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BULLETIN NUMBER 5

***Climate Change, Production Trends,
and Carrying Capacity of Pacific
Salmon in the Bering Sea and
Adjacent Waters***



**Edited by: E. Farley, Jr., T. Azumaya, R. Beamish, M. Koval, K. Myers,
K.B. Seong and S. Urawa**

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Maxim Koval, Katherine Myers, Ki Baik Seong, and Shigehiko Urawa**

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Preface

Dramatic fluctuations in the ocean growth and survival of many Asian and North American salmon populations over the past decade have been attributed to changes in the Bering Sea and other marine ecosystems. The absence of scientific observations for salmon, ecologically related species, and environmental conditions in the North Pacific Ocean has limited our understanding of these changes and how they affect salmon populations and economies around the Pacific Rim. International research efforts to address these issues were developed by the NPAFC, as part of its Science Plan. The research plan, called BASIS (the Bering-Aleutian Salmon International Survey), began in 2002 as a coordinated program of cooperative research on Pacific salmon in the Bering Sea. The goal of BASIS research was to clarify the mechanisms of biological response by salmon to the conditions caused by climate change in the Bering Sea.

The International Symposium on Bering-Aleutian Salmon International Surveys (BASIS): Climate Change, Production Trends, and Carrying Capacity of Pacific Salmon in the Bering Sea and Adjacent Waters was held in the Sheraton Seattle Hotel, Seattle, WA, USA on November 23-25, 2008. The Symposium was hosted by the North Pacific Anadromous Fish Commission (NPAFC) and organized by the Symposium Steering Committee (T. Azumaya, R. Beamish, E. Farley, Jr. (chairperson), K.B. Seong, V. Sviridov, and S.

Urawa) in cooperation with the NPAFC Secretariat. Local arrangements were made by the Local Organizing Committee (H. Bartlett, J. Helle, K. Myers, and J. Seeb) formed by the host country, the United States.

The purpose of the symposium was to summarize BASIS research conducted during 2002 to 2006 and increase our understanding about how climate change will affect salmon growth and survival in the North Pacific Ocean. The symposium topics were:

1. Overviews of Climate Change, Bering Sea Ecosystems, and Salmon Production
2. Biological Responses by Salmon to Climate and Ecosystem Dynamics
 - 2.1. Migration and Distribution of Salmon
 - 2.2. Food Production and Salmon Growth
 - 2.3. Feeding Habits and Trophic Interactions
 - 2.4. Production Trends and Carrying Capacity of Salmon

There were 34 oral, and 30 poster presentations followed by a session of discussion and summary on BASIS 2002-2006 (Where do we go from here?). This bulletin includes 33 papers which were peer reviewed and edited. Reviewers are listed at the end of the bulletin.

Opening Remarks

Birth of Bering-Aleutian Salmon International Survey (BASIS)

Fran Ulmer, President of NPAFC from 1999 through 2001, initiated discussions with members of the Committee on Scientific Research and Statistics (CSRS) that led to the formation of BASIS (Bering-Aleutian Salmon International Survey). I met with Fran several times during the Annual Meeting in Tokyo in 2000. Fran believed that the NPAFC was a unique organization that could provide the forum to support international research that would be beneficial to each nation. Her belief was that collaborative research supported by each nation with a common objective would provide more extensive research results than research accomplished by each country working independently. She asked me what were the major science issues within the CSRS? Were any of the major issues common to all the member countries?

Fran and I discussed the new ecosystems studies with emphasis on juvenile salmon in the Gulf of Alaska initiated by NOAA Auke Bay Laboratory's Ocean Carrying Capacity Program (OCC) in 1995. The OCC program worked with Canadian Department of Fisheries and Oceans biologists developing gear to sample juvenile salmon off shore. Large trawls towed near the surface proved to be successful in capturing juvenile salmon in the ocean along the continental shelf. Earlier, the Russians, Japanese, and Canadians had been successful in developing different types of surface nets to sample juvenile salmon in coastal and offshore waters. In the late 1990's, in response to declining ocean survival of sockeye salmon returning to Bristol Bay, the OCC program initiated early marine studies on juvenile sockeye salmon in the southeastern Bering Sea. I discussed these studies with Fran and also pointed out that western Alaska stocks of chum salmon in the Yukon and Kuskokwim rivers were declining and little was known of the early marine life history of North American salmon in the Bering Sea. Only a few small studies had looked at early marine survival of salmon in Bristol Bay and near the mouth of the Yukon River.

At the Annual Meeting in Tokyo Fran met with Kate Myers, University of Washington, several times and the three of us met several times. Fran talked with Canadian, Japanese, and Russian scientists about collaborative research at this time as well. Kate's extensive experience working with the Japanese in salmon research on the high seas in both the North Pacific Ocean and the Bering Sea provided an international background to our discussions. We discussed the declining stocks in the eastern Bering Sea that included not only sockeye salmon in Bristol Bay but also stocks of chum salmon from the Yukon and Kuskokwim rivers. At the same

time chum salmon stocks in Japan and Russia also were experiencing declines. The commonality of the use of the Bering Sea by Asian and North American stocks of salmon suggested that ocean conditions in the Bering Sea may be responsible for the declines.

Kate Myers initiated discussions in the Science Subcommittee (SSC) at the Tokyo meeting about our discussions of collaborative research in the Bering Sea. The SSC (V. Karpenko, Russia, Chair; R. Beamish, Canada; S. Urawa, Japan; and K. Myers, U.S.A.) drafted a new Science Plan and included in the plan suggested coordinated research by the Parties in the Bering Sea.

In early December 2000, Fran held a teleconference with U.S. delegates to the NPAFC to discuss the "Next Steps" towards further development of the NPAFC Science Plan, and "our common goal of more focused and more coordinated Bering Sea salmon research." Fran's call to action and identification of potential funding sources quickly led to development by the OCC staff (S. Ignell and E. Farley) and K. Myers of a new research initiative for international cooperative research on salmon in the Bering Sea. Kate Myers recommended the new international research program be called "BASIS" (Bering-Aleutian Salmon International Survey), because the results would provide a solid scientific foundation for addressing current and future research, management, and conservation issues concerning salmon in the Bering Sea.

Discussions with Fran about collaborative international research became more focused at the Research Planning and Coordinating Meeting (RPCM) in Seattle in March 2001, chaired by Y. Ishida of Japan. Kate and I met with Fran several times during this meeting. The United States presented its BASIS proposal, which was well received by international participants. Discussions continued in the SSC (M. Fukuwaka substituted for S. Urawa), and R. Beamish and K. Myers were tasked with developing a fully-coordinated BASIS research plan in two weeks (NPAFC Doc. 525). Shortly after the meeting, the draft BASIS plan was completed, reviewed and amended by all national parties, and submitted to F. Ulmer for her further consideration and use for seeking financial support.

At the 2001 Annual Meeting of the NPAFC in Victoria, Canada, plans for making BASIS a reality progressed. In the CSRS meeting, chaired by Y. Ishida, the draft BASIS plan developed in Seattle in April was expanded and the four countries – Canada, Japan, Russia, and the United States of America – agreed to plan and coordinate the new interna-

tional research plan (NPAFC Doc. 582). A BASIS Working Group (BWG) was formed to coordinate individual national plans and draft an “Annual Implementation Plan” for joint BASIS research. The BWG appointments were: Canada – R. Beamish; Japan- S. Urawa and T. Azumaya; Russia – V. Karpenko, S. Sinyakov, and V. Lapko; U.S.A. – J. Helle, D. Eggers, and K. Myers.

This was Fran’s final meeting as NPAFC President, and in her closing remarks she said, “The revolutionary BASIS science plan is an example of an approach that can provide valuable insights into salmon and their environment in a way that has not been previously attempted. We are moving quickly to become the cutting-edge of scientific collaboration for the new millennium. I believe BASIS will help us achieve this collaboration.”

The spring RPCM in 2002 was held on March 12–13 in Vancouver, British Columbia. The BWG prepared a detailed draft Agenda (NPAFC Doc. 592) for a major meeting to take place in Vladivostok, Russia, to plan the research and cruise activity for the summer/fall of 2002.

The BASIS Working Group Meeting in Vladivostok on May 27–28, 2002 was attended by additional delegates from each country (NPAFC Doc. 599). In addition to the official working group members, two from Canada, one each from Japan and the U.S.A., 14 from Russia and 3 from the Secretariat participated in the meeting. J. Helle was elected Chair of the BWG. Russia appointed O. Temnykh to replace V. Lapko on the official working group.

During the Vladivostok meeting detailed discussions were held about preparations for the upcoming field season. Financial support for BASIS research from internal and external sources was discussed. Vessel support for the extensive sampling would be provided by fisheries agencies in Japan and Russia – the *RV Kaiyo maru*, and the *RV TINRO*. The U.S.A. would charter two private fishing vessels, the *FV Northwest Explorer* for mid-ocean sampling and the *FV Sea Storm* for more coastal sampling. Because each country would use different nets for sampling during this ecosystem research in the epipelagic zone, detailed discussions concerned how and where to calibrate the gear between the three countries’ vessels. Discussions also took place on how to compare and calibrate different methods for sampling plankton, oceanography, salmon tagging, age and maturity, food habits and bioenergetics, migration and growth models, ecologically related species, parasites and diseases, and stock identification. Protocols for collecting samples and exchange of samples and data were discussed. Contact persons within each country were appointed for each sampling method. These people would coordinate the exchange of data and samples for each method. Timetables for reports, publications, workshops, and symposia were discussed. By the end of this meeting the plans and commitments were in place to launch ships from Japan, Russia, and the U.S.A. that would sample nearly the entire Bering Sea with synoptic surveys of

salmon. These three ships met near Attu in the remote western Aleutian Islands in 2002 to tow their nets side by side in the ocean swells to calibrate their gear. I will never forget the excitement expressed in the message I received from J. Murphy, Chief Scientist, aboard the *FV Northwest Explorer* about the sight and communications with each nation’s ships doing side-by-side cooperative research in the open ocean. It was a day that none of the participants will ever forget!

Fran delivered a keynote address, “BASIS as a Model for International Scientific Collaboration: the Project is Greater than Just the Sum of its Parts,” at the NPAFC’s BASIS Workshop in Sapporo, Japan, in October 2004 (NPAFC Tech. Rep. 6). In this address, she reminded us that “policy makers, regulators, fishermen, community leaders, university faculty, foundation and grant-giving organizations and media representatives must be educated about BASIS. They need to know about the progress underway at NPAFC to provide a new paradigm for international science and information sharing. I for one, plan to do so whenever the opportunity presents itself.”

At a 1-day symposium “Science Bridging Five Nations: The Bering-Aleutian Salmon International Survey,” held at the 2005 Annual Meeting of the American Fisheries Society in Anchorage, Alaska, Fran reviewed the history and importance of BASIS: “This process is unique in its level of cooperation and productivity. Although it has an unusual foundation: a treaty signed by the member nations enabling them to share data and resources for a common mission (the protection of anadromous fish), its success lies in something else: mutual trust and respect among the participating scientists and the shared vision that no one country can accomplish this mission alone.”

The Birth of BASIS can be attributed to the visualization, persistence, and international coordination of Fran Ulmer. She had a special ability to listen and talk to scientists from different countries and backgrounds and get them to plan and execute a cooperative research program that had a common goal that would provide mutual benefits to all the parties.



Photo by J.H. Davis

John H. (Jack) Helle
Chairman of the BASIS
Working Group (2002–2007)

Greetings

BASIS (Bering-Aleutian Salmon International Survey) evolved out of a shared goal: to learn more about the complex Bering Sea ecosystem and how changing conditions, caused in part by climate change, are impacting salmon and inter-related species. NPAFC scientists were interested in migration patterns, feeding patterns, juvenile survival and growth, and many other areas of research. Since no one nation had sufficient resources to do all of the data accumulation and analysis that was needed, and since salmon move over vast areas beyond any one nation's boundaries, the idea of sharing research efforts evolved. This could not have happened without the mutual respect and trust of the researchers

from the member nations that grew over time.

A great deal has been accomplished through BASIS, in spite of meager funding. I am proud that I was able to play a small role in helping to get it launched, and I am glad that it continues today.

I have two hopes for the future: 1) that BASIS will obtain some additional funding to continue data collection and help analyze, publish and disseminate the results of the research that is done on the Bering Sea. 2) that BASIS will be used as an example of international, collaborative research for other regions of the world.



*Fran Ulmer
Former NPAFC President*

Distribution and CPUE Trends in Pacific Salmon, Especially Sockeye Salmon in the Bering Sea and Adjacent Waters from 1972 to the mid 2000s

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Abstract: We present the mean CPUE distributions of five species of Pacific salmon in the Bering Sea and adjacent waters, based on long-term data from Japanese research-gillnet operations, 1972–2002. Many populations of three abundant Pacific salmon species (pink, chum, and sockeye salmon), have feeding migrations in the Bering Sea. There are two distinct patterns in the fluctuations in CPUE of major North Pacific salmon species in the Bering Sea. The CPUEs of pink and Chinook salmon increased after 1988 and remained high to 2005. The CPUEs of sockeye and chum salmon were low prior to 1977, peaked in 1980, declined until 1989, and then increased again until 2005. The trends in CPUE of sockeye and chum salmon seem to coincide with fluctuations in Bering Sea sea surface temperatures (SST) with higher densities of sockeye and chum salmon in the Bering Sea during warm periods and lower densities during cool periods, especially in sockeye. These increases and decreases in CPUE seem to coincide with the hypothesized regime shifts in 1977 and 1989. We also discuss the effects of the semi-decadal fluctuations in the Bering Sea SST, and related fluctuations in sockeye salmon abundance.

Keywords: horizontal distribution, CPUE trends, SST, Bering Sea, sockeye salmon

INTRODUCTION

Japanese high-seas salmon research has been conducted since 1952. Until recently, we used research driftnets as the standard gear for most salmon research programs (Takagi 1975). We have many data from these surveys that were conducted during the months of June, July and August (Ishida and Ogura 1992). The Bering-Aleutian Salmon International Surveys (BASIS) began in 2002, and was designed to cover both the high seas and waters within the 200 naut. mi. limit of the USA and Russia in the Bering Sea using a surface trawl net. Today the surface trawl net is the semi-standard fishing gear for salmon research in the North Pacific Ocean. Although, the time series data obtained from trawl net surveys are not yet adequate, Japanese gillnet surveys will likely decrease in the near future because of the high cost of supporting both trawl and gillnet surveys for salmon. Studies on the horizontal distribution of major Pacific salmon species using data from Japanese research gillnet surveys have been reviewed (Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978; Takagi et al. 1981). However, the results of Japanese research cruises conducted after 1972 are

not well described in these articles. In this paper, we present a retrospective analysis of driftnet data collected from 1972 to 2008, especially on the distribution of each species, classified by age. We think mean CPUE horizontal distribution patterns by species, by month, and by ocean age will be a helpful tool for further understanding the nature of Pacific salmon.

After the late 1980s many researchers described the synchrony observed between fish stock fluctuations and climate fluctuations (e.g., Kawasaki et al. 1991). Beamish and Bouillon (1993) introduced the relationships between Pacific salmon catches and decadal-scale climate trends. The Bering Sea is a major feeding area for the many economically important salmon stocks of both Alaskan and Asian origin. While there is coherence in long-term trends in climate change effects on salmon production at basin scales, analysis of CPUE trends in this area may further contribute to our knowledge of relationships between salmon population abundance and climate change.

The objectives of this paper were to 1) map CPUE in relation to sea surface temperature (SST) by age and month, 2) compare temporal trends in CPUE by species, 3) compare

temporal trends in CPUE and SST, 4) compare CPUE and fork length of sockeye salmon (*Oncorhynchus nerka*) to the Bristol Bay sockeye salmon catch, and 5) compare sockeye salmon fork length to walleye pollock (*Theragra chalcogramma*) abundance.

MATERIAL AND METHODS

We analyzed catch data obtained by Japanese research-gillnet operations (Takagi 1975) for distribution patterns in mean CPUE from 1972 to 2002, because Japanese research-gillnet operations have decreased since 2002. To describe the distributions, we stratified the whole area by 2-degree latitude and 5-degree longitude grid sections, following Azumaya and Ishida (2000). We calculated the long-term mean density of each species by age group and month. We used the mean CPUE for each month for the density index. The mean CPUE in each grid was calculated as follows:

$$\text{CPUE} = \text{total catch in number} / \text{total effort (in units of 30 tans of research-gillnet)}.$$

Mean monthly SST data were provided for $2^\circ \times 2^\circ$ grids from 1972 to 2002 by the Japan Meteorological Agency. The proportions of maturing and immature fish in each grid were calculated based on maturity definitions that are based on gonad weight (Takagi 1961; Ishida et al. 1961; Ito et al. 1974). We estimated fish age by scale observations following Ito and Ishida (1998). In this paper we used the "European" system for age designation, in which the winters in fresh water after hatching and the winters in sea water are identified and separated by a period. Because estimated freshwater ages of sockeye and Chinook salmon (*O. tshawytscha*) varied by reader, we did not determine freshwater ages of sockeye and Chinook but we did use ocean ages. In these cases, an x.2 fish has spent an unknown number of winters in fresh water, and two winters in sea water.

Although the main research areas of Japanese research-gillnet operations have been restricted since 1992, we have been able to maintain the summer research operations in the Bering Sea. Therefore, we analyzed the mean July CPUE in the Bering Sea from 1972 to 2008 to obtain the long-term density trends in salmon in the Bering Sea. To detect the trends in decadal fluctuation patterns or longer-term trends, we used five-year running means (5YRM) for both salmon CPUE and SST. A five-year running mean is an effective filter to exclude annual fluctuations.

The Bristol Bay sockeye salmon stock is a large stock in the North Pacific. We used commercial catch statistics for Bristol Bay as an index of sockeye salmon abundance. We compiled this catch data from INPFC Statistics Year Books, NPAFC Statistics Year Books, and from Eggers (2004) for 1993. We also calculated the annual mean fork length (FL) of sockeye salmon of each ocean age caught by Japanese research-gillnet operations in July. The mean FL in each year was calculated as the arithmetic average of all samples from

Japanese research-gillnet operations in the Bering Sea in July. We also calculated the growth rate of sockeye salmon between age x.1 and x.2 as: growth rate of t year = average fork length of age x.2 sockeye salmon in July in t year – average fork length of age x.1 sockeye salmon in July in t - 1 year.

RESULTS

Horizontal Distribution of Sockeye Salmon Mean CPUE

Most age x.1 sockeye salmon were immature. In June, age x.1 sockeye salmon were mainly distributed in the North Pacific Ocean where SST ranged from 5–8°C; a few were distributed in the Bering Sea, but few in areas < 5°C (Fig. 1). In July, some portion of immature age x.1 sockeye salmon entered the Bering Sea, but the rest remained in the North Pacific Ocean either along the Aleutian archipelago, or in the Gulf of Alaska. The SST over most of the distribution area ranged from 7–10°C, but ranged from 9–12°C in the Gulf of Alaska. In August, most age x.1 sockeye salmon appeared along the Aleutian archipelago and the eastern coast of Kamchatka. The catch of age x.1 sockeye salmon occurred at temperatures < 11°C.

In June, catch of age x.2 sockeye salmon mainly occurred in waters ranging from 5–8°C (Fig. 2). Around the eastern part of the Aleutian archipelago and the Alaska Peninsula, especially in the eastern Bering Sea near Bristol Bay, CPUE of maturing sockeye salmon was high. In other waters, the proportion of maturing fish was < 50%. In July, age x.2 sockeye salmon CPUE was high around the Alaska Peninsula and the eastern portion of the Gulf of Alaska. The proportion of maturing fish was also high around Kamchatka, but CPUE was not high. The CPUE of immature age x.2 sockeye salmon was high in the North Pacific Ocean along the Aleutian archipelago. The catch of immature age x.2 sockeye salmon occurred in waters at 7–9°C, and the catch of maturing age x.2 sockeye salmon in waters at 7–12°C. In August, a small catch of maturing age x.2 sockeye salmon occurred around Kamchatka, but they were not found in the other waters. A catch of immature x.2 sockeye salmon occurred in both the Bering Sea and North Pacific Ocean at 8–11°C.

Most age x.3 sockeye salmon were maturing fish. In June, the catch of age x.3 sockeye salmon occurred in waters at 3–9°C, and CPUE was high around the Alaska Peninsula and along the eastern Aleutian archipelago (Fig. 3). In July, maturing age x.3 sockeye salmon occurred in waters at 7–12°C, with two high CPUE areas, one around the Alaska Peninsula, and another near Kamchatka. In August, a few maturing sockeye salmon were distributed around Kamchatka, the Aleutian archipelago, and northern waters of the Bering Sea, but none occurred in the central portion of the Bering Sea.

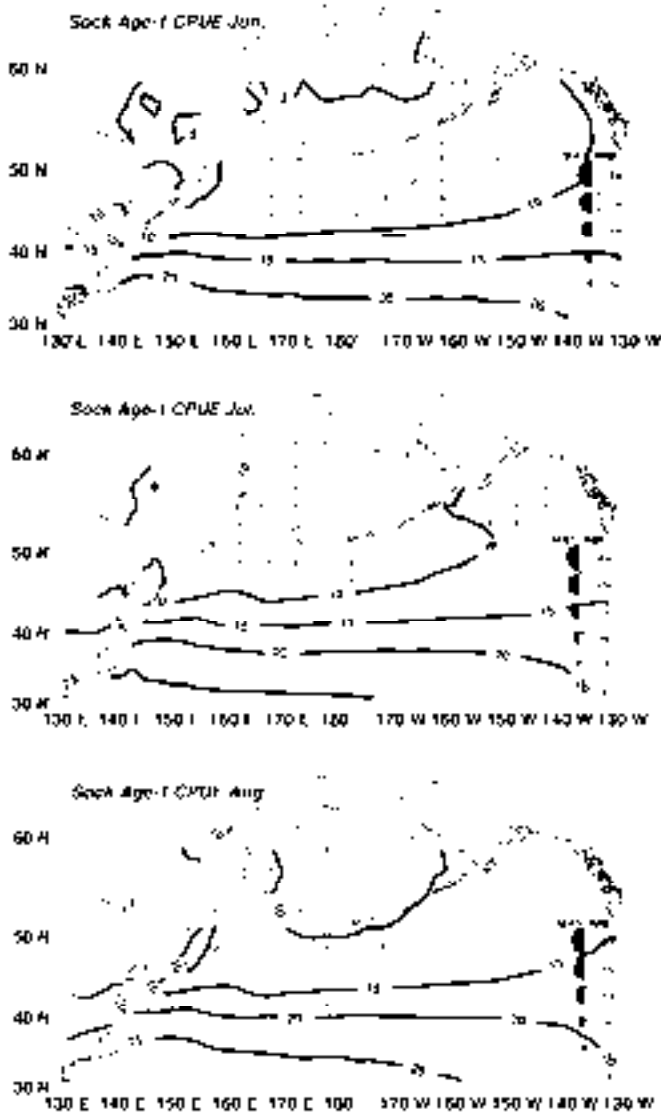


Fig. 1. Monthly ocean distribution of ocean age .1 (x.1) sockeye salmon in the North Pacific Ocean. Circle size indicates catch per unit effort (CPUE). Solid symbols indicate maturing fish (MAT), open symbols indicate immature fish (IMM), X indicates 0 CPUE. Lines indicate Sea Surface Temperature (SST).

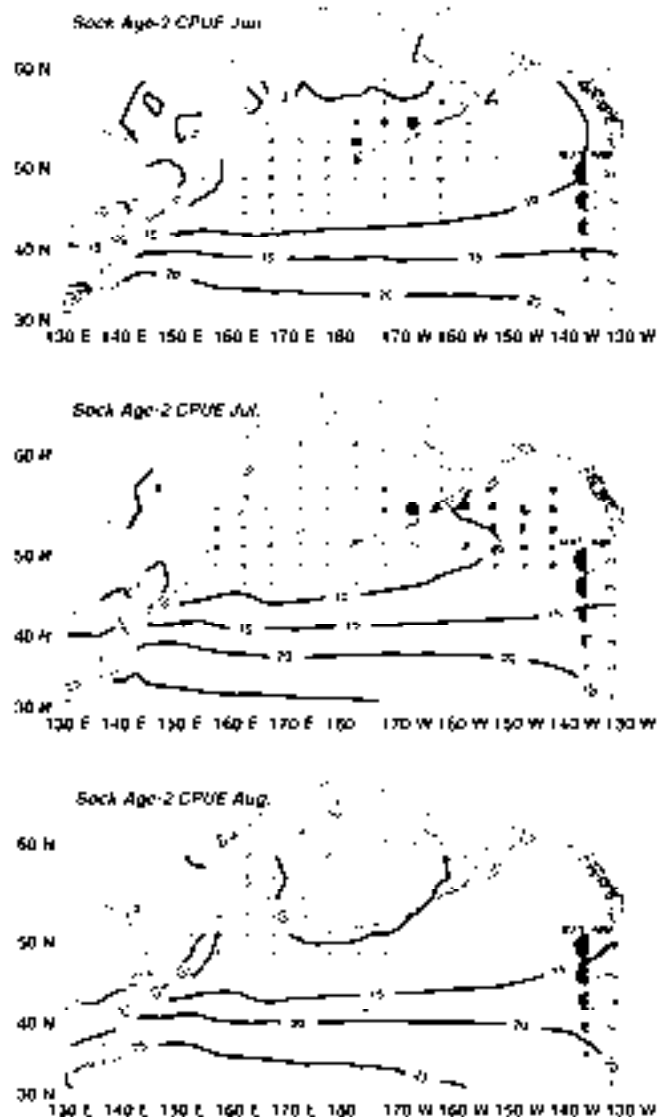


Fig. 2. Monthly ocean distribution of age x.2 sockeye salmon in the North Pacific Ocean. Symbols as in Fig. 1.

Horizontal Distribution of Chum Salmon Mean CPUE

Most age 0.1 chum salmon (*O. keta*) were immature. In June, the distribution of age 0.1 chum salmon occurred in waters at 5–10°C, but did not occur in the Bering Sea (Fig. 4). In July, the catch of age 0.1 chum salmon occurred broadly in waters at 7–12°C. High densities were recorded in the central part of the Bering Sea and the central North Pacific between 170°E–170°W, but few occurred in the eastern Bering Sea. In August, the catch of age 0.1 chum salmon mainly occurred in waters < 12°C. High CPUEs occurred in the central and northeastern Bering Sea.

In June, the catch of age 0.2 chum salmon mainly occurred in waters at 6–10°C (Fig. 5). Small catches also

occurred in waters at 3–6°C including the Bering Sea, and 10–13°C. No catch occurred in the northwestern portion of the Gulf of Alaska. The proportion of maturing fish was < 25 % in all waters. In July, catches of age 0.2 chum salmon occurred broadly in waters at 7–15°C. High CPUEs occurred in the central Bering Sea at 7–8°C, and in the Gulf of Alaska at 10–12°C. Around Kamchatka, the proportion of maturing fish was higher than in other waters. In August, catches of age 0.2 chum salmon occurred in waters < 15°C. High CPUEs occurred in the Bering Sea.

In June, catches of age 0.3 chum salmon occurred in waters < 17°C. The catches of immature age 0.3 chum salmon only occurred in waters at 5–9°C (Fig. 6). The proportion of maturing chum was higher in coastal areas on both sides

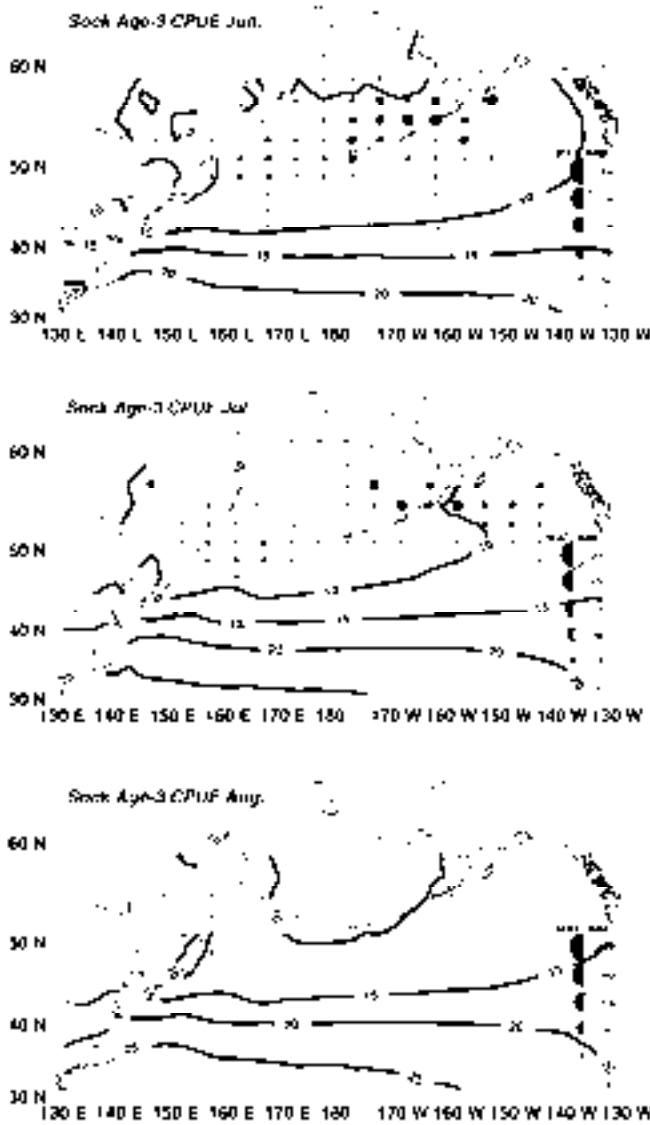


Fig. 3. Monthly ocean distribution of age x.3 sockeye salmon in the North Pacific Ocean. Symbols as in Fig. 1.

of the North Pacific Ocean than in offshore waters. In July catch of age 0.3 chum salmon occurred in waters < 13°C. The two areas of high CPUE were around Kamchatka and in the Bering Sea. The proportion of maturing chum salmon was high in the waters around Kamchatka and near Bristol Bay. In August, the catch of age 0.3 chum salmon occurred in waters < 14°C. The proportion of maturing fish was lower than that in July.

Most age 0.4 chum salmon captured were maturing. In June, the catch of age 0.4 chum salmon occurred in waters at 3–17°C (Fig.7). High CPUEs occurred near Bristol Bay, the central Bering Sea, and around Kamchatka. In July, catches of age 0.4 chum salmon occurred in the Bering Sea in waters at 7–9°C; CPUE was low elsewhere. In August, catches of age 0.4 chum mainly occurred in waters at 10–12°C in the

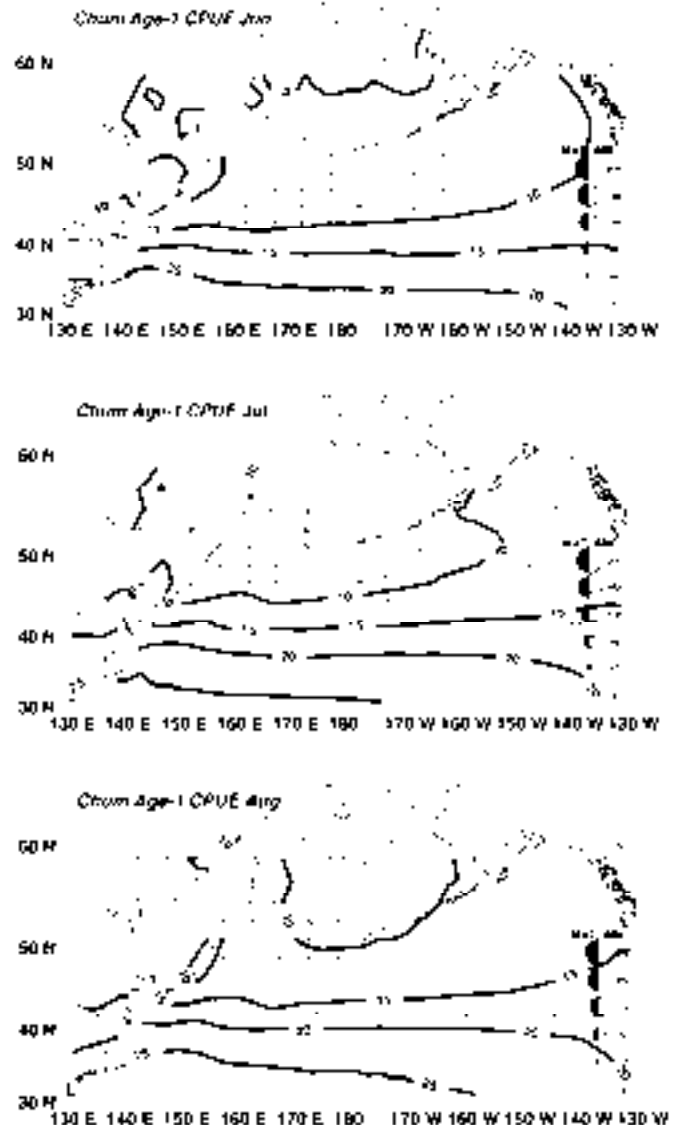


Fig. 4. Monthly ocean distribution of age 0.1 chum salmon in the North Pacific Ocean. Symbols as in Fig. 1.

central North Pacific Ocean between 160°W and 180°; few were captured elsewhere.

Horizontal Distribution of Pink Salmon Mean CPUE

Because they have a two-year life span, all pink salmon (*O. gorbuscha*) caught in research-gillnet operations were maturing. In June, catches of pink salmon occurred broadly in waters at 3–17°C, and high CPUEs occurred in waters of the western North Pacific at 5–10°C (Fig.8). In July, two areas of high CPUE distribution occurred, one in the western North Pacific, especially around Kamchatka at 8–11°C, and another in the central Bering Sea at 6–7°C. In August, catches of pink salmon only occurred in waters off the Asian coast.

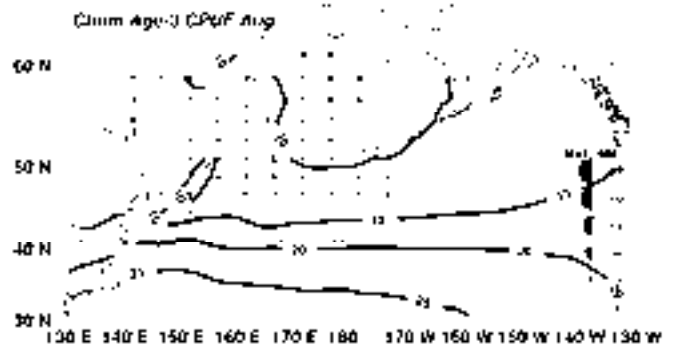
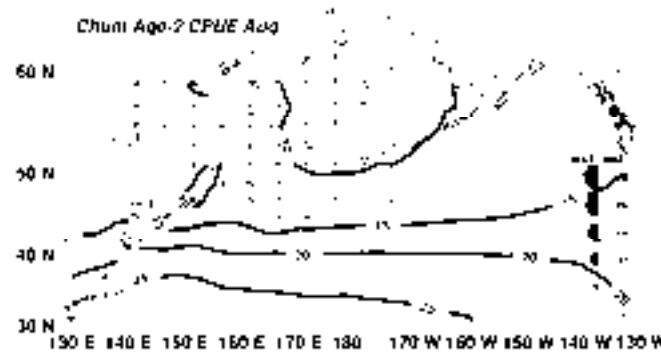
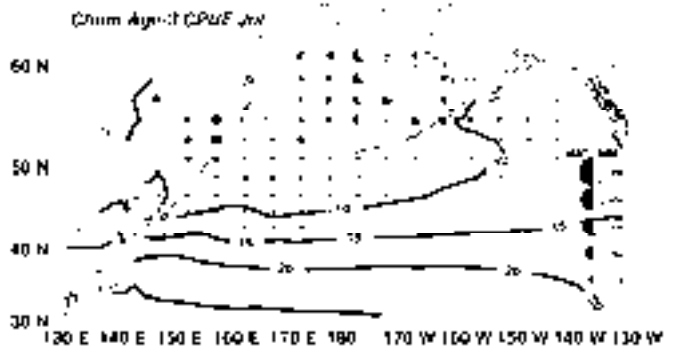
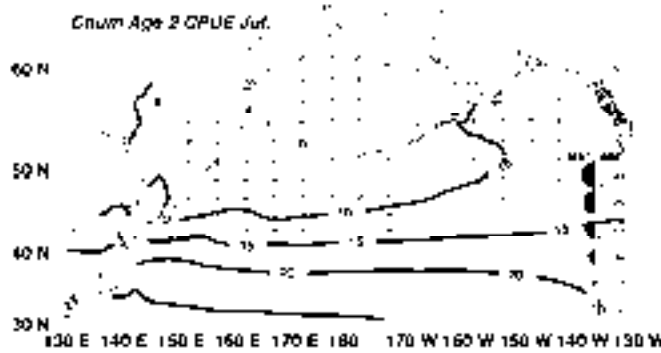
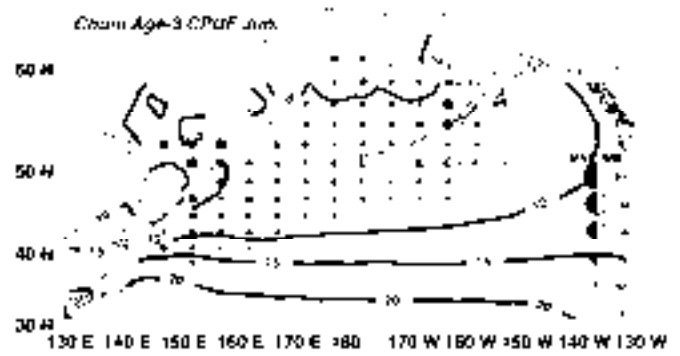
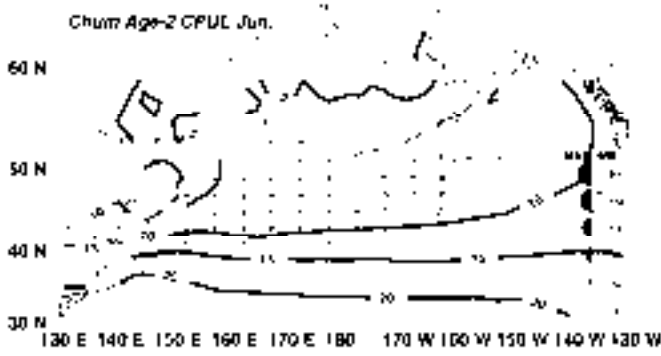


Fig. 5. Monthly ocean distribution of age 0.2 chum salmon in the North Pacific Ocean. Symbols as in Fig. 1.

Fig. 6. Monthly ocean distribution of age 0.3 chum salmon in the North Pacific Ocean. Symbols as in Fig. 1.

Horizontal Distribution of Coho Salmon Mean CPUE

All coho salmon (*O. kisutch*) caught by research-gillnet operations were maturing, because their growth period includes one winter in the sea. In June, catches of coho salmon occurred in waters at 5–13°C. The high CPUEs occurred at 7–11°C in the central North Pacific between 160°E and 160°W. CPUEs were low in other waters. Few catches occurred in the Bering Sea. In July, catches of coho salmon occurred at 7–16°C, however, coho salmon were rare in research-gillnet samples. In August, catches of coho salmon occurred in waters at 8–14°C. Coho salmon CPUEs around Kamchatka were higher than those in the central North Pacific.

Horizontal Distribution of Chinook Salmon Mean CPUE

In June, the catch of age x.1 Chinook salmon occurred in waters at 3–7°C in the Bering Sea, and 6–9°C in the central North Pacific (Fig. 10). In July, the catch of age x.1 Chinook salmon occurred in waters at 7–11°C. In August, catches of age x.1 Chinook salmon occurred in waters < 13°C.

In June, catch of age x.2 Chinook salmon occurred widely at temperatures > 2–10°C, including the North Pacific, Bering Sea, Okhotsk Sea, and Gulf of Alaska (Fig. 11). In July, the catch of age x.2 Chinook salmon occurred widely at 7–12°C. In August, the catch of age x.2 Chinook salmon occurred in waters < 13°C.

In June, catches of age x.3 Chinook salmon occurred

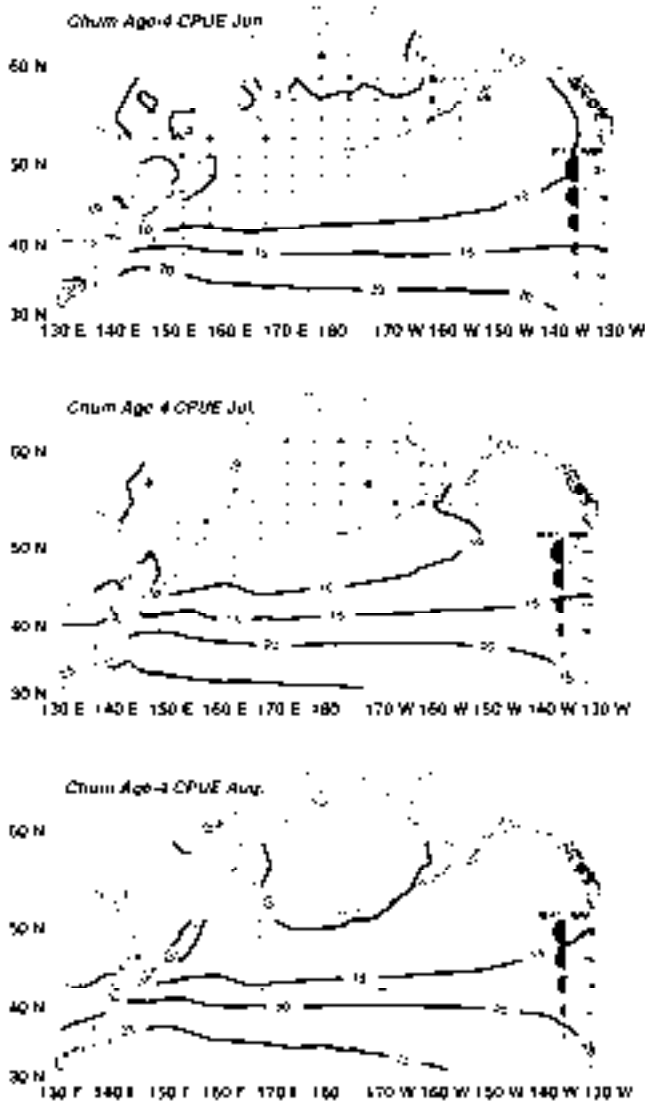


Fig. 7. Monthly ocean distribution of age 0.4 chum salmon in the North Pacific Ocean. Symbols as in Fig. 1.

in waters at 3–10°C in the Bering Sea, the North Pacific, and the Sea of Okhotsk (Fig. 12). In July, age x.3 Chinook salmon occurred widely at temperatures < 12°C. In August, catches of age x.3 Chinook salmon were small, but occurred in waters < 12°C.

The catch records of age x.4 Chinook salmon in research gillnets were few. In June the catch of age x.4 Chinook occurred in waters at 4–8°C (Fig. 14). In July the highest catch of age x.4 Chinook salmon occurred at 7–8°C in the Bering Sea, and at 9–10°C in the western North Pacific. In August, catches of age x.4 Chinook salmon were not recorded anywhere.

CPUE Fluctuation of Salmon in the Bering Sea

There were two patterns of CPUE fluctuation, one for sockeye and chum salmon (Fig 14A), the other for pink and

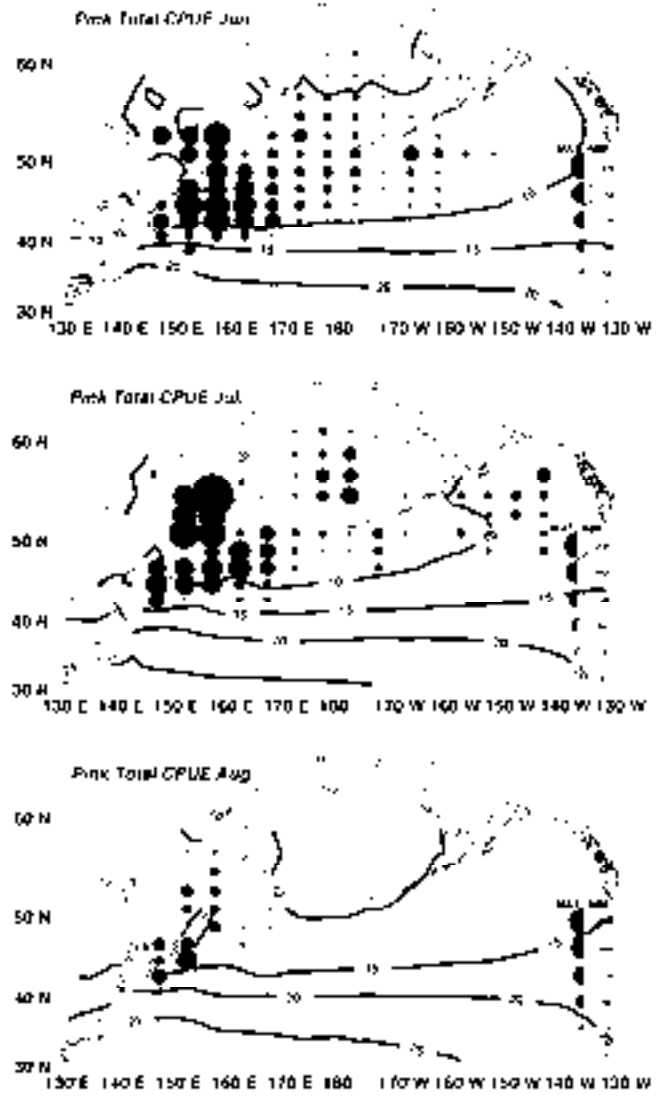


Fig. 8. Monthly ocean distribution of age 0.1 pink salmon in the North Pacific Ocean. Symbols as in Fig. 1.

Chinook salmon (Fig. 14B). Until 1977, the CPUEs for sockeye and chum salmon were low; they then became high by 1980, became low again by 1989, and then became high until the present. The CPUEs of pink and Chinook salmon became high and remained so after 1988; prior to 1988 CPUEs were consistently low (Fig. 14B). Among these four species, the 5-year running mean (5YRM) CPUE trends in sockeye and chum salmon were similar to the 5YRM SST fluctuation, especially in sockeye (Fig. 15). It seems that sockeye salmon density was higher in warm periods than in cool periods in the Bering Sea. There was positive linear correlation between 5YRM SST and 5YRM CPUE of sockeye salmon (Fig. 16).

After 1980, commercial catches of the sockeye salmon in Bristol Bay have remained at high levels (Fig. 17). The five-year running mean of sockeye commercial catches after 1980 had two modes, one was in 1983, and the other was in

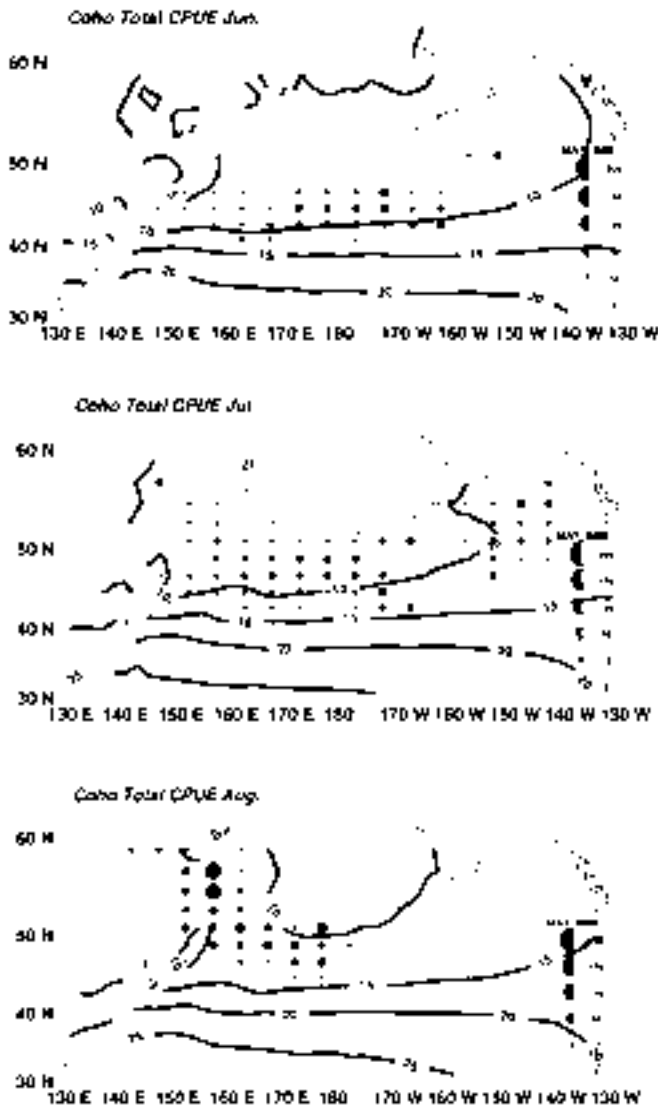


Fig. 9. Monthly ocean distribution of age x.1 coho salmon in the North Pacific Ocean. Symbols as in Fig. 1.

1994. The 5YRM CPUE of sockeye salmon by Japanese research-gillnet operations also had two modes: one was in 1981 and the other was in 1995. The high and low fluctuation patterns of both index values were very similar.

Size Trends of Sockeye Salmon Caught in the Bering Sea

The mean FL of age x.1 sockeye salmon in the Bering Sea was low between 1972 and 1976 (excluding 1973 (Fig. 18)). After 1977, the mean FL became larger (exceeding 340 mm) until 1984. In 1986, the mean FL of age x.1 sockeye salmon was the smallest (about 290 mm), and then increased up to 1994. After 1995, the mean FL of age 0.1 sockeye salmon fluctuated between 319–348 mm. The trends in mean FL of age x.2 and older sockeye salmon were opposite

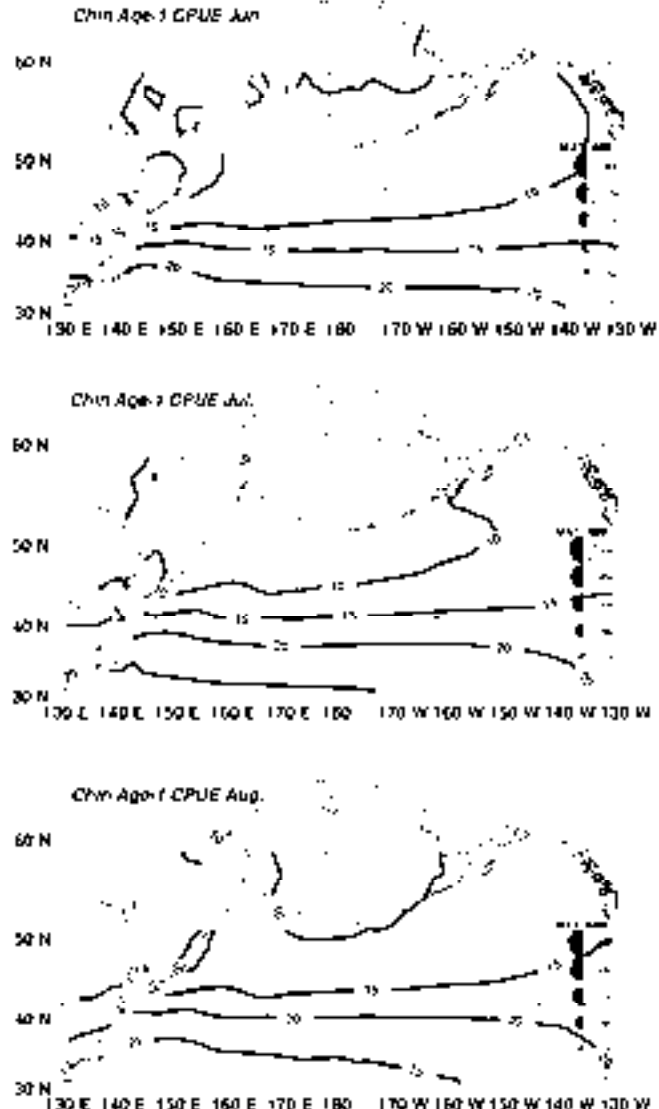


Fig. 10. Monthly ocean distribution of age x.1 Chinook salmon in the North Pacific Ocean. Symbols as in Fig. 1.

to the trend in age 0.1 fish. The mean FL of age 0.2 sockeye salmon was largest in 1976, and exceeded 510 mm between 1986 and 1990. The trend in mean FL of age x.3 sockeye salmon was similar to that of age x.2. The calculated growth between age x.1 and x.2 were large from 1974–1977 and 1986–1989. During these periods, mean FL of age x.1 sockeye salmon was small.

Although the mean FL of age x.1 sockeye salmon fluctuated annually, 5YRM showed clear oscillations. The oscillation pattern of the 5YRM of FL of age x.1 sockeye salmon showed two peaks, one in 1978–1983 and the other in 1992–1995 (Fig. 19). The peaks and valleys of this oscillation pattern were similar to the trends in 5YRM commercial catches of Bristol Bay sockeye salmon.

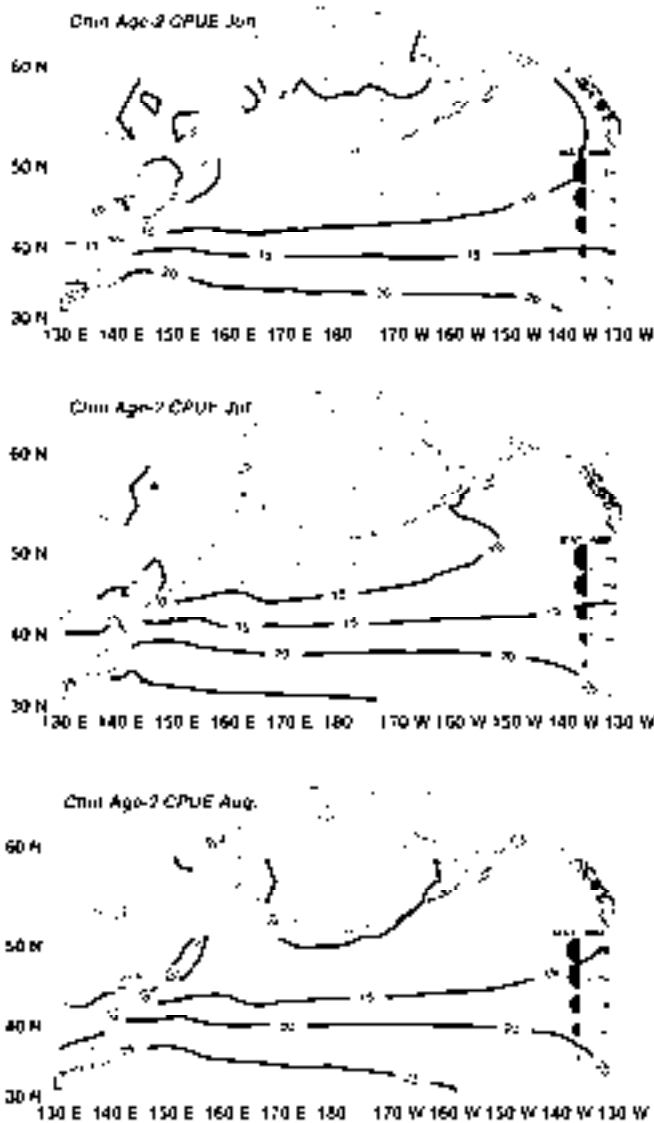


Fig. 11. Monthly ocean distribution of age x.2 Chinook salmon in the North Pacific Ocean. Symbols as in Fig. 1.

DISCUSSION

After overwintering, many populations of Pacific salmon migrate to the Bering Sea to feed. During the summer, age x.1 and age x.2 immature sockeye salmon appeared in the central Bering Sea, although some part of the population remained around the Aleutian archipelago. Recent genetic analysis has revealed that most immature sockeye salmon sampled in the central Bering Sea, were Bristol Bay stocks (Habicht et al. 2005). Thus, both the Bering Sea and the southern portion of the Aleutian archipelago are important feeding grounds for Bristol Bay sockeye stocks. Horizontal distribution patterns in this study showed that older chum salmon intrude into the cool Bering Sea earlier than younger chum in spring, but in summer, the most abundant salmon in the Bering Sea was age 0.1 chum salmon and the second

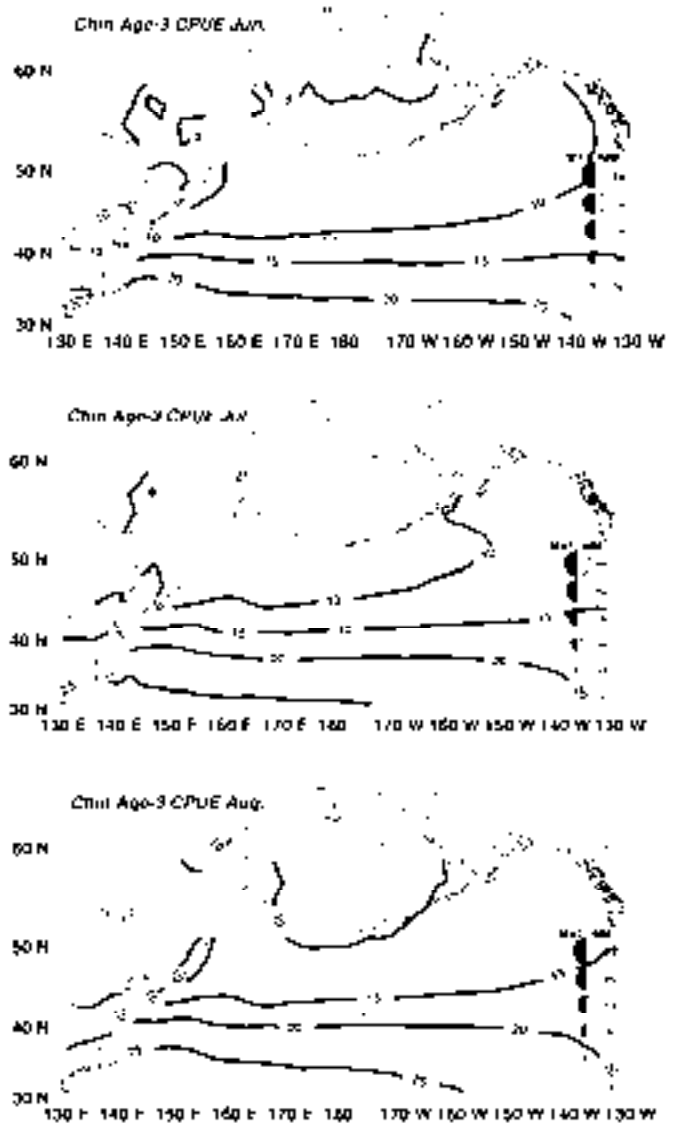


Fig. 12. Monthly ocean distribution of age x.3 Chinook salmon in the North Pacific Ocean. Symbols as in Fig. 1.

was age 0.2 immature chum salmon. Maturing pink salmon were more abundant in the western part of the North Pacific than in the Bering Sea. Although maturing pink salmon of eastern Kamchatka and western Alaska stocks appear in the Bering Sea in June (Myers et al. 1996), they must return to their natal rivers by August. Maturing coho salmon were relatively rare in the Bering Sea in each month, but abundant in the northern North Pacific Ocean. Although Chinook salmon were rather few, they occurred widely in the Bering Sea and northern North Pacific Ocean from June to August. It seems that the Bering Sea is not an important feeding area for most stocks of coho salmon. Although there are many maturing pink salmon feeding in the Bering Sea, their feeding period is shorter than that of other Pacific salmon which have a longer ocean life. Immature and maturing Chinook salmon appear in all seasons in the central Bering Sea, but

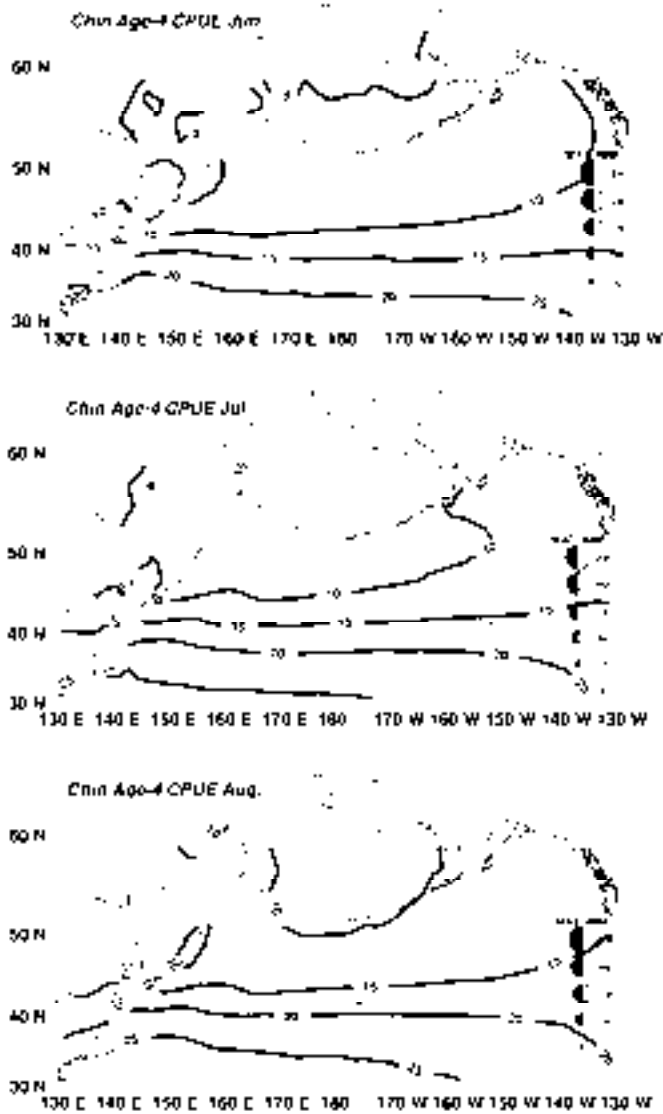


Fig. 13. Monthly ocean distribution of age x.4 Chinook salmon in the North Pacific Ocean. Symbols as in Fig. 1.

the species is not abundant. The Bering Sea is an important feeding area for salmon which have a long ocean life period (chum, sockeye and Chinook salmon). For other salmon, the subarctic region of North Pacific Ocean is a more important area than the Bering Sea, as a feeding migration area.

Azumaya et al. (2007) described the upper and lower thermal limits for 5 Pacific salmon (sockeye, chum, pink, coho, and Chinook salmon) based on data from several BASIS cruises and Japanese research-gillnet operations, however ocean-age differences in thermal limits for each species were not considered. In this study, we showed the different distribution patterns for each ocean-age class. For example, in June, age 0.1 chum salmon occurred at temperatures > 5°C; older chum salmon occurred in waters < 4°C. Apparently, older chum salmon enter the cool Bering Sea earlier than younger chum.

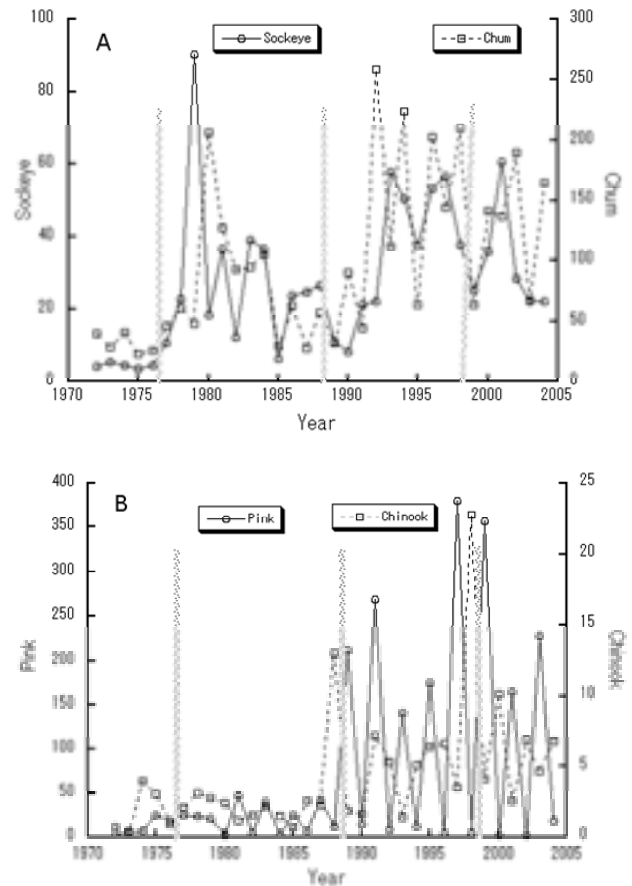


Fig. 14. Mean July CPUE trends in Japanese research-gillnet surveys for four Pacific salmon species in the Bering Sea. Panel A shows sockeye and chum salmon, and Panel B, pink and Chinook salmon. Pale gray vertical lines indicate the hypothesized regime shifts.

In this study, we showed the time series of fluctuations in CPUE in salmon and SST in the Bering Sea from 1972 to recent years. There are two patterns in CPUE fluctuation, one for pink and Chinook salmon, the other for sockeye and chum salmon. The CPUE of pink and Chinook salmon increased and remained at high levels after 1988. Before 1988, the mean CPUE for these two species was rather low. The regime shift in 1988/1989 might have affected the change in these CPUE trends. Based on tagging experiments, most Chinook salmon distributed in the central Bering Sea belong to either the Arctic-Yukon-Kuskokwim (AYK) or Bristol Bay stocks (Major et al. 1978; Myers et al. 1984). However, our CPUE time series trend was very different from the commercial catches of the AYK and the Bristol Bay stocks.

In our data, the 5YRM CPUE trends in sockeye and chum salmon are similar to the 5YRM SST fluctuation. It seems that sockeye salmon densities were higher in warm than in cool periods in the Bering Sea. Some researchers have hypothesized that the ocean condition shifted to a high production regime in 1977 and then shifted back to a low production regime in 1989 (Beamish and Bouillon 1993; Hare and Mantua 2000). However, during the hypothesized

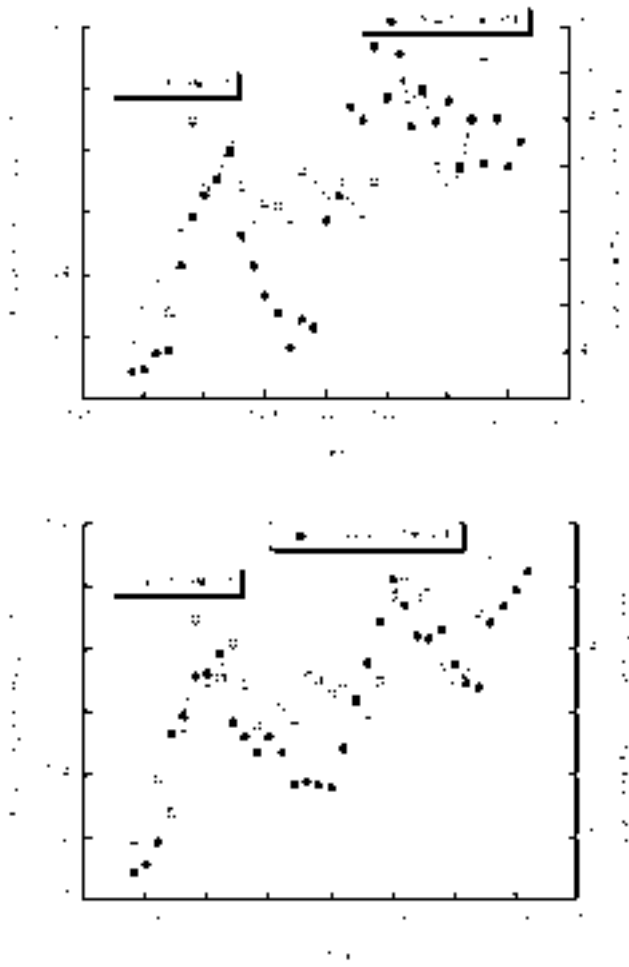


Fig. 15. Trends in 5-year running means (5YRM) for July CPUE (Japanese research vessels) of chum (upper panel), and sockeye (lower panel) salmon in the Bering Sea. Hatched lines indicate the 5-year running mean of July sea-surface temperatures in the Bering Sea.

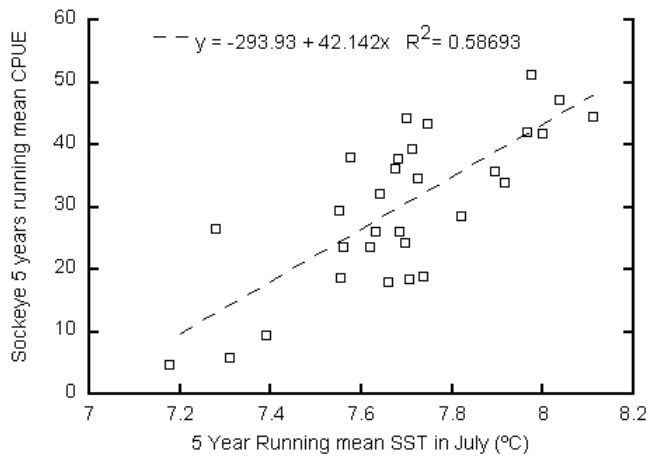


Fig. 16. Relationship between July 5YRM CPUE (Japanese research vessels) in the Bering Sea, and July 5YRM SST in the Bering Sea.

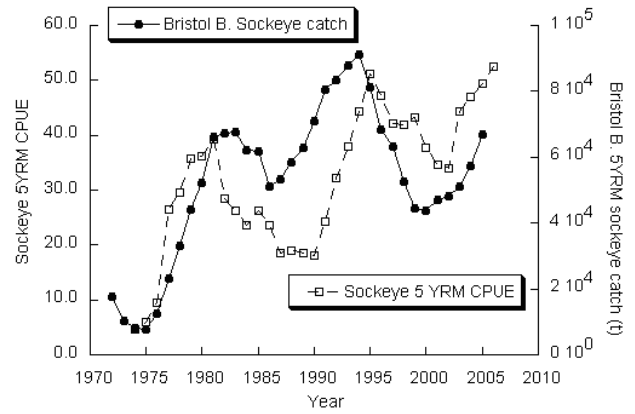


Fig. 17. Five-year running mean trends in the Bristol Bay sockeye salmon commercial catch and 5YRM CPUE (Japanese research vessels) in the Bering Sea.

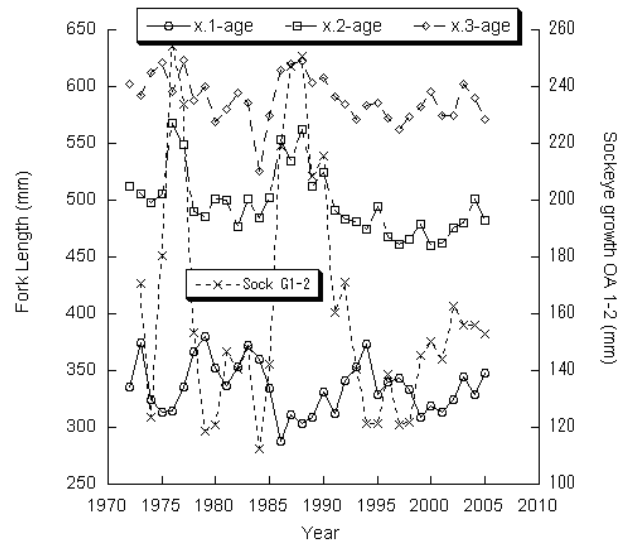


Fig. 18. Trends in mean July fork length of sockeye salmon at each ocean age (x.1, x.2, and x.3), and calculated growth rate between age x.1 and x.2 fish in the Bering Sea.

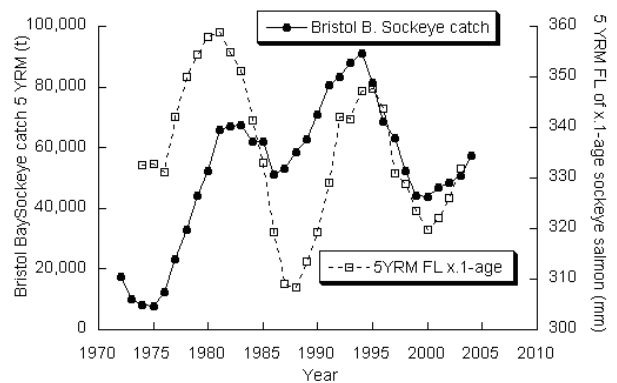


Fig. 19. Trends in the 5YRM sockeye salmon commercial catch in Bristol Bay and the 5YRM July fork length of age x.1 sockeye salmon caught by Japanese research vessels in the Bering Sea.

low production regime, the mean CPUE of four Pacific salmon species (sockeye, chum, pink and Chinook salmon) in the Bering Sea were at high levels. Our data showed a positive linear correlation between 5YRM SST and 5YRM CPUE of sockeye salmon. Additionally, the 5YRM sockeye salmon CPUE oscillation was similar to the 5YRM commercial catch of Bristol Bay sockeye salmon. These results indicate that warm periods lead to a high abundance of Bristol Bay sockeye salmon. We showed the similarity in oscillation patterns between size trends of age x.1 sockeye salmon and abundance of Bristol Bay sockeye salmon stocks. When the 5YRM FL of age x.1 sockeye salmon became large, the Bristol Bay sockeye salmon abundance increased. Farley et al. (2007a) showed that the warmer sea temperatures during the spring and summer increased the productivity in the eastern Bering Sea, enhancing sockeye salmon growth; and Farley et al. (2007b) support the “bigger is better” hypothesis for sockeye salmon (Beamish and Mahnken 2001). Our analysis in the central Bering Sea also supports his hypothesis for sockeye salmon populations.

We observed two periods with small mean FL of age x.1 sockeye salmon from 1972 to 2005. One was from 1974 to 1977, and the other from 1986 to 1989. During these periods, the mean FL of age x.2 and age x.3 sockeye salmon was larger than usual. In both periods calculated growth rates between age x.1 and age x.2 sockeye in summer were very high. On the other hand, during 1978–1984 and 1992–1998 with large mean FL of age x.1 sockeye salmon, the mean FL of age x.2 and age x.3 sockeye salmon were small. These results indicate the occurrence of intra-population, density-dependent effects on growth after age x.1 in sockeye salmon in the Bering Sea. Ruggerone and his colleagues pointed out that the population abundance of Asian pink salmon affected the growth of the Bristol Bay sockeye salmon population, based on scale analysis (Ruggerone et al. 2003, 2005), but they did not mention intra-population competition. In our data, mean pink salmon CPUE in the Bering Sea was low between 1972 and 1989, so interspecies competition between Asian pink salmon and Bristol Bay sockeye salmon stocks should have been at low levels. However, large fluctuations in growth of sockeye salmon at sea occurred during this period. Intra-population competition may be more important than interspecific competition on the growth of Bristol Bay sockeye. Farley et al. (2007a) pointed out that age 0 year walleye pollock were important food items for juvenile sockeye salmon along the eastern Bering Sea shelf. According to a recent assessment, the estimated abundance of age 1 walleye pollock was high around 1979 and 1993, and low around 1988 and 2005 (Ianelli et al. 2008). This fluctuation pattern is similar to the mean FL of age x.1 sockeye salmon in the central Bering Sea (Fig. 20). Considering this, abundance of YOY walleye pollock along the eastern Bering Sea shelf should be one of the key factors affecting the growth and survival of juvenile Bristol Bay sockeye salmon. When age 1 walleye pollock are abundant, we can expect numerous

YOY walleye pollock as a food organism for age x.1 sockeye salmon in the eastern Bering Sea. An abundant food supply may accelerate the early growth of age x.0 sockeye salmon in the eastern Bering Sea shelf.

In this study, we showed that SST fluctuations affected some characteristics of Pacific salmon. The SST and other oceanographic components were, in turn, influenced by climate change. Among the climate indices, the PDO was well associated with Alaskan sockeye stocks (Mantua et al. 1997; Hare et al. 1999). The PDO was an index of SST fluctuation; it was also associated with our SST data on the central Bering Sea. The detected regime shifts in the PDO occurred in 1977 and 1989. After the 1977 regime shift, the Bering Sea became warmer and the mean FL of age x.1 sockeye salmon increased until 1985. Mean FL became smaller in 1986 and 1987 (Figs. 18 and 19). After the 1989 regime shift, mean FL of age x.1 sockeye salmon increased until 1995. The

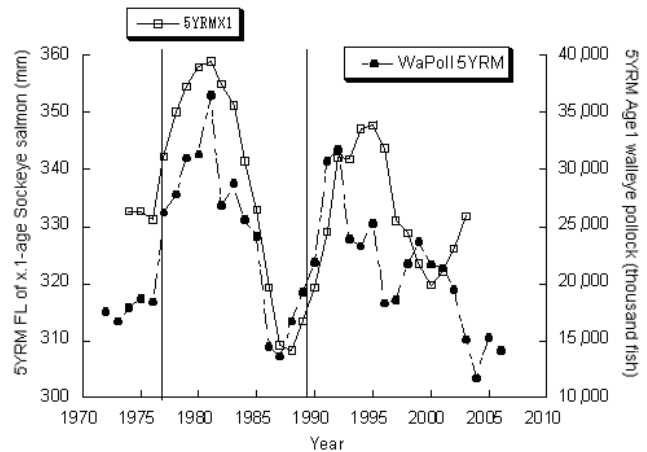


Fig. 20. Trends in the 5YRM July fork length of age x.1 sockeye salmon caught by Japanese research vessels in the Bering Sea, and the 5YRM of estimated abundance of age 1 walleye pollock (from Ianelli et al. 2008) in the Western Bering Sea.

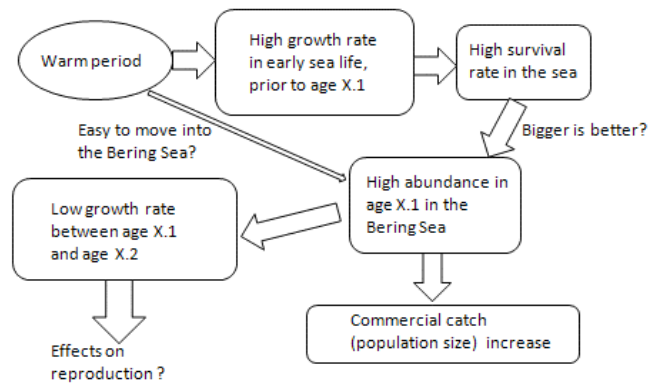


Fig. 21. Suggested connection for some characteristic changes in sockeye salmon stocks that migrate in the Bering Sea during the summer, in warm periods.

1977 regime shift marked a significant increase in many Alaskan salmon stocks (Hare and Francis 1994), but trends after the 1989 regime shift were unclear. Some researchers indicated the occurrence of a 1998 regime shift (Minobe 2002). If it is true, we can now identify three regime shifts, 1977, 1989, and 1998, in our time series of CPUE and SST data in the Bering Sea. Among these three years, both the SST and CPUE showed two up-and-down cycles with the minimum value around each regime shift year. Additionally, we can see a similar trend in the commercial catch of Bristol Bay sockeye salmon. What has happened to sockeye salmon during the warm periods (such as around 1980 and 1996)? We propose a possible process affecting sockeye salmon characteristics in Fig 21. In warm periods, salmon grow faster during early marine life in the eastern Bering Sea, with the larger size resulting in higher survival rates. The result of higher early life survival is a higher abundance of age x.1 sockeye salmon. If, after age x.1, the survival rate of salmon is semi-constant, then a high abundance of age x.1 fish results in an increased commercial catch (population size). Because of intra-population density effects, growth rates between age x.1 and age x.2 sockeye salmon become lower because of the influence of a high density of age x.1 fish. Effects of slower growth rates are unclear, but may affect reproduction through the adult size, fecundity, or egg quality.

In this paper, we have shown the possibility of semi-decadal fluctuations in the Bering Sea SST, and related fluctuations in sockeye salmon abundance, although cause and effects of the fluctuations are still unclear. Climate change and its effects on the salmon populations are one of the serious problems affecting salmon population management (Beamish 2007).

ACKNOWLEDGEMENTS

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Stock Origins of Chum Salmon (*Oncorhynchus keta*) in the Gulf of Alaska during Winter as Estimated with Microsatellites

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Abstract: A microsatellite baseline incorporating over 53,000 chum salmon (*Oncorhynchus keta*) sampled from over 380 locations in Asia and North America was applied to estimate stock composition in mixed-stock fishery samples from the Gulf of Alaska. High resolution of these mixed-stock samples was possible, with 1 reporting group developed for Korean populations, 7 groups for Japanese populations, 8 groups for Russian populations, 15 groups for Alaskan populations, 5 groups for Canadian Yukon River populations, 16 groups for British Columbia populations, and 5 groups for Washington populations. In February 2006 samples from the Gulf of Alaska (145°W), chum salmon in more northern areas (54°N) were primarily of North American origin (55% British Columbia, 30% Alaska), but in more southern areas (48°N), nearly 40% of chum salmon sampled were of Japanese origin (Sea of Okhotsk and Pacific coasts of Hokkaido), and 30% were of Russian origin (Kamchatka and northeast Russia). Ocean age-1 chum salmon spending their first winter in the Gulf of Alaska were almost entirely from southeast Alaska (39%), Prince William Sound (31%), or southern British Columbia (26%). However, by the second winter, 30% of ocean age-2 chum salmon were identified as of Asian origin (18% Japanese, 12% Russian).

Keywords: chum salmon, winter, Gulf of Alaska, stock identification, microsatellites

INTRODUCTION

Stock composition information is important in determining areas of ocean rearing of stocks of immature chum salmon (*Oncorhynchus keta*), and the migration routes used by immature salmon to reach seasonal rearing areas, as well as the routes used by maturing chum salmon to return to natal rivers. Although scale pattern analysis has been used in chum salmon stock identification (Tanaka et al. 1969; Ishida et al. 1989), stock identification based upon analysis of genetic variation has been the main method used in stock identification applications. Initial applications centered on allozymes, whereby the genetic structure of populations potentially contributing to a mixed-stock fishery was determined (Okazaki 1982a,b; Wilmot et al. 1994; Winans et al. 1994; Seeb and Crane 1999a; Efremov 2001) and then this structure was used to estimate the stock composition of samples from mixed-stock fisheries (Beacham et al. 1987; Urawa et al. 1997, 2000, 2009; Wilmot et al. 1998; Winans et al. 1998; Seeb and Crane 1999b). Additionally, sequence variation in mitochondrial (mt) DNA has been used to evaluate population structure (Ginatulina 1992; Sato et al. 2001, 2004) and to estimate stock compositions of chum salmon in the Bering

Sea and North Pacific Ocean (Moriya et al. 2007; Sato et al. 2009). Microsatellites have also been demonstrated to be effective in determining population structure of chum salmon and estimating stock composition in fisheries in local areas in both Asia (Beacham et al. 2008b,c) and North America (Beacham et al. 2008a), as well as providing high resolution stock composition estimates for complex mixed-stock samples in North Pacific and Bering Sea sampling (Beacham et al. unpub. data).

Accurate, cost-effective identification of chum salmon to region of origin is important to our understanding of stock-specific responses to recent climatic regime shifts in the north Pacific Ocean (Welch et al. 2000; Mueter et al. 2002). Identification of marine factors responsible for survival variation observed in salmon stocks requires identification of fish sampled in marine environments to stock of origin as an initial step. The potential mixing of many chum salmon stocks throughout their marine existence necessitates identification of fish from mixed-stock samples for delineation of stock-specific migration pathways and marine feeding areas (Brodeur et al. 2003), and for evaluation of physiological status during spawning migrations (Cooke et al. 2004).

In the present study, mixed-stock samples from the Gulf

of Alaska were analyzed for stock composition through analysis of 14 microsatellites by incorporating a 381-population baseline including populations from Korea, Japan, Russia, Alaska, the Yukon Territory, British Columbia, and Washington. Comparisons of presence and absence of specific stocks of salmon in the areas surveyed are outlined.

MATERIALS AND METHODS

Baseline Populations

The baseline survey consisted of the analysis of over 53,000 chum salmon from 381 populations from Korea, Japan, Russia, Alaska, Canada, and Washington, with the sampling sites or populations surveyed in each geographic region outlined by Beacham et al. (unpub. data). Information on regional population structure has been outlined previously for Japanese populations (Beacham et al. 2008b), Russian populations (Beacham et al. 2008c), western Alaska populations (Beacham et al. 2009b) and British Columbia populations (Beacham et al. 2008a). Pacific Rim population structure of chum salmon was reported by Beacham et al. (2009a).

Marine Samples and Laboratory Analysis

A series of six samples was collected during a research cruise in the Gulf of Alaska during February 2006 between approximately latitude 48°N–53°N along longitude 145°W (Fig. 1). The age of virtually all individuals in these six samples was determined by analysis of scales, and variation in stock composition attributable to both location and age was conducted subsequently.

Laboratory Analysis

Tissue samples from the marine samples were collected, preserved in 95% ethanol, and DNA subsequently extracted. Extracted DNA from 2006 Gulf of Alaska samples was sent to the Molecular Genetics Laboratory (MGL) at the Pacific Biological Station for subsequent analysis. Once extracted DNA was available, surveys of variation at 14 microsatellite loci were conducted: Ots3 (Banks et al. 1999), Oke3 (Buchholz et al. 2001), Oki2 (Smith et al. 1998), Oki100 (Beacham et al. 2008b), Omm1070 (Rexroad et al. 2001), Omy1011 (Spies et al. 2005), One101, One102, One104, One111, and One114 (Olsen et al. 2000), Ots103 (Nelson and Beacham 1999), Ssa419 (Cairney et al. 2000), and OtsG68 (Williamson et al. 2002).

PCR DNA amplifications were conducted using DNA

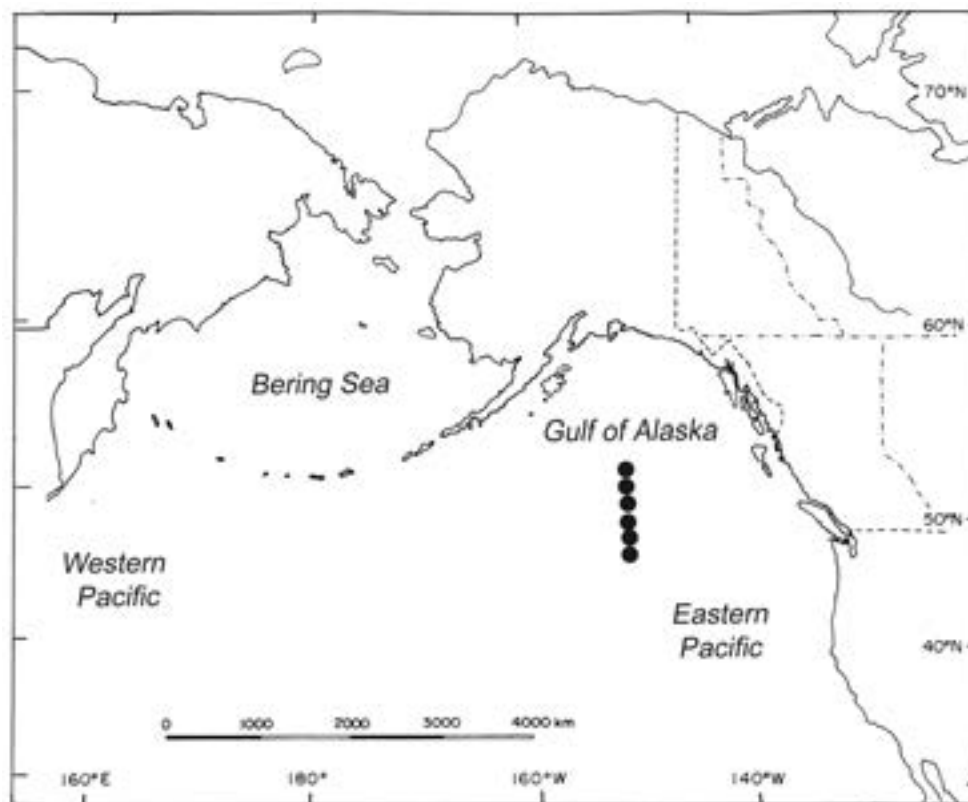


Fig. 1. Map indicating the locations of six samples collected during a February 2006 cruise of the *R/V Kaiyo-maru* in the Gulf of Alaska and eastern Pacific Ocean.

Engine Cycler Tetrad2 (BioRad, Hercules, CA) in 6- μ l volumes consisting of 0.15 units of Taq polymerase, 1 μ l of extracted DNA, 1x PCR buffer (Qiagen, Mississauga, Ontario), 60 μ M each nucleotide, 0.40 μ M of each primer, and deionized H₂O. The thermal cycling profile involved one cycle of 15 min at 95°C, followed by 30–40 cycles of 20 sec at 94°C, 30–60 sec at 47–65°C and 30–60 sec at 68–72°C (depending on the locus). Specific PCR conditions for a particular locus could vary from this general outline and were outlined by Beacham et al. (2009b). PCR fragments were size fractionated in an ABI 3730 capillary DNA sequencer, and genotypes were scored by GeneMapper software 3.0 (Applied Biosystems, Foster City, CA) using an internal lane sizing standard.

Estimation of Stock Composition in Mixed-stock Samples

The BAYES routine of Pella and Masuda (2001) was modified by our laboratory to a C++-based program (cBayes), which is available from our laboratory website (Neaves et al. 2005). In the analysis, ten 20,000-iteration Monte Carlo Markov chains of estimated stock compositions were produced, with initial starting values for each chain set at 0.90 for a particular population that was different for each chain. Estimated stock compositions were considered to have converged when the shrink factor was < 1.2 for the 10 chains (Pella and Masuda 2001), and thus the starting values were considered to be irrelevant (uninformative prior). Stock composition estimates converged before 20,000 iterations, and no further improvements in the estimates were observed in excess of 20,000 iterations. Therefore, 20,000 iterations was set as the standard in the analysis. The last 1,000 iterations from each of the 10 chains were then combined, and for each fish the probability of originating from each population in the baseline was determined. These individual probabilities were summed over all fish in the sample, and divided by the number of fish sampled to provide the point estimate of stock composition. Standard deviations of estimated stock compositions were determined from the last 1,000 iterations from each of the 10 chains incorporated in the analysis.

RESULTS

Winter distribution of chum salmon along 145°W longitude in 2006 was evaluated between 48°N and 53°N. In the most northerly location sampled (53°N), sample size was modest (N=32), but chum salmon originating from the central coast of British Columbia (19%), the Fraser River (15%) in southern British Columbia, and southeast Alaska (12%) were identified as the most relatively abundant stocks (Table 1). Contributions were also identified from chum salmon originating from southern coastal British Columbia (8%) and Prince William Sound (7%). Asian chum salmon detected were limited to those from Kamchatka (8%) and northeast

Russia (3%). Sampling at 52°N indicated that chum salmon from southeast Alaska (23%), the Fraser River (23%), Prince William Sound (15%), and the west coast of Vancouver Island (13%) accounted for 74% of the chum salmon sampled. Asian chum salmon accounted for 8% of the fish sampled from this location, with the largest stock from the Sea of Okhotsk coast of Hokkaido (5%). Sampling at 51°N indicated that chum salmon from southeast Alaska were the most relatively abundant stock (22%), followed by chum salmon from Prince William Sound (17%) and the Fraser River (9%) (Table 1). Chum salmon from Norton Sound and the lower Yukon River constituted approximately 11% of the individuals sampled. Asian chum salmon were estimated to constitute 26% of the individuals sampled, with Russian chum salmon identified almost exclusively from Kamchatka (7%) and northeast Russia (8%), and Japanese chum salmon almost exclusively from the Sea of Okhotsk coast and Nemuro Strait region of Hokkaido (10%). Sampling from these three sites indicated an increasing proportion of Asian chum salmon from north to south, a dominant presence of chum salmon from southeast Alaska and Prince William Sound in the samples, little evidence of chum salmon from northern British Columbia, and evidence of chum salmon from southern British Columbia, Washington, and western Alaska.

In the southern section of the survey, starting at 50°N, the single most abundant stock was the Sea of Okhotsk coast of Hokkaido (13%), followed by the southeast Alaska (12%) and Prince William Sound stocks (10%) (Table 1). Asian chum salmon accounted for 39% of the sample (23% Japanese, 16% Russian), with the Russian contribution largely accounted for by Kamchatka and northeast Russia stocks. Chum salmon from northern North America in Kotzebue Sound (3%), Norton Sound (7%), and the Yukon River (3%) were also identified as present in the sample. Asian chum salmon increased substantially in relative abundance in the sample from 49°N, with Japanese (34%) and Russian (35%) chum salmon substantial contributors to the catch. Japanese chum salmon were largely from the Pacific coast (21%) and Nemuro Strait (12%) regions of Hokkaido. Russian chum salmon were largely from northeast Russia (24%), Magadan (6%), and Kamchatka (4%). North American chum salmon were largely from southeast Alaska (12%) and Washington (12%). Asian chum salmon again dominated at the most southern sampling site (48°N), with 66% of the fish sampled of Asian origin. Japanese chum salmon, at 37% of the fish sampled, were largely from the Sea of Okhotsk coast (28%) and Pacific coast (9%) regions of Hokkaido. Russian chum salmon, constituting 28% of the fish sampled, were largely from Kamchatka (12%), northeast Russia (7%), and Sakhalin Island (6%). Chum salmon from North America were identified as originating mainly from southeast Alaska (15%) and Prince William Sound (9%). Asian chum salmon dominated at the southern sampling sites, with Japanese chum salmon estimated to be largely derived from the Sea of Okhotsk, Nemuro Strait, and Pacific coastal regions of Hok-

Table 1. Estimated stock compositions (percentage, SD in parentheses) of six mixed-stock samples of chum salmon sampled in the Gulf of Alaska during February 2006. Region codes are: QCI (Queen Charlotte Islands), BC (British Columbia), ECVI (east coast Vancouver Island), WCVI (west coast Vancouver Island).

Latitude	53°01' N	52°09' N	50°52' N	49°52' N	48°53' N	47°54' N
Longitude	145°00' W	144°58' W	144°52' W	144°53' W	144°49' W	144°49' W
Date	16 February	16 February	17 February	17 February	18 February	18 February
Number of samples	32	64	130	136	34	111
Honshu Sea of Japan	0.0 (0.4)	0.0 (0.2)	0.1 (0.3)	1.3 (2.6)	0.3 (1.7)	0.0 (0.2)
Honshu Pacific	0.0 (0.3)	0.0 (0.2)	0.3 (0.7)	0.2 (0.6)	0.3 (1.4)	0.1 (0.5)
Hokkaido Sea of Japan	0.0 (0.3)	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)	0.3 (1.3)	0.0 (0.1)
Hokkaido Sea of Okhotsk	0.4 (1.5)	4.9 (2.8)	3.3 (2.0)	13.1 (4.7)	0.6 (2.2)	27.8 (5.2)
Nemuro Strait	0.0 (0.2)	0.0 (0.1)	6.2 (2.5)	2.3 (3.3)	11.8 (6.7)	0.1 (0.4)
Hokkaido eastern Pacific	0.0 (0.2)	0.0 (0.1)	0.7 (1.5)	0.0 (0.2)	11.6 (6.0)	3.4 (3.5)
Hokkaido western Pacific	0.0 (0.3)	0.0 (0.2)	0.8 (1.4)	6.0 (3.6)	9.1 (6.4)	5.7 (3.3)
Sakhalin	0.0 (0.4)	0.0 (0.2)	0.0 (0.1)	0.0 (0.1)	0.0 (0.3)	5.7 (2.5)
Magadan	0.1 (1.0)	2.6 (2.6)	0.2 (0.7)	2.4 (1.8)	6.1 (5.5)	3.0 (2.4)
Northern Sea of Okhotsk	0.0 (0.2)	0.0 (0.2)	0.4 (1.1)	0.0 (0.1)	0.1 (1.2)	0.0 (0.3)
West Kamchatka	5.9 (6.5)	0.3 (1.1)	4.3 (3.3)	9.3 (3.2)	3.3 (4.8)	12.3 (4.4)
East Kamchatka	1.9 (3.9)	0.0 (0.5)	2.4 (2.6)	0.1 (0.6)	0.9 (2.4)	0.0 (0.3)
Northeast Russia	3.3 (4.7)	0.0 (0.3)	7.7 (2.6)	4.5 (2.1)	24.1 (8.9)	7.4 (4.0)
Kotzebue Sound	0.0 (0.5)	0.2 (0.8)	0.9 (1.8)	2.5 (1.7)	0.2 (1.3)	0.0 (0.2)
Norton Sound	1.2 (3.1)	2.9 (3.4)	6.1 (4.4)	7.1 (4.5)	1.7 (3.2)	4.2 (2.9)
Yukon lower summer	1.8 (3.6)	0.2 (1.0)	4.4 (3.4)	1.1 (2.3)	0.1 (0.9)	0.3 (1.2)
Yukon upper Alaska fall	0.0 (0.4)	0.0 (0.2)	0.2 (0.8)	1.7 (1.5)	0.1 (0.8)	0.7 (1.1)
Yukon mainstem Canada	0.0 (0.4)	0.0 (0.2)	0.0 (0.3)	0.4 (0.8)	0.0 (0.3)	0.0 (0.3)
Yukon Porcupine Canada	0.0 (0.4)	0.0 (0.1)	0.0 (0.2)	0.1 (0.4)	0.0 (0.2)	0.0 (0.3)
Nushagak summer	0.0 (0.5)	0.0 (0.4)	0.4 (1.2)	0.1 (0.6)	0.0 (0.5)	0.0 (0.4)
Kuskokwim Bay/ River	0.5 (2.2)	0.1 (0.5)	0.1 (0.7)	1.7 (2.8)	0.4 (1.7)	0.4 (1.2)
Northeast Bristol Bay	0.0 (0.5)	3.6 (4.0)	0.0 (0.3)	1.8 (2.4)	0.1 (0.6)	0.1 (0.4)
Southwest Bristol Bay	0.0 (0.4)	0.0 (0.3)	0.1 (0.6)	0.0 (0.2)	0.0 (0.4)	0.0 (0.1)
North Peninsula	0.0 (0.2)	0.0 (0.4)	2.7 (1.7)	1.2 (1.4)	0.0 (0.3)	0.0 (0.2)
Southwest Peninsula	0.6 (2.2)	0.0 (0.2)	0.0 (0.3)	0.1 (0.6)	0.2 (1.0)	0.0 (0.1)
Southeast Peninsula	0.3 (1.2)	0.1 (0.5)	0.1 (0.4)	0.0 (0.2)	0.0 (0.4)	0.1 (0.3)
Kodiak Island	0.0 (0.3)	0.0 (0.2)	0.0 (0.2)	1.6 (1.1)	0.0 (0.2)	0.0 (0.1)
Prince William Sound	7.2 (6.5)	15.3 (5.8)	16.8 (3.7)	9.6 (3.0)	0.4 (1.5)	9.3 (3.0)
SE Alaska	12.2 (10.4)	23.2 (8.0)	21.8 (4.8)	11.8 (4.0)	12.2 (6.2)	15.0 (3.9)
Taku	0.1 (0.8)	0.7 (2.0)	0.1 (0.5)	0.1 (0.6)	0.0 (0.4)	0.0 (0.3)
QCI west	1.9 (4.0)	0.0 (0.4)	0.1 (0.4)	0.3 (0.8)	0.0 (0.5)	0.0 (0.3)
QCI east	0.1 (0.9)	0.4 (1.5)	0.1 (0.4)	0.1 (0.5)	0.4 (1.7)	0.1 (0.4)
QCI Skidegate	0.1 (0.8)	0.2 (1.1)	0.0 (0.2)	0.6 (1.2)	0.0 (0.4)	0.1 (0.4)
BC north	2.4 (6.9)	0.6 (1.9)	1.2 (2.2)	0.3 (1.0)	0.9 (2.7)	0.1 (0.5)
Skeena	0.0 (0.7)	0.5 (1.6)	0.1 (0.6)	0.0 (0.2)	0.0 (0.6)	0.3 (0.9)
BC Grenville	6.0 (10.5)	0.1 (0.8)	0.0 (0.4)	0.1 (0.4)	0.2 (1.3)	0.1 (0.6)
BC central	19.4 (10.4)	0.5 (1.7)	4.4 (2.9)	0.5 (1.2)	0.7 (2.5)	0.3 (1.0)
BC Rivers Inlet	0.2 (1.3)	0.0 (0.5)	0.1 (0.4)	0.1 (0.4)	0.0 (0.4)	0.0 (0.3)
Johnstone Strait	0.2 (1.6)	0.3 (1.4)	0.0 (0.2)	0.0 (0.3)	0.0 (0.4)	0.3 (0.7)
BC south	8.4 (8.4)	2.8 (4.7)	0.4 (1.1)	2.9 (3.1)	0.6 (2.4)	0.7 (1.3)
ECVI	4.0 (6.9)	0.5 (1.6)	0.3 (1.0)	2.1 (2.7)	0.2 (1.4)	0.0 (0.3)
WCVI	0.5 (2.6)	13.1 (4.6)	3.7 (2.0)	7.1 (2.7)	0.3 (1.5)	0.0 (0.2)
Fraser	15.2 (9.1)	22.6 (7.1)	9.2 (3.1)	4.5 (2.7)	0.9 (2.9)	2.3 (1.9)
North Puget Sound	0.1 (1.1)	1.4 (3.5)	0.0 (0.3)	0.4 (1.5)	1.0 (3.1)	0.2 (0.7)

Table 1 (continued).

Latitude	53°01' N	52°09' N	50°52' N	49°52' N	48°53' N	47°54' N
Longitude	145°00' W	144°58' W	144°52' W	144°53' W	144°49' W	144°49' W
Date	16 February	16 February	17 February	17 February	18 February	18 February
South Puget Sound	2.2 (4.3)	0.1 (0.5)	0.0 (0.2)	0.0 (0.1)	0.6 (2.3)	0.0 (0.1)
Hood Canal	0.0 (0.3)	1.5 (2.9)	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)
Juan de Fuca Strait	3.2 (5.9)	1.0 (2.4)	0.0 (0.1)	0.0 (0.2)	10.0 (7.0)	0.0 (0.1)
Coastal Washington	0.2 (1.2)	0.0 (0.2)	0.0 (0.1)	0.7 (1.3)	0.0 (0.3)	0.0 (0.1)
Values by region						
Japan	0.4 (1.7)	4.9 (2.8)	11.3 (92.9)	23.0 (3.7)	34.1 (8.1)	37.1 (4.8)
Russia	11.3 (7.5)	3.0 (2.6)	15.1 (3.8)	16.3 (3.8)	34.5 (8.7)	28.4 (5.2)
Western Alaska	3.6 (4.6)	6.9 (3.5)	12.2 (3.3)	16.0 (3.6)	2.6 (3.8)	5.6 (2.9)
Central/Southeast Alaska	20.3 (10.7)	38.7 (8.3)	41.6 (5.5)	24.4 (4.4)	12.9 (6.3)	24.4 (4.4)
Canada Yukon	0.0 (0.7)	0.0 (0.3)	0.1 (0.4)	0.4 (0.9)	0.0 (0.5)	0.1 (0.5)
Northern British Columbia	30.2 (12.7)	3.2 (4.4)	6.1 (3.7)	2.1 (2.2)	2.4 (4.0)	1.0 (1.7)
Southern British Columbia	28.3 (11.7)	39.3 (7.5)	13.6 (3.5)	16.6 (3.7)	2.0 (4.2)	3.2 (2.2)
Washington	5.8 (5.2)	4.0 (4.6)	0.1 (0.4)	1.2 (1.9)	11.6 (6.9)	0.2 (0.7)

kaido. Russian chum salmon were identified as primarily from Kamchatka and northeast Russia.

Stock composition showed considerable differences among the age-classes of chum salmon evaluated. Chum salmon typically spend 1–4 winters rearing in the ocean. Ocean age-1 chum salmon spending their first winter in the ocean were almost entirely from southeast Alaska (39%), Prince William Sound (31%), or southern British Columbia (26%) (Table 2). No ocean age-1 individuals were identified as Asian in origin. However, by the second winter, 30% of chum salmon of ocean age-2 were identified as of Asian origin (18% Japanese, 12% Russian). Ocean age-2 North American fish were estimated to be from British Columbia (27%), Prince William Sound (18%), western Alaska (13%), and southeast Alaska (8%). Asian chum salmon accounted for 36% of ocean age-3 chum salmon (20% Japanese, 16% Russian), with ocean age-3 North American chum salmon ranging from western Alaska to Washington (Table 2). Ocean age-4 chum salmon were predominately (66%) Asian in origin (36% Japanese, 30% Russian). Higher proportions of ocean age-4 chum salmon from North America were generally observed in more northerly stocks (central and southeast Alaska 14%, southern British Columbia 4%, and Washington 4%).

DISCUSSION

The present microsatellite stock identification study indicated that various stocks of Asian and North American chum salmon stocks intermingled in the central Gulf of Alaska during winter. A similar result was obtained by allozyme analysis for chum salmon collected in the same region during the winter of 1996 (Urawa et al. 1997).

Ocean age-1 chum salmon spending their first winter in the ocean in the Gulf of Alaska along 145°W were all of

North American origin, primarily from regions directly adjacent (Prince William Sound, southeast Alaska) to the sampling locations. No migration of ocean age-1 (2004 brood year) Asian chum salmon into the region was observed. Allozyme stock identification has indicated that Japanese chum salmon inhabit in the western North Pacific Ocean during their first winter, move into the Bering Sea in the summer, and migrate into the Gulf of Alaska for their second winter (Urawa 2000, 2004; Urawa et al. 2001, 2009). The present study supported this migration model, and indicated that ocean age-2 Asian chum salmon had moved into the Gulf of Alaska after the second summer of marine rearing (2003 brood year), as did chum salmon from western Alaska. However, Russian chum salmon of this age were primarily of northeast Russia origin, with virtually no 2003 broodyear chum salmon from Kamchatka observed. Substantial differences in survival rates, broodyear spawning abundances, or sampling variation could account for the observed differences in age composition between northeast Russia and Kamchatka, but perhaps the results may reflect a differential migration pattern between chum salmon of northeast Russia and Kamchatka origin chum salmon of this age. Older Russian chum salmon were primarily of Kamchatka origin, so it is possible that the lack of 2003 brood year salmon from Kamchatka may reflect a slower rate of migration into the Gulf of Alaska of this stock. In the Gulf of Alaska, Russian chum salmon originated primarily from northeast Russia and Kamchatka, so these differences reflect either differences in survival and spawning abundance, or a more eastward migration pattern of these stocks compared with other stocks in Russia.

Japanese chum salmon in the Gulf of Alaska originated entirely from the Sea of Okhotsk coast, Nemuro Strait, and Pacific coast regions of Hokkaido. Production from these areas accounts for about 75% of total production of Japanese

Table 2. Estimated stock compositions (percentage, SD in parentheses) by age of 519 chum salmon sampled in the Gulf of Alaska during February 2006. Region codes are as outlined in Table 1.

	All	Ocean age 1	Ocean age 2	Ocean age 3	Ocean age 4	Undetermined
Number of samples	519	30	212	162	104	12
Honshu Sea of Japan	0.0 (0.1)	0.0 (0.4)	0.0 (0.2)	0.0 (0.3)	0.0 (0.3)	0.0 (1.0)
Honshu Pacific	0.0 (0.1)	0.0 (0.4)	0.0 (0.1)	0.1 (0.4)	0.3 (0.9)	0.0 (0.9)
Hokkaido Sea of Japan	0.0 (0.0)	0.0 (0.3)	0.0 (0.3)	0.0 (0.1)	0.0 (0.1)	2.7 (5.8)
Hokkaido Sea of Okhotsk	11.7 (1.8)	0.0 (0.3)	8.1 (2.7)	12.1 (3.3)	24.9 (5.3)	1.0 (3.8)
Nemuro Strait	1.4 (1.1)	0.0 (0.2)	0.0 (0.1)	4.7 (3.1)	0.6 (1.8)	2.0 (5.0)
Hokkaido eastern Pacific	2.6 (1.0)	0.0 (0.3)	1.7 (1.9)	3.0 (2.0)	3.7 (2.5)	1.4 (4.3)
Hokkaido western Pacific	5.6 (1.3)	0.0 (0.3)	8.2 (2.3)	0.3 (0.9)	6.6 (3.2)	1.6 (4.3)
Sakhalin	1.0 (0.5)	0.0 (0.3)	1.6 (1.0)	0.1 (0.3)	1.8 (1.7)	0.0 (0.6)
Magadan	1.5 (0.8)	0.0 (0.6)	0.4 (0.8)	0.0 (0.3)	6.7 (3.1)	0.0 (1.0)
West Kamchatka	6.9 (1.6)	0.1 (0.9)	0.6 (1.1)	15.1 (3.5)	9.4 (4.2)	0.0 (0.9)
East Kamchatka	0.9 (1.5)	0.0 (0.6)	0.3 (0.7)	0.3 (1.1)	2.2 (4.2)	0.0 (1.0)
Northeast Russia	7.2 (1.4)	0.0 (0.2)	9.2 (2.2)	0.4 (1.0)	9.3 (3.2)	0.0 (0.5)
Kotzebue Sound	1.9 (0.8)	0.0 (0.4)	2.1 (1.2)	0.1 (0.4)	0.0 (0.3)	0.0 (0.9)
Norton Sound	4.8 (1.5)	0.0 (0.5)	8.5 (2.5)	7.4 (3.0)	0.3 (1.0)	7.0 (7.3)
Yukon lower summer	0.2 (0.6)	0.0 (0.6)	0.1 (0.5)	0.6 (1.4)	4.5 (2.9)	0.4 (2.6)
Yukon Upper Alaska fall	0.9 (0.6)	0.0 (0.3)	1.5 (1.3)	0.6 (0.9)	0.0 (0.1)	0.0 (0.7)
Yukon mainstem Canada	0.1 (0.3)	0.0 (0.3)	0.4 (0.9)	0.0 (0.3)	0.0 (0.1)	0.0 (0.9)
Yukon White	0.0 (0.0)	0.0 (0.3)	0.0 (0.0)	0.1 (0.3)	0.0 (0.1)	0.0 (0.6)
Yukon Porcupine Canada	0.0 (0.1)	0.0 (0.3)	0.1 (0.5)	0.1 (0.3)	0.0 (0.1)	0.0 (0.7)
Nushagak summer	0.1 (0.4)	0.0 (0.2)	0.0 (0.1)	1.5 (1.9)	0.0 (0.2)	0.3 (2.4)
Kuskokwim Bay/ River	0.3 (0.7)	0.0 (0.4)	0.3 (0.8)	0.2 (0.9)	0.2 (0.8)	0.7 (2.7)
Northeast Bristol Bay	0.9 (1.2)	0.0 (0.3)	0.8 (1.3)	0.3 (1.0)	0.1 (0.6)	0.0 (0.6)
North Peninsula	0.9 (0.5)	0.0 (0.3)	1.7 (1.0)	0.0 (0.1)	2.3 (1.9)	0.0 (0.8)
Southwest Peninsula	0.0 (0.1)	0.3 (1.3)	0.1 (0.3)	0.0 (0.3)	0.1 (0.4)	0.0 (0.5)
Southeast Peninsula	0.1 (0.2)	0.0 (0.4)	0.6 (1.0)	0.0 (0.1)	0.0 (0.3)	0.0 (0.9)
Kodiak Island	0.4 (0.3)	0.0 (0.2)	0.6 (0.6)	0.6 (0.6)	0.0 (0.1)	0.0 (0.6)
Prince William Sound	11.3 (1.6)	30.5 (10.6)	17.9 (2.9)	4.1 (1.8)	2.8 (2.7)	1.0 (4.4)
SE Alaska	18.0 (2.2)	38.7 (12.0)	7.5 (3.6)	18.2 (3.8)	9.3 (3.9)	42.5 (15.5)
Taku	0.1 (0.3)	0.6 (2.7)	0.0 (0.2)	0.3 (0.8)	0.0 (0.3)	9.3 (8.9)
QCI west	0.0 (0.1)	0.5 (2.2)	0.1 (0.4)	0.0 (0.2)	0.1 (0.6)	0.0 (1.2)
QCI east	0.1 (0.3)	1.0 (3.3)	0.0 (0.3)	0.0 (0.2)	0.0 (0.3)	0.0 (1.6)
QCI Skidegate	0.1 (0.2)	0.1 (0.7)	0.1 (0.4)	0.0 (0.2)	0.2 (0.7)	0.0 (1.4)
BC north	0.3 (0.8)	0.3 (1.7)	0.5 (1.2)	0.3 (1.1)	0.9 (1.9)	0.3 (2.7)
Skeena	0.0 (0.1)	0.4 (1.8)	0.0 (0.2)	0.0 (0.2)	0.0 (0.2)	0.1 (2.2)
BC Grenville	0.4 (0.7)	0.2 (1.7)	6.5 (3.5)	0.0 (0.3)	1.6 (2.2)	0.0 (1.1)
BC central	1.7 (1.0)	0.6 (2.4)	2.7 (2.0)	3.5 (2.7)	3.4 (3.7)	0.0 (2.5)
BC Rivers Inlet	0.0 (0.1)	0.1 (0.8)	0.0 (0.2)	0.0 (0.1)	0.7 (1.9)	0.0 (1.1)
Johnstone Strait	0.0 (0.2)	0.4 (1.6)	0.0 (0.2)	0.0 (0.2)	0.0 (0.3)	0.0 (1.7)
BC south	3.6 (1.5)	6.4 (7.3)	4.1 (2.6)	0.4 (1.2)	0.1 (0.5)	14.0 (14.7)
ECVI	1.5 (1.7)	10.0 (9.3)	2.3 (2.3)	5.5 (3.3)	0.1 (0.7)	12.6 (15.4)
WCVI	4.6 (1.2)	0.6 (2.4)	4.4 (1.7)	5.2 (2.3)	1.8 (1.5)	0.0 (1.3)
Fraser	7.3 (1.6)	8.9 (8.1)	6.4 (2.4)	7.1 (2.9)	2.2 (2.8)	1.9 (6.1)
North Puget Sound	0.0 (0.2)	0.0 (0.5)	0.5 (1.1)	0.3 (1.1)	3.7 (3.7)	0.7 (3.1)
South Puget Sound	0.2 (0.4)	0.0 (0.6)	0.0 (0.1)	2.6 (1.7)	0.0 (0.1)	0.0 (0.7)
Hood Canal	0.2 (0.4)	0.0 (0.3)	0.0 (0.1)	0.9 (1.5)	0.0 (0.1)	0.1 (1.3)
Juan de Fuca Strait	1.0 (0.8)	0.0 (0.3)	0.1 (0.4)	3.5 (1.8)	0.0 (0.2)	0.0 (0.8)
Coastal Washington	0.0 (0.2)	0.0 (0.3)	0.0 (0.1)	0.2 (0.7)	0.0 (0.1)	0.0 (0.7)

Table 2 (continued).

	All	Ocean age 1	Ocean age 2	Ocean age 3	Ocean age 4	Undetermined
Values by region						
Japan	21.3 (1.9)	0.0 (0.9)	18.0 (2.8)	20.2 (3.3)	36.0 (4.9)	8.7 (7.8)
Russia	17.5 (2.0)	0.2 (1.4)	12.2 (2.6)	16.0 (3.4)	29.5 (5.2)	0.0 (2.0)
Western Alaska	9.3 (1.5)	0.0 (1.2)	13.2 (2.6)	10.8 (2.7)	5.1 (2.7)	8.3 (7.6)
Central/Southeast Alaska	30.6 (2.4)	69.6 (9.9)	28.3 (4.2)	23.0 (3.9)	14.4 (4.9)	43.6 (14.7)
Canada Yukon	0.1 (0.3)	0.0 (0.6)	0.5 (1.0)	0.2 (0.5)	0.0 (0.2)	0.0 (1.6)
Northern British Columbia	2.7 (1.3)	3.7 (5.9)	10.0 (3.9)	4.2 (2.9)	7.0 (4.6)	9.8 (10.3)
Southern British Columbia	17.1 (1.9)	26.4 (9.1)	17.1 (2.9)	18.3 (3.8)	4.3 (3.1)	28.6 (12.9)
Washington	1.4 (0.8)	0.1 (1.0)	0.6 (1.1)	7.4 (2.7)	3.7 (3.7)	0.8 (3.6)

chum salmon, so if Japanese chum salmon are present, substantial contributions from these regions would be expected. However, it is noteworthy that few chum salmon from Honshu or the Sea of Japan coast of Hokkaido were observed in the sampling in the Gulf of Alaska, so chum salmon from these regions either do not migrate as far east as other Japanese chum salmon, or they were south of 48°N during winter residence in the Gulf of Alaska.

Chum salmon from North America were distributed in the more northerly regions sampled in the Gulf of Alaska, and, conversely, Asian chum salmon were more prevalent in the southern regions. Chum salmon from western Alaska were observed in the Gulf of Alaska in winter after two summers of marine residence, but not after one summer. Urawa et al. (2000) indicated that western Alaskan stocks were rarely present among ocean age-1 chum salmon, and increased among ocean age-2 and -3 in the central Gulf of Alaska during the summer of 1998. Therefore, western Alaska chum salmon might not migrate to the Gulf of Alaska after one summer of rearing. Chum salmon from northern British Columbia were only observed in significant proportions in the most northern sample (53°N), perhaps indicative of a more northerly distribution in the Gulf of Alaska for chum salmon from this region. Fraser River chum salmon were also more prevalent at more northern sampling locations in the Gulf of Alaska. Clearly, there was a nonrandom distribution of chum salmon in the Gulf of Alaska during the winter of 2006.

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Preliminary Genetic Analysis of Juvenile Chum Salmon from the Chukchi Sea and Bering Strait

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Abstract: The arctic region has experienced warming in recent years, resulting in decreased summer sea ice cover and increased sea surface temperatures. In September 2007, the U.S. BASIS survey extended surface trawling into the Chukchi Sea. Juvenile (young-of-the-year) chum salmon were collected at most stations. Genetic methods using microsatellite and SNP loci were applied to identify the origin of a subset of juvenile chum salmon collected in the Chukchi Sea and Bering Strait. Most of the juvenile chum salmon caught in the Bering Strait were from populations of the Anadyr-Kanchalan river system of northeastern Russia and the majority of fish collected in the Chukchi Sea site were from populations of northwestern Alaska.

Keywords: genetic stock identification, juvenile chum salmon, Bering Sea, Chukchi Sea

INTRODUCTION

The sea surface temperature in the arctic marginal seas has increased since the mid-1960s. The extent of arctic summer sea ice cover has decreased dramatically in recent years (Steele et al. 2008). In 2007, the NOAA ship *Oscar Dyson* was used for the U.S. BASIS survey of the eastern Bering Sea, which extended northward for the first time into the Chukchi Sea. Along with juvenile Chinook (*Oncorhynchus tshawytscha*), pink (*O. gorbuscha*) and sockeye salmon (*O. nerka*) and various forage fish species, juvenile (young-of-the-year) chum salmon (*O. keta*) were caught in most of the trawl hauls in the surface waters of the Chukchi Sea (Moss et al. 2009). The objective of this study was to identify the populations or regional groupings of populations that contribute to the juvenile chum salmon collected in this northern region.

MATERIALS AND METHODS

Genetic methods were applied to identify the origin of the juvenile chum salmon collected from two locations, the Bering Strait (three trawl hauls pooled; n = 185) on September 13, 2007, and the eastern Chukchi Sea (one trawl haul; n = 186) on September 7, 2007 (Fig. 1). A microsatellite baseline that is compatible with data assembled by Fisheries and

Oceans Canada (Beacham et al. 2008) is being developed and will be coupled with data from single-nucleotide-polymorphism (SNP) markers from nuclear and mitochondrial loci (M.R. Garvin, unpub. data; Garvin and Gharrett 2007). For our study, nine microsatellite loci (Oki100, Omy1011, One101, One102, One104, One114, Ots103, Ots68, and Ssa419) and 21 SNPs representing one mitochondrial and nine nuclear loci were used (M.R. Garvin, unpub. data). A preliminary 89-population genetic baseline currently incorporates sufficient genetic information of western Alaskan and Asian populations for stock identification analysis of chum salmon caught in the Bering and Chukchi seas. Eight regional groupings were used for this analysis. Baseline simulations for the eight regional groupings and estimates of stock proportions present in the juvenile chum salmon from Bering Strait and Chukchi Sea were made using the program SPAM 3.7b (Debevec et al. 2000).

RESULTS AND DISCUSSION

Regional estimates of origin of the juvenile chum salmon caught in the Bering Strait and Chukchi Sea indicate an eastward, then northward migration route used by northeastern Russian populations (Anadyr-Kanchalan rivers) and a westward, then northward route used by western Alaskan populations from coastal waters in late summer-early fall

(Table 1). Most of the juvenile chum salmon caught at the Bering Strait location were from the Anadyr-Kanchalan rivers of northeastern Russia with small contributions from the Kamchatka Peninsula and northwestern Alaska. Approximately two-thirds of the juvenile chum salmon caught in the Chukchi Sea location were from Kotzebue Sound, with lesser contributions from populations on the Seward Peninsula and in Norton Sound. It would be necessary to process additional samples to determine whether juvenile chum salmon from these northernmost populations also have a southward

migration component. A previous study suggests that the movement of juvenile chum salmon in this region may be more complex: juvenile chum salmon from northeastern Russia populations were caught in the fall of 2002 south of St. Lawrence Island (Farley et al. 2004), indicating a southeasterly component in their migration route, at least in some years. It is not known if northeastern Russian fish continue through the Bering Strait and into the Chukchi Sea.

The Chukchi Sea lies over the shallow continental shelf in the Arctic Ocean—and is unique among the arctic margin-



Fig. 1. Location (solid circles) of juvenile chum salmon samples genetically analyzed in this study from the Chukchi Sea and Bering Strait, collected during the 2007 fall U.S. BASIS survey using the NOAA ship *Oscar Dyson*.

Table 1. Estimates and standard errors of regional proportions assigned to juvenile chum salmon samples from the Bering Strait (n = 184) and Chukchi Sea (n = 183) using genetic methods based on nine microsatellite and 10 SNP loci. Number of populations in each grouping is given in parentheses after the region name.

Region ¹	Bering Strait		Chukchi Sea	
	Estimate	SE	Estimate	SE
Western Asia (19)	0	0	0	0
Kamchatka Peninsula (6)	0.0600	0.0044	0.0030	0.0002
Northeastern Russia (3)	0.7650	0.0563	0	0
Kotzebue Sound (4)	0	0	0.6915	0.0511
Seward Peninsula–Norton Sound (9)	0.0925	0.0068	0.2710	0.0200
Yukon River (11)	0.0443	0.0033	0.0304	0.0022
Kuskokwim (6)	0.0349	0.0026	0.0040	0.0003
Bristol Bay–Washington (31)	0.0033	0.0002	0	0

¹Baseline simulations of these eight groupings indicated at least 80% correct assignment for simulation allocations set to 100%, except for the Kuskokwim grouping, which was 67%, with mis-allocation primarily to the Yukon and Seward-Norton regions.

al seas in that waters are transported from the North Pacific via the Bering Sea into the Chukchi Sea (Weingartner 1997). While movement of juvenile chum salmon from northeastern Russian and northwestern Alaska populations coincides with the northward flow of water from the Bering Sea shelf into the Bering Strait and Chukchi Sea, juvenile chum salmon from the Yukon River do not appear to follow this northward flow. For the locations sampled in this study there is little contribution from Yukon River populations. The winter habitat of juvenile chum salmon that utilize the northern Bering and Chukchi seas is unknown.

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Stock Distribution Patterns of Chum Salmon in the Bering Sea and North Pacific Ocean during the Summer and Fall of 2002–2004

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Abstract: Stock origin and ocean distribution of chum salmon in the Bering Sea and its adjacent North Pacific waters during the summer and fall of 2002–2004 were estimated using a mitochondrial DNA control region. The percentage of immature chum salmon samples was more than 97% in the fall of 2002 and 2003, and 80–88% in summer 2003 and 2004. The genetic stock identification (GSI) and GSI-estimated CPUE (catch per unit effort) suggested that immature chum salmon were mostly from Japanese and Russian stocks, and they were widely distributed in the Bering Sea. The abundance of North American stocks was much lower than that of Asian stocks in the Bering Sea, while it increased in the North Pacific Ocean in the fall of 2003. In the central Bering Sea, Japanese chum salmon stocks were most predominant among regional stocks. All regional stocks were distributed in proportion to sea surface temperatures (6.6–11.9°C) available during each survey period. The distribution pattern and abundance of chum salmon CPUE in the Bering Sea was different among years and seasons, while those changes were not significantly related to the favorable sea surface temperature range in the Bering Sea.

Keywords: chum salmon, genetic stock identification, mitochondrial DNA, distribution, Bering Sea

INTRODUCTION

Chum salmon (*Oncorhynchus keta*) are the most widely distributed salmon species around the Pacific Rim and are considered an important commercial fisheries resource. Estimation of stock origins of chum salmon is important to clarify the stock assessment and the patterns of ocean migration.

Stock identification of chum salmon on the high seas has been attempted with tagging methods, thermal otolith marking, and genetic characters (e.g. Ishida et al. 1989; Wilmot et al. 1998; Seeb and Crane 1999; Urawa et al. 2000b). Off-shore tagging experiments indicated that maturing Japanese chum salmon were widely distributed in the Bering Sea and North Pacific Ocean in summer (Ogura and Ito 1994). Otolith-marked chum salmon were collected in the Bering Sea and North Pacific Ocean, and of those, approximately 90% were found to have been released from Japanese hatcheries (Sato et al. 2009). Genetic stock identification (GSI) analysis were performed using allozyme and mitochondrial DNA

(mtDNA) markers, and the results showed that Japanese and Russian chum salmon stocks are predominant in the central Bering Sea during summer and fall (Urawa et al. 2004, 2005, 2009; Moriya et al. 2007, 2009). Those results support the ocean migration model of Japanese chum salmon that shows that immature fish inhabit mainly the Bering Sea after overwintering in the North Pacific Ocean (Urawa 2000; Urawa et al. 2001). However, it is still unclear whether or not the marine distribution of particular stock shows inter-annual changes.

Marine habitat conditions affect salmonid ocean distribution. Ocean temperatures should be an important factor affecting the ocean distribution of chum salmon (Urawa et al. 2000a). Welch et al. (1995) also postulated thermal limits and sea surface temperature (SST) as determinants of salmonid distribution in the open ocean. However, the relationships between distribution pattern of specific stocks and SST are unclear.

Japanese scientists have participated in the Bering/Aleutian Salmon International Survey (BASIS) program to clar-

ify the effect of environmental factors on the distribution of Pacific salmon in the Bering Sea. In the 2002 and 2003 summer and fall seasons, biological data on Pacific salmon and oceanographic data were collected in the Bering Sea and its adjacent North Pacific waters (Azumaya et al. 2003; NPAFC 2004). In summer 2004, biological and oceanographic surveys for Pacific salmon were also conducted in the Bering Sea and North Pacific Ocean (Azumaya et al. 2005). The objective of the present study was to clarify the inter-annual changes in ocean distribution patterns of chum salmon stocks and to examine the relationships between stock distribution patterns and marine habitat conditions, particularly SST. We estimated the stock origin and ocean distribution of chum salmon in the Bering Sea and North Pacific Ocean during the summer of 2004 using a mtDNA marker. The 2004 estimates were compared with the previous 2002–2003 data and the relationships between stock-specific distribution and SST were examined using randomization tests.

MATERIALS AND METHODS

Fish Samples and DNA Extraction

Samples of chum salmon were collected from 18 stations in the Bering Sea and North Pacific Ocean (50°38'N–57°58'N, 175°14'E–170°00'W) aboard the research vessel R/V *Kaiyo maru* between 24 June and 8 July 2004 (Table 1). A net was trawled in the surface layer (down to 50m) for 1 hour at 5 knots. We calculated the catch per unit effort (CPUE) of chum salmon as the number of chum salmon caught per one hour of trawling at a station. Whole blood samples were collected from the caudal vasculature or gills of chum salmon ($n = 1,014$) and frozen at -40°C . DNA was isolated from the whole blood samples by a Puregene™ DNA purification kit (QIAGEN Inc., Valencia, CA) following the manufacturer's instructions. DNA was extracted at the laboratory of the National Salmon Resources Center, Fisheries Research Agency.

MtDNA Analysis and GSI Estimation

Thirty mtDNA haplotypes of chum salmon that were collected from the Bering Sea and North Pacific Ocean were detected by the DNA microarray method (Moriya et al. 2005) and assigned origins (Japanese, Russian, or North American stocks) using a previously reported mtDNA dataset (Yoon et al. 2008) as baseline data. This baseline data was created from about 4,200 individuals from 96 populations of chum salmon in the Pacific Rim. In previous simulation studies using this baseline data, estimates for the Japanese and North American regions were about 90% accurate (91.6% for Japanese stocks and 94.5% for North American stocks), whereas an estimate for the Russian region was 80.2% accurate (Moriya et al. 2009).

Stock contributions of the mixed samples were estimat-

ed via a conditional maximum likelihood (Pella and Milner 1987; Masuda et al. 1991). A conjugate-gradient searching algorithm using a square root transformation was used because it provides good performance with large baselines and small stock differences (Pella et al. 1996). Standard deviations and 90% symmetric confidence intervals were estimated by 1,000 bootstrap resamplings of the baseline and mixture samples. Estimates were made to individual stock and then pooled to regional stock groups: Japan, Russia, and North America. These regional stock groups were categorized based on previous genetic analysis for the baseline data set of 96 populations of chum salmon in the Pacific Rim (Yoon et al. 2008). Computations were performed with the Statistics Programs for Analyzing Mixtures (SPAM version 3.7b), which was originally developed by Debevec et al. (2000).

Estimation of Stock-specific CPUE

GSI-estimated CPUE of chum salmon by stock origin in the Bering Sea and North Pacific Ocean was calculated for five areas: central Bering Sea (55°57'N–58°30'N, 179°42'E–174°42'W), southern Bering Sea (51°41'N–54°40'N, 179°42'E–174°59'W), eastern Bering Sea (53°05'N–56°00'N, 169°57'W–170°34'W), western Bering Sea (52°52'N–56°10'N, 172°30'E–177°29'E), and North Pacific Ocean (49°50'N–53°29'N, 164°46'W–174°49'W) in each survey period (2002 fall, 2003 summer and fall, and 2004 summer). The GSI data during summer and fall of 2002 and 2003 were referenced from Moriya et al. (2009). CPUE data for chum salmon during 2002–2004 are shown in Fig. 1.

Randomization Test

The randomization test of cumulative frequency was used to show the difference in distribution for each regional stock group and SST (Perry and Smith 1994). In this test, the Cramer-von Mises test statistics and 999 permutations of random combinations of 2 variants were used for the significance (Syrjala 1996). Relationships between the distribution of each regional stock and SST were tested by the randomization test for cumulative functions of CPUE and stations over SST in each year. The randomization test was calculated using an EXCEL macro.

RESULTS

Distribution and Maturity

A total of 2,149 chum salmon were collected in summer of 2004. Chum salmon were widely distributed in the survey areas during 2002–2004 (Fig. 1). The abundance of chum salmon in the Bering Sea was higher than the abundance in the North Pacific Ocean during summer/fall 2003 and sum-

Table 1. Survey areas and stations, sampling locations, date of collection, sea surface temperature, number of genetic samples, and stock contribution estimates of immature chum salmon in the Bering Sea and North Pacific Ocean during the summer of 2004. SST, sea surface temperature; N, number of genetic samples; SD, standard deviation; CI, symmetric confidence interval.

Areas/Stations	Latitude	Longitude	Date	SST	N	Estimate ± SD (90% CI)		
						Japan	Russia	North America
Central Bering Sea								
H07	57°58'N	174°42'W	Jun 29	8.7	72	0.674±0.125 (0.493-0.919)	0.196±0.157 (0.001-0.466)	0.130±0.135 (0.000-0.365)
H09	56°01'N	174°42'W	Jun 30	8.2	76	0.613±0.122 (0.415-0.838)	0.243±0.160 (0.008-0.518)	0.143±0.135 (0.000-0.364)
H20	56°21'N	179°52'W	Jul 6	8.3	80	0.599±0.129 (0.423-0.863)	0.191±0.175 (0.001-0.510)	0.210±0.172 (0.001-0.470)
H21	57°20'N	179°53'W	Jul 6	8.4	53	0.596±0.148 (0.366-0.868)	0.361±0.166 (0.064-0.613)	0.043±0.088 (0.000-0.261)
Total				8.4*	281	0.647±0.087 (0.525-0.798)	0.236±0.113 (0.060-0.427)	0.117±0.098 (0.000-0.295)
Southern Bering Sea								
H11	54°10'N	175°02'W	Jul 1	7.9	84	0.333±0.147 (0.124-0.615)	0.581±0.193 (0.214-0.846)	0.087±0.138 (0.000-0.395)
H18	54°35'N	179°46'E	Jul 5	7.7	93	0.475±0.141 (0.271-0.763)	0.367±0.206 (0.022-0.684)	0.158±0.173 (0.000-0.460)
Total				7.8*	177	0.389±0.126 (0.188-0.610)	0.488±0.161 (0.205-0.723)	0.123±0.120 (0.000-0.355)
Eastern Bering Sea								
H03	53°05'N	170°22'W	Jun 27	7.6	57	0.257±0.144 (0.047-0.523)	0.607±0.203 (0.243-0.908)	0.136±0.168 (0.001-0.472)
H04	53°56'N	170°01'W	Jun 27	7.2	34	0.470±0.174 (0.175-0.750)	0.474±0.203 (0.093-0.804)	0.056±0.109 (0.000-0.332)
H05	55°04'N	170°01'W	Jun 28	8.5	34	0.535±0.148 (0.312-0.804)	0.157±0.208 (0.001-0.595)	0.309±0.208 (0.003-0.590)
H06	55°40'N	170°05'W	Jun 28	9.1	42	0.655±0.163 (0.380-0.945)	0.177±0.184 (0.003-0.530)	0.168±0.154 (0.003-0.430)
Total				8.1*	167	0.462±0.108 (0.292-0.654)	0.430±0.150 (0.157-0.660)	0.108±0.110 (0.000-0.322)
Western Bering Sea								
H22	55°57'N	175°17'E	Jul 7	8.8	75	0.177±0.127 (0.007-0.442)	0.522±0.265 (0.084-0.906)	0.300±0.254 (0.001-0.685)
H23	55°05'N	175°14'E	Jul 7	7.9	77	0.190±0.124 (0.028-0.424)	0.542±0.295 (0.060-0.927)	0.268±0.284 (0.001-0.717)
H24	53°57'N	175°16'E	Jul 8	8.1	21	0.143±0.114 (0.000-0.360)	0.367±0.367 (0.002-0.959)	0.490±0.348 (0.006-0.905)
H25	52°58'N	175°16'E	Jul 8	7.2	13	0.160±0.110 (0.000-0.366)	0.138±0.165 (0.002-0.465)	0.703±0.191 (0.313-0.980)
Total				8.0*	186	0.156±0.090 (0.008-0.330)	0.557±0.187 (0.247-0.855)	0.267±0.179 (0.012-0.576)
North Pacific Ocean								
H01	50°53'N	170°10'W	Jun 26	8.8	65	0.498±0.156 (0.273-0.811)	0.198±0.213 (0.005-0.607)	0.305±0.195 (0.002-0.570)
H02	51°49'N	170°00'W	Jun 26	8.6	71	0.450±0.137 (0.257-0.720)	0.327±0.207 (0.002-0.655)	0.223±0.181 (0.006-0.543)
H13	51°40'N	175°06'W	Jul 2	8.3	56	0.412±0.118 (0.230-0.618)	0.416±0.223 (0.011-0.743)	0.173±0.194 (0.000-0.542)
H14	50°38'N	180°00'	Jul 3	7.4	11	0.282±0.143 (0.091-0.545)	0.018±0.045 (0.001-0.041)	0.700±0.153 (0.421-0.907)
Total				8.6*	203	0.431±0.100 (0.273-0.610)	0.337±0.163 (0.060-0.591)	0.233±0.141 (0.033-0.482)

*Average SST in each survey area.

mer 2004. However, their distribution patterns in the Bering Sea were different among those three years and seasons. In 2002, chum salmon were mainly collected in the southern Bering Sea between 172°30'W–177°30'W (Fig. 1A). In 2003, chum salmon were widely distributed in the survey areas of the Bering Sea, but the CPUE in fall was higher than that in summer (Fig. 1B, C). In 2004, about 30% of chum salmon were caught at a single station (H18, see Fig. 1D). The percentage of immature chum salmon samples was > 97% in the fall of 2002 and 2003. On the other hand, the occurrence of immature fish was < 90% in summer 2003 and 2004 (80.2% in 2003 and 88.1% in 2004).

Genetic Stock Identification

The stock composition of immature chum salmon in the Bering Sea and North Pacific Ocean in the summer of 2004 is shown in Table 1. The stock composition in the central Bering Sea (H07, H09, H20, and H21) was 59.6–67.4% Japanese, 19.1–36.1% Russian, and 4.3–21.0% North American stocks. The estimated stock composition of chum salmon in the southern Bering Sea (H11 and H18) was 33.3–47.5% Japanese, 36.7–58.1% Russian, and 8.7–15.8% North American stocks. Chum salmon in the eastern Bering Sea (H03–06) were estimated to be 25.7–65.5% Japa-

nese, 15.7–60.7% Russian, and 5.6–30.9% North American stocks. The stock composition in the western Bering Sea (H22–H25) was 14.3–19.0% Japanese, 13.8–54.2% Russian, and 26.8–70.3% North American stocks. In the North Pacific Ocean (H01, H02, H13, and H14), the stock composition was estimated to be 28.2–49.8% Japanese, 1.8–41.6% Russian, and 17.3–70.0% North American chum salmon.

CPUE Distribution

GSI-estimated CPUE analysis of immature chum salmon indicated that Asian (Japanese and Russian) stocks were widely distributed in the surveyed areas, and were relatively abundant in the central and southern Bering Sea (Fig. 2, Table 2). Particularly, Japanese stocks were predominant in the central Bering Sea during 2002–2004. Stock abundance in the southern Bering Sea fluctuated highly among years. The CPUE of Russian stocks was higher than that of Japanese and North American stocks in the western Bering Sea during 2002–2004. The abundance of North American stocks was much lower than that of Asian stocks in the Bering Sea (Fig. 2, Table 2). In the North Pacific Ocean, North American stocks showed a high CPUE in fall 2003, while their CPUE was almost the same or lower than other stocks in summer 2003 and 2004 (Fig. 2).

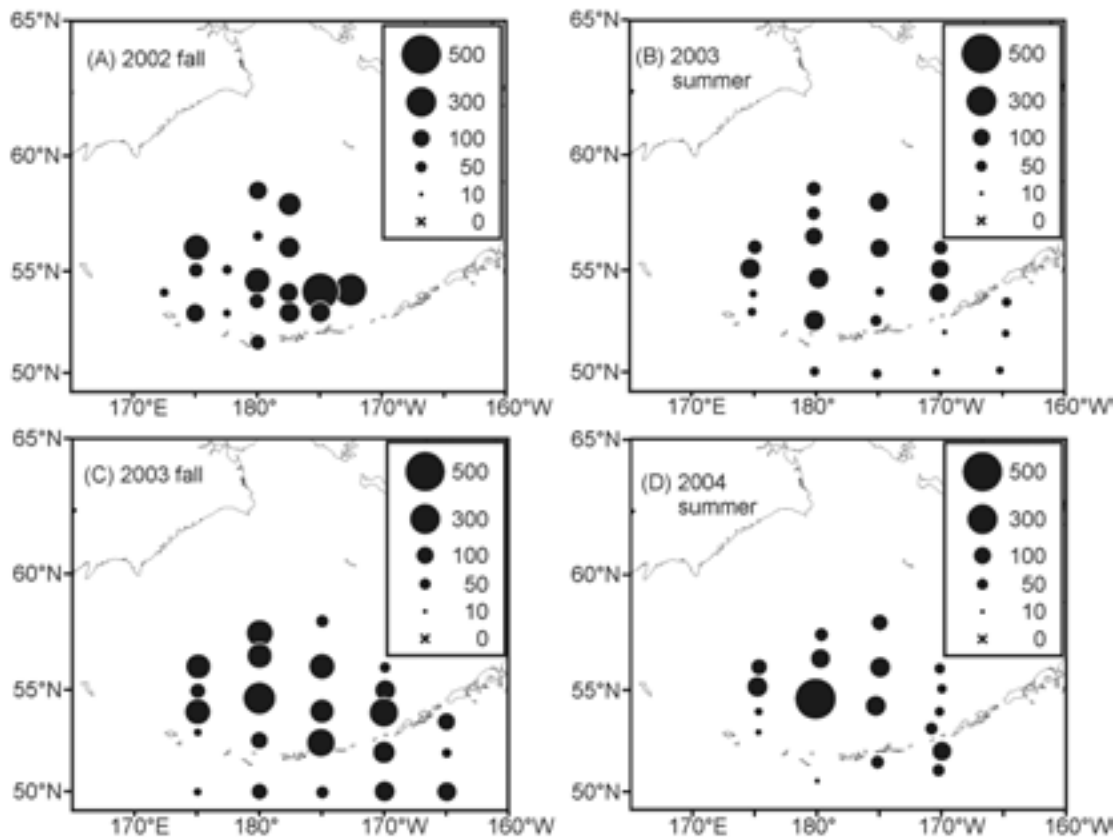


Fig. 1. Catch per unit effort (CPUE) distribution of chum salmon in the Bering Sea and North Pacific Ocean in the fall of 2002 (A), the summer (B) and fall (C) of 2003, and the summer of 2004 (D). CPUE indicates the number of catches per one-hour trawl.

Table 2. Estimation of stock-specific CPUE of immature chum salmon in five surveyed areas of the Bering Sea and North Pacific Ocean during the summer and fall of 2002-2004. CPUE, the number of catches per one hour trawl; St., number of stations in each survey area; CI, symmetric confidence interval. Genetic-estimated CPUE data from 2002-2003 were calculated using GSI data from Moriya et al. (2009).

Seasons (sampling date)/Areas	St.	Mean SST	CPUE (Mean \pm SD (90% CI))		
			Japan	Russia	North America
2002 fall (Sep 3-18)					
Central Bering Sea	4	10.2	72.8 \pm 10.9 (55.3-90.6)	40.5 \pm 14.7 (12.0-61.7)	6.5 \pm 10.2 (0.0-29.8)
Southern Bering Sea	7	9.0	55.3 \pm 18.6 (33.4-89.5)	87.2 \pm 39.0 (11.1-131.2)	25.5 \pm 33.1 (0.0-94.0)
Western Bering Sea	6	9.9	27.1 \pm 9.6 (15.9-46.1)	41.5 \pm 19.7 (3.5-63.7)	12.3 \pm 12.3 (0.0-47.3)
2003 summer (Jun 28-Jul 18)					
Central Bering Sea	5	8.0	55.7 \pm 10.5 (38.4-72.8)	26.3 \pm 13.0 (3.9-47.0)	10.6 \pm 8.6 (0.0-27.6)
Southern Bering Sea	4	7.7	46.6 \pm 10.2 (30.2-64.6)	29.8 \pm 14.2 (3.9-51.4)	10.7 \pm 11.0 (0.0-32.7)
Western Bering Sea	4	7.3	38.4 \pm 6.5 (15.3-37.0)	22.4 \pm 8.8 (8.5-43.7)	6.2 \pm 6.4 (0.2-27.5)
Eastern Bering Sea	3	9.1	58.7 \pm 9.9 (39.4-72.4)	34.3 \pm 13.5 (11.7-55.0)	9.4 \pm 9.7 (0.0-29.0)
North Pacific Ocean	7	9.5	7.0 \pm 2.4 (3.9-11.3)	13.6 \pm 5.8 (3.9-23.1)	9.3 \pm 5.6 (0.4-18.9)
2003 fall (Aug 30-Sep 19)					
Central Bering Sea	4	10.8	89.8 \pm 17.0 (63.6-119.1)	58.4 \pm 24.0 (17.1-96.3)	23.1 \pm 18.2 (0.3-58.1)
Southern Bering Sea	4	9.3	104.8 \pm 19.9 (74.6-139.8)	63.7 \pm 27.6 (19.7-110.3)	45.5 \pm 23.5 (10.7-86.8)
Western Bering Sea	4	10.1	36.3 \pm 10.7 (20.5-55.6)	64.8 \pm 20.5 (28.3-95.0)	24.1 \pm 17.8 (0.4-56.4)
Eastern Bering Sea	3	10.7	34.9 \pm 13.1 (15.3-56.1)	67.2 \pm 25.4 (22.8-106.0)	44.0 \pm 22.9 (10.7-84.2)
North Pacific Ocean	7	11.7	20.7 \pm 6.0 (11.7-28.7)	23.4 \pm 14.7 (3.1-46.4)	56.3 \pm 14.2 (26.9-69.8)
2004 summer (Jun 26-Jul 8)					
Central Bering Sea	4	8.4	79.6 \pm 10.7 (64.6-98.2)	29.0 \pm 13.9 (7.4-52.5)	14.4 \pm 12.1 (0.0-36.3)
Southern Bering Sea	2	7.8	154.2 \pm 50.0 (74.5-241.9)	193.5 \pm 63.8 (81.3-286.7)	48.8 \pm 47.6 (0.0-140.8)
Western Bering Sea	4	8.0	13.0 \pm 7.5 (0.7-27.5)	46.4 \pm 15.6 (20.6-71.2)	22.2 \pm 14.9 (1.0-48.0)
Eastern Bering Sea	4	8.1	25.6 \pm 6.0 (16.2-36.3)	23.9 \pm 8.3 (8.7-36.6)	6.0 \pm 6.1 (0.0-17.9)
North Pacific Ocean	4	8.3	33.3 \pm 7.7 (21.1-47.2)	26.1 \pm 12.6 (4.6-45.7)	18.0 \pm 10.9 (2.5-37.3)

Relationships between Stock-specific Distribution and SST

Associations between cumulative frequencies of genetic-estimated CPUE for three regional stocks and cumulative frequency of SST in each survey period were estimated based on stock CPUE and SST data at each survey station. All regional stocks were distributed in proportion to the available SST (6.6–11.9°C) in each survey period (Fig. 3). The test values for statistical significance in 2002 fall indicated negative values (Japanese stock, $P = 0.085$; Russian stock, $P = 0.401$; North American stock, $P = 0.534$) (Fig. 3A). In the 2003 summer and fall, the randomization test showed non-significant correlations between the distribution of each regional stock and observed SST (summer: Japanese stock, $P = 0.187$; Russian stock, $P = 0.972$; North American stock, $P = 0.699$) (Fig. 3B); (fall: Japanese stock, $P = 0.052$; Russian stock, $P = 0.981$; North American stock, $P = 0.508$) (Fig. 3C). In the summer of 2004, the test values for statistical significance also indicated negative values (Japanese stock, $P = 0.876$; Russian stock, $P = 0.749$; North American stock, $P = 0.1$) (Fig. 3D).

DISCUSSION

Our genetic stock estimates and GSI-estimated CPUE indicated that immature chum salmon were mostly of Asian (Japanese and Russian) origin, and were widely distributed in the surveyed areas of the Bering Sea during summer and fall. The abundance of immature North American stocks was lowest in the Bering Sea during 2002–2004. Previous allozyme analysis indicated that the relative abundance of immature North American stocks was low in the Bering Sea and high in the eastern North Pacific Ocean (Urawa et al. 2005, 2009). Many otolith-marked chum salmon released from North American hatcheries were found in the southern Bering Sea and eastern North Pacific Ocean (Urawa et al. 2005, 2009). These results suggest that the North American stocks are mainly distributed in the North Pacific Ocean.

Japanese stocks were predominant in the central Bering Sea during summer and fall of 2002–2004 compared to chum salmon stocks from all other countries. Allozyme analyses also indicated that Japanese immature chum salmon were most abundant in the central Bering Sea during summer and fall 2002 and 2003 (Urawa et al. 2004, 2005). Why do

Japanese chum salmon migrate and distribute themselves in the central Bering Sea? Urawa et al. (2005, 2009) suggested that one reason may be related with their overwintering habitats. Japanese chum salmon stay in a narrow region of the western North Pacific Ocean in the first winter and in the Gulf of Alaska during the following winters (Urawa 2000). During the overwintering period, chum salmon prefer water with low temperatures between 4°C and 8°C (Nagasawa 2000). The habitat in this temperature range was more widely available in the eastern North Pacific than the western North Pacific Ocean (Urawa et al. 2005). For Japanese chum salmon in the eastern North Pacific, the shortest homing migration route is through the Bering Sea (Urawa 2000; Urawa et al. 2005). MtDNA analysis of chum salmon in the North

Pacific Ocean in spring 2006 indicated that the abundance of Japanese stocks was higher in the central (180°) than in the western (165°E–175°E) North Pacific Ocean (Sato et al. 2007). Perhaps Japanese chum salmon start to move into the Bering Sea in late June or early July as estimated by Urawa et al. (2001, 2005, 2009), and then rapidly move into the central Bering Sea.

The CPUE distribution of chum salmon in the Bering Sea was different among years and seasons. The chum salmon CPUE in fall 2002 was higher than in fall 2003, while the CPUE in summer 2003 was lower than in summer 2004. The CPUE of chum salmon in fall 2003 was also higher than in summer 2003. Previous studies indicated that the density and distribution of chum salmon in the Bering Sea fluctuates

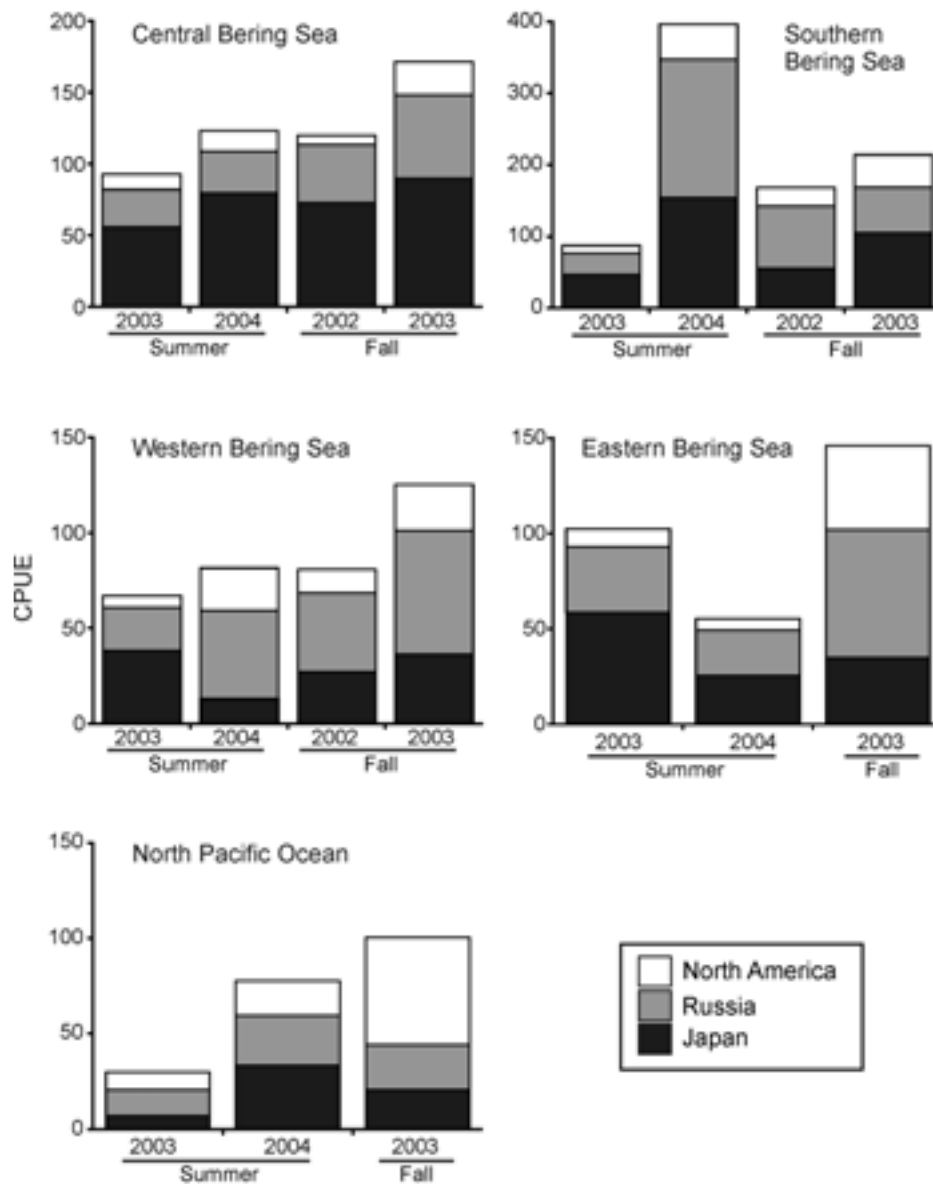


Fig. 2. Estimation of stock-specific CPUE of immature chum salmon in the five surveyed areas of the Bering Sea and North Pacific Ocean during 2002-2004. CPUE as in Fig. 1.

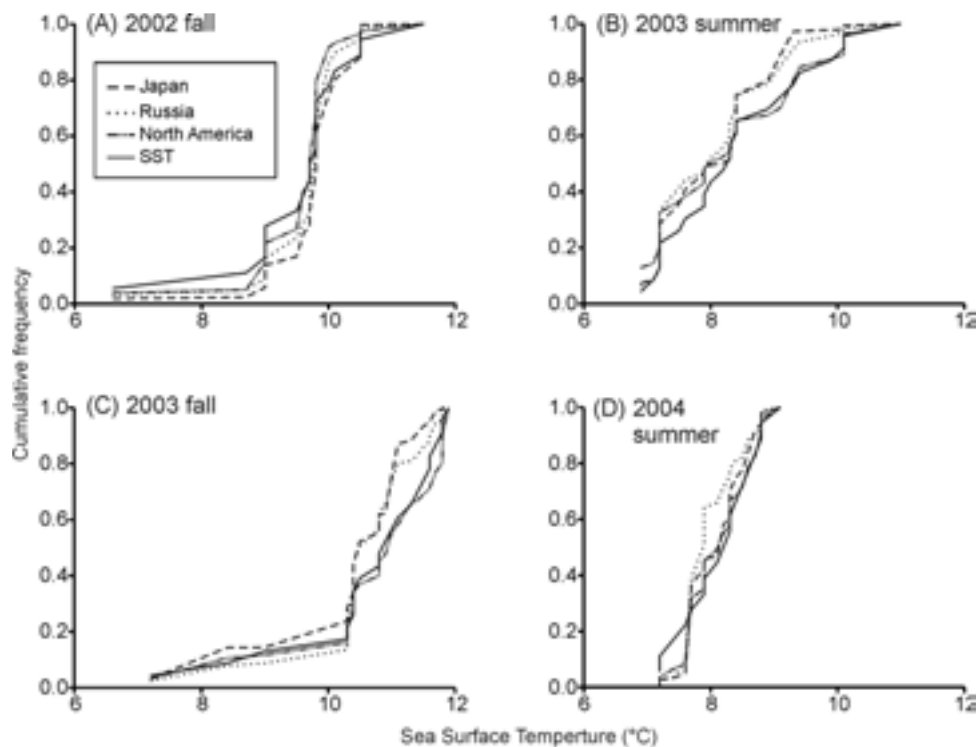


Fig. 3. Relationships between cumulative frequencies of GSI-estimated CPUE of immature chum salmon for three regional stocks (Japan, Russia, and North America) and sea surface temperature (SST) in the fall of 2002 (A), the summer (B) and fall (C) of 2003, and the summer of 2004 (D).

between odd and even years, because the interaction between pink (*O. gorbuscha*) and chum salmon changes their density and distribution (Azumaya and Ishida 2000). On the other hand, most pink salmon leave from the offshore of the Bering Sea by August for their spawning migration. Thus, pink salmon may influence the spatial and temporal distribution and abundance of chum salmon during early and mid summer, while pink salmon may have no impact on the distribution of immature chum salmon in the late summer and fall.

Myers et al. (2007) reported that there was a strong negative relation between the relative abundance of Russian chum salmon and SST in the central Bering Sea. They estimated that this correlation might reflect the influence of ocean temperature on run timing: in warm SST years Russian salmon may mature faster and leave the central Bering Sea sooner, resulting in lower CPUEs in July. However, this may not be the case for immature fish. Our randomization test showed non-significant correlations between the distribution of each regional stock of immature chum salmon and observed SST during each survey period. These results suggest that a response to SST may be different for maturing and immature chum salmon.

Azumaya et al. (2007) showed that the upper thermal limit was 15.6°C for chum salmon and that the southern limit of chum salmon distribution was located in the Transition Domain (43°N) in summer. In our study, all regional stocks were distributed in proportion to the available SST (6.6–

11.9°C) during summer and fall. This SST range is basically within the “preferred” temperature range of chum salmon. Furthermore, SST anomalies (relative to 1970–2000 mean values) in the Bering Sea for summer and fall of 2002–2004 showed +0–2°C (Japan Meteorological Agency, data citation: 19 December, 2008). These results suggest that chum salmon can inhabit most areas of the Bering Sea in summer without being affected by thermal limitations. In other words, SST may not be the main factor limiting the distribution of immature chum salmon in summer in the Bering Sea. The ocean distribution and migration patterns of salmon may be affected by the abundance of food organisms, interactions within or between species, ocean conditions, timing and location of spawning, as well as winter habitat (Urawa et al. 2005, 2009). In future studies, we should clarify factors influencing the migration and distribution of chum salmon in the ocean.

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Salmon in the Arctic and How They Avoid Lethal Low Temperatures

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Abstract: With climate change, scientists and others are interested in the future of Pacific salmon in the Arctic. Chum, pink, sockeye, coho, and chinook salmon have been encountered in the Beaufort Sea, well within Canadian Arctic waters. Chum is the only salmon species regarded as natal to the Mackenzie River watershed, although both pink and chum salmon appear to be natal to Alaska's North Slope rivers. It is not possible to say whether apparent recent increases in the frequency of occurrence of salmonids in the Arctic is an effect of climate change, but it appears there are either increases in the survival of natal fish from the Mackenzie, or in the wandering of non-natal fish to the Mackenzie, or both. We propose three hypotheses to explain how chum salmon survive cold marine winter conditions, and thereby persist in the North American Arctic: (1) Bering Sea Refuge – young salmon migrate to the Bering Sea and Gulf of Alaska where they remain until they are ready to return to spawn; (2) Atlantic Layer Beaufort Refuge – salmon remain in the Beaufort Sea, wintering offshore deep under pack ice; and (3) Freshwater Beaufort Refuge – salmon remain in the Beaufort Sea region, wintering in the brackish, under-ice Mackenzie River plume or in fresh water adjacent to the Beaufort Sea. As a preliminary test of these hypotheses, we examined the strontium-to-calcium ratios (Sr:Ca) of otoliths from chum salmon from the Colville (Alaska's North Slope) and Tanana (Yukon River drainage) rivers. Yukon River chum salmon were assumed to reside in the Gulf of Alaska and the Bering Sea. Otolith Sr:Ca ratios were similar between rivers, implying that fish from each group lived in similar environments, but also exhibited significant fluctuations often associated with migrations between freshwater and marine environments. Age compositions and sizes of adult chum salmon from the upper Mackenzie River watershed did not differ from chum from a Yukon River tributary. We are not able to refute any of our hypotheses, but the most parsimonious explanation is that arctic chum salmon live in the North Pacific for most of their marine life, rather than in the Beaufort Sea region. Because of the long distance to migrate between the mouth of the Mackenzie and the North Pacific Ocean, we suggest salmon may spend their first winter deep within the Beaufort Sea (i.e., a combination of Hypotheses 1 and 2). Additional elemental and isotopic signature measurements will enable a more thorough testing of these hypotheses, allow us to understand how chum salmon survive cold winter conditions, and thereby better predict potential climate change effects on salmon in the Arctic.

Keywords: salmon, Arctic, Beaufort Sea, Bering Sea, chum salmon, climate change, oceanography, Mackenzie River; low temperature

INTRODUCTION

The subarctic North Pacific Ocean, especially the Bering Sea and Gulf of Alaska (Fig. 1), is a major rearing area for many Pacific salmon. Differences in the distribution and growth of salmon in this region between warm and cold years imply that salmon productivity and growth closely track the thermal regimes and productivity of marine waters. Thus, future effects of climate change may be

significant. Northward ecological community shifts must have occurred at the end of the last ice age, and recent shifts have been documented in the Bering Sea (Mueter and Litzkow 2008). Extensive shifts in species distributions are projected in consequence to changing sea-ice and temperature distributions (Vermeij and Roopnarine 2008). Kaeriyama (2008) predicts distributional changes for chum salmon, with the Arctic becoming increasingly important as ecosystems continue to shift over time.

What is the potential of the Arctic Ocean, including the Chukchi and Beaufort seas for Pacific salmon? With climate change, will this area become a major salmon rearing environment? Will arctic watersheds become important salmon producers? In order to answer these types of questions, we need to better understand the current importance of the Arctic for Pacific salmon, the factors that currently limit salmon production there, and how these factors are likely to respond to climate change.

After briefly describing the oceanography of North American Arctic Ocean and reviewing the status of Pacific salmon in it, we propose three hypotheses to explain the persistence of salmon in the Arctic. The Bering Sea Refuge, the Atlantic Layer Beaufort Refuge, and the Freshwater Beaufort Refuge hypotheses differ primarily in where salmon are purported to spend their winters. We present results on strontium-to-calcium ratios (Sr:Ca) of otoliths from northern chum salmon, examine size and age-frequency data as a preliminary testing of these hypotheses, and identify additional research to further test these hypotheses. Understanding how

salmon from the Arctic are able to survive winter will enable us to better anticipate future climate change impacts.

OCEANOGRAPHY

We focus on the North American portion of the Arctic known to have Pacific salmon, which includes Alaska’s North Slope and the Western Canadian Arctic. Various rivers, including the Colville, drain this portion of the coast, but the Mackenzie River, with a mean annual discharge of 9130 m³/s (Water Survey of Canada, http://www.wsc.ec.gc.ca/staflo/index_e.cfm?cname=main_e.cfm, accessed 12 June 2009), is by far the largest (Fig. 1).

Although the oceanography of the Arctic Ocean is perhaps not as thoroughly observed as most ocean areas to the south due to difficulty of year-round access, a reasonable understanding of ice motion, stratification, seasonality of shelf regions, and ocean currents has been developed during the past three decades. There is a vigorous inflow through Bering Strait (85 km wide, 50 m sill depth; Woodgate and

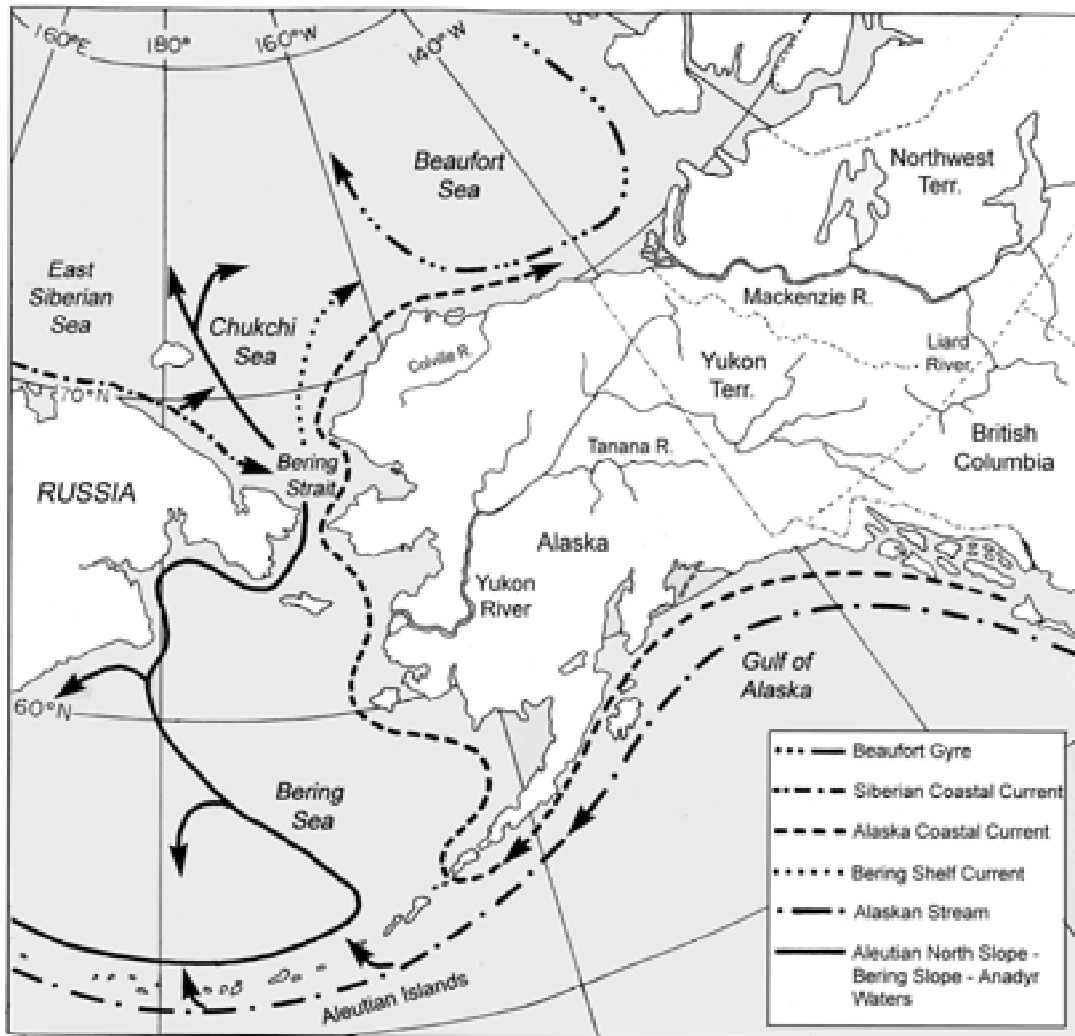


Fig. 1. Study area showing major rivers and ocean currents.

Aagaard 2005) into the western Arctic Ocean, and ice motion of the permanent pack is characterized by a clockwise drift within the Beaufort Gyre (Fig. 1; Aagaard 1984). Due to the strong inflow, the upper layers of the western Arctic Ocean derive largely from the Pacific Ocean (McLaughlin et al. 1996; Yamamoto-Kawai et al. 2008), whereas the deeper water below 200 m or so originates in the Atlantic Ocean (Macdonald et al. 1989). Surface waters (< 50 m) tend to be less salty because of freshwater inflow from the large pan-arctic drainage basin (Carmack et al. 2008). Surface water also undergoes a strong modulation in temperature, exhibiting near freezing temperatures (-1.2 to -1.8 °C) in winter and warmer temperatures in open water around the ocean margin in summer. Below the surface water there is a cold halocline that exhibits near freezing temperatures throughout the year (50–200 m). Below about 200 m where Atlantic water is encountered, the temperatures exceed 0°C throughout the year and salinity increases to above 34.8 (Fig. 2; Carmack et al. 1989). The Alaska Coastal Current forms part of a long transport system that moves fresh water, contained in low-salinity surface water, northward along the North American coast and into the Chukchi Sea where the current then moves eastward along the Alaskan northern coast. Below the surface waters, however, the Beaufort Undercurrent runs eastward along the shelf slope (Aagaard 1984). Carmack and Macdonald (2002) describe the complex seasonal influence of the Mackenzie River on the oceanography of the Beaufort Sea; whether the Mackenzie River plume goes west into the Beaufort Gyre, or east into Amundsen Gulf, is influenced each year by the amount of persistent summer ice cover, its proximity to shore, and the direction, strength, and persistence of prevailing winds.

STATUS OF PACIFIC SALMON IN THE ARCTIC

Of all Pacific salmon, chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon have the broadest distributions, occasionally being encountered west of the Lena River in Siberia, and east of Canada's Mackenzie River (Heard 1991; Salo 1991; Stephenson 2006). Documentation from the 1881 Alaskan voyage of the Revenue-Steamer Corwin (Bean 1883), to our knowledge, provides the first published records of Pacific salmon in Arctic North America. Bean (1883) reported pink and chum salmon in the Bering Strait, chum salmon in Hotham Inlet (Kotzebue Sound), and pink salmon in the Colville River. There is also anecdotal evidence of increased numbers of pink salmon in northern-draining rivers of the Russian north (V. Karpenko, Kamchatka Research Institute of Fisheries and Oceanography, Petropavlovsk-Kamchatsky, Russia, pers. comm.). Recent reviews of salmon in the Canadian Arctic (Babaluk et al. 2000; Stephenson 2006; Irvine et al. 2009) document the capture of Chinook (*O. tshawytscha*), sockeye (*O. nerka*), and coho (*O. kisutch*) salmon, in addition to chum and pink salmon, but note there is no clear evidence of recent increases in abundance. Numbers of chum salmon estimated at individual locations in the Western Canadian Arctic over the years ranged from 1 to 5000 (Stephenson 2006); Irvine et al. (2009) estimated that at least several hundred chum salmon returned to the Liard River in the upper Mackenzie River watershed (Fig. 1) during two years of intensive study.

Coho, sockeye, and Chinook salmon are rare east of Point Hope (western North Slope Alaska), and pink salmon east of Prudhoe Bay (central North Slope Alaska) are generally considered to be vagrants (Craig and Haldorson 1986). Chum salmon appear to be the only species natal to the Mackenzie River watershed as they are the only spe-

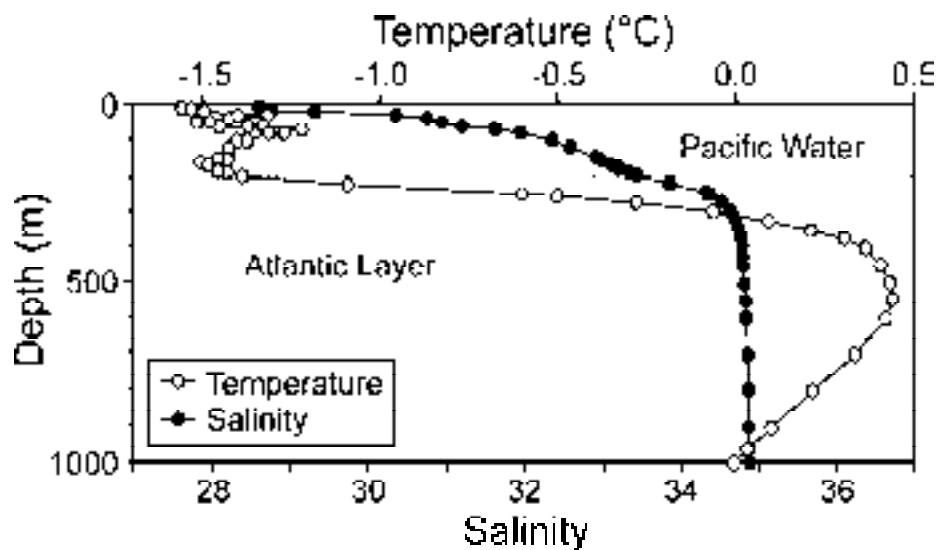


Fig. 2. Typical vertical profiles of temperature (open circles) and salinity (closed circles) for the southern Beaufort Sea of the Canada Basin. Water above about 200 m is cold and comes predominantly from the Pacific Ocean via Bering Strait, whereas water deeper than 200 m is warmer and comes from the Atlantic Ocean via the Barents Sea and Fram Strait.

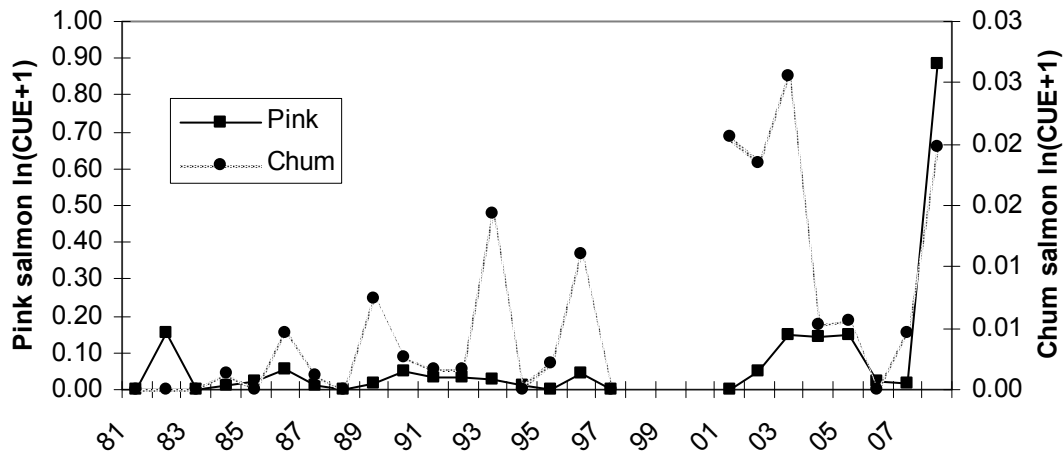


Fig. 3. Catch per unit effort for pink and chum salmon from a nearshore marine fyke net survey in the North Slope, Alaska (data from Fechhelm et al. (2008) and Bob Fechhelm, LGL Ecological Research Associates, Bryan, Texas, USA, pers. comm.).

cies consistently captured in good numbers in upstream areas with many individuals exhibiting pre-reproductive development. Traditional knowledge supports this theory; chum is the only salmon species with a name in the Inuvialuktun and Dene languages of this area (Coad and Reist 2004; Stephenson 2006). Closer to the Bering Strait, both pink and chum salmon are reported from various rivers in the Prudhoe Bay area, including the Colville (Craig and Haldorson 1986). We assume pink and chum are natal in many of these streams, but this has not been confirmed.

Salmon abundance time series are rare. One exception is the monitoring program operated ~50 km west of Prudhoe Bay to evaluate potential effects of oil and gas exploration in the area (Craig and Haldorson 1986; Fechhelm et al. 2008). Small numbers of pink and chum salmon have been caught in most years in a nearshore fyke net, which has been maintained since 1981, and larger numbers of pink salmon were caught in 2008 (Fig. 3). It is impossible to know if the high 2008 pink salmon catches reflect a spike in actual abundance, or are some sort of artefacts.

The Canadian Arctic Salmon Sampling Program monitors salmon caught by subsistence harvesters, aboriginal and commercial fishers, and others in and near the Mackenzie River. During the past decade, salmon catches have increased, especially for pink and chum salmon (J. Reist, unpubl. data). While it is not possible to know if the apparent increase in frequency of occurrence is a climate change effect, something appears to have changed to either increase the survival of natal fish from the Mackenzie, the wandering of non-natal fish to the Mackenzie, or both.

To summarise, salmon in the Arctic are uncommon. All five species have been captured, and while there is some evidence implying recent increases in abundance, this does not necessarily mean additional spawning in the Arctic. Chum and pink salmon are encountered more frequently than coho, sockeye, and Chinook salmon, and there is general agreement that only chum salmon are natal to the Mackenzie

River watershed while chum and pink salmon are probably natal to several rivers in Alaska's North Slope.

WHERE DO ARCTIC SALMON OVERWINTER?

While recent dramatic reductions in the extent of summer ice coverage in the Arctic have been well-documented (e.g., Stroeve et al. 2008), ice coverage during winter continues to extend beyond the Arctic Ocean southward into the Bering Sea. The ability of salmonids to tolerate cold waters varies among species, but in general, acclimatized salmon can survive subzero temperatures provided they do not come in contact with ice crystals (Brett and Alderdice 1958; Fletcher et al. 1988).

We focus here on chum salmon because they are the only species thought to return regularly to the Mackenzie River. We present three hypotheses (Bering Sea Refuge, Atlantic Layer Beaufort Refuge, and Freshwater Beaufort Refuge) to explain how chum salmon are able to persist in the Arctic. In all cases, chum salmon fry are transported downstream by river flows, arriving at the mouth of the Mackenzie (or other) River in June/July of the year following spawning. We assume chum usually spend three winters at sea (occasionally two or four) as found by Irvine et al. (2009) for chum from the Liard River, returning to the mouth of their spawning river in late summer or early autumn. Each hypothesis differs in where chum spend their winters, meaning that the temperatures and salinities fish are exposed to in the marine environment also vary. Although incomplete, our understanding of the physical and chemical oceanography of the Arctic Ocean is sufficient to speculate on the influence of these conditions on chum salmon.

Hypothesis 1 - Bering Sea Refuge

According to this hypothesis, after arriving in the ocean, young-of-the-year chum salmon are carried north (offshore)

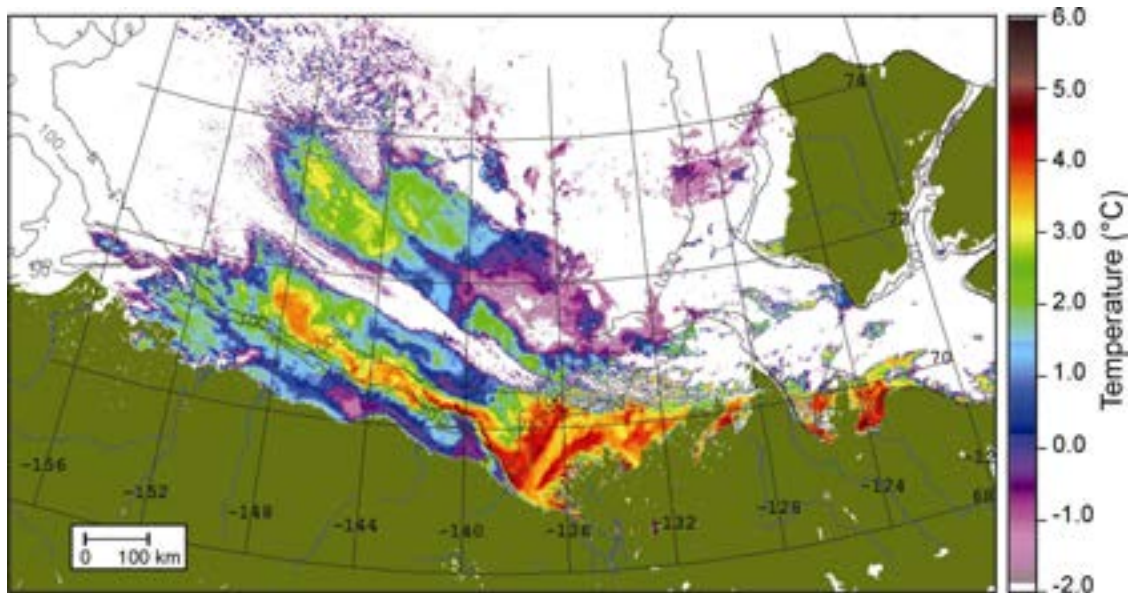


Fig. 4. A satellite thermal image taken of the Southern Beaufort Sea on 17 September 2008. The influence of the Mackenzie Plume likely extends westward at least as far as 142° W where it connects with a continuous band of what is probably warm Alaskan coastal water (SeaWiFS data were obtained from OCDP Archive, NASA/Goddard Space Flight Center).

and sometimes west towards the icepack in the Mackenzie plume (Fig. 4). From there young chum are transported west towards the Chukchi Sea either by means of wind-driven longshore currents, as proposed by Fechhelm and Fissel (1988) for Arctic cisco (*Coregonus autumnalis*), and/or by taking advantage of the westerly flowing Beaufort Gyre near the ice edge, which in some years also transports substantial amounts of Mackenzie River water (Macdonald et al. 1999). To arrive in the Bering Sea before freeze-up, young Mackenzie River chum salmon need to cover the distance (~1800 km) at a speed of ~24 km/d (assuming 75 days to complete the migration). Young chum salmon from Alaskan North Slope rivers, with a shorter distance to swim to reach the Bering Strait, rely chiefly on wind-driven currents to move them west.

Because the dominant flow leaving the Bering Sea is northward (Woodgate and Aagaard 2005), young chum exiting the Chukchi Sea would normally have to swim against the current, perhaps saving energy by remaining close to the Asian side of the Bering Strait where currents are generally slowest (Fig. 1). Alternatively, fish could be assisted by occasional southerly flow reversals consequent to periods of northerly winds (see Woodgate et al. 2006).

Once in the Bering Sea, arctic chum salmon probably adopt a migratory strategy similar to that proposed by Myers et al. (2007) in their conceptual model for Pacific salmon in the open ocean. According to Myers et al., salmon move southeastward towards the Gulf of Alaska in fall, and back to the Bering Sea in summer. After typically three winters in the Bering Sea and Gulf of Alaska, arctic chum salmon return to the Mackenzie (or other) River, taking advantage of the Alaska Coastal current, arriving at the mouth of their

natal river in late summer or early autumn.

Although this hypothesis requires young chum salmon to migrate a long distance, it is attractive because for the majority of their life, arctic chum salmon occupy the same environment as many chum from the North Pacific.

Hypothesis 2 - Atlantic Layer Beaufort Refuge

This hypothesis proposes that young-of-the-year chum salmon carried north towards the icepack avoid freezing temperatures by swimming down to water of Atlantic origin (> 200 m) in fall. After wintering at depth in these waters, which exceed 0°C throughout the year (Fig. 2), chum return towards the surface, and spend the ice-free period within the Beaufort Sea actively feeding and growing. This seasonal vertical migratory pattern is repeated typically during three years at which point the salmon return to the Mackenzie (or other) River and migrate upstream to spawn.

This hypothesis is appealing from the standpoint that salmon do not need to migrate over the long distance required to reach the Chukchi Sea, or swim against the current to enter the Bering Sea. Furthermore, from what we know about the replenishment process for the Atlantic layer, heat has been sustained here reliably over a long time-frame and is not affected by either local ice conditions or weather. Other studies have reported chum in the North Pacific at the depths and temperatures required under this hypothesis. For instance, Walker et al. (2000) recorded chum in very cold waters (-1°C to 1°C), possibly several hundred metres deep. Ueno (1992) found that chum salmon were frequently caught in trawls at depths exceeding 200 m.

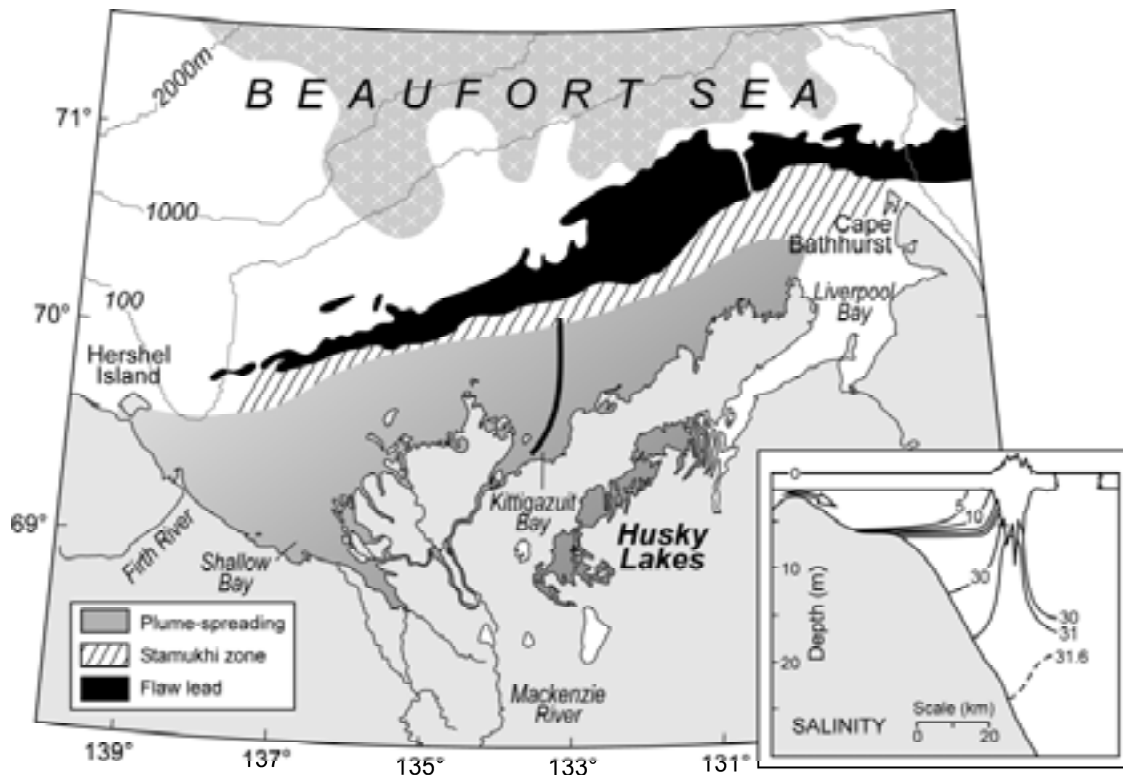


Fig. 5. A diagram showing the disposition toward the end of winter (May) of Mackenzie River water that has invaded the nearshore under the ice of the Canadian Beaufort Shelf. The inset section shows the depth and salinity of the brackish water, which extends out to the rough ice (stamukhi) located at the end of the landfast ice zone. This seasonal, under-ice lake covers approximately 16,000 km² by the end of winter (Macdonald et al. 1995).

Hypothesis 3 - Freshwater Beaufort Refuge

In this case, chum salmon adopt a strategy similar to other arctic fish species. For instance, Dolly Varden (*Salvelinus malma*) and several coregonine species common in the Arctic spend their summers in the Beaufort Sea, typically near the coast, but retreat into fresh or brackish waters, at temperatures at or close to zero in winter, thereby avoiding sub-zero (-1.9 °C) temperatures associated with more saline water during winter (Fig. 2; Craig 1984; Craig 1989). Fish may also over-winter in groundwater-influenced stream environments, near the bottoms of coastal lakes, or within parts of the Mackenzie River plume that flows underneath a large portion of the landfast ice (Fig. 5; Macdonald et al. 1995).

The Freshwater Beaufort Refuge Hypothesis is also attractive because salmon do not have to migrate long distances, including an upstream migration through the Bering Strait. However, as chum salmon elsewhere are not known to rely on fresh or brackish refugia as a means of avoiding cold marine environments, if it occurs, this strategy would likely be a specific adaptation to the Arctic. Furthermore, fish over-wintering in the plume under the ice would endure very uncertain conditions where they might be exposed to either below-freezing water near the bottom or frazil ice formation at interfaces.

PRELIMINARY TESTING OF HYPOTHESES

While the most direct way to test these hypotheses would be to sample the proposed winter environments for arctic chum salmon, the likelihood of capturing salmon during winter in the Arctic is extremely low. Most winter fish sampling techniques are not only dangerous but tend to be passive, and unlikely to catch uncommon non-migrating fish. If arctic salmon are in the Bering Sea, they will be mixed with many more numerous salmon populations. Genetic techniques could theoretically be applied to identify arctic salmon in the Bering Sea, but an inadequate baseline for arctic salmon and small sample sizes makes this approach impractical at this time. Fortunately we can take advantage of the different chemical signatures of the various environments potentially used by arctic salmon to evaluate the hypotheses. We can also compare growth and age patterns of salmon from the Arctic with salmon from other northern areas.

If Hypothesis 1 (Bering Sea Refuge) is correct, salmon are exposed to relatively constant salinity (maximum 34.45) during their marine period, but significant seasonal variability in temperatures (-2.7 to 15.6 °C, Azumaya et al. 2007). If Hypothesis 2 (Atlantic Layer Beaufort Refuge) is correct, fish are exposed to winter salinities similar to those in Hypothesis 1, but reduced summer salinities, and lower

minimum and maximum temperatures (~1 and ~8 °C). With Hypothesis 3 (Freshwater Beaufort Refuge), salinity profiles are much more variable, with the lowest minimum values for fish retreating to fresh or brackish water in winter. In addition, salmon wintering in the Mackenzie plume would probably be exposed to colder winter temperatures than those retreating to fresh water.

As a preliminary test of the Freshwater Beaufort Refuge Hypothesis, we examined the Sr:Ca ratios of otoliths from six returning adult chum salmon collected in the Colville River and six returning adult chum salmon collected in the Tanana River, a major tributary of the Yukon River (Fig. 1). Secor et al. (1995), Zimmerman (2005), and others have documented that the ratio of Sr to Ca is generally greater in otolith material precipitated in marine rather than in fresh water, and that analysis of Sr:Ca ratios across fish otoliths can reveal their migratory histories between marine and freshwater environments. We also compared the size and age of chum salmon from the Liard River with those caught in the Porcupine River, another tributary of the upper Yukon River. The life

history of chum salmon from the Yukon River and tributaries is similar to that of other non-arctic chum; they migrate to the ocean during their first summer and remain in marine waters until they return to spawn (Salo 1991). We hypothesized that if Colville River chum salmon overwintered in marine waters of the Bering Sea/Gulf of Alaska, similar to Yukon River chum salmon, then the two groups would have similar otolith Sr:Ca profiles, sizes, and age compositions. If Colville chum wintered deep within the Beaufort Sea, or within the freshened water of the Mackenzie River plume or adjacent areas (i.e., Hypotheses 2 and 3), their otolith Sr:Ca profiles might exhibit larger oscillations, particularly for Hypothesis 3. Otolith Sr:Ca profiles for chum wintering in fresh or brackish waters should exhibit larger oscillations than Tanana River chum salmon, similar to those of Arctic char *Salvelinus alpinus* (Halden et al. 1995), inconnu *Stenodus leucichthys* (Howland et al. 2001), and other anadromous salmonids that annually migrate between high and low salinity environments. If chum salmon remain in the Beaufort Sea region, their growth (i.e., size at age) should

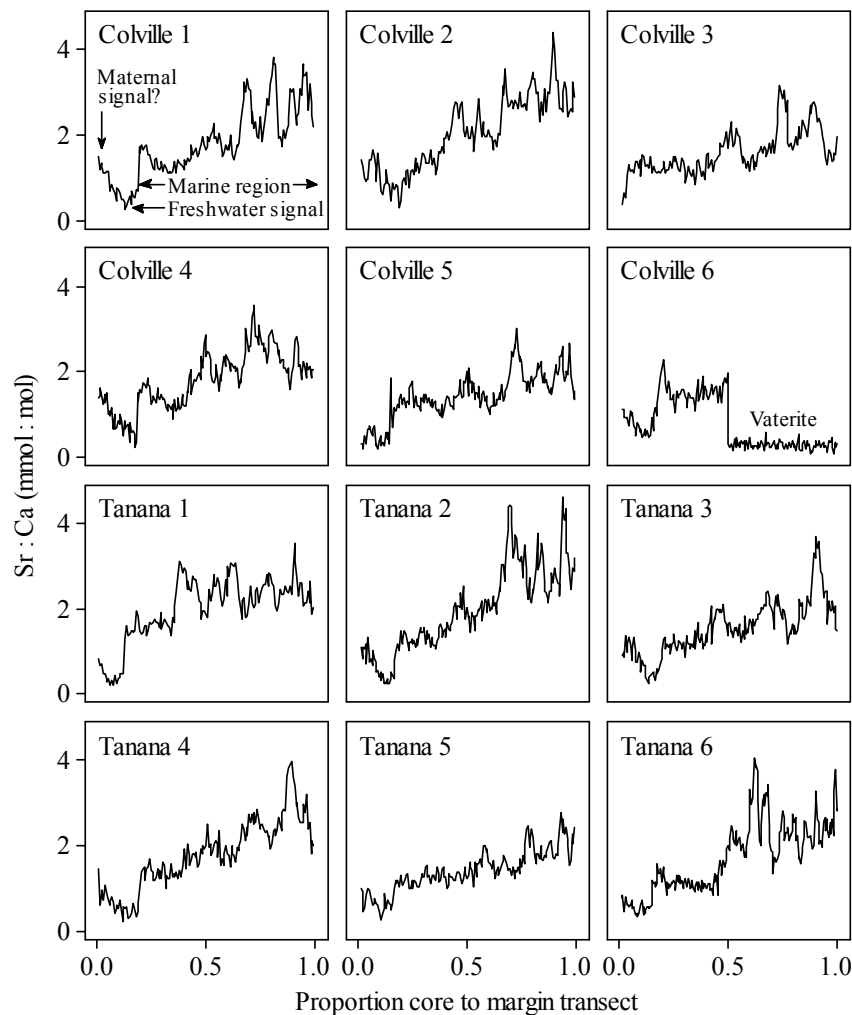


Fig. 6. Lifetime otolith Sr:Ca profiles of six Colville River chum salmon (top two rows) and six Tanana River (Yukon River drainage) chum salmon (bottom two rows).

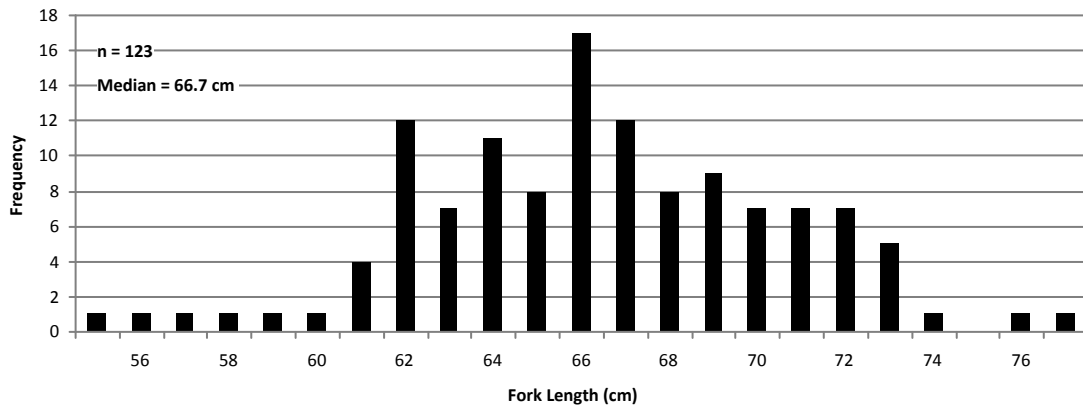


Fig. 7. Length frequency distribution of adult chum salmon from the Liard River (from Irvine et al. 2009).

be depressed compared to fish in the Bering Sea and North Pacific Ocean, and perhaps they might return to spawn as older fish, due to the colder winter temperatures.

Using methods described by Brown et al. (2007), Sr and Ca concentrations were measured in chum salmon from the Tanana and Colville rivers, at a series of points from the core of each otolith (precipitated early in life) to its margin (precipitated late in life). These data were converted to molar ratios of Sr:Ca using equivalency equations presented by Brown and Severin (2008), and plotted as ontogenetic profiles (Fig. 6). In these preliminary analyses, comparisons were limited to descriptive assessments of patterns of Sr:Ca variation (Fig. 6).

Strontium:Ca profiles of the Colville River chum salmon were similar to those of Tanana River chum salmon (Fig. 6), suggesting these fish experienced similar environments throughout life. Freshwater regions near the core were narrow and all fell in the range of Sr:Ca < 1 mmol:mol. Several members of each group had an elevated region of Sr:Ca (> 1 mmol:mol) in the core that is probably a maternal contribution of marine Sr via the egg, a phenomenon documented by Arai and Miyazaki (2002) for chum and Volk et al. (2000) for other anadromous salmonids. All chum salmon from the Colville and Tanana river groups exhibited an initial rise in Sr:Ca to levels ranging between approximately 1 and 2 mmol:mol. A general increasing ontogenetic Sr:Ca trend was evident for chum salmon within both groups rising to maximum levels ranging from just under 3 mmol:mol (Fig. 6, Colville 5 and Tanana 5) to just over 4 mmol:mol (Fig. 6, Colville 2 and Tanana 2). An exception to this trend was sample Colville 6, for which the outer region consisted of vaterite. Vaterite regions of otoliths are visually distinctive and have been shown to exhibit very low levels of Sr that do not reflect environmental chemistry (Brown and Severin 1999; Tzeng et al. 2007).

Somewhat surprisingly, chum salmon from both groups exhibited Sr:Ca oscillations in the latter portion of their profiles that spanned as much as 2 mmol:mol. Oscillations of this magnitude are normally associated with migrations be-

tween freshwater and marine environments (e.g., Brenkman et al. 2007). Because the Tanana River chum salmon are not thought to migrate annually between marine and fresh waters, the oscillations seen in their Sr:Ca profiles may reflect physiological responses within the marine environment, as reported by Arai and Miyazaki (2002) for chum salmon from the Otsuchi River in Japan. We are not able to refute any of our hypotheses based on these results.

Chum salmon captured in the Liard River ranged between 55 and 78 cm fork length (Fig. 7) and 2000 and 6200 g. Four-year-old fish predominated, with some three- and five-year-olds also caught; approximately 61% of the catch was male, and 39% female (n = 167, Irvine et al. 2009). Irvine et al. (2009) compared these results with those for chum from the Yukon River watershed as documented by Boyce (2001, 2002), Boyce and Vust (2002), and Boyce and Wilson (2001). In the Porcupine River, a tributary of the Yukon, for the four years considered, returning chum ranged in age from three to six years. The majority were age three to five with age-four fish being the most common, the same as found for chum from the Liard. Male and female chum caught in weirs in the Yukon did not differ in abundance, while in the Liard, males were caught most frequently, perhaps a result of sex-biased sampling by gill nets. Irvine et al. (2009) did not find significant differences between the sizes of male and female chum of each age caught in the Liard and those in the Yukon, although in some cases, sample sizes from the Liard River were small.

Similar growth patterns for chum from the Mackenzie and Yukon rivers support Hypothesis 1 (Bering Sea Refuge). Furthermore, if chum salmon are living in the Beaufort Sea region (Hypotheses 2 and 3) for a significant period of their lives, one would expect that subadult fish would have been reported in some of the many sampling projects that have been conducted along the Beaufort Sea coast of Canada and Alaska (e.g., Kendel et al. 1975; Percy 1975; Bond 1982; Craig 1984; Craig et al. 1985; Bond and Erickson 1989, 1992; Jarvela and Thorsteinson 1999; Brown 2008; Fechhelm et al. 2008; and many more); yet subadult size chum salmon

have never been reported, other than in recent surveys in the Chukchi Sea (Kondzela et al. 2009; Moss et al. 2009). We believe these lines of evidence are most consistent with the Bering Sea Refuge Hypothesis although the long distance chum would need to migrate between the Canadian Arctic and the Bering Sea needs to be considered.

The speed required for chum to reach the Bering Sea in their first season (~24 km/d) is significantly greater than their normal swimming speed. Even if the chum migration is assisted by currents, it may not be possible to reach the Chukchi Sea in the first year, so perhaps chum spend their first winter in the Beaufort Sea below 200 m to avoid freezing temperatures. Adopting this strategy would give them extra time to complete their migration, and also provide them the opportunity to reach a larger size, when they would presumably be more capable of migrating against the current to reach the Bering Sea. We note that Japanese chum salmon spend their first winter in a narrow region of the western North Pacific, arriving at the Bering Sea in their second summer-fall (Myers et al. 2007).

Although we are unable to exclude any of the three hypotheses based on our preliminary evaluation, the most parsimonious explanation is that arctic chum salmon live in the North Pacific for most of their marine life, rather than the Beaufort Sea region. Because of the long distance to migrate between the mouth of the Mackenzie and the North Pacific Ocean, they may spend their first winter deep within the Beaufort Sea (i.e., a combination of Hypotheses 1 and 2). However, it is not possible to eliminate the Freshwater Beaufort Refuge Hypothesis due to the surprising range of otolith Sr:Ca values for chum salmon from the Colville and Tanana river samples.

FUTURE WORK NEEDED TO TEST HYPOTHESES

We recommend additional elemental and isotope analyses to fully test our hypotheses. For instance, Arai and Hirata (2006) found that, in addition to Sr, concentrations of Mg, Zn, and Ba also differed between the freshwater and seawater growth zones of chum otoliths. Unfortunately, elemental results can sometimes be confusing due to natural variability in elemental concentrations within environments. In addition, temperature and salinity, the two primary environmental parameters to differentiate among our hypotheses, can have an interactive effect on otolith microchemistry (Elsdon and Gillanders 2002). In contrast, the $^{87}\text{Sr}:^{86}\text{Sr}$ ratios for particular freshwater systems tend to be constant and often different from those in the ocean (Kennedy et al. 2002). Milton and Chenery (2003) described anadromous migrations of a tropical shad by examining variation in the ratio of $^{87}\text{Sr}:^{86}\text{Sr}$ isotopes, along linear transects. The dietary history of a fish is recorded in the organic matrix of its otolith; $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ are particularly useful at tracing this history since these stable isotopes are more enriched in marine versus freshwater prey (Hesslein et al. 1993; Doucett et al. 1999;

Weber et al. 2002; L. Godbout, unpubl. data). Measures of these stable isotopes in prey from locations associated with the hypotheses (Gulf of Alaska, Bering Sea, Beaufort Sea, Mackenzie River plume and nearby freshwater habitats) as well as in salmon otoliths from Mackenzie River chum salmon will allow one to determine in which environments salmon are most likely to have lived. Isotopic signatures of salmon prey are likely to differ among the various locations, as there is evidence for differences in salinities and food webs among locations. For instance, $\delta^{13}\text{C}$ is enriched in Bering Sea zooplankton compared to Beaufort Sea zooplankton (Saupe et al. 1989) and this difference is likely to occur at other trophic levels.

Measures of stable oxygen isotopes can also be used to reconstruct the water temperatures at which fish lived. This is possible because there is temperature-dependent fractionation during the formation of the otolith; increases in water temperature result in lower $\delta^{18}\text{O}$ (Høie et al. 2004). Because the slopes of fractionation equations are constant among species (Storm-Suke et al. 2007), a general fractionation equation could be used to describe the thermal conditions in relative terms. This approach would be useful to differentiate between the Bering Sea Refuge and Atlantic Layer Beaufort Refuge hypotheses.

Additional exploration can be done at lower levels of temporal resolution of life histories by measuring isotopic signatures from tissue samples such as muscle and scales. Finally, additional fish growth patterns, as reflected by otolith and/or scale growth, should be compared among arctic salmon and other reference fish of known history.

In summary, to thoroughly evaluate the hypotheses proposed, which would allow one to evaluate potential climate change effects on arctic salmon, we recommend that elemental and isotopic signatures be measured in:

- Otoliths and tissue from arctic and more southerly salmon populations;
- Tissue from fish of known habitats; and
- Prey and water samples from the Bering Sea, Beaufort Sea, Mackenzie River plume and nearby freshwater habitats

Fortunately some of this work has been completed. For instance, the Canadian Arctic Salmon Sampling Program has been gathering salmon samples from the western Canadian Arctic since 1986. The U.S. Fish and Wildlife Service have access to salmon samples from the Prudhoe Bay region. Similarly, reference fish samples are available from all areas, and some have been analysed for elemental and isotopic ratio levels. However, fewer environmental samples, especially of salmon prey, have been collected and essentially no relevant laboratory analyses of these samples have been completed.

Anticipating climate effects on arctic salmon is an international issue. Much valuable information has resulted from events such as the International Polar Year, and through the cooperative research by agencies such as the North Pacific

Anadromous Fish Commission. We encourage a continuing collaborative approach among scientists to better understand likely impacts of climate on salmon and other creatures in the Arctic.

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Stock-Structured Distribution of Western Alaska and Yukon Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) from United States BASIS Surveys, 2002–2007

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Abstract: We describe migratory patterns of western Alaska and Yukon Chinook salmon (*Oncorhynchus tshawytscha*) using stock-structured distribution data from United States Bering-Aleutian Salmon International Surveys (BASIS), 2002–2007. Juvenile Chinook salmon were distributed within water depths less than 50 m and their highest densities were found close to river mouths of primary Chinook salmon-producing rivers in the eastern Bering Sea (Yukon, Kuskokwim, and Nushagak rivers) through their first summer at sea. This reflects a later marine dispersal from freshwater entry points than typically found in Gulf of Alaska stream-type Chinook salmon and resulted in the presence of juvenile Chinook salmon in shallow, non-trawlable habitats during the surveys. Juvenile Chinook salmon stock proportions in the northern shelf region (north of 60°N) were: 44% Upper Yukon, 24% Middle Yukon, 31% Coastal Western Alaska, and 1% other western Alaska stock groups. Juvenile Chinook salmon stock proportions present in the southern shelf region (south of 60°N) were: 95% Coastal Western Alaska, 1% Upper Yukon, and 4% other western Alaska stock groups. It is believed that these stock mixtures do not support significant northward migration of stocks from the southern shelf, and reflect limited mixing of salmon from the two production regions during their first summer at sea. Spatial distribution patterns and coded-wire tag recoveries provide evidence that the distribution of Yukon River Chinook salmon extends northward into the Chukchi Sea during their first summer at sea. Although the juveniles present in the Chukchi Sea represent a minor portion of the total Yukon River juvenile population, continued warming of the Arctic could increase the proportion of Yukon River Chinook salmon migrating north into the Chukchi Sea.

Keywords: Bering Sea, Chinook salmon, distribution, migration, stock structure

INTRODUCTION

Migratory corridors used by Chinook salmon (*Oncorhynchus tshawytscha*) and their distribution within the corridors provide key information on the early marine ecology and life-history strategies of juvenile salmon important to their growth and survival (Brodeur et al. 2000). Juvenile Chinook salmon from western Alaska and Yukon, Canada enter the marine waters of the eastern Bering Sea during the spring and summer and migrate along the coast of western Alaska during their first summer in the ocean (Healey 1991). An understanding of the underlying migratory patterns of salmon is also required to interpret and apply research survey data to population studies of Chinook salmon (Farley et

al. 2005).

Although much of the historical work on salmon migration has relied on tagging and marking research (Hartt and Dell 1986; Orsi and Jaenicke 1996; Farley et al. 1997; Courtney et al. 2000), genetic methods have expanded the ability of research surveys to define migratory behavior of salmon in the ocean (Seeb et al. 2004; Templin et al. 2005). Recent developments in single nucleotide polymorphism (SNP) markers and genetic baselines provide efficient and accurate assignment of Chinook salmon to freshwater origin (Smith et al. 2005; Templin et al. 2005). SNP data can be collected and scored very rapidly compared to other genetic markers, thus increasing its power and efficiency to discriminate stock origins.

Farley et al. (2005) initially described migratory pathways of juvenile Chinook salmon in the eastern Bering Sea using information on juvenile salmon size distribution. Reconstructing migration corridors from size data capitalizes on the fact that much of the variability in juvenile size reflects the time of ocean entry. Dispersal patterns of juvenile salmon from points of ocean entry are apparent in the spatial distribution of size, with the largest juvenile salmon (earliest out-migrants) distributed the greatest distance from their point of ocean entry. In the following analysis, migratory patterns of juvenile western Alaska and Yukon Chinook salmon are described using information on ocean distributions and freshwater origin from coded-wire tags and genetic stock identification methods.

METHODS

Juvenile Chinook salmon were collected with surface rope trawls during the U.S. Bering-Aleutian Salmon International Survey (BASIS) on the eastern Bering Sea shelf from 2002–2007 (Table 1). Start dates of the survey ranged from August 14 to August 21; end dates ranged from September 20 to October 8 (Table 1). Variation in start and end dates each year reflected changes in vessel availability and survey coverage and design. The initial survey design (2002 and 2003) used transect-based sampling along latitude and longitude lines (Farley et al. 2005). A grid-based sampling design with stations at each degree of longitude and 30 minutes of latitude was used from 2004 to 2007.

Juvenile Chinook salmon and other pelagic fish were collected with surface rope trawls built by Cantrawl Pacific Limited of Richmond, British Columbia (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.). Trawls were 198 m long, had hexagonal mesh in wings and body, and included a 1.2-cm mesh liner in the codend (Murphy et al. 2003). Trawls were

towed at the surface at an average speed of 4.3 knots, resulting in an average vertical mouth opening of 14 m and horizontal mouth opening of 58 m. Sampling depths were slightly deeper than the vertical opening as the center of the trawl often was just below the surface during the trawl deployment. Water depths shallower than 20 m were considered non-trawlable and were not sampled. Nor' eastern Trawl Systems 5-m alloy doors with 60-m bridle lengths were deployed typically 360 m astern of the boat. Buoys were secured to the wing-tips and center of the headrope to help keep the trawl at the surface and wingtip buoy wakes were monitored to ensure the headrope was maintained at the surface during the tow. Trawl speeds were adjusted to keep the trawl at the surface and trawl doors in the water. A Simrad FS900 net sounder was used to monitor the fishing dimensions and trawl geometry during each tow. All trawls were towed astern of the vessel for 30 min at each station. Catch per unit of fishing effort, CPUE, was used to describe salmon spatial distributions and the standardized unit of fishing effort was effort during a 30-min trawl set. Average area swept by the trawl at each station was 0.25 km².

Stations were sampled between 07:30–21:00 hours (Alaska Standard Time), and typically four stations were sampled each day. Stations were sampled during daylight with the exception of the first station of each day. The first station of the day was sampled just after sunrise, and occasionally sampling would occur during sunrise depending on the schedule set for vessel operations by the chief scientist. Salmon catch rates from the crepuscular time-period were not significantly different from other daylight samples (Farley et al. in press). Sample dates differed by location due to the order in which stations were sampled during the survey. Average sample dates were estimated with a weighted average date with weights provided by the catch at each station.

Standard research trawl protocols were used to process the trawl catch. All salmon were sorted and counted by spe-

Table 1. Number of surface trawl stations sampled during U.S. BASIS surveys on the eastern Bering Sea shelf by year and vessel, 2002–2007.

Year	Vessel	Start Date	End Date	Number of Trawl Stations
2002	<i>F/V Sea Storm</i>	20-Aug-02	07-Oct-02	152
	<i>F/V Northwest Explorer</i>	08-Sep-02	06-Oct-02	44
2003	<i>F/V Sea Storm</i>	21-Aug-03	08-Oct-03	151
2004	<i>F/V Sea Storm</i>	14-Aug-04	30-Sep-04	143
2005	<i>F/V Sea Storm</i>	14-Aug-05	06-Oct-05	127
2006	<i>F/V Sea Storm</i>	14-Aug-06	20-Sep-06	105
	<i>F/V Northwest Explorer</i>	21-Aug-06	04-Sep-06	53
2007	<i>F/V Sea Storm</i>	15-Aug-07	08-Oct-07	136
	NOAA Ship <i>Oscar Dyson</i>	05-Sep-07	26-Sep-07	50

cies and life-history stage; all juvenile Chinook salmon were examined for a missing adipose fin. Snouts were removed from juvenile Chinook salmon with a missing adipose fin and examined for the presence of a coded wire tag at the Auke Bay Laboratories in Juneau, Alaska. Individual lengths and weights were collected from a subsample of up to 50 Chinook salmon and genetic samples were collected from these fish.

Kriging models implemented in ArcGIS software package (ESRI 2006) were used to construct the spatial distribution map of juvenile Chinook salmon on the eastern Bering Sea shelf. The spatial mean was removed with a local polynomial regression model prior to fitting the Kriging model and the spatial covariance of juvenile Chinook salmon was modeled with a spherical variogram (Cressie 1991). The spatial model was used to estimate the distribution of juvenile Chinook salmon in non-trawlable habitats with the addition of boundary conditions. Boundary conditions were created by adding with zero catch points on land at spatial scales matching the survey sampling grid.

Freshwater stock origins of juvenile Chinook salmon were determined from coded-wire tag (Jefferts et al. 1963) recoveries and from genetic stock identification analysis. Coded-wire tags were assigned to freshwater origin using the coast-wide mark database maintained by the Pacific States Marine Fisheries Commission (<http://www.rmfc.org/>) and by coded-wire tag release information provided by the Whitehorse Rapids Fish Hatchery (YRJTC 2009).

A coast-wide baseline of 42 SNP genetic markers for

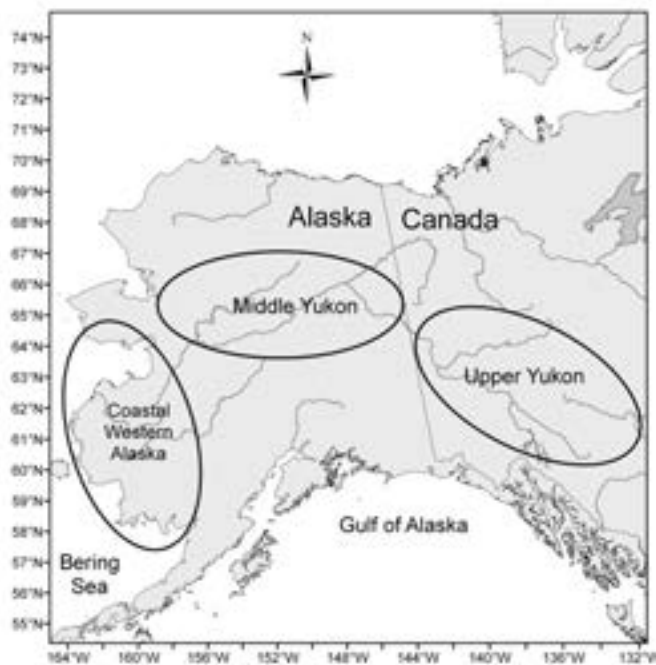


Fig. 1. Approximate locations of regional genetic stock groups of juvenile Chinook salmon (Coastal Western Alaska, Middle Yukon, and Upper Yukon) captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf.

Chinook salmon (updated from Templin et al. 2005) was used to assign freshwater origin of juvenile Chinook salmon. SNP data were obtained from 1,356 juvenile Chinook salmon collected during 2002–2006 following the methods of Seeb et al. (2009), and stock mixtures were estimated for three locations on the eastern Bering Sea shelf. Mixed stock proportions at each location were estimated using conditional maximum likelihood models implemented in the SPAM 3.7 mixed-stock software program (Debevec et al. 2000). Accuracy of mixed stock assignment to freshwater origins considered in this analysis was greater than 90% using the 42-SNP baseline (Templin et al. 2005).

Chinook salmon outside of the eastern Bering Sea were not assumed to be present in the area sampled by the U.S. BASIS survey during their first summer at sea (juvenile life-history stage); therefore, only Chinook salmon stocks from eastern Bering Sea river systems were considered in the mixed stock analysis. Stock groups included in the analysis were: the Upper Yukon River stock group, the Middle Yukon River stock group, the Coastal Western Alaska stock group, and an ‘Other’ stock group (Fig. 1). The Coastal Western Alaska stock group included the Lower Yukon Chinook salmon stocks and all other western Alaska stock groups outside of the Yukon River except the Upper Kuskokwim River and North Alaska Peninsula stock groups. For simplicity, these two stock groups were combined into a single ‘Other’ stock group. The Lower Yukon stock group included Alaskan tributary streams draining the Andreafsky Hills and Kaltag Mountains; the Middle Yukon stock group included Alaskan tributary streams in the upper Koyukuk River and Tanana River basins; the Upper Yukon stock group included Canadian tributary streams draining the Pelly and Big Salmon mountains (Lingnau and Bromaghin 1999).

Juvenile mixtures in the northern shelf region (north of 60°N) were compared with expected adult stock mixtures in the Yukon River. Expected adult stock mixtures were estimated by the average mixtures present in historical and recent commercial and subsistence harvests in the Yukon River (DuBois and DeCovich 2008; Bue and Hayes 2009). These estimates were not corrected for potential stock selective harvest.

RESULTS

Juvenile Chinook salmon were primarily distributed within water depths less than 50 m through their first summer at sea (middle of August through the middle of October). The highest densities of juvenile Chinook salmon were found close to river mouths of primary Chinook salmon-producing rivers in the eastern Bering Sea (Yukon, Kuskokwim, and Nushagak rivers) (Fig. 2). Juvenile Chinook salmon were distributed as far north as the Chukchi Sea and the southern extent of their distribution was along the north shore of Bristol Bay. The migratory corridor of juvenile Chinook salmon was broader in the northern shelf (north of 60°N) than in the

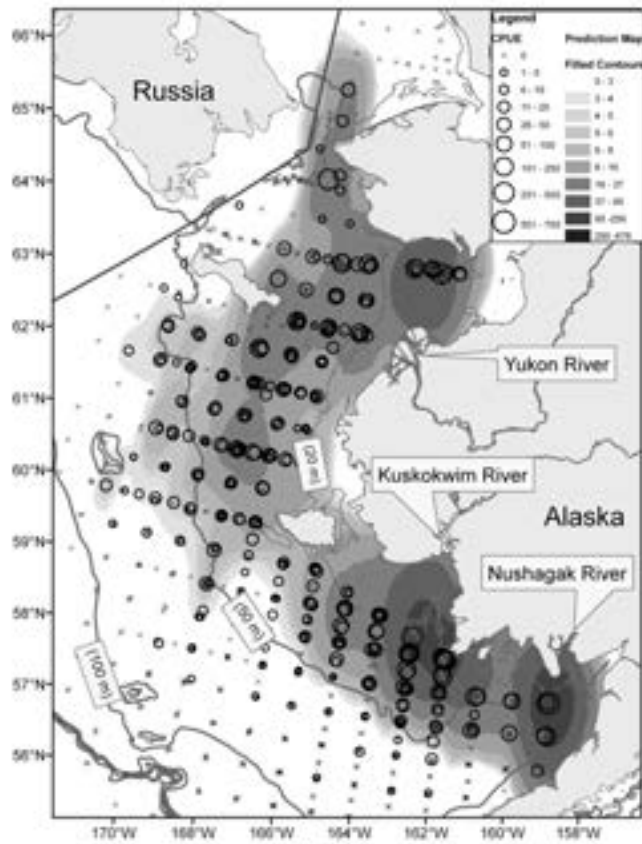


Fig. 2. Distribution of juvenile Chinook salmon during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2007. Distribution is based on catch per unit of effort (CPUE) with a 30-min trawl haul used as the standard unit of effort. Individual trawl catches are overlaid on the CPUE prediction surface from a Kriging spatial model. Contours are shaded at geometric intervals of the prediction surface.

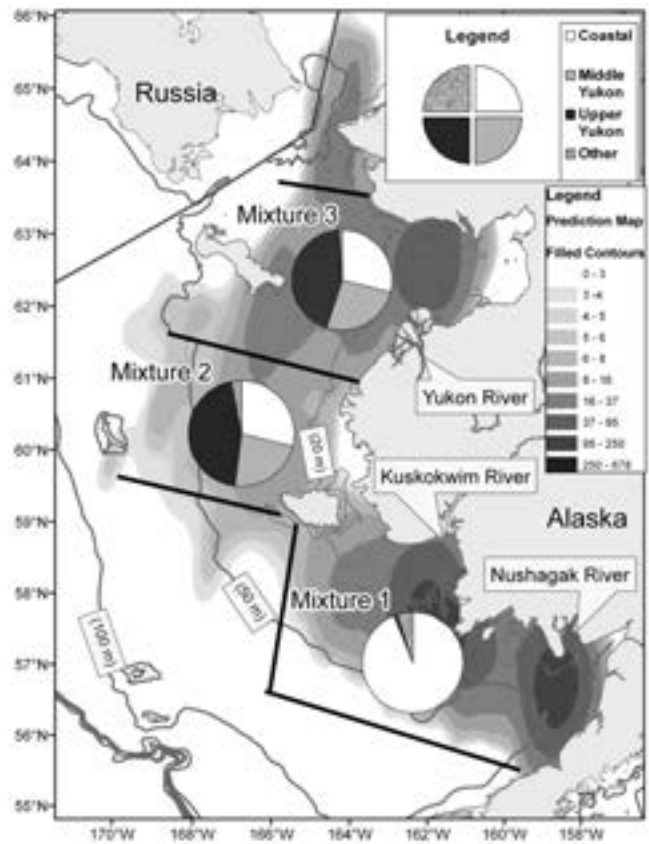


Fig. 3. Genetic stock mixtures of juvenile Chinook salmon (Coastal Western Alaska, Middle Yukon, Upper Yukon, and ‘other’ stock groups) captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2006. Mixtures are overlaid on a map of juvenile Chinook salmon distribution and black bars identify the spatial extent of samples used for each mixture. Genetic mixtures are overlaid on the CPUE prediction surface from a Kriging spatial model. Contours are shaded at geometric intervals of the prediction surface.

Table 2. Estimated stock mixtures of juvenile Chinook salmon (with 95% confidence intervals) collected during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf by region and location, 2002–2006. Average sample dates and DNA sample sizes are included.

Stock Mixture	Region	Location	Average Sample Date	Sample Size	Stock Group			
					Coastal Western Alaska	Middle Yukon	Upper Yukon	Other
1	Southern Bering Shelf	< 167°W	24-Aug	819	0.95 (0.89–0.98)	0.00 (0.00–0.00)	0.01 (0.00–0.01)	0.04 (0.02–0.11)
2	Northern Bering Shelf	60°N<>62°N	24-Sep	238	0.31 (0.23–0.37)	0.23 (0.15–0.30)	0.44 (0.37–0.52)	0.02 (0.00–0.08)
3	Northern Bering Shelf	62°N<>64.5°N	10-Sep	299	0.30 (0.25–0.35)	0.26 (0.20–0.32)	0.43 (0.37–0.50)	0.01 (0.00–0.03)
2 & 3	Northern Bering Shelf	60°N<>64.5°N	14-Sep	537	0.31 (0.26–0.35)	0.24 (0.20–0.29)	0.44 (0.40–0.49)	0.01 (0.00–0.03)

southern shelf region. Peak densities of juvenile Chinook salmon occurred in the shallowest water depths sampled during the survey. Significant numbers of juvenile Chinook salmon were estimated to be present in water depths shallower than could be sampled by the trawl gear (20 m).

Average sample dates of the genetic mixtures differed due to the order in which stations were sampled during the survey (Table 2). The average sample date of mixtures 1, 2, and 3 were: August 24, September 24, and September 10, respectively. The average sample date of mixtures 2 and 3 combined was September 16.

Stock mixtures differed by region and location (Table 2, Fig. 3). In the southern Bering Sea shelf (mixture 1), stock proportions were: 95% Coastal Western Alaska, 1% Upper Yukon, and 4% other western Alaska stock groups. In the northern Bering Shelf, mixture 2 contained 44% Upper Yukon, 23% Middle Yukon, and 31% Coastal Western Alaska stocks, and 2% other western Alaska stock groups. Mixture 3 was similar to mixture 2 with 43% Upper Yukon, 26% Middle Yukon, 30% Coastal Western Alaska, and 1% other western Alaska stock groups. Stock proportions from mixtures 2 and 3 combined, were 44% upper Yukon, 24% Middle Yukon, 31% Coastal Western Alaska stocks, and 1% other Western Alaska stock groups.

Stock proportions between juvenile populations and adult harvests were similar enough to discount significant bias due to incomplete sampling of the juvenile population within the northern shelf region. The proportion of the Coastal Western Alaska stock group in the juveniles from the northern shelf region (mixtures 2 and 3 combined, 31%, SD

= 3%) was slightly higher than the proportion in the harvest (21%, SD = 8%), but within the range expected for Yukon River harvests (DuBois and DeCovich 2008). The proportion of the Middle Yukon River stock group in the juvenile population (24%, SD = 3%) was similar to the proportion observed in historic harvests (23%, SD = 10%). The proportion of the Upper Yukon stock group in the juvenile population (44%, SD = 3%) was lower than the average proportion in historic harvests (56%, SD = 8%), but higher than the proportion in recent harvests. The Upper Yukon stock group comprised 37% and 36% of the total harvest in 2007 and 2008, respectively (Bue and Hayes 2009).

Coded-wire tags all matched tag codes from the Whitehorse Rapids Fish Hatchery located near Whitehorse, Yukon. Coded-wire tag codes from juvenile Chinook salmon released by the Whitehorse Rapids Fish Hatchery in 2002 included release location codes (Table 3). Tag codes from 2007 only included information on agency and year of release. However, as no other tagged Canadian juvenile Chinook entered the ocean in the Bering Sea in 2007, it was possible to assign origin to the Whitehorse Rapids Fish Hatchery.

Coded-wire tags were recovered at the mouth of the Yukon River and just south of the Bering Strait (Fig. 4). Coded-wire tags from 2002 were recovered near the mouth of the Yukon River at 63°N and at 64.1°N. Coded-wire tags recovered from 2007 were all recovered just south of the Bering Strait at 65.2°N, confirming the presence of a northward migration corridor for juvenile Yukon Chinook salmon.

All coded-wire tagged juveniles were age-0 (or fall-type Chinook salmon), a known life-history feature of Chinook

Table 3. Coded-wire tag recoveries from juvenile Chinook salmon captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf, 2002–2007. Release information provided by the Whitehorse Rapids Fish Hatchery (YRJTC, 2009).

Freshwater Origin	Tag Code	Release Data		Recovery Data				
		Date	Weight (g)	Date	Latitude	Longitude	Length (mm)	Weight (g)
Whitehorse Rapids Hatchery: Michie Creek	185061	2-Jun-02	3.2	4-Oct-02	63.0°N	166.0°W	155	49
Whitehorse Rapids Hatchery: Michie Creek	185106	10-Jun-02	3.2	3-Oct-02	64.1°N	164.5°W	193	79
Whitehorse Rapids Hatchery: Wolf Creek	185102	2-Jun-02	3.1	3-Oct-02	64.1°N	164.5°W	153	43
Whitehorse Rapids Hatchery	18	2007	--	13-Sep-07	65.2°N	168.1°W	176	58
Whitehorse Rapids Hatchery	18	2007	--	13-Sep-07	65.2°N	168.1°W	125	18
Whitehorse Rapids Hatchery	18	2007	--	13-Sep-07	65.2°N	168.1°W	179	58

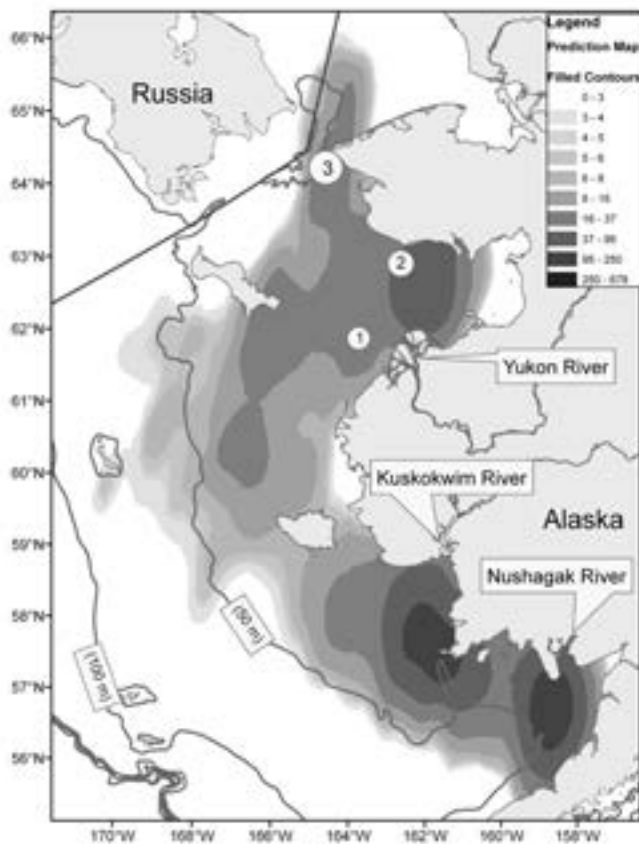


Fig. 4. Locations of coded-wire tag recoveries of Whitehorse Rapids Fish Hatchery Chinook salmon from the Yukon River during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2007. Circles indicate coded-wire tag recovery locations and are overlaid on a map of juvenile Chinook salmon distribution. Numbers in each circle indicates the number of coded-wire tags recovered at each location and are overlaid on the CPUE prediction surface from a Kriging spatial model. Contours are shaded at geometric intervals of the prediction surface.

salmon produced from the Whitehorse Rapids Fish Hatchery. The size of hatchery juveniles (125–193 mm; 18–79 g) were significantly smaller than the average size of juvenile Chinook salmon captured during the survey (213 mm, 127 g), and hatchery juveniles still had visible parr marks at the time of capture (average date of September 10). The presence of parr marks on hatchery juveniles indicates an ocean entry date much later than most wild juvenile Chinook salmon on the eastern Bering Sea shelf and is consistent with their classification as ocean-type Chinook salmon.

DISCUSSION

The estuarine and early ocean habitats of juvenile salmon in the Bering Sea differ from juvenile salmon habitats in the Gulf of Alaska. Juvenile salmon occupy a broad shallow shelf with relatively stable waters in the Bering Sea. In the Gulf of Alaska, juvenile salmon occupy habitats ranging from a network of narrow corridors associated with fjords

in southeast Alaska, to the narrow shelf and highly dynamic waters of northern California (Brodeur et al. 2000; Orsi et al. 2000). Migratory corridors of juvenile salmon in summer are largely thought to be constrained to epipelagic waters over the continental shelf once they reach the open ocean in the Gulf of Alaska (Brodeur et al. 2000; Orsi et al. 2000; Fisher et al. 2007). Juvenile salmon migratory corridors in all open ocean regions are most likely defined by oceanographic, not bathymetric features; however, the close association of these features in the Gulf of Alaska (Mundy 2005) often results in the use of the continental shelf to describe juvenile salmon migratory corridors. The broad continental shelf of the Bering Sea provides the opportunity to investigate biological and physical features such as water mass types and frontal regions that structure migratory pathways of juvenile salmon.

Juvenile Chinook salmon were primarily distributed within water depths < 50 m throughout their first summer at sea (middle of August through the middle of October) and the highest densities of juvenile Chinook salmon were found close to river mouths of primary Chinook salmon-producing rivers in the eastern Bering Sea (Yukon, Kuskokwim, and Nushagak rivers). This reflects a later dispersal from freshwater entry points than typically found in Gulf of Alaska stream-type Chinook salmon (Fisher et al. 2007). This is likely the effect of later ocean entry dates and slower marine dispersal rates of juvenile Chinook salmon on the eastern Bering Sea shelf.

Foraging behavior of salmon within the Coastal Domain may play a key role in defining juvenile Chinook salmon habitat and dispersal rates during their first summer at sea. The Coastal Domain is typically found in water depths < 50 m on the eastern Bering Sea Shelf (Schumacher and Stabeno 1998) and is associated with reduced water column stability, tight pelagic-benthic coupling, and high benthic productivity (Grebmeier et al. 2006). These structural components of the Coastal Domain favor forage fish species such as capelin and Pacific sand lance, which are the principal prey of juvenile Chinook salmon (Farley et al. in press). It is possible that feeding behavior of Chinook salmon on these forage fish species may be contributing to a delayed dispersal from the Coastal Domain. An apparent preference for the Coastal Domain is also seen in coho salmon (Farley et al. 2005) which also preferentially feed on the forage fish species in the Coastal Domain (Farley et al. in press).

The adequacy of the U.S. BASIS survey design for juvenile Chinook salmon populations differed by region. The broad migratory corridor of juvenile Chinook salmon and later survey sampling dates in the northern Bering Shelf region resulted in most juvenile Chinook salmon from this region present within trawlable habitats (> 20 m). The narrow migratory corridor and earlier sampling dates in the southern shelf region resulted in a higher proportion of the juvenile salmon population present in non-trawlable habitats. The inability to distinguish between primary stock groups contrib-

uting to the southern shelf index area also limits our ability to evaluate how well the survey reflects juvenile Chinook salmon stocks in this region.

Stock mixtures of juvenile salmon did not support significant northward migration of stocks from the southern shelf, reflecting limited mixing of salmon from different production regions during their first summer at sea. Juvenile Chinook salmon in the southern region were primarily from the Coastal Western Alaska stock group (95%). Therefore, the presence of juveniles from the southern region would increase the proportion of juvenile Chinook salmon assigned to the Coastal Western Alaska stock group. Similarity in juvenile salmon stock mixtures from both spatial strata in the northern region indicates that if juveniles from the southern shelf region were migrating north, they would need to be equally present in both northern spatial strata. This is unlikely, given the apparent dispersal rates of juvenile Chinook salmon from the southern region. Comparisons between stock proportions of the juvenile population in the northern shelf region and Yukon River harvests also did not support significant northward migration of southern stocks. If significant numbers of juvenile Chinook salmon from southern shelf were migrating north, the estimated proportions of the Coastal Western Alaska stock group would be significantly higher in the northern shelf region than expected for Yukon River Chinook salmon. The proportion of Coastal Western Alaska stocks in the northern shelf region was within the range expected for Yukon River Chinook salmon. Stock differences between the juveniles and historic harvests are most likely the result of reduced production of the Upper Yukon stock group relative to historic returns to the Yukon River (Bue and Hayes 2009). Limited northward migration of juvenile Chinook salmon from the southern shelf region is consistent with the interpretation of size and distribution data summarized by Farley et al. (2005).

Coded-wire tag recoveries of Yukon River Chinook salmon near the Bering Strait provide evidence that Yukon River Chinook salmon distributions can extend northward into the Bering Strait. The combined pattern of juvenile Chinook salmon distribution and coded-wire tag recoveries (Fig. 4) suggests that Yukon River Chinook salmon distributions can also extend into the Chukchi Sea. Although the proportion of Yukon River Chinook salmon that are believed to migrate into the Chukchi Sea is small relative to their total marine distribution, anticipated changes in Arctic climate and sea-ice levels could alter the proportion of Yukon River salmon migrating into the Chukchi Sea (Moss et al. 2009). The northward extension of juvenile Chinook salmon distribution into the Chukchi Sea was primarily due to catches in 2007—a year with record loss of Arctic sea ice and an exceptionally warm summer (Moss et al. 2009). Northward advection or migration of Yukon River Chinook salmon is in contrast to the lack of significant northward advection or migration observed in juvenile Chinook salmon from the southern shelf region. This may reflect differences in marine

habitats (water depths, freshwater discharge levels, seasonal currents, surface temperatures, prey fields, e.g.) or simply differences in the behavior or life-history of juvenile Chinook salmon from the two regions.

Life-history differences between wild and hatchery fish can result in different marine distributions; therefore it is not appropriate to characterize the distribution of Yukon River stocks with hatchery coded-wire tag recoveries alone. Stock identification data are needed to adequately describe marine distributions. Wild Yukon River Chinook are characterized as stream-type Chinook salmon (also known as spring-type as they generally enter the marine habitat in the spring) (Gilbert 1922). Hatchery Yukon River Chinook salmon are characterized as ocean-type Chinook salmon (also known as fall-type as they enter the marine habitat in the fall), which have a freshwater age of zero (age-0) (YRJTC 2009). However, life histories of wild and hatchery Yukon River Chinook salmon are not completely unique. Several unmarked or wild juvenile Chinook salmon were similar in size to or smaller than hatchery Chinook salmon and had visible parr marks during September. This suggests that ocean-type or age-0 juveniles are present in wild populations; although, they are believed to represent only a minor portion of the total juvenile population. Size and timing of ocean entry of Yukon River Chinook salmon summarized by Martin et al. (1987) also suggests the presence of age-0, -1, and older Chinook salmon in wild Yukon River stocks. The presence of freshwater age-0 Yukon River Chinook salmon in wild populations emphasizes the importance of freshwater age plasticity in stream-type Chinook salmon as part of their natural life-history variation and not simply an artifact of hatchery rearing (Beckman and Dickhoff 1998).

The following conclusions can be made concerning the U.S. BASIS survey data as it applies to juvenile Chinook salmon populations on the eastern Bering Sea shelf. Juvenile Chinook salmon are present in non-trawlable habitats; therefore, the effect of non-trawlable habitats needs to be considered when applying survey data to juvenile Chinook salmon populations, particularly in the southern shelf region. Limited mixing of juvenile Chinook salmon from different production regions (northern and southern shelf regions) is thought to occur during their first summer at sea. However, stock mixtures of juvenile Chinook salmon within each region will be needed to evaluate the status of managed stock groups. Although Yukon River Chinook salmon stocks can extend northward into the Chukchi Sea, the proportion of Yukon River Chinook salmon present in the Chukchi Sea is small relative to the total marine distribution of juvenile Yukon River salmon. However, it is also important to recognize that changes in Arctic climate and the loss of sea ice could increase the proportion of Yukon River Chinook salmon present in the Chukchi Sea during their first summer at sea.

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Reproduction of Short-Term Vertical Movements Observed Using Archival Tags on Chum Salmon (*Oncorhynchus keta*) by a Simple Model

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Azumaya, T., and T. Nagasawa. 2009. Reproduction of short-term vertical movements observed using archival tags on chum salmon (*Oncorhynchus keta*) by a simple model. N. Pac. Anadr. Fish Comm. Bull. 5: 61–69.

Abstract: Vertical movement patterns of chum salmon (*Oncorhynchus keta*) during their homing migration were examined using archival tags. Vertical movements through the thermocline with a periodicity of less than 1 h were observed during the day in the North Pacific. To examine the dynamics of these short-term vertical movements, we developed a simple one-dimensional vertical movement model. It is assumed that chum salmon have an optimal body temperature and that they regulate their dive behavior to depths with relatively high prey densities in a manner that conserves their body temperature. The model reproduced the short-term vertical movements such as those observed from archival tagging data. The model provides evidence that the high frequency movements allow conservation of the body temperature at an optimal level during foraging dives for prey.

Keywords: chum salmon, vertical movements, archival tag, model

INTRODUCTION

It is known that chum salmon (*Oncorhynchus keta*) are widely distributed in the North Pacific Ocean and adjacent waters. Japanese stocks of chum salmon remain in the North Pacific Ocean and the Bering Sea for one to seven years before returning to spawn in their natal rivers. Recent studies using archival tags have determined the characteristics of swimming patterns and the ambient environmental conditions to which homing adult chum salmon are exposed (Wada and Ueno 1999; Tanaka et al. 2000; Walker et al. 2000; Friedland et al. 2001; Ishida et al. 2001; Azumaya and Ishida 2005). These studies demonstrated that diel vertical movements are pronounced in the open ocean on time scales of days. Chum salmon remain near the surface at night, but they show short-term vertical movements lasting < 1 hour during the day. Thus they experience a wide range of water temperatures, occasionally higher than 10°C. It has been suggested that these night/day behaviors of chum salmon are related to feeding and/or searching for prey (Walker et al. 2000; Ishida et al. 2001). Euphausiids (*Thysanoessa longipes*), walleye pollock (*Theragra chalcogramma*) and atka mackerel (*Pleurogrammus monoptyerygius*) comprise more fractions of stomach contents of chum salmon in the afternoon than in the morning (Osamu Sakai, National Research Institute of Far Seas Fisheries Research Institute, Shizuoka, Japan, pers. comm.). Age-0 walleye pollock > 55 mm fork length (FL) appear to migrate through the thermocline on a diel basis (Swartzman et al. 2002). Larval or juvenile atka mackerel are mainly distributed above depths of 50–60 m

throughout the day according to observations made using a split-beam echo-sounder system operating at 38 and 120 kHz (Orio Yamamura, Hokkaido Fisheries Research Institute, Hokkaido, Japan, and Osamu Sakai, National Research Institute of Far Seas Fisheries Research Institute, Shizuoka, Japan, pers. comm.). Iguchi and Ikeda (2004) reported that *T. longipes* also showed diel distributions, occurring mainly between 30–300 m at night and dropping to between 150–500 m during the day. Thus, prey distribution for chum salmon during the day might extend to depths of 50–60 m. Chum salmon have been observed diving to such depths for prey (Wada and Ueno 1999; Azumaya and Ishida 2005).

Azumaya and Ishida (2005) reported that the difference between the ambient and body cavity temperatures of chum salmon increased during the course of short-term vertical movements through the thermocline during the day. The water temperatures experienced by chum salmon while below the thermocline were occasionally lower than the lower thermal limit (2.7°C) for the species as determined by Azumaya et al. (2007). Azumaya and Ishida (2005), using a heat budget model, suggested that chum salmon used short-term vertical movements to maintain their body cavity temperature within their thermal tolerance while actively diving to feed in water even colder than that considered physiologically suboptimal for them. However, how their diving behavior might be modified under various environmental conditions remains unclear. To examine the dynamics of high frequency vertical movements by chum salmon we developed a simple one-dimensional vertical movement model.

MATERIALS AND METHODS

Archival Tags

Archival tagging operations were conducted in the Bering Sea during July 1998. Archival tags (Northwest Marine Technology, Inc., WA, USA) were inserted into the abdominal body cavity of chum salmon on board the research vessel. Wada and Ueno (1999) reported on these tagging operations. The tags consisted of a cylindrical stainless steel tube, 1.6 cm in diameter and 10 cm long, with a 20-cm-long Teflon light/external temperature sensor stalk protruding from one end. The tag weight in air was 52 g. The external sensor stalk of the tag was allowed to trail out of the fish at the site of the incision. The archival tags measured and recorded both external (ambient) and internal (body cavity) temperatures, pressure (depth), and ambient light intensity near the tagged fish every 256 (Chum #894) or 512 (Chum #256) seconds. Temperature was measured with a resolution of 0.2°C. Depth was measured with a resolution of 1 m to a depth of 126 m, and 3 m at depths > 126 m. The two tagged chum salmon were released in the Bering Sea and recovered along the coast of Hokkaido, Japan within 68 and 87 days, respectively, after their release (Table 1).

Heat Budget Model

The heat budget model consisted of the ambient and body cavity temperatures (Stevens and Sutterlin 1976; Holland et al. 1992; Brill 1994; Kitagawa et al. 2001; Azumaya and Ishida 2005). The equation for the body cavity temperature in the heat budget model can be written as

$$Tb_{t+\Delta t} = k(Ta_{t+\Delta t} - Tb_t)\Delta t + Tm\Delta t + Tb_t \quad (1)$$

where: Tb is body temperature, Ta is ambient temperature (°C), t is time (s), Δt is a time step, k is the whole-body heat-transfer coefficient $1.48 \times 10^{-3} (\text{s}^{-1})$ between the fish and the water, and Tm is the internal heat production

$2.14 \times 10^{-4} (\text{°C} \cdot \text{s}^{-1})$ of the fish (Azumaya and Ishida 2005). Here, we neglected Tm because this term is smaller than k by about 1 order of magnitude. In this study, we focused on the movement on 4 September for Chum #894 and that on 11 August for Chum #256, because on these days the differences between body cavity temperatures and ambient temperatures were relatively large, and short-term vertical movements were documented within the archival tag data. In order to check the reproducibility of the heat budget model on 4 September for Chum #894 and on 11 August for Chum #256, the body cavity temperature was predicted using equation (1). The time steps (Δt) in equation (1) were 256 and 512 seconds which were periods equal to the sampling intervals of the archival tags of Chum #894 and Chum #256, respectively. The resulting temperature profiles were compared with the observed body cavity temperatures.

One-dimensional Vertical Movement Model

To model the vertical movements of chum salmon, we developed a one-dimensional vertical movement model. The model was kept simple to determine the mechanism for the vertical movements of chum salmon. The model included a heat budget component for body temperature and a separate component to model active swimming. The direction of active swimming was assumed to be only vertical, either upward or downward. This directional swimming speed was a constant value: 1 body length/second ($\text{BL} \cdot \text{s}^{-1}$) (Ware 1978; Azumaya and Ishida 2004). We could not distinguish whether chum salmon preferentially swim either toward an area with their preferred SST or toward an area with abundant zooplankton. Therefore, in this study, we defined their average body cavity temperature during the day (range: 4.6°C–7.3°C) as the optimal body temperature ($5.95^\circ\text{C} \pm 1.35^\circ\text{C}$ SD), and set a rule for directional swimming as follows: if the body cavity temperature was within the range of the optimal body temperatures, chum salmon would swim toward the zone with abundant zooplankton; if the body cavity temperature was below optimal body temperature, chum

Table 1. Release and recapture information for two chum salmon tagged with archival tags in the Bering Sea and recovered in Hokkaido, Japan. Days at sea: days between release and recovery days. Distances: shortest distance between release and recovery sites. Age was determined from scales (Ito and Ishida 1998)*. FL = fork length.

Fish No.	Release				Recapture						
	Date	Location	FL (mm)	Age	Date	Location	FL (mm)	Days at liberty	Distance (km)	Sex	Swimming speed ($\text{m} \cdot \text{s}^{-1}$)
256	July 5 1998	Bering Sea 54° 30'N 179° 30'W	650	5	Sep. 10 1998	Shibetsu coast 43° 54'N 145° 06'E	690	68	2,797	female	0.475
894	July 18 1998	Bering Sea 56° 30'N 177° 30'W	570	4	Oct. 10 1998	Shibetsu coast 43° 51'N 145° 06'E	598	87	2,964	female	0.394

*Fish of age-1 migrate to the sea after emergence from the stream gravel in March to April and spend several months in coastal waters. In the next year, the age of the fish is age-2.

salmon would swim toward the warmer sea surface. They would then remain in surface waters until their body cavity temperature was within the range of the optimal body temperatures. Chum would then swim back toward the zone with abundant zooplankton. The body cavity temperature in the model was calculated using the heat budget component of equation (1). The forcing of the model by the vertical density-distribution of zooplankton assumed a normal distribution with a standard deviation of 10 m. The vertical integration of the density of zooplankton was assumed to be constant. The mean position of zooplankton changed in a sinusoidal manner, with a period of 24 hours from maximum density occurring at the sea surface during the night to maximum density occurring at 60 m during the day. The vertical profile of the ambient water temperature as another driver of the model was approximated by an exponential curve as follows:

$$T_{t+\Delta t} = \exp(-aZ_{t+\Delta t} + b) \quad (2)$$

where: $Z_{t+\Delta t}$ is the vertical position (m) of the fish at $t+\Delta t$, and a and b are the attenuation coefficients ($0.028\text{--}0.046\text{ m}^{-1}$) and constants ($2.6\text{--}2.7$) of water temperature, respectively. The values of a and b in equation (2) were estimated from the depth and ambient temperatures of the archival tag data on the target days using the least squares method for each target date. The vertical position of the fish in the model was calculated at each time step as follows:

$$Z_{t+\Delta t} = Z_t + w(BL)\Delta t \quad (3)$$

where: $w(BL)$ is swimming speed ($0.6\text{ m}\cdot\text{s}^{-1}$) (Table 1), and is a function of the body length, because the swimming speed was assumed to be $1\text{ BL}\cdot\text{s}^{-1}$. The model was numerically integrated by time step (Δt), 0.1 seconds, and was run for 24 hours. The start position of the fish was at the surface. The value Δt in equation (1) also corresponded to the one-dimensional vertical movement model. Data from the model were output every 256 or 512 seconds, periods equal to the sampling intervals of the archival tags of Chum #894 and Chum #256, respectively. In order to check the reproducibility of the body cavity temperatures by the heat budget component, the difference between the body cavity temperature calculated by one-dimensional movement model and the body cavity temperatures predicted using the heat budget component of equation (1) and the ambient temperature output every 256 or 512 seconds from the one-dimensional vertical movement model were examined. When the body cavity temperature was predicted using the heat budget model and output data from the model, the time steps (Δt) in equation (1) were 256 and 512 seconds, corresponding to Chum #894 and Chum #256, respectively.

According to equations (2) and (3), the vertical movement of chum salmon will be affected by the vertical profile of the ambient temperature and swimming speed. Substituting for Z from equation (3) into equation (2) and substituting

T_a from equation (2) into equation (1), and integrating with respect to time t , equation (1) becomes

$$T_b(t) = \left(\frac{T_{a_{ini}}k}{k-aw} \right) \exp(-aw(BL)t) + \left(T_{b_{ini}} - \frac{T_{a_{ini}}k}{k-aw(BL)} \right) \exp(-kt) \quad (4)$$

where: $T_{a_{ini}}$ (10°C) and $T_{b_{ini}}$ (10°C) are the initial values of T_a and T_b , respectively. The value $T_{b_{ini}}$ includes b in equation (2). The depth that chum salmon are able to reach, while maintaining a body cavity temperature above 5°C in one dive was quantitatively examined using equation (4) with respect to the swimming speeds and attenuation coefficients of water temperature.

RESULTS

Archival Tags

Chum #256 and Chum #894 were recovered after 68 and 87 days at sea, respectively. On 4 September, Chum #894 showed pronounced oscillatory vertical movements during the day (Fig. 1, top). Chum salmon experienced water $< 2^\circ\text{C}$ and $> 10^\circ\text{C}$ during a typical 24-h period. A relatively large difference between ambient and body cavity temperatures corresponded with periods of diving into the cold water. Although the ambient temperature changed corresponding to the vertical excursions, the body cavity temperature did not reflect the variation in the ambient temperature (Fig. 1, bottom). Rather, the changes in observed body cavity temperatures were less extreme and lagged slightly behind ambient temperatures, because it takes time for heat to transfer between the water and the body cavity and to reach equilibrium. Thus, the daytime variability in body cavity temperatures ($\pm 2.3^\circ\text{C}$) was smaller than that in the ambient temperature ($\pm 3.6^\circ\text{C}$). On 11 August, Chum #256 seemed to remain for relatively long periods (up to 60 minutes) at a depth of about 50 m, where it experienced an ambient temperature $< 4^\circ\text{C}$ (Fig. 2, top). However, the body cavity temperature did not decrease to $< 5^\circ\text{C}$, and the SD ($\pm 2.8^\circ\text{C}$) of body cavity temperature was smaller than that of the ambient temperature ($\pm 4.5^\circ\text{C}$) during the day (Fig. 2, bottom).

The body cavity temperature predicted by the heat budget model (thin line) was generally quantitatively similar to the observed body cavity temperature (thick line) in Chum #894 (Fig. 1, bottom). The correlation between the body cavity temperature predicted by the heat budget model and the observed value was significant ($R^2 = 0.88$, $P < 0.01$). On the other hand, for Chum #256, the body cavity temperature predicted by the heat budget model (thin line) was dissimilar to the observed value (thick line, Fig. 2, bottom). The predicted body cavity temperature decreased to the ambient temperature, whereas the observed body cavity temperature did not. The correlation between the predicted body cavity temperature and the observed profile for Chum #256 was not significant ($R^2 = 0.026$, $P > 0.01$).

One-dimensional Vertical Movement Model

Figure 3 shows the vertical movement of chum salmon simulated by the one-dimensional vertical movement model in the case of output every 256 seconds (the same

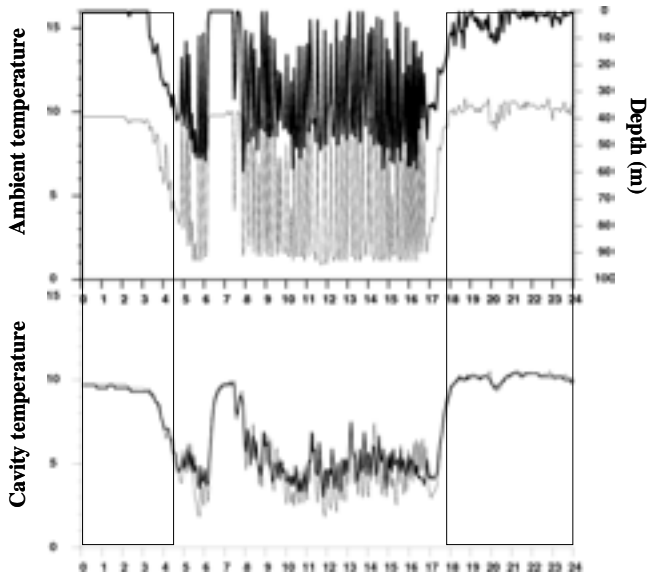


Fig. 1. Time series of archival depth data (top panel, thick line), archival ambient temperature (top, thin line), archival observed body cavity temperature (lower, thick line), and body cavity temperature predicted by the heat budget model (lower, thin line) over a 24-hour period on 4 September for Chum #894. For both panels, the shaded period is night.

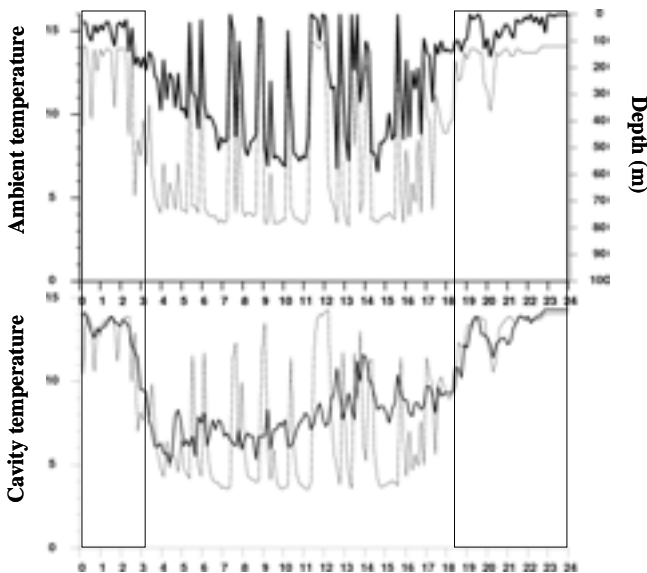


Fig. 2. Time series of archival depth data (top panel, thick line), archival ambient temperature (top, thin line), archival observed body cavity temperature (lower, thick line), and body cavity temperature predicted by the heat budget model (lower, thin line) over a 24-hour period on 11 August for Chum #256. For both panels, the shaded period is night.

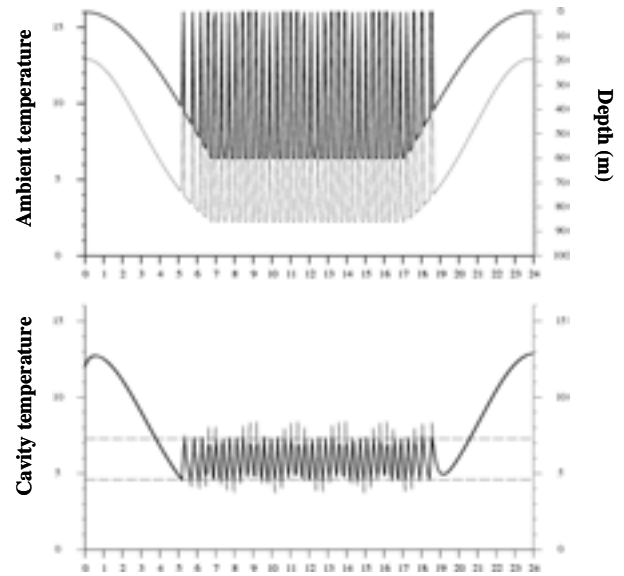


Fig. 3. Time series of modeled depth (top panel, thick line), modeled ambient temperature (top, thin line), modeled body cavity temperature by the one-dimensional movement model (lower, thick line), and body cavity temperature predicted by the heat budget model (lower, thin line) over a 24-hour period using an output interval of 256 seconds (the same as the archival tag data on 4 September for Chum #894). Horizontal dashed lines are a minimum optimal (4.6°C) and a maximum optimal (7.3°C) temperature, respectively. The range from 4.6°C to 7.3°C of the thin dashed lines is the optimal body temperature.

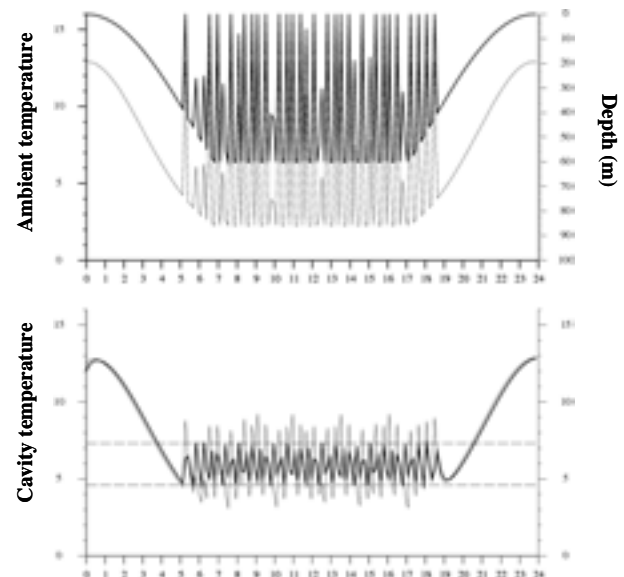


Fig. 4. Time series of modeled depth (top panel, thick line), modeled ambient temperature (top, thin line), modeled body cavity temperature by the one-dimensional movement model (lower, thick line), and body cavity temperature predicted by the heat budget model (lower, thin line) over a 24-hour period using an output interval of 512 seconds (the same as the archival tag data on 11 August for Chum #256). Horizontal dashed lines are a minimum optimal (4.6°C) and a maximum optimal (7.3°C) temperature, respectively. The range from 4.6°C to 7.3°C of the thin dashed lines is the optimal body temperature.

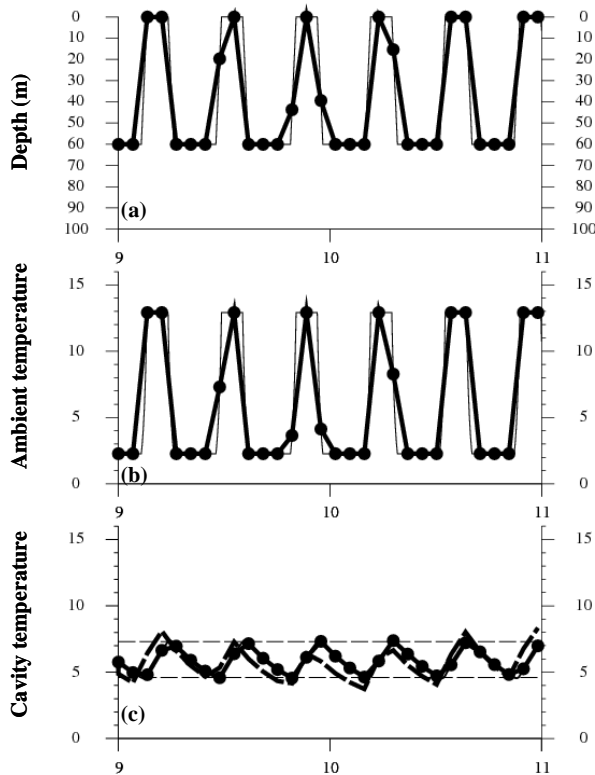


Fig. 5. Detailed time series of modeled depth, modeled ambient temperature, and modeled body cavity temperature by the one-dimensional vertical movement model from 0900 to 1100 hours in model time using an output interval of 0.1 seconds (thin line). Time series output interval of 256 seconds from the one-dimensional vertical movement model is shown by the thick line and dots. Time series of body cavity temperature predicted by the heat budget model using output data of ambient temperature is shown by the dashed line. (a) depth, (b) ambient temperature, (c) body cavity temperature. Horizontal dashed lines are a minimum optimal (4.6°C) and a maximum optimal (7.3°C) temperature, respectively. The range from 4.6°C to 7.3°C of the thin dashed lines is the optimal body temperature.

as the tag data for Chum #894). The calculated vertical movements were similar to the observed diel movements of chum salmon. The model-generated profile also remained near the sea surface (depth of < 10 m), when zooplankton were distributed at the sea surface (at night). Body cavity temperatures and the ambient temperature during the night were equivalent to one another. The density of zooplankton that chum salmon encountered was almost constant during the night (not shown). The variation in ambient temperature was considerably larger than that in body cavity temperature, and similar to the observed values when zooplankton were distributed at depth of 60 m (daytime). The body cavity temperature predicted by the heat budget model (thin line) using output data from the one-dimensional movement model was generally similar to the body cavity temperature (thick line) output by the one-dimensional movement model. Although the temperatures of the cold water where zooplankton were distributed during the day were not the optimal temperatures for chum salmon, they were predicted to swim into the cold

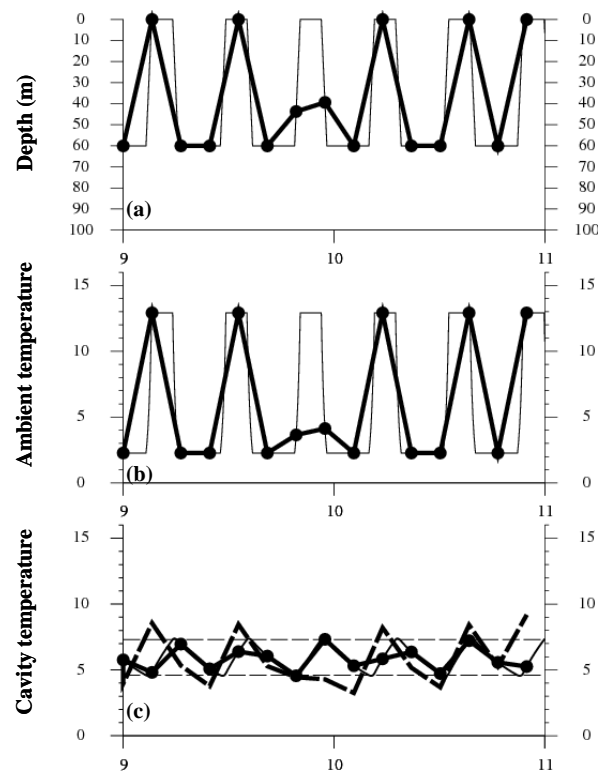


Fig. 6. Detailed time series of modeled depth, modeled ambient temperature, and modeled body cavity temperature by the one-dimensional vertical movement model from 0900 to 1100 hours in model time using an output interval 0.1 seconds (thin line). Time series of output interval of 512 seconds from the one-dimensional vertical movement model is shown by the thick line and dots. Time series of body cavity temperature predicted by the heat budget model using output data of ambient temperature is shown by the dashed line. (a) depth, (b) ambient temperature, (c) body cavity temperature. Horizontal dashed lines are a minimum optimal (4.6°C) and a maximum optimal (7.3°C) temperature, respectively. The range from 4.6°C to 7.3°C of the thin dashed lines is the optimal body temperature.

water to encounter zooplankton. Because the body cavity temperature of the chum salmon remained within range of optimal body temperatures, the results of the one-dimensional movement model suggest that high frequency movements are related to both conservation of body temperature and the acquisition of the prey.

In the case of output every 512 seconds (the same as the tag data for Chum #256), the one-dimensional movement model produced a profile in which the chum salmon remained in water that was colder than the optimal body temperature for chum at 0600, 1000, 1200, 1400 and 1600 hours in model time (Fig. 4, top). The body cavity temperatures output by the one-dimensional vertical movement model (thick line), however, did not decrease to the ambient temperature. Furthermore, the body cavity temperature predicted by the heat budget model (thin line) using output data from the one-dimensional movement model was not equivalent to the body cavity temperature output by the one-dimensional movement model (thick line). The predictions from the one-

dimensional movement model suggest that changes in body cavity temperature should be less variable than ambient temperature changes, and that body temperatures remain above the minimum observed ambient temperature. The features seen in the one-dimensional movement model were similar to the archival tag observations.

DISCUSSION

Chum salmon # 256 remained for up to 60 minutes at depths near 50 m and at ambient temperatures < 4°C during the day. However, the body cavity temperature did not decrease to the ambient temperature, as shown in Fig. 2 (bottom). On the other hand, the body cavity temperature predicted by the heat budget model was not consistent with the observed body cavity temperature; rather, it decreased to the ambient temperature. Why was the heat budget model not able to reproduce the daytime body cavity temperature observed for Chum #256? The nighttime body cavity temperature predicted by the heat budget model was consistent

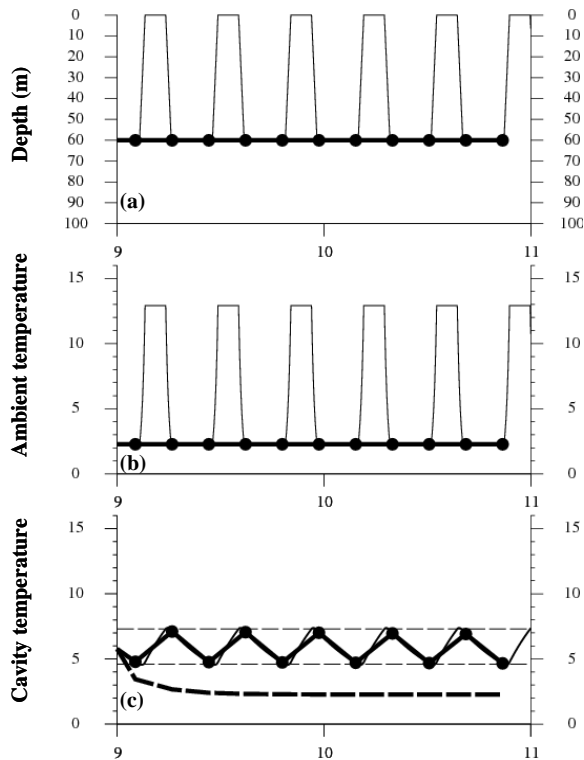


Fig. 7. Detailed time series of modeled depth, modeled ambient temperature, and modeled body cavity temperature by the one-dimensional vertical movement model from 0900 to 1100 hours in model time using an output interval of 0.1 seconds (thin line). Time series of an output interval of 665 seconds from the one-dimensional vertical movement model is shown by the thick line and dots. Time series of body cavity temperature predicted by the heat budget model using output data of ambient temperature is shown by the dashed line. (a) depth, (b) ambient temperature, (c) body cavity temperature. Horizontal dashed lines are a minimum optimal (4.6°C) and a maximum optimal (7.3°C) temperature, respectively. The range from 4.6°C to 7.3°C of the thin dashed lines is the optimal body temperature.

with the one observed, and the body cavity temperature of Chum #894 predicted by the heat budget model was also good. When T_m was included in the heat budget model, it did not have any effect on the results (not shown). In the one-dimensional vertical movement model experiment, the parameters of the model were the same except for the output interval. Thus, we suggest that the inconsistency is not due to the parameters of the heat budget model, but that the reproducibility of the heat budget model was affected by the sampling interval.

In this study, the time series of depth, and ambient, and body cavity temperatures were integrated by a 0.1-second time step in the one-dimensional movement model. The differences between this time series of output every 0.1 seconds and the time series of output every 256 or 512 seconds were then examined. Figures 5 and 6 show the detail of time series from 0900 to 1100 hours in model time. With output every 256 seconds (Fig. 5a, b, c), the output time series (thick line) of depth, and ambient and body cavity temperature were similar to the time series of output every 0.1 seconds (thin line). However, with output every 512 seconds, there was no third peak in the output time series (thick line) of depth and ambient temperature before 1000 hours in model time (Fig. 6a, b), although there were six peaks in the time series output every 0.1 seconds of depth and ambient temperature (thin lines). Thus, the output time series (thick line) of depth, and

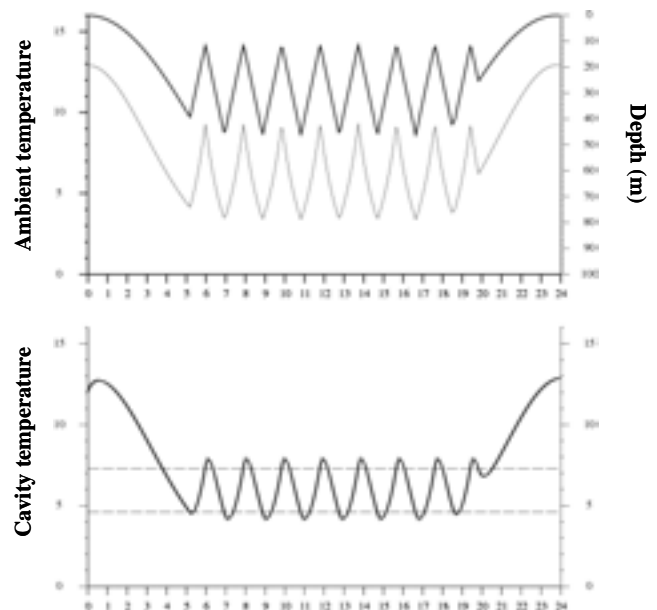


Fig. 8. Time series of modeled depth (top panel, thick line), modeled ambient temperature (top, thin line), and modeled body cavity temperature by the one-dimensional movement model (lower, thick line), and body cavity temperature predicted by the heat budget model of 256 seconds (the same as the archival tag data on 4 September for Chum #894, but utilizing a swimming speed 0.01 m·s⁻¹). Horizontal dashed lines are a minimum optimal (4.6°C) and a maximum optimal (7.3°C) temperature, respectively. The range from 4.6°C to 7.3°C of the thin dashed lines is the optimal body temperature.

ambient temperature did not reflect the time series of output every 0.1 seconds (thin line) well. The likely cause was that the output interval of 512 seconds (dots, Fig. 6) was either the same or larger with respect to the period of variation in the time series of output every 0.1 seconds (thin line). On the other hand, the phase difference between the ambient temperature and the body cavity temperature was about 90 degrees (Azumaya and Ishida 2005), and data was output at the peaks and valleys in the time series of output every 0.1 seconds. Thus, the feature of the time series of output every 512 seconds (Fig. 6, thick line) for body cavity temperature was similar to the time series of output every 0.1 seconds (Fig. 6c, thin line). However, the body cavity temperature predicted by the heat budget model (dashed line) using ambient temperature (thick line) from the one-dimensional movement model was not equivalent to the body cavity temperature output by the one-dimensional movement model (thick line) before 1000 hours in model time, because body cavity temperature was predicted by the heat budget model using the ambient temperature indicated by the dot before the peak. These features were also seen in the time series of Chum # 256. Hanawa and Mitsudera (1987) reported that when the sampling frequency is not at least 2x higher than the highest frequency of the input signal, aliasing can occur. Thus, it is possible that during the day the movement of Chum #256 derived from the archival tag data was not practical.

Figure 7 shows a time series with an output interval of 665 seconds as an extreme case of the occurrence of alias-

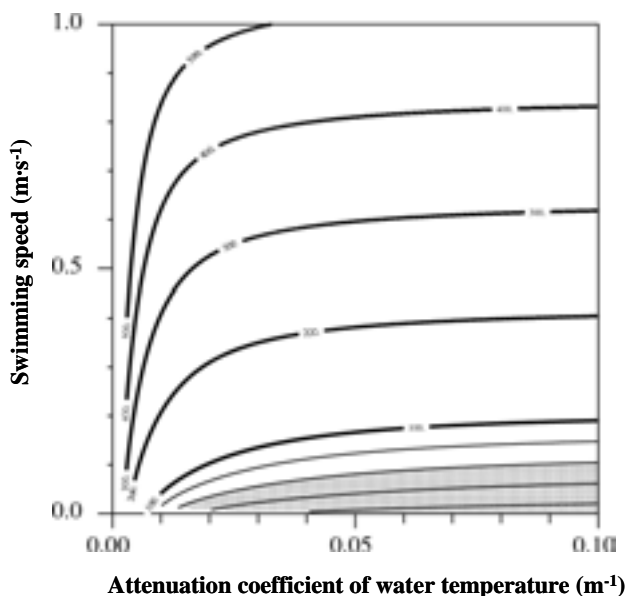


Fig. 9. Depth that chum salmon are predicted to be able to reach in one dive while maintaining their body cavity temperature at $> 5^{\circ}\text{C}$ with respect to swimming speed and the attenuation coefficient of water temperature. Thick curves are for 500, 400, 300, 200 and 100 m, and thin curves are for 80, 60, 40 and 20 m. Shaded area indicates < 60 m, where zooplankton are not distributed during the day in the model.

ing. Although there were no variations in the time series of output every 665 seconds for depth and ambient temperature (thick line) (Fig. 7a, b), there were variations in the time series of output every 665 seconds for body cavity temperature (thick line) (Fig. 7c). In this case the output interval (dots) and the period of variation (thin line) of the time series of output every 0.1 seconds were the same. Variation was not seen in the time series for body cavity temperature predicted by the heat budget model (dashed line), because the ambient temperatures at the dots were constant. Thus, there is a discrepancy between the body cavity temperature predicted by the heat budget model (dashed line) and the body cavity temperature predicted by a model with output every 665 seconds (thick line). Furthermore, the body cavity temperature predicted by the heat budget model (dashed line) was less than the optimal body temperature of the model. If the archival tag records the depth and the ambient temperature only when the chum salmon were diving as shown in Fig. 7a, it can be interpreted that chum salmon were able to remain in the cold water with a body cavity temperature higher than the ambient temperature. These results suggest that the time series data on vertical movements of Chum #256 exhibited aliasing. Thus, we note the existence of aliasing in the time series data.

In the one-dimensional movement model, we assumed the swimming speed of chum salmon to be $1\text{BL}\cdot\text{s}^{-1}$ ($0.6\text{ m}\cdot\text{s}^{-1}$). Swimming speed estimated from the horizontal distance between tag release and recovery over the course of a fish's time at sea has been estimated at nearly $1\text{BL}\cdot\text{s}^{-1}$ (Table 1). The same value has been observed directly using a current meter (Tanaka et al. 2005). However, vertical swimming speed estimated from the change in depth per unit time observed in archival tag data was considerably lower: $0.003\text{--}0.015\text{ m}\cdot\text{s}^{-1}$ (Azumaya and Ishida 2005). We examined this difference between vertical and horizontal swimming speed of chum salmon using the one-dimensional vertical model. Figure 8 shows the model result at a swimming speed of $0.01\text{ m}\cdot\text{s}^{-1}$. The result was cyclic vertical excursions with a period of about 120 minutes, not similar to our daytime observations. Further, the chum salmon were not predicted to dive to depths of 60 m where zooplankton occur at a relatively high densities because the model predicted that their body cavity temperature would decrease to less than optimal before they reached 60 m. This suggests that chum salmon subjected to the observed temperature profiles might not be able to encounter food during the day at swimming speeds ranging from $0.003\text{--}0.015\text{ m}\cdot\text{s}^{-1}$. By contrast, model results using a swimming speed of $1\text{BL}\cdot\text{s}^{-1}$ were similar to daytime archival tag observations (Fig. 3). The vertical swimming speed that was estimated from archival tag data was an underestimation due to aliasing as previously mentioned. Therefore, we consider the vertical swimming speed of $1\text{BL}\cdot\text{s}^{-1}$ to be appropriate.

The one-dimensional movement model suggests that short-term vertical movement of chum salmon resulted

from both optimizing body temperature and the requirement to dive to feed on prey. Thus, both the swimming speed ($w(BL)$) and the attenuation coefficient (a in equation (4)) of ambient temperature play critical roles in regulating the depth to which chum salmon are able to dive. The depth that chum salmon are able to reach under the observed temperature conditions, while maintaining a body cavity temperature above 5°C in one dive, with respect to swimming speed and the attenuation coefficient, was examined using equation (4). Results of this analysis are shown in Fig. 9.

When swimming speed is taken as a constant, the depth that chum salmon can reach becomes shallower (deeper) as the attenuation coefficient becomes larger (smaller). This implies that chum salmon are not able to dive into the cold water that is close to the freezing point in the Okhotsk Sea, nor into the diathermal layer characterized by the minimum temperatures found in the North Pacific Ocean and the Bering Sea. This suggests that chum salmon cannot use the layer of maximum temperature located beneath the mixed layer at a depth of about 300 m for wintering in the Bering Sea, although Chinook salmon (*O. tshawytscha*) are known to overwinter in this layer (Walker et al. 2006). On the other hand, if the attenuation coefficient is taken as a constant, then the depth that is reached becomes deeper (shallower) as swimming speed becomes higher (lower). This implies that chum salmon of larger body size can dive to deeper depths and suggests that during the day the average vertical distribution of chum salmon of small body size (i.e., younger age) should be shallower than that of chum of larger body size (older age) because swimming speed is a function of the body length in this study. Assuming that the whole-body heat-transfer coefficient depends on the body size, the average vertical distribution of chum salmon of small body size should be much shallower than that of fish of larger body size - but only if the water temperature profile associated with preferred feeding depth exceeds the thermal capacities of smaller fish.

In conclusion, the one-dimensional vertical movement model could reproduce the observed short-term vertical movements. Chum salmon have an optimal body temperature, and the model results were consistent with the hypothesis that chum salmon regulate their short-term movements in relation to body temperature while foraging for prey. If the body temperature of chum salmon is in the range of the optimal body temperature, they will be able to obtain the prey in water that is colder than the optimal body temperature. In the case of Chum #256, it is possible that aliasing occurred in the data due to the short-term vertical movements and the sampling intervals.

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Stock-Specific Distribution and Abundance of Immature Sockeye Salmon in the Western Bering Sea in Summer and Fall 2002–2004

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Abstract: Seasonal stock-specific distribution and abundance of immature sockeye salmon (*Oncorhynchus nerka*) in the western Bering Sea in summer 2003 and fall 2002–2004 were determined using scale pattern analysis of Bering-Aleutian Salmon International Survey (BASIS) samples. Most (nearly 100%) of the sockeye salmon in BASIS catches were immature. Four age groups, 1.1, 1.2, 2.1 and 2.2, accounted for more than 90% of immature fish. Sockeye salmon of Asian (primarily Kamchatka) origin dominated catches throughout the region. In general, abundance of immature sockeye salmon was highest in the northwestern Bering Sea, where sockeye salmon of North American origin (primarily Bristol Bay stocks) were more abundant than in the southwestern Bering Sea. Estimated abundance of immature sockeye salmon in the western Bering Sea in 2002–2004 was high compared to estimated run sizes of adult returns, particularly in Asia. BASIS stock assessment methods may have overestimated the abundance of salmon or adult run-size statistics may be inaccurate, or both. Nevertheless, our stock-composition estimates were corroborated by other (genetic) studies. We concluded that the western Bering Sea in summer–fall is an important area of intermixing of immature sockeye salmon of Asian and North American origin.

Keywords: abundance, age, biomass, distribution, immature, scale pattern analysis, sockeye salmon, stock identification, western Bering Sea

INTRODUCTION

The Bering-Aleutian Salmon International Survey (BASIS) was initiated in 2002 to detect and monitor changes in climate-ocean and ecosystem states and Pacific salmon (*Oncorhynchus* spp.) in the Bering Sea (NPAFC 2001, 2003, 2004, 2005). One of the major objectives of BASIS was to estimate seasonal stock-specific distributions of salmon in the Bering Sea. Previous stock identification research indicated that ocean foraging areas of sockeye salmon can be distant from their spawning grounds (e.g., Konovalov 1971; French et al. 1976; Forrester 1987). Prior to BASIS research, very little was known about the stock composition of immature sockeye salmon (*O. nerka*) migrating in the Bering Sea in summer–fall, particularly inside of the Russian Federation’s Exclusive Economic Zone (REEZ). Previous marine stock-identification research in the Russian Far East focused primarily on maturing salmon during their prespawning migrations (e.g., Konovalov 1971; Temnykh et al. 1994, 1997; Temnykh 1996; Varnavskaya 2001; Bugaev 2003a,b,c). Aggregations of maturing sockeye salmon in western Bering Sea waters adjacent Kamchatka and contiguous waters of the western North Pacific Ocean likely include only Asian-origin

stocks (Bugaev 2003b). However, immature sockeye salmon in this oceanic region might include a mixture of Asian and North American stocks. Historical stock-identification research by the International North Pacific Fisheries Commission (INPFC) indicated only that “some portion” of immature sockeye salmon of North American origin (primarily Bristol Bay) were distributed in the central and western Bering Sea in summer–fall (at least to 60°N and west to 166°E; French et al. 1976).

Habicht et al. (2005) used genetic (DNA) methods to identify the origin of sockeye salmon in BASIS samples from 2002–2003. The results of Habicht et al. indicated that sockeye salmon of Bristol Bay origin were the dominant stock in all regions of the Bering Sea in summer–fall, except in the southwestern REEZ where Russian (Kamchatka) stocks dominated. Bugaev (2004, 2005, 2006) used scale pattern analysis to estimate the stock composition of immature sockeye salmon in 2002–2004 BASIS samples from the REEZ. In general, Bugaev’s preliminary results were similar to those of Habicht et al. (2005). In this paper, we update the results of (Bugaev et al. 2004, 2005, 2006), briefly review BASIS data on distribution and abundance of immature sockeye salmon, and provide provisional estimates of

the abundance and biomass of Asian and North American sockeye salmon in the western Bering Sea.

MATERIALS AND METHODS

Analysis of scale patterns has been used since the 1950s to estimate the regional stock composition of salmon caught in mixed-stock fisheries on the high seas. Major et al. (1972) outlined the basic principles and procedures of scale pattern analysis. Our methods were similar to those described by Bugaev (2003a, 2004, 2005, 2006). Briefly, we used scale pattern analysis of representative (baseline) samples of Asian and North American sockeye salmon to estimate the proportions of these stock groups in BASIS (mixture) samples and their potential abundance in the western Bering Sea.

Mixture Samples

Mixture samples of sockeye salmon and associated biological and catch data were collected by the staff of the TINRO-Center in trawl catches of the RV *TINRO* in the western Bering Sea in summer (July–August) 2003 and fall (September–October) 2002–2004 (NPAFC 2003, 2004, 2005). A standard midwater rope trawl (PT/TM 80/396 m) was used to survey the upper epipelagic layer (~upper 40 m).

Shipboard sampling of sockeye salmon included determination of maturity and collection of a scale sample from each fish. Maturity was determined by visual evaluation of the stage of gonad maturation (Pravdin 1966). All fish at stages II and II–III were considered immature (e.g., Mosher 1972; Bugaev 1995; Ito and Ishida 1998). The body area of scale collection was recorded using a classification scheme developed by TINRO-Center (Bugaev et al. 2009). Collection of preferred scales (Clutter and Whitesel 1956; Knudsen 1985; Davis et al. 1990) was not always possible, as salmon caught in trawls frequently lose many scales. Both preferred and non-preferred scales were used to estimate age composition. Only preferred scales were used to estimate stock composition, because different rates of scale growth on different parts of the fish's body can influence the results of scale pattern analysis.

Ages of immature sockeye salmon in the mixture samples were determined in the laboratory by counting the number of freshwater and marine annuli on scales, which is the standard method accepted for Pacific salmon (e.g., Ito and Ishida 1998). Age was designated by the European method, whereby the number of freshwater annuli and number of ocean annuli are separated by a dot (Koo 1962). For example, a 1.2 fish has one freshwater annulus and two ocean annuli on its scale, and is in its third summer–fall in the ocean. Although juvenile sockeye salmon (.0 fish) were present in BASIS trawl catches, samples were insufficient for stock-identification analysis due to scale loss during trawl operations.

Samples of immature sockeye salmon collected in Dis-

tricts 8 and 12 (Fig. 1) accounted for approximately 90% of all biostatistical and scale data. Therefore, we pooled samples from individual districts into two geographic regions—a “northern” region that included samples from Districts 1–8 and a “southern” region that included samples from Districts 9–12. The total mixture sample from all districts (3,691 fish) was used to estimate age composition by year, season, and region, and a subset of preferred scales from this sample (2,678 fish) was used to estimate stock composition.

Baseline Samples

Baseline scale samples were collected by regional fishery agency personnel (KamchatNIRO, ChukotNIRO, Sevostroybvod (North-East Fishery Protection Service), and the Alaska Department of Fish and Game) from adult sockeye salmon returning to principal commercial watersheds in Asia and North America in 2003–2005. Scale samples and associated age data from 36 stocks of sockeye salmon of Asian (Kamchatka and Chukotka) and North American (Alaska) origin were used to form the baselines (Fig. 2).

Two different baselines were formed for each stock and adult return year (2003–2005) by pooling samples of the four most common age groups of adult sockeye salmon by freshwater age: (1) ages 1.2 + 1.3 and (2) ages 2.2 + 2.3. These baselines were used to estimate stock composition of fish of the same freshwater age group in the previous year's (2002–2004) mixture sample of immature ocean ages .1 and .2 sockeye salmon. This approach was taken to reduce the effects of year-to-year variation in scale growth patterns caused by environmental factors. However, pooling by ocean age (.2 + .3 fish) was necessary to obtain a sufficient number of scales for each stock in the two baselines.

For each baseline stock, we selected a stratified random

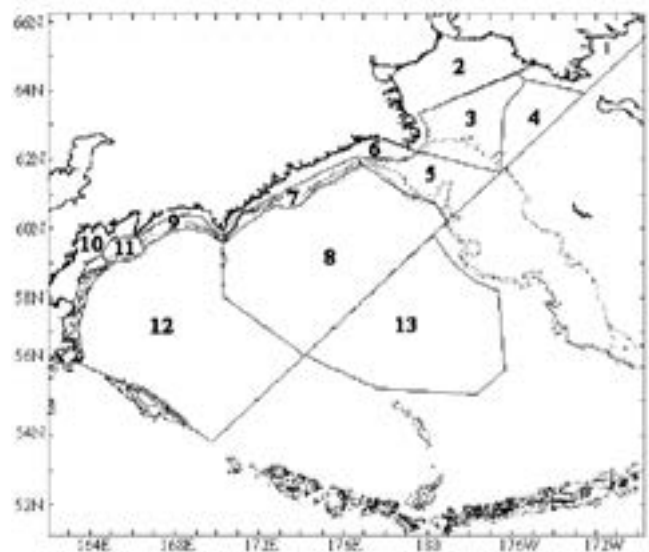


Fig. 1. TINRO-Center biostatistical districts in the western Bering Sea (Shuntov 1986; Volvenko 2003).

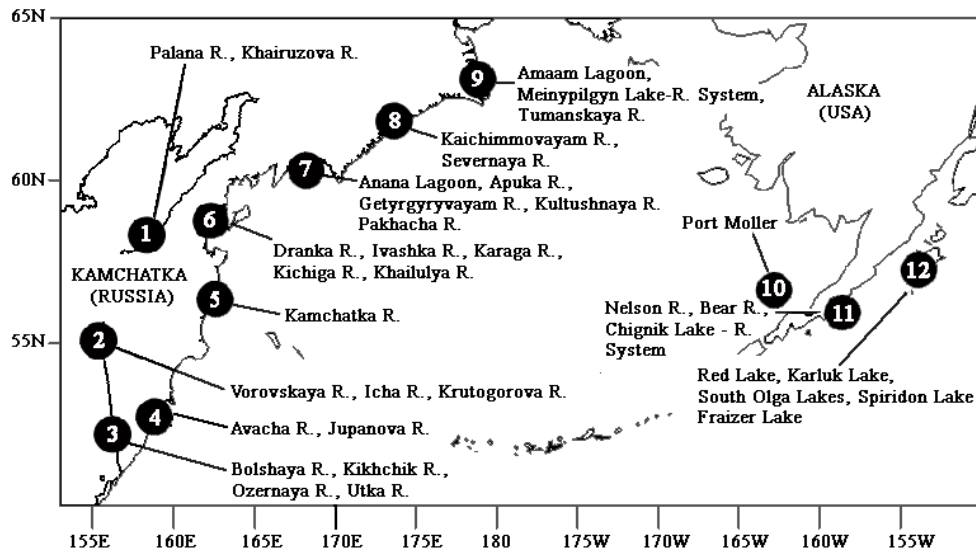


Fig. 2. Locations (numbered black circles) of 12 sockeye salmon stock groups represented in the 2003–2005 scale pattern baselines. The baseline scale samples and associated data were collected by scientists of KamchatNIRO, ChukotNIRO, Sevvostrybvod, and the Alaska Department of Fish and Game. 1 = northwestern Kamchatka, 2 = western Kamchatka, 3 = southwestern Kamchatka, 4 = southeastern Kamchatka, 5 = eastern Kamchatka, 6–8 = northeastern Kamchatka, 9 = Chukotka, 10 = central Alaska (Bristol Bay), 11 = southwestern Alaska (Alaska Peninsula), 12 = Kodiak Island.

sample of scales that accounted for spatial and temporal population structure (early-, mid-, and late-run timing). This method varied somewhat depending on available sample size. When sample size was small the entire sample was used in the analysis.

Scale Measurement

Scales were measured using an optical digitizing system (Biosonics model OPR-513, OPRS, BioSonics Inc., Seattle, WA, USA (Davis et al. 1990)). Measurements were made in the freshwater and first annual ocean zone along an axis perpendicular to the boundary of the sculptured and unsculptured fields of the scale (Fig. 3). Scale pattern variables were calculated from inter-circulus measurements. Variables included the total radius of the freshwater zone (FW), total radius of the first ocean zone (O1), total number of circuli in the first ocean zone (C1), six triplets (TR) in the first ocean zone, and six reverse triplets (RTR) in the first ocean zone (Fig. 3).

Estimates of Stock Composition

The 36 baseline stocks were combined into a reduced number of stock groups according to similarity in scale pattern variables, as determined by *t*-tests ($P < 0.05$), hierarchical cluster analysis of Euclidian distances between stock centroids, and canonical discriminant analysis (Bugaev 2007).

Computer simulations were used to evaluate the accuracy of the baseline stock groups using a maximum-likelihood estimation procedure (Millar 1987, 1990; Patton et al. 1998). The estimation procedure included 500 iterations of random-

ly sampled scales in the model (with replacement) for 100% representation by one baseline in the simulated mixture.

The baseline data were used to calculate maximum likelihood estimates of stock composition of sockeye salmon in the mixture samples (Patton et al. 1998). Confidence intervals (95%) of the stock composition estimates were calculated from bootstrap resampling (500) of the baseline and mixture samples (Efron and Tibshirani 1986).

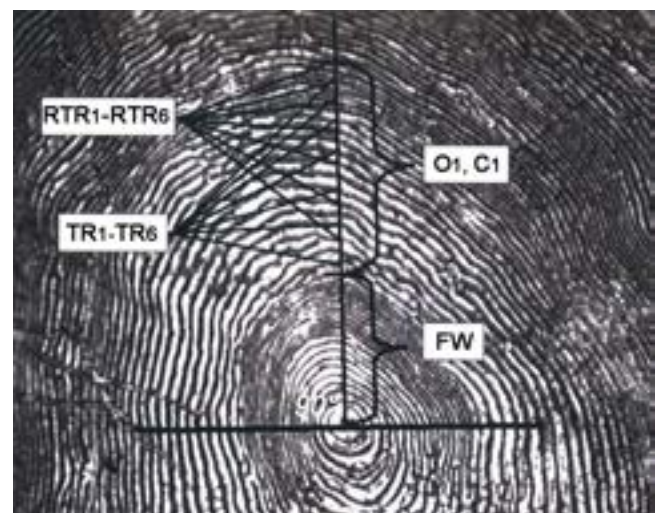


Fig. 3. Image of a sockeye salmon scale showing the scale pattern variables used for stock identification. FW = the total radius of freshwater zone, O1 = total radius of the first annual ocean growth zone, C1 = number of circuli in the first annual ocean growth zone, TR1–TR6 = radii of groups of three circuli (triplets) in the first ocean zone (six triplets), RTR1–RTR6 = radii of groups of three circuli (reverse triplets) in the first ocean zone (six reverse-triplets).

Estimates of Distribution and Abundance

We reviewed information on the distribution and abundance of immature sockeye salmon during BASIS research in the western Bering Sea in summer 2003 and fall 2002–2004 (Glebov 2007). Estimates of the abundance and biomass of sockeye salmon in the Bering Sea REEZ were provided by the TINRO-Center. The TINRO-Center estimates were calculated from BASIS trawl catch data using an area-swept formula with a fishing efficiency coefficient of 0.3 for immature salmon (Temnykh et al. 2003). The TINRO-Center estimates were stratified by year, season, maturity group, and biostatistical district. For each year and season, we pooled the TINRO-Center estimates for immature sockeye salmon into northern (districts 2–8) and southern (districts 9–12) areas (Fig. 1), and apportioned these estimates to stock (Asia and North America) using our estimates of stock composition weighted by age group. As a rough measure of the validity of these estimates, we compared them to published information on the abundance of adult sockeye salmon runs in Asia and North America.

RESULTS

Age Composition of Immature Sockeye Salmon

The 2002–2004 catches of immature sockeye salmon in the western Bering Sea were dominated (84.8 to 94.6%) by four age groups (1.1, 1.2, 2.1, and 2.2), which we referred to as “available age groups” because sample sizes of the other age groups were not large enough for scale pattern analysis (AAG; Table 1). Over the entire survey period, percentages of young immature sockeye salmon in their second ocean summer (primarily 1.1 and 2.1 fish) were higher

(~50–80% of total) than those of older ocean age groups of immature sockeye salmon. In fall 2002–2004, percentages of 1.1 sockeye salmon were higher than percentages of 2.1 sockeye salmon in the northern districts, while percentages of the two age groups were relatively similar in the southern districts. From summer to fall 2003, percentages of 1.1 sockeye salmon increased and percentages of 2.1 sockeye salmon decreased in northern districts. Immature sockeye salmon in their third ocean summer (primarily 1.2 and 2.2 fish) ranged from approximately 20–40% of the total sample. In fall 2002, percentages of 1.2 and 2.2 fish were higher than percentages of 1.1 and 2.1 fish in the northern districts. Samples sizes of other age groups of sockeye salmon were usually < 10% of the total sample in each year, season, and area stratum.

Stock-Specific Differences in Scale Patterns

Bugaev (2007) reported the detailed results of a statistical evaluation of differences in the scale patterns of local stocks of adult sockeye salmon of Asian and North American origin that were used in the baseline models. In general, the results of cluster and canonical analyses indicated that sockeye salmon of Ozernaya River (western Kamchatka) origin, which is the main stock in Asia, were well differentiated from other stocks. In contrast, stocks of eastern Kamchatka origin (Kamchatka River and a group of minor stocks of northeast Kamchatka origin) were often similar in scale structure to sockeye salmon of Alaskan origin (primarily Bristol Bay stocks). The scale patterns of adult 2.2 + 2.3 sockeye salmon of Asian and North American origin were significantly different (t -tests, $P < 0.05$). This result was important to our objective to estimate abundance and biomass of Asian and North American sockeye salmon in the western Bering Sea,

Table 1. The age composition (% of total sample size) of immature sockeye salmon in BASIS trawl catches by the R/V *TINRO* in the western Bering Sea. N = sample size, AAG = available age groups for identification by scale pattern analysis. North = Districts 1-8 and South = Districts 9-12 (Fig. 1). Juvenile (age x.0) sockeye salmon were not included in the analysis because of scale loss during trawl operations.

Year-Season Area	N	Age composition (%)											AAG %		
		0.1	0.2	0.3	1.1	1.2	1.3	1.4	2.1	2.2	2.3	3.1		3.2	4.1
2002-Fall															
North	438	1.4	2.1	-	23.1	30.4	3.2	-	14.2	19.6	1.8	1.0	3.2	-	87.3
South	642	2.8	2.9	0.1	22.6	20.6	2.2	-	22.6	19.0	2.9	3.3	0.9	-	84.8
2003-Summer															
North	527	2.6	1.0	0.4	36.8	11.4	0.2	-	38.9	5.5	0.4	2.1	0.6	0.2	92.6
South	447	5.1	1.6	0.7	29.5	16.1	1.8	-	26.8	14.3	0.4	2.2	1.3	-	86.8
2003-Fall															
North	310	2.9	1.6	-	51.6	11.0	1.6	-	21.0	7.4	0.6	1.9	0.3	-	91.0
South	566	5.5	0.9	-	32.0	14.0	1.1	0.2	29.2	12.0	0.9	3.4	1.1	-	87.1
2004-Fall															
North	295	1.7	0.7	-	42.7	16.3	-	-	29.8	5.8	-	2.7	-	0.3	94.6
South	466	6.4	1.3	0.4	36.9	10.5	-	-	39.5	3.2	-	1.3	0.4	-	90.1

because 2.2 and 2.3 are the dominant age groups of the two major Asian stocks of sockeye salmon—Lake Kuril (Ozernaya River) and Lake Azabache (Kamchatka River). For 1.2 + 1.3 sockeye salmon, there were fewer statistically significant differences between Asian and North American stocks, as well as between Asian stocks, than were found for 2.2 + 2.3 fish (*t*-tests, *p* < 0.05). In general, this was due to similarity in scale patterns of 1.2 + 1.3 sockeye salmon of eastern Kamchatka and Alaska origin, and to the wide diversity in scale phenotypes of minor stocks of western Kamchatka and eastern Kamchatka origin. In addition, there was considerable annual variation in differences in scale growth patterns between 1.2 + 1.3 stocks, which was likely due to annual changes in freshwater and early ocean foraging conditions. Nevertheless, similar trends were observed in all age 1.2 + 1.3 baselines, and errors due to annual variation in scale patterns were considered to be standard throughout the entire period of observations.

Accuracies of Stock Identification Models

Computer simulations indicated that the accuracies of the maximum-likelihood stock identification models were relatively high (mean 84.5–91.2%; Tables 2–7). While baseline-dependent simulations might overestimate the true accuracy of the models, we considered these accuracies adequate for identification of stocks at the regional level. Three models (1.2 + 1.3 fish in 2003 and 2004, 2.2 + 2.3 fish in 2003) included a multi-regional stock, i.e., a stock composed of stocks originating in both Asia and North America (Table 2, no. 2; Table 3, no. 5; Table 4, no. 4). Four models included a multi-regional stock composed of local stocks originating in both eastern and western Kamchatka (age 2.2 + 2.3 in 2002 and 2003; 1.2 + 1.3 in 2004, 2.2 + 2.3 in 2005) (Table 3, no. 5, Table 4, no. 5; Table 7, no. 4). To estimate biomass

and abundance of sockeye salmon by region, the estimated proportions of multi-regional stocks in the mixture sample were later apportioned to the component regional stock with the highest abundance of adult returns.

Stock Composition Estimates

Regional stocks of Asian origin dominated all time-area strata of 2.1+2.2 immature sockeye salmon, while proportions of stocks of North American origin (primarily Bristol Bay) were relatively high in time-area strata of 1.1+1.2 immature sockeye salmon (Table 8).

In fall 2002, estimated percentages of the 1.1+1.2 multi-regional stock (primarily sockeye salmon of Bristol Bay origin) were relatively high in both northern (51.7%) and southern areas (44.1%), and estimated percentages of 2.1+2.2 Bristol Bay sockeye salmon were relatively low in both the northern (23.6%) and southern areas (2.6%).

In summer 2003, estimated percentages of all age groups of Bristol Bay sockeye salmon were lower in northern (34.4% of 1.1+1.2 fish and 18.3% of 2.1+2.2 fish) and southern (11.3% of 1.1+1.2 fish and 0.9% of 2.1+2.2 fish) areas than in fall 2002.

In fall 2003, estimated percentages of 1.1+1.2 Bristol Bay sockeye salmon were slightly higher in the northern area (53.6%) and considerably lower in the southern area (17.7%) than in fall 2002, and estimated percentages of 2.1+2.2 Bristol Bay sockeye salmon were relatively low in both the northern (10.9%) and southern areas (6.3%).

In fall 2004, estimated percentages of 1.1+1.2 Bristol Bay fish were lower in the northern area (27.2%) than in 2002 and 2003, and were similar to fall 2003 in the southern area (20.4%). For 2.1+2.2 fish, no sockeye salmon of Bristol Bay origin were detected in either the northern or southern areas in fall 2004.

Table 2. Evaluation of the accuracy of a 5-region maximum likelihood estimate model for ages 1.2 and 1.3 sockeye salmon in 2003, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size.

Regional stock	N	Maximum likelihood estimate/standard deviation				
		1	2	3	4	5
1. Northeastern Kamchatka + Chukotka	303	0.8889	0.0642	0.0028	0.0381	0.0035
		0.0694	0.0474	0.0072	0.0391	0.0087
2. Central (Bristol Bay) and Southwestern Alaska + Northeastern and Southeastern Kamchatka	477	0.0673	0.8239	0.0003	0.0730	0.0078
		0.0686	0.0831	0.0024	0.0779	0.0146
3. Kodiak I.	150	0.0177	0.0069	0.9869	0.0030	0.0001
		0.0204	0.0139	0.0215	0.0089	0.0010
4. Eastern (Kamchatka R.) and Northeastern Kamchatka	231	0.0254	0.0924	0.0095	0.8770	0.0034
		0.0336	0.0762	0.0201	0.0832	0.0084
5. Western and Southwestern Kamchatka	301	0.0007	0.0126	0.0005	0.0089	0.9852
		0.0023	0.0180	0.0029	0.0125	0.0171
Mean accuracy (%)						91.24

Table 3. Evaluation of the accuracy of a 6-region maximum likelihood estimate model for ages 2.2 and 2.3 sockeye salmon in 2003, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size.

Regional stock	N	Maximum likelihood estimate/standard deviation					
		1	2	3	4	5	6
1. Northeastern Kamchatka + Chukotka	337	0.8144	0.0234	0.0096	0.0047	0.0830	0.0002
		0.0827	0.0256	0.0157	0.0103	0.0521	0.0024
2. Central Alaska (Bristol Bay)	150	0.0092	0.9321	0.0180	0.0043	0.0959	0.0003
		0.0237	0.0569	0.0312	0.0156	0.0722	0.0023
3. Eastern (Kamchatka R.), Southeastern, and Northwestern Kamchatka	220	0.0803	0.0176	0.9170	0.0001	0.0365	0.0000
		0.0527	0.0310	0.0463	0.0009	0.0370	0.0000
4. Kodiak I.	200	0.0079	0.0079	0.0012	0.8599	0.0459	0.0000
		0.0126	0.0194	0.0040	0.0817	0.0506	0.0000
5. Southwestern Alaska + Northeastern Kamchatka	384	0.0864	0.0186	0.0030	0.1310	0.7360	0.0000
		0.0726	0.0374	0.0114	0.0829	0.0971	0.0000
6. Southwestern Kamchatka (Ozernaya R.)	100	0.0018	0.0004	0.0512	0.0000	0.0027	0.9995
		0.0054	0.0028	0.0316	0.0004	0.0079	0.0033
Mean accuracy (%)							87.65

Table 4. Evaluation of the accuracy of a 6-region maximum likelihood estimate model for ages 1.2 and 1.3 sockeye salmon in 2004, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size.

Regional stock	N	Maximum likelihood estimate/standard deviation					
		1	2	3	4	5	6
1. Kodiak I.	279	0.9586	0.0037	0.0109	0.0043	0.0017	0.0031
		0.0343	0.0074	0.0156	0.0104	0.0046	0.0061
2. Central Alaska (Bristol Bay)	195	0.0302	0.8038	0.0374	0.0873	0.0396	0.0053
		0.0323	0.1092	0.0519	0.0829	0.0420	0.0175
3. Eastern Kamchatka (Kamchatka R.) + Chukotka	295	0.0006	0.0618	0.8421	0.0860	0.0611	0.0384
		0.0040	0.0580	0.0974	0.0785	0.0503	0.0357
4. Southwestern Alaska + Northeastern Kamchatka	333	0.0001	0.0935	0.0917	0.8029	0.0409	0.0038
		0.0017	0.1012	0.0910	0.1102	0.0522	0.0150
5. Northeastern and Northwestern Kamchatka	200	0.0064	0.0249	0.0171	0.0163	0.8192	0.0595
		0.0112	0.0343	0.0268	0.0315	0.0793	0.0644
6. Western and Southwestern Kamchatka	349	0.0041	0.0123	0.0008	0.0032	0.0375	0.8899
		0.0094	0.0232	0.0057	0.0098	0.0520	0.0734
Mean accuracy (%)							85.28

Distribution and Assessment of Relative Abundance

Catches of immature sockeye salmon were highest in Districts 8 and 12 (Fig. 4). Average catches were approximately 100–500 fish/km². In 2002 and 2003, catches of sockeye salmon at some stations were very high (≥ 1000 fish/km²). In District 8, sockeye salmon were distributed throughout the entire area in fall 2002–2003 or concentrated in the northern part of the district in summer 2003 and fall 2004. In District 12, catches were highest west of 167–168°E, and substantially lower near the border of the

REEZ. Seasonal variation in 2003 might reflect southward migration of some immature sockeye salmon from northern districts in fall (Glebov 2007).

Estimates of Abundance and Biomass of Immature Sockeye Salmon

The estimated maximum abundance/biomass of immature sockeye salmon occurred in fall 2002 (77 million fish/92 thousand t in Districts 5–8; 75 million fish/86 thousand t in southern District 12; Table 9). Estimated abundance and

Table 5. Evaluation of the accuracy of a 5-region maximum likelihood estimate model for ages 2.2 and 2.3 sockeye salmon in 2004, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size.

Regional stock	N	Maximum likelihood estimate/standard deviation				
		1	2	3	4	5
1. Eastern Kamchatka (Kamchatka R.) + Chukotka	325	0.9233	0.0892	0.0645	0.0038	0.0464
		0.0602	0.0593	0.0542	0.0089	0.0585
2. Central (Bristol Bay) and Southwestern Alaska	423	0.0155	0.7835	0.0345	0.0098	0.0090
		0.0319	0.1006	0.0607	0.0260	0.0245
3. Kodiak I.	293	0.0369	0.0923	0.8870	0.0030	0.0034
		0.0472	0.0726	0.0773	0.0093	0.0125
4. Southwestern Kamchatka (Ozernaya R.)	202	0.0044	0.0205	0.0126	0.9825	0.0001
		0.0103	0.0318	0.0217	0.0280	0.0012
5. Southeastern Kamchatka	32	0.0199	0.0145	0.0014	0.0009	0.9411
		0.0319	0.0255	0.0067	0.0046	0.0635
Mean accuracy (%)						90.35

Table 6. Evaluation of the accuracy of a 5-region maximum likelihood estimate model for ages 1.2 and 1.3 sockeye salmon in 2005, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size.

Regional stock	N	Maximum likelihood estimate/standard deviation				
		1	2	3	4	5
1. Central Alaska (Bristol Bay)	150	0.9121	0.1155	0.0077	0.0134	0.0384
		0.0852	0.0875	0.0175	0.0275	0.0501
2. Eastern (Kamchatka R.) and Northeastern Kamchatka	411	0.0585	0.7520	0.0583	0.0053	0.0466
		0.0836	0.1150	0.0501	0.0155	0.0658
3. Southwestern Alaska + Kodiak I.	401	0.0000	0.0392	0.9259	0.0058	0.0085
		0.0002	0.0371	0.0501	0.0097	0.0137
4. Northwestern, West, and Southwestern Kamchatka	453	0.0199	0.0201	0.0049	0.8930	0.0203
		0.0267	0.0242	0.0095	0.0677	0.0301
5. Northeastern and Southeastern Kamchatka	220	0.0095	0.0732	0.0032	0.0825	0.8862
		0.0218	0.0658	0.0080	0.0638	0.0805
Mean accuracy (%)						87.38

biomass of immature sockeye salmon were very high in two biostatistical districts (8 and 12). In the northern area (District 8) estimated abundance and biomass in fall 2003 were substantially lower in fall 2003 than in fall 2002 and 2004. In the southern area (District 8) in fall, there was a declining trend in estimated abundance and biomass over the three-year period. In 2003, estimated abundance/biomass decreased from summer to fall in the northern area and increased from summer to fall in the southern area.

Abundance and Biomass of Asian and North American Stocks

In all time and area strata, estimates of abundance and biomass of immature sockeye salmon (1.1+1.2+2.1+2.2 fish)

were consistently higher for Asian stocks than for North American stocks (Table 10). Estimates of abundance and biomass of North American stocks were highest in the northern area in fall 2002 and summer 2003. Although estimated percentages of North American stocks in the northern area were similar in fall 2002 and 2003, the estimated total abundance and biomass of immature sockeye salmon was substantially lower in fall 2003 than in fall 2002. In the southern area in fall, the estimated abundance and biomass of North American stocks decreased over the period from 2002 to 2004.

For Asian stocks, estimates of abundance and biomass of immature sockeye salmon (1.1+1.2+2.1+2.2 fish) were further apportioned to two groups: (1) eastern Kamchatka+Chukotka stocks and (2) western Kamchatka stocks. In the northern

Table 7. Evaluation of the accuracy of a 6-region maximum likelihood estimate model for ages 2.2 and 2.3 sockeye salmon in 2005, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size.

Regional stock	N	Maximum likelihood estimate/standard deviation					
		1	2	3	4	5	6
1. Chukotka	76	0.8430	0.0106	0.0294	0.0068	0.0009	0.0168
		0.0641	0.0157	0.0253	0.0182	0.0041	0.0188
2. Central Alaska (Bristol Bay) + Kodiak I.	450	0.0048	0.6571	0.0295	0.0004	0.1229	0.0278
		0.0165	0.1505	0.0485	0.0030	0.1186	0.0399
3. Eastern Kamchatka (Kamchatka R.)	150	0.0460	0.1349	0.9344	0.0417	0.0148	0.0000
		0.0392	0.0773	0.0554	0.0359	0.0248	0.0000
4. Northeastern Kamchatka + Northwestern Kamchatka	142	0.0702	0.0051	0.0002	0.9045	0.0004	0.0185
		0.0522	0.0110	0.0014	0.0517	0.0031	0.0267
5. Southwestern Alaska	195	0.0164	0.1595	0.0065	0.0018	0.8059	0.0106
		0.0296	0.1252	0.0190	0.0064	0.1288	0.0329
6. Southwestern Kamchatka (Ozernaya R.)	150	0.0196	0.0328	0.0000	0.0448	0.0551	0.9263
		0.0324	0.0408	0.0000	0.0375	0.0620	0.0576
Mean accuracy (%)							84.52

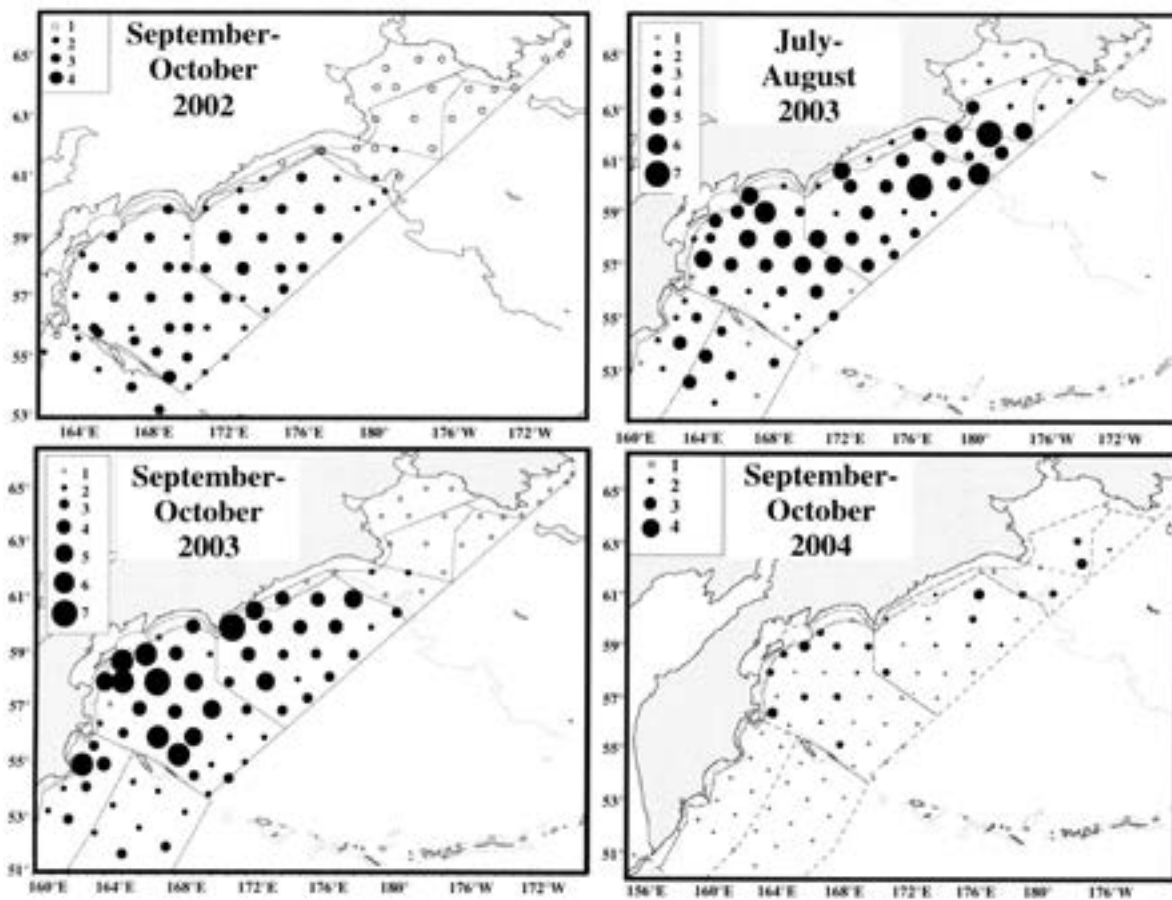


Fig. 4. The spatial distribution and relative abundance of sockeye salmon determined by BASIS research in the western Bering Sea, 2002-2004. Note that scales vary among years. The size of the circles indicates relative abundance (number of fish/km²). Upper left panel (2002): 1 = no catch, 2 = 1–10, 3 = 11–100, 4 = 101–1000. Upper right and lower left panels (2003): 1 = no catch, 2 = < 50, 3 = 51–100, 4 = 101–250, 5 = 251–500, 6 = 501–1000, 7 = > 1001. Lower right panel (2004): 1 = no catch; 2 = 1–10; 3 = 11–100; 4 = 101–500.

Table 8. Evaluation of the accuracy of a 6-region maximum likelihood (MLE) estimate model for ages 2.2 and 2.3 sockeye salmon in 2005, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). CI (95%) = 95% confidence interval, N = sample size, SD = standard deviation. Geographic locations of regional stocks are shown in Fig. 2. CAK = Central Alaska (Port Moller, Bristol Bay), Chuk = Chukotka, EKam = Eastern Kamchatka, Kodiak I. = Kodiak Island, NEKAM = Northeastern Kamchatka, NWKAM = Northwestern Kamchatka, SEKAM = Southeastern Kamchatka, SWAK = Southwestern Alaska, SWKAM = Southwestern Kamchatka, WKAM = Western Kamchatka.

Year & Season	Bering Sea Area	Age	N	Regional stock	MLE	SD	CI (95%)
2002 Fall	Northern	1.1-1.2	193	NEKam-Chuk	0.2696	0.0503	0.1656-0.3707
				CAK-SWAK-NEKam-SEKam	0.5167	0.0576	0.4003-0.6386
				Kodiak I.	0.0162	0.0140	0.0000-0.0467
				EKam-NEKam	-	-	-
				WKam-SWKam	0.1975	0.0336	0.1283-0.2692
		2.1-2.2	135	NEKam-Chuk	0.1641	0.0504	0.0458-0.2278
				CAK	0.2355	0.0690	0.1003-0.3943
				EKam-SEKam-NWKam	0.4408	0.0721	0.2919-0.5902
				Kodiak I.	-	-	-
				SWAK+ NEKam	-	-	-
	Southern	1.1-1.2	214	NE Kam.-Chuk	0.2466	0.0455	0.1473-0.3384
				CAK- SWAK-NEKam-SEKam	0.4537	0.0614	0.3198-0.5910
				Kodiak I.	-	-	-
				EKam- NEKam	0.0581	0.0397	0.0000-0.1445
				WKam-SWKam	0.2416	0.0356	0.1733-0.3218
		2.1-2.2	232	NE Kam.-Chuk	0.1104	0.0316	0.0372-0.1441
				CAK	0.0264	0.0359	0.0000-0.1201
				EKam-SEKam-NWKam	0.6137	0.0548	0.4729-0.7077
				Kodiak I.	-	-	-
				SWAK-NEKam	-	-	-
2003 Summer	Northern	1.1-1.2	180	SWKam	0.2495	0.0361	0.1908-0.3667
				Kodiak I.	0.0132	0.0114	0.0000-0.0419
				CAK	0.3437	0.0793	0.1607-0.5288
				EKam-Chuk	0.2858	0.0659	0.1531-0.4354
				SWAK-NEKam	0.3017	0.0798	0.1187-0.4675
				NEKam-NWKam	-	-	-
				WKam-SWKam	0.0556	0.0354	0.0000-0.1358
				EKam-Chuk	0.4444	0.0617	0.3205-0.5913
				CAK-SWAK	0.1829	0.0609	0.0000-0.2246
				Kodiak I.	-	-	-
	Southern	1.1-1.2	120	SWKam	0.3727	0.0567	0.3095-0.5796
				SEKam	-	-	-
				Kodiak I.	0.0085	0.0099	0.0000-0.0344
				CAK	0.1138	0.0699	0.0000-0.2583
				EKam-Chuk	0.1225	0.0708	0.0000-0.3013
		2.1-2.2	127	SWAK-NEKam	0.5800	0.0994	0.3445-0.7744
				NEKam-NWKam	0.0370	0.0442	0.0000-0.1369
				WKam-SWKam	0.1382	0.0569	0.0227-0.2725
				EKam-Chuk	0.5471	0.0647	0.4179-0.6864
				CAK-SWAK	0.0088	0.0422	0.0000-0.0831
Kodiak I.	-	-	-				
SWKam	0.4441	0.0654	0.2893-0.5709				
SEKam	-	-	-				

Table 8 (continued).

Year & Season	B.S. Area	Age	N	Regional stock	MLE	SD	CI (95%)
Fall	Northern	1.1-1.2	178	Kodiak I.	-	-	-
				CAK	0.5358	0.0650	0.3849-0.6654
				EKam-Chuk	0.3852	0.0600	0.2599-0.5126
				SWAK-NEKam	-	-	-
				NEKam-NWKam	-	-	-
		WKam-SWKam	0.0790	0.0397	0.0000-0.1761		
		2.1-2.2	86	EKam-Chuk	0.4370	0.0756	0.2876-0.5833
				CAK-SWAK	0.1094	0.0644	0.0000-0.2285
				Kodiak I.	-	-	-
				SWKam	0.4536	0.0745	0.3266-0.6241
	SEKam			-	-	-	
	Southern	1.1-1.2	225	Kodiak I.	-	-	-
				CAK	0.1766	0.0555	0.0509-0.2708
				EKam-Chuk	0.4085	0.0607	0.2616-0.5242
				SWAK-NEKam	0.0499	0.0564	0.0000-0.1865
				NEKam-NWKam	-	-	-
		WKam-SWKam	0.3650	0.0485	0.2533-0.4716		
		2.1-2.2	200	EKam-Chuk	0.2327	0.0477	0.1354-0.3478
				CAK-SWAK	0.0626	0.0442	0.0000-0.1385
				Kodiak I.	-	-	-
SWKam				0.7047	0.0509	0.6030-0.8324	
SEKam	-			-	-		
2004 Fall	Northern	1.1-1.2	163	CAK	0.2725	0.0764	0.0693-0.4306
				EKam-NEKam	0.6508	0.0883	0.4355-0.8604
				SWAK-Kodiak I.	0.0767	0.0410	0.0114-0.1830
				NWKam-WKam-SWKam	-	-	-
				NEKam-SEKam	-	-	-
		2.1-2.2	115	Chuk	0.1239	0.0448	0.0211-0.2214
				CAK-Kodiak I.	-	-	-
				EKam	0.5773	0.0726	0.4120-0.7185
				NEKam-NWKam	0.1114	0.0548	0.0000-0.2133
	Southern	1.1-1.2	155	CAK	0.2039	0.0706	0.0378-0.3372
				EKam-NEKam	0.4822	0.1028	0.2603-0.6995
				SWAK-Kodiak I.	0.1239	0.0409	0.0484-0.2201
				NWKam-WKam-SWKam	-	-	-
				NEKam-SEKAM	0.1900	0.0706	0.0286-0.3498
		2.1-2.2	163	Chuk	0.0552	0.0253	0.0000-0.0929
				CAK-Kodiak I.	-	-	-
				EKam	0.2057	0.0460	0.1150-0.3130
				NEKam-NWKam	0.2744	0.0548	0.1709-0.3960
SWAK	-	-	-				
SWKam	0.4647	0.0584	0.3526-0.5856				

Table 9. The estimated abundance and biomass of immature sockeye salmon in the epipelagic zone of the western Bering Sea in 2002–2004. Coefficient of trawl catch = 0.3. Data source: TINRO-Centre, Vladivostok. The locations of biostatistical districts are shown in Fig. 1.

Year-Season	Biostatistical districts												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
Abundance (millions of fish)													
2002-Fall	-	-	-	-	0.5	-	0.1	76.6	-	-	-	75.3	152.5
2003-Summer	-	0.3	5.8	0.6	13.1	-	0.9	50.1	1.1	-	-	40.0	111.7
2003-Fall	-	-	-	-	0.2	-	2.5	30.1	0.2	-	-	68.2	101.3
2004-Fall	-	-	0.1	-	0.7	-	0.1	72.9	-	-	-	48.2	122.0
Biomass (thousands of tons)													
2002-Fall	-	-	-	-	0.6	-	0.2	91.6	-	-	-	86.1	178.4
2003-Summer	-	0.2	3.8	0.4	8.8	-	0.7	39.1	0.6	-	-	30.0	83.8
2003-Fall	-	-	-	-	0.1	-	2.3	26.3	0.2	-	-	61.7	90.6
2004-Fall	-	-	0.1	-	0.5	-	0.1	63.9	-	-	-	44.3	108.9

Table 10. Estimates of the number (no., millions of fish) and biomass (thousands of metric tons) of immature sockeye salmon (1.1+1.2+2.1+2.2 fish) of Asian and North American origin in the western Bering Sea in 2002–2004. The northern area includes Districts 1–8 and the southern area includes Districts 9–12 (Fig. 1).

Year-Season B.S. Region	Total abundance and biomass		Regional stock					
			Asia			North America		
	no.	tons	%	no.	tons	%	no.	tons
2002-Fall								
Northern	77.18	92.36	58.9	45.46	54.40	41.1	31.72	37.96
Southern	75.30	86.06	76.9	57.91	66.18	23.1	17.39	19.88
2003-summer								
Northern	70.68	53.07	57.0	40.29	30.25	43.0	30.39	22.82
Southern	41.04	30.78	65.2	26.76	20.07	34.8	14.28	10.71
2003-Fall								
Northern	32.82	28.72	60.6	19.89	17.40	39.4	12.93	11.32
Southern	68.46	61.90	84.9	58.12	52.55	15.1	10.34	9.35
2004-Fall								
Northern	73.80	64.60	77.0	56.83	49.74	23.0	16.97	14.86
Southern	48.15	44.30	83.9	40.40	37.17	16.1	7.75	7.13

area, percentages of the total estimated abundance/biomass were consistently higher for eastern Kamchatka+Chukotka stocks (40.9% in fall 2002, 36.3% in summer 2003, 40.5% in fall 2004, and 71.6% in fall 2004) than for western Kamchatka stocks (18.0% in fall 2002, 20.7% in summer 2003, 20.1% in fall 2004, and 5.4% in fall 2004). In the southern area, percentages of the total estimated abundance/biomass were higher for eastern Kamchatka+Chukotka stocks in fall 2002 (52.2%), summer 2003 (35.6%), and fall 2004 (60.0%) than for western Kamchatka stocks in fall 2002 (24.7%), summer 2003 (29.6%), and fall 2004 (23.9%). In fall 2003,

percentages of the total estimated abundance/biomass of immature sockeye salmon were substantially higher for western Kamchatka (52.4%) than for eastern Kamchatka+Chukotka (32.5%).

DISCUSSION

Maturity, Age Composition, and Distribution

Glebov (2007) reviewed information on the distribution and migrations of sockeye salmon during BASIS surveys in

the western Bering Sea in summer and fall 2002–2006. Most (nearly 100%) of the sockeye salmon in trawl catches by the RV *TINRO* in summer and fall 2002–2004 were immature. A single maturing sockeye salmon was caught during the summer 2003 survey. The near absence of maturing sockeye salmon in trawl catches in the western Bering Sea was expected, because prespawning aggregations of maturing sockeye salmon in the western Bering Sea (primarily of eastern Kamchatka origin) are usually completed by the second half of July (Bugaev 2003a,d). Juvenile (ocean age .0) sockeye salmon were more prevalent than maturing fish in BASIS trawl catches in the western Bering Sea. However, we could not use scale pattern analysis to estimate stock composition of juvenile salmon because of scale loss during BASIS trawl fishing operations. While it seems reasonable to assume that juvenile sockeye salmon in summer–fall BASIS catches in the western Bering Sea were of Asian origin, similarities in scale patterns indicated possible intermixing of eastern Kamchatka, Chukotka, and Alaskan stocks during their first ocean year. This issue will likely be resolved by future genetic (DNA) stock identification analyses.

The age structure of immature sockeye salmon in the western Bering Sea during the 2002–2004 BASIS surveys was typical for this period of ocean life (French et al. 1976; Burgner 1991). For our stock-identification analysis, we used baselines composed of the four dominant age groups of sockeye salmon (1.2, 1.3, 2.2 and 2.3). These age groups account for about 90% of all adult returns of sockeye salmon in Asia and North America (Burgner 1991; Bugaev 1995).

Comparison of Stock Composition Estimates to Other Studies

The results of preliminary scale pattern analyses indicated that the western Bering Sea in summer and fall is an area of intermingling of immature sockeye salmon of Asian and North American origin, and that there is considerable spatial, seasonal, and annual variation in the proportions of Asian and North American origin stocks distributed in this region (Bugaev 2004, 2005, 2006). In general our results were similar to these preliminary analyses. Nevertheless, there were some notable differences. For example, in fall 2002 catches our estimated percentages of Alaskan stocks were 10–20% higher than those of Bugaev (2004), while our estimated percentages of western Kamchatka stocks were correspondingly lower. In summer 2003 catches, our estimated percentage of Alaskan stocks in the southwestern Bering Sea (Districts 9–12) was 34.8%, which was 25.9% lower than the preliminary estimate (Bugaev 2005). Brood-year specific baselines were not available for use in preliminary analyses, and likely resulted in errors in the models when there was significant interannual variation in freshwater and early marine scale growth patterns.

In general, the results of genetic stock identification studies corroborate our scale pattern analysis results. A direct

comparison of our stock composition estimates with those of genetic analyses of 2002–2004 BASIS mixture samples (Habicht et al. 2005; Gritsenko et al. 2007) is not possible because of differences in experimental design among studies. For example, investigations differed in the number and geographic range of stocks included in the baseline models, the number of mixture samples analyzed, and the biological (age), spatial, and temporal stratification of results. Nevertheless, a broad comparison of the results of these studies with respect to estimated proportions of immature sockeye salmon of Asian and North American origin is possible.

Habicht et al. (2005) used a DNA baseline (13 microsatellite and two single nucleotide polymorphism (SNP) markers) to estimate stock proportions of immature sockeye salmon in summer–fall 2002–2003 BASIS samples. Their mixture samples were pooled over years. Similar to our results, Habicht et al. estimated that immature sockeye salmon of Asian origin were the dominant (~80%) stock in the southwestern Bering Sea. In contrast to our results, Habicht et al. estimated that Asian stocks accounted for < 50% of immature sockeye salmon in the northwestern Bering Sea. However, their Asian baseline was not comprehensive, including only Kamchatka River and Lake Kuril populations. Updated estimates using a more comprehensive (SNP) baseline indicated that Asian populations dominated BASIS catches in both southern (~94%) and northern (~62%) areas of Bering Sea (Districts 8 and 12, Fig. 4) in fall 2002–2004 (C. Habicht, chris.habicht@alaska.gov, pers. comm.).

Gritsenko et al. (2007) analyzed fall 2004 BASIS samples of immature sockeye salmon from the Bering Sea REEZ using genetic (SNP) analysis. Their estimated percentage of Asian stocks in the northwestern Bering Sea (72%) was similar to that of C. Habicht (chris.habicht@alaska.gov, pers. comm.). Our results also indicated that Asian stocks dominated BASIS samples from this region in fall 2004, although the total percentage of Asian stocks was substantially higher among age 2.1+2.2 fish (94%) than age 1.1+1.2 fish (65%; Table 8).

Our results and those of other (genetic) studies corroborate conceptual models of ocean migrations of sockeye salmon of Asian and North American origin in the western Bering Sea (French et al. 1976; Burgner 1991; Myers et al. 2007). The results of BASIS stock identification studies provide quantitative evidence that immature sockeye salmon of Asian (Kamchatka) origin are the dominant regional stock of this species in the western Bering Sea in fall. In addition, percentages of sockeye salmon of North American origin were higher in the northwestern Bering Sea (Districts 1–8) than in the southwestern Bering Sea (Districts 9–12). These results conform to known patterns of distribution of sockeye salmon originating from both continents, and are reasonable considering the geographic proximity of the northwestern Bering Sea to Alaska.

Distribution and Abundance of Sockeye Salmon Stocks in the Western Bering Sea

Abundance of sockeye salmon in Asia and North America was relatively high during the early 2000s (Eggers and Irvine 2007). However, BASIS estimates of abundance of immature sockeye salmon in the western Bering Sea (Table 9) were very high compared to estimated annual runs (catch + escapement) of sockeye salmon in Asia and North America. For example, the estimated total annual Pacific-Rim run of sockeye salmon averaged 79 million sockeye salmon in 2003–2005 (G. Ruggerone, Natural Resources Consultants, Seattle, pers. comm.). High estimates of abundance of immature sockeye salmon in the western Bering Sea might be explained, in part, by the presence of multiple brood years and age-classes of immature sockeye salmon that would have returned to their natal streams over a period of several years. The western Bering Sea, however, includes only a portion of the total area of known ocean distribution of Asian and North American sockeye salmon (Myers et al. 2007). We speculate that BASIS stock assessment methods, in particular the use of a fishing-efficiency coefficient of 0.3, may have resulted in overestimation of the abundance of immature salmon in the western Bering Sea.

In addition, official run-size statistics for adult salmon may be inaccurate. For example, official statistics indicated that total annual runs of adult sockeye salmon in Russia averaged 10.8 million fish in 2004–2006 (Anonymous 2005, 2006, 2007). Our estimates of abundance of immature sockeye salmon of Asian origin in the western Bering Sea in fall were 103 million fish in 2002, 78 million fish in 2004, and 97 million fish in 2005 (Table 10). Historically high catches (~ 15–18 thousand t) of sockeye salmon on the west coast of Kamchatka (the Ozernaya River), which exceeded the maximum recorded for the past one hundred years, have occurred since 2002 (Bugaev and Bugaev 2003). This likely contributed to the high abundance of immature sockeye salmon of Asian origin in the western Bering Sea in 2002–2004. The abundance of sockeye salmon of northeastern Kamchatka origin has also increased, although official statistics on catches and escapement in this area are not accurate because of extensive poaching. In recent years a similar poaching problem has occurred in the Kamchatka River Basin, as a result of its proximity to a number of human settlements.

Ecological conditions apparently also played an important role in the distribution and abundance of immature sockeye salmon in the western Bering Sea in summer–fall 2002–2004 (Shuntov et al. 2007). In principle, summer–fall foraging and migratory strategies of sockeye salmon in the western Bering Sea are relatively stable. Western Kamchatka (Ozernaya River) sockeye salmon are the most abundant regional stock of sockeye salmon in Asia. Our estimates indicated a relatively stable and high abundance of immature sockeye salmon of western Kamchatka origin in the western Bering Sea in 2002–2004. Estimated percentages of sockeye

salmon of eastern Kamchatka, northeastern Kamchatka, and Chukotka origin, which are indigenous to the western Bering Sea, were also relatively stable and high. Our results, as well as those of other stock identification studies (Habicht et al. 2005; Gritsenko 2007), indicated significant foraging migrations of immature sockeye salmon of Alaskan origin in the western Bering Sea. Alaskan stocks dominate total Pacific Rim runs of sockeye salmon (Eggers and Irvine 2007), and Bristol Bay stocks accounted for an average of 50% (37 million fish) of total annual Pacific Rim runs in 2003–2005 (G. Ruggerone, Natural Resources Consultants, Seattle, pers. comm.). In general, BASIS estimates of total abundance of immature sockeye salmon were highest in the northern districts (2–8) of the western Bering Sea, except in fall 2003 (Table 9). The estimated abundance of North American stocks, primarily Bristol Bay, was higher in the northwestern Bering Sea than in the southwestern Bering Sea (Table 10). This may reflect northwestward shifts in distribution immature sockeye salmon of North American origin that resulted from large-scale ecosystem changes and favorable ecological conditions for foraging salmon in the western Bering Sea in the early 2000s (Shuntov and Sviridov 2005). These changes included weaker winter monsoons, stronger summer monsoons, below normal ice cover, increased sea surface temperature, and increased inflow of Pacific waters into the Bering Sea (Glebova 2007; Basyuk et al. 2007; Shuntov et al. 2007). These changes may have also influenced the distribution and abundance of salmon predators. Differences between estimated abundances of immature and adult salmon might be explained in part by high ocean mortality due to increased abundance of predators. For example, Sviridov et al. (2004) and Bugaev and Shevlyakov (2007) observed high numbers of wounded and scarred salmon during research vessel surveys in the REEZ. Further research, however, is needed to clarify the dynamics of distribution and abundance of sockeye salmon of Asian and North American origin in the western Bering Sea against the background of ecosystem changes at the beginning of the 21st century.

Stock-specific ocean assessments of distribution and abundance of immature sockeye salmon can serve as pre-season indicators of adult returns, providing a useful decision-making tool for fishery managers. In the REEZ, this issue has usually been addressed by analysis of data on the distribution of salmon during feeding migrations in waters adjacent to the area of reproduction of certain regional stock groups (e.g., Shuntov et al. 1989a,b; Yerokhin 2002). Nevertheless, this method seems to lead to frequent errors in run forecasting. Ocean stock assessment methods for salmon, e.g., trawl fishing efficiency coefficients, need further evaluation and refinement. Stock assessments performed at multiple life stages of salmon can result in more complete and accurate management recommendations. New genetic tools have the potential to provide a rapid and precise procedure for real-time ocean stock assessment of immature salmon. The use of this approach in the western Bering Sea

might improve assessments of the potential abundance of sockeye salmon returning to all regions in Asia and some regions of North America. In addition, trawl survey research would benefit from activities that provide practical tools that can be used by managers to forecast the runs of major species and stocks.

CONCLUSIONS

We conclude that the western Bering Sea is an important area of intermixing of immature sockeye salmon of Asian and North American origin. In principle, this phenomenon has been known for a long time (e.g., Konovalov 1971), however, the results of scale pattern and genetic stock identification analyses (Habicht et al. 2005; C. Habicht, chris.habicht@alaska.gov, pers. comm.) have provided new quantitative evidence of the extent of intermixing of sockeye salmon of Asian and North American origin in the western Bering Sea. We speculated that there might have been a substantial increase in “visitors” to the western Bering Sea from stocks originating in Alaska and western Kamchatka in the early 2000s. Stock-specific changes in abundance and distribution might have resulted from complex interactions between density-dependent and ecosystem factors. However, the temporal span of observations from BASIS research is not yet sufficient to understand the dynamics of stock-specific distribution and abundance of sockeye salmon or to provide accurate run forecasting tools for fishery management.

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Stock-Specific Distribution and Abundance of Immature Chinook Salmon in the Western Bering Sea in Summer and Fall 2002–2004

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Abstract: Seasonal stock-specific distribution and abundance of Chinook salmon (*Oncorhynchus tshawytscha*) were determined using scale pattern analysis of Bering-Aleutian Salmon International Survey (BASIS) samples and catch data collected in the western Bering Sea in summer 2003 and fall 2002–2004. Chinook salmon were sparsely distributed in this region, which greatly limited the number of samples available for stock identification research. Research trawl catches of immature Chinook salmon were highest in northern areas, and catches throughout the region were dominated by fish in their second ocean summer. Estimated percentages of immature Chinook salmon of North American (Alaska) origin (50.2–71.2%) were consistently higher than those of Asian (Russia) origin. The highest estimated abundance of immature Chinook salmon was in summer 2003 (~21 million North American and ~20 million Asian fish). These estimates were extraordinarily high compared to adult returns to Asia and North America in 2004–2006, and we concluded that BASIS stock assessment methods overestimated the abundance of this species. Nevertheless, our results provided the first quantitative evidence of the extensive distribution of immature Chinook salmon of North American origin in the western Bering Sea in summer and fall. We concluded that the western Bering Sea ecosystem is an important summer–fall foraging area for immature Chinook salmon of both Asian and North American origin.

Keywords: abundance, age, biomass, Chinook salmon, distribution, immature, scale pattern analysis, stock identification, western Bering Sea

INTRODUCTION

The Bering-Aleutian Salmon International Survey (BASIS) was initiated in 2002 to detect and monitor changes in climate-ocean and ecosystem states and Pacific salmon (*Oncorhynchus* spp.) in the Bering Sea (NPAFC 2001, 2002, 2003, 2004). In addition to ichthyological, hydrobiological, and hydrological research, a major focus of BASIS was to estimate seasonal stock-specific distribution and abundance of salmon in the Bering Sea. Chinook salmon (*O. tshawytscha*) are the least abundant species of Pacific salmon (Heard et al. 2007), which increased the difficulty of obtaining adequate BASIS samples for stock identification research. Prior to BASIS research, limited evidence from tagging experiments and stock identification studies using scale pattern analysis indicated that western Alaska was the dominant regional stock of Chinook salmon in the northwestern and central Bering Sea in summer and in the southeastern Bering Sea (west of 170°W) in winter (Major et al. 1978; Myers et al. 1987, 1996, 2004; Myers and Rogers 1988; Healey 1991). Bugaev (2004, 2005) reported preliminary stock-identification results from scale-pattern analyses of Chinook salmon in

BASIS samples from the western Bering Sea in 2002–2003. Bugaev's results indicated intermixing of Chinook salmon of Asian (Kamchatka Peninsula) and western Alaska origin in the western Bering Sea portion of the Russian Exclusive Economic Zone (REEZ). In this paper, we briefly review information from BASIS surveys on the distribution, abundance, and biological characteristics of Chinook salmon in the western Bering Sea, and update and extend earlier stock identification results reported by Bugaev (2004, 2005). Our primary objectives were to estimate the proportions and potential abundance of major stocks of Chinook salmon of Asian and North American origin in the western Bering Sea in summer and fall 2002–2004.

MATERIALS AND METHODS

Analysis of scale patterns has been used since the 1950s to estimate the regional stock composition of salmon caught in mixed-stock fisheries on the high seas. Major et al. (1972) outlined the basic principles and procedures of scale pattern analysis. Our methods were similar to those described by Bugaev (2004, 2005) and Bugaev et al. (2004). Briefly, we

used scale pattern analysis of representative (baseline) samples of Asian and North American Chinook salmon to estimate the proportions of these stock groups in BASIS (mixture) samples and their potential abundance in the western Bering Sea.

Mixture Samples

Mixture samples of Chinook salmon and associated biological and catch data were collected by the staff of the TINRO-Center from trawl catches of the RV *TINRO* in the western Bering Sea in summer (July–August) 2003 and fall (September–October) 2002–2004 (NPAFC 2003, 2004, 2005). A standard midwater rope trawl (PT/TM 80/396 m) was used to survey the upper epipelagic layer (~upper 40 m).

Shipboard sampling of Chinook salmon included determination of maturity and collection of a scale sample from each fish. Maturity was determined by visual evaluation of the stage of gonad maturation (Pravdin 1966). All fish at stages II and II–III were considered immature (e.g., Mosher 1972; Bugaev 1995; Ito and Ishida 1998). The body area of scale collection was recorded using a classification scheme developed by TINRO-Center (Bugaev et al. 2009). Collection of preferred scales (Clutter and Whitesel 1956; Knudsen 1985; Davis et al. 1990) was not always possible as salmon caught in trawls frequently lose many scales. Both preferred and non-preferred scales were used to estimate age composition. Only preferred scales were used to estimate stock composition, because different rates of scale growth on different parts of the fish's body can influence the results of scale pattern analysis. A similar approach has been used for age determination and stock identification of salmon in incidental catches by commercial trawl fisheries in the eastern Bering Sea (Myers and Rogers 1988; Patton et al. 1998; Myers et al. 2004).

Ages of immature Chinook salmon in the mixture samples were determined in the laboratory by counting the number of freshwater and marine annuli on scales, which is the standard method accepted for Pacific salmon (e.g., Ito and Ishida 1998). Age was designated by the European method, whereby the number of freshwater annuli and number of ocean annuli are separated by a dot (Koo 1962). For example, a 1.1 Chinook salmon has one freshwater annulus and one ocean annuli on its scale, and is in its second summer–fall in the ocean. Although juvenile Chinook salmon (x.0 fish) were present in BASIS trawl catches, samples were insufficient for stock-identification analysis due to scale loss during trawl operations.

Samples of immature Chinook salmon collected in Districts 8 and 12 (Fig. 1) accounted for approximately 90% of all biostatistical and scale data. Nevertheless, when samples were stratified by district the number of scales was not sufficient to obtain statistically reliable results. Therefore, the mixture samples were pooled over all districts. Samples

from a total of 756 Chinook salmon were used for age composition estimates, and only 480 fish were used for stock composition estimates.

Baseline Samples

Baseline scale samples were collected by biologists from KamchatNIRO, Sevvostrybvod (North-East Fishery Protection Service), and the Alaska Department of Fish and Game from the “preferred” body area of adult Chinook salmon in rivers or terminal area fisheries in marine waters in 2004 and 2005. The five baselines used in our analysis included samples from the most abundant stocks of adult Chinook salmon in major watersheds of Kamchatka and western Alaska (Fig. 2). In Kamchatka, these watersheds included the Kamchatka River (eastern Kamchatka) and the Bolshaya River (western Kamchatka). Commercial catches in these two rivers accounted for up to 90% of the total catch of Chinook salmon in Asia, and Kamchatka River catches alone accounted for up to 80% of this total. North American baselines were composed of the three most abundant stocks of Chinook salmon in western Alaska (Yukon, Kuskokwim, and Nushagak rivers), which accounted for ~90% of the total catch of Chinook salmon in western Alaska in 2004–2006 (NOAA 2008). The Yukon River baseline is also representative of Chinook salmon of Canadian Yukon origin. The known geographical distribution of Chinook salmon in the Bering Sea also played an important role in the selection of North American baseline samples. Earlier stock identification research using tags, scale patterns, and parasites indicated that the Yukon, Kuskokwim, and Nushagak rivers are the major stocks of Chinook salmon distributed in the eastern and central Bering Sea (Major et al. 1978; Myers et al. 1987; Myers and Rogers

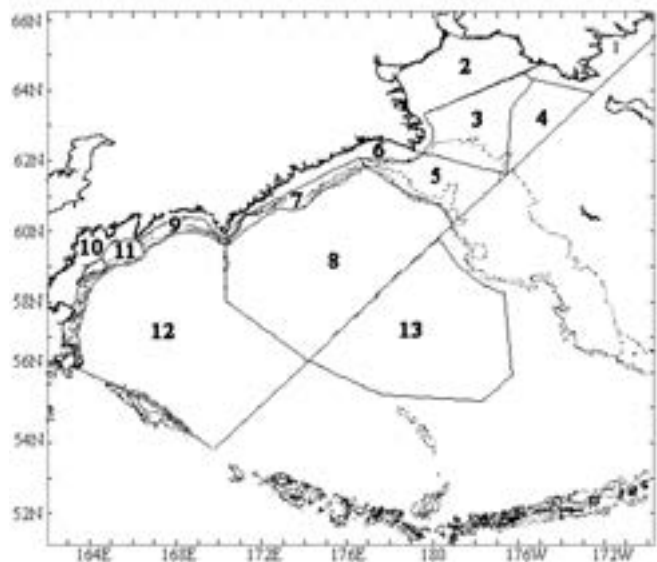


Fig. 1. TINRO-Center biostatistical districts in the western Bering Sea (Shuntov 1986; Volvenko 2003).

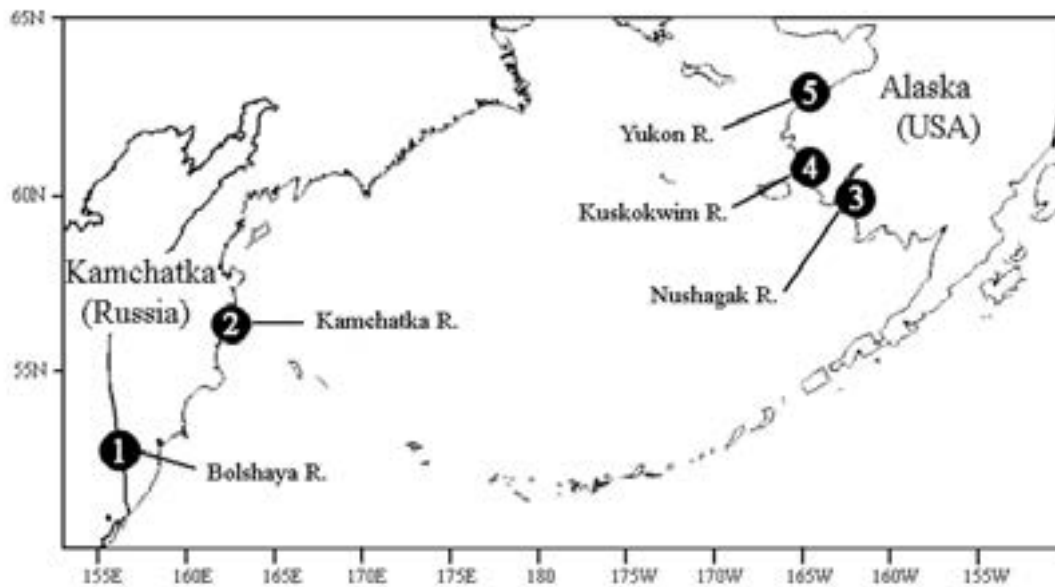


Fig. 2. Locations (numbers in black circles) of major Chinook salmon watersheds in Kamchatka and Alaska represented in the 2004–2005 scale pattern baselines. The Yukon River watershed includes the Canadian Yukon.

1988; Urawa et al. 1998; Klovatch et al. 2002; Myers et al. 2004).

In general the highest accuracies in scale-pattern models are obtained by using baseline samples composed of fish of the same freshwater age group and brood year as fish in the mixture samples (e.g., Myers et al. 1987). This approach minimizes the effects of year-to-year variation in scale growth patterns caused by environmental factors. Because the abundance of Asian Chinook salmon is very low, however, sufficient samples for baselines were obtained only by pooling samples over ocean age group. In the rivers of Kamchatka and western Alaska, the majority (> 90%) of adult Chinook salmon spent from 2–4 winters (ages 1.2, 1.3, and 1.4) in the ocean (Healey 1991). Scale data for these three dominant age groups were pooled into separate baselines for each major stock, which increased the variance of scale pattern variables.

For each baseline stock, we selected a stratified random sample of scales that accounted for spatial and temporal population structure (early-, mid-, and late-run timing). This method varied somewhat depending on available sample size. When sample size was small the entire sample was used in the analysis. In total, the scale baselines included samples from 1,598 fish.

The average age of fish in the baselines was approximately 1.3. Immature Chinook salmon in the mixed-stock samples were predominantly age 1.1 (up to 80%). Thus, a 2-year lag time was needed to minimize interannual variation between mixed-stock and baseline samples. The 2002 mixed-stock samples were analyzed with baselines samples from adult salmon returns in 2004, and the 2003 mixed-stock samples were analyzed with baselines from 2005 returns. Because baseline samples from 2006 adult salmon returns were

not available at the time of this study, the 2004 mixed-stock samples were analyzed with 2005 baseline samples. Differences between the age and brood year of Chinook salmon in the baselines and mixed-stock samples probably reduced the accuracy of the stock composition estimates. Previous studies, however, have indicated that scale patterns are relatively consistent for particular local stocks or complexes of stocks over long periods of time (e.g., Major et al. 1972).

Scale Measurement

Scales were measured using an optical digitizing system (Biosonics model OPR-513, OPRS, BioSonics Inc., Seattle, WA, USA (Davis et al. 1990)). Measurements were made in the freshwater and first annual ocean zone along an axis perpendicular to the boundary of the sculptured and unsculptured fields of the scale (Fig. 3). The structure of these two scale growth zones has been used for many years to differentiate local stocks of Pacific salmon in mixed-stock catches in the North Pacific Ocean (e.g., Davis et al. 1990). Scale pattern variables were calculated from inter-circulus measurement. Variables included the total radius of the freshwater zone (FW), total radius of the first ocean zone (O1), total number of circuli in the first ocean zone (C1), five triplets (TR) in the first ocean zone, and five reverse triplets (RTR) in the first ocean zone (Fig. 3).

Estimates of Stock Composition

Differences and similarities in the baseline stocks were evaluated using *t*-tests ($P < 0.05$), hierarchical cluster analysis of Euclidian distances between stock centroids, and canonical discriminant analysis (Bugaev 2007).

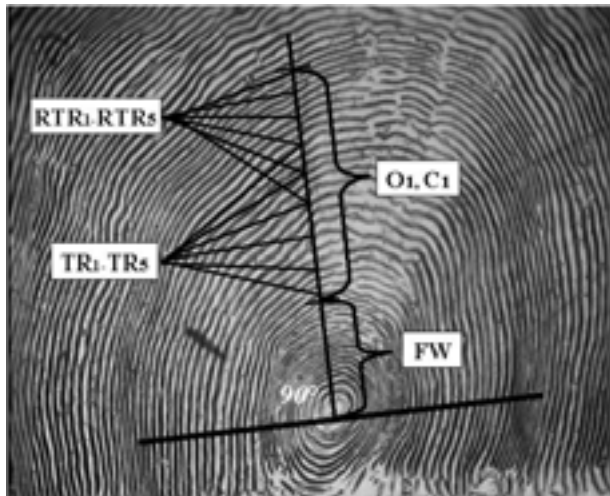


Fig. 3. Image of a Chinook salmon scale showing the scale pattern variables used for stock identification. FW = the total radius of the freshwater zone, O1 = total radius of the first annual ocean growth zone, C1 = number of circuli in the first annual ocean growth zone, TR1-TR5 = radii of groups of three circuli (triplets) in the first ocean zone (five triplets), RTR1-RTR5 = radii of groups of three circuli (reverse-triplets) in the first ocean zone (five reverse-triplets).

Computer simulations were used to evaluate the accuracy of the baseline stock groups using a maximum-likelihood estimation (MLE) procedure (Millar 1987, 1990; Patton et al. 1998). The estimation procedure included 500 iterations of randomly sampled scales in the model (with replacement) for 100% representation by one baseline in the simulated mixture.

The baseline data were used to calculate MLEs of stock composition of Chinook salmon in the mixture samples (Patton et al. 1998). Confidence intervals (95%) of the stock composition estimates were calculated from bootstrap resampling (500) of the baseline and mixture samples (Efron and Tibshirani 1986).

Estimates of Distribution and Abundance

We reviewed information on the distribution and abundance of immature Chinook salmon during BASIS research in the western Bering Sea in summer 2003 and fall 2002–2004 (Glebov 2007). Estimates of the abundance and biomass of Chinook salmon in the Bering Sea portion of the Russian Federation Exclusive Economic Zone (REEZ) were provided by the TINRO-Center. The TINRO-Center estimates were calculated from BASIS trawl catch data using an area-swept formula with a fishing efficiency coefficient of 0.3 for immature salmon (Temnykh et al. 2002). The TINRO-Center estimates were stratified by year, season, maturity group, and biostatistical district (Fig. 1). We apportioned the estimates for immature fish to stock (Asia and North America) using our estimates of stock composition weighted by age group. As a rough measure of the validity of these estimates, we compared them to published information on the abundance of adult Chinook salmon runs in Asia and North America.

RESULTS

Maturity and Age Composition in Mixture Samples

Size-weight characteristics and stage of gonad development indicated that most Chinook salmon in summer–fall BASIS catches in the western Bering Sea were either juvenile (x.0) or immature fish. Mature fish were not observed in the catches. Juvenile Chinook salmon were not included in the analysis because of scale loss during trawl fishing operations.

Age 1.1 fish dominated (75.5–87.9%) mixed-stock samples of immature Chinook salmon in BASIS trawl catches in the western Bering Sea in summer and fall 2002–2004 (Table 1). Percentages of age 1.2 fish were relatively low (8.6–18.8%), and those of other age groups were very low. Ages 1.1 and 1.2 fish accounted for more than 90% of the mixture samples of immature Chinook salmon stratified by year and season.

Table 1. The age composition (% of total sample size) of immature Chinook salmon in BASIS trawl catches by the R/V *TINRO* in the Western Bering Sea in 2002–2004. N = sample size, AAG = percentage of available age groups used for stock identification by scale pattern analysis (only ages 1.1 and 1.2 fish were analyzed). Locations of biostatistical districts are shown in Fig. 1. Juvenile (x.0 fish) Chinook salmon were not included in the analysis because of scale loss during trawl operations.

Year	Season	Biostat. districts	N	Age composition (%)									AAG (%)
				0.1	0.2	0.3	1.1	1.2	1.3	1.4	2.1	2.2	
2002	Autumn	1-12	133	-	0.8	-	76.0	18.8	3.0	-	1.5	-	94.8
2003	Summer	1-12	421	1.7	1.2	0.2	75.5	18.3	2.4	0.2	0.2	0.2	93.8
	Autumn	1-12	144	0.7	0.7	0.7	80.6	11.8	4.9	-	-	0.7	92.4
2004	Autumn	3-12	58	1.7	-	-	87.9	8.6	-	-	1.7	-	96.6

Evaluation of Scale Patterns and Accuracies of Models

Bugaev (2007) reported the detailed results of a statistical evaluation of the scale patterns of local stocks of adult Chinook salmon of Asian and North American origin that were used in the baseline models. In general, the results of cluster and canonical analyses demonstrated a relatively wide range in centroid means of the 2004 and 2005 baselines. Asian and North American stocks of Chinook salmon were clearly distinguishable in the 2004 baselines. In the 2005 baselines, however, the centroids of the Yukon and Kamchatka rivers were similar. In principle, this might result in underestimation or overestimation of the proportions of Chinook salmon of eastern Kamchatka or Alaska origin in

the 2003 mixed-stock samples. The results of *t*-tests indicated statistically significant differences ($P < 0.05$) in most pairwise comparisons of baselines. One notable exception was that the 2005 Bolshaya and Nushagak river baselines were not significantly different ($P = 0.36$). However, the most abundant Asian stock (Kamchatka R.) in the 2005 baseline was significantly different ($P < 0.05$) from all North American stocks.

Computer simulations of Chinook salmon baselines (pooled ages 1.2+1.3+1.4) indicated reasonably high mean accuracies (86% for the 2004 and 89% for the 2005 baselines; Tables 2, 3). The accuracy of the 2004 Kuskokwim R. baseline was particularly low (60%), however, errors in the estimates were largely apportioned to geographically adja-

Table 2. Evaluation of the accuracy of a 5-stock maximum likelihood estimate model for ages 1.2 + 1.3 + 1.4 Chinook salmon in 2004, as indicated by computer simulations of 100% representation by one stock group (indicated by grey shading). N = sample size.

Baseline stock	Maximum likelihood estimate/standard deviation					
	N	1	2	3	4	5
1. Bolshaya R.	111	<u>0.9881</u> 0.0216	<u>0.0787</u> 0.0560	<u>0.0003</u> 0.0019	<u>0.0044</u> 0.0080	<u>0.0013</u> 0.0056
2. Kamchatka R.	241	<u>0.0063</u> 0.0192	<u>0.8011</u> 0.0914	<u>0.0000</u> 0.0003	<u>0.0067</u> 0.0232	<u>0.0136</u> 0.0240
3. Nushagak R.	150	<u>0.0000</u> 0.0000	<u>0.0000</u> 0.0000	<u>0.9677</u> 0.0458	<u>0.0023</u> 0.0073	<u>0.1439</u> 0.0657
4. Yukon R.	186	<u>0.0048</u> 0.0107	<u>0.1190</u> 0.0727	<u>0.0003</u> 0.0025	<u>0.9477</u> 0.0509	<u>0.2382</u> 0.0967
5. Kuskokwim R.	239	<u>0.0008</u> 0.0038	<u>0.0012</u> 0.0057	<u>0.0317</u> 0.0459	<u>0.0389</u> 0.0439	<u>0.6030</u> 0.1125
Mean accuracy (%)						86.15

Table 3. Evaluation of the accuracy of a 5-stock maximum likelihood estimate model for ages 1.2 + 1.3 + 1.4 Chinook salmon in 2005, as indicated by computer simulations of 100% representation by one stock group (indicated by grey shading). N = sample size.

Baseline stock	Maximum likelihood estimate/standard deviation					
	N	1	2	3	4	5
1. Bolshaya R.	121	<u>0.9781</u> 0.0260	<u>0.0080</u> 0.0148	<u>0.0029</u> 0.0068	<u>0.0090</u> 0.0165	<u>0.0386</u> 0.0268
2. Kamchatka R.	150	<u>0.0074</u> 0.0196	<u>0.8462</u> 0.0951	<u>0.0026</u> 0.0105	<u>0.0571</u> 0.0768	<u>0.0069</u> 0.0178
3. Nushagak R.	150	<u>0.0009</u> 0.0039	<u>0.0012</u> 0.0074	<u>0.9244</u> 0.0737	<u>0.0305</u> 0.0315	<u>0.0606</u> 0.0735
4. Yukon R.	100	<u>0.0126</u> 0.0171	<u>0.1322</u> 0.0935	<u>0.0003</u> 0.0029	<u>0.8481</u> 0.1070	<u>0.0509</u> 0.0602
5. Kuskokwim R.	150	<u>0.0010</u> 0.0049	<u>0.0124</u> 0.0281	<u>0.0698</u> 0.0728	<u>0.0553</u> 0.0688	<u>0.8430</u> 0.0973
Mean accuracy (%)						88.80

Table 4. Maximum likelihood estimates (MLE) of stock composition of immature Chinook salmon in trawl catches of the R/V *TINRO* in the western Bering Sea in 2002–2004. N = sample size, SD = standard deviation, CI = confidence interval.

Year	Season	Biostat. dist.	Age	N	Stock/river	MLE	SD	CI (95%)
2002	Autumn	1-12	1.1 + 1.2	87	Bolshaya	-	-	-
					Kamchatka	0.4981	0.0853	0.2941-0.6489
					Nushagak	0.0320	0.0323	0.0000-0.1132
					Yukon	0.0004	0.0020	0.0000-0.2466
					Kuskokwim	0.4695	0.0916	0.2019-0.6266
2003	Summer	1-12	1.1 + 1.2	242	Bolshaya	0.0036	0.0124	0.0000-0.0390
					Kamchatka	0.4756	0.0496	0.3341-0.5980
					Nushagak	0.5208	0.0478	0.3947-0.6539
					Yukon	-	-	-
					Kuskokwim	-	-	-
	Autumn	1-12	1.1 + 1.2	103	Bolshaya	-	-	-
					Kamchatka	0.4148	0.0704	0.2272-0.5812
					Nushagak	0.5852	0.0704	0.4123-0.7507
					Yukon	-	-	-
					Kuskokwim	-	-	-
2004	Autumn	3-12	1.1 + 1.2	48	Bolshaya	-	-	-
					Kamchatka	0.2882	0.0919	0.0998-0.4640
					Nushagak	0.7105	0.0883	0.5077-0.8600
					Yukon	0.0013	0.0439	0.0000-0.1389
					Kuskokwim	-	-	-

cent stocks (Yukon and Kuskokwim rivers). While baseline-dependent simulations might overestimate the true accuracy of the models, we considered these accuracies adequate for identification of stocks at the regional level.

Stock Composition Estimates

Although mixture samples sizes were small, particularly in 2002 and 2004, Alaskan stocks dominated (50.2–71.2%) BASIS catches of immature Chinook salmon in the western Bering Sea in 2002–2004 (Table 4). There were no statistically significant estimates (either not detected or confidence intervals included 0.0) for Chinook salmon of western Kamchatka or Yukon River origin. Although confidence intervals were broad, the dominant stocks of Chinook salmon of western Alaska origin were Kuskokwim River in fall 2002 and Nushagak River in summer–fall 2003 and fall 2004.

Distribution and Assessment of Relative Abundance

Typically, Chinook salmon either did not occur in BASIS catches or were present in low abundance (1–50 fish/km²; Fig. 4). The highest catches of Chinook salmon occurred in the northern districts (1–8). The maximum abundance of Chinook salmon (average of 251–500 fish/km²) occurred in summer of 2003. This high level of abundance of Chinook salmon was comparable to that of more abundant salmon species, including sockeye salmon (*O. nerka*). In

general, however, Chinook salmon were sparsely distributed in the western Bering Sea, which greatly limited the number of samples available for stock identification research.

Estimates of Abundance and Biomass

The maximum estimated abundance/biomass of immature Chinook salmon during the entire study period was in District 8 (3.2–30.1 million fish/4.7–36.4 thousand tons) (Table 5). The estimated abundance/biomass of immature Chinook salmon was also relatively high in District 12 (1.5–2.6 million fish/3.4–4.5 thousand tons). In 2003, the estimated abundance of immature Chinook salmon was nearly three times higher in summer than in fall. In fall, estimated abundance of immature Chinook salmon was relatively high in both 2002 and 2003, and was much lower in 2004.

Estimated abundance and biomass of immature Chinook salmon of Asian origin ranged from 6–20 million fish and 10–25 thousand tons (Table 6). Estimated abundance and biomass of immature Chinook salmon of North American origin ranged from 4–21 million fish and 7–27 thousand tons.

DISCUSSION

Maturity, Age Composition, and Distribution

Glebov (2007) reviewed information on the maturity

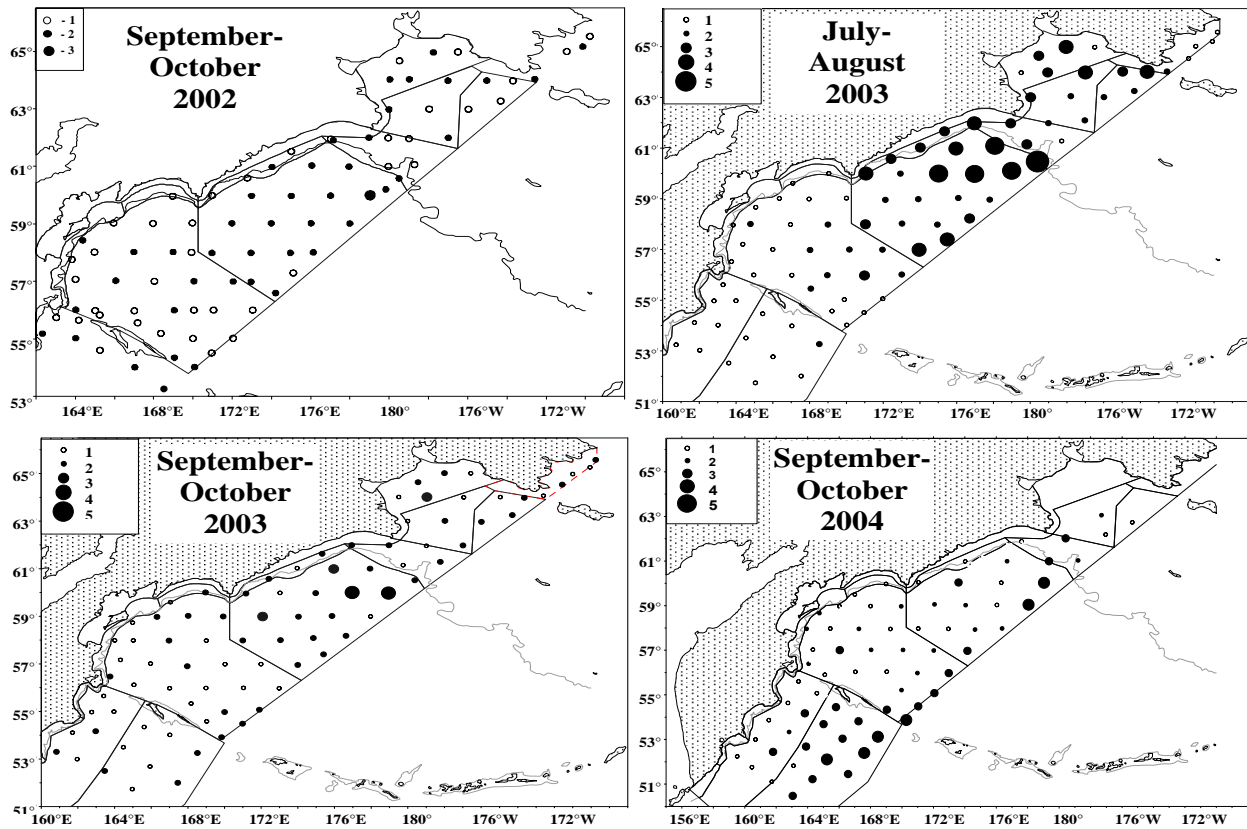


Fig. 4. The spatial distribution and relative abundance of Chinook salmon determined by BASIS research in the western Bering Sea, 2002–2004. Note that scales vary among years. The size of the circles indicates relative abundance (number of fish/km²). Upper left panel (2002): 1 = no catch, 2 = 1–10, 3 = 11–100. Upper right and lower left panels (2003): 1 = no catch, 2 = 1–50, 3 = 51–100, 4 = 101–250, 5 = 251–500. Lower right panel (2004): 1 = no catch; 2 = 1–10; 3 = 11–50; 4 = 51–100; 5 = > 100.

Table 5. The estimated abundance and the biomass of immature Chinook salmon in the epipelagic zone of the western Bering Sea in 2002–2004. Coefficient of trawl catch = 0.3. Data source: TINRO-Centre, Vladivostok. The locations of biostatistical districts are shown in Fig. 1.

Year	Season	Biostatistical districts												Total
		1	2	3	4	5	6	7	8	9	10	11	12	
Abundance (millions of fish)														
2002	Autumn	0.06	0.47	0.47	0.08	0.26	-	0.05	8.87	-	-	-	1.72	11.98
2003	Summer	0.02	1.63	2.08	1.43	2.18	-	1.20	30.11	-	-	-	2.36	41.01
	Autumn	0.07	0.53	0.23	0.50	0.49	-	0.10	10.83	0.07	-	-	1.54	14.36
2004	Autumn	-	-	0.08	-	0.48	-	-	3.22	-	-	-	2.58	6.36
Biomass (thousands of tons)														
2002	Autumn	0.38	2.39	0.81	0.05	1.08	-	0.11	9.87	-	-	-	4.54	19.23
2003	Summer	0.13	2.33	2.19	1.27	3.43	-	1.56	36.35	-	-	-	4.01	51.27
	Autumn	0.48	1.59	0.50	1.83	1.13	-	0.10	15.60	0.09	-	-	3.44	24.76
2004	Autumn	-	-	0.10	-	0.80	-	-	4.73	-	-	-	3.96	9.59

Table 6. Estimates of the abundance and biomass of immature Chinook salmon (1.1+1.2 fish) of Asian and North American origin in the western Bering Sea in 2002–2004. Dist. = biostatistical district (Fig. 1), no. = abundance in millions of fish, t = biomass in thousands of metric tons.

Year	Season	Dist.	Total		Asia			North America		
			no.	t	%	no.	t	%	no.	t
2002	Fall	1-12	11.98	16.46	49.8	5.97	8.20	50.2	6.01	8.26
2003	Summer	1-12	41.01	51.27	47.9	19.64	24.56	52.1	21.37	26.71
	Fall	1-12	14.36	24.76	41.5	5.96	10.28	58.5	8.40	14.48
2004	Fall	3-12	6.36	9.59	28.8	1.83	2.76	71.2	.53	6.83

and distribution of Chinook salmon during BASIS surveys in the western Bering Sea in summer and fall 2002–2006. Both juvenile (x.0) and immature Chinook salmon were caught during the surveys. The age structure of immature Chinook salmon in the western Bering Sea during the 2002–2004 BASIS surveys indicated the western Bering Sea is a particularly important rearing area for young (1.1) fish.

We could not use scale pattern analysis to estimate freshwater age composition or stock composition of juvenile salmon because of scale loss during BASIS trawl fishing operations. While it seems reasonable to assume that juvenile Chinook salmon in summer–fall BASIS catches in the western Bering Sea were of Asian origin, similarities in scale patterns of adult salmon of known origin indicated possible intermixing of Kamchatka and western Alaska stocks during their first ocean year. This issue will likely be resolved by future genetic (DNA) stock identification analyses of juvenile Chinook salmon collected in the northern Bering Sea and the Chukchi Sea in summer–fall.

The overall pattern of seasonal migration patterns of immature Chinook salmon in the Bering Sea is a northwestward movement in spring, followed by a southeastward movement in fall (Radchenko and Chigirinsky 1995). During BASIS surveys in summer 2003, immature Chinook salmon were most abundant along the northeastern boundary of the Aleutian Basin (Glebov 2007; Fig. 4). In fall 2002–2004, when immature Chinook salmon began to migrate out of the western Bering Sea, abundance was relatively low except near the eastern border of the REEZ.

Similar distribution patterns of immature Chinook salmon were observed in previous trawl surveys by TINRO-Center in this region (Radchenko and Chigirinsky 1995). These surveys showed that in summer, young (age 1.1) immature Chinook salmon were distributed primarily in the western Aleutian Basin and the shelf and continental slope of the Navarin region. Radchenko and Chigirinsky (1995) speculated that young immature Chinook salmon distributed in this region were of North American origin, as indicated by their small size compared to Kamchatka stocks. By late August and September, older age groups of immature Chinook salmon, likely a mix of Asian and North American stocks, were distributed primarily over the Shirshov Ridge and eastward

near the eastern border of the REEZ. In late fall (October–November) older (maturing) Chinook salmon moved into the western Bering Sea, as immature Chinook salmon left the region. Radchenko and Chigirinsky (1995) concluded that distribution of Chinook salmon corresponded well with the distribution of their primary prey, i.e., fish in shelf zones and gonatid squids in the basins.

Comparison of Stock Composition Estimates to Other Studies

Preliminary analyses by Bugaev (2004, 2005) demonstrated the predominance of immature Chinook salmon of eastern Kamchatka and western Alaska origin in BASIS catches in the western Bering Sea in 2002 and 2003. Our reanalysis of these data with brood-year-specific baselines, however, resulted in a substantial increase in estimated percentages of immature Chinook salmon of western Alaskan origin in fall 2002 (~30% increase) and fall 2003 (~20% increase). Preliminary and updated estimates for Chinook salmon of western Alaskan origin in summer 2003 were similar (~50% of total), which was surprising given the high estimated abundance of immature Chinook salmon in the western Bering Sea in summer 2003 (41 million fish; Table 5). Bugaev et al. (2004) estimated that 74% of ages 1.1 and 1.2 immature Chinook salmon in research driftnet catches in the western Bering Sea in July–August 2003 were of North American origin. In each case, the results were clearly influenced by errors in the MLE models, as well as variation in the quality of the scale samples. We suggest that our results should be interpreted as an approximate range of values based on the 95% confidence intervals of our point estimates, e.g., 40–65% of Chinook salmon in summer 2003 samples from the western Bering Sea were of North American origin.

Overall, the results of these scale pattern analyses provided the first quantitative estimates of the stock composition of immature Chinook salmon of Asian and North American origin in the western Bering Sea in summer and fall. While researchers had previously assumed that Chinook salmon of western Alaskan origin were the dominant regional stock in the western Bering Sea (e.g., Radchenko and Chigirinsky 1995), this was corroborated by our stock com-

position estimates (Table 4). The highest percentage of fish of Alaskan origin was in 2004, when there was a significant concentration of Chinook salmon at the eastern boundary of the REEZ. All Asian fish were of East Kamchatka (Kamchatka R.) origin.

Comparison of BASIS Abundance Estimates with Adult Run Sizes

Low catches of immature Chinook salmon during BASIS surveys in the western Bering Sea were expected, as Chinook salmon are the least abundant species of Pacific salmon in Asia and North America (Heard et al. 2007). The upper range of the BASIS estimates of abundance of immature Chinook salmon in the western Bering Sea in 2002–2004, however, was extraordinarily high (41 million fish in summer 2003; Table 5) compared to the production of Chinook salmon in Kamchatka and western Alaska (including the Canadian Yukon).

A conservative estimate of average annual runs (commercial, sport, and subsistence catches + escapement) of Chinook salmon returning to both Kamchatka and western Alaska in 2004–2006 is approximately 1 million fish (TINRO-Center 2005, 2006; Anonymous 2007; NOAA 2008; Jones et al. 2009; D. Molyneaux, Alaska Department of Fish and Game, pers. comm.). Thus, estimates of the abundance of immature Chinook salmon from R/V *TINRO* trawl surveys greatly exceeded (6–40 times) the estimated abundance of annual returns of adult Chinook salmon to rivers in Kamchatka and western Alaska. The estimate of the magnitude of annual adult runs in Kamchatka and western Alaska is conservative because it includes estimates of total runs for only the five major “index” stocks used in our scale pattern analysis.

Trends in the annual abundance of adult returns of Chinook salmon to Kamchatka and western Alaska in the early 2000s varied between regions (Heard et al. 2007). In 2004–2006, estimated average annual returns to western Kamchatka (Bolshaya River) were low and relatively stable (~75,000 fish), while estimated returns to eastern Kamchatka (Kamchatka River) increased substantially after 2003 (~190,000 fish) (TINRO-Center 2005, 2006; Anonymous 2007). In addition, there were exceptionally high annual average runs in the Kuskokwim (~360,000 fish) and Nushagak (~230,000 fish) after 2003, while runs in the Yukon River decreased to a relatively low and stable level (~220,000 fish) in 2004–2006 (NOAA 2008; Jones et al. 2009; D. Molyneaux, Alaska Department of Fish and Game, pers. comm.). These stock-specific trends in abundance are reflected to some degree in our regional stock composition and abundance estimates for immature Chinook salmon in 2002–2004.

Run size estimates for Kamchatka and western Alaska Chinook salmon would be higher than 1 million fish if interceptions by ocean salmon fisheries, bycatch by commercial groundfish fisheries, and removal by poaching (particularly

in Kamchatka) were taken into account. In addition, there are numerous small runs of Chinook salmon in Kamchatka and western Alaska for which run size estimates are unavailable. BASIS samples of immature Chinook salmon included fish that would have returned primarily over a period of two to four years. Natural and fishing mortality rates of immature Chinook salmon at sea are not well known, but could be substantial. However, none of these factors alone or in combination are sufficient to explain the high estimated abundance and biomass of Chinook salmon in summer 2003 BASIS catches. In addition, the western Bering Sea includes only a portion of the total area of known ocean distribution of Chinook salmon of Kamchatka and western Alaska origin. There is no evidence that Chinook salmon returning to other regions of Asia or North America are distributed in the western Bering Sea.

We speculate that BASIS stock assessment methods, e.g., the use of a fishing-efficiency coefficient of 0.3, may have resulted in overestimation of the abundance of Chinook salmon. Errors in trawl assessment methods may be exceptionally high for species in low abundance, e.g., only 119 Chinook salmon were caught during the 2002 BASIS trawl fishing operations (Temnykh et al. 2003). Volvenko (2000) discussed other problems with estimation of salmon abundance by trawl sampling. Murphy et al. (2003) compared research trawls and fishing power of vessels used for BASIS research in 2002.

CONCLUSIONS

Our results corroborated previous studies indicating that western Alaska is the dominant regional stock of Chinook salmon in the Bering Sea (e.g., Major et al. 1978; Myers et al. 1987; Myers and Rogers 1988; Healey 1991; Myers et al. 2004). Future genetic studies are needed to validate and refine our estimates. The seasonal stock-specific distribution patterns of Chinook salmon observed in 2002–2004 might have resulted from recent changes in ecosystem conditions in the western Bering Sea that occurred at end of the 20th century and the beginning of the 21st century (Shuntov and Sviridov 2005). On the other hand, the 2002–2004 distributions might represent a long-term, stable balance between abundant stocks of North American origin and scarce stocks of Asian origin. The BASIS estimates of abundance of salmon in western Bering Sea in the early 2000s were extraordinarily high compared to production of Chinook salmon in Kamchatka and western Alaska, including the Canadian Yukon. We concluded that BASIS stock assessment methods for Chinook salmon need to be reevaluated. Nevertheless, our results provided new quantitative evidence of the important role of the western Bering Sea ecosystem as a summer–fall foraging area for immature Chinook salmon of both Asian and North American origin.

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Preliminary Records of Otolith-Marked Chum Salmon found in the Bering Sea and North Pacific Ocean in 2006 and 2007

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Abstract: We examined otolith marks on chum salmon caught in the North Pacific Ocean and Bering Sea during the spring and summer of 2006 and 2007. Otolith marks were detected in 190 of 8,295 immature and maturing fish. Of these marked salmon, 13 fish were found in the North Pacific Ocean and 177 fish were found in the Bering Sea. Approximately 90% of the marked salmon were released from Japanese hatcheries. Other marked fish originated from hatcheries in Alaska, Russia, and the Republic of Korea. Our results suggest that otolith-marked chum salmon released from NPAFC countries are detectable in the Bering Sea and North Pacific Ocean. Our study demonstrated that otolith marking is a useful tool for identifying hatchery of origin of individual chum salmon in the ocean. We believe this technique will be useful for the international management of anadromous salmon stocks.

Keywords: chum salmon, otolith mark, distribution, Bering Sea, North Pacific Ocean

INTRODUCTION

Chum salmon (*Oncorhynchus keta*) are the most widely distributed salmon species in the Pacific Rim (Salo 1991). Chum salmon are also an important commercial fisheries resource in North Pacific countries. Determining the ocean distribution and origins of chum salmon will provide valuable information to help clarify stock-specific patterns of ocean migration for stock assessment.

Stock identification of chum salmon in the offshore waters of the Bering Sea and North Pacific Ocean has been attempted using a wide variety of techniques including tagging, identification of scale characteristics, otolith thermal marking, and/or genetic characters (e.g. Ishida et al. 1989; Ogura and Ito 1994; Wilmot et al. 1998; Seeb and Crane 1999; Urawa et al. 2000). Otolith thermal marking uses short-term temperature fluctuations to induce distinctive structural marks on the otoliths of incubating fish, and is a

widely-used technique for identifying origins of hatchery-produced salmonids (Volk et al. 1999). Otolith mark/recovery experiments have provided significant new stock-specific information on the offshore ocean distribution and migration patterns of Pacific salmon (Farley and Munk 1997; Kawana et al. 1999; Carlson et al. 2000; Urawa et al. 2000; Myers et al. 2004). These recovery experiments have mainly focused on chum and pink salmon in the Gulf of Alaska. Urawa et al. (2009) indicated stock-specific chum salmon distribution in the Bering Sea and the adjacent North Pacific Ocean by combining genetic and otolith marking information.

In the spring and summer of 2006 and 2007, scientists from Japanese institutes surveyed salmon stocks in the Bering Sea and North Pacific Ocean (Fukuwaka et al. 2006, 2007; Morita et al. 2006, 2007). Approximately 8,000 chum salmon otolith samples were collected during these surveys. In this paper, we present the results from those surveys.

MATERIALS AND METHODS

Fish Samples

Chum salmon were collected from the Bering Sea and North Pacific Ocean during research cruises of the R/V *Kaiyo maru* between April 24 and June 17, 2006 (41°01'N–55°29'N, 154°47'E–159°47'W; Fig. 1A), the R/V *Wakatake maru* between June 15 and July 14, 2006 (41°00'N–58°30'N, 179°00'E–180°; Fig. 1B) and between June 14 and July 12, 2007 (41°00'N–58°30'N, 176°00'E–178°00'W; Fig. 1C)

(Fukuwaka et al. 2006, 2007; Morita et al. 2006). Cruises were also conducted by the R/V *Hokko maru* between June 30 and July 15, 2007 (Fig. 1D) and between July 22 and August 3, 2007 (52°38'N–59°23'N, 174°55'E–170°11'E; Fig. 1E) (Morita et al. 2007). Sagittal otoliths from 8,295 of 11,943 fish caught in the North Pacific Ocean and Bering Sea in 2006 and 2007 were collected onboard ship (Table 1). Otoliths were examined for the presence of an otolith mark at the laboratory of National Salmon Resources Center, Fisheries Research Agency, Japan. We also collected a scale from each sampled fish, and gonad weight was measured to

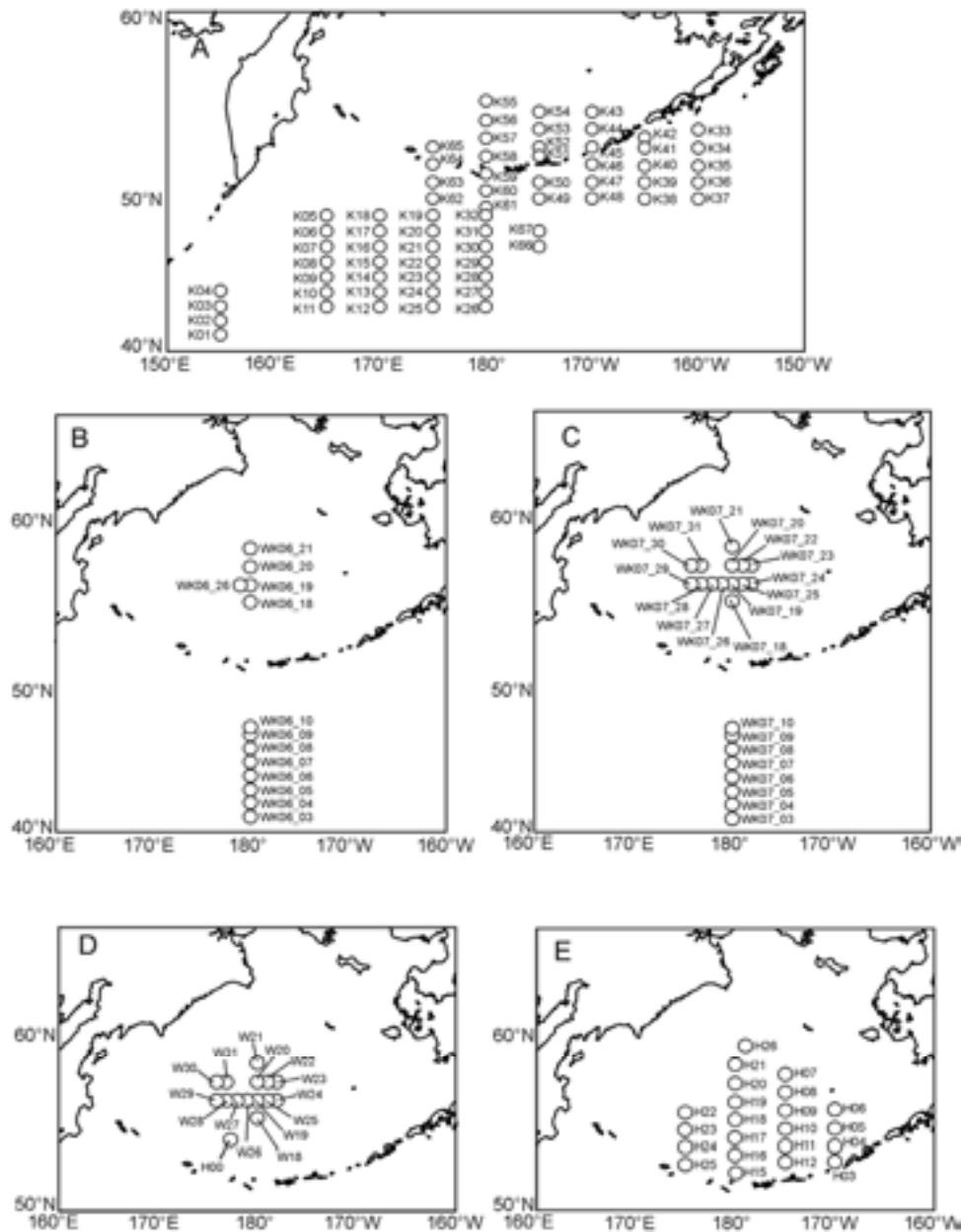


Fig. 1. Sampling locations of chum salmon in the North Pacific Ocean and Bering Sea during Japanese research cruises of R/V *Kaiyo maru* between April 24 and June 17, 2006 (A), R/V *Wakatake maru* between June 15 and July 14, 2006 (B), and between June 14 and July 12, 2007 (C), R/V *Hokko maru* between June 30 and July 15 (D), and between July 22 and August 3, 2007 (E).

the nearest gram. Fish age was determined by counting scale annuli, and maturity was determined from gonad weights (Takagi 1961). The criteria used to categorize maturity by gonad weight are shown in Table 2.

Detection of Otolith Thermal Marks

One otolith from each pair was mounted on a glass slide using Thermoplastic Cement (Buehler Ltd., Lake Bluff, IL) and then ground to expose the primordia using Doctor-Lap (MARUTO Instrument Co. Ltd., Tokyo, Japan) and Fibermet Discs (0.3, 1, 3, 9, and 12 μ, Buehler Ltd.). If a sample was overground, the other sagittal otolith was used. Otolith microstructure was examined under a compound microscope and compared to the mark patterns of voucher specimens archived on the NPAFC website (<http://npafc.taglab.org>). All otoliths were read independently by two readers (a beginner and an experienced reader). When disagreements between otolith readers occurred, they accessed the NPAFC database and re-checked the details of the mark pattern. After discussion, the experienced reader made the final decision.

RESULTS

Otolith marks were detected in 190 of 8,295 chum salmon (2.29%) caught in the Bering Sea and North Pacific Ocean in 2006 and 2007 (Table 1). Of the marked salmon, 13 of 1,885 fish (0.69%) were found in the North Pacific Ocean during the spring of 2006 and five of 335 fish (1.49%) were recovered in the early summer of 2006. Twelve of 847 fish (1.41%) were found in the Bering Sea during the summer of 2006. In the summer of 2007, 160 of 4,899 fish (3.3%) were recovered in the Bering Sea. These latter samples included two alizarin complexone (ALC) marked fish. Most of the marked chum salmon that we recovered were from Japanese hatcheries (Table 1).

Bering Sea Recovery

During early summer of 2006, five Japanese maturing chum salmon originally from the Chitose, Shari, Ichani, and Shizunai hatcheries in Hokkaido were caught in the central and eastern waters of the Bering Sea. In the summer of 2006 and 2007, 28 marked maturing fish were also recovered in the Bering Sea basin (Table 1). Those marked fish were released from eight Japanese hatcheries (Ichani, Shari, Nijibetsu, Shizunai, Tokushibetsu, Tsurui, Tonbetsu, and an unspecified hatchery in Hokkaido), the Paratimsky Hatchery in Kamchatka and an unidentified hatchery in either Russia or Alaska (Table 1).

We found a total of 144 immature otolith-marked chum salmon in the Bering Sea (Table 1). Of these marked fish, the origins of 137 fish were identified as follows: 130 from 13 Japanese hatcheries (Tokushibetsu, Shari, Nijibetsu,

Table 1. Number of chum salmon caught (Catch), sampled (OT), and number of otolith-marked chum salmon detected in the Bering Sea (BS) and North Pacific Ocean (NP) on the Japanese research vessels *Kaiyo maru*, *Wakatake maru*, and *Hokko maru* in 2006 and 2007. M, maturing fish; I, immature fish; T, surface/midwater trawl; H, hook-and-line; G, gillnet; U, unidentified origin.

Year/season	Sampling date	Research vessel	Survey area (stations)	Gear	Catch	OT	Number of otolith-marked fish by country of origin												
							Japan		Korea		Russia		Alaska		U.I.		Total		
							M	I	M	I	M	I	M	I	M	I	M	I	
2006 spring	April 24 - May 15	<i>Kaiyo maru</i>	NP (K01-32, 66-67)	T, H	1,294	1,022	4	3	0	0	0	0	0	0	0	0	3	4	6
2006 early summer	May 26 - June 17	<i>Kaiyo maru</i>	NP (K33-42, 46-50, 59-64)	T	978	863	1	0	0	0	1	0	1	0	0	0	0	3	0
	May 26 - June 17	<i>Kaiyo maru</i>	BS (K43-45, 51-58, 65)	T	360	335	5	0	0	0	0	0	0	0	0	0	0	5	0
2006 summer	June 15 - 22	<i>Wakatake maru</i>	NP (WK06_03-10)	G	123	102	0	0	0	0	0	0	0	0	0	0	0	0	0
	July 10 - 14	<i>Wakatake maru</i>	BS (WK06_18-21, 26)	G	1,173	847	1	7	0	0	0	0	0	0	1	3	2	10	0
	June 14 - 21	<i>Wakatake maru</i>	NP (WK07_03-10)	G	250	227	0	0	0	0	0	0	0	0	0	0	0	0	0
2007 summer	June 29 - July 12	<i>Wakatake maru</i>	BS (WK07_18-31)	G	1,175	1,079	8	27	0	1	1	0	0	1	0	0	9	29	0
	June 30 - July 15	<i>Hokko maru</i>	BS (H00, W18-31)	T	2,740	1,802	16	59	0	0	0	0	0	0	0	2	16	62	0
	July 22 - August 3	<i>Hokko maru</i>	BS (H03-26)	T	3,850	2,018	1	37	0	0	0	0	0	0	0	2	1	43	0
Total					11,943	8,295	36	133	0	1	2	0	1	6	1	10	40	150	0

Table 2. Criteria used to categorize maturity by gonad weight of chum salmon (modified from Takagi (1961)).

Sex	April - late May	June			July		
		Early	Mid	Late	Early	Mid	Late
Female	≤ 10 g	< 15 g	< 15 g	≤ 20 g	< 25 g	< 25 g	< 25 g
Male	≤ 1 g	≤ 2 g	≤ 3 g	≤ 3 g	≤ 3 g	≤ 5 g	≤ 5 g

Tokachi, Yakumo, Tonbetsu, Ichani, Shizunai, Chitose, Teshio, Tsurui, and unspecified hatcheries in Hokkaido and Katagishi Hatchery on the Pacific coast of Honshu); one from the Yang-Yang Hatchery in the Republic of Korea; six from four Alaskan hatcheries (Macaulay, Wally Noerenberg, Port Armstrong, and Haines). One otolith-marked fish (age 0.1, male, 334 mm in fork length) was caught at station WK07-31 (56°30'N, 176°00'E; Fig. 1C) on July 12, 2007 and is the first record of a Korean chum salmon found on the high-seas.

North Pacific Ocean Recovery

In the North Pacific Ocean during the spring of 2006, seven maturing otolith-marked chum salmon were collected: five Japanese fish were caught in the central and eastern North Pacific Ocean (175°E, 180°, and 165°W) and one Russian and one Alaskan fish were both caught at station K46 (52°08'N, 170°04'W) in the eastern North Pacific Ocean. Those fish originated from four Japanese hatcheries (Chitose, Nijibetsu, Tsurui, and Shizunai in Hokkaido), the Ozerkovsky Hatchery in western Kamchatka, and the Macaulay Hatchery in southeast Alaska. No maturing fish were recovered in the central North Pacific Ocean during the summers of 2006 and 2007.

Six immature otolith-marked chum salmon were found in the North Pacific Ocean in the spring of 2006. Three of those fish were released from two Japanese hatcheries (Nijibetsu and Ichani in Hokkaido), but the hatchery origins of the other three marked fish could not be identified. These samples were collected from the central North Pacific Ocean (43°00'N–45°06'N, 174°50'E–179°48'W). In the summer of 2006 and 2007, no otolith-marked immature fish were detected in the central North Pacific Ocean.

DISCUSSION

This study demonstrated that otolith marks were detected in 190 of 8,295 immature and maturing fish in the survey areas of North Pacific Ocean and Bering Sea during 2006 and 2007. Of these marked salmon, 13 fish were found in the North Pacific Ocean and 177 fish were found in the Bering Sea. Approximately 70–90% of the otolith-marked immature chum salmon originated from Japanese hatcheries, and they were mainly found in the central Bering Sea.

Our study indicated that the recovery number and percentage of otolith-marked samples were very low (0.69–3.3%). The number and percentages of otolith-marked fish

released were approximately 19–146 million (1.0–7.9%) from Japan, 7–49 million (2.5–13.7%) from Russia, 267–477 million (58.9–96.4%) from Alaska, and 0.6–1.4 million (11.5–23.8%) from Washington, Oregon, California, and Idaho, between 2001 and 2006 (data from NPAFC website: www.npafc.org). However, about 89% of the recovered otolith-marked chum salmon were released from Japanese hatcheries.

The survey areas in our study were limited. Particularly, in the summer of 2006 and 2007, otolith samples were collected from limited areas of the central North Pacific Ocean and central (high-seas) Bering Sea. Previous tagging and genetic studies indicated that Asian (Japanese and Russian) stocks were widely distributed in the Bering Sea and North Pacific Ocean (Sato et al. 2009; Urawa et al. 2009). It may be that the limited survey design influenced the number and percentages of otolith-marked chum salmon recovered.

Why did Japanese otolith-marked fish dominate the recovery from the survey areas of the central Bering Sea? Almost all Japanese stocks migrate into the central Bering Sea during the summer (Urawa et al. 2009). United States stocks from central Alaska, southeast Alaska, Washington, and Oregon were mainly distributed in the Gulf of Alaska and central North Pacific Ocean, while the Russian stocks are mainly distributed in the western Bering Sea and north-west Pacific Ocean (Myers et al. 1996). Further, most of the otolith-marked fish originating in United States and Russia are released from Prince William Sound and southeast Alaskan hatcheries and Sakhalin Island hatcheries, respectively (NPAFC website: www.npafc.org). Therefore, it seems logical that we did not recover any otolith-marked fish released from United States or Russian hatcheries.

Our present study indicates that 10 maturing Japanese chum salmon were collected from the survey areas of the North Pacific Ocean (175°E, 180°, and 165°W) and southern Bering Sea in the spring and early summer, and 26 maturing fish originating in Japan were caught in the survey areas of the central Bering Sea during summer. On the other hand, 130 immature fish originating from Japanese hatcheries were caught in the survey areas of the Bering Sea during summer. Urawa et al. (2009) estimated that maturing Japanese chum salmon in Gulf of Alaska migrate into the Bering Sea during June, followed by young chum salmon from the western North Pacific Ocean and by immature Japanese fish from the Gulf of Alaska. Maturing chum salmon migrate out of the Bering Sea by August, while immature fish remain there to feed (Urawa et al. 2009). Our results reflect the migration patterns of maturing and immature Japanese chum salmon.

Hatcheries in southeast Alaska and Prince William Sound annually released approximately 270–460 million otolith-marked chum salmon from 2001 to 2006; the Japanese released 19–146 million otolith-marked fish from 2001 to 2006 (NPAFC website: www.npafc.org). Neave et al. (1976) estimated that immature chum salmon of North American stocks migrate to the north and west in the Gulf of Alaska during spring and early summer, and that they remain in the Gulf of Alaska (primarily south of 50°N and east of 155°W) during the late summer and winter. A previous tagging study also indicated that immature chum salmon released from Prince William Sound and southeast Alaskan hatcheries were distributed in the Gulf of Alaska and central North Pacific Ocean and adjacent Bering Sea waters during summer (Myers et al. 1996). Previous genetic and otolith mark analyses suggested that Prince William Sound and southeast Alaska immature chum salmon are distributed in the northern Gulf of Alaska and southern Bering Sea during summer (Urawa et al. 2009). Our otolith mark recoveries suggest that the Prince William Sound and southeast Alaska fish are mainly distributed in the Gulf of Alaska and central North Pacific Ocean, and that some of these fish may extend into the survey areas in the central Bering Sea.

Russian hatcheries released approximately 306–387 million chum salmon from 2001 to 2006. Of these, approximately 7.9–49 million fish (2.5–13.7%) were otolith-marked. Previous genetic stock identification studies estimated that Japanese and Russian stocks were dominant in the Bering Sea basin during summer and fall, and that their abundances were almost equivalent (Sato et al. 2009; Urawa et al. 2009). However, in our study the number of otolith-marked fish of Russian origin was much lower than those of Japanese origin. In Russia, wild populations are the basis of most of the salmon harvest (Zaporozhets and Zaporozhets 2004). A previous study of wild and hatchery fish production and recruitment in the Tym River, one of the largest rivers on Sakhalin Island, indicated that returning numbers of wild chum salmon were five times greater than those of hatchery origin during 1960–1998 (Kovtun 2000). The low recovery of Russian otolith-marked fish in the high-seas ocean samples suggests that Russian chum salmon stocks include a considerable number of wild fish.

An otolith-marked fish released from the Yang-Yang Hatchery in the Republic of Korea was collected in the central Bering Sea during the summer of 2007. This was the first record of recovery of a Korean otolith-marked salmon on the high seas. This finding suggests that Korean chum salmon may migrate to the Bering Sea during the summer as do other Asian stocks.

In conclusion, we have demonstrated that otolith-marked chum salmon released from the NPAFC countries were widely distributed in the Bering Sea and North Pacific Ocean. Otolith marking is a useful tool for identifying the hatchery of origin of individual chum salmon in the ocean. We believe this technique will be useful for the international

management of anadromous salmon stocks in the North Pacific Ocean.

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Stock-Specific Distribution and Abundance of Immature Chum Salmon in the Western Bering Sea in Summer and Fall 2002–2003

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Abstract: Seasonal stock-specific distribution and abundance of immature chum salmon (*Oncorhynchus keta*) in the western Bering Sea in summer 2003 and fall 2002–2003 were determined using scale pattern analysis. Results indicated that immature chum salmon were predominantly of Asian (Russian and Japanese) origin. There was considerable spatial and temporal variation in estimated proportions of regional stocks of chum salmon. Russian stocks dominated catches in the southwestern Bering Sea. Japanese and North American stocks were most abundant in the northwestern Bering Sea. Despite low estimated percentages of North American (western Alaska) chum salmon (average $\leq 10\%$), estimated total abundance of immature chum salmon in the western Bering Sea was very high in the early 2000s. Thus, we concluded that the western Bering Sea ecosystem is an important summer-fall foraging area for immature chum salmon of both Asian and North American origin.

Keywords: abundance, age, biomass, chum salmon, distribution, immature, scale pattern analysis, stock identification, western Bering Sea

INTRODUCTION

The Bering-Aleutian Salmon International Survey (BASIS) was initiated in 2002 to detect and monitor changes in climate-ocean and ecosystem states and Pacific salmon (*Oncorhynchus* spp.) in the Bering Sea (NPAFC 2001). In addition to ichthyological, hydrobiological, and hydrological research, a major focus of BASIS was to estimate seasonal stock-specific distribution and abundance of salmon in the Bering Sea. A number of recent publications have reported the results of stock identification of chum salmon (*O. keta*) in BASIS research vessel catches. Allozyme- and DNA-based genetic characteristics were used to identify chum salmon in BASIS samples collected in the central Bering Sea and adjacent North Pacific waters in summer–fall 2002–2004 (Sato et al. 2004, 2009; Urawa et al. 2004, 2005, 2009; Moriya

et al. 2007, 2009). Bugaev et al. (2006) used scale pattern analysis in a preliminary assessment of the distribution of regional stocks of chum salmon in the western Bering Sea, inside the Russian Federation Exclusive Economic Zone (REEZ), in fall 2002 and summer–fall 2003. Collectively, the results of genetic and scale pattern stock-identification studies indicated that the majority of chum salmon in the central and western Bering Sea were of Asian (Russian and Japanese) origin. In this paper, we briefly review information from BASIS surveys in the REEZ on the distribution, abundance, and biological characteristics of chum salmon in the western Bering Sea, and update and extend earlier stock identification results reported by Bugaev et al. (2006). Our primary objectives were to estimate the proportions and potential abundance of regional stocks of chum salmon in the western Bering Sea in fall 2002 and summer–fall 2003.

MATERIALS AND METHODS

Analysis of scale patterns has been used since the 1950s to estimate the regional stock composition of salmon caught in mixed-stock fisheries on the high seas. Major et al. (1972) outlined the basic principles and procedures of scale pattern analysis. Our methods were similar to those described by Bugaev et al. (2006). Briefly, we used scale pattern analysis of representative (baseline) samples of Asian and North American chum salmon to estimate the proportions of these stock groups in BASIS (mixture) samples and their potential abundance in the western Bering Sea.

Mixture Samples

Mixture samples of chum salmon and associated biological and catch data were collected by the staff of the TINRO-Center from BASIS trawl catches of the RV *TINRO* in the western Bering Sea (REEZ) in summer (July–August) 2003 and fall (September–October) 2002–2003 (NPAFC 2003, 2004). A standard midwater rope trawl (PT/TM 80/396 m) was used to survey the upper epipelagic layer (~upper 40 m).

Shipboard sampling of chum salmon included determination of maturity and collection of a scale sample from each fish. Maturity was determined by visual evaluation of the stage of gonad maturation (Pravdin 1966). All fish at stages II and II–III were considered immature (e.g., Mosher 1972; Bugaev 1995; Ito and Ishida 1998). The body area of scale collection was recorded using a classification scheme developed by TINRO-Center (Fig. 1). Collection of preferred scales (Clutter and Whitesel 1956; Knudsen 1985; Davis et al. 1990) was not always possible, as salmon caught in trawls frequently lose many scales. Preferred scales were collected from body areas A or B, but if these scales were missing scales were collected from areas C and D. Both preferred and

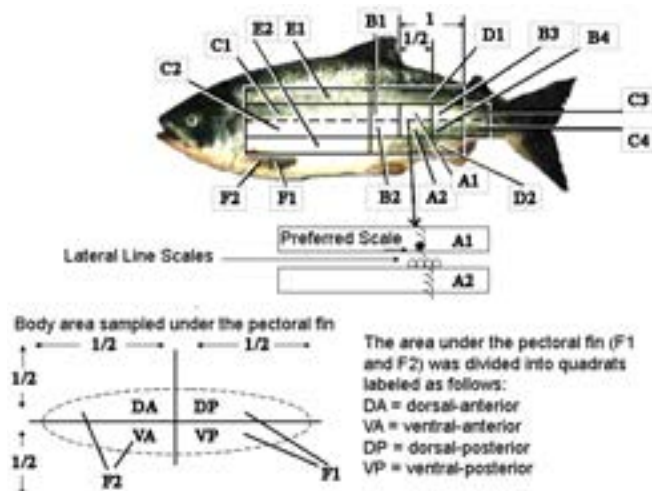


Fig. 1. Classification scheme for coding the body area of scale collection used by TINRO-Center during BASIS trawl surveys.

non-preferred scales were used to estimate age composition. Only preferred scales were used to estimate stock composition, because different rates of scale growth on different parts of the fish’s body can influence the results of scale pattern analysis. In all cases, the quality of scales was evaluated visually before inclusion in our analyses.

Ages of immature chum salmon in the mixture samples were determined in the laboratory by counting the number of freshwater and marine annuli on scales, which is the standard method accepted for Pacific salmon (e.g., Ito and Ishida 1998). Age was designated by the European method, whereby the number of freshwater annuli (always zero for chum salmon) and number of ocean annuli are separated by a dot (Koo 1962). For example, an age 0.1 chum salmon has one ocean annulus on its scale and is in its second summer–fall in the ocean. Although juvenile chum salmon (0.0 fish) were present in BASIS trawl catches, samples were insufficient for stock-identification analysis due to scale loss during trawl operations.

Samples of immature chum salmon collected in Districts 8 and 12 (Fig. 2) accounted for approximately 90% of all biostatistical and scale data. Therefore, we pooled samples from individual districts into two geographic regions – a “northern” region that included samples from Districts 1–8 and a “southern” region that included samples from Districts 9–12. The total mixed-stock sample from all districts (4,837 fish) was used for age composition estimates, and a subset of preferred scales from this sample (3,877 fish) was used to estimate stock composition.

Baseline Samples

Baseline scale samples were collected by regional fish-

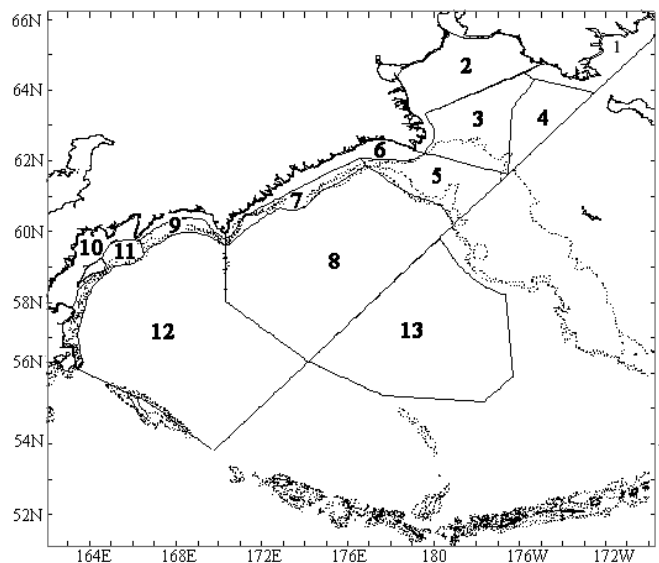


Fig. 2. TINRO-Center biostatistical districts in the western Bering Sea (Shuntov 1986; Volvenko 2003).

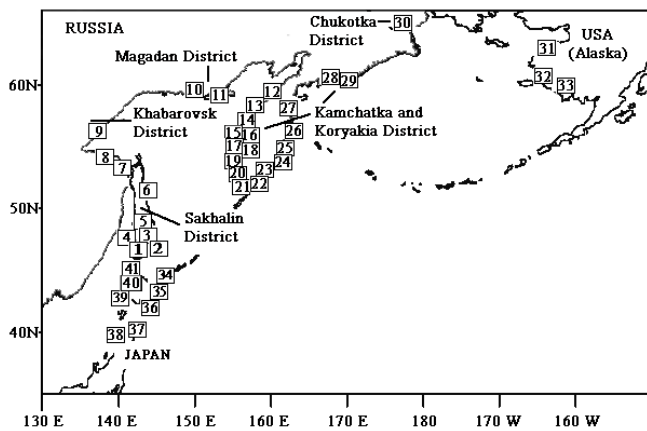


Fig. 3. Locations (indicated by numbers) of 41 chum salmon stocks represented in the 2003 scale pattern baselines. Russia, Sakhalin District: (1) Taranai R., (2) Mordvinov Bay, (3) Belaya R., (4) Kalininka R., (5) Naiba R., (6) Tym' R.; Khabarovsk District: (7) Amur R., (8) Aldoma R., (9) Uda R.; Magadan District: (10) Taiu R., (11) Yama R.; Kamchatka and Koryakia District: (12) Palana R., (13) Icha R., (14) Krutogorova R., (15) Vorovskaya R., (16) Kol' R., (17) Pymta R., (18) Kikhchik R., (19) Utka R., (20) Bolshaya R., (21) Opala R., (22) Zhirovaya R., (23) Avacha R., (24) Nalycheva R., (25) Zhupanova R., (26) Kamchatka R., (27) Khailulya R., (28) Impuka R., (29) Apuka R.; Chukotka District: (30) Anadyr' R.; USA (western Alaska): (31) Yukon R., (32) Kuskokwim R., (33) Nushagak R. (Bristol Bay); Japan (Hokkaido and Honshu): (34) Nishibetsu R., (35) Abashiri R., (36) Tokachi R., (37) Tsugaruishi R., (38) Gakko R., (39) Urappu R., (40) Tokushibetsu R., (41) Ishikari R. Scales were collected by personnel from KamchatNIRO, SakhNIRO, MagadanNIRO, TINRO-Center KhBr, ChukotNIRO, Sevvostryvod, Alaska Department of Fish and Game (Anchorage, Alaska), and the National Salmon Resources Center (Sapporo, Japan).

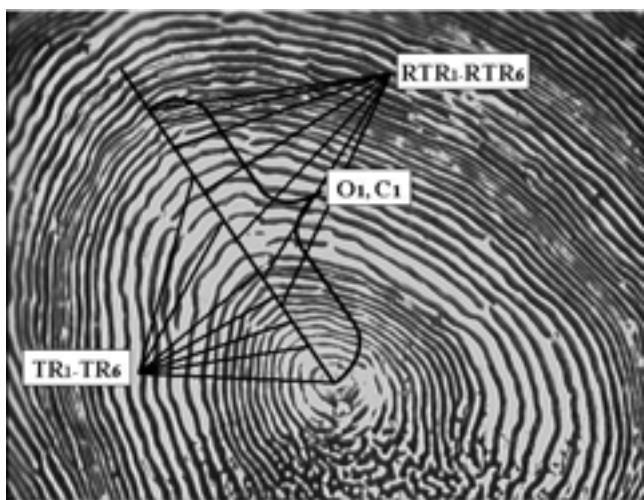


Fig. 4. Image of a chum salmon scale showing the scale pattern variables used for stock identification. O1 = total radius of the first annual ocean growth zone, C1 = number of circuli in the first annual ocean growth zone, TR1-TR6 = radii of groups of three circuli (triplets) in the first ocean zone (six triplets), RTR1-RTR6 = radii of groups of three circuli (reverse-triplets) in the first ocean zone (six reverse-triplets).

ery agency personnel from adult chum salmon returning to principal commercial watersheds in Asia and North America in 2003. Scale samples from 41 stocks of Asian and North American origin were used to form the baselines (Fig. 3). For each stock, we selected a stratified random sample of scales from the two dominant age groups (0.3 and 0.4) that accounted for spatial and temporal population structure (early-, mid-, and late-run timing). This method varied somewhat depending on available sample size. When sample size was small the entire sample was used in the analysis. Scale baselines for 2003 included a total of 5,055 chum salmon specimens, and on average the baseline for each stock consisted of 50–100 scales in every age group.

Scale Measurement

Scales were measured using an optical digitizing system (Biosonics model OPR-513, OPRS, BioSonics Inc., Seattle, WA, USA (Davis et al. 1990)). Measurements were made along the maximum radius of the scale in the first annual zone (Fig. 4). Scale pattern variables were calculated from inter-circulus measurement. Variables included the total radius of the first ocean zone (O1), total number of circuli in the first ocean zone (C1), six triplets (TR) in the first ocean zone, and six reverse triplets (RTR) in the first ocean zone (Fig. 4).

Estimates of Stock Composition

The 41 baseline stocks were combined into a reduced number of regional stocks according to similarity in scale pattern variables, as determined by *t*-tests ($p < 0.05$), hierarchical cluster analysis of Euclidian distances between stock centroids, and canonical discriminant analysis (Bugaev et al. 2007).

Computer simulations were used to evaluate the accuracy of the regional-stock models using a maximum-likelihood estimation (MLE) procedure (Millar 1987, 1990; Patton et al. 1998). The estimation procedure included 500 iterations of randomly sampled scales in the model (with replacement) for 100% representation by one baseline in the simulated mixture.

The baseline data were used to calculate MLEs of stock composition of chum salmon in the mixture samples (Patton et al. 1998). Confidence intervals (95%) of the stock composition estimates were calculated from bootstrap resampling (500) of the baseline and mixture samples (Efron and Tibshirani 1986).

Estimates of Distribution and Abundance

We reviewed information on the distribution and abundance of immature sockeye salmon during BASIS research in the western Bering Sea in summer 2003 and fall 2002–2003 (Zavolokina and Zavolokin 2007). Estimates of the abundance and biomass of chum salmon in the Bering Sea

REEZ were provided by the TINRO-Center. The TINRO-Center estimates were calculated from BASIS trawl catch data using an area-swept formula with a fishing efficiency coefficient of 0.3 for immature salmon (Temnykh et al. 2003). The TINRO-Center estimates were stratified by year, season, maturity group, and biostatistical district. For each year and season, we pooled the TINRO-Center estimates for immature chum salmon into northern (districts 1–8) and southern (districts 9–12) areas (Fig. 1), and apportioned these estimates to three regional stocks (Russia, Japan, and USA) using our estimates of stock composition weighted by age group. Russian-origin chum salmon were further apportioned to three regional stocks: (1) continental coast of the Okhotsk Sea (Magadan) and Kamchatka (Okhotsk-Kamchatka), (2) Sakhalin (Kuril)-Amur, and (3) Chukotka (Fig. 3). As a rough measure of the validity of these estimates, we compared them to published information on the abundance of adult chum salmon runs in Asia and North America.

RESULTS

Age Composition of Immature Chum Salmon

In the western Bering Sea, estimated percentages of immature chum salmon in BASIS catches of immature and maturing chum salmon (not including 0.0 fish) were 98.4% ($n = 819$) in northern districts and 97.9% ($n = 907$) in southern districts in fall 2002, 82.6% ($n = 1250$) in northern districts and 89.4% ($n = 652$) in southern districts in summer 2003, and 98.8% ($n = 640$) in northern districts and 96.7% ($n = 569$) in southern districts in fall 2003.

Three age groups (0.1, 0.2 and 0.3) accounted for 99% of immature chum salmon samples in BASIS trawl catches in the western Bering Sea (Table 1). Age 0.4 fish accounted for less than 1% of samples collected in northern districts in summer 2003 and fall 2003. All districts and time periods were dominated the two age groups (0.1 and 0.2), and north-

ern districts (1–8) consistently had higher percentages of 0.1 fish than southern districts. Percentages of 0.1 chum salmon increased in both the northern and southern areas from summer to fall 2003, while percentages of all older age groups decreased. We referred to 0.1, 0.2, and 0.3 fish as “available age groups” because sample sizes of 0.4 chum salmon were not large enough for scale pattern analysis (AAG; Table 1).

Stock-Specific Differences in Scale Patterns

Bugaev et al. (2007) reported the detailed results of a statistical evaluation of differences in the scale patterns of local stocks of adult chum salmon of Asian and North American origin that were used in the baseline models. The results of hierarchical cluster analysis were used to combine the 41 baseline stocks of chum salmon (Fig. 3) into eight regional stocks for each age group (0.3 and 0.4 fish). The results of t -tests ($p < 0.05$) indicated statistically significant differences in 75% ($n = 28$) of the pairwise comparisons of age 0.3 regional stocks and 79% ($n = 28$) of age 0.4 comparisons ($n = 28$).

Unfortunately, the Sakhalin-Amur regional stock did not include baselines from rivers of the southern Kuril Islands. We assumed that the scale patterns of chum salmon of southern Kuril origin (Kunashir and Iturup islands) were similar to those of Sakhalin-Amur origin, because their ocean foraging areas are known to overlap during the first marine year. This issue requires further investigation, however, because age 0.3 chum salmon of Kalininka River (southwest Sakhalin) origin clustered with fish of Japanese origin, rather than with other Sakhalin-Amur origin stocks. This exception has also been observed at the genetic level (Varnavskaya 2001).

The Kamchatka baselines included samples from rivers of both coasts of Kamchatka. While the scale patterns of eastern and western Kamchatka stocks differed, high phenotypic diversity in the mixed-stock sample can increase errors in identification at lower-level hierarchical clusters. Therefore, we used higher-level hierarchical clusters to character-

Table 1. The age composition (% of total sample size) of immature chum salmon samples in the trawl catches of the R/V *TINRO* in the western Bering Sea. Age 0.4 immature chum salmon were not used in subsequent analyses because of low sample sizes. Juvenile (age 0.0 fish) chum salmon were not included in the analysis because of scale loss during trawl operations. N = sample size, AAG = available age groups for identification by scale pattern analysis, North = Districts 1–8, South = Districts 9–12 (Fig. 1).

Year	Season	Biostatistical area	N	Age composition (%)				AAG (%)
				0.1	0.2	0.3	0.4	
2002	Fall	North	806	75.8	21.1	3.1	-	100.0
		South	888	43.2	50.0	6.8	-	100.0
2003	Summer	North	1033	50.6	39.2	9.2	1.0	99.0
		South	583	46.5	37.7	15.8	-	100.0
	Fall	North	632	82.8	12.8	4.3	0.2	99.8
		South	550	75.1	21.6	3.3	-	100.0

ize Kamchatka stocks.

The Okhotsk Coast baselines included samples from rivers tributary to the continental coast of the Okhotsk Sea (Magadan District, Fig. 3). In some cases, baselines from the western and northeastern coasts of Kamchatka also clustered with Okhotsk Coast baselines. A similar trend has been observed at the genetic level for chum salmon of Okhotsk Coast (Tauf and Ola rivers) and western Kamchatka origin (Varnavskaya 2001). It is likely that the phenotypic similarity in scale patterns of these stocks depends directly on genotype. For both age groups, the Okhotsk Coast regional cluster included the Tym' River (northeastern Sakhalin) baseline. We cannot explain this phenomenon, however, the probable error in identification of regional stocks would likely be small given the low abundance of Tym' River chum salmon (annual commercial catch of roughly 100–200 tons).

For both age groups, the Chukotka regional stock included only Anadyr River baseline data. The Anadyr River accounts for 80–90% of the commercial harvest of chum salmon in the Chukotka region (Makoedov et al. 2000). Therefore, we considered our assumption that one baseline is representative of the entire region to be reasonable.

The Japanese regional stock included baselines from both Hokkaido and Honshu, and the scale patterns of chum salmon from both areas were relatively homogenous. The only exception was the Tsugaruishi River baseline, which formed a single cluster with the Kalininka River baseline of age 0.3 fish. Moreover, for age 0.3 fish the Avacha River (eastern Kamchatka) baseline clustered with the Japan regional stock group. Again, we assumed that any probable error in our analysis caused by these exceptions would be low because of the high abundance of Japanese chum salmon relative to chum salmon originating in the Kalininka and Avacha rivers.

The Alaska regional stock included chum salmon baselines only from western Alaska (Yukon R., Kuskokwim R., and Nushagak R.), which formed a homogeneous cluster for age 0.3 fish. For age 0.4 fish, Alaska clustered with eastern Kamchatka. At a lower level, however, the stocks formed separate clusters. Until additional data are available, however, an explanation for similarities and differences in scale patterns between chum salmon originating in western Alaska and East Kamchatka is premature.

Accuracies of Stock Identification Models

Computer simulations indicated that the accuracies of the MLE stock identification models were relatively high (means of 91.6% for 0.3 fish and 94.0% for 0.4 fish; Tables 2 and 3). While baseline-dependent simulations might overestimate the true accuracy of the models, we considered these accuracies adequate for identification of chum salmon stocks at the regional level.

Stock Composition Estimates

Regional stocks of Asian origin (Russia and Japan) dominated all time, area, and age strata of immature chum salmon in the 2002 and 2003 BASIS mixture samples from the western Bering Sea REEZ (Table 4). Estimated proportions of Japanese chum salmon were higher in the northern area than in the southern area. Estimated proportions of Alaska chum salmon, which were also higher in the northern area, were either low (< 12% of the total) or were not statistically significant (95% CI included zero). Russian stocks, particularly Sakhalin-Amur and Okhotsk-E. Kamchatka, dominated all strata in fall 2002 and summer 2003. In fall 2003, estimated proportions of Sakhalin-Amur chum salmon were very low (not statistically significant), and chum salmon of Japanese origin dominated most strata. In most fall 2003 strata, the dominant stocks of chum salmon of Russian origin were Okhotsk-eastern Kamchatka or Okhotsk-western Kamchatka, or both. The estimated proportions of Chukotka stocks were very low and not statistically significant except for a few strata in summer 2003 (0.1 and 0.2 fish in the northern area).

Distribution and Assessment of Relative Abundance

In general, the highest catches of immature chum salmon during BASIS trawl-fishing operations were observed in the northern region (District 8; Fig. 5). Catches typically ranged from 2,000–5,000 fish/km², and in a few cases were higher. Catches were similar in summer and fall periods. In the southern region (District 12), catches in general did not exceed 200–2,000 fish/km². Fall catches of immature chum salmon were slightly higher than summer catches.

Estimates of Abundance and Biomass of Immature Chum Salmon

The abundance and biomass of immature chum salmon were estimated for each statistical district based on catch distribution data (Table 5). In the northern districts (1–8), the highest abundance and biomass of immature chum salmon were observed in summer 2003 (583 million fish and 475 thousand tons), and the lowest—in fall of same year (206 million fish and 136 thousand tons). In the southern districts (9–12) there was less interannual variation in the abundance and biomass of immature chum salmon. The highest abundance and biomass of immature chum salmon were observed there in fall 2002 (151 million fish and 129 thousand tons).

Abundance and Biomass of Asian and North American Stocks

In September–October 2002, stocks of Japanese and Russian origin accounted for most of the estimated abundance and biomass of immature chum salmon (0.1+0.2+0.3

Table 2. Evaluation of the accuracy of an 8-region maximum likelihood estimate model for age 0.3 chum salmon in 2003, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size, Chuk = Chukotka, Sakh = Sakhalin, Kam = Kamchatka, Okh = Okhotsk Coast.

Regional stock	N	Maximum likelihood estimate/standard deviation							
		1	2	3	4	5	6	7	8
1. Chuk.	100	<u>0.9705</u>	<u>0.0061</u>	<u>0.0003</u>	<u>0.0132</u>	<u>0.0053</u>	<u>0.0189</u>	<u>0.0004</u>	<u>0.0000</u>
		0.0402	0.0108	0.0018	0.0187	0.0109	0.0251	0.0021	0.0000
2. Sakh.- Amur R.	353	<u>0.0031</u>	<u>0.8801</u>	<u>0.0208</u>	<u>0.0236</u>	<u>0.0348</u>	<u>0.0040</u>	<u>0.0104</u>	<u>0.0024</u>
		0.0081	0.0762	0.0337	0.0397	0.0518	0.0096	0.0221	0.0083
3. Japan	480	<u>0.0000</u>	<u>0.0239</u>	<u>0.8860</u>	<u>0.0254</u>	<u>0.0144</u>	<u>0.0002</u>	<u>0.0090</u>	<u>0.0023</u>
		0.0000	0.0381	0.0711	0.0388	0.0264	0.0019	0.0217	0.0088
4. West & East Kam.	500	<u>0.0034</u>	<u>0.0197</u>	<u>0.0130</u>	<u>0.8348</u>	<u>0.0482</u>	<u>0.0058</u>	<u>0.0082</u>	<u>0.0000</u>
		0.0123	0.0381	0.0282	0.1031	0.0774	0.0180	0.0203	0.0000
5. Okh. & West Kam.	380	<u>0.0029</u>	<u>0.0302</u>	<u>0.0180</u>	<u>0.0500</u>	<u>0.8494</u>	<u>0.0107</u>	<u>0.0062</u>	<u>0.0000</u>
		0.0093	0.0519	0.0338	0.0779	0.1057	0.0255	0.0146	0.0000
6. Okh. & East Kam.	226	<u>0.0201</u>	<u>0.0065</u>	<u>0.0057</u>	<u>0.0295</u>	<u>0.0275</u>	<u>0.9537</u>	<u>0.0027</u>	<u>0.0045</u>
		0.0363	0.0128	0.0116	0.0402	0.0387	0.0404	0.0064	0.0099
7. Alaska	300	<u>0.0000</u>	<u>0.0207</u>	<u>0.0271</u>	<u>0.0182</u>	<u>0.0085</u>	<u>0.0025</u>	<u>0.9631</u>	<u>0.0000</u>
		0.0000	0.0282	0.0358	0.0253	0.0152	0.0052	0.0377	0.0000
8. Japan & Sakh.	50	<u>0.0000</u>	<u>0.0128</u>	<u>0.0291</u>	<u>0.0053</u>	<u>0.0119</u>	<u>0.0042</u>	<u>0.0000</u>	<u>0.9908</u>
		0.0000	0.0200	0.0371	0.0100	0.0175	0.0079	0.0000	0.0155
Mean accuracy (%)									91.61

Table 3. Evaluation of the accuracy of an 8-region maximum likelihood estimate model for age 0.4 chum salmon in 2003, as indicated by computer simulations of 100% representation by one regional stock group (indicated by grey shading). N = sample size, Chuk = Chukotka, Sakh = Sakhalin, Kam = Kamchatka, Okh = Okhotsk Coast.

Regional stock	N	Maximum likelihood estimate/standard deviation							
		1	2	3	4	5	6	7	8
1. Sakh. & Amur R.	380	<u>0.9317</u>	<u>0.0210</u>	<u>0.0000</u>	<u>0.0196</u>	<u>0.0076</u>	<u>0.0062</u>	<u>0.0092</u>	<u>0.0003</u>
		0.0517	0.0328	0.0000	0.0284	0.0154	0.0120	0.0195	0.0022
2. Japan 1	313	<u>0.0283</u>	<u>0.9278</u>	<u>0.0000</u>	<u>0.0144</u>	<u>0.0153</u>	<u>0.0012</u>	<u>0.0092</u>	<u>0.0028</u>
		0.0431	0.0532	0.0000	0.0253	0.0246	0.0036	0.0188	0.0064
3. Chuk.	16	<u>0.0000</u>	<u>0.0002</u>	<u>0.9958</u>	<u>0.0102</u>	<u>0.0041</u>	<u>0.0250</u>	<u>0.0095</u>	<u>0.0000</u>
		0.0000	0.0021	0.0121	0.0154	0.0085	0.0338	0.0150	0.0000
4. East Kam.	214	<u>0.0071</u>	<u>0.0140</u>	<u>0.0005</u>	<u>0.8713</u>	<u>0.0237</u>	<u>0.0151</u>	<u>0.0061</u>	<u>0.0000</u>
		0.0173	0.0273	0.0038	0.0816	0.0428	0.0300	0.0162	0.0000
5. Alaska	215	<u>0.0141</u>	<u>0.0157</u>	<u>0.0000</u>	<u>0.0413</u>	<u>0.9293</u>	<u>0.0103</u>	<u>0.0006</u>	<u>0.0000</u>
		0.0244	0.0256	0.0000	0.0520	0.0551	0.0174	0.0029	0.0000
6. West Kam.	497	<u>0.0029</u>	<u>0.0034</u>	<u>0.0002</u>	<u>0.0292</u>	<u>0.0089</u>	<u>0.9188</u>	<u>0.0175</u>	<u>0.0000</u>
		0.0072	0.0085	0.0027	0.0409	0.0175	0.0588	0.0304	0.0000
7. Okh.	203	<u>0.0096</u>	<u>0.0115</u>	<u>0.0035</u>	<u>0.0110</u>	<u>0.0111</u>	<u>0.0200</u>	<u>0.9450</u>	<u>0.0000</u>
		0.0166	0.0200	0.0105	0.0187	0.0187	0.0313	0.0450	0.0000
8. Japan 2	100	<u>0.0063</u>	<u>0.0064</u>	<u>0.0000</u>	<u>0.0030</u>	<u>0.0000</u>	<u>0.0034</u>	<u>0.0029</u>	<u>0.9969</u>
		0.0098	0.0105	0.0000	0.0059	0.0000	0.0057	0.0056	0.0067
Mean accuracy (%)									93.96

Table 4. Maximum likelihood estimates (MLE) of regional stock composition of chum salmon in trawl catches of the R/V *TINRO* in the western Bering Sea in 2002–2003. SD = standard deviation, CI = confidence interval, B.S = Bering Sea, W = west, E = East, Kam = Kamchatka.

Year & Season	B.S. Area	Age	N	Regional stock	MLE	SD	CI (95%)
2002 Fall	Northern	0.1	566	Chukotka	0.0023	0.0018	0.0000–0.0083
				Sakhalin-Amur	0.3184	0.0297	0.1885–0.3329
				Japan	0.4088	0.0298	0.3431–0.4871
		W. & E. Kam.	-	-	-		
		Okhotsk-W. Kam.	0.0001	0.0002	0.0000–0.0694		
		Okhotsk-E. Kam.	0.2632	0.0230	0.2398–0.3503		
		Alaska	0.0049	0.0087	0.0000–0.0455		
		Japan-Sakhalin	0.0023	0.0018	0.0000–0.0041		
		0.2	156	Chukotka	0.0028	0.0036	0.0000–0.0152
				Sakhalin-Amur	0.4429	0.0602	0.2511–0.5225
				Japan	0.4077	0.0580	0.2996–0.5495
				W. & E. Kam.	-	-	-
				Okhotsk-W. Kam.	-	-	-
				Okhotsk-E. Kam.	0.1438	0.0358	0.0699–0.2395
		0.3	23	Alaska	-	-	-
	Japan-Sakhalin			0.0028	0.0036	0.0000–0.0039	
	Sakhalin-Amur			0.4810	0.1439	0.1711–0.7325	
	Japan 1			0.3652	0.1305	0.1250–0.6273	
	Chukotka			-	-	-	
	E. Kam.			-	-	-	
	Alaska			-	-	-	
	W. Kam.			-	-	-	
	Okhotsk			0.1379	0.0885	0.0000–0.3261	
	Japan 2	0.0159	0.0566	0.0000–0.2584			
	Southern	0.1	309	Chukotka	-	-	-
				Sakhalin-Amur	0.5388	0.0420	0.3939–0.5780
				Japan	0.2754	0.0353	0.2090–0.3616
W. & E. Kam.				-	-	-	
Okhotsk-W. Kam.				-	-	-	
Okhotsk-E. Kam.				0.1858	0.0291	0.1459–0.2759	
0.2		384	Alaska	-	-	-	
			Japan-Sakhalin	-	-	-	
			Chukotka	-	-	-	
			Sakhalin-Amur	0.4251	0.0444	0.2429–0.4416	
			Japan	0.1428	0.0264	0.1029–0.2184	
			W. & E. Kam.	-	-	-	
0.3	57	Okhotsk-W. Kam.	0.1625	0.0448	0.0755–0.3214		
		Okhotsk-E. Kam.	0.2696	0.0327	0.2187–0.3871		
		Alaska	-	-	-		
Japan-Sakhalin	-	-	-	-			
					Sakhalin-Amur	0.4806	0.0972
Japan 1	0.2174	0.0838	0.0662–0.3846				

Table 4 (continued).

Year & Season	B.S. Area	Age	N	Regional stock	MLE	SD	CI (95%)
2003 Summer	Northern	0.1	436	Chukotka	-	-	-
				E. Kam.	0.0003	0.0039	0.0000–0.0000
				Alaska	0.0188	0.0211	0.0000–0.0695
				W. Kam.	-	-	-
				Okhotsk	0.2827	0.0721	0.1540–0.4220
				Japan 2	0.0002	0.0039	0.0000–0.0000
				Chukotka	0.0256	0.0064	0.0299–0.0891
				Sakhalin-Amur	0.2081	0.0348	0.1028–0.2652
				Japan	0.3268	0.0332	0.2522–0.3893
		W. & E. Kam.	0.0615	0.0300	0.0000–0.1177		
		Okhotsk-W. Kam.	0.0538	0.0337	0.0143–0.1515		
		Okhotsk-E. Kam.	0.2109	0.0273	0.1591–0.2867		
		Alaska	0.0879	0.0211	0.0561–0.1437		
		Japan-Sakhalin	0.0254	0.0064	0.0000–0.0000		
		0.2	342	Chukotka	0.0105	0.0046	0.0036–0.0393
		Sakhalin-Amur		0.2454	0.0370	0.1477–0.3013	
		Japan		0.2835	0.0377	0.2031–0.3645	
		W. & Kam.		-	-	-	
	Okhotsk-W. Kam.	-		-	-		
	Okhotsk-E. Kam.	0.3293		0.0314	0.2932–0.4306		
	Alaska	0.1209		0.0273	0.0634–0.1704		
	Japan-Sakhalin	0.0104		0.0046	0.0000–0.0002		
	0.3	69		Chukotka	0.0155	0.0198	0.0000–0.0974
	Sakhalin-Amur		0.3450	0.0973	0.0758–0.5079		
	Japan		0.2502	0.0896	0.0528–0.4131		
	W. & E. Kam.		0.0392	0.0674	0.0000–0.1687		
	Okhotsk-W. Kam.		-	-	-		
	Okhotsk-E. Kam.		0.2197	0.0781	0.0898–0.3946		
	Alaska		0.1149	0.0678	0.0000–0.2526		
	Japan-Sakhalin		0.0155	0.0197	0.0000–0.0215		
	Southern		0.1	195	Chukotka	0.0164	0.0105
	Sakhalin-Amur	0.4342			0.0595	0.2639–0.5016	
	Japan	0.0347			0.0228	0.0000–0.0839	
W. & E. Kam.	0.0346	0.0504			0.0000–0.1037		
Okhotsk-W. Kam.	0.0140	0.0648			0.0000–0.1672		
Okhotsk-E. Kam.	0.4059	0.0545			0.3110–0.5549		
Alaska	0.0439	0.0216			0.0081–0.0855		
Japan-Sakhalin	0.0163	0.0105			0.0000–0.0000		
0.2	203	Chukotka			0.0096	0.0062	0.0000–0.0662
Sakhalin-Amur		0.4222		0.0519	0.2718–0.4893		
Japan		0.1133		0.0360	0.0573–0.2024		
W. & E. Kam.		-		-	-		
Okhotsk-W. Kam.		-		-	-		

Table 4 (continued).

Year & Season	B.S. Area	Age	N	Regional stock	MLE	SD	CI (95%)
2003 Fall	Northern	0.3	87	Okhotsk-E. Kam.	0.3474	0.0433	0.2605–0.4660
				Alaska	0.0979	0.0307	0.0356–0.1489
				Japan-Sakhalin	0.0096	0.0063	0.0000–0.0000
				Chukotka	0.0231	0.0138	0.0000–0.1087
				Sakhalin-Amur	0.3534	0.0834	0.1742–0.5024
				Japan	0.0843	0.0454	0.0001–0.1632
				W.-E. Kam.	0.0724	0.0779	0.0000–0.2024
				Okhotsk-W. Kam.	0.0286	0.0559	0.0000–0.1682
				Okhotsk-E. Kam.	0.4152	0.0753	0.2761–0.5769
		Alaska	-	-	-		
		Japan-Sakhalin	0.0230	0.0138	0.0000–0.0005		
		Chukotka	0.0064	0.0044	0.0000–0.0199		
		Sakhalin-Amur	-	-	-		
		Japan	0.5433	0.0324	0.4489–0.5797		
		W. & E. Kam.	-	-	-		
	Southern	0.2	70	Okhotsk-W. Kam.	0.2077	0.0319	0.1492–0.2901
				Okhotsk-E. Kam.	0.2048	0.0267	0.1568–0.2720
				Alaska	0.0314	0.0151	0.0138–0.0866
				Japan-Sakhalin	0.0064	0.0039	0.0000–0.0011
				Chukotka	-	-	-
				Sakhalin-Amur	0.0338	0.0693	0.0000–0.1390
				Japan	0.5778	0.0755	0.4249–0.6919
				W. & E. Kam.	-	-	-
				Okhotsk-W. Kam.	0.0234	0.0855	0.0000–0.1908
		Okhotsk-E. Kam.	0.3650	0.0778	0.2121–0.5209		
		Alaska	-	-	-		
		Japan-Sakhalin	-	-	-		
		0.3	35	Chukotka	-	-	-
				Sakhalin-Amur	0.1438	0.1039	0.0000–0.3133
				Japan	0.7766	0.1039	0.5489–0.9280
W. & E. Kam.	0.0045			0.0459	0.0000–0.1016		
Okhotsk-W. Kam.	-			-	-		
Okhotsk -E. Kam	0.0751			0.0568	0.0000–0.2108		
Alaska	-			-	-		
Japan-Sakhalin	-			-	-		
Chukotka	0.0051			0.0035	0.0000–0.0188		
0.1	375	Sakhalin-Amur	-	-	-		
		Japan	0.4460	0.0364	0.3573–0.4993		
		W. & E. Kam.	0.0340	0.0284	0.0000–0.0950		
		Okhotsk-W. Kam.	0.3609	0.0443	0.2735–0.4433		
		Okhotsk-E. Kam.	0.1091	0.0247	0.0651–0.1690		
		Alaska	0.0398	0.0168	0.0204–0.0890		
		Japan-Sakhalin	0.0051	0.0035	0.0000–0.0002		

Table 4 (continued).

Year & Season	B.S. Area	Age	N	Regional stock	MLE	SD	CI (95%)
		0.2	114	Chukotka	0.0087	0.0074	0.0000–0.0348
				Sakhalin-Amur	0.0040	0.0437	0.0000–0.0893
				Japan	0.5333	0.0672	0.3746–0.6616
				W. & E. Kam.	0.0374	0.0551	0.0000–0.1209
				Okhotsk-W. Kam.	0.1841	0.0916	0.0002–0.3646
				Okhotsk-E. Kam.	0.2139	0.0571	0.1228–0.3704
				Alaska	0.0098	0.0167	0.0000–0.0551
				Japan-Sakhalin	0.0088	0.0074	0.0000–0.0095
		0.3	20	Chukotka	-	-	-
				Sakhalin-Amur	0.1146	0.2104	0.0000–0.5452
				Japan	0.3283	0.1944	0.0000–0.6136
				W. & E. Kam.	0.0419	0.1353	0.0000–0.3112
				Okhotsk-W. Kam.	0.3386	0.2144	0.0000–0.6291
				Okhotsk-E. Kam.	0.1314	0.1070	0.0000–0.3392
				Alaska	0.0452	0.0662	0.0000–0.1885
				Japan-Sakhalin	-	-	-

fish) in the western Bering Sea (99.6% in the northern area; 99.9% in the southern area; Table 6). In the northern area, two regional stocks of Russian origin were dominant: Sakhalin (Kuril)-Amur (34.8% of total abundance and biomass) and Okhotsk-Kamchatka (23.4%). These two regional stocks were also dominant in the southern area (Districts 9–12): Sakhalin-Amur (47.5%) and Okhotsk-Kamchatka (32.1%). The estimated abundance and biomass of chum salmon of Japanese origin were substantially lower in the southern area than in the northern area (Table 6). The estimated abundance and biomass of chum salmon of USA (Alaska) origin and Chukotka origin (0.3% of total abundance and biomass in northern districts; 0.0% in southern districts) were low in comparison to other regional stocks.

In July–August 2003, Russian and Japanese stocks again accounted for most (89.7%) of the estimated abundance and biomass of immature chum salmon in the northern area: Japan (35.4% of total), Sakhalin (Kuril)-Amur (23.5%), Okhotsk-Kamchatka (28.9%), Alaska (10.3%), and Chukotka (1.9%). It is notable that for the entire period of observations in 2002–2003, this was the highest estimate for USA (Alaska) chum salmon. In the southwestern Bering Sea, Japan stocks accounted for a much lower percentage of the total biomass and abundance of immature chum salmon than in the northwestern Bering Sea, and percentages of Sakhalin-Amur (41.6% of total) and Okhotsk-Kamchatka (44.3%) stocks were higher. Estimated abundance and biomass of chum salmon of Alaska origin and Chukotka origin (1.4% of total) were low in comparison to other regional stocks.

In September–October 2003, percentages of Japan stocks increased to 56.7% of the total abundance and biomass of

immature chum salmon in the northwestern Bering Sea and 46.8% in the southwestern Bering Sea (Table 6). Percentages of Okhotsk-Kamchatka stocks were also high: 38.8% in the northwestern Bering Sea and 48.7% in the southwestern Bering Sea. Estimated percentages of chum salmon of Chukotka origin (0.6% in both northern and southern districts) and Alaska origin were low throughout the western Bering Sea in comparison to other stocks.

DISCUSSION

Stock-Specific Coherence of Scale-Pattern Baselines

Numerous studies have demonstrated stock-specific coherence in salmon age and scale structure (e.g., Koo 1955; Clutter and Whitesel 1956; Foerster 1968; Anas and Murai 1969; Kulikova 1970, 1975; Mosher 1972; Bugaev 1995; Kaev 1998). Age 0.3 and 0.4 fish typically account for more than 80% of adult chum salmon returns to both continents (Salo 1991). Interannual variation in environmental conditions, however, can affect scale growth. Therefore, the use of mixture and baseline samples from fish of the same brood year is often recommended for scale pattern analysis (Bugaev 2003a,b, 2004). Because of time and labor constraints, however, we used only two baselines composed of ages 0.3 and 0.4 adult chum salmon in 2003 to identify regional stock origins of three age groups (0.1, 0.2, and 0.3) of immature chum salmon in mixed-stock samples from 2002 and 2003.

The hierarchical clustering of chum salmon scale-pattern baselines was similar to that obtained with genetic (allozyme) data (Varnavskaya 2001; Bugaev et al. 2007). The

few differences between scale pattern and genetic results are most likely related to the effects of ecological conditions on the early marine growth of chum salmon. Kulikova (1975) found regional stock groups similar to ours using scale data, even though marine ecological conditions changed substan-

tially between the early 1970s and 2000s. In principle, this confirms that the scale patterns of chum salmon are relatively stable over time at the level of regional stock groups. This trend can be explained to some extent by genetic isolation of local stocks. While phenotype strongly depends on an organism's genotype, scale growth is also strongly influenced ecologically. The issue is which factor – genetics or environment – plays a more important role in determining scale growth patterns. The genetic component of phenotypic diversity in scale patterns is most likely evident at the macro-level, i.e., in the highly abundant regional groups of stocks that are geographically isolated during the early marine period. The ecological component is likely more important at the micro-level, i.e., it determines interannual variations in scale structure within specific local stocks. General phenotypic differences in scale structure determined genetically at a regional (macro) level would likely override ecological effects determined at a local (micro) level.

Thus, in practice the scale-pattern baselines used in our analysis should provide reliable results for geographic region of origin of chum salmon migrating in the western Bering Sea, even though our baselines emphasized the phenotypic diversity of Asian stocks. For identification of chum salmon stocks in the eastern Bering Sea, however, baselines from a much broader spectrum of chum salmon populations of North American origin should be used (e.g., Patton et al. 1998).

Overall, statistical tests indicated that chum salmon stocks originating in Asia and North America could be reliably distinguished in mixed-stock samples from the western Bering Sea using regional stock groups (Bugaev et al. 2007). We caution, however, that the reliability of our results is determined not only by parameters used in the model, but also by the quality of scales in the mixed-stock samples. This is always an important consideration in studies using potentially poor-quality scale samples from fish caught by trawl gear.

Distribution and Abundance of Chum Salmon in the Western Bering Sea

Detailed information on the distribution, abundance, and biological characteristics of chum salmon sampled during BASIS research in the western Bering Sea was reported by Zavolokina and Zavolokin (2007). Immature chum salmon dominated BASIS catches of immature and maturing chum salmon in all areas and time periods. Our age composition estimates indicated that the northwestern Bering Sea is a particularly important foraging area for young (age 0.1) immature chum salmon in fall. As expected, the percentage of mature fish in the survey area was higher in summer than fall, as summer is the period of active prespawning migrations of chum salmon in the sea. In September–October, most prespawning migrations of chum salmon were completed and the percentage of immature individuals increased. Juvenile

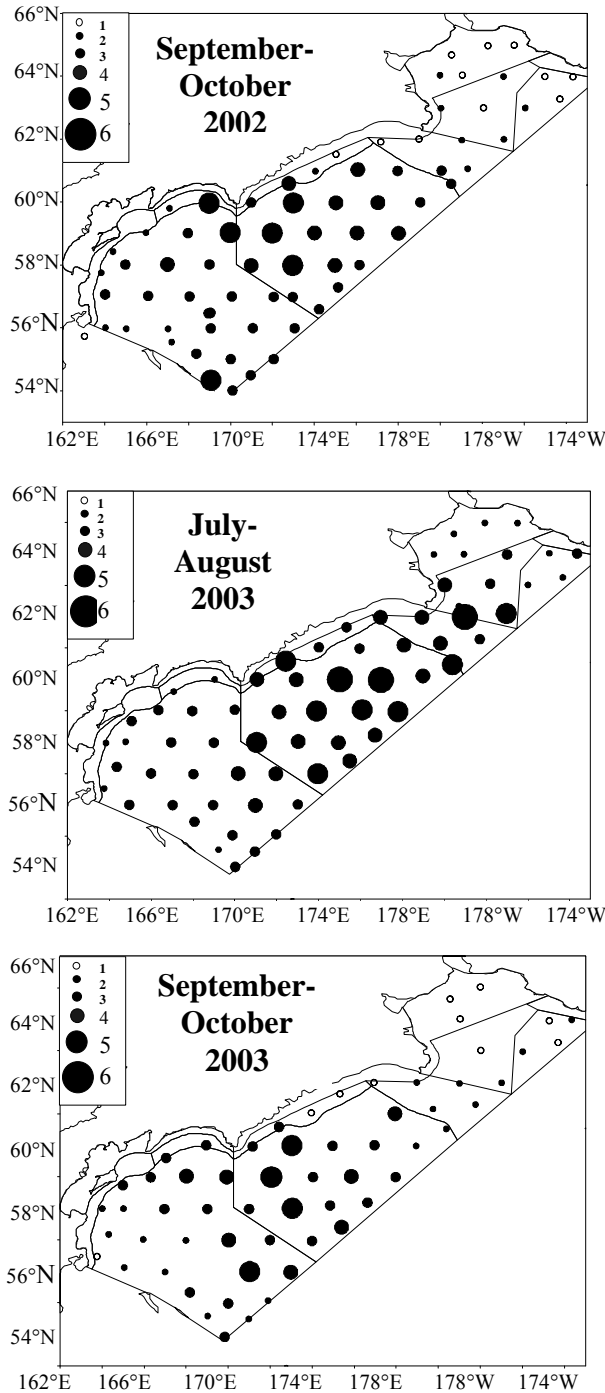


Fig. 5. The spatial distribution and relative abundance of chum salmon determined by BASIS research in the western Bering Sea, 2002-2003. The size of the circles indicates relative abundance (number of fish/km²): 1 = no catch, 2 = 1–200, 3 = 201–1000, 4 = 1001–2000, 5 = 2001–5000, 6 = >5001.

Table 5. The estimated abundance and the biomass of immature chum salmon in the epipelagic zone of the western Bering Sea in 2002–2003. Coefficient of trawl catch = 0.3. Data source: TINRO-Center, Vladivostok.

Year	Season	Biostatistical districts												Total
		1	2	3	4	5	6	7	8	9	10	11	12	
Abundance (millions of fish)														
2002		0.0	0.1	0.5	0.7	3.2	-	1.8	297.8	0.1	-	-	151.1	455.2
2003	Summer	0.1	0.8	54.2	1.8	61.7	-	10.9	453.5	0.4	-	-	121.7	705.1
	Fall	-	-	0.1	0.3	1.1	-	0.6	204.0	1.4	-	-	132.7	340.2
Biomass (thousands of tons)														
2002	Fall	0.1	0.3	0.7	1.3	5.6	-	1.9	178.4	0.1	-	-	128.5	316.8
2003	Summer	0.2	2.2	100.8	3.2	68.7	-	9.1	290.7	0.6	-	-	118.9	594.4
	Fall	-	-	0.2	0.8	1.0	-	0.8	133.1	1.5	-	-	109.1	246.3

(ocean age .0) chum salmon were more prevalent than maturing fish in BASIS trawl catches in the western Bering Sea. We could not use scale pattern analysis to estimate stock composition of juvenile salmon, however, because of scale loss during BASIS trawl fishing operations. While it seems reasonable to assume that juvenile chum salmon in summer–fall BASIS catches in the western Bering Sea were of Asian origin, similarities in scale patterns (age 0.4 chum salmon in 2003) indicated possible intermixing of eastern Kamchatka and western Alaskan stocks during their first ocean year.

When comparing the results of BASIS surveys from different periods, it is notable that the estimated percentage of the Sakhalin-Amur stock, which was high in fall 2002 and relatively high in the summer 2003, was very low in fall 2003. We hypothesize that in 2003 we observed a summer–fall migration of Sakhalin-Amur chum salmon out of the western Bering Sea. Considering the complicated nature of hydrological and hydrobiological conditions in 2003 (e.g., Basyuk et al. 2007; Shuntov et al. 2007), this scenario is plausible. Nevertheless, we cannot rule out methodical errors due to interannual variations in scale patterns, resulting from differences in the age composition and brood year of chum salmon in baseline and mixture samples.

In all cases, stock composition estimates for western and eastern Kamchatka stocks were low. Hence, we suggest that the majority of mixed samples identified as the Okhotsk-Kamchatka stock consisted of chum salmon originating in the Magadan and Khabarovsk regions. However, we cannot exclude the possibility that northeastern Kamchatka stocks also contributed substantially to estimated percentages of this regional stock, as the western Bering Sea is their traditional foraging area. This and other issues discussed above will likely be clarified through future applications using genetic (DNA) stock identification methods.

The overall pattern of immature chum salmon distribution in the western Bering Sea in summer–fall 2002–2003

was similar to the average summer–fall data from 1982–2004 (Shuntov et al. 2006). However, there was a substantial increase in the estimated biomass of chum salmon in the western Bering Sea in the early 2000s (~146–684 thousand tons, or more than 2–10 times), as compared to the 1990s (~40–60 thousand tons), which likely reflects strong interannual variation in freshwater survival at early life stages of chum salmon (Shuntov and Sviridov 2005; Shuntov et al. 2007).

Comparison of Stock Composition Estimates to Other (genetic) Studies

To compare of our scale pattern results with those of genetic analyses of BASIS samples from the central Bering Sea (Sato et al. 2004, 2009; Urawa et al. 2004, 2005, 2009), we summarized our stock composition estimates by major chum salmon-producing nation (Russia, Japan, and USA). These summary estimates showed some stable trends characteristic of the entire observation period: (1) Asian-origin stocks always dominated BASIS catches in the western Bering Sea, (2) percentages of Japanese chum salmon were highest in the northwestern Bering Sea, and (3) percentages of Russian chum salmon were highest in the southwestern Bering Sea. Both scale pattern and genetic results demonstrated the dominance (average 50–70%) of Russian chum salmon stocks at the boundary of the REEZ (near 178°E) in August–September 2002 and 2003, while percentages of Japanese chum salmon in this area averaged 20–40%, and percentages of USA chum salmon were low (average never exceeded 10%). The similarity in results obtained by different stock-identification techniques validates their use to complete BASIS modeling objectives.

The development of seasonal models of the migrations of regional stocks of chum salmon in the western Bering Sea will require additional research. The results of the 2003 sur-

veys, however, indicated that in fall immature Japanese chum salmon migrate from the central Bering Sea to the western Bering Sea. Thus, our results also validate previous observations and models of migration of chum salmon of Asian and American origin in the Western Bering Sea (Neave et al. 1976; Fredin et al. 1977; Urawa 2004).

Comparison of Abundance Estimates of Immature Chum Salmon to Adult Returns

In 2002–2003, the BASIS estimates of abundance of immature chum salmon in the western Bering Sea were very high. The summer survey of 2003 is most illustrative of this point, as our estimates show very high abundances of chum salmon of Japanese (~ 217 million fish) and USA (~ 64 million fish) origin in the western Bering Sea. Again, we emphasize that the abundance of immature chum salmon in western Bering Sea in the early 2000s was very high compared to the 1990s (Shuntov et al. 2007). Compared to average annual (1996–2005) coastal and inshore catches of chum salmon in Asia and North America (Eggers et al. 2003; Karpenko and Rassadnikov 2004, and archival commercial fisheries statistics of KamchatNIRO)—about 300,000 tons by Japan (200,000 tons), Russia (30,000 tons) and the USA (70,000 tons), the estimated abundance of immature chum salmon in the western Bering Sea was notably higher than the potential abundance of coastal runs. The total catch of Pacific salmon, including chum salmon, in the Russian Far East is uncertain, however, due to the extensive poaching. Expert assessments by scientists of KamchatNIRO indicated that recent annual coastal and inshore catches of chum salmon might be as high as 70,000 tons.

If the average weight of an individual chum salmon is 3.0 kg, then potential annual catches in Asia and North America would be approximately 100 million chum salmon. Assuming an average exploitation rate by coastal and inshore fisheries of 70% (average spawning escapement of 30%), then total annual chum salmon runs to Asia and North America would approximate 140–150 million individuals. The estimated abundances of immature chum salmon from BASIS trawl survey data were approximately 2–7 times higher than this approximate estimate of total annual adult returns. The abundance of adult returns is much less than the abundance of immature salmon in the ocean, however, because most chum salmon do not mature until ages 0.3 or 0.4. Nevertheless, the 2002–2003 RV *TINRO* surveys covered only a portion of the entire area of the distribution of chum salmon of Japanese, Russian, and western Alaska origin in the Bering Sea and North Pacific Ocean (e.g., Sato et al. 2009; Urawa et al. 2009). Our results may indicate a very high level of ocean mortality for immature chum salmon. In principle, high mortality could have resulted from increased competition for food or predation due to increased abundance of salmon and mesopelagic fish species, including salmon predators such as North Pacific daggertooth (*Anotopterus*

Table 6. Estimates of the abundance and biomass of Asian and North American (USA) stocks of immature chum salmon in the western Bering Sea in 2003.

Year	Season	Western Bering Sea area	Total abundance and biomass			Regional stock							
			Millions of fish	Thousands of tons	%	Russia		Japan		USA			
2002	Fall	Northern	303.94	187.85	58.5	177.80	109.89	41.1	124.92	77.21	0.4	1.22	0.75
		Southern	151.22	128.58	79.6	120.37	102.35	20.3	30.70	26.10	0.1	0.15	0.13
2003	Summer	Northern	582.91	474.97	54.3	316.52	257.91	35.4	206.35	168.14	10.3	60.04	48.92
		Southern	122.17	119.48	87.3	106.65	104.31	9.2	11.24	10.99	3.5	4.28	4.18
2003	Fall	Northern	206.11	135.68	40.9	84.30	55.49	56.7	116.86	76.93	2.4	4.95	3.26
		Southern	134.10	110.60	49.9	66.92	55.19	46.8	62.76	51.76	3.3	4.42	3.65

pharaoh) and longnose lancetfish (*Alepisaurus borealis*), in the western Bering Sea in the early 2000s (Shuntov and Sviridov 2005). Methodical errors in assessing the relative abundance of immature chum salmon in the BASIS trawl survey area are also highly possible to cause the overestimation of chum salmon abundance, as suggested by Bugaev and Myers (2009a, b).

CONCLUSIONS

Our results provided new evidence for the important role of the western Bering Sea ecosystem as a summer–fall foraging area for immature chum salmon of Asian and North American origin. Similar to the results of BASIS genetic stock-identification studies in the central Bering Sea (e.g., Sato et al. 2009; Urawa et al. 2009), Asian stocks dominated BASIS trawl catches of immature chum salmon in the western Bering Sea. In addition, estimated percentages of Japanese stocks were higher in northern areas, and percentages of Russian stocks were higher in southern areas. Estimated percentages of western Alaska stocks in the western Bering Sea were relatively low, but estimated abundance and biomass were high compared to rough estimates of total adult returns in North America. In fall, Japanese stocks apparently migrated into the western Bering Sea from the central Bering Sea, which validated previous observations and models of migration. In contrast, western Alaska stocks apparently migrated out of the western Bering Sea in fall. There was substantial interannual variation in the regional stock composition of chum salmon of Russian origin. Additional BASIS research is needed to further develop seasonal models of the migrations of regional stocks of Asian and North American chum salmon in the western Bering Sea.

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Behavior of Yukon River Chinook Salmon in the Bering Sea as Inferred from Archival Tag Data

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Abstract: Understanding the vulnerability of Chinook salmon to variability in climate and fishing mortality is complicated by a lack of information on migration and behavior. An archival tag placed on a Chinook salmon in the Bering Sea in 2002 was recovered in the Yukon River in 2004. During eight seasons the fish displayed a wide variety of behaviors. In summer, it was usually within the top 50 m. In the first winter it remained near 125 m, while in the second it remained within the top 50 m. Fall was a transition period between summer and winter, and in spring the fish underwent large (> 340 m) vertical movements. Temperatures experienced by the fish ranged from 1°C to 12°C. A comparison of sea surface temperatures and temperature profiles derived from tag data with oceanographic data indicated the fish was mostly in the central and southern Bering Sea Basin, with part of its second summer and final homeward migration on the eastern Bering Sea shelf. Data from another tag on a maturing Yukon River Chinook salmon indicated it moved directly from the Basin to the Yukon in three weeks. Neither fish spent substantial amounts of time in the area of groundfish fishery operations.

Keywords: Chinook, Bering Sea, Yukon, tags, vertical distribution, temperature, behavior

INTRODUCTION

Chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*) constitute the overwhelming majority of salmon caught incidentally in U.S. groundfish trawl fisheries, creating economic and social problems for western Alaska communities (Myers and Rogers 1988; Myers et al. 2003, 2004; Berger 2008; NPFMC 2008). Although Chinook salmon are the least abundant of the Pacific salmon in North America, they contributed over 900,000 fish (nearly 50,000 per year) to the Bering Sea trawl bycatch from 1990 to 2008. The vulnerability of Chinook salmon to the trawl fishery is likely due at least partially to the fact that Chinook are the deepest diving of Pacific salmon (Walker et al. 2007).

Western Alaskan Chinook salmon stocks may also be affected by climate change. There is no evidence from tag recoveries that Chinook salmon from the Arctic-Yukon-Kuskokwim (AYK) region of western Alaska leave the Bering Sea (Myers et al. 1996). Current climate model projections indicate that by 2050 mean sea surface temperatures (SSTs) in high latitudes could increase 2°C over 1990 values (IPCC 2001, 2007).

The thermal habitat of the Bering Sea varies greatly with season. During winter, storms create a deep mixed layer of cold water in the open water portions. In spring and summer, cold bottom water from melting ice forms on the eastern shelf, and a diathermal layer with a minimum temperature

around 100–200 m forms in the basin. A warmer stratified layer with a thermocline also develops in summer, both in the basin and on the shelf. Chinook encounter all of these conditions.

Understanding the vulnerability of Chinook salmon to variability in ocean temperature and fishing mortality is complicated by a lack of information on migration and behavior. An archival tag placed on a Chinook salmon in the Bering Sea in 2002 was recovered in the Yukon River in 2004. The data from this tag cover eight seasons of the travels of this fish, and shed important light on the behavior of both immature and maturing Chinook salmon in the Bering Sea. An additional tag covers the homeward migration of a Chinook salmon from the Bering Sea Basin to the Yukon River.

MATERIALS AND METHODS

Tags

Data from two archival tags were analyzed. One tag (1401) was a model LTD_1100-300, a small circuit board potted in a clear urethane, manufactured by Lotek Marine Technologies (www.lotek.com). Model LTD_1100-300 tags are 27- x 16- x 8-mm lozenges, weigh 2 g in water, and record date, time, temperature, and pressure (depth). For this model the pre-set maximum depth from which data could be recorded was 300 m (actually functional to 340 m). The

other tag (1899) was a DST CTD tag manufactured by Star-Oddi (www.star-oddi.com). Housed in a 46- x 17-mm cylindrical ceramic shell, these tags weigh 13 g in water and record date, time, conductivity (salinity), temperature, and depth data.

Fish were captured for tagging by Japanese research vessels in 2002 and 2006 in the eastern part of the central basin of the Bering Sea (Fig. 1). The Chinook salmon carrying tag 1401 (hereafter, “fish 1401”) was caught with longline gear on 7 July 2002 (Alaska Daylight Time) at 56°30′N, 179°00′W. At tagging, the fork length of the fish was measured as 562 mm. The age of the fish was determined from a scale as 1.2 (1 winter in fresh water, 2 winters at sea). The tag was attached to the fish just anterior to the dorsal fin using two 76-mm stainless steel pins, with labeled U.S. and Japanese plastic disk tags placed on the pins on the other side of the fish. The fish carrying tag 1899 (“fish 1899”) was caught by trawl on 6 June 2006 at 54°50′N, 175°08′W. The fork length of the fish at tagging was 850 mm. The tag was attached to the fish in the same body location, but was affixed with stainless steel wire and a small oval plastic plate on the opposite side of the fish.

Both fish were recaptured in fisheries in the Yukon River (Fig. 1). Fish 1401 was captured 72 km upstream from Kotlik, Alaska on 21 June 2004. Fish 1899 was captured at Mountain Village, Alaska on 30 June 2006. Tag 1401 contained 16,246 data points for both temperature and depth

for the period the fish was at liberty; data were collected at 1-h (15,336 points) and 2-h (910 points) intervals. Tag 1899 contained 4,012 data points each for temperature, depth, and salinity for the time the fish was at liberty, collected at 8-min intervals.

Sources of Oceanographic Data and Data Analysis

To determine the ocean location of tagged fish after release, temperature and depth data from the tags were compared with oceanographic data from several sources in addition to published information. MODIS satellite data provided images with estimates of sea surface temperatures (SST) throughout the year (oceancolor.gsfc.nasa.gov/cgi/13). Temperature data from tags were screened for surface (less than 5 m depth) values (for some periods, fish 1401 was not within 5 m of the surface). Surface temperatures from tags were often relatively constant for several days to over a week. Surface temperature values were visually compared to images from corresponding dates (Aqua sea surface temperature sensor, 11 μ nighttime, eight-day composite, nine-km resolution). Data from Argo floats in and near the Bering Sea yielded temperature-depth profiles, primarily in the eastern basin (floats.pmel.noaa.gov). Profile data were compared to data from tags. The Pacific Marine Environmental Laboratory (PMEL, National Oceanic and Atmospheric Administration) provided data collected from four moorings

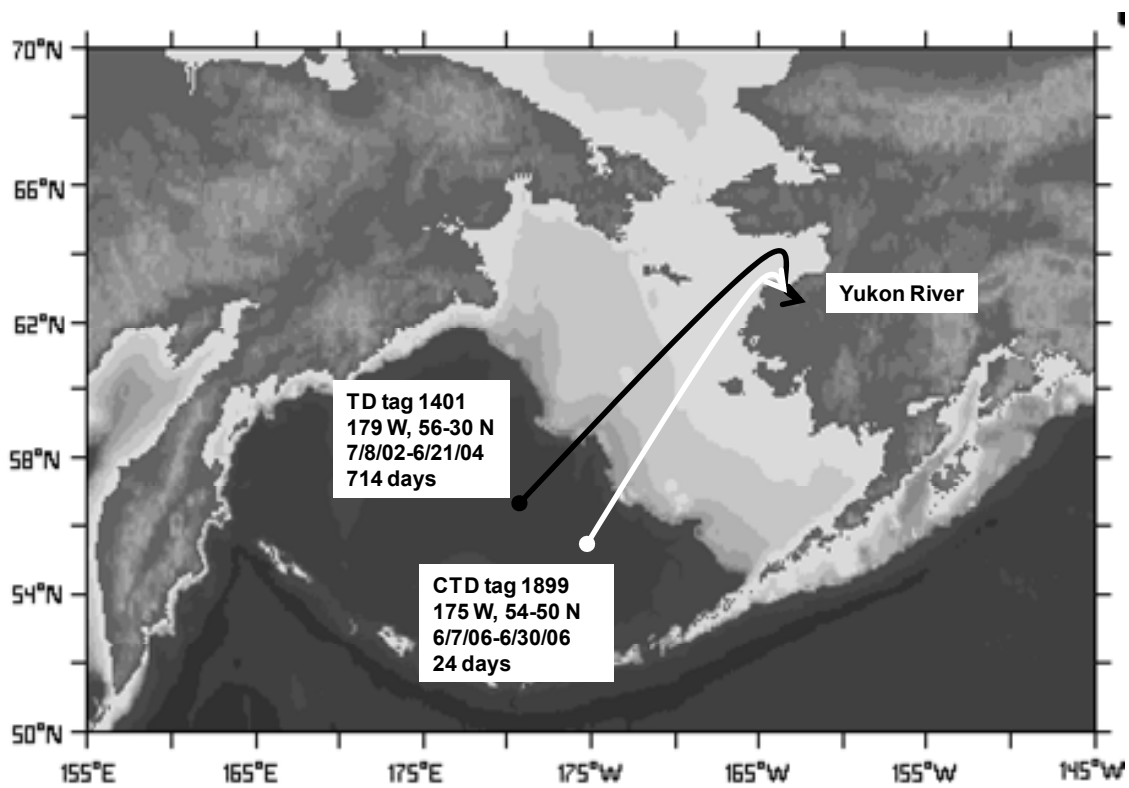


Fig. 1. Tagging and recovery locations of two Yukon River Chinook salmon tagged with archival tags in the Bering Sea. (Base map modified from a map on the PMEL website: <http://www.pmel.noaa.gov/np/pages/seas/bseamap2.html>).

on the eastern Bering Sea shelf: M2 (56.9°N, 164.1°W), M4 (57.9°N, 168.9°W), M5 (59.9°N, 171.7°W) and M8 (62.2°N, 174.7°W) (P. Stabeno and D. Kachel, pers. comm. Phyllis. Stabeno@noaa.gov and Dave.Kachel@noaa.gov). Only M2 and M4 collected data in 2002–2004. Temperature-depth profiles were constructed from mooring sensor data for dates of interest, and these were compared to tag data.

RESULTS

Fish 1401 underwent major changes in behavior during the two years it was at large (Fig. 2). In summer 2002, temperature/depth profiles (compiled from data on the tag) in the two months following tagging were similar to those from the tagging vessel and Argo floats in the Bering Sea Basin (Fig. 3). They did not match data from moorings in the eastern Bering Sea shelf, or sea surface temperatures as measured by satellite for most other regions of the Bering Sea. Beginning in October 2002, the fish began an overall descent in the water column that culminated in its remaining at approximately 125 m depth during the winter, until it gradually returned to surface waters in March 2003 (Fig. 4A). Because the fish remained at a constant depth well below the surface, it was not possible to construct temperature profiles or compare data to SSTs. However, the fish experienced near-constant water temperatures of 4°C at 125 m, a relatively warm temperature for the Bering Sea in winter at that depth. Temperatures of 4°C were not recorded by moorings on the eastern Bering

Sea shelf or by Argo floats in the Bering Sea Basin north of about 54°N. However, moorings in the Aleutian Islands did record 4°C temperatures at depths of 142–453 m in Tanaga and Amukta passes in the winter of 2002–2003, and similar temperatures at Seguam Pass at 145–154 m in the winter of 2001–2002 (Stabeno et al. 2005).

In spring (April 2003) fish 1401 undertook a series of movements between the surface and 350 m (maximum depth the tag was capable of recording) or more (Fig. 5A). The deep vertical movements by the fish in April 2003 indicate the fish was either in the Bering Sea Basin or near the shelf break. In summer 2003 temperature profiles show three different patterns, roughly June, July, and August (Figs. 6 and 7). In all periods the water column is highly stratified with a sharp thermocline around 20–40 m. In June and August temperatures below the thermocline were 3°–4°C, while in July temperatures were 1°–2°C. Maximum depths were about 140 m in June and July, but below 300 m in August. It appears the fish moved from the basin onto the eastern Bering Sea shelf in June and moved off again later in August. The coldest (1°–2°C) waters at relatively shallow depths (40–80 m) in July were typical of the “cold pool” on the eastern Bering Sea shelf south of St. Lawrence Island, and found around 60° N in 2003 (Schumacher et al. 1983; Stabeno et al. 2001; Wang et al. 2007). Temperatures at mooring M2 (56.9°N) on the shelf (Fig. 7A) during June and August are similar to those on the tag, but in July deepwater temperatures are warmer (3.3°C), as are deep temperatures at mooring M4

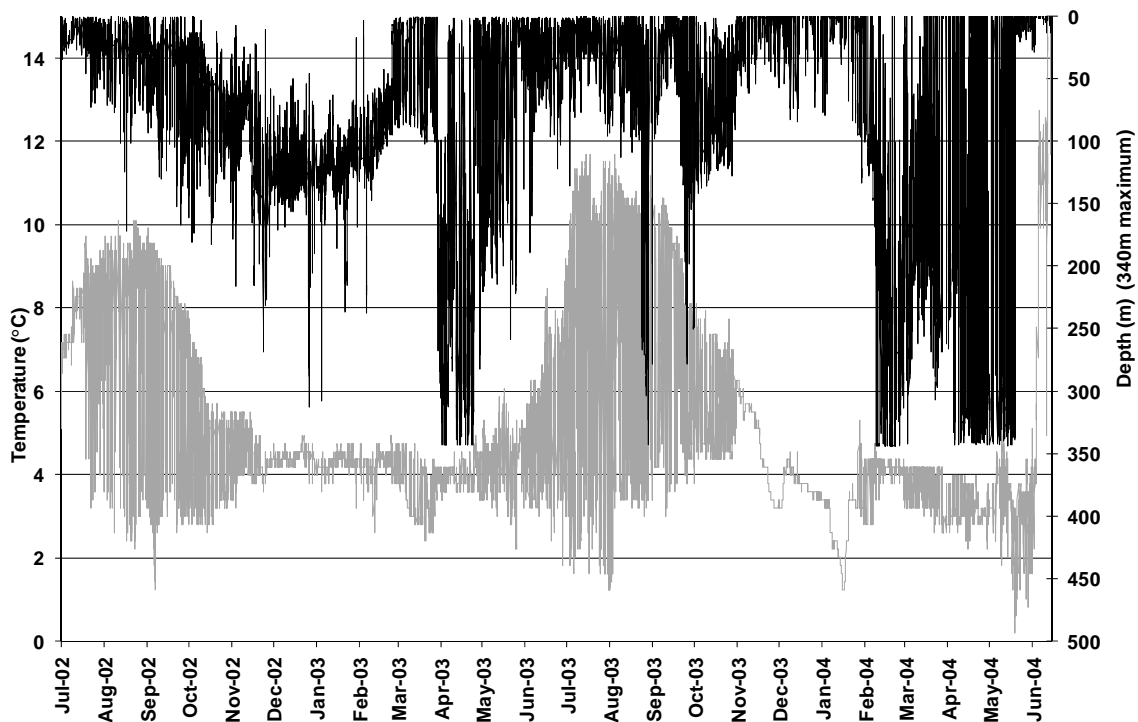


Fig. 2. Temperature (gray) and depth (black) data record from tag 1401 on a Chinook salmon tagged at 56°30'N, 179°00'W in the Bering Sea on 2 July 2002 and recovered near Kotlik, Alaska, in the Yukon River on 16 June 2004. Maximum depth the tag could record was 340 m.

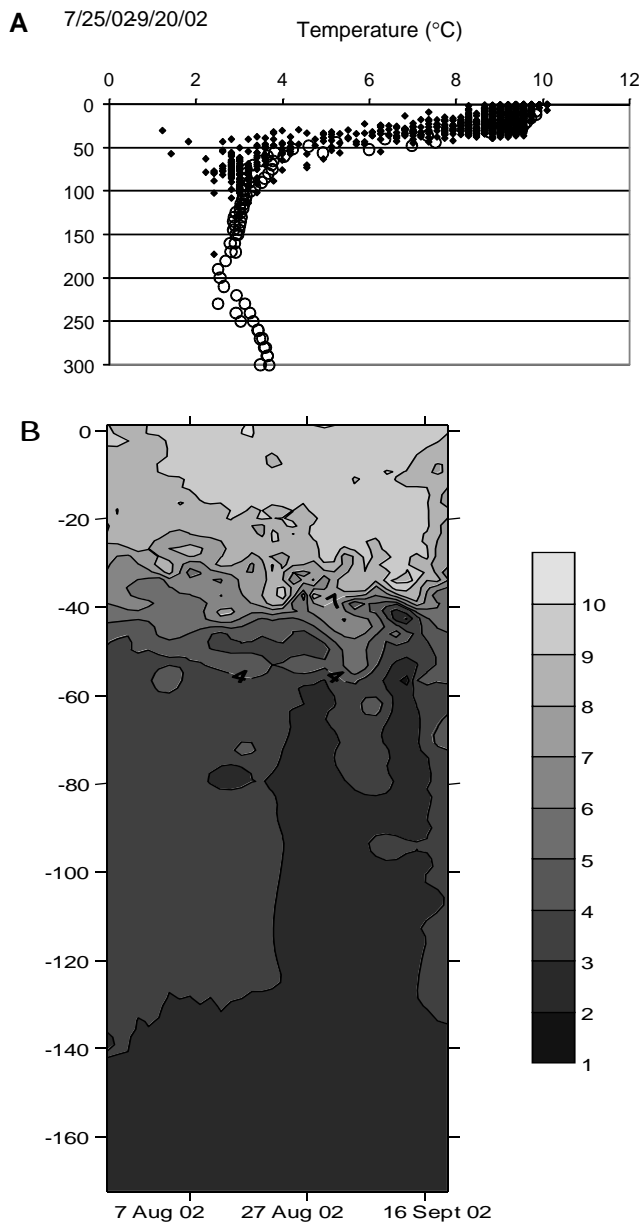


Fig. 3. Temperature-depth profiles from tag 1401 on a Chinook salmon in the Bering Sea in summer 2002. In (A) solid marks are data from tag, 25 July – 20 September; open circles are data from PMEL Argo float 11490, 26 July 2002 at 176.058° W, 57.072° N and 5 August 2002 at 175.889° W, 56.693° N. (B) includes data from the tag only and shows changes in the temperature-depth profile over time.

further north (57.9°N; temperature of 2.9°C). Fish 1401 was likely both further north and farther toward the edge of the shelf. Maximum depths on the tag were greater than 80 m, while the maximum sensor depths of M2 and M4, near the bottom, are 62 m and 67 m, respectively.

As autumn approached in 2003 fish 1401 did not substantially change its vertical behavior, remaining mostly above 100 m (Fig. 4B). Surface temperatures gradually declined and daily temperature ranges decreased. In early

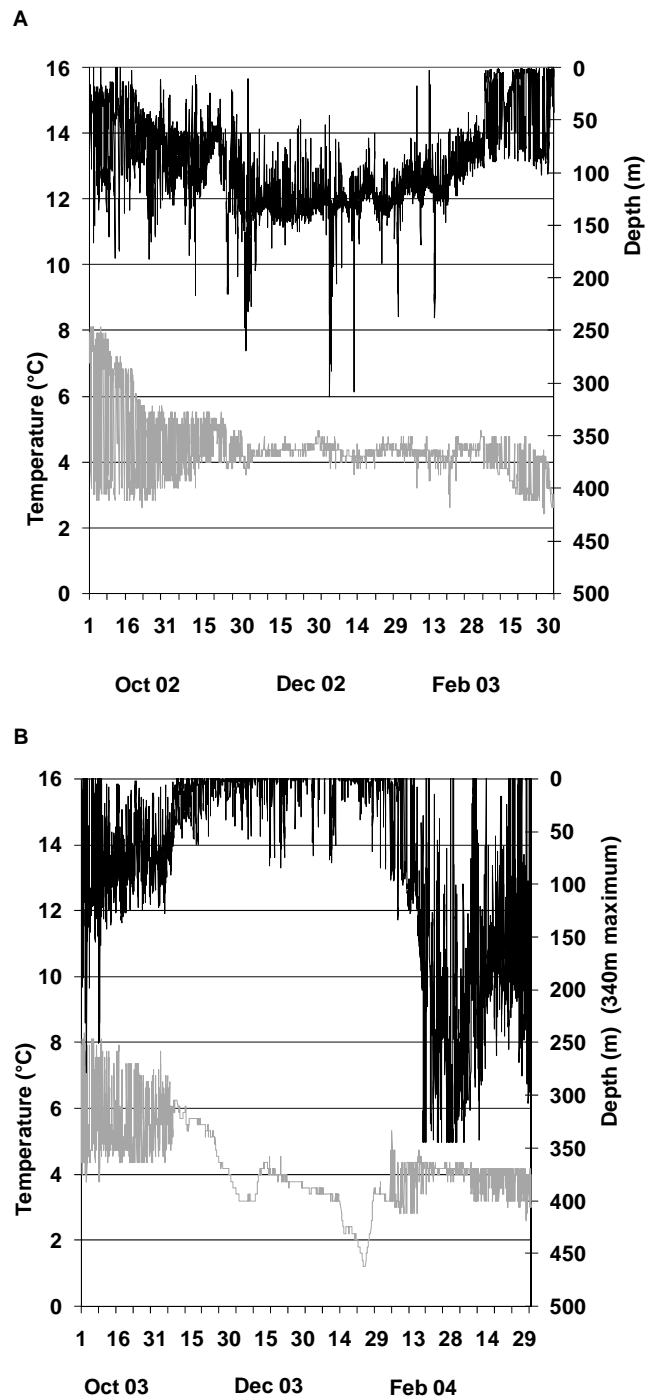


Fig. 4. Temperature (gray) and depth (black) data records from tag 1401 on a Chinook salmon tagged in the Bering Sea for (A) winter 2002-2003 and (B) winter 2003-2004. Maximum depth tag could record was 340 m.

November, temperature ranges abruptly changed to a single temperature (6°C) at all depths recorded by the tag (down to 70 m), presumably following a storm that mixed waters to at least that depth. In contrast to the previous winter, the fish continued moving between the surface and relatively shallow (50–70 m) depths. Temperatures dropped over the

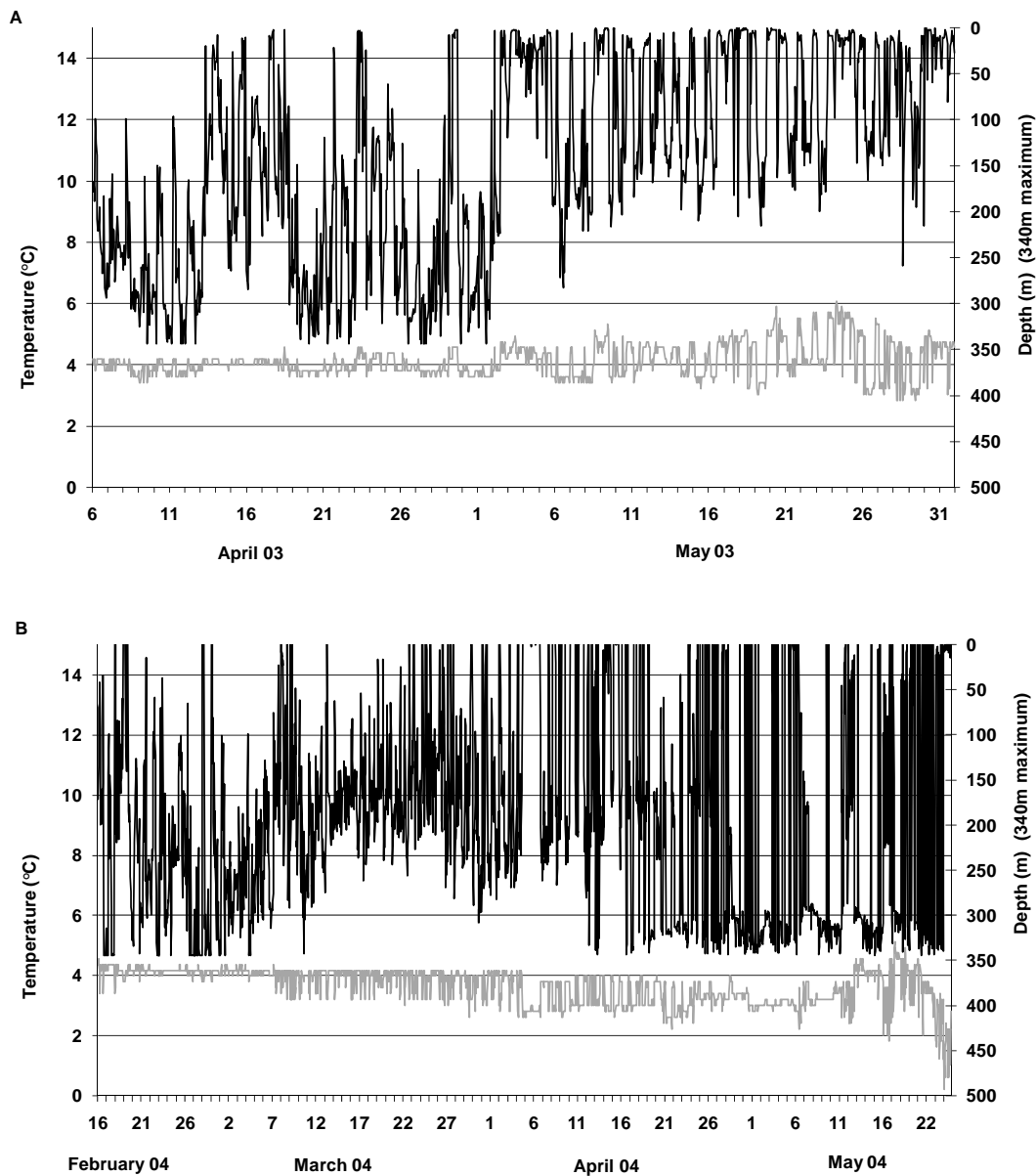


Fig. 5. Temperature (gray) and depth (black) data records from tag 1401 on a Chinook salmon tagged in the Bering Sea for deep diving periods in (A) spring 2003 and (B) late winter and spring 2004. Maximum depth the tag could record was 340 m.

course of the winter, reaching 1.2°C in January 2004. While temperatures were uniform with depth, precluding construction of informative profiles, SSTs were similar to those from satellite imagery in the southern and central portions of the Bering Sea, but were warmer than the range of SSTs in the western, northern, or eastern portions of the Bering Sea.

In late winter and spring of 2004 the fish resumed the deep vertical movements it made in spring 2003, indicating the fish was in the Bering Sea Basin or near the shelf break (Fig. 5B). During this period there are intervals when the fish does not return to the surface, though generally the fish is moving between the surface and depths of over 340 m. As in 2003 there is a relatively small temperature range

(2.5°–4.4°C) despite the large range of depths. In February the fish was encountering temperatures of about 4°C even at depth. Again, these temperatures match those in the southern Bering Sea just north of the eastern Aleutians. After three months of this behavior, it abruptly ceased deep vertical movement on 26 May. Later on this day it encountered its coldest temperatures of 0.2°–1.8°C at depths of about 20 m. This may be the edge of the cold pool, which in 2004 was north of about 58°N. At this point the fish had begun its return to the Yukon, which it reached around 12 June. During this 17-day journey the fish was mostly above 30 m and temperatures were mostly 2°–4°C.

For most of the period fish 1401 was at liberty it showed

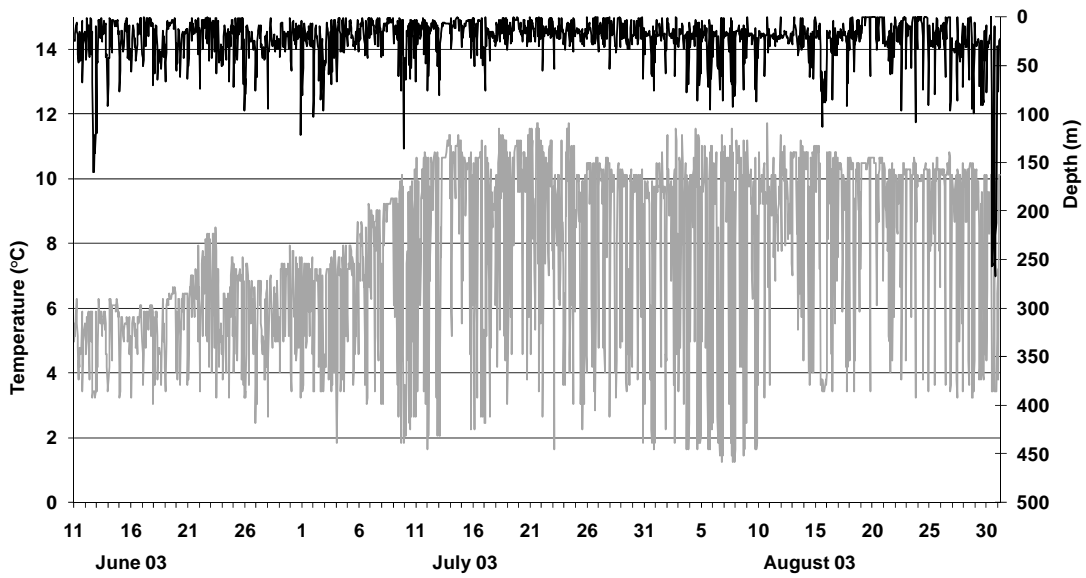


Fig. 6. Temperature (gray) and depth (black) data records from tag 1401 on a Chinook salmon tagged in the Bering Sea for summer 2003.

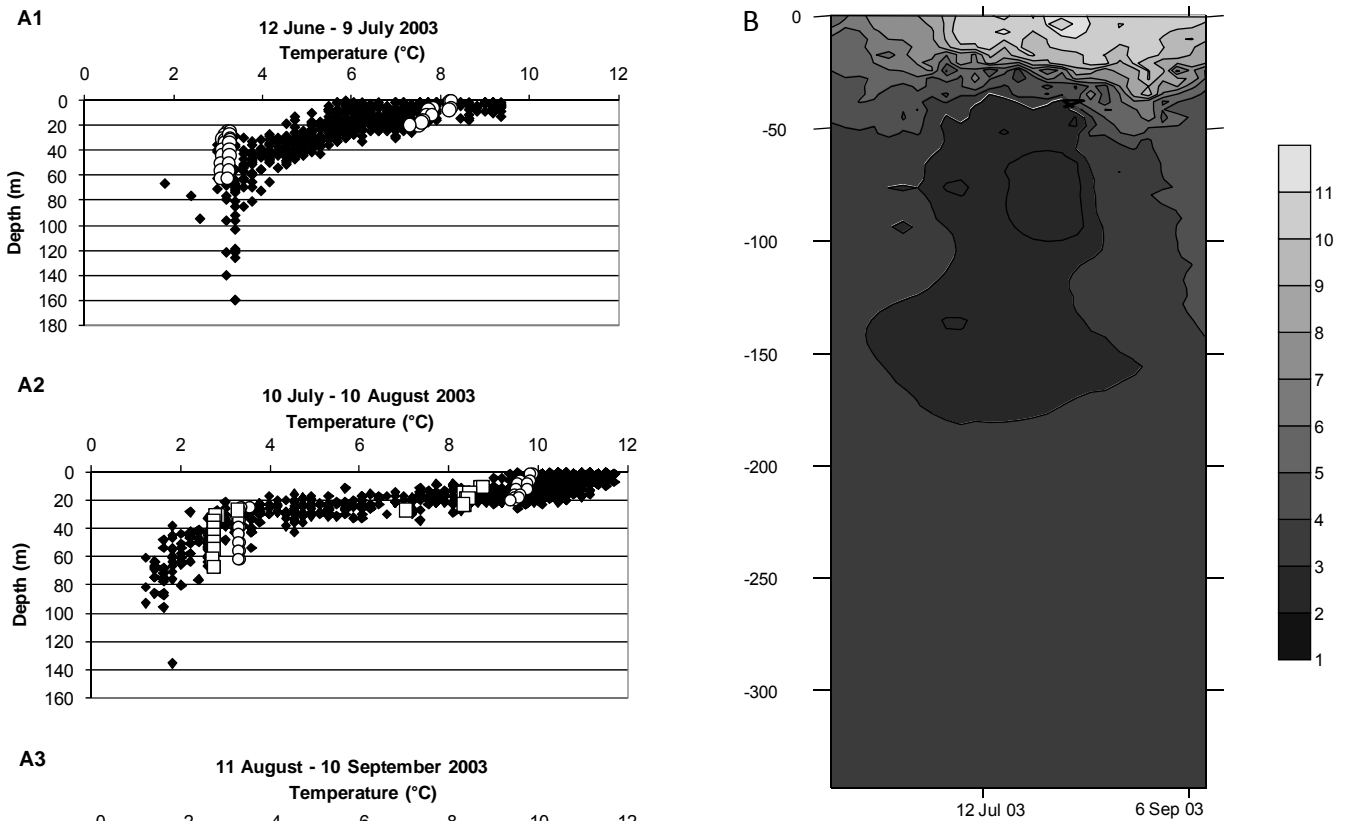


Fig. 7. Temperature-depth profiles from tag 1401 on a Chinook salmon in the Bering Sea in summer 2003. Profiles from two moorings on the eastern Bering Sea shelf are included in (A): M2, at 56.9°N, 164.1°W (open circles), and M4 at 57.9°N, 168.9°W (open squares). Maximum sensor depths are 62 m for M2 and 67 m for M4. Representative data from two days within the time range of the tag data were plotted (A1: 22–23 June for M2 only; A2: 20–21 July for both moorings; A3: 11–12 August for M2 only). (B) includes data from the tag only and shows changes in the temperature-depth profile over time.

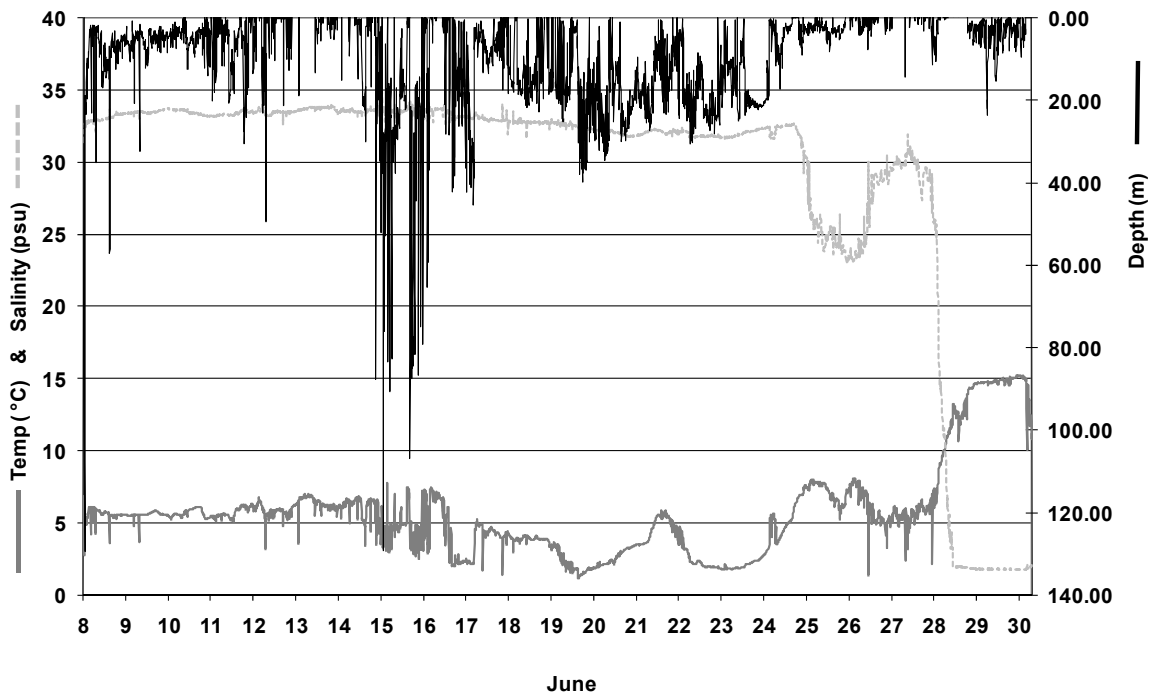


Fig. 8. Temperature (medium gray), depth (black), and salinity data (light gray, dotted line) record from tag 1899 on a Chinook salmon tagged at 54°50'N, 179°00'W in the Bering Sea on 7 June 2006 and recovered near Mountain Village, Alaska, in the Yukon River on 30 June 2006.

diel behavior patterns, with the exception of the deep diving periods of late winter and early spring. However, these patterns differed with season. In summer the fish was nearer the surface at night and moved deeper during the day. During the first autumn transition the fish remained about 25 m below the surface at night but initially made small upward vertical movements during the day, coming to the surface, and later made larger vertical movements down to 100 m. In the first winter, the fish remained at about 125 m during the night, and made small (to 50 m) vertical movements toward the surface during the day. In the second winter, fish 1401 remained near the surface, making small (40 m) movements downward during the day. During the deep dive periods of late winter and spring, there was no apparent diurnal pattern.

Fish 1899 was at liberty only 24 days after tagging. Data from tag 1899 show the fish at depths less than 40 m until it reached the mouth of the Yukon River, except for two days midway through the journey when it made dives to 100 m (Fig. 8). Temperatures ranged from 6°C to 8°C. The fish covered a minimum of 1040 km (great circle distance) in the 22 days until it entered the Yukon (as indicated by a sharp drop in salinity), implying a minimal travel rate of 1.96 km/h (0.64 body lengths/s). Given the distance and necessary rate of travel, it is likely this fish moved in a relatively direct line from the tagging location to the Yukon.

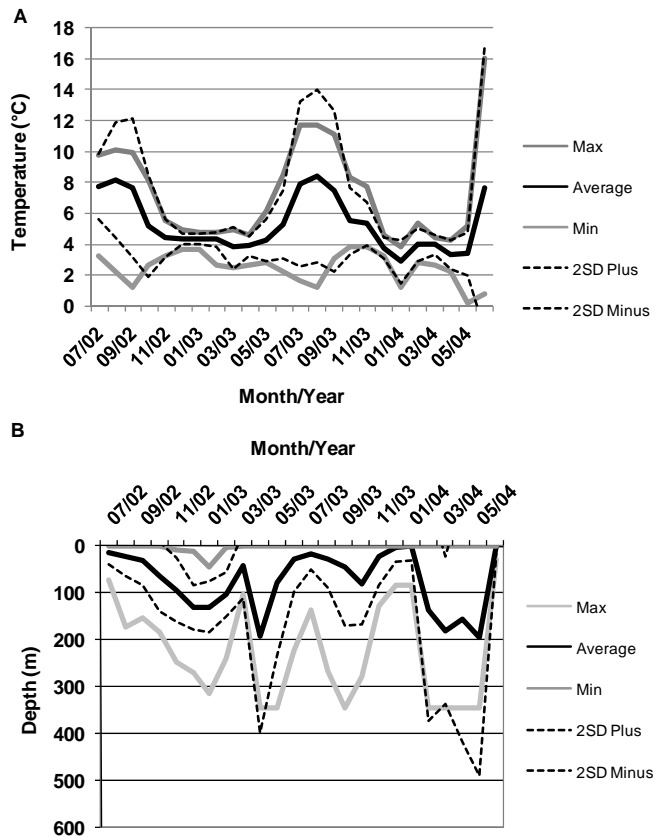


Fig. 9. Temperature and depth variation for data from tag 1401. Averages and standard deviations were calculated as means of monthly values and deviations from the monthly means. Positive value deviations for depth were constrained to zero for plotting.

DISCUSSION

The most striking feature of the data from tag 1401 is the great variability in the fish's behavior leading to large differences in the temperatures the fish experienced (Figs. 2, 9). The behavior varied between seasons and even between the same season in different years. The general pattern seemed to be one of high variance in depth but not temperature in winter and spring, when the water column is more homogeneous due to cooling and mixing, and large variance in temperature but not depth in summer and fall, due to much shallower dives through highly stratified surface waters.

Fish 1401 moved below the shallow (less than 40 m) thermocline to cooler waters below in the summer. There is a diurnal pattern to the movement, as seen in many species of Pacific salmon (Walker et al. 2000, 2007), where the fish is near the surface at night and makes occasional deeper vertical movements during the day. This may be related to feeding, with fish feeding on organisms that come to the surface at night, and moving deeper during the day to search for food or as a thermoregulatory behavior (Azumaya and Ishida 2005).

A diurnal pattern of dives continued through both winters, but was not as pronounced as in summer and fall. In the first winter, the pattern was reversed, with the fish moving toward the surface during the day. The average depth in the first winter increased, perhaps to avoid the cold turbulent surface waters and perhaps for feeding on other organisms at that depth. Water temperatures at that depth were warmer than the surface and may have been more optimal for growth. In the second winter, before it returns to spawn, the fish was much shallower, in surface waters (less than 50 m). Having obtained sufficient size to spawn, perhaps it was more important to position closer to its home river than to feed extensively or put on more somatic growth. The colder surface waters would also conserve energy.

One puzzling and dramatic feature of the behavior of fish 1401 was the very deep periodic dives undertaken in late winter and spring. The frequency and constancy with which the dives occur over a period of time, and at only one period of the year, make it unlikely that they are to escape predators. The behavior occurs in years both as an immature and a maturing fish, so is not likely a feature of maturation or sensing a migratory path. The dives are quite possibly related to feeding. In late winter and early spring, some fish and squid prey species may be overwintering at depth to avoid predation, because there is less food at the surface before development of the spring phytoplankton bloom and the zooplankton that feed on it. The diet of Chinook salmon caught deeper than 200 m in trawl fisheries in the winter is almost entirely squid; fish at shallower depths fed on a mixture of euphausiids, discarded fish offal, squid, and fish (Davis et al. 2009). If food is more abundant at depth, why didn't fish 1401 simply remain there? Perhaps Chinook have difficulty enduring the continual pressure, or perhaps there is

a small thermoregulatory benefit from the slight temperature differences between the surface and deeper waters. The fish reached depths over 300 m, and although at this season the mixed layer was very deep and temperatures were relatively uniform with depth, temperatures at depth were sometimes 1°C higher than at the surface, indicating that this was below the mixed layer; later in the spring, surface temperatures were slightly warmer. Thus although the temperature variation was small and the fish did not remain deep, thermoregulatory behavior cannot be ruled out.

Detailed information on behavior of Chinook salmon has come from other archival tags on fish off the coasts of southeastern Alaska and California. Chinook tagged by Murphy and Heard (2001, 2002) exhibited a wide range of behaviors, e.g., some fish remained near the surface at night and were deeper (40 m) during the day, some fish reversed this pattern, and some had mixed or no apparent patterns. Similarly, Hinke et al. (2005a) saw no consistent diel pattern but described four different patterns of vertical distribution in data from 15 Chinook salmon off northern California and southern Oregon: a shallow night pattern around 10 m; a shallow day pattern at 0–80 m; a deep (mostly night) pattern around 55 m; and a deeper pattern around 100 m (60–280 m). Data from two fish that overwintered at sea showed a seasonal shift in depth, with fish in the upper 150 m in fall and on average at 200 m in winter (rarely shallower than 100 m) (Hinke et al. 2005b). Data from fish at liberty in all months demonstrated a strong preference for waters between 8°C and 12°C throughout the year. They proposed that variation in depth use across individuals was probably due to thermoregulatory behaviors related to changes in local thermal conditions, while the seasonal cycle in depth use was regulated by bioenergetic needs (loss of surface productivity during winter drove the fish to seek prey resources at greater depths). Azumaya and Ishida (2005) also concluded that vertical movements played an important role in maintenance of an advantageous body temperature in chum salmon migrating from the Bering Sea to Japan.

The temperature preference of the California Chinook salmon was in marked contrast to the temperatures experienced by fish 1401 (1–11°C, excluding the final few days before entering the Yukon). Fish 1401 spent most of its time at temperatures below 8°C, except for summers. At another extreme, Wurster et al. (2005) used oxygen isotopes to estimate temperatures inhabited by Chinook salmon in Lake Ontario, and found that these fish inhabited waters of 19–20°C for up to two months during the summer. Otoliths cannot resolve features as fine as daily vertical movements, but clearly these fish tolerated much warmer temperatures than those off of California and Oregon or in the Bering Sea. Winter temperatures could not be determined, due to lack of otolith growth in that season, but May and November temperatures were below 10°C. The overall seasonal cycle of temperatures looked much like an annual cycle of water temperatures.

The Chinook tagged by Hinke et al. seem to have re-

mained along the California and Oregon coast. Chinook caught incidentally by commercial trawl operations off the Washington, Oregon, and California coasts were found from the surface to 482 m (Erickson and Pikitch 1994). Few were caught in summer, mostly above 220 m; catches were larger and deeper (100–482 m) in winter. Russian trawl fisheries captured Chinook salmon incidentally on the northwestern Bering Sea shelf at depths to 360 m throughout the year, with the majority (90%) at 50 to 400 m (Radchenko and Glebov 1998a, b). In 1997–2000 over 90% of the eastern Bering Sea groundfish trawl Chinook bycatch was caught at fishing depths between 25 m and 175 m; less than 3% were deeper than 300 m. In the winter depth distribution showed a bimodal tendency, with the bulk of fish at 25–75 m and a smaller peak at 200–300 m (Walker et al. 2007). Chinook were slightly deeper in autumn than winter in both the U.S. and Russian trawl fisheries.

Most of the bycatch of Chinook by the eastern Bering Sea trawl fishery has been concentrated along the shelf break, especially just north of the easternmost Aleutian Islands (“horseshoe area”). This pattern closely follows that of fishing effort by the fleet (NPFMC 2008). The locations we have inferred from the data on tag 1401 do not overlap the fishing areas to a great degree except for the first winter, which may be near the horseshoe area. Neither do catch locations of Chinook by the Japanese mothership salmon fishery (1952–1992) which was restricted to basin waters (Major et al. 1978; Major 1984) or catches by research vessels in the central Bering Sea. Bugaev and Myers (2009) found that while Chinook salmon were sparsely distributed in the western Bering Sea, scale pattern estimates of immature fish of North American (Alaska) origin were consistently greater than those of Asian (Russia) origin, indicating that this area is an important summer–autumn foraging area for North American as well as Asian stocks. Thus it is not clear if trawl bycatch concentrations are actually concentrations of Chinook salmon or merely the result of fishing effort. In the winter of 2002–2003 fish 1401 was very likely near the Aleutian Islands in the southeastern Bering Sea (4°C temperatures at 125 m), and if other Chinook salmon choose this area, it could account for some of the bycatch in the horseshoe area. The water column through the passes is well-mixed by strong tidal currents, and northward transport provides an important source of nutrients to the Bering Sea (Stabeno et al. 2005). Chinook may seek the horseshoe area as both an area of high productivity and a thermal refuge.

The future of Chinook salmon in the Bering Sea is uncertain. Their low abundance and use of deeper habitat makes them susceptible to trawl fisheries. The geographical range of Chinook salmon is large, stretching from central California to the northern Bering Sea, and there are transplanted populations in the Great Lakes, New Zealand, and Chile. Studies of behavior and thermal habitat in several areas demonstrate a wide variety of behavior and thermal tolerances. This great flexibility gives some cause for opti-

mism that they can adapt to changing oceanographic conditions.

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Stock-specific Ocean Distribution and Migration of Chum Salmon in the Bering Sea and North Pacific Ocean

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Abstract: Chum salmon (*Oncorhynchus keta*) is a major pelagic fish species in the Bering Sea and North Pacific ecosystems. The stock-specific ocean distribution of chum salmon was estimated by genetic stock identification (GSI) and hatchery otolith marks. Fish were caught by 1-h trawls at 98 stations in the Bering Sea, North Pacific Ocean and Gulf of Alaska during the early summer (June/July) and late summer/early fall (August/September) of 2003. Tissue samples were collected from chum salmon (n = 3,980) and run for 20 allozyme loci to estimate the stock composition of mixtures. In addition, otoliths were collected from chum salmon (n = 4,424) and examined for mark patterns to determine hatchery origin. The GSI-estimates combined with catch data (CPUE) indicated that the ocean distribution patterns of immature chum salmon were different among eleven regional stocks. Japanese stocks were mainly distributed in the Bering Sea during summer and early fall. The distribution of Russian (primarily northern Russian) stocks was similar to that of Japanese chum salmon, but they also spread into the North Pacific Ocean. Northwest Alaska stocks including fall runs in the Yukon River were relatively abundant at the southern edge (50°N) of the Gulf of Alaska and eastern North Pacific Ocean. Alaska Peninsula/Kodiak Island stocks were widely distributed in the Bering Sea and North Pacific Ocean. The southeast Alaska (SEAK)/North British Columbia (BC) stocks were distributed throughout the northern Gulf of Alaska, the eastern North Pacific Ocean and the southern Bering Sea. The distribution of the South BC/Washington stocks was similar to that of the SEAK/North BC stocks, but extended into the central Bering Sea. The samples included otolith-marked chum salmon released from Alaska (n = 66), Canada (n = 3), Japan (n = 23) and Russia (n = 6). The recovery sites of marked fish were largely consistent with the marine distribution of those regional stocks estimated by GSI. The seasonal migration patterns of Japanese chum salmon in the Bering Sea were assessed from the best available information.

Keywords: genetic stock identification, otolith mark, chum salmon, ocean distribution, migration route, Bering Sea, North Pacific Ocean, Gulf of Alaska

INTRODUCTION

The Bering Sea provides major feeding habitats for various salmon stocks originating from Asia and North America. A better understanding of salmon community structure will clarify the mechanisms of the salmon population response to recent environmental changes (Myers et al. 2007). Chum salmon (*Oncorhynchus keta*) is a dominant pelagic fish in the Bering Sea during summer and fall especially after pink salmon (*O. gorbuscha*) have moved to coastal areas for spawning (Nagasawa and Azumaya 2009).

Genetic stock identification (GSI) techniques using allozyme variation were established for estimating stock compositions of high-seas chum salmon (Seeb et al. 1995, 2004; Wilmot et al. 1998; Winans et al. 1998; Seeb and Crane 1999a, 1999b). The previous allozyme analyses suggested that Japanese and Russian stocks were predominant in chum salmon mixtures in the central Bering Sea (Urawa et al. 1997, 1998, 2004; Winans et al. 1998), while North American stocks were predominant in the Gulf of Alaska (Urawa et al. 2000). In addition, mitochondrial DNA (mtDNA) markers were recently used to estimate the stock origins of chum

salmon in the Bering Sea (Moriya et al. 2007, 2009; Sato et al. 2009a), however the resolution of the mtDNA analysis was limited to identifying only three regional stocks (Japan, Russia and North America).

Otolith marking is an effective tool for determining the hatchery origin of individual salmon in both high seas and coastal waters (Volk and Hagen 2001). Otolith-marked salmon are annually released from hatcheries in Canada, Japan, Korea, Russia and the United States under the coordination of the North Pacific Anadromous Fish Commission (NPAFC) (Josephson 2007). The total number of otolith-marked chum salmon released in 1999–2002 was approximately 1.3 billion juveniles (11.8% of the total hatchery releases in the North Pacific Rim countries).

This study used allozyme and otolith markers to estimate stock origins of maturing and immature chum salmon in the Bering Sea and North Pacific Ocean, including the Gulf of Alaska, during the summer and early fall of 2003, and to determine the ocean distribution and migration patterns of eleven regional stocks.

MATERIALS AND METHODS

Fish Samples

Trawl surveys were conducted at 98 stations in the Bering Sea and North Pacific Ocean by the research vessel *Kaiyo maru* during the early summer (June 28 to July 18) and the late summer/early fall (August 2 to September 19) of 2003 (NPAFC 2004). At each station a trawl net was towed at the surface for one hour at a speed of 5 knots. The average opening of the net during towing was 53 m in width and 54 m in height. A total of 9,600 chum salmon were caught during the two survey periods.

Maturity of fish was determined from gonad weights (Takagi 1961). Age was determined by visual examination of scale samples and designated by the European method, in which the number preceding the period is the number of freshwater annuli (zero for chum salmon) and the number following the period is the number of ocean annuli (Koo 1962).

For GSI, tissue samples (liver, heart and muscle) were collected from 3,980 chum salmon, and immediately deep frozen until allozyme analysis at the National Salmon Resources Center (NASREC) in Sapporo, Japan. In addition, otoliths were collected from 4,424 chum salmon to determine their hatchery origins at the Mark, Tag, and Age Laboratory, Alaska Department of Fish and Game, Juneau, Alaska, USA.

Allozyme Analysis

Tissue samples were examined for protein electrophoretic variation on horizontal starch gels using standard procedures described by Aebersold et al. (1987). Standard

nomenclature for loci and alleles was used as outlined in Shaklee et al. (1990). Alleles were compared and standardized for 20 polymorphic loci (ALAT*, mAAT-1*, sAAT-1,2*, mAH-3*, ESTD*, G3PDH-2*, GPI-A*, GPIB-1,2, mIDHP-1*, sIDHP-2*, LDH-A1*, LDHB-2*, sMDHA-1*, sMDHB-1,2*, mMEP-2*, sMEP-1*, MPI*, PEPA*, PEPB-1*, and PGDH*) (see Table 1 in Kondzela et al. 2002 and Table 2 in Urawa et al. 2006).

Baseline and Statistical Estimates

We used the simplified baseline data set (124 stock groups/20 loci) formulated in Seeb et al. (1997) with additional data from Japan (the Gakko R., Hei R., Katagishi R., Kido R., Koizumi R., Kurobe R., Orikasa R., Naruse R., Sho R., Tedoru R., and Uono R. in Honshu, and the Abashiri R., Shikiu R., Shizunai R., Yubetsu R., and Yurrapu R. in Hokkaido) (Urawa et al. 2006). Estimates of stock contributions were made with a conditional maximum likelihood algorithm (Pella and Milner 1987) by using the Statistical Package for Analyzing Mixtures (SPAM version 3.7) developed by Debevec et al. (2000). Standard deviations of stock estimates were estimated by 1,000 bootstrap resamplings of the baseline and mixture samples.

Based on genetic similarity and 100% simulation analysis among baseline stocks, eleven reporting regions were selected. These included five regions in Asia: 1) Japan, 2) Sakhalin, 3) Premorye, 4) Amur, and 5) north Russia (north Okhotsk coast, Kamchatka and Anadyr); and six regions in North America: 6) northwest Alaska summer, 7) fall Yukon, 8) Alaska Peninsula/Kodiak Island, 9) Prince William Sound (PWS), 10) southeast Alaska/north British Columbia (BC), and 11) south BC/Washington. Estimates were made to individual stocks and then pooled into regional stock groups. Simulation studies indicated that most reporting regions showed greater than 90% accuracy when true group contributions were 100% (Table 1).

Stock-specific CPUE (number of fish caught per 1-h trawl) was calculated by using the GSI estimates and catch data of chum salmon.

Otolith Analysis

The left sagittal otoliths were mounted on glass slides using thermoplastic cement, and then ground to expose the primordia. If the left sagittal otolith was not adequate for identification, the right sagittal otolith was used. Otolith microstructures were observed under a light microscope, and the microstructure patterns were compared to the otolith mark patterns of voucher specimens deposited in the NPAFC database (www.npafc.taglab.org). Otolith mark patterns are presented in the uniform hatch code notation (Johnson et al. 2006).

Table 1. Mean estimated contribution and standard deviations for 1,000 simulations where each region comprises 100% of the mixture (n = 400). Shaded cells are correct allocations and should equal 1.00.

Reporting region	Japan		Sakhalin Island		Premorye		Amur	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1. Japan	0.964	0.020	0.039	0.028	0.151	0.072	0.001	0.003
2. Sakhalin Island	0.005	0.009	0.903	0.037	0.011	0.018	0.002	0.006
3. Premorye	0.004	0.009	0.003	0.007	0.826	0.081	0.000	0.001
4. Amur River	0.001	0.002	0.003	0.005	0.000	0.001	0.961	0.043
5. North Russia	0.006	0.007	0.015	0.014	0.001	0.002	0.012	0.019
6. Northwest Alaska Summer	0.009	0.011	0.017	0.018	0.002	0.006	0.004	0.009
7. Fall Yukon	0.002	0.005	0.002	0.003	0.000	0.001	0.000	0.001
8. Alaska Peninsula/Kodiak	0.007	0.007	0.006	0.006	0.006	0.008	0.017	0.029
9. Prince William Sound	0.000	0.001	0.001	0.002	0.000	0.000	0.000	0.002
10. Southeast Alaska/North BC	0.001	0.002	0.001	0.003	0.001	0.002	0.000	0.000
11. South BC/Washington	0.001	0.002	0.002	0.004	0.000	0.002	0.000	0.000

Reporting region	North Russia		NW Alaska Summer		Fall Yukon		AK Peninsula/Kodiak	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1. Japan	0.010	0.010	0.010	0.010	0.002	0.003	0.006	0.007
2. Sakhalin Island	0.004	0.008	0.002	0.004	0.000	0.001	0.001	0.002
3. Premorye	0.000	0.001	0.000	0.001	0.000	0.000	0.000	0.001
4. Amur River	0.003	0.005	0.001	0.002	0.000	0.001	0.002	0.005
5. North Russia	0.902	0.036	0.013	0.014	0.001	0.002	0.013	0.014
6. Northwest Alaska Summer	0.025	0.021	0.895	0.049	0.041	0.040	0.005	0.008
7. Fall Yukon	0.002	0.004	0.064	0.043	0.954	0.040	0.001	0.003
8. Alaska Peninsula/Kodiak	0.040	0.025	0.007	0.008	0.001	0.001	0.935	0.030
9. Prince William Sound	0.004	0.007	0.001	0.002	0.000	0.001	0.010	0.013
10. Southeast Alaska/North BC	0.004	0.007	0.000	0.002	0.000	0.000	0.018	0.019
11. South BC/Washington	0.002	0.004	0.000	0.001	0.000	0.000	0.007	0.009

Reporting region	Prince William Sound		SE Alaska/N BC		S BC/Washington	
	Mean	SD	Mean	SD	Mean	SD
1. Japan	0.001	0.002	0.004	0.005	0.001	0.002
2. Sakhalin Island	0.000	0.001	0.001	0.003	0.000	0.001
3. Premorye	0.000	0.000	0.000	0.002	0.000	0.000
4. Amur River	0.001	0.002	0.001	0.003	0.001	0.002
5. North Russia	0.008	0.011	0.007	0.009	0.001	0.003
6. Northwest Alaska Summer	0.001	0.002	0.002	0.004	0.000	0.001
7. Fall Yukon	0.000	0.001	0.001	0.002	0.000	0.000
8. Alaska Peninsula/Kodiak	0.034	0.024	0.074	0.041	0.010	0.011
9. Prince William Sound	0.938	0.029	0.009	0.013	0.003	0.006
10. Southeast Alaska/North BC	0.006	0.011	0.863	0.052	0.010	0.013
11. South BC/Washington	0.008	0.011	0.036	0.027	0.973	0.017

RESULTS

Abundance, Maturity and Age Composition

Early Summer

Chum salmon were caught at all sampling stations (n = 37) in the Bering Sea and adjacent North Pacific Ocean during June and July 2003 (Fig. 1A). The highest CPUE

(number of fish caught per one-hour trawl) was recorded in the eastern North Pacific Ocean (51°N, 165–170°W). Most (94%) chum salmon were immature in the North Pacific Ocean, while the percentage of maturing fish averaged 25% in the Bering Sea (Fig. 1B). The age composition of immature chum salmon was 15.9% age 0.1, 41.8% age 0.2, 36.6% age 0.3 and 4.2% age 0.4 in the Bering Sea, and 39.6% age 0.1, 39.6% age 0.2, 17.4% age 0.3 and 2.7% age 0.4 in the

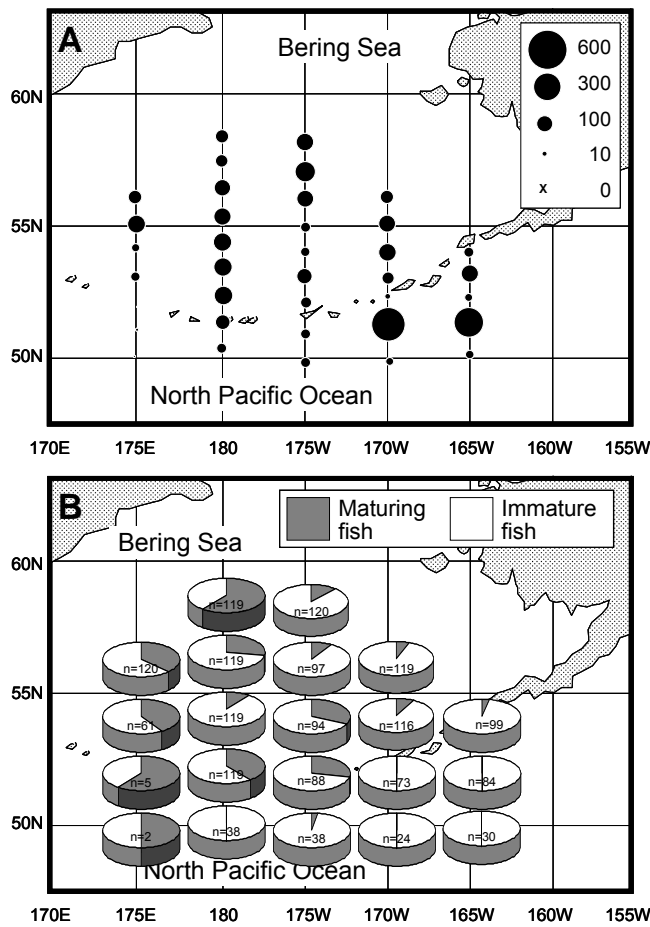


Fig. 1. CPUE distribution (A) and percent composition of maturing and immature fish (B) of chum salmon caught in the Bering Sea and North Pacific Ocean during June and July 2003. CPUE = number of fish caught per 1-h trawl, n = number of samples.

North Pacific Ocean. Therefore the major age-classes were 0.2 and 0.3 fish in the Bering Sea, and 0.1 and 0.2 in the North Pacific Ocean. Young chum salmon (age 0.1) were most prevalent in the central North Pacific Ocean (50–52°N, 175°E–175°W) and southern Bering Sea (52–54°N, 180–175°W).

Late Summer/Early Fall

In August and September, chum salmon were widely distributed in the Bering Sea and North Pacific Ocean except for the central Gulf of Alaska (50–53°N, 145°W), and they were most abundant in the southern Bering Sea (Fig. 2A). The majority of chum salmon were immature at every station (Fig. 2B). The age composition of immature chum salmon was 44.9% age 0.1, 38.6% age 0.2 and 14.4% age 0.3 in the Bering Sea, and 32.6% age 0.1, 45.5% age 0.2 and 19.4% age 0.3 in the North Pacific Ocean and Gulf of Alaska. Thus age 0.1 and 0.2 fish were predominant over the entire area. Young chum salmon (age 0.1) showed a trend of occurring in marginal habitat: north in the Bering Sea, and south in the eastern North Pacific Ocean and the Gulf of Alaska.

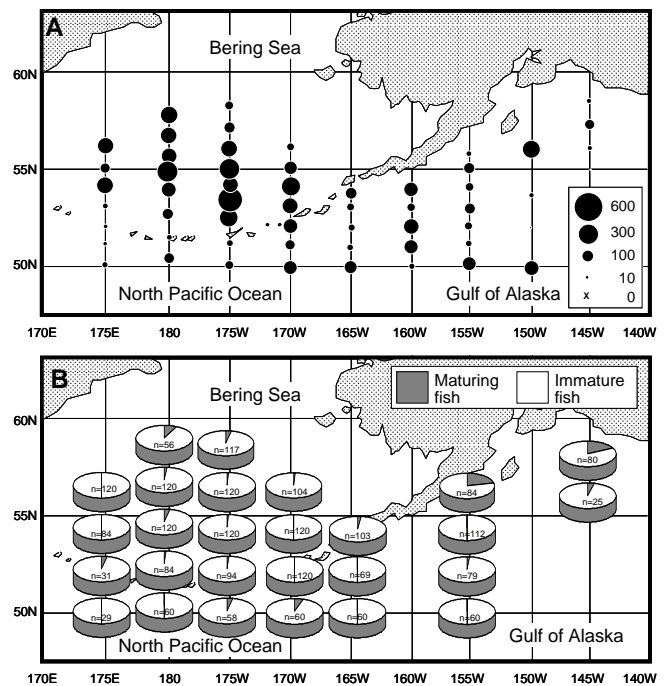


Fig. 2. CPUE distribution (A) and percent composition of maturing and immature fish (B) of chum salmon caught in the Bering Sea, North Pacific Ocean and Gulf of Alaska during August and September 2003. CPUE = number of fish caught per 1-h trawl, n = number of samples.

Stock-specific Distribution Estimated by GSI

Early Summer

The GSI-estimated stock composition of maturing chum salmon was 45–71% Japanese and 21–42% Russian stocks in the Bering Sea (Fig. 3A, Table 2). Russian stocks comprised 52% of maturing fish in the central North Pacific Ocean (50–52°N, 175°E–175°W). The percentage of North American stocks was 37% in the eastern Bering Sea (53–56°N, 170°W), but less than 20% in the other areas. The estimated CPUE of Japanese and Russian maturing chum salmon was extremely high in the Bering Sea (except for the eastern waters), and low in the North Pacific Ocean (Fig. 3B). The majority of Russian maturing fish originated from the Sakhalin and north Russia regions, and they were most abundant in the western and southern Bering Sea (Table 2). The distribution of Japanese maturing fish also shifted west of 175°W in the Bering Sea with the highest CPUE at the central stations (Fig. 3B). Most of North American maturing fish in the Bering Sea originated from the northwest Alaska and Alaska Peninsula/Kodiak Island regions (Table 2).

The estimated stock composition of immature chum salmon in the Bering Sea was similar to that of maturing fish, with Japanese and Russian stocks accounting for 37–68% and 25–45% of fish mixtures, respectively (Fig. 4A, Table 3). In the central and eastern North Pacific Ocean, however, the stock composition was almost equal for the three major

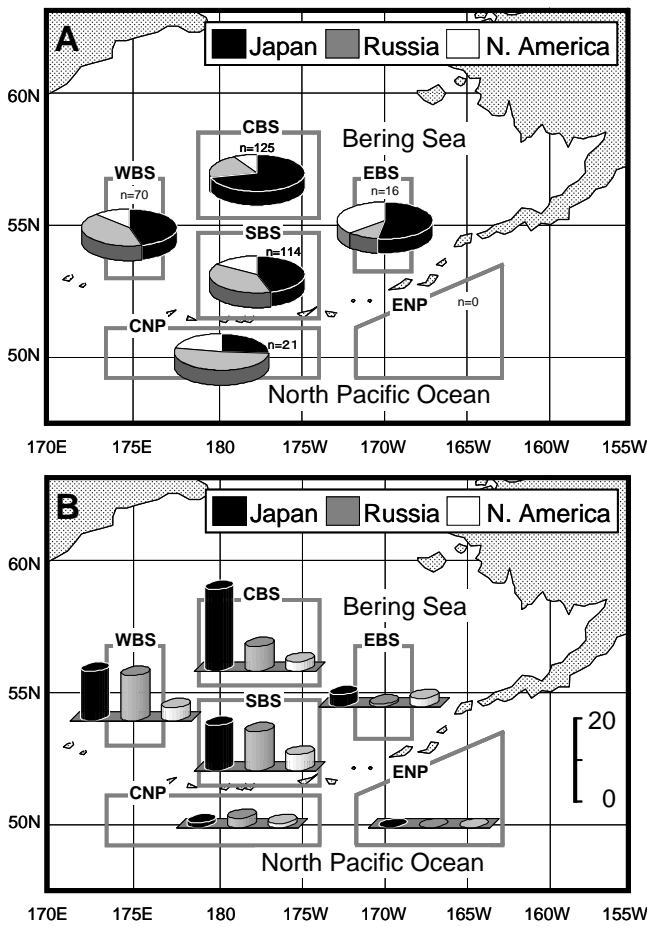


Fig. 3. GSI-estimated stock composition (A) and mean CPUE (B) of maturing chum salmon caught in the Bering Sea and North Pacific Ocean during June and July 2003. CPUE = number of fish caught per 1-h trawl, n = number of samples, CBS = central Bering Sea (55-58°N, 180-175°W), EBS = eastern Bering Sea (53-56°N, 170°W), SBS = southern Bering Sea (52-54°N, 180-175°W), WBS = western Bering Sea (53-56°N, 175°E), CNP = central North Pacific Ocean (50-52°N, 175°E-175°W), ENP = eastern North Pacific Ocean (50-53°N, 165-170°W).

groups: 25–39% for Japanese, 39–44% for Russian and 23–31% for North American stocks. Japanese immature chum salmon were mainly distributed in the eastern North Pacific Ocean and the Bering Sea, with the highest CPUE in the central Bering Sea (Fig. 4B). Russian immature fish were also abundant in the same areas, but their highest CPUE was recorded in the eastern North Pacific Ocean. North Russian stocks comprised 68–89% of Russian immature fish (Table 3). North American immature stocks (except for fall Yukon and PWS fish) were abundant in the eastern North Pacific Ocean, while they were relatively scarce in the Bering Sea and central North Pacific Ocean (Fig. 4B, Table 3).

Late Summer/Early Fall

Maturing chum salmon were rare in the survey areas during August and September, and thus were not adequate for GSI.

Table 2. GSI-estimated mean stock contribution and standard deviation for maturing chum salmon caught in the Bering Sea, and North Pacific Ocean in 2003. Estimated mean CPUE (number of fish caught per 1-h trawl) is indicated in parentheses. N = number of samples, NWAk = Northwest-Alaska summer, AP = Alaska Peninsula, PWS = Prince William Sound, SEAK = Southeast Alaska, NBC = North British Columbia, SBC = South British Columbia, WA = Washington.

Sampling Area/ Date	N	JAPAN				RUSSIA				NORTH-AMERICA				Total		
		N	Amur R.	Premorye	N. Russia	Amur R.	Premorye	N. Russia	Sakhalin	Total	Fall Yukon	NWAk	AP/Kodiak		PWS	SEAK/NBC
Western Bering Sea (53-56°N, 175°E)																
June 30 -	70	0.459±0.104	0.288±0.080	0.039±0.044	0.009±0.017	0.009±0.017	0.083±0.044	0.419±0.102	0.000	0.091±0.061	0.027±0.040	0.027±0.040	0.000	0.003±0.015	0.000	0.122±0.075
July 1		(11.3)	(7.1)	(1.0)	(0.2)	(0.2)	(2.0)	(10.3)	(0.0)	(2.2)	(0.7)	(0.7)	(0.0)	(0.1)	(0.0)	(3.0)
Central Bering Sea (55-58°N, 180-175°W)																
July 2-11	125	0.708±0.070	0.104±0.049	0.015±0.026	0.007±0.011	0.007±0.011	0.086±0.057	0.213±0.077	0.000	0.032±0.032	0.029±0.029	0.029±0.029	0.002±0.007	0.008±0.015	0.009±0.010	0.079±0.045
		(18.6)	(2.7)	(0.4)	(0.2)	(0.2)	(2.3)	(5.6)	(0.0)	(0.8)	(0.8)	(0.8)	(0.1)	(0.2)	(0.2)	(2.1)
Southern Bering Sea (52-54°N, 180-175°W)																
July 4-10	114	0.453±0.091	0.267±0.085	0.008±0.020	0.003±0.009	0.111±0.067	0.389±0.108	0.002±0.006	0.002±0.006	0.105±0.064	0.034±0.038	0.034±0.038	0.005±0.013	0.011±0.016	0.002±0.007	0.158±0.080
		(10.3)	(6.1)	(0.2)	(0.1)	(2.5)	(8.9)	(0.0)	(0.0)	(2.4)	(0.8)	(0.8)	(0.1)	(0.2)	(0.0)	(3.6)
Eastern Bering Sea (53-56°N, 170°W)																
July 12-14	16	0.526±0.186	0.028±0.064	0.062±0.112	0.000	0.013±0.045	0.103±0.136	0.000	0.042±0.070	0.134±0.127	0.134±0.127	0.000	0.088±0.096	0.106±0.093	0.371±0.168	
		(2.7)	(0.1)	(0.3)	(0.0)	(0.1)	(0.5)	(0.0)	(0.2)	(0.7)	(0.7)	(0.0)	(0.4)	(0.5)	(1.9)	
Central North Pacific Ocean (50-52°N, 175E-175°W)																
June 29 -	21	0.259±0.167	0.366±0.154	0.092±0.117	0.001±0.010	0.065±0.098	0.523±0.198	0.001±0.007	0.001±0.007	0.147±0.125	0.007±0.031	0.000	0.008±0.031	0.055±0.061	0.218±0.139	
July 8		(1.1)	(1.5)	(0.4)	(0.0)	(0.3)	(2.1)	(0.0)	(0.0)	(0.6)	(0.0)	(0.0)	(0.0)	(0.2)	(0.9)	

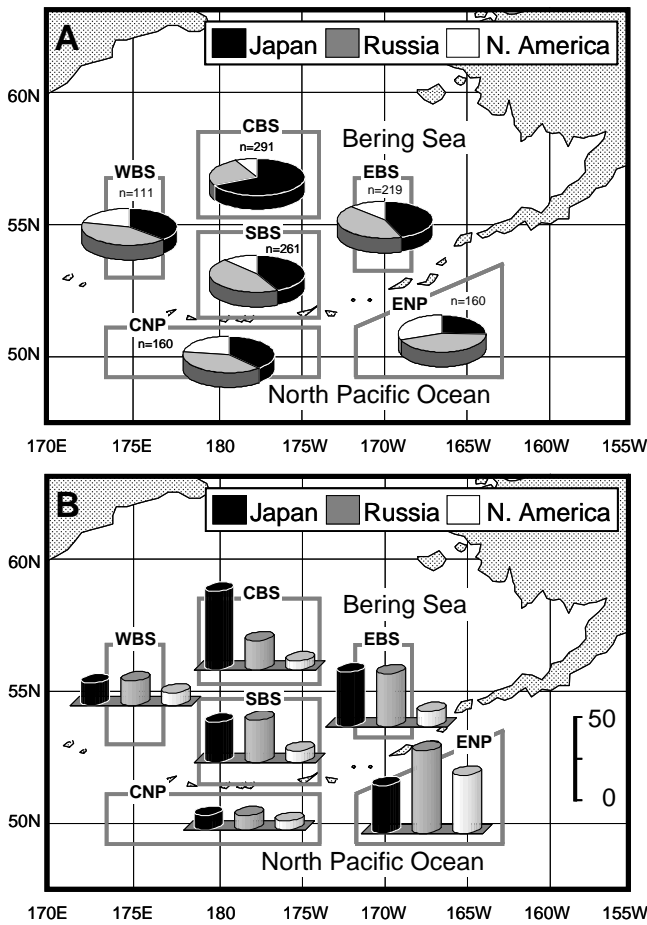


Fig. 4. GSI-estimated stock composition (A) and mean CPUE (B) of immature chum salmon caught in the Bering Sea and North Pacific Ocean during June and July 2003. CPUE = number of fish caught per 1-h trawl, n = number of samples, CBS = central Bering Sea (55–58°N, 180–175°W), EBS = eastern Bering Sea (53–56°N, 170°W), SBS = southern Bering Sea (52–54°N, 180–175°W), WBS = western Bering Sea (53–56°N, 175°E), CNP = central North Pacific Ocean (50–52°N, 175°E–175°W), ENP = eastern North Pacific Ocean (50–53°N, 165–170°W).

Asian immature chum salmon predominated in the Bering Sea and central North Pacific Ocean, where the estimated stock composition was 24–45% Japanese, 29–52% Russian and 13–30% North American stocks (Fig. 5A, Table 3). North American immature chum salmon were the major stocks in the eastern North Pacific Ocean (57%) and the Gulf of Alaska (86%). Japanese and Russian stocks were most abundant in the central and southern Bering Sea, whereas North American stocks were most abundant in the eastern Bering Sea and eastern North Pacific Ocean (Fig. 5B).

The GSI-estimated CPUE distribution indicated that Japanese immature chum salmon were mainly distributed in the Bering Sea, and rarely in the Gulf of Alaska (Fig. 6A). They were most abundant in the central and southern Bering Sea. Russian immature chum salmon had a distribution similar to the Japanese stocks, but their distribution extended south to the adjacent North Pacific Ocean (Fig. 6B). Among

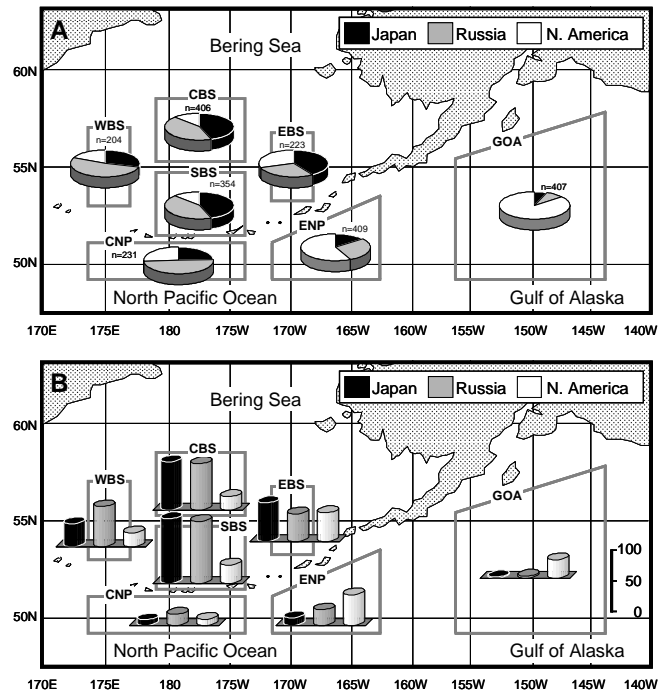


Fig. 5. GSI-estimated stock composition (A) and mean CPUE (B) of immature chum salmon in the Bering Sea, North Pacific Ocean and Gulf of Alaska during August and September 2003. CPUE = number of fish caught per 1-h trawl, n = number of samples, CBS = central Bering Sea (55–58°N, 180–175°W), EBS = eastern Bering Sea (53–56°N, 170°W), SBS = southern Bering Sea (52–54°N, 180–175°W), WBS = western Bering Sea (53–56°N, 175°E), CNP = central North Pacific Ocean (50–52°N, 175°E–175°W), ENP = eastern North Pacific Ocean (50–53°N, 165–170°W), GOA = Gulf of Alaska (50–58°N, 145–155°W).

Russian immature chum salmon, north Russian stocks accounted for 68–86% in all areas (Table 3). Sakhalin stocks appeared mainly in the central and southern Bering Sea, while the abundance of Premorye and Amur River stocks were low in the survey areas.

Fall Yukon chum salmon had a unique distribution, appearing at the southern edge of the sampling areas (50°N) in the eastern North Pacific Ocean and Gulf of Alaska (Fig. 6C). Most of those chum salmon were young age 0.1 fish (2001 brood year). Northwest Alaska summer runs had a wide ocean distribution, and they were relatively abundant in the eastern waters of the Bering Sea and North Pacific Ocean and the Gulf of Alaska (Fig. 6D). Alaska Peninsula/Kodiak Island chum salmon were also widely distributed in the Bering Sea and North Pacific Ocean including the Gulf of Alaska (Fig. 6E). Prince William Sound (PWS) fish were not abundant, although they appeared in the southern Bering Sea, eastern North Pacific Ocean and Gulf of Alaska (Fig. 6F). Southeast Alaska (SEAK)/north BC fish were distributed near the continental shelf waters of the eastern North Pacific Ocean and Gulf of Alaska, and the southern Bering Sea (Fig. 6G). South BC/Washington stocks had a distribution similar to that of SEAK/north BC stocks, except that they also appeared in the central Bering Sea (Fig. 6H).

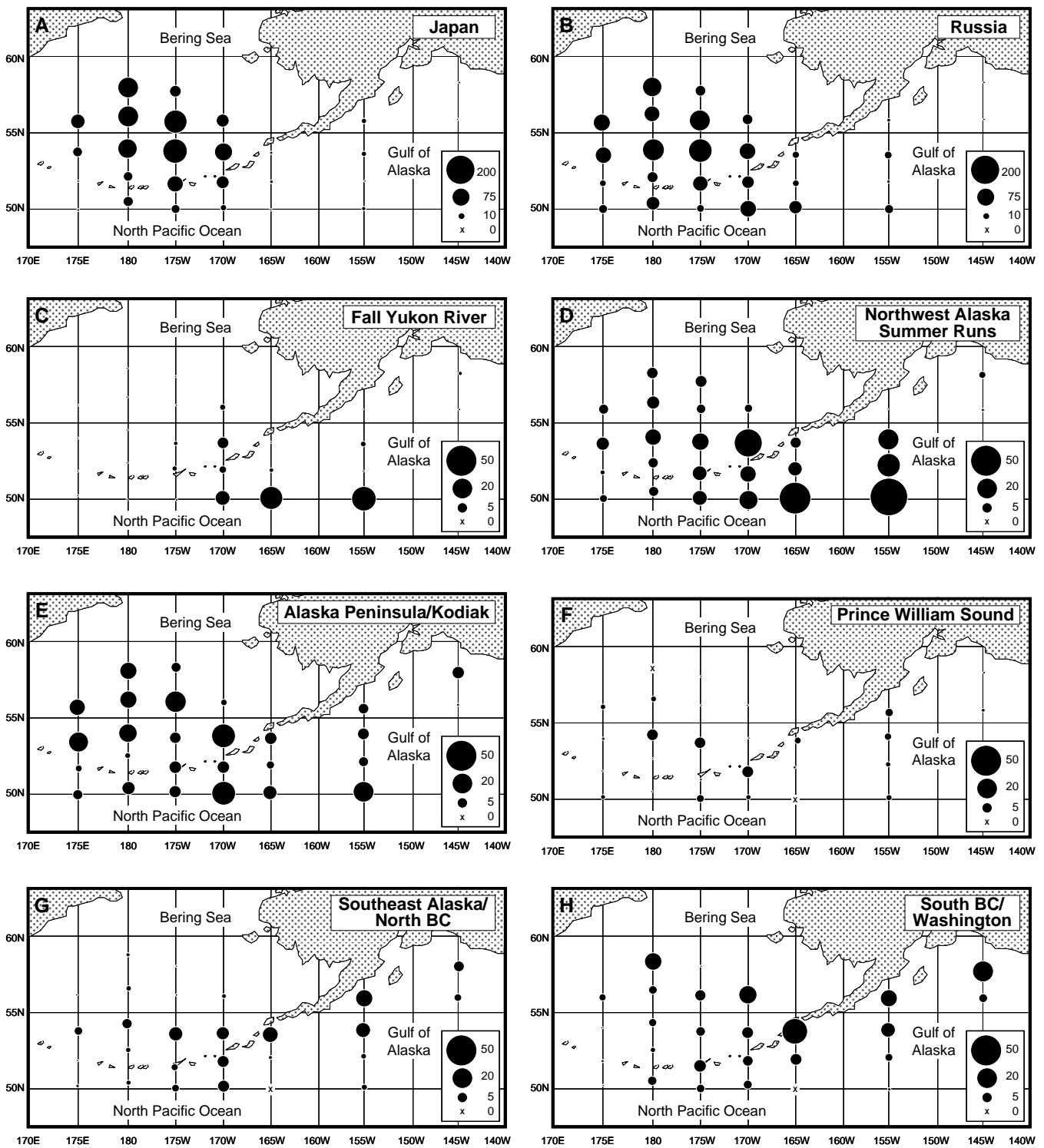


Fig. 6. GSI-estimated CPUE distribution of immature chum salmon in the Bering Sea, North Pacific Ocean and Gulf of Alaska during August and September 2003 by regional stocks. CPUE = number of fish caught per 1-h trawl. Number of mixture samples at each station is indicated in Fig. 2B.

Otolith Mark Recoveries

A total of 107 otolith-marked chum salmon (2.4% of all examined fish) were recovered in the Bering Sea and North

Pacific Ocean including the Gulf of Alaska (Figs. 7–9). The biological information on all recovered fish is recorded in Table 4. Hatchery origins of nine fish were not identified, mainly because of duplicate mark patterns among hatchery stocks.

Table 3. GSI-estimated mean stock contribution and standard deviation for immature chum salmon caught in the Bering Sea, North Pacific Ocean and the Gulf of Alaska in 2003. Estimated mean CPUE (number of fish caught per 1-h trawl) is indicated in parentheses. N = number of samples, NWAk = Northwest Alaska summer, AP = Alaska Peninsula, PWS = Prince William Sound, SEAK = Southeast Alaska, NBC = North British Columbia, SBC = South British Columbia, WA = Washington.

Sampling Area/ Date	N	JAPAN	RUSSIA					NORTH AMERICA						
			N. Russia	Premorye	Amur R.	Sakhalin	Total	Fall Yukon	NWAk	AP/Kodiak	PWS	SEAK/NBC	SBC/WA	Total
Western Bering Sea (53-56°N, 175°E)														
June 30 - July 1	111	0.374±0.074 (15.1)	0.282±0.073 (11.4)	0.082±0.045 (3.3)	0.001±0.004 (0.0)	0.050±0.050 (2.0)	0.414±0.088 (16.7)	0.000 (0.0)	0.041±0.039 (1.7)	0.087±0.054 (3.5)	0.028±0.037 (1.1)	0.023±0.027 (0.9)	0.033±0.030 (1.3)	0.212±0.067 (8.6)
Sep 16-18	204	0.298±0.052 (37.3)	0.439±0.064 (55.0)	0.026±0.022 (3.2)	0.044±0.026 (5.5)	0.014±0.023 (1.8)	0.523±0.067 (65.6)	0.000 (0.0)	0.042±0.031 (5.2)	0.114±0.047 (14.2)	0.004±0.009 (0.5)	0.011±0.013 (1.4)	0.008±0.010 (1.0)	0.179±0.056 (22.4)
Central Bering Sea (55-58°N, 180-175°W)														
July 2-11	291	0.676±0.053 (53.7)	0.168±0.042 (13.4)	0.048±0.023 (3.8)	0.000 (0.0)	0.033±0.030 (2.6)	0.249±0.053 (19.8)	0.001±0.002 (0.1)	0.004±0.008 (0.3)	0.047±0.027 (3.7)	0.004±0.009 (0.3)	0.006±0.011 (0.5)	0.015±0.013 (1.2)	0.075±0.030 (6.0)
Sep 6-15	406	0.446±0.074 (78.9)	0.296±0.059 (52.2)	0.025±0.029 (4.4)	0.015±0.015 (2.6)	0.094±0.047 (16.7)	0.430±0.076 (75.9)	0.000 (0.0)	0.050±0.039 (8.9)	0.067±0.043 (11.9)	0.002±0.006 (0.3)	0.001±0.005 (0.1)	0.004±0.008 (0.7)	0.124±0.057 (21.9)
Southern Bering Sea (52-54°N, 180-175°W)														
July 4-10	261	0.430±0.055 (27.5)	0.400±0.059 (25.5)	0.027±0.023 (1.7)	0.010±0.011 (0.7)	0.013±0.018 (0.8)	0.450±0.062 (28.7)	0.002±0.005 (0.1)	0.078±0.043 (5.0)	0.020±0.020 (1.3)	0.004±0.010 (0.2)	0.013±0.016 (0.8)	0.003±0.006 (0.2)	0.119±0.051 (7.6)
Sep 8-13	354	0.448±0.056 (106.5)	0.321±0.053 (76.4)	0.016±0.015 (3.7)	0.016±0.014 (3.8)	0.074±0.042 (17.6)	0.427±0.063 (101.6)	0.001±0.003 (0.2)	0.039±0.030 (9.4)	0.038±0.024 (9.1)	0.021±0.019 (5.1)	0.015±0.017 (3.7)	0.010±0.009 (2.4)	0.125±0.042 (29.8)
Eastern Bering Sea (53-56°N, 170°W)														
July 12-14	219	0.445±0.053 (37.3)	0.386±0.061 (32.4)	0.022±0.016 (1.8)	0.000 (0.0)	0.024±0.032 (2.0)	0.431±0.063 (36.2)	0.000 (0.0)	0.017±0.022 (1.4)	0.038±0.029 (3.2)	0.026±0.023 (2.2)	0.007±0.015 (0.6)	0.036±0.026 (3.0)	0.124±0.046 (10.4)
Sep 3-5	223	0.407±0.054 (63.4)	0.246±0.054 (38.4)	0.028±0.022 (4.3)	0.001±0.003 (0.1)	0.016±0.014 (2.5)	0.291±0.058 (45.3)	0.024±0.016 (3.7)	0.099±0.045 (15.3)	0.068±0.035 (10.6)	0.000 (0.0)	0.024±0.025 (3.7)	0.087±0.031 (13.6)	0.302±0.056 (47.0)
Central North Pacific Ocean (50-52°N, 175E-175°W)														
June 29 - July 8	160	0.387±0.071 (9.8)	0.279±0.072 (7.1)	0.037±0.030 (0.9)	0.022±0.019 (0.6)	0.046±0.034 (1.2)	0.385±0.081 (9.7)	0.000 (0.0)	0.092±0.053 (2.3)	0.101±0.054 (2.6)	0.020±0.022 (0.5)	0.005±0.010 (0.1)	0.010±0.014 (0.2)	0.228±0.074 (5.8)
Sep 9-19	231	0.242±0.059 (9.0)	0.412±0.074 (15.2)	0.032±0.029 (1.2)	0.024±0.017 (0.9)	0.025±0.028 (0.9)	0.494±0.080 (18.3)	0.000 (0.0)	0.096±0.050 (3.5)	0.061±0.041 (2.3)	0.027±0.034 (1.0)	0.037±0.039 (1.4)	0.043±0.024 (1.6)	0.264±0.070 (9.8)
Eastern North Pacific Ocean (50-53°N, 165-170°W)														
July 14-18	160	0.252±0.045 (32.5)	0.389±0.055 (50.0)	0.009±0.014 (1.1)	0.002±0.005 (0.3)	0.039±0.024 (5.0)	0.438±0.058 (56.5)	0.002±0.005 (0.3)	0.124±0.041 (15.9)	0.073±0.038 (9.5)	0.006±0.012 (0.8)	0.046±0.030 (5.9)	0.058±0.024 (7.5)	0.309±0.056 (39.8)
Aug 30 - Sep 3	409	0.141±0.038 (12.4)	0.249±0.050 (21.8)	0.025±0.018 (2.2)	0.007±0.007 (0.6)	0.007±0.013 (0.6)	0.289±0.052 (25.3)	0.054±0.020 (4.7)	0.172±0.048 (15.1)	0.075±0.034 (6.5)	0.039±0.028 (3.5)	0.070±0.033 (6.1)	0.160±0.034 (14.0)	0.569±0.054 (49.9)
Gulf of Alaska (50-58°N, 145-155°W)														
Aug 5-17	407	0.057±0.021 (2.0)	0.058±0.032 (2.0)	0.002±0.004 (0.1)	0.007±0.007 (0.3)	0.016±0.014 (0.6)	0.083±0.036 (2.9)	0.029±0.020 (1.0)	0.299±0.039 (10.4)	0.132±0.043 (4.6)	0.036±0.024 (1.3)	0.170±0.049 (6.0)	0.193±0.036 (6.8)	0.859±0.038 (30.1)

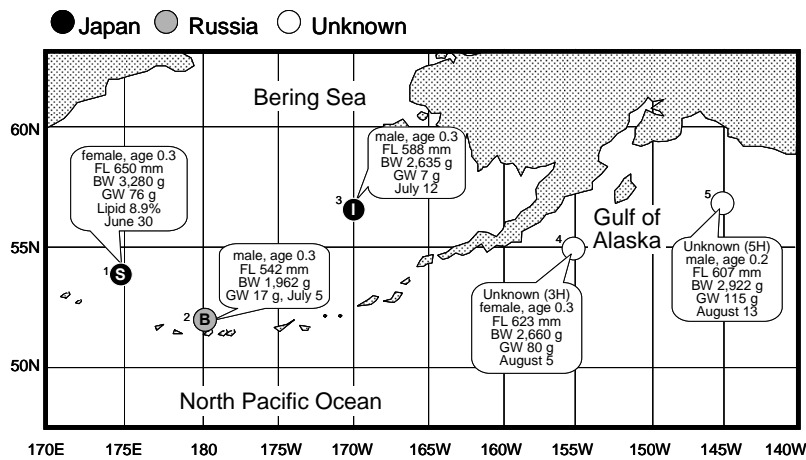


Fig. 7. Distribution of otolith-marked maturing chum salmon in the Bering Sea, North Pacific Ocean and Gulf of Alaska in the summer of 2003. Japanese hatcheries: I = Ichani, S = Shizunai; Russian hatchery: B = Bereznykovsky. Sex, age, fork length (FL), body weight (BW), gonad weight (GW), lipid content of muscle (if available), and catch date are indicated in each column. Numerals indicate sample numbers listed in Table 4.

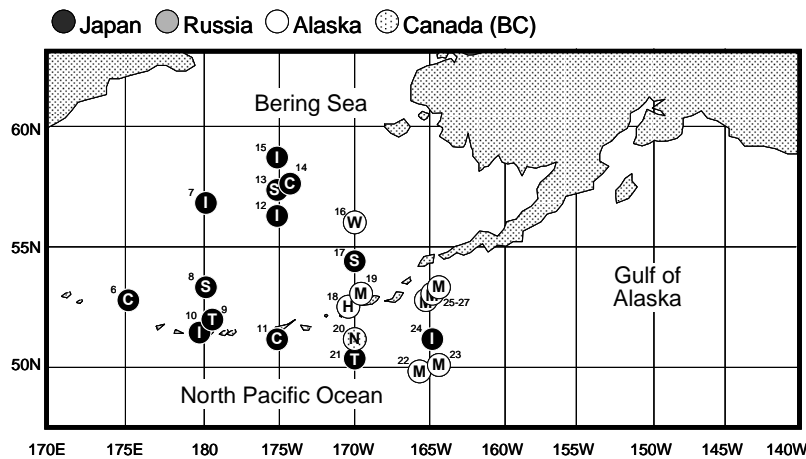


Fig. 8. Distribution of otolith-marked immature chum salmon in the Bering Sea, North Pacific Ocean and Gulf of Alaska in June and July 2003. Japanese hatcheries: C = Chitose, I = Ichani, S = Shizunai, T = Tokushibetsu; Alaskan hatcheries: H = Hidden Falls, M = Macaulay/Gastineau, W = Wally Noerenberg; Canadian hatchery: N = Nitinat. Numerals indicate sample numbers listed in Table 4.

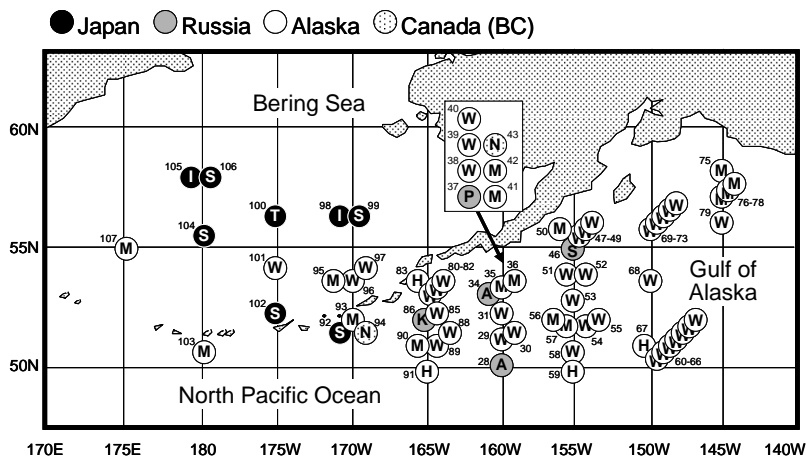


Fig. 9. Distribution of otolith-marked immature chum salmon in the Bering Sea, North Pacific Ocean and Gulf of Alaska in August and September 2003. Japanese hatcheries: I = Ichani, S = Shizunai, T = Tokushibetsu; Russian hatcheries: A = Armansky, K = Ketkinsky, P = Paratunsky, S = Sokolovsky; Alaskan hatcheries: H = Hidden Falls, M = Macaulay/Gastineau, W = Wally Noerenberg; Canadian hatchery: N = Nitinat. Numerals indicate sample numbers listed in Table 4.

Table 4. List of otolith-marked chum salmon caught in the Bering Sea and North Pacific Ocean during the 2003 *Kaiyo maru* trawl survey. Mark patterns are presented in hatch code notation (Johnson et al. 2006). F = female, M = male, IM = immature fish, MAT = maturing fish, NID = not identified.

No	Original hatchery	Hatch code	NPAFC-ID	Date of catch	Location of catch		Fork length (mm)	Body weight (g)	Sex	Ocean age	Maturity
					Latitude	Longitude					
1	Shizunai	2,3H	JP99-03	June 30	53°50'N	174°59'E	650	3,280	F	3	MAT
2	Bereznykovsky	4H	RU99-18	July 5	52°35'N	179°44'E	542	1,962	M	3	MAT
3	Ichani	2,8nH	JP99-09	July 12	56°00'N	170°03'W	588	2,635	M	3	MAT
4	NID	3H	NID	August 5	55°03'N	155°15'W	623	2,660	F	3	MAT
5	NID	5H	NID	August 13	56°53'N	144°45'W	607	2,922	M	2	MAT
6	Chitose	2,5n-3nH	JP01-03	June 30	53°05'N	174°44'E	338	367	F	1	IM
7	Ichani	2,8nH	JP00-08	July 4	55°40'N	179°58'W	410	747	M	2	IM
8	Shizunai	2,6nH	JP01-04	July 5	53°25'N	179°42'W	344	345	M	1	IM
9	Tokushibetsu	2,1n-4nH	JP00-09	July 6	51°34'N	179°44'W	469	1,313	M	2	IM
10	Ichani	2,7nH	JP01-08	July 6	51°34'N	179°44'W	314	329	M	1	IM
11	Chitose	2,5n-3nH	JP01-03	July 8	50°49'N	175°03'W	320	328	F	1	IM
12	Ichani	2,7nH	JP01-08	July 10	55°49'N	175°00'W	344	474	F	1	IM
13	Shizunai	2-3H	JP00-03	July 11	57°03'N	175°20'W	451	1,016	F	2	IM
14	Chitose	2,6nH	JP00-01	July 11	57°03'N	175°20'W	464	1,153	F	2	IM
15	Ichani	2,8nH	JP00-08	July 11	57°49'N	175°00'W	420	847	F	2	IM
16	Wally Noerenberg	3,2H	AK01-14	July 12	56°00'N	170°03'W	365	548	M	1	IM
17	Shizunai	2-3H	JP00-03	July 13	54°02'N	170°34'W	426	827	F	2	IM
18	Hidden Falls	3,3H	AK00-10	July 14	53°19'N	170°32'W	535	1,963	M	2	IM
19	Macaulay/Gastineau	5H4	AK00-07	July 14	53°19'N	170°32'W	494	1,586	F	2	IM
20	Nitinat	3-1H3	CA01-34	July 15	50°50'N	169°48'W	315	372	F	1	IM
21	Tokushibetsu	2,3n-3nH	JP01-01	July 15	49°52'N	170°14'W	332	410	M	1	IM
22	Macaulay/Gastineau	5H4	AK00-07	July 16	50°03'N	165°14'W	444	971	F	2	IM
23	Macaulay/Gastineau	5H5	AK00-08	July 16	50°03'N	165°14'W	480	1,219	M	2	IM
24	Ichani	2,8nH	JP00-08	July 17	51°06'N	165°12'W	451	1,029	M	2	IM
25	Macaulay/Gastineau	6H6	AK99-02	July 18	52°49'N	164°54'W	526	1,574	F	3	IM
26	Macaulay/Gastineau	5H	AK00-05	July 18	52°49'N	164°54'W	503	1,591	M	2	IM
27	Macaulay/Gastineau	5H3	AK00-06	July 18	52°49'N	164°54'W	504	1,514	F	2	IM
28	Armansky	5,3H	RU01-03	August 2	49°49'N	160°00'W	386	669	M	1	IM
29	Wally Noerenberg	3,2H	AK01-14	August 2	50°50'N	160°10'W	381	587	M	1	IM
30	Wally Noerenberg	3,2H	AK01-14	August 2	50°50'N	160°10'W	320	349	F	1	IM
31	Wally Noerenberg	5,2H	AK00-14	August 3	51°54'N	160°15'W	499	1,505	F	2	IM
32	NID	3,3H	NID	August 3	52°51'N	160°10'W	404	767	M	x	IM
33	NID	4H	NID	August 3	52°51'N	160°10'W	436	911	M	2	IM
34	Armansky	5,3H	RU01-03	August 3	52°51'N	160°10'W	470	1,071	F	2	IM
35	Macaulay/Gastineau	6H	AK99-01	August 3	52°51'N	160°10'W	557	1,893	M	3	IM
36	Macaulay/Gastineau	5H4	AK00-07	August 3	52°51'N	160°10'W	487	1,373	F	2	IM
37	Paratunsky	3,2nH	RU01-13	August 4	53°50'N	160°05'W	496	1,361	F	2	IM
38	Wally Noerenberg	5,2H	AK00-14	August 4	53°50'N	160°05'W	507	1,565	M	2	IM
39	Wally Noerenberg	5,2H	AK00-14	August 4	53°50'N	160°05'W	473	1,346	M	2	IM
40	Wally Noerenberg	5,2H	AK00-14	August 4	53°50'N	160°05'W	521	1,575	M	2	IM
41	Macaulay/Gastineau	6H6	AK99-02	August 4	53°50'N	160°05'W	548	1,885	F	3	IM
42	Macaulay/Gastineau	6H	AK99-01	August 4	53°50'N	160°05'W	588	2,348	F	3	IM
43	Nitinat	5H	CA00-22	August 4	53°50'N	160°05'W	488	1,384	M	x	IM
44	NID	4H	NID	August 4	53°50'N	160°05'W	510	1,556	M	2	IM
45	NID	5H	NID	August 4	53°50'N	160°05'W	525	1,707	F	2	IM
46	Sokolovsky	4,3H	RU01-18	August 5	55°03'N	155°15'W	428	1,000	F	1	IM
47	Wally Noerenberg	3,2H	AK01-14	August 5	55°03'N	155°15'W	364	522	M	1	IM
48	Wally Noerenberg	5,2H	AK00-14	August 5	55°03'N	155°15'W	526	1,660	M	2	IM
49	Wally Noerenberg	3,2H	AK01-14	August 5	55°03'N	155°15'W	409	846	F	1	IM
50	Macaulay/Gastineau	5H4	AK00-07	August 5	55°03'N	155°15'W	436	1,019	M	2	IM
51	Wally Noerenberg	5,2H	AK00-14	August 6	54°00'N	155°13'W	539	1,741	M	2	IM
52	Wally Noerenberg	5,2H	AK00-14	August 6	54°00'N	155°13'W	500	1,406	F	2	IM
53	Wally Noerenberg	3H	AK01-15	August 6	53°03'N	155°13'W	452	1,121	F	x	IM
54	Wally Noerenberg	5,2H	AK00-14	August 7	52°08'N	154°52'W	499	1,458	F	2	IM

Table 4 (continued).

No	Original hatchery	Hatch code	NPAFC-ID	Date of catch	Location of catch		Fork length (mm)	Body weight (g)	Sex	Ocean age	Maturity
					Latitude	Longitude					
55	Wally Noerenberg	3,2H	AK01-14	August 7	52°08'N	154°52'W	372	530	F	1	IM
56	Macaulay/Gastineau	5H	AK00-05	August 7	52°08'N	154°52'W	522	1,708	F	2	IM
57	Macaulay/Gastineau	6H	AK99-01	August 7	52°08'N	154°52'W	588	2,374	F	3	IM
58	Wally Noerenberg	3,2H	AK01-14	August 7	51°09'N	154°59'W	409	771	M	1	IM
59	Hidden Falls	3,3H	AK01-13	August 8	50°07'N	154°59'W	387	726	F	1	IM
60	Wally Noerenberg	3,2H	AK01-14	August 9	49°50'N	150°02'W	393	734	F	1	IM
61	Wally Noerenberg	3,2H	AK01-14	August 9	49°50'N	150°02'W	419	859	F	1	IM
62	Wally Noerenberg	3,2H	AK01-14	August 9	49°50'N	150°02'W	400	771	M	1	IM
63	Wally Noerenberg	3,2H	AK01-14	August 9	49°50'N	150°02'W	393	723	F	1	IM
64	Wally Noerenberg	3,2H	AK01-14	August 9	49°50'N	150°02'W	393	765	M	1	IM
65	Wally Noerenberg	3,2H	AK01-14	August 9	49°50'N	150°02'W	355	552	M	1	IM
66	Wally Noerenberg	3,2H	AK01-14	August 9	49°50'N	150°02'W	369	568	M	1	IM
67	Hidden Falls	3,2H	AK01-12	August 9	49°50'N	150°02'W	405	815	F	1	IM
68	Wally Noerenberg	3,2H	AK01-14	August 11	53°50'N	149°59'W	429	936	M	1	IM
69	Wally Noerenberg	5,2H	AK00-14	August 12	55°52'N	150°15'W	511	1,537	M	2	IM
70	Wally Noerenberg	3,2H	AK01-14	August 12	55°52'N	150°15'W	435	978	M	1	IM
71	Wally Noerenberg	5,2H	AK00-14	August 12	55°52'N	150°15'W	549	1,931	M	2	IM
72	Wally Noerenberg	3,2H	AK01-14	August 12	55°52'N	150°15'W	372	581	M	1	IM
73	Wally Noerenberg	3H	AK00-13	August 12	55°52'N	150°15'W	519	1,670	M	2	IM
74	NID	5H	NID	August 12	55°52'N	150°15'W	478	1,241	M	2	IM
75	Macaulay/Gastineau	6H	AK99-01	August 13	57°50'N	144°59'W	580	2,328	M	3	IM
76	Macaulay/Gastineau	5H4	AK00-07	August 13	56°53'N	144°45'W	504	1,446	M	2	IM
77	Macaulay/Gastineau	5H6	AK00-09	August 13	56°53'N	144°45'W	508	1,675	M	2	IM
78	Macaulay/Gastineau	4H5	AK01-22	August 13	56°53'N	144°45'W	449	1,180	M	1	IM
79	Wally Noerenberg	5,2H	AK00-14	August 14	55°50'N	145°04'W	386	732	M	1	IM
80	Wally Noerenberg	5,2H	AK00-14	August 30	53°29'N	165°00'W	513	1,586	F	2	IM
81	Wally Noerenberg	5,2H	AK00-14	August 30	53°29'N	165°00'W	501	1,269	F	2	IM
82	Wally Noerenberg	5,2H	AK00-14	August 30	53°29'N	165°00'W	496	1,298	F	2	IM
83	Hidden Falls	3,3H	AK00-10	August 30	53°29'N	165°00'W	497	1,401	M	2	IM
84	NID	5H	NID	August 30	53°29'N	165°00'W	562	1,676	M	2	IM
85	Wally Noerenberg	3,4H	AK98-12	August 30	53°11'N	164°59'W	575	2,120	F	4	IM
86	Ketkinsky	3,4H	RU99-15	August 30	53°11'N	164°59'W	520	1,298	M	3	IM
87	NID	5H	NID	August 30	53°11'N	164°59'W	550	2,002	F	3	IM
88	Wally Noerenberg	5,2H	AK00-14	August 31	51°59'N	164°59'W	528	1,580	M	2	IM
89	Wally Noerenberg	3,2H	AK01-14	August 31	51°59'N	164°59'W	409	745	F	1	IM
90	Macaulay/Gastineau	5H3	AK00-06	August 31	51°59'N	164°59'W	564	2,121	M	2	IM
91	Hidden Falls	3,3H	AK00-10	September 2	49°59'N	164°59'W	495	1,251	F	2	IM
92	Shizunai	2-3H	JP00-03	September 3	52°11'N	170°04'W	475	1,141	F	2	IM
93	Macaulay/Gastineau	5H3	AK00-06	September 3	52°11'N	170°04'W	493	1,216	M	2	IM
94	Nitinat	5H3	CA00-23	September 3	52°11'N	170°04'W	543	1,994	M	2	IM
95	Macaulay/Gastineau	6H3	AK99-04	September 4	54°00'N	170°17'W	548	1,940	F	3	IM
96	Wally Noerenberg	3,2H	AK01-14	September 4	54°00'N	170°17'W	412	842	F	1	IM
97	Wally Noerenberg	3H	AK01-15	September 4	54°00'N	170°17'W	400	677	M	1	IM
98	Ichani	2,8nH	JP00-08	September 5	55°59'N	169°57'W	534	1,622	F	3	IM
99	Shizunai	2-3H	JP00-03	September 5	55°59'N	169°57'W	500	1,459	F	2	IM
100	Tokushibetsu	2,3n-3nH	JP01-01	September 7	55°59'N	175°00'W	359	579	F	1	IM
101	Wally Noerenberg	3,2H	AK01-14	September 8	53°59'N	175°00'W	385	595	M	1	IM
102	Shizunai	2,6nH	JP01-04	September 9	51°40'N	175°00'W	372	636	M	1	IM
103	Macaulay/Gastineau	5H6	AK00-09	September 11	50°29'N	179°49'W	490	1,285	F	2	IM
104	Shizunai	2,6nH	JP01-04	September 13	55°29'N	179°42'W	384	690	M	1	IM
105	Ichani	2,8nH	JP00-08	September 15	57°29'N	179°59'E	421	820	F	2	IM
106	Shizunai	2,6nH	JP01-04	September 15	57°29'N	179°59'E	367	519	F	1	IM
107	Macaulay/Gastineau	6H	AK99-01	September 16	55°03'N	175°18'E	537	1,526	M	3	IM

Early Summer

Three otolith-marked maturing chum salmon (age 0.3) were found in the Bering Sea between June 30 and July 12 (Fig. 7). Those marked fish were released from the Ichani and Shizunai hatcheries in Hokkaido, Japan, and the Berznykovsky Hatchery in Sakhalin, Russia.

Thirteen Japanese immature chum salmon originally released from four hatcheries (Chitose, Ichani, Shizunai and Tokushibetsu) in Hokkaido were recovered in the Bering Sea ($n = 10$) and adjacent North Pacific Ocean ($n = 3$) (Fig. 8). In addition, eight Alaskan chum salmon from the Wally Noerenberg (PWS), Hidden Falls and Macaulay hatcheries (SEAK) and one Canadian fish from the Nitinat Hatchery on southern Vancouver Island were found in the eastern waters of the North Pacific Ocean and Bering Sea (Fig. 8).

Late Summer/Early Fall

Two otolith-marked maturing chum salmon (ages 0.2 and 0.3) were found in the northern Gulf of Alaska on August 5 and 13, 2003, but their hatchery origins were not determined due to mark duplication (Fig. 7).

Eight Japanese immature chum salmon released from the Ichani, Shizunai and Tokushibetsu hatcheries (Hokkaido) were caught in the Bering Sea ($n = 7$) and eastern North Pacific Ocean near the Aleutian Islands ($n = 1$) (Fig. 9). Five Russian chum salmon released from the Armansky (North Okhotsk), Ketkinsky and Paratunsky (Kamchatka), and Sokolovsky (Sakhalin) hatcheries were recovered in the eastern North Pacific Ocean and Gulf of Alaska (Fig. 9). Thirty-eight fish released from the Wally Noerenberg Hatchery (PWS) were found in the Gulf of Alaska ($n = 23$), eastern North Pacific Ocean ($n = 12$), and eastern Bering Sea ($n = 3$). Nineteen fish from the Macaulay and Hidden Falls hatcheries (SEAK) were recovered in the Gulf of Alaska ($n = 9$), eastern North Pacific Ocean ($n = 7$), central North Pacific Ocean ($n = 1$) and Bering Sea ($n = 2$). One of them was caught in the western Bering Sea ($55^{\circ}03'N$, $175^{\circ}18'E$) (Fig. 9, Table 4). Two Canadian fish from the Nitinat Hatchery were detected in the eastern North Pacific Ocean (Fig. 9).

DISCUSSION

The present GSI study clearly indicated the stock-specific distribution, migration and abundance of maturing and immature chum salmon in the Bering Sea and North Pacific Ocean. Their distribution and migration patterns in the ocean were variable among eleven regional stocks in Asia and North America. Past long-term high-seas tagging experiments have been useful in designating the major ocean distributions of maturing chum salmon (e.g. Yonemori 1975; Neave et al. 1976; Ogura 1994; Myers et al. 1996), however, distributional information for immature fish is sparse due to the limited recoveries of tagged fish over the years. The recent mass otolith marking programs provide a good opportunity to identify the distribution and abundance of hatchery

chum salmon in the ocean. For example, the total number of tagging recoveries for immature chum salmon originating from central and southeast Alaska was only 19 fish over 40 years (1956–1995; Myers et al. 1996), whereas 57 immature chum salmon originating from hatcheries in PWS and southeast Alaska were recovered in the open ocean during the single summer and fall period of 2003.

Ocean Distribution and Migration of Japanese Stocks

Past tagging recoveries suggested that Japanese immature chum salmon were distributed along the Aleutian Islands in the North Pacific Ocean during July and August (Yonemori 1975; Neave et al. 1976). However, our GSI study clearly indicated that Japanese immature fish were widely distributed in the Bering Sea during the summer and fall, while a considerable number of fish appeared in the eastern North Pacific Ocean in the early summer (late June and July). On the other hand, most Japanese maturing fish were already present in the central and western waters of the Bering Sea in the early summer, and had disappeared by late summer. Japanese chum salmon inhabit the western North Pacific Ocean during the first winter and the central Gulf of Alaska during the following winters (Urawa and Ueno 1997; Urawa 2000, 2004). Genetic monitoring surveys in salmon fisheries in the Unimak and Shumagin islands (near Unimak Pass in the eastern Aleutian Islands) indicated that the component of Japanese chum salmon stocks increased between mid June and mid July with a peak in late June (Crane and Seeb 2000; Seeb et al. 2004). Young fish (age 0.1) of Japanese origin also migrate from the western North Pacific Ocean into the Bering Sea in the summer (Urawa et al. 1998, 2001). Nagasawa and Azumaya (2009) also reported that age 0.1 chum salmon stayed in the North Pacific Ocean at $5\text{--}10^{\circ}\text{C}$ in June and appeared in the Bering Sea in July. Our results as well as other known information suggest that Japanese maturing chum salmon move from the Gulf of Alaska into the Bering Sea mainly in June, and are followed by immature fish in late June and July.

The ocean distribution of immature chum salmon is affected by water temperatures (Azumaya et al. 2007; Fukuwaka et al. 2007). It is not known exactly how long immature chum salmon stay in the Bering Sea to feed, but sea surface temperature (SST) data suggest that they may migrate out of the Bering Sea to their winter habitat in the Gulf of Alaska by late November when SST decrease to less than 4°C . During the winter period, chum salmon prefer water temperatures between 4°C and 6°C (Ueno et al. 1997). The habitat in this temperature range is more widely available in the Gulf of Alaska than in the western waters of the North Pacific Ocean (Neave et al. 1976; Urawa 2000). For Japanese chum salmon overwintering in the Gulf of Alaska, the shortest homing migration route is through the Bering Sea. In addition, the Bering Sea is one of most productive ecosystems in the world, and provides favorable feeding habitats

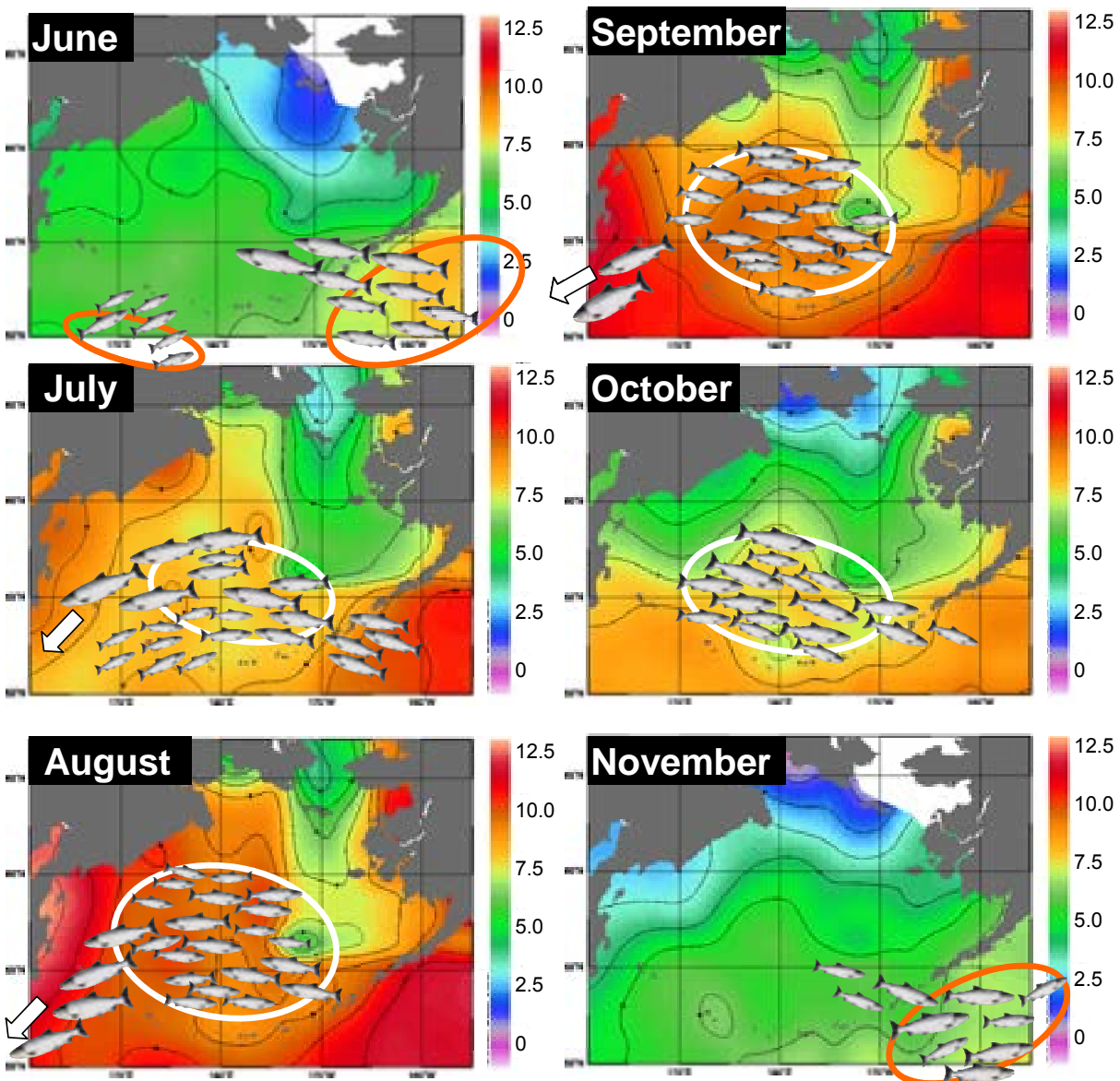


Fig. 10. Estimated migration pattern of Japanese chum salmon in the Bering Sea and North Pacific Ocean with the 10-year average of sea surface temperatures ($^{\circ}\text{C}$; http://www.emc.ncep.noaa.gov/research/cmb/sst_analysis/). Orange and white circles indicate the estimated major ocean distributions of Japanese chum salmon during winter and summer/fall, respectively (Urawa 2000, 2004).

for salmon during summer and fall.

In the western Bering Sea within the Russian EEZ, Russian chum salmon were the predominant stocks (over 60%) in May and June, while the percentage of Japanese stocks increased from several percent in May to 60% in August (Seeb et al. 2004). This GSI estimate as well as past tagging experiments (Yonemori 1975; Neave et al. 1976; Ogura 1994; Myers et al. 1996) indicates that Japanese maturing chum salmon migrate in the waters off the Kamchatka Peninsula and the Kuril Islands between July and September, heading southwest to northern Japan where mature salmon runs occur between September and December.

A total of 23 otolith-marked chum salmon released from four Japanese hatcheries in Hokkaido were recovered in this

study, and most of those fish were found in the Bering Sea. Sato et al. (2009b) also recorded many otolith marked chum salmon in the Bering Sea ($n = 177$) and North Pacific Ocean ($n = 13$) during the spring and summer of 2006 and 2007, most (90%) of which were of Japanese origin. Those otolith mark recoveries support the ocean distribution of Japanese chum salmon estimated by GSI analysis.

The estimated seasonal migration patterns of Japanese chum salmon in the Bering Sea and North Pacific Ocean are summarized in Fig. 10 along with 10-year averages of SST. After overwintering, maturing chum salmon in the Gulf of Alaska migrate into the Bering Sea during June, followed by young fish (age 0.1) from the western North Pacific Ocean and by immature fish from the Gulf of Alaska. Maturing fish

migrate out of the Bering Sea by August, while immature fish remain in the Bering Sea to feed. In late October or November when the water temperature decreases in the Bering Sea, immature fish move southeast to the Gulf of Alaska. They migrate between summer feeding grounds in the Bering Sea and winter habitat in the Gulf of Alaska until they return to spawn along the shortest migration route through the Bering Sea.

Ocean Distribution of Russian Stocks

Our GSI analysis suggested that Russian immature chum salmon were abundantly distributed in the Bering Sea similar to the Japanese stocks, but their distribution also spread into the adjacent North Pacific Ocean. Most of the Russian chum salmon in the Bering Sea and North Pacific Ocean were of north Russian (north Okhotsk coast, Kamchatka and Anadyr) origin. Sakhalin immature chum salmon were mainly distributed in the central and southern Bering Sea. Other Russian stocks (Amur River and Premorye) may not be abundant in the Bering Sea. Tagging recoveries (Myers et al. 1996) suggested that immature chum salmon from the Amur River and Sakhalin were mainly present in the western North Pacific Ocean, and immature fish from North Okhotsk coast and Kamchatka were distributed in both the Bering Sea and North Pacific Ocean. Russian immature chum salmon inhabit the central North Pacific Ocean during winter (Urawa and Ueno 1997).

Our study indicated that northern Russian maturing chum salmon were most abundant in the western Bering Sea in the early summer. Tagging experiments indicated that maturing fish from the eastern Kamchatka and Anadyr regions were distributed in the Bering Sea, while other stocks (Amur River, Prymoyre, Sakhalin, northern Okhotsk and western Kamchatka) appeared mainly in the western North Pacific Ocean between May and July (Neave et al. 1976; Ogura 1994; Myers et al. 1996). Because Russian stocks include summer runs, the timing of spawning runs may limit their oceanic distribution to western waters.

Ocean Distribution of North American Stocks

As suggested by past results (Urawa et al. 2000, 2004), our GSI study indicated that North American stocks were predominant in the Gulf of Alaska, but not in the Bering Sea. It is noteworthy that young chum salmon from the Yukon River fall runs appeared at the southern margin (50°N) of our survey areas in the eastern North Pacific Ocean and Gulf of Alaska. Northwest Alaska summer runs also appeared in the same area as well as in the Bering Sea. Other GSI studies estimated that the contribution of northwest Alaska stocks among immature chum salmon in the Gulf of Alaska was 15% in summer 1998 (Urawa et al. 2000), 11–14% (ages 0.2–0.4 only) in January 1996 (Urawa et al. 1997), and 3–16% in February 2006 (Beacham et al. 2009). Most tagged

immature chum salmon recovered in northwest Alaska were released in the Gulf of Alaska and around the eastern Aleutian Islands, whereas tagged maturing fish were released in both the Gulf of Alaska and the Bering Sea (Neave et al. 1976; Myers et al. 1996). Thus it may be that young chum salmon migrate from the northwest Alaska coast to the Gulf of Alaska for overwintering, and considerable numbers of fish remain there until maturing, unlike Japanese stocks that migrate seasonally between the Gulf of Alaska and Bering Sea.

Our study confirmed that immature chum salmon from the Alaska Peninsula/Kodiak Island region were widely distributed in the Bering Sea and North Pacific Ocean (east of 175°E), although the tagging recoveries indicated a limited distribution in the northern Gulf of Alaska and around the Aleutian Islands east of 178°W (Neave et al. 1976; Myers et al. 1996).

The ocean distribution of PWS chum salmon was not clear in our GSI study, because of the low abundance of PWS stocks in the survey areas. However, a large number of otolith-marked chum salmon released from the Wally Noerenberg Hatchery (WNH) located in PWS were found in the open ocean. This hatchery annually releases approximately 75–100 million chum salmon fry with otolith marks. According to our recovery records, WNH immature chum salmon were mainly distributed in the Gulf of Alaska and eastern North Pacific Ocean, and some were present in the eastern and southern Bering Sea (east of 175°W).

Both our GSI and otolith mark recoveries indicated that SEAK/North BC immature stocks were widely distributed throughout the northern waters of the Gulf of Alaska and eastern North Pacific Ocean, and the southern Bering Sea. South BC/Washington stocks shared a similar ocean distribution with SEAK/North BC stocks, but they were also distributed in the central Bering Sea. In the Bering Sea, there were few records of tagging recovery for immature and maturing chum salmon originating from central and southeast Alaska, BC and Washington (Myers et al. 1996). Compared with the past tagging recovery records, the present GSI and otolith mark recoveries suggest a wider ocean distribution of chum salmon stocks originating along the Gulf of Alaska and northwest coast of North America than previously acknowledged.

CONCLUSIONS

Our study using genetic and otolith marks provides new information on stock-specific ocean distribution of chum salmon originating from Asia and North America. The distribution patterns apparently differ among regional stocks. Japanese and north Russian chum salmon are predominant in the Bering Sea during summer and fall. North American stocks are mainly distributed in the Gulf of Alaska and eastern North Pacific Ocean, and some stocks also intermingle in the Bering Sea. Japanese chum salmon have a strong sea-

sonal migration pattern between the Bering Sea (summer/fall) and Gulf of Alaska (winter/spring), responding to sea-water temperatures. The ocean distribution and migration patterns of salmon may be also affected by the abundance of food organisms, interactions within or between species, ocean conditions (salinity, depth, currents, e.g.), and timing and location of spawning as well as winter habitat. Further long-term studies are required to clarify factors affecting the migration and distribution of salmon in the ocean.

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Do Sea Surface Temperatures Influence Catch Rates in the June South Peninsula, Alaska, Salmon Fishery?

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Abstract: The influence of sea surface temperature (SST) on sockeye salmon catch per unit effort (CPUE) for the June south Alaska Peninsula fishery and on the run size of the western Alaska sockeye salmon was investigated for the period 1975–2008. CPUE was positively related to the size of the western Alaska sockeye salmon run but not to SST over the pooled time period. Time-stratified analysis before and after 1994/1993 revealed significant negative relations between the June fishery CPUE and winter and spring SST in the area to the east of the fishery. There were positive relations between the size of the western Alaska run and SST for temperature time series in the central Bering Sea, eastern Aleutian Islands, and between Kodiak and the Shumagin islands for one- and two-year lags prior to the adult return. Time-stratified analysis showed that there were significant changes in the influence of temperature on the June fishery CPUE and in the size of the western Alaska run. Combined the results suggest that warming temperatures in the Bering Sea have shifted regions of importance to the west for all ocean ages.

Keywords: sockeye salmon, sea surface temperature, ocean distribution, migration, western Alaska, Bering Sea, Alaska Peninsula, CPUE

INTRODUCTION

During June a coastal net fishery takes place on the Pacific Ocean side of the Alaska Peninsula and eastern Aleutian Islands targeting maturing sockeye salmon (*Oncorhynchus nerka*) with an incidental harvest of maturing chum salmon (Rogers 1986). Annual catches are typically between one and two million sockeye salmon and about one quarter that number for chum salmon (*O. keta*). Tagging studies have identified the majority of the sockeye salmon catch as of Bristol Bay origin (Eggers et al. 1991). Results of genetic stock identification show that the majority of the chum salmon catch is of western Alaska origin with one-quarter to one-third of Asian origin (Seeb and Crane 1999).

Most of the variance in June fishery sockeye salmon catches can be explained by a positive linear relation between catches and the total western Alaska sockeye salmon abundance alone ($P = 5.8 \times 10^{-7}$, $R^2 = 0.55$). Catch per unit effort (CPUE) in the fishery has been highly variable over time but is not closely related to changes in the management of the fishery (Fig. 1). For example, the depth of nets allowed in the fishery was reduced and restricted for the first time in 1990 following the year with the highest CPUE on record. Following modest CPUE in 1990 and 1991, the sockeye salmon CPUE in 1992 and 1993 were the third and fourth highest on record. Since 1994 the average June south Peninsula fishery sockeye salmon CPUE has dropped by about 30% while western Alaska sockeye salmon abundance has been above average. Years such as 1996 with near record re-

turns of sockeye salmon to Bristol Bay but unexpectedly low CPUE in the June fishery have prompted speculation that the availability of salmon to the fishery is influenced by environmental conditions along the migratory path of salmon at sea (Poetter 2009).

The freshwater reproductive and early life history of salmon is relatively attractive for study, but salmon populations experience most of their mortality at sea (Groot and Margolis 1991). Variability in marine survival is thus closely related to the abundance of returns. There has been considerable work aimed at understanding the influence of climatic variables such as sea surface temperature (SST) on growth, distribution and production of salmon (Beamish and Boullion 1992; Francis and Hare 1994; Adkison et al. 1996). These studies have focused on large-scale effects frequently related to the regime shift in about 1977 that marked the beginning of the present period of high production. Both Rogers (1987) and Isakov et al. (2000) studied the effects of temperature on growth of Bristol Bay sockeye salmon and found the greatest effects in the early marine life history stages. Francis and Hare (1994) have shown that the abundance of western Alaska sockeye salmon adult returns is correlated with winter temperatures on Kodiak Island two years prior. Welch et al. (1995, 1998) have shown that salmon distributions at sea have sharp thermal limits that vary by area during different months of the year.

Nagasawa et al. (2005) found a strong positive relation between sea surface temperature trends along the dateline in the Bering Sea in July and trends in CPUE of immature

sockeye and chum salmon in Bering Sea research gillnet surveys ($P = 8.15 \times 10^{-7}$, $R^2 = 0.586$). Greater abundance of immature fish with warmer temperatures would be consistent with a greater proportion of western Alaska sockeye salmon using a larger area in the Bering Sea for a longer period in the summer. This would correspond to a reduced distribution in the North Pacific during the following winter and spring. Perry et al. (2005) relate distribution shifts for marine fishes to SST changes in the North Sea using CPUE data and suggest “profound impacts on commercial fisheries through continued shifts in distribution and alteration of community interactions”. They also found that species with rapid generational turnover were more likely to show changes in marine distribution.

Because the June fishery is restricted to a relatively small nearshore area, changes in the migratory path of maturing salmon could have a large impact on availability to the fishery. Thus previous research suggests that SST might influence June CPUE both via changes in western Alaska sockeye salmon abundance and changes in ocean distribution and migration patterns (Beamish and Bouillon 1993; Francis and Hare 1994; Welch et al. 1995, 1998; Nagasawa et al. 2005; Perry et al. 2005). For example, later departure from the Bering Sea after summer feeding would limit the extent of eastward migration in the Subarctic Current in the winter. Reduced eastward distribution in winter would result in a westward migration farther offshore in the Alaskan Stream in spring with lower availability to the June fishery. The purpose of this study is to evaluate the potential importance of SST at specific ocean areas and times on the June fishery CPUE and to determine whether the importance of those locations has changed in concert with changes in the June fishery CPUE.

First I hypothesize that the June fishery CPUE is positively related to western Alaska sockeye salmon abundance and to SST in five regions of the North Pacific and Bering Sea from 1975–2008 and that there are significant changes

in those relations before and after 1994/1993. Second, I hypothesize that the abundance of western Alaska sockeye salmon has been positively related to SST in those five regions from 1975–2008 and that those relations also changed before and after 1994/1993.

MATERIALS AND METHODS

Sea Surface Temperature

Five locations were chosen to evaluate the influence of temperature by region on the June south Peninsula fishery catch rates (Fig. 2). T. Nagasawa (nagasat@affrc.go.jp, unpublished data) provided time series of SST for the Bering Sea and for an area near the eastern Aleutian Islands which includes the location of the June south Peninsula fishery. He has identified these areas as particularly important for immature sockeye salmon at sea. A Kodiak winter air temperature time series was constructed from the Alaska Climate Research Center (<http://climate.gi.alaska.edu/Climate/Location/Time-Series/Data/adqT>) to serve as a surrogate for SST, according to Francis and Hare (1994). An average for each year was computed by averaging the monthly average air temperatures for the period November through March, where March is the identified year. Time series of direct observation of SST are lacking for the winter and spring from the Gulf of Alaska and North Pacific Ocean in the vicinity of the Alaska Peninsula. However a global time series of average monthly SSTs (Smith-Reynolds Optimum Interpolation SSTs) is available for sub-sampling online at the NOAA site (http://nomads.ncdc.noaa.gov/cgi-bin/ncdc-ui/define-collection.pl?model_sys=sst&model_name=ersst&grid_name=999). For the Gulf of Alaska area between 55°N–60°N, 140°W–150°W, I extracted the minimum monthly average SST for each year, usually occurring in February or March in order to test whether the degree of extreme cold might keep fish

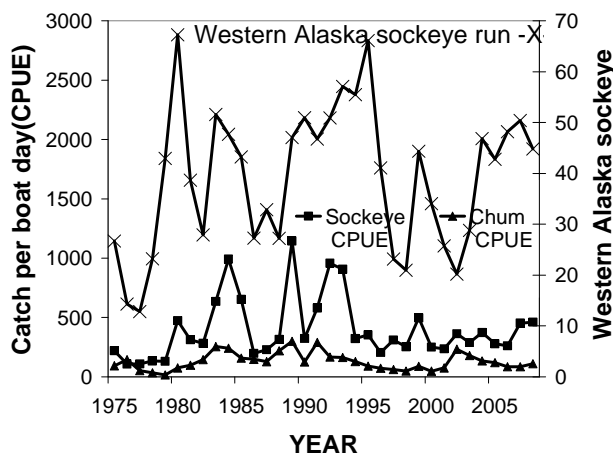
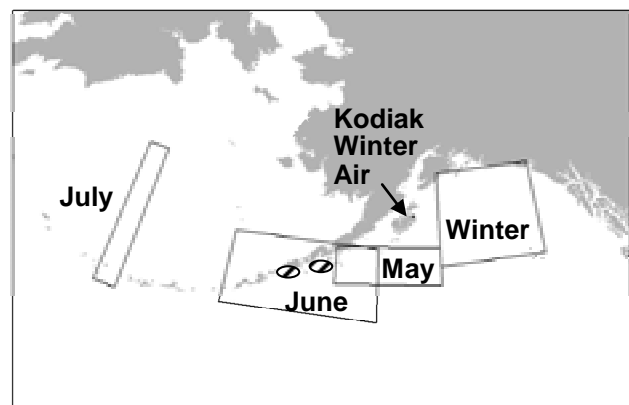


Fig. 1. Western Alaska sockeye run size and June south Peninsula fishery catch per boat per day for sockeye and chum salmon, 1975–2008.



○ - Locations of June South Peninsula Fishery
 □ - Boundaries of Sea Surface Temperature Areas

Fig. 2. Location of the June south Peninsula fishery and areas of temperature time series.

farther offshore. For the area offshore and between Kodiak and the Shumagin islands bounded by 54°N–56°N, 150°W–160°W, I extracted the May average SST. Maturing adult salmon migrate through this area in the period immediately preceding the fishery. The four time series of SST and one SST surrogate are shown in Table 1.

Catch per Unit Effort

Catch and effort information for the June south Penin-

sula fishery were obtained from the Alaska Department of Fish and Game (ADF&G) (Poetter 2009). The abundance of the western Alaska sockeye salmon run was computed from ADF&G data files as the sum of catch plus escapement for Chignik, the north Alaska Peninsula and Bristol Bay. Abundance, catch, effort and CPUE data are shown in Table 2.

Catches may not be simply dependent on availability of sockeye salmon during June along the south Peninsula. Throughout most of the period of this study, 1975–2008, fishing time in the June fishery was regulated based on fore-

Table 1. Temperature by time and area for the North Pacific Ocean and Bering Sea.

Year	July Bering Sea ¹	June Eastern Aleutian ¹	May Kodiak-Shumagin ²	Kodiak winter Air ³	Gulf winter monthly minimum ²
1972	7.28	5.22	5.06	-2.51	2.87
1973	7.03	5.53	5.09	-1.78	4.06
1974	8.10	6.21	5.62	-1.29	3.83
1975	6.63	5.23	4.84	-2.53	4.53
1976	6.85	5.65	4.85	-2.42	4.07
1977	7.95	7.13	5.59	1.68	5.46
1978	7.43	6.55	5.84	0.23	4.77
1979	7.55	7.39	5.88	1.97	4.47
1980	7.98	6.29	5.35	0.63	4.29
1981	8.58	7.69	6.38	1.99	4.84
1982	6.85	5.96	4.96	0.42	4.07
1983	7.60	7.31	6.19	2.41	4.79
1984	8.10	7.73	6.05	1.43	5.28
1985	7.30	5.91	5.12	1.62	4.77
1986	7.95	6.24	5.64	0.58	4.84
1987	7.20	6.34	5.64	1.92	5.12
1988	7.55	6.63	5.39	0.28	4.91
1989	7.78	6.15	5.70	-1.03	3.70
1990	8.20	6.79	6.22	-0.50	3.99
1991	7.80	6.56	5.56	-0.83	4.34
1992	6.98	7.23	5.97	0.09	4.88
1993	7.73	7.19	6.35	-0.14	4.29
1994	7.50	6.96	5.79	0.83	4.94
1995	7.88	6.40	6.00	-0.90	4.47
1996	8.43	6.97	6.45	0.39	4.42
1997	8.35	7.83	6.18	0.34	4.54
1998	8.03	6.73	5.92	0.56	5.42
1999	7.15	5.92	4.78	-2.14	4.29
2000	8.05	6.69	5.75	-0.97	4.19
2001	7.15	7.13	5.99	1.46	5.11
2002	8.03	6.89	5.78	-0.88	4.17
2003	8.25	6.97	6.27	1.83	5.80
2004	8.10	6.99	6.27	-0.31	4.86
2005	7.91	NA ⁴	7.11	1.33	5.14
2006	7.24	NA	5.65	-0.98	4.40
2007	7.30	NA	5.09	-2.77	3.77
2008	7.44	NA	4.68	-0.87	4.21

¹Provided from T. Nagasawa

²NOAA NCEP Smith-Reynolds Optimum Interpolation SST

³Alaska Climate Research Center average of monthly values

⁴Data not available

Table 2. Effort, catch and CPUE for the June south Alaska Peninsula fishery and total western Alaska sockeye salmon abundance.

Year	Days fished	Units of gear	Gear days	Sockeye catch (x 1000)	Sockeye CPUE	Chum catch (x 1000)	Chum CPUE	Western Alaska sockeye run (millions)*
1975	10	109	1,090	240	220	101	93	26.7
1976	19	149	2,831	305	108	410	145	14.3
1977	17	131	2,227	242	109	116	52	12.8
1978	23	159	3,657	487	133	122	33	23.2
1979	33	198	6,534	851	130	104	16	42.9
1980	30	226	6,780	3,206	473	509	75	67.3
1981	24	243	5,832	1,821	312	564	97	38.6
1982	30	251	7,530	2,119	281	1,095	145	27.9
1983	11	281	3,091	1,964	635	786	254	51.6
1984	5	280	1,400	1,388	991	337	241	47.7
1985	9	305	2,745	1,791	652	434	158	43.3
1986	8	298	2,384	471	198	352	148	27.3
1987	12	290	3,480	794	228	443	127	32.8
1988	8	301	2,408	757	314	527	219	27.2
1989	5	305	1,525	1,745	1,144	455	298	47.1
1990	13	321	4,173	1,345	322	519	124	51.0
1991	8	334	2,672	1,549	580	773	289	46.8
1992	8	321	2,568	2,458	957	426	166	50.9
1993	10	328	3,280	2,974	907	532	162	57.1
1994	14	324	4,536	1,461	322	582	128	55.5
1995	18	331	5,958	2,105	353	537	90	66.1
1996	16	313	5,008	1,029	205	360	72	41.1
1997	18	292	5,256	1,628	310	322	61	23.1
1998	18	283	5,094	1,289	253	246	48	21.0
1999	10	277	2,770	1,375	496	245	88	44.4
2000	18	278	5,004	1,251	250	239	48	34.0
2001	5	128	640	151	236	48	75	25.7
2002	9	181	1,629	591	363	379	233	20.2
2003	9	177	1,593	453	288	282	179	28.8
2004	19	190	3,610	1,348	373	482	134	46.8
2005	19	190	3,610	1,004	278	428	119	42.8
2006	19	188	3,572	932	261	300	84	48.2
2007	19	185	3,515	1,590	452	298	85	50.4
2008	19	196	3,724	1,714	460	411	110	44.8

* Catch plus escapement for Chignik, north Alaska Peninsula and Bristol Bay.

casts of abundance of Bristol Bay sockeye salmon. Effort, measured as the product of the total number of days the fishery was open and the total number of vessels fishing during the month, varied over a wide range as the result of management measures and variable participation by fishermen. Adding effort as an independent variable in step-wise multiple regression only results in a small change in the amount of variance explained in the relation between June fishery catches and total western Alaska sockeye salmon abundance ($P = 2.15 \times 10^{-7}$, $R^2 = 0.63$ vs. $P = 5.8 \times 10^{-7}$, $R^2 = 0.55$). Because management measures had a relatively small effect on catches, CPUE should be a measure of the availability

of salmon to the June fishery. The time series of CPUE for sockeye salmon and the CPUE for chum salmon have a significant linear positive relation ($P = 4.4 \times 10^{-5}$, $R^2 = 0.42$). However, total abundance data are only available for sockeye salmon, so the balance of the analysis was restricted to sockeye salmon.

Regressions

Regressions and step-wise multiple regressions were performed between time series of annual June south Peninsula fishery CPUE, the abundance of the western Alaska

sockeye salmon run, and five SST time series for the areas in Fig. 2 for the same year and for lags in temperature preceding the catch by 1, 2, and 3 years. Adult returns in a single year incorporate several ages since out-migration. Rogers (1987) and Isakov et al. (2000) have shown that age since out-migration is most important with respect to the influence of temperature on growth and subsequent survival. This analysis, similar to that of Francis and Hare (1994) but different from Rogers (1987) and Isakov et al. (2000) was conducted from the perspective of year of adult return which results in a dilution of the power of the analysis.

The analysis was performed for all years combined and separately for the periods 1975–1993 and 1994–2008 in order to detect changes that might be associated with the apparent shift in CPUE in the fishery. An important consequence of partitioning the 34-year time series is the reduction in sample size by a factor of two with a consequent reduction in analytical power.

Ryding and Skalski (1999) found a non-linear relation between SST and survival for hatchery released coho salmon

(*O. kisutch*) in Washington State which they evaluated with quadratic regressions and interpreted as reflective of an optimum for survival of salmon in the marine environment. In this study, all linear regressions were evaluated for evidence of such an optimal relation and a quadratic model was fit for the case where it occurred in the Bering Sea.

RESULTS

Time-Pooled Analysis

June CPUE and SST

There were no areas with statistically significant relations between June fishery CPUE and SST over the period 1975–2008.

June CPUE and Western Alaska Run Size

There is a significant positive relation between CPUE in the June fishery and total western Alaska sockeye salmon abundance ($P = 0.001$, $R^2 = 0.284$, $b = 9.9$) over the period

Table 3. Results of regression analysis of sea surface temperature with June south Peninsula sockeye salmon CPUE (A) and with the run size of the western Alaska sockeye salmon (B). Asterisks * and ** indicate $P < 0.05$ and $P < 0.01$, respectively. Bold italic categories reflect a decrease in importance across time-stratified analysis.

A. June south Peninsula sockeye salmon CPUE										
Area	Time-pooled analysis				Time-stratified analysis					
	Lag (years)	P	R ²	b (°C)	1975–1993			1994–2008		
May Kodiak-Shumagin	0	0.760	0.003	25.7	0.137	0.125	244.8	0.002	0.521	-100.8
Kodiak Winter Air	0	0.800	0.002	-8.5	0.964	0.000	-2.6	0.005	0.473	-46.0
May Kodiak-Shumagin + Kodiak Winter Air								<i>P</i>	<i>R²</i>	<i>b</i>
								0.006	0.578	-65.73 -23.18
Western Alaska Sockeye run size	0	<i>0.001**</i>	<i>0.284</i>	<i>9.9</i>	<i>0.002**</i>	<i>0.450</i>	<i>15.2</i>	<i>0.193</i>	<i>0.126</i>	<i>2.3</i>
June south Peninsula CPUE			400			458			327	

B. Western Alaska sockeye salmon run size										
Area	Time-pooled analysis				Time-stratified analysis					
	Lag (years)	P	R ²	b (10 ⁶ /°C)	1975–1993			1994–2008		
July Bering Sea	1	<i>0.009**</i>	<i>0.263</i>	parabolic	0.138	0.129	b (10 ⁶ /°C) parabolic	0.034*	0.430	parabolic
June Eastern Aleutian	1	0.124	0.080	6.6	0.037*	0.231	10.3	<i>0.698</i>	<i>0.016</i>	<i>-4.0</i>
	2	0.017*	0.175	9.3	0.073	0.177	8.7	0.054	0.297	17.3
May Kodiak-Shumagin	1	0.155	0.062	6.7	0.061	0.191	14.2	<i>0.860</i>	<i>0.002</i>	<i>1.2</i>
	2	0.024*	0.150	10.4	0.0498*	0.208	14.6	<i>0.180</i>	<i>0.134</i>	<i>10.0</i>

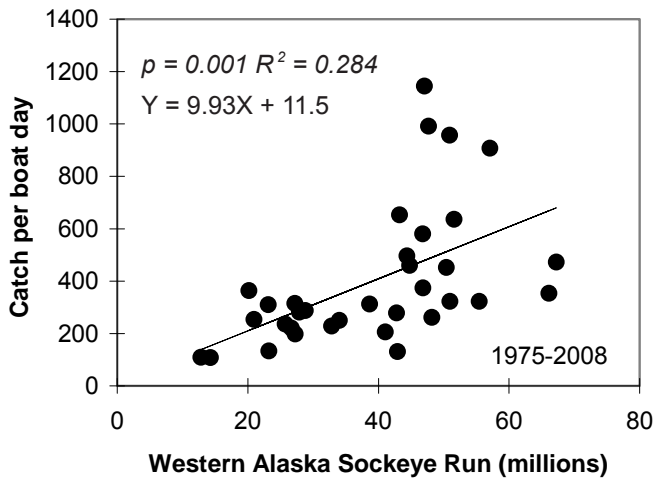


Fig. 3. Relation between June south Peninsula sockeye CPUE and the size of the western Alaska sockeye run, 1975–2008.

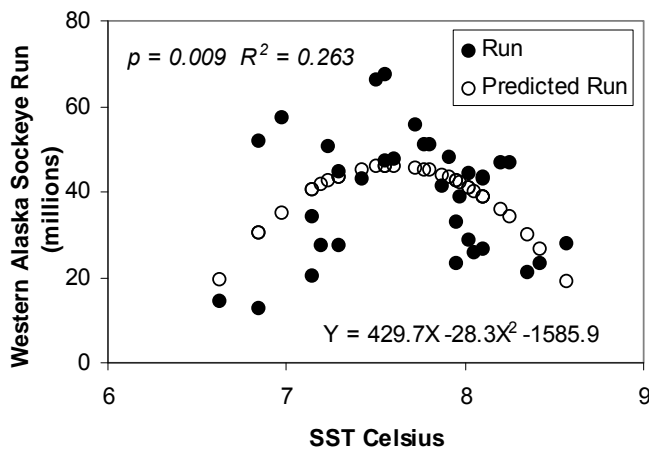


Fig. 4. Relation between western Alaska adult sockeye salmon abundance and previous year July Bering Sea dateline sea surface temperature, 1975–2008.

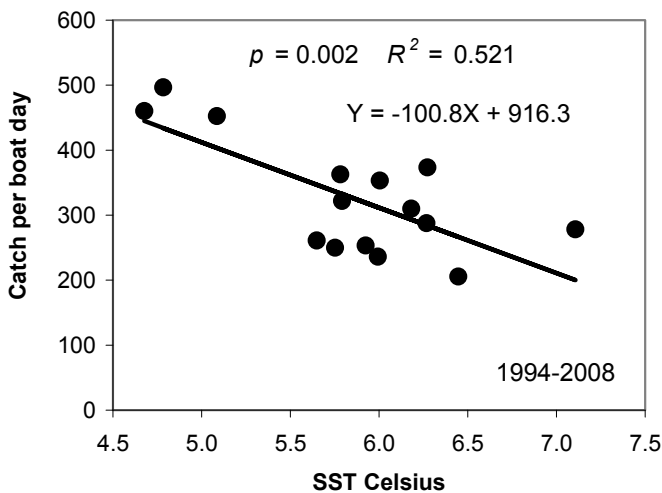


Fig. 5. Relation between June south Peninsula sockeye salmon CPUE and May Kodiak-Shumagin SST 1994–2008.

(Table 3A, Fig. 3). Addition of each of the temperature time series to the abundance of the western Alaska sockeye salmon run size in step-wise multiple regression did not result in significant improvement in the explanatory power with respect to the June fishery CPUE. This was true at lags in temperature with respect to the year of adult returns of one, two and three years.

Western Alaska Run Size and SST

There are significant positive relations between total western Alaska sockeye salmon abundance and July Bering Sea, June eastern Aleutian and May Kodiak-Shumagin SST (Table 3B). A narrow range of July Bering Sea temperatures produced uniformly large returns of sockeye salmon to western Alaska the next year. The temperature range 7.40–7.93°C corresponds to average returns one year later of 52 million, with a minimum return of 41 million fish. Cooler years averaged 29 million and warmer years averaged 34 million adult sockeye salmon returning to western Alaska. While there was no significant relation between the abundance of western Alaska sockeye salmon and a linear model for the previous year July Bering Sea SST, the relation with the parabolic model was significant ($P = 0.009$, $R^2 = 0.263$) for temperatures the summer previous to the adult return (Fig. 4).

Temperatures two years prior to the adult return were positively related to the adult return for both June eastern Aleutian SST ($P = 0.017$, $R^2 = 0.175$, $b = 9.3$ M/°C) and May Kodiak-Shumagin SST ($P = 0.024$, $R^2 = 0.150$, $b = 10.4$ M/°C). One-year lags in temperature ahead of year of adult return did not produce significant results for these same areas over the 1975–2008 time period.

For time-pooled analysis the null hypothesis that there are no significant relations between June fishery CPUE and SST is not rejected ($P < 0.05$) but the null hypothesis of no significant relation between June CPUE and the size of the western Alaska sockeye salmon run is rejected ($P < 0.01$).

Time-Stratified Analysis

June CPUE and SST

The only significant relations between June south Peninsula sockeye salmon CPUE and SST occur for the period 1994–2008 for May Kodiak-Shumagin ($P = 0.002$, $R^2 = 0.521$, $b = -100.8$) and Kodiak winter air temperature ($P = 0.005$, $R^2 = 0.473$, $b = -46.0$) (Table 3A, Fig. 5). Cooler winter and spring temperatures to the east of the fishery are related to higher CPUE in June.

June CPUE and Western Alaska Run Size

The significant positive relation from 1975–2008 between June fishery CPUE and the size of the western Alaska run is split before and after 1994/1993 with a significant relation for the early period ($P = 0.002$, $R^2 = 0.450$, $b = 15.2$) but not for the late ($P = 0.193$, $R^2 = 0.126$, $b = 2.3$). In step-wise multiple regressions for the period 1994–2008 the size

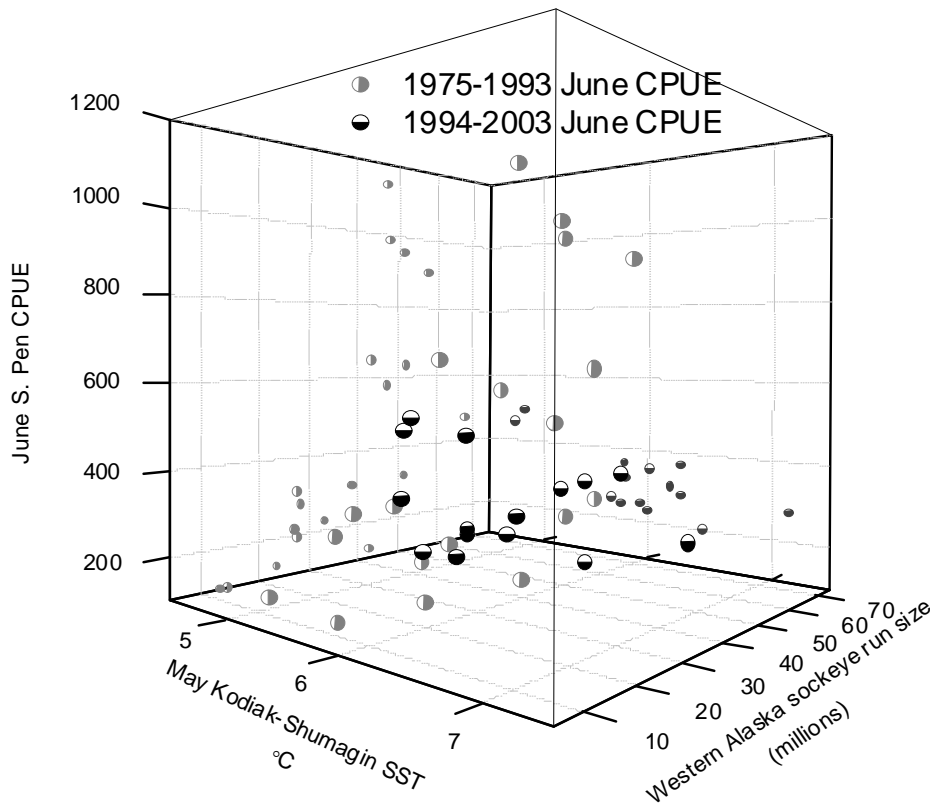


Fig. 6. The combined effect of May Kodiak-Shumagin SST and the size of the western Alaska sockeye salmon run on June south Peninsula sockeye CPUE for time-stratified analysis. Small grey symbols on the CPUE/western Alaska run size plane and small black symbols on the CPUE/May Kodiak-Shumagin SST plane show the shift of dominant influence on June CPUE from the size of the western Alaska sockeye salmon run for 1975–1993 ($P = 0.002$, $R^2 = 0.450$) to the May Kodiak-Shumagin SST from 1994–2008 ($P = 0.002$, $R^2 = 0.521$). See Figs. 3 and 5.

of the western Alaska sockeye salmon run adds only a little explanatory power with respect to the June fishery CPUE compared to those of each of May Kodiak-Shumagin and Kodiak winter air temperature time series alone.

The combined effects of temperature and the size of the western Alaska sockeye salmon on the June south Peninsula sockeye salmon CPUE over the period 1975–2008 appear to have been dominated by the positive relation with size of the western Alaska sockeye salmon run, but since 1994 temperatures immediately to the east of the fishery have had a significant effect. The combined effects of different dominant influences on June CPUE before and after 1994/1993 are shown in a composite 3D view of June CPUE against western Alaska run size and May Kodiak-Shumagin SST with the respective 2D linear relations shown in the background (Fig. 6).

Western Alaska Run Size and SST

For immature sockeye salmon (one-year lag) the area of greatest influence on the size of the adult return in the early period was the June eastern Aleutian Islands ($P = 0.037$, $R^2 = 0.231$, $b = 10.3$), while in the later period the region of greatest importance had shifted to the central Bering Sea ($P = 0.034$, $R^2 = 0.430$) with very little influence of temperature in the June eastern Aleutian and May Kodiak-Shumagin ar-

ea ($P = 0.698$, $R^2 = 0.016$, $b = -4.0$; $P = 0.860$, $R^2 = 0.002$, $b = 1.2$, respectively). The influence of a narrow range of temperatures in the central Bering Sea on the size of the western Alaska sockeye salmon run increased from the early period (Table 3B, Fig. 7). For juvenile sockeye salmon (two-year

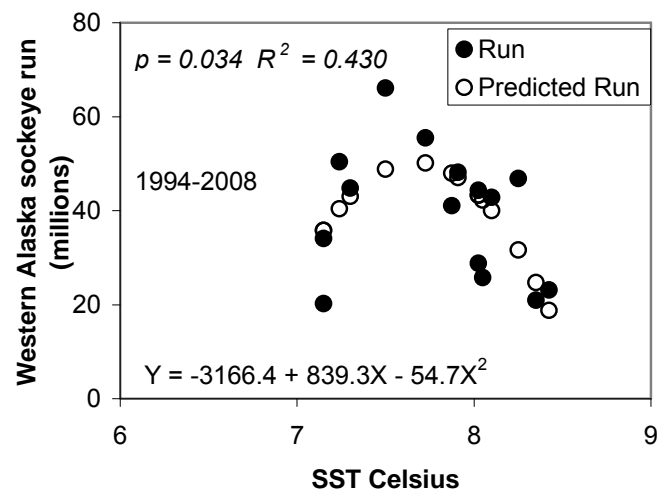


Fig. 7. Relation between western Alaska adult sockeye salmon abundance and previous July Bering Sea dateline sea surface temperature, 1994–2008.

lag) the greatest decline in area of importance was for the May Kodiak-Shumagin which had been more important than the June eastern Aleutians in the early period but became less important in the later period. For juvenile sockeye salmon the June eastern Aleutians area has become somewhat more important in the recent period ($P = 0.054$, $R^2 = 0.297$, $b = 17.3$).

For time-stratified analysis, the null hypothesis that there are no changes in significance of relations across the time strata for the influence of SST on June CPUE is rejected for two of the five areas examined ($P < 0.01$). Kodiak-Shumagin May SST and Kodiak winter air temperatures both have had a significant negative relation with June CPUE since 1994 but not before. The null hypothesis of no change in significance for the influence of the size of the western Alaska sockeye salmon run on June CPUE is also rejected ($P < 0.01$). The positive relation of western Alaska sockeye salmon on June CPUE from 1975–1993 is not significant for the later period.

The null hypothesis that there are no changes in the significance of relations across the time strata for the influence of SST on the size of the western Alaska sockeye salmon run is also rejected ($P < 0.05$). For one year of lag between SST and abundance, the Bering Sea became more important and the eastern Aleutians area became less important after 1993. For two years of lag of SST to adult run size, the Kodiak-Shumagin area became less important after 1993.

DISCUSSION

There is a clear pattern of decreasing influence of temperature on western Alaska sockeye salmon run size for most maturity stages of sockeye salmon in areas to the east of the Bering Sea, and an increase in the influence of temperature in the central Bering Sea with time. For maturing sockeye salmon, June south Peninsula CPUE was positively correlated with the abundance of the western Alaska sockeye salmon run before 1994 ($P = 0.002$, $R^2 = 0.450$, $b = 15.2/M$ run) but not after.

If the abundance of maturing adults is primarily driven by marine mortality then juvenile sockeye salmon appear to be about 50% more sensitive to temperature than immature sockeye salmon for the time-pooled analysis (b_2/b_1 ; $(9.3 + 10.4)/(6.6 + 6.7) = 1.48$). For the 1975–1993 period in time-stratified analysis the influence of temperature by age is not apparent, but for the combined maturity stages temperatures in May to the east of the Shumagin Islands were about 50% more important than temperatures in June to the west of the Shumagins for survival to adult maturity. Apparently at sea younger western Alaska sockeye salmon initially utilized waters offshore of the eastern Aleutian Islands, Alaska Peninsula, Kodiak, and the Shumagin Islands and only as immatures relied significantly on waters of the Bering Sea (Table 3B).

Time-stratified analysis by maturity stage in the eastern Aleutians and Kodiak-Shumagin areas shows that the in-

fluence of temperature on the survival of immature fish to adult maturity virtually vanished for the 1994–2008 period which suggests that there was a reduction in use of these areas during the later period. In contrast, the effect of temperature on immature sockeye salmon survival to adult maturity increased in the central Bering Sea between the early and late periods in time-stratified analysis. These apparent shifts in use are probably a combination of changes in both the seasonality of use and annual use. The selection of the May–June time period was intended primarily to address the adult maturity stage with respect to the June south Peninsula fishery, and analysis of other seasons might produce different results for younger maturity stages.

Earlier work by Francis and Hare (1994), Rogers (1987), and Isakov et al. (2000) found evidence for the importance of Gulf of Alaska temperatures for growth and survival of juvenile sockeye salmon. Both studies relate the influence of temperature to possible ocean distribution early in marine life. The later period in the time-stratified analysis of this study continues well after the years of the earlier studies, and it appears that shifts in areas of influence and implied shifts in migration patterns have occurred. Temporal-spatial shifts in oceanic habitat utilization over time are probably normal.

Unlike the studies mentioned above, this analysis included temperatures from the central Bering Sea. It is interesting that a narrow range of SST in the middle of the Bering Sea is correlated with strong production of western Alaska sockeye salmon, probably reflecting an environmental optimum to which these populations are adapted. This effect has been stronger since 1994 than from 1975–1993.

Spatial Considerations

The apparent shifts in area of use for juvenile and immature sockeye salmon are likely to have occurred for maturing fish as well. If the June south Alaska Peninsula fishery location were in a position central to the shoreward distribution of sockeye salmon returning to the Bering Sea then variations in run size should be reflected in a positive relation with the June fishery CPUE. The data show that this was the case before 1994 but not since, which suggests that the fishery takes place at the eastern and shoreward margins of the migration of sockeye salmon toward the Bering Sea.

Warmer temperatures in the Bering Sea likely lead to expansion of the margins of optimal habitat for immature sockeye salmon up to about 7.6°C. Above that temperature the location of the optimal habitat is likely further north, although the areal extent of optimal habitat may start to diminish. Warmer July temperatures also imply a longer duration of suitable habitat in the Bering Sea. The combination of more northerly distributions and longer durations in the Bering Sea must result in shorter durations and less geographic extent for immature sockeye salmon in the North Pacific through the next winter. Apparently the eastward extent of immature sockeye salmon has been reduced enough by ex-

tended use of the Bering Sea to lead to reduced CPUE of maturing salmon in the south Peninsula fishery the following June.

One model which is consistent with the aggregate of these results focuses on the role of the Alaskan Stream in the homeward migration of maturing salmon. The Alaskan Stream may act as a collector and conveyor to the west for salmon across a wide area of the eastern North Pacific Ocean. If photoperiod were the dominant factor over SST on the timing of northward departure from the Alaskan Stream toward the Alaska Peninsula and Aleutian passes into the Bering Sea this would be consistent with the observed stable timing of catches in the June south Peninsula fishery. If SST were the dominant factor in the timing of the initiation of migration northward into the Alaskan Stream then warmer conditions would result in a more westerly distribution within the Alaskan Stream prior to departure toward the Alaska Peninsula and Aleutian passes. This is consistent with the observed lower CPUE in the June fishery in spite of high abundance during the warm period from 1994–2005. Homeward migration may also be more protracted in time and space for warmer years where the onset of migration occurs earlier. The corollary is that the distribution of returning adults in cooler years would be relatively more concentrated in time and space and further to the east which is consistent with the observed higher CPUE in cooler springs. If ocean distributions are far enough to the east of the June fishery, the abundance of western Alaska sockeye salmon could become the dominant factor in the June fishery CPUE instead of nearby spring SST. The interplay of these factors, and doubtless many others, must be variable and subtle.

French and Bakkala (1974) found “Evidence of varying catch rates of Bristol Bay sockeye salmon by the Japanese mothership fishery west of longitude 175°W (rates have varied between years from 2.2 to 35.2% of the total run) suggests that the distribution of maturing sockeye salmon shifts to the east in fall and winter and that the magnitude and extent of this movement governs the availability of sockeye salmon to the Japanese fishing fleet.” This variability is remarkably similar to the results for the June fishery CPUE, with the difference that the June fishery harvest rate on Bristol Bay stocks is much smaller (ave. ~3%, range 2–8%). It seems likely that variations in east-west distribution would have reciprocal influence on catch rates in each fishery and that SST is a major factor contributing to variations in the east-west distributions.

Changes in Temperature Trends

The influence of temperatures from the years 2006–2008 on trends in the time series is significant. All three of the time series west of Kodiak had significant warming trends from 1975–2005 but the addition of the last three years of data has diminished the significance those trends. Data are not available for the June eastern Aleutian SST time series

since 2004, but cooling for the July Bering Sea dateline and May Kodiak-Shumagin time series since 2005 has decreased the slope of the those temperature relations since 1975 by a factor of two in just three years (decreased R^2 by a factor of three and increased $P > 0.05$). If warming SSTs account for the reductions in the June fishery CPUE since 1994 it will be interesting to see if cooling will reverse that effect. June fishery CPUE increased in 2007 and 2008, which were the coldest and seventh coldest temperatures for the May Kodiak-Shumagin area in the 34-year analysis period. Temperatures from the years 2006–2008 for July Bering Sea on the dateline were in the cooler half of the 34-year temperature range but not at the coldest end of that range.

CONCLUSIONS

A variety of management measures were implemented for the June south Peninsula fishery throughout the period of this study and while those measures are certain to have produced variations in CPUE it is notable that environmental factors are still apparent in the relation between CPUE and SST. One interpretation of these results is that there may be a geographic cline from east to west for the importance of environmental factors on all stages of marine life for western Alaska sockeye salmon and that there may have been a shift to the west for this cline around 1994. The evidence of an optimum temperature in the Bering Sea with respect to adult abundance suggests that the extended period of high western Alaska sockeye salmon production is a consequence of a historically unprecedented period of near-optimal utilization of the Bering Sea.

Implementation of a similar analysis but with the incorporation of ocean age-specific returns as those data become available should further clarify the potential for shifts in regions of importance for the marine survival of sockeye salmon. Sea surface temperature databases performed well relative to the Kodiak winter air time series with respect to effects on juvenile (two-year lag) and immature sockeye salmon.

To the extent that the Alaskan Stream may be an important factor in the migration of maturing salmon south of the Alaska Peninsula and Aleutian Islands, some means to measure and understand its movement is needed. Finer spatial resolution for measurement of SST from satellite observations might be enough to provide some insight into variations in the position of the Stream and the consequences for CPUE of nearshore fisheries. Salinity is also important for salmon migration (Fujii 1975) and it should not be neglected in spite of the difficulty in measuring it remotely.

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Changes in Size and Growth of Anadyr Chum Salmon (*Oncorhynchus keta*) from 1962–2007

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Abstract: Annual changes in body size and growth of Anadyr chum salmon (ages 0.3 and 0.4) in 1962–2007 were studied. Regression analysis showed that the fork length and weight of Anadyr chum salmon significantly decreased from the 1960s to the 2000s. Mean body length of Anadyr chum salmon was highest in 1972 and 1979, and lowest in 1991 and 1994. The most pronounced decrease in chum salmon body size occurred from the early 1980s to the mid 1990s. In 1962–1980 and 1997–2007, mean fork length and weight remained relatively stable. The first-year growth of Anadyr chum salmon, estimated from intersclerite distances, did not change significantly from 1962 to 2007. Growth reduction began in the second year, and the greatest reduction occurred in the third year. There was a significant negative correlation between annual total catches of Pacific salmon and Anadyr chum salmon fork length, body weight, and growth during the second, third and fourth years. Our results may corroborate the conclusions of other researchers that climatic and oceanic conditions can strongly affect the carrying capacity for Pacific salmon and other fish.

Keywords: chum salmon, Russia, fork length, body weight, growth, scale, Anadyr River

INTRODUCTION

Decreases in Pacific salmon production have been observed in many populations (Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996; Kaeriyama 1998; Volobuev 2000; Kaev 2003; Helle et al. 2007; Kaeriyama et al. 2007; and others). In an analysis of the data on fluctuations in chum salmon (*Oncorhynchus keta*) of Asian and American populations from 1953–1988, Ishida et al. (1993) discovered a reduction in body size, scale radius, and width of the third-year group of 0.4-age fish. Bigler et al. (1996) found that 45 of 47 North Pacific salmon populations, comprising five species from North America and Asia, decreased in mean body size. Based on data from 1960 to 2006, Helle et al. (2007) observed that most American populations of Pacific salmon declined in body weight from the 1970s to the early 1990s and increased in body size after the mid 1990s. It is generally supposed that one of the main causes of these changes is density-dependent growth of Pacific salmon in the ocean.

The present paper discusses the data on inter-annual changes in body length, weight, and growth of Anadyr chum salmon from 1962 to 2007. The availability of long-term data gave us an opportunity to identify the periods characterized by either changeable or relatively stable characteristics.

MATERIALS AND METHODS

This study was based on body-size and scale-measurement data obtained from chum salmon returning to the Anadyr River. Adult chum salmon were sampled annually from 1962–2007, except for 1963, 1967, 1969, 1970 and 2005. Fish samples were collected in the Anadyrskiy estuary using a trap net and from the spawning grounds of the Anadyr River (Fig. 1). We analyzed scales of ages-0.3 and -0.4 chum salmon, which are the dominant age-groups of spawners in the Anadyr River (Putivkin 1999).

A total of 2,930 chum salmon (age 0.3 – 1640, age 0.4 – 1290) was sampled. A similar number of males and females was sampled in each year. Fork length and body weight were measured, and scales were collected. Scales were taken from the chum salmon in the preferred body area, located a few rows above the lateral line and below the posterior insertion of the dorsal fin.

Scale measurements included the length along the long axis, the number and length of annual zones, and intersclerite (intercirculus) distances (Fig. 2). Measurements were performed using the Biosonics Optical Pattern Recognition System (OPRS; BioSonics, Inc., Seattle, Washington, USA). Increments in fork length during each year of marine life were estimated from the measured distances between adja-

cent annuli on the fish scale using a direct proportion between body and scale growth (Pravdin 1966): $L_c/L_i = S_c/S_i$, where L_c and S_c = fork length and scale radius of the captured fish; and L_i and S_i = the same at age i . Annual growth was estimated by intersclerite distances of chum salmon scales.

The inter-annual trends in chum salmon body size and growth (mean \pm 95% confidence interval) were evaluated by simple linear regression analysis: $y = ax + b$, where the independent variable (x) is return year and the dependent variable (y) is either mean body length, weight, or intersclerite distance in that year.

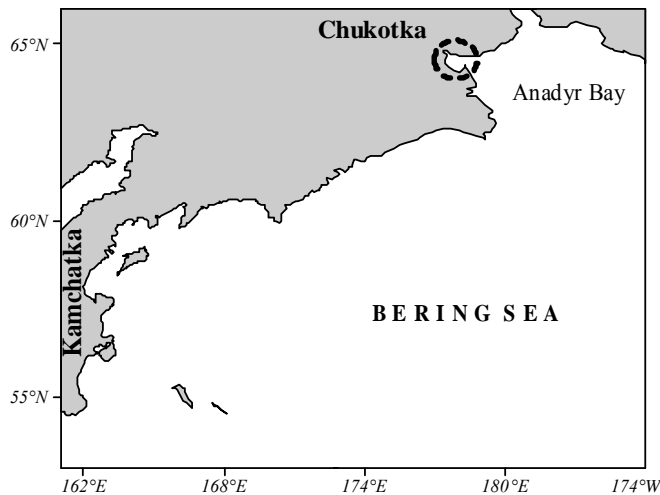


Fig. 1. Map showing the location of our sampling area (Anadyrskiy estuary, Chukotka autonomous Okrug, Far East, Russia).

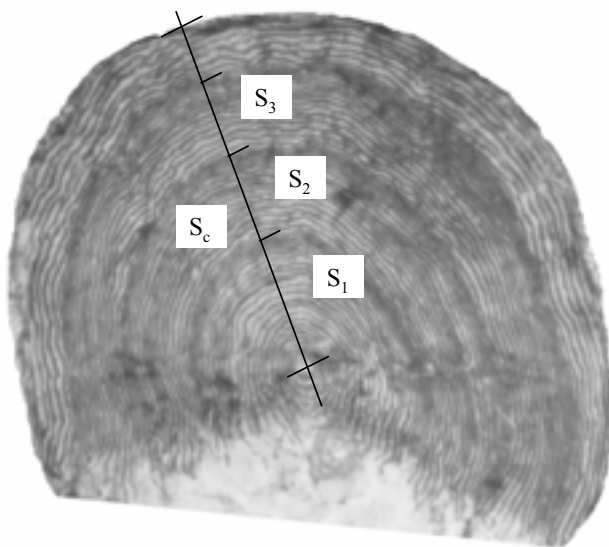


Fig. 2. The scale of an age-0.3 chum salmon collected in August 2003 in the Anadyrskiy estuary, showing the measurement axis (black line) and variables. S_1 – S_3 = scale radius of individual annuli, S_c = radius of the whole scale.

RESULTS

Inter-annual Changes in Body Size

Body size of Anadyr chum salmon decreased from the 1960s to 2000s (Tables 1, 2; Fig. 3). In 1962–1980, mean fork length (weight) was 66.8 ± 1.3 cm (3.7 ± 0.2 kg) for age 0.3 chum salmon and 71.2 ± 1.6 cm (4.5 ± 0.3 kg) for age 0.4 chum salmon. In 1990–2007, chum salmon body size decreased to 61.4 ± 0.8 cm (3.1 ± 0.2 kg) for age 0.3 chum salmon and 64.5 ± 1.1 cm (3.6 ± 0.3 kg) for age 0.4 chum salmon.

Regression analysis showed a significant negative trend in mean body sizes of both 0.3-age and 0.4-age chum salmon from 1962 to 2007 (Fig. 3). However, during these years inter-annual trends in mean body size were variable. From 1962–1980, mean fork lengths of chum salmon did not show any trends, and were relatively stable. A significant decrease in body size began in the early 1980s and continued to the mid 1990s. In 1994–1995, mean fork length of Anadyr chum salmon was the smallest in the study period (approximately 58–59 cm for age 0.3 and 60–61 cm for age 0.4). After 1994–1995, the length and weight of chum salmon increased. However, this trend lasted only for two or three years, and did not reach the levels seen in the 1960s–1970s. In the late 1990s to the mid 2000s, chum salmon body size remained stable. Fork length averaged 62 cm for age 0.3 and 65 cm for age 0.4 fish during this time period.

Inter-annual fluctuations in mean body weights of Anadyr chum salmon were similar to those observed in mean body length. Mean body weight was highest in the 1960s–1970s (~ 3.1 – 4.3 kg for age 0.3 and ~ 3.8 – 5.3 kg for age 0.4 fish) and lowest in the mid 1990s (~ 2.5 – 2.8 kg for age 0.3 and ~ 2.7 – 3.0 kg for age 0.4 fish (Tables 1, 2).

Inter-annual Changes in Growth

First-year growth, estimated from intercirculus distances, did not change significantly from 1962 to 2007 (Fig. 4). There was a positive trend in annual scale growth in the first year, but slope coefficients were low and statistically non-significant (0.3 age fish: 0.04, $p = 0.12$; 0.4 age fish: 0.05, $p = 0.09$). During the second, third, and fourth years at sea, annual scale growth declined significantly from the 1960s through the mid 2000s. Slope coefficients of linear regressions for the second, third and fourth years of growth were, respectively, as follows: -0.07 , -0.19 and -0.18 (Fig. 4).

Annual scale growth of chum salmon during the second, third, and fourth years was greatest during the 1960s and 1970s (Fig. 4). The mean annual growth in length during this period was 18, 14, and 9 cm in the second, third, and fourth years, respectively. The lowest growth of chum salmon occurred in 1994–1995. Annual growth decreased to 16 cm in the second year, 9 cm in the third year, and 7 cm in the fourth year. Thus, the largest decrease occurred in the third year of the chum salmon life cycle.

Table 1. Average fork length (cm), body weight (g), and intercirculus distances (μm) for age-0.3 chum salmon from 1962–2007. CI = confidence interval, N = number of samples.

Year	Length (cm)	95% CI	Weight (g)	95% CI	Intercirculus distance (μm)						N
					1 year	95% CI	2 year	95% CI	3 year	95% CI	
1962	67.5	1.4	3,946	234	47	2	44	1	47	2	42
1964	68.6	1.0	3,989	188	53	3	51	3	53	3	52
1965	64.6	1.2	3,068	200	52	2	43	2	47	2	41
1968	66.9	1.5	3,563	231	47	2	47	2	47	2	28
1971	62.3	1.3	3,308	221	47	2	45	1	45	2	44
1972	70.3	1.1	3,583	204	47	2	47	1	47	2	41
1973	67.3	1.3	3,479	285	49	2	45	2	47	2	24
1974	68.1	1.3	4,238	264	49	1	48	1	49	2	49
1975	65.0	1.1	3,493	228	50	1	44	1	44	2	59
1976	65.0	3.4	3,290	562	46	4	44	9	44	10	4
1977	68.5	0.9	4,070	194	48	1	43	1	42	1	47
1978	67.0	0.9	3,922	181	46	1	46	2	46	2	50
1979	69.6	1.1	4,279	232	44	2	41	2	42	2	49
1980	64.7	1.0	3,713	204	49	2	45	2	43	2	44
1981	66.4	1.5	3,654	336	49	2	44	2	46	2	33
1982	63.6	1.1	3,576	257	50	2	46	1	44	1	48
1983	63.3	0.9	3,722	188	46	1	44	1	46	2	52
1984	62.1	0.9	3,385	196	48	2	43	1	45	2	44
1985	60.5	1.1	3,242	204	49	2	46	1	43	2	48
1986	62.2	1.3	3,375	322	47	2	45	2	47	3	34
1987	63.1	1.0	3,579	195	47	1	44	1	42	2	60
1988	63.2	0.8	3,693	191	46	1	45	1	42	1	56
1989	61.8	1.0	3,234	211	47	1	45	2	47	2	44
1990	61.5	1.1	3,548	227	46	1	44	1	44	2	48
1991	59.1	1.2	2,840	190	48	1	45	1	40	2	47
1992	61.6	1.1	2,767	188	49	1	44	1	42	1	53
1993	61.6	1.1	2,547	191	49	1	43	1	40	2	41
1994	58.1	0.9	2,524	160	50	1	43	1	40	2	44
1995	59.2	2.0	2,786	318	49	2	41	2	37	3	18
1996	61.8	1.1	3,042	182	51	1	42	1	38	2	36
1997	61.7	1.3	3,216	235	49	1	43	1	42	2	41
1998	61.3	1.2	3,019	219	51	1	42	2	39	2	34
1999	61.8	1.7	3,112	275	53	2	42	2	40	2	21
2000	62.2	1.1	3,388	203	50	1	42	1	39	1	46
2001	63.2	1.3	3,414	250	52	1	45	1	46	2	39
2002	63.8	1.4	3,492	249	50	1	44	1	44	1	32
2003	63.0	0.9	3,050	154	50	1	44	1	44	1	40
2004	61.0	1.2	3,076	211	47	1	42	1	41	1	43
2006	61.8	1.3	3,234	227	49	1	45	1	41	2	35
2007	61.2	1.4	3,217	234	50	2	45	1	42	2	29

Table 2. Average fork length (cm), body weight (g), and intercirculus distances (μm) for age-0.4 chum salmon from 1962–2007. CI = confidence interval, N = number of samples.

Year	Length (cm)	95% CI	Weight (g)	95% CI	Intercirculus distance (μm)								N
					1 year	95% CI	2 year	95% CI	3 year	95% CI	4 year	95% CI	
1962	68.7	1.2	4,165	267	47	2	44	2	42	2	44	2	45
1968	72.7	0.9	4,434	193	48	1	47	1	49	2	46	1	63
1972	73.1	1.1	4,092	218	46	1	44	1	44	2	47	2	47
1973	73.9	1.1	4,409	232	48	2	46	1	47	2	45	2	49
1974	71.8	2.5	4,556	585	49	4	48	2	53	7	49	6	10
1976	68.7	3.1	4,194	849	50	6	42	4	39	5	43	4	7
1977	72.6	1.2	4,812	415	44	3	43	3	42	3	43	5	10
1978	70.4	1.1	4,405	245	46	1	43	1	44	2	48	2	48
1979	74.6	1.6	5,298	413	43	1	42	2	41	2	45	3	28
1980	70.3	1.7	4,871	452	43	1	44	2	42	2	45	3	21
1981	70.9	1.0	4,529	236	49	1	46	1	43	1	47	2	54
1982	67.5	1.2	4,344	279	50	2	44	2	43	2	44	2	40
1983	66.7	1.3	4,348	247	46	1	43	1	41	2	47	2	45
1984	66.3	1.1	4,012	247	47	1	44	1	44	2	45	2	43
1985	65.7	1.1	4,376	277	46	2	44	1	42	2	44	2	41
1986	63.7	1.4	3,712	339	48	2	44	2	39	3	45	4	28
1987	65.2	1.0	3,903	207	48	2	46	2	41	2	43	2	46
1988	66.4	0.9	4,399	258	47	1	43	2	40	1	46	3	44
1989	67.4	1.1	4,319	255	47	2	44	2	43	2	46	2	45
1990	65.7	1.0	4,330	257	46	1	45	1	46	2	44	2	49
1991	63.5	1.2	3,564	255	47	1	46	1	42	2	43	2	44
1992	65.9	1.4	3,515	292	50	2	45	1	38	2	41	2	36
1993	65.8	1.7	3,138	319	47	2	42	2	38	2	39	2	32
1994	59.6	1.0	2,660	158	47	1	42	1	38	2	38	2	49
1995	61.1	1.1	2,971	205	48	1	40	1	35	1	36	2	51
1997	64.7	1.0	3,771	224	48	1	43	1	38	1	41	2	50
1998	63.8	2.0	3,363	328	51	2	43	2	38	2	39	2	27
1999	64.1	0.9	3,564	185	52	2	42	1	38	2	40	1	44
2000	67.1	1.3	4,344	272	51	1	41	1	39	1	39	2	45
2001	66.5	1.2	4,074	242	51	1	43	1	41	2	46	3	45
2002	66.9	1.8	4,209	318	53	1	44	1	43	2	47	2	31
2003	66.1	5.3	3,700	1131	49	10	41	3	42	9	43	8	4
2004	65.3	2.3	3,825	390	47	2	41	2	39	2	40	3	23
2006	62.3	1.2	3,345	227	49	1	45	1	40	2	43	2	38
2007	64.2	3.9	3,680	1084	49	5	42	5	37	3	38	3	5

Biological Characteristics of Anadyr Chum Salmon and Abundance of Pacific Salmon

We used the total catches of Pacific salmon by Russia, USA, Japan, and Canada as the measure of their abundance in the North Pacific Ocean (data source: NPAFC Statistical Yearbooks). Pearson's correlation coefficients between catches of Pacific salmon and some biological characteristics of Anadyr chum salmon are shown in Table 3 and Fig. 5. A statistically significant negative relationship between total catches of Pacific salmon and Anadyr chum salmon body

size (length and weight) and scale intercirculus distances for the second, third and fourth years was observed. These relationships were observed for both age groups (0.3 and 0.4). The growth of chum salmon during the first year of life and total Pacific salmon abundance were not significantly correlated.

There was no relationship between the scale growth and body size of Anadyr chum salmon and the abundance of Anadyr chum salmon. Pearson's correlation coefficients among the Anadyr chum salmon catches and fish body size and growth were non-significant.

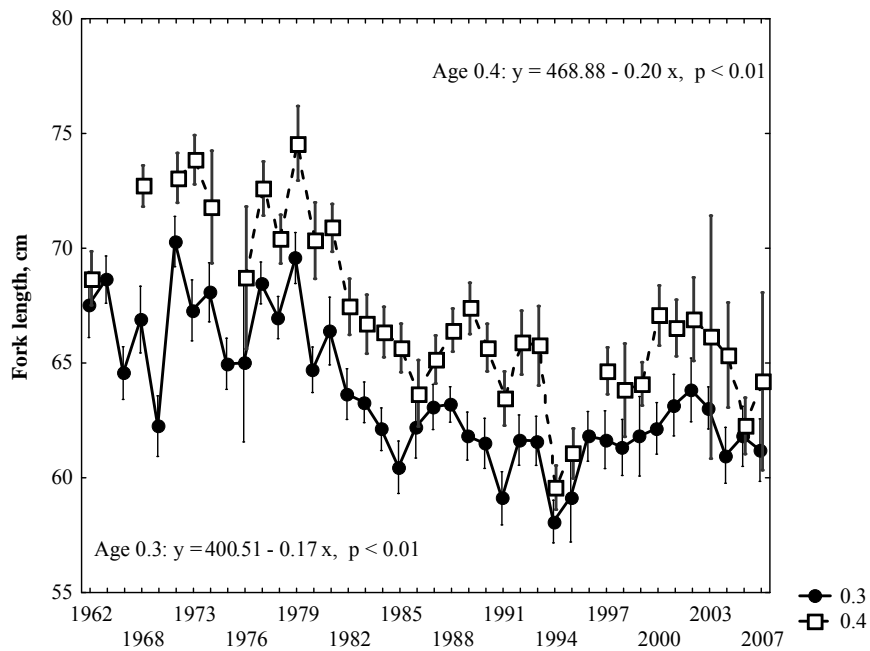


Fig. 3. Changes in mean fork length (cm) of Anadyr chum salmon (ages 0.3 and 0.4) from 1962–2007. Bars = 95% confidence interval.

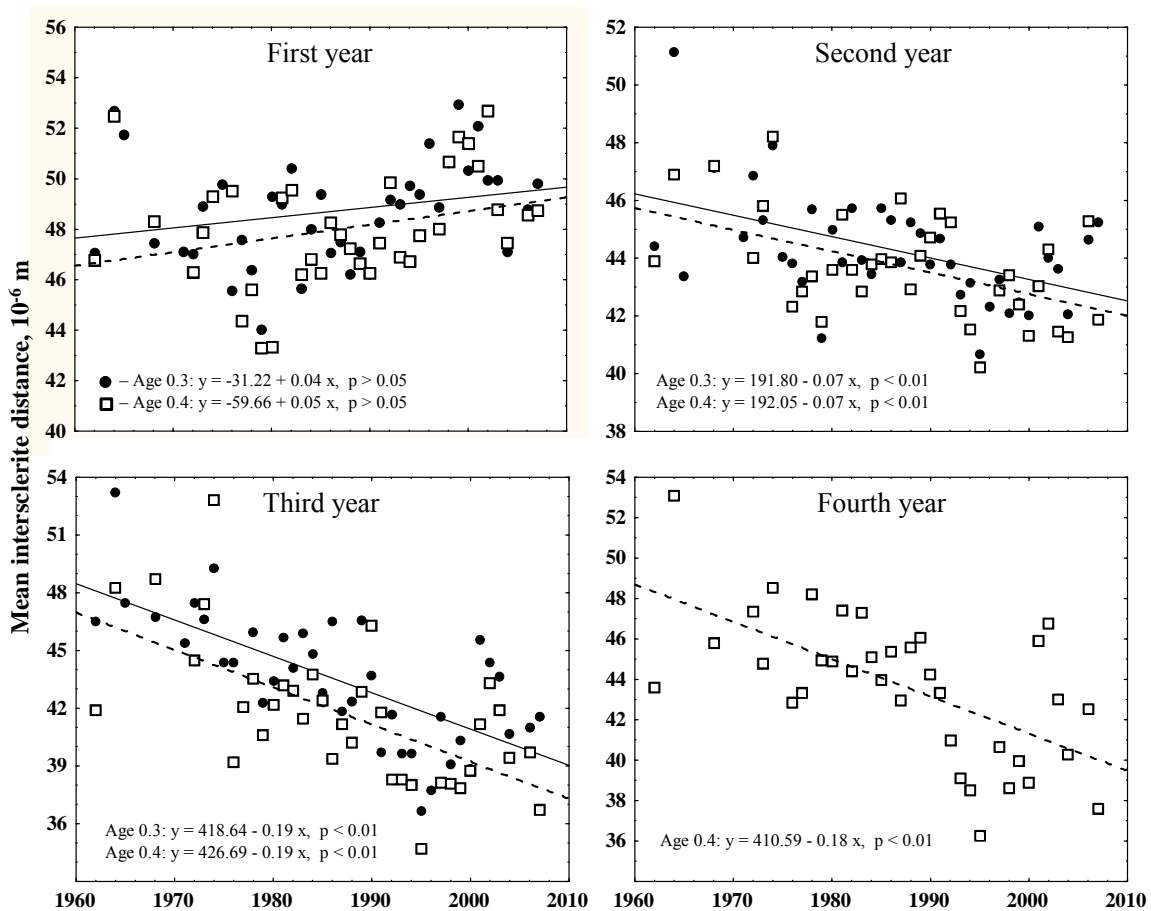


Fig. 4. Changes in mean intersclerite distances of Anadyr chum salmon from 1962–2007. Solid and dashed regression lines indicate for ages 0.3 and 0.4 fish, respectively.

Table 3. Pearson correlation coefficients relating mean body size and intercirculus distances of Anadyr chum salmon to the total catch of Pacific salmon in the North Pacific Ocean.

Age	Fork length	Body weight	Intersclerite distance			
			1st year	2nd year	3rd year	4th year
0.3	-0.78	-0.61	0.18	-0.55	-0.67	-
	$P < 0.01$	$P < 0.01$	$P = 0.29$	$P < 0.01$	$P < 0.01$	
0.4	-0.72	-0.50	0.12	-0.50	-0.61	-0.59
	$P < 0.01$	$P < 0.01$	$P = 0.51$	$P < 0.01$	$P < 0.01$	$P < 0.01$

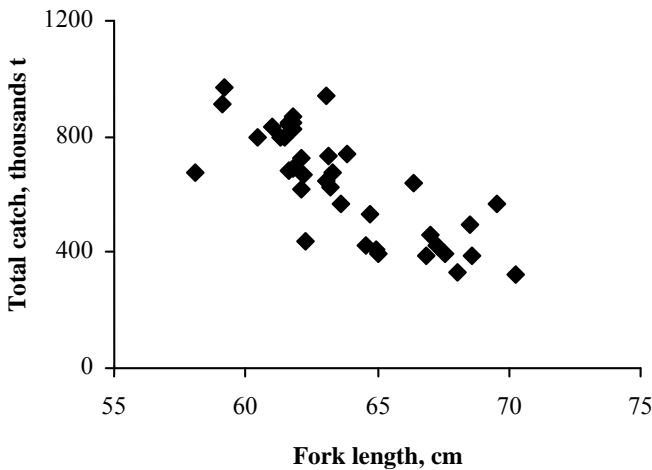


Fig. 5. Mean fork length of Anadyr chum salmon (age 0.3) and the total catch (thousands of metric tons, t) of Pacific salmon in the North Pacific Ocean from 1962–2007 (Catch data source: NPAFC Statistical Yearbooks).

DISCUSSION

The observed declines in body size and annual growth of Anadyr chum salmon that accompanied the large increase in Pacific salmon total abundance may indicate a density-dependent response by Anadyr chum salmon resulting from a decreased food supply. As noted above, growth declines of Anadyr chum salmon started during the second year of life. In the first year (based on scale growth), statistically significant changes in chum salmon growth were not observed. Perhaps feeding conditions in western Bering Sea where Anadyr chum salmon are believed to forage during the first year of life year did not change substantially during the study period. This corresponds with the conclusions of other authors about relatively abundant food resources and a sufficient food supply for Pacific salmon in the western Bering Sea (Shuntov 2001; Shuntov and Temnykh 2004; Naydenko 2007; Zavolokin et al. 2007).

Alternatively, several studies noted that annual scale growth during first year of marine life for many other popu-

lations of Pacific salmon did not decrease but even increased during recent decades (Kaeriyama et al. 2007; Martinson et al. 2008). Therefore, not only food conditions but also other factors, for example, size-selective mortality (Farley et al. 2007), can determine salmon growth in the first year of marine life.

Figures 3 and 4 show that there were both less favorable and more favorable periods for Anadyr chum salmon growth and probably survival. In 1962–1980, fork length and body weight of Anadyr chum salmon were the highest. And from the early 1980s to the mid 1990s, fish size sharply decreased. Shifts in Anadyr chum salmon sizes, taking into account a 3–4 year lag, coincided well with the 1976–1977 climatic regime shift (Hare and Francis 1995; Mantua and Hare 2002). These results may corroborate the conclusions of other researchers that climatic and oceanic conditions can strongly affect carrying capacity for Pacific salmon and other fish (Myers et al. 2001; Kaeriyama et al. 2007; Martinson et al. 2008).

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Forage Base of Pacific Salmon in the Western Bering Sea and Adjacent Pacific Waters in 2002–2006

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Zavolokin, A.V. 2009. Forage base of Pacific salmon in the western Bering Sea and adjacent Pacific waters in 2002–2006. *N. Pac. Anadr. Fish Comm. Bull.* 5: 165–172.

Abstract: The objective of this study was to estimate the total relative biomass of the forage base (zooplankton + nekton) of Pacific salmon (*Oncorhynchus* spp.) in the upper epipelagic zone of the western Bering Sea and adjacent Pacific waters in summer and fall 2002–2006. Zooplankton biomass was estimated from plankton survey data, and nekton biomass was estimated from salmon diet data using a mathematical model of selective feeding. In 2002–2006, estimated total relative biomass of the salmon forage base varied from 690–1590 mg/m³. Biomass was lowest in fall 2004, and was highest in fall 2002. Copepods and chaetognaths dominated the potential forage base. Squids and fishes were 15–22% (average 19%) of the overall biomass. The biomass of fish was highest in the continental shelf area (Anadyr Bay). Squids were more abundant in deep-water regions of the Bering Sea and adjacent Pacific waters. Walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and Pacific sand lance *Ammodytes hexapterus* were the dominant nekton species in the northwestern shelf region. Shortarm gonate squid *Gonatus kamtschaticus*, boreopacific gonate squid *Gonatopsis borealis*, Atka mackerel *Pleurogrammus monopterygius*, and myctophids were prevalent items in the salmon forage base in deep-water areas. In general, the results indicated that immature salmon in both summer and fall were concentrated within deep-water regions of the western Bering Sea, where their forage (overall and preferred prey items) was also concentrated, and were much less numerous in the Pacific waters off the Commander Islands and in the western Bering Sea shelf zone, where their forage was less concentrated.

Keywords: micronekton, plankton, forage base, model of selective feeding, Pacific salmon, Bering Sea

INTRODUCTION

Estimation of salmon prey abundance is an important objective of research for understanding how ocean conditions affect the marine survival and production of Pacific salmon. As a rule, researchers use plankton sampling to estimate the Pacific salmon forage base. However not only plankton, but also micronekton, constitute a significant part of Pacific salmon diets. Small nekton species dominate chinook and coho salmon diets, and are important in sockeye, chum, and pink salmon diets, especially for adult fish (Andrievskaya 1966; Pearcy et al. 1988; Volkov et al. 1997; Davis et al. 2000; Kaeriyama et al. 2000; Chuchukalo 2006; Karpenko et al. 2007; and many others).

Total estimation of the abundance of the forage base of fish can be performed using several types of gear. Small plankton species are caught by relatively small nets whereas micronekton species are caught with either larger nets or small trawls (see, e.g., Viitasalo et al. 2001; Schabetsberger et al. 2003). However in this case researchers need to use compensatory coefficients for combining the data from different types of gear. In our work, we used a standard approach (plankton net) for zooplankton sampling combined

with a mathematical model of fish selective feeding for estimating small-size nekton species biomass.

The purpose of this work was the assessment of the overall salmon forage base using data from plankton sampling and modeled estimates of micronekton (small-size fishes and squids) biomass. The composition of the Pacific salmon forage base and its year-to-year variability and spatial distribution are described.

MATERIALS AND METHODS

Study Area

The study was based on data collected as part of the Bering-Aleutian Salmon International Survey (BASIS) by TINRO-Centre in the upper epipelagic zone of the western Bering Sea and adjacent Pacific waters. Surveys were conducted in September–October 2002, July–August and September–October 2003, September–October 2004, June–July 2005, and August–October 2006. The study area included four large districts (Fig. 1). One district was located primarily in the shelf zone (Anadyr Bay and adjacent waters), and other districts were located in deep-water areas of

the Bering Sea and in adjacent Pacific waters (Commander Basin, western Aleutian Basin, and Pacific waters).

Forage Base Estimation

The forage base was defined as all plankton and nekton species that are prey of Pacific salmon. The Pacific salmon forage base included two parts: zooplankton and small-size nekton species (micronekton) with body lengths that do not exceed 15 cm.

Zooplankton data

The published data of A.F. Volkov (Volkov et al. 2007) were used to describe the plankton component of the Pacific salmon forage base in the western Bering Sea in summer and fall of 2002–2006. Plankton were sampled and analysed by a unified approach, accepted at the TINRO-Centre (Volkov 1996). Zooplankton samples were obtained with a Juday net (0.1 m² mouth opening; 0.168-mm mesh net). The Juday net was towed in the upper 50 m of the water column. Because Pacific salmon ingested primarily large zooplankton prey (> 3 mm), zooplankton biomass was evaluated only for items > 3 mm. The total number of plankton stations sampled is shown in Table 1.

Micronekton data

That Pacific salmon have high trophic plasticity is well known (Andrievskaya 1966; Pearcy et al. 1988; Volkov et al. 1997; Davis et al. 2000; Kaeriyama et al. 2000; Efimkin 2003; Temnykh et al. 2004; Kuznetsova 2005; Chuchukalo 2006; Karpenko et al. 2007; Naydenko et al. 2007; and others). Their ration composition changes depending on the forage base. Therefore, the relative biomass of the unknown components of the Pacific salmon forage base can be estimated using data on their diets.

This task was accomplished by a mathematical model of

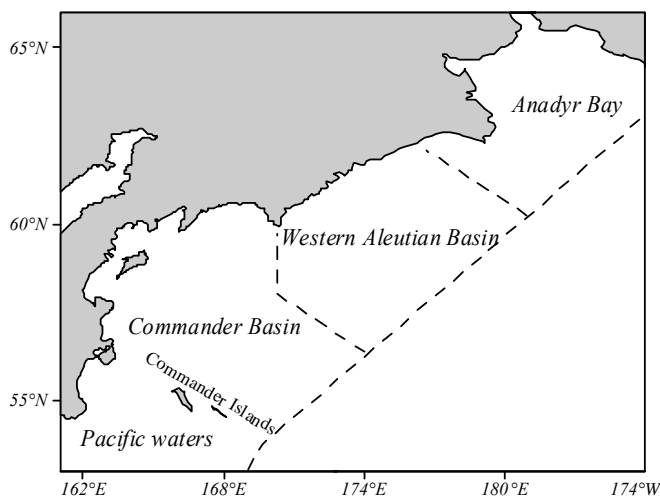


Fig. 1. Map of the study area for planktonic and trophological samples.

selective feeding. Firstly, this model included trophological circulation from Krogius et al. (1969):

$$q_i = \varepsilon_i p_i / \sum_{j=1}^n \varepsilon_j p_j, \quad i = 1, \dots, n, \quad (1)$$

where q_i is the fraction of i -th food species in the predator's ration, p_i is the fraction of the same species in the total biomass of forage base, and ε_i represents feeding electivities. Values q_i, p_i, ε_i are probabilities (fractions), so the sum over all $i = 1, \dots, n$ foraging objects must be equal to 1 for every one of these variables.

Numerical values of electivities ε_i can be obtained by solving the next system of n linear equations (Sukhanov 1988):

$$\left. \begin{aligned} \varepsilon_1 + \varepsilon_2 + \dots + \varepsilon_{n-1} + \varepsilon_n &= 1 \\ q_2 p_1 \varepsilon_1 + (q_2 - 1) p_2 \varepsilon_2 + \dots + q_2 p_{n-1} \varepsilon_{n-1} + q_2 p_n \varepsilon_n &= 0 \\ q_3 p_1 \varepsilon_1 + q_3 p_2 \varepsilon_2 + (q_3 - 1) p_3 \varepsilon_3 + \dots + q_3 p_{n-1} \varepsilon_{n-1} + q_3 p_n \varepsilon_n &= 0 \\ \dots &\dots \\ q_n p_1 \varepsilon_1 + q_n p_2 \varepsilon_2 + \dots + q_n p_{n-1} \varepsilon_{n-1} + (q_n - 1) p_n \varepsilon_n &= 0 \end{aligned} \right\} (2)$$

If some j -th food species were not caught by gear and therefore not included in the forage base, but it was considered prey, then not only electivities $\varepsilon_1, \varepsilon_2, \dots, \varepsilon_n$ but also fractions of this food species in the total biomass of forage base (p_j) must be estimated. So the model (1) becomes non-linear. Parameter estimation needs to be performed not by solving system equation (2), but by using a special gradient algorithm, that fits model (1) into our data. To accomplish this, the Marquardt method was used (Bard 1979). To uphold the restrictions for model parameters (it must be in the range of 0 and 1), a penalty function (Bunday 1984) was added to the model algorithm. The program for parameter estimation was performed using the algorithmic language TMT-Pascal 3.90.

The algorithm scheme of the model used to evaluate the unknown components of the Pacific salmon forage base is shown in Fig. 2. Input data for this model are the Pacific

Table 1. Survey date (day.month.year) and total number of plankton stations and analyzed stomachs of Pacific salmon.

Survey date	Total number of	
	Plankton stations	Analyzed stomachs
Aug 31 – Oct 9, 2002	82	1,721
July 15 – Aug 24, 2003	86	2,816
Sep 14 – Oct 25, 2003	86	2,545
Sep 11 – Oct 23, 2004	70	3,121
June 17 – July 21, 2005	93	2,341
Aug 24 – Oct 12, 2006	110	4,109

salmon feeding spectra, zooplankton species composition, and the initial values of parameters. The base of the program includes a model of fish selective feeding, a restriction procedure, and an algorithm that fits parameters by the Marquardt method. Output data are the feeding electivities and the required fractions of small fishes and squids in the total biomass of the forage base. For more detailed information see Sukhanov and Zavolokin (2006).

Table 2 shows an example of input data for the estimation of unknown fractions of small-size fishes and squids. It includes feeding habits of five predators q_i (pink, chum, sockeye, coho, and chinook salmon) and zooplankton species composition p_i . Initial values of electivities are calculated based on feeding spectra and zooplankton data using equation (1). Each unknown fraction (fish larvae p_1 , Pacific sand lance p_2 and squid larvae p_3) in the total biomass of the forage base was assigned an initial value of 0.05.

Estimated fractions (mean \pm standard error) of small-size nekton in the total biomass of the Pacific salmon forage base were: $p_1 = 0.099 \pm 0.018$, $p_2 = 0.076 \pm 0.018$ and $p_3 = 0.033 \pm 0.017$. Based on the biomass of the planktonic component of the salmon forage base (1,424 mg/m³ – Table 2) and estimated values of parameters, the relative biomass of each unknown component of the Pacific salmon forage base was calculated.

Stomach contents that were used for modeled estimates of micronekton biomass were analyzed aboard the vessel using the method described by Chuchukalo and Volkov (1986). Stomachs were removed from up to 25 fish of each size-class (10–30, 31–40, 41–50, 51–60 cm) at each station. Stomach contents of each size-class of fish were mixed and weighed. Prey composition was determined to the lowest possible taxonomic category and the percentage of each prey item was estimated visually. The total number of stations and stomachs analyzed is shown in Table 1.

RESULTS AND DISCUSSION

Pacific Salmon Forage Base Composition

Zooplankton dominated the Pacific salmon forage base in the western Bering Sea (Fig. 3). Micronekton were approximately 20% of the forage base. In the northwestern shelf region, the majority of micronekton consisted of small-size fishes. In the deep-water areas, the percentages of fishes and squids were approximately equal.

In the shelf region, the plankton component of the Pacific salmon forage base was dominated by copepods (mainly *Calanus glacialis*) and chaetognaths (Fig. 3). Furthermore, the fraction of euphausiids (mainly *Thysanoessa inermis* and

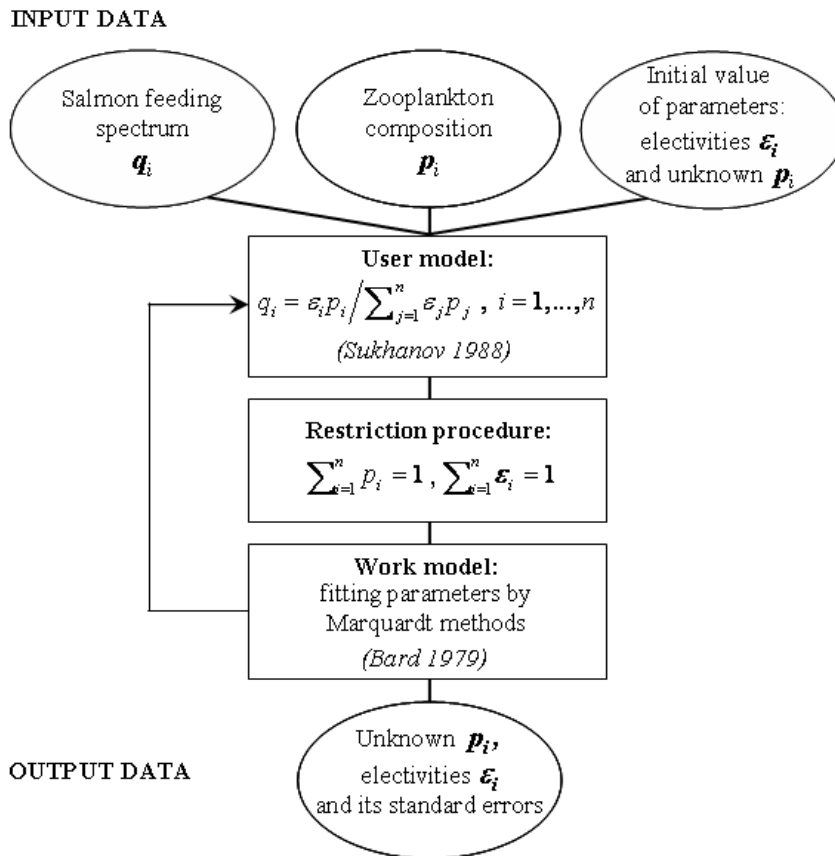


Fig. 2. Scheme of the model used to estimate the fraction of squid and fish from the total zooplankton biomass.

Table 2. Feeding habits of Pacific salmon of size group 10-30 cm and zooplankton composition in the deep-water basins of the western Bering Sea in fall 2002.

Species	Pink	Chum	Sockeye	Coho	Chinook	Plankton
Copepods						
<i>Neocalanus plumchrus</i>	0.120	0.084	0.073	-	-	0.493
<i>N. cristatus</i>	0.005	0.013	0.085	-	-	0.010
<i>Eucalanus bungii</i>	-	-	-	-	-	0.025
Euphausiids						
<i>Thysanoessa longipes</i>	0.377	0.166	0.428	-	-	0.041
Amphipods						
<i>Themisto pacifica</i>	0.438	0.574	0.186	0.002	-	0.008
<i>Primno macropa</i>	0.018	0.014	0.006	-	-	0.001
Decapods						
Zoea	-	0.010	0.042	-	-	0.001
Megalopa	0.017	0.002	0.009	0.030	0.010	0.001
Chaetognaths						
	0.024	0.116	0.171	-	-	0.420
Fishes						
Larvae	-	0.004	-	0.870	0.698	-
<i>Ammodytes hexapterus</i>	-	0.017	-	0.092	0.284	-
Squid larvae						
	0.001	-	-	0.006	0.008	-
Total zooplankton biomass, mg/m³						1424

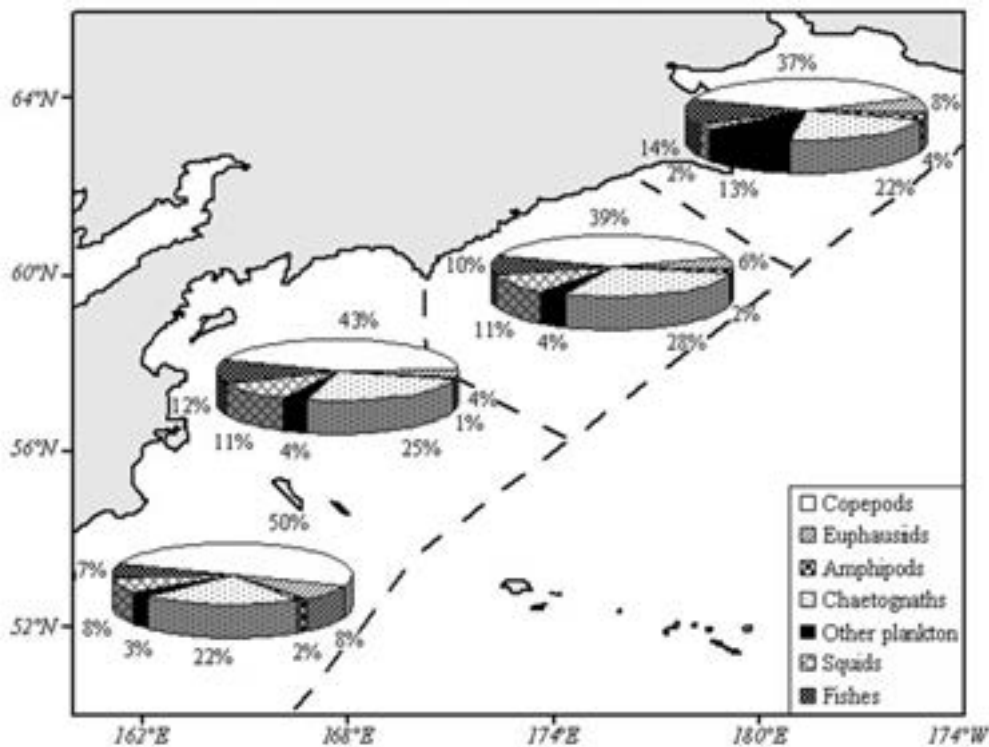


Fig. 3. Salmon forage base composition in the western Bering Sea and adjacent Pacific waters in 2002–2006.

Th. raschii) was relatively high. The dominant species of the nekton component of the Pacific salmon forage base were walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and Pacific sand lance *Ammodytes hexapterus*. The percentage of fish larvae was substantial as well.

Within the deep-water regions, most of the plankton component of the Pacific salmon forage base consisted of copepods (mainly *Neocalanus plumchrus*) and chaetognaths (Fig. 3). The fraction of euphausiids in deep-water regions was lower than that in the shelf region. The prevalent species of euphausiid was *Thysanoessa longipes*. The nekton component of the Pacific salmon forage base was dominated by two species of gonatid squids (boreopacific gonate squid *Gonatopsis borealis* and shortarm gonate squid *Gonatus kamtschaticus*), small mesopelagic fishes (primarily, northern lampfish *Stenobranchius leucopsarus*), and juvenile Atka mackerel *Pleurogrammus monopterygius*.

The percentage of the most preferred prey items of Pacific salmon such as amphipods and pteropods was very low. In 2002–2006, they contributed about 3.5% and 1.1% of the total forage base in Anadyr Bay and deep-water regions, respectively.

Inter-annual dynamic of Pacific Salmon Forage Base

The cumulative values for relative biomass estimates of the components of the Pacific salmon forage base varied greatly from year to year. In the shelf region, these values were highest (1,380 mg/m³) in 2002 and lowest in 2003 and 2004 (440–520 mg/m³) (Fig. 4a). Inter-annual dynamics of the cumulative values of the relative biomass of plankton species exhibited a similar pattern (Fig. 4b). Fish biomass was relatively stable and varied from 70 to 120 mg/m³, except for 2006 (Fig. 4c). Squid biomass values for squid were very low in the shelf region, particularly in fall. Squid were abundant only in summer 2003 (Fig. 4d).

Within deep-water regions, cumulative values for relative biomass estimates of the Pacific salmon forage base were highest in summer of 2003 (1,600 mg/m³) and lowest in fall of 2004 (600 mg/m³) (Fig. 5a). Dynamics of the cumulative values of relative abundance estimates of zooplankton were similar to those of the entire forage base of Pacific salmon (Fig. 5b). Fish biomass varied greatly from 40 mg/m³ in fall 2004 up to 190 mg/m³ in fall 2002 (Fig. 5c). Squid biomass was more stable (90–140 mg/m³), and did not vary substantially during these years (Fig. 5d).

In 2002–2006, relative biomass of the preferred prey of Pacific salmon (amphipods, pteropods, euphausiids, small-size fishes and squids) varied from 130–300 mg/m³ in Anadyr Bay (Fig. 4e) and from 220–430 mg/m³ in the basins and Pacific waters (Fig. 5e). In the shelf region, relative biomass of the preferred prey was lowest in fall 2004 and summer 2005 and the highest in fall 2006. In the deep-water regions, minimum relative biomass of the preferred prey of Pacific salmon occurred in fall 2004, and maximum relative

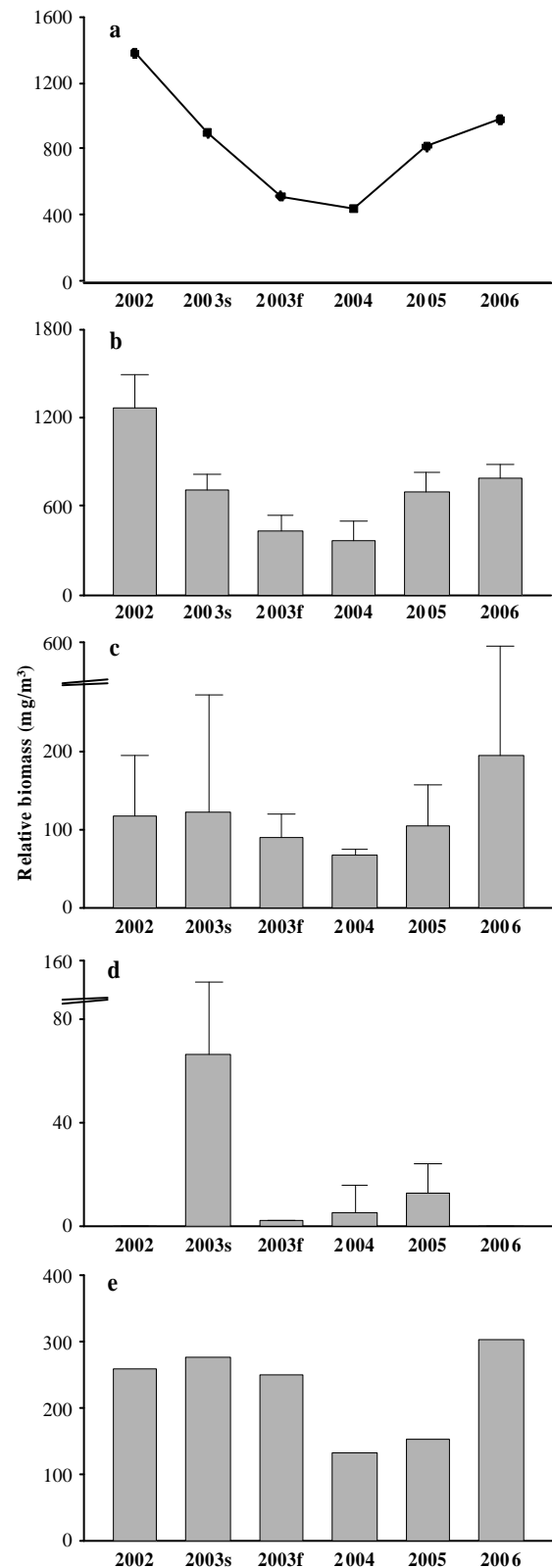


Fig. 4. Trends in relative biomass (mg/m³) of the Pacific salmon forage base in Anadyr Bay in 2002-2006. a = Total forage base, b = zooplankton, c = fishes, d = squids, e = preferred salmon prey (amphipods, euphausiids, pteropods, micronekton), 2003s = summer 2003, 2003f = fall 2003.

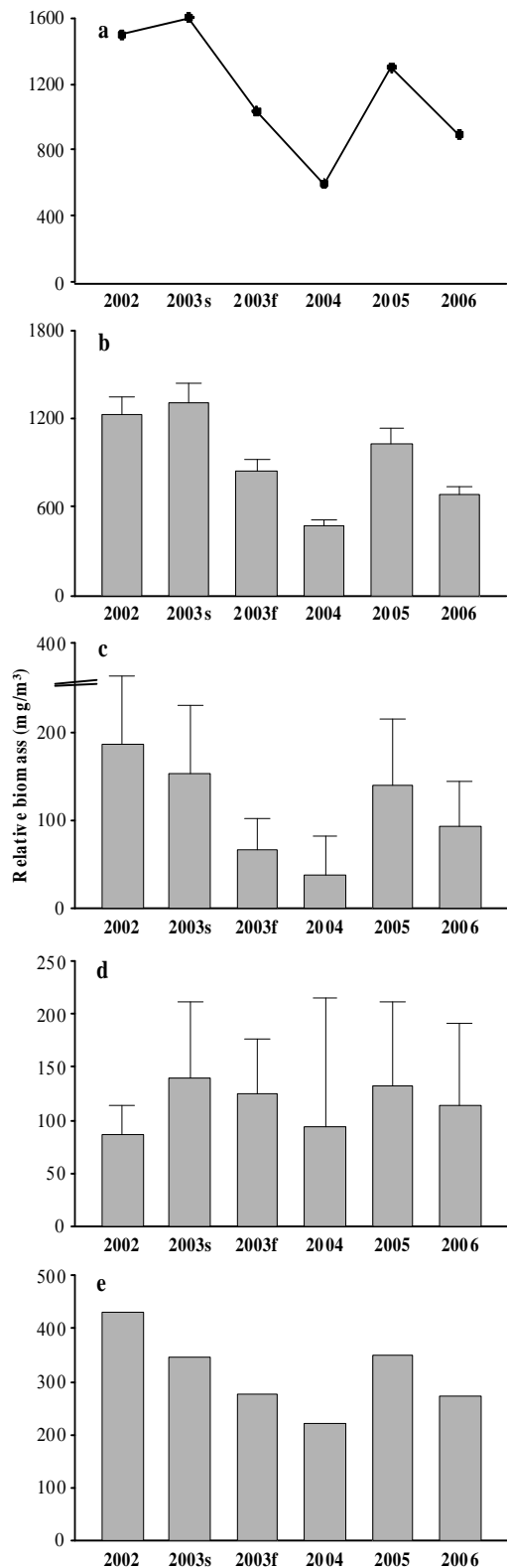


Fig. 5. Trends in relative biomass (mg/m^3) of the Pacific salmon forage base in deep-water regions of the western Bering Sea and adjacent Pacific waters in 2002-2006. a = Total forage base, b = zooplankton, c = fishes, d = squids, e = preferred salmon prey (amphipods, euphausiids, pteropods, micronekton), 2003s = summer 2003, 2003f = fall 2003.

biomass was in fall 2002.

Spatial Distribution of Pacific Salmon Forage Base Relative Biomass

The highest concentrations of zooplankton were confined mainly to the deep-water regions – the Commander and Aleutian basins. Zooplankton relative biomass estimates were slightly lower in the Pacific waters and Anadyr Bay (Table 3).

Small-size fishes were located primarily within the Commander Basin area. Furthermore, their relatively high concentrations were observed in the north-western shelf and in the Aleutian Basin. Small-size squids were abundant only in the deep-water basins and Pacific waters. In the shelf zone they were rare (Table 3).

For the entire forage base biomass, the maximum values were in the Commander and Aleutian basins and the minimum values were in Anadyr Bay. That the preferred prey items of Pacific salmon showed a similar pattern of distribution is interesting to note. Their relative biomass estimates were highest in the deep-water regions of the Bering Sea (Table 3).

High concentrations of the Pacific salmon forage base (overall and preferred prey items) in the basin areas may be the cause of observed distributions of immature Pacific salmon, that is, in both summer and fall immature Pacific salmon were concentrated primarily within deep-water regions of the western Bering Sea, and were much less numerous in the Pacific waters off the Commander Islands and in the shelf zone (Fig. 6).

CONCLUSION

In 2002–2006, cumulative values for relative biomass estimates of the Pacific salmon forage base varied significantly (from 600 to 1,600 mg/m^3 in deep-water regions and from 400–1400 mg/m^3 in the shelf zone). Relative biomass estimates were the lowest during fall 2004 and the highest in fall 2002 and summer 2003.

The highest cumulative values for relative biomass estimates of the Pacific salmon forage base were observed in the Commander and Aleutian basins of the western Bering Sea. This result provides evidence that deep-basin areas are the most favorable for Pacific salmon feeding. The lowest relative biomass estimates of the forage base were in the shelf region.

The potential forage base of Pacific salmon was dominated by planktonic organisms (copepods, chaetognaths, and euphausiids). The fraction of micronekton comprised about 20% of the potential forage base. In the shelf zone (Anadyr Bay) prevalent micronekton species were walleye pollock, capelin, Pacific sand lance, and fish larvae. Within the deep-water regions, the micronekton community was dominated by gonatid squids, small mesopelagic fishes, and juvenile

Table 3. Relative biomass (mg/m³) of the Pacific salmon forage base in the western Bering Sea and adjacent North Pacific waters in 2002-2006. Mean values and standard errors are shown. Preferred prey include amphipods, pteropods, euphausiids, small-size fishes and squids.

Group	Pacific waters	Commander Basin	Aleutian Basin	Anadyr Bay
Zooplankton	897 ± 144	986 ± 160	892 ± 125	708 ± 130
Fish	75 ± 18	152 ± 27	111 ± 40	115 ± 18
Squid	83 ± 13	143 ± 33	119 ± 28	14 ± 11
Preferred prey	268 ± 74	370 ± 39	325 ± 49	231 ± 25
Overall	1,055 ± 153	1,281 ± 197	1,122 ± 170	837 ± 139

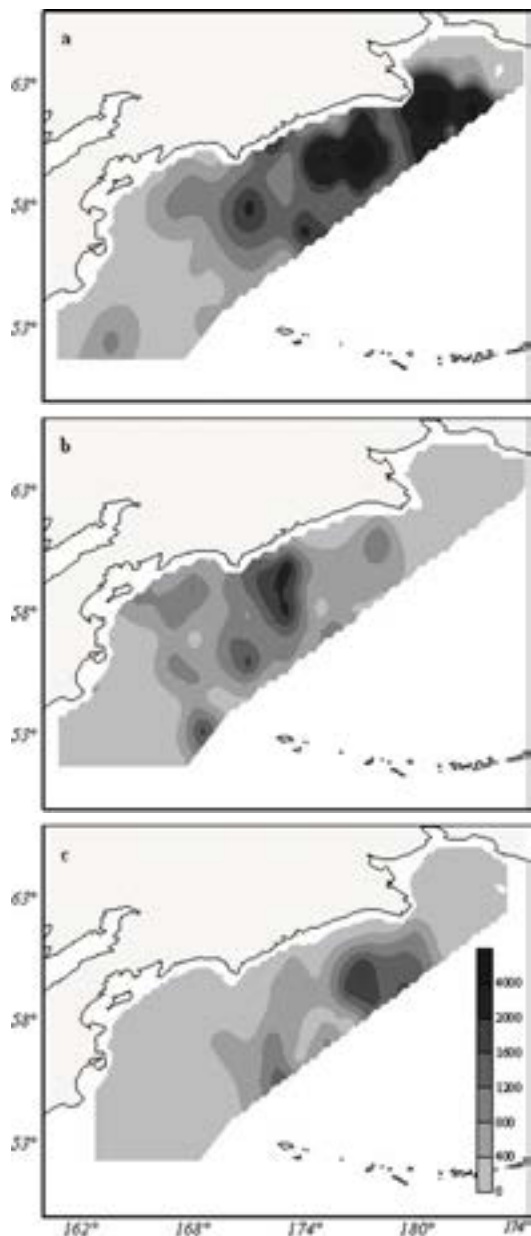


Fig. 6. Spatial distribution of immature Pacific salmon relative abundance (number of fish/km²) in the western Bering Sea and adjacent Pacific waters in July-August 2003 (a), September-October 2003 (b), and June-July 2005 (c).

Atka mackerel.

The method used for estimation of small-size nekton biomass has some restrictions. Firstly, estimated values rely on the planktonic component of the forage base. Therefore, inaccuracies and uncertainties in plankton sampling, processing and calculating may affect micronekton biomass estimates. Secondly, this method requires data on feeding habits for all large predatory fish in the epipelagic ecosystem. Further, it is important to note that feeding habits of fish used for estimation of small-size nekton biomass must differ. The more the feeding spectra of predators differ, the higher the accuracy of estimates.

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Bias-Corrected Size Trends in Chum Salmon in the Central Bering Sea and North Pacific Ocean

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Abstract: We estimated bias-corrected mean fork lengths of gillnet-caught chum salmon using a size selectivity estimate of the gillnet to test how the bias correction affects the estimated temporal pattern of chum salmon body size, during 1971–1994 and 1994–2007. Results showed bias-corrected mean fork lengths were smaller than uncorrected means. Therefore, when examining ontogenetic changes in fish size (e.g. the growth trajectory) using data collected by research gillnets, the uncorrected mean fork length can overestimate the true value. Comparison of temporal trends in bias-corrected mean fish lengths to uncorrected means showed similar results because both illustrated a decrease in chum salmon fork length in 1971–1994, and a stable fish size after 1994. Uncorrected mean values of chum salmon fork length for fish caught using research gillnets can be used as a proxy for fish size to examine temporal trends. We conclude that interpreting temporal trends using either uncorrected or bias-corrected data will support the same general conclusions regarding long-term changes in chum salmon body size.

Keywords: chum salmon, ocean survey, fish size, temporal trend, gillnet selectivity, sampling bias

INTRODUCTION

The Bering-Aleutian Salmon International Survey (BASIS) of the North Pacific Anadromous Fish Commission (NPAFC), begun in 2002, established the trawl as the standard fishing gear to collect salmon (NPAFC 2001). One of the scientific issues stated in the BASIS plan was to investigate the key biological, climatic, and oceanographic factors affecting long-term changes in Bering Sea food production and salmon growth rates. However, information on long-term changes in salmon growth is difficult to obtain from BASIS surveys because the research began only a short number of years ago. Since 1972, Japanese research vessels have monitored salmon stock condition in the Bering Sea and North Pacific by catching fish using a research gillnet consisting of ten different mesh sizes (Takagi 1975, 1996). These Japanese monitoring surveys provide valuable information on long-term changes in salmon growth because their standardized methods and data series were established several decades ago and have not changed.

Analysis of the temporal trend in chum salmon fork lengths from Japanese research gillnet surveys showed a decrease in fish size from the 1970s to the 1990s, and not much change in fish size through the middle of the next decade

(Fukuwaka et al. 2007). The temporal trend in fish size from high seas research surveys correlated with age and size at maturation of Ishikari River chum salmon (Fukuwaka et al. 2007). Fish size at maturation of other populations of chum salmon and other species of Pacific salmon has shown similar trends, with a decrease in size into the 1990s and an increase in size in recent years (e.g. Helle and Hoffman 1998; Eggers and Irvine 2007; Helle et al. 2007; Shaul et al. 2007).

Recent studies have shown that estimates of fish size are biased in catches from multi-mesh research gillnets due to the size selectivity of this fishing gear (Finstad et al. 2000; Finstad and Berg 2004; Fukuwaka et al. 2008). The data series on immature and maturing chum salmon body size collected at sea by Japanese research monitoring programs are based on catches in a multi-mesh research gillnet. As long-term changes in salmon body size are of primary interest to the BASIS program, the objective of our study was to test how the temporal pattern of uncorrected values of chum salmon fish length compares to bias-corrected values using data collected in Japanese salmon research gillnet surveys from 1971 to 1994 and 1994 to 2007. We estimated bias-corrected mean fork lengths of gillnet-caught chum salmon using a size selectivity estimate based on comparison of the research gillnet catches of the R/V *Wakatake maru* moni-

toring surveys and the mid-water trawl catches of the R/V *Kaiyo maru* BASIS surveys reported in Fukuwaka et al. (2008).

MATERIALS AND METHODS

Chum salmon fork length and ocean age from scale collections were determined for each mesh size in catches of a standard salmon research gillnet from Japanese monitoring surveys conducted in the central Bering Sea and North Pacific between 170°E and 170°W from June 11 to July 20, 1971–2007. High-seas salmon monitoring surveys using this standardized research gillnet began in 1972, however, measurements of chum salmon fork length caught by the same gear were available from surveys in 1971, and therefore were included in this study. The gillnet configuration comprised variable-meshes representing a geometric series of factor 1.14 (identical number of 50-m by ca. 7-m panels of 48-, 55-, 63-, 72-, 82-, 93-, 106-, 121-, 138-, and 157-mm meshes composed of nylon monofilament line; Takagi 1975). To maintain the gillnet’s stretch while fishing, additional panels of 115- or 121-mm mesh were attached at both ends, however, catches in these meshes were not included in our analysis. In recent years, three 50-m panels of each research mesh size were used in gillnet operations. However, before 1993 sometimes four to six 50-m panels of each mesh size were used. Because the same number of panels of each mesh size was used in each fishing operation, the change in the number of panels over the time period does not affect the relative catch efficiency of each mesh size. We set the maximum catch efficiency of the 157-mm mesh to 1.0 and estimated the efficiencies of each mesh size relative to

catches in that mesh size.

To correct for the bias in fish size caused by gillnet sampling, we weighted fork length by the reciprocal of the catch efficiency. Catch efficiency of the research gillnet was estimated by inter-calibrating research gillnet catches with trawl catches conducted during the 2002–2004 BASIS cruises (Fukuwaka et al. 2008). Annual mean fork length was estimated using the following equation:

$$\bar{l}_{corr} = \frac{\sum l \frac{n_{l,m}}{E_m(l)}}{\sum \frac{n_{l,m}}{E_m(l)}}$$

where *l* was the mid point of length class, *n_{l,m}* was the number of fish at length class *l* caught in gillnet mesh *m*, and *E_m(l)* was the catch efficiency of gillnet mesh *m* for length class *l*. Although the number of fish caught, *n_{l,m}*, was assumed to have a Poisson error (Fukuwaka et al. 2008), we did not evaluate the bias caused by the sampling error in this study. Because sample size was large for all age groups except age-0.5 (age-0.1 *n* = 67-1338, age-0.2 *n* = 139-1585, age-0.3 *n* = 178-1719, age-0.4 *n* = 27-573, and age-0.5 *n* = 0-28; Table 1), we assumed the bias caused by sampling error in mean fork length was much smaller than the bias caused by gillnet selectivity. The average % difference between uncorrected and bias-corrected values was estimated for each age group:

$$\% \text{ difference} = 100 \times \frac{\bar{l}_{uncorr} - \bar{l}_{corr}}{\bar{l}_{corr}}$$

To compare the temporal trends in the annual mean fork length of uncorrected and bias-corrected values, we estimated the correlation coefficient between year and the uncorrected and bias-corrected sizes for two time periods,

Table 1. Correlation coefficient (*r*) and significance (*P*) between year and uncorrected and bias-corrected mean fork lengths of chum salmon caught in the central Bering Sea and North Pacific in summer. The symbol N indicates the range of the number of fish used for estimation of annual mean fork lengths in each time period. Values are presented for two time periods (1971–1994 and 1994–2007) and chum salmon age groups (0.1–0.5).

Period	Age	Uncorrected		Bias-corrected		N
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
1971–1994	0.1	0.068	0.753	-0.073	0.736	144–1338
	0.2	-0.800	< 0.001	-0.752	< 0.001	192–1585
	0.3	-0.831	< 0.001	-0.792	< 0.001	274–1719
	0.4	-0.869	< 0.001	-0.836	< 0.001	27–573
	0.5	-0.539	0.001	-0.517	0.011	0–28
1994–2007	0.1	0.443	0.112	0.276	0.340	67–883
	0.2	-0.113	0.700	-0.191	0.513	139–1018
	0.3	0.319	0.267	0.187	0.522	178–883
	0.4	0.391	0.167	0.133	0.649	37–324
	0.5	0.117	0.689	0.346	0.226	2–25

1971–1994 and 1994–2007. The significance of the correlation coefficient was tested using a *t*-test. The data were separated into the two time periods because a previous study showed the correlation coefficient of uncorrected annual mean fork length was significantly negative in 1972–1994 and not significant in 1994–2004 (Fukuwaka et al. 2007).

RESULTS

Bias-corrected mean fork lengths of chum salmon were smaller than means calculated from raw data (Fig. 1). However, the difference was less in the oldest age group. Average % difference was 3.2% for age-0.1 fish, 3.4% for age-0.2 fish, 5.2% for age-0.3 fish, 2.9% for age-0.4 fish, and 1.4% for age-0.5 fish.

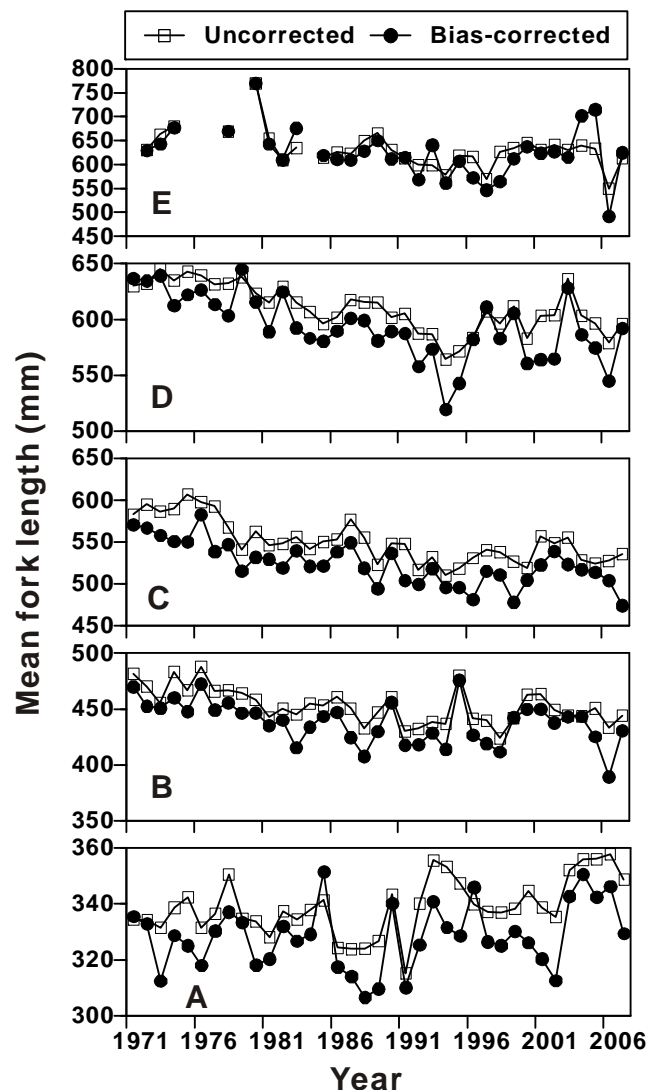


Fig. 1. Annual change in mean fork length of chum salmon of age-0.1 (A), age-0.2 (B), age-0.3 (C), age-0.4 (D), and age-0.5 (E) caught in the central Bering Sea and North Pacific in summer, 1971–2007. The data series shows values for uncorrected fish size calculated from mean fish length of gillnet catches (open squares) and bias-corrected mean fish lengths (solid circles).

for age-0.5 fish. For age-0.5 fish some bias-corrected means were larger than uncorrected means (Fig. 1E). The difference between corrected and uncorrected fork lengths was statistically significant (*t*-test, $\alpha = 0.05$) in 32 of 37 years for age-0.1 fish, 33 of 37 years for age-0.2 fish, 37 of 37 years for age-0.3 fish, 25 of 37 years for age-0.4 fish, and 3 of 27 years for age 0.5 fish. The difference between mean fork lengths and less difference in the oldest age group were caused by a heavier weight (i.e. the reciprocal of catch efficiency) applied to estimate for smaller fish.

The temporal trend of bias-corrected mean chum salmon fork length was similar to that calculated from uncorrected data (Fig. 1). Correlation coefficients (*r*) between corrected and uncorrected means were 0.771 ($P < 0.001$) for age-0.1 fish, 0.886 ($P < 0.001$) for age-0.2 fish, 0.853 ($P < 0.001$) for age-0.3 fish, 0.915 ($P < 0.001$) for age-0.4 fish, and 0.829 ($P < 0.001$) for age-0.5 fish. Over the time period 1971–1994, both time series of mean fork lengths of age-0.2, -0.3, -0.4, and -0.5 fish decreased significantly, but the correlation coefficients between year and bias-corrected means were smaller than those from uncorrected data (Table 1). Mean fork length of age-0.1 fish showed no significant temporal trend in 1971–1994. After 1994, mean fork lengths of all age groups were relatively stable and showed no significant trend.

DISCUSSION

The temporal trend of bias-corrected mean fork length was similar to that of uncorrected mean fork length of chum salmon caught using a salmon research gillnet. Although some authors have not considered the bias in fish size caused by gillnet sampling (e.g. Ishida et al. 1993; Azumaya and Ishida 2000; Fukuwaka et al. 2007), temporal trends of uncorrected values follow the same trends as unbiased values. The temporal correspondence between uncorrected mean sizes from research gillnet catches and sizes of mature fish caught in weirs in fresh water, which may be less size selective (Ishida et al. 1993; Fukuwaka et al. 2007), further supports the usefulness of uncorrected data as a proxy for unbiased values. However, for studies of ontogenetic changes in chum salmon size (e.g. the growth trajectory), researchers should account for the overestimation of true mean fork length when using uncorrected data from research gillnet catches.

The salmon research gillnet was designed to be non-selective with regard to fish size (Takagi 1975). This design was based on the assumptions that (1) gillnet panels of a geometric mesh size series offset the individual selectivity of each single mesh panel and (2) each mesh size had a common maximum efficiency, or fishing intensity. These assumptions have a theoretical basis in Balanov's principle of geometric similarity, which states that the selectivity curves for different mesh sizes must be similar because all meshes and all fish of the same species are geometrically

similar (Hamley 1975). However, the second assumption is not valid when gillnet efficiency increases with mesh size (reviewed by Hamley 1975). Fukuwaka et al. (2008) recently determined that the catch efficiencies of the salmon research gillnet increases with mesh size and fish size, which suggests that the second assumption is not necessarily true. The unidirectional bias toward larger size we observed in this study was caused by the higher catch efficiency for large fish than for small fish in research gillnet catches. When the bias is not unidirectional in the research gillnet catch the reason may be a large sampling error caused by small sample size. In addition, lower correlation coefficients for temporal trends in bias-corrected mean fork length might be the result of small sample sizes being caught in small mesh sizes. Because variance in numbers and sizes of fish caught in small mesh sizes can increase with heavier weights (reciprocals of catch efficiency) in the bias-correction, bias-corrected mean fork length may be unreliable if small numbers of fish are caught in small mesh sizes.

Although studies of ontogenetic changes in chum salmon size from research gillnet data should correct for the over-estimation of true mean fork length, we conclude that interpreting temporal trends using uncorrected or bias-corrected data will support the same general conclusions regarding long-term changes in chum salmon body size.

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Alaska Sockeye Salmon Scale Patterns as Indicators of Climatic and Oceanic Shifts in the North Pacific Ocean, 1922–2000

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Martinson, E.C., J.H. Helle, D.L. Scarnecchia, and H.H. Stokes. 2009. Alaska sockeye salmon scale patterns as indicators of climatic and oceanic shifts in the North Pacific Ocean, 1922–2000. *N. Pac. Anadr. Fish Comm. Bull.* 5: 177–182.

Abstract: Climate regime shifts can alter the community structure of marine species in the North Pacific Ocean. In this study, we use a regime shift detection algorithm to determine whether regime shifts are recorded as shifts in the mean fish length indices at the smolt, juvenile, immature, and mature life stages based on measurements of increments on scales of adult age-2.2 sockeye salmon (*Oncorhynchus nerka*) that returned to the Karluk River, Kodiak Island over a 77-year time period (1924–2000). Fish length was expected to increase with cool-to-warm climate shifts (1926, 1958, 1977, and 1998) and decrease with warm-to-cool climate shifts (1943, 1947, 1971, and 1989). Regime shifts were not consistently observed as statistical shifts in the time series of fish length indices. At contemporaneous lags, shifts in the mean temperature of the North Pacific were detected as shifts in length in 1958 (+), but not in 1926 (+), 1943 (-), 1971 (-), and 1977 (+). Shifts in the atmospheric circulation and sea level pressure of the North Pacific were detected as negative shifts in length in 1989 (-), but not in 1926 (+), 1947 (-), 1977 (+), 1998 (+). Shifts in length indices were associated with the 1957–58 El Niño, the warm-to-cool shift in 1989, and preceded the 1976–77 climate shift in the North Pacific Ocean. Fish length indices from salmon scales may be useful predictors for major and more recent shifts in the status of the ecosystem of the North Pacific Ocean.

Keywords: sockeye salmon, scale, climate, regime shifts

INTRODUCTION

In the 20th century, climate and oceanic conditions shifted between cool and warm regimes in the North Pacific Ocean (Mantua et al. 1997; Yasunaka and Hanawa 2005). Warm regimes (1925–46, 1977–88, 1998–2000) were characterized by a more intense and eastward Aleutian Low pressure cell, increased cyclonic circulation, increased Ekman pumping velocity, cooler conditions in the central North Pacific Ocean, and warmer conditions in the eastern North Pacific Ocean. Cool regimes (1947–1976 and 1989–97) showed opposite trends (Mantua et al. 1997).

Changes in the ecology of the North Pacific Ocean also occurred in response to these climatic regime shifts. Following the 1976–77 cool-to-warm shift, the commercial harvest increased for Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), and Pacific salmon (*Oncorhynchus* spp.), and decreased for shrimp, capelin (*Mallotus villosus*), and Pacific herring (*Clupea pallasii*) (Hare and Mantua 2000). The mid-1940s and mid-1970s climate regime shifts were identified in tree ring growth, a proxy for temperature at

coastal land-based stations along the Gulf of Alaska (Wilson et al. 2006).

Climatic and oceanic conditions affect the marine growth rates of Pacific salmon. For sockeye from the Karluk River on Kodiak Island, Alaska, the scale growth during the middle and later part of the marine juvenile growing season was correlated with summer sea surface temperatures in the Gulf of Alaska ($r = 0.49$, $P < 0.01$, $n = 40$) (Martinson 2004). The 1976–77 regime shift was associated with a positive change in immature marine scale growth when the 1976–77 shift was included as a covariate in the model of growth and population density (Martinson et al. 2008). The positive salmon growth and sea-surface temperature relationship is likely indirectly due to increased food availability from increased transport of warm water and species from south to north and increased sunlight and energy for photosynthesis, plankton growth, and food available for salmon.

Monitoring projects on Pacific salmon provide long-term biological time series with records from the 1920s to the present (Martinson et al. 2008). Biological time series are useful for reconstructing and understanding ecological responses to climate change (Helle and Hoffman 1995;

Ruggerone and Rogers 1998; Isakov et al. 2000; Batten and Welch 2004; Martinson et al. 2008). Relating biological time series to climatic and oceanic time series will help us understand and develop hypotheses on the mechanisms by which climate change might alter large marine ecosystems.

The purpose of this study was to determine whether shifts in physical atmospheric and oceanic conditions were recorded in the growth patterns on scales of sockeye salmon that originated from the eastern North Pacific Ocean. A regime shift detection algorithm was used to determine whether climatic regime shifts were recorded as abrupt changes, called shifts, in the patterns of scales of sockeye salmon (*Oncorhynchus nerka*) from the Karluk river and lake, on Kodiak Island, Alaska, from 1924 to 2000. Karluk sockeye are distributed primarily on the continental shelf of the eastern North Pacific as juveniles, in the central and western Pacific Ocean during the immature stage, and in the central and eastern North Pacific Ocean as maturing fish (Myers et al. 1996). Because Karluk sockeye originate in the middle of the latitudinal distribution of North American sockeye, we hypothesize that the indices of fish length estimated from scale radius measurements would increase in response to cool-to-warm regime shifts (+) and to decrease in response to warm-to-cool regime shifts (-).

MATERIAL AND METHODS

Fish length indices

Fish lengths at the end of the freshwater period and at times of marine annulus formation were estimated indirectly from incremental measurements on the scales of adult age-2.2 sockeye salmon that returned from the ocean to the weir on the Karluk River system on Kodiak Island, 1924–2000. Historical field notes indicate that scales were taken a few rows above the lateral line using either a scrape method (1924–51) or with forceps (1952–2000). Some bias may have resulted if scrape samples were not taken consistently from an area immediately (2–3 rows) above the lateral line (Clutter and Whitesel 1956; Scarnecchia 1979). In using scale radius to estimate fish length, we assumed that the growth along the radius of the scale was proportional to the increase in fish length and that the distance between adjacent annuli on a scale depicted one year of somatic growth (Dahl 1909; Fukuwaka and Kaeriyama 1997).

One scale per fish was measured, resulting in 30 to 50 scales per year ($n = 69$ years) for a total of 3,116 scales. Data were missing for the years 1945, 1947, 1958, 1965, 1966, 1969, and 1979. The missing values were estimated using a smoothing technique to establish a continuous time series for the statistical analysis. For each year, scales were selected at equal time intervals throughout the collection period from the early run (May 1–July 21) spawning migration. Mea-

Table 1. Results of the regime shift detection test for smolt (FW), juvenile (L1), immature (L2), and maturing (L3) body length as estimated from scale measurements of age-2.2 sockeye salmon that returned to the Karluk River on Kodiak Island, Alaska, 1924–2000.

Length Variable	Regime			Shift		
	No. of Years	Years	Mean (mm)	Year	Direction	Confidence Interval
FW	14	1922-1935	0.709930			
	63	1936-1998	0.639646	1936	↓	5.58E-06
L1	15	1922-1936	1.712347			
	20	1937-1956	1.673877	1937	↓	0.040799
	17	1957-1973	1.709088	1957	↑	0.12392
	15	1974-1988	1.788408	1974	↑	0.00345
	7	1989-1995	1.672092	1989	↓	0.000692
L2	3	1996-1998	1.778136	1996	↑	0.035939
	50	1923-1972	2.445125			
L3	27	1973-1999	2.587601	1973	↑	2.05E-09
	33	1924-1957	2.735112			
L3	17	1958-1973	2.837429	1958	↑	0.001023
	17	1974-1990	2.975105	1974	↑	5.39E-05
	8	1991-1998	2.842775	1991	↓	0.000865
	2	1999-2000	2.984582	1999	↑	0.105114

measurements were made using imaging software along a reference line drawn from the focus to the edge of the scale along the longest axis of the anterior portion of the scale (Narver 1968). A mark was placed at the end of the freshwater growth zone, at the end of each annulus, and at the edge of the scale.

Four fish length indices were calculated for the analysis. Smolt length (FW) was estimated as the total radius from the focus of the scale to the end of freshwater growth. Juvenile length (L1) was estimated as the total radius from the focus to the end of the 1st marine annulus on the scale. Immature length (L2) was estimated as the total radius from the focus to the end of the 2nd marine annulus. Maturing length (L3) was estimated as the total radius from the focus to the edge of the scale, at the time of capture in river. For each length index, mean values were constructed by year.

Statistical Analysis

The hypotheses we tested were that fish length indices would increase in response to cool-to-warm (+) climate

shifts (1926, 1958, 1977, and 1998) and decrease in response to warm-to-cool (-) climate shifts (1943, 1947, 1971, and 1989). The North Pacific Ocean mean winter SST shifted in 1926 (+), 1943 (-), 1958 (+), 1971 (-) and 1977 (+) (Yasunaka and Hanawa 2005). North Pacific atmospheric circulation and sea level pressure shifted in 1926 (+), 1947 (-), 1977 (+), 1989 (-), and 1998 (+) (Mantua et al. 1997). We expected eight shifts in each of the four fish length indices time series for a total of 32 possible shifts. All four time series were assumed independent.

To statistically detect shifts in the mean state of each fish length index time series we used a sequential *t*-test analysis of regime shifts (STARS) (Rodionov 2005). The STARS program automatically detects shifts in the time series as the sequential data points enter the model and estimates the magnitude of the shift over the duration of the regime (Rodionov 2004). The confidence level of the difference between the mean values of neighboring regimes is based on the Student's two-tailed *t*-test with unequal variance (TTEST procedure in Excel) at a 90% significant level and a default cutoff length of 10 years. For the one-tailed test and hypotheses

Shifts in the mean for FW, 1922-1998

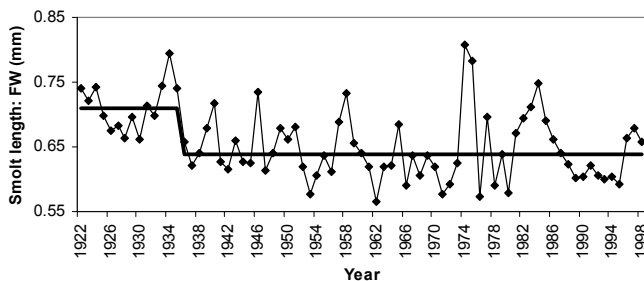


Fig. 1. Regime shift detection for smolt length (FW) in years 1922-1998 estimated from scale measurements of age-2.2 sockeye salmon that returned to the Karluk River on Kodiak Island, Alaska, 1924-2000. A shift occurred in 1936. Data are missing for 1943, 1945, 1956, 1963, 1964, 1967, 1977.

Shifts in the mean for L2, 1923-1999

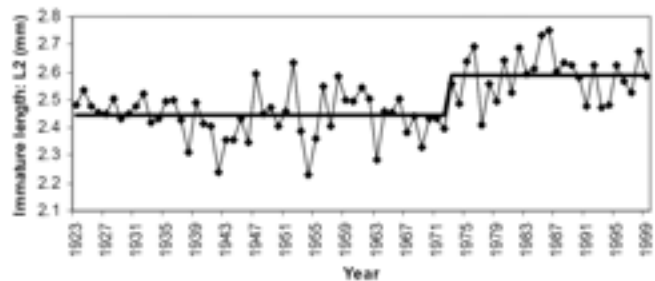


Fig. 3. Regime shift detection for immature length (L2) in years 1923-1999 estimated from scale measurements of age-2.2 sockeye salmon that returned to the Karluk River on Kodiak Island, Alaska, 1924-2000. A shift occurred in 1973. Data are missing for 1944, 1946, 1957, 1964, 1965, 1968, 1978.

Shifts in the mean for L1, 1922-1998

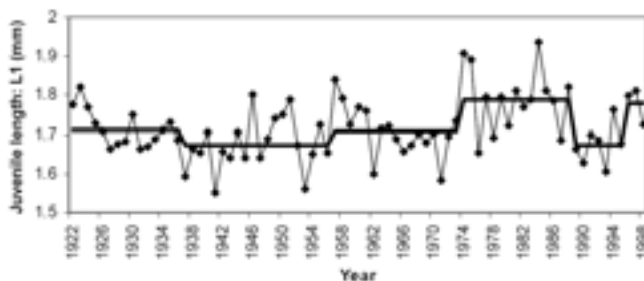


Fig. 2. Regime shift detection for juvenile length (L1) in years 1922-1998 estimated from scale measurements of age-2.2 sockeye salmon that returned to the Karluk River on Kodiak Island, Alaska, 1924-2000. Shifts occurred in 1937, 1957, 1974, 1989, 1996. Data are missing for 1943, 1945, 1956, 1963, 1964, 1967, 1977.

Shifts in the mean for L3, 1924-2000

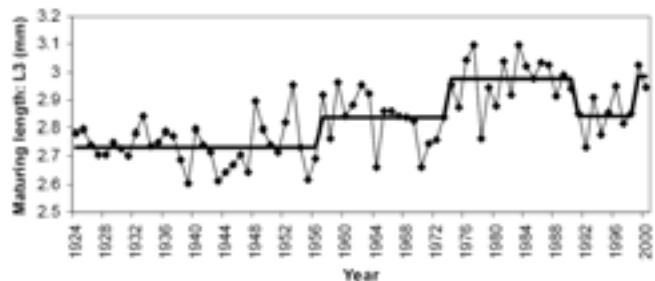


Fig. 4. Regime shift detection for maturing length (L3) in years 1924-2000 estimated from scale measurements of age-2.2 sockeye salmon that returned to the Karluk River on Kodiak Island, Alaska, 1924-2000. Shifts occurred in 1958, 1974, 1991, and 1999. Data are missing for 1945, 1947, 1958, 1965, 1966, 1969, 1979.

there is a 5% probability that two of the 32 shifts will occur by random chance. A significant shift means there is a difference in the mean level between the two regimes. The STARS algorithm was written in Visual Basic and is available from the Bering Climate website (<http://www.beringclimate.noaa.gov/regimes/index.html>).

RESULTS

Of the 32 possible shifts, only two shifts occurred in the same year and direction that was hypothesized (Table 1). A hypothesized positive shift occurred in 1958, but not 1926, 1977, and 1998. In this shift, the maturing fish length index (L3) had a significant positive shift in 1958 from 2.73511 mm in a 33-year regime (1924–1957) to 2.8374 mm in a 17-year regime (1958–1973). A hypothesized negative shift occurred in 1989, but not 1943, 1947, and 1971. In this shift, the juvenile fish length index (L1) had a significant negative shift in 1989 from 1.78841 mm in a 15-year regime (1974–1988) to 1.67210 mm in a seven-year regime (1989–1995). Similarly, with a one-year time lag between regime shift and fish length shift, an additional match between climate and length shifts occurred in 1958. This low frequency of matches in regime shifts and fish length shifts by exact year and a one-year lag is about the same as expected by random chance.

Of the eleven fish length shifts observed among the four time series, nine occurred in years with no specific hypothesis for shifts. Smolt length (FW) had a negative shift in 1936 (Fig. 1). Juvenile length (L1) had positive shifts in 1957, 1974, and 1996, and negative shifts in 1937 and 1989 (Fig. 2). Immature length (L2) had a positive shift in 1973 (Fig. 3). Maturing length (L3) had positive shifts in 1958, 1974, and 1999 and a negative shift in 1991 (Fig. 4). None of the eleven shifts occurred in the opposite direction than was hypothesized.

DISCUSSION

Climate regime shifts in the North Pacific Ocean were not consistently observed as statistical shifts in the time series of indices of fish length for sockeye salmon that returned to the Karluk River on Kodiak Island, Alaska. At contemporaneous lags, shifts in the sea surface temperatures in the North Pacific Ocean were detected as shifts in fish length in 1958 (+), but not in 1926 (+), 1943 (-), 1971 (-) and 1977 (+) (Yasunaka and Hanawa 2005). Shifts in the atmospheric circulation and sea level pressure of the North Pacific were detected as shifts in length in 1989 (-), but not 1926 (+), 1947 (-), 1977 (+), and 1998 (+) (Mantua et al. 1997). The influence of underlying and interacting cycles (i.e. predators, prey, competitors, generation length) and density-dependent effects on the growth of salmon may confound the exact year when a regime shift affected the marine growth of Karluk sockeye (Martinson et al. 2008). Despite the low number of matching shifts, some patterns in shifts were found. The

shifts in fish length indices coincided with the 1957–58 El Niño, the 1989 warm-to-cool regime shift, and preceded the 1976–77 cool-to-warm regime shift in the North Pacific Ocean.

First, the 1957–58 El Niño event that warmed the Gulf of Alaska and North Pacific Ocean was shown as positive shifts in the juvenile and maturing length and as a positive outlier in the smolt length index. During the 1998 El Niño, immature chum salmon were larger and had an earlier growing season than in the cooler waters of the 1999 La Nina in the central North Pacific Ocean (Martinson and Helle 2000). For Karluk sockeye salmon, the El Niño events were not consistently associated with increases in fish length. However, the 1958, 1983, and 1998 El Niño events were observed as positive outliers in the smolt length index rather than in the length incurred in salt water.

Second, the 1989 negative shift in the L1 index corresponded with reduced atmospheric circulation and sea level pressure shift in the North Pacific Ocean (Mantua et al. 1997). Both the 1989 shift and the mid-1990s shift in L1 corresponded with shifts in the Arctic Oscillation, an index of atmospheric pressure in the Bering Sea (www.beringclimate.noaa.gov).

Third, all three marine fish length indices had shifts during the early 1970s. Several possible reasons could explain the occurrence of shifts three and four years (1973–74) prior to the 1977 cool-to-warm regime shift and following two very cold winters in 1971–72. First, the 1971–72 cold winters increased winter winds and storms in the Gulf of Alaska. Storms bring nutrients from deep layers to the surface at an upwelling rate of 10–30 m/yr in the middle of the Alaska gyre. Upwelled nutrients are then transported to the continental shelf by Ekman flow away from the gyre center (Coyle and Pinchuk 2003). Nutrients in the form of nitrates are also transported by deepwater flow to the shelf (Coyle and Pinchuk 2003). Second, 1973 was also an El Niño year. Regime shifts are correlated with and appear to begin as El Niño events (Yasunaka and Hanawa 2005). Third, the one-year time lag between the L2 shift in 1973 and the L1 and L3 shifts in 1974 may be due to an offshore process in the central or western North Pacific Ocean that propagated into the Gulf of Alaska. Therefore, these indices of fish length may be useful predictors several years in advance of future changes in the ecosystem structure in the North Pacific Ocean.

Two possible brood-year effects occurred in the time series where shifts in body size during an earlier life stage were detected as shifts during a later life stage. For example, the negative shift in L1 in 1989 corresponded with a negative shift in L3 in 1991 and the positive shift in L2 in 1973 corresponded with a positive shift in L3 in 1974. In addition, waters in the Gulf of Alaska were cold in 1991 and warm in 1974 (Hare and Mantua 2000). A combined brood-year effect and temperature-related anomalies in production in the Gulf of Alaska may account for the shifts in length.

The coherence in the timing of the shifts in L1 and

L3 time series indicates that a similar process affected the growth of juvenile and maturing sockeye salmon from the Karluk River. Both juvenile and maturing salmon spend a portion of their life in the eastern North Pacific Ocean, while immature salmon occur in the central and western North Pacific Ocean (Myers et al. 1996). In addition, fewer shifts in the L2 than the L1 and L3 time series indicate that fish in the central North Pacific Ocean may occupy a more stable environment than fish in coastal waters of the Gulf of Alaska and the eastern North Pacific Ocean.

From a regional perspective, similar shifts occurred in the indices of fish length at maturing of sockeye salmon that returned to the Karluk River in the Gulf of Alaska and to Bristol Bay in the eastern Bering Sea. For example, the mid-1970s and the late 1980s shifts in the L3 time series for Karluk sockeye salmon were also detected as shifts in the mean age-specific length of adult Bristol Bay sockeye, however only after the data were filtered for the effects of sockeye and pink salmon abundance (Ruggerone et al. 2007). Coherence in the response of length changes in sockeye salmon from the Gulf of Alaska and Bering Sea indicate that similar processes affected recent shifts in the final body size at maturity of sockeye salmon in the two regions.

Even though most shifts in the fish length indices did not match shifts in climate regime indices, the indices of fish length have some potential as predictors of major ecosystem change in the North Pacific Ocean. For example, shifts in juvenile, immature, and maturing lengths occurred several years in advance of the 1976–77 major climate and ecosystem change in the North Pacific Ocean. The overall increases in the fish length indices over time and especially around the 1958 El Niño and the 1976–77 regime shift indicates that further increases in sea-surface temperatures would possibly increase the body length of these sockeye salmon originating from the eastern North Pacific.

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Energy Density and Length of Juvenile Pink Salmon *Oncorhynchus gorbuscha* in the Eastern Bering Sea from 2004 to 2007: a Period of Relatively Warm and Cool Sea Surface Temperatures

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Abstract: Juvenile pink salmon (*Oncorhynchus gorbuscha*) were examined in the eastern Bering Sea from 2004 to 2007 to assess the influence of ocean temperature on whole body energy content (WBEC), length, and diet. Fish were collected during the United States Bering-Aleutian Salmon International Study (U.S. BASIS) surveys in the eastern Bering Sea. Warmer spring and summer sea surface temperatures prevailed from 2004 to 2005 on the eastern Bering Sea shelf, whereas cooler spring and summer sea surface temperatures occurred from 2006 to 2007. Juvenile pink salmon changed diet between the warm and cool years. Walleye pollock *Theragra chalcogramma* dominated the diet (> 50% wet mass) in warm years, while walleye pollock were nearly absent from the diet in cool years. Juvenile pink salmon lengths were significantly longer in warm years but WBEC was significantly lower. We interpret our results to indicate that length is not always a reliable measure of energy status.

Keywords: pink salmon, *Oncorhynchus gorbuscha*, Bering Sea, energy density, whole body energy content (WBEC), diet, growth

INTRODUCTION

Juvenile Pacific salmon (*Oncorhynchus* spp.) early marine survival has been linked to early marine growth rate within nearshore environments (Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007). Size-selective mortality of juvenile salmon is believed to occur during two time periods. The first period occurs after entering the nearshore marine environment and is attributed to predation (Parker 1968; Willette et al. 1999). The second period is during the first winter at sea and is attributed to size and energy reserves (Beamish et al. 2004; Moss et al. 2005). The growth rate of juvenile salmon is linked to climate-driven processes that regulate ocean productivity (Farley et al. 2007). Thus, early marine survival of Pacific salmon is thought to be a reflection of the carrying capacity of the ecosystem they inhabit.

In the eastern Bering Sea, ocean productivity is hypothesized to oscillate, benefitting either pelagic or benthic habitats (Hunt et al. 2002; Mueter et al. 2007). The oscillating control hypothesis (OCH) predicts that the timing of the ice retreat and spring sea surface temperatures (SST) will dictate how ocean productivity is distributed between pelagic

and benthic environments in the southeastern Bering Sea. Early ice retreat and higher spring SSTs will lead to higher pelagic production during warm years, and conversely, late ice retreat and lower spring SSTs will lead to lower pelagic production and higher benthic production during cool years (Hunt et al. 2002). Research on salmon ecology indicates that juvenile salmon growth and early marine survival are regulated by bottom-up control in the eastern Bering Sea ecosystem (Straty 1974; Farley et al. 2007; Farley et al. in press).

In this paper, we test the impact of warm versus cool oceans on the condition of juvenile pink salmon (*O. gorbuscha*). The data are from trawl surveys conducted on the eastern Bering Sea shelf during late August to early October 2004 through 2007. A previous study on juvenile pink salmon suggests that their size was significantly different, being larger in warm spring SSTs and smaller in cool spring SSTs, and that diet and relative abundance shifted between spring SST states (Farley et al. in press). Our analysis expands on previous work by adding data for another year and includes energy density measurements of juvenile pink salmon.

MATERIAL AND METHODS

Field Methods

Fisheries and oceanographic data were collected during the U.S. BASIS trawl surveys conducted from 2004 to 2007 (Fig. 1). Salmon and other fish species were collected following methods described in Farley et al. (2005). At each station, diet analysis was performed on a random sample of up to 10 juvenile pink salmon for each of the following size bins: < 100 mm, 100–200 mm, and 200–300 mm. Contents of the stomachs in each size bin were pooled and then sorted to the lowest taxonomic group. The resulting prey groups were weighed (nearest 0.001 g). At each station, pink salmon were weighed (nearest 1.0 g) and measured (fork length to nearest 1.0 mm; hereafter referred to as length) on board, and the first two juvenile pink salmon from each trawl haul were labeled and frozen whole for laboratory analyses. This systematic sampling allowed us to obtain a representative sample of the juvenile pink salmon captured in our trawl.

Laboratory Methods

Juvenile pink salmon energy densities were determined using bomb calorimetry. Prior to bomb calorimetry analysis we obtained a whole fish wet weight (g), and removed oto-

liths and stomach contents. Fish were dried in a VWR 1324 convection oven at 60–65°C until a constant weight (within 0.005 g) was obtained; dried fish were stored in a desiccator until further processing. We homogenized individual fish using a pulverizer for 30 s then transferred the sample to a mortar and pestle and pulverized further until a uniform powder was obtained. For each sample, we pressed pellets weighing approximately 0.15 g and stored them in a desiccator until further processing. These pellets were then combusted in a Parr 1425 Semimicro calorimeter to determine whole body energy content (WBEC). The values generated by the calorimeter were converted from Cal g⁻¹ dry weight to J g⁻¹ dry weight. Total energy (J) represents the calculated energy for the entire fish and was calculated by multiplying WBEC by the dry weight of the fish.

Statistical Methods

The eastern Bering Sea was split into two areas north and south of 60°N latitude, based on the potential for pink salmon to be from different stock groups and to minimize the effects of survey timing between the two areas. For example, the southern area was surveyed earlier in the field season while the northern area was completed in the fall. Also, the southern area was intended to more closely match the area discussed by Hunt et al. (2002) with regards to the OCH. We defined the southeastern Bering Sea (SEBS) to include all stations to the south of 59.75°N and the northeastern Bering Sea (NEBS) to include all stations to the north of 59.75°N.

Earlier studies have determined the size and prey of juvenile salmon in the eastern Bering Sea (Farley et al. 2005; Farley et al. in press). In an effort to test the effects of the OCH we pooled our sampling years into warm and cool years. We defined warm and cool years based on whether they had positive or negative spring SST anomalies (www.beringclimate.noaa.gov). Warm years are represented by 2004 and 2005; cool years are represented by 2006 and 2007 (Fig. 2).

Juvenile pink salmon diet data were split by cool and warm years into the two regions, NEBS and SEBS. Prey items were pooled into common groups and expressed as percent wet weight. Dominant prey categories included: walleye pollock (*Theragra chalcogramma*), squid and octopus, pteropod, Pacific sand lance (*Ammodytes hexapterus*), other, other fish (ofish), larvacea, euphausiid, decapoda, copepod, capelin (*Mallotus villosus*), and amphipoda. The group ‘other’ represents: cnidaria, mysida, *Evadne* sp., insecta, polychaeta, bivalvia, cumacea, haploids, and chaetognatha. The group ‘ofish’ represents: hexagrammidae, cottidae, pleuronectidae, *Pleurogrammus monopterygius*, *Gadus macrocephalus*, *Clupea pallasii*, *Lumpenus fabricii*, teleostei, and *Sebastes* sp.

We tested for differences in juvenile pink salmon lengths between cool and warm years (i.e. spring SSTs) for the NEBS and SEBS regions. In an effort to account for the effect of growth during the survey we fitted a series of length models as a function of Day of Year by region (i.e. SEBS

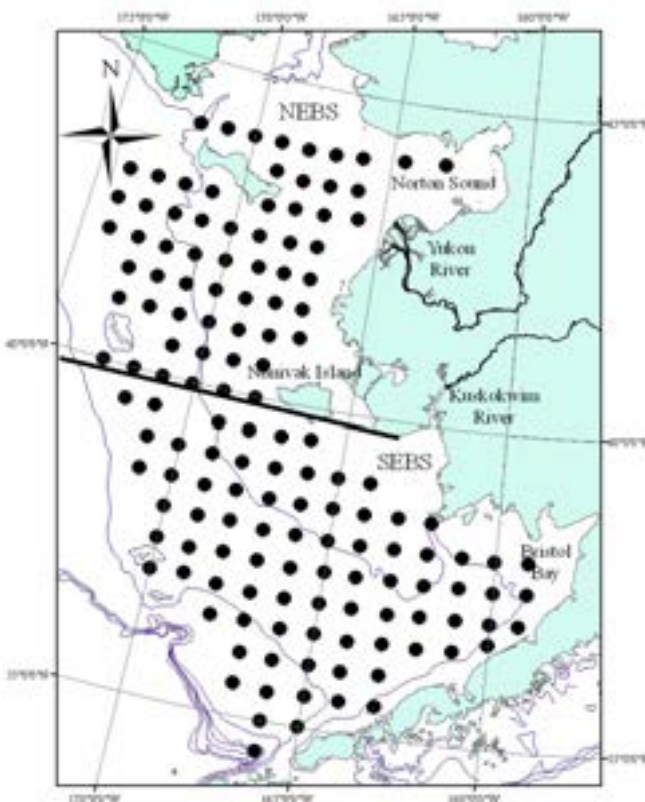


Fig. 1. Study area in the eastern Bering Sea. Solid line demarcates the area where the northeastern Bering Sea (NEBS) and the southeastern Bering Sea (SEBS) were split for our statistical analyses.

and NEBS) and selected the best fitting models using F-tests and the Akaike Information Criterion (AIC) (Tables 1 and 2). The first model tested for the effect of Day of Year, the second model tested for the effect of Day of Year and spring SST, and the third model included an interaction term to test for variable slope. We evaluated whether the interaction between Day of Year and spring SST was significant to determine if the slopes were different. If the interaction term was not significant, we compared the remaining two models

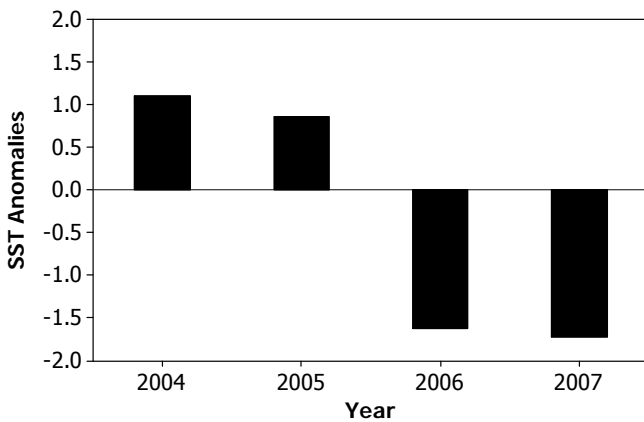


Fig. 2. Sea surface temperature anomalies based on mean May SSTs for the southeastern Bering Sea from 1948 to 2008. Mean May SSTs were averaged over the area 54°18'N to 60°00'N;161°12'W to 172°30'W using data from the NCEP/NCAR project (Kalnay et al. 1996). The SST anomalies are deviations from the mean May SST value (2.33°C) for the 1970–2000 period normalized by the S.D. (0.76°C). Warm years are represented by 2004 and 2005 while cool years are represented by 2006 and 2007.

to determine whether there was a significant difference in length between cool and warm years (spring SST effect).

Similarly, we tested for differences in total energy between cool and warm years for the NEBS and the SEBS regions. We fitted a series of three energy content models as a function of length between cool and warm years for each region (Tables 3, 4). The first model tested for the effect of length, the second model tested for the effect of length and spring SST, and the third model included an interaction term to test for variable slope. Each model was evaluated using the *p*-values and models were selected using the results of F-tests and the AIC. We used log transformed (total energy) and log transformed (length (mm)). First, we tested whether the slopes were constant by evaluating whether the interaction effect between spring SST and length was significant. If slopes were not significantly different, we compared the remaining models for the best performance. If the interaction term was significant, then differences in lengths were evaluated using an ANOVA.

RESULTS

Diet

Diets of juvenile pink salmon differed between warm and cool years in the eastern Bering Sea (Fig. 3). Walleye pollock were a major diet component in warm years and nearly absent in cool years; walleye pollock made up over 50% of the diet by wet weight of juvenile pink salmon in the SEBS during warm years. Overall, fish (i.e. walleye pollock, Pacific sand lance, capelin, and ofish) were larger compo-

Table 1. Series of models testing the effect of day of year and ocean condition on lengths in the SEBS. Model performance was evaluated using the results of F-tests and the AIC.

SEBS Fork Length Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β1	β2	β3						
M1: $y = \beta_0 + \beta_1 \cdot x_1 + \text{error}$	< 0.001			2325	1,003,564				20,727
M2: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \text{error}$	< 0.001	< 0.001		2324	855,534	M1&M2	401.9	< 0.001	20,357
M3: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + b_3 \cdot (x_1 \cdot x_2) + \text{error}$	< 0.001	0.172	0.942	2323	855,532	M2&M3	0.005	0.942	20,359

y is fork length; *x*₁ is day of year; *x*₂ dummy variable for ocean condition; β₀, β₁, β₂, and β₃ are regression coefficients.

Table 2. Series of models testing the effect of day of year and ocean condition on lengths in the NEBS. Model performance was evaluated using the results of F-tests and the AIC.

NEBS Fork Length Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β1	β2	β3						
M4: $y = \beta_0 + \beta_1 \cdot x_1 + \text{error}$	< 0.001			2764	1,223,348				24,706
M5: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \text{error}$	< 0.001	< 0.001		2763	1,193,424	M4&M5	74.6	< 0.001	24,639
M6: $y = \beta_0 + \beta_1 \cdot x_1 + \beta_2 \cdot x_2 + b_3 \cdot (x_1 \cdot x_2) + \text{error}$	< 0.001	< 0.001	< 0.001	2762	1,107,779	M5&M6	213.5	< 0.001	24,435

y is fork length; *x*₁ is day of year; *x*₂ dummy variable for ocean condition; β₀, β₁, β₂, and β₃ are regression coefficients.

Table 3. Series of models testing the effect of length and ocean condition on energy content in the SEBS. Model performance was evaluated using the results of F-tests and the AIC.

SEBS Energy Content Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β_1	β_2	β_3						
M7: $y = \beta_0 + \beta_1 x_1 + \text{error}$	< 0.001			167	0.61				-463.5
M8: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \text{error}$	< 0.001	0.003		166	0.58	M7&M8	8.94	0.003	-470.3
M9: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 (x_1 x_2) + \text{error}$	< 0.001	0.116	0.093	165	0.57	M8&M9	2.86	0.093	-471.2

y is log transformed total energy content; x1 is log transformed fork length; x2 dummy variable for ocean condition; β_0 , β_1 , β_2 , and β_3 are regression coefficients.

Table 4. Series of models testing the effect of length and ocean condition on energy content in the NEBS. Model performance was evaluated using the results of F-tests and the AIC.

NEBS Energy Content Models	P-values (coefficients)			Res. DF	RSS	F-Test	F	P-value	AIC
	β_1	β_2	β_3						
M10: $y = \beta_0 + \beta_1 x_1 + \text{error}$	< 0.001			120	0.45				-331.3
M11: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \text{error}$	< 0.001	0.030		119	0.43	M10&M11	4.77	0.031	-334.1
M12: $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 (x_1 x_2) + \text{error}$	< 0.001	0.934	0.893	118	0.43	M11&M12	0.02	0.893	-332.1

y is log transformed total energy content; x1 is log transformed fork length; x2 dummy variable for ocean condition; β_0 , β_1 , β_2 , and β_3 are regression coefficients.

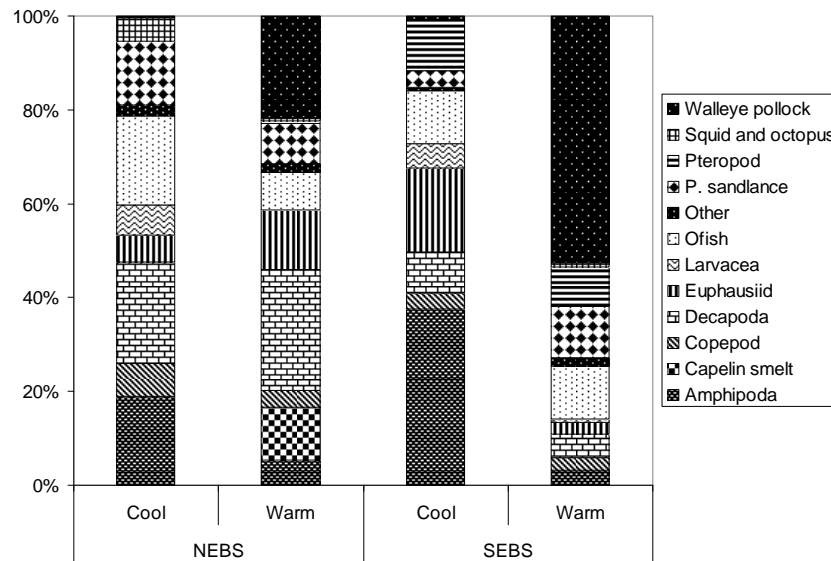


Fig. 3. Comparison of juvenile pink salmon diets in the northeastern Bering Sea (NEBS) and the southeastern Bering Sea (SEBS) during warm (2004 and 2005) and cool (2006 and 2007) years.

nents of the diet in warm years than in cool. In cool years, amphipoda, copepod, decapoda, euphausiids and larvacea comprised from 60 to 70% of the diet. Interestingly, larvacea were present in the diets during cool years and nearly absent in warm years.

Diets were also different between the NEBS and SEBS. Although amphipoda, decapoda, and copepods were important diet components in both regions, decapoda were three times higher in the NEBS. Overall, fish comprised a larger

percentage of the diet in the SEBS, with walleye pollock dominating the fish component. Capelin and squid and octopus were present in the diets in the NEBS and nearly absent in the SEBS, while pteropods were present in the SEBS and nearly absent in the NEBS.

Length Comparison

Juvenile salmon were significantly longer during the

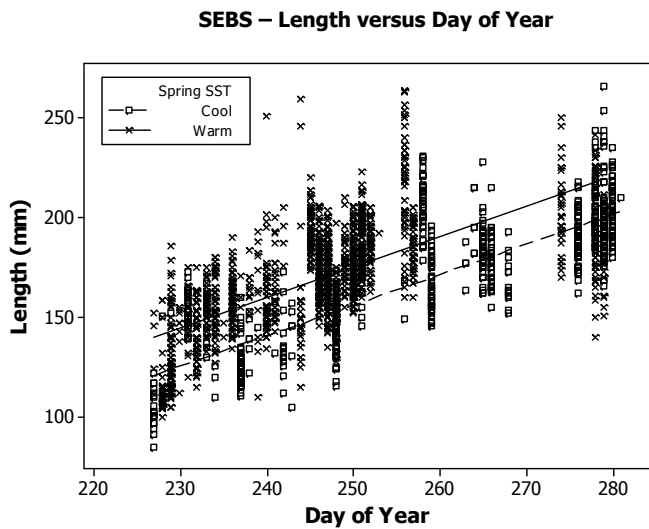


Fig. 4. Plot of juvenile pink salmon lengths versus Day of Year from fish collected in the southeastern Bering Sea (SEBS). Results of an analysis of covariance (ANCOVA) showed that on a given sampling day (Day of Year) juvenile pink salmon are significantly larger during warm years than cool years ($P < 0.01$).

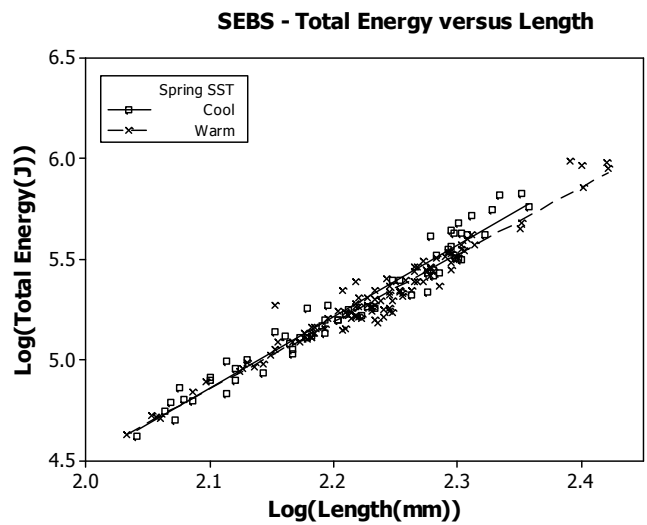


Fig. 6. Plot of log transformed (total energy (J)) versus log transformed (length (mm)) from juvenile pink salmon collected in the southeastern Bering Sea. Results of an analysis of covariance (ANCOVA) showed that total energy is significantly higher during cool years in the SEBS.

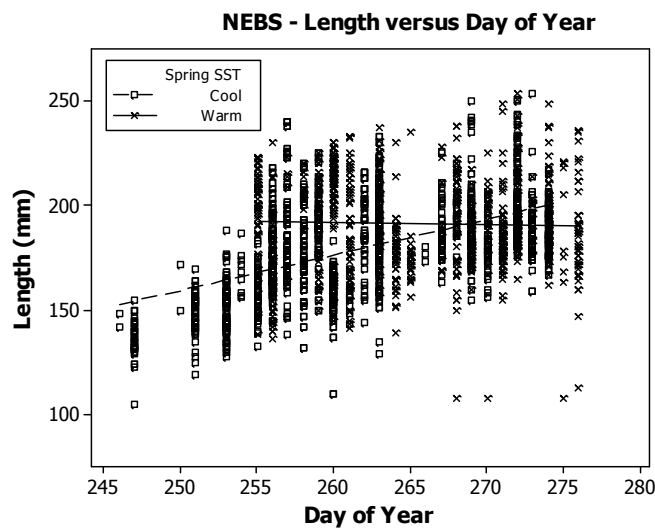


Fig. 5. Plot of juvenile pink salmon lengths versus Day of Year from fish collected in the northeastern Bering Sea (NEBS). Results of an analysis of covariance (ANCOVA) showed that there is significant interaction ($P < 0.01$) between climate and Day of Year reflecting that the slopes are different.

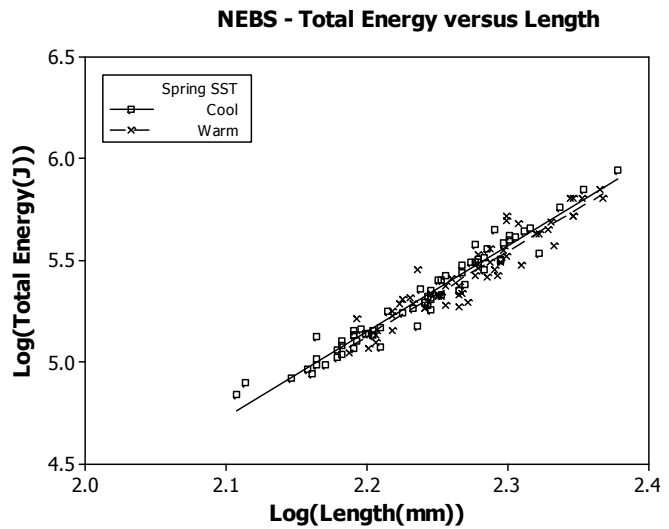


Fig. 7. Plot of log transformed (total energy (J)) versus log transformed (length (mm)) from juvenile pink salmon collected in the northeastern Bering Sea. Results of an analysis of covariance (ANCOVA) showed that total energy is significantly higher during cool years in the NEBS.

warm years in both regions. In the SEBS, we determined that the interaction term between spring SST and Day of Year was not significant (Table 1, M3: $P = 0.942$), which allowed us to assume constant slopes and to test M1 and M2 for best performance. M2 was significantly different from M1 ($P = 0.003$) and had a lower AIC value. We selected M2 which included both an effect for Day of Year and spring SST and determined that, for a given Day of Year, juvenile pink salmon were 19 mm longer in warm years (Fig. 4). In the NEBS, the interaction between spring SST and Day of

Year was significant (Table 2, M6: $P < 0.001$), indicating that the slopes were not constant (Fig. 5). This prevented us from testing for differences in lengths between cool and warm years using the general linear models. Using an analysis of variance (ANOVA), we tested for differences in lengths on a dataset that constrained the sampling days to include Day of Year between 255 and 275; this was the period of greatest overlap between cool and warm years in the NEBS. In the NEBS, we found that fish were significantly longer ($P < 0.01$) in warm years; mean length was 184.0 mm in cool

years and mean length was 191.8 mm in warm years.

Total Energy Comparison

Juvenile pink salmon had higher total energy during cool years in both the SEBS and NEBS (Figs. 6, 7). We determined that the interaction between spring SST and log transformed (length (mm)) was not significant in the SEBS (Table 3, M9: $P = 0.093$) or the NEBS (Table 4, M12: $P = 0.893$). We compared the remaining two models in each region and found similar results with M8 and M11 being the most parsimonious models. These models included a term for length as well as a term for spring SST. Spring SST was significant in the SEBS ($P = 0.003$) and the NEBS ($P = 0.030$), where fish total energy content values in cool years had consistently higher predicted values in both regions. Using the best models (i.e. M8 and M11) we calculated the predicted total energy for a 200-mm fish and determined that there is a difference of 23.0 kJ in the SEBS and 21.7 kJ in the NEBS, between cool and warm years.

DISCUSSION

Our results highlight a possible uncoupling between length and total energy content for juvenile pink salmon captured on the eastern Bering Sea shelf. Previous studies indicated that larger juvenile Pacific salmon during their first year at sea have a survival advantage over smaller conspecifics (see Farley et al. 2007). Presumably, larger juvenile salmon after their first year at sea would be better fit (higher lipid reserves) to survive their first winter at sea. This study found that juvenile pink salmon were significantly longer in warm years but, for a given size, had significantly lower total energy. Higher marine growth has been linked with higher adult salmon survival (Beamish et al. 2004; Moss et al. 2005) and higher energy reserves in some fish (Eurasian perch, *Perca fluviatilis*) are thought to be important for winter survival (Huss et al. 2008). Thus, a critical aspect of our results is what biological characteristic of juvenile pink salmon will best represent their ability to survive the first winter at sea.

On the eastern Bering Sea shelf, juvenile pink salmon were able to store more energy in cool years than in warm years. A similar study that compared age-0 walleye pollock diet, length, energy density and overwinter survival between cool and warm SST states found that age-0 walleye pollock captured during warm years were significantly larger, but had significantly lower energy density and reduced overwinter survival (Moss et al. 2009). Although more work is needed to determine the biological significance of having higher energy reserves, it may mean these fish can avoid starvation and death during their first winter at sea while fish with lower energy content cannot. Thus, studies that focus only on length as a measure of energetic status may increase the probability of incorrectly forecasting adult returns or recruitment, as over-winter mortality of juvenile fish is likely

a function of a combination of factors including energy reserves prior to winter.

Energy density of juvenile pink salmon is likely a function of prey quality, prey quantity, and temperature. Different prey items can have very different WBEC values and presumably individual prey species can have variable energy content depending on season and geographical region. Fish and squid tend to have relatively high WBEC when compared with copepods, euphausiids, hyperiid amphipods, pteropods, and larvacea (Davis et al. 1998). Juvenile pink salmon diets contain more fish in warm years and predominantly contain amphipods, copepods, decapods, euphausiids and larvacea in cool years. It appears that salmon have diets with higher energy content during warm years, yet have lower total energy. In Prince William Sound and the Gulf of Alaska, juvenile pink salmon survival and growth were positively correlated with pteropod dominated diets and high gut fullness (Armstrong et al. 2008). Pteropods have lower WBEC than many of the common diet items (Davis et al. 1998) consumed by juvenile pink salmon suggesting that perhaps prey quantity is more important than prey quality. If prey densities are insufficient during warm years on the eastern Bering Sea shelf, density-dependent factors between juvenile pink salmon and their prey could be a factor limiting WBEC. Water temperature may also play an important role in fish energy density. A laboratory study where juvenile coho salmon (*O. kisutch*) were fed *ad libitum* in two temperature treatments found that the fish in the cooler temperature treatment had higher WBEC than the fish in the warmer temperature treatment (Heintz 2009). The hypothesis for this result is that fish allocate more energy to storage when sea temperatures are cooler. Perhaps this observation helps partially explain the higher WBEC in juvenile pink salmon during the cool years.

Our findings show that juvenile pink salmon were significantly longer in warm years. However, based on the constant slopes illustrated in Fig. 4 the apparent growth rates in the SEBS were not significantly different during our sampling period. This suggests that either these fish must have had different growth rates prior to our sampling, or the outmigration timing was different. Although it is unknown what growth rates were prior to our survey it is very likely that earlier outmigration during warm years could have given these juvenile pink salmon a jump on growth that was difficult to overcome by the juveniles in the cool years. In the spring in the eastern Bering Sea, fish may be benefitting from higher pelagic productivity during years with warm SSTs, as predicted by the OCH.

Broad-scale climate changes in the Bering Sea could have far-reaching impacts on the marine ecosystem and the fisheries that it supports (Grebmeier et al. 2006; Mueter et al. 2007). The OCH describes a mechanism that may drive the flow and magnitude of primary production between the pelagic and benthic communities. In the summer and fall, juvenile pink salmon occupy the pelagic zone of the east-

ern Bering Sea and provide insights into the effects of this changing environment. The linkage between the “critical size and period” hypothesis (Beamish and Mahnken 2001) and the OCH (Hunt et al. 2002) could explain the variability of juvenile pink salmon populations as well as many other commercially important species that inhabit the eastern Bering Sea. However, the impact on survival of pink salmon being longer and leaner is unknown and will require future research on threshold requirements of WBEC during the physiologically stressful winter months.

ACKNOWLEDGEMENTS

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Juvenile Pink and Chum Salmon Distribution, Diet, and Growth in the Northern Bering and Chukchi Seas

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Abstract: Loss of non-seasonal sea ice and a general warming trend in the Bering Sea has altered the composition, distribution, and abundance of marine organisms inhabiting the region. Juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon were found in significant numbers throughout the Chukchi Sea and Bering Strait regions during early autumn 2007, reflecting significant utilization of Arctic marine habitat by Pacific salmon. Linear models of juvenile pink and chum salmon body size corrected for Day of Year were parameterized to estimate daily growth rates and habitat-specific differences in body size using 6 years of survey data. Model results revealed that juvenile pink salmon inhabiting the eastern Bering Sea grew at an average rate of $1.17 \text{ mm}\cdot\text{day}^{-1}$ and juvenile chum salmon grew at a rate of $1.21 \text{ mm}\cdot\text{day}^{-1}$. The U.S. BASIS survey area was expanded northward to include the Chukchi Sea during 2007, where larger juvenile pink and chum salmon were found in higher abundances relative to pink and chum inhabiting the eastern Bering Sea. Food habits analyses revealed that juvenile pink and chum salmon fed upon high energy prey in the Chukchi Sea, and that the majority of chum salmon encountered there were from either Alaskan or Russian stocks.

Keywords: pink salmon, chum salmon, Chukchi Sea, eastern Bering Sea, growth

INTRODUCTION

Loss of non-seasonal sea ice and a general warming trend in the Bering Sea has altered the composition, distribution, and abundance of marine organisms inhabiting the region (Grebmeier et al. 2006). Juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon were found in significant numbers throughout the Chukchi Sea and Bering Strait regions during early autumn, reflecting significant utilization of Arctic marine habitat. Marine migration rate plays a key role in the distribution of juvenile salmon within the Bering Sea (Farley et al. 2005). Bering-Aleutian Salmon International Survey (BASIS) research cruises have determined that juvenile pink and chum salmon are consistently distributed the greatest distance from shore as compared with other Pacific salmon species, reflecting high dispersal rates and minimal utilization of nearshore estuarine habitat. Pink salmon consume large amounts of food in order to sustain rapid growth during the early marine life-history stage (Healey 1980); and offshore movements of chum salmon generally coincide with a decline in nearshore food resources and a period when fish attain a body size that allows them to capture and consume prey resources located farther from shore (Simenstadt and Salo 1982).

Environmental conditions can limit or enhance growth

during the early marine life-history stage, which influences over-winter survival and recruitment (Farley et al. 2009; Moss et al. 2009). Climate can affect salmon growth and survival directly through physiological influences such as the effect of water temperature on metabolism, or indirectly through altering migration pathways and the availability of prey resources. The effect of ocean temperature and prey quality on juvenile pink salmon growth rate has been quantified for Gulf of Alaska stocks (Cross et al. 2008), and early marine growth shown to affect over-winter survival during the first year of marine life (Moss et al. 2005). In addition to the potential for thermal conditions to constrain growth, there is also evidence that salmon are food-limited during the offshore migration in the Bering Sea and North Pacific Ocean (Ruggerone et al. 2003; Aydin et al. 2004; Kaeriyama et al. 2004), and that climate variability could alter the distribution and abundance of prey resources.

All five species of Pacific salmon are distributed in the epipelagic waters of the eastern Bering Sea during their first marine summer and fall (Farley et al. in press). Early marine growth is known to positively influence marine survival, and salmon populations that have typically inhabited the Bering Sea are expanding their range into Arctic waters. Therefore, the objective of this study is to document and describe the distribution of juvenile pink and chum salmon in the Chukchi

Sea, and to quantify differences in habitat-specific growth across the Bering and Chukchi seas. In order to accomplish these goals, linear models of juvenile pink salmon body size and Day of Year are parameterized to estimate daily growth rates and to quantify habitat-specific differences in body size. Variability in water temperature and food habits of juvenile pink and chum salmon in the northern Bering and Chukchi seas are also reported.

MATERIALS AND METHODS

Biological Sampling

Juvenile pink and chum salmon were collected in the Bering Strait region and Chukchi Sea aboard the NOAA fisheries research vessel *Oscar Dyson* from September 2nd – September 29th 2007 (Fig. 1), using a midwater rope trawl (model 400/580) made by Cantrawl Pacific Limited of Richmond, B.C., Canada (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.). The net is approximately 198 m long, has hexagonal mesh in the wings and body, and a 1.2-cm mesh liner in the codend, and has a mouth opening of approximately 55 m horizontally and 15 m vertically. It was towed at or near the surface for 30 minutes at speeds between 3.5 and 5 knots at each station, retrieved, and the contents emptied onto a sorting table on deck. Nekton samples were then moved to an onboard laboratory by conveyer belt where standard biological measurements including fork length and body weight

were recorded.

Food habits of juvenile pink and chum salmon were examined on board by removing and pooling the contents of the entire food bolus from the stomachs of up to 10 randomly selected individuals. Stomach contents were weighed to the nearest 0.001 g, sorted, and identified to the lowest feasible taxonomic group. Individual prey groups were weighed and divided by the total weight of prey contained in the stomachs and the proportional contributions of each prey group to the diet were calculated.

Growth Rate Estimation and Habitat-specific Differences in Body Size

Variation in juvenile salmon length and body weight across ocean habitats can provide insight into how juvenile salmon respond to environmental conditions. However, a number of confounding factors such as water temperature, prey availability, and prey quality can act to limit direct interpretations of habitat quality to growth rate or body size. The effect of growth during the course of a survey is an important confounding factor in the U.S. BASIS survey, which was in excess of 50 days during 2007. To correct for the effect of growth during the survey a simple linear regression model with Gaussian error was used to model length as a function of Day of Year (growth rate term) and habitat type with habitat terms estimated as dummy variables or factors for each type of habitat (Venables and Ripley 1999), which was performed using six years (2002–2007) of survey data on body size. The interaction between habitat type and growth rate was not considered, as three of the five habitat categories contained a date range of less than five days. This was considered inadequate to describe habitat-specific growth rates. Habitat types selected for the analysis included two from the eastern Bering shelf region: coastal (bottom depth < 50 m) and middle (100 > bottom depth > 50 m), and three from the Arctic region: Bering Strait (64.0–65.5°N) (bottom depth < 100 m), southern Chukchi Sea (66.0–68.0°N) (bottom depth < 100 m), and northern Chukchi Sea (68.5–70.0°N) (bottom depth < 100 m) (Fig. 1).

RESULTS

Spatial Distribution and Growth

Higher densities of juvenile pink and chum salmon were observed within the vicinity of the Bering Strait and the Chukchi Sea as compared with the eastern Bering Sea during 2007 (Fig. 2). Relatively high densities of pink and chum were also encountered on the eastern Bering Sea shelf within the vicinity of St. Lawrence Island (63.5°N, -170.0°W), south of St. Lawrence to the Pribilof Islands (57.0°N, -170.0°W), and west of Nunivak Island (60.0°N, -166.0°W) (Fig. 2). Sea surface temperatures in the northern Chukchi Sea (10.8°C) were higher on average than the other two areas sampled

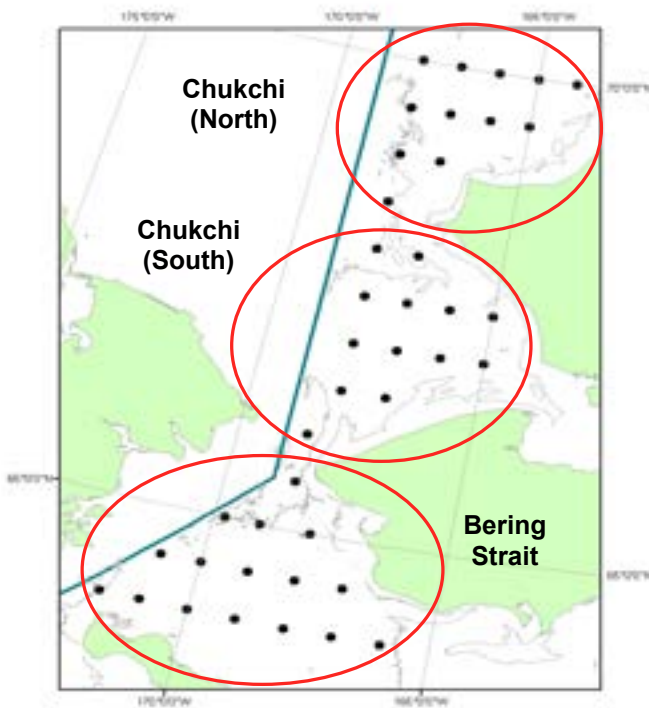


Fig. 1. Survey station locations sampled in the Bering Strait region, southern Chukchi Sea, and northern Chukchi Sea.

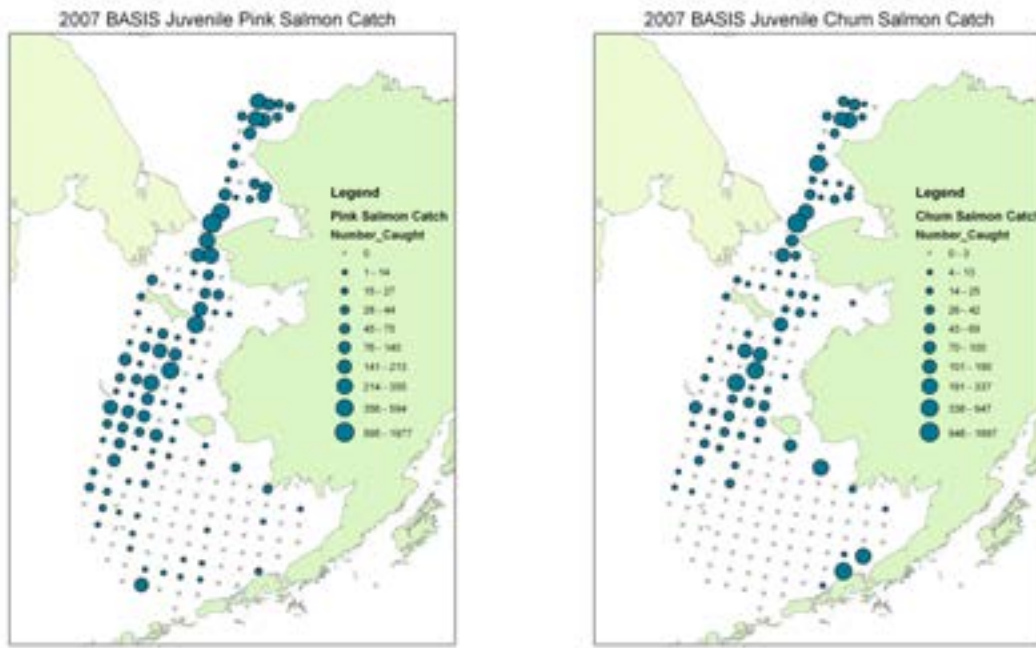


Fig. 2. Relative abundance of juvenile pink and chum salmon inhabiting the eastern Bering Sea, Bering Strait, and Chukchi Sea during late August and early September 2007. Circle size represents catch per unit effort for a 30-minute surface trawl.

in 2007. The southern Chukchi Sea temperatures averaged 9.3°C, and those for the Bering Strait region averaged 8.7°C. Juvenile pink salmon grew less on average (1.17 mm•day⁻¹) than chum salmon (1.21 mm•day⁻¹) during 2007 (Fig. 3). Pink salmon grew at rates comparable to the six-year mean (1.18 mm•day⁻¹) during 2007, whereas juvenile chum salmon grew at above average rates (1.48 mm•day⁻¹). During 2007, pink and chum salmon inhabiting the Bering Strait and Chukchi Sea were also larger on average than those inhabiting the lower latitudes of the eastern Bering Sea (Fig. 4).

Juvenile Pink and Chum Salmon Food Habits

Juvenile pink and chum salmon preyed heavily upon high-energy content prey including fish (5,011 J•g⁻¹), euphausiids (3,110 J•g⁻¹), and appendicularia (3,177 J•g⁻¹) (Tables 1, 2). Pink and chum salmon inhabiting the northern Chukchi Sea preyed most heavily upon fish (> 0.61 of diet by weight). Chum salmon inhabiting the southern Chukchi Sea and northern Bering Sea preyed most heavily upon euphausiids (42%, 36% of diet by weight, respectively), while pink salmon preyed most heavily upon crab megalopa (69%, 39% of diet by weight, respectively) (Table 1).

DISCUSSION

Climate-induced changes in the Bering Sea have caused a thinning and reduction of sea ice and a northward redistribution of subarctic species (Hunt et al. 2002; Overland et al. 2004; Grebmeier et al. 2006). The recent temperature increase in Arctic waters can be attributed to a lack of sea

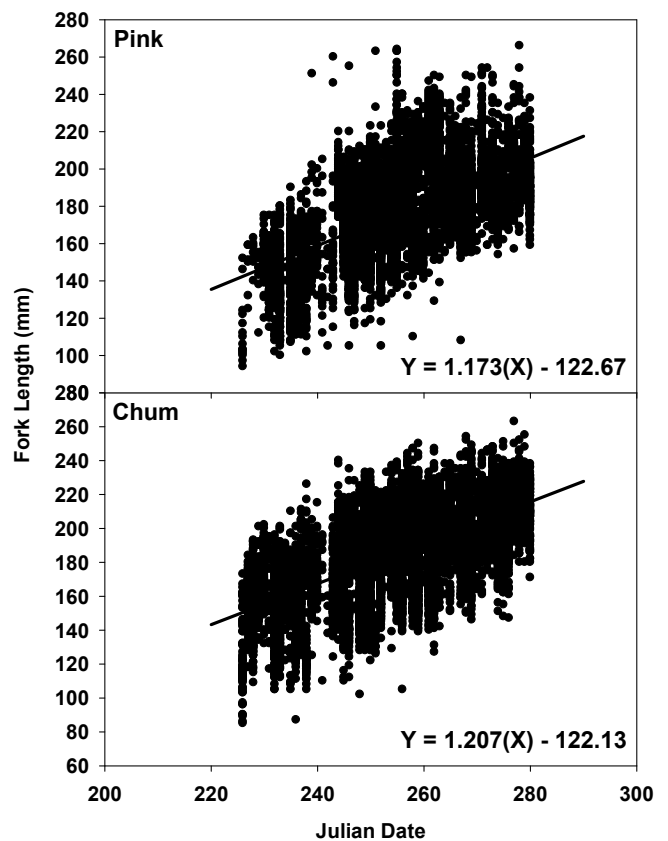


Fig. 3. Linear models representing daily growth of juvenile pink (n = 6,828) and chum (n = 8,769) salmon collected in U.S. BASIS surveys from 2002–2007.

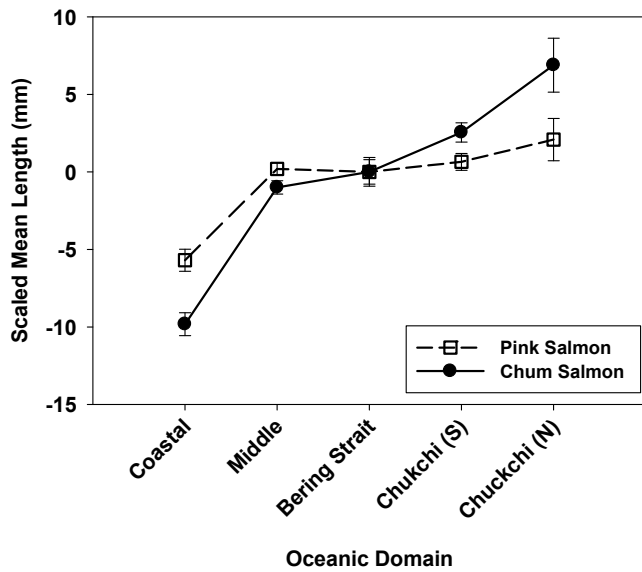


Fig. 4. Estimated average fork length (mm) of juvenile pink and chum salmon by oceanic domain (habitat) during the U.S. BASIS cruise in 2007. Standard error estimates of average length are included.

ice that would normally reflect solar radiation, compared to darker, ice-free ocean water that absorbs solar radiation. Such climate-induced changes may affect salmon feeding and overwintering grounds by influencing inter- and intra-specific competition related to the availability and quality of ocean habitat (Welch et al. 1998). Climate-induced changes may also influence the interactions among the wide variety of salmon stocks in the North Pacific Ocean. During 2007, sea surface temperatures were greatest in the northern Chukchi Sea, followed by temperatures in the southern Chukchi Sea and the Bering Strait. Higher water temperatures combined with a longer photoperiod during summer months could have allowed for longer daily foraging bouts, and more energetically favorable conditions for growth compared to cooler, deeper, eastern Bering Sea waters. It has previously been suggested that cool spring sea surface temperatures lead to slower growth and marine survival of juvenile salmon, and that warmer spring sea surface temperatures lead to more rapid growth (Farley et al. in press). Further, it has been shown that the fastest growing juvenile pink salmon experience higher survival to adulthood (Moss et al. 2005; Cross et al. 2008). Therefore, the combination of increased light and higher water temperatures in the Chukchi Sea is likely resulting in increased lower trophic level productivity, which

Table 1. Prey composition of juvenile pink and chum salmon captured in the northern Chukchi Sea, southern Chukchi Sea, and the Bering Strait region during early autumn 2007.

Prey	Pink salmon			Chum salmon		
	Chukchi North	Chukchi South	Bering Strait	Chukchi North	Chukchi South	Bering Strait
Copepoda	0.008	0.010	0.228	0.009	0.001	0.042
Amphipoda	0.000	0.005	0.015	0.000	0.057	0.058
Euphausiacea	0.268	0.250	0.130	0.241	0.418	0.361
Pteropoda	0.000	0.002	0.000	0.000	0.000	0.000
Chaetognatha	0.000	0.000	0.010	0.000	0.000	0.004
Appendicularia	0.038	0.005	0.006	0.025	0.150	0.214
Coelenterata	0.000	0.000	0.000	0.000	0.174	0.193
Megalopa	0.075	0.687	0.389	0.032	0.192	0.027
Fish	0.611	0.041	0.222	0.693	0.008	0.101

Table 2. Prey energy density (wet weight) and percent indigestible values of prey identified in juvenile pink and chum salmon diet.

Prey	Percent indigestible	Energy content (J·g ⁻¹)	Literature sources
Copepoda	9.04	2,624.2	Davis et al. 1998, Boldt and Haldorson 2002
Amphipoda	12.99	2,465.6	Davis et al. 1998, Boldt and Haldorson 2002
Euphausiacea	10.35	3,110.2	Davis et al. 1998, Boldt and Haldorson 2002
Pteropoda	10.00	2,612.1	Model default value
Chaetognatha	8.50	2,213.0	Davis et al. 1998, Boldt and Haldorson 2002
Appendicularia	10.00	3,177.2	Davis et al. 1998, Boldt and Haldorson 2002
Coelenterata	10.00	1,975.8	Davis et al. 2003, Model default value
Megalopa	8.50	2,980.4	Nishiyama 1977, Boldt and Haldorson 2002
Fish + Squid	8.98	5,010.6	Nishiyama 1977, Boldt and Haldorson 2002

is cascading up the food chain to fishes that prey upon zooplankton.

A closer examination of habitat-specific differences in length showed that pink and chum salmon body size increased from coastal waters seaward across the eastern Bering Sea shelf. Similar differences in size patterns have been reported for pink and chum inhabiting the Gulf of Alaska (Farley et al. 2005; Cross et al. 2008). Chum salmon growth rates were above average in 2007, which may have been the result of earlier ocean entry and seaward migration than that in a 'typical' year. The observed growth rate differences suggest that environmental conditions in the northern Chukchi Sea were better for supporting growth, which could be due to the presence of higher quality prey, as well as more energetically favorable water temperatures and a longer photoperiod for these visually foraging fish. High quality prey items in the northern Chukchi Sea likely enhanced juvenile pink and chum salmon growth as well, and given a potential for high growth rates in the Chukchi Sea, juvenile pink and chum salmon that inhabit this region will likely benefit from the shallow shelf habitat. The combined effects of prey quality, prey availability, and water temperature which support chum salmon growth and survival in Arctic waters should be further investigated using bioenergetics models. Bioenergetics model simulations can be used to reveal the combined influence of biophysical factors such as juvenile pink and chum salmon physiology, prey quality, and thermal experience.

Juvenile chum salmon captured in the Bering Strait region were primarily from northern Russia (Kondzela et al. 2009), and may have been passively transported from coastal Siberia to the eastern Bering Strait by the Anadyr Current. Climate-based effects on the Arctic and northern Bering Sea ecosystem may cause a trophic feedback loop and increase competition for zooplankton prey (Aydin et al. 2000). The ability to predict the effects of climate change on the growth and survival of marine organisms is needed, and results from this study suggest that juvenile pink and chum salmon inhabiting the Arctic are currently benefiting from present conditions.

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Review of BASIS Salmon Food Habits Studies

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Abstract: The BASIS food habits studies of sockeye, chum, pink, and Chinook salmon conducted in 2002–2006 were summarized. These studies identified important ($\geq 10\%$ of prey composition by weight) prey taxa of salmon. Salmon diet composition differed between the western region, where diets contained more zooplankton, and the eastern region, where diets contained more ichthyoplankton and nekton. Salmon feeding conditions, growth, and survival in the eastern region were more favorable in relatively warm years, as compared to cool years. However, warmer conditions may not be favorable for all salmon species, such as chum salmon. These studies significantly increased the available information on salmon food habits during the fall in the western, central, and eastern regions. Salmon diet composition shifted from zooplankton to fish and squid, or to larger sizes of fish prey, with increasing salmon body size, age, or maturity. Continued monitoring of salmon food habits will contribute to understanding how future climate changes will affect salmon populations in the Bering Sea.

Keywords: sockeye, chum, pink, Chinook, food habits, Bering Sea

INTRODUCTION

Shifts in Bering Sea climate-ocean processes and fish assemblages favored by current warming trends (Hunt et al. 2002; Stabeno et al. 2007) prompted the North Pacific Anadromous Fish Commission (NPAFC) to initiate the Bering-Aleutian Salmon International Survey (BASIS) for the period 2002–2006 (NPAFC 2001). The BASIS plan called for trawling surveys across the Bering Sea to be conducted throughout the year to investigate ocean conditions, conduct plankton tows, and sample salmon biological characteristics, including salmon food habits.

Prior to BASIS, the broadest seasonal coverage of salmon food habits sampling was in the western Bering Sea. In the decades before 2000, salmon food habits studies were reported by numerous investigators sampling in the western Bering Sea (e.g., Ito 1964; Andrievskaya 1966; Machidori 1968; Karpenko 1982; Karpenko and Maksimenkov 1988; Chuchukalo et al. 1995; Klovach et al. 1996; Koval and Karpenko 1998; Bugaev and Shaporev 2002; Karpenko et al. 2007). In the central Bering Sea, summer data collections were more frequently reported than fall collections (e.g., Kanno and Hamai 1972; Azuma 1992; Tadokoro et al. 1996; Davis et al. 1998; Davis et al. 2000). Results of food habits studies had not been reported in the eastern Bering Sea

since the 1970s (e.g., Nishiyama 1974; Straty 1974; Carlson 1976), and in the Aleutians since the 1990s (Carlson et al. 1998).

Spatial variation among salmon species and life-history groups in the Bering Sea is produced by migrations of juvenile salmon from fresh water to nearshore and coastal areas in the late summer–fall, movement of immature and maturing fish to over-wintering areas, and subsequent spring–summer return of immature fish to deep-water feeding areas and maturing fish to near-shore areas for their return to freshwater spawning areas (e.g., Farley et al. in press; Myers et al. in press). Salmon prey organisms also have differing distributions with respect to regions (western, central, eastern Bering Sea) and to temporal-depth distribution (Volkov et al. 2007a; Volkov and Kosenok 2007). Salmon feeding characteristically exhibits both plasticity and selectivity in behavior (Shuntov et al. 2007) that reflect both the flexibility in consuming prey that is available (Naydenko et al. 2007) and selecting prey from preferred items depending on salmon size and life-history stage (Zavolokin et al. 2007).

Our objective was to summarize Russian, Japanese, and U.S. BASIS food habits results from studies of sockeye (*Oncorhynchus nerka*), chum (*O. keta*), pink (*O. gorbuscha*), and Chinook salmon (*O. tshawytscha*) during 2002–2006. This review outlines methods used for routine collection of

food habits data and describes important prey taxa of salmon in the Bering Sea. In addition, we included studies comparing salmon diets across geographical regions, water column depths, between relatively warm and cold time periods, and among seasons. We have also included information on changes in salmon diets associated with salmon body size and maturity stage.

METHODS USED IN BASIS FOOD HABITS STUDIES 2002–2006

During 2002–2006, BASIS trawling cruises surveyed large regions of the western, central, and eastern Bering Sea (Fig. 1). In multiple year surveys, the western Bering Sea was surveyed by the R/V *TINRO*, the central basin was surveyed by the R/V *Kaiyo maru*, and the eastern Bering Sea shelf was surveyed by the F/V *Sea Storm*. In addition, in 2002 the F/V *Northwest Explorer* surveyed westward along the Aleutian chain, in the deep areas of the central basin, and along the eastern Bering Sea shelf. In 2002–2006 the R/V *Wakatake maru* conducted gillnet and longline surveys and monitored salmon food habits in the central region.

Food habits data gathered during the BASIS period used several different approaches. The express method, developed by TINRO Centre, allowed for quick examination of stomach contents while on board the research vessel (Chuchukalo and Volkov 1986; Volkov et al. 1995; Temnykh et al. 2003). At each trawl operation, a maximum of 25 fish

per species was grouped into 10-cm fork length (FL) size groups (< 10 cm FL, 10–20 cm FL, 20–30 cm FL, etc.). After associated biological information (i.e., length, weight, maturity, etc.) was collected, stomachs were removed and examined in a fresh condition, without fixation. Contents of the stomachs within each salmon size grouping were combined. In the process of combining stomach contents, the number of empty stomachs and the degree of stomach fullness (based on five categories) of each individual stomach sample was recorded. An average degree of prey digestion characterizing the combined contents of all the stomachs in the size group was noted using a five-step scale based on visual condition of the prey. The total weight of the combined stomach contents was determined, prey species composition was identified to the lowest possible taxonomic level, and the percent composition was measured by weight. Standardization across research vessels was accomplished by placing TINRO specialists on survey vessels operating in each region of the Bering Sea.

Japanese food habits specialists on board the R/V *Kaiyo maru* used a different method of data collection (Yamamura et al. 2002). After fish measurement, individual salmon stomachs were removed and preserved in a 10% formalin-seawater solution for examination after the cruise. In the laboratory, stomach contents were sorted to the lowest taxon possible and prey items were weighed. Samples of prey items were dried at 52°C in a drying oven for 24 hours and in desiccators for 1.5–2 days, after which prey items were weighed again to

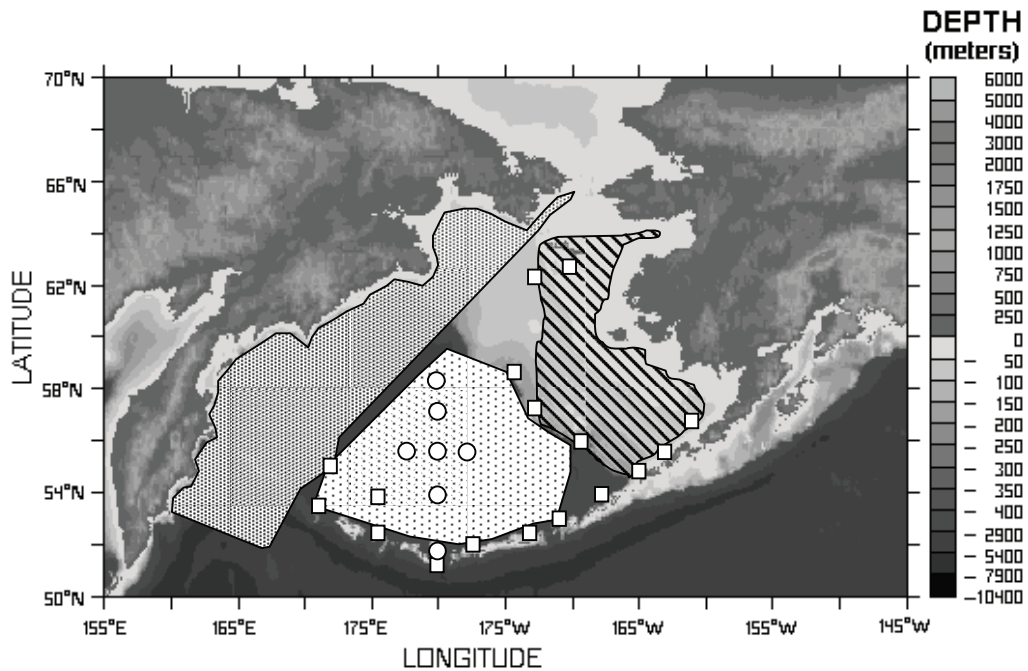


Fig. 1. The regions of the Bering Sea where BASIS cruises collected samples for salmon food habit studies. Map source: <http://www.beringclimate.noaa.gov>. Dense stippling indicates the western region surveyed by the R/V *TINRO*. Sparse stippling indicates the central region surveyed by the R/V *Kaiyo maru* and the diagonal pattern shows the eastern region surveyed by the F/V *Sea Storm*. Squares indicate approximate survey locations of the F/V *Northwest Explorer* in the Aleutian, central, and eastern regions, and circles indicate approximate survey locations of the R/V *Wakatake maru* in the central region.

the nearest mg. Prey composition was expressed as percentage of dry weight.

Researchers on the F/V *Northwest Explorer* and R/V *Wakatake maru* took yet another approach. They examined a maximum of 10 fish per species per fishing operation (trawl, longline, or gillnet), which were obtained from a range of fish sizes (Ueno et al. 1998). After collecting salmon biological data, fresh fish stomachs were removed and examined individually on board. Total prey weight was calculated as the difference between full stomach weight and weight of the stomach after removal of the contents. Degree of stomach fullness and digestion were recorded and the contents separated into the lowest taxon possible. The percent volume in each prey category was estimated by eye.

Salmon life-history stage was determined for juvenile, immature, and maturing salmon. Juvenile fish have not yet completed one winter at sea because they are caught in the same year that they entered the marine environment. Immature fish have spent at least one winter at sea and will remain at sea for one or more winters before returning to fresh water to spawn. Maturing fish will return to spawn in the current year. Salmon life-history stages were identified on BASIS cruises based on one or several of the following characteristics: survey month, fish age, length and weight, and gonad weight or condition (Ishida and Miyaguchi 1958; Ishida et al. 1961; Takagi 1961; Ito et al. 1974).

RESULTS FROM BASIS SALMON FOOD HABITS STUDIES

During the 2002–2006 Bering Sea cruises of the R/V *TINRO*, R/V *Kaiyo maru*, F/V *Sea Storm*, F/V *Northwest Explorer*, and R/V *Wakatake maru* 6,358 sockeye, 13,562 chum, 5,219 pink, and 2,120 Chinook salmon were sampled for their stomach contents (Table 1). Most stomach samples (45.6%) obtained from these studies came from the western region, while 28.8% were from the central region, 25.1% from the eastern region, and 0.6% from the Aleutian Islands region. Differences in the number of samples obtained from various regions occurred for a number of reasons, including the number of survey stations in each region, the number of researchers available for processing food habits samples, and whether stomach contents were combined or fish diet data were based on the examination of individual fish.

Major Prey Items of Salmon in the Bering Sea

Particular taxa of zooplankton, squid, and fish species were shown to be important prey ($\geq 10\%$ of the prey composition by weight) of sockeye, chum, pink, and Chinook salmon in the Bering Sea (Figs. 2, 3). Zooplankton prey, including euphausiids (*Thysanoessa longipes* and *Thy. raschii*) and crab megalopa and zoea, were identified as important prey for all these salmon species (Fig. 2). The hyperiid amphipod, *Themisto pacifica*, was an important component in

the diet of sockeye, chum, and pink salmon from the smallest sizes (10 cm FL) to fish up to 60 cm in length. The shelled pteropod, *Limacina helicina*, was also an important component of the diet for a wide size range of sockeye, chum, and pink salmon. Prey items such as medusae and comb jellies, the hyperiid amphipod, *Primno abyssalis*, the unshelled pteropod, *Clione limacina*, and chaetognaths (*Sagitta* spp.) were important in chum salmon diets, exclusively. The euphausiid, *Thy. longipes*, was an important component of stomach contents observed from a wide range of Chinook salmon body sizes (20–70 cm FL).

Squid, Atka mackerel (*Pleurogrammus monopterygius*), lampfishes (*Stenobranchius* spp.), Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), and wall-eye pollock (*Theragra chalcogramma*) were important nekton ($\geq 10\%$ of the prey composition by weight) in sockeye, chum, pink, and Chinook salmon diets (Fig. 3). Other species of fish identified as significant components ($\geq 10\%$ of the prey composition by weight) of Chinook salmon diets included herring (*Clupea pallasii*), whitespotted greenling (*Hexagrammos stelleri*), prowlfish (*Zaprora silenus*), sablefish (*Anoplopoma fimbria*), and rockfishes (*Sebastes* spp.).

Salmon Food Habits among Regions

Bering Sea salmon food habits data showed differences between salmon diets collected in the western and eastern Bering Sea (Volkov et al. 2007b; Farley et al. in press). Diets of salmon collected in the western region contained more zooplankton, and those collected from the eastern region contained more ichthyoplankton and nekton.

In the western region, hyperiid amphipods, pteropods, and small squids were the basic prey of planktivorous salmonids, such as sockeye, pink, and chum salmon (Volkov et al. 2007b). Juvenile pink salmon most commonly consumed planktonic crustaceans including hyperiid amphipods (*The. pacifica*, *The. libellula*, and *P. macropa*), euphausiids (*Thy. longipes*), copepods (*Neocalanus plumchrus*), and pteropods (*L. helicina*; Naydenko et al. 2007). Juvenile Chinook salmon in this area consumed zooplankton (Naydenko et al. 2005). Salmon diets contained relatively few euphausiids because of their low abundance in surface waters during the day when salmon were actively feeding (Volkov and Kosenok 2007). Copepods and chaetognaths, while abundant in zooplankton collections, were not important in salmon diets suggesting the habitat provided a high abundance of more preferable food for salmon (Volkov et al. 2007b). Salmon selected prey that were heavily pigmented (e.g., *Themisto* spp. and *L. helicina*), large bodied (e.g., young squid, pollock, and Atka mackerel), or possessed luminous photophores (e.g., myctophids and euphausiids; A. Zavolokin, zavolokin@tinro.ru, pers. comm.).

Eastern Bering Sea zooplankton collections were dominated by small-sized copepods, chaetognaths, and ichthyoplankton, primarily larval and juvenile pollock, and crab

Table 1. Salmon food habits data collected during BASIS cruises in the western, central, eastern, and Aleutian Islands (< 20 nm from shore) regions of the Bering Sea. Groups (N): number of groups of stomachs examined by the express method (see text). Stomachs (N): the number of individual stomachs that were combined into groups, or examined individually. – indicates no samples examined. *indicates group number not applicable because stomach samples were examined individually.

Region	Vessel	Year	Season	Sockeye		Chum		Pink		Chinook		Contact Person
				Groups (N)	Stomachs (N)	Groups (N)	Stomachs (N)	Groups (N)	Stomachs (N)	Groups (N)	Stomachs (N)	
Western	<i>TINRO</i>	2002	Summer-Fall	99	571	124	834	23	240	24	61	Volkov
		2003	Summer-Fall	151	807	178	1,102	43	514	56	186	Volkov
		2004	Fall	179	986	187	1,208	65	673	82	267	Volkov
		2005	Summer	143	433	225	888	146	873	65	153	Volkov
		2006	Summer-Fall	95	145	151	1,580	48	748	48	154	Volkov
Central	<i>Kaiyo maru</i>	2002	Summer		–	*	395		–		–	Sakai
		2002	Fall		–	*	575		–		–	Sakai
		2002	Fall	*	47	*	238	*	1	*	63	Davis
		2003	Summer		–	*	255		–		–	Sakai
		2003	Fall		–	*	189		–		–	Sakai
		2003	Fall	23	463	45	803		–		–	Volkov
		2004	Summer	3	37	38	544		–	5	30	Volkov
	2006	Spring	27	357	59	849	22	375	4	57	Volkov	
	<i>NW Explorer Wakatake maru</i>	2002	Fall	*	46	*	166		–	*	34	Davis
		2002	Summer	*	139	*	242	*	40	*	89	Davis
		2003	Summer	*	155	*	183	*	168	*	77	Davis
		2004	Summer	*	143	*	180	*	142	*	114	Davis
		2005	Summer	*	112	*	152	*	124	*	27	Davis
		2006	Summer	*	72	*	91	*	35	*	32	Davis
Eastern		<i>NW Explorer Sea Storm</i>	2002	Fall	*	5	*	71		–	*	23
	2003		Fall	54	394	50	247	18	175	6	17	Volkov
	2004	Fall	100	677	161	879	96	517	102	329	Volkov	
	2005	Fall	103	600	157	581	89	437	84	272	Volkov	
	2006	Fall	41	127	309	1,228	26	144	60	119	Volkov	
Aleutians	<i>NW Explorer Wakatake maru</i>	2002	Fall	*	39	*	65		–	*	16	Davis
		2002	Summer	*	2	*	7		–		–	Davis
		2003	Summer		–	*	4	*	10		–	Davis
		2004	Summer		–	*	1	*	2		–	Davis
		2005	Summer	*	1		–	*	1		–	Davis
		2006	Summer		–	*	5		–		–	Davis

larvae. These same ichthyoplankton and crab larvae also dominated the contents of salmon stomachs (Naydenko et al. 2007; Volkov et al. 2007b; Farley et al. in press). The small-size fraction (< 1.3 mm) of zooplankton was most abundant in the eastern region, and the large-size fraction (> 3.3 mm) dominated throughout the year in other regions (Volkov et al. 2005). The biomass of the zooplankton forage base, comprising organisms consumed by sockeye, chum, and pink salmon, was determined primarily from the abundance of organisms in the large-size fraction of zooplankton (Volkov et al. 2005). In 2002–2006 differences in zooplankton size composition, taxonomic and trophic structure, and zooplankton production available for fish consumption led researchers to conclude that the eastern Bering Sea was ap-

proximately 30% less productive than the western Bering Sea (Volkov et al. 2007a). In 2006–2008 the large-size fraction of zooplankton increased in the eastern Bering Sea affecting salmon diet composition by increasing the proportion of zooplankton, particularly euphausiids, and decreasing nekton in sockeye, chum, pink, and Chinook salmon diets (Volkov et al. 2007b). Sockeye and chum salmon consumed juvenile rockfishes, age-0 pollock, capelin, sand lance, and sablefish (Davis et al. 2004; Naydenko et al 2005; Volkov et al. 2007b; Farley et al. in press), and Chinook salmon consumed young herring, capelin, pollock, rockfishes, and sablefish (Davis et al. 2004).

In the central region the large-size fraction of zooplankton, which included hyperiid amphipods, pteropods, eu-

Fork length of salmon predator

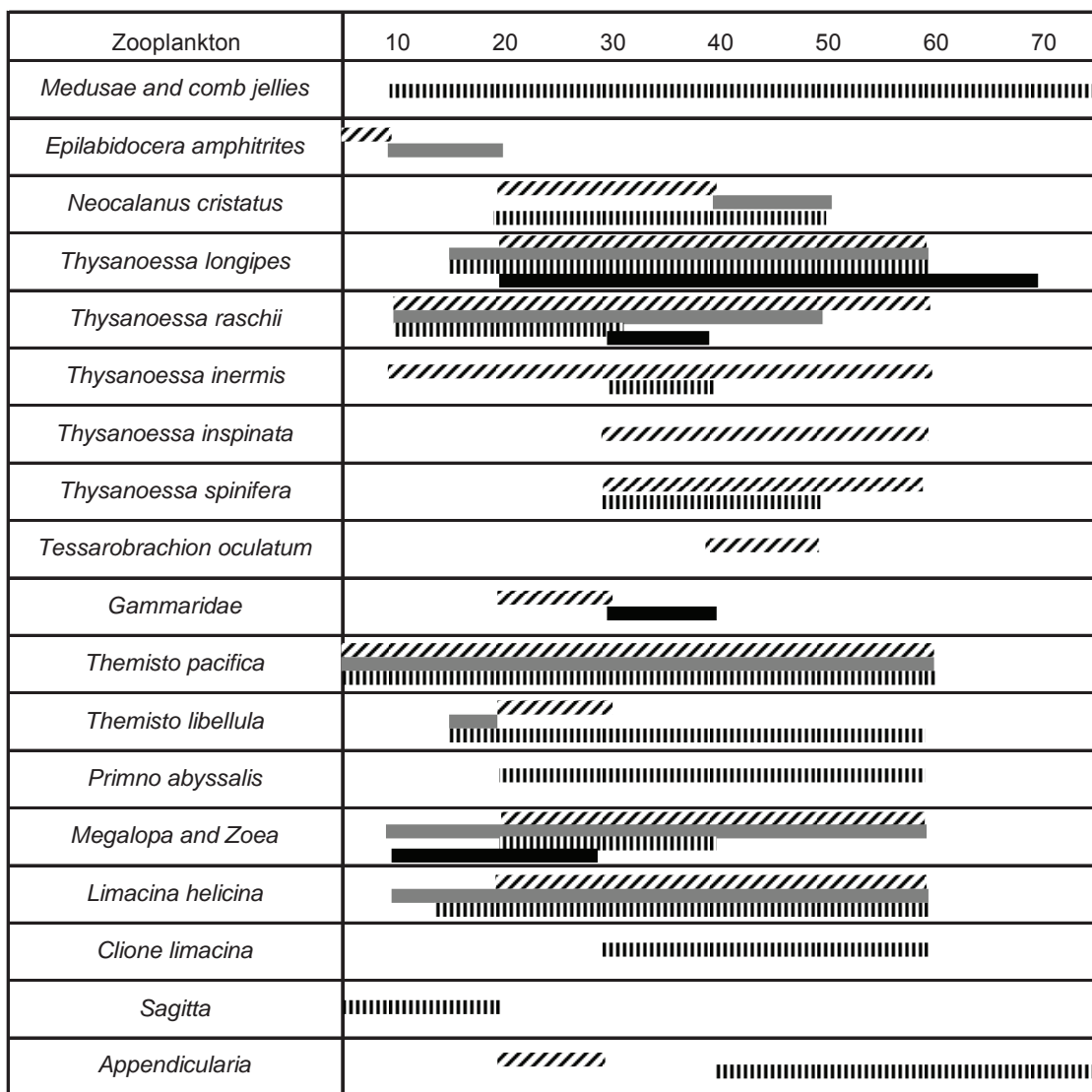


Fig. 2. List of the major zooplankton prey items consumed by salmon in the Bering Sea by fork length (cm) of the salmon predator. A prey item is considered major if it comprises at least 10% of the diet by weight for a region and size group. Diagonal pattern = sockeye salmon, gray = pink salmon, vertical pattern = chum salmon, black = Chinook salmon.

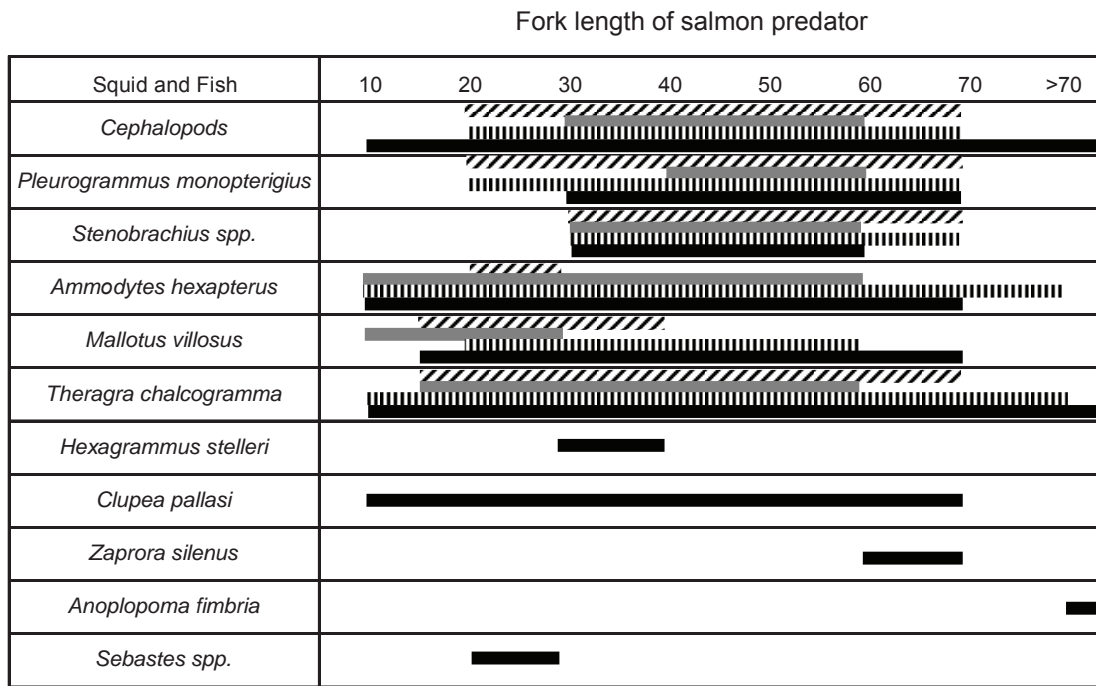


Fig. 3. List of the squid and major fish prey items consumed by salmon in the Bering Sea by fork length (cm) of the salmon predator. A prey item is considered major if it comprises at least 10% of the diet by weight for a region and size group. Diagonal pattern = sockeye salmon, gray = pink salmon, vertical pattern = chum salmon, black = Chinook salmon.

phausiids and coelenterates (*Aglantha digitale*; Volkov et al. 2007a), were the common prey items found in the stomach contents of sockeye, chum, and pink salmon (Davis et al. 2004; Volkov et al. 2007b). Fish consumed by immature sockeye, chum, and Chinook salmon in the central Bering Sea differed from fish observed in stomachs collected in the eastern region. In the central region, salmon consumed *S. leucopsarus* and juvenile fish including Atka mackerel, sculpins, and flatfish (Davis et al. 2004; Naydenko et al. 2005). Squid predominated in the diets of Chinook salmon collected from the central basin and fish were the primary prey of Chinook salmon collected on the eastern shelf (Davis et al. 2004).

If salmon consumption of zooplankton does not significantly affect the salmon’s forage base, then recent increases in salmon abundance are unlikely to change the trophic relationships in the Bering Sea (Naydenko 2009). Patterns in food habits characteristics may represent adaptive strategies intended to lessen density-dependent interactions and maximize utilization of available feeding grounds (Sviridov et al. 2004).

Salmon Food Habits Associated with Water Depth

Patterns in salmon prey composition have been associated with different water column depths. Sockeye salmon caught in shallow waters of the western Bering Sea contained more chaetognaths and copepods than sockeye salmon collected from deeper waters, where more amphipods,

euphausiids, and squids were observed in stomach contents (Temnykh et al. 2003; Naydenko et al. 2005). In the shallow northern areas of the western Bering Sea *The. libellula* predominate in diets of young chum salmon, while in deeper southern areas and the deep water of the central Bering Sea basin, *The. pacifica* is more common (Temnykh et al. 2003; Davis et al. 2004).

The ratio of euphausiids and fish offal, identified as originating from pollock (Buser et al. 2009), observed in Chinook salmon stomach contents was significantly higher in samples collected at shallow depths (< 200 m), and the ratio of squid was significantly higher in salmon collected at deeper depths (201 to 600 m; Davis et al. 2009). Changes in prey composition of salmon diets among habitats of differing water depths likely reflect changes in the distribution and abundance of salmon prey organisms available in those habitats.

Shifts in Salmon Food Habits Associated with Relatively Warm and Cool Years

The five years of BASIS (2002 – 2006) captured variation in environmental conditions in the Bering Sea including relatively warm and cool years. Oceanographic indices formulated from eastern Bering Sea shelf conditions show that 2002 to 2005 were relatively warm years, and 2006 was a relatively cool year (Fig. 4). These indices show levels of water column stability, nutrient conditioning, and the influence of thermal conditions on distributions of fishes. The

switch from warm to cool years during the BASIS study period provided a natural experiment to measure effects on salmon food habits in response to climate and ecosystem change.

Warmer spring sea surface temperatures on the eastern Bering Sea shelf were associated with increased marine growth and survival of juvenile western Alaska sockeye salmon and changes in primary prey composition of juvenile sockeye salmon during relatively warm years (2002–2003), as compared to cool years (2000–2001; Farley et al. 2007). When cool springtime conditions prevailed in the eastern region, Pacific sand lance was an important component (by weight) of juvenile salmon diets. However, when warm springtime conditions prevailed, age-0 pollock were the primary prey and sockeye salmon had an improved body

condition (Farley et al. 2007). Similarly, later comparisons of juvenile salmon collected in the southeast and northeast Bering Sea shelf showed a shift in diets for all species across the shelf in a cool year (2006; Farley et al. in press). Under cool conditions, the importance of sand lance dramatically increased in the diets of juvenile salmon in both areas, while the importance of age-0 pollock (southeast and northeast areas) and euphausiids and other zooplankton (northeast area) was reduced. Authors concluded cold spring sea surface temperatures on the eastern Bering Sea shelf contribute to lower growth and survival for western Alaska juvenile salmon (Farley et al. in press).

Environmental changes are likely to have complex effects on different salmon species from inter-specific interac-

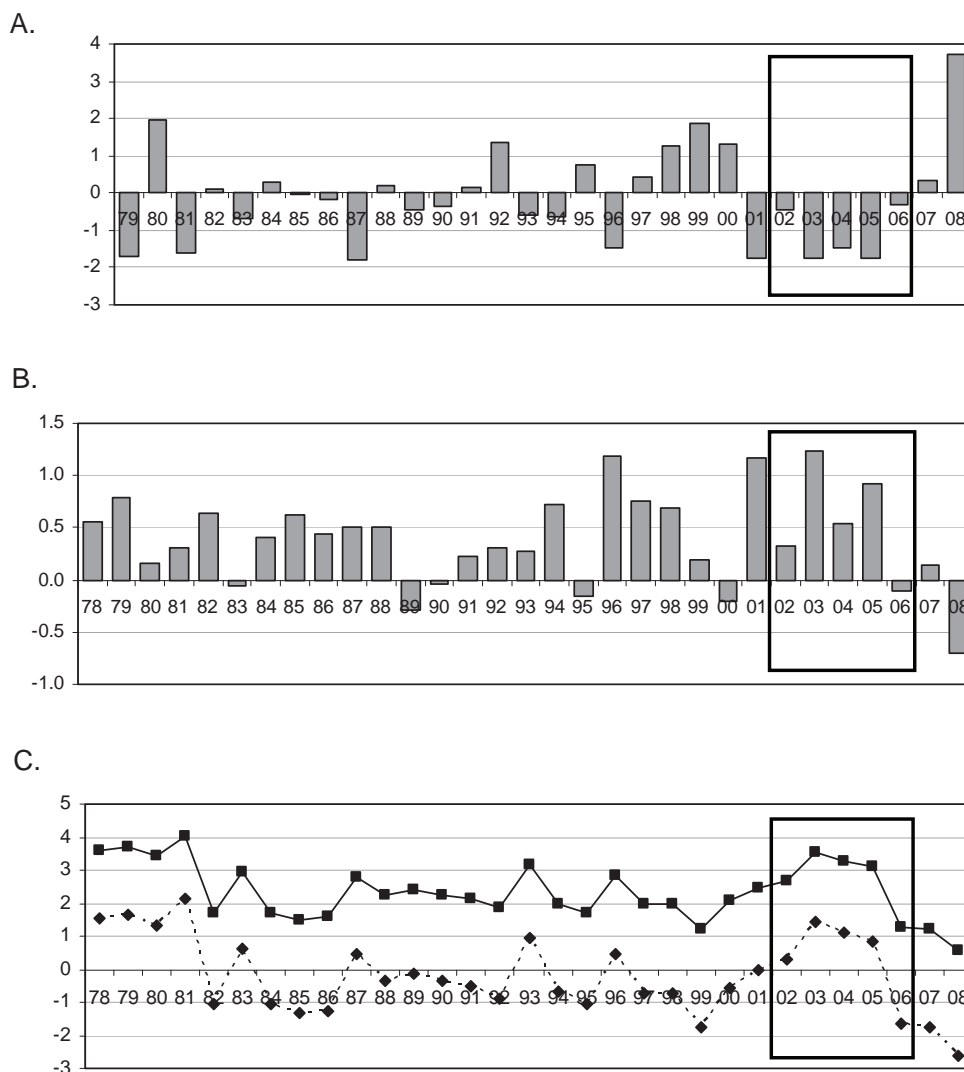


Fig. 4. Several eastern Bering Sea shelf climate indices show that 2002–2005 were characterized as relatively warm years, and 2006 was a cool year. Rectangular boxes highlight the BASIS years 2002–2006. Data source for indices: <http://www.beringclimate.noaa.gov>. A. Ice cover index shows the average ice concentration anomalies from January 1 to May 31 at locations between 56° to 58°N, 163° to 165°W, normalized relative to values from 1981 to 2000. B. Winter (January to March) sea surface temperature anomalies in the 5° by 5° grid centered at 55°N, 170°W, normalized relative to values from 1950 to 2000. C. May sea surface temperatures (solid line) and anomalies (dotted line) in the area 54° to 60°N, 161° to 172°W. Anomalies normalized relative to values from 1961 to 2000.

tions, prey availability, and bioenergetics (Beauchamp et al. 2007). For example, abundance of several species of large medusae, which consume some of the same prey as chum salmon, was higher in relatively warm years (2004, 2005) than in relatively cool years (2006, 2007) suggesting possible increased food competition between jellyfish and chum salmon in warming climate conditions (Cieciel et al. 2009). Using average total lipid content as a measure of chum body condition, researchers showed a significant negative correlation between sea surface temperature and lipid content of chum salmon muscle (T. Kaga, tkaga@fra.affrc.go.jp, pers. comm.). Increased water column stability and observed shifts to increased abundance and biomass of smaller-sized zooplankton taxa in relatively warm years might affect the feeding conditions of higher trophic levels in the eastern Bering Sea (Coyle et al. 2008).

Salmon Food Habits among Seasons

The 2002–2006 BASIS cruises significantly increased data collection of salmon food habits data during the fall season in all regions (Fig. 5; NPAFC 2003; Temnykh et al.

2003; Farley et al. 2004; NPAFC 2004; Farley et al. 2005; Glebov et al. 2005; NPAFC 2005; Farley et al. 2006; Glebov et al. 2006; Kuznetsova 2006; NPAFC 2006; Naydenko et al. 2007; Temnykh et al. 2007; Volkov et al. 2007b; Farley et al. in press). New food habits data were obtained from the Aleutians area in summer and fall (Murphy et al. 2003; Davis et al. 2004), and temporal coverage in the central Bering Sea was extended to spring (Azumaya et al. 2003, 2005).

In the eastern region in 2007, the percentage of empty stomachs observed was higher in Chinook salmon stomach samples collected in winter (45%) than in summer (8%), suggesting longer time periods between meals in winter (Davis et al. 2009). The diversity of squid species observed in Chinook salmon diets was higher in winter than summer, when more fish (particularly juvenile walleye pollock) were consumed (Davis et al. 2009).

In the central region, sockeye salmon consumed a higher proportion of euphausiids in fall than summer, and squids present in summer stomach samples disappeared in the fall samples (Davis et al. 2004). In 2002–2003, chum salmon shifted from consuming zooplankton, mostly euphausiids in summer, to lampfishes in fall (NPAFC 2005). Chinook

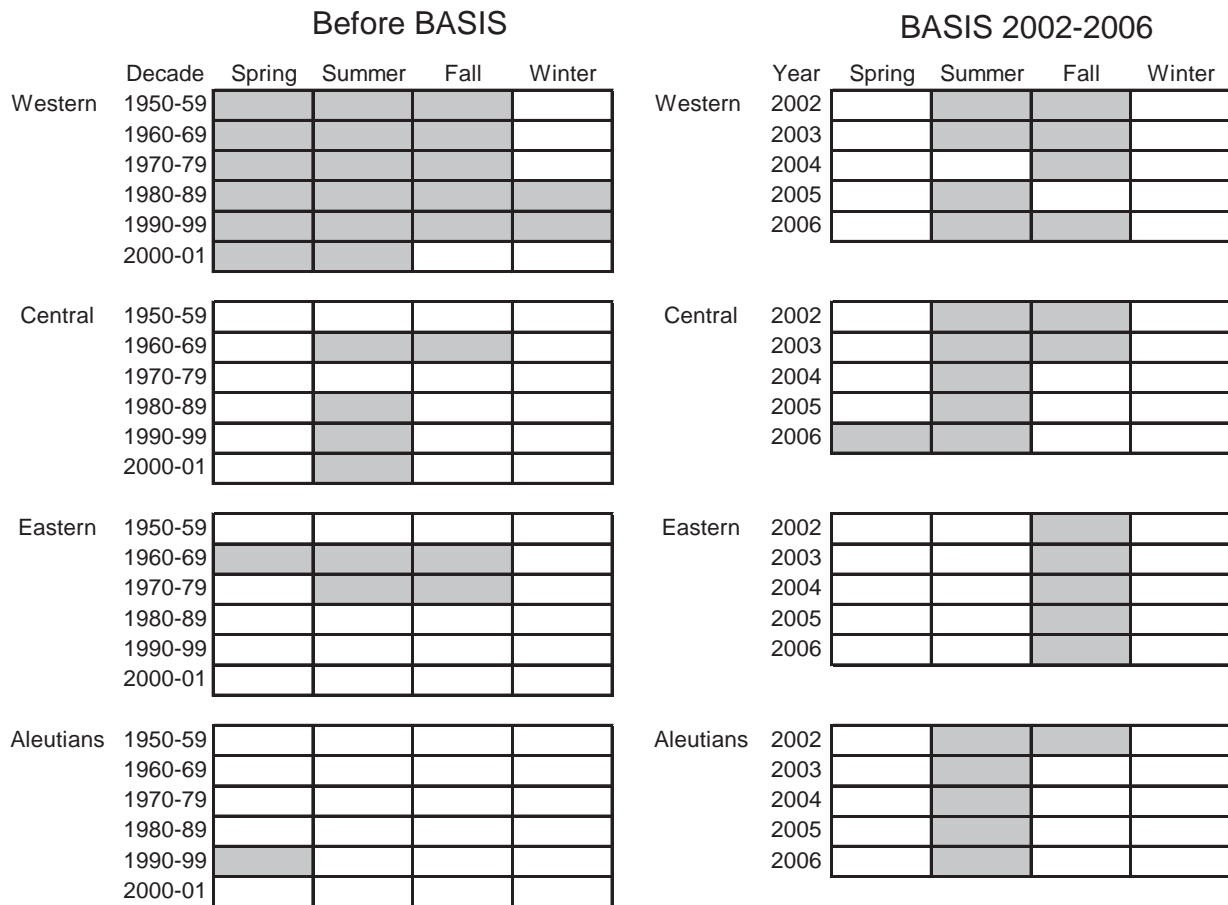


Fig. 5. Shaded boxes indicate the time period by decade (before BASIS) and BASIS years (2002–2006) when salmon food habits data were collected by season in the western, central, eastern, and Aleutian Islands regions of the Bering Sea. Spring = March–May, summer = June–August, fall = September–November, winter = December–February.

salmon stomach samples collected during the summer contained euphausiids, squid, and fish, however, in fall stomach samples contained primarily squid (Davis et al. 2004; Myers et al. in press).

Salmon Food Habits Associated with Salmon Biological Characteristics

Patterns in salmon food habits have been associated with variations in body size, age, or maturity of the salmon predator. For example, as chum salmon grow they prey more intensively on lampfish, pollock, Atka mackerel, sand lance, or capelin, depending on the geographic area (Naydenko et al. 2005).

In the western region, small chum salmon (< 20 cm FL) fed mostly on hyperiid amphipods (*The. pacifica*) and large chum salmon (> 50 cm FL) fed mostly on fish (Atka mackerel; Temnykh et al. 2003). In the western region and more southerly waters off Kamchatka, medusae consumption was a distinctive feature of chum > 51 cm. This might reflect adaptations by maturing chum, which could require more easily digested prey (Dulepova and Dulepov 2003). Sockeye salmon < 50 cm FL preyed on hyperiid amphipods, euphausiids, pteropods, and juvenile squid, while larger fish preyed more intensively on nekton (Naydenko et al. 2005). Chinook salmon juveniles consumed mostly plankton, including large crab larvae and euphausiids, and larger fish consumed few zooplankton (Naydenko et al. 2005). The diurnal feeding activity of immature salmon (< 30 cm FL) had similar feeding rhythms, regardless of whether they were nekton or zooplankton consumers, with most activity occurring between mid-day and dusk (Volkov and Kosenok 2007). Older immature and maturing individuals had less defined diurnal patterns (Volkov and Kosenok 2007).

Juvenile sockeye, chum, and pink salmon in the eastern region preyed on nektonic animals including, larvae and age-0 walleye pollock, sand lance, capelin, and bottom fish larvae. All sizes of chum salmon consumed larval and age-0 pollock, crab larvae, and coelenterates (Naydenko et al. 2005; Volkov et al. 2007a). Prevalence of fish in the diet of juvenile sockeye, chum, and pink salmon was associated with the high concentration of juvenile fish prey, especially age-0 pollock (Kuznetsova 2006). Small Chinook (≤ 40 cm FL) salmon preyed predominately upon fish (sand lance, juvenile pollock, larval fishes) and large individuals (≥ 60 cm FL) preyed almost exclusively on squid (Naydenko et al. 2005).

In the eastern region, pteropods often dominated the diets of ocean age-1 and older sockeye and chum salmon (NPAFC 2004). In Bristol Bay juvenile sockeye up to 10 cm FL fed mostly on copepods. Larger juveniles (10–30 cm FL) consumed mainly juvenile pollock, pteropods, copepods, hyperiid amphipods, euphausiids, and crab megalopa (Kuznetsova 2006), whereas large sockeye salmon (50 to 60 cm FL) consumed mostly euphausiids. The proportion of fish (juvenile pollock and capelin) in the diet of pink salmon increased with

pink salmon body size (Kuznetsova 2006). Examining Chinook salmon winter diets, investigators found that the ratio of euphausiids to fish body weight was significantly higher in immature than maturing fish (Davis et al. 2009).

CONCLUSIONS

In 2002–2006 BASIS food habits studies of sockeye, chum, pink, and Chinook salmon identified important prey taxa of salmon including, euphausiids, crab megalopa and zoea, hyperiid amphipods, pteropods, chaetognaths, gonatid squids, Atka mackerel, lampfishes, Pacific sand lance, capelin, walleye pollock, herring, whitespotted greenling, prowlfish, sablefish, and rockfish. Monitoring the abundance and distribution of these prey organisms using a standardized method will be useful for evaluating the feeding status of salmon in the Bering Sea. Investigations comparing salmon diets among areas of the Bering Sea showed the largest difference in salmon diets between the western and eastern regions. Diets of salmon collected in the western region contained more zooplankton, while salmon collected in the eastern region contained more ichthyoplankton and nekton. Salmon stomach samples collected from deep waters contained more prey species that were either deep dwelling or vertically migrating themselves. Studies showed salmon feeding differed in relatively warm years, as compared to cooler years, suggesting some salmon species will do better under warming climate conditions than others.

The BASIS food habits studies significantly increased the available information on salmon food habits during the fall in the western, central, and eastern regions. Limited studies suggest salmon food habits vary by season but more studies in the same sampling area in more than one season are required. Salmon prey composition shifts with increasing salmon body size, enabling large salmon to feed on relatively large-size fish such as young pollock, Atka mackerel, and lampfishes. As sea temperatures and environmental variability increase in the future, it is important that we continue to monitor salmon food habits, growth, and body condition if we are to understand how these changes will affect salmon populations in the Bering Sea.

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Jellyfish and Juvenile Salmon Associations with Oceanographic Characteristics during Warm and Cool Years in the Eastern Bering Sea

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Abstract: We explored possible associations between jellyfish biomass (*Aequorea* spp., *Aurelia labiata*, *Chrysaora melanaster*, and *Cyanea capillata*), juvenile salmon (*Oncorhynchus keta*, *O. nerka*, *O. gorbuscha*, *O. kisutch*, and *O. tshawytscha*) abundance, and oceanographic characteristics (temperature, salinity, chlorophyll-*a*, and bottom depth) during two warm years (2004, 2005) and two cool years (2006, 2007) in the eastern Bering Sea from the annual Bering-Aleutian Salmon International Surveys (US BASIS). A significant difference was observed in the mean relative biomass of the four jellyfish species in response to the various conditions in warm versus cool years. Our results indicated that juvenile *O. tshawytscha* were significantly associated with cooler temperatures in only cool years and shallower bottom depths in all years. Juvenile *O. kisutch* were associated with shallower than average bottom depths for all years and juvenile *O. keta* had only cool-year associations with lower salinities and shallower bottom depths. Similar spatial distributions were seen between jellyfish and juvenile salmon, suggesting the possibility of competition. Immature *O. keta* were significantly associated with the same physical ocean factors as *Aequorea* spp. during fall warm years, indicating a potential for interaction.

Keywords: jellyfish, salmon, climate, eastern Bering Sea

INTRODUCTION

How large marine ecosystems respond to shifts in climate is one of the major issues facing fisheries managers today (Kafarowski 2003; Moser and Leurs 2008). The response by management to these changes could impact the future utilization of marine resources. Having the ability to predict the effects of climate change on community structure at either a small or large scale would enhance a manager's ability to adequately maintain marine resources.

On the eastern Bering Sea shelf, shifts between warm and cool climate states have impacted the pelagic ecosystem in profound ways. For instance, anomalously cold spring sea surface temperatures (SST) (Overland 2008) were believed to lower pelagic productivity, reducing the number of age-0 *Theragra chalcogramma* (walleye pollock) (Moss et al. 2009), Bristol Bay *Oncorhynchus nerka* (sockeye salmon) (Farley et al. 2007) and Kuskokwim *O. keta* (chum salmon) and *O. tshawytscha* (Chinook salmon) (Farley et al. in press). However, jellyfish have shown an opposite shift in abundance, declining during years with warm SSTs (Brodeur et al. 2008a). Zooplankton species composition was also affected by changing SSTs, shifting from larger oceanic zooplankton in cool years to smaller zooplankton species during warm years (Coyle et al. 2008).

The planktonic nature of jellyfish makes them subject to

the same physical properties of the water column that affect the vertical migration of pelagic fish and other planktonic organisms (Kjørboe et al. 1990). Current, temperature, salinity, predator-prey interactions, competition, and light have measurable effects on gelatinous zooplankton and, in turn, the fish and other zooplankton that occupy similar habitats (Kjørboe et al. 1990; Pagès and Gili 1992). Jellyfish associations have been documented worldwide between many species of fish and jellyfish on many occasions (Mansueti 1963; Hamner and Schneider 1986; Brodeur 1998a; Hay et al. 1990). These fish and jellyfish associations occur for several reasons but in Alaska, specifically with the jellyfish *Cyanea capillata* (lion's mane), *Aurelia labiata* (moon jelly), and *Chrysaora melanaster* (sea nettle), they seem to occur because of spatial and dietary resource overlap, which has been observed with young-of-the-year *T. chalcogramma* (Brodeur 1998b; Brodeur et al. 2000; Purcell and Sturdevant 2001). The *O. keta* diet includes a large portion of gelatinous species, making potential associations for predation possible (Arai 1988; Purcell and Arai 2001; Arai et al. 2003). We know that jellyfish biomass on the eastern Bering Sea shelf can be substantial (Brodeur et al. 2002), but it is not clear what effect this large biomass has on salmon abundance, either through competition, predation, or as refuge from potential predators.

In this paper, we explore possible associations among

oceanographic characteristics, jellyfish biomass, and juvenile and immature salmon abundance in the eastern Bering Sea. The data come from pelagic trawl and oceanographic surveys (Bering-Aleutian Salmon International Surveys, BASIS) along the eastern Bering Sea shelf during August through early October, 2004–2007. The surveys were conducted during two anomalously warm (2004 and 2005) and cool (2006 and 2007) spring SST years. Our objective was to determine if a particular species of jellyfish or salmon were associated with oceanographic characteristics on the shelf. Testing for significant associations among salmon, jellyfish, oceanographic characteristics, and bottom depths could provide insight into where these marine organisms distribute themselves and whether or not salmon have the potential to compete with or utilize jellyfish as a resource in various climate states.

MATERIALS AND METHODS

We conducted trawl surveys from mid-August to early October in 2004–2007 across the eastern Bering Sea shelf as part of the BASIS survey. The sampling grid covered the shelf off western Alaska, from 159°W to 174°W longitude and 54.5°N to 64°N latitude (Fig. 1). All stations were approximately 30 nautical miles (55.6 km) apart. The number of stations sampled each year was dependent upon weather.

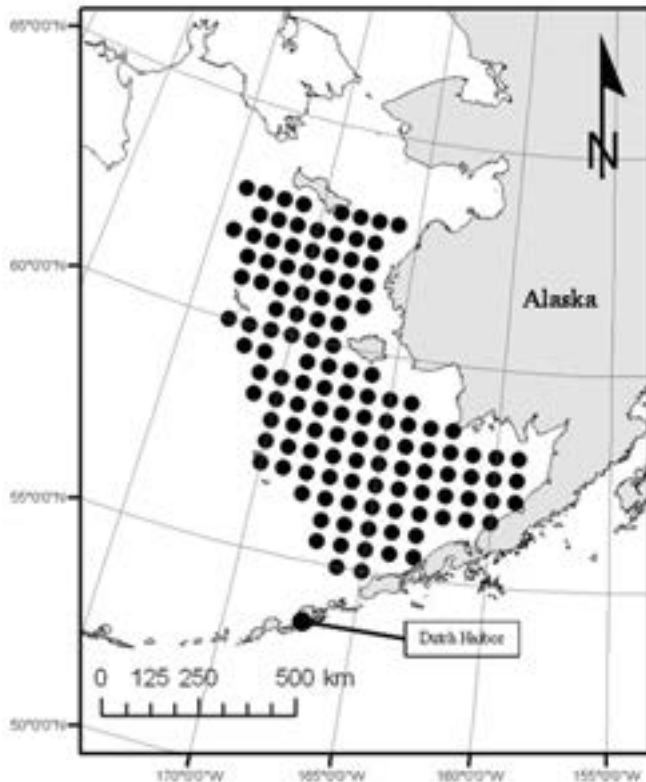


Fig. 1. The U.S. Bering-Aleutian Salmon International Surveys (BASIS) station grid for fall 2004–2007 in the eastern Bering Sea.

For our purposes and to maintain consistency among years, only stations from 55.5°N to 63.5°N latitude and those located on the shelf were included in the analysis (Fig. 1).

Fish and jellyfish were collected using a midwater rope trawl, towed at or near the surface, with typical spreads of 66.4 m horizontally and 14.6 m vertically. All sampling was performed during daylight hours. The salmon collected were sorted by species and counted. The salmon species included in this paper are: juvenile *O. keta*, *O. nerka*, *O. gorbuscha* (pink salmon), *O. kisutch* (coho salmon), and *O. tshawytscha* and immature *O. keta*. Every medusa caught in the codend of the trawl net was sorted to species. The first 50 intact individuals of each species were weighed (wet weight in kilograms). Wet weights were taken for all remaining individuals and pieces to calculate total biomass of each species (Suchman and Brodeur 2005). The jellyfish typically encountered by the trawl were *Chrysaora melanaster*, *Cyanea capillata*, *Aequorea* sp., and *Aurelia labiata*. Detailed BASIS field sampling methods can be found in Farley et al. (2005).

Oceanographic data were collected at each station immediately prior to deploying the trawl. Vertical profiles of temperature and salinity were measured with a Sea-Bird Electronics Inc. (SBE) Model 25 or Model 9 conductivity-temperature-depth profiler (CTD). Sampling occurred across domains on the shelf. Oceanographic characteristics include salinity, temperature (°C), chlorophyll-*a* (µg/L), and bottom depth (m). All oceanographic characteristics were average values by station from 0 to 15 m. Chlorophyll-*a* was determined from *in situ* fluorescence that was calibrated with discrete chlorophyll samples. The chlorophyll-*a* values for 2007 were incomplete and have not been included in this analysis.

Frequency, composition, relative biomass, and distribution

We analyzed survey data from 532 stations over 4 years to determine how often we caught specific species, the annual variation in composition, and the annual variation in relative biomass. To account for the frequency of a jellyfish occurring in the net during sampling, we calculated the percent for each species by weight (kg) for each year. Species composition was calculated by pooling data from each trawl catch into warm and cool years and then calculating a percentage. A one-tailed Z-test at the 99% confidence limit was used to test for significant differences between the warm and cool year proportions for each species. For changes in biomass, we calculated relative biomass (kg/km²) for each station and then pooled warm and cool years and applied a single factor ANOVA. To determine if the two warm years were similar in terms of biomass, we ran an additional single factor ANOVA on the 2004–2005 data, and on the 2006–2007 data. Mean relative biomass was calculated to examine differences in individual years. Catch distribution plots were

Table 1. Average values for oceanographic characteristics, temperature (°C), salinity, and chlorophyll-a (µg/L) for warm and cool years in the eastern Bering Sea from 2004–2007. The average of each characteristic is based on values from the top 15 m of the water column at all stations in the U.S. BASIS surveys (Bering-Aleutian Salmon International Surveys) sample area. The column “designation” labels the year as either warm or cool based on spring sea surface temperatures taken from the NOAA Bering Climate web page (available at: <http://www.beringclimate.noaa.gov/data>). The data originated from the M2 mooring located in the southeast Bering Sea (56.9°N, 164.1°W).

Year	Designation	Characteristic	Average	Std. Error	Minimum	Maximum
2004	warm	Temperature	10.81	0.13	7.09	14.00
2005	warm	Temperature	8.99	0.24	5.06	13.24
2006	cool	Temperature	8.98	0.11	4.34	11.67
2007	cool	Temperature	5.61	0.20	1.57	11.78
2004	warm	Salinity	31.31	0.06	28.93	32.35
2005	warm	Salinity	31.37	0.06	29.89	32.56
2006	cool	Salinity	31.06	0.11	23.27	32.93
2007	cool	Salinity	31.56	0.05	30.37	33.00
2004	warm	Chlorophyll-a	2.04	0.10	0.45	9.31
2005	warm	Chlorophyll-a	2.45	0.13	0.56	9.28
2006	cool	Chlorophyll-a	1.60	0.09	0.39	5.73
2007	cool	Chlorophyll-a	-	-	-	-

Table 2. Species composition by year for the fall U.S. BASIS (Bering-Aleutian Salmon International Surveys) surface trawl survey. Values are in percent and are calculated from total catches (kg).

Year	<i>Aequorea</i> sp.	<i>Aurelia labiata</i>	<i>Chrysaora melanaster</i>	<i>Cyanea capillata</i>	Other species
2004	25.9	1.2	65.1	6.1	1.6
2005	19.0	0.5	65.3	7.5	7.7
2006	27.4	0.7	61.1	10.0	0.8
2007	2.5	0.1	93.8	3.4	0.1

made of each species during warm and cool years to show distributions within a sample area and the potential for interactions through distribution overlap between jellyfish and salmon species (Figs. 3–5).

Associations

To identify associations between habitat characteristics, salmon species and jellyfish species, we developed general frequency distributions for each variable (salmon catch per unit effort (CPUE), salinity, chlorophyll-a, temperature, bottom depth, and jellyfish weight per unit effort (WPUE)) by constructing their empirical cumulative distribution functions (cdf) (Figs. 6–9). We statistically compared the cdfs of oceanographic characteristics, bottom depth, salmon species and jellyfish species using a modified version of the methods described in Perry and Smith (1994). The probability associated with each observation in a cdf simplifies to 1/n where n represents the number of hauls or sets in the sampling grid per year. The cdf for each habitat variable ($x_i; i = 1, n$) is constructed to incorporate the survey design

$$(1) \quad f(t) = \sum_i \frac{1}{n} I(x_i)$$

with the indicator function

$$I(x_i) = \begin{cases} 1, & \text{If } x_i \leq t \\ 0, & \text{Otherwise} \end{cases}$$

and where, t represents an index, ranging from the lowest to the highest value of the habitat variable at a step size appropriate for the desired resolution. In our analysis, bottom

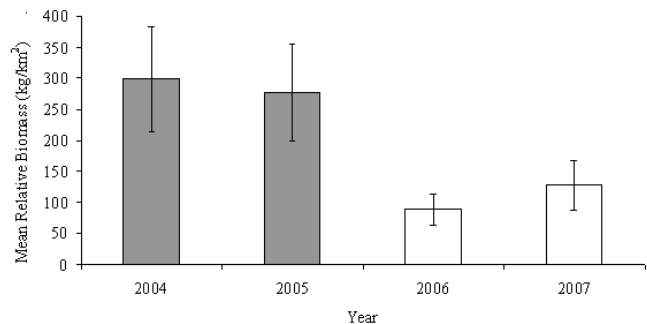


Fig. 2. Mean relative biomass by year for combined jellyfish species in the eastern Bering Sea from the U.S. BASIS (Bering-Aleutian Salmon International Surveys) surface trawl surveys. Filled bars represent the warm years, open bars, the cool years, with standard error shown.

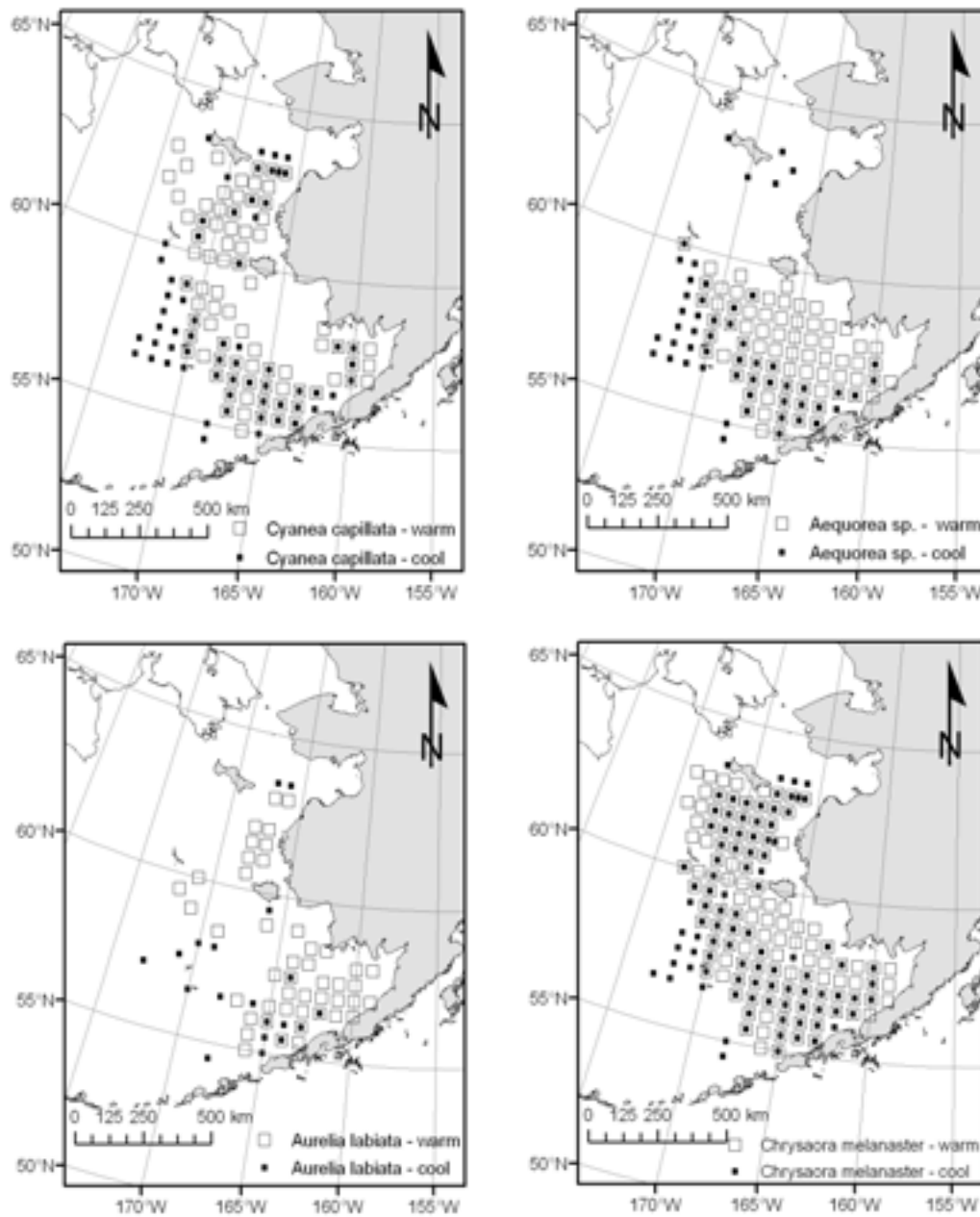


Fig. 3. Catch distribution plots for jellyfish species from the U.S. BASIS survey (Bering-Aleutian Salmon International Surveys) during fall warm and cool years. Open white squares represent catch locations during warm years (2004–2005) for each species and black filled squares represent cool years (2006–2007).

depth ranged from 0–130 m at step size 10, temperature ranged from 4° to 13°C at step size 1, salinity ranged from 29 to 33 parts per thousand at step size 0.5, and average chlorophyll-*a* ranged from 0–5 µg/L with a step increase of 1.

Each salmon and jellyfish species was associated with a habitat characteristic by

$$(2) \quad g(t) = \sum_i \frac{1}{n} \frac{y_i}{\bar{y}} I(x_i)$$

where y_i is the number or weight of individuals of a particular species in set i and \bar{y} is the estimated mean catch of a par-

ticular species. We used the test statistic described in Perry and Smith (1994) to test the strength of the associations by assessing the degree of difference between the 2 curves $g(t)$ and $f(t)$ (Figs. 6–9). The maximum absolute vertical distance between $g(t)$ and $f(t)$ was estimated using

$$(3) \quad \max_{\nabla t} \left| \sum_i \frac{1}{n} \left(\frac{y_i - \bar{y}}{\bar{y}} \right) I(x_i) \right|$$

We modeled the distribution of the test statistic under the null hypothesis of random association between individ-

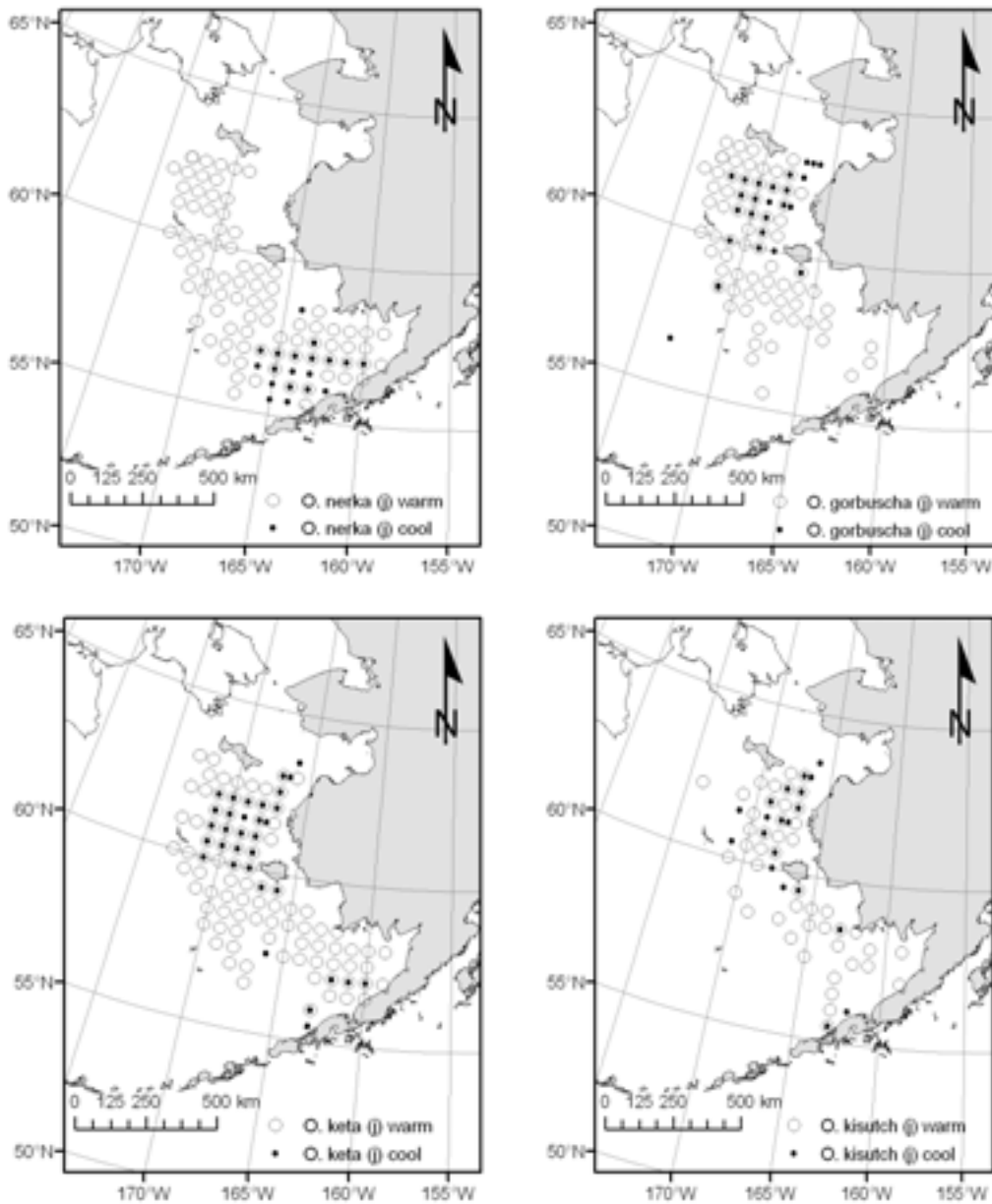


Fig. 4. Catch distribution plots for juvenile salmon species (*Oncorhynchus* spp.) from the U.S. BASIS survey (Bering-Aleutian Salmon International Survey) during fall warm and cool years. Open white circles represent catch locations during warm years (2004–2005) for each species and black filled circles represent cool years (2006–2007).

ual salmon species (CPUE) and jellyfish species (WPUE) with habitat characteristics through Monte-Carlo sampling (see Perry and Smith (1994) for details). The pairings of $(1/n)[y_i - \bar{y}]/\bar{y}(1/n)$ and x_i were randomized over all i and the test statistic was calculated for the new pairs. This was repeated 1000 times to produce a pseudo-population of test statistics under the null hypothesis. Afterwards, the original test statistic for a given species and oceanographic characteristic was compared with increasing (sorted) values from the randomized procedure and the number of pseudo-test statistics that were equal to or greater than the original test statistic were counted. The probability of obtaining a test

statistic for a given species and variable (habitat characteristic, salmon species, or jellyfish species) is equal to (1- the number of pseudo-test statistics greater than or equal to the test statistic/1000).

RESULTS

Analysis of oceanographic characteristics from our surveys showed that the average sea surface temperatures (top 15 m) were lower in 2005, 2006, and 2007 than those measured in 2004 (Table 1). Average salinities (top 15 m) were lowest in 2006 and highest in 2007. Warm/cool year differ-

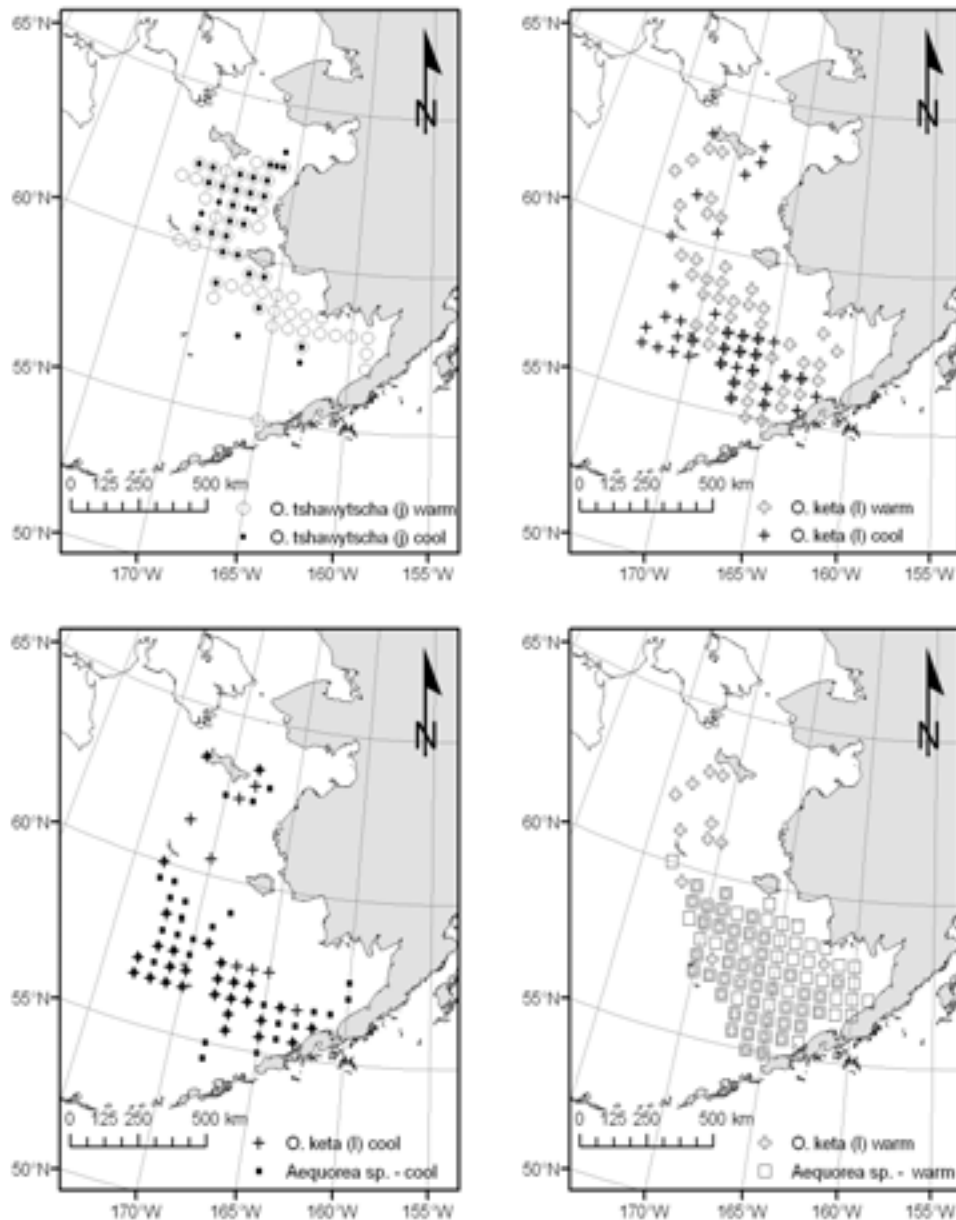


Fig. 5. Catch distribution plots for juvenile salmon (*Oncorhynchus* spp.) and jellyfish species from the U.S. BASIS survey (Bering-Aleutian Salmon International Surveys) during fall warm and cool years. Open white symbols represent catch locations during warm years (2004–2005) for each species and black filled symbols represent cool years (2006–2007).

ences were not observed (Table 1). The average chlorophyll-*a* (top 15 m) was also lowest in 2006 compared to the two warm years (Table 1).

In warm years, the frequency at which the four jellyfish species occurred in our nets was 94% *Chrysaora melanaster*, 72% *Cyanea capillata*, 60% *Aequorea* sp., and 39% *Aurelia labiata*. The frequency of occurrence in cool years differed significantly from warm years with 81% *C. melanaster*, 44% *Cyanea capillata*, 39% *Aequorea* sp., and 14% *A. labiata* ($P < 0.01$, $Z = 4.964, 6.336, 4.435, 6.437$). Species composition (percent catch) remained relatively the same from 2004–2006 with *C. melanaster* having the highest composi-

tion (61–65%), followed by *Aequorea* sp. (19–27 %) (Table 2). In 2007, *C. melanaster* dominated the composition at 94% with all other species decreasing dramatically (Table 2). Relative biomass for combined jellyfish species was significantly higher in warm than in cool years ($F_{1,497} = 35.04$, $P < 0.01$). There was no difference in the mean relative biomass for individual warm years ($F_{1,234} = 0.13$, $P = 0.72$) or individual cool years ($F_{1,261} = 2.68$, $P = 0.10$) (Fig. 2).

Chrysaora melanaster was seen at almost every station on our survey grid in warm years. During cool years we noted a slight decrease in distribution but the majority of our sampling grid was still occupied by *C. melanaster* indicat-

Table 3. Fall associations based on cumulative frequencies for juvenile salmon CPUE (catch per unit effort) and jellyfish WPUE (weight per unit effort) with temperature in the eastern Bering Sea. Table A shows the p -values resulting from the differences in the cumulative frequencies of each species and the oceanographic characteristic temperature collected during the annual U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Table B shows the trends associated with the statistically significant results between species and temperature. For example, *Oncorhynchus nerka* was significantly associated with warmer than average temperatures in 2005. Salmon species life-history stages are indicated by (j) = juvenile and (l) = immature.

A.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	0.195	0.554	0.149	0.351
<i>O. nerka</i> (j)	0.13	0.047	0.03	0.458
<i>O. gorbuscha</i> (j)	0.024	0.829	0.012	0.776
<i>O. tshawytscha</i> (j)	0.355	0.315	< 0.001	0.009
<i>O. kisutch</i> (j)	0.143	0.001	< 0.001	0.001
<i>O. keta</i> (l)	0.034	0.003	0.876	0.444
<i>Aequorea</i> sp.	< 0.001	0.052	0.175	0.504
<i>Aurelia labiata</i>	0.549	0.049	0.612	0.081
<i>Chrysaora melanaster</i>	0.769	< 0.001	0.002	0.742
<i>Cyanea capillata</i>	0.359	0.086	0.274	0.82

B.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	-	-	-	-
<i>O. nerka</i> (j)	-	warmer	warmer	-
<i>O. gorbuscha</i> (j)	cooler	-	cooler	-
<i>O. tshawytscha</i> (j)	-	-	cooler	cooler
<i>O. kisutch</i> (j)	-	warmer	warmer	cooler
<i>O. keta</i> (l)	cooler	warm/cool	-	-
<i>Aequorea</i> sp.	warmer	warmer	-	-
<i>Aurelia labiata</i>	-	warmer	-	-
<i>Chrysaora melanaster</i>	-	cooler	cooler	-
<i>Cyanea capillata</i>	-	-	-	-

ing distribution overlaps with all species of salmon during both warm and cool years (Figs. 3–5). The distribution of *Aurelia labiata* was mainly south of 60°N in the Bristol Bay area and at coastal locations in areas north of 60°N allowing for physical overlap with distributions of juvenile *O. nerka*, *O. keta*, *O. kisutch*, and *O. tshawytscha* (Figs. 3–5). *Cyanea capillata* was distributed throughout the survey location with the exception of an area south of 60°N near the coast; there were distribution overlaps with all species of salmon (Figs. 3–5). *Aequorea* sp. was distributed south of 60°N, mainly along the coast and offshore during both warm and cool years; physical overlaps in distribution were seen with *O. nerka* and immature *O. keta* during warm and cool years and juvenile *O. keta* during warm years only (Figs. 3–5).

Temperature, salinity, and chlorophyll-*a* had multiple significant associations in multiple years with salmon and jellyfish; all associations between species and characteristics varied in their trends (Tables 3–5). Juvenile *O. tshawytscha* were significantly associated with cooler temperatures in only cool years and shallower bottom depths in all years ($P < 0.05$) (Tables 4, 6). Juvenile *O. kisutch* were associated

with shallower than average bottom depths for all years ($P < 0.05$) (Table 6). Juvenile *O. keta* had only cool-year associations with lower salinities and shallower bottom depths ($P < 0.05$) (Tables 5, 6). For the most part, immature *O. keta* were associated with cooler temperatures in warm years, and higher salinities and deeper bottom depths in all years ($P < 0.05$) (Tables 4–6). Although less consistent among years, we did find juvenile *O. nerka* were associated with warmer SSTs while juvenile *O. gorbuscha* were associated with cooler SSTs.

In terms of differences between warm and cool years, the only jellyfish species to demonstrate any such difference was *Aequorea* sp., which associated with warmer than average temperatures only in warm years (2004–2005) ($P < 0.05$) (Table 3). *Aequorea* sp. was significantly associated with higher salinities and deeper depths in all years ($P < 0.05$) (Tables 4, 6). Chlorophyll-*a* did not show any warm/cool-year influenced association for any species but there were some significant year-specific associations (Table 5).

Table 4. Fall associations based on cumulative frequencies for juvenile salmon CPUE (catch per unit effort) and jellyfish WPUE (weight per unit effort) with salinity in the eastern Bering Sea. Table A shows the *p*-values resulting from the differences in the cumulative frequencies of each species and the oceanographic characteristic salinity collected during the annual U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Table B shows the trends associated with the statistically significant results between species and salinity. For example, *Oncorhynchus nerka* was significantly associated with higher than average salinities in 2004. Salmon species life-history stages are indicated by (j) = juvenile and (l) = immature.

A.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	0.349	0.404	< 0.001	0.032
<i>O. nerka</i> (j)	0.017	0.699	0.643	0.644
<i>O. gorbuscha</i> (j)	0.52	0.919	< 0.001	0.578
<i>O. tshawytscha</i> (j)	< 0.001	0.085	< 0.001	0.542
<i>O. kisutch</i> (j)	< 0.001	< 0.001	0.034	0.217
<i>O. keta</i> (l)	< 0.001	< 0.001	0.002	0.007
<i>Aequorea</i> sp.	< 0.001	< 0.001	< 0.001	0.001
<i>Aurelia labiata</i>	0.314	0.02	0.034	0.04
<i>Chrysaora melanaster</i>	0.032	0.023	0.959	0.037
<i>Cyanea capillata</i>	0.422	0.001	0.001	0.152
B.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	-	-	lower	lower
<i>O. nerka</i> (j)	higher	-	-	-
<i>O. gorbuscha</i> (j)	-	-	lower	-
<i>O. tshawytscha</i> (j)	lower	-	lower	-
<i>O. kisutch</i> (j)	lower	lower	lower	-
<i>O. keta</i> (l)	higher	higher	higher	higher
<i>Aequorea</i> sp.	higher	higher	higher	higher
<i>Aurelia labiata</i>	-	lower	low/high	low/high
<i>Chrysaora melanaster</i>	higher	-	-	lower
<i>Cyanea capillata</i>	-	higher	higher	-

DISCUSSION

Our analysis reveals several associations regarding warm and cool spring SST habitat associations of the eastern Bering Sea salmon and jellyfish species examined. Juvenile *O. tshawytscha* and *O. kisutch* tended to associate with shallow depths and low salinity water, indicating that they maintained a 'nearshore' distribution during both warm and cool SST years. Juvenile *O. keta* were associated with lower salinity and shallow depths during years with cool SSTs. In contrast, immature *O. keta* were associated with deeper locations during warm SST and higher salinity during all years, indicating an offshore distribution during warm SST years. Juvenile *O. nerka* tended to be associated with warmer SSTs across cool and warm SST years, whereas juvenile *O. gorbuscha* tended to be associated with cooler SSTs across all years. Among the jellyfish, *Aequorea* sp. were associated with offshore locations during all years examined, whereas *Aurelia labiata* tended to be at nearshore locations during most years. *Chrysaora melanaster* was not associated with either depth or salinity but was associated with cooler SSTs

during years with warm SSTs, indicating that their distribution may have shifted to regions with cooler SSTs during years with warm SSTs.

The significant associations between juvenile salmon and habitat are consistent with known distributions of juvenile salmon in the eastern Bering Sea. Farley et al. (2005) found that juvenile *O. tshawytscha* and *O. kisutch* were distributed in nearshore locations, juvenile *O. keta* were distributed from nearshore to across the inner front (50 m depth) and juvenile *O. nerka* were distributed farther offshore in depths to 100 m during a year with warm SSTs. The distributions of juvenile *O. nerka* and *O. keta* shifted to nearshore locations during years of cool SSTs, whereas the distribution of juvenile *O. tshawytscha* and *O. kisutch* remained the same during warm and cool SST years (Farley et al. in press). The eastern Bering Sea shelf is a migratory corridor for juvenile western Alaska salmon emigrating from freshwater rearing areas in the north Pacific Ocean (Farley et al. 2005). The timing at which these juvenile salmon migrate is a function of water temperature and growth rate (Straty 1974; Burgner 1991; Healey 1991; Heard 1991; Salo 1991; Sandercock

Table 5. Fall associations based on cumulative frequencies for juvenile salmon CPUE (catch per unit effort) and jellyfish WPUE (weight per unit effort) with chlorophyll-a in the eastern Bering Sea. Table A shows the p-values resulting from the differences in the cumulative frequencies of each species and the oceanographic characteristic chlorophyll-a collected during the annual U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Table B shows the trends associated with the statistically significant results between species and chlorophyll-a. Example, *Oncorhynchus gorbuscha* is significantly associated with lower than average chlorophyll-a in 2006. Salmon species life-history stages are indicated by (j) = juvenile and (l) = immature. Chlorophyll-a data were unavailable for 2007.

A.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	0.489	0.726	0.115	-
<i>O. nerka</i> (j)	0.485	0.129	0.101	-
<i>O. gorbuscha</i> (j)	0.233	0.491	0.043	-
<i>O. tshawytscha</i> (j)	0.597	0.022	0.001	-
<i>O. kisutch</i> (j)	0.396	0.319	0.677	-
<i>O. keta</i> (l)	0.293	< 0.001	0.044	-
<i>Aequorea</i> sp.	0.878	< 0.001	0.760	-
<i>Aurelia labiata</i>	0.119	0.122	0.766	-
<i>Chrysaora melanaster</i>	0.006	0.016	0.05	-
<i>Cyanea capillata</i>	0.19	0.408	0.604	-

B.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	-	-	-	-
<i>O. nerka</i> (j)	-	-	-	-
<i>O. gorbuscha</i> (j)	-	-	lower	-
<i>O. tshawytscha</i> (j)	-	lower	lower	-
<i>O. kisutch</i> (j)	-	-	-	-
<i>O. keta</i> (l)	-	higher	lower	-
<i>Aequorea</i> sp.	-	higher	-	-
<i>Aurelia labiata</i>	-	-	-	-
<i>Chrysaora melanaster</i>	higher	lower	lower	-
<i>Cyanea capillata</i>	-	-	-	-

1991; Ocean Carrying Capacity Program 1999). In addition, juvenile western Alaska salmon generally emigrate from freshwater rearing areas during ice breakup, and changes in river discharge and flow rates (Burgner 1991; Healey 1991; Salo 1991; Sandercock 1991). Thus, variability in the timing of lake and river ice breakup, which influences flow and discharge rates (Scrimgeour et al. 1994) can affect when juvenile salmon enter the eastern Bering Sea and thus, the amount of time they have to grow and emigrate offshore. Therefore, it is likely that the associations found here among three of the juvenile salmon species and their habitats is simply an artifact of their migration patterns during warm and cool SST years and not due to an affinity to particular habitat characteristics. We note that juvenile *O. tshawytscha* and *O. kisutch* may have been an exception as these juvenile salmon maintained consistent habitat associations and had consistent distributions during both warm and cool SSTs (Farley et al. in press). However, it is equally likely that juvenile *O. tshawytscha* and *O. kisutch* are found nearshore due to their tendency to feed on shallow water or coastal domain forage fish species such as *Ammodytes hexapterus* (sand lance)

(Farley et al. in press; Murphy et al. 2009).

Our conclusions regarding associations between jellyfish and eastern Bering Sea oceanographic characteristics could be biased due to the type of trawl sampling performed during the surveys. The BASIS research cruises targeted juvenile salmon in the top 15 m of the water column. Thus, it is possible that our net did not catch a representative sample of the jellyfish species, making it difficult to associate jellyfish biomass with oceanographic characteristics. The jellyfish captured by our net during the BASIS survey ranged in size from 1.5–67.5 cm (K. Ciciel, unpub. data). A comparison between our jellyfish catch per unit effort (CPUE) and the RACE (Resource Assessment and Conservation Engineering Division, NMFS) bottom trawl CPUE revealed that the trends in relative CPUEs were similar during warm and cool SST years (Lauth 2008). *Chrysaora melanaster* was observed as the most frequently occurring jellyfish species in both warm and cool years during the BASIS surveys. Brodeur et al. (2002, 2008b) had similar findings and documented that *C. melanaster* dominated the jellyfish catch in both abundance and biomass during the RACE bottom trawl

Table 6. Fall associations based on cumulative frequencies for juvenile salmon CPUE (catch per unit effort) and jellyfish WPUE (weight per unit effort) with bottom depth in the eastern Bering Sea. Table A shows the p -values resulting from the differences in the cumulative frequencies of each species and bottom depth collected during the annual U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Table B shows the trends associated with the statistically significant results between species and bottom depth. For example, *Oncorhynchus gorbuscha* was significantly associated with shallower than average bottom depths in 2006. Salmon species life-history stages are indicated by (j) = juvenile and (l) = immature.

A.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	0.149	0.206	< 0.001	0.016
<i>O. nerka</i> (j)	0.088	0.229	0.006	0.138
<i>O. gorbuscha</i> (j)	0.064	0.605	0.014	0.218
<i>O. tshawytscha</i> (j)	0.004	0.001	< 0.001	< 0.001
<i>O. kisutch</i> (j)	< 0.001	< 0.001	< 0.001	< 0.001
<i>O. keta</i> (l)	< 0.001	< 0.001	0.537	0.35
<i>Aequorea</i> sp.	< 0.001	< 0.001	< 0.001	< 0.001
<i>Aurelia labiata</i>	0.306	0.052	0.073	0.026
<i>Chrysaora melanaster</i>	0.863	0.007	0.58	0.984
<i>Cyanea capillata</i>	0.034	0.002	0.068	0.416
B.				
Species	2004	2005	2006	2007
<i>Oncorhynchus keta</i> (j)	-	-	shallower	shallower
<i>O. nerka</i> (j)	-	-	deep/shallow	-
<i>O. gorbuscha</i> (j)	-	-	shallower	-
<i>O. tshawytscha</i> (j)	shallower	shallower	shallower	shallower
<i>O. kisutch</i> (j)	shallower	shallower	shallower	shallower
<i>O. keta</i> (l)	deeper	deeper	-	-
<i>Aequorea</i> sp.	deeper	deeper	deeper	deeper
<i>Aurelia labiata</i>	-	shallower	-	deeper
<i>Chrysaora melanaster</i>	-	shallower	-	-
<i>Cyanea capillata</i>	shallow/deep	deeper	-	-

surveys in the Bering Sea. Therefore, we believe that our analysis is not biased and provides a true assessment of the relative biomass of the four jellyfish species analyzed.

One of our objectives was to assess whether or not jellyfish and salmon on the eastern Bering Sea shelf have the potential to directly compete during fall for resources. Our results indicated that juvenile salmon and jellyfish do not target similar oceanographic characteristics but do overlap in terms of distribution. During these times of shared distributions it is possible that both groups are targeting preferred prey resources which also overlap between jellyfish and juvenile salmon (BASIS data, unpublished; Purcell and Sturdevant 2001; Zavolokin et al. 2008). Therefore, we see potential for competition between jellyfish and salmon based on diet and spatial overlap. Similar results between fish and jellyfish were described by Purcell and Sturdevant (2001) and the possibilities for salmon/jellyfish diet and spatial overlap were discussed by Zavolokin et al. (2008). Due to our lack of diet analysis, we are severely limited in the assumptions we can make.

Immature *O. keta* and *Aequorea* sp. did show potential

for interaction, as these two species tended to be associated with deeper and higher salinity water during each year. They also overlap spatially. In addition, the *O. keta* diet includes a large portion of gelatinous species at times, but because of relatively rapid digestion rates and water loss, quantifiable numbers and identifications are not known (Arai 1988; Purcell and Arai 2001; Arai et al. 2003). *Aequorea* sp. could potentially be a prey item for immature *O. keta*. In laboratory studies it was fed successfully to immature *O. keta* (Arai et al. 2003). Thus, it is possible to suggest that immature *O. keta* are distributing themselves in areas of higher concentrations of prey resources and not with particular sea temperatures, bottom depths, or salinities. We note that the relative biomass of *Aequorea* sp. was low compared to the dominant jellyfish species *C. melanaster* (Cieciel and Eisner 2008), and it is likely that if competition for resources between *Aequorea* sp. and immature *O. keta* were to occur, it would be at low levels.

Our data also indicate a significant decrease in jellyfish biomass between warm and cool SST years. Jellyfish catch composition remained relatively constant from 2004–2006

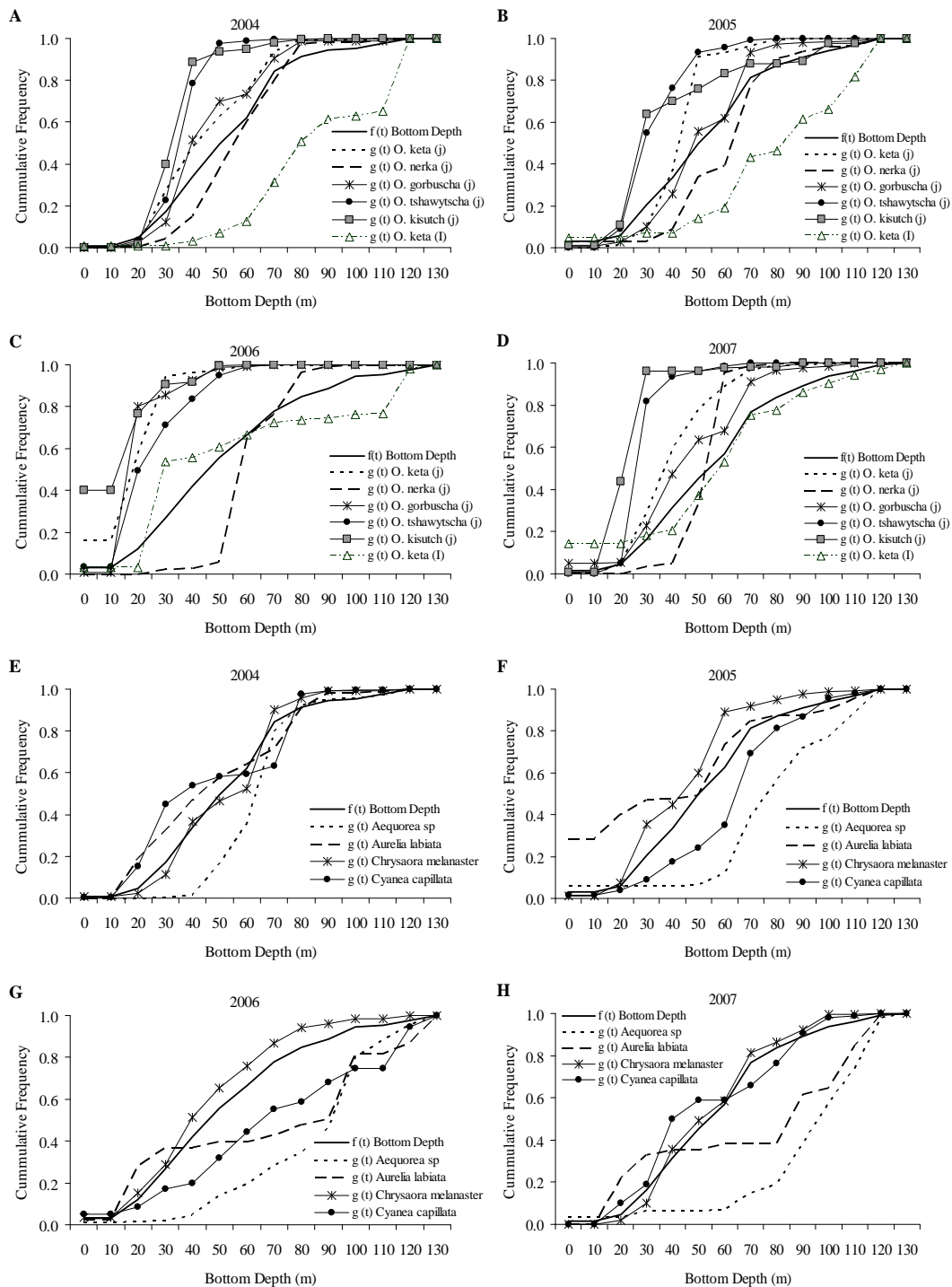


Fig. 6. Cumulative distribution functions for bottom depth with salmon species (A–D) and jellyfish species (E–H) for all years from the annual fall U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Life stage of salmon is indicated by j (juvenile) or l (immature).

with *C. melanaster* as the dominant species followed by *Aequorea* sp., *Cyanea capillata*, and *Aurelia labiata*. However, during 2007 the catch composition changed with all species recorded in low numbers and in some cases nearly absent, with the exception of *C. melanaster*. Both temperature and seasonal variation can affect jellyfish species composition.

For example, in the East China Sea the composition of jellyfish shifted from (in order of highest abundance) *Aequorea* sp., *Cyanea* sp., and *Stomolophus meleagris* in April (cooler waters) to *S. meleagris*, *Aequorea* sp., and *Cyanea* sp. in June (warmer waters) (Cheng et al. 2006). We note that the average fall SST during 2007 in the eastern Bering Sea was

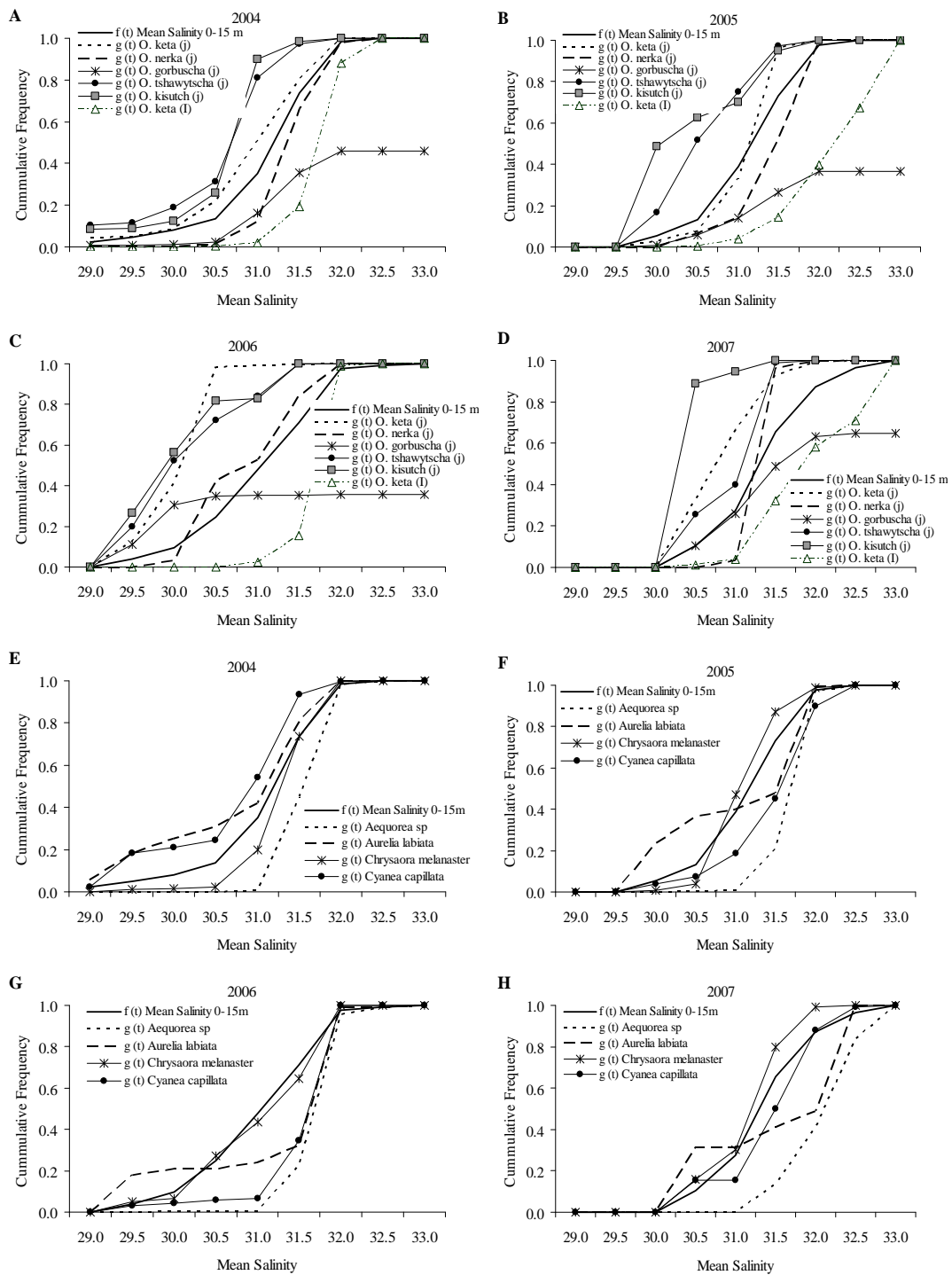


Fig. 7. Cumulative distribution functions for mean salinity with salmon species (A–D) and jellyfish species (E–H) for all years from the annual fall U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Life stage of salmon is indicated by j (juvenile) or I (immature).

5.61°C compared to substantially higher SST averages during 2004–2006 (8.9°, 8.9°, 10.8°C). Sea temperature effects growth rates of jellyfish at early life-history stages (Purcell 2007; Wilcox et al. 2007), can alter respiration rates (Møeller and Riisgård 2007), and impact their distributions (Decker et al. 2007). Similar shifts in the relative abundance of pelagic

fish species in relation to warm (higher abundance) and cool (lower abundance) SST years have been found for western Alaska salmon (Farley et al. in press) and age-0 pollock (Moss et al. 2009). These later studies related shifts in relative abundance to bottom-up control of the eastern Bering Sea ecosystem. Because the biomass of jellyfish decreased

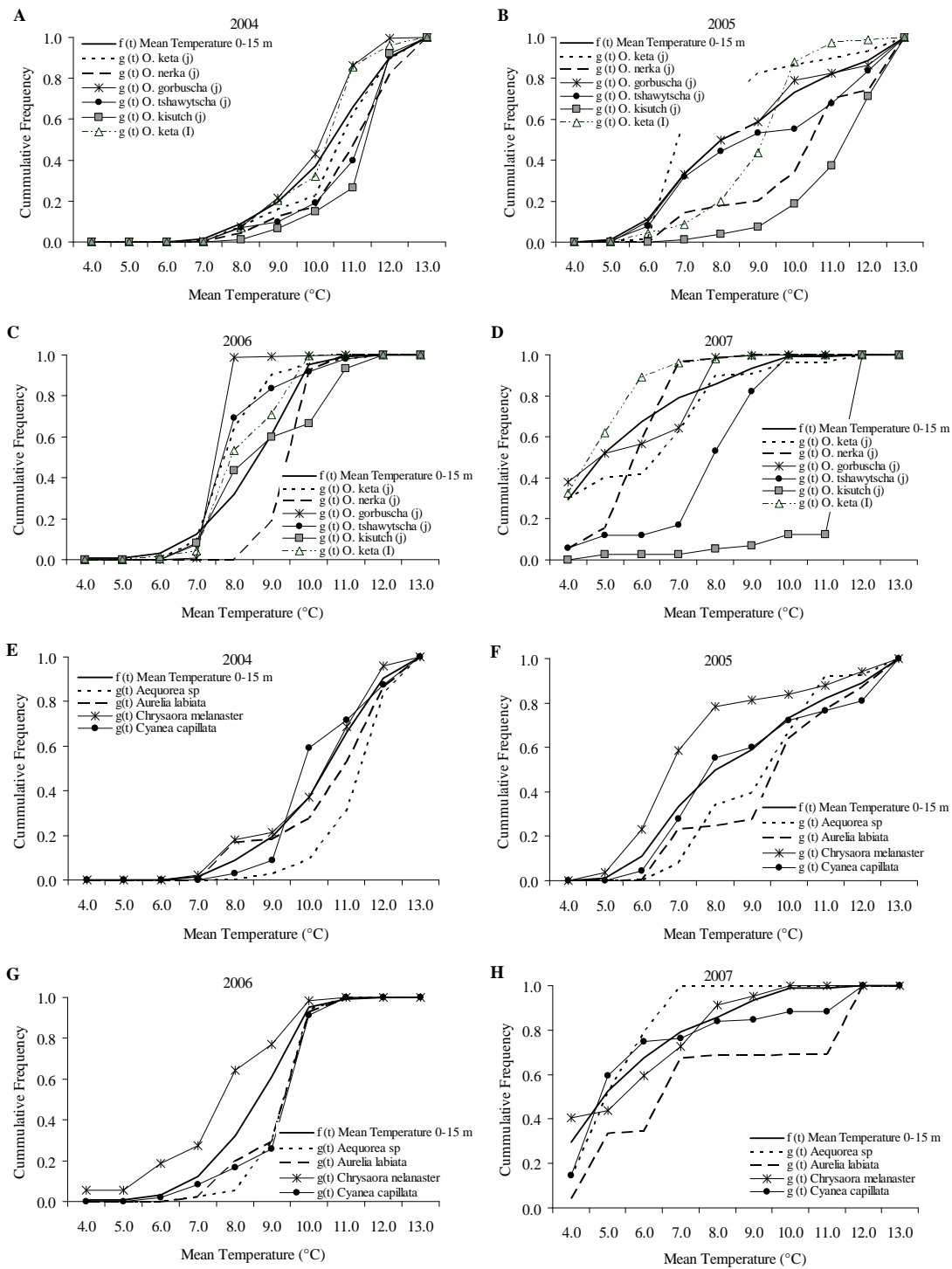


Fig. 8. Cumulative distribution functions for mean temperature with salmon species (A–D) and jellyfish species (E–H) for all years from the fall U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Life stage of salmon is indicated by j (juvenile) or I (immature).

during cool years, it is likely that similar bottom-up processes regulate their growth and abundance levels on the eastern Bering Sea shelf.

The relative abundance data for juvenile salmon and jellyfish were collected using a systematic, non-random survey sampling design. Thus, our data violate the assumptions re-

quired to utilize classical statistical models (e.g., ANOVA), where independence of observations and normal distribution are necessary to reduce bias in determining the strength of an association. The analysis we chose to examine the habitat association of fish species is non-parametric in the sense that no specific statistical distribution is assumed for either fish

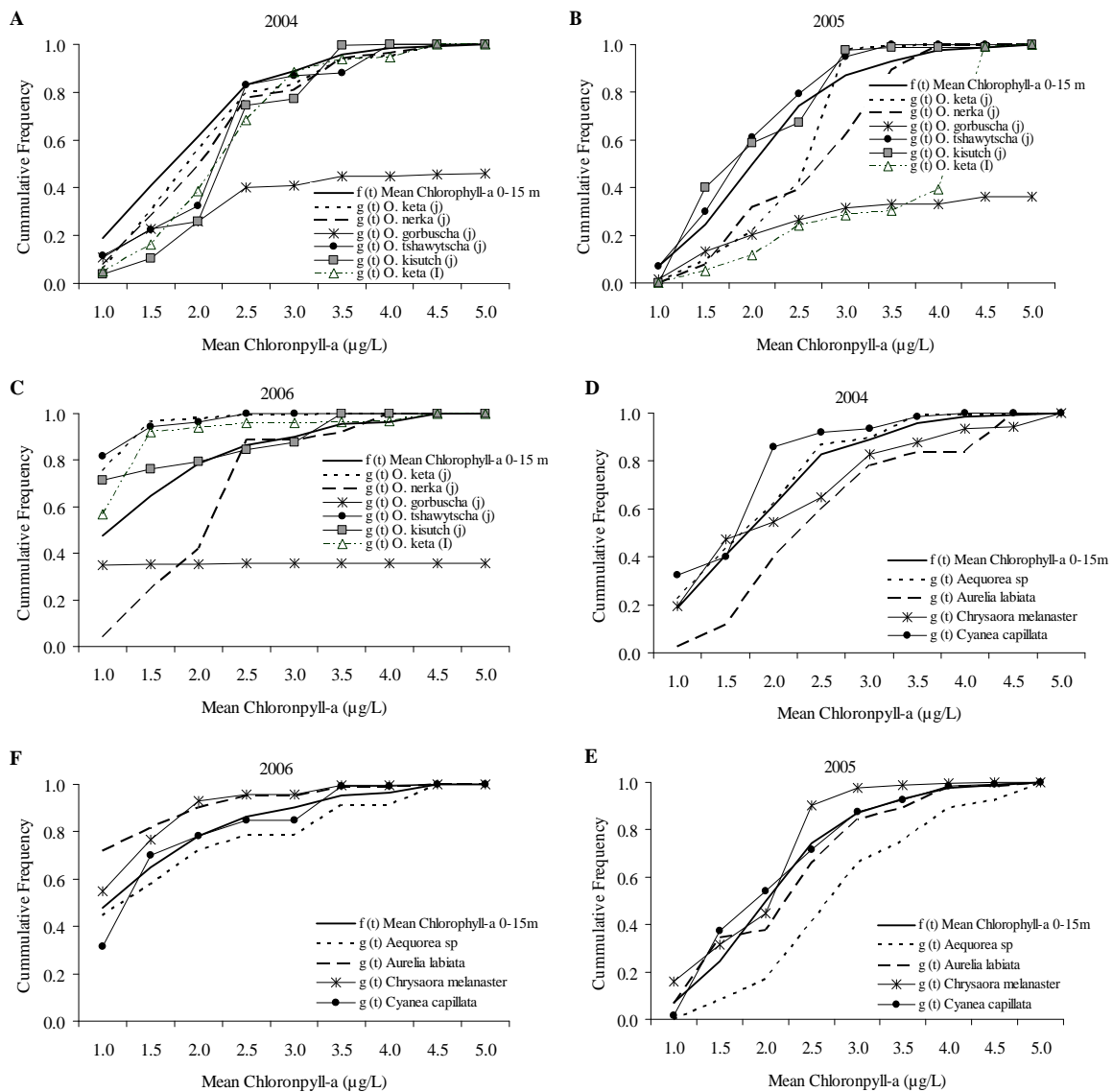


Fig. 9. Cumulative distribution functions for mean chlorophyll-a with salmon (A–C) and jellyfish species (D–F) for years 2004–06 from the fall U.S. BASIS survey (Bering-Aleutian Salmon International Surveys). Life stage of salmon is indicated by j (juvenile) or I (immature).

catch or habitat variables. The method allows for quantitative comparisons with observed habitat conditions to identify fish species which are randomly distributed with respect to a particular habitat (Perry and Smith 1994). The method takes explicit account of the survey design, and has been used on other fish catch data sets to determine habitat associations for fish where the fish were caught using survey designs similar to ours (Perry and Smith 1994; Brodeur et al. 1999; Vögler et al. 2008) or from commercial catch data (Reynolds 2003). In addition, the randomization tests are often more powerful than their standard counterparts in non-standard situations such as the survey design and analysis we present here.

Our habitat associations with juvenile salmon and jellyfish are simple univariate associations. We understand that bottom depth and temperature may be correlated and that a more powerful approach would have been to include both

variables using a bivariate distribution, such as that suggested in Perry and Smith (1994). However, our findings that some of the juvenile salmon species and the jellyfish species do not actively select a particular habitat temperature or chlorophyll-a range was surprising, considering the differences in these habitat characteristics among years.

In conclusion, while some salmon species appear to associate with certain habitat characteristics, it is more plausible that these associations are an artifact of their growth, migratory pathways, and preferred prey. We did see potential for direct competition based on spatial overlap and similar diets on the eastern Bering Sea shelf during fall between jellyfish and juvenile salmon. This analysis provides more of an understanding of adult jellyfish species within the eastern Bering Sea ecosystem, in that the biomass of many species may be regulated by bottom-up processes.

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Genetic Techniques Provide Evidence of Chinook Salmon Feeding on Walleye Pollock Offal

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Abstract: Declining runs of Chinook salmon in western Alaska have focused interest on the ocean condition and food habits of Chinook salmon in the Bering Sea, including potential mortality from bycatch in the pollock fishery. Examination of Chinook salmon stomach contents collected in the eastern Bering Sea by the U.S. North Pacific Groundfish Observer Program (NOAA Fisheries) revealed isolated pieces of skin, bones, and fins (offal) belonging to large-bodied fish which were physically identified as either walleye pollock (*Theragra chalcogramma*) or Pacific cod (*Gadus macrocephalus*). To confirm the species identification of the offal, we matched DNA sequences of these offal samples to known sequences of walleye pollock and Pacific cod. Novel mitochondrial DNA (mtDNA) primers were designed to amplify a 174-base pair (bp)-long section of the cytochrome c oxidase subunit I (COI) gene, which was sequenced and compared with sequences downloaded from the GenBank database. Typically, much longer sections (~700 bp) of DNA are used for species identification but due to the state of digestion of the samples, long sequences of DNA were no longer present. The specific design of our primers, however, allowed us to make positive identification and differentiation of walleye pollock and Pacific cod. Of the 15 offal samples, nine yielded usable sequences, all of which were positively identified as walleye pollock. Our results clearly demonstrate the utility of a short COI sequence for species identification of Chinook salmon stomach contents that might otherwise be unidentifiable due to either the state of digestion, or because the salmon consumed isolated body parts (offal) rather than whole fish. These results suggest that walleye pollock offal supplements the diet of Chinook salmon during winter.

Keywords: Chinook salmon, walleye pollock, offal, genetics, food habits

INTRODUCTION

Understanding the ecology of a species is a fundamental component in developing conservation and management plans. Recent declines of Chinook salmon (*Oncorhynchus tshawytscha*) returns to western Alaska have prompted restrictions on commercial fishing (Hayes et al. 2008). Changes in abundance can often be attributed to variability in conditions during the marine life history (Botsford et al. 2002), yet there are large gaps in our understanding of the feeding ecology of Chinook salmon during their time at sea. Food habits studies are basic to gaining insights into salmon marine life history (Beamish and Mahnken 2001; Armstrong et al. 2008).

Stomach content analyses from Chinook salmon gathered in summer and fall in the North Pacific, Gulf of Alaska, and the Bering Sea indicate they feed primarily on fish and gonatid squids, although euphausiids, crab larvae, and other invertebrates can also be found in Chinook salmon diets (e.g., Volkov et al. 1995; Kaeriyama et al. 2004; Davis et al. 2005, 2009a; Volkov et al. 2007; Weitkamp and Sturdevant 2008). However, little is known about the food habits of

Chinook salmon at sea during winter, primarily because of the difficulty in conducting winter surveys.

Our samples were obtained from stomach samples collected by U.S. groundfish observers during the winter walleye pollock (*Theragra chalcogramma*) fishery in the eastern Bering Sea. Analysis of these samples revealed the presence of skin, flesh, fins, and bone (Davis et al. 2009b). Visual examination of skin pigmentation, fin and bone morphology, flesh consistency, and myotome structure revealed that among the possible prey species of Chinook salmon, walleye pollock and Pacific cod (*Gadus macrocephalus*) were the only reasonable possibilities. However, due to the condition of the tissues, further identification to the species level was not possible for all samples. Instead, we used genetic techniques to make positive species identifications.

Genetic identification is possible by comparing DNA sequences from unknown samples to those of known taxa. This approach can become quite costly if one must secure, extract, and sequence DNA from all possible candidate taxa. Although DNA sequences are available on public databases (GenBank), they often stem from different genes in different taxa, thus preventing direct comparison for species identifi-

cation. In a recent standardization effort, Hebert et al. (2003) proposed that a single gene sequence was sufficient to differentiate between the majority of species on the planet and suggested using the mitochondrial DNA (mtDNA) gene, cytochrome *c* oxidase subunit I (COI). The COI gene has been termed the “barcode of life” and sequences from different species have been compiled in order to provide a database by which sequences from new or unknown species can be compared (Ratnasingham and Hebert 2007). This effort has been extended to fish (Ward et al. 2005), and COI sequences are now available for a wide variety of species on GenBank (www.ncbi.nlm.nih.gov) and on the Fish Barcode of Life database (www.fishbol.org; Ward et al. 2009).

Genetic tools have been used to determine the identification of prey species after partial digestion by amplifying relatively small (162 bp and 327 bp) sections of mtDNA (Parsons et al. 2005). Short sequences have also helped to identify highly degraded DNA samples using the barcoding gene, COI (Hajibabaei et al. 2006). In this study, our objective was to identify the fish species of offal found in the stomach contents of Chinook salmon. To achieve this objective, we developed novel primers for gene amplification of short DNA fragments, and compared those sequences to reference data from a public database (GenBank) and to positive control DNA samples from known species.

MATERIALS AND METHODS

Laboratory Analysis

Chinook salmon stomach samples were obtained from the winter pollock fishery during January to March, 2007 in the eastern Bering Sea and examined by Davis et al. (2009b). Offal refers to fish body parts (e.g., head, tail, spine, skin) that are discarded after processing. When Chinook salmon stomach contents were identified as fish offal they were collected and frozen at -20°C. In total, 15 samples were selected for genetic analysis (Table 1). Samples were thawed and divided into subsamples, which were then soaked in a 2% bleach solution to reduce contamination. To account for differing degrees of digestion present in each sample and the effect of bleach on our target DNA, we used two different soak times per sample. One subsample was soaked for 1 min and a second subsample for 3 min. After bleach soaking, each subsample was rinsed twice in distilled water and then preserved in a 95% ethanol solution according to the protocol outlined in Mitchell et al. (2007). This procedure reduced DNA contamination from Chinook salmon and other prey items by destroying the DNA in the external layers of the tissue.

A sample of walleye pollock positive control DNA was extracted from fin tissue (collected in the northeast Bering Sea) using the same protocol as that for the offal samples. Two Pacific cod positive control DNA samples were obtained from the study by Cunningham et al. (2009).

Offal DNA was extracted with a Qiagen DNeasy® micro-extraction kit following the manufacturer’s protocol (Qiagen Inc., Valencia, CA). Novel primers were designed that amplified DNA from walleye pollock and Pacific cod in order to reduce the likelihood of contamination from other prey sources and from the salmon itself.

Walleye pollock, Pacific cod, and Atlantic cod (*G. morhua*) sequences were downloaded from GenBank and aligned in BioEdit (Ibis Biosciences, Carlsbad, CA). Primers were designed using Primer 3 (Rozen and Skaletsky 2000). The forward (5’ – TTGGGATGGACGTAGACACA – 3’) and reverse (5’ – AGCCCCAACTGTAAAGAGG – 3’) primers amplified a 174-bp-long fragment of the mtDNA COI gene to avoid problems with amplification of large fragments from degraded DNA.

The reaction mixture comprised 20 ng of DNA, 1 X reaction buffer, 2 mM MgCl₂, 0.2 mM dNTPs, 0.5 μM forward primer, 0.5 μM reverse primer, and 0.5 U DNA Taq polymerase. The polymerase chain reaction (PCR) conditions were as follows: preheating at 94°C for two min; 40 cycles of 94°C denaturation for 30 sec, 55°C annealing for 90 sec, and 72°C extension for 90 sec; and a final 72°C extension for three min. The PCR products were examined on 1% agarose gels and directly sequenced in both directions with PCR primers on a high-throughput capillary sequencer at the University of Washington High-Throughput Genomics Unit (Dept. of Genome Science, University of Washington).

Table 1. Offal samples chosen for genetic testing, including month of collection and the tissue type analyzed. All samples were collected in the eastern Bering Sea during January to March, 2007. Offal, in this study, refers to fish body parts (e.g. head, tail, spine, skin) that are discarded after processing.

Sample No.	Collection Month	Tissue Type
8-20	February	Fin
20-9A	February	Bone and Muscle
28-11	February	Skin
43-28D	March	Fin
48-13A	March	Skin
50-7A	March	Fin
51-8A	March	Skin
52-2C	January	Skin
52-3A	January	Bone and Muscle
52-4	January	Skin
52-5A	January	Skin
59-13B	February	Muscle
59-16	February	Muscle
60-19	February	Muscle
84-16	March	Muscle

Data Analysis

The sequence fluorograms were aligned using Sequencher™ (Gene Codes Inc. Ann Arbor, MI). Low-quality base calls at the end of sequences were removed, and sequences were checked for consistency between forward and reverse sequences. Samples with low and/or confounding peaks in the sequence chromatogram were rejected. In addition to the fish offal sequence data, known sequences of walleye pollock (accession numbers AF081699 and DQ174028) and Pacific cod (accession number AF081697) retrieved from the GenBank database were included in the analysis as reference points to compare with our sequences. An Atlantic cod sequence (accession number DQ173997) was also downloaded from GenBank and included in our analysis as a genetic outgroup.

Phylogenetic analyses were conducted in MEGA4 (Tamura et al. 2007) using the neighbor-joining method (Saitou and Nei 1987) with Kimura two-parameter distances (Kimura 1980) including all three codon positions. In order to evaluate the reliability of the tree, bootstrap values were generated with 1000 iterations and only those values above 50 were reported and indicated at the nodes.

RESULTS

All samples of positive control walleye pollock and Pacific cod DNA amplified with our primers and produced usable haplotypes. Additionally, nine of the 15 offal samples yielded usable haplotypes. Samples 28-11, 51-8A, 52-2C, 52-5A, 59-16, and 60-19 were amplified but rejected due to low and/or confounding peaks. Of those six rejected haplotypes, four were from skin samples (Table 1). However,

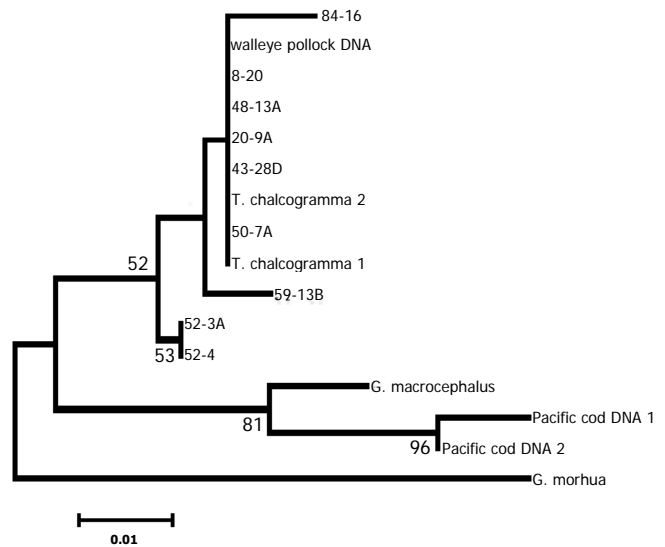


Fig. 1. Neighbor-joining tree showing the evolutionary relationship of nine offal sample haplotypes, three known DNA sample haplotypes and four known haplotypes (from GenBank). The tree is labeled as follows: walleye pollock = *T. chalcogramma* 1 (accession number AF081699) and *T. chalcogramma* 2 (accession number DQ174028); Pacific cod = *G. macrocephalus* (accession number AF081697); and Atlantic cod = *G. morhua* (accession number DQ173997). Offal sample haplotypes are labeled by sample numbers as in Table 2. Walleye pollock positive control DNA sample haplotype is labeled walleye pollock DNA (GenBank accession number GQ302982). Pacific cod positive control DNA sample haplotypes are labeled as Pacific cod DNA 1 (GenBank accession number GQ302983) and Pacific cod DNA 2 (GenBank accession number GQ302984). The tree was generated with Kimura two-parameter distances. Bootstrap values indicated at nodes were generated with 1000 replicates and only values above 50 are reported.

Table 2. Biological characteristics of Chinook salmon stomachs containing fish offal identified using genetic techniques. Sequences are available on the GenBank database and can be accessed using the GenBank accession number of each sample. Chinook salmon stomach samples collected by U.S. groundfish observers in the walleye pollock fishery operating in the eastern Bering Sea during January to March, 2007. Chinook salmon age determined from scales, where the number before (after) the period is the number of winters spent in fresh water (ocean). The X indicates that age could not be determined. Chinook salmon biological data and percentage of stomach content weight comprising fish offal from Davis et al. (2009b).

Fish Offal Sample No.	GenBank Accession No.	Chinook Salmon					Fish Offal	
		Sex	Maturity	Fork Length (cm)	Body Weight (kg)	Age	Species Identification	% of Stomach Content Weight
8-20	GQ302973	female	immature	44	0.94	1.2	pollock	100
20-9A	GQ302974	male	immature	52	1.67	1.2	pollock	100
43-28D	GQ302975	male	maturing	77	5.41	1.4	pollock	100
48-13A	GQ302976	female	maturing	82	5.92	1.4	pollock	100
50-7A	GQ302977	female	maturing	62	2.66	1.3	pollock	100
52-3A	GQ302978	female	immature	77	5.74	1.4	pollock	100
52-4	GQ302979	female	immature	47	1.6	X.X	pollock	54
59-13B	GQ302980	male	immature	59	2.34	1.2	pollock	95
84-16	GQ302981	female	immature	67	3.75	1.3	pollock	45

there was no obvious difference in DNA quantity among tissue types. No correlation was detected between the amount of DNA extracted and the duration of soak time in the bleach solution. The length of usable DNA sequences ranged from 108 bp to 152 bp but all sequences were trimmed to a length of 108 bp. Sequences were uploaded to the GenBank database (see Table 2 for offal sample accession numbers; see caption of Fig. 1 for positive control accession numbers). There was a total of 13 variable sites, four of which were diagnostic for differentiating walleye pollock from Pacific cod. Although our primers were designed to amplify DNA from both species, the neighbor-joining tree generated from the sequence data proved to be sufficient for differentiating the two (Fig. 1).

All offal haplotypes showed a closer relationship to the control sample of walleye pollock DNA and the walleye pollock sequences from GenBank than they did to the control samples of Pacific cod DNA and the Pacific cod sequence from GenBank, indicating the offal samples were in fact pieces of walleye pollock (Fig. 1). This relationship was supported by a bootstrap value of 52%. The Pacific cod positive controls were more closely related to each other (96% bootstrap value) and to the Pacific cod sequence (81% bootstrap value) than they were to any other sequence. All pollock samples were more closely related to Pacific cod than they were to the sequence of Atlantic cod from GenBank.

DISCUSSION

Nine of the fish offal samples collected from Chinook salmon stomach contents were identified as originating from walleye pollock (Table 2) due to their genetic similarities with known walleye pollock DNA and sequence data (Fig. 1). Those samples that did amplify but were rejected because of low and/or confounding peaks were likely contaminated by other contents of the stomach from which they were gathered. Four out of six of the rejected sample haplotypes were from skin tissue (Table 1), which was the thinnest tissue type. It is possible that the contamination from other stomach contents completely permeated the tissue. It is also possible that the exclusion of these samples may have introduced a degree of bias in our results, however, because the primary aim of this study was to demonstrate the presence of pollock offal, and not to quantify it, this possible bias is unlikely to have affected our results.

Our results clearly demonstrated the utility of a short COI sequence for species identification of Chinook salmon stomach contents. The specificity of our primer design was possible because morphological characters allowed the identification of offal as either cod or pollock. Further species identification was possible by sequencing the DNA and comparing results with known sequences. Much longer sequences are more typical for identifying species (Ward et al. 2009). The relatively short (108 bp) sequences are likely responsible for the low bootstrap values in the neighbor-joining tree

(i.e., 52% for the grouping of all pollock together), but they were sufficient to distinguish two species and, importantly, they could be obtained from degraded DNA (Hajibabaei et al. 2006).

This technique may prove invaluable for identifying fish prey from stomach contents that might be unidentifiable due to the state of digestion, or when isolated body parts are consumed rather than whole fish. Future DNA research will focus on the development of techniques for identification of invertebrate salmon prey, such as cephalopods and cnidarians, which can be difficult to identify in the absence of fresh or intact specimens.

Our results suggest fish offal derived from pollock might supplement the diet of Chinook salmon during winter. The scavenging of commercially discarded fish parts has been well documented in seabirds (Bertellotti 2000; Garthe and Scherp 2003). However, consumption of offal by Chinook salmon has yet to be investigated for the possible changes in feeding strategy and behavior it may elicit in the affected populations. Currently, only direct mortality of Chinook salmon in the pollock fishery has been well documented (Berger 2008). Future research will be needed in order to determine the positive or negative consequences for Chinook salmon survival through the winter and the magnitude of the direct and indirect effects of offal consumption on the total population.

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The Role of Pacific Salmon in the Trophic Structure of the Upper Epipelagic Layer of the Western Bering Sea during Summer-Autumn 2002–2006

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Abstract: Pacific salmon are among the dominant fish in the epipelagic layer of the subarctic Pacific Ocean and are considered the principle consumers of forage resources. In recent years (1990s and 2000s) most Pacific salmon stocks have increased two-fold in abundance. Many researchers consider that such high abundance may increase interspecific competition for food and influence density-dependent factors during periods of limited food availability and may change salmon characteristics such as length, weight, fecundity, and the average age of populations. Long-term data series on Pacific salmon and their food resources have traditionally been collected during Russian surveys in the pelagic zone of the Far Eastern Seas and adjacent waters of the northwestern North Pacific Ocean. More recently (summer–autumn, 2002–2006) surveys have been conducted by TINRO-Centre in the epipelagic zone of the western Bering Sea as part of the international BASIS program. The integration of the results of these programs make it possible to better understand the status of Pacific salmon and their role in North Pacific pelagic communities.

Keywords: Pacific salmon, competition, forage resources, trophic structure, carrying capacity

INTRODUCTION

Over the last 25 years researchers have documented a significant increase in the abundance of many Pacific salmon populations, including Asian stocks. Based on data collected during anadromous migrations (catch size and value, densities of fish on spawning grounds, e.g.), it is estimated that the abundance of Pacific salmon may be twice as high compared to levels of stocks in the 1950s–1970s (Temnykh et al. 2003, 2004; Shuntov and Temnykh 2004, 2008; Temnykh 2005).

The possible effect(s) of these high population levels on intra- and inter-specific competition among salmon for food resources have been discussed in many scientific publications. There is some consensus among researchers that the North Pacific is now overpopulated by salmon, and that tissue degeneration of salmon (for example, the occurrence of ‘flabby chum’) is possibly caused by limited forage resources on marine feeding grounds (Klovach 2000, 2003; Gritsenko and Klovach 2002; Mikodina et al. 2002). Some studies suggest that density-dependent factors result in changes in some parameters of salmon stocks such as length, weight, age, and fecundity (Ishida et al. 1993, 2000; Bigler et al. 1996; Kaeriyama 1996; Davis et al. 1998; Azumaya and Ishida 2000).

However, the extensive and detailed results on the structure and dynamics of nekton and plankton communi-

ties, including their trophic structuring, obtained during many complex large-scale surveys to the Far Eastern Seas and Northwest Pacific, summarized and published in Russian journals and monographs (Shuntov et al. 1993a,b, 2007; Volkov 1996; Shuntov 2001; Dulepova 2002; Temnykh 2004, 2008; Kuznetsova 2005; Chuchukalo 2006; Shuntov and Temnykh 2008) allow us to create a clearer picture of the status of Pacific salmon and their role in North Pacific pelagic communities.

Long-term data series on Pacific salmon and their food resources have traditionally been collected during Russian surveys in the pelagic zone of the Far Eastern Seas and adjacent waters of the northwestern North Pacific Ocean. More recently (summer–autumn, 2002–2006) surveys have been conducted in the epipelagic zone of the western Bering Sea by TINRO-Centre as part of the international BASIS program. The integration of the results of these programs make it possible to better understand the status of Pacific salmon and their role in North Pacific pelagic communities.

MATERIALS AND METHODS

Data on food habits of Pacific salmon and the distribution and composition of plankton were collected by the research vessel *TINRO* of the Pacific Fisheries Research

Center (TINRO) in the western Bering Sea in summer 2003 and autumn 2002–2006, including surveys that were part of the international research program BASIS (Bering-Aleutian Salmon International Survey).

To sample salmon and other epipelagic nekton a standard midwater rope trawl RT/TM was used. Technical characteristics of the trawl are provided in Table 1. The trawl hydrodynamic plate had floats on the headrope. The trawl had quadrangular mesh in the body and wings and a small-mesh (1 cm) codend. The trawl was fished with 4 bridles, each 112 m long and 1.9 cm thick. One 220-kg chain is attached to the footrope and 2 weights (200 kg each) are attached in front of the footrope to sink the trawl. V-shaped conical midwater trawl doors (6 m² and 1.3 tons each) were used.

Trawls were conducted round-the-clock and lasted one hour. The trawling course was adjusted according to weather and hydrological conditions. The trawl hydrodynamic plate was maintained at 0 m level. The position of the plate was verified by acoustic readings and by sight.

Standard methods, developed by Volkov and Chuchukalo (1986) and widely applied at TINRO-Centre, were used for sampling and processing fish stomach contents. The contents of all stomachs from fish of the same species and

of similar size in each trawl catch were combined into one sample. Prey items were identified and measurements of total prey weight and weights of all prey components were recorded. Daily food rations were calculated by the methods of Novikova (1949), Yurovitsky (1962), Kogan (1963), and Gorbatenko (1996). The total consumption by nektonic consumers was determined as:

$$B = b * R * n$$

where B is the weight of the food consumed by nektonic consumers (tons); b is mean nekton biomass (tons) during a certain period; R is daily ration; n is duration of the period (days (summer = 92, and autumn = 91 days)). Size, age, and seasonal, year-to-year, and regional differences were taken into account in the calculations. The consumption of forage resources by nekton was calculated for the western Bering Sea in summer 2003 and autumn 2002–2006. These calculations were compared with the same calculations for the western Bering Sea in autumn 1986, 1987, and 1990, the southern Okhotsk Sea in summer 1991 and 2003 and autumn 2006, and the Pacific waters of the Kuril Islands in summer 1995, 2004, 2006 and 2007.

Table 1. Specifications of the trawl RT/TM 80/396.

Parameters	Average and its intervals (min-max)
Headrope	80 m
Perimeter of the trawl opening	396 m
Hydrodynamic plate	6 m ² , 0.6x10 m
Length of the trawl	30 m
Vertical opening*	32.2 m (26-40 m)
Horizontal opening*	49.0 (42-61 m)
Speed of trawling	4.8 knots (4.0-5.7 knots)
Length of warps	256 m (245-280 m)
Square of water surface per 1 hour	0.44 km ² (0.34-0.53 km ²)

*vertical and horizontal openings were measured by Simrad FS20/25 vertical and horizontal scanning trawl sonars.

Table 2. Juday net catchability coefficients for certain groups of plankton (from Volkov 1996).

Plankton size group	Catchability coefficient (CC)
Small (< 1.2 mm)	1.5
Medium (1.2–3.2 mm)	2.0
Large (> 3.2 mm):	
euphausiids < 10 mm	2.0
euphausiids 10–20 mm	5.0
euphausiids > 20 mm	10.0
chaetognaths < 10 mm	2.0
chaetognaths 10–20 mm	5.0
chaetognaths > 20 mm	10.0
hyperiid < 5 mm	1.5
hyperiid 5–10 mm	5.0
copepods < 5 mm	2.0
copepods > 5 mm	3.0

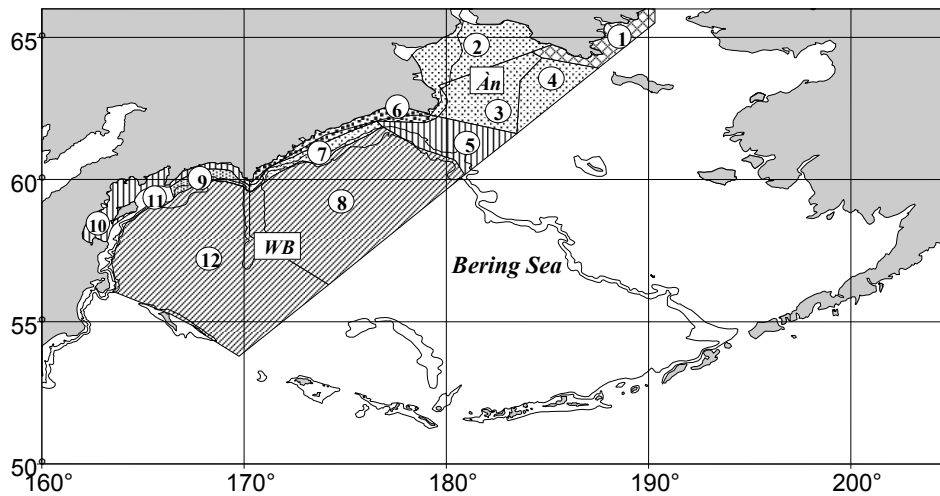


Fig. 1. Map of biostatistical regions covered in 5 surveys by TINRO-Centre on the R/V *TINRO* as part of the international research program BASIS (Bering-Aleutian Salmon International Survey) in the epipelagic layer of the western Bering Sea in 2002–2006. 1, Bering Strait; 2, north-western Anadyr Bay; 3, southeastern Anadyr Bay; 4, eastern Anadyr Bay; 5, Navarin region; 6, Koryak shelf; 7, Koryak slope; 8, western Aleutian Basin; 9, Olutorskiy slope; 10, shelf of Karaginskiy and Olutorskiy bays; 11, Karaginskiy slope; 12, Commander Basin; An, Anadyr Bay; WB, western Bering Sea basins (from Shuntov et al. 1986, 1988a, b).

Plankton samples were collected with a Juday net (nylon, mouth area 0.1 m², mesh size 0.168 mm) from 0–50 and 0–200 m both during the day and at night just before trawling. The samples were divided into three size fractions: small (animals < 1.2 mm in length), medium (1.2–3.2 mm), and large (> 3.2 mm). Species composition was determined for each fraction, and weight (as displaced volume), size, and developmental stage determined for each species. The results on abundance and biomass were multiplied by catchability coefficients (CC) of the Juday net (Table 2).

All data were averaged by standard biostatistical regions proposed for the Russian EEZ by Shuntov et al. (1986,

1988a, b) (Fig. 1).

RESULTS AND DISCUSSION

Composition of the Epipelagic Nekton Community

The epipelagic nekton community of the western Bering Sea in summer–autumn consists of walleye pollock, Pacific salmon, squids and also the mezopelagic fishes, capelin, atka mackerel and Pacific herring (Fig. 2). This nekton community (biomass, physiological condition, distribution, and migration patterns, e.g.) determines the principle trophic rela-

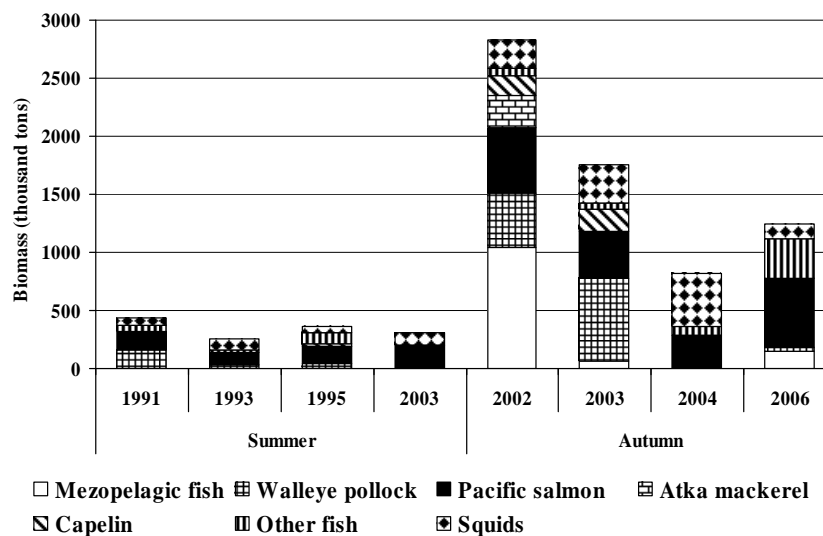


Fig. 2. The biomass (thousand tons) of nekton in the upper epipelagic layer in the western Bering Sea during summer and autumn (from Shuntov et al. 1993b, 2007; Radchenko 1997; Temnykh et al. 2003, 2004; Shuntov and Temnykh 2004, 2005; Shuntov and Sviridov 2005; Temnykh 2005, 2006; Glebov et al. 2006; Starovoytov 2007; with modifications).

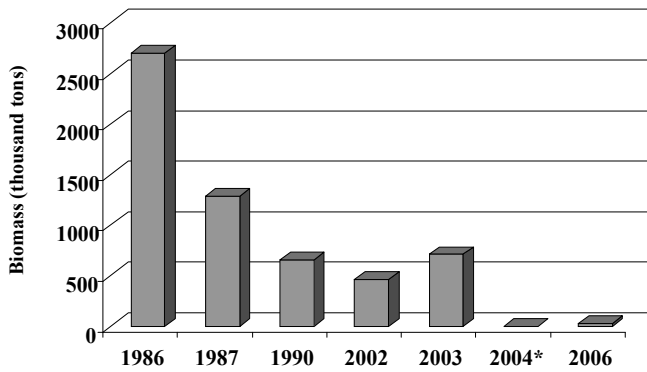


Fig. 3. Walleye pollock biomass in the upper epipelagic layer in the western Bering Sea during autumn 1986–1987, 1990 and 2002–2006. *Only a part of the shelf was surveyed. (Shuntov et al. 1993a; Shuntov and Sviridov 2005; Glebov et al 2006).

tionships within the epipelagic community. Walleye pollock and Pacific salmon are always present in the pelagic community in summer–autumn, and are the most important influence. Pollock distribution in the western Bering Sea is very variable and depends on the stock and environmental conditions (Shuntov et al. 1993b; Stepanenko 1997, 2001; Shuntov and Sviridov 2005; Glebov et al 2006). For example, the relative biomass of adult pollock at the sea floor can be high, while the biomass of juvenile pollock in the epipelagic zone can be low. The migrations of juvenile pollock from the eastern to the northwestern Bering Sea in 2004 and 2006 were reduced considerably, so the relative biomass of pollock in the western Bering Sea in these years was low (Fig. 3) (Nikolaev and Stepanenko 2006). By contrast, salmon biomass has increased 3-fold since the 1980s such that their share of the total fish biomass in the upper pelagic layer of

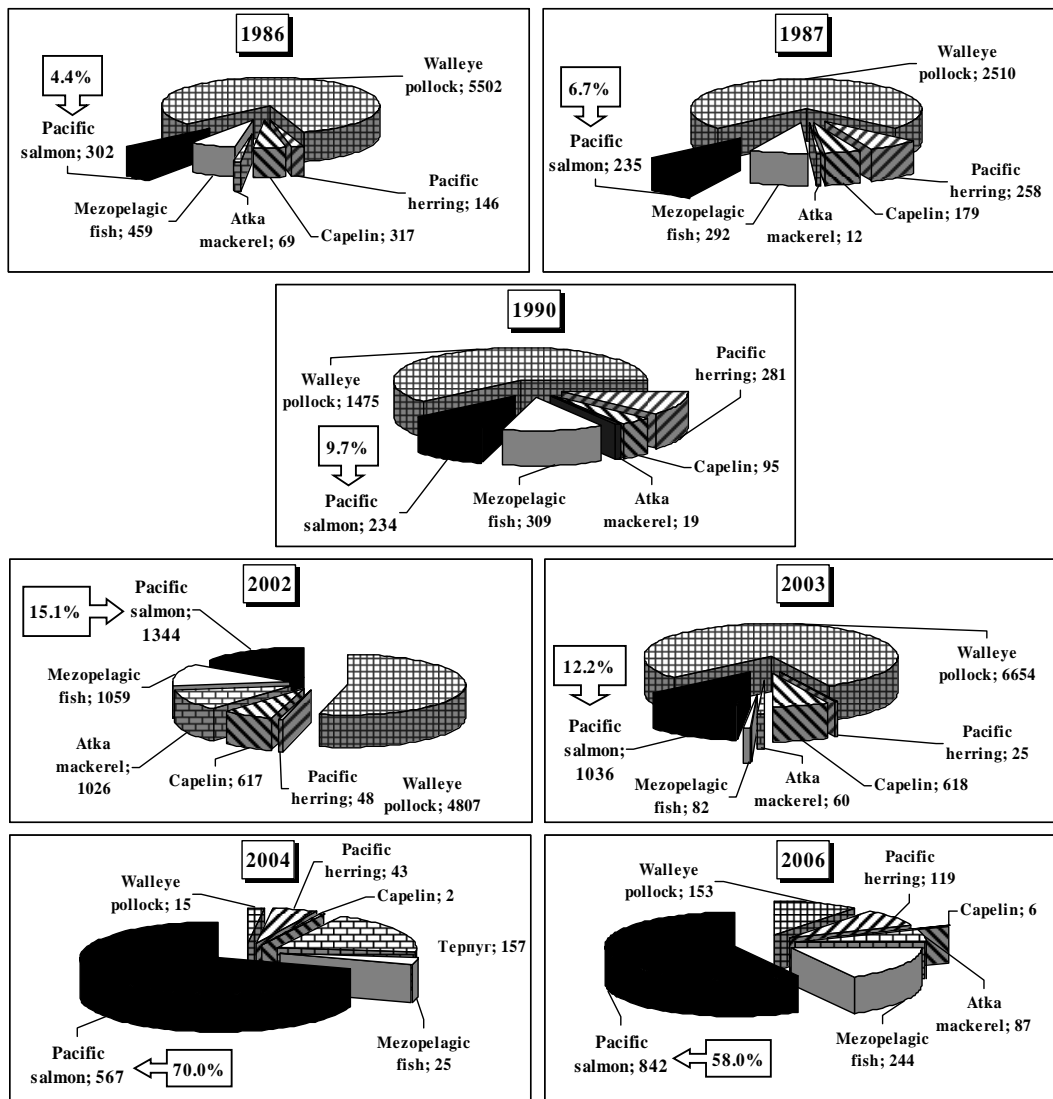


Fig. 4. The consumption (thousand tons) of total forage resources by fish in the upper epipelagic layer in the western Bering Sea during autumn 1986–1987, 1990, and 2002–2006 (Naydenko 2007).

the western Bering Sea increased to 21–53% in 2002–2006 (Shuntov et al. 1993a, 2007; Temnykh et al. 2003; Shuntov and Temnykh 2004, 2005; Glebov et al. 2006; Starovoytov 2007).

Trophic Structure of the Nekton Community

Changes in the abundance and structure of the main consumers have affected the trophic structure of the nekton community. The volumes of consumption, energy flows, and trophic roles of many major species, including salmon, have changed.

In the epipelagic zone of the western Bering Sea the total consumption of resources by fish alone reached from 3.5 to 8.9 million tons in years when pollock biomass was high (for example, in 1986–1987, 1990, and 2002–2003). In 2004 and 2006 consumption decreased to 1 million tons (Fig. 4). Accordingly, the share of pollock in total consumption declined from 80 to 10%, and the share of food consumption by salmon increased from 4.4 to 58–70% (Fig. 4). Pacific salmon consumed 52% of total food consumption by nekton (fishes and squids) in summer 2003, and 39–41% in autumn 2004 and 2006 (Fig. 5). However, the role of salmon in the trophic structure of the upper pelagic layer is still not as important as that of pollock.

For example, in autumn 2002 and 2003, pollock consumed almost 1/3 of the total stock of euphausiids (3.5 and 3.1 million tons, respectively) but their grazing was estimated as 1/30 of the total stock in the autumn of 2004 and 2006, when pollock abundance was low (Naydenko 2007). In the same years (2004 and 2006) grazing on copepods had decreased by 10–20-fold (Table 3), but the decrease in hyperiid grazing was not so dramatic because of active consumption of this group by salmon, atka mackerel and other nekton species (Naydenko 2007).

Despite an increase in abundance, Pacific salmon consumed a much smaller part of forage resources compared to walleye pollock. For example, in autumn 2004 and 2006 salmon consumed 167–179 thousand tons of euphausiids, 87–230 10³ tons of hyperiids, 4–27 thousand tons of copepods, and 6–130 thousand tons of pteropods (Naydenko 2007). Consumption of zooplankton by salmon was higher in summer (for example, up to 1754 thousand tons in summer 2003) (Fig. 6).

Thus in autumn of 2002 and 2003 the predominant path-

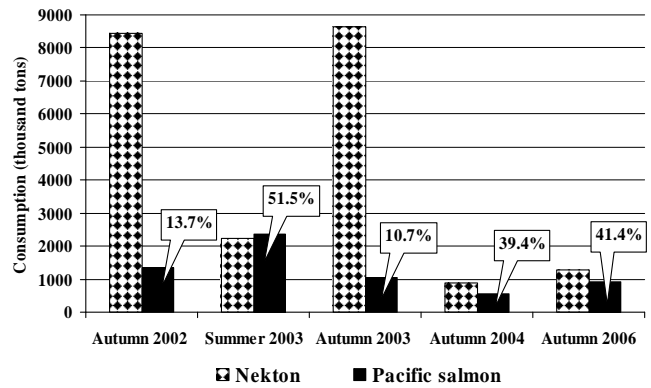


Fig. 5. The consumption (thousand tons) of total forage resources by Pacific salmon and other nektonic consumers in the upper epipelagic layer in the western Bering Sea during summer 2003 and autumn 2002–2006 (Naydenko 2007).

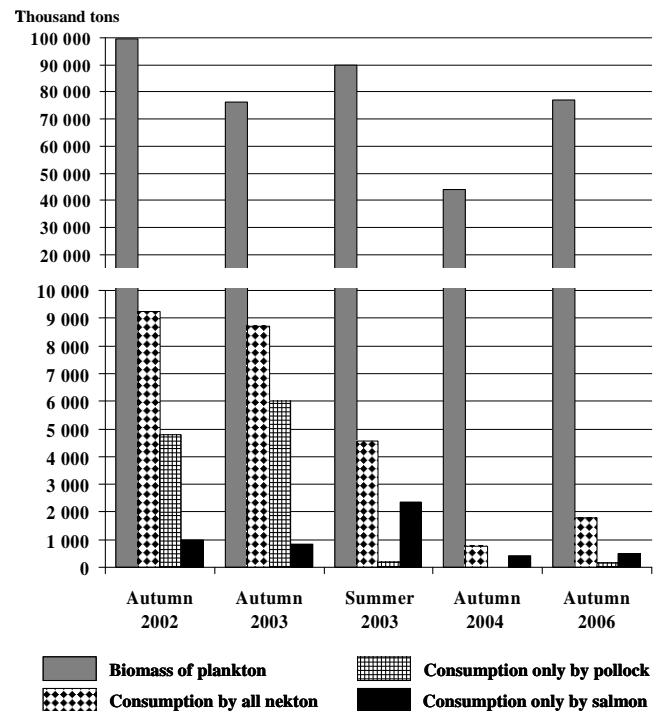


Fig. 6. The biomass of zooplankton and its consumption (thousand tons) by nektonic consumers in the epipelagic layer of the western Bering Sea.

Table 3. The main zooplankton groups (103 tons) in the upper pelagic layer of the western Bering Sea in autumn 2002–2006 and their grazing by nektonic consumers (numerator = consumption by all nektonic consumers, denominator = consumption only by fish) (Naydenko 2007).

Years	Euphausiids		Copepods		Hyperiids	
	Biomass	Consumption	Biomass	Consumption	Biomass	Consumption
2002	9,067	4,082/3,514	43,722	2,337/2,333	2,424	1,047/1,042
2003	10,059	4,141/3,095	80,438	2,075/2,071	1,833	577/569
2004*	14,429	709/222	10,145	120/118	1,796	294/293
2006	8,568	1,089/716	27,035	226/224	1,794	219/209

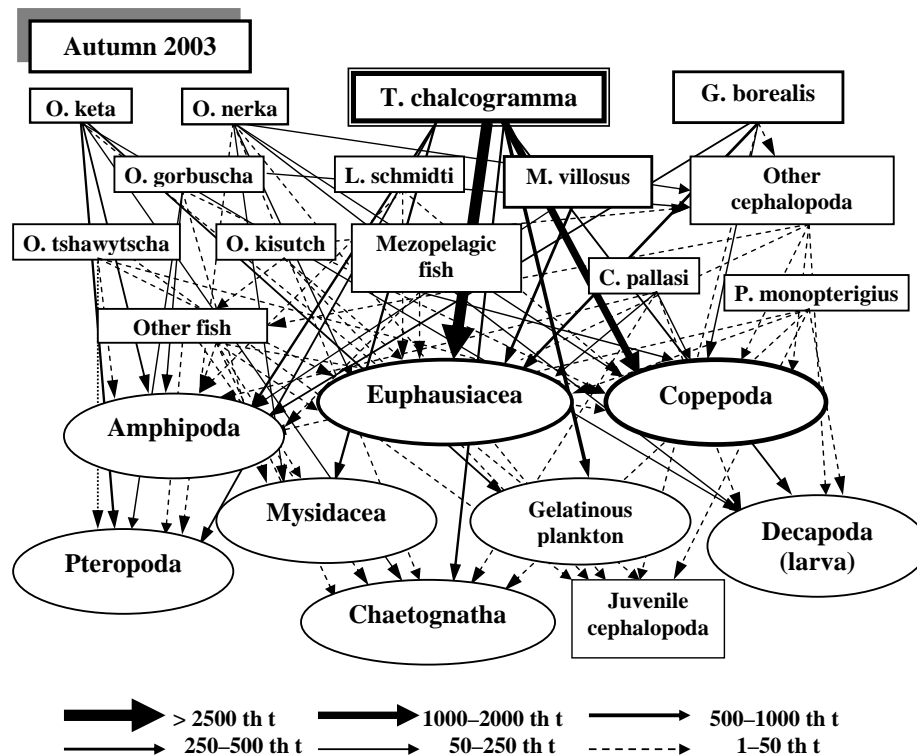


Fig. 7. Schematic of the basic trophic relationships of dominant nektonic species and major zooplankton groups in the upper epipelagic zone of the western Bering Sea in autumn 2003 (thickness of arrows indicates volumes of autumn consumption, thousand tons (th t)).

way of energy flow in pelagic communities of the western Bering Sea led from two zooplankton groups, euphausiids and copepods, toward walleye pollock (Fig. 7). In autumn 2004 and 2006 Pacific salmon and squids (and in some cases atka mackerel, capelin or mezopelagic fishes) were the major consumers, such that the trophic links were directed not only toward euphausiids and copepods but also other zooplankton groups such as hyperiids, pteropods, and larval decapods (Fig. 8). On the whole, the energy flows from zooplankton toward higher trophic levels of the epipelagic community have decreased considerably. Most likely these energy flows switched to plankton predators (jellyfishes, chaetognaths, or other copepods). Unfortunately, the trophic relationships within the pelagic zooplankton community in the western Bering Sea are not well understood. It should be noted that with the substantial increase in the abundance of predatory plankton, serious shifts in trophic relationships and the direction of energy flow in the epipelagic zone of the western Bering Sea in the last 20 years were not observed.

The observed increase in plankton resources, a result of lower consumption rates and high plankton biomass, should contribute to a satisfactory foraging environment for pelagic nekton species, including Pacific salmon.

Based on estimates by Shuntov (2001), Dulepova (2002), Shuntov and Temnykh (2007) and Volkov et al. (2004, 2007a), the total stock of zooplankton in the epipelagic layer of the subarctic northwestern Pacific, including

the Okhotsk and Bering seas, has decreased by 134.5 million tons over two decades (from 722.5 million tons in 1980 to 587.8 million tons in 2000), i.e. approximately 20%. The decrease has been noted everywhere, from inner shelf areas to the deep ocean. However, the large-size fraction of zooplankton, the most important prey for nektonic planktivores, showed other changes: a slight decrease from 1980 to the early 1990s (from 560.8 to 500.5 million tons, or 8%) and a slight increase in succeeding years (up to 520.1 million tons). Generally, despite a decrease in the total abundance of macroplankton, the biomass levels are rather high. In the western Bering Sea macroplankton biomass is estimated at 81.4 million tons, of which about 60% is concentrated in deepwater areas (Shuntov 2001; Dulepova 2002; Shuntov and Temnykh 2007). This conclusion is very important in the estimation of forage resources, because the main feeding grounds for Pacific salmon are located in deepwater areas where the biomass of nekton is usually lower.

Not all zooplankton species are equally consumed by nekton. Only a few species are actively consumed. However, in the epipelagic zone of the western Bering Sea the abundance of these preferred species is sufficient. For example, the total biomass of five species (*Thysanoessa longipes*, *Neocalanus plumchrus*, *Themisto pacifica*, *Clione limacina*, and *Limacina helicina*) which are the most important food items of nekton was estimated at 15–19 million tons, which exceeds the consumption of these species by several times.

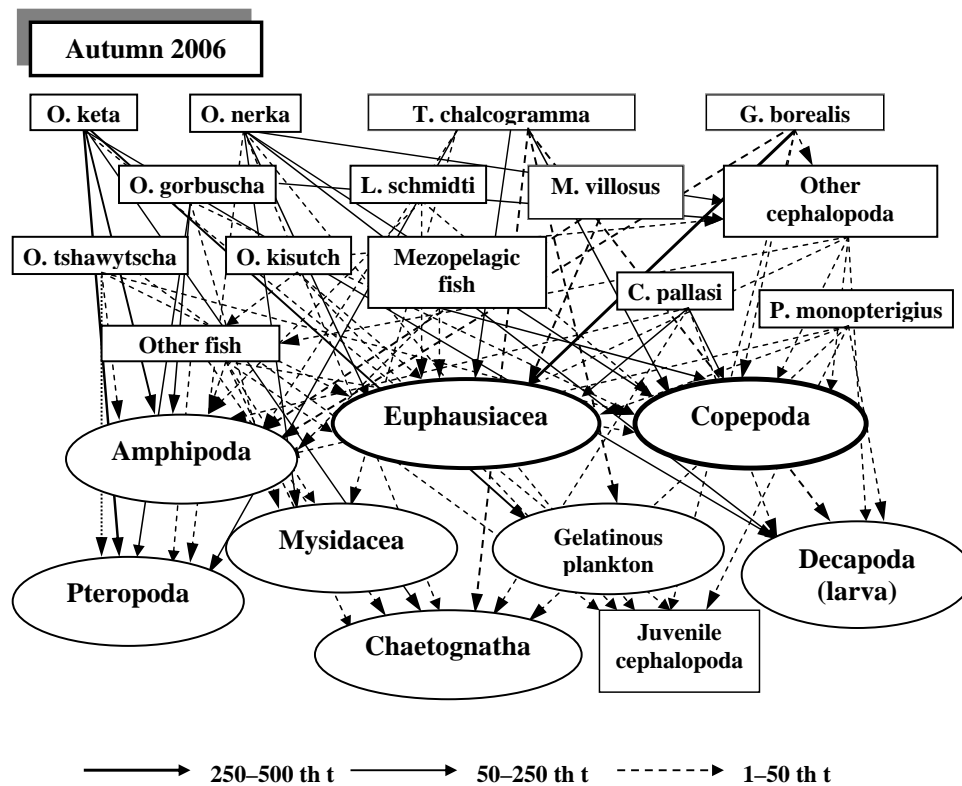


Fig. 8. Schematic of the basic main trophic relationships of dominant nektonic species and major zooplankton groups in the upper epipelagic zone of the western Bering Sea in autumn 2006. (thickness of arrows indicates volumes of autumn consumption, thousand tons (th t)).

If we take zooplankton production into account, the difference between zooplankton biomass and zooplankton consumption by nekton will be even higher. A satisfactory food supply for salmon in the western Bering Sea is also shown by stable and high values of their daily rations, and a permanent preference for feeding on hyperiids, pteropods, and euphausiids.

Besides zooplankton, small fishes and squids also make up a considerable part of the salmon diet. Their mean concentration is estimated to be 0.1–3.9 g/m² depending on the region surveyed (Shuntov and Temnykh 2007), compared with the mean concentrations of preferred macroplankton such as pteropods (1–2 g/m²), hyperiids (2–8 g/m²), and euphausiids (15–25 g/m²). Small pelagic nekton are able to compensate for the lack of zooplankton forage resources, for example, in the eastern Bering Sea where larval fish and bottom-dwelling invertebrates form the base of salmon diet when large-size zooplankton are not abundant (Volkov et al. 2007a, b).

Other important factors that contribute to satisfactory foraging environments for Pacific salmon are the spatial dissociation of the main consumers and the timing of migrations and feeding. Pacific salmon, juvenile atka mackerel, and squids feed mainly in deepwater areas of the western Bering Sea. The forage resources in deepwater areas are affected by these fishes and squids during summer–autumn (especially in summer during salmon migrations and graz-

ing on zooplankton by juvenile atka mackerel). By contrast, the main feeding grounds of pollock, capelin and herring are located in shallow waters of Anadyr Bay and at Cape Navarin. The consumption of zooplankton by these fishes is very high in autumn, especially when pollock are abundant. The example of walleye pollock, atka mackerel, and sockeye and chum salmon distribution in the western Bering Sea in autumn 2003 is shown in Fig. 9. In 2004 and 2006 the consumption of forage resources was highest in deepwater areas (Fig. 10).

Some competition for food among salmon and other abundant nekton species is possible where feeding grounds and/or migration dates overlap, however such situations are mitigated by plasticity and electivity in salmon feeding, as well as by excess forage reserves. All salmon species have a high feeding plasticity and are able to change from one food source to another, depending on the state of forage resources. This ability is well illustrated by the different feeding habits of Pacific salmon in the western and eastern regions of the Bering Sea.

CONCLUSIONS

Any fluctuations in the biomass of major consumers lead to changes in the trophic structure of pelagic communities. However, even multiple variations in highly fluctuating species’ biomass, such as that of walleye pollock, result

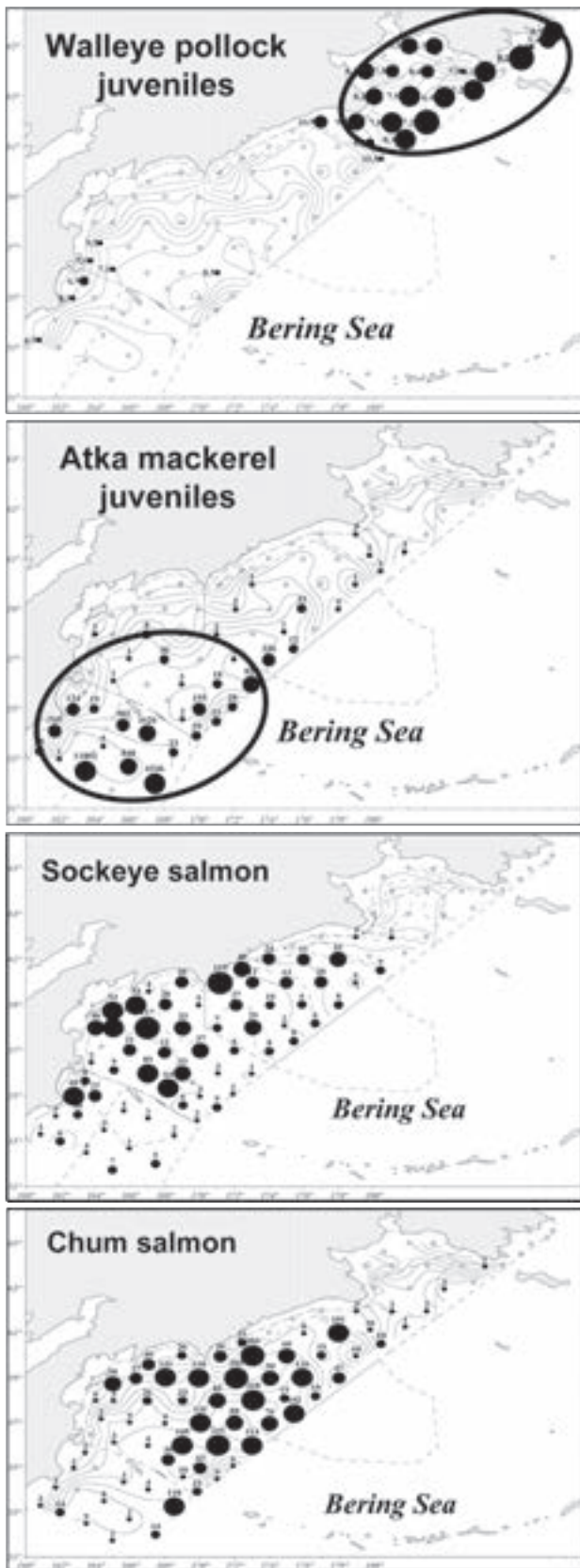


Fig. 9. Distribution of the walleye pollock, atka mackerel, and sockeye, and chum salmon in the western Bering Sea in autumn 2003.

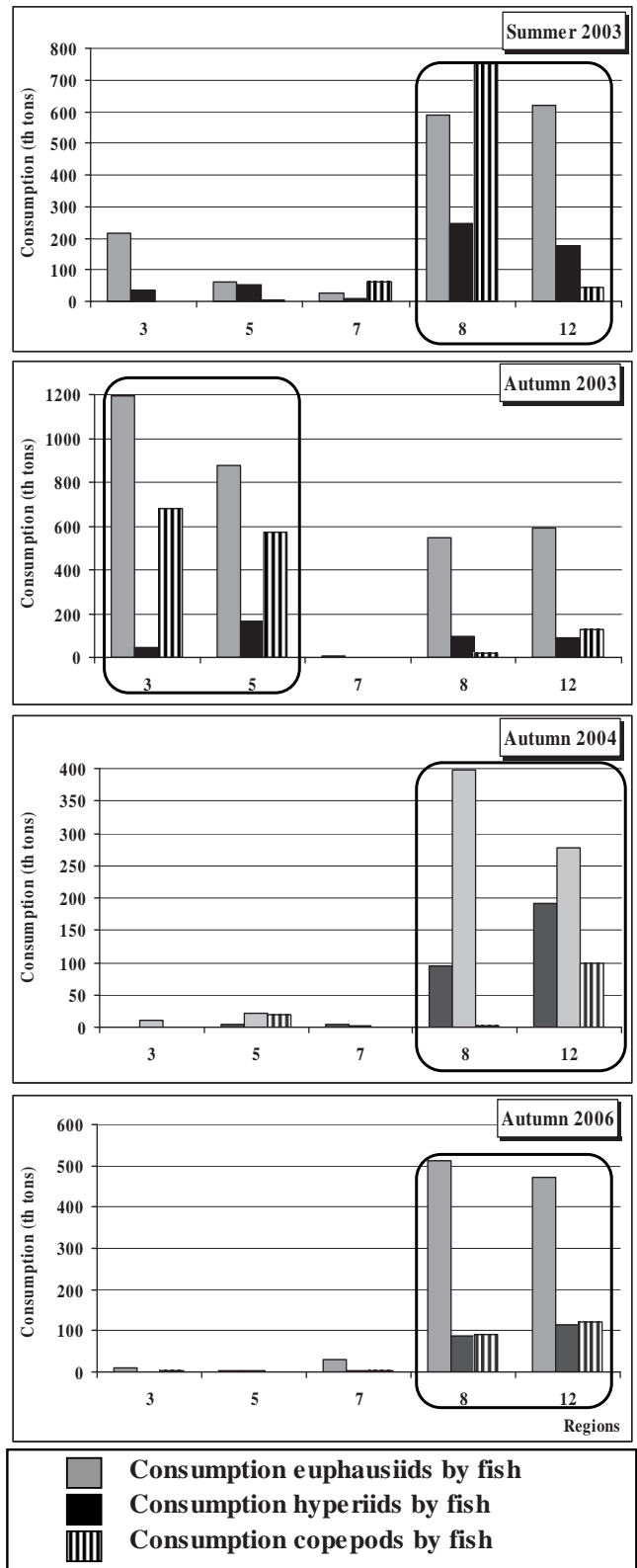


Fig. 10. The consumption (thousand tons) of zooplankton forage groups by nektonic consumers in the upper epipelagic layer in the different regions of western Bering Sea during summer 2003 and autumn 2003, 2004, and 2006 (Naydenko 2007). See Fig. 1 for designation of regions.

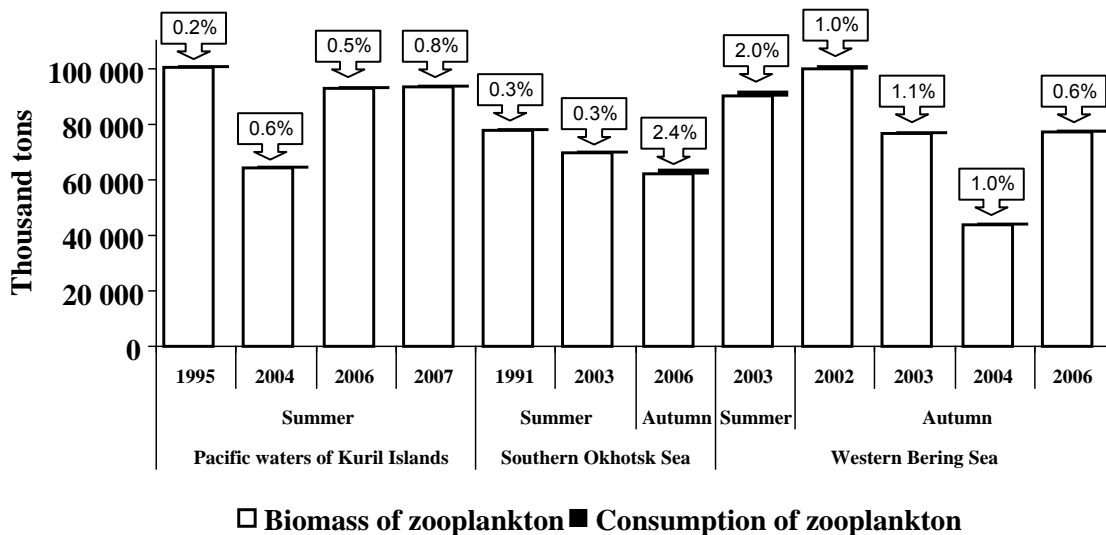


Fig. 11. The biomass of zooplankton (thousand tons — white columns) and its consumption (arrows indicate %) by Pacific salmon in the epipelagic layer of the Okhotsk and Bering seas and Pacific waters of the Kuril Islands (from Naydenko 2007, 2008, with modifications).

only in changes in trophic relationships and the direction of energy flow (namely a change to grazing on euphausiids and copepods by pollock). The contribution of Pacific salmon to the consumption of forage resources in all the areas we investigated is not significant and changes from only 0.2 to 2.4% of total zooplankton biomass (without production), depending on region and year (Fig. 11). It follows that the recent increase in Pacific salmon abundance is unlikely to cause serious shifts in the trophic structure of the upper pelagic zone of the Far Eastern Seas.

The carrying capacity of the pelagic layer for Pacific salmon (in relation to the sufficiency of the forage supply) is not a constant value and depends on multiple factors such as the amount of forage resources, the abundance of major consumers, and the spatial dissociation and migration timing of salmon and other major consumers. According to our data (a high total stock of zooplankton compared with its low consumption by nekton and the spatial dissociation of major consumers), the carrying capacity of the upper epipelagic layer of the Far Eastern Seas and the Pacific waters of eastern Kamchatka and the Kuril Islands in relation to Pacific salmon is high.

Our conclusion that salmon production in the North Pacific is not limited by zooplankton abundance on foraging grounds contradicts the conclusions of Klovach (2003) that large-scale hatchery production and release of chum salmon by the Japanese fishery was impacting salmon returns to the Russian Far East and North America, primarily because of the high abundance of salmon in marine foraging habitats. Klovach (2003) reached these conclusions using indirect production characteristics (changes in length, weight and the physiological state of salmon under conditions of high abundance) and without taking into account quantitative estimates of zooplankton biomass and consumption values of forage resources by salmon and other nekton species.

It is also necessary to note that our conclusions are based on data obtained in the Far Eastern Seas in summer and autumn only. Such calculations cannot be performed for open waters of the North Pacific in winter and spring because of a lack of data. There are vague and contradictory opinions on the feeding conditions for salmon in winter–spring. According to some researchers, zooplankton biomass in the North Pacific in winter is considerably lower compared to summer (Nagasawa 1999, 2000; Ishida et al. 2000) and results in unsatisfactory feeding conditions. Others doubt these estimates and suggest that zooplankton abundance is underestimated because of methodical problems (Shuntov 2001). Quantitative studies of both zooplankton and salmon feeding habits in winter–spring are necessary, including information on daily rhythms of feeding activity, and studies of feeding of other nekton species on common winter feeding grounds. Other important problems in estimating forage reserves are definition of energy values and the biochemical composition of the food necessary to assess trophic relationships in communities and ecosystems. Because many problems are still unsolved it remains tenuous at best to attempt to make realistic estimates of the carrying capacity of pelagic waters over a broad spatial and temporal range.

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Winter Food Habits of Chinook Salmon in the Eastern Bering Sea

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Abstract: This is the first study of winter diets of Chinook salmon in the eastern Bering Sea. We analyzed Chinook salmon stomach samples collected by U.S. observers on board commercial groundfish trawlers from January to March and July to August, 2007. The proportion of empty stomachs was higher in winter (45%) than summer (8%), suggesting longer time periods between meals in winter. Diversity of squid species in Chinook salmon diets was higher in winter than summer, when more fish, particularly juvenile walleye pollock, were consumed. All age groups of Chinook salmon collected in winter consumed fish offal, likely generated by fishery catch-processing activities, however, fish offal was not observed in summer samples. In winter, the ratio of euphausiids and fish offal weight to Chinook salmon body weight was significantly higher in samples collected at shallow depths (< 200 m), and the ratio of squid was significantly higher in salmon collected at deeper depths (201–600 m). The ratio of euphausiids to fish body weight was significantly higher in immature than maturing Chinook salmon.

Keywords: Chinook salmon, food habits, eastern Bering Sea, winter

INTRODUCTION

In response to the significant environmental and biotic changes seen in the Bering Sea ecosystem in the late 1990s, the Bering-Aleutian Salmon International Survey (BASIS) was established as an international cooperative program of the North Pacific Anadromous Fish Commission (NPAFC 2001). Monitoring salmon food habits during BASIS cruises was planned in order to model the pelagic food web dynamics of the Bering Sea ecosystem. In 2002–2006 BASIS greatly increased the spatial and seasonal coverage of information on salmon food habits in the Bering Sea, particularly for the late-summer and fall period (Davis et al. 2009).

Since 2000 declining Chinook salmon (*Oncorhynchus tshawytscha*) returns to western Alaska resulted in either a reduced or closed commercial harvest in western Alaska (Bue and Hayes 2006). Because Chinook salmon stocks from this area have not maintained expected yields above escapement levels, which would provide for subsistence and commercial harvests (Hayes et al. 2008), information is needed to understand the effects of fishing and ocean conditions on growth, maturation, and survival of Arctic-Yukon-Kuskokwim (AYK) Chinook salmon.

Chinook salmon food habits studies have been conducted in the western (Karpenko 1979, 1982; Karpenko and Maksimenkov 1988; Shuntov et al. 1993; Volkov et al. 1995; Glebov 1998; Karpenko et al. 1998; Koval and Karpenko 1998; Temnykh et al. 2003; Klovach and Gruzevich 2004; Smorodin et al. 2004; Volkov et al. 2007), eastern (Carlson et al. 1998; Murphy et al. 2003; Davis et al. 2004; Volkov et

al. 2007), and central (Ito 1964; Murphy et al. 2003; Davis et al. 2004; Volkov et al. 2007) Bering Sea. Originally, winter surveys were included in the BASIS plan, however, no winter BASIS cruises occurred during 2002–2006.

Unlike sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon, Chinook salmon appear to remain in the Bering Sea throughout the winter, as evidenced by catches in winter walleye pollock (*Theragra chalcogramma*) fisheries and the recovery of an archival tag from a Yukon River Chinook salmon at liberty for two years (Radchenko and Glebov 1998a; Myers et al. 2003; Berger 2008; Walker and Myers 2009). The mean estimated bycatch of Chinook salmon in Bering Sea and Aleutian Islands U.S. groundfish fisheries in 2001–2006 was 60,150 fish. This figure dramatically increased in 2007 to an estimated 129,530 fish (Berger 2008). Chinook salmon are caught in both the winter “A” (January 20–June 10) and the summer–fall “B” (June 10–November 1) pollock fishery seasons (NOAA 2008). The months during which these Chinook salmon are caught suggest observers on pollock fishing vessels are well positioned to sample them during time periods not sampled during BASIS cruises. Therefore, Chinook salmon samples collected from the observer program could enhance the seasonal coverage from which food habits data were obtained.

Our goal was to examine winter Chinook salmon food habits samples collected by U.S. groundfish observers sampling in the eastern Bering Sea, and determine the major prey types consumed during this season. We wanted to determine if differences in prey composition occurred with respect to depth of fishing, time period of the day when fishing oc-

curred, and Chinook salmon ocean age, and maturity stage.

MATERIALS AND METHODS

Frozen Chinook salmon stomach samples, fish scales, and biological data were collected by U.S. groundfish observers aboard commercial catcher-processors in the walleye pollock midwater trawl fishery during winter (January–March) and summer (July–August), 2007. Trawl gear fishing depth (average gear depth measured by various instrumentation), trawl gear deployment and retrieval time (tow time period), and Chinook salmon biological characteristics (fork length, body weight, sex, and maturity) were recorded by observers from bridge data and from Chinook salmon when stomach samples were collected. Trawl fishing depth was grouped into three categories (< 200 m, 201–400 m, 401–600 m) and tow time period was divided into four six-hour periods of the day (0001–0600 hr, 0601–1200 hr, 1201–1800 hr, and 1801–2400 hr). When a tow was not completed within one time period, a stomach sample was attributed to the time period when at least 50% of the tow was conducted. Observers classified Chinook salmon maturity as either immature or maturing based on appearance of the gonads (immature ovaries are approximately uniform in thickness and contain tiny eggs; immature testes are thin pinkish translucent tubes; AFSC 2007). Chinook salmon ocean age (count of annuli in the ocean zone of the scale) was determined from scales (Davis et al. 1990).

Chinook salmon stomach contents were counted, weighed, and identified to the lowest possible taxonomic group. When possible, estimates of prey size were obtained by measuring squid (mantle length), fish (standard length), and pollock otoliths (maximum length). Pollock standard length and age were estimated based on otolith maximum size, and the pollock subopercle size, from information provided by T. Buckley (Troy.Buckley@noaa.gov, pers. comm.). When fish offal was observed in stomach contents, it was identified by the presence of distinct isolated prey fish body parts, such as wads of skin, individual fins, sections of vertebral column, or the head from a large-bodied fish. The presence of individual body parts in the stomach was inconsistent with fish prey consumed whole, which is typical for Chinook salmon. Samples of fish offal were frozen and analyzed using genetic techniques by Buser et al. (2009) to confirm the fish species identification.

The prey composition was summarized in two ways. First, results were summarized at a high level of detail with regard to prey identification. Individual stomach samples were grouped by ocean age and season, and the prey weights in each prey group were summed, then divided by the total prey weight in each stratum. A second approach aggregated data for statistical comparison of winter prey composition of the major prey categories (euphausiids, squid, fish, and fish offal) to fishing depth zones, tow time period, Chinook salmon ocean age, and maturity. For each individual stom-

ach sample containing prey, the weight of each of the four prey categories was divided by the fish's body weight to get a prey index (PI). The PI was arcsine square-root transformed for statistical analysis (Zar 1984). The transformed PI was compared among strata with the Kruskal Wallis or the Wilcoxon rank sum test. Only the winter samples were statistically analyzed because summer samples were too few in number.

RESULTS

A total of 282 Chinook salmon stomach samples was collected in winter (91%) and summer (9%) 2007 (Table 1). Samples were collected along the eastern Bering Sea slope in a northwesterly to southeasterly axis, with summer samples extending further to the northwest than winter samples (Fig. 1). Half the Chinook salmon collected in winter (50%) were ocean age-2 and most of the summer samples (64%) were ocean age-3 fish. Winter samples were collected from significantly (t -test, one tail, $P < 0.001$) deeper depths (mean 308 m, range 51–569 m) than summer samples (mean 138 m, range 95–272 m; Table 1; Fig. 2). Among winter samples, the age frequency in samples from each fishing depth and tow time period were not equal (both χ^2 , $df = 2$, $P < 0.001$). More young fish were collected from the deepest depth strata and more ocean age-3 fish were collected in afternoon tows than would be expected if the age composition were equal across tow time periods.

Results showed qualitative differences in samples collected during winter and summer. In winter, Chinook salmon had a high percentage of empty stomachs (20–54%; Table 1). The squid species identified from stomach contents included a variety of species including *Berryteuthis magister*, *Gonatopsis (Go.) borealis*, and a mixture of other *Gonatus*

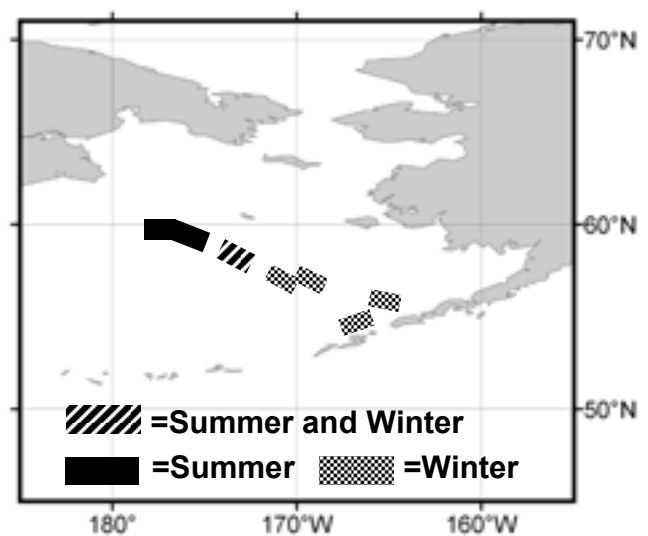


Fig. 1. Areas in the eastern Bering Sea where U.S. ground fish observers collected Chinook salmon stomach samples in winter and summer, 2007.

Table 1. Total number of Chinook salmon stomach samples, percent age composition, and body size at age for samples collected by groundfish observers in 2007. Winter is January–March and summer is June–August. Fishing depth is the depth where the tow was conducted. Fork length, body weight, and salmon maturity from data provided by observers. Tow time period indicates the six-hour time period of the day when at least 50% of the tow duration occurred.

Description	Winter	Summer
Total number of Chinook samples	257	25
mean fishing depth m (sd; min, max)	308 (177; 51, 569)	138 (56; 95, 272)
tow time period		
0001 to 0600 hours (% of seasonal samples)	28	16
0601 to 1200 hours (% of seasonal samples)	19	12
1201 to 1800 hours (% of seasonal samples)	30	52
1801 to 2400 hours (% of seasonal samples)	23	20
Ocean age-1		
number (% of seasonal total)	5 (2)	0
mean fishing depth m (sd)	155 (195)	
number immature (% of age group)	5 (100)	
mean fork length cm (sd)	28 (4.5)	
mean body weight kg (sd)	0.25 (0.11)	
proportion empty stomachs (for age group)	0.20	
Ocean age-2		
number (% of seasonal total)	128 (50)	9 (36)
mean fishing depth m (sd)	382 (144)	136 (60)
number immature (% of age group)	107 (84)	5 (56)
mean fork length cm (sd)	52 (5.0)	64 (6.6)
mean body weight kg (sd)	1.71 (0.61)	3.63 (1.08)
proportion empty stomachs (for age group)	0.52	0.00
Ocean age-3		
number (% of seasonal total)	89 (35)	16 (64)
mean fishing depth m (sd)	258 (176)	139 (56)
number immature (% of age group)	50 (56)	7 (44)
mean fork length cm (sd)	66 (5.1)	73 (5.9)
mean body weight kg (sd)	3.58 (1.14)	5.27 (1.30)
proportion empty stomachs (for age group)	0.54	0.19
Ocean age-4 or more		
number (% of seasonal total)	35 (14)	0
mean fishing depth m (sd)	191 (168)	
number immature (% of age group)	17 (49)	
mean fork length cm (sd)	76 (6.5)	
mean body weight kg (sd)	5.68 (1.90)	
proportion empty stomachs (for age group)	0.40	

species (Table 2). Fish offal was present in the diets of all age groups, ranging from 3.7% in ocean age-3 fish to 22.8% in ocean age-1 fish. By comparison, in summer Chinook salmon had a low percentage of empty stomachs (0–19%; Table 1). Two species of squid were identified from samples collected in summer, including *B. magister* and *Gonatus (G.) kamtschaticus*, the latter identified only in summer samples (Table 2). In the summer stomach samples, whole young pollock were common, but euphausiids, fish offal, and plas-

tic debris were not found in these samples.

Comparison of Chinook salmon fork length to fish and squid prey size in winter showed a positive relation between predator size and maximum size of squid and fish consumed (Fig. 3). In summer, there is no relation between Chinook salmon size and either squid or fish prey size. In summer Chinook salmon might consume fish and squid that are smaller, or younger, than those encountered in winter.

Twenty-one of 23 pairs of walleye pollock otoliths recovered from Chinook salmon stomach contents were collected from summer samples (Table 3). All pollock otoliths were recovered from whole fish consumed naturally by Chinook salmon. One pair of pollock subopercles was recovered from fish offal found in a winter Chinook salmon stomach sample. Most commonly, ocean age-3 Chinook salmon consumed age-1 pollock. The otoliths collected in the winter samples were found in two ocean age-4 Chinook salmon that consumed an age-1, and an age-3 or possibly age-4 pollock. The pollock subopercles were recovered from a Chinook salmon 77 cm long. The subopercle bones were likely from an age-5+ pollock, approximately 50 cm in size, a fish too large for the Chinook salmon to swallow whole.

Among winter samples, results of nonparametric analysis indicated that prey composition was different among fishing depth zones and between maturity groups (Table 4). The PI of euphausiids in stomach contents of fish collected at depths < 200 m was significantly higher than observed in the diet of fish collected at depths from 201–600 m (Kruskal Wallis test, $df = 2, P < 0.001$). The opposite was true for the PI of squid (Table 4; Fig. 4). The PI of squid was significantly greater in Chinook caught at 201–600 m than at depths < 200 m (Kruskal Wallis test, $df = 2, P < 0.001$). The PI of fish offal in the diet was significantly higher in Chinook salmon caught at depths < 200 m than fish caught at 401–600 m (Kruskal Wallis test, $df = 2, P < 0.01$). The value of fish offal PI in stomach contents of fish sampled at 201–400 m was intermediate between shallow and deep samples and was not significantly different from either. Fish PI was not significantly different among depth strata. Euphausiid PI was significantly higher among immature Chinook salmon than maturing fish, but the PI of the other prey types were not different between maturity groups (Wilcoxon rank sum test, $df = 1, P < 0.01$). The PI of euphausiids, squid, fish, or fish offal were not significantly different among tow time periods or Chinook salmon ocean ages.

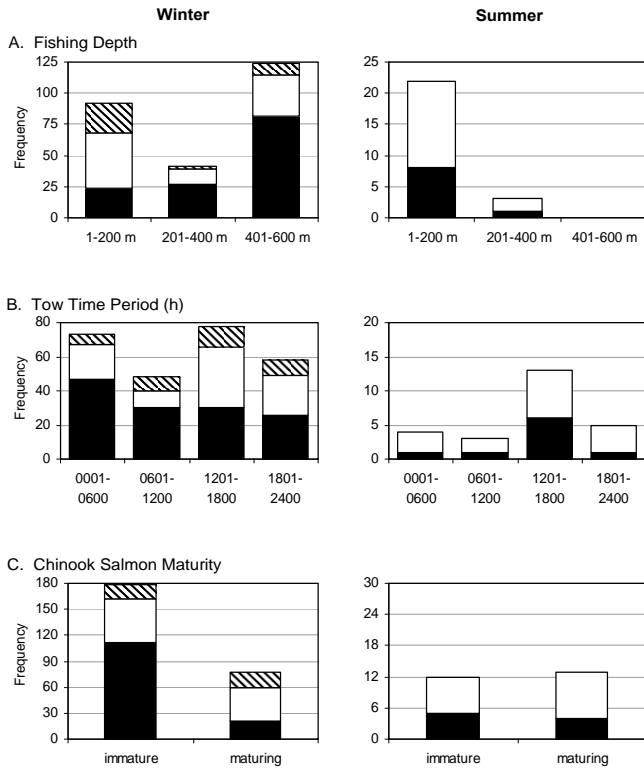


Fig. 2. Comparison of Chinook salmon age composition in samples collected in winter (left panels) and summer (right panels) in the eastern Bering Sea, 2007. Note difference in frequencies (y-axis) between winter and summer samples. Solid fill = Ocean age-1 and -2; open fill = ocean age-3; diagonal fill = ocean age-4 and -5. A. Age composition among fishing depth zones (m). B. Age composition among tow time periods of the day (hr). C. Age composition of immature and maturing fish.

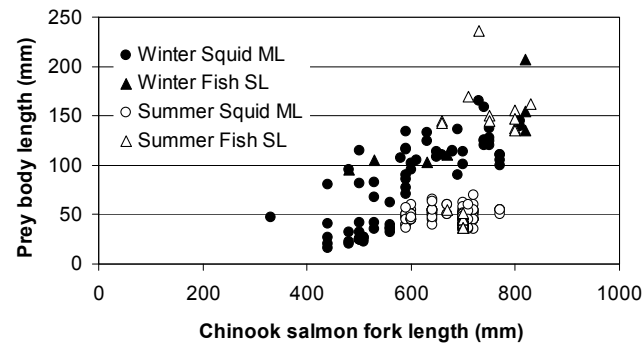


Fig. 3. Comparison of squid and fish prey size with Chinook salmon fork length of fish in which the prey were observed.

Table 2. Percent prey composition of Chinook salmon stomach samples collected by groundfish observers in 2007. Percent prey composition calculated by adding prey weights in each category for each ocean age group and season, then dividing by the total prey weight in each stratum. Mean and range of prey weight calculated from among stomach samples that contain prey. Stomach index was the total prey weight (g) divided by fish body weight (g) times 100. Mean stomach index was averaged over the number of stomach samples containing prey. Fish offal and plastic material (n, mean wt) based on the number of stomachs and average weight among stomachs containing those materials.

Prey items	Percent prey composition by weight					
	Winter 2007				Summer 2007	
	Ocean age-1	Ocean age-2	Ocean age-3	Ocean age-4 & -5	Ocean age-2	Ocean age-3
Total Euphausiacea	22.8	4.9	13.2	0.9	0.0	0.0
Total Other/Unid Crustaceans	0.0	0.9	0.0	0.4	0.0	0.0
Total Cephalopods	47.4	73.9	80.7	81.6	45.2	26.7
<i>Beryteuthis magister</i>	47.4	49.8	29.3	38.2	14.0	10.7
<i>Gonatopsis borealis</i>	0.0	12.5	50.1	43.5	0.0	0.0
<i>Gonatus kamtschaticus</i>	0.0	0.0	0.0	0.0	31.2	15.9
<i>Gonatus pyros</i>	0.0	2.1	0.0	0.0	0.0	0.0
<i>Gonatus berryi</i>	0.0	1.2	0.3	0.0	0.0	0.0
Unidentified Cephalopods	0.0	8.2	1.0	0.0	0.0	0.1
Total Pisces	7.0	5.7	2.3	12.1	54.8	73.3
Bathymasteridae	0.0	0.0	0.0	0.0	0.0	0.1
<i>Mallotus villosus</i>	0.0	0.0	1.4	0.0	0.0	0.0
<i>Stenobranchius leucopsarus</i>	0.0	2.6	0.0	0.0	0.0	0.0
<i>Ammodytes hexapterus</i>	0.0	0.5	0.0	0.0	0.0	0.0
<i>Blepsias bilobus</i>	0.0	0.0	0.0	0.0	0.0	16.4
<i>Theragra chalcogramma</i>	0.0	1.3	0.0	1.5	50.3	56.3
<i>Leuroglossus schmidti</i>	0.0	0.0	0.1	0.0	0.0	0.0
Unidentified Pisces	7.0	1.2	0.8	10.6	4.5	0.5
Fish Offal	22.8	15.1	3.7	4.8	0.0	0.0
Plastic Debris	0.0	0.0	0.1	0.2	0.0	0.0
Number of stomachs	5	128	89	35	9	16
% empty stomachs	20	49	54	40	0	19
Mean prey weight (g) (sd)	1.43 (1.18)	16.20 (27.26)	29.42 (37.68)	56.39 (72.20)	28.33 (38.62)	72.24 (39.45)
Range prey weight (g)	0.4-3.1	0.1-155.1	0.1-165.9	0.1-244.0	1.6-127.30	1.1-145.8
Mean stomach index (sd)	0.547 (0.191)	0.781 (1.006)	0.803 (0.999)	1.049 (1.348)	0.721 (0.831)	1.465 (0.779)
Fish offal (n, mean wt)	1, 1.3 g	7, 21.0 g	5, 8.9 g	3, 18.8 g	0	0
Plastic debris (n, mean wt)	0	0	1, 1.1 g	1, 2.0 g	0	0

age-0 and older Chinook salmon consumed primarily nekton. Young Chinook salmon (21–40 cm FL) consumed up to 87% juvenile squids (including *B. magister*) and the remaining component of the diet was euphausiids (Sobelevskii and Senchenko 1996). In the winter, fish species consumed by Chinook salmon included capelin (*Mallotus villosus*), northern lampfish (*Stenobranchius leucopsarus*), Pacific sand lance

(*Ammodytes hexapterus*), and walleye pollock. Some of the same species were identified from earlier winter Chinook salmon diet studies, including Myctophidae and capelin (Glebov 1998). Squid identified in winter 2007 diet samples included several species of gonatid squid, including *B. magister*, *Go. borealis*, *G. pyros*, and *G. berryi*. *G. kamtschaticus* has been identified in winter diets of Chinook salmon

Table 3. Estimated body length (SL, mm) and age of walleye pollock (year) based on pollock otoliths and subopercles collected from Chinook salmon stomach contents in the eastern Bering Sea, 2007. Pollock otoliths were recovered from whole fish consumed naturally by Chinook salmon and pollock subopercles were obtained from salmon consumption of pollock offal. Identical lengths listed for Chinook salmon indicate multiple otolith samples obtained from a single salmon stomach. Otolith length is the maximum dimension of the larger otolith of the pair. Conversion of otolith length and subopercle size to estimated pollock length and age from information provided by T. Buckley (Troy.Buckley@noaa.gov, pers. comm.).

Chinook salmon capture month	Chinook salmon fork length (cm)	Chinook salmon ocean age	Pollock otolith maximum length (mm)	Other pollock bone	Estimated pollock SL (mm)	Estimated pollock age (years)
Jan	82	4	7.12		143	1
Mar	79	4	14.90		348	3 or 4
Mar	77	4	n/a	subopercle	~500	5+
Aug	80	3	7.34		147	1
Aug	80	3	6.68		135	1
Aug	80	3	7.94		161	1
Aug	80	3	7.87		160	1
Aug	80	3	7.78		157	1
Aug	74	3	6.49		130	1
Aug	74	3	6.96		140	1
Aug	74	3	6.28		126	1
Aug	74	3	7.62		153	1
Aug	71	3	8.29		168	1
Aug	72	3	8.12		164	1
Aug	73	2	7.52		151	1
Aug	73	2	10.94		231	2
Aug	75	3	8.19		166	1
Aug	75	3	6.84		138	1
Aug	75	3	7.50		151	1
Aug	83	3	8.75		177	1
Aug	83	3	6.98		141	1
Aug	83	3	7.78		157	1
Aug	66	3	7.70		155	1
Aug	66	3	7.56		152	1

(Glebov 1998), however, we observed this species only as juveniles in samples collected during the summer.

While Chinook salmon routinely inhabit waters considerably deeper than 50 m, this is the first study to examine the stomach contents of Chinook salmon caught at considerably greater depths (51–569 m). Salmon trawl surveys that include analysis of salmon food habits generally operate in the upper 50 m of the water column (NPAFC 2001; Volkov et al. 2007; Efimkin et al. 2008; Fukuwaka et al. 2008). Chinook abundance estimates have been obtained to depths of 120 m (Walker et al. 2007) and Chinook salmon bycatch in commercial trawling operations has been reported to 360 m in the northeastern Bering Sea, 300 m in the eastern Bering Sea, and 482 m in U.S. west coast trawl fisheries (Erickson and Pikitch 1994; Radchenko and Glebov 1998a,b; Walker et al. 2007). While some Chinook salmon might have entered the trawl at shallower depths during descent or ascent of the fishing gear, depth-recording data storage tags placed

on Chinook salmon show these fish routinely dive to 250 m in spring in southeast Alaska (Murphy and Heard 2001) and inhabit depths to at least 350 m during winter and early spring in the Bering Sea (Walker and Myers 2009). If Chinook salmon generally remain for several hours to feed within the broad 200-m depth intervals where they are caught, then we can assume the difference in the prey composition among the depth categories likely reflects true differences in the diet of fish caught in different depth habitats.

We observed that Chinook salmon stomach contents varied with fishing depth, with more euphausiids and fish offal in the stomach contents of Chinook salmon caught at < 200 m and more squid in the stomach contents of Chinook salmon caught at > 200 m. The preponderance of euphausiids in the stomach contents of Chinook salmon captured at < 200 m might result from higher abundance of these organisms at shallow depths. Preference for a particular depth range is characteristic of euphausiid species, and most of the species

Table 4. Results of nonparametric analysis for differences between prey category and fishing depth zones (1-200, 201-400, 401-600 m), tow time period of the day (0001-0600, 0601-1200, 1201-1800, 1801-2400 hr), maturity (immature, maturing), and Chinook salmon ocean age (age-1 and -2, age-3, and age-4 and -5) for the winter samples. Kruskal Wallis nonparametric chi-square test used to compare prey components with fishing depth zone, tow time period, and Chinook salmon ocean age. Wilcoxon rank sum test used to compare prey composition and maturity. Prey index (PI) = weight of prey component divided by fish body weight. The PI was arcsine square root transformed before statistical analysis. Critical value of $P = 0.05$, ns = not significant.

Analysis	Prey components	Test statistic	df	P-value	Comparison of factors with significant P-values
Prey components and fishing depth zone		chi-square			
	Euphausiid PI	60.7602	2	< 0.001	1-200 > 201-400 and 401-600
	Squid PI	68.2755	2	< 0.001	1-200 < 201-400 and 401-600
	Fish offal PI	11.8835	2	< 0.01	1-200 > 401-600*
Prey components and tow time period		chi-square			
	Euphausiid PI	7.1513	3	ns	
	Squid PI	3.3642	3	ns	
	Fish offal PI	2.9347	3	ns	
Prey components by maturity		corrected-z			
	Euphausiid PI	2.5786	1	< 0.01	immature > maturing
	Squid PI	-1.9158	1	ns	
	Fish offal PI	-0.0045	1	ns	
Prey components and ocean age		chi-square			
	Euphausiid PI	2.217	2	ns	
	Squid PI	1.277	2	ns	
	Fish offal PI	0.0797	2	ns	

*Fish offal PI for the middle fishing depth range, 201-400 m, was not significantly different from fish offal PI in the shallow (1-200 m) or deep (401-600 m) depth range.

distributed in this area of the eastern Bering Sea generally have a maximum vertical range of 0 to 400 m (Mauchline 1980).

The preponderance of fish offal in the stomach contents of Chinook salmon captured at < 200 m might reflect the greater abundance of this material at shallower depths. Several other authors have described an inverse relationship between the amount of fish offal in stomach contents and water column depth (Hovde et al. 2002; Orlov and Moukhametov 2007). Perhaps the horizontal spread of fish offal away from the surface increases with depth, thus increasing the number of potential scavengers consuming it.

Piscine scavenging on offal generated from fish processing has been reported primarily from the diets of demersal fish, including Greenland halibut (*Reinhardtius hippoglossoides*; Hovde et al. 2002; Roman et al. 2007), Pacific halibut (*Hippoglossus stenolepis*; Orlov and Moukhametov 2007), Pacific black halibut (*R. hippoglossoides mat-*

suurae) and Kamchatka flounder (*Atheresthes evermanni*; Orlov and Moukhametov 2004), yellowfin sole (*Limanda aspera*; Brown et al. 2005), belligerent sculpin (*Megalocottus platycephalus*) and starry flounder (*Platichthys stellatus*; Tokranov and Maksimenkov 1995), great sculpin (*Myoxocephalus polyacanthocephalus*; Glubokov and Orlov 2005), southern cod (*Patagonotothen ramsayi*) and channel bull blenny (*Cottoperca gobio*; Laptikhovskiy and Arkhipkin 2003), Argentine hake (*Merluccius hubbsi*) and bigeye grenadier (*Macrourus holotrachys*; Laptikhovskiy and Fetisov 1999), and black dogfish (*Centroscyllium fabricii*; Punzon and Herrera 2000). However, consumption of fish offal has not been previously reported for any salmon species, including Chinook salmon. In winter, we found Chinook salmon feeding on fish offal identified as originating from walleye pollock (Buser et al. 2009). Food resources might be scarce in winter causing some Chinook salmon having a demersal distribution to scavenge offal discarded by the pollock fish-

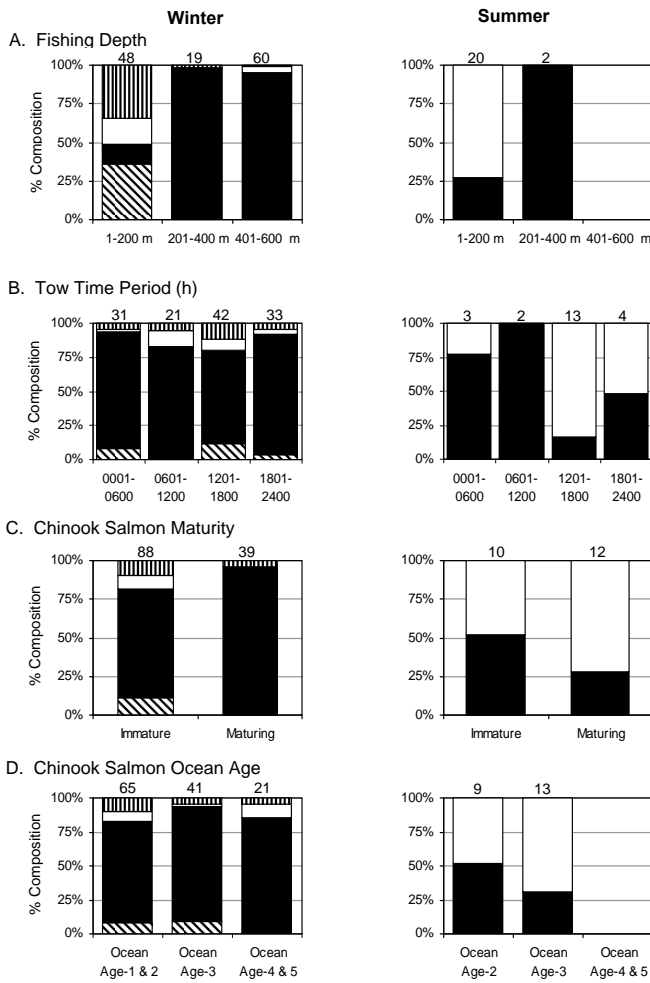


Fig. 4. Comparison of Chinook salmon diets for fish collected in winter (left panels) and summer (right panels) in the eastern Bering Sea, 2007. The percent composition is the mean prey index (PI = weight of prey category/fish body weight) among fish that contain prey. Sample size of fish that contain prey in each category is shown above each histogram. Histogram patterns include the major prey categories: Diagonal fill = euphausiids; solid fill = cephalopods; open fill = pisces; vertical fill = fish offal. A. Chinook salmon diet comparison among fishing depth zones (m). B. Chinook salmon diet comparison among tow time periods of the day (hr). C. Chinook salmon diet comparison between immature and maturing fish. D. Chinook salmon diet comparison among ocean age groups.

ery, thus supplementing their natural diet. Proximity and attraction to fish offal could affect distribution of Chinook salmon by motivating them to move to areas where fish are processed and chunks of fish are discarded.

Our study found immature Chinook salmon contained more euphausiids in their stomach contents than maturing fish (Table 4; Fig. 4). Analyses of Chinook salmon food habits by other investigators working in the Bering Sea have observed that small Chinook (< 40 cm) salmon consume more zooplankton, such as euphausiids, decapods, large crustaceans, and pteropods. Larger (> 40 cm) Chinook salmon consume more nekton, such as squid and fish (Glebov 1998;

Farley et al. 2006; Volkov et al. 2007).

We did not observe a statistical difference in the proportion of various prey types in Chinook salmon of different ages. Because of the small number of stomach samples obtained from the youngest (ocean age-1) fish (n = 5; Table 1), data for ocean age-1 and -2 fish were combined. Combining the data from these age groups likely obscured potential differences in diet between small (young) and larger (older) fish. If the number of ocean age-1 fish collected in winter could be increased in future studies, we suspect that significant differences in diet between young and older Chinook salmon will be found.

Consumption of age-0 walleye pollock by Chinook, sockeye, and chum salmon was reported in earlier studies of food habits in the Bering Sea (Davis et al. 2004; Farley et al. 2007; Volkov et al. 2007). Our study showed the age of pollock consumed by Chinook salmon extends beyond consumption of juvenile (age-0) pollock to older age groups such as age-3 and possibly age-4 pollock (Table 3). This suggests pollock of the same age-class are susceptible to predation by Chinook salmon for several years, rather than escaping from salmon predation after the first year of life. Pollock might be vulnerable to predation by Chinook salmon until age-4, when pollock fully recruit into the eastern Bering Sea pollock fishery (Wespestad 1993). The impact of salmon predation on pollock abundance has not been estimated, but future estimates will need to account for the successive years that a single cohort of pollock is vulnerable to salmon predation.

Future research will include analysis of samples collected by observers in 2008, which we anticipate will improve information on interannual and seasonal changes, and effects of Chinook body size on Chinook salmon diets in the eastern Bering Sea.

CONCLUSIONS

This was the first study of winter diets of Chinook salmon in the eastern Bering Sea, and we found their diets varied by fishing depth and maturity group. The ratio of euphausiids and fish offal in the diet was significantly higher in Chinook salmon collected at shallower depths (< 200 m), and the ratio of squid was significantly higher in Chinook salmon collected at deeper depths (201–600 m). Euphausiids were more common in the diet of immature Chinook salmon than maturing fish. The percentage of empty stomachs was higher in winter than summer, suggesting wintertime feeding might occur after longer time periods between meals than in summer. In winter, Chinook salmon of all age groups consumed fish offal, which was likely generated by human fishing activities. Consumption of fish offal could also have deleterious effects, therefore the implications of scavenging by Chinook salmon needs to be further explored. Future studies examining the winter and summer samples collected by groundfish observers will allow for a more detailed examination of Chinook salmon food habits with respect to

inter-annual and seasonal variability.

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A Comparison of the Diets of Hatchery and Wild Coho Salmon (*Oncorhynchus kisutch*) in the Strait of Georgia from 1997–2007

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Sweeting, R.M., and R.J. Beamish. 2009. A comparison of the diets of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia from 1997–2007. N. Pac. Anadr. Fish Comm. Bull. 5: 255–264.

Abstract: Wild and hatchery-reared coho salmon (*Oncorhynchus kisutch*) have now co-existed in the Strait of Georgia for over 30 years, and have exhibited considerable variation in marine survival rates. This study is the first to compare diets of juvenile hatchery and wild coho salmon during the critical early marine period of this species. From 1997–2007, over 10,000 stomachs from juvenile coho salmon captured in the Strait of Georgia were examined. Diets in July were dominated by decapods (primarily crab megalops) and fish (primarily herring). In September, euphausiids and amphipods (primarily hyperiids) dominated. The variability between hatchery and wild coho salmon diet was larger in September than in July. Prey volume, stomach fullness and fork length were significantly correlated between hatchery and wild coho salmon in the July and September surveys. While coho salmon captured in September surveys had significantly higher percentages of empty stomachs than those from July, there were no significant differences in the percentage of empty stomachs between hatchery and wild coho salmon in either survey. Shifts in diet composition occurred both annually and seasonally, but the trends for both groups of coho salmon were the same. Thus, we conclude there were no significant differences observed between hatchery and wild coho salmon in either appetite (volume of prey in the stomach) or in diet (composition of stomach contents) in either July or September surveys from 1997–2007 in the Strait of Georgia, British Columbia, Canada.

Keywords: coho salmon, hatchery, wild, diet, seasonal, Strait of Georgia, interaction, survival

INTRODUCTION

Coho salmon (*Oncorhynchus kisutch*) are an anadromous Pacific salmonid found on the west coast of North America from California to Alaska. Typically, young coho salmon spend 1–2 years in freshwater rivers and lakes before undergoing a spring transformation (termed “smoltification”) and subsequent migration to the marine environment in the late spring or early summer. Smolts spend several weeks to months in the near-shore or estuarine regions prior to a second major migration to winter feeding grounds in October–November (Groot and Margolis 1991). For the coho populations utilizing the Strait of Georgia, British Columbia, this winter feeding ground is off the southwest coast of Vancouver Island (Fig. 1). Adult coho salmon then return to spawn in their natal rivers in the following late summer/early fall. Although some small programs had been initiated in the 1960s, enhancement of coho salmon productivity in British Columbia began in the 1970s with the multiple goals of increasing commercial and recreational fishing opportunities and providing economic opportunity for First Nation, coastal and other public groups (Lehmann and Irvine 2005). Currently, there are eight major hatcheries producing coho salmon which utilize the Strait of Georgia as an early rearing

area, as well as a number of smaller facilities. Total production of coho salmon (Fig. 2) was 8–10 million throughout most of the 1990s, but has declined recently. Wild salmon stocks are currently not consistently monitored, and assessment data exists only for a few streams.

Coho salmon stocks utilizing the Strait of Georgia historically supported a strong commercial and recreational fishery. Beginning in the early 1980s, however, a long-term decline in coho marine survival began (Beamish et al. 2002, 2008). Throughout the 1990s, marine survival averaged < 2%, down from the 10–15% range observed in the early years of enhancement. Furthermore, in the 1990s adult coho began remaining in the over-winter feeding grounds on the west coast until immediately prior to entering the river system for spawning, rather than returning to the Strait of Georgia in early spring (Beamish et al. 2008). Combined with low marine survival, this effect was disastrous to the fishery. In 1995, management decisions closed the commercial fishery in the Strait of Georgia and in 1998 placed further restrictions on the recreational fishery. At this time, a mass marking program (adipose fin clip) for hatchery coho salmon was also instituted to provide relief for wild coho salmon stocks (via non-retention of unclipped coho). Hatchery coho salmon were dominating the population at this time (Sweet-

ing et al. 2003), but that trend appears to have been recently reversed (Beamish et al. 2008). The mass marking program initiated in the late 1990s provided an excellent opportunity to differentiate between large numbers of hatchery and wild coho salmon compared to the low numbers (typically 2–5% of releases) of fish implanted with coded wire tags (CWTs). In 1997 only 10% of the all hatchery coho salmon were adipose fin-clipped, whereas from 1998–2007 the clip rate averaged 76% (range 67–89%).

Beginning in 1997, we conducted juvenile Pacific salmon surveys in the Strait of Georgia and surrounding waters

in the summer (July) and early fall (September). As part of these surveys, we analyzed coho salmon stomach fullness (“appetite”) and volumes (including the prevalence of empty stomachs), as well as identifying the percentage of prey items (the “diet”) present in the stomach. In this paper, we summarize 11 years of surveys in July and September in the Strait of Georgia (1997–2007) and examine the hypothesis that juvenile hatchery-reared and wild coho have similar appetites (assessed as average stomach prey volumes) and diets (assessed as percentages of group prey items) during these critical early months in the marine environment.

MATERIALS AND METHODS

Annual surveys have been conducted in the Strait of Georgia in July and September from 1997–2007, with the exception of July 2003. Over this time period, the track lines (Fig. 1) and the fishing gear have remained constant. The fishing platform in most years has been the CCG vessel *W.E. Ricker*, but there have been some surveys using charter vessels (the *M/V Frosti* and *M/V Viking Storm*). To our knowledge, there does not appear to be any impact of fishing platform on catch, individual fish size or dietary data in these surveys. Details of the fishing gear and survey design can be seen in previous papers (Beamish et al. 2000; Sweeting et al. 2003). The gear used in these surveys is a modified 250/350/14 midwater rope trawl (Cantrawl Pacific Ltd., Richmond, British Columbia) with an average opening of approximately 14 by 32 meters under nominal fishing conditions. All sets are 30 minutes in duration and are conducted at 5 knots, as much as possible, under wind and tide conditions. To assess the vertical as well as horizontal distributions of juvenile coho salmon within the water column, the fishing effort was partitioned into 15-meter strata, roughly the height of the net opening. Thus, fishing was conducted at the surface, at 15m, at 30m, etc. This stratification was, however, weighted to surface tows such that ~half of our effort was surface tows (48% of the July survey sets, and 50% of the September survey sets). These surveys are part of a number of long-term projects investigating the Strait of Georgia ecosystem (Beamish et al. 2000, 2004; Sweeting et al. 2003). To normalize effort among surveys and years, catch data is expressed as catch per unit effort (CPUE) or, in this case, catch per hour. Survey dates, total number of sets, total coho catch, CPUE and average fork length data for the July and September surveys are shown in Tables 1 and 2, respectively.

Upon retrieval of the net, the entire catch was emptied into totes and immediately separated into individual species. All juvenile coho salmon were counted, examined for adipose clips, and checked for coded wire tags. Fork lengths were measured (to the nearest mm); sub-samples were then taken (n = 15–30) for a more intensive analysis including fork length, body weight (to the nearest 0.1 g, when weather conditions permitted), removal of otoliths and dietary anal-



Fig. 1. Map of the Strait of Georgia and surrounding area, showing survey track lines in effect since 1997.

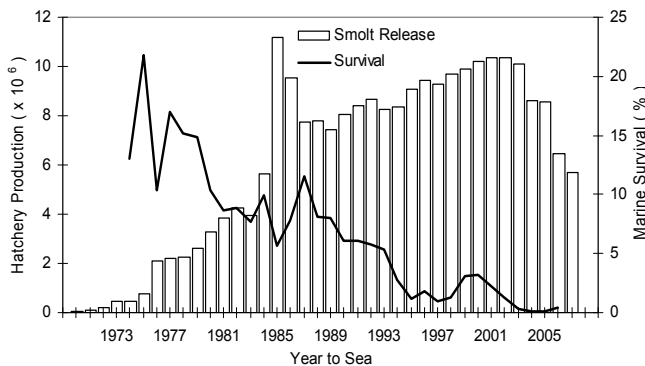


Fig. 2. Production (open bars) and marine survival (solid line) for British Columbia hatcheries releasing coho into the Strait of Georgia. Data from DFO.

Table 1. Total catch, average CPUE, and average fork length (mm) of juvenile coho salmon captured during July surveys in the Strait of Georgia from 1997-2007.

Year	Date	Number of sets	Total catch	CPUE (± SD)	Fork length (mm) (± SD)	N
1997	June 17–20, July 06–11	53	522	15.0 (42.8)	159.2 (22.54)	520
1998	June 30–July 09	60	1,245	38.1 (57.6)	172.8 (23.27)	1,220
1999	June 30–July 08	78	1,649	41.8 (66.2)	167.6 (22.31)	1,639
2000	July 11–July 20	72	4,628	126.1 (221.5)	199.7 (23.33)	3,361
2001	July 07–July 15	76	4,299	116.8 (168.5)	185.7 (21.31)	2,957
2002	July 02–July 11	86	1,887	42.8 (59.7)	170.3 (22.84)	1,887
2003	NO SURVEY	-	-	-	-	-
2004	July 04–July 13	91	2,709	59.7 (83.6)	178.9 (28.19)	2,257
2005	July 14–July 21	76	416	11.0 (23.9)	190.9 (24.28)	414
2006	July 09–July 20	65	3,338	102.4 (333.1)	194.0 (23.66)	2,257
2007	July 08–July 15	74	1,293	41.7 (64.6)	153.6 (23.17)	1,236

Table 2. Total catch, average CPUE, and average fork length (mm) of juvenile coho salmon captured during September surveys in the Strait of Georgia from 1997-2007.

Year	Date	Number of sets	Total catch	CPUE (± SD)	Fork length (mm) (± SD)	N
1997	September 08–22, 25–27	110	2,399	28.8 (53.9)	243.2 (21.75)	2,399
1998	September 08–10, 12–16, 23–24	78	1,510	38.4 (79.5)	243.2 (27.70)	1,385
1999	August 31–September 08	73	2,022	55.2 (121.4)	229.3 (21.80)	1,600
2000	September 09–10, 14–24, October 01	82	1,546	32.5 (42.5)	247.6 (22.92)	1,536
2001	September 16–27	87	2,040	46.6 (78.5)	254.5 (23.28)	1,794
2002	September 20–28	74	643	16.9 (40.9)	245.6 (23.13)	566
2003	September 13–22	77	843	21.8 (42.8)	231.8 (22.08)	752
2004	October 07–18	64	355	11.0 (27.0)	251.9 (24.20)	355
2005	September 14–21, 28–29	63	507	16.1 (29.2)	252.1 (24.80)	506
2006	September 08–21, October 01	59	626	21.0 (44.8)	258.8 (21.12)	626
2007	September 17–25	71	328	10.2 (41.3)	224.1 (26.48)	287

ysis. Obtaining the body weight data also allowed for the calculation of individual condition factor, using the standard formula:

$$\text{Condition Factor (K)} = \text{Weight (g)} / \text{Length (mm)}^3 \times 100,000 \text{ (Ricker 1975)}$$

Diet analysis involved opening the stomach from the cardiac to pyloric constrictions and removal of the contents to a Petri dish. For each stomach, a visual estimate of fullness (%) and prey volume (cc) was determined from these fresh stomach contents. Stomach volumes estimated to be less than 0.1 cc were considered empty. Thus, all stomach analyses were performed on the ship, with no preservation. This diet analysis and methodology has been performed for the entire time series by the same experienced person and all stomach contents were examined within an hour of capture. Stomach contents were broken down (by %) to the genus level (or species, when possible), as well as to life-history stage. The subsequent contribution of each food group to the overall diet was calculated as the percent contribution of each prey group (in cc) to the total volume examined over the survey. To scale for differences in fish sizes, we calculated a stomach volume index for each fish:

$$\text{Stomach Volume Index} = \text{Stomach volume (cc)} \cdot 100 / \text{body weight (g)}$$

For ease of analysis and discussion, the diet items are organized into major prey groups: amphipods (hyperids and gammarids), decapods (crab and shrimp), euphausiids (primarily *Euphausia pacifica*), fish (primarily herring, but including sandlance, smelt, juvenile hake, juvenile walleye pollock, larval fishes and fish remains), and a category called “other”, which includes a wide range of low frequency items. Items in this final category are rare in the coho diet and, as a category, rarely exceeded 2–3% of the total coho salmon stomach prey volume.

Finally, it is important to acknowledge that the ‘wild’ coho salmon discussed throughout this paper were in fact mostly wild, with a percentage of unclipped hatchery-reared fish as not all hatchery fish received adipose fin clips. The hatchery coho salmon group, on the other hand, is composed entirely of fish of hatchery origin.

Statistical Tests

Basic descriptive statistics were performed utilizing built-in Excel (Microsoft) programs. All other statistical tests were performed using InStat (GraphPad Software,

USA). All data were initially examined for normality (InStat) and significance was accepted at the $\alpha = 0.05$ level. Student's *t*-tests were used to assess within-survey differences in fork length, weight, condition factor, stomach volume and fullness between hatchery and wild fish. If the data were determined to be non-parametric, then Welch's approximate *T*-test was used (InStat), which does not assume equal variances.

RESULTS

Over the course of this study (1997–2007), over 10,000 juvenile coho salmon stomachs were examined: 5,937 in July surveys and 4,677 in September (Table 3). For July surveys, the number of stomachs assessed represented an overall average of 35.8% of the total catch of juvenile coho salmon (range: 17% to 59%). For September surveys, the 4,677 stomachs examined represented an overall average of 41.9% of the total catch over the time series (range: 23% to 52%). The lower percentage values represent years of high juvenile coho salmon catch (e.g., the high catches in the 2000, 2001 and 2006 July surveys also have the three lowest percentages of juvenile coho salmon stomachs assessed). There was also no impact of depth of capture on the fork length, diet or appetite of juvenile coho salmon (data not shown). Catches and CPUE of juvenile coho salmon did decrease with depth, as noted in the literature.

There were no consistent differences in the percentages of empty stomachs in the July and September surveys between juvenile hatchery and wild coho salmon, other than the July surveys of 2004, 2005 and 2006 (Fig. 3). The overall 1997–2007 average percentage of coho with empty stomachs in the July surveys were 5.6% (± 5.93 SD) and 6.3% (± 4.31 SD) between hatchery and wild, respectively, which was not significantly different ($t = 0.302$; $P = 0.766$). There were also no significant differences in the overall percentage of empty stomachs between hatchery and wild coho salmon in the September surveys: 16.1% ± 10.00 and 18.7% ± 7.81 , respectively ($t = 0.679$; $P = 0.505$). There was, however, a

clear seasonal difference, as the average percent of empty stomachs in the 11 September surveys was approximately three times larger than that seen in the 10 July surveys for both hatchery ($t = 2.88$; $P < 0.01$) and wild ($t = 4.56$; $P < 0.01$) coho salmon.

The average lengths, weights, condition factors, estimated prey volumes and stomach fullness as well as the calculated stomach volume index for the summer surveys from 1997–2007 are shown in Table 4. Coho salmon determined to be of hatchery origin were significantly larger than non-hatchery coho salmon in eight of the 10 years of summer surveys, and to be significantly heavier in seven of 10 years. These differences also appeared in the average condition factor calculations (Table 4), with the wild coho having significantly larger *K* values in six of 10 years. These differences in condition factor, while significant, were quite small. There was only a single significant difference in the average volume of prey in the stomachs between hatchery and wild coho salmon in the summer surveys, observed in the July 2006 survey. Furthermore, there were no consistent differences in either stomach fullness or in the calculated stomach volume index in the July surveys (Table 4).

Summary data from the September surveys are shown in Table 5. The average fork lengths of hatchery coho salmon in the September surveys were again significantly longer than wild coho in 10 of 11 years and significantly heavier in nine of 11 survey years, as seen in the July surveys. Average condition factor was only significantly different between the two groups of coho salmon in the September 1997 and 2000 surveys. There were no significant differences in average prey volume or in average stomach fullness between the two groups of coho salmon in any September survey from 1997–2007 (Table 5). The range of average stomach volumes in the September surveys (1.0–5.0 cc for hatchery; 1.2–2.0 cc for wild) was slightly larger than those observed in July (0.7–2.4 cc for hatchery; 0.7–1.9 cc for wild), presumably reflecting the larger average size of these juvenile coho salmon after a further 2 months. The average stomach volume index calculated for wild coho salmon was greater

Table 3. Total number of stomachs of juvenile hatchery and wild coho salmon examined during July and September surveys in the Strait of Georgia from 1997–2007. Hatchery coho were determined by the absence of an adipose fin.

Year	July		September	
	Hatchery	Wild	Hatchery	Wild
1997	114	157	60	483
1998	221	338	227	342
1999	264	483	241	403
2000	309	476	266	445
2001	389	474	224	362
2002	276	367	109	225
2003	-	-	166	267
2004	281	350	59	120
2005	53	192	67	151
2006	205	425	74	220
2007	212	351	69	97
Total	2,324	3,613	1,562	3,115

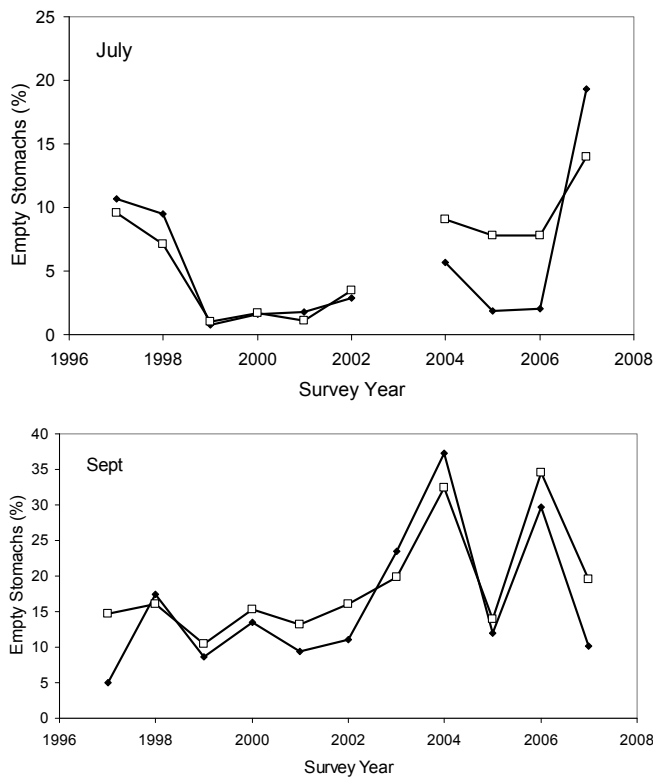


Fig. 3. Percentage of empty stomachs (total volume of prey ≤ 0.1 cc) in juvenile salmon from July and September surveys in the Strait of Georgia, 1997–2007. Closed diamonds represent hatchery coho salmon and open squares denote wild juvenile coho salmon.

than for hatchery fish in almost every September survey, but significantly so for only one of the 11 years (2005). The stomach volume index values for September surveys were also generally lower than the values calculated for the July surveys.

Diet composition of both hatchery and wild coho salmon captured in the July surveys (Fig. 4A, B) were dominated (by percent volume) by two categories: decapods (primarily crab megalops) and fish (primarily herring). In hatchery coho salmon, decapods comprised an average of 49.8% (± 25.37 SD; range: 16.7–87.7%) of stomach prey volume and fish contributed 37.3% (± 28.6 SD; 3.5–77.1%). In wild coho salmon, decapods ranged from 25.2% to 71.5% of the diet volume (average: 44.4% ± 19.58 SD) while the percentage of fish the diet volume ranged from 15.8–69.7% (average: 42.3 ± 23.2 SD). Amphipods, euphausiids and items from the “others” category combined generally comprised roughly 10% of the total stomach volume for both groups of coho (Table 6), although amphipods were significant in the diet in some years (e.g., 2001 and 2005). Furthermore, while there was some yearly variability observed (Fig. 4A, B), the shifts in diet composition were similar between both groups of juvenile coho salmon.

In the September surveys (Fig. 5A, B), decapods were no longer a major diet category in either hatchery-reared or

wild coho salmon (average: 3.5% ± 3.00 SD vs. 3.5% ± 3.46 SD, respectively). Fish still contributed about 1/3 of the total volume of diet of both groups of coho. For hatchery coho salmon the average was 30.9% ± 29.09 SD (range: 3.6–92.4%), while for wild coho salmon the average was 31.7% ± 22.24 SD). Euphausiids were now a major diet item in both hatchery (average: 34.6% ± 24.17 SD; range: 3.3–69.5%) and wild coho salmon (average: 35.1 ± 21.32 SD), followed by amphipods (average for hatchery fish: 26.9% ± 17.7 SD; range: 3.1–70.9%; average for wild fish: 26.2% ± 14.65 SD; range: 3.1–50.1%).

The lack of significant differences between juvenile hatchery and wild coho salmon in either July or September allows one to combine the two groups and examine seasonal differences in juvenile coho salmon diet in the marine environment (Table 6). While some annual variability exists, the differences in diet between July and September were significant. The dominance of decapods in July surveys (46.7%) is replaced by a significantly ($P = 0.003$) increased presence of amphipods (26.5%, especially gammarids) and euphausiids (34.8%) ($P = 0.001$). Fish remained approximately 1/3 of the diet (by percent volume) in both July and September ($P > 0.05$, ns).

DISCUSSION

An examination of over 10,000 stomach volumes and diet compositions between hatchery and wild juvenile coho salmon in their early ocean residence failed to disclose any significant differences. Annual variability in diet composition was observed during the 11 years of this study, presumably reflecting variability in prey availability due to climate and ocean conditions. However, the changes in diet composition were seen in both hatchery and wild coho salmon smolts, and overall differences were not significantly different. Comparing the combined July diet with the combined September diet (Table 6), a seasonal shift in diet composition was also observed, that was generally larger and more consistent than annual variability. Again, both groups of coho salmon responded similarly. These results suggest that in the early marine phase (July through September of their first ocean year), there is little difference between hatchery and wild coho salmon in terms of appetite or diet.

In the July surveys, the major dietary items consisted of decapods and fish. The decapods consumed were primarily crab megalops (probably *Cancer* spp.), with significant contributions by crab zoea and larval shrimp. The fish consumed were primarily juvenile herring, although a wide range of species were observed being consumed by both hatchery and wild coho salmon, including bay pipefish, Pacific sand-lance, sculpins, poachers, and various juvenile and larval fish (hake, pollock, rockfish, smelts) that also utilize the Strait of Georgia as early nursery or rearing areas. Fish remains, too digested to be identified to a specific species, and fish eggs were also included in this category. Of particular interest,

Table 4. Average fork lengths (mm) (\pm standard deviation, n), weights (g) (\pm SD, n), condition factors (\pm SD), prey volumes (cc) (\pm SD), fullness (%) (\pm SD) and stomach volume index (SVI) (\pm SD) for clipped (hatchery) and non-clipped (wild) juvenile coho salmon sampled from July surveys in the Strait of Georgia from 1997-2007. An asterisk (*) denotes a significant difference between the two groups at the 0.05 level. The sample size for condition factor and SVI is equal to that for weights, whereas the sample size for prey volume and stomach fullness is equal to fork lengths. Note that no survey was conducted in July of 2003.

Year	Fork length (mm)		Weight (g)		Condition factor		Prey volume (cc)		Stomach fullness (%)		Stomach volume index	
	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild
1997	162.5 (19.55)(112)	167.0 (26.56)(156)	61.6 (24.28)(50)	67.3 (37.95)(78)	1.14 (0.13)	1.17 (0.12)	1.0 (1.01)	1.2 (1.68)	29.7 (20.31)	29.8 (20.86)	2.31 (2.03)	1.98 (2.01)
1998	179.1 (18.54)(221)	180.3 (27.12)(338)	69.1 (24.75)(202)	77.0 (43.59)(301)	1.17 (0.09)	1.20* (0.10)	0.9 (1.16)	1.1 (1.69)	29.2 (22.50)	31.3 (22.81)	1.21 (1.26)	1.41 (2.59)
1999	175.3 (19.54)(264)	170.5* (22.90)(483)	64.1 (24.51)(255)	61.2 (25.99)(472)	1.14 (0.09)	1.16* (0.09)	0.7 (0.51)	0.7 (0.50)	31.2 (19.34)	33.4 (19.79)	1.07 (0.73)	1.27* (0.82)
2000	206.1 (19.12)(309)	193.6* (30.16)(476)	110.5 (31.91)(253)	94.6* (50.98)(407)	1.21 (0.07)	1.21 (0.11)	1.8 (1.41)	1.7 (1.86)	33.6 (17.57)	33.0 (18.33)	1.60 (1.23)	1.76 (1.34)
2001	191.6 (18.68)(389)	182.8* (24.07)(474)	86.4 (26.44)(233)	77.4* (33.68)(305)	1.19 (0.09)	1.23* (0.20)	1.2 (1.00)	1.2 (1.11)	32.9 (16.60)	32.4 (17.15)	1.34 (1.01)	1.55* (1.10)
2002	176.9 (19.31)(276)	164.5* (26.99)(367)	67.4 (24.49)(276)	58.7* (32.14)(366)	1.17 (0.09)	1.20* (0.10)	1.6 (2.08)	1.4 (1.92)	37.2 (22.12)	36.0 (22.06)	2.25 (2.34)	2.31 (2.35)
2003	NO SURVEY											
2004	194.4 (21.77)(281)	176.5* (30.00)(350)	90.9 (34.42)(240)	72.7* (44.06)(302)	1.20 (0.08)	1.23* (0.11)	2.1 (2.42)	1.9 (2.55)	39.3 (21.23)	36.5 (21.53)	2.44 (2.63)	2.64 (2.61)
2005	204.0 (19.55)(53)	189.9* (25.51)(192)	107.9 (31.40)(53)	89.0* (34.17)(192)	1.24 (0.06)	1.24 (0.09)	1.6 (1.44)	1.3 (2.14)	34.8 (15.40)	29.2* (17.57)	1.55 (1.45)	1.51 (1.88)
2006	207.7 (21.41)(205)	188.1* (26.10)(425)	117.3 (35.67)(175)	89.1* (42.74)(378)	1.25 (0.07)	1.26 (0.08)	2.4 (2.60)	1.9* (2.22)	43.8 (22.39)	40.9 (22.83)	2.08 (2.18)	2.23 (2.36)
2007	165.6 (19.95)(212)	150.3* (27.18)(351)	52.1 (19.95)(197)	42.1* (32.11)(332)	1.07 (0.10)	1.09* (0.11)	1.6 (2.69)	1.5 (2.8)	30.5 (24.20)	32.5 (23.45)	2.72 (3.38)	2.97 (3.34)

Table 5. Average fork lengths (mm) (\pm standard deviation, n), weights (g) (\pm SD, n), condition factors (\pm SD), prey volumes (cc) (\pm SD), fullness (%) (\pm SD) and stomach volume index (SVI) (\pm SD) for clipped (hatchery) and non-clipped (wild) juvenile coho salmon from September surveys in the Strait of Georgia from 1997-2007. An asterisk (*) denotes a significant difference between the two groups at the 0.05 level. The sample size for condition factor and SVI is equal to that for weights, whereas the sample size for prey volume and stomach fullness is equal to that of fork lengths.

Year	Fork length (mm)		Weight (g)		Condition factor		Prey volume (cc)		Stomach fullness (%)		Stomach volume index	
	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild
1997	245.6 (21.24)(60)	246.2 (22.39)(483)	173.4 (54.26)(56)	177.1 (22.39)(423)	1.14 (0.08)	1.17* (0.11)	1.1 (1.47)	1.3 (1.74)	28.0 (23.54)	18.1 (23.39)	0.73 (0.85)	0.67 (0.86)
1998	248.9 (24.66)(228)	234.8* (31.95)(344)	192.8 (61.95)(227)	169.0* (82.00)(341)	1.21 (0.09)	1.22 (0.09)	2.2 (3.85)	1.9 (3.71)	24.3 (28.41)	22.8 (25.29)	1.05 (1.60)	1.02 (1.73)
1999	231.2 (22.04)(241)	224.4* (22.31)(403)	146.5 (43.17)(238)	135.1* (40.08)(394)	1.15 (0.06)	1.16 (0.08)	1.4 (3.86)	1.5 (3.64)	17.6 (19.72)	20.5 (21.29)	0.99 (2.46)	1.08 (2.40)
2000	258.3 (17.90)(266)	244.2* (25.32)(445)	207.8 (47.43)(264)	183.0* (66.86)(442)	1.18 (0.07)	1.21* (0.09)	1.2 (1.91)	1.2 (2.33)	19.7 (18.50)	19.9 (18.49)	0.56 (0.84)	0.68 (1.07)
2001	262.1 (22.89)(224)	248.1* (25.25)(362)	223.1 (61.14)(175)	189.6* (62.87)(270)	1.22 (0.10)	1.21 (0.08)	2.3 (4.77)	1.8 (3.27)	18.9 (20.69)	18.4 (19.17)	1.16 (2.29)	1.10 (1.86)
2002	257.0 (17.12)(109)	242.4* (26.05)(225)	210.8 (41.70)(97)	180.0* (67.94)(215)	1.21 (0.08)	1.21 (0.08)	2.7 (3.91)	2.2 (3.26)	26.4 (23.13)	25.4 (22.74)	1.12 (1.64)	1.28 (1.83)
2003	240.1 (20.42)(166)	229.0* (23.60)(267)	160.7 (41.91)(104)	141.5* (39.83)(193)	1.15 (0.06)	1.16 (0.06)	1.0 (1.61)	1.4 (2.46)	19.5 (20.54)	25.3 (24.27)	0.61 (0.99)	0.86 (1.48)
2004	269.6 (16.42)(59)	251.1* (28.59)(120)	225.5 (45.97)(55)	190.6* (75.12)(107)	1.14 (0.07)	1.15 (0.08)	1.9 (3.81)	2.1 (4.10)	20.2 (24.88)	19.6 (23.24)	1.04 (2.21)	1.11 (2.14)
2005	263.6 (23.08)(67)	247.7* (25.92)(151)	230.6 (73.85)(67)	194.9* (61.82)(151)	1.23 (0.07)	1.24 (0.07)	1.2 (1.93)	1.6 (3.35)	18.7 (16.23)	19.7 (17.83)	0.52 (0.77)	0.82* (1.45)
2006	272.5 (19.20)(74)	257.5* (24.59)(220)	252.0 (59.77)(63)	223.3* (75.33)(185)	1.25 (0.10)	1.24 (0.08)	2.6 (4.35)	2.2 (3.82)	23.7 (25.95)	23.3 (26.54)	0.89 (1.66)	0.96 (1.83)
2007	234.6 (36.02)(61)	220.0* (29.65)(97)	179.5 (130.66)(60)	141.4 (97.62)(97)	1.24 (0.11)	1.23 (0.09)	5.5 (12.78)	2.0 (5.34)	35.7 (24.05)	29.7 (24.01)	1.71 (2.90)	1.27 (1.78)

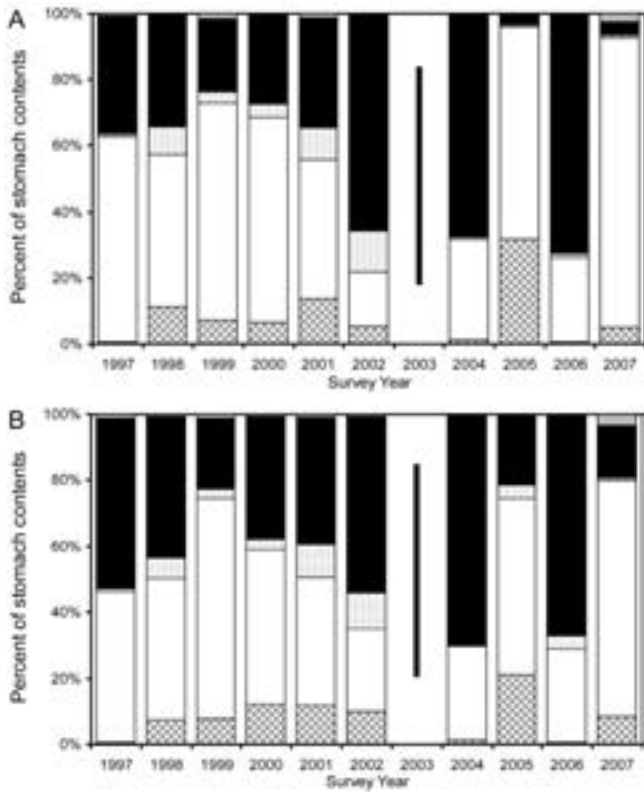


Fig. 4. Prey groups, by percent volume, in stomachs of (A) clipped and (B) non-clipped juvenile coho salmon captured in July surveys in the Strait of Georgia from 1997-2007. Prey groups are as follows: Amphipods (cross-hatch), Decapods (white), Euphausiids (stippled), Fish (diagonal stripe) and Other (black). See text for details. No survey in 2003.

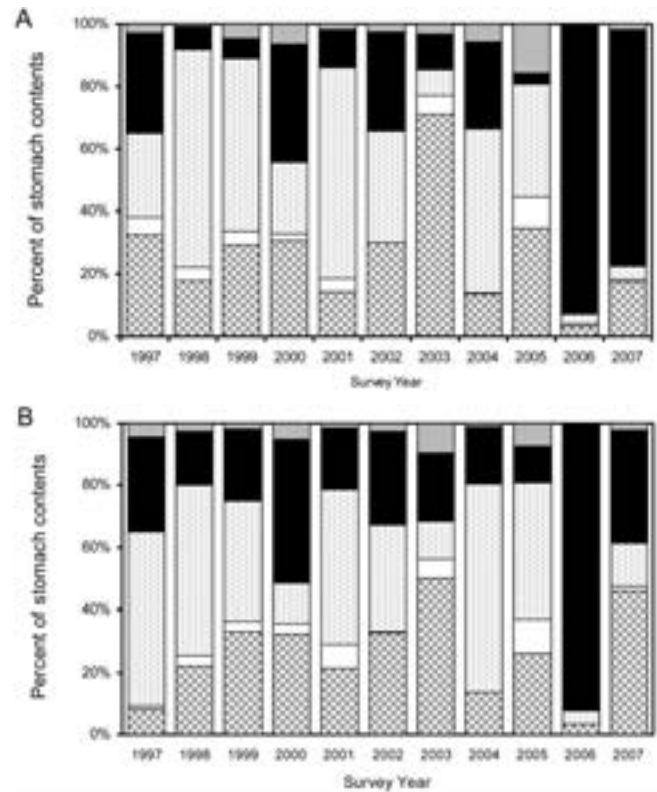


Fig. 5. Prey groups, by percent volume, in stomachs of clipped and non-clipped juvenile coho salmon captured in September surveys in the Strait of Georgia from 1997-2007. Prey groups are as follows: Amphipods (cross-hatch), Decapods (white), Euphausiids (stippled), Fish (diagonal lines) and Other (black). See text for details.

Table 6. Diet composition (percent of total volume) of juvenile coho salmon from July and September surveys in the Strait of Georgia from 1997-2007. Recall that no survey was conducted in July of 2003. Asterisks by the long-term averages of each prey group in July denote significant ($P < 0.05$) differences from the September diets. See text for details of diet groups.

	July					September				
	Amphipod	Decapod	Euphausiid	Fish	Other	Amphipod	Decapod	Euphausiid	Fish	Other
1997	0.6	53.7	1.0	43.8	0.8	20.4	3.4	41.1	31.5	3.6
1998	9.4	43.4	7.4	38.4	0.5	20.0	3.7	62.2	12.4	1.7
1999	7.6	66.0	3.3	21.8	1.3	31.3	3.7	46.9	14.8	3.4
2000	9.2	54.5	3.7	32.2	0.4	31.6	2.9	17.5	42.2	5.8
2001	12.8	40.3	9.9	35.9	1.1	17.9	5.9	58.5	16.1	1.6
2002	7.6	20.9	11.7	59.2	0.5	31.3	0.3	34.8	31.1	2.5
2003	-	-	-	-	-	60.5	6.2	10.1	16.7	6.5
2004	1.2	29.5	0.6	68.9	0.1	13.4	0.3	59.5	23.3	3.4
2005	26.6	58.7	2.3	12.4	0.1	30.4	10.3	39.9	7.9	11.6
2006	0.6	26.9	2.8	69.5	0.3	3.1	0.6	3.9	92.2	0.3
2007	6.6	79.6	0.9	10.0	2.9	31.8	1.1	9.13	56.1	1.9
Average (SD)	9.1* (7.61)	46.7* (19.54)	4.7* (3.99)	38.7 (22.69)	0.8* (0.91)	26.5 (14.63)	3.5 (3.08)	34.8 (21.57)	31.3 (24.76)	3.8 (3.14)

however, was the lack of differences in the proportions of dietary categories between the hatchery and wild coho salmon. The lack of significant differences in the percentage contribution of the major food groups to the two diets within each survey suggested that both groups of coho salmon tended to prey on the same species. Furthermore, while there was annual variation observed in the overall diets, the shifts and trends were the same between both groups.

In the September surveys, the individual coho salmon were much larger, having fork lengths an average of 36% greater than in the July surveys. Euphausiids and amphipods became the primary diet categories in September, with fish continuing as major contributors. The shift by juvenile coho salmon to euphausiids and amphipods in the late summer/early autumn may reflect the shift in physiological demands from a diet coupled to increasing overall size to one related to deposition of lipid/energy stores, as suggested by Beamish and Mahnken (2001). Caloric values in the literature suggest that euphausiids (3,111 Joules/g wet wt) and hyperid amphipods (3,952 cal/g dry weight) have more energy per gram than crab larvae (2,981 J/g wet wt) (Davis et al. 1998). However, we note that similar species in different regions and/or seasons may exhibit much different values. Furthermore, the amphipod composition in July diets from 1997–2007 was ~90% hyperids (range: 47.7–99.7%), whereas in September, gammarids comprised over 50% of the amphipod category (range: 27.5–65.5%) (data not shown).

Healey (1980) examined stomach contents in juvenile coho salmon in the Strait of Georgia in 1975 and 1976, using a purse seine (approximately 480 m x 48 m). The average fork lengths of the coho salmon in the 1975 study ranged from an average of 168 mm in June to 263 mm in September, well within the ranges observed for those same months in our study. Healey found that amphipods (type not noted), decapods (primarily crab megalops), and fish (predominantly unidentifiable fish remains, but also herring and sandlance) accounted for 26.6%, 28%, and 34.6%, respectively, of diet items in 1975 and 40.5%, 11% and 28.9% of the diet items, respectively, in 1976. Thus, both the major diet items and the large interannual variability of the diet items in his study were similar to the results from our study.

Size of juvenile hatchery-reared coho salmon entering the marine environment has been shown by many authors to be a critical factor in initial marine survival as well as adult returns (e.g., Bilton 1978; Bilton et al. 1982; Beamish and Mahnken 2001; Kallio-Nyberg 2004; Chittenden et al. 2008), and we have also reported strong correlations between the average size of both hatchery and wild coho salmon and the hatchery marine survival rates in the July surveys (Sweeting et al. 2003; Beamish et al. 2008). There is less information on the impact of size on wild coho survival rates (e.g. Holtby et al. 1990), but the data supports the advantage of size. Saloniemi et al. (2004) demonstrated that wild Atlantic salmon (*Salmo salar*) had higher survival rates of similar sized hatchery-reared progeny and that this was par-

ticularly greater in years of poor survival. The ‘advantage’ of size has been attributed to several wide-ranging impacts: increased hypo-osmoregulatory capacity, enhanced predator avoidance due greater swimming speeds, and wider ranges of prey prospects. In this study, the larger hatchery coho salmon did not possess significantly greater prey volumes in their stomachs in either the July or September surveys, indicating that the food available to the fish was accessed similarly by both groups. This held true even when the size effect was scaled using a stomach volume index. Due to the difficulty of weighing small amounts of stomach material while at sea, we utilized a volume/weight index. This index is similar to indices used in other studies (e.g., Armstrong et al. 2008; Boldt and Haldorson 2002; Brodeur et al. 2007), with similar results and conclusions. Also, there were no significant correlations between fish size and the proportion of any prey group in the diet (data not shown). Thus, the proposed difference in marine survival incurred by larger fish does not appear to be due to increased consumption rates (i.e., “appetite”) or prey choice (i.e., “diet”)

Another index of appetite, and perhaps survival, is the percentage of empty stomachs. The lack of differences observed between the two groups suggests that both hatchery and wild coho salmon were encountering and consuming food items equally. The range of empty stomach percentage observed in our studies (10–20% in July surveys, 5–35% in September surveys) are higher than earlier studies performed in the same study area (e.g., Landingham et al. 1998; Barraclough and Fulton 1968), but roughly similar to those noted for juvenile coho salmon by Brodeur et al. (2007) and Weitkamp and Sturdevant (2008) in other areas but over similar years. The larger percentage of empty stomachs observed in September surveys than in July surveys suggests that food becomes a limiting factor in the fall, and supports published models on the importance of overwinter survival (e.g., Beamish and Mahnken 2001).

In conclusion, a decade of examining stomach volumes and contents failed to demonstrate any significant differences between hatchery and wild juvenile coho salmon in either July or September in the Strait of Georgia, despite some clear differences in size between the two groups. While annual variability existed, hatchery and wild coho salmon tended to follow the same trends and shifts in diet. Seasonal variability in diet was significantly greater than annual shifts, and seemed to support the hypotheses of increased energy storage becoming more important than growth per se in the fall/winter months.

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Growth Rate Potential of Juvenile Chum Salmon on the Eastern Bering Sea Shelf: an Assessment of Salmon Carrying Capacity

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Abstract: Spatial and temporal variation in growing conditions for juvenile salmon may determine the survival of salmon after their first year at sea. To assess this aspect of habitat quality, a spatially explicit bioenergetics model was used to predict juvenile chum salmon (*Oncorhynchus keta*) growth rate potential (GRP) on the eastern Bering Sea shelf during years with cold and warm spring sea surface temperatures (SSTs). Annual averages of juvenile chum salmon GRP were generally lower among years and regions with cold spring SSTs. In addition, juvenile chum salmon GRP was generally higher in offshore than in nearshore regions of the eastern Bering Sea shelf during years with warm SSTs; however, the distribution (catch per unit effort) of juvenile chum salmon was not significantly ($P < 0.05$) related to GRP. Shifts from warm to cold SSTs in the northern region do not appear to affect summer abundance of juvenile Yukon River chum salmon, whereas the abundance of juvenile Kuskokwim River chum salmon drops precipitously during years with cold SSTs. From this result, we hypothesize that size-selective predation is highest on juvenile Kuskokwim chum salmon during cold years, but that predation is not as great a factor for juvenile Yukon River chum salmon. Although not addressed in this study, we also hypothesize that the smaller Yukon River chum salmon captured during years with cold SSTs likely incur higher size-selective mortality during winter.

Keywords: Bering Sea, juvenile chum salmon, growth rate potential, climate variability

INTRODUCTION

Larger juvenile Pacific salmon (*Oncorhynchus* spp.) during their first year at sea have a survival advantage over smaller juvenile salmon from the same cohort (Farley et al. 2007a). Ocean conditions are believed to play a pivotal role in constraining early marine growth of juvenile salmon. For instance, sized-based natural mortality of juvenile coho salmon (*O. kisutch*) was hypothesized to be linked to available nutrients regulating the food supply and hence competition for food (Beamish and Mahnken 2001). Farley et al. (2007b) suggested that bottom-up control of the trophic structure on the eastern Bering Sea (EBS) shelf affected the size and condition of juvenile sockeye salmon (*O. nerka*). Moss et al. (2005) found that juvenile pink salmon with an above-average growth trajectory during their first summer at sea had higher marine survival rates. Presumably, the above-average growth for juvenile pink salmon would occur during years with higher marine productivity. Thus, linking salmon prey demand to prey supply and their dependence on habitat could provide insight into the complex dynamics among marine productivity and growth and survival of salmon.

A leading hypothesis for ocean productivity on the EBS

shelf suggests that spring sea surface temperature (SST) affects prey availability to pelagic consumers. Specifically, cold spring temperatures negatively affect the productivity of prey (Hunt and Stabeno 2002), which will potentially impact salmon growth and survival. Seasonal sea ice extent and timing of ice retreat are believed to affect the timing, magnitude, and persistence of the spring phytoplankton bloom. When sea ice extends to the southern EBS shelf during March and April, an early and short-lived spring phytoplankton bloom occurs in cold water. Cold SST limits copepod growth (Coyle and Pinchuk 2002), thus much of the annual phytoplankton production sinks to the bottom of the ocean. Alternatively, when sea ice is absent during March and April, the bloom occurs substantially later in the season (May and June). The warmer temperatures and later bloom timing allow copepods to graze on phytoplankton, such that secondary production remains in the pelagic system. According to this hypothesis, zooplankton production during years with reduced sea ice (warm spring SST) is not limited by food availability, providing abundant prey for pelagic fish consumers.

To develop an understanding of the link between juvenile chum salmon prey demand and supply, we used a bioen-

ergetics model to estimate growth rate potential (GRP) over a 4-year period within the EBS shelf as a measure of habitat quality for juvenile chum salmon. The utility of applying bioenergetics models to examine juvenile salmon GRP in marine waters was discussed in Farley and Trudel (2009). Data on juvenile chum salmon and ocean conditions come from BASIS surveys conducted along the EBS shelf during mid-August to early October 2004 to 2007. Sea temperatures and ice extent on the shelf varied during this time period, with warm spring and summer SSTs and reduced sea ice extent during 2004 and 2005 and colder spring and summer SSTs and increased sea ice extent during 2006 and 2007.

Prior information on juvenile chum salmon size and diet data collected during research surveys along the EBS shelf (mid August to October 2000 to 2006) were reported in Farley et al. (in press). The results suggested that shifts in diet and size of juvenile chum salmon occurred between years with warm and cold spring SSTs. The juvenile chum salmon size and diet data presented here include one more year (2007) and are the focal data for the GRP models. We focus on 2004 to 2007 because during these years, the EBS shelf was consistently surveyed during the same time period, sampling the same station grid in the southern and northern EBS (Fig. 1). The EBS shelf was separated into northern and southern regions in order to address stock-specific differences in juvenile chum salmon because Yukon River juvenile

chum salmon are distributed in the northern EBS and juvenile Kuskokwim River chum salmon are distributed in the southeastern Bering Sea during fall (Farley et al. 2005). We report the diet and size data for these years; however, the objectives of this study were to compare juvenile chum salmon GRP among years with warm and cold spring SSTs and to examine whether GRP is a useful index of habitat quality for juvenile chum salmon on the EBS shelf. A bioenergetics model was used to test whether (1) GRP was significantly higher during years with warm spring sea temperatures; (2) salmon densities were positively related to GRP; and (3) larger, faster growing salmon occurred during years with higher GRP.

MATERIALS AND METHODS

Study Area and Sampling Protocols

Stations along the EBS shelf were sampled during August–September, 2004–2007 (Fig. 1). Juvenile chum salmon were collected following methods described in Farley et al. (2005). Fish were collected using a mid-water rope trawl that was 198 m long, with a typical spread of 55 m horizontally and 15 m vertically. The trawl is constructed with hexagonal mesh in the wings and body, and a 1.2-cm mesh liner in the codend. Trawl stations were located along longitudinal meridians spaced every 55.6 km (i.e., along longitudinal meridians at stations spaced every 30 degrees of latitude). The rope trawl was towed at 6.5 to 9.3 km/h with the head rope at or near the surface. Trawl stations were sampled during daylight hours (0730–2100, Alaska Daylight Savings Time) and all tows lasted 30 min and covered 2.8 to 4.6 km. A Seabird SBE-911 conductivity-temperature-depth (CTD) device was deployed at each station to measure the vertical profiles (from near bottom to surface) of ocean temperature. Observed SSTs at 5 m depth taken from CTD profiles were used for bioenergetics modeling. At each trawl station, juvenile chum salmon were selected at random (maximum 50) and standard biological attributes, including fork length (nearest 1.0 mm) and body weight (nearest 1.0 g) were measured on board.

Regions along the EBS shelf were defined as northern (stations sampled north of 60N, including stations sampled along 60N) and southern (stations sampled south of 60N).

Bioenergetics Model

GRP of juvenile chum salmon over the EBS shelf was estimated using the bioenergetics model developed by Ware (1978) with incorporated modifications to the model developed by Trudel and Welch (2005). This model was parameterized for sockeye salmon and accounts for optimal cruising speed:

$$G_{i,s} = \tau \cdot I_{i,s} - (SMR_{i,s} + ACT_{i,s}) \quad (1)$$

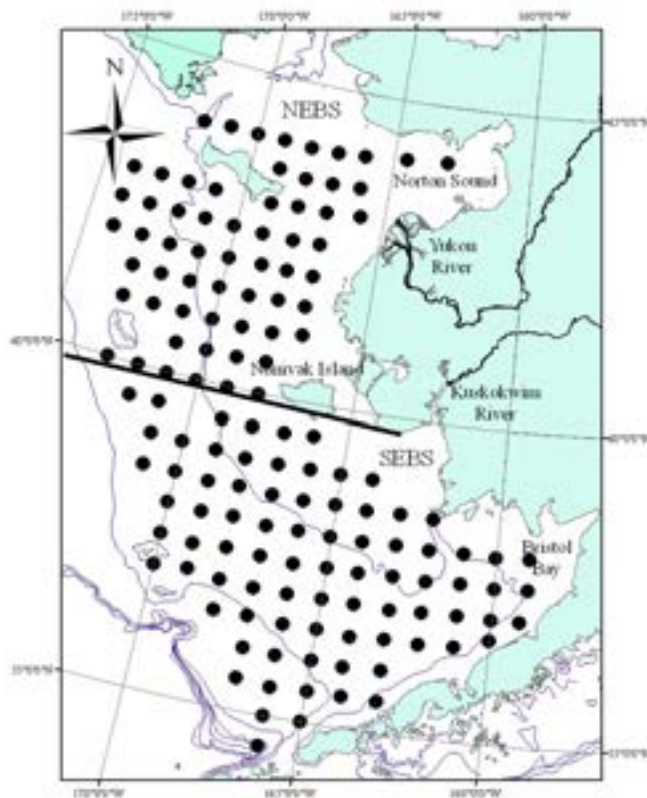


Fig. 1. Area surveyed for juvenile chum salmon during August–September 2004 to 2007, Bering-Aleutian Salmon International Survey (BASIS) research cruises.

where $G_{i,s}$ is the GRP (cal/s) for juvenile chum salmon during year i at station s , τ is the proportion of food that can be metabolized (Trudel and Rasmussen 2006), $I_{i,s}$ is the feeding rate (cal/s), $SMR_{i,s}$ and $ACT_{i,s}$ are, respectively, the standard metabolic rate (cal/s) and activity costs (cal/s). For simplicity, we assumed that τ was constant and not affected by water temperature (Table 1), as the sum of fecal and urinary losses and specific dynamic action is often nearly constant in bioenergetics models (Trudel and Rasmussen 2006).

The relationship between salmon feeding rate and prey density was assumed to be described by a type II functional response (Holling 1965; Ware 1978):

$$I_{i,s} = ED_{i,s} \cdot \frac{\rho_{i,s} \gamma_{i,s} U_{i,s}}{1 + \rho_{i,s} \gamma_{i,s} h_{i,s} U_{i,s}} \quad (2)$$

where ρ is prey density (g/cm³), γ is the cross-sectional area of the reactive field (cm²), U is the optimum swimming speed (cm/s), h is handling time of prey (s/g), and ED is sum of prey caloric content (cal/gwet), and was estimated as:

$$ED_{i,s} = \sum_{z=1}^p ED_{i,s,z} \quad (3)$$

where p = the number of prey species z . Consumption rates were equal to zero when no prey were available. The equations for handling time were developed in Farley and Trudel (2009):

$$h = \alpha_4 \bar{W}_i^{CB-1} \quad (4)$$

$$\alpha_4 = \frac{1}{CA \cdot f(T)} \quad (5)$$

where \bar{W}_i is the average chum salmon weight (g), CA and CB are, respectively, the weight coefficient and exponent for maximum feeding rate for chum salmon, and $f(T)$ is the Thornton and Lessem (1978) temperature-dependence function for cold-water fish species (see Table 1 for definition and parameters).

The energetic costs associated with the standard metabolic rates and activity costs of juvenile chum salmon were modeled using the empirical models derived by Trudel and Welch (2005). Specifically, standard metabolic rates were modeled as a function of weight and water temperature (°C):

$$SMR_{i,s} = \alpha_1 \bar{W}_i^\beta e^{\phi T_{i,s}} \quad (6)$$

where α_1 , β , and ϕ are regression coefficients (Table 1). Activity costs were modeled as a function of weight and swimming speed:

$$ACT_{i,s} = \alpha_0 \bar{W}_i^\delta U_{i,s}^\lambda \quad (7)$$

where α_0 , δ , and λ are regression coefficients (Table 1). We used the optimal cruising speed model derived by Trudel and

Welch (2005) to estimate the swimming speed of juvenile chum salmon (Table 1).

Prey Biomass

Gut contents from subsamples of juvenile chum salmon at each trawl station were analyzed to characterize prey consumption (Fig. 2). Prey analyses determined that the following prey items were important for juvenile chum salmon (those with percent wet weight greater than 5%): pagurids (northern region only), *Oikopleura* spp., euphausiids, cnidaria, brachyura, amphipods, and fish including age-0 wall-eye pollock (*Theragra chalcogramma*) and Pacific sand lance (*Ammodytes hexapterus*). The typical size ranges of age-0 pollock and sand lance in the diets of juvenile chum salmon were between 28 to 67 mm total length (TL) and 55 to 80 mm fork length (FL), respectively. Prey that were less than 5% wet weight were lumped into “other fish” and “other zoop” categories.

Fish prey density (g/cm³) at each station was determined as:

$$\rho_{i,s} = \sum_{z=1}^f \frac{N_{i,s,f} \cdot \theta \cdot \bar{W}_f}{\phi \cdot V_{i,s}} \quad (9)$$

where $N_{i,s,f}$ is the number of prey (f = age-0 pollock or sand lance) caught in the trawl at each station, θ is the proportion of prey items captured in trawls that fell within the size range that juvenile chum salmon fed upon (dimensionless), \bar{W}_f is the average weight (g) for each prey item, ϕ is the catchability coefficient (dimensionless), and $V_{i,s}$ is the volume sampled at each station (cm³). Volume sampled at each station was estimated by multiplying the distance trawled (cm) by the vertical (cm) and horizontal (cm) spread of the net opening. The catchability coefficient ($\phi = 0.016$) for age-0 pollock and sand lance was determined following methods described in Farley and Trudel (2009).

The average weight of these prey was 1.7 g for age-0 pollock and 1.2 g for sand lance. Laboratory analyses of subsamples of age-0 pollock taken during the 2005 survey indicated that the average caloric content was 4,424 cal/gdry; caloric content for Pacific sand lance (4,209 cal/gdry) was obtained from Robards et al. (1999). The estimates of catchability, proportion of prey items, caloric content, and weight were held constant for each station, among years.

Zooplankton prey were collected using a 65-cm bongo sampler with 505-micron mesh net. The net was towed obliquely to near bottom (max 200 m depth) and the volume of water flowing through the net was measured using a General Oceanics 2030R flowmeter. Zooplankton samples were preserved in a buffered-formalin (5%) solution and processed at the University of Alaska Fairbanks laboratory.

Zooplankton prey density (g/cm³) at each station was determined as:

Table 1. Definitions of symbols used in the text. Note that subscripts *i* and *s* represent year (*i* = 2004 to 2007) and station and overbars denote mean quantities within the definitions of *i*.

Symbol	Parameter description	Value	Source
<i>ACT</i>	Activity costs (cal/s)		
<i>E</i>	Total energy content of juvenile chum salmon (cal)		
<i>ED_f</i>	Caloric content of juvenile salmon (cal/g _{wet})	1,176	2
<i>ED₁</i>	Caloric content of age-0 pollock (cal/g _{wet})	885	2
<i>ED₂</i>	Caloric content of sand lance (cal/g _{wet})	842	2
<i>ED_{is}</i>	Weighted average of caloric content of juvenile salmon prey at year <i>i</i> and stations <i>s</i> (cal/g _{wet})		
<i>G</i>	Growth rates (cal/s)		
<i>I</i>	Feeding rates (cal/s)		
<i>N</i>	Number of prey caught at a station		
<i>SMR</i>	Standard metabolic rates (cal/s)		
<i>T</i>	Sea surface temperature (°C; 5m below surface)		
<i>V</i>	Volume sampled by the net (cm ³)		
<i>W</i>	Chum salmon weight (g)		
<i>W_p</i>	Prey weight (g)		
<i>ϕ</i>	Catchability coefficient of the net (dimensionless)	0.016	7
<i>τ</i>	Proportion of food that can be metabolized (dimensionless)	0.7	1
<i>θ</i>	Proportion of prey items captured in the net that is within the size range that juvenile salmon fed upon (dimensionless)		
Consumption:			
$I = \frac{\rho\gamma U}{1 + \rho\gamma h U}$			
<i>ρ</i>	Prey density (cal/cm ³)		
<i>γ</i>	Cross-sectional area of the reactive field (cm ²)		
<i>U</i>	Swimming speed (cm/s)		
<i>h</i>	Handling time (s/cal)		
Cross-sectional area of the reactive field:			
$\gamma = \alpha_3 \cdot W^{\beta_3}$			
<i>α₃</i>	Intercept (cm ²)	1	1
<i>β₃</i>	Coefficient, <i>γ</i> versus <i>W</i>	0.69	1
Handling time:			
$h = \frac{W^{CB-1}}{ED_p \cdot CA \cdot f(T)}$			
<i>CA</i>	Intercept for maximum feeding rates (g/s)	4.56 E-06	5
<i>CB</i>	Allometric exponent of maximum feeding rate	-0.275	5
<i>f(T)</i>	Temperature adjustment for maximum food consumption rates		

Table 1 (continued).

Symbol	Parameter description	Value	Source
Temperature adjustment function:			
$f(T) = K_a \cdot K_b$			
$K_a = \frac{(0.58 \cdot L1)}{1 + 0.58 \cdot (L1 - 1)}$			
$L1 = \exp(G1 \cdot (T - 3))$			
$G1$			
$K_b = \frac{(0.5 \cdot L2)}{1 + 0.5 \cdot (L2 - 1)}$			
$L2 = \exp(G2 \cdot (24 - T))$			
$G2$			
Standard metabolic rates*:			
$SMR = \alpha_1 \cdot W^\beta \cdot e^{\varphi \cdot T}$			
α_1	Intercept (cal/s)	4.76×10^{-5}	4
β	Coefficient, SMR versus W	0.87	4
φ	Coefficient, SMR versus T (1/°C)	0.064	4
Swimming costs*:			
$ACT = \alpha_0 \cdot W^\delta \cdot U^\lambda$			
α_0	Intercept (cal·s ⁻¹)	1.74×10^{-6}	4
δ	Coefficient, ACT versus W	0.72	4
β_3	Coefficient, ACT versus U	1.6	4
Swimming speed:			
$U = \omega \cdot W^v \cdot \exp^{\kappa \cdot T}$			
ω	Intercept (cm/s)	11.1	4
v	Coefficient, U versus W	0.097	4
κ	Coefficient, U versus T (1/°C)	0.040	4

1. Ware (1978); 2. This study; 3. Beauchamp et al. (1989); 4. Trudel and Welch (2005); 5. Davis et al. (1998); 6. Moss and Farley (unpubl. data); 7. Farley and Trudel (in press).

*The oxygen consumption rates were converted from mg O₂/h to cal/s using an oxy calorific equivalent to 3.24 mg O₂/cal (Elliott and Davison 1975).

$$\rho_{i,s} = \sum_{z=1}^p N_{i,s,z} \cdot \bar{W}_{i,s,z} \tag{10}$$

where $N_{i,s,z}$ and $\bar{W}_{i,s,z}$ are the number and average weight of zooplankton species z ($z = 1$ to p) at station s during year i .

GRP (cal/s) was converted to cal/d by multiplying $I_{i,s}$ by the number of seconds in a 15-hour day (estimated time juvenile chum salmon spend feeding per day during August and September) and by multiplying $SMR_{i,s}$ and $ACT_{i,s}$ by the

number of seconds in a 24-hour day.

Estimated daily GRP (cal/d) at each station s was then expressed as a percentage of body weight (% body weight/d) for each station s by dividing estimated daily GRP (cal/d) by the total energy per fish (cal) as in Perry et al. (1996):

$$\bar{E}_{i,s} = ED_f \cdot \bar{W}_i \tag{11}$$

where $\bar{E}_{i,s}$ is the average total energy per fish (cal), ED_f is the

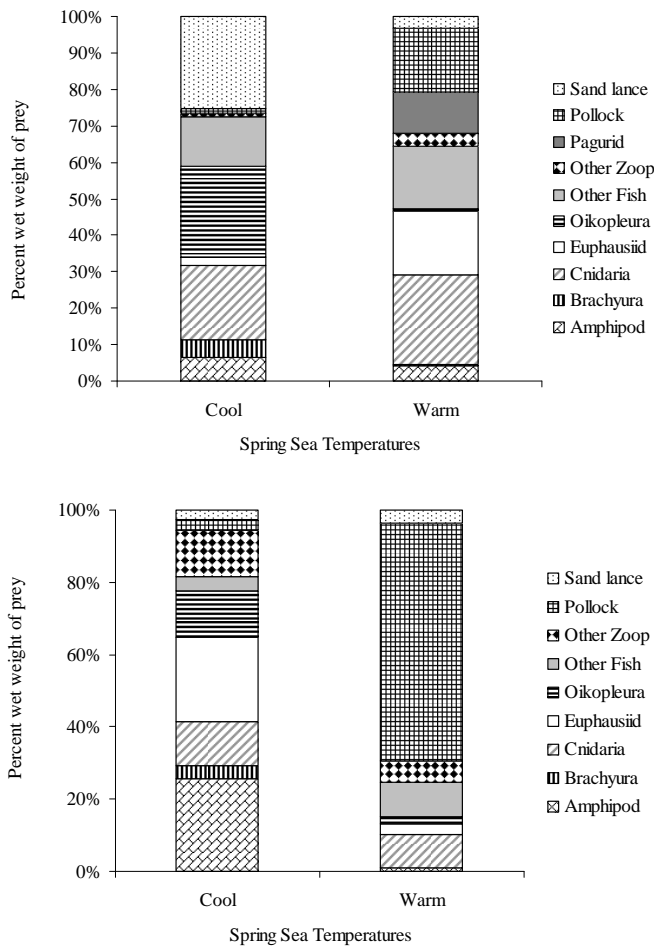


Fig. 2. Juvenile chum salmon prey composition (percent wet weight) in the northern (upper) and southern (lower) regions of the eastern Bering Sea shelf during warm (August to October, 2004 and 2005) and cold (August to October 2006 and 2007) years.

caloric content in juvenile chum salmon ($\text{cal/g}_{\text{wet}}$), and \bar{W}_i is the average weight (g) of juvenile chum salmon. Annual averages of juvenile chum salmon weight were used as opposed to average weight of these fish at each station because there were stations within a year where no juvenile chum salmon were caught. The caloric content of juvenile chum salmon was determined from subsamples of the juvenile chum salmon caught during the 2004 and 2005 (no data available for 2006 and 2007) surveys using bomb calorimetry and averaged $5,107 \text{ cal/g}_{\text{dry}}$. (There was no significant difference in average caloric content of juvenile chum salmon between years; ANOVA- Fixed effect, $F = 1.0$, $P = 0.32$). The units ($\text{cal/g}_{\text{dry}}$) were converted to ($\text{cal/g}_{\text{wet}}$) by multiplying $5,107 \text{ cal/g}_{\text{dry}}$ by 23% ($W_{\text{dry}}/W_{\text{wet}}$), the average value obtained from the subsample (2004 to 2005) of juvenile chum salmon dried for the bomb calorimetry process. These estimates of growth (% body weight/d) were considered to be juvenile chum salmon GRP on the EBS shelf and were the primary statistic used in subsequent models.

Spring SSTs

Spring SSTs ($^{\circ}\text{C}$) during May 2002 to 2008 in the southeastern Bering Sea are shown in Fig. 3. Mean May SSTs were averaged over $54^{\circ}18' \text{ N}$ to $60^{\circ}0' \text{ N}$, $161^{\circ}12' \text{ W}$ to $172^{\circ}30' \text{ W}$ (data from www.beringclimate.noaa.gov). Index values were calculated as the deviations from the mean May SST value (2.33° C) for the 1970–2000 period divided by the standard deviation (0.76° C). Years with cold SSTs were defined as those years when the index values of SSTs were at or below 0 (2006 to 2008); years with warm SSTs were defined as those years when the index values of SSTs were above 0 (2002 to 2005).

Model Applications

The bioenergetics model was used to test the following hypotheses:

Hypothesis 1: GRP is significantly higher during years with warm spring temperatures. This hypothesis was tested using two-way analysis of variance (ANOVA-Fixed Effect) with S-plus software (Insightful 2001) where year (2004 to 2007) and region (northern and southern) were the categorical variables and GRP was the dependent variable. These data were also pooled by oceanographic domain (see Kinder and Schumacher 1981) and two-way ANOVA was used to test for significant differences between nearshore (coastal domain – depths $< 50 \text{ m}$; well-mixed vertical structure, low salinity, warm water temperature, low stratification) and off-shore (middle domain – depths $> 50 \text{ m}$ and $< 100 \text{ m}$; strong two-layer vertical structure, moderate salinity, high stratification) domains within each region (northern and southern) among years. If a significant difference ($P < 0.05$) occurred, a Sidak multiple comparison test was used to calculate the 95% ($\alpha = 0.05, 0.01, 0.001$) confidence intervals for all pairwise differences between the dependent variable means (Insightful 2001). The level of significance between the pairwise differences was determined by examining those confidence intervals that excluded zero for the three values of alpha.

Hypothesis 2: Juvenile chum salmon are distributed in areas of high GRP on the EBS shelf. Within each region, regression analysis was used to examine the relationship between $\text{GRP}_{i,s}$ and catch per unit effort ($\text{CPUE}_{i,s}$ – defined as the number of juvenile salmon caught during a 30-min trawl haul during year i at station s and hereon referred to as relative abundance). The natural logarithm of ($\text{CPUE}_{i,s} + 1$) was used to reduce the wide variability in $\text{CPUE}_{i,s}$. Year was used as a factor within the regression analysis and an interaction between relative abundance and year was included to account for year effects. Juvenile chum salmon GRP and relative abundance were also compared graphically by year to provide perspective on the distribution of juvenile chum salmon in relation to regions of high and low GRP on the EBS shelf.

Hypothesis 3: Juvenile chum salmon size and growth

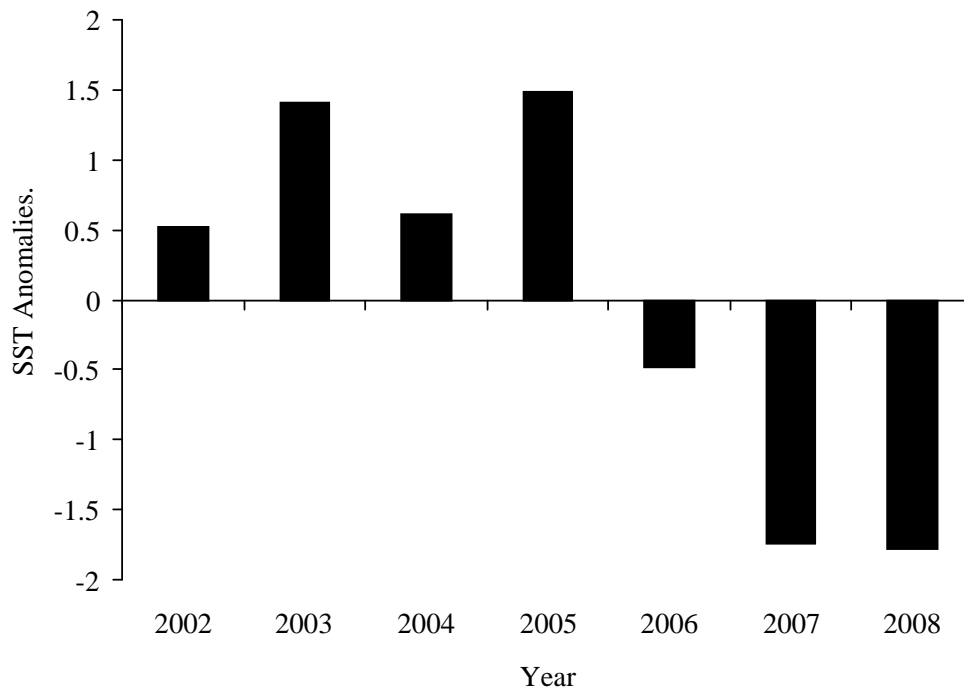


Fig. 3. Anomalies of sea surface temperatures (bar, SSTs, °C) during May 2002 to 2008 in the southeastern Bering Sea (data obtained from <http://www.beringclimate.noaa.gov>). Mean May SSTs are averaged over the area 54°18' N to 60°0' N, 161°12' W to 172°30' W using data from the National Centers for Environmental Protection and the National Center for Atmospheric Research (NCEP/NCAR) reanalysis project (Kalnay et al. 1996). The anomalies are the deviations from the mean May SST value (2.33° C) for the 1970–2000 period normalized by the standard deviation (0.76° C).

rates were significantly higher during years with higher GRP. Differences in annual length within region were determined using two-way ANOVA where year was the categorical variable and length was the dependent variable. Because GRP was generally higher during years with warm spring SST (2004 and 2005) than during years with cold SST (2006 and 2007), the length data were pooled into warm and cold years within each region. Growth rate (mm/day) within each region for warm and cold years was estimated from the slope of the regression of Day of Year on length (dependent variable). The difference in slopes between warm and cold years within each region was determined using analysis of covariance.

RESULTS

Hypothesis Tests

Hypothesis 1: In general, mean annual GRP was positive during 2004 and 2005 and negative during 2006 and 2007 in both regions (Table 2). Juvenile chum salmon GRP differed significantly among years in the northern (ANOVA; $f_{[3,154]} = 43.31$, $P < 0.001$) and southern (ANOVA; $f_{[3,331]} = 40.09$, $P < 0.001$) regions. In the northern region, the pairwise comparison among years indicated that average GRP was significantly higher during 2004 than 2006 and 2007 ($P < 0.001$) and GRP was higher during 2005 than 2006 ($P <$

0.001) and 2007 ($P < 0.01$). Average GRP was also higher during 2004 than 2005 ($P < 0.001$). In the southern region, GRP was significantly higher during 2004 and 2005 than during 2006 and 2007 ($P < 0.001$). These analyses indicate that juvenile chum salmon GRP was higher during warm than cold years in both regions of the EBS.

In the northern region, juvenile chum salmon GRP was positive in the middle domain during all years except 2007 and negative during all years except 2004 in the coastal domain (Table 3). Juvenile chum salmon GRP differed significantly among domains (ANOVA; $f_{[7,288]} = 1814.1$, $P < 0.001$), year (described above) and the interaction between domain and year in the southern region ($P < 0.001$), whereas only the domain (ANOVA; $f_{[7,150]} = 520.6$, $P < 0.001$) and year (described above) were significant and not the interaction term ($P = 0.40$) in the northern region. In the southern region, the middle domain had significantly higher GRP than the coastal domain during all years (2005 and 2006, $P < 0.001$; 2007, $P < 0.05$) except 2004. Juvenile chum salmon GRP in the coastal domain of the southern region was significantly higher during 2004 than all other years ($P < 0.001$). In the middle domain of the southern region, juvenile chum salmon GRP was significantly higher during 2004 and 2005 than 2006 and 2007 ($P < 0.001$).

Hypothesis 2: Relative abundance of juvenile chum salmon was highest during the warm years of 2004 and 2005 in the southern region, whereas relative abundance increased

Table 2. Annual averages (\pm SE) of juvenile chum salmon growth rate potential (GRP; % body weight per day) during mid-August – mid-September (southern region) and mid-September to early October (northern region) 2004 to 2007 along the eastern Bering Sea shelf. The number of stations (N) is included.

Year	Northern			Southern		
	N	GRP	SE	N	GRP	SE
2004	42	2.90	0.18	82	3.37	0.20
2005	38	0.58	0.44	81	3.01	0.45
2006	42	-1.04	0.32	89	-0.17	0.30
2007	37	-1.78	0.30	83	-0.25	0.25

Table 3. Annual averages (\pm SE) of juvenile chum salmon growth rate potential (GRP; % body weight per day) within the coastal and middle domains during mid-August – mid-September (southern region) and mid-September to early October (northern region) 2004 to 2007 along the eastern Bering Sea shelf. The number of stations (N) is included.

Region	Year	Coastal			Middle		
		N	GRP	SE	N	GRP	SE
Northern							
	2004	33	2.65	0.21	9	3.81	0.18
	2005	27	-0.16	0.40	11	2.39	0.97
	2006	35	-1.39	0.28	6	0.99	1.21
	2007	32	-1.95	0.25	5	-0.72	1.61
Southern							
	2004	28	2.95	0.37	47	3.75	0.18
	2005	25	-0.12	0.73	46	4.49	0.48
	2006	23	-2.00	0.22	56	0.75	0.40
	2007	27	-1.06	0.31	44	0.55	0.36

Table 4. Annual averages (\pm SE) of juvenile chum salmon length (mm) during mid-August – mid-September (southern region) and mid-September to early October (northern region) 2004 to 2007 along the eastern Bering Sea shelf. The number of juvenile chum salmon sampled (N) is included.

Year	Northern			Southern		
	N	Length	SE	N	Length	SE
2004	471	205.6	0.97	844	179.9	0.79
2005	253	199.6	1.11	649	172.5	0.88
2006	576	156.2	0.57	30	179.9	3.02
2007	755	193.5	0.90	577	178.1	1.57

during the cold years of 2006 and 2007 in the northern region (Fig. 4). The regression of GRP and relative abundance indicated that the relationship was not significant in either the northern ($P = 0.30$) or southern regions ($P = 0.30$). These results show that juvenile chum salmon were not distributed in areas of highest GRP during any year. As shown in Fig. 5, the highest catch of juvenile chum salmon generally occurred in water depths < 50 m (coastal domain), an area where GRP was generally at or below zero (Table 3). Areas with the highest GRP occurred offshore in deeper water during each year (middle domain; Table 4); however, the offshore area tended not to have many juvenile chum salmon, especially

during the cold years of 2006 and 2007.

Hypothesis 3: Juvenile chum salmon length differed significantly among years in the northern (ANOVA; $f_{[3,2051]} = 623.13$, $P < 0.001$) and southern (ANOVA; $f_{[3,2096]} = 9.32$, $P < 0.001$) regions (Table 4). In the northern region juvenile chum salmon were significantly larger during 2004 and 2005 than during 2006 and 2007 ($P < 0.001$). In addition, juvenile chum salmon were significantly larger during 2004 than 2005 ($P < 0.01$) and during 2007 than 2006 ($P < 0.001$). In the southern region, juvenile chum salmon were significantly smaller during 2005 than during 2004 ($P < 0.001$) and 2007 ($P < 0.01$). These results indicate that juvenile chum

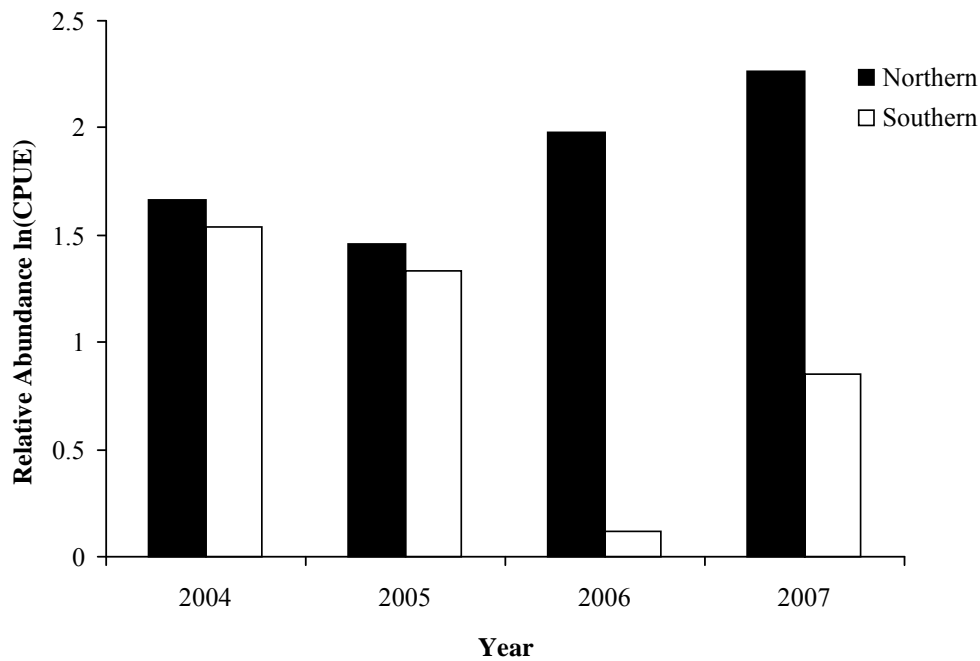


Fig. 4. Relative abundance (natural logarithm of catch per unit effort defined as the number of juvenile chum salmon captured in a 30-min surface trawl) of juvenile chum salmon in the northern (solid bar) and southern (clear bar) regions of the eastern Bering Sea during 2004 to 2007.

salmon were significantly larger during warm years within the northern region, but not within the southern region.

Juvenile chum salmon growth rates were significantly lower ($P < 0.001$) in the northern region during warm years (slope = 0.27 mm/day; regression statistics: $F = 5.73$, deg (1, 722), $P = 0.02$) as opposed to cold years (slope = 2.53 mm/day; regression statistics: $F = 1384$, deg (1, 1329), $P < 0.001$). Growth rates of juvenile chum salmon in the southern region were also significantly higher ($P < 0.001$) during cold years (slope = 1.27 mm/day; regression statistics: $F = 1533$, deg (1, 1491), $P < 0.001$) than warm years (slope = 1.53 mm/day; regression statistics: $F = 978.3$, deg (1, 605), $P < 0.001$).

A schematic of these results is shown in Table 5 for reference.

DISCUSSION

Our findings suggest a possible connection between GRP of juvenile chum salmon during late summer - early fall and spring SSTs along the EBS shelf. On average, salmon GRP was lower during years with cold rather than warm spring SSTs (supporting Hypothesis 1). However, juvenile chum salmon were not distributed in areas of highest GRP on the EBS shelf. In the southern region, many juvenile chum salmon were distributed in water depths < 50 m (coastal domain), areas on the shelf with significantly lower GRP (opposing Hypothesis 2). Juvenile chum salmon were larger during years with warm rather than cold SSTs in the northern region, but not so in the southern region. In addition, growth rate of juvenile chum salmon was significantly higher during

cold rather than warm years in both regions (opposing Hypothesis 3). Juvenile chum salmon were also more abundant during cold years in the northern region, but relative abundance in the southern region declined dramatically during cold years.

The critical-size and critical-period hypothesis for juvenile salmon suggests two periods of high mortality linked to the size (growth rate) of juvenile salmon. The first stage may occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker 1968; Willette et al. 1999). The second stage is thought to occur following the first summer at sea, when smaller individuals may not have sufficient energy reserves to survive late fall and winter conditions (Beamish and Mahnken 2001). In our study, juvenile chum salmon were collected at the end of the first summer's growing season. We found that in the southern region, juvenile chum salmon were similar in size among years but their relative abundance dropped dramatically during cold years. These results suggest that perhaps smaller, slower growing individuals during years with lower GRP experienced higher size-selective mortality early in their marine residence. In the northern region, size-selective mortality does not appear to take place during early marine residence. In this case, years with lower GRP had higher relative abundance, suggesting that predation is minimal in the northern regions during years with cold SSTs. However, it is possible that these smaller individuals may experience higher size-selective mortality during their first winter at sea, thus reducing survival later in their marine life history (see Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007b).

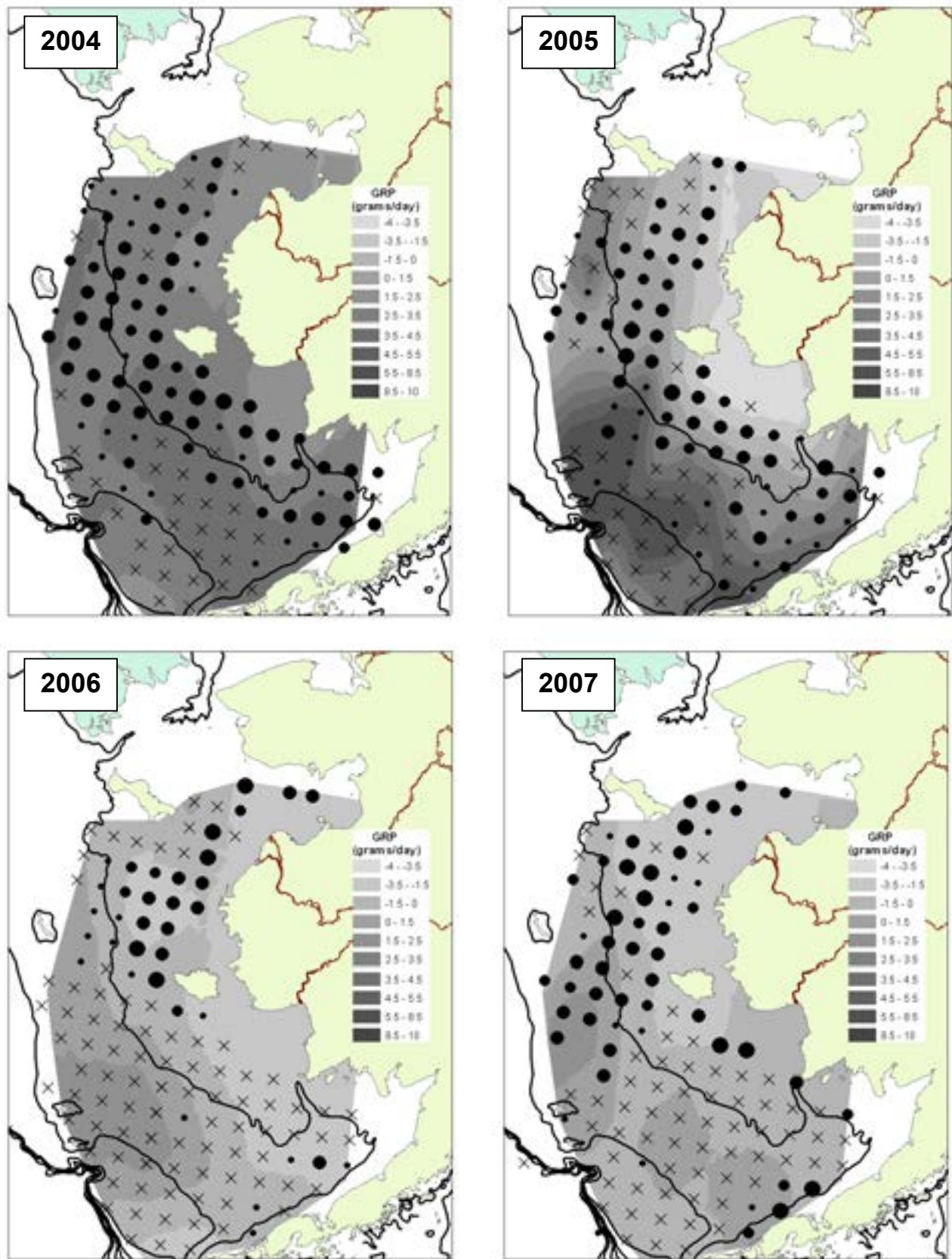


Fig. 5. Contour plot of juvenile chum salmon growth rate potential (GRP; % body weight per day) in relation to the natural logarithm of catch per unit effort of juvenile chum salmon captured in 2004 - 2007.

Table 5. Summary of the hypothesis tests for juvenile chum salmon growth rate potential (GRP), catch per unit effort (CPUE), fork length (FL), and growth rate (GR) within the northern and southern regions of the Bering Sea during years with warm (2004 and 2005) and cold (2006 and 2007) sea surface temperatures. Dash (-) indicates no difference in hypothesis test between warm and cold years.

Region	Hypothesis	Warm	Cold
Northern	GRP	High	Low
	CPUE	Low	High
	FL	Small	Large
	Growth Rate	Low	High
Southern	GRP	High	Low
	CPUE	High	Low
	FL	-	-
	Growth Rate	Low	High

We found that juvenile chum salmon growth rates were higher in both regions during years with cold SSTs and reduced GRP. These results appear to be at odds with similar studies of juvenile chum salmon in coastal waters that found that higher growth rates occurred during years with warmer SSTs (Karpenko 1987; Kawamura et al. 2000). We note that juvenile chum salmon were significantly larger during warm years than cold years in the northern region. As marine survival is a function of size for juvenile salmon, perhaps the smaller juvenile salmon dedicated more energy to growth during the latter part of their first summer's growing season. In the southern region, it is likely that smaller, slower growing juvenile chum salmon were not surviving, thus only the faster growing individuals of the population were surveyed. This result is supported by the fact that the relative abundance of juvenile chum salmon in the southern region was much less during years with cold SSTs when compared to years with warm SSTs.

Our goal was to use GRP as an indicator of habitat quality during years with cold and warm spring SSTs rather than to provide precise quantitative estimates of growth rates for juvenile chum salmon. For instance, juvenile chum salmon GRP was negative during some years and shelf habitats indicating that these salmon may be losing rather than gaining weight. The annual estimates of juvenile chum salmon average GRP varied from -1.78% to 3.37% body weight per day for fish that ranged in length between 156 mm to 205 mm FL. Smaller juvenile chum salmon (41 mm FL) fed a varying ration of prey items in an experimental holding tank gained an average of 5.4% body weight (g) per day (LeBrasseur 1969). Larger juvenile chum salmon (90 mm to 160 mm FL) captured in coastal waters off Vancouver Island, British Columbia, Canada, attained daily growth rates between 0.34% to 3.28% (Perry et al. 1996). Juvenile salmon growth rate is size-dependent, and daily growth rate decreases as the fish get larger (Brett 1974). Thus, our highest GRP estimates may not be out of line with experimental estimates, and seem to be in line with marine research estimates of juvenile chum salmon daily growth rate.

Bioenergetics models are particularly sensitive to changes in energy density, composition of stomach contents, and biomass of potential prey (Beauchamp et al. 1989). Our estimates of available prey biomass were generated using a number of assumptions that could potentially lead to a bias of under-over-estimating the number of dominant prey (age-0 pollock and Pacific sand lance) available to juvenile chum salmon on the EBS shelf. For instance, euphausiids make up 20% of juvenile chum salmon diet by wet weight in the southern EBS during cold SST years, yet the bongo nets used to sample these important prey items typically underestimate euphausiids (Ken Coyle, University of Alaska Fairbanks, Fairbanks, AK, pers. comm.), thereby lowering biomass estimates of euphausiids used in GRP models. Thus, the most plausible explanation for negative GRP is that our estimates of prey biomass were biased low. However, because we maintained these assumptions for all years, comparisons of the relative differences in juvenile salmon GRP would likely provide robust estimates of changes in juvenile chum salmon GRP among the years examined.

Juvenile chum salmon GRP was estimated using average caloric content of juvenile chum salmon collected during 2004 and 2005 (warm years). Caloric content of juvenile chum salmon was not available during 2006 and 2007 (cold years). Decreasing the caloric content of juvenile chum salmon increases their estimated GRP. Thus, if caloric content of juvenile chum salmon were lower during cold years, our estimates of juvenile chum salmon GRP could be biased low. However, a recent paper comparing differences in caloric content of age-0 fish on the EBS found that the caloric content of these fish was significantly higher during years with cold SSTs (Moss et al. 2009). Thus, it is likely that juvenile chum salmon caloric content could have been higher during years with cold SSTs, suggesting that our estimates of juvenile chum salmon GRP are biased high.

Our study provides evidence that energetic limitation influences habitat quality on the EBS shelf for juvenile chum salmon during years with cold spring SSTs. Declining GRP in coastal waters is one possible reason why juve-

nile chum salmon begin to migrate offshore and away from shelf habitats. Our study also highlights differing responses of Yukon vs. Kuskokwim River juvenile chum salmon to changing ecosystem states. For instance, shifts from warm to cold SSTs in the northern region do not appear to affect summer abundance of juvenile Yukon River chum salmon, whereas the abundance of juvenile Kuskokwim River chum salmon drops precipitously during years with cold SSTs. From this result, we hypothesize that size-selective mortality from marine entry to late summer is highest in juvenile Kuskokwim chum salmon during cold years, but that size-selective mortality during early marine life is not a factor for juvenile Yukon River chum salmon. Although not addressed in this study, we hypothesize that the smaller Yukon River chum salmon captured during years with cold SSTs and lower GRP likely incur higher size-selective mortality during winter. As such, this work is an instructive case study and is a framework for future research on juvenile salmon energetics in large marine ecosystems.

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Climate, Growth and Population Dynamics of Yukon River Chinook Salmon

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Abstract: Harvests of Yukon Chinook salmon increased in the mid-1970s, then declined during 1998 to 2007 in response to fewer returning salmon. We examined annual growth of age-1.3 and age-1.4 Yukon Chinook salmon scales, 1965–2004, and tested the hypothesis that shifts in Chinook salmon abundance were related to annual growth at sea. Annual scale growth trends were not significantly correlated with salmon abundance indices, sea surface temperature, or climate indices, although growth during the first year at sea appeared to have been affected by the 1977 and 1989 ocean regime shifts. Chinook salmon scale growth was dependent on growth during the previous year, a factor that may have confounded detection of relationships among growth, environmental conditions, and abundance. Scale growth during the second year at sea was greater in odd-numbered years compared with even-numbered years, leading to greater adult length of age-1.3 salmon in odd-numbered years. The alternating-year pattern in Chinook salmon growth was opposite that observed in Bristol Bay sockeye salmon, and it may be related to the higher trophic level of Chinook salmon and indirect competition with pink salmon. This finding highlights the need to investigate alternating-year patterns in salmon growth, prey abundance, and factors that influence these patterns, such as pink salmon.

Keywords: Yukon River, Chinook salmon, growth, abundance, climate, scales

INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) returning to western Alaska represent a major proportion of wild Chinook salmon in North America and Asia. Average harvest (commercial and subsistence) of Chinook salmon in western Alaska, which includes Bristol Bay and the Arctic-Yukon-Kuskokwim (AYK) region, averaged approximately 0.9 ± 0.2 million (SD) salmon per year during 1981–2004 (e.g., Eggers et al. 2005; JTC 2008; Whitmore et al. 2008). However, harvests of Chinook salmon have undergone substantial shifts during the past 40 years. For example, harvests of Yukon and Kuskokwim Chinook salmon (two major stocks) tended to be low during the 1960s through the mid 1970s, high from the late 1970s through the mid 1990s, and low from the late 1990s through the mid 2000s (Fig. 1). These harvest patterns appear to be related to the 1977 ocean regime shift (Hare and Mantua 2000) and the 1997 El Niño (Kruse 1998) that influenced many marine species in the Bering Sea and North Pacific Ocean. Harvests of chum (*O. keta*) and coho salmon (*O. kisutch*) also declined in the late 1990s (AYK SSI (Arctic – Yukon – Kuskokwim Sustainable

Salmon Initiative) 2006). The recent decline in harvests triggered multiple “disaster” declarations for this region by state and federal governments because salmon are highly important for subsistence fisheries and the economy of this region (www.aykssi.org/Home.htm).

Growth of salmon is believed to be an important factor influencing survival (Beamish et al. 2004; Farley et al. 2007). Furthermore, annual scale growth measurements of Bristol Bay and Chignik sockeye salmon (*O. nerka*) since the 1950s provided evidence that greater early marine growth was a key mechanism that influenced the doubling of Alaska sockeye salmon abundance after the 1977 ocean regime shift (Ruggerone et al. 2005, 2007a). Survival of Chinook salmon has also been linked to the alternating-year pattern of pink salmon (*O. gorbuscha*) abundance (Grachev 1967; Ruggerone and Goetz 2004; Ruggerone and Nielsen 2004).

In this investigation, we examined trends in annual scale growth of Yukon River Chinook salmon from 1965 to 2004. Salmon scales are known to be correlated with salmon body size (Clutter and Whitesel 1956; Henderson and Cass 1991; Fukuwaka and Kaeriyama 1997; Ruggerone et al. 2009). We tested the following hypotheses:

- 1) Harvests of Yukon Chinook salmon were associated with annual growth in fresh water and/or in the ocean;
- 2) Growth of Chinook salmon was associated with major ocean-climate events, i.e., the 1977 and 1989 ocean regime shifts and the 1997 El Niño event;
- 3) Growth of Chinook salmon at sea exhibited an alternating-year pattern that may be associated with Asian pink salmon abundance; and
- 4) Annual growth of Chinook salmon was dependent on the previous year's growth.

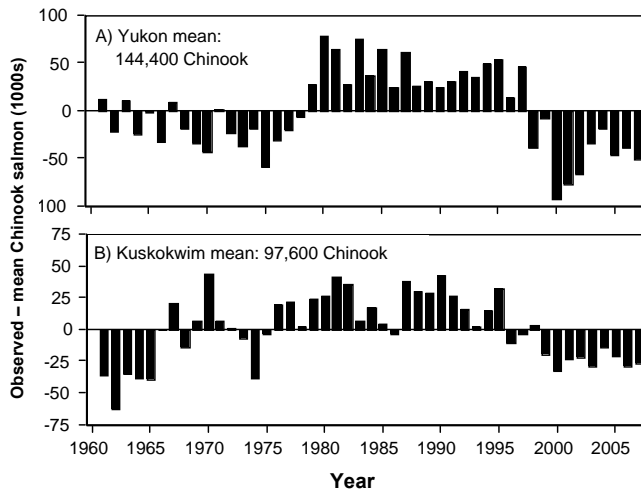


Fig. 1. Catch trends of Yukon and Kuskokwim Chinook salmon, 1961–2007. Values are total catch (subsistence, commercial, sport, personal use). Data sources: Ruggerone et al. 2007b; JTC 2008; Whitmore et al. 2008.

MATERIALS AND METHODS

Scale Collection and Measurements

Scales from adult Chinook salmon from the Yukon River were obtained from the Alaska Department of Fish and Game (ADFG) archive in Anchorage, Alaska. Yukon River scales have been collected annually since 1965 for quantifying age composition. As a means to minimize year-to-year variability in scale growth caused by size-selective gillnets, we selected scales for measurement only when they were from Chinook salmon captured with large mesh (8.5 inch stretched measure) set gillnets (commercial or test fisheries) located in the lower river (river km 20–30). Only scales collected in June and July were measured to ensure fish were from the same stocks.

We measured approximately 50 scales from each of the two dominant Chinook age groups (1.3 and 1.4) or ~100 scales per year. These fish spent one winter in fresh water and three (age-1.3) or four (age-1.4) winters in the ocean. Scales were selected for measurement only when: 1) we agreed with the age determination previously made by ADFG, 2) the scale shape indicated that the scale was removed from

the preferred area (Koo 1962), and 3) circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis.

Scale measurements followed procedures described by Hagen et al. (2001). After selecting a scale for measurement, the scale was scanned from a microfiche reader and stored as a high resolution digital file. The high resolution image (3352 x 4425 pixels) allowed the entire scale to be viewed and provided enough pixels between narrow circuli to ensure accurate measurements of circuli spacing. We used Optimas 6.5 image processing software to collect measurement data using a customized program. The scale image was displayed on an LCD monitor, and the scale measurement axis was defined as the longest axis extending from the scale focus. Distance (mm) between circuli was measured within each growth zone, i.e. from the scale focus to the outer edge of the first freshwater annulus (FW1), spring plus growth zone (FWPL), each annual ocean growth zone (SW1, SW2, SW3, SW4), and from the last ocean annulus to the edge of the scale (SWPL). Data associated with the scale such as date of collection, location, sex, fish length, and capture method were included in the database.

Standardized Scale Growth

Unequal numbers of male and female Chinook salmon scales were available for measurement in most years for age-1.3 salmon and in one year for age-1.4 salmon. Female Chinook salmon were much less common among age-1.3 salmon, whereas male Chinook salmon were less common among age-1.4 Chinook salmon, owing to differences in age at maturation. Male and female Chinook salmon had different growth rates (Ruggerone et al. 2007b). Therefore, scale growth indices were developed that equally weighted male and female scale growth during each year while utilizing all available scale measurement data:

$$\text{Annual mean growth (Z)} = [n_M (\text{Growth } Z_M) + n_F (\text{Growth } Z_F)] / [n_M + n_F],$$

where n_M and n_F are sample sizes of male and female salmon, and $\text{Growth } Z_M$ and $\text{Growth } Z_F$ represent the normalized mean growth of male and female salmon, respectively. Normalized growth is the number of standard deviations above or below the long-term mean.

Environmental Data and Analyses

Seasonal sea surface temperatures (SST) and climate indices that might influence growth of Chinook salmon were obtained from the Bering Climate web page (www.bering-climate.noaa.gov). Climate indices examined included the Pacific Decadal Oscillation index (PDO), Aleutian Low, Arctic Oscillation index, and the North Pacific index. Correlation analyses were conducted to determine whether an-

nual growth of Chinook salmon scales was associated with climate indices and/or seasonal SST. Serial autocorrelation among residuals was examined, and correlation tests were re-examined using differenced values when autocorrelation was significant.

Chinook and Pink Salmon Relationships

Pink salmon in the Bering Sea were highly abundant in odd-numbered years compared with even-numbered years (Davis et al. 2005). In order to remove the effects of time trends and to highlight differences in Chinook salmon scale growth between even- and odd-numbered years, we calculated the first difference of each scale growth variable and adult length-at-age:

$$\text{Differenced growth } (DG_i) = G_i - G_{i-1},$$

where G is normalized scale growth or adult length in year i.

RESULTS

Annual Growth Trends by Life Stage

Freshwater scale growth (FW1 and FWPL) of age-1.3

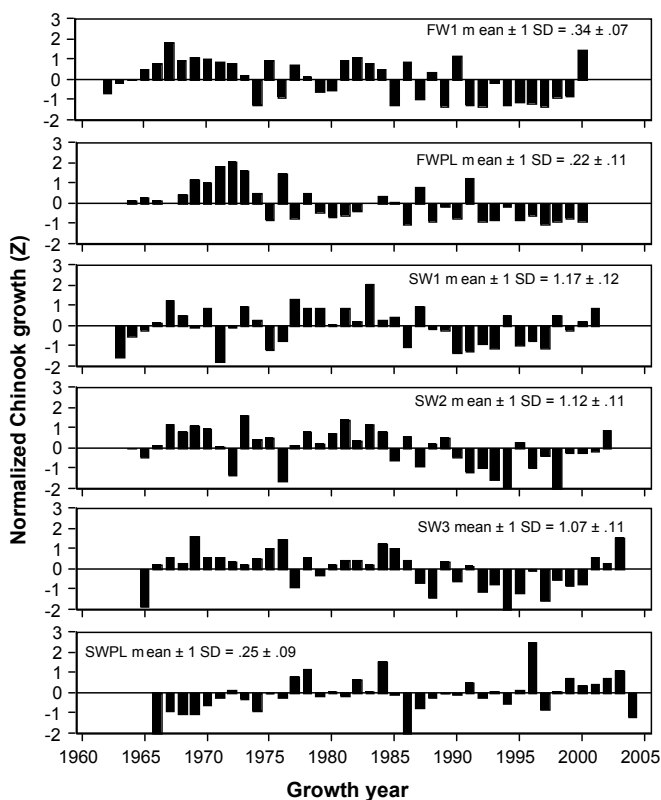


Fig. 2. Mean annual growth of age-1.3 Yukon Chinook salmon during each life stage, growth years 1962–2004. Values are standard deviations above and below the long-term mean. The long-term unweighted mean of male and female scale measurements is shown.

and age-1.4 Yukon Chinook salmon tended to be relatively high from the 1960s through the early 1970s, intermediate from the mid 1970s through the early 1980s, then typically below average after 1984 until rebounding in 1999 or 2000 (Figs. 2, 3). Mean annual growth was typically within two standard deviations of the long-term mean. During the first year at sea (SW1), scale growth was variable but tended to be intermediate prior to the mid 1970s, high during and immediately after the 1977 regime shift, and below average after the 1989 regime shift. Growth during the second, third, and fourth year at sea was typically above average prior to the mid-1980s, below average from the mid-1980s through 1990s, then higher beginning in the early 2000s. In contrast, scale growth during the homeward migration, which can be influenced by scale resorption, tended to be below average prior the mid-1970s and variable thereafter.

Adult length of age-1.3 Chinook salmon did not show a long-term pattern; whereas, the length of age-1.4 Chinook salmon was relatively high during the 1960s through 1982, intermediate through 1993, and typically below average from 1994 through 2002 (Fig. 4).

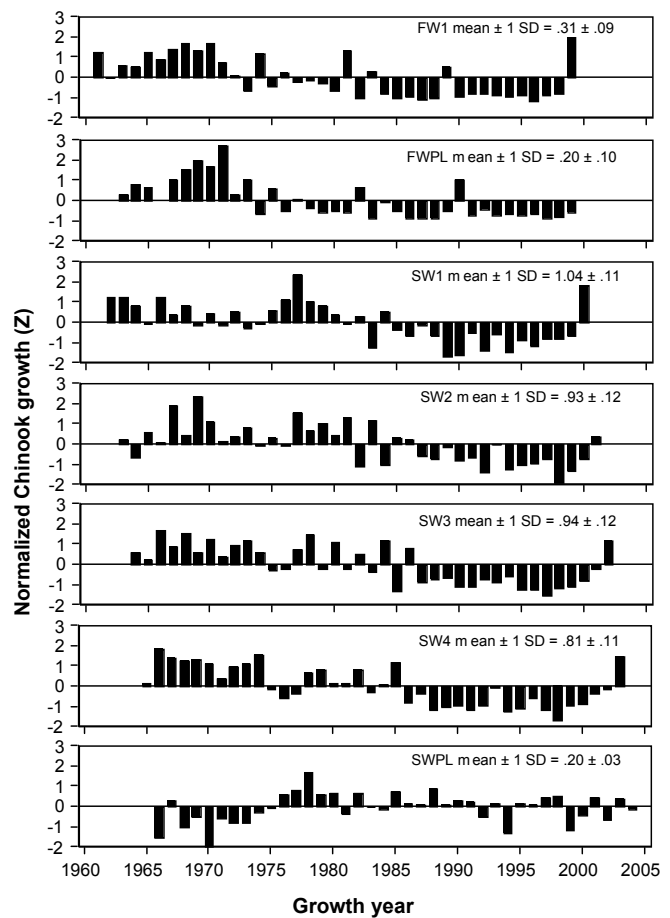


Fig. 3. Mean annual growth of age-1.4 Yukon Chinook salmon during each life stage, growth years 1961–2004. Values are standard deviations above and below the long-term mean. The long-term unweighted mean of male and female scale measurements is shown.

Climate Shift, Chinook Salmon Abundance and Growth

Harvests of Yukon Chinook salmon since 1965 were not correlated with annual marine growth of Chinook salmon scales except for a weak positive correlation with scale growth during the homeward migration ($r = 0.38$; $n = 32$, $P < 0.05$). Harvests were negatively correlated with spring plus growth during the smolt migration ($r = -0.41$; $n = 32$, $P < 0.05$).

Scale growth patterns were compared with the 1977, 1989, and 1997/98 climate events. Distinct shifts in scale growth during each life stage were not visibly associated with these climate events. The most noticeable pattern

occurred during the first year at sea (SW1) in which scale growth tended to be intermediate (age-1.4 salmon) or variable (age-1.3 salmon) prior to the mid-1970s, high immediately after the 1977 regime shift, and below average after the 1989 regime shift (Figs. 2, 3). Scale growth during subsequent life stages tended to follow this pattern, although the pattern was less defined.

Annual scale growth was compared with SST and climate variables, but statistically significant and meaningful relationships were not detected ($P > 0.05$). Scale growth was sometimes weakly correlated with SST and climate variables, but this correlation was largely caused by autocorrelation even when utilizing the first difference of variables.

Growth in Relation to Asian Pink Salmon

Adult length of age-1.3 Chinook salmon (differenced values to remove long-term trend) was significantly longer when returning in odd-numbered versus even-numbered years (ANOVA: $df = 1, 35$; $F = 21.181$; $P < 0.001$). The alternating-year pattern was consistent throughout all years, 1968–2004, although it was less apparent during the mid to late 1990s (Fig. 5A). In contrast, the alternating-year pattern of age-1.4 Chinook salmon length switched in the early 1990s (Fig. 5B). Age-1.4 Chinook salmon tended to be smaller during odd-numbered years prior to 1992, while they tended to be larger in odd-numbered years during 1992–2004. Length of age-1.4 salmon was not significantly different between even and odd years within each period ($P > 0.05$), owing to the small number of years within each period.

We examined annual scale growth patterns (differenced) to determine the life stage in which growth varied between odd- and even-numbered years. Among age-1.4 Chinook salmon, SW2 scale growth was significantly greater during odd-numbered years at sea (Fig. 6B; $df = 1, 36$; $F = 33.869$; $P < 0.001$), whereas SW3 growth was significantly greater during even-numbered years (Fig. 6C; $df = 1, 36$; $F = 23.715$; $P < 0.001$). No differences in growth were detected during other life stages of age-1.4 Chinook salmon. Age-1.4 Chinook salmon experienced relatively high growth in odd-numbered years of their second year at sea followed by relatively high growth during the third year at sea. These fish returned to the Yukon River during even-numbered years in which length-at-age was relatively high prior to the early 1990s (Fig. 5B).

Age-1.3 Chinook salmon also exhibited an alternating-year pattern during SW2 where differenced growth was greater during odd-numbered years at sea (Fig. 6A; $df = 1, 36$; $F = 3.165$; $P = 0.084$). Greater SW2 growth during odd-numbered years of age-1.3 was associated with greater adult length among fish that returned in odd-numbered years (Fig. 5A). An alternating-year pattern was not detected among other life stages of age-1.3 Chinook salmon.

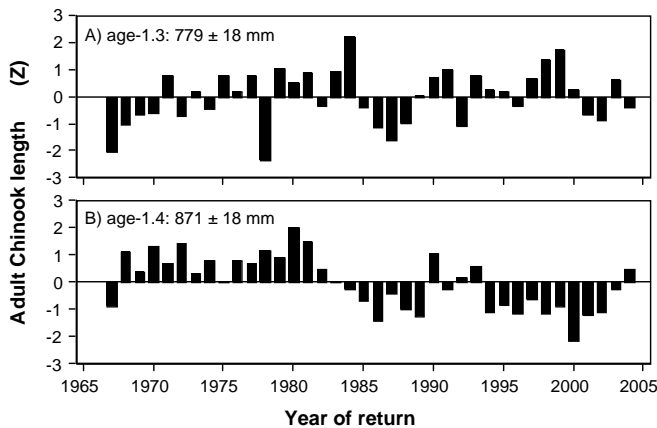


Fig. 4. Normalized length of age-1.3 and age-1.4 adult Yukon Chinook salmon, 1967–2004. Mean length \pm 1 SD is shown. Each value is the mean of male and female salmon in the ADFG database for all Chinook salmon sampled with 8.5-inch mesh in the lower Yukon River ($n = 30,600$ measurements).

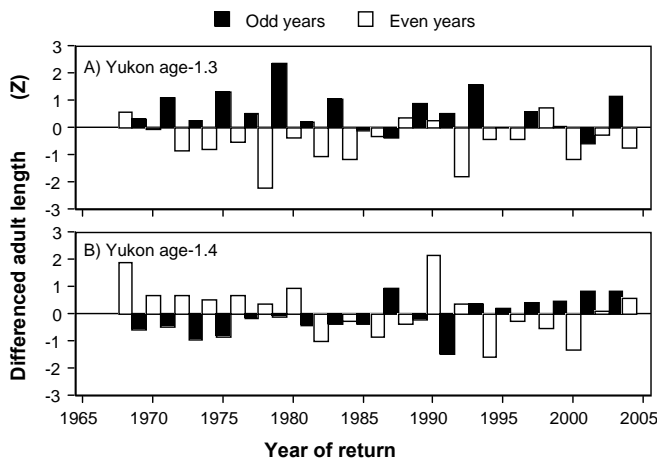


Fig. 5. Differenced length of age-1.3 and age-1.4 adult Yukon Chinook salmon, 1968–2004. Fish returning during odd-numbered years are shown by black bars, and fish returning during even-numbered years are shown by white bars. Values are the first difference of normalized adult length. Values are based on the ADFG database for all salmon sampled with 8.5-inch mesh in the lower Yukon River (30,600 measurements).

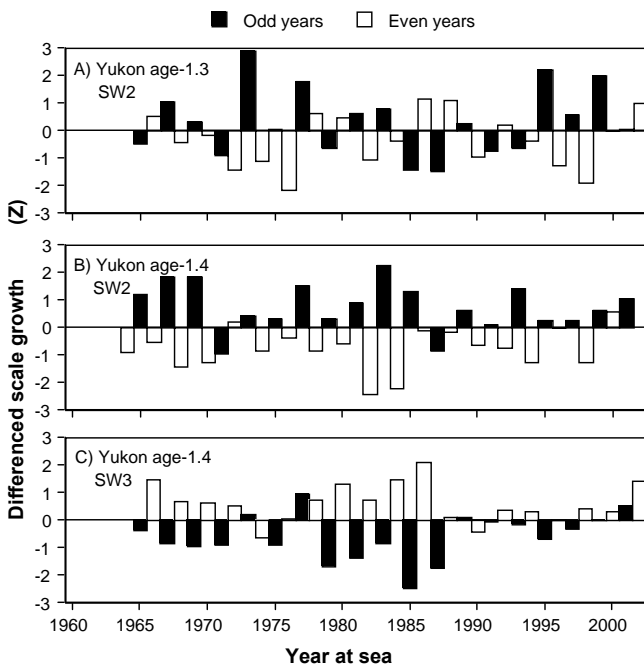


Fig. 6. Index of Yukon Chinook salmon growth during the second (A, B) and third (C) years at sea, 1964–2002. Odd-numbered years are represented by black bars, and even-numbered years are shown by white bars. Index is the first difference of normalized scale growth.

Growth in Relation to Prior Growth

Scale growth of Yukon Chinook salmon during each life stage in fresh water (FWPL) and the ocean (SW1, SW2, SW3, SW4) was significantly and positively correlated with growth during the previous life stage ($P < 0.05$; Fig. 7). On average, 60% of the variability in annual Yukon scale growth was explained by growth during the previous life stage. These relationships were consistent for both age-1.3 and age-1.4 Chinook salmon. Spring growth during the smolt migration period (FWPL) was correlated with total freshwater growth. Growth during the first year at sea was correlated with total freshwater growth, but it was most highly correlated with growth during early life in fresh water (i.e., circuli 1–4). Growth during each subsequent year in the ocean was correlated with the previous year’s growth, but growth was most highly correlated with maximum scale growth, as defined as the spacing among the five widest circuli.

Autocorrelation was present in the scale growth time series. However, autocorrelation was non-significant in the residuals of the scale growth regressions described above, indicating the regression models were not significantly influenced by time (L. Conquest, University of Washington, pers. comm.). Statistical significance of the regressions was tested by reducing the degrees of freedom to account for autocorrelation within the variables (Pyper and Peterman 1998) and all regressions were statistically significant.

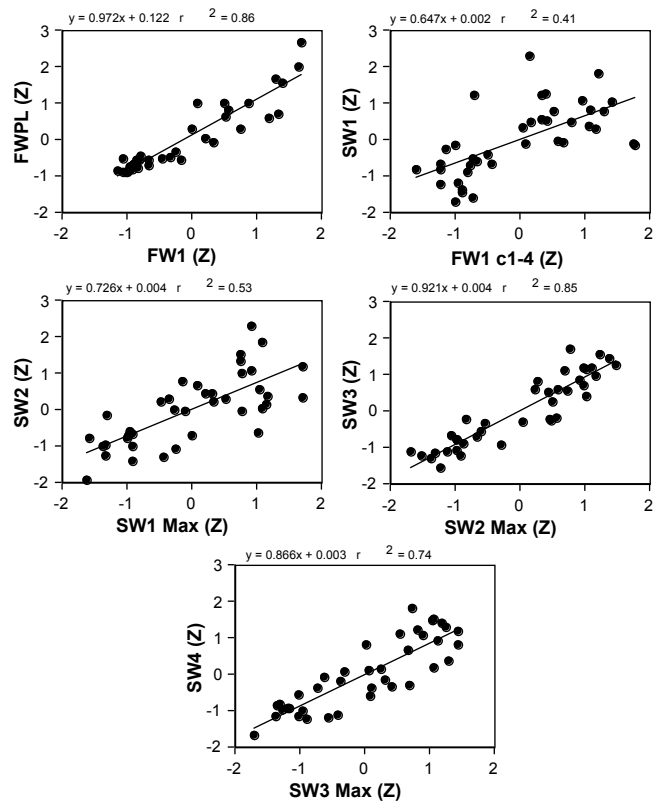


Fig. 7. Relationship between average scale growth during each life stage of age-1.4 Yukon Chinook salmon and average scale growth during the previous year. Independent variables include: total growth in fresh water (FW1), the first four circuli of freshwater growth excluding the scale focus (FW1 c1-4) and width of five maximum circuli during each year in the ocean (SW1, SW2 and SW3). All values are normalized. Relationships for age-1.3 Chinook salmon were similar, and are not shown here (Ruggerone et al. 2007b).

DISCUSSION

Yukon and other Chinook salmon harvests in western Alaska tended to reflect the 1977 ocean regime shift (abundance increase) and the 1997/98 El Niño event (abundance decrease). Both of these broad-scale climate events had a significant impact on the southeastern Bering Sea and on salmon production (Rogers 1984; Kruse 1998; Hunt et al. 2002; Peterman et al. 2003). In contrast, the 1989 regime shift (Hare and Mantua 2000), which was associated with a significant decline in adult size and abundance of Bristol Bay sockeye salmon (Ruggerone et al. 2007a), did not have an apparent effect on Chinook salmon abundance in western Alaska.

Harvests of western Alaska Chinook salmon changed relatively rapidly in response to the 1977 and 1997/98 climate events, and these abundance levels persisted for a number of years. The rapid decline in the late 1990s suggests that Chinook salmon abundance and survival may have been initially influenced during late marine life. The persistence of relatively low harvests after the 1997/1998 El Niño suggests

that the El Niño event may have affected multiple year-classes that occupied the ocean during this period. Additionally, the El Niño event may have altered the abundances and/or distributions of other marine species, leading to a prolonged influence on Chinook salmon abundance.

Adult length and annual scale growth at sea of Yukon Chinook salmon did not appear to be closely linked to shifts in abundance of Chinook salmon. Furthermore, no positive correlation existed between scale growth during each life stage and ocean conditions such as sea surface temperature. Scale growth during the first year at sea appeared to have been affected by the 1977 (growth increase) and 1989 (growth decrease) ocean regime shifts.

Mean scale growth of Chinook salmon at sea was dependent on the previous year's growth, and this dependency may have confounded potential relationships between growth and abundance or environmental conditions. Additional research indicated that scale growth of individual Yukon and Kuskokwim Chinook salmon was dependent on scale growth during the previous life stage (Ruggerone et al. 2009). Adult length of individual Chinook salmon tended to be positively correlated with scale growth in fresh water, indicating an important link between growth at sea and growth and habitat quality in fresh water. Adult length of individual Chinook salmon was also correlated with marine scale growth, especially cumulative scale growth after the first year at sea.

The dependence of growth on prior growth of Chinook salmon is an unusual finding compared with analyses of Bristol Bay sockeye growth where there was no significant positive correlation between scale growth of adjacent life stages (Ruggerone, unpublished analyses). Instead, Bristol Bay sockeye salmon exhibited a significant negative correlation between scale growth in the second year versus first year at sea, possibly reflecting the need to grow fast in the second year if growth in the first year was below average (Ruggerone et al. 2005). The dependency of Chinook salmon growth on prior growth may reflect the tendency of Chinook salmon to consume relatively large, mobile prey such as fishes and squid (Davis et al. 2005) and the greater ability of larger Chinook salmon to capture these prey.

Previous studies indicated that Chinook salmon growth and survival was influenced by competition with pink salmon, especially when Chinook salmon initially entered marine waters (Grachev 1967; Ruggerone and Goetz 2004; Ruggerone and Nielsen 2004). Pink salmon are exceptionally abundant in the central Bering Sea during odd- versus even-numbered years (Davis et al. 2005). For example, during the 1990s, catch per unit effort (CPUE) in Japanese research nets during odd-numbered years indicated that pink salmon were 580% more abundant than sockeye salmon and 87% more abundant than chum salmon (Davis et al. 2005). However, we did not detect direct competition between pink salmon and Chinook salmon, possibly because Yukon Chinook salmon do not overlap with Asian pink salmon until the second year at sea and because pink salmon from western

Alaska are not abundant (JTC 2008; Whitmore et al. 2008).

Instead, growth of age-1.3 and age-1.4 Chinook salmon during the second year at sea (SW2) was greater during odd-numbered years, i.e., years when pink salmon were highly abundant. Growth of age-1.4 Chinook salmon during the third year at sea (SW3) was lower during odd-numbered years, but this pattern may reflect the dependency of growth on previous year's growth, as discussed previously. The alternating-year pattern in scale growth led to greater adult length-at-age in odd-numbered years, especially among age-1.3 Chinook salmon. These growth patterns were also detected in Kuskokwim Chinook salmon (Ruggerone et al. 2007b).

The alternating-year pattern of Yukon Chinook salmon was opposite to that observed among Bristol Bay sockeye salmon, which experienced lower growth during odd-numbered years (Ruggerone et al. 2003, 2005). Diet overlap is much greater between pink and sockeye salmon versus pink and Chinook salmon. Chinook salmon also feed on higher trophic level prey (Davis et al. 2005). The cause of the alternating-year pattern of Chinook salmon growth is unknown, but it may be related to a cascading effect of pink salmon on the epipelagic food web. If so, this finding would indicate indirect competition between pink and Chinook salmon in offshore areas. Future studies of salmon diets on the high seas should attempt to identify prey species that contribute to these alternating-year patterns in salmon growth and to identify the extent to which prey life history contributes to this pattern.

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Salmon Distribution in Northern Japan during the Jomon Period, 2,000–8,000 Years Ago, and Its Implications for Future Global Warming

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Abstract: In Japan, the present southern limit for main chum salmon spawning is the Tone River in Chiba Prefecture on the Pacific side and the Tedor River in Ishikawa Prefecture on the Japan Sea side (about 36° North) of the Island of Honshu in Japan. Historic chum salmon distributions along the coast of the Tohoku Region, from Aomori to Fukushima Prefecture on the Pacific side, were examined based on archeological evidence dating to the Jomon Period, 8,000–2,000 years ago. The oldest salmon remains were found in the northern part of the Tohoku Region, such as in Hachinohe, from the Initial Jomon Period (8,000–6,000 years ago). Salmon remains were found in Miyako from the Early Jomon Period (6,000–5,000 years ago), in Oofunato from the Middle Jomon Period (5,000–4,000 years ago), in Rikuzentakada from the Late Jomon (4,000–3,000 years ago), and Naruse in Sendai Bay from the Final Jomon (3,000–2,000 years ago). These shifts of salmon remains from north to south appear to reflect a change in salmon distribution coincident with decreasing temperatures after the Jomon Marine Transgression peaked 6,000 years ago. Based on these observations of the past, we expect that global warming will reduce salmon production in Japan, if sea surface temperatures rise again. If so, then managers and scientists should start searching for adaptive measures now to mitigate future global warming. Such mitigation might include focusing on stock enhancement with late-run stocks, allowing more natural spawning, a greater emphasis on hatchery feeding programs, and adaptively changing the number of juvenile salmon released from hatcheries.

Keywords: chum salmon, distribution, salmon remains, Jomon Period, global warming

INTRODUCTION

Chum salmon (*Oncorhynchus keta*) have the widest natural geographic distribution of all Pacific salmon species. Chum salmon in Asia are found from Korea to the Arctic coast of Russia and west to the Lena River. Chum salmon in North America are found from Monterey, California to the Arctic coast and east to the Mackenzie River (Salo 1991). The spawning distributions of all species of Pacific salmon are limited by environmental conditions, and these conditions are usually assumed to be the most challenging at the limits of each species' range. Because Japan includes the southern limit of chum salmon distribution, Japanese chum salmon will almost surely be affected by global warming. Because Pacific salmon have been such an important part of the Japanese diet, even a small change in the Japanese chum salmon harvest will have harsh consequences for the people that depend on these fish.

There are two conventional approaches to forecasting the effect(s) that global warming may have on salmon distribution. The first approach is to observe present salmon distribution in the North Pacific and note the accompanying sea surface temperatures that salmon prefer. Then these preferred temperatures can be combined with predicted future sea surface temperatures from global simulation models. Welch et al. (1998) and Kaeriyama (2008) used this approach to predict that the distributions of sockeye and chum salmon will be reduced to the northern part of the North Pacific Ocean in coming years. Notably, Kaeriyama (2008) predicted that chum salmon will disappear from Japan by 2100.

The second approach to predicting the effects of climate change is to examine the archeological record, looking for changes in salmon distribution, and then to compare variation in the archeological record to what is known about variation in the climate record. For example, stream conditions in the Columbia River basin in western North America were

reconstructed using paleoecological data from 7,000–6,000 years ago when regional temperatures were up to 2°C warmer than at present. Using this approach, Chatters et al. (1995) concluded that salmon were 30–60% less abundant during this time, relative to the present. In Japan, approximately 6,000 years ago the southern limit of chum salmon distribution was located in the northern part of Honshu, far north of the current limit. Also, 6,000 years ago the seawater temperature was approximately 5°C warmer than the conditions today (Ishida et al. 2001).

Our first purpose with this paper is to examine the chum salmon distribution in Tohoku Region during the Jomon period, based on archeological evidence, and then to relate variation in ancient remains of salmon parts to what is known about variation in ocean temperature. In Japan, the ancient people that lived in Hokkaido utilized chum salmon. Therefore, large-scale changes in the abundance of chum salmon parts in the archeological record can be assumed to mirror changes in chum salmon abundance at the time the archeological remains were deposited. Our broader goal is to begin thinking about appropriate adaptive measures to protect salmon in the Tohoku Region from the effects of future global warming.

MATERIALS AND METHODS

Yamada (2005) reviewed literature on archeological

sites in Tohoku Region of Japan (the northeastern portion of Honshu Island) and described archeological sites containing salmon remains. These salmon remains were mapped according to the following periods: Initial Jomon (8,000–6,000 years ago), Early Jomon (6,000–5,000 years ago), Middle Jomon (5,000–4,000 years ago), Late Jomon (4,000–3,000 years ago), and Final Jomon (3,000–2,000 years ago). Fish remains in the Satohama Shell Midden in Miyagi Prefecture were examined intensively from the Early to the Final Jomon periods (Tohoku History Museum 1987). Although there were many fish remains dating from the Early Jomon Period onward, salmon remains were only found at this location during the Final Jomon Period (Table 1). Finally, summaries of the environmental conditions in the Jomon Period (Table 2) were taken from several sources (Sawa 1987; Matsushima 1988; Yamashiro 1999; Ishida et al. 2001).

RESULTS

Salmon Remains in the Tohoku Region

The oldest salmon remains were found in the northern part of the Tohoku Region, such as in Hachinohe, and these remains date to the Initial Jomon Period, 8,000–6,000 years ago, when sea surface temperatures were warmer than the present (Table 2). Thereafter, salmon remains were found in Miyako, and these remains date to the Early Jomon Period,

Table 1. Fish remains in Satohama shell midden in Miyagi Prefecture in the southern part of the Tohoku Region. Numbers indicate the frequency of appearance of fish remains; '+' indicates that fish remains were found, but in small numbers.

Fish species	Common name	Chronology (Year B.P.)				
		Initial Jomon (8,000–6,000)	Early Jomon (6,000–5,000)	Middle Jomon (5,000–4,000)	Late Jomon (4,000–3,000)	Final Jomon (3,000–2,000)
<i>Chondrichthyes</i>	Sharks		+	+		+
<i>Clupea pallasii</i>	Pacific herring		12	5		24
<i>Engraulis japonicus</i>	Japanese anchovy					1
<i>Anguilla japonica</i>	Japanese eel		1	+		1
<i>Conger myriaster</i>	Conger eel		2	2		4
<i>Oncorhynchus</i> sp.	Pacific salmon					+
<i>Hemiramphus sajori</i>	Japanese halfbeak		11	2		
<i>Mugil cephalus</i>	Flathead mullet		+			
<i>Lateolabrax japonicus</i>	Japanese seabass		10	3		8
<i>Seriola quinqueradiata</i>	Japanese yellowtail		3	4		
<i>Trachurus japonicus</i>	Jack mackerel		9	2		1
<i>Pagrus major</i>	Red seabream		8	3		
<i>Acanthopagrus schlegelii</i>	Black seabream					2
<i>Halichoeres poecilopterus</i>	Multicolorfin rainbowfish			1		
<i>Scomber</i>	Mackerel		1	10		+
<i>Thunnus</i> sp.	Tuna		+			
<i>Scorpaena onaria</i>	Rock fish		12	6		2
<i>Hexagrammos otakii</i>	Fat greenling		12	4		8
<i>Platycephalus indicus</i>	Flat head		2			
<i>Pleuronectidae</i>	Righteye flounder		2			2
<i>Stephanolepis cirrhifer</i>	Thread-sail filefish		12			
<i>Tetraodontidae</i>	Puffers		2	+		4

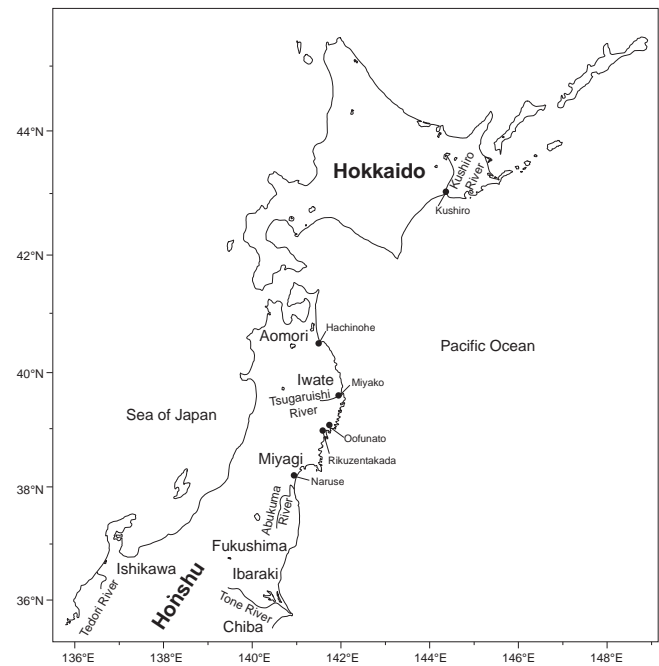
Table 2. A summary of environmental conditions and effects on salmon production in the Kushiro River on the Island of Hokkaido in Japan and in the Columbia River in the Pacific Northwest of North America.

Chronology	Year B.P.	The Kushiro River in Hokkaido	The Columbia River in North America	
Initial Jomon	8,000	Jomon marine transgression Sea surface was 3-5m higher than at present in Japan	Poor for salmon 200 days above 10° C	
	6,000			
Early Jomon	5,000	Paleolithic Kushiro Bay		
		+5° C		
Middle Jomon	4,000	Start of cooling		
		Seawater retreated		
Late Jomon	3,000	Present coastline		Optimum for salmon 130 days above 10° C
Post Jomon	1,200			Good for salmon 100 days above 10° C
Satsumon	700	Present Kushiro River		
Ainu	Present			
References		Sawa (1987) Matsushima (1988) Yamashiro (1999) Ishida et al. (2001)	Chatters et al. (1995)	

6,000–5,000 years ago; in Oofunato, dating to the Middle Jomon Period, 5,000–4,000 years ago; in Rikuzentakada from the Late Jomon, 4,000–3,000 years ago; and Naruse in Sendai Bay, dating to the Final Jomon, 3,000–2,000 years ago (Figs. 1, 2). These shifts in salmon remains from north to south appear to reflect changes in salmon distribution caused by decreasing temperatures after the Jomon Marine Transgression.

Salmon Remains in the Satohama Shell Midden

Various kinds of fishes, such as seabass and yellowtail from the Early to Final Jomon periods, were found in the Satohama Shell Midden, in Miyagi Prefecture in the southern part of the Tohoku Region (Fig. 1). However, salmon remains were found only from the Final Jomon Period, when average sea surface temperatures were similar to those at present (Table 1). Salmon remains were not found in the Early to Middle Jomon periods (Table 1), when temperatures were generally higher than at present (Table 2).

**Fig. 1.** Map indicating many of the place names that are included in the text.

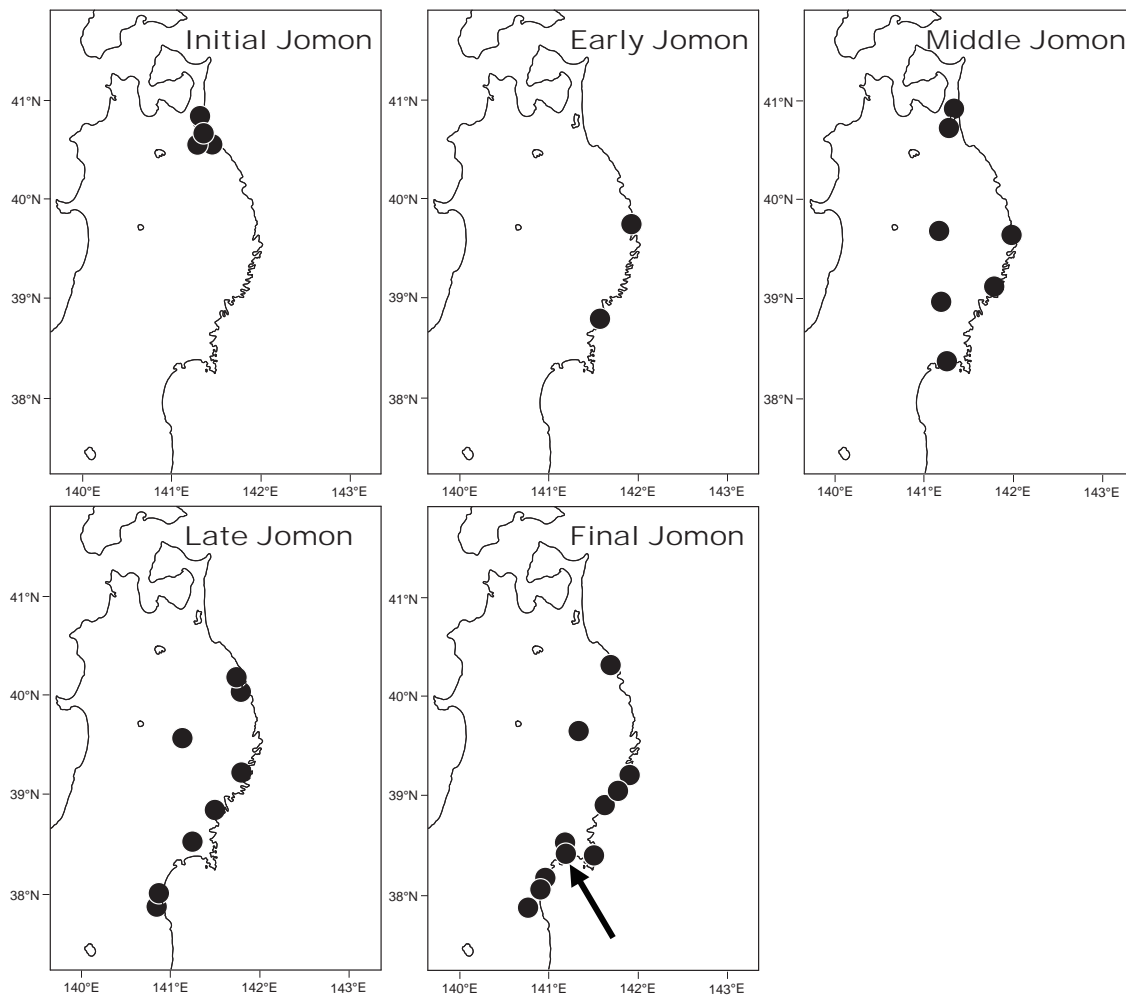


Fig. 2. Distribution of salmon remains in the Tohoku Region from the Initial to the Final Jomon periods. The arrow indicates the location of the Satohama shell midden.

DISCUSSION

We propose that the shifts of salmon remains from north to south reflect a change in salmon distribution that was due to decreasing temperatures after the Jomon Marine Transgression peaked 6,000 years ago (Table 2). If so, then a northward shift in salmon distribution might occur in the ocean, under conditions caused by future global warming. Because of the importance of chum salmon in the Japanese diet, it is essential that managers begin planning as soon as possible, looking for adaptive measures to counteract the effects of global warming. We know quite a bit about the timing of chum salmon returning to natal rivers, the timing of chum salmon juveniles entering sea water, and the timing of the chum salmon migration into offshore waters.

Currently, the southern limit for chum salmon returns in Japan is the Tone River in Chiba Prefecture on the Pacific side and the Tedoru River in Ishikawa Prefecture on the Japan Sea side of the Island of Honshu. Returning chum salmon may move to bottom depths ranging from 150 to 460 m to

avoid the high temperatures (12–20°C) of surface waters found in the waters off Iwate Prefecture, and follow temperatures close to their thermal preference (3–11°C), which are found near the bottom waters off Iwate Prefecture in the Tohoku Region during autumn. This movement pattern appears to be an adaptation of chum salmon near the southern limit of their range (Ueno 1992). Chum salmon return to the Tohoku Region from September to February, depending on river of origin (Okazaki 1982). Recently, surface seawater temperatures have ranged from 17–22°C in September to 5–10°C in February along the Tohoku Region (Tomosada 1982).

Although these observations about chum salmon timing and distribution reflect general trends, there are two stocks of chum salmon returning to this area, each with different timing characteristics. The early-run stock in the Abukuma River returns in October, and the late-run stock in the Tsugaruishi River returns in December (Okazaki 1982). Because the late-run stock returns when the coastal waters are currently about 8°C cooler than when the early-run stock returns, an

emphasis on the use of the late-run stock in hatcheries might be appropriate under global warming conditions.

In the Tohoku Region, the time of entry of chum salmon juveniles into sea water is from March to June, depending on the river (Mayama and Ishida 2003). Recent seawater temperatures along the Tohoku Region have ranged from 5–8°C in March to 12–15°C in June (Tomosada 1982). Recently, juvenile chum salmon have remained in coastal water masses with plentiful food resources and physiologically optimal surface temperatures and salinities until they reached about 70–80 mm fork length, at which time they were able to migrate offshore, avoiding high (over 12–13°C) sea surface temperatures and high (over 34 psu) salinities (Mayama and Ishida 2003). Under warmer conditions, juveniles will need to enter sea water earlier, before coastal water temperatures rise. Therefore, managers should consider using an enhanced hatchery feeding program so that juveniles can grow rapidly prior to release.

The measures we have considered so far are steps humans can take artificially, mainly at hatcheries, but other adaptive measures might be taken naturally by chum salmon themselves in natal rivers. At present, hatchery practices are to capture returning chum salmon with fishing weirs set near the mouths of rivers, so that there is virtually no natural spawning. In order to increase natural adaptations, it might be necessary to move the fishing weirs to the upper parts of rivers or at least allow a portion of the chum salmon returns to escape into spawning areas there. By increasing the number of chum salmon allowed to spawn naturally, thereby allowing chum salmon to enter naturally into coastal waters to migrate to limited offshore waters, we may produce chum salmon that return to Japan with the timing best adapted to warmer conditions.

Global warming could affect the ocean carrying capacity of chum salmon in ways that may be difficult to predict. During the ocean life stage, chum salmon are currently distributed in waters with the sea surface temperature ranging from 2–11°C (Brodeur 1988). Welch et al. (1998) and Kaeriyama (2008) have predicted that the carrying capacity of salmon in the North Pacific will be reduced under global warming conditions. With changing abundances of different species and stocks originating from many jurisdictions, it will be very difficult to regulate the size of each stock. However, competition may be stronger within stocks than among stocks of the same species, and among different species. Therefore, it might be possible to reduce the competition among Japanese chum salmon by adaptively changing the number of juveniles released from the hatcheries, based on monitoring the abundance and body size of returning chum salmon.

In summary, there may be additional adaptive measures to increase chum salmon survival that have not yet been proposed. However, we recommend that planners begin looking for mitigation measures in four areas. First, late-run chum salmon stocks deserve special attention, as these may be the best adapted chum salmon to return to Japanese hatcheries

under warmer conditions. Second, we recommend that managers begin research into the effects of feeding programs to support early release, so Japanese chum salmon will move out of coastal waters earlier. Third, we recommend increasing the number of naturally spawning chum salmon, and monitoring their survival and fitness to see if natural selection will lead to fish better adapted to warmer conditions. Finally, we recommend that Japanese hatchery planners consider adjusting the number of chum salmon released, as global warming may reduce the ocean carrying capacity. However, even with the measures we recommend, and even with measures not yet identified, the spawning distribution of Japanese chum salmon may still shift northward as the climate continues to change.

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Trends in Run Size and Carrying Capacity of Pacific Salmon in the North Pacific Ocean

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Kaeriyama, M., H. Seo, and H. Kudo. 2009. Trends in run size and carrying capacity of Pacific salmon in the North Pacific Ocean. *N. Pac. Anadr. Fish Comm. Bull.* 5: 293–302.

Abstract: Pacific salmon (*Oncorhynchus* spp.) play an important role as keystone species and as ecosystem services in the North Pacific ecosystem. Our objective is to evaluate the trends in and causes of variation in run size and carrying capacity of Pacific salmon, and to predict their future production dynamics. Salmon catch data indicate that the abundance of Pacific salmon has declined since the end of the twentieth century, despite the healthy condition of stocks. At the beginning of the 21st century, chum (*O. keta*) and pink salmon (*O. gorbuscha*) maintained high abundance commensurate with a sharp increase in hatchery-released populations. However, sockeye salmon (*O. nerka*) have shown a reduction trend since the late 1990s. The abundance of coho (*O. kisutch*), Chinook (*O. tshawytscha*), and masu (*O. masou*) salmon, which spend more than one year in fresh water, has declined sharply since the 1980s due to degraded environmental conditions in freshwater habitats (e.g., habitat loss, urbanization, and river channelization). The significant positive correlation between the carrying capacity (K) of three species (sockeye, chum, and pink salmon), defined as the replacement level of Ricker's recruitment curve, and the Aleutian Low Pressure Index (ALPI) indicate that their carrying capacity is synchronous with long-term trends in climate change. The carrying capacity of the three species is expected to continue the downward trend seen since the 1998/99 regime shift.

Keywords: carrying capacity, long-term climate change, Pacific salmon, run size

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) play an important role as keystone species and ecosystem services in the North Pacific ecosystem. They are important not only as fisheries resources but also as a keystone species in these ecosystems. Pacific salmon are also a key species for sustaining the biodiversity and productivity of riparian ecosystems because they supply marine-derived nutrients to rivers (e.g., Kaeriyama and Minagawa 2008).

Since the 1976/77 regime shift, catches of Pacific salmon have been increasing throughout the North Pacific Ocean, coinciding with favorable oceanic conditions and a successful artificial enhancement program (Beamish and Bouillon 1993; Kaeriyama 1998). The most abundant species caught is pink salmon (*O. gorbuscha*), followed by chum (*O. keta*) and sockeye salmon (*O. nerka*). Catches have been increasing almost steadily in coastal Japan, Russia, and central and southeast Alaska. Catches in western Alaska increased through the mid-1990s but have been decreasing recently. Salmon catches in British Columbia and the western United States (Washington, Oregon, and California) have been decreasing since the late 1980s (Eggers 2004). We estimated the carrying capacity of Pacific salmon from catch and/or abundance data which are based on the expansion rate of

the terminal run in each regional population (D. E. Eggers, Alaska Department of Fish and Game, Douglas.Eggers@alaska.gov, unpublished data), using the equilibrium level on the Ricker recruitment curve (e.g., Kaeriyama and Edpalina 2004; Yatsu and Kaeriyama 2005). However, this expansion rate did not always accurately reflect the run size (catch and escapement, millions of individuals) when based on catch data, with the result that the run size of chum salmon was overestimated.

Since 1999, the North Pacific has been characterized by consistent spatial patterns in the sea level pressure anomaly (SLPA), sea surface temperature (SST), and the reversed Pacific Decadal Oscillation (PDO) (Bond et al. 2003; Chavez et al. 2003; Peterson and Schwing 2003; Rodionov and Overland 2005). These persistent changes in the North Pacific resulted in a new climate regime shift in 1998/99 (Minobe 2002; Chavez et al. 2003; Rodionov and Overland 2005).

The purpose of this paper is to update and extend the estimated run size and carrying capacity values of Pacific salmon proposed by Kaeriyama and Edpalina (2004) in order to assess near-future fluctuation(s) in carrying capacity in relation to long-term climate change and the biological interaction between wild and hatchery salmon.

MATERIALS AND METHODS

We used INPFC (1979), Fredin (1980), Kaeriyama and Edpalina (2004), Eggers (2004), White (2008), and URLs: www.cf.adfg.state.ak.us and <http://salmon.fra.affrc.go.jp/> to obtain catch data for Pacific salmon. Also, we used the Aleutian low-pressure index (ALPI) derived from Beamish and Bouillion (1993), the Pacific decadal oscillation (PDO)

derived from Mantua et al. (1987) and URLs: http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/climate/clm_indx_alpi.htm and <http://jisao.washington.edu/pdo/>, as indices of long-term climate change. We estimated run size of sockeye, chum, and pink salmon from catch data using the expansion rate, which indicates the exploitation rate (catch per run size of three species) (D. E. Eggers, Alaska Department of Fish and Game, Douglas.Eggers@alaska.gov, unpublished data).

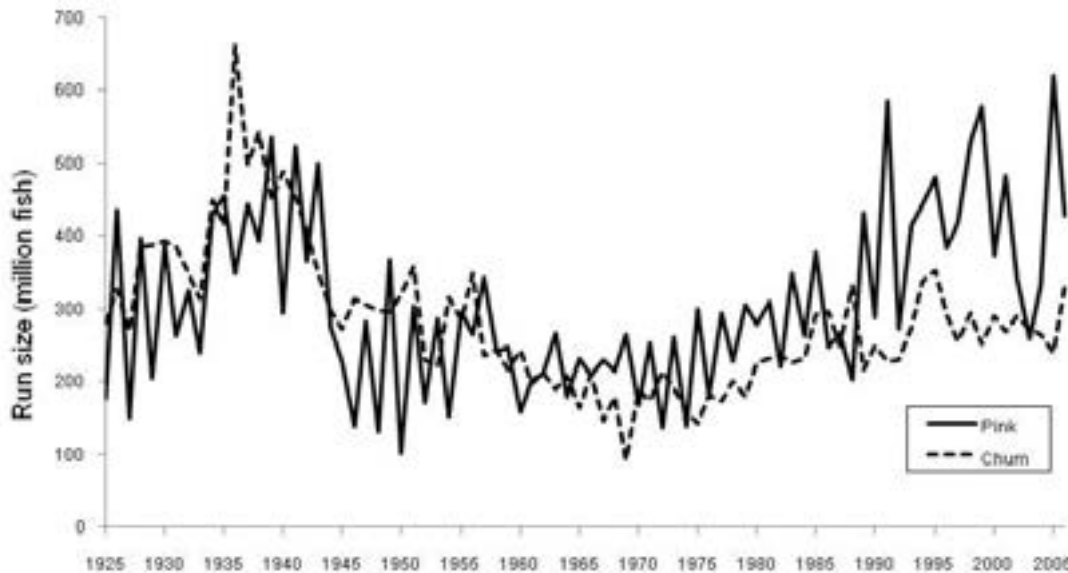


Fig. 1. Annual changes in run sizes estimated by Eggers' expansion rate of pink (solid line) and chum salmon (broken line). The expansion rate of chum salmon was 43% on the high seas, 11% in coastal Russia, 10% in western Alaska, 10% in central Alaska, 10% in southeast Alaska, and 10% in BC/Washington/Oregon (D.E. Eggers, Douglas.Eggers@alaska.gov, unpublished data).

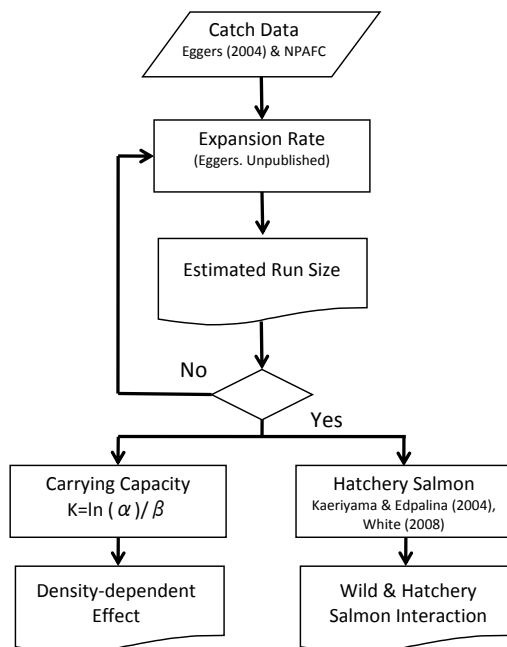


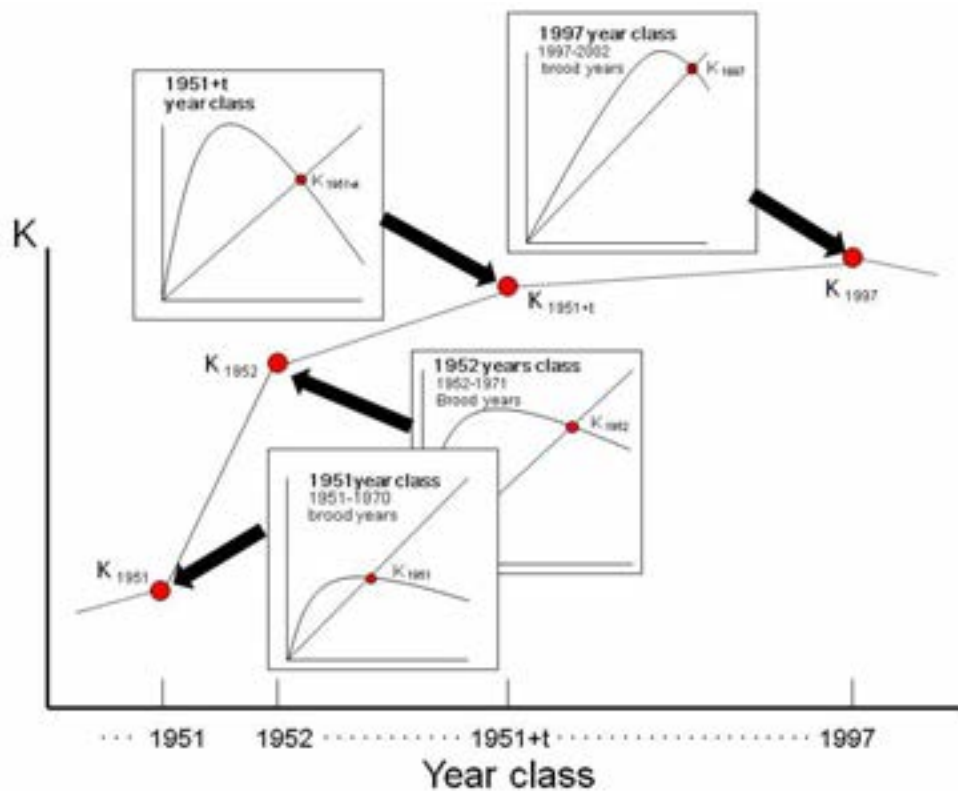
Fig. 2. Flow chart for estimating run size and carrying capacity of Pacific salmon.

However, the run sizes using Eggers' expansion rate were overestimated. For instance, the run size of chum salmon exceeded the run size of pink salmon (Fig. 1). As the result of trial and error using random exploitation rates (Fig. 2), we decided on a new expansion rate (Table 1).

Parameters for the Ricker recruitment curve ($R = \alpha Pe^{-\beta P}$) were estimated for each of the three species by the Levenberg-Marquardt method (Marquardt 1963). Parameters were calculated by regression analysis and the index of carrying capacity (K) for salmon was defined as the unfished equilibrium level ($\ln(\alpha)/\beta$) (Ricker 1975). The time span of data used to estimate the parameters (α , β , K) for year-class, t , was 10 generations of odd- and even-year groups for pink salmon, and 20 brood years for sockeye and chum salmon from year-class t to $t + 20$ (Fig. 3). The choice of 10 generations or 20 brood years was based on the appearance of bidecadal cycles of climate conditions (Minobe 2000). The run size of salmon released from hatcheries was based on Kaeriyama and Edpalina (2004) and White (2008) in order to compare run sizes between wild and hatchery salmon.

Table 1. Catch rate per run size of pink, chum, and sockeye salmon in the North Pacific Ocean. The expansion rate shows exploitation rate (catch per run size).

Area	Pink salmon	Sockeye salmon	Chum salmon
Japan; Coastal	49%	None	0%
Japanese: Japan Sea	57%	None	None
Japanese: High Seas Immature	None	46%	43%
Japanese: High Seas Maturing	56%	32%	22%
Russian: Coastal	50%	30%	20%
Western Alaska	None	30%	20%
Central Alaska	62%	30%	20%
PWS Hatchery	White (2008)	None	None
Southeast Alaska	55%	40%	20%
Southeast Alaska Hatchery	White (2008)	None	White (2008)
B.C./Washington/Oregon	55%	40%	20%

**Fig. 3.** Schematic diagram of temporal changes in carrying capacity of Pacific salmon.

RESULTS AND DISCUSSION

The catch of sockeye, chum, and pink salmon comprised more than 90% of the total catch of Pacific salmon. Temporal changes in the catch had roughly a 30- or 40-year periodicity, corresponding to long-term climate change indicators such as the PDO and the regime shift (Fig. 4). The general trend in Pacific salmon production was similar for both North American and Asian populations. Increased production began in the late 1970s, reaching historic levels in 1995. Catches declined slightly thereafter but were the second highest in history in 2003. In both the eastern and

western Pacific, the catches of salmon generally increased substantially after the regime shift in 1977 (Beamish 2008). Recent trends in catch show increases in pink and chum, steadiness in Chinook (*O. tshawytscha*), and decreases in sockeye, coho (*O. kisutch*), and masu (*O. masou*) salmon (Fig. 5). In particular, masu and coho salmon which spend a long time in fresh water have shown significant decreasing trends since the 1980s. Japanese masu salmon decreased from more than 2000 tons in the 1960s to about 500 tons by 2000. This decreasing trend is attributed to losses of suitable habitat in fresh water (Kaeriyama and Edpalina 2004).

The run sizes of the three major species (sockeye, chum,

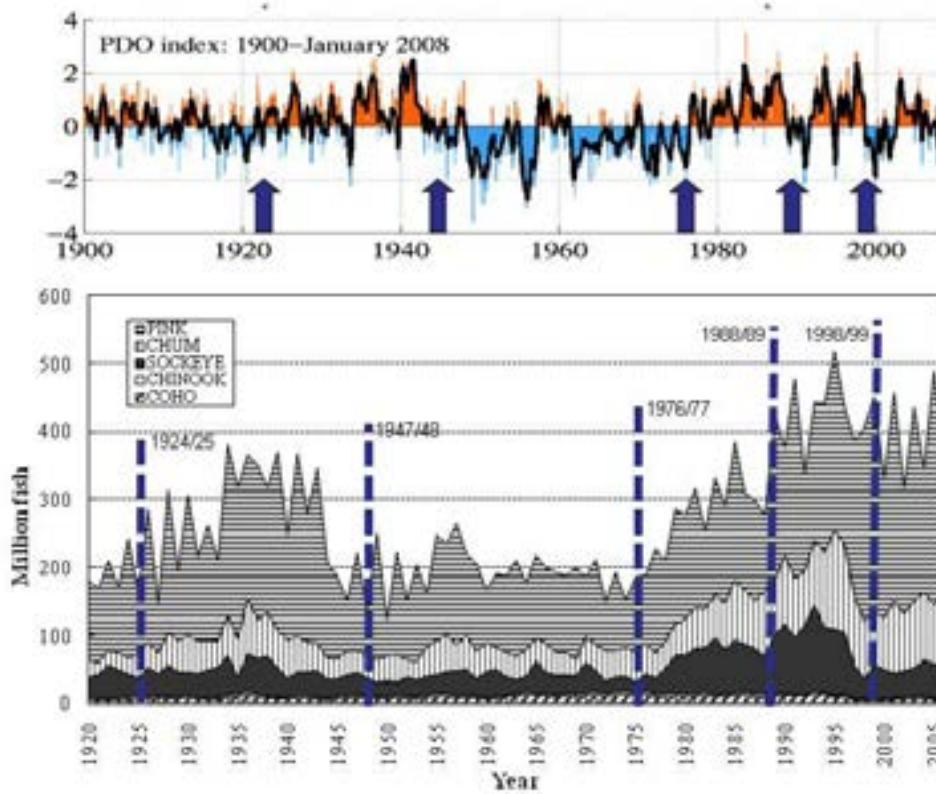


Fig. 4. Annual changes in catches of Pacific salmon (1920–2006) and the Pacific Decadal Oscillation (PDO; 1900–2008). Bars and arrows show regime shift years.

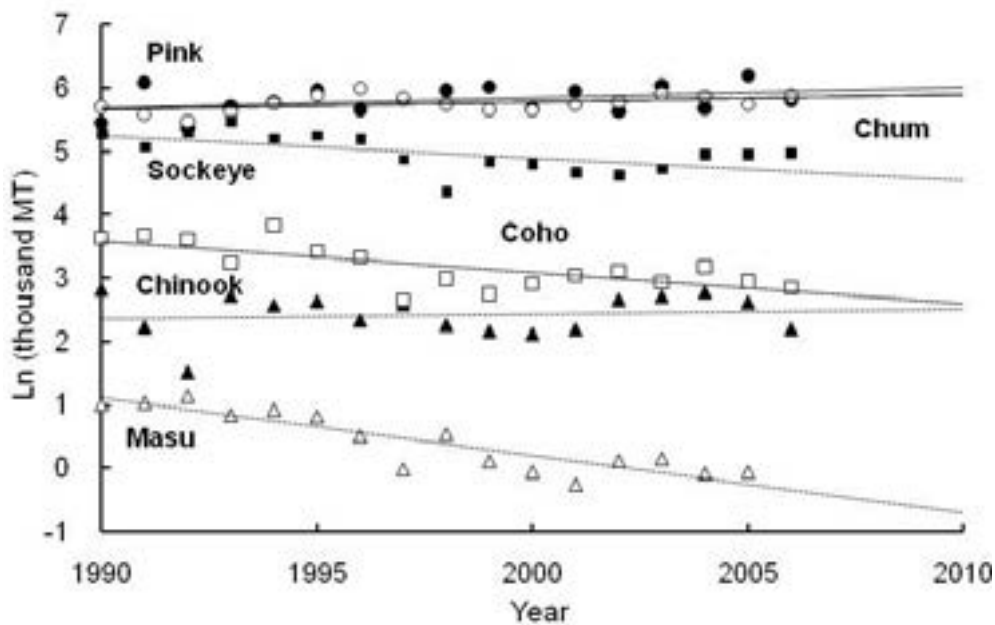


Fig. 5. Recent trends in catches of Pacific salmon since 1990. Lines indicate the results of a simple linear regression analysis between time (year) and natural logarithm of catch by species.

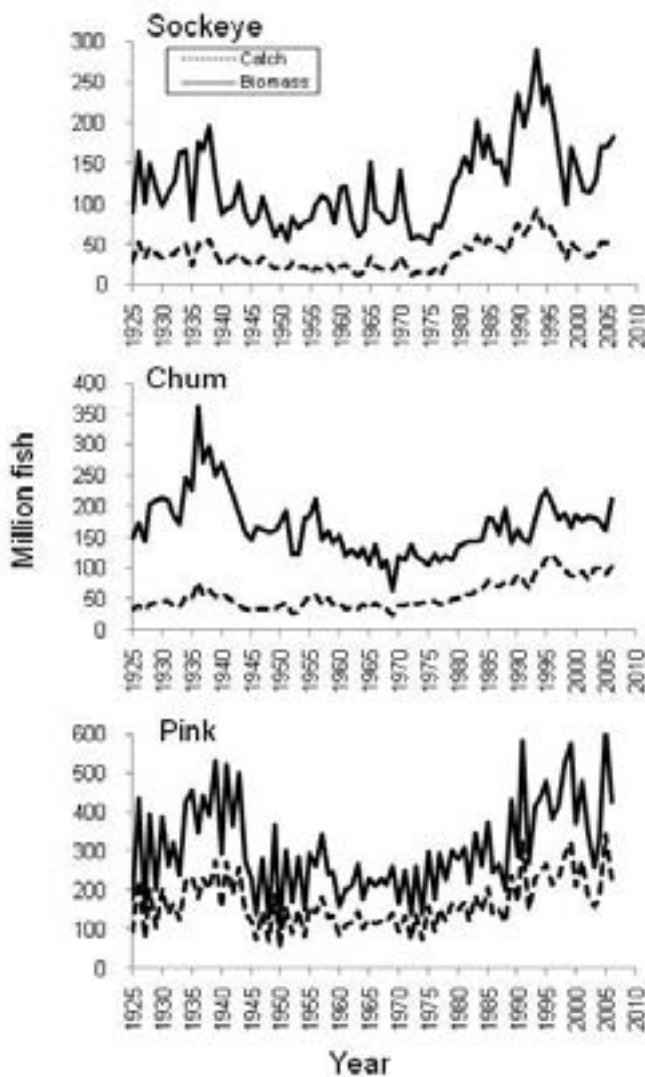


Fig. 6. Annual changes in catch and run sizes of sockeye, chum, and pink salmon in the North Pacific Ocean during 1925–2006.

and pink salmon) were 1.9–3.7 times more than catch values (sockeye: 3.7 ± 0.82 , chum: 3.3 ± 1.09 , pink salmon: 1.85 ± 0.06), and showed increases in the late 1970s and the early 1990s (Fig. 6). Although catch and run sizes of chum salmon have increased since the late 1970s, wild chum salmon showed a decreasing trend. In contrast, hatchery chum salmon are increasing exponentially in Japan and southeast Alaska, comprising more than 80% of catch and more than 40% of run size (Fig. 7). Means (\pm SD) of the rate of change in hatchery salmon run size since the 1990s were $2.1 (\pm 2.83)$ % in sockeye, $46.9 (\pm 6.06)$ % in chum, and $9.3 (\pm 4.28)$ % in pink salmon (Table 2, Fig. 8).

Results for chum salmon showed that increases in run size might lead to a reduction in body size and increases in the average age at maturity of the population suggesting a population density-dependent effect (Kaeriyama 1998). Data for Alaskan sockeye salmon also showed that greater marine growth contributed to greater survival and abundance, which

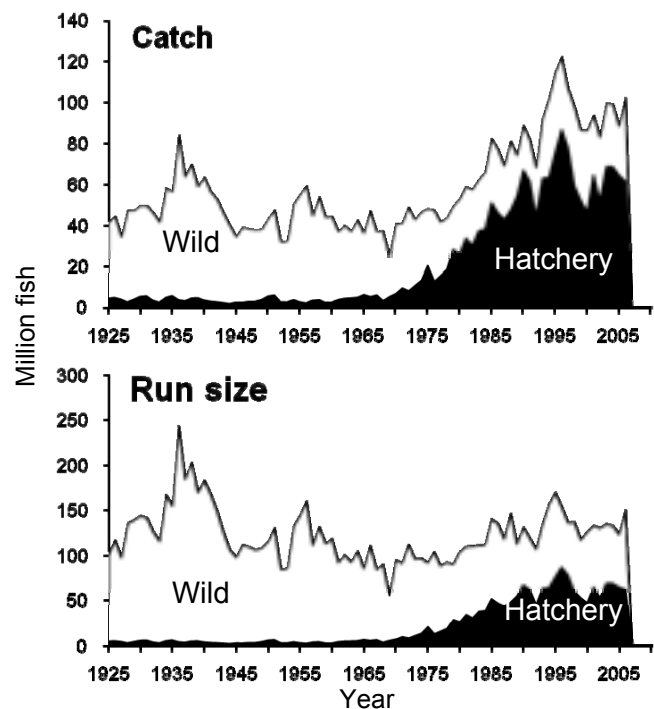


Fig. 7. Annual changes in catch and run size of wild and hatchery chum salmon during 1925–2006.

in turn led to density-dependent growth (Ruggerone et al. 2007). The biomass of wild chum salmon in the 1990s decreased to 50% below that of the 1930s, despite significant increases in hatchery populations. The density-dependent growth resulting from increases in hatchery salmon might affect wild chum salmon populations. This indicates that biological interaction between wild and hatchery populations is an important issue in the sustainable management of Pacific salmon production at the ecosystem level.

The carrying capacity of three species (sockeye, chum, and pink salmon) has decreased since the 1925 year-class, was minimal during 1945–1955 year-classes, increased during 1956–1975 year-classes, and remained constant during 1976–1997 year-classes (Fig. 9). Relationships between the carrying capacity of three species was significantly correlated with the Aleutian Low Pressure Index (ALPI) (Fig. 9; $R^2 = 0.868$, $F = 462$, $P < 0.001$, $n = 72$). Therefore, we predict that their carrying capacity will be significantly synchronized with the long-term trends in climate change. The carrying capacity of sockeye, chum, and pink salmon achieved peaks in 1985, 1993, and 1994 year-classes (Fig. 7). The total catch of Pacific salmon has declined slightly since the late 1990s (Fig. 4). Following a strong El Niño in 1997, the climate of the North Pacific underwent a rapid transition in late 1998. The PDO reversed direction and remained negative. These persistent changes in the atmosphere, upper ocean fields and ecosystem structure show that a new climate regime shift occurred in 1998/99 (Chavez et al. 2003; Peterson and Schwing 2003; Rodionov and Overland 2005).

Table 2. Annual changes in run size (millions of fish) of sockeye, chum, and pink salmon in the North Pacific Ocean. Wild = salmon derived by natural spawning; Hatchery = salmon released from hatcheries.

Year	Sockeye salmon			Chum salmon			Pink salmon		
	Wild	Hatchery	Total	Wild	Hatchery	Total	Wild	Hatchery	Total
1925	89.3	-	89.3	95.3	4.3	99.6	177.8	-	177.8
1926	165.3	-	165.3	112.0	4.7	116.7	436.3	-	436.3
1927	100.0	-	100.0	93.3	3.9	97.2	150.7	-	150.7
1928	148.9	-	148.9	133.3	2.4	135.7	396.8	-	396.8
1929	120.3	-	120.3	135.7	3.8	139.5	203.6	-	203.6
1930	97.5	-	97.5	138.8	5.2	144.0	387.2	-	387.2
1931	114.1	-	114.1	136.3	5.5	141.8	262.3	-	262.3
1932	128.8	-	128.8	122.6	3.3	125.9	324.9	-	324.9
1933	162.6	-	162.6	113.2	2.3	115.5	239.4	-	239.4
1934	167.4	-	167.4	162.4	4.7	167.1	429.4	-	429.4
1935	80.2	-	80.2	149.4	5.6	155.0	454.6	-	454.6
1936	176.5	-	176.5	239.6	3.6	243.2	347.9	-	347.9
1937	167.2	-	167.2	180.5	3.0	183.5	442.8	-	442.8
1938	195.3	-	195.3	198.4	4.4	202.8	392.7	-	392.7
1939	134.6	-	134.6	165.5	4.6	170.1	534.0	-	534.0
1940	87.7	-	87.7	179.7	3.4	183.1	293.0	-	293.0
1941	94.4	-	94.4	165.1	2.8	167.9	522.9	-	522.9
1942	96.7	-	96.7	146.6	2.5	149.1	366.4	-	366.4
1943	125.8	-	125.8	123.3	2.1	125.4	500.1	-	500.1
1944	89.9	-	89.9	104.3	1.6	105.9	275.2	-	275.2
1945	74.3	-	74.3	95.3	2.3	97.6	228.7	-	228.7
1946	82.8	-	82.8	109.3	2.2	111.5	138.1	-	138.1
1947	108.4	-	108.4	106.7	2.7	109.4	281.3	-	281.3
1948	82.6	-	82.6	103.3	2.7	106.0	131.2	-	131.2
1949	60.0	-	60.0	104.3	3.7	108.0	368.2	-	368.2
1950	72.9	-	72.9	109.7	5.4	115.1	101.7	-	101.7
1951	54.3	-	54.3	124.3	5.9	130.2	303.2	-	303.2
1952	84.0	-	84.0	81.8	2.5	84.3	171.5	-	171.5
1953	69.5	-	69.5	82.9	2.4	85.3	286.5	-	286.5
1954	76.8	-	76.8	128.8	3.6	132.4	151.6	-	151.6
1955	81.2	-	81.2	142.0	2.5	144.5	295.8	-	295.8
1956	98.4	-	98.4	158.3	1.9	160.2	263.9	-	263.9
1957	110.9	-	110.9	107.9	3.3	111.2	343.1	-	343.1
1958	104.9	-	104.9	128.0	3.6	131.6	241.2	-	241.2
1959	74.8	-	74.8	110.8	2.2	113.0	248.0	-	248.0
1960	119.3	-	119.3	115.9	2.2	118.1	157.5	-	157.5
1961	121.7	-	121.7	88.1	3.7	91.8	202.8	-	202.8
1962	79.5	-	79.5	95.8	4.3	100.1	211.1	-	211.1
1963	60.6	-	60.6	87.7	4.5	92.2	265.8	-	265.8
1964	68.6	-	68.6	99.6	4.8	104.4	179.6	-	179.6
1965	151.8	-	151.8	79.0	6.1	85.1	232.3	-	232.3

Table 2 (continued).

Year	Sockeye salmon			Chum salmon			Pink salmon		
	Wild	Hatchery	Total	Wild	Hatchery	Total	Wild	Hatchery	Total
1966	92.3	-	92.3	105.5	5.1	110.6	209.2	-	209.2
1967	87.1	-	87.1	78.1	5.9	84.0	229.1	-	229.1
1968	76.0	-	76.0	86.9	3.1	90.0	215.1	-	215.1
1969	80.6	-	80.6	49.7	5.1	54.8	264.2	-	264.2
1970	141.4	-	141.4	88.1	6.6	94.7	166.6	-	166.6
1971	93.5	-	93.5	81.7	9.3	91.0	252.4	-	252.4
1972	56.4	-	56.4	104.1	7.9	112.0	137.3	-	137.3
1973	60.4	-	60.4	85.2	10.5	95.7	261.7	-	261.7
1974	58.2	-	58.2	83.7	13.0	96.7	138.6	0.0	138.6
1975	52.4	-	52.4	71.5	20.0	91.5	299.6	0.0	299.6
1976	73.5	-	73.5	91.2	12.4	103.6	178.7	0.0	178.7
1977	72.3	-	72.3	73.0	15.2	88.2	293.9	0.2	294.0
1978	95.2	0.0	95.2	74.0	18.2	92.2	226.6	0.3	226.9
1979	125.9	0.3	126.2	61.8	28.0	89.8	303.2	1.6	304.8
1980	133.8	0.7	134.5	77.9	25.7	103.6	275.8	2.3	278.1
1981	158.6	0.4	159.0	76.2	33.5	109.7	305.6	4.4	310.0
1982	138.7	0.1	138.7	80.4	29.9	110.3	213.4	6.6	220.1
1983	202.4	0.2	202.6	73.9	37.1	111.0	341.7	5.9	347.6
1984	157.2	0.4	157.6	74.1	37.8	111.9	258.1	5.3	263.4
1985	182.7	0.8	183.5	89.2	50.9	140.1	362.6	14.2	376.7
1986	150.2	1.3	151.5	89.5	46.0	135.5	239.1	9.0	248.1
1987	151.2	1.0	152.2	75.4	42.7	118.1	244.7	22.0	266.7
1988	121.9	1.7	123.5	99.4	47.2	146.6	189.0	13.9	202.8
1989	195.7	2.0	197.8	58.3	54.1	112.4	399.3	31.8	431.0
1990	231.9	4.2	236.1	64.2	66.9	131.1	247.4	41.2	288.6
1991	190.3	5.4	195.7	57.6	61.4	119.0	546.1	39.8	585.9
1992	228.6	4.2	232.8	62.4	44.3	106.7	256.9	14.7	271.6
1993	285.3	5.1	290.3	71.9	62.8	134.7	393.5	20.7	414.2
1994	218.7	4.2	222.8	93.5	63.3	156.8	402.1	41.3	443.4
1995	244.9	1.5	246.4	94.3	75.6	169.9	455.7	24.8	480.4
1996	204.4	2.8	207.2	67.1	86.8	153.9	353.3	29.6	382.8
1997	148.9	3.0	151.9	58.5	77.9	136.4	384.3	34.0	418.3
1998	95.8	2.5	98.3	77.8	59.1	136.9	490.1	38.7	528.7
1999	166.8	3.6	170.4	65.1	52.0	117.1	524.7	52.0	576.7
2000	140.7	2.1	142.8	79.8	46.4	126.2	332.7	40.4	373.1
2001	112.9	3.3	116.3	68.6	64.5	133.1	434.2	47.2	481.5
2002	109.8	3.6	113.4	78.3	52.0	130.3	311.7	30.8	342.5
2003	126.0	4.8	130.7	66.4	68.5	134.9	199.8	59.8	259.6
2004	167.5	3.6	171.0	64.3	68.6	132.9	301.5	30.6	332.1
2005	168.3	2.8	171.0	58.8	64.3	123.2	551.9	69.1	621.0
2006	179.2	2.6	181.8	88.9	61.5	150.4	401.8	26.7	428.5

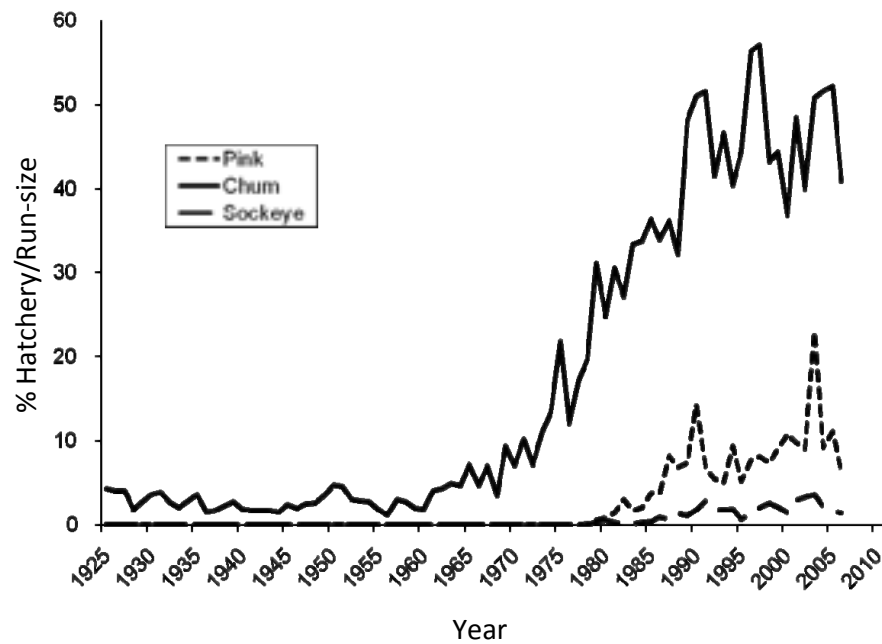


Fig. 8. Annual change in the percentage of hatchery salmon in Pacific salmon runs during 1925–2006.

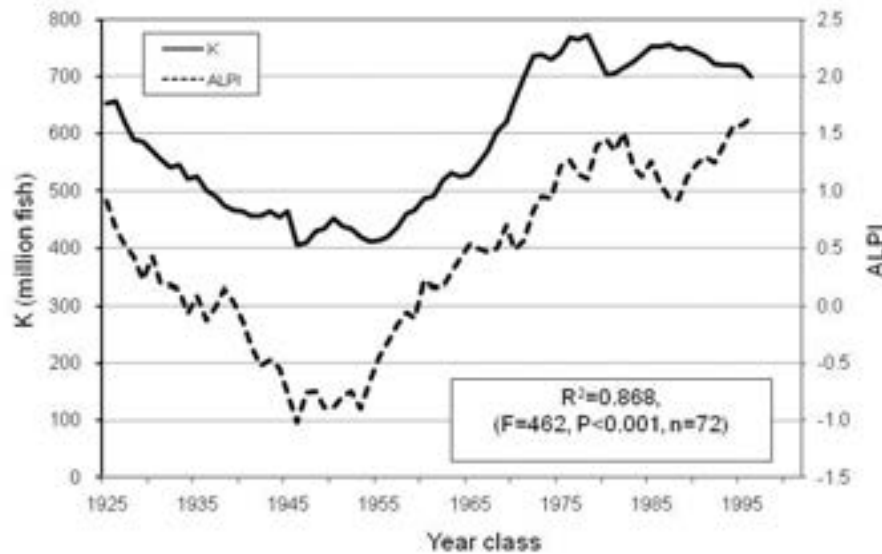


Fig. 9. Temporal changes in the Aleutian low pressure index (ALPI) and carrying capacity (K) of three species of Pacific salmon (sockeye, chum, and pink) for 1925-1997 year-classes.

In the 1998/99 change over the North Pacific, sea-surface temperatures and the upper water heat storage increased abruptly both in the Kuroshio/Oyashio Extension region in the western subarctic ocean and the central North Pacific, accompanied by cooling in the eastern North Pacific (Minobe 2002). These suggest that carrying capacities would have gradually changed to a downward trend since the 1998/99 regime shift.

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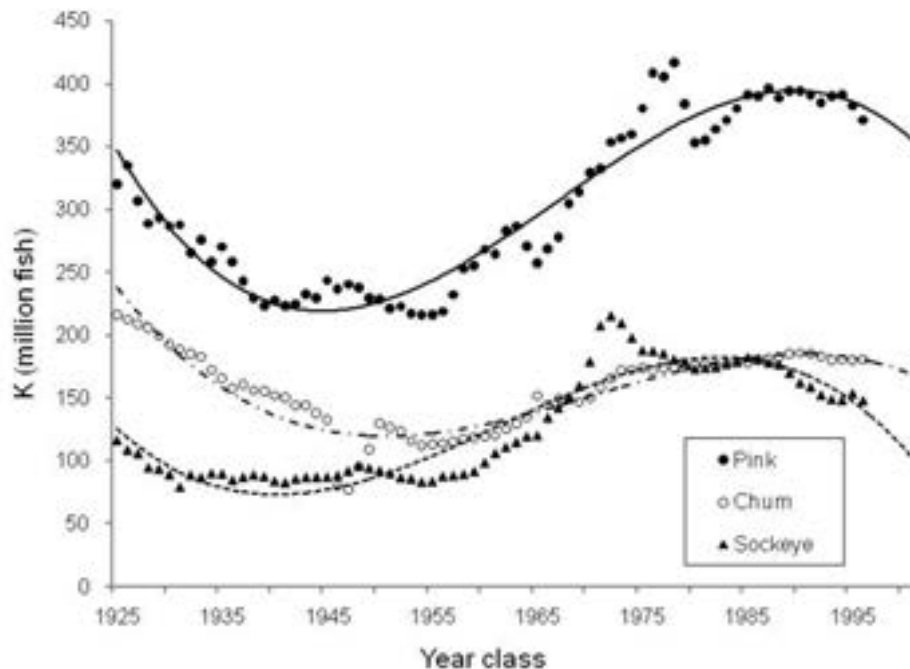


Fig. 10. Temporal changes in carrying capacity of sockeye, chum, and pink salmon for 1925-1997 year-classes.

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Body Size of Maturing Chum Salmon in Relation to Sea Surface Temperatures in the Eastern Bering Sea

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Abstract: During their last season at sea, some chum salmon from North America and Japan are known to forage in the southeast Bering Sea. Body size of mature chum salmon from North America and Japan was compared with sea surface temperatures in the winter, spring, and summer in the southeast Bering Sea during three time periods: pre-regime shift 1960–76, regime shift 1977–94, and post-regime shift 1995–2006. During the 1977–94 time period, mean correlation coefficients between body size and sea surface temperatures were positive and largest during the winter and spring. During the 1960–76 and 1995–2006 time periods, correlation coefficients were usually smaller and often negative. We conclude that chum salmon from many locations around the Pacific Rim were present in the eastern Bering Sea during the winter and spring of 1977–1994. We suggest that differences in oceanographic parameters and population density of salmon during the three time periods may influence migration pathways of salmon in the North Pacific Ocean and Bering Sea. Research on migration patterns of salmon in relation to these factors is necessary to elucidate these issues.

Keywords: chum salmon, body size, sea surface temperatures, Bering Sea

INTRODUCTION

Chum salmon (*Oncorhynchus keta*) from western Alaska and from as far south as the state of Washington (Fig. 1) can occur in the eastern Bering Sea during their last summer in the ocean (Wilmot et al. 1998). Chum salmon from Japan and Russia also occur in the eastern Bering Sea even during their last summer in the ocean (Wilmot et al. 1998; Urawa et al. 2005, 2009; Sato et al. 2009). Because the last year in the ocean is important in determining final size at maturity in chum salmon (Helle 1979) we suggest that a positive relation between body size at maturity and environmental parameters, such as sea surface temperature (SST), in the Bering Sea would indicate the presence of the chum salmon in that area.

In the Bering Sea, spring temperatures and the timing of the sea ice retreat in the spring are important in determining annual production in the pelagic zone (Napp et al. 2000; Hunt et al. 2002; Jin et al. 2007). During cold years when more ice is present, the spring phytoplankton bloom occurs in March or April, whereas during warm years when the ice retreats earlier, the spring bloom occurs during May or June (Stabeno et al. 2001; Baier and Napp 2003). During warm years, the later timing of the spring phytoplankton bloom coincides with the optimal time for the feeding and growth of zooplankton which, in turn, provides more food for pe-

lagic species such as salmon (*Oncorhynchus* spp.) (Hunt et al. 2002). This is a possible mechanism by which climate change may affect the growth of salmon.

We consider sea surface temperatures (SST) to be a surrogate for prey availability for chum salmon in the eastern Bering Sea. Thus, we examine the relation between SST in the winter/spring/summer and body size of chum salmon from North America and Japan during three time periods: pre-ocean regime shift, 1960–1976; ocean regime shift, 1977–1994; and post-ocean regime shift, 1995–2006 (Helle et al. 2007). Our hypothesis is that body size of mature chum salmon in the eastern Bering Sea that relates positively to SST during their last growth season at sea suggests their presence in the eastern Bering Sea.

MATERIALS AND METHODS

Size data used for this study of chum salmon from North America are from Helle et al. (2007). Data on body size of chum salmon from Japan are from Fukuwaka et al. (2007). For the years 1960–2006 body sizes of maturing chum salmon of North American and Japanese (Hokkaido) origin were compared to winter, spring, and summer SST in the southeastern Bering Sea during climate-ocean regime periods.

Mean Body Weight Estimates

Mean body size of Pacific salmon during the year of migration back to natal rivers were estimated from commercial fisheries harvest statistics from Kotzebue in northern Alaska to the state of Washington from 1960 to 2006 (Helle et al. 2007). Mean body size was calculated as the total biomass (kg) of chum salmon captured during year t divided by the numbers of salmon captured (N) during year t (Helle et al. 2007). Regions included Kotzebue, Norton Sound, Kuskokwim, Yukon (both summer and fall runs), Bristol Bay, central Alaska, southeast Alaska, northern British Columbia, and the state of Washington (Fig. 1). Mean size of central Alaska chum salmon was calculated as the average of the mean body sizes of chum salmon from the Alaska Peninsula, Chignik, Kodiak, Cook Inlet, and Prince William Sound areas. Weights were not available for chum salmon of Japanese origin. Fork length measurements of chum salmon from Japan were available from fish that returned to the Ishikari River on the Japan Sea coast of Hokkaido Island (Fukuwaka et al. 2007). We did not have size-at-age information for the stocks discussed in this paper. However, we are aware that differences in size-at-age or maturation of chum salmon could influence the interpretation of our results (see Helle and Hoffman 1995). In addition, we have not attempted to evaluate the complex effects of gear selectivity on body size of commercial salmon catches. We assume the correlations

between body size and SST in each area are valid.

Sea Surface Temperature (SST)

Winter, spring, and summer SST in the eastern Bering Sea were used to reflect ocean conditions experienced by salmon in the eastern Bering Sea. These were compared to body sizes of adult salmon returning to the eastern and western North Pacific Ocean. The three SST periods used were: January 15–April 15 (winter), May (spring), and June, July, and August (summer). The winter, spring, and summer SST periods also reflect climatic processes that occurred during the past winter: ice cover ($r = 0.50$; $P < 0.05$), winter surface air temperatures on St. Paul Island in the southeast Bering Sea ($r = 0.59$; $P < 0.01$), spring wind mixing, and the summer bottom temperature ($r = 0.82$; $P < 0.001$) for the period 1982–2003 (www.beringclimate.noaa.gov). Sea surface temperatures recorded at the Mooring 2 buoy (M2, 57°N, 164°W) were available from the National Oceanic and Atmospheric Administration's Bering climate website (<http://www.beringclimate.noaa.gov>) and Pacific Marine Environmental Laboratory staff. Winter, spring, and summer SST had been calculated as an average monthly sea surface temperature from the NCEP/NCAR Reanalysis at M2 in the southeastern Bering Sea (54.3–60.0°N, 161.2–172.5°W). The SST data are from the NCEP/NCAR Reanalysis project (Kalnay et al. 1996). Before 1982, the NCEP data are the

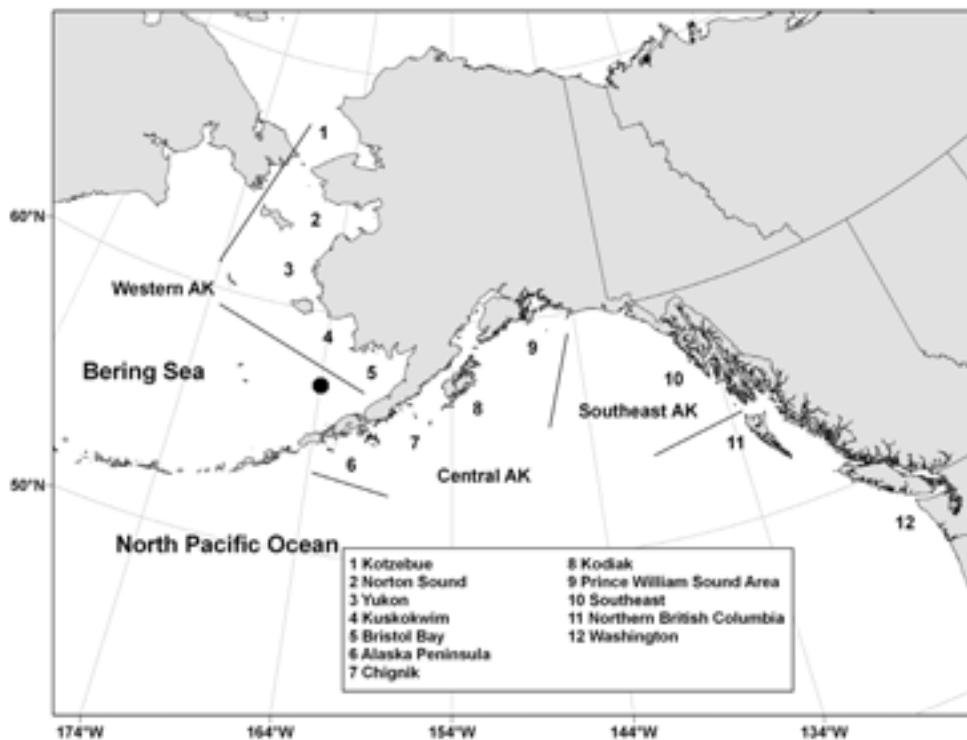


Fig. 1. Locations of salmon populations examined for changes in body size over time in Alaska (AK) (U.S.A.), British Columbia (Canada), and Washington (U.S.A.). The black dot marks the location of the biophysical mooring site M2 in the eastern Bering Sea. Mooring operated by NOAA, Pacific Marine Environmental Laboratory, Seattle, Washington.

optimally interpolated *in situ* SST based on the Reynolds and Smith reanalysis (1994). From 1982–2006, the NCEP analysis used both *in situ* and satellite data.

Relation between Body Size and SST

The Pearson product moment correlation coefficient was used to describe the relationships between mean body size of salmon populations and SST in the Bering Sea. The coefficient measures the tendency of the variables to increase or decrease together. The coefficient is calculated by dividing the covariance between the two variables by the product of their standard deviations. We decided not to test the significance of individual correlation coefficients because we were looking for regional patterns over time.

Comparisons were made between salmon body size and SST during three time periods. The periods were: pre-ocean regime change, 1960–76; ocean regime change, 1977–94; and post-ocean regime change, 1995–2006. Designations for these time periods were the same used by Helle et al. (2007). The post-ocean regime change was estimated to have begun in 1995 because chum salmon size in North America increased in 1994–1995 after declining from the late 1970s through the early 1990s (Helle and Hoffman 1995; Helle et al. 2007). Comparisons were made between salmon size and SST in the eastern Bering Sea because some populations from North America are known to migrate from the North Pacific Ocean to the Bering Sea (Myers et al. 1996; Wilmot et al. 1998).

RESULTS

Sea Surface Temperatures in the Eastern Bering Sea

Multi-year and annual variation occurred in the average SST in the eastern Bering Sea during January–April from 1960–2006 (Fig. 2). Multi-year variation indicates that temperatures were warm in 1960–70, cool in 1971–76, warm in 1977–80, cool in 1982–2002, warm in 2003–05, and cool in 2006. Temporal trends show SST dropped steeply between 1969 and 1976, rose between 1976 and 1977, and declined from 1981 through 1992. The coolest years were 1964, 1971, 1973–76, 1992, and 1999. The warmest years were 1969, 1977–1981, 2001, 2003, and 2005.

Sea surface temperatures over time in spring and summer showed much less variation than winter temperatures (Fig. 2). Comparisons of SST during the three seasons within each time period again show the most variation during winter (Fig. 3).

Relation between Body Size and Sea Temperature

Time series graphs of body size and SST for winter, spring, and summer and three time periods within each season are presented in Figs. 4–12. Generally, the correlation coefficients were small or negative during 1960–76 in all three seasons (Table 1). The largest correlation coefficient between body size and SST during the 1960–76 time period was -0.31 for Japanese male chum in winter (Table 1). For

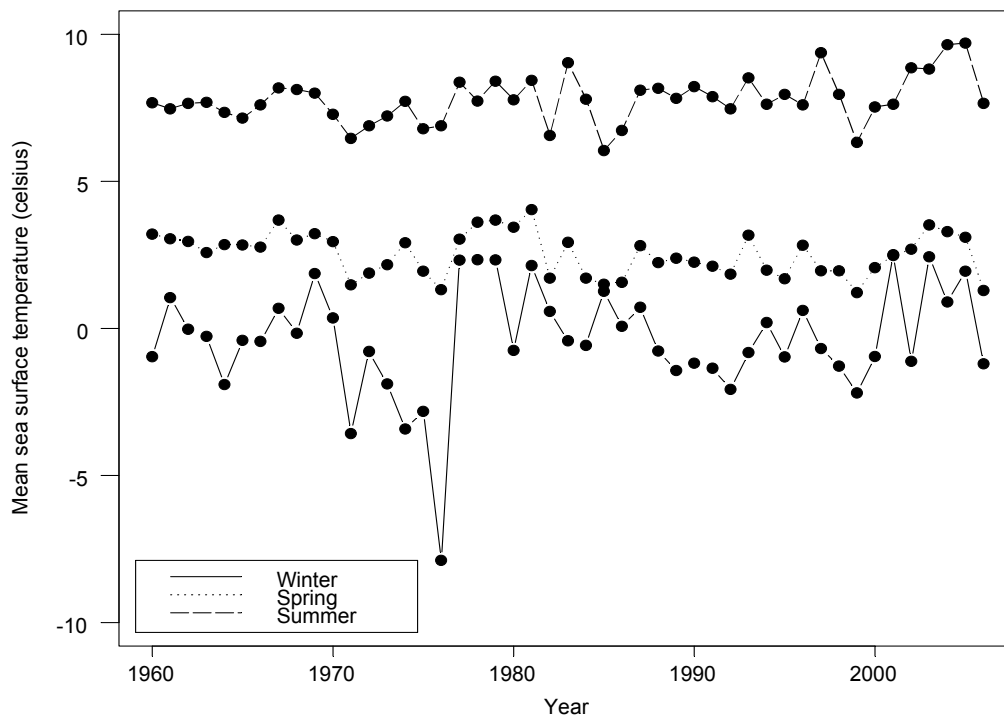


Fig. 2. Mean sea surface temperatures at the M2 mooring buoy during winter (January–April), spring (May), and summer (June–August) in the eastern Bering Sea from 1960 to 2006.

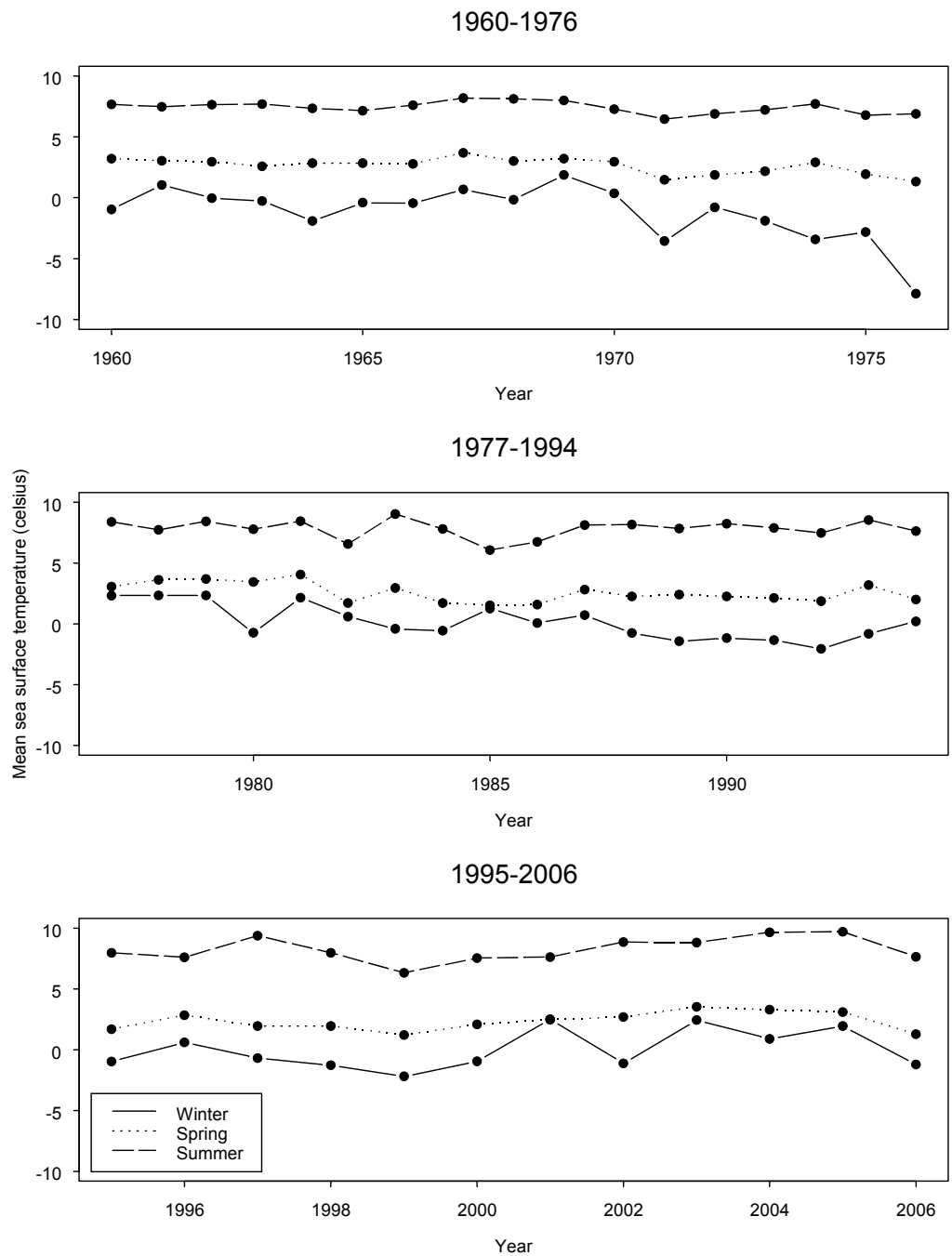


Fig. 3. Mean sea surface temperatures at the M2 mooring buoy in winter (January–April), spring (May), and summer (June–August) in the eastern Bering Sea during three time periods: 1960–1976, 1977–1994, and 1995–2006.

the 1977–94 time period, correlation coefficients were mostly positive. During the 1995–2006 time period, mean correlation coefficients were smaller than those in 1976–94. Nearly all of the correlation coefficients from central Alaska south to the state of Washington were negative from all three SST databases (Table 1). Seasonally, the mean positive correlation coefficients decreased from winter to summer for the 1977–94 and 1995–2006 time periods.

Winter

Winter SST was more positively correlated with body size than spring or summer SST for the 1977–94 and 1995–2006 time periods. Little relation is evident between body size and winter SST in 1960–76 (Fig.4). However, body size and winter SST comparisons tended to track quite closely during 1977–94 (Fig. 5). Correlation coefficients between body size and winter SST were generally larger and positive

Table 1. Pearson correlation coefficients relating mean body size of chum salmon to mean sea surface temperature (SST) in the eastern Bering Sea during winter (January–April), spring (May), and summer (June–August). Correlations were not computed when less than 10 years of paired data were available.

Area	Winter SST			Spring SST			Summer SST		
	1960–1976	1977–1994	1995–2006	1960–1976	1977–1994	1995–2006	1960–1976	1977–1994	1995–2006
Japan females ¹	0.10	0.68	0.18	0.25	0.72	0.19	0.26	0.22	0.05
Japan males ¹	-0.31	0.59	0.16	-0.21	0.54	0.32	-0.21	0.15	0.11
Kotzebue	–	0.48	0.38	–	0.38	0.51	–	0.18	0.17
Norton Sound	–	0.35	-0.02	–	0.39	0.05	–	0.19	-0.07
Yukon River summer	–	0.17	0.40	–	0.31	0.41	–	0.23	-0.06
Yukon River fall	–	0.61	–	–	0.59	–	–	0.47	–
Kuskokwim	–	0.63	-0.27	–	0.34	-0.15	–	0.09	-0.30
Bristol Bay	-0.06	0.63	0.51	0.07	0.24	0.34	0.04	0.07	0.11
Central Alaska	-0.23	0.48	-0.35	0.10	0.08	-0.46	0.28	0.003	-0.45
Southeast Alaska	-0.20	0.45	-0.52	0.12	0.28	-0.48	0.24	-0.02	-0.41
N. British Columbia	–	0.42	-0.29	–	0.47	-0.38	–	0.22	-0.58
Washington	–	0.45	-0.54	–	0.23	-0.44	–	-0.02	-0.15
Mean positive correlations	0.10	0.50	0.33	0.13	0.38	0.30	0.21	0.18	0.11

¹Mean fork lengths of four-year-old chum salmon from the Ishikari River were used in calculating the correlations with mean sea surface temperature.

during the 1977–94 time period. The largest correlation coefficients during 1977–94 in winter were from Japanese and western Alaska chum populations. During 1995–2006, the comparisons between body size and winter SST were often negative, especially from central Alaska populations south to the state of Washington (Fig. 6).

Spring

Spring SST and mean body size correlation coefficients were larger for the 1977–94 ($R = 0.38$) and 1995–2006 time periods ($R = 0.30$), and smaller for the 1960–76 time period ($R = 0.13$). Similar to the comparison with body size and winter SST in 1960–76, the comparison of body size with spring SST shows little relation (Fig. 7). There appears to be a strong relation between body size and spring SST in both female and male Japanese chum salmon; however, the rest of the stocks compared with spring SST during this time were quite variable (Fig. 8). During the 1977–94 time period, correlation coefficients between body size and spring SST were largest from Japanese, Yukon River Fall, and Northern British Columbia stocks (Table 1). During the 1977–94 time period, correlation coefficients between body size and spring SST were generally lower than they were in winter with two exceptions – Japanese female chum and northern British Columbia chum. During 1995–2006 time period, the comparison of body size and spring SST, like the winter SST in 1995–2006, there was a tendency toward a negative relation in the stocks from central Alaska south to the state of Washington (Fig. 9).

Summer

The mean positive correlations between body size and

SST were smaller in summer than in winter and spring. The mean positive correlations in the summer were largest in 1960–76 ($R = 0.21$) and 1977–94 ($R = 0.18$), and smaller in 1995–2006 ($R = 0.11$). Comparison of body size and summer SST of five populations during 1960–76 shows little relation (Fig. 10). Comparison of body size and summer SST during both 1977–94 and 1995–2006 also show little relation (Figs. 11 and 12). During the 1977–94 time period, the mean positive correlation coefficients between body size and summer SST were all smaller than those during winter or spring (Table 1). During the 1995–2006, the correlation coefficients for body size and summer SST were all negative as was seen with winter and spring SST.

DISCUSSION

Body size of adult chum salmon, pink salmon (*O. gorbuscha*), and sockeye salmon (*O. nerka*) from Alaska south to the state of Washington was negatively related to interspecific and intraspecific population abundance from 1977 to 1994 (Helle et al. 2007). Salmon body size declined significantly as population numbers increased from 1977 through the early 1990s (Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996). This relationship between body size (weight) and population abundance was not strong during time periods before 1977 (1960–1976) and after 1994 (1995–2005), even though body size was generally larger after 1994 (Helle et al. 2007). Because body size increased abruptly after 1994, Helle and Hoffman (1998) suggested that there may have been an ocean regime shift. Of these three time periods, the period between 1995 and 2005 was the most favorable for salmon because ocean resources supported salmon of both large size and large population abundance (Helle et al. 2007). Shuntov and Temnykh (2009) in this volume

Years 1960-1976

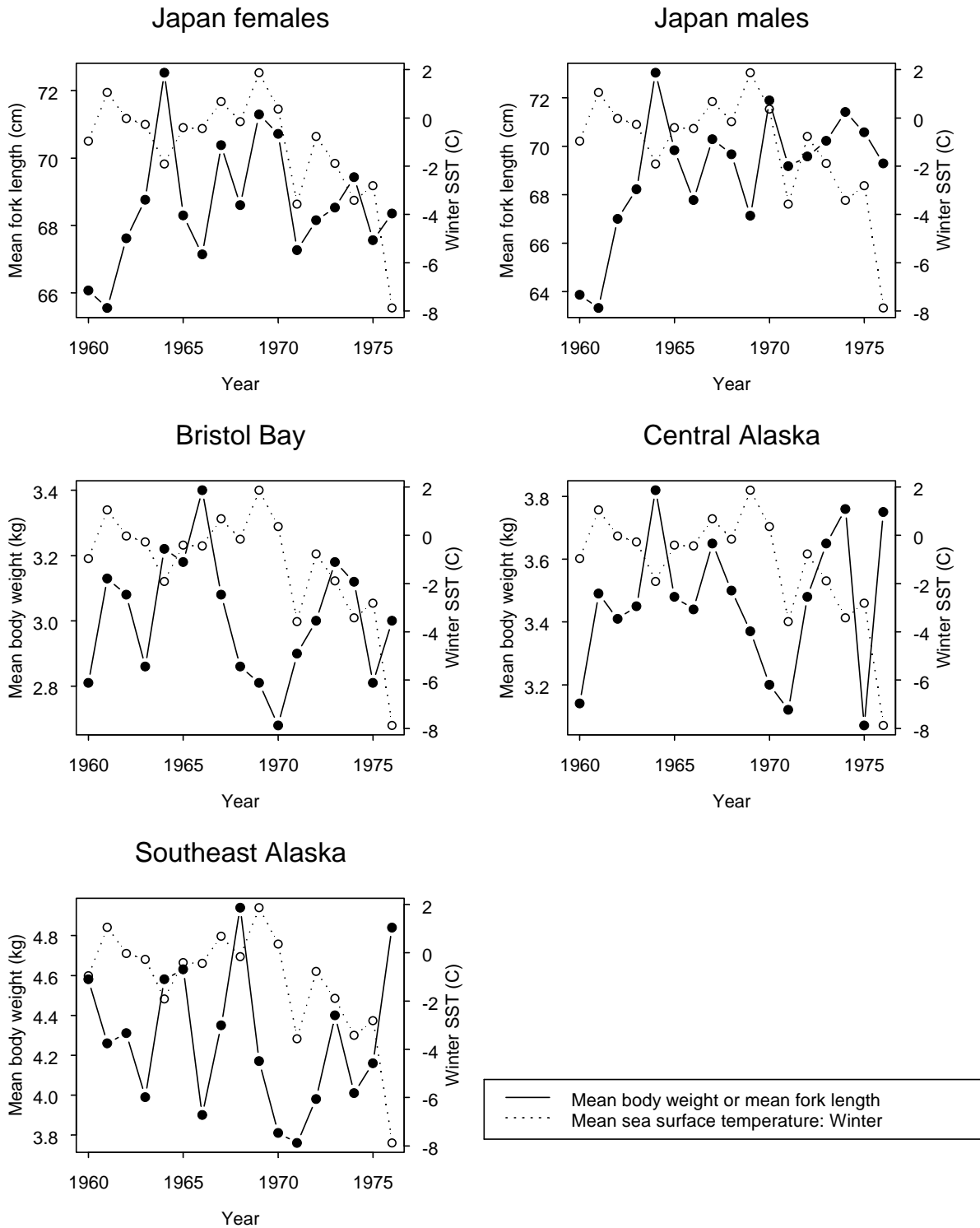


Fig. 4. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in winter (January–April) for chum salmon populations during the 1960–1976 time period.

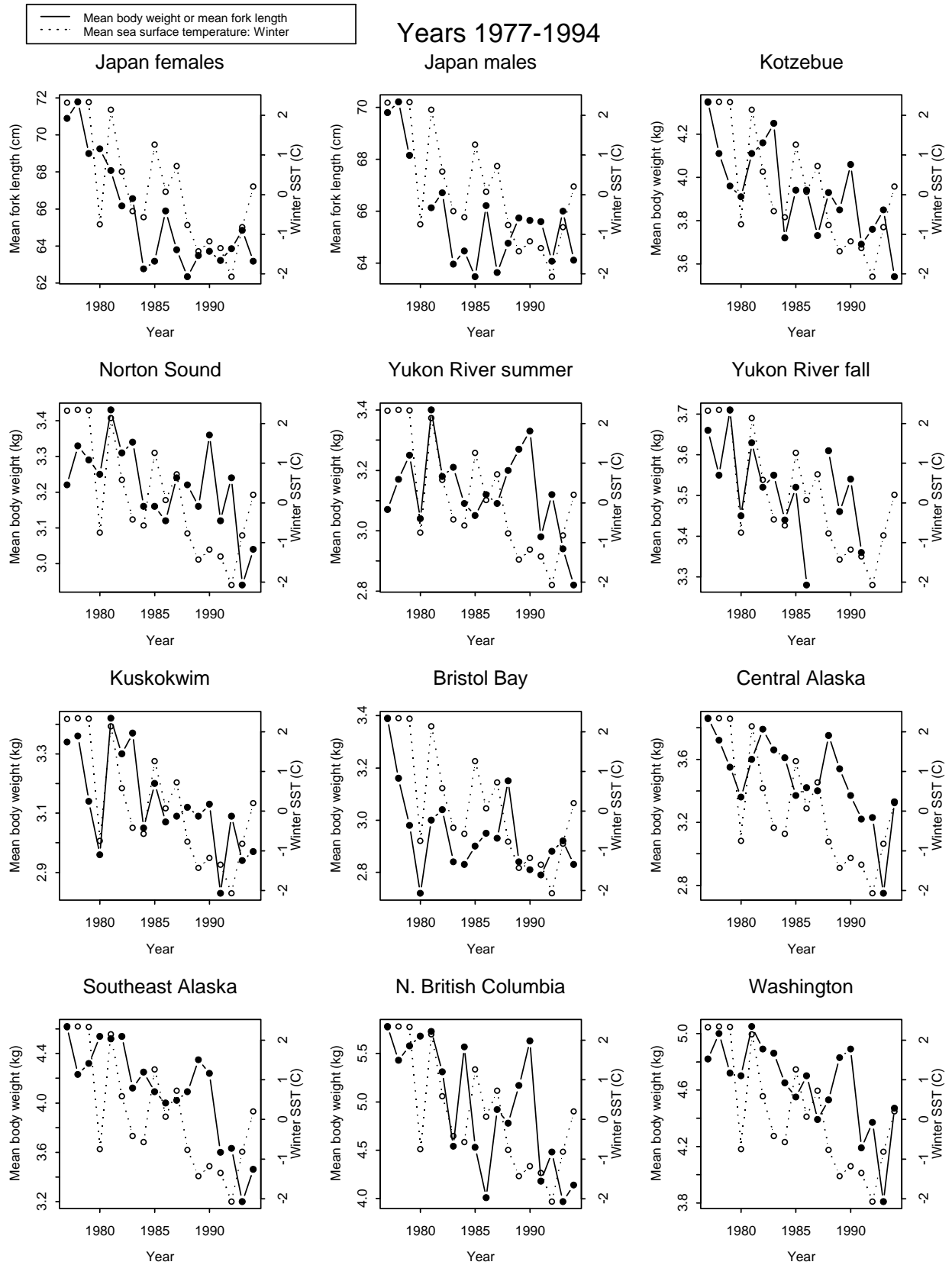


Fig. 5. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in winter (January–April) for chum salmon populations during the 1977–1994 time period.

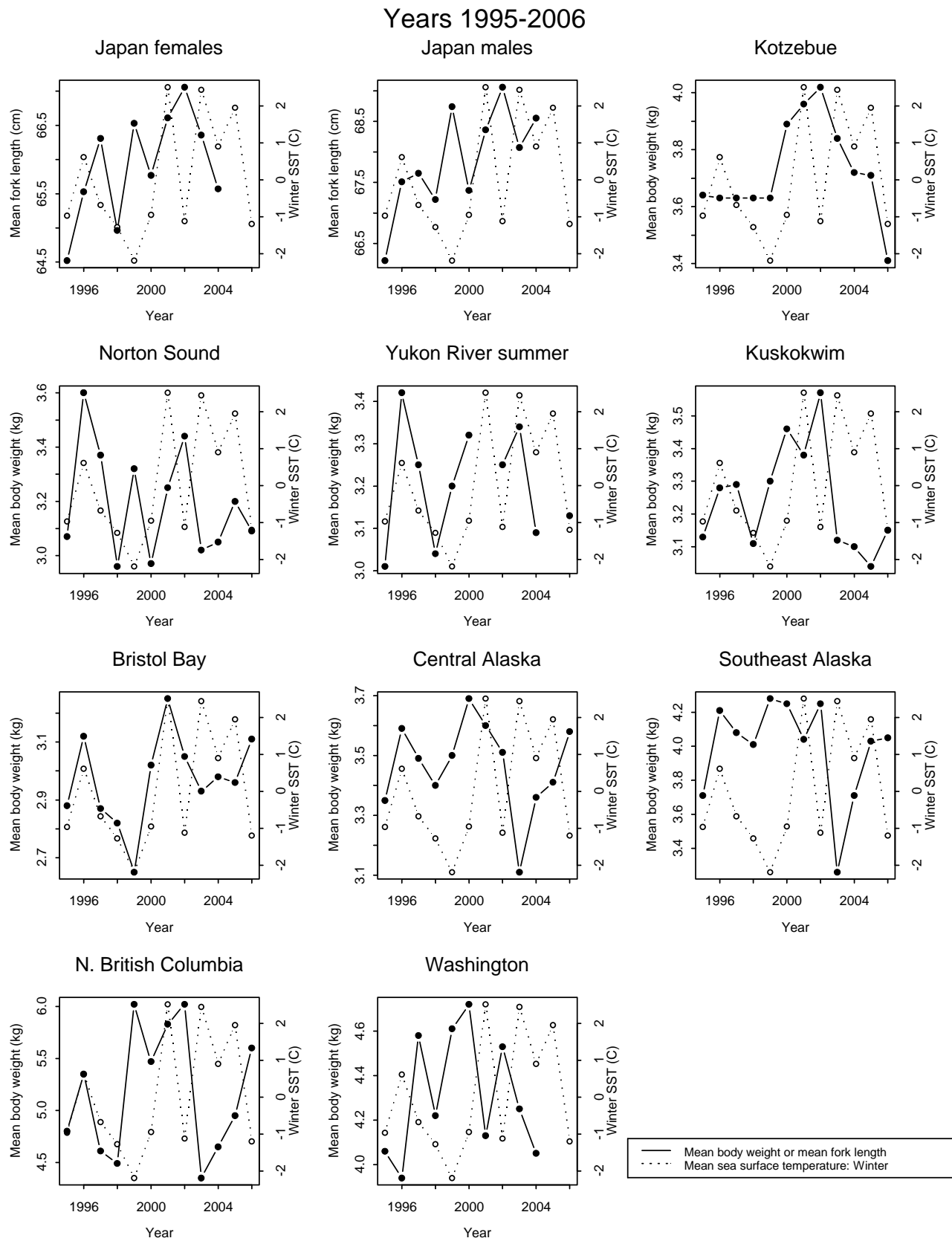


Fig. 6. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in winter (January–April) for chum salmon populations during the 1995–2006 time period.

Years 1960-1976

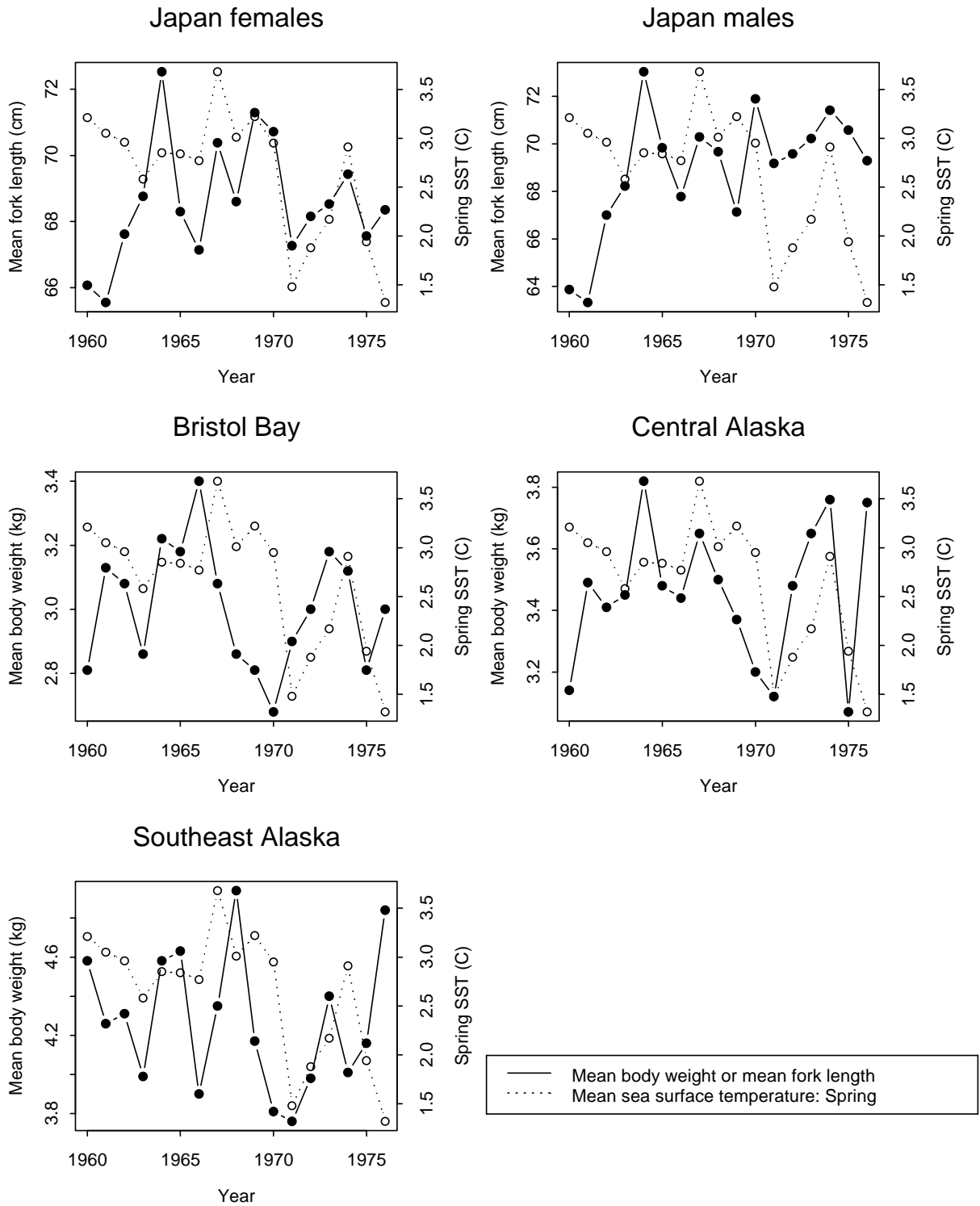


Fig. 7. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in spring (May) for chum salmon populations during the 1960–1976 time period.

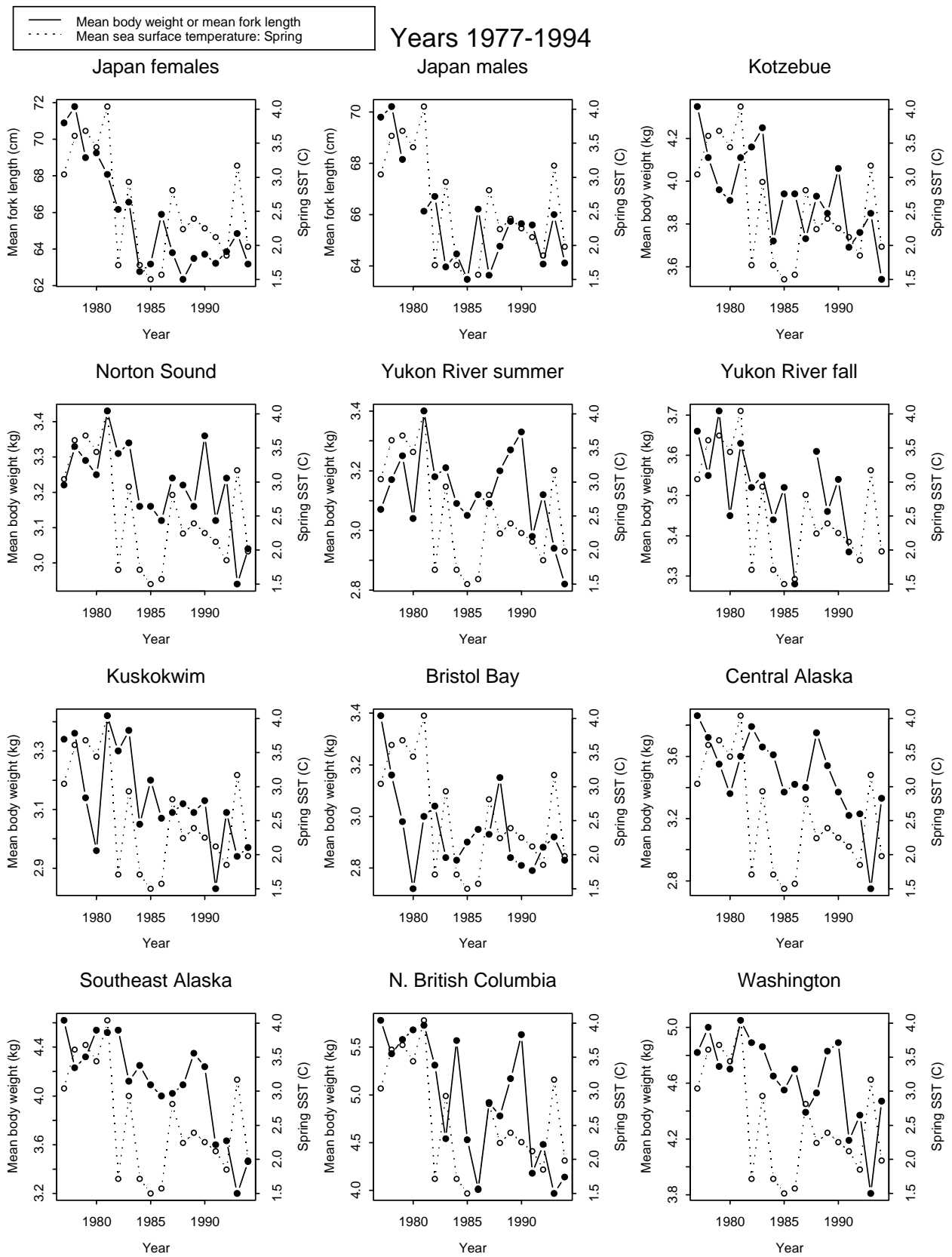


Fig. 8. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in spring (May) for chum salmon populations during the 1977–1994 time period.

Years 1995-2006

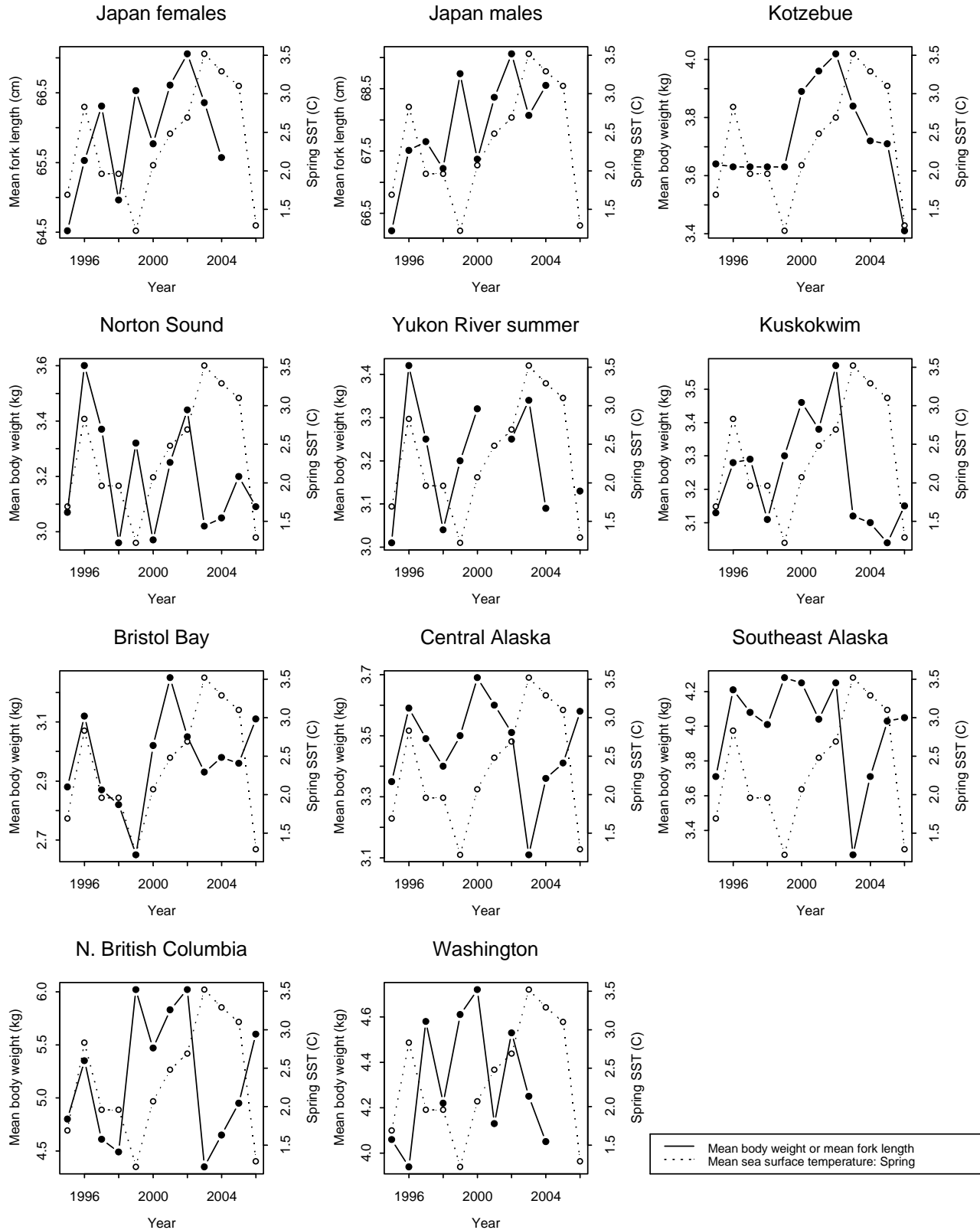


Fig. 9. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in spring (May) for chum salmon populations during the 1995–2006 time period.

Years 1960-1976

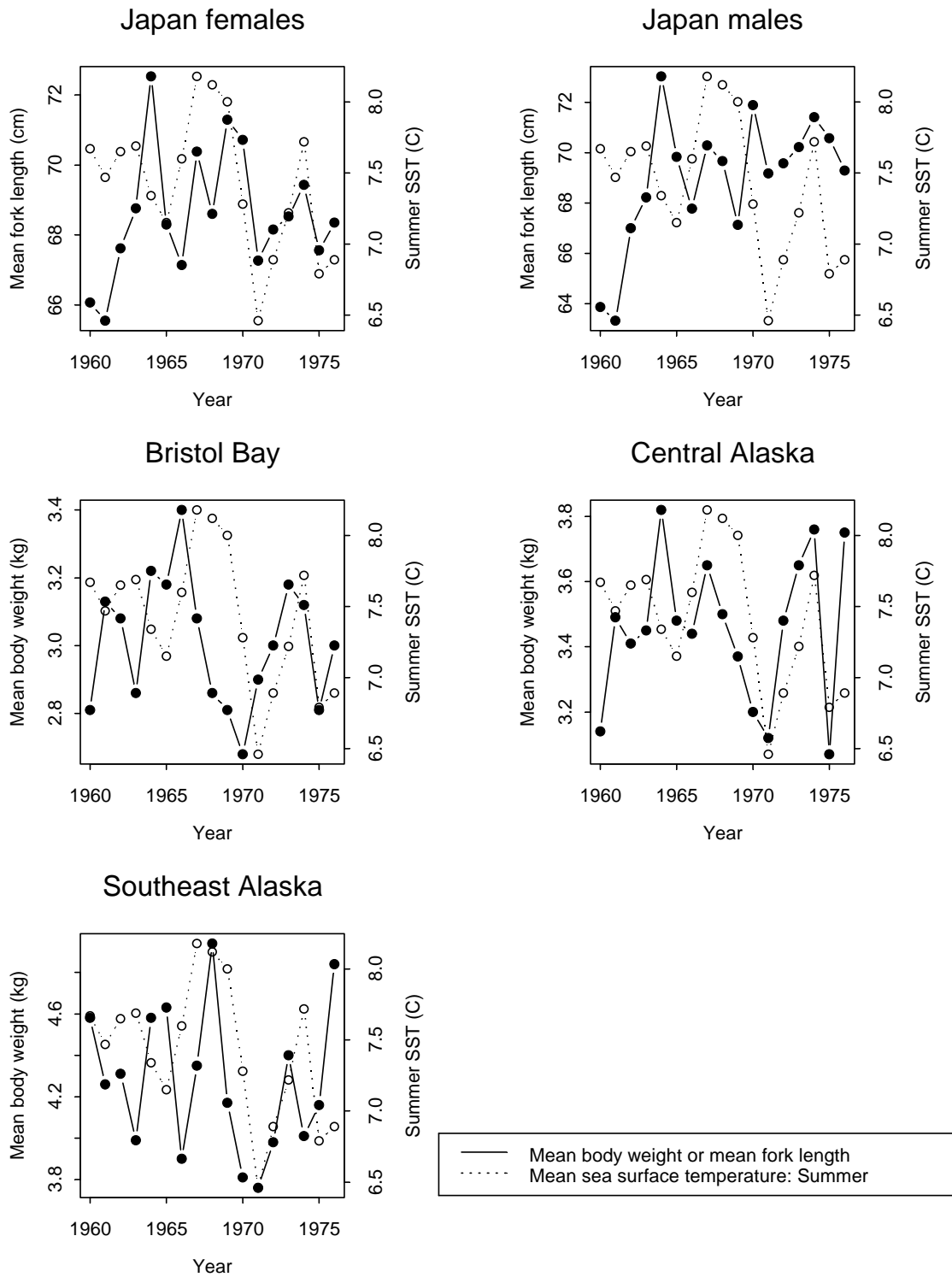


Fig. 10. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in summer (June–August) for chum salmon populations during the 1960–1976 time period.

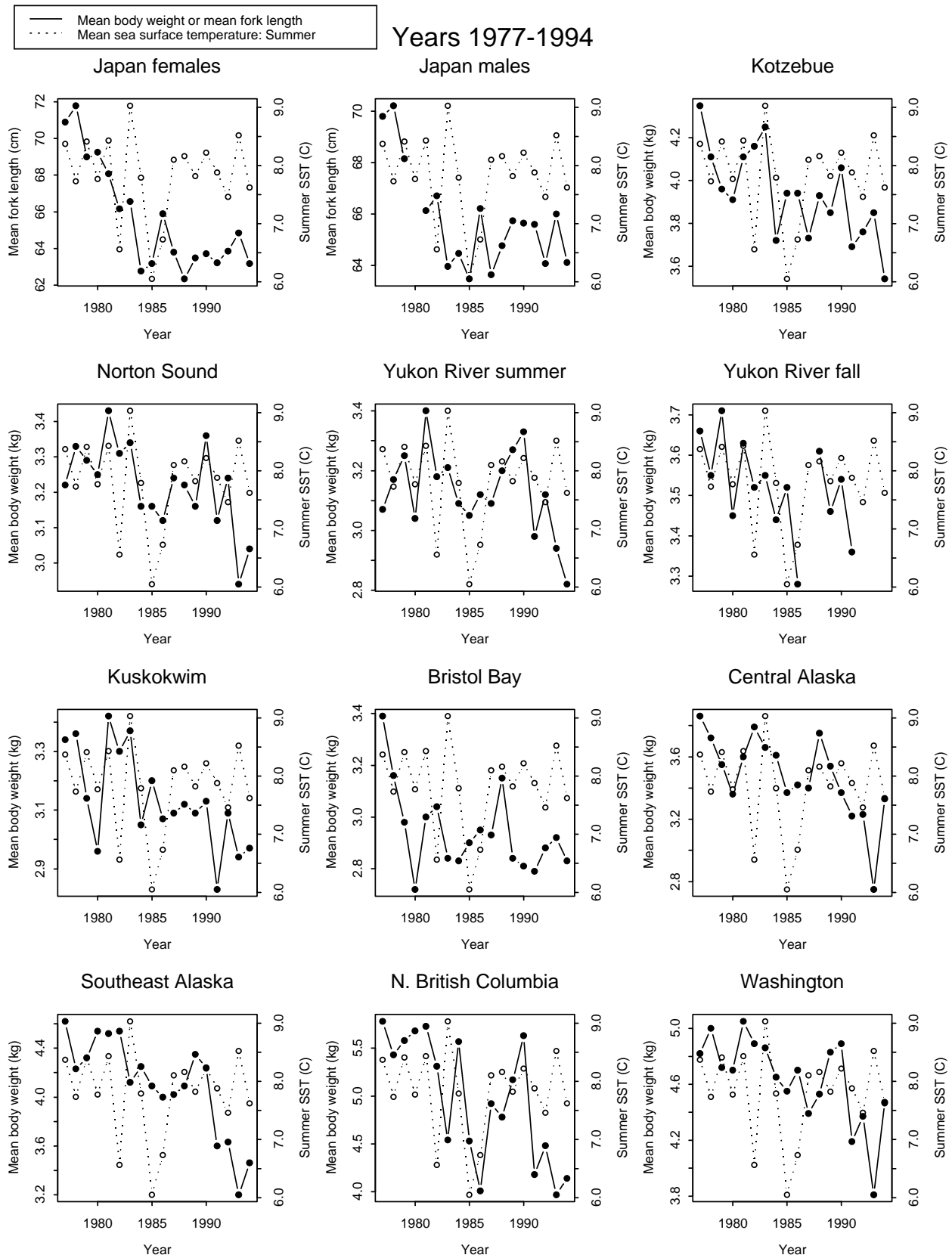


Fig. 11. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in summer (June–August) for chum salmon populations during the 1977–1994 time period.

Years 1995-2006

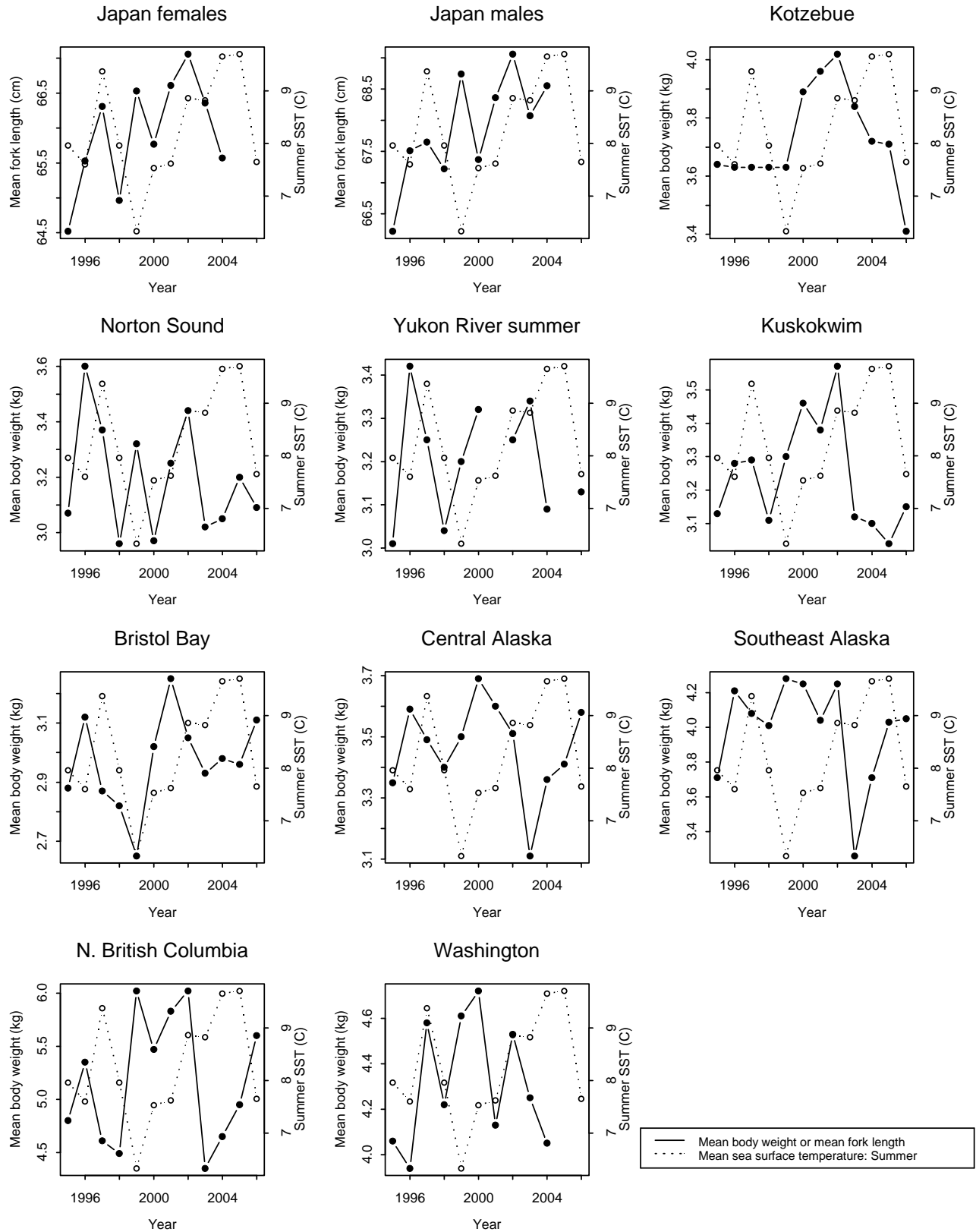


Fig. 12. Time-series of mean body weight or fork length (solid circles and lines) and sea surface temperatures (open circles and dotted lines) in summer (June–August) for chum salmon populations during the 1995–2006 time period.

provide a comprehensive discussion of biological responses to climate and ocean regime changes in the Bering Sea.

The last year in the ocean is important in determining final size at maturity in chum salmon (Helle 1979). Chum salmon from western Alaska and from as far south as the state of Washington can occur in the eastern Bering Sea during their last summer in the ocean (Wilmot et al. 1998). Chum salmon from Japan and Russia also occur in the eastern Bering Sea during their last year at sea (Wilmot et al. 1998; Urawa et al. 2005, 2009).

Correlation analysis was used to estimate the relation between body size and SST. Correlation coefficients were positive between the body size of adult salmon and winter SST in the eastern Bering Sea for the 1977–94 time period, and mixed positive and negative in 1960–76 and 1995–2006. Also, correlation coefficients were mostly larger during the 1977–94 time period compared to values during 1960–76 and 1995–2006.

Winter SST at the M2 buoy present a measure of the severity of the winter over the shelf of the southeast Bering Sea (Bond and Adams 2002). The oceanographic and climate changes associated with the anomalously cold winters and springs from 1971–1976 (McLain and Favorite 1976) are clearly represented in the winter SST data from the M2 mooring. The dramatic warming between 1976 and 1977 is also documented in the M2 mooring data and is known as the Ocean Regime Shift (ORS) of 1976–77 (Pearcy 1992; Miller et al. 1994; Hare and Francis 1995). Cooling of the sea surfaces in the eastern Bering Sea from the early 1980s through 1992 coincided with a reduction in the body size of salmon as indicated by the generally larger correlations between body size of salmon and SST during the 1977–94 period.

Several mechanisms could explain why body size was positively related to SST during the period following the ORS during the 1977–94 period when body size was declining. One factor that may influence the coincidental reductions in body size of salmon and the cooling of SST is increased competition for food resources among chum, pink, and sockeye salmon (Martinson et al. 2008; Helle et al. 2007; Ruggerone et al. 2003).

Winter/spring SST increases are thought to increase the metabolic rates of zooplankton and fish (Hunt et al. 2002). Possibly, the decline in body size was linked to reduced annual pelagic production that was, in turn, related to the change in the timing of the ice retreat and the spring bloom.

Perhaps differences in the occurrence of larger correlation coefficients between SST and body size among the three time periods are related to the migration routes of maturing salmon. Previous studies have indicated that maturing and immature chum salmon populations from Washington, British Columbia, southeast Alaska, central Alaska, western Alaska, and Asia are at times present in the eastern Bering Sea (Urawa et al. 2005; Wilmot et al. 1998). There could have been more of these Pacific Rim populations in the

eastern Bering Sea following the ORS (1977–94) than were present in the periods before and after the ORS. Correlation coefficients were larger between body size and winter SST of chum salmon from the more southerly areas of the eastern Bering Sea and Japan in 1977–94 compared to chum salmon from the more northerly areas of the eastern Bering Sea and eastern North Pacific Ocean. For example, we found that correlation coefficients between body size and winter SST from the southeastern Bering Sea were higher than those for chum salmon from the eastern North Pacific. These differences may indicate a more localized stock-specific response to changes in SST.

During the 1977–94 time period, correlation coefficients were on average lower and positive between body size and spring SST than they were between mean body size and winter SST (Table 1). Perhaps most of the populations we compared were present in the eastern Bering Sea before May. Sea surface temperature and body size correlation coefficients were on average lower during the summer than they were in the spring. Most of the western Alaska chum salmon populations are entering the rivers during June and July so correlation coefficients between body size and summer SST would be expected to be lower. The Yukon River Fall chum salmon population had the largest correlation coefficient during this time and would be expected to be in the eastern Bering Sea later than most of the other populations.

For the 1995–2006 time period, the largest correlations were between winter SST and the body size of chum salmon from Bristol Bay, southeast Alaska and the state of Washington. The Bristol Bay area is within the front of the ice edge in the spring, therefore this stock, if present at that time, would be expected to respond to temperature changes in the area. The correlation coefficient for Bristol Bay was positive while the correlation coefficients for populations from central Alaska south to the state of Washington were negative. The central Alaska, southeast Alaska, and North British Columbia populations showed much steeper declines in body size in 2003 than did the Bristol Bay population. Perhaps these populations were not present in the southeastern Bering Sea at that time. During the 1960–1976 time period, correlations between winter SST and body size were generally low and mostly negative. Stock distribution in the eastern Bering Sea needs to be monitored to understand the results of our analyses.

For most of the southern populations, correlation coefficients between body size and winter and spring SST were mostly negative during the 1995–2006 time period and positive for these populations in 1977–94. During the 1977–94 time period, body size of both North American and Japanese populations was generally large (although decreasing after 1980), population abundances were increasing, and sea surfaces were cooling (Helle et al. 2007; Fukuwaka et al. 2007). During the 1995–2006 time period, chum salmon body size increased abruptly in the mid-1990s but did not reach sizes comparable to those during the early 1970s, population

abundances were high but decreasing, and sea surfaces were warming. Warmer SST that resulted in higher productivity during the 1995–2006 time period may have reduced the density-dependent effects of large population abundances on growth rates of chum salmon. On the other hand, these fish may not have been present in the eastern Bering Sea.

The purpose of our study was to learn if SST in the eastern Bering Sea were related to body size of maturing chum salmon from North America and Japan. We assumed that larger correlation coefficients between body size and SST would indicate the presence of those populations in the eastern Bering Sea. Larger correlations between body size and SST were more common during 1977–94 than they were during either 1960–76 or 1995–2006. Helle et al. (2007) found that the relation between body size of chum, pink, and sockeye salmon and population abundance was also stronger during the 1977–94 time period. They found that population abundance was also larger during 1977–94. Perhaps population density was responsible for southern chum salmon populations moving up into the Bering Sea during 1977–94. Understanding stock distribution in relation to SST, prey availability and population abundance may be necessary to account for differences we have observed among these parameters and the three time periods.

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Current Status and Tendencies in the Dynamics of Biota of the Bering Sea Macroecosystem

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Abstract: In the analysis of the long-term changes in the biota of the macroecosystems of the Bering Sea, many researchers focus on a) global greenhouse warming, b) decadal changes in climate and oceanological regimes, and c) cascading changes at different trophic levels. We think that the association of the majority of significant biological events in the Bering Sea with irreversible greenhouse warming is not justified. The relation between the dynamic processes in the populations, communities and ecosystems of the sea with the decadal changes in the climate regime is obvious. However, due to the sheer complexity of natural events, no identical recurrence of such changes has been observed, even during time periods with similar climatic conditions. Up until now, the cause-and-effect mechanisms of the transformations in populations and communities remain insufficiently studied. Here we present a critical assessment of the hypotheses of cascade transformations, including the chain of events following the overharvest of whales. In the 1990s–2000s, a significant amount of information has been collected on the biota in the Bering Sea, representing middle and higher trophic levels (zooplankton, zoobenthos, nekton, nektobenthos, sea birds and mammals). The abundance and biomass assessments of the majority of these animals, with few exceptions, suggest that they are at medium or high multi-annual levels. We conclude that normal functioning of the biota in the Bering Sea macroecosystem ensures its ability to support both biological and fish productivity at a high level.

Keywords: ecosystem, global warming, regime shift, pelagic and bottom communities, trophic relationships

INTRODUCTION

Important changes in Bering Sea biota have resulted in the expansion of ecosystem investigations there. Today there are literally hundreds of references that discuss the complex nature of the Bering Sea, in general, and the ecology of its populations, communities and ecosystems, in particular. This research is often characterized by a variety of viewpoints, particularly when it comes to interpretations of cause-and-effect mechanisms within the dynamics of Bering Sea ecosystems. Further, this research has led scientists into a wide range of subject areas including studies on the effects of global warming, research on the cyclic dynamics of climate-oceanologic factors that influence biota, and studies of anthropogenic influences on marine ecosystems.

Since the late 20th century, an underlying theme of many publications on the changes in the biota of either ecosystems, communities, or individual species has been an assumption of some (often negative) relation to global warming caused by the greenhouse effect. In some studies on the Bering Sea and adjacent waters, modern events have been related to global warming, and forecasts have been made of their influence on Pacific salmon (*Oncorhynchus* spp.) un-

til the end of the 21st century. Such predictions have included the abundant bloom of coccolithophorids (*Emiliania huxleyi*) in the late 1990s on the eastern shelf of the Bering Sea, the mass mortality of puffins (*Puffinus tenuirostris*) in the same area in 1997, the multi-year decrease in abundance of sea lions (*Eumetopias jubatus*) and fur seals (*Callorhinus ursinus*), increased mortality and the redistribution of gray whales (*Eschrichtius robustus*) to the Arctic, significant changes in phytoplankton community structure, a decrease in primary production, and other negative effects.

At the same time, it has been emphasized (and we agree) that the negative effect(s) of warming can be seen, first of all, not in temperature *per se*, but in “secondary effects” (a decrease in the forage base, ice reduction, e.g.) (Sukhanova and Flint 1998; Bering Ecosystem Science Study Plan 2004; Macklin and Hunt 2004; PICES 2004; Grebmeier et al. 2005; Hare et al. 2007; Shuntov and Temnykh 2008a).

We do not, however, share the opinion that there is a prevailing influence of the greenhouse effect on the dynamics of the modern climate and/or the world ocean regime. No clear global tendencies can be tracked in any of the large number of publications on the multiannual dynamics of the climate-oceanological conditions in the Bering Sea or the

North Pacific Ocean, including the most recent work (Luchin et al. 2002; Minobe 2002; Khen et al. 2004, 2006; Ponomarev et al. 2007; Darnitskiy and Ishchenko 2008). Further, in addition to the obvious interannual variations, cyclicity in climate patterns for periods from several years to several dozen years has been acknowledged for decades.

The assumption that known climate changes have a natural cyclic pattern seems substantially more convincing. Based on this assumption, the modern climate state is a “common link” in the chain of the cycle of other planetary events, in which the nature epochs come to replace each other sequentially, with a different periodicities, in a wave-like manner. The statements regarding the essential role of geo-physical and cosmo-physical factors provide a reliable, fundamental basis for the cyclic changes in the atmosphere, hydrosphere and biosphere (Sidorenkov 2004; Elizarov 2005; Monin and Sonechkin 2005; Kasimov and Klige 2006a, b). Here, the instability in the slope and the rotation rate of the earth, the activity of the gravitational forces of the moon, sun and planets (the “generic tides” which direct the processes in all parts of the earth), as well as the dynamics of solar activity, are also taken into consideration.

Beginning in the late 20th century, special attention has been paid to the influence of the decadal variability in climate-oceanological processes on biota. This cyclicity has been well tracked using atmospheric and hydrological parameters. The term “regime shift” (meaning a rather sudden change in climate processes) has become very common in the scientific literature. In particular, the years 1976/77, 1988/89 and 1998/99 have been recognized as such historical milestones. At the same time, it has been emphasized that in the different areas of the North Pacific, climate and hydrobiological events within regimes can also occur with specific differences, sometimes in the opposite direction (Bakun and Broad 2001; Hunt and Stabeno 2002; Macklin and Hunt 2004; King 2005).

In light of the above-mentioned approaches and results, nevertheless, it is difficult to agree with much of the published literature. For example, the recently developed concept of regime shifts may result in changes in our previous views on the stability of marine ecosystems. However, ecosystems have never been stable. In fact, nearly all publications (including those cited above) on changes (especially the sudden ones) in climate regimes speak about the ecosystem response to such changes in the form of different transformations. Further, all such examples refer only to the individual components of an ecosystem rather than populations or communities.

Natural communities are not rigidly integrated systems. They are characterized by multi-annual dynamics and abundance fluctuations. In fact some species can enter a community and leave it without any significant consequences. The varying cyclicity in the abundance dynamics of different populations and species living within the same ecosystem supports the idea that relationships within communities are

flexible. As a result, not all events will necessarily develop according to a “falling dominoes” principle (an example of such a cascade in the ecosystem of the Bering Sea: killer whales (*Orcinus orca*) switch from feeding whales to sea lions and after that to the sea otters – resulting in a decrease in the number of the sea otters (*Enhydra lutris*); an increase in the number of the sea urchins (*Strongylocentrotus* spp.); a destruction of algae; essentially the destruction of the near-shore ecosystem) (Estes et al. 1998). To describe the response of communities to the environmental changes, Shuntov (2000) suggested the example of a chess game, where a limited set of rules exists but with a very large number of possible results. In such an example, the reaction of biota to the same climate influence can be different in different regions. In other words, each has its own individual chess game. This is the essence of the “provinciality” principle described in the middle of the 20th century by the Russian fisheries scientist G.K. Izhevskiy (1961, 1964). The dynamics in the abundance and state of the population of each species in the ecosystem is a result of the complex activities and the influence of various factors, including the cosmo-physical, climate-oceanological, and biological. All these factors are constantly overlapping each other and can act in different combinations. Each group of factors at certain stages can either enhance or neutralize the action of others. Because it is difficult to estimate the total influence of all factors, variations in population abundance are generally unpredictable. Therefore, because of the lack of reliable population data, it is possible to speak only about the ‘tendencies’ in the dynamics in abundance of populations (Shuntov et al. 1993). It looks like ‘the effect of the black box’ works there as well.

Regrettably, we think that there are very few sufficiently thorough investigations of the structure and functioning of marine macroecosystems over vast sea and ocean territories. This is because it is much easier to study individual components of ecosystems rather than the ecosystem itself. We also emphasize that almost everywhere the lower trophic levels (phytoplankton, bacteria and protozoa), the production of which is many times larger than the total production at higher trophic levels, have been poorly studied and rarely quantitatively estimated.

Much more reliable information has been collected on the composition and qualitative characteristics of biota at the middle and higher trophic levels. For some of them, i.e. meso- and macro-zooplankton, as well as nekton (fish and squids), the studies included in the BASIS program achieved good results. During the same years, the new information on zoobenthos and nektobenthos (bottom fish and commercial invertebrates) obtained as a result of the national research programs of Russia and the USA, has been added to the database.

The results of 20 years of ecosystem observations allow us to evaluate the current state of the pelagic and bottom communities in the Bering Sea taking into consideration inter-annual and multi-annual dynamics. We will be able to

determine regularities in the dynamics of these communities of the Bering Sea and to define the functional characteristics of these communities in the 1980–2000s, during which several so-called regime shifts occurred.

MATERIALS AND METHODS

Due to the significant differences in the methods of collection and treatment of zooplankton and nekton, the data from expeditions of different research institutions and countries, as well as those obtained in different years, are often difficult or even impossible to compare (Shuntov et al. 2007a).

For this reason, the materials of 160 expeditions of TINRO-Centre in the far-eastern seas, beginning 1980, were used. In addition to the data on the benthos (1000 stations) and bottom fish (13,000 trawls), the database of new information at TINRO-Centre on the macroecosystem biota during 1980–2000 includes the results of about 25,000 trawls (out of them about 4000 trawls were conducted in the Bering Sea). These data were systematized and combined in a series of catalogs on the composition and quantitative distribution of nekton in the far-eastern seas and the northwest Pacific Ocean (Shuntov 2003, 2004, 2005, 2006). These data as well as data from 10,000 plankton stations (> 2600 in the Bering Sea) were used for the study of multi-year trends in the nekton and plankton communities of the far-eastern seas (including the western Bering Sea) during the last 25 years. Data on average plankton and nekton biomass were systematized for the far-eastern seas, for the years 1980–1990, 1991–1995, 1996–2006), 48 standard statistical regions, and three different topographic zones (inner shelf, outer shelf, deep-water basins) (Shuntov and Temnykh 2008b; Volkov 2008).

RESULTS

Status and Multi-annual Dynamics of the Zooplankton Community

The mean multi-annual total biomass of zooplankton is approximately one-and-one-half times less in the Bering Sea than in the Okhotsk Sea: 755 mg/m³ and 1,106 mg/m³, respectively (Shuntov et al. 2007b). The concentration of macroplankton (the main food source of nekton older than those at the fry stage) in those seas is approximately the same.

Inter-annually, the average total biomass of zooplankton in the Bering Sea and other comparable regions normally varies by not > 1.5–2 times (Volkov et al. 2007). In total, no distinct differences in the biomass of zooplankton in either ‘warm’ or ‘cold’ years were observed. However, an increased biomass was more often observed in colder years. As a rule, in the absence of the growth spurts and significant decreases in the zooplankton biomass in individual years in the western Bering Sea, plankton stocks do not differ much in different periods of years (Table 1).

Therefore, over 20 years, the zooplankton resources in the western Bering Sea, in general, and macroplankton, in particular, remained at a high and relatively stable level.

In contrast to the relative stability of the total zooplankton stock, the ratio of different plankton species and groups can differ distinctly in different years. For example, inverse tendencies in the dynamics of copepod biomass on the one hand, and euphausiid and arrow worm biomass on the other, are observed (Volkov et al. 2004, 2007). However, data on the abundance of specific zooplankton species or groups in the Bering Sea are lacking, such that in most cases conditions (whether favourable or limiting) for successful reproduction are unknown. In particular, no sufficient explanation has been found for the significant decrease in macroplankton abundance in the early 2000s on the eastern shelf of the Bering Sea, or the recent increase in density beginning in 2006 (Volkov et al. 2007).

Multi-annual Dynamics of Benthos

Regular monitoring of the status and quantitative distribution of benthos from the 1950s to the 2000s has been conducted only in the western Bering Sea. From the 1950–1960s to the 1980s no appreciable changes or transformations in the composition of benthic communities were observed (Shuntov 2001; Dulepova 2002). Of course, this conclusion does not exclude the presence of some differences in biomass distribution, the configuration of the borders of bottom communities, the level of total benthos biomass and/or the ratio of different taxa within them. We assumed that these differences were within the range of the natural dynamics that is typical for relatively stable communities. In the 2000s, the TINRO benthos surveys on the shelf of the western Bering Sea were repeated (Nadtochiy et al. 2008). In general, the new data confirmed our previous conclusions on the stability of the benthic communities at a macroecosystem scale (Fig 1).

Table 1. Total biomass of zooplankton/macroplankton (millions of tons) at night in the upper epipelagic layer of the western Bering Sea during different time periods (Shuntov and Temnykh 2007).

Year	Inner shelf	Outer shelf	Deep-water regions	Total
1986-1990	7.87/5.23	20.75/14.56	61.21/49.99	89.83/69.87
1991-1995	2.64/1.9	19.63/14.8	63.81/52.35	86.08/69.06
1996-2006	6.74/5.16	19.52/16.58	70.08/53.65	96.34/81.39

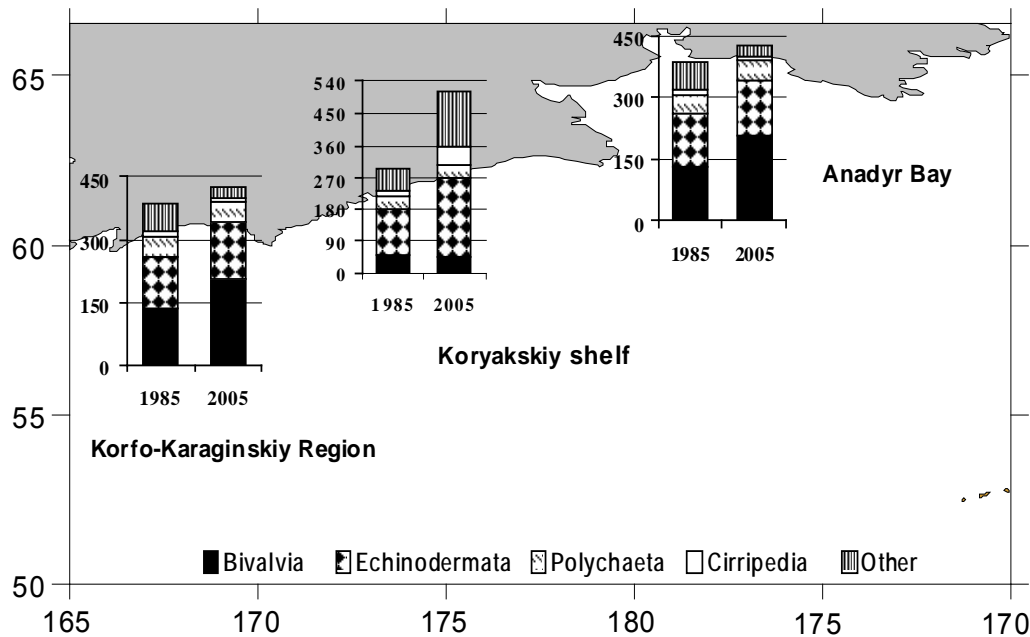


Fig. 1. Composition and biomass (g/m²) of macrozoobenthos in the western Bering Sea from 1980–2000 (Nadtochiy et al. 2008)

Based on the data collected in all the three areas of the western Bering Sea, it is possible to say that the general appearance and location of the benthic population on the shelf of the Bering Sea have remained consistent over several decades.

Status and Multi-annual Dynamics of the Nektobenthic Community

The biomass of benthic fish species increased from the 1980s to the 2000s on the western Bering Sea shelf (Fig. 2). Some changes have also been observed in the structure of nektobenthic communities over the last 20 years. The most typical feature of the structure of the bottom communities in the western Bering Sea in the 1980s was the absolute predominance of cod – almost 70% in Anadyr Bay and about 83% on the Koryakskiy Shelf (Borets 1997). A dramatic increase in the abundance of this species, combined with an increase in reproduction, beginning in the late 1970s, occurred in many parts of the far-eastern seas, including the eastern Bering Sea (Fig. 3). Up until now, cod, together with flat-fish and sculpins, remain the main species contributing to the biomass. Based on data discussed above, it can be assumed that ‘modern’ levels of bottom fish abundance in the western Bering Sea should be considered relatively high.

The biomass dynamics of the main commercial bottom fish species from the 1980s to 2007 in the eastern Bering Sea are shown in Fig. 3. In that area, monitoring the status and dynamics of the populations of bottom fishes and crabs is conducted more systematically and regularly. One of the main conclusions based on those assessments is that in the 1980s–2000s the abundance of bottom fishes on the shelf of

the eastern Bering Sea was similar to levels in the 1960s–1980s. In the 2000s, a gradual decrease in abundance was seen only for cod (*Gadus macrocephalus*) and Greenland turbot (*Reinhardtius hippoglossoides*). Other important species in bottom communities have remained at high levels in recent years (about the same as levels in the 1980s.).

State and Multi-annual Dynamics of Nektonic Communities

Figure 4 shows changes in nekton density in 48 statistical areas of the northwestern Pacific Ocean. In the 1980s nekton density in the epipelagic zone of most areas was very high. In the early 1990s it decreased, and since the middle of the 1990s it has begun to increase again, but still has not reached the 1980s values. The very high abundance of nekton in the 1980s was the result of a massive decrease in populations of walleye pollock in northern boreal waters and the western Pacific sardine in southern boreal waters. In the early 1990s, the decrease in abundance of these fish, especially the western Pacific sardine, was so significant and sharp that it could not be compensated by an increase in abundance of a large number of fish and squid species - such as herring, Pacific saury, Pacific salmon, Japanese anchovy, Atka mackerel, Pacific squid and others.

The above-mentioned dynamics in nekton density are typical for the entire far-east region, including the western Bering Sea. Throughout the area nekton density showed a sharp decrease in all zones in the first half of the 1990s. In the following decade, it did not change appreciably in either the outer shelf or shelf edge waters of the Bering Sea (Fig. 4, Table 2).

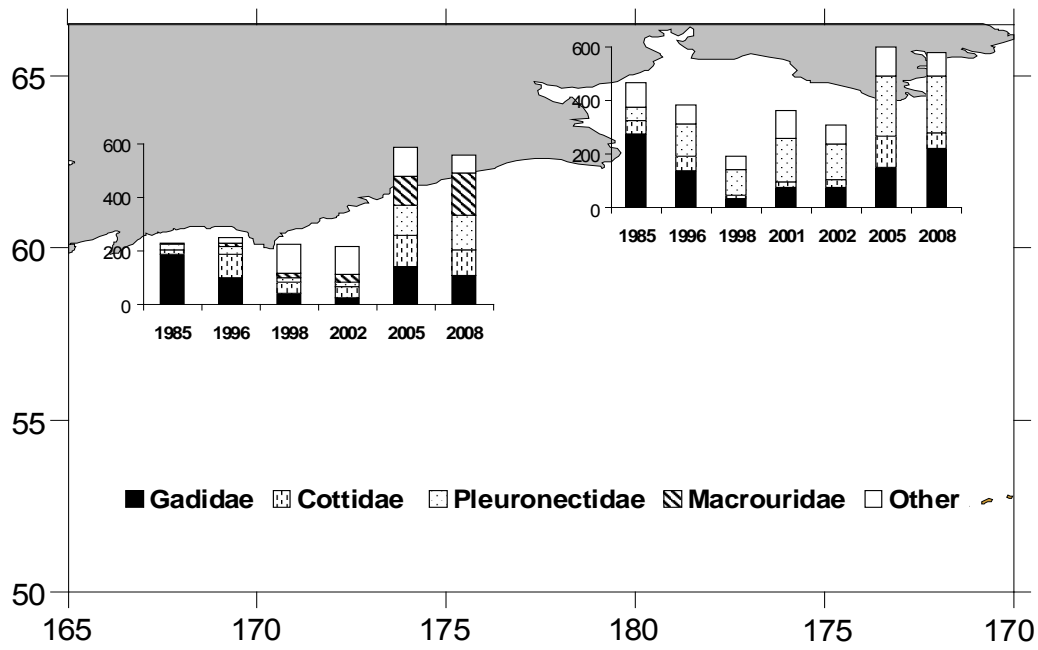


Fig. 2. Composition and biomass (thousand tons) of benthic fishes in the northwestern Bering Sea during 1985–2002.

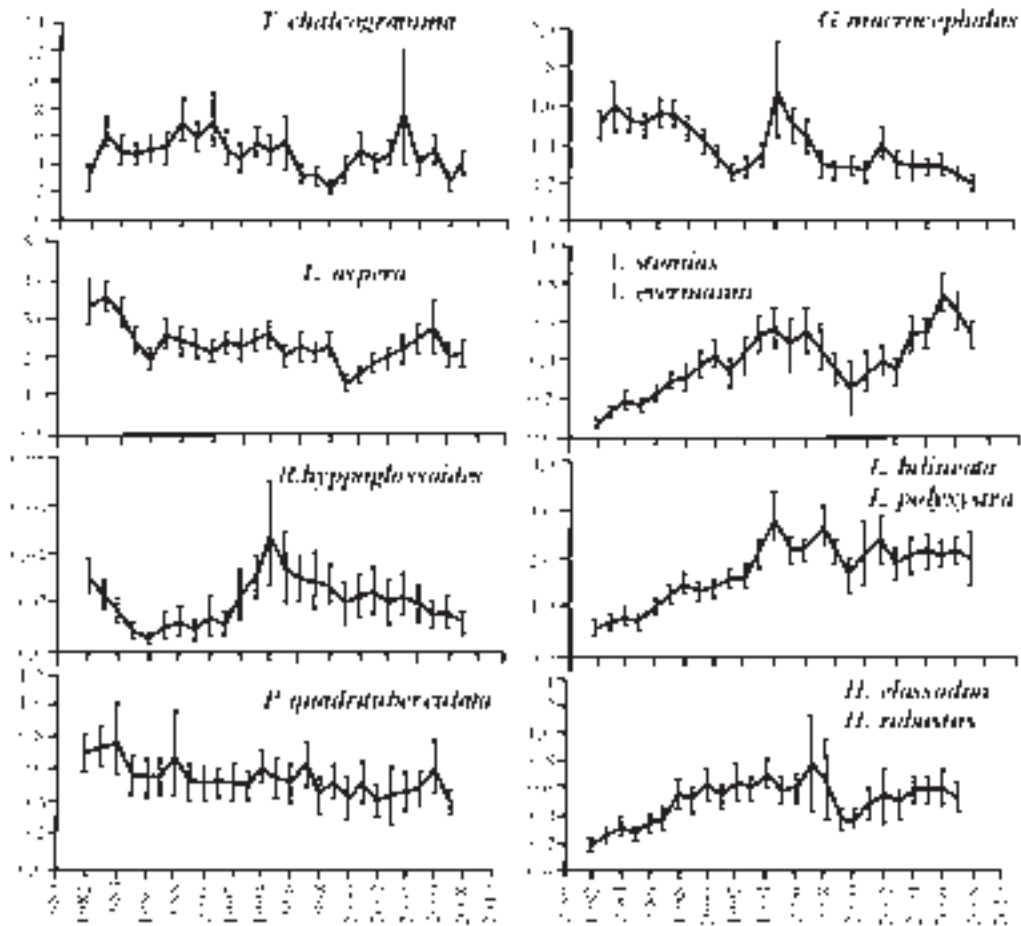


Fig. 3. Biomass dynamics (million tons) of major commercial fish species on the shelf of the eastern Bering Sea during 1982–2007 (Lauth 2007).



Fig. 4. Average biomass (tons/km²) of nekton species in the epipelagic layer of biostatistical areas of the far-eastern seas and adjacent Pacific waters in 1979–1990 (A), 1991–1995 (B) and 1996–2004 (C). 1 = up to 1, 2 = 1.1–5.0, 3 = 5.1–20.0, 4 = over 20 t/km², circled numbers = average biomass in the biostatistical area (Shuntov et al. 2007b).

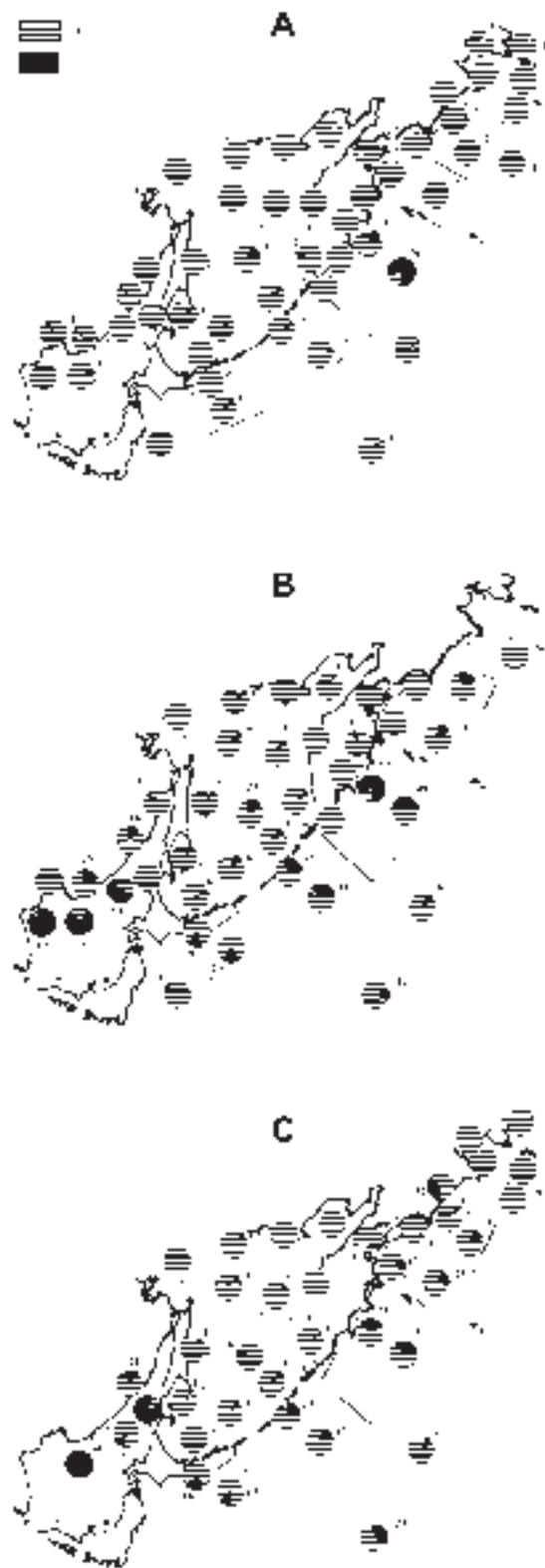


Fig. 5. Ratio of different nekton components in the epipelagic layer of different biostatistical areas of the far-eastern seas and adjacent Pacific waters in 1979–1990 (A), 1991–1995 (B) and 1996–2004 (C). 1 = fishes, 2 = squids, numbers = percentage of squids and crustaceans (Shuntov et al. 2007b).

Table 2. Dynamics in relative biomass averages (tons/km²) of nekton species in upper epipelagic layer of the far-eastern seas and northwestern Pacific Ocean during 1979–2004 (Shuntov and Temnykh 2008b).

Topographic zone	1979–1990	1991–1995	1996–2004
Bering Sea (western)			
Inner shelf	9.3	2.8	6.0
Outer shelf and the shelf edge	23.2	22.0	19.7
Deepwater regions	7.6	0.8	2.0
Far-eastern region*			
Inner shelf	13.0	4.5	8.1
Outer shelf and the shelf edge	23.4	8.4	15.8
Deepwater regions	8.1	1.5	3.3

*Hereafter within the borders of the biostatistical areas in Fig. 4.

In the epipelagic zone in both the western and eastern regions, walleye pollock was always dominant. At present, its population density still continues to remain relatively high.

At present, the total nekton biomass in the Bering Sea is slightly lower when compared with levels in the 1980s, mainly due to the decrease in the abundance of walleye pollock. The abundance of the walleye pollock stocks in both the western and eastern Bering Sea is low. The ‘shortage’ of this species in the total nekton biomass seems to be within the range of 5–10 million tons. However, in the nekton community there are at least two groups, squids and Pacific salmon, with abundance levels that are now higher than in the 1980s.

In the 1980s, fish were dominant in nekton communities of the epipelagic zones almost everywhere (with the exception of Pacific waters off Kamchatka) (Fig. 5). However, in the 1990s and 2000s, the squid share increased significantly. The squid biomass increased several times in the second half of the 1990s and 2000s (Fig. 5). These changes cannot be explained simply by a decrease in the abundance of consumers (primarily fish). Most probably, the changes are a result of the combined effects of many different factors, among which may be favorable conditions for reproduction for at least some squid species (Shuntov et al. 2007b). As a rule, the majority of squids are beyond the edge of the inner shelf (Table 3). However, in the second half of the 1990s and 2000s biomass of squids increased noticeably in the inner shelf waters as young squid are carried there by the currents.

Abundance of salmon in nekton communities of the far-eastern seas has increased more than three times in comparison with the 1980s. For example, in the summer of 2003 up to 1 million tons of all salmon species (chum predominated) were observed in the Russian zone of the Bering Sea. In recent years, the biomass of the salmon feeding in the North Pacific Ocean has been estimated to be as high as 3.5–4.5 million tons. However, as it has been noted above, the rise in abundance of these species did not compensate for the reduction in nekton biomass in the mid-1990s.

DISCUSSION

After examining the multiannual tendencies and trends in the changes occurring in both the pelagic and bottom communities of the western Bering Sea over 20 years, it is possible to come to a number of conclusions.

The stability of the plankton and benthos biomass in the western Bering Sea (as well as in all the far-eastern seas) over the long term illustrates a relative stability in the plankton and benthic communities commensurate with the observed dynamics in climate-oceanological conditions and changes in the biomass of the main consumers of plankton and benthos. This conclusion is significant, especially because of the regularly emerging assumptions about both the shortage of food and the severe competition for food in both the pelagic and bottom communities. For example, at the end of the 20th century, this subject was discussed widely in relation to the increase in salmon abundance. The conclusions about the limited carrying capacity of the sub-Arctic epipelagic zone for salmon were based on deductions about the effect of density factors on the salmon food supply (Ishida et al. 1993; Bigler et al. 1996; Volobuev 2000; Klovatch 2003). Such deductions were often based on the indirect assessments rather than actual data on the quantitative assessments of the biomass of plankton and its main consumers.

In accordance with the results of our assessments, in the 1980s, the zooplankton biomass in the Bering Sea comprised about 600 million tons in summer. The annual zooplankton consumption by nekton comprised only about 50% of the total biomass (Shuntov et al. 1993). Although plankton consumption by all nekton species in the ecosystem in general is quite large, it does not look very significant and probably does not exceed 10% of plankton production. For about the last 15 years, the total nekton abundance has decreased and zooplankton abundance remains at the mean multi-annual level. This allows us to conclude that only a few per cent of zooplankton production are consumed by nekton (Shuntov and Temnykh 2004). In the western Bering Sea specifically, zooplankton consumption by nekton comprised not more than 11% of the total zooplankton biomass in the 2000s. Consumption of zooplankton by salmon was not more than

Table 3. Dynamics of relative biomass averages (kg/km²) of squids in the upper epipelagic layer of the far-eastern seas and northwestern Pacific Ocean during 1979–2004 (Shuntov and Temnykh 2008b).

Topographic zone	1979–1990	1991–1995	1996–2004
Bering Sea (western)			
Inner shelf	0.9	< 0.1	77
Outer shelf and the shelf edge	88.2	9.7	465
Deepwater regions	122	125	340
Far-eastern region			
Inner shelf	6.4	32	60
Outer shelf and the shelf edge	93	68.2	365
Deepwater regions	128	319	483

1% of the total zooplankton biomass (Naydenko 2007)

In addition to the above-mentioned data on plankton, the conclusions of sufficient food provision of the nekton in the upper epipelagic zone are also confirmed by our data on the density and stocks of small-sized nekton (young and small fish and squid < 50 mm length) (Table 4). The concentration densities of food objects represented by small nekton (5–10 g/m²) in the epipelagic zone is an order of magnitude lower than the total macroplankton biomass; however, it is comparable to the density of hyperiids (2–8 g/m²), an important component of the fish forage base.

Salmon are not very important in the trophic relationships of nekton species. In the mid-1990s their share was 5% of the total nekton biomass in the epipelagic layers of the far-eastern seas, in the 2000s, 6%. Salmon biomass is appreciable outside shelf areas. For example, in the 2000s in the western deepwater areas of the Bering Sea their share averaged about 50% of the total nekton biomass. For most of their marine life, salmon are spatially separated from mass nekton consumers (including walleye pollock) on the shelf and at the shelf edge. Thus the pressure on forage resources decreases. However, because there is usually an adequate food supply does not necessarily mean that competition for food does not exist from time to time. For many years there have been descriptions in the literature of a decrease in salmon growth rates when abundance is high. However, a decrease in the growth rate does not necessarily indicate a strict regulation of abundance, especially by means of an increase in mortality due to a serious food shortage. The vast literature on the feeding of nekton and nektobenthos generally confirms our conclusions. Competition for food in pelagic and bottom communities does not reach levels at which abundance becomes limited (Napazakov 2003; Kuznetsova 2005; Chuchukalo 2006; Shuntov et al. 2007b).

These conclusions do not exclude the possibility of the limitation of a number of larval and fry stages of fish and commercial invertebrates when both pelagic and the majority of the benthic species in the early stages of development are found together in pelagic growth zones and layers. In these growth zones, the early life stages are more dependent

on each other when their ability to maneuver vertically, and especially horizontally, is limited.

Predators are the main factors in the functioning of marine pelagic and bottom communities. A significant amount of information on the rate of losses due to predators has been accumulated over the years, which allows us to consider the quantitative effects of predation. Table 5 shows the loss rate of walleye pollock from predators and cannibalism.

According to the data collected by TINRO expeditions in the 2000s, the number of generations of pink salmon in the Okhotsk and Bering seas on average decreases by one-third over seven months (November–June) (Shuntov and Temnykh 2008b).

Recent studies have confirmed previous conclusions that strict control of the abundance of commercial crustaceans, crabs and shrimps, occurs from the ‘top down’. In 1998–2002 in the western Bering Sea, bottom fish with a biomass of about 700,000 tons consumed 25,000 tons of shrimp and snow crabs per month (Napazakov 2003). From the 1980s until now (see above), the biomass of bottom fish has doubled, which means that the rate of consumption of crustaceans has also doubled. Considering the above-mentioned significant consumption rate of commercial crustaceans, it should be noted that with the exception of cod, walleye pollock and halibut, no other predatory species (grenadiers, sculpins, lords, skates, e.g.) are caught for commercial purposes. By approximate calculations, even a 10% harvest of these fishes will result in about a 10% increase in the number of the unconsumed crabs and shrimp compared with their present total allowable catches (Chuchukalo 2006; Shuntov and Temnykh 2007c). As we know, current fisheries management practices are based on approaches that are very different from ours. They are concerned with a targeted impact on communities with the goal of producing changes in the ratios of species and groups. Modern fisheries management is traditionally based on two concepts – the determination of allowable catch quotas for specific populations and the conservation of resources (Shuntov 2004).

In summary, it is possible to make two general conclusions about the structure, dynamics and function of the biota

Table 4. Dynamics of relative biomass averages (g/m²) of small-size nekton species (fishes and squids) in the upper epipelagic layer of the far-eastern seas and the northwestern Pacific Ocean during 1979–2004 (Shuntov and Temnykh 2007).

Topographic zone	1979–1990	1991–1995	1996–2004
Bering Sea (western)			
Inner shelf	3.9	2.1	1.9
Outer shelf and the shelf edge	3.7	0.1	1.9
Deepwater regions	0.3	0.2	0.5
Far-eastern region			
Inner shelf	2.4	1.4	1.7
Outer shelf and the shelf edge	1.8	0.4	1.1
Deepwater regions	1.2	0.8	1.2

Table 5. Annual consumption (million tons) of walleye pollock in the Okhotsk and Bering seas in the 1980s (Shuntov and Dulepova 1993).

Cause of mortality	Okhotsk Sea	Bering Sea
Large walleye pollock (cannibalism)	0.6	0.9
Other predatory fish	2.2	4.5
Marine mammals and birds	0.4	1.5
All predators	3.2	6.9
Commercial catch	1.8	2.0*
Walleye pollock production	5.0-7.5	10.0–12.5

in the Bering Sea:

a) At present the vast ecosystem of the Bering Sea is capable of sustaining a high level of biological and fisheries production;

b) Natural events (climate-hydrological, community and population factors) are the most important factors influencing the dynamics of marine biota. At present, anthropogenic influences and even fisheries do not play a key role in determining trends in the abundance dynamics of the majority of the populations or in the structural transformations of the communities of the Bering Sea.

CONCLUSION

As we begin the 21st century, it is clear that significant progress has been achieved in our understanding of the functioning of marine ecosystems, including that of the Bering Sea. However, as we have discussed, our understanding of the cause-and-effect mechanisms impacting the dynamics of natural events and processes is mainly based on retrospective analyses. There have been few (or no) successful predictions of future events based on theoretical knowledge. This illustrates the unreliability of hypotheses and suggestions. Nevertheless, despite the complexity of functioning of populations, communities and ecosystems, we can be assured that future studies in the areas that have been defined in recent years will bring good results. At the same time, however, there are doubts regarding the sufficiency of traditional methods and approaches (Shuntov et al. 2007a). Doubts emerge from the fact that significant changes in communities are mainly caused by the dynamics of limited number

of species (such as walleye pollock or Pacific sardine). The contribution of the majority of species to dynamics of communities is imperceptible. Even neighbouring populations of the same species can ‘behave strangely’ in the similar situations. Dramatic and considerable increases or decreases in abundance of certain species or populations as a rule occur suddenly for investigators. In our opinion, obvious progress in understanding the mechanisms of reorganization of biota will be connected only with the advent of new “nonconventional” hypotheses.

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The Salmon MALBEC Project: A North Pacific-scale Study to Support Salmon Conservation Planning

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Abstract: The Model for Assessing Links Between Ecosystems (MALBEC) is a policy gaming tool with potential to explore the impacts of climate change, harvest policies, hatchery policies, and freshwater habitat capacity changes on salmon at the North Pacific scale. This article provides background information on the MALBEC project, methods, input data, and preliminary results pertaining to (1) hatchery *versus* wild salmon production in the North Pacific Ocean, (2) rearing, movement, and interactions among Pacific salmon populations in marine environments, (3) marine carrying capacities, density-dependent growth, and survival in Pacific salmon stocks, and (4) climate impacts on productivity in salmon habitat domains across the North Pacific. The basic modeling strategy underlying MALBEC follows the full life cycle of salmon and allows for density-dependence at multiple life stages, and it includes spatially explicit ecosystem considerations for both freshwater and marine habitat. The model is supported by a data base including annual run sizes, catches, spawning escapements, and hatchery releases for 146 regional stock groups of hatchery and wild pink, chum, and sockeye salmon around the North Pacific for the period 1952–2006. For this historical period, various hypotheses about density-dependent interactions in the marine environment are evaluated based on the goodness-of-fit between simulated and observed annual run sizes. Based on the information we used to inform our ocean migration table, interactions among stocks that originate from geographically distant regions are greatest in the Bering Sea in summer–fall and in the eastern sub-Arctic in winter–spring. While the model does not reproduce the observed data for some specific stock groups, it does predict the same overall production pattern that was observed by reconstructing run sizes with catch and escapement data alone. Our preliminary results indicate that simulations that include density-dependent interactions in the ocean yield better fits to the observed run-size data than those simulations without density-dependent interactions in the ocean. This suggests that for any level of ocean productivity, the ocean will only support a certain biomass of fish but that this biomass could consist of different combinations of stocks, stock numbers and individual fish sizes. MALBEC simulations illustrate this point by showing that under scenarios of Pacific-wide reduced hatchery production, the total number of wild Alaskan chum salmon increases, and that such increases are large where density-dependent effects on survival are large and small where they are not. Under scenarios with reduced freshwater carrying capacities for wild stocks, the impacts of density-dependent interactions also lead to relative increases in ocean survival and growth rates for stocks using ocean habitats where density-dependence is large.

Keywords: MALBEC, North Pacific, salmon, density-dependence, hatchery-reared, wild, conservation, computer simulation

INTRODUCTION

A multi-investigator team has been synthesizing data and expert knowledge in order to develop a new simulation model: Salmon MALBEC (Model for Assessing Links Between Ecosystems), to support Pacific salmon conservation planning at the scale of the North Pacific basin and its large river drainages. MALBEC is designed to pursue three main objectives: (1) to integrate existing knowledge about impacts to Pacific salmon ecosystems, (2) to evaluate integrated impacts and conservation strategies for reducing risks posed by those impacts; and (3) to identify high priority research needs. The model allows users to explore hypotheses about Pacific salmon at the North Pacific scale, e.g., the effects of competition among salmon stocks (and species) in the North Pacific, the response of salmon stocks and species to climate change, the impacts of freshwater habitat degradation on local and remote stocks, and the possible effects of large hatchery programs on natural and hatchery stocks from other regions. MALBEC is a policy gaming tool with potential to explore the impacts of climate change, harvest policies, hatchery policies, and freshwater habitat capacity changes, and it is not meant to address the kinds of questions for which stock assessment models are designed, e.g., setting harvest and escapement policies for a single population.

In this article we review background information on the MALBEC project, methods, input data, and preliminary results pertaining to: (1) hatchery *versus* wild salmon production in the North Pacific Ocean, (2) rearing, movement, and interactions among Pacific salmon populations in marine environments, (3) marine carrying capacities, density-dependent growth, and survival of Pacific salmon stocks, and (4) climate impacts on productivity in salmon habitat domains across the North Pacific.

Background

The modeling strategy underlying MALBEC is based on a SHIRAZ framework (Scheuerell et al. 2006) that follows the full life cycle for salmon, allows for density dependence at multiple life stages, and includes spatially explicit ecosystem considerations for both freshwater and marine habitat. The model is supported by a data base including annual run sizes, catches, spawning escapements, and hatchery releases for pink, chum, and sockeye salmon populations around the North Pacific for the period 1952–2006. We focused on pink, chum and sockeye salmon because these are the most abundant species of Pacific salmon, and because of the relative availability of historical run-size, catch, and hatchery production information. For this historical period, various hypotheses about density-dependent interactions in the marine environment are evaluated based on the goodness-of-fit between simulated and observed annual run sizes. Future scenarios for North Pacific chum, sockeye, and pink salmon for the period 2007–2050 are based on specified changes in

the carrying capacity or productivity for marine or freshwater habitat or both due to human or natural causes, e.g., changing climate, land and water use impacts on freshwater habitat, or changes in harvest or hatchery policies.

Key challenges in the development of MALBEC have revolved around integrating recent advances in the understanding of salmon ecosystems. These advances include: the role of biocomplexity in the sustainability of Bristol Bay's sockeye salmon fisheries (Hilborn et al. 2003); the role of shifting freshwater habitat mosaics in supporting biocomplexity in salmon (Stanford et al. 2005); the ocean ecology of Pacific salmon, especially interspecific and intraspecific competition of salmon in marine environments (Ruggerone et al. 2003; Ruggerone and Nielsen 2004), and climate impacts on salmon via effects on habitat and food webs in freshwater and marine environments (Beamish and Bouillon 1993; Hare and Francis 1994; Mantua et al. 1997; Pyper et al. 2001, 2002).

MATERIALS AND METHODS

The Model

The basic approach to MALBEC is to explicitly model survival rates, growth rates, and movement between habitat areas of Pacific salmon populations in six-month time steps, from the egg through to spawning. Habitats are defined in terms of area and prey items, so that the total feeding load in any given habitat in time is the sum of all salmon in the combined area-food group. We represent a schematic of these dynamics in Fig. 1. Survival and growth rates are scaled to be a function of the total feeding load relative to the carrying capacity within a given habitat area.

MALBEC uses a multi-stage Beverton and Holt stock recruitment relationship (Moussalli and Hilborn 1986) for predicting survival rates through 6-month time step life-history stanzas (one for overwinter, and one for summer) for every modeled stock. Fish surviving to the end of any stanza are predicted to (possibly) vary with total fish abundance relative to the carrying capacity in shared habitat(s). The multi-stanza Beverton-Holt survival function is derived by assuming that behavioral activity levels (foraging times, dispersal rates) are proportional to abundance and that mortality rates are proportional to activity (so mortality rates vary linearly with abundance). For any brood year b , the basic prediction equation is:

$$N_{b,i,j+1,t+1} = \frac{\alpha_{h(i,j),t} s_{i,j} N_{b,i,j,t}}{1 + \frac{\rho \eta_{h(i,j),t}}{\omega_{h(i,j),t} C_{h(i,j),t}}} \quad (1)$$

Equation 1: Predicted numbers of stock i during stanza j in habitat h and at time t .

Here, $s_{i,j}$ is the maximum survival rate for stock i fish through stanza j absent competition/predation effects, $h(i,j)$

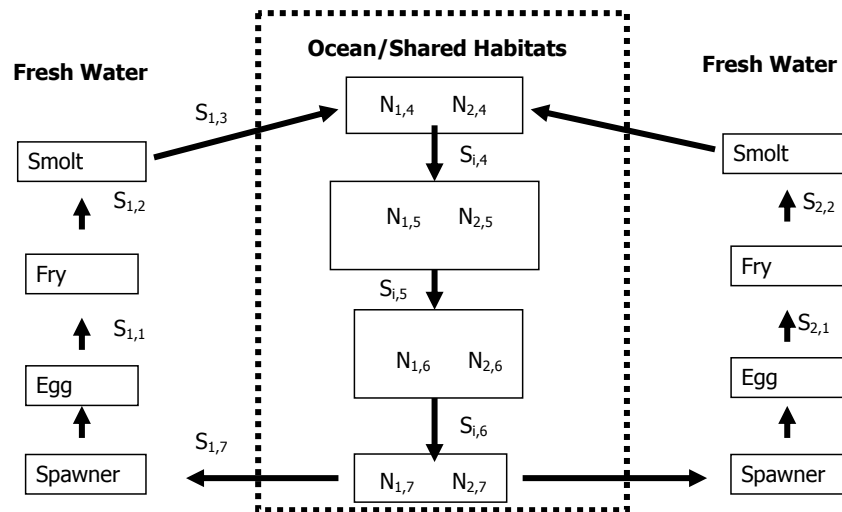


Fig. 1. Schematic of the MALBEC modeling approach. Each box represents a different habitat area, and relative box sizes represent habitat-specific carrying capacities so that larger boxes can support more fish. Fish of each stock i and stanza j are assumed to survive from stage j to stage $j+1$ at a rate of $S_{i,j}$, moving from one habitat area to the next. When density dependence is invoked, survival and growth (not shown) are scaled to vary with the ratio of density to carrying capacity in each habitat area. As the carrying capacity in an area goes down, survival and growth for stocks i at stage j go down. Similarly, as total fish numbers N increase, survival and growth go down.

is a habitat code number for the habitat used by stock i during stanza j , $C_{h(i,j)}$ is the carrying capacity of habitat $h(i,j)$ for stanza- j fish (measured as total abundance of competing fish needed to drive the survival rate down by 50%, i.e. to $s_{ij}/2$), and $N_{b,i,j,t}$ is the sum of weighted abundance using habitat $h(i,j)$ in time t . MALBEC can incorporate time-varying capacity and productivity changes by including time series of scaling coefficients representing time-varying changes in carrying capacity ($\omega_{t,h(i,j)}$) and survival ($\alpha_{i,t}$) where these are available from other analyses.

Instead of treating competing fish of different stanza ages as having equivalent feeding loads or competitive effects, we weight the relative effects of consumption by stanza age. Walters and Post (1993) suggest that the best size-dependent weighting (ϕ_j) should be the sum of body length squared. We model relative changes in body length using the von Bertalanffy growth equation $BL_j = BL_\infty(1 - e^{-K(j-t_0)})$ (von Bertalanffy 1938), where BL_∞ is the asymptotic size, K the metabolic parameter, and t_0 the theoretical time at length 0. Here we assume $K = 0.4$ (Berg 1962) and $t_0 = -0.5 \text{ j}^{-1}$. Assuming that Pacific salmon stocks share the same asymptotic size then relative competitive weights are $\phi_j = (1 - \exp(-K(j-t_0)))^2$. In any given habitat h used by stock i at stanza j , the sum of weighted numbers η , or feeding load, is given as:

$$\eta_{h(i,j),t} = \sum_i \sum_j N_{h(i,j),t} \phi_j \quad (2)$$

Equation 2: Sum of length weighted numbers where h is the habitat index of stock i at stanza j and time t .

The density-dependent survival effects of competing fish are scaled by ρ . If competitive effects are assumed not

to exist, ρ is set to 0 and fish survive from stanza to stanza at $s_{i,j}$, absent any density-dependent interactions. For egg-to-fry stages where habitats are typically not shared with other stocks, ρ is set to 1 and recruitment is predicted using the classical Beverton-Holt stock recruitment relationship. When density-dependent survival is invoked, ρ is estimated in the fitting procedure described below.

Growth is modeled using the same functional form as Equation 1, where γ is the strength of the density-dependent growth effect, $G_{o_{ij}}$ the maximum growth rate (in kg per stanza) and $G_{i,j,t}$ is the growth increment.

$$G_{b,i,j+1,t+1} = \frac{G_{o_{i,j}}}{1 + \frac{\gamma \eta_{h(i,j),t}}{C_{h(i,j),t}}} \quad (3)$$

Equation 3: Predicted body size in kg for stock i , in stage j as a function of base growth rate ($G_{o_{ij}}$), density-dependent growth effect γ , weighted numbers in habitat $h(i,j),t$ and habitat carrying capacity C .

The model thus predicts numbers and body sizes from stage to stage according to Equation 1 and Equation 3, respectively. Stage and stock-specific habitats h , baseline survival s and maximum growth rates G_0 are specified in model input data sections below. For odd-numbered (first half of the year) stanzas, returns R are given as a function of maturity M at stanza j :

$$R_{b,i,t} = \sum_j N_{b,i,j,t} M_{i,j} \quad (4)$$

Equation 4: Predicted returns for stock i , brood year b , and

time t .

MALBEC has the option of driving the model using either observed or predicted spawners. If the former option is used, the number of spawners at each time step (S) are prescribed to be the observed values in our historical data series. The historical period model simulations discussed in this article use this approach. In contrast, all simulations for the 2007–2050 period use predicted spawners, S , which are computed as the product of numbers and proportions mature at stanza j : $S_{b,i,j,t} = N_{b,i,j,t} M_{i,j}$. In all cases, the total spawning stock biomass for each stock (W) is summed across all stanzas and is given as:

$$W_{b,i,t} = \sum_j S_{b,i,j,t} G_{b,i,j,t} \tag{5}$$

Equation 5: Predicted total spawning stock biomass for stock i , brood year b , and time t .

Egg production is defined in terms of species-specific fecundity $F_{sp(i)}$, spawners in the previous brood year $S_{b-1,i}$ and the ratio of current predicted spawning weight W . For all fitting results shown, the number of spawners is prescribed to be the observed value for each population group for each year in the 1952–2006 simulation period. All forward simulations use predicted eggs (E) given by

$$E_{b,i,t} = F_i S_{b,i,t} \frac{W_{i,b-1}}{W_{i,0}} \tag{6}$$

Equation 6: Egg production for stock i , brood year b at time t .

The next brood year’s fry numbers are calculated as

$$N_{b,i,0,t+1} = \frac{\alpha_{h(i,0),t} S_{i,0} E_{b-1,i,t}}{1 + \frac{E_{b,t}}{\omega_{h(i,0),t} C_{h(i,0),t}}} \tag{7}$$

Equation 7: Predicted egg to fry production for stock i , brood year b , time $t+1$.

Time-varying Survival and Carrying Capacity Multipliers

MALBEC can model time-varying survival $\alpha_{h(i,j),t}$ or capacity $\omega_{h(i,j),t}$ effects. In this case we use time-varying $\alpha_{h(i,j),t}$ based on the analysis of Peterman et al. (1998). For carrying capacity anomalies there are two options. The first is to prescribe $\omega_{h(i,j),t}$ using oceanographic anomaly series. The second is to treat them as a vector of estimated process-error $\omega_{t,h(i,j)}$ parameters. In this way, we can use the model to predict what capacity changes the salmon experienced, propa-

gate historical capacity uncertainty forward and compare fit anomaly values to observed oceanographic anomalies.

Model Fitting

We estimated γ , ρ , and carrying capacities of habitats in the first (egg-to-fry) life-history stanza by minimizing log-normal likelihoods between observed and predicted values for run size and body size for 29 stocks having sufficient data to do so (stocks with size and abundance data used in the fitting procedure are indicated with asterisks in Table 1). Historical and recent time series of stock-specific mean body weight data were taken from INPFC (1979) and North Pacific Anadromous Fish Commission (NPAFC) Statistical Yearbooks (1992–2008). For a prescribed coefficient of variation ($\sigma = 0.3$), we fit a likelihood to observed run size data (x) with:

$$L_1 = \sum_i \sum_t \log \left[\frac{1}{x_i \sigma \sqrt{2\pi}} e^{-\frac{(\ln(x_i) - \log(R_{i,t}))^2}{2\sigma^2}} \right] \tag{8}$$

Equation 8: Likelihood of observed (x) and predicted (R) returns.

and another likelihood to observed mean body size as:

$$L_2 = \sum_i \sum_t \log \left[\frac{1}{G_{obs,i,t} \sigma \sqrt{2\pi}} e^{-\frac{(\ln(G_{obs,i,t}) - \log(G_{pred,i,t}))^2}{2\sigma^2}} \right] \tag{9}$$

Equation 9: Likelihood of observed (G_{obs}) and predicted (G_{pred}) mean weight for stock i at time t .

The sum of total log-likelihood is given simply as $L_1 + L_2$. For both total run and mean body size time series we fixed the observation error coefficients of variation (σ) to be 0.3 for both mean body size and total return data.

Hatchery capacities in early life-history stages were assumed known at their entered values. Carrying capacities of habitats for all stages beyond egg-to-fry were entered as model inputs with very large values (10^{10}) so that there is no density dependence at those stages unless later modified.

Statistical Features in Development

MALBEC is programmed in both AD model builder (available from www.otter-rsch.com/admodel.htm) and with a graphical user interface in Visual Basic 6. The Visual Basic version was used to generate all maximum likelihood fits shown in this document. Fitting the model using AD model builder will allow for integrating across all parameters to propagate parameter uncertainties forward using Markov Chain Monte Carlo simulations. The specification of priors for estimated parameters will be central to the success of this

approach.

Model Input Data

Salmon Abundance

Our goal was to produce total abundance estimates of wild and hatchery salmon rather than indices of abundance so that production could be compared from region to region. When possible, we utilized local estimates of wild *versus* hatchery salmon abundance (run), catch, and spawning escapement. We did not attempt to identify the proportion of spawners represented by hatchery strays because few data are available, therefore hatchery estimates may be low to some extent. In most regions, spawning escapements did not extend back to the 1950s, therefore regressions of harvest rate on $\text{Log}_e(\text{catch})$ during recent years were used to predict harvest rate (and run size) from reported catch during earlier years. The degree of reliance on this approach varied with region and species. Although we extended the abundance time series of each stock back to 1952, the MALBEC model fitting primarily relied upon years when both catch and escapement data were available (except for stocks in Russia). Sockeye salmon statistics were undoubtedly the most reliable, followed by pink salmon, then chum salmon. A description of the hatchery and wild salmon database and production trends is available from G. Ruggerone (Natural Resources Consultants, Seattle, WA, GRuggerone@nrccorp.com), but the database is briefly described here.

The largest portion of data on salmon populations on the west coast of North America came from 120 populations of pink, chum, and sockeye salmon previously described in Pyper et al. (2001, 2002), Mueter et al. (2002), and Peterman et al. (1998). In Alaska, the data base was updated with catch and spawning escapement values from recent regional reports. For most pink and chum stocks escapement counts were peak rather than total estimates. Therefore, we applied expansion factors based on data or information provided by regional biologists regarding the ratio of total spawners to spawners at the peak of the run and the fraction of streams surveyed.

In British Columbia, we supplemented the above data sets with recent run reconstructions of wild salmon (K. English, LGL Limited, Sidney, B.C., Canada, pers. comm.), which accounted for unmonitored streams and ocean-troll fisheries. Hatchery salmon estimates in British Columbia were based on annual releases and survival of salmon estimated from coded-wire-tag data or from literature values (e.g., Mahnken et al. 1998). United States west coast estimates of salmon abundance (primarily Washington State and Columbia River) were provided by state biologists and Pacific Fishery Management Council (PFMC) reports, but some estimates required additional expansions.

In Russia, we relied upon catch and escapement statistics for each district as provided in annual reports by Russia to NPAFC since 1992. Escapement estimates were not avail-

able prior to 1992, therefore the regression of harvest rate on $\text{Log}_e(\text{catch})$ was used to estimate earlier salmon abundance from catch reported by the International North Pacific Fisheries Commission (INPFC 1979). For Kamchatka pink salmon, we used recent run reconstruction estimates dating back to 1957, as described by Bugaev (2002). Russian statistics did not identify hatchery *versus* wild salmon, therefore hatchery releases in Russia after 1971 (W.J. McNeil, pers. comm.; Morita et al. 2006) and assumed approximate survival rates were used to estimate hatchery production. Russian hatchery releases prior to 1971 were not available, except for the Sakhalin and Kuril Islands region, but they were likely small compared with recent years (Zaporozhets and Zaporozhets 2004). Russian hatchery releases prior to 1971 were not available. Chum survival rates were based on recent data and information provided by Zaporozhets and Zaporozhets (2004) collected for Kamchatka chum hatcheries (N. Kran, Sevvostrybvod, Petropavlovsk-Kamchatsky, Russia, pers. comm.). Survival rates of chum salmon were lower in southern regions of Russia and during years prior to the 1990s when hatchery fish quality was reportedly lower. Survival of hatchery pink salmon increased from approximately 1.4% in 1971–1983 to 5.1% in 1989–1997, owing to improved hatchery practices (Tarasyuk and Tarasyuk 2007; Kaev and Geraschenko 2008). Russian pink salmon survival was assumed to be lower (2–3%) than Japanese pink salmon survival (Hiroi 1998).

Abundances of Japanese hatchery salmon were largely available from NPAFC and regional hatchery program documents (e.g., CCAHSHP 1988; Hiroi 1998; Eggers et al. 2005; NASREC 2007). Although most production of pink salmon in Japan was previously thought to originate from hatcheries, we used recent estimates of hatchery *versus* wild pink salmon production provided by Morita et al. (2006). Although this finding appears to be controversial, more recent information also supports the relatively high proportion of wild *versus* hatchery pink salmon in Japan (K. Morita, moritak@affrc.go.jp, pers. comm.). Recent evidence indicates that Japan also produces wild chum salmon but estimates were not available (Y. Ishida, ishiday@affrc.go.jp, pers. comm.). The small production of hatchery chum salmon in South Korea was updated from Seong (1998) and included with Japanese hatchery estimates unless noted otherwise (S. Kang, kangsk@momaf.go.kr, pers. comm.). Small numbers of pink salmon return to North Korea, but quantities were unavailable (Kim et al. 2007).

Annual harvests of salmon in the Japanese high seas fisheries (mothership, land-based, and the more recent fishery in the Russian Exclusive Economic Zone) were reported by Eggers et al. (2005) and updated in November 2008 by M. Fukuwaka (fukuwaka@fra.affrc.go.jp, pers. comm.). Estimates of adult equivalent harvests were calculated using proportions of mature and immature salmon in the catch (e.g., Fredin et al. 1977; Harris 1988; Radchenko 1994) and monthly mortality schedules for each species (Ricker 1976).

Some sockeye salmon harvested in the mothership fishery, and to a much lesser extent chum and pink salmon, were from North American rivers, especially rivers in western Alaska (Fredin et al. 1977; Harris 1988). These salmon were allocated to western Alaska, except for Alaska pink salmon whose harvest averaged less than 25,000 fish per year. The high seas catch of Asian salmon was allocated to hatchery and wild salmon based on the proportion of hatchery *versus* wild salmon returning to all of Asia in that year. The proportion of hatchery or wild fish returning to each region was used to allocate the high seas catch to that region. Estimated historical catches of Bristol Bay sockeye salmon by the Japanese high seas salmon driftnet fisheries (1950–1991) were included in our abundance estimates for Bristol Bay sockeye salmon. For other species, we assumed that all fish in historical high seas catches and recent catches by foreign driftnet fisheries operating inside the Russian Exclusive Economic Zone were of Asian origin. The remaining high seas catch (after removing Bristol Bay sockeye salmon) was split into hatchery and wild fish based on the proportion of hatchery *versus* wild salmon returning to all of Asia in that year. Next, we used the proportion of hatchery or wild fish returning to each region to allocate the high seas catch to that area. These are very simple assumptions that do not account for the proportions of immature and maturing fish in the high seas salmon driftnet fishery catches.

MALBEC Stock Groups

We grouped individual populations of pink, chum, and sockeye salmon into large geographic regions and aggregated data into composite time series (1950–2006) that describe historical salmon dynamics on this regional level. Regions were delineated based on geographic context, patterns of ocean migration, and our ability to separate and assign catches from mixed-stock fisheries. Even- and odd-year pink salmon returns to the same region are treated as separate stocks in the model. In regions that produce both hatchery and wild salmon, we stratified data to separate hatchery and wild stock groups. The data were stratified into a total of 146 regional stock groups (Table 1). The approximate geographic locations of stock groups are shown in Fig. 2.

Marine Habitat Data

Key processes used to describe the life history of salmon in MALBEC are rearing (stock-specific habitats), movement (seasonal migration patterns), and trophic interactions (diet). Initial constraints in the model limit life-history input data to two seasonal habitat stanzas per year (extended “winter” and “summer” seasons). Our goal was to synthesize published information on the marine life histories of salmon to fit this input-data scheme at the scale of the North Pacific. Primarily, we used information in the peer-reviewed bulletin series of the INPFC and NPAFC. Historical data (1955–1992) on marine life histories of pink, chum, and sockeye salmon of Asian and North American origin are summarized in INPFC

bulletins (French et al. 1976; Neave et al. 1976; Takagi et al. 1981; Hartt and Dell 1986; Myers et al. 1993). These data, as well as some updated information, are also reviewed by species in *Pacific Salmon Life Histories* (Burgner 1991; Heard 1991; Salo 1991). In addition, we incorporated more recent (1993–2006) marine life-history information reported in NPAFC bulletins, technical reports, and scientific documents (available online at www.npafc.org) and scientific journals (e.g., Seeb et al. 2004), and used data on early marine life histories of North American and Asian salmon reviewed by Beamish et al. (2003), Karpenko (2003), Mayama and Ishida (2003), and Brodeur et al. (2003). For many salmon populations, however, our only source of stock-specific data on open ocean rearing habitats and seasonal movements was INPFC/NPAFC tagging studies (Myers et al. 1996; Klovach et al. 2002; documents reporting INPFC/NPAFC tag recovery data are archived at NPAFC, Vancouver, B.C.; high seas coded-wire-tag recovery data are archived at the Regional Mark Processing Center, Pacific States Marine Fisheries Commission, Portland, Oregon).

Time Varying Carrying-Capacity Multipliers from Plankton Data

Climate-driven bottom-up forcing of changes in marine carrying capacity is one mechanism for salmon population change that can be examined in MALBEC simulations. It is generally accepted that North Pacific salmon production responds to changes in climate (Beamish and Bouillon 1993; Hare and Francis 1994; Mantua et al. 1997). In MALBEC we examine the impact of changes in carrying capacity for the modeled ocean habitats with time-varying carrying capacity indices. Climate-related changes in carrying capacity for salmon are evident at decadal time scales when measured across large regions and sub-regions of the North Pacific basin (Beamish and Bouillon 1993; Klyashtorin 1998; Beamish et al. 1999), and this is especially true for the historic 1950–2006 period of interest in the MALBEC project.

Here we approximate such decadal to interannual changes in habitat carrying capacity using time series of annually or seasonally resolved estimates for phytoplankton or zooplankton production (Preikshot 2007). In the simplest implementation of this approach, relative changes in carrying capacity values result in changes in the survival and growth rates for salmon occupying the affected MALBEC defined habitat area. Thus, in all MALBEC marine habitat areas, normalized time series of zooplankton biomass are used to simulate variations in the marine carrying capacity of Pacific salmon. This approach can be used to examine the impacts of future climate changes on the marine carrying capacity for salmon if the space-time patterns of phytoplankton and zooplankton production can be estimated.

Field Derived Time Series

Where available, we used zooplankton biomass time series from field studies for the past few decades as proxies

Table 1. Stocks and seasonal habitats used in MALBEC (w = winter, s = summer). Habitat w0 = egg-to-fry stage. Habitat stanzas 4-6 are not shown, but use the same data as habitat s3 and habitat w3. Stocks with size and abundance data used in the fitting procedure are indicated with asterisks next to the stock name.

Stock no.	Stock name	Hab w0	Hab s1	Hab w1	Hab s2	Hab w2	Hab s3	Hab w3
1	Fraser sockeye hatchery	Fras sockeye hatchery	GSPS lakes	GSPS lakes	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton
2	*Inner GSPS sockeye wild	GSPS sockeye streams	GSPS lakes	GSPS lakes	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton
3	Washington & WCVI sockeye hatchery	WCVI sockeye hatchery	WCVI lakes	WCVI lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
4	Washington & WCVI sockeye wild	WCVI sockeye streams	WCVI lakes	WCVI lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
5	CCBC sockeye hatchery	CCBC sockeye hatchery	CCBC lakes	CCBC lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
6	*CCBC sockeye wild	CCBC sockeye streams	CCBC lakes	CCBC lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
7	Skeena/Nass sockeye hatchery	Skeenas sockeye hatchery	Skeenas lakes	Skeenas lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
8	*NBC sockeye wild	Skeenas sockeye streams	Skeenas lakes	Skeenas lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
9	SEAK sockeye hatchery	SEAK sockeye hatchery	SEAK lakes	SEAK lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
10	SEAK sockeye wild	SEAK sockeye streams	SEAK lakes	SEAK lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
11	PWS sockeye hatchery	PWS sockeye hatchery	PWS lakes	PWS lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
12	PWS sockeye wild	PWS sockeye streams	PWS lakes	PWS lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
13	Cook Inlet sockeye hatchery	Cook sockeye hatchery	Cook lakes	Cook lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
14	*Cook Inlet sockeye wild	Cook sockeye streams	Cook lakes	Cook lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
15	Kodiak sockeye hatchery	Kodi sockeye hatchery	Kodi lakes	Kodi lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
16	*Kodiak sockeye wild	Kodi sockeye streams	Kodi lakes	Kodi lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
17	*Chignik & South Peninsula sockeye wild	Chig sockeye streams	Chig lakes	Chig lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
18	*North Peninsula sockeye wild	NPen sockeye streams	NPen lakes	NPen lakes	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton
19	*Bristol Bay Westside sockeye wild	BB Westside sockeye streams	BB Westside lakes	BB Westside lakes	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton
20	*Bristol Bay Eastside sockeye wild	BB Eastside sockeye streams	BB Eastside lakes	BB Eastside lakes	EBS zoop	ESA micronekton	WBS zoop	ESA micronekton
21	AYK sockeye hatchery	AYK sockeye hatchery	AYK lakes	AYK lakes	EBS zoop	ESA micronekton	WBS zoop	ESA micronekton
22	AYK sockeye wild	AYK sockeye streams	AYK lakes	AYK lakes	EBS zoop	ESA micronekton	WBS zoop	ESA micronekton
23	Anadyr sockeye wild	Anad sockeye streams	Anad lakes	Anad lakes	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton
24	*East Kamchatka sockeye wild	EKam sockeye streams	EKam lakes	EKam lakes	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton
25	West Kamchatka sockeye hatchery	WKam sockeye hatchery	Wkam lakes	Wkam lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
26	*West Kamchatka sockeye wild	WKam sockeye streams	Wkam lakes	Wkam lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
27	Okhotsk sockeye hatchery	Okho sockeye hatchery	Okho lakes	Okho lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
28	Okhotsk sockeye wild	Okho sockeye streams	Okho lakes	Okho lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
29	East Sakhalin sockeye hatchery	ESak sockeye hatchery	ESak lakes	ESak lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
30	Hokkaido sockeye hatchery	HokP sockeye hatchery	HokP lakes	HokP lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
31	GSPS chum hatchery	GSPS chum hatchery	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
32	*GSPS chum wild	GSPS chum streams	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
33	WCVI chum hatchery	WCVI chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
34	WCVI chum wild	WCVI chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
35	CCBC chum hatchery	CCBC chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
36	*CCBC chum wild	CCBC chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
37	NBC & Southern SEAK chum hatchery	Skeena chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
38	NBC & Southern SEAK chum wild	Skeena chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
39	Northern SEAK & Yakutat chum hatchery	SEAK chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
40	Northern SEAK & Yakutat chum wild	SEAK chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
41	PWS chum hatchery	PWS chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
42	*PWS chum wild	PWS chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
43	Cook Inlet chum hatchery	Cook chum hatchery	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton

Table 1 (continued).

Stock no.	Stock name	Hab w0	Hab s1	Hab w1	Hab s2	Hab w2	Hab s3	Hab w3
44	Cook Inlet chum wild	Cook chum streams	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
45	Kodiak chum hatchery	Kodi chum hatchery	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
46	*Kodiak chum wild	Kodi chum streams	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
47	Chignik & South Peninsula chum hatchery	Chig chum hatchery	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
48	Chignik & South Peninsula chum wild	Chig chum streams	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
49	North Peninsula chum hatchery	NPen chum hatchery	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
50	*North Peninsula chum wild	NPen chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
51	Bristol Bay chum hatchery	BB chum hatchery	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
52	*Bristol Bay chum wild	BB chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
53	AYK chum hatchery	AYK chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
54	AYK chum wild	AYK chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
55	*Kotzebue & Beaufort chum wild	Kotz chum streams	CS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
56	Kotzebue & Beaufort chum hatchery	Kotz chum hatchery	CS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
57	Anadyr chum wild	Anadyr chum streams	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
58	*East Kamchatka chum wild	EKam chum streams	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
59	West Kamchatka chum hatchery	WKam chum hatchery	OS zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
60	*West Kamchatka chum wild	WKam chum streams	OS zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
61	Okhotsk chum hatchery	Okho chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
62	Okhotsk chum wild	Okho chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
63	Amur chum hatchery	Amur chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
64	Amur chum wild	Amur chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
65	East Sakhalin chum hatchery	ESak chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
66	East Sakhalin chum wild	ESak chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
67	Primorye chum hatchery	Prim chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
68	Primorye chum wild	Prim chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
69	Hokkaido chum hatchery	HokP chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
70	Korea chum hatchery	Korea chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
71	GSPS pink hatchery	GSPS pink hatchery	GSPS zoop	ESA micronekton	ESA zoop			
72	GSPS oddpink hatchery	GSPS pink hatchery	GSPS zoop	ESA micronekton	ESA zoop			
73	*GSPS pink wild	GSPS pink streams	GSPS zoop	ESA micronekton	ESA zoop			
74	*GSPS oddpink wild	GSPS pink streams	GSPS zoop	ESA micronekton	ESA zoop			
75	WCVI pink hatchery	WCVI pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
76	WCVI oddpink hatchery	WCVI pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
77	WCVI pink wild	WCVI pink streams	ACC zoop	ESA micronekton	ESA zoop			
78	CCBC pink hatchery	CCBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
79	CCBC oddpink hatchery	CCBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
80	*CCBC pink wild	CCBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
81	CCBC oddpink wild	CCBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
82	NBC & Southern SEAK pink hatchery	NBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
83	NBC & Southern SEAK oddpink hatchery	NBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
84	NBC & Southern SEAK pink wild	NBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
85	NBC & Southern SEAK oddpink wild	NBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
86	Northern SEAK & Yakutat pink hatchery	SEAK pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
87	Northern SEAK & Yakutat oddpink hatchery	SEAK pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
88	*Northern SEAK & Yakutat pink wild	SEAK pink streams	ACC zoop	ESA micronekton	ESA zoop			

Table 1 (continued).

Stock no.	Stock name	Hab w0	Hab s1	Hab w1	Hab s2	Hab w2	Hab s3	Hab w3
89	Northern SEAK & Yakutat oddpink wild	SEAK pink streams	ACC zoop	ESA micronekton	ESA zoop			
90	PWS pink hatchery	PWS pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
91	PWS oddpink hatchery	PWS pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
92	*PWS pink wild	PWS pink streams	ACC zoop	ESA micronekton	ESA zoop			
93	PWS oddpink wild	PWS pink streams	ACC zoop	ESA micronekton	ESA zoop			
94	Cook Inlet pink hatchery	Cook pink hatchery	AS zoop	ESA micronekton	ESA zoop			
95	Cook Inlet oddpink hatchery	Cook pink hatchery	AS zoop	ESA micronekton	ESA zoop			
96	Cook Inlet pink wild	Cook pink streams	AS zoop	ESA micronekton	ESA zoop			
97	Cook Inlet oddpink wild	Cook pink streams	AS zoop	ESA micronekton	ESA zoop			
98	Kodiak pink hatchery	Kodi pink hatchery	AS zoop	ESA micronekton	ESA zoop			
99	Kodiak oddpink hatchery	Kodi pink hatchery	AS zoop	ESA micronekton	ESA zoop			
100	*Kodiak pink wild	Kodi pink streams	AS zoop	ESA micronekton	ESA zoop			
101	Kodiak oddpink wild	Kodi pink streams	AS zoop	ESA micronekton	ESA zoop			
102	Chignik & South Peninsula pink hatchery	Chig pink hatchery	AS zoop	ESA micronekton	ESA zoop			
103	Chignik & South Peninsula oddpink hatchery	Chig pink hatchery	AS zoop	ESA micronekton	ESA zoop			
104	*Chignik & South Peninsula pink wild	Chig pink streams	AS zoop	ESA micronekton	ESA zoop			
105	Chignik & South Peninsula oddpink wild	Chig pink streams	AS zoop	ESA micronekton	ESA zoop			
106	North Peninsula pink hatchery	NPen pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
107	North Peninsula oddpink hatchery	NPen pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
108	North Peninsula pink wild	NPen pink streams	EBS zoop	ESA micronekton	EBS zoop			
109	North Peninsula oddpink wild	NPen pink streams	EBS zoop	ESA micronekton	EBS zoop			
110	Bristol Bay pink hatchery	BB pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
111	Bristol Bay oddpink hatchery	BB pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
112	Bristol Bay pink wild	BB pink streams	EBS zoop	ESA micronekton	EBS zoop			
113	AYK pink hatchery	AYK pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
114	AYK oddpink hatchery	AYK pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
115	AYK pink wild	AYK pink streams	EBS zoop	ESA micronekton	EBS zoop			
116	AYK oddpink wild	AYK pink streams	EBS zoop	ESA micronekton	EBS zoop			
117	Kotzebue & Beaufort pink hatchery	Kotz pink hatchery	CS zoop	ESA micronekton	EBS zoop			
118	Kotzebue & Beaufort oddpink hatchery	Kotz pink hatchery	CS zoop	ESA micronekton	EBS zoop			
119	Kotzebue & Beaufort oddpink wild	Kotz pink streams	CS zoop	ESA micronekton	EBS zoop			
120	Kotzebue & Beaufort pink wild	Kotz pink streams	CS zoop	ESA micronekton	EBS zoop			
121	Anadyr pink wild	Anad pink streams	EKC zoop	ESA micronekton	WBS zoop			
122	Anadyr oddpink wild	Anad pink streams	EKC zoop	ESA micronekton	WBS zoop			
123	East Kamchatka pink hatchery	EKam pink hatchery	EKC zoop	ESA micronekton	WBS zoop			
124	East Kamchatka oddpink hatchery	EKam pink hatchery	EKC zoop	ESA micronekton	WBS zoop			
125	*East Kamchatka pink wild	EKam pink streams	EKC zoop	ESA micronekton	WBS zoop			
126	East Kamchatka oddpink wild	EKam pink streams	EKC zoop	ESA micronekton	WBS zoop			
127	West Kamchatka pink hatchery	WKam pink hatchery	OS zoop	WSA micronekton	OS zoop			
128	West Kamchatka oddpink hatchery	WKam pink hatchery	OS zoop	WSA micronekton	OS zoop			
129	*West Kamchatka pink wild	WKam pink streams	OS zoop	WSA micronekton	OS zoop			
130	West Kamchatka oddpink wild	WKam pink streams	OS zoop	WSA micronekton	OS zoop			
131	North Okhotsk pink hatchery	Okho pink hatchery	OS zoop	WSA micronekton	OS zoop			
132	North Okhotsk oddpink hatchery	Okho pink hatchery	OS zoop	WSA micronekton	OS zoop			

Table 1 (continued).

Stock no.	Stock name	Hab w0	Hab s1	Hab w1	Hab s2	Hab w2	Hab s3	Hab w3
133	North Okhotsk pink wild	Okho pink streams	OS zoop	WSA micronekton	OS zoop			
134	North Okhotsk oddpink wild	Okho pink streams	OS zoop	WSA micronekton	OS zoop			
135	East Sakhalin pink hatchery	ESak pink hatchery	OS zoop	WSA micronekton	OS zoop			
136	East Sakhalin oddpink hatchery	ESak pink hatchery	OS zoop	WSA micronekton	OS zoop			
137	East Sakhalin pink wild	ESak pink streams	OS zoop	WSA micronekton	OS zoop			
138	East Sakhalin oddpink wild	ESak pink streams	OS zoop	WSA micronekton	OS zoop			
139	Hokkaido pink hatchery	HokP pink hatchery	OS zoop	WSA micronekton	OS zoop			
140	Hokkaido oddpink hatchery	HokP pink hatchery	OS zoop	WSA micronekton	OS zoop			
141	Hokkaido pink wild	HokP pink streams	OS zoop	WSA micronekton	OS zoop			
142	Hokkaido oddpink wild	HokP pink streams	OS zoop	WSA micronekton	OS zoop			
143	Amur pink wild	Amur pink streams	JS zoop	JS micronekton	JS zoop			
144	Amur oddpink wild	Amur pink streams	JS zoop	JS micronekton	JS zoop			
145	Primorye pink wild	Prim pink streams	JS zoop	JS micronekton	JS zoop			
146	Primorye oddpink wild	Prim pink streams	JS zoop	JS micronekton	JS zoop			

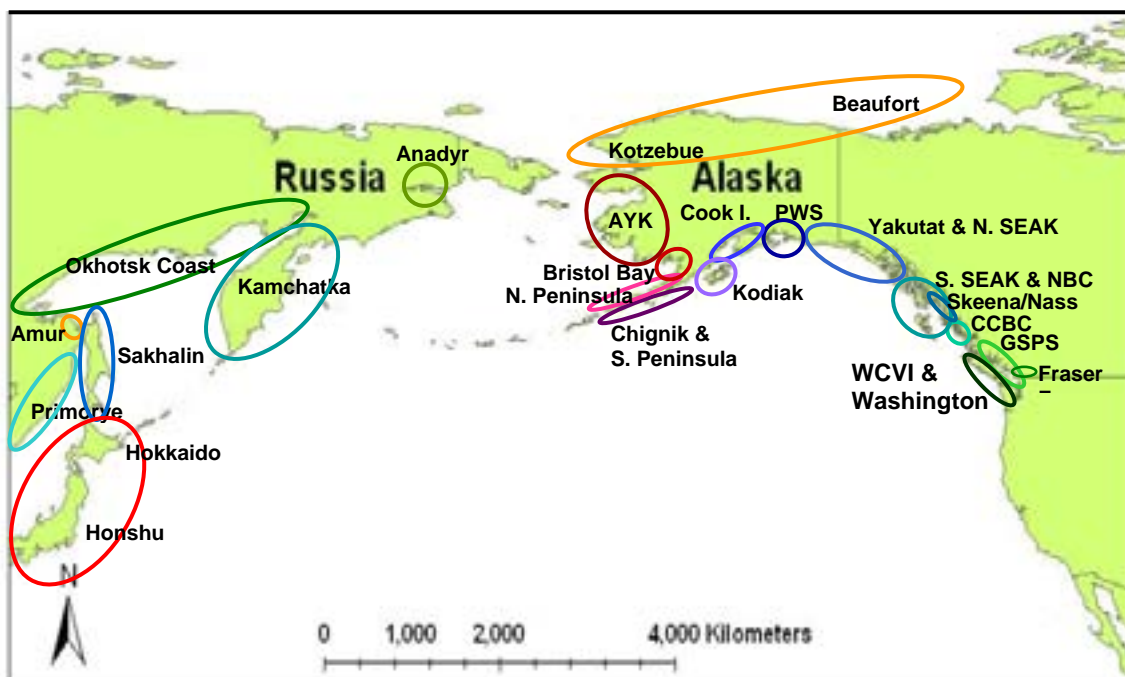


Fig. 2. The approximate geographic locations of regional stock groups used in MALBEC. Stock groups are listed in Table 1. Korea is not shown. AYK = Arctic-Yukon-Kuskokwim, CCBC = central coast British Columbia, GSPS = Georgia Strait (BC) and Puget Sound (WA), PWS = Prince William Sound, SEAK = southeast Alaska, WCVI = west coast Vancouver Island (BC).

for salmon carrying capacity in the MALBEC marine habitat areas. Time series of zooplankton data were obtained for the following regions: the Sea of Okhotsk (Naydenko 2003), the Oyashio (Sugisaki 2006), the Eastern Bering Sea (Napp 2006) and Ocean Station Papa, Gulf of Alaska (Brodeur et al. 1996).

This means that there are also nine MALBEC marine habitat areas for which we have no data. Also, even where measurements exist they may not necessarily be integrated

over all of a particular MALBEC-defined habitat. There has also been an intensive effort to systematically collate long-term zooplankton data, e.g., the Scientific Committee on Oceanic Research Working Group 125 (see www.wg125.net) and the Global Plankton database of the National Oceanic and Atmospheric Administration (www.st.nmfs.gov/plankton/).

Ecopath/Ecosim-Model Derived Time Series

Ecosystem modeling software such as Ecopath with Ecosim has been used to study changes in fish populations and explore bottom-up and top-down mechanisms driving these changes (Christensen and Walters 2004; Walters et al. 2000). When these models are used to infer historic phytoplankton and zooplankton production changes necessary to explain observed changes in upper trophic level populations, e.g., salmon, the resultant time series are correlated to climate indices linked to the ecosystem being modeled (Preikshot 2007; Field et al. 2006; Aydin et al. 2003). Time series of phytoplankton or zooplankton production emergent from Ecosim models used for several North Pacific sub-domains were obtained from previous studies and applied to the most closely related MALBEC habitats. Specifically, we used Ecosim phytoplankton production time series for the British Columbia Shelf (Preikshot 2007), the Strait of Georgia (Preikshot 2007), the Northeast Pacific Gyre (Aydin et al. 2003), the Oyashio (Megrey et al. 2007), and the Northeast Pacific Basin (Preikshot 2007).

Biophysical Model Hindcast Time Series

The Japan Agency for Marine-Earth Science and Technology (JAMSTEC) Frontier Research Center for Global Change (FRCGC) provided zooplankton simulation data produced by a wind-forced biophysical model of the North Pacific Ocean (Aita et al. 2007). This research was done using the *North Pacific Ecosystem Model for Understanding Regional Oceanography* (NEMURO), which covers the whole North Pacific basin with a spatial resolution of 1° latitude by 1° longitude with simulated fields for 1948 to 2002. We developed area-averaged zooplankton time series for each of the following MALBEC-defined marine habitats from the NEMURO gridded fields: Alaska Current, Alaska Coastal Current, Alaska Stream, California Current, Eastern Bering Sea, Chukchi Sea, East Kamchatka Current, Eastern Subarctic, Georgia Strait/Puget Sound, Japan Sea, Okhotsk Sea, Western Bering Sea, and Western Subarctic.

Simulation and Gaming

The model is designed so that a variety of policy scenarios may be examined in the graphical user interface. In particular we built in the capability to change hatchery releases, marine and/or freshwater carrying capacities, and harvest policies. For example, users might ask how specific stocks will perform with changes in habitat capacity caused by land or water use changes that impact freshwater habitat, or by changes in climate that impact freshwater and marine habitat. Users can either sketch carrying capacity changes into the model directly, or prescribed past and future carrying capacity changes can be read in from text files.

The model has three simulation modules built in that allow users to examine different future scenarios. One simulation module allows users to simulate total returns across a

range of hatchery release scenarios and different hypotheses about the strength of density-dependent interactions in shared marine habitat areas. The results are organized so that users may examine total returns, biomass or biomass \times price per kg (\$ value) for wild and/or hatchery stocks by individual stock, species or region. This allows users to ask, for example, what total returns of wild Alaskan sockeye salmon will be if worldwide hatchery production is reduced or increased by a specific fraction. Hatchery policies can be implemented according to jurisdiction, i.e., hatchery production in Canada, the continental USA, Alaska, Russia, Japan, and Korea can each be varied independently.

The second simulation module allows users to examine the impacts of protecting and/or degrading freshwater habitat carrying capacities on total salmon production. In this habitat module, users specify a series of protected freshwater areas whose capacity will be preserved and a range of future relative changes in freshwater carrying capacities for all other regions. Here, for example, users can ask what total salmon returns will be by region across a range of freshwater carrying capacity changes in all but the protected areas.

Lastly, MALBEC has a module that predicts total salmon production as a function of the total number of wild salmon stocks. Using this module users may do simulations that randomly reduce the production of individual wild stocks (ranging from one stock to all wild stocks) by a specific proportion, and then MALBEC estimates how total salmon production overall will be affected.

Here we provide some example results from two simulations: (1) where we change hatchery carrying capacities across a range of hypotheses about density dependence in ocean habitats, and (2) where we evaluate the relative abundance and biomass of wild salmon across a range of numbers of wild stocks affected by declines in egg-to-fry freshwater habitat carrying capacity.

Marine Habitat Capacity Fitting and Simulation

We tested the ability of MALBEC to reproduce the observed run-size data under prescribed marine habitat carrying capacity forcings derived from three different sources of habitat productivity information. This was accomplished by fitting the model and specifying time- and area-specific variations in marine carrying capacities directly linked with plankton biomass time series. The plankton time series data were obtained from three different sources: (1) zooplankton biomass time series developed from field measurements; (2) phytoplankton production time series estimated from fisheries-ecosystem-type models (i.e., driven by changes to the upper portion of the oceanic food web); and (3) zooplankton biomass time series produced by the atmosphere-forced coupled oceanographic-ecosystem NEMURO modeling system (Aita et al. 2007). Three separate MALBEC simulations were then run using each of these three input data sets for the ocean habitat areas defined in the model. In all cases

every effort was made to use time series that would cover a significant portion of the 1952–2006 period or, at the very least, span a few decades in which at least one North Pacific ‘ecosystem regime shift’ (Hare and Mantua 2000) in relative production had occurred. We compared the log likelihoods for each simulation’s salmon abundance predictions compared with our historical simulation to evaluate the model performance using these different sources of marine carrying capacity variations.

RESULTS AND DISCUSSION

Hatchery Versus Wild Salmon Production in the North Pacific Ocean

Our historical salmon abundance estimates are used as input data to the model. Wild pink salmon were the most numerous adult salmon in the North Pacific Ocean and Bering Sea during 1952–2006, averaging approximately 256 million pink salmon per year or approximately 70% of combined wild chum, sockeye, and pink salmon (Fig. 3). Pink salmon abundance declined from the 1950s through the early 1970s, and then increased 82%, on average, after the 1976/77 regime shift compared with the previous 15 years. Sockeye salmon abundance averaged 63 million salmon per year, and production increased 88% after the regime shift. Wild chum salmon abundance averaged approximately 47 million fish per year. However, in contrast to pink and sockeye salmon, wild chum salmon abundance did not increase after the regime shift and abundance was lower than that during the 1950s and early 1960s. Total abundance of the three species averaged 495 million wild salmon during the 1990s. Wild sockeye salmon abundance was greatest in western Alaska (e.g., Bristol Bay), whereas chum salmon abundance was relatively high in mainland Russia, and pink salmon abundance was high in all regions except western Alaska and Washington State and south (not shown).

Abundance of adult hatchery salmon increased steadily from the 1950s to the 1990s (Fig. 3), in part due to increasing releases of juvenile salmon (Mahnken et al. 1998). Improved marine survival rates related to changes in climate and ocean conditions might also be an important factor for at least some hatchery stocks. Abundance of hatchery chum salmon (all regions) exceeded that of wild chum salmon in the early 1980s (Fig. 3), largely in response to high hatchery production in Japan and increasing production in Alaska (not shown). During the 1990s, hatchery production of adult fish averaged 76 million chum, 51 million pink, and 2.9 million sockeye salmon per year (excluding spawning channel sockeye salmon), leading to a combined hatchery and wild salmon abundance of 625 million salmon per year. Regions contributing the greatest to overall hatchery production include Japan (83% of total hatchery chum production), central Alaska (59% of hatchery pink and 87% of hatchery sockeye salmon), southeast Alaska (approximately 10% of hatchery

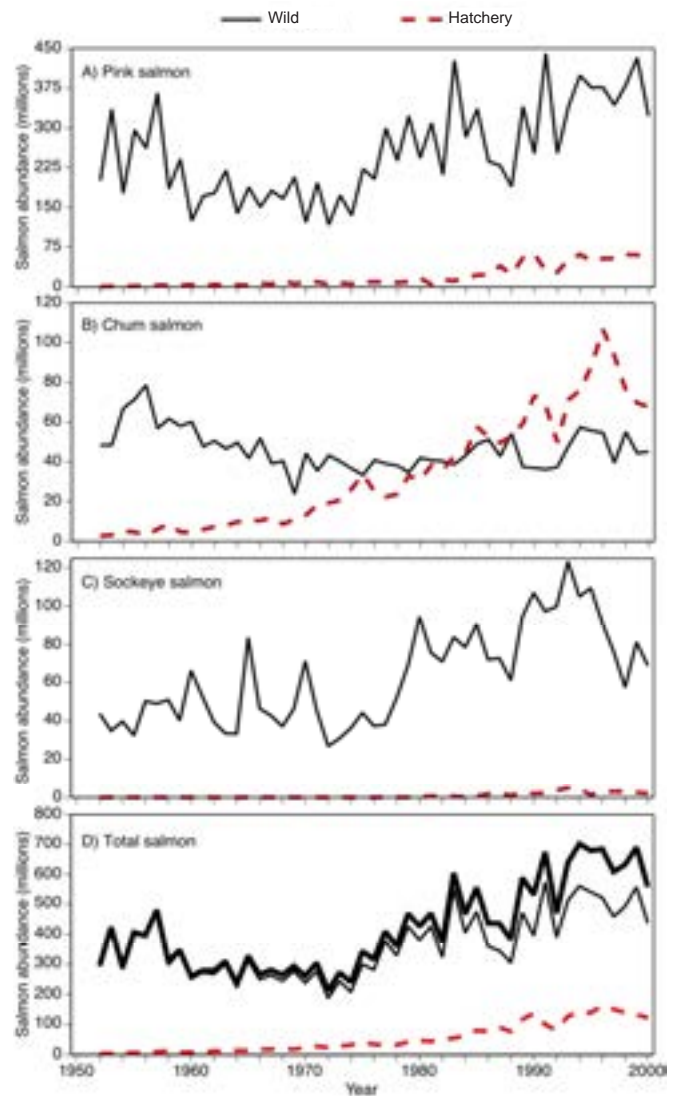


Fig. 3. Trends in abundance (catch and escapement) of wild (solid lines) and hatchery (broken lines) pink, chum, and sockeye salmon, 1952–2000. The heavy solid line in panel D indicates the total of hatchery and wild salmon.

pink, chum, and sockeye salmon), and southern Russia (26% of pink salmon).

During the 1990s, Asian hatchery chum and pink salmon averaged 76% and 58%, respectively, of total species abundance in Asia. In North America, hatchery chum and pink salmon averaged 31% and 18% of total species abundance. Regions where hatchery salmon contributed significantly to total abundance included Japan, Prince William Sound, Southeast Alaska, and Kodiak. Hatchery salmon represented more than 70% of total pink and chum salmon in Prince William Sound, and more than 50% of chum salmon in Southeast Alaska. Hatchery sockeye salmon contributed relatively little to total abundance except in Kodiak, Prince William Sound, and Japan.

These data show that hatchery salmon contribute signif-

icantly to overall abundance of salmon in some regions and that hatchery chum salmon abundance has exceeded that of wild chum salmon since the early 1980s. Our efforts to estimate hatchery and wild salmon abundances involved many assumptions because resource agencies typically do not report estimates of hatchery *versus* wild salmon returning to each region and because spawning counts are often indices rather than total abundance estimates. Reasonably accurate estimates of wild salmon production are necessary for developing spawning escapement goals that provide the potential for maintaining high harvest levels. We therefore encourage agencies to document and report numbers of hatchery and wild salmon in both catch and spawning escapements.

Rearing, Movement, and Interactions in the Marine Environment

Our input data on marine habitats are based on the premise that Pacific salmon in the open ocean have stock-specific distribution and migration patterns. In general, the results of stock identification studies using a variety of methods indicate that the ocean distribution patterns of salmon have a hierarchical geographic structure in which stocks that are genetically similar or geographically adjacent to each other in freshwater habitats, or both, have ocean distribution and migration patterns more similar to each other than to those of genetically or geographically distant populations (Myers et al. 2007). Individual populations or life-history variants within populations usually occupy only a portion of the entire oceanic range occupied by larger groups of populations, e.g., regional stock complexes.

Variation in the marine life history of salmon occurs at many different spatial and temporal scales (Fig. 4). Because the temporal scale of life-history variation in MALBEC is limited to two, 6-month stanzas per year, large marine ecosystems are the most appropriate spatial scale for this model. The prevailing theory among experts is that salmon in the

open ocean move across broad fronts to the south and east in winter and spring and to the north and west in summer and fall (e.g., French et al. 1976; Burgner 1991; Shuntov et al. 1993; Myers et al. 2007). While spatial and temporal variation in salmon diets is considerable, it is generally well-accepted that sockeye, pink, and chum salmon occupy the same or similar trophic levels at all life-history stages (e.g., Johnson and Schindler 2008).

Rearing habitats in MALBEC are designated by region and prey names. We devised a simple classification scheme of 13 marine ecoregions and two diets (zooplankton, micronekton) to describe winter–spring (W, January–June) and summer–fall (S, July–December) rearing, movement, and interactions of MALBEC stock groups (Fig. 5, Table 1). Micronekton prey typically include small forage fish, squid, and euphausiids (Brodeur and Yamamura 2005). If coho and Chinook salmon and steelhead are included in future versions of MALBEC, both their summer and winter diets in the open ocean can be categorized as micronekton prey.

Because of our underlying assumptions about salmon distributions and movements, interactions in MALBEC will be greatest among species and stocks that originate from the same or adjacent geographic regions. Based on the information we used to inform our ocean migration table, interactions among stocks that originate from geographically distant regions will be greatest in the Bering Sea in summer–fall and in the eastern sub-Arctic in winter–spring. We emphasize that our current understanding of stock-specific distribution and movement patterns of salmon in the open ocean, particularly in winter and early spring, is extremely limited. There are little or no published data for many salmon populations. We encourage the NPAFC to coordinate cooperative salmon research efforts in international waters that will provide data on rearing, movements, interactions, abundance, and stock origins of hatchery and wild salmon in winter and early spring.

Model Fitting

While our results are preliminary, we were able to fit the model to all stock data (e.g., Figs. 6, 7) and to estimate density-dependent growth and survival effects. Our preliminary results indicated that simulations including density-dependent interactions in the ocean yielded better fits to the observed run-size and growth data than those simulations without density-dependent interactions in the ocean. These results indicate that increases in the production in one area and/or one population group could affect growth and survival of salmon in population groups with overlapping marine distributions. Much work remains to validate model fits. In particular fits to body size need to be corrected for changes in age composition for each stock where the age structures are currently assumed stationary at input values.

The model reproduced general patterns observed in the total run data but consistently had difficulty predicting run

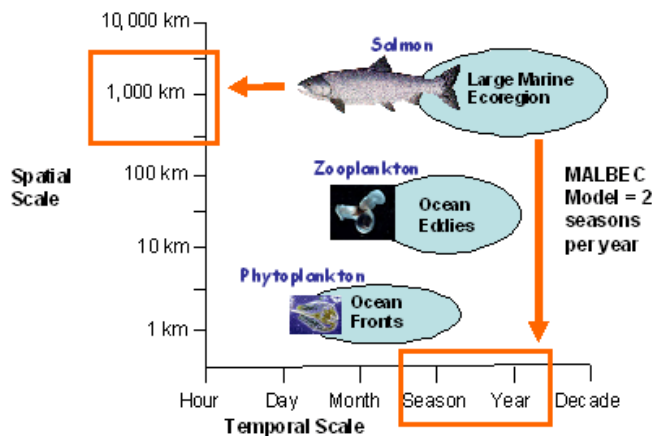


Fig. 4. Spatial and temporal scales of variation in the marine life history of salmon. In MALBEC, the spatial scale is large marine ecoregions and the temporal scale is two seasons per year.

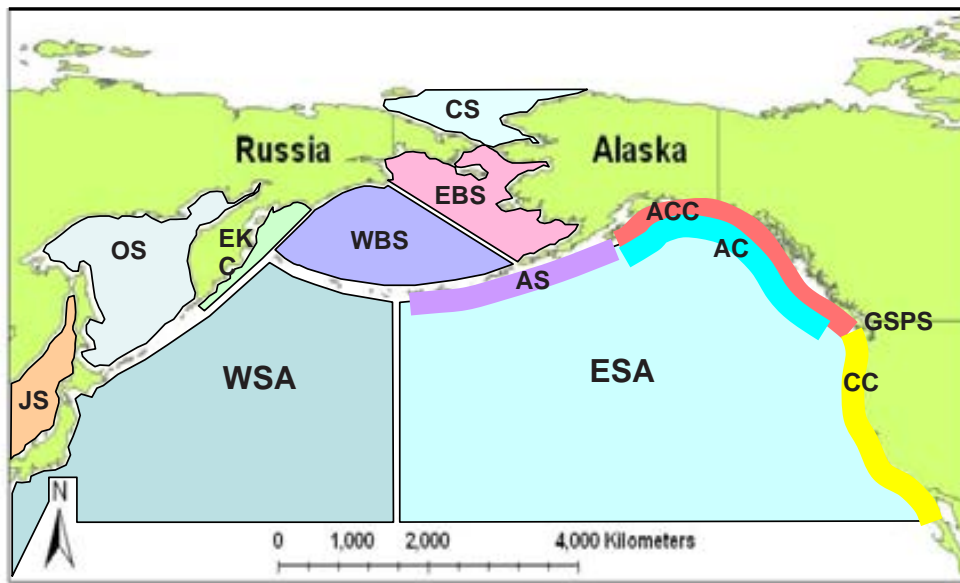


Fig. 5. Large marine ecoregions used to describe ocean distribution of MALBEC stock groups. AC = Alaska Current, ACC = Alaska Coastal Current, AS = Alaska Stream, CC = California Current, CS = Chukchi Sea, EBS = Eastern Bering Sea, EKC = Eastern Kamchatka Current, ESA = Eastern Sub-Arctic, GSPS = Georgia Strait and Puget Sound, JS = Japan Sea, OS = Okhotsk Sea, WBS = Western Bering Sea, WSA = Western Sub-Arctic.

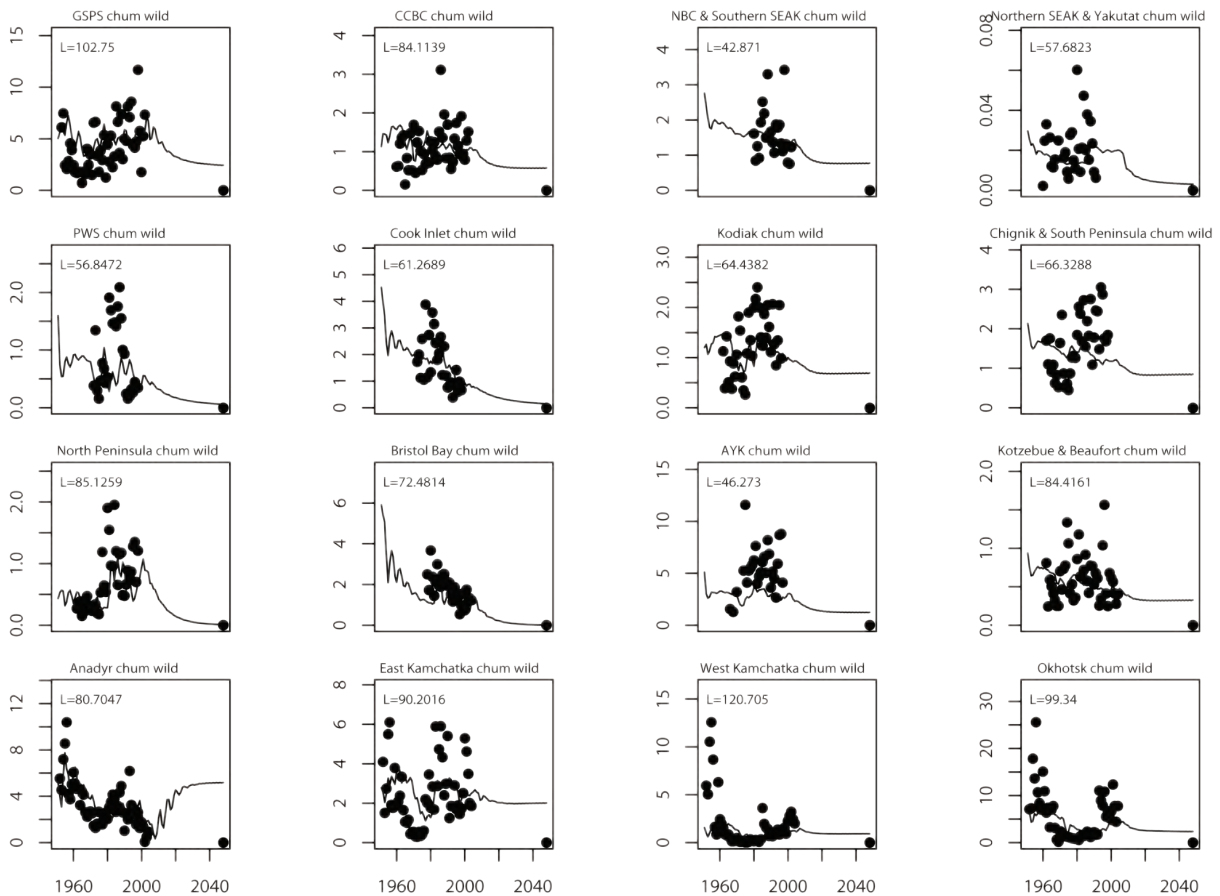


Fig. 6. Model fit to total run size for wild chum salmon using time-varying survival rate multipliers (α_t). Historical run-size data are shown with solid dots, MALBEC simulation output is shown with light solid lines, and abundances are given in millions of fish. The geographic location of each stock group is shown in Fig. 2.

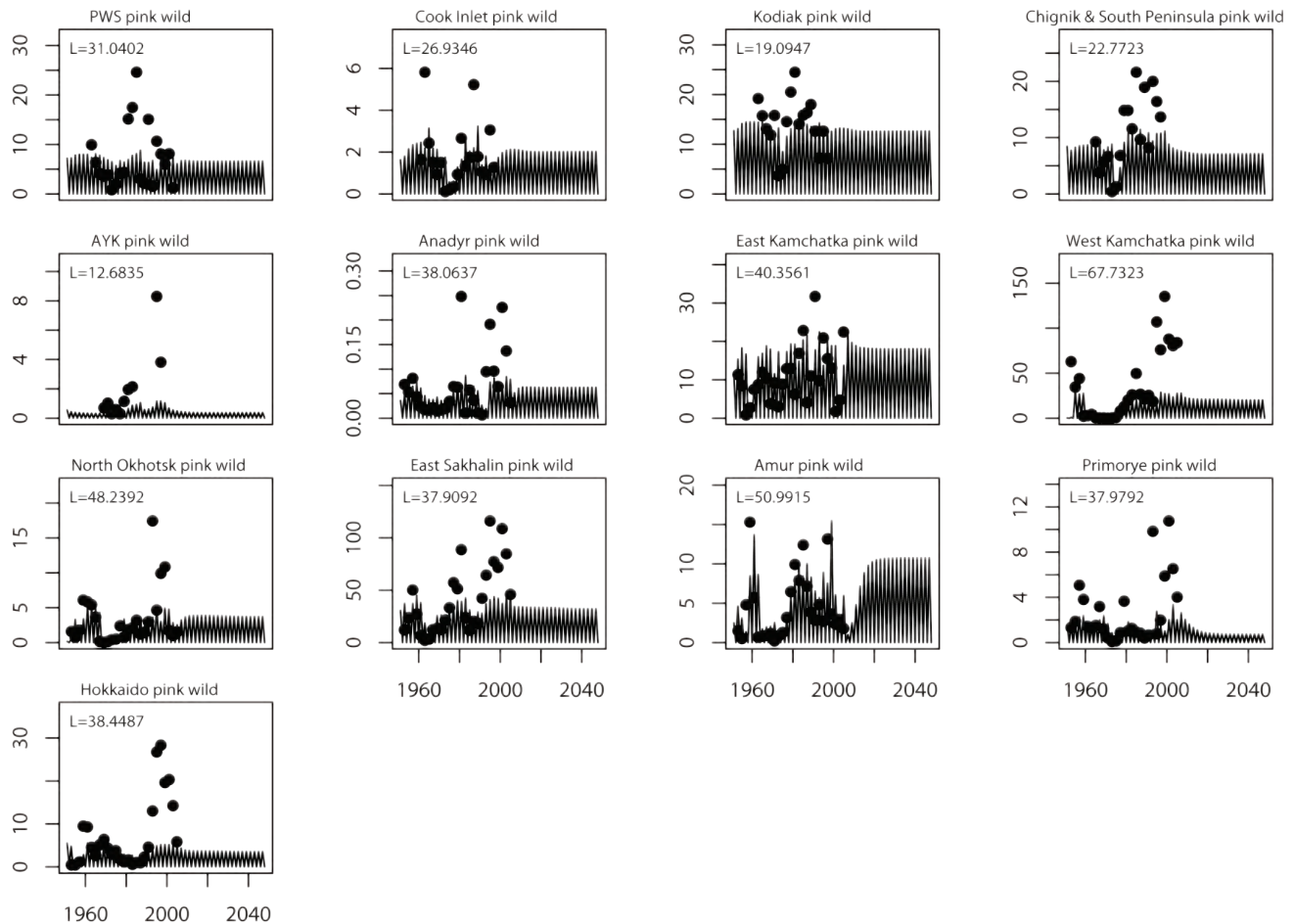


Fig. 7. Model fit to total run size for wild pink salmon using time-varying survival rate multipliers (α_t). Historical run-size data are shown with solid dots, MALBEC simulation output is shown with light solid lines, and abundances are given in millions of fish. The geographic location of each stock group is shown in Fig. 2.

sizes for some stock groups, even with time varying Ricker $\alpha_{i,t}$ values. Our simulation did not predict some of the very dramatic declines that occurred in some stocks, for example, in western Kamchatka chum salmon in the 1950s (Fig. 6). Likewise it did not capture some of the very large increases that occurred in pink salmon population sizes in the late 20th century, for example, in Prince William Sound (PWS) in the 1980s or in east Sakhalin in the 1990s (Fig. 7). It should be noted that freshwater rearing capacities for hatchery stocks are not fit to the data in the same way as they are for wild stocks. While hatchery performance is plotted in Figs. 6 and 7, the predicted returns depend on freshwater carrying capacity changes in hatcheries that go into the model as input in addition to changes in marine survival rates caused by competition and density-dependent interactions that the model predicts.

While the model run size predictions for some specific stock groups have large errors, the predicted aggregate run-size variations for all stocks are similar to those in the historical data. Using the maximum likelihood fit to data series designated high quality, the model predicts that total pink,

chum, and sockeye salmon abundance was, at its peak, approximately 700 million wild and hatchery salmon (Fig. 8), while the estimated observed abundance was 634 million wild and hatchery salmon during the 1990s. Rogers (2001) reported total Pacific salmon numbers of all species at approximately 600 million fish in the peak years of the 1990s. MALBEC offers the additional advantage of tracking total biomass, which better incorporates density-dependent growth and survival effects.

MALBEC Simulations Using Prescribed Variations in Marine Carrying Capacities with Density-Dependent Growth and Survival

It is important to note that estimates of density-dependent effects (on both growth and survival) will be confounded with carrying capacities (Equations 1, 4). High carrying capacity ($C_{j>0}$) values can be compensated by higher estimates of ρ , and vice-versa (Equation 1). The shared habitat effects of stock interactions will depend on the ratio of ρ and/or γ to C , so that in those areas where capacities are either

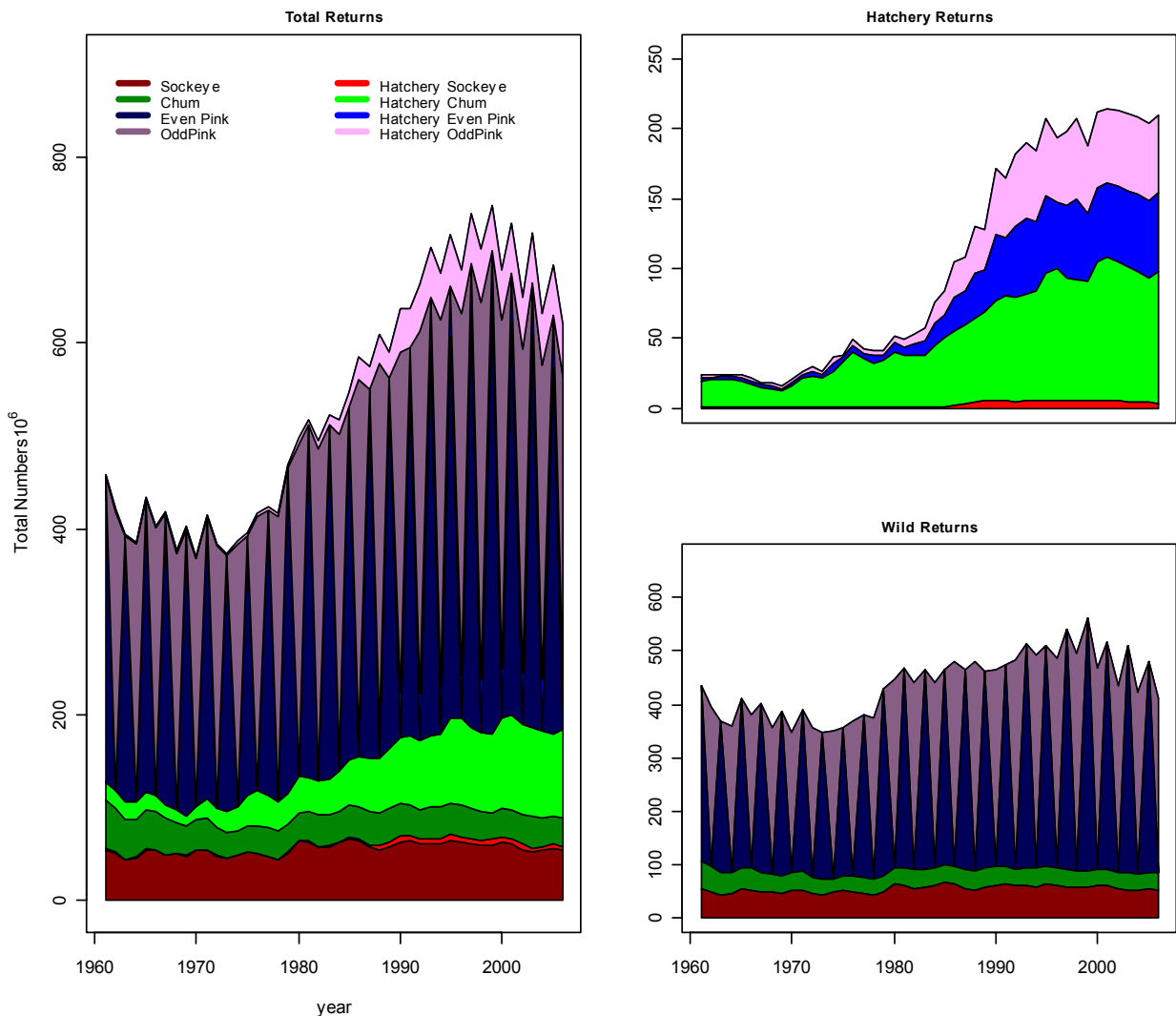


Fig. 8. Reconstructed salmon returns (numbers in millions of fish) estimated using MALBEC: total salmon returns (left panel), total hatchery salmon returns (upper right panel), and total wild salmon returns (lower right).

modeled to be low, and/or fish densities high, then density-dependent effects must be stronger to explain the observed data. Total run data do not contain information about both density-dependent parameters and carrying capacities. That is, the total number of eggs produced to support subsequent generations can be affected by density-dependent processes that lead to population-level responses that include smaller adult body sizes (from density-dependent effects on growth), or fewer numbers (density-dependent effects on mortality). Changes external to individual populations can exert density-dependent controls by such pathways as altered fish densities or reduced marine carrying capacities in shared marine habitats. Regardless, the policy consequences are the same: there are limits to salmon production and these limits are determined by the combined effects of habitat carrying capacities and total fish densities.

Density-dependent interactions suggest that for any level of ocean productivity, each ocean habitat will only support a

certain biomass of fish but this biomass could consist of different combinations of stocks, stock numbers, and individual fish sizes. We show results from two simulations to illustrate this point in Figs. 9–11. In Fig. 9 we show that scenarios for reduced total North Pacific hatchery production cause the total number of wild Alaskan chum salmon to increase, and that such increases are largest where density-dependent effects on survival are large and small where they are not. In Figs. 10 and 11 we show how the numbers of total salmon biomass change as a function of changes in the freshwater rearing capacity for wild salmon. The isopleths on these figures show that the relative total abundance and biomass of wild salmon can be conserved near the current state even as the freshwater carrying capacity is reduced for an increasing number of wild stocks because of compensating increases in marine growth and survival in shared marine habitats. Not shown in these figures is the improved performance of hatchery stocks as wild stocks are in decline, again because

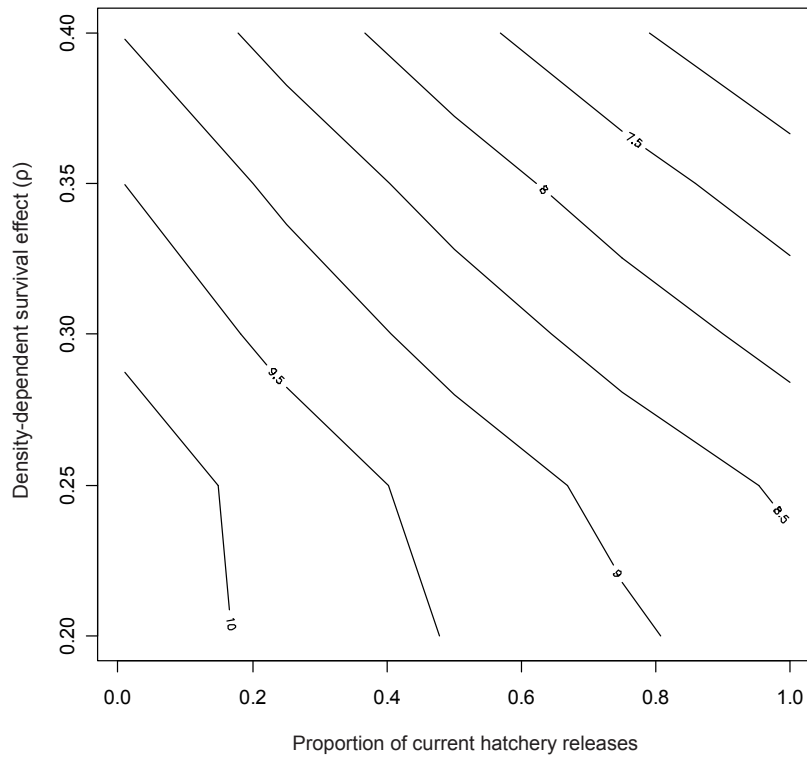


Fig. 9. Example of predicted changes in total wild Alaskan chum numbers (in millions) as a function ρ and relative hatchery production.

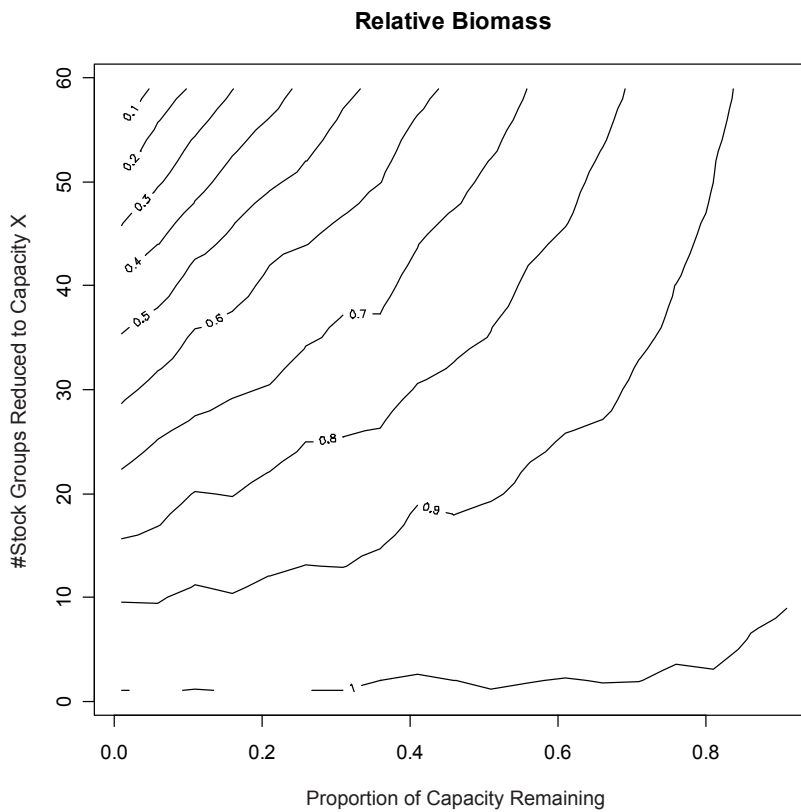


Fig. 10. Example of total relative wild salmon biomass as a function of number of wild stock groups (y axis), with egg-to-fry capacity reduced by the proportion of current carrying capacity (x axis). For this simulation, ρ was set to 0.34 and γ set to 0.5.

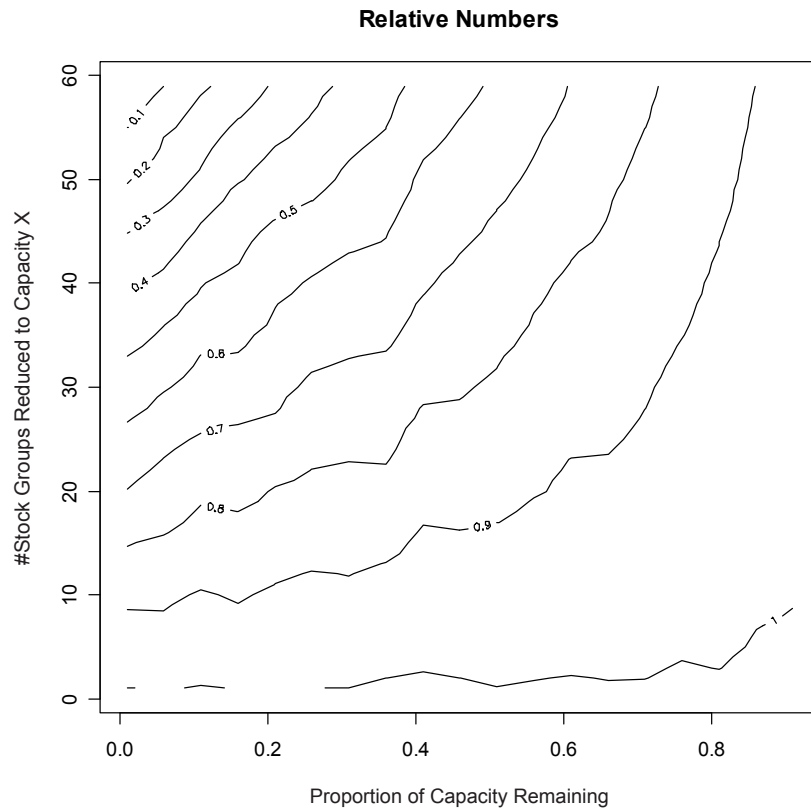


Fig. 11. Example of total relative wild salmon numbers as a function of number of wild stock groups (y axis), with egg-to-fry capacity reduced by the proportion of current carrying capacity (x axis). For this simulation, ρ was set to 0.34 and γ set to 0.5.

the model predicts that marine survival rates increase in response to reduced fish densities in shared marine habitats. If hypotheses about density-dependent growth and survival effects in the ocean are true, then an important policy choice involves tradeoffs between the relative abundance of hatchery *versus* wild salmon using shared marine habitats.

Time-Varying Productivity in Salmon Habitat Domains across the North Pacific

The inclusion of time-series anomalies in carrying capacity (from the different estimates of plankton biomass) did not dramatically improve the model fit over simulations that did not include these data, but based on log likelihood values alone the simulations using NEMURO summer zooplankton fields performed the best of the three simulations that used time-varying carrying capacity information (Table 2). It is important to note that simulations that included the time-varying Ricker $\alpha_{i,t}$ parameter series of Peterman et al. (2003) outperform these plankton-based time series of spatially and temporally varying marine carrying capacities by 100s of log likelihood units. This result is not surprising, since the relative $\alpha_{i,t}$ values were derived from stock recruitment data and should be expected to give the best fit.

MALBEC's ability to accurately project future changes in abundance of each salmon population group will depend

on the accuracy of projected changes in carrying capacity of salmon in both freshwater and marine habitat areas and its ability to accurately capture the dynamics of multi-stock interactions. It is important to note that future salmon production will not just be a function of density-dependent interactions and carrying capacity variations modeled with MALBEC. Salmon numbers will also respond to changes in overall predator regimes associated with any future climate changes, i.e., following from Walters and Korman (1999), relative changes in predation risk to carrying capacity will affect future outcomes. Another limitation with MALBEC's relatively coarse spatial resolution is that it assumes density-dependent effects (ρ, γ) are the same across all areas whereas the dynamics underlying apparent production limits might be occurring in very narrow spatio-temporal windows. If salmon population dynamics are determined by such fine scale dynamics then MALBEC's stock-level predictions will be unreliable.

SUMMARY AND CONCLUSIONS

Our historical salmon abundance dataset shows that hatchery fish contributed significantly to overall abundance of salmon in some regions, and that hatchery chum salmon abundance exceeded that of wild chum salmon beginning in the early 1980s. Our estimates involved many assump-

Table 2. ρ , γ and log likelihood values for simulations using different sources of prescribed marine habitat carrying-capacity time series. Stock-specific time-varying survival rate multipliers (Ricker α parameters) of Peterman et al. (2003) were not used in any of these simulations.

Source of marine habitat carrying-capacity time series	Rho	Gamma	Log(likelihood)
None	0.707	0.652	2914.52
EcoPath	0.387	0.411	2954.2
Zooplankton field data	0.641	0.631	2915.64
NEMURO summer	0.704	0.652	2914.07
NEMURO winter	0.707	0.652	2914.5

tions because resource agencies do not routinely report these numbers. We therefore encourage agencies to document and report numbers of hatchery and wild salmon in both catch and spawning escapements.

Published data were used to assign 146 regional stock groups of Asian and North American hatchery and wild pink, chum, and sockeye salmon to marine habitats during seasonal (winter–spring, summer–fall) life-history stanzas. However, current understanding of stock-specific distribution and movement patterns of salmon in the open ocean, particularly in winter and early spring, is extremely limited. There are little or no published data for many salmon populations. We encourage NPAFC to coordinate cooperative salmon research efforts in international waters that will provide data on rearing, movements, interactions, abundance, and stock origins of hatchery and wild salmon in winter and early spring.

While our results are preliminary, we were able to fit the model to all stock data and to estimate density-dependent growth and survival effects. Simulations that include density-dependent interactions in the ocean yield better fits to the observed run-size and growth data than those simulations without density-dependent interactions. These results indicate that increases in salmon production in one area and/or one population group could affect growth and survival of population groups with overlapping marine distributions. Much work remains to validate model fits. In particular fits to body size need to be corrected for changes in age composition for each stock where the age structures are currently assumed stationary at input values.

We used three different time series of zooplankton biomass to simulate variations in the marine carrying capacity of salmon in all MALBEC habitats. If the space-time patterns of phytoplankton and zooplankton production can be estimated, this approach can be used to examine the potential impacts of future climate changes on the marine carrying capacity of salmon. Additional climate or ecosystem indices associated with any future changes in carrying capacity of salmon, e.g., changes in overall predator or competitor densities, also need to be evaluated.

Next Steps

While much progress has been made in the Salmon

MALBEC project, this effort aims to tackle several important issues in the near future. One high priority next step is an evaluation of climate change impacts on the carrying capacity for salmon in both freshwater and marine habitat areas for the 2007–2050 period. Key challenges in developing carrying capacity change scenarios for salmon lie in linking scenarios for surface temperature and precipitation changes to hydrologic and freshwater carrying capacity changes, and linking scenarios for changes in upper ocean properties (e.g., temperatures, currents, and upwelling) to meaningful measures of food-web productivity and predation risks. Physical climate scenarios are now readily available from the archives of the Intergovernmental Panel on Climate Change (IPCC), but to our knowledge no one has yet extended these into full life-cycle salmon habitat change scenarios.

We also plan to use the results of the Pacific Rim River Typology Project, a remote-sensing based classification of salmon-producing rivers across the north Pacific Rim to better estimate habitat-defined freshwater carrying capacities for salmon. Because the MALBEC framework is scalable, we hope that MALBEC will be used for regional evaluations of interstock interactions in salmon production basins like the Puget Sound/Georgia Basin, or the Skeena or Columbia river basins, where large numbers of individual populations have the opportunity to interact at various stages of their life cycle in shared habitats.

Our ultimate goals are to integrate various combinations of scenarios for conservation, habitat change, hatchery production, and harvest policy to reflect possible futures for Pacific salmon, and to use MALBEC to test the outcomes of various policy decisions in the face of climate and management uncertainty. To that end, we also plan to make the MALBEC software available for the research and management community to explore conservation, hatchery, harvest, and habitat change scenarios of their own choosing.

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Summary and Future Plan of BASIS

Dramatic fluctuations in the ocean growth and survival of many Asian and North American salmon populations over the past decade have been attributed to changes in the Bering Sea and other marine ecosystems. The absence of scientific observations for salmon, ecologically related species, and environmental conditions in the North Pacific Ocean has limited our understanding of these changes and how they affect salmon populations and economies around the Pacific Rim. International research efforts to address these issues were developed by the North Pacific Anadromous Fish Commission (NPAFC) as part of its Science Plan. The research plan called BASIS (the Bering-Aleutian Salmon International Survey), began in 2002 as a coordinated program of cooperative research on Pacific salmon in the Bering Sea. The goal of BASIS research was to clarify the mechanisms of biological response by salmon to the conditions caused by climate change in the Bering Sea.

Climate models predict a gradual increase in atmospheric temperature, with the greatest increases occurring in sub-arctic and arctic regions. The evidence for current warming trends is the pole-ward retreat of seasonal sea ice cover in the Arctic (Fig. 1). Continued warming is predicted to have a profound effect on Bering Sea ecosystems. For instance, a presentation at the BASIS Symposium by Nicholas Bond showed that climate warming will increase water column stability on the eastern Bering Sea shelf, limiting the flux of nutrients into the photic zone and perhaps negatively impacting primary and secondary productivity.

Large-scale climate cycles are affecting regional climate trends. For instance, shifts in the position the Far Eastern Low and Aleutian Low pressure systems determine whether or not the Bering Sea experiences warming or cooling and also affects the velocity of ocean currents. The position of these atmospheric low pressure systems (NE and W, respectively) during 2002 to 2005 brought warmer air to the Bering Sea during winter and was related to decreased storm

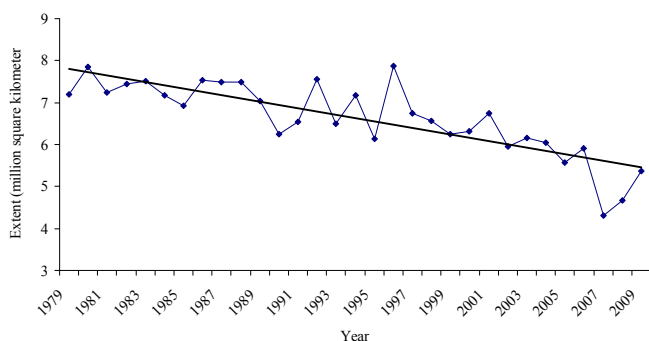


Fig. 1. Average monthly Arctic sea ice extent September 1979 to 2009. (Data courtesy of the National Snow and Ice Data Center).

activity during summer. The position of these low pressure systems shifted again (SW and E, respectively) during 2006, resulting in colder arctic air covering much of the Bering Sea during winter and summer which increased storm activity.

The BASIS research initiated by the NPAFC could not have been more timely. The surveys began during 2002, a time of anomalously warm spring and summer sea temperatures. These warm sea temperatures continued through 2005, switching to anomalously cold during 2006 to 2008 (Fig. 2). Thus many of the papers within these proceedings offer perspective on how salmon and other nekton responded to changing climate states. All papers were peer-reviewed with the objective to provide a broad spectrum of research results from a team of international scientists working on the biological response of Pacific salmon and other nekton to climate change and variability in the Bering Sea and Arctic ecosystems.

The papers in these proceedings are the culmination of oral and poster presentations given at the BASIS Symposium during November 23–25, 2008 in Seattle, Washington. Ed Farley chaired a steering committee consisting of Tominori Azumaya, Richard Beamish, Ki Baik Seong, Vladimir Sviridov, and Shigehiko Urawa. There are four topics within the general theme of the biological responses by salmon to climate and ecosystem dynamics: (1) migration and distribution of salmon; (2) food production and salmon growth; (3) feeding habits and trophic interaction; and (4) production trends and carrying capacity of salmon. During the symposium, NPAFC

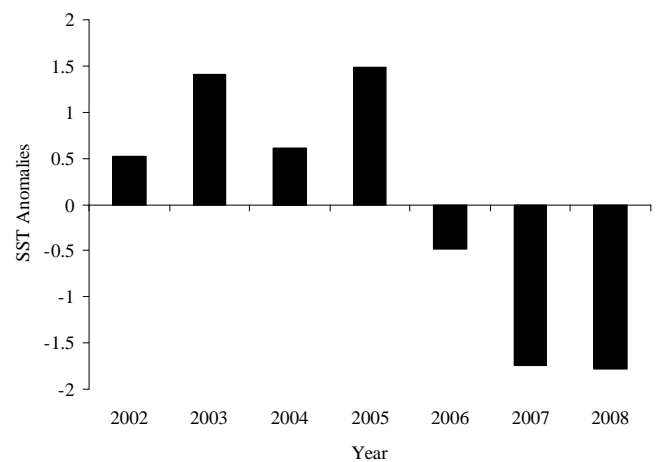


Fig. 2. Anomalies of sea surface temperatures (bars, SSTs, °C) during May 2002 to 2008 in the southeastern Bering Sea (data obtained from <http://www.beringclimate.noaa.gov>). Mean May SSTs are averaged over the area 54°18'N to 60°0'N, 161°12'W to 172°30'W using data from the National Centers for Environmental Protection and the National Center for Atmospheric Research (NCEP/NCAR) reanalysis project (Kalnay et al. 1996). The anomalies are the deviations from the mean May SST value (2.33°C) for the 1970–2000 period normalized by the standard deviation (0.76°C).

commemorated the efforts from research and contract vessels: *Kaiyo maru* and *Wakatake maru* (Japan), *TINRO* (Russia), and *Sea Storm* and *Northwest Explorer* (USA) for their expertise and support in conducting BASIS research surveys.

The success of the symposium was due to the steadfast dedication of the NPAFC Secretariat: Vladimir Fedorenko, Shigehiko Urawa, Wakako Morris, and Denise McGrann-Pavlovic. In addition, the papers within this Bulletin were published one year after the Symposium because of the timely management by Shigehiko Urawa and the symposium editorial group members. Approximately 60 reviewers contributed to peer reviews of original manuscripts, and Natalie Moir worked closely with authors for the final editions.

Migration and Distribution of Salmon

There are 14 papers utilizing a combination of stock identification techniques including genetics, hatchery otolith thermal marks, scale pattern analysis, temperature-depth archival tags, and otolith microchemistry used to describe the distribution, vertical migration, and potential migratory pathways/overwintering grounds for juvenile, immature, and maturing salmon. New information on the distribution of juvenile chum salmon in the Arctic during fall presented by Chris Kondzela indicated a large percentage of juvenile chum salmon captured in Bering Strait were from the Anadyr-Kanchalan river system of northeastern Russia, whereas the majority of juvenile chum salmon captured in the Chukchi Sea region were from northwestern Alaska. Jim Irvine used otolith microchemistry to examine whether or not juvenile chum salmon from the Mackenzie River (Arctic) over-winter in the Beaufort Sea region and determined that they could not rule out this possibility. Shunpei Sato found that Asian chum salmon stocks dominated the catch in the central Bering Sea during summer months, whereas Alexander Bugaev found that Japanese and North American stocks were primarily distributed in the northern sections of the Russian EEZ and Russian stocks were primarily distributed in the southern region of the Russian EEZ during summer and fall. Terry Beacham found that immature chum salmon captured in the Gulf of Alaska during winter were primarily from North America in the northern region and from Asia in the southern region. Tomonori Azumaya developed a new model linking chum salmon bioenergetics to their high-frequency vertical migrations, as determined from archival tags data to describe why these vertical migrations optimize their feeding opportunities while minimizing their energetic requirements. Shigehiko Urawa clarified the stock-specific ocean distributions of Asian and North American chum salmon by using genetic and otolith marks, and he modeled the seasonal migration patterns of Japanese chum salmon between the Bering Sea and North Pacific Ocean, which mainly responded to changing seawater temperatures.

Papers from Toru Nagasawa and Pat Martin offer new information on the influence of sea surface temperatures on im-

mature and maturing sockeye salmon distributions and CPUE trends in the Bering Sea. New information on stock structure of immature sockeye salmon in the Russian EEZ indicated the presence of Bristol Bay and Asian stocks of sockeye salmon in the northwestern Bering Sea during summer and fall. Papers on Chinook salmon distribution by James Murphy and Alexander Bugaev suggested that juvenile western Alaska Chinook salmon maintain distinct stock-specific distributions during their first year in the ocean, but are intermixed with Russian Chinook salmon in the northwestern Bering Sea the following years at sea. In addition, Robert Walker describes how information from an archival temperature depth tag placed on an immature Chinook salmon was used to infer that this fish over-wintered in the Bering Sea before migrating back to the Yukon River the following summer.

Food Production and Salmon Growth

There are six papers examining salmon size and growth as a proxy to ocean productivity. There is a long history of researchers using size at age to determine when or if density-dependent growth occurs for salmon in the ocean inferring an ocean carrying capacity. The Japanese scientists have one of the best time series on salmon length, where salmon were collected using variable mesh research gillnets during open ocean surveys in the North Pacific. Masa-aki Fukuwaka determined that bias-corrected mean fork lengths for chum salmon captured using research gillnets were smaller than uncorrected means, but concluded that the temporal trends in salmon size were not different. Ellen Martinson used scales collected from adult sockeye salmon returning to the Karluk River from 1922 to 2000 to suggest that fish length indices from salmon scales can be useful predictors of climate variability - shifts and ecosystem status. Alexander Zavolokin determined that Russian chum salmon tend to be distributed in regions where high concentrations of forage are found but can experience density-dependent growth patterns during their second, third, and fourth years at sea indicating that ocean conditions can affect ocean carrying capacity for these salmon. Alex Andrews showed how shifts between warm and cold ocean temperatures among years can alter juvenile pink salmon diets, size, and whole body energy content. Jamal Moss found that juvenile pink and chum salmon captured in the Chukchi Sea fed on high energy prey and had higher growth rates than those captured further south.

Feeding Habits and Trophic Interaction

Many fisheries resource managers are turning from single species management to an ecosystem approach to management in order to provide a comprehensive framework for living marine resource decision making. A necessary component of an ecosystem approach to management is the study of fish food habits and trophic interaction. There are six papers in these proceedings examining this topic. Svetlana Naydenko

showed that in the western Bering Sea juvenile walleye pollock consumed a large portion of the forage resource during 2002 and 2003 and Pacific salmon, squids, Atka mackerel, herring, and capelin were the dominate consumers of the available forage during 2004 to 2006. She concluded that salmon production is not limited by zooplankton abundance. Kristen Cieciel examined the relationship between jellyfish and juvenile and immature salmon distributions and found that in some years there could be a potential for competition for food resources. Nancy Davis with Thaddaeus Buser have several papers on salmon diets. One paper reveals that salmon diets shifted between warm and cold years and that there is a difference in salmon stomach contents amongst regions of the Bering Sea. The others indicate that immature Chinook salmon feed on fish offal during winter months in the Bering Sea, where the offal is identified as walleye Pollock body parts discarded from high seas factory trawlers. Rusty Sweeting examined diets of juvenile hatchery and wild coho salmon collected in the Strait of Georgia and found no differences in appetite or diet of these fish during the summer growing months.

Production Trends and Carrying Capacity of Salmon

There are seven papers addressing this topic. Vyacheslav Shuntov suggests that climate warming will not impact carrying capacity for salmon in the western Bering Sea and that current models indicate that the carrying capacity for salmon in the Bering Sea is much higher than present abundance levels. Greg Ruggerone presents a different view on carrying capacity, suggesting that the large increase in the abundance of hatchery salmon impact wild salmon stocks by limiting growth via density-dependent processes in the ocean, increasing their mortality rates. Ed Farley found that pelagic productivity on the eastern Bering Sea was highest during years with warm SSTs, as abundance levels of juvenile salmon and age-0 pollock are much higher than during years with cool SSTs. A model assessing links between ecosystems presented by Nate Mantua suggests that for any level of ocean productivity, the ocean will only support a certain biomass of fish. Masahide Kaeriyama shows prediction models for the impact of global warming on the ecosystems of the North Pacific Ocean and concludes that (1) global warming will decrease salmon carrying capacity by reducing their preferred ocean habitat; (2) an increase in density-dependent effects on growth of salmon, thus potentially reducing their marine survival; (3) Hokkaido chum salmon will no longer migrate to the Sea of Okhotsk, an important rearing region for juvenile chum salmon. In addition, Yukimasa Ishida examined archeological remains of chum salmon from sites along the Japan coast and determined that global warming will reduce salmon production in Japan if sea surface temperatures rise such as they had in the past.

Future BASIS Research

There was a lively discussion at the end of the symposium

regarding future research for BASIS and a resounding commitment to continue this vital research by Parties within NPAFC. Since the meeting, Parties within NPAFC agreed to continue BASIS into Phase II (2009–2013). The Phase II plan (NPAFC 2009) will focus on the following research questions:

- 1) How will climate change and climate cycles affect anadromous stocks, ecologically related species, and the Bering Sea ecosystems?
- 2) What are the key climatic factors affecting cyclical changes in Bering Sea food production and pelagic fish communities?
- 3) How will climate change and climate cycles impact the available salmon habitat in the Bering Sea?
- 4) How will climate change and climate cycles affect Pacific salmon carrying capacity within the Bering Sea?

There was a general sense of satisfaction knowing that BASIS research captured the response of the Bering Sea pelagic ecosystem to cyclic patterns in climate. There was no question that the North Pacific Anadromous Fish Commission BASIS research strengthened our knowledge of the effects of climate variation on pelagic ecosystems of the Bering Sea. This research also fostered unprecedented cooperation among NPAFC Parties and is a model for future collaborative research efforts in the North Pacific Ocean.

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