NORTH
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TECHNICAL REPORT 4

Joint Meeting *on Causes of Marine Mortality of Salmon in the North Pacific and North Atlantic Oceans and in the Baltic Sea*

Edited by: **IBSFC**
NASCO
NPAFC
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Vancouver, Canada

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Vancouver, B.C., Canada, March 14-15, 2002

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Published by: **North Pacific Anadromous Fish Commission** **Tel: (604) 775-5550**
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Foreword

The Joint Meeting on Causes of Marine Mortality of Salmon in the North Pacific and North Atlantic Oceans and in the Baltic Sea was held in Vancouver, British Columbia, Canada, on March 14-15, 2002. The Joint Meeting was co-organized and co-sponsored by International Baltic Sea Fishery Commission (IBSFC), International Council for the Exploration of the Sea (ICES), North Atlantic Salmon Conservation Organization (NASCO), North Pacific Anadromous Fish Commission (NPAFC), and North Pacific Marine Science Organization (PICES). The Organizing Committee consisted of representatives from each of these five international organizations, and was co-chaired by Dr. Yukimasa Ishida of NPAFC and Dr. Malcolm Windsor of NASCO. All necessary arrangements were made by the NPAFC Secretariat (Local Organizer) in cooperation with the Organizing Committee.

Over 140 scientists, industry representatives, and fisheries officials from 15 countries attended the Joint Meeting. There were 21 oral and 16 poster presentations of scientific papers followed by a synthesis and discussion session. Extended abstracts of the presented papers are included in this Technical Report as well as a synthesis of the Joint Meeting. The material presented in this Technical Report has not been peer reviewed, and does not necessarily reflect the views of IBSFC, ICES, NASCO, NPAFC, PICES, or their Parties. Some work may be preliminary. The material has been edited for clarity and publication purposes only.

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b. Human induced factors

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Opening Remarks

Ladies and Gentlemen:

On behalf of five International Organizations, the Co-Chairs, Yukimasa Ishida and I would like to welcome you to this Symposium. This is something of a unique occasion. As far as I know, five International Fisheries Organizations have never before cooperated to arrange such a meeting. So the North Pacific Anadromous Fish Commission (NPAFC), International Baltic Sea Fishery Commission (IBSFC), International Council for the Exploration of the Sea (ICES), North Pacific Marine Science Organization (PICES) and North Atlantic Salmon Conservation Organization (NASCO) would like to warmly welcome you to what is, in fact, something of an experiment. We want to examine whether there are common factors driving salmon abundance in the Pacific, the Baltic and the Atlantic. We want to bring scientists and managers together to seek common factors, exchange ideas, think new thoughts and tell us where the gaps in research are and where there are new possibilities for international cooperation.

The situation facing some wild salmon populations in the Baltic, Atlantic and Pacific is severe indeed, and appears to be linked to poor survival at sea. There are real concerns that some salmon populations will be lost. This meeting is, therefore, timely, although we must realize that while some factors may be within our control and can be counteracted there may be little we can do about changes in ocean climate, other than adjust our management regimes to the new situation and hope that conditions improve.

We are all very pleased that there has been such a good response to this meeting and we are excited by the prospect of looking at this subject from new angles. Although we are all international in scope, this meeting extends our viewpoint wider to a Northern Hemisphere perspective.

We hope that the next two days will give new impetus, forge new relationships and deepen our understanding. We want this to be open-minded, informal and hard-hitting so we very much encourage everyone to participate.

We will now start immediately on the first session, to be chaired by Yukimasa Ishida and David Meerburg, which will cover the present status of salmon stocks and fisheries.

Malcolm Windsor
Co-chair of the Organizing Committee

Status of Salmon Stocks and Fisheries in the Baltic Sea

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* * *

Keywords: Restoration wild stocks, Salmon Action Plan 1997–2010

Before the damming of many rivers destroyed the spawning and nursery areas of the salmon in the Baltic there were 80–120 salmon rivers in the region. Pollution, habitat destruction and overfishing had also contributed to this serious decline of the wild salmon populations.

Today, there are about 40 rivers with significant production of wild salmon smolts:

- 13 discharging into the Gulf of Bothnia
- 14 discharging into the Main Basin
- 12 discharging into the Gulf of Finland.

To compensate for the loss of salmon production caused by construction of dams, hatcheries have been built on the affected rivers and reared salmon are released. The salmon fishery is mainly based on reared fish. In recent years reared fish might have constituted about 90% of the catch, but there are indications that the proportion of wild salmon in the catch is higher than previously estimated.

The first action to protect the wild salmon stocks was taken in the mid-seventies when closed seasons were introduced. These were extended in 1981, but in spite of these measures by the early nineties most salmon populations were depleted, only producing between 5–20% of their potential. They were outside safe biological limits.

A very important step to strengthen the production of the wild salmon was taken by IBSFC in 1991 with the introduction of a regulatory system, based mainly on annual TACs for the Baltic Sea and the individual fishery zones of the Contracting Parties. In 1991 the TAC for the whole Baltic was 760,000 units of salmon.

A dramatic increase in the so called M-74 syndrome, which in the period 1992–1996 caused high mortality rates among the offspring of sea-run females (more than 50%), led to a further decline in the wild salmon populations, in particular in the Gulf of Bothnia.

In response to this critical situation, IBSFC established the "Salmon Action Plan 1997–2010" with the following long term objectives:

- The production of wild salmon should gradually increase to attain by 2010 for each salmon river a natural production of wild Baltic salmon of at least 50% of the best estimate potential and within safe genetic limits, in order to achieve a better balance between wild and reared salmon;
- Wild salmon populations shall be re-established in potential salmon rivers.

In implementing the Salmon Action Plan the Commission agreed upon:

- principles for salmon enhancement activities;
- a list of rivers where self-sustaining wild populations should exist by 2010 (29 rivers);
- a list of wild salmon Index Rivers (12) and monitoring methods;
- management measures to optimize the harvesting of the surplus of reared salmon and to minimize genetic impact on wild salmon;
- the definition of terminal fishery areas where the fishery is targeted on reared salmon and where no, or few, wild salmon occur.

It is expected that in the rivers listed for self-sustaining wild populations reared fish should not be released after 2005 so that these populations could become fully sustainable by 2010. An important element of the Action Plan was the setting of the annual TAC in accordance with the long term management objective. Therefore the TACs have been established at comparatively low levels. Since 1997 the TAC for the whole Baltic was in the range of 510–540,000 units of salmon.

There are two management units with separate TACs:

- Main Basin and Gulf of Bothnia	(TAC for 2002: 450,000 units of salmon)
- Gulf of Finland	(TAC for 2002: 60,000 units of salmon)

These TACs reflect the different status of the stocks in these regions.

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As a result of actions taken in implementing the Salmon Action Plan 1997–2010 and the occurrence of a strong brood-year class in 1990, the number of wild salmon smolts, in particular in the Gulf of Bothnia, has increased significantly in recent years.

In the Gulf of Bothnia increased parr densities were observed in almost all rivers in 1996–2000. Improved parr densities are expected to result in good smolt runs in 2001–2002 (3–4 year old smolts) and good spawning runs in 2002–2005. However, in a small number of rivers the improvement in the status of salmon stocks is slow. The wild smolt run of 1.16 million in the Gulf of Bothnia and in the Main Basin in the year 2000 represents about 72% of the potential production as presently estimated for the rivers concerned. Analysis of smolt origin in the Gulf of Bothnia and the Main Basin indicates that the proportion of the wild smolts has increased from about 6% in 1997 to about 20% in 2001.

In its assessment of the status of wild Baltic salmon in 2001, the International Council for the Exploration of the Sea (ICES) considered that “most stocks are improving but still not all”.

The present TAC system, set to safeguard wild salmon, is effective, but it also limits the harvest of the surplus of reared salmon. IBSFC is now focusing on management measures which would allow an increase in the catch of reared salmon by establishing terminal fishery areas where mainly reared salmon are caught fishing techniques would be used which allow release of live wild salmon. IBSFC has defined a terminal fishery area as “a distinct coastal area, where the fishery is targeted on reared salmon, and where no or few wild salmon occur or the fishing technique used allows release of live wild salmon".

The feasibility of establishing a terminal fishery area depends on the geographical distance to the nearest wild salmon river and the route and timing of the spawning migration of the wild populations. There are two problems IBSFC is, or might be, faced with in the years to come:

- it is possible that the M-74 syndrome may continue to fluctuate rapidly, without any possibility of predicting its level;
- an increased seal population adversely affects the operation and economic viability of the salmon fishery in the northern part of the Baltic Sea (ICES sub-division 29-32).

Overview of the Report of the Working Group on North Atlantic Salmon

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* * *

Keywords: Atlantic salmon, conservation limits

In establishing annual regulatory measures for the international mixed stock fisheries at Greenland and Faroes, the North Atlantic Salmon Conservation Organization (NASCO) requests scientific information from the International Council for the Exploration of the Sea (ICES). ICES convenes a Working Group on North Atlantic Salmon annually to:

- review information on all homewater and distant water fisheries exploiting Atlantic salmon;
- provide an overview of the status of stocks contributing to these fisheries;
- report on the expected abundance for subsequent seasons;
- evaluate the attainment of conservation limits or other biological reference points for these stocks.

Specific information is provided for the regional Commissions of NASCO:

- the North-East Atlantic Commission (NEAC) relating to the Faroes mixed stock fishery (and the stocks contributing to the fishery) and the fisheries and stocks of Russia, Scandinavia, Iceland, Ireland, United Kingdom, France and Spain;
- the North American Commission (NAC) relating to the fisheries and stocks of the USA and Canada;
- the West Greenland Commission (WGC) relating to the fishery and the stocks contributing to this fishery.

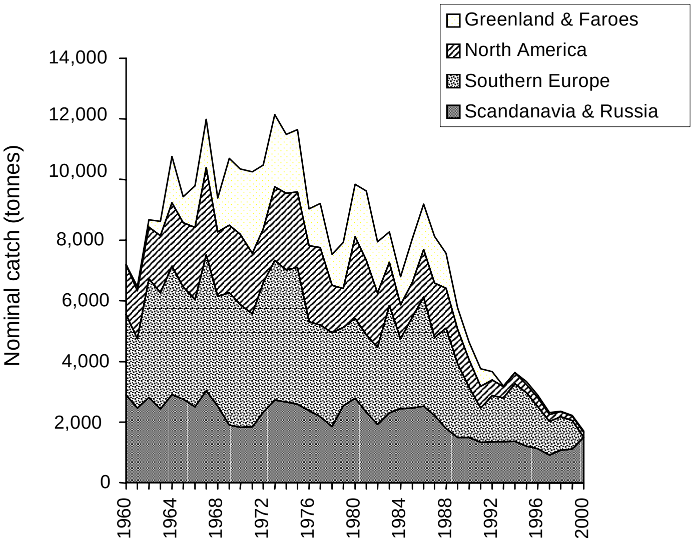
The report of the Working Group is evaluated by the ICES Advisory Committee on Fisheries Management which provides catch advice relative to the attainment of conservation limits for the internationally regulated fisheries at Greenland and Faroes.

Catches of North Atlantic salmon were highest (10,000 to 12,000 tonnes) between 1964 and 1977 (Fig. 1). Catches declined dramatically since this period due primarily to stock declines and resulting management measures which restricted the catches further. The total catch is now less than 3,000 tonnes and is taken mainly in the NEAC area. An additional 30% approximately of the declared catch has been estimated as unreported catch resulting from under-reporting of the nominal catch and estimated illegal landings where information is available.

It is important to note that apart from the US, the vast majority of North Atlantic salmon derive from wild spawned eggs with only a small proportion of sea run salmon eggs (maximum 1.4%) being diverted to hatchery programmes.

Run-reconstruction estimates of pre-fishery abundance (PFA) of maturing 1SW salmon (i.e. grilse) from the northern stocks of the North-East Atlantic declined significantly from 1985 to 1995 (Fig. 2a). An improvement in the PFA has occurred since 1995 with the result that the stocks appear to be attaining their conservation limits. The PFA of non-maturing 1SW salmon (i.e. those fish destined to return as multi-sea-winter salmon, MSW) from the same area showed a similar decline but they have not recovered as well, although they also appear to be at or above the conservation limit (Fig. 2b). However, the status of these stocks is still a cause for concern.

Fig. 1. Nominal catches of salmon in four North Atlantic regions 1960–2000.



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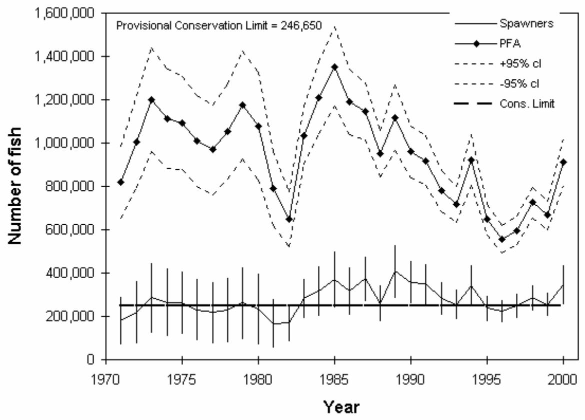
The estimated PFA for maturing 1SW salmon from the southern areas of the North-East Atlantic was volatile during the period 1971 to 1998. Three distinct periods are noted leading to an overall decline in the past 14 years (Fig. 3a). There is concern that the estimated PFA and the estimated number of fish spawning are below the conservation limit. A more serious situation exists for non-maturing salmon from the southern areas of the North-East Atlantic where there has been a sharp decline in PFA since 1971 resulting in fewer recruits being generated than required to meet the conservation limit (Fig. 3b).

For stocks originating in North America, the run-reconstruction estimates of pre-fishery abundance of non-maturing 1SW salmon have been the lowest on record in recent years (Fig. 4). In addition to the steady decline in non-maturing and maturing salmon over the last 10 years, maturing 1SW salmon (grilse) have become an increasingly large percentage of the North American stock complex. The estimated returns to, and spawners in, US rivers in 2000 were below the 1999 estimate and also below the 5-year and 10-year means, respectively. North American stocks remain low relative to the 1970s. The 1SW non-maturing component continues to be low with river returns and total production being the lowest recorded. In addition, returns in 2000 of maturing 1SW salmon (grilse) to North American rivers were also low. It is therefore unlikely that any improvement in 2SW salmon returns will occur in 2001.

Fig. 2. Estimated recruitment (PFA), conservation limit and spawning escapement of maturing and non-maturing salmon in Northern Europe, 1971–2000.

a) Maturing 1SW recruits (potential 1SW returns) and 1SW spawners (and 95% confidence limits)



b) Non-maturing 1SW recruits (potential MSW returns) and MSW spawners (and 95% confidence limits)

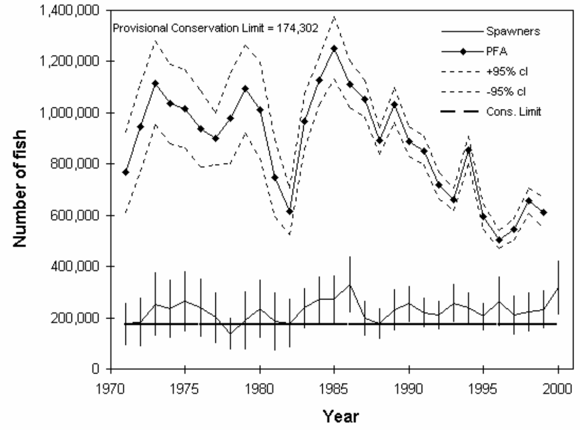
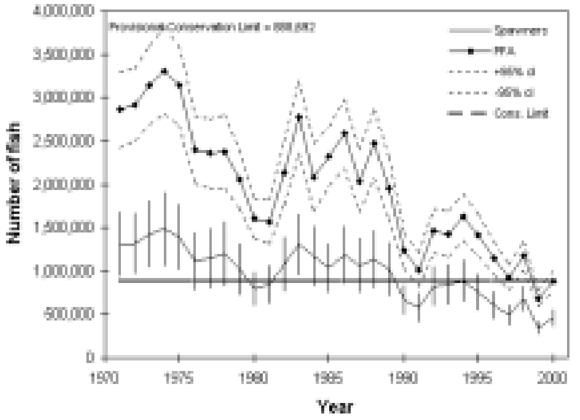


Fig. 3. Estimated recruitment (PFA), conservation limit and spawning escapement of maturing and non-maturing salmon in Southern Europe, 1971–2000.

a) Maturing 1SW recruits (potential 1SW returns) and 1SW spawners (and 95% confidence limits)



b) Non-maturing 1SW recruits (potential MSW returns) and MSW spawners (and 95% confidence limits)

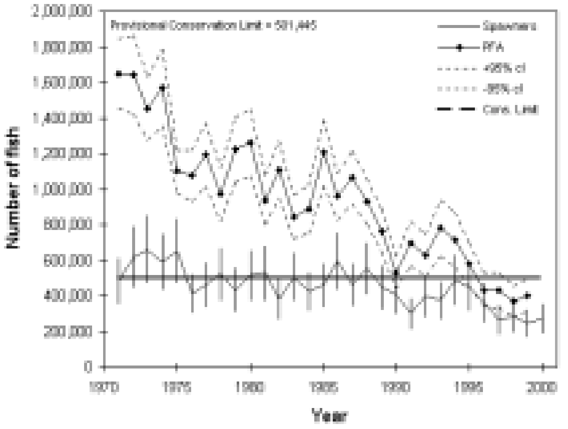
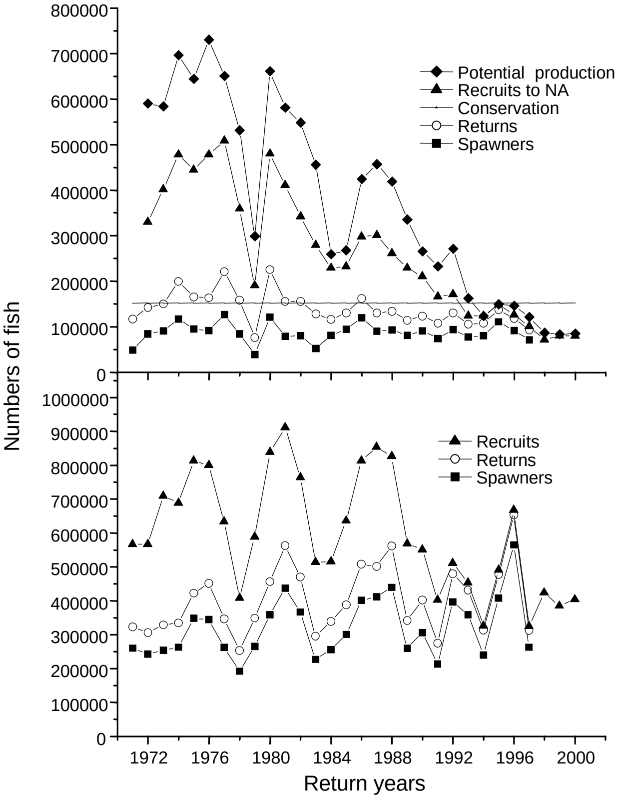


Fig. 4. Top panel: comparison of estimated potential 2SW production prior to all fisheries, 2SW recruits available to North America 1971–2000, and 2SW returns and spawners for 1971–97 (as 1998–2000 data for Labrador are unavailable). The horizontal line indicates the 2SW spawner requirements. Bottom panel: comparison of potential maturing 1SW recruits 1971–2000, and returns and 1SW spawners for 1971–97 return years as Labrador data for 1998–2000 are unavailable.



The stock status and the catch advice for each of the NASCO Commission areas can be summarized as follows:

North East Atlantic Commission area: The Northern stocks are at or above the conservation limits but no extra exploitation is advised particularly on non-maturing salmon stocks destined to return as multi-sea-winter salmon.

Stocks in the southern part of the North-East Atlantic are in a tenuous state with recruitment prior to any fishery taking place being below the requirements for conservation. Severe reductions in exploitation are, therefore, required and mixed-stock fisheries pose particular threats to these stocks.

North American Commission area: Many areas are below the conservation limit requirements and exploitation should be directed specifically at stocks which are shown to be above CL.

West Greenland Commission area: Many of the stocks being fished at West Greenland are severely below the required conservation limits and there should be no exploitation on stocks in the West Greenland area.

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Status of Salmon Stocks and Fisheries in the North Pacific Ocean

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* * *

Keywords: Pacific salmon, stock assessment, catch, recruitment

Overall, the status of Pacific salmon stocks and fisheries is currently viewed as favorable by scientists around the Pacific – although there are some areas of definite concern. Stocks in the Pacific Northwest of the United States are at historically low levels. Along the west coast of Canada, coho salmon stocks have been a concern for several years, and restrictions to coho and other fisheries have led to general increases in spawning stock sizes. Stocks of salmon in Alaska are generally at very high levels, although some salmon stocks declined rapidly in Western Alaska in the late 1990s. Stock status in the Russian Far East is somewhat mixed. In Japan, survival rates for chum salmon, the primary species, declined in the late 1990s but abundance is still at relatively high levels. The total commercial harvest, by weight, of Pacific salmon declined slightly more than 15% from 1993 to 2001, although the total harvest of pink and chum salmon remained almost constant throughout that period.

The situation for salmon stocks in the Pacific Northwest region of the United States is often referred to as one of “crisis” (e.g., NRC 1996, Lichatowich 1999). Stock trends are downward. In contrast, Alaska stocks that migrate in the Gulf of Alaska are generally at very high levels, although many stocks that migrate into the Bering Sea declined sharply in the late 1990s. For example, the commercial harvest of salmon in Bristol Bay reached a peak of over 44 million fish in 1995. The commercial catch of Bristol Bay sockeye salmon declined to just over 12 million in 1997, and then further declined to just over 10 million in 1998. In 2001, the commercial catch of Bristol Bay sockeye salmon was approximately 14 million. In Alaska, the period from 1900 to 1925 was the buildup period for the commercial fishery, when there was very little regulation. This period ended with the White Act, passed in 1924, which halted fishing at the midpoint of the run. From 1925 to 1945 major fishing districts were defined, and a number of management measures were introduced. Fishing effort increased up to 1930, when the number of fish traps was restricted. The commercial catch reached a peak of 126 million salmon in 1936. By the mid 1940s, the runs were severely over fished and catch trends were on their way down. Run sizes increased following the move to Alaskan state control in 1959, until 1970, when the run sizes dropped sharply. The all-species Alaska commercial harvest reached a low point of 22 million Pacific salmon in 1974 (Byerly et al. 1999). From the mid-1970s to the present, run sizes, salmon survival, sport and commercial fishery harvests have generally increased with peak in commercial catch (218 million salmon of all species) in 1995. The all-species catch reached 174 million salmon in the most recent year (2001).

The harvest of salmon in British Columbia increased from the late 1800s to a peak of about 30 million fish in the late 1920s and early 1930s. Harvest subsequently declined through the 1950s and 1960s, but then rebounded to record high levels of about 40 million fish in the early 1990s. This peak was followed by a rapid decline to the historical low harvest levels, about 8 million fish, in the late 1990s and early 2000s.

Sockeye and pink salmon are the most abundant species of salmon in Canada and account for most of the harvest. However, fisheries have been increasingly managed to conserve less abundant species and stocks, especially coho salmon from the interior Fraser River and interior Skeena River areas. The result of this management approach has been reduced harvest of both abundant species as well as less abundant species and stocks, a general increase in the proportion of the maturing fish reaching their spawning grounds, and increased escapement of many key stocks of concern during the past several years. Survival rate of juvenile salmon after entering the marine environment appears to be a key factor in the decline, and the recent partial recovery, of many salmon stocks throughout British Columbia.

The main stocks of pink and sockeye salmon remain in good condition in the Russian Far East; the Eastern Kamchatka stocks are an important exception. Catches of coho and chinook salmon have been declining in the Russian Far East. There is one principal stock of Russian chinook salmon in the Kamchatka River. By 1915 the

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annual pink salmon catch in Russia reached 200–215 thousand tonnes. This level of harvest was maintained until 1922 when the odd-year catch declined, although the even-year catch remained at approximately 300 thousand tonnes. From 1934 to 1944, the odd-year catch increased and even-year catches declined. The historical catch reached 380 thousand tonnes (or 532 thousand tonnes of Asian pink salmon if Japanese high-seas driftnet fisheries are included). Pink salmon production has declined from this peak, with the catch near 110 thousand tonnes throughout the 1990s though 2001.

The Russian chum salmon catch has been more stable than pink salmon catch. The fishery developed rapidly in major rivers, with most of the catch made up of summer races. The chum salmon catch reached a peak of 138 thousand tonnes in 1910; by 1916 the catch declined to 21.7 thousand. The chum salmon catch increased and was fairly stable within a range of 50 to 80 thousand tonnes up to the end of the 1940s, when the harvest decreased. Chum salmon stocks increased after 1975, but recently they have declined again. Currently, most of the catch is made up of fall races of chum salmon. Russian stocks of chum salmon are currently at low levels in many far eastern regions, except for the northern Okhotsk Sea region. Most sockeye catches are concentrated off the Kamchatka Peninsula. The sockeye catch reached a peak in 1928 at 39.7 tonnes. The stocks and catches declined in the 1930 and remained depressed until the 1970s. In 1995, the total harvest (including the catches of Russian and foreign driftnet fleet within the Russian economic zone) exceeded 20 thousand tonnes for the first time since the 1930s, and the stocks have remained high.

Salmon harvest in Japan increased from the late 1800s to a peak of about 170 million fish in the 1930s, followed by decline through the 1940s. Catch levels increased in the 1950s, declined to the late 1970s, then increased to the mid 1990s. There has been a recent decline in the survival and abundance of chum salmon, the dominant species in Japan, but overall abundance is still at high levels. Offshore catches of pink, chum, and sockeye salmon account for the large portion of the total Japanese salmon catch from the early 1930s to 1980s. Since the 1970s, the landing of offshore catch was gradually decreased, at the same time the landing of coastal fisheries for chum and pink salmon was increased.

Japan has an extensive system of salmon hatcheries that maintain much of the salmon production. Chum salmon are the primary species. Hatchery production of chum salmon in Japan increased up through 1980, when production stabilized near 1.0–1.2 billion juveniles in Hokkaido and in 0.8–1.0 billion juveniles in Honshu through the 1980s and 1990s. Although return rates for hatchery-released chum salmon declined in the late 1990s, the abundance of returning adults is still at historically high levels. Hatchery production of pink salmon in Japan increased up to 1985, and has remained stable at 120–140 million juveniles through the late 1980s and 1990s.

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Possible Effects of Ocean Currents on Survival of Japanese Chum Salmon during their First Winter in the North Pacific Ocean

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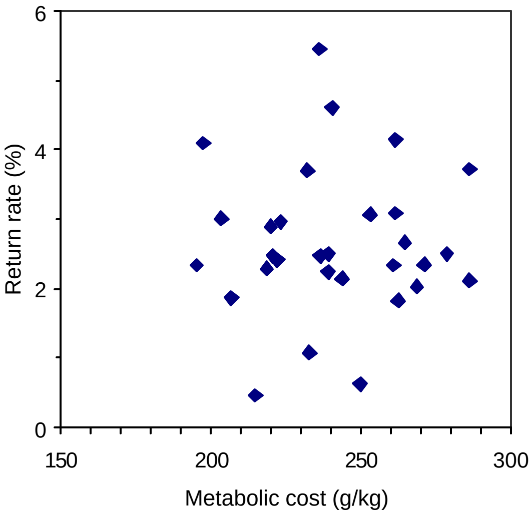
Keywords: Chum salmon, migration, energy cost, survival, winter, migration model

A number of studies have indicated that the survival of salmon was affected by several environmental factors in the ocean. However, even if there were significant correlation between the survival of salmon and sea surface temperature or the Aleutian Low index, the mechanism between them has not been well examined. Previously, we found that immature chum salmon swim against wind driven currents to maintain their position within preferred temperatures during their first winter in the North Pacific Ocean using the salmon migration model. We examined the interannual changes in wind driven current during the first ocean year in the North Pacific Ocean. The southward wind driven current velocity in wither, which transports immature chum salmon southward, was the smallest in 1971 and the largest in 1977 during the past 38 years. The velocity of the currents in 1971 was about one third in 1977. We are interested in how these changes in wind driven currents relate to the energetic costs of swimming and the mortality of chum salmon during winter in the first ocean year. The metabolic costs in the first winter were estimated by the salmon migration model and the relationship between the metabolic costs and return rates of Japanese chum salmon was examined. The standard deviation of energetic costs during winter was larger than other seasons. However, there is not a relationship between the metabolic costs during the first winter and return rates of Japanese chum salmon (Fig. 1). This result indicates that, although the ocean conditions affect the energetic costs of salmon during winter, they do not seem to influence the survival of salmon directly.

Fig. 1. Relationship between metabolic cost and return rate of Japanese chum salmon.



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A Climate Related Explanation for the Natural Control of Pacific Salmon Abundance in the First Marine Year

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* * *

Keywords: Ocean mortality, growth, competition, climate, coho

The belief that most natural losses of Pacific salmon occurred during the freshwater stage of their life cycle profoundly influenced how Pacific salmon were managed and researched in Canada for the past 50 years. It has only been recognized in the last few years that an understanding of the impacts of ocean habitat and climate are essential ingredients in the assemblage of considerations needed to manage salmon. We studied climate and ocean impacts on the productivity of coho salmon in the Strait of Georgia from 1996 to 2001. From September of 1996 to the end of 2001, we completed 27 surveys, 3,203 sets and sampled 123, 519 juvenile Pacific salmon (Table 1). Our study benefited from a managed fishing closure, an almost constant production of hatchery-reared coho that was approximately two times the production of wild smolts, and an abrupt increase in coho prey productivity in the Strait of Georgia in 2000. In the late 1990s, the total Canadian catch of all species of Pacific salmon declined to historic low levels. In the Strait of Georgia, coho marine survival declined from levels of 10–15% in the early 1980s to below 2% in the late 1990s. The number of adults produced declined from average abundances of 1.5 million in the 1980s[1] to less than 200,000 from 1996 to 1999[2]. The decline in production of coho and other species of salmon in 1999[2]. The decline in production of coho and other species of salmon in the 1990s followed a shift in large-scale climate indicators in 1989. The recent productivity increase was associated with another decadal-scale climate shift in mid-1998 (Beamish et al. 1998).

Productivity in the Strait of Georgia increased from 1999 to 2000, as indicated by a doubling of euphausiid biomass in 2000 (Fig. 1). Because euphausiids in the Strait of Georgia feed on phytoplankton (Parsons et al. 1969), there must have been an increase in phytoplankton. If phytoplankton production also doubled, there would be significant changes in productivity at lower trophic levels in 2000. As a consequence, coho and other

Fig. 1. Euphausiid biomass in the Strait of Georgia determined from hydroacoustic surveys in 1999 and 2000.

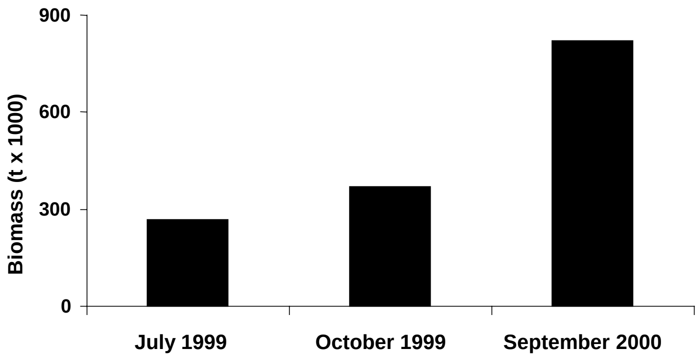

Table 1. Total catches (numbers) of ocean age 0 salmon from the Strait of Georgia surveys from September 1996 to November 2001.

Species	1996	1997	1998	1999	2000	2001	Grand Total
Chinook	1749	5674	3706	2789	4241	4254	22413
Chum	2748	7558	9064	7577	17818	8875	53640
Coho	2813	3370	2854	3635	6029	7331	26032
Pink	1520	138	4961	3	5592	79	12293
Sockeye	798	4920	659	1200	598	966	9141
Grand Total	9628	21660	21244	15204	34278	21505	123519

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[1] Total number of adults was determined by dividing catch by the exploitation rate, less 11% to account for adults from United States sources.

[2] Total number of adults was determined by multiplying the estimated number of hatchery and wild smolts produced in Canada by the estimated marine survival.

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Pacific salmon in the first marine year increased in size, fed more frequently, and contained larger volumes of prey in their stomachs (Fig. 2). The first evidence of improved marine survival occurred in 2001 for pink salmon and coho salmon as they spend only one winter in the ocean. Adult returns of pink salmon in 2001 were at historic high levels, following historic lows in 1997 and 1999. Preliminary marine survival estimates for coho show between a two and four-fold increase. The coho that returned as adults in 2001 were primarily from the faster growing individuals in the previous year. An analysis of marine circuli spacing in 2000 (the 1998 brood year) indicated that circuli spacing for the first 10 marine circuli was significantly larger in the coho that survived the winter compared to juveniles sampled in the previous year. The average spacing of the first 10 circuli of 50% of the fish returning in 2001 was equal to the average spacing of approximately 10% of the population in the previous year (Fig. 3). Scale circuli represent a permanent record of growth and circuli spacing is an accepted index of growth (Fisher and Pearcey 1990). Thus, it was clear that the faster growing coho in their first marine summer had significantly larger over-winter survival and hence contributed a greater proportion to the subsequent adult population. Because the abundance of juveniles in September of all years of the study was large relative to the total returns (Beamish et al. 2000), the late fall and winter mortality was an important contribution to the total natural mortality. The existence of this mortality, late in the first marine year, indicated that there were two major sources of natural mortality for coho: the well-known, early, predation-based mortality and this newly documented, later, growth-based mortality. The wide range in observed marine survival in the Strait of Georgia may indicate that growth-based mortality is more important than predation-based mortality.

Fig. 2. Biological data for ocean age 0 coho captured in July surveys in the Strait of Georgia from 1997 to 2001, expressed as anomalies for the time series. A. Anomaly of average fork lengths. B. Anomaly of average percentage of empty stomachs. C. Anomaly of average prey volume in stomachs.

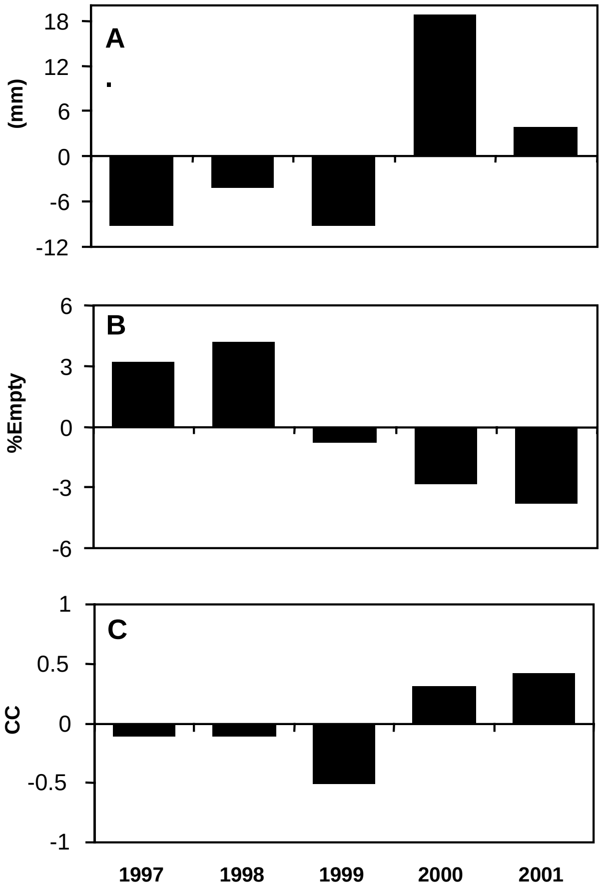
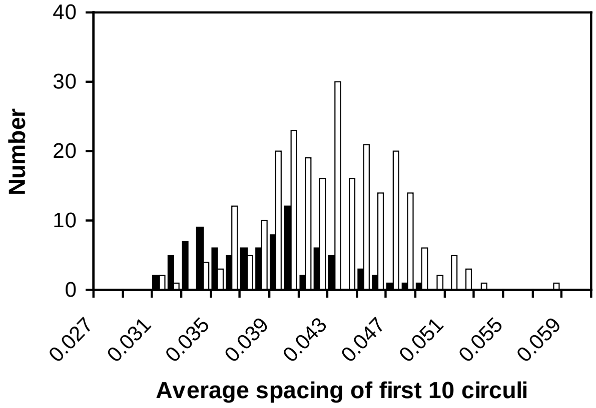


Fig. 3. Average spacing (in mm) of first 10 marine circuli for age 0 coho captured in 2000 (black bars, N = 87) and ocean age 1+ coho (open bars, N = 248) from the same brood year captured in 2001.



Our study provides additional evidence of the validity of the critical size and critical period hypothesis proposed by Beamish and Mahnken (1999, 2001). The hypothesis proposed that the later growth-based mortality related to the requirement to store enough energy to survive metabolic demands over a period of reduced feeding in the late fall and winter when there was a possible net deficit in energy. The beginning of he critical period was proposed to be more related to day length than to temperature, with the onset being at the fall equinox. A relationship between growth and natural mortality and a relationship between growth and ocean productivity is evidence that factors that reduce growth will contribute to increasing the natural loss of juvenile salmon in the ocean. Thus, during the periods of reduced prey abundance prior to the regime shift of 1998, competition from other coho and other species eating prey similar to coho contributed to reduced coho productivity through increased marine mortality. It is evident that, under such conditions, adding more coho or other salmon that compete for similar prey would reduce growth and subsequently increase growth-based mortality. It is also evident that climate and climate change play a vital role in the natural regulation of coho abundance through impacts on the production of prey. The relative importance of predation-based and growth-based mortality may vary among ecosystems and among species. The concept of a growth-based mortality probably would apply to Atlantic as well as Pacific salmon. A linkage between marine survival and climate, particularly at the decadal scale, should warn salmon managers that greenhouse gas induced climate change will affect marine survival. This means that there is a possibility that the pollutants we emit into the atmosphere may be just as harmful to salmon as those that we dump into their spawning and nursery habitats.

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Atlantic Salmon and Climate Variation in the North Atlantic

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Keywords: Atlantic salmon, climate, post-smolt survival, growth, nursery

The largest component of natural mortality affecting Atlantic salmon populations in the marine environment occurs during the first year at sea. The juveniles are referred to as post-smolts during this period, which begins after their migration to the ocean and continues up until the first winter. The stock complexes for Europe and North America appear to have different climate-controlling mechanisms reflecting theorized differences in post-smolt distribution and ecology.

The nursery zone for European post-smolts is located in the open ocean whereas North American post-smolts appear to utilize inshore habitats. Holm et al. (2000) described the distribution of European post-smolts from surface trawling operations in the Northeast Atlantic. The nursery is confined to a region within the Norwegian Sea, the northern extent of which would appear to be defined by current transport. In North America, post-smolts can be found in high numbers in the Labrador Sea during the fall of the year (Reddin and Short 1991). However, during the earlier part of the post-smolt period, i.e. through the spring and summer months, fish are also found in the Gulf of St. Lawrence, the coast of Nova Scotia, and elsewhere (Dutil and Coutu 1988; Ritter 1989; Friedland et al. 1999). Furthermore, North American stocks may not physically mix for many months after entering the ocean whereas it appears European stocks are concentrated in a single, albeit large, ocean area (Friedland and Reddin 2000).

If in some years the North American post-smolt nursery is distributed along the coast, it would function in fundamentally different ways than the European post-smolt nursery, thus affecting the climate response of the respective stock complexes. Predation losses for the North American stocks may be the result of more avian and mammalian predators emanating from specific rookery locations on the coast (Montevecchi et al. 1988); whereas European fish would be expected to face growth-mediated predation pressure associated with the dynamics of an oceanic ecosystem (Sogard 1997). Growth data provides a practical test for this idea. Inter-annual post-smolt growth variation for Scottish and Norwegian stocks correlated with survival supports the idea that mortality of these stocks is controlled by their growth (Friedland et al. 2000). However, similar growth signatures for North American stocks are uncorrelated with survival (Friedland and Haas 1996). It is important to qualify this observation by stating that the survival differences among stocks can, at times, be attributed to growth regardless of the pattern of inter-annual growth variation (Friedland et al. 1996).

A fundamentally different response to climate forcing due to the nature of the post-smolt nursery may be what is reflected in our current state of knowledge concerning climate forcing and recruitment of Atlantic salmon. From analyses of sea surface temperature distribution, spring thermal conditions have emerged as an important forcing in the recruitment of European salmon stocks. The relationship was first quantified for trends in the entire stock complex, i.e. for all sea age fish, using time series subjected to temporal averaging (Friedland et al. 1993). Subsequently, when examined for a distinct set of stocks from the centre of the European range using a time step of one month, the relationship became much clearer (Friedland et al. 1998a). However, similar relationships have not emerged in respect to the North American stock complex.

To date, the only evidence of climate forcing related to North American stocks is the relationship between 2SW salmon and winter thermal habitat in the Northwest Atlantic (Friedland et al. 1993). However, it is not clear if this relationship is related to survival given the season of the climate effect; instead, it has been suggested that this relationship may be related to maturity (Friedland et al. 1998b). It would appear that European salmon stocks in the Northeast Atlantic are responding to broad-scale climate forcing, such as temperature and factors likely to co-vary with temperature, much like other pelagic species. The response would appear to be related to the distribution of the post-smolt nursery. North American salmon stocks in the Northwest Atlantic do not appear to have a pelagically distributed nursery and climate forcing has not been detected either because researchers are not examining the correct variables, or other non-climate factors, such as predator abundance, are more important.

Age at maturation has important consequences on the total complement of eggs deposited during spawning. While age at maturity has a strong genetic component (Gjerde 1984), environment can also play a significant role (Saunders et al. 1983). Climate may be acting on this process in a number of different ways. Conditions that affect the growth of fish may determine whether an individual is physiologically ready to return to the river to spawn.

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There is evidence that growth at various times during the post-smolt year may be important to achieving maturity (Scarnecchia et al. 1989, 1991; Gudjonsson 1995; Duston and Saunders 1999), suggesting that hypotheses regarding genetic and temporally fixed mechanisms lack the plasticity realized by wild stocks (Thorpe 1986). Alternatively, some investigators have suggested that climate variations that extend migrations beyond a reasonable return distance contribute to a variable proportion of grilse in the return (Martin and Mitchell 1985). Some animals on migration routes away from home rivers are actually approaching maturation and likely regress when they fail to find their home rivers (Friedland et al. 1998b).

The unprecedented decline in Atlantic salmon abundance over the past few decades raises concerns over the future impact of climate change. With climate at the core of many of the factors contributing to the decline of stocks, the effects of further shifts, beyond the reactive norms to which salmon populations have adapted, now pose the threat of range shift for the species. If these climate changes are being accelerated by anthropogenic factors, the speed at which the changes occur may be beyond the time-scales salmon need to develop requisite survival adaptations, thus posing the threat of widespread extinctions.

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Temporal and Spatial Migration and Distribution of Atlantic Salmon, *Salmo salar* L., in the Northeast Atlantic Ocean

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Keywords: Wild salmon, escaped farmed salmon, post-smolts, kelts, archival tags

It has been suggested that the decline of Atlantic salmon in recent years has been caused by increased marine mortality. Many factors may affect salmon survival in the sea, although they are poorly understood (Fig. 1). In the Northeast Atlantic survival of salmon and sea surface temperatures have been shown to be correlated, suggesting that marine climate (directly or indirectly) is a key factor, particularly at the post-smolt stage (Friedland et al. 1998). There is limited information on the distribution and migration of Atlantic salmon at sea in space and time (e.g. Hansen and Quinn 1998), and until recently this was based solely on records from commercial fisheries. Understanding fluctuations in marine mortality of salmon is highly dependent on knowledge of the distribution and migration of salmon in space and time.

This paper summarises the conclusions from a recent study on the distribution and migration of post-smolts in the Norwegian Sea and from a salmon tagging program conducted at the Faroe Islands. Furthermore, we discuss the future possibilities to fill gaps in our knowledge by using information from archival tags attached to salmon.

Atlantic salmon smolts leave fresh water and the post-smolts migrate to the feeding areas in the ocean during late spring and summer (e.g. Thorpe 1988; Mills 1989). The duration of estuarine residence seems to be relatively brief. Further evidence, albeit indirect, of rapid migration comes from the fact that very few post-smolts are recorded in fjords and coastal waters during summer and autumn, although they are already present in oceanic areas in the Northeast Atlantic (Holm et al. 2000; Holst et al. 2000).

A number of post-smolts have been caught in oceanic areas of the Northeast Atlantic in recent years during pelagic trawl surveys in the Norwegian Sea in July and August (Holst et al. 1993; Holm et al. 2000; Fig. 2), and north of Scotland in May and June (Shelton et al. 1997). Based on the distribution of catches north of Scotland, the fish appear to move north-wards with the shelf edge current (Shelton et al. 1997). Further north, in the Norwegian Sea, post-smolts were caught beyond 70°N in July. Analysis of growth and smolt age distribution strongly suggested that most of the post-smolts originated from rivers in southern Europe (Holst et al. 1996).

When Atlantic salmon have reached catchable size, their marine distribution is easier to document. Many countries have had major tagging programs on smolts and adults, and some of these fish have been recaptured in the high seas fisheries. It is difficult to assess the true distribution of salmon at sea, as tag recoveries depend on the distribution of fishing effort. The absence of fishing pressure in an area does not demonstrate the absence of salmon, although it may be assumed that there is at least some general correspondence between the distribution of fish and fishermen.

Fig. 1. Factors influencing salmon at sea.

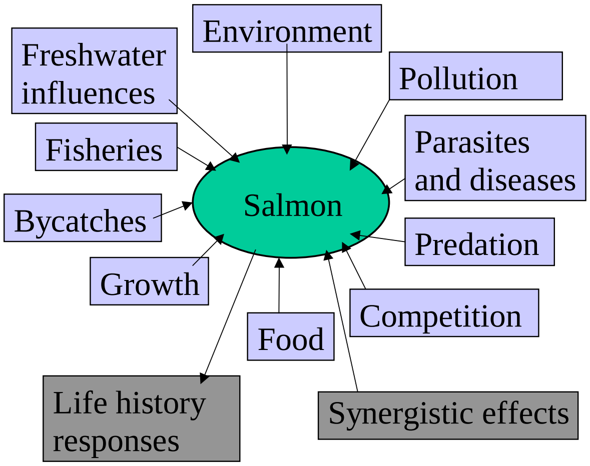

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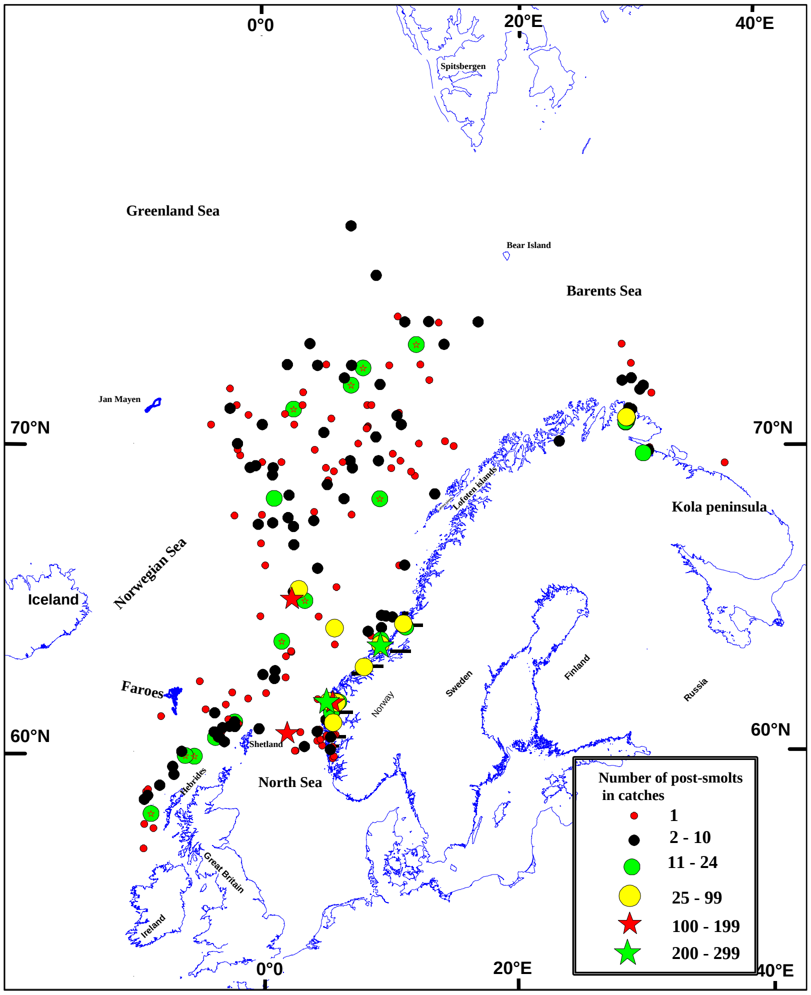
Fig. 2. Distribution of post-smolt catches in the Nordic Seas in 1990–2000. The size and colour of the symbols indicate the number of post-smolts in the catch (Holm et al. 2000).



In the Northeast Atlantic, salmon are found in large areas in the Norwegian Sea. In the 1970s there was an important commercial long-line fishery in the Norwegian Sea in February–May. Recoveries of fish in this fishery that had been tagged as smolts, and recaptures in coastal and freshwater fisheries of salmon tagged in the Norwegian Sea, suggested that Norwegian salmon were most abundant, although fish from the United Kingdom, Sweden and Russia were also present. Most of the fish tagged in the Norwegian Sea were recaptured in homewaters in the same year they were tagged, suggesting that they were maturing (Rosseland 1971). Towards the end of the 1970s, fishing for salmon in the Northern Norwegian Sea was banned, and fishing was limited to the area within the Faroese Exclusive Economic Zone (EEZ).

The abundance of salmon within the Faroese EEZ has been assessed from sampling of the fishery for a number of years. Jákupsstovu (1988) reported on a tagging program at sea from 1969–1976 in which 1,946 salmon caught on long-lines were tagged and released. The fish were tagged in more southerly parts of the Faroese EEZ, and 1SW fish were probably highly over-represented. In total, 90 fish were recovered: 33 in Scotland; 31 in Norway; 15 in Ireland; 8 in other European countries; and 3 at West Greenland. The majority of the tags were reported in homewaters in the same year as tagging occurred. However, it is interesting to note that some fish in the Faroese area may have been on their way westwards, as they were reported from the fishery at West Greenland later that year.

In the Norwegian Sea large numbers of escaped farmed salmon are present, and it has been estimated that up to 40% of the salmon in commercial catches at the Faroes are of farmed origin (Hansen et al. 1999). Some years ago a tagging program was carried out in the major fishing grounds north of the Faroes. From November–March in the 1992/93, 1993/94 and 1994/95 fishing seasons, 5,456 salmon (3,811 wild and 1,637 farmed) were caught by long-line, tagged and released (Hansen and Jacobsen 2000). In total, 106 fish (87 wild and 19 farmed) were recaptured. Wild salmon of Norwegian origin were most abundant in the area but Scottish and Russian salmon were also common. Some additional recaptures were reported from Ireland, Iceland, Spain, Sweden, Denmark, England, and even Canada (Table 1; Hansen and Jacobsen 2000), strongly suggesting that salmon originating from most areas of the distribution range are present at some life stage in this area, but in variable proportions at different times (Jacobsen et al. 2001). Of the escaped farmed salmon, 18 were recaptured in Norway and one at the west coast of Sweden.

At the NINA research station at Ims, in southwest Norway, 75 kelts were tagged with Kiwi temperature loggers and released back into the river (Hansen and Friedland unpublished data). After a journey lasting about 9 months, three fish returned to the river to spawn for a second time and were caught in a trap at the mouth of the river. The temperature was recorded every hour and showed a potential for determining the exact timing of sea entry, timing of the onset of the homing migration, migratory speed on the return migration, and timing of river entry. Further development and the use of archival tags on Atlantic salmon will improve the knowledge of the salmon's life history significantly and thus enhance assessments and salmon management.

Table 1. Number of wild salmon tagged at Faroes during the 1992/1993, 1993/1994 and 1994/1995 fishing seasons and subsequently captured in different countries. From Hansen and Jacobsen (2000).

Country	Tagged 1992/1993		Tagged 1993/1994		Tagged 1994/1995		Total	
	Rec.93	Rec.94	Rec.94	Rec.95	Rec.95	Rec.96	No	%
Norway	22	3	2		17	3	47	54.0
Scotland	8		1		3		12	13.8
Ireland	3		2		4		9	10.3
Sweden	2	1			1		4	4.6
Russia	1	1	3		1		6	6.9
Canada	1				3		4	4.6
Denmark	2						2	2.3
England	1						1	1.1
Iceland	1						1	1.1
Spain	1						1	1.1
Total	42	5	8	0	29	3	87	99.8

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Recent Changes in Atlantic (*Salmo salar*) and Pacific (*Oncorhynchus*) Salmon Stocks in the Context of Climatic Variations in the Northern Hemisphere

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Keywords: Atlantic salmon, Pacific salmon, sea surface temperature anomaly, decadal changes, interdecadal change

The study is based on the analysis of spatial and temporal features of winter climate in the North Atlantic and the North Pacific during the last four decades. In each ocean several large-scale subdomains with the coherent sea surface temperature anomaly (SSTA) fluctuations were defined with the use Ward's hierarchical clustering method. SSTA variations in the northeastern and southwestern North Atlantic are opposite to those in the northwestern and southeastern parts. This quadra-pole structure is clearly associated with the features of the North Atlantic Oscillation (NAO). At the same time, the SSTA fluctuations in the central North Atlantic appear to be connected with the Pacific/North American (PNA) teleconnection pattern in the middle troposphere, while there are no significant relationships with the atmospheric teleconnection patterns over the North Atlantic.

The spatial structure of the SSTA fluctuations in the North Pacific is characterized by two independent patterns: changes in the SSTA in the eastern and central North Pacific, and those in the northwestern and southwestern parts, are out of phase. The SSTA fluctuations in the central and eastern North Pacific are related to the PNA pattern, while those in two western regions are associated with the Western Pacific (WP) teleconnection pattern.

Principal component analysis (PCA) was used to define objectively the most important patterns of common variability in 39 physical time series in the North Atlantic and the North Pacific. The first principal component (PC1) which explained 20% of the total variance is associated with the NAO and its temporal pattern shows four distinct regimes between 1957 and 2000: 1957–1971; 1972–1976, 1977–1988 and 1989 through (at least) 2000, with the most abrupt transition in 1989. The last decade is characterized by strong positive NAO values (except for 1995–1997). The second PC (17% of total variance) is associated with the Southern Oscillation and Pacific Decadal Oscillation (PDO) pattern and shows the rather prominent shift in 1977. The 1990–1999 decade was the warmest in both oceans compared with the previous three decades.

The results of PCA and correlation analysis give some evidence for strong relationships in SSTA variations between the oceans. Thus, the SSTA fluctuations in the Northwest Atlantic and Northwest Pacific are out of phase ($r = -0.69$), while those in the eastern North Pacific and central North Atlantic are characterized by a significant positive correlation ($r = 0.65$).

Climatic variations in the North Atlantic during the last 40 years were characterized by a second, interdecadal, mode of variability. From the 1970s to the 1990s there was an intensification and eastward shift of low- and high-pressure anomaly cells over the whole area south of 50°N and a general strengthening of zonal flow over the North Atlantic north of 50°N. This was accompanied by a gradual spreading of warming of the surface waters in the North Atlantic from the southwest to the northeast south of 50–55°N in accordance with the shift of the high pressure anomaly cell. The situation in the North Pacific was more uncertain. SST changes in the 1970s–1980s were, in general, consistent with the changes in the atmospheric circulation. At the same time, the signs of the northeastward propagating warming appeared in the 1980s, and in the 1990s the warming was observed over most of the North Pacific.

The interdecadal changes in the North Atlantic are characterized by a warming trend during the 1970s–1990s which in many aspects, resembled the warming of the 1920s–1930s described by Bjerknes (1964). In particular, there were inconsistent changes in SST and local winds north of 50°N. In the North Pacific the heat exchange at the sea surface contributed to SSTA changes at interdecadal time scale to a larger extent than in the North Atlantic. Thus, the effect of oceanic circulation in the North Pacific on interdecadal SST changes is seen only in the periods of general lessening of atmospheric circulation.

To consider if there is any relationships between the observed climatic variations and the recent trends in Atlantic salmon and Far Eastern Russian pink, chum and sockeye salmon stocks, we applied PCA to isolate the patterns of common variability in the 40 physical and 37 biological time series characterizing the Atlantic and Pacific salmon stocks. Scores for the first two PCs are shown in Fig. 1 and the loadings on these two PCs are given

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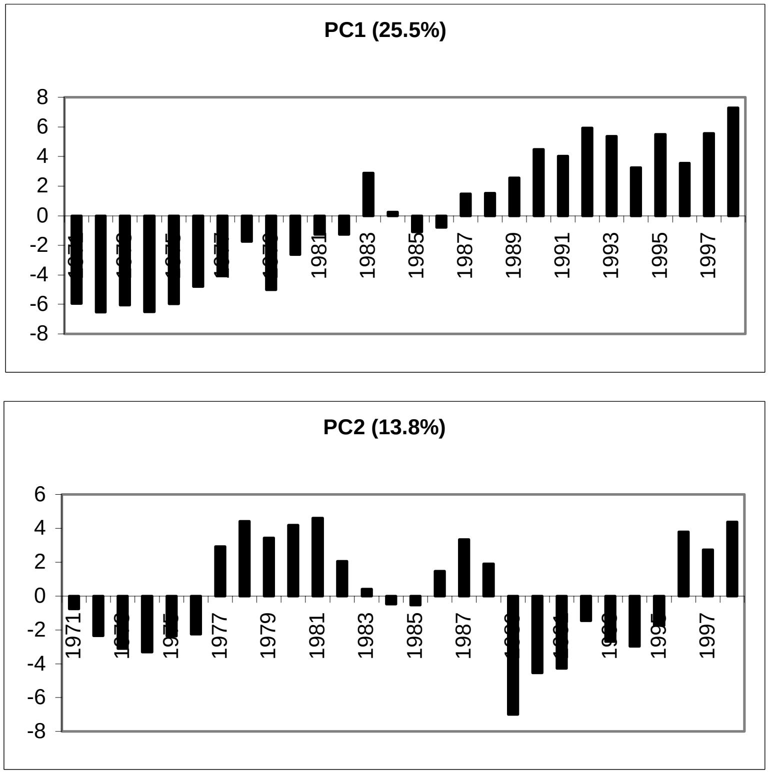
in Table 1. The PC loadings are correlations between individual time series and the associated PC score. Only statistically significant corrrelations are given in Table 1. The time series of PC1 illustrates an abrupt shift from negative to strongly positive values in 1987. High loadings (r > |0.4|) on PC1 occur for 6 of 9 time series for Pacific salmon stocks and for most time series of Atlantic salmon. All the Pacific salmon time series are positively correlated with PC1, while most Atlantic salmon stocks show the negative association with PC1. This indicates that the inverse reproductive patterns of the Pacific and Atlantic salmon stocks may be explained by these features of climate variations in the oceans under consideration.

The second principal component (PC2) shows three distinct regimes from 1971 to 1998, with abrupt shifts in 1977 and 1989 which are similar to climatic regimes defined in the North Atlantic, however, few biological time series have high loadings on PC2. There is a positive correlation between fluctuations of East Sakhalin pink salmon and Atlantic salmon in Labrador and Newfoundland areas.

Fig. 1. The first two principal component scores from a principal component analysis of the 77 climatic and salmon time series.



The analysis of the current tendencies in climatic changes in the North Atlantic and North Pacific allows some proposals regarding the situation with the salmons stocks in both oceans in the near future. In the North Atlantic, the recent period of warming appears to be close to its end and will be followed by a cool period. In this case, the state of most Atlantic salmon stocks will improve. In the Northwest Pacific, the cold regime that started in 1998 will result in decrease in abundance of pink salmon stocks in the western Pacific. At the same time, an abundance of West and East Kamchatka chum and sockeye stocks will not change essentially. This is associated with a weakening of the density-related dependence of these stocks on the stock of artificially propagated Japanese chum salmon, for which this cold period is unfavorable.

Table 1. Loadings on the first principal component from a principal component analysis of the 77 climatic and salmon time series. The loadings are correlation coefficient between each time series and the first PC score. Only statistically significant corrrelations are given.

Variable	Loadings
North Pacific	
Pacific Decadal Oscillations	0.47
Longitude of Aleutian Low	0.45
SSTA in Region 1P (eastern North Pacific)	0.78
Catches of pink salmon (West Kamchatka)	0.64
Catches of pink salmon (East Kamchatka)	0.84
Catches of pink salmon (East Sakhalin)	0.45
Catches of chum salmon (West Kamchatka)	0.46
Catches of sockeye salmon (West Kamchatka)	0.76
Catches of sockeye salmon (East Kamchatka)	0.60
North Atlantic	
Eastern Atlantic –Jet teleconnection pattern (TP)	0.55
SSTA in Region 5A (central North Atlantic)	0.87
North Atlantic Tripole	0.51
1 sea winter (SW) spawners (Northern Europe)	0.58
1SW returns (Salmon Fishing Area (SFA) 18, Northwest Atlantic	0.45
1SW returns (the Quebec rivers)	0.52
The Pacific Ocean	
SOI	-0.47
North Atlantic	
Catches of Atlantic Salmon (ICES area, I + IIab)	-0.82
1SW returns (Southern Europe)	-0.79
Multi sea winter (MSW) returns (Northern Europe)	-0.71
MSW returns (Southern Europe)	-0.74
1SW spawners (Southern Europe)	-0.74
Fishing-related mortalities as 2SW equivalents (Canada)	-0.94
Fishing-related mortalities as 2SW equivalents (Greenland)	-0.88
Fishing-related mortality as 2 SW equivalents (Northwest Atlantic)	-0.95
Weight of 1SW salmon caught at West Greenland (North American origin)	-0.61
Weight of 1SW salmon caught at West Greenland (European origin)	-0.81
Length of 1SW salmon caught at West Greenland (North American origin)	-0.48
Fork length of 1SW salmon caught at West Greenland (European origin)	-0.88
2SW recruitment (Labrador)	-0.90
2SW recruitment (Labrador + Newfoundland + West Greenland)	-0.93
2SW returns (SFA 15, Northwest Atlantic)	-0.66

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Tracking Environmental Bottlenecks in the Coastal Zone for Understanding and Predicting Oregon coho (*Oncorhynchus kisutch*) marine survival

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Keywords: Oregon coho, climate, El Niño, Pacific Decadal Oscillation, fishery forecasts

To better understand and predict Oregon coho (*Oncorhynchus kisutch*) marine survival, we developed a conceptual model that links four semi-independent environmental processes that influence coastal marine habitat important for coho survival. We hypothesize that these 4 processes are related to: (1) winter climate prior to smolt migration from freshwater to ocean, (2) the date of the spring transition from winter downwelling to spring/summer upwelling, (3) the spring upwelling season and (4) winter ocean conditions near the end of the maturing coho's first year at sea. We then parameterized a General Additive Model (GAM) with Oregon Production Index (OPI) coho smolt-to-adult survival estimates from 1969 to 1998 and environmental data representing each process (pre-smolt winter SST, spring transition date, spring upwelling wind indices, and post-smolt winter SST). The model explained a high and significant proportion of the variation in coho survival during the period of record (R2=0.73). In contrast to previous studies that have shown coherence among oceanographic variables that are related to coho survival, the variables in our GAM were essentially uncorrelated with each other. We suggest that it is this lack of coherence that explains a substantial amount of the year-to-year variability in coho marine survival. We have also explored connections between local/regional coastal ocean processes important in our GAM and large scale climate variations. We find that indices tracking ENSO, the PDO, and the Aleutian Low are generally well-correlated with winter coastal ocean temperatures, but poorly correlated with the spring transition date and springtime upwelling wind indices. However, conditional sampling of the local/regional data based on values of the large-scale climate indices identifies tendencies in several parameters that may help explain the documented correspondence between large scale climate indices and indices for coho salmon marine survival.

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Opposite Effects of Sea-Surface Temperature on Survival Rates of Pacific Salmon from Northern and Southern Areas

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Keywords: Marine survival, multi-stock model, Pacific salmon, regional scale, sea-surface temperature

Environmental conditions cause large variations in productivity of Northeast Pacific salmon (*Oncorhynchus* spp.). Management of salmon stocks could be improved by better understanding the sources of environmentally driven variability in their productivity. Large-scale climatic and oceanographic variability has been related to aggregate catches of Northeast Pacific salmon (Downton and Miller 1998; Hare et al. 1999). However, catch data may not reveal changes in productivity because catch reflects the confounded effects of fishing effort, spawner abundance, and hatchery production, and, if aggregated across stocks, may be dominated by changes in the most abundant stocks in a given area. Therefore, to identify environmental effects on recruitment, we used survival rates from eggs to adult recruits, adjusted for the effect of spawner abundance, as a more appropriate measure of productivity. Recent analyses show that such survival rates are positively correlated among stocks across local or regional spatial scales of several hundred kilometers, but not at larger scales (Peterman et al. 1998; Pyper et al. 2001; Pyper et al. in press). Coastal sea-surface temperatures (SST) have similar spatial correlation scales, suggesting that covariation in survival rates among salmon stocks is driven by regional-scale processes in the coastal ocean (Mueter et al. in press). The objectives of this study were to quantify SST effects on survival rates of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*) across multiple stocks, to examine differences in these effects among stocks from different areas, and to determine the relative importance of regional and large-scale measures of ocean temperature for explaining variability in survival rates.

Identifying environmental effects on survival rates of individual stocks are hampered by high variability in spawner and recruit data and short time series. To improve our understanding of effects of temperatures on salmon productivity, we examined relationships between recruitment and potential explanatory variables across a large number of stocks. We adopted a multi-stock approach similar to Myers et al. (1999) to estimate the effects of environmental variability, specifically sea surface temperature (SST), on multiple stocks of three species of salmon. We modeled stock-specific survival rates ($\log_e$(recruits-per-spawner)) as a function of spawner abundance (to account for density-dependent effects) and regional measures of SST. We used 120 stocks of pink (43 stocks), chum (40), and sockeye (37) salmon, with ocean-entry points ranging from Washington to western Alaska, as "replicates" to help identify the effects of SST more clearly than is possible with single-stock analyses. We averaged SST anomalies across the coastal areas occupied by a given stock during the first four months of ocean life. Monthly SST anomalies for selected coastal 2x2° grids were obtained from the COADS database (available at http://ferret.wrc.noaa.gov/las/main.html).

To model variations in $\log_e$(recruits-per-spawner), we fit a mixed-effects model to stock-recruit data for all stocks of a species and area (northern or southern) simultaneously. A mixed-effects model corresponding to the generalized Ricker model may be written as:

$$\log_e(R/S) = \alpha + a_i + \beta_i S + \gamma SST + g_i SST \qquad (1)$$

In this multi-stock model, the Ricker-*a* parameter consists of an overall fixed intercept (α) that is common to all stocks in a given area and a random, stock-specific deviation from the fixed intercept (a_i) that reflects the relative productivity of stock *i*. The stock-specific a_i values are assumed to follow a normal distribution. Similarly, the SST effect has two components: a common effect of SST (γ) that affects all stocks within an area equally and a stock-specific SST effect (g_i) that differs among stocks.

Initial parameter estimates for individual stocks showed strong geographical gradients in the SST effect across stocks for all three species. Specifically, SST had a different effect on stocks in Alaska (northern area) compared to stocks in British Columbia and Washington (southern area). We allowed for potential differences by assuming two area-specific mean effects of SST (γ), and stock-specific components (g_i) that vary around the common mean within

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each of the two areas. Here we report the estimated mean SST effects for each geographical area and the estimated variability of the SST effect among stocks.

We found strong geographical differences in estimated effects of SST on survival rates for all three species (Mueter et al. 2002). Warm anomalies in coastal temperatures were associated with increased survival rates of all salmon stocks in Alaska and with decreased survival rates of pink and sockeye salmon stocks in Washington and British Columbia. No apparent effects of SST on survival rates were found for chum salmon in the southern area. The magnitude of the SST effect differed among species and was strongest for pink salmon. The estimated effect suggests that an increase in SST corresponding to one standard deviation (~ 1°C) results, on average, in a 45% increase in recruits-per-spawner for Alaska pink stocks, and a 20% decrease in recruits-per-spawner for southern pink stocks. Our results suggest that temperature effects are much more consistent across adjacent stocks than indicated by single-stock analyses, and provide precise estimates of mean SST effects within each area.

To determine the relative importance of regional and large-scale measures of ocean temperature for explaining variability in survival rates, we used the Pacific Decadal Oscillation (PDO), a large-scale index of SST anomalies across the Northeast Pacific, as an alternative to regional SST in equation 1. Generally, regional-scale SST was a much better predictor of survival rates than PDO, suggesting that coastal conditions during the first few months at sea have a larger effect on survival rate and subsequent recruitment of salmon than large-scale variability related to the PDO index (Mueter et al. 2002).

We conclude that survival rates of pink, sockeye, and northern chum salmon are strongly affected by coastal processes related to variations in regional-scale SST during early ocean life, and that northern and southern stocks of Northeast Pacific pink and sockeye salmon respond in opposite ways to variations in coastal SST. Most likely, SST is a proxy for indirect effects on survival related to oceanographic differences between the two areas. Nevertheless, regional measures of SST may be useful predictors of salmon survival rates and future recruitment.

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Some Aspects of the Life History and Ecology of Atlantic Salmon (*Salmo salar* L.) in the Northwest Atlantic

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Keywords: Atlantic salmon, ecology, northwest Atlantic, data storage tags, post-smolt

In recent years, the numbers of North American multi-sea-winter and one-sea-winter salmon have been steadily declining with multi-sea-winter salmon declining at a faster rate than one-sea-winter salmon (Fig. 1). Although the source of the mortality and its potential cause(s) remain largely unknown, sea survival rates have declined substantially even with the almost complete closure of commercial fisheries at sea which should have resulted in dramatic increases in returns and survival rates; especially when the fisheries are located close to the natal river and are conducted during the main runs of salmon to the river (Dempson et al. 2001). In North America, there are regions in the southern area of the salmon's range where stocks have become close to being extirpated (Anon. 2002). Due to these declines in overall abundance and near extirpation in some areas, sea research has become particularly important if the cause(s) of the at-sea mortality is to be found.

Exploratory fishing in the Northwest Atlantic was begun by the Department of Fisheries and Oceans Canada in 1965 (Friedland and Reddin 1993). Surface gillnets of various mesh sizes were set out at dawn and fished for up to twelve hours depending on the weather and wave conditions. Nets were sometimes patrolled from a small open boat to obtain live salmon for tagging. Mortalities were sampled for biological characteristics, scales, and stomach contents. Salmon of all sea ages occurred seasonally over most of the Northwest Atlantic and were found concentrated in the Labrador Sea gyre throughout the year, at west Greenland in the summer and autumn, and along the eastern slope of the Grand Banks in the spring. Salmon were distributed as far east as the Irminger Sea (Fig. 2). Post-smolt salmon were first caught at sea in 1987 using gillnets of small mesh sizes not previously fished (Fig. 3). The highest concentration of post-smolts and adult salmon occurred in the mid-Labrador Sea area. Comparison of catch rates by research vessels in the Labrador Sea and by commercial and research vessels at Greenland indicated that in most years, for which there were comparable data, catch rates were similar in the Labrador Sea and at Greenland (Fig. 4). In some years, catch rates were higher in the Labrador Sea. This suggests that a substantial population of salmon exists in the Labrador Sea, comparable to that at West Greenland, and that at least in some years, this population may even exceed that at Greenland because the area utilized by salmon in the Labrador Sea is much larger than at Greenland.

Information collected in the Labrador Sea from age interpretation of scales of captured salmon, salmon caught with tags attached, and the distribution of recaptures of salmon tagged at sea indicated that salmon over the entire range in North America occur in the Labrador Sea. Stomach content analysis suggested that salmon were feeding opportunistically on whatever is abundant in the area. The distribution of salmon as measured by catch rates and temperatures, measured from the research vessels, indicated that salmon are found most abundantly in water with surface temperatures between 4 and 10°C (Fig. 5).

Water temperature has proven to be an important variable in the ecology of salmon at sea (Friedland and Reddin 1993; Reddin et al. 2000). Experiments with data storage tags (DSTs) were conducted on Atlantic salmon kelts obtained at enumeration facilities on Western Arm Brook, Campbellton and Highlands rivers, Newfoundland in 1998. In total, data on temperature are available from eleven of the returned tags. In order to verify the temperatures

Fig. 1. The number of Atlantic salmon in North America (Anon. 2001).

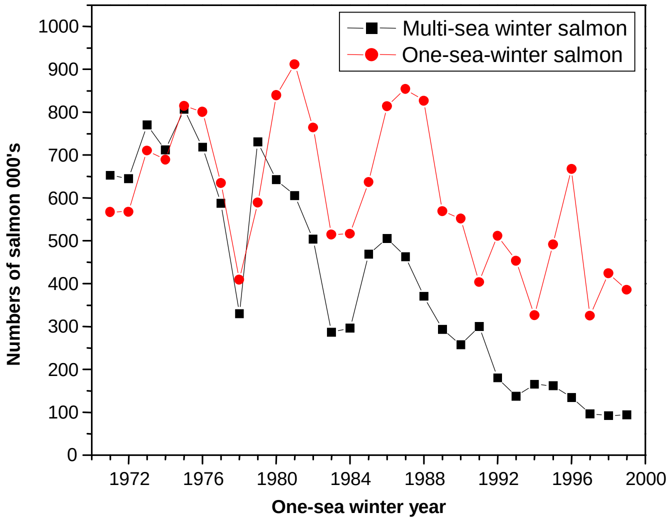

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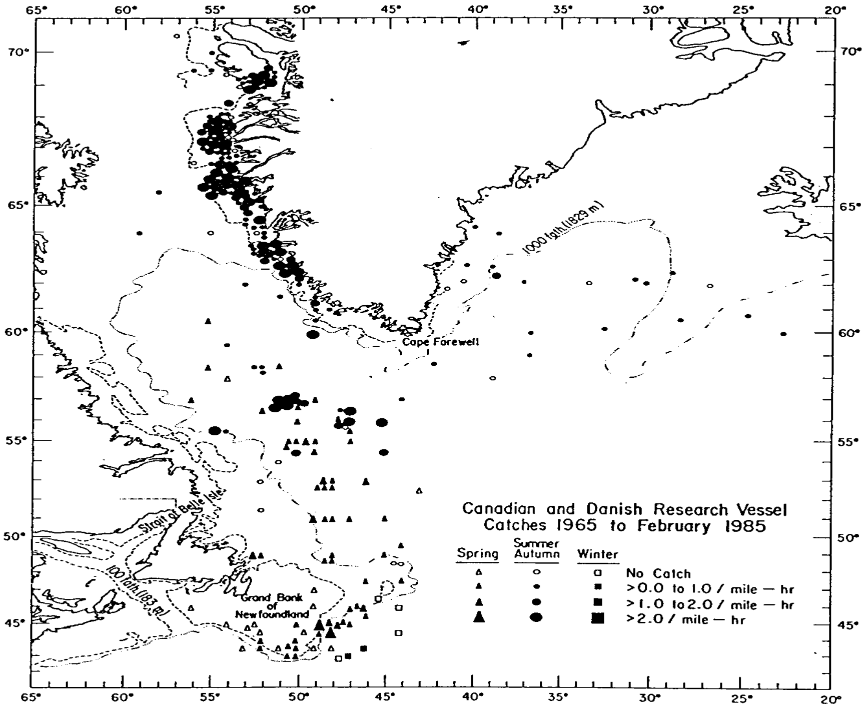
Fig. 2. Catch rates by Canadian and Danish research vessels from 1965–1985 (reproduced from Reddin and Friedland 1993).



recorded by the DSTs, kelts were tagged and held in a freshwater fluvarium. Water temperatures recorded by these DSTs were accurate. Comparison of the temperature profiles obtained using DSTs indicated that there were differences in the water temperatures experienced by salmon from different rivers and among salmon from the same river. Information collected by data storage tags is important for determining the marine ecology of salmon, adjusting marine climate change models for salmon and, in freshwater, water temperature protocols for opening/closing angling fisheries due to high water temperatures. Movements vertically in the water column were inferred from the daily temperature patterns and indicated extensive diurnal movements. The DST-tagged salmon spent most of their time in water from 5 to 17°C (Fig. 6).

In summary, there is a lot of information available to use as background for further studies on the ecology of salmon in the sea. This information should be utilized to design experiments to test hypotheses related to why natural mortality rates are apparently so high for salmon at sea in recent years.

Fig. 3. Locations of capture of post-smolts in the Northwest Atlantic in 1987-88 (reproduced from Reddin and Short 1990).

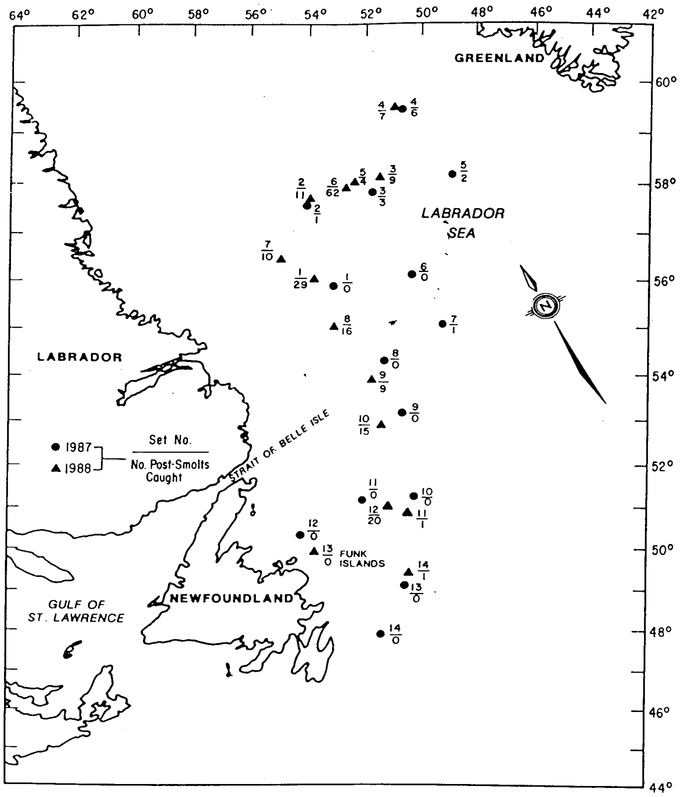


Fig. 4. Catch rates by research vessels in the Labrador Sea and by commercial vessels and research vessels at Greenland.

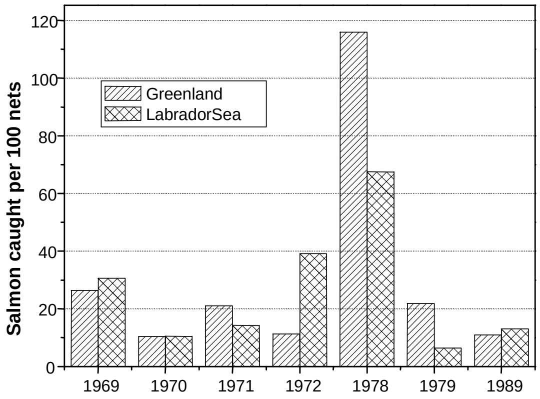


Fig. 5. Relationship between catch rate for salmon in the Northwest Atlantic and sea surface temperature.

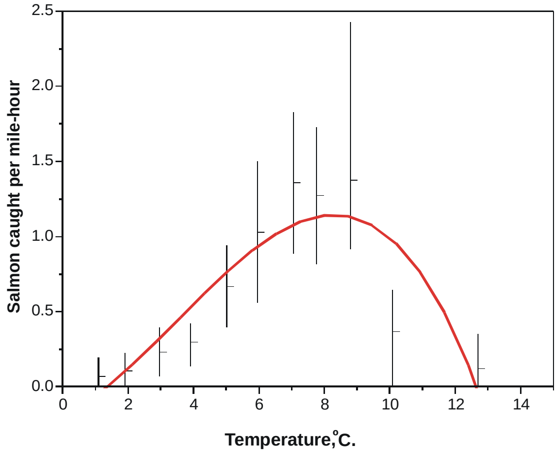
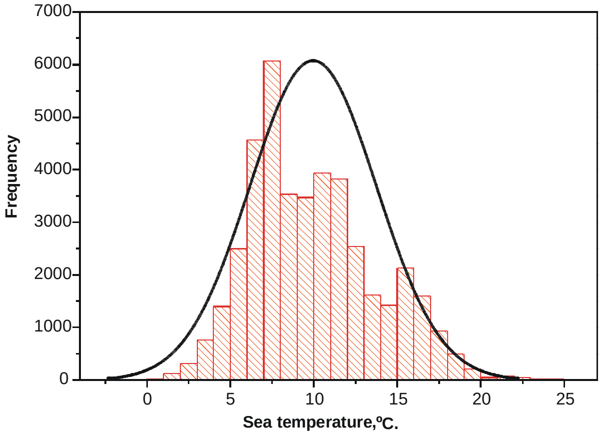


Fig. 6. Sea temperatures experienced by Atlantic salmon kelts tagged with data storage tags in 1998 at Highlands and Campbellton rivers and Western Arm Brook, Newfoundland.



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Marine Survival of Atlantic Salmon in the Baltic Sea

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Keywords: Salmo salar, Baltic Sea, post-smolt survival, marine environment, smolt quality

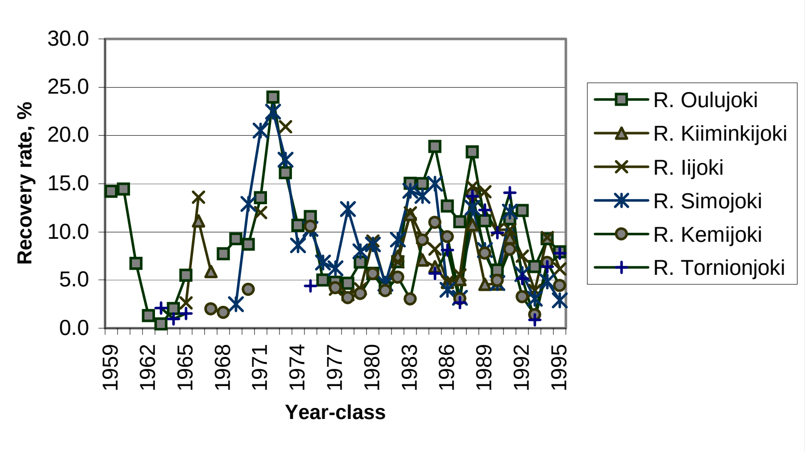
In the Baltic Sea, Atlantic salmon (*Salmo salar* L.) live in an environment very different from the oceanic conditions of the North Atlantic. As a brackish-water area, the Baltic Sea hosts a community where marine and freshwater organisms coexist. A general feature of the marine fish community is low in overall diversity. In the Main Basinprincipal southern feeding areas of Baltic salmon (Baltic Main Basin, Gulf of Finland) there are two significant marine prey fish species for young salmon to feed on during the first months of their migration in the open sea, the herring (*Clupea harengus* L.) and the sprat (*Sprattus sprattus* (L.)), and in the north (Bothnian Sea) only one, the herring (Salminen et al. 2001). Furthermore, the number and abundance of potential predators on young salmon is low in the open sea.

Located within the west-wind zone, the Baltic Sea is exposed to the cyclones from the west-southwest. Climatic variations, together with hydrological and hydrographic processes, strongly influence the temperature and ice conditions, the inflow of fresh water from rivers and the exchange of water with the North-Atlantic Ocean. These features have a significant controlling effect on different trophic levels and their processes, including the dynamics of the open-sea fish community. Human induced factors affecting the whole marine ecosystem of the Baltic include pollution and eutrophication. In the Baltic Sea, salmon live in a highly volatile environment.

Salmon populations of the Baltic Sea exhibit both long-term and short-term fluctuations (Svärdson 1955; Lindroth 1965; McKinnell, 1997; Niva 2001) (Fig. 1). Most authors agree that a substantial part of this variation arises from events during the smolt and post-smolt stages, but attempts to identify the ultimate factors causing early mortality have not been productive. Working hypotheses have linked variable survival to variable predation by marine mammals (review: Lindroth 1965), bird and fish predation (Lindroth 1955, 1965; Larsson and Larsson 1975; Lindroth 1977; Larsson 1985), starvation and disease (Österdahl 1965; Rahkonen et al.1997; Buchmann et al. 2001). No single dominant factor has yet to emerge suggesting that annual mortality levels are influenced by the interaction of a complex of different factors, whose relative importance is continuously changing.

Most of our knowledge on post-smolt mortality in the Baltic is based on tagging experiments using hatchery smolts, and may thus be biased by the study method itself and by hatchery practices affecting both smolt quality and the circumstances in which the fish encounter the marine habitat (release site and time). Specific tagging experiments have been carried out to identify the timing and duration of the critical period for survival (Lindroth 1977; Larsson 1985; Eriksson 1988, 1994; Salminen and Erkamo 1998) and the role of smolt quality and size (e.g. Lundqvist et al. 1988; Vehanen et al. 1993; Lundqvist et al. 1994). Long-term monitoring data have been used to search for synchronous trends in the recapture rates of different reared stocks (McKinnell 1997; Niva 2001) and for correlations between these and different environmental factors (Salminen et al. 1995). These experiments and analyses suggest that although the mortality rates of young salmon are highest during the first days and weeks of migration, the survival levels of hatchery fish are determined during a prolonged period in the marine habitat. Positive correlations between recapture rates, post-smolt growth, summer sea-surface temperatures and the availability of suitable prey fish suggest that the variability in

Fig. 1. Tag-recovery rates (Carlin tag) from releases of salmon smolts in different Finnish Rivers in smolt year-classes 1959–1995.



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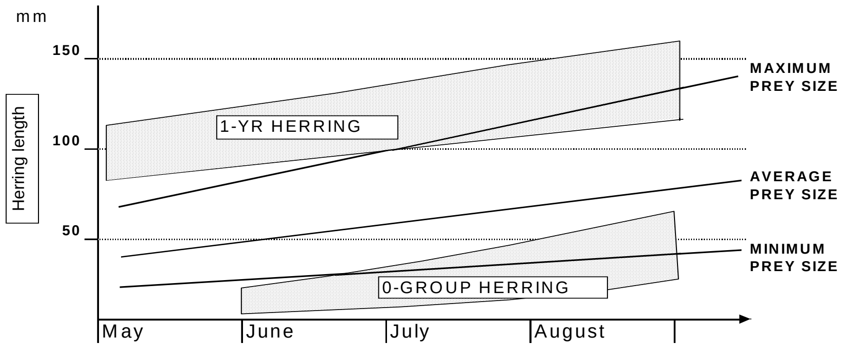
survival is mainly due to variable marine conditions affecting post-smolt growth rates, and thus, the vulnerability of the fish to some size dependent source(s) of mortality.

Tagging experiments have further indicated that in ranched Baltic salmon, the mean survival rates markedly increase (Virtanen et al. 1991; Vehanen et al. 1993; Lundqvist et al. 1994) while the annual variation in survival decreases with increasing smolt size (Salminen et al. 1995; Salminen 1996). In the long-migrating northern salmon stocks, smolt size also influences the distribution of feeding migrants between the northern and southern feeding areas (Salminen et al. 1994; Kallio-Nyberg et al. 1999). Small smolts tend to migrate further south than larger ones.

The higher and less variable survival of larger smolts may be due to their lower initial vulnerability to predation, further reduced by their rapid size increment at sea, which is probably attributed to better foraging opportunities. In the Bothnian Sea, large smolts are able to feed on 1-year old herring shortly after sea entrance while small smolts either have to postpone their shift to piscivory (the only option for an introduced, short-migrating ranching stock) until young-of-the-year herring become available later in the summer (Fig. 2), or to migrate further (an option for the local long-migrating stocks) (Salminen et al. 2001). Smaller, slow-growing individuals are subjected to a wider range of potential sources of mortality for an extended period of time. After an entire year of migration in the Bothnian Sea, the smallest smolts of the short-migrating ranching stock are still smaller than the largest ones at release (Salminen 1997).

Fig. 2. Schematic diagram showing the prey size preference of average salmon post-smolts (size at release 160 mm, average growth rates) during the first months after release in the Bothnian Sea, versus the available size distribution of the principal prey fish, the herring (based on data in Salminen et al. 2001).



Despite large seasonal and annual variability in the physical and biological features of the Baltic Sea, average post-smolt survival rates of salmon seem to be higher in this volatile environment than in the Atlantic Ocean (e.g. Ìsaksson 1994). This may be due to the lower salinity barrier, facilitating the migration of salmon smolts through the estuaries, where predators are usually abundant. On the other hand, the low salinity barrier may also give the managers of hatchery programs more freedom to manipulate smolt quality (e.g. size), despite possible associated deficiencies in smolt status. Overall predation levels on young salmon may also be lower in the Baltic compared to the Atlantic.

Are salmon different in the Baltic Sea compared to the Atlantic? The Baltic salmon provides two pieces of evidence of its genetic adaptation to freshwater or brackish water conditions. First, it has genetic resistance to *Gyrodactylus salaris* Malmberg, a freshwater ectoparasite that is fatal to the North Atlantic stocks of salmon (Bagge et al. 1990). The second piece of evidence of adaptive genetic divergence between Baltic and oceanic salmon is the short feeding migration, which is probably common for all eastern and southern stocks of Baltic salmon, though properly documented only for the River Neva salmon (Kallio-Nyberg and Ikonen 1992). Both these adaptations may partly reflect the dichotomous origin of Baltic salmon: after the last glacial period salmon probably colonized the Baltic Sea from two different directions, from the Atlantic Ocean and from the eastern ice-lakes (Koljonen et al. 1999).

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Effects of Freshwater Contaminants on Marine Survival in Atlantic Salmon

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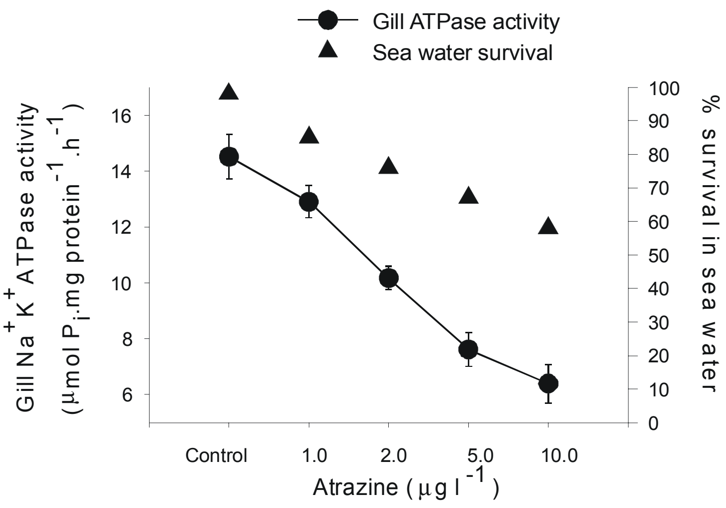
Keywords: Atlantic salmon, marine survival, endocrine-disrupting chemicals, pesticides, smoltification

There is increasing concern about the continuing decline of wild stocks of Atlantic salmon, *Salmo salar*, throughout the North Atlantic and the impact on commercial and recreational fisheries (Cairns 2001). Recent research has demonstrated that freshwater and marine environments cannot be considered in isolation and that conditions within the freshwater zone experienced by Atlantic salmon may be critical to their subsequent survival in the sea. In particular, exposure of juvenile salmon to a range of sub-lethal concentrations of freshwater contaminants, such as pesticides and endocrine-disrupting chemicals (EDCs), may operate to reduce survival in fish once they have migrated to sea (Madsen et al. 1997).

Freshwater contaminants may act in a number of ways to reduce marine survival. Pesticides such as atrazine may interfere with the parr-smolt transformation (PST), and reduce the ability of the fish to physiologically adapt to saline conditions (Hoar 1988). Atrazine is a widely used pre-emergent herbicide often applied to corn crops, and has high run-off in the first rain after field application (Solomon et al. 1996). Laboratory studies have indicated that smolts exposed in fresh water to environmental levels of atrazine have lower gill Na^+K^+ATPase activity and plasma ion concentrations. Subsequent exposure to seawater resulted in poor hypo-osmoregulatory performance and mortality (Fig. 1). Moreover, modification of the physiological processes involved during smoltification by atrazine may also delay or inhibit smolt migration (Moore et al. in press).

An extensive study has demonstrated a significant relationship between historical applications of an insecticide containing 4-nonylphenol (4-NP), a known EDC, and catch data for Atlantic salmon populations (Fairchild et al. 1999). This study suggested declines in catch were related to exposure during PST. To evaluate this, juvenile salmon were exposed to water-borne 4-NP (5 µg/L) or estrogen (100 ng/L) during the later stages of PST and their subsequent growth and survival followed for 5 months. Caged salmon smolts were also exposed in natural estuarine waters and seawater growth and survival monitored for 3 months. Relative to reference groups, there was a greater proportion of salmon exhibiting poor seawater growth in exposed groups from both laboratory and field experiments (Fig. 2). The response in all cases was bimodal, with growth effects occurring soon after treatments (Brown et al. 2001). Poor growth measured close to PST has been linked to reduced survival and fewer returns of adult salmon to their native streams (Beckman et al. 1999; Friedland et al. 1993). If the effects exerted by 4-NP are due to its estrogenic potential, then steroidogenic activity stemming from other sources (e.g. domestic sewage, agricultural, industrial) (Blackburn et al. 1999; Hewitt and Servos 2001; Sheahan et al. 2002) might negatively influence salmon populations.

Fig. 1. Effects of a 7-day exposure to the herbicide atrazine on seawater adaptability and survival (24 h) of Atlantic salmon smolts.



The Inner Bay of Fundy (iBoF) Atlantic salmon on the east coast of Canada are distinct genetically from other North American and European populations (mitochondrial DNA analysis), and make a good case study. iBoF Atlantic salmon usually enter rivers in the fall of the year, a high proportion return to spawn after one winter at sea, and survival between consecutive spawnings is high. These salmon are not generally known to migrate to the North Atlantic Ocean (DFO 1998). Recent

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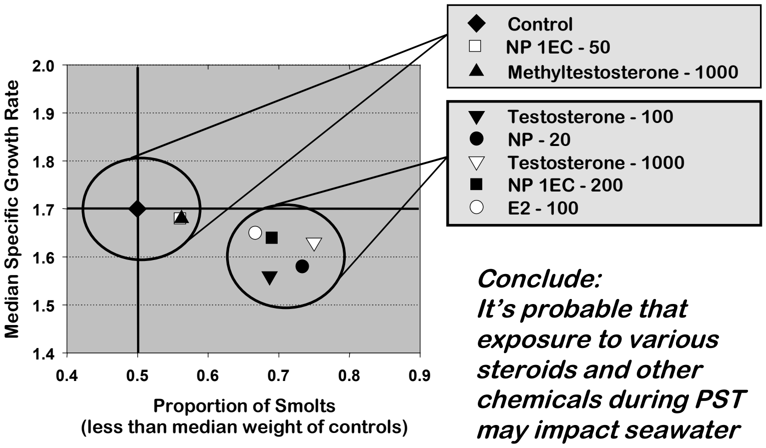
Fig. 2. Specific growth and weight of Atlantic salmon smolts two months after exposure to endocrine disrupting substances, and subsequent grow-out in seawater, St. Andrews Biological Station, 2001. (Legend: E2 = estradiol, NP = nonylphenol, NP1EC = nonylphenoxyacetic acid; units in legend are in µg/L for NP compounds and ng/L for hormones).



Conclude:
It's probable that exposure to various steroids and other chemicals during PST may impact seawater growth.

performance of iBoF Atlantic salmon populations has been poor. Stocks have been in decline since 1986, and conservation requirements have not been met since 1989. The rivers have been closed to fishing since 1990 (DFO 1998). The iBoF Atlantic salmon were designated as 'endangered' in 2001 (COSEWIC 2001).

Two rivers in the iBoF, the Big Salmon River and the Stewiacke River, account for more than half of the current production, and were historically the largest salmon producers (DFO 1998). The Big Salmon River population had the most pronounced reduction in population of any river in eastern Canada that we evaluated after nonylphenol exposure between 1977 and 1983 (1% of the expected return based on five-year mean in 1980) (Fairchild et al. 1999). This was a singular event in the recorded returns for this river.

In the environment, atrazine is derived primarily from intensive agriculture, and nonylphenol family compounds from sewage treatment plants (STP) and industrial effluents such as textile mills. Monitoring of salmon rivers and estuaries in the iBoF catchment has measured atrazine near agricultural fields (Lakshminarayana et al. 1992; O'Neill and Doull 1992) and nonylphenols in STP effluents (Bennie et al. 1998; Bennie 1999) in the low µg/L range. The concentration range of these measurements is similar to the range described above in experiments that had a negative effect on the growth and survival of smolts. In addition, laboratory studies have indicated that a combination of low environmental levels of atrazine and 4-NP may have a synergistic effect on smoltification, again reducing survival of smolts in seawater (Moore et al. in press).

The concern is that the iBoF salmon smolts may be exposed to atrazine while in streams, and then to nonylphenols in the lower river or estuary; that is, two or more pulses of exposure, a few days apart. This is a very similar pattern to that used in some of the experiments above, and matches the timing pattern of historical forestry spraying of nonylphenol very well. Based on the evidence presented above, it is conceivable that the exposure of the smolts to both atrazine and nonylphenol during downstream migration may subsequently affect growth and mortality of the smolts once they enter the iBoF.

Further work is continuing throughout the geographic range of the Atlantic salmon to determine the role of exposure to mixtures of contaminants on marine survival of salmon and model impacts of contaminants on populations.

Collaborating partners in this research include; K. Haya, L.E. Burridge, J. Sherry, D. Bennie, K. Burnison, D. MacLatchy, J.T. Arsenault, R. Evans, J.G. Eales, N. Lower, L. Greenwood, A.P. Scott, I. Katsiadaki and C. Waring. Laboratory and field work was conducted with the help of: D. Chaput, T. Jardine, D. Sephton, M. Lyons, K. MacKeighan, M. Villella, K. Moore, M. Brown; G. Chaput and the DFO salmon assessment crew; and M. Hambrook and staff of the Miramichi Salmon Conservation Centre.

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Mortality of Seaward-Migrating Post-smolts of Atlantic Salmon Due to Salmon Lice Infection in Western Norwegian Salmon Stocks

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Keywords: Post-smolt Atlantic salmon, salmon lice, infection, mortality

Since the early 1990s premature returns due to heavy salmon lice infections have been observed in Norwegian sea trout stocks. Following these observations it was hypothesized that salmon lice could also cause serious problems and mortality for seaward-migrating salmon post-smolts. However, due to the direct migration into the high seas of this species, evidence was hard to secure. In 1998 the Institute of Marine Research, Bergen, Norway in cooperation with the University of Bergen initiated fjordic surveys aimed at estimating the level of salmon lice infection in seaward-migrating post-smolts of western Norwegian salmon stocks and the impact of these infections on their survival. Through the development of a live-capture trawl device, Ocean-Fish-Lift, it has been possible to secure live samples of post-smolt salmon without removing any lice from the fish. Sampling of post-smolts has also taken place in the open ocean later in the season when the salmon lice have grown to their most aggressive stages. It has also been possible to run a controlled experiment to estimate the mortal level of salmon lice infection on wild salmon post-smolts.

The mean infection levels of copepodites and chalimus stages have been observed to vary from 0 to 104 per fish between years and fjords. The hydrographic features of the specific fjord and year seem to be major factors governing the infection level.

The controlled experiment suggested a mortal level of 11 adult salmon lice on wild post-smolts. This number is in close accordance with the oceanic observations, where no salmon taken during a period of 10 years were observed to carry more than 10 adult salmon lice in July.

Based on the observed infection levels and a conservative mortal limit of 15 adult salmon lice, estimates of up to 95% mortality due to salmon lice infection have been observed.

Although the reported mean numbers of adult female lice in fish farms in the area studied have been reduced to close to the allowed level of 0.5 adult females per fish in the spring, salmon lice still appear to be a problem for many wild salmon stocks in western Norway. In particular, rivers draining into the heads of long fjords seem to be adversely affected. As it seems unrealistic that salmon lice levels in fish farms will be further reduced in the near future, an additional measure for critically affected rivers would be to treat the smolts with a protective chemical against salmon lice infection during the migration to sea.

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Impacts of the fishery, disease, and contaminants on Baltic salmon (*Salmo salar* L.) in the sea

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Keywords: Baltic salmon, *Salmo salar*, disease, fishery, dioxin, PCB

Baltic salmon (*Salmo salar* L.) are normally subjected to the environment in the brackish Baltic Sea throughout their marine life, since few migrate into the Atlantic. This paper assesses the impacts of three factors, the fishery, disease and contaminants, on salmon survival during their marine phase in the Baltic. Two factors are strictly anthropogenic, whereas the third factor, prevalence of diseases, is weakly and the link is normally difficult to verify.

The salmon fishery in the Baltic takes place mainly in the offshore area, primarily with drift nets and long lines (Karlsson and Karlström 1994). Catch records and tag recoveries provide an overview of the offshore fishery. A low proportion of river recoveries of tagged salmon from the early 1960s to the early 1990s (Fig. 1), reflecting the high level of fishery exploitation, resulted in the loss of several river populations of salmon, and in severe reductions in the size of many of the populations that survived. The period of intense size-selective drift-net fishing coincided with a decline in spawner weight by age and a lower mean age of spawners (Fig. 2). When exploitation decreased in the early 1990s, salmon weight by age started to increase, indicating resilience to depressed weights; but other factors, such as smolt size, winter temperature, and changes in prey abundance may also have contributed to increased growth at sea.

Fig. 1. Percentage of tagged salmon recovered in rivers. Data are from Swedish tagging records during 1952–1997.

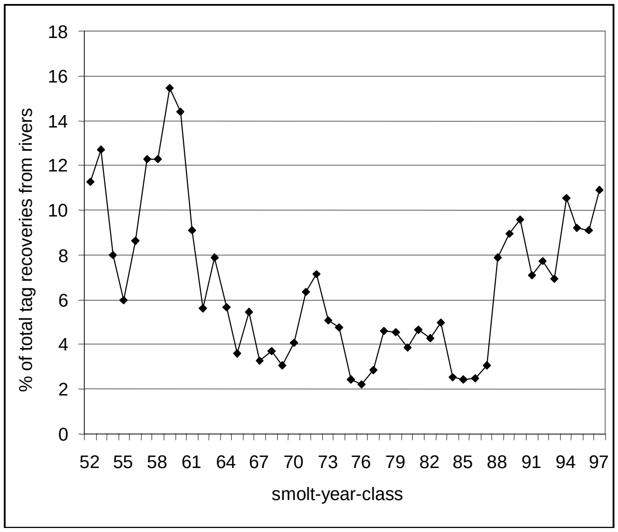

Fig. 2. Annual mean weight of spawners in the northern part of the Baltic, Gulf of Bothnia. Values from 1930-44 are based on catch statistics for the rivers Oulu and Torne. Values from 1952–2001 are based on Swedish tagging records.

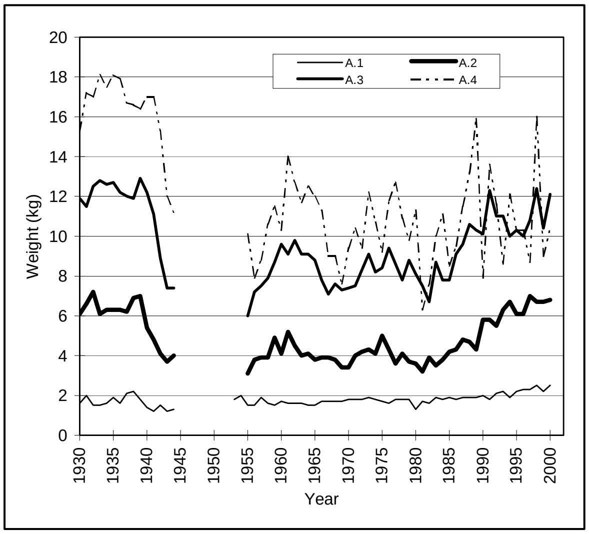

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Table 1. Notifiable diseases demonstrated in sea-run salmon in Swedish brood-stock fisheries during the period 1986–2001. The number of brood-stock holding facilities varied in the range from 8 to 12 and about 1000 fish were examined annually.

River	Disease (year of detection)
Torneälven	Furunculosis (1986)
Luleälven	Furunculosis (1986) and yersiniosis (2001)
Umeälven	Furunculosis (1990)
Ljusnan	Infectious pancreatic necrosis (IPN-V) serotype Sp (1998), renibacteriosis (1998) and furunculosis (1998)
Dalälven	Infectious pancreatic necrosis (IPN-V) serotype Ab (1992)
Mörrumsån	Furunculosis (1990)

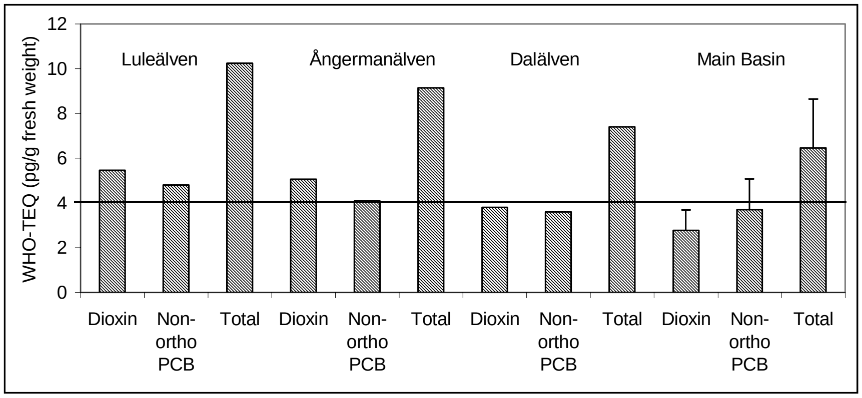
Discussions on salmon diseases during the 1990s focused on the high mortality in many salmon stocks, caused by M74, a syndrome resulting primarily from a low level of vitamin B1 (thiamine). Consequently, little is known about the impact of many other diseases on the marine survival of salmon. Records from sampling in Swedish brood-stock fisheries from 1986 to 2001 indicated the prevalence of viral and bacterial pathogens in salmon (Table 1). However, the presence of only one viral disease, IPN-V was demonstrated. Furunculosis was identified on several occasions during the period, and one case of renibacteriosis was recorded. The sources of infections are believed to be in the marine environment, since the diseases, with the exception of yersiniosis, have not been demonstrated in rivers where brood-stock holding facilities are located.

In the same period, the number of cases of IPN-V was low and sporadic in Swedish commercial fish farms along the Baltic coast. However, in recent years, more than 70% of these farms have been infected with BKD and furunculosis. The low rate of infection in salmon brood-stock fisheries may indicate that spreading of pathogens from commercial fish farming activities has been low in areas where salmon migrate. The future development will depend in part on disease regulations as well as industry efforts to control diseases.

Due to increasing human activity and resulting pollution in the Baltic region and elsewhere, persistent contaminants have accumulated (by means of air- and water-mediated transport), which can also affect salmon populations in the Baltic. The restricted water exchange between the Baltic and the North Atlantic has contributed to increased levels of persistent organochlorine compounds in Baltic salmon, compared to levels in neighbouring parts of the North Atlantic. Because the EU has established a maximum level of dioxin for fish and fish products intended for human consumption (4 pg WHO-TEQ/ g fresh weight, Council regulation 2375/2001), there is now a major interest dioxin levels in fish.

The toxicity of dioxins (PCDD/PCDF) to fish and mammals appears to be of the same order of magnitude (Van den Berg et al. 1998). For salmon and Baltic herring (*Clupea harengus*, data not shown), observed levels of dioxin are close to or exceed the threshold (Fig. 3). In addition, several dioxin-like PCBs (non-ortho PCB 77, 81, 126, 169) also have toxic effects, which add to that of the TEQ of dioxin. At the same time, no evidence unequivocally shows that current dioxin levels adversely influence salmon physiology. Monitoring of Baltic biota reveals decreasing concentrations of PCB and DDT from the 1970s (Olsson et al. 2000), whereas from 1988 to 1999, dioxin levels in Baltic herring were constant (Contaminant Research Group, Swedish Museum of Natural History, personal communication). Sweden and Finland currently have an exemption from the Council regulation that allows national marketing of fish that exceed the threshold level for dioxin. In Sweden, the exemption is based on recommendations from the Swedish National Food Administration to certain risk groups (i.e. women and girls of fertile age and high consumers) to restrict their consumption of fatty fish from the Baltic region. Expiration of this exemption on 31 December 2006 will influence the commercial fishery and trade in Baltic salmon.

Fig. 3. WHO-TEQ (pg/g fresh weight) levels of dioxin, non-ortho PCBs (dioxin-like PCB) and the summed levels in salmon in 2000 (Main Basin - 2001). Samples of muscle tissue of salmon spawners (n=10) from three rivers in the northern Baltic, Gulf of Bothnia, are pooled for analysis. Individual analyses are from feeding-salmon (mean and SD, n=10) in the Main Basin. The threshold of 4 pg/g fresh weight is indicated.



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Factors Affecting Survival of Hatchery-Reared Chum Salmon in Japan

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Keywords: Hatchery, growth, return rate, coastal ocean conditions

Most of the chum salmon in Japan are sustained by hatchery programs. Annual fry releases have increased since the mid 1970s to a plateau of 1.8–2.1 billion during the last two decades. The number of chum salmon returning to Japan has also increased dramatically since the mid 1970s and reached a historic peak (about 88 million returns) in 1996. This steady increase was realized by aggregate effects of successful hatchery programs and changes in oceanographic conditions (e.g. Kaeriyama 1998). However, annual returns began a gradual decline from 1997 to 2000. To evaluate potential effects of large-scale hatchery releases on the growth and survival of Japanese chum salmon annual scale growth and return rates of 1976–96 brood year stocks are analyzed.
Scales from age 0.3 females caught in five rivers of Hokkaido (Ishikari, Shari, Nishibetu, Tokachi, and Yurappu rivers) were measured, about 30–50 scales per brood year for each river population. The width between scale annuli is regarded as an indication of annual fish growth. Comparisons in mean annual growth of brood year stocks revealed differences among the river populations in the first year of ocean life. Comparisons in the second, third andfourth years found annual growth to be largely similar. This suggests that growth differences between populations during the first year likely stems from localized coastal water influences. In the 1980s, annual fluctuations in average fork length of age 0.3 females were stable despite an obvious decline in 1984. In the 1990s the variation increased suggesting that ocean conditions for growth of chum salmon might have changed in the 1990s as compared to those in the 1980s. While some researchers have reported a negative correlation between population abundance and somatic growth (e.g. Ishida et al. 1993; Kaeriyama 1996, 1998), adult returns in the Hokkaido river revealed no relationship between the average fork length and adundance of age 0.3 females, based on data for the last 20 years. However, as the brood population has been abundant in Hokkaido river, average age at maturity of brood year stocks has increased in the same period. These results indicate that increased population size may slow growth and delay maturation increasing average age of the population.

Return rates of 1976–93 brood year stocks were calculated for seven regions of Japan (Okhotsk, Nemuro, East and West Hokkaido Pacific coast, Japan Sea, Honshu Japan Sea, and Honshu Pacific coast regions). There was no significant relationship between the number of released fry and return rates in the seven regions. Correlation analysis for the return rates revealed significant positive relationships in three pairs of regions; Okhotsk-Nemuro, Nemuro-East Hokkaido Pacific coast, and Honshu-West Hokkaido Pacific coast regions. Cluster analysis determined the Okhotsk-Nemuro and Honshu-West Hokkaido Pacific coast regions to be similar groups. Since these regions, i.e., Okhotsk-Nemuro and Honshu-West Hokkaido Pacific coast regions, are geographically close each other, I examined the following coastal ocean conditions as possible factors affecting the return rates: (1) November-July sea surface temperature (SST) and (2) surface area of SST ranging 5–13°C, in which juveniles are distributed during the early ocean life. Original SST data were provided by Japan Meteorological Agency as 10-day mean sea surface temperatures analyzed for 1 temperature degree by 1 degree grid points (NEAR-GOOS Regional real time database). The above-noted two factors were calculated using a software package for marine geographic information systems, "GIS Marine explorer version 3.1" (Environment simulation laboratory Co. Inc., Kawagoe, Japan) across an area for each pair of regions (area for Okhotsk-Nemuro regions, 43°N–46°N latitude and 142°E–147°E longitude; area for Honshu-West Hokkaido Pacific coast regions, 35°N–43°N latitude and 140°E–146°E longitude excluding an area 35°N–41°N latitude and 143°E–146°E longitude). Sea surface temperatures for years 1976 through2000 were positively correlated with stock returns in Okhotsk-Nemuro regions, but not in Honshu-West Hokkaido Pacific coast regions. Alternately, increase in the surface area was associated with higher stock returns in the Honshu-West Hokkaido Pacific coast regions, but not in the Okhotsk-Nemuro regions. Although the underlying mechanisms to link these coastal ocean conditions to survival are not well known, results of this study suggest that in the northern regions (e.g. Okhotsk-Nemuro regions) ocean productivity is enhanced by warmer ocean temperatures and this increases the survival of juveniles and in the southern regions (e.g. Honshu-West Hokkaido Pacific coast regions) the formation of suitable area is a determinant for success of migration in the early ocean life.

Annual fluctuations of adult returns in Japan were pronounced in the 1990s.This occurance may be partly explained by fluctuations in survival rates of stocks in Okhotsk and Nemuro regions. From the late 1980s to the early 1990s, survival of stocks in these regions probably improved due to warmer SSTs in the early ocean life. These stocks obviously contributed to the increase in adult returns during the early-mid 1990s then SSTs shifted to normal levels after the mid 1990s. This change in SST might be the cause of recent declines of adult returns in the

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late 1990s. Since chum salmon are the most abundant of the salmon species in Japan their survival rates are a primary factor influencing total salmon returns.

This study suggests that survival of Japanese chum salmon may be strongly influenced by coastal ocean conditions and that the oceanographic factors affecting their survival probably differ among regions. Future studies should examine effects of hatchery techniques (e.g. size at release and timing of release), to assess the effect of hatchery practices on survival under variable oceanographic conditions.

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Life History Diversity, Marine Survival, and Viability of Pacific Salmon

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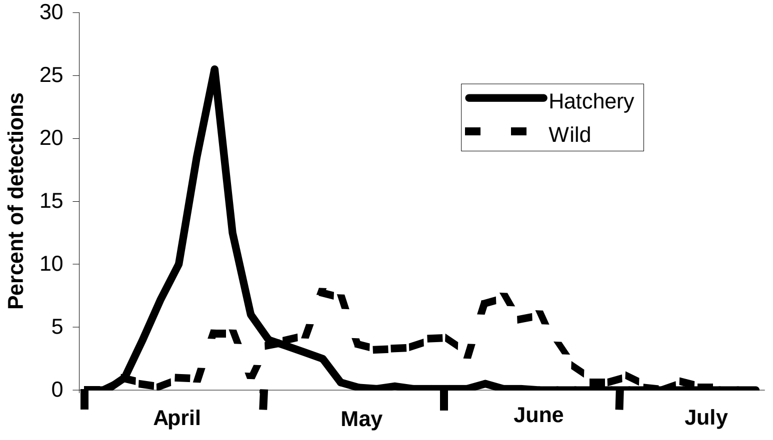
Keywords: Diversity, Pacific salmon, marine survival, life history

The hypothesis that ocean productivity to support salmon populations fluctuates between "good" and "bad" cycles that can span 2–3 decades, and that these fluctuations are negatively correlated between waters off Alaska and the Pacific Northwest, is gaining increasing acceptance. However, not all populations within a geographic area respond to common environmental conditions in the same way. Genetic and life history diversity among salmon and steelhead populations leads to considerable variability in their response to the marine environment. Conversely, events that occur during the marine phase of the life cycle can profoundly affect metapopulation structure and diversity of salmon and steelhead populations in fresh water. Some empirical examples illustrate that these patterns of genetic and life history diversity can be important on a variety of spatial and temporal scales.

Figure 1 shows the timing of arrival at a mainstem Snake River dam of outmigrating chinook salmon (*Oncorhynchus tshawytscha*) smolts that had been implanted with Passive Integrated Responder tags (PIT tags) as wild parr or as presmolts in hatcheries (Achord et al. 1996). The natural populations show a protracted outmigration timing over a more than 3-month period that reflects diversity within populations as well as differences among populations in mean outmigration timing. In contrast, hatchery smolts are typically released during a short temporal window in early spring. More recent research (J. Williams, Northwest Fisheries Science Center, personal communication) has shown that just a few days difference in date of ocean entry of spring/summer chinook salmon smolts collected at mainstem Columbia and Snake River dams and barged to the estuary can result in a 5- or 10-fold difference in marine survival rate. Similarly, recent genetic studies of juvenile chinook salmon during their first critical summer at sea show that stock composition of juveniles in nearshore waters changes dramatically during the course of the season (D. Teel, Northwest Fisheries Science Center, personal communication).

Snake River spring/summer chinook salmon, together with spring chinook from the mid and upper Columbia, are part of what is referred to as the stream-type lineage (Healey 1991; Myers et al. 1998); the ocean-type lineage includes other Columbia River and all coastal populations. Little is known of the ocean ecology of stream-type chinook salmon except that they are only rarely taken in continental shelf fisheries that typically harvest ocean-type populations at relatively high rates. Presumably, therefore, Columbia River stream-type chinook salmon utilize the marine environment in a very different way than do ocean-type populations, either moving off the continental shelf during times the ocean-type populations are vulnerable to harvest, or adopting behavioral patterns that make them less susceptible to harvest. This fundamental difference in utilization of the marine environment is associated with a deep evolutionary split and is not affected by environmental factors that may alter smolt age or migration or spawn timing (Myers et al. 1998). If the stream-type chinook salmon lineage was lost in the interior Columbia River basin, it is possible that spring-run fish would re-evolve from summer or fall chinook in the ocean-type lineage (a scenario that has occurred

Fig. 1. Detection of PIT-tagged juvenile Snake River spring/summer chinook salmon as they migrated though Lower Granite Dam in 1989. Wild fish were tagged as parr in late summer 1988 from streams in the Salmon, Imnaha, Grande Ronde, and Clearwater river basins; hatchery fish were tagged before release in spring 1989 at Lookingglass and Sawtooth Hatcheries. Percentages of total detections are plotted separately for hatchery and wild groups as sums over 3-day periods. Modified from Achord et al. (1996).



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repeatedly in coastal basins), although it likely would take a long time from the human perspective for this to occur. Even if it did occur, however, the resulting spring-run fish might not be yearling migrants, and there is no reason to expect that they would adopt the marine ecological patterns of the extirpated stream-type lineage. The result would be a profound (and long lasting) loss of diversity and overall productivity within the basin.

Fig. 2. Variation in adult size (weight measured in in-river fisheries or length of natural spawners) of coho salmon from Puget Sound and the Oregon and Washington coasts, 1972–1993. Source: Weitkamp et al. (1997).

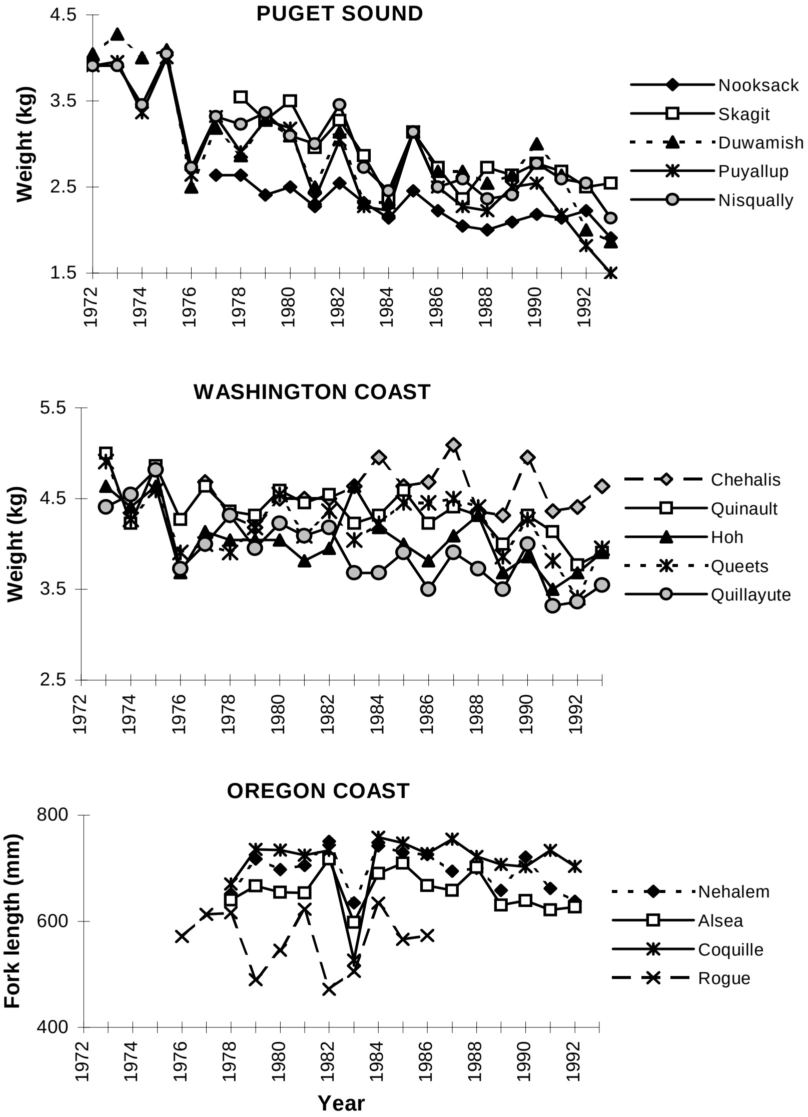

Figure 2, which shows patterns of variation in adult size of coho salmon (*O. kisutch*) over a 20-year period, provides evidence of geographic differences in marine ecology in this species as well (Weitkamp et al. 1997). A pronounced and steady decline in adult size was seen in Puget Sound, but not coastal populations. Although possible explanations for this pattern are numerous, human factors such as size-selective fisheries, genetic changes in hatcheries, and freshwater condition factor could differentially affect marine growth and survival of coho salmon. Second, the response to the large 1982–83 El Niño event was different in populations from the three areas. Oregon coast coho populations showed a pronounced reduction in adult size in 1983, but a similar reduction was not seen in populations from the Washington coast. Puget Sound also showed a sharp reduction in size, but the effect was greatest in 1984 rather than 1983. Although freshwater effects on adult size cannot be entirely ruled out, the most plausible explanation for these data is that populations from the three geographic areas utilize the ocean environment in different ways. Populations from the Washington coast apparently avoided most of the deleterious effects of El Niño experienced by the Oregon coast populations. The phenotypic effects of the El Niño were delayed a year in Puget Sound coho salmon, suggesting that either (a) the El Niño affected coho in their first year at sea in Puget Sound and their second year at sea in Oregon, or (b) the effects of El Niño persisted for an additional year in marine waters occupied by Puget Sound fish.

Collectively, these data demonstrate that interactions between life history, genetic, and ecological diversity of salmon populations and their freshwater and marine environments can profoundly affect their population dynamics and sustainability. For example, the wide diversity in outmigration timing and early marine life history that has evolved in Snake River chinook salmon provides a substantial buffer against fine-scale temporal changes in freshwater and marine risk factors. A variety of anthropogenic factors, including impediments to migration, instream flow management, harvest, and hatchery releases, can affect these life history traits and survival in both terrestrial and marine habitats. Effective recovery planning must recognize these complex relationships.

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Interactions and Potential Causes to the M74 Syndrome Affecting Sea-Run Baltic Salmon (*Salmo salar*) Populations

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Keywords: Baltic salmon, M74, thiamine deficiency, reproduction disorder

Baltic salmon (*Salmo salar*) populations originating from the Swedish East Coast have suffered from the reproduction disorder M74 since 1974. Between 1992–96 the mean frequency of M74 in Swedish compensatory rearing stations varied between 50 and 80%. The highest recorded incidence of M74 was in 1993 when 96% of all family groups from the River Ume developed M74. Since 1997 the mean annual frequency of M74 in Swedish compensatory rearing stations has been about 25%. Finnish and Estonian Baltic salmon have also demonstrated development of M74 in the 1990s. Several factors have been hypothesized to be involved in the aetiology including loading of man-made pollutants, lowered levels of antioxidant compounds and large-scale changes of the food web with accompanying alterations of the nutritional quality of the basic prey species for Baltic salmon (Norrgren et al. 1993a; Börjeson and Norrgren 1997). However, today it is evident that the primary cause of M74 is a deficiency in thiamine (Vitamin B_1) due to a poor maternal transfer (Amcoff et al. 1998a). M74-similar syndromes (EMS and Cayuga Syndrome) also affect several salmonid species in the North American Great Lakes (Fisher et al. 1995: Fitzsimons 1995; Marcquenski and Brown 1997). Thiamine is essential as a co-factor for three enzymes necessary in carbohydrate metabolism: the transketolase in the non-oxidative part of the penthose phosphate shunt; the pyruvate dehydrogenase complex in the junction between the glycolytic pathway and the citric acid cycle; and the a-ketoglutarate dehydrogenase complex in the citric acid cycle. The pentose phosphate shunt produces NADPH and ribose 5-phosphate, compounds necessary in reductive biosynthesis and for DNA ribonucleotides. Lowered thiamine content results in lowered activities of the thiamine dependent enzymes, which is considered to be the initial event in the development of clinical signs. Thiamine deficiencies have been shown to cause a variety of neuropathologies with lethal outcome in many different animals including humans (Evans 1975). In fish, typical symptoms are anorexia, instability, convulsions and darkening of the skin (Blaxter et al. 1974; Lehmitz and Spannhof 1977; Morito et al. 1986; Masumoto et al. 1987; Lundström et al. 1998a). Biochemical changes include accumulation of lactic acid, depletion of hepatic and muscular glycogen depots and altered activities of brain transmitter substances (Amcoff et al. in press a). Brain areas with extensive single cell necrosis are commonly found in M74-developing yolk-sac fry (Lundström et al. 1999a). The M74 syndrome is usually regarded as a yolk-sac fry thiamine deficiency with the progeny demonstrating M74-typical neurological disturbances followed by death prior to swim-up. Development of disease is predetermined by the maternally transferred concentration of thiamine to the offspring and yolk-sac fry with a thiamine content below the threshold limit interval of 0.34–0.47 nmol/g have lowered thiamine-dependent enzyme activities and will develop M74 (Amcoff et al. 1998b, 2000). Data show that offspring with thiamine levels just above the threshold limit interval have restrained enzyme activities, indicating that seemingly healthy Baltic salmon yolk-sac fry suffer from a sub-lethal thiamine deficiency (Amcoff et al. 2000). Thiamine deficiencies during early development in the rat reduce the activities and alter the cerebral distribution pattern of the thiamine-dependent enzyme, possibly due to tissue-selective vulnerability (Sheu et al. 1996). Whether sub-lethal thiamine deficiencies affect future performance in Baltic salmon is not known. By using thiamine antagonists that specifically bind to the thiamine-dependent enzymes most of the typical M74-symptoms may be reproduced (Amcoff et al. 1999, in press a). The M74-syndrome is female dependent, however, in severe cases adult salmon of both sexes develop thiamine deficiency and die before spawning. These fish manifest a typical in-coordinative behavior and have problems with the regulation of their swim-bladder pressure (Amcoff et al. 1998a). In addition, they have altered brain serotonergic and dopaminergic activities, possibly contributing to the aberrant behavior (Amcoff et al. in press b). Both adult fish and their offspring can be treated to full survival with thiamine treatments (Amcoff et al. 1998b).

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The Baltic Sea ecosystem is a contaminated environment and it has been suggested that the M74-syndrome is caused by maternal transfer of different organohalogen substances to the oocytes (Norrgren et al. 1993a). Studies on mammals show that exposure to polychlorinated biphenyls (PCBs) and dichloro-diphenyltrichloroethane (DDT) may give rise to a thiamine deficiency (Yagi et al. 1979; Pélissier et al. 1992). Asplund et al. (1999) and Vuorinen et al. (1997) showed that Baltic salmon tissues and eggs contain high levels of organohalogen compounds, though no clear connection with M74 development was found. Experimental studies to induce M74 have been performed by exposures to model substances like PCBs, polychlorinated naphtalenes (PCNs) and extracts from sediments and animal tissues (Norrgren et al. 1993b; Engwall et al. 1994; Holm et al. 1994; Amcoff et al. 1998c; Lundström et al. 1998b). However, none of these studies succeeded in inducing M74.

A common effect of organohalogen biotransformation is free radical generation with an accompanying consumption of free radical scavengers in addition to induced biotransformation sytems (Halliwell and Gutteridge 1996). M74-developing yolk-sac fry have reduced concentrations of ascorbic acid, a-tocopherol and ubiquinone, three of the most important antioxidant vitamins (Börjeson and Norrgren 1997). They also demonstrate altered activities of catalase, glutathion reductase, glutathion peroxidase and cytochrome P4501A, indicating that organohalogens may play a role in further worsening the situation for individuals with low thiamine content being on the edge of survival (Amcoff et al. 1999; Lundström et al. 1999b; Amcoff et al. 2000, in press a).

The cause of the low thiamine levels found in Baltic salmon is not completely resolved. A study by Karlsson et al (1999) showed that Baltic salmon have not changed their preference for herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) since the early 1960s, indicating that factors other than food choice have to be addressed. One factor that is of great interest is the presence and regulation of thiaminase, a thiamine-destroying enzyme present in herring and sprat.

In conclusion, the M74 syndrome is primarily caused by a maternally transferred thiamine deficiency from the female to the oocytes. The exact causes of the deficiency are not known. M74 still constitutes a severe threat to the survival of the remaining self-sustaining Baltic salmon populations.

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Self-Regulation of Japan Chum Salmon Abundance

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Keywords: Chum salmon, self-regulation, abundance

Japanese chum hatcheries have been releasing a large number of fry during the past 10–15 years. The biomass of Japanese chum reached 200,000 t by the early 1990s, and remained at that level until 1996. The emergence of such amounts of artificially bred fish could not but change the ecological environment in the North Pacific. We became witness of an experiment on a global scale. We were challenged by the need to comprehend the mechanism and the results of that experiment. We conducted our study between 1994 and 2001 from drift-netters which operated in the exclusive economic zone of Russia between Navarin Cape and the South Kurils from May till October.

Considerable changes have taken place in the North Pacific during these years. Catches of chum per net at the outset of our study were rather large which agreed with the high abundance of the Japanese stock. The number of fish in the Russian wild stocks of chum had concurrently gone down nearly everywhere. Alongside their rise in numbers, the average length and weight of the Japanese adult chum declined while their mean age increased (Ishida et al. 1993; Kaeriyama 1996). However, the increasing amount of culturing has had greater effects on the ecosystem than a simple arithmetic increment in the number of juveniles released. Both the greater volumes of culturing, together with increasing mean age, resulted in increased feeding times at sea. Our estimates indicate that, given the increased mean age of chum from 3 to 3.75 years, the number of fish found in the ocean at one time rises by 34%. VNIRO scientist A. Jarzhombek`s calculations indicate that the non-productive loss of energy in 1995 compared to 1970 was 34% higher as well, i.e. the functioning of the North Pacific epipelagic ecosystem became less effective. Low calorie organisms (coelenterates and tunicates) prevailed in the diet of chum. At the same time, a softening of muscle tissue in chum salmon was recorded by us in 1994. The average percentage of chum with this condition was, at that time, 35%. The seasonal dynamics of chum having softened muscles (flabby chum) followed the migration pattern features of the Japanese chum. It allowed us to assume that it was expressly Japanese chum that were exposed initially to the myopathy.

The situation began to change gradually. Catch rates dropped, chum began to consume food of high energy content: fish, squids and crustaceans. The percentage of flabby fish in catches decreased from 40% in 1996 to 7.4% in 2000 (Klovatch 2000). By 2000, the abundance of the East Kamchatka stocks of chum which had been especially subdued by Japanese chum abundance, had gone up. Total returns of the Japanese chum declined notably. Hence, it was 20% lower in 1998, and 30% lower in 2000 than in 1996 (Watanabe 2000). The age composition of catches had changed. The fish became younger. In 1996–1997 catches at sea consisted basically of five-year-olds, whereas the catches taken after 1998 began to consist mostly of four- year-olds (Gritsenko et al. 2000).

The factors causing that change were cooling in the North Pacific which began in mid-1990s, and the mechanisms of density dependence of chum in the ocean. It is impossible to quantify the role of those factors. That is why on the first factor we shall reduce ourselves to simply stating the actual condition. We shall examine the second group of factors in greater detail. The most pronounced phenomenon that occurred in the first half of the 1990s was mass myopathy in chum. We examined two hypotheses (parasitological and trophic) in order to track down the immediate causes of myopathy in chum. In 1997 Dr. P. Golovin conducted a clinical, pathalogoanatomic and microscopic studies of the muscles and the inner organs in chum, as well as helmintological examination of the intestine in order to detect organisms that might be causing softened muscles. No pathogenic organisms causing the softening of tissue in chum were found. The parasitological hypothesis did not prove to be correct. The second trophic hypothesis was corroborated by histological studies of the muscles of healthy and flabby chum. The muscles taken from all parts of body of healthy individuals of chum had normal structure. The fish with abnormal muscle structure had their destructive changes more pronounced in the groups of muscles localized immediately behind the head and under the dorsal fin.

The range of pathological changes found can be divided into three major groups. First, there were dystrophic changes observed in the muscle fibres which were expressed in damaging of the regularities in the cross-wise line pattern. In some parts the structure of fibres was totally broken and turned into a shapeless mass. The number of atypical muscular fibres reached 60%. The second group of pathological changes was notable for broad zones of necrosis resulting from complete disintegration of muscular fibres. The other part of fibres is subjected to partial

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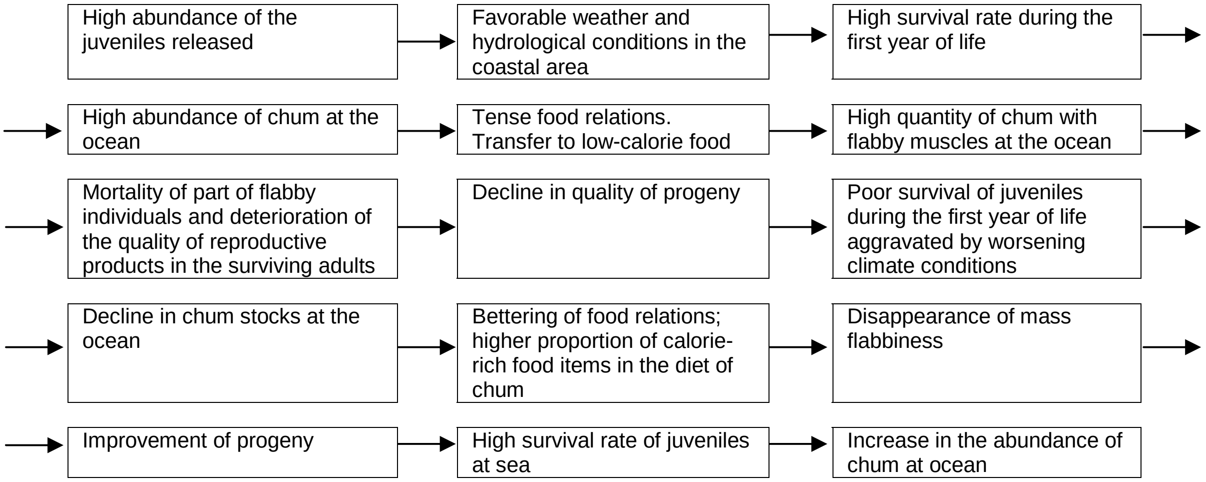
disintegration where a part of the fibrillar structure, sarcoplasm and nuclei remain. This group of muscular fibres is a potential source of rehabilitation processes. The third type of change was detected in the largest individuals where clear signs of muscular fibre regeneration were found.

We suggested that when chum salmon feed on jelly-like organisms, the expenditure of lipids and proteins is not compensated by ingestion, which causes destructive modifications and takes the form of muscle softening and changes in body shape. When feeding resumes the structure of muscular fibres is restored by regeneration, which was indeed observed in the largest fish. The process of destruction of the myofibrillar structure of the muscle fibres in chum salmon can, under favorable conditions, be replaced with their restoration. Therefore, worse feeding leads to the mobilization of reserve muscle proteins, and subsequently structural proteins. When protein products are severely limited during the growth of the fish, the destructive changes in the muscles will undoubtedly be so considerable that it will inevitably cause death. The mortality among a part of the abnormal specimens is essentially the realization of the regulatory mechanism in the period of great abundance of population (Lange and Klovatch in press).

The situation described is an example of population abundance control on the tissue level. In order to understand the mechanism of regulation we carried out a biochemical analysis of muscles, liver and gonads of normal and flabby female chum. We detected considerable differences between them in a number of characteristics. There were differing volumes of water, protein, lipids, carbohydrates and nucleic acids which points to a changed metabolism in organs and muscles. The metabolic changes included greater muscle energy reserve losses, and exhaustion of lipid reserves in the liver, offset by the carbohydrate component. The shift in metabolism allowed flabby females to form relatively valuable oocytes, in terms of their protein and lipid composition, at the expense of higher energy loss. However the RNA content, a matrix for synthesis of proteins, is lower in flabby fish oocytes than in healthy fish gonads, 0.209±0.047 and 0.441±0.0809% of dry weight, respectively. This causes low quality progeny from flabby chum females, and the lower survival rate is responsible for lowering the population abundance.

This is exactly what we observed in Japanese chum salmon. Although releases of juveniles from Japanese hatcheries have remained constant (about 2 billion) throughout the recent decades, the return of brood stock in recent years has been invariably going down. This picture indicates a higher rate of mortality in Japanese chum during the sea period of life as compared to the previous years. The recent decline in aggregations of large-sized chum in the ocean is another proof of the death of a significant part of fish occurring at the initial stage of the sea period of life. The self-regulation of the Japanese chum abundance is shown in Fig. 1.

Fig. 1. Scheme of Self-Regulation of Japan chum salmon abundance.



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Episodic Predation on Post-Smolt Atlantic Salmon (*Salmo salar*) by Northern Gannets (*Morus bassanus)*

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Keywords: Atlantic salmon, gannets, post-smolt predation, regime shift

Salmon population declines in both the Atlantic and Pacific Oceans appear to be related to the demise of juvenile salmon at sea (Hansen and Quinn 1998). Predation may play a role and could contribute to cumulative effects with other sources of mortality, e.g. aquaculture practices (Gross 1998), climate change (Welch et al. 2000), and pesticide use (Fairchild et al. 1999). It has proven difficult to document natural mortality of marine-phase salmon (Friedland 1998), and most predation on Atlantic salmon has been recorded in rivers and estuaries (Cairns 1998). We present evidence of varying levels of mortality among marine-phase, post-smolt Atlantic salmon in an analysis of a 25-year data set of the prey landed by northern gannets at a large breeding colony on Funk Island off the northeast coast of Newfoundland in the Northwest Atlantic. We explore the implications of these findings and recommend research strategies at gannet colonies that will enhance understanding of avian predation on post-smolt Atlantic salmon throughout the North Atlantic. We also indicate ways in which light-weight data loggers attached to avian predators can be used to enhance knowledge of the behavioral ecology and habitat use of marine phase Atlantic salmon.

Gannets are the largest marine birds that breed in the North Atlantic. They are opportunistic foragers that prey on a variety of pelagic fish and squid, including mackerel (*Scombrus scomber*), herring (*Clupea harengus*), Atlantic saury (*Scomberesox saurus*), short- and long-finned squid (*Illex illecebrosus* and *I. loligo*), capelin (*Mallotus villosus*) and sand lance (*Ammodytes* spp.) (Montevecchi and Myers 1997). During the course of this research from 1977 - 2001, there have been major changes in oceanographic conditions (Drinkwater 1996) and fisheries activities in the Northwest Atlantic (Carscadden et al. in press). A significant cold-water event in 1991 produced numerous changes in biological oceanography (e.g. Regehr and Montevecchi 1997). Gannets showed a marked dietary change from warm-water prey (mackerel, squid, saury) diets during the late 1970s and 1980s to cold-water prey (capelin, herring) through the 1990s. These dietary changes are indicative of larger-scale shifts in pelagic food webs (Montevecchi and Myers 1996).

Post-smolts are a minor dietary component for gannets during their breeding season. Through the late1970s and 1980s, salmon comprised on average < 1% (range = 0 to 2%) of the mass of the gannets' diet (Fig. 1). During the 1990s, however, consumption levels of salmon increased by an order of magnitude to more than 2.5% (range = 0 to 6%) of dietary mass. In 2001, the gannets' estimated level of consumption of salmon increased to more than 25% of the mass of the prey consumed. We attribute the decadal shifts in diet between the late 1970s/80s and the 1990s to biological responses to a physical oceanographic regime shift (Steele 1998) in the early 1990s in the Northwest Atlantic (Montevecchi and Myers 1996). The high level of predation on salmon by gannets in 2001 was attributed to variation associated with episodic avian predation and limited sampling effort. Predation on salmon is related to their presence and detection within avian foraging ranges (up to 180 km) around colonies (Fig. 2). Predation on salmon might increase when other large prey (e.g. mackerel) are absent or in reduced abundance within the gannets' foraging range. More intra-annual sampling over longer periods is needed at Funk Island and

Fig. 1. Atlantic salmon as a percentage of mass of prey eaten by northern gannets at the colony on Funk Island off northeastern Newfoundland in the Northwest Atlantic. Estimated percentage of the post-smolt biomass in the Northwest Atlantic preyed on by gannets from a bioenergetics model presented in Montevecchi et al. 2002.

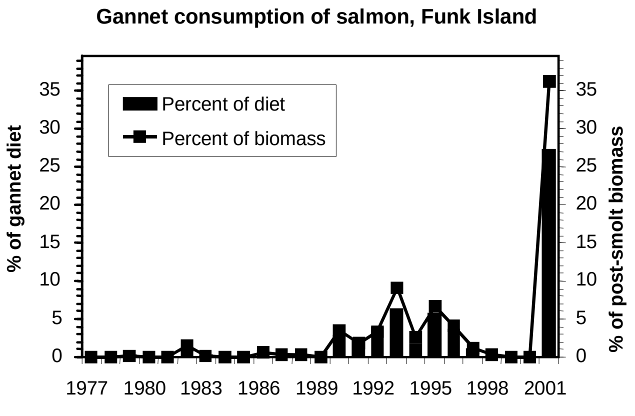

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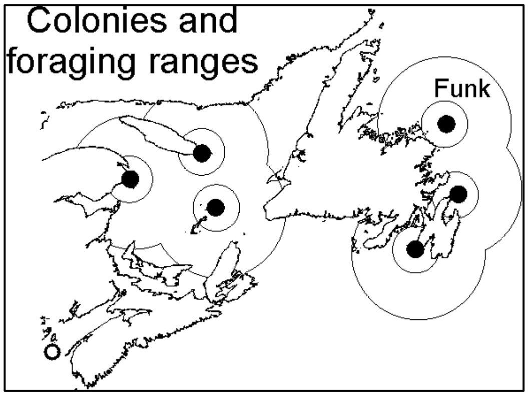
Fig. 2. Location of Funk Island and five other gannet colonies in North America. Circles around colonies represent average (60 km) and maximum (180 km) foraging ranges of gannets breeding in these colonies. Post-smolt Atlantic salmon from rivers in the Maritimes, New England and Newfoundland and Labrador pass through these foraging ranges.



especially at the other gannet colonies, referred to below, where dietary sampling is essentially nonexistent.

Predation by gannets may influence the population dynamics of North American Atlantic salmon. The migratory pathways of post-smolt Atlantic salmon pass through the foraging ranges of the six North American colonies of gannets, three of which are in the Gulf of St. Lawrence and three off eastern Newfoundland (Montevecchi et al. 1988; Reddin 1988; Fig. 2). Breeding populations of gannets at these colonies are increasing (Fig. 3).

Non-invasive, dietary sampling of gannets is an ecologically sound, cost-effective and efficient means of obtaining information about the natural mortality and behavioral ecology of marine-phase Atlantic salmon. There has, however, been very little sampling of gannet diets at colonies other than Funk Island, and even at Funk Island the intra-annual temporal extent of sampling is restricted. Systematic sampling of the diets of gannets at breeding colonies will greatly help quantify the predatory mortality that gannets impose on Atlantic salmon. It would be informative to expand dietary sampling regimes to gannet colonies in Europe, Norway (Montevecchi and Barrett 1987) and Iceland (Fig. 4). In view of recent findings that at least some Atlantic salmon of North American origin occur in the Northeast Atlantic (Tucker et al. 1999), such dietary sampling could be relevant for post-smolts from all origins.

Research with marine birds can also be used to collect data on the movements, behavior and ecology of Atlantic salmon at sea. Gannets equipped with stomach thermal sensors, externally attached compass recorders and miniaturized data loggers that record temperature and pressure (e.g. Benvenuti et al. 1998; Garthe et al. 2000) can also be used as sampling agents to collect information on the movements and behavioral ecology of post-smolt Atlantic salmon at sea. For example, the spatial and temporal movement patterns and thermal habitats of salmon can be derived from directional, water temperature and depth data obtained from gannets that catch salmon. Given the difficulty of tracking post-smolts at sea (Montevecchi et al. 1988; Ritter 1989), these research opportunities hold quite promising potential (e.g. Wilson et al. 2002).

Many people helped in field collections, especially Iain Stenhouse, Stefan Garthe, Gail Davoren, Nicholas Montevecchi, Janet Russell and Laura Dominguez who crewed our expeditions in the 1990s. Research was supported by grants from NSERC.

Fig. 3. Breeding populations of northern gannets in North America. Colonies (from top to bottom): Funk, Baccalieu, Cape St. Marys, Great Bird Rock, and Bonaventure Island. The population of gannets on Anticosti Island is too small to be plotted at this scale.

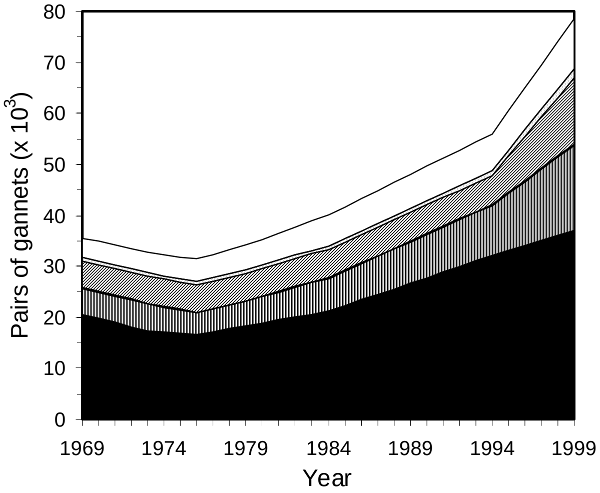
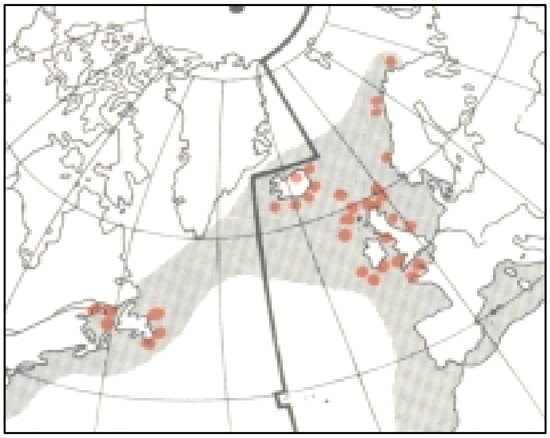


Fig. 4. Colonies of northern gannets throughout the North Atlantic Ocean.



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Impact of Predation by Salmon Sharks (*Lamna ditropis*) and Daggertooth (*Anotopterus nikparini*) on Pacific Salmon (*Oncorhynchus* spp.) Stocks in the North Pacific Ocean

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Keywords: Predation impact, salmon shark, daggertooth, salmon stocks, North Pacific.

Various species of fishes, seabirds and marine mammals are known as predators of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. However, there is little quantitative information about impact of predation by such predators on Pacific salmon populations. In this paper, we focus on predation by salmon sharks (*Lamna ditropis*) in oceanic offshore waters of the North Pacific Ocean and report on possible substantial impact of their predation on salmon stocks, based on the recent increase in salmon shark abundance on the high seas of the North Pacific Ocean. Also, we discuss predation impact by daggertooth (*Anotopterus nikparini*, formerly *A. pharao*) on salmon stocks, based on current information on their abundance and frequency of occurrence of slash marks on the lateral side of high-seas salmon caused by the attack of daggertooth.

We calculated annual CPUE (number/1000 tan of surface gillnets) of salmon sharks using the data collected by Japanese salmon research vessels that operated in the western and central North Pacific Ocean from 1972 to 2000. Salmon shark CPUE was low from 1984 to 1993 but increased sharply in 1996 and thereafter remained at a high level. A similar increase in salmon shark abundance has been reported from the Gulf of Alaska (Wright and Hulbert 2000). These results indicate that the North Pacific salmon shark population has recovered since the mid- or late 1990s. We estimate that the loss of high-seas salmon due to salmon shark predation was approximately $73\text{-}146\times10^6$ salmon ($113\text{-}226\times10^3$ metric tons) in 1989 when salmon shark CPUE was low (Nagasawa 1998). Thus, there is a possibility that the current increase in salmon shark abundance in the whole region of the North Pacific has increased mortality of salmon during the high-seas phase of the life history.

Daggertooth is a species that has been recently noticed as a predator of offshore salmon (Welch et al. 1991; Radchenko and Semenchenko 1996). Current Russian surface trawl surveys indicate that the abundance of daggertooth is not low in the western North Pacific and that it feeds on large numbers of salmon (Melnikov 1997). Slash marks from daggertooths are not frequently but sometimes found on salmon from high seas and coastal waters. The incidence of slash marks on salmon is usually low, ranging from less than 1% to 4 or 5%, in offshore waters (Ishida et al. 1991) but slightly higher (up to 12%) in coastal waters (Gilhousen 1989; Henderson et al. 1990). The species is widely distributed in offshore waters of the North Pacific Ocean (Nagasawa 1992), and its abundance seems to have been increasing since the early 1990's. Based on this information, we can regard daggertooth as significant salmon predators as well.

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Paleoclimate Variability in Ocean Conditions and the Production of North American Atlantic Salmon

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Keywords: Multidecadal climate cycles, thermohaline circulation, regime shifts, winter salmon mortality

Climate regime shifts related to changes in circulation variations, nutrient upwelling and productivity have been shown to influence the survival success of young salmon at sea in the North Pacific (Mantua et al. 1997; Beamish et al. 1999). A similar relationship to climate and salmon production in the North Atlantic is less clear. While the ecology of young European salmon appears to be correlated with climate (Friedland et al. 2000) the only climatic link to North American Atlantic salmon is shown between winter thermal habitat and catch (Friedland et al. 1993). However, the relationship between the season in which this climatic link occurs suggests that the precise mechanism controlling salmon survival remains unknown (Friedland et al. 1993).

Principal Component Analysis of global multiproxy paleoclimate datasets and instrumental records reveal a 50–75 year multidecadal climate oscillation centered over the North Atlantic (Mann et al. 1998). The original dataset examined in this reconstruction (Mann et al. 1998) was compiled from 1,082 nearly continuous land air/sea surface instrumental temperature grid points from 1902 onward. An extensive set of proxy data was then calibrated against the records, extending the reconstruction over the past millennium. The multidecadal oscillation is best described by the fifth eigenvector of reconstructed global climate and is observed back to 1650.

Although observational data is lacking in spatial coverage, climate model simulations using two independent, naturally forced integrations of the Geophysical Fluid Dynamics Laboratory (GFDL) coupled ocean-atmosphere model, reproduce the observed multidecadal patterns of variability (Delworth and Mann 2000). They further demonstrate that in both the model and observational data, sea surface temperature (SST) appears to carry the signal. The simulations suggest that the observed multidecadal fluctuations are driven by variations in the intensity of the Thermohaline circulation (THC) (Delworth et al. 1997). An intensified THC increases northward warm water transport and is associated with reduced cold, fresh water export via the East Greenland Current. These changes are also related to large-scale salinity variations in the Arctic Ocean, suggesting interactions between the Arctic and the North Atlantic are forcing the multidecadal oscillation (Delworth et al. 1997).

North American commercial salmon landings, used in this study as a measure of stock production since 1908, appear to follow a similar multidecadal cycle (Fig. 1). This suggests that large-scale THC changes have played an important role in altering salmon abundance over the past century, and that salmon production is higher when SSTs in the North Atlantic are anomalously cold. The connection is interesting as the Labrador Sea, an important feeding ground in the late summer and early autumn for salmon, is also the site of deep-water convection driving the THC. Further evidence for a multidecadal climate signal in this region is indicated by tree-ring climate reconstructions from coastal Labrador (D’Arrigo et al. 1996).

In this study, an updated version of the Kaplan et al. (1998) monthly SST anomaly (SSTA) reanalysis dataset is examined for the Northwest Atlantic region (40–65°N, 70–40°W). Thirty, monthly, 5°x5° SSTA data grid point locations are examined over the last 100 years and three, ten-year average, SSTA maps are used to show the ocean climate conditions corresponding to the high-low-high catches for 1920–30, 1945–55 and 1965–75, respectively (Fig. 2). The cold-warm-cold multidecadal cycle is clearly evident from the approximately 0.5°C SST change between these three periods, supporting the inverse relationship to salmon production and Northwest Atlantic SSTs.

An attempt to isolate the catch signal to a specific location and time of year is made by using monthly SSTA data for each grid point and statistically comparing it to the North American commercial salmon catch since 1908. The highest correlation is obtained from the southern, Northwest Atlantic for the January prior to the salmon going to sea. To the north, in the Labrador Sea, SSTAs throughout the year show low correlations with salmon production. Taking the highest January SSTA and catch correlation values reveals a 10°x10° box located on and to the east of the Scotian Shelf (40–50°N, 60–50°W). We apply a ten-year running mean to the combined SSTA signal, taken from these four data point locations, and reproduce the cold-warm-cold signal of the multidecadal

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Fig. 1. North American commercial salmon landings (1908–1991) [black line] shown against the reconstructed principal component (RPC) 5 from Mann et al. (1998) [grey line] indicating approximately 300 years of multidecadal variability. The RPC5 is negatively correlated with salmon production.

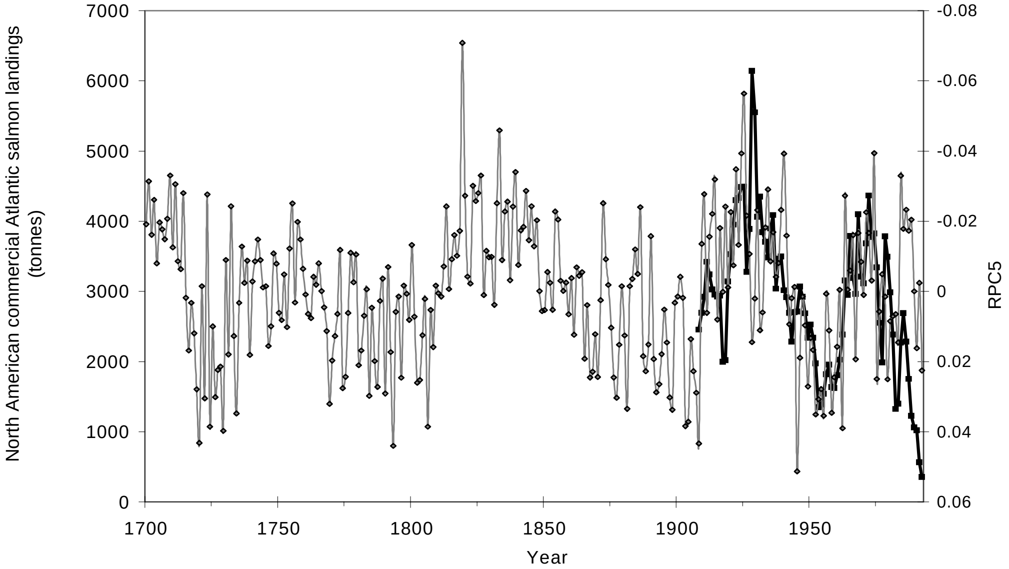
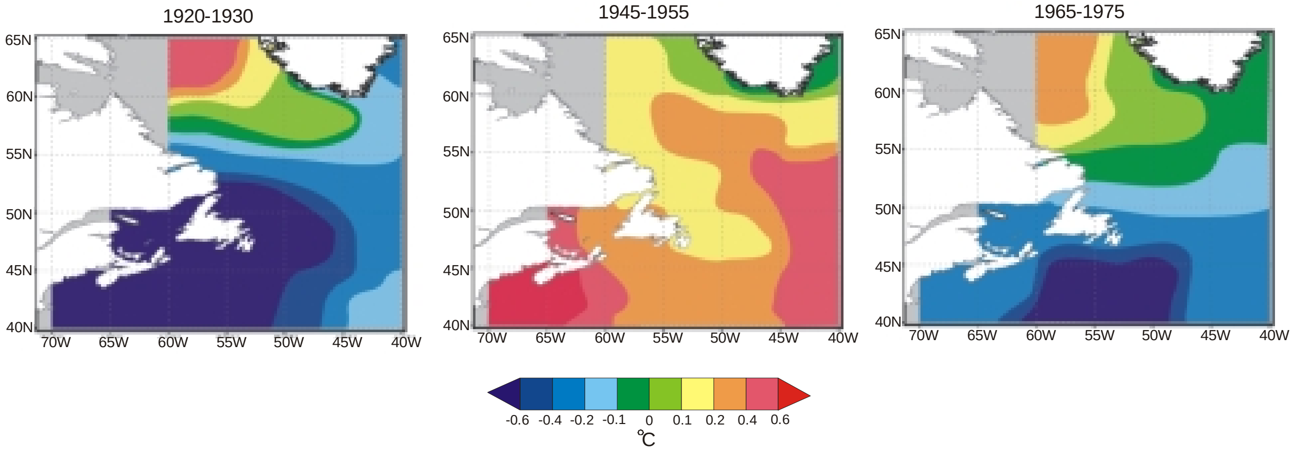


Fig. 2. 10-year average sea surface temperature anomalies showing the cold-warm-cold phase of the multidecadal cycle. The maps are drawn for time periods corresponding to high-low-high salmon production. The pattern shows that catch is negatively correlated with SST in the Northwest Atlantic.



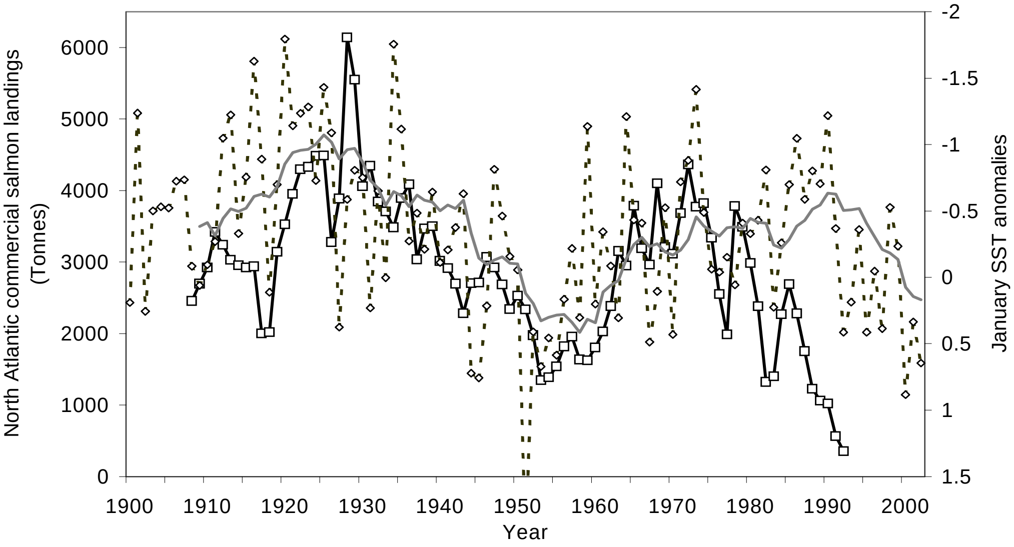
oscillation produced by principal component 5 over the past century. The correlation shows that salmon landings decrease (increase) when winter SSTs on and to the east of the Scotian Shelf are anomalously warm (cold) (Fig.3).

The results from this study suggest that large-scale multidecadal Northern hemisphere climate changes over the North Atlantic are negatively correlated with salmon production. The high correlation implies that climatic regime shifts, perhaps similar to those affecting North Pacific salmon (Mantua et al. 1997; Beamish et al. 1999) are also occurring in the North Atlantic. We can speculate that THC driven variations in the Greenland current and northward extent of warm water are altering the long-term climate of this region. However, a lack of investigation into changes in primary productivity and nutrient upwelling suggests we are still far from finding an oceanic link between the observed climate changes and those seen in salmon abundance.

Further investigation has revealed that the multidecadal signal can be traced over one hundred years of Northwest Atlantic SSTs, and can be isolated to a specific region in the winter months. This further supports the contention that winter climate conditions are affecting North American Atlantic salmon. The issue of an underlying mechanism is also advanced, as the temperature effect is no longer distant to the salmon juvenile rearing areas (Friedland et al. 1993), providing support for a freshwater winter mortality. Despite this, an oceanic overwintering influence cannot be ignored until the statistical correlations are investigated further.

The long-term climate regime shifts observed in this study bring us a step closer to understanding how climate controls salmon survival. However, the observed January correlation does not exist for the past few decades, as shown by a downward trend in salmon production in the late 1980s, despite declining SSTs (Fig. 3). For this location the trend is suggestive that recent declines in salmon abundance are not completely climate-related. However, the findings from this limited domain highlight our lack of understanding of the impact of climate on salmon and raise further concerns over the effect of future climate stress and its impact on salmonid populations.

Fig. 3. North American commercial salmon landings [black line] shown against January SST anomalies located at 40–50'N, 60–50'W [dashed black line]. A 10-year running average is drawn through the SST data [solid grey line]. Salmon production shows a strong negative correlation with SST anomalies from 1908–1980. The decline in salmon production in the 1980s is not consistent with the negative relationship observed prior to this.



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Long-term Trends in Annual Bristol Bay Sockeye Salmon Scale Growth at Sea in Relation to Sockeye Abundance and Environmental Trends, 1955–2000

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Keywords: Density-dependent growth, survival, scale, sockeye salmon, Bristol Bay, climate shift

Pacific salmon populations rearing in the North Pacific Ocean and Bering Sea increased substantially after the marine climate shift during the mid-1970s. Density-dependent growth has been observed among many stocks of Pacific salmon and it raises questions about the relationship between salmon growth at sea and salmon survival and production. For example, after the mid-1970s, did salmon growth decline during each stage of ocean life in response to greater salmon abundance, or did growth increase during certain periods of ocean life most critical to survival, followed by reduced growth during other periods when growth may be less important to survival?

We measured annual marine scale growth of Bristol Bay and central Alaska sockeye salmon, 1955 to 2000, in order to test whether annual salmon growth at sea was positively or negatively associated with the large increase in salmon abundance that began in the mid-1970s (see Hagen et al. 2001; Davis et al. 1990 for scale methods). Bristol Bay and central Alaska sockeye salmon runs more than doubled after the mid-1970s, a trend that was common to many stocks.

After the mid-1970s, sockeye salmon scale growth tended to be above average during the first two years at sea. This pattern was generally consistent among Kvichak age-2.2 and age-2.3 sockeye salmon (Figs. 1 and 2), but was especially pronounced among Chignik sockeye salmon (Fig. 3). During the first year at sea, Kvichak sockeye rear in the Bering Sea whereas Chignik sockeye rear in the North Pacific Ocean, indicating early marine growth was generally favorable in both regions after the mid-1970s. One exception to the trend was the somewhat above average growth of Kvichak age-2.2 sockeye salmon during the second year at sea beginning in the mid-1960s.

After the mid-1970s, scale growth of ocean age-3 Kvichak sockeye salmon tended to be below average during the third year at sea (Fig. 2), especially during odd-numbered years. Chignik scale growth during the third year at sea was variable due to the odd/even year pattern but somewhat below average after the mid-1970s (Fig. 3). Chignik salmon scale growth during the homeward migration was below average after the mid-1970s. These growth trends were opposite of that during the first two years at sea.

Scale growth during the second and third years at sea show an odd/even-year pattern that is inversely related to Asian pink salmon abundance (Ruggerone et al. unpublished analysis). For example, multivariate time series analysis indicated scale growth during the second year at sea (SW2) was negatively related to harvest of Eastern Kamchatka pink salmon (1,000 mt) and positively related to winter sea-surface temperature in the North Pacific Ocean (Fig. 4).

Previous analyses indicated adult length of Bristol Bay sockeye salmon was inversely related to adult sockeye salmon run size (Rogers and Ruggerone 1993). A new analysis of this relationship indicates Bristol Bay sockeye length also decreased in years of large Asian pink salmon runs during the previous year. However, salmon size was greater at a given salmon abundance during 1977–2000 compared with 1958–1976. These effects on length of female age-1.3 sockeye salmon are shown in the following multivariate time series equation (Fig. 5; Ruggerone et al. unpublished analysis):

$$\text{Length} = 571.7 - 0.339(\textit{sockeye run}) + 8.76(\textit{period};\ 0 \text{ or } 1) - 0.067(\textit{pink run},\ \text{y-1}) + \varepsilon$$

Bristol Bay sockeye salmon runs tended to be relatively low when scale growth during the first and second years at sea was below average. Sockeye runs increased when marine scale growth increased beyond average scale growth (Fig. 6), suggesting that greater growth during both the first and second years at sea were associated with greater salmon survival.

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This analysis suggests sockeye salmon growth during the first two years at sea was an important factor leading to the large abundance of western and central Alaska sockeye salmon since the mid-1970s. Although density-dependent growth may occur during early marine life, density-dependent growth is most apparent in the later stages of life when reduced growth likely has less effect on survival.

Fig. 1. Age-2.3 Kvichak sockeye salmon growth during first, second and third years at sea.

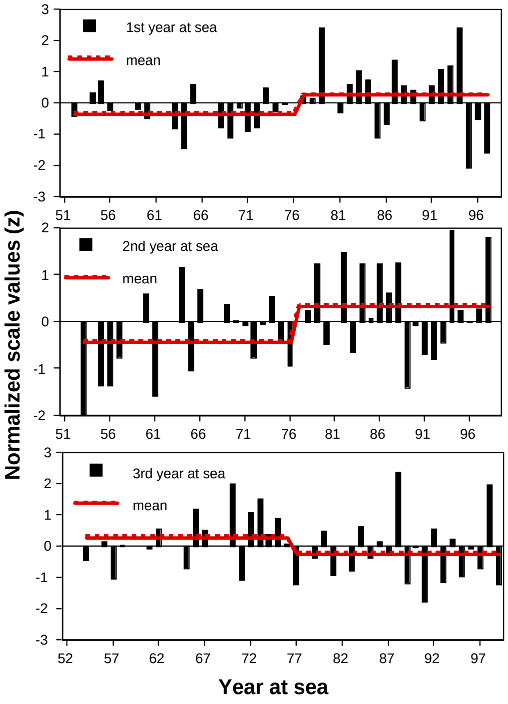


Fig. 3. Chignik sockeye salmon growth during first, second, third years at sea and during homeward migration.

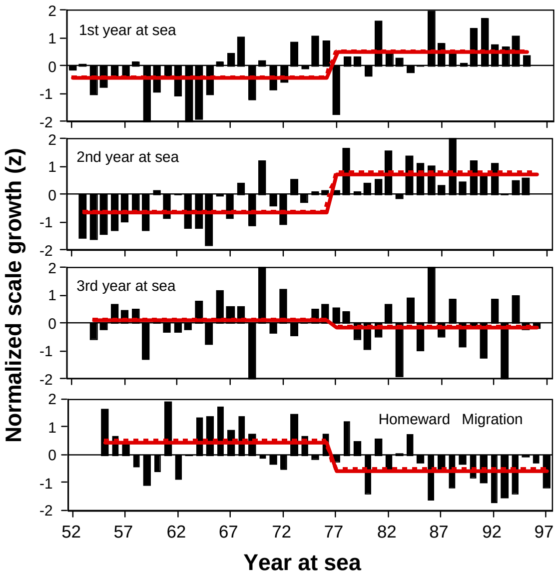


Fig. 2. Age-2.2 Kvichak sockeye salmon growth during first and second years at sea.

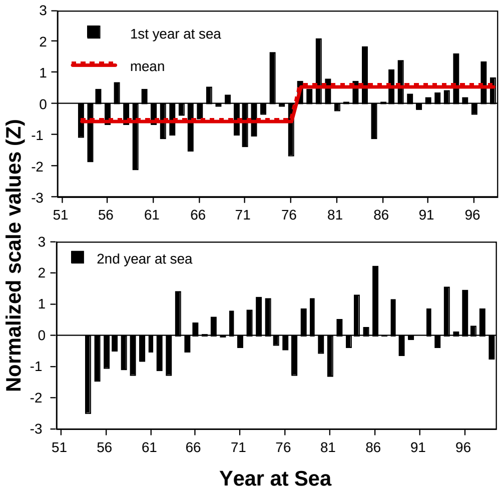


Fig. 4. Multivariate time series corrected plots showing the relationship between female age-1.3 sockeye length and Bristol Bay sockeye run, Asian pink salmon run (y-1), and time period.

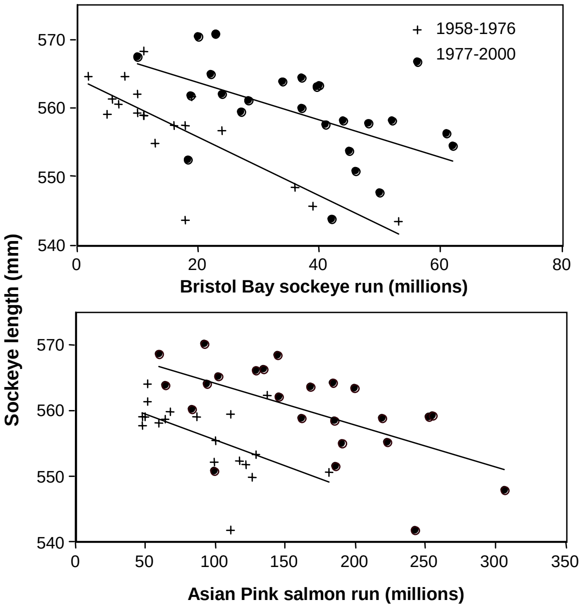


Fig. 5. Adult returns of sockeye salmon to Bristol Bay in relation to scale growth of age-2.2 Kvichak sockeye salmon during first two years at sea (lowess curve fit).

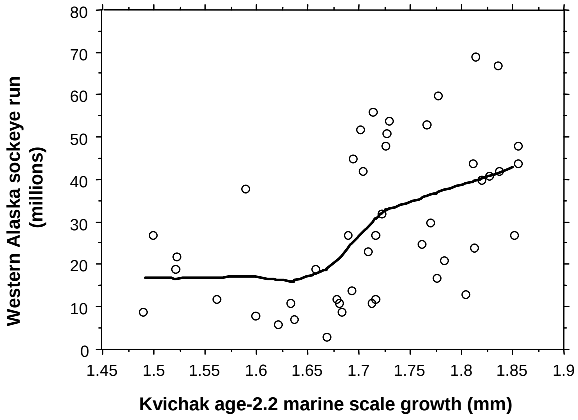
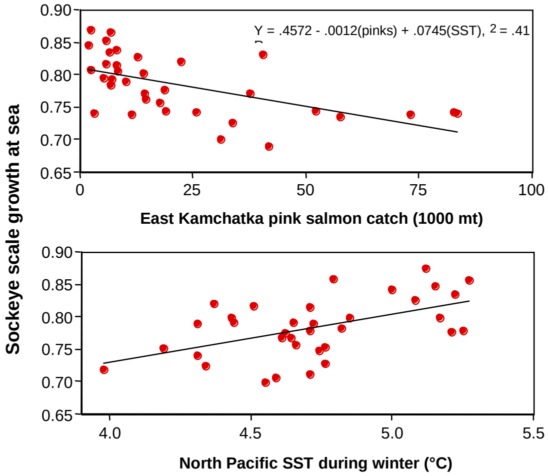


Fig. 6. Partial residual plots showing the effect of eastern Kamchatka pink salmon and North Pacific Ocean winter sea-surface temperature (°C) on Kvichak sockeye salmon scale growth during second year at sea.



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Bioenergetic Response of Coho Salmon to Climate Change

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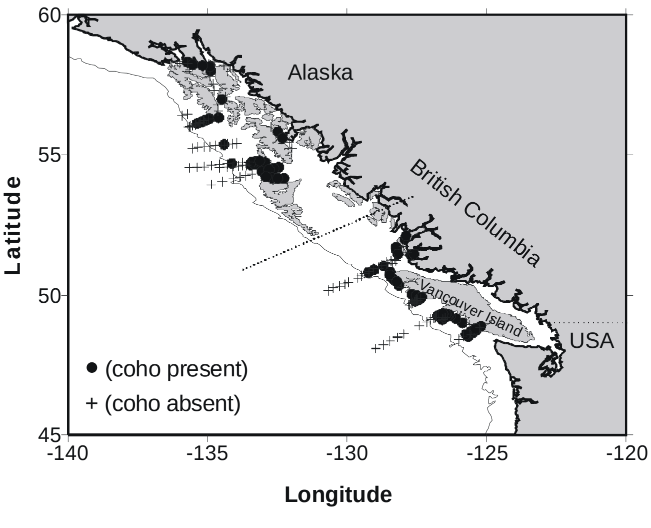
Keywords: Growth, food consumption, metabolic rates, bioenergetics, temperature, climate change, salmon, North Pacific Ocean

The marine survival and production of Pacific salmon and steelhead trout (*Oncorhynchus spp.*) have decreased tremendously during the last decade in British Columbia (BC), Washington, Oregon, and California (Hare et al. 1999; Beamish et al. 2000; Welch et al. 2000). Fisheries have been closed, and a number of stocks have been added to the endangered species list in the United States. This period was also the warmest on record. However, it is unclear how sea surface temperature (SST) influences the survival and production of salmon. Higher temperature may increase the metabolic rates of salmon, and hence, reduce the energy available for growth (Pyper and Peterman 1999). As mortality rates tend to be larger in small fish (Lorenzen 1996), a reduction in growth rate may thus reduce the survival of salmon. Warmer SST may also produce poorer ocean conditions for salmon growth through bottom-up processes. As warm water tends to be lighter, an increase in SST may increase the stability of the water column in the mixed layer and may prevent or reduce the upwelling of deep nutrient-rich water, and consequently, may decrease both primary and secondary productivity (Gargett 1997). Thus, in warmer years, salmon may have less food and reduced growth.

The objectives of this study were to assess how the growth rates of juvenile salmon were influenced by oceanographic and climatic conditions. We examined the effects of SST on food consumption rates of salmon. We also assessed the effects of prey quality and SST on salmon growth.

We collected juvenile coho salmon (*Oncorhynchus kisutch*) off the west coast of BC using a rope trawl and the *WE Ricker* in the spring (May–June), summer (July–August), and fall (October–November) of 1998, 1999, and 2000 (Fig. 1). For the purpose of this study, the area north of latitude 52°N was defined as Northern BC, while the area west of Vancouver Island (47–51°N) was defined as Southern BC (Fig. 1). Water temperature profiles were usually obtained before the net was deployed using a CTD. Each net tow consisted of towing the net at the surface (0–20 m) for 30 minutes at 5 knots. Up to 30 juvenile coho salmon were randomly selected from each net tow. Fork length and mass of coho were determined on board the research vessel. Otoliths and scales were removed for age determination. A skin sample was also taken from the operculum using a hole punch and preserved in 70% ethanol for DNA stock identification. Whole fish were then frozen individually at minus 20°C in pre-identified plastic bags for subsequent analyses. Energy density was determined on a subset of coho using a bomb calorimeter. Food consumption rates of juvenile coho salmon were estimated using a mass balance model of stable cesium (^{133}Cs) following the procedures presented in Rowan and Rasmussen (1996) and Trudel et al. (2000). ^{133}Cs concentration in salmon caught in the spring and fall and their food was determined by Inductively-Coupled Plasma Mass Spectroscopy.

Fig. 1. Sampling locations during the month of October 1998, 1999, and 2000.



Sea surface temperature (SST) was higher in 1998 by about 2–3°C due to a warm El Niño that was followed by a cool La Niña in 1999 and 2000.

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This El Niño corresponded to one of the strongest ever recorded. Surface nutrient concentrations were also much lower in 1998 than 1999 (Whitney and Welch in press). Nitrates were actually depleted at the surface during the summer of 1998 (Whitney and Welch in press), suggesting that primary productivity was reduced during that period.

Coho salmon were half the size and also had lower energy reserves in southern BC than in Alaska in October 1998, but not in 1999–2000 (Fig. 2–3). Thus, coho salmon collected in Southern BC in 1998 were in poorer condition, and had lower growth rates than those from Northern BC, but were similar in both regions after the 1997–98 El Niño. Food consumption rates of juvenile coho salmon averaged about 10% of their body weight per day and did not vary significantly between regions or years (Fig. 4). These estimates represent about 75% of their maximum physiological capacity, and are among the highest values reported in the literature for any wild fish (Trudel unpublished data). Thus, there are no indications that coho salmon were starving, despite ocean conditions being less favourable for salmon growth in Southern BC in 1998. These results also indicates that the growth differences observed in this study were not related to feeding rate differences.

To assess the potential effects of prey quality and SST on the growth of juvenile coho salmon, we used a bioenergetic model in conjunction with the feeding rates derived in this study. We used prey with low (700 cal/g) and high (900 cal/g) quality in these simulations. These values are within the range of published energy densities for zooplankton (Davis et al. 1998). SST was modelled using the temperature cycle provided in Brett (1983). These simulations were also performed by increasing the daily temperature by 3°C to simulate the effects of increased SST on salmon. We assumed that coho smolts entered the ocean weighing 10 g on May 15 (Sandercock 1991), and calculated their growth until October 15 of the same year.

Fig. 2. Size frequency distribution of coho salmon caught in Southern BC (gray bars) and Northern BC (black bars) in October 1998, 1999, 2000. Here, frequency is expressed as a percent of the total catch in a given area.

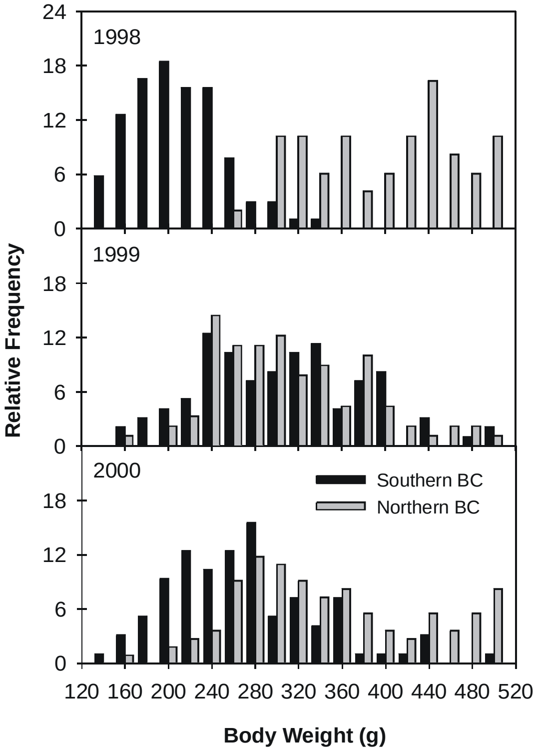


Fig. 3. Caloric contents (1 cal = 4.186 J) in coho salmon collected Southern BC (gray bars) and Northern BC (black bars) in October 1998, 1999, 2000. The error bars represent the 95% CI.

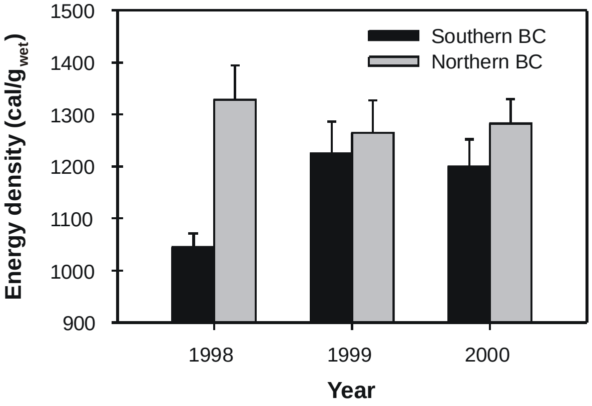


Fig. 4. Food consumption rates of juvenile coho during their first summer (May–October) in the ocean in 1998, 1999, 2000. The error bars represent the 95% CI and were determined using Monte Carlo simulations.

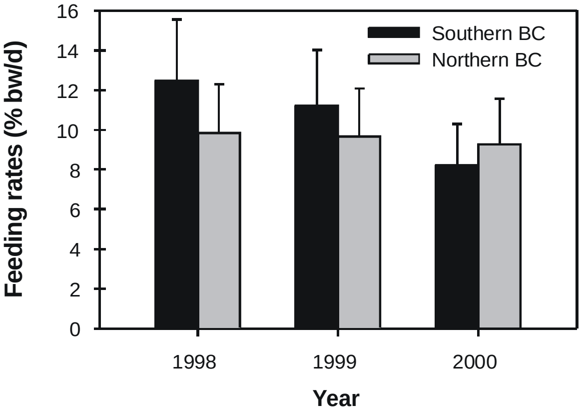
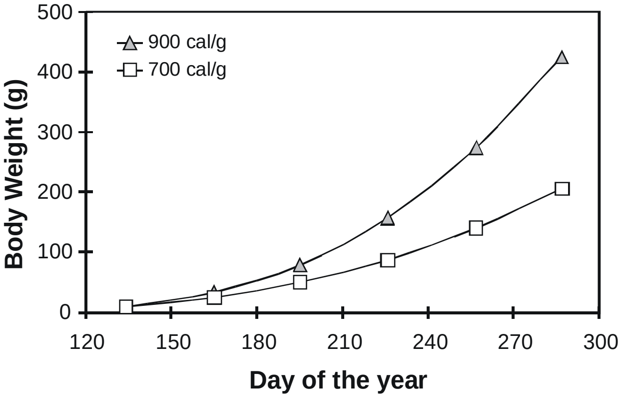


Fig. 5. Growth rates of coho salmon predicted using prey of low (700 cal/g_{wet}) and high quality (900 cal/g_{wet}).



Coho salmon reached a size of about 200 g and 400 g when they were feeding on prey of low and high quality, respectively (Fig. 5). This corresponds quite well to the mean size of coho salmon collected of Southern and Northern BC in 1998. Increasing SST by 3°C decreased the final size by only 10 g, suggesting that the direct effects of SST on salmon growth were negligible. Our analyses thus indicate that the effects of SST on salmon growth is mediated by changes in prey community structure and quality rather than by changes in food consumption and metabolic rates. These results also illustrate the importance of measuring bioenergetic parameters *in situ* for better understanding the effects of climate change on fish populations.

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Potential Interrelationships between Patterns of Migration and Marine Survival in Pacific Salmon

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Keywords: Pacific salmon, migration, distribution

There is a 10-fold difference in coho marine survival between different regions of the West Coast of North America. Survival is lowest in the south (Washington-Oregon) and highest in the north (Alaska). Salmon swimming through regions of different survival should have different fates, with the poorest-performing stocks spending the longest period in areas of poor survival, and the best-performing stocks spending the least amount of time in these areas. Permanent shelf-resident stocks would presumably have the worst productivity of all. However, the migration route and foraging grounds of most stocks of Pacific salmon are not well known.

We conducted multiple ocean surveys each year since 1995 to examine ocean growth, migration patterns, and expected survival of juvenile salmon along the West Coast from southern Vancouver Island to the Aleutians. The results show that juvenile salmon appear to remain strictly on the continental shelf until at least the start of winter, and that stocks migrating to the offshore do so by first swimming along the shelf to the Aleutian Islands before eventually moving offshore (Fig. 1). Figure 2 (A) shows a close-up view of the composite salmon catches (all species) from all October surveys off the West Coast (British Columbia to South East Alaska). Figure 2 (B) shows the distribution off the Alaska Peninsula in November–December 1997. These results indicate that juveniles were still on the continental shelf in early winter all the way to the Aleutians. Note the long multi-day transect moving in towards Kodiak from the offshore, and the abrupt occurrence of juvenile salmon in the catches at the shelf edge. This transect was made in late November, long after the juveniles were originally suggested to leave the shelf (Hartt and Dell 1986).

Large numbers of tagged juvenile salmon (all species) released from hatcheries (▲) have been caught on our surveys (●). These animals all moved north and west along the continental shelf (Fig 3). Although we have shown the great circle (minimum distance) lines connecting river mouths to recovery sites, the distributional studies demonstrate that the salmon must have navigated to remain strictly over the continental shelf despite this not being the shortest migration path.

Captures of CWT & PIT-tagged chinook and coho allow us to calculate migration rates (Fig. 4). Salmon caught in the summer exhibit a wide range of swimming speeds, with some moving at up to 2 body lengths/sec for months. By autumn (lower panels), migration rates are much slower, reflecting the fact that rapidly moving juveniles have travelled thousands of kilometers over the summer, and are thus no longer present in our study area. This suggest that there are at least two specific migration behaviours evident, with the slow speeds for fall-caught fish suggesting that these are animals taking up shelf-residence in particular areas of the shelf. This would expose them to different ocean conditions in different regions of the shelf (See Trudel et al. this volume).

Our research indicates that juvenile salmon undertake rapid long-distance migrations that are highly directed to maintain them over the continental shelf.

Fig. 1. Distribution of all positive juvenile salmon catches (●) from fall sampling efforts (1995 to present). Locations where no salmon were caught are indicated by a cross (x). The results show that juvenile salmon remain within the shelf ecosystem much longer than previously suspected. The black line shows the position of the shelf edge (1,000 m isobath). Note that no salmon were caught off the shelf.

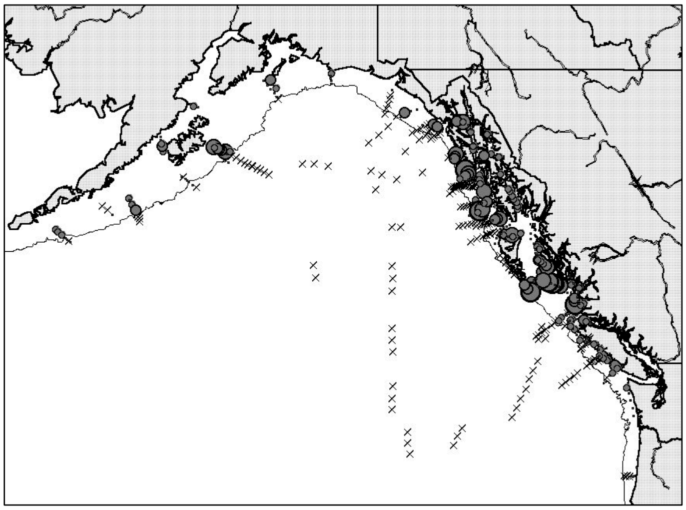

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Fig. 2. Distribution of juvenile salmon (all species combined) from Autumn and early Winter surveys, all years combined. (A) Juvenile salmon catches from all October surveys combined along the British Columbia and SE Alaska coastal zones. The 1,000 m isobath, delimiting the shelf break, is indicated. Note that all salmon catches were confined to the continental shelf. (B). A similar example but concentrating on a single early winter cruise to south of the Alaska Peninsula in early winter. Note the abrupt reoccurrence of juvenile salmon once the shelf break is reached SE of Kodiak Island (end of November). The subsequent survey lines in early December found no evidence for juvenile salmon leaving the shelf except on the far west survey line on December 7th, when 10% of the salmon catch was caught off shelf. The December 7th sampling is the only significant evidence we have obtained for off-shelf distribution of juvenile Pacific salmon, suggesting that most salmon stocks migrate along the shelf to the Aleutian Islands before moving to the offshore (See Fig. 3).

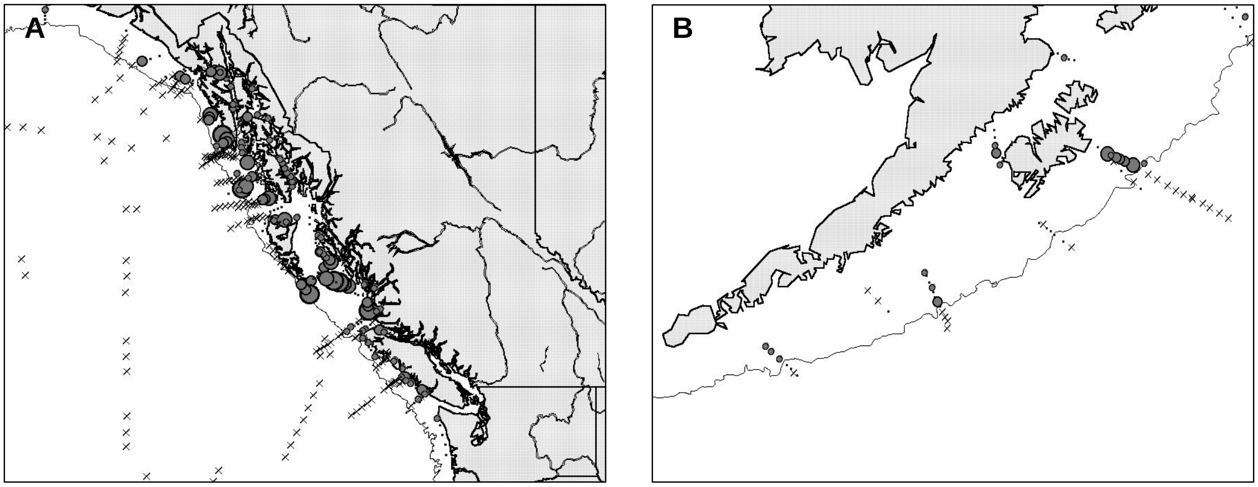


Fig. 3. Examples of long-distance recoveries of tagged Pacific salmon. Note the significant movements of some animals; chinook from the Sacramento Valley, California, have been caught off British Columbia, as have substantial numbers of endangered Snake R. chinook. Migration speeds for the Snake River chinook are the fastest we have recorded to date (>2BL/sec; see below). Great circle routes are drawn to show the relationship between release and recovery positions, but as the distribution of juvenile salmon catches makes clear, the animals do not leave the shelf ecosystem and must have therefore taken a migration path that maintained them over the continental shelf. The results suggest that juvenile coho may undertake larger-scale movements than chinook, since coho were caught farther away from their home streams, yet both species were caught on the same surveys.

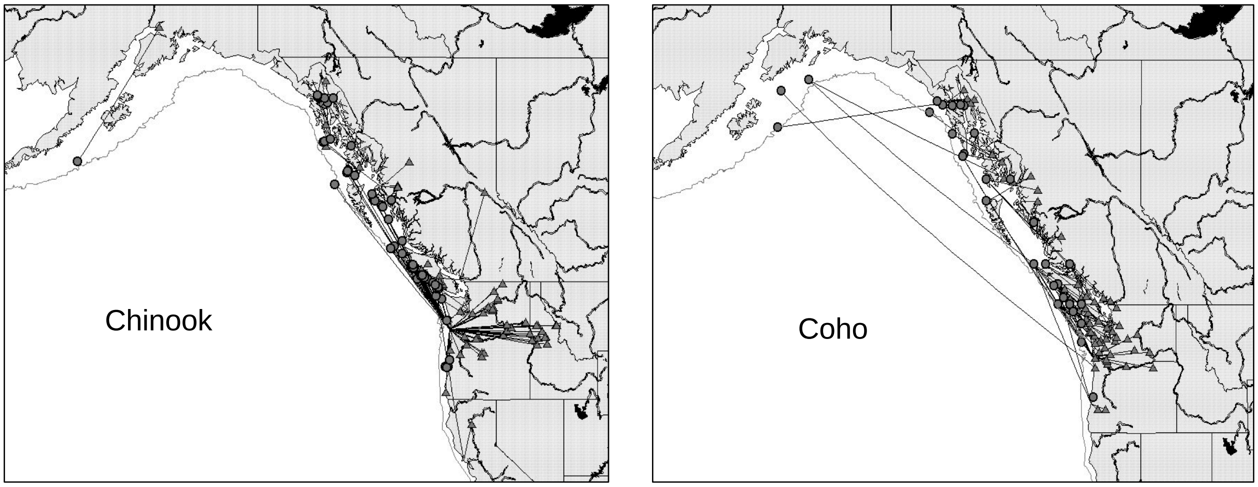
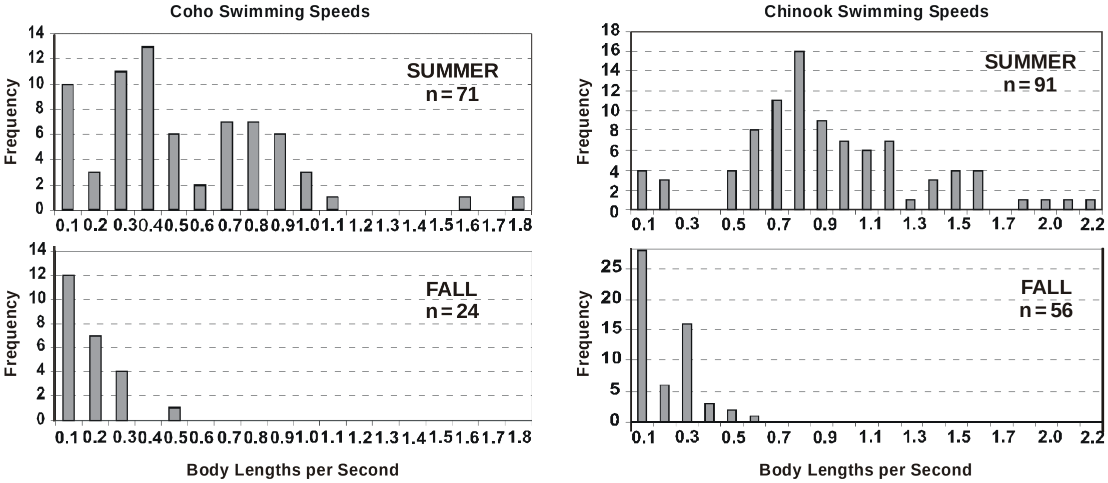


Fig. 4. Comparison of coho and chinook salmon swimming speeds, calculated from all CWT or PIT-tagged salmon returns (1995–2001). The top row shows the minimum possible swimming speed, calculated on the assumption that each animal remained over the shelf but followed the shortest shelf-bound path to the capture location.



There is evidence from tag recoveries that some coho and chinook move rapidly to the Aleutians, while we speculate that specific stocks remain in the coastal zone as long-term over-winter residents. These patterns of movement, interacting with regional differences in climate-induced carrying capacity, may explain the peculiar patterns of salmon productivity along the West Coast of North America that have been observed in recent years.

Our conclusions are based on the overall distribution of juvenile salmon catches relative to the shelf edge, and the observation that tagged hatchery smolts can in relatively short time periods move long distances before capture. Details of the movement patterns of individual animals in between the release and recovery positions are needed to address questions concerning possible stock-specific patterns of behaviour. A critical issue will be to develop methods to track the migration of individual stocks of salmon, and to then develop a predictive understanding of which stock groupings may be influenced most significantly by shifts in ocean climate. Because the continental shelf off the West Coast of North America is so narrow relative to its length (only 30–40 kms wide relative to a 4,000 km long migration path), this raises the possibility of developing an acoustic tracking array consisting of multiple cross-shelf listening lines. Such an array could provide a wealth of detail concerning the movement patterns of individual salmon over many months or years on the continental shelf.

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Rearing Origin and Distribution of Atlantic Salmon Post-Smolts in Penobscot Bay and the Near-shore Waters of the Gulf of Maine, USA

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Keywords: Atlantic salmon, post-smolt, rearing origin, mortality, trawl

Wild Atlantic salmon populations on the east coast of the United States have failed to recover despite sustained efforts to improve rearing conditions, reduce high seas fishing mortality and supplement populations with hatchery fish. Currently, differential mortality of cohorts and life history stages from factors such as competition, predation, pollution and disease is poorly understood. The smolting process (migration and transition from freshwater to marine environments) has been identified as a critical period and a potential population bottleneck for Atlantic salmon and other salmonids. The success of the transition to marine habitats by emigrating Atlantic salmon smolts is poorly understood because attempts to sample and monitor smolts in estuarine and near-shore marine areas have been extremely difficult.

The Penobscot River (Maine, USA) has hosted 75% of documented adult returns to East Coast US Rivers since 1986. Atlantic salmon smolts from the Penobscot River originate from natural spawning by adult escapement and hatchery releases of fry, parr and age 1+ smolts. The relative contribution of each source to smolt populations is unknown, but scale analyses indicate that adults originating from age 1 and 2-year smolt stocking have represented in excess of 85% of returning adults in recent years. The survival rates of hatchery smolts have declined by 10-fold over the past 15 years, resulting in sharp declines in adult returns, and has heightened concerns about progress on restoration goals. To provide future direction for coordinated management strategies, basic questions about the riverine, estuarine, and marine survival of each cohort need to be addressed. Partitioning of riverine, estuarine and marine mortality sources for smolts and post-smolts represents an important step that may allow for the identification of population bottlenecks.

In an effort to track individual cohorts with differing in-river rearing times, NOAA Fisheries has developed a coordinated research program focused on hatchery and naturally reared Atlantic salmon smolts in the Penobscot watershed. This coordinated program involves the elastomer marking and release of 170,000–180,000 age 1+ hatchery smolts annually, a rotary screw trap monitoring program at the head of tide, an estuarine and near-shore marine trawl survey program, and recovery of elastomer marks from returning adults trapped at a head-of-tide dam. In May 2001, NOAA Fisheries implemented a pair-trawl sampling approach to the capture and live release of post-smolts based on technology developed by investigators in Norway and Canada. We pair-trawled a modified mid-water trawl with an aluminum live box at the cod end throughout Penobscot Bay and near-shore waters of the Gulf of Maine. Atlantic salmon post-smolts were captured at 49 of 61 stations (80%) sampled during the survey and a total of 1458 Atlantic salmon post-smolts were captured. Recovery of 355 elastomer-marked fish allowed for evaluation of the relative contribution of different hatchery release groups to the post-smolt population. Analysis of scale samples indicates that post-smolt populations were dominated by age 1+ hatchery smolts (97%) and few naturally reared fish (smolts originating from natural spawning or fry and parr releases) were detected. However, the proportion of naturally reared fish increased in samples collected further offshore, suggesting that either naturally reared fish were migrating earlier, were moving more quickly to offshore waters, or that differential mortality was occurring between hatchery and naturally reared fish. Hatchery smolts are easily distinguished from naturally reared smolts, but a potentially confounding factor is the difficulty in distinguishing smolts originating from natural spawning from smolts surviving from fry and parr releases. Expansion of marking programs and refined image analysis approaches are being utilized to improve identification of smolts from these sources.

Effects from pollution, river acidification and other sources of physiological stress may negatively affect the timing of physiological transitions required to successfully osmoregulate in saltwater. The release of batch-marked smolts at different times and at different locations in the river is allowing for analysis of migration timing and measurement of enzymatic indicators of physiological transition. Sequential testing of Na+, K+, ATPase and citrate synthase levels in hatchery smolts prior to release, in the river at the head of tide during migration, and in estuarine and near-shore marine areas, is providing a continuum of data to allow for better understanding of this physiological transition. Ultrasonic telemetry studies in other US systems provide evidence that smolts that are not fully capable of osmoregulating in saltwater may hold in areas of lower salinity, possibly increasing their vulnerability to predation. In addition, the presence of multiple hydro-electric projects and associated impoundments in the

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watershed may delay the timing of emigration to marine systems. Although hatchery smolts are released in main stem areas below the majority of dams, naturally reared smolts are required to migrate through up to 6 hydro-electric projects prior to reaching estuarine areas. Current migration data suggest that smolts begin seaward migration at 10°C, but that in many years water temperatures quickly reach 18°–20°C in lower river areas. Rapidly warming river water temperatures can potentially result in increased physiological stress and predation from warm-water predators. Delayed migration can further increase smolt exposure to these potential mortality sources.

The early marine phase likely represents a critical growth period since suitable prey are abundant in near-shore marine waters. Diet samples collected from smolts and post-smolts as they move down river and into marine waters suggest that upon entering marine waters post-smolts begin feeding immediately and predominantly on herring larvae, which occur in high densities. As part of the continuing research we intend to evaluate this further by calculating relative growth rates using RNA/DNA ratios and additional stomach content analysis.

Heavy sea lice infestation potentially contributes to higher mortality of post-smolts. However, in our samples we found no sea lice infestation on post-smolts, though closely related lice species were documented on other species (e.g. lumpfish). A follow-up cruise in Spring 2002 will expand spatial and temporal coverage to further define migration pathways and near-shore distribution and to test hypotheses related to differential mortality of post-smolts originating from hatchery and naturally reared sources.

Injuries of Salmon in the Amur River and its Estuary as an Index of the Adult Fish Mortality in the Period of Sea Migrations

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Keywords: The Amur River Estuary, injures, anadromous salmon, white whale, harbour seal

During 1994–2000 we have observed injures on salmon in the Amur River Estuary to assess the salmon sea mortality. In the Amur River Estuary the portion of salmon injures made by marine mammals in 1994–2000 was large and accounted for 32.2–87.7% of total number of injured fishes. However, the portion of injured fishes made up only 1.7–13.9% of total salmon number. The number of slashes caused by drift nets and pelagic long-line fisheries was insignificant during the same period.

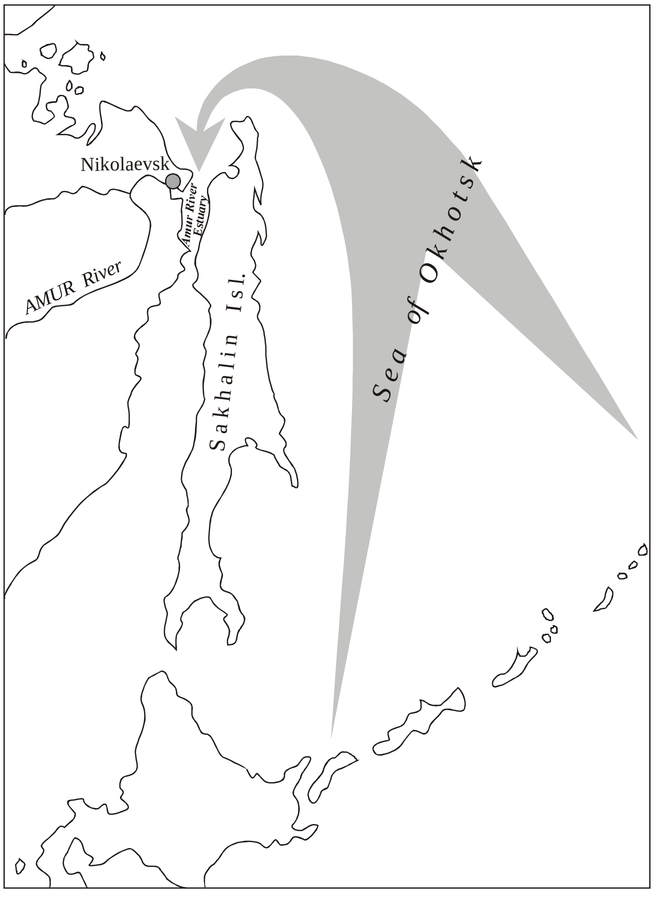
The predation is the second largest cause of mortality after the fishing mortality in the sea.

On the migration path from the Pacific ocean to the Amur River Estuary (Fig. 1) salmon can be consumed by different predators: killer whale; northern sea-lion and northern fur seal; among predator fishes: *Alepisaurus ferox*, daggertooth (*Anotopterus pharao*) and salmon shark.

In the Sakhalin Bay and in the Amur River Estuary white whale, harbour seal and kaluga sturgeon (among fish) eat salmon. The abundance and the distribution of white whale and habour seal in summer are connected with the salmon spawning migration in the Amur River Basin, as salmon is the main food for these animals during summer.

In Russia drift nets are not used for salmon fishing and injures due to drift nets are considered as an influence of the Japanese fleet. Slashes made by marine mammals were fresh and related to harbour seal in the estuary. Sores can be made by different gear or by parasites. Healed wounds are related to *Alepisaurus ferox* and daggertooth (*Anotopterus pharao*), (Fig. 2a) that attack salmon in the Pacific. We have begun to assess healed wounds since 1999. We suggest that northern fur seal does not make slash marks on salmon because they catch them successfully. We think that salmon shark and kaluga sturgeon swallow salmon without marks. Others predators eat salmon rarely.

Fig. 1. Direction of Pacific Salmon Migration to Amur River.



In Tables 1–3 is presented some data on wounded salmon in the Amur River Estuary during last 7 years.

Proportionately, the most injured salmon in the Amur River is pink salmon, the smallest Amur anadromous salmon weighing on average 1.2 kg. In years of low abundance of any salmon species, the portion of injured fishes increases. The number of slashes caused by drift nets (Fig. 2b) in our catches (1994–2000) was insignificant. Some years this type of slashes did not occur. We believe that low frequency of marks is synonymous with low marine mortality during this time. The insignificant proportion of injuries made by drift nets and the absence of pelagic long-line hooks reveal the current weakness of marine drift and long-line fishing of salmon.

In the Amur River Estuary the portion of salmon injures made by marine mammals (Fig. 2c,d) in 1994–2000 was large and accounted for 32.2–87.7% of the total number of injured fishes.

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Fig. 2. Wounds of Salmon in the Amur River Estuary.

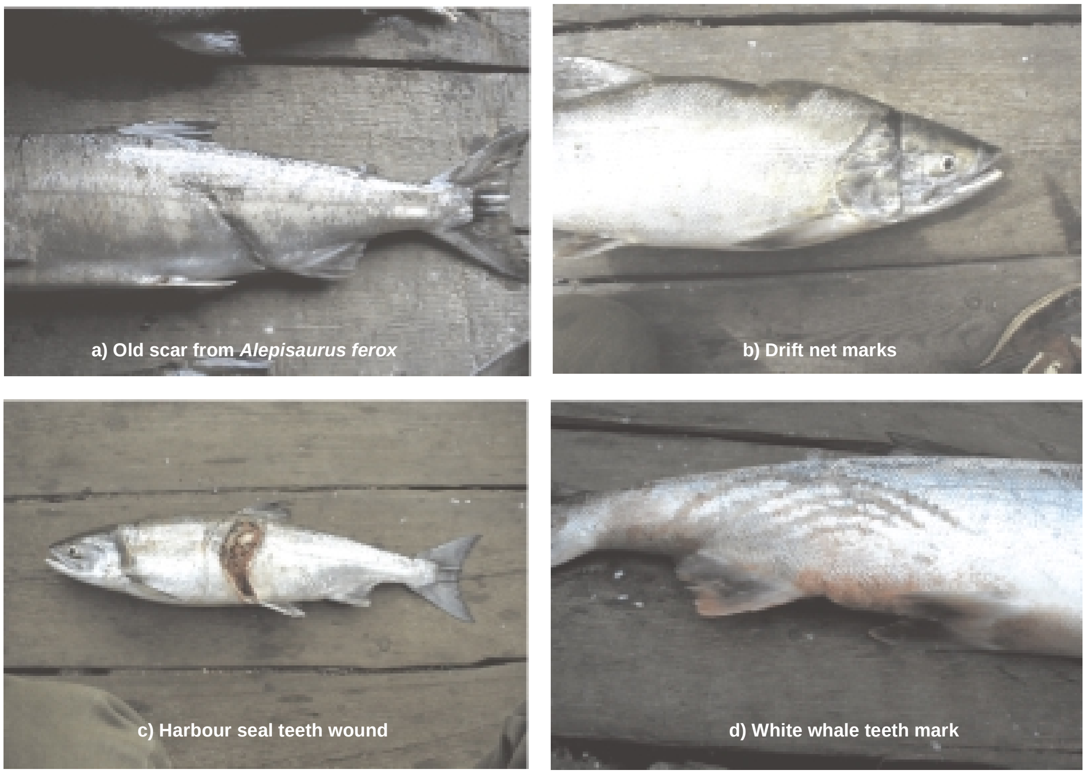


Table 1. Wounded pink salmon in the Amur River Estuary, 1994-2000 (in percentage terms of total number of wounded fish).

Year	Wound type										Number of wounded fish	Number of surveyed fish	Wound %
	Drift nets		Sea mammals		Lamprey wounds		Sores and absence of fins		Healed wounds				
	fish	%	fish	%	fish	%	fish	%	fish	%	fish	fish	%
1994	2	0.8	82	35.1	144	61.5	6	2.6	-	-	234	3000	7.8
1995	0	0	63	39.6	94	59.1	2	1.3	-	-	159	1650	9.5
1996	0	0	174	32.2	362	67.0	4	0.8	-	-	540	8800	6.1
1997	0	0	246	44.0	296	53.0	17	3.0	-	-	559	4010	13.9
1998	2	0.5	192	51.9	155	41.9	21	5.7	-	-	370	6530	5.7
1999	0	0	58	38.7	79	52.7	5	3.3	8	5.3	150	2650	5.7
2000	10	1.7	302	52.5	226	39.4	26	4.5	11	1.9	575	8900	6.5

Table 2. Wounded summer chum salmon in the Amur River Estuary, 1994-2000 (in percentage terms of wounded fish total number).

Year	Wound type										Number of wounded fish	Number of surveyed fish	Wound %
	Drift nets		Sea mammals		Lamprey wounds		Sores and absence of fins		Healed wounds				
	fish	%	fish	%	fish	%	fish	%	fish	%	fish	fish	%
1994	0	0	123	59.1	73	35.1	12	5.8	-	-	208	2600	8.1
1995	0	0	150	61.2	77	31.4	18	7.4	-	-	245	4400	5.6
1996	0	0	19	52.8	17	47.2	-	-	-	-	-	-	5.5
1997	0	0	302	83	53	14.5	9	2.5	-	-	364	4765	9.7
1998	0	0	104	76.4	24	17.7	8	5.9	-	-	136	2670	5.1
1999	0	0	125	63.5	30	15.2	30	15.2	12	6.1	197	4500	4.4
2000	3	0.8	219	60.2	55	15.1	37	10.2	50	13.7	364	4249	4.6

Table 3. Wounded fall chum in the Amur River Estuary, 1994-2000 (in percentage terms of wounded fish total number).

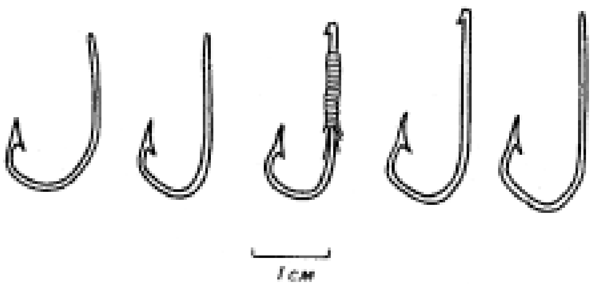
Year	Wound type										Number of wounded fish	Number of surveyed fish	Wound %
	Drift nets		Sea mammals		Lamprey wounds		Sores and absence of fins		Healed wounds				
	fish	%	fish	%	fish	%	fish	%	fish	%	fish	fish	%
1994	0	0	106	78	23	16.9	7	5.1	-	-	136	5100	2.7
1995	0	0	48	50	43	44.8	5	5.2	-	-	96	2000	4.8
1996	0	0	39	62.9	17	27.4	6	9.7	-	-	62	2200	2.8
1997	0	0	43	87.7	4	8.2	2	4.1	-	-	49	1500	3.3
1998	1	3.7	20	74.1	5	18.5	1	3.7	-	-	27	1200	2.3
1999	1	0.7	69	46.6	33	22.3	18	12.2	27	18.2	148	2500	5.9
2000	0	0	105	57.7	22	12.1	14	7.7	41	22.5	182	2370	1.7

However, the portion of injured fishes made up only 1.7–13.9% of the total salmon number. The number of white whales and harbour seals in the Amur River Estuary and in the Sakhalin Bay is large. Their abundance is not regulated by man as hunting for them has been prohibited for a long time. In this conditions we suggest the predation and fishing are largest causes of the adult Amur River salmon mortality.

We conclude that the investigations of wounds are necessary for the standard biological analysis of salmon in the main fishing regions of the Pacific, as this data gives additional information about the relative abundance of marine mammals, salmon mortality in the feeding period and the dynamics of fishing by some gear on the ways of sea migrations.

In comparison to the 1950s (Yenutina and Krykhtin 1957)when Japanese long line hooks were abundant on Amur River salmon, there were no long line hooks (Fig. 3) on Pacific salmon in Amur River Estuary during 1990–2001.

Fig. 3. Long line hooks from Pacific salmon in Amur River Estuary in 1956 (Yenutina and Krykhtin 1957).



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On Peculiarities of the Palana River Sockeye *(Oncorhynchus nerka)* Abundance (North-West Kamchatka)

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Keywords: Western Kamchatka, Palana River, sockeye salmon, age, abundance, pink salmon

In the basin of the Palana River, which flows into the Sea of Okhotsk at 59°06'N a large stock of sockeye *(Oncorhynchus nerka)* occurs. This stock is the third or fourth largest of this species in Asia. Reproduction and growth of this stock as juveniles occurs almost entirely in the Palana Lake basin prior to migration to the sea. While migrating to the Pacific Ocean sockeye smolts make a long migration along the Western Kamchatka coast southward and bypassing the southern extremity of Kamchatka peninsula (50°52'N). Mature fishes then make the reverse migration.

As shown in Table 1, sockeye smolt migration from Palana Lake to the sea occurs at ages 1–4 years of age. In Table 2, one can see the age structure of mature fishes from the commercial catches in 1994–2001.

As shown in Fig. 1, the abundance of the sockeye reveals a stable two year cycle of abundance (violated in 1983–1984 only): in 1979, 1981, 1985, 1987, 1989, 1993, 1995, 1997, 1999 and 2001 peaks of abundance are observed, and in1978, 1980, 1982, 1986, 1988, 1990, 1992, 1994, 1996, 1998 and 2000 – decreases of abundance. We suppose that this cyclic recurrence is connected with the pink salmon fluctuations, which, as is well known, has a two-year life cycle.

Table 1. Body Length of Smolts of Sockeye Migrating From the Palana Lake in 1995–2000.

Age	Body length, mm			Body weight, g			Number of fishes (%)
	Limits	Average	Error	Limits	Average	Error	
1995							
1+	50-62	57.15	1,07	0.80-2.40	1,74	0,12	13(10.2)
2+	71-107	89,35	0,64	3.60-11.80	6,67	0,15	113(88.3)
3+	87-100	93,5	6,5	6.20-9.40	7,8	1,6	2(1.5)
1996							
1+	47-57	52,67	2,96	1.20-2	1,73	0,27	3(11.1)
2+	66-100	82,5	1,32	2.20-10.70	5,84	0,31	24(88.9)
3+	-	-	-	-	-	-	-
1998							
1+	54-65	60,8	2,13	1.15-2.41	1,85	0,23	5(8.5)
2+	70-85	77,22	0,54	2.02-6.26	4,09	0,11	51(86.4)
3+	85-88	86,33	0,88	5.42-5.82	5,68	0,13	3(5.1)
1999							
1+	56-79	67,63	3,16	1,51-4,64	3,14	0,42	8(9,9)
2+	78-101	87,89	0,71	4,63-11,34	6,62	0,16	64(79,0)
3+	83-100	92,89	1,91	5,32-9,25	7,64	0,45	9(11,1)
2000							
1+	61-62	61.50	0.50	1.46-2.98	2.22	0.76	2(3.8)
2+	76-105	92.55	0.99	4.48-12.58	7.87	0.25	42(79.2)
3+	95-111	103.25	2.01	8.70-13.19	11.19	0.49	8(15.1)
4+	134	134.00	-	26.37	26.37	-	1(1.9)

Note. In 1997 the studies of dynamics sockeye smolt migration were not realized

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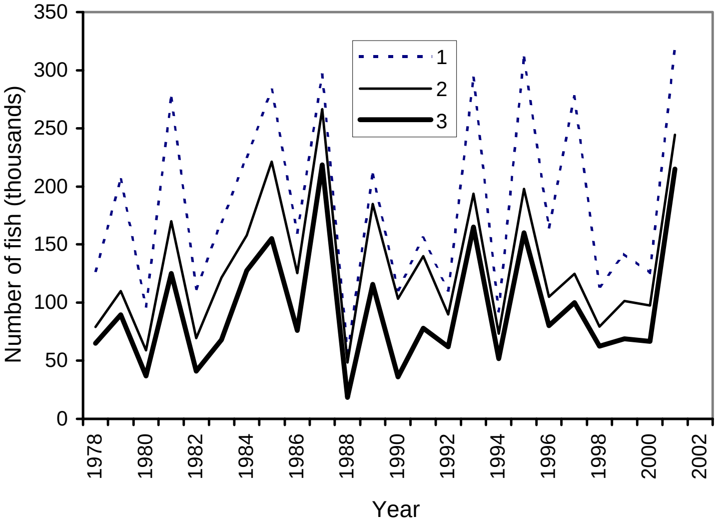
Table 2. Age Structure of the Palana River Mature Sockeye from the Commercial Catches in 1994–2001, %.

Year	1.2	1.3	1.4	2.2	2.3	2.4	3.2	3.3	3.4	Number of fishes
1990*	-	14.6	-	-	79.2	2.1	-	4.1	-	48
1994	0.7	18.4	-	10.9	54.8	2.0	1.0	12.2	-	294
1995	1.0	5.1	-	11.2	82.7	-	-	-	-	98
1996	-	9.7	-	50.0	40.3	-	-	-	-	72
1997	-	3.1	0.4	2.4	85.5	1.0	-	7.2	0.4	290
1998	8.4	9.4	0.7	26.2	50.7	1.0	1.8	1.8	-	286
1999	-	20.1	-	7.7	69.4	-	-	2.8	-	284
2000	-	9.4	-	-	86.4	1.1	-	3.1	-	287
2001	-	1.8	-	9.7	82.1	3.6	2.1	0.7	-	279

Note. The fist figure – duration of the fresh water life period, the second one – duration of the marine life period. * - fish caught at the Palana Lakespawning grounds.

Fig. 1. The Palana River sockeye abundance in 1978–2001: at the stock mature part (SMP) the ocean prior to the driftnet catch (1), at the approach to the river estuary (2) and the escapement into Palana Lake (3), in thousands of fish.



The researches recommend (Bugayev 2001) to consider the abundance dynamics of the Asian stocks of sockeye by periods of growth in the ocean: 1 – before 1984 inclusive, when the abundance of the dominant generations of the Western and North-Eastern Kamchatka pink salmon fluctuated in one phase, and 2 – starting in 1985, when a shift of the dominant generations of the Western Kamchatka pink salmon abundance from odd years to even ones occurred. As a result a high pink salmon abundance (dominant generations) was observed at Western and North-Eastern Kamchatka in different years unlike the previous period. Considering this, we have divided all the available data about the Palana River sockeye in generations of 1972–1981 and 1982–1999.

The average abundance of the Western Kamchatka pink salmon approaches to the coast in even years 1978–1984 (1986–2000) was made up of 36.9 (67.5) millions of fish, and in odd years 1977–1983 (1985–2001) – 80.6 (2.1) millions of fish. Starting in 1985 and up till present there has been a shift of abundant (dominant) generations from the odd years to even ones along with the change in pink salmon on this coast (Bugayev 2001). But this shift of pink salmon abundance has not considerably influenced the Palana River sockeye abundance.

Using the "STATISTICA" program we have calculated the coefficients of the multiple regression – R between the Palana River sockeye SMP and environmental factors and fish abundance by the forward stepwise method of inclusion at the generations of 1982–1995. In this work we have made a transform of all the initial indicators into natural logarithms as recommended by Borovikov and Borovikov (1998). Considering that for the Palana River sockeye the age at maturity for calculations was taken as 2.3, the abundance of SMP in this case is at the same time the abundance of generations (ZRPAL). This equation of the multiple regression looks like this:

LnZRPAL = 19.5504 + 0.0407*LnPINE-2 + 0.7758*LnSPKU – 0.4383*LnPINE-3 – 3.3311*LnLSMKU + 0.2658*LnPINW-0 + 0.1737*LnPINW-2 – 0.6267*LnOZZR + 0.2468*LnSPPAL + 0.0613*LnPINE-1; R = 0.997, P < 0.001, n = 14.

As it is seen from the equation of the multiple regression in our case the Palana River sockeye SMP is influenced by the following factors:

PINE-2 - the inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) during the second year of marine life of sockeye salmon of the Palana River, which returned at the studied year (SY), millions of fish;

SPKU - the abundance of the parent escapement of sockeye of all the age groups spawned in the Kuril Lake at the year of spawning of the studied generation of the Palana River sockeye, which returned at the studied year (SY), in thousands of fish;

PINE-3 - the inshore run of mature North-Eastern Kamchatka pink salmon (after driftnet harvesting) during the third year of marine life of the Palana River sockeye, which returned at the SY, millions of fish;

LSMKU - the body length of the Kuril Lake sockeye smolts at the age 2+, from which the return of mature sockeye happens at the SY, mm;

PINW-0 - the inshore run of mature Western Kamchatka pink salmon (after driftnet harvesting) one year prior to ocean migration of sockeye smolts of the Palana River (from Palana Lake) at the age 2+, which returned at the SY, millions of fish;

PINW-2 - the inshore run of mature Western Kamchatka pink salmon (after driftnet harvesting) during the second year of the Palana River sockeye, which returned at the SY, millions of fish;

OZZR - the SMP of the Ozernaya River sockeye at ocean prior to the beginning of the driftnet harvesting at the SY, in thousands of fish;

SPPAL - the abundance of the parent escapement of sockeye of all the age groups spawned in the Palana Lake at the year of spawning of the studied generation of sockeye, which returned at SY, in thousands of fish;

PINE-1 - the inshore run of mature of the North-East Kamchatka mature pink salmon (after driftnet harvesting) during the first year of marine life of the Palana River sockeye, which returned at SY, millions of fish.

The analysis of the dynamics of the Palana River sockeye generations' abundance of 1972–1981 is now of historical and scientific interest only, and will not be of practical use until the abundance of the Western and North-Eastern Kamchatka pink salmon dominating generations does not fluctuate in phase again.

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Extreme *Salmo*: the Risk-Prone Life History of Marine-Phase Atlantic Salmon and its Implications for Natural Mortality

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Keywords: Atlantic salmon, life history, growth-mortality trade-off, fasting

Although life history variation in Atlantic salmon (*Salmo salar*) has been examined in scores of scientific papers, the most remarkable features of the species' life history have been ignored in the literature. This paper examines marine growth and pre-spawning fasting in Atlantic salmon, two traits which set Atlantic salmon radically apart from other fish species. Atlantic salmon pre-fishery abundance in the Northwest Atlantic has decreased markedly since the 1980s due to increased marine mortality (Cairns 2001). Understanding the life history strategies behind the Atlantic salmon's growth and fasting patterns may be the key to explaining the species' decline.

Juvenile Atlantic salmon grow at rates typical of other stream fishes, but growth rates increase dramatically after sea entry. Salmon in the Northwest Atlantic increase in weight 75-fold between river exit and return after 1 sea winter, and > 200-fold between river exit and return after 2 sea winters. These growth rates are two orders of magnitude faster than those of other fish (herring, mackerel, capelin) which occupy the same pelagic habitat (Fig. 1).

Atlantic salmon typically return to natal rivers in early summer (early run) or in fall (late run). Adult Atlantic salmon stop feeding before they enter rivers, and continue to fast during their time in fresh water. The pre-spawning fast typically lasts about five months in early run fish. Late-run fish spend the summer at sea. Although they have the opportunity to feed during the pre-spawning summer, late-run fish are not larger than early-run fish (Fig. 2). This suggests that they either have a slower overall growth trajectory, or that they do not eat during the pre-spawning summer. Circulii spacing patterns in scales collected from late-run salmon returning to the Margaree River, Nova Scotia, suggest that these fish did not grow in the summer prior to river entry (G. Chaput, personal communication). Hence it is possible that both early- and late-run Atlantic salmon fast in the summer prior to spawning.

Survivorship of Atlantic salmon between river exit and return after 1 sea winter is typically < 10% in eastern North American stocks (Table 1). Survivorships of other ocean fish of similar size, estimated from allometric equations that relate natural mortality to body weight (Lorenzen 1996), are about 50–60% (Fig. 3). Atlantic salmon marine survivorship

Fig. 1. Growth of three species of pelagic fish in the Northwest Atlantic. Salmon weights assume a smolt age of 3 years. Data are from Cairns and Reddin (2000) for salmon and from Scott and Scott (1988) for mackerel and herring.

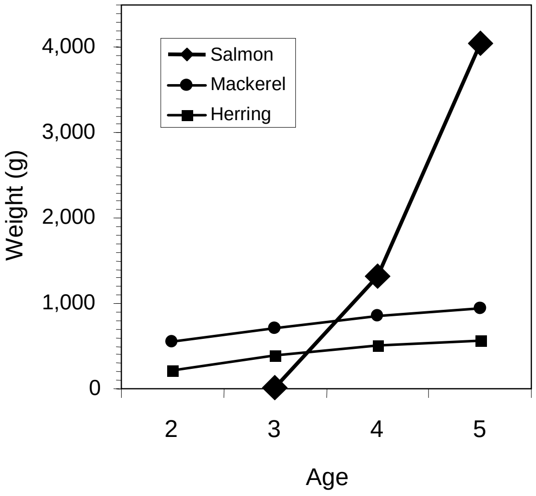

Fig. 2. Weights of 1SW and 2SW maiden Atlantic salmon vs. date of capture at the Millbank Trap, Miramichi River, 1986–1991. Data from G. Chaput.

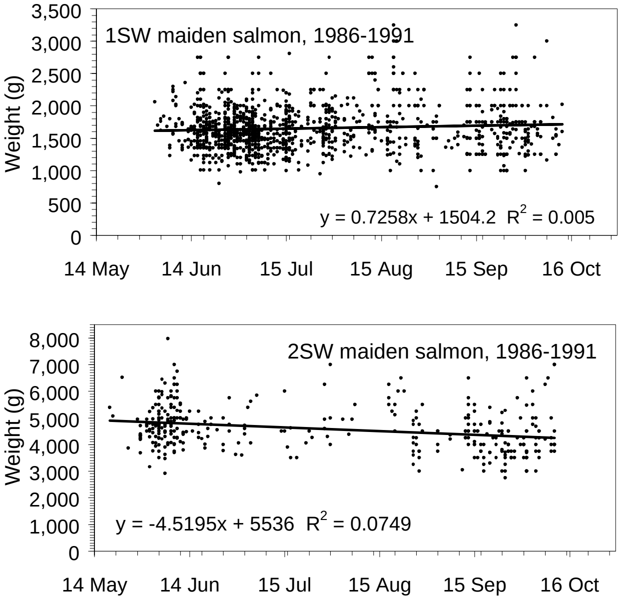

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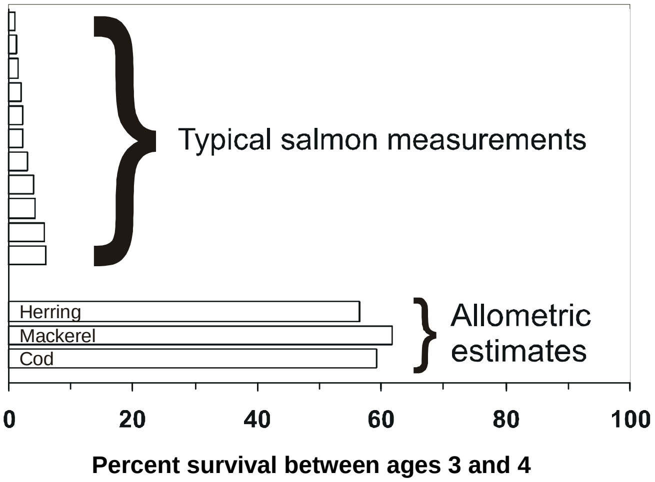
Table 1. Means, standard deviations, and coefficients of variation of annual sea survivals and sizes at return of Atlantic salmon in Eastern Canada.

Item	Location	Dates	Mean	SD	CV (%)	N	Mean of within-year CVs (%)
Size[a]							
Fork lengths (cm) of returning maiden 1SW salmon	Miramichi	1971-1999	53.6	2.0	3.7	29	5.6
Fork lengths (cm) of returning maiden 2SW salmon	Miramichi	1971-1999	73.8	1.6	2.2	29	4.5
Weights (g) of returning maiden 1SW salmon	Miramichi	1971-1991	1,578.0	78.9	5.0	21	16.9
Weights (g) of returning maiden 2SW salmon	Miramichi	1971-1991	4,468.1	224.8	5.0	21	15.7
Mortality[b]							
Survival between smolt exit and river return (%)	Bec-Scie	1988-1995	1.4	0.3	20.6	8	
Survival between smolt exit and river return (%)	de la Trinité	1984-1997	1.7	0.9	55.5	14	
Survival between smolt exit and river return (%)	Saint-Jean	1989-1996	0.4	0.1	24.3	8	
Survival between smolt exit and river return (%)	Catamaran	1990-1997	9.7	3.2	33.4	8	
Survival between smolt exit and river return (%)	Highlands	1993-1997	1.9	0.8	40.7	5	
Survival between smolt exit and river return (%)	Campbellton	1993-1997	6.6	2.3	34.4	5	
Survival between smolt exit and river return (%)	Western Arm Brook	1977-1997	4.8	2.8	58.3	21	
Survival between smolt exit and river return (%)	Northeast Trepassy	1986-1997	5.5	2.2	39.5	12	
Survival between smolt exit and river return (%)	Rocky	1990-1997	3.3	0.7	22.3	8	
Survival between smolt exit and river return (%)	Conne	1987-1997	5.3	2.4	45.8	11	

[a] Data from Moore et al. 1995 and G. Chaput.
[b] Data from compilation by Cairns and Reddin 2000

Fig. 3. Annual percent survival of marine-phase Atlantic salmon based on typical return rates of 1SW fish, and annual percent survival of Northwest atlantic fish based on Lorenzen's (1996) allometric estimates of natural mortality.



fluctuates greatly from year to year (CVs from 20.6% to 58.3%, Table 1). In contrast, sizes of returning adults show little inter-annual variation (CVs 5% or less, Table 1).

The following explanation of the Atlantic salmon's remarkable patterns of growth and fasting is proposed. Growth and mortality in fishes are thought to operate as trade-offs (Henning et al. 1993). Growth in fishes depends heavily on food availability and on water temperature. Water temperature is important because it influences the rate at which food can be procured and assimilated. The warmest temperatures in summer occur in the surface layer. To grow rapidly, salmon must feed aggressively, and also preferentially occupy the surface layer where warm temperatures enhance growth. But rapid growth is traded against higher mortality because vigorous feeding movements, especially in the photic zone near the surface, increases exposure to predation.

Food supplies and ocean temperatures fluctuate inter-annually, but sizes of returning Atlantic salmon show little inter-annual variability (Fig. 4). This suggests that Atlantic salmon have a target size at return, which they achieve by adjusting their feeding intensity and their use of the warm surface layer. These behaviours alter the risk of predation mortality. Thus in the face of fluctuating growth conditions, Atlantic salmon appear to adjust the mortality term, but not the growth term, of the growth-mortality trade-off.

Salmon that fast during the pre-spawning summer forego the opportunity for a major increase in somatic and gonadal weight which would increase their reproductive fitness. The timing of early runs cannot be attributed to the need to ascend obstacles when the spring run-off is high, because the spring run-off has usually finished before the run begins. Pre-summer fasting cannot be attributed to a need to physiologically prepare for spawning, because it is implausible that

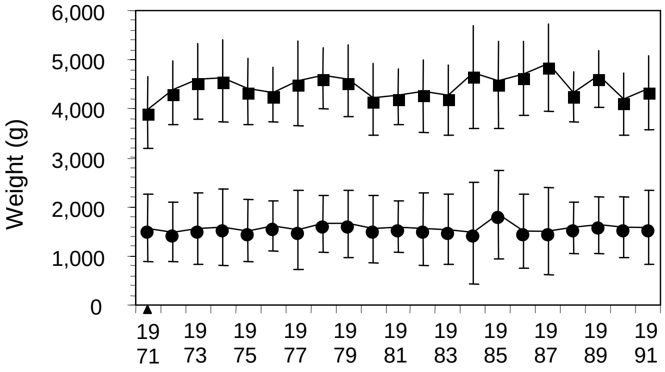


Fig. 4. Mean (± SD) weights of maiden 1SW (circles) and 2SW (squares) salmon captured in assessment traps in the Miramichi River. Data from G. Chaput.

such a preparation period needs to be five months long. Many vertebrate animals fast for extended periods, but the reasons for these fasts are obvious (e.g. lack of food during winter hibernation, requirement to incubate eggs or guard harems, inability to fly because of wing moult). To fast for five months during the normal growing season, as pre-spawning Atlantic salmon often do, is an extraordinary aberrancy that may, among vertebrates, be unique to salmonids.

The only viable explanation of the Atlantic salmon's pre-spawning fast appears to be that feeding imposes a fitness cost that is even higher than the fitness cost of fasting. Atlantic salmon sit on the high-growth/high-mortality end of the growth-mortality spectrum. At a certain body size, the high mortality due to aggressive feeding and use of the warm surface layer overtakes the advantage of further growth. At this size, fitness is better served by fasting. The body size at which fasting becomes more advantageous than feeding appears to vary geographically. In the Northwest Atlantic, salmon destined to grow to 2SW size travel to the northern Labrador Sea or southern Greenland. Salmon that don't make this journey return to natal rivers as 1SW fish. Among 1SW returnees, early-run fish, and possibly late-run fish as well, fast during the pre-spawning summer.

The lifestyle of marine-phase Atlantic salmon is highly risk-prone. The annual income of a professional gambler is likely to be more variable than that of a steady wage-earner. In similar vein, marine survivorships of Atlantic salmon can be expected to be highly volatile, and dependent on poorly-understood relations with food supply, temperature, and predators.

This paper has pointed out extraordinary features of salmon life history, and offered preliminary explanations for the life history strategies that underlie them. If we want to determine why Atlantic salmon are in difficulty, theoretical, observational, and experimental investigations of these features and their fitness consequences should be a research priority.

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Viral Diseases as a Possible Cause of Salmon Mortality in the North Pacific Ocean

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Keywords: IHNV, phylogeny, diversity, transmission

Many viruses have been isolated from wild fish species from marine ecosystems. Whether these viruses can initiate an infection, cause disease, and eventually cause mortality of fish in ocean environments is not well understood. However, mortalities linked to viral infections in cultured marine fish have been reported. Three major virus pathogens that have been associated with outbreaks of cultured fish in salt water include infectious salmon anemia, viral hemorrhagic septicemia virus, and infectious hematopoietic necrosis virus.

Infectious salmon anemia (ISA) is an established viral disease of cultured Atlantic salmon in the marine environment (Nylund et al. 1999). Outbreaks were first reported from Norwegian cultured Atlantic salmon (Thorud and Djupvik 1988), but reported mortalities due to ISA soon followed in Scotland (Rodger et al. 1998) and on the east coast of Canada (Lovely et al. 1999) in Atlantic salmon reared in salt water net pens. Wild fish in the waters near where the marine outbreaks occurred have tested positive for the virus, but do not exhibit any clinical signs of disease (Raynard et al. 2001).

Originally, viral hemorrhagic septicemia virus (VHSV) was identified in association with high mortalities of rainbow trout reared in fresh water culture facilities in central Europe. Since 1979, VHSV has been isolated from many species of fish present in salt water from the Atlantic Ocean near continental Europe, Baltic Sea, Kattegat, Skagerrak, and the North Sea (Mortensen et al. 1999). Most wild marine fish infected with VHSV show no clinical signs of disease though a few isolations were from skin lesions. However, there have been epizootics in cultured turbot reared in salt water from Germany, Scotland, and Ireland (King et al. 2001). In North America, VHSV was first isolated in 1990 from returning adult coho and chinook salmon (Eaton et al. 1991; Meyers and Winton 1995) and the virus is now known to be endemic to many north Pacific fish species (Meyers et al. 1994; Hershberger et al. 1999). No mortalities in wild or cultured fish from North America have been directly attributed to VHSV, but it has been speculated that VHSV infection may play a role in the population fluctuations observed in wild herring stocks in Alaska (Hershberger et al. 1999).

Infectious hematopoietic necrosis virus (IHNV) is the most significant viral pathogen of cultured salmonids in the Pacific Northwest. IHNV is primarily associated with epidemics in fresh water culture facilities (e.g. fish farms, hatcheries, and spawning channels) and can infect many species of Pacific salmonids (Bootland and Leong 1999). The virus is endemic to the waters of North America from Alaska to northern California and has been isolated from both wild and cultured fish in fresh water (Wolf 1988). In 1992 the first marine isolation of IHNV from an Atlantic salmon (*Salmo salar*) occurred during an outbreak at a salt-water net pen rearing facility near Vancouver Island in British Columbia, Canada (Armstrong et al. 1993). Subsequent IHNV outbreaks in neighboring facilities rearing Atlantic salmon have occurred intermittently (S. St-Hiliare, University of Guelph, Guelph Ontario, Canada, personal communication). IHNV has also been isolated from a returning adult sockeye (*Oncorhynchus nerka*) in salt-water (Traxler et al. 1997), and four other species of ocean-harvested wild fish (Kent et al. 1998; S. St-Hiliare, University of Guelph, Guelph Ontario, Canada, personal communication). The isolation of IHNV from wild and cultured fish in both salt and fresh water within the Pacific Northwest indicates that the virus is highly versatile in regard to host specificities and host environments during its infectious cycle.

In order to better understand the epidemiology of IHNV infections and their possible transmission patterns in both fresh and salt-water environments, a long-term project is underway to genetically characterize virus isolates throughout the entire geographic range of IHNV in the Pacific Northwest. The IHN virus RNA genome consists of 6 genes in the following order: the N, P, M, G, NV, and L, which code for the nucleoprotein, phosphoprotein, matrix protein, glycoprotein, nonvirion protein, and the polymerase, respectively (Kurath et al. 1995; Morzunov et al. 1995). We have extensively examined various genes of IHNV isolates from Alaska (Emmenegger et al. 2000), British Columbia (Anderson et al. unpublished data), Washington coastal rivers (Emmenegger and Kurath 2002), 12 mile region along the Snake River subbasin in Idaho (Troyer et al. 2000), the entire Columbia River basin (Garver et al. unpublished data), and watersheds from California and the southern Oregon coast (Kurath et al. unpublished

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data). The virus isolates were characterized by nucleotide sequencing and comparing genetic fingerprints using the ribonuclease protection assay. The data presented is a comprehensive phylogenetic analysis of a 303 nucleotide region in the G-gene of IHNV isolates throughout its North American range over the last 35 years.

Phylogenetic analysis of the partial sequences indicated that IHNV isolates clustered into three major clades U, M, and L, with maximum genetic diversities of 3.0%, 7.6%, and 3.3% respectively. These analyses indicated that the three major genetic groups of the virus isolates correlated with both their geographic origin and the long-distance migration patterns of the salmonid host stocks. Interestingly, the U clade is the largest clade by numbers of isolates and by geographic range, occurring from approximately the Columbia River to the farthest northern IHNV isolation in Alaska, and yet it has the lowest genetic diversity. Genetic homogeneity within the viral U and L clades suggests that viral transmission may occur during the marine life stage of the hosts. Possible hypotheses that may explain IHNV genetic homogeneity within specific regions of its range include: species/stock migration patterns in the ocean, a marine reservoir or carrier state of the virus in saltwater, oceanic features (i.e. small or large gyres), fish culture practices, host specific factors, and differences in coastal versus inland salmonid migration distances. In association with other climatic or ecological stressors, marine virus transmission could result in epidemics. Further sampling of salmonids and other fish species during their ocean migration is required in order to determine if IHNV infection is highly prevalent and contributes to the mortality of salmon in the North Pacific Ocean.

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Effect of Ocean Mortality and Growth on Ocean Life History of Pacific Salmon

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Keywords: Life history model, age at maturity, size at maturity, ocean growth

The objective of this study is to evaluate the effects of ocean mortality and growth on life history variability of Pacific salmon. Ocean mortality of Pacific salmon may be size-selective (Ricker 1976), and size-selective mortality may be caused by predation or gillnet fisheries. In general, Pacific salmon with high growth rate mature at younger ages within a year class. But body size of younger fish is smaller than of older fish. Healey (1987) found that the optimum life history model cannot explain such a life history variation within a sockeye salmon population. From the 1970s to the 1990s ocean growth rate was lower, and age at maturity of Pacific salmon increased and mean size at age decreased simultaneously. Pacific salmon life histories are characterized by "big-bang" reproduction and a multi-year life span, in which a fish lives two or more years, reproduces only one time, and dies after the reproduction. General life history models merely treat such a specific condition. Recently, the dynamic state variable approach was used to model salmon life history, and was used elsewhere to model life history of a plant that has "big-bang" reproduction and a multi-year life span similar to Pacific salmon (Mangel 1994; Rees et al. 1999). I examined whether this life history model could explain the within-population variability and temporal changes in age and size at maturity of Pacific salmon.

I used life history models with the "1-year look-ahead criterion" (Rees et al. 1999). The "1-year look-ahead criterion" is a criterion which a fish uses to decide whether to mature now or next year by comparing two expected fitnesses. In contrast, the regular optimal life history model compares fitness overlooking the possible future life span to treat a problem of when an individual organism matures in its life history. The "1-year look-ahead criterion" is convenient to simulate a life history in which individual body size or condition is variable and not predictable. Rees et al. (1999) indicated that the difference or bias was small in the results of simulations between with "1-year look-ahead criterion" or "life span overlooking criterion" for size and age at maturity.

First I considered the condition that a fish "knows" its mean future growth rate. I used life history models assuming a constant, size-selective, or age-selective ocean mortality. The condition is interpreted that a life history of fish is evolved to adapt a mean ocean growth. Models assuming a constant or size-selective mortality predicted a constant size at maturity regardless of age, while models assuming age-selective mortality predicted plasticity both in age at maturity and size at maturity within a year class (Table 1). Second, I considered the condition that a fish "knows" the mean and variance of its future growth. In this case, the predicted size at maturity was slightly larger than in the case that a fish knew only its mean growth rate. Finally, I considered the condition that individual fish expect different growth rates within a population. In this case, models predicted that size at maturity was positively correlated with age at maturity in a Monte Carlo simulation (Table 1, Fig. 1, rectangular plots). And in the similar condition but with mean growth rate decreased to 70%, age at maturity increased and mean size at age decreased (Table 1, Fig. 1, circle plots).

Table 1. The relationship between size at maturity and age at maturity, and changes in age at maturity and size at age at maturity under a condition that ocean growth is decreased to 70% in results of Monte Carlo simulations of life history models for Pacific salmon.

Expected growth	Ocean survival	Relation between size and age at maturity	Changes at decreased growth	
			Age at maturity	Size at age
Mean	Constant	Size is constant	Increase	No change
	Size-selective	Size is constant	Increase	No change
	Age-selective	Positive	Increase	No change
Mean and variance	Constant	Size is constant	Increase	No change
	Size-selective	Size is constant	Increase	No change
	Age-selective	Positive	Increase	No change
Individually different	Constant	Positive	Increase	Decreased
	Size-selective	Positive	Increase	Decreased
	Age-selective	Positive	Increase	Decreased

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Fig 1. Predicted age and size at maturity for female chum salmon using Monte Carlo simulations assuming that individual fish has a variability in growth and a variability in growth expectation with a constant ocean survival rate.

These analyses indicate that a simpler salmon life history model with the "1-year look-ahead criterion" can explain variability within a population and temporal changes in ocean life history of Pacific salmon than the ordinary optimum life history model (Healey 1987). Ocean survival of Pacific salmon may be size-selective (Ricker 1976). Individual variability in the expectation for ocean growth rate and size-selective mortality may produce the observed age and size variability of Pacific salmon which has ocean age variability, such as chum, sockeye, chinook salmon.

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Predation by Lamprey Smolts *Lampetra japonica* as a Main Cause of Amur Chum Salmon and Pink Salmon Mortality in the Early Sea Period of Life

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Keywords: Lamprey, chum salmon, pink salmon, elimination, the Amur River, the Okhotsk Sea

Investigations conducted between 1986-1993 using smolt trawls in the Amur Estuary and the adjacent sea area revealed that lamprey smolts preyed upon chum and pink salmon smolts. It was determined that 15% to 25% of lamprey smolts had the remains of salmon in their intestine. It was also determined that 2% to 31% of live salmon smolts collected showed signs of lamprey wounds. It was estimated that Lamprey consumed approximately 75% of the pink and chum salmon smolts migrating through the Amur Estuary.

The early sea period of life of pink and chum salmon in the Amur estuary and in the adjacent sea area was investigated between 1986 and 1993. It was observed that the sea migration of lamprey smolts occurred at the same time as the migration of salmon smolts (Fig. 1). Migration patterns of lamprey and salmon smolts in the Amur Estuary and in the adjacent sea area are similar (Fig. 2).

Most of salmon and lamprey traverse the Amur Estuary very quickly (approximately one day) and appear in the Sakhalin Bay. A smaller portion stays within the shoal waters of the southern portion of the Estuary for one to one and a half months. Very few of these smolts are from the Amur River; the majority of the smolts in the shoal waters are from local streams. The salmon smolts can grow up to 8.5 cm and the lamprey up to 21 cm during this period. Early migrating (until June) salmon smolts from streams in the southern portion of the Amur Estuary move directly into the Japanese sea (through the Nevelskoy Strait). The salmon that originate in the Amur River do not migrate southward. In July, a current appears periodically that carries salmon and lamprey smolts that have accumulated in the southern portion of the Amur Estuary northward into the Sakhalin Bay. It was discovered that the migrating lamprey smolts prey upon the smolts of chum and pink salmon. Wounds containing suction and lateral tooth marks were discovered on some of the recovered salmon smolts. These wounds are characteristic features of lamprey bites (Fig. 3).

No chum or pink salmon (size 33-88 mm) whose wounds had healed appeared in the catches. Only cherry salmon *Onchorhynchus masu* with lengths of 12 cm or greater were caught with healed lamprey wounds.

In the large catches the number of salmon recovered with lamprey injuries greatly exceeded the number of lamprey recovered. In the sampled catches 15% to 25% of lamprey had remains of salmon smolts in their intestines.

The lampreys initiated their attacks on salmon within the fresh waters of the Amur Estuary (2% to 5% of salmon showed injuries in fresh water). The lamprey predation increased drastically in the brackish waters of the Amur Estuary and the Sakhalin Bay (17% to 31% of salmon recovered in these areas showed Lamprey wounds). Theoretically, this high rate of predation would reduce the abundance of salmon in these spatial-temporal aggregations to a very low number of individuals (Table 1). Lampreys appeared frequently in catches containing large numbers of salmon smolts. However, lampreys were absent in catches containing low numbers of salmon smolts.

From 37% to 68% of the salmon smolts in the various spatial-temporal aggregations were preyed upon by lampreys. Due to the similarities in the migration patterns of the lampreys and the salmon, the major portion of pink and chum salmon mortalities was attributable to lampreys. During the years of study, 75% to 93% of the mortalities of chum salmon passing through the Amur Estuary were attributable to lampreys and from 73% to 96% of pink salmon

Fig. 1. Dynamic of Amur salmon and lamprey migration in the Amur Estuary (average long-term data).

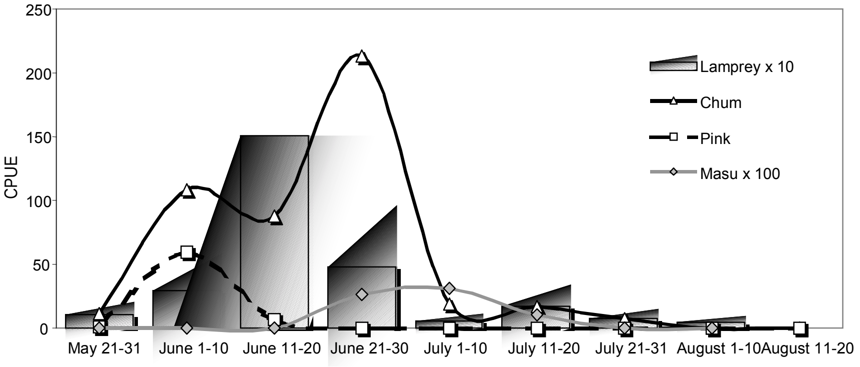

Fig.2. Generalized schema of salmon smolts and lamprey migrations in the Amur Estuary and in the adjacent sea areas.

Fig.3. Chum and pink salmon smolts wounded by lamprey from trawl catches in the Amur Estuary and the Sakhalin Bay.

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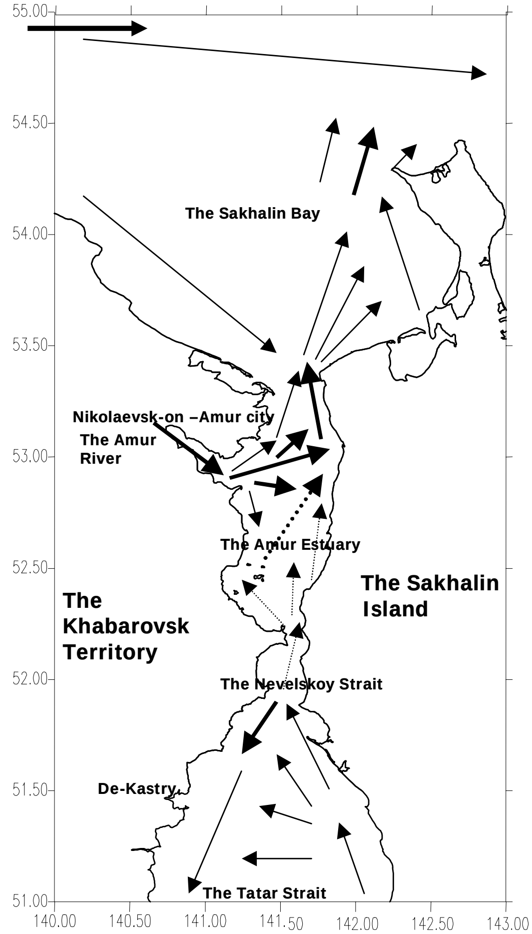

➞ constant main concentrations of salmon

→ constant low concentration of salmon

▪▪▪▪▪▶ periodically occurred migrations, caused of current from the Tatar Strait to the Sakhalin Bay through the Amur Estuary (main concentration)

┈┈▶ periodically occurred migrations (low concentration)

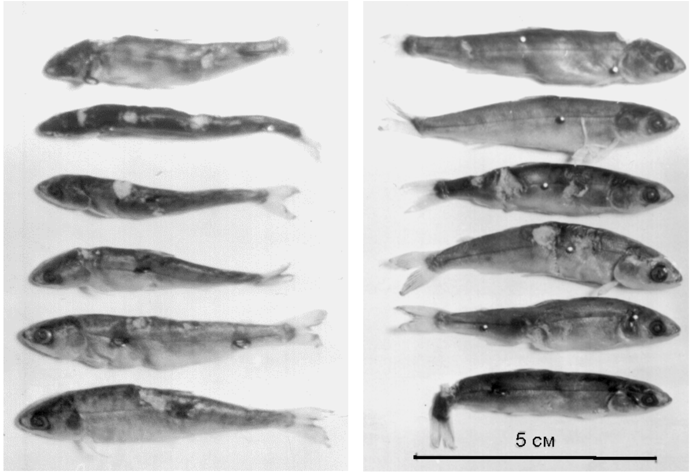

Table 1. Correlation of salmon smolts abundance and predators in fairway of the Amur Estuary.

Species	Portion in the catch, %
Chum salmon	64.04
Pink salmon	21.48
Lamprey	12.85
Arctic smelt	1.58
Ussuri whitefish	0.05

mortalities were attributable to lampreys. Predation by arctic smelts *Osmerus mordax dentex* and Ussuri whitefish *Coregonus ussuriensis* was considered a non-significant source of salmon mortality (maximum 0.04% to 0.15%), because these are not major predators in the Amur Estuary. However, these species consume a large number of salmon smolts in the estuary area of local streams.

One factor that accounts for decreased predation on salmon is a large biomass of smelt fry and *Neomysis sp*. Nearly all fish species present in the Amur Estuary prey upon these species during periods when their biomass peaks. In the saltwater areas of the Sakhalin Bay, trawl catches consisted only of salmon and lamprey. No other species were present.

Thus, for salmon smolt that migrate through the Amur Estuary, lampreys account for approximately 75% of all salmon smolt mortalities. They are by far the major source of salmon smolt mortality in this area during the early sea period of life.

Marine Survival of Hatchery Released Pink Salmon (*Oncorhynchus gorbuscha*) Estimated by Coded-Wire Tagging or Thermal Otolith Marking

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Keywords: Coded -wire tags (CWT), thermal marking, pink salmon

Four major hatcheries in Alaska's Prince William Sound produce pink salmon. In 1996, more than 0.6 billion pink salmon fry were released, all having received a thermal otolith mark unique to each hatchery. Additionally, more than one million fry received a coded wire tag, which allowed identification as to hatchery and specific release group. All survival estimates are based on recovered tags or marks. These two methods produced different results, which are discussed in this communication.

Thermal base marks were laid down in late 1995, at the 'eyed' stage of development, before hatching (Munk et al. 1993). All hatchery pink salmon eggs received thermal otolith marks. A distinct mark was used at each hatchery.

After the eggs hatched into fry in the spring of 1996, a portion of them received two additional marks, a half-length coded-wire tag applied using a Northwest Marine Technology tag injector (MKIV), and removal of the adipose fin to distinguish the fish from its untagged peers. Approximately 1 in 600 pink salmon received a tag. A total of 641.68 million pink salmon fry were released, of which 1.07 million had coded-wire tags.

Mark or tag recoveries were made in 1997 from the commercial fishery. Three components comprise the commercial fishery, the common property fishery, the cost recovery fishery, and the brood stock fishery. Otolith samples were collected systematically as the tenders were being offloaded at processing plants (Joyce and Evans 1998). Using timers set at a specified interval, technicians selected fish and removed the otoliths, working from the beginning of a tender delivery to the end. After all otolith samples had been collected, a weighted sample of 96 otoliths was created by systematically subsampling otoliths taken from each tender, based on the proportion of the total catch that each tender - or its respective processing plant- bought during that opening.

In sampling for coded-wire tags, 20 percent of the catch had to be examined, to compensate for the low tagging ratio and realize desired variance (Geiger and Sharr 1990; Peltz and Geiger 1990; Peltz and Miller 1990). In practice, virtually all tenders had to be sampled to achieve the desired sampling fraction.

The otolith-derived estimate of the contribution of hatchery *h* to district-period stratum *i*, C_{hi} was made as follows (Joyce and Evans 1998):

$$\hat{C}_{hi} = \frac{o_{hi}}{n_i} N_i \qquad (1)$$

where,

o_{hi} = Number of otoliths from hatchery *h* in the sample of stratum *i*,
n_i = Number of otoliths sampled from stratum *i* (usually 96),
N_i = Number of fish caught in stratum *i*.

The total catch over all strata is:

$$\hat{C}_h = \sum_{i=1}^{Q} \hat{C}_{hi} \qquad (2)$$

where,

Q = Number of recovery strata associated with the pink salmon harvest in question.

A variance estimate for $\hat{C}_h$ is given by:

$$\hat{V}(\hat{C}_h) = \sum_{i=1}^{Q} \frac{N_i^2 o_{hi}}{n_i^2} \left(1 - \frac{o_{hi}}{n_i}\right) \qquad (3)$$

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The original tagging ratios had to be expanded by an adjustment factor, due to apparent violations of assumptions concerning tag loss and differential mortality. An adjustment factor combined with the original tagging ratio is equivalent to estimating tag ratios in brood stock or from escapement surveys.

The adjustment factor a_h, for hatchery h, was estimated as the ratio of sampled salmon in the brood stock to the expected number of salmon sampled, based on tags found in the sample:

$$\hat{a}_h = \frac{s_h}{\sum_{i}^{T} \frac{x_i}{p_i}} \tag{4}$$

where

T = number of tag codes released from hatchery h,
p_i = tagging rate at release for the ith tag code (defined as number of tagged salmon released with the ith code divided by the total number of salmon in release group i),
x_i = number of tags of the ith code found in s_h and,
s_h = number of brood stock salmon examined in hatchery h.

The contribution of release group t to the sampled harvests and escapement, C_t, was estimated as:

$$\hat{C}_t = \sum_{i=1}^{L} x_{it} \left(\frac{N_i \hat{a}_h}{s_i p_t} \right), \tag{5}$$

where

x_{it} = number of group t tags recovered in the ith stratum,
N_i = total number of salmon in the ith stratum,
s_i = number of salmon sampled from the ith stratum,
p_t = proportion of group t tagged,
a_h = adjustment factor for hatchery of origin,
L = number of recovery strata associated with harvests, brood stock, and escapement in which tag code t was found.

A variance approximation for $\hat{C}_t$, derived by Clark and Bernard (1987) and Bernard and Clark (1996) was used:

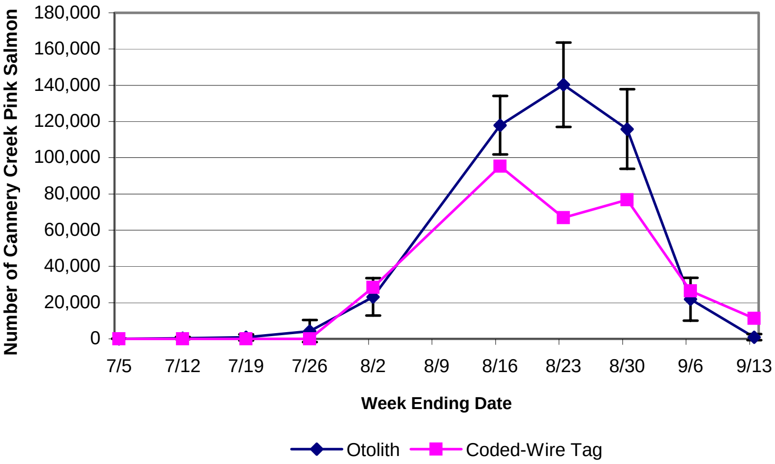
$$\hat{V}(\hat{C}_t) = \sum_{i=1}^{L} x_{it} * \left[\frac{N_i \hat{a}_h}{s_i p_t} \right] \left[\frac{N_i \hat{a}_h}{s_i p_t} - 1 \right] \tag{6}$$

The Prince William Sound hatchery component according to otolith data was 25.67 million pink salmon, while coded-wire tag data estimates totaled to 24.61 million fish. The number of wild fish was 1.11 million for otolith estimates, and 2.17 million for coded-wire tag estimates. Marine survival estimates by hatchery are presented in table 1. Otolith estimates were higher than the coded-wire tag methods three hatcheries, and had much narrower confidence intervals. In general, coded-wire tag estimates were similar to those calculated from otoliths, except where fish which had high tag loss rates for coded-wire tags comprised a large component of the catch (Fig. 1).

Table 1. Marine survival estimates, Prince William Sound hatchery pink salmon returning in 1997.

	Otolith		Coded-Wire Tag	
Hatchery	%Survival	95% Confidence Interval	%Survival	95% Confidence Interval
Solomon Gulch	3.04	3.01–3.07	3.25	2.93–3.57
Cannery Creek	4.10	4.03–4.17	3.78	3.12–4.43
W.H. Noerenberg	3.64	3.57–3.71	3.45	3.06–3.84
A.F. Koernig	6.40	6.28–6.52	5.71	4.82–6.59
Overall	4.00	3.97–4.03	3.84	3.63–4.04

Fig. 1. Number of Cannery Creek pink salmon caught in the Coghill District traditional pink salmon fishery in 1997.



In a related analysis, otoliths were used to classify coded-wire tag samples found to be missing tags. About 96% of those missing tags originated from hatchery fish, of which 31.3% were from Solomon Gulch hatchery, 29% from Cannery Creek hatchery, 28.3% from W.H. Noerenberg hatchery, and 7.77% from A.F. Koernig hatchery. The estimated rates of tag loss attributed to each hatchery were 19.2% for Solomon Gulch hatchery, 38.1% for Cannery Creek hatchery, 25.8% for W.H. Noerenberg hatchery, and 11.7% for A.F. Koernig hatchery.

Coded-wire tag estimates were probably consistently lower due to technicians missing tagged fish. Low tagging fractions for Prince William Sound pink salmon reduced the chance of including groups of fish, present in the harvest at low levels, in the coded-wire tag estimates.

Otolith marking of all fish in a release group appears to produce better estimates and narrower confidence limits, due to a reduced number of assumptions that need to be fulfilled, and a rigorous sampling protocol. The low number of possible differentiable marks limits the usefulness of thermal otolith marking.

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Comments on the Predation of Salmon by Seals in the Coastal Waters of Newfoundland and Labrador

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Keywords: Seal predation, seal/fisheries interactions, salmon mortality

There are six species of seals present in Newfoundland and Labrador waters, i.e. harp, hooded, harbour, grey, ringed and bearded seals. Approximately 7,000 seal stomachs containing food have been examined. There is little information to evaluate the importance of seal predation on salmon in either coastal areas or offshore areas; only two incidences of salmon have been documented in the stomachs of harp seals and none for any other species (Anon. 2000; Hammill and Stenson 2000). Despite this lack of evidence in the diet of seals sampled by DFO, all seals (with the exception possibly of bearded seals) are known to opportunistically take salmon in Newfoundland and Labrador waters.

Presently there is growing concern that seals are responsible for the declining returns of salmon in many Newfoundland and Labrador Rivers (e.g. Cairns 2001). To address some of the key aspects of this issue a River Observation Program was implemented in 1999 on rivers with counting facilities to identify which rivers have seal/salmon interactions, to document the frequency of occurrence and nature of the interactions, and to evaluate potential mitigation actions where problems exist (the program is ongoing). Furthermore, in 1997 a questionnaire dealing with seal/salmon interactions along the coast of Labrador was presented to commercial fishermen.

Participants in the River Observation Program recorded the date, location, time, sighting effort and activities of all mammalian and avian predators observed in the vicinity of the counting facility. In addition to this detailed logbook information, DFO personnel who spend significant amounts of time on rivers were interviewed in order to synthesize their existing knowledge of salmonid predation.

The seal/salmon questionnaire dealt with a wide range of fishery-related issues including when and where seal and avian predation problems occurred. A total of 89 commercial fishermen participated; however, several of the questions allowed the respondents to list more than one answer. Thus, for some results n is > 89 responses. Although the commercial fishery was closed in 1998, much of the information collected is relevant to current seal/salmon interaction issues.

Based on interviews with DFO personnel, seals were observed more frequently, and thought to be more of a predation threat, in rivers along the NE Coast of Newfoundland and parts of the Avalon Peninsula compared to the West Coast. Harp seals were the most commonly identified problem species along the NE Coast while harbour seals were the most common along the southern Avalon Peninsula.

Logbook information was collected for periods of 1–3 years from 7 rivers that have counting facilities. The longest series of data is from Northeast Brook in southern Newfoundland and the English River in Labrador; Table 1 summarizes seal observations at each of these study areas. In Northeast Brook 87.5% (1999), 80.0% (2000) and 77.4% (2001) of seals were sighted during late August and September. In the English River Estuary 77.0%, 73.0% and 88.8% of the seal sightings were made prior to mid-July in 1999, 2000 and 2001 respectively.

Table. 1. Seal Observations for Northeast Brook, Newfoundland and English River, Labrador. In both study areas the field seasons were approximately 70–90 days from early July to mid- or late September.

	Obs. Hours	Total Seals	Sighting Effort	% of Days with a sighting	Species (%)
N.E. Brook					
1999	30.0	16	0.48/hr	17.5	harbour
2000	30.0	21	0.63/hr	20.2	harbour
2001	30.0	25	0.74/hr	21.2	harbour
English R.					
1999	83.0	43	0.52/hr	23.3	26 ringed; 67 harp
2000	70.8	26	0.37/hr	16.3	19 ringed; 69 harp
2001	78.0	89	1.10/hr	20.0	8 ringed; 88 harp

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Based on limited logbook data only 2 seals were seen in the Campbellton River in 2001. Sightings were made on 8.7% of the observation days and the effort was 0.18 seals/hr. There was no reported seal predation at the Bishops Falls Fishway, Northeast River or the mouth of the Rocky River or the nearby Colinet River during the smolt and adult runs. Paradise River supports a significant population of harbour seals and individuals are seen almost daily at known haul-out sites and at predictable foraging sites (these data are still being analyzed).

Of those fishermen responding to the seal/salmon questionnaire, 45.8% indicated that the most significant challenges they faced during the season were interactions with seals. Other concerns included the presence of ice (20.4%), the occurrence of dirty water (19.0%) and the presence of sea gulls (14.8%; n = 142 responses). Seals and sea gulls were considered to be the two most important predators by 57.5% and 38.1% of the fishermen respectively (n = 134 responses).

Overall the fishermen felt that grey (29.1%), harp (28.6%) and harbour seals (23.4%) were the most problematic (n = 175 responses). Other species such as ringed, hooded and bearded seals were less of a concern. However, there were geographic differences in how fishermen ranked the various species (Table 2). Those setting nets along more exposed coastlines (Black Tickle, Charlottetown and Mary's Harbour) tended to have problems with highly migratory seal species such as harp seals while nets set in protected bays (Makkovik, Rigolet and Cartwright) were frequented by more sedentary species like harbour and grey seals.

Results of the interviews and River Observation logbooks indicate that there is considerable geographic variability in the occurrence of seal/salmon interactions as well as in the species of seal predator involved. Although some observations pertain to harbour seals and grey seals, many refer to harp seals. Satellite tags placed on harp seals during the mid-1990s indicated that they were migrating into Newfoundland and Labrador waters earlier and staying later in the spring compared to the 1980s. Tagging data also indicated that a portion of the population frequented inshore areas where they were not normally observed in such high numbers (Stenson and Sjare 1997).

Logbooks and observations made by commercial salmon fishermen along the coast of Labrador are consistent with the information provided by the tagging study. Changes in the timing of harp seal migrations into and out of Newfoundland waters during the 1990s is likely a response to changing availability of capelin and other prey species influenced by the cold oceanographic conditions at the time (Drinkwater 1996).

In addition to geographic variability, the logbook information provides good evidence for annual and seasonal variability within and between rivers. Data for several rivers suggests that the occurrence of harp seals is 'pulsed' and related to the presence of schooling, high-energy fish such as capelin, juvenile herring or smelt. Observations of harp seals in the English, Gander, Exploits, Campbellton and Humber Rivers also provide support for this link. Data from Northeast Brook suggests that at least in some areas harbour seals also exhibit pulses of activity. In two of the three years, the late August – September period of higher seal abundance overlapped with a run of juvenile herring and the presence of mackerel. Thus, a better understanding of the location and timing of schooling bait fish runs, and the timing of salmon runs, may be valuable for predicting, assessing the impact and mitigating seal/salmon interactions (particularly in relation to harp seals).

Table 2. The species composition of seals considered problematic by commercial salmon fishermen along the coast of Labrador. B. Tickle = Black Tickle; Chartown = Charlottetown; Mary's H. = Mary's Harbour. Harp and hooded seals are highly migratory: grey, ringed and bearded seals are seasonally sedentary; and harbour seals are considered resident.

Species	Makkovik %	Rigolet %	Cartwright %	B. Tickle %	Chartown %	Mary's H. %
Harp/Hooded	17.7	22.7	17.1	50.0	38.2	48.0
Grey, Ringed Bearded	52.9	36.4	55.2	30.0	44.1	40.0
Habour	29.4	40.9	27.7	20.0	17.6	12.0

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Euphausiid Availability Explains Marine Survival Variation for Barkley Sound Coho Salmon (*Oncorhynchus kisutch*) and Sockeye Salmon (*O. nerka*)

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Keywords: Salmon smolts, marine survival, euphausiids, interannual variability

We have been monitoring the population biology of euphausiids (*Thysanoessa spinifera*, *Euphausia pacifica*) from the southwest coast of Vancouver Island (SWCVI) since 1991, a period during which there have been significant ocean warming and cooling events. We have found recently that coho salmon (*Oncorhynchus kisutch*) and sockeye salmon (*O. nerka*) smolts originating in Barkley Sound feed on *T. spinifera* when they move to continental shelf waters along the SWCVI. Coho salmon ate 9–12 mm long *T. spinifera* and sockeye salmon fed on animals that were 3–5 mm in length. This information allowed us to test the null hypothesis that smolt abundance and food availability during the first marine year have no effect on the number of returning adults. The null hypothesis was rejected for both species. Results of multiple regression analyses showed that the parameter estimate for the smolt effect did not differ significantly from 1; therefore, smolt number had no compensatory or depensatory effect on returns. For coho, median *T. spinifera* abundance over June–August of the first marine year improved the regression fit and accounted for a significant proportion (23%) of the explained variation. Figure 1 shows results of a retrospective analysis of forecasts of marine survival for wild (Carnation Creek) coho salmon; data are presented as marine survival rate because Carnation Creek and Kirby Creek (another "wild indicator stream about 100 km away) have different smolt outputs. For sockeye salmon, the median biomass of *T. spinifera* over April–June of the first marine year improved the regression fit and explained 58% of the variation in the number of sockeye salmon returning to Great Central and Sproat Lakes. Fits of age-specific regressions for Great Central Lake are show in Fig. 2. Explained variation ranged between 70 and 98% depending on the lake and age-group for which the analysis was done.

Fig. 1. Results of retrospective analysis of forecasting accuracy of smolt-euphausiid regression for Carnation Creek wild coho salmon (top panel) and Robertson Creek Hatchery coho salmon. Solid circles – observed survival rate. Open circles – predicted survival rate. Error bars – 95% CL. K – observed marine survival rate for Kirby Creek coho salmon.

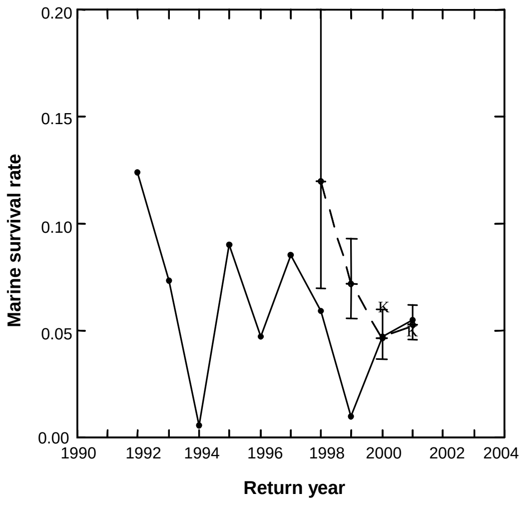
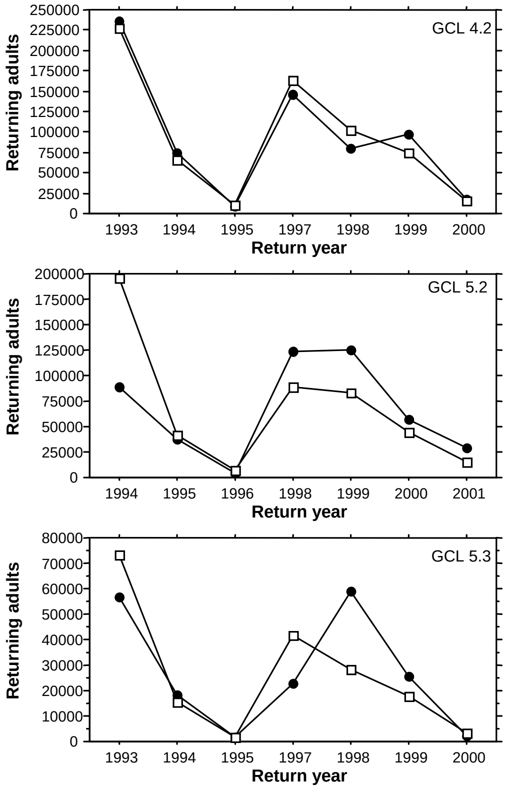


Fig. 2. Plots of observed (solid circles) and fitted estimates (open squares) of number of returning sockeye salmon by lake and age. This is a representative subset and is for the dominant age classes in Great Central Lake.



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Atlantic Salmon Autumn Pre-smolts in New Brunswick, Canada Rivers

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Keywords: Pre-smolts, movements, sonic tracking

In some Atlantic salmon (*Salmo salar*) rivers, juvenile salmon begin their movements toward the sea in autumn of the year before they become smolts. These fish are termed "pre-smolts", and we know very little about their ecology, behavior, physiology, and the adaptive reasons for their movements, and to what degree changes in these could be contributing to depressed salmon returns. Two hypotheses have been proposed for the autumn movements. The first holds that the fish have outgrown the winter shelters available to them among the substrate interstitial spaces in their home tributaries, and they move to locate larger shelters in the river's main stem. The second hypothesis is that the fish are staging toward the estuary in order to be able to rapidly enter the sea during favorable conditions in the following spring. Work involving the New Brunswick Wildlife Trust Fund, Bowater, J.D. Irving Limited, the Miramichi Salmon Association, the Tobique Salmon Association, DFO, the Université de Québec at Rimouski, and the Atlantic Salmon Federation has begun to document autumn pre-smolt abundance and movements on selected New Brunswick rivers.

Rotary Screw fish traps were installed in the autumn in the Gulquac (Saint John system), Rocky Brook (Miramichi system) and Little Main Restigouche rivers to enumerate pre-smolts and document movement timing. In 2001, pre-smolt blood samples were obtained for hormonal assays (T3, T4, Cortisol), and a sample of fish from Rocky Brook had sonic tags (VEMCO) surgically implanted in their body cavities. VR2 receivers were deployed for a distance of about 40 km along the Miramichi main stem to record signals from the sonically tagged fish in order to document their movements in the autumn and winter.

Pre-smolts were found in all the rivers monitored, although the numbers caught varied among sites and years. Within a given year, pre-smolt movements in the different rivers were initiated and peaked on roughly the same dates. Water temperature appears to be an important cue. Hormonal assays are not yet completed. Sonic tracking of pre-smolts in 2001–2002 was hampered by drought conditions and a warm winter. The former reduced water depths, and may have blocked the transmission of some of our signals. The latter resulted in unsafe ice conditions during much of the winter that prevented us from accessing the receivers to download information. The few fish that we have successfully tracked moved short distances and seem to have taken shelter in the first patches of coarse substrate they encountered during their downstream migration. More information may become available when we can download presently inaccessible receivers in the river.

Present results suggest that pre-smolts move to find winter shelter rather than as a staging movement.

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Ichthyophonus hoferi as One of Possible Causes of Increased Marine Mortality in Post-Smolts of Atlantic Salmon

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* * *

Keywords: Tuloma River, Atlantic salmon, histopathological examination, symptoms, *Ichthyophonus hoferi*

In July and August 2001 a number of adult Atlantic salmon (*Salmo salar*) from the Tuloma and Kola rivers (Kola Peninsula, Russia) were found to have multiple haemorrhages on the skin, necrosis of the fins and epidermis, extensive areas of scale loss, flat sores of 0.5–1.5 cm in diameter and epithelial tumours (Fig. 1). The muscles of examined fish were unnaturally soft.

In order to establish the cause of these symptoms, samples of liver, spleen, kidney and blood were cultured in mycological media. After 3 months' incubation at 4 – 5°C 9 cultures of a fungus identified as *Ichthyophonus hoferi* were derived.

Fig. 1. Hemorrhages and sores on the skin.

Histopathological examination of sections stained with hematoxylin-eosin revealed spores and fungal hyphae in the spleen, lumina of kidney tubules and the muscles below haemorrhages, sores and papillomas (Fig. 2). Spores were scarce, and their size was 3–10 µm. The lymphoid tissue in the spleen was reduced, kidneys showed necrosis of the tubules and haemorrahages in the parenchyma and body muscles exhibited lysis of muscle fibres and connective tissue in areas of localization of spores.

Epizootics of ichthyophonosis occasionally occur among commercial fish species in the North Atlantic, particularly in herring (McVicar 1977, 1982; ICES 1991; Hjeltnes and Skagen 1992; Karaseva et al. 1993; Sindermann and Chenoweth 1993; Karaseva and Donetskov 2001). *I.hoferi* attacks more than 70 species of fish, including salmon, and induces system mycosis (Lauckner 1984; McVicar 1977; Sindermann and Chenoweth 1993). Epizootics among salmonids thought to be caused by *I.hoferi* have been reported from trout farms in Europe and North America (Neish and Hughes 1980). In wild populations of salmonids a high prevalence of *Ichthyophonus hoferi* disease was reported for *Oncorhynchus tshawytscha* from the Yukon river (ICES 2001).

Symptoms of the disease are species-related and depend on the condition of individual fish (Neish and Hughes 1980). For example, Dorier and Degrange (1961) observed chaotic, spiral-wise movements of diseased farmed rainbow trout which develop when the nervous system has been affected. Some individuals ceased growth and became debilitated, while other, even severely affected, fish did not differ from healthy individuals.

Rucker and Gustafson (1953) noted that as the disease developed trout showed clear signs of agitation, and the skin along the lateral line and then in other areas of the body became darkened, and the belly was observed to protrude because of the increased size of the internal organs. However, the brain was seldom found to be affected.

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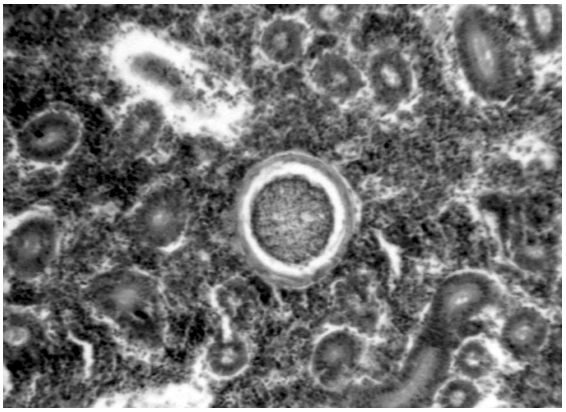
Fig. 2. A spore in the kidney tissue of Atlantic salmon.



The most comprehensive description of ichthyophonosis symptoms is given for herring, in which a major sign of the disease is small light nodules of connective tissue which develop beneath the skin and in the internal organs. However, the absence of such nodules does not prove that fish are uninfected with *I.hoferi* (Neish and Hughes 1980; Sindermann and Chenoweth 1993).

The symptoms of ichthyophonosis in Atlantic salmon are unknown. For example, nodules were not found in the salmon examined. However, external signs suggest that the development of symptoms in salmon follows the pattern typical of herring. A certain distortion of the clinical picture may be attributed to specific features of the physiological condition and immune status of fish.

According to a number of authors infection of fish with *I.hoferi* occurs during feeding on food containing viable spores of fungus (Rucker and Gustafson 1953; Dorier and Degrange 1961; Lauckner 1984). For example, Marshall and Orr (1955) referred to *I.hoferi* (*Ichthyosporidium*) as a parasite of Calanus.

According to data provided by Hansen and Pethon (1985) the diet of salmon at sea is dominated by crustaceans, squid and fish. Euphausiidae and Hyeriidae were the most frequent crustacean prey. No records of infection of these crustaceans with *I.hoferi* were found.

Calanus has not been identified as food for Atlantic salmon. However, it could be ingested by fish with other food. Besides, *Calanus finmarchicus* could play a role in the diet of post-smolts, and, hence, be a source of infection but at present only limited information is available on the diet of post-smolts.

Salmon show a dietary preference for other fish species. In samples obtained between 1969 and 1972 the frequency of occurrence of fish in salmon stomachs was on average 61.4% (Hansen and Pethon 1985). According to Grønvik and Klemetsen (1987), 85% of stomachs of salmon caught near Northern Norway contained herring. Therefore, it is quite likely that salmon may contract *I.hoferi* through feeding on infected herring.

Post-smolts may contract *I.hoferi* through transmission of the infectious agent from fish to fish during feeding migrations with herring shoals. For farmed salmon, feeds based on meal or mince of Clupeidae could be a source of infection. This possibility should not be disregarded, since the range of temperatures which spores can tolerate is unknown.

In the wild it is difficult to establish the cause of death of fish, except in the case of large-scale mortalities. For example, in 1991 during an outbreak of the disease in the Kattegat and Skagerrak the mortality of fish was so high that dead herring were found along the coast of Denmark (ICES 1991). Repercussions of the disease for wild populations of fish are, as a rule, identifiable only after an epizootic. They appear not only in the form of a decline in abundance but also as changes in population structure (Winters 1976; Neish and Hughes 1980).

Many attempts have been made to assess the magnitude or proportion of natural mortality caused by *Ichthyophonus* during an epizootic by using indirect methods (McVicar 1982; Munro et al., 1983; ICES 1993), but these were unsuccessful. Nevertheless, the results obtained and analysis of data available in the literature suggest that in recent years conditions have developed in northern seas which facilitate infection of both adults and post-smolts of Atlantic salmon with *I.hoferi*.

This is a dangerous disease, the consequences of which are difficult to assess for wild populations of fish. For shoaling species, ichthyophonosis often leads to mortality of a part of the population. Salmon represent both an intermediate (plankton-post-smolt) and a final (plankton-herring-predator) constituent of the food web, therefore, it can contract *Ichthyophonus*, and post-smolts are the most vulnerable link in this chain.

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A Synthesis of the Joint Meeting

Causes of Marine Mortality of Salmon in the North Pacific and North Atlantic Oceans and in the Baltic Sea

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INTRODUCTION

The increased marine mortality of some salmon stocks in recent years is a pressing concern in both the North Pacific and North Atlantic Oceans as well as in the Baltic Sea. In response to this situation a joint meeting, co-sponsored by IBSFC, ICES, NASCO, NPAFC and PICES, was held in Vancouver, Canada during 14–15 March, 2002 to review and exchange information on the causes of recent changes in marine mortality of salmon. The objectives of the meeting were to: (1) improve understanding of the mechanisms resulting in the increased mortality, (2) to identify research priorities, and (3) to stimulate enhanced cooperation and information exchange in the future. The meeting, which was the first of its kind to bring together five inter-governmental organizations to review information on salmon in the three areas, was attended by 142 delegates. Sessions were held on the status of salmon stocks and fisheries, and the possible factors associated with increased marine mortality of salmon, which were considered under three groupings - climate and oceanography, human-induced effects, and ecological factors. In addition there was a synthesis and general discussion session. A total of 21 oral and 16 poster papers was presented. In this synthesis we have summarised the main points that emerged from these presentations and the subsequent discussions, and have drawn some conclusions.

STATUS OF SALMON STOCKS AND FISHERIES

Baltic Sea

- more than half of the rivers historically known to support Atlantic salmon have been lost to production as a result of habitat loss in fresh water (mainly through hydro-electric developments);
- compensatory releases of hatchery smolts led to high exploitation of the remaining wild stocks, particularly in sea fisheries;
- in 1997, a Salmon Action Plan was adopted by the IBSFC, with the objective of achieving 50% of the estimated historical production of wild salmon by 2010 through reduced TACs and more focussed targeted harvesting of reared salmon;
- following the introduction of recent management measures, ICES had advised that most, but not all, wild salmon stocks are improving but there are concerns about the impacts of a neurological disorder, known as M74 syndrome, and seal predation.

North Atlantic

- there have been major reductions in salmon fisheries at sea but the abundance of salmon stocks has not responded;
- both European (particularly the southern component) and North American stocks, particularly multi-sea-winter stocks, have declined, with North American returns currently at the lowest recorded levels in history;
- for some monitored stocks marine mortality is currently double the level of the 1970s;
- it has been suggested on the basis of reconstructed climate cycles that the present abundance of North American Atlantic salmon is the lowest it has been for 300 years and that there is an increasing anthropogenic influence on these stocks.

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Pacific Ocean

- stock status varies regionally from favourable to endangered, and low marine survival is a problem for some stocks;
- US West Coast stocks are at very low levels and while Alaskan stocks are generally at high levels there is serious concern about Bering Sea stocks of chinook and chum salmon, probably due to reduced marine survival;
- in Canada, greatest concern is centered on several coho stocks that are at critically low levels of abundance; the other species of Pacific salmon are generally at low levels of abundance, but certain stocks of sockeye, chinook, and steelhead present serious conservation concerns; in most cases those stocks with the most serious conservation concerns are known to have reduced marine survival;
- stock status in the Far East is mixed but Russian coho and chinook salmon stocks have declined; the survival of Japanese hatchery chum salmon is high but declining.

On the basis of the information presented on status of stocks and fisheries, it is clear that there is concern about the low marine survival of some stocks in all three areas, that in response to these concerns there have been major reductions in marine fisheries, and that for some stocks these restrictive measures have not yet resulted in improvements in status. Particular concern was expressed about the status of stocks at the southern limits of the species' range, inevitably raising concerns about the effects of global warming. Some US stocks of both Pacific and Atlantic salmon have been designated under the Endangered Species Act.

FACTORS AFFEECTING SURVIVAL OF SALMON AT SEA

Research on salmon at sea has, until recently, been given relatively low priority rather than being considered fundamental to rational management. As a result the factors affecting survival of salmon at sea are poorly understood; new evidence, however, suggests that these factors may be driving abundance and need to be better incorporated into stock assessments. If the key to good management is knowledge, then it is important to develop a clearer understanding of this phase of the salmon's life-cycle. The joint meeting provided an opportunity to review new information on the factors affecting survival of salmon at sea.

Climate and oceanography

- marine survival of salmon stocks shows spatial coherence on scales related to regional ocean conditions. For example, in the North Pacific survival rates among stocks are positively correlated across local or regional spatial scales of several hundred kilometres but not at scales nearer to a thousand kilometres;
- environmental variability (e.g. sea surface temperature, upwelling) is correlated to salmon survival, and may provide a basis for forecasts useful to management;
- decadal-scale climate regimes lead to major changes in marine ecosystems, affect salmon production, and can have a profound effect on the population structure and diversity of salmon;
- links between the North Pacific and North Atlantic climatic regimes have resulted in common responses in salmon stocks. This was particularly marked for the climate regime shift in 1989, which resulted in low marine survival of Atlantic salmon and some stocks of Pacific salmon;
- while the precise factors affecting mortality at sea remain unclear, and may differ within and between ecosystems, changes in early marine growth of post-smolt salmon appear to be important;
- the effects of even small shifts in climate (on the timescale of a few years) can exceed the effect of long-term management actions on salmon population dynamics.

Human-induced effects

- exposure to sub-lethal concentrations of contaminants (e.g. pesticides and endocrine-disrupting chemicals) in fresh water or estuaries may delay or inhibit smolt migration, affect adaptation to marine conditions or lead to poor growth;
- other factors in fresh water (e.g. acidification, water temperature, factors affecting size and condition of smolts) may subsequently affect survival at sea. Appropriate targeting of management actions will require better identification of the relevance of these factors;
- there is concern about the impacts of aquaculture and hatchery practices in all three areas. In the North Pacific and Baltic, large-scale hatchery releases have led to concerns about the genetic impact of cultured salmon inter-

breeding with wild salmon and over-exploitation of wild salmon in fisheries. In the North Atlantic and in British Columbia, escapes of farm Atlantic salmon are a concern;

- diseases and parasites from aquaculture may cause problems for wild salmon:
  - in Norway it has been estimated that sea lice from salmon farms may result in up to 95% mortality of wild Atlantic salmon in some areas, despite target lice levels in farms conforming to regulatory requirements;
  - in the Baltic there are concerns about the spread of diseases, e.g. furunculosis, from coastal fish farms to wild salmon;
- high concentrations of persistent pollutants are a concern in the Baltic Sea and could have significant implications for the future of the salmon fishery. Eutrophication in the Baltic Sea is also a concern;
- human-induced changes in genetic diversity may reduce the resilience of salmon to environmental changes in both freshwater and marine environments. It is vital that in all three areas maintenance of biodiversity (life-history and genetic diversity) must be one of the key goals of salmon management.

Ecological factors

- the impact of predation on salmon stocks in all three areas is poorly understood but thought to be significant;
- in recent years the populations of many salmon predators, including species protected by legislation, have increased while salmon abundance has declined;
- there is little quantitative information on the impact of predators on salmon fisheries and stocks. However, the impact of some species is thought to be significant, e.g. salmon sharks in the North Pacific and pinnipeds in all three areas;
- much of the available information concerns predation in rivers and estuaries rather than at sea;
- the intensity of predation is variable and may be related to climate change and availability of other prey. For example, a significant cold-water event in the early 1990s led to a shift in diet of gannets off Newfoundland and an increase by an order of magnitude in the proportion of salmon post-smolts in the diet;
- in the Baltic, M74 syndrome, caused by thiamine deficiency, possibly related to pollution of the Baltic or changes in the prey species of salmon, has led to very high mortality of salmon fry and is a severe threat to the survival of the remaining wild populations of salmon;
- there is an urgent need to develop a basis for predicting the severity of M74 so that its impact can be taken into account in management decisions concerning the wild stocks of salmon.

DISSCUSSION

During the discussions a number of points emerged, including the following:

- the meeting had produced a valuable exchange of information. Efforts should be made to continue the dialogue, to enhance coordination of the work being undertaken in the three areas, and to improve cooperation in the development of new technologies for studying salmon at sea;
- it is likely that a variety of factors are influencing mortality of salmon at sea and that a clearer understanding of these will require a multi-disciplinary research effort, that there may be synergistic effects and that freshwater factors which may subsequently affect survival at sea should not be ignored;
- a priority area for research is to improve understanding of salmon migration patterns, distribution, and habitat utilization at sea, which may be stock-specific;
- a serious problem in understanding the marine phase of salmon is related to the scale, and therefore the cost, of research. There is a need to build on the progress being made. A number of suggestions as to the way forward were made, including:
  - the use of long-term cooperative studies in experimental marine areas;
  - analysis of historical scale collections;
  - use of electronic tags;
  - international cooperative research focusing on specific areas of the migratory range;
- salmon are highly prestigious species, in which there is much public interest. There is a need for effective communication so as to gain public support for scientific research on salmon at sea. NASCO has established an International Cooperative Salmon Research Board to identify research gaps and priorities and to seek funding from private sources to augment public spending.

CONCLUSIONS

The joint meeting demonstrated that progress is being made in understanding the factors affecting salmon at sea through ongoing research programmes in the three areas. Newly developed expertise and tools (such as electronic tags and live-capture trawls) will facilitate better and more cost-effective research on salmon at sea. The challenge will be to deploy these technologies effectively in the future. A priority for research is to increase understanding of distribution and migration at sea and there are likely to be cost savings and other benefits from internationally coordinated research. In order to assess trends in marine survival there is a need to maintain and critically appraise monitoring programmes. In particular, it should be recognised that information from hatchery salmon may not be representative of survival trends for wild salmon and that changes in hatchery practices can influence trends in marine survival of hatchery stocks.

The joint meeting demonstrated the benefits of, and the need to maintain and enhance, cooperation and information exchange within and between the North Pacific and North Atlantic Oceans and the Baltic Sea. There was strong agreement from those attending the workshop that there is substantial marine research on salmon now underway, the results from which would form the basis for an expanded international symposium on the marine survival of salmon. The development of such a symposium in the near future would provide a focus for international cooperation and exchange of information between scientists in the three areas on the problems facing salmon stocks in the marine environment, and provide an opportunity to communicate findings and ideas to the public so as to enhance support for research on salmon at sea.

APPENDIX 1

List of Participants

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Okhanov, Alexander
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Perry, Ted
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ISSN 1029-5917

Printed in Canada