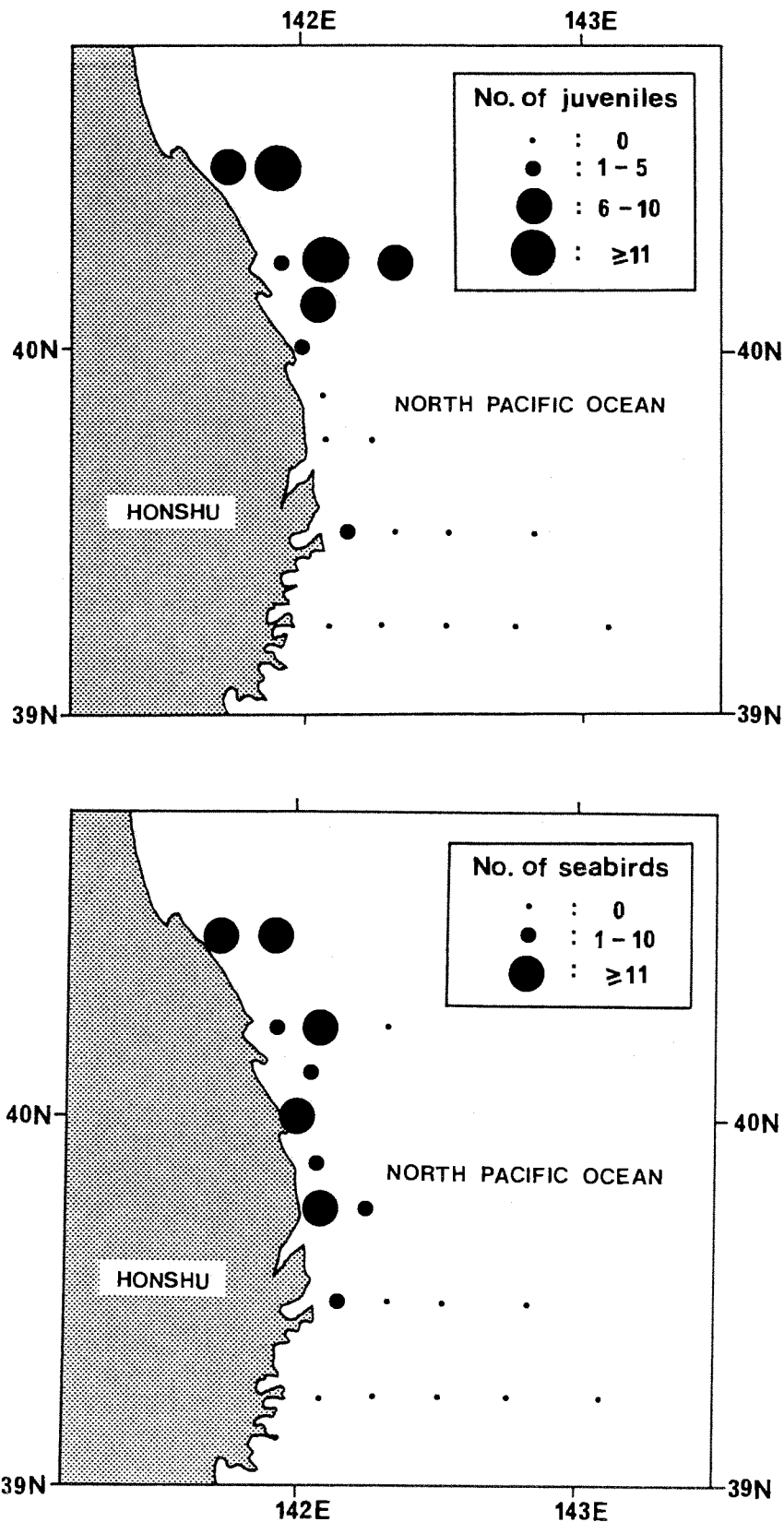


Fig. 3 Distribution of chum salmon juveniles (top) and seabirds (mainly black-tailed gulls) (bottom) in the western North Pacific Ocean off Sanriku, northern Honshu, from May 29 to June 2, 1980 (Nagasawa and Kaeriyama, 1995, with permission of the Hokkaido Salmon Hatchery). Juveniles were caught with dip nets by three crew persons for 20 min., and seabirds were observed during these juvenile chum salmon collections.



found in coastal waters of northern Japan. While the exact total population size of this species is not known, the breeding population on Kabu Island was estimated as about 30×10^3 pairs (Narita 1979). Watanuki et al. (1988) also reported that black-tailed gulls are ranked as the third most numerous seabirds breeding in Hokkaido ($36\text{--}40 \times 10^3$ pairs in a year in the 1980's). This species breeds from late February to late July on Kabu Island (Narita 1979).

Other seabirds

Some other seabirds breed in northern Japan (Watanuki et al. 1988). However, there is no evidence that such seabirds feed on chum salmon juveniles. Leach's storm-petrels feed on fishes from May to September, but the fishes taken were too digested to be identified to species (Watanuki 1985). While slaty-backed gulls take fishes for chicks in spring and summer, no salmonids were recorded in their diets (Watanuki 1984, 1988). If these species of seabirds would take salmon juveniles, their predatory impact on Japanese chum salmon populations would be significant because these birds' population sizes are high in Hokkaido (500×10^3 pairs of Leach's storm-petrels and $9.6\text{--}10.0 \times 10^3$ of slaty-backed gulls nesting per year in the 1980's; Watanuki et al. 1988). Furthermore, Kato et al. (1995) examined the food of Japanese cormorants (*Phalacrocorax filamentosus*) at Teuri Island but did not find chum salmon juveniles. The chick diets of spectacled guillemots (*Cepphus carbo*) on this island also did not include chum salmon juveniles (Minami et al. 1995). Several other species, such as other cormorants (*Phalacrocorax* spp.) and streaked shearwaters (*Calpnectris leucomelas*), also breed along the coasts of northern Japan, but there is no study on the feeding habits of these species in northern Japan.

Large numbers of sooty shearwaters (*Puffinus griseus*) and short-tailed shearwaters (*P. tenuirostris*) migrate off the Pacific coast of northern Honshu and Hokkaido in spring and summer (Ogi 1986; Watabe et al. 1987). Ogi (1986) found that sooty shearwaters feed mainly on Japanese sardine (*Sardinops melanostictus*) in this area but did not give any comment on salmonid juveniles as prey.

Murres (common murres *Uria aagle* and thick-billed murres *U. lomvia*) are distributed in small numbers off the southeast coast of Hokkaido in May and June (Ogi 1986). Although these birds prey on juvenile sockeye salmon (*Oncorhynchus nerka*) in the eastern Bering Sea and Bristol Bay (Ogi and Tsujita 1973), little information is available on their foods in Japan. Both species are known to feed mainly on Japanese sand lance in winter in the Japan Sea off the west coast of Hokkaido (Ogi and Shiomi 1991; Hashimoto 1993).

DISCUSSION AND CONCLUSIONS

Over 90 species of fishes have been reported to occur with chum salmon juveniles in Japanese coastal waters. Among these species, only nine species are recorded as predators. Stomach content analyses for some potential predatory fishes demonstrated that they consumed no salmonid juveniles. Under localized circumstances in which predatory fishes, such as Japanese dace and arabesque greenling, occur abundantly, these fishes may cause significant loss of juveniles. However, there is no evidence that fish predation has much impact on the number of returning adult salmon in Japan. Therefore, fish predation does not appear to be an important factor that can control the population level of Japanese chum salmon.

A possible reason for the lack of significant predation by predatory fishes on chum salmon juveniles is the escapement of juveniles from piscivores. With increased size, chum salmon juveniles are able to swim faster (Kobayashi and Ohkuma 1983). In Japan, almost all chum salmon populations are produced at hatcheries, and juveniles are fed before release. It is thus likely that the release of large hatchery-reared juveniles reduces predation mortality. Wakabayashi (1995) demonstrated that all chum salmon juveniles larger than 91 mm FL escaped predation by Japanese halibut in a tank study. Higher survival for larger-sized chum salmon juveniles has been suggested by Hiyama et al. (1972b) and Kobayashi (1980).

Based on the feeding habits, distribution, and abundance of rhinoceros auklets and black-tailed gulls in northern Japan, these species appear to be significant predators of chum salmon juveniles, and the impact of their predation may not be negligible. It also should be noted that the numbers of seabirds presented above are only those of nesting pairs and the actual numbers including immature birds are more numerous.

There is as yet little information about the impact of fish and seabird predation on chum salmon populations, and it should be emphasized that more field and experimental work is needed to assess it. In Japan, almost all chum salmon populations are produced artificially and large-sized juveniles are released currently. The vulnerability and behavioral responses of those juveniles to fish and avian predators should be the subject of future research.

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Appendix

Table 1. Fishes collected with chum salmon juveniles in coastal waters of northern Japan by purse seine (PS), gillnets (GN), larval fish net (LN), dip net (DN) and beach seine (BS) in spring-summer*. +=collected, J=juveniles, A=adults. Scientific names follow those recommended by Nakabo (1993).

Area	Japan Sea			Okhotsk Sea					North Pacific	
	PS	GN	LN	PS	GN	LN	BS	DN	PS	DN
Salmonidae										
<i>Oncorhynchus keta</i> (J)	+	+	+	+	+	+	+	+	+	+
<i>Oncorhynchus keta</i> (A)									+	
<i>Oncorhynchus gorbuscha</i> (J)				+		+	+			
<i>Oncorhynchus gorbuscha</i> (A)		+		+					+	
<i>Oncorhynchus masou</i> (J)		+		+	+					
Petromyzontidae										
<i>Lethenteron japonica</i>		+	+			+		+		
Lamnidae										
<i>Lamna ditropis</i>					+					
Triakidae										
<i>Mustelus manazo</i>					+					
Squalidae										
<i>Squalus acanthias</i>				+	+					
Clupeidae										
<i>Clupea pallasii</i>		+		+	+		+	+		
<i>Sardinops melanostictus</i>		+		+	+				+	+
Engraulidae										
<i>Engraulis japonicus</i>		+							+	
Cyprinidae										
<i>Tribolodon hakonensis</i>	+						+	+		
<i>Tribolodon brandti</i>							+			
Bathylagidae										
<i>Leuroglossus schmidtii</i>					+					
Osmeridae										
<i>Hypomesus transpacificus nipponensis</i>		+	+				+			
<i>Hypomesus pteriosus japonicus</i>				+				+		
<i>Mallotus villosus</i>						+				
<i>Osmerus eperlanus mordax</i>							+	+		
Salangidae										
<i>Salangichthys microdon</i>			+	+			+	+		
Myctophidae										
Myctophidae gen. sp.									+	
<i>Stenobranichius nannochir</i>						+				
Gadidae										
<i>Eleginus gracilis</i>					+		+	+		
<i>Gadus macrocephalus</i> (J)				+			+			
<i>Theragra chalcogramma</i> (J)	+			+			+			
<i>Theragra chalcogramma</i> (A)				+						
Hemiramphidae										
<i>Hemiramphus sajori</i>								+		+
Scomberesocidae										
<i>Cololabis saira</i>		+			+				+	+
Hypoptychidae										
<i>Hypoptychus dybowskii</i>								+		
Gasterosteidae										
<i>Gasterosteus aculeatus</i>	+	+	+	+	+	+	+	+	+	
Syngnathidae										
<i>Syngnathus schlegelii</i>							+			
Carangidae										
<i>Trachurus japonicus</i>									+	

* Data from Anonymous (1978, 1979, 1980a), Shirahata and Hatori (1979), Mishima and Shimazaki (1980a, b), Hashiba and Yasui (1980), Hashiba et al. (1981), Ito (1981), Hashiba and Otaki (1982), Kato (1982), and Ueno et al. (1990).

Appendix (continued)

Area	Japan Sea			Okhotsk Sea					North Pacific	
	PS	GN	LN	PS	GN	LN	BS	DN	PS	DN
Bramidae										
<i>Brama japonica</i>									+	
Mugilidae										
<i>Chelon haematocheilus</i>								+		
Zoarcidae										
<i>Neozarces steindachneri</i>							+			
<i>Zoarces elongatus</i>							+			
Stichaeidae										
Stichaeidae gen. sp.						+		+		
<i>Bryozoichthys lysimus</i>									+	
<i>Eumesogrammus praeciosus*</i>			+			+				
<i>Lumpennella longirostris</i>									+	
<i>Opisthocentrus dybowskii</i>							+			
<i>Opisthocentrus ocellatus</i>							+			
<i>Stichaeus nozawai</i>			+			+				
<i>Stichaeus</i> sp.						+				
Pholididae										
Pholidae gen. spp.						+			+	
<i>Pholis fasciata</i>						+	+			
<i>Pholis</i> sp.										
<i>Rhodymenichthys dolichogaster</i>							+			
Anarchichadidae										
<i>Anarchichas orientalis</i>				+		+			+	
Ptilichthyidae										
<i>Ptilichthys goodei</i>						+				
Trichodontidae										
<i>Arctoscopus japonicus</i>			+				+			
Ammodytidae										
<i>Ammodytes personatus</i> (J)	+	+	+	+	+	+	+		+	
<i>Ammodytes personatus</i> (A)	+	+	+	+	+					
<i>Ammodytes</i> sp.									+	
Gobiidae										
Gobiidae gen. sp.							+			
<i>Chaenogobius castaneus</i>								+		
<i>Chaenogobius laevis</i>								+		
Scombridae										
<i>Scomber japonicus</i>		+							+	
<i>Scomber tapeinocephalus</i>									+	
Scorpaeniformes fam. gen. sp.			+							
Scorpaenidae										
<i>Sebastes glaucus</i>		+								
<i>Sebastes schlegelii</i>	+		+			+				
<i>Sebastes</i> sp. (type A)			+							
<i>Sebastes</i> sp. (type B)			+			+				
<i>Sebastes</i> sp. (type C)			+			+				
Anoplopomatidae										
<i>Anoplopoma fimbria</i>									+	
Hexagrammidae										
<i>Hexagrammos lagocephalus</i>									+	
<i>Hexagrammos octogrammus</i>							+		+	
<i>Hexagrammos otakii</i>							+			+
<i>Hexagrammos stelleri</i>						+	+	+	+	
<i>Pleurogrammus azonus</i>	+	+	+	+	+	+		+	+	+

* This species was reported by Anonymous (1978, p. 78-86) but is not listed in Nakabo (1993).

Appendix (continued)

Area	Japan Sea			Okhotsk Sea					North Pacific	
	PS	GN	LN	PS	GN	LN	BS	DN	PS	DN
Cottidae										
Cottidae gen. sp.						+				
<i>Argyrocottus zanderi</i>							+			
<i>Blepsias bilobus</i>				+	+	+	+		+	
<i>Blepsias cirrhosus</i>						+	+		+	
<i>Enophyrus diceratus</i>						+				
<i>Gymnocanthus</i> sp.						+				
<i>Hemilepidotus gilberti</i>			+	+		+			+	
<i>Hemitripterus villosus</i>				+		+			+	
<i>Nautichthys pribilovius</i>						+				
<i>Myoxocephalus brandti</i>							+			
<i>Myoxocephalus stelleri</i>				+			+		+	
<i>Myoxocephalus</i> sp.							+			
<i>Porocottus allisi</i>							+			
Psychrolutiae										
<i>Malacocottus zonurus</i>						+				
Agonidae										
<i>Agonomalus proboscidalis</i>						+				
<i>Aspidophoroides bartoni</i>						+				
<i>Brachyopsis rostratus</i>							+			
<i>Occella dodecaedron</i>							+			
<i>Pallasina barbata</i>							+	+		
<i>Pallasina eryngia</i>										
<i>Percis japonicus</i>						+				
<i>Podothecus gilberti</i>						+				
<i>Tilesina gobbosa</i>			+			+				
Cyclopteridae										
<i>Aptocyclus ventricosus</i>						+				
<i>Eurimicrotremus birulai</i>				+	+	+				
Liparidae										
<i>Liparus agassizii</i>									+	
<i>Liparus tessellatus</i>			+							
<i>Liparus</i> sp.			+			+				
Pleuronectidae										
Pleuronectidae gen. sp. (A)			+							
Pleuronectidae gen. sp. (B)			+							
<i>Atheresthes evermanni</i>									+	
<i>Cleisthenes pinetorum herzensteini</i>							+			
<i>Kareicus bicoloratus</i>							+			
<i>Platichthys stellatus</i>							+			
<i>Pleuronectes herzensteini</i>				+						
<i>Pleuronectes punctatissimus</i>							+			
<i>Pleuronectes schrenki</i>							+			
<i>Pleuronectes obscurus</i>							+			
<i>Pleuronectes pinnifasciatus</i>							+			
Monacanthidae										
<i>Thamnaconus modestus</i>		+			+					
Tetradontidae										
<i>Takifugu porphyreus</i>	+				+					

Fluctuations in Abundance of Pink Salmon (*Oncorhynchus gorbuscha*) in the North Pacific Ocean

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Commercial exploitation of all species of salmon in Alaska commenced in 1878. It is assumed that major changes in the commercial catches reflect similar major changes in total abundance. These have been remarkably synchronous for all five species in Alaska. Following the initial harvest of virgin stocks, there was a gradual buildup of total yield, which remained high for more than half a century. In the fifties catches or abundances decreased for all species and remained low until the seventies, when salmon stocks again started to gain in strength. Today abundances are at the highest levels ever recorded.

Environmental data, such as time series of air temperatures, demonstrate similar changes. The period with low pink salmon catches in S.E. Alaska corresponds to a lowering of winter air temperatures. Air temperatures observed here at various locations follow the same temporal pattern, only the amplitude varies. Environmental changes can thus be described by observations from one location. The reduced production may be due to a lowering of the food production and a shortening of the growing season for the juvenile salmon.

Pink salmon is the dominant species in both S.E. Alaska and in the Russian Far East. The initial high level of catches of Pacific salmon in Russia lasted until the late forties. After a couple of decades of low abundance, the stocks started to gain in strength, which still continues today. However, the recovery was slower than observed in the eastern North Pacific Ocean. This similarity in pink abundance of the eastern and western stocks is most likely driven by large scale climatic factors.



INTRODUCTION

It has been known for a long time that variations in the catch curve may have the same general features in several districts when compared over periods of several years. Thus the Nushagak catch curve was almost identical with that of the Chignik system (Mathisen 1971). The last few decades have witnessed an expanding interest in the relationship between fish abundance and environmental variables such as coastal upwelling, temperature, precipitation, and others. A number of symposia have been held including Wooster (1983), Wooster and Fluharty (1985), Beamish and

McFarlane (1989), Beamish (1995). Since the present paper deals with pink salmon (*Oncorhynchus gorbuscha*) in S.E. Alaska there are two papers of particular interest, namely Marshall (1993) and Francis and Hare (1994). The author of this first paper used time series analysis to forecast salmon catches in Alaska. The second paper relates decade-scale shifts in climate to similar shifts in abundance of salmon and zooplankton.

The present paper is continuing this line of inquiry by relating the mean monthly air temperatures to pink salmon production in S.E. Alaska. There are distinct relationships between the smoothed curves for

air temperature and pink salmon abundance; but variability between years is great, proving that the final returns of pink salmon are governed by both the size of the escapement and the environment. This makes forecasting pink salmon extremely difficult and imprecise in nature when using only past catch levels. It will improve as better escapement data become available with more precise estimates of total runs, and clearer understanding of the relationship between survival and environmental variables is achieved.

MATERIALS AND METHODS

The catches for Alaska and S.E. Alaska have been obtained from the integrated fisheries data base of the Alaska Department of Fish and Game. Historically salmon was sold as a whole fish with different unit prices depending upon the species in question. After 1965 all trade has been on a weight basis. Since escapement is always reported in numbers of fish, the weight of catches has been converted to numbers by division with an average weight per fish. This declines through the fishing season. In the case of pink salmon the main reason is that the percentages of the smaller females increases as the season progresses. Normally average weight is determined at each processing plant by weighing about one hundred fish. There are errors involved due to selection of samples and counting of numbers of fish; but these have been considered to be randomly distributed, and no corrections have been applied.

The Russian catch statistics were taken from a publication compiled and issued in 1989 by the All-Russian Research Institute of Fisheries and Oceanography (VNIRO). The data for 1900 - 1986 have been corrected by the late Dr. A.I. Chigirinsky. Corrected data from subsequent years have been

provided by one of us.

For each species there are large year to year variations in reported catches. In order to bring out common trends between species the catches were expressed as a percentage of the maximum catch and a moving average of 5 years was calculated. A similar approach was used for air temperatures based on monthly mean values. These have been gathered at many places and for various lengths of time. The early records came from the U.S. Department of Agriculture (1921 & 1940), and then the U.S. Department of Commerce (1992) for the period 1950-1992.

No escapement records exist prior to 1960, however, Jaenicke (1995) has demonstrated a linear relationship between catch and total run of pink salmon in S.E. Alaska after this time (Fig.1). It therefore, becomes possible to use pink salmon catches as a proxy for total run. Practically this means that this salmon fishery is managed on a fixed fractional harvest of the total incoming run. Prior to 1960 most of the catches came from stationary traps. Although the total number of traps varied, those set in good locations were operated each year. This gave a stability to expended effort even though the catches of the five species varied drastically with pink and sockeye salmon being the dominant species in volume.

RESULTS

Total Catches in Alaska

On Fig. 2 are plotted the moving averages of the normalized commercial catches of all five species of Pacific salmon. For the numerically important species like pinks and chums (*O.keta*) the curves track each other very closely. For the more valuable species like

Fig. 1 Linear relationship between harvest and total return of pink salmon to S.E. Alaska during the period 1960-1995, (from Jaenicke 1995).

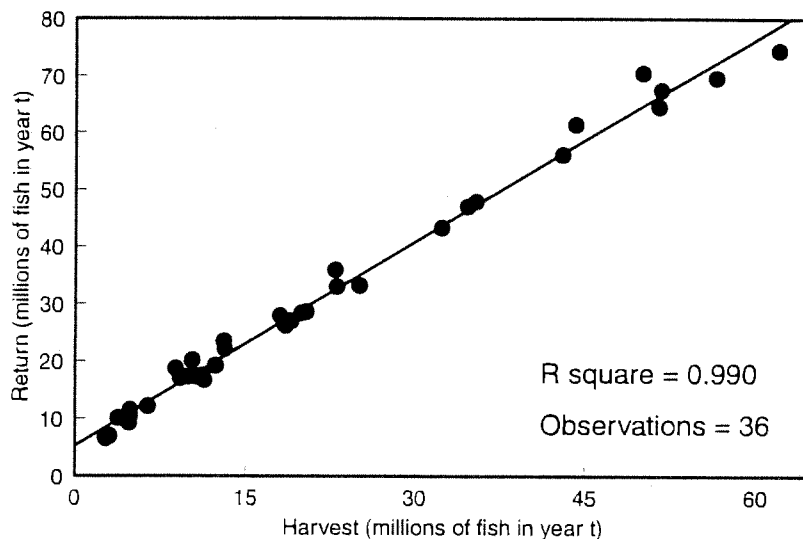
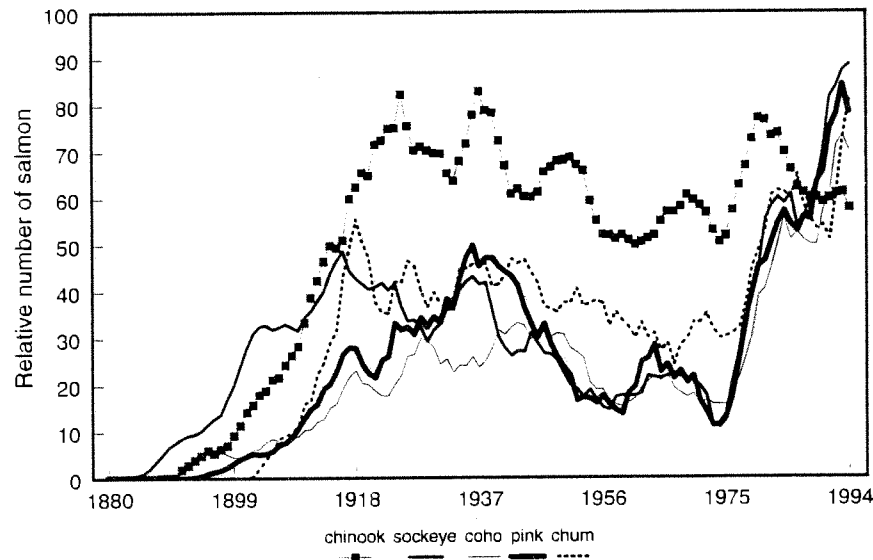


Fig. 2 Commercial catches of the five Pacific salmon species in Alaska, expressed as a 5-year moving average of percentages of maximum catch.



sockeye and chinook salmon the percentage catch of the total run is higher than for the less valuable species. Such a selective harvest rather than one proportional to abundance was especially pronounced for sockeye salmon during the early phases of commercial exploitation. Nevertheless, the catch curve for every species shows an initial period of high production with a decline appearing in the forties which lasted to the seventies. This was followed by a period of sharp increases in catch which is still ongoing.

Catches in S.E. Alaska

For the S.E. Alaska there was an initial emphasis on the harvest of sockeye salmon (Fig.3). But the two high production periods with a low one between them are well pronounced and covers the same time intervals as observed for Alaska as a whole. The recovery of chinook during the last period is less pronounced than for the other species. One reason might be a general increase in effort applied to this species inside and outside S.E. Alaska.

Russian Catches of Pacific Salmon

The catches in the Russian Far East are summarized in (Fig. 4). Pink salmon is the dominant species and a 5 year moving average of catches displays a similar pattern as seen in the eastern portion of the North Pacific Ocean with a period of stable production from 1910 to the early forties. Low production was seen in the sixties, but an increase in production commenced in the early seventies. The catch figures of chum salmon follow a similar picture

with chum lagging pinks by approximately 10 years. In both cases the recovery during the last period is slower for pink and chum salmon than seen along the North American continent. If individual years are plotted, there occurs large variations. The catches of chinook and coho remain relatively high.

In spite of local variability within and between districts in the Russian Far East and the eastern side of the North Pacific Ocean, the catches of species like pink salmon display a similar pattern of two high production periods with an intervening period of low production. They could be generated by the same climatic factors as observed in the eastern North Pacific Ocean.

Air Temperatures in S.E. Alaska

Air temperatures have been measured at a number of places for varying lengths of time in S.E. Alaska. Although the amplitude differs from one place to the next, a variety of locations display the same common features. In this paper it is, therefore, assumed that temperatures measured in Juneau, the set of records covering the longest uninterrupted number of years, serve as a proxy for climatic changes in S.E. Alaska from 1909-1993. Three time periods have been considered in Fig. 5, namely two high production periods 1928-1938, and 1978-1988, a low one 1963-1973. For each period, representing 11 years, a monthly mean was calculated by combining daily high and low air temperatures. The three sets of monthly means were averaged, and considered as the -0-reference line. For each of the three sets deviations from this line have been plotted. The results (Fig. 5), are similar for the summer months for all three

Fig. 3 Commercial catches of the five Pacific salmon species in S.E. Alaska, expressed as a 5-year moving average of percentages of maximum catch.

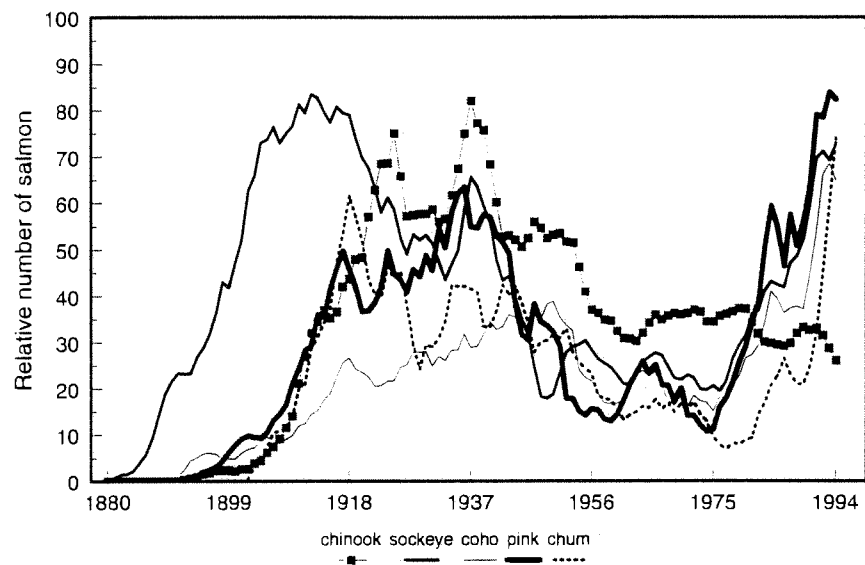


Fig. 4 Commercial catches of the five Pacific salmon species in the Far East of Russia, expressed as a 5-year moving average of percentage of maximum catch.

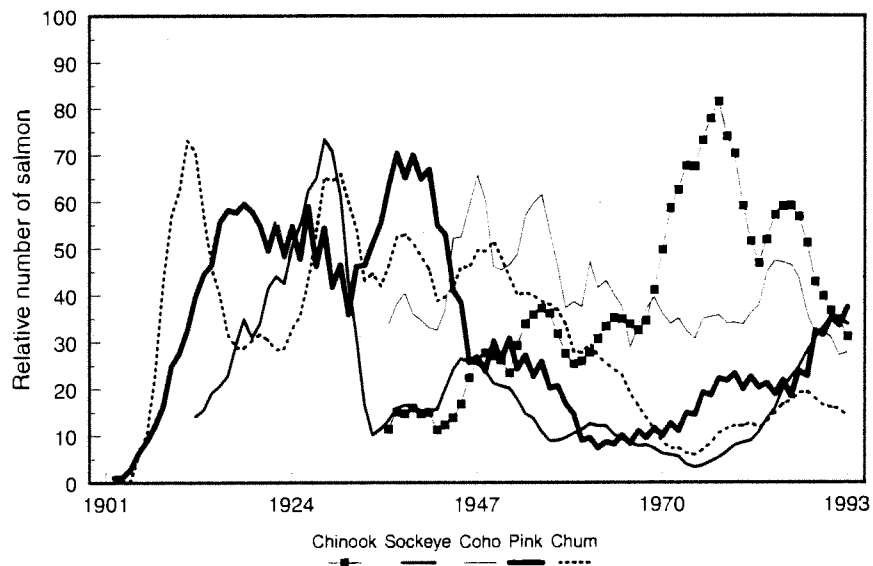
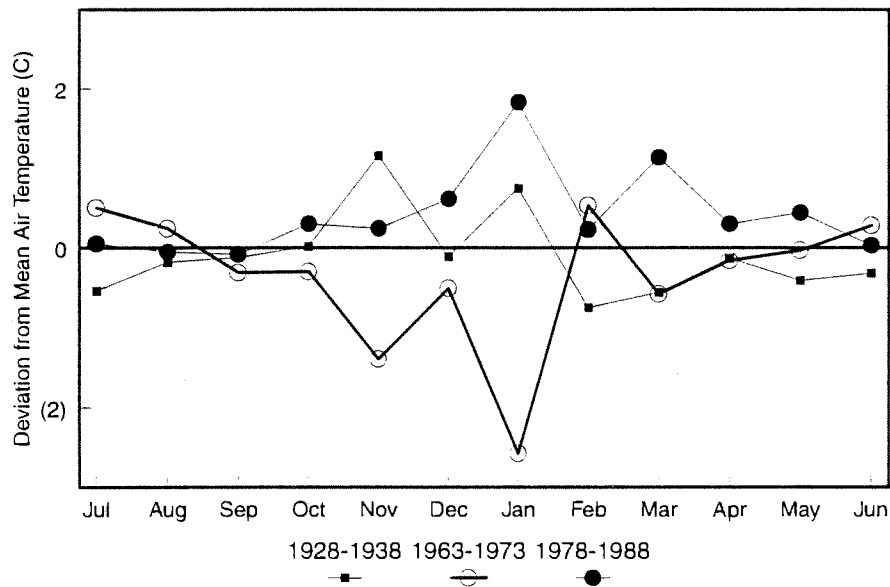


Fig. 5 Monthly means for three periods, 1928-1938, 1963-1973, and 1978-1988 have been averaged. The deviations of the three sets of monthly means from the overall mean have been plotted.



periods. The differences lie in the winter temperatures for October, November, December and January which are decidedly colder during the low production period.

The mean catches for three periods identified in Fig. 6 are essentially the same as used in Fig. 5. If the two figures are compared it is clear that low winter temperatures depress production of pink salmon in S.E. Alaska.

DISCUSSION

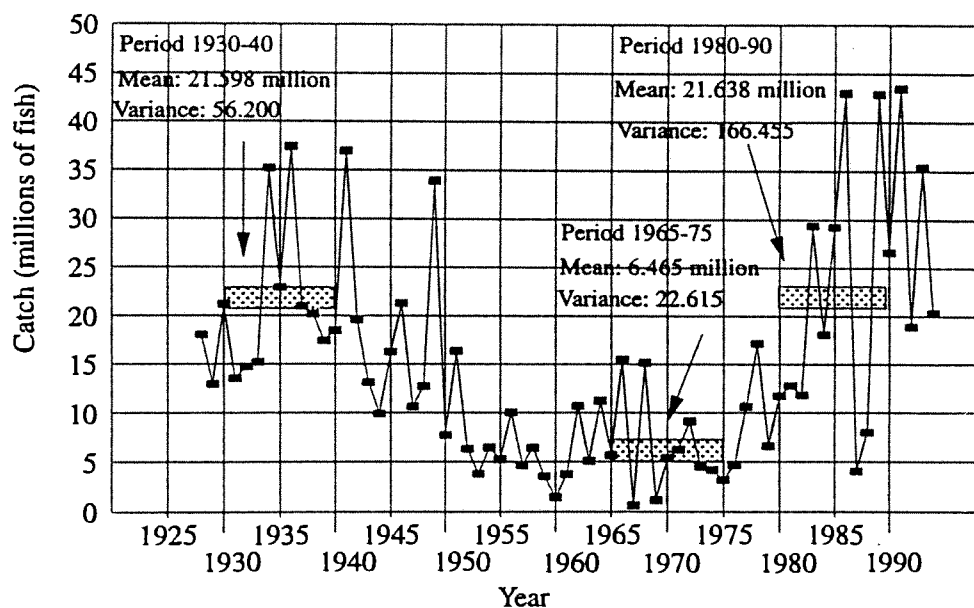
Attempts to use time series analysis of catches for prediction of future yearly salmon runs have only met with moderate success (Farley 1996). His errors varied approximately from ± 20 -25 %. A univariate model performed just as well as one where environmental processes were included. The underlying variability is great if catches for individual years are plotted without any smoothing process.

Generally good growth of immature pink salmon during first summer in the inshore waters enhances their survival (Courtney 1997). But an observed variability in catches from year to year and within districts clearly indicate that other factors also are

operating in conjunction with the temperature. Some can be abiotic in nature like precipitation while others are biological factors. Very little work has been done to clarify the role of predators and food competitors in the ecosystems occupied by salmon throughout its life span. For pink salmon a large escapement in one year may effect success of next spawning. It appears that the bottom fauna is enhanced from a large escapement and associated organic material introduced in the gravel, and developing scavengers may effect next year's egg deposition (Kline *et al.* 1990).

The changes observed in S.E. Alaska are only part of a larger picture of interannual variability in the North Pacific and the Bering Sea where a number of forcing mechanisms create atmosphere-ocean variability with varying time scales (National Research Council 1996). However, persistent changes in average air temperature will indicate major changes in pink salmon production with time lags not fully understood. This in itself is of great economic importance to the fishing industry. The present high salmon production has depressed the profit margin per production unit so any substantial reduction in catches carries immediate and large economic consequences.

Fig. 6 Average catches and associated variances of pink salmon in S.E. Alaska during three time periods, 1930-1940, 1965-1975, and 1980-1990.



CONCLUSIONS

Average winter air temperatures can serve as a proxy for total average pink salmon production over long time periods in S.E. Alaska. But the correspondence between salmon production and average air temperature is not accurate enough to use for yearly predictions of run sizes. While the emphasis in this paper has been on pink salmon in S.E. Alaska, it appears that the four other species of Pacific salmon there follow similar trends.

The salmon processing industry is in need of pre-season forecasts of long term and short term changes in abundance. The latter ones must come from other sources in addition to long term climatic changes.

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Predation Risk as an Opportunity for Compensatory Growth in Juvenile Coho Salmon?

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It is a common occurrence in the freshwater stages of anadromous salmonids that growth rates of large individuals within a cohort surpass those of smaller fish. Small size classes of fish are lost from the population due to emigration or mortality from predators. The present study explores the reasons for the apparent higher susceptibility of small individuals to predation. We used field and laboratory observations of size-dependent foraging strategies in age-0 coho salmon (*Oncorhynchus kisutch*) under predation risk. In laboratory stream tanks groups of juvenile coho salmon were given a choice of a safe habitat and a habitat offering the same amount of food but associated with simulated predation risk from a model predator. Fish were individually marked, their position and behaviour recorded over one week and their change in size assessed. Fish that made use of the risky pool were smaller and fewer in numbers than their counterparts in the safe pool. Fish distribution pattern

was remarkably stable over a 2-day period after predation simulation had been discontinued. Overall growth rates were depressed and the difference in growth rates between small and large individuals was reduced when compared with control experiments without simulated predation. We argue that large fish behaved in a risk-averse manner compared to small individuals, the latter making use of enhanced feeding opportunities indirectly provided by the presence of the predation threat. We speculate that in a natural environment, the presence of predators may serve to depress growth rates in a population through risk-avoidance behaviour, but may allow for growth compensation among size classes within a cohort. Before removal of predators as part of an enhancement scheme for salmonids, managers may consider the potential effect not only on mortality rates but also on growth patterns in a population of fish.

Genetic Variation in Asian Populations of Chum Salmon, *Oncorhynchus keta* (Walbaum)

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Asian chum salmon stocks represent a significant portion of all chum stocks feeding in the Pacific ocean. They are of great importance to fisheries of Pacific Rim countries. Effective stock identification in Pacific Ocean mixed-stock fisheries was impossible without a genetic characterization of Asian chum populations. Many aspects of understanding salmon life history, interspecies population structure and ecology in feeding areas in the Pacific Ocean demand knowledge about status and relative abundance of stocks from different continents and spawning regions. The application of mixed-stock fisheries identification techniques is revealing the migration routes of Pacific salmon of different origins in the Pacific Ocean.

The purpose of the present article is to summarize recently collected genetic data with previously published data (Winans et al. 1995) on Asian chum salmon, to characterize genetic diversity among local stocks, to estimate genetic flow and interspecies population structure and create a reliable baseline for identification of Asian chum populations in Pacific Ocean mixed-stock fisheries.

Up to 74 protein loci were screened in 57 sample collections (about 4 thousand fish) from the Northern

Coast of Okhotsk Sea, Chukotka, Northern, West and East Kamchatka, Sakhalin, Amur River, and Prymorie areas.

Genetic diversity was analyzed by several statistical methods - Cavally-Sforza and Edwards chord distances, Nei distances, multidimensional scaling and gene diversity analysis. Several well distinguished clusters were revealed. In general, they are in accordance with a geographical origin of populations. Clusters of the Anadyr River, Amur River and rivers from Sakhalin, Prymorie and Japan significantly differed from each other. In populations from the Northern part of the Okhotsk Sea and Kamchatka Peninsula the clustering of genetic traits is not so clear in spite of highly significant genetic differences among stocks. The G-test analysis revealed a highly significant heterogeneity within all geographical regions. The most different were the artificially reared populations of Sakhalin.

Estimates of genetic flow made by F-statistic analysis showed a significant correlation between gene flow and distances between river mouths ($r^2=0.208$, $P<0.001$).

An Attempt to Identify Okhotsk Sea Chum Salmon Origin and Life History by Means of Scale Features

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For the period of May 23 - October 10, 1994 scales of chum salmon were sampled that were caught by gillnets in the Pacific Ocean near Kuril Islands (Iturup-Urup-Simushir). For stock identification of the catches chum salmon scales were sampled from rivers Severyanka and Ilyushina (Kunashir), Rybatskaya and Kurilka (Iturup), Naiba (South Sakhalin), Tym (North Sakhalin), Taui and Kukhtui (north coast of the Okhotsk Sea) in 1994, and also from rivers Abashiri and Tokachi (North and South Hokkaido, respectively) in 1993. The most essential distinctions in biology of chum salmon of different populations are observed in terms of juvenile migrations from rivers and coastal feeding conditions. That is why main attention was paid to the peculiarities of scale growth in the area characterizing juvenile's sea life near home coasts. For emphasizing these peculiarities graphs describing the distance between the circuli of the first year of growth from different fish scales were compared so that circuli were being combined in order, from first sea annulus, but not from scale focus. Scales of only 4 yr old chum salmon were used for analysis. Circuli width graphs were identical for chum salmon of different rivers of the same area, but in comparing individuals from different areas, in 20 of 21 cases the distinctions were reliable. Four yr old fish from mixed catches were tested as separate groups with the same number of circuli inside each group. Individual fish

were counted as belonging to a population of chum salmon if the values of its circuli widths lay within the relevant confidence interval. From 474 fishes 224 have been identified, among them 123 - for some one region only, 56 - for two regions simultaneously, 31 - for three, 11 - for four, and 3- for five regions. The adjusted results show that the share of identified fish was less in groups with the most number of circuli, because scales of Hokkaido chum salmon of the 1993 return year and from two rivers only were used for the test.

During four years of observation for size and age composition of fish migrating to the Kuril straits no juvenile chum salmon were found. Probably chum salmon occur in the Okhotsk Sea only during the first and the last years of life. The rivers of South Hokkaido flow into the ocean far from the Okhotsk Sea. However some chum salmon from these rivers enter the Okhotsk Sea twice. Two zones of growth are seen on their scales in the first year of life. The large peak of the graph coincides with that of the Okhotsk Sea fish population. The small "peak", seen synchronously in all groups of chum salmon from Tokachi River, probably reflects fish putting on weight in ocean near Hokkaido. In the south-west part of the sea mature fish with such type of scales have been found in research catches that supports this idea.

Mark-recapture Estimation of Masu Salmon (*Oncorhynchus masou*) Smolt Numbers in the Masuhoro River, Northern Hokkaido

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In the spring of 1995 and 1996, a mark-recapture study was undertaken in the Masuhoro River to estimate the numbers of both wild and hatchery origin masu salmon smolts, that had been stocked the previous fall. A partial fence was installed in the Masuhoro River a short distance above the Soya Research Branch of the Hokkaido Fish Hatchery. Masu salmon smolts migrating downstream were diverted by the partial fence into rearing ponds at the Soya Branch. To sample migrating smolts below the partial fence, a rotary screw trap was operated 14.8 km downstream. In 1995, about 2,000 masu smolts were tagged with numbered streamer tags and released

at the upstream site, and 4% of tagged fish were recaptured at the downstream site. Population estimates were generated using the statistical program SPAS (Stratified Population Analysis System). Maximum likelihood estimates of the number of wild and hatchery origin smolts were 49,369 and 2,647 respectively. 95% confidence intervals were about 50% of the population estimates because of insufficient numbers of tagged smolts recaptured. In order to increase the accuracy and precision of the estimates, it is necessary to raise the sampling efficiency at each trapping site.

Change in Number of Sakhalin-Kuril Pacific Salmon in Connection with Hatchery Development

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For 50 years large changes in number of pink salmon reproducing in rivers of the Sakhalin-Kuril region have taken place. After the period of relatively stable reproduction when annual catches averaged 10-20 thousands tons between 1946-1970, considerable population growth occurred and, as a consequence, growth of catches. First peak of catches was observed in the second half of the 1970s. A second peak occurred at the end of the 1980s and beginning of the 1990s. For the period 1991-1995, pink salmon annual catch averaged 76 thousands tons. Changes of pink salmon catches differ between areas of the Sakhalin region. In north-western and north-eastern parts of the Sakhalin coast, in Terpenie Gulf and at Kunashir Island catch has increased 2-3 times, in south-eastern Sakhalin coast, Aniva Bay and at Iturup Island 6-7 times, while in south-western part of Sakhalin catches, in fact, did not change and even decreased in comparison with the

period 1965-1975.

We may suppose that change of stocks can be due as to general ecological causes and to development of fish culture. A six-fold times increase of catches was registered in regions possessing high-capacity hatcheries, and at Iturup Island catches increased 7-fold.

Construction of hatcheries, use of additional feeding for juveniles and optimum means for their release in natural waters favoured considerable growth of pink salmon numbers. Pink fishing is concentrated in places where hatcheries are located. Perfection of artificial propagation biotechnique caused the increase of return rates for pink salmon.

However, chum propagation has not led to considerable stock increase of this species up to the present time.

The Role of Riparian Vegetation in the Environment of Masu Salmon Juveniles, *Oncorhynchus masou*

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Much riparian vegetation in Hokkaido has been lost due to logging and construction activities. However, little is known how these activities influence habitat quality for masu salmon and their growth and survival. Shakotan River in midwestern Hokkaido was straightened to control floods in the middle reaches twenty years ago. As a result, riparian vegetation was lost from the streamside area. Fortunately, some of the riparian vegetation has recovered. The aim of this study was to estimate influences of a loss of riparian vegetation on stream temperature, and resultant consequences on growth and survival of masu salmon juveniles. Five study stations were established along the straightened stream to monitor changes in stream temperature, growth, condition factor and population density of juvenile masu salmon in 1994 and 1995. Stns. 0 (1995 only) and 1 were located in the upper reach where overhead tree cover varied between 30 and 60%. Stn. 2 was in the middle reach where there were

few riparian trees and overhead cover from grass was less than 15%. Stns. 3 and 4 were in the lower river with tree cover between 40 and 90%. The 1994 summer was so hot that stream temperature exceeded 20°C at Stns. 2, 3 and 4. Stream temperatures rose most rapidly in the middle reach with the least overhead cover. In contrast, the 1995 summer was cool and stream temperatures in Stns. 2-4 rarely exceeded 20°C. Masu salmon juveniles at Stns. 2-4 almost stopped growing, and their condition factor and population density also decreased from July to August in 1994. In contrast, masu salmon juveniles at Stns. 2-4 continued to grow and their condition factors rose from July to August in 1995. Furthermore, summer decreases in population density in this year were not higher than those in 1994. These results suggest that overhead cover by riparian vegetation contributes to maintaining low summer stream temperatures which enables rapid growth of masu salmon juveniles during the summer.

Regions of Optimal Reproduction of Pink Salmon

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Peculiarities of abundance dynamics of pink salmon often result in unsuccessful efforts to develop fishery forecasts and improve artificial propagation. Measures necessary to achieve success in fishery and artificial propagation of pink salmon require the consecutive solution of two tasks: 1) identification of regions of ecologically optimum conditions, and 2) determination of the environmental conditions favouring this optimum. To distinguish the regions of ecologically optimum conditions for pink salmon, we analysed the following reproductive parameters at the macro-scale: 1) effectiveness of reproduction (catch per square unit of spawning grounds); 2) complexity of population structure; 3) expressiveness of dominance phenomenon; 4) features of long-term variations in abundance. During the analysis we proceeded from an assumption that in the optimal zone one could observe the highest effectiveness of reproduction, the most complicated population structure, the least pronounced dominance phenomenon, and the least variable long-term changes in abundance. On the basis of analysis of the above parameters we concluded that Iturup Island was a zone of ecological optimum. In particular, a curve of long-term changes in abundance of pink salmon of Iturup Is. is smoothed and reflects variation with a

period of several decades. This indicates that reproduction of pink salmon of Iturup Island is determined first of all by long-term changes in oceanological regime and not by interannual variations of climatic conditions as it occurs in the continental regions of reproduction. In a broader sense, the whole south-western Sea of Okhotsk may be considered as a zone of optimum condition. Chukotski Peninsula and continental coast of the Sea of Okhotsk are zones of poor condition. Comparing the conditions of pink salmon existence in the zones of optimum and poor condition, one may conclude that reproduction of pink salmon is favored by: 1) proximity between oceanic feeding grounds and spawning grounds; 2) remoteness of spawning grounds from the continent and the stabilising influence of the ocean. Influence of the continent with the sharp seasonal changes in climatic conditions varying from year to year, presence of permafrost in some regions often negatively affect both the survival of embryos in the ground and conditions of juvenile survival in the beginning of their marine period of life. Duration of marine migrations of the juveniles may also negatively affect them. In contrast, the proximity of the ocean provides the stable conditions of existence.

XI. Closing Remarks

Thank you, Dr. Wakabayashi:

I appreciate this opportunity to deliver a few concluding remarks to this symposium, which represents a milestone in the relatively short history of NPAFC.

Dr. Low has very ably summarized the scientific presentations given over the past two days. There is, therefore, clearly no need for me to do so. Instead, with your permission, I would like to reflect briefly on the past and make a few comments on the future.

When the former INPFC initiated its research program some forty years ago, we knew little about the ocean distribution of salmonids in general and individual stocks or stock groups in particular. After some 35 years of research under the INPFC banner, we had learned a great deal about salmonid distribution and migrations in the ocean, and something about the factors affecting these life history features. But there is still much more to be learned in the area of species and stock interactions, and on the influence of oceanographic and ocean climatic factors on the abundance and distribution of salmonids. This is especially important in the face of anticipated ocean climate changes.

In the present symposium, the status of knowledge of stock conditions and of some of the factors affecting stock abundance, growth, and other related aspects of salmonid biology have been addressed. It will be left to the younger generation of scientists to build on this knowledge and to further our understanding of salmonid production, biology, and ecology in the North Pacific. I am sure that this symposium will not be the last to be organized by the member countries of the NPAFC to bring scientists of North Pacific countries together to share new information as it accumulates.

Long before the establishment of the NPAFC, our four countries had already initiated a series of scientific symposia on Pacific salmonids, with meetings having been held in Sakhalin, Alaska, and British Columbia. The present symposium and those that are certain to follow may be looked upon as an extension of those events started close to 20 years ago.

When I spoke at the closing of the inaugural meeting of the Committee on Scientific Research and Statistics of the NPAFC, which was held in

Vladivostok in June 1993, I noted that the participating scientists would be proud to tell their grandchildren of their involvement in that historic event, which heralded a new era of scientific cooperation among our four nations. I believe I can echo those words with respect to your participation in the first symposium organized under the auspices of the NPAFC.

I would be remiss if I did not take this moment to thank the many people involved with organizing the symposium, starting with Dr. Akira Taniguchi, Chairman of the Steering Committee, and the other members of the Steering Committee including Dr. Douglas Eggers (USA), Dr. Osamu Hiroi (Japan), Dr. Donald Noakes (Canada), Dr. Sergei Sinyakov (Russia), and Dr. Kiyoshi Wakabayashi (Japan), who personally carried a tremendous load during the course of the symposium to ensure its success. Thanks are also extended to the members of the local organizing committee, which included Dr. Yukimasa Ishida, Dr. Masahide Kaeriyama, Mr. Kiyoshi Katsuyama, Dr. Hiroshi Ueda, and Dr. Kohei Yamauchi for their attention to the numerous details associated with planning the symposium. And of course the members of the NPAFC Secretariat, under the directorship of Dr. Irina Shestakova, deserve our thanks and appreciation for their excellent administrative support. Particular mention must be made of Deputy Director Hisashi Endo's role throughout the period of development and organization of the symposium.

Before leaving the podium, on behalf of all of the symposium participants, I would like to offer a special word of gratitude to our Japanese hosts for their kind and generous hospitality during our stay in Sapporo. It is always a welcome pleasure to experience the warmth and generosity of our Japanese colleagues.

Finally, for those of you who are travelling out of Sapporo to return to your homes, I wish you a safe and pleasant journey.

Thank you and bon voyage.

Leo Margolis
First Chairman
Committee on Scientific Research and Statistics
1994-1996

X. Symposium Review

This symposium has been a successful venue to bring together 29 oral and 32 poster presentations on Pacific Rim salmonid stocks. It is clear from the presentations that salmon science has been examined from the most minute detail to the broad perspective of its ecosystem.

Historical catch records of the fisheries indicate that salmon has been important to the cultural activities and heritage of the people of four major nations that extends in an extensive geographical arc from northern Japan through the Russian Far East, to the entire coastal areas of Alaska, down to western Canada and farther south to northern California. In modern history, the salmon resource continues to feed the world, provides for a thriving commerce, and offers recreational experiences to millions of people.

The present World-wide catch of salmon amounted to 1.5 million metric tons annually, hatchery and wild-run fish combined. The North Pacific Rim catch amounted to almost 1 million metric tons of the total. By country, the percent catch contribution, by weight, averaged 48% by the United States, 27% by Japan, 20% by Russia, and 5% by Canada. Five salmonid species make up the bulk of the catch: pink (34%), chum (30%), sockeye (27%), coho (5%), and chinook (3%). The poster session by Dr. Irina Shestakova puts the gross value of the North Pacific salmon catch at more than \$1 billion annually.

This symposium has illustrated that there is successful hatchery technology to enhance natural runs of salmon stocks. Hatchery-reared salmon are being released into the North Pacific Ocean to augment natural salmon production and to rebuild depleted natural runs. The total number of juvenile salmon estimated to enter the North Pacific ocean system amounted to 20-30 billion fish per year. Hatchery releases accounted for 16-25% of the total. In 1995, hatchery releases were 5.2 billion fish. Forty-one percent of the hatchery releases were from Japan, 39% from the United States, 10% from Canada, and 10% from Russia. These fish went to sea and the survivors migrate back to their natal release areas as adult salmon.

Since the North Pacific ocean is the common grow-out area for juvenile salmon from all the North Pacific rim countries, the question of stock migration, distribution, and intermixing of the stocks has always captured the attention of scientists. During the days when high seas fishing operations were authorized, the subject of fish interception of one stock while fishing another was controversial among the user groups.

Since high seas salmon fishing has been prohibited under the international convention that established the NPAFC, the question of intermixing of

the stocks has remained important from a scientific point of view as more hatchery-raised fish are released into the ocean that would compete with stocks of many natural origins. As release numbers grow, they would affect the growth rates of fish and the overall carrying capacity of the oceans. Thus the distribution and migration of the stocks and research technology to identify fish from different stocks remain important science topics for the Commission.

The symposium also highlights the broader question of carrying capacity of the oceans and effect of environment on fish production. Can we produce more? What will be the impacts? We heard a report of interactions between juvenile chum salmon and fat greenling juveniles. We also heard a report of predation on salmon by salmon sharks. These presentations pointed out that prey-predator relationships are intricate and more research needs to be conducted among the ecologically related species.

Eventually, our studies of the oceans come back to the effects of Mother Nature. How do the various components of the environment affect salmon biology, population dynamics, and production? A speaker at the symposium stated that "Nature knows no bounds". However, mathematicians and computer simulation experts will attempt to simplify and simulate the ocean system. We heard a few reports on computer simulations. The take home message is pretty much the same -- we need more data and more research.

The NPAFC and its predecessor organization, INPFC, has provided the focal point for salmon research and coordination of national research programs on anadromous species in the North Pacific the past 40 years. This symposium indicates that such programs are still pertinent and the scientists have kept learning. We must all contribute freely to the advancement of salmonid science in the North Pacific Ocean because the salmon resource must be maintained to sustain our fish food supply, enhance our fisheries economy, and provide for recreational opportunities.

"Sustainable development" has been a global goal in recent years. In the North Pacific salmon case, such development should refer to the continued development of social and economic benefits to improve the quality of life associated with the use of the Pacific salmon resource. We must apply science to further achievement of this goal.

Loh-Lee Low
Chairman
Committee on Scientific Research and Statistics
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