

*NORTH
PACIFIC
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FISH
COMMISSION*



BULLETIN NUMBER 3

***A Review of the Research on the
Early Marine Period of Pacific Salmon
by Canada, Japan, Russia, and the
United States***



Edited by: Philip Symons

VANCOUVER, CANADA, 2003

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Preface

The International Workshop on Factors Affecting Production of Juvenile Salmon: Comparative Studies on Juvenile Salmon Ecology between the East and West North Pacific Ocean was held in Tokyo, Japan, on October 29, 2000. The Workshop was hosted by the North Pacific Anadromous Fish Commission (NPAFC), and co-organized by the NPAFC and the North Pacific Marine Science Organization (PICES). The Workshop Organizing Committee consisted of the NPAFC and PICES representatives, and was chaired by the Chairman of the NPAFC Committee on Scientific Research and Statistics. All necessary arrangements were made by the NPAFC Secretariat in cooperation with the Organizing Committee and local coordinators.

Over 80 scientists, industry representatives, and fisheries officials attended the Workshop. There were 5 review, 7 oral, and 14 poster presentations followed by a general discussion session. Extended abstracts of the oral and poster presentations were published as the NPAFC Technical Report No. 2, which also contains

opening remarks by the Chairman of the NPAFC Committee on Scientific Research and Statistics at that time and the Chairperson of the PICES Science Board, and a short review of the Workshop by the Chairman of the Organizing Committee.

This Bulletin is composed of four national review papers, which were originally presented at the Workshop by Canada, Japan, Russia, and the United States. Those papers were re-drafted after the Workshop in a format prepared by the Organizing Committee for easy comparison, and in order to include latest information. This Bulletin also includes an "Introduction", which summarizes the papers, prepared by the present Chairman of the NPAFC Committee on Scientific Research and Statistics, and indices on major topics by species and location names. The materials presented in this Bulletin were peer reviewed and edited. Biographies of the authors and reviewers are at the end of the bulletin.

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Introduction

The reports in this Bulletin summarize the studies of the early marine period of the life history of juvenile Pacific salmon. The format and contents of the four papers vary slightly because the reasons for juvenile salmon studies differ among the four countries. The research conducted by each country reflects the relative importance of the various species of salmon as well as the particular management issues. All reports document the history of the early marine studies and all reports provide a comprehensive list of publications. Authors note that not all material has been published in regular publications requiring some recognition of difficult to find reports and even, on occasion, personal communications. The authors of the four reports did not write a critical review, rather they summarized past studies by reporting results identified in the original papers. Not all statements are referenced so that the text is more readable. Readers who require more detail or specific references may need to review the list of references and refer to original papers. It is useful to use this Bulletin in association with the summaries of the life histories of Pacific salmon published in Groot and Margolis (1991. *Pacific salmon life histories*. UBC Press, Vancouver, Canada). The papers in Groot and Margolis (1991) also provide additional detail about the location of marine rearing areas of Pacific salmon for each country.

This introduction highlights the contributions of each paper by providing a very brief executive summary of each paper along with some commentary on the relationships of the results of the research among the four countries. The authors of each report provided a summary of their expectations of future issues and the reader is encouraged to find these sections in each paper as it is informed speculation that has many common themes among the four countries. The order of papers in the Bulletin is alphabetical and the same order is used in this summary.

Canada

Pacific salmon on the west coast of Canada have been a major focus for human society for thousands of years. Commercial harvests of Pacific salmon began about 1870, but the active management of Pacific salmon did not begin until much later. In fact, it wasn't until the 1990s that coho salmon were managed in a manner similar to the other species of Pacific salmon. In 1937, a formal agreement was ratified with the United States of America to establish the International Pacific Salmon Fisheries Commission to manage sockeye salmon in the Fraser River. In 1959, it was agreed to include Fraser River pink salmon in the agreement. In 1953, the International North Pacific Fisheries Commission was estab-

lished and activities associated with assessing the impact on Canadian salmon of the high seas Pacific salmon fishery consumed much of the Canadian research effort on Pacific salmon. Thus, it was not until 1955 that scientists started their investigations of the early marine phase of Pacific salmon. This early research was carried out to improve the ability to predict the number of returning adults. Underlying this research was a strong belief that abundance could be rebuilt to historic levels, even though the natural factors regulating abundance were completely unknown. One of the first studies by Parker in the mid-1960s remains as one of the best Canadian studies on the timing of early marine mortality. This study concluded that 55–77% of pink salmon died over the first 40 days in the ocean and 78–94% of those surviving, died over the remaining 410 days at sea.

In the early 1970s, the general abundance of all species of Pacific salmon continued to decline despite efforts to control fishing and protect freshwater habitat. A concern was that the rearing areas in estuaries might in some way be associated with the ability for the managed salmon stocks to recover. Emphasis shifted in the 1970s as studies focused on chinook and coho salmon, although chum salmon studies continued. Excellent research was conducted on the linkage between food available to juvenile salmon in the nearshore areas and the survival and behaviour of chinook, coho, and chum salmon. The dependence of juvenile salmon on estuaries was found to be specific with juvenile chinook salmon being most dependent on the estuary. It was about this time that it was discovered that chinook salmon had two distinct life history types. The ocean type juveniles remained in fresh water less than 12 months while the stream type remained in fresh water more than 12 months and entered the ocean at a considerably larger size. It was in the 1970s that Canada started its Salmonid Enhancement Program that originally was designed to double the production that existed in the early 1970s. Unlike the Japanese hatcheries studies, there was no direct linkage between the Salmonid Enhancement Program and the early marine research studies, perhaps because there was a strong belief that the ocean was not limiting production. However studies on salmon diets continued with results that were similar to the observations reported in the other papers in this Bulletin.

In the 1980s there was a strong emphasis on research on the early marine period of Pacific salmon. Juvenile sockeye migrations were monitored to determine if a relationship existed between the route to the high seas taken by juveniles and the route taken by the adults that returned. There was a large-scale study to determine the importance of estuarine rearing for chinook salmon. This

study was able to demonstrate that there was an interaction between hatchery and wild chinook salmon in the estuary that needed to be minimized if wild chinook salmon were to be maintained. New gear for capturing juvenile salmon were developed; first using a large beam trawl, then settling on a modified mid-water rope trawl that was capable of fishing on and near the surface. The largest study of the factors affecting the early marine survival of juvenile Pacific salmon, the marine survival of salmon, or MASS program, was conducted from 1987 to 1991. This was a multidisciplinary study involving fisheries and oceans scientists. The results of this large program are reported in the Canadian paper, however more material remains to be published.

One area that has received almost continual research attention is the Strait of Georgia. This is the most important rearing area for juvenile Pacific salmon as the adult returns from the juveniles that enter the Strait can account for up to about 40% of the Canadian Pacific salmon catch. The series of investigations are summarized in the Canadian report, including detail of diets and predation. One study of predators, identified the river lamprey (*Lampetra ayresi*) as a major predator of juvenile Pacific salmon. Although the river lamprey is a different species than the lamprey identified as a major predator in the Russian paper, the impacts were similar. Another study in Masset Inlet clearly showed that coho will eat both pink and chum juveniles, with a preference for pink salmon. A study of smolt size and early ocean growth of coho salmon concluded that large coho size as a juvenile did not give a constant survival advantage, but large smolts did survive better in years when marine survival was relatively poor. Offshore Pacific salmon research started in the 1990s after a pause of almost a quarter century. This work was strongly influenced by a co-operative research cruise on a Russian research vessel in the Gulf of Alaska. The results showed that juvenile Pacific salmon migrated northward along the coast with virtually no juveniles beyond the shelf break.

As hatcheries increased in prominence, several studies researched the potential impact of hatchery fish on wild fish. One study in the Campbell River area in the late 1980s showed that wild chinook fry represented 55% of the total catch of young salmon but consumed only 28% of the total rations available to the young salmon. Coho and chinook hatchery-reared smolts were only 28% of the catch, but consumed 65% of the available rations. Thus there was evidence that the hatchery-reared fish had a higher feeding rate than wild fish. In a Strait of Georgia study, in the 1990s, it was shown that the percentage of hatchery coho had increased from almost zero in the late 1960s to as high as 79% in the mid-1990s without an increase in coho abundance.

In general, the conclusions from the Canadian research are that there are similarities with the observations in the other papers in this Bulletin. Pink salmon prefer to eat small items, chum salmon prefer oikopleura, and coho

and chinook salmon consume more fish than the other salmon species. Rates of growth are rapid in the early marine period, but there is considerable uncertainty in the measures of these rates. There is evidence that these early rates of growth are related to marine survival, but the mechanism appears to be more complicated than size related predation. Canadian research showed that the conditions in the ocean can limit survival. In fact, there is solid evidence that the marine survival and resulting adult abundances are related to climate. The Canadian report concludes with a series of questions and recommendations such as why do some stocks of salmon have better marine survival than others and how do juvenile Pacific salmon survive the first marine winter. It is recommended that a plan be developed to adapt to the expected changes in climate. A team of experts is proposed to be the most efficient way of doing this and experts from NPAFC would make a significant contribution.

Japan

Japan may have the longest recorded history of commercial Pacific salmon fishing with records dating back over 400 years. At present, virtually all of the Pacific salmon produced in Japan, are produced artificially in hatcheries. Most of this production is chum salmon (about 90%). The remaining production is pink salmon (5% to 10%), with a small production (less than 1%) of masu salmon (*O. masou*). The artificial production of chum salmon has been very successful as indicated by the maximum return of 89 million fish in 1996 compared to average returns of about 3 million fish between 1900 and 1970. Returns have declined since 1996 for reasons that remained to be explained.

Artificial rearing of Pacific salmon started in 1876 but did not reach a large scale until 1888. At present there are 21 national, 13 prefectural, and 269 private hatcheries in Japan. The number of juveniles produced in these hatcheries increased from 800 million in the early 1970s to 2 billion in 1982. Production has remained at about 2 billion since 1982. The return rate, or marine survival, increased from 2% in the mid-1960s to over 3% after the 1984 brood year. The increase in return rate is believed to result from improved hatchery practices and improved ocean conditions. A return rate of about 3% means that 97% of the juveniles that entered the ocean died. A change in marine survival of only 1% makes a tremendous change in the number of adult fish that return. It is remarkable that the marine survival has been rather constant around the 2% to 3% rate.

The rivers that naturally produce chum salmon in Japan are almost all small, and without estuaries. Thus, the focus for Japanese research on the early marine period was in the near shore area in the early years and offshore areas in recent years. The objective of the research has been to optimize the timing of the release of juveniles from hatcheries and to maximize the production from

hatcheries. Most of this research has been on chum salmon, which are at the southern limit of their geographical range in Japan.

Japanese research has shown that juvenile chum salmon are in low abundance in the near shore areas in April. Their abundance increases rapidly from late May to early June and decreases rapidly by mid-June. The timing of the rapid decrease in abundance appears to be consistent among years. A decrease in the abundance of food organisms appeared to be the main stimulus for juvenile chum salmon to move offshore. However, offshore migrating chum salmon were concentrated in areas with a surface temperature from 9° to 13°C and a surface salinity from 31.0 to 33.9 psu. There were size-related distribution patterns that fell into size ranges of about 30–50 mm, 50–80 mm, 80–120 mm, and larger than 120 mm. Juveniles, 80–120 mm were in the process of migrating offshore.

Feeding of juvenile chum salmon was found to be very selective as observed in the studies of all countries. Japanese studies showed that the diet of juvenile chum salmon does not usually correlate well with zooplankton composition collected in the same area. It is clear that juvenile chum salmon actively searched for their prey. Harpacticoid and calanoid copepods were the most important prey items of juvenile chum salmon. Prey size was an important factor. As chum size exceeded 55 mm, diet changed to larger copepods and euphausiids. Studies using RNA-DNA ratios and triglyceride contents suggested that pink salmon and chum salmon differed in their early growth strategies. Chum salmon had faster growth rates and less energy storage in the early stages, but decreased growth rate and increased energy storage as growth progressed. Pink salmon had low energy and slow growth rates at first, but both increased as they grew.

Recent research has been through cooperative studies with Russian scientists. These studies found that juvenile chum salmon rear mainly in the southern and central Okhotsk Sea from summer through to November. They migrated out of this area through the Kuril Islands and into the western North Pacific Ocean in the late autumn and early winter. One study showed that 90% of the juvenile salmon were shallower than 40 m during this migration. A small percent (2.8%) were detected in water deeper than 70 m. In 1993 and 1996, the abundance of juvenile chum salmon in one area of the Okhotsk Sea was estimated to be 60–100 million fish and 200–334 million fish respectively. Chum salmon of Japanese and Russian origin reared in this area, thus this abundance estimate provided a general indication of the dominance of chum salmon in the surface waters in this area. Both the Japanese and Russian studies clearly showed that the Okhotsk Sea is a major rearing area for chum salmon as well as for pink salmon. Pink salmon juveniles appeared to have migration patterns similar to chum salmon. Large concentrations of juvenile pink salmon were observed in the southern Okhotsk Sea in October and November.

Movement offshore occurs late in the year. In general, little is known about the winter distributions of the juveniles and about the factors that affected their survival during the first marine winter.

Studies of early marine mortality identified relatively few predators. In a review paper, 90 fish species were recorded to occur in the same habitat as juvenile chum salmon, but only 9 were identified as predators of chum salmon in the near shore area. Predation was recognized as a major cause of mortality immediately after chum were released from the hatchery, but rates of predation by some species declined after a few weeks. Studies of predation by sea birds suggested that they might cause more mortality than fish predators. Japanese studies can be summarized as identifying five species of sea birds and 9 species of fish as major predators of chum salmon. However, there have been no quantitative studies of the impact of predation on the early marine survival of juvenile chum salmon.

In the studies of juvenile rearing areas in the Okhotsk Sea and in the western North Pacific Ocean off Kuril Islands, 24 species of fishes and two species of squid were observed in a common habitat. Juvenile salmon were the most abundant; followed by myctophids, arabesque greenling, squids, and the deep sea smelt (*Leuoglossus schmidtii*). It is apparent that this is an important summer feeding and rearing area. It could be hypothesized that juvenile salmon are not experiencing heavy predation at this time as major predators were not identified.

It is in the Okhotsk Sea where there will be an interaction between hatchery-reared and wild chum and pink salmon, however, there has been limited research to study interactions. All Pacific salmon producing countries now recognize the importance of studying the relationship between the two rearing types. Japan proposes to study where and when the predominately wild, Russian chum stocks mix with Japanese stocks in the Okhotsk Sea. Japan proposes to continue to improve the understanding of the mechanisms that regulate the marine survival of hatchery-reared chum salmon once they enter the ocean. A priority for Japanese research to improve the forecasts of the recruitment of returning adults is similar to the priority of Russian research. The decline in marine survival after 1996 does not appear random, although it does appear to be natural. A better understanding of where, when, and how much mortality occurs in the various seasons of the first ocean year, will help explain the mechanisms that caused the decline and thus will help optimize hatchery production. We can assume that the biological basis for chum behaviour and survival is similar for all stocks. Thus, the detailed investigations of Japanese scientists should provide insights on issues such as the importance of estuaries, the importance of growth in the first four weeks in the ocean, and the role of predators in recruitment, that will improve the management of all chum stocks in all countries.

Russia

The first extensive studies of the early marine period of Pacific salmon were carried out by Russian scientists beginning in the 1960s. Pacific salmon are an important part of the commerce and culture of Russians living along their Pacific coast as indicated by the establishment of research laboratories in Khabarovsk, Vladivostok, Yuzhno-Sakhalinsk, Petropavlovsk-Kamchatsky, and Magadan. Over the past decades, literally thousands of scientists and support staff have studied the ecology of juvenile salmon in the early marine period with an emphasis on assessing the abundance of the returning adult pink, chum, and sockeye salmon. Significant advances occurred in their research when small pelagic trawls were developed in 1981 and perfected for assessment use by the mid-1980s. Forecasts of returning abundances using estimates of spawning escapements were adjusted using information from abundances estimated both inshore and offshore and from growth. No other country uses information from juvenile surveys to complement their forecasts of the number of returning adults.

Russian studies emphasized related feeding to the availability of food. All juvenile Pacific salmon were found to exhibit selective feeding, but their food preferences became even more selective after their seaward migration. There results of the Russian studies were consistent with the observations in the other countries of feeding habits and migratory behaviour. For example, when chum salmon first enter the ocean, they feed extensively on harpacticoid copepods. These preferences changed to calanoid copepods and then to euphausiids as the juveniles grew. The Russian studies also showed that chum salmon remain in the near shore areas longer than pink salmon juveniles.

Hatcheries are a common approach for the management of Pacific salmon in Russia, as they are in Canada, Japan, and the United States. Hatcheries are used more extensively in the Sakhalin Islands than in any other region of the Russian Far East. There have been a number of studies in Russia that have attempted to assess the marine carrying capacity for juvenile Pacific salmon so that there is optimal use of both hatchery and wild production. There also were studies of the potential interaction between hatchery produced juveniles and wild juveniles in the juvenile rearing areas. These are difficult studies and they represent a challenge for future research by Russian scientists.

A common source of investigation among the four papers in this Bulletin has been the determination of the factors that cause the very large early marine mortality. In general, only a very small percentage (2% to 5%) of the juvenile salmon that enter the ocean, survive to return as adults. It is believed that predation causes most of this mortality shortly after the juvenile salmon enter the ocean. Another way of looking at this problem would be to determine why there are returns from virtually all

stocks when the early marine mortality is so large. Why, for example, in some years would the mortality not be 100%; in such cases the stock would be lost if it were pink salmon, or a brood year could be lost if it were a chum salmon.

Russian studies identified a relatively small number of predators of juvenile salmon in different areas that accounted for reductions in abundance ranging from 2% to 96%. The most important predator identified was the Arctic lamprey (*Lampetra japonica*), which consumed, up to 93% to 96% of the juvenile population in some years. Lamprey were considered to be a major predator because salmon were in contact with lamprey for 1.5 to 3.0 months, compared to shorter exposures for other predators such as Arctic smelt (*Osmerus mordax dentex*) and Ussuri whitefish (*Coregonus ussuriensis*). Lamprey predation was considered to affect juvenile salmon in the Sea of Okhotsk and north Sakhalin Island because the migration paths of the lamprey and salmon were similar. In the South-west Sakhalin, West and East Kamchatka, the main predators were Arctic smelt, Arctic char (*Salvelinus alpinus*), Siberian char (*Salvelinus leucomaenis*), where they consumed up to 70% of pink and chum juveniles. Russian studies clearly showed that significant amounts of mortality occurred later in the first marine year. Methods used to estimate the mortality of pink salmon, for example, showed that the mortality in some broods changed from 55% to 96% after migration offshore late in the first marine year.

Future research in Russia will emphasize the need to understand the interaction between hatchery and wild fish. It is no longer believed that the carrying capacity in the ocean is limitless. Thus, it is important to determine a rational combination of the two rearing types. The assessment of recruitment remains as the highest priority in Russian research. Although Russian forecasts have been very good, there is the expectation of improvement through the use of surveys before and after the offshore migration of juveniles. All countries are beginning to manage fisheries on an ecosystem basis and Russia will carry out early marine studies that investigate the impacts of fishing on the interrelationships among species.

United States

Research on the early marine period of Pacific salmon by United States has been distributed among 7 species including steelhead trout (*O. mykiss*) and the coastal cutthroat trout (*O. clarki clarki*). The investigations in the United States tend to be associated with two geographical areas; the area off the West Coast (Washington, Oregon and California); and the area off Alaska. Most studies off the West Coast have been on coho, chinook, and steelhead. Studies off Alaska have researched pink, sockeye, and chum, more than the other species. The objectives of the research have changed over the years. The original research tended to be

associated with defining the distributions of Pacific salmon of United States origin. Understanding where Pacific salmon produced in United States migrated and reared was important for the protection of Pacific salmon on the high seas and for cooperative management of stocks from Canada and the United States that were jointly fished. More recently, in addition to these international considerations, there was regional interest based on the insatiable curiosity of biologists to understand the biology and behaviour of Pacific salmon.

Off California, chinook salmon are the most abundant species. They are at the southern limit of their distribution and historically were relatively abundant. At present, the various stocks appear to be at record low levels or extinct. Chinook are virtually all the ocean type, spending about 40 days in estuaries or close to shore before moving off shore. In recent years, large numbers of juvenile chinook salmon have been released from hatcheries in California. In Oregon and Washington, the two most abundant species are chinook and coho salmon, but steelhead trout are a species of major interest. The total catches of Pacific salmon off California, Oregon, and Washington are only about 5% of the total catch in the United States in the last decade, but there is exceptional interest in the health and management of Pacific salmon in this area. There is a diversity of issues related to Pacific salmon produced in the Columbia River and in Puget Sound. A number of stocks have been identified as requiring special protection and there is growing concern about the interaction between wild and hatchery-produced salmon. Washington hatcheries produced large numbers of chinook, coho, and chum salmon, which some believe affect the abundance of wild salmon and others believe, are essential to support the important commercial and recreational fisheries. The research carried out on these "southern" stocks has identified a diversity of behaviours and even life history strategies. For example, the direction of coastal migrations of juvenile chinook salmon from Washington and Oregon is stock specific, with some moving north to waters off Canada and Alaska and some moving south to waters off Oregon and California. Juvenile steelhead trout were reported to move directly offshore soon after they enter the ocean early in the spring or summer.

Alaska is the world's largest producer of sockeye salmon and has the largest spawning population in Bristol Bay. Thus, a focus for research has been on the factors that affect the marine survival of juvenile sockeye salmon. Studies have concentrated on the variety of stock specific behaviours that may contribute to specific marine distributions and even subsequent recruitment. Sockeye salmon smolts enter Bristol Bay from May to mid-July and remain inshore until the fall when they move into the Bering Sea. The northwest extent of their distribution in the Bering Sea in the fall and winter remains to be determined. The area where juvenile sockeye salmon are distributed at the end of their first marine winter may be dif-

ferent for individual stocks or stock aggregates.

Alaska is also a major producer of pink and chum salmon. Catches of Pacific salmon in the Alaskan fishery increased to historic levels in recent years. Associated with these increases has been a well-organized attempt to understand the mechanisms that caused the increases and the occasional unexpected decrease. Current research is multi-disciplinary and is well-positioned to solve some problems common to all Pacific salmon management. In recent years, there has been a large production in hatcheries and the impact of hatchery-reared pink salmon on wild stocks has become an important area of research.

Studies of juvenile salmon during the first marine winter is one of the current priorities of the North Pacific Anadromous Fish Commission. Research reported in the paper from the United States identifies observations similar to research results in Asia. Most research in United States is now conducted using pelagic trawls. Although the size of the trawls differ among investigations, there has been considerable progress towards standardizing sampling methods. Observations, to date, indicate that pink and chum fry remain inshore longer than coho, sockeye and chinook juveniles which move into open water sooner. Faster growing individuals may move into open waters sooner. One difference between research in United States and in Asia is the emphasis on the importance of estuaries as rearing areas for juvenile salmon. The role of estuaries has been of general interest and thus their importance for salmon has received considerable attention in United States and in Canada.

Diets of juvenile Pacific salmon have been fairly well documented in the research in United States. There was a similarity in the types of prey consumed by the various salmon species with Asian studies, as was the selectivity in the feeding of pink and chum salmon. Coho and chinook salmon were reported to be more piscivorous and more opportunistic than pink, chum, and sockeye. Predation studies also produced common observations common to Asian studies. Despite some extensive studies that examined potential predators of juvenile salmon, studies within United States waters have found relatively few documented examples of large numbers of juveniles being consumed in the marine environment. In the most extensive study, nine fish and seabird predators were identified that apparently consumed about one half of the pink salmon juveniles in the study area. This is identical to the number of fish and sea bird predators identified in a Japanese study.

The report by the United States also contains some and concerns common to all countries. Current programs are assessing how the ocean environment affects not only Pacific salmon growth, bioenergetics, health, condition, feeding, but the role that juvenile salmon play in the ecosystem. There are cooperative programs in the Bering Sea with Japan and Russia, and also with Canada in the coastal waters shared by the salmon produced in Canada and the United States. There is a requirement to deter-

mine the timing of juvenile salmon movement from the coast waters to the high seas, beyond territorial limits.

Priorities for future research in the United States also share common themes among all countries. Interactions between hatchery and wild juveniles need to be determined. More information on the biology and behaviours during the first winter is a common priority as there is a possibility that this is an important period of early marine mortality. There is a common concern about the impacts of a changing climate. The general recognition of greenhouse gas induced climate change means that it is unlikely that there will be the kind of steady states and

random variability that is often proposed to affect the dynamics of Pacific salmon populations. Because the effects of global climate change on Pacific salmon will differ between oceanic regions, as well as among salmon species and stocks, future research by the United States is proposed to examine both regional and basin-wide factors that affect early marine survival.

Richard J. Beamish
Chairman of the NPAFC Committee
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A History of the Research on the Early Marine Life of Pacific Salmon Off Canada's Pacific Coast

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Keywords: Juvenile Pacific salmon, marine survival and growth, research history

Abstract: We review studies of the early ocean period of salmon life history conducted in the coastal areas off Canada's West Coast. The role of the ocean in the dynamics of salmon populations has received considerably less study than their life cycle in fresh water, even though Pacific salmon in general spend more time in the ocean than in fresh water and the survivals in the ocean are extremely low and variable. Feeding, growth and distribution studies from the late 1950s until the present have contributed to an improved appreciation of biology of salmon during the marine phase of their life history. However, conclusions about the processes that cause the high and variable mortality in the ocean remain speculative. How fishing impacts interact with natural processes also remain to be clarified. Recent studies have demonstrated that ocean and climate conditions are important contributors to the total marine mortality of a number of species, and to the stock and recruitment relationship. We suggest that it is time to conduct the definitive studies that will identify the processes that regulate the survival of Pacific salmon throughout their entire life cycle. We propose that an international effort to study the early marine period is the way to change the current beliefs and speculations into explanations.

INTRODUCTION

Pacific salmon have been an integral part of the culture on Canada's west coast for thousands of years. We now know that abundances have always fluctuated naturally (Finney et al. 2000), but that in the past 100 years fishing and degradation in freshwater habitat have intervened in these natural changes. Commercial harvests of Pacific salmon began on Canada's west coast about 1870. As stocks declined, it became necessary to manage salmon abundance, and to do this more information was required about their life histories. The Dominion of Canada Government was alarmed by the uncontrolled salmon fishery and gave the Reverend George Taylor \$7,000 Canadian to build the Pacific Biological Station through to its completion in 1908. However, it was not until 1955 that scientists started their investigations of the early marine phase of Pacific salmon.

This is a report on the history of these investigations and their key findings. The purpose is to provide a complete as possible summary of the information available on the early sea life of salmon in British Columbia waters

as a reference and information source for researchers attempting to work out the complex ecological relationships during this life phase. The approach for this review has been to consider published results of studies that were carried out in the ocean or were analyzed using the data from such investigations. Studies on smolts or fry in fresh water are not included even if they evaluated the impact of the ocean environment. Studies on the optimal size and time of release of juvenile hatchery salmon, for example, are referenced or not included. We constrained our report to the conclusions of the investigators and have not re-analyzed data or provided alternative interpretations. We have added commentary when it was necessary to put studies into historical perspective. We record the research results in chronological order and we provide a summary by topic. This leads to an apparent overlap of reports, but it also facilitates the review of material by readers who do not want to read through the entire report. We conclude with a list of questions that should be addressed and recommendations that relate to the expected impacts of ocean and freshwater habitat changes resulting from greenhouse gas accumulations.

CHRONOLOGICAL SUMMARY OF RESEARCH

Virtually all of the early work at the Pacific Biological Station on salmon focussed on propagation methods, migration, elucidation of life cycles, egg production, sex ratios, and freshwater mortality. Most research in the 1930s and 1940s was by R.E. Foerster on sockeye salmon (*Oncorhynchus nerka*), with some work on pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) by A.L. Pritchard and W.M. Cameron. The freshwater phase of the life history was given particular attention at a number of field stations along the Pacific coast, because it was believed that the factors most limiting to production were spawning and the development of the young alevin and fry in rivers, streams and lakes. This was consistent with the broadly accepted view in fisheries ecology that recruitment was determined in the egg and larval stages (Ricker 1954).

In 1953, Canada, Japan and the United States ratified a treaty, which established the International North Pacific Fisheries Commission (INPFC). Determining the distribution of Canadian salmon on the high seas became a priority. Scientists at the Pacific Biological Station initiated research in 1955 to determine where salmon originating in various rivers in Canada rear in the North Pacific Ocean. The active participation of Canada in the work of the INPFC brought about the funds and personnel to begin the study of the ocean phase of Pacific salmon.

The first research on juvenile salmon in the ocean (Table 1) occurred in 1955 by Ferris Neave who wrote, "In 1955 for the first time in the history of the Pacific salmon investigation, a sustained effort was made to find and catch young fish during the first few months of their life in the ocean." The objective of this pioneering program was to improve the prediction of adult returns. The main efforts were to find, catch, identify and tag salmon. Field operations were carried out from early June to early September in two study areas to facilitate comparisons: one in the north at Masset Inlet, Chatham Sound and adjacent waters (to catch fish from Skeena system) (Fig. 1) and one in the south in Queen Charlotte Strait, where concentrations of juvenile fish emerging from the northern exit of the Strait of Georgia were expected. A variety of gear types was used, including purse seines, beach seines, small-mesh gillnets, tow nets and mid-water trawls. The small juvenile salmon were examined for stomach contents, and lengths and weights were recorded. In addition, plankton samples were taken, and surface temperatures were determined. All five species were studied, but emphasis was on sockeye, pink and chum salmon. This fieldwork appears to have lasted for two years, although members of this research team carried out studies on a continuing

basis. It was apparently very easy to find and catch young salmon during the first two months of life in the ocean, a period when they frequented the shallow inshore waters in large concentrations. J. I. Manzer and G.T. Taylor reported on the results in an annual report, focussing on size, sex, food, distribution, abundance and movement of the young salmon. There was no indication that the studies could improve the prediction of returns, but the behaviour of young salmon when they first entered the ocean was documented. Juveniles were seen to move from near-shore areas to open water by late July to mid-August. An interesting observation was that sockeye were still moderately abundant in Queen Charlotte Strait in September. The diet studies indicated that the five species differed in feeding habits, with juvenile pink, chum and sockeye salmon feeding primarily on invertebrates, whereas juvenile coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon were more piscivorous. When chum and pink salmon occurred in the same locations, chum were found to be more catholic in their diet. Over 4,000 juveniles were tagged in Chatham Sound and Johnstone Strait using spaghetti tags, but very low numbers were recovered. A concurrent study of marine distributions of young salmon by LeBrasseur and Parker (1964) showed that seaward migrations of young salmon appeared to be related more to sea surface water temperature than to high concentrations of zooplankton or to any particular salinity levels.

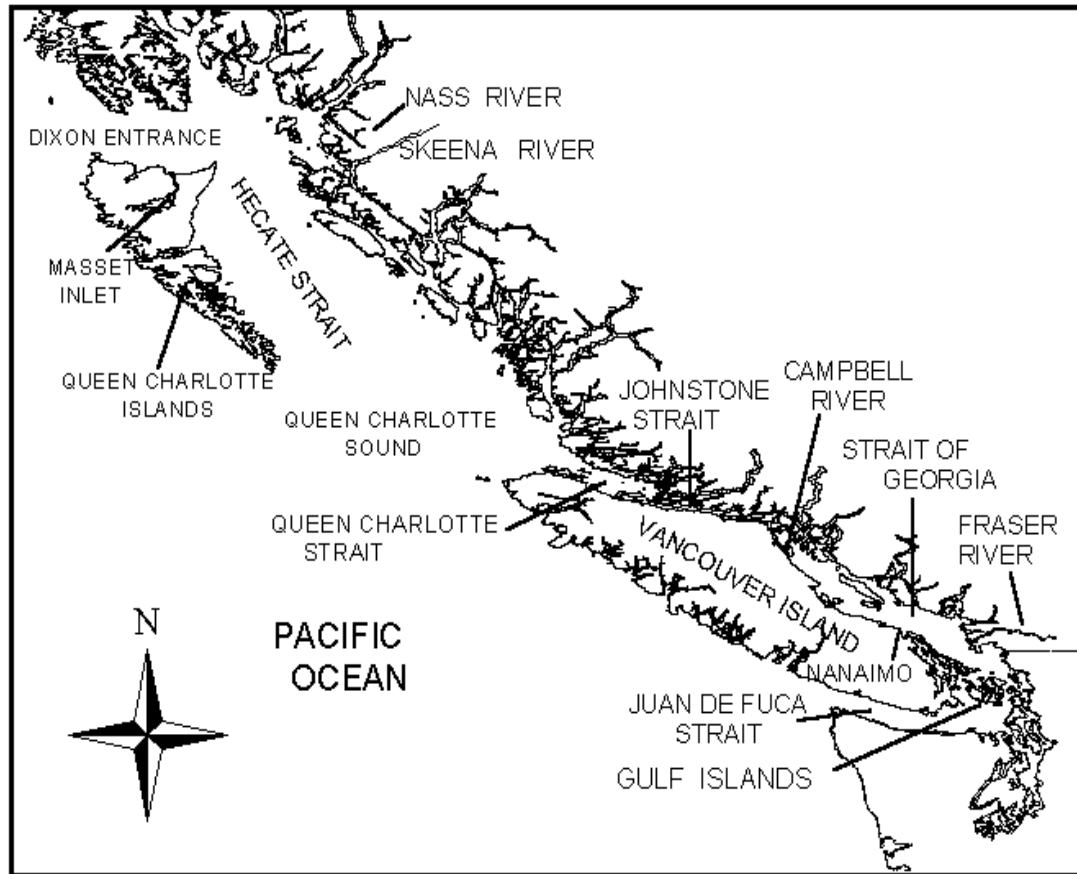
The period of the late 1950s appears to have been a time of broadening interest in the early oceanic phase of the life history of salmon. Steelhead trout (*Oncorhynchus mykiss*), however, which were later moved from the genus *Salmo* to *Oncorhynchus*, were not a priority. Early investigators were intrigued by the odd and even year life histories of pink salmon (Groot and Margolis 1991), and thus pink salmon received much more attention than in recent years. The general directive at the Pacific Biological Station was to examine the relationship between the many varying environmental factors and the survival of young salmon. A conclusion by Godfrey (1958) that the early marine environment encountered by Fraser River pink salmon was a determinant of adult abundance was one of the early indications that the ocean state played a role in the production of Pacific salmon. This may appear self-evident now, but the common view at the time was that density-related processes in fresh water determined the abundance of returning stocks. A prophetic, C.D. McAllister stated in 1960 that "it seems not impossible that winters with very sparse zooplankton, heavy cloud cover and unusual turbidity could be critical for the survival of young salmon" (McAllister 1961).

In the 1960s, the search for methods to forecast adult returns continued. There was a strong belief

Table 1. Major investigations of juvenile Pacific salmon

Investigator	Date of work	Type of Study
F. Neave J.I. Manzer G.T. Taylor R.J. LeBrasseur	1955–1957	Life history, migration, diet
R.R. Parker	1960–1971	Diet, early marine mortality, predation, early marine growth
J.I. Manzer M.P. Shepard	1953–1965	Diet, distribution and abundance
A.W. Argue R.W. Armstrong B. Hillaby D.E. Marshall	1963–1976	Migration, diet, distribution, abundance, growth
H. Goldfrey	1968–1974	Distribution and abundance
E.A.R. Ball	1974	Distribution and abundance
A.C. Phillips	1963–1978	Diet, distribution and abundance, early marine growth
W.E. Barraclough	1963–1978	Diet, distribution and abundance, early marine growth
J.D. Fulton	1967–1978	Diet
D.G. Robinson	1968–1976	Diet
J. Sibert	1972–1977	Diet
R.J. LeBrasseur	1964	Early marine growth
R.A.H. Sparrow	1967	Distribution and abundance
M.C. Healey J.F.T. Morris B.J. Waddell B. Hungar M. Abrahams	1974–1988	Distribution and abundance, diet, early marine growth, size selective mortality, (Nanaimo River estuary, Barkley Sound and Hecate Strait)
C.D. Levings C.D. McAllister M.S. Kotyk T.J. Brown	1970–2000	Hatchery vs. wild interactions, diet, distribution and abundance (Campbell River Estuary)
W.E. Dunford	1975	Distribution and abundance
W.E. Ricker	1976	Size selective mortality
D.A. Levy	1979–1985	Distribution and abundance, diet
T.J. Northcote	1979–1985	Distribution and abundance, diet
J-G.G. Godin	1980–1981	Diet
C. Groot	Barkley Sound (MASS, 1987–1991)	Migration
K. Cooke	Barkley Sound (MASS, 1987–1991)	Migration
B. Hargreaves B. Hungar B. Patten T. Carter	1982–1991	Predation, size selective mortality
K. Hyatt G.J. Steer P. Rankin I. Miki R. Traber D. Kolody	Barkley Sound (MASS, 1987–1991)	Early marine mortality, diet
R.J. Beamish C.M. Neville R. Sweeting J. King M. Folkes	1976–2000	Diet, early marine mortality, distribution and abundance, predation (Strait of Georgia and West Coast Vancouver Island)
C.W. Haegele	1990–1994	Diet
D.W. Welch	1980–2000	Migration, distribution and abundance, diet (High Seas)

Fig. 1. Major study areas.



that Pacific salmon abundance could be rebuilt to historic levels, but the factors limiting salmon were still “completely unknown”, according to R.R. Parker. In 1960–61, a field program was initiated at the Port John field station involving marking of half of the seaward migrating pink and chum fry from Hooknose Creek and observation of their movement, growth and survival after they entered salt water. This work was the start of a major study carried out over a 3 year period by R.R. Parker during which a wealth of data was produced as well as some classic publications. The main hypothesis being tested at this time was that annual survival in coastal waters determined, to a large degree, the numerical strength of the returning adult salmon populations because mortality rates in the high sea areas appeared to be low and relatively constant.

Separation of the natural mortality rates of Bella Coola pink salmon into two subsequent time periods was achieved by two-stage markings: tagging at age zero and at 40 days sea life. The two types of marking used were removal of the adipose and right ventral fins, and removal of the adipose and left ventral fins. Recovery was at the time of adult return. Samples were also retained for stomach analysis and the

usual measurement of size. It was observed that small schools of pink salmon from individual rivers formed larger aggregations close to shore. These aggregations remained inshore until June, then broke up into smaller schools in open areas of Queen Charlotte Sound. Pink and chum were captured together, but there were major differences in the diets of the two species. The composition of their food indicated that they were feeding selectively. Thus, although they shared a common habitat, the two species used it differently (a concept long ago reported for finches sharing arboreal habitats on the Galapagos Islands).

Parker (1965) found that during the first 40 days, the average daily loss to the pink salmon population was 2–4%. However, the average daily loss for the remaining period at sea (410 days) was 0.4–0.8%. Of the three brood years studied, 55–77% of pink salmon died over the first 40 days, and 78–94% of those remaining died over the remaining 410 days. However, he also found that the marine mortality was quite variable among the three years. He reported that the variability in coastal and ocean mortality was 36–38% of the average for the three brood years. The major predator was juvenile coho and it appeared that coho preferred to eat pink salmon compared to chum

salmon. Parker believed that squid could also be a predator, but he ruled out bird predation as a significant source of mortality.

This work became a standard reference for investigators proposing that brood year strength is determined very early after entry into the ocean. However, the significance of the large variability over only three years did not appear to influence subsequent thinking and management. In fact, R.R. Parker (1965) wrote that it was unwise to consider any portion of natural mortality in the ocean as a constant. He found that it was difficult to forecast returns using counts made in freshwater, and concluded that variation in marine survival "obscures the parental to filial generation relationships that are currently sought for in stock and recruitment curves".

In the late 1960s, there was a new emphasis on the trophodynamic relationships of salmon with other organisms. Research focussed on diets in relation to the changing distributions of juvenile salmon as they moved into the open water areas later in the summer. Studies were conducted by W.E. Barraclough, J.D. Fulton, D.G. Robinson, A.C. Phillips, and T.R. Parsons. Barraclough and Phillips (1978) reported on the early marine growth of juvenile salmon in the southern Strait of Georgia and Saanich Inlet as part of a larger study of production in the Fraser River plume (Parsons et al. 1969a, b). The project provided an opportunity to examine the extent to which the early marine life of various species of fish was dependent upon concentrations of zooplankton.

Understanding movements of immature coho and chinook salmon that were rearing at various locations in the Strait of Georgia and Johnstone Strait was the focus in the 1960s and early 1970s of a number of tagging studies (disc, Carlin and Floy spaghetti-anchor tags) conducted by A.W. Argue and D.E. Marshall (Argue and Heizer 1971; Heizer and Argue 1972; Argue and Heizer 1974). Of particular interest were movements of coho from winter rearing areas (Argue and Heizer 1974). Purse seining was the principal capture method and first ocean-year coho the main target species, although on occasion large numbers of juvenile pink salmon were caught and tagged during winter and early spring months (Heizer and Argue 1972).

The late 1960s and early 1970s was a somewhat unsettled period for fisheries research on Canada's west coast, and it appears to have influenced the kind of early marine research that was conducted. In the late 1960s, the management of fisheries research changed from an independent board to a government-run department. At the same time, a 'year class' of senior scientists was either retiring or leaving the Pacific Biological Station. There was an ominous and unexplained decline in Pacific salmon catch at this time, and this appeared to change the priority for

early marine studies from forecasting to understanding the productive capacity for young salmon in the coastal ecosystem. The preference for studying species also changed and coho and chinook salmon began to receive more attention. Chum salmon retained its priority, but pink and sockeye salmon were less studied. In particular, there was a strong emphasis on understanding the importance of estuaries as nursery areas for all species of salmon. There was interest in trying to use any improvement in understanding of the early marine period to increase salmon production. Areas for research included Alberni Inlet, Squamish River estuary, Nanaimo River estuary, Cowichan Bay, Saanich Inlet and the Strait of Georgia in general. In 1962, Ricker (1962) had calculated that it was possible to restore salmon abundance to levels of the late 1800s. These historic abundances were about double the numbers that existed at the time of his calculations.

The change in emphasis was characterized in the mid-1970s by the second Strait of Georgia program, which was never implemented as an integrated study. The objective was to provide fisheries information that was essential to management. Even though the full project was not supported, aspects of the plan were undertaken in the studies of M.C. Healey beginning in the 1970s. Healey tested the hypothesis that the movement of juvenile salmon out of the estuary or nearshore area was related to food availability. These studies were conducted in the Strait of Georgia and around the Nanaimo River estuary.

A growing recognition of ecological issues began in the 1970s arising from existing and proposed estuary developments (Hoos and Packman 1974). An Estuary Working Group under Environment Canada, led by Dr. Michael Waldichuk of the Pacific Environment Group, Fisheries and Marine Service, published a series of inventories of relevant bio-physical information, including information on juvenile salmon for British Columbia's major estuaries (e.g. Fraser River estuary, Hoos and Packman 1974; Cowichan-Chemainus River estuaries, Bell and Kallman 1976; Bella Coola River estuary, Leaney and Morris 1981). In 1975/1976 the Cowichan River estuary was the site of one of several focussed studies on distribution, abundance, residence times, growth and feeding of juvenile salmon (Argue et al. 1986) that arose from this enhanced concern for estuary habitat.

The dependence of juvenile salmon on estuaries was found to be species specific. An unexpected finding was that chinook fry used intermediate salinity estuarine waters as a nursery area (Healey 1980a, b). Prior to this finding it was believed that chinook fry that migrated seaward were unable to find nursery space in fresh water and were lost to the population. Young chinook salmon were unable to

make the transition to full sea water, however, and so were confined to estuarine waters of 20‰ or less until about 70 mm fork length. Chum salmon fry also made use of estuarine nursery habitats but, unlike chinook, chum were not restricted to the estuary and were able to use shallow marine nursery areas as well (Healey 1982c). Chum salmon remained well inshore when they first entered the ocean, and their diet in this early marine period was found to be associated with a detritus-based production. The residence of chum fry in the Nanaimo River estuary in particular was found to be associated with the abundance of their principal prey species, *Harpacticus uniremus*. Chum salmon left the estuary when this prey species declined sharply in abundance at the end of May. Thus young chum salmon were dependent on shallow marine habitats. The studies identified size selective mortality of chum, but it was only for a size range between 45 and 55 mm. This occurred at a time when 2–4 scale circuli were formed and at the time the juvenile chum salmon moved from the inshore area to an open water habitat. Like chum salmon, pink salmon made use of shallow marine nursery habitats for a few weeks following downstream migration. Unlike chum, however, pink salmon did not spend more than a day or two in estuarine habitats before moving to marine waters. Both pink and chum salmon left the near shore areas despite adequate feeding conditions, although as noted earlier, the departure of chum from the Nanaimo River estuary was associated with the decline in their main prey species. Thus, there was little evidence to relate the migration into open areas with decreasing food availability. Healey (1982c) suggested that the absence of a relationship may have been an indication that food resources were adequate in most habitats to allow for successful foraging, and that distribution may be controlled by another need such as avoiding predators or taking advantage of relatively warm nearshore temperatures to maximize growth efficiency. However, he did find that the emigration of pink and chum juveniles out of the Strait of Georgia and the regional distributions of chum, coho and chinook salmon juveniles in late summer were correlated with stomach contents. He assumed that food resources were low enough that the fish had to seek out the best feeding areas to satisfy their food requirements. For pink, chum and sockeye salmon, which are largely planktivorous, this meant that they had to leave the Strait of Georgia, whereas coho and chinook salmon, which are largely piscivorous, were able to satisfy their food requirements within the Strait. Healey (1980b) further suggested that the indication that food resources may be limiting in late summer should warn against the release of large numbers of hatchery juveniles, as this could overload the habitat.

Healey (1980b) and his co-workers also found

that the major concentrations of juvenile pink and sockeye and possibly chum salmon, occurred in the Gulf Islands across the Strait of Georgia from the Fraser River (Fig. 1). This small area, they concluded, had to support the bulk of the juvenile salmon that entered the Strait of Georgia. About 25 years later, it would be shown in the studies of Beamish and his colleagues that this area was no longer the main rearing area in the Strait of Georgia. In fact, the central area of the Strait of Georgia that Healey found to contain relatively low abundances of salmon would be shown to contain large numbers of juvenile chum, pink, coho and chinook salmon through to the fall of the first marine year (Beamish et al. 2000a). Healey and his colleagues, in the late 1970s and 1980s, provided much of the first information on the early marine period of juvenile salmon off the west coast of Canada. The results of their work have made a significant contribution to our understanding of the early marine life history.

The area of Masset Inlet was of concern during 1970–1980 since there appeared to be a significant decline in pink salmon returns. Masset Inlet was thought to be the primary rearing area for juvenile pink salmon from the Yakoun River. Thus, there were concerns that this decline may have been due to increased mortality during the early sea life period. A four year study of the early sea life of juvenile pink and chum salmon was started in Masset Inlet in 1982 by B. Hargreaves and R.J. LeBrasseur. Juvenile salmon and potential predators were collected with a variety of sampling gear including beach seines, two boat trawls, fish traps, and a purse seine. Hargreaves and LeBrasseur (1985) examined stomach contents of 15 potential predators, and found salmon remains in coho salmon, cutthroat trout (*S. clarki clarki*), silver-spotted sculpin (*Blepias cirrhosus*), buffalo sculpin (*Enophrys bison*), whitespotted greenling (*Hexagrammos stelleri*), Dolly Varden (*Salvelinus malma*), tidepool sculpin (*Oligocottus maculosus*), great sculpin (*Myoxocephalus polyacanthocephalus*) and possibly in Pacific staghorn sculpin (*Leptocottus armatus*). Although these potential predators were examined, they were not able to determine the cause of the decline in pink salmon numbers and the data were not analysed. Using a number of marine enclosure experiments, Hargreaves and LeBrasseur (1985) showed that coho salmon preferred pink salmon as prey even when small chum were available, but these net pen studies provided conflicting evidence of size dependent predation and even preference for chum rather than pink salmon in some situations. A consistent conclusion was that coho are an important potential predator of pink salmon juveniles and in some cases of chum salmon.

A difficulty with the early marine studies of salmon was that the gear available to catch salmon

could not be fished in all kinds of weather and in all areas. The reliance on purse seines with small mesh bunts, restricted sampling to areas where currents, including tides, were not excessive and to seas that were unusually calm. A technical improvement in gear could greatly affect the sampling ability. Purse seining and beach seining were effective methods of catching juvenile salmon close to shore, but sampling in the areas deeper than about 30 m would benefit from the development of new gear. A fisherman (Norm Sigmund) and two scientists (F. Bernard and B. Hargreaves) designed twin beam trawls that could fish the surface waters down to 10 m. The trawls were towed on either side of the *W.E. Ricker* at about 3 knots. This was a much-improved method of sampling compared to purse seining or the use of small trawls. The specifications for the gear, however, were not published.

The first major scientific survey using the new Bernard-Sigmund beam trawls on the *W.E. Ricker* was successfully completed between 23 July and 10 August 1990 by Hargreaves. These trawls were used to survey the distribution and abundance of juvenile salmon along the entire west coast of Vancouver Island from Juan de Fuca Strait to Cape Scott. A total of 329 trawl sets was completed over a 16 day period, providing much greater detail regarding the distribution and biology of juvenile salmon and other pelagic species than had previously been possible. The catches included a total of over 6,000 juvenile salmon, 1,100 juvenile sablefish (*Anoplopoma fimbria*) and 61,000 juvenile herring (*Clupea harengus pallasii*). The observations of distribution and abundance of the juvenile salmon showed a very different pattern than previously reported. Juvenile salmon were distributed evenly across the continental shelf and farther seaward to distances of at least 70 km offshore. This observation differed from the conventional wisdom, based on purse seine data collected during the 1950s to 1970s, that most juvenile salmon along the coast of Washington and British Columbia migrated within 15–20 km of the shore. Studies by scientists from the United States, and by Healey, also showed that large numbers of juvenile salmon were caught 50–70 km offshore. There was no indication that the nearshore Vancouver Island Coastal Current acted as either a conduit or as a cross-shelf barrier. A variety of potential predators of juvenile salmon was collected including various rockfish, Pacific hake (*Merluccius productus*), spiny dogfish (*Squalus acanthias*), blue shark (*Prionace glauca*) and chub mackerel (*Scomber japonicus*). Several specimens of black rockfish (*Sebastes melanops*) had juvenile salmon in their stomachs. A survey of the abundance and distribution of juvenile salmon and other pelagic species was also carried out between 15 June and 4 July 1992, off the west coast of Vancouver Island, in

which 480 trawl tows were completed and 5,418 juvenile salmon were caught. In 1992, all juvenile salmon were concentrated close to shore and very few were caught between 30–55 km offshore. The El Niño conditions that occurred along the North American coast in 1991–1992 may have strongly affected the distribution and abundance of juvenile salmon and many other fish species. There were large changes in ocean conditions including a 1.5–2.0°C increase in average sea surface temperature along the southwest coast of Vancouver Island. The abundance, distribution, migration routes and migration timing of all salmon species and other pelagic fish species differed significantly from 1991 to 1992. The high influx of mackerel seen in 1992 was, no doubt, the result of the warm water conditions in 1992. The results of three beam trawl surveys in 1990, 1991 and 1992 clearly indicated that there were large interannual variations in the abundance, distribution, migration routes and migration timing of the various species of salmon.

The beam trawl was eventually replaced by a rope trawl, because it was found that sampling only the surface 10 m did not effectively sample the populations of chinook and coho, as juveniles of these species occupied a greater depth range than chum, sockeye or pink salmon. Comparative fishing of the beam trawl and rope trawls in the Strait of Georgia in 1996 by R.J. Beamish (Beamish unpublished data) showed that the rope trawls were a more reliable method of sampling a population because they could be towed faster, at 5 knots, and could catch all sizes of salmon. The beam trawl was restricted to the surface and could not be towed fast enough to catch the larger salmon. Also, the rope trawl could be towed at all depths and thus could be used to study predators (and other species interacting with salmon in the ecosystem).

In the 1980s, there was a series of studies on juvenile salmon in the early marine period. These included studies by R.J. Beamish and co-workers to examine the predators of young salmon (Beamish et al. 1992; Beamish and Neville 1995). It had recently been discovered that there were large abundances of Pacific hake in the Strait of Georgia. Hake was a known predator of herring, and it was proposed that it was also an important predator of juvenile salmon. The belief that the productivity of salmon could be improved by reducing the abundance of predators had persisted since the 1960s. Extensive studies of hake diets continued for over 20 years with only a few hake being found with salmon in their stomachs. An important predator of juvenile Pacific salmon was identified by Beamish and staff. They identified river lamprey (*Lampetra ayresi*) as a major predator of juvenile salmon (Beamish and Youson 1987). An important component of these predation studies was

what was not found. Extensive studies of the diets of various species resident in the Strait of Georgia including Pacific hake, did not identify predators of juvenile salmon as important as spiny dogfish, river lamprey, and Pacific lamprey (*L. tridentata*) (Beamish and Williams 1976; Beamish et al. 1992; Beamish and Neville 1995). This was important, because it was clear that the sources of predation mortality from other fish were not mysterious. Discussions relating to predation-based mortality could be specific.

During the spring through winter months of 1988 to 1991, surveys were conducted by R. Beamish to examine the incidence of juvenile salmon in the diets of dogfish (Beamish et al. 1992). The study area was immediately offshore of the river into which hatchery fish were released from Big Qualicum Hatchery. At the time, this hatchery produced the largest number of salmon of all those releasing salmon into the Strait of Georgia. The study included the identification of dogfish stomach contents and the estimation of dogfish abundance in the study area. Spiny dogfish accounted for 94% to 98% of the total catch in all years of the bottom gillnet study and the percentage of dogfish feeding on salmon was different in all years: 11.9% in 1988, 0.8% in 1989, 1.1% in 1990 and 1.5% in 1991. The estimates of juvenile salmon predation indicated that a minimum of 1.4% in 1990 to a maximum of 10% in 1988 of the Big Qualicum Hatchery chinook and coho salmon releases were killed by spiny dogfish within four weeks of entering saltwater.

Surveys to study lamprey predation were conducted in the Fraser River plume and adjacent waters using a surface trawl (Beamish and Neville 1995). Using estimates of numbers of prey killed per lamprey from laboratory studies, it was determined that lamprey predation could account for 13% of all coho hatchery production from Strait of Georgia hatcheries in 1990 and 65% of all coho production in 1991.

Other studies carried out during this period included C. D. Leving's work on juvenile salmon in estuaries (particularly the Campbell River estuary), C. Groot and K.D. Cooke on sockeye migrations, and M. Healey's work with the Hecate Strait project. In the early 1980s, C. Levings began extensive studies of how juvenile salmon use the Campbell River estuary (Levings et al. 1986). His work, together with that of Healey, established that the use of estuaries and shallow water habitats (< 10 m) by juvenile salmon varies among species. Based on estimates of residency time, juvenile chinook and chum salmon are the species that reside the longest in estuaries. Most of the information from these two investigators is for these two species. There is significant stock variation in the use of estuaries by the other species of salmon, but in general the data supporting observations for other species are weak. There are also some popula-

tions of Fraser River sockeye salmon whose juveniles rear in the lower river or estuary or both (Levings et al. 1995).

The research of Levings and associates (Levings et al. 1986) found that the chinook fry population in the Campbell River estuary took about two and a half months to move from the inner estuary to fully marine habitats farther offshore. In estuaries on larger river systems with numerous tributaries, chinook fry and smolts were found to trickle through the estuary from March to August. It was believed that hatchery smolts and wild fry at the Campbell River estuary competed for resources such as habitat space and food. There was evidence of density-dependent growth of the latter in years when this small estuary was dominated by the larger hatchery fish.

The Hecate Strait (between the northern mainland of British Columbia and the Queen Charlotte Islands) project started in 1984 with the overall objective of conducting research into the ecological basis for multi-species stock assessment and management among groundfish, herring and salmon. This region serves as a temporary residence for all five species of juvenile Pacific salmon, particularly those originating from stocks in southern and central British Columbia. The objective of the juvenile salmon component, which was carried out by M. Healey was to determine the residency, growth, and food requirements of juvenile salmon and provide information on their growth and migratory paths. Weights of stomach contents and estimated daily rations of juvenile pink and chum salmon were small enough to limit growth rates, and the hypothesis that the limitation of growth during early ocean life affected survival and recruitment was not rejected (Healey 1980b). Haegele (1997) carried out a five-year study, from 1990 to 1994, in which he examined the diets of juvenile Pacific herring and juvenile salmon in the Strait of Georgia. The study by Haegele was designed to survey for Pacific herring in their first ocean year and most effort was in the open areas of the Strait of Georgia.

The work of the MASS program (Marine Survival of Salmon) was carried out between 1987 and 1991 in Barkley Sound, off the west coast of Vancouver Island. This study attempted to integrate biological and physical sciences that affected the dispersal and survival of salmon during their first few months at sea. There were three objectives: (1) to examine the direct effects of coastal circulation and water mass structure on the dispersion and migratory behaviour of juvenile salmon; (2) to determine the relationship between food chain productivity, food distribution and survival; and (3) to examine the predation mortality of young salmon. The stocks studied included sockeye salmon from the Alberni Inlet system, chinook and coho salmon from Robertson Creek

hatchery, and juvenile chinook and coho salmon of various origins on fishing banks off southwestern Vancouver Island. Work on the first objective was mainly to examine residence (distribution and abundance) of all five species in the inlet, and migrations of sockeye in particular, within Barkley Sound (Groot and Cooke 1988), on offshore banks (Morris et al. 1990; Morris and Welch 1992a, b; Morris et al. 1992, 1993, 1997) and along the west coast of Vancouver Island (Hargreaves et al. 1990). Hyatt et al. (1988, 1990) conducted work on sockeye salmon recruitment variations. The second objective was also addressed by the latter group (Hyatt et al. 1988, 1990) who (1) examined diets of juvenile sockeye migrating through Barkley Sound to identify prey sizes and taxa of greatest importance for early marine growth; (2) examined prey abundance in Barkley Sound to characterise the food available relative to the cropping potential of juvenile salmon; and (3) analysed scale samples from adult sockeye to provide an index of early marine growth rates (first year) associated with sockeye year classes exhibiting high versus low marine survivals. In general, this was the most ambitious study of factors affecting the early marine survival of Pacific salmon undertaken by Canada. To date, there have been few reviewed publications from this study.

Results from diet analyses suggested that there could be interspecific competition for food supplies as various species of juvenile salmon (sockeye, chinook and chum) migrating through Barkley Sound relied on similar prey taxa (early stage euphausiids, medium sizes of copepods and brackish water cladocerans) during the spring and early summer period. However, scale pattern analysis indicated that first year marine growth rates of juvenile sockeye salmon that experienced the lowest survival rate (1983 smolt year) were not significantly lower than growth rates achieved by juvenile sockeye showing one of the highest survival rates (1978 smolt year). Later, Beamish and Mahnken (1998) proposed that similar results from another sockeye salmon stock could be explained by hypothesising that only the individuals that grew to a critical size could survive the first marine winter. Thus, the slower growing ocean age 0 fish were expected to be rare in any sample of returning adults.

The work on the second objective of the MASS program (carried out by Morris et al. 1990) provided information on diet and feeding success, but was not able to confirm the original hypothesis that aggregations of salmon would be associated with local circulation.

Work on the third objective, was done by Hargreaves et al. (1988, 1990) and Hargreaves and Hungar (1990), who examined juvenile salmon abundance, distribution and predation mortality in Alberni

Inlet and Barkley Sound. Their objectives included (1) determining the abundance and distribution of juvenile chinook, coho, chum and sockeye salmon; (2) identifying and assessing the relative abundance of potential predators of juvenile salmonids; and (3) determining the intensity of predation by examination of the stomach contents of major predators. One hypothesis to explain the variability in marine survival of salmon was that variation in ocean conditions changed the abundance, distribution or species composition of predators. Variation in ocean conditions could be interannual, decadal or both. The Barkley Sound predation study was an intensive effort carried out by B. Hargreaves and co-workers between early-April and mid-July for each of the four years. Sockeye salmon juveniles were the most abundant in this region, although chinook salmon used the areas as a juvenile rearing area more than chum, coho and pink salmon. Resident Pacific hake, walleye pollock (*Theragra chalcogramma*) and spiny dogfish were the most important predators of the juvenile salmon. The results do not appear to have been published as a final analysis, but preliminary conclusions were that in 1989, about 12 million juvenile sockeye (> 50% of total production) and 7 million juvenile chinook (equivalent to about 75% of the hatchery production) may have been consumed by predators during the early sea life period in this region. These estimates were based on very small numbers of salmon observed in Pacific hake stomachs, so there is high uncertainty. The mortalities were much lower in 1990.

Shortly after the MASS program ended in 1991, there were some major changes in the ocean that resulted in declines in survival of a number of salmon species. The declining survival was followed by management decisions to reduce fishing impacts and this resulted in catches of all species declining to historic low levels. Coho salmon marine survival in particular declined to less than 2%. At this time, there were other major changes in the ocean ecosystems. Pacific sardines (*Sardinops sagax*) returned to Canadian waters after an absence of over 40 years. Chub mackerel first appeared as a new and important predator in 1991, and there was considerable evidence that they became the major predator of juvenile salmon in Barkley Sound.

In the 1990s there were dramatic declines in the production of coho and chinook salmon in the Strait of Georgia. The declines of adult chinook salmon occurred despite a more than doubling of production of smolts (Beamish et al. 1995). The decline in the abundance of adult chinook was proposed to result from a natural decline in the carrying capacity for chinook salmon in the Strait of Georgia (Beamish et al. 1995). A similar explanation was proposed for the decline in adult coho abundance in the late 1990s (Beamish et al. 2000b). The decline in marine

survival in the Strait of Georgia was shown to be synchronous with declines in average marine survival in Puget Sound and off the coast of Oregon (Beamish et al. 2000b). The synchrony in the declines in marine survival was similar to large scale shifts in climate indices which indicated that climate and climate change affected the ocean carrying capacity for juvenile Pacific salmon over a large area. It is interesting that another major climate shift occurred in 1998 which affected the productivity of the Strait of Georgia in 2000. This recent change resulted in better marine survival, and better growth (Beamish et al. 2000c, 2001a). As a result of this change, juvenile salmon had more volume in their stomachs and fewer empty stomachs (Beamish et al. 2000c, 2001a). Similar food items were consumed; juveniles simply ate more and grew to larger sizes.

During the 1990s, the use of the rope trawl provided a tool that could be used to estimate abundances using swept volumes. A fixed survey design with a randomised depth component and a large rope trawl that fished surface waters at a speed of approximately 5 knots was used to estimate the abundance of juvenile coho salmon in the Strait of Georgia (Beamish et al. 2000a). The estimates were 4.2 million in September 1996, 3 million in September 1997, and 3 million in September 1998; these were assumed to be minimal estimates as catchability by the net was probably lower than used in the analyses. Using hatchery marked percentages, it was estimated that 3.4 million wild juvenile coho salmon entered the Strait of Georgia from Canadian rivers in 1997. In the Strait of Georgia, abundance estimates of juvenile Pacific salmon were shown to be large for some species relative to the numbers that returned. Because abundances were larger late in the first marine year and mortalities over the fall and winter exceeded 90%, Beamish and Mahnken (2001) proposed that the natural regulation of adult returns of salmon occurred in two stages, an early predation-based mortality, and a fall/winter mortality that was related to growth.

Survival and behaviour of juvenile salmon in the Strait of Georgia were linked by Beamish and co-workers to changes in climate that produced persistent and distinct climate-ocean states called regimes (Beamish et al. 1997, 2000d). Regime shifts occurred in 1977, 1989 and in 1998 (Beamish et al. , 2000a, d, 2001b). These regimes are characterized by changes in ocean temperature, sea level heights and Fraser River flows. The pattern of marine survival of chinook and coho salmon was related to the particular regimes. The decline in survival of coho after the 1989 regime shift was also associated with a behavioural change that resulted in virtually all juvenile coho salmon leaving the Strait of Georgia in the late fall and not returning until the spawning migration in the following late summer (Beamish et al. 2000d).

This resulted in an absence of ocean age 1+ coho and a collapse of the sport fishery in the Strait of Georgia. The abundance estimates and the release of marked hatchery fish were combined to study the changes in the percentages of hatchery and wild coho salmon. The percentages of hatchery coho salmon in the late 1990s exceeded 70%, indicating that, under the current management approach, hatchery coho were replacing wild coho salmon (Beamish et al. 1998b; Sweeting et al. 2003).

Offshore salmon research in Canada began again in 1990 by D. Welch and staff, after a pause of a quarter century when research surveys stopped in 1967. The initial impetus for the new work was provided through a co-operative research cruise on the USSR research vessel *Tinro* in the Gulf of Alaska. This co-operative effort provided an opportunity to assess the performance of the rope trawl being used to sample salmon in the open ocean by the Soviet Union (Morris et al. 1991, 1992). After a number of small-scale trials, a rope trawl capable of being successfully fished offshore was developed in 1995 (Welch and Carlson 1995). During offshore trials in March of 1995, it proved possible to tow the net at 5 to 5.5 knots, very near the surface (headrope depth 2–3 m under calm conditions) using a chartered trawler. Substantial catches of young salmon (> 100 salmon per 1 hour tow) were reported at some offshore stations, establishing the usefulness of the net.

Following the autumn 1995 trials, the High Seas program began to focus on autumn and early winter surveys to study the migration pathways of juvenile salmon. This work showed that no juveniles were found beyond the region of the shelf break (i.e. waters of 200–1,000 m depth). During multiple cross-shelf transects consisting of a linear sequence of closely spaced tows, catches of juvenile salmon abruptly dropped to zero as the shelf break was reached. In over 550 tows, roughly divided between those on and off the shelf, virtually no juveniles were found beyond the shelf break. The only exceptions to this general rule were a few catches of juvenile coho found just seaward of the 1,000 m isobath, each catch consisting of just one or two fish.

The results from these surveys indicated, by the end of 1996, that all of the juvenile salmon appeared to be staying on the shelf at least as far as Kodiak until October. The sharpness of the distribution of juvenile salmon in the eastern Pacific was described as remarkable (Welch et al. 1995a, b, 1997). Earlier work had postulated that juvenile salmon from SE Alaska and British Columbia probably turned west and moved out into the open North Pacific in the autumn (Hart and Dell 1986). Stocks of coho and chinook salmon were known to contribute to winter fisheries. They must migrate to specific feeding grounds along the coast where they take up residence and

make up the majority of the salmon left in the fall, such as the locations in the Strait of Georgia (e.g. Saanich Inlet, Stuart Channel) and Johnstone Strait (e.g. Bauza Cove, Frederick Arm) where over several years thousands of coho were seined for tagging (Argue and Heizer 1971, Heizer and Argue 1972). These fall-caught salmon were proposed to have a much lower rate of migration than the summer-caught fish, since the latter do not move as far, and presumably stay on fairly well-defined coastal feeding grounds once they reach these regions.

SPECIFIC RESEARCH TOPICS

Estuaries and Nearshore Habitats

Juvenile Pacific salmon in their migration from inland rearing areas to oceanic feeding areas often pass through littoral estuarine habitats. Studies of juvenile salmon in estuaries have been carried out primarily by M. Healey, C.D. Levings, B.A. Bravender, (formerly B.A. Kask), K.S. Kotyk, and T.J. Brown. Healey (1980a, b, 1989, unpublished data) studied juvenile salmon in the Nanaimo and Nitinat estuaries in southern British Columbia and put together the results of a number of studies of juvenile salmon in other BC estuaries, such as the Fraser, Squamish, Courtney, and Somass in southern British Columbia (Kask and Parker 1971, 1972a, b, 1974; Barraclough and Phillips 1978; Birtwell 1978; Levy and Levings 1978; Levy et al. 1979; Morris and Leaney 1980; Levy and Northcote 1981; Healey 1982a). Some species remain in these habitats for several days and in some cases for several months (Reimers 1973; Dunford 1975; Healey 1979, 1980a, b; Levy and Northcote 1982). There have been many studies to assess timing of migration into estuaries, length of residence, distribution and abundance of juvenile fish, possible interactions among the different species of salmon and among hatchery and wild fish in estuarine areas.

Most young salmon enter estuaries in the spring, and move into the coastal oceans in the spring and early summer. Juvenile pink salmon were only found in any abundance in the Fraser River, and pink fry were found in the tidal marshes of the Fraser River delta only during their downstream migration. Pink fry were found to move into the tidal marshes at high tide and to leave on the first of the ebb, thus their residence time in the marsh (area) was found to be no more than one or two days (Levy et al. 1979). Most of the fry migrating seaward each day were found to move directly through the delta (area) and into the river plume (Barraclough and Phillips 1978). Healey (1980b, 1982b) found that pink fry were swept across the southern Strait of Georgia by the Fraser River plume, and congregated in dense schools close to

shore along the east coast of Vancouver Island. Healey (1982b) also found some pink fry, probably of Fraser River origin, rearing in the outer Nanaimo River estuary in May and June. Phillips and Barraclough (1978) and Healey (1980b, 1982b) found that juvenile pink salmon left the Nanaimo River estuary and other habitats in the southern Strait of Georgia in late June or July when they reached 80 mm fork length.

Chum salmon have shown similar behaviour in estuaries (Healey 1979; Levy et al. 1979; Levy and Northcote 1981; Healey 1982a, b, c). Chum fry were shown to disperse several kilometres within a few hours once they had reached the river mouth, although some remained in the estuary to rear. The first habitats occupied by the fry were found to be tidal creeks and sloughs high in the delta area, and also marsh habitats and intertidal areas. During high tide, the chum fry apparently congregated in the upper intertidal at the fringe of marshes, moving deep into the marsh along tidal creeks. At low tide, the fry were seen to retreat into tidal creeks that have flowing water at high tide, and into delta channels. Healey (1982a) noted that the preferred habitats appeared to be the junction of major and minor tributaries in the delta. Levy et al. (1979) found that abundances of pink and chum fry peaked in the tidal channels of the Fraser River during late April, that juvenile chinook were most abundant during late April and May, and that nearly all juvenile salmon moved into coastal waters by mid-June. Healey (1982a) examined the seasonal changes in catch of chum, coho, chinook and pink salmon in the Nanaimo river estuary. He found maximum catches in the inner estuary during April and May for chum salmon, and in the outer estuary during May and June for chum, coho and pink salmon. Most juvenile chinook salmon were caught later during June and July. Most salmon except for chinook had left the estuary by July.

Healey (1978) detailed the timing of arrival of Pacific salmon juveniles into the Strait of Georgia. Young salmon that enter the Strait of Georgia in spring and early summer spend between a few weeks and a few months exploiting the food resources there, and then move out to the open ocean. During even years, large numbers of juvenile pink salmon are present in the Strait of Georgia, most are from the Fraser River but some are from rivers that flow into the northern end of the strait. Pink fry migrate down the Fraser River in March and April and disperse quickly across the Strait of Georgia to occupy shallower near-shore nursery areas in the Gulf Islands region, although some are carried north into the central strait region or south into the San Juan Islands area. Juvenile pink salmon from central British Columbia also show the same behaviour (LeBrasseur and Parker 1964; Healey 1987). For the first few weeks the fry

stay close to shore often in large schools in just a few centimetres of water. They disperse along the shore but tend to accumulate in various places. In the Nanaimo area, the juvenile pink salmon move offshore in late May and also become abundant along the east side of the outer chain of the Gulf Islands (Fig. 1) (Barracough and Phillips 1978). By June offshore purse seine catches peaked in the Gulf Islands and the Nanaimo region, but by July they dropped dramatically, illustrating that most pink salmon had left the Strait of Georgia by that time. Apparently a few persist and leave in September and as late as March or April of their second ocean-year based on the purse seine catches by Argue in Johnstone Strait (Heizer and Argue 1972; Argue and Heizer 1974).

Chum salmon rear in the lower Fraser River and many other rivers flowing into the Strait of Georgia. Most chum salmon migrate downstream in April and May. Those from the Fraser River disperse similarly to pink salmon and occur with them in the nearshore areas. Juvenile chum salmon from smaller rivers disperse along shore after leaving the river mouths. Unlike pink salmon fry, many chum salmon rear in sloughs and side channels of the Fraser River delta and in other river estuaries for many weeks after migrating downstream (Dunford 1975; Healey et al. 1977a; Healey 1979 and unpublished data). Chum salmon and pink salmon fry are a similar size, both about 30–40 mm in length (0.25–0.4 g), when they migrate seaward.

Chum salmon fry from the early part of the run from the Nanaimo River remain in estuary nursery areas, whereas fry from the latter part of the run move directly into deeper water (Healey et al. 1977a; Healey 1979). Juveniles in the estuary nursery areas appeared to occupy waters of 1 m or less until late May when they moved from the shallow nearshore into deep water. They appeared to leave the Strait of Georgia more slowly than pink salmon, but catches declined after June no doubt due to their emigration. Some chum salmon, however, stay as late as October.

There was a decline in catches of chum, pink and yearling sockeye salmon in June and July in the Strait of Georgia which is coincident with an increase in the abundance of these species off the outer coast (Hartt 1980; Healey 1982b;). Healey (1982b) suggests that July is the time of outmigration for each of these species. However, in the 1990s, large numbers of chum and pink salmon were observed in September by Beamish (Beamish and Folkes 1998; Beamish et al. 2000a, 2001b), and in the 1970s Argue encountered significant numbers of immature pink and chum salmon, and a few sockeye, in Johnstone Strait as late as April (Heizer and Argue 1972; Argue and Heizer 1974). However, Beamish and Folkes (1998) showed that relatively large numbers of juvenile chum salmon

remained in the Strait of Georgia until late in the year, and that this behaviour was quite different from that observed during the studies of Healey and others during the 1960s and 1970s. It was possible that more chum salmon remained in the Strait of Georgia because of increased releases of hatchery reared chum salmon. However, except for 1992 and 1994, the total releases from Canada had not changed since the late 1980s. It appeared that pink and sockeye salmon were also found later in the year. Thus the behaviour change was believed to be real. The reason for the change in behaviour was unknown, although it was seen to coincide with a change in the pattern of the Aleutian Low Pressure Index (ALPI) about 1989–1990 (Beamish et al. 2000d). Another change which occurred at the same time was the earlier beginning of the increased Fraser River flows and a general increase in sea surface temperatures. Beamish and Folkes (1998) hypothesised that these changes led to improved feeding conditions for the juvenile chum salmon. The change in behaviour from the Healey studies may be related to physical changes resulting from the 1989 regime shift or from increased hatchery production of chum salmon. However, it may also represent a growth-related response.

Coho salmon smolts entered the Strait of Georgia during May and June from just about all the streams and rivers around the strait. They are rare in the open water before May, although a few were captured in the Fraser River plume in April (Barracough and Phillips 1978). Smolts became common in purse seine and trawl samples at the end of May and remained common throughout the summer. Tag returns suggested that whereas many coho rear in the open Pacific, some also rear to maturity in the open Strait of Georgia. Some also rear through the fall and winter months amongst islands of the southern Strait of Georgia and Johnstone Strait (Argue and Heizer 1971; Heizer and Argue 1972; Argue and Heizer 1974). Purse seine catches taken monthly in the Gulf Island region of the Strait of Georgia from May to October 1976, and weekly in the Nanaimo area (Fig. 1) from April to August 1975 and 1976, did not reveal any decline in the coho salmon catch that would signal the timing of an outmigration (Healey et al. 1977a; Healey 1978 and unpublished data; Schmidt et al. 1979; Healey 1980b). The extensive studies by Beamish and colleagues in the 1990s and early 2000s documented the migration of virtually all coho salmon out of the Strait of Georgia in 1991 and from 1995 to 2000 (Beamish et al. 2000a, d). Coded-wire tags in coho salmon caught outside of the Strait of Georgia indicated that few left the Strait of Georgia until late September (Beamish and Sweeting 1999). In Puget Sound, coho salmon left in August while chum and chinook salmon remained (Beamish et al. 1998a; Beamish and Sweeting 1999). The reason for

the change in behaviour from the mid- to late-1990s remains to be discovered but the change in behaviour was clear. It is important to note that the movement out of the Strait of Georgia without returning until the spawning migration of the following late summer was associated with a dramatic decline in marine survival.

Chinook salmon are produced in most medium to large rivers with the Fraser River producing the greatest numbers. Chinook have the most complex life history among Pacific salmon. Upon hatching and emerging from the gravel, some go directly to estuaries and rear in intermediate salinity waters, whereas some stay in fresh water. Thus, they migrate to sea as recently emerged fry from March to May, as underyearling smolts in June, and as yearling smolts from March to May of their second year (Rich 1920; Reimers 1971; Healey 1980b and unpublished data). Juveniles that rear in the estuary tend to leave it about the time that those reared in fresh water move downstream. Catches of underyearling smolts in open waters of the Strait of Georgia remained constant through July to November and declined during the winter (Healey 1980a, b). Yearling smolts were common in seine catches in the Strait of Georgia only during May to July after which they disappear from the Strait (Healey 1980a, b). Chinook salmon fry enter the estuary at a length of 40 mm (0.5 g), fingerling smolts are 60–80 mm in length (2–5 g), and yearling smolts are 80–110 mm, (5–18 g).

Barraclough and Phillips (1978) produced a series of distribution maps which suggested that most salmon found off the Fraser River estuary in April migrated across the Strait of Georgia, through Active and Porlier passes during May and June, and were virtually absent from the central Strait of Georgia by July. Distribution appeared to be influenced by tide and wind-generated surface currents and by the volume of fresh water discharge from the Fraser River. They found that during their migration across the Strait of Georgia, pink, chinook and coho salmon tended to be more confined to low salinity plume water than chum or sockeye salmon. During April to mid-June, the bulk of the juvenile salmon populations of pink, chum and chinook were close inshore rather than in the open waters of the Strait. The authors suggested that fry of these three species may remain for a time in the Fraser River estuary or in the proximate nearshore areas before resuming oceanward migration. They believed that entry of young salmon into the open Strait of Georgia may be a response to local environmental conditions resulting in the intermittent discharge of groups of fish into the Strait.

Holtby et al. (1989) found that downstream movements of chum and coho salmon were different, even though stream temperatures affected both. They found that the outmigration of chum was more predictable and more synchronous within a year than was

that of coho salmon. Coho salmon do not remain in estuaries, enter the ocean when larger, and have a more extended migratory period from fresh water than do chum salmon (Holtby et al. 1989). It was suggested that this difference might exist because peaks in productivity of large zooplankton may be less predictable in coastal waters, where juvenile coho salmon forage, than peaks of small epibenthos in estuaries, on which chum fry initially depend.

Healey (1979) and Levy et al. (1979), using release of marked fry in the Nanaimo and Fraser River estuaries, showed that chum salmon may spend up to three weeks rearing in the inner estuary, and appeared to be localized in their movement patterns. In addition to the twice-daily migration of fry from low tide regions to marshes and back again, Healey (unpublished data) demonstrated that there is also a seasonal migration seaward in the estuary. Thus, in the Nanaimo, Courtney and Cowichan River estuaries, chum salmon fry are found in the inner estuary in April and May and move into the outer estuary during May and June. Most chum salmon have moved out of estuarine habitats in southern British Columbia by mid July (Healey 1982a, b).

Almost all sockeye salmon migrate to sea in April and May as yearling smolts, but some migrate seaward as fry and rear in the Fraser River delta until July or August. In late April the yearling smolts are concentrated just off the river mouth, by late May they have dispersed rapidly south and east and are concentrated along the east and west sides of the outer Gulf Islands chain (Groot and Cooke 1987). By June most are concentrated in the Gulf Islands region, especially along the Vancouver Island shore (Barraclough and Phillips 1978; Healey 1978). Most sockeye leave the Strait of Georgia in late June and July through the northern passage (Groot and Cooke 1987). Timing of peak catches in the Fraser River plume and Gulf Islands region suggests that the smolts take 20 to 30 days to move through the Strait of Georgia. The sockeye fry that accompany the smolts downstream in the Fraser River in the spring rear in the estuary over the early summer and leave with the plume once they have reached 60–70 mm fork length.

DNA of ocean age 0 sockeye salmon sampled in the Strait of Georgia in one of the surveys conducted by R. Beamish was analyzed for 24 of the sample of 67 fish. Maximum likelihood analysis of microsatellite genotypes indicated that all fish were of Fraser River origin. Bayesian classification of these fish indicated that they originated from 12 different stocks: Pitt River, Weaver Creek, Birkenhead River, Portage Creek, Chilko River, Horsefly River, Mitchell River, Stuart River (early stock), North Thompson River, Lower Shuswap River, Little Shuswap River, and Lower Adams River (St-Hilaire

et al. 2002). A second DNA analysis was made from a sample of 63 ocean age 0 sockeye smolts collected in July 2001. The results from this analysis were compared to those from sockeye salmon in a baseline data set that contained information for the same 15 loci from 130 stocks from Washington to Russia (R. Withler, Pacific Biological Station, Nanaimo, BC, Canada, personal communications). All of the 63 ocean age 0 sockeye, except two, originated in the Fraser River drainage. The remaining two were from Lake Washington in Washington State, USA. Within the Fraser River about 18 different stocks were represented, indicating that small numbers of juvenile sockeye from a relatively large number of stocks remain in the Strait of Georgia in July.

Sockeye smolts have rarely been caught in the inner estuary and delta habitats of the Fraser and So-mass rivers, even though these systems are major producers of sockeye salmon (Levy et al. 1979; Morris and Leaney 1980). Sockeye smolts have been found in the outer Nitinat estuary, and the outer regions of other estuaries during their downstream migration, but the catches were considered small in comparison to the number of downstream migrants (Kask and Parker 1971; Barraclough and Phillips 1978). It therefore appears that sockeye smolts move quickly to nursery areas outside their natal estuaries. However, sockeye races from the Fraser River that migrate downstream as fry have been found within estuary habitats during April–June. They have been seen to migrate into the river plume after this time, where some remain until September (Healey 1980b).

Greer et al. (1980) examined the distribution of fish species on Roberts and Sturgeon Banks recorded in seine and trawl surveys. Levings and Kotyk (1983) carried out two trawling surveys for juvenile salmonids (chum, pink, coho, chinook and steelhead) in Discovery Passage and nearby channels in the northern Strait of Georgia. This was part of a sampling program established to examine the dispersal of wild chinook fry and juvenile marked chinook from release experiments at Quinsam hatchery into the Campbell River (Fig. 1) estuary. Chum salmon dominated the catches and peaked in abundance in late June, as did pink. Most chum salmon were probably from the Fraser River system. Chinook and coho salmon were less abundant and were primarily fish from the Quinsam hatchery. Steelhead trout and sockeye salmon were uncommon.

Argue et al. 1986 reported on habitat utilization and dispersal of juvenile coho and chinook from the Cowichan River estuary based on three years (1973, 1975, 1976) sampling with various net gears. Juvenile chinook and coho (ocean age 0) utilized the estuary from early April through June. Chinook then moved to deeper water at the head of Cowichan Bay, just past the estuary drop off, and to nearshore waters

around the perimeter of the bay. Coho smolts were not common on the estuary at any time, but were abundant near the drop off and at nearshore stations around the edges of the bay. Neither species was abundant at deep water stations (> 45 m) in the middle of Cowichan Bay. Juvenile chinook abundance outside Cowichan Bay in nearshore habitats peaked in July and August. Coho smolts were most abundant at outside sites when purse seine sampling started in June. Coded-wire tagged juveniles from the Cowichan River were recovered in the Bay through to the end of sampling in October. For coho smolts, there was evidence that later migrants from fresh water dispersed less from Cowichan Bay than earlier migrants.

Macdonald et al. (1988) examined the habitat utilization by juvenile salmonids in the Campbell River estuary. In this study, the authors wanted to characterise the microhabitats occupied by salmon by defining the physical features such as water velocity, salinity and temperature, and to investigate the importance of inter- and intra-specific aggression on micro-habitat selection. They found that water velocity, temperature, and salinity were the variables most important in characterising differences among micro-habitats. Coho salmon were observed in regions of higher salinities and water velocities than chinook salmon. Hatchery chinook salmon were found in lowest water velocities of all.

Macdonald et al. (1988) evaluated the importance of estuaries to juvenile chinook salmon survival. In late April of 1983–1985, 140,000 marked chinook salmon smolts were transported by helicopter from Quinsam hatchery to four release sites: riverine, estuarine, transition and marine, near Campbell River, British Columbia. At the marine site, fish were released directly into seawater. Beach seine data for four months after release showed that fish released directly into marine waters rarely dispersed to the Campbell River estuary. Fish released immediately adjacent to the mouth of the estuary (transition zone) had the widest immediate dispersal pattern, with many of them returning to the estuary. Estuarine zone fish displayed the most restricted distribution. Fish released to the river and estuary remained in the sampling area for a longer period (34–47 days) than those released in the marine or transition zone (20–23 days). Overall, fish released into the estuarine zone showed many signs of delayed seaward migration. They dispersed at lower rates, they travelled shorter distances immediately after release and were thus recaptured in greater numbers than chinook salmon deprived of estuarine residence.

Levings et al. (1983) carried out some preliminary marking experiments with juvenile chum and chinook salmon in May and June 1981 at three low tide refuges on Roberts and Sturgeons Banks at the

Fraser River estuary. They used spray marking with fluorescent grit. Residency periods of up to two days were documented. These experiments were part of a larger study investigating the juvenile salmonid use of foreshore habitats on Sturgeon and Roberts Bank in the Fraser River estuary. Preliminary results from this study suggested that the two species, chinook and chum salmon, may have different habitat preferences.

In summary, coho, yearling chinook and sockeye salmon all tend to rear to a large size in fresh water and spend little time in estuaries. Pink salmon migrate to the coastal ocean when very small and quickly move across the intertidal marshes and inner estuaries. Chum and sub-yearling chinook salmon, however, have much longer residence time in estuaries (Levy et al. 1979; Healey 1982a; Levy and Northcote 1982). Chum salmon are abundant in estuaries for two months in early spring, and chinook salmon throughout the spring, summer and fall. Pink and sockeye salmon spend very little time in estuaries. Habitats occupied by each species vary with fish size, tidal stage and time of year. The favourite habitats appear to be tidal creeks to marshes, the junction of major and minor tributaries in the intertidal zone, and the delta front.

Movement Patterns into Coastal Oceans

Peak migration of smolts into estuaries occurs in the spring and migration into the open ocean occurs in the late spring and early summer. Parsons et al. (1969a, b) and Stephens et al. (1969) suggested that the timing of movement into nearshore areas of the Strait of Georgia might be related to zooplankton abundance. The juvenile salmon that leave protected nearshore waters, inlets, and estuaries of the north-eastern Pacific enter the open coastal waters in large numbers by June (Healey 1980a, b). Most juvenile sockeye, chum and pink salmon spend several months in coastal "corridors" of around 30–40 km width, as they migrate northwards and westwards along the Gulf of Alaska. Some stocks of coho and pink salmon spend all of their marine life in coastal waters (Argue et al. 1983; Hartt and Dell 1986; Fisher and Percy 1987, 1988). However, juvenile steelhead generally migrate offshore into oceanic waters of the Gulf of Alaska, and are rarely found close to shore (Percy and Masuda 1982; Hartt and Dell 1986).

Pink salmon fry upon entering the sea at Bella Coola are initially shore oriented and form a narrow band extending into Burke Channel (Parker 1969b). With growth, they appear to move away from the shoreline and the fingerlings occupy more pelagic positions. At the end of May the fingerlings formed tight schools which were observed to migrate out of coastal waters to the more exposed waters of the Queen Charlotte Sound. Barraclough and Phillips

(1978) found that migration of fish across the Strait of Georgia could be rapid. Current velocities associated with discharge from the Fraser River could exceed 2.7 km/hr, which would mean that it would take only a few hours for juvenile salmon to cross the Strait. Groot and Cooke (1987) suggested that sockeye smolts move 6–7 km/day in the Strait of Georgia (i.e. about 0.7 to 0.8 body lengths per second at an average smolt length of 10 cm). Data from Parker (1965) and Healey (1967) suggest that pink salmon fry took 20–30 days to migrate about 70 km down Burke Channel in central British Columbia (i.e. about 0.6 to 0.8 body lengths per second). Healey (1989) used a default rate of 1 body length per second for sockeye, pink and chum salmon in his model of the coastal migration of salmon through Hecate Strait. Movements of coho and chinook were believed to be slower as movement of these species was thought to be more of a gradual dispersal than a directed migration.

Ocean type chinook enter the ocean at around 70–80 mm fork length, usually during their first summer, and these fish generally remain in coastal waters throughout their oceanic life (Healey 1982b; Healey and Groot 1987). Stream type chinook enter the ocean at a larger size and, after spending one year in fresh water, are also found in this band of juveniles migrating northwards. Healey (1983) suggested that stream and ocean type chinook salmon were different races. Information on ocean distribution and migration patterns of chinook also was recorded by Argue (1970). He found stream type chinook in their first ocean year in test troll catches throughout Juan de Fuca Strait during September and October, possibly indicating they were migrating to offshore waters. Stream type chinook migrate far offshore whereas ocean type chinook remain in coastal waters throughout their life. Ocean type chinook occur only in spawning populations south of about 56° N, but dominate in virtually all river systems from this latitude to the southern extremity of their range in California (Healey 1983). For example, Healey (1980a, b) reported high catches of juvenile ocean type chinook salmon in the southern Strait of Georgia during the period June to November, after which catches declined. Immature ocean type chinook salmon in their second ocean year were also abundant in the Strait of Georgia as demonstrated by sport fishery catches (Argue et al. 1983). Timing of seaward migration of stream- and ocean- types was similar. Stream type chinook smolts migrated in April and May, slightly later than recently emerged ocean type fry migrants, but before the downstream movement of ocean type smolts (Healey 1980a and unpublished data). First ocean year stream type chinook were present in the Strait of Georgia for about two months following downstream migration. Ocean type, however, remain abundant in the Strait of Georgia

throughout their first and second years of ocean life. (The patterns of scale or otolith growth zones are used to identify the particular life history type).

Argue et al. (1983) found that most emigration of coho from the Strait of Georgia took place prior to December of their first ocean year, as indicated by several years of marine tagging data covering all calendar months. There is, however, evidence that some coho continued to move out through Juan de Fuca Strait during winter and spring months in their second year (Argue 1970). In contrast, chinook tagging results showed modest levels of exchange at all ocean ages between the Strait of Georgia and the west coast of Vancouver Island.

Fraser et al. (1982) suggested that significant numbers of chinook salmon probably remained in the Strait of Georgia through to maturity, as indicated by substantial local sport and commercial troll fisheries and recoveries from many Strait of Georgia tag releases (Argue et al. 1983). A portion of the Fraser River chinook juveniles migrated out of the Strait of Georgia in a northwesterly direction through Johnstone Strait. This northwesterly direction had been proposed to be a dominant migratory route for many salmon stocks (Mason 1965). It was believed that these stocks remained relatively close to shore because of the rich feeding grounds off the continental shelf. According to Mason (1965), the highly productive troll fishery off the British Columbia and Alaska coasts, capturing primarily immature, feeding chinook salmon has confirmed this.

Healey (1967) examined the orientation of pink salmon during early marine migration from the Bella Coola River (Fig. 1) system for one summer only in 1966. He stated that the Bella Coola River and Burke Channel (Fig. 1) was a unique system in which to study the early marine migrations of Pacific salmon because they remained relatively distinct for much of their journey through the Channel. He noted that the movements of pink salmon fry down Burke Channel were saltatory: short periods of active migration were interspersed with longer periods when the juveniles did not migrate and accumulated in bays. Fry were sampled from these aggregations and their ability to orient using celestial cues was examined. During the early morning fry tended to prefer directions at right angles to their direction of migration, but at other times of the day they preferred the direction of migration. The preference for direction of migration was strongest at mid-day. Fry were better oriented on clear days than on cloudy days. These data indicate that the fry may use celestial cues to find directions during their oceanic migrations.

Healey and Groot (1987) compared the short migrations of ocean type chinook with the long distance migrations of sockeye to try to assess the sophistication of the direction finding mechanisms

required for each type of migration. During outward migration as juveniles to oceanic feeding grounds, both species apparently used compass orientation. During the homing migration, however, both species use a combination of compass and bicoordinate orientation until near the home stream mouth (at which time they use local environmental cues).

Sockeye salmon in southern British Columbia typically migrated seaward after one year in fresh water (Foerster 1968). Hartt (1980) and Hartt and Dell (1986) showed that juvenile sockeye, pink and chum salmon in the eastern Pacific migrate northward along the coast in a narrow band after leaving their natal river. This narrow band extends 1,800 km from southern Vancouver Island to Yakutat in Alaska and persists for about three months. Chinook are also found in this band but are stream type rather than ocean type (Healey 1983).

Sockeye salmon from the Fraser River can follow two routes out of the Strait of Georgia, either south through Juan de Fuca Strait or northwest through Johnstone Strait. Most juvenile sockeye salmon are thought to leave via the northern route (Groot and Cooke 1987). Upon leaving the Fraser River estuary, most smolts proceed along the mainland coast northward but some are flushed west across the Strait of Georgia by the Fraser River plume and tidal currents towards the Gulf Islands. Once among the Gulf Islands, these smolts turn north and migrate diagonally back across the Strait to join up with the smolts that have moved directly north from the river mouth (Groot and Cooke 1987). Groot and Cooke (1987) estimated that sockeye smolts migrated through the Strait of Georgia, a distance of about 200 km, in 30 days. To do this they had to travel 6–7 km per day. Johnson and Groot (1963) and Groot (1972) examined the rates of travel for sockeye smolts from Babine Lake (Fig. 1) (5–8 km/hr), with individual schools travelling at rates of 24.5–30.0 cm per second during active migration. At this rate, the smolts must swim for 6–8 hours per day. During their first summer in the Gulf of Alaska, juvenile sockeye salmon continued to travel rapidly along the coast of North America. Hartt (1980) estimated that to cover the distances of 1,150 and 2,770 km between the Fraser River mouth and the tagging sites in southern Alaska, the fish must have travelled 13.7–25.9 km/day. The average fork length at tagging was 20.8 cm. Thus, travelling at an optimum swimming speed of about two body lengths per second (Brett 1965), they must have swum on a direct course for 9–17 hr/day to get to the tagging site.

Healey and Groot (1987) concluded that ocean type chinook salmon remain in the region of their natal stream during their first summer at sea and then, during their first winter at sea, migrate northwards and establish a distribution along the coast within a

few hundred to 1,000 km of their natal stream. They maintain a relatively fixed coastal distribution throughout their ocean life, and migrate rapidly along the coast from the ocean feeding area to their home stream once mature. In contrast, sockeye salmon undertake a directed migration either north or northwest soon after entering the ocean. The following Spring, they migrate south and west into open waters of the Gulf of Alaska more than 1,000 km from their natal stream. Following their first winter at sea, they move continuously in a wide circle around the Gulf of Alaska throughout their ocean life and migrate rapidly from the open Gulf of Alaska directly to their home stream when mature.

Locally, returning chinook salmon congregate in particular areas as indicated by concentrations of fishing vessels during chinook salmon fisheries. The fact that chinook tend to occur at depth rather than near the surface (Argue 1970) suggests that the areas in which they aggregate may be characterized by bottom topographic features or oceanographic features below the mixed layer, that serve to congregate potential prey. Different size fish may also have different habitat requirements, a possibility suggested because the size composition of the catch changes dramatically along the west coast of Vancouver Island (Healey 1986). Also, chinook salmon from each brood year that are destined to mature at an older age appear to occupy the most northerly parts of a stock's geographic distribution.

Immature sockeye are distributed far offshore and appear to migrate actively throughout their life in the ocean. Their seasonal movements carry them in a large circuit off the Gulf of Alaska once each year. Their migration as immature fish may be a response to the seasonal movements of greatest ocean plankton production and thus serves to keep the sockeye in regions of good feeding. What is clear is that these fish are constantly on the move once they enter the ocean. In contrast, chinook salmon, once they have established a coastal distribution, appear to be relatively sedentary.

Little is known about what happens to immature sockeye after October or November of their first ocean year, when they have reached Kodiak Island. Because they are found well to the south in the Gulf of Alaska the following spring, French et al. (1976) concluded that there is a movement south and southwest in autumn and winter. Groot and Cooke (1987) examined the migration routes of juvenile and adult Fraser River sockeye salmon into and out of the Strait of Georgia. The purpose of their study was to determine if adults returned to the Strait of Georgia and Fraser River by retracing the same route taken by juveniles during their seaward migration. They suggested that the ability to predict the proportion and migratory routes of the Fraser River sockeye return-

ing to their home stream through Johnstone and Juan de Fuca straits would contribute significantly to the solution of international problems related to management. Migratory routes were determined by seining and trawling during 1982–1984. They noted that sockeye salmon returning to the Fraser River from their ocean feeding grounds migrated either via a northern or southern route around Vancouver Island with the proportion taking the northern route varying annually from 2 to 80% between 1954 and 1987. Sockeye smolts leaving the Fraser River on their way to the ocean were also seen to follow either route around Vancouver Island. This information, together with results of previous studies, showed that most juveniles left inland water by moving north by one of two patterns. In one migration, smolts leaving the Fraser River immediately turned north and continued to travel along the mainland coast. A second pattern was observed as a movement of smolts across the Strait of Georgia towards the Gulf Islands, a northward movement along the east side of these islands and then diagonally northward through the strait to join the smolts migrating across to the mainland shore. This suggested that Fraser River sockeye smolts have a north to northwestern directional tendency. The movement from the river mouth across the Strait of Georgia towards the Gulf Islands was assumed to result from a combination of strong river outflow and tidal currents. Comparison of the migratory patterns of the juveniles and the adults suggested that they were not related and the authors were unable to substantiate their hypothesis that the outward migration of the juveniles determines the inward migration of adults. They suggested that the smolts perform a one directional compass orientation (north to northwest) and that the adults show goal orientation homing to the Fraser River from their ocean feeding grounds by either following a northern or a southern route around Vancouver Island.

Diet and Growth Studies

Feeding within estuaries

Healey (1980a, b) examined the relationship between foraging success and residency in estuaries. He stated that the residence of chum fry was related to the seasonal abundance of their principal prey species, the copepod *Harpacticus uniremis*, in the Nanaimo River estuary. Estimates of amount of *H. uniremis* eaten by chum salmon was of the same order as estimates of its production, leading to the speculation that the abundance of chum was potentially limited by the production of this copepod (Healey 1979; Sibert 1979). The data indicated that food consumption by chum salmon was lowest when fish were most abundant in the estuary, and that emigration of the

majority of the chum coincided with a major decline in the population of *H. uniremis*.

Healey (1978) tried to establish a relationship between migration and food limitation. He found that movement of salmon juveniles away from the estuary did appear to be related to disappearance of their dominant food. But for the entire Strait of Georgia, he was unable to demonstrate food limitation. He suggested that demonstrating food limitation may be impossible because plankton samples generally have not revealed an abundance of the types of food that are in the stomachs of young salmon (Barraclough 1967; Barraclough and Fulton 1968; Barraclough et al. 1968; Robinson et al. 1968).

This absence of a relationship between movement away from shore and stomach contents may be an indication that food resources were adequate in most habitats to allow for successful foraging. Distribution of fish may be controlled by another need such as avoiding predators, or taking advantage of relatively warm nearshore water temperatures to maximize growth efficiency (Brett and Higgs 1970). The growth rate of juvenile pink, chum and chinook salmon during their first few weeks is very rapid (Healey 1979, 1980a, b) suggesting that food is not directly limiting at this time. After 15 June, when stomach contents declined, the fish began to show distributional patterns related to foraging success. Healey assumed that food resources were low enough that the fish had to seek out the best feeding areas to satisfy their food requirements. For pink, chum and sockeye salmon, which are largely planktivorous, this meant that they had to leave the Strait of Georgia. However, coho and chinook salmon, which are largely piscivorous, were able to satisfy their food requirements without migration.

Manzer (1956) examined diurnal variations in feeding intensity of pink, chum and coho salmon from June 8 to July 18 in Chatham Sound (Fig. 1) and adjacent waters. He noted diurnal variations in feeding intensity: pink, chum and coho salmon apparently did not feed with equal intensity from dawn to dusk, and their feeding rhythms during this time were not similar. Pink salmon fed relatively heavily during early morning and late afternoon and more lightly during 12:00 to 14:00 hours and possibly in the late evening, suggesting a bimodal diel feeding cycle. Parker and Vanstone (1966) found that juvenile pink salmon in central coastal British Columbia in late May fed most intensely in the afternoon and least intensely during the early morning. With chum, as with pink salmon, food consumption in Chatham Sound declined through the morning to a low between 12:00–14:00 hours. After that, food consumption increased in late evening (Narver 1968; McDonald 1973; Doble and Eggers 1978). Coho salmon, in contrast, appeared to consume food at about the same level of intensity

during the day, except possibly in late evening when feeding may have been reduced. Juvenile sockeye salmon are apparently crepuscular feeders.

LeBrasseur and Parker (1964) showed that the growth rate of juvenile pink salmon is extremely rapid during their first few months at sea. Phillips and Barraclough (1978) examined the early marine growth of several juvenile Pacific salmon species in the southern Strait of Georgia and Saanich Inlet using samples taken with a two boat surface trawl from April to July 1966–69, 1973, and 1975. Growth rates calculated from change in average size with time showed that pink salmon grew at rates of 3.5–4.0% body weight per day, and chum salmon at rates of 4–5% per day over the weight range of 0.5–10.0 g. Growth rates could not be calculated for sockeye, chinook or coho salmon because these fish did not show a consistent increase in size with time.

LeBrasseur and Parker (1964) found that young pink salmon grew at a rate of 6.35% body weight/day for their first 40 days, falling to a rate of 3.50%/day for the following 30 days. This study identified an average range of 3.5–5.0% body weight/day for Strait of Georgia pink salmon. Healey et al. (1977b) described comparable rates of 4.7–6.4% body weight/day for chum salmon in the Nanaimo River estuary during early marine residence. This was similar to rates of 4–5% body weight/day observed for chum in the open waters of the Strait of Georgia. He did not, however, find significant differences in growth rate between early and later estuarine residence. LeBrasseur and Parker (1964) also determined a reduction in size of sockeye with time in the open waters of the Strait of Georgia. They likened the offshore migration of young pink salmon at fork lengths of 60–70 mm to true smolting behaviour as exhibited by sockeye. Because sockeye are larger when they enter the marine environment, they do not spend much time in nearshore waters. Early emigration of large fish and continual addition of smaller downstream migrants may mask growth and account for the observed reversal in size of the offshore samples. It would also be possible that size selective mortality accounted for the observed changes. Chinook, coho and sockeye salmon had different size groups too, depending on how long the different races within a species reared in fresh water before entering the ocean.

Fish captured offshore appeared to grow at a greater rate than those captured inshore. Data for juvenile pink salmon captured by LeBrasseur and Parker (1964) indicated that larger fish tended to move offshore earlier than the rest of the population. Argue et al. (1986) reported similar findings for coho and chinook juveniles dispersing from Cowichan Bay. Thus, these larger fish would be most available to the surface trawl, leading to possible overestimation of mean size from offshore samples. Conversely,

the growth rate of the remaining nearshore fish may be artificially depressed due to loss of large fish to offshore areas and to recruitment of smaller downstream migrants or fish from areas closer inshore.

Parker (1971) found that a large part of the early mortality of pink and chum salmon was due to predation by coho smolts. He showed that there was greater selectivity by the predator for smaller prey resulting from late entry into the estuary, from slower growth rates, or from a preference for pink rather than chum salmon. He suggested that rapid growth might be important for survival of pink and chum salmon because that would allow them to grow out of a size class in which they were susceptible to predation.

Larkin (1988) examined the evidence for compensatory growth and mortality of sockeye salmon. Average total mortality of sockeye salmon at sea is around 90%, but varies from stock to stock and from year to year. Large smolt productions in sockeye have been associated with higher rates of marine mortality, e.g. for Cultus Lake (Foerster 1954) and Chilko Lake (Henry 1961). Mortality has also been shown to be lower when smolt size is larger. For pink salmon, a large production of seaward migrants may be associated with smaller adults returning (Davidson and Vaughan 1941; Hoar 1951; Neave 1953; Peterman 1978).

Diet composition

Diets have been described for salmon from a number of estuaries (LeBrasseur et al. 1969; Levy and Levings 1978; Sibert and Kask 1978; Fedorenko et al. 1979; Healey 1979, 1980b; Levy and Northcote 1981; Argue et al. 1986). The main conclusion from these studies is that salmon diets vary seasonally, geographically and annually. Thus salmon are opportunistic feeders and capable of exploiting a variety of taxa.

Parker (1969a) examined the diet of pink salmon fry. He noted that the pink fry entering the estuary fed incessantly, with diet consisting mainly of smaller zooplankters such as nauplii of copepods and barnacles, and oikopleura. With growth, the diet became mainly (80%) calanoid copepods. The pink salmon grew quickly (7% weight increase per day) and had catholic tastes, suggesting they are opportunistic feeders. The pink salmon fry appeared to leave the estuarine environment when food availability declined. He noted an afternoon maximum in feeding as indicated by relative stomach fullness.

Levy and Levings (1978) sampled the fish community of the Squamish River estuary during the period October 1975 to September 1976, using beach seines, gillnets and tidal creek enclosures. Juvenile salmonids used the estuary during spring and summer months (except for sockeye salmon). The salmonids

fed on estuarine crustaceans and insects, especially the mysid *Neomysis mercedis* and the amphipod *Anisogammarus confervicolus*.

Argue et al. (1986) sampled juvenile coho and chinook on the Cowichan River estuary and in Cowichan Bay using tow nets and pole, beach and purse seines. Estuarine benthic organisms and insects were most common by weight in the stomach contents of chinook and coho from March through May. Stomach contents of juveniles of both species caught from June onwards were dominated (content weight) by larval and juvenile fish (principally Pacific herring).

Healey (1980b) reported that the diets of chinook were similar over the course of the two years, with feeding on harpacticoid copepods important in March and early April, decapod larvae and amphipods in April and May, and mysids and insect larvae in May–July. Outside the intertidal area of the estuary, fish larvae, mainly herring, dominated the diet of juvenile chinook salmon from May to August, whereas calanoid copepods, decapod larvae and insects were occasionally important. Thus a change from a predominantly invertebrate diet to a predominantly fish diet occurred as young chinook salmon dispersed away from the intertidal area of the estuary. Using weights of stomach contents as an index of feeding conditions, he found that there was substantial variability from year to year. Poorest feeding conditions occurred in 1976 and the best conditions were in 1975 when population densities were the highest. There was a concomitant decline in the volume of stomach contents at these high juvenile densities.

Healey (1982a) summarized information on abundance, food requirements and production of the five major species of Pacific salmon in two estuaries in southern British Columbia and compared some of these features among seven other estuaries. He stated that the major prey of juvenile salmon in estuaries tends to be detritus feeders, suggesting that the food web supporting juvenile salmon is detritus based. Adult insects (mainly Diptera) were also a common occurrence in diets. Decapod larvae were important in the diet from seven of the nine estuaries considered in this report. Harpacticoid copepods, decapod larvae and cladocera were common in diet of chum salmon from several estuaries in southern British Columbia (Healey 1979 and unpublished data; Levy and Northcote 1981). Sibert and Kask (1978) compared diets of coho and chinook salmon among estuaries and among habitats within estuaries and concluded that each species had a distinctive feeding habit within an estuary but there was little similarity between estuaries. They said coho salmon had a narrow diet spectrum and their diet did not overlap with that of other species. Chinook salmon had a wider spectrum. Levy and Northcote (1981) compared chum and chinook salmon from marsh habitats of the

Fraser River estuary and concluded that chum salmon diet varied less from place to place than did chinook salmon diet. Thus, Healey (1982a) suggested that the range of feeding specificities among juvenile salmon correlated with the degree of dependence of the species on estuarine habitats. Chinook salmon, having great dependence on estuaries, appear less restricted in the types of food they can exploit. He also suggested that all the juvenile salmon, but particularly chinook and chum, appear to depend greatly on prey animals living near to or on the bottom, particularly in the inner estuary. He found that more pelagic forms were taken in the outer estuary but benthic food was still most important.

Kask et al. (1988a, b) examined the nearshore epibenthos of the Campbell River estuary and Discovery Passage, in relation to juvenile chinook salmon diets. Specifically, 284 epibenthic sled samples were collected from ten sites, which included established areas and newly created islands in the estuary as well as sites in the transition area immediately off the river mouth and in the marine zone. The epifauna was counted and compared to the food organisms present in juvenile chinook collected in the same areas. Comparisons were also made of the epibenthos and the diets of juvenile chinook in all three zones from 1982 to 1984. In the estuary, both wild and hatchery chinook relied on marine calanoids most likely transported in with the salt wedge (Brown et al. 1984) and freshwater cladocera flushed downstream from the lake and river habitat. The epibenthos (amphipods, harpacticoids, isopods, and cumaceans) contributed to the diet but usually comprised less than 15% of the total diet for either group. Once into the transition zone, the juvenile chinook salmon consumed mainly epibenthic amphipods and harpacticoids. These two groups alone made up 64–91% of the total diet. Calanoids made up a much smaller percent of the diet than in the estuary. The 14 wild fish analysed from the marine zone had eaten mainly harpacticoids (62%), barnacle cypris (24%) and decapod larvae (8%). Animals of benthic origin formed part of the diet in all three zones. They were most important in the transition zone followed by the marine and estuarine areas. Kask et al. (1986) compared the diet of juvenile salmon in the estuary and nearshore areas to that of previous studies and found differences in prey items between years and areas. In 1983, diets of all the chinook salmon analysed in all three zones changed from that recorded in 1982, demonstrating the opportunistic nature of chinook feeding preferences.

Following an experimental rehabilitation of the Campbell River estuary in 1981 to 1982, a program was established to monitor the use of the new, as well as the established, habitats of juvenile salmonids, particularly wild and hatchery chinook salmon. The

role of each of the nearshore habitats in providing food for the young fish was also monitored using an epibenthic sled (Kask et al. 1986). From March to December 1982, 146 nearshore samples were collected from three different habitat areas: estuary, transition and marine. Copepod nauplii, nematodes and harpacticoids dominated the estuarine and transition zones whereas harpacticoids, copepod nauplii and amphipods dominated in the marine zone. Densities of nearshore epibenthos were highest in the marine zone and lowest in the estuarine zone. Overall mean density of harpacticoids was almost 40 times greater in the marine zone than in the estuary. The epibenthic nearshore populations appeared to be most important in the diet of the juvenile chinook salmon in the transition zone, followed by the estuarine and marine zones. The transition and marine zones seemed to have the highest food potential, the dominant prey organisms occurring in the greatest densities in these nearshore areas. Epibenthic organisms never constituted more than 40% of the salmon diet in the estuarine zone. The proportion of epibenthos in the diet increased to over 99% in the wild chinook and 74% in marked chinook salmon (mainly harpacticoids and copepods). These fish also began to prey on pelagic euphausiids. Once in the marine zone, they reduced reliance on epibenthic harpacticoids and increased consumption of decapods (megalops and zoea) and pelagic amphipods. Pelagic calanoids, mainly *Neocalanus plumchrus*, were consistently present in stomachs of juvenile chinook in all three zones and often dominated their diet. Even in the estuarine zone, marine calanoids transported in with the salt wedge formed a major part of the food in both wild and marked fish. Amphipods were also important in all three zones.

Levings (1994a) continued the examination of feeding behaviour of juvenile salmon and the significance of habitat during the estuarine and early sea phases. He evaluated feeding success by using the Forage Ratio (FR), which is the ratio of weight of food in the stomach of a fish compared to the weight of the fish. Both forage ratios and food consumption have been found to vary between habitats and with environmental conditions. Post-smolt chum in British Columbia showed higher forage ratios in estuarine habitats (FR = 1.84) than in offshore areas (FR = 1.48) in the Strait of Georgia. The same trend was shown by post-smolt chinook salmon in the same area (Healey 1982b).

Bravender et al. (1996) surveyed the fish populations, juvenile salmon diets and epibenthic invertebrates in the Englishman River estuary in 1993. Chinook and chum salmon found between March and July were rearing in several low tide refuges. Most of the chinook salmon juveniles were hatchery fish from Big Qualicum River stock and reared in a side

channel in the Englishman River by Habitat Enhancement staff in Nanaimo. Diet analysis for chinook showed that insects dominated the diet. Forage ratios calculated for juvenile chinook were similar for those recorded for both the Nanaimo River and Campbell River estuaries.

Feeding outside of estuaries

Manzer (1956) examined the diet of young pink, chum, sockeye and coho salmon between June and August 1955 in Chatham Sound, in northern British Columbia. In general, food spectra were similar but the degree of importance of different groups varied. In general, pink and chum salmon were planktophagous, with copepods and oikopleura spp. being most important. Coho were mainly piscivorous (herring larvae and sandlance (*Ammodytes hexapteras*) most frequent). Sockeye salmon overlapped these two groups somewhat in their diet. They fed mainly on plankton but fish were also important. Samples of cohabiting pink and chum salmon showed that either all or many of the individuals consumed copepods, but this item made up a greater fraction of the food of pink salmon.

Godfrey (1968) presented data on the diets of chinook, coho and chum salmon captured in June 1965 in the Gulf Islands, Fraser River plume and central Strait of Georgia. He found that juvenile chum salmon consumed much smaller organisms than juvenile chinook and coho salmon. All three species fed on fish, zooplankton and terrestrial insects. Some chinook and coho salmon fed on sandlance, but this was not found in chum stomachs. He suggested that the frequency of occurrence of terrestrial insects indicated that surface feeding was of some importance to each of the three species.

Godin (1981) examined the stomach contents of pink salmon fry in the littoral zone of Departure Bay and Hammond Bay, Nanaimo, British Columbia. Stomach analyses showed that pink salmon fry fed mainly during daylight hours in May. Although the diurnal pattern of feeding differed slightly between the two bays, maximum mean prey biomass in the stomachs of the pink salmon occurred near or at dusk in both bays. The fry consumed similar items in both bays, but in differing proportions. Harpacticoid copepods, copepod nauplii, and barnacle larvae collectively comprised 93.1 and 86.2% of the diets of Departure Bay and Hammond Bay fish, respectively. About 38% of the diet of Departure Bay fish and 51% of the Hammond Bay fish consisted of epibenthic prey, mainly harpacticoid copepods. These data provided additional support for the importance of the detritus-microbe-consumer type food chain supporting the production of pink salmon during their early period of marine residency. In contrast to the diets

listed here, the diets of larger juvenile pink salmon in more offshore waters consisted mainly of larger, planktonic prey species (Barraclough and Fulton 1967, 1968). Chum salmon fry also fed on epibenthic invertebrates, mainly harpacticoid copepods, in nearshore marine habitats (Mason 1974; Feller and Kaczynski 1975; Sibert et al. 1977; Healey 1979). These fry fed mainly during daylight hours and little or no feeding occurred at night.

Healey presented some of the most detailed observations of diet of juvenile salmon, from within the Strait of Georgia, from Saanich Inlet, as well as in Hecate Strait (as part of the Hecate Strait program), and in the Barkley sound region (as part of the MASS project). Healey (1980b) provided an extensive summary of the diets of juvenile salmon in the Strait of Georgia from studies carried out by himself and various other authors from 1966–1977. Different items appeared to be important in different years. In 1966, sockeye smolts caught in the plume fed on insects, euphausiids and copepods. In 1967, they fed on copepods, insects and fish larvae. In late summer they fed on amphipods and insects. In 1975, sockeye salmon smolts fed on crab larvae and fish larvae, whereas in 1976, copepods and ctenophores were important. He suggested that overall sockeye smolts prefer copepods and insects, but also eat amphipods, euphausiids and fish larvae when available.

Phillips and Barraclough (1978) found evidence that there was an inverse relationship between abundance and size. Pink salmon captured in Fraser River plume in 1966 and 1968, years of high abundance, were smaller on average than those caught in 1967 or 1969, when abundance was low. To grow at a rate of 7% of body weight per day, pink salmon juveniles must eat almost continuously. While in transit to nearshore nursery areas, pink salmon fed on calanoid copepods in April and May in the Fraser River plume. However, in nearshore nursery areas during the same months, they fed on epibenthic prey, with harpacticoid copepods being the major food item (Kaczynski et al. 1973; Healey unpublished data). In late May, when pink salmon moved offshore, they again fed on zooplankton. Data provided by Healey (1980b) for Saanich Inlet for early June 1966 and 1968 were also typical of diets in the Strait of Georgia at that time. Pink salmon fed mainly on copepods in 1966. Of secondary importance in the diets were amphipods, insects, chaetognaths and the larvacean oikopleura. In 1968, euphausiid eggs dominated the diet, with oikopleura, insects, euphausiids, and copepods being of secondary importance (Barraclough and Fulton 1968; Barraclough et al. 1968). In late summer, pink salmon that remained in the Strait fed on amphipods and insects, with crab larvae, euphausiids and copepods being of secondary importance.

The diet of juvenile pink, chum and coho salmon

from the same samples taken in Saanich Inlet were compared by Healey in 1966 and 1968. The relative contribution of various food organisms changed in the same direction between years for all species. It appeared that copepods were less available in 1968 than in 1966, and because of this, pink salmon turned their attention to the next most available and preferred prey, which was euphausiid eggs. The belief that this was a choice, rather than a result of the eggs being overwhelmingly abundant, was indicated by the relatively low abundance of euphausiid eggs in the diet of chum and coho.

Healey (1980b) suggested that small food items are particularly important for pink salmon, including harpacticoid copepods during their residence in near-shore areas, and calanoid copepods and euphausiid eggs in late May and June before they leave the Strait. The importance of amphipods and insects in late summer was thought to reflect the scarcity of copepods at that time, as well as the large size of the remaining pink juveniles in the Strait of Georgia.

Healey (1980b) suggested that stomach contents give a good indication of success of feeding conditions. In Nanaimo River estuary areas the stomach contents increased with time: in April, stomach contents averaged 1–2% of body weight, whereas by late May they increased to 4–5% of body weight. Stomach contents of fish caught over deeper water ranged from 2–3% for most of April and May, increased to 3.5% in early June, and then dropped to less than 0.5% at the end of June. In July the stomach contents averaged about 1% of body weight. Clearly, fish left nursery areas and entered a depth zone where the foraging success was lower. Healey also found that the majority of pink salmon left the Strait of Georgia when foraging success was very poor. Barraclough et al. (1968) reported that stomach contents were poor for a brief period at the end of June 1968 in Saanich Inlet. Thus, movement of pink salmon away from beaches does not appear to be a response to poor feeding conditions but the movement of fish out of the Strait of Georgia in late June and early July may be a response to poor feeding conditions.

The average increase in the fork length of chum salmon from samples taken in the Fraser plume was 0.80 mm/day in 1966–69 (Phillips and Barraclough 1978) and from samples taken monthly in the Gulf Islands in 1976 was 0.72 mm per day. In nearshore nursery areas and estuaries, chum salmon fed mainly on harpacticoids (Kaczynski et al. 1973; Healey 1979), although Dunford (1975) found that chum in the upper Fraser marshes fed mainly on chironomid larvae and cladocera. In 1966 and 1968, chum that moved offshore fed mainly on oikopleura. This was also a dominant food item in the chum diet in the Nanaimo area during June 1975 (Healey unpublished data), and Chatham Sound in northern British Co-

lumbia (Manzer 1969). Chum salmon also appeared to prefer polychaetes and chaetognaths. They generally took larger prey than pink salmon and were less attracted to euphausiid eggs than pink salmon were.

Healey (1979) reported on regional diet differences found in the late summer of 1975. The regional comparison suggested that chum salmon prefer euphausiids over other items such as crab megalops. In 1975 and 1976 he recorded stomach content weights. In the Nanaimo River estuary, average contents varied from 1.2 to 5.9% body weight between March and June. There was no apparent seasonal trend, but stomach contents did tend to be low when chum were most abundant in the estuary. However, there were more chum salmon rearing in the estuary in 1975 than in 1976, and their stomach contents were greater on average in 1975, which suggested a relationship between carrying capacity of the estuary and food supply (Healey 1979). Similar changes in stomach contents were seen over time, as e.g. with pink salmon, but chum salmon tended to have more food in their stomachs. Seasonal changes suggested that the best feeding conditions for chum were in May. As with pink salmon, they left nearshore areas when feeding conditions were improving, and entered the pelagic zone where their feeding success appeared lower. Their departure from the Strait of Georgia in late June was associated with the lowest recorded stomach contents. Chum salmon also showed reduced stomach contents at this time in Saanich Inlet in 1968 (Barraclough et al. 1968).

Euphausiids dominated the diet of juvenile coho caught in Saanich Inlet in June of 1966 and 1968. Since diets of pink and chum salmon suggested that euphausiids were less abundant in 1966 and 1968, their predominance in the diet of coho suggests that they are a preferred prey. Coho salmon did show flexibility in the importance of secondary items, probably as these are taken with respect to availability. Coho also showed regional differences in diet. They showed a positive correlation between abundance and the amount of food in their stomachs in late summer 1975 and 1976, leading to apparently greater numbers remaining in the Strait in 1975, when feeding conditions were better.

Chinook salmon show a complex size distribution in the Strait (Healey 1980a, b). In the estuary, they were seen to feed on a wide variety of invertebrates and were much less dependent than chum salmon on small copepods. Chinook juveniles ate insect larvae and adults, amphipods, decapod larvae and calanoid copepods (Sibert and Kask 1978; Healey unpublished data). Upon leaving the estuary, larval and juvenile fish were the dominant prey of juvenile chinook, and invertebrates were a diet choice of secondary importance (Godfrey 1968; Beamish et al. 1976; Healey unpublished data). Prey such as

crab megalops, euphausiids and amphipods made up the invertebrate fraction. Diet was seen to change from year to year depending on availability of various organisms. Overall, chinook salmon appeared to prefer fish, particularly Pacific herring, but also liked larger invertebrates and appeared to have similar food preferences to coho. Healey (1980b) also found a relationship between chinook salmon abundance and feeding conditions similar to that for coho and chum salmon.

The way that the young salmon use nursery areas in the Strait of Georgia suggests resource partitioning (Healey 1978, 1980b). Pink, chum and chinook salmon that migrate downstream as fry spend most of their first month in the ocean in very shallow water close to shore. Chum and chinook salmon coexist in estuaries and pink and chum salmon in high salinity nurseries. All three species are opportunistic feeders, and often have the same diet components when they coexist. However, when dominant food items are the same, they generally are found in different proportions in the diets and the choice of secondary items differs. Chinook, particularly, feed on different things than chum salmon during estuarine residence. Harpacticoid copepods and shrimp larvae are dominant items for chum feeding, but chinook feed on harpacticoids for only a few days after migrating downstream, and after that concentrate on amphipods, insect larvae and adults, and mysids. Pink and chum salmon do feed on the same things but in different proportions.

The major concentration of juvenile pink and sockeye and possibly chum salmon, occurs around the Gulf Islands (Healey 1978, 1980b). Thus, just a small area of the Strait of Georgia was originally believed to support the bulk of the juvenile salmon population. Offshore movement appears to be unrelated to food abundances, and is apparently not timed to correspond to plankton blooms in the Strait of Georgia, as these blooms are beginning to decline in May. Juvenile pink, chum and sockeye salmon that are foraging over deep water in May and June may experience food shortages as their demands increase with growth. Thus it is hardly surprising that this is when the greatest differences in diets occurred: chum feed mainly on oikopleura, pink on small copepods and invertebrate eggs, and sockeye on copepods, amphipods and insects (Healey 1978). Stomach volume was low, perhaps indicating that these species leave the Strait of Georgia in response to poor feeding conditions (Healey 1980b, 1982a). After these juveniles left, feeding conditions appeared to improve for the young-of-the-year sockeye salmon entering the Strait. Juvenile sockeye salmon fed well and grew rapidly at the food densities found during July and August.

Healey (1980b) suggested that coho and chinook salmon do not depend as much on invertebrate food

resources as chum, pink and sockeye, and thus they face a different situation. In fact, a significant proportion of coho and chinook salmon remained within the Strait of Georgia to rear. Chinook stomach contents did not decline in late June, as did those in pink and chum salmon (Healey 1978, 1980b). Both coho and chinook salmon fed on larger invertebrates as well as fish: e.g., while pink and chum salmon in Saanich Inlet ate copepods, euphausiid eggs and oikopleura, coho fed on euphausiid adults and insects. In late summer, both coho and chinook salmon concentrated on amphipods, crab megalops and fish. Because of their preference for fish and large invertebrates, coho and chinook may not compete with pink, chum and sockeye salmon but may compete with each other.

Bravender et al. (1996) compared the diets of juvenile salmonids in the Englishman River estuary with the diets recorded for the Nanaimo River estuary by Healey (1980a) and the Campbell River estuary (Kask et al. 1986, 1988a, b; Macdonald et al. 1988). Juvenile chinook in the Englishman River estuary fed primarily on insects, mainly dipteran adults, but also other adult insects and larvae. In the Nanaimo River estuary, juvenile salmon fed on five taxonomic groups which changed in importance as the fish grew over the spring, with the salmon progressing from feeding on harpacticoid copepods in early spring, to decapod larvae, amphipods, mysids and insect larvae in early summer. In the Campbell River estuary, freshwater cladocerans and copepods were the most important components of the diet.

Healey (1991) also examined the diets and feeding rates of juvenile pink, chum and sockeye salmon in Hecate Strait during July and August 1986 and 1987, as part of the Hecate Strait program. The objectives of this study were to describe seasonal and species-specific patterns of feeding and to test assumptions and predictions of models relating feeding success of juvenile salmon during their first summer at sea to survival and recruitment. A wide variety of taxa was consumed by all three species, but only a few taxa made up most of the fishes' daily food intake. Diet composition was more similar among species within sampling periods than within species among sampling periods, although there were some apparent species-specific feeding preferences. Patterns of changing diet composition with increasing time and distance between samples were consistent with expected mesoscale patterns of plankton patchiness in coastal waters. Juvenile salmon fed selectively on larger sized taxa in the plankton community and larger salmon fed on larger prey. Young salmon did not switch to larger prey later in the summer, however. Weights of stomach contents and estimated daily ration were small enough to limit growth rates, and the hypothesis that limitation of growth during

early ocean life affects survival and recruitment cannot be rejected.

Haegerle (1997) collected information on herring, salmon and plankton abundance in the Strait of Georgia from 1990 to 1994. Purse seine and plankton tows were made on ten transects, each with five stations, around the perimeter of the Strait of Georgia during two weeks in both the late spring and late summer. Haegerle found that juvenile chinook, coho and chum salmon were much more common in late spring than late summer. He did not catch any juvenile pink or sockeye salmon. Major plankton species were copepods, crab larvae and euphausiids which were also the major prey of juvenile herring and chinook and coho salmon. Larvaceans and amphipods were of lesser abundance in the plankton but were targeted by the juveniles of chum, sockeye and pink salmon. Haegerle (1997) reported that there was no obvious correlation between plankton density and juvenile Pacific herring or salmon abundance. Both juvenile chinook and juvenile coho salmon ate mainly crab larvae, but they both also ate fish, mostly Pacific herring larvae and 0+ herring, along with amphipods, euphausiids, and insects. Chum salmon ate different things in different years: overall larvaceans were most common in spring, and amphipods and euphausiids and crab larvae in the summer. Sockeye and pink salmon juveniles had the most cosmopolitan diet feeding on all the above prey as well as ostracods. These results were similar to those of Healey (1978) except that Healey considered fish to be more important in the diet of chinook and coho salmon juveniles than did Haegerle (1997). Generally, salmon juveniles did not appear to target copepods, the principal prey of herring.

Perry et al. (1998) examined spatial variations in feeding and condition of juvenile pink and chum salmon feeding on the Vancouver Island continental shelf during the early summer of 1992. They found that juvenile pink salmon off northern Vancouver Island had more food in their stomachs, and were in better condition, than pink salmon off southern Vancouver Island. Juvenile chum salmon in the north also had more food material in their stomachs, and the authors suggested that these variations were associated with variations in zooplankton biomass, since they found more plankton in the north. There was a significant positive relationship between amount of food in pink salmon stomachs and their condition factor. However, no difference was found in the condition factor of chum salmon between northern and southern regions and there was no relationship between stomach contents and condition factor for chum salmon from the south. Using a bioenergetics model, the authors showed that pink salmon in the north had higher potential growth rates than those in the south, but chum salmon did not respond in the

same way. They suggested that chum salmon in the south were food limited.

Using diet comparisons, King and Beamish (2000) indicated that there could be a competitive interaction between ocean age 0 chum and coho salmon. Trawl surveys were carried out in the Strait of Georgia in June/July and September of 1997 and 1998. Onboard stomach analyses were done on 2,230 ocean age 0 coho and 1,558 ocean age 0 chum salmon. In June/July 1997, the three most abundant food items for coho were decapods, teleosts and euphausiids, while decapods, teleosts and amphipods were the top items for chum. In September 1997, amphipods replaced decapods for coho and ctenophores replaced teleosts for chum. In June/July 1998, the top three items for coho salmon were decapods, amphipods and teleosts, and for chum salmon were decapods, amphipods, and euphausiids. In September 1998 the top three items for coho were amphipods, euphausiids and decapods, and for chum were amphipods, euphausiids and ctenophores. The authors concluded that in early summer, chum are potential competitors of coho salmon in the Strait of Georgia, whereas by late summer, the chum were still competitors but also began to feed on gelatinous zooplankton. There was almost complete diet overlap between hatchery marked and unmarked coho.

Neville and Beamish (1999) compared the diets of ocean age-0 hatchery and wild chinook salmon from the Strait of Georgia between 1996 and 1998. Salmon were identified as hatchery or wild using otolith microstructure. Diet items were summarised into nine main categories and by percent volume and frequency of occurrence. Diet overlap was determined using a modified Morisita Index. There was a significant overlap in diet of hatchery and wild ocean age 0 chinook and this overlap persisted even with differences in size of the two types. The dominant diet items for both were amphipods, euphausiids, decapods and teleosts.

Beamish et al. (2001b) examined the hypothesis that during some ocean conditions, Pacific herring could also be a competitor of juvenile coho salmon. Traditional views were that the survival of coho might be linked to the abundance of herring as prey. Beamish and co-workers proposed that the abundance of coho salmon might also be linked to herring through diet overlaps, resulting in reduced coho growth and consequent higher winter mortalities. The critical size and critical period hypothesis of Beamish and Mahnken (1998, 2001) proposed that, during the first marine summer, coho must grow at a rate that would enable them to survive the first marine winter. The diets of ocean age 0 coho showed a preference for small fish, while Pacific herring age 1+ and 2+ preferred copepods and small eggs of invertebrates. However, decapods, amphipods, and euphausiids

were prey that were common to both diets. Beamish et al. (2001a) showed that there was no relationship between herring abundance and coho abundance, ruling out a direct linkage between coho and herring, either as prey or competition. However, once it is known that slower growing coho do not survive through the first marine winter as well as their faster growing siblings, then Beamish et al. (2001a) argued that it was possible that competition from herring contributed to the aggregate of factors that reduced growth of coho in their first marine year below a critical minimal level.

HATCHERY STUDIES

Most work regarding juvenile hatchery fish in the ocean has been 1) examination of interactions in estuaries by workers such as Levings (Levings 1985, 1986; Levings et al. 1986, 1987, 1989a, b; Levings 1990, 1991; Levings and Macdonald 1991; Levings 1993a, b, 1994a, b, c; Bravender et al. 1996; Levings and Bouillon 1997; Bravender et al. 1997a,b; Korman et al. 1997; Levings 1998; Bravender et al. 1999) and 2) determination of abundance and survival of hatchery fish in the Strait of Georgia (Beamish et al. 1998b, 2000a; Sweeting et al. 2003). Korman et al. (1997) analysed juvenile salmon population growth and abundance data collected in the Campbell River estuary in 1994 to describe chinook habitat use, residency timing, growth, and potential competitive interactions between wild chinook fry, hatchery chinook and other salmon species. The authors found that wild chinook fry densities were highest in estuarine zone sites, while hatchery chinook densities were generally higher than wild densities between the nearshore and deeper water habitats. Habitat type significantly affected the density of wild chinook in the estuary where their densities were greatest at riparian and intertidal island sites. Hatchery and wild chinook juveniles showed different patterns in their seaward emigration timing. The timing of peak abundance of hatchery chinook in the estuary coincided with the peak abundance of wild fry. This was considered a likely period of strong competitive interaction between hatchery and wild chinook salmon. Wild and hatchery juveniles were generally larger at transition zone sites compared to those from the estuarine zone. Growth rates of wild chinook tended to be slightly higher than growth rates of hatchery chinook. The inverse relationship between wild chinook fry size and total salmon biomass, assessed in mid-May, was similar to that established with earlier data, supporting the conclusion that growth of wild chinook in the Campbell River estuary may be density dependent.

McAllister and Brown (Pacific Biological Station, Nanaimo, BC, Canada, personal communica-

tions) also examined the use and residency of hatchery and wild chinook fry and juveniles in the Campbell River estuary. They examined these issues from 1982–1986 and in 1989, and concluded that the hatchery juveniles affected the growth and size of wild chinook fry in the estuary and that increases in rearing capacity resulting from the intertidal islands may also have reduced competitive effects on wild chinook growth. They concluded that wild chinook fry appeared to move seaward more rapidly in years of high total salmon biomass in the estuary than in years of low biomass, which could potentially lead to greater exposure of smaller chinook to larger predators outside the estuary.

Levings et al. (1986) examined the differential use of the Campbell River estuary by wild and hatchery-reared juvenile chinook salmon. Juvenile chinook were sampled by beach seine between March 1982 and December 1983 in the Campbell River estuary and adjacent waters of Discovery Passage to examine estuarine use by wild and hatchery fish. Wild juvenile chinook entered the estuary as migrant fry and were present in the estuarine zone mainly in late April to June, in the transition zone mid-May to July and in the marine zone in July. Maximum catches of wild stocks were similar in the estuarine and transition zones, but maximum catches of most hatchery stocks were higher in the transition zone. For both wild and hatchery chinook, catches in the marine zone were much lower than in the estuarine and transition zones. Wild fry resided in the estuary for 40–60 days, while most hatchery fish used the estuary for about one half of this time. Residency and growth rates of wild fish were similar to those recorded for wild fish in the Nanaimo estuary, where there were no hatchery fish (Healey 1980a). The potential for interaction between wild and hatchery fish was greatest in the transition zone, where hatchery fish were most abundant and because hatchery releases occurred when catches of wild fish were highest in this foreshore area. This study allowed some preliminary analysis of diet differences between hatchery reared and wild salmon. Comparisons of the percent numerical composition of the dominant taxa in stomachs were made from a number of established and new sites. Chi squared analysis showed significant differences at all stations in both years, with a predominance of marine calanoids in the hatchery fish diet, and an abundance of harpacticoids, calanoids, insects and freshwater cladocerans in the diet of the wild fish. Higher rates of growth were seen in the hatchery fish with earlier release dates and smaller mean sizes. These results indicated that chinook food limitation and interspecific or intraspecific interactions may be most significant in the transition zone. Here, catches of hatchery groups were highest, and in both 1982 and 1983,

large numbers of hatchery fish were released when the main migration of wild stocks to the transition zone was occurring (late May to early June). Using estimated peak biomasses for the two different groups, Levings and co-workers were able to estimate, based on size of fish, that hatchery chinook could consume up to four times as much food as wild fish. In late June the transition zone also supported high densities of pink and chum juveniles, many of which may be Fraser River outmigrants (Levings and Kotyk 1983). These two species could impose a food demand almost equivalent to that of the wild and hatchery chinook and their peak biomasses also occurred in mid to late June. Wild chinook fry in the Campbell River area in 1989 comprised a total of 55% of the total catch of young salmon in the estuary but appeared to consume only 28% of the total rations required by the young salmon. Chinook and coho smolts from the Quinsam hatchery were found to take the largest fraction of rations in the estuary (approximately 65%) even though they were found to make up only 28% of the average numbers caught. Hatchery chinook and coho salmon also dominated food consumption in the transition zone immediately outside of the estuary, consuming approximately 63% of the total.

This major study of the importance of estuaries for salmon showed that in two of the three years of the experiment, fish that experienced the estuary survived best (Levings et al. 1989b). There was evidence of changing ocean conditions in the third year and final conclusions remain to be published. Their unpublished summary appears to show that the total return of all age classes of chinook salmon, in all brood years, was a function of both estuarine and open ocean conditions. The survival experiments and the hatchery-wild interaction studies showed that the factors affecting chinook salmon survival in estuary and ocean habitats are likely not independent. Levings et al. (1989b) suggested that if wild chinook salmon are to be maintained, habitat space in the estuaries needs to be maintained or enhanced and interactions with hatchery fish need to be minimized. A very important conclusion was that the size and health of the fish as established in the estuary may affect their survival later in the ocean.

Beamish and staff had carried out a survey to determine juvenile coho abundance and distribution in the Strait of Georgia and in Puget Sound in 1997 (Beamish et al. 1998a). In addition, the survey provided data that enabled estimates of hatchery and wild coho to be determined prior to any fishery (Sweeting et al. 2003). These marked coho and catches from surveys in June/July and in September indicated that the proportion of juvenile hatchery coho salmon within the Strait of Georgia ranged from 76–79%. If estimates of smolts from enhanced adults

(i.e. hatchery fish spawning in the wild) were included as hatchery releases, estimates of hatchery percentages in the catch could be as high as 87%. Both hatchery and wild juvenile coho salmon remained in the Strait of Georgia until after September, several months after coho left Puget Sound. There was no difference in the fork length of coho with or without the left pelvic fin.

Beamish and Sweeting (1999) examined the patterns in the recapture rates among release locations of coded-wire tagged (CWT) juvenile coho salmon in the Strait of Georgia. Analysis of CWT recoveries from research surveys during 1995 to 1998 indicated that, in September, the production from Fraser River hatcheries dominated the recaptures. However, recaptures from the Fraser River hatcheries also tended to exceed the expected adult returns, indicating that early marine survival was higher for Fraser River stocks than for coho salmon juveniles released on the opposite side of the Strait. The relative proportions of CWTs from the nine major hatcheries seen in the September surveys generally persisted until the next fall, which indicated that the fall/winter mortality was non-selective across all of the hatcheries.

Zhang et al. (1995, 1998) found that otolith microstructure exhibited characteristic differences between hatchery reared and wild chinook salmon from the Cowichan River. The daily growth increments that formed in the otoliths of the hatchery-reared salmon after exogenous feeding were more regular in width and contrast than those in the otoliths of wild chinook salmon. Also, hatchery fish otoliths often showed a check when the fish were released from the hatchery. Samples were collected in early summer, late summer and late fall in 1995, 1996 and 1997. The percentage of wild fish dropped from 71.5% in late summer to 36.8% in the late fall of 1995, and more dramatically from 61.4% in the late summer to 19.2% in the late fall of 1996. There was also a general decrease in lengths of each rearing type from the 1995/1996 samples to the 1996/1997 samples, suggesting that ocean conditions were possibly less favourable for growth in 1996/1997. Hatchery fish were not found to be moving into the Strait of Georgia in the fall, and thus, differential mortality and/or utilisation of these waters accounted for this shift to a reduced percentage of wild juveniles.

EARLY MARINE GROWTH

Relationships between Marine Mortality and Environmental Correlates

Early studies focussed on the influence of fresh water factors on production of salmonids (Pritchard 1936; Davidson and Hutchinson 1943; Davidson et al. 1943; Pritchard 1947a, b; Neave 1949; Neave and

Wickett 1948; McKernan et al. 1950; Brett 1951; Wickett 1951, 1952; Neave 1953; Smoker 1954; Wickett 1954; Silliman 1970). However, examination of the relationship between ocean factors and survival of Pacific salmon began in the late 1950s. Vernon (1958) found that year class strength of pink salmon in the Fraser River was negatively correlated with the temperature encountered by juveniles when entering the Georgia Strait. He also showed that there was an inverse relationship between sea surface temperature in the Strait of Georgia during the seaward migration stage (April to August), and pink salmon catches (total run or percentage survival) of the following year. However, this apparently only held for the 1935–1957 data and not later data. Vernon (1956) suggested that the negative relationship between temperature and pink salmon survival might not be due to lethal temperatures, but due to warm surface waters forcing young fish to move to deeper strata where food may be less suitable or predation more intense. He suggested that because the Fraser River and its estuary are near the southern limit of the range for pink salmon, their abundance might be inversely related to sea temperature. Overall, low temperatures and high salinity appeared to be most favourable for survival. Wickett (1958) found that low sea surface temperatures along the coast in June were associated with reduced survival of pink salmon in central British Columbia.

Hunter (1959) examined the effects of temperature, stream discharge, sex ratio and population density in relation to egg to fry survival of pink and chum salmon in the central coastal region of British Columbia between 1947–1956. Within the limits of this study, temperature, stream discharge and sex ratio did not appear to affect the population, but population density was important. The density of spawners in preceding years also affected the survival in subsequent years. Predation was an important factor in keeping fry density low. Ocean survival, including the effect of fishing mortality, varied from 5.2% down to 0.7% for pink salmon, and from 2.6% to 0.85% for chum salmon. Ocean survival for pink salmon before fishing mortality ranged from 10.8% down to 1%. The combination of freshwater and ocean survival rates indicated that a variation of up to 190 times the lowest rate recorded was possible.

Holtby and Scrivener (1989) examined correlations between coho smolt survival at Carnation Creek, British Columbia and environmental factors. They found negative correlations between sea surface temperatures (SST) and smolt survival in the year of migration for coho salmon and also showed lower smolt survival during years of higher temperatures and low salinity. They suggested that variability in smolt survival was associated with variations in SST during the first few months of ocean residence. Holtby et al.

(1990) found positive correlations between salmon growth rates and upwelling. Holtby (1988) found that smolt size can be an important factor in determining smolt survival and that a size selective mortality agent was acting during some of the years in his study. Overall, he concluded that smolt survival was size dependent during years when smolt survival was poor, and when herring abundance was low, which is consistent with the hypothesis that variation from smolt to adult survival of the coho salmon of Carnation Creek resulted from changing predation intensity.

Holtby et al. (1990) examined the influence of smolt size and early ocean growth on marine survival of coho salmon over a 17-year period at Carnation Creek. Comparisons of overall marine survival were made both between years, using two smolt groups of different age and of different mean sizes, and within years, using observed smolt size distributions and smolt size distributions back calculated from the scales of returning adults. Large size did not give a consistent survival advantage, but large smolts did survive better in years when marine survival was relatively poor. Marine survivals were correlated with early ocean growth as estimated by the spacing of the first five ocean circuli on the scales of returning adults. Marine survival and early ocean growth were positively correlated with ocean conditions indicative of strong upwelling along the northwest coast of Vancouver Island. Neither smolt survival nor early ocean growth was correlated with regional coho smolt production. The authors suggested that interannual variability in smolt survival was driven by ocean conditions that determined smolt growth rates, which subsequently affected the susceptibility of smolts to a size selective predator. The authors also found that marine survival and early ocean growth were positively correlated, which suggested that marine survival of Carnation Creek coho salmon was closely related to ocean conditions off the west coast of Vancouver Island during the first four months of life. Conditions favourable to upwelling and subsequent transport of upwelled water onto the continental margin may have been conducive to fast growth for juvenile salmon migrating up the coast. Relatively fast growth was in turn associated with relatively high survival. They also found covariation of survival of coho salmon smolts and Pacific herring, suggesting some common underlying factor.

The marine survival of chum salmon was also correlated with sea surface salinity for April or for the spring months at Amphitrite Point, British Columbia (Scrivener 1987). This salinity was taken to be an indicator of the distribution of predators and of areas of upwelling and high plankton productivity in the nearshore zone off the west coast of Vancouver Island (Fulton and LeBrasseur 1985). In years of very low salinities, the plankton-rich subarctic boundary

between the Alaska Gyre with its coastal current and the California Current shifted northward. Very low survivals were obtained for chum salmon juveniles that entered the ocean during those springs. The marine survival of chum salmon was also related positively to fry size and the timing of movement into salt water (Scrivener 1987, Holtby and Scrivener 1989). Both were affected by logging.

Predation Studies

Parker (1969b) examined the predator-prey relationships among pink and chum salmon fry and coho salmon smolts in a central British Columbia inlet. For brood years 1961 to 1963, 56, 61 and 32 million pink fry, respectively, were estimated to have entered the sea. During the first 40 days of sea life, he estimated that 43, 34 and 19 million fish were lost to the populations, representing losses of 77%, 55% and 59%. Parker suggested that these losses were mainly due to predation by coho salmon smolts.

Parker (1971) suggested that pink salmon survival was higher than chum salmon due to a shorter life history and a faster growth rate. Parker (1971) proposed that selective predation on pink was responsible for enhancing and maintaining this superiority. He tested his hypothesis in the laboratory using coho as predators. Original and terminal length frequencies of both prey and predators were recorded. Populations were maintained until the numbers of prey were reduced. On the basis of experimental evidence, Parker (1971) concluded that coho salmon were size-selective when preying on both juvenile pink and chum salmon during early sea life. Hargreaves and LeBrasseur (1985) re-analyzed these data and calculated the expected number of pink and chum salmon fry remaining in each aquarium at the end of Parker's experiment if predation had been non-selective. They then compared these estimates with the actual number of pink and chum fry remaining, using the χ^2 goodness of fit test. Parker had reported in his paper that coho salmon predation was size selective for the smaller fish, regardless of species. Hargreaves and LeBrasseur's calculations suggested that there were fewer pink salmon fry remaining at the end of the experiment than the number expected if coho salmon predation had not been species selective. Hargreaves and LeBrasseur concluded that coho preferred pink salmon as prey which corroborated the results of their own field experiments.

Dunford (1975) implicated the Pacific staghorn sculpin as an important predator of juvenile salmon. Levy and Levings (1978) found that this sculpin was the most dominant fish in the Squamish River estuary. On several occasions in their study, staghorn sculpins were observed preying on juvenile chum salmon in tidal creek enclosures. The importance of this predation remains poorly understood. Slaney et al.

Slaney et al. (1985) suggested that because migrant juvenile sockeye salmon are fairly large, predation on them by other smaller juvenile salmonids in estuarine and marine environments is unlikely. Chum salmon fry, however, are preyed on by other larger juvenile salmonids during their short freshwater migration, in estuaries, and in their early marine rearing phase (Bakkala 1970). In addition to coho and chinook smolts, they are eaten by steelhead and cutthroat trout (*S. clarki clarki*) and Dolly Varden (*Salvelinus malma*) char. Although steelhead smolts prey on salmonid fry in both fresh water (Hunter 1959) and estuaries, they are seldom numerous enough to influence chum stocks (Slaney et al. 1985). Like coho smolts, resident and anadromous cutthroat trout have been considered major predators on chum fry (Pritchard 1936; Hunter 1959), but they are seldom as numerous as coho salmon, Dolly Varden or sculpins and few quantitative data on their impact on chum populations were found. In estuarine and marine habitats, steelhead trout and chum salmon are present at the same time, and they also may move through estuaries and offshore at the same time.

Coho, chinook, steelhead, cutthroat and Dolly Varden are all recorded as predators of pink salmon fry (Pritchard 1936; Hunter 1959; Parker 1965). Parker (1971) reported that coho smolts began to prey on pink fry soon after the fry emerged. The coho salmon followed the pink salmon fry downstream through the estuary and for the first weeks of their marine life. Using a series of multiple mark recapture experiments conducted as pink salmon fry moved out of the Bella Coola river and seaward along Burke channel, Parker calculated that fry losses were between 59 and 77% in the first 40 days after emergence, and that most of these losses were due to predation by coho smolts. Hargreaves (Pacific Biological Station, Nanaimo, BC, Canada, personal communication) also observed coho salmon predation on pink salmon fry in Masset Inlet, and suggested that coho salmon were the main cause of pink salmon fry losses in their early marine life. Models of coho salmon smolt predation on pink fry were developed by Bailey and Anderson (1974), Belford (1978), Peterman and Gatto (1978). They suggested that coho salmon predation can significantly affect pink salmon fry survival and that the extent of predation can be influenced by the duration of exposure.

A number of experimental approaches have indicated that smaller Pacific salmon suffer the highest mortality during early sea life (Hager and Noble 1976; Bilton et al. 1982a, b). Healey (1982c) found more direct evidence, showing that mortality of juvenile chum was strongly size selective over the size range of 45–55 mm fork length. Predation is generally considered to be the most likely cause of size

selective mortality of juvenile salmon.

Hargreaves and LeBrasseur (1985) examined predation on juvenile pink and chum salmon by yearling coho salmon in marine enclosures in Masset Inlet, on the north end of Hecate Strait, British Columbia. They used two net enclosures, each containing 1,500 chum and 500 pink salmon, and added yearling coho to each enclosure. However, the coho salmon had been used prior to this experiment as predators on juvenile pink salmon only as prey. In these experiments, pink salmon were always significantly larger than chum salmon. For the first half of the experiment coho salmon consumed more pink than chum, and more chum than pink during the latter half. They suggested that the change from feeding on pink salmon fry to feeding on chum was because the chance of encountering a pink salmon was much lower than encountering a chum salmon. Also the remaining pink salmon may have reached a size range in which they could not be eaten. In Parker (1971), whose data they reanalysed, the coho also chose pink over chum when the pink were significantly smaller than the chum. Overall then, there appears to be a preference for pink over chum salmon fry.

Withler (1955) reported what he considered was the first record of a young salmon being attacked by a young river lamprey (*Lampetra ayresi*). Roos et al. (1973) reported that river lamprey feed on young juvenile salmon and herring in the Strait of Georgia. Williams and Gilhousen (1968) also found that Pacific lamprey (*L. tridentata*) preyed on Pacific salmon.

Beamish and Williams (1976) examined the effects of river lamprey (*Lampetra ayresi*) predation on salmon and herring stocks in the Strait of Georgia. The numbers and potential importance of river lampreys were unknown until the surface waters of the Strait were fished with a small mesh purse seine. Beamish et al. (1976) carried out a study of the fishes inhabiting the surface waters of the Strait of Georgia during July and August 1974. River lamprey from 14 to 28 cm total length were commonly captured throughout the survey. There was evidence that some young salmon had been attacked by river lamprey. Numerous spiny dogfish also were captured in the surface waters, but most of these were feeding on ctenophores and did not appear to be competing with or feeding on the young salmonids. River lamprey and chinook salmon were found in equal numbers and chinook salmon comprised approximately 20% of the total number of young salmon captured. River lamprey were sufficiently common in the surface waters of the Strait of Georgia to be an important predator of young herring and salmon (Beamish and Youson 1987; Beamish and Neville 1995). Feeding adult lamprey entered the Strait of Georgia from the Fraser River in late spring or early summer and concentrated

in nearshore areas especially in the Gulf Islands. They actively fed on Pacific salmon and Pacific herring in the summer, and preferred Pacific herring. Laboratory studies indicated that one river lamprey could kill an average of one small fish per day. Using this feeding rate and an approximation of the population size, it was estimated that between 60 and 600 million fish could be killed by river lamprey during the active feeding period. Beamish and Neville (1995) determined that in 1990 and 1991, river lamprey killed a minimum of 20 million and 18 million chinook and a minimum of 2 million and 10 million coho salmon. In 1991, river lamprey in the Fraser River plume killed an equivalent of approximately 65 and 25% of the total Canadian hatchery and wild production of coho and chinook salmon, respectively. These estimates are probably low as these river lamprey feed in other areas and the abundance estimates are conservative. Beamish and Neville (1995) estimated that river lamprey predation in the Fraser River plume killed 39 million salmon in 1990 and 51 million salmon in 1991. Chinook salmon were preyed upon in the highest numbers followed by coho.

Estimates for chum salmon smolt production are difficult to determine: estimates of chum salmon mortality in 1990 and 1991 of 14.9 and 10.1 million smolts would account for 13.7 and 4.7 % of the total smolt production of chum from the rivers flowing into the Strait of Georgia and would thus not be considered a major source of early marine mortality. In 1991, juvenile sockeye mortality due to lamprey predation was 11.7 million or 2.3% of the estimated smolt production in the Fraser River. River lamprey left salt water by fall, returning to the Fraser River in preparation to spawn the next spring. Lamprey scars and wounds on all species of juvenile salmon in the Strait of Georgia were also routinely observed in the surveys conducted in the Strait of Georgia by Beamish and staff, confirming that both river lamprey and Pacific lamprey were predators of Pacific salmon.

Beamish and Smith (1976) carried out 129 mid-water trawls, 32 bottom trawls, and 184 purse seine sets resulting in examination of over 100,000 spiny dogfish in the Strait of Georgia during the 1970s. The spiny dogfish were found to feed almost exclusively on planktonic invertebrates, such as euphausiids and ctenophores. Predation on other fishes was rare. Juvenile dogfish occupying the off bottom waters of the Strait of Georgia were found in association with Pacific hake (*Merluccius productus*), wall-eye pollock (*Theragra chalcogramma*), salmon, Pacific herring (*Clupea pallasii*), northern smooth-tongue (*Leuroglossus stilbius schmidtii*), myctophids and several other species of small midwater fishes. During the summer, they were routinely captured in association with young salmon. At this time of year, young Pacific salmon of all species and Pacific her-

ring fed almost exclusively on euphausiids. Juvenile spiny dogfish captured in association with these Pacific herring and salmon also fed on euphausiids, but primarily on ctenophores: never on salmon and seldom on Pacific herring. Thus there was virtually no predation on young Pacific herring and salmon and very little competition for the same food source.

A Pacific Biological Station update reported preliminary results of the Beamish predation study near the Big Qualicum hatchery (1989 Pacific Biological Station science updates: July Aug Sept No. 9 Field work for the ocean salmon program mortality). He showed that predation rates on juvenile salmon declined dramatically in early July, coincidental with the appearance of large concentrations of juvenile herring. Virtually all species of predators switched to juvenile herring, although there was a low incidence of predation by dogfish and hake on juvenile chinook. It was suggested based on this observation that this information could be used to determine the correct timing of hatchery releases to increase survival of juvenile chinook salmon. Beamish et al. (1992) noted that large numbers of spiny dogfish moved into the area near the mouth of the Big Qualicum River, BC, at the time hatchery-reared chinook and coho salmon smolts were leaving the river in 1988 and 1989. A small percentage of the spiny dogfish preyed on the smolts, but the resulting smolt mortality was believed to have been large because of the large numbers of spiny dogfish in this area. Spiny dogfish also fed on adult salmon in the fall. The long-term decline in survival of chinook salmon produced at this hatchery was similar to the pattern of survival of other hatchery-reared salmon. Thus, they proposed that predation contributed to the decline. Jones and Geen (1977) found that 27 stomachs of 9,466 spiny dogfish contained Pacific salmon. In three other studies examining the role of spiny dogfish as predators of Pacific salmon (Chatwin and Foerster 1953; Godfrey 1968; Robinson et al. 1982), spiny dogfish were not found to be important predators of Pacific salmon (Chatwin and Foerster 1953).

Beamish and Neville (2001) examined the impact of predation-based mortality on juvenile chinook, coho and chum salmon in the Strait of Georgia using an Ecopath model of the ecosystem. Apart from lamprey and dogfish, which these authors had shown in the past to be important predators of juvenile salmon during the early marine period, the other predators of juvenile salmon in the Strait of Georgia did not appear to be major predators of juvenile salmon. Spiny dogfish predation has been shown to be highly variable, accounting for between 1.4 to 100% of hatchery releases of coho and chinook salmon from the Big Qualicum hatchery (Beamish and Neville 1992). In addition, both lamprey and spiny dogfish reduce predation on juvenile salmon by late summer. The re-

duction in predation by these species, and the general lack of potential predators in 616 survey tows in 1998 and 1999, indicated that predation mortality is probably not the only mechanism that regulates the numbers of mature fish that return. Beamish and Neville (2001) have suggested that the total natural mortality is made up of both an early predation-based mortality and a later carrying capacity mortality. They suggested that their inability to show that predation in the early marine period regulates the number of returning salmon is because the carrying capacity mortality occurred later in the year when the slower growing, smaller fish were unable to survive the first marine winter. The combination of predation and carrying capacity mortality determines the total mortality.

CONCLUDING THOUGHTS

Early studies tended to be based on individual interest rather than on a plan to test ideas about the factors regulating salmon abundance. Early workers (such as Foerster, Neave, Milne and Ricker) believed that the factors that limited survival occurred in fresh water. These beliefs lasted until the mid-1990s. The belief that freshwater factors limited salmon production meant that fishing and freshwater habitat were the factors that limited abundance. This resulted in the theory that stocks could be rebuilt and sustained at levels, perhaps double the historic average catch. The emphasis on increasing the "resource base" began in the 1960s and early 1970s as catches declined, despite the improving management. Bill Ricker's paper in 1976 "Two mechanisms that explain why stocks cannot be rebuilt to historic levels" is evidence that theories of salmon management were becoming inadequate (Ricker 1976). The most intensive effort to understand the early marine phase of Pacific salmon occurred in the 1990s with the MASS program, the Strait of Georgia program, and the High Seas program.

In general, it appears that there have been extensive studies of juvenile Pacific salmon. There is variation in the items eaten and in the proportion of these items. However, there are some consistent preferences. Pink salmon prefer small items, chum salmon prefer oikopleura, and coho and chinook salmon consume more fish species than the other salmon species. Rates of growth are rapid in the early marine period, but there is considerable uncertainty in the measures of these rates. There does appear to be a relationship between these rates of growth and movement, but the relationships probably are not simple. There also is evidence that the early rates of growth are related to marine survival.

Research eventually showed that the abundance of salmon can be limited in the ocean. This means that we need to know how the ocean affects produc-

tion to interpret fishing impacts correctly and to make effective use of enhancement. This new view is captured in a recommendation to Fisheries and Oceans Canada from the Pacific Fisheries Resource Conservation Council that reads "Now more than ever, information on the ocean life stage is required to understand what is happening" (Pacific Fisheries Resource Conservation Council (PFRCC) 2001). When the new millennium started, it was generally accepted that the final abundance of salmon was related to ocean conditions. The continued low catch of salmon remained an overriding concern. However, there was an abrupt change in abundance levels about 2000/2001 that clearly demonstrated the immediate impact of climate and climate change (PFRCC 2001).

FUTURE ISSUES OR QUESTIONS

1. Are estuaries necessary as nursery areas? Are there specific nearshore habitats that are critical to the survival of juvenile salmon? If so, how will climate change and sea level rise affect salmon production? Will the estuary of the Fraser River still be present?
2. Is the abundance of salmon determined only by predation in the first few months in salt water, or is brood year strength a combination of growth-related mortality and predation mortality?
3. Do additions of artificially reared juveniles into the ocean affect the survival of wild juveniles of the same species and the survival of other salmon species? What are the impacts of Atlantic salmon culture on Pacific salmon?
4. How do juvenile salmon survive their first marine winter when temperature is low and prey is less abundant?
5. How do juvenile salmon partition their estuarine and open ocean habitats so that the various species do not compete directly?
6. Where do stocks of juvenile salmon rear in the ocean and why do some stocks of each species survive better than other stocks?
7. What causes the fluctuations in survival in the ocean?
8. Which stocks remain on the shelf and what defines the area of the shelf that forms their marine feeding grounds?
9. When and how much mortality occurs on juvenile salmon between fresh water emigration and migration into deep coastal waters.
10. How can we use the information from past, present and future early marine studies to improve our forecasts of adult returns? Can biophysical models be developed?
11. How will global warming affect salmon on Canada's West Coast?
12. Why have the migration patterns of coho and sockeye salmon changed in the late 1990s?

RECOMMENDATIONS

We know that climate will change and in Canada, for example, we know that the Fraser River is the southern limit for a substantial amount of salmon production. Therefore, we need to have a plan to adapt to the impact of climate change and changed ocean conditions on the production of salmon. As a part of this plan, an international team could be set up to revise the plan, as new information becomes available. This team could be supported through NPAFC and would identify the questions relating to the impact of the ocean on salmon production. As many of these questions as possible might be addressed with the information from the material in this report. The remaining questions could be the focus for research by each country, with the intent of continued sharing of results. Team discussions would occur at the interim and annual meetings in order to minimize costs. A commitment of co-operation and support from team members and from national agencies should provide the ingredients for success.

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Japanese Studies on the Early Ocean Life of Juvenile Salmon

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Abstract: Almost all the salmon resources in Japan have been supported by artificial enhancement, and because of the success of this program the population size of chum salmon (*Oncorhynchus keta*) has increased dramatically since the early 1970s. About 90% of Japan's salmon catch is chum; 5–10% is pink salmon (*O. gorbuscha*) and 0.5% masu (*O. masou*). Therefore, biological research has focused on the early ocean life of juvenile chum salmon to establish the proper timing and size for release of juveniles from hatcheries, and, since the late 1960s, to study the distribution and movement of juvenile salmon in nearshore waters. Survey results indicated that juvenile chum salmon remained in coastal water masses with good food conditions and physiologically optimum surface temperature and salinity until they reached about 70–80 mm FL, when they were able to migrate offshore, avoiding high SST (over 12–13°C) and high salinity (over 34 psu). Japan-Russia cooperative juvenile salmon surveys were conducted in the Okhotsk Sea and the western North Pacific Ocean, from early summer to winter in 1988–1996. Results suggest that the Okhotsk Sea is an important nursery area for juvenile salmon originating from Russia and Japan.

INTRODUCTION

A Historical Overview of Importance of Salmon in Japan

Pacific salmon (genus *Oncorhynchus*) have been important to the Japanese life style since ancient times (the initial Jomon Period: 6,000 B.C.) (Ishida et al. 2001). Because of religious commandments relating to diet, the Japanese people depended on animal proteins from the sea, so the fishing industries had to make many technical innovations and contrivances to meet the demand for fish (Kobayashi 1980).

Originally, a native people, the Ainu, caught adult salmon for subsistence use as the salmon ascended their home rivers and streams for spawning. Commercial coastal fishing for salmon began in the 16th century in Hokkaido. It was operated by seasonal emigrants from Honshu Island. After 1800, coastal set nets were introduced, which helped to expand salmon fishing grounds in the coastal areas (Kobayashi 1980).

A Historical Overview of Abundance

Three of the seven species of anadromous Pacific salmon inhabit Japanese coastal and oceanic waters:

chum salmon or "sake" (*Oncorhynchus keta*), pink salmon or "karafuto-masu" (*O. gorbuscha*), and masu salmon or "sakura-masu" (*O. masou*). The distribution of the three species forms the southernmost limit of the genus *Oncorhynchus*. Their abundance increases from south to north, and the principal salmon production area in Japan is Hokkaido.

Chum salmon are produced in rivers on the coasts of Hokkaido and the northern part of Honshu in Japan. Pink salmon ascend rivers draining into the Okhotsk Sea and part of the Pacific Ocean. Masu salmon are distributed throughout Japan, but the anadromous type is found in rivers on the coast of the Okhotsk Sea, the Japan Sea and the northern part of the Pacific Ocean.

Total coastal catches of salmon fluctuated between 10–100 thousand tons from 1965 to 1982, and increased to over 100 thousand tons since 1983, reaching about 300 thousand tons in 1996 (Hiroi 1998). About 90% of Japan's salmon catch is chum; 5–10% is pink salmon and 0.5% masu. Therefore, biological research has been focused on chum salmon. Almost all the salmon resources in Japan have been supported by artificial enhancement. The present review of juvenile production is restricted to hatchery-produced chum salmon.

A Historical Overview of Size Changes over Time

Size of chum salmon adults returning to rivers of Hokkaido has decreased since the late 1970s (Kaeriyama 1989, 1992, 1996, 1998; Ishida et al. 1993). Annual decline in average fork length was 4.9 mm/year in female and 3.7 mm/year in males between 1979 and 1989 in Hokkaido (Kaeriyama and Urawa 1992). The body weight of returning adults has also declined with increasing number of returns. Additionally, the average age of returning adults has increased in conjunction with an increase in the stock size since the 1973 brood year (Kaeriyama 1989, 1992, 1996, 1998; Ishida et al. 1993). These phenomena are considered to reflect density-dependent effects, although density-dependent mortality is not yet found (Kaeriyama 1992, 1999).

Hatchery Production

According to historical documents, efforts to enhance spawning salmon by improving their natural spawning environment through primitive artificial spawning channels were practiced in the 18th century. Artificial salmon hatching techniques were introduced from the U.S.A. to Japan in 1876, but did not reach a large scale until 1888 when the first public salmon hatchery was established on a tributary of the Ishikari River in Hokkaido (Kobayashi 1980). At present, there are 21 national, 13 prefectural and 269 private hatcheries in Japan.

The number of adult chum salmon returning to Japan remained at an average of about 3 million fish between 1900 and 1970. However, adult returns have increased exponentially since the early 1970s, and reached about 89 million fish (58 million individuals in Hokkaido and 31 million individuals in Honshu) in 1996 (Fig. 1). During this period, the number of juveniles released from hatcheries increased from 800 million in the early 1970s to 2 billion in 1982, and has remained at about 2 billion

juveniles since then. Return rate (percentage of adult returns to released juveniles) has increased to 2% since the 1966 brood year and reached more than 3% after 1984 brood year. The rise in return rate was the result of successful artificial enhancement techniques, such as releasing after feeding (Kobayashi 1980; Mayama 1985; Kaeriyama 1989), as well as the influence of favorable ocean conditions in the North Pacific Ocean (Kaeriyama 1998).

Pink salmon are also produced in hatcheries. The number of juvenile pink salmon released increased from 40 million fish annually in the late 1970s to 130 million fish annually in 1987, and has remained at 140 million fish since the late 1980s. The number of adult salmon returning to Japan has increased since the 1985 brood year, reaching about 20 million fish in the 1994 brood year (Hiroi 1998; Kaeriyama 1999).

In the propagation of masu salmon in Japan, fry have been released in spring. This technique is similar to that used in the propagation of chum and pink salmon fry that migrate to the sea in early spring soon after their release. However, the release at the fry-stage has not been an effective method in areas where the river environment has deteriorated. Techniques for releasing yearling smolts of masu salmon have been studied since the early 1980s (Mayama 1990, 1991).

HISTORICAL OVERVIEW

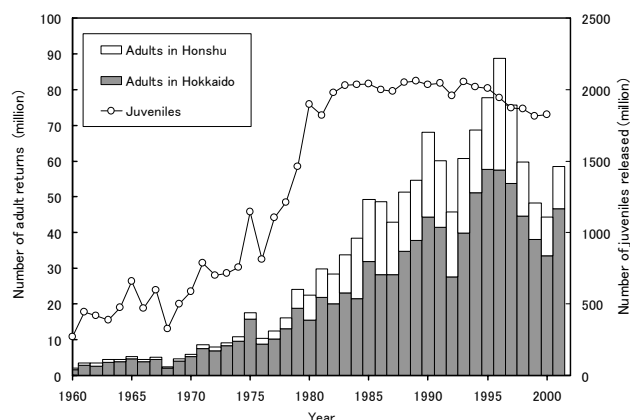
A Brief History on Early Ocean Life Studies

Because of the success of hatchery programs, populations of chum salmon increased dramatically in Japan over the last few decades. Nevertheless, we had no detailed information about the mortality of juvenile salmon during their ocean life.

In 1952, the National Hokkaido Salmon Hatchery (HSH) was established under the Fish Resource Conservation Law and began scientific research and enhancement activities to rebuild salmon populations. Until the early 1960s, research at HSH focused on freshwater life history and technical aspects of efficient hatchery production. During this time, Japanese high seas salmon surveys by the National Research Institute of Far Seas Fisheries (NRIFSF) (formerly the Far Seas Fisheries Research Laboratory) were conducted in conjunction with the high seas fisheries in spring and summer, the offshore fishing seasons for salmon since 1956 (Ishida and Ogura 1992). Thus, there were few studies on the early ocean life history of juvenile salmon after they had migrated down Japanese rivers.

Pioneering studies on migration ecology of juvenile chum salmon during their coastal life were carried out in the 1950s. However, migration timing and growth of juveniles were estimated from incidental

Fig. 1. Annual changes in numbers of adult returns and juvenile releases of chum salmon in Japan.



catches in coastal commercial set-nets in Hokkaido (Sano and Kobayashi 1952, 1953; Mihara 1958).

Until the early 1960s, chum salmon were released as unfed fry into streams as soon as the yolk sac was absorbed. Experiments on the release of chum salmon fry after a brief period feeding with dry food began in Hokkaido in 1962. To optimize timing of release of juveniles, a research program on the distribution and movement of juvenile salmon in coastal waters was begun in the late 1960s (Mayama 1985).

Seasonal changes in juvenile salmon distribution and growth in coastal areas were surveyed along the coasts of Hokkaido by the research division of HSH since 1969, using a purse seine and surface trawl. In 1971, a similar survey program was begun in northern Honshu under the auspices of the Fisheries Agency (Kaeriyama et al. 1993, 1994).

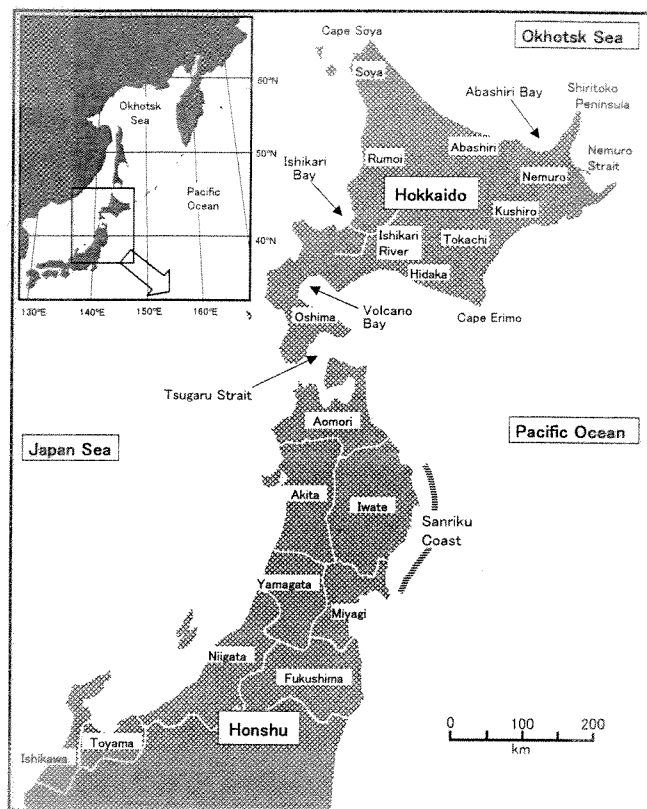
Results from these surveys indicated that the offshore movement of juvenile chum salmon is closely related to the environment of prey or physical oceanographic conditions. Physiological, ecological and morphological changes in the development of juvenile chum salmon during their early ocean life were also investigated. As a result, the early life history of juvenile chum salmon before their offshore migration had gradually become clear (Kaeriyama 1986; Irie 1990).

In the 1970s, surveys in about 20 areas along the coasts of Hokkaido and Honshu, including about 10 in the coastal waters of Hokkaido, described the local life patterns of juvenile chum salmon. Annual reports on the salmon enhancement programs including the coastal surveys have been published by HSH and various prefectures in Honshu. However, the survey areas were limited to the nearshore, i.e., from estuaries to about 5 km offshore, where small vessels could operate or coastal set nets were used.

A national research project entitled "Technical development of large-scale farming of anadromous salmon" was conducted with financial support from the Agriculture, Forestry, and Fisheries Research Council for five years (1977–1981) by seven national fisheries research institutes, sixteen prefectural fisheries experimental stations, and three universities. The research project included cooperative studies between nearshore and offshore research groups to elucidate migration routes of marked juvenile chum salmon originating from the Ishikari River (Fig. 2) entering the Japan Sea (Ito et al. 1980; Kato and Mayama 1980; Mishima and Shimazaki 1980; Mayama et al. 1982; Kato 1985). Migration and growth patterns of juvenile chum salmon during their offshore migration were clarified through this joint group research.

Since the 1980s, the biomass of Pacific salmon has increased throughout the North Pacific Ocean. Adult chum salmon returns increased to more than 50

Fig. 2. Map of the Japanese coastal waters with main study areas for juvenile salmon.



million fish until the late 1980s in Japan. The rapid increase in chum salmon abundance was regarded as a good example of the benefits of sea ranching. However, the Japanese salmon enhancement program was confronted with new problems such as a decrease in body size and an increase in age at maturity of chum salmon (e.g. Kaeriyama and Urawa 1992). At the same time, the Japanese high seas salmon fishery was prohibited in the U.S.S.R. 200-mile zone in 1977, and in the U.S.A. 200-mile zone in 1989, restricting availability of high seas data to Japanese scientists. More extensive cooperation with scientists in other nations as well as those of domestic organizations was deemed necessary to conserve salmon populations in the North Pacific Ocean (Nagasawa 1992).

General migration patterns and distribution of Japanese chum salmon juveniles were described by Irie (1990). However, their offshore migration routes to the North Pacific Ocean have not been identified. To investigate these offshore migration routes, Japan-Russia cooperative juvenile salmon surveys were conducted in the Okhotsk Sea and the western North Pacific Ocean in 1988–1996 (Ueno and Ishida 1996; Ueno et al. 1998). Results suggested that the Okhotsk Sea was an important nursery area for juvenile salmon originating from Japan and Russia (Ueno and Ishida 1996; Ueno et al. 1998).

Decreases in the high seas fishery catch following establishment of foreign 200-mile zones enhanced the significance of Japanese coastal fisheries. A new nine-year innovative "Marine Ranching Program (MRP)" was initiated by the Ministry of Agriculture, Forestry and Fisheries from 1980 till 1989, linking the governmental, academic and private sectors. Masu salmon was one of the target anadromous species, because it remains in coastal areas. In this research program, ecological surveys of juvenile masu salmon on migration clarified their feeding habits and growth during their coastal life (Kato 1983; Kiso 1995).

In the late 1990s, natural mortality from predators (Nagasawa 1998) and from environmental stress (Fukuwaka and Suzuki 1998, 2002) were studied during the early ocean life of juvenile chum salmon.

To advance research on juveniles, the National Salmon Resources Center (NASREC; formerly HSH) began a new monitoring program for otolith thermal marks in 1998 to obtain stock-specific biological information, including the early ocean life history in a wide coastal area around Hokkaido.

In October 1998, the National Fisheries Research Institutes were reorganized and the high-seas salmon research transferred from NRIFS to the Hokkaido National Fisheries Research Institute (HNFRI). The HNFRI conducts fishery surveys under national or international research plans on migratory fish such as salmon as well as on ground fish, mainly walleye pollock (*Theragra chalcogramma*), to measure the distribution and abundance of these species in the Subarctic region of the North Pacific Ocean. The HNFRI also collects information on biological characteristics of species, such as age, growth, maturation, migration, feeding habits, and population structure to establish appropriate fisheries management systems and to ensure the well-being of marine resources and ecosystems.

REVIEW OF RESULTS

Distribution and Abundance in Estuaries

The importance of estuaries as nursery areas has not been evaluated, because chum salmon have strong preferences for seawater and migrate to the sea soon after yolk absorption. Furthermore, few rivers have well defined estuaries; they empty directly into the sea, except along the Sanriku coast which is a Rias-type coastline with a lot of bays, peninsulas and capes. Many Japanese scientists have not distinguished between "estuary" and "coastal waters" in the strict sense of the words.

The coast of northern Japan, except for the Sanriku coast (Fig. 2) of the Pacific Honshu, has a simple shoreline and very few estuaries. Almost all rivers producing chum salmon are small and enter the open

sea. Therefore, there are few studies on juveniles in estuaries.

The distribution of juvenile chum salmon in estuaries was first reported by Sano and Kobayashi (1952). They observed that juvenile chum salmon released from a hatchery on the Japan Sea side of Hokkaido began to move down the river at the end of February. Juveniles congregated in the estuary, peaking in abundance in early and middle May, and moving offshore by late June (Sano and Kobayashi 1952, 1953). In these early studies on estuarine life, the relationship between fish distribution and environmental factors was not discussed because environmental data were not collected consistently.

Between 1952 and 1957, Mihara (1958) collected ecological information on the coastal life of juvenile chum salmon from 48 rivers in Hokkaido by means of questionnaires to coastal fishermen. The purpose was to plan a means of avoiding bycatch with coastal fishing nets. He reported that juvenile chum salmon released as unfed fry from February to June arrived in estuaries from late February to late July.

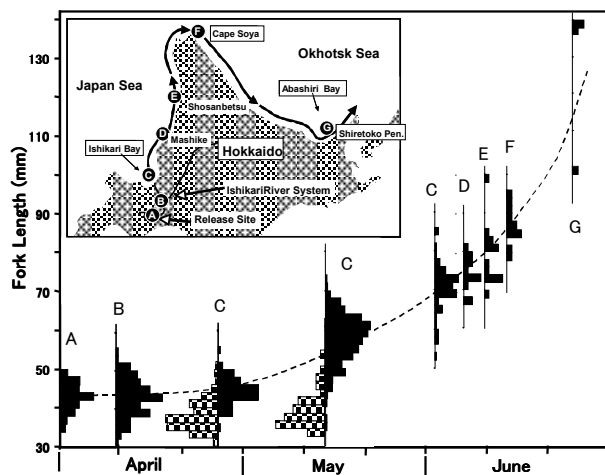
There are many small coastal rivers producing chum salmon in Japan, especially in Honshu. Juvenile chum salmon released into a small river on the Sanriku coast in northern Honshu arrived in the estuary within 24 hours (Seki 1978a; Iwata and Komatsu 1984), suggesting that growth and survival were more affected by the environment of the littoral zone around the estuaries than the freshwater habitat (Seki 1978a).

Chum salmon acquire salinity tolerance earlier than many other salmonids. Little information was available on adaptation during actual seaward migration until the observations by Iwata and Komatsu (1984).

Most chum salmon fry migrating from a small stream of the Sanriku coast were found in the surface layer (salinity 10–15 psu) of the estuary of the river. No fish were seen in the underlying seawater. Many fry remained in the brackish water for two days before migrating seaward (Iwata and Komatsu 1984). Iwata and Komatsu concluded that estuaries were an important area for the osmoregulatory adjustment of chum fry.

Juvenile chum salmon collected with a beach seine in the intertidal (littoral) zone of waters adjacent to the Ishikari River, Hokkaido (Fig. 2), from March to May were always small, ranging mainly from 30 to 45 mm, and averaging 37 mm in fork length (FL) (Fig. 3). Specific conditions for the short residence of smaller juveniles in the littoral zone were suggested (Mayama et al. 1982, 1983). A similar distribution pattern of small juveniles was observed in the coastal waters of Sanriku (Seki 1978a; Terazaki et al. 1982; Kaeriyama 1986) and the Nemuro Strait off eastern Hokkaido (Kasahara 1985).

Fig. 3. Seasonal changes in fork length distribution of juvenile chum salmon originating from the Ishikari River System, 1979. Histograms show lengths of juvenile chum salmon caught on beaches (left side) and offshore (right side) along the Ishikari coast. (Data from Ito et al. 1980; Kato and Mayama 1980, 1982; Mayama et al. 1982).



Juvenile chum salmon were often seen schooling in ports (Irie et al. 1981; Irie and Nakamura 1985; Seki and Shimizu 1997). The length of residence and growth of juvenile chum salmon in small harbors on the Pacific coast of eastern Hokkaido were surveyed during late April to early August by Irie and Nakamura (1985). The number of juvenile chum salmon found in these harbors increased from late April through early June and then decreased from mid-June through mid-July.

Estuarine environments containing important nursery areas for small and physiologically weak juveniles have been destroyed and lost because of recent construction and development in Japan. Research is needed to elucidate the habitat requirements of juvenile salmon in estuaries and adjacent waters of the littoral zone.

Diet of Juvenile Salmon in Estuaries

Information on the diet of juvenile salmon in estuaries is limited for the same reasons that data on distribution and abundance are scarce. Most chum salmon fry reach the estuaries within 24 hours after release from hatcheries on coastal rivers. They appear inactive on the first day, and begin feeding the following day (Iwata and Komatsu 1984).

Terazaki et al. (1982) and Terazaki and Iwata (1983) studied the feeding habits of juvenile chum salmon captured by beach seine in estuaries and the adjacent shore of the Ohtsuchi River of the Sanriku coast. Zooplankton was collected with vertical tows using a Norpac net at the same location. Epibenthic crustaceans such as *Jassa falcata* (Amphipoda) and harpacticoid copepods were major prey of juvenile chum salmon living in the littoral zone, including

estuaries in spite of abundant pelagic zooplankton. Terazaki and his colleagues suggested that juveniles could probably catch epibenthic animals more easily than zooplankton in shallow estuarine waters.

The main diet of juvenile chum salmon captured in areas of low salinity (< 21 psu) was terrestrial insects, mainly chironomid larvae, and epibenthic crustaceans such as amphipods. Harpacticoid copepods were dominant in stomach contents of juveniles captured in areas of relatively high salinity (21–30 psu) around estuaries of rivers in the Sanriku coast (Kaeriyama 1986). The results indicated a change in prey types from terrestrial origin to oceanic origin.

Irie (1987) found that juvenile chum salmon in small harbors in eastern Hokkaido mainly fed on harpacticoid copepods and gammarid amphipods. Juvenile salmon fed first on the abundant food organisms in their surroundings and also preferably on the relatively larger ones. Irie (1990) indicated that not only did increased food intake accompany growth, but also a shortage of food in the harbors, especially prey of larger size, was a major cause of migration.

Besides copepods, other principal prey items of juvenile chum salmon during their estuary life include insects, amphipods and fish larvae (Table 1).

When stomach contents of juvenile chum salmon and plankton net samples were compared at each sampling station, remarkable differences were usually found in their composition (Seki 1978a; Terazaki et al. 1982; Terazaki and Iwata 1983). Efficient methods for sampling prey animals are necessary to get useful information on food availability for juvenile chum salmon in estuaries.

Movement Patterns into Coastal Waters

There is limited information about environmental conditions during the movement of juvenile chum salmon from estuary to coastal waters. Because lengths of juvenile chum salmon in estuaries ranged mainly from 30 to 50 mm FL, movement of the juveniles from estuaries to coastal waters is estimated to have occurred successively as juveniles exceeded about 40–50 mm FL (Sano and Kobayashi 1952; Seki 1978a; Mayama et al. 1982, 1983; Terazaki et al. 1982; Kasahara 1985; Kaeriyama 1986). In the inner part of the bay at the southern end of the Sanriku coast, juvenile chum salmon moved from estuary to coastal waters when surface water temperatures rose to 13°C (Seki 1978a).

The abundance of juvenile chum salmon in small harbors decreased from mid-June through mid-July (Irie and Nakamura 1985). Juvenile chum salmon remained in the harbors for about one month and moved away when they grew larger than 45 mm FL. It seemed unlikely that most of the juvenile salmon migrated from the harbors due to changes in water temperature or salinity. It appeared that increased

Table 1. Information on the stomach contents of juvenile chum salmon sampled from various estuary waters and the littoral zone in Japan. continue...

Relative importance of												
Year	Month	Area ^{*1}	Number of fish examined	Fork length (mm)		Fishes	Eggs	Larvaceans	Polychaetes	Gastropods	Insects	Decapods
				Mean	Range							
Percentage composition in volume												
1981	May–Jun	Katsurakoi (Kushiro, HK)	126	46	32–74	22	-	-	+	-	2	3
1982	Apr–Jun	"	114	49	32–71	15	-	-	+	-	2	1
1983	Apr–May	"	43	45	32–70	35	-	-	+	-	4	1
Percentage composition in number												
1984	Apr	Konbumori (Kushiro, HK)	20	-	35–43	-	3.0	-	0.1	-	-	0.4
1984	May	"	80	-	33–52	-	2.6	-	0.9	-	0.6	0.7
1984	Jun	"	164	-	31–66	0.0	7.2	-	0.0	-	2.2	0.1
1984	Jul	"	36	-	38–54	-	6.4	-	0.1	-	0.4	0.0
Average number of prey animals found per stomach												
1978	Apr	Ohtsuchi (Iwate, HS)	3	50	40–61	-	-	-	-	-	-	0.7
1979	Mar–Apr	"	117	43	30–80	-	0.1	0.2	0.2	-	0.2	0.9
1980	May	"	14	54	40–80	0.4	0.0	0.1	0.2	-	4.0	0.2
1980	May	Ohkawa River (Miyagi, HS)	-	-	40–80	-	-	-	-	-	0.5	-
1980	Apr	Omose R. (")	-	-	45–65	-	-	-	-	-	18.4	-
1980	Apr–May	Koizumi R. (")	-	-	35–70	0.9	-	-	-	-	4.7	-
1980	Apr–May	Mitobe R. (")	-	-	35–70	-	-	-	-	-	2.7	0.1
1980	Mar	Ishikari Bay (HK)	10	-	32–44	-	-	3.1	-	0.3	-	-
1980	Apr	"	440	-	30–60	0.0	-	-	-	0.9	0.7	-
1980	May	"	301	-	30–50	0.0	0.4	0.0	-	0.3	0.8	-
Percentage frequency of occurrence of prey animals												
1981	May–Jun	Katsurakoi (Kushiro, HK)	126	46	32–74	16	-	-	3	-	24	28
1982	Apr–Jun	"	114	49	32–71	38	-	-	5	-	8	7
1983	Apr–May	"	43	45	32–70	10	-	-	2	-	10	5
1979	Apr	Toyama Bay (HS)	22	0.9g ^{*2}	-	-	6	-	-	-	36	-
1980	Mar	"	473	0.7g ^{*2}	-	-	-	3	2	-	52	1
1981	Mar	"	242	0.6g ^{*2}	-	0	1	-	-	-	59	-
1982	Mar–Apr	"	204	0.9g ^{*2}	-	-	-	-	-	-	64	-

*1: HK and HS in parentheses mean Hokkaido and Honshu, respectively.

*2: Mean body weight.

*3: Toyama Prefectural Fisheries Experimental Station.

food requirements accompanying their growth and a shortage of food in the harbors were major causes of migration. Irie (1990) concluded that small harbors were one of the important places for juvenile chum salmon during early physiological and ecological adaptations to ocean life.

Diet in Coastal Waters

Seasonal changes in food abundance appear to be one of the important factors affecting offshore movement of juvenile chum salmon from coastal waters.

Until the 1960s, very little was known about the feeding habits of juvenile chum salmon in coastal waters, though more was known about feeding of

...continued

prey animals in stomachs											
Copepods											
Euphausiids	Amphipods	Mysids	Total	Calanoids	Harpacticoids	Others	Ostracods	Cumaceans	Cladocerans	Others	Source
27	13	21	(13)	4	9	-	+	1	-	-	Irie 1987
27	19	2	(31)	11	20	-	+	1	-	-	"
3	15	-	(28)	4	24	-	-	1	-	-	"
-	26.6	0.1	(69.7)	32.2	37.5	-	-	0.1	-	-	Irie 1990
0.6	32.8	0.1	(48.7)	0.6	48.1	-	-	0.4	-	1.1	"
0.0	25.1	0.5	(65.1)	2.0	63.1	-	-	0.2	-	0.1	"
-	4.1	0.3	(87.8)	0.3	87.5	-	-	0.1	-	0.1	"
-	7.0	-	(104.0)	0.3	102.7	1.0	-	-	-	-	Terazaki & Iwata 1983
-	0.7	-	(67.1)	46.0	11.2	9.9	-	-	0.2	0.0	"
-	19.6	-	(2.1)	0.2	1.1	0.8	-	-	-	0.6	"
-	80.6	-	-	-	-	-	-	18.3	-	-	Kaeriyama 1986
-	7.9	-	-	-	-	-	-	-	-	-	"
-	-	-	(2.6)	-	2.6	-	-	-	-	-	"
-	3.8	-	(32.9)	24.6	8.3	-	-	-	-	-	"
-	-	-	(2.7)	2.7	-	-	-	-	-	-	Seki et al. 1981
0.7	0.9	-	(16.6)	11.8	4.8	-	-	-	-	0.0	"
0.3	0.3	-	(17.4)	16.0	1.4	-	-	0.1	-	0.3	"
7	58	14	-	29	63	-	1	7	-	-	Irie 1987
18	30	3	-	10	46	-	3	10	-	-	"
5	25	-	-	15	55	-	-	5	-	-	"
14	-	-	73	-	-	-	-	-	-	-	TPFES ²³ 1984
15	4	-	59	-	-	-	-	-	8	-	"
16	19	-	50	-	-	-	-	-	3	-	"
25	23	-	39	-	-	-	-	-	-	-	"

juveniles in fresh water in Japan. The first paper on feeding habits of juvenile chum salmon in coastal waters, published in 1971 (Okada and Taniguchi 1971), reported on the diets of juvenile chum and pink salmon along the Pacific coast of southern Hokkaido from May to June.

On the basis of several papers (Seki et al. 1981; Terazaki and Iwata 1983; Irie 1990) dealing with feeding habit of juveniles, copepods were regarded as the most important prey of juvenile chum salmon. Hyperiid amphipods (*Parathemisto japonica*), bran-

chiopods (cladocerans), terrestrial insects (dipterans and hymenopterans), decapod larvae, euphausiids, fish larvae (mainly sand lance), and larvaceans (appendicularians) are predominant prey in coastal waters (Table 2). Furthermore, cumaceans, polychaetes, mysids and eggs of invertebrates and fishes were frequently found in stomachs of juvenile chum salmon.

Prey of juvenile chum salmon vary with the salmon's movement from estuary to coastal waters and with their growth. Okada and Taniguchi (1971)

Table 2. Information on the stomach contents of juvenile chum salmon sampled from various coastal waters in Japan. continue...

						Relative importance of							
Year	Month	Area ^{*1}	Number of fish examined	Fork length (mm)		Fishes	Eggs	Larvaceans	Polychaeta	Sagittas	Gastropods	Bivalvia	Insects
				Mean	Range								
Occurrence of prey animals													
1970	Jun	Usujiri (Oshima, HK)	27	-	36–104	+	-	-	-	-	+	-	+
1970	May–Jun	Mori (Volcano Bay, HK)	67	-	"	+	+	-	-	-	+	-	+
Percentage composition in number													
1981	May	Kesennuma (Miyagi, HS)	-	-	-	5.6	-	11.1	-	-	-	-	-
1981	Jun	"	-	-	-	-	-	87.2	-	-	-	-	0.6
1984	May	Kushiro (HK)	7	-	40–70	0.6	-	-	-	-	-	-	2.8
1984	Jun	"	20	-	40–80	3.3	-	-	-	-	-	-	-
1984	Jul	"	80	-	70–140	0.5	-	2.2	2.2	-	-	-	23.8
1984	Aug	"	10	-	70–100	-	-	-	-	-	-	-	98.5
1985	Jun	Kushiro (HK)	11	-	110–130	26.4	-	-	-	-	-	-	-
1985	Jul	"	27	-	40–120	-	-	-	0.2	-	-	-	3.0
1993	Apr	Fukura (Yamagata, HS)	61	71	35–100	2.9	-	6.4	13.1	-	1.0	-	-
1994	Mar	"	29	51	-	0.2	-	59.6	-	-	-	-	-
1994	Apr	"	65	66	-	1.1	-	22.0	-	-	-	-	-
Average number of prey animals found per stomach													
1980	May–Jun	Otsuchi (Iwate, HS)	76	81	60–130	-	-	-	-	0.2	-	-	0.2
1980	May	Ishikari Bay (HK)	585	-	34–78	0.2	0.1	5.4	-	-	5.4	-	0.5
1987	May–Jun	Hidaka (HK)	283	-	-	4.9	-	165.7	5.1	1.7	-	46.6	6.1
1988	Jun–Jul	"	256	-	-	-	-	172.0	-	-	-	6.1	2.4
1995	Apr	Mashike (Rumoi, HK)	56	51	-	7.3	-	-	0.0	-	0.4	-	-
Percentage frequency of occurrence of prey animals													
1978	May	Kesennuma (Miyagi, HS)	327	-	40–125	29.1	-	-	-	-	-	-	4.6
1978	May–Jun	"	121	-	60–125	28.1	-	-	-	-	-	-	0.8
1977	Jul	Abashiri Bay (HK)	7	-	46–76	-	29	-	-	-	14	-	86
1978	May–Jul	"	63	-	38–63	46	3	-	-	-	24	-	25
1979	"	"	261	-	32–110	5	2	16	-	-	-	-	24
1980	"	"	140	-	29–110	14	3	14	-	-	-	-	21
1978	Apr–Jun	Rumoi (HK)	111	-	41–98 ^{*2}	27.9	0.9	4.5	3.6	-	12.6	-	5.4
1979	May	"	8	87.4 ^{*2}	74–96 ^{*2}	12.5	-	-	-	-	25.0	-	-
1978	May–Jun	Cape Soya (HK)	49	-	56–99 ^{*2}	22.4	-	2.0	-	-	-	-	-
1979	"	"	100	55.9 ^{*2}	35–85 ^{*2}	27.0	-	-	-	3.0	1.0	-	24.0
1978	May–Jun	East Soya (HK)	89	-	34–97 ^{*2}	13.5	-	1.1	3.3	-	1.1	-	28.1
1979	"	Soya (HK)	120	80.7 ^{*2}	58–100 ^{*2}	72.5	0.8	-	-	-	-	-	10.8
1979	Jun	East Soya (HK)	60	61.3 ^{*2}	37–88 ^{*2}	43.3	-	-	-	-	-	-	30.0
1979	Apr–May	Toyama Bay (HS)	1133	2.8g ^{*3}	-	1.1	3.8	3.2	-	-	0.3	-	10.4
1980	"	"	752	2.6g ^{*3}	-	7.2	3.8	2.9	-	1.0	1.0	-	14.5
1981	Apr–Jun	"	572	2.3g ^{*3}	-	1.0	6.0	5.9	-	-	1.7	-	25.4
1982	"	"	470	2.5g ^{*3}	-	1.0	3.9	-	-	-	-	-	15.2
1983	Jun	Aomori (Pacific, HS)	81	-	80–110	33	-	-	-	-	-	-	5

continue...

...continued

prey animals in stomachs													
Copepods													
Decapods	Euphausiids	Amphipods	Mysids	Cirripedes	Total	Calanoida	Harpacticoida	Others	Ostracods	Cumaceans	Cladocerans	Others	Source
+	+	+	-	-	+	+	-	-	+	-	-	+	Okada & Taniguchi 1971
+	+	+	+	-	+	+	+	-	+	+	-	-	"
-	9.8	68.5	-	-	(0.5)	-	0.5	-	-	-	-	5.6	Kaeriyama 1986
-	-	1.5	-	-	(1.1)	0.9	0.2	-	-	-	4.6	4.5	"
58.7	-	2.2	-	-	35.7	-	-	-	-	-	-	-	Irie 1990
8.6	-	7.7	-	-	80.2	-	-	-	-	-	-	0.2	"
21.2	1.1	18.7	0.3	-	24.3	-	-	-	2.0	0.6	3.2	-	"
-	-	1.5	-	-	-	-	-	-	-	-	-	-	"
46.9	0.3	2.7	-	-	22.8	-	-	-	0.3	-	-	0.6	Irie 1990
7.1	10.8	25.1	-	-	50.8	-	-	-	1.1	0.1	0.8	1.0	"
-	18.0	0.3	-	-	42.8	-	-	-	-	-	12.7	-	Suzuki et al. 1994
-	1.8	17.8	-	-	(15.7)	15.7	-	2.3	-	-	-	-	Suzuki et al. 1995
-	12.0	0.6	-	-	(19.0)	16.7	2.3	-	-	-	42.7	-	"
3.8	1.3	21.4	-	-	(125.3)	121.1	1.0	3.2	-	-	212.8	-	Terazaki & Iwata 1983
-	10.7	0.5	-	-	(92.6)	92.6	0.0	-	-	0.1	-	0.1	Seki et al. 1981
-	5.6	6.7	7.2	-	(58.0)	57.5	0.5	-	-	-	47.7	-	Seki & Shimizu 1998
11.8	5.1	15.2	17.4	16.9	(160.6)	160.6	-	-	-	4.8	5.1	0.0	"
4.0	-	1.0	-	-	(2.4)	1.7	0.7	-	-	-	-	0.2	Kawamura et al. 1998
-	-	51.7	-	-	-	21.4	6.7	-	-	-	-	9.8	Seki 1978b
-	-	50.4	-	-	-	3.3	-	-	-	-	-	4.1	"
14	14	100	-	-	-	100	-	-	-	-	-	-	Irie 1990
8	17	32	-	-	-	92	-	-	-	-	-	-	"
5	2	37	1	-	-	51	6	-	1	+	12	1	"
13	7	37	-	-	-	59	11	-	-	1	7	-	"
15.3	-	3.6	-	1.8	-	40.5	31.5	-	-	0.9	-	-	Suzuki et al. 1979
-	-	12.5	-	-	-	100.0	-	-	-	-	-	-	Suzuki et al. 1980
26.5	-	26.5	-	-	-	67.3	8.2	-	-	-	-	-	Suzuki et al. 1979
23.0	-	20.0	-	-	-	8.0	4.0	-	-	5.0	-	6.0	Suzuki et al. 1980
19.1	-	57.3	-	5.6	-	56.2	57.3	-	-	28.1	-	1.1	Suzuki et al. 1979
34.2	-	7.5	-	-	-	40.0	-	-	-	-	-	3.3	Suzuki et al. 1980
11.7	-	23.3	-	-	-	16.7	3.3	-	-	10.0	-	-	Suzuki et al. 1980
10.3	27.4	24.1	-	-	52.5	-	-	-	-	-	0.7	-	TPFES ⁴ 1984
-	21.8	13.8	-	-	49.8	-	-	-	-	-	21.3	-	"
-	19.8	9.7	-	-	17.2	-	-	-	-	-	14.2	-	"
1.9	10.7	1.9	-	-	16.7	-	-	-	-	-	1.0	-	"
-	20	42	-	-	7	-	-	-	7	-	-	-	Irie 1990

continue...

Table 2. continued

continue...

Year	Month	Area ^{*1}	Number of fish examined	Fork length (mm)		Fishes	Eggs	Larvaceans	Polychaeta	Sagittas	Gastropods	Bivalvia	Insects
				Mean	Range								
1985	May	Aomori (Pacific, HS)	25	-	60–120	4	4	4	-	-	-	-	4
1981	Jun	Hidaka (HK)	60	-	50–140	32	-	-	-	-	-	-	22
1982	Jul	"	51	-	50–120	14	-	12	-	-	-	-	6
1983	"	"	21	-	90–120	14	-	-	-	-	-	-	66
1981	Jul	Tokachi (HK)	29	-	70–120	10	-	-	-	-	-	-	28
1982	"	"	32	-	90–140	13	-	-	-	-	-	-	13
1983	"	"	50	-	60–110	8	-	10	-	-	-	-	16
1983	Jul	Kushiro (HK)	25	-	90–120	-	-	20	-	-	-	-	16
1984	"	"	86	-	100–120	1	-	1	-	-	-	-	16
1983	Jul	Akkeshi (kushiro, HK)	67	-	80–120	12	-	-	-	-	-	-	9
1984	"	"	30	-	90–130	3	-	7	-	-	-	-	3
1985	Aug	"	30	-	90–120	10	-	-	-	-	-	-	70

*1: HK and HS in parentheses mean Hokkaido and Honshu, respectively.

*2: Total length (mm).

*3: Mean weight (g).

*4: Toyama Prefectural Fisheries Experimental Station.

indicated a rapid rather than gradual change in prey size from small animals, such as micro-copepods (young *Parathemisto* spp.), decapod zoea and insects, to larger ones, such as adult *Parathemisto japonica* and euphausiids, as juveniles exceeded about 55 mm FL. Similar changes were observed by Irie (1990) and Suzuki et al. (1994).

Irie (1990) reported that, in small harbors in eastern Hokkaido, the prey size of juvenile chum salmon of about 43 mm FL increased rapidly. The juveniles appeared to feed on larger food organisms (amphipods, fish larvae and euphausiids) as they grew. Suzuki et al. (1994) evaluated the relation between fish size and selectivity of juvenile chum salmon feeding on pelagic zooplankton during their coastal life in the Japan Sea off northern Honshu, and suggested that juvenile chum salmon 50–60 mm FL selected large prey such as *Calanus sinicus*, euphausiid furcilia larvae and polychaetes. Larger juvenile chum salmon, i.e. >80 mm FL, during offshore migration were found to migrate actively in schools searching for food, and selectively fed on larger zooplankton found in patches and in high density (Irie 1990).

Another study on change in feeding patterns of juvenile chum salmon conducted on the southern Sanriku coast was reported by Kaeriyama (1986). He showed that juvenile chum salmon searched for larger, actively moving prey distributed patchily in the sea, and selectively fed on them. This feeding method of juveniles in coastal waters was therefore

regarded as "wide-foraging type", and differed from the "sit-and-wait type" of juveniles feeding in rivers. Suzuki and Fukuwaka (1998) reported that the change in foraging behavior of juveniles was influenced by abundance of large prey. Fingerlings intensified their foraging selectivity with an increase in the abundance of larger prey. On the contrary, the abundance of smaller prey did not influence prey size selectivity.

Food items of juvenile salmon do not usually correlate well with zooplankton fauna collected at the same sampling sites. The disagreements are caused by changes in feeding behavior associated with changes in developmental stage or body size, as mentioned above. Also, temporal movement of prey may cause differences. Seki and Shimizu (1998) collected juvenile chum salmon and zooplankton in coastal waters of southwestern Hokkaido. Zooplankton collected with simultaneous horizontal tow nets from seven different layers were most abundant at 30 m depth, and the density decreased markedly in near-surface layers. However, feeding was successful in chum salmon juveniles inhabiting shallow waters (5–15 m in depth). The authors suggested that prey organisms might become available to salmon juveniles in coastal shallow waters as a result of limited vertical migration of zooplankton and by up-welling. As described above for estuaries, efficient methods for sampling prey animals are required to obtain useful information on food availability for juvenile chum salmon.

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prey animals in stomachs													
Copepods													
Decapods	Euphausiids	Amphipods	Mysids	Cirripedes	Total	Calanoida	Harpacticoida	Others	Ostracods	Cumaceans	Cladocerans	Others	Source
16	8	88	-	-	-	-	-	-	12	-	4	-	Irie 1990
3	5	72	-	-	35	-	-	-	-	-	-	-	Irie 1990
8	8	24	-	-	49	-	-	-	14	-	-	-	"
-	19	10	-	-	33	-	-	-	-	-	-	-	"
10	14	17	-	-	38	-	-	-	-	-	-	-	Irie 1990
28	22	19	-	-	31	-	-	-	3	-	-	-	"
2	40	44	-	-	42	-	-	-	-	-	-	-	"
28	28	12	-	-	20	-	-	-	4	-	-	-	Irie 1990
57	7	9	-	-	22	-	-	-	7	1	-	-	"
25	6	36	4	-	40	-	-	-	15	-	3	-	Irie 1990
33	7	10	7	-	23	-	-	-	-	-	-	-	"
-	25	15	-	-	85	-	-	-	-	-	-	-	"

Timing and Speed of Movement to High Seas

Until the 1960s, migration and growth of juvenile chum salmon during their coastal life was estimated from by-catches in coastal commercial fisheries. These observations had shown that chum salmon disappeared from coastal areas at a specific time and body size every year.

Data on juvenile chum salmon in the coastal waters off Hokkaido, collected by means of questionnaires to coastal fishermen during 1952 to 1957, showed that juvenile salmon stayed in coastal waters from April to late June, and disappeared rapidly when sea surface temperature (SST) increased above 17°C (Mihara 1958). In this early study, SST conditions during offshore migration of juvenile chum salmon were similar among different areas around Hokkaido, although conditions at any one time varied widely among areas.

Japan is located at the southern limit of the geographical distribution of chum salmon. Along the coast, effects of the warm current are pronounced during spring and summer. Therefore, juvenile chum salmon must migrate offshore until the environment becomes inadequate. In order to delay the time of release and produce larger juveniles, the release of chum salmon juveniles after feeding was begun in the 1960's. It was necessary to clarify the time limit to determine the duration of feeding in the hatchery.

To establish the proper timing and size for release of juveniles from hatcheries, a research program was started in the late 1960s. Seasonal changes in juvenile distribution and growth in coastal areas were surveyed since 1969 using a purse seine and

surface trawl along the coasts of Hokkaido. A similar survey program started in northern Honshu in 1971. The survey areas were limited to near-shore, from estuaries to about 5 km offshore. Local life patterns of juvenile chum salmon off the coasts of Hokkaido and Honshu were monitored in about 20 areas, including a total about 10 coastal areas off Hokkaido.

The distribution and migration of juvenile chum salmon was investigated for five years, 1977–1981, using a purse seine at depths of 5–25 m, up to 5 km offshore on the Ishikari coast of the Japan Sea side of Hokkaido (Mayama et al. 1982, 1983; Mayama 1985). Juveniles were low in abundance in April, increased rapidly from late May to early June, and disappeared by mid-June. The rapid decrease in numbers of larger juveniles was found at the same time every year. The temperature at a depth of 5 m showed a linear increase with time, and reached 11–12°C in late May to early June, when abundance of juveniles had decreased. Salinity at the same depth decreased in April and mid-May (27.2–33.6 psu) as a result of an increasing amount of water from the river, and then increased rapidly in late May (33.3–34.0 psu). At this time, the effect of the Tsushima Warm Current increased, raising the water temperature and salinity, and seemed to produce some physiological effects that induced offshore migration of chum salmon juveniles.

Investigations by Irie (1985a, 1990) were conducted over a wide area in Abashiri Bay and adjacent waters of the Okhotsk Sea, and in the Pacific Ocean off Hokkaido and northern Honshu, and in Tsugaru Strait and adjacent waters of the Japan Sea. From all

results in each region, it appeared that offshore migrating juvenile chum salmon mainly concentrated in areas with SST from 9° to 13°C and surface salinity from 31.0 to 33.9 psu, and that upper limits were at about 14°C in temperature and 34 psu in salinity. These two studies suggested that juvenile chum salmon showed a certain preference for water temperature, salinity, and water masses. A similar relationship between oceanographic conditions such as SST and salinity and distribution of juvenile chum salmon has been found through surveys on the Japan Sea coasts of northern Honshu (Kaeriyama et al. 1993, 1994) and Pacific coasts (Koganezawa and Sasaki 1985; Kaeriyama 1986, 1989).

Kaeriyama (1986, 1989) observed differences in patterns of offshore migration between early and late seaward migrating juveniles off the Sanriku coast of the Pacific side of northern Honshu. The early migrating juveniles remained in the coastal waters for a long time (about 80 days) through early spring (February–March), and then migrated offshore as the Oyashio Current approached the coast (April–May), with SSTs ranging from 8–11°C. Late migrating juveniles remained in the coastal region for a shorter time (about 40 days), until late spring (April–May), and migrated offshore after retreat of the Oyashio Current from the coast (June) when SSTs ranged from 11° to 13°C.

The relation between size, or developmental stage, and offshore migration was investigated simultaneously (see section on growth patterns, below). Based on the ecological change that coincided with morphological or physiological changes, Kaeriyama (1986) and Irie (1985b, 1990) concluded that juveniles of 8–12 cm FL are in the process of offshore migration.

A decrease in abundance of food organisms appears to be the main cause of migration of juvenile chum salmon to offshore waters (Irie 1990). Kaeriyama (1986) identified two causes of offshore migration, as indicated previously, an active migration caused by the search for prey, and a passive migration arising from lack of food or escape from unsuitable environmental conditions such as high SST.

It became clear that juvenile chum salmon remained in coastal water masses with good food conditions and physiologically optimum SST and salinity, until they reached about 70–80 mm FL, when they were able to migrate offshore, avoiding high SST (over 12–13°C) and high salinity (over 34 psu). These results were used to propose an optimum size and time for release of juveniles to produce high survival during early sea life (Nogawa 1992).

While early life of juvenile chum salmon before their offshore migration had been clarified, the offshore migration routes to the North Pacific Ocean were not identified.

A national research project on anadromous salmon enhancement was conducted from 1977 to 1981. The project included a cooperative study between nearshore and offshore research groups to describe the migration patterns and growth of juvenile chum salmon originating from the Ishikari River on the Japan Sea side of Hokkaido. Four million chum salmon fry were marked by europium, one of the rare earth elements, and released in a tributary of the Ishikari River in April 1979 (Kato and Mayama 1980; Mayama et al. 1982).

The nearshore research group, including HSH, captured juvenile chum salmon with a purse seine and beach seine in the coastal area of Ishikari Bay, and also with stationary trap nets along the coasts of the northern Japan Sea, and Cape Soya (Mayama et al. 1982). Using the research vessel *Hokusei-maru* of Hokkaido University, the University and NRIFSF collected juvenile chum salmon in offshore waters of the Japan Sea and off the Okhotsk Sea coast (Mishima and Shimazaki 1980; Ito et al. 1980).

Europium was detected in scales and livers of juvenile chum salmon collected in the coastal waters along Hokkaido (Kato 1985). After leaving the natal waters around the river mouth of the Ishikari River, juveniles migrated northward along the Japan Sea coast, appeared on the east coast of Cape Soya, and were collected in offshore waters 8 to 16 km from the coast, from Abashiri Bay to the Shiretoko Peninsula, facing the Okhotsk Sea (Fig. 3) (Ito et al. 1980; Ito 1982; Kato and Mayama 1980, 1982; Kato and Kitaguchi 1981; Mayama et al. 1982; Kato 1985). The migration route of the marked juveniles was very similar to the path of the Tsushima and Soya Warm Current running along the northern part of Hokkaido. Mean fork length and body weight were 126 mm and 26.4 g, in the areas between Abashiri Bay and Shiretoko Peninsula in late June, and body weight was 10 times that of juveniles in Ishikari Bay.

General offshore migration patterns and distribution of juvenile chum salmon in coastal waters originating in Japan were reported by Irie (1985a, b, c, 1990).

Studies of Early Sea Mortality

Progressive hatchery technologies have led to a great increase in the stock size of Japanese chum salmon. Hatchery-reared chum salmon reach the sea within several days after release into rivers (Mayama et al. 1982; Kaeriyama 1986; Seki et al. 1997). During early sea life, mortality of juvenile chum salmon has been estimated to be high, but little is known about natural mortality of released juveniles in estuaries and coastal waters of Japan. This subject has received little discussion despite a marked increase in survival rate with favorable oceanic

conditions, and a successful artificial enhancement program in Japan.

As shown in the following section, predation by fishes, seabirds and mammals has been considered a major factor in early sea mortality of juvenile Pacific salmon (Nagasawa 1998). Nevertheless, the physical environment, particularly salinity and water temperature in coastal waters, also affects the abundance of adult chum salmon. Mayama (1985) suggested that inadequate coastal water temperature and timing of fry release strongly influence the survival of Japanese hatchery-reared chum.

From experiments with marked juvenile chum salmon to determine the effect of release timings on return rate in the Pacific coast of Hokkaido, optimal timing for release was estimated as the later period when coastal water temperature exceeds 5°C (Seki and Shimizu 1996).

To investigate factors regulating abundance of hatchery-reared chum salmon, Fukuwaka and Suzuki (2000) examined survival, distribution, and nutritional condition of juveniles in the coastal waters of the Japan Sea off Honshu, the southern limit of chum salmon distribution in the western North Pacific. Survival during ocean life correlated negatively with the number of released juveniles and high coastal SST. When density of juveniles increased, the weight of their stomach contents decreased. These results indicated that chum salmon abundance affected prey availability, and a restricted nursery area intensified intraspecific competition of chum salmon juveniles for food resources. The coastal carrying capacity may regulate abundance of chum salmon along the Japan Sea coast of Honshu, where ocean survival is lower than on the Pacific side (Kaeriyama 1989).

Hayano et al. (1997) examined whether ocean survival was affected by abundance of potential prey organisms in shallow coastal waters of the northern Japan Sea, Hokkaido. Harpacticoid copepods, *Harpacticus* spp., an important prey of juvenile chum salmon, were predominant in 1991 and 1992, but were at a very low level in 1990 (Asami and Hirano 1993). Juvenile chum salmon released into the Shokanbetsu River during this investigation, returned after 2–5 years. Return rates of adults released as juveniles in 1990, 1991 and 1992 were 0.09%, 0.31% and 0.34% respectively (in 1992 only ages 2–4 years were used to estimate return rate, it being already high). Return rate in the 1990 class was lowest, prompting Hayano et al. (1997) to suggest that this may have been due to low density of harpacticoid copepods during the release of juvenile chum salmon.

Fukuwaka and Suzuki (2002) estimated early sea mortality rate during coastal life using large-scale mark-recapture experiments. To estimate daily mortality in early coastal life, they analyzed the data record of nine mark-recapture experiments. These

marked fish were released from hatcheries in 1992–1997 into rivers flowing into the Japan Sea coast of Honshu. Estimated instantaneous mortality rates in coastal waters ranged from 0.033 to 0.268 day⁻¹ in the 14–43 days after release. High mortality may therefore occur in a short period after release. Censuses of juvenile salmon abundance after their early sea life may be needed to assess the abundance of salmon entering the Pacific basin.

The objective of this study was to assess the usefulness of a mark-recapture model, assuming different sampling effort, for estimating the mortality rate of chum salmon during their early coastal life. Results indicated that large-scale mark-recapture experiments are useful for estimating mortality during early sea life, which is considered to be a critical period for Pacific salmon.

Few studies on the natural mortality of hatchery juveniles in estuaries and coastal waters have been carried out in Japan. We need to identify the survival mechanism of hatchery-reared chum salmon and factors reducing their survival in order to establish optimum management in coastal waters.

Studies of Predation

Juvenile chum salmon may be most vulnerable to predators when entering and adapting to the sea because of poor adjustment to the new habitat, osmoregulatory stress, low food availability and open shallow waters (Kawamura et al. 2000). White-spotted charr (*Salvelinus leucomaenis*) predation on juvenile chum salmon in coastal waters in southeastern Hokkaido was greatest immediately after the salmon were released from the hatchery, but low after about two weeks (Takami and Aoyama 1997). These results suggest that fish predation on juvenile chum salmon during the seaward migration from hatcheries may be significant in coastal waters near the river mouth. However, release of large hatchery-reared juveniles may reduce mortality from fish predation.

Generally speaking, predation is thought to be a major source of natural mortality of juvenile salmonids during their early sea life. Nagasawa and Kaeriyama (1995) provided the first review of predation by fishes and seabirds on Japanese chum salmon juveniles in their early ocean life. In this report, they recorded only four species of fishes as predators. Three years later, Nagasawa (1998) published a revised review on this predation by fishes and seabirds using additional new information (e.g. Nagasawa and Mayama 1997). Although over 90 fish species had been reported to occur with chum salmon juveniles, only nine were recorded as predators in river-mouths and at sea (Table 3). The author discussed the impact of predation by fishes on juvenile chum salmon, suggesting that fish predation might cause substantial loss of chum salmon juveniles in localities where

Table 3. Recorded predators of juvenile chum salmon in coastal and estuarine waters in Japan. (From Nagasawa 1998; based on various sources, and Kawamura et al. 2000).

Predators		Sources
Fishes		
Japanese dace	<i>Tribolodon hakonensis</i>	Nagasawa 1998
Far Eastern dace	<i>T. brandti</i>	"
White spotted charr	<i>Salvelinus leucomaenis</i>	"
Japanese halibut	<i>Paralichthys olivaceus</i>	"
Japanese sea perch	<i>Lateolabrax japonicus</i>	"
Spiny dogfish	<i>Squalus acanthias</i>	"
Arabesque greenling	<i>Pleurogrammus azonus</i>	"
Pink salmon	<i>Oncorhynchus gorbuscha</i>	"
Masu salmon	<i>O. masou</i>	"
Seabirds		
Rhinoceros auklet	<i>Cerorhinca monocerata</i>	Nagasawa 1998
Black-tailed gull	<i>Larus crassirostris</i>	"
Slaty-backed gull	<i>L. schistisagus</i>	Kawamura et al. 2000
Japanese cormorant	<i>Phalacrocorax capillatus</i> (<i>P. filamentosus</i>)	"
Red-breasted merganser	<i>Mergus serrator</i>	"

these predatory fishes, especially Japanese dace (*Tribolodon hakonensis*) and arabesque greenling (*Pleurogrammus azonus*), were abundant. However, there has been no quantitative study on the impact of fish predation during the early ocean life of juvenile chum salmon in Japan.

There is, however, limited information about seabird predation on pelagic fish in coastal waters of Japan (Watanuki 1990). A review paper by Nagasawa (1998) indicated that rhinoceros auklets (*Cerorhinca monocerata*) and black-tailed gulls (*Larus crassirostris*) have been recorded as predators of juvenile chum salmon. These seabirds breed abundantly in northern Japan, and the impact of their predation on Japanese chum salmon populations may be significant.

Kawamura et al. (2000) also suggested that large numbers of seabirds present in inshore waters of their study area, the Japan Sea coast of Hokkaido, were a significant potential hazard to the survival of juvenile chum salmon during their seaward migration and early coastal life. They observed beak marks on the sides of juvenile chum salmon, and three species of seabirds feeding on juvenile chum salmon: slaty-backed gull (*Larus schistisagus*), black-tailed gull, and Japanese cormorant (*Phalacrocorax filamentosus*).

Furthermore, based on a census of seabirds and their feeding behavior on juvenile chum salmon around the same river mouth, Kawamura and Kudo (2001) estimated the loss of chum salmon juveniles by gulls at 11.1 % of the total fish released. Consumption may have been underestimated because of the restricted area of observations and the limited

number of predator species examined. They concluded that predation by seabirds (gulls, cormorants, and red-breasted merganser, *Mergus serrator*, and possibly rhinoceros auklets) has more impact than predation by fish on survival of juvenile chum salmon during seaward migration and early coastal life. Thus five seabirds, and nine fish species, are regarded as major predators of juvenile chum salmon in estuarine and coastal waters of Japan (Table 3).

When considering the relation between the physical environment and risk of fish predation, Fukuwaka and Suzuki (1998) suggested that nearshore distribution of juvenile chum salmon minimized the overlap with oceanic predators, and the extension of the riverine plume may decrease the predation rate of juvenile chum salmon by marine predators.

There is yet little information about the impact of fish and seabird predation on chum salmon populations, and it should be emphasized that more field and experimental work is needed to assess it.

Studies of Salmonid Growth Patterns in Estuaries, Coastal Oceans and High Seas

In Japan, nearly 100% of juvenile chum salmon are reared in hatcheries and released into small rivers in spring. Until the early 1960s when feeding chum salmon fry with dry food was begun, fry migrated from hatchery ponds to streams as soon as the yolk sac was absorbed. As a result, juvenile chum salmon might arrive at the estuaries almost within 24 hours in small coastal rivers (Seki 1978a; Iwata and Komatsu 1984). Information on size of offshore migrants had not yet been obtained, except that from by-catches of

juveniles (Sano and Kobayashi 1952, 1953; Mihara 1958).

The size of juvenile chum salmon stayed in estuaries and small harbors ranged from about 30 to 50 mm FL, and moved to coastal waters as they exceeded a certain size, 45–50 mm FL (Sano and Kobayashi 1952; Seki 1978a; Mayama et al. 1982, 1983; Terazaki et al. 1982; Kasahara 1985; Irie and Nakamura 1985; Kaeriyama 1986).

Growth of chum salmon juveniles originating in the Ishikari River System was traced using europium-marked fish in coastal waters from the Japan Sea side through the Okhotsk Sea side (Ito et al. 1980; Kato and Mayama 1980; Kato and Kitaguchi 1981; Ito 1982; Mayama et al. 1982, 1983; Kato 1985). In the coastal areas of Ishikari Bay, mean fork length and body weight were 43 mm and 0.6 g in early April, which was a little larger than those in the river. They grew to 64 mm and 2.1 g in early May (Kato 1985). Juvenile chum salmon were 60–80 mm FL and 2.5–4.0 g in body weight just before they disappeared from the Ishikari coast (Mayama et al. 1982, 1983). Europium-marked fish were 87 mm mean FL and 5.7 g mean weight off the coast of Cape Soya, northern Hokkaido, in mid-June. Juveniles around Cape Soya were much larger than those in the Japan Sea coastal areas during the same period. Mean fork length and mean weight were greatest, 126 mm and 26.4 g, in the areas between Abashiri Bay and the Shiretoko Peninsula of the Okhotsk Sea coast in late June. Thus, the body weight in Abashiri Bay-Shiretoko Peninsula was 10 times that of juvenile chum salmon in Ishikari Bay. These results on growth of juvenile chum salmon during offshore migration indicate that juveniles occupy different areas as they attain a larger size.

Many marked juvenile chum salmon have been released from hatcheries in Japan for various research programs. Growth patterns of juvenile salmon during early life can be estimated using data on size of juveniles recaptured in coastal waters. Specific growth rates (SGR) of juvenile chum salmon are exponential during early life, and are calculated for both body weight and fork length as follows: $SGR = (L_n - L_0) / t$ (LeBrasseur and Parker 1964), where t is days after release, L_n is the size at t days after release, and L_0 is the size at release.

Almost all juvenile chum salmon released from hatcheries in Japan arrive at the estuary within a few days without growing in fresh water. The growth rates of juveniles recaptured in estuarine and coastal waters were therefore regarded as representative of growth during early sea life. Average specific growth rates of juvenile chum salmon vary from 0.0222 to 0.0631 in body weight, and 0.005 to 0.020 in fork length (Table 4). Higher values were noted in long distance migrants such as juveniles recaptured in areas between Abashiri Bay and the Shiretoko Penin-

sula of the Okhotsk Sea coast (Ito et al. 1980). Annual differences in SGR of juvenile chum salmon during coastal life were greater than differences at any one time in south-north geographical cline.

Swimming behavior of a school tends to become more active with size of juvenile chum salmon. Juveniles appear to feed on larger food organisms as they grow. Therefore, distribution patterns of juvenile chum salmon during early ocean life closely follow changes in body size or developmental stage.

During the 1980s, size and developmental stage at time of migration offshore were investigated simultaneously. Physiological, ecological and morphological changes in the developmental process of chum salmon during early life were studied by Kaeriyama (1986) and Irie (1990). Kaeriyama (1986) classified early life developmental stages of chum salmon into alevin (20–38 mm FL), fry (38–50 mm FL), pre-fingerling (50–80 mm FL), and post-fingerling (80–120 mm FL), the period from fry to fingerling comprising the juvenile stage. Irie (1990) also observed great changes in the inshore/offshore distribution of juvenile chum salmon among size classes of about 30–50 mm, 50–80 mm, 80–120 mm and larger than 120 mm FL. Early and later seaward migrating groups migrated offshore at the transition from juvenile to young (about 120 mm FL) and the post-fingerling stage (about 80 mm FL), respectively (Kaeriyama 1986, 1989). On the basis of ecological changes such as feeding habits, swimming behavior and distribution, which coincided with morphological or physiological changes, Irie (1990) considered that juveniles of 80–120 mm FL are in the process of migrating offshore.

Growth patterns of juvenile chum and pink salmon were examined using biological data collected by dip-net, gillnet, purse seine, and surface trawl in the Okhotsk Sea and the western North Pacific Ocean from July to February. During early summer, variation in fork length was relatively narrow, being only 80 to 130 mm. During mid-summer, fork lengths of most juvenile chum salmon caught off the Pacific coast of Hokkaido and off the Okhotsk coast of Iturup and Kunashiri islands ranged from 70 to 140 mm. In contrast, off the Pacific coasts of the Kunashiri and Iturup islands, both small sized (70–110 mm FL) and large sized juveniles (160–210 mm FL) were observed (Ueno and Ishida 1996). Large sized juvenile chum salmon were collected in coastal waters of Iturup Island in early August in 1990. The mean size was 187.3 mm FL and 62.5 g body weight. The mean number of circuli on the scales was 21.0, and the maximum radius of scales was 0.85 mm. The mean number of circuli on the scales indicated that the juveniles emerged between mid-December and mid-March, suggesting that they originated from rivers in Hokkaido or Honshu (Ueno et al. 1992). Fork lengths of juvenile chum salmon were about 200 mm

Table 4. Information on the specific growth rate (SGR) of marked juvenile chum salmon released from hatcheries during the early sea life in Japan.

Year	River system ^{*1}	Mean size at releasing		Recaptured juveniles			Specific growth rate (SGR) ^{*2}	Remarks	Source
		Fork length (mm)	Weight (g)	Number of fish	Weight (g) or Fork length (mm)	Days after release			
Growth rate in body weight									
1953	Ishikari R. (Ishikari, HK)	30.6 ⁻³	0.27	-	-	-	0.0421		Kobayashi 1977
1979	"	40.0	0.58	11	1.46–3.61	65	0.0222		Kato & Mayama 1982
"	"	"	"	10	2.64–4.48	66–73	0.0260		"
"	"	"	"	9	4.42–6.99	68–74	0.0325		"
"	"	38.3	0.54	29	0.87–8.40	44–50	0.0382		Ito et al. 1980
"	"	"	"	11	0.87–4.94	63–69	0.0368		Ito 1982
"	"	"	"	3	28.69–36.93	64–66	0.0631		Ito et al. 1980
1980	Saroma Lake (Abashiri, HK)	-	1.46-4.49	31	1.43–8.12	19–33	0.0464		Ito 1982
1965	Yurappu R. (Oshima, HK)	36.2-40.1	0.44-0.65	21	1.05–5.00	26–58	0.0392		Kobayashi & Abe 1977
1982	Katagai R. (Toyama, HS)	44	0.7	24	0.9–4.2	30–60	0.0467	"Small" fish at release in late Feburary	TPFES ^{*4} 1984
"	"	52	1.2	113	1.3–4.8	15–40	0.0509	"Large" fish at release in mid-March	"
Growth rate in fork length									
1979	Ishikari R. (Ishikari, HK)	40.0	0.58	11	57–74	65	0.0083		Mayama et al. 1982
"	"	"	"	10	66–80	66–73	0.0090		"
"	"	"	"	9	81–94	68–74	0.0111		"
"	"	38.3	0.54	29	48–99	44–50	0.0133		Ito et al. 1980
"	"	"	"	3	137–139	64–66	0.0200		"
1981	Oh R. (Miyagi, HS)	47	-	47	65–95	23–68	0.0116	Seaward migrants in later spring (May)	Kaeriyama 1986
1982	"	48	-	10	50–120	14–80	0.0104	Seaward migrants in early spring (Feb-Mar)	"
1982	"	49	-	10	85–110	49–59	0.0113	Seaward migrants in later spring (April)	"
1983	Kitakami R. (Miyagi, HS)	53	-	20	62–99	10–39	0.0118	Offshore migrating group (pelagic item feeder)	"
1983	"	53	-	26	52–93	12–49	0.0107	Neritic staying group (coastal item feeder)	"
1983	"	53	-	3	58–66	17–45	0.0050	Inshore group (insect feeder)	"
1994	Akaishi R. (Aomori, HS)	44.6	0.9	15	62–90	1–36	0.0086		HSH ^{*5} 1995
"	"	52.5	1.5	19	44–79	1–44	0.0080		"
1995	"	50.2	1.4	17	45–66	1–22	0.0086		HSH 1996
1996	"	46.0	0.7	10	42–70	0–40	0.0090		HSH 1997
1997	"	59.5	2.1	37	55–112	0–35	0.0136		NSRC ^{*6} 1998
"	"	48.4	1.0	52	41–96	9–40	0.0161		"
1998	"	66.6	3.1	36	60–88	18–27	0.0074		NSRC 1999
"	"	48.9	1.1	28	55–74	18–27	0.0135		"
1999	"	51.8	1.3	54	51–79	16–32	0.0099		NSRC 2000
2000	"	54.6	1.5	11	56–75	27–31	0.0056		NSRC 2001
1994	Kawabukuro R. (Akita, HS)	44.6	0.9	15	62–90	1–36	0.0086		HSH 1995
1994	Fukura Bay (Yamagata, HS)	73.8	3.2	12	66.2–98.8	11–28	0.0068		HSH 1995
1984	Miomote R. (Niigata, HS)	55.0	1.5	111	42.1–76.6	6–23	0.0136		Ishikawa et al. 1993

continue...

Table 4. continued.

Year	River system ^{*1}	Mean size at releasing		Recaptured juveniles			Specific growth rate (SGR) ^{*2}	Remarks	Source
		Fork length (mm)	Weight (g)	Number of fish	Weight (g) or Fork length (mm)	Days after release			
1992	Miomote R. (Niigata, HS)	50.1	1.6	104	-	4–25	0.0165		Ishikawa et al. 1993
1994	"	46.5	1.0	501	38.1–81.6	0–43	0.0126		HSH 1995
1996	"	55.8	1.1	22	50–91	5–36	0.0083		"
1997	Hime R. (Niigata, HS)	52.4	1.1	70	49–92	10–41	0.0082		NSRC 1998
1995	Shou R. (Toyama, HS)	57.4	1.7	103	47–85	1–26	0.0101		HSH 1996
1996	"	52.5	1.4	142	46–86	1–30	0.0111		HSH 1997
1994	Tedori R. (Ishikawa, HS)	66.1	2.3	18	75.2–101.2	24–42	0.0100		HSH 1995
1995	"	69.3	2.8	60	73–115	24–52	0.0062		HSH 1996
"	"	61.8	1.9	21	70–100	26–49	0.0094		"
1996	"	70.0	2.2	43	67–123	29–52	0.0101		HSH 1997
"	"	63.7	2.8	47	75–121	16–53	0.0113		"
1997	"	63.3	2.0	15	82–114	19–37	0.0142		NSRC 1998
1998	"	74.1	3.5	12	76–116	30–43	0.0135		NSRC 1999
"	"	79.7	4.2	134	58–104	3–32	0.0068		"
1999	"	62.2	2.0	51	67–120	6–36	0.0157		NSRC 2000
"	"	73.9	3.1	65	83–128	20–43	0.0104		"
"	"	64.7	2.2	25	73–126	16–50	0.0128		"
2000	"	71.5	3.0	27	74–101	19–42	0.0055		NSRC 2001
"	"	58.6	1.6	11	72–102	25–51	0.0087		"

*1: HK and HS in parentheses mean Hokkaido and Honshu, respectively.

*2: $SGR = (LnSt - LnSo)/t$, ST: size at recapture, So: size at release from hatchery, t: day after release.

*3: body length.

*4: Toyama Prefectural Fisheries Experimental Station.

*5: Hokkaido Salmon Hatchery.

*6: National Salmon Resources Center.

in September in the Okhotsk Sea, and then gradually increased to about 230 mm in the western North Pacific Ocean by February. Pink salmon grew faster than chum salmon (Fig. 4).

Growth and nutritional conditions of juvenile chum and pink salmon migrating to the Okhotsk Sea and the North Pacific Ocean were examined using biochemical indices such as protein contents, the RNA-DNA ratio, and percentage of triglyceride in dorsal muscle as well as biological data such as fork length, body weight, and condition factor. Both chum and pink salmon exhibited good growth, especially chum salmon captured in late August to early September, judging from the protein content and the RNA-DNA ratio. The relationships of RNA-DNA ratios and triglyceride contents suggested different strategies for survival between the two species. Chum salmon showed higher growth rates and less energy storage in earlier stages, but decreased growth rate and increased energy storage as growth progressed. Pink salmon had both low energy and low

growth rates at first, but both these gradually increased as growth progressed (Azuma 1996).

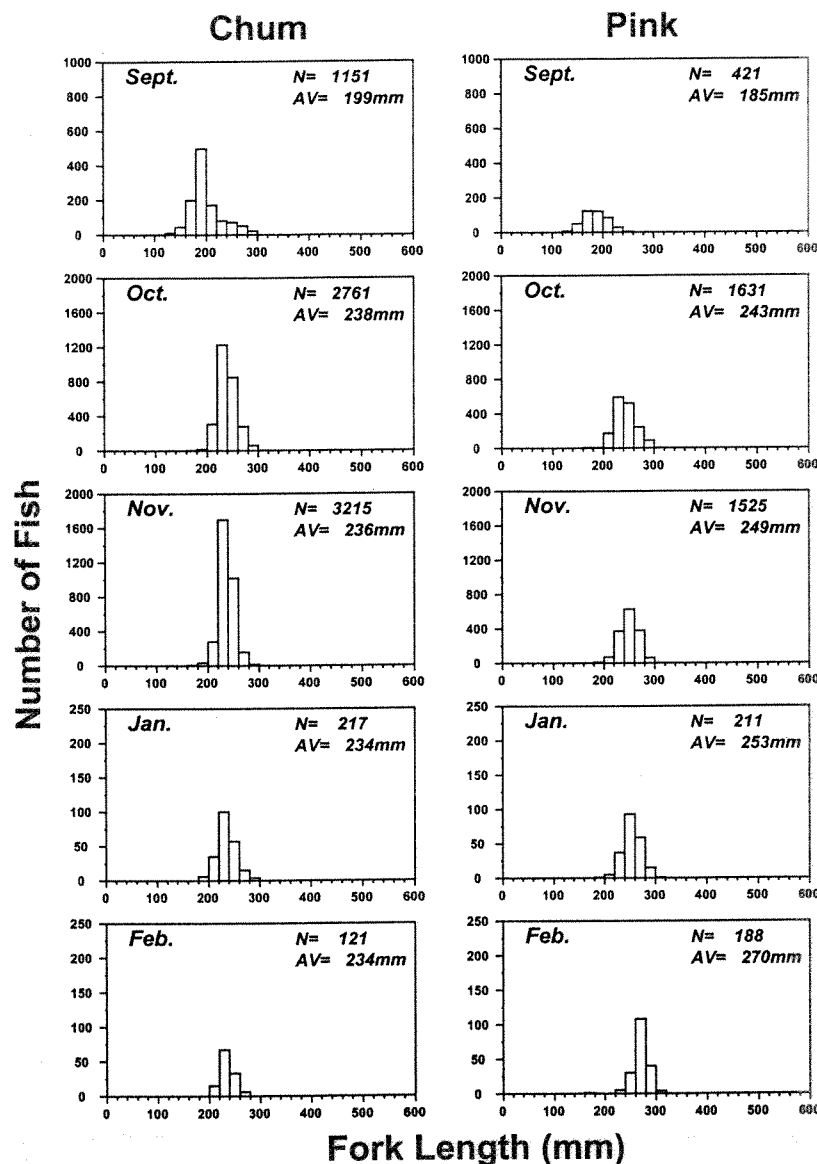
Studies of Hatchery versus Wild Fish Interactions

Until about 1900 when large scale salmon hatcheries were introduced, chum salmon stocks in Japan were maintained by wild populations. However, recent chum salmon resources have been entirely supported by artificial reproduction. Since little research on salmon was done before the advent of hatcheries, we have no studies on the interactions between hatchery and wild fish in Japan.

High Seas Work

Juvenile chum salmon originating in Japan migrate along the coast of Honshu and Hokkaido during early summer. However, their offshore migration routes to the North Pacific Ocean were not identified.

Fig. 4. Seasonal changes in fork length of juvenile chum and pink salmon caught by research vessels from 1988–1996. (Data from Ueno and Ishida 1996; Ueno 1998).



To investigate the offshore migration routes of juvenile chum salmon, Japan-Russia cooperative juvenile salmon surveys were conducted in the Okhotsk Sea and the western North Pacific Ocean, using a purse seine, dip-nets, drift gillnet and a surface trawl, from early summer to winter in 1988–1996 (Ueno and Ishida 1996; Ueno 1998). The results indicated that juvenile chum salmon mainly occurred in the southern and central waters of the Okhotsk Sea from summer to mid-autumn. Then they migrated out from the Okhotsk Sea to the waters off the Kuril Islands in the western North Pacific in late autumn. In winter they were distributed in the western North Pacific Ocean (Fig. 5). Pink salmon juveniles appear to have similar migration patterns (Fig. 6). Migrating chum and pink salmon juveniles were mainly concentrated in waters with surface temperatures higher than 10°C in

August, but shifted to waters with lower temperature, from 5° to 10°C, during September to February (Fig. 7).

A trawl and acoustic survey of salmon juveniles was conducted in the Okhotsk Sea and Pacific Ocean off the Kuril Islands in October and November of 1996. The echoes from juveniles were weak, about –32dB to –43dB, but salmon juveniles were detected. Ninety percent of detected fish were in the zone shallower than 40 m, and 2.8 percent were detected in water deeper than 70 m, where the temperature was 1° to 4°C (Sakai and Ueno 1998). Juvenile chum salmon were concentrated in a limited area of the Okhotsk Sea; abundance was estimated at 60–100 million fish in 1993, and 200–334 million fish in 1996 (Ueno 1998).

Fig. 5. Seasonal changes in distribution of juvenile chum salmon caught by research vessels from 1988–1996. "X" indicates no catch; size of circle indicates abundance of juvenile salmon caught by purse seine, surface trawl, dip net, and drift net. (Data from Ueno and Ishida 1996; Ueno 1998).

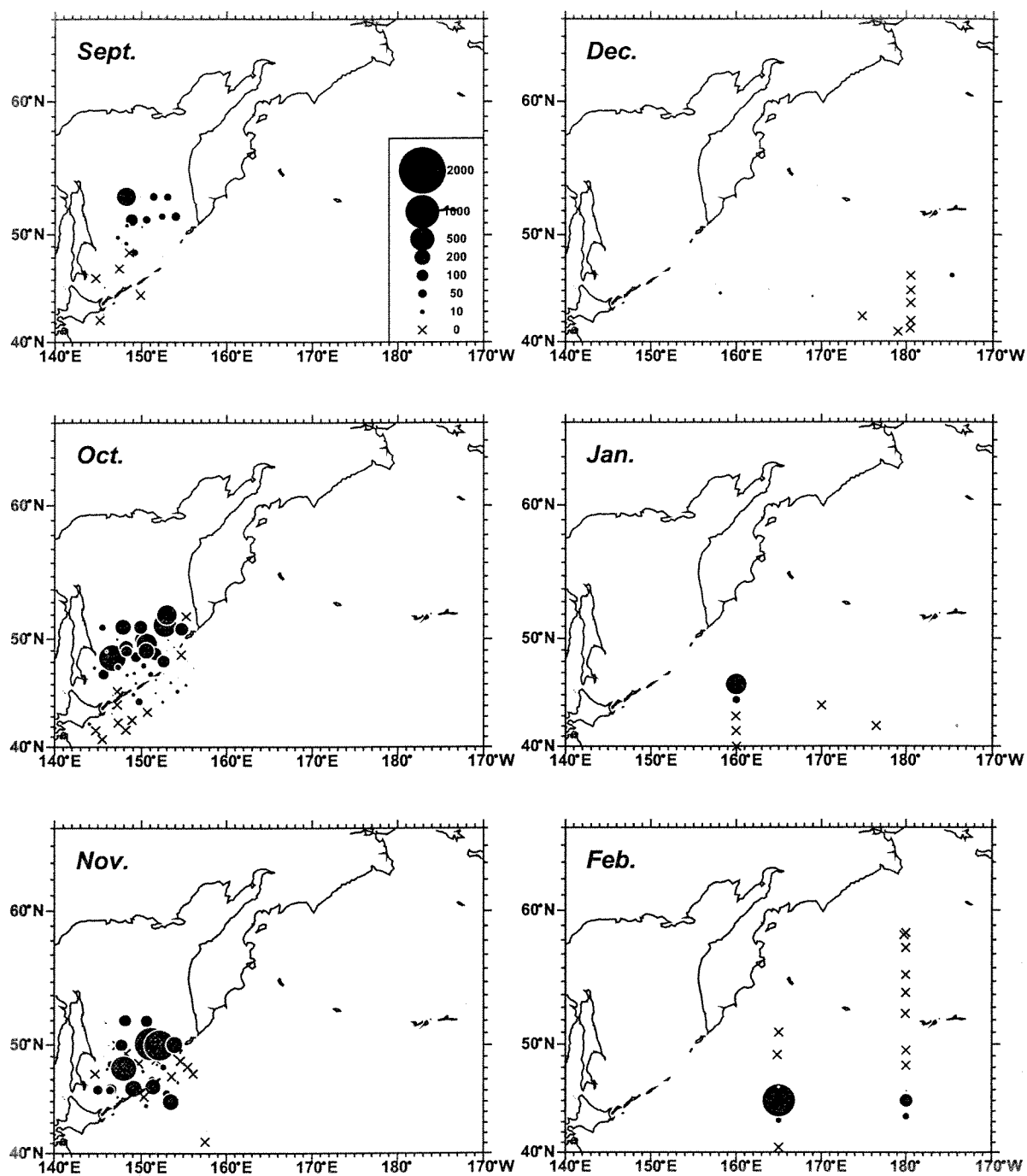


Fig. 6. Seasonal changes in distribution of juvenile pink salmon caught by research vessels from 1988–1996. "X" indicates no catch; size of circle indicates abundance of juvenile salmon caught by purse seine, surface trawl, dip net, and drift net. (Data from Ueno and Ishida 1996; Ueno 1998).

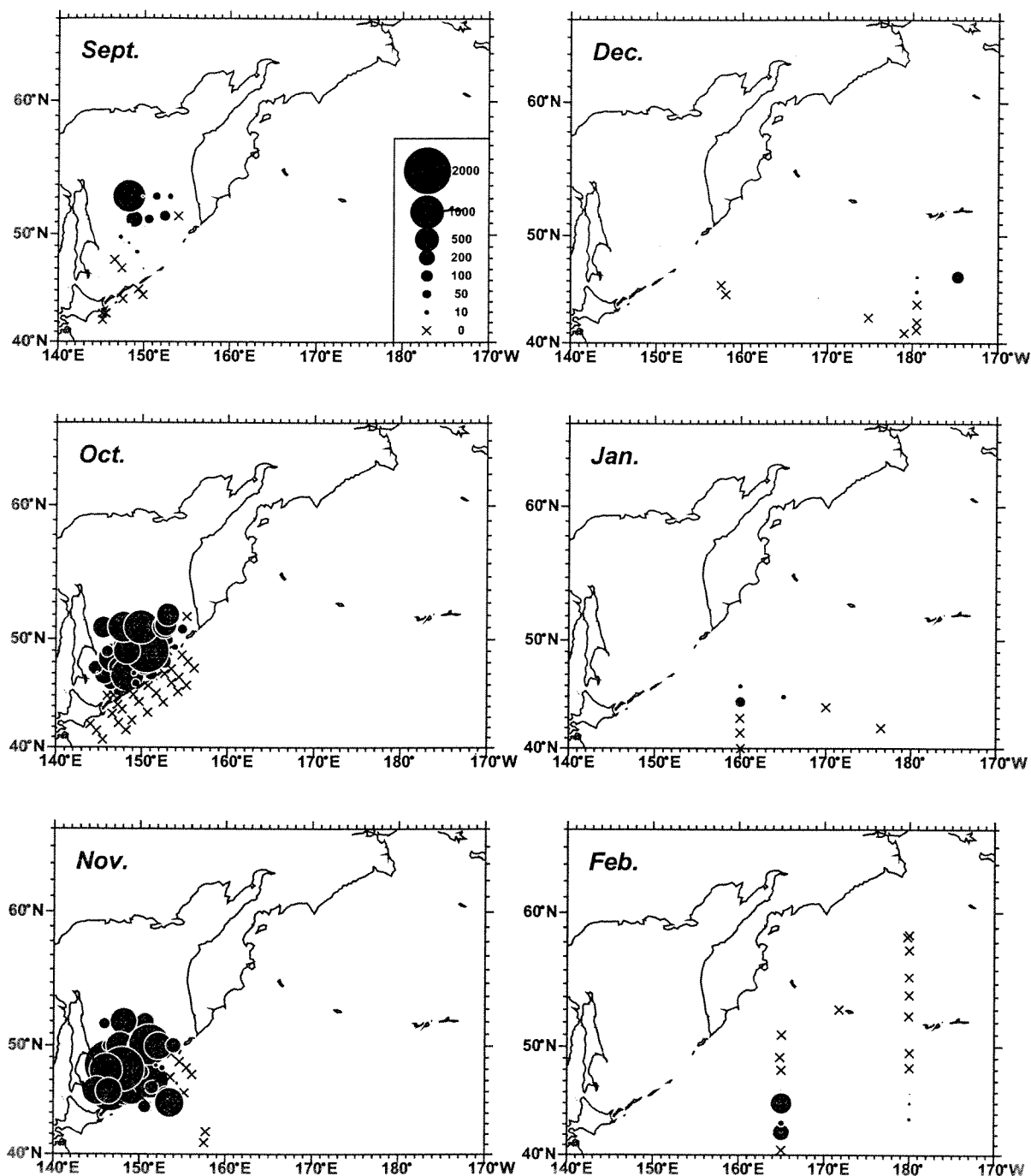
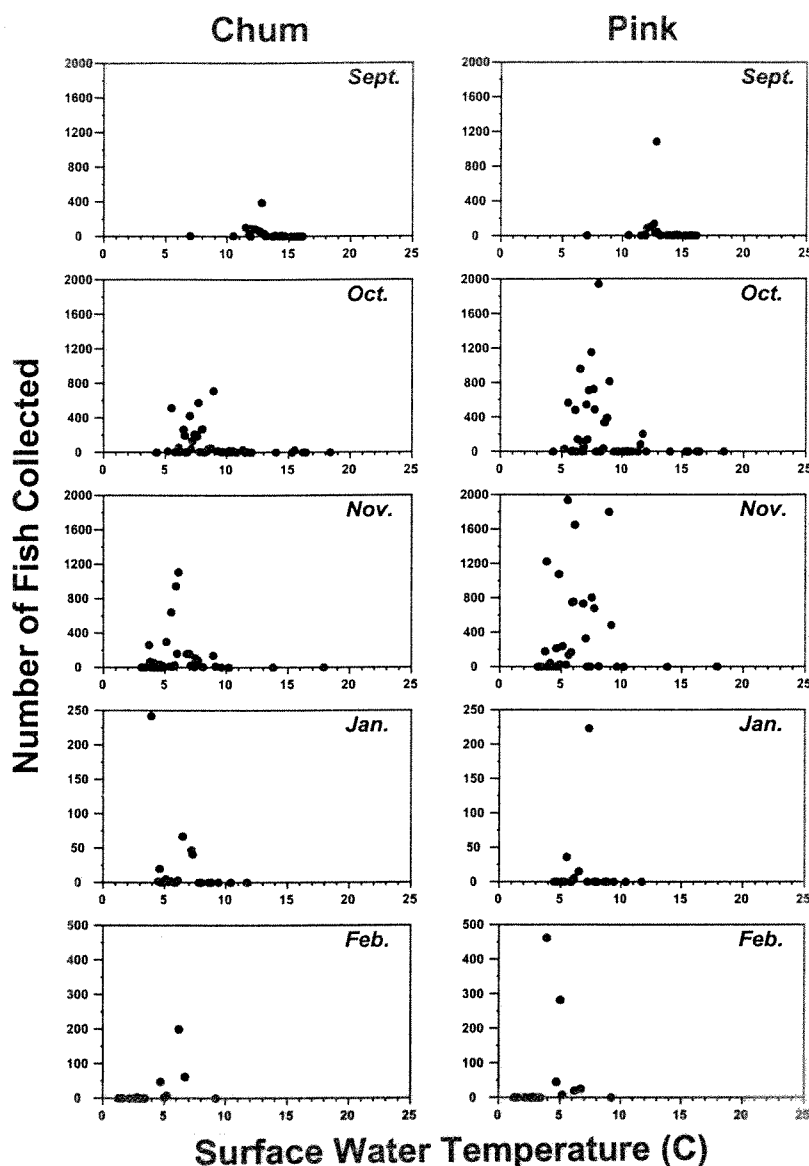


Fig. 7. Seasonal changes in surface water temperature and number of juvenile chum and pink salmon caught by research vessels from 1988–1996. (Data from Ueno and Ishida 1996; Ueno 1998).



To investigate trophic relations and feeding habits of juvenile salmon and other major pelagic fishes, the stomach contents of juvenile pink, chum, masu, sockeye (*O. nerka*), chinook (*O. tshawytscha*), and coho salmon (*O. kisutch*), Atka mackerel (*P. monopterygius*), and Arabesque greenling were examined from collections taken in the Okhotsk Sea and Pacific waters off the Kuril Islands during autumn of 1993 (Tamura et al. 1999). The major prey of pink, chum, and sockeye salmon were planktonic Amphipoda, *Themisto* sp. and *Primno* sp. Chum and pink salmon also fed on a variety of invertebrates such as Gastropoda, Copepoda, Euphausiacea, and *Sagitta* spp. Masu, chinook, and coho salmon mainly fed on Cephalopoda and fishes (Table 5). Prey species (diet niche) overlap was highest between pink and chum salmon, which were the most abundant species in

these waters. Prey species composition in their stomach contents is considered to reflect planktonic species composition in the environment.

Stock origins of juvenile chum salmon in the Okhotsk Sea were identified by morphological characters such as pyloric caeca counts and by genetic characters such as allele frequencies (Ueno et al. 1998). The results indicated that juvenile chum salmon from southern stocks such as Japan, Sakhalin, and Primorye migrated northwards through the southern part of the Okhotsk Sea in July and were distributed in the central part of the Okhotsk Sea in August and September. In October and November, they migrated southwards to the central and southern part of the Okhotsk Sea and moved to the North Pacific Ocean through the straits of the northern and central Kuril Islands. Northern Russian stocks such as

Table 5. Information on the stomach contents of age .0 Pacific salmon sampled in the southern Okhotsk Sea and the Pacific coast waters off Kuril Islands during October and November 1993.

Species	Number examined	Fork length (mm)	Percentage composition by weight									Source
			Fishes	Sagittas	Squids	Pteropods	Insects	Decapods	Euphausiids	Amphipods	Copepods	
Pink	637	180-340	1.2	11.4	0.8	6.2	+	6.1	14.5	59.5	0.5	Tamura et al. 1999
Chum	424	160-300	2.2	21.6	0.7	4.8	+	0.5	16.1	52.6	1.4	Tamura et al. 1999
Sockeye	33	220-290		36.3	3.4	0.1		0.1	7.1	52.6	0.5	Tamura et al. 1999
Masu	25	250-400	95.3						3.5	1.2		Tamura et al. 1999
Chinook	17	270-350	25.2	0.1	72.4	0.0		0.4		1.9		Tamura et al. 1999
Coho	14	220-340			99.5					0.5		Tamura et al. 1999

Magadan and western Kamchatka were distributed in the northern and eastern part of the Okhotsk Sea, and followed the southern stocks (Ueno et al. 1998). Among juvenile chum salmon (age 0.0) caught in the Okhotsk Sea, the Japanese regional stock was predominant (71%) in October, but its contribution to the sample decreased to 36% in November. Juvenile chum salmon migrating to Pacific waters east of the Kuril Islands in November were composed of 57% Japanese, 30% Russian and 13% Alaskan stocks. Young chum salmon (age 0.1) caught in winter in the western North Pacific Ocean consisted of 29% Japanese, 65% Russian and 6% Alaskan stocks in January, and 37% Japanese, 45% Russian and 18% North American stocks in February (Urawa et al. 1998).

Twenty-four species of fishes and two squid species were identified in the southern Okhotsk Sea and western North Pacific Ocean off Kuril Island in October and November 1993 during juvenile salmon surveys. Juvenile salmonids (*Oncorhynchus* spp.) were the most abundant, followed by myctophids, juvenile Arabesque greenling, and gonatids including boreopacific gonate squid (*Gonatopsis borealis*) and probably schoolmaster gonate squid (*Berryteuthis magister*). Deep-sea smelts (*Leuroglossus schmidtii*) were also abundant. Juvenile Arabesque greenling were abundantly taken in the Okhotsk Sea in October but disappeared from its surface waters in November probably because they settled onto the continental shelf. There were marked differences in the oceanic distributions of Arabesque greenling and Atka mackerel, suggesting that these species segregate their habitats. Deep-sea smelts mostly occurred in the Okhotsk Sea, but myctophids were caught only in the North Pacific Ocean. Nagasawa et al. (1995) suggested that the surface layer of the southern Okhotsk Sea provides favorable habitats for the feeding and growth of juvenile fishes such as salmonids and Arabesque greenling from summer to mid-autumn, but

ends its role in late autumn when sea surface temperatures decrease and those juveniles leave.

Juvenile salmon studies suggest that the Okhotsk Sea is an important nursery ground for juvenile salmon originating from Russia and Japan.

FUTURE ISSUES AND QUESTIONS

Four future issues for juvenile salmon studies are identified.

- 1) Assessment of juvenile salmon abundance. Are there reliable methods for assessing the change in abundance of juvenile salmon?
- 2) Stock identification and estimation of stock composition of juvenile salmon by genetic methods and otolith thermal marks. Where and when do juveniles of Japanese stocks mix with Russian stocks? Do these stocks affect survival and growth of each other?
- 3) Investigation of factors affecting survival and abundance of juvenile salmon during their early ocean life. What are the main factors affecting survival and abundance of juvenile chum salmon released into rivers in Japan?
- 4) The life history of other salmon species, such as pink, masu and sockeye salmon, should also be studied in order to improve salmon management in Japan.

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Review of Russian Marine Investigations of Juvenile Pacific Salmon

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Keywords: Russian, Pacific salmon, *Oncorhynchus* spp., juvenile ecology, abundance, north-west Pacific Ocean

Abstract: In the coastal waters of the far eastern seas of Russia, different gears were used for juvenile salmon surveys depending on the geomorphological and hydrological conditions of the region. In offshore waters, pelagic rope-trawls were used to collect juvenile salmon in the same areas from year to year. For the future it is recommended that monitoring in these standard areas continue, and that a new investigation on biological interactions of enhanced and wild salmonids be undertaken.

INTRODUCTION

Data on the marine biology of juvenile Pacific salmon were first collected during occasional sampling and investigation of other marine fishes, usually Pacific herring (*Clupea pallasii*), as well as during sampling directed at juvenile salmonids in coastal waters (Baranenkova 1934; Semko 1939; Gribanov 1948; Piskunov 1955, 1959). Regular studies of juvenile Pacific salmon were undertaken by I. B. Birman in the early 1960s, after a laboratory was established in Kamchatka in 1960 to investigate the marine life of salmon (Birman 1985). Originally, only the ecology of juveniles in the open sea and the North Pacific was studied, but later coastal water ecology was included.

These Russian marine investigations of juvenile Pacific salmon have addressed three topics:

- 1) juvenile ecology during early marine life in estuaries and coastal waters;
- 2) life of juvenile salmon during autumn, and assessment of their brood abundance;
- 3) the role of juvenile salmon in coastal and marine ecosystems of Russia's far eastern seas and the north-west Pacific Ocean.

This report reviews the results and prospects for further study of these and some other topics.

METHODS AND MATERIALS

Work reviewed in this paper was carried out by Russian scientists and their foreign colleagues in the waters of Russia's far east, and published in Russia and abroad. In addition, some data, including personal reports of investigators, were provided to the

author at his request. The author acknowledges and thanks all people who have provided such data.

Various investigators used different methods of collecting data. Methods depended on geomorphological peculiarities of the survey areas as well as goals and technical requirements (Fig. 1). The sampling areas, methods and results are summarized in Table 1.

RESULTS

Early Marine Life of Pacific Salmon

Data on ecology of juvenile salmon during early marine life were first collected in the 1930s from the estuaries of some west Kamchatka rivers, from Avacha Bay, and from the Kamchatka River (Baranenkova 1934; Semko 1939; Gribanov 1948). Kamchatka scientists were the first to describe feeding and distribution patterns, and biological parameters of some salmon species in coastal waters. Later, investigations were conducted more regularly, and focussed on specific problems in the area. The results of these investigations are reviewed from south to north along the far east coast.

Primorye chum salmon

Investigations into the biology of juvenile chum salmon (*Oncorhynchus keta*) were carried out in the spring–summer seasons of 1986–1990 along the west side of Peter the Great Bay and on the Sea of Japan's coastal waters from Provotny Cape to Olga Bay (Goriaynov 1991, 1993, 1998a). The major goal of these investigations was to gather data on the food requirements of Primorye chum salmon during their

Fig. 1. Main Investigation areas of Pacific salmon juveniles. Coastal waters: 1-Primorye, 2-Iturup Island, 3-Southeast Sakhalin, 4-Southwest Sakhalin, 5-Nyiskiy Bay, 6-Sakhalin Bay, 7-Tauy Bay, 8-Western Kamchatka, 9-Avacha Bay, 10-Karaginskii Bay; I-fall surveys TINRO-Centre; II-Winter Surveys TINRO-Centre.

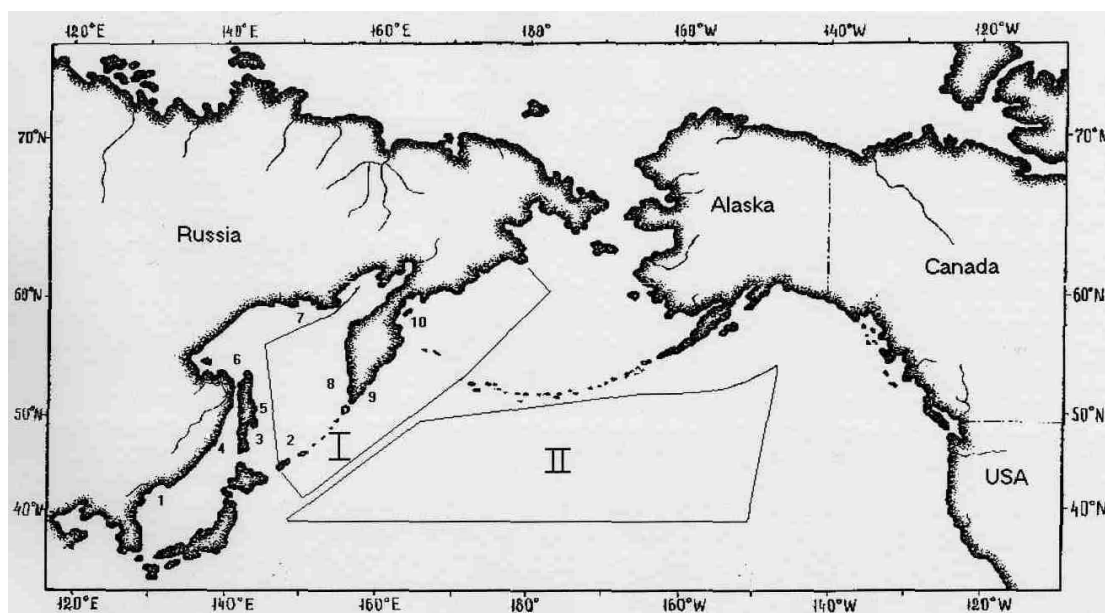


Table 1. Studies on juvenile salmon conducted in Russian waters (main cruises) and types of data collected.

Region	Investigator	Dates	Gear	Physical oceanography	Zooplankton	Food	Growth	Migration	Predators
<i>TINRO-Centre</i>									
N-W Pacific	Erokhin V.G.	1985–1986	Trawl	+	+	+	+	-	-
"	Borisovskii Yu.G.	1987	"	+	+	+	+	-	-
N-W, N-E Pacific	Rassadnikov O.A.	1988–1991	"	+	+	+	+	-	-
N-W Pacific	Rassadnikov O.A.	1992	"	+	+	+	+	-	-
Bering sea	Shuntov V.P.	1986	"	+	+	+	+	-	-
"	Ozhereliev A.V.	1988	"	+	+	+	+	-	-
Bering sea, Pacific Kuril Is.	Sobolevskii E.I.	1987, 1993	"	+	+	+	+	-	-
Bering sea, Sea of Okhotsk, Pacific Kuril Is.	Boldyrev V.Z.	1990	"	+	+	+	+	-	-
"	Volkov A.F.	1990	"	+	+	+	+	-	-
Sea of Okhotsk, Pacific Kuril Is.	Rassadnikov O.A.	1990–1991	"	+	+	+	+	-	-
"	Gorbatenko K.M.	1992	"	+	+	+	+	-	-
"	Shuntov V.P.	1993	"	+	+	+	+	-	-
Sea of Okhotsk	Radchenko V.I.	1994	"	+	+	+	+	-	-
Sea of Okhotsk, Pacific Kuril Is.	Moroz I.F.	1994–1995	"	+	+	+	+	-	-
"	Gorbatenko K.M.	1995–1996	"	+	+	+	+	-	-
Sea of Okhotsk	Radchenko V.I.	1996	"	+	+	+	+	-	-
Sea of Okhotsk, Pacific Kuril Is.	Efimkin A.Ya.	1996	"	+	+	+	+	-	-
Sea of Okhotsk	Shuntov V.P.	1997	"	+	+	+	+	-	-
"	Melnikov I.V.	1998–1999	"	+	+	+	+	-	-
Sea of Japan (Peter the Great Bay)	Goriaynov A.A.	1986–1990	Trawl, beach seine, lift net	+	+	+	+	+	-

continue...

Table 1. continued.

Region	Investigator	Dates	Gear	Physical oceanography	Zooplankton	Food	Growth	Migration	Predators
Amur branch TINRO-centre									
Sakhalin Bay	Rosly Yu.S., Novomodny G.V.	1987–1993	Trawl	+	-	+	+	-	+
Magadan branch TINRO-centre									
Ola estuary	Frolenko L.A.	1975–1978	Beach seine	+	+	+	+	-	-
Tauy Bay	Popov S.A., Semenova N.R.	1981–1982	Beach seine	+	+	+	+	-	-
"	Kostarev N.V.	1986–1988	Pelagic trawl, Isaacs- Kidd trawl, trap, gill net	+	+	+	+	+	+
"	Afanasyev N.N. et al.	1988–1990	Pelagic trawl Isaacs- Kidd trawl	+	+	+	+	+	-
Sea of Okhotsk	Volobuyev V.V.	1986–1990	trawl	+	+	+	+	-	-
SakhNIRO									
S-W Sakhalin	Shershnev A.P.	1964–1970	Bottom trawl, beach seine, Isaacs- Kidd trawl	+	+	+	+	+	+
"	Ivankov V.N. et al.	1985–1988	Beach seine	+	+	+	+	+	+
S-E Sakhalin	Shershnev A.P., Rudnev V.A.	1973–1976	Bottom trawl, beach seine, Isaacs- Kidd trawl	+	+	+	+	+	+
"	Shubin A.O. et al.	1988–1993	Trawl	+	+	+	+	+	+
"	Ivankov V.N. et al.	1988–1992	Beach seine	+	+	+	+	+	+
N-E Sakhalin	Churikov A.A., Gritsenko O.F.	1971–1974	Beach seine, gill net	+	-	-	+	+	+
"	Ivankov V.N. et al.	1988–1993	Beach seine	+	+	+	+	+	+
Iturup Is.	Kayev A.M., Chupakhin V.M.	1974–1987	Beach seine, landing net	+	+	+	+	+	-
KamchatNIRO									
Karaginskii Bay	Karpenko V.I.	1975–1983, 1985–1987, 1989, 1991	Trawl, beach seine, purse seine, lift net	+	+	+	+	+	+
"	Erokhin V.G.	1984	"	+	+	+	+	+	+
"	Maslov A.V.	1988	"	+	+	+	+	+	+
"	Goncharov D.V.	1992	"	+	+	+	+	+	+
"	Maximenkov V.V.	1993, 1995	"	+	+	+	+	+	+
"	Kondrashenkov E.L.	1997	"	+	+	+	+	+	+
Bering Sea	?	1965	Gill net	+	+	+	+	+	-
"	Sklyarov Yu.M.	1966	"	+	+	+	+	+	-

continue...

Table 1. continued.

Region	Investigator	Dates	Gear	Physical oceanography	Zooplankton	Food	Growth	Migration	Predators
Bering Sea	Davydov I.V.	1967	Gill net	+	+	+	+	+	-
"	Karpenko V.I.	1975–1979	"	+	+	+	+	+	-
"	Shershneva V.I.	1981	"	+	+	+	+	+	-
"	Shushunov P.I.	1981–1982	Trawl	+	+	+	+	+	-
"	Kisljakov V.P.	1984, 1986, 1987	"	+	+	+	+	+	-
"	Dekshtein A.B.	1988	"	+	+	+	+	+	-
"	Sinjakov S.A.	1989–1990	"	+	+	+	+	+	-
"	Smorodin V.P.	1994, 1998, 2000	"	+	+	+	+	+	-
Avacha Bay	Karpenko V.I.	1974	Beach seine, Gill net	+	-	+	+	+	+
"	Vasilets P.M., Maximenkov V.V.	1995–2000	Beach seine	+	-	+	+	+	+
Bolshaya estuary	Leman V.N.	1989–1990, 1994–1999	Beach seine	+	+	+	+	+	+
"	Tokranov A.M., Maximenkov V.V.	1990–1992	Beach seine	+	+	+	+	+	+
Sea of Okhotsk (coastal waters)	Bazarkin V.N.	1987	Beach seine, purse seine, lift net	+	+	+	+	+	+
"	Grigoryev S.S.	1988	"	+	+	+	+	+	+
Sea of Okhotsk (open waters)	Grachev L.E.	1964–1967	Gill net	+	+	+	+	+	-
"	Sklijarov Yu.M., Shershneva V.I.	1966	"	+	+	+	+	+	-
"	Shershneva V.I.	1968, 1973, 1981	"	+	+	+	+	+	-
"	Dguravlev V.M.	1971	"	+	+	+	+	+	-
"	Kaun A.N.	1972, 1973	"	+	+	+	+	+	-
"	Kisljakov V.P.	1975, 1977–1979	"	+	+	+	+	+	-
"	Safronov S.G.	1980	"	+	+	+	+	+	-
"	Shershneva V.I.	1982, 1986	Purse seine	+	+	+	+	+	-
"	Shushunov P.I., Sinjakov S.A.	1984	"	+	+	+	+	+	-
"	Shushunov P.I.	1981–1982	Trawl	+	+	+	+	+	-
"	Kisljakov V.P.	1983–1984	"	+	+	+	+	+	-
"	Erokhin V.G.	1985, 1986, 1989, 1991, 1993, 1995, 1997	"	+	+	+	+	+	-
"	Bezljudny A.M.	1986	"	+	+	+	+	+	-
"	Shershneva V.I.	1987	"	+	+	+	+	+	-
"	Shisterov M.V.	1990	"	+	+	+	+	+	-
"	Smorodin V.P.	1999	"	+	+	+	+	+	-
Sea of Japan	Nikolayev A.S.	1964, 1966	Gill net	+	+	+	+	+	+
"	Grachev L.E.	1965	"	+	+	+	+	+	+
"	Bezrukov A.A.	1970, 1972, 1973	"	+	+	+	+	+	+
"	Karpenko V.I.	1974	"	+	+	+	+	+	+
"	Kisljakov V.P., Shershneva V.I.	1975	"	+	+	+	+	+	+
"	Safronov S.G.	1976	"	+	+	+	+	+	+
Pacific ocean	Birman I.B.	1961	"	+	+	+	+	+	+
"	Kuznetsov A.I.	1961	"	+	+	+	+	+	+

continue...

Table 1. continued.

Region	Investigator	Dates	Gear	Physical oceanography	Zooplankton	Food	Growth	Migration	Predators
Pacific Ocean	Grachev L.E.	1963, 1966	Gill net	+	+	+	+	+	+
"	Davydov I.V.	1965	"	+	+	+	+	+	+
"	Shershneva V.I.	1966, 1967, 1970, 1972	"	+	+	+	+	+	+
"	Piskunova L.V.	1972	"	+	+	+	+	+	+
"	Kaun A.N.	1973	"	+	+	+	+	+	+

early marine life in coastal waters. To obtain these data, investigators assessed the productivity of coastal waters in areas where fish hatcheries were located and operated. The results permitted the evaluation of possible increases in hatchery production, and provided management recommendations for chum salmon produced at hatcheries in the south Primorye. The results led to technological improvements in chum salmon hatchery production, specifically regarding the timing, quantity, and frequency of releases. Release success was correlated with the development and production of the main crustacean forage species. Implementation of the recommendations increased hatchery production efficiency.

Sampling of zooplankton in 1991 (April 19–June 18) documented the presence of 32 species, but only 3–4 of these were abundant: *Acartia clausi*, *Oithona similis*, *Paracalanus minutus*, and *Calanus plumchrus*. Zooplankton biomass varied from 50 to 437 mg/m³, the maximum occurring in the Barabashevka River estuary and Narva Bay in mid May. The food composition of juvenile chum salmon included 26 taxa, of which copepods (*P. minutus*, *Tortanus discaudatus*) and euphausiids (*Euphausia pacifica*) were the main groups. Stomach fullness reached 133–446 ‰ (Puschina and Goriaynov 1994). Young mysids, decapod larvae and fish larvae were minor components of the diet of juvenile chum salmon.

Although the main downstream migration of juvenile chum salmon occurs in April, a high growth rate is observed later in May: fork lengths increase from 32–42 to 48–60 mm, and weights from 460–590 to 850–2100 mg, daily growth rate in length was from 0.17 to 0.65 mm. At Iturup Island and southwestern Sakhalin Island, daily growth rate was 0.26–0.6 mm (Ivankov and Shershnev 1968; Shershnev 1968). For comparison, in southern Alaska daily growth rate was 0.4 mm (Murphy et al. 1988), and at Hokkaido Island, 0.21–0.39 mm (Irie 1990).

Juvenile chum salmon begin their seaward migration at fork lengths of 55–65 mm, and the duration of coastal habitation in Peter the Great Bay is 0.5–1.5 months. The number of circuli on the scales reaches six, though when migrating to sea most juveniles have no scales. A new circulus appears approximately at each 4–5 mm increment in fork length (Goriaynov 1993).

Survival of juvenile chum salmon depends on their growth in coastal waters, which in turn is determined by the abundance and availability of their food. The coefficient of return of chum salmon to the Narva River decreased more than three times (from 5.2% to 1.6%) when juvenile numbers increased by six times. In addition, return coefficients depend on the average daily growth rate in weight of different generations of juveniles. Release of juvenile chum salmon from hatcheries increases their abundance in coastal areas, and high densities create competition for food because of a limitation in coastal food resources. This is exacerbated in Southern Primorye waters by a relatively short favorable feeding period, associated with a rapid warming of water, leading to the migration of juveniles offshore. This does not occur in more northern areas of salmon production.

Growth rate of juvenile chum salmon may therefore be a reliable indicator of feeding conditions. It affects the number of generations of maturing salmon present at one time, their sizes which affects reproductive effectiveness, and the potential salmon production capacity of this area (Goriaynov 1998b).

Iturup Island chum and pink salmon

In this area, wild and hatchery salmon reproduction are of nearly equal importance. However, very high hydrological activity and such indicators as temperature, salinity, upwelling, and high productivity mean that food availability is likely not crucial to survival of juvenile salmon during their first weeks of marine life. The major objectives of the study on juvenile pink salmon (*O. gorbuscha*) and chum salmon during early marine life in this area were to assess the biological parameters affecting their condition and abundance. Knowledge of these factors is essential for stock assessment and management (Chupakhin and Kayev 1980; Kayev and Chupakhin 1980, 1982, 1986). Investigations were begun in 1974, and continued regularly until the late 1980s. After that, data were collected only occasionally. Some recent data have not yet been published. The specifics of downstream migration, feeding and migration of juvenile pink and chum salmon have received most attention, including formation and growth of scales in the spring-summer season. Eco-

logical groups have been identified in juvenile chum salmon under different feeding conditions, and patterns of individual growth and survival (Kayev 1992). Thus growth patterns in some juvenile broods were used to forecast commercial escapement (Kayev 1979, 1983, 1986, 1999). In addition, juvenile condition while feeding in coastal waters of Iturup Island allows prediction of further growth, and of the numbers and age composition of adults returning to spawn.

Research in this area was begun in the 1960s by V.N. Ivankov (Ivankov and Shershnev 1968), and was continued through the 1970s and 1980s by A.M. Kayev and V.M. Chupakhin (Chupakhin and Kayev 1980; Kayev and Chupakhin 1980). Juvenile salmon were caught in shallow coastal waters and in the zone of stationary trap nets located more than 2 km from the home-river estuary.

Juvenile salmon biology was studied in Kurilsky and Kuybyshevsky bays where both wild and hatchery fish intermingled. The bays have similar geomorphological and physical and hydrological characteristics where juveniles enter from rivers and are released from hatcheries in May and June. In recent years about 50 million pink fry were released annually from the Kurilsky hatchery into Kurilsky Bay, whereas natural spawning grounds in the Kurilka and Rybatskaya rivers produce only 20–30 million fry (O.A. Shubin, SakhNIRO, Komsomolskaya Str. 196, Yuzhno-Sakhalinsk, personal communication). Juveniles in coastal waters are generally observed around the beginning of May, and by the end of May and in June their numbers have considerably increased. By mid-June, offshore migration begins, as at this time temperatures in shallow water increase noticeably, promoting juvenile migration offshore. During this period, the diet of juvenile pink and chum salmon changes, pink salmon in particular switching to more pelagic organisms. Feeding of juvenile salmon may therefore be divided into three stages: 1) feeding in warm, shallow coastal waters, 2) feeding in open bays, and 3) feeding during migration from bays to the open waters of Kurilsky and Kuybyshevsky bays (Chupakhin and Kayev 1980).

The open waters of Kurilsky and Kuybyshevsky bays are influenced by the warm Soya Current and the cold Oyashio Current, which are prominent oceanographic features of the coastal waters determining the seasonal appearance of food organisms here. As a result of the interaction of these two currents at Iturup Island in the coastal waters of the Sea of Okhotsk, three bioproductive zones can be identified. Annually in coastal waters, about 40 species of zooplankton appear belonging to 18 taxonomic groups (Efanov et al. 1990). From small rivers of Iturup Island, pink and chum salmon migrate downstream to the sea where they inhabit coastal waters for 2–3 months. This period may be divided into

two, the first being in shallow waters, and the second in open areas and bays. Water temperatures and juvenile growth determine the time juveniles remain to feed in these zones. The optimal temperature is from 6° to 14°C, and salinity from 20 to 32.5‰.

Juvenile salmon are much smaller in shallow coastal waters than in open areas and bays. Lengths differ on average by 1.5 to 1.8 times, weight by 5 to 9 times, and the sea zone variability (salinity gradients) is higher. Stomach fullness is almost the same in the two areas, but variability is higher in coastal waters. The stomach fullness of chum salmon is usually 1.5 times higher than that of pink salmon, and on average exceeds 200‰. Nevertheless, interannual differences in size and fullness of stomachs are significant, and are used to estimate survival and return rates of different generations.

As in other coastal areas, the food spectrum of juvenile salmon in shallow waters is usually narrower than in open areas or small bays. The diet of chum salmon narrows after their seaward migration. This defines lower indicators of the food overlap of the two species of juveniles in the first zone near beaches after seaward migration, 50%, in comparison with those in the second zone, bays, 80%. While in the first zone (May–June) the main food components are representatives from river insect drift and small coastal crustaceans, in the second zone and period (June–July, early August) they are calanoida, amphipoda and euphausiacea. Chum salmon in the first period usually consume benthic and epibenthic organisms (gammaridae, polychaeta and fish eggs as well as aerial insects); pink salmon prefer crustaceans that inhabit the water mass (Kayev and Chupakhin 1980, 1986). Chum salmon change their predominant food from harpacticoida to calanoida and euphausiids as they grow (Kayev 1983). In pink salmon, this change in diet is not so obvious, but prey sizes increase as the fish grow.

By mid-August most juvenile salmon have migrated from the bays to the open Sea of Okhotsk, and only a few remain in the zone of stationary trap nets. In some years this migration begins earlier, in July; nevertheless, juveniles are seldom caught in the open sea, and then only in small numbers.

Food availability (food supply per fish) in coastal waters as estimated from growth parameters can be used to predict the rate of return of mature fish. For characterizing growth features of chum of different generations Kayev (1979) used asymmetries in the size compositions of juveniles. The coefficient of asymmetry of fork length for juveniles was used to estimate the return rate of mature salmon: right asymmetry (a predominance of small fish) suggested a low return rate, and left asymmetry (predominance of larger fish) a high rate of return (Poljakov 1975). In the case of juvenile pink salmon, the rate of scale formation was used as an index of feeding conditions

and growth. For this purpose, annually at the end of the first 10 days of July the proportion of juveniles with fully formed scales was identified. This index was significantly correlated ($r = 0.87$; $p < 0.01$) with brood year survival of pink salmon during their life at sea (Chupakhin 1986).

As the example of wild populations of fall chum salmon of Iturup and Sakhalin islands showed (Kayevev 1983, 1985), when fish with a limited population adaptability are exposed to highly variable thermal conditions and low temperature shock, mortality is high. Unfavorable environmental conditions can cause a change in the size structure of fish populations (Kayevev 1983). Chum salmon mortality is highest in coastal waters when water temperatures change rapidly. This mortality is both direct and indirect; indirect salmon mortality results from thermally induced reduction in abundance and availability of their prey. Food availability is estimated from the growth rate of juvenile salmon in different brood generations (Kayevev 1989a, 1989b). The survival rate of brood year-classes is well correlated with variations in this indicator; survival shows an exponential relation to food abundance. This method of predicting survival has permitted a five-fold increase in precision in estimates of numbers of salmon in general, and a 2.5-fold increase in the precision of predicted spawning escapement numbers.

With water temperatures down to 1–3°C during stormy weather, stomach fullness indices of older juvenile salmon differed from those of recent downstream migrants; older fish fed better than recently arrived migrants. At low temperatures, yolk-sac fry fed poorly compared with fish at other stages (Kayevev 1992). Fork length (FL) perfectly corresponded with condition factor and stomach fullness in all groups including those migrating downstream and those in coastal waters. The analysis of the condition factor variability of juveniles also supports the assumption of a critical situation among juveniles at this early marine stage and particularly juveniles with remnants of yolk sac. Critical condition threatening survival can therefore arise both from poor food availability and from low temperatures resulting in poor feeding.

Juvenile salmon in coastal waters feed selectively, especially immediately after switching to exogenous feeding. This was concluded from analysis of food composition both in different coastal locations and at different times of day. The stage of tide also influenced food composition (Karpenko 1979, 1981; Kayevev et al. 1993). As juveniles grow they observe both total coincidence of the food composition and plankton composition and their differences. Food selectivity depends first on improved swimming and hunting abilities as juveniles grow, and is reflected not only in the plankton composition of their diet, but also the variety of species consumed other species than plankton. The influence of broad-

ened ocean diet is apparent from higher fat content. Scale growth can also be used to successfully estimate abundance of various brood years, and the numbers returning to spawn (Kayevev 1989a, 1994). Research into the ecology of juvenile salmon during early marine life reduced the error in spawning escapement estimates of chum salmon to Iturup Island by a factor of 1.7. A similar improvement in estimates was realized for Iturup Island pink salmon (Chupakhin 1986).

Sakhalin Island chum and pink salmon

Investigations have been conducted in three coastal areas of the Island; the south-west, the south-east including Terpeniya Bay, and the north-east. Hatchery salmon production has been developed more intensively at Sakhalin Island than in any other region of Russia, and a major objective of work on the ecology of juvenile salmon has been to assess the survival of both wild and hatchery produced salmon in shelf waters. A second objective was to assess the productivity of coastal waters to determine the carrying capacity for and distribution of salmon in various areas of the Sakhalin region. Chum and pink salmon have been the major species of investigation.

The first systematic investigations of chum and pink salmon biology in south-west Sakhalin were carried out by Shershnev (1971a) from 1964 to 1970. The goal was to study habitat requirements, migration, behaviour, growth and development patterns, and causes of mortality in the coastal waters of the area. Studies were conducted not only in areas of natural reproduction, but in areas near hatcheries. Results have been published in a number of articles in journals on the ecology, early marine life and limiting factors of chum and pink juvenile salmon. The investigations have also provided specific values on juvenile mortality, particularly mortality from predation, at various life stages in coastal waters (Shershnev 1968, 1970, 1971b, 1973, 1974, 1975).

Juvenile salmon inhabit coastal waters of southwestern Sakhalin Island during May and July, in some years remaining until mid-August. During that time, zooplankton reach high biomass densities of 300–530 mg/m³ both in shallow coastal waters and in bays (Shershnev 1971a). Harpacticoida are the most abundant zooplankters during the first weeks after juvenile salmon arrive, and make up the bulk of their diet. Later these juveniles begin to consume mysids, gammarids, and fish larvae, primarily in bays. Immediately after downstream migration, more than half the juvenile chum salmon's food by weight is insects, and these also make up 23.3% of the juvenile pink salmon diet (Shershnev 1975). Stomach fullness of the fish is also high, reaching 450⁰/₀₀₀. Favorable temperature during spring and summer, and good food availability promote growth, development

and survival of juveniles in that brood year. As juvenile chum and pink salmon grow, they migrate to bays and begin to prey on larger organisms (mysids, euphausiids), smaller prey (haracticoida) becoming less significant. At the same time, however, competition for food both within and among species intensifies.

Juvenile pink and chum salmon migrating downstream in April and May at a size of 30–40 mm double their fork length and increase their weight 8–9 times by mid-August. The highest growth rates occur after their migration to bays and open coastal waters (Shershnev 1973). By this time chum salmon have 8–9 scale circuli, and pink salmon 6–8 circuli, the fastest rate of circuli formation coinciding with the fastest growth from July to August. During this feeding period, the condition factor of juvenile chum salmon in coastal waters increases from 1.04 in May to 1.15 in August (Shershnev 1975).

As these juvenile salmon grow, predation by their chief predators, immature white spotted char (*Salvelinus leucomaenis*), saffron cod (*Eleginus gracilis*) and sculpins (*Cottidae*), decreases. These predators consume more than 11% of a year class present in shallow waters, and about 31% in bays; white spotted char are responsible for about 80% of this predation (Shershnev 1975). In offshore waters, juvenile chum salmon are found in the stomachs of greenlings (*Hexagrammidae*) and rockfishes.

In the late 1980s, with the reconstruction of the majority of Sakhalin Island's salmon hatcheries, investigations into the early marine life of salmon in the area resumed (Ivankov et al. 1999), particularly in areas with hatcheries. The major goal of the investigations was to assess the carrying capacity of coastal waters in order to improve the efficiency of hatchery use. Research results achieved not only this goal, but also provided information on comparative feeding conditions for juvenile salmon over a period of twenty years.

In waters of south-east Sakhalin Island and in Terpeniya Bay, work was conducted during two periods, the 1970s, and late 1980s to 1990s. During the earlier period, juvenile salmon were studied during their migration from coastal areas to open waters (Shershnev et al. 1982). Later, emphasis was placed on the ecology of juvenile salmon in estuaries and coastal waters (Shubin 1994; Shubin et al. 1996; Ivankov et al. 1999). The major goal of the investigation was to assess carrying capacity of coastal waters and feeding conditions for juvenile salmon, again for the purpose of improving the efficiency of salmon hatcheries. The effect of predation on survival of both hatchery and naturally produced fish was also investigated.

In Nyiskiy Bay (north-east Sakhalin Island) the main purpose of investigations in the 1970s was to document predation on juvenile salmon and their

resulting survival (Churikov 1975). Later, in the 1990s, trophic relations of juvenile chum salmon and their survival in coastal waters became the main focus of investigations (Ivankov et al. 1999).

Both naturally and hatchery produced juvenile salmon remain in Mordvinov Bay when conditions for feeding in coastal waters, particularly for pink salmon, are unfavorable. Pink salmon as small as 39 mm and 380 mg can be found 8 km offshore by the end of June. They are found in the stomachs of white spotted char, sculpins, saffron cod, and rock greenling (*Hexagrammus lagocephalus*); the first two species are major predators (Ivankov et al. 1999). A portion of both naturally and hatchery produced juvenile salmon from this region migrate through the brackish waters of Tunaycha Lake, but while pink salmon pass straight through, chum salmon remain there to feed. Juvenile chum remain after mid-May for a couple of months, and grow 39 mm in length (from 45.5 mm to 83.9 mm) and 3.7 g in weight (from 0.634 g to 4.389 g) during that time. Incidentally, on July 7, 1990, six juvenile (1+ years) sockeye salmon (*O. nerka*), that had been released from the Okhotsky hatchery, were caught in this lake.

In more northern areas of eastern Sakhalin Island, juvenile salmon are usually smaller, and feed and grow near the shore for only a short period. In this area, juvenile pink salmon predominate in catches (Ivankov et al. 1999). Chum salmon juveniles are usually bigger, and, though not as numerous, are caught in larger numbers in some net catches. Juvenile chum salmon feed in Nyisky Bay, increasing in fork length by 25 mm, and in weight by more than 1 g. Judging from the sizes of juveniles in this Bay, they remain 1.0–1.5 months, which is longer than they remain inshore at south-western Sakhalin Island (Andreyeva et al. 1994).

Sakhalin Bay chum and pink salmon

The chief objective of research in this area was to assess predation and survival on juvenile chum salmon from the Amur River during their migration to Sakhalin Bay. The work was conducted between 1986 and 1993, but most results were obtained in the early 1990s (Karpenko and Rosly 1989; Rosly and Novomodny 1996). These results indicated that, of all the possible predators in the Bay, the most important on post-migrant juvenile chum and pink salmon was Arctic lamprey (*Lampetra japonica*), which consumed, in some years, up to 93–96% of the juvenile population.

Arctic lamprey probably greatly reduce salmon stocks not only from the Amur River, but also from the Sea of Okhotsk and north Sakhalin Island because the migration paths of these stocks are similar. Lamprey begin preying on juvenile salmon in the Amur estuary, and continue through the Amur Strait and

Sakhalin Bay where different stocks of fish mix. Predation rates increase here. Because migrating salmon are in contact with lamprey for 1.5–3.0 months, reduction of these stocks may also be significant (Rosly and Novomodny 1996).

Predation on juvenile salmon by other species, Arctic smelt (*Osmerus mordax dentex*) and Ussuri whitefish (*Coregonus ussuriensis*) is less than that by lampreys. Exposure to these predators is usually relatively short, from mid-May to June, and in June and July these predators shift mainly to eating mysids, which act as a good buffer between predators and juvenile salmon. Rosly and Novomodny (1996) estimated that in 1989, under the most favorable conditions, predators removed 0.04% of juvenile chum and 0.15% of pink salmon while they were in the lower Amur River and its estuary.

Salmon of the north coast of the Sea of Okhotsk

The major goal of research in this area was to assess feeding conditions in some bays during construction and operation of the salmon hatcheries. Data collection began in the early 1980s, before construction of salmon hatcheries (Popov and Semyonova 1983). The most complete set of data was collected from 1988 to 1990 (Afanasyev and Mikhailov 1994; Afanasyev et al. 1994a, 1994b). The work was conducted both close inshore and in offshore waters in the open area of Tauyskaya Guba. Feeding, distribution, migration and growth of juvenile chum and pink salmon were studied during the first weeks of marine life. Results assessed feeding and survival, and permitted the development of recommendations to improve hatchery practices concerning optimum production capacity, feeding methods, and timing and sizes of releases from hatcheries.

Downstream migration of juvenile salmon begins here in the second week of May, and lasts until the end of June or July. Usually juveniles migrate both west and east along the coast. In rivers that have no estuaries, juvenile salmon move immediately to offshore waters, returning with incoming tides. Juvenile salmon from the Tauy and Motykleyka rivers fed in the tidal zone along the coast in June and July. They remained in the coastal waters of the Tauyskaya Guba a little more than 2.5 months on average; as they grew, they moved to outer, more open waters. Stocks disperse during this movement (Afanasyev et al. 1994a).

Downstream pink salmon migrants averaged 30 mm fork length and 152 mg; juvenile chum salmon were 35 mm and 321 mg. After a short adaptation period with low growth, both species began to grow rapidly in June and July, chum salmon in the Arman sky estuary increasing from 36 to 50 mm and from 317 to 1017 mg. In coastal waters to the east and west of the Arman River estuary, juvenile pink

salmon increased in length by a factor of 1.7 (from 32 to 54 mm) and in weight by a factor of 8.3 (from 147 mg to 1217 mg) between the time they migrated from the river and arriving in the deep waters of the Tauyskaya Guba. The biggest juvenile pink salmon was captured in the Tokarev Bay. Over the same path and time, juvenile chum increased in length by a factor of 1.5 (from 36 mm to 54 mm) and in weight by a factor of 4.1 (317 mg to 1310 mg) (Afanasyev et al. 1994b).

The food spectrum of juvenile salmon in the Tauyskaya Guba varied among areas, but remained relatively stable with time. Juveniles began to consume small harpacticoida, and shifted to larger organisms, gammarids, calanoida, mysids and other crustaceans, as they grew. The most commonly eaten organism was harpacticoida, followed in order by fish larvae and eggs, calanus, amphipoda, decapod larvae, and mysids.

Growth and food consumption generally varied together among areas. For example, in the Olskaya group of rivers, the daily growth of juvenile pink salmon was 5.1% at a daily ration of 10.1–13.1% body weight, and in the Arman sky area daily growth was 5.6% at a ration of 11.2–13.2% body weight. Chum salmon in the Olskaya rivers grew at 2.8% daily at a ration of 7.7–9.9% body weight, and in the Arman sky area they grew 3.8% on a daily ration that was 8.5–19.0% body weight (Afanasyev et al. 1994b).

West Kamchatka salmon

Technical difficulties permitted only intermittent investigations into juvenile salmon biology in this area. In 1987–1988 two complete surveys were conducted in the majority of estuaries in west Kamchatka rivers, from the Opala River in the south to Voyampolka River in the north (Karpenko 1998). In 1990–1992, detailed surveys were conducted in the estuaries of the Bolshaya River (Maximenkov and Tokranov 1994). Feeding, distribution, behaviour, and feeding-growth patterns were studied. Some predatory fish were identified as well. More recently, juvenile salmon were occasionally sampled in the estuaries of some rivers, mainly the Bolshaya River (Table 1).

Juvenile pink salmon, while small immediately upon leaving the estuaries, migrate great distances offshore (Karpenko and Safronov 1985). Juvenile chum salmon appear in coastal waters later, and at a larger size. Juvenile coho (*Oncorhynchus kisutch*), sockeye and chinook (*O. tshawytscha*) salmon migrate downstream at the same time as chum salmon, and co-habit coastal waters for a long time. Because individuals of these species live to different ages, fish of various ages are found in coastal waters at different times. The last to appear are chinook salmon, of which juveniles of age 0+ sometimes make up more

than 50% of all juvenile chinook salmon present. In V.N. Leman's opinion (VNIRO, Verkhnyaya Krasnoselskaya Str. 17, Moscow, personal communication), downstream migration by juvenile chinook salmon age 0+ is usual.

Most juvenile pink salmon migrate to coastal waters in June, and in the beginning of July they move offshore, remaining only a short time in shallow water. In rough seas, juveniles are found deeper. In July, juvenile chum and coho salmon predominate in western Kamchatka river estuaries; in some of these, juvenile masu salmon (*O. masou*) also occur. Age structures of juvenile sockeye and chinook salmon usually include 0+ and 1+ ages, and coho and masu three ages (0+, 1+ and 2+). In some areas, 0+ juveniles of these species are by far the most numerous.

The appearance of the different species in coastal waters is determined by conditions at the time they pass through the estuaries, particularly in the Bolshaya River. This timing influences subsequent feeding, growth and migration of each species in coastal waters. Species that migrate downstream at a young age when small (pink, sockeye and chum salmon) are planktivores and remain for a relatively long time in coastal waters; those species that migrate downstream at an older age (coho and chinook) are larger, eat bigger prey, and migrate offshore sooner.

East Kamchatka salmon

Avacha Bay and the Kamchatka River estuary are the main locations for juvenile salmon in east Kamchatka, and their biology was investigated here and in coastal waters of north-west Kamchatka. Results were published in a monograph (Karpenko 1998), and therefore only some of the most recent data are reviewed here.

The ecology of juvenile salmon in Avacha Bay has been investigated from time to time since the 1930s (Baranenkova 1934; Gribanov 1948; Karpenko 1979; Safronov 1998; Vasilets et al. 1998). Initially feeding and survival of juvenile wild salmon was investigated. In the mid-1990s, two salmon hatcheries began operating in the watersheds of the Avacha and Paratunka rivers. These two hatcheries have been releasing about 30 million juveniles annually. Since the mid-1990s, therefore, the Avacha Bay ecosystem has been investigated because of its importance as a feeding area for various species of juvenile salmon.

Juvenile salmon were also occasionally sampled in the estuaries of the Kamchatka River. The purpose was to familiarize researchers with the area, and to study its features particularly as they affected sockeye salmon (Bugaev and Karpenko 1983; Bugaev 1995).

The most regular and long standing investigations on the ecology of the five species of Pacific salmon (pink, chum, sockeye, coho and chinook salmon) have been conducted in the south-west Bering Sea (Karpenko 1991, 1998). Data were first obtained from this area in the 1960s (Andrievskaya 1968; Nikolayeva 1972). For more than 20 years, starting in 1975, annual ichthyological surveys have been conducted here. Special methods were developed and later applied in some other far eastern areas (Karpenko et al. 1997). Investigations conducted in this area evaluated the role of early marine life on later abundance of adult salmon of that brood class. The role of major limiting factors was also investigated. A method of correcting fishing estimates nearly a year prior to when fishing occurs was also developed for pink salmon (Karpenko 1982a, 1982b, 1982c, 1983, 1985, 1989, 1994). In addition, a preliminary database for computation of production of crustacean forage species and evaluation of the role of juvenile salmon in coastal ecosystems was compiled.

To estimate the effect of feeding by juvenile salmon on the food base, the diet and time each species inhabited specified areas of coastal waters was considered. Over a 20 year period, the total stock of zooplankton in the upper 10 m of Karaginskii Bay in June–August was estimated to have increased from 7,760 to 34,640 tons. Food requirements of juvenile pink, chum and sockeye salmon, the main planktivores, were 18.2 to 12,032.5 tons to be consumed from 335.6 to 20,756.3 tons of zooplankton. The juvenile salmon therefore ate between 0.23% and 46.2% of the total stock of zooplankton, pink salmon being the main consumers (up to 45.1% of the total stock) (Karpenko et al. 1999) (Table 2).

The main fish species in the north-eastern Kamchatka estuaries and coastal waters were flounders, *Pleuronectidae* (frequency, 50%), three-spine stickleback, *Gasterosteus aculeatus* (47.1%) and juvenile chum salmon (36.9%) (Vasilets et al. 1999). Species of juvenile salmon other than pink, chum and sockeye occur less frequently and remain for only a short time. They therefore have less effect on these coastal communities.

Feeding periods and growth patterns, distribution, and migration have therefore been documented for the majority of areas, providing information on factors affecting survival of juvenile salmonids and the abundance of their resulting brood classes (Table 3).

Autumn Assessment of Juvenile Salmon

The studies of Pacific salmon that have continued the longest are those on their biology in autumn following the period of highest mortality. These studies began in the 1960s, though some preliminary

Table 2. Consumption of forage resources by Pacific salmon juveniles during sojourn in Karaginskii Bay (June–early August).

Year	Parameters	Forage resources & consumption in tons	% of resource consumed
1985	Forage resources	7,763.83	-
	Consumption pink	10.22	0.13
	chum	7.96	0.10
	Total	18.18	0.23
1987	Forage resources	19,120.24	-
	Consumption pink	107.91	0.56
	chum	115.61	0.60
	sockeye	11.17	0.06
	Total	234.69	1.22
1988	Forage resources	26,007.60	-
	Consumption pink	11,735.05	45.10
	chum	297.43	1.14
	Total	12,032.48	46.26
1992	Forage resources	34,229.07	-
	Consumption pink	11,058.27	32.30
	chum	85.51	0.26
	sockeye	5.44	0.02
	Total	11,149.22	32.58
1993	Forage resources	34,642.55	-
	Consumption pink	156.38	0.45
	chum	58.02	0.17
	Total	214.40	0.62

Table 3. Food and predators of pink and chum juveniles in the coastal waters of Russia's Far East seas.

Area and salmon spp	Feeding Period	Food Item	Predators	% reduction of salmon
Primorye, chum	April–May (June)	Copepoda	-	-
Iturup Island, pink	May–June	Copepoda	-	-
Iturup Island, chum	May–June	Copepoda	-	-
S-E Sakhalin, pink	June–July	Copepoda, fish eggs, Hyperiididae	White spotted & Arctic char, Arctic smelt	-
S-E Sakhalin, chum	June–July	Copepoda, fish eggs, Hyperiididae	White spotted & Arctic char, Arctic smelt	-
S-W Sakhalin, pink	May–June	-	White spotted char, saffron cod, sculpins	-
S-W Sakhalin, chum	May–July	Harpacticoidae, Amphipoda, Insecta	White spotted char, saffron cod, sculpins	41.7
N-E Sakhalin, pink	May–June	-	Arctic smelt	7.7–51.6
N-E Sakhalin, chum	May–July	Mysidae, Insecta, Hyperiididae	Arctic smelt	11.1
Sakhalin Bay, pink	May–July	-	Arctic lamprey, Arctic smelt, Ussuri whitefish	67–96
Sakhalin Bay, chum	May–July	-	Arctic lamprey, Arctic smelt, Ussuri whitefish	28–93
North coast Sea of Okhotsk, pink	May–July	Harpacticoidae, Amphipoda, Copepoda	Arctic smelt, Arctic char	-
North coast Sea of Okhotsk, chum	May–July	Amphipoda, Insecta, Harpacticoidae	Arctic smelt, Arctic char	-
West Kamchatka, pink	May–July	Copepoda, Harpacticoidae	White spotted char, Arctic smelt, Kamchatka trout*	40–50
West Kamchatka, chum	May–July	Harpacticoidae, Insecta	White spotted char, Arctic smelt, Kamchatka trout*	-
Avacha Bay, pink	May–July	Copepoda, Insecta	-	-
Avacha Bay, chum	May–July	Insecta, Copepoda	-	-
Karaginskii Bay, pink	June–July	Copepoda, Harpacticoidae, fish larvae	Arctic smelt & char, white spotted char	11.2–28.8
Karaginskii Bay, chum	June–July	Insecta, Cumacea, Gammaridae	Arctic smelt & char, white spotted char	1.8–16.8

**Oncorhynchus mykiss* or *Parasalmo mykiss*.

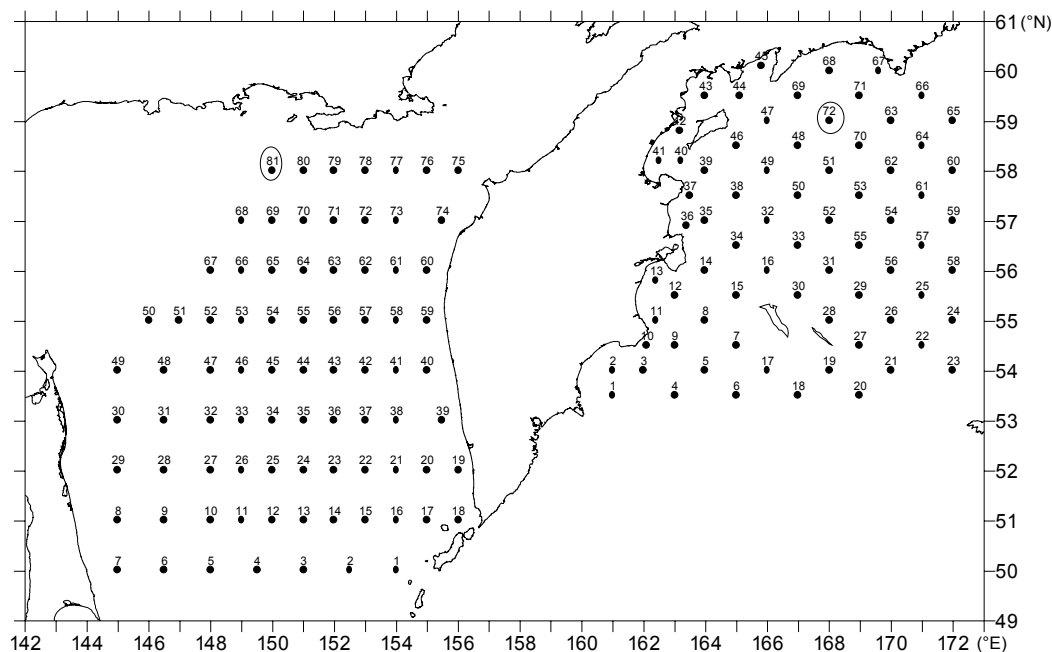
data were collected earlier. Small mesh drift nets were used initially to catch juvenile salmon until 1981, when pelagic trawls were used (including large trawls, 108/528 and 118/620 m). The work has been conducted by two institutions, KamchatNIRO and TINRO-centre, and surveys have been carried out in the waters of the east Sea of Okhotsk, west Bering Sea, east Sea of Japan (through 1976), the Kuril area, and the north-west Pacific. Trawl surveys have been conducted in a standard pattern of stations (Figs. 1, 2).

Since the 1960s KamchatNIRO has investigated juvenile salmon biology during fall in Kamchatka waters of the Sea of Okhotsk and the Bering Sea, and in winter in the eastern Sea of Japan. Originally these surveys were combined with investigations of anadromous salmon species when small mesh (20–40 mm) drift nets for catching juveniles were added to gear used to catch adult salmon. Beginning in the 1970s, the work was conducted from vessels equipped only with small mesh drift nets which were fished in late August to November (January to March in the Sea of Japan), when juvenile salmon had already migrated away from coastal waters. Due to a shortage of needed equipment, catching juvenile salmon with drift nets was labour-intensive. It required good weather, and it often was unproductive. The data were not always sufficient for correctly estimating brood abundance. However, the main features of the ecology of all salmon species were identified during that time; habitation times, distribution,

migration, feeding, major biological parameters, growth rates, interspecific interactions, and some other features (Andrievskaya 1966, 1968, 1970, 1988; Birman 1969, 1985). However, the problem of brood abundance assessment was not solved. Only with the inauguration of trawl fishing for juvenile salmon did the collection of data on abundance of individual broods of juvenile salmon of the various species become possible.

Trawling for juvenile salmon was conducted for the first time in the Bering Sea in 1981. KamchatNIRO organized an expedition of three vessels. One of them was to catch juvenile salmon with a mid-water trawl of 32.5 m, the second was to use drift nets, and the third was to conduct hydrological and hydrobiological surveys. Prior to 1985 KamchatNIRO used variously modified trawls to try to catch juvenile salmon near the surface. In 1985 the Kamchatrybprom Laboratory of Fishing Gear for Commercial Fishing invented a special pelagic trawl 54.4/192 m. Since then, this trawl has been used in all areas to assess juvenile salmon (Fig. 2). Data collected using these trawls are remarkably representative, allowing investigators to estimate the number and production of salmon in different feeding areas. This new gear allowed Kamchatka scientists to obtain better information on juvenile salmon biology in autumn. Most important, it permitted the development of a method of assessing abundance that has been used to correct fishing forecasts 8–9 months prior to fishing (Karpenko et al. 1997, 1998).

Fig. 2. Location of trawl stations in the Sea of Okhotsk and Bering Sea in September–October 1985–2000 (cruises by KamchatNIRO). At stations 72 and 81 (ringed), eight trawl samples were collected over a 24-hr period (day and night); at all other stations only one trawl sample was taken.



The results of research on juvenile salmon in autumn using close-mesh drift net catches are summarized by Birman (1969, 1985). Birman described the length of time juvenile salmon remained in different zones of the coastal waters of the Sea of Okhotsk and Bering Sea, their migrations, growth, feeding and other factors that influence the numbers and productivity of each brood class. A comparative analysis of juvenile growth rates in different feeding areas showed regional differences arising from the particular food resources and predator abundance. Later research determined that growth rates were typically higher in the Okhotsk Sea compared with those in other areas of the north Pacific Ocean (Karpenko 1987b). Most planktivorous fish in this area, i.e., pink, sockeye and chum salmon, consumed those organisms that had the highest caloric content: crustaceans—hyperiids, *Parathemisto japonica*.

Estimated abundance of juveniles in the fall were used to correct commercial forecasts of pink salmon approaching their spawning areas in north-eastern and western Kamchatka (Karpenko et al. 1998). Note that if in one area the forecast correction was relatively small because of a local isolated stock, in the Sea of Okhotsk juveniles congregated from different origins for fattening: West Kamchatka, East Sakhalin, Magadan area, Japan etc. Usually the captured juveniles are from mixed stocks, and cannot be identified as to origin. This requires a special systemic analysis to separate and estimate the numbers in each stock, and the use of such techniques is not always successful (V.G. Erokhin, KamchatNIRO, 18, Naberezhnaya Str., Petropavlovsk-Kamchatsky, personal communication). In addition, methods used to estimate mortality of pink salmon at different stages in their life at sea suggested that mortality in some broods changed from 55.4% to 95.8% after migration offshore (Karpenko 1995, 1998). Data on numbers of other juvenile salmon species are also used to estimate the numbers in brood classes and the conditions promoting survival at sea, as well as to investigate the role of juvenile salmon in ocean ecosystems.

TINRO-center began investigations of juvenile Pacific salmon biology with its first voyage to the north-west Pacific Ocean in the winter of 1985–86 (Erokhin 1990; Erokhin et al. 1990). A large pelagic trawl (112/528 m) was used for fishing. Work in the area continued until 1992; since 1988 the area covered was expanded to the north-east Pacific Ocean (Table 1).

In the autumn of 1986, with its voyage to the western Bering Sea, TINRO-centre began assessing juvenile salmon (Shuntov 1989b). However, only two expeditions have been sent to this area. Since 1990, the Sea of Okhotsk and Pacific waters around the Kuril Islands have become major areas of investigation (Shuntov 1989a) (Table 1). These investigations not only enabled the gathering of good informa-

tion on ecology of Pacific salmon during autumn and winter, but also regularly collected data on feeding of juveniles, which was important for prediction of adult salmon abundance (Shuntov et al. 2000). It was also found that in some years pink salmon in particular remained for the winter in the southern part of the Sea of Okhotsk (Radchenko et al. 1991, 1997; Zhigalov 1992).

Data collection during TINRO-centre voyages in the fall was thorough in order to obtain a variety of data on ecosystems of the far eastern seas and north-western Pacific Ocean. To this end, the major areas of the Sea of Okhotsk and Bering Sea where juvenile salmon feed and fatten were subdivided into smaller biostatistical areas (Shuntov 1989a, 1989b). The estimated numbers of juvenile salmon so obtained were used to correct estimates of returning mature salmon, which were later further refined using the results from spring surveys of anadromous maturing salmon (Shuntov and Chigirinskii 1995). To conduct this detailed work, scientists from different fisheries institutes, and also from the Russian State Academy, were invited to participate.

Data collected over many years from these expeditions to the Sea of Okhotsk shed light on the role of age 0+ pink and chum salmon in the trophic structure of the epipelagic zone. In the fall and winter of 1994–95 these juvenile salmon consumed mainly hyperiid amphipods — 3–4.3 thousand tons or 35.5–42.3% of their daily production (Dulepova 1998). Daily consumption of other organisms, with the exception of euphausiids, did not exceed 3% of daily production. Interspecific competition with other species that consume the same crustacea could be intense.

By September, juvenile salmon in both coastal and open waters of the Sea of Okhotsk are a mix of stocks from different origins. The identification of their origins helped to confirm the distribution and migration routes of the different stocks of juvenile pink salmon that had been suggested from classical fisheries research (Varnavskaya et al. 1998; Varnavskaya 2001). At first juveniles migrate along the coasts of origin, then later move offshore (Shuntov 1994a). As the water cools, the fish migrate to the southern Sea of Okhotsk where some remain over winter (Radchenko et al. 1991, 1997; Zhigalov 1992). Estimates of abundance of juveniles in the Sea of Okhotsk over many years have permitted forecasts of return rates of spawners (Radchenko 2001), and elucidated their return migration routes to different coastal areas (Shuntov et al. 2000).

Voyages to the Bering Sea were made periodically in 1986–1992, but did not always cover the fall period optimally. As a result the data were not as satisfactory as those from the Sea of Okhotsk, but some worthwhile conclusions were drawn nevertheless (Radchenko 1994a; Shuntov 1994b; Sobolevsky

et al. 1994). For instance, juvenile pink salmon were found to migrate off north-eastern Kamchatka coasts in wide fronts, and to spread along the Komandorskaya gully in a generally south-eastern direction. Shuntov (1994a) stated that "there are no noticeable pink migrations to the Kuril waters". The last surveys by KamchatNIRO confirmed this. Juvenile pink salmon usually migrate in two or three directions; there are one or two routes heading southeastward, and a third, with the smallest fish, heading along the Kamchatka coast (Smorodin et al. 2001). Migrations in similar directions are followed by other salmonids, in particular by juvenile chum and sockeye salmon. Sockeye salmon have somewhat different feeding, growth, and distribution patterns from other species (Radchenko 1994b; Sobolevski et al. 1994; Karpenko 1998).

Juvenile Pacific salmon, when surveyed by trawl under optimal conditions (in September), provide data not only for estimating a brood year's abundance, but in some cases also for estimating mortality over the entire marine life, including before fall migration to wintering grounds. For instance, Karpenko and Smorodin (2001) determined from two surveys in September–October, 2000, that monthly mortality rates of juvenile pink and chum salmon were about 3%.

Investigation of Coastal and Marine Ecosystems

Data obtained on the biology of Pacific salmon during their early marine and first autumn of life permitted an evaluation of their role in coastal marine ecosystems in some regions. For instance, detailed surveys in the estuary of the Bolshaya River (west Kamchatka) revealed the interrelations among species in this watershed, including major trophic interrelations (Tokranov 1994; Maximenkov and Tokranov 1999, 2000). Three ecologically distinct groups of fish make up the community in the estuary; permanent inhabitants, 19.3%; migrants, 35.5%; and temporary residents, 45.2%. Six species are the main representatives of the fish community of the Bolshaya River estuary: starry flounder (*Platichthys stellatus*), belligerent sculpin (*Megalocottus platycephalus platycephalus*), pink and coho salmon, threespine stickleback (*Gasterosteus aculeatus*), and ninespine stickleback (*Pungitius pungitius*). Juvenile salmon play an important role in interspecies relations despite their short time in the estuary, but starry flounder and threespine stickleback (permanent residents) are the main consumers there.

Similar investigations have been conducted in Avacha Bay since the 1990s. To date they have provided preliminary data on trophic relationships among fish in this watershed (Vasilets et al. 1998). As in the Bolshaya River estuary, threespine stickleback and belligerent sculpin are the main consumers.

In addition, some data have been obtained for the first time on feeding interactions between juvenile wild and hatchery produced salmon (Karpenko 1987a, 1998; Karpenko and Safronov 1999). This research has proven timely because of the increased releases from two hatcheries, Paratunsky and Ketkino, which have recently reached full production capacity. So, estimated carrying capacity of Avacha Bay is very important now.

Year-to-year investigations on the biology of juvenile salmon in coastal waters of southwest Bering Sea revealed the role of some fish in ichthyocenosis (Karpenko and Maximenkov 1988, 1990). These investigations also showed the scale of predation by juvenile salmon on various species of crustaceans and other animals inhabiting coastal waters, and allowed analysis of the predator-prey relationship (Karpenko 1982a, 1994, 1998; Karpenko et al. 1999). Juvenile salmon were found to consume about one third of the total stock (biomass plus production) of planktonic crustaceans in the area; at the same time about one third of each year's migrating yearling pink and chum salmon were consumed by predators. These findings emphasize the need for assessment of the production capacity of areas where salmon hatcheries are to be installed and operated (Karpenko and Safronov 1999).

From 1% to 63% of juvenile pink salmon migrating downstream in the Khailyulya River are consumed by Arctic char (*Salvelinus alpinus*) (Tyller 1999). This predator, together with Arctic smelt (*Osmerus mordax dentex*) and white spotted char (*Salvelinus leucomaenis*) consume sufficient juvenile salmon in estuaries and marine coastal waters over 1.5–2.0 months to reduce their numbers (Karpenko 1998). Both food supply and predators, therefore, regulate salmon stock abundance in the marine environment.

The most successful assessments were those conducted on juvenile salmon in the autumn by TINRO-centre scientists. Detailed data were collected on abundance and biological state (characteristics) of salmon, as well as on co-habitants in and physical characters of water masses (Shuntov et al. 1993). The numerical abundance and biomass of major fish species, including their larvae and eggs, as well as the plankton and nekton, were assessed in the majority of areas. This detailed information permitted the tracking of changes in the ecosystems of the far eastern seas and the north-west Pacific Ocean, and the assessment of the effects of these changes (Radchenko 1994a; Shuntov 1994a; Lapko 1996; Dulepova 1997; Shuntov and Dulepova 1997; Shuntov et al. 1997).

In some areas of the Bering Sea during summer and fall Pacific salmon stocks make up 60% of the fish biomass (Radchenko 1994a), of which pink and chum salmon are the main species in the western part

of the Bering Sea, and sockeye, chinook, and, in summer, pink salmon are the main species in the eastern part. Salmon stocks are expanding into the North Pacific Ocean to feed. In the 1990s, their consumption of food organisms increased almost a third in comparison with the 1980s, and it is still increasing owing to immigration of many southern salmon populations to feed.

In the Sea of Okhotsk in the 1980s, salmon stocks comprised about 1% of the total biomass of fish during the summer–fall, and in the early 1990s this increased to 4.6% (Lapko 1996). There followed a period of rapid increase in the stocks of these species, which continues to the present. However, the number of returning adults has fluctuated considerably, especially those of pink salmon even in adjacent years (Shuntov and Dulepova 1997). This is confirmed by the results of the most recent annual trawl surveys by the TINRO-centre (Shuntov et al. 2000; Lapko and Glebov 2001).

FUTURE INVESTIGATIONS

Russian investigations of the marine life of Pacific salmon have identified the major causes of mortality in juvenile salmon, and developed methods of assessment necessary for predicting abundance of returning spawners of the two main species, pink and chum salmon.

Further investigations will address the following four topics.

- 1) Use of defined standard areas for monitoring and identifying causes of mortality, and abundance of each year's brood class. As mentioned above, the methods of investigation can be specific and different for each standard area.
- 2) Assessment of interrelations between wild and hatchery produced salmon in areas where these stocks mix to feed. This work has been done both where hatcheries were already operating, and where their construction was expected. Depending on the specific goals, investigations take the form of monitoring or surveying. The overall goal is to determine what is a rational combination of the two types of salmon production, sustainable natural production and efficient hatchery production.
- 3) Efforts must continue to improve methods of stock assessment of Pacific salmon, through assessment of juvenile abundance in the fall, and to use stocks more efficiently. Mesosurveys are assessments performed in standard near-shore areas that are considered to be the main feeding grounds of specific salmon stocks and populations (e.g., the

shelf waters of east and west Kamchatka, Sakhalin, the north shelf of the Sea of Okhotsk (Fig. 2), etc.). Macrosurveys are assessments in large offshore and oceanic areas (Fig. 1). Mesosurveys occur in August–September, prior to offshore migration, and mixing of juvenile salmon stocks that originate from different reproductive areas. This permits assessment of the abundance of each stock. Macrosurveys are conducted later, in October–November, to obtain data on total abundance throughout a large area such as the Sea of Okhotsk, the Bering Sea, or the north Pacific Ocean. The two types of survey provide important data both for predicting escapement to the commercial fishery, and for evaluating pelagic community interactions.

- 4) Ecosystem studies are the fourth topic of investigation in the marine life of Pacific salmon. Such studies utilize data gathered both during standard monitoring and during investigation of specific components of the ecosystem in the area under investigation.

Integration and organization of the studies on the above topics will continue to contribute to the conservation and efficient use of Pacific salmon stocks in the far east basin.

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Research Conducted by the United States on the Early Ocean Life History of Pacific Salmon

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Abstract: Research on juvenile Pacific salmon in coastal U.S. waters began almost 50 years ago in Southeast Alaska, and has continued somewhat sporadically since then. The National Marine Fisheries Service (NMFS), through its various laboratories in Alaska and along the West Coast of the United States, has done much of the research on the early life history of many Pacific salmon stocks in all habitats of U.S. waters, including their period of residence in coastal and oceanic waters. In addition, several of the leading universities in this region (University of Washington, Oregon State University, University of Alaska) have contributed greatly to our knowledge of salmon in their early ocean residency. Much of the early research was done using fine-mesh purse seines, but recently surface fine-mesh trawl nets and gill nets have been used more widely. A large number of programs are actively sampling in coastal waters at the present time, and the geographic and temporal coverage is the most complete it has ever been. In this paper, we provide a brief overview of many of the studies that have been done, synthesize their major findings, and discuss some of the areas where we believe future efforts should be concentrated.

INTRODUCTION

There has been considerable recent interest by a large number of investigators in the early marine life history of salmonids (*Oncorhynchus* spp.) in the North Pacific Ocean. Some of this interest is derived from the recognition that relatively high rates of mortality occur in salmon in the first few months at sea, a period termed by Hartt (1980) as the “first critical summer”. Indeed, it has been shown that cohort mortality at sea is often equivalent to that in freshwater (Bradford 1995). Much of the current research on salmonids in the ocean has focussed on understanding processes related to this early ocean mortality (Percy 1984a, 1992; Emmett and Schiewe 1997; Brodeur et al. 2000). Such an understanding may lead to better predictability of salmon returns and other management benefits (Bisbal and McConnaha 1998; Beamish et al. 2000).

The purpose of this paper is to review studies on juvenile salmon conducted in coastal waters of the United States. We define juvenile salmon as those

that are in their first year in the marine environment prior to the time that the first marine annulus forms on their scales. Pacific salmon inhabit coastal waters in the Eastern Pacific from southern California all the way to the Beaufort Sea. However, they occur in substantial numbers only from northern California to the Bering Sea, and the geographic coverage of our review encompasses the U.S. continental shelf across this range. Naturally, salmon are highly migratory and do not recognize international boundaries. A substantial amount of research has been done on juvenile salmon in Canadian coastal waters and is reviewed by Beamish et al. in this volume. We will not include studies of immature salmon after their first ocean year or maturing salmon, which were reviewed by Burgner (1992) and Myers et al. (2000). We instead focus on exposed coastal and oceanic regions and semi-enclosed areas such as Puget Sound, the inside waters of Southeast Alaska, and Prince William Sound. The voluminous U.S. studies that have specifically examined juvenile salmon utilization of smaller estuaries are beyond the scope of this review.

Our aim is to highlight studies that have examined abundance and distribution patterns of juvenile salmonids during their early ocean existence. In addition to sampling salmon, most studies collected ancillary data on the biotic and abiotic conditions in which they were caught. Secondary information on the salmon themselves, such as growth, condition, diseases, food habits and stock origin, was also gathered generally at a later period in the laboratory. We cannot cover all these studies in detail; however, we discuss many of them briefly, especially in terms of their contribution to the understanding of salmon survival.

HISTORICAL OVERVIEW OF THE IMPORTANCE OF SALMON TO THE UNITED STATES

Seven anadromous species of the genus *Oncorhynchus* are native to the U.S. waters: sockeye or “red” salmon (*O. nerka*), chum or “dog” salmon (*O. keta*), pink or “humpback” salmon (*O. gorbuscha*), coho or “silver” salmon (*O. kisutch*), chinook or “king” salmon (*O. tshawytscha*), steelhead trout (*O. mykiss*), and coastal cutthroat trout (*O. clarki clarki*). Spawning stocks of sockeye salmon are distributed in U.S. waters from the Columbia River to Kotzebue Sound, Alaska, and the world’s largest spawning population of sockeye salmon is in Bristol Bay, Alaska. Significant spawning populations of chum salmon range from Tillamook Bay, Oregon, to Kotzebue Sound, Alaska. Spawning stocks of pink salmon are distributed primarily from Washington to Norton Sound, and the largest populations are in central Alaska (Prince William Sound and Kodiak Island) and southeastern Alaska. Coho salmon spawning stocks are distributed in numerous streams from Monterey Bay, California, to Norton Sound, Alaska. Commercially important spawning stocks of chinook salmon occur primarily in large rivers from the Sacramento River, California, to the Yukon River, Alaska. The historical distribution of steelhead trout spawning stocks extended from the eastern Bering Sea (north side of the Alaska Peninsula and Unimak Island in the Aleutians) to the California-Mexico border, and the center of abundance is the Columbia River basin and adjacent rivers to the north and south (Burgner et al. 1992). Coastal cutthroat trout are distributed from northern California to Prince William Sound, Alaska.

Pacific salmon have been important to the native peoples of North America as a food for subsistence, a commodity for trade, and a cultural icon for many thousands of years. Sediment core data from salmon nursery lakes in Alaska, spanning the past two millennia, indicate that from AD 1200 to 1900 salmon abundance was relatively high and coincided with human population growth and high use of salmon

fishing gear (Finney et al. 2002). At the time of arrival of the first European explorers, Native American fishermen were using a wide variety of methods to catch salmon, including bare hands, clubs, spears, gillnets, dip nets, traps, and weirs (e.g., Netboy 1974; Roppel 1986; Lichatowich 1999). Annual subsistence harvest in Alaska was probably more than 12 million salmon (Wertheimer 1997). Russian fur traders, established their first permanent settlement in Alaska on Kodiak Island in 1784, and supplied dried and salted salmon to Native American hunters, but their later attempts in the 1850s–1860s to market salted salmon were not successful (Roppel 1986).

The first U.S. salmon cannery began operating on the Sacramento River in California in 1864 and the first salmon hatchery was built on the McCloud River (a tributary of the Sacramento River) in 1872 (Lichatowich 1999). The U.S. salmon canning industry expanded rapidly northward to the Columbia River in 1866, southeastern Alaska in 1878, Cook Inlet and Kodiak in 1882, and Bristol Bay in 1884 (Browning 1974), and followed a boom and bust cycle as natural salmon runs were exploited and depleted. In Alaska, the number of salmon canneries peaked at 159 in 1929, and the salmon pack peaked at 8,454,348 cases canned in 1936 (Freeburn 1976). Commercial fisheries, first established to supply salmon to the canneries, used a wide variety of gear (e.g., beach seines, purse seines, drag seines, gillnets, traps, fish wheels, ocean trolling), and there were often conflicts over catch allocation among fishermen using different gear and between fishermen and processors over salmon prices. As the years passed, improvements in cold storage techniques and transportation systems opened new national and international markets for fresh and frozen U.S. salmon. After World War II, Alaska salmon runs declined, likely due to overfishing during a period of low ocean productivity, but prior to the expansion of the walleye pollock fishery in the 1970s, Alaska’s salmon industry was regarded as the single most valuable U.S. commercial fishery in the North Pacific Ocean (Browning 1974). Sport or recreational salmon fisheries developed concurrently with commercial salmon fisheries.

Historically, ocean salmon fisheries were largely unregulated, and freshwater commercial and sport salmon fisheries were managed by the states. Alaskan fisheries were managed by the federal government from the purchase of Alaska in 1867 through 1959. Since the establishment of the U.S. 200-mile fishery Conservation Zone in 1976, the federal government has managed ocean salmon fishing from 3 miles offshore. The recognition of Native American fishing rights by the federal courts has led to a resurgence of tribal ceremonial and subsistence salmon fisheries since the late 1960s. Treaty tribes in western Washington and major tribes in the Columbia

River Basin are apportioned an equal share of the annual commercial salmon harvest and function as co-managers with the State. Since the 1990s, subsistence fisheries have taken precedence over all other fisheries in federally reserved waters in Alaska, and the federal government now manages these fisheries.

Over the past 200 years, the cumulative effects of overfishing, unfavorable climate, poor hatchery practices, human development, and environmental degradation have resulted in the decline or extirpation of many natural salmon populations. Since 1991, 27 anadromous salmon and steelhead trout stocks in the U.S. Pacific Northwest have been listed as threatened or endangered under the federal Endangered Species Act (ESA). Even in areas with pristine habitats and healthy salmon runs, commercial salmon fisheries are experiencing difficulties because of the loss of foreign markets, overcapitalization of fisheries, competition with farmed salmon, increasing management restrictions, and reduced harvests forced by the ESA. The estimated landed value of the Alaska commercial salmon catch has declined from \$489 million in 1994 to \$141 million in 2002 (Alaska Department of Fish and Game (ADFG), Commercial Fisheries, Juneau, USA, personal communication). Public awareness and understanding of the ecological and economic problems facing the salmon industry are now at an all-time high. New sectors of the industry involving marketing, research, management, conservation, restoration, education, information, and ecotourism are developing. Perhaps more than ever before, Pacific salmonids seem to be important to the United States as a natural, economic, and cultural resource.

TRENDS IN COMMERCIAL SALMON LANDINGS

In the U.S. Pacific Northwest region (Washington, Oregon, Idaho, and California), commercial landings in metric tonnes of most salmon species peaked prior to 1920, and from then until the late 1980s and early 1990s, there was a decline in chinook, coho, and pink salmon landings, no clear trend in sockeye salmon landings, and chum salmon landings declined until the late 1950s and then increased (Kope and Wainwright 1998; Fig. 1). Over the same period, commercial fisheries shifted from predominantly freshwater (terminal) to ocean (mixed-stock) fisheries, and much of the natural production in this region was replaced by hatchery production. In the 1990s, the predominant species by weight in the commercial landings in Washington, Oregon, and California (total of 149,007 mt from 1990 through 1999) were chinook (29%) and chum (27%) salmon, followed by sockeye (20%), pink (12%), and coho (12%) salmon (National Marine Fisheries Service (NMFS), Fisheries Statistics and Economics Division,

Silver Spring, MD, USA, personal communication). There are no commercial salmon harvests in Idaho.

In Alaska, commercial salmon fisheries began in the 1880s and landings increased to a peak of 290,000 mt in 1936, then declined steadily through the 1950s to a level below 100,000 mt (Fig. 2). Conservation measures in the 1960s and favorable climate conditions in the late 1970s led to a sharp increasing trend that continued to the mid-1990s (Wertheimer 1997), with a peak in 1995 at 412,000 mt (ADFG, Commercial Fisheries, Juneau, USA, personal communication). In the 1990s, the predominant species by weight in the commercial landings in the Alaska region (total of 3,318,693 mt from 1990 through 1999) were pink (41%) and sockeye (38%) salmon, followed by chum (14%), coho (6%), and chinook (1%) salmon (NMFS, Fisheries Statistics and Economics Division, Silver Spring, MD, USA, personal communication).

Fig. 1. Time series of commercial catches in metric tonnes from the U.S. West Coast (Washington, Oregon, and California) for the period 1900–2001. The dotted line indicates the long-term mean. The 1900–1980 data are from Shepard et al. (1985) and the 1981–2001 data are from the Pacific States Marine Fisheries Commission PacFIN database.

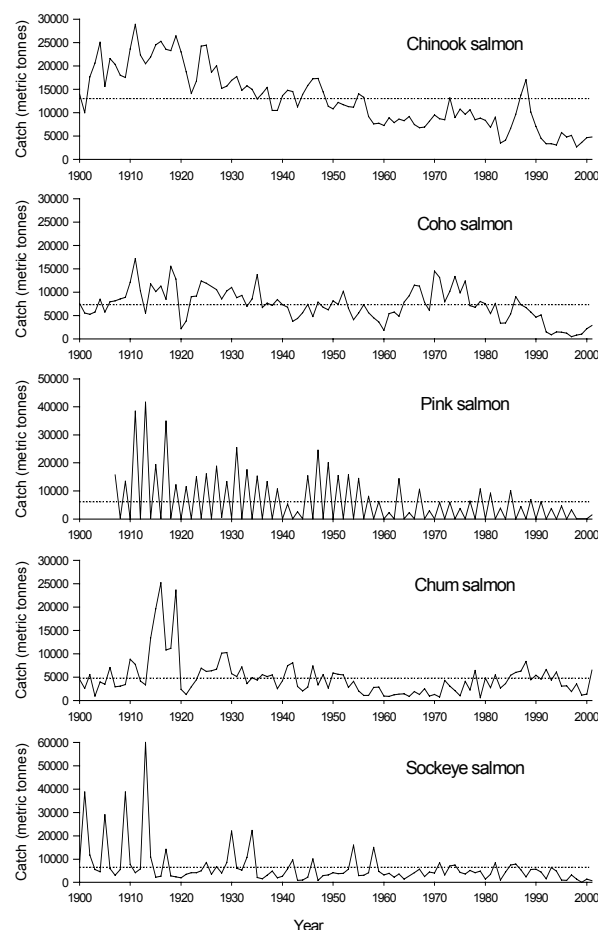
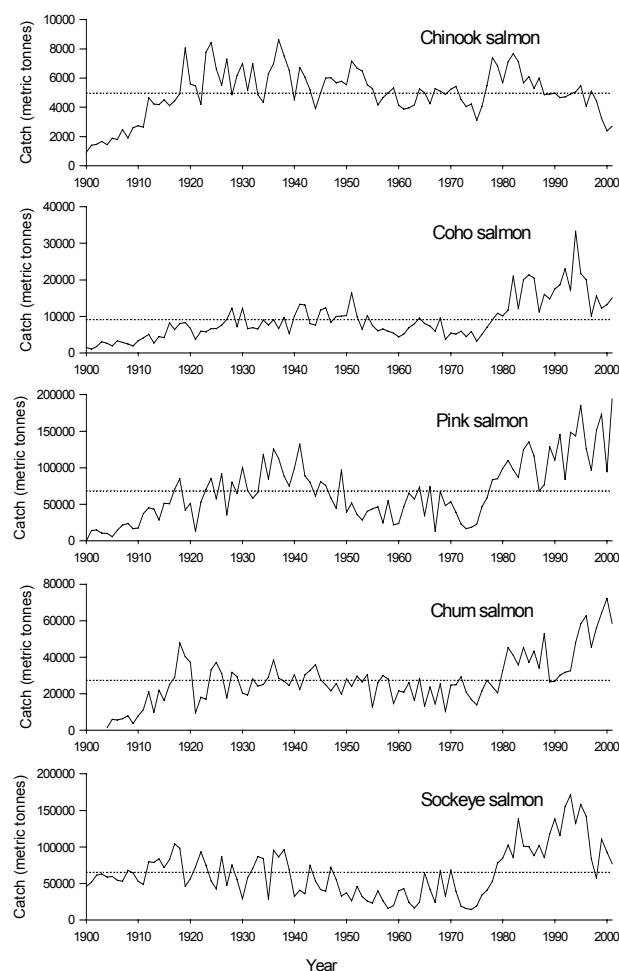


Fig. 2. Time series of Alaska commercial salmon catches in metric tonnes for the period 1900–2001. The dotted line indicates the long-term mean. Data sources: 1900–1949 (INPFC 1979; annual catches in numbers of fish were converted to rough estimates of catches in metric tonnes by using a constant annual average weight of individual fish of each species, calculated from data in Table 93, as follows: sockeye – 2.78 kg, chum – 3.4625 kg, pink (odd years) – 1.6975 kg, pink (even years) – 1.62375 kg, coho – 3.36875 kg, and chinook – 8.3175 kg); 1950–2000 (National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD); 2001 (preliminary data, Alaska Department of Fish and Game, Juneau, AK).



In both the Alaska and U.S. Pacific Northwest regions, precipitous early declines in commercial landings were largely due to overfishing and the lack of adequate (science-based) fishery management before the 1950s (Royce 1988). The two regions also seem to have inverse salmon production regimes linked to climate, and, in particular, to wind stress at the ocean's surface (e.g., Francis and Sibley 1991; Mantua et al. 1997; Hare et al. 1999).

STATUS OF NATURALLY SPAWNING STOCKS

California

Mills et al. (1997) reviewed the status of naturally reproducing California salmon and steelhead populations. Virtually all stocks had declined to record or near-record low levels from 1980 to 1995. Klamath and Sacramento basin fall-run chinook salmon were consistently below escapement goals. The Sacramento winter-run chinook salmon was listed under the ESA as threatened in 1990 and endangered in 1994. Spring run chinook salmon were extinct in the San Joaquin River basin, and there were few spawners in the Klamath, Smith, and Sacramento river basins. Many steelhead trout stocks in California were also close to extinction. Coastal cutthroat trout were depleted. Coho salmon spawners (historically near 1 million fish) had decreased to approximately 5,000 natural spawners per year. A few chum salmon, never a significant native species in California, still remain in the Sacramento River basin and Trinity River. Historically small runs of pink salmon in the Sacramento and Russian rivers are probably extinct.

Oregon and Washington

Kostow (1997) reviewed the status of salmon and steelhead trout in Oregon in the early 1990s. Sockeye and chum salmon populations were depressed or nearly extinct throughout their range in Oregon. The status of chinook and coho salmon populations varied by geographic region. Along the mid- to north coast chinook salmon populations were considered to be in good condition, while they were depressed on the south coast, and in the Columbia and Snake rivers. Many coastal populations of coho salmon were small and declining, and Columbia River Basin coho salmon populations were depressed to extinct. Most coastal and inland steelhead trout populations were stable or slightly declining. The run sizes of most species of salmon and steelhead trout in Washington State increased through the 1970s and 1980s, and then declined in the 1990s (Johnson, T.H., et al. 1997).

Idaho

Hassemer et al. (1997) reviewed the status of Idaho salmon and steelhead trout. All naturally reproducing anadromous sockeye salmon, chinook salmon (spring, summer, and fall), and steelhead trout populations in the Snake River, except Clearwater River drainage chinook salmon and Snake River steelhead trout, have been listed as endangered under the ESA.

Alaska

Wertheimer (1997) reviewed the status of Alaska salmon and steelhead trout. In the 1990s, there were predominantly no trends or increasing trends in spawning escapements for all species evaluated. The high productivity of stocks was attributed to pristine rearing and spawning habitats, effective salmon management policies within the state, the elimination of high seas driftnet fisheries, increased hatchery production, and favorable climate conditions.

TRENDS IN CLIMATE, ABUNDANCE, AND BODY SIZE

A growing body of scientific evidence supports hypotheses about the direct and indirect effects of climate change on the ocean production of salmon (e.g., see reviews by Percy 1997; Kruse 1998; Myers et al. 2000; Hare and Mantua 2001; Hollowed et al. 2001). Most U.S. research has focused on two natural climate phenomena that affect the abundance and growth of salmon, the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). ENSO is a short-term climate change event (lasting about 8–15 months) that occurs at irregular intervals (every 3–7 years) and alternates between two phases, the El Niño (warm) phase and the La Niña (cool) phase. Percy (1992) reviewed the effects of the 1957–58 and 1982–83 El Niño events on Oregon coho salmon, which included northward shifts in ocean distribution of juveniles, reductions in ocean growth and survival of juveniles, jacks (precociously mature), and adults, and low fecundity. Although the long-term effects of the 1997/1998 ENSO are not yet understood completely, there were no apparent effects on body size of returning adult coho salmon to the Columbia River as there was in 1983 (Percy 2002).

The PDO is a multi-decadal (20–30 year) ENSO-like pattern of North Pacific climate change (Mantua et al. 1997; Zhang et al. 1997; Hare and Mantua 2001). The PDO seems to drive an inverse relation between salmon abundance in the Alaska and U.S. West Coast regions, e.g., during a positive PDO phase, the abundance of Alaska salmon is high, and the abundance of U.S. West Coast salmon is low (Francis and Sibley 1991; Hare et al. 1999; Hollowed et al. 2001). An abrupt change between positive and negative PDO phases is called a *regime shift*. Conceptual models suggest that an enhanced Aleutian Low (atmospheric) pressure system may be the physical forcing mechanism that links the positive PDO phase to enhanced production of Alaska salmon (Hare 1996; Francis et al. 1998).

A dramatic increasing trend in the abundance of Alaska salmon that began in the late 1970s has been correlated with many factors. Among these are a

change in Alaska salmon management policies, the elimination of Asian high-seas driftnet fisheries, enhancement by Alaska hatcheries, increase in Alaska salmon fishing effort, warm seawater temperatures in the North Pacific, increase in productivity (zooplankton biomass) in the eastern subarctic Pacific, and a regime shift to a positive PDO phase in 1976–77 (e.g., Rogers 1984; Rogers and Ruggerone 1993; Brodeur and Ware 1995; Farley and Murphy 1997; Mantua et al. 1997; Wertheimer 1997; Downton and Miller 1998; Eggers 1998). Hare and Mantua (2001) hypothesized that a sharp negative shift in the PDO climate index in fall of 1998 may signify a climate change event that will reverse salmon production trends established by the winter 1976–77 regime shift. Since the late 1990s Western Alaska has experienced extremely low chinook and chum salmon returns, but annual returns of salmon to south-central and southeast Alaska have sometimes reached historical highs (e.g., McNair and Geiger 2001; Eggers 2002). In general, salmon returns to many U.S. Pacific Northwest streams have improved since the late 1990s.

A multi-decadal decrease in body size and increase in age at return of many stocks of U.S. salmon is well established (Helle and Hoffman 1995; Bigler et al. 1996; Helle and Hoffman 1998). Several retrospective studies of scale patterns indicate that growth reductions in Alaska salmon occur during their second or third summers in the ocean, and are negatively correlated with high salmon abundance (Isakov et al. 2000; Sands et al. 2001; Ruggerone et al. 2003). Percy (1992) reviewed evidence of ocean carrying capacity (density-dependent mortality or growth) effects in salmon. Density-dependent effects on salmon growth in summer may be linked to increased ocean mortality during winter, particularly in years when winter seawater temperatures are warmer than average (Beamish and Manhken 2001; Ruggerone et al. 2003).

The variability in ocean life history patterns of salmon that we see today reflects their evolutionary response to changing climatic conditions (Percy 1992). Run reconstructions from salmon-derived nutrients in nursery lake sediment cores showed multi-centennial regimes of anomalously low or high salmon abundance in Alaska, which correspond to major paleoclimatic changes (Finney et al. 2002).

TRENDS IN HATCHERY PRODUCTION

Mahnken et al. (1998) reviewed annual production rates from the U.S. Pacific Northwest (Washington, Oregon, Idaho, and California) and Alaska hatcheries from 1950–1992. Since the early 1970s, production of pink, chum, and sockeye salmon has increased, and since 1985, the production of coho salmon, chinook salmon, and steelhead trout has decreased. In 1992, an estimated 1.8 billion juvenile

Pacific salmon were released into the North Pacific Ocean by U.S. hatcheries, enhancement and ocean ranching programs (Heard 1998).

Since 1993, the North Pacific Anadromous Fish Commission (NPAFC) has compiled and published statistics on the annual releases of juvenile hatchery salmon by country and area (North Pacific Anadromous Fish Commission 1997–2002, Table 1). Among U.S. states, Alaska is the major producer of hatchery salmon, accounting for an average of 77% of the annual (1993–1998) releases into the North Pacific Ocean. Alaskan hatcheries are the major producers of sockeye, pink, and chum salmon, and Washington hatcheries are the major producers of coho and chinook salmon. Hatchery production of sockeye and pink salmon is highest in the central Alaska region, and hatchery production of chum salmon is highest in the southeast Alaska region. There is no hatchery salmon production in the Arctic-Yukon-Kuskokwim region of Alaska. Hatchery production of steelhead trout is highest in Washington and Idaho.

OVERVIEW OF MAJOR FIELD RESEARCH PROGRAMS

Table 2 summarizes some of the major sampling programs conducted in coastal waters of the U.S. by geographic region and includes type of sampling undertaken for each program. The majority of field research has been conducted by National Marine Fisheries Service (NMFS) laboratories on the West Coast and Alaska, or by universities funded in part by NMFS. However, new sources of funding have recently become available through other programs such as GLOBEC (Global Ocean Ecosystem Dynamics) that have juvenile salmon as one of their primary target species (U.S. GLOBEC 1996). Our coverage of these studies has been grouped by geographic region (Fig. 3), progressing from south to north, for ease of presentation.

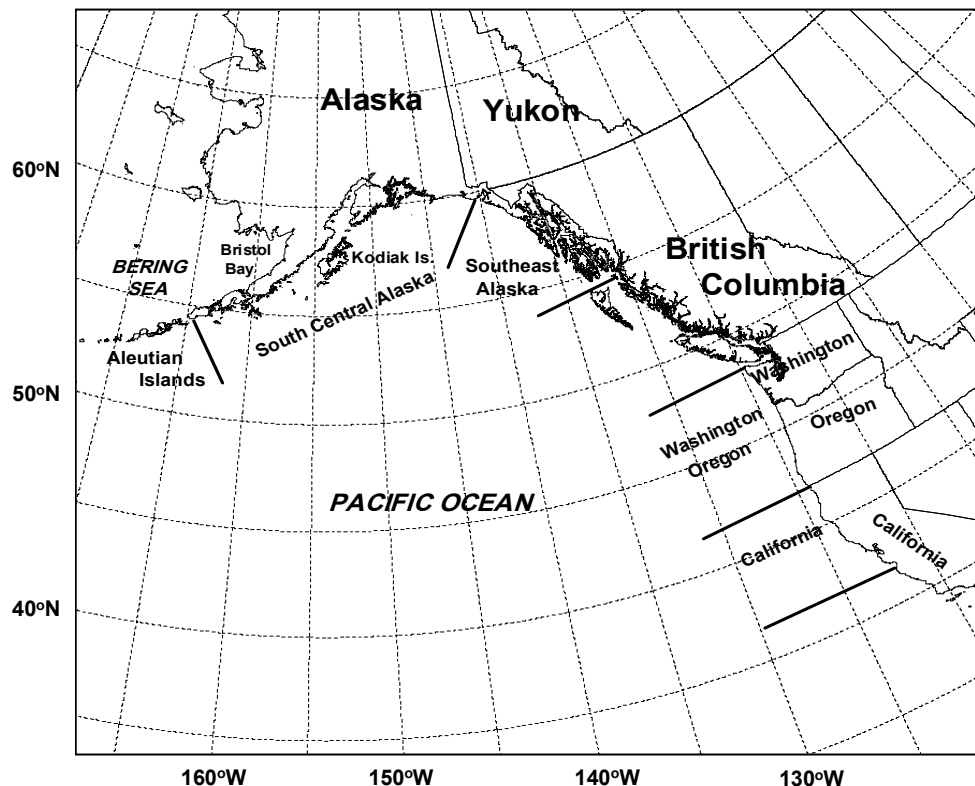
Table 1. Hatchery releases of juvenile salmon (millions of fish) by species in Alaska, Washington, Oregon, Idaho, and California in 1993–1998.

Region	Year	Sockeye	Pink	Chum	Coho	Chinook	Steelhead	All Species	Source*
Alaska	1993	54.8	819.2	468.7	14.6	11.4	0.1	1368.8	NPAFC 1997
	1994	69.7	790.3	407.2	17.8	9.8	-	1294.8	NPAFC 1998
	1995	81.4	920.5	473.2	17.4	6.7	<0.05	1499.3	NPAFC 1999
	1996	75.3	999.1	535.4	21.0	7.0	<0.05	1637.8	NPAFC 2000
	1997	76.5	773.3	478.1	23.2	7.6	0.0	1358.7	NPAFC 2001
	1998	70.6	872.5	479.2	21.6	8.7	<0.05	1452.6	NPAFC 2002
Washington	1993	3.5	-	59.8	63.2	139.1	11.0	276.6	NPAFC 1997
	1994	8.6	3.5	60.0	56.4	141.7	9.8	280.0	NPAFC 1998
	1995	16.3	0.1	59.1	57.0	159.3	10.6	302.4	NPAFC 1999
	1996	13.2	4.6	58.9	59.6	151.4	10.6	298.3	NPAFC 2000
	1997	27.4	-	46.8	52.6	151.1	11.3	289.2	NPAFC 2001
	1998	21.1	5.1	45.0	54.1	143.9	12.2	281.3	NPAFC 2002
Oregon	1993	-	-	-	4.5	17.3	2.4	24.2	NPAFC 1997
	1994	-	-	-	14.9	48.8	6.6	70.3	NPAFC 1998
	1995	-	-	-	13.1	60.6	6.8	80.5	NPAFC 1999
	1996	<0.05	-	-	13.5	56.2	6.5	76.2	NPAFC 2000
	1997	-	-	-	10.3	37.0	6.4	53.7	NPAFC 2001
	1998	0.1	-	-	8.2	27.0	6.1	41.3	NPAFC 2002
California	1993	-	-	-	0.8	49.0	5.6	55.4	NPAFC 1997
	1994	-	-	-	0.7	60.4	6.4	67.5	NPAFC 1998
	1995	-	-	-	0.9	60.2	5.8	66.9	NPAFC 1999
	1996	-	-	-	0.2	59.0	5.3	64.5	NPAFC 2000
	1997	-	-	-	0.8	50.3	3.7	54.8	NPAFC 2001
	1998	-	-	-	0.9	59.7	3.5	64.0	NPAFC 2002
Idaho	1993	-	-	-	-	4.9	7.8	12.7	NPAFC 1997
	1994	<0.05	-	-	-	7.8	8.1	15.9	NPAFC 1998
	1995	-	-	-	0.6	7.7	8.7	17.1	NPAFC 1999
	1996	-	-	-	-	1.8	8.9	10.7	NPAFC 2000
	1997	-	-	-	-	1.5	8.5	10.0	NPAFC 2001
	1998	<0.05	-	-	-	3.3	7.8	11.1	NPAFC 2002

*NPAFC: North Pacific Anadromous Fish Commission

Table 2. Studies on juvenile salmon conducted in U.S. coastal waters and types of sampling done in each study.

Geographic Region	Principal Investigators	Dates	Gear	Physical	Plankton	Food	Growth	Migration	Predators
California	McFarlane, Grimes, Norton	1996–2002	Surface trawl	x	x	x	x	x	
Washington/ Oregon	Miller, Williams, Sims	1980	Purse seine	x		x			
	Pearcy, Fisher, Brodeur	1979–1985	Purse seine	x	x	x	x	x	x
	Dawley, Ledgerwood, Jensen	1979–1980	Purse seine						
	Casillas, Brodeur, Emmett, Peterson	1998–2002	Surface trawl	x	x	x	x	x	x
	Emmett, Bentley, Krutzikowsky	1998–2002	Midwater trawl	x					x
	Brodeur, Emmett	2000–2002	Surface trawl	x	x	x	x	x	x
	Pearcy, Fisher	1985	Gill net	x				x	
SE Alaska	Hartt, Dell	1964–1968	Purse seine			x	x	x	
	Jaenicke, Celewycz	1983–1984	Purse seine	x	x	x	x	x	
	Jaenicke, Brodeur	1982	Gill net	x		x		x	
	Orsi, Wertheimer, Heard	1997–2002	Surface trawl	x	x	x	x	x	x
	Helle, Carlson, Welch	1995–2002	Surface trawl	x	x	x	x	x	
N. Gulf of Alaska/ Aleutians	Hartt, Dell	1964–1968	Purse seine			x	x	x	
	Helle, Carlson, Welch	1995–2002	Surface trawl						
	Haldorson, Boldt	1998–2001	Gill net	x	x	x	x		x
	Helle, Haldorson, Beauchamp, Myers	2001	Surface trawl	x	x	x	x	x	
Bering Sea	Hartt, Dell	1964–1968	Purse seine			x	x	x	
	Straty, Jaenicke	1966–1969	Purse seine	x	x	x	x	x	x
	Farley, Helle, Guthrie	1999–2002	Surface trawl	x	x	x	x	x	

Fig. 3. Locations of geographic areas covered in this review.

Central California

The Tiburon/Santa Cruz Laboratory of NMFS has conducted limited sampling for juvenile salmon in the Gulf of the Farallones, off San Francisco Bay, since 1997. Primary objectives of these studies are to monitor growth, physiological condition, and contaminant levels of juvenile chinook salmon and compare these factors to those measured on fish collected earlier in the year in San Francisco Bay (MacFarlane and Norton 2002). Near-surface pelagic trawls were used to collect the juvenile salmon, and concurrent depth-stratified and surface (neuston) plankton tows were taken to compare food availability with the juvenile salmon diets. Environmental data (water column temperature and salinity, transmissivity, fluorescence, and currents) are collected concurrently with the salmon, the associated fish community, and the plankton samples. Preliminary results from 1997 suggest that salmon grow rapidly in coastal waters at the expense of depleting energy reserves (MacFarlane and Norton 2002). This work is continuing, and the ultimate goal is to assess how interannual variations in ocean conditions, including such major perturbations as El Niño/Southern Oscillation (ENSO) events, affect the distribution and survival of juvenile chinook salmon.

Washington and Oregon

Substantial effort has been expended on studies of the marine distribution and ecology of juvenile salmonids, particularly coho and chinook salmon, in coastal waters off Washington and Oregon. One of the earliest and most extensive of these studies was conducted by Oregon State University (OSU) under the direction of W.G. Pearcy and colleagues and was funded by NMFS and OSU Sea Grant. Pilot cruises were conducted in June of 1979 and 1980 followed by multiple cruises run from May through September 1981 to 1985, for a total of 17 cruises. Fine-mesh purse seines were set at predetermined station locations to capture juvenile salmonids and associated biota. Sampling generally ranged from northern Washington (48°N) to Cape Blanco (43°N) in southern Oregon, although in July 1984 the sampling was extended to northern California and off Vancouver Island, British Columbia. In addition to purse seining, some environmental (temperature, salinity, and ambient light) and biological (chlorophyll and zooplankton) sampling was done at each station. Details of sampling, environmental conditions, and catch of juvenile salmon and other nekton can be found in Brodeur and Pearcy (1986) and Pearcy and Fisher (1990).

Scientific studies resulting from this sampling were numerous and details are available in Pearcy

(1992). Analyses were done on salmonid growth based on scale analysis (Fisher and Pearcy 1988; Pearcy et al. 1990; Fisher and Pearcy 1995), and migration based on recoveries of coded-wire tags (CWT) and external tags (Pearcy and Fisher 1988; Fisher and Pearcy 1995). Feeding ecology (Peterson et al. 1982; Brodeur 1989; Brodeur and Pearcy 1990; Pearcy et al. 1990; Brodeur 1991) and food consumption (Brodeur and Pearcy 1987; Brodeur et al. 1992) were also studied. The diets of adult salmon and non-salmonid fishes were examined for potential predation on juvenile salmon (Brodeur et al. 1987). A strength of this research was that sampling occurred under highly contrasting oceanographic conditions from strong upwelling to anomalous ENSO conditions, and the effects of this variability on salmon survival and the ecosystem in general were examined (Pearcy et al. 1985; Brodeur and Pearcy 1992; Pearcy 1992).

Personnel at the NMFS Point Adams Field Station conducted similar fine-mesh purse seining studies in coastal waters during three cruises from May until early September 1980. Sampling was done on transects mainly in the vicinity of the Columbia River plume. Although all five species of salmon and both species of trout were captured, the majority of the catch was juvenile coho and chinook salmon (Miller et al. 1983). In addition to information on abundance and distribution, some studies were done on the size, direction of migration, and food habits of juvenile salmon, as well as the environmental conditions in which the salmon were caught (Miller et al. 1983; Emmett et al. 1986; Loch and Miller 1988).

A much smaller and shallower purse seine was used to sample juvenile salmon in the very nearshore regions in the mouth of the Columbia River and adjacent littoral areas north and south of the river mouth in 1979 and 1980. Sampling was conducted intermittently at several sites from May through September. Subyearling chinook salmon was the dominant juvenile salmonid caught, although many other forage fishes such as smelts (Osmeridae) and anchovy (*Engraulis mordax*), were also caught (Dawley et al. 1985a; Miller 1992).

An additional type of diel sampling was done by a pelagic small-mesh gillnet at one station off the central Oregon Coast in 1985 from the Hokkaido University training ship, *Oshoro maru*. Nets were set simultaneously at two depth levels over four different time periods. The salmonid catch consisted primarily of juvenile coho salmon (Pearcy and Fisher 1988) that were found to be residing in the upper two meters of the water column. Additional data were collected on physical conditions, zooplankton biomass, and size, growth, and feeding habits of the juvenile salmon.

Beginning in 1998, researchers from NMFS and OSU have been sampling the coastal waters from

northern Washington to central Oregon using large surface trawls. Multiple cruises have been conducted each year, generally during May, June, and September. The purpose of these studies, funded by Bonneville Power Administration (BPA), is to assess the importance of the Columbia River Plume to juvenile salmon survival. Trawling is done from both chartered fishing boats and fishery research vessels, and is accompanied by extensive surface and depth-integrated plankton sampling, water column physics, and chlorophyll measurements, and some ancillary measurements including currents, light transmission, and acoustics.

One of the goals of this research is to compare how the pelagic community has changed since the previous intense sampling period in the early 1980s (Emmett and Brodeur 2000). Salmon catches during the 1990s were dominated by juvenile chinook salmon, as opposed to the earlier sampling when coho salmon were predominant. The non-salmonid community has also changed somewhat, with large increases in sardine (*Sardinops sagax*) and a corresponding drop in northern anchovy and squid (Emmett and Brodeur 2000). Process studies have examined the diel vertical distribution and catch rates (Emmett et al. unpublished manuscript) and feeding chronology and selectivity (Schabetsberger et al. 2003) of juvenile salmon in the Columbia River plume. Studies presently underway include analysis of juvenile salmon growth, bioenergetics, health, condition, genetic composition, habitat associations, and feeding habits relative to available prey.

A parallel study has been underway to sample potential predators along two transects near the mouth of the Columbia River (Emmett et al. 2001). Nighttime sampling, again using surface trawls, was conducted biweekly from April through August during 1998–2001. Substantial seasonal and interannual variation in the abundance of potential predators and juvenile salmon was observed reflecting major changes in oceanographic conditions during the study period (Emmett and Brodeur 2000; Emmett et al. 2001).

Sampling for juvenile salmon and associated biota off the U.S. West Coast has been a component of the GLOBEC Northeast Pacific Program. The main goal of this program is to assess how the physical environment affects the ecosystem, including juvenile salmon and their prey. A number of retrospective, monitoring, modeling, and field process studies have been funded to attain this goal. The study site chosen for this research extends from central Oregon to northern California and bridges a major oceanographic and zoogeographic break at Cape Blanco in southern Oregon. The first field sampling took place in June and August of 2000 and involved the coordinated activities of three vessels. Continuous underway sampling of physical, biological, and acoustical

properties of the water column was carried out on one research vessel, while biological sampling (depth-stratified plankton tows, shipboard laboratory studies, bird and marine mammal observations) was done on a second research vessel. The salmon sampling was done by surface trawl using the gear previously described for BPA work on the third vessel, a chartered fishing boat, in close proximity to the other sampling. Both mesoscale grid and fine-scale opportunistic trawling were conducted. Catches of juvenile salmon were relatively low in 2000 compared to BPA collections further north at about the same time, despite the presence of strong upwelling and high zooplankton biomass. Analyses of salmon and other nekton distributions in relation to biophysical parameters are presently being conducted, along with analyses of juvenile salmon growth, condition, genetic stock composition, diseases, and trophic interactions with predators and prey (Brodeur et al. 2003). A second major field season was completed during the summer of 2002.

Puget Sound

There has never been a comprehensive NMFS field research program on juvenile salmonids in the marine waters of Puget Sound and the Strait of Juan de Fuca. Investigations from the early 1960s to present by the University of Washington, School of Aquatic and Fishery Sciences (SAFS; formerly the School of Fisheries, the College of Fisheries, and its research branch, the Fisheries Research Institute) form the only comprehensive major field research program in this region. The results, reports, and publications from these studies are summarized in the SAFS annual or biennial report series, *Research in Fisheries* (Fisheries Research Institute 1960–1996). An online database of reports and publications at the SAFS Publications internet website can be used to access information on historical and ongoing studies of juvenile salmon in Puget Sound and adjoining estuaries (<http://www.fish.washington.edu/Publications/>).

Many field investigations by federal, state, county, city, and tribal agencies, private consulting firms, non-profit organizations, and other universities, particularly with respect to the effects of human activities on juvenile salmonids and their habitats, have also contributed to our knowledge of the early marine life history and ecology of juvenile salmonids in Puget Sound. The results of SAFS and other studies were synthesized and reviewed by Iwamoto and Salo (1977), Simenstad et al. (1982), and Weitkamp (2001). These reviews include some previously unpublished data with respect to early marine survival, timing and size at entry, species residence times, habitat utilization, food habits, growth, and predation. Status reviews of U.S. West Coast salmon, steelhead and cutthroat trout by NMFS also provide a useful

synthesis of information from Puget Sound field investigations, particularly on migratory timing and size at entry of fry and smolts (Weitkamp et al. 1995; Busby et al. 1996; Hard et al. 1996; Gustafson et al. 1997; Johnson, O.W., et al. 1997, Myers et al. 1998; Johnson et al. 1999).

The combined results of field investigations conducted since the 1950s show that Puget Sound is a very important early marine habitat for anadromous juvenile salmonids. The investigations were conducted with a variety of gear, including beach seines, trap nets, tow nets, purse seines, and trawls, and also included some tagging and marking studies to determine movement and migration patterns. Five species of Pacific salmon occur naturally in Puget Sound and the Strait of Juan de Fuca, although coho, chinook, and chum salmon are more prevalent than pink and sockeye salmon. Juvenile chinook and chum salmon apparently make more extensive use of estuarine and nearshore habitats in Puget Sound than juveniles of other salmon species. Steelhead and cutthroat trout also occur naturally in Puget Sound. Some salmon and trout populations rear to adults in Puget Sound, never migrating to the Pacific Ocean. Salmon and steelhead trout populations in Puget Sound have been continuously enhanced with artificially propagated fish since the early 1900s; however, we are not aware of comprehensive investigations of hatchery and wild juvenile salmonid interactions in Puget Sound. Historically, Puget Sound salmon have had higher marine survival rates than coastal salmon populations. Water pollution and shoreline development, among other factors, have contributed to the decline of Puget Sound salmonid populations, some of which are listed as threatened or endangered under the U.S. ESA or are candidates for listing. Recent field investigations in Puget Sound have primarily involved assessment of the effects of pollution and shoreline development or habitat restoration on juvenile salmonids.

Coastal Waters off Southeast Alaska

Small mesh experimental gillnetting similar to that described earlier for research off Oregon, was conducted off Southeast Alaska by the research vessel *Oshoro maru* in July 1982 as part of a cooperative U.S./Japan survey (Jaenicke et al. 1984). Information was gathered on the species composition, size, depth and direction of travel, and food habits of all (mostly coho) juvenile salmon caught.

During the summers of 1983 and 1984, juvenile salmon were the primary focus of a study to examine the nearshore ecosystem off Southeast Alaska and northern British Columbia (1984 only) using fine-mesh purse seines. Sampling was done with a seine, mainly during the daytime. About half of the sampling was done in protected bays and passages in

inside waters of Southeast Alaska (Jaenicke and Celewycz 1994). Purse-seine sampling in outside waters was augmented by temperature measurements and surface (neuston) and oblique plankton tows down to 50 m. Catch rates and size of salmonids are presented in Jaenicke and Celewycz (1994), and their feeding habits relative to plankton availability were examined by Landingham et al. (1998).

During October 1995, scientists from the newly formed Ocean Carrying Capacity (OCC) program at the NMFS Auke Bay Laboratory worked jointly with biologists from the Canadian Department of Fisheries and Oceans Biological Station in Nanaimo, British Columbia on a survey along the coastal waters of Southeast Alaska. The objective of the survey was to compare the effectiveness of two gear types (Bernard-Sigmund Beam trawls and mid-water rope trawl) at catching juvenile salmon at sea. Paired trawling between two vessels along the coastal waters of Southeast Alaska indicated that the mid-water rope trawl was more efficient at catching juvenile salmon in the ocean. Incidental catch of juvenile salmon in coastal waters of Southeast Alaska by the mid-water rope trawl indicated large numbers of juvenile pink, chum, and coho salmon still present in this region during October. Sampling for juvenile salmon by the OCC group continued off Southeast Alaska in 1996 (Carlson et al. 1996) and 1998 (Carlson et al. 1998).

The early marine life history of juvenile Pacific salmon has been studied since 1997 as part of the Southeast Alaska Coastal Monitoring (SECM) project of the NMFS Auke Bay Laboratory. Although the majority of this sampling took place in inshore waters (Orsi et al. 2000), stations were sampled along a transect off Icy Point, just north of Cross Sound, and off Cape Edward just to the south. Cruises are conducted on a monthly basis from May to October of each year. The sampling platform was the NOAA ship *John N. Cobb*, and hauls were made using a Nordic 264 trawl. Also collected were physical data (continuous thermosalinograph and CTD at each station) and zooplankton (vertical 0–20 m NORPAC, oblique bongo). Catch rates for salmon (mainly pink and chum salmon) were highest inshore and most juveniles were caught within 25 km of shore (Murphy et al. 1999). Sablefish, herring, and capelin were the dominant non-salmonid species caught. Additional work is underway to examine seasonal habitat use by salmonids during migration using CWT and thermal marks, diet and lipid analysis, and determination of potential predators (Orsi et al. 2001a).

Inside Waters of Southeast Alaska

A comprehensive synthesis of research on marine ecology of juvenile salmon in southeast Alaska was presented by Heard et al. (2001). An ongoing program to monitor habitat use by juvenile salmon in

southeast Alaska was described by Orsi et al. (2001a). The reader is referred to these detailed reviews for a historical summary as well as a description of the ongoing research on juvenile salmon in southeast Alaska.

Southeast Alaska has many large islands along the coast that provide a maze of bays and channels between the islands and the mainland (Fig. 3). Many rivers and streams flow from the islands and mainland into the bays and provide ideal spawning and rearing areas for all species of Pacific salmon and other anadromous species (e.g. cutthroat trout and Dolly Varden char (*Salvelinus malma*)). Research on the early marine life history of juvenile salmon concentrated on developing methods to capture these small fish in the marine waters.

Studies on juvenile salmon were started in the mid-1950s in southeast Alaska by the U.S. Fish and Wildlife Service (USFWS), Bureau of Commercial Fisheries (BCF; predecessor of NMFS), and the Fisheries Research Institute (FRI) of the University of Washington, and were primarily focussed on methods for capturing juvenile salmonids. Large pile-driven and floating traps, both with leads to shore, were the primary method used to capture adult salmon in the 1950s in southeast Alaska (Dumont and Sundstrom 1961; Scudder 1970). These traps also caught juvenile salmon, and starting in the mid-1950s, investigators attempted to relate numbers of juvenile pink salmon in traps to adult returns one year later (Mattson and Sears 1963). These studies were terminated after 1958, as traps would no longer be used as a commercial sampling gear after the state of Alaska assumed control of salmon management in 1960 from the federal government.

A small floating trap was developed in 1957 for capturing juvenile salmon by J.W. Martin of FRI (Martin 1958). Also in 1957, beach seines, gill nets, paired towed hoop nets, a floating trap, and an Isaacs-Kidd midwater trawl were tested and evaluated, but these methods generally had only minor success in capturing juvenile salmon (Mattson and Sears 1963). In 1958 a Lampara seine was tested in bays and open water channels by BCF and this proved to be the most successful method to date for capturing juvenile salmon (Sears 1958).

In 1962–65, Martin, then with BCF, successfully captured large numbers of juvenile pink and chum salmon using a round haul seine in bays and channels throughout Southeast Alaska and in large numbers in lower Chatham Strait as late as 10 September during 1963 (Martin 1964; 1966). The pink salmon ranged in size from 135–200 mm and the chum salmon from 135–165 mm (Martin 1964). Martin also tried to capture juvenile salmon using baited floating longlines but was not successful. Bailey et al. (1975) used dip nets from boats and floating traps anchored nearshore to capture pink and chum salmon juveniles

for a study on food habits in the mid-1960s.

Beach seines were later used to capture juvenile salmon in northern Southeast Alaska by Orsi and Landingham (1985) and Celewycz et al. (1994). Beach seines and dip nets were used by Mortensen and Wertheimer (1988) to capture juvenile salmon in Auke Bay. Juvenile salmon were captured nearshore with beach seines and offshore with a small surface trawl in Auke Bay in 1986–89 (Mortensen et al. 2000). Jaenicke et al. (1985) used paired beach seines opened in opposite directions to study the migrations of juvenile salmon in Southeast Alaska channels in the early 1980s. In 1983 and 1984, Jaenicke and Celewycz (1994) used both drum and table purse seines to capture juvenile salmon and associated species throughout the passages of Southeast Alaska as described previously for the outside waters. Orsi et al. (1987) and Orsi (1987) evaluated trolling with small lures and herring bait for capturing juvenile chinook and coho salmon in 1985. Finally, in the most recent sampling, a Nordic trawl fished at the surface has become the gear of choice for sampling juvenile salmon in the channels as part of the SECM project described previously (Orsi et al. 1997; Murphy et al. 1999).

Pink and chum salmon fry and sockeye, coho, and chinook salmon smolts migrate out of the rivers and streams into the marine waters as early as late February and generally are gone from freshwater by early June. Pink and chum salmon migrate along the shores and feed in the littoral areas. Sockeye, coho, and chinook salmon smolts move away from the shore into open water sooner than smaller pink and chum salmon fry. In June and July all species of salmon are moving away from shore into the channels and in August and September most juvenile salmon have entered the Gulf of Alaska (GOA) where they move northward and westward along the continental shelf. Some Alaska and more southerly stocks of juvenile chinook salmon may stay in the inside waters of Southeast Alaska through December (Orsi and Jaenicke 1996).

Coastal North Pacific Ocean to Aleutian Islands

Some of the earliest directed sampling for juvenile salmon was undertaken by the Fisheries Research Institute (FRI) of the University of Washington, under contract to NMFS. The sampling began in 1964 and continued until 1968 using fine-mesh purse seines towed as a semicircle for a half hour and then pursed as in normal operations (Hartt 1980; Hartt and Dell 1986). Sampling mainly occurred from July through October from the coastal waters off Southeast Alaska to Attu Island in the Aleutian Islands. Juvenile salmon were found along the coastal waters from southern Southeast Alaska to as far west as Unimak Pass. The dominant species of juvenile

salmon caught within this region consisted of sock-eye, chum, and pink salmon. During the summer (July–August), these juvenile salmon were generally found along the continental shelf from nearshore to the 200-m contour. Coho and chinook salmon were also caught but were farther offshore (beyond the 200-m contour) by late summer.

One of the objectives of the FRI study was to determine the migration routes and speed of juvenile salmon during their early ocean migration. An extensive tagging operation was undertaken and with the exception of steelhead trout that migrated directly to the open ocean, most juvenile salmon migrated northward in a counter-clockwise direction around the coastal waters of the Gulf of Alaska after entering the ocean (Hartt and Dell 1986). Other information gathered during the surveys included growth (derived from change in length) and food habits data (Andrews 1970; Hartt and Dell 1986).

During 1993, the North Pacific Anadromous Fish Commission (NPAFC) and the North Pacific Marine Science Organization (PICES) agreed to jointly examine the effects of changes in productivity in the North Pacific Ocean on salmon populations. Primary issues of concern were (1) identifying factors that affect current changes in ocean productivity and how these changes affect salmonid carrying capacity, and (2) identifying factors that affect changes in growth, age and size at maturity, marine distribution, and survival of Pacific salmon. In response to this call for marine research on Pacific salmon the NMFS Auke Bay Laboratory in Juneau, Alaska, initiated the OCC research program. Since its inception, the OCC program has conducted three broad-scale field studies (1996, 1997, and 1998) of the coastal waters of the North Pacific Ocean (Carlson et al. 1996, 1997, 1998). The surveys occurred during July and August and generally sampled between southern Southeast Alaska and Attu Island using a mid-water rope trawl rigged to fish in near surface waters. In addition to trawl sampling, some environmental (CTD) and biological (zooplankton) sampling was done at selected stations and genetic samples of salmon were taken for stock identification analysis.

Examination of juvenile salmon catch data indicated that species dominance, distribution, and migration characteristics were similar to those found for juvenile salmon in the earlier studies by FRI. Analyses of salmon otoliths for hatchery thermal marks indicated a large proportion (roughly 20–30%) of the juvenile pink and chum salmon captured during the OCC surveys were from hatcheries located in Southeast Alaska and Prince William Sound (Farley and Munk 1997; Carlson et al. 2000). Further analyses of the growth and condition factor of hatchery juvenile pink and chum salmon were presented in Farley and Carlson (2000), and Auburn and Ignell (2000) examined their feeding habits with

respect to habitat.

Fine mesh gill nets and surface trawls were the main sampling gear used to collect juvenile salmon as part of a multidisciplinary GLOBEC effort by University of Alaska scientists under the direction of Dr. L. Haldorson. The sampling has taken place several times a year (summer and fall) since 1998 along the Seward hydrographic line extending from Seward Alaska across the shelf out into the Gulf of Alaska. An extended suite of physical, biological, and acoustical measurements was taken concurrently with the salmon from a different vessel. Juvenile pink and chum salmon were the main fishes caught inshore, whereas coho salmon and other non-salmonids (saury, rockfishes, capelin) were common offshore (Boldt 2001). Dietary and caloric analyses have been conducted on the pink salmon (Boldt and Haldorson in press) and bioenergetic consumption estimates were estimated (Boldt and Haldorson 2002).

The large-scale field studies conducted by the OCC program and FRI have provided a basis for future planned juvenile salmon studies in the coastal waters of the Gulf of Alaska. These surveys have shown that juvenile salmon have a strong preference for coastal waters (continental shelf near the Alaska Coastal Current) along the Gulf of Alaska over offshore waters (near the Alaska Stream). The strong preference by juvenile salmon for the coastal waters is not fully understood but may be related to survival. In order to further understand this relationship, the OCC program conducted cruises in July and August of 2001 in the coastal Gulf of Alaska from Yakutat to the western end of Kodiak Island as part of the Gulf of Alaska GLOBEC program. The main objective of the program is to quantify the relationships between biological and physical oceanographic processes that affect the distribution of juvenile salmon in the coastal Gulf of Alaska. The OCC program conducted a pilot survey of the area west of Prince William Sound within the project survey area during August 2000 and in July 2001 and 2002. Details of sampling and catch of juvenile salmon and other associated nekton for the first year can be found in Farley et al. (2000a).

Prince William Sound

Sampling for juvenile salmon started in Prince William Sound by the Bureau of Commercial Fisheries in July and August 1957 (Kirkwood 1962). These studies lasted only one year, and various types of gear were evaluated such as beach seines, gill-nets, a small shrimp trawl towed at the surface, and a cone-shaped net towed between two skiffs. Juvenile pink and chum salmon were caught with all gear types except for gill-nets, which were generally fouled with adult salmon. Pink salmon close to shore were

around 100 mm while those captured 0.15 km or more offshore were greater than 130 mm. The largest pink salmon caught were around 155 mm, which Kirkwood (1962) concluded is the size at which they leave the sound. Researchers caught chum salmon in southwestern Prince William Sound in September and late October 1961 using a midwater trawl. These fish, which were deposited in a museum collection, were later measured and the circuli on their scales counted to determine growth (Helle 1979). The fish ranged from 140–200 mm and were noteworthy considering they were captured in Prince William Sound so late in the year.

Much of the earlier research focused on pink salmon, the dominant salmon in terms of production in Prince William Sound, and its utilization of near-shore habitats in the first few weeks after entering marine waters (Cooney et al. 1981). A major oil spill in the region in 1989 led to substantial research on the biological effects of the oil on juvenile salmon and other biota in the sound (Sturdevant et al. 1996; Wertheimer and Celewycz 1996; Willette 1996; Paul and Willette 1997). A subsequent program entitled Sound Ecosystem Assessment (SEA) examined the role of juvenile pink salmon and other forage fishes in Prince William Sound (Willette et al. 1999; Cooney et al. 2001; Willette et al. 2001). Results from the SEA program have been summarized in a special journal volume dedicated to this program (Cooney et al. 2001).

Eastern Bering Sea

Similar to that reported above, the Fisheries Research Institute conducted substantial sampling inside Bristol Bay and along the north side of the Alaska Peninsula using purse seines (Hartt and Dell 1986). Most of the catch was sockeye salmon collected between 18 and 54 km offshore. Dell (1963) reported that juvenile sockeye (age .0) ate euphausiids and fish in Bristol Bay.

The Auke Bay Laboratory initiated research on the distribution and migration of juvenile sockeye salmon in Bristol Bay during 1966–67 and 1969–72 (Straty 1974; Carlson 1976; Straty and Jaenicke 1980; Straty 1981). The surveys were conducted using purse seines and occurred within inner Bristol Bay east of Port Heiden and along the coastal waters of the Alaska Peninsula west of Port Heiden (outer Bristol Bay). In addition to purse seining, some environmental (sea temperature and salinity) and biological (zooplankton) sampling took place at selected stations throughout the survey area. A summary of this research on the horizontal and vertical distribution, migration routes and rates, food habits, and predators of juvenile sockeye in Bristol Bay is given by Straty (1974).

These studies found that juvenile sockeye salmon from all river systems entering Bristol Bay follow the same southwesterly seaward migration route along the coastal waters of the eastern Bering Sea. The migration rate of juvenile sockeye salmon through inner Bristol Bay is rapid, whereas their migration rate slows once they enter outer Bristol Bay, presumably due to increased food resources encountered in this region. The seasonal timing of this migration can be influenced by annual differences in environmental conditions, such as time of ice breakup on lakes and anomalously cold sea temperatures. For example, during 1971, a year characterized by anomalously cold sea temperatures from spring through fall, juvenile sockeye salmon were virtually absent in outer Bristol Bay in early July; whereas, they were abundant in this area during 1967, a year with warm spring through fall sea temperatures.

The Auke Bay Laboratory's OCC program renewed research on juvenile salmon in Bristol Bay and the eastern Bering Sea during 1999–2002. The primary goal of the annual assessment is to establish and verify the linkages between adult sockeye salmon survival and annual variations in biological characteristics of juvenile sockeye salmon. The surveys have generally occurred within the coastal and middle domains of the eastern Bering Sea between 166°W and 158°W during July, August, and September. The primary sampling gear was a mid-water rope trawl rigged to fish in near surface waters. Biological (zooplankton) and physical (CTD) oceanographic data were also collected at every trawl station. Initial results of the surveys have indicated that environmental conditions found during early marine residence of juvenile sockeye salmon affect their distribution, migration, and growth. Further details of sampling, catch of juvenile salmon and other associated nekton, as well as environmental conditions can be found in Farley et al. (1999, 2000a, 2001a, c).

In September/October 2002, Auke Bay Laboratory's OCC program initiated juvenile salmon surveys with a chartered fishing vessel *Sea Storm* in the eastern Bering Sea north from Bristol Bay off the Kuskokwim and Yukon rivers and into Norton Sound. These surveys extended north and west of St. Lawrence Island to the Russian boundary. Another chartered OCC vessel, *Northwest Explorer*, and the Japanese research vessel *Kaiyo maru* fished stations throughout the Bering Sea west to the Russian boundary and south to the Aleutian Islands. A Russian research vessel *TINRO* fished stations throughout the Russian portion of the Bering Sea. These three vessels met in the area north of Attu Island in the Aleutian Islands and did side-by-side tows to calibrate their trawl gears. All of these surveys were coordinated within a multiyear NPAFC sponsored research plan: Bering-Aleutian Salmon International Survey (BASIS).

MOVEMENTS IN COASTAL WATERS

Overview

A large body of U.S. research has focused on the timing of movements, distribution, migration routes, and migration rates of juvenile salmonids in coastal marine waters. Much of the field work has emphasized coastal surveys of juvenile salmon distribution, recoveries of tagged and marked fish to determine stock-specific migration routes and migration rates, and investigations of the relations between juvenile salmon movements and various biotic (species, stock, age, size, growth, physiology, and behavior) and abiotic factors (natal stream locations, shoreline and basin bathymetry, current patterns, and oceanographic conditions).

In warm U.S. regions (California), juvenile salmon tend to move quickly through river estuaries in late winter, spring, and early summer to cool, upwelling coastal waters (e.g., MacFarlane and Norton 2002). In cold U.S. regions (Alaska) timing of movements to coastal waters tends to correspond to spring ice breakup in rivers and maximal water temperatures along migration corridors (e.g., Straty 1974; Orsi et al. 2000). In general, juvenile sockeye, pink, and chum salmon from U.S. West Coast populations (Oregon and Washington) move to coastal waters earlier in the spring or summer and at a larger size than those from Alaskan populations (e.g., Hartt and Dell 1986; see reviews by Heard 1991; Salo 1991; Burgner 1992). In contrast, coho salmon do not show a clear geographic pattern for timing of outmigration, which generally peaks in May when smolts measure 90–115 mm fork length (Weitkamp et al. 1995). Some juvenile pink, chum, coho, and chinook salmon entering inside marine waters (e.g., Puget Sound, Washington, and Southeast Alaska) in the spring or summer do not move to coastal waters until late fall, winter, or the following spring, and *resident* fish may remain in inside waters or river estuaries for most or all of their marine life (e.g., Jensen 1956a, b; Haw et al. 1967; Wright 1968; Williams et al. 1975; Myers 1980; Hartt and Dell 1986; Orsi et al. 1987).

Timing of movements of juvenile chinook salmon to U.S. coastal waters varies by life history type. *Ocean-type* chinook salmon migrate to coastal waters in their first year, some immediately after hatching in the spring (30–45 mm), but most as fry (60–150 days post hatching) or fingerlings, which migrate in late summer and fall (Myers et al. 1998). Small, slow growing ocean-type chinook salmon may rear for extended periods in estuarine, inside, or coastal waters near their natal streams before moving to more distant coastal waters (Reimers 1973; Myers 1980; Kjelson et al. 1982; Nicholas and Hankin 1988; Fisher and Percy 1990; but see MacFarlane and Norton 2002). In contrast, large *stream-type* chinook

salmon smolts typically move quickly from freshwater to coastal areas in the winter, spring, or early summer of their second year; however, juveniles from some Southeast Alaska stocks reside in the inside waters of Southeast Alaska (Orsi and Jaenicke 1996). Some stream-type chinook salmon from Southeast Alaska (Stikine, King Salmon, and Chilkat rivers) may remain in the coastal waters of Southeast Alaska throughout their lives (ADFG 1997). Most *spring* chinook salmon stocks (adults return to rivers in the spring) have a stream-type life history as juveniles, and most *fall* chinook salmon stocks have an ocean-type life history as juveniles.

Steelhead and cutthroat trout juveniles exhibit diverse life histories with respect to timing of movements to U.S. coastal waters. Timing of juvenile steelhead trout movement to coastal waters, however, appears to be size-specific (at approximately 160 mm; see review by Burgner et al. 1992). Juvenile *half-pounder* steelhead trout of the Rogue, Klamath, Mad, and Eel rivers of southern Oregon and northern California return to fresh water after only 2–4 months in the ocean, overwinter in fresh water, and then move to coastal waters again in the following spring (e.g., Snyder 1925; Kesner and Barnhart 1972; Everest 1973). Coastal cutthroat trout, which range from northern California to Southeast Alaska, typically migrate as juveniles to marine waters in late winter or spring, feed in marine waters in summer, and then overwinter in freshwater (Loch and Miller 1988; Percy et al. 1990; Johnson et al. 1999). Some precociously maturing steelhead and cutthroat trout, and male chinook salmon spawn in freshwater before their first ocean migration (Shapovalov and Taft 1954).

At first entry to U.S. coastal marine waters, small juvenile salmon typically are distributed in shallow, littoral habitats (beach areas between low and high tide). As summer progresses and fish grow, juvenile salmon move to neritic habitats (shallow, pelagic areas near shore or over a continental shelf, from low-tide mark down to a depth of about 200 m). The extent of distribution of juvenile salmon over and beyond the continental shelf varies regionally, annually, seasonally, and by species and stock (e.g., Straty and Jaenicke 1980; Straty 1981; Miller et al. 1983; Hartt and Dell 1986; Percy and Fisher 1990; Jaenicke and Celewycz 1994; Carlson et al. 2000). Vertical distribution of juvenile salmon in neritic habitats is influenced by biotic (species, age, size, forage location) and abiotic (water temperature, salinity, season, light, turbidity, currents, tides, and bottom topography) factors (e.g., Orsi and Wertheimer 1995). Seasonal habitat use is linked to species, stock, water temperature, and zooplankton distribution (e.g., Orsi et al. 2000).

Broad-scale field investigations and tagging experiments along the North American coastline from

Cape Flattery, Washington, to Attu Island at the end of the Aleutian Island chain have established that in summer (July–August) juvenile salmon are concentrated in neritic waters throughout the Gulf of Alaska westward to Unimak Pass (Hartt and Dell 1986; Carlson et al. 1996, 1997, 1998, 2000). Concentrations of juvenile salmon over the continental shelf, the net direction of their movements, and their rapid migration rates are associated with the relatively narrow, intense, counter-clockwise Alaska Coastal Current (e.g., Hartt and Dell 1986). The extent of offshore distribution of juvenile salmon varies regionally, and roughly corresponds to the width of the continental shelf. For example, one major distribution ranges from nearshore to 93 km offshore off southern Southeast Alaska (shelf width approximately 75 km) and another from nearshore to as far as 185 km offshore in the region west of Prince William Sound (shelf width nearly 200 km) (Carlson et al. 2000). Similar broad-scale juvenile salmon surveys were initiated throughout U.S. waters in the Bering Sea in 2002 by the OCC program.

Tagging and transplanting studies have shown that the direction of movement and migratory routes of salmon in coastal waters are inherited or specific to regional stock groups (e.g., Brannon and Hersberger 1984; Hartt and Dell 1986; Brannon and Setter 1987; Nicholas and Hankin 1988; Myers et al. 1996). Genetic and regional diversity in migration timing, distribution, migration routes, and migration rates of juvenile salmon in coastal waters are keys to their short-term and evolutionary success. In the following sections, we review some of the major results of U.S. field research (arranged by geographical location) on the timing of movements, distribution, migration routes, and migration rates of juvenile salmon in coastal waters.

California

Chinook salmon is the most abundant species in the California region, and is considered to have an ocean-type life history throughout this region. Even though some juveniles migrate as yearlings, the majority of California chinook salmon migrate to coastal waters as sub-yearling fry in winter and spring, a tendency linked to poor river conditions in summer (low flows and high temperatures; Myers et al. 1998). Juvenile chinook salmon leaving California's Central Valley spend about 40 days transiting the San Francisco Estuary (mean migration rate of $1.7 \text{ km} \cdot \text{day}^{-1}$), primarily in May and June, and enter the ocean in the Gulf of the Farallones (MacFarlane and Norton 2002). Migration rates, calculated from coded-wire tagged juveniles caught in the estuary, were $1.7\text{--}13.5 \text{ km} \cdot \text{day}^{-1}$ (5–38 days estuarine residence times) (Table 3). An earlier study showed that juvenile chinook

salmon fry migrated through the upstream delta at $10\text{--}18 \text{ km} \cdot \text{day}^{-1}$, and tended to remain in the estuary for almost 2 months (Kjelson et al. 1982).

Less is known about coastal movements of other species of juvenile salmon in the California region. Tag recovery data show that at least some California coho salmon juveniles move northward along the coast and are distributed from the outer coast of Vancouver Island, B.C., to Yakutat, Alaska, in July and August (e.g., Hartt 1980; Hartt and Dell 1986; Myers et al. 1996).

Pearcy et al. (1990) hypothesized that California steelhead trout populations may reside for their entire marine life in the strong upwelling coastal zone off northern California and southern Oregon. However, coastal recoveries of California steelhead trout tagged as immatures and adults in offshore waters of the northeastern Pacific (between $45\text{--}54^\circ\text{N}$ latitude, west to approximately 160°W longitude) show that at least some California steelhead trout move well offshore during juvenile or subsequent life history stages (Myers et al. 1996).

Oregon, Washington, and Columbia River

The two most abundant juvenile salmon species in research catches along the Oregon and Washington coasts are coho (highest catches inshore of 37.2 km) and chinook (usually inshore of 27.9 km) salmon (Pearcy and Fisher 1990; Brodeur et al. 2003). All Puget Sound and coastal Oregon and Washington chinook salmon populations are considered to be ocean-type fish, and the Columbia River has both ocean- and stream-type chinook salmon. Juvenile chum, pink, and sockeye salmon, as well as steelhead and cutthroat trout also occur in this region.

In Oregon, coho salmon smolts move rapidly through river estuaries to coastal waters in May (e.g., Myers 1980). Upon ocean entry, juvenile Oregon and Washington coho salmon tend to be advected southward of their natal streams by coastal surface currents in May and June, and by August and September most have reversed their direction and are caught northward of their natal streams (Pearcy and Fisher 1988). The maximum migration rates against southward-flowing surface currents for marked juvenile hatchery coho salmon caught within 10 days after release were over $18.8 \text{ km} \cdot \text{day}^{-1}$, equivalent to 1.7 body lengths (BL) per second (s), which is within the range of optimal cruising speeds ($1\text{--}3 \text{ BL} \cdot \text{s}^{-1}$) for small ($< 20 \text{ cm}$) pelagic fishes (Pearcy and Fisher 1988). Many Oregon and Washington coho salmon may reside in the coastal waters off Oregon, Washington, and northern California during their first summer, and many remain there perhaps during their entire ocean life (Miller et al. 1983; Percy and Fisher 1987, 1988). More recent genetic and CWT

Table 3. Summary of information on migration rates of juvenile salmon in U.S. waters.

Region	Species	Location	Migration Rates (km•day ⁻¹)	Source
California	chinook	estuary	1.7–13.5	MacFarlane and Norton (2002)
	chinook	river delta	10.0–18.0	Kjelson <i>et al.</i> (1982)
Oregon-Washington	chinook	outer coast	4.1	Fisher and Pearcy (1995)
	coho	outer coast	18.8	Pearcy and Fisher (1988)
	chum	Puget Sound	4.0–14.0	Bax (1982, 1983a)
Southeast Alaska	chinook	inside waters	0.3	Orsi and Jaenicke (1996)
	chinook	inside waters	1.3	Orsi <i>et al.</i> (2000)
	chinook	outer coast	6.9	Orsi and Jaenicke (1996)
	chinook	outer coast	19.1	Orsi <i>et al.</i> (1987)
	coho	inside waters	3.2	Orsi <i>et al.</i> (2000)
	coho	outer coast	28.6	Orsi <i>et al.</i> (2000)
	pink	inside waters	5.5–22.2	Martin (1966)
	pink	outer coast	10.0–45.0	Sakagawa (1972)
	chum	inside waters	1.6–2.4	Orsi <i>et al.</i> (2000)
	sockeye	outer coast	6.5–26.7	Hartt and Dell (1986)
	all species	outer coast	18.5	Royce <i>et al.</i> (1968)
Bering Sea-Aleutian Islands	sockeye	outer coast	3.9–6.7	Hartt and Dell (1986)

recovery data suggest that some Puget Sound and southern British Columbia coho salmon also reside along the Oregon and Washington coasts during their first summer at sea (Teel *et al.* in press). In years of unfavorable ocean conditions (e.g., El Niño years), however, Oregon and Washington juvenile coho salmon may make more extensive northward movements. Recovery of juvenile coho salmon show that at least some Washington, Columbia River, and Oregon coho salmon juveniles migrate far to the north and west, and are distributed from Southeast Alaska to waters well offshore of Kodiak Island, Alaska (e.g., Hartt 1980; Hartt and Dell 1986; Myers *et al.* 1996, 2001a). In Southeast Alaska, coded-wire tagged U.S. West Coast (Columbia River Basin and Washington) coho salmon juveniles have been recovered only in outer coast waters, to which they migrate at much faster rates (28.6 km•day⁻¹) than Southeast Alaska stocks distributed in inside waters (Orsi *et al.* 2000).

The direction of coastal migrations of juvenile chinook salmon from the Washington-Oregon regions is stock-specific (Nicholas and Hankin 1988). Northward-migrating stocks move to waters off Washington, British Columbia, or Alaska. These include Oregon coastal stocks from streams north of Cape Blanco, Puget Sound stocks, Columbia River Basin stocks from the Willamette and Klickitat rivers (spring runs), lower Yakima River (fall runs), and summer- and fall-runs from the mainstem Columbia River and its tributaries. Southward-migrating stocks include Oregon

coastal stocks from natal streams located south of Cape Blanco and Columbia River Basin fall-run chinook salmon from the Snake and Deschutes rivers. These stocks apparently remain in waters off Oregon and California. Migration rates of stream-type juvenile chinook salmon off the coast of Oregon and Washington (primarily Columbia River stocks) average 4.1 km•day⁻¹ (Fisher and Pearcy 1995). Chinook salmon juveniles from Oregon and Washington have been caught in both inside and outside waters off Southeast Alaska (Orsi and Jaenicke 1996).

The median date of ocean entry of stream-type chinook salmon from the Columbia River is generally prior to May 15 (Miller *et al.* 1983; Dawley *et al.* 1985b). Their abundance off Oregon and Washington is much higher in May–June than in August–September, indicating rapid northward movement (Fisher and Pearcy 1995). Columbia River Basin stream-type stocks have been caught off Southeast Alaska only in outside waters, and they migrate at much faster rates (19.1 km•day⁻¹) than the stream-type stocks of Southeast Alaska, which are distributed almost exclusively in inside waters (Orsi *et al.* 1987). Early (June) recoveries off Southeast Alaska of stream-type chinook salmon juveniles from the Columbia River Basin, indicate a critical, early marine-entry period for these stocks (Orsi *et al.* 2000). By August, tag recoveries show that the coastal distribution of juveniles from these stocks extends to the northern Gulf of Alaska (Hartt and Dell 1986).

Subyearling (ocean-type) chinook salmon juveniles from the Columbia River Basin are more abundant in Oregon and Washington neritic habitats in late summer than in spring and early summer (Fisher and Pearcy 1995; Brodeur et al. 2003). In spring and early summer, ocean-type chinook salmon juveniles are distributed primarily in littoral habitats in estuarine or coastal waters, and offshore movement appears to be strongly size dependent at a minimum size of approximately 130 mm FL (Miller et al 1983; Fisher and Pearcy 1995).

There is comparatively little information on migration patterns of sockeye, chum, and pink salmon juveniles in this region. Much of the U.S. marine research on Oregon and Washington chum salmon juveniles was conducted in Puget Sound. Upon release, hatchery chum salmon juveniles in inside waters (Hood Canal, Puget Sound, Washington) actively disperse, many across open waters to the opposite shore, and then passively migrate close to shore at rates that vary annually and seasonally ($4\text{--}14\text{ km}\cdot\text{day}^{-1}$) depending on residual surface-water outflows (Bax 1982, 1983a).

Juvenile coastal cutthroat and steelhead trout are distributed in coastal waters off the Oregon and Washington coasts in early summer (Pearcy et al. 1990; Brodeur et al. 2003). Juvenile cutthroat trout tend to be distributed closer to shore (9.4–27.8 km) than steelhead trout, but occasionally catches of both species are highest well offshore (37.2–46.3 km) in May and June. Juvenile cutthroat trout have been caught as far as 66 km offshore, and some make substantial alongshore movements ($> 250\text{ km}$). By September, most cutthroat and steelhead trout juveniles have left coastal waters, with cutthroat trout returning to freshwater and most steelhead trout migrating far offshore (see sections below on Timing and Speed of Movement and High Seas Work). Juvenile coastal cutthroat trout in Puget Sound, Washington, are usually distributed in shallow ($< 3\text{ m}$ deep) water, and may not migrate more than 50 km from their natal stream (see review by Johnston 1982). Columbia River steelhead trout juveniles migrate northward and farther offshore than most chinook and coho salmon juveniles from the Oregon-Washington region (Miller et al. 1983).

Southeast Alaska

Southeast Alaska juvenile salmon rear in the inside waters of the Alexander Archipelago before moving to outside coastal waters, where they migrate northward along the coast or move progressively offshore (e.g., Hartt and Dell 1986; Jaenicke and Celewycz 1994; see review by Heard et al. 2001). Pink salmon are usually the most abundant species of juvenile salmon in research catches in this region, and are often associated with juvenile chum salmon

and to a lesser extent with sockeye salmon, which are also abundant. The distributions of Southeast Alaska juvenile pink, chum, and sockeye salmon in research catches tend to be highly aggregated or patchy compared to those of coho and chinook salmon (e.g., Hartt and Dell 1986; Jaenicke and Celewycz 1994).

In March to early June, most Southeast Alaska salmon juveniles are distributed in littoral, inside-water habitats (e.g., Jaenicke et al. 1985; Mortensen and Wertheimer 1988). Peak abundance of juvenile salmon in neritic habitats is in June and July (Orsi et al. 2000). Migrations of juvenile salmon in coastal waters off Southeast Alaska peak in August (Hartt and Dell 1986; Jaenicke and Celewycz 1994). A substantial portion of coho salmon juveniles in Southeast Alaska, however, resides in inside waters until late fall (Orsi et al. 1987; Jaenicke and Celewycz 1994).

Along the outer coast, juvenile salmon are generally concentrated within 25 km of shore, and catches of all species decline with distance offshore, although pink and chum salmon tend to be distributed closer to shore than other species (e.g., Hartt and Dell 1986; Murphy et al. 1999; Orsi et al. 2000). Hartt and Dell (1986) described outer coastal migrations of juvenile salmon as a “band” of fish, only 37 km wide in areas off Southeast Alaska, where the continental shelf is narrow, and extending farther offshore in the northern Gulf of Alaska, where the shelf is wider. In August, Jaenicke and Celewycz (1994) caught juvenile salmon as far as 74 km offshore of Southeast Alaska. In some years, the majority of juvenile salmon in research catches off Southeast Alaska in August are in waters beyond the continental shelf, indicating that annual and seasonal changes in the Alaska coastal current affect offshore distribution (Jaenicke and Celewycz 1994).

Peak movements of Southeast Alaska pink salmon juveniles to coastal waters are in late July–early August, and variation in migration rates ($5.5\text{--}22.2\text{ km}\cdot\text{day}^{-1}$) corresponds to seasonal and annual changes in net transport by wind-induced surface currents (Martin 1966). Royce et al. (1968) estimated that all species of juvenile salmon and steelhead trout migrate from Dixon Entrance to Yakutat Bay at a rate of about $18.5\text{ km}\cdot\text{day}^{-1}$. Sakagawa (1972) estimated that northward migration rates of pink salmon ranged from $10\text{ km}\cdot\text{d}^{-1}$ to $45\text{ km}\cdot\text{day}^{-1}$ (average of $17\text{ km}\cdot\text{day}^{-1}$), that about $17\text{ km}\cdot\text{day}^{-1}$ of the speed is due to the coastal current, and that the maximum speed of active migration of pink salmon is $28\text{ km}\cdot\text{day}^{-1}$.

Sakagawa (1972) developed a conceptual model of juvenile salmon movements from Cape Flattery, Washington to Yakutat Bay, Alaska. In inside waters, movements of juvenile salmon are influenced by tidal currents, but net movement is outward to the open coast (outside waters). Along the open coast,

net movement of most juvenile salmon is northward (in outside waters). Some juvenile salmon move back and forth between inside and outside waters while migrating northward, and a few move southward. Some juvenile salmon do not migrate and remain in inside waters. Catch per unit effort (with purse seines fishing to a depth of approximately 40 m) is not significantly affected by time of day. Most of the northerly migration of juvenile salmon in the Gulf of Alaska can be accounted for by ocean current transport. High variability in nearshore currents and possibly in fish behavior, however, tends to obscure any direct relationship between migration speed and calculated transport in the Alaska Coastal Current.

Research by the NMFS (OCC and SECM) indicates that distribution and migration rates of juvenile salmon in neritic habitats off Alaska in May–October differ by species, stock, and habitat (Farley and Munk 1997; Carlson et al. 2000; Orsi et al. 2000). This research has provided some of the first stock-specific information on migration rates of Alaska hatchery salmon juveniles (determined by recoveries of thermally otolith-marked or coded-wire tagged fish). Recoveries of thermally otolith-marked hatchery fish show that by late July–early August, southeast Alaska hatchery pink salmon juveniles are distributed northwest along the continental shelf from Cape Spencer (off Southeast Alaska) to an area offshore from the Kenai Peninsula in the northern Gulf of Alaska (Farley and Munk 1997; Carlson et al. 2000). In inside waters off Southeast Alaska, juvenile chum salmon released from a hatchery near Juneau were caught primarily in June and migrated at 1.9 (June) and 1.6 (July) $\text{km}\cdot\text{day}^{-1}$. Juvenile chum salmon released from another hatchery were caught primarily in July and migrated at speeds of 2.2 (June) and 2.4 (July) $\text{km}\cdot\text{day}^{-1}$ (Orsi et al. 2000). Along the outer coast in late July, hatchery chum salmon juveniles were distributed northwest along the continental shelf from Cape Spencer, Southeast Alaska, to Cape Hinchinbrook, Prince William Sound (Farley and Munk 1997; Carlson et al. 2000).

Southeast Alaska chinook and coho salmon juveniles are caught in inside waters from June through October; however, chinook salmon catches are highest in July in inshore habitats (average migration rate of 1.3 $\text{km}\cdot\text{day}^{-1}$), and coho salmon catches are highest in June in strait habitats (average migration rate of 3.2 $\text{km}\cdot\text{day}^{-1}$; Orsi et al. 2000). An earlier study within the Alexander Archipelago and adjacent coastal waters showed that stream-type Southeast Alaska chinook salmon juveniles in inside waters migrate slower (0.3 $\text{km}\cdot\text{day}^{-1}$) than British Columbia (0.9 $\text{km}\cdot\text{day}^{-1}$) and Columbia River Basin (6.9 $\text{km}\cdot\text{day}^{-1}$) stocks in outside waters (Orsi and Jaenicke 1996).

Experimental fishing with commercial trolling gear at five depth intervals (0.1–7.5 m, 7.6–15.0 m,

15.1–22.5 m, 22.6–30.0 m, and 30.1–37.5 m) indicates that in September juvenile coho salmon are caught in significantly shallower water than juvenile chinook salmon, and that juvenile chinook salmon move progressively deeper with increasing age and size (Orsi and Wertheimer 1995). Surface gillnet catches of juvenile coho salmon are highest at night (Jaenicke et al. 1984).

Prince William Sound, Cook Inlet, and Kodiak Island

In April and May, juvenile pink and chum salmon enter Prince William Sound, Alaska, and are distributed in shallow, littoral habitats (Cooney et al. 1978; Wertheimer and Celewycz 1996; Boldt 2001). When they reach approximately 60–70 mm in length, they move to neritic habitats, and by mid-August, most have moved through southwest passages of Prince William Sound to outside waters, where they migrate westward over the continental shelf of the Gulf of Alaska (Cooney et al. 2001).

Recoveries of thermally otolith-marked hatchery fish show that by late July–early August most Prince William Sound hatchery pink salmon juveniles are distributed in the vicinity of the Kenai Peninsula and Kodiak Island (Gore Point and Marmot Island), and that their range extends to areas off the south side of the Alaska Peninsula and as far west as Mitrofanina Island (750 km west of Prince William Sound) (Farley and Munk 1997; Carlson et al. 2000). Pink salmon juveniles released from one hatchery in southwest Prince William Sound may move directly to the Gulf of Alaska in July without rearing in inside waters (Boldt 2001). By October a few Prince William Sound hatchery pink salmon juveniles remain over the continental shelf along the Seward hydrographic transect (approximately 90 km from Prince William Sound) (Boldt 2001).

Emigration of pink and chum salmon juveniles into Cook Inlet begins in late May and peaks in June, substantially later than these species enter Prince William Sound (Moulton 1997). Pink salmon is the most abundant species in June, and chum salmon is the most abundant species in July. Pink, sockeye, coho, and chinook salmon apparently move quickly through northern Cook Inlet, while chum salmon juveniles remain in this region longer than the other species. Pink and chum salmon juveniles form small aggregations (10–50 fish) near the surface, with peak fish densities usually in the 15–20-m depth range. The highest and most diverse catches of all species of juvenile salmon are associated with tide rip lines or floating debris (Moulton 1997).

Large numbers of juvenile salmon (estimated annual average production > 0.5 billion; peak production > 1.5 billion) enter coastal waters throughout the Kodiak region (Stern 1976). In late May and late

June, both pink and chum salmon juveniles are abundant in littoral habitats around Kodiak Island (Tyler 1972; Gosho 1977; Harris and Hartt 1977). By late July, as they increase in size, most Kodiak Island pink and chum salmon juveniles move to neritic habitats. Outmigration of juvenile pink salmon from Kodiak Island bays, fjords, and channels peaks in August, although large diurnal schools of juvenile pink and chum salmon can be found in intertidal areas of Kodiak Island bays in August (Harris and Hartt 1977). Post-smolt sockeye salmon remain in Chignik Lagoon (south side of Alaska Peninsula) for about four to six weeks, initially occupying littoral areas and gradually moving into deeper waters of the lagoon before moving to outside waters (Dahlberg 1968; Phinney 1968). In August, local stocks of juvenile salmonids of all species are caught in outside waters of the Kodiak region (Hartt and Dell 1986). In addition, by late August the distribution of juvenile sockeye salmon from as far south as the Fraser River and juvenile coho and chinook salmon and steelhead trout from as far south as Oregon extends to the highly productive marine waters of Cook Inlet-Kodiak region (Hartt and Dell 1986; Myers et al. 1996). The small size of juvenile salmon distributed in the Shelikof Strait, between Kodiak Island and the mainland, in August indicates that they may be primarily from local (Kodiak region) stocks (Farley et al. 2000b, 2001b).

Eastern Bering Sea and Aleutian Islands

Most of the U.S. data on ocean distribution and migration patterns of juvenile salmon in the eastern Bering Sea pertain to Bristol Bay sockeye salmon (Straty 1974; Straty and Jaenicke 1980; Straty 1981; Hartt and Dell 1986; Isakson et al. 1986; Farley et al. 1999, 2000a, 2001a, c). Bristol Bay sockeye salmon usually spend one or two years in freshwater before migrating to the ocean. Sockeye smolts (approximately 4–15 g in weight) leave freshwater rearing areas from mid May to mid July, and throughout much of the summer are found in concentrated schools around the perimeter of Bristol Bay and along the north side of the Alaska Peninsula (most within 93–111 km of shore) (Hartt and Dell 1986). In general, movements from the river mouths are nearshore along the southeast and south side of Bristol Bay to Port Moller, and offshore beyond Port Moller. Tidal currents appear to influence direction of movement, which is variable (Hartt and Dell 1986). In cold years juvenile sockeye salmon distribution may be restricted to warmer waters around the margins of Bristol Bay, and in warm years they may be distributed in cooler waters farther offshore (Straty 1974; Farley et al. 1999, 2000a, 2001c). The southwestward extent of distribution of juvenile sockeye salmon along the north side of the Alaska Peninsula

in July, August, and September may also be influenced by sea temperatures, with fish moving farther southward (west of Port Moller) earlier in the year in warm years (Straty and Jaenicke 1980; Hartt and Dell 1986; Isakson et al. 1986; Farley et al. 1999, 2000a, 2001a, c). Migration routes through Bristol Bay seem to correspond to areas with the steepest salinity gradients (Straty 1974; Straty and Jaenicke 1980; Straty 1981). Juvenile sockeye salmon in the eastern Bering Sea appear to be most abundant at or near the surface (upper 1 m at night, 2-m depth during the day) (Straty 1974). Juvenile sockeye salmon are scarce or absent in summer (June–October) sampling in neritic waters off the Aleutian Islands (Hartt and Dell 1986; Carlson et al. 1996, 1997).

Gradual offshore movements of juvenile sockeye salmon, northwestward into the Bering Sea, may continue through fall before salmon move southward through the Aleutian Passes into the North Pacific Ocean. The northwestward extent of their distribution in the Bering Sea in fall and winter is not known. Overwintering of juveniles in the Bering Sea may occur in some years (see section on High Seas Work). The area where juvenile sockeye salmon are distributed at the end of their first winter at sea may be different for individual stocks or populations, and also may be the approximate location from which maturing salmon begin their return migrations (Rogers 1988).

Historical marking studies indicate some separation in major stocks of juvenile Bristol Bay sockeye salmon as far seaward as Port Moller (Straty 1974). Differences that may contribute to stock-specific distributions include time of outmigration, travel distance from the lake system of origin, age, and size. Annual variation in time of outmigration is caused by time of ice breakup, water temperature, and wind action in nursery lakes. All Bristol Bay stocks have early, middle, and late components, but the average time of outmigration is earliest for Ugashik and Egegik smolts, intermediate for Kvichak (later in cold than in warm years), and latest for Naknek and Wood River smolts (Rogers 1988). There is substantial annual variation in the abundance and distribution of sockeye salmon juveniles in Bristol Bay on a given date, which is caused by annual variation in smolt production and migration timing in each lake system and spring weather conditions that affect the beginning of outmigration (Rogers 1977). Due to differences in migration timing, the distributions of Egegik and Ugashik smolts may not overlap those of the majority of smolts from the Naknek and Kvichak rivers, and may be well separated from the Nushagak stocks, and the separation may be greater in cold years because of greater delay in Kvichak and Wood River migrations (Rogers 1988). For example, Ugashik or Egegik River smolts may arrive at the outer boundary of Bristol Bay in mid-July, whereas Wood

River fish may not arrive there until the end of September (Bax 1985; Rogers 1988). By the time they reach Port Moller, juvenile Bristol Bay sockeye salmon stocks may be well mixed. Estimated travel rates of Bristol Bay sockeye salmon juveniles in the Bering Sea between Port Moller and Unimak Island ($3.9\text{--}6.7\text{ km}\cdot\text{d}^{-1}$) are slower than those of British Columbia stocks migrating northward in the Alaska coastal current (Skeena River, $6.5\text{--}13.9\text{ km}\cdot\text{day}^{-1}$; Fraser River, $14.1\text{--}26.7\text{ km}\cdot\text{day}^{-1}$) (Hartt and Dell 1986).

Hartt and Dell (1986) provided limited information on the distribution of other species of juvenile salmon in the eastern Bering Sea and Aleutian Islands. Most of their sampling was done from late June to September 1964–1968 in neritic waters beyond the 46-m depth contour with fine-mesh purse seines. Pink and chum salmon fry (less than 1 g in weight) begin to migrate into Bristol Bay in July (Rogers 1977). Hartt and Dell (1986) had only small catches of juvenile chum salmon in July in the eastern Bering Sea and Aleutians, which were probably composed of local stocks, but these catches increased in August in the eastern Bering Sea. Pink salmon juveniles were scarce or absent in their catches throughout the region. Juvenile coho salmon were caught in small numbers in the eastern Bering Sea in July, August, and September. Juvenile chinook salmon first appeared in eastern Bering Sea catches in late June, and were caught in all subsequent time periods. The westernmost catches of juvenile chinook salmon were south of the central Aleutian Islands during July. Data were inadequate for inferring migration patterns between juvenile and age .1 stages, but indicated that western Alaskan stocks migrated farther offshore than stocks from other North American production areas to the south. The mixing of juvenile age .0 and immature age .1 chinook salmon in both coastal and offshore waters appeared to be unique compared to other Pacific salmon species. There was no evidence of overlap in distribution of Bering Sea and Gulf of Alaska salmon stocks at the juvenile stage for any species. The direction of local movements of all species of salmon juveniles in the eastern Bering Sea was variable, apparently influenced by strong tidal currents and rich feeding conditions.

OCC research in the eastern Bering Sea in July–September indicates substantial annual, seasonal, and spatial variation in distribution by species and life history stage of juvenile chum, pink, coho, and chinook salmon (Farley et al. 1999, 2000a, 2001a, c). No juvenile salmon were caught during extensive research trawl surveys in neritic waters off the Aleutian Islands in July–August 1996–1997 (Carlson et al. 1996, 1997). There are no reported catches of steelhead trout juveniles in the eastern Bering Sea and Aleutian Islands, although steelhead trout populations

occur in some streams along the north side of the Alaska Peninsula and eastern Aleutian Islands (see review by Burgner et al. 1992).

Martin et al. (1986) provides limited information on coastal movements of Yukon River salmon juveniles. The peak outmigration of juvenile chinook salmon probably occurs during or shortly after ice breakup (early June), and there is no indication that juvenile chinook salmon utilize littoral coastal habitats in the vicinity of the Yukon Delta. Outmigration of juvenile pink salmon peaks before mid June, and pink salmon juveniles seem to move rapidly through delta habitats to the delta front. Outmigration of juvenile chum salmon peaks in late June, and juvenile chum salmon use coastal habitats and the delta front from June through early August. Similar movements of juvenile chum salmon were observed in Norton and Kotzebue Sound (see review by Martin et al. 1986). Millions of juvenile chum salmon are dispersed by high river discharges through numerous tributary channels into coastal habitats surrounding the Yukon delta, and catches in coastal habitats decreased as water temperatures increased to $18\text{--}21^{\circ}\text{C}$ in mid-July.

In conclusion, while general information on broad-scale and regional movements of juvenile salmon in U.S. coastal waters is probably sufficient, better field data on local, stock-specific movements is needed in almost every region. At the limits of coastal distribution of juvenile salmon (California, Arctic–Yukon–Kuskokwim, and Aleutian Islands), even the most basic information on juvenile salmon movements is sometimes lacking. Coastal field investigations in many U.S. regions have been conducted only in summer in neritic habitats, and for most species and stocks we do not have any information on October–December movements. There are few or no data on movements of small juvenile salmon in littoral habitats along most of the outer U.S. coastline. Better field data on spatial and temporal variation in stock-specific movements, distribution, migration routes and rates of juvenile salmon in marine habitats both on and off the continental shelf will improve our ability to estimate their abundance, growth, and survival.

DIET IN COASTAL WATERS

A substantial body of literature has accumulated on the food habits and feeding ecology of juvenile salmon in coastal waters of the U.S. Some of this information is presented by species and life history stage in Brodeur (1990). These studies fall into the broad categories of food habits, feeding selectivity, daily ration, and food consumption.

Food items preyed upon by juvenile salmon have been studied extensively in protected areas such as southeast Alaska and Puget Sound. Pink and chum

salmon near shore feed on a variety of plankton but copepods predominate (Bailey et al. 1975). Simenstad et al. (1982) summarized diet information for juvenile salmonids from 16 different estuaries in Puget Sound and along the Washington coast. Juvenile pink salmon were found to feed almost exclusively on small zooplankton such as copepods and larvaceans. Juvenile chum showed a more diverse diet including epibenthic crustaceans (haracticoid copepods) and emergent insects, and switch to planktonic prey at a larger size. Chum salmon juveniles appear to be more selective than pink salmon. Juvenile sockeye salmon consume larger zooplankton prey (e.g., euphausiids, juvenile shrimp, and decapod larvae). Because of their larger size when entering the estuaries, juvenile coho salmon forage on large planktonic or small nektonic prey, including decapod larvae, fish larvae and juveniles, and euphausiids. Finally, juvenile chinook salmon utilize a broad trophic spectrum due to their extended residence in some estuaries, ranging from insects, amphipods, mysids, and nekton. Other estuarine and nearshore food studies have documented the diversity of prey items in relation to fish size, seasonality, and various habitats (e.g. Landingham and Mothershead 1988; Murphy et al. 1988; Landingham et al. 1998).

The general diets of juvenile salmon in coastal waters are fairly well known for all salmon species in much of the continental shelf region off the West Coast and Alaska (Table 4). Quantitative studies of the diet of juvenile salmonids in the California Current include those by MacFarlane and Norton (2002) and Norton (2002) for California; Peterson et al. (1982), Emmett et al. (1986), Loch and Miller (1988), Brodeur and Percy (1990), Percy et al. (1990), Brodeur (1991), and Schabetsberger et al. (2003) for Oregon and Washington; Andrews (1970), Jaenicke et al. (1984), Landingham et al. (1998), and Auburn and Ignell (2000) for outside waters of Southeast Alaska; Cooney et al. (1981), Sturdevant et al. (1996), Moulton (1997), and Boldt (2001) for northern Gulf of Alaska; and Straty (1974) and Carlson (1976) for the Bering Sea. These studies find some intraspecific differences in type and size of prey consumed by salmonids with coho and chinook salmon and cutthroat trout tending to be mainly piscivorous, steelhead trout more omnivorous, and pink, chum, and sockeye salmon more planktivorous. Diet composition changes markedly with ontogeny toward larger and more evasive prey in later juvenile stages (Brodeur 1991; Boldt 2001). Interannual and seasonal differences in prey availability can lead to major differences in diet composition (Brodeur and Percy 1990).

Quantitative examination of feeding selectivity, daily ration, and food consumption are less common and even completely lacking for juvenile salmon in several systems. Feeding selectivity has been ad-

ressed by Brodeur et al. (1987), Brodeur (1989), and Schabetsberger et al. (in press) for juvenile coho and chinook salmon off Oregon and Washington. They found that juvenile salmon are highly opportunistic in their feeding habits but tend to select the most visually obvious prey within the suitable size range. These studies, along with that of Landingham et al. (1998), show that salmon often consume prey associated strictly with the near surface neustonic layer.

Brodeur and Percy (1987) estimated the daily ration of juvenile coho salmon based on the diel trajectory of stomach content weight and laboratory-derived evacuation rates. Coho salmon juveniles were found to feed primarily at the crepuscular (dawn and dusk) periods. These ration estimates (2.4–3.7% body weight per day depending on the temperature) were found to yield similar estimates of food consumption compared with estimates made using bioenergetic models (Brodeur et al. 1992). Studies of the overall consumption of juvenile salmon utilizing bioenergetic models suggest very little if any food limitation in coastal waters. Brodeur et al. (1992) found that juvenile chinook and coho salmon have the potential to easily exhaust the available fish prey resources during anomalous low-productivity years (e.g. during the 1983 El Niño), but generally they consume substantially less than 1% of the total production during normal years. Based on bioenergetic consumption estimates, juvenile pink salmon in Prince William Sound, Alaska were also estimated to have consumed less than 1% of the total annual zooplankton production in the sound (Boldt and Haldorson 2002). However, their impact may be more severe (up to 8.2%) in a restricted geographic nearshore area where pink juveniles generally reside in the sound. Also, if standing stocks of zooplankton were assumed to be stable over a 10-day period, consumption of some key zooplankton groups such as large calanoid copepods and hyperiid amphipods ranged from 15–19% of the standing stock in Prince William Sound (Boldt and Haldorson 2002).

MARINE PREDATION

Predation is likely to be the major source of mortality for most juvenile salmon when they first enter the marine environment. Juvenile salmon may be preyed upon by a variety of predators in the estuarine and coastal environments, including adult salmon, other fishes, seabirds, and marine mammals (Fresh 1997). In some cases, introduced species such as striped bass (*Morone saxatilis*) in the Coos Bay Estuary in Oregon have been estimated to consume many juvenile and adult salmonids (Johnson et al. 1992). However, despite some extensive studies examining potential predation on juvenile salmon, there have been relatively few documented examples of large numbers of juveniles being consumed in marine

Table 4. Studies on juvenile salmon feeding habits conducted in U.S. coastal waters.

Geographic Region	Species	Month	Year	Number Examined	Main Prey	Source
California	chinook	May–Sept.	1995–1999	146	fishes, decapods, euphausiids, copepods	Norton (2002)
Washington/ Oregon	coho	June	1979	220	fishes, euphausiids, amphipods	Peterson et al. (1982)
	chinook			146	fishes, euphausiids, amphipods	
	chum			41	euphausiids, amphipods, decapods	
	chinook	May–Sept.	1980	174	fishes, decapods, amphipods	Emmett et al. (1986)
	coho			137	fishes, euphausiids, amphipods, pteropods	
	cutthroat	May–June	1980	17	fishes, mysids, decapods	Loch and Miller (1988)
	coho	June–Sept.	1984	217	fish, decapods, euphausiids, insects	Brodeur (1989)
	chinook			118	fish, decapods, euphausiids, copepods	
	cutthroat	May–Aug.	1981–1985	67	fish, decapods, euphausiids	Pearcy et al. (1990)
	steelhead			98	fish, decapods, euphausiids, amphipods	
	coho	May–Sept.	1980–1985	1652	fish, decapods, euphausiids, pteropods	Brodeur and Percy (1990)
	chinook			844	fish, decapods, euphausiids, amphipods	
	chum			109	euphausiids, fish, chaetognaths, copepods	
	sockeye			32	euphausiids, fish, amphipods, copepods	
	chinook	June	2000	249	amphipods, fish, decapods, euphausiids	Schabetsberger et al. (2003)
	coho			98	amphipods, fish, euphausiids	
SE Alaska	sockeye	NA	1967–1968	996	euphausiids, fish larvae, pteropods, copepods	Andrews (1970)
	coho	July	1982	45	fish, euphausiids, amphipods, decapods	Jaenicke et al. (1984)
	chum			17	euphausiids, amphipods, copepods	
	pink			14	euphausiids, amphipods, copepods	
	sockeye			5	euphausiids, amphipods, copepods	
	pink	July–Aug.	1983–1984	452	amphipods, fish, euphausiids, tunicates	Landingham et al. (1998)
	chum			210	tunicates, fish, amphipods	
	sockeye			279	fish, amphipods, euphausiids, copepods	
	coho			127	fish, decapods	
	pink	Oct. –Nov.	1995	227	pteropods, fish, hyperiids, euphausiids	Sturdevant et al. (1997)
	chum			120	larvaceans, euphausiids, hyperiids	
	coho			70	fish, euphausiids, hyperiids	
	sockeye			10	euphausiids, pteropods, gelatinous	
	pink	July	1996	130	euphausiids, hyperiids, calanoids, fish	Auburn and Ignell (2000)
	sockeye			120	euphausiids, calanoids, fish, hyperiids	
	chum			112	euphausiids, hyperiids, calanoids, fish	
	coho			147	fish, euphausiids	
N. Gulf of Alaska/ Aleutian Islands	pink	July–Aug.	1996	110	euphausiids, hyperiids, pteropods, fish	Auburn and Ignell (2000)
	sockeye			99	euphausiids, fish, decapods	
	chum			80	hyperiids, euphausiids, fish	
	coho			80	fish, euphausiids, decapods	
	pink	July–Oct.	1998	104	pteropods, hyperiids, larvaceans, copepods	Boldt (2001)
Bering Sea	sockeye	June–Sept.	1969–1970	>1200	fish, euphausiids, copepods, pteropods	Straty (1974)
	sockeye	June–Sept.	1966–1967	160	copepods, fish, decapod larvae	Carlson (1976)

waters (e.g., Buckley 1999). However, because of the high abundance of some potential predators, a relatively low incidence of predation over a long period of time can lead to a high cumulative mortality on some populations.

Pearcy (1992) reviewed what was known about predators on juvenile salmon along the U.S. West Coast. Few marine fish predators have been identified, but those that were identified as predators include salmonids (Fresh et al. 1981; Stuart and Buckman 1985; Brodeur et al. 1987; Pearcy et al. 1990) and non-salmonids such as rockfish (*Sebastes* spp.) and Pacific whiting (*Merluccius productus*) (Brodeur et al. 1987; Emmett et al. 2001). However, many of these studies were done in coastal waters, and much of the predation could be occurring in the very near-shore region and in river mouths, where predators may be attracted to large pulses of migrants, particularly in systems with hatcheries (Emmett 1997; Peterson and Brodeur 1997).

Documenting bird and marine mammal predation may be even more problematic because of the difficulties in collecting specimens for stomach analysis. Common murre *Uria aalge* have been shown to aggregate and actively feed during release periods of a hatchery near the mouth of Yaquina Bay (Bayer 1986). Salmonids were an important part of the diet of common murre collected in coastal waters offshore of several estuaries along the Oregon Coast (Mathews 1983). Based on the occurrence of PIT tags at a single colony on a man-made island in the lower Columbia River, Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*) were estimated to consume more than 50,000 juvenile salmon and steelhead trout (Collis et al. 2001). The annual consumption of juvenile salmon by terns alone has been estimated to be 8.1 million (1997) and 12.4 million (1998) fish, based upon bioenergetic modeling (Roby et al. 2003). Pinnipeds such as harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*) appear to be the major marine mammal predators on salmon in the Pacific Northwest (Everitt et al. 1981; Brown and Mate 1983; Zamon 2001; Laake et al. 2002), although much of the impact is on returning adult runs in estuaries.

In Alaskan waters, there have also been a number of studies on predation on juvenile salmon. Early observations of predators upon juvenile salmon in estuaries or nearshore ocean waters include Dolly Varden char (Lagler and Wright 1962), Pacific herring *Clupea harengus* (Thorsteinson 1962) and wall-eye pollock *Theragra chalcogramma* (Armstrong and Winslow 1968). Wing (1985) found juvenile salmon in troll-caught adult coho salmon in Southeast Alaska. Dolly Varden char, great sculpin, *Myoxocephalus polyacanthocephalus*, Pacific staghorn

sculpin, *Leptocottus armatus* and buffalo sculpin, *Enophrys bison*, were all found to prey on juvenile salmon (Mortensen et al. 2000). As a component of a multiyear study analyzing salmon habitats in Southeast Alaska, Orsi et al. (2000) examined diets of 19 potential fish predators and found only four species consumed juvenile salmon. Only sablefish *Anoplopoma fimbria* and adult coho salmon were found to be important predators.

Probably one of the most concerted efforts to examine predation on juvenile salmon in U.S. waters has been accomplished as part of the SEA program in Prince William Sound (Willette et al. 2001). The target species in this study was juvenile pink salmon, a species that is released by the millions from hatcheries each year, in addition to the substantial wild production. Based on field estimates of predator abundance and diet, these authors were able to estimate the consumption of juvenile pink salmon by key predators. They found that Pacific herring and wall-eye pollock were the dominant piscivorous fish predators. Willette et al. estimated that nine fish and avian predator groups consumed approximately half of the annual production of pink salmon in the Sound. Finally, predation pressure appears to be less in the nearshore environment than offshore in the Sound. In one of the most quantitative estimates of predation impact by seabirds, Scheel and Hough (1997) estimated that seabirds foraging near a hatchery in Prince William Sound consumed between 1.1 and 2.4% of the hatchery production of pink salmon during their study period. Willette (2001) suggests that the seasonal availability of prey such as copepods in inshore regions influenced the offshore migration and subsequent consumption of juvenile salmon. Populations of marine birds and mammals are fairly high throughout much of Alaska, and a number of important salmon predators, including several seals, whales, eagles, gulls, and terns, have been identified (Straty 1974; Meachum and Clark 1979).

GROWTH AND MORTALITY PATTERNS IN ESTUARIES AND COASTAL OCEANS

Juvenile salmon generally exhibit little growth in most estuaries. For example, Reimers (1973) found that juvenile chinook salmon in the Sixes River Estuary in southern Oregon grew at a rate of $0.07 \text{ mm} \cdot \text{day}^{-1}$ in the summer which was attributed to food limitation. Growth rates of juvenile chinook salmon were estimated to be relatively low ($0.18 \text{ mm} \cdot \text{day}^{-1}$) in the San Francisco Estuary but increased rapidly ($0.6 \text{ mm} \cdot \text{day}^{-1}$) in the coastal ocean (MacFarlane and Norton 2002). Estimates of yearling chinook salmon growth rate in the Columbia River estuary and coastal ocean based on CWT recoveries were on the

order of $1.05 \text{ mm} \cdot \text{day}^{-1}$ in length and 1% body weight $\cdot \text{day}^{-1}$ (Fisher and Pearcy 1995). Fisher and Pearcy (1988) observed substantial variability in marked and unmarked juvenile coho salmon growth rates over five years of sampling (range $0.36\text{--}2.20 \text{ mm} \cdot \text{day}^{-1}$ in length). They showed that coho salmon survival is positively correlated to early (March–June) upwelling, even in low upwelling years, but growth of smolts caught in coastal waters was not. Growth rates of coho salmon jacks returning after one summer at sea were related to the cumulative upwelling strength for the whole summer (March–September) and showed substantial differences between poor and moderate upwelling years. In juvenile coho salmon maturing after more than one summer at sea captured off Oregon and Washington from 1998 to 2000, growth rates ranged from 0.63 to $1.61 \text{ mm} \cdot \text{day}^{-1}$ in length, with the highest growth rates occurring in fish caught off southern Oregon (Brodeur et al. 2003). Overall, growth rates of CWT coho salmon during their first four months at sea were between 1.8 and $2.5\% \text{ BW} \cdot \text{day}^{-1}$, which may be close to their predicted physiological maximum rates, but they decreased to about $0.6\% \text{ BW} \cdot \text{day}^{-1}$ by the second summer of life (Fisher and Pearcy, unpublished manuscript, available from J. Fisher, Oregon State University, Corvallis). Mathews and Buckley (1976) found growth rates of $1.7\% \text{ BW} \cdot \text{day}^{-1}$ for Puget Sound coho salmon during their first summer at sea.

Juvenile salmon grow rapidly in the marine environment. Larger pink salmon move from the near-shore habitats to the middle of the bay (Mortensen and Wertheimer 1988). Mortensen et al. (2000) documented that greater early growth in juvenile pink salmon resulted in higher survival to adults. This higher survival resulted from less predation. Taylor et al. (1987) showed that the earliest emigrants from Auke Creek stayed longer in Auke Bay than did later emigrants from the stream. Murphy et al. (1999) sampled juvenile salmon with a rope trawl in May, June, July, August, and October in northern southeast Alaska. They found that the mean length of coho salmon increased more each month than the other species. Mean length of sockeye salmon showed the lowest rate of increase, and pink and chum salmon showed similar size increases and were intermediate in growth rate between coho and sockeye salmon.

In Prince William Sound, Willette et al. (2001) found that juvenile pink salmon that have higher sustained growth rates shortly after entering the marine environment tend to suffer lower predation rates. They also showed that the growth rates of hatchery fish are directly related to the density of zooplankton available to them, especially during years when the total release from the hatchery was > 20 million fish. This suggests that there is density-dependent growth limitation in the system and Willette et al. suggest

that these juveniles may adopt foraging strategies that maximize their growth rates.

ENVIRONMENTAL CORRELATES WITH SURVIVAL AND LIFE HISTORY

Population models indicate that long-term survival prospects of most salmon stocks are dependent on both freshwater and ocean conditions (Lawson 1993). Perhaps the most intensely studied population of salmon with respect to ocean environmental conditions relating to survival has been that of coho salmon in the Oregon Production Index (OPI) area from southern Washington to northern California. Early studies had suggested that the magnitude of the coastal upwelling, or factors associated with upwelling early in the summer during smolt outmigration, have an effect on the return of adult OPI coho salmon the following year (Scarnecchia 1981; Nickelson and Lichatowich 1984; Anderson and Wilen 1985; Nickelson 1986). Nickelson (1986) showed that there was a threshold level of upwelling intensity below which marine survival of hatchery coho salmon was always low ($< 5\%$) but above which survival was high. Contrary to previous observations, he found that the smolt-to-adult relationship was linear for wild, public hatchery and private hatchery fish analyzed separately, thus implying that a density-independent relationship existed. However, more recent work extending the time series of OPI into the 1980s and 1990s shows that this relationship has disintegrated (Lawson 1997) and, in fact, there has been an inverse, but insignificant, relationship between upwelling and OPI survival from 1982–1992 (Pearcy 1997).

Cole (2000) examined sea surface temperatures (SST) available from satellite data and found that OPI coho salmon survival was enhanced during cool years in their first spring, but warm temperatures during their first winter negatively affected survival. A recent study by Logerwell et al. (2003) looked at four uncorrelated environmental factors hypothesized to be important in the early life history of OPI coho salmon. These include (1) climate conditions as the smolts enter the ocean, (2) the spring transition between downwelling and upwelling, (3) ocean conditions during the spring upwelling, and (4) winter conditions at the end of the first year at sea. They found that their model predicted a substantial amount of the variability in OPI survival, and suggest that the model may have utility in predicting ocean survival.

Recent work has used the extensive coded-wire database to examine survival at the individual stock level and determine environmental factors related to these survival levels. Coronado and Hilborn (1998) examined the geographic patterns in survival of coho salmon from Oregon to Alaska based on CWT returns. They found that large-scale regions had simi-

lar patterns of survival that most likely are related to where the smolts first enter the ocean. However, these authors did not attempt to relate these survival patterns to marine variables. Ryding and Skalski (1999) used CWT data from hatcheries on or near the U.S. west coast to isolate marine effects. They found that some variables (June SST, spring transition timing) were not linearly related to survival, implying that some optimal conditions exist for these variables. Hobday and Boehlert (2001) examined a large number of coho salmon stocks (225 river systems) throughout this species' range in North America and six environmental variables calculated on spatial and temporal scales appropriate for early ocean influences of each stock. These authors found that survival was influenced most by environmental conditions occurring in late summer, and that these conditions most affected salmon in the southern region, followed by those of the northern region and then Puget Sound. Mixed-layer depth was found to be the most critical variable affecting juvenile salmon survival and size of jacks and adults. Koslow et al. (2002) examined salmon survival relative to a large suite of environmental variables specific to certain regions of the ocean and collapsed the data using Principal Component Analysis. These relationships were examined for both early marine residence and the winter-spring period prior to spawning migrations. They were able to identify components of the environment that accounted for a substantial part of variability in hatchery and wild coho salmon survival. Included among these were upwelling, cool surface temperatures, strong wind mixing, deep mixed layer, and strong transport of the California Current. In contrast to the results of Ryding and Skalski (1999), all relationships with survival were found to be linear. More recent studies have addressed the effects of ocean climate variables on Columbia River chinook salmon populations (Levin 2003).

There have been surprisingly few studies of this type looking at the relationship between salmon survival and environmental variables outside of the Pacific Northwest. Kope and Botsford (1990) examined the relationship between chinook salmon recruitment in central California and variables such as upwelling, sea surface height and temperature and found better relationships with survival in the final ocean year than the first summer. Botsford and Lawrence (2002) examined patterns of covariability in coho and chinook salmon and Dungeness crab (*Cancer magister*) catch rates throughout the California Current in relation to environmental data collected at the same spatio-temporal scales. Coho salmon were found to vary synchronously from Northern Washington to Central California on annual time scales whereas chinook salmon vary on longer time scales with population-specific patterns. Attempts at correlating salmon recruitment and climate in Alaskan

waters have shown some correlations but generally at lags that seem difficult to associate with direct causal mechanisms (e.g., Quinn and Marshall 1989; Adkinson et al. 1996; Downton and Miller 1998). Clearly more studies could be done as time series of survival and environmental conditions attain sufficient length for suitable analyses.

STUDIES OF HATCHERY VERSUS WILD FISH INTERACTIONS

Mahnken et al. (1998) reviewed annual production trends (1900–1992) and survival trends (1970–1990) for hatchery salmon in the Pacific Northwest (Washington, Oregon, Idaho, and California) and Alaska. Despite a long history of concerns about hatchery and wild stock interactions (predation, competition), there have been few field investigations focusing directly on this issue (Fresh 1997; Heard 1998), perhaps largely because of the difficulty in identifying the hatchery or wild origin of individual fish in mixed-stock catches at sea.

In the Pacific Northwest, concerns about declining salmon survival rates, rapidly expanding public and private sea ranching operations, and intensive shoreline development and pollution have prompted numerous field investigations of the estuarine and early marine life history of juvenile salmon since the 1960s (e.g., Sims 1970; Johnson 1973; Reimers 1973; Moore et al. 1977; Schreiner 1977; Myers 1978; Rasch and O'Conner 1979; Myers 1980; Simenstad et al. 1980; Bax 1982; Durkin 1982; Kjelson et al. 1982; Myers and Horton 1982; Pearce et al. 1982; Simenstad and Salo 1982; Bax 1983b; Miller et al. 1983; Percy 1984a, b; Dawley et al. 1985a, b; Fisher and Percy 1988; Percy and Fisher 1988; Percy et al. 1989; Fisher and Percy 1990; Percy and Fisher 1990; Percy et al. 1990). Although the focus of most studies was not to evaluate hatchery and wild stock interactions, many provide at least some data pertinent to this issue.

A variety of techniques have been used to identify hatchery or wild stocks or both in mixed-stock catches (e.g., tags, fin clips, dye marks, scales, hatchery species and release dates, external parasites, visceral fat, fish size, and fin erosion). Evidence from these and other similar studies demonstrates overlap in spatial and temporal distribution and food habits of hatchery and wild juvenile salmon in estuarine and coastal habitats, and sometimes predation of larger hatchery juveniles on smaller hatchery or wild juveniles. Species, time, and size (age, growth rate) at marine entry, and distribution and abundance of prey appear to be the most important factors influencing the overlap in utilization of marine habitats by hatchery and wild juvenile salmon. The potential for negative effects (decreased growth and survival) from hatchery and wild stock interactions exists, if prey resources are limited or foraging success is poor.

In Alaska, an increasing percentage of hatchery salmon releases have had thermal marks placed on their otoliths since the mid-1990s (approximately 60% in 2000) (Scott et al. 2001). A number of NMFS Auke Bay Laboratory field investigations have demonstrated that thermally-marked hatchery salmon releases are sufficient to enable recoveries in inland, coastal, and high seas salmon surveys (e.g., Farley and Munk 1997; Carlson et al. 2000; Farley and Carlson 2000; Orsi et al. 2000; Farley et al. 2001d; Orsi et al. 2001b). These studies are providing valuable new information on the ocean distribution, migration, growth, and abundance of juvenile hatchery salmon (see section on coastal movements); however, differentiation of unmarked hatchery fish and wild fish in mixed-stock catches is still problematic.

Over the past decade a system of major hatcheries in Prince William Sound have produced 70–80% of large pink salmon returns to that region (averaging 27 million fish per year). This development has created controversy over potential impacts of hatchery production on local wild stocks. These hatcheries have released over 650 million juvenile pink salmon into Prince William Sound annually (McNair 2002) and some scientists have suggested that this number of hatchery fry can have a deleterious impact on smaller numbers of wild fry probably through density-dependent interactions in early marine life history stages. Hilborn and Eggers (2000) examined a series of factors and argued that pink salmon hatchery production in Prince William Sound has essentially replaced wild stock production that would have occurred in the absence of hatcheries. These authors also believe that the large hatchery program was reducing the basic productivity of local wild stocks. Wertheimer et al. (2001), however, analyzed the same data sets and concluded that hatcheries were supplementing wild stock production with a net gain of 17.5–23.7 million pink salmon to fisheries annually in the region. A further detailed modeling study that examined a broad series of bio-environmental variables (Wertheimer et al. in press) concluded that variable regional conditions in the marine environment, rather than numbers of hatchery fry, best explain the changes over time in wild stock production of pink salmon in Prince William Sound.

Pioneering research by the University of Alaska in Prince William Sound where 100% of hatchery releases are thermally otolith-marked, found no significant differences in caloric content of wild and thermally otolith-marked hatchery juvenile pink salmon caught at the same geographic locations (Boldt 2001). Significant geographical differences in caloric content of both hatchery and wild stock groups indicated extended periods of local mixing of hatchery and wild juveniles, and low caloric content at some locations may have been related to local prey depletion (Boldt 2001). Since the late 1990s, U.S.

GLOBEC and many other programs have focused their research efforts on climate and physical and biological oceanographic effects on the distribution, growth, and survival of juvenile salmon in coastal waters (see overview of major field research programs). Pearcy (1997) predicted that a change to less favorable ocean conditions would result in more evidence of density-dependent interactions between hatchery and wild salmon stocks.

MOVEMENT TO THE HIGH SEAS, TIMING AND SPEED OF MOVEMENT

Broad syntheses of catch, biological, and stock identification data by Canadian, Japanese, and U.S. scientists of the INPFC provided conceptual models of the movements of juvenile salmonids to the high seas (Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978; Takagi et al. 1981; Hartt and Dell 1986; Burgner et al. 1992). Among salmonid populations known to migrate to the high seas, those of juvenile steelhead trout appear to move offshore relatively soon after ocean entry in the spring or early summer, whereas those of juvenile Pacific salmon move offshore later in the fall or early winter following ocean entry. As described in our overview of major field investigations, however, most U.S. research on juvenile salmonids has emphasized spring and summer (April–September) work in inside and coastal waters (mainly within 200 km from the shoreline). There has never been a comprehensive U.S. field research effort to determine the timing and extent of movements of juvenile salmon and steelhead trout from coastal waters to the high seas (international waters, beyond the U.S. 200-mile zone). Among all U.S. geographical regions, salmonid species, and populations, western Alaska salmon (sockeye, chum, pink, coho, and chinook salmon) and Pacific Northwest steelhead trout seem to make the most extensive high seas migrations as juveniles. Juvenile salmon from many U.S. populations may never migrate far offshore, but nevertheless make extensive migrations to inside and coastal waters distant from their rivers of origin (see section on movements in coastal waters). The proportions of U.S. salmonids migrating to the high seas and those remaining in coastal waters are not known.

The most comprehensive U.S. research on movements of western Alaska juvenile salmon to the high seas has focused largely on Bristol Bay sockeye salmon. Investigations by the NMFS Auke Bay Laboratory in the eastern Bering Sea from the mid 1960s to the early 1970s, indicated that juvenile Bristol Bay sockeye salmon begin their seaward movements in mid-August from the area along north side of the Alaska Peninsula beyond Port Moller (Straty 1974; Carlson 1976; Straty and Jaenicke 1980; Straty 1981). The timing of seaward movements of juve-

niles coincides with the departure from the high seas of major runs of adult sockeye salmon to Bristol Bay and adult pink salmon to eastern Kamchatka Peninsula. By mid-September large numbers of juvenile sockeye salmon are distributed to at least 167 km offshore in the eastern Bering Sea (east of 166°W). Pioneering winter high-seas gillnet research by the NMFS Northwest and Alaska Fisheries Science Center from 1962–1970 indicated that by January and early February relatively few juvenile sockeye salmon remain in the Bering Sea, and that they are broadly distributed across the central and eastern North Pacific (north of 46°N, between at least 175°E to 150°W) (French and McAlister 1970; Bakkala 1971; Bakkala and French 1971; French and Bakkala 1974). Estimated migration routes of juvenile Bristol Bay sockeye salmon from the Bering Sea to the North Pacific are through the Aleutian passes, and their winter high seas distribution in the North Pacific extends southward to at least about 46°N in the central North Pacific and 48–51°N south of the Alaska Peninsula. Their migrations cover an estimated horizontal distance of 1,300–1,850 km at a rate of at least 14.8–18.5 km·day⁻¹ (French and Bakkala 1974). These and other estimates of travel rates (Table 3) are probably conservative because a cooperative Japan-U.S.-Canada high-seas trawl survey in 1992 found that juvenile sockeye salmon are distributed in international waters of the central and eastern North Pacific early in December, which would require much faster migration rates for some individuals (Nagasawa et al. 1994). A field research program on juvenile Bristol Bay sockeye salmon initiated by Auke Bay Laboratory in 1999 is providing additional information on the extent of their seaward movements in July–September (see section on coastal movements) (Farley et al. 1999, 2000a, 2001c).

In the eastern North Pacific Ocean in summer (through August), most juvenile salmon are concentrated in coastal and inland waters, but opportunistic sampling has shown that juvenile coho and chinook salmon occur in small numbers in high seas areas as early as July and August, and that some juvenile steelhead trout move to the high seas as early as June (e.g., Hartt and Dell 1986; Burgner et al. 1992). A few coded-wire tagged juvenile steelhead trout released from U.S. Pacific Northwest coastal and Columbia River hatcheries in April have been recovered in July in the international waters of the eastern North Pacific during cooperative Japan–U.S. tagging programs (Percy and Masuda 1982; Myers et al. 2001b). These data, however, are insufficient to estimate exact timing, migration speeds, and migration routes of juvenile steelhead trout to the high seas. A cooperative Japan–U.S.–Canada high-seas trawl survey in 1992 found that juvenile sockeye, chum, pink, coho, and chinook salmon were distributed in international waters of the Gulf of

Alaska in December (Nagasawa et al. 1994). Fall and winter research in this region has been inadequate to indicate the exact migration routes and precise travel rates of juvenile salmon moving offshore.

HIGH SEAS WORK

High-seas salmon research, which focused primarily on investigations of the distribution of immature and adult salmon in spring and summer (April–September), was conducted as part of the U.S. research commitment to the INPFC (see annual reports of U.S. research in International North Pacific Fisheries Commission (INPFC) 1955–1992). Tagging and fine-mesh purse-seine fishing operations by FRI in 1964–1968, designed to study movements of juvenile salmon, were conducted primarily in coastal waters, where juveniles are concentrated in summer (see section on coastal movements) (Hartt and Dell 1986). High-seas tagging operations by FRI with longlines in the Gulf of Alaska, 1964–1966, were coordinated with similar operations by Canada and Japan, and provided some information on high seas distributions of juvenile salmon. Research by the NMFS Northwest Fisheries Science Center with multi-meshed gill-nets in winter (January–March 1962–1970) provided partial information on the high-seas distribution of juvenile salmon during their first winter at sea (French and Mason 1964; French et al. 1969; French and McAlister 1970; see INPFC Annual Reports, 1962–1970). Fisheries-oceanographic research by the U.S. Fish and Wildlife Service defined major oceanographic features and related them to the high-seas distribution of salmon (see INPFC Annual Reports, 1959–1971). A comprehensive analysis by FRI of Canadian and U.S. (1955–1990), Russian (1983–1990), and Japanese (1981–1989) research vessel data provided some information on the high-seas distribution and growth of juvenile steelhead (Burgner et al. 1992). The results of international cooperative NPAFC winter research on juvenile salmon in the 1990s, during trans-Pacific cruises of the Japanese R/V *Kaiyo maru*, are summarized by Mayama and Ishida (this volume).

Historically, most work by NMFS on the high seas emphasized research on Bristol Bay sockeye salmon. To capture juvenile sockeye salmon in winter, net panels with small meshes (508 mm and 635 mm stretched mesh) were added to a standard string of panels with larger meshes for capturing older immature and adult salmon. These small-mesh panels, however, may not have been fine enough to capture the smallest size groups of juvenile salmon. The gill-net survey data showed that juvenile sockeye salmon are distributed over a broad oceanic region in January–March (170°E–145°W, 45–57°N). Occurrence in winter of juvenile sockeye salmon in the Bering Sea and western North Pacific Ocean (near 170°E)

was relatively low, and major concentrations were in the central (near 46°30'N) and eastern (48–51°N, 165–155°W) North Pacific (French and Bakkala 1974). In the Bering Sea, juvenile sockeye salmon were distributed farther south than older sockeye salmon, but experimental fishing to the north beyond the northern stations where sockeye salmon were caught was not possible because of sea ice (French and Mason 1964). There was considerable annual variation in the average size of juvenile sockeye salmon in winter, and fish caught in the Bering Sea tended to be larger than those caught in the North Pacific (French 1966). French and Bakkala (1974) concluded from age composition data that many of the juvenile sockeye salmon in their winter high seas catches were of Bristol Bay stocks. These fish migrated to the northeastern Pacific Ocean by January and February of their first year at sea, and predominated in winter catches eastward from 175°E to about 160°W and possibly to 155°W in years of high abundance. Estimated migration routes of juvenile Bristol Bay sockeye salmon from the Bering Sea to the North Pacific were through the Aleutian passes, between 179°E and 169°W (see above section on movements to the high seas) (Royce et al. 1968; French and Bakkala 1974).

In winter, juvenile sockeye salmon were generally not caught in the Bering Sea or North Pacific Ocean at extremes of cold or warm SSTs. The largest catches were at 3.5°–5.5°C SST (French and Bakkala 1974). In the North Pacific Ocean, catches of juvenile sockeye salmon were often associated with a specific water mass, called the Oyashio Extension (originating as western Subarctic water and extending eastward to about 150°W in the Gulf of Alaska). This water mass was characterized by low salinities, a weak eastward current, and a 200 to 400 m deep core of cold (< 3.6°C) water (French and McAlister 1970; Bakkala 1971). In some years, however, when this water mass (combined with eastward flowing Subarctic Current waters and called the Western Subarctic Intrusion) shifted northward, juvenile salmon remained at about the same latitudes (near or south of 50°N) in the Transition area waters, which are characterized by relatively warm temperatures of 4–9°C at 200 m (French and Bakkala 1974). In addition to looking at the effects of large water masses, the importance of local, transient oceanographic features, e.g., the sharp temperature-salinity fronts where salmon were sometimes concentrated, were also investigated (e.g., Favorite et al. 1971, 1972). Synoptic, repetitive high seas fishing and oceanographic sampling at fixed locations was often not possible, but an important conclusion from this work was that proper interpretation of high-seas catch statistics requires data on short-term changes in local environmental conditions (Favorite et al. 1972). This type of intensive fisheries-oceanographic field research to

define high-seas salmonid habitats is beyond the scope of any U.S. high-seas salmon research since conducted.

The U.S. high-seas data for other species of juvenile salmon are even more limited than for sockeye salmon. What little information is available has been summarized in INPFC joint comprehensive reports on distribution and origin of salmon in offshore waters by Canada, Japan, and the United States (Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978; Takagi et al. 1981). Few juvenile chum salmon were caught during U.S. winter surface gillnet and longline surveys, perhaps because of their small size or other factors related to gear selectivity, feeding behavior, or vertical distribution (Neave et al. 1976). Tagging data show that some West Coast and Alaska populations of pink and coho salmon make extensive high-seas migrations (Myers et al. 1996). United States and Canadian longline catches of pink salmon in the Gulf of Alaska showed that by November at least some juvenile pink salmon are distributed offshore, and that by January and February pink salmon, averaging 30 cm long, are broadly distributed across the southern Gulf (45–51°N, 133–156°W) (Royce et al. 1968; Hartt and Dell 1986). High-seas catch data from areas west of 180° W longitude in January–March showed that both pink and coho salmon were distributed south of 46°N (Godfrey et al. 1975; Takagi et al. 1981). Catch data have also shown that in January–March coho salmon are distributed in the central Gulf of Alaska (50°N, 150–160°W) (Godfrey et al. 1975). NMFS observer data indicated that in December at least some juvenile chinook salmon are distributed in the international waters of the central Bering Sea (Florey 1975).

Juvenile steelhead trout first appear in high seas catches in June, and in the Gulf of Alaska from spring through fall, their numbers decrease in coastal catches and increase in high seas catches (Pearcy and Masuda 1982; Hartt and Dell 1986; Burgner et al. 1992). Hartt and Dell (1986) and others have hypothesized that steelhead trout migrate directly offshore from the point of ocean entry, but there are no data on migration routes and travel rates (see section above on movements to the high seas). Most juvenile steelhead trout from U.S. basins probably remain in the Gulf of Alaska throughout their first summer and fall, although the known westward range of juvenile steelhead trout in summer extends to 180° longitude in the central North Pacific Ocean (Burgner et al. 1992). There are too few samples of juvenile steelhead trout from high seas surveys to describe their winter distribution. By the following spring, their high-seas range extends across the North Pacific (125°W–155°E), and has shifted southward (generally south of 52°N in the Gulf of Alaska and south of 48°N in the central North Pacific; Burgner et al.

1992). Japan–U.S. research gillnet surveys in the central Gulf of Alaska in summer 1993–2000 showed that juvenile steelhead trout were distributed at all latitudes sampled from 49°N to 56°N (8–13°C SST), and were most frequent in catches at 52°N (10°C SST) (Myers et al. 2001b). In this region, mesoscale (200–300 km) and small (< 200 km) eddies may influence primary productivity and the distribution of juvenile steelhead trout and their prey (primarily small fish and squid) (Onishi et al. 2000; Myers et al. 2001b).

Evidence from high-seas tagging studies has shown that the ocean ranges of many U.S. salmonid stocks from California to arctic Alaska extend into international waters of the North Pacific Ocean and Bering Sea (Myers et al. 1996). There are little or no stock-specific data, however, on juvenile salmon in high-seas areas from September through March. Future high-seas investigations should be coordinated with investigations of coastal juvenile salmon so that we can determine the relative importance of both habitats to the growth and survival of specific stocks of juvenile salmon during their first fall and winter at sea.

RECOMMENDATIONS FOR FUTURE STUDIES

The studies described in this paper, together with those conducted by other nations in the North Pacific Rim, have significantly advanced our understanding of where and when juvenile salmon occur in coastal waters, and have substantially augmented our knowledge of the biology of these juveniles. All the studies described have attempted to sample the physical and biotic environment where juvenile salmon were caught, in an attempt to determine habitat preferences. This has had somewhat limited utility, especially in the early marine life stages of salmon shortly after leaving their river systems, since they may have to traverse less preferred and perhaps even unfavorable areas to arrive at their optimal habitats. These measurements need to be continued and perhaps broadened to include finer-scale and depth-stratified oceanographic and biological dynamics that may be sensed by these juveniles.

An enormous amount of information has been gathered on the movement patterns of juvenile salmon in coastal waters. Much of the early information was based on tagging at sea (Hartt and Dell 1986; Myers et al. 1996). In recent years, the proliferation of releases of coded-wire tagged (Pearcy and Fisher 1988) and thermally-marked (Farley and Munk 1997) hatchery salmon has provided a wealth of information on where fish from different stocks reside in coastal waters, as well as rough estimates of growth and migration speeds. Directional purse seines and fine-mesh gillnets provide some information on direction of movements. New advances in

miniaturization allow widespread application of acoustic and data-storage tags on juvenile salmon as they enter the ocean (Boehlert 1997; Walker et al. 2000). Promising new technology is being developed for moored arrays of listening devices in coastal waters for detecting the presence of juvenile salmon and monitoring their movements and behavior (Boehlert 1997; Klimley et al. 1998).

Determining early ocean mortality factors and rates may continue to be elusive for several years to come. Unique individual tagging of all hatchery fish will add much information on the timing and direct causes of mortality. It will also aid in understanding wild and hatchery salmon interactions in the coastal environment. In the future, we hope to see greater U.S. research emphasis on local interactions between hatchery and wild juvenile salmon and their prey resources, possible density-dependent interactions, and the influence of these early marine interactions on adult salmon production in changing ocean regimes (Noakes et al. 2000; Levin and Williams 2002).

Logistic complications and safety concerns have generally limited most coastal sampling at sea to daytime and late spring through early fall collections of juvenile salmon. More information is needed on the nocturnal depth distribution, aggregation, and movement patterns of juvenile salmon. More winter sampling will help determine whether there exists a second ‘critical period’ in the life of salmon (Beamish and Mahnken 2001), or at least whether their habitat preferences change at this time of the year.

Obviously, juvenile salmon are not alone in the coastal environment, and in many cases, they may play a minor role in the ecosystem relative to other more plentiful fishes and invertebrates. However, the juveniles themselves may be critically affected by what happens around them, especially by the abundance of predators, competitors, and prey. As described in this review and elsewhere (Brodeur 1990), much is known about the feeding habits and food preferences of juvenile salmon, although more research is clearly needed on consumption rates relative to food availability so that some estimation of the carrying capacity of the coastal environment for juveniles is achieved (Cooney 1984; Cooney and Brodeur 1998). Similarly, competitors and predators of juvenile salmon have been identified (Fresh 1997), but their impact on juvenile salmon survival has seldom been measured. Understandably, such measurements are difficult to accomplish in the field. It may be that these data gaps can be filled by simulation modeling, perhaps by either individually-based bioenergetics models or general ecosystem models focussing on juvenile salmon. However, the models are generally wanting for appropriate field data in some areas at the present time.

At present, there has been little or no U.S. re-

search on changes in abundance and body size of salmon caused by rapid global warming from the combined effects of man-made greenhouse gas emissions (e.g., carbon dioxide, methane, nitrous oxide and the fluorocarbons) and the Arctic Oscillation, a natural climate phenomenon that has been in its warm phase for the past 30 years (Thompson and Wallace 1998). Global warming is likely to affect marine distribution, growth, and survival, and is likely to affect the amount of ocean habitat available to juvenile and adult salmon (Welch et al. 1998). Because the effects of global climate change on salmon will differ between oceanic regions, as well as among salmon species and stocks, new U.S. research on both regional and trans-oceanic scales is highly recommended.

Recent years have seen the expansion of several studies as well as the initiation of new studies examining juvenile salmon in the ocean. In fact, the last several years have probably witnessed more sampling activity in U.S. waters over a broader geographic and temporal scale than in any previous period. The future looks equally promising with many new programs starting up (e.g., U.S. GLOBEC; BASIS), but a continuation of the effort already in place is necessary if we are to make critical advances in our knowledge of juvenile salmon distribution, behavior, and ecology when they first enter the ocean.

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Authors Biographies

Richard (Dick) Beamish
Senior Author for Canadian Review Paper



Dick Beamish is the Senior Scientist and former Director at the Pacific Biological Station in Nanaimo, British Columbia, Canada. He has published over 250 scientific articles on a range of topics from climate impacts on fish, to new species of fish. For the past 11 years he has been a Commissioner of the International Pacific Halibut Commission. He was appointed as the Department of Fisheries and Oceans representative on the New Pacific Fisheries Resource Conservation Council, an independent body that advises the Minister of Fisheries and Oceans on salmon and related management issues. He also was appointed by Canada to be a member of the four person Committee for Scientific Cooperation for the Pacific Salmon Commission. He currently is the chairman for the Committee on Scientific Research and Statistics (CSRS) for the North Pacific Anadromous Fish Commission. In February of 1999, he was awarded the Order of Canada for his discovery of the problem of acid rain in North America. As well, he was recently appointed as a Fellow of the Royal Society of Canada. He teaches a course each year on Pacific coast fisheries management at Malaspina University College and produces videos on famous scientists whose careers in aquatic science would be inspirational to students. His work on age determination included the recognition that many fish are long-lived and he has also contributed to the understanding of the impacts of climate on fish populations. Dick Beamish has been married for 33 years and has two daughters. He plays rugby, grows rhododendrons, and makes chocolates.



Mike Healey
Co-Author for Canadian Review Paper



Mike Healey received his PhD from the University of Aberdeen, Scotland in 1969. From 1970 until 1990, Professor Healey was a scientist with the federal government working on freshwater fisheries from 1970 to 1974 and salmon fisheries from 1974 to 1990. In 1990 he joined the faculty at UBC as director of the Westwater Research Centre. Since 1995 he has been cross appointed in the Institute for Resources and Environment and Sustainability, the Fisheries Centre and the Department of Earth and Ocean Sciences. Mike Healey is recognized internationally as an expert in the ecology of Pacific salmon and as an expert in the design of resource management systems. He has served as a consultant to government and industry in Canada, the United States and Asia on the management of fish and fish habitat and on restoration of aquatic ecosystems. For the past five years he has been an advisor on ecosystem restoration to the CALFED Bay-Delta program in California. He is presently on sabbatical at the University of Rhode Island where he is writing a book on ecosystem based management of coastal resources.



Isobel Pearsall
Co-Author for Canadian Review Paper

Born in Manchester, England, Isobel Pearsall did her undergraduate degree in Biology at Oxford University between 1984 and 1987. After working abroad in Japan for a number of years, she did her MSc in Biology at Dalhousie University, Nova Scotia, Canada between 1990–1992 and then her Ph.D. at the University of British Columbia in Vancouver, Canada between 1992–1998. She worked at the Pacific Biological Station as a post-doctoral fellow between September 1999 and January 2001. Since that time, she has established her own consulting business, and works primarily in fisheries and forestry consulting. She lives in Nanaimo on Vancouver Island, Canada, with her husband and two children. She enjoys kayaking and camping, organic gardening, and wine-making.

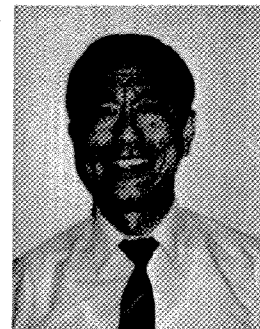


Hiroshi Mayama
Senior Author for Japanese Review Paper

Hiroshi Mayama studied fishery biology at the Tokyo University of Fisheries, Japan. He has been employed at the National Salmon Resources Center (formerly the Hokkaido Salmon Hatchery), Sapporo in Hokkaido, for thirty-five years, where he has occupied position of research scientist in areas of salmon enhancement. Until 1970s, his research work focused on early life history of chum salmon to clarify the proper timing and size for effective release of juveniles from hatcheries. In 1985 he was appointed chief of ecology section of the research division of the Hokkaido Salmon Hatchery, Fishery Agency of Japan, and turned his attention to enhancement of masu salmon resources. He received a Ph.D. in Fisheries from the Hokkaido University, Japan in 1990 for his study on freshwater life and propagation technology of masu salmon. At present, he is director of research division of the National Salmon Resources Center.

Yukimasa Ishida
Co-Author for Japanese Review Paper

Yukimasa Ishida served for 16 years as research scientist at the National Research Institute of Far Seas Fisheries (NRIFS) in Shimizu, Japan and for 3 years as the Research Coordinator of Oceanography and Resources at the Hokkaido National Fisheries Research Institute in Kushiro, Japan. He started salmon research at NRIFS and studied salmon stock identification using scale pattern analysis. He also had interested in growth variation and carrying capacity of Pacific salmon. He surveyed salmon ecology in the North Pacific Ocean, Bering Sea and Okhotsk Sea several times. He served as CSRS Chairman from 1999 to 2001. Now he is a Director of Kuroshio Research Division, National Research Institute of Fisheries Science, in Kochi, Japan.



Vladimir Karpenko
Senior Author for Russian Review Paper

Vladimir Karpenko is the Head of the Bering Sea Program and Chief Scientist of the Laboratory of Marine Salmon Investigations at KamchatNIRO, Russia. He was born in Ukraine. But from 1954 to 1973 he lived in Primorye Territory. In 1973 he graduated Far Eastern Fishery University and began his work as the Junior Scientist of the Laboratory of Marine Salmon Investigations at KamchatNIRO. Then he continued the scientific researches as the Senior Scientist (1984–1990), and as the Head Laboratory (1991–1997). During three years Vladimir Karpenko was a Deputy Director (1998–2001). From 2002 he is Chief Scientist of the Laboratory. In 1983 he finished Ph. dissertation (Institute of Marine Biology, Vladivostok) and in 1997 – Doctor's dissertation at Russian Federal Institute of Fisheries and Oceanography in Moscow. His laboratory conducts international cooperative research on stocks origins, distribution, migration, abundance, and ecology of Pacific salmon in the North Pacific Ocean, Bering Sea, and Okhotsk Sea. He is best known for his research on the early marine life history of juvenile salmon, relationships between salmon and other commercial fish species, and the role of salmon juveniles in coastal ecosystems. He is an international expert on methods used to catch Pacific salmon in coastal and offshore marine waters and to estimate the brood abundance of pink salmon and others species. Besides, Vladimir Karpenko is an international expert of IUCN SSG. He has more than 80 published works.





Richard Brodeur
Senior Author for the United States Review Paper

Richard Brodeur is a Research Fisheries Oceanographer working in the Fish Ecology Division of the Northwest Fisheries Science Center, NOAA Fisheries, and is based in Newport, OR. Ric received his B.S. in Fishery Science from the University of Massachusetts, his M.S. in Oceanography from Oregon State University, and his Ph.D. in Fisheries from the University of Washington. His dissertation research examined the feeding ecology of juvenile salmon and its relationship to ocean carrying capacity. Following a year-long postdoctoral position at Pacific Biological Laboratory in Nanaimo, B.C. Canada, he began his career working on early life history and recruitment dynamics of walleye pollock in the Gulf of Alaska and Bering Sea for the Alaska Fisheries Science Center based in Seattle. He worked in this study for eight years but in 1999, he returned to Oregon to work again on habitat preferences and trophic ecology of juvenile salmon. Over the years, Ric has been heavily involved with the North Pacific Marine Science Organization (PICES) serving on several committees and working groups and organizing a number of special sessions. He is also on the Scientific Steering Committee of the U.S. GLOBEC program. During a temporary assignment to a lab in Monterey, California, he led a team of scientists in developing a NOAA Strategic Plan to study salmon in the ocean. He has published on a variety of topics ranging from satellite oceanography to fish bioenergetics to fisheries acoustics, but has focused much of his research on juvenile salmon.



John H. (Jack) Helle
Co-Author for the United States Review Paper

John H. (Jack) Helle is Chairman of BASIS (Bering-Aleutian Salmon International Survey) Working Group for the NPAFC. He was appointed to his present position of Program Manager in 1996 for Ocean Carrying Capacity Research (OCC) with the National Oceanic and Atmospheric Administration (NOAA Fisheries) at the Alaska Fisheries Science Center's Auke Bay Laboratory in Juneau, Alaska. Previous research assignments at Auke Bay Laboratory included: directing salmonid stock identification research from 1982 to 1995, project leader for Pink and Chum Salmon Investigations at Olsen Bay Field Station from 1965 to 1981, and fishery research biologist at the Olsen Bay Field Station from 1960-1964. He received his B.S. (1958) and M.S. (1961) degrees in Fishery Management from the University of Idaho, spent a year as an Honorary Research Fellow (1964-65) at Marischal College, University of Aberdeen, Scotland, and completed the Ph.D. (1979) degree in Fisheries Science at Oregon State University. Jack Helle has been married (Marilyn) for 43 years and has two daughters.

Katherine (Kate) Myers
Co-Author for the United States Review Paper

Katherine ("Kate") W. Myers is a fishery research biologist with a B.Sc. in Fisheries from the University of Washington (1976), an M.Sc. in Fisheries from Oregon State University (1980), and a Ph.D. in Fisheries from Hokkaido University (1998). Throughout her career, Kate's work has focused on the biology, life history, ecology, and stock interactions of Pacific salmon and steelhead trout in river estuaries and in the North Pacific Ocean and Bering Sea. Kate is currently the Principal Investigator of the long-term (since 1953) High Seas Salmon Research Program at the School of Fishery and



Aquatic Sciences, University of Washington, Seattle, which conducts international cooperative research on salmon and steelhead trout in the North Pacific Ocean and Bering Sea. Her research specialties include tagging experiments to determine salmon ocean distribution and migration patterns, scale pattern analyses for age, growth, and stock composition of salmon in mixed-stock research and commercial fishery catches, and marine food habits studies of salmon for bioenergetic and carrying capacity models. Her contributions to this NPAFC Bulletin were funded by the Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service (NOAA Contract 50-ABNF-1-0002).

Reviewers Biographies

Sandy Argue
Reviewer for the Canadian Paper

Sandy Argue currently is A/Director Seafood Development for the British Columbia Ministry of Agriculture, Food and Fisheries (MAFF). His career in fisheries spans 40 years starting with Pacific Region, Fisheries and Oceans Canada (DFO), first as a Summer Student, then as Senior Management Biologist for the Johnstone Strait - Strait of Georgia Division. In this capacity during the 1960s and 1970s he conducted extensive tagging and nearshore seining surveys for juvenile chinook and coho salmon. He left DFO in 1978 to take a position as Senior Scientist for tuna stock assessment with the South Pacific Commission in Noumea, New Caledonia. In 1984 he returned to Canada where he consulted in fisheries resource assessment and management until returning to DFO Pacific Region in the International and Intergovernmental Affairs Division. In this capacity he advised the Canadian government on fisheries issues under negotiation with the United States and other Pacific nations. In 1994 he assumed the position of International Advisor at DFO and in 2001 he began working with MAFF.



Kees Groot
Reviewer for the Canadian Paper

Kees Groot was born in Modjokerto, on Java, Indonesia, in 1928. After spending three years in a concentration camp during the Second World War, he went to Holland in 1946 and studied biology at the Universities of Amsterdam and Leyden. He immigrated to Canada in 1956 and a year later joined the Fisheries Research Board of Canada (now the Department of Fisheries and Oceans) as a fish behaviourist (ethologist) at the Pacific Biological Station in Nanaimo, British Columbia. There, under the guidance of Dr. J.R. (Roly) Brett, he worked on problems related to a major threat to Fraser River salmon because of a proposal to build multiple dams on the main stem of this river for the generation of hydroelectric power. After this multiple dam construction plan was rejected because of the high likelihood that migrating salmon stocks would be destroyed, he concentrated his studies on long distance migration, orientation, and navigation of Pacific salmon and used the data of these studies to obtain his Ph. D. degree (cum laude) at the University of Leyden in Holland in 1965. In 1966, soon after receiving his doctorate degree, Kees Groot was appointed Biological Director of the Netherlands Institute of Sea Research in Holland. In 1968 he was invited to return to Canada and again join the staff of the Pacific Biological Station at Nanaimo. His studies then have centered on 1) problems of Pacific salmon migration, specifically on how these fish find their way during long distance journeys, 2) on problems related to salmonid enhancement, and 3) on the potential effects of global climate change on Canada's west coast fisheries resources. Kees Groot has acted as research supervisor for a number of M.Sc. and Ph.D. candidates of British Columbia universities and has taught as visiting professor at Simon Fraser University and, several times, at the Bamfield Marine Station. In 1993 he retired from the Department of Fisheries and Oceans, became scientist emeritus and started his own biological consulting business - Yellow Point Bio-Research.





Masahide Kaeriyama
Reviewer for the Japanese Paper

Masahide Kaeriyama is a Professor of Marine Ecology at the Department of Marine Science and Technology, School of Engineering, Hokkaido Tokai University, Japan. His research has focused on the life history and population dynamics of Pacific salmon, particularly on feeding ecology and trophic dynamics of Pacific salmon in the ocean, population density-dependent effect, salmon as the key to upstream transport of marine nutrients onto land ecosystems, and aspects related to biological interaction between wild and hatchery salmon. He is author or co-author of more than 30 scientific papers. He serves on the Affiliate Professor of Fisheries, University of Alaska Fairbanks, on the Lecturer in Fish Biology, Hokkaido University, on the Member of counseling committee of the Ichthyological Society of Japan and the Japanese Society of Fisheries Science.



Hiroshi Kawamura
Reviewer for the Japanese Paper

Hiroshi Kawamura was born in Fukuoka, Kyushu of Japan, in 1950. He received his MA from Hokkaido University and dropped out of the doctoral course to work at Hokkaido Fish Hatchery, in 1975. He had studied on migration behavior and predation of juvenile chum salmon, and a life history of masu salmon at Erimo, Makkari and Mashike branches and Eniwa Center of the Hatchery since 1975. Now his study is focused on stock enhancement, conservation and restoration of masu and chum salmon at Kumaishi Branch.

Victor Bugayev
Reviewer for the Russian Paper

Victor Bugayev is an ichthyologist, pisciculturist, and fishery biologist, and has been working in Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO) since 1973, as Scientific Worker in 1973–1983, Senior Scientist Worker in 1983–1990, and Leading Scientist Worker in 1991–2002. Every year he did 2–3 months or more scientific ichthyologist expedition in different rivers and lakes in Kamchatka Peninsula. He published more than 120 scientific articles on growth of fishes and determination of age composition using the scales, influence of feeding and climate on year-to-year variations on growth of sockeye salmon, life history of threespine stickleback in Kamchatka and masu salmon in Asia, etc., and published a book “Asian Sockeye Salmon *Oncorhynchus nerka* (freshwater period, local structure, abundance dynamics)” in 1995. He received his Ph.D. in Biological Science from Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), Moscow, Russia, in 1994. Victor Bugayev was awarded with a medal “Honorary Workman of Fish Industry of Russian Federation” in 2002.



William (Bill) Heard
Reviewer for the United States Paper

Bill Heard has been a student of Pacific salmon ecology and other Alaska fishes at NOAA's Alaska Fisheries Science Center's Auke Bay Laboratory for over 40 years. He originally came to Alaska as a graduate student from Oklahoma State University where he received his first degree in zoology and a Master's degree in fisheries. After working in warm water fisheries in Oklahoma, Alabama, and Arkansas, the lure of Alaska became too much and he has lived and worked in the Great Land since 1960. Initially working with sockeye salmon and associated fishes at Brooks Lake in Bristol Bay, he subsequently has studied pink, coho, and chinook salmon, mostly in Southeast Alaska where he has been associated with the year-round Biological Field Station at Little Port Walter. Presently he is Program Manager for Marine Salmon Interactions where research is focused on early marine ecology of salmon, stock enhancement aquaculture, hatchery-wild stock interactions, long-term monitoring of biophysical parameters and variability in salmon populations, and strategies to help protect ESA listed species. He currently resides in Auke Bay with his wife and is an avid enthusiast of sport fishing, along with boating, birding, diving, hiking, and most other elements of Alaska's natural history.





William (Bill) Percy
Reviewer for the United States Paper

William (Bill) Percy is a Professor Emeritus of Biological Oceanography in the College of Oceanic and Atmospheric Sciences at Oregon State University. His research interests include fisheries oceanography and the ocean ecology of salmonids, and is author of a book on the Ocean Ecology of North Pacific Salmonids. In the past he has published papers on the ecology and distribution of coastal and deep-sea animals, including benthic and pelagic fishes, squids and shrimps. He received his B.S. and M.S. degrees from Iowa State University and his Ph.D. from Yale. He has served on committees of U.S.

GLOBEC and PICES and was awarded American Fisheries Society-Oscar E. Sette, Outstanding Marine Fishery Biologist Award and the American Institute of Fishery Research Biologists, Outstanding Achievement Award. He is presently the co-chair of Independent Multidisciplinary Science Team for Oregon Salmon Plan.
