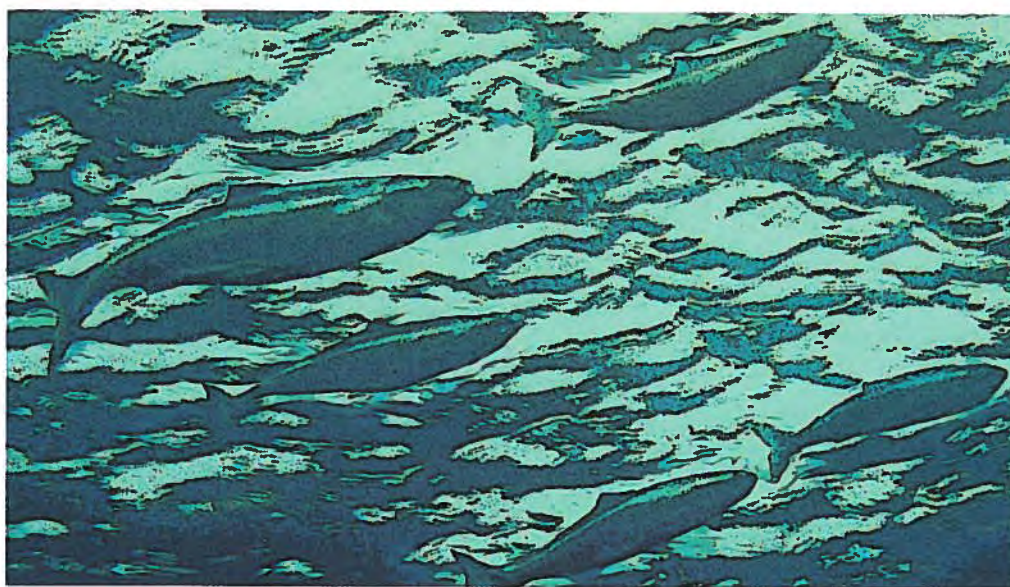


***NORTH
PACIFIC
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BULLETIN NUMBER 2

Recent Changes in Ocean Production of Pacific Salmon



**Edited by: John H. (Jack) Helle, Yukimasa Ishida,
Don Noakes and Vladimir Radchenko**

Consulting Editor: Philip Symons

Technical Editors: Hiroko Omori and Wakako Morris

VANCOUVER, CANADA, 2000

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In Memoriam
Harry Richard (Dick) Carlson, Ph.D.
1940-1999



Photo credit Chris Kondzela

This second Bulletin of the North Pacific Anadromous Fish Commission is dedicated to the memory of Dr. Richard (Dick) Carlson (1940-1999). Dick was a well-known American marine fisheries biologist at the Alaska Fisheries Science Center's Auke Bay Laboratory (National Marine Fisheries Service, U.S.A.) for 31 years. At the time of his sudden death he was Chief Scientist for the Ocean Carrying Capacity Program and was widely respected for his research in support of the science goals of the North Pacific Anadromous Fish Commission.

Preface

This Bulletin is a compilation of papers presented at an International Symposium on Recent Changes in Ocean Production of Pacific Salmon, held in Juneau, Alaska, U.S.A., November 1-2, 1999, under the auspices of the North Pacific Anadromous Fish Commission. The symposium was the second held by the Commission and was hosted by the government of the United States of America.

The symposium steering and editorial committee comprised of scientists from the Parties was appointed by the Committee on Scientific Research and Statistics.

The Steering and Editorial Committee members were:

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Local arrangements for the symposium were facilitated by a local organizing committee led by Hal Geiger of the Alaska Department of Fish and Game and Steve Ignell of the Auke Bay Laboratory and assisted by Debbie Hart and Paula Johnson from these organizations. Symposium participants were taken on a tour of the spawning grounds of the fall chum salmon on the Chilkat River near Haines by ferry and bus. These spawning grounds are well-known as a gathering place for thousands of bald eagles and a wide area for the last salmon feast of the season.

The symposium *Recent Changes in Ocean Production of Pacific Salmon*, attracted an audience of approximately 80 people in addition to the presenters of the oral and poster presentations. Two Keynote addresses at the Symposium presented perspectives on climate change: 1) Dr. E.N. (Joe Friday, Jr. (Director, Board on Atmospheric Sciences in Climate, National Academy of Sciences, U.S.A.) discussed the outlook for natural resources in the future in terms of climate variability and climate change, and 2) Dr. Bruce P. Finney (University of Alaska Fairbanks) presented a retrospective look at climate variability and salmon production in Alaska during the past 100 years.

The symposium presentations addressed four major Topics: 1) Physical and Biological Factors Affecting Ocean Production of Pacific Salmon, 2) Detection of Trends, Patterns, and Changes in Historical Salmon and Environmental Data, 3) Forecasts and Models of Pacific Salmon Dynamics, and 4) New Research Methods and Techniques in Ocean Salmon Research. Both oral and poster presentations summarized research results in these four Topics.

In summary the following key research issues have been identified at the 1999 NPAFC Symposium: ocean regime changes, hatchery and wild salmon interactions, archival tags, stock identification, bycatch, feeding behavior of salmon in coastal areas and offshore, coastal habitat degradation, and carrying capacity for juvenile and adult salmon in the marine environment. These key issues should be incorporated into the new NPAFC Science Plan to promote scientific activities within the NPAFC member nations.

Research papers were presented and submitted at the symposium by scientists of the Parties – Canada, Japan, Russia, and the United States of America. All papers were peer-reviewed and revised by the authors before final review and acceptance for publication by the Editorial Committee. A professional editor, Dr. Philip Symons, facilitated the review and revision process with the authors.

The staff of the North Pacific Anadromous Fish Commission needs special recognition in all aspects of management of this symposium, from the planning to the production of the final publication of the proceedings. One of the things that make the staff of the North Pacific Anadromous Fish Commission unique is their ability to organize and facilitate oral and written presentations at meetings and symposia in three different languages – English, Japanese, and Russian. In addition, they provide people at meetings that fluently translate scientific talks into clearly understood translations in your language. I know I speak for the Steering and Editorial Committee members and all the scientists and other participants in the symposium when I congratulate and thank all the staff members for their consistently superb work, done cheerfully under sometimes stressful time constraints: Vladimir Fedorenko, Hiroko Omori, Wakako Morris, and Denise McGrann-Pavlovic. We also thank our interpreters, Ms. Kondo-Blum and Ms. Safarova-Downey for their outstanding contributions to the Symposium.

Jack Helle
Chairman
Editorial Committee

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I. Opening Remarks

Welcome to Alaska, welcome to Juneau, and welcome to the second symposium sponsored by the North Pacific Anadromous Fish Commission, *Recent Changes in Ocean Production of Pacific Salmon*. Those of you that went on the tour of the Chilkat River chum salmon spawning areas at Haines yesterday probably are not talking to me today after the brutal weather I subjected you to up at Herman Creek and at the Bald Eagle Preserve. Listening to me talk about my favorite subject, chum salmon, in the freezing, numbing wind, snow, and rain was an unforgettable, or should it be forgettable or perhaps unforgivable, experience? I'm sure in the future if I'm permitted to arrange a tour, people that were on this one will be checking the weather and looking for excuses to do something else.

We have two distinguished guests in the audience that I would like to introduce to you right now. First, Alaska's Lieutenant Governor, and Commissioner of the North Pacific Anadromous Fish Commission, Fran Ulmer. Second, Mrs. Shirley Carlson from Juneau. Most of you knew Dick, Shirley is his wife. Dick died from injuries after he was struck by a car on the side of the highway near his home on July 21. A poster is on the wall that celebrates some of Dick's research activities. Most of the papers presented here in the next two days will be published in the proceedings of the Symposium as Bulletin Number 2 of the North Pacific Anadromous Fish Commission. This Bulletin will be dedicated to Dr. H. Richard (Dick) Carlson.

Dick was born in Elgin, Illinois, on June 29, 1940. He was a young 59 years old. He attended South Dakota State University and transferred to Humboldt State University in Arcata, California, to finish his B.S. degree in fisheries in 1963. He completed a M.S. degree in fisheries in 1968 at the University of Connecticut and his Ph.D. degree in 1985 at Oregon State University. Dick also graduated from the U.S. Coast Guard Officer Candidate School in Yorktown, Virginia, and was commissioned ensign and lieutenant and served on active duty in the Gulf of Mexico in 1963-66.

He started working at the Auke Bay Laboratory in 1960-61 as a seasonal temporary in the Herring Investigations Program. After his stint in the Coast Guard, he came back to the Auke Bay Laboratory and worked for the Salmon Investigations Program in Bristol Bay. He accepted a permanent research biologist position in 1968 with the Marine Fisheries Investigations Program. His research on rockfish behavior and life history resulted in several papers that first demonstrated homing ability to certain reefs.

Dick was the first American scientific observer on the Japanese research vessel the *Oshoro Maru*. Dick

was also the first scientist to use a submersible submarine to observe groundfish in southeastern Alaska.

He also worked with the U.S./Canada Salmon Treaty Research Program from 1986 through 1994. In 1995, he transferred to the new Ocean Carrying Capacity Research Program. Dick was very pleased to get back on the high seas and was the program's Chief Scientist until his death.

Dick's love of the ocean caused him to spend much time under the ocean surface. As a diver for Auke Bay Laboratory, he logged an astounding 3887 dives! He also dove in California, Hawaii, Fiji, Tahiti, Australia, New Zealand, Scotland, Mexico, and Honduras. For 17 years he observed and marked starfish and monitored their distribution and longevity in Auke Bay. A paper describing these observations was published in the *Journal of Marine Biology* in 1999, shortly before his death.

Dick and Shirley were famous for their hospitality. One of our Russian colleagues told me that they considered Dick and Shirley their adopted American parents. They made sure that our foreign visitors felt they always had a home to go to in Juneau.

He was supposed to make an oral presentation at this symposium. His co-authors Ed Farley and Kate Myers finished the paper and will present it for him. It will be a very fitting memorial to have the proceedings of this Symposium – Bulletin Number 2 of the North Pacific Anadromous Fish Commission – dedicated to Dr. H. R. (Dick) Carlson.

I have two more distinguished guests to introduce and they are our keynote speakers. Dr. Elbert W. (Joe) Friday, Jr., Director of the Board on Atmospheric Sciences and Climate in the U.S. National Research Council, Washington, D.C. Dr. Friday will speak to us on "Climate Variability and Climate Change: What Do We Really Know?" His talk will follow Lieutenant Governor Ulmer's Welcome Address. The next distinguished guest is Dr. Bruce Finney, University of Alaska Fairbanks. Dr. Finney's keynote address will be the first talk tomorrow – "A Long-Term Perspective on Climate Variability and Salmon Production in the Northeast Pacific Ocean." These two keynote talks will provide the background and insights for helping to understand how climate variability and climate change are involved in our symposium subject – *Recent Changes in Ocean Production of Pacific Salmon*.

Jack Helle
Chairman
Symposium Steering Committee

Synthesis and Review of US Research on the Physical and Biological Factors Affecting Ocean Production of Salmon

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Myers, K.W., R.V. Walker, H.R. Carlson, and J. Helle. 2000. Synthesis and review of US research on the physical and biological factors affecting ocean production of salmon. N. Pac. Anadr. Fish Comm. Bull. No. 2: 1-9.

Keywords: NPAFC, Pacific salmon, research plan, United States, ocean, carrying capacity

Abstract: This paper is a synthesis and review of the results of US research in the 1990s on the physical and biological factors affecting ocean production of Pacific salmon (*Oncorhynchus* spp.). The review follows the outline of US research under the North Pacific Anadromous Fish Commission Science Plan, which addresses issues concerning the ocean production of salmon. The research includes studies on juvenile salmon in coastal waters, ecology of salmon in the Gulf of Alaska, retrospective analyses of long-term data series, development and application of stock identification techniques, and international cooperative high seas salmon research. Our review indicates that climate-induced variation in productivity and fishing are the two major factors affecting ocean production of salmon, but the underlying mechanisms are not well known. To understand the processes linking climate, ocean productivity, and salmon production, we need stock-specific information on salmon distribution, abundance, and migration patterns with respect to environmental conditions. We recommend continuation of this research, with a strong emphasis on (1) the development of new technologies and international baselines for salmon stock identification, (2) ship-board research and monitoring programs to provide a platform for process studies, as well as data on interannual variation in ocean growth, distribution, and run timing of key stocks, and (3) the development and dissemination of international databases useful for research on ocean production of salmon.

INTRODUCTION

This year the North Pacific Anadromous Fish Commission's (NPAFC) Science Sub-Committee (SSC) is charged with developing a new science plan for the year 2000 (Y2K) and beyond (NPAFC 1999). This task includes a review of the results of NPAFC's scientific research program in the 1990s, as well as new information presented at this symposium. The ultimate goal of NPAFC's research program is conservation of salmon (*Oncorhynchus* spp.). And so, we may ask, "Are Pacific salmon Y2K-safe?" The focus of this symposium and resulting bulletin is salmon in the ocean, but we must keep in mind that salmon begin and end their lives in fresh water. Without healthy freshwater ecosystems, there will be no salmon. Y2K-safe science, therefore, should consider factors that affect growth and survival of salmon over the entire salmonid ecosystem, including both freshwater and ocean habitats.

The picture of salmon on the cover of the symposium proceedings is a computer adaptation of an

underwater photograph of salmon swimming on the high seas, taken in the 1960s by A.C. Hartt near Adak Island in the central Aleutians. According to Mr. Hartt, high-seas salmon are like "gray ghosts," that is, very difficult to see and photograph underwater. Over the next two days, we will be discussing the factors that affect the survival of these gray ghosts during their extensive ocean feeding migrations. There are many posters and papers presenting the detailed results of individual research projects and programs. Our objective in this paper is to "set the stage" for the presentations that follow by giving a brief overview of US high seas salmon research issues, programs, methods, results, and recommendations.

Research Issues

The main issue or question underlying the need for ocean salmon research has always been: "Why didn't the salmon come back from the sea?" This question, asked since time immemorial by native

† deceased

salmon fishermen of the North Pacific Rim, was asked once again in 1997 and 1998, when Bristol Bay, Alaska, sockeye salmon (*O. nerka*) failed to return in forecasted numbers. The NPAFC treaty promotes conservation of salmon by prohibiting all directed fishing for anadromous stocks in international waters (NPAFC 1993). In the 1970s, fisheries scientists defined conservation as the wise use of (fishery) resources. In the 1990s, conservation has a much broader meaning involving "long-term sustainability of ecosystems." Accordingly, the present NPAFC Science Plan addresses two critical research issues: (1) factors affecting current trends in ocean productivity and impacts on carrying capacity (i.e., biomass of salmonids that can be supported by their ecosystem), and (2) factors affecting changes in biological characteristics (growth, size and age at maturity, oceanic distribution, survival, and abundance). These issues were formulated as areas of salmon research that could be conducted in cooperation with other research organizations, especially the North Pacific Marine Science Organization (PICES)—to bring to the NPAFC forum new scientific expertise and information, particularly in the areas of ocean and atmospheric sciences.

North Pacific Research Programs

Concerns in the 1990s about salmon carrying capacity in the North Pacific Ocean, the effects of oil pollution, global warming, ocean interactions between hatchery and wild fish, endangered species, illegal high seas fishing, and salmon bycatch in non-target ocean fisheries have spawned a multitude of US and international programs that are investigating various aspects of ocean production of salmon and other marine species. Some of the major programs are as follows:

- Ocean Carrying Capacity (OCC) Program, US National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory—funded by the US Department of Commerce, National Oceanic and Atmospheric Administration (NOAA)
- US Global Ocean Ecosystems Dynamics (GLOBEC) Northeast Pacific Program (US National Science Foundation Division of Ocean Sciences, NOAA Coastal Ocean Program Office)
- Fisheries Oceanography Coordinated Investigations (NOAA)
- Climate Change and Carrying Capacity (CCCC) Program (PICES)
- Exxon Valdez Oil Spill (EVOS) Trustee Council, including the Sound Ecosystem Assessment

(SEA) Program and the Gulf Ecosystem Monitoring (GEM) Program

- North Pacific Marine Research Program (Federal grant to the University of Alaska Fairbanks)

The OCC Program, which is described in this paper, is the only program directly funded to conduct US salmon research in the NPAFC forum (National Marine Fisheries Service 1995).

Research Approaches

Most US programs are using similar research approaches, including (1) retrospective/comparative analysis, (2) mathematical modeling, (3) 3-dimensional (distribution and depth) surveys, (4) process (mechanism) studies, (5) data acquisition and management, and (6) long-term observation (monitoring) programs. The use of multiple approaches in investigations of ocean production of salmon is essential because of problems or difficulties associated with individual components.

Retrospective (historical) or comparative analyses are one of the major methodological approaches, but most historical salmon data were not collected with current research objectives in mind. For example, the number of salmon in commercial catches is often the only historical measure of salmon abundance, which is a poor substitute for total biomass in salmon carrying-capacity research. Salmon catch data are affected by changes in fishing strategy, effort, and gear, management activities, and other factors. Often, retrospective analyses show a correlation between various physical and biological factors and salmon growth or catch, but correlations are not proof of cause and effect and explain nothing about underlying mechanisms.

Mathematical modeling is a useful tool for generating hypotheses, but models can be designed to show whatever result we want. Models, therefore, must be validated with field data. Ocean field surveys are very expensive. Environmental data from remote sensing is becoming more readily available, but we still need to go to sea in ships to collect data on salmon and 3-dimensional environmental data. Process studies are vital to discovering underlying mechanisms, but difficult to carry out either in the laboratory or on ships at sea.

International systems to acquire, manage, and exchange long-term data series are essential to North Pacific salmon research, but salmon databases are often considered to be proprietary information. Long-term monitoring programs are the key to understanding variation in biological and physical factors affecting ocean production of salmon. Governments, however, are usually reluctant to fund long-term programs.

US SCIENCE PLAN

The US Science Plan under NPAFC includes five major areas of research (NPAFC 1999), (1) juvenile salmon studies, (2) Gulf of Alaska salmon ecology, (3) retrospective analyses, (4) stock identification, and (5) high seas salmon studies. Field and laboratory investigations are conducted on salmon in both coastal and high seas habitats, primarily in the Bering Sea, central North Pacific Ocean, and Gulf of Alaska, where US salmon are most abundant. Samples and data for retrospective analyses are obtained from historical high seas and Alaska salmon research and management programs, as well as from new techniques like sediment-core sampling. Accurate stock identification in mixed-stock ocean samples is a key aspect of every phase of the research.

Coastal Juvenile Salmon Studies

Ocean production of salmon in terms of numbers of fish is closely linked with their early ocean survival. Juvenile salmon spend their first summer at sea in open coastal areas over the continental shelf or in protected marine waters, straits, sounds, and river estuaries. Coastal studies are focusing on field monitoring, models of salmon production, and process studies, including (1) repeated measurements of habitat and stock-specific life history characteristics, (2) modeling salmon production based on interannual variability in early marine survival and growth, and (3) trophic dynamics of salmon and their predators.

At present, there are two main programs, one in southeastern Alaska and one in western Alaska. The southeastern Alaska program, initiated in 1997, is investigating seasonal (May–October) interactions between hatchery and wild salmon stocks and their potential impact on marine carrying capacity (Murphy et al., 1997, 1999; Orsi 1997; Orsi and Murphy 1997; Orsi et al. 1997, 1998a, b, c, d, e, this volume; Murphy 1998). The western Alaska Program, initiated in 1999, is investigating effects of climate on growth, migration, and distribution of juvenile Bristol Bay sockeye salmon in the eastern Bering Sea (Farley et al. 1999; Ocean Carrying Capacity Program 1999). Sampling for juvenile salmon was also conducted during broad-scale coastal surveys of the northeastern North Pacific, Gulf of Alaska, Bering Sea, and Aleutian Islands from 1996–1999 (Carlson et al. this volume).

The results of coastal juvenile salmon studies indicate that spatial and temporal variations in their distribution and migration patterns are most closely associated with changes in feeding conditions and distribution of prey. There is a strong relationship between early marine growth and survival. High growth rates are associated with high temperatures. As juvenile salmon grow, they move farther away

from shore and the points of ocean entrance; they are better able to avoid fish, bird, and marine mammal predators; and they can feed on a greater diversity and size range of prey. Variations in early marine growth and survival are most often related to climate-induced changes in distribution and abundance of predator and prey populations. These are chaotic events that cannot be predicted with a high degree of certainty. Thus, coastal ocean field monitoring programs are needed if our objective to forecast salmon carrying capacity in the North Pacific Ocean is to be met.

Gulf of Alaska Salmon Ecology

The components of an ongoing program of research on Gulf of Alaska salmon ecology (1995–present) include studies of (1) broad-scale ocean distribution and migration patterns of salmon (Carlson et al. 1996, 1997, 1998a,b, 1999), (2) fine-scale processes or factors influencing distribution, behavior, and growth, (3) diet overlap and prey selectivity (Sturdevant et al. 1997; Auburn-Cook and Ignell this volume), (4) genetic stock identification (Guthrie et al. this volume), (5) distribution of thermally-marked hatchery salmon (Farley and Munk 1997; Carlson et al. this volume), and (6) salmon growth and size (Farley and Carlson this volume).

From 1996–1999, Gulf of Alaska salmon ecology studies focused on broad-scale field surveys of distribution and migration of salmon in the Alaska Coastal Current (ACC) and Alaska Gyre. The results have corroborated the findings of earlier studies conducted in the 1950s, 1960s, and 1970s. But with new stock identification techniques (genetics, thermal marking, coded-wire tags, and data-storage tags), we have enhanced capability over these earlier studies to investigate growth, distribution, and migration patterns of individual stocks at various life-history stages along their ocean migration routes.

Variation in life-history strategies of salmon, especially spatial and temporal variation in distribution and migration patterns, is a key to their evolutionary success. The results of Gulf of Alaska salmon ecology studies indicate that ocean distribution and migration patterns of salmon are stock-specific, although patterns may be broadly overlapping, particularly with those of other stocks originating from the same geographic region. Salmon in the Gulf of Alaska partition utilization of coastal and offshore feeding areas on the basis of species, maturity, age, size, feeding behavior, food preferences, run timing, and other factors. Productivity and predation by marine mammals, birds, and fish are higher in the ACC than in the Alaska Gyre. Availability of prey resources may not be a limiting factor for production and growth of juvenile salmon in the Gulf of Alaska. Body size of juvenile salmon increases as they mi-

grate westward in the ACC, reducing predation risk and improving their ability to move against currents. Juvenile salmon move offshore in late fall or winter, coincident with decreasing sea temperature and prey availability in the ACC. Immature and adult salmon are able to optimize growth and survival potential through seasonal movements between the coastal and offshore areas. Salmon carrying capacity may be regulated primarily by climate-induced changes in productivity. Competition is most likely to occur among fish of the same species, stock, age, and maturity group, exhibited as density-dependent changes in ocean growth and survival.

Retrospective Analyses

Retrospective studies characterize past variability in climate and salmon population parameters over various time and space scales, and are a key component to understanding effects of climate change on the abundance and life-history of US salmon populations. Past and current research on Alaska salmon includes analyses of (1) freshwater scale growth patterns of Karluk lake sockeye salmon (early 1900s-present; Nelson, Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, U.S.A., personal communication), (2) marine scale growth patterns of Kvichak River sockeye salmon (1920–1997; Isakov et al. this volume), (3) marine scale growth patterns of Yukon River chum salmon (*O. keta*) (1965–1996; Sands, University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau Center, personal communication), (4) Auke Creek pink salmon (*O. gorbuscha*) scale growth and total pink salmon production from Southeast Alaska (1979–1996; Jaenicke et al. 1994; Murphy et al. 1998), (5) historical salmon research in the Karluk Lake area (1880-present; Gard and Bottorff, University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau Center, personal communication), (6) long-term changes in salmon abundance using high-resolution paleoenvironmental analysis of sediment cores (1500-present; Finney 1998), and (7) time-series of salmon catch, escapement, growth data and environmental data (Helle and Hoffman 1995; Bigler et al. 1996; Farley and Murphy 1997; Eggers 1998; Farley and Quinn 1998; Hare et al. 1998; Helle and Hoffman 1998; Wing and Pella 1998).

Retrospective analyses using a variety of techniques have established that there are interannual, decadal, and longer-term fluctuations in the ocean growth and production or survival of salmon. Variation in salmon scale growth patterns reflects changes in feeding behavior and conditions. When salmon are not feeding, circuli are not formed on scales, and in starving fish scales may be resorbed, e.g., in spawning adult salmon. Density-dependent survival is correlated with early ocean (coastal) growth on

scales, and density-dependent growth is correlated with scale growth in subsequent years, when fish are distributed offshore. Spatial and temporal trends in scale growth patterns reflect trends in ocean productivity and climate indices. Differences in scale growth between years of high and low salmon production indicate size-selective mortality, where predation risk is higher for slower-growing individuals. The results of the historical Karluk Lake research and sedimentary ^{15}N analyses from core samples indicate that the long-term decline in Karluk Lake sockeye salmon was primarily precipitated by, and continued by, overfishing in the commercial fishery, not from insufficient spawning but from changes to the fertility of Karluk Lake. Overfishing greatly reduced the quantities of marine-derived nutrients released back into Karluk Lake each year in the decomposing bodies of sockeye salmon adults. Time series analyses of catch, escapement, and growth data indicate that both management (e.g., changes in escapement policy and fishing) and climatic factors have significantly affected Alaska sockeye salmon populations in the past.

Stock Identification Research

NPAFC-related stock identification research is focused on the development of international genetic baselines (e.g., Hawkins et al. 1998; Seeb et al. 1998), standardization and coordination of otolith marking methods (e.g., Hagen 1999; Munk 1999; Volk and Hagen 1999), and application of new and historical techniques (tagging, parasites, and scale pattern analysis) to research and high-seas enforcement questions (e.g., Bernard and Myers 1996; Myers et al. 1996; McKinnell et al. 1997; Patton et al. 1998; Urawa et al. 1998; Wilmot et al. 1998; Winans et al. 1998; Wilmot et al. 1999; Guthrie et al. this volume; Walker et al. 2000).

Thermal marking of otoliths is a promising new technique for high seas stock identification, but the number of available marks is limited (Ignell et al. 1997; Farley and Munk 1997; Hagen 1999; Carlson et al. this volume). International standardization and supplementation with other marks may be necessary for future high seas applications (Munk 1999; Volk and Hagen 1999).

International genetic baselines have been established for chum, sockeye, and chinook salmon (*O. tshawytscha*). International genetic baselines for sockeye salmon can accurately separate Asian and North American fish, but are not accurate at distinguishing among North American stocks. There is no international baseline for coho salmon (*O. kisutch*). All baselines need more samples from Russian stocks.

The combined results of genetic stock identification, scale pattern analysis, and parasite analysis sug-

gest that the areas of intermingling of Asian and North American salmon in the Bering Sea and North Pacific Ocean are wider than that shown by direct evidence from tag experiments. Our present understanding of stock-specific distribution, migration patterns, and abundance of salmon in offshore waters is limited. Much work remains to validate the results of genetic and other indirect methods of stock identification of salmon on the high seas.

International Cooperative High Seas Salmon Research

Cooperative research on the high seas (international waters) is critical to understanding salmon carrying capacity (density-dependent growth) in the North Pacific Ocean and Bering Sea. The US high seas salmon research program involves international cooperative studies with Canadian, Japanese, and Russian scientists, including: (1) shipboard field studies on salmon distribution, migration patterns, abundance, and growth (e.g., Davis and Tadokoro 1994; Carlson et al. 1998b; Ishida et al. 1998a,b; Ueno et al. 1998; Carlson et al. 1999; Yamaguchi et al. 1999), (2) food habits studies and bioenergetic modeling (e.g., Tadokoro et al. 1996; Aydin 1998; Davis et al. 1998; Aydin et al. this volume; Davis et al. this volume; Walker et al. this volume), (3) growth studies using historical scale collections (e.g., Walker et al. 1998), (4) salmon life-history and carrying capacity modeling (e.g., Pearcy et al. 1999; Aydin et al. this volume), and (5) behavior studies using data storage tags (e.g., Walker et al. 2000).

The results of international cooperative research indicate that high seas distribution of salmon is most closely associated with distribution of their prey. Most growth occurs in summer months. Sea temperature is the most important physical factor affecting growth, but bioenergetic models indicate that prey consumption is more important to growth in offshore waters than temperature. Density-dependent prey limitation probably takes place in winter, when lipid stores are critical to salmon survival. High seas food-habit and bioenergetic studies provide evidence of feeding competition and density-dependent growth in summer. Behavior studies using data storage tags are providing significant new information on behavior of salmon with respect to ambient sea temperatures and depth. Summer data from tagged fish show considerable diurnal and shorter-term variation in ambient temperatures and swimming depth, indicating that non-lethal sea surface temperatures do not regulate the behavior of salmon on the high seas. These results do not minimize the potential problems associated with global warming, but warmer ocean temperatures in winter are associated with increased production of Alaska salmon. In the absence of large-scale high seas salmon fisheries, climate-

induced change in ocean productivity, acting through the food chain, is the major factor affecting high seas production of salmon.

CONCLUSION

Our review of US research indicates that climate-induced variation in productivity and fishing are the two major factors affecting ocean production of salmon, but the underlying mechanisms are not well known. To understand the processes linking climate, ocean productivity, and salmon production, we need stock-specific information on salmon distribution, abundance, and migration patterns with respect to environmental conditions. We recommend continuation of this research, with a strong emphasis on (1) the development of new technologies and international baselines for salmon stock identification, (2) shipboard research and monitoring programs to provide a platform for process studies, as well as data on interannual variation in ocean growth, distribution, and run timing of key stocks, and (3) the development and dissemination of international databases useful for research on ocean production of salmon.

"The historical perspective suggests that salmonid stocks waxed and waned in different parts of their range with interdecadal, centenary, and millenary fluctuations in past ocean climates. Since anadromous salmonids of the genus *Oncorhynchus* have persisted during the past 50–100 million years (McPhail 1997), they must have evolved mechanisms to enable them to adapt to large-scale climatic changes" (Percy 1997). Fluctuations in salmon abundance and climate are normal. This underscores the importance of ocean conservation of salmon and protection of freshwater habitats during periods of low ocean productivity.

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Recent Changes in the Pelagic Nekton Community Off Oregon and Washington in Relation to Some Physical Oceanographic Conditions

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Abstract: Since approximately 1977, there have been dramatic declines in West Coast salmonid (*Oncorhynchus* spp.) resources and salmonid marine survival. At the same time, there are indications that the pelagic nekton fauna off Oregon and Washington has shifted in species composition and abundance since the late 1970s. While Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasii*), American shad (*Alosa sapidissima*), Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and Pacific sardine (*Sardinops sagax*) populations off the Northwest coast have increased in abundance since 1977, ocean survival of salmonids, and populations of northern anchovy (*Engraulis mordax*), eulachon (*Thaleichthys pacificus*), and market squid (*Loligo opalescens*) declined. Northwest sea surface temperatures have shown a strong warming trend since 1977. Our results suggest that salmon marine survival is affected by the interplay between biological and physical factors in the northern California Current.

INTRODUCTION

Recent studies indicate that the biological community structure and dynamics of the California Current ecosystem are affected by a complex series of atmospheric/ocean interactions occurring remotely and locally at varying time scales (Francis and Hare 1994; Brodeur et al. 1996). There is also evidence that both lower and higher trophic levels undergo substantial shifts in abundance and species composition, and that these changes are usually out of phase with those occurring in the Gulf of Alaska (Hollowed and Wooster 1992, 1995; Brodeur et al. 1996; Hare et al. 1999). Examples of large fluctuations in pelagic fish composition include long-term changes in the abundance of northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) populations in the California Current system (Baumgartner et al. 1992) and the synchronous rise and fall of anchovy and sardine populations off Peru and other regions (Lluch-Belda et al. 1992). Furthermore, large annual fluctuations in pelagic and demersal fish recruitment have been documented for the Northeast Pacific Ocean (Hollowed et al. 1987; McFarlane and Beamish 1992; Beamish 1993).

Since approximately 1977, there have been dra-

matic declines in West Coast salmonid (*Oncorhynchus* spp.) populations. While much of this decline undoubtedly relates to loss and impairment of freshwater habitat (Gregory and Bisson 1997), ocean conditions have changed markedly since the 1970s, coinciding with the declines in salmonid marine survival (Pearcy 1992, 1997; Francis and Hare 1994; Beamish et al. 1995; Hare et al. 1999). At the same time, there are indications that the pelagic nekton off Oregon and Washington has shifted in both species composition and abundance since the late 1970s. Evidence includes reduced abundance of northern anchovy and market squid (*Loligo opalescens*), and the increased abundance of Pacific sardine, chub or Pacific mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and Pacific hake (*Merluccius productus*) (NMFS unpublished data, and personal observations).

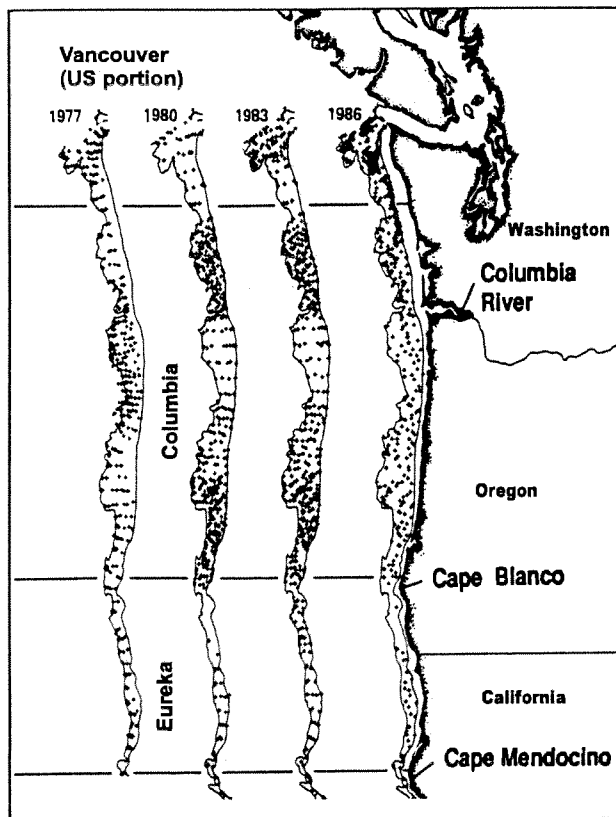
The purpose of this paper is to summarize pelagic nekton collections off Oregon and Washington since 1977, and relate these data to ocean environmental conditions. We also relate changes in a Northwest salmon population [i.e., ocean survival for Oregon Production Index Area coho salmon (*Oncorhynchus kisutch*)] to changes in the abundance and species composition of the pelagic nekton.

METHODS AND MATERIALS

Nekton Data

Pelagic nekton abundances and species compositions came from four different sources. The first was the direct measurement of Pacific hake and incidental catches of pelagic fishes captured during the National Marine Fisheries Service's (NMFS) **Triennial Trawl Survey** of groundfish resources on the Northwest shelf (Dark and Wilkins 1994; Wilkins 1996). Triennial survey data were available from 1977 through 1998. Although the survey was not designed to target small pelagic species, the survey consists of a randomized design with standardized effort each year, thus permitting comparisons of catches between survey periods. All trawling was done using a Nor'Eastern¹ trawl constructed with 8.9 cm nylon mesh in the body and lined with 3.2 cm mesh to retain small fish. Surveys were conducted from July to October from northern Washington to Monterey Bay, California. Typical trawl sampling locations and the geographic range of fishery statistical regions are

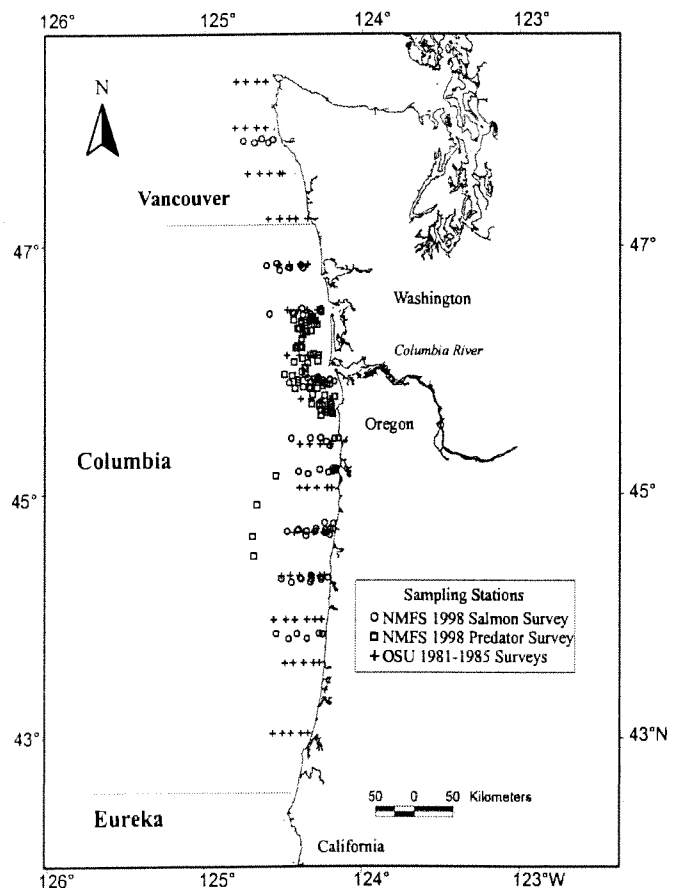
Fig. 1. Examples of geographic distribution and sampling effort of the NMFS Triennial Trawl Survey on the US continental shelf from 1977 to 1986. Also shown are three fishery statistical regions, Vancouver (U.S. portion), Columbia, and Eureka (modified from Dark and Wilkins 1994).



shown (Fig. 1). For this study, only data from the Columbia Statistical Region, which extends from northern Washington to southern Oregon, were used. This region overlaps with the Oregon Production Index Area used to estimate coho salmon marine survival and all other pelagic nekton data sources used in this study.

The second source of data on pelagic nekton abundance off Oregon and Washington was from purse seine collections conducted from May to September of 1981 to 1985 by Oregon State University (OSU) [see Brodeur and Pearcy (1986) and Pearcy and Fisher (1990) for sampling dates and details]. Briefly, fine mesh (32 mm) herring purse seines were fished along east-west transects from Cape Flattery off Northern Washington to Cape Blanco off Oregon. The net size varied from 457 m to 495 m in length and 20 m to 60 m in depth among the 15 cruises. It is important to note that most of these collections were conducted during daylight. These data will be referred to as the **OSU 1981–1985 Survey**. Locations of their sampling stations are shown (Fig. 2).

Fig. 2. Location of stations sampled by surface trawl during the NMFS Salmon Survey, Predator Survey and OSU purse seine survey.



¹Reference to trade name does not mean endorsement by NOAA, National Marine Fisheries Service.

The third data set consists of the nekton captured during a NMFS pelagic trawl survey for juvenile salmonids off Washington and Oregon during June and September of 1998, and May, June, and September of 1999. This survey sampled as far north as La Push, Washington and south to Cape Perpetua, Oregon (Fig. 2). Sampling consisted of one-half hour surface tows of a 264 Nordic rope trawl (built by Nor'Eastern Trawl Systems, Inc.) along transects perpendicular from shore, at a variety of locations. The Nordic rope trawl, which has variable mesh sizes (162.6 cm at mouth to 8.9 cm at cod end with a 1.5 cm cod-end liner), has a fishing mouth opening of approximately 30 m x 20 m. Initial trawls were conducted in as shallow water as was possible (30 m depth); farthest seaward sampling was conducted approximately 50 km from shore. Except for a couple of trawls, all sampling was conducted during daylight. These data will be referred to as the **NMFS Salmon Survey**.

The fourth data set came from the NMFS 1998 and 1999 pelagic and midwater trawling survey of juvenile salmonid fish predators off the mouth of the Columbia River (Fig. 2). This sampling consisted of trawling for two nights every two weeks from April to mid-August. Initial sampling gear was a standard Pacific hake net, which is a large variable-mesh rope trawl (mouth opening 60 m x 28 m) fished as close to the surface as possible. However, from mid-June on, a Nordic 264 surface rope trawl (as in the NMFS salmon survey) was used. Sampling during this study was conducted chiefly at night. Pacific hake and many other semi-demersal and pelagic species have nocturnal behavior and move near the surface, where juvenile salmonids appear to reside, during night. These data will be referred to as the **NMFS 1998 Predator Survey**.

To compare among the last three data sets, and to adjust for different gear (purse seine catches and trawl catches) and effort, all data were transformed to percentage of total catch for a particular year. The NMFS triennial survey data, however, are presented as estimates of species biomass by metric ton (mt) (Wilkins 1996 and personal communication, Alaska Fisheries Science Center, Seattle, WA). Finally, to examine long-term changes in small fish and squid commonly eaten by predatory fishes and birds, these species numbers were summed and represented as a forage nekton category while large piscivorous fishes were grouped as predators.

Hatchery coho salmon ocean survival data from the Oregon Production Index Area were used as a general description of annual ocean salmon survival. However, wild salmon generally survive at much higher rates (Nickelson 1986) and salmonid ocean survival can vary widely depending on species, stock, and location. Percent hatchery coho salmon marine survival was determined by dividing estimated adult

hatchery returns (catch and escapement) by number of juvenile hatchery releases (see Pacific Fishery Management Council 2000 for data).

Physical Data

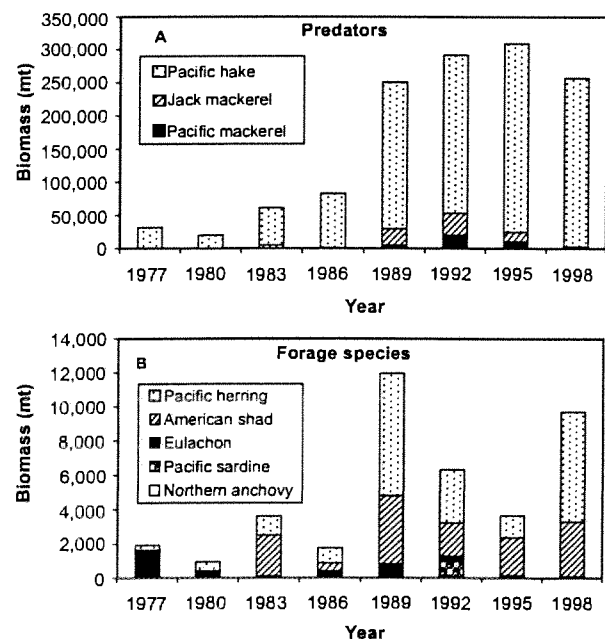
Physical oceanographic data were obtained from a variety of sources. Of particular interest were long-term records of physical conditions relevant to the Pacific Northwest. Sea surface temperatures were obtained from the Scripps Institute of Oceanography Shore Station web site for Charleston, Oregon, and Neah Bay, Washington (ftp://nemo.ucsd.edu/pub/shore/monthly_means/). Upwelling data were obtained from NOAA's Pacific Fishery Environmental Laboratory, Pacific Grove, California (Jerrold Norton, PFEL, pers. comm., and <http://www.pfeg.noaa.gov/index.html>).

RESULTS

NMFS Triennial Trawl Survey

The estimated abundances of the dominant pelagic fishes, separated by adult size and feeding habits into either forage fishes or predators, during the NMFS triennial trawl surveys indicate that a large change in the pelagic fish community occurred between 1977 and 1995 (Fig. 3). Pacific sardine, chub mackerel, jack mackerel, Pacific herring (*Clupea pallasii*), American shad (*Alosa sapidissima*) and

Fig. 3. Estimated biomass of three fish predators (A) and five forage fish (B) species caught during National Marine Fisheries Service (NMFS) triennial trawl survey of fish abundance on the continental shelf in the Columbia Region (data provided by Mark Wilkins, NMFS).

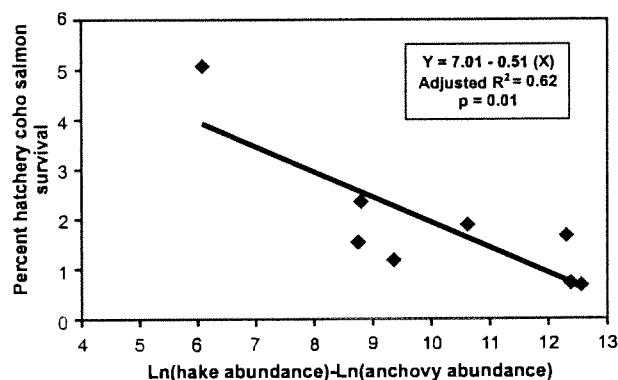


Pacific hake increased in abundance while northern anchovy and eulachon (*Thaleichthys pacificus*) declined. The Pacific hake population showed over a five-fold increase, from less than 50,000 mt in 1977 to over 284,000 mt in 1995. Both forage nekton and predatory nekton increased substantially beginning in 1989 (Fig. 3).

There appears to be a relatively strong inverse relationship between jack mackerel abundance and coho salmon marine survival [linear regression of $\ln(\text{jack mackerel abundance})$ on percent coho salmon marine survival, $p = 0.12$, $R^2 = 0.41$] given the small data set. There was an even stronger inverse relationship between Pacific hake abundance and coho salmon marine survival [linear regression of $\ln(\text{Pacific hake abundance})$ on percent coho salmon marine survival, $p = 0.068$, $R^2 = 0.52$].

However, if we assume that hake predation on salmon is mediated by northern anchovy abundance (i.e., when anchovy is abundant, predation on salmonids is reduced), we can build a more realistic model of hake predation effects. The regression of $\ln(\text{Pacific hake}) - \ln(\text{northern anchovy})$ on percent coho salmon survival produces a $p = 0.007$ with a $R^2 = 0.80$ (Fig. 4). Using the regression formula from this analysis, we predict a 2.08% ocean survival of coho salmon juveniles which outmigrated to sea in 1998, most of which will be returning as adults in 1999. This is a much higher ocean survival than recent years (< 1% since 1992).

Fig. 4. Relationship between Oregon Production Index coho salmon percent marine survival and predation pressure of Pacific hake [defined by $\ln(\text{hake abundance}) - \ln(\text{anchovy abundance})$].



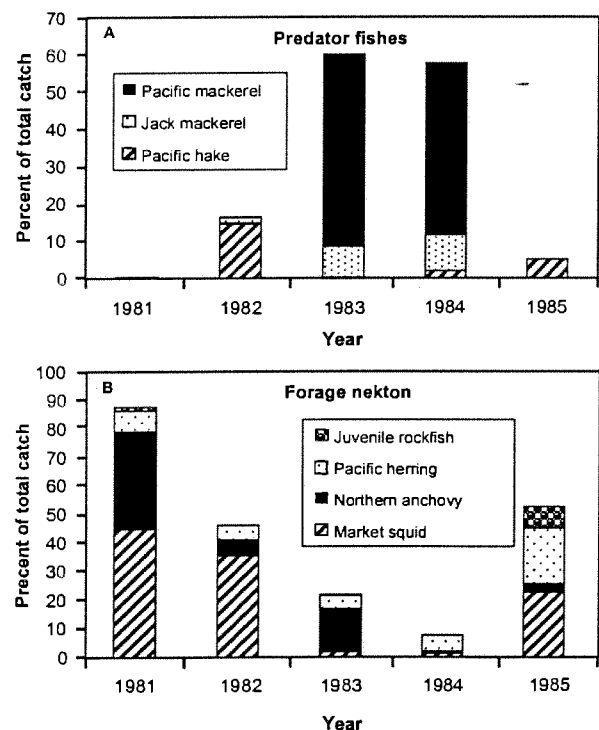
OSU 1981–1985 Survey

The pelagic nekton species composition off Oregon and Washington also changed from 1981 to 1985. The percentage of forage nekton (Fig. 5), in particular, fluctuated dramatically. In 1981, forage nekton comprised over 87% of the catch, dropped to 8% in 1984, and then rebounded to 52% in 1985. Northern anchovy showed the largest drop in percent

abundance from 1981 to 1985, declining from 34% to 3%, respectively. One forage species, Pacific herring, increased from 7.2% of the catches in 1981 to 19.3% in 1985. Meanwhile, the large predatory fish Pacific hake showed increases in relative abundance from 1981 to 1985 (Fig. 5). Pacific and jack mackerel were very large percentages of the catches only in 1983 and 1984, which were warm El Niño years.

Juvenile salmonids were an important component of the pelagic nekton community during these annual surveys (Fig. 6). Juvenile coho salmon were the most abundant salmonid captured, and were consistently more abundant than juvenile chinook salmon (*O. tshawytscha*). Coho salmon were particularly abundant in 1985 (19.5% of the catch). Chinook salmon were also a large percentage of the catch in 1985 (5.6%).

Fig. 5. Percent of total purse seine catches of major species of predator fishes (A) and forage nekton (B) off Oregon/southwest Washington from 1981 to 1985 by Oregon State University.



NMFS Salmon Survey

The composition of pelagic nekton captured during the NMFS 1998/1999 salmon survey was much different than that identified by the OSU 1981–1985 surveys. Particularly striking was the dominance of Pacific sardine in the catches, 18% and 59% in 1998 and 1999, respectively (Fig. 7), whereas sardines were rarely captured during the OSU 1981–1985 surveys. Other dominant forage nekton included Pacific herring, 59% of the catch in 1998 and 18% in 1999.

Fig. 6. Percent of total catch comprised of salmonids during the OSU purse seine survey (A) and the NMFS trawl surveys (B).

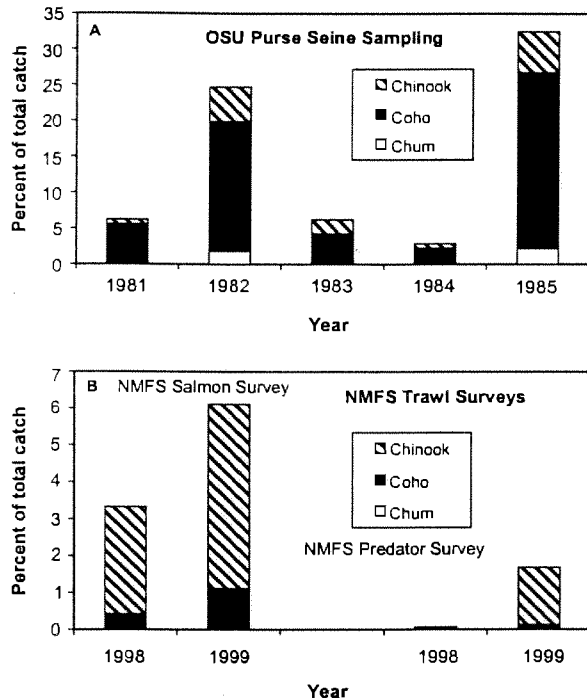
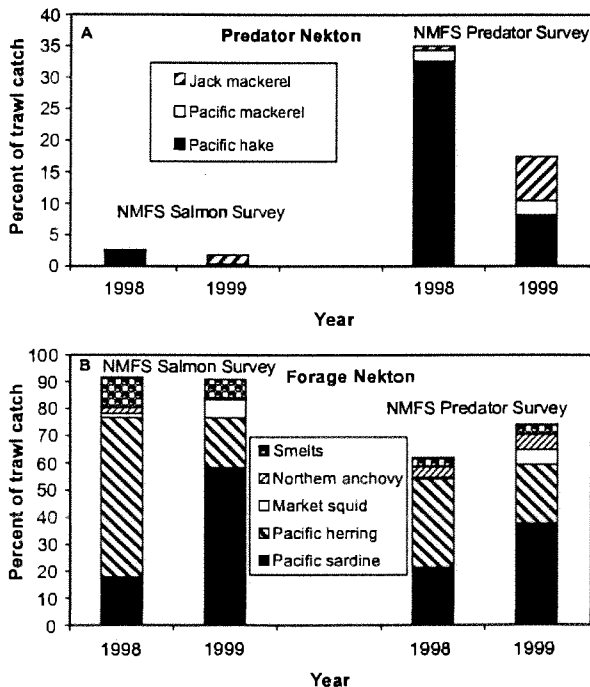


Fig. 7. Percent of total surface and near-surface trawl catches off Oregon/southwest Washington composed of predator fishes (A) and forage fishes (B).



In contrast, market squid, an important component of the pelagic nekton in the early 1980s (Brodeur and Pearcy 1992), were only 2% and 7% of the NMFS catches in 1998 and 1999, respectively. Overall, forage nekton composed over 90% of the catches during 1998 and 1999. However, the forage nekton species were different than those during the OSU 1981–1985 surveys. The major predator in 1998 was Pacific hake, but it only comprised 2.3% of the catch in 1998 and 0.3% in 1999 (Fig. 7).

Unlike the OSU 1981–1985 survey, few juvenile coho salmon were captured and they comprised a very small portion of the catches (0.4% in 1998, and 1.2% in 1999) (Fig. 6). However, the percentage of the catch made up by juvenile chinook salmon (3.0% in 1998 and 5.0% in 1999) was not much different than that observed during the OSU 1981–1985 surveys.

NMFS 1998 Predator Survey

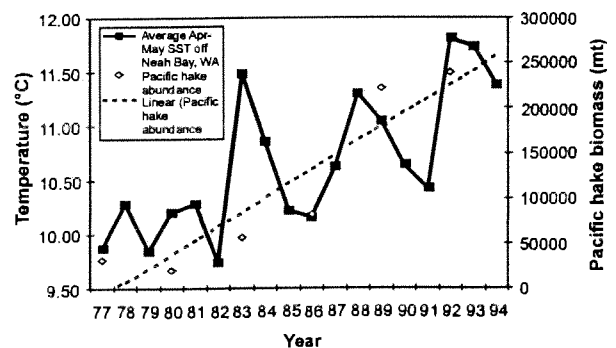
This survey showed similar catches to the NMFS Salmon Survey, with Pacific sardine and Pacific herring being the dominant forage nekton (Fig. 7). However, this survey also caught large numbers of Pacific hake (33% and 8% of the catch in 1998 and 1999, respectively). This was probably related to time of the collections, which were conducted at night. The percentages of forage fish catches were lower than the NMFS salmon survey due to the preponderance of adult Pacific hake and jack mackerel, but both surveys were relatively similar in species composition.

Physical Data

Upwelling

Seasonal upwelling has been shown to be a significant predictor of salmon ocean survival in the past (Nickelson 1986; Lawson 1997). Cumulative sum plots of upwelling anomalies at 45°N 125°W (Fig. 8)

Fig. 8. Cumulative sum of spring, summer, and fall upwelling anomalies at 45°N 125°W.

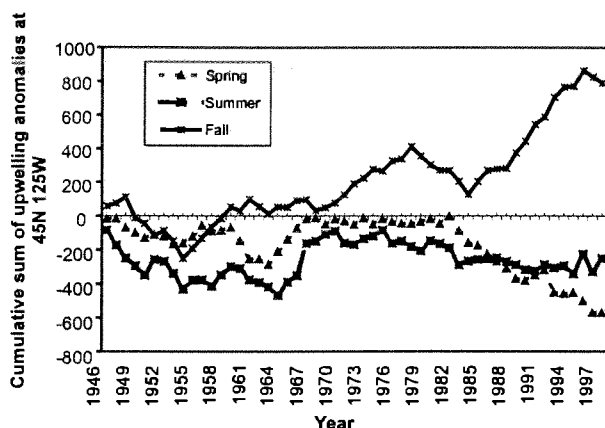


showed that, from about 1982 until 1998, spring upwelling anomalies were almost consistently negative (less spring upwelling). Fall upwelling during the same period showed the opposite trend with relatively consistent positive anomalies (Fig. 8). Summer upwelling showed no consistent trends.

Sea surface temperatures

Lawson (1997) found that winter sea surface temperatures at Charleston, Oregon explained a significant amount of the variation in salmon ocean survival. While sea surface temperatures (SST) at Charleston appear to be warmer since 1985, early trends in SST data are unclear because of missed data points. The more complete SST series from Neah Bay, however, showed a strong warming trend since 1977, with April–May averages rising from slightly below 10.0°C in 1977 to 11.8°C in 1994 (Fig. 9). When we plotted Neah Bay average SST and Pacific hake abundance, as measured by trawl survey in the Columbia Statistical Region (Fig. 9), we found that as summer SST increased, Pacific hake became more abundant. Ware and McFarlane (1995) documented a similar trend off British Columbia.

Fig. 9. The relationship between Pacific hake abundance in the Columbia Statistical Region and sea surface temperatures off Neah Bay, Washington.



DISCUSSION

During the past 20 years many studies have indicated that changing ocean conditions play a large role in the recent decline in abundance of many salmonid stocks (Percy 1992, 1997; Coronado and Hilborn 1998). While physical factors and food supply are generally thought to be important mechanisms regulating ocean salmon survival, interspecific interactions (competition and predation) with other nekton species are coming under increasing scrutiny (Percy 1992; Emmett 1997; Fresh 1997; Nagasawa 1998). Unfortunately, no regular systematic surveys of the pelagic nekton and the associated oceanographic

physical conditions have been made. In this paper, we have examined changes in pelagic nekton species composition and biomass trends over the last two decades off the Pacific Northwest using a variety of data sources. While the data compiled during this study were from different fishing survey designs, gear types and years, they nevertheless provide evidence that the pelagic nekton community of the northern California Current has changed dramatically since the late 1970s.

The decline in the percentage of coho salmon in the pelagic nekton community off Oregon and Washington from the early 1980s to 1998/1999 probably reflects a variety of factors. A major factor has been the reduced number of hatchery salmon being released. In the early 1980s commercial (for profit) salmon hatcheries were releasing millions of coho salmon smolts, but these are now shut down (Weitkamp et al. 1995). Other causes of reduced ocean abundance of juvenile coho salmon include less freshwater production and decreased marine survival. The reduced percentage of chum salmon (*O. keta*) captured in 1998/1999 versus the 1980s may reflect their overall decline in abundance. However, while Columbia River and Hood Canal stocks are presently listed as threatened, most coastal stocks do not appear to be declining in abundance (Johnson et al. 1997). The relatively stable percentages of chinook salmon in nekton catches (between 1980s and 1998/1999) probably relates to continued large hatchery releases, adequate freshwater production, and perhaps better marine survival than coho salmon.

The NMFS triennial trawl survey results suggest that Pacific hake, Pacific herring, American shad, Pacific and jack mackerel, and Pacific sardine populations off the Northwest have increased, while northern anchovy and eulachon populations have decreased. These changes are concurrent with the decrease in survival of juvenile salmon. Although we do not have any direct evidence that this relationship is causal, species interactions undoubtedly occur, and probably play a role in determining pelagic nekton species composition. Off British Columbia, predation by increased numbers of Pacific hake since 1977 caused the marked decline in their primary forage fish, Pacific herring (Ware and McFarlane 1995). Furthermore, there appears to be a relationship between forage fish abundance and salmon ocean survival. Holtby (1988) showed that smolt-to-adult survival rates of Carnation Creek, B.C., coho salmon were significantly greater during years when age-1 Pacific herring were abundant in and around Barkley Sound, Canada. Our data also appear to support the Fisher and Percy (1988) hypothesis that increased predation, perhaps resulting from decreased alternative prey (i.e., forage fish such as anchovy), was responsible for the low coho salmon marine survival in the early 1980s.

The data presented here, unlike those for British Columbia waters, indicate that Pacific herring off Oregon and Washington have increased since the late 1980s, where northern anchovy has, until recently, been the dominant forage fish (Richardson 1981). The decline in northern anchovy may be related to a host of factors, including increased predation by Pacific hake and mackerel, competition with other similar sized species such as sardines and herring, or changes in wind stress, upwelling and other oceanographic conditions during spawning and larval development. Older and larger Pacific hake and mackerel feed on northern anchovy (Livingston and Alton 1982; MBC Applied Environmental Sciences 1987). We find it likely that increased predation on northern anchovy has been a factor reducing its abundance since 1977. Furthermore, adult anchovies may suffer a higher predation rate than either Pacific herring or Pacific sardine because northern anchovy are more susceptible to predation throughout their entire life history (smaller adult size) (Hart 1973).

One of the most obvious changes that occurred in the pelagic nekton community off Oregon and Washington since 1977 is the present high abundance of Pacific sardines. Although they were reported as early as 1984 (Brodeur and Pearcy 1986), Pacific sardines apparently arrived in great numbers to waters of the Pacific Northwest sometime between 1989 and 1992 (Hargreaves et al. 1994). There is evidence that the West Coast population of Pacific sardines, which is centered in California, is rapidly increasing and has expanded its range north into British Columbia and even into Alaskan waters (Hargreaves et al. 1994; Beamish et al. 2000). Sardines are now spawning off Oregon and Washington (Bentley et al. 1996) and British Columbia (Beamish et al. 2000). At about the same time, the northern anchovy population in this region evidently crashed. They have declined from being one of the dominant fish caught in the early 1980s cruises to mainly an incidental species in the 1990s. Historically a relatively large population of northern anchovy used to spawn in the plume of the Columbia River (Richardson 1981), but spawning now appears to be restricted to a narrow nearshore area adjacent to Willapa Bay, Washington (Emmett et al. 1997; unpublished data).

Pacific hake, one of the most abundant pelagic fish in the California Current system, also appears to be altering its range and distribution. Evidently, recent warmer ocean temperatures and slower southerly-flowing currents have prompted Pacific hake to migrate faster and earlier from their California spawning grounds (Dorn 1995; McFarlane and Beamish 1999). There are also indications that Pacific hake may have shifted their spawning area farther north (Horne and Smith 1997; Beamish et al. 2000). Finally, Pacific hake has had several years of good recruitment since 1977, so that their overall

abundance is relatively high (Dorn 1996; Wilkins 1996). The OSU purse seining survey and the NMFS salmon survey surface trawling were conducted primarily during daylight, and evidently underestimated Pacific hake abundance because of hake's diurnal migrational behavior. During darkness Pacific hake migrated to the surface, where they were susceptible to capture by surface trawl during the NMFS predation study.

Pacific and jack mackerel also have become an important component of the pelagic ecosystem off Oregon and Washington, at least during the summer months. They apparently invaded the region around the time of the 1983 El Niño and became the dominant fishes caught in the purse seine sampling during 1983 and 1984 (Brodeur and Pearcy 1986, 1992). Pacific mackerel were also common in British Columbia at that time (Ashton et al. 1985), and in recent years they have been found as far north as northern British Columbia (Beamish et al. 2000). Although a large proportion of the population is believed to return to Southern California in the winter to spawn, some Pacific mackerel eggs and larvae have been found off Oregon (Emmett, unpublished data).

Perhaps the only study off Washington and Oregon comparable to ours in terms of spanning several decades was the analysis of Soviet bottom trawl data collected from 1965 to 1985 by Ermakov and Stepanenko (1996). They also showed dramatic fluctuations in the catch of pelagic forage species such as Pacific herring, American shad, northern anchovy and smelts, but the overall biomass was dominated by Pacific hake throughout this period. They found, as we did, that chub mackerel and sardines only began to occur in their catches from 1980 to 1985. They attributed some of the declines in fish populations to fishing, but many species that were not the direct target of fisheries also fluctuated in abundance.

The change in the pelagic nekton community off the Pacific Northwest appears to be related to changes in atmospheric and oceanic circulation since 1977 (Mantua et al. 1997). In particular, the increasing ocean temperatures and less southerly current transport may be related to an unprecedented series of El Niño events, especially in the 1990s (Trenberth and Hoar 1996). These warming events, beginning with the 1982–83 event, undoubtedly increased the range of geographic area species such as chub mackerel and other warm water species can occupy from off California to off the Pacific Northwest (Pearcy et al. 1985; Brodeur and Pearcy 1992). There is increasing evidence for a 1989 regime shift (Beamish et al. 2000; Hare and Mantua 2000), and this is reflected in a dramatic increase in both forage and predator nekton at this time. In this example, the response is far too rapid to be related to an influx of new recruits, but is more likely a shift in distribution of these species.

This pelagic community change also coincides with the decline in coho salmon ocean survival. We suspect that ocean-migrating juvenile coho salmon are being "squeezed" by both competitors and predators, and that smolts are finding reduced ocean habitats containing appropriate or optimum water temperatures and feeding conditions (Fisher and Pearcy 1988; Pearcy 1992). Besides having to evade numerous predators (large mackerel and Pacific hake), coho salmon may also be suffering from competition with small individuals of these and other species. Small mackerel and hake feed primarily on euphausiids, a common prey of juvenile salmonids (Peterson et al. 1982; Brodeur et al. 1987; Brodeur and Pearcy 1992). At the same time, northern anchovy, eulachon, and market squid populations appear to have crashed, thus diminishing any predatory "buffer" or alternative prey to predators in place of salmonids. Sardines could also be acting as competitors with juvenile salmon for food. As a potential result of this competition, juvenile salmon ocean growth may now be reduced, thus prolonging their availability to predators. Studies are presently underway by NMFS and others to identify the growth rates and fish predators of juvenile salmonids and to quantify their predation rates in coastal waters.

CONCLUSIONS

The pelagic nekton fauna off the Oregon coast has changed markedly since 1977. In the late 1970s and early 1980s market squid, eulachon, and northern anchovy were a large proportion of the pelagic nekton fauna. Starting in the late 1980s and early 1990s, however, these species were evidently replaced by Pacific sardine, Pacific mackerel, and jack mackerel. Pacific hake also became more abundant beginning in the late 1980s. The cause of this species change is uncertain; however, it correlates well with increasing sea surface temperatures and other oceanographic conditions. The shift in the pelagic nekton fauna (particularly the increase in Pacific hake and the decrease in northern anchovy) appears to be strongly associated with the decline in coho salmon ocean survival. The actual mechanisms whereby Pacific hake, northern anchovy, or possibly mackerel affect ocean survival of salmonids is uncertain, but predation and competition could both be playing a role.

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Winter Zooplankton Biomass in the Subarctic North Pacific, with a Discussion on the Overwintering Survival Strategy of Pacific Salmon (*Oncorhynchus* spp.)

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Keywords: Winter zooplankton biomass, North Pacific Ocean, Pacific salmon, *Oncorhynchus* spp., offshore distribution, survival strategy

Abstract: Zooplankton biomass was investigated using a North Pacific standard plankton (NORPAC) net in a wide area of the northern North Pacific Ocean (including the Gulf of Alaska and Bering Sea) in November to December 1992, January 1996, and February 1998. Data are compared with results from the literature obtained in summer (June or July), and discussed in relation to the winter ocean distribution of salmonids. In all of the western and central Pacific, Gulf of Alaska and Bering Sea, the winter zooplankton biomass was low, being, in January or February, about 10% of the summer biomass. There was also a regional difference in zooplankton biomass in the North Pacific: it was higher in the western Pacific than in the central Pacific and Gulf of Alaska. The biomass appeared to decline in January in the western and central Pacific. Five species of salmonids [sockeye (*Oncorhynchus nerka*), chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon] were mostly captured in the Subarctic Domain and northern Transitional Domain at sea surface temperatures lower than 8°C, where the zooplankton biomass remained quite low as well. These salmonids may have a survival strategy to overwinter in cold waters to reduce metabolic consumption under poor food conditions of offshore waters.

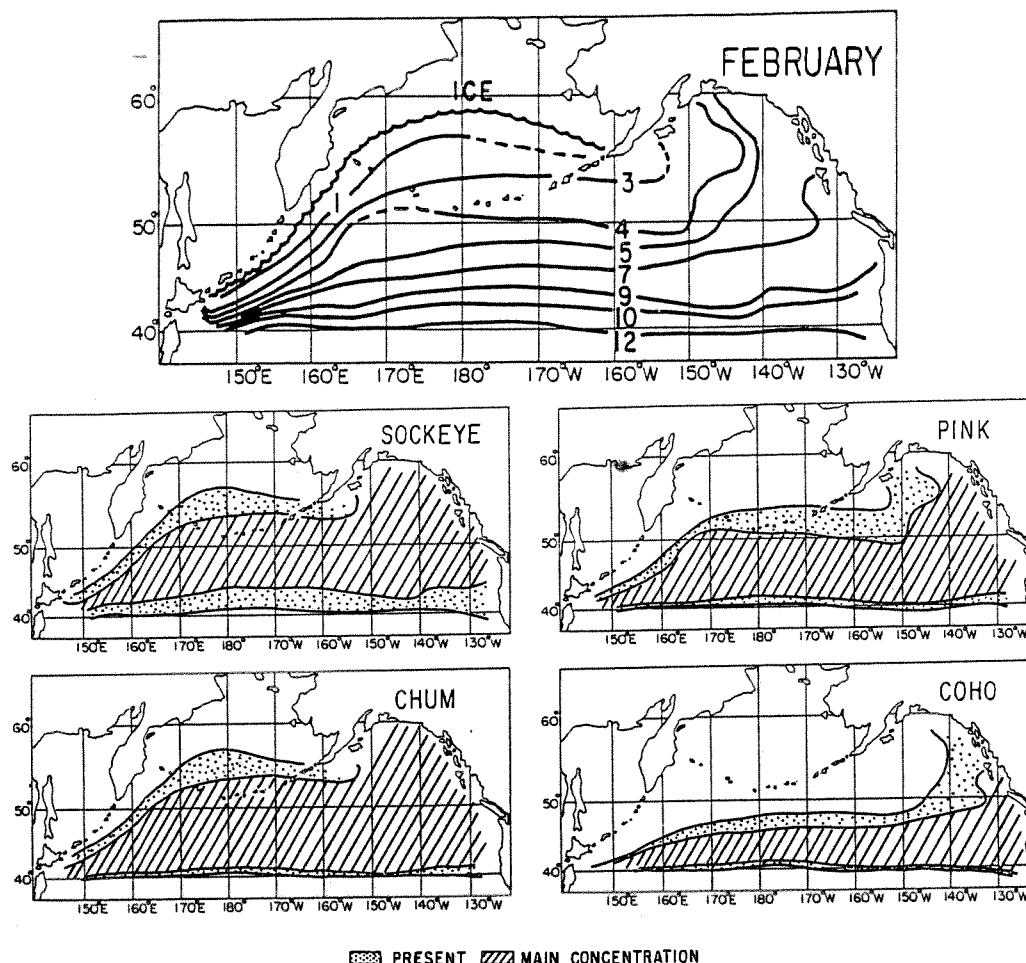
INTRODUCTION

Our current knowledge about the biology of Pacific salmon (*Oncorhynchus* spp.) on the high seas of the North Pacific Ocean is based largely on offshore surveys conducted by scientists of Japan, Canada and the U.S.A. from 1950's to 1992 under the auspices of the International North Pacific Fisheries Commission (INPFC) (e.g., French et al. 1976 for sockeye salmon, *O. nerka*; Neave et al. 1976 for chum salmon, *O. keta*; Takagi et al. 1981 for pink salmon, *O. gorbuscha*; Godfrey et al. 1975 for coho salmon, *O. kisutch*; Major et al. 1978 for chinook salmon, *O. tshawytscha*; Machidori and Kato 1984 for masu salmon, *O. masou*; Burgner et al. 1992 for steelhead trout *O. mykiss*; Hartt and Dell 1986 for juvenile salmonids). However, since most of the offshore surveys were conducted during the spring and summer, we have only fragmentary information on the autumn and winter offshore life of salmonids. A few papers deal with the biology and distribution of offshore salmonids during the autumn and winter (e.g., French and Mason 1964; French and McAlister 1970; Shimazaki and Nakayama 1975; Erokin 1991; Sobolevskiy et al. 1994; Glebov and Rassadnikov

1997; Startsev and Rassadnikov 1997). This lack of information is due to difficulty in conducting surveys on the high seas under rough weather and ocean conditions in the autumn and winter.

The winter distribution of Pacific salmon in offshore waters has been a mystery for a long time. In his book, Percy (1992, p.90) stated "Least is known about the high seas distribution of salmon during the winter." To rectify this situation, Japanese salmon scientists conducted large-scale surveys, together with U.S., Canadian and Russian scientists, in the winters of 1992, 1996 and 1998 in offshore waters of the North Pacific Ocean under the auspices of the new international organization, North Pacific Anadromous Fish Commission (NPAFC) (Nagasawa et al. 1994; Ueno et al. 1997; Ishida et al. 1999). Prior to the surveys, Manzer et al. (1965) hypothesized that four species of salmonids (sockeye, chum, pink, and coho salmon) would be widely distributed northward from the 12°C isotherm at about 40°N near the Subarctic Boundary in winter (Fig. 1). However, Japan's winter surveys produced very different results (Ueno et al. 1999) and revealed that all species of salmonids have narrower latitudinal ranges than hypothesized, and occur in northern cold waters at sea

Fig. 1. Sea surface isotherms and hypothesized distribution of four species of Pacific salmon in February in the North Pacific Ocean and Bering Sea (modified from Manzer et al. 1965).



surface temperatures (SSTs) from 4 to 8°C (Fig. 2). This raised a question "Why do Pacific salmon overwinter in the northern cold waters?"

The winter surveys included zooplankton sampling and oceanographic observations to understand the winter habitat of offshore salmonids. The aims of the present paper are to elucidate the food conditions, measured as zooplankton biomass, for salmonids overwintering in the oceanic subarctic Pacific and to discuss the results in relation to the winter ocean distribution of salmonids.

MATERIALS AND METHODS

Survey Area

Zooplankton were sampled during three cruises of the R/V *Kaiyo maru* (2,630 gross tons) of the Fisheries Agency of Japan in a wide area of the northern North Pacific Ocean (including the Gulf of Alaska and Bering Sea) in late November to mid-December 1992, January 1996, and February 1998 (Fig. 3). The first and second cruises were conducted

as trans-Pacific surveys (from Tokyo to Seattle), whereas the third covered the western and central North Pacific and Bering Sea. During the 1992 cruise, sampling was done at 27 stations along three south-to-north transects [157°E (ca. 38°N to 45°30'N) in the western Pacific, 179°30'W (ca. 41°N to 46°N) in the central Pacific, and 145°W (ca. 44°30'N to 51°N) in the Gulf of Alaska] and two diagonal transects connecting the south-to-north transects. Only four samples were taken in November in the western Pacific, and the majority of sampling was conducted in December. For the 1996 cruise, approximately the same locations were planned for sampling but, due to rough weather, samples were taken at 23 different locations (especially in the central Pacific) along three south-to-north transects [160°E (ca. 40°N to 46°N), 168°W (ca. 41°30'N to 49°N), and 145°W (ca. 48°30'N to 56°N)] and two diagonal transects. During the 1998 cruise, sampling was conducted at 19 stations along two south-to-north transects [165°E (ca. 40°30'N to 51°N) and 180° (ca. 43°30'N to 58°30'N)] and one diagonal transect. As a rule, sampling stations were set at

Fig. 2. Distribution of CPUE (number of fish caught by trawl net per hour) of Pacific salmon (all species combined) in the North Pacific Ocean and Bering Sea in November to December 1992 (top), January 1996 (middle), and February 1998 (bottom) (modified from Ueno et al. 1999). Sea surface temperatures at 4 and 8°C are shown. Dotted lines show the borders of the Subarctic Domain (SD), Transitional Domain (TD), and subtropical waters (STW). Note that salmonids had narrower distributional ranges than hypothesized (see Fig. 1) and occurred in northern cold waters at sea surface temperatures less than 8°C. SB, Subarctic Boundary.

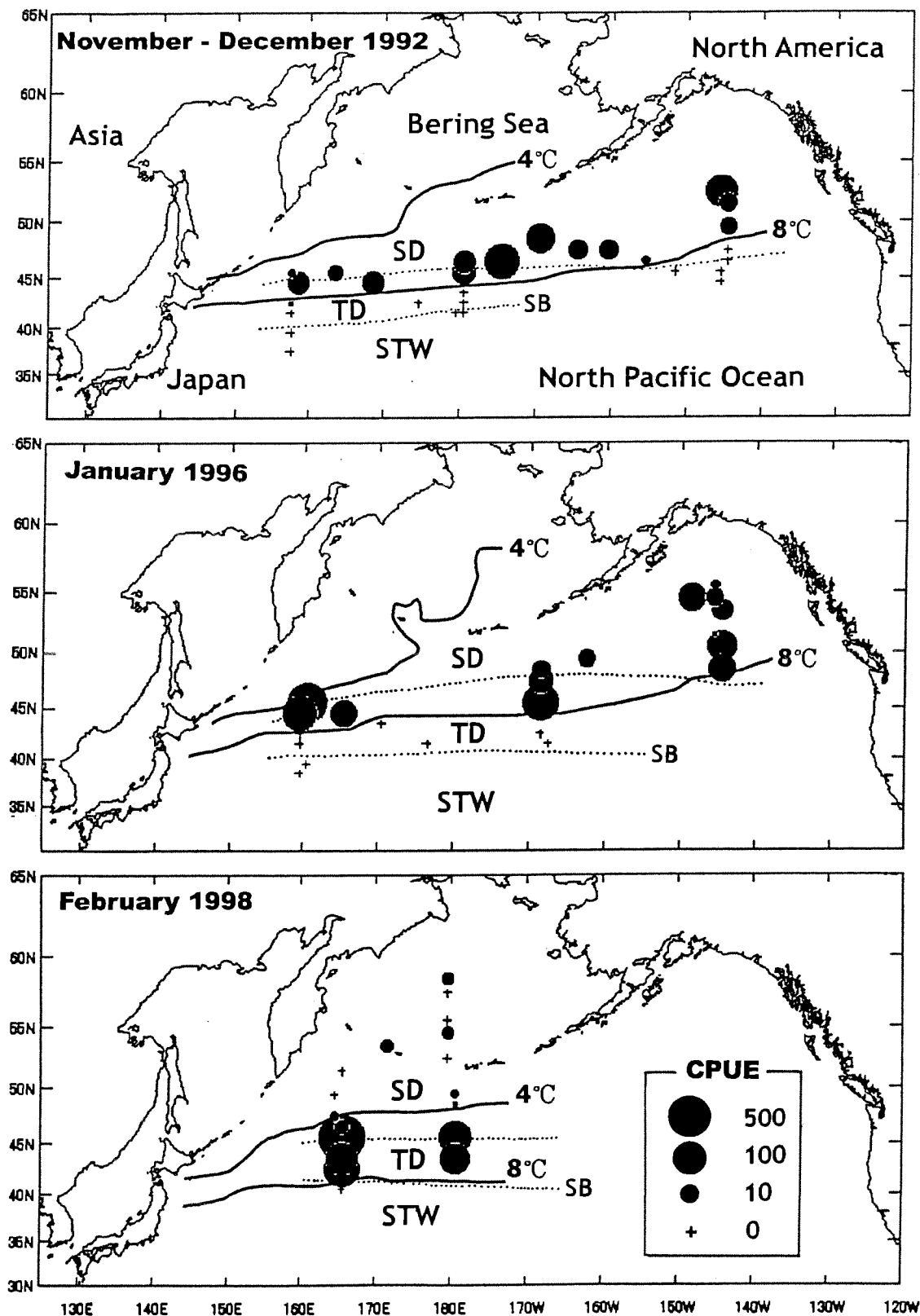
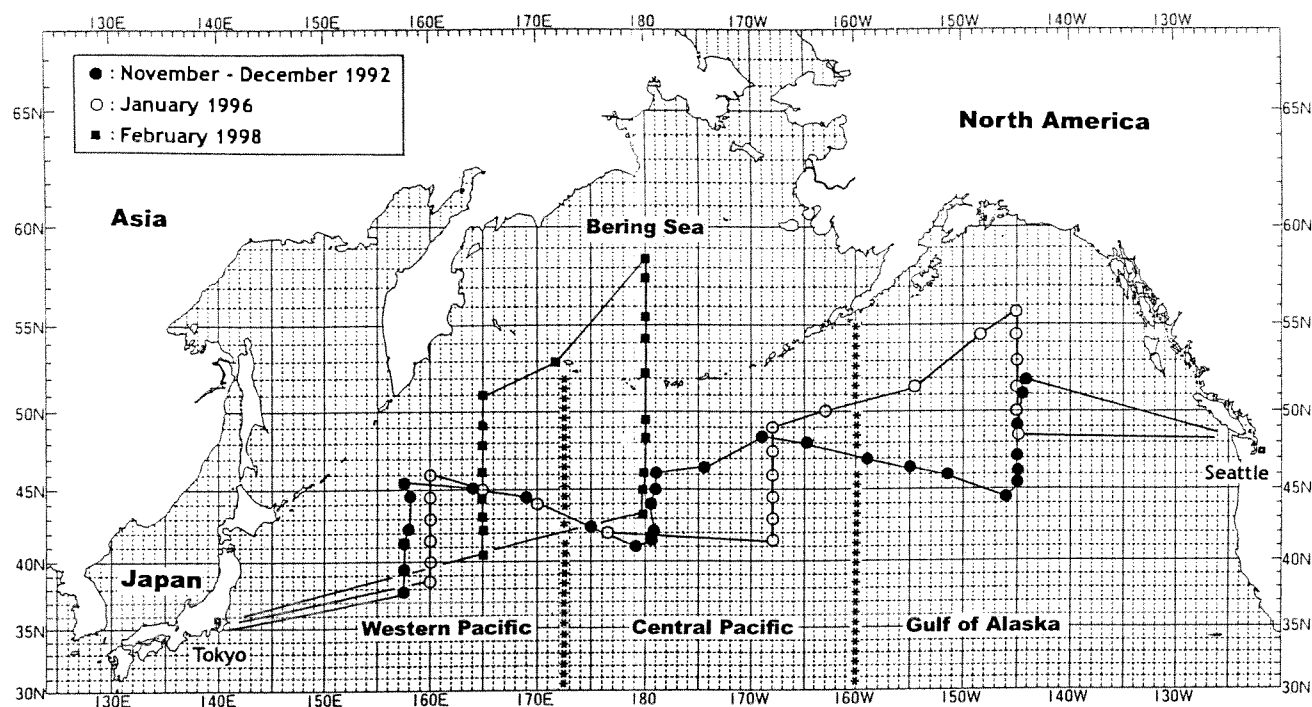


Fig. 3. Sampling stations of zooplankton in the North Pacific and Bering Sea during three cruises of the R/V *Kaiyo maru* in November to December 1992, January 1996, and February 1998. The survey area is divided into four regions: western Pacific (west of 172°30'E), central Pacific (172°30'E to 160°00'W), Gulf of Alaska (east of 160°00'W), and Bering Sea. Asterisk lines show the longitudinal borders separating the North Pacific into three regions.



every one degree of latitude for the south-to-north transects and at every five degrees of longitude for the diagonal transects.

Oceanographic Survey

At each sampling station, an oceanographic observation was made using a CTD sensor "Octopus" in order to collect data on water temperature, conductivity, salinity, and depth from 0 to 1,000 m. In case of high winds and rough seas, a Seabird CTD (Model 19) was used to collect data on water temperature and salinity to a depth of 800 m. While the R/V *Kaiyo maru* was underway, vertical thermal structure (0 to 760 m) was determined using an XBT at every one degree of longitude and 30-minute degree of latitude.

Zooplankton Sampling and Examination

Zooplankton was collected using a North Pacific standard (NORPAC) net (0.45 m diameter, 1.95 m length, 0.335 mm mesh size) (Motoda 1957) at each station. The plankton net was towed vertically from 150 m to the surface at a speed of 1 m per second. Sampling was usually done from the morning to the early evening. Filtered water volume was measured using a calibrated flow meter (Rigosha Co. Ltd., Japan). Samples were fixed in 10% borax-buffered formalin in seawater and sent to the National Research Institute of Far Seas Fisheries in Shimizu for

analysis.

Zooplankton was sorted to the following categories in the laboratory: euphausiids, copepods, pteropods, appendicularians, chaetognaths, ostracods, jellyfishes (medusae and ctenophores), salps, fishes, squids, and others (polychaets, decapods, eggs etc.). For each category, wet weight was measured. Zooplankton biomass used herein is defined as total wet weight of all categories collected per m³ at each station. Detailed data on zooplankton biomass and wet weight of each category at each location are found in Nagasawa et al. (1997, 1999).

Regional and Seasonal Comparison of Zooplankton Biomass

To examine regional differences in zooplankton biomass, the survey area was divided into four regions: western Pacific (west of 172°30'E), central Pacific (172°30'E to 160°00'W), Gulf of Alaska (east of 160°00'W), and Bering Sea (Fig. 3). Also, based on salinity and temperature data, three oceanographic regions were distinguished in the North Pacific: subtropical waters, Transitional Domain, and Subarctic Domain. The subtropical waters and Transitional Domain were located, respectively, south and north of the Subarctic Boundary, which was denoted as a vertical 34.0 psu isohaline from the surface to 200–400 m (Dodimead et al. 1963; Favorite et al. 1976). The northern edge of the Transitional Domain was

recognized as the surface isohaline of 33.0 psu (Favorite et al. 1976).

Also to examine seasonal changes in zooplankton biomass in each region, the winter zooplankton biomass data from each region were compared with data on the biomass of zooplankton collected in summer months (June or July) of 1994–1996 along transects at 165°00'E (40°00'N/41°00'N to 51°00'N) in the western Pacific (Nagasawa and Ishida 1995, 1997a), at 179°30'W (38°30'N to 51°30'N) in the central Pacific (Tadokoro et al. 1995; Nagasawa and Ishida 1997b), and at 179°30'W (52°30'N to 58°30'N) in the Bering Sea (Tadokoro et al. 1995; Nagasawa and Ishida 1997b). The summer zooplankton sampling was conducted at every one degree of latitude along these transects, and a NORPAC net was used for collection. Since the locations of summer transects were close to those of winter transects, and since the same sampling gear was employed, seasonal comparisons are possible. In addition, the data (June to July from 1980 to 1989) from Brodeur et al. (1996, p.87) are referred to for seasonal variations in zooplankton biomass in the Gulf of Alaska.

RESULTS

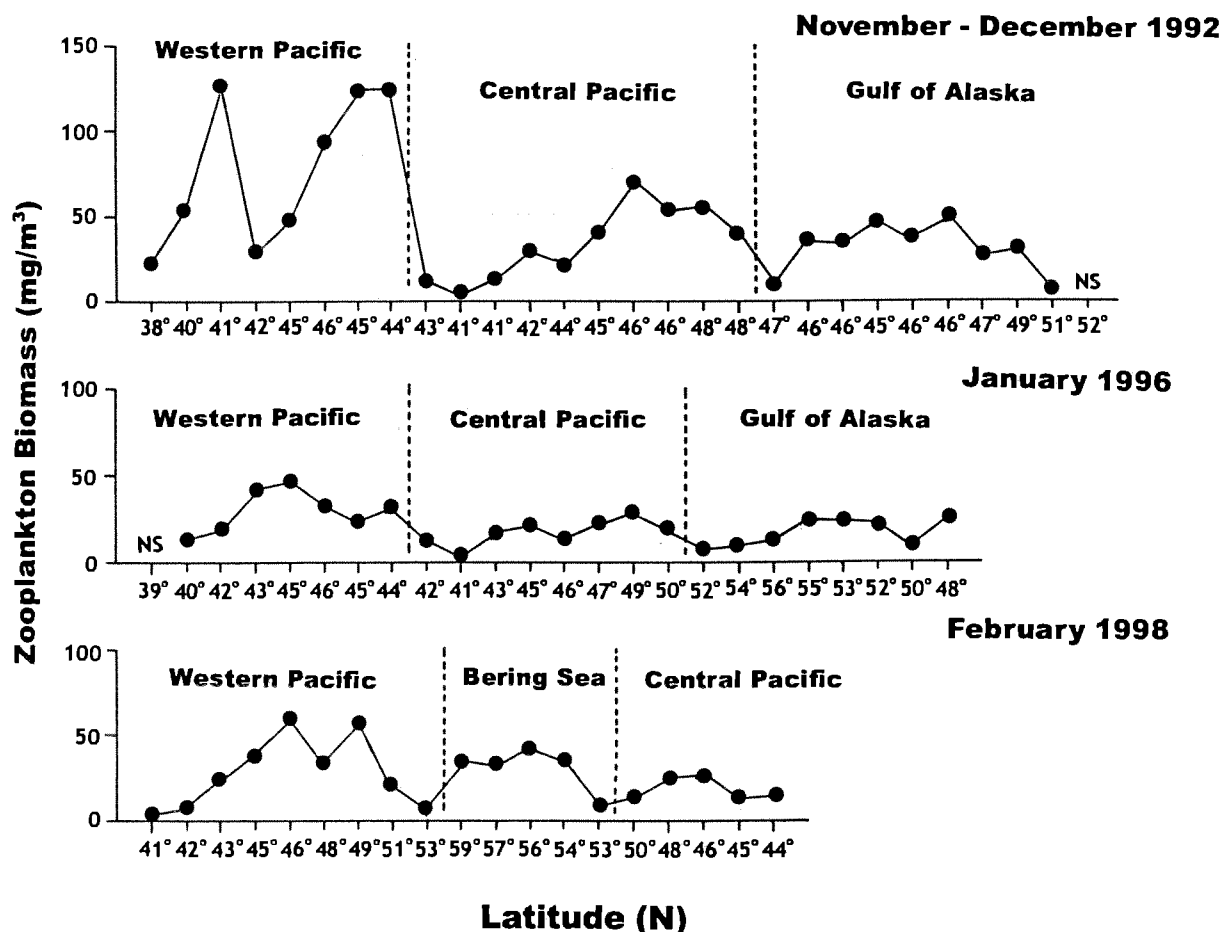
Salmonid Catches in Relation to Oceanographic Features

Five species of Pacific salmon (sockeye, chum, pink, coho, and chinook salmon) were caught during the three cruises. These species were caught in narrow latitudinal ranges at low SSTs from 4 to 8°C (Fig. 2). Although some fish were collected in the southern Transitional Domain (especially in February) and Bering Sea, most of the salmonids were taken in the Subarctic Domain and northern Transitional Domain. No salmonids were caught in subtropical waters. There was no difference in distribution pattern in the North Pacific between salmonid species, except for chinook salmon, some of which were collected in the Bering Sea in February (Ueno et al. 1999).

Winter Zooplankton Biomass

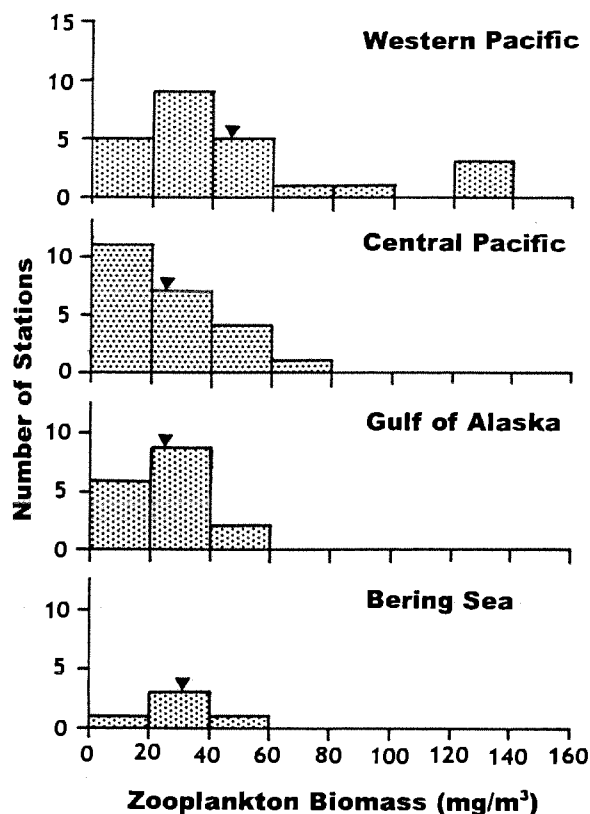
The winter zooplankton biomass varied among sampling locations, areas, and dates (Fig. 4). The mean winter zooplankton biomass (all months com-

Fig. 4. Variations in zooplankton biomass at sampling stations in the western and central Pacific, Gulf of Alaska, and Bering Sea in November to December 1992 (top), January 1996 (middle), and February 1998 (bottom). NS, no sampling.



bined) was highest (45.1 mg/m^3) in the western Pa-Pacific, followed by the central Pacific and Gulf of Alaska, where the biomass had nearly identical values (25.4 mg/m^3 and 25.0 mg/m^3 , respectively) (Fig. 5). Although only February data were available for the Bering Sea, the mean zooplankton biomass was 32.3 mg/m^3 . The mean monthly biomasses of zooplankton collected from the North Pacific Ocean were 46.1, 21.5, and 25.1 mg/m^3 for November to December, January, and February, respectively.

Fig. 5. Frequency distribution of winter zooplankton biomass (all months combined) in the western and central Pacific, Gulf of Alaska, and Bering Sea. Closed triangles represent the means.



In the western Pacific, the mean zooplankton biomass was highest in the northernmost Subarctic Domain, followed by the Transitional Domain and the southernmost subtropical waters (Fig. 6). Although the data in November-December, January, and February were taken from different years, the biomass appeared to decrease in January in these three regions. A similar southward decrease in regional zooplankton biomass was observed in the central Pacific in December: the biomass was highest in the Subarctic Domain and decreased toward the subtropical waters. As in the western Pacific, the mean zooplankton biomass was lower in January 1996 in the Subarctic Domain and Transitional Domain than in December 1992. In both the western and central Pacific, there was no marked difference in mean zoo-

plankton biomass between January 1996 and February 1998, when the biomass was low. In the Gulf of Alaska, sufficient sampling was available only from the Subarctic Domain, where the mean zooplankton biomass showed similar values in January 1996 and February 1998.

Zooplankton Composition

Copepods were most abundant at 53 (82.8%) of 64 sampling stations in the western and central Pacific and Gulf of Alaska (Fig. 7), where they usually accounted for over 50% of the zooplankton biomass. These copepods were small-sized individuals (mostly copepodites of *Neocalanus* spp.). In the western and central Pacific, chaetognaths usually followed copepods in abundance, but euphausiids or amphipods were the second most abundant at some stations. In the Gulf of Alaska, copepods were followed by pteropods in December (sometimes the latter was more abundant than the former) and by gelatinous zooplankton (jellyfishes and salps), euphausiids and pteropods in January. Although zooplankton samples were collected only in February from the Bering Sea, jellyfishes were the most abundant, followed by copepods or chaetognaths. A similar trend was observed in the northern Subarctic Domain of the western and central Pacific in February.

Comparison of Summer and Winter Zooplankton Biomass in Areas with Salmonids

The mean summer (July) zooplankton biomass at locations with salmonid catches in the western Pacific was as high as 217.4 mg/m^3 (Nagasawa and Ishida 1995, 1997a). However, the mean winter zooplankton biomass at the stations where salmonids were taken in this region was less than 100 mg/m^3 and decreased with time (83.0 mg/m^3 in November to December, 34.6 mg/m^3 in January, and 29.0 mg/m^3 in February, Fig. 8).

Similarly, the mean zooplankton biomass at locations with salmonid catches in the central Pacific was high (244.7 mg/m^3) in the summer (June) (Tadokoro et al. 1995; Nagasawa and Ishida 1997b), but remained at low levels in the winter (52.3 mg/m^3 in December, 21.4 mg/m^3 in January, and 19.7 mg/m^3 in February, Fig. 8).

In the Gulf of Alaska, the mean zooplankton biomass decreased from a high of 226.4 mg/m^3 in the summer (June to mid-July) (Brodeur et al. 1996) to 21.6 mg/m^3 in December and 18.7 mg/m^3 in January (Fig. 8). In the Bering Sea, there was a big decrease in mean zooplankton biomass from summer (July) to winter (February) at locations with salmonid catches. The biomasses in these months were 275.2 g/m^3 (Tadokoro et al. 1995; Nagasawa and Ishida 1997b) and 37.1 mg/m^3 , respectively (Fig. 8).

Fig. 6. Monthly variations in mean winter zooplankton biomass in the Subarctic Domain, Transitional Domain, and subtropical waters of the western and central Pacific and Gulf of Alaska. The histograms and error bars represent the means and 1 standard deviation, respectively. Numerals indicate sample sizes. NS, no sampling.

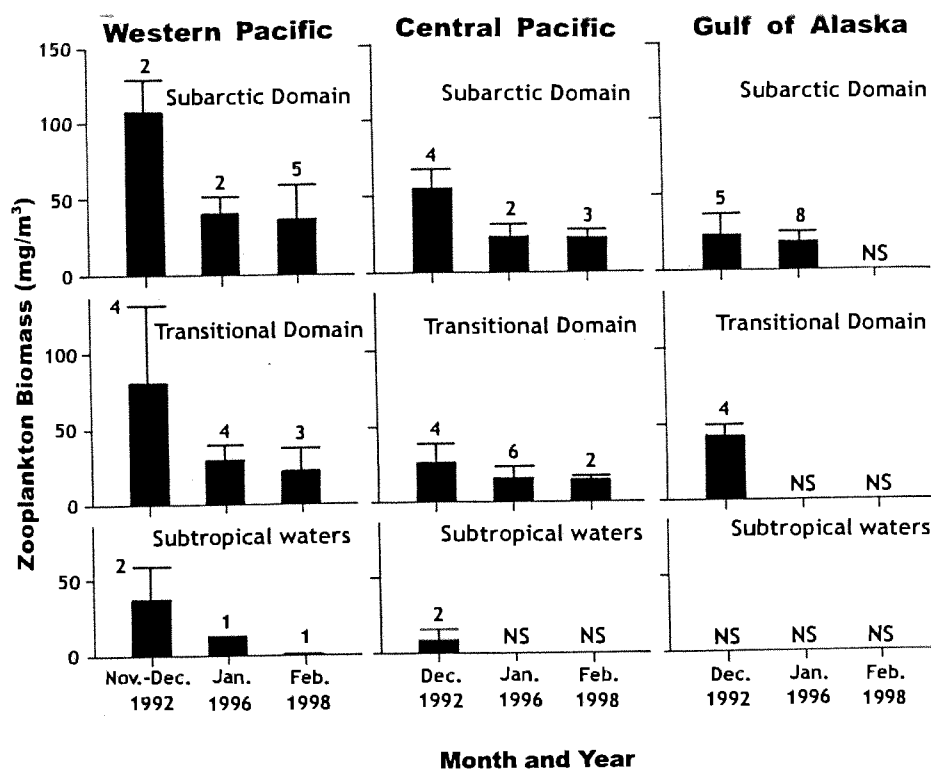


Fig. 7. Variations in percentage of the most abundant (lines) and second most abundant (dashed lines) categories of zooplankton at sampling stations in the western and central Pacific, Gulf of Alaska, and Bering Sea in November to December 1992 (top), January 1996 (middle), and February 1998 (bottom).

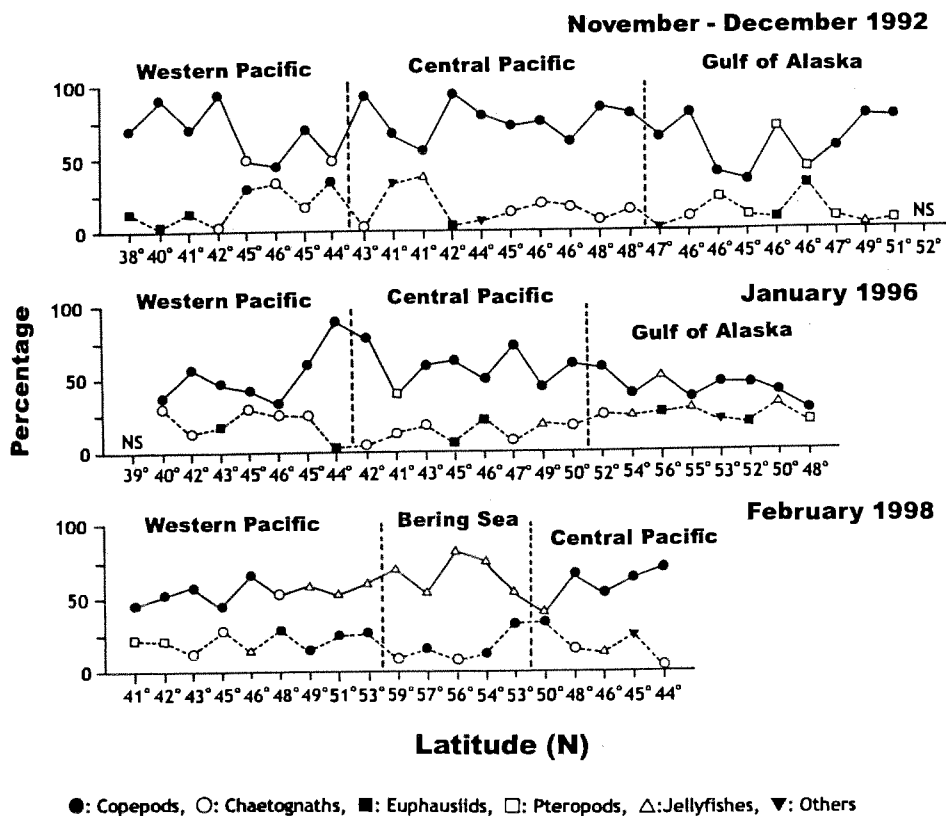
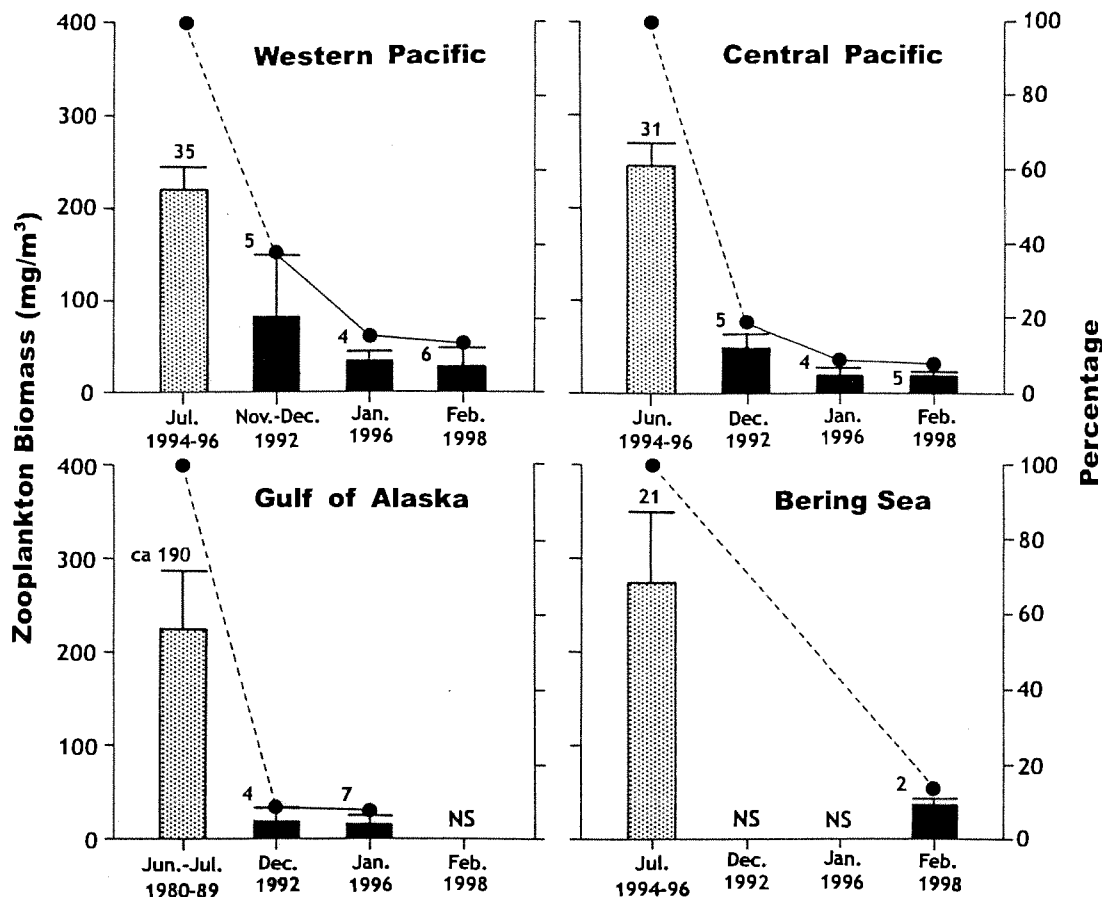


Fig. 8. Summer-to-winter changes in zooplankton biomass (bars) and its relative percentage of the summer value (closed circles) at locations where salmonids were caught in the western and central Pacific, Gulf of Alaska, and Bering Sea. The summer data for the Gulf of Alaska were taken from stations in a wide region, where no information on salmonid occurrence was available (Brodeur et al. 1996). The histograms and error bars represent the means and 1 standard deviation, respectively. Numerals indicate sample sizes. NS, no sampling.



As compared to the summer biomass, the mean winter zooplankton biomass decreased from 38.2% (November to December) to 13.3% (February) in the western Pacific, from 21.4% (December) to 8.1% (February) in the central Pacific, and from 8.6% (December) to 8.3% (January) in the Gulf of Alaska (Fig. 8). It was 13.5% (February) of the summer biomass in the Bering Sea.

DISCUSSION

One of the most important findings in the present study is that the zooplankton biomass in the oceanic waters where salmonids were overwintering was low, being, in January or February, about 10% of the summer biomass. Although Pacific salmon feed on various organisms in the open ocean and their diets overlap (Pearcy et al. 1988), they fall largely into two groups in terms of their feeding habits: planktivorous species (e.g., pink, sockeye, and chum salmon) and non-planktivorous species (e.g., coho and chinook salmon) (Ito 1964; Brodeur 1990). Our findings imply that the prey or food conditions, as measured by

the zooplankton biomass, in oceanic subarctic waters are unfavorable for planktivorous salmonids in winter.

There may be two ways that planktivorous salmonids could overwinter in the open ocean with low zooplankton biomass, namely, a change in diet, and a reduction in metabolic consumption. As for diet, according to Ishida et al. (1997), there are some seasonal variations in composition of stomach contents between the summer and winter, but each species of overwintering salmonid retains its basic feeding habits even during winter. It is thus unlikely that food change is important as a survival method of overwintering in planktivorous salmonids. In contrast, the winter distribution pattern of salmonids, irrespective of feeding habits, is markedly different from that in summer. Overwintering salmonids were caught in northern cold waters of narrow latitudinal ranges at SSTs from 4 to 8°C. In summer, salmonids occurred widely at SSTs lower than 15°C, and each species had a specific SST range in its distribution (Takagi 1983). The metabolic rates of salmonids remain low at low temperatures but increase exponentially with increasing temperature (Brett 1964; Brett et al. 1969;

Welch et al. 1998). Thus, the cold environment may provide an advantage to overwintering salmonids by suppressing their metabolic rates, thereby preventing energy loss under poor food conditions. In addition, the zooplankton biomass was slightly higher in the Subarctic Domain, where many overwintering salmonids were caught, than in the Transitional Domain, and food conditions in the Subarctic Domain appear to be a little more favorable (Fig. 6). If salmonids had as wide ocean distribution in the winter as suggested by Manzer et al. (1965), they would consume more metabolic energy due to higher water temperatures in southern waters (the southern Transitional Domain), and the zooplankton biomass in addition was actually lower than in northern waters (the Subarctic Domain and northern Transitional Domain). Based on these considerations, I propose a "Salmon Overwintering Strategy" (SOS) hypothesis, that, under poor food conditions in winter in the subarctic Pacific, salmonids remain in northern cold waters to reduce energy loss. This answers the question "Why do Pacific salmon overwinter in the northern cold waters?" However, some chinook salmon were caught in the Bering Sea in February, when other species occurred mainly in the Subarctic Domain and Transitional Domain. We need more explanations for the specific distribution of chinook salmon. This could also give some suggestions on the reasons why other salmonid species do not occur in the Bering Sea in winter.

Nomura et al. (this volume) reported that the lipid content in the muscle of both pink and chum salmon caught during the winter was low. These authors also found that neutral lipids in the muscle of overwintering fish were less than 3% of the summer value for chum salmon, and less than 23% of the summer value for pink salmon. Since salmonids use neutral lipids as an energy source, these results indicate that overwintering salmonids are probably starving compared to their summer condition. Some salmonids may die due to starvation under poor food conditions during the winter.

Winter zooplankton biomass is known to remain low in the subarctic Pacific (Parsons and Lalli 1988; Odate 1994; Brodeur et al. 1996; Sugimoto and Tadokoro 1998; Mackas and Tsuda 1999). This low winter zooplankton biomass is closely related to the seasonal downward migrations of the calanoid copepods *Neocalanus plumchrus*, *N. cristatus*, *N. flemingeri*, and *Eucalanus bungii* (Fulton 1973; Miller et al. 1984).

The present study has also shown that the winter zooplankton biomass was higher in the western Pacific than in the central Pacific and the Gulf of Alaska. Sugimoto and Tadokoro (1997) reported that the summer zooplankton biomass was higher in the western and central Pacific than in the Gulf of Alaska. Based on the material collected from the R/V *Kaiyo*

maru cruise in January 1996, Shiimoto and Asami (1999) found that the winter chlorophyll *a* concentration and cell density of diatoms *Thalassiosira* were higher in the region west of 180° than east of 180°. They also found that there was a negative relationship between naked ciliate numbers and copepod biomass and suggested that grazing by abundant copepods on naked ciliates in the western region indirectly results in, due to reduction in feeding pressure by the ciliates, the high abundance of *Thalassiosira* (and also high chlorophyll *a* concentration). Similar results about the high winter chlorophyll *a* concentration in the western region were reported by Shiimoto et al. (in press) based on the material collected from the R/V *Kaiyo maru* cruise in November and December 1992. These observations indicate that there are differences in winter primary and zooplankton production between the western and eastern North, which may provide different regional food conditions for overwintering salmonids.

Much remains to be studied on the winter biology of salmonids in the subarctic Pacific. Although the zooplankton biomass is focused on in this paper, micronektonic animals, such as very small squids, are also one of the stomach contents of overwintering salmonids (Ishida et al. 1997). We need more information about the biology, distribution, and abundance of prey animals in the overwintering area of salmonids.

CONCLUSIONS

The winter zooplankton biomass is quite low, declining to about 10% of the summer biomass in the subarctic Pacific, where Pacific salmon (*Oncorhynchus* spp.) overwinter in cold subarctic waters at sea surface temperatures lower than 8°C. The "Salmon Overwintering Strategy (SOS)" hypothesis proposes that under winter poor food conditions of the open ocean, salmonids stay in cold waters in order to reduce their metabolic consumption. This hypothesis may be applicable to non-planktivorous salmonids (e.g., coho salmon) as well as planktivorous salmonids (e.g., pink, chum, and sockeye salmon), because coho salmon were caught in the same cold waters as those planktivorous species. The cold environment appears to be advantageous to the winter survival of salmonids.

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Movements, Food and Predators of Juvenile Chum Salmon (*Oncorhynchus keta*) Entering the Coastal Sea of Japan off Northern Hokkaido in Warm and Cool Years

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Keywords: Chum salmon; coastal life; seawater temperature; open coastal waters; predation; seabird

Abstract: The coastal ecology of juvenile chum salmon (*Oncorhynchus keta*) was studied in the Sea of Japan off Mashike in northern Hokkaido, Japan, from March to June 1995–1998. Spring surface seawater temperatures (SSTs) were consistently higher than the 10-year average in 1995 and 1998 (SST-H years), and consistently lower in 1996 and 1997 (SST-L years). Peak catch rates of juvenile chum salmon occurred within 500 m from shore in May when the juveniles were approximately 70 mm and 3 g in size. Mean fork length and body weight increased faster during SST-H years than SST-L years even though stomach fullness was lower in SST-H years. Stomach contents were primarily fish larvae, sand lance, and terrestrial insects during SST-H years, and neritic and oceanic zooplankton during SST-L years. Predation by juvenile masu salmon (*O. masou*) on juvenile chum salmon was the only observed occurrence of fish predation not thought to be associated with net feeding. Beak scars and feeding on juvenile chum salmon by seabirds were observed. We concluded that seabirds were the primary predators of juvenile chum salmon during early marine life, and their predation is likely to be higher in SST-H years than SST-L years.

INTRODUCTION

Chum salmon (*Oncorhynchus keta*) stocks in Japan have been increasing in abundance since the 1970s, but the stocks in the Sea of Japan off Hokkaido have been lower than those in the Sea of Okhotsk and the Pacific Ocean off Hokkaido (Kaeriyama 1989). Reasons for this may be the Tsushima warm current, predation, and competition for prey (Kaeriyama 1989; Kawamura et al. 1998). Juvenile fat greenling (*Hexagrammos otakii*) is a potential competitor for prey in the coastal waters of the Sea of Japan (Kawamura et al. 1998). Except for the Ishikari and Suttu Bays, the coast along the Sea of Japan has a simple shoreline and very few estuaries. We call the waters off this shoreline open coastal waters. Estuaries are thought to be important areas for juvenile chum salmon to grow while avoiding predators (Pearcy 1992). Early marine life of juvenile chum salmon has been studied in inshore waters of the east and west sides of the Pacific Ocean, but most surveys

have been limited to estuarine and marsh nursery grounds (Kaczynski et al. 1973; Mason 1974; Healey 1979; Congleton et al. 1981; Bax 1982; Kaeriyama 1986; Murphy et al. 1988; Pearcy et al. 1989; Irie 1990). Little is known about the early marine life of juvenile chum salmon inhabiting open coastal waters in the Sea of Japan (Kawamura et al. 1998). To examine the relationship between survival of juvenile chum salmon and environmental factors in open coastal waters, we studied the early marine ecology of juvenile chum salmon, annual variations in environmental factors, and predation in open coastal waters in the Sea of Japan off northern Hokkaido, Japan.

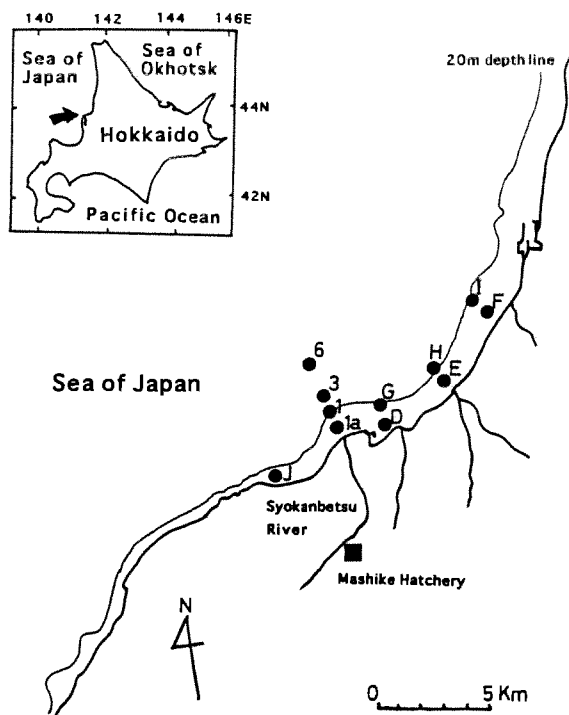
MATERIALS AND METHODS

Sampling Sites and Gear

We sampled at eleven stations in inshore waters off Mashike in the Sea of Japan off Hokkaido from 1995 to 1998 (Fig. 1). The survey was carried out

six to nine times from mid-May to mid-June, 1995 to 1998. We captured juvenile salmon inhabiting the layer between the surface and two meters depth with a Sayori net towed at a speed of approximately two knots for thirty minutes at seven to ten stations each sampling period. The Sayori townet had a mouth opening eight meters wide and five meters deep. The net was eighteen meters long with wing nets seven meters either side, and towed by two fishing boats. Thirteen million juvenile chum salmon are released in the Syokanbetsu River from the Mashike Branch of Hokkaido Fish Hatchery from early April to mid-April every year (Fig.1). The juveniles weighed about one gram and were about fifty millimeters in fork length. We defined CPUE as numbers of fish caught per 30-min. tow with the Sayori townet.

Fig. 1. Map showing the sampling sites in waters off Mashike in the Sea of Japan off northern Hokkaido, Japan. Near shore sampling stations (1a, D, E, F and J) within 500 m of the shore. Stations 1, 3, 6, G, H and I are coastal water sites.



Environmental Factors

We have obtained seawater temperature data from the water supply of the abalone culture center of Mashike fishermen's association since 1985. The water is pumped from seven meters depth near sampling station D (St. D) (Fig.1). We also measured the seawater temperature and salinity with a sensor attached to the bottom of the mouth of the Sayori townet. Salinity, seawater temperature and transparency were measured at stations 1, 3, 6, D and E.

Stomach Content and Growth Analysis

Sampled fish were fixed in five percent neutral formalin for seven hours and then transferred to seventy percent ethanol. In the laboratory, we measured fork length (FL) to 0.1 mm, body weight (BW) to 1 mg, stomach content weight (SCW) to 1 mg, and calculated stomach fullness (SF) as a percentage body weight:

$$SF = ((SCW)/(BW-SCW)) \cdot 100$$

Prey items in stomachs were counted and identified to species whenever possible. Specific growth rate (SGR) of juvenile chum salmon was calculated in body weight and fork length as follows;

$$SGR = \ln(Wt_2 - Wt_1) / (t_2 - t_1) \cdot 100$$

where Wt_1 and Wt_2 are mean body weight at day t_1 and t_2 , respectively. For SGR in fork length, we multiplied by 1000 rather than 100.

Predators

Fish

To examine stomach contents, we captured some carnivorous fish with gill nets set in inshore waters, 400 m (9.8 m depth) and 800 m (11.2 m depth) from shore near the Syokanbetsu River mouth during seaward migration and early marine life of chum salmon juveniles, early April to late April, 1997 (Fig. 1). Two hundred and seventy-eight arabesque greenling (*Pleurogrammus azonus*), six Masu salmon (*O. masou*) and 96 long shanny (*Stichaeus grigorjewi*) were captured. In 1999, we examined 72 stomachs of arabesque greenling captured by a small set net located in northern inshore waters 90 km from Mashike in early June. We also examined 20 stomachs of juvenile masu salmon caught by the Sayori townet in 1996 and 1998.

Seabirds

To examine the fluctuations in abundance of seabirds and to determine their predation on juvenile chum salmon, we established an observation station near the Syokanbetsu River mouth. We counted seabirds and observed their feeding behaviour with binoculars from 10 a.m. to 6 p.m. several times every ten days, from early February to late June in 1999. We used the highest count each ten days as a measure of abundance of seabirds. To compare the timing of seabird's migration among years, we recorded the first sightings of rhinoceros auklet (*Cerorhinca monocerata*) from a fishing boat during the Sayori townet surveys, 1995 to 1998, as an index of avian fish predators.

RESULTS

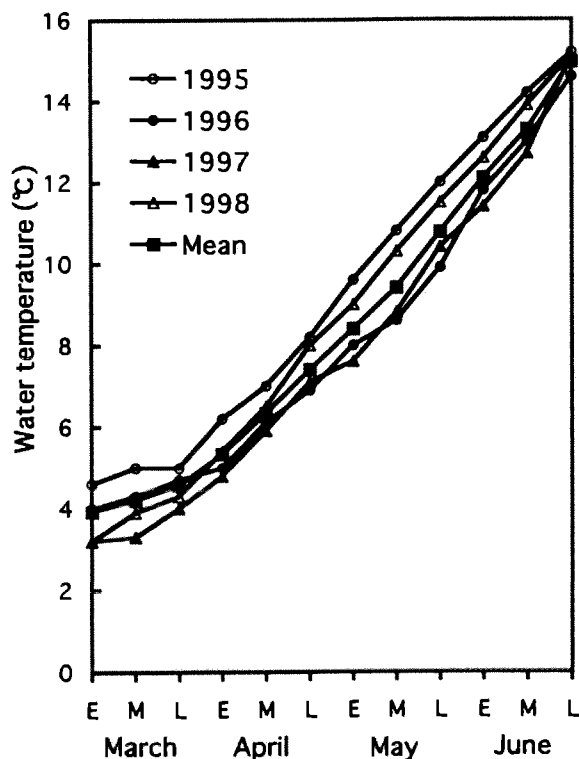
Environmental Factors

Surface seawater temperatures from early March to late June in 1995 and 1998 were higher (high temperature years) and those during the same months in 1996 and 1997 were lower (low temperature years) than the mean seawater temperature over ten years from 1985–1994 (Fig. 2). The difference in surface seawater temperatures between high temperature years and low temperature years was more than 2°C in mid-May. The fluctuations in salinity ranged from 26‰ to 34‰ with no trend. Transparency ranged from 4 meters to 22 meters one kilometer off-shore, also with no trend.

Seaward Distribution and Critical Size

We captured fourteen species of fish including two unidentified fish larvae from mid-March to late June, 1995 to 1998. Chum salmon juveniles were numerically predominant, followed by juvenile fat greenling. Also, threespine stickleback (*Gasterosteus aculeatus*), Japanese needlefish (*Hemiramphus sajori*), surf smelt (*Hypomesus pretiosus*), juvenile masu salmon, and juvenile and larval pacific sand

Fig. 2. Seawater temperatures (7 m depth) off the coast of Mashike during the period from March to June, 1995 to 1998. Mean is the average over 10 years from 1985 to 1994. The high temperature years 1995 and 1998, and low temperature years 1996 and 1997 are shown separately. E, early; M, mid; L, late.



lance (*Ammodytes personatus*) were abundant in in-shore waters. The other species, walleye pollock (*Theragra chalcogramma*) larvae, Japanese anchovy (*Engraulis japonica*), needlefish (*Strongylura anastomella*), Temmink's surfperch (*Ditrema temmincki*), and adult Japanese icefish (*Salangichthys microdon*) were caught in low numbers from late April to late June. Jelly fish (*Aurelia aurita* and *Beroe cucumis*) were more abundant in 1996 and 1997 than in 1995 and 1998.

Juvenile chum salmon were distributed similarly in all four years of the study (Fig. 3). Juvenile chum salmon inshore waters were distributed in two groups, near shore and in coastal waters. The near shore group, within 500 meters of the shore, had one peak CPUE in May, when a large number of juveniles was present, but exhibited low CPUEs in April during sea entry. The coastal waters group was captured more than one kilometer from shore and showed two peaks in CPUE, except in 1997, the first in April, and the second in late May to early June. The timing of the first peak coincided with the dispersal of juvenile chum salmon during sea entry, and the second was composed of juveniles migrating offshore. The coastal waters group was less abundant than the near shore group. In high temperature years, juvenile chum salmon migrated offshore earlier, from late May to early June, than in low temperature years (early June to mid-June in 1996).

Mean fork length of the near shore group decreased from late May to early June in 1995 and 1998 (Fig. 4) as larger individuals moved away. The timing of peaks in mean fork length was different among years; the peaks in high temperature years were earlier than in low temperature years. However, mean fork length at the peaks was similar among years, being 73 ± 0.9 mm (mean \pm SD), ($n = 1046$) in 1995, 78.2 ± 3.9 mm (6) in 1996, 74.9 ± 5.0 mm (232) in 1997, and 74.3 ± 7.1 mm (3270) in 1998. Except for a few juveniles in 1996, maximum fork length of the near shore group ranged from 73 mm to 74.9 mm. Similarly maximum mean body weight ranged from 3.2 g to 3.6 g. Mean fork length in the coastal waters group was larger (< 80 mm) after late May than the near shore group in 1995 and 1996.

The distribution of juvenile fat greenling < 60 mm in fork length was similar to that of juvenile chum salmon. Juvenile fat greenling from near shore stations was distributed similarly to the near shore group of juvenile chum salmon, with one peak of CPUE from mid-April to early May (Fig. 3). The juvenile fat greenling had moved from pelagic to demersal waters by mid-May.

Juvenile masu salmon showed a different distribution from chum salmon and fat greenling juveniles. Juvenile masu salmon were similarly distributed in both near shore and coastal stations (Fig. 3), but the

Fig. 3. CPUE of chum salmon, fat greenling and masu salmon juveniles caught at near shore or coastal water stations. Index of CPUE shows the average value per one net tow plus one. E, early; M, mid; L, late.

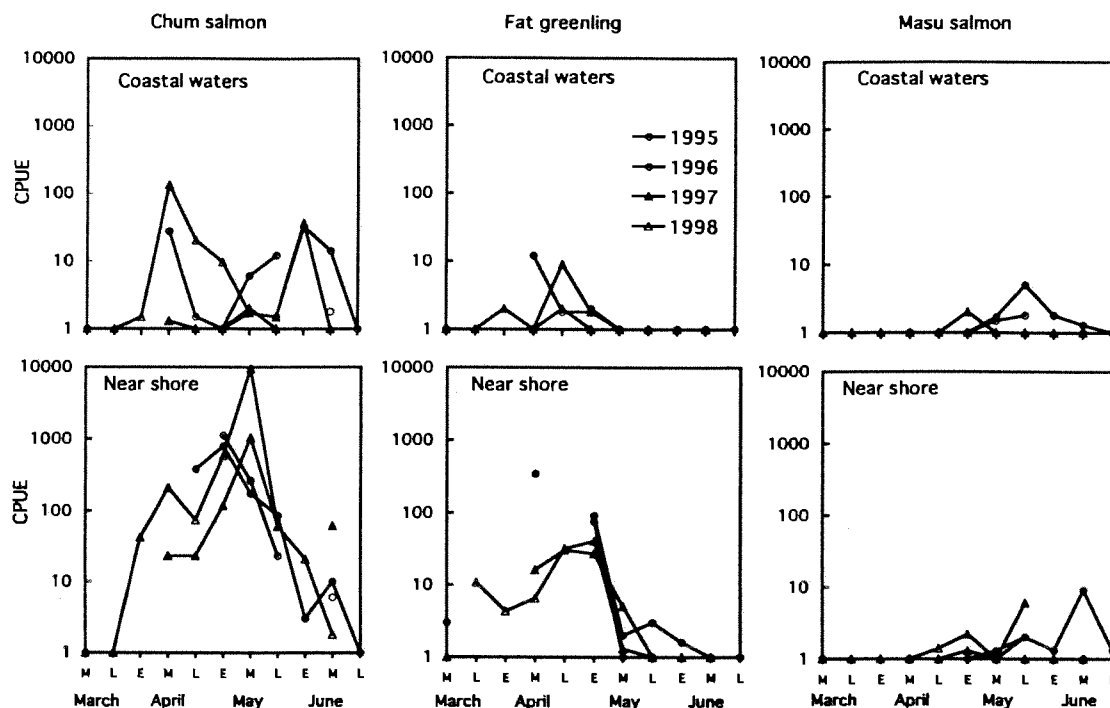
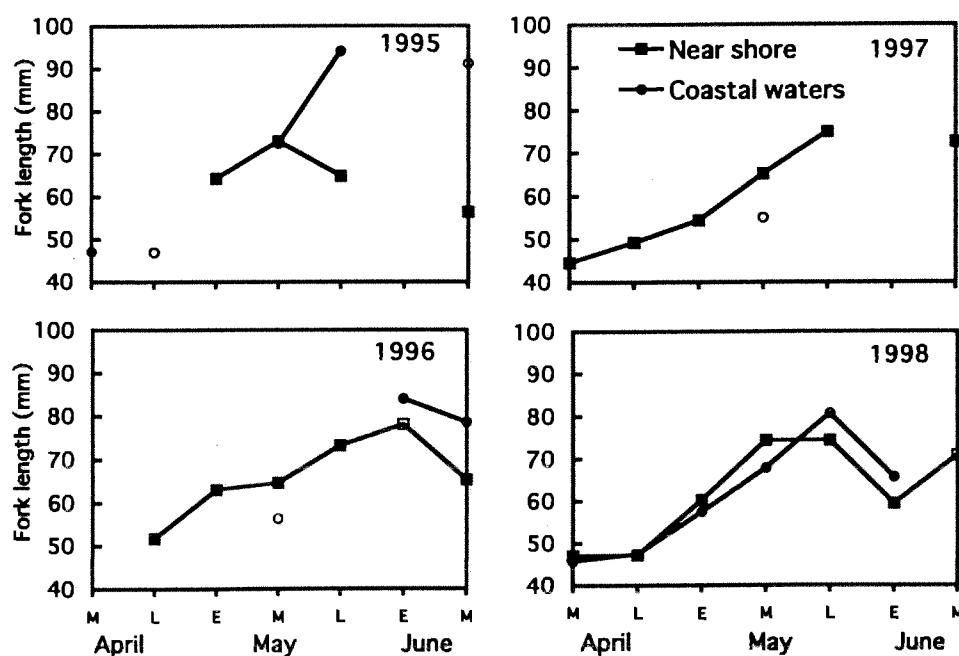


Fig. 4. Mean fork length of juvenile chum salmon caught at near shore or coastal water stations from mid-April to mid-June, 1995 to 1998. Sample sizes: near shore juveniles, 3–4116 fish; coastal waters, 1–261 fish. Open symbols indicate less than ten fish. E, early; M, mid; L, late.



juveniles entered the sea one month later than juvenile chum salmon. Masu salmon juveniles had one peak of CPUE from May to mid-June.

Prey Quantity and Growth

Stomach fullness of juvenile chum salmon was below 1% for a short time after sea entry, but it increased hereafter (Fig. 5). There was a difference in time and magnitude at the peak of stomach fullness between high temperature years and low temperature years. Though high temperature years had lower levels and unclear peak in stomach fullness in May and June, low temperature years showed a high peak in stomach fullness on late April or early May. Juvenile chum salmon of the near shore and coastal waters groups showed similar fluctuations in stomach fullness.

The stomach content composition of juvenile chum salmon captured in May showed differences between high temperature years and low temperature years. In high temperature years, stomach content composition were mainly composed of fish larvae, sand lance and terrestrial insects, but those in low temperature years consisted of neritic and oceanic zooplankton, *T. discaudatus*, *Oikopleura* spp, *Neocalanus plumchrus*, *Eucalanus bungii bungii* and *Pseudocalanus newmani*. On the other hand, epibenthic organisms, harpacticoid copepods were frequently found in the stomach of the juveniles for a short time after sea entry.

Growth of juvenile chum salmon was higher in high temperature years than in low temperature years (Fig. 6). Comparing the SGR in fork length and body

weight from late April to mid-May, SGR in high temperature years also showed higher levels (0.016 and 0.023 in fork length, 0.054 and 0.077 in body weight) than low temperature years (0.009 and 0.015, 0.030 and 0.053).

Predators

Fish

We examined the stomach contents of adults of three species, arabesque greenling, long shanny and masu salmon, and juvenile masu salmon from early April to early June, when juvenile chum salmon were abundantly distributed in inshore waters. Few juvenile chum salmon ($n = 10$) were found in the stomachs of adult Arabesque greenling ($n = 72$) caught by a small set net in early June. As the juvenile chum salmon ingested were undigested relative to other stomach prey, we concluded that arabesque greenling attacked the juvenile chum salmon while they were in the set net. The diet of arabesque greenling ($n = 278$) caught by a gill net near the Syokanbetsu river mouth, in contrast to that of arabesque greenling caught in the set net, was composed of euphausiids (*Thysanoessa inermis*) only.

Juvenile masu salmon ($n = 20$) captured with a Sayori tow net ate few chum salmon juveniles from late April to early June. Smaller juvenile chum salmon, less than 50 mm in fork length, were eaten by three of 20 masu salmon juveniles. Adult masu salmon ($n = 6$) caught by gill net near the river mouth in early April fed only on euphausiids.

Fig. 5. Mean stomach fullness of juvenile chum salmon caught at near shore or coastal water stations from mid-April to mid-June, 1995 to 1998. Sample sizes: near shore, 3–849 fish; coastal waters, 1–244 fish. Open symbols indicate less than ten fish. E, early; M, mid; L, late.

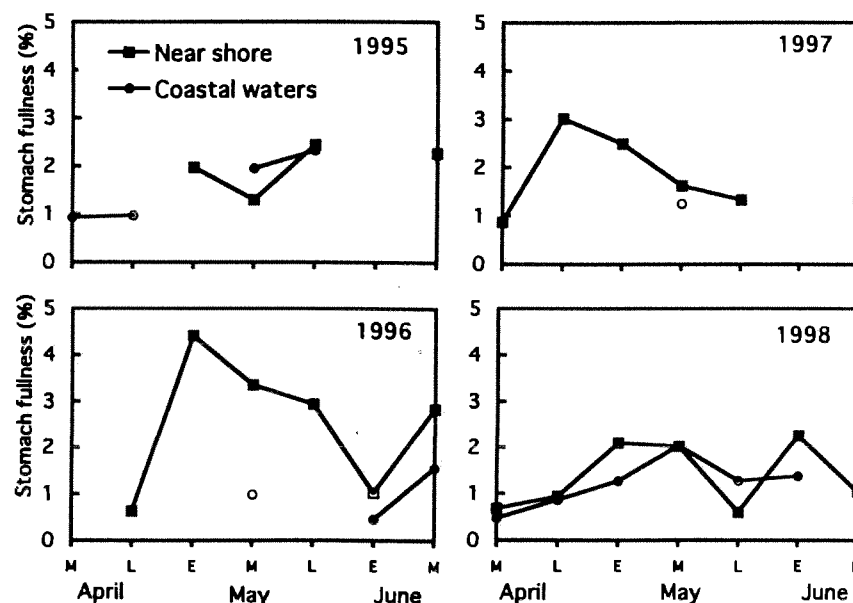
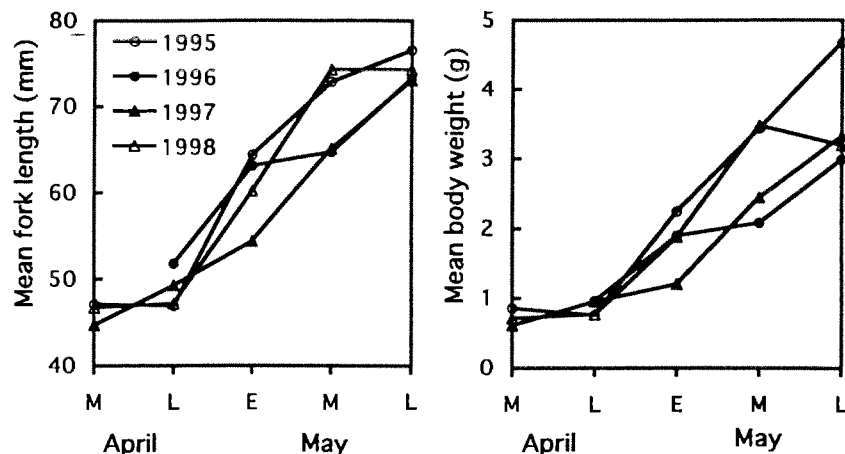


Fig. 6. Size (length and weight) of juvenile chum salmon caught in near shore waters off Mashike in high temperature and low temperature years during the period of growth until offshore migration. Sample sizes: 68–4165 fish. E, early; M, mid; L, late.



Most maturing long shanny ($n = 96$) captured by gill net from early April to mid-April had empty stomachs. Juvenile chum salmon were never found in the stomach contents of long shanny.

Seabirds

Gulls, ducks and cormorants showed three different patterns of abundance in the Syokanbetsu River mouth from February to June in 1999 (Fig. 7). Firstly, slaty-backed gull (*Larus schistisagus*), black-tailed gull (*Larus crassirostris*) and red-breasted merganser (*Mergus serrator*) showed a peak in abundance in late April when juvenile chum salmon actively migrated to the sea and entered the coastal waters. About one thousand five hundred gulls flocked around the mouth of the river in late April. Secondly, Japanese cormorant (*Phalacrocorax capillatus*) increased during the coastal life of juvenile chum salmon. Thirdly, harlequin duck (*Histrionicus histrionicus*) decreased in number from mid-April to mid-June. We observed three species, slaty-backed gull, black-tailed gull and Japanese cormorant feeding on juvenile chum salmon. We found juvenile chum salmon captured in inshore waters with beak marks (Fig. 8). The ratio of injured juveniles ($n = 3$) to total catch ($n = 1113$) was 0.27 percent at sampling site D in late April.

Rhinoceros auklet migrated to inshore waters from late April to early May in high temperature years, and from mid-May to late May in low temperature years, but we did not see them feed on juvenile chum salmon.

DISCUSSION

Our study showed the relationship between the early open coastal life of juvenile chum salmon and annual fluctuations in seawater temperature. The

early marine life has four parts: (1) Movement to the sea when juveniles are transported to the sea by the river, tide and wind. (2) Adaptation period when juveniles appear to move near the bottom for a short time to avoid predators, judging from the results of

Fig. 7. Changes in numbers of seabirds every ten days in the vicinity of the Syokanbetsu River mouth during pre-and post-seaward migration of juvenile chum salmon. E, early; M, mid; L, late.

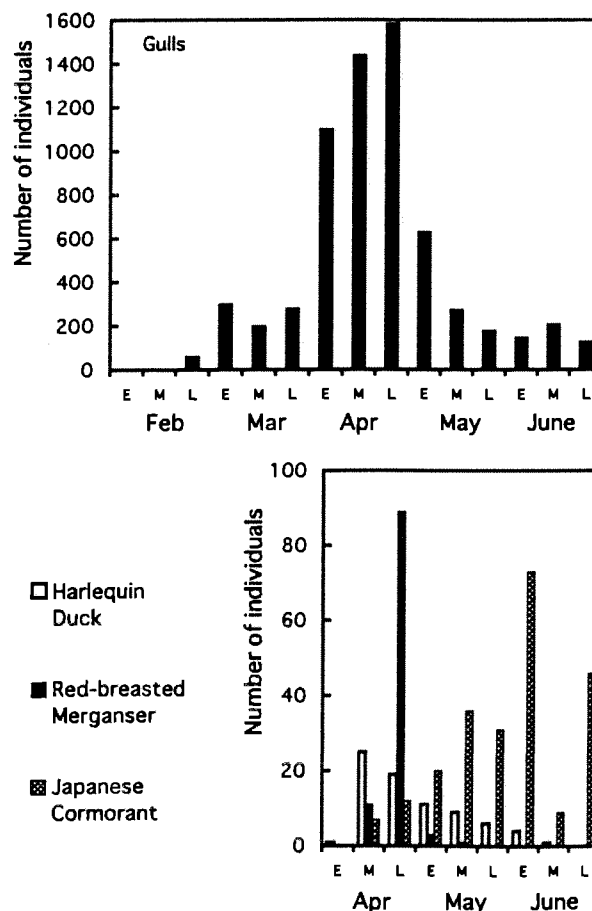
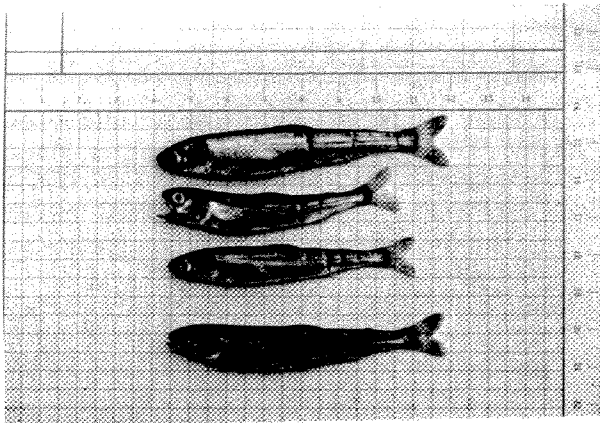


Fig. 8. Juvenile chum salmon with beak marks of seabirds. The juveniles were captured in a Sayori townet in inshore waters (St. D). Bottom fish has no beak marks, for comparison.



stomach content composition and low CPUE near the surface. The diet of juvenile chum salmon during the adaptation period was basically epibenthic organisms, such as harpacticoid copepods, and was consistent with other studies (Kaczynski et al. 1973; Feller and Kaczynski 1975; Healey 1979; Sibert 1979; Murphy et al. 1988; Pushchina and Goryainov 1994). (3) Growth period when the juveniles actively fed on prey organisms near the surface. (4) Offshore migration period when the juveniles migrated offshore after reaching a critical size (73 to 76 mm in mean fork length, 3.2 to 3.6 g in mean body weight).

Juvenile chum salmon remained in near shore waters off Mashike until they reached a critical size. They may have remained in this restricted zone near shore because of better availability and variety of food, and establishment of orientation for navigation in the ocean. Juvenile chum salmon occupy marsh and estuary habitats with shallow and low salinity waters before migrating into the coastal ocean (Kaczynski et al. 1973; Mason 1974; Healey 1979; Congleton et al. 1981; Mayama et al. 1982, 1983; Kaeriyama 1986; Murphy, et al. 1988; Percy et al. 1989). The juveniles we studied, however, had no estuarine habitat as a nursery ground. The coastal topography off Mashike may be one of the causes of low survival of chum salmon juveniles in the Sea of Japan.

Prey availability and growth of juvenile chum salmon were affected markedly by environmental factors, especially seawater temperature. In high temperature years, chum salmon juveniles had a higher growth rate and consumed many fish larvae and terrestrial insects. However, stomach fullness in high temperature years showed lower peaks. This lower stomach fullness may reflect intra- and/or inter-species competition for food and habitat in high temperature years (Kawamura et al. 1998). Brodeur and Percy (1990) similarly found that oceanographic

conditions could affect the feeding ecology of pelagic planktivores off the Oregon and Washington coasts. Quality of food and energy efficiency for food availability may affect growth of juvenile chum salmon. Fish larvae seem to be better prey than zooplankton copepods.

It is hypothesized that high mortality of Pacific salmon (*Oncorhynchus* spp.) occurs during early marine life (Parker 1968; Bax 1982; Healy 1982; Percy 1992). Juvenile chum salmon during entering and adapting to the sea may be most vulnerable to predators because of poor adjustment to the new habitat, osmoregulation, food availability and open shallow waters.

The results from stomach contents of carnivorous fish showed that we could not regard adult arabesque greenling and juvenile masu salmon as significant predators. Predation may largely depend on the spatial and temporal difference in availability of food and habitat among juvenile chum salmon and two other carnivorous fish. Murphy et al. (1988) observed that juvenile coho salmon (*O. kisutch*) did not feed on chum and pink salmon (*O. gorbuscha*) juveniles in estuarine basins in Alaska because of differences in diet and timing of migration.

Predation on juvenile Pacific salmon by avian predators (common murre, *Uria aalge*; ring-billed gull, *Larus delawarensis*; western gull, *L. occidentalis*; Brandt's cormorant, *Phalacrocorax penicillatus*; pelagic cormorant, *P. pelagicus*; common merganser, *Mergus merganser*) has been reported in several rivers and coastal waters in north America (Bayer, 1986; Ruggerone 1986; Wood 1987a, b). There is limited information about seabird predation on pelagic fish in coastal waters in Japan (Watanuki 1987, 1988; Nagasawa 1998). Our findings first showed that slaty-backed gull, black-tailed gull and Japanese cormorant could feed on juvenile chum salmon, and that juvenile chum salmon with beak marks of seabirds were captured in inshore waters off Hokkaido. Carss and Marquiss (1991) have also illustrated bird-damaged fish in the UK. Red-breasted merganser appears to consume juvenile chum salmon in the river mouth like other seabirds. The large number of seabirds present in inshore waters off Mashike, are a significant potential hazard to the survival of juvenile chum salmon during their seaward migration and early coastal life in the Sea of Japan off Hokkaido.

It is important for the survival of juvenile chum salmon to compare the effect of environmental factors in open coastal waters between high temperature years and low temperature years. In high temperature years, environmental conditions are as follows: the sea is calm, the period of flood from rivers is short, extension seaward of brackish waters is weak,

critical seawater temperature, 13°C, occurs early (Kaeriyama 1989; Irie 1990), and duration of food availability is short. These environmental factors may depress the survival of chum salmon juveniles during early marine life. Irie (1990) has already shown that juvenile chum salmon off Hokkaido have a preference for the coastal waters with low temperature (8–13°C) and low salinity (31.0–33.9‰). As the preferred conditions are apparently restricted in time and space in high temperature years, intra- and/or inter-species competition may become stronger (Kawamura et al. 1998). In addition, predation by seabirds on juvenile chum salmon may be higher in high temperature years because of calm water and a longer feeding period because of their earlier arrival. Consequently, changes in environmental factors in low temperature years may improve the survival of juvenile chum salmon in the open coastal waters off the northern coast of the Sea of Japan.

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Variation in Summer Distribution of the Prey of Pacific Salmon (*Oncorhynchus* spp.) in the Offshore Gulf of Alaska in Relation to Oceanographic Conditions, 1994–98

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Keywords: Pacific salmon, squid, SST minimum, latitudinal feeding zones

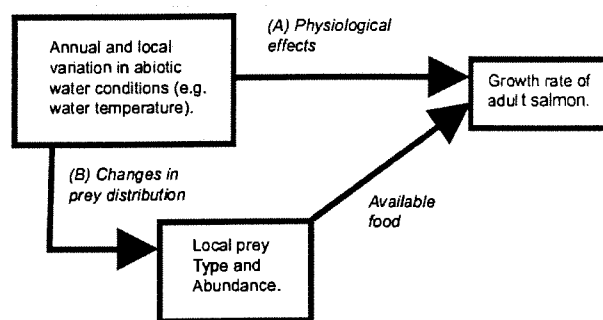
Abstract: We present the results of Pacific salmon (*Oncorhynchus* spp.) food habits studies from five years of high seas salmon research cruises along a July transect in the northeastern Pacific (50°–56°N, 145°W, 1994–98). The results suggest that there are two distinct latitudinal summer feeding zones for salmon associated with the July latitudinal sea surface temperature minimum. The southern zone is high in micronektonic squid between 6–12 mm mantle length, primarily the species *Berryteuthis anonychus*. The warmer, northern zone is higher in mesozooplankton in both net samples and salmon stomachs. The difference in the diet and body weights of pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*) was substantial between the two regions. The latitude of the border between the two zones varied between 51°–54°N over the years of the study, a distance of over 300 km. This variation in the biogeography of salmon prey may explain part of the previously noted relationship between ocean sea surface temperature and the adult body weight of salmon.

INTRODUCTION

The statistical relationships describing variation in adult Pacific salmon (*Oncorhynchus* spp.) body weights and environmental factors in the North Pacific Ocean have, to date, focused on large-scale correlations rather than on mechanisms. For example, several studies have reported a negative correlation between ocean temperature and the adult body weights of salmon that feed in the Gulf of Alaska (Hinch et al. 1995; Cox and Hinch 1997; Pyper and Peterman 1999). This correlation may be explained by a direct physiological mechanism linking temperature and growth, or by an indirect linkage through salmon prey (Fig. 1). Investigating the mechanisms behind such correlations requires measuring processes that act on smaller scales of time and space.

Correlation is only useful for prediction if the mechanism behind it remains constant. Therefore, it is important to determine which mechanisms play roles in determining salmon growth, and which mechanisms have the potential for “breaking down” in the face of large scale climatic change. Due to the difficulty of sampling on a fine scale across the North Pacific, relationships between ocean conditions and future salmon growth remain open to speculation (e.g., Welch et al. 1998).

Fig. 1. Two possible mechanisms underlying previously observed negative correlations between sea surface temperature and salmon body weight. Water temperature may either affect salmon (A) directly, through physiological interactions, or (B) indirectly, through prey.



Many salmon returning to North American waters put on up to 90% of their final adult body weight in the high seas of the Gulf of Alaska, mostly during the spring and summer prior to maturation (Ishida et al. 1998). Previous studies of salmon feeding suggest the existence of two distinct latitudinal “zones” of feeding for adult salmon in the portions of the Gulf offshore of the continental shelf. In the southern zone (south of 50–53°N), many of the larger salmon feed on the micronektonic squid *Berryteuthis anonychus*, while between 53°N and the northern continen-

tal shelf, squid are largely absent and lower trophic-level zooplankton dominate salmon diets (LeBrasseur 1966; Pearcy et al. 1988).

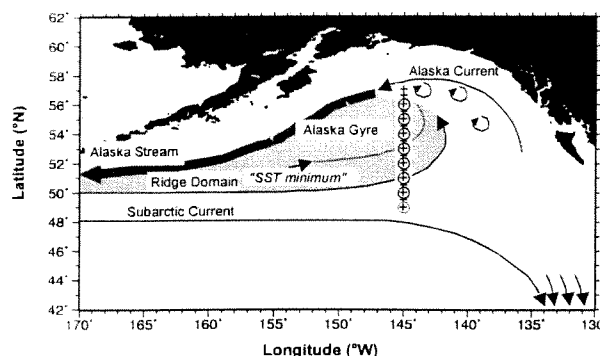
Within the Gulf of Alaska, there are several distinct oceanographic regions surrounding the central, cyclonic-circulating Alaska Gyre (Fig. 2). The structure of the water column in each of these regions possesses unique properties, reflecting differing sources of water (Musgrave et al. 1992). Thus, the Subarctic Current, entering the gyre along its southern border and carrying waters from the west, will be distinguishable from the upwelling center of the Alaska Gyre (Ridge Domain) in which water rises from intermediate depths to the surface (Van Scoy et al. 1991), and from the Alaska Current, where coastal and Subarctic Current waters meet and form the Alaska Stream, in a region rich with mesoscale eddies (Musgrave et al. 1992).

The borders between water masses may create important biological boundaries (Brandt 1993). In studying trends in the ocean, an important question to ask is "what is a fixed point?" If data are taken at a fixed latitude and longitude over a number of years, a biological trend at that location may result from changes occurring within a single water mass, or from a shifting spatial positioning of an adjacent water mass. The Alaska Gyre may shift from east to west on an interannual basis (Royer and Emery 1987; Musgrave et al. 1992), while the Subarctic Current may shift to the north and south (Hollowed and Wooster 1992). Pearcy et al. (1988) associated the north/south variation in salmon diet with the latitude of the Subarctic Current. However, at the time, not enough data existed to examine this hypothesis against a background of shifting oceanographic boundaries.

The difference in food types across the north/south boundary play an important role in determining salmon growth. Squid are a higher-energy food than zooplankton, and salmon growth models suggest that salmon feeding on squid may grow at a much faster rate (Davis et al. 1998; Aydin unpublished results). At the same time, squid may compete with smaller salmon for access to zooplankton. If shifting oceanographic boundaries change the biogeographic range over which salmon and squid overlap, and this boundary movement is associated with changes in sea surface temperature, a correlation between temperature and salmon size and growth may be the result—and this relationship may change substantially with long-term climate shifts.

In this study, we report the results of five years of studies on summer salmonid food habits studies, conducted between 1994–98. Specifically, we examine the link between physical ocean conditions and salmon prey variation during the sampling period. We examine prey distribution with respect to the temperature and salinity of the water column, and

Fig. 2. Transect line of the T/S *Oshoro maru* at 145°W in the Gulf of Alaska, early July 1994–98. Circles indicate gill-net stations, while crosses indicate oceanographic stations. Stations shown by dashed symbols were only sampled in a few years. Between years, annual variation may shift the boundaries of the oceanographic regions with respect to the transect line: boundaries shown are approximate.



with respect to the annual variability of the position of oceanographic features such as fronts, water masses, and eddies. The primary purpose of this study is to examine salmon prey in relation to these shifting water masses.

MATERIALS AND METHODS

Study Area

The data for this study were collected by the Japanese research vessel *Oshoro maru* along a transect line running from 50°N to 56°N along 145°W in 1994–98 (Fig. 2). Stations were sampled between 1 July and 11 July in each year. Gillnet sampling was conducted at every degree of latitude, while oceanographic and plankton sampling were conducted at every half degree. In 1994, oceanographic and plankton data collection alternated between 145°W and 146°W; this relatively slight longitudinal variation was ignored in the analysis. Due to weather conditions and time limitations in 1995, fishing stations at 50°, 51° and 52°N were cancelled and replaced with a single fishing station at 51.5°N. The sampling methods and resulting oceanographic data from each cruise are published annually by Hokkaido University (e.g., Faculty of Fisheries 1998).

Oceanographic and Zooplankton Sampling

Vertical casts to 1500 or 3000 meters depth were made with a Neil Brown Mark IIIB CTD at each half degree of latitude. Temperature (°C) and salinity (psu, practical salinity units) were recorded continuously. Values of σ_t , the water density anomaly from 1000 g/m³, were calculated by shipboard computer.

Zooplankton samples were collected by a 150 m depth-to-surface tow of a twin plankton NORPAC net (0.45 m ring diameter; 0.35 mm mesh size (#200

filtering cloth; 1.8 m length) while the ship drifted (speed 0 knots). Samples were bottled with formalin and wet weight of each sample was determined. For most samples, gelatinous zooplankton was removed before bottling.

Salmon Sampling

During July in the offshore Gulf of Alaska, maturing stocks of sockeye salmon (*O. nerka*) and pink salmon (*O. gorbuscha*) east of 155°W longitude are primarily fish from Central Alaska, Southeastern Alaska, British Columbia, and Washington (Myers et al. 1996). In addition, immature sockeye are found from other North American stocks including Bristol Bay, although their numbers increase to the west of 155°W, south of the Aleutian Islands. Coho salmon (*O. kisutch*) may be from any North American stock. Immature chum salmon (*O. keta*) in the region are a mix of North American and Asian fish (Myers et al. 1996, Urawa et al. this volume). Variation in prey availability in the study region may affect any or all of these stocks. Other salmonid species were not caught in large enough numbers to be analyzed in this study.

Salmon surface gillnet gear (0–6 m fishing depth) was set prior to sunset and retrieved at sunrise at each station. The gillnet consisted of 47 to 49 panels of 50 m-long tans (total length 2.45 km). The net was divided into panels of commercial gear and research gear, with 25–30 tans of research gear (multiple mesh sizes for non-size selective sampling) used at each station.

Biological data—scale samples, species, fork length (mm), body weight (g) sex, and gonad weight (g)—were taken from the first 60 fish of each species from each mesh size, which included almost all fish from the research mesh. Stomach contents were examined from up to 30 fish of each species in each gillnet set. Stomachs were sub-sampled from both commercial and research meshes as fish were being processed, with an attempt to apportion the collection among all size classes present. The methods used for stomach examination were similar to those of Percy et al. (1988), and are described in Kaeriyama et al. (this volume). Total prey weights were determined, and percent volume of each identifiable prey type was estimated visually.

The freshwater and ocean age class of each fish were determined by counting the number of freshwater and ocean annuli on acetate impressions of scales. Maturity of salmonids in the samples was determined from gonad weights. The criteria used for determining maturity is reported by Takagi (1961). Log-transformed catch-per-unit-effort (CPUE) of each gillnet operation was calculated from the total number of each species, age, and maturity class of salmon caught in the research (non-selective) gillnet. The

research gear from an overnight net set, or approximately 30 tans of mixed-mesh gear, was considered to be a single unit of effort.

Data Analysis

Oceanographic analysis

Summary CTD data at standard depths were used to determine latitude/depth isopleths using the Generic Mapping Tools software package (Wessel and Smith 1995). The depths of the top and bottom of both the seasonal and permanent pycnoclines at each station were estimated by locating the standard depths closest to the inflection points of curves fitted to the σ_t plot. The strength of the density gradient across the pycnocline was calculated as the buoyancy frequency N (Mann and Lazier 1996, p. 62) across each pycnocline. Due to the smoothing procedure used across standard depths, the pycnocline depth was not resolvable to an accuracy greater than ± 5 m. Daily mixing and precipitation was evident in the upper 10 m of the water column, so stratification in the upper 10 m could not be determined reliably.

Many physical properties of the water column may be correlated during a single sampling period: for example, sea surface temperature may show a strong correlation with mixed-layer depth. If a biological variable is related to either variable, it would not be clear which of the physical variables has a direct effect on the biological process. This is important to consider if scenarios of climate change predict changes in the relationships between physical variables.

Principal Components Analysis (PCA) was used to determine the common modes of variability for eight oceanographic variables: sea surface temperature (SST) and salinity, 100 m temperature and salinity, seasonal pycnocline depth and maximum buoyancy frequency, and permanent pycnocline depth and maximum buoyancy frequency (Mathsoft 1995). These principal components were used to determine relationships between physical and biological properties during the study period. Using transformed principal components rather than individual variables such as SST emphasizes that oceanographic properties tend to covary.

Oceanographic domain determination

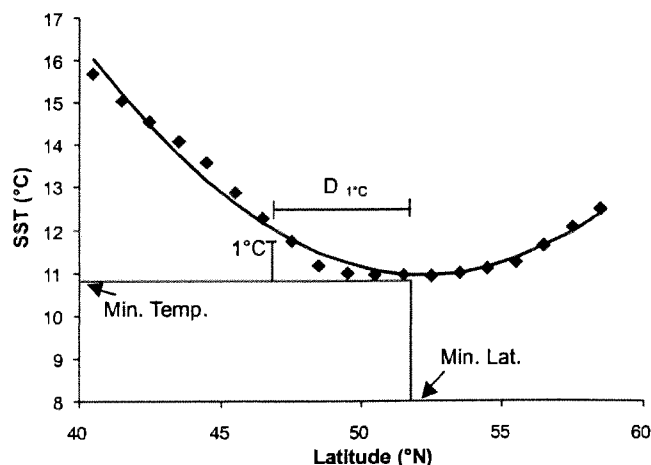
Two data sources were used to determine regional oceanographic boundaries. The first set of data was the CTD temperature, density, and salinity data collected along the transect. The second set was the July monthly averaged $1^\circ \times 1^\circ$ resolution SSTs for the years 1981–present, calculated as described in Reynolds and Smith (1994) and published electronically in the Integrated Global Ocean Services System

Products Bulletin (IGOSS). All boundaries were considered to occur halfway between two sampling stations, so every station was placed on one side of an oceanographic boundary.

The boundary between the Subarctic Current and the Ridge Domain was placed between the two CTD stations showing the largest change in depth of the 4°C temperature isotherm, which rises from below 300 m in the Subarctic Current to near 100 m in the Ridge Domain. This differs slightly from the method of marking the boundary at the latitude where the 4° isotherm rises above 100 m (Pearcy et al. 1988), because along 145°W the relatively weak Ridge Domain did not rise above 100 m during the course of this study.

In addition to this Ridge/Subarctic Boundary, it has been suggested by Aydin et al. (1998) that SST in the Alaska Gyre has a latitudinal minimum associated with a potential temperature discontinuity, which occurs at a boundary between central Gyre upwelling waters and water moving into the Alaska Gyre from the west. A plot of a single year of IGOS data along the transect shows that the SSTs along 145°W between 40°N and 58°N in a given year may be fit with little error to a quadratic curve with three parameters: the latitude of minimum temperature, the minimum temperature, and the "curvature" or rate of change of the north/south warming trend (Fig. 3). These three parameters were fitted to the curve for each year using the Solver routine in Microsoft Excel®, and the calculated latitude of minimum temperature (hereafter SST minimum) was used as a boundary distinct from the Subarctic Current/Ridge Domain boundary.

Fig. 3. Points show actual 1x1° IGOS sea surface temperatures for a single year. The solid line represents the smoothed 2nd degree curve fit using three parameters. The parameters may be manipulated to have specific physical meaning. In this case, the three parameters are minimum latitude (the latitude at which temperature is at a minimum), minimum temperature (the fit temperature at this minimum) and $D(1^\circ)$, or the distance in degrees latitude required for the temperature to rise 1°C from the minimum.



The boundary between the Ridge Domain and the Alaska Current was placed at the latitude of northern descent of the 4°C isotherm from 100 m to below 300 m (Pearcy et al. 1988). Salinity plots (not shown) were also used to determine the presence of the Alaska Current.

The Alaska Current may create eddies that move into the Ridge Domain, obscuring the Ridge Domain's presence while transporting coastal water, or water from the southern portions of the Subarctic Current, into the Ridge Domain (Thomson and Gower 1998). Locations where mesoscale features appeared during the study were reported in Onishi et al. (2000) and are examined here for correlation with biological variables.

Zooplankton analysis

Zooplankton density measurements (mg/m^3) were log-transformed, and all stations at which $\ln[\text{density}]$ was greater than 7 were excluded from the analysis as representing the combined weights of gelatinous and non-gelatinous zooplankton. The cut-off was determined after examining the statistical distribution of the raw data. Therefore, the samples should not be considered to represent concentrations of gelatinous zooplankton.

Due to this exclusion, and equipment difficulties, raw zooplankton measurements were not available at all stations. For each station, we averaged all undiscarded log-transformed zooplankton measurements taken within a 100 km radius during the same year. The distance of 100 km was chosen because (1) it would include multiple measurements at most gillnet stations, (2) it would leave mesoscale features, generally 200+ km in size, resolvable, (3) it would provide smoothing over the area in which a salmon travelling 30–50 km a day may have been feeding, and (4) a spatial study by Rand and Hinch (1998) showed that zooplankton concentrations in the Gulf were strongly autocorrelated to a range of 100 km, with correlation in some years falling off sharply outside that distance.

The difference between day and night sampling in integrated 0–150 m zooplankton tows is not significant in high latitude areas in the summer and is not taken into account in this analysis (Sugimoto and Tadokoro 1997). Phytoplankton data were also considered, as proxied by secchi depth (Sugimoto and Tadokoro 1997). However, due to the amount of error inherent in this method, limited analysis was performed on these data.

Salmon stomach contents and squid density estimation

The patchy nature of prey distribution requires the use of detailed bioenergetics simulation modeling

and Monte Carlo techniques to determine the effect of each prey type on salmon growth (Aydin, unpublished data). Details of the abundance and importance of individual prey types in the salmon diet are presented in Kaeriyama et al. (this volume).

An index of micronektonic squid abundance was calculated for each gillnet station using food habits data from pink, sockeye, and coho salmon. Chum salmon do not feed on squid often enough to be used for this index. The formula used was:

$$\text{SquidIndex} = \ln \left[\frac{N_{\text{squid}, \text{species}} + \frac{1}{2}}{N_{\text{total}, \text{species}} - N_{\text{squid}, \text{species}} + \frac{1}{2}} \right] - \alpha_{\text{species}}$$

$$BW \geq BW_{\text{cutoff}, \text{species}}$$

$$\text{species} = \{\text{pink}, \text{coho}, \text{sockeye}\}$$

This formula gives three comparable estimates of the squid index at each station, provided all three species, pink, coho, and sockeye salmon, are sampled at the station. $N_{\text{total}, \text{species}}$ is the number of fish stomachs sampled in a given species, where only fish with body weights above BW_{cutoff} are used. $N_{\text{squid}, \text{species}}$ is the number of those fish with stomachs containing non-larval squid. The correction α is used to calibrate the estimates with respect to each other. The body weight cutoff and correction α for each species are given in Table 1.

The squid index is an empirical logistic variable (Cox and Snell 1989). If prey capture is considered to be a Poisson process, the squid index is approximately proportional to $\ln[\text{density}]$ in the range $-3 < \text{Index} < 3$, where [density] is the numerical density of squid in the foraging area. Thus, this corrected squid index may be treated as a log-CPUE index, which uses the salmon as the sampling gear, and the differing α for each of pink, sockeye and coho constituting empirical "gear corrections" for species-specific behavior. In this study, the three estimates of squid density were pooled into a single estimate for each gillnet station. The empirical corrections were determined by a site-by-site analysis of over 11,000 pink, sockeye and coho salmon stomachs collected between 1956 and 1998 (Aydin, unpublished data).

Table 1. Estimated empirical corrections for calculating a squid density index from sockeye, pink, and coho salmon. Corrections were calculated from over 11,000 fish sampled between 1956–98 (Aydin unpublished data).

Species	Body weight cutoff (g)	Alpha offset (intercept)
Sockeye	1000	-0.03
Pink	1000	-0.41
Coho	500	+0.60

Determining relationships between variables

Each of the biological variables described above—zooplankton density, squid index values, CPUE and body weight of salmon (by species and age) and the prey weight—was analyzed with respect to physical variables. The physical variables considered were year, latitude, ocean domain/boundaries, and the principal components of the eight water column variables. The relationship between biological and physical variables was examined by constructing Generalized Linear Models (GLMs) for the potential biological/physical relationships (McCullagh and Nelder 1989).

The process used to select the best statistical models for each variable was a manual stepwise model selection procedure, where linear first-order interactions of each of the physical variables were examined in turn, and second- and higher-order interactions were examined where appropriate.

RESULTS

CTD sampling occurred at 83 stations while NORPAC sampling included 131 zooplankton samples over these stations, five of which were discarded due to the presence of gelatinous material. A total of 876 pink, 1,124 sockeye, 412 coho and 1,320 chum salmon was measured at 33 gillnet stations. From these, a total of 2,471 stomach samples was taken. For sockeye and chum, ocean ages .1–.3 made up over 99% of the samples. For calculating the squid index, 1,738 pink, coho and sockeye stomachs came from fish with body weights above the species-specific cutoffs, with at least 22 and an average of 51 being sampled for squid at each station.

Oceanographic Variables Along 145°W, 1994–98

In 1995, precipitation caused measurements of sea surface salinity to be anomalously low at a few stations (< 29 psu). These salinity values were replaced with salinity values at 1 m depth, which were all greater than 32 psu. No other corrections were made in the oceanographic data prior to analysis.

In all years, a seasonal thermocline was visible between 20–50 m depth. At most stations, the seasonal thermocline was the point of highest buoyancy frequency in the water column, although in 1995 and 1998 some strong surface stratification was visible in the top 5 m. In all years, mixed-layer water temperatures were highest in the south, decreased to a minimum between 51–53°N, and increased again in the north. The mixed layer was generally shallower and stronger in the north and weaker and deeper in the south. Temperatures were warmest in 1997 and cooler in 1996 and 1998. In 1997, the mixed layer

was shallow with strong stratification along the entire transect.

The maximum gradient in the permanent pycnocline occurs between 80–120 m at most stations. The exceptions are between 51–53°N in 1997, when the pycnocline was deeper, and between 55–57°N in 1995, when the pycnocline was not visible. This latter anomaly is due to the presence of a strong downwelling (clockwise) eddy between 55–57°N, which is also shown by the intrusion of 6°C water to depths of 200 m. Dynamic topography maps confirm the presence of this eddy in 1995 and numerous weaker eddies along the transect line (Onishi et al. 2000).

Principal Components Analysis

The first two principal components (PCs) together account for 58% of the variation in the oceanographic variables used in the PCA, while the first five PCs account for 91% of the variation (Table 2). By convention, only variables accounting for the first 90% of the variation are retained for further analysis (Mathsoft 1995). An examination of PC5 revealed that it was the result of a single anomalous data point in 1995 at 55.5°N, where the permanent pycnocline was not evident. Therefore, PCs 5–8 were not analyzed further.

PC1 is a measure of the properties of the seasonal thermocline. It represents the combined surface water characteristics of sea surface temperature, mixed-layer depth, and mixed-layer strength. Stations with maximum values of PC1 show very warm surface-layer temperatures with SSTs between 12–14°C, while stations with minimum values have surface-layer temperatures below 10°C. PC1 values show interannual variability, with 1997 having a warmer, shallower mixed layer, and 1996 and 1998 being cooler and more well-mixed on the surface.

PC1 values tend to increase from south to north (Fig. 4).

The remaining three principal components reflect processes in the permanent pycnocline that are associated with the oceanic domains. For example, PC2 indicates dilute surface waters and a deeper, less stratified permanent pycnocline, typical of the Alaska Current. Because PC2–PC4 are indicators of oceanographic domain characteristics, they are redundant with the domain definitions (Subarctic Current, Ridge Domain, Alaska Current) determined by examination of the TS plots.

Oceanographic Boundaries

In all years, the Ridge Domain of ~4°C water was evident along the transect, rising from below 300 m to depths of 100–200 m (Fig. 5). In 1994, the rise was between 50° and 51°N, and in 1995–97 the rise was between 51° and 53°N. In 1998, a weak rise occurred at 51°N and a sharper rise occurred between 53° and 54°N, with an intrusion of warmer water to 150 m between the two rises, perhaps due to an eddy reported by Onishi (2000). The sharper northern rise was chosen for the Ridge Domain boundary. In all years, north of 55°–56°N the Ridge Domain was not evident, either due to eddy activity in the north or the presence of the Alaska Current.

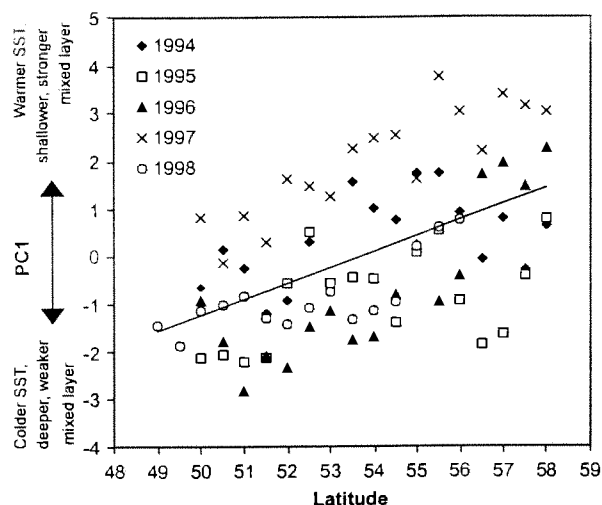
The SST minimum from IGOSS data ranged between 50°30'N and 53°30'N. The minimum was furthest to the south in 1997 and furthest to the north in 1996 (Fig. 5). The minima generally corresponded with locations of SST minima seen in the *Oshoro maru* data, except in 1995 when turbulent conditions may have affected shipboard measurements.

All three of the first-order models for PC1 (pooled by domain, pooled north or south of the SST minimum, and fit linearly to latitude) were significantly better than the null model at explaining the

Table 2. Principal components of oceanographic data. The eigenvectors (loading coefficients) are shown for all eight principal components. The individual and cumulative percent of variance explained by each component are also shown. For the first four PCs, coefficients with absolute values > 0.35 are shown in bold (cutoff is arbitrary).

Variable	Principal Component							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
T0	0.55	0.22		-0.11		-0.40	-0.68	
S0	0.14	-0.39	0.40	-0.45	-0.57	0.34	-0.11	
T100	-0.17	0.25	-0.46	-0.82				
S100	0.20	-0.49	-0.49	0.10	-0.13			0.67
Sdepth	-0.46	-0.24	0.12		-0.35	-0.77		
Sstm	0.59		0.17			-0.31	0.72	
Pdepth	-0.21	0.53	0.38		-0.20	0.13		0.67
Pstm	-0.11	-0.40	0.44	-0.29	0.70			0.25
Percent of variance explained								
Individual	30	28	15	10	8	6	2	1
Cumulative	30	58	73	83	91	97	99	100

Fig. 4. The first principal component of the eight oceanographic variables sea surface temperature and salinity, 100 m temperature and salinity, mixed-layer depth and maximum buoyancy frequency, and permanent pycnocline depth and maximum buoyancy frequency, regressed vs. latitude ($R^2 = 0.28$, $p < 0.001$). The first PC's primary components are SST, mixed-layer depth, and mixed layer buoyancy frequency.



latitudinal variation in PC1. However, the SST minimum explained a greater proportion of the variance (32% of the total variance) compared with 21% and 18% for latitude and domain, respectively (Table 3). Using latitude as an additive term in the two-pool SST minimum model did not increase the amount of variance explained.

This result indicates that in any given year, variation in the common mode of sea surface temperature and seasonal mixed-layer variation is best explained by distinguishing two zones, with a discontinuity located at the yearly SST minimum. PC1 varied significantly among the five years in both the north and the south, with high values in 1994 and 1997 (1-way ANOVA, $p < 0.005$).

Table 3. Percent of variance explained by single- and two-term linear models for PC1, $\ln[\text{Zooplankton}]$, and Squid Index values. "N/S" indicates the term defined as north or south of the IGOSS SST minimum. Single-term models are listed as "n.s." if they were not significantly different from the null model (F-Test, $p > 0.05$). Two-term models are listed as "n.s." if they were not significantly different from a single-term model that contained one of the two terms (F-Test, $p > 0.05$).

Independent Terms	DEPENDENT VARIABLE		
	PC1	$\ln[\text{Zooplankton}]^1$	Squid Index
Single-term models			
Latitude	21%	n.s.	33%
Domain	18%	11%	n.s.
N/S	32%	21%	41%
Two-term models			
N/S + Latitude	n.s.	n.s.	43%
N/S + PC1	-	n.s.	51%
Latitude + PC1	-	n.s.	55%

¹after removal of stations in the Alaska Current.

Zooplankton

Stepwise linear model selection of the explanatory variables showed that log-transformed zooplankton measurements were significantly different between domains (1-way ANOVA, $p < 0.04$). The average zooplankton density was lowest in the Subarctic Current (average: 180 g/1000 m³), and highest in the Ridge Domain (average: 253 g/1000 m³), with a middle value in the Alaska Current (average: 221 g/1000 m³; Fig. 6).

The north to south change from high to low zooplankton density along the transect was correlated with domain boundaries, and the change was steep and evident in the zooplankton data, especially between 1996–1998. However, within the Ridge Domain further patchiness was evident. An area of low

Fig. 5. Vertical transect of water temperature (°C; numbers and contours of 0.5°C) along 145°W to a depth of 500 m, 1994–1998. Shading indicates water below 4°C. The location and boundaries of the Subarctic Current (sc), Alaska Current (ac) and the IGOSS sea surface temperature minimum (Tmin) are shown. The area between the Subarctic and Alaska Currents is considered to be the Ridge Domain. Oceanographic regions were determined from temperature and salinity profiles as discussed in the text.

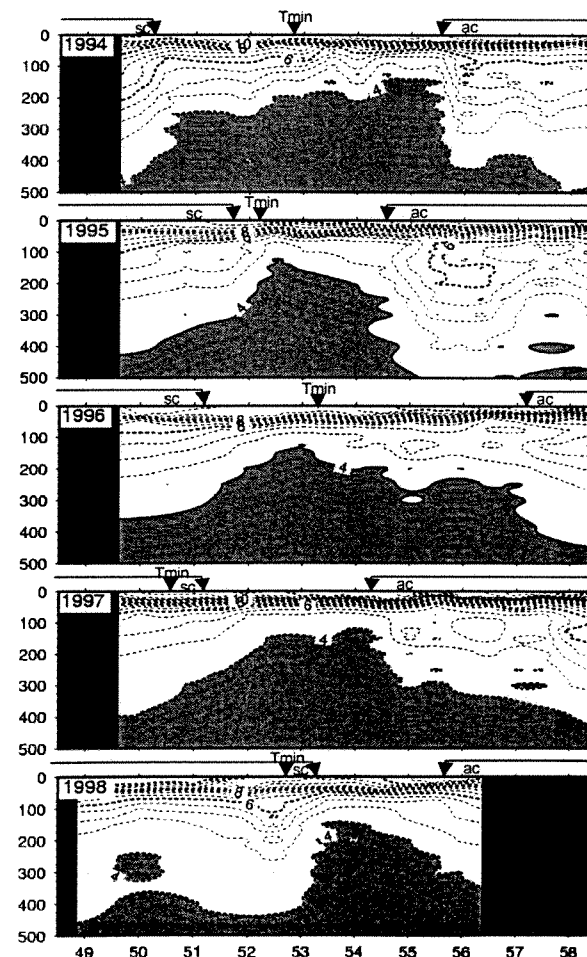
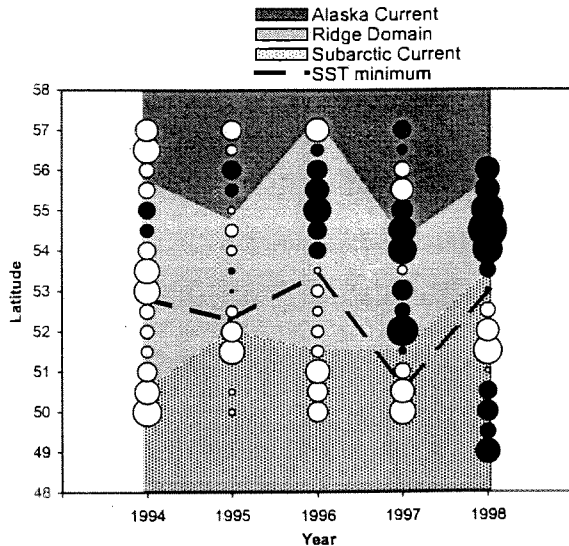


Fig. 6. Oceanographic regions and boundaries from Fig. 5 (shaded areas) and 0–150 m integrated zooplankton densities (wet weight, mg/m³; circles), by year and latitude. The area of each circle is proportional to the difference between the log-transformed, 100 km-smoothed zooplankton density at each station and the log-transformed mean value of all stations. Black circles are greater than the mean value, and white circles are less than the mean value. The largest circles are approximately ± 3 s.d. from the mean.



zooplankton density between 51–53°N in 1998 corresponds with the mesoscale eddy mentioned above. In 1995, there seems to be a discontinuity in zooplankton values at the SST minimum, as well (Fig. 6).

When the stations in the Alaska Current were removed, the southern boundary between areas of high and low zooplankton densities was more strongly associated with the SST minimum than the Ridge/Subarctic Boundary. A 1-way ANOVA between the two models showed a significant difference in the amount of variance explained ($p < 0.05$), with the SST minimum break explaining 21% of the zooplankton variance south of the Alaska Current, while the Ridge/Subarctic Current partitioning explained only 11% (Table 3). Relationships between zooplankton and either PC1 or latitude were not significant.

Zooplankton showed a weak positive correlation with phytoplankton as proxied by secchi depth ($r = 0.11$). This is probably due to the effect of mesoscale vertical concentration and dilution features, such as the 1998 eddy, acting on both phytoplankton and zooplankton. Zooplankton showed a significant increase in the northern zone between 1994 and 1998 (1-way ANOVA, $p < 0.005$), but did not vary significantly between years in the south.

Squid Indices

In most years, salmon were not collected far enough to the north to examine squid or salmon in

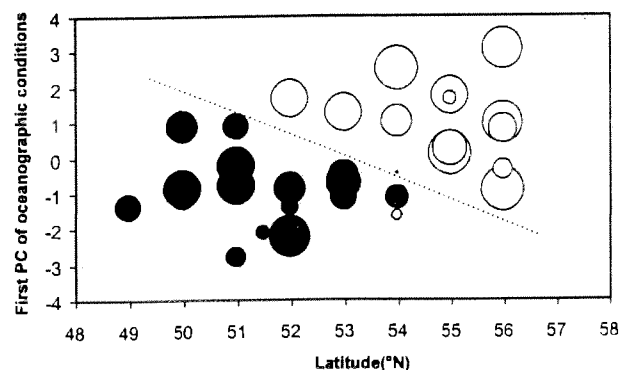
the Alaska Current. Therefore, all Alaska Current stations were removed from analysis of squid density and salmon biological characteristics. Examination of squid specimens from stomachs indicated that over 90% of the squid found in salmon stomachs were *Berryteuthis anonychus*, with the remainder being *Gonatus onyx* or unidentified species.

Examined station-by-station, the squid index values calculated separately for pink, sockeye, and coho salmon were highly correlated ($r = 0.75$ to 0.85 , $p < 0.001$), confirming that most of the variation in index values was due to factors common to all three species varying between stations, such as the environmental density of squid. Values of the pooled index ranged from -2.5 and 2.5 across all stations. This corresponds to a range of from 5% to 95% squid in stomachs.

The pooled squid index showed significant first-order interactions with latitude, PC1, and the SST minimum. However, it was not immediately possible to choose a “best” model from among the multiple interactions of the three variables on squid densities, as the three explanatory variables were not independent, and several of the two-term models had significant explanatory power (Table 3).

To clarify the situation, squid index values were plotted versus both latitude and PC1 (Fig. 7). While PC1 and latitude are not orthogonal, this graph shows the relationship of squid abundance to the three variables. Squid index values were higher in the south, and at colder surface temperatures with deeper seasonal mixed layers. More importantly, there was a sharp linear boundary between high and low squid index values (dotted line in Fig. 7). In any given year, all positive squid index values were on the southern end of the transect, and all negative values were on the northern end of the transect.

Fig. 7. Squid index values plotted by latitude and the first principal component of oceanographic conditions for all stations, 1994–1998. Size of circles indicates the distance of the squid index value from the mean over all stations. Black circles are larger than the mean, while negative circles are smaller than the mean. The largest circles are approximately ± 2.5 squid index units from the mean. The dotted line shows the division between high and low squid densities fitted by eye.



The latitude of the cutoff varied from year to year (Fig. 8). The latitudes at which squid abundance drops and the SST minimum occurs each year are significantly correlated (Table 4). The correlation between the Ridge/Subarctic Boundary and the squid boundary is not significant. Within each zone, squid index values were not significantly different between years. When squid, zooplankton, and PC1 were examined on a station-by-station level within each year and region, there were no significant correlations.

Fig. 8. Latitudes of north/south borders between possible oceanographic or biological regions, using four criteria. Diamonds and dotted line, Ridge/Subarctic Boundary; solid squares and bold line, IGOSS temperature minimum; open circles, cutoff determined by the dotted line in Fig. 7; triangles, latitude south of which all squid index values are positive, north of which all values are negative.

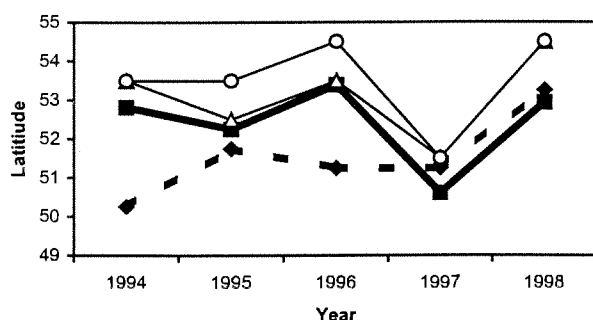


Table 4. Correlation between the latitude of the yearly boundary between high and low squid index values and the yearly boundary between the IGOSS SST minimum and the Ridge/Subarctic Boundary. Two methods of determining the squid cutoff latitude: one uses the switch between positive and negative values, and one uses the dotted line in Fig. 6.

	Ridge/ Subarctic Border	IGOSS SST minimum	Squid positive/ negative cutoff
IGOSS SST minimum	0.12		
Squid positive/negative cutoff	0.42	0.86(*)	
Squid latitude/PC1 cutoff	0.37	0.97(**)	0.90(*)

(*) $p < 0.05$ (**) $p < 0.01$

Salmon CPUE and Body weight

Log-transformed CPUE for salmon showed few significant differences between ocean domains or across the SST minimum. The CPUE of most of the species and ocean age classes showed catches increasing linearly from the south to the north, most likely representing return migration patterns rather than feeding distribution. Ocean age .1–.2 sockeye had highest catches in the Ridge Domain, possibly due to the abundance of southern British Columbia stocks. Pink salmon, ocean age .2 and .3 chum salmon, and ocean age .3 sockeye salmon showed significant differences in CPUE by year (1-Way ANOVA, $p < 0.05$), which are probably related to the

interannual variation in the population size of each stock (Myers et al. 1999).

Of the 14 age and maturity classes caught in large enough numbers for analysis, three groups of chum salmon showed significantly larger body weights north of the SST minimum, while coho, pink, and maturing .2–.3 sockeye salmon showed significantly larger body weights to the south (Table 5). These latter species feed exclusively on squid in the southern zones, while the chum feed on zooplankton in both zones. Ocean age .1 sockeye were not significantly different in size between the two zones.

Within the southern and the northern zones, several of the species/age-class combinations showed significant interannual variation in body weight (1-way ANOVA, $p < 0.05$). Specifically, the fish with the largest average body weights—coho, ocean-age .3 chum and maturing ocean-age .2 sockeye salmon—were larger in 1996 and 1998 than in any other year. These coincide with the years that temperatures were coolest overall, and the SST minimum boundary and the squid were the farthest to the north (Fig. 8). Conversely, ocean age .1 sockeye salmon, both in the south and the north, were significantly larger in 1997 than in any other year (1-way ANOVA). This coincides with the year that waters were warmest and the SST minimum and squid were farthest to the south.

DISCUSSION

The analysis of zooplankton and micronektonic squid along the transect line supports the existence of a biological boundary affecting salmon feeding ontogeny between 50–54°N, associated with the July sea surface temperature minimum (Tables 3–4 and Figs. 6–8). This boundary was noted by LeBrasseur (1966), who described the predominance of squid in salmon diets in the Subarctic Current. Pearcy et al. (1988) similarly noted a biological boundary along 155°W in 1984 and 1985, but associated the boundary with the border between the Subarctic Current and the Ridge Domain. However, our analysis shows that the SST minimum is more strongly correlated with the biological boundary than the Ridge/Subarctic border.

The importance of the latitudinal position of the SST minimum boundary in determining salmon growth is suggested by the body weights of the largest salmon, which have the highest predation rates on squid (Kaeriyama et al. this volume). All of these species are larger in 1996 and 1998, when the boundary was farther to the north, and smaller in 1997 when the boundary was farther to the south (Fig. 8).

It is possible that sea surface temperature, which is warm in 1997 and cold in 1996 and 1998, is a contributing physiological factor, causing poor growth in warm years. However, such a physiological effect of

Table 5. Average body weights by species, ocean age, and maturity status, of salmon caught south and north of the SST minimum. North/South *p*-value shows significance of difference between north and south for all years pooled using a 2-tailed *t*-test.

Species	Ocean age	Maturity ¹	N	Body weight north (kg)	Body weight south (kg)	North/South <i>p</i> -value	Significantly higher in:
Chum	.1	IM	332	0.75	0.67	<0.0001	North
		MT	28	0.77	0.84	0.55	
	.2	IM	763	1.29	1.18	<0.0001	North
		MT	100	1.52	1.41	0.21	
	.3	IM	54	1.68	1.59	0.62	
		MT	43	2.60	1.93	0.01	North
Coho	.1	MT	412	2.82	3.06	0.01	South
Pink	.1	MT	876	1.30	1.53	<0.0001	South
Sockeye	.1	IM	68	0.50	0.54	0.10	
		MT	39	0.79	0.95	0.57	
	.2	IM	82	1.75	2.01	0.07	
		MT	641	2.27	2.65	<0.0001	South
	.3	IM	2	2.78	-		
		MT	292	2.96	3.15	0.03	South

¹IM, immature; M, mature.

sea surface temperature should act similarly for all salmon groups, but ocean age .1 sockeye salmon are larger in 1997 than in the colder years. These smaller fish, feeding mainly on zooplankton, grow larger in years in which their overlap with squid is minimized. Chum salmon, also zooplankton feeders, are larger in the north in all years (Table 5), supporting the idea that the difference in prey distribution on either side of the boundary is a determining factor in growth. This pattern suggests that the squid are a competitor with the chum and smaller sockeye for food.

There is no evidence of a small-scale, station-by-station negative correlation between squid and zooplankton within each region, perhaps due to mesoscale zooplankton structure associated with eddies (Fig.6). Zooplankton density is lower to the south and higher to the north, while the density of the micronektonic squid *Beryteuthis anonychus*, as indexed from salmon stomach sampling, is higher in the south than in the north. It is possible, but not confirmable, that lower densities of zooplankton are evidence of top-down control of zooplankton by squid and salmon.

The latitude of the SST minimum varies from year to year between 51°N in 1997 and 54°N in 1998, a distance of over 300 km. In the north, zooplankton density increased from 1994 to 1998 but it did not differ significantly in the south. Within each region, squid density did not vary significantly from year to year. Therefore, the processes determining the latitude of the SST minimum may be more important to salmon prey distribution than the variation in the amount of food within each region.

The mechanistic link between the SST minimum and the northern boundary of squid distribution is not clear. The SST minimum may represent a density or

temperature gradient unsuitable for squid. More likely, Aydin *et al.* (1998) suggest that the SST minimum may be a proxy for a frontal structure between internal Alaska Gyre waters and waters from the west. It is also possible that the SST minimum is a better proxy for the Subarctic Current than the 4°C vertical isotherm, or that squid respond to multiple conditions, entering the Gyre in the Subarctic Current and spreading north to the SST minimum. Surveys conducted in the 1950s–1970s show that Oyashio waters are associated with a cold front within the Ridge Domain which varies substantially in its eastern extent from year to year (Favorite and Hebard 1961; USBCFBL 1969). This component of westward transport, associated with the SST minimum, may be linked to squid distribution.

Fronts may propagate across the North Pacific and vary substantially from year to year (Yuan and Talley 1996). Percy *et al.* (1996) found a similar biological border further to the south that was important for larger species such as Pacific pomfret (*Brama japonica*) and Neon Flying Squid (*Ommastrephes bartrami*). The role of fronts in salmonid feeding has been cause for speculation (e.g., Brandt 1993), and the behavior of these fronts under climate-change scenarios may be critical to determining changes in salmon biogeography.

Because the squid are sampled from salmon themselves, it is possible that the change is not representative of squid abundance but of the changing ability of salmon to capture squid on one side of the border, or that at warmer temperatures catching squid ceases to be profitable causing salmon to switch to zooplankton. However, the fact that the switch occurs in pink, sockeye, and coho salmon simultaneously, three species with differing energy budgets,

suggests that the change is due to the presence or absence of squid.

The determination of the SST minimum as a proxy for the border between two distinct feeding modes of salmon has implications for both salmon growth and future populations. Because SST records exist in the region back to the 1950s, it would be worthwhile to examine the variation in this border back through time with large-scale salmonid growth trends, to determine the importance of this mechanism in salmon growth overall. Such retrospective studies in combination with continuing modeling on salmon growth would improve our ability to understand the consequences of global climate change.

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Feeding Ecology of Sockeye and Pink Salmon in the Gulf of Alaska

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Abstract: The feeding ecology of sockeye (*Oncorhynchus nerka*) and pink (*O. gorbuscha*) salmon in the Gulf of Alaska was investigated during early summers of 1994–1999. The dominant prey of salmon were squids (mainly *Beryteuthis anomychus*) in the Subarctic Current, and zooplankton (e.g., euphausiids, copepods, and pteropods) in the Alaskan Gyre during 1994–1996 and 1998. Food competition occurred between sockeye and pink salmon. Pink salmon appeared to feed on more diverse prey at a lower trophic level than sockeye salmon. The feeding and growth of sockeye and pink salmon were affected by the El Niño event during spring and summer of 1997.

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are distributed widely and grow in oceans, which are typically more productive than freshwaters (Gross 1987). For Pacific salmon, oceanic foraging conditions and food relationships are important to growth. They are omnivorous and opportunistic feeders. Major categories of prey found in stomach contents of Pacific salmon usually include either one or a combination of fish, squid, euphausiids, amphipods, copepods, pteropods, larval crustaceans, gelatinous zooplankton, polychaetes, chaetognaths, appendicularians, ostracods, heteropods, mysids, and shrimps (Percy et al. 1988). By switching their diets to micronekton (squid and fish), salmon can sustain themselves through seasons or even years of low zooplankton production (Kaeriyama et al. 1998). Pink salmon (*O. gorbuscha*) fed predominantly on larger food items (squid and fish) in even years and small food items (euphausiids, amphipods, and copepods) in odd years. This relationship suggests a possible feeding interaction with abundance of pink salmon (Ito 1964). The composition of food of sockeye salmon (*O. nerka*) depends on the availability and relative abundance of the food items, which vary with season and location (Burgner 1991).

At the same time, Pacific salmon are selective feeders. In general, chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon tend to feed on large prey (fish and squid), while sockeye, chum (*O. keta*), and pink salmon feed on small prey (zooplankton). Prey selectivity in Pacific salmon is related to inter- and intra-specific differences in functional morphology, physiology, and behavior. In feeding strategy, juvenile chum salmon switch their feeding tactics from “sit-and-waiting” in the river to “wide-foraging” in the sea (Kaeriyama 1986).

Pacific salmon production in the North Pacific Ocean increased dramatically in the late 1970s, possibly owing to enhanced early ocean survival (Percy 1992; Percy et al. 1999). The increase in the number of salmon has prompted interest in possible density-dependent effects on survival, growth, and production of salmon stocks around the Pacific rim (e.g., Helle 1989; Kaeriyama 1989, 1998). However, the population density-dependent effect on feeding ecology of Pacific salmon has not been proven yet. On the other hand, Pacific salmon runs to some western Alaska river systems were very poor in 1997 and 1998. Sockeye salmon returning to Bristol Bay were smaller than average. Both reduced size and weak

runs of Bristol Bay sockeye salmon in 1997 and 1998 implied that ocean conditions were unusually poor for growth and survival (Kruse 1998).

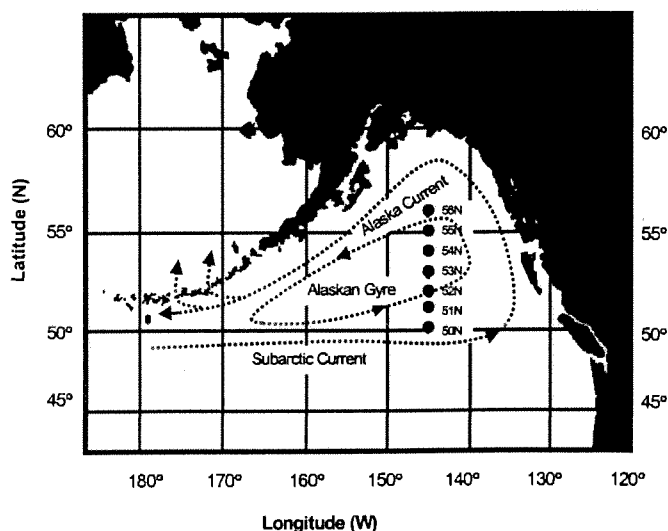
The objective of this paper is to describe the feeding ecology of sockeye and pink salmon in the Gulf of Alaska, and to discuss the basic principles of food and feeding habits, the relationship between feeding ecology and ocean environmental condition, and inter- and intra-specific interaction.

MATERIALS AND METHODS

Fish Collection

Sockeye and pink salmon were collected from late June to middle July, 1994–1998, in non-selective research gillnet operation aboard the *Oshoro maru*, training vessel of the Hokkaido University, at stations located in 1-degree latitude intervals along a transect 145°W from 50°N to 56°N (Fig. 1). In this area, there are three oceanic regions: the Subarctic Current, Alaskan Gyre, and Alaska Current (Percy et al. 1988). Total length and mesh size of gillnet were 2.35–2.50 km (47–50 tans, 50 m/tan) and 48–157 mm, respectively. Gillnet gear was set in the evening, allowed to soak overnight, and was retrieved the following morning. Each fish was weighed to the nearest gram and measured to the nearest millimeter in fork length (FL) on board. Scale samples were collected to determine the age of fish for growth estimation. At each fishing station the CTD model II was lowered to a depth of 3,000 m. The data from the CTD were used to plot temperature isopleths along the 145°W transect.

Fig. 1. Sampling locations in the Gulf of Alaska. Samples were collected from late June 1994 to middle July 1999 in non-selective research gillnet operations aboard the *Oshoro maru*, training vessel of the Hokkaido University.



Stomach Analysis

Stomachs from the esophagus to the pyloric valve were collected from up to 20 fish of each species in each gillnet operation, and preserved in 10% formalin-seawater solution for later stomach analysis in 1997 and 1998. In 1994–1996, fresh stomach contents were used to estimate percent volume of each prey category. This was done in the shipboard laboratory. Stomach contents were classified to 12 taxa (Table 1), then were identified to the lowest identifiable taxon, and counted and weighed by species. We estimated caloric values of each prey in the stomach content using the data provided by Davis et al. (1998).

Table 1. Prey animals and food items of sockeye and pink salmon in the Gulf of Alaska.

Food items	Species
EU Euphausiids	<i>Thysanoessa longipes</i> <i>Thysanoessa inermis</i> <i>Thysanoessa</i> spp. <i>Euphausia</i> spp. Other euphausiids
CO Copepods	<i>Neocalanus cristatus</i> <i>Eucalanus bungii</i> Other copepods
AM Amphipods	<i>Hyperia medusarum</i> <i>Hyperia</i> spp. <i>Themisto pacifica</i> <i>Themisto japonica</i> <i>Themisto</i> spp. <i>Primno macropa</i> <i>Phronima sedentaria</i> Other amphipods
DE Decapods	Decapods
SQ Squids	<i>Berryteuthis anonychus</i> Other squids
PT Pteropods	<i>Limacina</i> spp. <i>Clio</i> spp. <i>Clione</i> spp.
FI Fishes	<i>Anoplopoma fimbria</i> Other fish egg and larva
PO Polychaetes	Polychaetes
CH Chaetognaths	Chaetognaths
GE Gelatinous zooplankton	Coelenterates Ctenophores Salps
OT Other animals	Halocypridids Cumacea Octopoda Ostracods Barnacles Debris
UI Unidentified material	

Carbon Isotope Ratio of Salmon Muscle Tissue

Muscles of Pacific salmon were collected from behind the head of 1–3 fish of each species at each station, and frozen on board during early summer sampling in 1999. These samples were thawed and rinsed with distilled water in the laboratory at Hokkaido University. Samples were dried at about 60°C for 24 hours and homogenized. Fat animals tend to possess lower carbon isotope ratios than lean ones (McConnaughey and McRoy 1979). Lipid levels for mature salmon should be considerably higher than for immature salmon (Welch and Parsons 1993). Therefore, lipids were removed from samples to avoid apparent differences in trophic level with maturity of salmon. The carbon isotope ratio was measured by a MAT252/B mass spectrometer fitted with a dual inlet system and double collector. As per convention, the $\delta^{13}\text{C}$ isotope values were reported as per mil ^{13}C enrichments relative to PDB standard in the conventional manner:

$$\delta (\text{‰}) = 10^3 [R(\text{sample})/R(\text{standard}) - 1],$$

where R is again the $^{13}\text{C} : ^{12}\text{C}$ ratio. All marine samples analyzed here produce negative δ values since they are isotopically light (^{13}C -depleted) compared to the standard (McConnaughey and McRoy 1979).

Data Analysis

Stomach contents were analyzed by 5 methods: frequency of occurrence (FO) method, numerical (N) method, volume (V) method, wet-weight (W) method, and the modified index of relative importance (IRI) method (Pinkas et al. 1971). The IRI was used to characterize the diet of each species and to rank prey taxa:

$$\text{IRI} = (N + W) \text{FO}$$

where N is numerical percentage, W is weight percentage, and FO is frequency of occurrence in percent.

The Shannon-Wiener formula (H') was used to measure food niche breadth:

$$H' = -\sum p_i \log p_i$$

where p_i is the proportion of the IRI of species i in the stomach.

The simplified Morishita's index (C_H) was used to calculate overlap of food niche between species pairs; values range from 0 (no overlap) to 1 (complete overlap):

$$C_H = \frac{2 \sum_i^n p_{ij} p_{ik}}{\sum_i^n p_{ij}^2 + \sum_i^n p_{ik}^2}$$

where p_{ij} and p_{ik} are proportions of the IRI of prey species i found in the predator species j and k , respectively.

To estimate taxonomic similarity between samples from stomach contents, the average linkage clustering method was used (Krebs 1998). Student's t -test and nonparametric Mann-Whitney test were used to compare growth characters and food niche of sockeye and pink salmon in 1997 and 1998 respectively.

RESULTS AND DISCUSSION

Comparison Between Stomach Content Analysis Methods

The prey spectrum of sockeye and pink salmon comprised at least 20 taxa (Table 1). The five taxonomic groups of greatest importance using IRI were squids, calanoid copepods, hyperiid amphipods, euphausiids, and pteropods. In four methods of stomach contents analysis, squids were the most important prey for both sockeye and pink salmon (Tables 2 and 3).

Figure 2 shows the stomach contents of pink salmon in 1998 by stations and by stomach content analysis methods. In the FO (frequency of occurrence) method, percentages of prey species are more evenly spread than in other methods. In the N (numerical) method, small organisms such as copepods were numerous and therefore accounted for high percentages, and large animals such as squid and fish had lower percentages because of small numbers. Results found in both the W (weight) and V (volume) methods were opposite to those in the N method.

While the N method furnishes information about feeding behavior, V and W methods reflect nutritional value of prey. The FO method differs from the two former measures because it is not a quantity of food, but of fish qualified by their diet content (Tirasin and Jørgensen 1999). The IRI was calculated by summing the numerical and weight percentage values, and multiplying by the frequency of occurrence rate (Pinkas et al. 1971). The IRI method assumes that different measures contain substantially independent information, and that the use of compound indices prevents loss of information. Incorporating the different measures was thought to cancel out the biases in individual components and seemed to provide a more accurate description (Tirasin and Jørgensen 1999). Therefore, the IRI method may be the best for evaluating stomach contents.

Table 2. Stomach contents of sockeye salmon in the Gulf of Alaska in 1997 and 1998. FO is frequency of occurrence percentage, N is numerical percentage, W is wet weight percentage of a prey animal per fish, and IRI is percentage of total IRI for all prey taxa. $IRI = (N+W) FO$.

IRI = (N+W) FO.

	50N				51N				52N				53N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997																
Euphausiids	0.0	0.0	0.0	0.0	12.5	5.4	0.0	1.1	17.1	3.4	3.8	3.0	17.0	3.9	10.3	6.0
Copepods	9.5	23.0	0.0	3.7	12.5	4.3	0.0	0.9	22.9	92.8	43.0	76.3	21.3	92.2	70.1	85.6
Amphipods	9.5	6.1	0.0	1.0	4.2	1.1	0.0	0.1	22.9	2.8	1.0	2.1	19.1	2.8	1.1	1.9
Decapods	4.8	4.7	0.0	0.4	0.0	0.0	0.0	0.0	2.9	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Squids	42.9	11.3	97.3	77.5	37.5	41.3	100.0	85.5	14.3	0.3	26.1	9.3	12.8	0.2	9.7	3.1
Pteropods	19.0	53.1	0.0	16.8	16.7	43.5	0.0	11.7	14.3	0.5	25.9	9.3	12.8	0.7	0.2	0.3
Fish	9.5	0.9	2.6	0.6	4.2	1.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.1	0.1	0.0	2.1	0.0	0.3	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	4.8	0.9	0.0	0.1	12.5	3.3	0.0	0.7	2.9	0.1	0.0	0.0	14.9	0.2	8.3	3.1
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998																
Euphausiids	0.0	0.0	0.0	0.0	18.8	10.8	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	15.4	15.4	0.0	2.0	6.3	10.8	0.0	0.8	16.7	93.3	0.5	21.1	0.0	0.0	0.0	0.0
Amphipods	15.4	26.9	0.0	3.6	18.8	8.1	0.0	1.7	16.7	1.9	0.0	0.4	7.7	4.2	0.0	0.2
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	69.2	57.7	100.0	94.4	50.0	67.6	98.0	94.8	58.3	4.3	94.3	77.8	76.9	75.0	100.0	97.4
Pteropods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.4	20.8	0.0	2.3
Fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	0.0	0.0	0.0	0.0	6.3	2.7	2.0	0.3	8.3	0.5	5.2	0.6	0.0	0.0	0.0	0.0
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

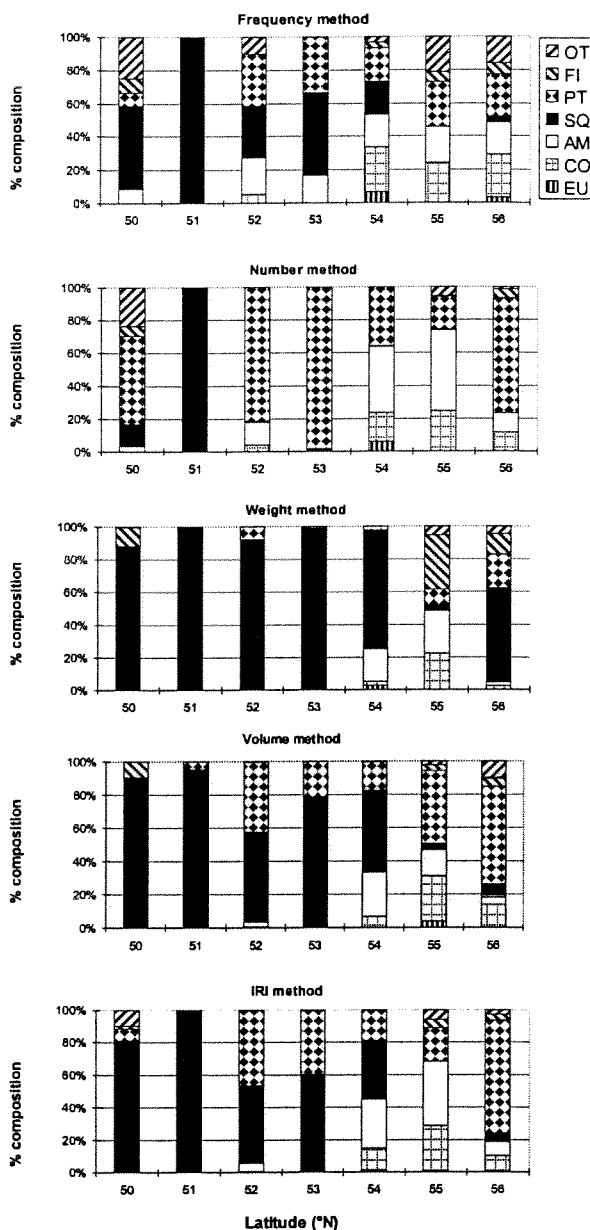
	54N				55N				56N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997												
Euphausiids	14.7	4.7	6.5	3.2	12.5	0.1	0.4	0.1	25.0	59.5	27.0	64.7
Copepods	26.5	91.2	90.1	94.9	28.1	99.3	70.5	90.6	0.0	0.0	0.0	0.0
Amphipods	8.8	0.4	0.9	0.2	21.9	0.4	0.7	0.4	8.3	0.6	0.1	0.2
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3	0.6	0.1	0.2
Squids	5.9	0.1	0.3	0.0	18.8	0.1	23.0	8.2	13.9	0.5	1.6	0.9
Pteropods	14.7	2.8	0.4	0.9	6.3	0.1	0.1	0.0	19.4	31.8	2.6	20.0
Fish	2.9	0.0	0.2	0.0	3.1	0.0	0.0	0.0	5.6	2.6	66.1	11.4
Polychaetes	8.8	0.3	0.9	0.2	3.1	0.0	0.0	0.0	13.9	3.9	2.1	2.5
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	17.6	0.5	0.7	0.4	6.3	0.0	5.3	0.6	5.6	0.4	0.4	0.1
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998												
Euphausiids	0.0	0.0	0.0	0.0	8.3	0.5	0.0	0.1	8.0	0.7	0.0	0.2
Copepods	25.0	11.0	0.7	5.9	25.0	13.7	0.5	12.7	24.0	1.8	0.2	1.7
Amphipods	21.4	8.8	1.1	4.3	16.7	10.9	0.2	6.6	20.0	24.9	0.2	18.0
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.3	0.0	0.0
Squids	28.6	1.0	94.2	54.5	16.7	0.9	76.2	45.8	12.0	0.4	73.6	31.8
Pteropods	21.4	79.0	3.2	35.3	16.7	19.9	0.3	12.0	16.0	69.2	1.1	40.3
Fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	1.5	0.2	0.5
Polychaetes	0.0	0.0	0.0	0.0	8.3	6.2	17.7	7.1	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	8.3	47.9	5.1	15.7	0.0	0.0	0.0	0.0
Others	3.6	0.1	0.8	0.1	0.0	0.0	0.0	0.0	8.0	1.2	24.7	7.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 3. Stomach contents of pink salmon in the Gulf of Alaska in 1997 and 1998. *FO* is frequency of occurrence percentage, *N* is numerical percentage, *W* is wet weight percentage of a prey animal per fish, and *IRI* is percentage of total IRI for all prey taxa. $IRI = (N + W) FO$.

	50N				51N				52N				53N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997																
Euphausiids	-	-	-	-	0.0	0.0	0.0	0.0	20.8	23.0	40.0	29.0	8.8	5.3	10.7	2.3
Copepods	-	-	-	-	0.0	0.0	0.0	0.0	25.0	59.4	47.5	59.0	32.4	85.4	84.8	91.6
Amphipods	-	-	-	-	20.0	2.5	0.4	1.4	16.7	7.4	9.5	6.2	32.4	6.0	2.8	4.7
Decapods	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	-	-	-	-	20.0	3.8	81.0	42.4	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Pteropods	-	-	-	-	20.0	91.8	2.8	47.3	20.8	8.0	2.5	4.8	20.6	3.1	0.8	1.3
Fish	-	-	-	-	20.0	0.6	15.8	8.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	-	-	-	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	-	-	-	-	20.0	1.3	0.0	0.6	16.7	2.1	0.5	1.0	5.9	0.2	0.1	0.0
Total	-	-	-	-	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998																
Euphausiids	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	4.0	0.1	0.4	0.0	0.0	0.0	0.0
Amphipods	8.3	3.4	0.0	0.4	0.0	0.0	0.0	0.0	22.2	13.8	0.3	5.3	16.7	0.4	0.0	0.1
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	50.0	13.5	88.0	80.6	100.0	100.0	100.0	100.0	31.1	0.4	92.0	48.0	50.0	1.3	98.9	60.1
Pteropods	8.3	53.9	0.2	7.2	0.0	0.0	0.0	0.0	31.1	81.6	7.5	46.3	33.3	98.3	1.1	39.8
Fish	8.3	5.6	11.5	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	25.0	23.6	0.3	9.5	0.0	0.0	0.0	0.0	10.4	0.2	0.1	0.0	0.0	0.0	0.0	0.0
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

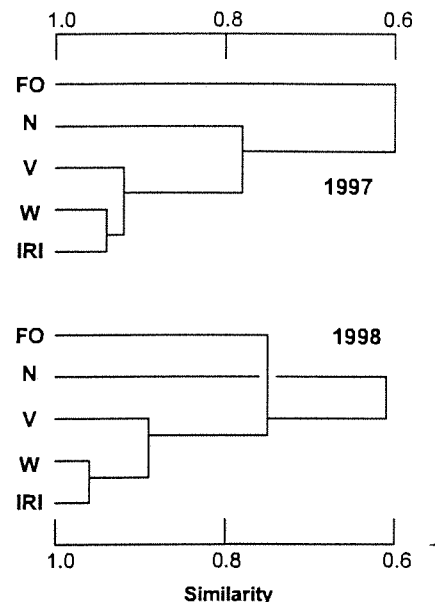
	54N				55N				56N			
	FO	N	W	IRI	FO	N	W	IRI	FO	N	W	IRI
1997												
Euphausiids	23.8	5.1	9.1	6.6	7.5	0.3	0.3	0.1	22.7	24.4	61.6	42.6
Copepods	26.2	86.0	86.9	88.0	22.5	68.7	67.7	73.8	0.0	0.0	0.0	0.0
Amphipods	14.3	0.2	0.3	0.2	22.5	20.6	7.0	15.0	13.6	0.4	0.6	0.3
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	4.8	0.0	1.0	0.1	10.0	0.3	22.3	5.4	4.5	0.0	5.1	0.5
Pteropods	23.8	8.6	2.5	5.2	17.5	6.2	1.7	3.4	25.0	71.0	22.8	51.2
Fish	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	9.1	0.2	4.9	1.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	7.1	0.0	0.1	0.0	20.0	3.9	0.9	2.3	22.7	4.0	4.9	4.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1998												
Euphausiids	6.7	6.0	2.7	1.4	0.0	0.0	0.0	0.0	3.2	0.1	0.0	0.0
Copepods	26.7	17.5	2.2	13.1	24.2	24.3	22.3	28.4	25.8	11.1	2.4	10.4
Amphipods	20.0	40.1	20.2	30.1	21.2	49.4	25.8	40.0	19.4	12.1	2.0	8.1
Decapods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squids	20.0	0.6	72.8	36.6	0.0	0.0	3.7	0.0	3.2	0.1	57.7	5.6
Pteropods	20.0	35.6	1.9	18.7	27.3	20.6	9.4	20.5	25.8	70.0	20.6	69.6
Fish	3.3	0.1	0.2	0.0	6.1	0.1	33.2	5.1	6.5	5.5	12.5	3.5
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gelatinous zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	3.3	0.1	0.0	0.0	21.2	5.6	5.6	6.0	16.1	1.3	4.7	2.9
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Fig. 2. Stomach contents of pink salmon in the Gulf of Alaska at 145°W longitude in 1998 calculated by five different methods. Number of samples was from 10 to 20 individuals at each station. EU = euphausiids, CO = copepods, AM = amphipods, SQ = squids, PT = pteropods, FI = fish, OT = other species.



The similarity between the five methods results in similar outcomes for the stomach contents of sockeye salmon collected in 1997 and 1998 (Fig. 3). The most similar pair was the IRI and W methods. The results from the N and FO methods were very different from the IRI method. To evaluate the feeding ecology of salmon, we therefore mainly used the IRI method, but depending on the situation also employed the W method.

Fig. 3. Dendrograms of stomach contents of sockeye salmon from the Gulf of Alaska in 1997 and 1998. Degree of overlap and cluster analysis between stomach content analysis methods were calculated by the simplified Morishita's index and the average linkage within group. IRI = index of relative importance method, W = weight method, V = volume method, N = numerical method, FO = frequency of occurrence method.



Comparison of Feeding Ecology Between Sockeye and Pink salmon

We investigated the carbon isotope ratio of Pacific salmon in the Gulf of Alaska during summer in 1999 (Fig. 4). Trophic levels of nekton-feeders (e.g., coho and chinook salmon, and steelhead trout) were higher than those of plankton-feeders (e.g., sockeye, pink, and chum salmon). In the Gulf of Alaska, sockeye salmon appear to be positioned between coho and pink salmon, with the potential for significant trophic competition to occur (Welch and Parsons 1993). Our results indicate that the trophic level of sockeye salmon was higher than the trophic levels of pink and chum salmon in the southern stations (the Subarctic Current; 50–53°N). However, there was no difference in trophic level among these three species at the northern stations (the Alaskan Gyre; 54–56°N).

We calculated the breadth and overlap of feeding niche of sockeye and pink salmon based on the Shannon-Wiener formula and the simplified Morishita index, respectively (Table 4). The high degree of food niche overlap between sockeye and pink salmon indicates that their food niche may be the same. Sockeye salmon ate more large prey (e.g., squid) than pink salmon (Figs. 5–6). The breadth of the food niche of pink salmon was wider than that of sockeye salmon in both years, although not significantly so (U-test; $p > 0.05$).

Fig. 4. Carbon isotope ratios of Pacific salmon collected in the Gulf of Alaska (145°W) during early summer of 1999. Symbols are means for various species, bars indicate standard error. Number of samples was from one to three individuals of each species in each station.

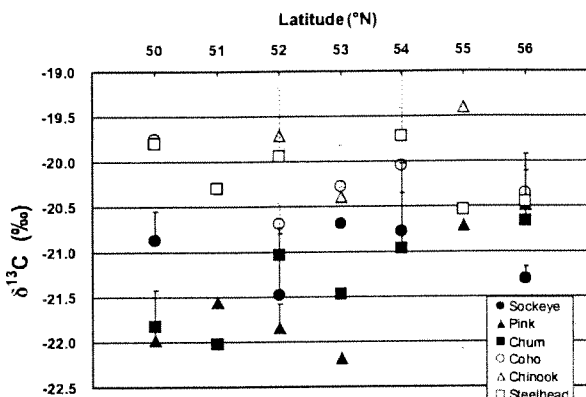


Table 4. Breadth (Shannon-Wiener index) and overlap (simplified Morishita's index) of food niche between sockeye and pink salmon in the Gulf of Alaska, 1997–1998.

Station	1997			1998		
	Overlap	Breadth		Overlap	Breadth	
		Sockeye	Pink		Sockeye	Pink
50N	-	0.719	-	0.978	0.254	0.696
51N	0.724	0.520	1.017	0.998	0.265	0.000
52N	0.895	0.838	1.034	0.682	0.580	0.887
53N	0.995	0.610	0.372	0.810	0.127	0.678
54N	0.995	0.258	0.462	0.813	1.004	1.373
55N	0.963	0.362	0.875	0.309	1.541	1.368
56N	0.827	1.019	0.936	0.783	1.344	1.071
Ave	0.900	0.618	0.783	0.768	0.731	0.868
SD	0.099	0.266	0.265	0.231	0.569	0.477

These results suggest that there is a potential for food competition between sockeye and pink salmon. Pink salmon appear to feed on more diverse prey at a lower trophic level than sockeye salmon.

The Effect of the El Niño Event on the Feeding Ecology and Growth of Sockeye and Pink Salmon

Squids, mostly *Berryteuthis anonychus*, dominated the stomach contents of sockeye salmon by both W and IRI methods in the Subarctic Current from 1994 to 1998. An exception was 1997, when squids and copepods were the most important prey. In the Alaskan Gyre, squids had the highest or second-highest percentages from 1994 to 1996 and 1998. In 1997, however, squids were rarely observed in the stomachs of sockeye salmon, and copepods were their most important prey (Fig. 5). Pink salmon also showed a similar pattern, although their diet was much more diverse (e.g., copepods, pteropods, and amphipods) than that of sockeye salmon (Fig. 6).

Fig. 5. Mean percent composition of stomach contents of sockeye salmon in the Subarctic Current (50–53°N 145°W) and the Alaskan Gyre (54–56°N 145°W) of the Gulf of Alaska during early summer from 1994 to 1998. Number of samples was from 10 to 20 individuals at each station. The mean percent composition evenly weighted for stations is shown by the volume method in 1994–1996, and by the IRI method in 1997 and 1998. EU = euphausiids, CO = copepods, AM = amphipods, DE = decapods, SQ = squids, PT = pteropods, FI = fish, PO = polychaetes, GE = gelatinous zooplankton, OT = other species.

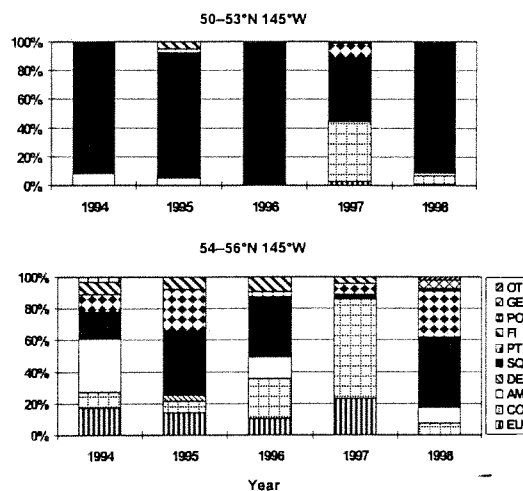
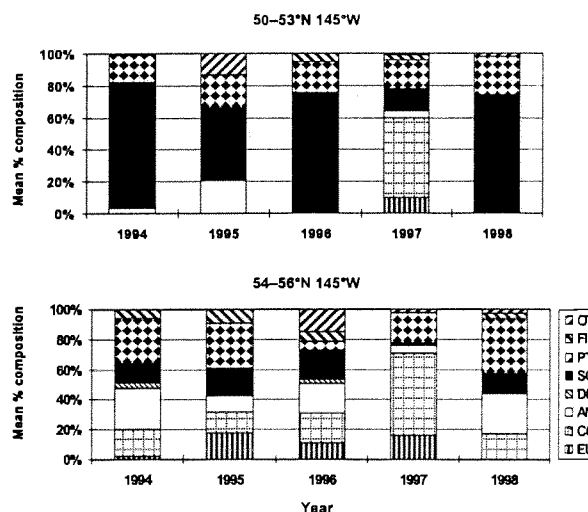


Fig. 6. Mean percent composition of stomach contents of pink salmon in the Subarctic Current (50–53°N 145°W) and the Alaskan Gyre (54–56°N 145°W) of the Gulf of Alaska during early summer from 1994 to 1998. Number of samples was from 10 to 20 individuals at each station. The mean percent composition evenly weighted for stations is shown by the volume method in 1994–1996, and by the IRI method in 1997 and 1998. EU = euphausiids, CO = copepods, AM = amphipods, DE = decapods, SQ = squids, PT = pteropods, FI = fish, OT = other species.



The degree of food niche overlap between sockeye and pink salmon was higher in 1997 than in 1998, and the breadth of food niche of both species was lower in 1997 than in 1998 although not significantly so (U-test; $p > 0.05$; Table 4).

The Gulf of Alaska was affected by the El Niño event in 1997 (Freeland 1998). In 1997, early-July mean sea surface temperature (SST: 12.4°C) was 2.5°C warmer than in the other years (Fig. 7). The caloric value of prey consumed in 1998 was higher than that in 1997, because in 1998 pink salmon fed predominately on squids which provided higher potential energy than zooplankton (Fig. 8). The body weight and condition factor of both species plus fork length for sockeye salmon were significantly higher in 1998 than in 1997 (t -test; $p < 0.05$; Table 5). Returning Bristol Bay sockeye salmon were smaller than average in 1997–1998 (Kruse 1998). Typically, smaller fish are associated with strong runs: density-dependent growth or changes in marine environmental conditions are commonly postulated as causes (Helle and Hoffman 1995). The combination of smaller body size and weak runs of Bristol Bay sockeye salmon in 1997 and 1998 implies that ocean conditions were unusually poor for growth and survival (Kruse 1998). Therefore, these results suggest that the salmonid feeding ecology in 1997 was affected by the El Niño event, which resulted in the difference in annual growth of both species.

Fig. 7. Vertical profile of seawater temperature (°C) of the surface layers in the Gulf of Alaska (145°W) in early July from 1996 to 1998.

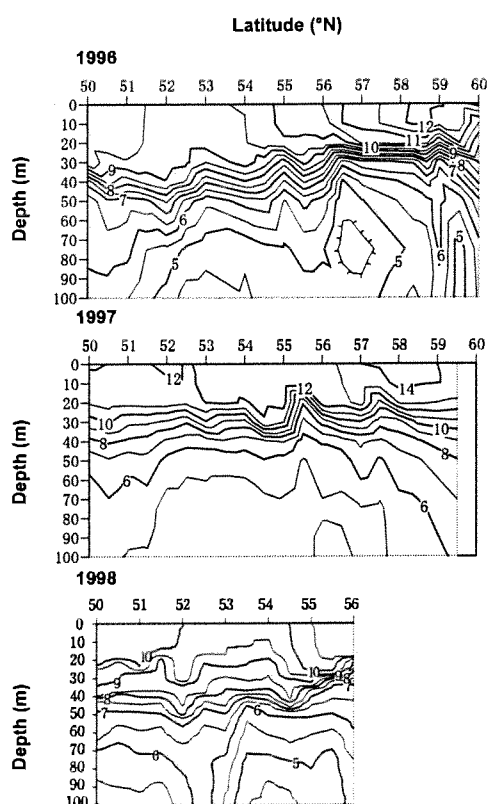


Fig. 8. Caloric value of organisms in stomach contents of pink salmon caught in the Gulf of Alaska (145°W) during early summer of 1997 and 1998. The caloric value was estimated from each prey weight in stomach contents of pink salmon using the data provided by Davis et al. (1998). EU = euphausiids, CO = copepods, AM = amphipods, SQ = squids, PT = pteropods, FI = fish, OT = other species.

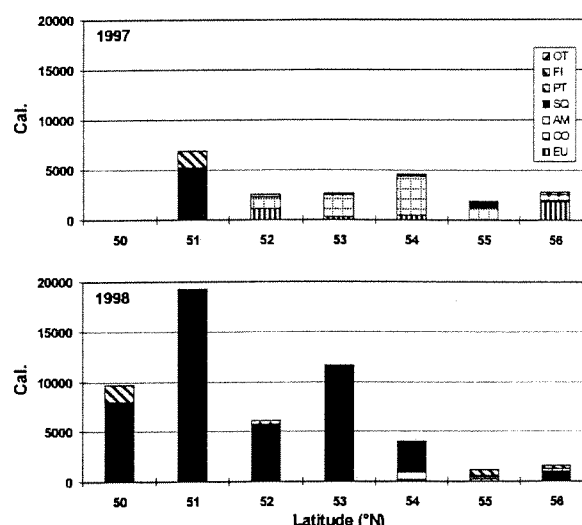


Table 5. Fork length, body weight, and condition factor of sockeye and pink salmon in the Gulf of Alaska, 1997–1998. The P indicates result of t -test comparison between 1997 and 1998 in each growth character.

and 1998 in each growth character.							
	1997			1998			P
	Mean	SD	No	Mean	SD	No	
Sockeye salmon							
Fork length (mm)	564	51	674	571	62	586	0.019
Body weight (g)	2367	667	674	2579	699	586	<0.001
Condition factor	12.9	1.5	674	13.4	1.5	586	<0.001
Pink salmon							
Fork length (mm)	480	37	228	484	29	581	0.159
Body weight (g)	1374	316	228	1433	350	581	0.023
Condition factor	12.2	0.9	228	12.4	1.4	581	0.008

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Diet Comparisons Indicate a Competitive Interaction between Ocean Age-0 Chum and Coho Salmon

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Abstract: Systematic trawl surveys were conducted within the Strait of Georgia in June/July and September of 1997 and 1998. Stomachs of 2230 coho (*Oncorhynchus kisutch*) and 1558 chum (*O. keta*) ocean age-0 salmon were analysed. A large hatchery marking program was conducted for coho but not for chum salmon allowing us to compare diets of hatchery-marked and unmarked coho. There was almost complete diet overlap between hatchery-marked and unmarked coho throughout the seasons of both years. The seasonal patterns in diet composition illustrate that in early summer chum are potential competitors of coho in the Strait of Georgia. By late summer, chum are still competitors but they begin to feed upon gelatinous zooplankton. The implications of all diet comparisons are that chum and hatchery-reared coho are competitors of non-hatchery coho during their first marine summer. In the Strait of Georgia, the catch per unit effort indicates that chum salmon is two to four times more abundant than coho. If coho final brood year strength is determined via first summer growth and winter mortality (according to the critical-size-and-critical-period hypothesis), then the high abundance of chum and the overlap in chum and coho diets could explain, at least in part, the recent increase in natural marine mortality of coho.

INTRODUCTION

In the 1990s there has been a drastic decline in the marine survival of coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia (Beamish et al. 2000a). This has led to historic low returns of wild coho resulting in restrictions in fishing effort. Beamish and Mahnken (1999) proposed that coho brood year strength is determined in two major stages. The first stage is the commonly accepted early marine, predation based, mortality (Percy 1988). The second stage is based on the concept that to survive their first winter in the ocean, juvenile coho have to obtain enough food in summer to achieve a threshold amount of growth. This 'critical-size-and-critical-period' hypothesis is based on previous work which illustrated that mortality for juvenile coho reared in net pens increased greatly within the first fall through winter period (Mahnken et al. 1983) as a function of summer food intake.

Within the Strait of Georgia, there have been climate and ocean changes in the 1990s that have been linked to behavioural changes in coho (Beamish et al. 1999). Briefly, an increase in westerly winds and an increase in Fraser River discharge, led to changes in the estuarine circulation resulting in lower salinities and higher sea levels. Changes in estuarine

circulation have implications for nitrate entrainment and primary productivity (St. John et al. 1993; Yin et al. 1997a, 1997b). These regional ecosystem changes were associated with changes in climate conditions in the North Pacific. Changes in oceanic conditions, such as those observed in the Strait of Georgia in the 1990s (Beamish et al. 1999), could affect the carrying capacity for coho. According to the critical-size-and-critical-period hypothesis, reduced first summer marine growth and increased mortality results from reduced food availability or increased intra- and inter-specific competition or both. Higher abundance of competitors relative to coho abundance increases competition. Within the Strait of Georgia large numbers of chum salmon (*O. keta*) are released by hatcheries providing a potential source of increased inter-specific competition. More obviously, hatchery released coho are sources of increased intraspecific competition for non-hatchery (wild) coho.

To the best of our knowledge, previous studies on juvenile coho or chum salmon diet composition have focused on fish that have survived their first ocean winter (i.e. ages greater than ocean age 0) and not on the early marine phase. Brodeur and Percy (1990) compared the diets of ocean age-0 coho, chinook (*O. tshawytscha*), chum and sockeye (*O. nerka*) caught off Oregon and Washington in 1980–1985.

Unfortunately large-scale marking programs were not used by hatcheries during the 1980s and Brodeur and Pearcy (1990) were unable to compare diets between hatchery and non-hatchery coho. In the 1980s, coho marine survival was average and, on the basis of the critical-size-and-critical-period hypothesis, little intra- or inter-specific competition during the early marine phase would be expected. Brodeur and Pearcy (1990) observed low diet overlap among coho, chinook, chum and sockeye at the lowest taxonomic levels, but observed some similarities in major prey groups. Coho and chinook consumed teleosts and large zooplankton; and chum and sockeye had more diverse diets of smaller zooplankton. Similar observations were made by Landingham et al. (1998) for ocean age-0 salmon caught in southeastern Alaskan marine waters in 1983 and 1984. Within British Columbian waters Perry et al. (1996) investigated the diet of ocean age-0 chum salmon (and pink—*O. gorbuscha*) off the west coast of Vancouver Island during a single cruise in 1992. They did not compare chum (or pink) diets to coho, and their sample size for chum stomachs was small ($n = 261$), but they reported that chum mainly consumed larvaceans, euphausiids and calanoid copepods.

Given the recent declines in coho marine survival and the continued release of large numbers of hatchery coho and chum salmon into the Strait of Georgia during the 1990s, we decided to examine the diet composition of coho and chum salmon during their early marine phase to determine if there was potential intra- and inter-specific competition for food. Recent large-scale hatchery marking programs for coho salmon made diet comparisons between hatchery-marked and unmarked coho possible. Unfortunately, hatchery-reared chum were not marked. Our trawl surveys conducted in the Strait of Georgia provided large sample sizes ($n > 1000$) of ocean age-0 coho and chum salmon sufficient for diet overlap investigations. Here we report on the diet analyses conducted during surveys in the early- and late-summers of 1997 and 1998 for ocean age-0 coho and chum salmon caught throughout the Strait of Georgia.

METHODS

Fish Collection

Four trawl surveys were conducted in June/July and September, 1997 and 1998, aboard the R/V *W. E. Ricker* (June 17–July 10, 1997, September 8–27, 1997, June 22–July 15, 1998, and September 8–16, 1998). Mechanical failure of the *W. E. Ricker* in September 1997, necessitated use of the fishing vessel *Frosti* to finish the survey (September 19–27). Beamish et al. (2000b) compared catch per unit effort

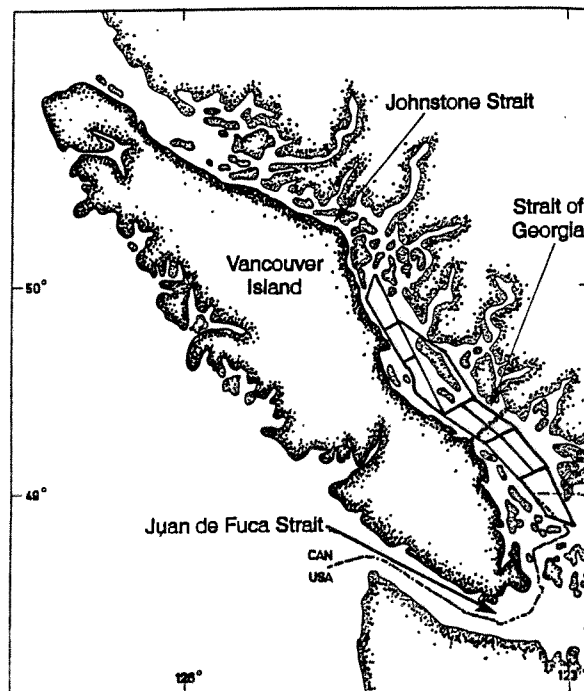
between the two vessels and did not determine any significant differences. A midwater rope trawl (model 250/350/14) built by Cantrawl Pacific Limited, Richmond, B.C., was fished at a towing speed of approximately 5 knots. The net was held open with Model P USA Jet Doors that can be fished at the surface or any depth. The opening of the net was approximately 14 m deep by 30 m wide, and was estimated using a backwards-looking net sounder (Simrad FS3300). The net was towed approximately 3 boat lengths (180 m) from the stern. Specifications on the gear are outlined in Beamish et al. (2000b).

The ocean age-0 salmon used in this diet study were collected as part of a juvenile salmon abundance survey conducted throughout the Strait of Georgia (Fig. 1). Beamish et al. (2000b) provide details on the survey and sampling design. Briefly, fishing was conducted along track lines that formed a gridlike pattern and provided coverage for virtually all of the strait (Fig. 1). The first set of every day was always a surface tow, but thereafter sets were fished at randomly determined depths at the surface and at intervals of 15 m. Most salmon ($> 80\%$) were caught within the top 45 m, so catch per unit effort of each survey was expressed for all depths fished and for sets between 0–45 m.

Stomach Analyses

All diet analyses were conducted onboard from a random subsample of each catch. The forklength of each fish was measured to the nearest millimeter (mm) and weights to the nearest gram (g) were mea-

Fig. 1 Survey track lines throughout the Strait of Georgia.



sured when sea conditions permitted. Condition factor ($\text{g}\cdot\text{cm}^{-3}$) was calculated using available weight and forklengths. The cardiac and pyloric portions of each stomach were removed and the total volume of contents was estimated to the nearest 0.1 cc. The contents were flushed into a petrie dish in order to identify prey items. When necessary, 10x magnification was used to determine prey composition. Rather than count individual prey items, the relative contribution of a prey item to the overall stomach contents was estimated as a percentage of the total volume. This differs from the traditional numerical percentage approach to estimating the percentage ratio of contents, but it does allow for substantially more stomachs to be analysed. Prey were identified to the lowest taxonomic group possible, usually to order in invertebrates and to species in teleosts. The percentage of stomachs with each specific prey group was calculated for each survey for coho and chum. Prey were combined into major groups if overall that combination occurred in at least 3 surveys and in 5 % of the stomachs at least once. If prey groups did not meet this criterion, they were classed as "other". As we were interested in comparing coho and chum diets, we compiled a composite list of major prey groups for both species. We were also interested in comparing hatchery and non-hatchery coho diets, so the coho stomachs were reanalysed using these two categories. Empty stomachs were defined as containing less than 0.1 cc of all contents.

Diet Composition and Overlap

Any unidentifiable material resulting from excessive digestion was excluded from analysis. We used three measures of importance for each of the major prey groups of coho and chum salmon. Percent frequency of occurrence (%F.O.) was the percentage of stomachs containing at least one prey item. The proportion of contents importance (%C) was the average percentage of the individual volume of stomach contents that were made up of a prey group. The total volume importance (%V) was the percentage ratio of the total volume of the prey item consumed by all fish to the total volume of all prey items consumed by all fish. Pinkas et al. (1971) introduced the Index Relative Importance (IRI) which is calculated as a linear combination of a prey's numerical importance, volumetric importance and frequency of occurrence. We did not count individual prey items for calculating numeric importance and were unable to calculate IRI according to Pinkas et al. (1971). However, we used a modified index of relative importance (RI) such that;

$$RI = \%F.O. \times (\%C + \%V) \quad (1)$$

Both indices (IRI and RI) relate how much of a prey item an individual fish eats, how many fish eat that prey item and, overall, how much that prey contributes to the total amount of food consumed by all fish examined. Similar to IRI (Pinkas et al. 1971), RI also ranges from zero, when a prey item is not present at all, to 20,000 when a prey item is consumed as a monodiet (i.e. %F.O., %C and %V all measure 100%). We expressed RI as a percentage (%RI) for easier comparison of relative prey item importance and used three-way graphs to indicate which measures of diet (%F.O., %C or %V) were most influential in the determination of %RI. Cortés (1997) proposed that the percent index of relative importance and three-dimensional graphical representations of the diet measures used to calculate the index be used as standardized measures in dietary analyses.

To estimate diet overlap between coho and chum, we calculated the Morisita-Horn index of overlap (Horn 1966);

$$O = \frac{2 \sum_i^n p_{ij} p_{ik}}{\sum_i^n p^2_{ij} + \sum_i^n p^2_{ik}} \quad (2)$$

where n = total number of prey item groups

p_{ij} = proportion of prey item used by coho

p_{ik} = proportion of prey item used by chum

The Morisita-Horn index was calculated separately for total volume importance (%V) and index of relative importance (%RI) as the measurements of proportion of prey items. The overlap index varies between 0 (no overlap) and 1.0 (complete overlap). We considered values ≥ 0.6 to reflect significant overlap. We used %V since it reflects an overall contribution and is not influenced by small prey items unless they are consumed often and in large quantities. We used the %RI since it is a composite measurement that provides an integrated expression of diet.

Hatchery-marked vs. Unmarked Coho

In 1997 and 1998, approximately 50 and 60% respectively of coho released from hatcheries into the Strait of Georgia were marked by a fin clip or by a coded wire tag insertion (Beamish et al. 1998). In order to identify potential intra-specific competition between hatchery and non-hatchery coho, the three measures of prey importance (%F.O., %C and %V) along with the corresponding %RI were calculated for hatchery-marked and for unmarked coho as above. The Morisita-Horn index of overlap was also calculated to measure overlap between hatchery-marked and unmarked coho diets.

RESULTS

A total of 2,230 coho stomachs and 1,558 chum stomachs were examined. The catch per unit effort within the top 45 m for chum was approximately two to four times higher than that for coho (Table 1). For coho, condition in early-summer 1998 and late-summer 1997, 1998 were similar, but in early-summer 1997 was lower than in the other three periods (ANOVA $F = 3.61$, $p = 0.01$, Table 1). The condition of chum in early-summer 1998 was higher than in early-summer 1997, and condition in both years increased by late-summer though was not different between years (ANOVA $F = 15.95$, $p < 0.0001$, Table 1). Coho were always larger and in better condition (ANOVA $F = 23.52$, $p < 0.0001$) than chum.

The mean percentage of coho stomachs containing prey items was 87.7% with survey percentages ranging from 76.9 (late-summer 1998) to 95.1% (late-summer 1997). Generally, the percentage of stomachs containing prey items in late summer was lower

than in early summer. The opposite was true for chum, though there was less variability across surveys. The mean percentage of chum stomachs containing prey items was 86.9% with a range of 83.2% in early-summer 1997 to 90.6% in late-summer 1998. In each survey, at least 85% of all the coho and chum stomachs examined contained identifiable prey items. The stomachs of chum in early-summer 1997 were an exception since the percentage was 75.9%. The main focus during that survey was coho salmon, so chum stomachs were not processed quickly. The mean volume (cc) contained in stomachs was always higher in coho than in chum (Table 1).

The most frequently occurring prey items in coho stomachs were amphipods (gammarids and hyperiids), decapods, euphausiids and teleosts—primarily sandlance (*Ammodytes hexapterus*) and herring (*Clupea harengus*) (Table 2). For chum, the predominant prey items were chaetognaths, calanoid copepods, hyperiid amphipods, decapods, euphausiids and ctenophores (Table 3).

Table 1. Summaries for each survey. For each species, the total number of sets in which that species was caught, the total number caught, the catch per unit effort (CPUE) for all sets (and sets between 0–45 m only), and the total number of stomachs examined are denoted by survey. Based on the number of stomachs examined, the percentage of stomachs containing prey items and the percentage of stomachs containing items that were identifiable are listed. For all fish whose stomachs were examined, fork-length, weight and condition factor are also listed.

	Survey Date			
	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
Number of sets	69	128	85	95
COHO SALMON				
Number of sets with species	31	98	57	73
Number caught	524	2277	1235	1326
CPUE all depths	14	37	28	29
(0–45 m)	(19)	(44)	(43)	(35)
Number of stomachs examined	272	652	573	733
Percentage of stomachs with prey items	94.5	84.1	95.1	76.9
Percentage of stomachs with identifiable items	98.9	91.1	100.0	98.4
Mean (stdev) volume (cm ³) in stomachs examined	1.10 (1.43)	1.22 (2.91)	0.99 (1.39)	1.52 (3.33)
Mean (stdev) forklength (mm) of fish examined	166 (31)	246 (23)	180 (24)	242 (34)
Mean (stdev) weight (g) of fish examined	64 (33)	175 (50)	74 (38)	181 (77)
Mean (stdev) condition factor ($\times 10^2$) of fish examined	1.14 (0.19)	1.22 (0.45)	1.19 (0.14)	1.22 (0.21)
CHUM SALMON				
Number of sets with species	37	78	43	68
Number caught	1086	4869	4804	3789
CPUE	28	78	105	82
(0–45 m)	(41)	(93)	(160)	(101)
Number of stomachs examined	191	260	408	699
Percentage of stomachs with prey items	83.2	85.4	88.2	90.6
Percentage of stomachs with identifiable items	75.9	86.9	98.8	93.0
Mean (stdev) volume (cm ³) in stomachs examined	0.16 (0.35)	0.37 (0.53)	0.26 (0.31)	0.74 (0.88)
Mean (stdev) forklength (mm) of fish examined	121 (26)	191 (25)	126 (15)	186 (15)
Mean (stdev) weight (g) of fish examined	20 (14)	76 (27)	21 (8)	73 (15)
Mean (stdev) condition factor ($\times 10^1$) of fish examined	0.92 (0.21)	1.13 (0.17)	1.01 (0.11)	1.15 (0.45)

Table 2. The percentage of coho salmon stomachs containing specific prey items. Parentheses are used to denote the lowest taxon group identified. Bold denotes phylum or subphylum of invertebrates. Teleosts were identified to species (in parentheses) except for the family Agonidae and for larval fish.

	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
Annelida				
(Hirudinea)		0.15		
Arthropoda				
(Insecta)	0.74	5.37	0.87	0.68
(Chaetognatha)			0.17	0.82
Tunicata				
(Oikopleuridae)				0.27
Crustacea				
(Cirripedia)				0.41
Copepoda				
(Calanoida)		2.61	2.44	1.64
(Harpacticoida)			0.17	
Amphipoda	1.47 undesignated			1.23 undesignated
(Gammaridea)	1.47	19.94	2.62	25.51
(Hyperidea)	2.21	27.61	45.90	50.34
(Decapoda)	72.79	11.04	82.02	13.37
(Euphausiacea)	7.72	43.40	27.75	31.24
(Ostracoda)				0.14
(Mysidacea)				0.82
(Ctenophora)		0.15		
Mollusca				
Cephalapoda				
(Octopoda)	0.36			0.14
(Teuthoidea)			0.17	
Gastropoda				
(Opisthobranchia)				0.27
Unidentified invertebrate		0.46		0.27
Teleosts				
(Agonidae)		0.15		
Ammodytidae				
(<i>Ammodytes hexapterus</i>)	15.07	0.31	3.14	0.55
Clupeidae				
(<i>Alosa sapidissima</i>)			0.17	
(<i>Clupea harengus</i>)	10.07	3.53	8.38	3.27
Embiotocidae				
(<i>Cymatogaster aggregata</i>)				0.14
Gadidae				
(<i>Merluccius productus</i>)				0.14
Salmonidae				
(<i>Oncorhynchus nerka</i>)		0.15		
(<i>O. tshawytscha</i>)		0.31		
Larval fish	2.21		0.70	
Unidentified fish	6.25	7.06	8.55	2.86

Table 3. The percentage of chum salmon stomachs containing specific prey items. Parentheses are used to denote the lowest taxon group identified. Bold denotes phylum or subphylum of invertebrates. Teleosts were identified to species (in parentheses) except for larval fish.

	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
Annelida				
(Polychaeta)			0.25	6.01
Arthropoda				
(Insecta)	2.56	0.77		
(Chaetognatha)		2.69	20.10	7.87
Tunicata				
(Oikopleuridae)			9.80	2.00
Cnidaria				
(Scyphozoa)	2.56	2.69		1.00
Crustacea				
(Cirripedia)				0.14
Copepoda				
(Calanoida)	2.56	6.54	10.54	3.29
(Cyclopoida)		0.38		
(Harpacticoida)			0.25	
Amphipoda				
(Gammaridea)		1.92		1.14
(Hyperidea)	15.90	42.69	67.65	49.07
(Decapoda)	28.21	5.38	19.36	2.58
(Euphausiacea)	7.69	18.07	20.34	9.87
(Ostracoda)			0.25	
(Mysidacea)				

continued...

Table 3. continued.

	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
(Ctenophora)		36.15	3.92	47.78
Mollusca				
Gastropoda				
(Opisthobranchia)		1.92		2.43
Unidentified invertebrate				0.14
Teleosts				
Ammodytidae				
(<i>Ammodytes hexapterus</i>)	0.51			
Clupeidae				
(<i>Clupea harengus</i>)	8.72	0.38	0.98	0.14
Larval fish	2.05	3.15		
Unidentified fish	4.10		0.25	

Early-summer 1997

In the early-summer of 1997, the top three important prey items for coho, as measured by %RI, were decapods, teleosts and euphausiids (Fig. 2A). Important prey items for chum were decapods, teleosts and amphipods (Fig. 2B). The relative importance of decapods in coho was influenced by both %V and %C, while the decapod relative importance in chum was mainly influenced by %C (Fig. 2B). Amphipod %RI in chum diets was influenced by %F.O. and %C (Fig. 2B). The diet overlap between coho and chum in early-summer 1997 was large i.e. approximately 0.8 (Fig. 3).

Late-summer 1997

In September 1997, the top three important prey items for coho were euphausiids, amphipods and teleosts (Fig. 4A). The relative importance of amphipods was primarily influenced by %F.O. and %C. Ctenophores replaced teleosts as important prey items for chum and the order of the top three important prey items was slightly different than for coho: amphipods, ctenophores and euphausiids (Fig. 4B). Unlike that for coho, the relative importance of amphipods was influenced by %F.O., %C and %V. The diet overlap measured by %V was moderate, though overlap measured by %RI was greater than 0.6 (Fig. 3).

Early-summer 1998

Generally, coho diet was less varied than chum (Fig. 5A). Two different prey items dominated the diet of coho and chum with decapods largely important for coho and amphipods largely important for chum (Fig. 5B). The relative importance in both cases was influenced by all three diet measurements (Fig. 5). Unlike early-summer of the previous year, teleosts were not a major component of chum diet. The overlap in coho and chum diets was very small i.e. < 0.3 (Fig. 3).

Fig. 2. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in early-summer 1997. The area contained within each prey item box represents the index of relative importance (i.e. %F.O. (%C + %V)).

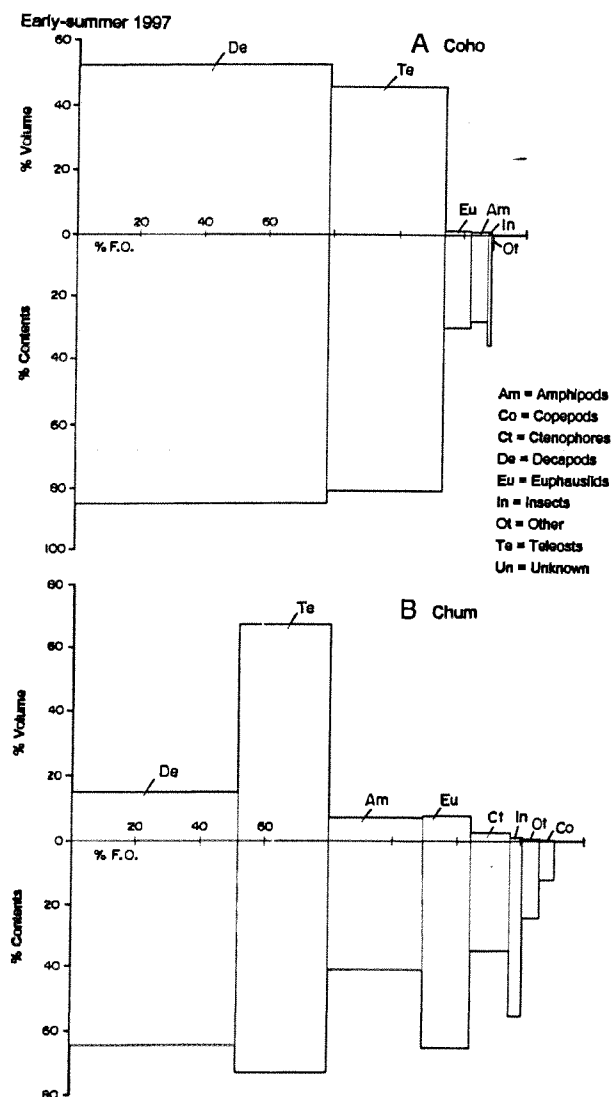


Fig. 3 Coho and chum diet overlap measured by the Morisita-Horn Index for proportion of total volume (vertical stripes) and for percentage index of Relative Importance (horizontal stripes). An overlap index value greater than 0.60 is generally considered to reflect significant overlap.

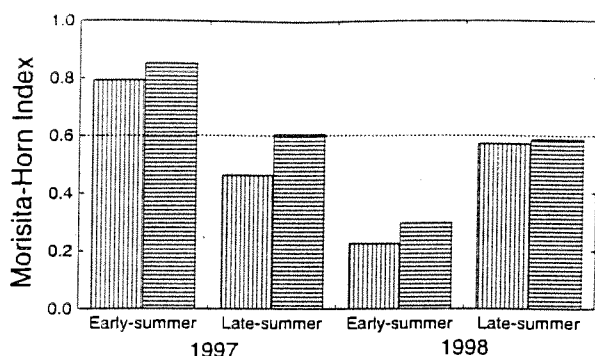


Fig. 4. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in late-summer 1997. The area contained within each prey item box represents the index of relative importance.

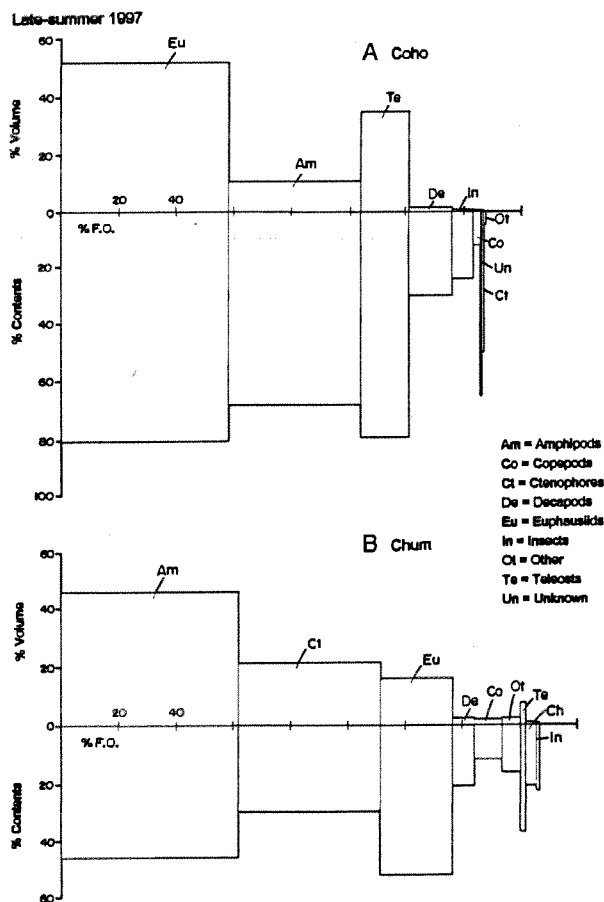
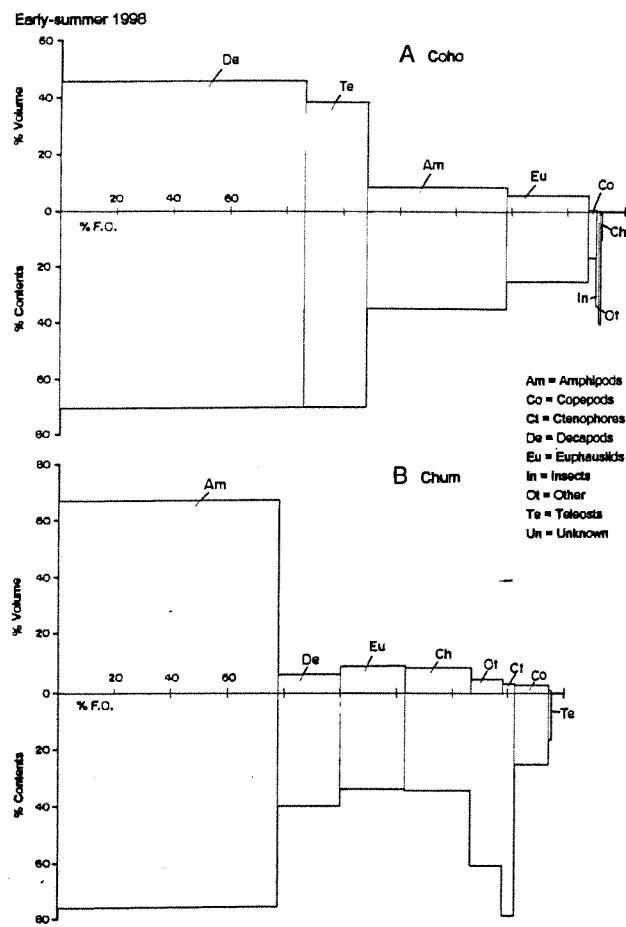


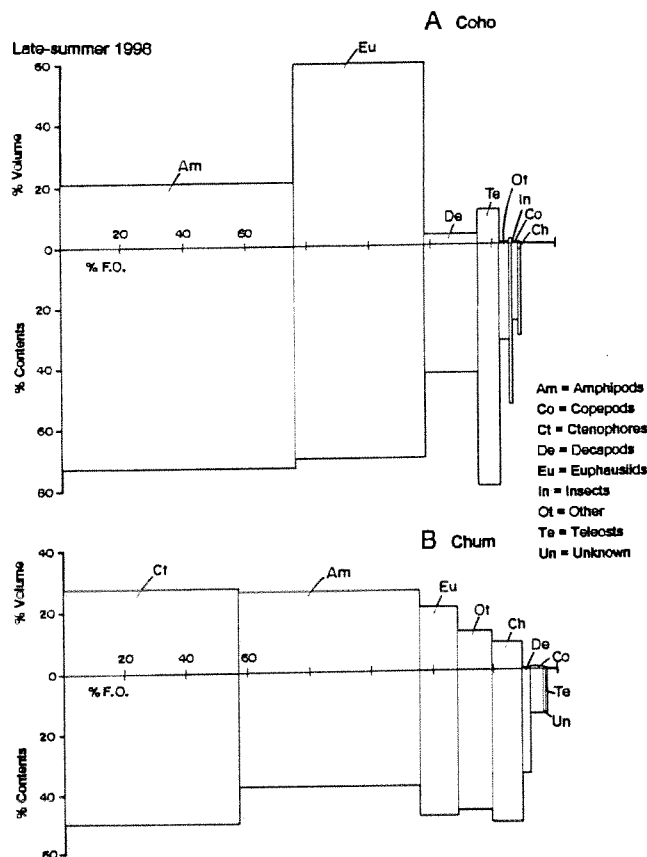
Fig. 5. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in early-summer 1998. The area contained within each prey item box represents the index of relative importance.



Late-summer 1998

For coho, the top three prey items in late-summer 1998 were amphipods, euphausiids and decapods (Fig. 6A), %C influenced the %RI values for amphipod and decapod prey groups. The higher %F.O. for decapods gave this prey group a higher %RI than teleosts which had a high %C. For chum, ctenophores, amphipods and euphausiids were the top three prey items, though chaetognaths and other prey were closely matched to euphausiids (Fig. 6). The %RIs of these prey groups were influenced by all three diet importance measurements. The overlap between chum and coho was only slightly lower than 0.60 (Fig. 3).

Fig. 6. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in late-summer 1998. The area contained within each prey item box represents the index of relative importance.



Hatchery vs. Non-hatchery Marked Coho

There were no differences between length, weight or mean volume consumed of hatchery-marked or unmarked coho except for late-summer 1998 when hatchery-marked coho were longer (ANOVA $F = 463.73$, $p < 0.0001$) and heavier (ANOVA $F = 205.08$, $p < 0.0001$) than unmarked coho (Table 4). Despite these differences in length and weight, there was no difference in condition factor between hatchery-marked and unmarked coho during any of the surveys (ANOVA $F = 1.62$, $p = 0.12$, Table 4).

For all four surveys, the top three prey items for hatchery-marked and unmarked coho were the same as those identified above for all coho. There were no differences between the rankings of all prey items based on %RI. The overlap in diet between marked and unmarked coho was close to complete for all four surveys (Fig. 7).

DISCUSSION

The major items in the diet of coho were similar in the early-summer of 1997 and 1998 and there was a general similarity in the diets in the late-summer, although the percentages differed slightly. Chum diets varied between years for the early-summer, with teleosts important in 1997 and not important in 1998. Chum switched to ctenophores in late-summer. The early-summer 1997 diet comparison between coho and chum showed that diet overlap can be quite high. The early-summer 1998 diet comparison illustrates that diet overlap can also be quite low. This implies that potential interspecific competition may at times also be high or low. Changes in oceanic conditions and carrying capacity or changes in relative abundance of competitors might alter the degree of diet overlap and competition in different seasons and years.

Diet composition studies from previous decades or on salmon older than ocean age 0, have shown that coho are mainly piscivorous and that chum feed mainly on small zooplankton and gelatinous zooplankton (Brodeur and Percy 1990; Perry et al. 1996; Tadokoro et al. 1996; Landingham et al. 1998). We have illustrated that chum may not begin feeding on gelatinous zooplankton until late in their first ocean summer. More importantly, we have illustrated that some major prey of chum, such as teleosts, are similar to coho. Possibly the presence of particular prey items in a diet (e.g. teleosts in chum diets) is an indication of a lower availability of preferred prey items.

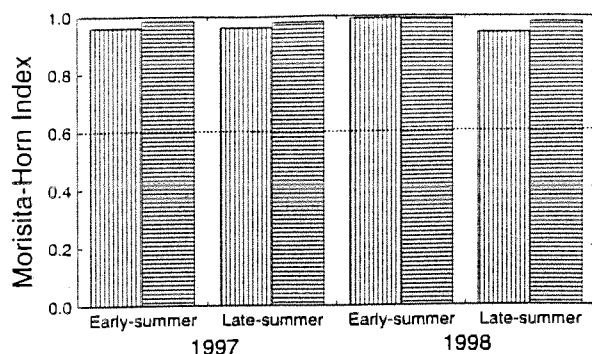
Hatchery released coho are likely strong competitors for non-hatchery coho in the Strait of Georgia. Our analysis here compared hatchery marked vs. unmarked fish, which does mean that hatchery-reared (but not marked) fish are likely included in the unmarked category. However, given the strong indication of diet overlap, it is likely that hatchery coho and non-hatchery coho diets are very similar. This has obvious implications for wild coho survival during periods when marine carrying capacity is low and the production of hatchery coho entering the ocean is higher than wild coho production.

Brodeur and Percy (1990) and Landingham et al. (1998) noted that larval and juvenile teleosts were present (but not dominant) in chum diets. Here, the diet overlap between chum and coho in early-summer 1997 was influenced by the dominance of teleosts (herring and larval fish) in the chum diet. In early-summer of the following year, teleosts were not dominant in chum diet and overlap with coho was low. In late-summer (1997 and 1998), diet overlap was moderate and influenced by the dominance of euphausiids and amphipods in both species' diet in both years. Though coho consumed gammariid am-

Table 4. Summaries for hatchery-marked (Mark.) and unmarked (Un.) coho caught and examined in each survey. Based on the number of stomachs examined, the percentage of stomachs containing prey items and the percentage of stomachs containing items that were identifiable are listed. For all fish whose stomachs were examined, forklengths, weights and condition factors are also listed.

	Survey Date							
	1997				1998			
	Early-summer	Late-summer	Early-summer	Late-summer	Early-summer	Late-summer	Early-summer	Late-summer
	Mark.	Un.	Mark.	Un.	Mark.	Un.	Mark.	Un.
Number of stomachs examined	94	178	238	414	220	353	300	433
Percentage of stomachs with prey items	93.6	94.9	85.7	82.1	96.4	94.3	76.7	77.1
Percentage of stomachs with identifiable items	98.9	98.9	92.0	91.8	100.0	100.0	99.3	97.7
Mean (stdev) volume (cc) in stomachs examined	1.07 (1.38)	1.12 (1.47)	1.36 (3.81)	1.15 (2.24)	0.94 (1.20)	1.02 (1.50)	1.68 (3.50)	1.41 (3.20)
Mean (stdev) forklength (mm) of fish examined	162 (16)	169 (37)	247 (20)	246 (25)	179 (19)	180 (27)	249 (34)	237 (32)
Mean (stdev) weight (g) of fish examined	58 (18)	68 (39)	179 (53)	173 (49)	70 (25)	76 (44)	192 (70)	173 (81)
Mean (stdev) condition factor ($\times 10^{-1}$) of fish examined	1.12 (0.16)	1.15 (0.20)	1.22 (0.45)	1.22 (0.45)	1.18 (0.13)	1.19 (0.13)	1.22 (0.30)	1.22 (0.10)

Fig. 7 Hatchery-marked and unmarked coho diet overlap measured by the Morisita-Horn Index for proportion of total volume (vertical stripes) and for percentage index of Relative Importance (horizontal stripes). An overlap index value greater than 0.60 is generally considered to reflect significant overlap.



phipods, hyperiid amphipods were more common in coho and chum diets.

Our trawl survey allowed us to examine a large number of stomachs collected throughout the Strait of Georgia. We therefore, do not believe that our results were strongly biased by the sampling program. The exclusion of fish with empty stomachs and digested matter from diet analyses likely did not strongly bias the results since small percentages of stomachs were empty or contained digested matter.

The results presented here do support the hypothesis that diet overlap could have biological consequences if food resources were limited. In early-summer 1997 when diet overlap between coho and chum was high, the condition of coho was significantly lower than in early-summer 1998 when diet overlap was low. While the mean volume of prey consumed by chum is far lower than that consumed by coho, the catch per unit effort of chum is 2 to 4 times higher than that for coho. In early-summer

1998, overlap was low and coho condition was better than the previous year. Beamish and Folkes (1996) noted that in the 1990s, chum salmon within the Strait of Georgia appeared to remain within the ecosystem later in the year than in previous decades. In addition to the diet similarities and the large abundance of chum, the longer residence in the strait may increase competition. During the 1990s, changes in the Strait of Georgia ecosystem, carrying capacity and behaviour of chum, coupled with continued high release of hatchery-reared chum, may have resulted in increased inter-specific competition for coho. The critical-size-and-critical-period hypothesis suggests that inter-specific competition can partially account for the observed decline in coho marine survival if competition reduces the growth of an increasing number of coho such that their size is below the minimum size required to survive the first marine winter. The overlap in the diets of coho and chum during the summer growth period, and the higher abundance of chum compared to coho, is evidence (if the critical-size-and-critical-period hypothesis is valid) that chum juveniles could contribute to the marine mortality of coho.

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Density-Dependence of Chum Salmon in Coastal Waters of the Japan Sea

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Abstract: To investigate factors regulating abundance of hatchery-reared chum salmon (*Oncorhynchus keta*), we examined survival, distribution, and nutritional condition of juveniles in the coastal waters of the Japan Sea. Over the past 10 years, the number of returning chum adults has fluctuated around 600,000 along the coast of Honshu. Survival during ocean life correlated negatively with the number of released juveniles and sea surface temperatures in coastal waters. To investigate factors affecting nutritional condition of juveniles, we collected chum salmon juveniles off Yamagata, Honshu, in March–May from 1994 to 1996. When density of juveniles increased the weight of their stomach contents decreased, indicating a negative effect of chum abundance on prey organisms. Results indicate that a restricted nursery area intensifies 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, Japan.

INTRODUCTION

Anadromous Pacific salmon (*Oncorhynchus* spp.) migrate between freshwater habitats and the ocean. Smolts are vulnerable to high mortality soon after they enter the sea (Pearcy 1992). In some salmon stocks, year-class strength is determined in early ocean life (Hartt 1980; Pearcy 1992). Hatchery-reared chum salmon (*O. keta*) reach the sea within several days after release in a river (Mayama et al. 1982; Kaeriyama 1986). During early sea life, chum salmon suffer high mortality (Bax 1983), and distribution is limited to coastal waters (Fukuwaka and Suzuki 1998a; see review by Salo 1991). Biotic and abiotic environments in coastal waters may be influenced by drainage from the land, tidal action, or human activity, and may change temporally and spatially.

The survival of hatchery-reared Pacific salmon is often depressed in southern regions of a species' distribution (Mahnken et al. 1998). In Japan, most chum salmon populations are sustained by hatcheries. In the last 20 years, an inverse density-dependence has been observed between the number of juvenile chum salmon released and the number of adults returning (McNeil 1991). However, on the Japan Sea coast (western coast of Honshu), ocean survival is lower than on the Pacific side (eastern coast) of Japan,

which is a serious problem for Japan's salmon enhancement program.

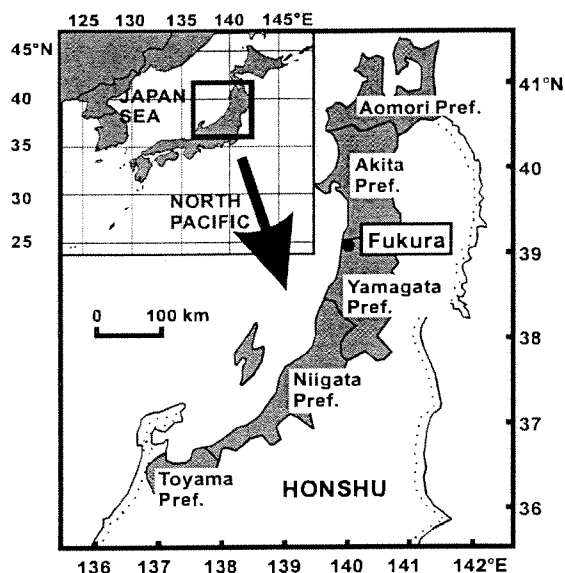
For ocean management of hatchery-reared salmon, factors depressing their survival need understanding. Thus, the objectives of this study are: 1) to test for density-dependence in ocean survival, 2) to identify environmental factors affecting ocean survival, and 3) to hypothesize the regulatory mechanisms of hatchery-reared adult chum salmon along the Japan Sea coast.

MATERIALS AND METHODS

Study Area

The coastal waters of the Japan Sea off Honshu, Japan, are near the southern limit of chum salmon distribution in the western North Pacific (Salo 1991). On this coast, the geographical range of industrial hatchery production of chum salmon extends from the Aomori Prefecture to the Toyama Prefecture (Fig. 1). The northern areas of the coast are characterized by open sand beaches and narrow estuaries at river mouths (Coastal Oceanography Research Committee, Oceanographical Society of Japan 1985). The coastal waters of the Japan Sea are strongly affected by the Tsushima Current. Currents generated by tides are relatively small. The Tsushima Current is

Fig. 1. Map of study site. Solid shaded area indicates prefectures along the Japan Sea coast of Honshu, Japan, where chum salmon juveniles are produced in hatcheries.



characterized by a high temperature (minimum 8°C at 100 m depth) and high salinity (> 34.1 psu) water mass flowing northward along the continental shelf (Kawabe 1982). River discharges increase in the spring due to snow melt; these discharges result in freshwater plumes in nearshore regions (Coastal Oceanography Research Committee, Oceanographical Society of Japan 1985) and these plumes are the chief habitat of juvenile chum salmon (Fukuwaka and Suzuki 1998a).

Abundance and Survival

The number of released chum salmon juveniles, the number of adults caught in rivers, and the number of adults caught in coastal waters were provided by the National Salmon Resources Center (NSRC 1998a, b, 1999a, b) (formerly the Hokkaido Salmon Hatchery: HSH 1993–1997) and the Fisheries Agency of Japan (FAJ) (Honshu Keison Zousyoku Shinkoukai 1991) in 1970–1998. The age composition of adults caught in rivers was provided by NSRC and FAJ (HSH 1972–1995, NSRC 1999a). The number of returning adults was equivalent to the sum of the numbers of adults caught in rivers and in coastal waters. The number of adults in each year-class was determined by the age composition. For 1992–1998 year-classes, we cannot calculate numbers of adults completely, because age at maturity of chum salmon ranges from 2–6 years.

To evaluate effects of numbers of released juveniles and coastal environmental variables on ocean survival, we used step-wise multiple regression ($p \leq 0.05$ to add and $p \geq 0.10$ to remove; Sokal and Rohlf

1995). The significance of the regression coefficient was tested using the t -test. The survival rate through the entire ocean life was calculated using the equation: $S_i = A_i / J_i$, where S_i is the survival rate of the i -th year-class, A_i is the number of returning adults in the i -th year-class, and J_i is the number of released juveniles in the i -th year-class. The survival rate and the number of released juveniles used in the analysis were log-transformed.

As coastal environmental variables, we used sea surface temperature (SST) and salinity within 50 km off the Niigata Prefecture and Yamagata Prefecture in early May, because the spatial distribution of chum salmon juveniles was restricted within coastal waters (Fukuwaka and Suzuki 1998a). In early May, SST reached near the upper limit of distribution of juvenile chum salmon and river plumes extended to off-shore (Fukuwaka and Suzuki 1998a). SST and salinity data were provided by the Niigata Prefectural Fisheries Experimental Station (1970–1983, 1970–1997) and the Yamagata Prefectural Fisheries Experimental Station (1985, 1993).

Nutritional Condition of Juveniles

We set a line transect from the mouth of the Gakko River to the southern edge of Tobishima Island off Fukura, Yamagata Prefecture, Japan (Fukuwaka and Suzuki 1998a). The shoreline of the southern area of the river mouth is an open sandy beach and the northern area is a rocky shore. We placed five sampling stations along the line transect at 2, 5, 10, 15, and 20 km from shore. At these stations, water depth was 10 to 200 m.

At all sampling stations from March to May in 1994 to 1996, we collected chum salmon juveniles with surface trawls, zooplankton with a modified NORPAC net, and we simultaneously measured water temperature and salinity using a CTD (Fukuwaka and Suzuki 1998a; Suzuki and Fukuwaka 1998). Surface trawls were towed at ca 4 km·h⁻¹ by 2 vessels trawling parallel to the shoreline in one set of 30 minutes, or three sets of 15 minutes at each station. The net was 8 m wide and 4 m deep at the mouth and equipped with 25 to 34 mm stretched mesh in the body and 7.5 mm mesh in the cod end. Catch per unit effort (CPUE) was calculated as number of collected juveniles per 30 minutes net trawl. Collected juveniles were fixed in 10% buffered formalin. Fork length of juveniles was measured to the nearest 0.01 mm and body weight was measured to the nearest 0.001 g. Stomach content weight of juveniles was measured to the nearest 0.001 g for 30 specimens at each station (Suzuki and Fukuwaka 1998).

The condition factor was used to evaluate fish condition: $CF = BW / FL^3 \cdot 10^6$, where CF is the condition factor, BW is the body weight of juveniles, and FL is the fork length. Relative stomach content

weight was used as an index of stomach fullness: $RSC = SCW / BW \cdot 10^2$, where RSC is the relative stomach content weight, SCW is the stomach content weight, and BW is the body weight.

To estimate prey abundance, a modified NORPAC net with a flow meter was towed vertically from the bottom or, at deeper stations, 20 m depth to the surface. Collected zooplankton was fixed in 10% buffered formalin and the number of individuals in each taxon counted (Suzuki and Fukuwaka 1998). Zooplankton taxa were divided into two size groups: smaller taxa, such as *Evadne nordmanni*, *Podon leuckarti*, euphausiid calyptopis larvae, or *Oikopleura* sp.; and large taxa, such as euphausiid furcilia larvae, polychaetes, *Calanus sinicus*, or *Neocalanus plumchrus* copepodid V stage.

The relationship between environmental factors and nutritional conditions was analyzed by linear regression. The correlation coefficient of the relationship was tested using the *t*-test. Because environmental factors were correlated with each other, we used path analysis to evaluate the strength of effect of environmental factors on nutritional condition of juveniles (Sokal and Rolf 1995). The path coefficient was tested using the *t*-test.

RESULTS

Juvenile-Adult Relationship

Numbers of chum salmon released as juveniles along the Japan Sea coast of Honshu increased from 1970 to 1980, but gradually decreased thereafter (Fig. 2A). The mean number of juveniles released (1970–1998) was 203 million ($SD \pm 74.8$ million). The mean number of returning adults was 510,000 ($SD \pm 190,000$) in this period. The number of returning adults fluctuated around 600,000 in recent years (1989–1999) (Fig. 2B). Mean year-class survival at sea was 0.318% ($SD \pm 0.145\%$). Year-class survival declined from 1970 to 1982, but increased thereafter (Fig. 2C).

Ocean survival was correlated negatively with number of released juveniles and coastal SST in early

May (Table 1). This indicates that ocean survival is density-dependent, and related to water temperature.

Nutritional Condition of Juveniles

The condition factor and the relative stomach content weight (RSC) of chum salmon juveniles were correlated positively with SST and negatively with surface salinity in coastal waters off Fukura, Yamagata (Figs. 3 and 4). The regression equations for the relationships are condition factor = $0.147 \cdot SST + 4.98$ ($R^2 = 0.218$, $p < 0.001$; Fig. 3A), condition factor = $-0.0618 \text{ salinity} + 8.37$ ($R^2 = 0.141$, $p < 0.001$; Fig. 3B), $RSC = 0.634 \text{ SST} - 4.96$ ($R^2 = 0.346$, $p < 0.001$; Fig. 4A), and $RSC = -0.235 \text{ salinity} + 8.71$ ($R^2 = 0.174$, $p < 0.001$; Fig. 4B). SST was 8.6–14.2°C and salinity was 18.5–34.0 psu in March to May in 1994–1996.

Fig. 2. Annual changes in numbers of released juveniles (A), returning adults (B), and ocean survival rate of year-class (C) for hatchery-reared chum salmon in 1970–1998 along the Japan Sea coast of Honshu, Japan.

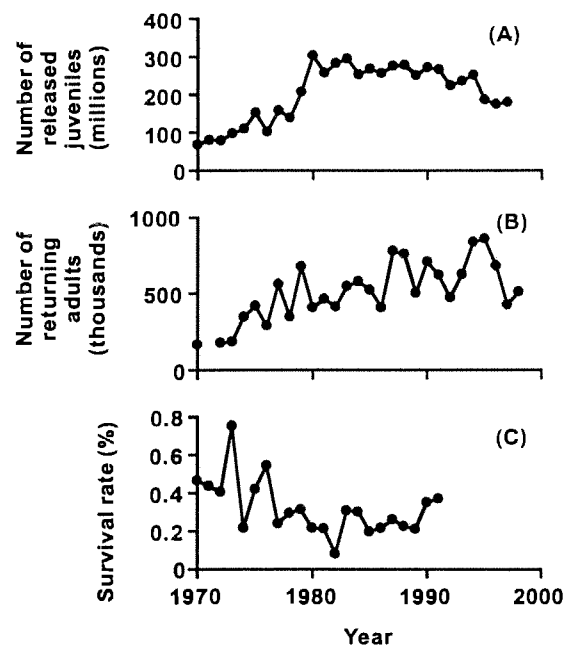
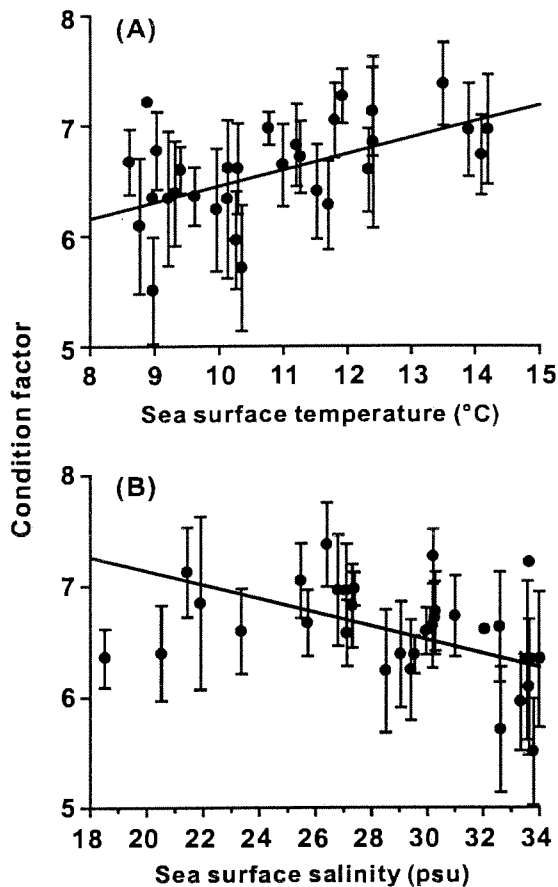


Table 1. Stepwise multiple regression analysis between ocean survival and number of released juveniles, coastal sea surface temperature in early May of the year of release, and coastal surface salinity in the same period, for 1970–1991 year-classes of chum salmon along the Japan Sea coast of Honshu. The degrees of freedom in the significance test are 19.

Variable	Standard partial regression coefficient	Partial regression coefficient	<i>t</i>	<i>p</i>
Intercept		-1.39	-3.64	0.0017
Number of released juveniles	-0.474	$-1.14 \cdot 10^{-9}$	-2.76	0.0125
Sea surface temperature	-0.393	-0.0719	-2.29	0.034
Surface salinity	Not added			

Fig. 3. Regressions of condition factor of chum salmon juveniles on sea surface temperature (A), and on sea surface salinity (B) in the coastal water off Fukura, Japan Sea, 1994–1996. Vertical bars, standard deviation. Regression equations: condition factor = $0.147 \cdot \text{SST} + 4.98$, $R^2 = 0.218$, $p < 0.001$, $n = 465$; condition factor = $-0.0618 \cdot \text{salinity} + 8.37$, $R^2 = 0.141$, $p < 0.001$, $n = 465$.

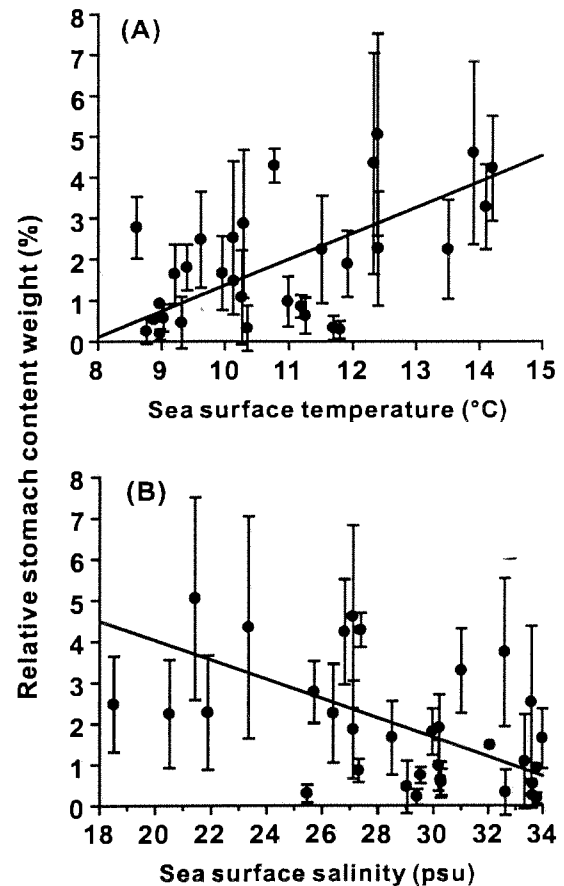


The relative stomach content weight (RSC) was negatively correlated with CPUE (Fig. 5). The regression equation is $\text{RSC} = -0.0251 \cdot \text{CPUE} + 2.96$ ($R^2 = 0.174$, $p < 0.001$). This indicates that intraspecific competition for food occurs in chum salmon juveniles. In the path diagram, the correlation between density of juveniles (CPUE) and stomach content weight was not significant (Fig. 6). CPUE of juveniles was negatively correlated to prey abundance, which affected stomach content weight significantly, and therefore CPUE affected stomach content weight indirectly. SST and salinity affected biotic factors such as prey abundance or CPUE of juveniles, and stomach content weight of juveniles.

DISCUSSION

We found that survival of chum salmon correlated with coastal sea surface temperature and number of juveniles released from hatcheries along the

Fig. 4. Regression of relative stomach content weight of chum salmon juveniles on sea surface temperature (A), and sea surface salinity (B) in the coastal water off Fukura, Japan Sea, 1994–1996. Vertical bars, standard deviation. Regression equations: $\text{RSC} = 0.634 \cdot \text{SST} - 4.96$, $R^2 = 0.346$, $p < 0.001$, $n = 465$; $\text{RSC} = -0.235 \cdot \text{salinity} + 8.71$, $R^2 = 0.174$, $p < 0.001$, $n = 465$.



Japan Sea coast of Honshu. The survival rate of hatchery-reared fish may be affected by biotic and abiotic environmental factors in freshwater, coastal, and oceanic habitats. The spatial extension of estuaries, coastal water temperatures, and coastal salinity also affected the marine survival of hatchery-reared Pacific salmon (Blackbourn 1990; Coronado and Hilborn 1998; Mahnken et al. 1998; Willette et al. 1999). Long-term or decadal-scale climate changes also affect the production of salmonids in the North Pacific (e.g. Beamish et al. 1999). Density-dependence is often a cause to depress the survival rate in hatchery-reared salmon stocks, such as the North American stocks of coho salmon and of the Prince William Sound stocks of pink salmon (e.g. Coronado and Hilborn 1998; Willette et al. 1999). Coastal environmental factors at release or numbers of released juveniles may be a key to the success of enhancement programs for Pacific salmon.

Fig. 5. Regression of relative stomach content weight on CPUE of chum salmon juveniles in the coastal water off Fukura, Japan Sea, 1994–1996. Vertical bars, standard deviation. Regression equation: $RSC = -0.0251 \cdot CPUE + 2.96$, $R^2 = 0.174$, $p < 0.001$, $n = 465$.

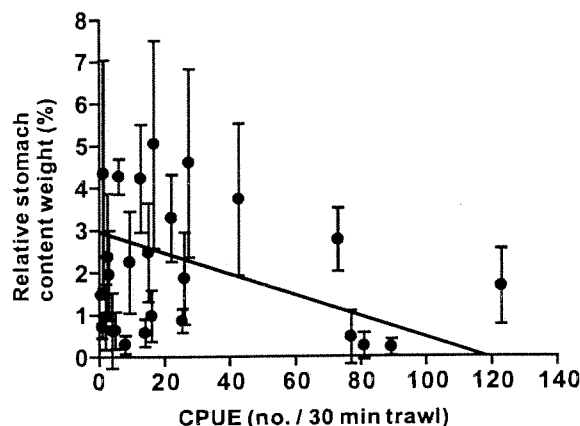
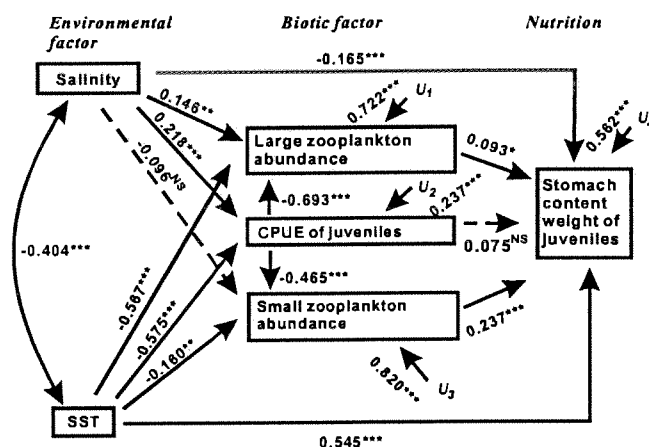


Fig. 6. Path diagram illustrating the relationships among environmental factors, biotic factors, and nutritional condition of chum salmon juveniles in the coastal water off Fukura, Japan Sea, 1994–1996. U is a residual variable. Arrows indicate the effect of one variable on another; dashed arrows not statistically significant ($p > 0.05$). Path coefficients are printed near the arrows. ***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; NS, $p > 0.05$.



Survival of chum salmon correlated negatively with coastal sea surface temperature. Mortality of chum fry and small fingerlings in the early sea life accounted for over 90% of the whole sea mortality in our study area (Fukuwaka and Suzuki 1998b). Year-class strength of hatchery-release chum salmon is determined by early sea mortality, which may be affected by coastal environment or predation by piscivorous fish or sea birds (Bax 1983). However, Nagasawa (1998) could not find any evidence that predation by fish in early sea life has much impact on abundance of Japanese chum salmon stocks. Early sea survival of salmonids was affected by coastal

environment such as SST or salinity, as well as prey abundance, primary production, or number of released juveniles (Blackbourn 1990; Coronado and Hilborn 1998; Willette et al. 1999).

The temporal and spatial distribution of environments suitable for survival of chum salmon juveniles may be narrow in coastal waters of the Japan Sea. Sea surface temperature in our study area reached near the upper limit for chum salmon juveniles in May. Coastal water temperature at release time strongly affects the survival of Japanese hatchery-reared chum salmon (Mayama 1985). Spatial distribution of chum salmon juveniles was restricted within a river plume in coastal waters (Fukuwaka and Suzuki 1998a).

Intraspecific competition for food within a limited distribution may cause density-dependent early sea mortality of chum salmon juveniles released from hatcheries. The analysis of nutritional condition indicates that the food consumption by chum salmon juveniles correlates negatively with their density through reduction in abundance of prey organisms (Fig. 6). Aggregated distribution of juveniles might exacerbate intraspecific competition (unpublished data). Early sea survival of slower growing chum salmon was lower than that of faster growing fish in the Nanaimo River, British Columbia (Healey 1982). Food competition may cause reduction of somatic growth in early sea life of chum salmon. Early sea distributions of Pacific salmon are restricted in estuaries or coastal waters (Percy 1992). Intraspecific competition may strongly affect early sea survival and growth not only of hatchery-reared chum salmon but also of other salmonid species, such as chinook salmon (*O. tshawytscha*) (Wissmar and Simenstad 1988; Simenstad 1997).

CONCLUSIONS

Density-dependent sea survival occurred in juvenile hatchery-reared chum salmon along the Japan Sea coast of Honshu, Japan. Survival is negatively correlated with high coastal SST during early sea life. The food consumption by juveniles correlated negatively with density through reduction in abundance of prey organisms. These results indicate that intraspecific competition for food within a narrow nursery area limited by environmental factors strongly affects early sea survival for hatchery-reared chum salmon. The coastal carrying capacity may regulate abundance of chum salmon along the Japan Sea coast of Honshu, Japan.

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Tissue Degeneration in Chum Salmon and Carrying Capacity of the North Pacific Ocean

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Keywords: Chum salmon, flabby muscles, dense concentrations of salmon.

Abstract: Seasonal, geographic and interannual occurrence of chum salmon (*Oncorhynchus keta*) with softened (flabby) muscles was related to oceanic abundance of salmon, their lengths, and maturity. The relative frequency of flabby chum was different in various years, and varied during the feeding season in various parts of the ocean; however, their frequency was greatest where concentrations of salmon were dense. The proportion of flabby chum varied with size and degree of maturity. As chum grew and became mature the frequency of flabbiness decreased. I suggest that during growth and maturation flabby individuals either die or recover, depending on the extent to which they were affected. The cause of tissue degeneration is most likely poor quality food where salmon aggregate. However, the condition is probably exacerbated by high densities in some regions. This suggests that the carrying capacity of the North Pacific is nearly reached.

INTRODUCTION

In recent years the abundance of Pacific salmon has reached a high level. Over 900,000 tons were taken by all nations in the North Pacific in 1995. This value is close to the historic maximum. This period of increase in the abundance of natural salmon stocks coincided with a period of large scale enhancement. The result was the creation of a large stock of chum salmon (*Oncorhynchus keta*), particularly by Japan. In terms of biomass this is the largest stock of salmon in the Pacific. Since the early 1980s Japan has been releasing nearly two billion young chum salmon annually. By 1990 the return of chum released from hatcheries in Honshu and Hokkaido (Japanese chum) exceeded 200,000 tons. The appearance of such a quantity of fish in the ocean, which had never before been recorded in conventional ranching areas, could not help but change the ecology of the area. Japanese chum salmon began to predominate in regions which had previously been occupied mostly by chum from Russian rivers (Russian chum), and chum salmon became the main consumer of food resources in the North Pacific. Signs now indicate that the raised abundance has begun to affect the stocks of salmon, primarily chum salmon themselves. Hence, beginning from the 1970s the rise in the abundance of chum from Japanese hatcheries was accompanied by a decline in most of the Asian stocks. From the 1970s the increase in chum salmon reared at Japanese hatcheries was associated

with a drop in their mean length and weight, and a rise in the mean age at maturation (Ishida et al. 1993; Kaeriyama 1996).

We noted another phenomenon possibly caused by high density of salmon in feeding areas. In 1994 we found and described mass softening of chum salmon body tissues. The proportion of fish having softened skeletal muscles varied between 35 and 60 percent in various areas and seasons. Such fish also had an unusual herring-shaped elongated body (Gritsenko et al. 1995). We call this condition "flabby chum".

This paper describes the spatial and temporal distribution of flabby chum, and its relationship with salmon densities. Causes and mechanisms of degeneration of tissue are suggested.

MATERIALS AND METHODS

Studies were conducted between April and October, 1994–1998, in the Bering Sea and North-West Pacific in waters adjacent to the East Kamchatka and Kuril Islands beyond territorial waters, but within Russia's 200-mile economic zone. Driftnets of 60 mm mesh size were used. In addition, pink salmon (*O. gorbuscha*) taken from fixed seines off southwest and southeast Sakhalin in 1995 were examined.

Fish to be examined were collected from nets immediately after lifting the catch on deck. Species composition of the catch was determined, and condition of all species of salmon was visually evaluated.

Chum and other species of salmon were classified by body shape and degree of tissue resiliency into "fair" or "normal" (n), "poor" or "flabby" (f), and intermediate (sf). Normal fish were salmon-shaped with elastic muscles, while flabby ones were elongated, with herring-like bodies, and a noticeable loss of resiliency in muscles, and loss of scales. Sampling for quality of salmon was occasional in 1994 and 1995, and throughout the whole season of investigations in 1996–1998. In 1996 sampling was from four ships simultaneously over the entire summer feeding area of Asian salmon; these data were used to describe the spatial and temporal changes in chum salmon quality.

Sampled salmon were measured for length (mm fork length), and the state of maturity of gonads was assessed. The stages of chum gonad maturity were estimated according to the scale by Murza and Christoforov (1991) as follows: Stage I (juveniles), gonads are like a thin transparent thread, blood vessels are absent, sex is not determined; Stage II, ovaria are a bit larger, semitransparent, color is yellow or sky-blue; there is one major blood vessel in each gonad; the largest oocytes are visible; testes are elastic and pink; Stage III, the gonads fill about 1/3 of the abdominal cavity, not transparent; the ovary color is yellow, the testis pale-pink, testis borders do not flow when cut, the oocytes have different sizes; Stage IV, gonads are of maximal size and occupy the greater part of the cavity, blood vessels are well developed, oocytes are full size, testis borders flow when cut, there is one drop of sperm when the abdomen is pressed; Stage V, eggs (ovulation), or liquid sperm (spermiation) flow from genital pores when abdomen is pressed. During intermediate stages (II-III, III-IV) gonad size is the same as in the preceding stage, and gonad cell content is the same as at the next stage.

We examined published references on fish pathology. The most common pathology appears to be infestation with endoparasitic protozoans such as mixo- and microsporidia, which may cause a pronounced softening of the muscles in some sea fish (Shulman 1966; Voronin 1983). Therefore a parasitological analysis of tissues was carried out in 1997 to investigate the possible causes and mechanisms of degenerative changes. Muscles, kidneys and liver of 125 samples (100 f and 25 n) were examined microscopically to determine the presence of endoparasitic protozoans and helminths. Intestines of chum salmon (from pylora to anus) were also examined for helminths (Golovin and Klovatch 1999).

RESULTS AND DISCUSSION

Seasonal and Geographic, Occurrence of Flabby Chum Salmon

Flabby chum salmon exhibited a herring-shaped body, softened musculature, and, as a rule, a considerable loss of scales. Body height/length ratio in normal chum varied within 0.23–0.27; in flabby chum (f) and (sf) this ratio was between 0.18 and 0.22. Condition factor of flabby chum was usually lower than in normal individuals. Among the other species of salmon few fish had an unusual body shape and flabby muscles.

Flabby chum salmon were abundant among large catches indicating dense concentrations. The condition appears to be associated with high densities at feeding grounds. Some individual pink salmon with a similarly degenerated skeletal musculature had previously been recorded off Southeast Sakhalin during years of extremely high abundance, for instance in 1991. In 1995 we examined pink salmon taken from fixed seines off Southeast and Southwest Sakhalin. There were no flabby fish among the small stock of pink salmon off Southwest Sakhalin, but they did occur there in the mixed concentrations of Russian and Japanese chum salmon, and in the abundant chum stock off Southeast Sakhalin.

In 1996 our surveys covered the entire range of Asian chum salmon between the northern Bering Sea and South Kuril Islands, including the Bering Sea (regions 1 and 2 in Fig. 1), East Kamchatka (region 3), and the Pacific side of the North and South Kuril Islands (regions 4 and 5). The monthly variations in percentage of flabby chum salmon in the Bering Sea on the one hand, and off East Kamchatka and North Kurils on the other hand followed opposite trends (Fig. 1). The proportion of flabby fish off East Kamchatka between May and August increased from 26.6% to 82%, whereas in the Bering Sea it decreased between June and October from 61% to 3.2%. This occurrence of flabby chum coincides with the migration of Japanese chum (Kondo et al. 1965; Neave et al. 1976; Ogura 1994; Myers et al. 1996) which appear in Russian waters in late May and June (Fig. 2). A few fish move to East Kamchatka, but most pass to the Bering Sea through the Aleutian chain straits and scatter in the northern part of that sea. In August the maturing Japanese chum migrate south along Kamchatka intermingling with chum feeding in that area. Later these stocks join and move along the Kuril chain to the islands of Japan. The highest proportion of flabby chum in the Bering Sea occurred in late June (about 60%), at East Kamchatka in August (about 80%), and off South Kurils in October (about 80%). At these times the proportion of Japanese chum in these areas is the largest, hence concentrations of chum are the most dense.

Fig. 1. Geographical and seasonal distribution of "flabby" chum salmon in 1996.

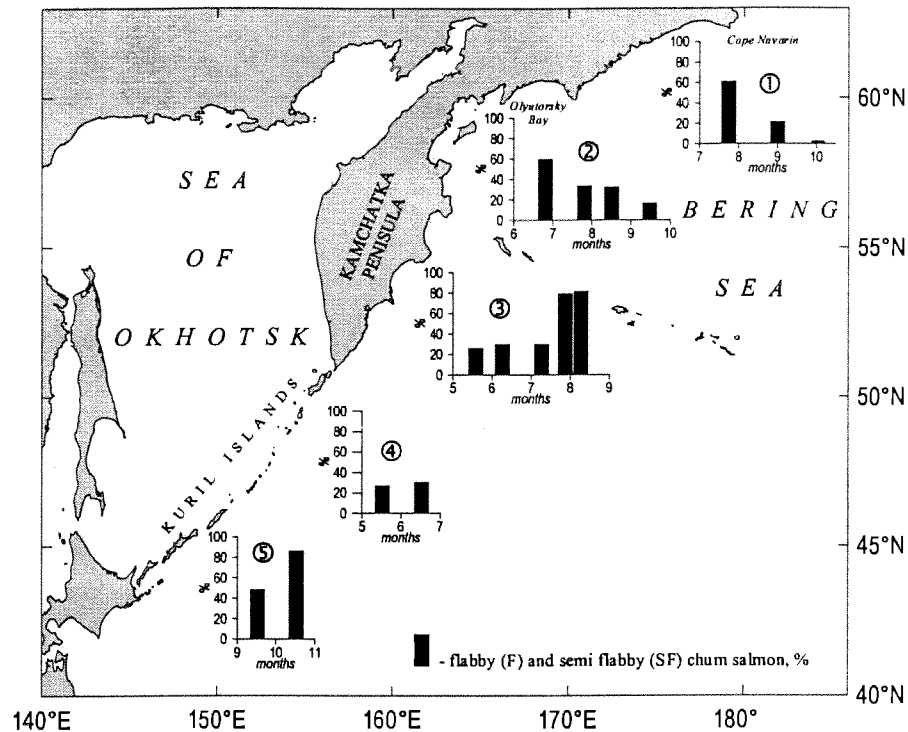
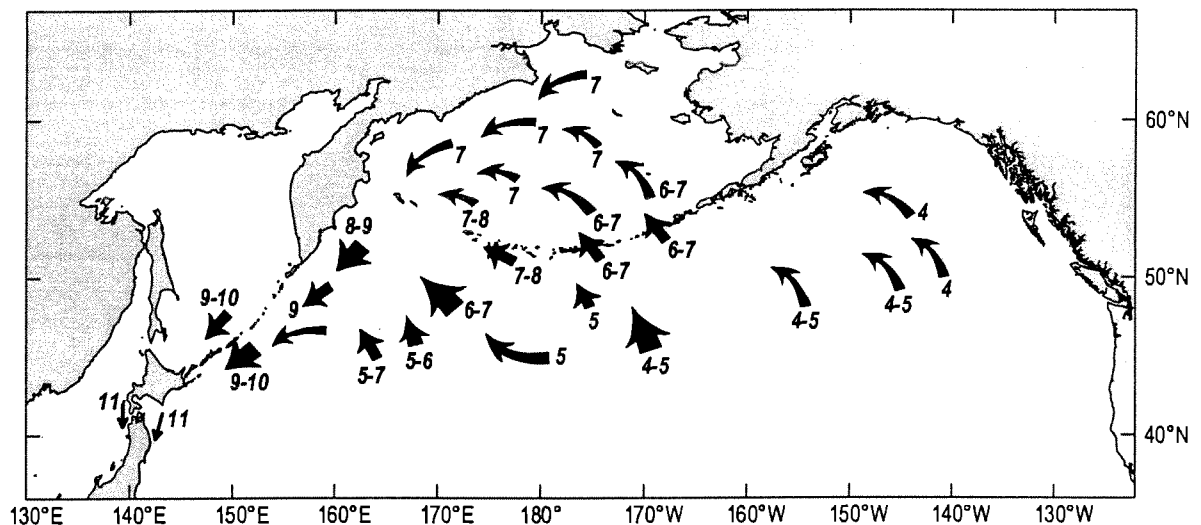


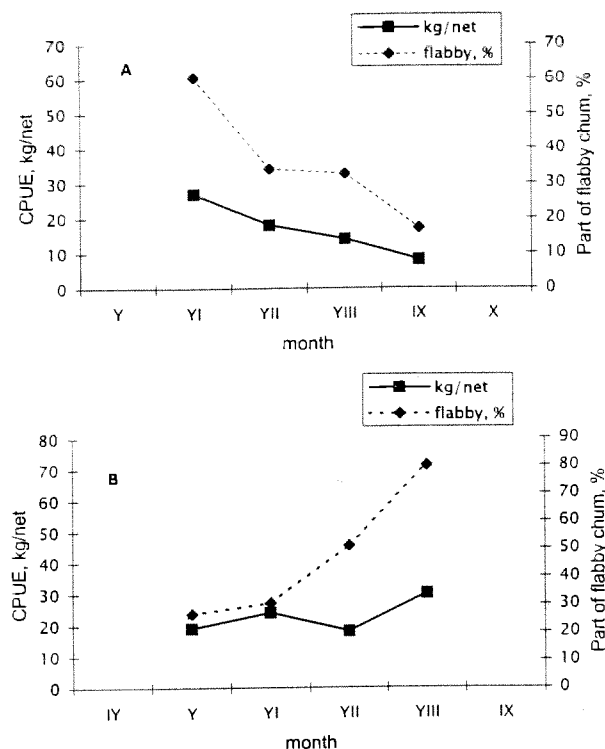
Fig. 2. Hypothesized migration route of maturing chum salmon originating from Japan. Figures beside arrows indicate month (from Ogura 1994).



The proportion of flabby individuals in catches usually varied according to the changes in CPUE (Fig.3). The correlation between the proportion of flabby individuals and catch rates in the Bering Sea was high ($r = 0.96$), while in the Pacific waters of Kamchatka it was lower ($r = 0.68$). Studies of vertical migrations in salmon have shown that they shift diurnally from the surface down to 15 m or more at night. Occurrence in the surface layer varies among the species of salmon, and depends on a number of fac-

tors, in particular the surface water temperature. Chum, sockeye (*O. nerka*) and pink salmon remain mostly near the surface at 7–8°C in summer months in the Bering Sea, whereas during the same months off East Kamchatka they descend to 10–15 m where the temperature is 1–2°C lower than 10–11°C at the surface (Ishida et al. 1997). At these depths fish become inaccessible to the netting (9 m deep). Catch rate and surface water temperature data for the entire summer showed that catches peaked at 7–8°C. Thus,

Fig. 3. CPUE (kg/net) and proportion of flabby chum salmon (%). A, Bering Sea; B, Pacific ocean off East Kamchatka.



at water temperatures higher than 8°C, CPUE reflects salmon densities to a lesser extent than at lower temperatures.

The occurrence of flabby chum varied among years. Over the five years of observation the maximum was in 1996 (average 40%), the minimum in 1998 (average 12%). This interannual variation coincides with the trend in world catches of Pacific salmon. The largest catches of salmon in the North Pacific were recorded in 1995. In 1996 catches on the American coast decreased notably, and in 1997 they began to decline on the Asian coast as well. In 1998 catches in all areas were lower than in 1997 (Beamish et al. 1998). Our CPUE data also show a downward trend in salmon concentrations at sea, especially in the Bering Sea. For example, in August–September 1995 catches of salmon in the Bering Sea were 20 kg per net. For the same period in 1996 they were 12 kg per net; in 1998, 5 kg per net. The proportion of flabby chum decreased simultaneously, from 27.3% in August 1996 to 18.6% in August 1998.

Relation of Flabby Chum Salmon to Length and Maturity

The proportion of flabby chum varied among fish of various sizes and stages of maturation. The maximum frequency occurred among fish under 50 cm (there were no fish under 40 cm in catches); the

lowest frequency was among the largest individuals of over 65 cm (Fig. 4). To determine the relation between quality of chum and the degree of maturation we selected the size group 51–60 cm, which was the most numerous in catches, and included individuals with gonads of different degrees of maturity. The largest proportion of flabby fish was among those having gonads at stages II and II-III of maturity; the lowest proportion was among the maturing fish with gonads at stages III-IV and IV of maturity (Fig. 5).

A histological analysis of chum muscles revealed a deterioration in muscle fibres. In addition, some displacement of liver and spleen was observed. However, some muscle fibres showed signs of regeneration, suggesting that degeneration of muscle tissue in chum may be reversible, given improved conditions. Histology experts from the Moscow University suggest that recovery or death of affected individuals may depend on whether or not the reproductive system has been affected.

Though the condition is not entirely understood there seems little doubt that chum salmon with flabby muscles occur when densities are high in areas of feeding at sea.

Fig. 4. Frequency of chum salmon of various lengths with N, normal muscles; SF, semi flabby muscles; F, flabby muscles. A, May–June 1996; B, May–June 1998; C, July–August 1997. Pacific ocean off East Kamchatka.

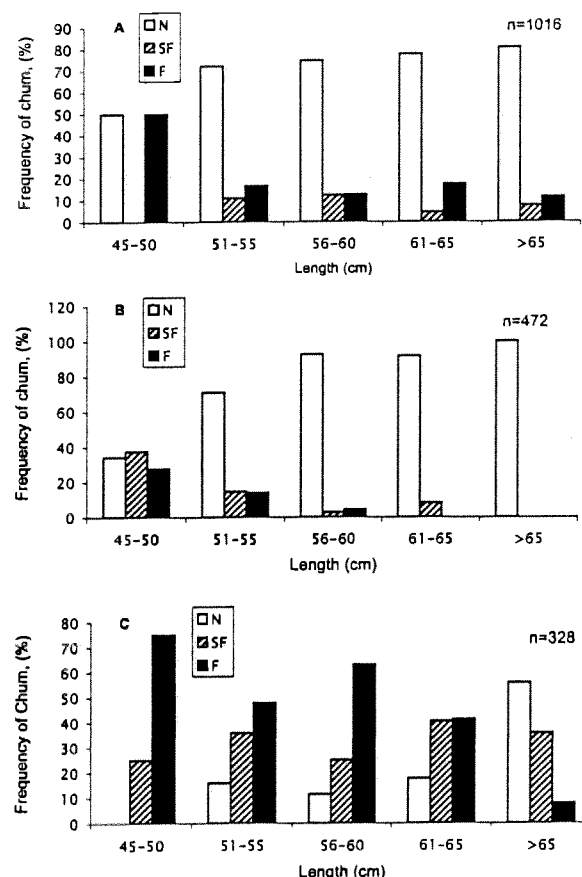
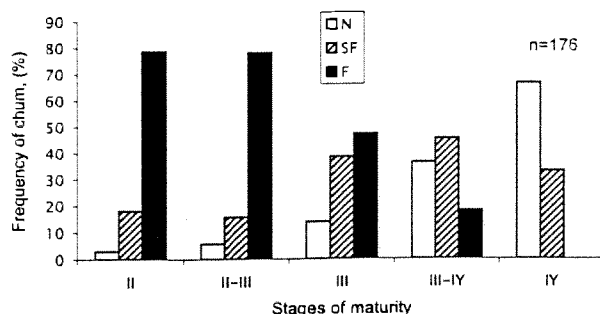


Fig. 5. Frequency of chum salmon of various stages of maturity with N, normal muscles; SF, semi flabby muscles; F, flabby muscles. Pacific ocean off East Kamchatka. July–August 1997.



Possible Causes of Flabby Chum Salmon Muscles.

I considered two hypotheses of possible causes of softening chum muscles: (1) presence of some pathogenic organism; (2) feeding of chum on inferior food where fish are concentrated.

Clinical and pathological examination of the sub-skin and deeper layers of the muscles did not reveal any noticeable changes of the skin in flabby fish, or the presence of visible cysts or capsules of parasitic protozoans or helminths. Dissection of muscle tissue from various parts of the body, kidneys and liver of the fish did not show the presence of any agents. Microscopic examination of the muscle tissue, kidneys and liver of fish immediately after capture excluded the presence of protozoans of myxosporidia, etiological agents that can cause various muscle pathologies in fish, including softening of muscle tissue.

Electron microscopic examination of muscle and liver samples from chum having normal and soft musculature was made to identify smaller parasitic protozoans (myxosporidia). None of the samples contained protozoans.

Since the condition of the intestine in fish, especially of its rear absorbent part can affect metabolic processes, we analyzed the intestines of flabby and normal chum for parasites. All the fish contained helminths in intestines: cestodes, nematodes, proboscis worms and individual flukes. Invasion intensity was 3–10 to 50–90 ind./fish. However, even under a high infestation rate the helminths found did not cause any significant pathology of intestinal walls, while their number did not correlate with the resiliency of muscles of the fish examined (Golovin and Klovatch 1999).

Thus, the clinical, pathology-anatomy and microscopic examination of the muscles and inner organs of chum, as well as helminthological analysis of the intestines ruled out parasites as a factor causing flabbiness of chum salmon muscles at sea.

Our five years' study of the food habits of chum

at sea showed that in large measure food consists of salps, jelly-fish and ctenophores marked by jelly structure and low caloric value, and containing 94% water (near 100% in some regions in certain periods). The caloric value of jelly-fish is 136 cal/g, whereas that in crustaceans is 589–743 cal/g, in fish 1185 cal/g (Davis et al. 1998). The high frequency of coelenterates as food of chum in the Bering Sea and the Pacific in the 1990s was also pointed out by Ishida et al. (1997), Volkov et al. (1997), and Ueno et al., (1998).

In the 1960s the abundance of salmon was much lower than at present, and the importance of jelly-fish and ctenophores as food for chum was lower. Ctenophores and jelly-fish were recorded as food items of chum only during years of high abundance of pink salmon, even more so during its mass pre-spawning migration (Andriyevskaya 1966).

It is known that the chemical composition of fish reflects their diet (Love 1976). Food of low-caloric value may change the chemical composition of the body. The relationship between the lipid composition of gut content and body muscles has been shown for larvae of Atlantic cod (*Gadus morhua*) (Lochmann et al. 1996). During starvation or inadequacy of necessary food components, lipids are first utilized, independently of their location in the body, and proteins of white muscles are utilized secondly. This causes cod muscles to become flabby (Love 1976). Juvenile steelhead salmon (*O. mykiss*) grow best when their food contains 13% lipids and 0.5% unsaturated fatty acids by dry weight (Gershanovich et al. 1988). Experiments have shown that salmon require 9.5% unsaturated fatty acids by dry weight in their food (Bogut and Opacak 1996).

The availability of food in different years may be indicated by the mean condition factor of chum salmon in the area of East Kamchatka in July, 1996–1998: in 1996 the mean condition factor was 1.08; it was 1.14 in 1997, and 1.21 in 1998. Correspondingly the highest frequency of flabby chum salmon in catches was noted in 1996, and the lowest in 1998.

I suggest that when chum feed on jelly-like organisms the loss of polyunsaturated fatty acids is not replaced by those ingested, which causes loss of lipids in musculature and destructive changes; muscles soften and body shape is modified. This is a hypothesis which needs further verification. However, there seems little doubt that flabby chum occur primarily in regions of high density, which may be an indication that the carrying capacity of epipelagic waters of the North Pacific is being exceeded.

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Food Habits of Juvenile Salmon in the Gulf of Alaska July–August 1996

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Auburn, M.E., and S.E. Ignell. 2000. Food habits of juvenile salmon in the Gulf of Alaska July–August 1996. N. Pac. Anadr. Fish Comm. Bull. No. 2: 89–97.

Keywords: Competition, diet, chum, coho, pink, sockeye, prey.

Abstract: Four species of juvenile salmon, pink (*Oncorhynchus gorbuscha*), sockeye (*O. nerka*), chum (*O. keta*), and coho (*O. kisutch*) salmon, were collected during July and August, 1996, using a midwater trawl in near surface waters of the Gulf of Alaska from Southeast Alaska to the Alaska Peninsula. Stomach contents of these salmon were examined to identify important prey items. Crustaceans, principally hyperiid amphipods and euphausiids, and fish were the primary prey. Decapod larvae, calanoid copepods, and pteropods were also commonly found in the juvenile salmon diets. The proportions of prey type varied by habitat and regions for each of the four salmon species examined. The variation in large prey types and the small proportion, 3%, of empty stomachs suggest that the availability of prey resources does not appear to be a limiting factor for production and growth of juvenile salmon examined in this study.

INTRODUCTION

In the past few years, considerable attention has been given to the diminished size of salmon in the North Pacific Ocean and Bering Sea (Helle 1989). This concern has prompted new studies of salmon diet and energetics, which are key to assessing the ocean's capacity to support recent levels in salmon production. Data on the similarity in diet between species, years, and areas provide insight into life history strategies such as ocean migrations, foraging behavior, and nutritional adaptations. Such studies enlarge our understanding of the trophic relations of salmonids in coastal and oceanic ecosystems of the North Pacific. They also provide data needed for models of salmon energetics and marine ecosystems.

Studies of feeding behavior and interspecific competition of juvenile salmon during marine residency can also provide insight on energy budgets and stock productivity. Changes in the abundance of inter- and intra-specific competitors can be reflected by changes in diet when prey resources are limiting for salmon (Tadokoro et al. 1996). Competition in foraging among species may suggest limited food resources and lower productivity (Healey 1978; Peterman 1984). At times, this competition may be limited to specific regions, time periods, and/or species. For example, earlier studies on juvenile salmon from waters in Southeast Alaska and northern British Columbia (Healey 1978; Landingham et al. 1998) showed that in some circumstances, the same major taxonomic prey shifted in proportions spatially and temporally between species; in other circumstances, diet overlap was apparent. Similarly, Peterson

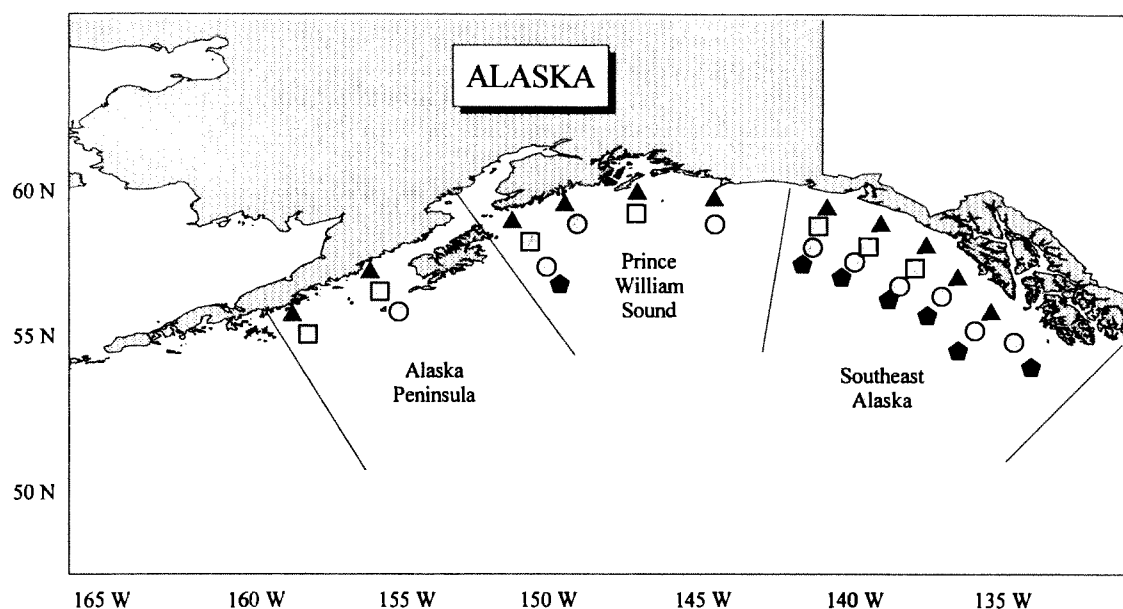
et al. (1982) and Brodeur et al. (1987) showed both diet overlap and similarity in feeding patterns for juvenile salmon off Oregon, suggesting a mixture of foraging strategies characterized by both prey availability or by prey selection.

This study describes the food habits of juvenile salmon taken in coastal waters of the Gulf of Alaska during July and August 1996. Diets of juvenile pink (*Oncorhynchus gorbuscha*), sockeye (*O. nerka*), chum (*O. keta*), and coho (*O. kisutch*) salmon are summarized and compared across four habitat types, extending from nearshore to oceanic waters, and across three regions from Southeast Alaska to the Alaskan Peninsula. The broad extent of the sampling area allows us to examine the diet characteristics of juvenile salmon as they enter coastal waters in Southeast Alaska and move north and westward along their migratory pathway. This pathway, with its changing current structure, continental shelf width and topography, nutrient inputs, and eddy activity, thus provides important insight into the plasticity of salmon foraging in diverse coastal habitats.

MATERIAL AND METHODS

Rope trawl surveys were conducted in near surface waters on the chartered fishing vessel F/V *Great Pacific*, a 38 m stern ramp trawler, in waters from Southeast Alaska to the Aleutian Islands in the North Pacific Ocean from 21 July to 22 August 1996 (Fig. 1; Carlson et al. 1996). The trawl was towed for five nmi at 5.0 knots in near shore (0–10 nmi offshore), shelf, slope (200 m depth contour), and oceanic waters (out to 60–120 nmi offshore). The net was 198 m long and was

Fig. 1. Sampling locations for juvenile salmon used in the diet analyses. Symbols represent the four habitat types: triangles – nearshore; squares – shelf; circles – slope; and hexagon – oceanic.



fished from the surface to a depth of approximately 18 m with a 52 m horizontal opening. The total catch of juvenile salmon in 1996 was 9,484, consisting of 4,701 pink, 1,932 chum, 1,405 coho, 1,414 sockeye, and 31 chinook (*O. tshawytscha*) salmon, and one steelhead (*O. mykiss*). A subsample of these fish was sorted, identified, and frozen whole for laboratory analysis of food habits. In the laboratory, each fish was measured to the nearest mm fork length, blotted dry, and weighed to the nearest 0.01 g. The stomach (from the pharynx to the pylorus) was removed and placed in a 7.5% formalin solution for 4–6 weeks, then transferred to 50% isopropyl alcohol for later analysis.

Data Collection

When available, 10 stomachs per species in each of four different habitats (near shore, shelf, slope, and oceanic) were selected and analyzed per transect. Relative stomach fullness was visually estimated and categorized using a scale of 1–6 (where 1 = trace, 2–5 = fullness in fourths, and 6 = distended stomachs). The state of digestion was noted as fresh, partially digested, or mostly digested. The stomachs were weighed to the nearest milligram, the contents removed, and then the stomachs were weighed empty. The contents were identified to major taxonomic groupings and enumerated. Larval and juvenile fish in the stomach contents were identified and measured (total length (TL)), when possible. Unidentifiable gelatinous material and incidental prey (barnacle cyprids, terrestrial insects, gammarids, and chaetognaths) were encountered in some of the stomachs. In

most cases these prey types occurred infrequently and were pooled into an “other” category.

Data Analysis

Stomach contents were identified to general taxa to provide a summary of diet composition. Comparisons of prey composition were made between species, habitat types and regions (off Southeast Alaska, Prince William Sound, and Alaska Peninsula). Prey weight data were predominantly used in the analyses as the importance of small prey such as oikopleura can be misrepresented when the data are reported as numerical or frequency percentages. Nevertheless, numerical and frequency of occurrence data were included in the tables for reader comparison. All three measures (number, weight, and frequency of occurrence) of each prey taxon were expressed as percentages.

Diet overlap by species and by area was estimated using the Schoener Index of Overlap, which is also known as the Percent Similarity Index (PSI; Schoener 1974). The PSI is computed as:

$$PSI_{jk} = \sum \min(p_{ij}, p_{ik}) = 1 - 0.5(\sum |p_{ij} - p_{ik}|),$$

where p is the proportion of the biomass of the i^{th} prey category in n taxonomic categories consumed by fish species (or habitat areas) j and k . Note that when prey are generalized into major taxa (as in this study), the PSI may overestimate diet similarity due to the use of summary prey categories; taxa used in a prey category identified from one species or area may not be the same taxa as those in that category collected from another species or area (Sturdevant et al. 1997).

RESULTS

Detailed analysis of stomach contents was performed on a total of 872 juvenile salmon (240 pink, 213 sockeye, 192 chum, and 227 coho salmon). Nearly all of the stomachs (97%) contained some food. Crustacean species most commonly encountered by the four juvenile salmon species within all habitats and regions were the euphausiid, *Thysannoessa spinifera*, and the common hyperiid, *Themisto pacifica*. Pteropods, mainly *Limacina helicina*, decapods, *Brachyura cancridae* megalops, and *Calanus pacificus* copepods were also frequent prey in the diets. Of the various families of fish found in the diets (Table 1), 30-35 mm Osmerid larvae were the most abundant.

Southeast Alaska

Of the three survey areas in our study, fork lengths were notably smaller for juvenile salmon sampled from the southeastern Alaska transects. Pink salmon were smallest (89–182 mm, \bar{x} = 126 mm) followed by chum salmon (95–194 mm, \bar{x} = 128 mm), sockeye salmon (107–143 mm, \bar{x} = 143 mm), and coho salmon (111–279 mm, \bar{x} = 206 mm).

Nearshore waters

Euphausiids and fish were the two most important food items as measured by percent wet weight (Table 2). Pink and chum salmon fed primarily on euphausiids, whereas sockeye and coho salmon fed primarily on fish. Coho salmon had the least diverse diet with fish comprising over 93% of the prey weight; sockeye salmon had the most diverse diet that included euphausiids, hyperiid amphipods, and calanoid copepods as secondary food items.

Shelf waters

Euphausiids and calanoid copepods were two important food items (Table 2). Pink and chum salmon fed primarily on euphausiids, whereas sockeye salmon fed primarily on calanoid copepods and coho salmon fed primarily on fish. Coho salmon had the least diverse diet with fish comprising over 87% of the prey weight. Pink and chum salmon had the most diverse diet that included calanoid copepods and fish as secondary food items.

Slope waters

Hyperiid amphipods and euphausiids were the two most important food items consumed in this habitat (Table 2). Pink salmon fed primarily on hyperiid amphipods, sockeye and chum salmon fed primarily

Table 1. List of prey organisms recorded from examination of the stomach contents of juvenile pink, sockeye, coho, and chum salmon in July–August 1996. Listed are prey types which were identified and categorized into general taxa categories. Genera and species are listed where positive identification was possible. This list includes prey that was encountered infrequently.

Gastropoda	Decapoda
Pteropoda	Brachyura
<i>Limacina helicina</i>	(Cancridae)
<i>Clione</i> sp.	(Majidae)
<i>Clio</i> sp.	Anomura
	(Paguridae)
Cephalopoda	(Lithodidae)
<i>Gonatus</i> sp.	Pandalidae
Insect	Hyperiidea
Diptera	<i>Themisto pacifica</i>
	<i>Hyperoche</i> sp.
	<i>Primno</i> sp.
Calanoida	Chaetognatha
<i>Calanus pacificus</i>	<i>Sagitta elegans</i>
<i>Calanus marshallae</i>	
<i>Epilabidocera longipedes</i>	Larvaceans
<i>Metridia pacifica</i>	<i>Oikopleura dioica</i>
<i>Eucalanus bungii</i>	
<i>Neocalanus</i> sp.	Osteichthyes
<i>Centropages abdominalis</i>	Hexagrammidae
<i>Pseudocalanus</i> sp.	Gadidae
<i>Acartia</i> sp.	Osmeridae
Cirripedia	Salmonidae
<i>Lepas</i> sp.	Cottidae
Euphausiacea	
<i>Thysannoessa spinifera</i>	
<i>T. raschii</i>	
<i>Euphausia pacifica</i>	

on euphausiids, and coho salmon fed primarily on fish. Hyperiid amphipods were also important for sockeye salmon and euphausiids important to pink salmon. Sockeye salmon had the most diverse diet that included calanoid copepods and fish as well as hyperiids and euphausiids.

Oceanic waters

Euphausiids were most important in this habitat for pink, sockeye, and coho salmon, whereas chum salmon consumed primarily gelatinous material (Table 2). Pink salmon had the least diverse diet, followed by chum salmon.

Prince William Sound

Average fork lengths of juvenile salmon sampled from Prince William Sound Alaska transects generally increased in comparison to Southeast Alaska. Pink salmon were smallest (102–196 mm, \bar{x} = 126 mm) followed by chum salmon (55–263 mm, \bar{x} = 137 mm), sockeye salmon (89–263 mm, \bar{x} = 137 mm), and coho salmon (132–345 mm, \bar{x} = 232 mm).

Table 2. Summary of prey consumed by juvenile salmon caught in trawls off Southeast Alaska, 21–28 July 1996: %N, percent by number; %W, percent by wet weight; and %FO, percent frequency of occurrence. Unidentified gelatinous and incidental prey are combined into an "Other" category. Prey weight data reported in the text are in bold type.

Prey taxon	Pink			Sockeye			Chum			Coho		
	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO
Near shore												
Hyperidea	14.9	14.5	60.0	17.6	10.6	60.0	1.6	0.4	42.5	0.7	0.0	10.0
Euphausiacea	6.0	64.9	43.3	20.0	27.3	55.0	2.9	74.9	55.0	12.4	4.4	32.0
Calanoida	6.7	9.2	43.3	24.0	12.9	60.0	1.3	2.5	32.5	0.0	0.0	0.0
Fish	2.2	6.1	30.0	26.1	45.9	50.0	1.5	9.8	35.0	6.1	93.6	72.0
Decapoda	1.1	2.8	43.3	1.9	2.6	20.0	1.0	6.7	22.5	45.1	1.8	42.0
Pteropoda	14.3	1.5	63.3	10.3	0.7	20.0	5.2	1.3	57.5	32.5	0.1	24.0
Larvaceans	53.8	1.1	33.3	0.0	0.0	0.0	86.4	4.1	45.0	2.3	0.0	2.0
Other	1.0	0.0	26.7	0.0	0.0	0.0	0.1	0.4	5.0	1.0	0.0	3.0
Number of stomachs		(30)			(20)			(40)			(50)	
Shelf												
Hyperidea	0.8	1.4	30.0	0.3	0.2	20.0	0.7	0.2	33.3	0.7	0.0	10.0
Euphausiacea	2.2	39.0	30.0	15.8	25.0	35.0	2.1	48.4	46.7	10.8	9.3	40.0
Calanoida	33.0	31.3	73.3	73.4	72.5	95.0	16.6	20.6	76.7	0.0	0.0	0.0
Fish	4.9	22.7	3.3	0.4	0.8	15.0	3.8	23.2	23.3	3.0	87.8	95.0
Decapoda	0.1	0.2	6.7	0.0	0.0	0.0	0.0	0.1	3.3	0.6	0.2	30.0
Pteropoda	23.1	4.0	90.0	9.9	0.8	80.0	6.2	1.4	76.7	84.5	0.7	45.0
Larvaceans	35.7	1.2	20.0	0.0	0.0	0.0	70.2	3.0	30.0	0.0	0.0	0.0
Other	0.1	0.2	3.3	0.2	0.7	8.0	0.3	0.2	10.0	0.2	2.0	5.0
Number of stomachs		(30)			(20)			(30)			(20)	
Slope												
Hyperidea	43.9	61.1	75.0	27.7	21.8	75.0	64.6	39.1	63.3	3.1	0.0	22.0
Euphausiacea	5.4	17.1	62.5	22.2	39.7	62.5	7.2	48.6	43.3	20.6	28.4	32.0
Calanoida	6.4	12.5	50.0	11.4	12.7	40.0	8.9	3.2	46.7	0.0	0.0	0.0
Fish	0.1	0.6	12.5	2.6	15.9	32.5	0.6	1.0	23.3	3.7	62.3	74.0
Decapoda	0.6	2.0	35.0	1.3	2.5	22.5	1.2	1.8	26.7	1.9	0.8	34.0
Pteropoda	43.4	6.6	72.5	34.0	2.9	77.5	17.0	1.1	50.0	70.2	0.9	48.0
Squid	0.0	0.0	0.0	0.0	3.7	5.0	0.0	0.0	0.0	0.5	7.5	22.0
Other	0.2	0.1	7.5	0.7	0.8	14.0	0.5	5.2	6.7	0.0	0.0	0.0
Number of stomachs		(40)			(40)			(30)			(50)	
Oceanic												
Hyperidea	16.9	4.8	93.3	6.8	4.5	78.0	62.7	7.1	91.7	0.7	0.1	37.0
Euphausiacea	25.8	82.1	50.0	47.7	70.6	80.0	0.9	2.2	41.7	53.6	72.2	44.4
Calanoida	13.9	4.0	40.0	19.0	17.5	55.0	2.6	3.0	16.7	0.0	0.0	0.0
Fish	0.8	6.8	16.7	2.3	4.5	35.0	2.1	6.5	50.0	2.7	23.2	55.6
Decapoda	0.7	0.6	40.0	0.2	0.3	20.0	0.7	1.8	16.7	3.3	1.0	29.6
Pteropoda	41.3	1.3	30.0	23.2	1.6	50.0	25.5	2.9	83.3	38.7	0.5	81.5
Other	0.6	0.5	10.0	0.7	1.0	5.0	5.9	76.6	45.0	1.0	3.0	7.4
Number of stomachs		(30)			(40)			(12)			(27)	
	n = 130			n = 120			n = 112			n = 147		

Nearshore waters

Euphausiids and decapod larvae were the two most important food items (Table 3). Pink, sockeye, and chum salmon fed primarily on euphausiids, and coho salmon fed primarily on fish. Hyperiid amphipods were of secondary importance for pink and chum salmon, whereas decapod larvae were found in the stomachs of sockeye, chum, and coho salmon. Larvaceans were also important for chum salmon, and euphausiids were fed upon by coho salmon. Pink salmon had the least diverse diet with euphausiids comprising over 75% of the prey weight.

Shelf waters

Fish were the most important food item for juvenile salmon, followed by euphausiids and hyperiid amphipods (Table 3). Sockeye and coho salmon fed primarily on fish, pink salmon on euphausiids, and chum salmon on hyperiid amphipods. Fish were also very important to pink and chum salmon. Sockeye salmon consumed the least diverse diet with fish comprising over 84% of the prey weight.

Table 3. Summary of prey consumed by juvenile salmon caught in trawls off shore from Prince William Sound, Alaska, 29 July to August 3, 1996: %N, percent by number; %W, percent by wet weight; and %FO, percent frequency of occurrence. Unidentified gelatinous and incidental prey are combined into an "Other" category. Prey weight data reported in the text are in bold type.

Prey taxon	Pink			Sockeye			Chum			Coho		
	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO
Near shore												
Hyperidea	49.3	16.9	63.3	41.3	9.8	65.0	56.9	13.1	56.7	2.0	0.2	37.5
Euphausiacea	19.8	75.9	73.3	32.9	68.5	75.0	16.3	41.9	56.7	28.3	26.0	47.5
Calanoida	8.1	2.8	36.7	2.2	0.5	15.0	1.0	0.3	20.0	2.0	0.2	12.5
Fish	0.2	0.2	16.7	0.1	0.8	10.0	0.3	0.2	16.7	3.0	52.3	62.5
Decapoda	2.4	3.8	66.7	21.6	20.2	55.0	13.9	12.4	43.3	62.8	21.3	90.0
Pteropoda	8.6	0.1	53.3	0.9	0.0	15.0	1.7	0.0	23.3	0.7	0.0	12.5
Larvaceans	10.6	0.0	20.0	0.0	0.0	0.0	6.5	31.3	6.7	0.0	0.0	0.0
Other	0.9	0.4	13.0	1.1	0.2	5.0	3.5	0.9	10.0	1.0	0.2	7.0
Number of stomachs		(30)			(20)			(30)			(40)	
Shelf												
Hyperidea	14.9	6.6	93.3	25.0	4.3	80.0	83.6	39.3	83.3	13.9	1.4	43.3
Euphausiacea	9.5	47.3	56.7	1.6	0.6	33.3	3.9	16.5	66.7	1.0	1.1	20.0
Calanoida	6.0	3.7	40.0	1.3	0.3	23.3	3.5	2.3	36.7	0.0	0.0	3.3
Fish	3.5	36.4	43.3	21.0	84.7	63.3	3.5	38.8	60.0	12.5	59.2	60.0
Decapoda	0.5	0.5	33.3	1.1	0.5	30.0	1.5	1.9	53.3	56.3	11.4	53.3
Pteropoda	65.3	3.2	56.7	47.4	0.9	50.0	3.1	0.2	43.3	13.6	0.1	30.0
Other	0.9	0.4	6.7	0.4	8.7	6.0	0.8	0.1	6.7	2.4	0.3	10.0
Number of stomachs		(30)			(30)			(30)			(30)	
Slope												
Hyperidea	85.7	40.2	100.0	39.6	5.7	90.0	91.3	74.9	95.0	1.7	0.1	20.0
Euphausiacea	3.0	30.1	95.0	57.9	94.0	100.0	2.4	22.0	95.0	92.5	8.7	90.0
Calanoida	2.2	13.6	65.0	0.0	0.0	0.0	1.1	0.4	45.0	0.6	0.0	10.0
Fish	0.2	3.2	50.0	0.5	0.2	60.0	0.2	0.5	45.0	3.5	91.0	60.0
Decapoda	0.6	7.6	30.0	0.0	0.0	0.0	1.0	1.8	40.0	1.8	0.3	30.0
Pteropoda	8.0	3.8	60.0	1.6	0.0	30.0	3.8	0.3	85.0	0.0	0.0	0.0
Other	0.2	1.4	15.0	0.3	0.0	10.0	0.3	0.0	10.0	0.0	0.0	0.0
Number of stomachs		(20)			(10)			(20)			(10)	
Oceanic												
Hyperidea	15.5	9.3	100.0	-	-	-	-	-	-	-	-	-
Euphausiacea	0.0	0.2	10.0	-	-	-	-	-	-	-	-	-
Calanoida	1.4	3.9	60.0	-	-	-	-	-	-	-	-	-
Fish	0.7	9.2	30.0	-	-	-	-	-	-	-	-	-
Decapoda	2.7	36.8	80.0	-	-	-	-	-	-	-	-	-
Pteropoda	79.6	49.3	100.0	-	-	-	-	-	-	-	-	-
Other	0.0	0.5	10.0	-	-	-	-	-	-	-	-	-
Number of stomachs		(10)			(0)			(0)			(0)	
	n = 90			n = 60			n = 80			n = 80		

Slope waters

Euphausiids and hyperiid amphipods were the two most important food items (Table 3). Pink, and chum salmon fed primarily on hyperiids, coho salmon fed primarily on fish, and sockeye salmon fed primarily on euphausiids. Euphausiids were also important prey for pink and chum salmon, and calanoid copepods were

consumed by pink salmon. Diets of sockeye and coho salmon were dominated by one prey type.

Oceanic waters

Diet information was only available for pink salmon collected from this habitat. Pteropods were the most important food item followed by decapod larvae (Table 3).

Alaska Peninsula

Data collected off the Alaska Peninsula were limited to examinations of juvenile pink salmon from shelf and slope waters and sockeye salmon from nearshore and shelf waters (Table 4). Average fork lengths for pink salmon (84–170 mm, \bar{x} = 120 mm) were similar to Southeast Alaska, while sockeye salmon (147–229 mm, \bar{x} = 185 mm) were considerably larger.

Nearshore waters

Diets of sockeye salmon consisted of decapod larvae, fish, and euphausiids.

Shelf waters

Hyperiid amphipods followed by euphausiids were important prey for pink salmon; decapod larvae followed by fish were important prey for sockeye salmon.

Oceanic waters

Pink salmon fed primarily upon hyperiid amphipods and decapod larvae.

Diet Overlap Among Species and Regions

Diets of pink and chum salmon were the most closely related; they had the highest similarity indices in four of the seven habitats with complete diet information (Table 5). The low correlation between pink and chum salmon in oceanic waters off Southeast Alaska arose from the high consumption of gelatinous species by chum salmon there. The most dissimilar diets occurred between coho and either pink or chum salmon. Sockeye diets were similar to diets of all other species, partially due to their lack of specialization in foraging as shown by the wide variety of prey items contained in their stomachs.

Coho salmon had the largest diet overlap in nearly all habitats and geographical areas where they fed consistently on fish (Tables 6 and 7). Percent similarity indices for coho salmon averaged 60.1 across all the habitats, which means that on the average over 60% of the prey biomass in their stomachs was similar among areas. Sockeye and chum salmon were the most diverse foragers with diet overlap indices averaging 37% across all habitats. Much of the spatial dissimilarity in chum diets resulted from the occasional occurrence of gelatinous prey items, or larvaceans in their stomachs (Tables 2–4).

Table 4. Summary of prey consumed by juvenile salmon caught in trawls off the Alaska Peninsula, 4–9 August, 1996: %N, percent by number; %W, percent by wet weight; and %FO, percent frequency of occurrence. Unidentified gelatinous and incidental prey are combined into an "Other" category. Prey weight data reported in the text are in bold type. Data for chum and coho salmon from the Alaska Peninsula were unavailable.

Prey taxon	Pink			Sockeye			Chum			Coho		
	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO
Near shore												
Hyperidea	-	-	-	2.2	1.2	42.5	-	-	-	-	-	-
Euphausiacea	-	-	-	79.9	19.8	56.5	-	-	-	-	-	-
Calanoida	-	-	-	0.4	0.2	47.8	-	-	-	-	-	-
Fish	-	-	-	0.1	31.4	30.4	-	-	-	-	-	-
Decapoda	-	-	-	16.5	47.0	91.3	-	-	-	-	-	-
Pteropoda	-	-	-	0.2	0.0	17.4	-	-	-	-	-	-
Other	-	-	-	0.5	0.5	17.3	-	-	-	-	-	-
Number of stomachs		(0)			(23)			(0)			(0)	
Shelf												
Hyperidea	98.7	72.5	100.0	83.5	7.1	80.0	-	-	-	-	-	-
Euphausiacea	0.2	18.9	40.0	0.7	8.6	40.0	-	-	-	-	-	-
Calanoida	0.8	6.3	70.0	0.1	0.1	10.0	-	-	-	-	-	-
Fish	0.0	0.0	0.0	0.7	22.0	60.0	-	-	-	-	-	-
Decapoda	0.0	1.9	10.0	14.7	64.1	100.0	-	-	-	-	-	-
Other	0.2	0.4	40.0	0.4	0.0	20.0	-	-	-	-	-	-
Number of stomachs		(10)			(10)			(0)			(0)	
Slope												
Hyperidea	93.9	79.8	100.0	-	-	-	-	-	-	-	-	-
Euphausiacea	0.3	0.5	50.0	-	-	-	-	-	-	-	-	-
Calanoida	0.3	0.3	40.0	-	-	-	-	-	-	-	-	-
Decapoda	5.3	19.5	70.0	-	-	-	-	-	-	-	-	-
Other	0.2	0.1	10.0	-	-	-	-	-	-	-	-	-
Number of stomachs		(10)			(0)			(0)			(0)	
	n = 20			n = 33			n = 0			n = 0		

Table 5. Percent similarity indices (PSI) of diet overlap between pairs of juvenile salmon species within habitat type and geographical area of capture.

Region	Habitat	Diet Overlap Indices					
		Pink-Sockeye	Pink-Chum	Pink-Coho	Sockeye-Chum	Sockeye-Coho	Chum-Coho
Southeast Alaska (SE)	Nearshore	47.4	78.7	12.4	43.4	52.2	16.1
	Shelf	58.3	85.4	33.1	47.6	11.5	33.5
	Slope	57.0	63.0	19.4	69.4	49.7	31.1
	Oceanic	85.7	18.9	80.7	17.1	77.0	13.3
Prince William Sound (PWS)	Nearshore	83.0	60.2	30.6	64.8	47.6	39.2
	Shelf	43.4	62.6	39.8	44.8	62.1	43.4
	Slope	36.0	79.3	12.3	27.9	9.0	9.6
Alaska Peninsula (AP)	Shelf	15.7					

Table 6. Percent similarity indices (PSI) of diet overlap between habitat types and areas for chum and coho salmon. The PSI measures the similarity in diet for chum and coho salmon among habitats and regions.

		Southeast Alaska				Prince William Sound	
Region	Habitat	Nearshore	Shelf	Slope	Oceanic	Nearshore	Shelf
Chum							
SE	Nearshore						
	Shelf	65.7					
	Slope	55.8	54.2				
	Oceanic	15.1	13.6	21.4			
PWS	Nearshore	54.0	45.9	58.2	12.5		
	Shelf	14.3	42.6	61.0	20.2	32.1	
	Slope	25.4	23.5	64.1	12.3	37.4	58.7
Coho							
SE	Nearshore						
	Shelf	92.5					
	Slope	67.6	72.5				
	Oceanic	28.7	33.2	52.9			
PWS	Nearshore	58.5	61.8	51.0	56.5		
	Shelf	62.2	60.9	61.2	25.8	65.2	
	Slope	95.7	96.8	71.3	32.3	61.4	60.7

Table 7. Percent similarity indices (PSI) of diet overlap between habitat types and areas for pink and sockeye salmon. The PSI measures the similarity in diet for pink and sockeye salmon among habitats and regions.

		Southeast Alaska				Prince William Sound				Alaska Peninsula		
Region	Habitat	Nearshore	Shelf	Slope	Oceanic	Nearshore	Shelf	Slope	Oceanic	Nearshore	Shelf	
Pink Salmon												
SE	Nearshore											
	Shelf	58.5										
	Slope	44.9	35.9									
	Oceanic	81.7	52.9	28.5								
PWS	Nearshore	85.3	43.9	39.2	84.8							
	Shelf	65.7	70.4	31.8	64.8	57.9						
	Slope	61.3	52.7	76.3	44.5	54.3	47.7					
	Oceanic	23.8	19.1	22.7	18.1	16.8	23.8	25.3				
Alaska	Shelf	41.6	27.0	86.5	28.7	40.9	30.1	67.7	15.7			
	Slope		18.1		2.5	64.0	6.6	21.6	8.0	49.0	29.7	75.3
Sockeye Salmon												
SE	Nearshore											
	Shelf		39.6									
	Slope		89.7	40.2								
	Oceanic		50.2	45.0	64.1							
PWS	Nearshore	40.2	26.7	53.5	74.8							
	Shelf		52.3		3.4	23.3	11.9		6.7			
	Slope		33.2	25.4	45.6	75.3	74.4		5.1			
AP	Nearshore	55.2	21.5	40.1	26.5	42.4	34.4	21.2				
	Shelf	38.4	7.7	32.2	16.0	27.5	27.5	12.5				76.9

Pink salmon diets were used for spatial comparisons among regions because pink salmon occurred in all habitats and regions where juvenile salmon were encountered. When compared across habitats but within regions, pink salmon diets were more similar within Southeast Alaska (SE) than within Prince William Sound (PWS; Table 7). Comparisons between these two regions showed that diet consistency within a region was no greater than between regions. In fact, the highest diet overlap in these two regions was cross-regional, occurring between the nearshore habitats of SE and PWS.

DISCUSSION

Planktonic crustaceans were present in the diets of all four salmon species. Euphausiids were the primary food item for pink, sockeye, and chum salmon in most region/habitat strata. Hyperiid amphipods were the next most important crustacean, with decapod larvae, pteropods, and calanoid copepods being occasionally important in the diets. Fish, however, were the primary food item for coho salmon in nearly all cases and were often important to the other species, particularly in nearshore and shelf waters off Southeast Alaska and in shelf waters off Prince William Sound.

Despite the importance of euphausiids and fish in juvenile salmon diets, prey types still varied extensively by habitat and region, particularly for sockeye and chum salmon. Each one of the secondary food items, e.g., hyperiid amphipods, decapod larvae, etc., were occasionally very important, but it is unclear if these changes in importance were due to changes in prey availability, selection of particular prey within certain strata, or foraging competition.

We suspect that some combination of these three processes, particularly prey availability and prey selection, was found in our data. For example, prey selection in some form was apparent throughout our study area. Diet overlap rates between species were more often below 50% than above. In several strata, the diet overlap between coho salmon and other species even dropped below 10%. Many of these differences were due to the larger body size and distinct feeding behavior of coho salmon, who predominately fed on osmerid larvae, one of the largest prey items which typically ranged from 30 to 35 mm in length. Salmon, particularly coho salmon, are known both to feed opportunistically and to select prey on the basis of size, availability, and ease of capture (Ricker 1937; Brooks and Dodson 1965; Carlson 1976; Eggers 1978; Murphy et al. 1988). The piscivorous tendency of coho salmon may alleviate foraging competition with other species, lowering its diet overlap when large prey items are available. Size-selective foraging can also incur energetic advantages for the preda-

tor by increasing consumption for a given number of prey items.

Prey selection combined with prey availability may best explain the preponderance of gelatinous zooplankton in the chum diets collected from Southeast Alaska oceanic habitat, particularly given a selective preference for gelatinous taxa by chum salmon (Welch and Parsons 1993; Landingham et al. 1998). Alternatively, the incidence of gelatinous zooplankton could suggest competition between pink and chum salmon in this habitat (incurring prey switching); consumption of this energetically less favorable prey (Davis et al. 1998) has been shown to increase in areas of high pink salmon abundance (Tadokoro et al. 1996). There was little evidence, however, for a competitive feeding strategy—at least in some of the areas and habitats in our study. For instance, diet similarity of pink and chum salmon (the two most abundant species in the survey; Carlson et al. (1996)) off Southeast Alaska was higher in the nearshore than the slope area, even though catch rates of these species were also highest nearshore.

Differences in prey among regions and habitats suggest the possibility that juvenile salmon feeding (particularly pink and chum salmon) was associated more with availability than with preference for specific organisms (e.g., LeBrasseur 1966). Pink salmon in Southeast Alaska consumed a much higher percentage of fish, one of the largest prey items, than pink salmon in Prince William Sound even though the Southeast Alaska pink salmon were smaller in size. Similarly, smaller chum salmon in nearshore waters of Southeast Alaska consumed a much higher percentage of fish than the larger chum salmon in shelf waters of the same region (see Carlson et al. (1996) for data on sizes of juvenile salmon by habitat type). We would have expected the opposite—that the larger fish would have an increased proportion of larger prey items—if feeding was predominately size-based; thus the data suggest the importance of prey availability in the diets of juvenile salmon migrating in the coastal GOA.

In summary, variations in foraging of juvenile salmon along the coastal waters of the northern Gulf of Alaska appear to be associated with both selection and availability of prey. The small proportion, 3%, of empty stomachs along with sustained high diet overlap indices in areas of high pink and chum salmon abundance suggest that the availability of prey resources does not appear to be a major limiting factor for production and growth of juvenile salmon examined in this study. A more definitive analysis of foraging strategy is beyond the scope of this study, however, as it would require joint analysis of stomach contents and prey availability (Landingham et al. 1998), the latter of which was not collected during the cruise. Further small-scale studies integrating data on feeding behavior,

prey size and abundance, growth, and energetics of juvenile salmon in coastal waters of the Gulf of Alaska would shed additional insight into salmon foraging tactics, particularly with respect to feeding and migration strategies and the growth potential of juvenile salmon during their first year at sea.

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Diel Catches and Food Habits of Sockeye, Pink, and Chum Salmon in the Central Bering Sea in Summer

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Keywords: Sockeye salmon, pink salmon, chum salmon, diel catch, diel feeding habits, salmon stomach contents, salmon prey composition, Bering Sea

Abstract: Sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon caught by gillnet in the central Bering Sea were observed for diel changes in prey composition and stomach content weight. Sockeye salmon catches peaked after sunrise, and pink salmon catches increased dramatically between sunset and sunrise. Chum salmon abundance was low, but catches increased after sunrise and in the middle of the day. Sockeye, pink, and chum salmon fed throughout the day and peaks in feeding activity varied. Sockeye feeding increased after sunset, while pink salmon showed two periods of increased feeding activity, one after sunset and another at noon. Chum salmon stomachs contained prey at all times of the day, although there was a peak in feeding activity in the mid-afternoon. Sockeye, pink, and chum salmon stomach contents contained fish during the day, and increased their feeding on euphausiids and copepods during the night. A shift in salmon prey between daytime and nighttime feeding periods suggests that sampling throughout the diel cycle is required to provide an accurate assessment of salmon feeding ecology.

INTRODUCTION

Previous studies of diel changes in immature and maturing salmon food habits in the North Pacific Ocean have included trawling and serial sampling with gillnets in the waters off eastern Kamchatka (Machidori 1968; Ueno et al. 1969; Chuchukalo et al. 1995; Volkov et al. 1995a,b), the Okhotsk Sea (Shimazaki and Mishima 1969; Gorbatenko and Chuchukalo 1989; Chuchukalo et al. 1995; Volkov et al. 1995a, b), Gulf of Alaska (Percy et al. 1984), and the Bering Sea (Azuma 1992; Chuchukalo et al. 1995; Radchenko and Chigirinsky 1995). Machidori (1968) reported on experiments using gillnets and concluded that feeding activity of immature and maturing sockeye (*Oncorhynchus nerka*) and chum (*O. keta*) salmon was greater during the day than at night and that light was necessary for salmon feeding. Other studies using shorter sampling intervals have concluded that sockeye salmon feed most actively in late afternoon until midnight (Ueno et al. 1969), and that by morning, sockeye salmon stomachs are empty (Chuchukalo et al. 1995). Alternatively, sockeye salmon have been reported to feed after sunset and

continue through the night (Percy et al. 1984; Azuma 1992). Results for maturing pink salmon (*O. gorbuscha*) were more varied with experiments indicating intensive feeding immediately after sunrise and sunset (Shimazaki and Mishima 1969), in the evening and shortly after midnight (Ueno et al. 1969), and a somewhat less active feeding period in the mid-morning (Percy et al. 1984). In coastal areas off western Kamchatka, maturing pink salmon fed actively during the day and ceased feeding at night (Gorbatenko and Chuchukalo 1989). From earlier studies of immature and maturing chum salmon, active feeding periods have been found immediately after sunrise and sunset (Shimazaki and Mishima 1969; Ueno et al. 1969), and alternatively, chum salmon have been observed to show little or no diel variation in their feeding activity (Percy et al. 1984; Azuma 1992). Inconsistency in results suggest that feeding periods of immature and maturing salmon at sea may change in response to several factors including day length, physical characteristics of the water column, and prey availability. However, for salmon food habit surveys to be useful in estimating prey consumption, sampling must be conducted to reflect

the shifts that might occur in the diel feeding activities (Davis *et al.* 1998).

In odd years, maturing pink salmon are abundant in the central Bering Sea in the summer, which may contribute to shifts in chum distribution and may indirectly influence the growth of chum salmon (Azumaya and Ishida; this volume). Increased consumption of gelatinous zooplankton by chum salmon has been observed when pink salmon abundance was high in the Bering Sea (Tadokoro *et al.* 1996). However, no previous study in the central Bering Sea has reported salmon food habits over the 24-hour period for sockeye, pink, and chum salmon. In this study, we conducted gillnet operations throughout the diel period and examined changes in catch, stomach content weight, and prey composition of sockeye, chum, and pink salmon.

MATERIALS AND METHODS

Environmental Conditions

Sea surface temperature (SST), percent cloud cover, and weather conditions were recorded every hour during the 24-hour sampling period (July 11–12, 1997). Sunrise and sunset time and moon phase were also recorded. At noon (local time, GMT+12) a CTD probe was lowered to 1000 m to measure temperature and salinity.

Gillnet Operations

Gillnet operations were conducted between 57°33'N, 178°41'W and 57°27'N, 178°20'W in the central Bering Sea (Nagasawa *et al.* 1997). Eight operations were conducted in a 24-hour period start-

ing at 0600 hrs and ending at 0500 hrs the following day using a surface gillnet (length = 950 m, fishing depth = 0–6 m, mesh size = 115 mm; Table 1). The gillnet set locations were 7.0 to 9.2 km apart. Setting the gillnet required five to six minutes after which it was allowed to soak for two hours. The duration of gillnet retrieval ranged from 16 to 23 min. Although vertical movements of high-seas salmon are different between daylight and dark periods, salmon spend a portion of time at the surface during all periods of the day (Walker *et al.* 1999, 2000), thereby making it possible for gillnets to catch salmon at the surface throughout the diel cycle. To catch salmon from a narrow range of sizes, a single mesh size was used. The mesh size (115 mm) was selected because it is efficient at catching immature and maturing salmon in the Bering Sea in summer.

Salmon Examination

After each gillnet retrieval, the catch was sorted by species and counted. If the number of individuals per species was greater than 50, the catch was subsampled due to logistical constraints (Table 1). Fork length, and body and gonad weight were measured and a scale sample was collected. The salmon stomachs were removed and frozen individually. After thawing, the stomach samples were weighed on a balance before and after removal of the stomach contents, and the weight of the contents obtained by subtraction. A stomach content index (SCI) was calculated as the ratio of measured prey weight to salmon body weight times 100, and differences in day and night catches and mean weight of stomach contents were compared using chi-square and one-way ANOVA.

Table 1. Salmon catches from eight consecutive gillnet sets on 11–12 July 1997 in the Bering Sea. Sample is the number of salmon sampled for stomach contents. Gillnet set and retrieval time is the local time (GMT+12) when setting and retrieval of the net began. Sunrise time is 03:11 (local) and sunset time is 20:47 on 11 July. Sunrise time is 03:12 on 12 July. Shading indicates periods in darkness.

Set number	SST (°C)	Gillnet set and retrieval time	Sockeye		Pink		Chum		Coho		Chinook		Total	
			Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample
1	8.3	0600–0800	25	25	140	67	6	6	1	1	0	0	172	99
2	8.5	0859–1100	29	29	145	35	10	10	0	0	0	0	184	74
3	8.5	1159–1400	24	24	129	21	26	26	0	0	5	5	184	76
4	8.6	1459–1700	16	16	114	51	5	5	0	0	3	3	138	75
5	8.6	1758–1959	27	27	117	39	9	9	0	0	0	0	153	75
6	8.6	2100–2259	23	23	221	50	9	9	0	0	0	0	253	82
7	8.4	0300–0500	21	21	278	50	9	9	0	0	0	0	308	80
8	8.3	0300–0500	68	50	273	20	20	20	0	0	0	0	361	90
Total			233	215	1417	333	94	94	1	1	8	8	1753	651
% Sampled				92		24		100		100		100		37

Prey composition was determined by separating the stomach contents into twelve prey categories (euphausiids, copepods, amphipods, crab larvae, squid, pteropods, fish, polychaetes, chaetognaths, gelatinous zooplankton, other, and unidentified), and visually estimating the percent volume of each category following the method of Pearcy et al. (1984). Combining less important groups reduced the number of prey categories to eight and the weight of these major prey categories was estimated by multiplying the percent volume of each group by the total measured stomach content weight, assuming the density of all prey was similar.

The degree of digestion was qualitatively described using an index described by Pearcy et al. (1984). Prey were categorized as either fresh, medium, or digested. Fresh prey was intact with no obvious digestion; medium digested prey, such as fish and squid, was missing skin, and euphausiids were opaque; and digested fish consisted of white flesh and bones, and crustaceans were in pieces. Usually digested prey, with the exception of gelatinous forms, was identifiable to prey category. The digestion index was noted as a general guide to the condition of the stomach contents.

RESULTS

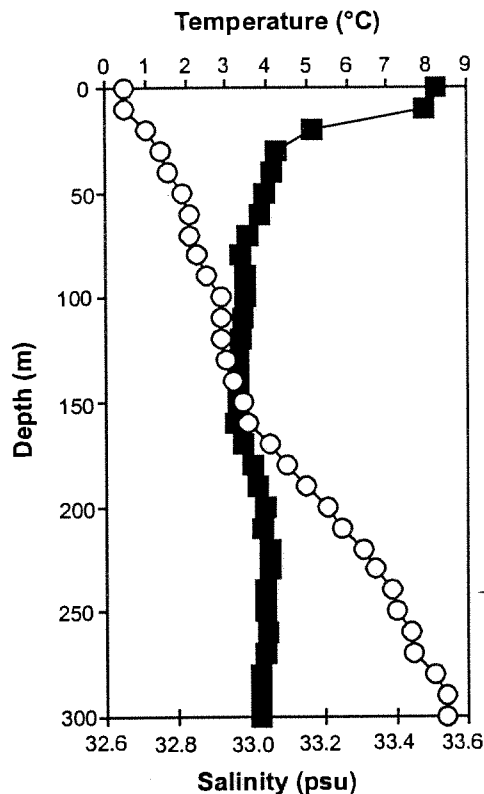
Environmental Conditions

The duration of daylight was approximately 17 hours when these operations were conducted (sunrise = 0311 hrs, sunset time = 2047 hrs). The moon phase was waxing to the first quarter and a continuous 100% cloud cover persisted during the diel period, which included drizzling rain between 2300 and 0200 hrs. Hourly sea surface temperatures ranged from 8.3° to 8.6°C (Table 1). The maximum seawater temperature was located at the surface and temperatures decreased to 4.48°C at 100 m (Fig. 1). The temperature minimum was located at 80 m (3.36°C), and a shallow thermocline was located between 10 and 20 m, where temperatures decreased rapidly from 7.90° to 5.11°C and continued to decrease to 4.23°C at 30 m.

Diel Salmon Catch

A total of 1,753 salmon was caught in eight gillnet operations (Table 1). Pink salmon was the most abundant salmon in the catch (81%), followed by sockeye (13%), chum (5%), chinook (1%), and coho salmon (< 1%). Sockeye, chum, and pink salmon were caught in all eight time periods, but coho ($n = 1$) and chinook ($n = 8$) salmon were caught only in the morning and afternoon. A relatively large catch of

Fig. 1. Upper water layer profile of temperature (closed box) and salinity (open circle) in the central Bering Sea at 57°30'N, 178°30'W on 10 July 1997 compiled from conductivity-temperature-depth probe data. Temperature decreased rapidly from 8.3°C at the surface to 4.2°C at 30 m depth.



pink, chum, and sockeye salmon was obtained immediately after sunrise (0300–0500 hrs; Table 1). The smallest catch of sockeye salmon occurred in late afternoon (1500–1700 hrs). Sockeye salmon catches were not independent of day and nighttime gillnet sets (χ^2 ; $p = 0.03$; $df = 1$). More sockeye salmon were caught during daylight and less during the night than would have been expected if catches had been equal in every time period. Pink salmon catches were also small in the afternoon and early evening (1500–2000 hrs) but increased dramatically immediately after sunset and remained at a high level until after sunrise (0300–0500 hrs). Pink salmon catches were not independent of day and night gillnet sets, as few salmon were caught during the day and more at night than would have been expected with equal catches in each time period (χ^2 ; $p = < 0.001$; $df = 1$). Chum salmon catches were relatively small throughout the sampling period, although chum catches increased shortly after sunrise (0300–0500 hrs) and after noon (1200–1400 hrs). The catch of chum salmon was independent of whether the gillnet was fishing during the day or night (χ^2 ; $p = 0.19$; $df = 1$).

Salmon Biological Characteristics

Sockeye salmon in gillnet catches were 62% male, predominantly immature (92%), and mostly ocean age .2 (94%) fish (Table 2). A few ocean age .3 sockeye salmon were caught and there was no catch of ocean age .1 fish. The mean fork length of sockeye salmon was significantly different among time periods (ANOVA; $p < 0.001$; $df = 7$). Although the Tukey multiple comparisons test did not detect which means were significantly different from one another ($p > 0.50$), the greatest difference in mean fork length was in the time interval before and after sunset (1500–1700 hrs, mean = 517 mm; 1800–2000 hrs, mean = 470 mm). However, a comparison of fork lengths of sockeye salmon caught in daytime versus nighttime sets was not significantly different (p

= 0.66; $df = 1$). Two-thirds (66%) of the pink salmon were males, and all the fish were maturing ocean age .1. There was no significant difference in mean fork lengths among time periods ($p = 0.27$; $df = 7$), or between catches in daytime and nighttime gillnet sets ($p = 0.21$; $df = 1$). Half (51%) of the chum salmon were female and approximately half (53%) were maturing. Ocean age .2, .3, and .4 chum salmon were caught, but ocean age .3 was the most abundant age group (61%). The mean fork lengths of chum salmon caught during each time period were not significantly different, either among time periods ($p = 0.68$; $df = 7$), or between daytime and nighttime catches ($p = 0.81$; $df = 1$). The food habits data were not stratified for predator size because the fork length among individuals of each salmon species was similar between day and nighttime periods.

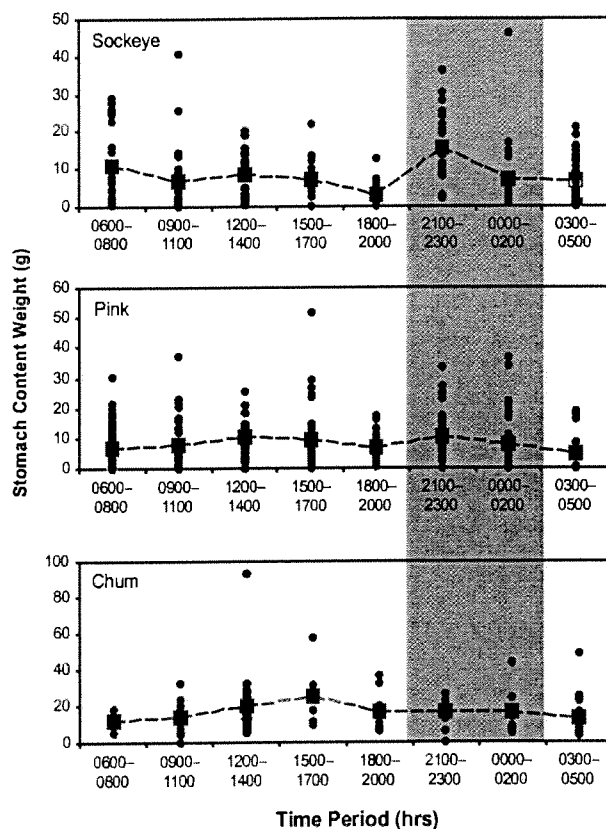
Table 2. Fork length (mm; sd = standard deviation), body weight (g), sex and maturity ratios, and age composition of sockeye, pink, and chum salmon caught in consecutive gillnet sets. Totals are data combined for all time periods. Shading indicates periods in darkness.

Species	Time period	Sample size	Fork length		Body weight		Percent female	Percent immature	Percent ocean age			
			mean	sd	mean	sd			1	2	3	4
Sockeye	0600–0800	25	485	29	1435	316	24	96	0	96	4	0
	0900–1100	29	478	26	1272	218	34	97	0	96	4	0
	1200–1400	24	494	45	1448	444	21	79	0	88	12	0
	1500–1700	16	517	50	1652	702	31	38	0	81	19	0
	1800–2000	27	470	21	1179	143	67	100	0	100	0	0
	2100–2300	23	492	26	1371	272	57	100	0	100	0	0
	0000–0200	21	480	26	1290	264	19	95	0	100	0	0
	0300–0500	50	478	22	1244	181	40	100	0	90	10	0
	Total	215	484	32	1333	336	38	92	0	94	6	0
Pink	0600–0800	67	455	19	1198	154	30	0	100	0	0	0
	0900–1100	35	460	22	1234	167	31	0	100	0	0	0
	1200–1400	21	458	17	1209	134	43	0	100	0	0	0
	1500–1700	51	460	24	1268	190	27	0	100	0	0	0
	1800–2000	39	451	17	1153	135	49	0	100	0	0	0
	2100–2300	50	453	22	1165	169	34	0	100	0	0	0
	0000–0200	50	455	21	1170	166	34	0	100	0	0	0
	0300–0500	20	460	16	1201	153	35	0	100	0	0	0
	Total	333	456	20	1202	165	34	0	100	0	0	0
Chum	0600–0800	6	531	55	1845	592	50	50	0	33	67	0
	0900–1100	10	546	77	2149	1125	50	30	0	40	30	30
	1200–1400	26	526	50	1784	515	42	39	0	24	64	12
	1500–1700	5	569	48	2104	559	40	0	0	20	40	40
	1800–2000	9	533	60	1898	1032	44	67	0	22	67	11
	2100–2300	9	524	38	1629	454	67	67	0	33	56	11
	0000–0200	9	547	50	1862	299	44	44	0	22	78	0
	0300–0500	20	526	43	1667	394	55	60	0	21	68	11
	Total	94	533	52	1822	640	51	47	0	26	61	13

Diel Food Habits of Sockeye Salmon

Stomach contents of sockeye salmon illustrated a diel pattern where prey weight was significantly greater among fish caught during the night than during the day (ANOVA; $p < 0.001$; $df = 1$; Fig. 2). There was one peak in stomach contents weight immediately after sunset (2100–2300 hrs; Table 3). The proportion of stomach contents in a fresh state of digestion was higher during the sunset to early morning hours than in the mid- to late afternoon. Mean stomach content weight decreased from mid-to late afternoon and was at a minimum before sunset (1800–2000 hrs). Few empty stomachs ($n = 3$) were collected from sockeye salmon, regardless of the sampling period, indicating that sockeye were able to find prey during all periods. Sockeye shifted from nighttime feeding on euphausiids and copepods to daytime feeding on fish and crab larvae.

Fig. 2. Stomach content weight of sockeye, pink, and chum salmon. Time period is the time of day when the fish was caught. The solid square and dashed line indicate the mean value for each time period. Solid circles represent the value for each fish examined. Shading indicates time periods in darkness.



Diel Food Habits of Pink Salmon

Stomach contents of pink salmon caught during the day and night were not significantly different from one another (ANOVA; $p = 0.07$; $df = 1$; Fig. 2), although there was increased feeding activity after noon (1200–1400) and immediately after sunset (2100–2300 hrs; Table 4). Empty stomachs ($n = 22$) were collected from midnight until late afternoon and the number of empty stomachs collected from pink salmon was higher than for sockeye and chum salmon. Pink salmon fed on fish during all time periods. During the night, euphausiids and copepods were important prey and during the day fish and crab larvae were the predominant prey.

Diel Food Habits of Chum Salmon

There was no significant difference between day and nighttime weight of stomach contents of chum salmon (ANOVA; $p = 0.90$; $df = 1$; Fig. 2). In every sampling period, chum had more prey in their stomachs than either pink or sockeye salmon (Table 5). Unlike the diel feeding of sockeye and pink salmon, chum salmon had an increase of stomach content weight in the middle to late afternoon (1500–1700), when fish were a major component of the diet, and showed no peak in prey weight after sunset. The afternoon period when stomach content weight was at a maximum (1500–1700) was also the time interval with the smallest sample size ($n = 5$) and, therefore, may not have been representative. Chum salmon, like sockeye salmon, had few empty stomachs ($n = 2$), suggesting chum salmon were able to find food at all times of the day. Chum salmon diet was more diverse than that of sockeye and pink salmon. In addition to fish, squid, euphausiids, and copepods, chum salmon also ate gelatinous zooplankton (medusae, ctenophores, and salps), appendicularians, and pteropods. The proportion of fish in chum stomachs decreased from evening through night and then gradually increased again from morning to afternoon. Chum salmon fed on gelatinous zooplankton during the day and night, although it was a less important component of the diet during the early morning daylight hours (0300–0800). Similar to feeding of sockeye and pink salmon, chum salmon increased their feeding on euphausiids during the night.

DISCUSSION

We caught sockeye, chum, and pink salmon at the surface (0–6 m) during each of the six daylight gillnet operations, providing evidence that these species spent some portion of their time at the surface during daylight periods. Previous gillnet studies have

Table 3. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of sockeye salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

Sockeye Salmon	Time Period							
	0600–0800	0900–1100	1200–1400	1500–1700	1800–2000	2100–2300	0000–0200	0300–0500
Sample size	25	29	24	16	27	23	21	50
Empty stomachs (%)	0	0	0	6	4	0	0	2
Degree of digestion (%)								
fresh	0	0	0	0	0	83	95	37
medium	72	7	0	6	15	17	5	42
digested	28	93	100	88	81	0	0	18
Stomach content weight								
mean	10.74	6.81	8.52	7.35	3.12	15.60	7.30	6.82
sd	9.24	8.62	5.82	5.20	2.59	8.70	10.21	5.56
SCI								
mean	0.75	0.55	0.63	0.50	0.27	1.15	0.56	0.56
sd	0.68	0.71	0.44	0.34	0.24	0.57	0.72	0.44
Estimated mean weight of major prey categories (g)								
euphausiids	1.4	0.1	0.2	0.0	0.0	3.8	4.0	0.4
copepods	2.6	0.2	0.3	0.6	0.0	10.2	2.0	2.3
crab larvae	0.1	1.2	3.5	4.2	1.2	1.2	0.6	0.1
squid	0.3	0.1	0.2	0.2	0.2	0.2	0.6	0.5
fish	5.7	5.0	4.3	2.3	1.3	0.2	0.1	3.5
other ¹	0.6	0.3	0.1	0.1	0.4	0.0	0.0	0.1
Estimated mean volume of major and minor prey categories (%)								
euphausiids	6.9	2.4	2.5	0.3	0.6	30.1	71.7	10.7
copepods	13.5	2.8	2.2	7.5	0.6	52.7	13.0	20.1
amphipods	5.0	3.7	0.0	0.0	1.3	0.0	1.0	1.2
crab larvae	3.5	34.8	47.4	58.4	34.6	12.9	3.7	0.7
squid	4.7	3.3	1.6	0.9	5.7	2.5	10.0	13.5
pteropods	0.9	0.7	0.1	0.0	0.0	0.0	0.0	2.2
fish	63.6	49.0	45.3	25.3	42.5	1.8	0.6	47.3
polychaetes	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
chaetognaths	0.1	0.0	0.4	0.0	0.0	0.0	0.0	0.0
gelatinous zooplankton ²	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
other ³	0.2	4.7	0.1	1.3	10.0	0.0	0.0	2.4
unidentified material	0.8	0.0	0.4	0.0	1.1	0.0	0.0	0.0

¹includes amphipods, pteropods, polychaetes, chaetognaths, appendicularians, mysids, and unidentified prey.

²includes medusae, ctenophores, and salps.

³includes appendicularians and mysids.

Table 4. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of pink salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

Pink Salmon	Time Period							
	0600-0800	0900-1100	1200-1400	1500-1700	1800-2000	2100-2300	0000-0200	0300-0500
Sample size	67	35	21	51	39	50	50	20
Empty stomachs (%)	4	12	5	4	0	0	10	35
Degree of digestion (%)								
fresh	0	0	0	0	5	70	10	20
medium	30	14	43	14	44	26	54	30
digested	66	74	52	82	51	4	26	15
Stomach content weight								
mean	6.61	7.79	10.33	9.29	6.56	10.64	7.67	4.59
sd	6.61	8.53	6.50	9.07	4.00	6.95	8.46	6.17
SCI								
mean	0.56	0.65	0.85	0.73	0.57	0.90	0.69	0.38
sd	0.56	0.70	0.52	0.66	0.34	0.59	0.64	0.53
Estimated mean weight of major prey categories (g)								
euphausiids	0.1	0.1	1.0	0.0	0.0	1.2	2.7	1.6
copepods	0.4	0.6	0.2	0.5	0.4	3.6	2.7	0.5
crab larvae	0.4	1.6	3.1	3.6	2.1	2.8	0.5	0.0
squid	0.1	0.2	1.5	0.5	0.4	0.7	0.6	0.1
fish	5.5	5.2	4.4	4.6	3.6	2.2	1.0	2.1
other ¹	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.2
Estimated mean volume of major and minor prey categories (%)								
euphausiids	2.1	1.3	6.2	0.5	0.0	10.6	21.9	15.5
copepods	6.9	5.3	1.6	4.4	3.5	27.5	32.5	8.7
amphipods	3.8	0.9	0.9	0.5	1.0	0.4	0.7	2.7
crab larvae	19.3	38.3	31.3	48.9	35.6	30.4	12.5	1.6
squid	3.3	2.6	7.9	3.4	7.3	7.0	4.2	2.1
pteropods	1.4	0.0	0.0	0.1	0.3	0.6	0.0	1.7
fish	58.0	39.9	46.9	38.0	52.2	23.5	16.2	32.9
polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
gelatinous zooplankton ²	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
other ³	0.7	0.0	0.8	0.2	0.1	0.1	2.0	0.0
unidentified material	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0

¹includes amphipods, pteropods, polychaetes, chaetognaths, appendicularians, mysids, and unidentified prey.

²includes medusae, ctenophores, and salps.

³includes appendicularians and mysids.

Table 5. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of chum salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

Chum Salmon	Time Period							
	0600–0800	0900–1100	1200–1400	1500–1700	1800–2000	2100–2300	0000–0200	0300–0500
Sample size	6	10	26	5	9	9	9	20
Empty stomachs (%)	0	10	0	0	0	11	0	0
Degree of digestion (%)								
fresh	0	0	0	0	0	33	22	50
medium	0	80	8	0	44	56	78	45
digested	100	10	92	100	56	0	0	5
Stomach content weight								
mean	12.03	14.06	19.86	25.20	16.36	16.47	16.10	13.35
sd	4.34	9.73	16.75	19.90	11.00	8.62	11.99	11.28
SCI								
mean	0.74	0.73	1.04	1.24	0.83	1.07	0.85	0.77
sd	0.50	0.48	0.54	0.99	0.32	0.64	0.50	0.52
Estimated mean weight of major prey categories (g)								
euphausiids	0.2	0.0	0.1	0.4	0.0	3.5	2.3	1.0
copepods	0.0	0.0	0.3	0.2	0.1	1.6	1.0	0.7
squid	0.5	0.5	1.1	0.3	0.5	0.5	1.5	– 0.3
pteropods	4.9	0	0.3	0.3	0.4	2.6	0.3	0.4
fish	3.0	3.8	12.5	22.6	10.9	3.0	1.9	6.0
gelatinous zooplankton ¹	0.7	8.2	2.5	0.7	2.9	2.3	3.4	0.3
appendicularians	0.4	1.5	0.8	0.1	0.3	0.7	2.8	3.9
other ²	2.3	0.0	2.2	0.6	1.1	2.1	2.9	0.7
Estimated mean volume of major and minor prey categories (%)								
euphausiids	1.7	0.0	0.8	1.4	0.0	17.8	16.1	7.3
copepods	0.8	0.1	2.5	1.4	0.3	10.0	8.1	5.2
amphipods	0.8	0.1	0.1	0.0	0.0	3.3	6.7	2.8
crab larvae	0.0	0.0	2.3	2.0	0.6	0.0	0.0	0.0
squid	4.2	3.5	5.0	2.0	3.9	3.3	6.7	3.2
pteropods	40.8	0.3	2.0	1.0	2.8	13.9	3.3	3.1
fish	16.7	14.5	57.9	83.2	68.0	15.6	7.8	32.3
polychaetes	1.7	0.1	0.2	0.0	0.0	1.1	0.6	0.0
chaetognaths	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
gelatinous zooplankton ¹	7.5	52.4	14.0	4.0	17.8	12.8	25.0	2.5
other ³	6.7	19.0	4.2	1.0	4.4	3.3	13.9	41.0
unidentified material	19.2	0.0	11.0	4.0	2.2	7.8	13.4	2.8

¹includes medusae, ctenophores, and salps.

²includes amphipods, crab larvae, polychaetes, chaetognaths, mysids, and unidentified prey.

³includes appendicularians and mysids.

generally shown that catches were generally higher during the night than during the day (Taguchi 1963; Manzer 1964; Takagi 1971; Pearcy et al. 1984; Azuma 1991). Based on these studies, it was hypothesized that perhaps salmon remained at depth during the day (Taguchi 1963; Manzer 1964). Although no consistent diel pattern was shown for short duration tracking of sockeye, pink, and chum using ultrasonic tags (Ogura and Ishida 1995), recent archival tag data recovered from salmon released on the high seas and recovered after many days in the coastal areas of Alaska and Japan have corroborated that salmon generally remain at the surface (< 10 m) during the night and, therefore, are susceptible to capture by gillnets (Wada and Ueno 1999; Walker et al. 2000). During the day, these data have shown that salmon swimming behavior by depth is highly variable because the fish are making continuous dives and ascents from the surface to a depth of approximately 50 m, or more (Walker et al. 2000). This behavior makes them vulnerable to capture by gillnets in the daytime when salmon return to the surface between dives.

Our results showed that sockeye salmon have a diel rhythm to their food habits with a peak in feeding activity in the evening after sunset (2100–2300 hrs). Earlier studies have reported a diel pattern to sockeye salmon feeding, where the most active feeding time was in the late afternoon before sunset until midnight (Ueno et al. 1969), or late in the evening (Pearcy et al. 1984; Azuma 1992). Azuma (1992) observed a secondary feeding period in the morning soon after sunrise (0400–0600 hrs), as did we (0600–0800 hrs). In our study in the central area of the Bering Sea, we noted a distinct change in the prey composition over the diel period from euphausiids and copepods in sockeye salmon stomachs collected at night to a striking predominance of fish and crab larvae in stomach contents sampled during the day. Pearcy et al. (1984), sampling in the Gulf of Alaska, likewise observed a shift in sockeye salmon prey composition from euphausiids at night to amphipods during daylight periods. In the western Bering Sea, Chuchukalo et al. (1995) observed that sockeye salmon fed primarily on euphausiids and squids at night and the proportion of copepods, hyperiid amphipods, and pteropods increased during the day.

We observed a pattern in pink salmon food habits characterized by two peaks in feeding intensity, one at night after sunset, and another at mid-day. Earlier studies have observed that pink salmon have a diel rhythm to their food habits, and feeding activity increased immediately after sunset and continued through the night (Shimazaki and Mishima 1969; Ueno et al. 1969; Pearcy et al. 1984). In the Bering Sea, we observed that at night pink salmon decreased the proportion of fish and increased the proportion of

euphausiids and copepods in their stomach contents. Shimazaki and Mishima (1969) saw no evidence of a switch in prey types between day and night in the Okhotsk Sea. However, in the Gulf of Alaska there was a clear increase in feeding on euphausiids during the night (Pearcy et al. 1984).

We observed that chum salmon stomachs contained relatively large volumes of prey at all times of the day, and there was a peak in feeding in the mid-afternoon. Earlier diel experiments on chum salmon have shown varied results regarding the period of the day when feeding is most active. Feeding indices of chum salmon collected after sunset and sunrise were greater than those for chum collected during the day and night in the Okhotsk Sea and in the North Pacific off eastern Kamchatka (Shimazaki and Mishima 1969; Ueno et al. 1969). Pearcy et al. (1984) found no suggestion of diel periodicity of stomach fullness in chum salmon. The chum they observed fed predominately on salps in the afternoon and euphausiids from sunset until mid-day. Azuma (1992) concluded that the peak time for chum salmon feeding was in the morning, and that chum salmon were adapted to quickly digest large volumes of relatively non-nutritious prey organisms. The most interesting observation in our study was that chum salmon collected during the day were feeding substantially on fish. Unfortunately, our catch of chum salmon was small, but we speculate that chum salmon may shift their behavior from feeding predominantly on gelatinous zooplankton to fish during the day, thereby substantially increasing the caloric and nutritious quality of their diet.

The qualitative digestion index is well established in previous high seas salmon food habits studies (Pearcy et al. 1984; Azuma 1994). However, there is an inherent problem associated with using this index. There is only one value (fresh, medium, or digested) assigned to each stomach and a problem arises when the contents of the stomach are not at the same stage of digestion. This can happen when there are large and small prey items present in one stomach, when prey is in different locations in the stomach (front to back), when prey is positioned in the exterior or interior of the food bolus, and when prey of different digestibility are located in one stomach sample (for example, euphausiids digest more quickly than hyperiid amphipods). We reported the digestion index to provide a general qualitative description of the condition of the prey in the stomachs in each time period. Development of a more comprehensive and objective measure of the level of digestion would be a useful contribution for future studies of salmon food habits.

If we assume that salmon feed actively only at night on zooplankton and fish, and that fish is present in salmon stomach contents during the day because

fish is digested more slowly than zooplankton; then we would expect stomach content weight to decrease over succeeding daylight hours until it reached a minimum before sunset. However, this was not our result. In this experiment, stomach content weight is actually higher in daylight than dark periods for chum salmon, and sockeye and pink salmon have at least one daylight time period when there is about the same amount of food in the stomachs as during the dark periods. These results suggest that fish were feeding throughout the 24-hour period, whenever prey was available. Nighttime competition for euphausiids may be intense, particularly when pink salmon are abundant, and when the period of darkness is short during summer at high latitudes. Therefore, a day-time switch to feeding on fish by sockeye, pink, and chum salmon may be a mechanism to decrease competition for food.

Our results emphasize that daily periods of increased feeding activities are different for each salmon species and that the prey composition shifts between day and night feeding periods. Although studies of salmon food habits that rely on sampling at one time of day highlight the difference in prey composition between salmon species, this type of study may fall short of examining the full spectrum of prey species taken by salmon predation. Therefore, sampling salmon throughout the diel cycle is required to provide an accurate assessment of salmon feeding ecology. Future investigations of diel feeding of salmon would benefit if sampling were intensified at dawn and dusk, when sockeye, pink, and chum salmon switch from feeding on fish during the day to zooplankton and squid at night. A diel trawl study using a short tow duration could sample a wide portion of the water column, increase the number of samples collected within a 24-hour period, and substantially reduce the time fish are held in the fishing gear digesting their meals. Further insight into the temporal variability of salmon diel feeding habits would be gained by repeating diel experiments in locations where these studies have been previously conducted and expanding these experiments to other seasons.

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Seasonal Habitat Use and Early Marine Ecology of Juvenile Pacific Salmon in Southeastern Alaska

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Abstract: Habitat use and early marine ecology of juvenile (age-0) Pacific salmon (*Oncorhynchus* spp.) were studied monthly at inshore, strait, and coastal habitats along a seaward migration corridor in southeastern Alaska from May through October 1997–99. A total of 31,853 fish from 40 taxa were captured with 283 surface trawl hauls; juvenile salmon made up 61% of the total catch. Predation on juvenile salmon was observed in 4 of 19 fish species examined, and occurred in 33 (5%) of the 661 predators examined. Juvenile salmon catches typically peaked in June and July and in strait habitats, where two Alaska hatchery chum salmon (*O. keta*) stocks made up > 50% of the chum salmon sampled. Of the juvenile chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) stocks of known origin, marine migration rates averaged 1 and 3 km/d for Alaska stocks and 19 and 29 km/d for Columbia River Basin stocks. Our results imply that seasonal habitat use patterns of juvenile salmon are related to favorable temperatures and zooplankton abundance and are also linked to species and stock of salmon. Long-term ecological monitoring of key juvenile salmon stocks is needed over varying environmental conditions to understand relationships among habitat use, marine growth, year-class strength, and ocean carrying capacity.

INTRODUCTION

Increasing evidence for relationships between Pacific salmon (*Oncorhynchus* spp.) production and shifts in climate has renewed interest in processes governing year-class strength in salmon (Beamish 1995). However, actual links tying salmon production to climate change are poorly understood. Synoptic time series of ocean conditions and salmon life-history characteristics are needed to adequately identify mechanisms linking production to climate change (Pearcy 1997). In addition, the presence of mixed stocks with different life-history characteristics confounds research attempts to assess marine growth, survival, distribution, migration, and ocean carrying capacity.

The ocean's carrying capacity for salmon is related to their tolerance for environmental change, density, food supply, and the density of competitors and predators. In their review of implications for stock enhancement of salmonids in the North Pacific Ocean, Cooney and Brodeur (1998) argued that much more knowledge about the distribution of forage resources and the interactions of predators is needed if enhancement of selected species is to proceed without risk of deleterious

effects. An understanding of the spatial, temporal, and ecological overlap between stocks and species of salmon, habitat characteristics, juvenile salmon condition, prey resources, and predators is required to understand factors governing the marine survival and production of salmon.

An ocean survey of juvenile salmon was initiated in 1997 to monitor the early marine ecology of juvenile salmon along a primary migration corridor in the northern region of southeastern Alaska (Orsi et al. 1997). We report three years of findings on habitat use, migration, and growth of juvenile salmon in the region, as well as physical and biological habitat characteristics, fish species composition, and predation on juvenile salmon.

MATERIALS AND METHODS

Study Area

Twenty four stations in inshore, strait, and coastal habitats were sampled at approximately monthly intervals in marine waters of the northern region of southeastern Alaska from May through October 1997–99

(Fig. 1). Stations were located along a seaward migration corridor used by juvenile salmon extending 250 km from inshore waters within the Alexander Archipelago along Chatham Strait and Icy Strait, through Cross Sound, and to offshore waters in the Gulf of Alaska (Orsi et al. 1998). All sampling occurred during daylight, between 07:00 and 20:00 hours.

Sampling stations were selected based on 1) the existence of historic data in the region, 2) the necessity to sample multiple habitat types along the migration corridor transited by juvenile salmon, and 3) vessel and sampling gear constraints. Historical biological and oceanographic data were available for Auke Bay Monitor (ABM), False Point Retreat (FPR), Lower Favorite Channel (LFC), and Icy Strait (Bruce et al. 1977; Mattson and Wing 1978; Ziemann and Fulton 1990). The Taku Inlet (TKI) station represents conditions near a large glacial river system of large wild stock production along the mainland. The Chatham Strait transect represents a mixing area of two major stocks of chum salmon (*O. keta*) entering the strait habitat from the south (Hidden Falls hatchery) and north (Douglas Island Pink and Chum (DIPAC) hatchery). The Cross Sound, Icy Point, and Cape Edward transects represent coastal habitats adjacent to and in the Gulf of Alaska.

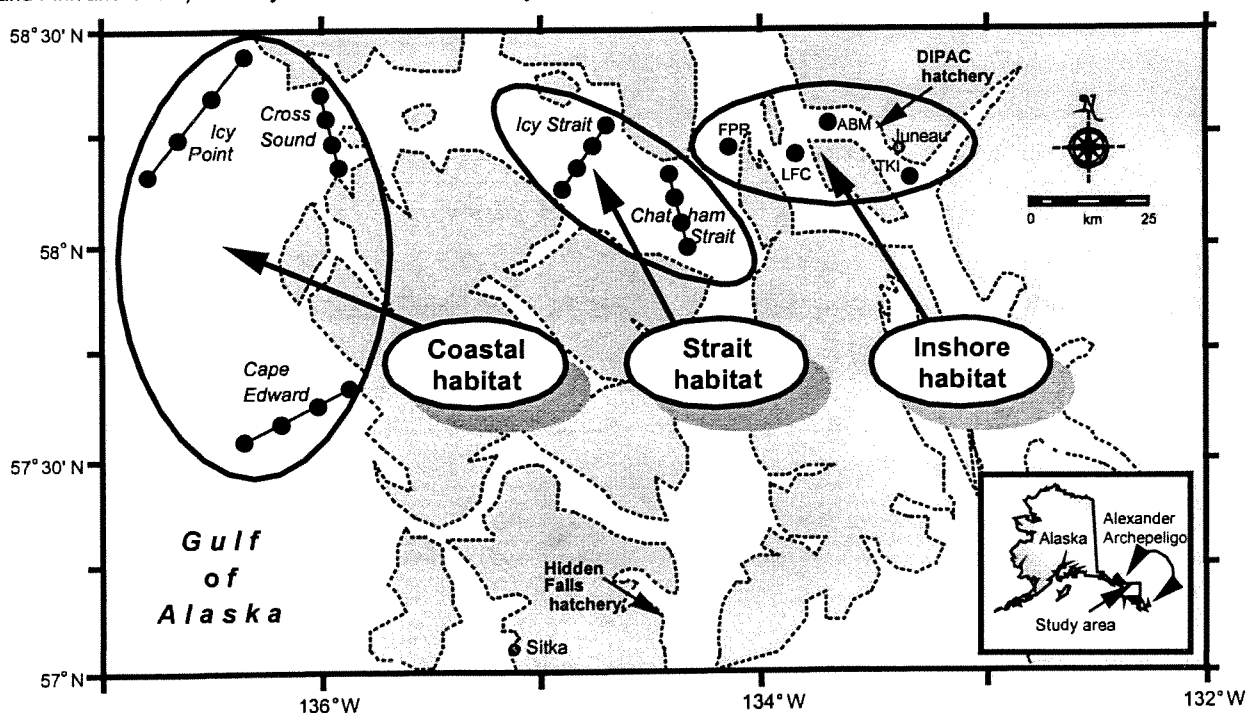
Vessel and sampling gear constraints limited operations to distances ≥ 1.5 and ≤ 65 km offshore, and ≥ 75 m depths; as a result, no trawling occurred at the ABM station. Sea conditions of < 2.5 m and winds < 12.5 m/sec were necessary to operate the sampling gear safely.

Oceanography and Fish Sampling

Physical and biological oceanographic sampling at each station included thermosalinograph data taken at 2 meters (m) and one 20 m vertical plankton haul. Surface temperature and salinity data were collected at 1-minute intervals with a SeaBird¹ SBE-21 thermosalinograph. One shallow (20 m) vertical haul was done using a conical NORPAC plankton net (50 cm diameter frame, 243 μ m mesh), the standard for previous zooplankton sampling programs in the region.

Fish were sampled with a Nordic 264 rope trawl modified to fish the surface water directly astern of the NOAA ship *John N. Cobb*, a 29 m research vessel. The trawl was 184 m long, with a mouth opening of 24 m \times 30 m (depth \times width), and was spread apart by a pair of 3 m foam-filled Lite trawl doors, each weighing 544 kg (91 kg submerged). Earlier gear trials with this vessel

Fig. 1. Stations sampled monthly in inshore, strait, and coastal marine habitats of the northern region of southeastern Alaska, May–October 1997–99. Up to 24 stations were sampled: four stations (ABM: Auke Bay Monitor, FPR: False Point Retreat, LFC: Lower Favorite Channel, TKI: Taku Inlet) in inshore habitats, two transect lines (four stations each) in strait habitats, and three transect lines (four stations each) in coastal habitats. Localities of the two primary salmon hatcheries in the region are identified: DIPAC (Douglas Island Pink and Chum) hatchery and Hidden Falls hatchery.



¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

and trawl indicated the actual fishing dimensions of the trawl to be 24 m vertical (head rope to foot rope) and 24 m horizontal (wingtip to wingtip). Trawl mesh sizes from the jib lines aft to the cod end ranged from 162.6 to 10.1 cm over the 129.6 m meshed portion of the rope trawl and a 6.1 m long, 0.8 cm knotless liner was sewn into the cod end. For each haul, the trawl was fished 20 min at 1.5 m/sec (3 knots), covering approximately 1.9 km (1.0 nautical mile) across a station. The effective sampling volume of water swept by the rope trawl during one haul was estimated to be $1.07 \times 10^6 \text{ m}^3$. This volume was calculated by multiplying the cross section of the trawl mouth opening (576 m^2) by the horizontal distance covered by one trawl haul (1,852 m), and dividing by a factor of four to account for surface orientation of juvenile salmonids (i.e., the top 6 m). Over-water trawl speed was usually monitored from the vessel using an electromagnetic current meter (Marsh McBirney, Inc., Model 2000-21). Station coordinates were targeted as the midpoint of the trawl haul; however, current, swell, and wind conditions dictated the direction of the trawl haul.

After each haul, fish were anesthetized, identified, enumerated, measured, labeled, bagged, and frozen. Fish were measured to the nearest millimeter (mm) fork length (FL) with a Limnotera FMB IV electronic measuring board (Chaput et al. 1992). All salmon were screened for coded-wire tags (CWTs). Juvenile salmon were poured through a portable CWT detector, and larger salmon were examined for missing adipose fins. After the juvenile salmon in each haul were processed, the stomachs of potential predators of juvenile salmon were examined.

Laboratory Processing and Data Analysis

Zooplankton settled volumes (ZSV) from the 20 m vertical tows were estimated by quantifying the amount of zooplankton settled for 24 hours in an Imhof 1,000 ml cone. Mean ZSV from all stations within a habitat was averaged, summarized by month, and pooled across years.

Apparent growth rates of pink salmon (*O. gorbuscha*) and chum salmon between June and July in the strait habitats were estimated by subtracting the average FL in July from that in June and dividing by the number of days between sampling periods. The number of days between sampling periods was estimated by subtracting the weighted date of sampling for July by the weighted date of sampling from June, with weights supplied by the number of each species of juvenile salmon captured and measured each day of sampling. Growth rate variance was estimated by summing the FL variance during each period and dividing by the squared number of days between sampling periods. Otolith marks were used to determine stock-specific growth rates for DIPAC and Hidden Falls hatchery chum salmon in 1997 and 1998.

Methods used to estimate stock-specific growth rates were similar to those described above.

Origin information was obtained for chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and chum salmon from CWTs (Jefferts et al. 1963) or thermally induced otolith marks (Hagen and Munk 1994). Independent tag readers verified all CWT codes and otolith marks. Release data for CWT codes and otolith marks were obtained from regional mark coordinators. Release and recovery data enabled migration rates to be determined by dividing marine distances traveled by the number of days at sea.

RESULTS

Seasonal Habitat Characteristics

From 1997 through 1999, data were collected from 319 surface thermosalinograph readings, 335 vertical zooplankton hauls, and 283 rope trawl hauls (Table 1). After 1997, limited rope trawling occurred in May due to the absence of juvenile salmon, but oceanographic data were collected. Inclement weather, particularly in coastal habitats, restricted sampling opportunities, thereby reducing the number of stations sampled some months.

Seasonal patterns were apparent in the temperature and salinity data (Fig. 2). Average surface temperatures ranged from 6.9 to 13.4°C and differed among habitats by up to 2.5°C monthly. Seasonal temperature patterns were consistent among habitats. Each year, temperatures were lowest in May, increased to a peak in July or August, then declined to near the spring minimum by October. Inshore habitats generally warmed first in spring, and coastal habitats cooled last in fall. Average surface salinities ranged from 16.7 to 31.8 PSU and differed among habitats by up to 19 PSU monthly. Seasonal salinity patterns were similar in inshore and strait habitats, but differed in coastal habitats. At inshore and strait habitats, salinity declined from May to July, then increased by October. In coastal habitats, salinities were relatively constant each month and year. Salinities were lowest in inshore habitats and highest in coastal habitats.

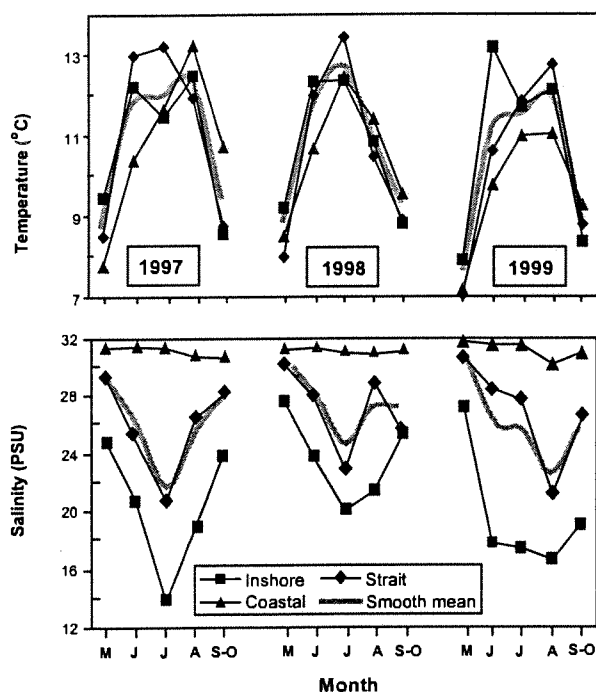
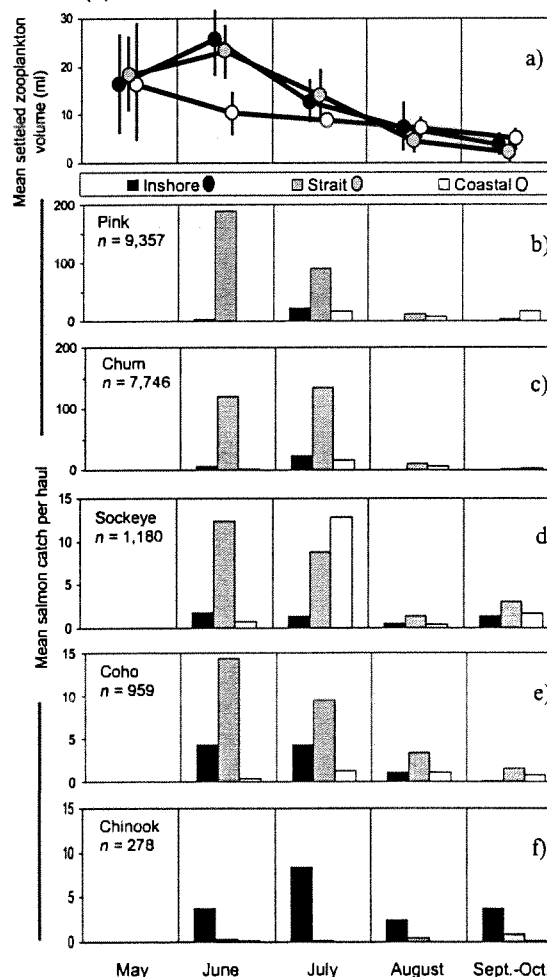
Interannual differences in the environment among habitats were also observed (Fig. 2). Lower temperatures prevailed in 1999 than in the two prior years, particularly in coastal habitats. Between years, annual peak temperature varied < 1°C in inshore and strait habitats and ~ 2°C in coastal habitats. Minimum salinities for all habitats occurred later in 1999 (August) than in 1997–98 (July).

Mean ZSV varied seasonally and among habitats (Fig. 3), ranging between 0 and 50 ml at the individual stations. In May, ZSV was similar at all three habitats, ~ 15 ml. However, seasonal patterns differed by habitat type from June through August. In inshore and strait

Table 1. Number of thermosalinograph*, zooplankton, and rope trawl samples collected monthly at inshore (I), strait (S), and coastal (C) habitats in marine waters of the northern region of southeastern Alaska, May–October 1997–99.

Month	Year	Thermosalinograph 2 m depth			Zooplankton 20 m vertical depth			Rope trawl 0–24 m depth		
		I	S	C	I	S	C	I	S	C
May	1997	4	8	8	4	8	8	3	8	8
	1998	4	9	1	7	8	1	2	9	0
	1999	4	8	4	6	8	4	0	4	0
June	1997	4	8	8	4	8	8	3	8	8
	1998	4	8	12	7	8	12	3	8	12
	1999	4	8	11	6	8	11	3	8	11
July	1997	5	9	8	4	8	8	3	8	8
	1998	4	12	16	6	12	16	3	12	16
	1999	4	8	11	6	8	11	3	8	11
August	1997	4	9	8	4	8	8	3	8	8
	1998	6	12	8	8	12	7	4	12	8
	1999	4	12	8	6	12	8	3	12	8
Sept.–Oct.	1997	4	5	8	7	5	12	3	4	7
	1998	4	4	7	7	4	7	3	4	7
	1999	4	8	8	6	8	8	3	8	8
Total		63	128	128	88	125	122	42	121	120

*Thermosalinograph data from 2 m depth; zooplankton data from 20 m vertical hauls, 50 cm diameter frame, 243 μ m mesh conical net; rope trawl data from 0–24 m depth, 20 min. haul.

Fig. 2. Surface (2 m) temperatures and salinities from inshore, strait, and coastal marine habitats, May–October 1997–99.**Fig. 3.** Mean settled volumes of zooplankton from 20 m vertical hauls (a) and mean catch per rope trawl haul of juvenile salmon (b–f) from inshore, strait, and coastal marine habitats, May–October 1997–99. One standard deviation about the mean is shown (a).

habitats, ZSV increased to ~ 25 ml in June and also remained 5–15 ml higher than in coastal habitats through July, declining sharply from June through August. At coastal habitats, ZSV declined slowly from May through October. In October, ZSV was similar again at all three habitats, ~ 5 ml.

Catch and Ecological Interactions

A total of 31,853 fish from 40 taxa were captured, including all five species of juvenile Pacific salmon and steelhead (*O. mykiss*); salmonids made up 61% of the total catch (Table 2). Of the 19,521 salmonids sam-

pled, over 98% were juveniles: 9,357 pink salmon, 7,746 chum salmon, 1,180 sockeye salmon (*O. nerka*), 959 coho salmon, and 278 chinook salmon; only 129 were immatures (125 chinook salmon, 3 chum salmon, 1 sockeye salmon) and 144 were adults. Non-salmonid species making up > 1% of the catch included 4,992 sablefish (*Anoplopoma fimbria*), 2,849 capelin (*Mallo-
tus villosus*), 2,671 Pacific herring (*Clupea harengus*), and 406 squid (Gonatidae). Juvenile pink and chum salmon were typically the primary catch components each year. Interannual differences in catch composition occurred, notably as the large catches of juvenile sablefish in 1997 and juvenile pink salmon in 1998.

Table 2. Catches of fishes and squid sampled with 283 rope trawl hauls, May–October 1997–99.

Common name	Life-history stage	Scientific name	Number caught					%
			1997	1998	1999	Total		
Pink salmon	J	<i>Oncorhynchus gorbuscha</i>	1,107	7,267	983	9,357	29.4	
	A		5	14	74	93	0.3	
Chum salmon	J	<i>O. keta</i>	3,565	2,748	1,433	7,746	24.3	
	J+		0	1	2	3	0.0	
	A		0	11	0	11	0.0	
Sockeye salmon	J	<i>O. nerka</i>	237	434	509	1,180	3.7	
	J+		1	0	0	1	0.0	
	A		0	1	3	4	0.0	
Coho salmon	J	<i>O. kisutch</i>	215	371	373	959	3.0	
	A		5	18	12	35	0.1	
Chinook salmon	J	<i>O. tshawytscha</i>	113	104	61	278	0.9	
	J+		29	58	38	125	0.4	
Steelhead	J	<i>O. mykiss</i>	1	0	0	1	0.0	
	A		0	1	0	1	0.0	
Sablefish	J	<i>Anoplopoma fimbria</i>	4,795	196	1	4,992	15.7	
	J+		0	5	161	166	0.5	
Capelin	J-A	<i>Mallotus villosus</i>	399	550	1,900	2,849	8.9	
Pacific herring	J-A	<i>Clupea pallasii</i>	599	783	1,289	2,671	8.4	
Squid	J	Gonatidae	231	166	9	406	1.3	
Walleye Pollock	J-A	<i>Theragra chalcogramma</i>	100	47	102	249	0.8	
Soft Sculpin	J-A	<i>Psychrolutes sigalutes</i>	27	40	106	173	0.5	
Spiny dogfish	A	<i>Squalus acanthias</i>	10	81	10	101	0.3	
Crested sculpin	J-A	<i>Blepsias bilobus</i>	46	28	14	88	0.3	
Pacific spiny lumpsucker	J-A	<i>Eumicrotremus orbis</i>	45	11	9	65	0.2	
Wolf-eel	J	<i>Anarrhichthys ocellatus</i>	1	57	2	60	0.2	
Pacific sand lance	J	<i>Ammodytes hexapterus</i>	53	0	2	55	0.2	
Pacific sandfish	J-A	<i>Trichodon trichodon</i>	12	24	17	53	0.2	
Prowfish	J-A	<i>Zaprora silenus</i>	9	5	20	34	0.1	
Greenling	J	<i>Hexagrammos</i> spp.	0	18	0	18	0.1	
Rockfish	J	<i>Sebastes</i> spp.	13	5	0	18	0.1	
Bigmouth sculpin	J	<i>Hemitripterus bolini</i>	5	3	3	11	0.0	
Starry flounder	A	<i>Platichthys stellatus</i>	2	4	4	10	0.0	
Three-spined stickleback	J-A	<i>Gasterosteus aculeatus</i>	1	4	1	6	0.0	
Black rockfish	A	<i>Sebastes melanops</i>	0	4	1	5	0.0	
Smooth lumpsucker	A	<i>Aptocyclus ventricosus</i>	3	1	1	5	0.0	
Arrowtooth flounder	J	<i>Atheresthes stomias</i>	5	0	0	5	0.0	
Dolly Varden	A	<i>Salvelinus malma</i>	0	0	3	3	0.0	
Lingcod	J	<i>Ophiodon elongates</i>	0	1	2	3	0.0	
Blue shark	A	<i>Prionace glauca</i>	0	1	1	2	0.0	
Salmon shark	A	<i>Lamna ditropis</i>	1	1	0	2	0.0	
Poacher	J	Agonidae	1	1	0	2	0.0	
Flatfish	J	Pleuronectidae	0	2	0	2	0.0	
Silverspotted sculpin	J-A	<i>Blepsias cirrhosus</i>	0	0	2	2	0.0	
Unknown fish	J	—	0	2	0	2	0.0	
Pacific saury	A	<i>Cololabis saira</i>	0	1	0	1	0.0	
Jack mackerel	A	<i>Trachurus symmetricus</i>	1	0	0	1	0.0	
Pacific pomfret	A	<i>Brama japonica</i>	1	0	0	1	0.0	
Eulachon	J	<i>Thaleichthys pacificus</i>	0	0	1	1	0.0	
Quillfish	J	<i>Ptilichthys goodei</i>	1	0	0	1	0.0	
Pacific cod	J	<i>Gadus macrocephalus</i>	0	0	1	1	0.0	
Total			11,633	13,069	7,151	31,853	100.0	

*J = Juvenile age-0+ fish, first year at sea; J+ = age-1+ fish one ocean-winter old; A = adult of spawning age; J-A = inclusive of all life history stages.

Predation on juvenile salmon was low. They were eaten by 4 of the 19 fish species examined for predation, and occurred in 33 (5%) of 661 stomachs (Table 3). The four fish species identified as predators of juvenile salmon were age 1+ sablefish, adult coho salmon, adult Pacific sandfish (*Trichodon trichodon*), and adult spiny dogfish (*Squalus acanthias*). Of these, age 1+ sablefish and adult coho salmon were the primary predators.

Habitat Use and Growth of Juvenile Salmon

Habitat use by juvenile salmon differed by month and species (Fig. 3). Seasonally, catch rates of juvenile salmon were lowest in May and highest in June and July. All species were most abundant in strait habitats except chinook salmon, which were found primarily in inshore habitats. Pink and coho salmon were most abundant in June, whereas chum, sockeye, and chinook salmon were most abundant in July. Average densities of juvenile salmon were highest in strait habitats during June and July (i.e., 1.1 fish per 1,000 m³); with a peak single catch density of 5.6 fish per 1,000 m³. Both juvenile salmon abundance and ZSV volume in strait habitats seasonally declined from July to August (Fig. 3).

Offshore distribution across the Icy Point transect in the coastal habitat reflected the width of the coastal migration band of juvenile salmon in the Gulf of Alaska (Fig. 4). Data from the Cape Edward offshore transect were not used because it was not sampled in 1997, nor

consistently sampled monthly in 1998-99. Offshore distribution of juvenile salmon was generally < 25 km from shore. Catches of all five species generally declined with distance offshore; however, a higher proportion of pink and chum salmon than the other three species were closer to shore.

Apparent growth of juvenile pink and chum salmon was compared to surface temperature and ZSV in the strait habitats in June and July (Fig. 5). From 1997 through 1999, apparent growth (mean mm per day) of both species declined from ~ 1.6 to < 1 mm/d, as mean temperature declined from ~ 13 to 11.5°C, and as mean ZSV declined from 24 to 13 ml. In 1997 and 1998, stock specific growth rates for the DIPAC and Hidden Falls hatchery chum salmon were similar to the mixed stock growth rate estimates. Although mixed stock estimates of growth rate had higher variances, no obvious bias appeared to be present. The similarity between the mixed stock and stock specific growth rates may be due to the high proportion (50%) of the DIPAC and Hidden Falls stocks in our samples during June and July.

Stock-specific Distribution and Migration

Recoveries of 1,575 otolith-marked juvenile chum salmon provided information on stock composition and stock-specific migration (Table 4). Hatchery chum salmon stocks made up 44–55% of the catch in June and July, whereas unmarked fish made up 75–100% of the catch in August through October. In 1997 and

Table 3. Number of potential predators of juvenile salmon examined (n_{ex}) and the actual number of those predators observed (n_{obs}) to have eaten juvenile salmon as a prey item from samples collected by rope trawl, May–October 1997–99.

Predator species	Life-history stage*	1997			1998			1999			Total		
		n_{ex}	n_{obs}	%	n_{ex}	n_{obs}	%	n_{ex}	n_{obs}	%	n_{ex}	n_{obs}	%
Sablefish	J+	0	0	0.0	4	1	25.0	66	24	36.3	70	25	35.7
Coho salmon	A	6	0	0.0	18	2	11.1	12	2	16.7	36	4	11.1
Pacific sandfish	A	8	2	25.0	3	0	0.0	16	0	0.0	27	2	7.4
Spiny dogfish	A	10	0	0.0	80	1	1.3	10	1	10.0	100	2	2.0
Walleye Pollock	A	42	0	0.0	31	0	0.0	65	0	0.0	138	0	0.0
Chinook salmon	J+	29	0	0.0	52	0	0.0	42	0	0.0	123	0	0.0
Pink salmon	A	5	0	0.0	14	0	0.0	81	0	0.0	100	0	0.0
Sablefish	J	17	0	0.0	0	0	0.0	0	0	0.0	17	0	0.0
Pacific herring	A	14	0	0.0	0	0	0.0	0	0	0.0	14	0	0.0
Starry flounder	A	3	0	0.0	3	0	0.0	4	0	0.0	10	0	0.0
Chum salmon	A	0	0	0.0	8	0	0.0	0	0	0.0	8	0	0.0
Black rockfish	A	0	0	0.0	4	0	0.0	1	0	0.0	5	0	0.0
Sockeye salmon	A	0	0	0.0	0	0	0.0	4	0	0.0	4	0	0.0
Dolly Varden	A	0	0	0.0	0	0	0.0	3	0	0.0	3	0	0.0
Chum salmon	J+	0	0	0.0	0	0	0.0	1	0	0.0	1	0	0.0
Salmon shark	A	0	0	0.0	1	0	0.0	0	0	0.0	1	0	0.0
Blue shark	A	0	0	0.0	1	0	0.0	0	0	0.0	1	0	0.0
Jack mackerel	A	1	0	0.0	0	0	0.0	0	0	0.0	1	0	0.0
Pacific promfret	A	1	0	0.0	0	0	0.0	0	0	0.0	1	0	0.0
Pacific cod	A	0	0	0.0	0	0	0.0	1	0	0.0	1	0	0.0
Total		136	2	1.5	219	4	1.8	306	27	8.8	661	33	4.9

*J = juvenile age-0+ fish, first year at sea; J+ = age-1+ fish, one ocean-winter old; A = adult of spawning age.

Table 4. Sample size (*n*) and stock composition of juvenile chum salmon examined for otolith marks in straits, June–October 1997–98. Estimates of stock composition have been corrected for the unmarked Hidden Falls hatchery component (60% of the Hidden Falls stock were marked; 100% of Douglas Island Pink and Chum (DIPAC) stock were marked).

Year	Month	<i>n</i>	Unmarked (%)	DIPAC (%)	Hidden Falls (%)	Total (%)
1997	June	50	46	49	5	100
	July	258	51	12	37	100
	August	215	75	10	15	100
	Sept.-Oct.	11	100	0	0	100
1998	June	354	45	36	19	100
	July	378	56	19	25	100
	August	2	100	0	0	100
	Sept.-Oct.	7	81	0	19	100

Fig. 4. Mean catch per rope trawl haul of juvenile salmon related to distance offshore along the Icy Point transect, June–October 1997–99.

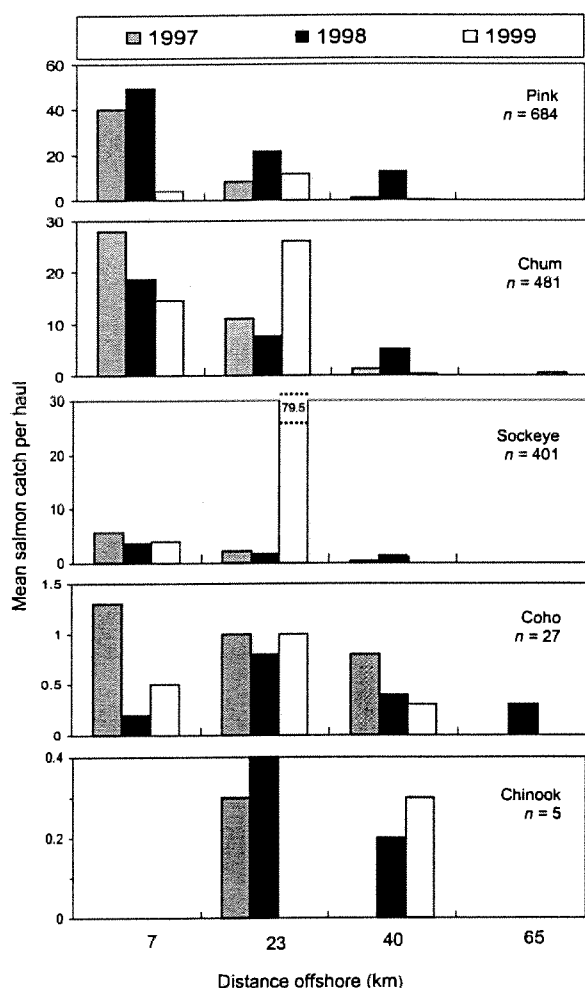
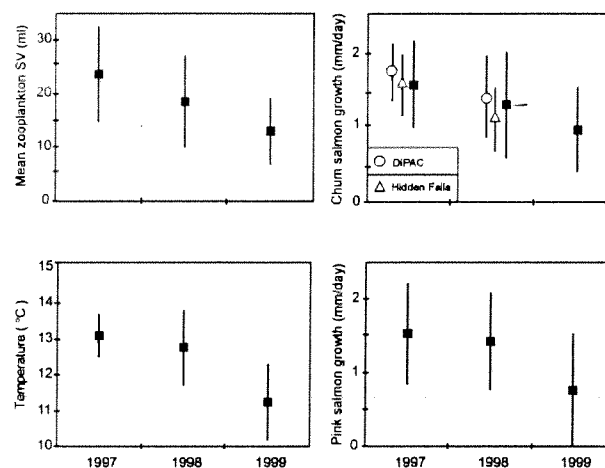


Fig. 5. Relationships between temperature and zooplankton to apparent growth rates of juvenile pink and chum salmon stocks in the strait habitats, June–July 1997–99. Stock-specific growth rates from otolith mark recoveries are included for DIPAC and Hidden Falls hatchery chum salmon stocks. One standard deviation about the mean is shown.



1998, DIPAC chum salmon migrated 1.9 and 1.6 km/d and were present predominantly in June, whereas Hidden Falls chum salmon migrated 2.2 and 2.4 km/d and were present predominantly in July.

Recoveries of 68 CWT chinook and coho salmon indicated differences in habitat use by species, stock, and ocean-age group (Table 5). CWT chinook salmon (33) were recovered primarily in inshore habitats, whereas CWT coho salmon (35) were recovered primarily in strait habitats. Alaska stocks were recovered primarily in inshore and strait habitats, whereas, Columbia River Basin (CRB) stocks were recovered exclusively in coastal habitats. By ocean-age group, age 1.0 juvenile chinook salmon (26) were present in all habitats and older, age 0.1, 1.1, 1.2, and 1.3 immature chinook salmon (7) were present exclusively in strait and coastal habitats.

Of the 61 CWT juvenile chinook and coho salmon (age 1.0) recovered, temporal occurrence within habitat differed by stock and species (Table 5). Alaska stocks of chinook salmon were present from June through October, principally in inshore habitats in July. Their average migration rate was 1.3 km/d. Alaska stocks of coho salmon were present from June through October, principally in strait habitats in June. Their average migration rate was 3.2 km/d. In contrast, CRB stocks of chinook salmon (4) and coho salmon (1) were recovered exclusively in coastal habitats in June and July; their average migration rates were 19.1 and 28.6 km/d.

DISCUSSION

The initial marine stage of juvenile salmon ecology has been studied in Canada and Alaska (LeBrasseur and Parker 1964; Healey 1967; Bailey *et al.* 1975; Cooney *et al.* 1978; Mortensen *et al.* 2000). Our study examined the next marine stage, the migration of juvenile salmon from littoral waters to the neritic waters farther offshore, involving routes through complex and highly diverse habitats. The patterns and timing of seaward dispersal are influenced by many factors, including natal stream localities, shoreline and basin bathymetry, current patterns, biological and oceanographic conditions, and a host of physiological and behavioral changes. According to Sheridan (1962), migration timing of juvenile salmon to the open ocean is keyed to take advantage of optimal water temperatures, salinities, and food availability. In our study, before juvenile salmon arrived in the habitats, temperatures were relatively low, but their arrival at successive habitats along the migration corridor corresponded with peaking temperatures. Additionally, in spring as juveniles arrived at inshore and strait habitats, ZSV increased and was soon at a seasonal peak. In contrast, when most juvenile

salmon reached the coastal habitat later in the season, the ZSV were already declining. However, by that time juvenile salmon rely on neustonic fauna and fish prey, taxa different from and larger than those captured in our small-mesh zooplankton samples (Landingham *et al.* 1998). Consequently, our low estimates of ZSV in the coastal habitats may not have been indicative of food supplies for arriving salmon. Therefore, in most habitats we studied, the timing of seaward migration of juvenile salmon coincided with seasonal peak periods of temperature and zooplankton.

In our study, the spatial and temporal occurrence of juvenile salmon in the marine waters of southeastern Alaska was relatively consistent between years and habitats, with peak salmon abundance in June and July. Juveniles were absent from these habitats in May because at that time in their life history they are distributed in shallow, littoral habitats (Jaenicke *et al.* 1985; Mortensen and Wertheimer 1988; Wertheimer and Celewycz 1996). Mortensen *et al.* (2000) found that peak emigration of pink and chum salmon fry from Auke Bay, Alaska, occurred in April and May; even late emigrants with the longest residencies were virtually absent by mid-July. In our study, juvenile salmon abundance peaked in most habitats in June and July, and declined in August through October. Thus, juvenile salmon migrate in the northern region of southeastern Alaska from littoral to neritic habitats from May to June and disperse to offshore habitats or travel outside the study area from July to August.

Adaptations of salmonids to oceanographic and feeding conditions are important because environmental conditions vary widely over their geographic range. Food requirements and fish behavior change with the physical and biological characteristics of habitat. Neither sea surface temperatures nor salinities have been found to consistently determine the distribution patterns

Table 5. Age and origin of recovered coded-wire tagged chinook and coho salmon sampled by rope trawl, May–October 1997–99.

Species	Age*	Origin	Number of coded-wire-tagged fish recovered					Total
			May	June	July	August	Sept.-Oct.	
Inshore habitat								
Chinook	1.0	Southeastern Alaska	—	5	9	4	3	21
Coho	1.0	Southeastern Alaska	—	3	2	—	—	5
Strait habitat								
Chinook	1.0	Southeastern Alaska	—	—	1	—	—	1
	1.1	Southeastern Alaska	3	—	1	—	—	4
	1.2	Southeastern Alaska	1	—	—	—	—	1
	1.3	Southeastern Alaska	—	—	—	1	—	1
Coho	1.0	Southeastern Alaska	—	17	7	3	1	28
Coastal habitat								
Chinook	1.0	Columbia River Basin	—	4	—	—	—	4
	0.1	Olympic Pen. Washington	—	1	—	—	—	1
Coho	1.0	Columbia River Basin	—	—	1	—	—	1
	1.0	Southeastern Alaska	—	—	1	—	—	1
Total for all habitats			4	30	22	8	4	68

*European age notation: number preceding decimal point denotes the number of freshwater winters and the number following the decimal point denotes the number of ocean winters.

of salmon (Groot and Margolis 1991), yet differences in thermal tolerance among species have been noted. Coho and chinook salmon are most tolerant of high temperatures, sockeye salmon prefer cooler water, and pink and chum salmon show the least tolerance for high temperature (Brett 1952; Groot and Margolis 1991; Groot et al. 1995). Although salmon do not necessarily optimize their distribution within the range of physical environments they traverse, the physical environment affects their physiology and metabolism (Groot et al. 1995). For example, temperature significantly influences the rate of digestion in juvenile salmon and other fish (e.g., Brett and Higgs 1970; Bailey et al. 1975). In a laboratory study, Brett et al. (1969) demonstrated that optimal growth of juvenile sockeye occurred at 15°C under high rations and at 5°C under low rations. This shift to lower temperatures for optimum growth at lower rations occurred because the efficiency of food conversion improved, even though absolute growth rates also declined with temperature. Brett's experimental temperature range of 5-17°C brackets average temperatures observed in our study. Fish growth and tolerance for low temperatures were also influenced by water salinity (Brett 1952; Brett et al. 1969), and juvenile salmon are known to occupy waters of "sub-optimal" quality when motivated by food availability (Birtwell et al. 1999).

Predation on juvenile salmon observed in our study was estimated at 5%. This rate may have been artificially high because the trawl concentrated predators and prey. However, we observed predation in only 4 of the 19 species of salmon predators examined, so if net-induced predation was prevalent, other predator species should have been implicated. For example, walleye pollock (*Theragra chalcogramma*) have been identified as a major predator on juvenile salmon in Prince William Sound, Alaska (Willette et al. 1999), yet out of the 138 we examined over three years, none ate juvenile salmon. Strong year classes of key predators, such as sablefish, adult coho salmon, and spiny dogfish, may also impact salmon survival. Other studies have also identified predation on juvenile salmon by adult coho salmon (Wing 1985) and spiny dogfish (Beamish et al. 1992). The latter study noted that only a small percentage of predators actually preyed on salmon, but the resulting salmon mortality was believed to be high because of the large numbers of predators in the area. The availability of alternative prey resources may also buffer the effect of predation on salmon (Willette et al. 1999), and predation in other habitats or by avian predators (Scheel and Hough 1997) may be significant.

Density-dependent effects commonly indicate that carrying capacity has been exceeded. During the 1970s and 1980s, unprecedented hatchery production of salmonids occurred around the Pacific rim (Heard 1995). Coincident with this production were changes in forage fish communities, indicating environmental change. Declines in lipid-rich forage species, such as capelin,

and increases in lipid-poor species, such as gadids and flatfish, were correlated with trophic shifts and population declines among piscivorous seabirds (Anderson et al. 1997; Duffy 1998; Anderson et al. 1999) and with decadal-scale shifts in the Gulf of Alaska (GOA) oceanographic regime (Piatt and Anderson 1996). Evidence also exists for long-term changes in the prey resources of salmon and planktivorous forage fish (e.g., Brodeur and Ware 1992; Frost and Bollens 1992; Cooney et al. 1994; Tanasichuk 1998a, b; Aydin et al. 1999). If oceanographic regime shifts caused changes in GOA fish communities, coincident with increased hatchery production of salmon and decreased production of zooplankton prey resources, fish trophic interactions could have influenced food supplies. Abundance of competing planktivores is an important aspect of carrying capacity (Sturdevant 1999). Possible density-dependent food limitation among salmon has been documented in diminished size and older age of maturity of salmon stocks from numerous localities (Bigler et al. 1996). Studies focusing on the estimation of carrying capacity in southeastern and southcentral Alaska showed little impact of salmon on availability of their prey (Bailey et al. 1975; Cooney 1993). In contrast, studies off British Columbia and Washington indicated juvenile salmon cropped prey resources, which initiated emigration (Healey 1982; Simenstad and Salo 1982). Our results suggest that declining ZSV from July to August contributed to the emigration of juvenile salmon. This is consistent with Healy's (1982) proposal that poor feeding conditions in mid-summer resulted in the emigration of juvenile pink and chum salmon from the Strait of Georgia. Simenstad and Salo (1982) also suggested that foraging success and the availability of preferred prey items in Hood Canal, Washington, were related to migration rates of juvenile salmon out of estuarine and nearshore areas. They calculated a neritic carrying capacity for juvenile chum salmon of 10 to 70 fish per 1,000 m³ (Simenstad and Salo 1982). Our highest estimated densities for all species of juvenile salmon ranged from 1.1 to 5.6 fish per 1,000 m³, although further analysis of the diet and available prey fields of juvenile salmon in our region is needed to estimate its carrying capacity, and to link the spatial and temporal occurrence of salmon with localized feeding conditions.

The offshore distribution pattern of our juvenile salmon in coastal waters was similar to that found in other studies. Along the Icy Point coastal transect, most of our juvenile salmon occurred < 25 km of shore in all years; few occurred > 40 km. Off the coast of Oregon and Washington, Miller et al. (1983) found concentrations of juveniles only < 28 km of shore. Hartt and Dell (1986) characterized the coastal migration of juvenile salmon as a 37 km-wide band of fish off the coast of southeastern Alaska, where the continental shelf is narrow, and the band extends farther offshore in the north-

ern Gulf of Alaska where the shelf widens. Distribution of juvenile salmon off the coast of southeastern Alaska has been documented to at least 74 km offshore in August (Jaenicke and Celewycz 1994).

Apparent growth of fish in our strait habitats tracked interannual changes in temperature and ZSV. Both stock-specific and mixed stock estimates of chum salmon growth showed a similar decline with temperature and ZSV. In Auke Bay, Mortensen et al. (2000) found that water temperature was the main factor determining growth of juvenile pink salmon during their early marine period, but prey limitation was also implicated. Mortensen et al. (2000) showed that early spring emigrants exposed to 5–7°C had lower growth rates than later emigrants exposed to 9–11°C. We found interannual temperature declines on the order of 2°C coincident with declining growth rates in strait habitats in June and July. Therefore, our findings for slightly older juvenile pink and chum salmon in strait habitats support the conclusions of Mortensen et al. (2000).

Stocks of juvenile chinook and coho salmon appear to have marine migration rates differing by origin and species. We determined migration rates for Alaska stocks to be 1.3 km/d for chinook salmon and 3.2 km/d for coho salmon, whereas migration rates for CRB stocks of these species were 19.1 and 28.6 km/d. Off the coast of Oregon and Washington, Fisher and Percy (1994) found chinook salmon stocks (primarily CRB) migrating 4.4 km/d and Percy and Fisher (1988) found northward-migrating coho salmon stocks traveling 11.0 km/d within 10 days of release. Off southeastern Alaska, Orsi and Jaenicke (1996) found stream-type (age 1.0) chinook salmon of Alaska stocks migrating 0.3 km/d, British Columbia stocks migrating 0.9 km/d, and CRB stocks migrating 6.9 km/d. Thus, it appears juvenile chinook salmon migrate slower than coho salmon, and CRB stocks of both species migrate rapidly along the Alaska coast.

CWT juvenile stream-type chinook salmon from the CRB captured off southeastern Alaska in June have important implications to the life-history strategies of these stocks, many of which are threatened or endangered. Our recoveries of CRB juvenile chinook salmon in June are significant because previous recoveries of these fish off Alaska have occurred only in September and October (Hartt and Dell 1986; Orsi and Jaenicke 1996). Our documented 3–4 month earlier occurrence of these stocks off Alaska indicates they may have a critical marine-entry period. Therefore, any natural or artificial impediments delaying entry of these stocks to the estuary could jeopardize their opportunities to initiate ocean migration at the proper time, thereby minimizing their access to suitable marine habitat and impacting survival.

Our results suggest juvenile salmon have seasonal habitat use patterns synchronous with environmental changes, and display distinct species- and stock-

dependent migration patterns. A long-term seasonal monitoring program during the early marine life-history stage of juvenile salmon enables researchers to adequately identify complex stock-specific information and trophic interaction necessary to understand relationships among habitat use, marine growth, year-class strength, and ocean carrying capacity.

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Feeding and Energy Characteristics of Juvenile Pink Salmon During Fall Marine Migrations

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Keywords: Juvenile pink salmon, feeding migrations, daily ration, metabolism

Abstract: Spatial distribution and energy metabolism of juvenile pink salmon (*Oncorhynchus gorbuscha*) feeding in the east part of the Sea of Okhotsk during September–October 1980–1990 were studied. In inshore waters caloric density of 40–100 g individuals increases rapidly, reaching a plateau at an average of 1,100–1,200 cal/g for fish with body weight about 120–150 g. In September juvenile pink salmon on the open Sea of Okhotsk feeding grounds begin their migration to wintering grounds. Body caloric content, daily rations (8.6–9.5% of total body caloric content), energy expenditures for growth (3.2–3.6%) and metabolism peak during this period when water temperature (11–12°C) is most favorable. By October, with the decrease in water temperature to 8–9°C, body caloric density declines to 900–1000 cal/g, daily rations to 6.0–8.5%, and energy expenditures for growth to 1.5–1.9%. At the same time, energy expenditures for swimming increase from 3.6–4.0% of total caloric content in September to 5% in October. These increased expenditures for active metabolism are caused by increased swimming of juveniles migrating to the southern areas of the Sea and to the Pacific Ocean.

INTRODUCTION

Juvenile pink salmon (*Oncorhynchus gorbuscha*) disperse widely from their reproductive areas to feeding grounds in the Sea of Okhotsk by fall of the year in which they hatch. For example, in 1995 pink salmon fingerlings from the South Kuril Islands reached 55°N by September of that year (Varnavskaya et al. 1998), and juveniles from the northern rivers arrived in waters above the South Kuril basin by the end of fall and beginning of winter (Shuntov 1989).

Abundance forecasts of Western Kamchatka pink salmon returning to spawn from the ocean are made from catches of juveniles caught by trawl in the Sea of Okhotsk. The reliability of these forecasts depends on the sampling of the stocks of feeding juveniles. They must be sampled at a stage of migration along the coast when they have left the shoal waters, where it is difficult or impossible to operate the trawl, but before they have had time to mix with stocks from other areas. Among physiological indicators of stages of feeding migration, energy content of the fish is especially important. Our study examines the energy content of juvenile pink salmon and its use in swimming and growth during fall migrations in the Sea of Okhotsk.

METHODS

Juvenile pink salmon were caught with a pelagic trawl in summer and fall in the eastern Sea of Okhotsk (51–58°N, from the coast of Kamchatka to 148°E) from August to October in 1982, 1986, 1989, 1990, 1991, 1995 and 1997. They were also caught using purse seines and beach seines along a 160 km coastal zone between 51–58°N in July to September, 1984, and June to August, 1987 and 1988. Fish growth in some stocks was estimated from catches separated by several days up to half a month according to the formulae:

$$\Delta W = (W_t - W_0)/t \quad \text{and} \quad (1)$$

$$\Delta L = (L_t - L_0)/t \quad (2)$$

where ΔW and ΔL are the daily increments in weight and length (fork length), respectively, W_t and L_t are weight and length of fish at time t , and W_0 and L_0 are weight and length of fish in the earlier catch.

To evaluate the cost of migration, we calculated a value we called migration intensity (i) as a fish's real length increment (ΔL) divided by the difference between average lengths of fish in a group with larger fish (L_{\max}) and a comparable group with a smaller average length (L_{\min}) at two stations where capture of the groups was separated by an interval of time (t):

$$i = \Delta L / (L_{\max} - L_{\min}) / t \quad \text{or} \quad (3)$$

$$i = \Delta L t / (L_{\max} - L_{\min}) \quad (4)$$

Values of "i" range between 0 and 1. The further the values deviate from 1, the more heterogeneous the groups. Migration vectors are directed from stations with smaller average fish length towards stations with average larger fish.

Food consumption by fish was estimated from indices of stomach fullness, calculated as the ratio of weight of food in the stomach to body weight ($^{\circ}/_{\infty}$). We calculated daily rations according to the method of Romanova and Kogan (Kogan 1963), which is based on calculation of speed of digestion as it varies with feeding intensity. Standard basal metabolism was calculated using the following equations suggested by Vinberg (1956):

$$Q = (0.498/q)W^{0.76} \quad (5)$$

$$R = 24k4.86Q10^{-3}C^{-1} \quad (6)$$

where Q is oxygen consumed in ml/sample per hour, q is temperature coefficient for metabolism up to 20°C, W is body weight (g), R is metabolic expenditure (g/sample per day), k is a coefficient of activity equal to 1 for standard metabolism, and C is total caloric content of the body, kcal/g of wet weight.

Energy expenditures for metabolism and growth where rations and growth increments were observed were calculated using the basic equation of balance (Vinberg 1956):

$$0.8r = \Delta W + R \quad (7)$$

$$K_2 = 100\Delta W / 0.8r \quad (8)$$

where r is ration (g/samples per day), ΔW is weight increment (g/samples per day), and K_2 is coefficient of use, or expenditure of assimilation, of the physiologically useful portion of food for growth. We used caloric content of various food organisms as given in the literature (Table 1). Fish food caloric content was assumed to be 1.0 kcal/g.

RESULTS AND DISCUSSION

Migration Routes and Sizes of Juvenile Pink Salmon

After emigrating to sea in April–May, and while adapting to the new habitat conditions, juveniles from the rivers of the western Kamchatka remain for a time in the inshore zone within 24–32 km of the shore. Catches made with a beach seine near river mouths in 1987 and 1988, and with a purse seine within 8–160 km of the coast revealed that only in June–July are juvenile pink salmon, chum salmon (*O. keta*) and sockeye salmon (*O. nerka*) observed in inshore waters. No juvenile salmon were caught beyond the 32 km zone. The narrow coastal zone of low salinity (29–30‰) surface water, resulting from river outflow, stretches along the complete west coast of Kamchatka. Thirty-two to 100km offshore salinities reach 33‰ (Davidov 1975). The inshore surface layer is characterized not only by low salinity, but by higher temperature (6–8°C) than offshore (4–6°C). By the beginning of August, water temperatures offshore increase to 8–10°C, while those inshore remain at 6–8°C.

The change in offshore water temperatures through July into August is associated with a redistribution of foraging juveniles of the various salmonid species present. Fingerling pink salmon begin to migrate towards open waters, assembling 160–192 km off the coast of Kamchatka in August (Yerokhin 1998). There are no juvenile salmon in the open Sea of Okhotsk during this period. In September, however, pink and chum salmon feed extensively throughout this Sea, while juvenile sockeye salmon continue to forage in inshore waters.

The September–October feeding migrations of juvenile pink salmon in the eastern Sea of Okhotsk follow two main routes, a long one and a short one (Varnavskaya et al. 1998). The longer route has two branches. An inshore branch proceeds north along the coast of Kamchatka to 58°N, swings westward

Table 1. Plankton caloric content (cal/g wet weight). OS = Sea of Okhotsk, AO = Atlantic Ocean, NPO = North Pacific Ocean.

Groups of organisms	Caloric density (kcal/g wet weight)	Area	Reference
Copepoda	1.5	OS	Shershneva 1991
Euphausiacea	1.39	OS	Shershneva 1991
Amphipoda, hyperiidea	1.31	OS	Shershneva 1991
Amphipoda, gammaridea	1.409	AO	Davis 1993
Chaetognatha	0.69	OS	Shershneva 1991
Appendicularia	0.86	AO	Davis 1993
Pteropoda	0.624	NPO	Davis et al. 1998
Cephalopoda	1.125	NPO	Davis et al. 1998

before entering Shelikhov Bay, and then moves southward along meridians 151–152°E. Juveniles following this inshore branch are fingerlings from rivers of western Kamchatka. The offshore branch of the long route proceeds southward. Fish using this offshore branch are from Kamchatka and Shelikof Bay, and also from the southern Okhotsk Sea, and Sakhalin. Fish in this offshore branch therefore have mixed origins.

The shorter migration route proceeds northward to 53–54°N, then westward to 149–150°E, then southward along 147–156°E. The largest juvenile pink salmon from the shorter route mix with juveniles from the longer route, and together they migrate towards the southern Kuril basin along the western periphery of this region. The smaller fish on this shorter route continue feeding in the area 51–53°N, 150–153°E until their body weight is sufficient for further migration southward.

Size groups of pink salmon in September–October coincide with these migration routes. The direction and relative intensity of migrations were determined using equation 4. Indices of "i" coincide in direction and value with fish united in separate areas (Fig. 1). The pink migrations along the coast of Kamchatka run in a northerly direction. Fish following this route are mostly small, and their abundance in inshore waters in September is higher than that of large fish (Fig. 2). Migrations along the western periphery with a southerly trajectory consist mainly of large salmon. Local migrations of low intensity ("i" from 0.1 to 0.3) occur in the southern part of this area between 150–154°E during the fall period of feeding migrations (of both large and small fish), and appear circular around the limits of food accumulation.

The intensity of migration to the warmer southern part of the sea is insignificant in September, but begins to increase by the end of the month, and continues doing so through October and November. Large fish that emigrated earlier are the first arrivals. In the western part of the Sea of Okhotsk, migrations are concluded by late migrating pink salmon from the northwest of Kamchatka, with schools of fish from Shelikhov Bay and the Magadan coast. These fish are characterized by slow growth, smaller sizes, and poor nutritional condition. These fish migrate southward in conjunction with the 6–7°C isotherm, and leave the northern part of the sea at the end of October and early November (Shuntov 1989; Karpenko et al. 1996, 1998). The migrations of juvenile pink salmon are closely related to processes of energy accumulation through food consumption, and its expenditure for growth, metabolism and swimming.

Daily Rhythm of Feeding by Juvenile Pink Salmon

The peak in stomach contents occurred between 17:00 and 21:00 hrs, when the index reached 100⁰/₁₀₀₀, but at other times of day it was lower or near this level (Figs. 3–5). Maximum stomach fullness indicates either that this is the most intensive feeding period, or that feeding was reduced or even stopped, and only digestion and removal of the food from the stomach continued. Some researchers have shown that the speed of food evacuation from the stomach (speed of digestion) is directly proportional to stomach fullness (Brett and Glass 1973; Hoar et al. 1983; Amineva and Jarzombek 1984; Smith 1986; Jarzombek 1996). The occurrence of individuals with extremely full stomachs is rare in nature. While the

Fig. 1. Size distribution (cm), and direction and intensity (i) of migrations of "small" (A) and "large" (B) juvenile pink salmon in September 1995, and of large juveniles in September 1997 (C).

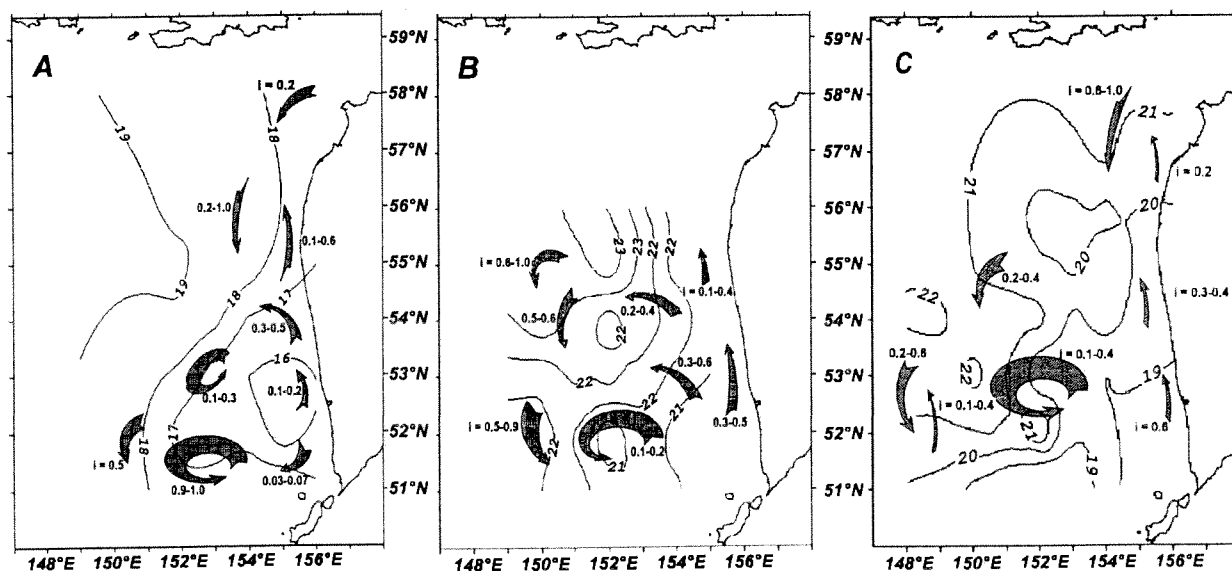


Fig. 2. Percentage of "large" pink salmon of all juvenile. A-1995, B-1997.

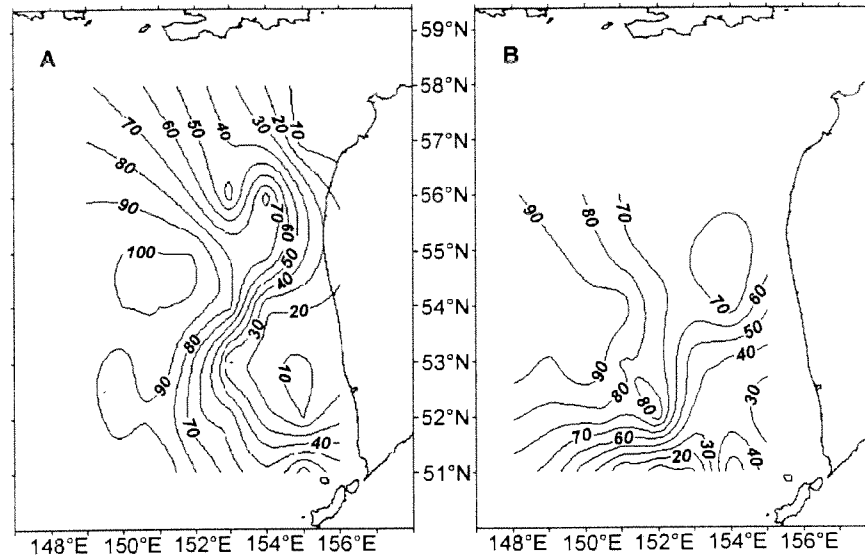


Fig. 3. Daily dynamics of feeding juvenile pink salmon in Sea of Okhotsk. October 1982 (A), September 1986 (B), October 1991 (C).

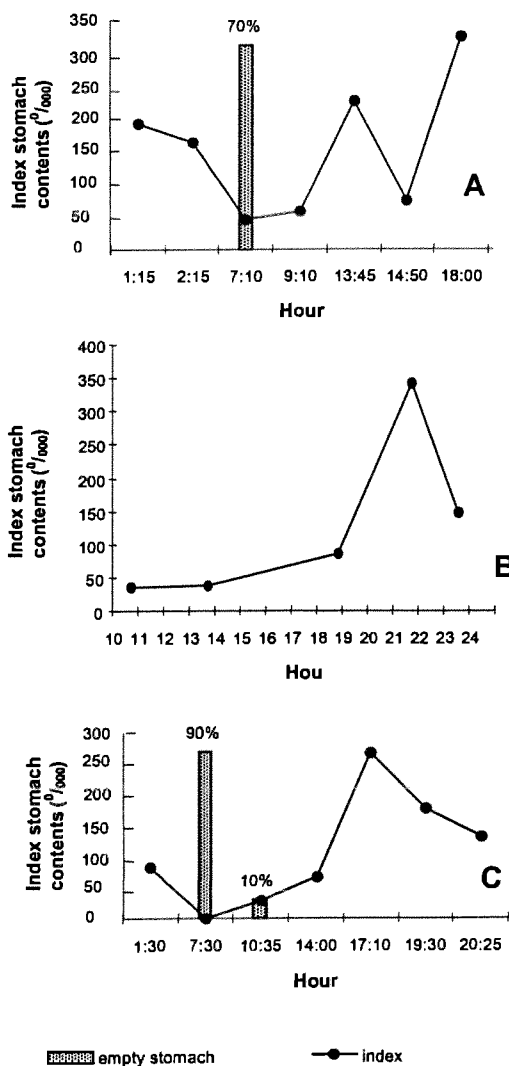


Fig. 4. The degree of pink salmon stomach fullness (0-empty, 4-full) in the Sea of Okhotsk. September 1997.

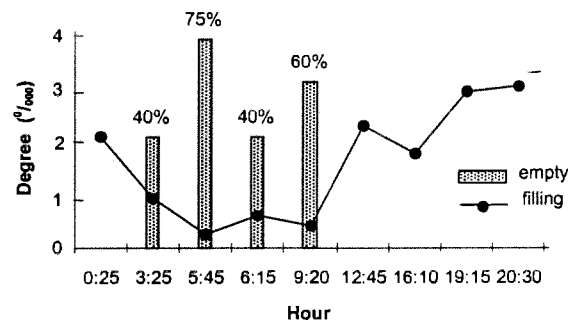


Fig. 5. Daily dynamics of juvenile pink salmon feeding in the Sea of Okhotsk. September to the beginning of October 1991.

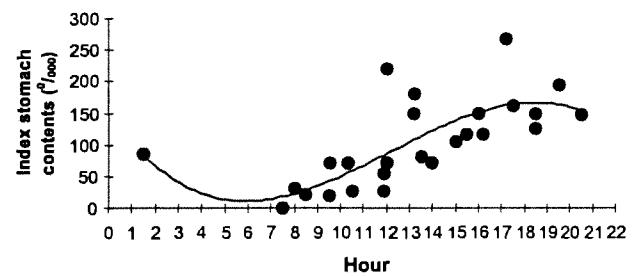


Table 2. Daily dynamics of feeding juvenile pink salmon in the Sea of Okhotsk, September 1995. Limits: 0- empty, 4- full.

Period	Empty stomach (%)	Degree of stomach fullness	
		Average	Range
morning	24	1.48	0-3
afternoon	0	2.10	1-4
evening	0	2.53	1-4

range in stomach fullness of individual fish was 25–450⁰/₀₀₀, the range in average indices was much less (150–250⁰/₀₀₀). We reasoned that the variability in speed of digestion was limited in comparison to range in individual speeds of digestion, and in calculating speed of digestion we assumed it was constant for the fish we sampled during the day. Generally 70–90% of fish had empty stomachs in the morning (Table 2, Figs. 3 and 4). We concluded that fish only began feeding in the morning after a pause during the night. From 07:00–13:00 hrs, speed of stomach evacuation was about 0.3% of average weight of fish per hour. We calculated rate of digestion during the evening assuming that when stomachs reached maximum fullness, fish stopped feeding. In one case, speed of digestion between 17:00 and 21:00 hrs was 0.40–0.48% of average body weight per hour (Fig. 3C). Analysis of the daily rhythm of feeding by juvenile pink salmon in 1982 and 1986, and at different periods in 1991 showed that speeds of stomach evacuation ranged from 0.3–0.5% of body weight per hour.

The hourly rate of feeding, as a percentage of full daily ration, clearly shows that the predawn pause in consumption lasts 3–4 hrs (Fig. 6). At this time, fish have empty stomachs, but digestion continues in the pyloric appendage and bowel. There is another pause in feeding in the evening between 17:00 and 20:00 hrs, after the period of maximum

stomach fullness. Food digestion and evacuation of the stomach continue at this time.

Daily rations of food consumed by juvenile pink salmon were estimated for different years and locations using the observed diurnal feeding rhythm. Overall, fish caught in September and October throughout our sampling area weighed between 70 and 140 g, and consumed from 5–12 g of food a day, or 5.9–9.5% of their body weight (Table 3).

Energy Accumulation

In September, the caloric content of pink salmon fingerlings increased with length, at least up to 25 cm (Table 4). Differences in caloric content of fish inshore and offshore were not consistent. The relation between body weight and caloric content varied among years and locations (Figs. 7–9), but showed a consistent pattern of first increasing and then decreasing with weight at any one time or place. Between

Fig. 6. Hourly rations of juvenile pink salmon as a percentage of total daily ration.

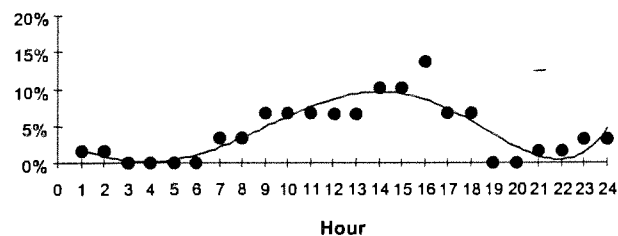


Table 3. Energy metabolism of juvenile pink salmon in the Sea of Okhotsk.

Date & location	Prey caloric density (kcal/g wet weight)	Predator caloric density (kcal/g wet weight)	Average body weight of fish (g)	Daily ration (g)	Daily ration (prey's caloric density converted to predator's)		T° C water	Expenditure for body growth		Expenditure for active metabolism		Number of fish
					g	ratio of body weight (%)		g	ratio of body weight (%)	g	ratio of body weight (%)	
1982, October 53° N, 154°30' E	0.898	1.030	74.80	5.064	4.415	5.90	8°	1.419	1.90	2.113	2.82	62
1986, September, 14–19 52–54° N, 150°30'–152°30' E	1.316	1.439	125.13	11.77	10.764	8.60	12°	4.014	3.21	4.597	3.67	50
1991, September, 20–25 South-west	1.271	1.103	130.18	10.747	12.387	9.52	11°	4.66	3.58	5.250	4.03	72
1991, October, 2–5 North-west	1.119	0.916	104.86	7.019	8.582	8.18	8°	1.604	1.53	5.262	5.02	50
1991, October, 11 54°N; 152°E	1.004	0.916	138.83	10.74	11.772	8.48	9°	2.291	1.65	7.127	5.13	70

Table 4. Average caloric content (cal/g) over years 1982, 1986, 1989, 1990, 1991, 1995 of juvenile pink salmon in the Sea of Okhotsk.

Location	Body length (cm)	September		October		Number of fish
		offshore	inshore	offshore	inshore	
"North"	below 19	-	-	817.1	879.4	20
	19–25	1376	1175	1033.4	864.5	78
	above 25	971.1	994.5	1004.9	-	29
"South"	below 19	1047	1021	1030	-	67
	19–25	1219.2	1194.6	1591	-	77

Fig. 7. Pink salmon caloric density in the Sea of Okhotsk, 1989: September, 52–53°N; 153–154°E (A); September 1991, 54°N (B); beginning October 1991, 56–57°N, 149–154°E (C).

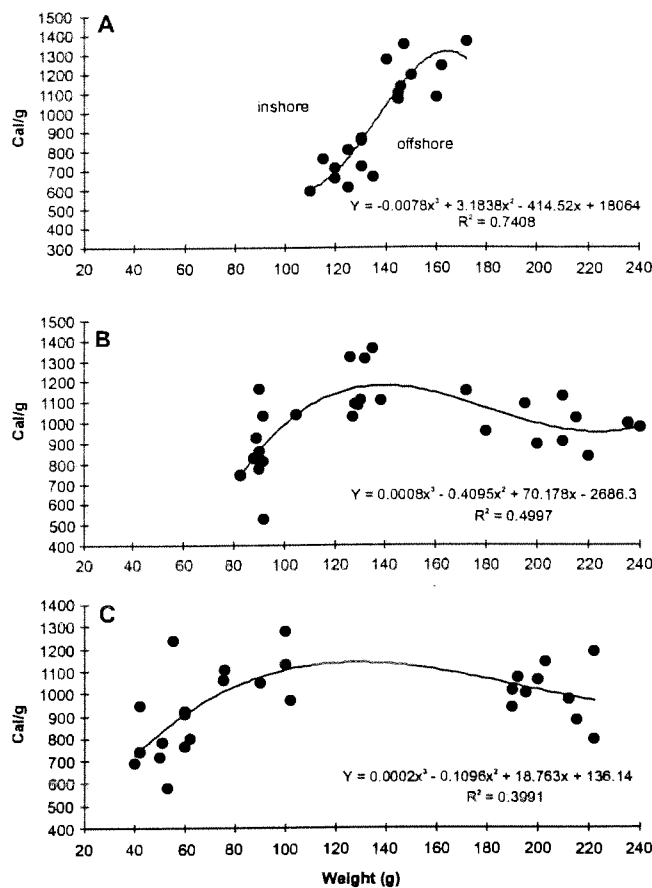


Fig. 8. Pink salmon caloric density in Sea of Okhotsk. September 1990, 51–54° N, 153–154° E (A); September 1991, 54° N (B); beginning October 1991, 56–57° N, 149–154° E (C).

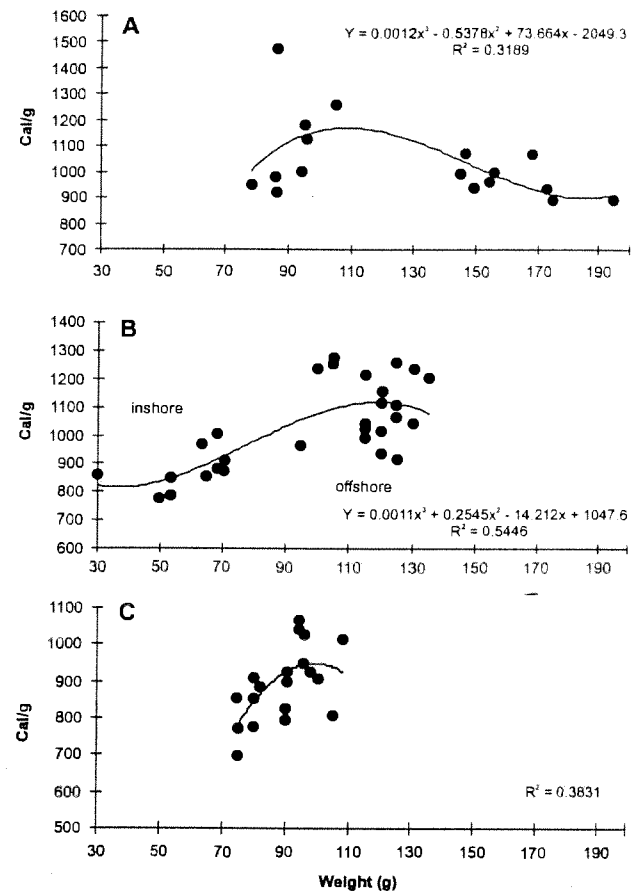
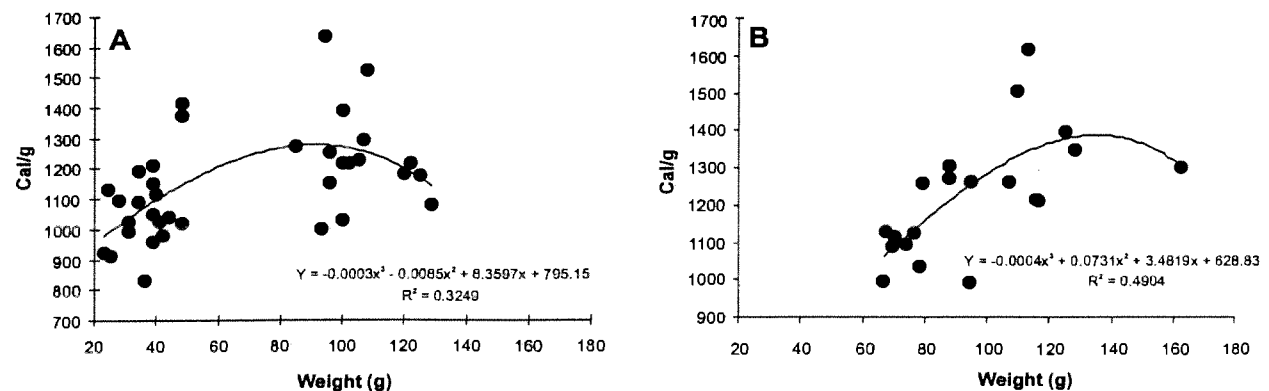


Fig. 9. Pink salmon caloric density in Sea of Okhotsk. September 1995, 52° N, 150–155° E (A); September 1997, 52–53° N, 148–154° E (B).



40 and 100 g, caloric content of fish rose rapidly, reaching a peak at around 1,100–1,200 cal./g for fish weighing 100–140 g in inshore waters, and for 120–160 g fish offshore in the Sea of Okhotsk. With further growth, caloric density (cal./g) declined.

Energy Expenditures by Juvenile Pink Salmon

Daily energy expenditures for fish growth range from 3.2–3.6% of body weight, and expenditures for metabolism 3.7–4.0% when temperatures are around 11° and 12°C (Table 3). Daily ration at this time is 9.0–9.5% of body weight (Table 3).

According to Vinberg (1956), energy lost in urine and excrement is 20% of food consumed, the physiologically useful portion of energy in food being, on average, 80% ($= r_{phys}$). In September, juvenile salmon expend 46–47% of this physiologically useful energy in food (r_{phys}) on growth, and 53% on active metabolism. With the decrease in temperature in October, ration is reduced by up to 6.0–8.5%, and growth increment is reduced by up to 1.7–1.9% of body weight per day. As a result, energy expenditure of assimilation (K_2) is reduced by 29–40%, while energy expenditure for active metabolism is simultaneously increased up to 60–70% of r_{phys} . Active swimming and intensification of migration by juveniles to the southern part of the Sea of Okhotsk and further to the Pacific Ocean cause the increase in expenditure for active metabolism. The reduction in growth and simultaneous increase in active metabolism are especially obvious in the northern part of the Sea of Okhotsk. In northern regions (56–57°N) during the first ten days of October 1991, the coefficient of expenditure of assimilation (K_2) of juvenile pink salmon decreased by 23.4%, but expenditures for active metabolism increased up to 76.6% of r_{phys} . From here juvenile pink salmon must migrate south

to wintering grounds, while fish located south of 55°N need only make low intensity local feeding migrations. Energy expenditures for active metabolism are higher than those for resting basal metabolism calculated by the formula of Vinberg (1965) (Table 5). Depending on the stage of feeding migration and physiological state, expenditures for active metabolism are 6–8 times higher than the level of basal metabolism in September–October.

CONCLUSIONS

From the beginning of August, pink and chum salmon start to leave the inshore waters for warmer offshore waters. In September, aggregations of juvenile pink and chum salmon form, as a result of localized migrations, where food is plentiful. Favorable temperatures allow indices of caloric body content, daily rations, energy expenditures for growth and metabolism to reach maximum values, marking the completion of this stage of short range feeding migrations, and readiness for prolonged migration. By the end of September and in October, juvenile pink salmon reach lengths of 24–26 cm and weights of 130–180 g earliest in the outer western regions of the sea. Large fish are the first to begin migration to wintering grounds.

With the commencement of prolonged migrations, behavioural strategy of juvenile fish changes. Movement is unidirectional and extends beyond feeding grounds, and consequently feeding is diminished. Food intake (ration) is reduced. The classical description of the positive dependency of feeding efficiency on food density, suggested by V.S. Ivlev (1977) is apparent. As intake of food energy is reduced, the balance of its use is altered toward a reduction for growth, and an increase for swimming.

Table 5. Basal metabolism of juvenile pink salmon calculated by formula $R=24kQ4.86 \cdot 10^{-3}C^{-1}$ (Vinberg 1956)

Date & location	Average body weight of fish (g)	Value «k» for fish at rest	Expenditure for basal metabolism		Real value «k» (the relation of active to basal metabolism)
			g	ratio of body weight (%)	
October 1982. 53° N, 154°30' E	74.80	1	0.430	0.57	4.9
14–19 September 1986. 52–54° N, 150°30'–152°30' E	125.13	1	0.754	0.60	6.1
September 20–25 1991. South-west	130.18	1	0.888	0.68	5.9
October 2–5 1991. North-west	104.86	1	0.625	0.60	8.4
October 11 1991. 54°N, 152°E	138.83	1	0.883	0.64	8.1

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Size of Sockeye Salmon Smolts and Freshwater Age of Adults in Azabachye Lake (Kamchatka River Basin)

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Keywords: Annulus, migration, scale, stock

Abstract: Analysis of age composition of early-run sockeye salmon (*Oncorhynchus nerka*) spawners in Azabachye Lake, in the lower reaches of the Kamchatka River, showed that in 1997 45% had spent only one year in fresh water (1.2, 1.3, 1.4). Previously, 80–99% spent two years in freshwater (2.1, 2.2, 2.3, 2.4, 2.5). The freshwater zone of scales from spawners of age 1.2, 1.3 and 1.4, caught in Azabachye Lake qualitatively resembled those of sockeye from tributaries in the lower and middle reaches of Kamchatka River. I hypothesized that high abundance of sockeye of one-year freshwater life in the basin of Azabachye Lake in 1997 arose from presence of spawners from lower and middle Kamchatka River, and that they had come to the lake as juveniles in 1993 to take advantage of excellent feeding there. In 1994, the largest sockeye smolts ever observed between 1979 and 1996 migrated out of Azabachye Lake. A significant correlation ($r_s = 0.66$ – 0.82 , $p < 0.05$ – 0.01 , $n = 17$) was obtained between the numbers of sockeye spawners with one freshwater year on their scales and length-weight of smolts leaving the Lake three years earlier.

INTRODUCTION

Azabachye Lake is the big sockeye salmon (*Oncorhynchus nerka*) nursery lake in the Kamchatka River basin. The lake plays an important role for reproduction of this species as it is a feeding area not only for local sockeye salmon (stock A) but also for juveniles from the low and middle reaches of the Kamchatka River (group E) migrating to the lake at age 0+ (Bugayev 1983, 1995a).

Sockeye salmon migrating to the lake at age 0+ start feeding and form a zone of closely-spaced circuli on their scales which is not an annulus. Smolts of group E migrate from the lake at age 1+, and smolts of the Azabachye stock migrate from the lake at age 2+. Annually spawners mainly of age 2.3 return to Azabachye Lake. Sockeye salmon spawners of group E return to the tributaries of the middle and lower reaches of the Kamchatka River at age 1.3 (Bugayev 1983, 1995a).

One-year old fry of group E have two zones of closely-spaced circuli (the first, indistinct, an accessory; the second, distinct, an annulus). Two-year old smolts of stock A have on their scales two distinct zones of closely-spaced circuli (annuli). Individuals from stock A and group E can be differentiated by the distinctness of the zones of closely-spaced circuli (and to a smaller extent by the number of circuli in the growth zone), infection by *Diphylllobothrium sp.* plerocercoids and the number of gill rakers (Bugayev

1983, 1986, 1995a; Bugayev and Bazarkin 1987). Photos of scales from stock A and group E sockeye salmon have been published earlier (Bugayev 1986, 1987, 1995a).

Early run sockeye salmon in Azabachye Lake make up 80% of the stock, late run 20% (Ostroumov 1972). Analysis of age composition, of spawners of early run sockeye in Azabachye Lake from 1982–1998 indicates that in 1997 45% ($n = 332$) of the fish had spent only one-year in freshwater (1.2, 1.3, 1.4). This is contrary to the generally accepted idea that 80–99% of sockeye from this lake spend two years in freshwater (ages 2.1, 2.2, 2.3, 2.4, 2.5) (Bugayev 1995a). This paper presents an analysis of the current situation.

MATERIAL AND METHODS

Data on age composition of early-run sockeye salmon from Azabachye Lake were collected from 1982 to 1998. In addition, data on length and weight of sockeye smolts of stock A and group E migrating from Azabachye Lake in 1984–1996 were collected. Individuals of group E and stock A were identified according to methods presented in Bugayev and Bazarkin (1987).

Data on run abundance of sockeye of Azabachye Lake at the mouth of the Kamchatka River and at the mouth of the Azabachya tributary were obtained from fisheries statistics, and from estimates of spawner

abundance on the spawning grounds. Sockeye from Azabachye Lake, were distinguished from fish sampled in coastal and river catches by structure of scales and infection by *Diphyllbothrium* sp. (Bugayev 1986).

The annual ocean abundance of mature sockeye returning to Azabachye Lake between 1977 and 1998 (prior to beginning of gillnet fishing season) was estimated on the basis of gillnet catches in the Russian economic zone (Bugayev and Dubynin this volume) and on the occurrence of Azabachye sockeye salmon in the run at the mouth of the Kamchatka River.

In this article we calculated Spearman's rank correlation coefficients (r_s) using the program "STATISTICA" (Borovikov and Borovikov 1998). When percentage data are used in regressions, they usually need to be transformed (e.g., arcsine transformation) (Zar 1984). I used an arcsine transformation on my percentage data.

RESULTS

Earlier analysis of the age composition of sockeye salmon spawners in Azabachye Lake (1982–1994) indicated that on average 5.3% migrated from the lake at age 1+ (1.2, 1.3, 1.4), 92% at age 2+ (2.1, 2.2, 2.3, 2.4, 2.5), and 2.7% at age 3+ (3.2, 3.3, 3.4) (Bugayev 1995b). Between 1995 and 1998, however, 22.9% migrated at age 1+, 71.7% at age 2+, and 5.4% at age 3+. The age at migration appeared to be different during these two periods (Table 1).

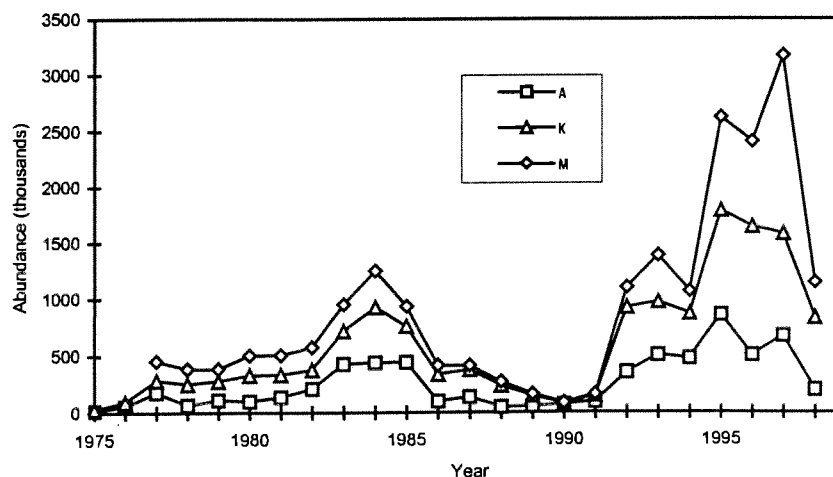
Abundance of sockeye salmon in Azabachye Lake between 1982 and 1994 was lower than in the period 1995–1998 (Fig. 1). Between 1982 and 1994, the average abundance of mature fish at sea was 672,000 fish, whereas in the period 1995–1998, it was 2,335,000 fish. At the mouth of the Kamchatka River the early run averaged 526,000 in the early period, while in the later period it averaged 1,460,000,

Table 1. Age composition of spawners of early-running sockeye of Azabachye Lake in 1982–1998, %.

Year	Freshwater and sea years of age ¹											n
	1.2	1.3	1.4	2.1	2.2	2.3	2.4	2.5	3.2	3.3	3.4	
1982	-	1.2	-	-	32.5	63.9	2.4	-	-	-	-	83
1983	1.0	1.0	-	-	7.0	88.0	2.0	-	-	1.0	-	100
1984	-	2.5	-	-	10.2	83.1	-	-	-	4.2	-	118
1985	-	5.1	-	-	10.1	76.8	2.0	1.0	-	4.0	1.0	99
1986	-	2.2	-	-	13.0	80.4	3.3	-	1.1	-	-	92
1987	-	0.7	-	-	8.7	86.6	4.0	-	-	-	-	150
1988	-	-	0.6	0.6	14.4	76.9	6.3	-	0.6	0.6	-	173
1989	-	2.5	0.5	-	7.5	78.4	8.6	-	0.5	2.0	-	199
1990	1.0	1.0	-	-	39.3	44.1	9.2	-	0.5	4.4	0.5	206
1991	11.6	2.2	-	-	34.8	43.4	2.2	-	4.4	1.4	-	362
1992	2.3	12.8	-	-	7.1	72.9	1.5	-	-	3.4	-	266
1993	1.3	2.6	0.4	-	14.7	72.3	6.9	-	-	0.9	0.9	231
1994	1.6	15.3	-	-	7.1	71.1	1.6	-	0.4	2.5	0.4	242
1995	7.0	1.7	-	-	30.4	46.8	4.1	-	4.7	5.3	-	171
1996	5.8	12.7	-	0.4	13.1	57.0	2.0	0.4	2.9	5.7	-	244
1997	2.8	40.6	1.6	-	6.5	44.1	1.6	-	-	2.8	-	322
1998	2.0	14.3	2.9	-	13.3	66.6	0.6	-	-	0.3	-	308

¹The first figure in the head of the table is the length of the freshwater life-period; the second figure is the length of the marine life-period.

Fig. 1. Abundance of Azabachye Lake sockeye salmon (1975–1998) at sea (M), at the mouth of the Kamchatka River (K), and at the mouth of Azabachya tributary (A).



and at the mouth of the Azabachye tributary numbers averaged 255,000 from 1982 to 1994, and 557,000 between 1995 and 1998.

Freshwater age and abundance at sea between 1982 and 1998 ($n = 17$) appeared to be linked. The percentage of age 1.3 fish (the most common age group with one freshwater year) among those returning was positively correlated with the abundance of mature fish at sea ($r_s = 0.583$, $p < 0.05$). The correlation coefficient (r_s) between frequency of this age group and abundance of the run at the mouth of the Kamchatka River was 0.570 ($p < 0.05$), and between this age and abundance at the mouth of the Azabachye tributary was 0.532 ($p < 0.05$). When the percentage of all age 1+ (1.2, 1.3, 1.4) migrants was used to calculate Spearman's rank correlation coefficients over the same period (1982–1998, $n = 17$), $r_s = 0.601$ ($p < 0.05$) with abundance at sea, $r_s = 0.606$ ($p < 0.01$) with abundance at the mouth of the Kamchatka River, and $r_s = 0.551$ ($p < 0.05$) with abundance at the mouth of the Azabachye tributary. There seems little doubt that increasing proportions of spawners that migrated to sea at age 1+ were positively related to increasing abundance of stock A spawners (those spawning in the Lake).

Length and weight of sockeye salmon smolts migrating from Azabachye Lake over the period 1984–1996 peaked in stock A in 1994 and group E

sockeye in 1993 (Fig. 2). Frequency of sockeye spawners with one freshwater year (various sea years) were positively correlated with length and weight over the years 1984–1995 (Table 2). In stock A, the correlation was stronger between age and length (Fig. 3) than between age and weight (Fig. 4), while in group E the reverse was true.

When these correlations between age and abundance, and size and abundance are considered together, one can conclude that as smolts reach a larger size at a younger freshwater age, the abundance of adult fish in the sea and in the river appears to increase. When data on males and females were examined separately, some significant correlations were obtained for males, but more rarely among females (Table 3).

DISCUSSION AND CONCLUSIONS

At least two hypotheses can be proposed to explain the correlation between the younger (higher proportion of 1+) bigger smolts and their greater abundance as returning adults. The first hypothesis is that improved growing conditions in Lake Azabachye between 1995 and 1998 resulted in faster growing fish that migrated to sea earlier in their lives. These fish would all be offspring of stock A parents (who themselves came from the lake), and the greater

Fig. 2. Body length (L) and weight (W) of sockeye salmon smolts of stock A (age 2+) and group E (age 1+), migrating from Azabachye Lake in 1984–1996.

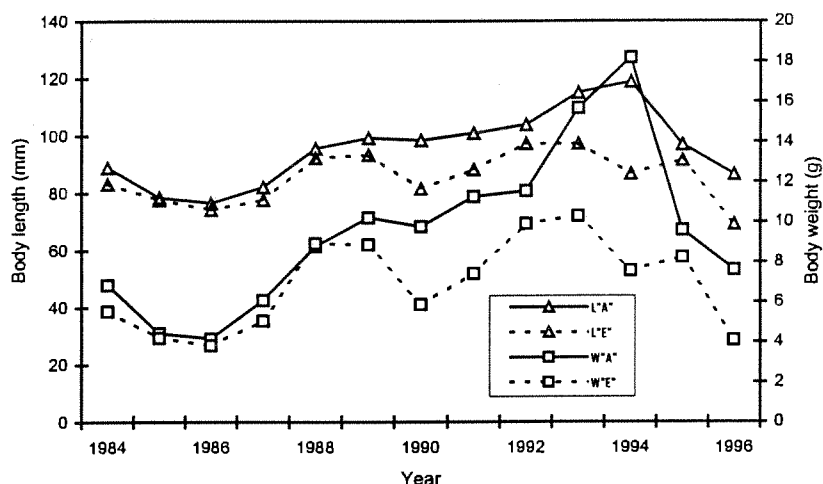


Table 2. Spearman's rank correlation coefficient (r_s) between occurrence in 1987–1998 in Azabachye Lake of sockeye spawners with one freshwater year on their scales and body length and weight in sockeye smolts migrating from Azabachye Lake in 1984–1995.

Stock, group	Age	Body length		Body weight	
		r_s		r_s	
A	1.3	0.685 *		0.664 *	
A	1.2, 1.3, 1.4	0.818 **		0.776 *	
E	1.3	0.336		0.378	
E	1.2, 1.3, 1.4	0.601 *		0.664 *	

Note. * - $p < 0.05$, ** - $p < 0.01$.

Fig. 3. Relation between frequency of sockeye spawners of ages 1.1, 1.3 and 1.4 and their mean length as smolts for stock A migrating from Azabachye Lake.

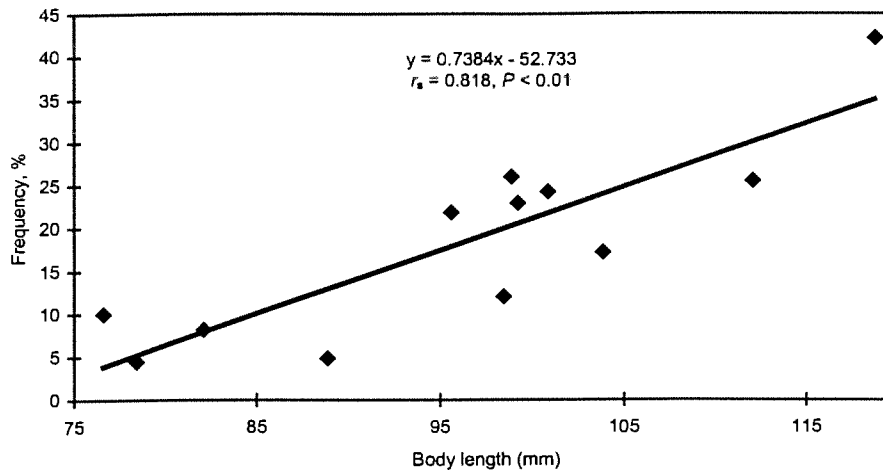


Fig. 4. Relation between frequency of sockeye spawners of ages 1.1, 1.3 and 1.4 and their mean weight as smolts for stock A migrating from Azabachye Lake.

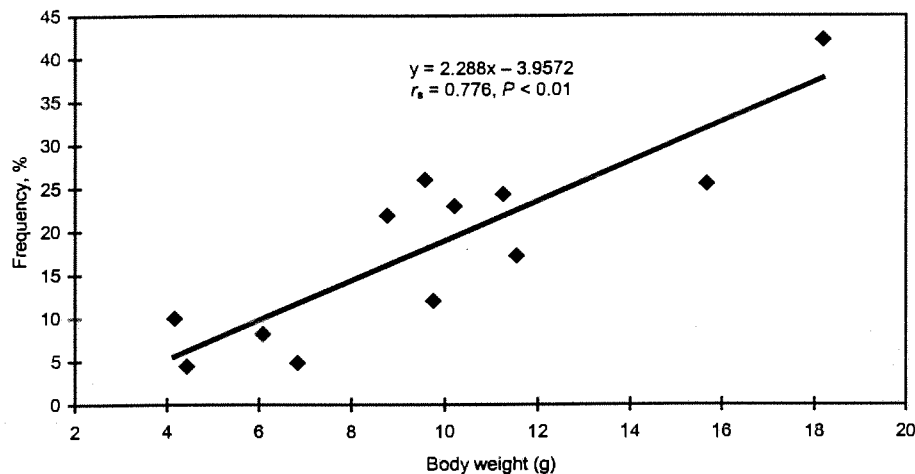


Table 3. Spearman's rank correlation coefficient (r_s) between occurrence in 1987–1998 in Azabachye Lake of sockeye spawners with one freshwater year on their scales and body length and weight of sockeye smolts migrated from Azabachye Lake in 1984–1995 when separated by sex.

Stock, group	Age	Sex	Body length r_s	Body weight r_s
A	1.3	Female	0.719 **	0.684 *
A	1.2, 1.3, 1.4	Female	0.718 **	0.690 *
A	1.3	Male	0.671 *	0.636 *
A	1.2, 1.3, 1.4	Male	0.797 **	0.755 **
E	1.3	Female	0.484	0.540
E	1.2, 1.3, 1.4	Female	0.438	0.539
E	1.3	Male	0.371	0.413
E	1.2, 1.3, 1.4	Male	0.594 *	0.671 *

Note. * - $p < 0.05$, ** - $p < 0.01$.

abundance of returning adults presumably would have arisen from either or both an improved survival of fry experiencing better feeding in the lake, and or greater survival in the sea as a result of arriving there as larger smolts.

The second hypothesis is that a portion of the fish rearing in Azabachye Lake were group E fish, which normally spawn in the lower and middle

reaches of Kamchatka River. The independent support for this hypothesis is that many of the adults returning to the lake with one freshwater year of life (1.2, 1.3, 1.4) have two closely spaced circuli on their scales typical of the scales of group E fish. These adults appear to have returned to the lake instead of the river to spawn. They possibly did so because of an advanced state of maturity, which prevented them

from reaching their native spawning grounds 100–200 km upstream from the lake. The presence of stock A fish in the lake may have acted as an incentive to group E fish to remain there. Also, Ilyin et al. (1983) found in the basin of Azabachye Lake that if sockeye on the point of spawning were transported from one tributary to another, they remained in the new location. Therefore I currently favour this second hypothesis.

After some years of successful spawning in Azabachye Lake by group E fish, returning there may have become an inherited behavioural pattern. This lake from time to time has provided a better than normal food supply because of periodic eruption of volcanoes of the nearby Kluchevskaya group. This provided natural fertilization of the lake in the form of volcanic ash. Group E fish returning to spawn in the Kamchatka River from 1982–1991 have rate of return between 0.4 and 10.1 (average 4.2), whereas the rate of return of stock A over the same period is 0.2 to 55.5 (average 18.9). If this greater survival of stock A fish is linked to rearing in the lake, group E fish which spawned in the Lake would presumably experience the same advantage, which would strengthen their numbers in the Lake.

In the pleistocene era and later a large lake existed in the lower reaches of the Kamchatka River in the area of the Yelovka River and Kamakovskaya lowland lakes (lakes Kurazhechnoye, Kobylkino, Sobachye, Urokolon and others) located upstream from lakes Nizovtsevo, Krasikovskoye, Azabachye, and Kursin (Kurenkov 1967; Krogius 1983). It is likely, therefore, that current stock A and group E populations had the same ancestors. This could facilitate straying of group E spawners to Azabachye Lake. Gene exchange between the two populations would enhance both the genetic and phenotypic resemblance between these two populations (Mina 1986).

The assumption of straying of group E to Azabachye Lake is not contradicted by the literature. Quinn (1985) showed, for example, that sockeye populations inhabiting two closely located lakes had straying rates of 0.2%. To determine the degree of straying by group E fish to Azabachye Lake, marking studies will be needed. Age 0+ individuals of group E can be marked (e.g. with magnetic tags) as they enter Azabachye Lake, and then their movements and residence times in the lake can be followed.

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Time of Annulus Formation on Scales of Chum Salmon in the North Pacific Ocean in 1998 and 1999

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Abstract: Scales ($n = 552$) of chum salmon (*Oncorhynchus keta*) collected in the North Pacific Ocean in May 1998 and 1999 and April 1999 were used to compare time of annulus formation between years, regions, and ages. May samples were collected from approximately the same location and time, during two years of very different ocean conditions, 1998 a strong El Niño year and 1999 a strong La Niña year. Sea surfaces were generally warmer during 1998 than in 1999 in the eastern North Pacific Ocean. Fish were generally longer in 1998. In 1999, fish length increased from west to east in the North Pacific Ocean. Annulus formation occurred earlier in 1999 than in the warmer El Niño year (1998); possible causes are discussed. Annulus formation generally occurred earlier in the eastern North Pacific Ocean than in the central and western North Pacific Ocean. Northern fish formed the annulus before southern fish in both years. Younger fish generally completed the annulus before older fish. Younger fish also had a greater number of circuli beyond the annulus.

INTRODUCTION

Annuli on chum salmon (*Oncorhynchus keta*) scales are thought to form completely between January and June in the North Pacific Ocean. Annulus formation was complete in chum salmon in the Gulf of Alaska during February or March (Bilton and Ludwig 1966). In the Bering Sea, Sea of Okhotsk, and western North Pacific Ocean annuli form between March and June (Kobayashi 1959; Sakurai 1996). Birman (1960) reported annulus formation through early May in chum salmon in the central North Pacific Ocean. Annulus formation in chum salmon occurs later in the spring than annulus formation in the other species of Pacific salmon (Salo 1991).

Causes of variability in time of marine annulus formation in salmon are poorly understood. Knowledge of time of annulus formation is necessary in order to understand variations in seasonal growth. Annulus formation in Pacific salmon (*Oncorhynchus* spp.) may be influenced by seasonal decrease in growth (Salo 1991), low winter temperatures and unfavorable feeding conditions (Birman 1960), and photoperiod (Barber and Walker 1988). Koo (1961) states that all the summer growth on chum salmon scales takes place between May and August and that

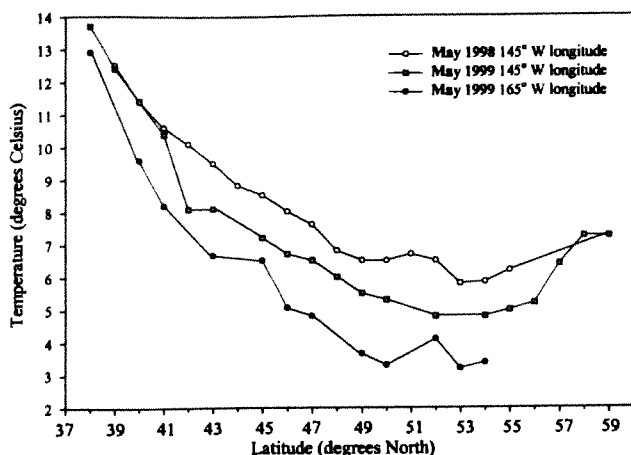
the narrow winter band (annulus) is added to the scales between September and April.

If time of annulus formation in chum salmon is related to seasonal growth at sea, then looking at chum salmon scales during the springs of 1998 (an El Niño year) and 1999 (a La Niña year) could provide some insights into time of annulus formation. Sea surfaces were generally warmer and temperatures higher during 1998 than 1999 in the eastern North Pacific Ocean (Fig. 1). We compare time of annulus formation in chum salmon in the eastern North Pacific Ocean in 1998 and in the western, central, and eastern North Pacific Ocean in 1999 (Fig. 2). Also, we consider the influence of age, length, stage of maturity, latitude, and longitude on time of annulus formation.

METHODS

Chum salmon scales, lengths, and sea surface temperatures were sampled from one station and two transects in the North Pacific Ocean in April 1999, May 1998, and May 1999 (Fig. 1). Scales were sampled from 252 chum salmon captured with gill-nets (Wilmot et al. 1999) fishing near the Kamchatka Peninsula (48°N, 163°E) during mid-April 1999 (Fig. 1). Scales were sampled from chum salmon caught using

Fig. 1. Sea surface temperature profile of the sampling locations in the North Pacific Ocean in May 1998 and in May 1999. Temperatures were taken at the head rope of the trawl.



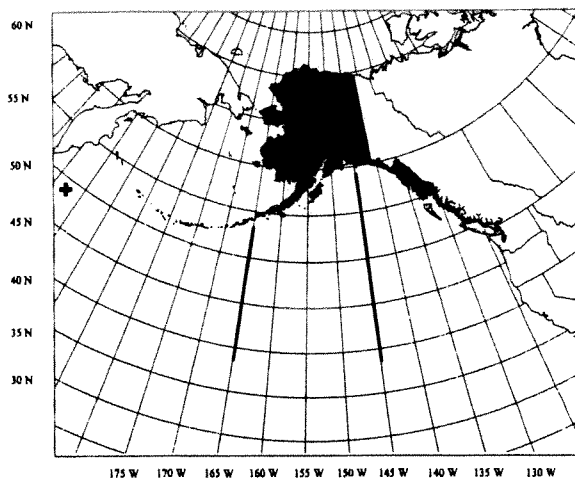
a surface trawl in the central (165°W, 51°N to 41°N) North Pacific Ocean in 4–9 May 1999 ($n = 58$), eastern (145°W, 43°N to 59°N) North Pacific Ocean in 13–19 May 1998 ($n = 70$), and eastern (145°W, 44°N to 59°N) North Pacific Ocean in 16–22 May 1999 ($n = 110$) (Carlson et al. 1998, 1999). Lengths were taken from tip of snout to fork of tail (FL) (Table 1 and Table 2). Temperatures were recorded near the head rope of the surface trawl (Fig. 2) using a YSI 30/50 salinity temperature probe¹.

Two scales were collected from the preferred area on the body of the fish, two to four rows above the lateral line and in a line between the posterior insertion of the dorsal fin and anterior insertion of the anal fin (Anas 1963). Scales were then placed on gum cards with the outer, sculptured side facing up. Impressions of the scales were made by placing gum cards scale-side down on plastic acetate cards and applying heat and pressure to the cards (Arnold 1951). The acetate impressions of the scales were then magnified (80x) and viewed using an Eberbach¹ scale projector.

Ages are represented by the European (decimal) method, where the number of freshwater annuli on the left is separated by a decimal from the number of marine annuli on the right. Chum salmon do not over-winter in fresh water after emergence from stream gravel, so the fresh water age is always zero (Koo 1962). For fish that had not begun to form the last marine annulus, we added one to the number of annuli formed to represent the correct age.

A reference line was drawn along an axis through the focus and along the marginal ridge that

Fig. 2. Sampling locations for April 1999 in the western (48°N, 163°E), May 1998 in the central (165°W), and May 1999 in the eastern (145°W) North Pacific Ocean.



bisected the anterior part of the scale. We identified whether the last annulus had formed and described the stage of development of the annulus using criteria similar to Hyun et al. (1998):

AF1: Annulus formation had not begun.

AF2: Annulus formation had begun.

AF3: Annulus formation was complete, with new growth and new circuli.

Fish that did not have an annulus near the edge but had the same amount of growth as fish with a new annulus near the edge were considered AF1. AF2 scales had a clear indication of a forming annulus due to narrow closely spaced circuli on the edge. AF3 scales had new circuli formed on the edge after the completed annulus. For AF3 scales, we counted the number of circuli beyond the last annulus. Counts began with the first complete broad circulus after the last winter annulus and ended on the last circulus forming near or on the edge. Circuli were included in counts if continuous within 1 cm to the right and left of the projected reference line (Tanaka et al. 1969).

We looked for annual and regional differences in completion of annuli and formation of new circuli. Regional differences were examined between the eastern, central, and western North Pacific Ocean, and between northern and southern regions of the eastern North Pacific Ocean. Annual differences were compared between May 1998 and May 1999 in the eastern Pacific Ocean. Effects of age and stage of maturity were also evaluated.

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1. Maturing chum salmon annulus formation in the North Pacific Ocean in 1998 and 1999. Age is represented by the European (decimal) method, the number of years spent in fresh water after emergence to the left of the decimal followed by the number of winters spent in saltwater. Length (mm) is measured from tip of snout to fork of tail (FL). Reliability of mean length is represented by 95% confidence interval (C.I.). Number of samples is represented by *n*. Stages of annulus formation, AF1, AF2, and AF3, are described in Methods section. N/A, no data available.

Age European method	May 1998 13 th –19 th 145°W (Eastern)	May 1999 19 th –22 nd 145°W (Eastern)	May 1999 4 th –8 th 165°W (Central)	April 1999 date N/A 163°E (Western)
0.3				
Mean FL±95% C.I. (<i>n</i>)	614±20 (49)	594±12 (58)	545±63 (4)	507±7 (58)
Annulus incompletely formed (AF 1&2)	8%	3%	0%	86%
Annulus with new circuli (AF 3)	92%	97%	100%	14%
Mean no. new circuli (range)	2.9 (0–6)	3.2 (0–6)	3.8 (3–5)	0.2 (0–2)
0.4				
Mean FL±95% C.I. (<i>n</i>)	688±22 (18)	630±21 (18)	592±18 (17)	535±4 (178)
Annulus incompletely formed (AF 1&2)	17%	0%	35%	98%
Annulus with new circuli (AF 3)	83%	100%	65%	2%
Mean no. new circuli (range)	2.0 (0–3)	2.7 (2–4)	1.3 (0–4)	0.05 (0–2)
0.5				
Mean FL±95% C.I. (<i>n</i>)	670±80 (3)	N/A	600±45 (4)	560±16 (16)
Annulus incompletely formed (AF 1&2)	0%		25%	100%
Annulus with new circuli (AF 3)	100%		75%	0%
Mean no. new circuli (range)	1.3 (1–2)		1.0 (0–2)	0.0

Table 2. Immature chum salmon annulus formation in the North Pacific Ocean in 1998 and 1999. Age is represented by the European (decimal) method, the number of years spent in fresh water after emergence to the left of the decimal followed by the number of winters spent in saltwater. Length (mm) is measured from tip of snout to fork of tail (FL). Reliability of mean length is represented by 95% confidence interval (C.I.). Number of samples is represented by *n*. Stages of annulus formation, AF1, AF2, and AF3, are described in Methods section. N/A, no data available.

Age European method	May 1998 date N/A 145°W (Eastern)	May 1999 16 th –18 th 145°W (Eastern)	May 1999 6 th –9 th 165°W (Central)	April 1999 date N/A 163°E (Western)
0.1				
Mean FL±95% C.I. (<i>n</i>)	N/A	287±6 (4)	285 (1)	N/A
Annulus incompletely formed (AF 1&2)		0%	0%	
Annulus with new circuli (AF 3)		100%	100%	
Mean no. new circuli (range)		6.5 (5–8)	6.0	
0.2				
Mean FL±95% C.I. (<i>n</i>)	N/A	411±9 (19)	400±9 (25)	N/A
Annulus incompletely formed (AF 1&2)		0%	8%	
Annulus with new circuli (AF 3)		100%	92%	
Mean no. new circuli (range)		2.5 (1–4)	2.2 (0–4)	
0.3				
Mean FL±95% C.I. (<i>n</i>)	N/A	428±80 (11)	554±71 (3)	N/A
Annulus incompletely formed (AF 1&2)		40%	67%	
Annulus with new circuli (AF 3)		60%	33%	
Mean no. new circuli (range)		1.0 (0–6)	0.8 (0–4)	
0.4				
Mean FL±95% C.I. (<i>n</i>)	N/A	N/A	554±71 (4)	N/A
Annulus incompletely formed (AF 1&2)			25%	
Annulus with new circuli (AF 3)			75%	
Mean no. new circuli (range)			1.3 (0–2)	

RESULTS

Eastern North Pacific Ocean (145°W) in May 1998

In May 1998, maturing chum salmon caught along 145°W longitude had formed the annulus in 92% of age-0.3, 83% of age-0.4, and all of age-0.5 fish (Table 1). Mean number of circuli beyond the last annulus was 2.9 for age-0.3, 2.0 for age-0.4, and 1.3 for age-0.5 fish (Table 1). Samples were small for age-0.5 fish. Preferred scales were not available on immature samples.

Eastern North Pacific Ocean (145°W) in May 1999

In May 1999, most fish captured along 145°W longitude had completed the annulus (Table 1 and Table 2). Maturing fish formed the annulus earlier than immature fish. Most maturing fish (97% of age-0.3 and 100% of age-0.4 fish) and all immature age-0.2 fish had formed the annulus, whereas only 60% of immature age-0.3 had formed the annulus. Maturing age-0.3 fish had more new circuli and were larger than immature age-0.3 fish (Tables 1 and 2). Mean number of circuli formed after the last annulus was 2.5 for immature age-0.2 fish and 1.0 for age-0.3 immatures. Maturing age-0.3 fish had an average of 3.2 circuli beyond the last annulus, and maturing age-0.4 chum had 2.7.

Central North Pacific Ocean (165°W) in May 1999

Maturing fish had completed the annulus in all age-0.3 fish, 65% of age-0.4 fish, and 75% of age-0.5 fish (Table 1). Mean number of new circuli decreased with age, 3.8 for age-0.3, 1.3 for age-0.4, and 1.0 for age-0.5 fish. Sample sizes were small for age-0.3 and age-0.5 fish.

Immature fish had completed the annulus in all age-0.1 fish, 92% of age-0.2, 33% of age-0.3 fish, and 75% of age-0.4 fish. Mean number of new circuli was 6.0 for age-0.1, 2.2 for age-0.2, 0.8 for age-0.3 fish, and 1.3 for age-0.4 fish (Table 1). Sample sizes for age-0.1, age-0.3, and age-0.4 fish were small.

Western North Pacific Ocean (163°23' E) in April 1999

In April 1999, most maturing fish were still forming the annulus (Table 1). However, there was a difference by age in completed annulus formation. About 14% of age-0.3 fish, 2% of age-0.4, and none of the age-0.5 fish had completed annulus formation. Of the fish that had completed annulus formation, younger fish had more new circuli than older fish. Mean number of circuli was 0.2 for age-0.3 and 0.1 for age-0.4 fish, and zero for age-0.5 fish (Table 1).

All of the chum salmon sampled were maturing fish. Because dates and areas of collection differed from those of other samples, these fish were not compared to data from 145°W and 165°W during May.

Northern and Southern Regions of the Eastern North Pacific Ocean (145°W) in May 1998 and 1999

Maturing age-0.3 chum salmon captured along 145°W were divided into two groups, the southern region (44°N–55°N) and northern region (56°N–59°N) in both years. Our division was based upon separating the sample into two nearly equal size subsamples. In May 1998, northern fish formed the annulus earlier than southern fish. By mid-May, most northern fish had formed the annulus, whereas up to half of the southern fish were still forming it (Fig. 3). Northern fish had more new circuli (mean = 3.1) than southern fish (mean = 1.8; Fig. 4) in 1998. Mean fork length of northern fish was 639 mm and 538 mm for southern fish in 1998. In May 1999, all northern fish and 92% of the southern fish had formed the annulus (Fig. 3). Northern and southern fish had similar mean numbers of circuli: 3.2 and 3.1 (Fig. 4). Northern fish were longer (mean = 608 mm) than southern fish (mean = 568 mm).

DISCUSSION

Annulus completion in the spring varied by ages and stages of maturity. In general, younger fish formed the annulus before older fish of the same stage of maturity. Mean number of new circuli decreased with age. For maturing and immature fish of the same age, maturing fish had formed the annulus to a greater extent and there were more new circuli on their scales (Tables 1, 2).

Fig. 3. Percent of annulus formation on scales of maturing age-0.3 chum salmon from the northern (56°N–59°N) and southern (44°N–55°N) regions of the 145°W longitude line in May 1998 and May 1999. AF3 = annulus has completed and new circuli formed beyond the annulus. AF1 and AF2 = annulus formation is not complete.

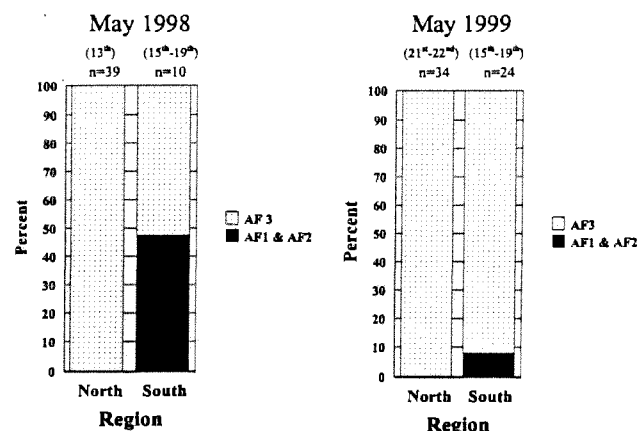
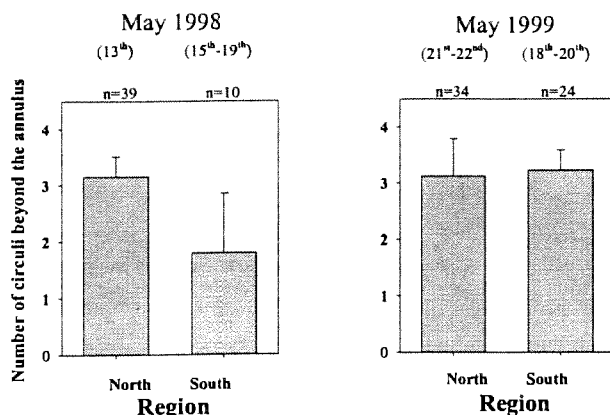


Fig. 4. Number of circuli beyond the last annulus on scales of maturing age-0.3 chum salmon from northern (56°N–59°N) and southern (44°N–55°N) regions of 145°W longitude in May 1998 and 1999.



Annulus formation also varied between locations and years (Table 1). Maturing chum salmon captured in 1998 in the eastern North Pacific Ocean (145°W) had fewer circuli beyond the annulus and formed the annulus later than fish captured at the same location in 1999 (Figs. 1, 2). Sea surfaces were generally warmer in the eastern North Pacific Ocean in 1998 than in 1999 (Fig. 2). In the eastern North Pacific Ocean (145°W), the northern region had a higher proportion of chum salmon with completed annuli than in the southern region in both 1998 and 1999 (Fig. 3). In 1999 where fish were captured, southern (49–55°N) sea surface temperatures were 5–6°C and northern (56–59°N) temperatures 6–7.5°C; in 1998, southern (44–54°N) sea surface temperatures were 6–8.5°C, and northern (59°N) temperatures near 7.5°C. In 1998, the northern fish averaged one more new circulus than southern fish. However, in 1999 the mean number of new circuli was similar in both regions (Fig. 4).

Sea surface temperatures in 1998 reflect the warming influence of El Niño (Fig. 2). Presumably, the warmer waters resulted in larger fish. In 1998 (El Niño year), fish of the same age in the eastern North Pacific Ocean (145°W) were considerably longer than fish sampled there in 1999 (non-El Niño year). Further, maturing fish of the same age from the warmer waters of the eastern North Pacific Ocean in 1999 were also longer than maturing fish of the same age sampled in the cooler waters of the central North Pacific Ocean in 1999 (Table 1). The positive relationship between sea surface temperature and length is clear; however, the relationship between sea surface temperature and annuli and circuli formation is more complex.

Ricker (1962) suggested that stock differences could influence time of annulus formation. Large differences in size (length) exist between stocks of chum salmon in North America (Helle 1984). We

compared samples of chum salmon from the western (163°E), central (165°W) and eastern (145°W) North Pacific Ocean. Wilmot et al. (1999) estimated that the stock composition of western samples (near the Kamchatka Peninsula) were primarily of Russian origin (86%). Central chum salmon were mostly of Asian origin: 53% Russian, 25% Japanese, 13% western Alaska, and 9% North American south of the Bering Sea (Urawa et al. 1999). Urawa et al. (1999) estimated that eastern chum salmon were primarily of North American origin (85%). Clearly, western and central chum salmon were mostly of Asian origin and eastern chum salmon were primarily of North American origin. Annulus formation and formation of new circuli were more advanced in the eastern North Pacific Ocean; however, sea surfaces were warmer and sampling occurred about two weeks later in the eastern than in the central and western region (Table 1). Also, eastern fish were longer. Therefore, using our data we cannot separate stock differences in annulus formation between areas.

Perhaps population density, if it affects growth, could influence annulus formation. Following the 1976 regime shift (Hare and Francis 1995) in the North Pacific Ocean, salmon size (hence growth) dropped sharply relative to increasing population numbers from about 1980 through the early 1990s (see Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996). Chum salmon sizes started to increase again in 1995 (Helle and Hoffman 1998). Comparing annulus formation in the late 1980s and early 1990s to the early 1970s or the late 1990s could address this question of how population density affects growth and annulus formation.

Barber and Walker (1988) concluded that photoperiod could be a major factor in marine annulus formation in sockeye salmon (*O. nerka*). Bugayev (1982) also concluded that photoperiod was important in annulus formation in sockeye salmon in fresh water. Annulus formation may be a function of food availability, particularly in the spring, when annulus formation is taking place. Brodeur and Ware (1992) clearly show differences in food production in the North Pacific Ocean before and after the regime change in 1976–1977. But differences in food availability between years in the spring would have to exist to answer the question of how food availability affects annulus formation. Further, chum salmon in the spring of 1999 may have had a growth advantage from the warmer El Niño conditions the year before. Data on growth and annulus formation from more years would be necessary to answer these questions.

Our data, from two years of very different ocean temperature (El Niño in 1998 and La Niña in 1999) indicate that annulus formation in chum salmon may be influenced by factors more important than sea surface temperature alone. Warmer sea surfaces and longer body size in the final year at sea during the El

Niño year in 1998 did not significantly increase the proportion of complete annuli nor the number of new circuli formed after the annulus compared to fish in 1999.

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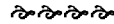
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Present State of Asian Coho Salmon (*Oncorhynchus kisutch*) Stocks

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Abstract: Data from pelagic trawl surveys by TINRO-center from 1987 to 1996 in the Okhotsk Sea indicate that coho abundance is underestimated by coastal observations. The approximate Asian coho spawning biomass is 7,300–16,000 tons for the 1990s. Ways of improving Asian coho salmon resource management are discussed. Collection of precise fishery and escapement statistics must be expanded in areas previously considered as non-traditional for coho. More attention must be paid to protection of coho spawning grounds from illegal fishing. Spawning stock abundance estimates must be substantiated by marine survey results. If Asian coho reproduction can be successful throughout the area around the Russian Far East, an artificial rearing program is highly recommended, which would not likely be detrimental to wild populations.

INTRODUCTION

Integrated studies of pelagic ecosystems have been conducted by the TINRO-center in far-eastern seas since 1984 until the present. This program has collected a significant database on common plankton and nekton species biology and ecology. The trophic structure of planktonic and nektonic communities has been examined, and some regulations and trends of community structure dynamics were found for recent years (Shuntov et al. 1997). The program on Pacific salmon sea life studies was conducted as a part of this integrated project in 1991–1995. Its next stage is from 1996–2001. Findings of this program added to and fundamentally changed some previous understandings on seasonal distribution, diet ration and feeding habits of Pacific salmon, and their role in pelagic ecosystems (Shuntov and Chigirinsky 1995). For all salmon species, seasonal and inter-annual abundance dynamics were estimated, the whole spectrum of prey organisms was assessed, and stock differentiation studies were executed by different methods.

Pink salmon (*Oncorhynchus gorbuscha*) migration patterns were analyzed and described for Asian stocks by Shuntov (1994). A significant part of the local pink salmon stocks was discovered to be overwintering in the Okhotsk Sea during January–March (Radchenko et al. 1991, 1997a). From an analysis of collected samples, the scleritogramm method was developed for differentiation of the Sakhalin and

western Kamchatka regional stocks (Temnykh 1996; Temnykh et al. 1997). Natural mortality rates of pink salmon at sea during the 1990s were estimated for the Okhotsk Sea populations (Radchenko 1998). The possibility of large-scale re-distributions of anadromous pink salmon aggregations between spawning areas was shown (as an example in 1993) (Shuntov 1994; Shuntov et al. 1995). This supports Glubokovsky's (1995) hypothesis on pink salmon population organization by the fluctuating stock principle, which regards such re-distributions as an important mechanism of genetic information exchange between pink salmon populations.

Migration patterns have also been described for chum salmon (*O. keta*). In particular, size group segregation of chum salmon has been found for feeding aggregations in the Bering Sea (Shuntov 1989a, b; Sobolevsky et al. 1994). It was noted that chum feeding aggregations usually appeared in areas of downwelling (anticyclonic eddies, flow convergency zones, etc.) (Radchenko and Chigirinsky 1995). Other data support previous hypotheses that maturing chum spent some time in near-bottom layers in the shelf zone (Radchenko and Glebov 1998), where their diet composition significantly changed.

The ecology of sockeye salmon (*O. nerka*), which feed and migrate in the Bering Sea, was described by Radchenko (1994). Sockeye aggregations adhere to well-stratified waters during their feeding migration. The prevalence of inter-zonal zooplankton and micronekton species in the sockeye diet

(Chuchukalo et al. 1994) indicated the sockeye salmon's probable preference for feeding in the thermocline zone. It was also found that immature sockeye use an insignificant part of the Okhotsk Sea area for their feeding migration (Radchenko et al. 1997b). Average natural mortality and growth rates at sea were estimated for sockeye salmon belonging to the eastern Kamchatka stocks (Radchenko 1994).

For chinook salmon (*O. tshawytscha*), vertical segregation by size has been found for feeding aggregations in the western Bering Sea (Radchenko and Glebov 1998). Chinook in their second marine year mostly spend their feeding migration in the upper pelagic layer where they feed upon zooplankton and gonatid squid juveniles. Older chinook dwell near the bottom layers where they feed on adult squids. Accordingly, overwintering on the north-western Bering Sea shelf is possible for older chinook.

Unfortunately, the studies cited above do not deal with coho salmon (*O. kisutch*). Coho salmon were only mentioned in the annual surveys with respect to their late return to the spawning grounds. Fragmented information was usually collected on coho, and much of this information was not published. Relatively recent summaries of data on coho described the pattern and conditions of their migration in the far-eastern seas (Glebov and Rassadnikov 1997). Further analyses presented in this study resulted in some new findings, in particular the possible underestimation of coho abundance in stocks migrating to feed and returning to spawn along the far-eastern seas' coast.

MATERIALS AND METHODS

Data on coho salmon distribution and biology were collected in the far-eastern seas and adjacent Pacific waters during integrated ecosystem expeditions in 1986–1996. Coho salmon were not abundant in our trawl survey catches due to their relatively low abundance, and their late and short migrations to spawning areas in comparison with pink, chum, and sockeye salmon. However, the data collected suggest that coho are widely distributed through the far-eastern seas—more widely than was previously thought. This also raised questions about estimates of coho salmon abundance in coastal areas.

Trawl surveys were conducted by research vessels of TINRO-center Fleet Base (Vladivostok, Russia). Vessels were middle tonnage trawlers. Hauls were executed by pelagic rope trawls, measuring roughly 108/528 m (trawl length on the topping lift/trawl mouth perimeter). The length of the wings was 32.6 m and the rope mesh size in the wings was 11 m. The conical part of the trawl (75.4 m) was made with nets with mesh size from 1,200 to 60 mm. The trawl bag (length 30–40 m) had a mesh size of 30

mm and a small-mesh insert 15 m long and mesh size of 6–12 mm. The width of the trawl mouth was about 50–55 m and the height 45–50 m. Thus, in 1 hour an area of 0.49 km² was swept at a tow speed of 5.0 knots (swept volume 0.023 km³). The trawl hauls (typically one-hour duration) were conducted using a pre-established scheme of stations around the clock. The trawl surveys were concentrated in a 0–50 m layer, and the tow speed was kept relatively constant at 5 knots. Wire lengths, roughly reflecting distance from trawl mouth to vessel were 350–400 m. The upper trawl panel was kept at the sea surface.

Salmon biomass and numbers in the epipelagic layer were calculated by square method (Shuntov et al. 1988) such that

$$B(orN) = \frac{Sq}{sk} \quad (1);$$

where B is fish biomass, N are numbers, S is survey area, q is average arithmetic catch over the whole survey area, s is the area swept in a one-hour haul, and k is a factor of trawl catchability. This factor (k) takes into account body size, form and mobility of fish, and their propensity to form schools. After long-term testing, the factor (k) has been estimated for different marine species, and for salmon was 0.3 (Shuntov et al. 1988, 1995).

Some data collected from Japanese commercial salmon fishery vessels were also used here to describe coho migration. These data were mostly collected in Pacific waters off the northern Kuril Islands and eastern Kamchatka in May–August of 1993–1998. Commercial salmon gill nets with mesh size 60–65 mm and a research net with mesh size 57.5 mm were deployed overnight usually for 12–14 hours. Net set length usually was 4 km, net height was 6 m.

RESULTS

Asian Coho Salmon Distribution and Migrations

Coho salmon are harvested along with other Pacific salmon species in coastal waters in the Russian Far East. They spawn in rivers around the southwestern Bering Sea, eastern and western Kamchatka, northern and western Okhotsk Sea, and the Sakhalin, Shantar and Hokkaido Islands. The main Asian populations of coho salmon spawn in the larger Kamchatka Peninsula rivers: the Kamchatka River (up to 70% of coho salmon harvested on the eastern Kamchatka coast) and Bolshaya River (up to 40% harvested on the western coast). The Okhota River coho population occurs chiefly on the continental Okhotsk Sea coast. Wild coho stocks of the Sakhalin and the Bering Sea coast are at low abundance currently, and are not harvested commercially. Coho also hardly

ever occurred in the northern Korea and Japan rivers (Zolotukhin 2000).

Coho, chinook, masu (*O. masou*) and sockeye salmon spend one to three years in freshwater, but coho, like pink salmon, spend only 1+ years at sea (Sandercock 1991). Coho aged 1.1+ predominate among spawners in the Kamchatka rivers (Gribanov 1948; Zorbidi 1975, 1993). Coho of the same age also predominate on the continental Okhotsk Sea coast, but in several rivers coho aged 2.1+ are slightly more numerous (Rogatnykh 1985). All spawner age groups occur in the Sakhalin rivers, but they are for the most part (more than 80%) aged 2.1+ (Zhulkov 1978). Coho salmon migrating through the Pacific waters off the northern Kuril Islands and entering the Okhotsk Sea through the northern straits of the Kuril Archipelago were aged 1.1+ to 2.1+ (Table 1). Coho salmon aged 3.1+ also occurred.

Juvenile coho aged 1.0+ and 2.0+ migrate from the inshore zone to the outer shelf and offshore over an extended period. The migration begins in July in the eastern Okhotsk Sea. The earliest catch of coho smolt (fork length 16 cm) occurred 16 July 1991

above the 200 m depth contour off northwestern Kamchatka (Fig. 1a). Coho juveniles have been sampled in the Okhotsk Sea from July to December. In October–November most juvenile coho left the Okhotsk Sea through the middle and northern straits of the Kuril Archipelago (Fig. 1b). In late November, almost all juvenile coho migrated in the Pacific waters off middle Kuril Islands (Fig. 1c). In the western Bering Sea, juvenile coho occurred from the second half of September to November, and in Pacific waters off Kamchatka up to late October–November (Fig. 2).

Coho salmon overwinter within the subarctic frontal zone, which is 4° latitude wide on average. This frontal zone defines the southern limit of the subarctic circulation. The subarctic halocline, which provides the stratification between the mixed layer and the underlying ocean, emerges there near the sea surface. The associated temperature front is an important salmon boundary. Coho demonstrate the most southern distribution among salmon species during winter. Optimal water temperature was approximately 9–10°C for coho salmon feeding in winter (Glebov and Rassadnikov 1997).

Table 1. Average fork length (fl, cm) and body weight (kg) of different coho age groups in Pacific waters off the northern Kuril Islands (fishery region 3) and in the Okhotsk Sea near the western Kamchatka coast (fishery region 4), June 18–July 21, 1995.

Region	Age groups	Fork length (cm)		Weight (kg)		Fish numbers	Sample* numbers
		Range	Mean±δ	Range	Mean±δ		
3	1.1+	47–66	57.9±0.34	1.7–3.6	2.54±0.05	94	17
	2.1+	48–66	58.3±0.35	1.8–3.8	2.61±0.05	78	17
	3.1+	59–61	60.0	2.4–2.8	2.60	2	2
4	1.1+	54–59	56.9±0.55	2.25–2.8	2.55±0.06	11	2
	2.1+	54–64	58.4±0.75	2.0–3.45	2.72±0.11	14	2

*One sample includes fish collected from driftnet fishery.

Fig. 1. Seasonal juvenile coho catch distribution in the Okhotsk Sea and adjacent Pacific waters in: a) July–August, 1991–1996. (1 July; 2 early; 3 mid; 4 late August). Russian EEZ in the Pacific ocean and some place-names are indicated in the inset; b) September–October, 1991–1996 (1 mid September; 2 late September; 3 early October; 4 mid October; 5 late October); and c) November, 1986–1994 (1 early; 2 mid; 3 late). Crosses, fishing but no catch.

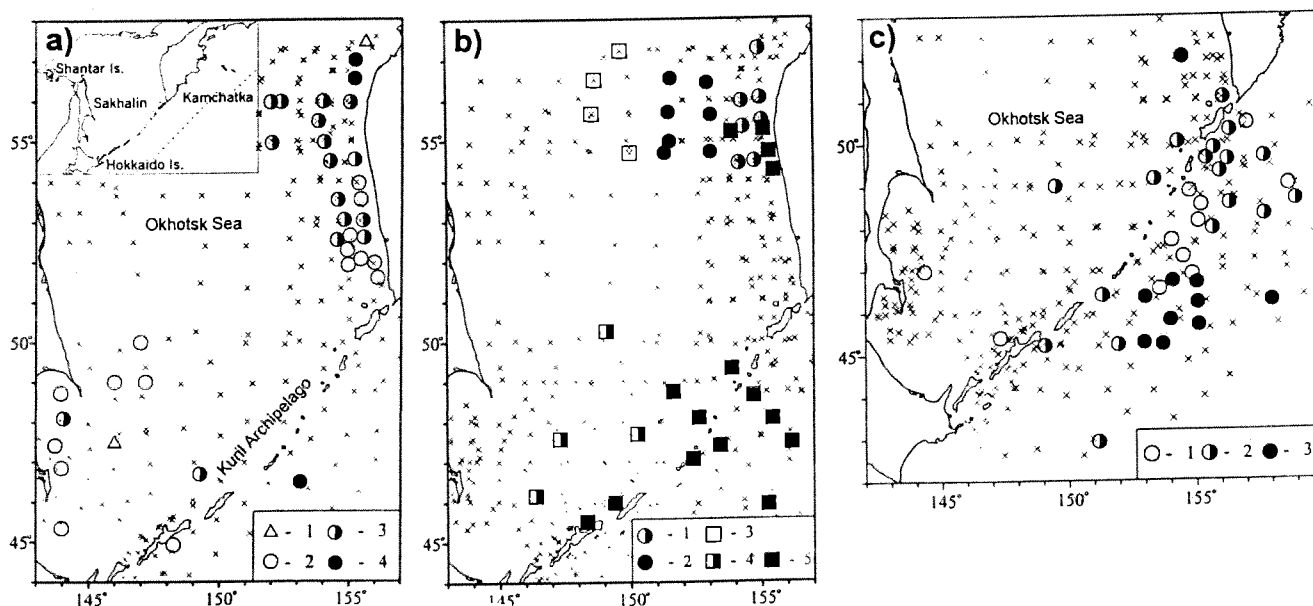
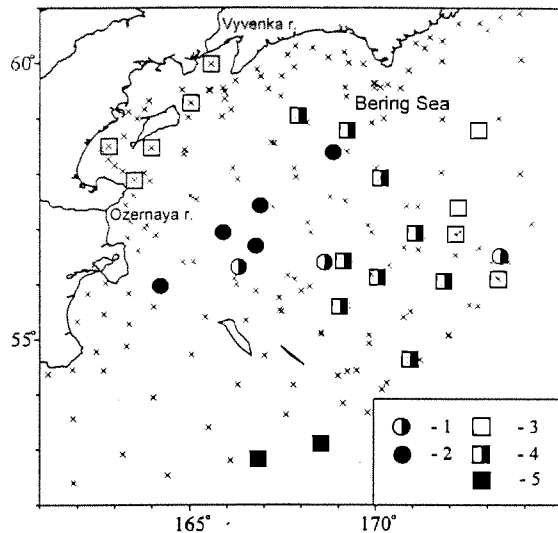


Fig. 2. Seasonal juvenile coho catch distribution in the southwestern Bering Sea September–October 1986–1994. (1 mid September; 2 late September; 3 early October; 4 mid October; 5 late October). Crosses, fishing but no catch.



Most chum, sockeye, and chinook salmon feeding in Russian waters were immature. Unlike these species, coho migrated later and over a brief period from the wintering localities to inshore areas near natal rivers through the Russian exclusive economic zone (EEZ). In the 1990s, the earliest seasonal coho catch was from salmon driftnet fishing in the area $50^{\circ}10' \text{ N } 160^{\circ}55' \text{ E}$ on 12 June 1998. Coho aged 1.1+ and 2.1+ occurred there, in Pacific waters off the northern Kuril Islands, and began to enter the Okhotsk Sea from the second week of June (Figs. 3, 4). In July, coho occurred northward up to 55° N along the western Kamchatka coast and up to 51° N near Sakhalin and in the central Okhotsk Sea. In August, coho migration continued through the middle and northern Kuril Archipelago straits. Two migration routes are available in the Okhotsk Sea, a northern and southern route (Fig. 5). The percentage of coho migrating through each pathway varied each year. Coho distribution density increased on the western Kamchatka shelf (trawl survey catches increased to 12 fish per one-hour haul) and reached 57° N in August. Most of the migration through the Kuril Archipelago straits finished by late August.

In the western Bering Sea, the earliest catch of coho salmon (54–64 cm) was 30 June 1993, by trawl. In July, coho salmon reached the Kamchatka coastal waters but still occurred in the offshore Bering Sea until the third week of October. In the Pacific waters off eastern Kamchatka, coho first appeared in abundance in early July. At this time, coho occurred near the Russian EEZ shore. Their migration also continued there until late October.

Fig. 3. Seasonal adult coho catch distribution in the Okhotsk Sea and adjacent Pacific waters in July, 1991–1996 (1 early; 2 mid; 3 late). Crosses, fishing but not catch.

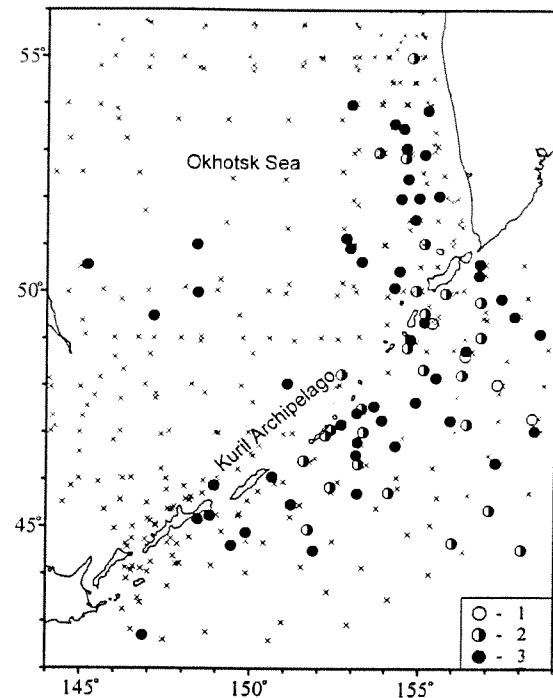


Fig. 4. Seasonal adult coho catch distribution in the Okhotsk Sea and adjacent Pacific waters in August, 1991–1996 (1 early; 2 mid; 3 late). Crosses, fishing but not catch.

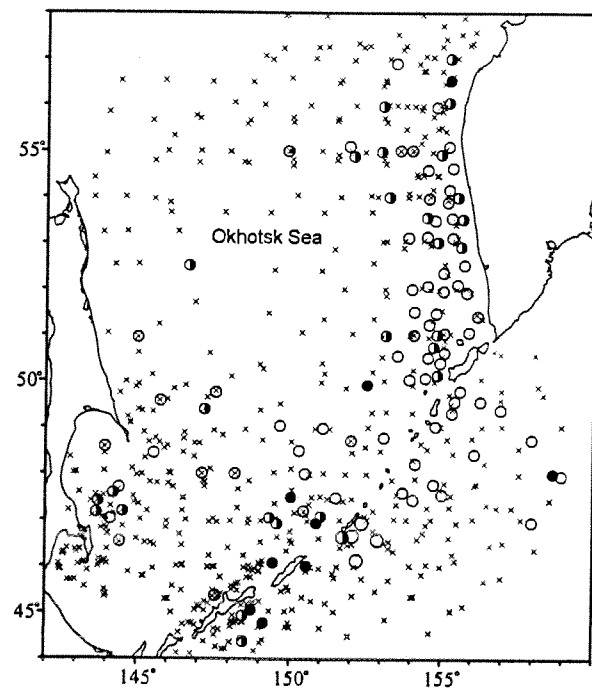


Fig. 5. Adult coho catch distribution in the Okhotsk Sea and adjacent Pacific waters a) 1992 and 1994, b) 1993 and 1995. Kamchatkan rivers: 1 Icha; 2 Krutogorova; 3 Kikhchik; 4 Bolshaya; 5 Nalycheva; 6 Zhupanova; 7 Kamchatka. Crosses, fishing but no catch.

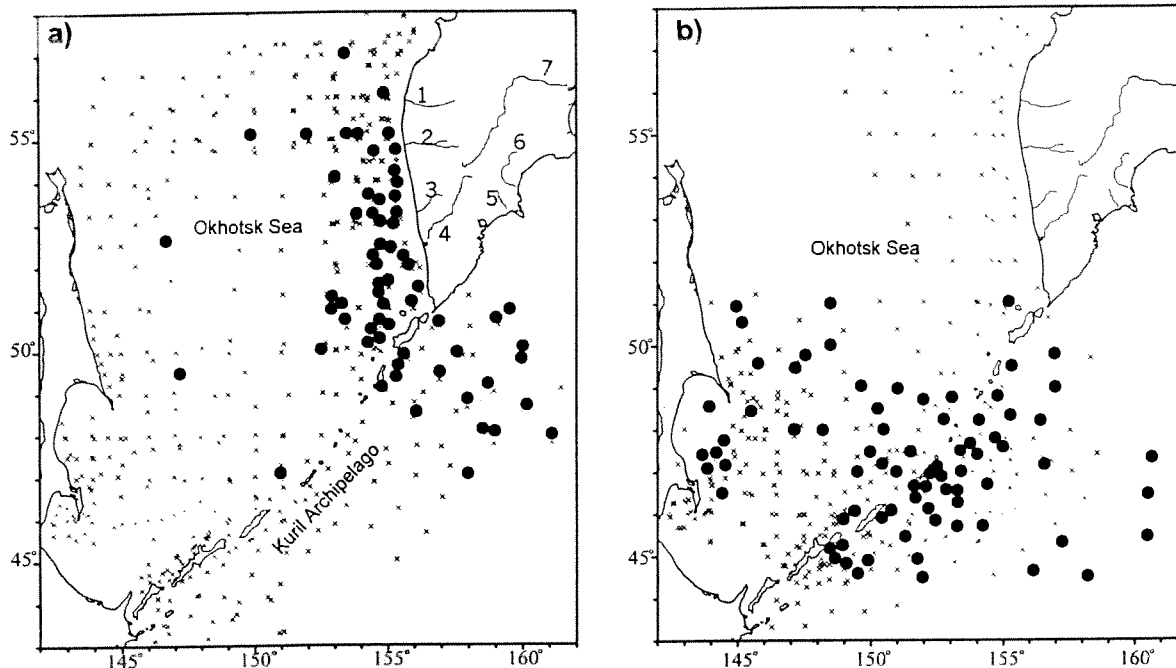
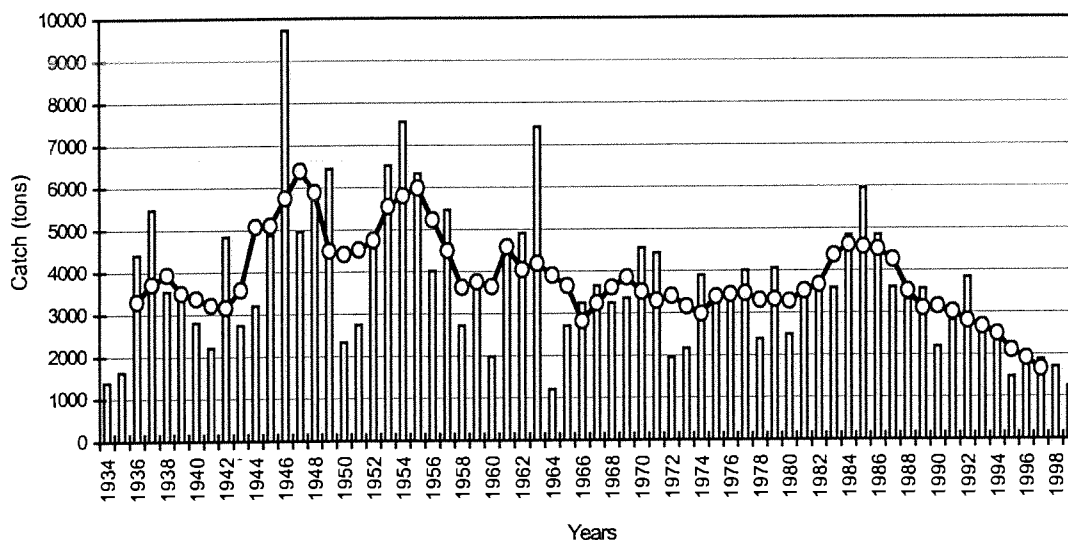


Fig. 6. Coho salmon catch in the Russian Far East (Eastern and western Kamchatka and the Okhotsk Sea continental coast), 1934–1999. Solid line indicates 5-years moving average.



Coho Salmon Fishery and Stock Assessments

During the last 20 years, coastal catches of coho salmon varied from 1,476 metric tonnes (t) in 1995 to 5,993 t in 1985, with an average annual catch of 3,224 t (Fig. 6). In the second half of the 1940s–1950s, the coho salmon harvest exceeded 4,000 t, as a rule. Then, in the 1960s to early 1980s, it varied usually between 3,000 and 4,000 t. In the 1980s, Rus-

sian coho catch grew to nearly 6,000 t in 1985, and then began to decrease gradually. In the second half of the 1990s, coho coastal catch exceeded 2,000 t in 1997 only. In addition, the foreign fleet caught 580 to 710 t of Asian coho at sea. However, the driftnet fishery alone could not explain the decrease in coastal coho catch. The coho catch at sea totalled only 35 and 234 t in the first years of the decrease in coastal catch, 1994 and 1995 (Table 2).

Table 2. Foreign fishery fleet Pacific salmon catches in the Russian Exclusive Economic Zone, 1993–1998.

Year	Pink	Chum	Sockeye	Coho	Chinook	Masu	Total
1993	4948	8597	7705	187	419	0	21856
1994	797	14264	3670	35	187	0	18953
1995	3008	18796	6146	234	126	8	28318
1996	900	14710	5644	628	159	1	22042
1997	1857	13488	9150	579	462	1	25537
1998	918	12013	2645	709	329	3	16617

In 1979–1984, the average number of coho spawners was estimated by the KamchatNIRO scientists at 0.26–0.43 million fish in the main part of the spawning area on the western coast of the Kamchatka Peninsula, southward from Icha River (Nepomnyaschi 1985; Yanovskaya et al. 1989). Zorbidi (1993) estimated the coho spawning stock to be 0.3 to 1.25 million fish over the whole western Kamchatka coast between 1986 and 1993. Coho spawning biomass was estimated as 1,000–4,000 t, combined catch and escapement, with a mean individual weight of 3.19 kg. On the continental Okhotsk Sea coast, coho spawning numbers were estimated to be 0.16–0.43 million fish, or 650–1,760 t in 1980–1985 (Rogatnykh 1985). A high abundance of coho salmon occurred in the continental Okhotsk Sea coast in 1992 and 1993 (at the same time as the high pink salmon catch). In 1992, the coho salmon harvest reached 446 t in that area. In 1993, coho abundance was estimated at 580,000 fish (about 2,400 t), from which 774 t were caught. Therefore, according to coastal survey data, anadromous coho abundance totaled 1,500–5,400 t in the 1990s, and in 1992–1993 up to 6,400 t in the northern Okhotsk Sea (for this rough estimate, sums of minimum and maximum values were used).

If these coho abundance estimates (1,500–6,400 t) were correct, the Russian annual catch (569–1,987) in the Okhotsk Sea between 1990 and 1998 was notably less than allowable. In the 1950s–1960s, coastal catch averaged 27% in total anadromous coho abundance on the western Kamchatka. According to Zorbidi (1975), anadromous coho abundance was 0.62–5.0 million fish (average 2.1 million), or 2,140–17,250 t (average 7,250 t) there. Of course, coho abundance was undoubtedly higher in the 1950s–1960s, than in the 1990s. Average coho harvest was three times higher in that period on the western Kamchatka: 1,980 versus 640 t. If the same exploitation rate (27%) of coho salmon resources occurred for the 1990s, it would have implied an average abundance of coho stock on the western Kamchatka of about 2,400 t (640 t fish). This is less than the average estimated value for 1990–1998.

The eastern Kamchatka coho stock abundance was roughly assessed at 0.6–3.1 million fish (average 1.7 million), or 1,620–9,610 t (average 5,270 t) in

1950s–1960s (Zorbidi 1975). In 1984, about 0.54 million coho spawners were estimated in the Kamchatka River system, which includes the main coho spawning grounds on the east side of the peninsula (Nepomnyaschi 1985). This stock contributed 51% of the total coho spawner numbers estimated in the eastern Kamchatka region (except the Bering Sea coast). However, the Kamchatka River portion annually contributed up to 70% in coho salmon catch there. In 1993, this portion increased to 83.5% (Zorbidi 1993). This suggests that coho stocks from other rivers may be underexploited by the commercial fishery. Nevertheless, according to official statistics, the portion of coho catch from the total stock is incredibly high; in 1984, it reached 3,830 t, that was estimated to be 70.1% of catch plus escapement numbers (5,460 t) on the eastern Kamchatka.

Coho stocks on the Bering Sea coast are insignificant compared to those in the eastern Kamchatka. Coho catches in the Bering Sea are usually small during trawl surveys. In July of 1992, coho salmon biomass was estimated at about 12 t, and in July 1993, 26 t. According to official statistics of foreign drift-net fisheries, annual coho salmon catch does not exceed 1 t in the southwestern Bering Sea.

Trawl surveys of Pacific salmon at sea allow the estimation of oceanic stock abundance, in addition to coastal abundance estimates (Radchenko 1998). In mid July of 1991 and 1992, estimated coho biomass was relatively small at 160 and 1,600 t in the Okhotsk Sea. Later in 1992 (from July 28 to August 7), noticeable coho aggregations occurred eastward from the northern Kuril straits. During the R/V *Professor Levandov* cruise, coho biomass in these aggregations was estimated at 12,200 t (5.28 million fish). Apparently, the pelagic survey in 1992 coincided with the coho migration that year. Later, from August 1–12, 1992, about 6,230 t, or 1.95 million t of coho were estimated in the area near western Kamchatka during another survey using the R/V *Professor Kaganovsky*. The two surveys overlapped by one week. Thus, it is possible that the same coho stock was only partly assessed on both surveys. Also, some of the coho caught eastward from the northern Kuril straits may have been fish belonging to the eastern Kamchatka stock migrating through this area to their own natal rivers. However, biomass of the eastern Kamchatka

stocks did not likely exceed their average level (5,270 t). The total catch of the eastern Kamchatka coho appeared not to be higher in 1992 than the average for the previous five years (2,200 versus 2,266 t). It may be much less, since the eastern Kamchatka coho are fished in the coastal zone and begin entering rivers in July, far north of the R/V *Professor Levanidov's* survey area.

The possibility that part of the coho aggregations were assessed twice in adjacent areas in 1992 was examined assuming maturing coho migrate 50 miles/day. In this case, a double assessment appeared to be possible for approximately 2,300 t, if all the coho migrated to western Kamchatka. Of course, such unidirectional migration is unlikely. In late July–August 1993, coho biomass was estimated at 1,520 t in the central and western Okhotsk Sea, and in 1995 at 1,110 t. Despite this unreliable estimate, in 1992 the total biomass of coho migrating in the Okhotsk Sea could not have been less than 10,900 t (sum of both survey estimates minus a possible overestimate due to overlapping and potential eastern Kamchatka coho biomass: $12,200 + 6,230 - 2,300 - 5,270 = 10,900$ t). Based on research recommendations, the quota for the coho salmon commercial fishery was increased from 500 to 1,500 t on the western Kamchatka. Coho harvest reached 1,226 t there, and 1,947 t for the whole Okhotsk Sea coast in 1992.

High coho abundance was also estimated in western Kamchatka waters in August 1996. During the pelagic trawl survey from August 5–21, 1996, coho biomass was estimated at 8,000 t. The coho portion of the total salmon biomass reached 7.1% there even though pink and chum salmon were migrating through that area (Radchenko et al. 1998). Note that adult coho could occur in the Okhotsk Sea until December (Rogatnykh 1985), although trawl catches were limited to July through August.

DISCUSSION

Seasonal variability in coho abundance has been analyzed in the Okhotsk Sea. In early July 1991, coho biomass was estimated at 160 t in the survey area near western Kamchatka. At the end of July 1992, coho biomass was an order of magnitude higher at 1,600 t. In early August, it increased sharply and briefly in 1992 and 1996. After August, the biomass decreased again due to coho migrations into local rivers and northwards. In 1996, coho salmon coastal catch (645 t) was almost equal to the average catch for western Kamchatka in the 1990s: 640 t. The estimated level of coho salmon biomass at 8,000 t also seems close to the average, assuming average catch level. The estimated variance in biomass calculated for the survey data provided a range for the estimate of 6,300–9,700 t. These estimates were 1.5–4 times

higher than values given by coastal observations, i.e. coho catch+escapement for the western Kamchatka in the 1990s (1,500–6,400 t) appeared to be too low in comparison with marine survey data.

The harvest rate for coho salmon was between 57.5–73.6% (average 63%) on the eastern Kamchatka coast in 1993–1997. For example, coho salmon spawning biomass totaled 1,601 t on the eastern Kamchatka, including a harvest at 1,085 t (0.45 million fish) and an escapement of 520 t (0.21 million fish) in 1997. As indicated above, this harvest rate appears too high and likely is incorrect. If a harvest rate of 63% was true for coho in the 1950s–1960s, coho spawning stock abundance on the eastern Kamchatka would be 1,110–4,510 t, or 0.36–1.45 million fish. Therefore, the average eastern Kamchatka coho stock abundance was 3,210 t, or 1.04 million fish in those years. This is notably less than the 5,270 t, or 1.7 million fish, of Zorbidi's (1975) estimates. The harvest rate of 38.9% obtained from anadromous coho biomass (Zorbidi 1975) seems more reliable. In the second half of the 1990s, the Kamchatka River coho stock declined, as reflected by a significant reduction in coho harvest. The average annual coho catch amounted to 1,356,200 t on the eastern Kamchatka in 1990–1998, or 60.1% of the salmon harvest in 1950–1969 (2,052,200 t). If the same percentage catch was assumed for the total anadromous run in the 1990s, coho spawning stock would be estimated at 1,070–6,350 t, (average 3,710 t) in eastern Kamchatka. There is no reason to presume that the coho harvest rate by the commercial fishery in the Soviet controlled economy was less than in the 1990s.

The main causes of the underestimation of coho abundance included an illegal fishery in river tributaries, in particular on the spawning grounds (S. Sinyakov, KamchatNIRO, Naberezhnaya 18, Petropavlovsk-Kamchatsky 683602, Russia, personal communication). In addition, small coho stocks were likely underestimated in rivers distant from densely populated regions. It should be noted that the coho run extends through the whole autumn, but beach and river seine fisheries are usually completed in September, seldom as late as October. A part of the coho stock, the so-called fall run, enters the rivers under ice (Gribanov 1948) and can not be utilized by the commercial fishery. The estimated biomass of fall run coho was 430–560 t (0.14–0.18 million fish) in the eastern Kamchatka in 1984 (Nepomnyaschi 1985). This late run was poorly covered by coastal observations in recent years.

In our opinion, coho salmon stocks are underexploited by the commercial fishery on the eastern Kamchatka, except for populations in the Kamchatka River and four other rivers: the Ozernaya River (not the well known river in western Kamchatka flowing

from Kurilskoye Lake), and Vyvenka, Zhupanova, and Nalycheva rivers. These well exploited rivers and their fishing grounds are in the immediate vicinity of processing facilities and populated areas. However, the quota for the commercial coho fishery may be increased for active fishery grounds too, as was shown for the western Kamchatka region in 1992. In any case, strict protection of coho salmon spawning grounds from illegal fisheries must be ensured.

Juvenile coho population estimates from in-river monitoring support our suggestion on the total abundance of this species. In the Okhotsk Sea, coho juveniles occurred from August to November (Figs. 1, 2). The autumn trawl surveys rarely coincided with the migration time of juvenile coho, and its partial estimation was conducted only in the eastern Okhotsk Sea. In September–October 1994, juvenile coho numbers were estimated at 6.6 million fish (1,910 t) above the western Kamchatka shelf and in adjacent areas.

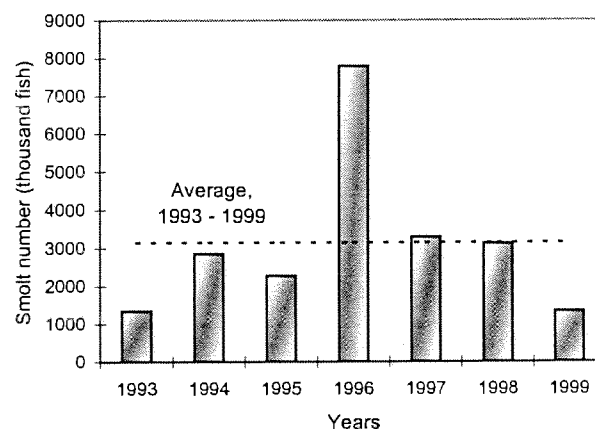
In 1996, the number of coho salmon smolts was estimated at 3.7 million fish from four rivers of the southwestern Kamchatka coast (two tributaries of the Bolshaya River, Bystraya and Klyutchevaya, and also Krutogorova and Kikhchik rivers). In 1997, coho outmigrant numbers were even higher (up to 5.1 million fish) from three monitored rivers, the Bystraya, Krutogorova, and Kikhchik. The total area of coho spawning grounds was assessed at 5–6 km². The Bystraya and Klyutchevaya rivers contribute only 0.47–0.52 km² (Ostroumov 1975, 1989). All spawning grounds were not utilized by coho in years of low stock abundance. Meanwhile, using data on coho spawning occurrence in the northwestern Kamchatka rivers, total juvenile coho abundance can be assessed to be at least 2.5 times higher than for monitored rivers (9.3–12.8 versus 3.7–5.1 million fish). If natural mortality rates for coho outmigrants are assumed to be 2% daily (Mathews and Buckley 1976; Karpenko 1998), the abundance of western Kamchatka juvenile coho stocks is 4.97–6.84 million fish 40 days after leaving freshwater.

According to the information above, abundance of the continental adult coho stocks in the northern Okhotsk Sea was assessed at 650–1,750 t from a total of 1,500–5,400 t in the whole Okhotsk Sea area, i.e. approximately 1.3–2 times less than the western Kamchatka stock abundance. If the ratio of juvenile to adult coho numbers is the same for these two regions, then approximately 2.49–5.26 million outmigrants must enter the Okhotsk Sea from the northern coast rivers. In this case, the total coho outmigrant abundance from wild stocks would be 7.46–12.1 million fish (1,110–1,810 t) in the Okhotsk Sea in summer. By October, the stock could decrease to 6.48–10.57 million fish. This estimation was consistent with the results from the autumn survey in 1994.

According to our estimate of coho spawning stock abundance in the Okhotsk Sea (1.97–3.04 million fish), coho salmon returns can be estimated at 28.8–30.4% of smolt output on average. This survival rate appears underestimated for salmon spending one year at sea. For example, pink salmon survival in the Okhotsk Sea was estimated at 25.2–61.6%, average 50% in the 1990s (Shuntov 1994; Radchenko 1998). This is consistent with our views on Asian coho salmon stock underestimation.

Besides wild stocks, 2.2–7.8 million coho smolts were annually released from the Sakhalin and northern Okhotsk Sea hatcheries in 1994–1998 (Fig. 7). Relatively low coho abundance at sea (in comparison with other salmon species) and its flexibility in food choice (wide spectrum of juvenile fish (Glebov

Fig. 7. Coho smolts released from Russian hatcheries, 1993–1998.



1998)) suggest a promising outlook for further development of hatchery production, of course, on a large scale, which would not be detrimental to wild populations. Juvenile coho are common in Sakhalin rivers (Gritsenko 1973), but this does not ensure high returns and catches. However, the progressive technology of hatcheries (release of fed juveniles, etc.) could change this situation and maintain coho abundance in the region at a significantly higher level.

CONCLUSIONS

Asian coho stocks are underestimated. This has hindered the rational exploitation of this resource, and lead to an under-representation of its role in freshwater and marine ecosystems.

The pelagic survey employed for estimation of Pacific salmon abundance can provide data to clarify coastal observation results. These data should now be included in the monitoring system for salmon populations.

Further development of Asian coho hatcheries could increase coho abundance, harvest and importance in Russian Pacific salmon catches in the near future.

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Changing the Balance: Interactions between Hatchery and Wild Pacific Coho Salmon in the Presence of Regime Shifts

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Abstract: Nearly 5 billion salmon are released from enhancement projects on an annual basis into the Pacific Ocean by Canada, Japan, Russia, and the United States. Although these large-scale enhancement programs contribute substantially to salmon fisheries in the North Pacific, there is growing evidence to suggest that these hatchery fish may negatively affect wild salmon stocks both from a genetic and ecological perspective. There is also some evidence that hatchery fish have replaced wild fish particularly chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) stocks. The percentage of hatchery fish in the waters off southern British Columbia, marine survival and climate trends, and hatchery policies and practices are used to examine potential interactions between hatchery and wild stocks. Shifts to lower productivity regimes such as occurred in 1989/90 may amplify the negative interactions. Decisive management action such as significantly reducing harvest pressure and protecting freshwater habitat may reduce these effects, but longer-term solutions are likely only if enhancement activities are viewed in a broader ecological context.

INTRODUCTION

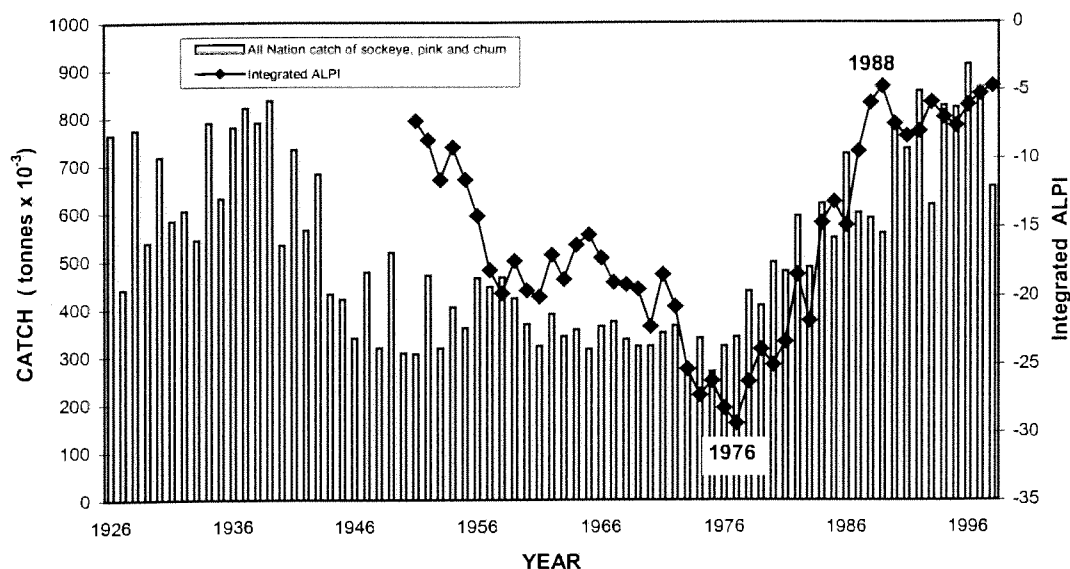
Salmon production in the north Pacific has fluctuated widely this century and there is some evidence to suggest such fluctuations have occurred naturally for hundreds and perhaps thousands of years (Finney et al. 1998; Beamish et al. 1999). An increase in production started in 1977 and coincided with significant shifts in climate and the ecosystem of the north Pacific (Ebbesmeyer et al. 1991; Beamish and Bouillon 1993). By the mid-1980s, total Pacific salmon catch exceeded 900,000 t annually. Salmon catches in Canada began to decline sharply around 1990, again coincidentally with a significant shift in the climate/ocean environment of the north Pacific (Beamish et al. 2000). Declines in salmon catch occurred for coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon despite large additions of hatchery-reared fry and smolts. These declines have resulted in managers in both Canada and the United States adopting restrictive harvest strategies and other conservation measures to protect wild salmon stocks.

In addressing these complex salmon management issues, it is important to take into consideration the significant salmon enhancement activities around the Pacific, because the introduction of these hatchery

fish constitutes a major human intervention in our ecosystem. Each year, nearly five billion juvenile salmon from hatcheries, spawning channels, and lake enrichment programs are released into the north Pacific by Canada, United States, Japan, and Russia (Mahnken et al. 1998). These fish, henceforth referred to as "hatchery fish", contribute substantially to fisheries in each country (Beamish et al. 1997) but scientific evidence is accumulating that suggests these large-scale enhancement activities also have significant adverse effects on both wild salmon production as well as the entire ecosystem (Meffe 1992; Thomas and Mathisen 1993; NRC 1996; Grant 1997; Brannon et al. 1998; Waples 1999).

When salmon enhancement programs were being initiated, there was a common belief that the productive capacity of the Pacific Ocean was vastly underutilized with respect to wild salmon production (Perry 1995). In part, this belief stemmed from the relatively large catches of wild salmon in the early part of this century compared to the much smaller catches during the 1950s and 1960s (Fig. 1). In a review of the Canadian initiative in 1980, the long-term objective of the program was to double salmon production from previous levels to 86,000 t annually. There was, at that time, no evidence to suggest to the program

Fig. 1. All nation catch of sockeye, pink, and chum salmon (bars) and the Integrated Aleutian Low Pressure Index (Beamish et al. 1999).



managers that the capacity of the ecosystem was incapable of sustaining this level of production. Salmon enhancement was seen as a means to compensate for declining freshwater production (lost through overfishing, urbanization or the construction of control structures/dams on rivers) or to take advantage of unproductive (or barren) freshwater systems (Beamish et al. 1997; Bradford and Irvine 2000).

Salmon enhancement has been practiced intensively in British Columbia since the early 1970s (SEP—Program Coordination and Assessment Division. 1998). In each of the last 20 years, nearly 500 million hatchery or enhanced salmon have been produced and released in British Columbia coastal waters (Table 1). Sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon production from hatcheries, artificial spawning channels or lake enrichment (fertilization) programs represents about 85 percent of the total production. Chinook and coho salmon are of particular significance to the sport fishery and on average 42.5 million chinook and 17.6 million coho fry and smolts are released from hatcheries and other enhancement projects annually (Table 1). The United States also releases significant numbers of hatchery salmon each year (Beamish et al. 1997; Didier 1998; Mahnken et al. 1998). Alaskan salmon enhancement began in the mid-1970s and is primarily focused on the production of sockeye, pink, and chum salmon with recent combined annual releases for these three species in the neighborhood of 1.25 billion fish (Beamish et al. 1997; Mahnken et al. 1998). Salmon enhancement in Washington State began in 1895 and by the early 1950s more than 100 million chinook and coho salmon were being produced and released each year (Beamish et al. 1997).

In contrast to the situation in British Columbia and Alaska, the bulk of the Washington, Oregon, Idaho, and California enhancement efforts are focused on the production of chinook and coho salmon. In the 1990s, approximately 250 million hatchery chinook and 68 million hatchery coho, or roughly five times the Canadian production for these two species combined, were released annually by Washington, Oregon, Idaho, and California (Table 2).

By the mid-1980s concerns and questions were being raised about the dramatic drop in survival for hatchery coho and chinook salmon in British Columbia. Marine survival for coho salmon decreased from about 20% in the mid-1970s to less than 2% by the 1990s. During the same period, marine survival for chinook salmon decreased from about 7% to less than 1%. Similar concerns had been raised in the United States (Washington State) in the early-1970s about its hatchery programs and, in retrospect, this was an ominous foreshadowing of the problems in British Columbia. To address this issue, several studies were initiated to determine the optimal size and time of release of hatchery salmon to maximize survival (Bilton et al. 1982). Despite these efforts, the marine survival for hatchery chinook and coho salmon continued to decline.

In this paper, we examine trends in the marine survival of coho stocks at the southern end of their freshwater distribution as well as the relative abundance of wild and hatchery coho in the Strait of Georgia. The implications of various past and current hatchery practices are discussed from a genetic, ecological, and fisheries perspective. Finally, the plausible effects of regime shifts are examined.

Table 1. Releases of juvenile salmon from Salmon Enhancement Program facilities in British Columbia (SEP—Program Coordination and Assessment Division, 1998).

Brood Year	Chinook	Chum	Coho	Pink	Sockeye *	Total
1977	13,620,370	54,031,652	5,058,281	31,029,220	201,309,000	305,048,523
1978	14,253,404	54,524,319	4,857,722	1,268,250	141,574,350	216,478,045
1979	16,379,080	82,652,695	8,756,923	36,254,543	220,701,122	364,744,363
1980	19,850,845	106,217,696	7,719,900	38,852,965	199,054,901	371,696,307
1981	17,428,192	129,893,114	12,277,121	92,109,022	211,604,372	463,311,821
1982	24,854,529	166,389,988	17,760,471	10,928,339	218,317,433	438,250,760
1983	29,374,066	178,391,768	22,625,999	106,863,812	144,301,195	481,556,840
1984	34,864,768	167,775,075	25,259,448	16,512,153	254,991,214	499,402,658
1985	42,761,623	158,534,388	19,141,208	80,406,993	175,808,962	476,653,174
1986	53,840,001	198,818,282	22,594,254	55,936,910	200,924,044	532,113,491
1987	63,693,726	199,054,154	17,819,451	61,138,919	158,654,299	500,360,549
1988	64,528,141	228,053,816	22,030,433	106,523,161	231,737,734	652,873,285
1989	63,628,249	203,541,458	23,276,342	70,654,343	223,568,392	584,668,784
1990	66,461,805	218,150,978	22,413,456	77,412,349	258,861,158	643,299,746
1991	59,540,198	200,152,670	22,147,770	62,785,065	277,228,098	621,853,801
1992	58,038,721	228,417,050	18,718,352	45,940,900	276,430,119	627,545,142
1993	51,094,315	216,634,268	19,220,749	65,091,522	192,659,518	544,700,372
1994	54,176,102	215,923,666	23,264,803	67,425,282	160,575,488	521,365,341
1995	45,370,507	155,671,013	20,343,257	60,366,993	120,842,893	402,594,663
1996	57,483,942	140,238,676	17,087,290	14,779,572	252,059,228	481,648,708
Average	42,562,129	165,153,336	17,618,662	55,114,016	206,060,176	486,508,319

* includes lake enrichment projects

Table 2. Estimated enhanced salmon releases from Washington, Oregon, California, and Idaho, 1993–1997.

Year	Chinook	Coho	Chum	Pink	Sockeye	Total
1993	210,387,445	68,586,446	59,773,153	0	3,492,161	342,239,205
1994	258,621,084	72,053,589	59,997,531	3,482,400	8,628,644	402,783,248
1995	287,691,217	71,591,160	59,141,900	100,000	16,397,960	434,922,237
1996	259,185,757	72,288,540	58,651,021	4,591,440	5,792,978	400,509,736
1997	232,847,517	55,067,267	42,048,963	0	14,470,295	344,434,042
Average	249,746,604	67,917,400	55,922,514	1,634,768	9,756,408	384,977,694

METHODS

Marine survival estimates for coho were determined using hatchery released coho that were tagged with a coded wire inserted in the nose (Beamish et al. 2000). The survival rate estimate was made by expanding the number of coded wire tags (CWT) recovered by the appropriate tagging percentage for each hatchery and calculating the percentage of total hatchery fish that survived. For the Strait of Georgia, the brood year survival was calculated using the number of hatchery fish released directly or indirectly into the Strait of Georgia and dividing the release

estimate into the estimate of the number that were caught in fisheries and returned to spawn. For Puget Sound, marine survival was calculated from CWT data stored at the Pacific States Marine Fisheries Commission regional mark information system (Pinix 1998). The Oregon Production Index (OPI) measures the survival of coho that enter the Pacific Ocean from California, Oregon, and southern Washington, north to Willapa Bay. The survival index is determined by summing the Washington, Oregon, and California smolt releases and dividing this number into the estimated adult and jack returns. Releases from private hatcheries or enhancement facilities are

not part of the index. Data from 1972–1995 are from Pacific Fisheries Management Council (PFMC 1997). In addition to examining the estimated survival rates, all survival estimates were subtracted by the mean of the time series and divided by the standard deviation to produce standardized anomalies.

Estimates of the percentage of hatchery and wild coho salmon were obtained from samples of juvenile salmon collected using trawl gear (Beamish and Folkes 1998; Sweeting et al. in review). The trawl net was a modified rope trawl with an average opening of 14 m (depth) by 30 m (width) and was towed at an average speed of 5 kt (2.6 m/s). The gear was trawled throughout the surface waters of the Strait of Georgia from the Canadian Coast Guard vessel *W.E. Ricker*. Surveys were conducted in May and September in both 1997 and 1998 (Sweeting et al. in review). Similar but larger rope trawls that have an opening of about 50 m X 50 m have been used to study the abundance and distribution of Asian stocks of Pacific salmon (Shuntov et al. 1988, 1993). All juvenile coho salmon were examined visually for clipped fins as well as with a coded wire tag detector to determine if a CWT had been inserted into the head. The heads of all fish with a CWT were frozen and the tag was removed and decoded at a later date. In addition, one hundred coho were randomly selected and the otoliths were examined for rearing type using the microstructure of the otolith (Zhang et al. 1995). Whenever possible, the left otolith was used in the determination, but if the left otolith was crystalline or if it was missing in the sample, the right otolith was used.

RESULTS

Average survival rates for coho salmon stocks associated with the OPI (3.2% survival) were approximately one third the rates observed for Strait of Georgia (9.4% survival) and Puget Sound (8.1% survival) stocks. In all three areas, marine survival rates after ocean year 1990 decreased substantially (Fig. 2). Compared to average survival rates prior to 1990, the observed reductions in survival were on the order of 60% for Strait of Georgia (from 11.2% to 4.6%) and OPI (from 3.9% to 1.3%) coho stocks, and 40% for Puget Sound (from 9.0% to 5.4%) coho stocks (Fig. 2). Lower than average marine survival was estimated for Puget Sound stocks in the early and mid-1970s while survival rates for Strait of Georgia and OPI coho stocks were either above average or average for the period prior to 1990. An intervention analysis (Hipel and McLeod 1994) of the standardized anomaly series (Fig. 2) identified a significant shift in 1990 in the Strait of Georgia and Puget Sound survival trends and in 1991 in the OPI (Table 3). These changes in marine survival coincided with significant shifts in the Aleutian Low Pressure Index and

Fig. 2. Marine survival rates and survival rate anomalies for hatchery coho released into the Strait of Georgia, Puget Sound, and stocks contributing to the Oregon Production Index (OPI) (Beamish et al. 2000). The dashed line in each of the six panels identifies ocean year 1990.

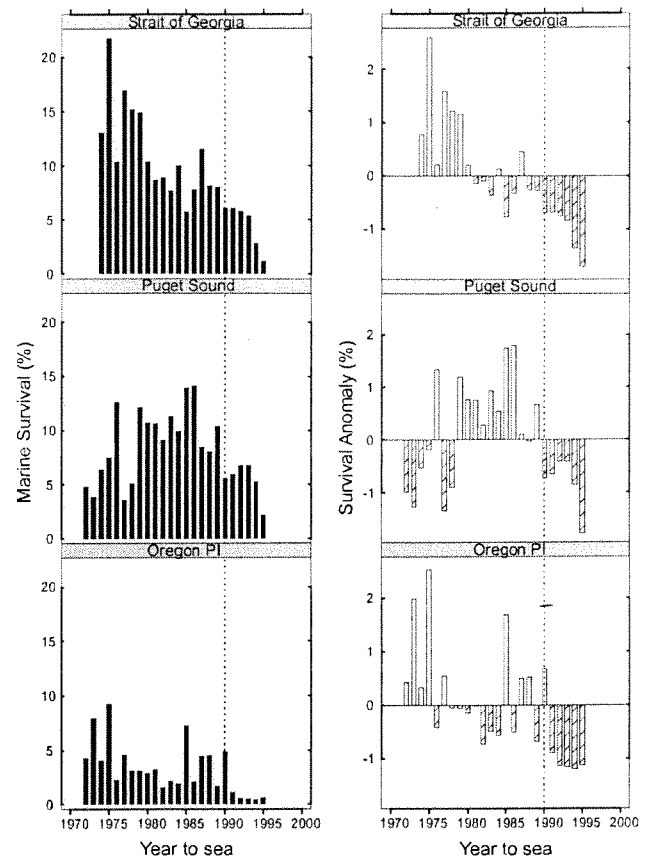


Table 3. Step intervention parameters, ω_0 , and estimated (standard errors) for the coho marine survival data.

Series	Year	ω_0 (se)
Strait of Georgia	1990	-4.61 (2.22)
Oregon Production Index	1991	-3.23 (1.00)
Puget Sound	1990	-0.73 (0.22)

other ocean-climate indices around 1990 (Beamish et al. 1999).

In 1997, 2,925 ocean age 0 coho were caught in the Strait of Georgia trawl surveys. An additional 2,760 ocean age 0 coho were caught in similar surveys in 1998. Based on fin clips and CWTs, approximately 75% of the juvenile coho caught in the Strait of Georgia in the 1997 survey were of hatchery origin. A similar estimate (70%) was obtained from the 1998 survey (Sweeting et al. in review). On average, hatchery coho were larger than wild coho in the

May survey with mean lengths of 136 mm and 125 mm, respectively. The size difference had largely disappeared by the September survey with mean lengths for hatchery and wild coho of 268 mm and 263 mm, respectively (Sweeting et al. in review). Percentages of hatchery fish estimated using the otolith microstructure were similar: 72.5% in 1997 and 71.5% in 1998. A high percentage (> 85%) of fish with one crystalline otolith were determined to be of hatchery origin.

DISCUSSION

A comparison of survival for hatchery and wild coho salmon is difficult primarily because of the lack of good data for wild stocks. Spatial and temporal differences in marine survival have been noted but the general trends in marine survival for both wild and hatchery coho salmon from the same geographic region appear to be similar (Coronado and Hilborn 1998). It is generally accepted that survival in the early freshwater stages of development is substantially better for hatchery reared salmon. There is also some evidence (Nickelson et al. 1986; Solazzi et al. 1990; Reisenbichler 1996) to suggest that hatchery fry out-planted in streams have better survival rates than wild fry due to a size advantage for the hatchery fish. This may be important since in some cases fry releases have been significant with more than 10,000 fish/km of stream out-planted in years when the streams were likely to be already fully seeded by progeny from wild spawners (Pitre and Cross 1992). It is plausible that both short and long term ecological and genetic consequences resulted from these activities although no quantitative studies have been conducted. There are also potential disease concerns because fish health checks are typically not conducted when the fry are out-planted into watersheds associated with the hatchery. Although the same pathogens are likely present in both the hatchery and the watersheds, the pathogens could be inadvertently amplified in the hatchery and spread to the wild fish (Noakes et al. 2000). Solazzi et al. (1990) also noted that the hatchery coho generally returned to spawn earlier than the wild coho but the resultant offspring from the adult hatchery coho had poorer survival. It is quite likely that differences in spawning time are designed to buffer the effects of environmental variation and that the percentage of early and late spawning wild coho shifts over time to adapt. These shifts could be in response to changes in either spawning or rearing habitat or food availability in fresh or saltwater. If wild coho were replaced by hatchery coho as a result of hatchery fry being out-planted, it is plausible that the stocks' ability to adapt to adverse environmental conditions has been seriously impaired. Solazzi et al. (1990) also found that for the 30 streams in Oregon

considered in their study, the number of adult coho caught in fisheries or returning to spawn was not substantially influenced by the level of enhancement.

The information for British Columbia is much more limited with only three wild indicator streams actively monitored for Strait of Georgia coho stocks and no experiments on the same or similar scale to Solazzi et al. (1990). Although reasonably good estimates of the number of juvenile coho (and other salmonids) released from hatcheries are available, the same is not necessarily true for indicator stocks where wild juveniles are tagged and released. In some years, a high percentage (more than 60%) of the adults returning to the wild indicator streams do not have coded wire tags (Simpson et al. 1999). These untagged fish are either stray hatchery fish from nearby hatcheries or represent the returns from wild juveniles that were missed during the tagging and monitoring programs conducted each year. The low straying rates for both coho and chinook salmon (Sandercock 1991; Labelle 1992; Candy and Beacham 2000) suggest that these fish are more likely returns of wild juvenile salmon that were not tagged. The exclusion of the unmarked adult fish as well as potential problems stemming from not tagging an unknown portion of the wild juvenile coho may result in a biased estimate of the marine survival for the wild fish (Noakes et al. 2000). The marine survival of the tagged fish may not be representative of the entire population given differences observed in other systems (Solazzi et al. 1990).

It is possible, however, to examine the relative abundance of hatchery and wild coho. Surveys of juvenile salmon in the Strait of Georgia and BC coastal waters indicated that between 70% and 80% of the juvenile coho salmon are now of hatchery origin (Beamish et al. 1998; Sweeting et al. in review). Also, some hatchery managers have suggested that up to 50% of the salmon spawning in rivers with hatcheries are first generation hatchery fish. These are in addition to the hatchery fish that may stray into streams without hatcheries to spawn with wild salmon (Simpson et al. 1999). Depending on one's point of view, these fish and their offspring could be viewed as 'wild' fish although there are serious genetic issues to consider (Hindar et al. 1991).

Estimates of the percentage of hatchery coho in the Strait of Georgia have been made over time (Cross et al. 1991; Sweeting et al. in review). The percentage of hatchery fish has increased from about 25% in the early 1980s to nearly 50% in 1990 and to approximately 75% in 1998 (Table 4). These estimates suggest a gradual replacement of wild fish with hatchery fish over time. If the annual rate of replacement (either through differences in marine survival between hatchery and wild salmon or differential harvest rates) was approximately 5% per year, then a

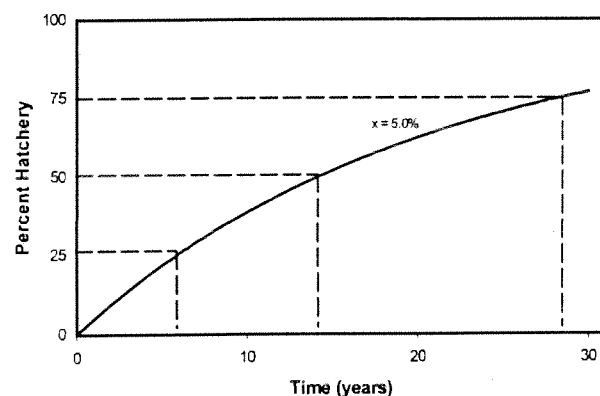
Table 4. Approximate percentage of hatchery origin Strait of Georgia coho salmon. Estimates from Cross et al. (1991) and Sweeting et al. (in review).

Period	Percentage
1980–1984	24
1985–1988	39
1989	45
1997–1998	75–80

simple calculation shows the proportion of hatchery fish would be approximately 25%, 50%, and 75% after 5, 13, and 28 years of enhancement, respectively (Fig. 3). This rate is only slightly higher than the rate of increasing hatchery percentage reported in Sweeting et al. (in review). It appears that the rate of replacement may have changed over time and was perhaps slightly less than 5% from the mid-1970s to the late-1980s and slightly more than 5% in the 1990s (Table 4 and Fig. 3). This could be due to changes in ecosystem productivity or some sort of positive feedback mechanism whereby the shift to hatchery fish accelerates as the proportion of hatchery fish increases. It is important to note that the increase in the percentage of hatchery coho has occurred at the same time the total abundance has declined.

Beamish and Mahnken (1998, 1999) proposed that coho salmon abundance is controlled according to a critical size and critical period hypothesis. They propose that early marine survival occurs in two major stages. In the first stage, marine mortality is primarily predator based occurring shortly after entry into salt water. The size of the coho smolts as well as their density and the abundance of predators are all contributing factors at this stage. The second stage of significant marine mortality occurs in the fall and winter although slower growing salmon may also die during the summer months. Juvenile salmon not reaching a critical size by the fall equinox are unable

Fig. 3. Estimated percentage of hatchery fish over time (years since enhancement began) assuming average annual replacement rates (i.e. hatchery fish replacing wild fish) of 5.0%. The percentage of hatchery fish would be approximately 25%, 50%, and 75% after 5, 13, and 28 years, respectively.



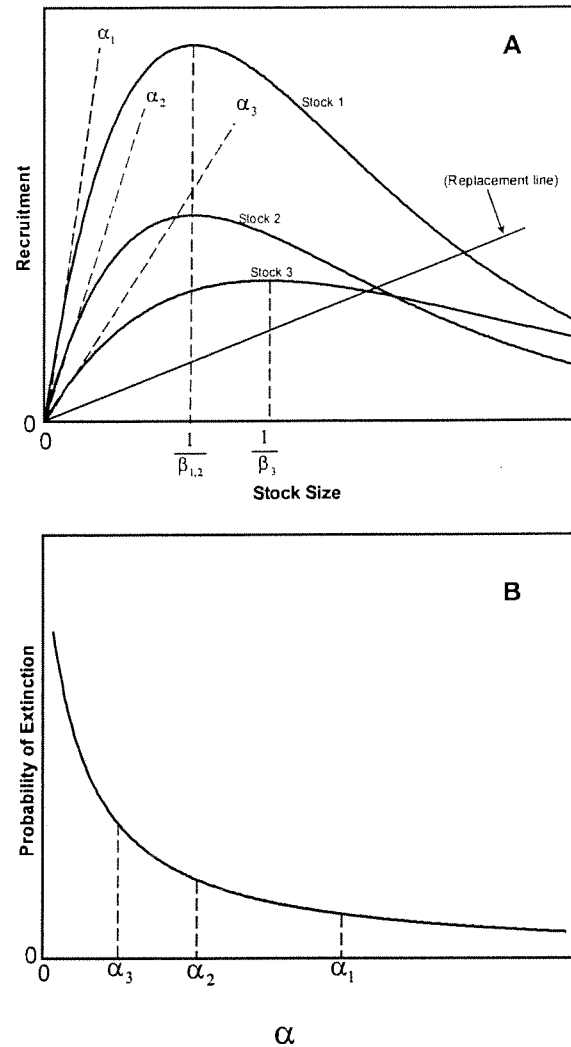
to survive until the next season. Both density dependent and density independent factors are important to the phase of growth related mortality. The negligible difference in the size of hatchery and wild fish in the fall (as observed during the September surveys) tends to support this size selective hypothesis although a faster growth rate of wild fish would also be an explanation. Since hatchery fish are larger than wild fish when they first enter the ocean (as observed during the May surveys), this may result in an advantage for hatchery fish during the size related, predation based mortality stage, ensuring that a greater percentage of hatchery fish than wild fish reach a critical size by the fall. This could, in part, explain the observed shift in the percentage of hatchery coho over time (Table 4). According to this view, the overall abundance of both wild and hatchery coho are governed through the critical size and critical period theory limited both by the overall carrying capacity of the ocean and through competitive interactions with other salmonids or other species such as herring (*Clupea harengus*) and hake (*Merluccius productus*).

Another likely factor contributing to the relative shift from wild to hatchery fish is non-selective mixed stock fisheries. In mixed stock fisheries, the catch is composed of salmon from a variety of wild and hatchery stocks and the various stocks are frequently subjected to differential harvest rates. This is particularly true when fewer wild salmon are mixed with a large number of co-migrating hatchery salmon. Because of the non-selective nature of these fisheries, significant portions of less abundant stocks can be intercepted during an intensive fishery opening where the capacity of the fishing fleet is excessive. The problem is compounded when stocks are in decline, such as after the regime shifts in 1990. The actual harvest rate (calculated only after the fishing season ends) can be much higher than the pre-season target harvest rate if salmon abundance is declining, thus increasing the probability of smaller runs of salmon being fished to near extinction levels. If the form of the production function for the stocks under consideration is known or can be assumed, it is possible to estimate an appropriate harvest rate for the mixed stock fishery. For instance, assuming a Ricker type production function Paulik et al. (1967) developed a method to determine an appropriate harvest rate. Differences in productivity may be a function of both density-independent and density-dependent factors as well as the current state of the stock. In reality, the complex interactions present in the ecosystem are likely to result in these factors being significantly confounded and difficult to separate. This is an important concept to consider in developing strategies to manage mixed stock fisheries and is often overlooked when stocks are considered in isolation during the assessment and management process.

If a Ricker stock recruitment function is considered appropriate, the density-independent factor, α , will be the determining factor at low levels of abundance with more productive stocks ($\alpha_1 > \alpha_2 > \alpha_3$) being able to withstand a higher harvest rate (Fig. 4A). Routeledge and Irvine (1999) showed that if the harvest rate is too high for too long (perhaps only a few generations), the lower productivity stocks will eventually become extinct and that the probability of extinction is a function of α (Fig. 4B). Climate shifts are likely to result in changes to the density independent component of the recruitment function (α) and perhaps to the density dependent component (β) through various complex ecological interactions. A shift to a less productive regime (such as occurred in 1990) will tend to reduce α , further compounding both the overall and relative declines of hatchery and wild coho. Also, hatchery stocks tend to have higher values of α (relatively few adults are required to produce a large number of juveniles) than wild stocks and are thus less likely to become extinct than wild stocks. A shift in climate may also increase the relative difference in α between hatchery and wild stocks and may, in part, explain the shift towards a higher percentage of hatchery fish in the combined population.

Enhancement activities have changed over the past century but it is clear that some practices have negatively affected wild stocks (Meffe 1992; NRC 1996; Brannon et al. 1998; Waples 1999; Noakes et al. 2000). The practices have tended to reduce genetic diversity in some cases (Withler 1988; Withler and Beacham 1994). In other instances, transfers within and between watersheds were done with little or no evaluation of the genetic consequences (Foerster 1946, 1968; Ricker 1987; Williams 1987; Roos 1991; Withler et al. 2000). While some limited degree of straying is generally believed to be beneficial in increasing local genetic diversity, the consequences of these larger scale and uncontrolled interventions are not known although they are commonly thought to be negative. The ecological consequences of enhancement have been equally significant through both biological and fisheries interactions. Climate shifts to lower productivity regimes and the inability to detect and react to these changes quickly have compounded the problem. The net result has been an overall decrease in coho abundance and an increase in the percentage of hatchery fish that seems to be accelerated by changes in environmental factors. It is clear a better understanding of the mechanisms controlling abundance and links to climate change is necessary.

Fig. 4. A. Ricker stock recruitment curves for three hypothetical stocks. Each stock is defined by a unique density-independent parameter, α . Stocks 1 and 2 have the same density-dependent parameter, β . **B.** Probability of stock extinction as a function of the Ricker α parameter. The replacement line represents the point where the stock (escapement) is just adequate to maintain the population at a fixed level of production.



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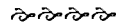
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Density Interactions between Pink Salmon (*Oncorhynchus gorbuscha*) and Chum Salmon (*O. keta*) and their Possible Effects on Distribution and Growth in the North Pacific Ocean and Bering Sea

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Key words: Pink salmon, chum salmon, interaction, density, distribution, growth, Pacific Ocean

Abstract: The long-term mean spatial and temporal distributions of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in the North Pacific Ocean were investigated using data collected on board Japanese salmon research vessels from 1972 to 1998. The distribution patterns of chum salmon differed between odd- and even-number years, and were more concentrated to the west in even-number years of low pink salmon abundance. In the Bering Sea, the density of pink salmon was higher in odd-number years than in even-number years, and density of chum salmon showed an opposite trend (higher in even than in odd-number years). Also chum salmon distribution shifted southeastward in odd-number years. These results suggest that there is a possible interaction between pink and chum salmon. The mean fork length of maturing pink salmon decreased from 1972 to 1998. Decreasing trends in fork length of age 3–5 chum salmon were also found during the same period. Significant negative relationships between density and mean growth of age 2–4 chum salmon were observed in the Bering Sea, although there was no relationship between density of pink salmon and mean growth of chum salmon directly. These results suggest that the growth of age 2–4 chum salmon is affected by intra-species in the Bering Sea and the abundance of pink salmon influenced the growth of chum salmon indirectly.

INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) is the most abundant salmon species, followed by chum salmon (*O. keta*) in the North Pacific Ocean. For two decades, the abundance of Pacific salmon especially pink and chum salmon has been high and hatchery production has increased, while the body size of both fish has decreased accordingly. Recent research indicated density-dependent effects on growth for some salmonid stocks in the marine environment (Peterman 1978; Rogers 1980; Beacham and Starr 1982; McGie 1984; Ishida et al. 1993). For chum and pink salmon direct and indirect evidence indicated that density-dependent effects were observed in the early marine environment (Birman 1960). Tado-koro et al. (1996) examined the abundance and stomach contents of salmonids in later life and the biomass of prey organisms, and suggested that there might be a limitation in the available prey resource for production of salmonids. This implied competitive interaction between pink and chum salmon during their marine life stages. Ishida et al. (1993) concluded that density-dependent factors explained 35%

of the decrease in average size of chum salmon in the central North Pacific. Walker et al. (1998) also showed that scale-edge growth of chum salmon was negatively correlated with Asian pink and chum salmon abundance, and pink salmon abundance might influence the third-year growth of chum salmon in the North Pacific Ocean. Smoker (1984) examined the effect of interaction between pink and chum on stock dynamics using a model which contrasted genetic and nongenetic mechanisms of determination of maturation age of chum salmon. From his model results, the genetic mechanism (high heritability of maturation age) lead to results similar to observed stock dynamics.

However, it is not clear how chum salmon are affected by the pink salmon abundance, and whether the growth of chum salmon is a result of intra- or inter-species interaction in offshore waters of the North Pacific Ocean. In this study, we examine the monthly long-term mean distribution, interannual changes in abundance of pink and chum salmon, and a possibility of inter-species interaction between pink and chum salmon.

MATERIAL AND METHODS

The data used were collected on board Japanese salmon research vessels in offshore waters of the North Pacific Ocean from 1972 to 1998. The total number of operations during the 27 year period from 1972 to 1998 in the North Pacific Ocean was 9,562 (Fig. 1). However, the number of operations in the eastern North Pacific Ocean was smaller than that in the western North Pacific Ocean. Salmon research vessels have used research-type gillnets and commercial-type gillnets. We analyzed the data obtained by research-type gillnets because this gear is non-selective (containing 10 different mesh sizes ranging from 48 to 157 mm; Takagi 1975). To describe the distribution of pink and chum salmon, data from the area between 30°N–65°N, 130°E–130°W were stratified by month, by 2 degree latitude by 5 degree longitude areas ($2^\circ \times 5^\circ$ grid), and by species. To describe monthly changes in distribution of pink and chum salmon, indexes of the long-term mean density of each species over the $2^\circ \times 5^\circ$ grid were calculated for each month of the year. The number of fish caught and the number of tans of gillnets fished were summed monthly and the density index (catch-per-unit effort, CPUE) in each grid was calculated as follows:

CPUE = total catch in number/total effort (in units of 30 tans of gillnet).

The proportions of maturing and immature fish in each grid were calculated based on Takagi's (1961) maturity definition, which is based on gonad weight.

RESULTS

Horizontal Distribution of Pink and Chum Salmon

Pink salmon were distributed in a wide zonal band along the 42°N line from 142°E to 165°W in April and May, and were the most abundant around 155°E (Fig. 2). However, pink salmon were not distributed in the area north of 50°N. In June and July, pink salmon extended their distribution to the area south of 62°N in the Bering Sea. The density of pink salmon between 150°E and 165°E and between 42°N and 55°N exceeded 100 fish per 30 tans. The area of relatively high density shifted westward from April to July. In August and September, pink salmon were distributed only in the coastal area, and they were not caught in offshore waters in October. The monthly changes in distribution of pink salmon densities appear to indicate their return migration to the spawning area.

In April and May, chum salmon were widely distributed in the area east of 145°E and north of 40°N in the western North Pacific, but the center of distribution for maturing fish was farther north than that of immature fish (Fig. 3). From June to July, the distribution of maturing chum salmon shifted progressively northwestward to the coast of Kamchatka, and northeastward to the Alaska coast. Immature chum salmon were widely distributed from 40°N to 60°N and they were most abundant in the Bering Sea. In August and September, maturing fish were rarely caught in offshore waters. In October, when fishing

Fig. 1. The distribution of operations (1972 to 1998) used in calculating area averages for this study. The western North Pacific (160°E–170°E, 38°N–52°N, 170°E–180°, 38°N–48°N), the Bering Sea (175°E–175°W, 55°N–59°N) and the eastern North Pacific (140°W–150°W, 48°N–58°N).

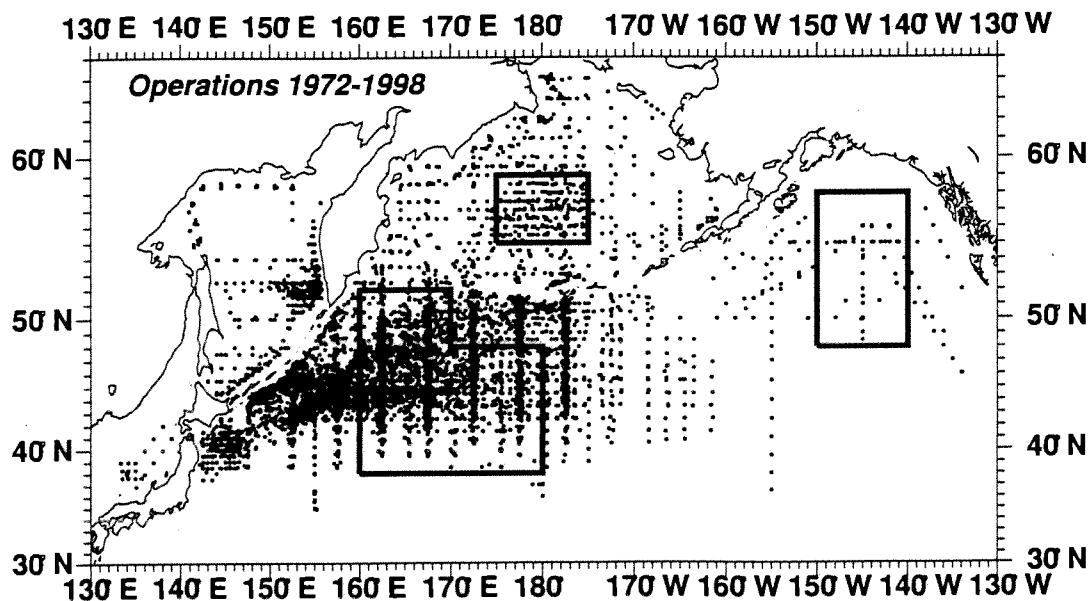


Fig. 2. Densities of pink salmon in the North Pacific Ocean in March to October averaged over 27 years, 1972–1998.

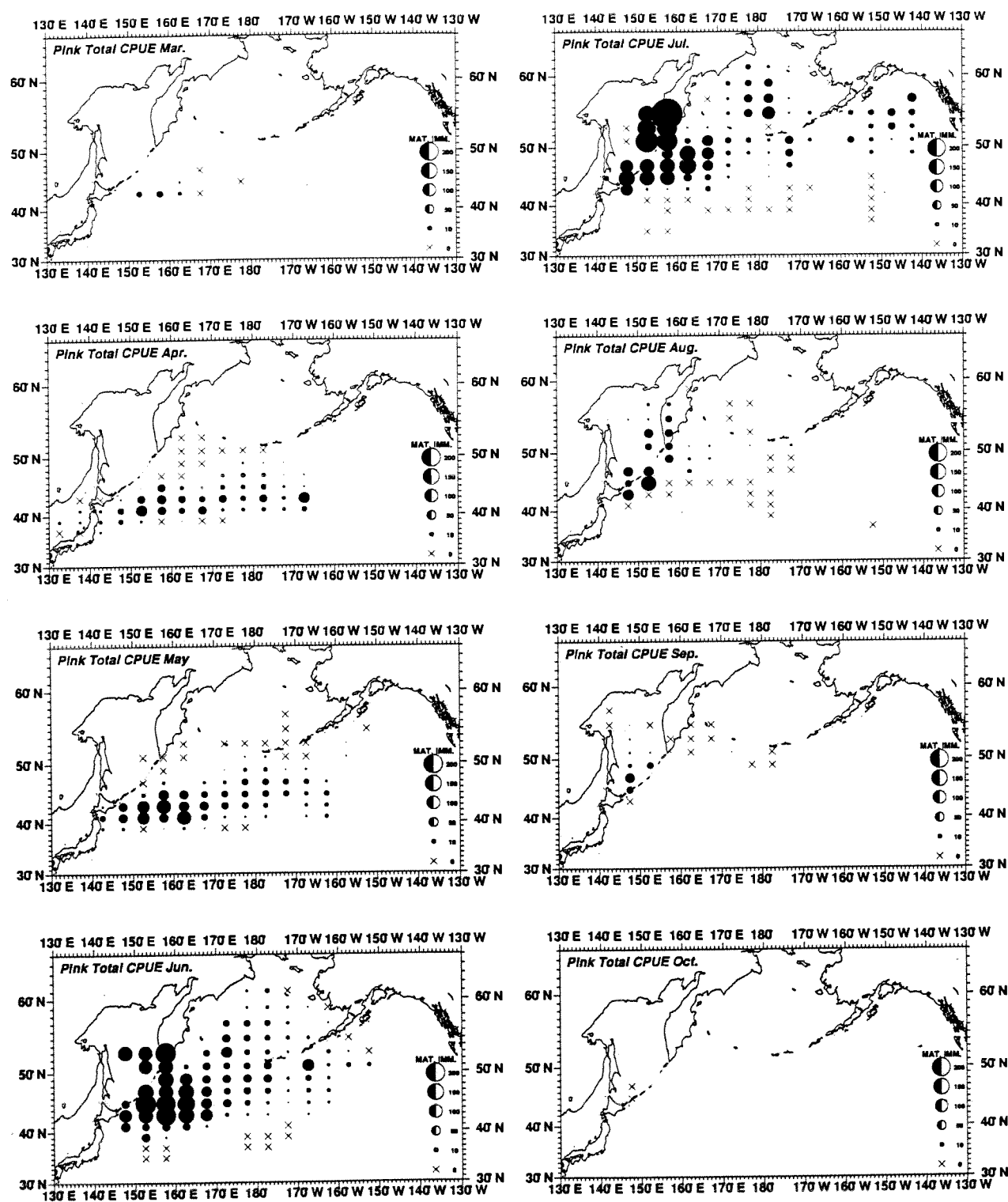
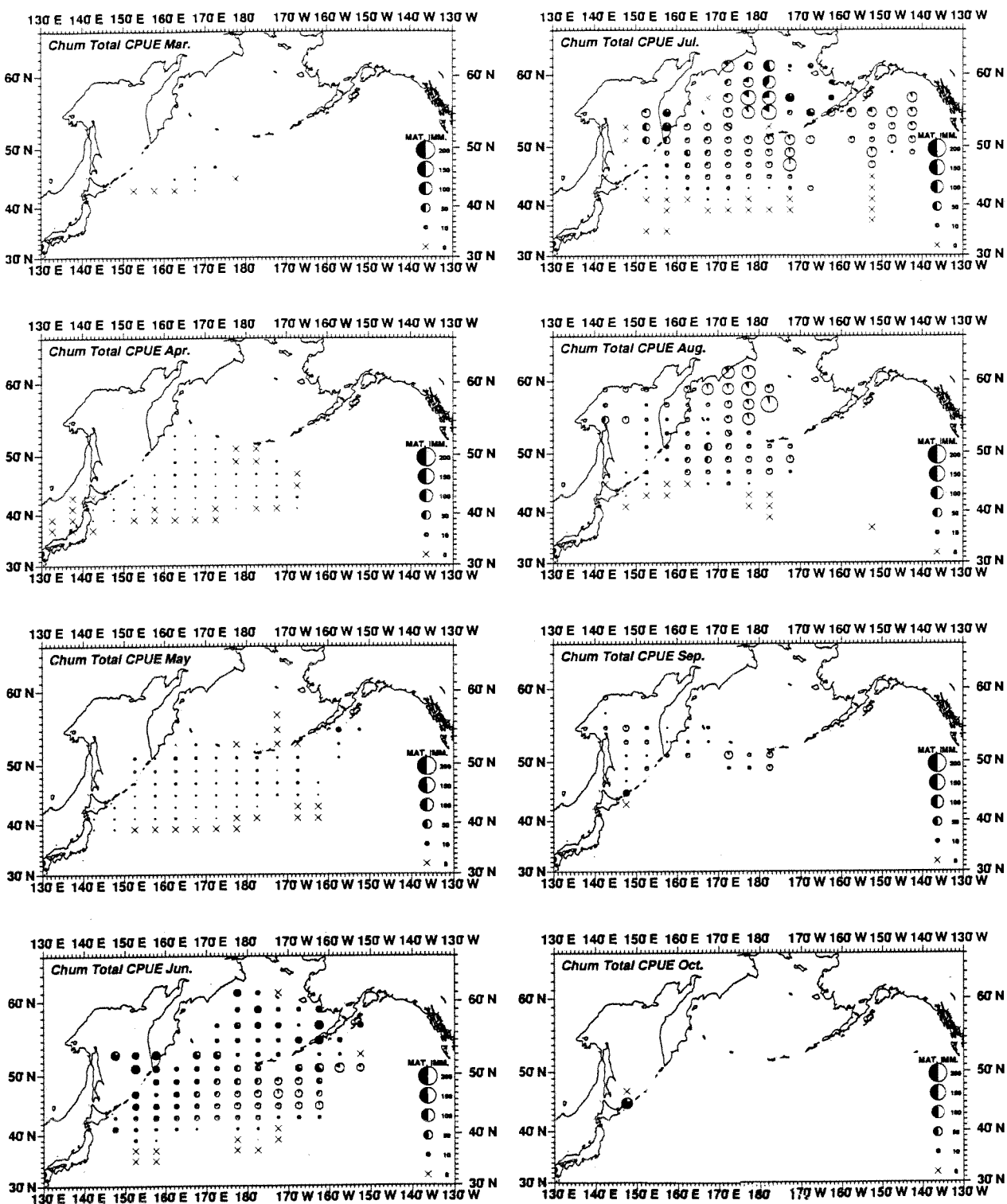


Fig. 3. Densities of chum salmon in the North Pacific Ocean in March to October averaged over 27 years, 1972–1998.



operations were limited to near the coast, the proportion of maturing fish was high. The proportion of immature fish in offshore waters increased as the season progressed and immature chum migrated from south to north in offshore waters. These results show that the distributions of pink salmon and chum salmon have overlapped in offshore waters, especially in the western North Pacific and in the Bering Sea from April to July.

Pink salmon were more widely distributed in odd-number years than in even-number years (Fig. 4). Moreover, the density of pink salmon was also higher in odd-number years than in even-number years except in the Gulf of Alaska. Particularly in the Bering Sea, odd-number year density exceeded 50 fish per 30 tans, while they were less than 10 fish per 30 tans in even-number years. Thus, a difference in the distribution and density of pink salmon between odd and even-number years is evident in offshore waters of the North Pacific Ocean.

No difference in chum salmon density between odd and even-number years was observed in the western North Pacific (Fig. 5). However, the density of chum salmon in the Bering Sea was lower in odd-number years and higher in even-number years, and was especially clear. On the contrary, in the eastern North Pacific, the density was higher in odd-number years, and lower in even-number years, though the difference was less distinct.

Pink salmon densities in odd-number years relative to even-number years were highest in areas north

of 45°N in the western North Pacific and in the Bering Sea (Fig. 6a). These areas correspond to regions where chum salmon densities were the lowest in odd-number years relative to even-number years (Fig. 6b). Chum salmon densities were also higher in odd-number relative to even-number years between 180° to 170°W around 46°N, and in the Gulf of Alaska. From these results, it appears that the change in distributions of chum salmon was associated with the odd/even year fluctuations of pink salmon density.

Interannual Changes in Relative Abundance of Pink and Chum Salmon

To examine interannual variations in relative abundance (density index) of pink and chum salmon, three major survey areas were defined as follows: the western North Pacific (160°E–170°E, 38°N–52°N, 170°E–180°, 38°N–48°N), the Bering Sea (175°E–175°W, 55°N–59°N) and the eastern North Pacific (140°W–150°W, 48°N–58°N), where Japanese salmon research vessels conducted gillnet fishing operations (Fig. 1). The densities of salmon in each area in July were averaged for each year, and a time series of densities of salmon in each area was estimated.

In the western North Pacific, the density of pink salmon in odd-year lines prior to 1985 was higher than that in even-year lines (Fig. 7a). After 1985, the interannual changes in density of pink salmon did not show the odd/even year fluctuation and ranged from

Fig. 4. The distribution of pink salmon in odd- (a) and even- (b) numbered years in July.

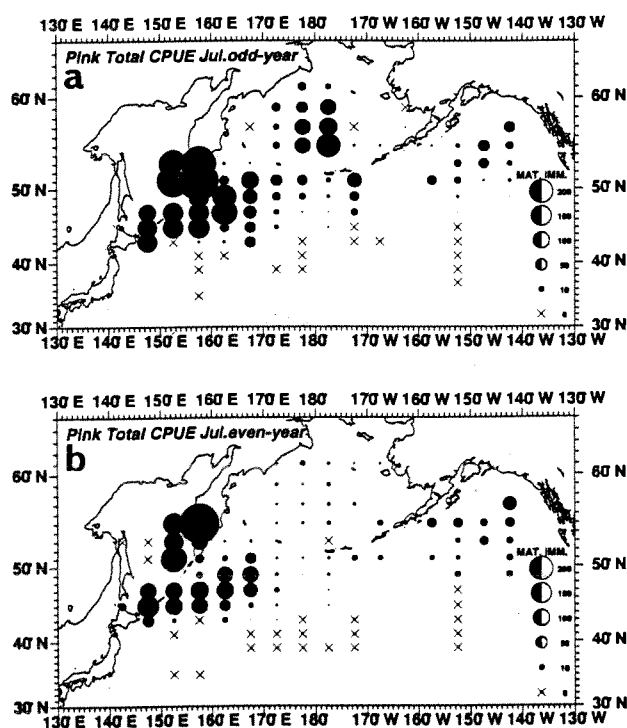


Fig. 5. The distribution of chum salmon in odd- (a) and even- (b) numbered years in July.

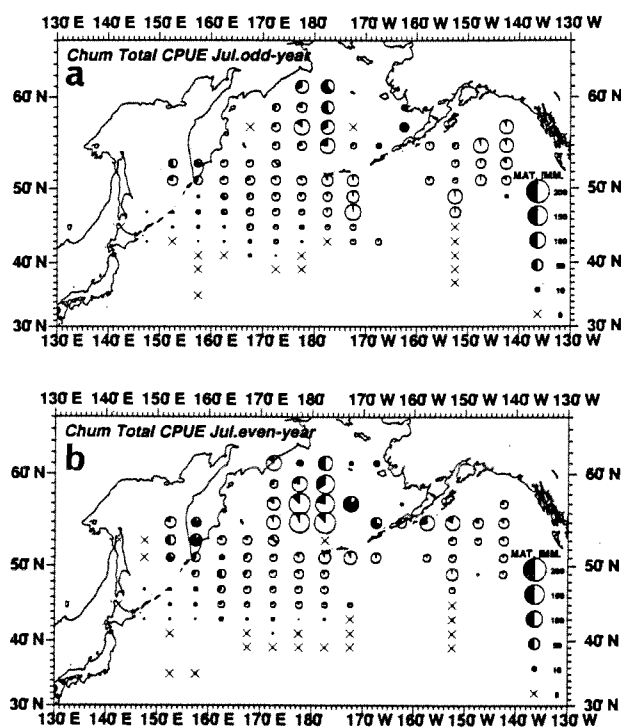
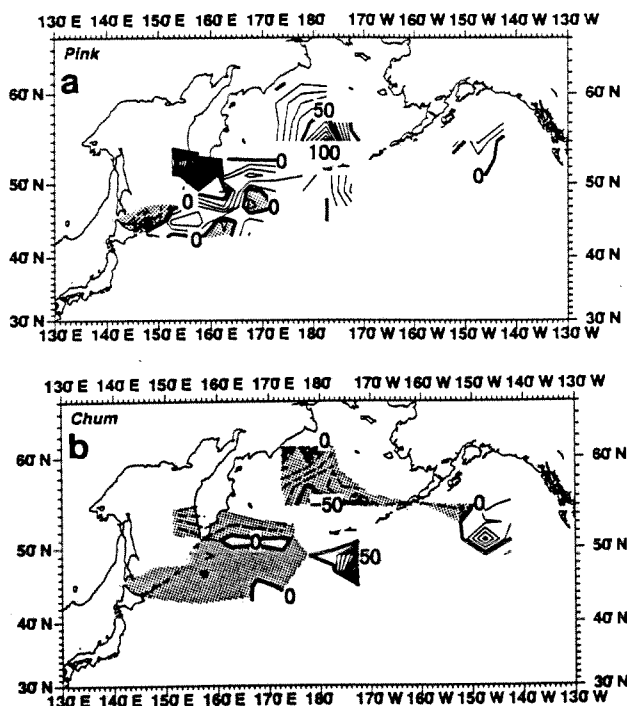


Fig. 6. Density of pink salmon (a) and chum salmon (b) in odd-numbered years relative to density in even-numbered years in the North Pacific Ocean and Bering Sea. (a) Pink salmon, (b) Chum salmon. The contour interval is 10 fish per 30 tans and negative contours (= density in odd-number years lower than that in even-number years) are dashed, and the area between is shaded.

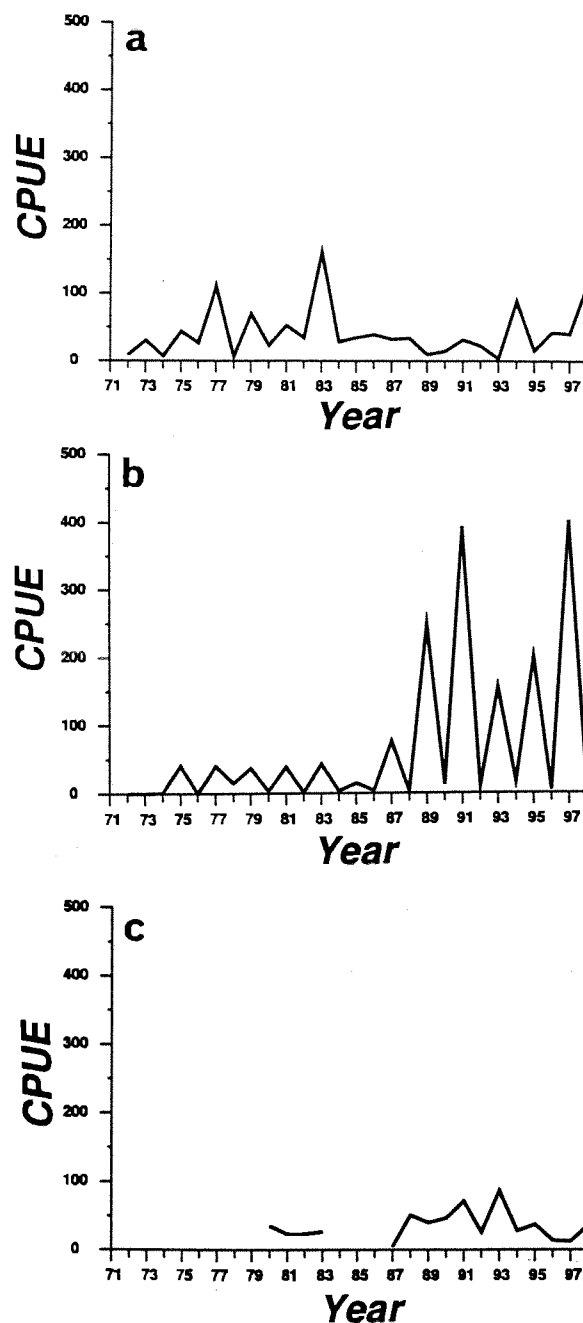


3 to 15 fish per 30 tans. In the Bering Sea, the inter-annual changes in the density of pink salmon were more variable than those in the western North Pacific. Densities of the odd-year lines remained at about 40 fish per 30 tans until 1989 (Fig. 7b). From 1985 to 1998, the odd-year lines increased sharply to about 200 fish per 30 tans. Conversely, densities in even-year lines remained stable at roughly 5 fish per 30 tans from 1972 to 1998. The densities of pink salmon in odd-year lines was higher than those in even-year lines. There was a significant difference in densities between odd and even-year lines (t test, $p < 0.05$). In the eastern North Pacific, the variation in the density of pink salmon did not show an odd/even year fluctuation such as in the Bering Sea (Fig. 7c). The density of pink salmon ranged from 20 to 80 fish per 30 tans.

Immature chum salmon were predominant in the western North Pacific, the Bering Sea and the eastern North Pacific in July (Fig. 8a). In the western North Pacific, the density of maturing and immature chum salmon slightly increased from the 1970s to 1990s. The total density of chum salmon was about half or less than that of pink salmon in the western North Pacific.

In the Bering Sea, the interannual changes in density of maturing and immature chum salmon showed clearly increasing trends from the 1970s to

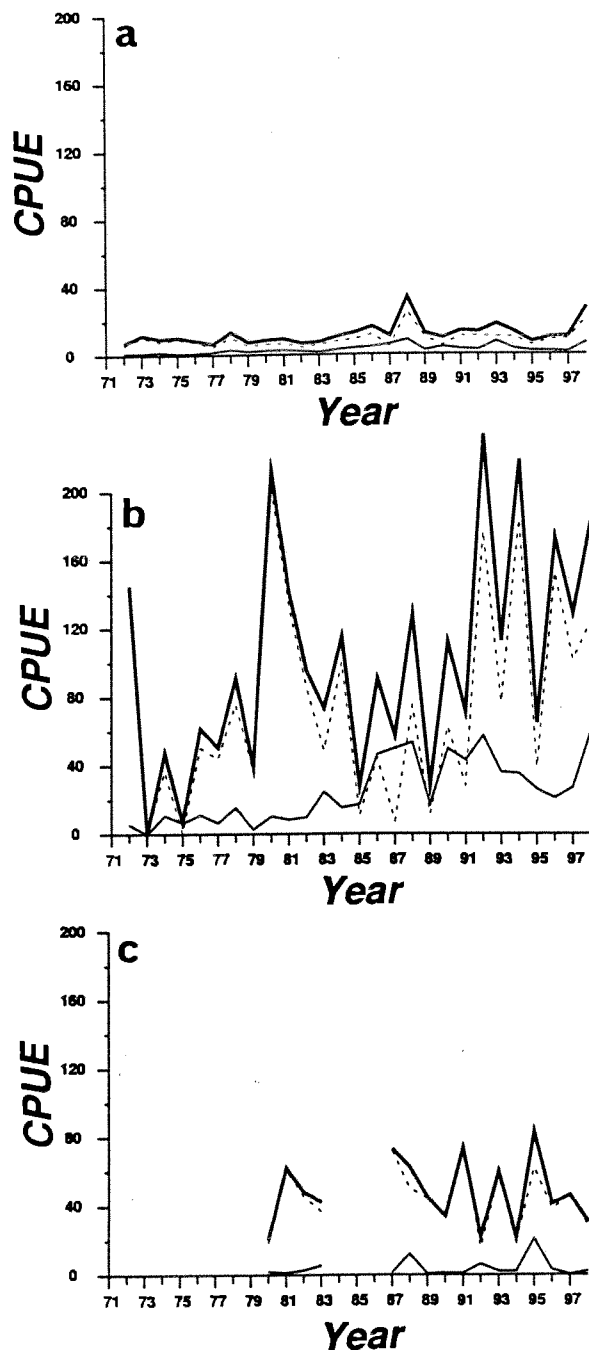
Fig. 7. Time series of the density of pink salmon in July in (a) the western North Pacific, (b) the Bering Sea and (c) the eastern North Pacific, respectively.



1990s (Fig. 8b). Moreover, CPUE of immature chum salmon in even-number years was distinctly higher than that in odd-number years. However, the densities of the immature chum salmon and pink salmon in odd and even years were out of phase, although the correlation between pink and chum salmon was not significant statistically. As pink salmon were abundant in odd-number years, immature chum salmon abundance was low. The density of maturing chum salmon did not show the same odd/even year fluctuation as immature chum salmon but did increase from

the 1970s to 1990s. Odd/even year fluctuations in density of immature chum salmon in the eastern North Pacific was out of phase with that in the Bering Sea (Fig. 8c). When chum salmon abundance in the Bering Sea was high, the abundance in the eastern North Pacific was low.

Fig. 8. Time series of the density of chum salmon in July in (a) the western North Pacific, (b) the Bering Sea and (c) the eastern North Pacific, respectively. Thin solid line, density of maturing chum salmon. Broken line, density immature maturing chum salmon. Thick solid line, total density of chum salmon.



There was a discrepancy in distributions of immature chum salmon in odd-number years and even-number years (Fig. 6), although the distributions of maturing chum salmon in the Bering Sea did not fluctuate. Densities of immature chum salmon in the Bering Sea and the eastern North Pacific were out of phase. The changes in immature chum salmon density in the Bering Sea reflected the changes in distributions of chum salmon in the eastern North Pacific. These results suggest that the variations in pink salmon abundance in the Bering Sea affect the distribution of immature chum salmon in the Bering Sea and the eastern North Pacific.

Interannual Changes in Age-specific Fork Length and Growth of Pink and Chum Salmon in the Bering Sea

Interannual changes in age-specific fork length and growth of pink and chum salmon in the Bering Sea were investigated. The age-specific fork lengths of salmon in each area were averaged for each year. For chum salmon, the differences in mean fork length from age t to age $t+1$ were calculated as the age-specific growth at age $t+1$ for each cohort. Because Ishida et al. (1998) reported that growth rate from spring to summer was greater than that in other seasons, age-specific growth at age $t+1$ was regarded as growth from age t to age $t+1$ for that cohort. Thus, the age-specific growth in this study was the change in mean fork length per year.

Mean fork length of maturing pink salmon in the Bering Sea generally decreased over the period of the study (Fig. 9). Mean fork length also showed an odd/even year fluctuation in phase with density, such that fork length in odd-year lines was greater than that in even-year lines. Mean fork length of chum salmon at age 4 and age 5 in the Bering Sea decreased (Fig. 10). The mean fork length at age 2 was around the value of 350 mm and stable. These variations in mean fork length did not show an odd/even year fluctuation similar to density. This result indicated that the size reduction of chum salmon during marine life stage had occurred by age 3.

Growth of chum salmon was negative in the Bering Sea at ages 3 and 4 (Fig. 11). This result indicated that size reduction of chum salmon was due to decreasing growth at ages 3 and 4 in the Bering Sea, and odd/even year fluctuations were found in growth of chum salmon except in 1990 (Fig. 11). The timing of size reduction of chum salmon was consistent with observations of Ishida et al. (1993), Kaeriyama (1998) and Walker et al. (1998) who showed that the growth reduction of Japanese and Russian chum salmon mainly occurred in the third year of ocean life based on analysis of scale patterns. In the present study, the decline of growth in chum salmon at age 4 was also found in the Bering Sea. The fluctuations of

Fig. 9. Time series of the fork length (mm) of pink salmon in July in the Bering Sea. The straight line is the linear regression of fork length on year.

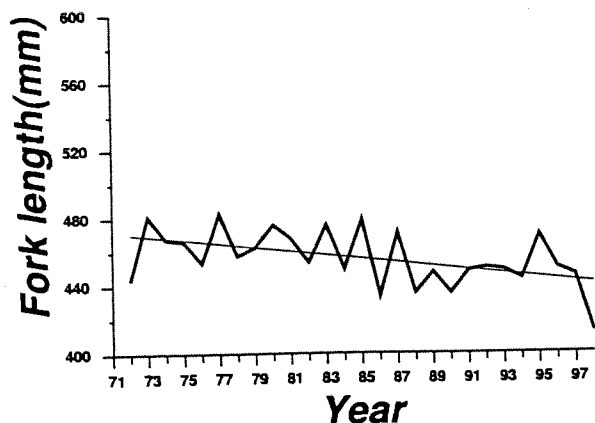


Fig. 10. Time series of the fork length (mm) of chum salmon in July in the Bering Sea. The straight line is the linear regression of fork length on year.

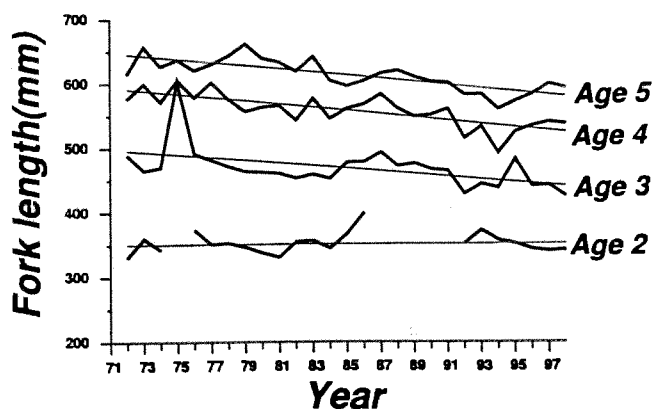
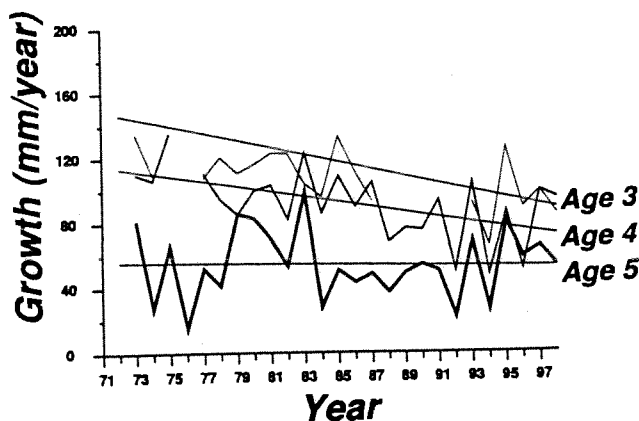


Fig. 11. Time series of the growth (mm/year) of chum salmon in July in the Bering Sea. The straight line is the linear regression of growth on year.



growth of chum salmon may be caused by density-dependent or environmental factors or both. The reason for the decline in growth of chum salmon at age 4 in the Bering Sea is discussed in the next section.

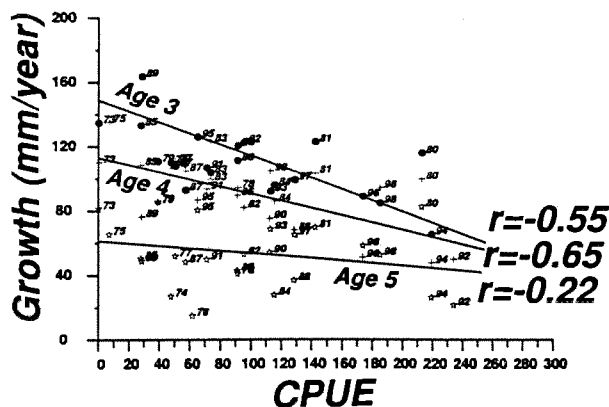
Relationship between Abundance and Growth of Salmon in the Bering Sea

For Pacific salmon, several papers have suggested that density-dependence may limit growth within stocks, among stocks, and among species in the ocean (Kaeriyama 1998, 1996a, b; Ogura et al. 1991; Kaeriyama and Urawa 1992). Helle and Hoffman (1995) have documented age-specific declines in the average size of two North American chum salmon populations. Bigler et al. (1996) also found a decline in average body size in Pacific salmon populations. Ishida et al. (1993) concluded that density-dependent factors explained 35% of the decrease in average size of chum salmon, and the remaining 65% may be explained by ocean conditions and the abundance of other salmon species. If the ocean distribution pattern of pink and chum salmon overlaps as shown in this study and food is limiting, then the significant trophic interaction between species found by Myers (1994) and Bigler et al. (1996) could result in density-dependent limitation of growth. In this study, to examine the possibility of inter- and intra-species density-dependent limitations on growth, we investigated the relationship between age-specific growth and the abundance of salmon. The fork lengths of chum salmon in each year were not compared with the density-dependent factors, because fork lengths of chum salmon are a sum of both physical environmental and density-dependent factors prior to catch. Age-specific growth ($FL_{t+1} - FL_t$) for each cohort was therefore used instead of mean fork length. The abundance of salmon was the index of total density of both immature and maturing salmon.

For pink salmon, fork length of odd-year lines with high density was larger than that of even-year lines with low density. Although the density-dependent limitations on growth among pink salmon was not seen at first sight, the correlations between fork length of pink salmon and density of odd-year lines in the Bering Sea were significant ($p < 0.05$). This result showed that there was density dependent growth of pink salmon of odd-year lines. Ishida et al. (1996) suggested that the discrepancy in fork length between odd- and even-year lines was due to genetic factors. There were no significant correlations between the density of pink salmon and the growth of chum salmon at each stage in the Bering Sea ($p > 0.05$). This result indicated that the growth of chum salmon was independent of the abundance of pink salmon. However, significant negative correlations

with a lag of 0 year were found between the density of chum salmon and the growth of chum salmon at age 3 and 4 ($r = -0.55$, $r = -0.65$, $p < 0.05$), respectively (Fig. 12). When the total density of chum salmon in the Bering Sea was high, the growth of chum at age 3 and 4 decreased. Apparently the growth of chum salmon in this area depends on the abundance of chum salmon itself. The growth of chum at age 5 did not depend on the total density of chum.

Fig. 12. Relationship between density of chum salmon and growth of chum salmon in the Bering Sea.



DISCUSSION AND CONCLUSION

The most important conclusion of this study is that density of chum salmon in the Bering Sea fluctuates between odd and even years, and this variation is out of phase with density of pink salmon in the Bering Sea and with chum salmon in the eastern North Pacific. The difference in the density and distribution of chum salmon between odd and even-number years suggested that chum salmon distributions were affected by pink salmon, and shifted from the Bering Sea to the eastern North Pacific as result of inter-species interaction between pink and chum salmon. A second important finding is that there is no significant relationship between the growth of chum salmon and density of pink salmon, and that growth of pink and chum salmon depend on the abundance of their own species in the Bering Sea. Although pink salmon were the most abundant species in the North Pacific Ocean, the growth of chum salmon was not affected by the abundance of pink salmon. This suggests that the growth of salmon during their marine life is affected by intra-species density. Therefore, for the growth of salmon, there is a possibility of intra-species interaction rather than inter-species interaction in the Bering Sea.

The distribution of chum salmon shifted from the Bering Sea to the eastern North Pacific, altering densities and growth of chum salmon, when abundance of pink salmon increased in the Bering Sea. This

suggests that the abundance of pink salmon influenced the growth of chum salmon indirectly. A comparison of pink and chum salmon stomach contents between odd- and even-number years to examine diet overlap would be useful to examine whether pink and chum salmon interact in their feeding. Diet studies are also needed to examine the possibility of intra- or inter-species interaction in the western North Pacific.

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Long-term Changes in the Biological Parameters of Chum Salmon of the Okhotsk Sea

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Keywords: Salmon, length, weight, age, size, fertility, spawning

Abstract: Chum salmon (*Oncorhynchus keta*) of the Okhotsk Sea return to their rivers to spawn in early and late runs. Runs differ in spawning time, areas and periods of spawning, and age, size and fertility of the fish. Length, weight and fertility of chum salmon increase when spawning run abundance is low. During periods of high abundance of stocks, weight and fertility decrease. Age at maturity and run abundance are inversely related. The biological characteristics of the Okhotsk Sea chum salmon stock is presumably affected by the abundance of the local stocks as well as by the total salmon population in the North-West Pacific. Changes in the climatic and oceanological conditions may affect ocean carrying capacity, and in turn affect the biological characteristics of the chum salmon stock in the Okhotsk Sea.

INTRODUCTION

The continental coast of the Okhotsk Sea is one of the main areas of Pacific salmon reproduction and fishery in the western Pacific Ocean. The coastline extends about 3,500 km from the Uda River in the southwest to the Penzhina River in the northeast. Sockeye salmon (*Oncorhynchus nerka*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) reproduce in the coastal lakes and rivers. Chum and pink salmon are more numerous than the other species. Chum salmon make up 40–45% of the total quantity of salmon stocks.

Chum salmon are heterogeneous as a species and may be divided into two ecological forms, early and late run forms, which differ in spawning migration time, reproduction areas and biological characteristics, such as length and weight, fertility, gonado-somatic index (GSI) and genome structure (Volobuev 1984; Volobuev et al. 1990; Volobuev and Rogatnykh 1997; Mednikov et al. 1998) (Fig. 1).

This report describes some of the intraspecific diversity of chum salmon of the Okhotsk Sea, and examines the relation between stock abundance and changes in some biological parameters, such as length and weight, fertility, and age at maturity over a period of 37 years.

MATERIAL AND METHODS

The material in this paper was collected chiefly by the author and fish biologists of the salmon research laboratory during their field trips to the main salmon rivers entering the Okhotsk Sea, the Gizhiga, Yama, Taui and Kukhtui rivers, from 1960 to 1996. Data for the Uda River were collected from 1967 until 1988.* The quantity of chum salmon sampled at each river annually varied from 400 to 1000, averaging 500–600 specimens. Newly caught fish were measured for fork length, whole fish weight, and weight of gonads, and scale samples were taken for the age identification. Fertility was determined first by counting the number of eggs in 20 gram samples, and then in one gram samples. The results were multiplied by the total gonad weight. CPUE was calculated as the average quantity of fish per specified piece of fishing gear. GSI was the ratio between the gonad weight and fish weight, and represented as a percentage.

*Salmon rivers of the continental coast of the Okhotsk Sea are divided into relatively large, up to 300–400 km in length, medium and small rivers running for only a few tens of km. The Gizhiga, Yama, Taui, Kukhtui, and Uda rivers are of the first category. The hydrological, hydrogeological and climatic conditions in this type of river are much more diversified than those of smaller rivers. This fact results in intraspecific heterogeneity of chum salmon. Major rivers are inhabited by both early and late runs of chum salmon. Early runs prevail in small rivers.

Food composition was determined by counting and weighing stomach contents accompanied by calculation of stomach fullness indices ($\%_{000}$), the ratio between stomach content weight and fish weight multiplied by 10,000. Content of oxygen in the water, as well as concentration of hydrogen ions were measured by L-7, portable field analyzer ("Horiba", Japan). The speed of river current was measured using a GR-51 current meter.

Chum salmon abundance in rivers was visually determined from an airplane at a distance of 100–150 m. A correction factor was used to compensate for possible errors.

RESULTS

Spawning Migration

Spawning runs of chum salmon to coastal rivers consist of both early and late runs. However, some rivers have only one run. Early run chum salmon enter spawning rivers from the second part of June until the end of July. The end of the early run overlaps the beginning of the late run. The late run lasts until mid September. Where two runs occur, the first peaks in July, the other in August (Fig. 1a).

Reproductive Environments

The Okhotsk Sea chum spawn from July through November, in some rivers continuing until January (Volobuev 1984). Early run chum spawn from July through August in small and large rivers, and

tributaries of the first and second categories at a depth from 0.3 to 1.5 m. Spawning occurs at water temperatures of 9.8–14.0°C; current speed 0.2–0.8 m/sec; pH 6.7–7.3, oxygen content 9.0–11.5 mg/L.

No phreatic discharge (from the ground water saturated zone) was found in the early run spawning areas. Eggs are incubated within the intragravel flow. Topography of the early run spawning areas is similar to that of pink salmon (Volobuev et al. 1992).

Reproduction of late-run chum occurs in the middle and upper reaches of large and medium-length rivers. Spawning occurs mainly in September–October in tributaries, streams, creeks, springs and limnocren. Late run chum reproduce in spring-type spawning areas and gravitate to phreatic discharge zones. Current speed at spawning areas varies from 0.03 to 0.8 m/sec; depth from 0.2 to 2.0 m; pH from 6.3 to 6.8, oxygen content from 9.5 to 13.5 mg/L. Water temperature in different streams may vary from 4 to 9°C, reaching 1.1–2.4°C by the end of the winter (Volobuev and Rogatnykh 1997).

Incubation Period and Development

Observations of the late run chum embryo development in the natural environment showed incubation lasted 117–122 days, and 353–405 degree-days. Fry leave the gravel and in April begin to feed mainly on larvae and pupae of chironomids in warmer spawning areas. Index of stomach fullness ranged from 223 up to 356‰. Stomach fullness index for fry migrating to the sea was much lower, 83–120‰ (Table 1).

Fig.1. Timing of various parameters of early and late run chum salmon of the Tau River, a) CPUE, b) gonado-somatic index (GSI), c) length, d) weight, e) frequency of males (%), and f) fertility.

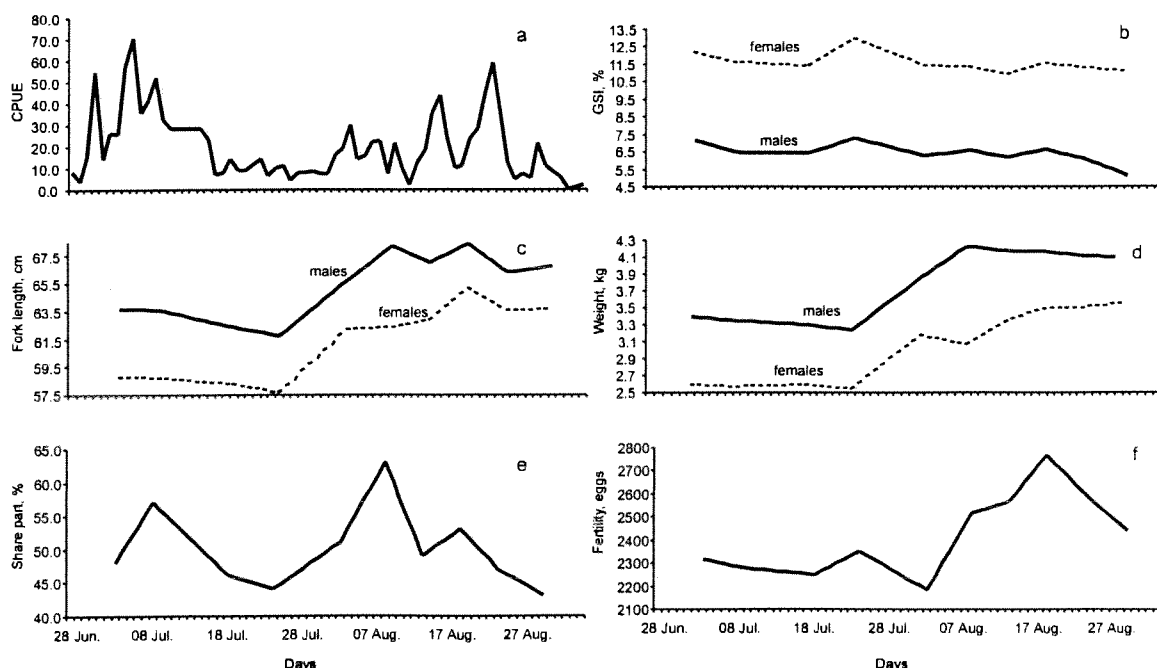


Table 1. Biological characteristics of late run chum fry (Tau River basin) migrating to the sea (mean \pm SD).

	Years			
	1980–1985	1986–1990	1991–1996	1980–1996
Fork length, mm	36.2 \pm 0.73	35.5 \pm 0.29	36.1 \pm 0.12	36.0 \pm 0.27
Weight, mg	359.5 \pm 9.51	344.1 \pm 14.9	353.1 \pm 17.7	352.8 \pm 7.9
Yolk sac weight, % of total body weight	4.06 \pm 0.58	6.10 \pm 1.77	5.83 \pm 2.76	5.36 \pm 1.14
Stomach fullness index, ‰	159.0 \pm 15.9	67.0 \pm 17.7	126.3 \pm 30.8	120.4 \pm 15.5
Percentage of feeding fish, %	49.0 \pm 2.40	38.3 \pm 2.01	33.2 \pm 7.9	40.4 \pm 3.40
Coefficient of fatness	1.04 \pm 0.06	1.08 \pm 0.02	1.06 \pm 0.05	1.06 \pm 0.03
Number sampled	1353	1440	1295	4088

Migration

Downstream migration of fry starts simultaneously with a rise in water level, and lasts from mid May until late June with a peak in late May to early June. The majority of fry migrate at night, from 0:00 to 3:00 a.m. Dates of downstream migration and diurnal activity for early and late run chum fry are the same. The main biological characteristics of late chum fry migrating downstream when averaged over 5 year periods appear to have remained the same from 1980 to 1996 (Table 1).

Biological Characteristics of Spawning Stocks

Length and weight

Chum salmon of the Okhotsk Sea coastal area are characterized by sexual dimorphism for length and weight: males are usually larger than females. The minimum recorded length of Okhotsk Sea chum salmon was 47.0 cm (female); maximum recorded length 83.0 cm (male), weight 1.18 kg and 10.35 kg, respectively. Chum salmon of the Yama River tend to be the largest in length and weight; chum salmon of the Gizhiga River tend to be the smallest (Table 2).

Average long-term length and weights for odd and even year chum salmon showed that even year generations of chum salmon are basically 0.5–1.1 cm and 0.07–0.20 kg larger than those of the odd years. Odd year generations are apparently suppressed by high abundance of pink salmon, which have similar feeding requirements (Kostarev 1964).

Analysis of the long-term changes in average length and weight showed an increase in these values during the depression in abundance of the 1970s, presumably due to total reduction in abundance of Asian salmon and their food in the salt water environment (Fig. 2a and 2b). Average decline in weight, of 0.4–0.5 kg, and length, of 3–4 cm was recorded in the late 1980s and early 1990s. Changes in length and weight are inversely proportional to chum salmon abundance. Correlation coefficients between body length and population abundance ranged from -0.55 to -0.84 ($p \leq 0.05$). Correlation coefficients between weight and abundance varied from -0.36 to -0.68 ($p \leq 0.05$).

Absolute fertility

It is known that absolute fertility (number of eggs) is correlated with fish length. The absolute fertility of the Okhotsk Sea chum salmon ranges from 1008 to 4830 eggs. The average long-term annual fertility for the main populations varies from 2633 to 3008 eggs (Table 2). Some increase in fertility occurred in the 1970s, and a decline in the 1980s–1990s (Fig. 2 c). Fertility and abundance of chum salmon are also inversely proportional to length ($r = -0.86$ to -0.95 , $p \leq 0.05$).

Age composition

Chum salmon reproducing in coastal rivers return to spawn mainly at the age of 3–5 (0.2+ to 0.5+) years. Spawning at the age of 0.1+ to 0.6+ is rare. Age groups maturing at age 0.3+ make up 58.9% of spawning Okhotsk Sea chum salmon. The long-term average age at spawning is 3.19–3.51 years (Table 2).

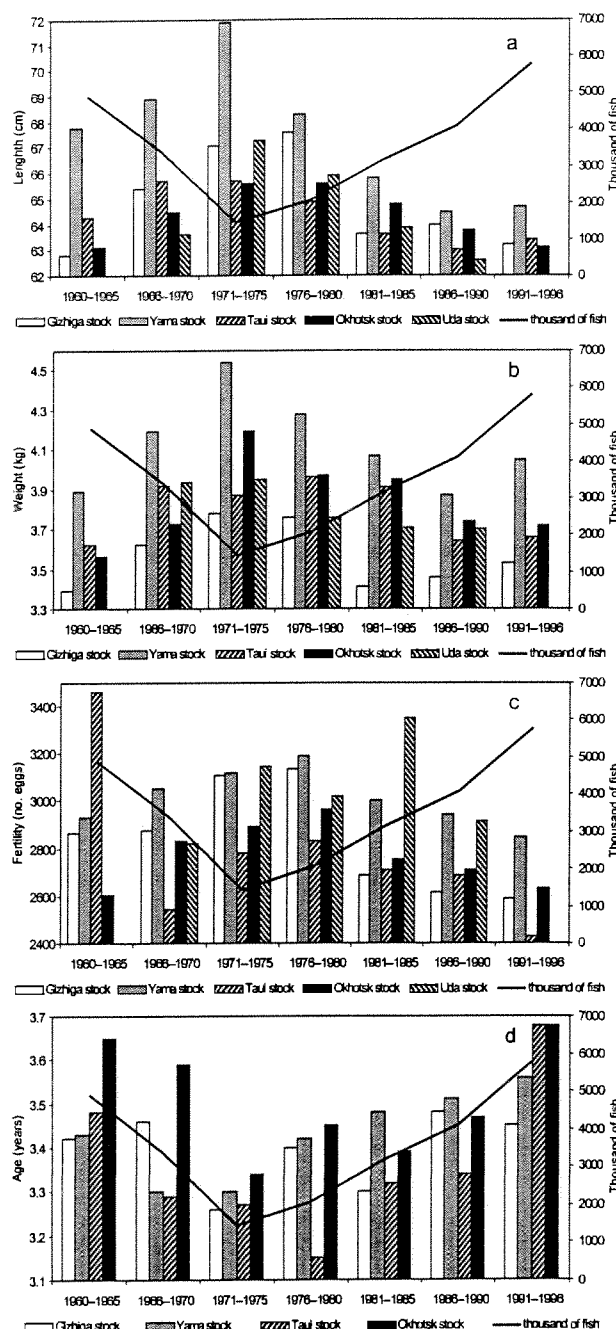
A decrease in average age at maturity in the 1970s and 1980s and increase in the 1990s occurred (Fig. 2d). In the mid 1990s age 0.4+ to 0.5+ made up 82–92% of chum salmon spawning in 1995 and 1996, respectively. In comparison with length, weight and fertility, age at maturity and abundance of chum salmon during spawning season were directly proportional ($r = 0.57$ to 0.79 , $p \leq 0.05$). Average age at maturity, which was 3.21 to 3.31 years in the 1970s, increased to 3.41–3.64 years in the 1990s. Similar values were recorded for chum salmon of Japanese origin (Kaeriyama 1998).

DISCUSSION AND CONCLUSION

Both early and late runs of Okhotsk chum salmon differ in spawning time and areas, reproduction ecology and main biological characteristics. Similar differences are known in Alaska, Kamchatka, Amur River, and Yukon River (Salo 1991). Along the coast of the Okhotsk Sea these temporal forms or ecotypes can be sympatric, inhabiting the same river basin, or allopatric, inhabiting different drainage-basin systems. Chum, as well as the majority of *Oncorhynchus* salmon, are

Table 2. Okhotsk Sea chum salmon length, weight, fertility and age at maturity (1960–1996).

River	Length, cm		Weight, kg		Fertility, eggs		Age 0.3+ spawning %	Age 0.3+ among generations %	Average age of spawners (years)
	Mean \pm SD	Range in annual means	Mean \pm SD	Range in annual means	Mean \pm SD	Range in annual means			
Gizhiga	64.7 \pm 0.39	61.1–69.7	3.56 \pm 0.05	3.01–4.23	2830 \pm 22.3	2366–3459	57.1	58.0	3.39
Yama	67.4 \pm 0.49	63.4–75.2	4.13 \pm 0.05	3.57–4.66	3008 \pm 22.8	2443–3375	54.8	54.5	3.43
Tau	64.3 \pm 0.31	61.1–70.3	3.79 \pm 0.05	3.22–4.85	2633 \pm 24.1	2195–3124	56.3	58.9	3.36
Kukhtui	64.3 \pm 0.27	61.3–67.0	3.83 \pm 0.05	3.02–4.38	2741 \pm 19.4	2234–2981	48.3	52.0	3.51
Uda	65.0 \pm 0.41	61.3–68.9	3.82 \pm 0.05	3.33–4.18	2940 \pm 18.1	2599–3940	62.8	-	3.19

Fig. 2. Long-term changes in (a) length, (b) weight, (c) fertility and (d) mean age-at-maturity of coastal chum salmon stocks of the Okhotsk Sea. Trend line indicates numbers of spawning chum salmon.

relegated to monotypic polymorphous species. The existence of ecological forms of chum salmon can be considered an adaptation to environment, or a species life strategy to enhance survivability and stability of the population in time and space.

Changes in biological parameters of Okhotsk Sea chum salmon are associated with long-term fluctuations in abundance of chum salmon stocks, and are caused by density-dependent factors and availability of food. During the period of low abundance in the 1970s, the numbers of Pacific salmon (including chum salmon) declined by three compared with stock levels of the 1930s. This resulted in increases in length, weight and fertility, and a reduction in age at maturity. (Fig. 2a–2d).

The period from 1936 until 1939 saw the first peak in salmon yield in the North Pacific in the twentieth century. Chum salmon biomass during spawning reached 500,000–600,000 tonnes and amounted to 47% of the total biomass of all six salmon species (Neave 1961; Salo 1991). The next increase in abundance of salmon stocks in Pacific Rim countries began in the early 1980s. This increase was caused by the favorable hydrological conditions in ocean feeding areas, and intensification of artificial reproduction of salmon by Pacific countries. As a result, by the mid 1990s hatchery output totalled 5.5 billion juveniles per year (Heard 1998). Most impressive is the output by Japanese chum salmon hatcheries: coastal chum salmon yield increased from 12,000 tonnes in the 1960s to 250,000 tonnes in the 1990s (Hiroi 1998).

As a result, the total catch of salmon in Russia, Japan, Canada and the USA by 1995 reached 1 million tonnes, with chum salmon comprising about 36% (NPAFC 1995; Klyashtorin and Rukhlov 1998; Noakes et al. 1998). Salmon stocks increased more than three times compared with levels in the 1970s. This increase affected the biological structure of the stock: the average age at maturity increased, and the length, weight and fertility of chum salmon decreased.

Size and weight of chum salmon decreased significantly between 1987 and 1990 in the Anadyr River compared with long-term values; in spawning runs from 1992 until 1994 the average weight of fish decreased by 0.8–0.9 kg, and the length by 4–5 cm

(Putivkin 1999). A decrease in length and weight, and increase in age at maturity were also observed for salmon of Japanese and North American origins (Ishida et al. 1993; Ricker 1995; Bigler et al. 1996; Helle and Hoffman 1995, 1998).

Analysis of biological parameters of Okhotsk Sea chum salmon over time has shown a deterioration during the past decade. This is probably associated with the increase in abundance of Asian (Russian and Japanese) salmon stocks, and intensification of competition for food among the different species. The level of biomass production, maturation rate and size of spawning runs are affected by the total number of Asian and North American salmon feeding simultaneously in the North Pacific. Inadequate food resources in the ocean and intensification of competition may have caused reduction in the Okhotsk Sea chum salmon weight, length and fertility, and an increase in age at maturity.

The North Pacific ecosystem has a limited carrying capacity for salmon production. Further increases in hatchery production of Pacific salmon will likely result in further deterioration of fish size and commercial value of yield. Moreover, increases in hatchery production have a negative impact on the wild salmon populations, reducing their genetic diversity and ability to adapt (Hindar et al. 1991; Nielsen et al. 1994; Altukhov et al. 1996; Berejikian et al. 1997). The number of artificially reared salmon fry of Asian origin in the 1990s amounted to 2.6 billion, including more than 2.2 billion chum (NPAFC 1998).

Currently at least two factors are influencing the development of the North Pacific ecosystem. These factors are the release of large numbers of hatchery-reared fry, and climatic shifts that affect the hydrological regime and food reserves. These factors ultimately are probably causing the changes in the biological parameters of the Asian and North American salmon populations.

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Factors Influencing Abundance of Sockeye Salmon (*Oncorhynchus nerka*) from the Ozernaya River, Southwest Kamchatka

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Keywords: Competition, escapement, smolts, sockeye, salmon, Russia

Abstract: Numbers of sockeye salmon (*Oncorhynchus nerka*) returning to the Ozernaya River (including driftnet catches at sea) are greatly influenced by four factors. The first is the parent escapement of sockeye in Kuril Lake. The second factor is the length and weight of sockeye smolts migrating from Kuril Lake. The third is the inshore abundance of West and North-East Kamchatka juvenile pink salmon (*O. gorbuscha*) one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+ (representing competition between pink salmon underyearlings and migrating sockeye salmon smolts). Finally, the fourth factor is the inshore abundance of West and North-East Kamchatka mature pink salmon during the first, second and third years of sockeye salmon at sea.

INTRODUCTION

In the basins of the rivers Ozernaya and Kamchatka in some years catch of sockeye salmon (*Oncorhynchus nerka*) made up 90–95% of the total sockeye catch in Asia (Anonymous 1989). Since 1985 through the present, catches of sockeye from the Ozernaya River rank first among catches of Asian sockeye surpassing catches of sockeye from the Kamchatka River (Bugayev 1995). At present, various mutually compatible explanations have been proposed for the increased sockeye abundance in the Ozernaya River spawning in Kuril Lake in the mid-late 1980s.

During the first years after natural fertilization of Kuril Lake in 1981 with ash from Alaid volcano, and with artificial mineral fertilizer in 1981, 1982, 1985, 1987 and 1989, and optimum levels of spawning, sockeye salmon abundance increased in the Ozernaya River (Kurenkov 1988; Dubynin and Bugayev 1988; Milovskaya 1991; Milovskaya and Selifonov 1993).

Ever since the very high abundance of pink salmon (*O. gorbuscha*) in West Kamchatka in 1983, the abundance of pink salmon in West and North-East Kamchatka began to fluctuate in counterphase from 1985 through the present, although before 1985 (1970–1984) the abundance of pink salmon in both areas fluctuated in phase (Bugayev 1995; Bugayev et al. 1996). Bugayev (1995) showed abundance of inshore runs of Kamchatka pink salmon were correlated with length and weight of mature sockeye salmon of the Ozernaya River. Bugayev (1995) as-

sumed that (in addition to fertilization and optimum levels on the spawning grounds in Kuril Lake), sockeye abundance increased as a result a sharp decrease in pink salmon abundance in the West Kamchatka, starting from 1985. When pink salmon increased in abundance in West Kamchatka in 1994, 1996 and 1998 the abundance of sockeye salmon in the Ozernaya River appeared to decrease.

Since the beginning of limitation of Japanese driftnet fishing and introduction of marine economic zones in 1977–1978 to the present, the pressure of the remaining Japanese driftnet fishing and of the Russian fishery, beginning in 1994, has fallen mostly on Asian sockeye stocks, mainly on sockeye from the Ozernaya and the Kamchatka rivers. As a result, we were able to assess the commercial harvest of sockeye from the Ozernaya and Kamchatka rivers in the Russian economic zone and to estimate numbers of these sockeye in the sea in the year of return to spawn (including driftnet catches). This paper is devoted to the analysis of fluctuations of sockeye abundance from the Ozernaya River.

MATERIAL AND METHODS

Annual returns of sockeye salmon to the Ozernaya River from 1976–1998 (the 1971–1992 brood years) were used in the study.

Previously, Selifonov (1982, 1987, 1989) used catches by the Japanese driftnet fishery at sea from 1952–1975 to calculate the rate of harvesting of sockeye from the Ozernaya River. Later (up to 1996),

M.M. Selifonov (Naberezhnaya Street 18, Kamchat-NIRO, Petropavlovsk-Kamchatsky, 683602 Russia, personal communication) used only expert visual assessment of the rate of harvesting by driftnets to forecast abundance at sea of sockeye from the Ozernaya River.

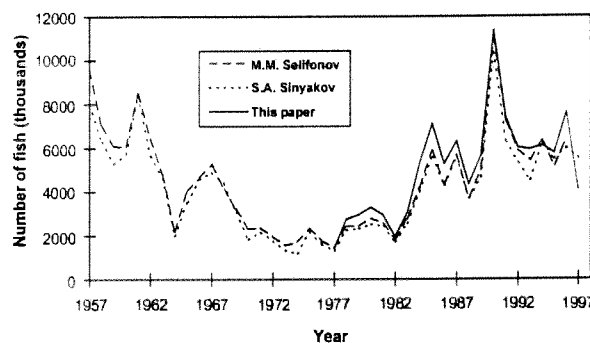
An expert visual assessment by Sinyakov of the rate of harvesting sockeye from the Ozernaya River by Japanese and Russian driftnet fishing is also available (S.A. Sinyakov, Naberezhnaya Street 18, Kamchat-NIRO, Petropavlovsk-Kamchatsky, 683602 Russia, personal communication, Milovskaya et al. 1998). It allowed investigators to assess the mature sockeye stock from 1940–1996, and to calculate the correlation between rate of return and smolt body weight. The results of the investigation showed that rate of return of adult sockeye to the Ozernaya River increased with their smolt body weight (Milovskaya et al. 1998). Unfortunately, the methods of assessment of the rate of harvesting sockeye from the Ozernaya River by Japanese and Russian driftnet fishing have not been published by Selifonov and Sinyakov (personal communication).

Differentiation between Japanese and Russian driftnet catches in Russia's economic zone, including the Ozernaya River, has only been performed on catches from 1995–1997 (A.V. Bugayev, Kamchat-NIRO, Petropavlovsk-Kamchatsky, 683602, Russia, personal communication). These investigations showed that sockeye salmon of Asian origin comprised the major portion of catches of Japanese and Russian driftnet fisheries in the Russian economic zone. This simplifies assessment of the rate of harvesting sockeye from the Ozernaya and Kamchatka rivers by driftnet starting from 1977 through the present. If salmon fishing in the Russian economic zone continues, assessment of sockeye salmon stock will be possible in the future as well. In general, sockeye salmon from the Ozernaya River comprise the majority of salmon caught in driftnets in the Russian economic zone.

For our estimates we have used the ratio (percent) of number of mature sockeye in inshore runs (escapement and total Russian domestic catches on the coast and in the rivers, omitting the Russian and Japanese highseas driftnet catches) between the Ozernaya and Kamchatka rivers from 1977–1998. We assumed that driftnet catches of sockeye from the Ozernaya and Kamchatka Rivers were correlated with the number of individuals returning to the Ozernaya and Kamchatka rivers. If the catches of sockeye from the Ozernaya River are excluded from the total, the remaining sockeye in the catches are from the Kamchatka River and other sources. We assumed also that of these remaining sockeye, 80% were from the Kamchatka River, and 20% were stocks from small Asian and other (American) rivers.

For example, in the 1996 inshore run of sockeye salmon, 4.844 million fish were from the Ozernaya River, and 2.885 million were from the Kamchatka River. Ozernaya River sockeye made up 62.67% of the total. The total Russian and Japanese driftnet catches of sockeye salmon was 10,940 tons in 1996. The catch of sockeye from the Ozernaya River was 6,860 tons, and from the Kamchatka River and other rivers was 4,080 tons (Kamchatka River – 3,260 tons, other stocks – 820 tons). The total number of mature sockeye salmon of Ozernaya River origin in the sea (before the beginning of the Russian and Japanese driftnet fisheries) was 7.588 million fish (Fig. 1), and from the Kamchatka River was 4.189 million fish. This standard approach can be easily reproduced. It can be used in the future to reveal any errors in the above assumptions.

Fig. 1. Number of mature sockeye salmon from the Ozernaya River at sea before the beginning of the drift net fishery, 1957–1997, in thousands of fish. Data from M.M. Selifonov and S.A. Sinyakov by personal communication.



The estimated abundance of sockeye from the Ozernaya River was compared with data provided by M.M. Selifonov and S.A. Sinyakov (personal communications) (Fig. 1). Our results on sockeye salmon from the Ozernaya River, in general, are similar to the earlier estimates from 1977–1997. In general, our evaluation of abundance of sockeye from the Ozernaya River was somewhat higher than the estimates of Selifonov and Sinyakov. However, in some years (1997, for example) the results are contradictory. In this paper we use our own estimates of abundance of sockeye salmon from the Ozernaya River (Fig. 1).

Bugayev (1995) showed that abundance of pink salmon off West and North-East Kamchatka influences the ocean growth-rate of sockeye from the Ozernaya River. Thus, in 1970–1984 with an increase in abundance of both West and North-East Kamchatka pink salmon, growth of mature sockeye from the Ozernaya River declined. In 1985–1991 a negative correlation remained only for West Kamchatka pink salmon; for North-East Kamchatka the pink salmon correlation changed from negative to positive (Bugayev 1995).

On the basis of the above, we separated our investigations on abundance of sockeye from the Ozernaya River from 1971–1992 into two periods (for addition and the more detailed picture): 1971–1981, and 1982–1992.

In this article we first used Spearman's regression method to calculate correlation coefficients of ranges (r_s).

Second, by forward stepwise regression in program "STATISTICA" we calculated coefficients of multiple regression (R) (Borovikov and Borovikov 1998). Forward stepwise regression means that at every step some independent variable is included in the model. Thus, a lot of the most important variables can be defined. This allows us to reduce the number of variables described by the correlation. In using forward stepwise regression independent variables are included in the regression equation until it satisfactorily describes the dependent variable, RBS, which is the return by brood year class of mature sockeye salmon of the Ozernaya River while in the ocean (i.e., including driftnet catches at sea). Inclusion of variables is defined by the F-criterion (Borovikov and Borovikov 1998). The 15 independent variables tested are listed in Table 1.

RESULTS

According to Selifonov (1975) and Bugayev (1995) there are 14 age patterns among sockeye salmon from the Ozernaya River, but most are rare. The major age patterns are the following: 2.2, 2.3, 3.2 and 3.3 (the first figure indicates years in freshwater and the second the years of marine life). These patterns from 1940–1975 comprised on average up to 98.4% of this sockeye stock. Patterns 2.2 (31.0%) and 2.3 (53.6%) on average comprised up to 84.6% of this stock (Selifonov 1982). As a result, success in forecasting return by brood year of sockeye salmon from the Ozernaya River depends, first, on accuracy of forecasting the proportion of individuals belonging to the two main age patterns, 2.2 and 2.3 (Selifonov 1975; Bugayev 1995).

Our investigations showed (Table 2) that there is a close correlation between the abundance of spawning adults in all 14 age patterns and the return by brood year in major age patterns 2.2, 2.3, 3.2, 3.3 from 1971–1992 ($n = 22$), $r_s = 0.876$, $p < 0.001$ (Fig. 2). There is a positive correlation between body length or weight of smolts and rate of return as adults ($r_s = 0.693$, $p < 0.001$, Fig. 3; $r_s = 0.715$, $p < 0.001$, Fig. 4).

Table 1. Fifteen independent variables used in forward stepwise regression to define the dependent variable, RBS, return by brood year class of mature sockeye salmon in the Ozernaya River.

Independent Variable	Description
ES	the parent escapement of sockeye into Kuril Lake, in thousands of fish;
L2	length of sockeye smolts migrating from Kuril Lake at the age 2+, mm.
W2	weight of sockeye smolts migrating from Kuril Lake at the age 2+, g.
WP0	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) one year prior to ocean migration of sockeye smolts of the Ozernaya River (from Kuril Lake) at age 2+, millions of fish.
WP1	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) during the first year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WP2	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) during the second year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WP3	inshore run of mature West Kamchatka pink salmon (after driftnet harvesting) during the third year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
EP0	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) one year prior to ocean migration of sockeye smolts from the Ozernaya River (from Kuril Lake) at the age 2+, millions of fish.
EP1	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) during the first year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
EP2	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) during the second year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
EP3	inshore run of mature North-East Kamchatka pink salmon (after driftnet harvesting) during the third year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WEP0	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) one year prior to ocean migration of sockeye smolts from the Ozernaya River (from Kuril Lake) at age 2+, millions of fish;
WEP1	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) during the first year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WEP2	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) during the second year of marine life of sockeye salmon of the Ozernaya River, millions of fish.
WEP3	total inshore runs of mature West and North-East Kamchatka pink salmon (after driftnet harvesting) during the third year of marine life of sockeye salmon of the Ozernaya River, millions of fish.

Table 2. Spearman correlation coefficients (r_s) between return by brood year and length and weight of smolts, and between rate of return and length and weight of smolts for sockeye salmon in the Ozernaya River.

Parameters ¹	Return by brood year	Rate of return (RBS/ES)
1971–1992		
ES	0.876***	-
L2	-0.317	0.693***
W2	-0.45	0.715***
	n=22	n=22
1971–1981		
ES	0.764**	-
L2	-0.309	0.591
W2	-0.396	0.469
	n=11	n=11
1982–1992		
ES	0.802**	-
L2	0.218	0.591
W2	-0.009	0.633*
	n=11	n=11

* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

ES - parent escapement of sockeye salmon, thousands;
L2 - body length of sockeye salmon smolts at age 2+, mm;
W2 - body weight of sockeye salmon smolts at age 2+, g.

Fig. 2. Relation between return by brood year of sockeye salmon of the Ozernaya river and parent escapement, 1971–1992 brood years.

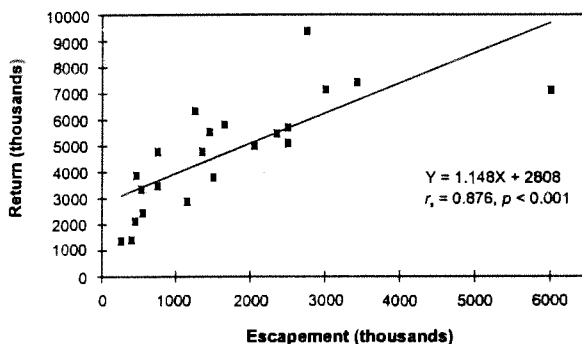


Fig. 3. Relation between rate of return of sockeye salmon from the Ozernaya River and their body length as age 2+ smolts, 1971–1992 brood years.

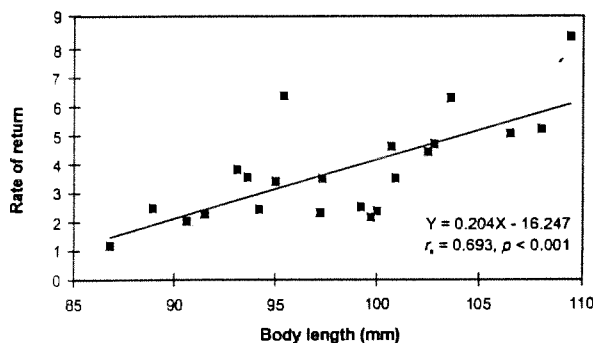
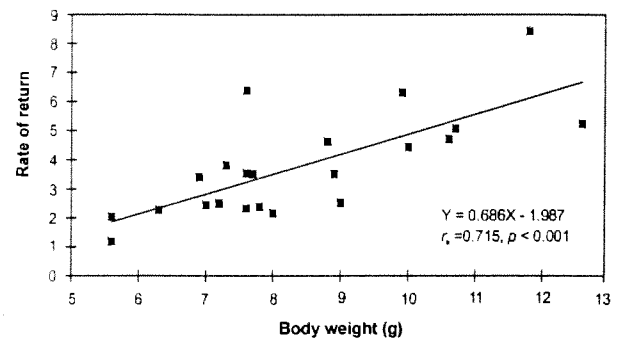


Fig. 4. Relation between rate of return of sockeye salmon from the Ozernaya River and their body weight as age 2+ smolts, 1971–1992 brood years.



During the period 1971–1981 ($n = 11$) the correlation between abundance of spawners and return by brood year was $r_s = 0.764$ ($p < 0.01$) (Fig. 5). In the later period, 1982–1992 ($n = 11$), the correlation between abundance of spawners and abundance of returning offspring was $r_s = 0.802$ ($p < 0.01$) (Fig. 6). The positive correlation between rate of return and smolt body weight in this period was $r_s = 0.633$ ($p < 0.05$) (Table 2).

Optimum escapement of pink salmon to West Kamchatka has been estimated by various investigators as 37–50 million fish (V.I. Karpenko and N.B. Markevich, Nabereznaya Street 18, KamchatNIRO, Petropavlovsk-Kamchatsky, 683602 Russia, personal communication). Only twice during the period 1983 to 1994 did abundance of West Kamchatka pink salmon spawners significantly exceed 50 million fish. For North-East Kamchatka the optimum escapement of pink salmon is estimated to be 13–25 million fish (V.I. Karpenko and N.B. Markevich, personal communication).

In the 1982–1992 period, there was no significant correlation between abundances of West and North-East Kamchatka pink salmon during the second sea-year of sockeye salmon and returns of sockeye salmon to the Ozernaya River ($r_s = -0.600$, $p > 0.05$, $n = 11$). However, if the 1992 brood year of sockeye salmon which migrated to sea as 2+ smolts in 1995 is omitted, the negative correlation is significant ($r_s = -0.745$, $p < 0.05$, $n = 10$) (Fig. 7). These sockeye would have competed with West Kamchatka pink salmon underyearlings from the 1994 brood year, in which year the pink salmon spawning grounds were seriously over-stocked, resulting in an unusually high abundance of pink salmon underyearlings, but anomalously low number of returning mature pink salmon. Correlation of sockeye salmon returns with abundance of returns in their brood year was not significant ($r_s = 0.358$, $p > 0.05$, $n = 10$).

During the period 1982–1992, a significant negative correlation was found ($r_s = -0.624$, $p < 0.05$, $n = 11$) between abundance of pink salmon inshore (after

Fig. 5. Relation between return of brood year of sockeye salmon to the Ozernaya River and parent escapement, 1971–1981 brood years.

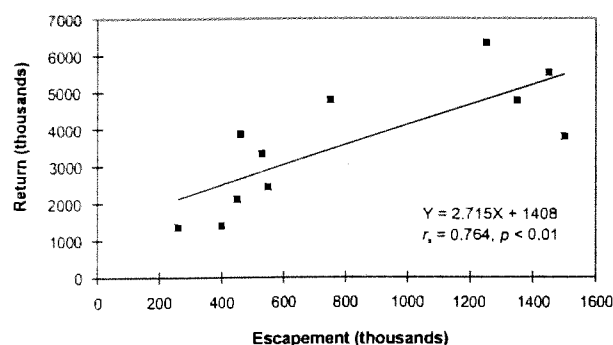


Fig. 6. Relation between return by brood year of sockeye salmon of the Ozernaya River and parent escapement, 1982–1992 brood years.

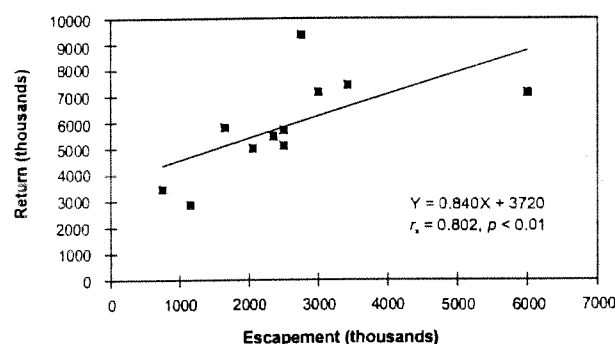
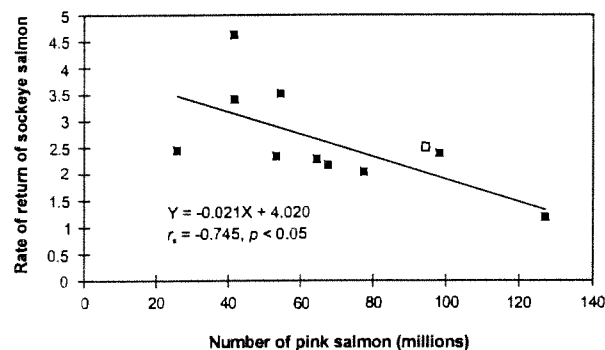


Fig. 7. Relation between rate of return of sockeye salmon (the 1982–1992 brood years) to the Ozernaya River and total inshore number of mature pink salmon off the coasts of West and North-East Kamchatka during the second year of marine life of sockeye salmon. The open square for 1992 data was omitted from the calculation of the significant correlation and regression.



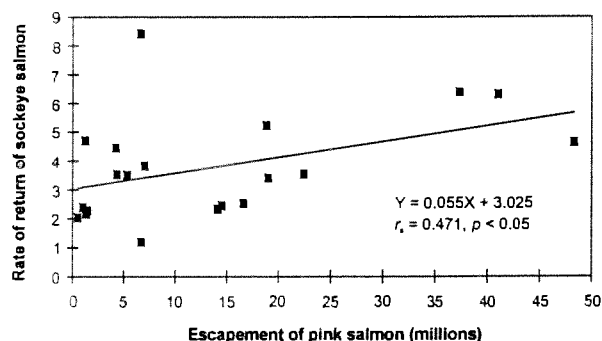
Russian and Japanese driftnet harvesting) in West Kamchatka (one year prior to ocean migration of sockeye smolts from Kuril Lake ad age 2+), and rate of return of sockeye salmon to Ozernaya River in the year following their contact at sea as age 2+ smolts with age 0+ pink salmon).

We assumed that this correlation resulted from the influence of West Kamchatka pink salmon under-yearling abundance on migrating sockeye salmon

smolts during their first year of marine life. When we replaced inshore run abundance of West Kamchatka pink salmon with abundance of pink salmon escapement in this area we also obtained a significant correlation ($r_s = 0.627$, $p < 0.05$, $n = 11$) for sockeye salmon during the 1982–1992 brood years. Correlation with sockeye return by brood years was not significant, $r_s = -0.436$, $p > 0.05$ ($n = 11$).

The abundance of pink salmon spawners in West Kamchatka one year prior to ocean migration of sockeye smolts was significantly and positively correlated with the rate of return of those sockeye salmon (over 1971–1992 brood years), when years with serious over spawning by pink salmon (1983, 1994), were excluded ($r_s = 0.471$, $p < 0.05$, $n = 20$) (Fig. 8). Correlation with sockeye return by brood year was not significant ($r_s = -0.254$, $p > 0.05$, $n = 20$).

Fig. 8. Relation between rate of return of sockeye salmon (the 1971–1992 brood years) to the Ozernaya River and the escapement of West Kamchatka pink salmon one year prior to the ocean migration of sockeye salmon smolts at age 2+ (the last freshwater year). Data from the 1983 return of sockeye (return, 5.07 million; pink escapement, 111.2 million) and the 1994 return of sockeye (return, 2.50 million; pink escapement, 81.1 million) were omitted from the figure and calculation of correlation and regression.



The 1974 brood year of sockeye salmon was unusual. The abundance of West Kamchatka pink salmon was low but the rate of return of sockeye salmon was equal to 8.42 times the average (which is extremely rare). Without brood year 1974, the correlation coefficient r_s is 0.551 ($p < 0.05$, $n = 19$). The regression equation is: $Y = 0.064X + 2.624$ (mean of X and Y as in Fig. 8); correlation with sockeye return by brood year was not significant, ($r_s = -0.227$, $p > 0.05$, $n = 19$). The correlation coefficient between abundance of the parent escapement in West Kamchatka pink salmon (one year prior to smolts ocean migration) and returns by brood year in sockeye from the Ozernaya River was also not significant ($r_s = 0.190$, $p > 0.05$, $n = 19$).

It is clear that no single factor (abundance of parent sockeye spawners, smolt length and weight, abundance of pink salmon at sea) influences brood year rate of return of sockeye salmon to the Ozernaya River alone. We therefore performed multiple re-

gression analysis (r) of the cumulative effect of all the investigated factors.

For the period 1971–1992 the regression equation of brood year abundance for sockeye from the Ozernaya River is:

$$\text{LnRBS}(1971-1992) = -6.61 + 0.8006 \cdot \text{LnES} + 2.1465 \cdot \text{LnL2} + 0.1182 \cdot \text{LnWP0} + 0.0943 \cdot \text{LnWP3} - 0.1462 \cdot \text{LnWEP1} - 0.1371 \cdot \text{LnWEP2}; r = 0.952, p < 0.001, n = 22.$$

For the period 1971–1981 the regression equation of brood year abundance for sockeye from the Ozernaya River is:

$$\text{LnRBS}(1971-1981) = -30.79 + 0.9574 \cdot \text{LnES} - 0.6814 \cdot \text{LnWEP0} + 0.3378 \cdot \text{LnWP3} + 7.5250 \cdot \text{LnL2} - 0.6152 \cdot \text{LnEP1} + 0.3172 \cdot \text{LnWP0} + 0.0951 \cdot \text{LnWP1}; r = 0.998, p < 0.01, n = 11.$$

For the period 1982–1992 the regression equation of brood year abundance for sockeye salmon of the Ozernaya River is:

$$\text{LnRBS}(1982-1992) = -8.72 + 0.9529 \cdot \text{LnES} + 2.3267 \cdot \text{LnL2} - 0.2366 \cdot \text{LnEP0} - 0.1242 \cdot \text{LnWP2} - 0.1867 \cdot \text{LnEP2} + 0.3316 \cdot \text{LnWEP0} - 0.2029 \cdot \text{LnEP3} + 0.0713 \cdot \text{LnWP0} + 0.1221 \cdot \text{LnW2}; r = 1.000, p < 0.01, n = 11.$$

The two highest multiple correlation coefficients are for the 1971–1981 brood years, $r = 0.998$, $p < 0.01$ ($n = 11$) and the 1982–1992 $r = 1.000$, $p < 0.01$ ($n = 11$). Note that the highest Spearman correlations for return by brood years are for the total 1971–1992 period (Table 2).

In this forward stepwise regression analysis, six of 15 independent variables were included in the first equation (the 1971–1992 period); seven variables were included in the second equation (the 1971–1981 period); and nine variables were included in the third equation (the 1982–1992 period). The multiple correlation coefficients for the entire 1971–1992 period was lower than for the two periods when separated. This again, justifies classifying the data according to the periods 1971–1981 and 1982–1992.

The difference between the initial (observed) values of the dependent variable and the predicted values is called the residual. To assess adequacy of the models it is necessary to perform an analysis of residuals (Borovikov and Borovikov 1998). Because we have only 11 (1971–1981 and 1982–1992) and 22 (1971–1992) data points, we have used graphical methods (Borovikov and Borovikov 1998). Graphical residual analysis of the three given models showed that residuals were randomly dispersed and there were no grounds to suggest that residuals were correlated among themselves. Neither were there any

distinguishing residuals. Therefore the above models adequately describe the data (Borovikov and Borovikov 1998).

During the period 1971–1992 sockeye returns by brood years were greatly influenced by the parent escapement of sockeye to Kuril Lake, and by the length of sockeye smolts migrating from Kuril Lake, positively influenced by the abundance of West Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake age 2+ (representing strength of competition between pink salmon underyearlings and migrating sockeye salmon smolts), by the abundance of West Kamchatka pink salmon during the third sea year of sockeye salmon, by the total abundance of West and North-East Kamchatka pink salmon during the first sea year of sockeye salmon, and by the total abundance of West and North-East Kamchatka pink salmon during the second sea year of sockeye salmon.

During the 1971–1981 period, sockeye returns by brood year were greatly influenced by the parent escapement of sockeye to Kuril Lake, the total abundance of West and North-East Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+ (representing competition between pink salmon underyearlings and migrating sockeye salmon smolts), the abundance of West Kamchatka pink salmon during the third sea year of sockeye salmon, the length of sockeye smolts migrating from Kuril Lake, the abundance of North-East Kamchatka pink salmon during the first sea year of sockeye salmon, the abundance of West Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at the age 2+, and the abundance of West Kamchatka pink salmon during the first sea year of sockeye salmon.

During the period 1982–1992 sockeye returns by brood years were greatly influenced by the parent escapement of sockeye to Kuril Lake, the length of sockeye smolts migrating from Kuril Lake, the abundance of North-East Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+ (representing competition between pink salmon underyearlings and migrating sockeye salmon smolts), the abundance of West Kamchatka pink salmon during the second sea year of sockeye salmon, the abundance of North-East Kamchatka pink salmon during the second sea year of sockeye salmon, the total abundance of West and North-East Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+, the abundance of North-East Kamchatka pink salmon during the third sea year of sockeye salmon, the abundance of West Kamchatka pink salmon one year prior to ocean migration of sockeye smolts from Kuril Lake at age 2+, and the weight of sockeye smolts migrating from Kuril Lake.

DISCUSSION

As we have shown, the abundance of sockeye of the Ozernaya River is greatly influenced by three factors: 1 - the parent escapement of sockeye salmon to Kuril Lake; 2 - length and weight of sockeye smolts migrating from Kuril Lake; and 3 - abundance at sea of mature pink salmon off West and North-East Kamchatka. The first two factors belong to the period of spawning and freshwater life of sockeye. These factors have already been studied by various investigators (Selifonov 1975, 1988; Milovskaya et al. 1998). The possible influence of the third factor, abundance of pink salmon during the year of their maturation, has previously been only assumed (Krogus 1965; Birman 1985; Bugayev, 1995). Pink salmon dominate other salmonids in abundance, and greatly influence the ocean habitat and abundance of other Pacific salmon species (Birman 1985). However, this influence is indirect, taking place apparently through competition for the food resource.

The abundance of sockeye salmon of the Ozernaya River is also influenced by a fourth factor, the abundance of immature pink salmon (under-yearlings). However, we have no direct data on abundance of immature pink salmon at sea, and therefore must consider indirect data only.

After an exceptional escapement of pink salmon to the spawning grounds in West Kamchatka in 1983, the abundance of West and North-East Kamchatka pink salmon began to fluctuate in counterphase. This no doubt changed the food relationships among sockeye, chum (*O. keta*) and pink salmon at sea (Andriyevskaya 1975; Birman 1985; Welch and Parsons 1993; Karpenko 1998). We think it is necessary to analyse periods in the sea before 1985 (1984 and more early years) and begin from 1985 separately.

Birman (1985), Welch and Parsons (1993), Ricker (1995), Bigler et al. (1996) and Karpenko (1998) have all shown that abundance and growth rates of salmon at sea are interrelated. Birman (1985) suggested that in any area where abundance of pink salmon is high, reproductive capacity of local sockeye stocks is to a certain extent limited.

Krogus (1965) suggested that an increase in length and weight of sockeye from the Ozernaya River in the 1950s resulted mainly from a decline in pink salmon abundance. Later (Bugayev 1995) found that prior to 1984 the correlation between sockeye weight-length parameters and pink salmon abundance was different than that from 1985 through 1991. The mechanism whereby West and North-East Kamchatka pink salmon affect abundance and rate of return of sockeye salmon from the Ozernaya River should be sought among the competitive food relationships of these species during their marine life, and also in the specific distributions at sea of mature and immature individuals of these two species in

feeding areas during years of high and low abundance.

Abundance of Pacific salmon species during their downstream migration and early marine life is greatly influenced by predatory fish such as Arctic charrs (*Salvelinus malma* and *S. leucomaenis*), Asian smelt (*Osmerus mordax dentex*) and others.

Predation on salmon smolts depends mainly on density and intensity of downstream migration (Gorshkov et al. 1989) and on (overlap) of migration times of salmon smolts and predatory fish (Karpenko 1994). In coastal waters and in zones of estuaries smolts usually concentrate where there are high gradients of temperature and salinity; for migration through such zones smolts require a certain adaptation period (Karpenko 1994, 1998). Predatory fish affect Pacific salmon smolts in two ways: by consuming smaller fish they increase average smolt size and, in addition, by decreasing salmon abundance they optimize the food supply for the remaining smolts (Karpenko 1998).

According to a number of investigators (Kononov 1971; Birman 1985) the marine habitat of sockeye salmon from the Ozernaya River is not limited to adjacent areas. According to Kononov (1971) sockeye smolts of the Ozernaya River migrate along the Western coast of Kamchatka far to the north. Birman (1985) assumed that sockeye salmon smolts from the Ozernaya River concentrating in Kamchatkan coastal waters of the sea of Okhotsk interacted with abundant stocks of juvenile pink salmon from various rivers of West Kamchatka and probably from the Northern coast of the Sea of Okhotsk.

Most sockeye smolts from the Ozernaya River disperse during the year of downstream migration through coastal waters from 51° to 58°N (Erokhin 1998; Karpenko et al. 1998). During the last ten days of August and in early September sockeye salmon smolts feed in coastal waters up to 60 miles offshore. As a rule, pink and chum salmon under-yearlings by this time migrate to warm open waters, lowering food and habitat competition with sockeye salmon smolts.

As Karpenko et al. (1998) and Erokhin (1998) showed, in September and October feeding areas for smolts of pink salmon, chum and sockeye in the Sea of Okhotsk are separated. Pink salmon stay in offshore waters, sockeye salmon remain in coastal waters and chum concentrate in a so called "buffer zone" between these two populations. In years of high abundance, pink salmon apparently restrict chum to coastal waters. Chum then share feeding areas with sockeye salmon. The most productive feeding areas are always occupied by large gatherings of pink salmon (Erokhin 1998; Karpenko et al. 1998).

There are two ways for sockeye and chum salmon to avoid pink salmon. First, they may migrate to the north as they are tolerant of lower tem-

peratures than pink salmon (Erokhin 1998; Karpenko et al. 1998). Second, they may choose a different spectrum of food.

The factors influencing abundance of sockeye salmon and of their food competitors during marine life are multiple and various. Therefore, when abundance of pink salmon influences abundance of sockeye salmon of the Ozernaya River, the correlations may have several explanations. These explanations can supplement one another, but they do not provide complete answers to every question. Complex year-to-year investigations are required for this. We believe that our work will assist in planning investigations leading to an understanding of the mechanism underlying the correlations.

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Review of Ocean Salmon Research by Japan from 1991 to 1998

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Abstract: Scientists of the National Research Institute of Far Seas Fisheries, Shimizu, Japan, conducted various surveys on Pacific salmon (*Oncorhynchus* spp.) in the northern North Pacific Ocean and adjacent seas from 1991 to 1998. The major results are summarized as follows: 1) chum salmon (*O. keta*) juveniles originating in Japan occurred in the Okhotsk Sea in summer and migrated into the western North Pacific from fall to winter; 2) growth variation of Pacific salmon was due to both intra- and inter-specific density dependent effects; 3) the abundances of phytoplankton, zooplankton, and Pacific salmon (especially pink salmon *O. gorbuscha*) which varied both temporally and spatially in offshore waters were related to each other, suggesting a top-down control of production; 4) salmon sharks (*Lamna ditropis*) caused a high ocean mortality of Pacific salmon; 5) there was a positive relationship between summer offshore catches of chum and sockeye salmon (*O. nerka*) and their coastal returns, which suggests a possible method of forecasting salmon returns; and 6) Pacific salmon were distributed in lower temperature waters and may be adapted to lower food resources in winter. Issues for future salmon research are discussed.

INTRODUCTION

An international workshop on future salmon research in the North Pacific Ocean was held at the National Research Institute of Far Seas Fisheries (NRIFSF) in Japan on November 11, 1991, just after the last annual meeting of the International North Pacific Fisheries Commission (INPFC). The workshop summary reported that the major focus of research would clearly shift from issues of interception to such problems as stock interaction, climate change, effects of artificial propagation, and carrying capacity of the North Pacific Ocean for Pacific salmon (*Oncorhynchus* spp.) (Ishida et al. 1992). To establish an effective mechanism of international cooperation to promote the conservation of anadromous stocks in the North Pacific Ocean, Canada, Japan, the Russian Federation and the United States of America signed a convention and formed the North Pacific Anadromous Fish Commission (NPAFC) on February 11, 1992 (NPAFC 1993a). At the 1993 Annual Meeting of the NPAFC, the Committee on Scientific Research and Statistics (CSRS) identified the following two critical issues for research by the Parties: 1) factors affecting current trends in ocean productivity, and 2) factors

affecting changes in biological characteristics such as growth, size and age at maturity, oceanic distribution, survival, and abundance of Pacific salmon (NPAFC 1993b). The CSRS also developed the NPAFC Science Plan to address these two critical issues by three areas of study: 1) salmonid life history, 2) salmonid population dynamics, and 3) salmonid habitat and ecosystem (NPAFC 1994). The purposes of this paper are to review the results of ocean salmon research conducted by the NRIFSF from 1991 to 1998, and to discuss issues for future research.

Juvenile Salmon Studies

The migration routes and distribution of Japanese juvenile chum salmon (*O. keta*) were surveyed in near shore waters around Hokkaido in northern Japan from 1977 to 1985 (Irie 1990). Migrating juvenile chum salmon were mainly concentrated in areas with surface temperatures from 9 to 13°C and surface salinities from 31.0 to 33.9 psu; the upper limits were about 14°C and 34psu. The juvenile chum salmon originating in the Japan Sea coast and the Pacific coast of Honshu migrated along the coast of Hokkaido during their offshore migration. However, their offshore

migration routes to the North Pacific Ocean were not identified.

To clarify the offshore migration routes of juvenile salmon, Japan-Russian cooperative surveys were conducted in the waters off southeastern Hokkaido, Sakhalin, and the Kuril Islands, using a purse seine, a surface trawl, dip-nets, and drift nets in the summers of 1988–1992 (Fig. 1). The results suggested two possible migration routes of juvenile chum salmon after they enter the coastal waters: 1) juvenile chum salmon migrate to offshore waters of the Okhotsk Sea, and 2) they migrate within coastal waters near the Kuril Islands (Ueno and Ishida 1996).

To examine the first possible migration route, the NRISF conducted drift gillnet and surface trawl operations in the Okhotsk Sea and the Pacific waters off Hokkaido and the Kuril Islands from early summer to late autumn in 1993–1996 (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 Pacific waters off the Kuril Islands in late autumn (Fig. 2). 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).

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 Primorie 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 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 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).

In addition to these migration studies, potential predators of chum salmon juveniles off the Japanese

coast and in coastal waters of the Kuril Islands were reviewed based on various sources of the literature (Nagasawa 1998a). Two species of seabirds (rhinoceros auklets *Cerorhinca monocerata* and black-tailed gulls *Larus crassirostris*) and two species of fishes (arabesque greenling *Pleurogrammus azonus* and Japanese dace *Tribolodon hakonensis*) were thought to be significant predators.

Fig. 1. Seasonal changes in distribution of juvenile chum salmon caught by research vessels from 1988–1992. Symbols indicate no catch (x) and size of circle indicates abundance of juvenile salmon caught by purse seine, surface trawl, dip net, and drift net. Early summer (a), mid summer (b) and total (c). (Fig. 1 from Ueno and Ishida 1996).

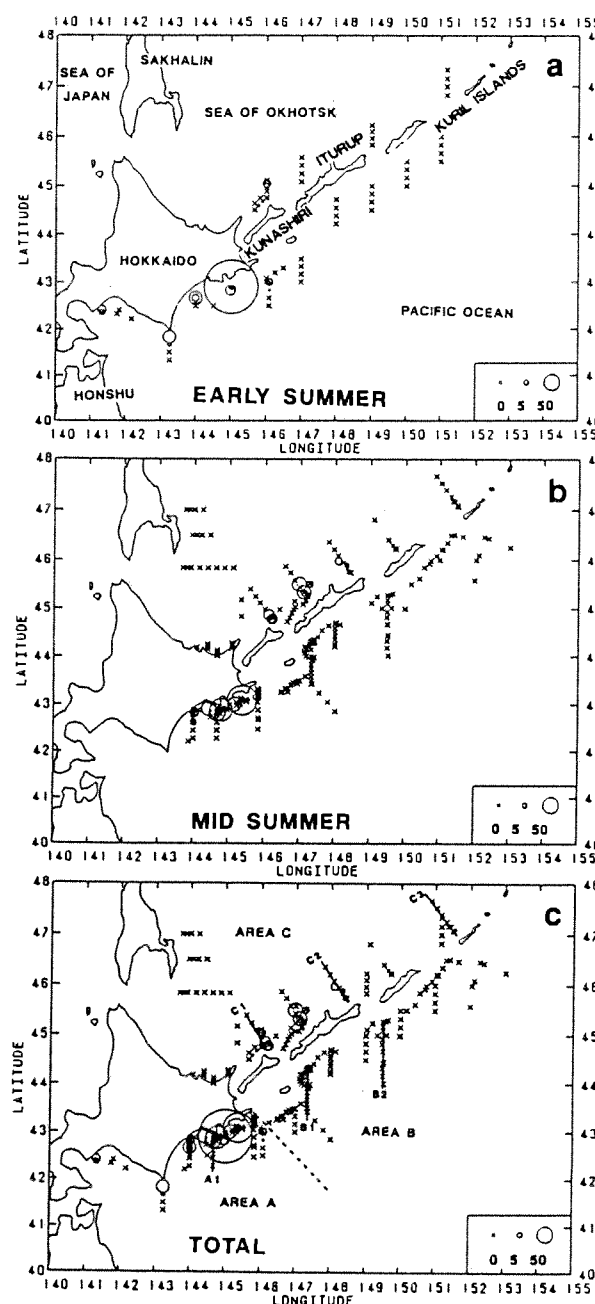
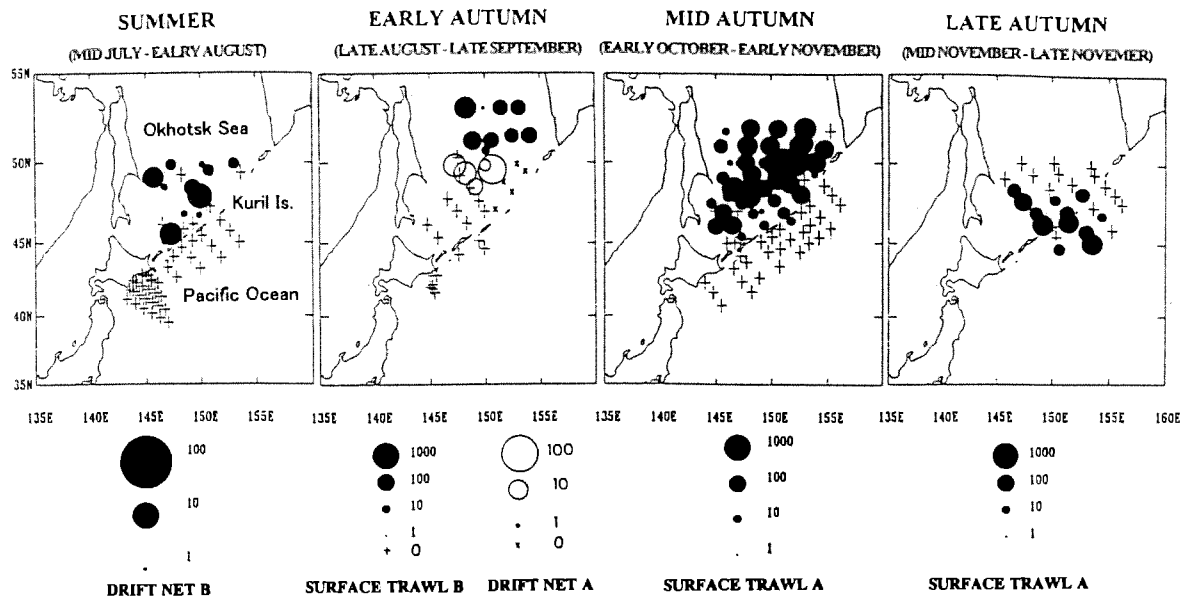


Fig. 2. Seasonal distributions of juvenile chum salmon caught by research vessels from 1993 to 1996. (Fig. 2 from Ueno 1998).



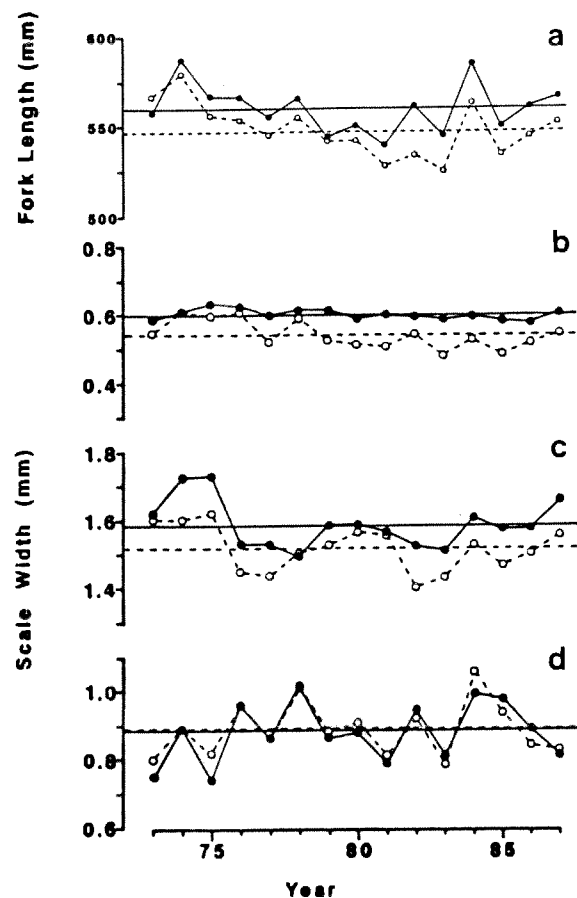
Juvenile salmon studies suggest that the Okhotsk Sea is an important nursery ground for juvenile salmon originating from Russia and Japan. Future issues for the juvenile salmon studies are: 1) assessment of juvenile salmon abundance, 2) stock identification and estimation of stock composition of juvenile salmon by genetic methods and otolith thermal marks, and 3) investigation of factors affecting survival and abundance of juvenile salmon in the Okhotsk Sea.

Salmon Growth Studies

Growth variation of coho salmon (*O. kisutch*) in the western North Pacific Ocean from 1973 to 1987 was examined based on fork lengths and scale measurements (Ogura et al. 1991). Average fork lengths of coho salmon in July in the area of 44°–50°N latitude and 160°E–180° longitude showed long-term variation, decreasing after 1975 and increasing from 1983 to 1987. Growth also showed strong odd-even year fluctuation (Fig. 3-a). The scale measurements indicated that long-term variation of growth occurred during the freshwater period and during the first year of ocean life (Fig. 3-b, c). Substantial odd-even year fluctuation in growth occurred only during the second year of ocean life (Fig. 3-d). These results suggested that intraspecific density-dependent growth is an important factor during the freshwater stage, and interspecific density-dependent growth is important during the second year of ocean life, the latter due primarily to the overlap of diet between coho and pink salmon (*O. gorbuscha*) (Anderson and Wilen 1985; Ito 1964).

Changes in age composition and size of adult chum salmon from rivers in Japan, Russia, and

Fig. 3. Average fork length and scale measurements of coho salmon in the western North Pacific Ocean from 1973 to 1987. Fork length (a), freshwater zone (b), the first year ocean zone (c), and the second year ocean zone (d). Open circles and broken line indicate freshwater age group one (age 1.1), solid circles and solid line indicate freshwater age group two (age 2.1), and horizontal lines indicate averages over all years for each age group. (Fig. 2 and Fig. 3 from Ogura et al. 1991).



Canada were also examined based on body weight and scale measurement data collected from 1953 to 1988 (Ishida et al. 1993). A significant increase in mean age was found in Japanese and Russian stocks after 1970 when the number of Japanese chum salmon began to increase exponentially, but not in the Canadian stock. Significant decreases in mean body weight, mean scale radius, and mean width of the third-year zones of age 0.3 chum salmon also occurred in Japanese and Russian stocks after 1970. Based on the Japanese salmon research vessel data from 1972 to 1988, significant negative relationships between catch-per-unit-effort (CPUE) and mean body weight of chum salmon were observed in summer in the central North Pacific Ocean where the distribution of Japanese and Russian stocks overlapped (Fig. 4). These results suggest that density dependence is one of the possible causes for the recent changes in age and size of chum salmon in the North Pacific Ocean.

Seasonal growth patterns of chum, coho, pink and sockeye salmon (*O. nerka*) in the North Pacific Ocean were described from the biological data collected using non-selective salmon gillnets by the Japanese salmon research program (Takagi 1975; Ishida et al. 1998). Maturity was determined from gonad weights (Takagi 1961; Ito et al. 1974). Seasonal change in fork length and body weight was similar between sockeye and chum salmon, and between pink and coho salmon. Seasonal change in condition factors was very similar among the four species, that is, condition factors increased in spring, peaked in summer, decreased in fall, and were lowest in winter (Fig. 5). Average growth rate in weight during maturation was significantly higher than during immaturity for sockeye, pink, and coho salmon (*t*-test, $p < 0.05$) (Ishida et al. 1998). For chum salmon, there was no significant difference in growth rate between immature and maturing fish (Ishida et al. 1998).

The potential influence of changes in sea surface temperature (SST) in the North Pacific Ocean on Japanese chum salmon adult return rates and growth rates was examined (Ishida et al. 1995). SST near the Kuril Islands (45°N, 150°E) in July ($r = -0.36$, $p < 0.05$) and SST in the central North Pacific (49°–45°N, 170°E–170°W) in winter and spring ($r = -0.61$, $p < 0.01$; $r = -0.53$, $p < 0.01$, respectively) showed significant decreasing trends from 1947 to 1988. Average return rates after the mid 1960s were higher than before the mid 1960s, when chum salmon fry were not fed prior to release at Japanese hatcheries. Return rate was negatively correlated with winter and spring SST in the central North Pacific after the mid 1960s ($r = -0.76$, $p < 0.01$; $r = -0.81$, $p < 0.01$, respectively) (Fig. 6-a). Mean body weight of age 0.3 chum salmon returning to the Ishikari River was positively correlated with the preceding three spring SST in the central North Pacific (Fig. 6-b). These results suggest that chum salmon production is enhanced in Japan by

Fig. 4. Relationship between CPUE and mean body weight of chum salmon caught by Japanese salmon research vessels in the central North Pacific in June and July from 1972 to 1988. Tan is a gillnet length unit of 50 m. * $p < 0.05$. (Fig. 6 from Ishida et al. 1993).

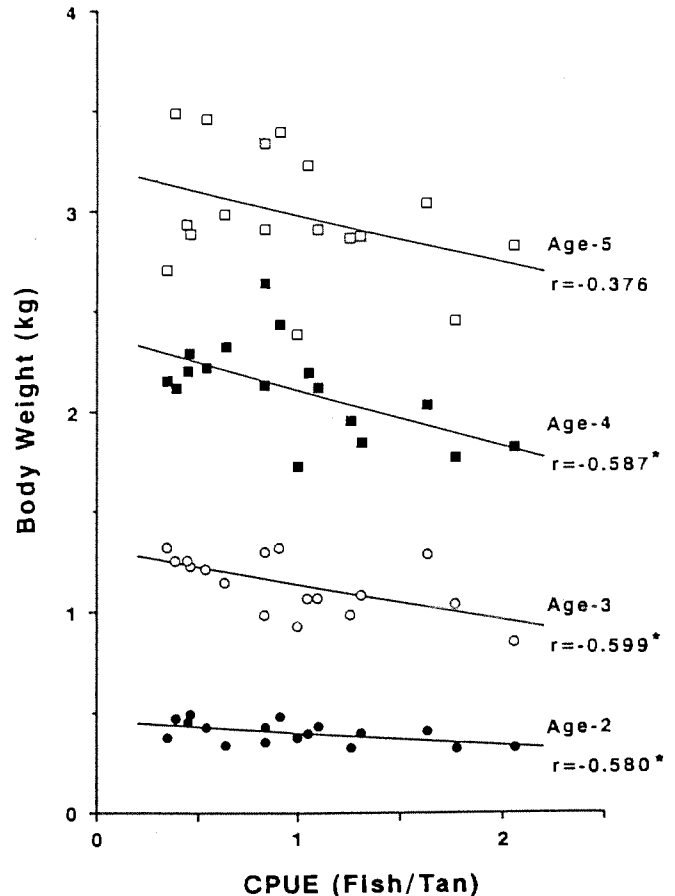


Fig. 5. Average condition factors of Pacific salmon after numbers of months at sea. Open circles, immature fish; closed circles, maturing fish. (Fig. 3 from Ishida et al. 1998).

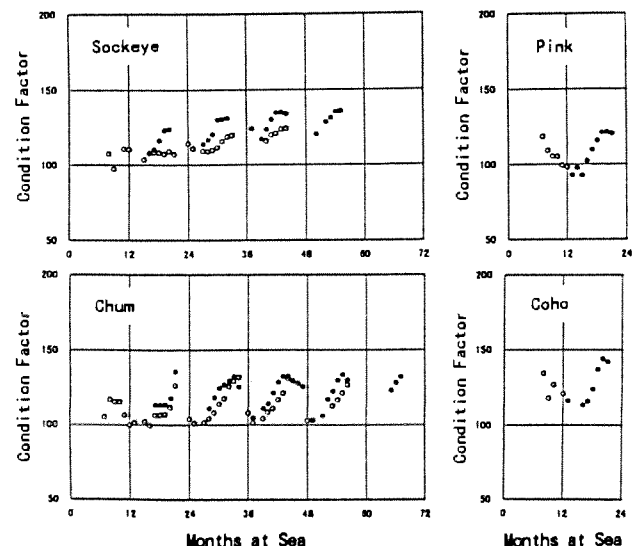
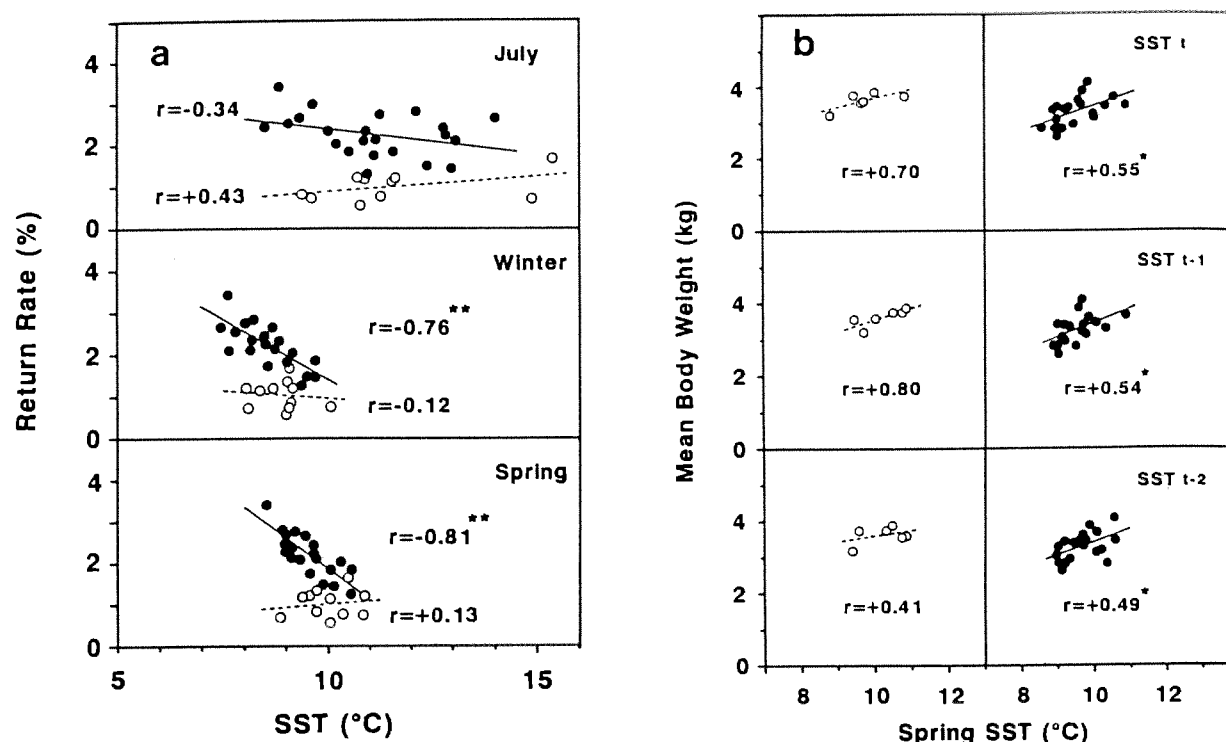


Fig. 6. Relationship between SST (near Kuril Island in July and in the central North Pacific in winter and spring) and return rates of Japanese chum salmon ($*p < 0.05$, $**p < 0.01$) (a), and relationship between the preceding three spring SSTs in the central North Pacific and mean body weight of age 0.3 chum salmon returning to the Ishikari River (b). Open circles, data for release years prior to 1966; solid circles, data for release years 1966 and subsequent year. (Fig. 3 and Fig. 5 from Ishida et al. 1995).



hatchery technology but that yields have been reduced by declining growth rates caused by decreasing SST and increasing fish density in the central North Pacific.

These studies suggest that salmon growth is variable and affected by intra- and inter-specific density dependent factors and also environmental factors such as SST in the North Pacific Ocean. Future objectives for salmon growth studies are: 1) examination of trade-off between increased number and decreased growth of Pacific salmon from biological and economical view points, 2) clarification of effects of reduced growth on reproduction, and 3) investigation of bioenergetics of salmon growth and environmental factors such as food conditions and SST.

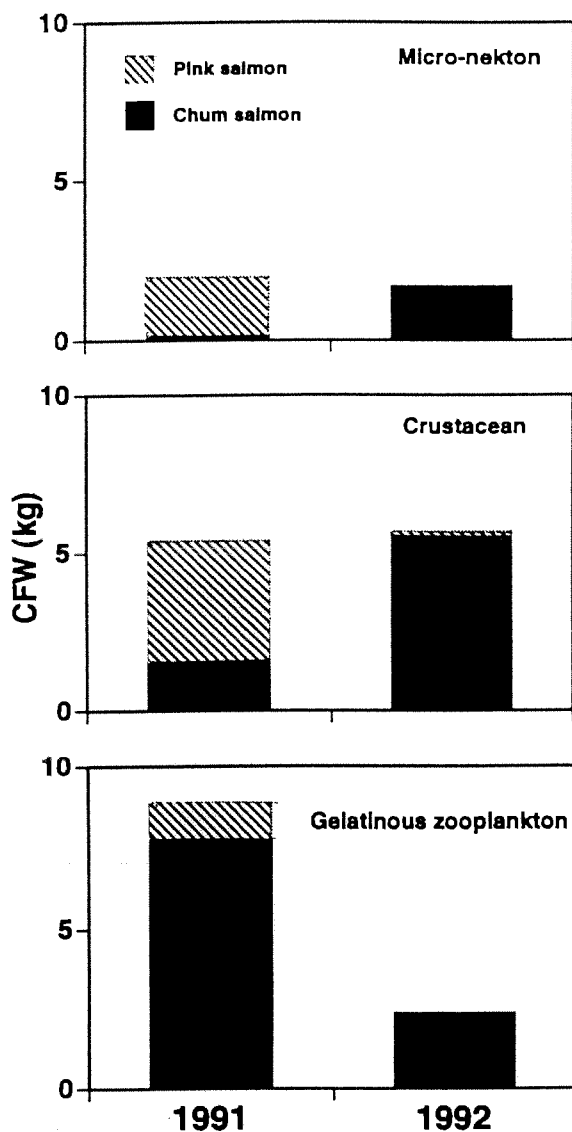
Carrying Capacity Studies

The abundance and stomach contents of salmonids (*Oncorhynchus* spp.) and biomass of prey organisms were examined in the central subarctic Pacific and Bering Sea in summer of 1991 and 1992 (Tadokoro et al. 1996). Salmonids were caught by surface longline using a standardized fishing effort. Chum (*O. keta*) and pink (*O. gorbuscha*) salmon were the predominant species, representing 44% and 36% of the total catch ($n = 1275$) in 1991. In 1992, chum salmon composed 85% of the total catch ($n = 603$), but

the catch of pink salmon decreased to 1% of the total catch due to the odd/even year fluctuation of pink salmon abundance in the study area. It was found that chum salmon changed their dominant diet from gelatinous zooplankton (pteropods, appendicularians, jellyfishes, chaetognaths, polychaetes and unidentified materials) in 1991, when pink salmon were abundant, to a diet of crustaceans (euphausiids, copepods, amphipods, ostracods, mysids and decapods) in 1992, when pink salmon were less abundant (Fig. 7). Local crustacean biomass (wet weight; mg/m^3) had significant negative correlation with CPUE (catch number per 30 longline) of pink salmon in 1991 ($r = -0.586$; $p = 0.026$) and that of chum salmon in 1992 ($r = -0.616$; $p = 0.014$) (Tadokoro et al. 1996). These results suggest that there is a limitation in the available prey resource for production of salmonids.

Year-to-year variations in biomass of phytoplankton (surface chlorophyll *a* concentration) and macrozooplankton (wet weight obtained by a North Pacific standard plankton net operation above 150 m), and abundance of pink salmon (catch per unit effort of pink salmon) from 1985 to 1994 in the subarctic North Pacific in summer were studied by Shiimoto et al. (1997). After 1989, phytoplankton biomass and pink salmon abundance showed corresponding yearly patterns, whereas the pattern shown by macrozooplankton biomass was always the inverse of that shown by

Fig. 7. Captured food weight (CFW: kg/total catch) for chum and pink salmon in 1991 and 1992. Micronekton includes squid and fish; crustaceans include euphausiids, copepods, amphipods, ostracods, mysids and decapods; and gelatinous zooplankton include pteropods, appendicularians, jellyfish, chaetognaths, polychaetes and unidentified materials. (Fig. 4 from Tadokoro et al. 1996).

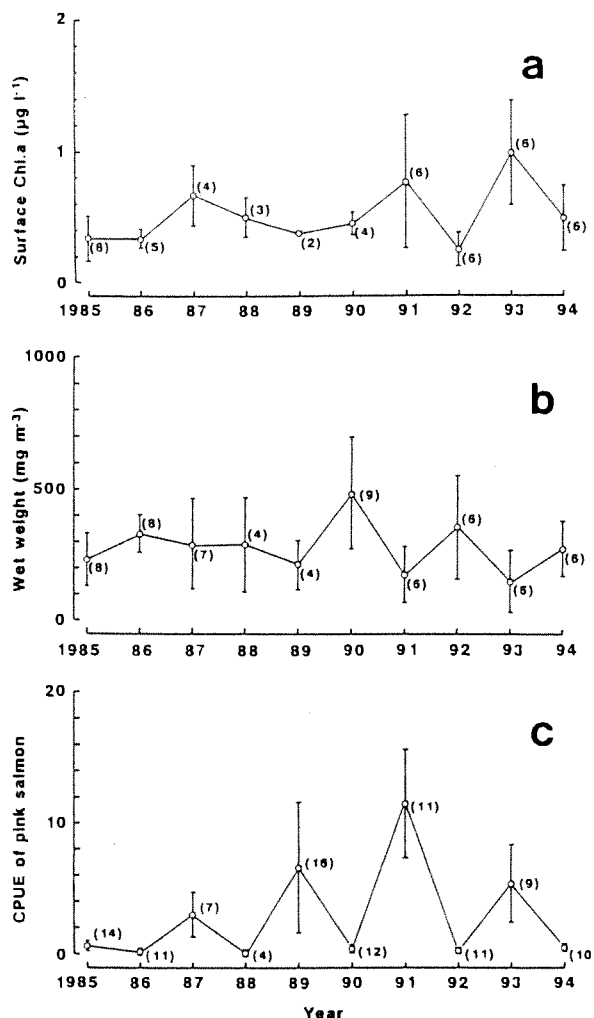


phytoplankton and salmon. These patterns suggest that macrozooplankton biomass remained low when pink salmon were abundant due to the intense feeding impact of pink salmon, which in turn allowed phytoplankton biomass to remain high as a result of the lesser grazing effect of macrozooplankton. The opposite phenomenon probably occurred when pink salmon was not abundant. Prior to 1989, macrozooplankton biomass was high while phytoplankton biomass and pink salmon abundance were low (Fig. 8). Macrozooplankton biomass apparently remained high due to a lesser feeding impact of the pink salmon, and phytoplankton biomass remained low due to the

intense grazing effect of macrozooplankton. These results suggest that feeding by pink salmon possibly structures summer macrozoo- and phytoplankton biomass in the subarctic North Pacific. Similar relationships among phytoplankton, macrozooplankton, and salmonid biomass were observed in the North Pacific and Bering Sea in the summers of 1992 and 1993 (Nagasawa et al. 1999).

Salmon sharks (*Lamna ditropis*) were observed to be opportunistic feeders, but occupied the highest trophic level in the food web of subarctic waters (Nagasawa 1998b). Salmonids were the major prey item for salmon sharks in the subarctic North Pacific Ocean. Although the importance of each species of Pacific salmon eaten by salmon sharks varied among regions, sockeye salmon were the most frequent prey, followed by chum, pink, coho, and chinook (*O. tshawytscha*) salmon. The conservatively estimated abundance of salmon sharks was about 2 million fish

Fig. 8. Mean yearly chlorophyll a concentration (a), mean wet weight of macrozooplankton (b), mean CPUE of pink salmon for each year (c). Number of samples in parentheses, error bars \pm SD. (Fig. 2 from Shiimoto et al. 1997).



in 1989 (Nagasawa 1998b). Of these fish, salmon shark older than 5 years (595×10^3 fish) occurring in subarctic waters appeared to have consumed $73\text{--}146 \times 10^6$ salmonids ($113\text{--}226 \times 10^3$ metric tons) from spring to autumn in 1989, which corresponded to 12.6–25.2 % of the total annual run of Pacific salmon for that year. These results suggest that predation by salmon sharks is responsible for significant mortality of Pacific salmon during their marine phase.

These studies suggest on the one hand that the salmon exercise top-down control of primary and secondary production in the North Pacific Ocean. On the other hand, linkages between climate change and salmon abundance suggest bottom-up control of salmon production in the North Pacific Ocean (Beamish and Bouillon 1993). Future issues for Japanese carrying capacity studies are: 1) confirmation of top-down and bottom-up control, 2) monitoring investigation of long-term salmon production and climate variability relating to top-down and bottom-up control, and 3) investigation of effects of top predators such as sharks, seabirds, and marine mammals on salmon production.

Forecast Studies

Estimates of high-seas abundance of salmon may be useful predictors of annual run strength. Abundance (CPUE: fish caught by gillnet with mesh sizes from 112 to 130 mm) was calculated using the data collected on board Japanese salmon research vessels in offshore waters of the North Pacific Ocean from 1972 to 1995 (Ishida and Ito 1998). These data were stratified by month, 2-degree latitude by 5-degree longitude areas (2×5 areas), species, and maturity, and related to the returns of Japanese chum salmon and Bristol Bay (Alaska) sockeye salmon. Significant correlations and high average CPUE were found in several areas. There were significant ($*p < 0.05$, $**p < 0.01$) positive correlations between CPUE of maturing chum salmon in central Bering Sea in July ($r = 0.46^*$ to 0.74^{**}) and the return of Japanese chum salmon in the same year as the samples (Fig. 9-a). The abundance of immature sockeye salmon in areas south of the Aleutian Islands ($r = 0.47^*$ to 0.65^{**}) and central Bering Sea ($r = 0.48^*$ to 0.64^*) in July was significantly and positively correlated with the returns of Bristol Bay sockeye salmon the following year (Fig. 9-b). These correlations suggest that estimates of abundance of salmon in offshore areas based on CPUE of sampling operations could be used to develop pre-season forecasts of Japanese chum salmon and Bristol Bay sockeye returns.

A significant positive relationship between the return rates of age 0.2 adults (R_2) and age 0.3 adults (R_3) was observed for chum salmon populations in Japan Sea side of Hokkaido during the 1989–1993 brood years: $R_4 = 5.891R_3$ ($r^2 = 0.969$, $p < 0.025$). The

return rate of age 0.3 adults in 1997 was actually 0.97%, although it was estimated as 2.65% from the above formula and the return rate (0.45%) of age 0.2 adults in 1996. This result suggests that age 0.3 adults of the 1993 brood-year cohort might have had a lower return rate in 1997 because of some influence during the offshore migration period from autumn of 1996 to summer of 1997, despite their high return rate at age 0.2 (Kaeriyama et al. 1998).

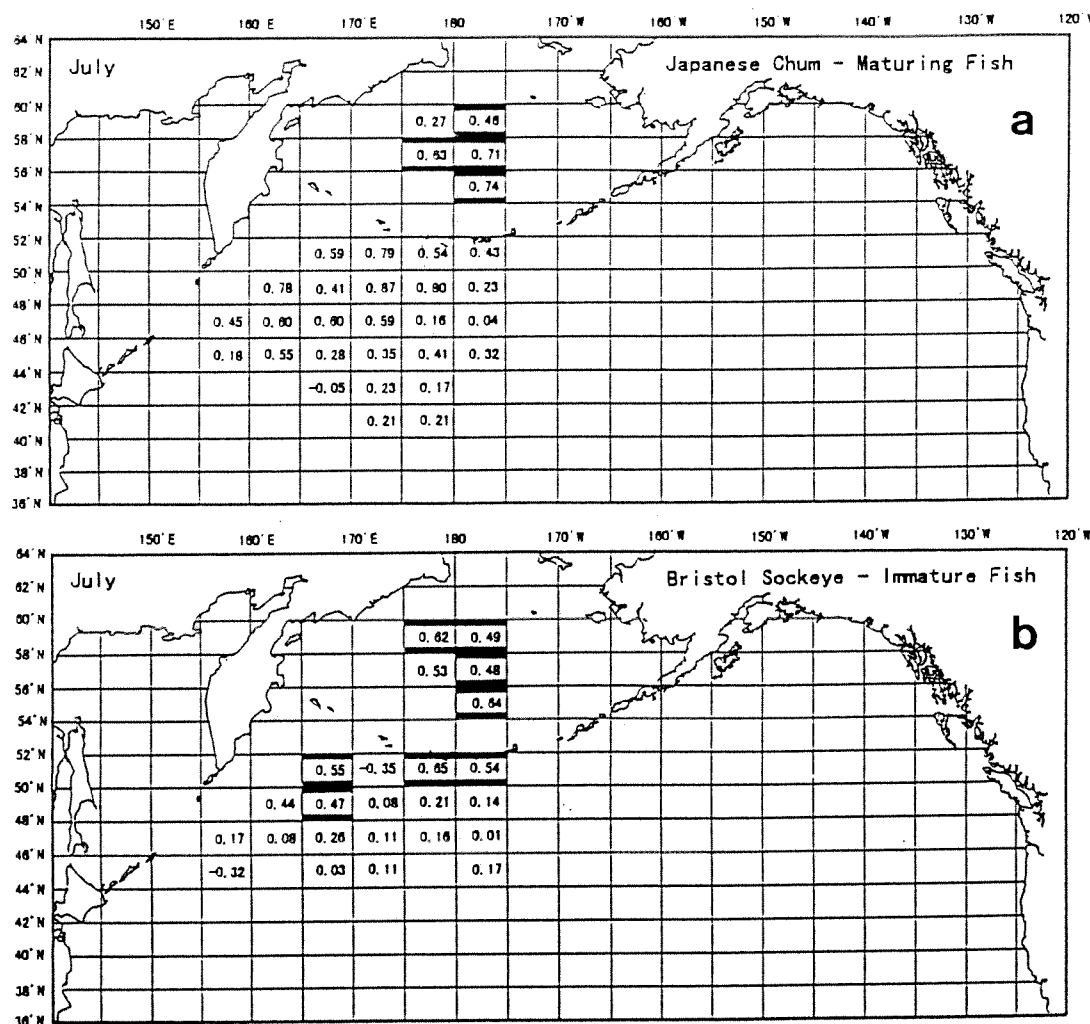
Relatively high positive correlation coefficients were found between survival rates of Russian pink salmon and the SST in the Okhotsk Sea and the waters off the East Kamchatka in August of years of fry emigration. The survival rates of pink salmon from Alaska were also positively related to SSTs in the waters along the West Coast of North America in August. These seasons correspond to the period when mortality rate is the highest in the ocean life of pink salmon. These results suggest that survival rates of pink salmon are affected by SST changes at a local level (Azumaya et al. 1998).

The forecast studies suggest that several possible methods may be useful in the North Pacific Ocean. Reliable salmon forecasts are one of the main objectives of salmon research; they are needed not only for salmon harvest management and conservation of stocks, but also for the efficient operation of salmon fisheries and processing industries. Future issues for forecast studies are: 1) inclusion of additional biological characters such as age composition and body size in forecasts, 2) cost and benefit analysis of forecast research in offshore waters, and 3) development of quick and accurate stock assessment tools, e.g. by surface trawl and/or acoustic surveys.

Winter Salmon Studies

Oceanographic and biological data collected in the trans-Pacific survey during early winter (1992), mid-winter (1996) and late winter (1998) were analyzed (Ueno et al. 1999). The seasonal changes of the distribution of sockeye, chum (except for juvenile), and coho salmon strongly indicated that they migrate eastwards from the western or central North Pacific to the eastern North Pacific in the winter. Strong eastward water transport in the upper ocean associated with the storms in the western North Pacific may accelerate the eastward migration of these salmonids. A high density of juvenile chum and pink salmon was observed in the western North Pacific Ocean in mid-winter. Sea surface temperature at 8°C indicated the southern boundary of salmon distribution in the North Pacific Ocean (Fig. 10). These results suggest that only subarctic waters are suitable for wintering salmon. Low temperatures in the subarctic waters seem to decrease the metabolic rate. The northern boundary of salmon distribution corresponded with about 4°C at sea surface in the North Pacific Ocean in

Fig. 9. Correlation coefficients between density (CPUE) of maturing chum salmon in $2^\circ \times 5^\circ$ areas in July of year t and return of Japanese chum salmon in year t (a), and correlation coefficients between density (CPUE) of immature sockeye salmon in $2^\circ \times 5^\circ$ areas in July of year t and return of Bristol Bay sockeye salmon in year $t+1$ (b). Shaded areas indicate higher average CPUE and significant correlation coefficients ($p < 0.05$). (Fig. 2 and Fig. 3 from Ishida and Ito 1998).



late winter. However, a few chinook salmon occurred in waters north of this boundary, where the SSTs ranged from 1°C to 4°C .

The use of measurements of total lipid content and lipid classes in the white muscle and liver of pink and chum salmon was examined for their potential to describe trophic condition during their ocean life (Azuma *et al.* 1998; Nomura *et al.* 1999). In winter, the total lipid contents of chum and pink salmon were extremely low and the total lipid content of the white muscle of pink salmon varied by capture location. The total lipid content in the white muscle of immature chum salmon was significantly lower than in maturing chum salmon in spring. The total lipid of the white muscle in maturing pink salmon in the Japan Sea was significantly higher than in pink salmon in the North Pacific Ocean. In summer, the total lipid content of the white muscle increased in both species, but a significant difference in the total lipid content was

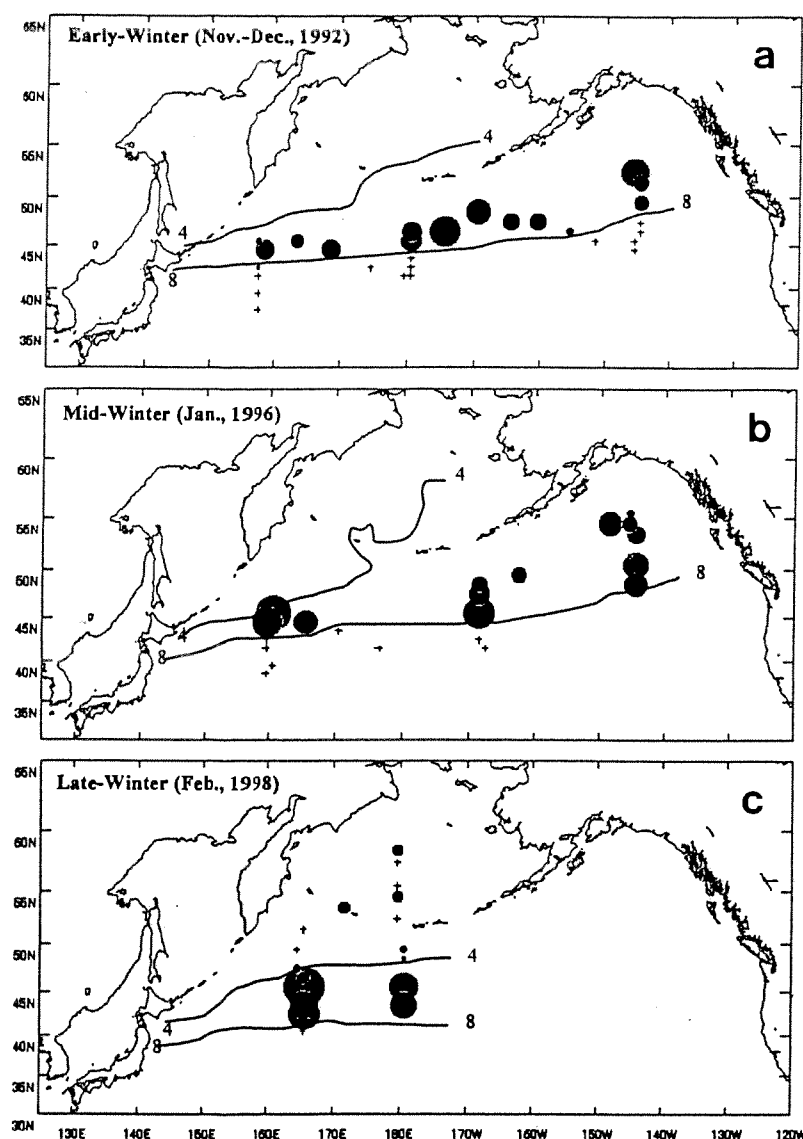
observed according to the capture locations. The extremely low lipid contents in winter suggest that chum and pink salmon are confronted with great energetic challenge during this season.

The winter salmon studies suggest that winter is one of the critical periods for salmon population in the North Pacific Ocean. Future issues for the winter salmon studies are: 1) investigation of migration routes and environment conditions of Pacific salmon using archival tag data in winter, and 2) examination of effect of possible food shortage on salmon survival and growth in winter.

CONCLUSIONS

The eight year ocean salmon research by Japanese scientists in cooperation with scientists of Canada, the Russian Federation and the United States of America have begun to solve many questions identified by the

Fig. 10. Distribution of salmon abundance (CPUE) and sea surface temperature in early winter (November–December, 1992) (a), mid winter (January 1996) (b), and late winter (February 1998) (c) in the North Pacific Ocean. (Fig. 2 from Ueno et al. 1999).



NPAFC Science Plan, and revealed new issues for future salmon research. In order to promote the future ocean salmon research, we need to concentrate our effort on specific waters, such as the Okhotsk Sea and Gulf of Alaska for juvenile salmon studies, and the Bering Sea for salmon growth, carrying capacity, and forecast studies. Winter salmon studies are also needed to clarify the critical period for the salmon ocean life. These issues should be incorporated into a revised NPAFC Science Plan scheduled in 2000 and investigated by the scientists under the cooperation of Pacific Rim countries.

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Long-term Changes in the Climate and Ocean Environment in the Okhotsk Sea and Western North Pacific and Abundance and Body Weight of East Sakhalin Pink Salmon (*Oncorhynchus gorbuscha*)

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Keywords: Pink salmon, climate change, Aleutian Low, sea ice, population biology, zooplankton biomass, carrying capacity

Abstract: Trends in catch of East Sakhalin pink salmon (*Oncorhynchus gorbuscha*) were closely related to the climate and ocean environment in the Okhotsk Sea and western North Pacific. During the period when the intensity of the Aleutian Low strengthened from 1977 to 1988, the area of sea ice expanded in the Okhotsk Sea, but both sea surface temperature (SST) and zooplankton biomass decreased in the western North Pacific, and pink salmon catch declined. Conversely, after the Aleutian Low weakened in 1989, the area of sea ice sharply decreased in the Okhotsk Sea, and pink salmon catch dramatically increased. It is thus suggested that during the period of the intensified Aleutian Low, juveniles have a higher mortality due to decreased SST in the Okhotsk Sea, and overwintering immature fish have a higher mortality due to decreased SST and zooplankton biomass in the western North Pacific. The reverse occurs with a weakened Aleutian Low. With an increase in catch after 1989, the body weight of adult pink salmon increased, suggesting that the carrying capacity of the western North Pacific Ocean for this stock has since increased.

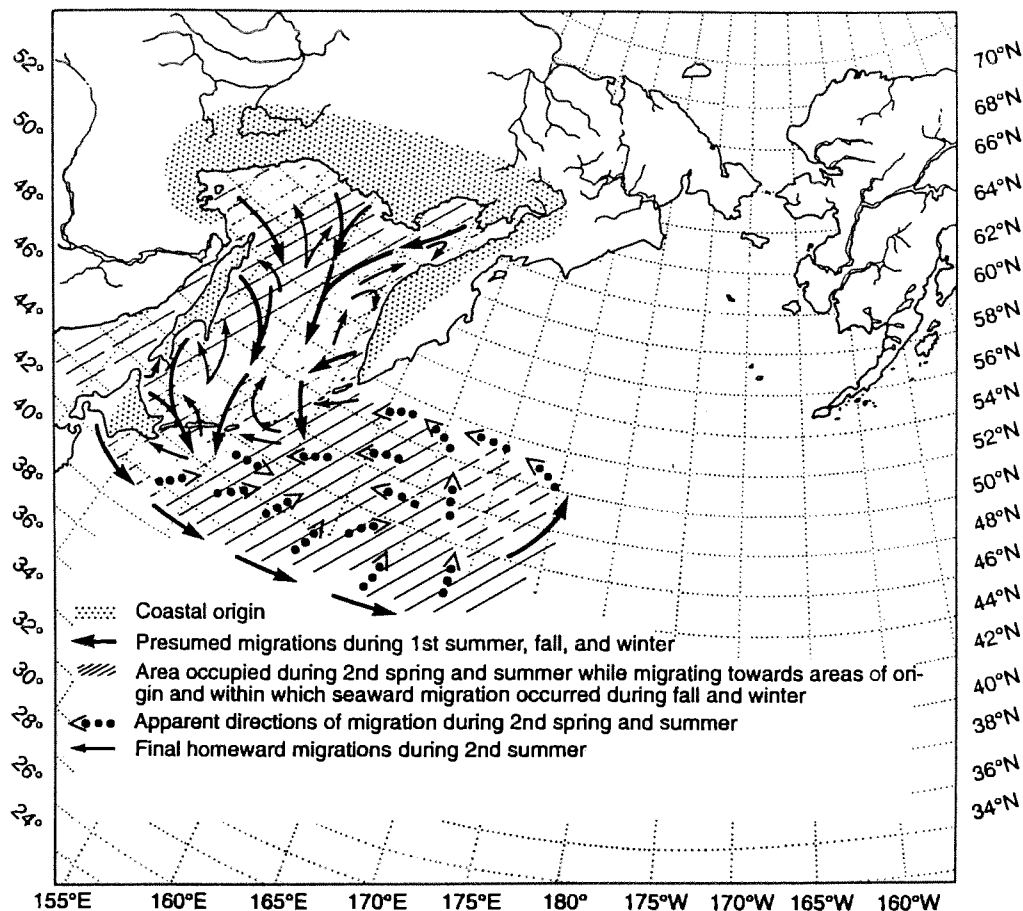
INTRODUCTION

There has been increasing evidence that long-term production trends of Pacific salmon (*Oncorhynchus* spp.) are related to climate change (Beamish 1993; Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Francis 1995; Beamish et al. 1995, 1997b, 1997c, 1999a, 1999b; Brodeur and Ware 1995; Klyashtorin and Smirnov 1995; Adkinson et al. 1996; Gargett 1997; Klyashtorin 1997; Mantua et al. 1997; Francis et al. 1998; Downton and Miller 1998). However, most of the studies deal with the stocks of salmon in North America or total catches in the whole North Pacific, and there are few studies focusing on the salmon production in Asia related to climate (Krovnin 1998). Large-scale climate change is indeed thought to have widely affected salmon production in the North Pacific Ocean (Beamish and Bouillon 1993; Klyashtorin and Smirnov 1995; Klyashtorin 1997; Beamish et al. 1999b). Its influence, however, may differ between North American and Asian salmon stocks as the stocks use different oceanic regions for growth (especially in the early ocean life histories), although high-seas distributions overlap, and each region has its own oceanographic

conditions and biological production. It may be that Asian salmon in the western North Pacific show different climate-related production patterns from North American salmon. Moreover, there is little information on the mechanisms linking climate change to salmon production. We need more information on the whole scenario from the climate through the ocean environment (including water temperature and zooplankton) to salmon production.

East Sakhalin pink salmon (*O. gorbuscha*) are one of the biggest stocks of Pacific salmon in Asia with catch exceeding 100,000 metric tonnes in 1991. The species is distributed as juveniles in the Okhotsk Sea from summer to autumn and occurs as immature and maturing fish in the western North Pacific Ocean in winter and spring (Fig. 1) (Takagi et al. 1981; Shuntov 1994). Studying this stock enables us to evaluate the effects of changes in the climate and ocean environment off Far East Asia on a local Asian stock. In the present paper, I examine data collected largely from the early 1950s to the early 1990s to relate production trends of East Sakhalin pink salmon to long-term changes in the climate and ocean environment in the Okhotsk Sea and western North Pacific. Specifically, since it is known that two climatic

Fig. 1. Distribution and migration of Far Eastern Asian pink salmon, including East Sakhalin stock [from Heard (1991) who modified Fig. 94 in Takagi et al. (1981), with the permission of the University of British Columbia Press].



regime shifts occurred in 1977 and 1989 (Beamish et al. 1997a, 1997b), I focus on fluctuations in stock of East Sakhalin pink salmon in relation to these regime shifts. I also relate annual changes in body size to the stock size to infer shifts in ocean carrying capacity for pink salmon.

MATERIALS AND METHODS

Pink Salmon Data

Data on East Sakhalin pink salmon used in this paper were provided to the Government of Japan by the Government of the Soviet Union and currently the Government of the Russian Federation. Annual catch data during the period from 1952 to 1997 included those of pink salmon from West Sakhalin and the Kuril Islands, but as catches in these areas were low and their exact values were unknown, the non-corrected data were used as catch data for East Sakhalin pink salmon. Data on the number of pink salmon annually caught from 1958 to 1993 were also used. Data on the annual mean body weight of East Sakhalin pink salmon were based on the measure-

ments of adult fish that had returned to their spawning rivers in July from 1958 to 1993 (excluding 1976 and 1984 when no data were available).

Climate Data

The Aleutian Low pressure system dominates the climate of the northern North Pacific Ocean from late in the year to the spring of the next year. For winters and springs of 1899–1990, Beamish and Bouillon (1993) calculated the area (square kilometers) of the North Pacific Ocean covered by the Aleutian Low pressure system less than 100.5 kPa. They used the sum of the winter and spring Aleutian Low values as an index of historical weather over the North Pacific Ocean and called it the Aleutian Low Pressure Index (ALPI). In the present study, data on the winter (January to March) ALPI anomaly from 1949 through 1997 were obtained from an appendix table in Beamish et al. (1997b), and 4-year running means were calculated to compare with the catch of East Sakhalin pink salmon and the sea surface temperature (SST) and zooplankton biomass in the western North Pacific Ocean.

Sea Ice Area Data

As SST and zooplankton biomass data in the Okhotsk Sea were not available for the present study, data on sea ice area were used as an index of the ocean environment. Part of the Okhotsk Sea is covered with sea ice during the winter (Aota and Ishikawa 1993). Annual data on accumulated sea ice concentration in the Okhotsk Sea south of 50°N from the period 1969–1992 were taken from Fig. 13 in Aota and Ishikawa (1993), and 4-year running means were calculated. The accumulated sea ice concentration was defined as the sum of daily percentages of a survey area covered with sea ice from January 1 to May 31 of each year (Aota and Ishikawa 1993).

Sea Surface Temperature Data

SST data in the western North Pacific Ocean were provided by Dr. K. Tadokoro (National Research Institute of Far Seas Fisheries, present address: Ocean Research Institute, University of Tokyo). He analyzed the SST data taken from 1961 to 1990 in an oceanic area (the Oyashio region, see below for definition) from the east coast of northern Honshu and Hokkaido to 145°E and from 40°N to 43°N. In the present paper, annual values of 48-month running means were used.

Zooplankton Biomass Data

Zooplankton biomass data used in this study were taken from Fig. 12 in Odate (1994). Based on 17,242 zooplankton samples collected in the western North Pacific off the east coast of Tohoku, Japan from 1951 to 1990, this author showed long-term changes in zooplankton biomass in three regions (i.e., the Kuroshio, Oyashio, and Kuroshio-Oyashio transition regions). The Oyashio region was defined as waters less than 5°C at 100 m in depth (Odate 1994), and the zooplankton biomass data in this region were used in the present study. The gear used for zooplankton sampling was a MARUTOKU net (net opening 0.45 m, net length 0.80 m, and mesh size 0.33 mm), which was vertically towed from 150 m in wire length (not depth) to the surface. The zooplankton collected was fixed in formalin on board and brought to the laboratory, where necessary sorting was done and the wet weight was measured. The zooplankton biomass was defined as the wet weight (g) of zooplankton per surface square meter, excluding large juvenile fish and gelatinous zooplankton (Odate 1994). In the present paper, annual values of 48-month running means of the zooplankton biomass were used.

RESULTS

Changes in Catch and Body Weight of East Sakhalin Pink Salmon

East Sakhalin pink salmon were commercially caught on the high seas of the western North Pacific by Japanese salmon fisheries until 1976 (Fig. 2). The 200-mile exclusive economic zone was established in 1977, when the Japanese high-seas fisheries ended. Despite this absence of fisheries, East Sakhalin pink salmon catch began to decrease in 1978 and remained low until 1988 (Fig. 2). Catch sharply increased in 1989 and thereafter, the highest ever recorded catch occurring in 1991.

The annual mean body weight of both male and female adult pink salmon showed similar trends in relation to catch fluctuations (Fig. 2). With increasing catch from the late 1960s to 1977, body weight declined. During the period from 1978 to 1988 when catch decreased, body weight remained low. In 1989 and afterward, catch increased and body weight was higher than that recorded from 1977 to 1988.

There is a negative relationship between annual catch number of pink salmon and annual mean body weight of adult fish (Fig. 3): in years when catch was high (low), the body weight was low (high). The relationship for the period from 1989 to 1993 was different from that for 1958 through 1988.

Changes in ALPI over the North Pacific and Sea Ice Area in the Okhotsk Sea

The ALPI increased in the 1970s and peaked in 1979 (Fig. 4). Subsequently, the ALPI decreased in the 1980s but remained at a high level from 1977 to 1987. This indicates that the intensity of the Aleutian Low strengthened during this period.

Annual changes in sea ice area showed similar trends to those of ALPI (Fig. 4). Sea ice area in the southern Okhotsk Sea steadily began to increase in 1975 and peaked in 1978. Although sea ice area was at an intermediate level from 1982 to 1985, it remained relatively high until 1988. Sea ice area abruptly decreased in 1989 and 1990.

Changes in SST and Zooplankton Biomass in the Western North Pacific

SST in the Oyashio region of the western North Pacific was relatively high from the mid-1960s to the early 1970s (Fig. 5). It decreased irregularly from 1971 to 1983, remained low until 1989, and increased sharply in 1990.

Fig. 2. Annual changes in catch (top) and body weight (bottom) of pink salmon along East Sakhalin, Russia, from the 1950s to 1990s. The regime shifts of 1977 and 1989 are indicated by vertical lines. A horizontal bar indicates the period of Japanese high-seas salmon fisheries from 1952 to 1976.

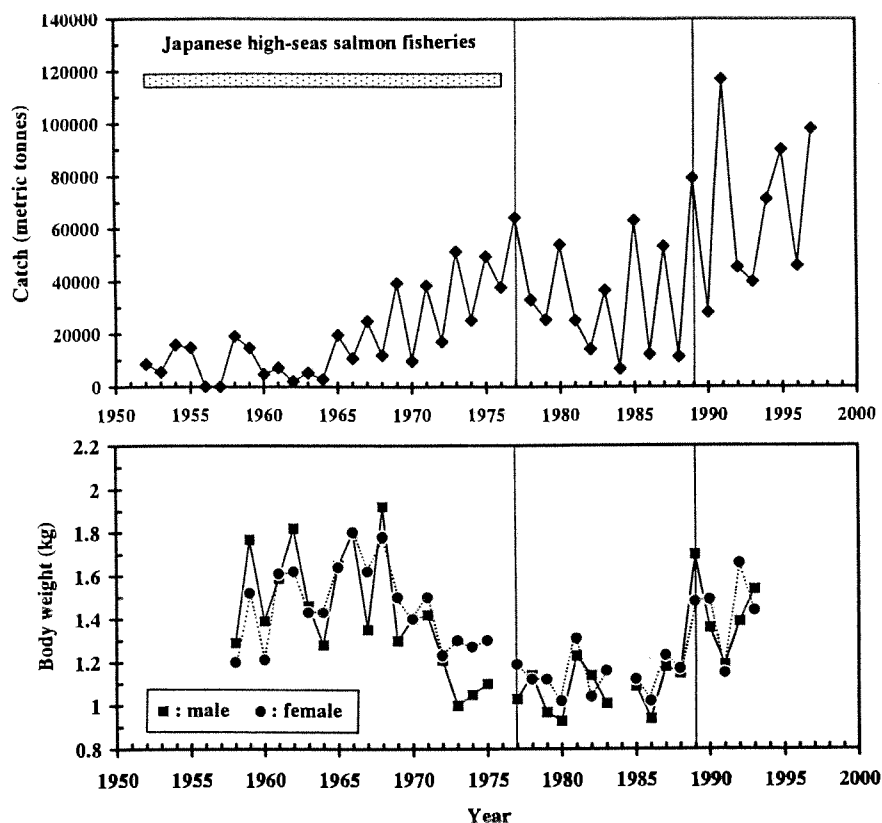


Fig. 3. Relationship between body weight of male (top) and female (bottom) adult pink salmon and catch number along East Sakhalin from 1958 to 1993.

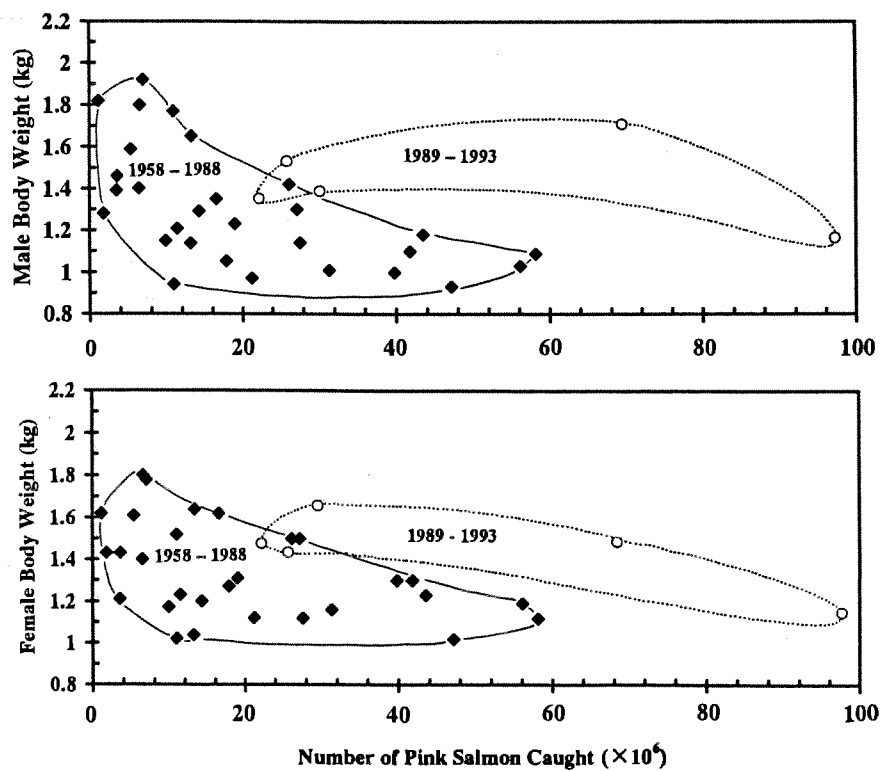


Fig. 4. Long-term changes in winter Aleutian Low Pressure Index (ALPI) anomaly over the North Pacific (top) and accumulated sea ice concentration in southern Okhotsk Sea south of 50°N (bottom). The regime shifts of 1977 and 1989 are indicated by vertical lines.

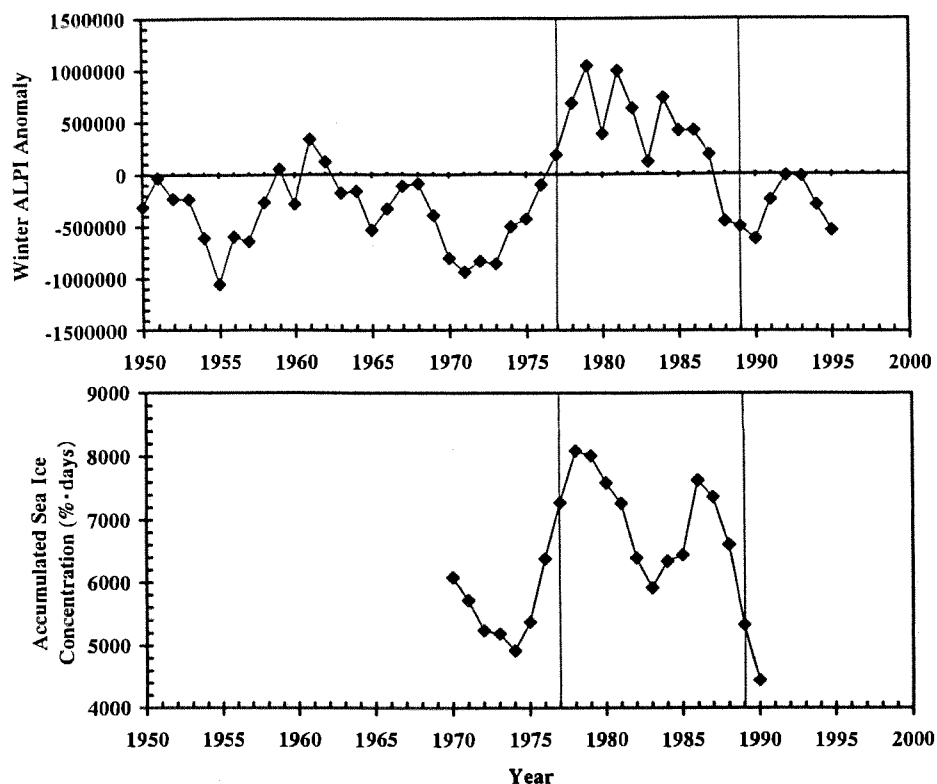
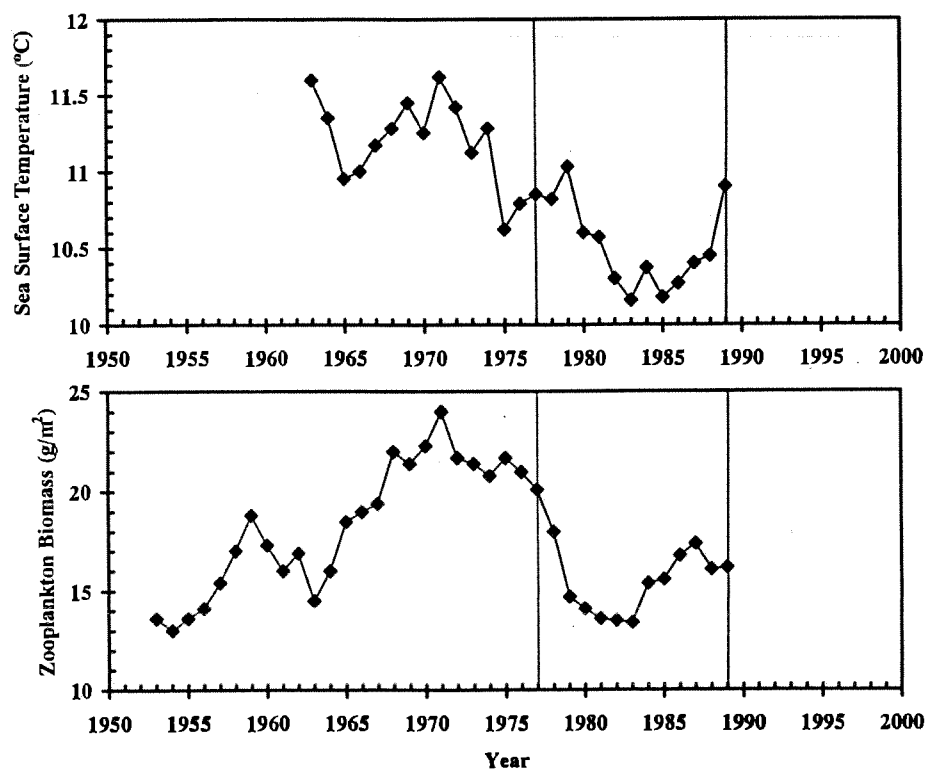


Fig. 5. Long-term changes in sea surface temperature (top) and zooplankton biomass (bottom) in the Oyashio region of the western North Pacific. The regime shifts of 1977 and 1989 are indicated by vertical lines.



Annual changes in zooplankton biomass in the Oyashio region were similar to those in SST (Fig. 5). While zooplankton biomass was high from the mid-1960s to the mid-1970s, it declined sharply in 1978 and remained low thereafter.

DISCUSSION

The present study shows that catch trends in East Sakhalin pink salmon were closely related to changes in the climate and ocean environment in the Okhotsk Sea and western North Pacific Ocean. Through the mid-1970s to the late 1980s when the Aleutian Low intensified, sea ice area expanded in the Okhotsk Sea, both SST and zooplankton biomass remained low in the western North Pacific, and pink salmon catch in East Sakhalin declined in spite of the disappearance of Japanese high-seas salmon fisheries. However, after 1989 when the intensity of the Aleutian Low weakened, sea ice area sharply decreased in the Okhotsk Sea, and East pink salmon catch dramatically increased, although corresponding SST and zooplankton data were not unfortunately demonstrated for the western North Pacific. These relationships imply that weakening of the Aleutian Low provides favorable ocean environments for pink salmon in the Okhotsk Sea and western North Pacific.

East Sakhalin pink salmon stay as juveniles in the Okhotsk Sea from summer to autumn before migrating to the western North Pacific in early winter (Takagi et al. 1981; Shuntov 1994). An extensive winter sea ice cover is thought to delay an increase in SST in the Okhotsk Sea in spring and early summer. This would create unfavorable conditions for juvenile pink salmon. Shershnev and Chupakin (1992) showed that higher returns of Northeast Sakhalin pink salmon are closely associated with higher coastal June–July SST. During the period when the Okhotsk Sea is widely covered with sea ice, decreased SST (and possibly decreased biological production) may induce a high mortality of juvenile pink salmon. The expansion of sea ice area in the Okhotsk Sea has a close relationship with intensifying of the Aleutian Low (Parkinson 1990; Tachibana et al. 1996). In years when the Aleutian Low is strong, winter northwest winds bring cold air from Siberia, which enhances the formation and movement of sea ice in the Okhotsk Sea. The abrupt decrease in sea ice cover in this sea corresponded well to the weakening of the Aleutian Low in 1989 (Tachibana et al. 1996). Therefore, the production of East Sakhalin pink salmon may be indirectly controlled by annual changes in the intensity of the Aleutian Low over the North Pacific.

The present study also shows that long-term trends in pink salmon catch are closely related to the marine environment in the western North Pacific, where immature and maturing pink salmon reside

from winter to spring. This implies that SST and zooplankton biomass in the western North Pacific are responsible for the survival or mortality of pink salmon. From this viewpoint, one possible explanation for low catches of pink salmon during the period of the intensified Aleutian Low is lower survival of overwintering fish owing to decreased SST and zooplankton biomass in the western North Pacific. Specifically, as winter zooplankton biomass remains at a low level (about 10% of the summer biomass) in the western North Pacific (Nagasawa this volume), overwintering salmon appear to survive under very poor food conditions. In addition, Blackburn (1993) suggested that temperatures experienced by maturing adult salmon may affect the development of eggs or sperm and the subsequent survival rate of the eggs and fry in fresh water. If this is true, another possible explanation is that colder ocean temperatures in the western North Pacific during the period of the intense Aleutian Low reduce the survival of eggs and fry, leading to the low production of pink salmon.

Note that East Sakhalin pink salmon decreased from the mid-1970s to the late 1980s, while during this period the production of northern North American (Alaskan) stocks increased (Beamish 1993; Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Francis 1995; Klyashtorin and Smirnov 1995; Beamish et al. 1997a, 1999b; Klyashtorin 1997; Mantua et al. 1997; Francis et al. 1998; Downton and Miller 1998). Stocks on southern North America (southern British Columbia, Washington, Oregon, California) showed decreasing trends during this period (Beamish et al. 1995, 1997a, 1999a). The reason why East Sakhalin pink salmon exhibited opposite production trends from northern North American stocks but similar trends to southern North American stocks is at least partly that a climate change (the Aleutian Low in the present study) causes different oceanographic changes among various regions of the North Pacific and adjacent seas. An abrupt shift in the North Pacific climate, including intensifying of the winter Aleutian Low, began in the winter of 1976–1977 (Miller et al. 1994; Graham 1994). This shift led to weather changes in various regions of the North Pacific Ocean (Nitta and Yamada 1989; Trenberth 1990; Trenberth and Hurrell 1995; Minobe 1997; Yasuda and Hanawa 1997; Kachi and Nitta 1997; Nakamura et al. 1997; Mantua et al. 1997; Minobe and Mantua 1999). The shift also resulted in changes in the ocean environment and biological production (Venrick et al. 1987; Ebbesmeyer et al. 1991; Tanimoto et al. 1993; Polovina et al. 1995; Hayward 1997; Sugimoto and Tadokoro 1997, 1998; McGowan et al. 1998). After the climatic regime shift in the mid-1970s, anomalous northerly winds on the one hand increased mixing and horizontal advection, and resulted in cooling in the central and western North Pacific (Miller et al.

1994). In the Gulf of Alaska on the other hand, warm moist air was brought from the south, warming the coastal ocean (Mantua et al. 1997). Both SST and zooplankton biomass increased in the Gulf of Alaska after the mid-1970s (McFarlane and Beamish 1992). Brodeur and Ware (1992) and Brodeur et al. (1996) also found that zooplankton biomass in the Gulf of Alaska doubled between the two periods (1952–1962 and 1980–1988). These observations were opposite to the decreasing trends in SST and zooplankton biomass found in the western North Pacific (present study). The regional differences in response of the ocean environment to climate change may result in regional differences in salmon survival and production. When we analyze relationships between long-term shifts in salmon production and climate/ocean environment, we need to study the relationships at both regional and whole North Pacific scales.

The catch of East pink salmon was extremely high after 1989, and the body weight of adult pink salmon was also greater after 1989 than that recorded from 1958 to 1988. It is well known that there is a population density-dependent effect in species of Pacific salmon: when salmon are abundant, their body size is smaller, and *vice versa* (Ishida et al. 1993; Helle and Hoffman 1995; Kaeriyama 1999). If this is the case, the body weight of East Sakhalin pink salmon should have decreased after 1989 with increasing abundance. However, the results found in the present study were opposite, suggesting that the ocean's carrying capacity for East Sakhalin pink salmon improved after 1989.

For future work, it is necessary to analyze details of relationships between the climate/ocean environments in the Okhotsk Sea and catches of stocks of Far Eastern Asian salmon. Many commercially important salmon stocks of Russia and Japan, including East Sakhalin pink salmon, utilize the Okhotsk Sea, and information linking long-term changes in salmon stocks to the climate/ocean environments is essential for efficient fisheries management. With global warming, air temperature is expected to dramatically increase in the 21st century over the Okhotsk Sea (cf. Wakatsuchi 1996), and changes in the ocean environment and related biological production should therefore be monitored carefully.

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Identification of Pink Salmon (*Oncorhynchus gorbuscha*) Runs in the Ocean off the Kuril Islands, Russia

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Keywords: Pink salmon, Pacific Ocean, runs, migration

**Abstract:** We conducted studies in the Pacific waters off the Kuril islands to obtain data on catch-per-unit-effort and some biological characteristics of pink salmon (*Oncorhynchus gorbuscha*), migrating to spawning rivers in the Okhotsk Sea Basin. The pink salmon return migration in this basin within the Kuril waters lasts four months. Large intraspecific units—temporal groups—are formed in the ocean, hundreds of miles from the coast. The homing migration of pink salmon in marine waters has three distinct runs—two in summer (early- and late-summer runs), and one in the fall. The numbers and timing of the Okhotsk Sea pink salmon runs in the ocean correspond to the numbers and timing of runs near shores and in rivers. This allows differentiation of spawning runs far out at sea long before they reach shore.

## INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) reproducing in rivers of the Okhotsk Sea Basin have a complex population structure. Populations near the shores and in rivers are distinguished by the timing of their runs, and have been called second rank populations (Gritsenko 1981). The Okhotsk Sea pink salmon have three such populations: two summer runs, early and late, and a fall run. The early pink salmon run near the shores occurs in July (northern coast of the Okhotsk Sea), the late run in August (western Kamchatka and eastern Sakhalin), and the fall run in September (southern Kuril Islands) (Ivankov 1967; Birman 1981; Gritsenko 1981; Takagi et al. 1981; Golovanov 1982).

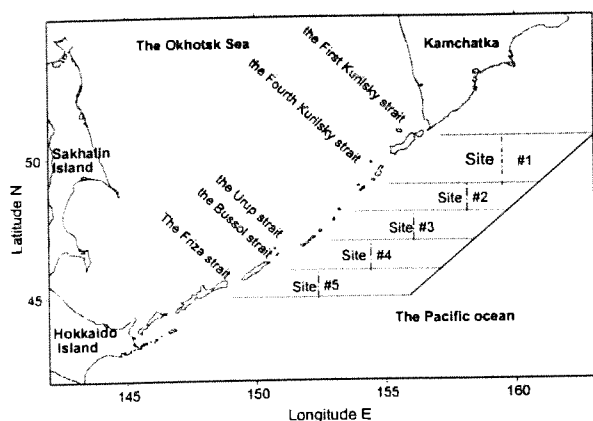
Where are these groups formed—in the ocean or in the Okhotsk Sea? We suggest that different temporal groups of Okhotsk Sea pink salmon found near the coast gather in the ocean. If so, we have an opportunity to distinguish pink salmon stocks by run timing and biological characteristics while they are far from shore. However, there is also a possibility that all three temporal groups of pink salmon begin their return migration together from their wintering sites in the Pacific Ocean by following the 2°C isotherm. Then early summer pinks may continue through the Kuril waters to the Okhotsk Sea spawning grounds, while late summer and fall pinks may stop in waters off the Kuril Islands or in the Okhotsk Sea to feed.

We decided to determine whether the Okhotsk Sea pink salmon run had a temporal structure in the ocean during their return to their spawning areas.

## MATERIALS AND METHODS

Data were obtained from 1996–1999 during the Sakhalin Research Institute of Fishery & Oceanography studies with the objective of assessing abundance of pink salmon in spawning runs far from Sakhalin shores. The studies were conducted in the Pacific waters off the Kuril Islands within the Russian Exclusive Economic Zone between 45°N and 50°50'N, from mid or end of May to early or mid August, using 6 or 7 ships each year. Occasional observations were made in the second half of August to early September of 1994–96. In 1999 surveys began in late April. Driftnets were used for sampling. To investigate the spatial distribution of salmonids, ships were located at five survey sites within the Kuril waters (site # 1—from 50°50'N to 49°01'N; sites # 2, 3, 4, 5—at every 1 degree of latitude from 49° to 45°N). Sites extended great distances east and west, and therefore they were divided into eastern and western parts. At site # 1 the boundary was at 159°E, site # 2 at 158°E, site # 3 at 156°E, site # 4 at 154°E, site # 5 at 152°E (Fig. 1). In May–June sampling was mostly in the east survey area; in July–August and early September sampling was in the west, 60–80 miles east from the straits of Kuril Islands. Sites 5–3 (45°00'–48°00'N)

Fig. 1. Survey area and location of the research sites.



were considered as the south, and sites 2–1 (48°01'–50°50'N) as the north of the study region. Sampling was conducted without intermission and simultaneously at all five survey sites to allow us to trace the changes in abundance and biological characteristics of the salmon. Sea surface temperature (SST) was measured daily where driftnets were set, using the ship's remote thermometers (Fig. 2).

Catch-per-unit-effort (CPUE) was used as a measure of pink salmon abundance at sampling sites. On the charts (Figs. 3–5) CPUE was calculated as mean catch per month based on the total number of stations within the area 1° latitude to 3° longitude at sites 5–2, and 1°50' latitude to 3° longitude at site 1, which were east and west of the mid boundary. On the graphs (Figs. 9–10) CPUE has been calculated as mean catch per driftnet during 5 days within the sampling site. Data from stations located only within an area of 1° latitude and 1° longitude were used.

In 1996–1999 driftnets used for sampling were of a standard length (50 meters), and mesh size (55 mm Russian size). In addition, we used data collected in 1994–1995, when drift net mesh size was primarily 65 mm. Usually there were 80 drift nets in a line in May–June, and 25–40 in July–August. Lines of nets were set at night for 10–12 hours. In total there were from 342 to 579 sets.

We recorded sex ratios in catches, the gonad somatic index determined as the ratio of gonad weight to the weight of eviscerated fish (GSI, %), fork length (FL) and body weight. One sample consisted of 100 individuals. During 1996–1997, biological data were collected once every ten days; each season 5,500–6,000 fish were examined. During 1998–1999 biological data were collected once every five days; each season 11,000–12,000 fish were examined. Fish and gonad weights were estimated by weighing in groups. Biological data on pink salmon were obtained only from fish caught in nets with mesh size of 55 mm.

Fig. 2. Sea surface temperature at driftnet stations in sites 1–5, 1997–1999.

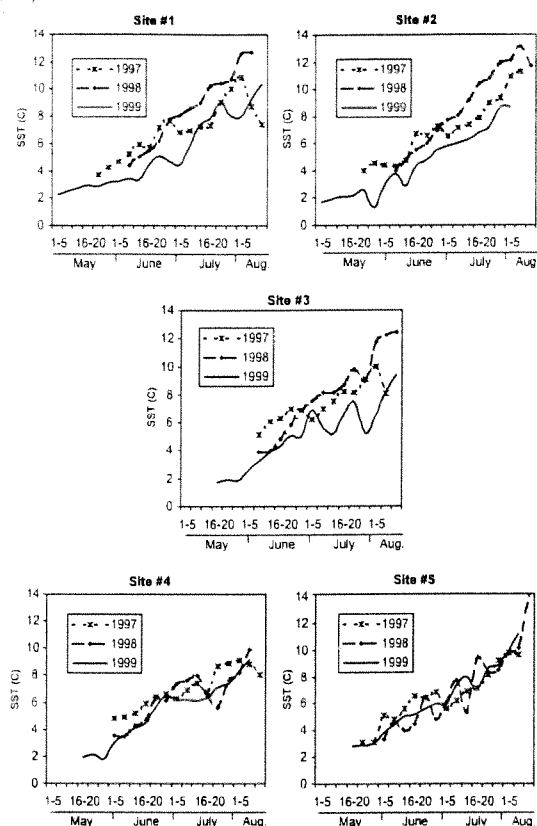


Fig. 3. CPUE of pink salmon in the Pacific waters off the Kuril islands, 1994–1995 (mesh size 65 mm).

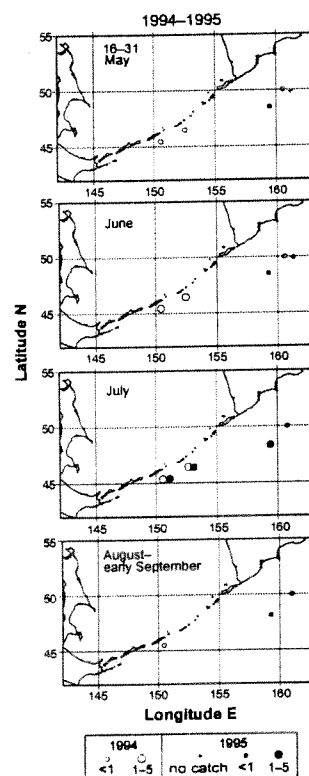


Fig. 4. CPUE of pink salmon in the Pacific waters off the Kuril islands, 1996 and 1997 (mesh size 55 mm).

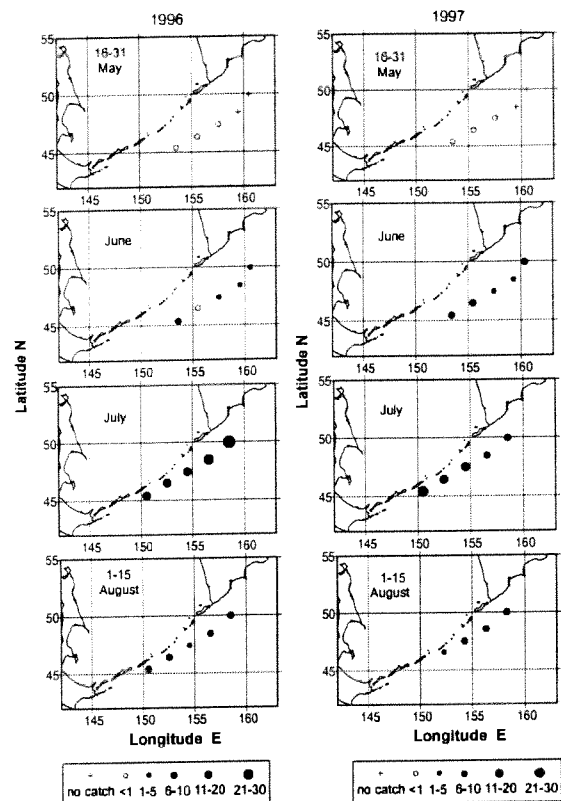


Fig. 5. CPUE of pink salmon in the Pacific waters off the Kuril islands, 1998 and 1999 (mesh size 55 mm).

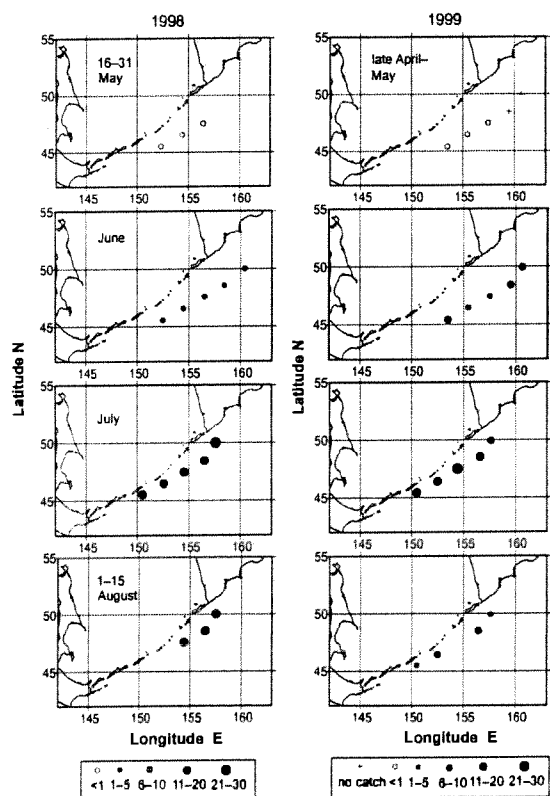


Fig. 6. Pink salmon fork length and percent of males during May–August 1998 and 1999 (arrows indicate boundary of runs).

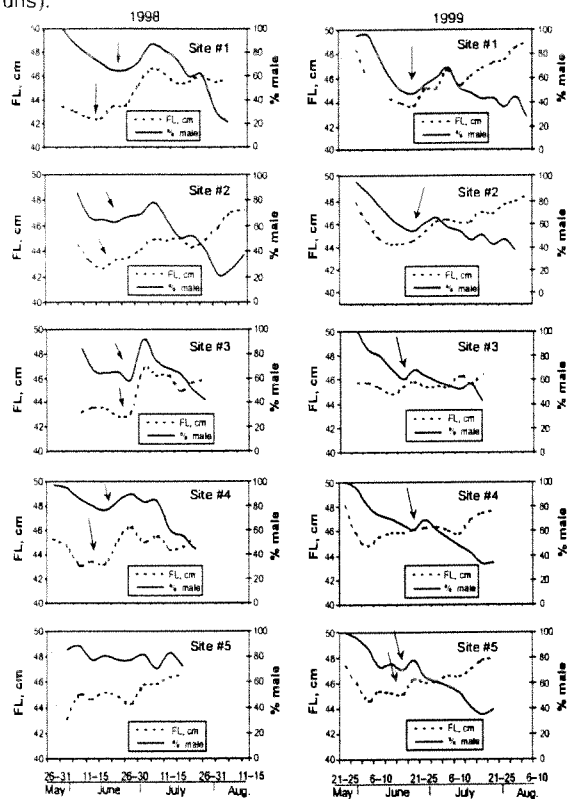
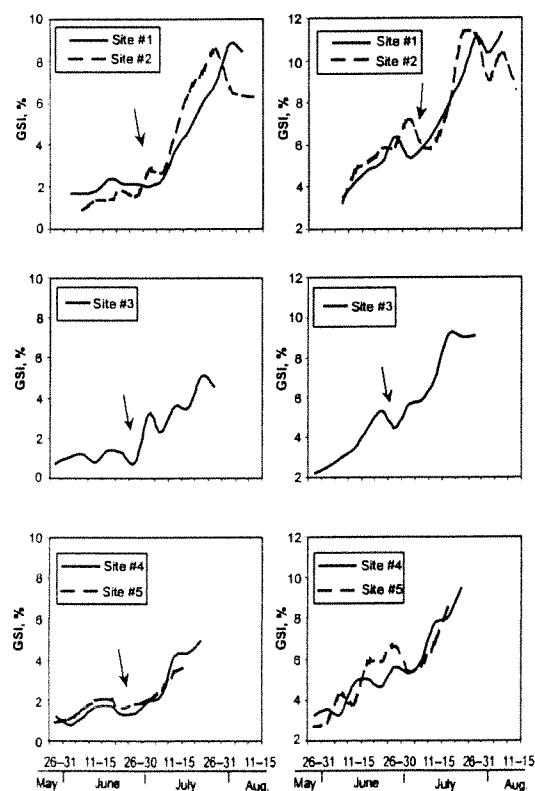
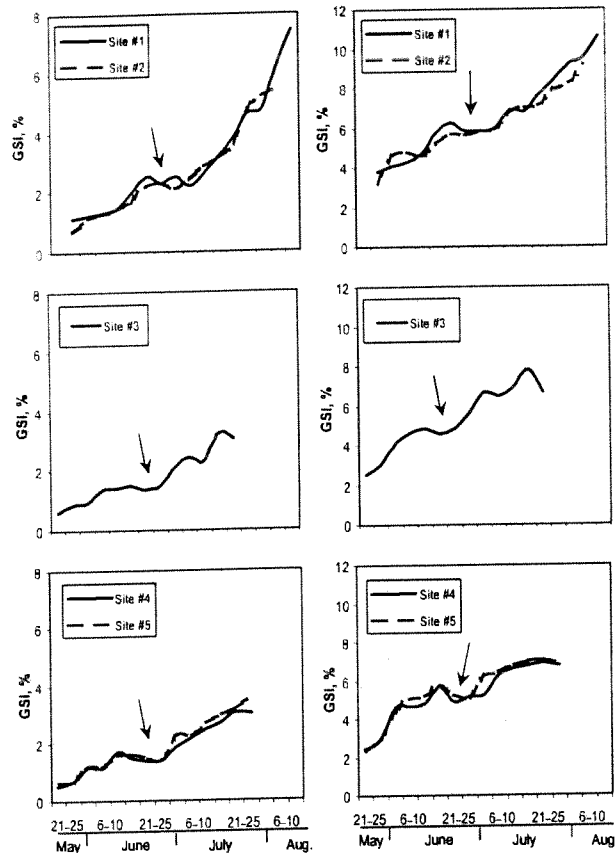


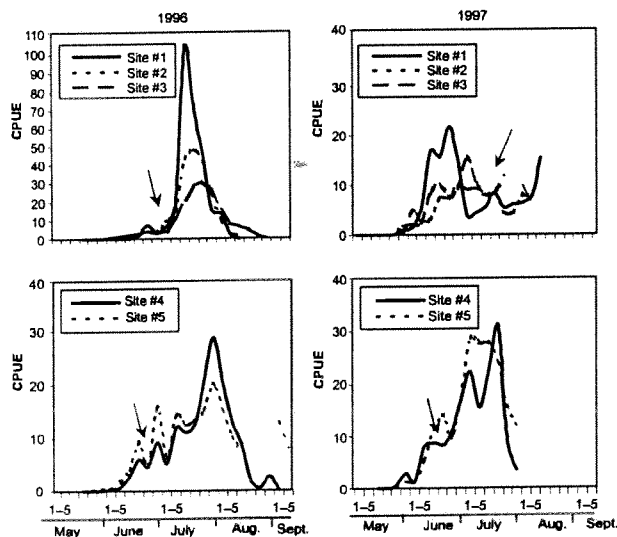
Fig. 7. Pink salmon GSI for males (left) and females (right) in May–August 1998 (arrows indicate boundary of runs).



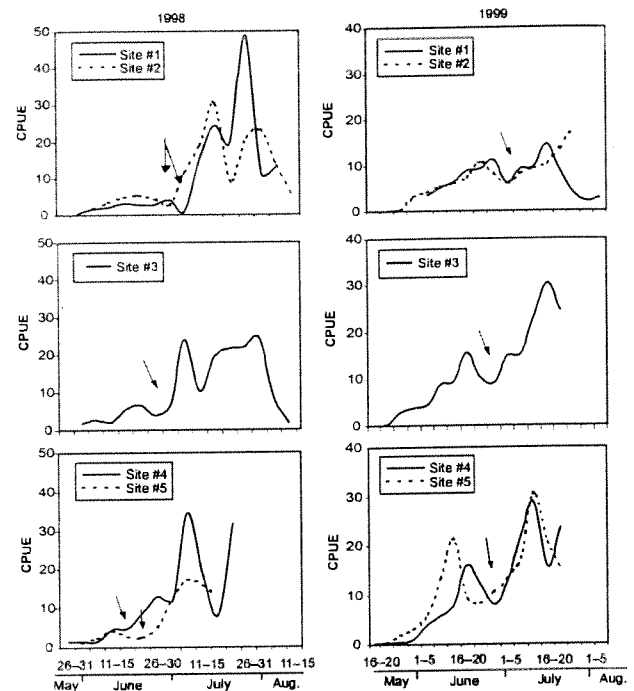
**Fig. 8.** Pink salmon GSI for males (left) and females (right) in May–August 1999 (arrows indicate boundary of runs).



**Fig. 9.** Pink salmon CPUE during May–August 1996 and 1997 (arrows indicate boundary of runs).



**Fig. 10.** Pink salmon CPUE during May–August 1998 and 1999 (arrows indicate boundary of runs).



## RESULTS

The first pink salmon migrating to spawning streams around the Okhotsk Sea shores were caught in driftnets 200 miles to the north of the Kuril Islands in late April. In the southern part of the study region, pink salmon began appearing regularly in catches around 16–20 May, and in the northern part of the region 10–15 days later. Within this period SSTs were 2.2–2.8°C (Fig. 2). In late May to early June pink salmon were distributed throughout the Pacific waters off the Kuril Islands, but in low abundance (CPUE 0.01–0.03 fish/net, Figs. 3–5). The proportion of males in May catches was 95–100% (Fig. 6). Gonad maturity index was low: GSI of males was 0.6–1.0% and of females 2.5–3.2% (Figs. 7, 8).

After early June abundance of pink salmon increased, the peak occurring between 16–20 of June in the southern area, and between 25–30 of June in the northern area, when CPUE was 15–20 fish/net (Figs. 9, 10) in some years. The proportion of males gradually decreased to 30–40%, but GSI slowly increased: for males, to 1.8–2.5%; for females, to 5.6–6.2%. By the end of June CPUE always decreased, appearing to end the pink salmon run.

CPUE began to increase in late June to early July when SST was higher than 4.8–6.0°C (Fig. 2). Maximum CPUE of pink salmon occurred in mid to late July: in the southern area CPUE increased to 30–35 fish/net, in the northern area to 80–100 fish/net. In late July to early August CPUE for pink salmon in

the Kuril waters sharply decreased (Figs. 9, 10). Sex ratios in July changed gradually in favour of females, reaching 60–70% by the end of the month (Fig. 6). Fish maturity substantially increased, with the male GSI rising to 5–6%, and female GSI to 8–10% (Figs. 7, 8).

In 1998 the more frequent sampling showed that all observed changes were interrelated. Over the wide area from 46° to 51°50'N, changes in CPUE and biological properties occurred at each site in turn, from south to north, over a very short period of 10–15 days (Figs. 6, 7, 10). The same picture was observed in 1999, when in late June to early July the CPUE decrease and increase of pink salmon were accompanied by a sharp increase in length and percentage of males (Fig. 6). Maturity decreased in this period (Fig. 8.). As in 1998, this change occurred at all sites during a short period and from south to north. (Figs. 6, 8, 10).

The majority of ships left the survey areas in August and September, but occasional observations showed that the pink salmon run in Kuril waters continued during this period. Through August and early September at some sampling sites off the Kuril Islands the CPUE of pink salmon reached 5–10 fish/net, while the percentage of males was higher comparatively than those at the end of July. Pink salmon were 50–60% males at the fifth site in early September of 1994, and at the first site in the third week of August, 1995. During the third week of July and the first week of August, 1996, the percentage of males increased from 22–36% to 50–58% at sites # 1 and # 2, and GSI simultaneously decreased (male GSI was almost 2%; female GSI 1%). In the third week of July, 1997, the percentage of adult male pink salmon in catches increased from 41% to 49–52%. This was accompanied by some decrease in maturity and an apparent rise in their size-weight indices. Fish weight, for instance, increased from 1.26–1.28 kg. in the first half of July to 1.40–1.48 kg. by the end of July. The percentage of males at site # 2 in the early half of August, 1998, increased from 21% to 38%, again accompanied by a decrease in maturity and a rise in their size-weight indices. During this period at site # 5 the proportion of males was stable at 48% until mid-August, but the size of fish was significantly larger, comparable to sizes at the end of July. At the end of July beginning of August of 1999, the proportion of males in some catches of pink salmon rose from 26–35% to 49–51% at sites 1 and 2. Because these observations in August–September were unsystematic, are not presented in tables and figures.

## DISCUSSION

The maps of salmon seasonal distribution (Fig. 3–5), show pink salmon moving into the waters off

the Kuril Islands in May. Pink salmon become most abundant in July, but their run in Kuril waters continues in August and even in early September. Superficially there appears to be one pink salmon run, but lasting in Kuril waters for four months, exceeding by three times the duration of the run near shore. However, the CPUE of pink salmon off the Kuril Islands and the changes in their biological characteristics show that homing migrations occur in three distinct runs, characterized by their temporal patterns. Early summer pinks constitute the first run during late May–June. They are followed by the late summer pinks (the end of June–July). The final fall run of pink salmon occurs through August–September.

The end of early summer and the beginning of late summer pink salmon runs are marked by the decrease-increase in CPUE at the turn of June and July, accompanied by the increase in percentage of males in catches, and also the increase in fish length and decrease in their maturity. This change occurred rapidly, in 10–15 days. In 1996–1997 the changes in CPUE and biological indices were not often visible due to the low frequency of sampling. In 1998–1999 with the higher frequency of sampling, the concurrent change in CPUE and biological indices was apparent. The CPUE decrease-increase occurred not only at the turn of June and July, but also during July. These changes in CPUE and biological indices have not been linked to the beginning and end of separate runs because the June–July changes occur sequentially from south to north, and the later changes, in July and August, were never associated with definite dates, and never accompanied by significant changes in biological indices.

The temporal separation between early summer and late summer runs in the ocean is apparent, but we still have insufficient data from July and August to clearly distinguish the fall run. However, pink salmon certainly occur in Kuril waters till early September with larger proportion of male adults in some runs compared with July. It is not clear yet whether pink salmon enter the Kuril straits from southwest or, on the contrary, from the northwest, nor how wide their migration band is.

The three seasonally spaced runs of Okhotsk Sea pink salmon differ both in abundance and ecology. The Okhotsk Sea pinks overwinter in a zone of the North Pacific Current in two stock groups (Yerokhin 1990). The northern less abundant group of pink salmon is distributed from 42° to 44°N, and spends the winter at SST 2–6°C, mean SST 4.5°C. The southern group is larger in number and distributed from 38° to 42°N. This group spends the winter at SST 4.3–9.6°C, on average 5.6–6.5°C. In spring, pinks migrate northwestward to the spawning areas by following the 2°C isotherm line (Yerokhin 1990). We observed pink salmon runs in the Kuril waters at

SST 2.2–2.8°C, while the temperature of the Okhotsk Sea off the mainland coast was 0°C. However, it is not the main body of the Okhotsk Sea pink salmon population but only early summer groups that pass through the Kuril straits in May and June at low SST. The early summer run and the groups of pink salmon described by Yerokhin (1990) may be identical. Some 1-year old pink salmon stay in the southeast Okhotsk Sea until January (Radchenko et al. 1991). However, it is uncertain yet whether this group is the same as a stock overwintering in the north. Late summer pink salmon follow the early summer run when SST rises to 5–6°C. SSTs are even higher, 10–12°C, when the fall run replaces the early summer run.

Currently there is only one stock of pink salmon in the Okhotsk Sea Basin which is abundant enough to support a commercial fishery. This stock originates from the northern Okhotsk Sea coast and migrates in July (Golovanov 1982). Therefore we believe that pink salmon from this region constitute the bulk of the early summer run migrating into the waters off the Kuril Islands in May and June. The minority of the same run originates from another traditional spawning area—the Kuril Islands (Ivankov 1967, 1997) and eastern Sakhalin. The abundant late summer stock from western Kamchatka, eastern Sakhalin and, partially, from the south of Kuril Islands makes up the July run. In August–September a relatively small fall pink salmon run arrives in this area, the majority of which migrates to spawn in rivers of southern Kuril and Hokkaido islands.

According to Takagi et al. (1981), pink salmon of northern Okhotsk Sea migrate to spawn mainly through the northern straits of Kuril Islands. According to Shuntov (1994), pink salmon of western Kamchatka and the majority of pink salmon of eastern Sakhalin migrate towards those northern straits. Our observations show that both early and late summer runs migrate towards the Kuril straits in a broad line 500 kilometers in width, and they are found outside the Kuril straits between the Freeze Strait and the First Kuril Strait. In June and July dense aggregations of pink salmon, first early, then late runs, occur not only in the vicinity of the Kuril straits north of 47°N, but also in the Freeze, Urup and Bussol straits (Fig. 3–5). The existence of pink salmon runs near these straits should be taken into account when considering pink salmon spawning migrations proposed by Takagi et al. (1981) and Shuntov (1994).

Fluctuations in timing and abundance of runs, and sampling limitations hinder conclusions about run structure. Nevertheless, the run structure we have proposed is in accordance with conclusions drawn earlier from the distribution of spawning areas, and it appears to be a reasonable picture of what is occurring in the ocean.

## CONCLUSION

Studies of pink salmon homing migration in waters off the Kuril Islands suggest that it lasts 4 months. The run timing is complex. During May–June a stock of Okhotsk Sea pink salmon, corresponding to an early summer run, migrates through Kuril waters. Pink salmon form large aggregations in July during the migration of the late summer run, which constitutes the bulk of the Okhotsk Sea pink salmon population. Abrupt changes in pink salmon CPUE and in length, sex ratios and maturity at the turn of June–July indicate the end of the early and beginning of the late summer runs. Early and late summer runs migrate to a spawning area at different SSTs. The fall run of Okhotsk Sea pink salmon appears in the Kuril basin around July–August. Low abundance of this run makes it difficult to differentiate from the previous run. On the whole, pink salmon occurring in Kuril waters may be divided into three runs: early and late summer, and fall runs. Each run continues for about one month, and is identifiable by characteristics similar to those of runs near the spawning areas: increase in CPUE during the run, decrease in proportion of males, and increase in maturity. The pink salmon runs that we have distinguished in the ocean correspond to those arriving at the spawning grounds.

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## Ocean Distribution of Columbia River Upriver Bright Fall Chinook Salmon Stocks

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Key words: Chinook salmon, migration, El Niño, ocean regime shift, Columbia River, Snake River, Endangered Species Act

**Abstract:** We used log-linear model analysis of coded-wire tag data that incorporates fishing effort to investigate the summer ocean distribution of three components of the Columbia River upriver bright fall chinook salmon (*Oncorhynchus tshawytscha*) stock—Priest Rapids hatchery, Lyon's Ferry hatchery, and Hanford Reach wild. The hatchery (Priest Rapids hatchery) and wild (Hanford Reach wild) components from the Hanford Reach region have the same ocean distribution, but have significantly different maturation rates and/or catchability coefficients. The Lyon's Ferry hatchery component did not migrate as far north as the other two components. Cohorts from all components move farther north with age. For the Priest Rapids hatchery and Hanford Reach wild releases, the percentages of the age 3–, 4–, and 5–year old cohorts residing in Alaska were 11%, 46%, and 55%, respectively. For the Lyon's Ferry hatchery releases, the percentages of the age 3–, 4–, and 5–year old cohorts residing in Alaska were 2%, 24%, and 41%, respectively. Lack of recoveries in the nearshore coastal waters of central British Columbia suggests that most of this chinook salmon stock migrates west of Vancouver Island and the Queen Charlotte Islands. Ocean distributions were fairly consistent from year to year, especially for the age 4– and 5–year old cohorts, indicating little impact from the 1982–83 El Niño event.

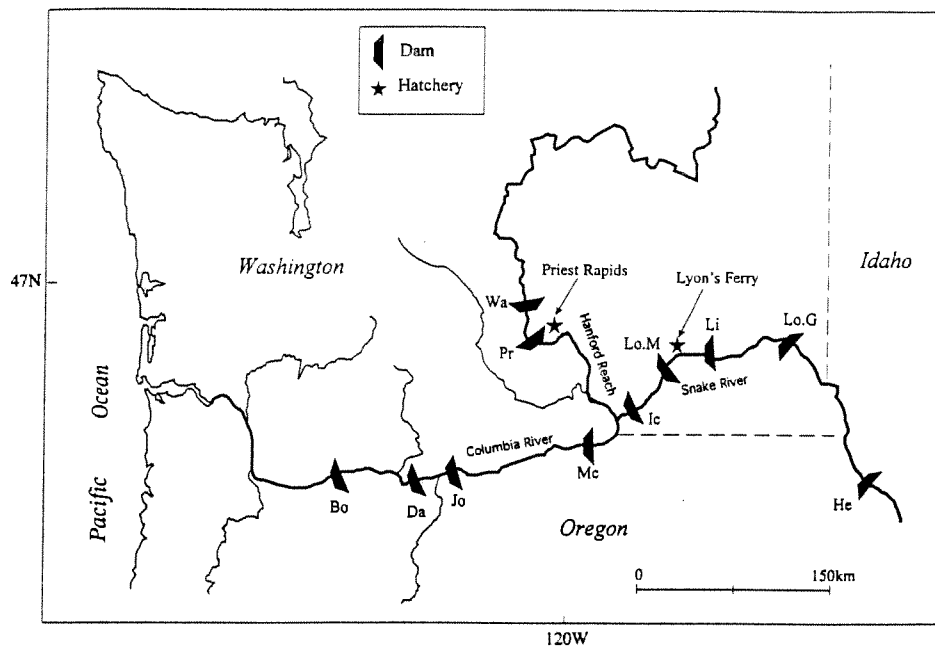
### INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) populations entering the Columbia River are categorized by return timing into spring, summer and fall segments. Typically, fall chinook are “ocean-type” (i.e., juveniles migrate downstream to the ocean during their first year of life as sub-yearlings) while spring and summer chinook are “river-type” (i.e., juveniles spend one year in freshwater before migrating downstream as yearlings). For management purposes, fall chinook that spawn above the confluence with the Snake River (river km 521) are referred to as “upriver brights” because they maintain their bright color throughout their upstream migration. Historically, the upriver bright stock spawned throughout the upper mainstem regions of the Columbia and Snake Rivers. Completion of Grand Coulee Dam in 1941 on the Columbia River and Hell's Canyon Dam in 1967 on the Snake River, both without adult fish passage facilities, greatly reduced natural upstream spawning areas. Four dams on the lower Columbia River (completed between 1938 and 1968) and four

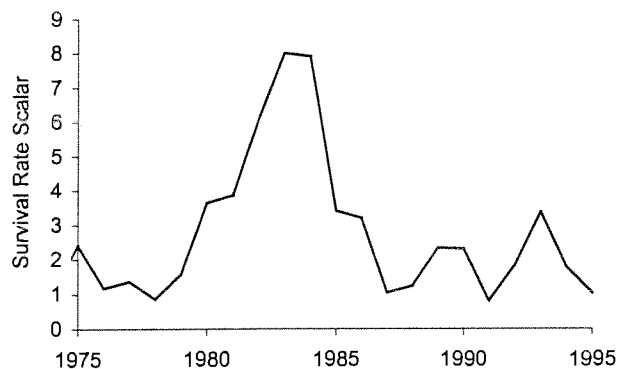
more on the lower Snake River (completed between 1961 and 1975) reduced spawning areas even further (Fig. 1).

Today, most production for the upriver bright stock comes from Priest Rapids hatchery and from naturally spawning fish in the Hanford Reach (referred to as the Hanford Reach wild component) located between Priest Rapids Dam and the confluence with the Snake River. These two components of the upriver bright stock are considered healthy (CTC 1999). The 1982–1984 brood years had exceptional smolt and juvenile survival (CTC 1996; Fig. 2) and produced the largest adult returns in over 40 years (Dauble and Watson 1990; Fig. 3). Natural production in the Snake River is now limited to the region between Lower Granite and Hell's Canyon dams. Some Snake River hatchery production comes from Lyon's Ferry hatchery located between Lower Monumental and Little Goose dams. Snake River fall chinook are severely depressed, and this component of the upriver bright stock was listed as “threatened” under the US Endangered Species Act in 1991.

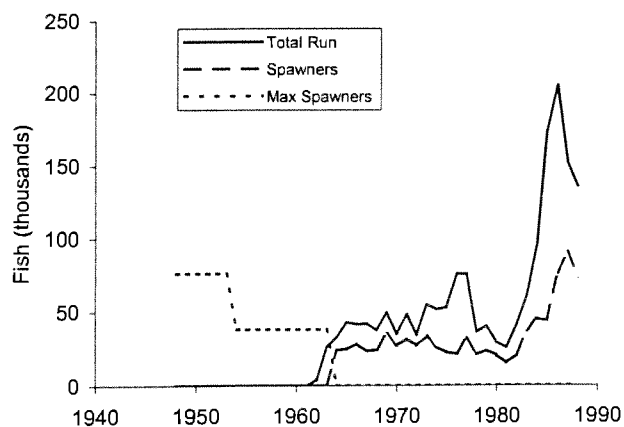
**Fig. 1.** Production areas for the Columbia River upriver bright stock. The acronyms of dam names are as follows: Bo = Bonneville, Da = The Dalles, Jo = John Day, Mc = McNary, Pr = Priest Rapids, Wa = Wanapum, Ic = Ice Harbor, Lo.M = Lower Monumental, Li = Little Goose, Lo.G = Lower Granite, and He = Hell's Canyon.



**Fig. 2.** Estimated brood year survival rate scalars (EV Scalars) for the upriver bright stock (Source: CTC 1996).



**Fig. 3.** Hanford Reach total run size and spawning estimates 1948–1988 (Source: Dauble and Watson 1990).

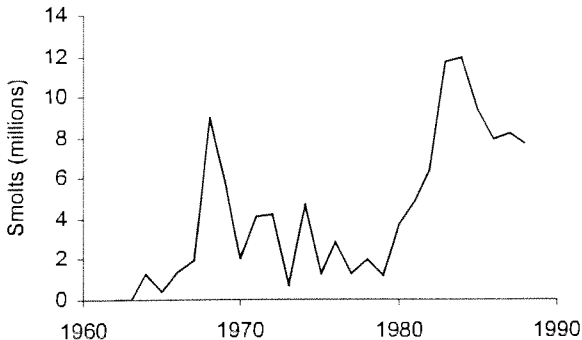


Adults from the upriver bright stock are distributed in coastal ocean waters from northern California to the Gulf of Alaska where they are harvested primarily by ocean troll fisheries in Alaska and British Columbia. Returning adults (ages two through seven) are harvested by commercial non-Indian net fisheries in the lower Columbia River below Bonneville Dam and by tribal fisheries between Bonneville and McNary dams. Although harvests are coordinated and managed by state, federal, and international agencies, these fisheries are “non-selective” in that fishermen cannot selectively harvest the various components of the upriver bright stock (Rutter 1997). Non-selective fishing gears and commingling stocks make it difficult, if not impossible, to design harvest management strategies that assign optimal exploitation rates to individual stock components. This problem becomes acute when seeking to balance the conflicting objectives of protecting weak stocks and harvesting strong stocks, all of which are exploited by a common fishery. Full knowledge of the ocean distributions of individual stock components would allow managers to identify potential windows of opportunity for selective harvesting.

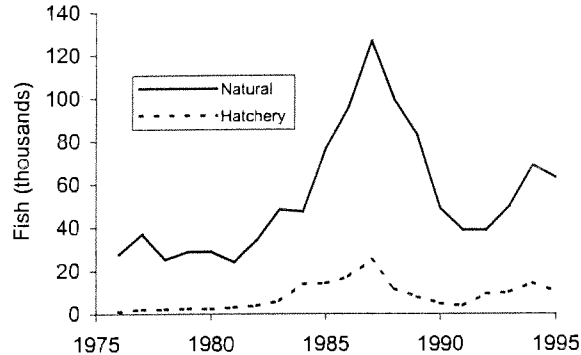
Beyond management implications, understanding the ocean distribution of the upriver bright stock may provide clues to understanding annual recruitment variability. Smolts from the strong 1982–1984 brood years entered the ocean during and just after the 1982–1983 El Niño event (Wooster and Fluharty 1985). Of interest to fishery oceanographers is the impact, if any, of this event on the upriver bright

ocean distribution and recruitment success of the 1982–1984 brood years. Although hatchery production peaked in 1983 and 1984 (Dauble and Watson 1990; Fig. 4), hatchery contribution to the total run, as indicated by hatchery escapement contributions, has averaged only 12% since 1976 (PFMC 1998; Fig. 5). Thus, increased hatchery production alone cannot explain the large returns from the 1982–1984 broods.

**Fig. 4.** Smolt production from Priest Rapids Hatchery and Ringold Facilities, 1962–1988 (Source: Dauble and Watson 1990).



**Fig. 5.** Natural and hatchery contributions to total upriver bright escapement (Source: PFMC 1994).



A growing body of evidence suggests that for many species, including salmon, broad scale natural environmental factors and decadal scale climate shifts play a significant role in juvenile survival in the ocean and subsequent recruitment variability (Ware and McFarlane 1989; Hollowed and Wooster 1992; Beamish 1993). Research to date has focused on correlating long time series of environmental variables with those of fish stock abundances (e.g., Francis and Hare 1994). Correlations have been highest for sockeye (*O. nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon, which inhabit the offshore ocean environment. For coho (*O. kisutch*) and fall chinook, which spend most of their marine life along the continental shelf, the correlations are less strong

and the mechanisms affecting recruitment variability are less well understood. Several authors have asserted that the ocean regime shift during the late 1970s created generally unfavorable conditions for chinook and coho stocks and favorable conditions for sockeye, pink, and chum stocks (Beamish and Bouillon 1993, Francis 1993, NRC US 1996). The 1982–1984 broods from the upriver bright stock appear to contradict this conclusion.

Understanding ocean environment effects on recruitment success also is critical to evaluating and designing salmon rehabilitation programs because ocean effects can mask the effects of human activities (NRC US 1996). Downstream smolt survival in the Columbia River is affected by a variety of human activities and has been studied extensively (see NRC US 1996, NMFS 1995, and 2000 for comprehensive reviews of downstream survival factors). Predicting the impacts of expensive and controversial in-river recovery actions, such as reservoir draw-downs to increase river flows, increased spill to reduce turbine mortalities, and barging smolts around dams to improve downstream survival, all have high levels of uncertainty in part because the effects of ocean conditions are poorly understood.

Despite a plethora of data on salmon fisheries, estimating ocean residence proportions has been difficult. We define the term “ocean residence proportion” to mean the proportion of an individual cohort residing in a particular ocean region at a given instant in time. Healey (1991) provides a comprehensive review of the state of knowledge on the ocean distribution of chinook salmon. General ocean distributions by species and broad geographic regions have been determined from high seas tagging programs (Godfrey 1956; Manzer et al. 1965; Godfrey et al. 1975; Hartt and Dell 1986) and from incidental salmon catches in high seas gillnet fisheries for squid (Major et al. 1978). While some ocean-type chinook from Washington and Oregon have been reported as far west as the Alaskan Peninsula (Dahlberg et al. 1986), most appear to remain along the continental shelf from Oregon to southeast Alaska (Healey 1991).

For almost three decades, the regional coded-wire-tag program has provided the most accurate data on individual stock distributions (Johnson 1990). Each year millions of microtags are placed in the snouts of outmigrating salmon smolts from throughout the Pacific northwest. Fish containing tags are marked externally with an adipose fin clip, and management agencies sample about 20% of the landed catch for marked fish. Recovery data are summarized and stored in a master database (Regional Mark Information System; [www.rmis.org](http://www.rmis.org)) maintained by the Pacific States Marine Fisheries Commission, Portland, Oregon. The coded-wire-tag releases are mostly from hatchery stocks and are commonly used as sur-

rogates for nearby wild stocks. Researchers tacitly assume that the hatchery and wild components have the same ocean distribution and behavior.

The Priest Rapids hatchery, Lyon's Ferry hatchery, and Hanford Reach wild components of the upriver bright stock have continuous time series of coded-wire-tag data dating back to the 1975, 1984, and 1986 brood years, respectively. These time series offer an opportunity to investigate three questions regarding the ocean distribution of the upriver bright stock: (1) Did the 1982–1983 El Niño event affect the ocean distribution of adults from the Priest Rapids hatchery stock? (2) Do the Priest Rapids hatchery and Hanford Reach wild components from the Hanford Reach area have the same ocean distribution? and (3) Do the adults from the Priest Rapids hatchery and Lyon's Ferry hatchery have the same ocean distribution? The primary goal of this paper is to investigate these three questions. We use a modified version of the coded-wire-tag analysis techniques described in Cormack and Skalski (1992) that incorporates fishing effort into the analysis. We also estimate ocean residence proportions for each stock and investigate how including fishing effort influenced the analysis.

## MATERIALS AND METHODS

### Mathematical Model

The number of coded-wire-tag recoveries in a given region and time period depends on several factors, including local abundance and the amount of fishing and sampling effort. For example, observing twice the number of recoveries may be due to twice the number of marked fish available, twice the fishing effort, or twice the sampling effort. Most analyses of coded-wire-tag data to determine ocean residence proportions simply report the relative distribution of expanded coded-wire-tag recoveries (i.e., number of recoveries divided by the sampling fraction), without correcting for differences in fishing effort between regions (e.g., Healey and Groot 1987). Since relative fishing effort between regions and years has changed significantly over the past two decades, we use a modified version of the Cormack and Skalski (1992) model that incorporates fishing effort:

$$E(n_{i,j}) = R_i \cdot \Theta_{i,j} \cdot f_j \cdot F_j \quad (1)$$

where  $E(n_{i,j})$  is the expected number of fish from release code  $i$  found in the inspected sample from catch  $j$ ,  $R_i$  is the number of tagged fish released with code  $i$ ,  $\Theta_{i,j}$  is the probability that a fish from release code  $i$  is caught in catch  $j$ ,  $f_j$  is the fraction of catch  $j$  examined for tags, and  $F_j$  is the total number of fishing effort units used to capture catch  $j$ . We assumed a scaled Poisson error distribution (i.e.,  $\text{Var}(n_{i,j}) = \phi\mu_{i,j}$ ,

where  $\phi$  is a constant of proportionality between the mean and variance) and fit the model in a log-linear form using standard statistical packages (GLIM; SPlus; GLMStat) and including cells containing zero recoveries:

$$\ln(n_{i,j}) = \ln(R_i f_j F_j) + \ln(\Theta_{i,j}) \quad (2)$$

In the form of Equation (2) there are no weighting factors and the offset terms are the  $\ln(R_i f_j F_j)$  terms. For hypothesis testing and model selection, the  $\ln(\Theta_{i,j})$  can be partitioned into an additive factorial model representing different treatment effects (e.g., stock A vs stock B, hatchery vs wild, recovery area, brood year, recovery age).

We tested for the effects of fishing effort by including fishing effort as an independent continuous variable:

$$\ln(n_{i,j}) = \ln(R_i f_j) + \ln(F_j) + \ln(\Theta_{i,j}) \quad (3)$$

Again there are no weighting factors, but now the offset terms are the  $\ln(R_i f_j)$ .

To investigate the three questions posed in the introduction, we used a stepwise forward selection procedure to build four models: (1) using only recoveries from the Priest Rapids hatchery releases in 1978–1990; (2) using recoveries from Priest Rapids hatchery and Hanford Reach wild releases in 1986–1990; (3) using recoveries from Priest Rapids hatchery and Lyon's Ferry hatchery releases in 1984–1990; and (4) using recoveries from the Lyon's Ferry hatchery releases in 1984–1990. At each step we used deviance, Pearson  $\chi^2$ , Akaike Information Criteria, and QQ plots as our criteria for including factors in the model. We did not use recoveries from releases after 1990 because fishing effort data beyond 1995 were still preliminary for some regions.

Intuitively, the ocean residence proportions for a cohort at a given age can be estimated from the relative proportions of the observed recoveries in the appropriate year once they are adjusted for regional differences in sampling fractions and fishing efforts. Release size (i.e., the number of tagged fish released) does not affect residence proportion estimates. To estimate ocean residence proportions, we re-index the variables for clarity:

$$E(n_{by,a,r}) = R_{by} \cdot \Theta_{by,a,r} \cdot f_{ry,r} \cdot F_{ry,r} \quad (4)$$

where  $by$  = brood year (note that the year in which smolts enter the ocean is  $by + 1$ ),  $a$  = recovery age,  $r$  = recovery region and  $ry$  = recovery year ( $ry = by + a$ ). We separate the  $\Theta_{i,j}$  into two components as follows:

$$\Theta_{by,a,r} = ORI_{by,a} \cdot L_{ry,a,r} \quad (5)$$

where  $ORI_{by,a}$  (Ocean Recovery Index) is the probability that a tagged fish from brood year  $by$  survives to age  $a$ , does not mature and leave the ocean prior to age  $a$ , and is caught by one unit of fishing effort, and  $L_{ry,a,r}$  is the fraction of the tagged fish released in brood year  $by$  surviving to age  $a$ , not maturing prior to age  $a$ , and are located in region  $r$  at age  $a$ . This characterization assumes that the  $ORI_{by,a}$  and  $L_{ry,a,r}$  are independent (i.e., surviving to age  $a$  and maturing prior to age  $a$  are independent of being located in region  $r$ ). The  $ORI_{by,a}$  also can be thought of as survival/maturation/catchability indices, since they represent all three of these factors.

We call the  $L_{ry,a,r}$  the summer ocean residence proportions and note that when summed over regions they must sum to one:

$$\sum_r L_{ry,a,r} = 1 \quad (6)$$

If the recoveries are separated by age, substituting Equation (5) into Equation (4) and rearranging terms gives a year, age, and region specific recovery rate index ( $I_{by,a,r}$ )

$$\frac{E(n_{by,a,r})}{R_{by} \cdot f_{ry,r} \cdot F_{ry,r}} = ORI_{by,a} \cdot L_{ry,a,r} = I_{by,a,r} \quad (7)$$

Note that the  $I_{by,a,r}$  are simply the expected catch-per-unit-effort of expanded recoveries standardized by release size:

$$I_{by,a,r} = \frac{e_{by,a,r} / F_{ry,r}}{R_{by}} \quad (8)$$

where  $e_{by,a,r}$  are the expanded recoveries ( $n_{by,a,r} f_{ry,r}$ ).

For each year and age, summing the  $I_{by,a,r}$  over all regions ( $r$ ) gives the relative ocean recovery index:

$$\sum_r I_{by,a,r} = ORI_{by,a} \cdot \sum_r L_{ry,a,r} = ORI_{by,a} \quad (9)$$

Note that if catchability (i.e., the probability of a fish of age  $a$  being captured by one unit of fishing effort) is assumed constant over all regions and years and the maturation rates prior to age  $a$  are assumed constant over all years,  $ORI_{by,a}$  is an index of relative survival to age  $a$ .

Substituting Equation (9) into Equation (7) and rearranging terms gives an estimate of the summer ocean residence proportions:

$$\hat{L}_{by,a,r} = \frac{I_{by,a,r}}{\sum_r I_{by,a,r}} \quad (10)$$

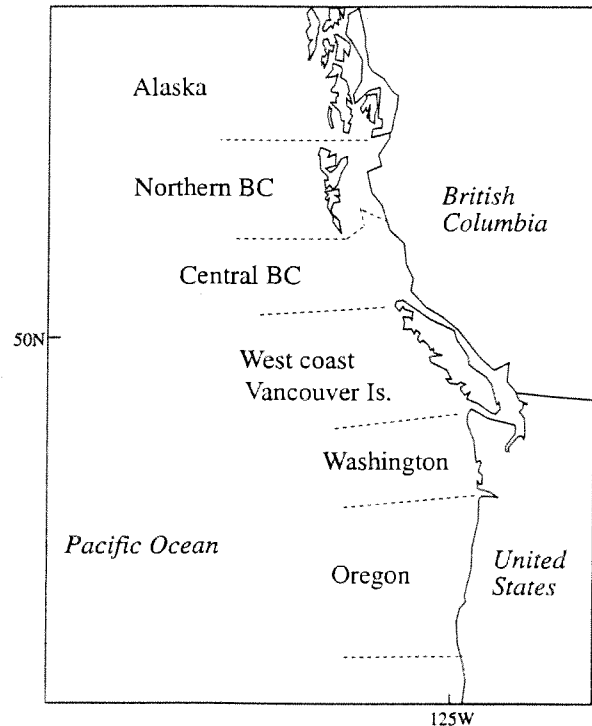
Note that for each brood year and age this estimator is simply the fraction of the coded-wire-tag recoveries in each area, adjusted for sampling fraction and fishing effort. The release size  $R_{by}$  has no effect because it cancels in both the numerator and denominator.

We computed observed ocean residence proportions for each year and age by summarizing recoveries by brood year, age, and region and using Equation (10). To estimate the ocean residence proportions, we used the selected model from the general linear model analysis to predict recoveries from standardized fishing efforts and sampling fractions and substituted the predicted values into Equation (10).

### Geographic Regions

We defined six geographic regions to describe the ocean distribution of the upriver bright stock (Fig. 6): (1) Alaska (Alaska statistical regions 101–115, 116, 152, 154, 157, 181, 189); (2) northern British Columbia (Canadian statistical areas 1–5); (3) central British Columbia (Canadian statistical areas 6–12, 30); (4) west Vancouver Island (Canadian statistical areas 21, 22–27); (5) Washington coast (including Washington statistical area 4B located at the west entrance to the Strait of Juan de Fuca to account for the tribal fishery); and (6) Oregon coast (including the region south of Cape Falcon). Regions were selected such that they provided sufficient coded-wire-tag data for statistical analysis and adequate resolution for biological interest. Recoveries from Strait of Juan de Fuca, Georgia Strait, and California troll fisheries were excluded due to the low number of recoveries from those areas.

Fig. 6. Geographic regions used to delineate summer ocean residence proportions for the Columbia River upriver bright stock.



### Coded-Wire-Tag Data

We extracted release and recovery records from the Pacific States Marine Fisheries Commission coded-wire-tag database for tag codes used by the Pacific Salmon Commission Chinook Technical Committee (CTC) to estimate ocean exploitation rates for the Priest Rapids hatchery, Hanford Reach wild, and Lyon's Ferry hatchery components of the upriver bright stock (CTC 1999, Appendix Table C-2). Table 1 and Fig. 7 summarize the release data.

For each year we limited recovery records to the summer period (15 April–30 September) and to those made by commercial ocean troll gear (fishery codes 10–19). Washington recoveries included both Treaty and non-Treaty fisheries. Oregon recoveries included those from both north and south of Cape Falcon. Records that had expanded recoveries  $\leq 1$  were eliminated to remove data for which sampling fractions were unknown or unreliable. Recovery site fields were used to assign area codes corresponding to geographic regions.

### Fishing Effort Data

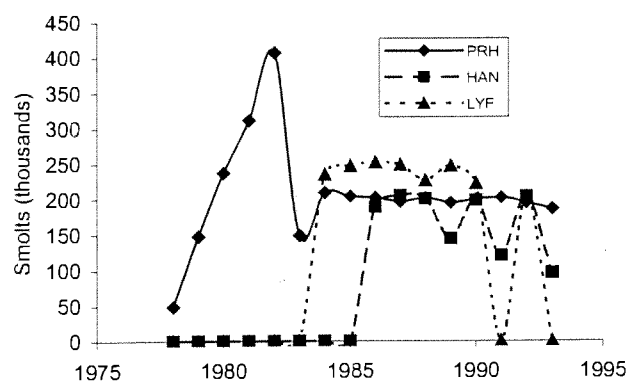
One unit of fishing effort was defined to be one vessel-day of commercial troll fishing during which it was legal to retain chinook salmon. Effort data were obtained from various state and Canadian agencies. We restricted effort data to the summer period (15 April through 30 September) during periods when chinook salmon were legal to retain (Table 2; Fig. 8). Washington and Oregon fisheries did not include any chinook non-retention periods and Alaska provided data for both chinook retention and non-retention fisheries. Canadian data consisted of total effort (i.e., chinook retention and non-retention) by region and chinook retention season dates. For Canadian data, we apportioned the total effort for each region to the chinook fishery in direct proportion with the open season data. For example, if it was legal to retain chinook for only 25% of the total troll season, then 25% of the total troll effort was apportioned to chinook effort. No Canadian effort data were available for 1981 and 1982. To estimate effort in these two

**Table 1.** Coded-wire-tag release data for the Columbia River upriver bright stock used in this analysis. All releases were subyearlings released in the year following the brood year.

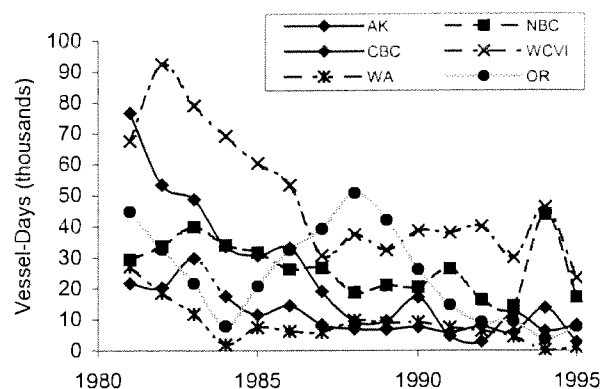
| Brood Year | Priest Rapids Hatchery |                 | Hanford Reach Wild |                 | Lyon's Ferry Hatchery |                 |
|------------|------------------------|-----------------|--------------------|-----------------|-----------------------|-----------------|
|            | Tag Code               | Number Released | Tag Code           | Number Released | Tag Code              | Number Released |
| 1978       | 631821                 | 48,130          |                    |                 |                       |                 |
| 1979       | 631948                 | 147,145         |                    |                 |                       |                 |
| 1980       | 632155                 | 194,649         |                    |                 |                       |                 |
|            | 632261                 | 42,089          |                    |                 |                       |                 |
| 1981       | 632252                 | 262,176         |                    |                 |                       |                 |
|            | 632456                 | 48,700          |                    |                 |                       |                 |
| 1982       | 632611                 | 204,141         |                    |                 |                       |                 |
|            | 632612                 | 202,388         |                    |                 |                       |                 |
| 1983       | 632859                 | 74,392          |                    |                 |                       |                 |
|            | 632860                 | 74,170          |                    |                 |                       |                 |
| 1984       | 633221                 | 103,665         |                    |                 | 633226                | 78,417          |
|            | 633222                 | 105,224         |                    |                 | 633227                | 78,064          |
| 1985       |                        |                 |                    |                 | 633228                | 78,504          |
|            |                        |                 |                    |                 | 633638                | 49,325          |
|            |                        |                 |                    |                 | 633639                | 49,325          |
|            |                        |                 |                    |                 | 633640                | 49,325          |
|            |                        |                 |                    |                 | 633641                | 49,325          |
|            |                        |                 |                    |                 | 633642                | 49,325          |
| 1986       | 634128                 | 201,779         | 634152             | 188,916         | 634259                | 126,076         |
| 1987       |                        |                 |                    |                 | 634261                | 125,570         |
|            | 635226                 | 196,221         | 635232             | 205,103         | 635214                | 124,345         |
| 1988       |                        |                 |                    |                 | 635216                | 124,394         |
|            | 635249                 | 201,608         | 635252             | 200,630         | 630226                | 113,193         |
| 1989       |                        |                 |                    |                 | 630228                | 113,285         |
|            | 630732                 | 194,530         | 630755             | 144,164         | 635544                | 123,640         |
| 1990       |                        |                 |                    |                 | 635547                | 123,233         |
|            | 634057                 | 199,469         | 634115             | 198,056         | 634143                | 111,784         |
| 1991       |                        |                 |                    |                 | 634160                | 110,748         |
|            | 634341                 | 201,647         | 634527             | 120,507         |                       |                 |
| 1992       | 635010                 | 194,622         | 635017             | 203,591         | 635012                | 203,177         |
| 1993       | 635540                 | 185,683         | 635704             | 95,897          |                       |                 |



**Fig. 7.** Coded wire tag releases from three components of the Columbia River upriver bright stock: Priest Rapids Hatchery, Hanford Reach Wild, and Lyon's Ferry Hatchery.



**Fig. 8.** Commercial ocean troll fishing effort (vessel-days) during the summer period (15 April to 30 September) by region and year. For identification of region abbreviations, see Fig. 6.



**Table 2.** Summary of summer (15 April to 30 September) commercial ocean troll chinook salmon effort data (vessel-days) by area used to analyze summer ocean residence proportions for the Columbia River upriver bright stock.

| Year | Alaska | Northern BC | Central BC | West Vancouver Island | Washington | Oregon | Total   |
|------|--------|-------------|------------|-----------------------|------------|--------|---------|
| 1981 | 76,691 | 29,344      | 21,629     | 67,622                | 27,100     | 44,868 | 267,254 |
| 1982 | 53,371 | 33,679      | 20,288     | 92,395                | 18,600     | 32,603 | 250,936 |
| 1983 | 48,734 | 39,886      | 29,729     | 78,999                | 11,800     | 21,541 | 230,689 |
| 1984 | 33,641 | 34,075      | 17,625     | 69,251                | 1,900      | 7,832  | 164,324 |
| 1985 | 30,628 | 31,720      | 11,537     | 60,306                | 7,500      | 20,738 | 162,429 |
| 1986 | 33,079 | 26,298      | 14,475     | 53,315                | 6,198      | 32,487 | 165,852 |
| 1987 | 19,077 | 26,636      | 8,386      | 30,677                | 5,888      | 39,308 | 129,972 |
| 1988 | 9,507  | 18,845      | 6,944      | 37,441                | 9,788      | 50,762 | 133,287 |
| 1989 | 9,585  | 21,078      | 6,792      | 32,449                | 8,945      | 42,123 | 120,972 |
| 1990 | 17,172 | 20,540      | 7,542      | 38,638                | 9,218      | 26,188 | 119,298 |
| 1991 | 4,718  | 26,484      | 5,879      | 38,003                | 7,489      | 14,868 | 97,441  |
| 1992 | 2,881  | 16,501      | 7,827      | 40,077                | 6,323      | 9,173  | 82,782  |
| 1993 | 12,036 | 14,536      | 5,799      | 30,119                | 4,546      | 9,487  | 76,523  |
| 1994 | 6,434  | 44,027      | 13,941     | 46,360                | 225        | 3,781  | 114,768 |
| 1995 | 8,420  | 17,362      | 2,778      | 23,669                | 1,146      | 7,872  | 61,247  |

years, we assumed that CPUEs were similar to those in 1983–1985. Thus, for each Canadian region we divided the 1981 and 1982 chinook catches by the average 1983–1985 chinook CPUEs to estimate the 1981 and 1982 chinook efforts.

### Sampling Fractions

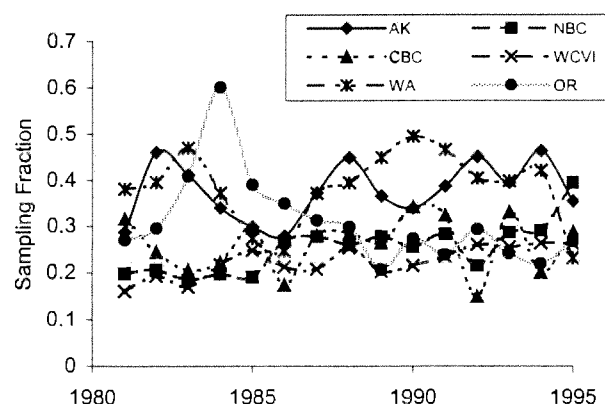
The Regional Mark Information System contains landed catch and sampled catch data by sample period and sample region. At our request, Pacific States Marine Fisheries Commission staff provided us with these data aggregated by year and our six geographic regions. From these data we computed annual sampling fractions by sample division (Table 3; Fig. 9).

### RESULTS

The log-linear model analysis for Priest Rapids hatchery recoveries from brood years 1978 to 1990 indicated that region effects were most significant,

followed by year and age effects (Table 4). The final selected model (model 1 in Table 4) also included the Region·Age and Year·Age interaction terms, but not the Region·Year interaction term, which was rejected

**Fig. 9.** Fractions of the landed catch sampled for coded-wire-tags by region and year.



**Table 3.** Sampling fractions by area and year determined from data provided by the Pacific States Marine Fisheries Commission.

| Year | Alaska | Northern BC | Central BC | West Vancouver Island | Washington | Oregon |
|------|--------|-------------|------------|-----------------------|------------|--------|
| 1981 | 0.2876 | 0.1983      | 0.3167     | 0.1610                | 0.3812     | 0.2705 |
| 1982 | 0.4605 | 0.2056      | 0.2449     | 0.1931                | 0.3955     | 0.2959 |
| 1983 | 0.4116 | 0.1848      | 0.2058     | 0.1701                | 0.4691     | 0.4091 |
| 1984 | 0.3402 | 0.1978      | 0.2227     | 0.2170                | 0.3721     | 0.6011 |
| 1985 | 0.2988 | 0.1903      | 0.2957     | 0.2476                | 0.2735     | 0.3899 |
| 1986 | 0.2785 | 0.2672      | 0.1743     | 0.2119                | 0.2463     | 0.3491 |
| 1987 | 0.3725 | 0.2779      | 0.2809     | 0.2074                | 0.3714     | 0.3127 |
| 1988 | 0.4480 | 0.2597      | 0.2852     | 0.2531                | 0.3944     | 0.2981 |
| 1989 | 0.3653 | 0.2782      | 0.2639     | 0.2023                | 0.4481     | 0.2065 |
| 1990 | 0.3395 | 0.2560      | 0.3423     | 0.2147                | 0.4943     | 0.2734 |
| 1991 | 0.3868 | 0.2825      | 0.3235     | 0.2340                | 0.4652     | 0.2386 |
| 1992 | 0.4495 | 0.2151      | 0.1492     | 0.2600                | 0.4044     | 0.2932 |
| 1993 | 0.3941 | 0.2868      | 0.3314     | 0.2552                | 0.3981     | 0.2412 |
| 1994 | 0.4624 | 0.2914      | 0.2008     | 0.2632                | 0.4208     | 0.2191 |
| 1995 | 0.3545 | 0.3942      | 0.2881     | 0.2629                | 0.2311     | 0.2665 |

**Table 4.** Results of log-linear model analysis for Priest Rapids Hatchery (PRH) releases from 1978 to 1990 (R = region effects; A = age effects; Y = brood year effects; main = Constant + R + A + Y; Dev = deviance; AIC = Akaike Information Constant).

| Main model plus                | Dev | Pearson $\chi^2$ | df  | Scale | Scaled $\Delta$ Dev | $\Delta$ df | p-value | AIC |
|--------------------------------|-----|------------------|-----|-------|---------------------|-------------|---------|-----|
| 1. R.A + Y.A                   | 251 | 299              | 180 | 1.66  | 45                  | 24          | 0.006   | 430 |
| 2. A.T + Y.T                   | 185 | 222              | 161 | 1.38  | 22                  | 4           | 0.000   | 237 |
| 3. R.A + R.S + Y.S + Y.A + S.A | 228 | 271              | 202 | 1.34  | 20                  | 2           | 0.000   | 362 |
| 4. A.R                         | 134 | 156              | 102 | 1.53  | 56                  | 10          | 0.000   | 208 |

based on its poor QQ plot. When fishing effort was treated as an independent variable (Equation 3), it was significant, but not as significant as the other main effects.

When recoveries from both the Priest Rapids hatchery and Hanford Reach wild components were analyzed in the same model (for brood years 1986–1990), region effects were again most significant followed by age and year effects (model 2 in Table 4). Adding the “Type” effect (i.e., hatchery for Priest Rapids hatchery or wild for Hanford Reach wild) to the model did not reduce the deviance. The final selected model (model 2 in Table 4) included the Age·Type and Year·Type interaction terms.

The results from comparing the two hatchery components (Priest Rapids hatchery and Lyon’s Ferry) indicated that year was the most significant effect, followed by region, age, and stock. The final selected model (model 3 in Table 4) included the following interaction terms: Region·Age, Region·Stock, Year·Stock, Year·Age, and Stock·Age.

For the Lyon’s Ferry hatchery releases, the most significant effect was year, followed by age and region. The final selected model (model 4 in Table 4) also included the Age·Region interaction term. The Year·Age interaction term was rejected based on its poor QQ plot.

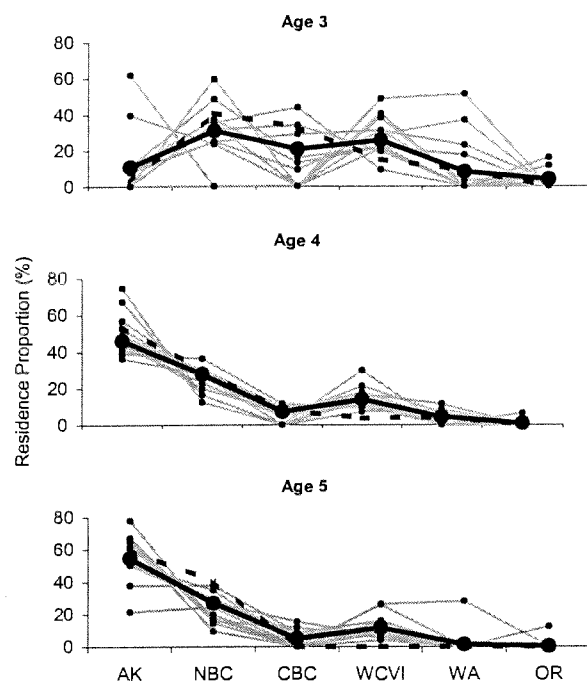
The results from model 2 in Table 4 indicate that the Priest Rapids hatchery and Hanford Reach wild releases had the same summer ocean distributions (i.e., the “Type” factor was not significant). Also, the

fact that the Region·Year interaction term was not included in selected models 1 and 2 in Table 4 suggests that these two stock components had the same general distribution each year. Table 5 shows the predicted summer ocean residence proportions for ages 3, 4, and 5 for these two upriver bright components based on the model 1 from Table 4. These proportions were fairly constant between years, although the age five recoveries in 1983 from the 1978 brood year showed the most northerly distribution (Fig. 10). Cohorts move further north as they get older. The percentages of the age 3–, 4–, and 5–year old cohorts residing in Alaska were 11%, 46%, and 55%, respectively. For all ages, fewer fish were located in the central BC region than in the regions immediately to the north (northern BC) and south (west Vancouver Island). The differences were most pronounced for ages four and five.

For the Lyon’s Ferry hatchery component, the predicted summer ocean residence proportions for ages 3, 4, and 5 based on the model 4 from Table 4 also are given in Table 6. Again, these cohorts move further north as they get older, but not as far north as for the Priest Rapids hatchery and Hanford Reach wild components. The percentages of the age 3–, 4–, and 5–year old cohorts residing in Alaska were 2%, 24%, and 41%, respectively. For all ages, fewer fish were located in the central BC region than in the regions immediately to the north (northern BC) and south (west Vancouver Island) and the differences were most pronounced for ages four and five.

**Table 5.** Estimated summer ocean residence proportions for releases from Priest Rapids hatchery and the Hanford Reach wild component based on Model 1 in Table 4 and from Lyon's Ferry Hatchery based on Model 4 in Table 4.

| Age                                                  | Alaska | Northern BC | Central BC | West Vancouver Island | Washington | Oregon |
|------------------------------------------------------|--------|-------------|------------|-----------------------|------------|--------|
| <i>Priest Rapids hatchery and Hanford Reach wild</i> |        |             |            |                       |            |        |
| 3                                                    | 0.1082 | 0.3097      | 0.2074     | 0.2560                | 0.0806     | 0.0381 |
| 4                                                    | 0.4597 | 0.2771      | 0.0715     | 0.1390                | 0.0441     | 0.0086 |
| 5                                                    | 0.5471 | 0.2691      | 0.0488     | 0.1178                | 0.0143     | 0.0028 |
| <i>Lyon's Ferry hatchery</i>                         |        |             |            |                       |            |        |
| 3                                                    | 0.0172 | 0.0583      | 0.1939     | 0.3046                | 0.2493     | 0.1767 |
| 4                                                    | 0.2367 | 0.1457      | 0.0410     | 0.2663                | 0.2645     | 0.0457 |
| 5                                                    | 0.4055 | 0.2484      | 0.1027     | 0.2433                | 0.0001     | 0.0000 |

**Fig. 10.** Observed and predicted ocean residence proportions by age for Priest Rapids Hatchery and Hanford Reach Wild components of the Columbia River upriver bright stock.

Although the Priest Rapids hatchery and Hanford Reach wild stocks appear to have the same summer ocean distribution, the significant Age-Type term in model 3 of Table 4 suggests that hatchery and wild fish have different recovery patterns by age. Table 6 indicates that for releases from Priest Rapids hatchery, more age four fish were recovered than age five fish (70% vs 30%). Whereas, for the Hanford Reach wild releases, more age five fish were recovered than age four fish (44% vs 56%).

## DISCUSSION

By including fishing effort in the analysis, we tacitly assume that the effect of one vessel-day of effort is equivalent in all regions. Admittedly, this is probably not true. However, the alternative of excluding fishing effort makes the even more unreasonable assumption that the effects of fishing effort are constant over all years and regions. Given the magnitude of the differences in fishing effort by year and region (Table 2; Fig. 8), it seems most appropriate to include fishing effort in the analysis. Our results indicate that although fishing effort was not as significant as other factors, it was a significant variable and excluding it would have led to a different model selection for the Priest Rapids hatchery stock. Thus, we encourage other researchers to include fishing effort in analyses of coded-wire-tag data. We have included the data used (Table 2) for this purpose.

**Table 6.** Summary of age four and five unexpanded recoveries from the Priest Rapids hatchery and Hanford Reach wild components by brood year.

| Brood Year | Priest Rapids Hatchery |                  | Hanford Reach Wild |                  |
|------------|------------------------|------------------|--------------------|------------------|
|            | Age 4 Recoveries       | Age 5 Recoveries | Age 4 Recoveries   | Age 5 Recoveries |
| 1986       | 33                     | 9                | 28                 | 35               |
| 1987       | 3                      | 2                | 6                  | 15               |
| 1988       | 11                     | 9                | 7                  | 7                |
| 1989       | 37                     | 15               | 18                 | 23               |
| 1990       | 51                     | 26               | 29                 | 31               |
| 1991       | 2                      | 1                | 0                  | 2                |
| 1992       | 8                      | 7                | 19                 | 28               |
| 1993       | 52                     | 17               | 16                 | 14               |
| Total      | 197                    | 86               | 123                | 155              |
|            | (70%)                  | (30%)            | (44%)              | (56%)            |

Our results suggest that the ocean distribution of the upriver bright stock is relatively constant from year to year, at least during the 1980s. There is some indication (Fig. 9) that the warm water off the west coast of Vancouver Island during the 1982–3 El Niño pushed the distribution of age five fish into northern British Columbia and Alaska. However, there were only five recoveries (four in Alaska and one in northern British Columbia), so the sample size was too small to make this result statistically significant. Since adult chinook salmon tend to live well below the surface, they may be less susceptible to changes in sea surface temperatures than other salmon species. However, Tabata (1985) reported that between November 1982 and March 1983 there was a widespread subsurface warming from nearshore to approximately 200 km from the BC coast. Thus, it is possible that El Niño-induced subsurface warming may affect the ocean distribution of chinook salmon.

The general lack of age four and age five recoveries in the central BC area relative to recoveries in the northern BC and west Vancouver Island regions suggests that the majority of each cohort migrates to the west of Vancouver Island and the Queen Charlotte Islands. Most of the fishing effort and recoveries in the central BC area are located in the nearshore areas of Queen Charlotte Sound.

Our results shown in Table 6 indicate that the Priest Rapids hatchery and Hanford Reach wild stocks have the same ocean distribution, but not the same maturation rate and/or catchability. It is possible to simulate the results shown in Table 6 by either assigning both stocks the same catchability and different maturation rates or by assigning both stocks the same maturation rates and different catchabilities. Both factors likely contribute, since both are related to size, and hatchery and wild fish from the same brood year may have different growth rates.

Our finding that the Priest Rapids hatchery and Lyon's Ferry hatchery stocks have different ocean distribution patterns (Lyon's Ferry hatchery cohorts do not migrate as far north as Priest Rapids hatchery cohorts) indicates that some selective harvesting is possible. The fact that the strong Priest Rapids hatchery and Hanford Reach wild components migrate farther north than the weak Lyon's Ferry hatchery component implies that harvesting Columbia River fall chinook in Alaska may offer the greatest total yield while protecting the weaker Snake River stock.

## CONCLUSIONS

Our major conclusions are the following:

- The Priest Rapids hatchery and Hanford Reach wild components from the Hanford Reach re-

gion have the same ocean distribution, but have significantly different maturation rates and/or catchability coefficients;

- The Snake River hatchery (Lyon's Ferry hatchery) component did not migrate as far north as the other two components;
- Harvesting Columbia River fall chinook in Alaska may offer the greatest total yield while protecting the weak Snake River stock;
- Cohorts from all components move farther north with age. For the Priest Rapids hatchery and Hanford Reach wild releases, the percentages of the age 3–, 4–, and 5–year old cohorts residing in Alaska were 11%, 46%, and 55%, respectively. For the Lyon's Ferry hatchery releases, the percentages of the age 3–, 4–, and 5–year old cohorts residing in Alaska were 2%, 24%, and 41%, respectively;
- Lack of recoveries in the nearshore coastal waters of central BC suggests that most of the upriver bright stock migrates west of Vancouver Island and the Queen Charlotte Islands;
- Ocean distributions were fairly consistent from year to year, especially for the age 4– and 5–year old cohorts, indicating little impact from the 1982–83 El Niño event.

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## Ocean Growth of Sockeye Salmon from the Kvichak River, Bristol Bay Based on Scale Analysis

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**Keywords:** Bristol Bay, sockeye, salmon, scales, growth

**Abstract:** Growth measurements were taken from 9,414 legible scales of Kvichak sockeye salmon (*Oncorhynchus nerka*), yielding a long time series (1914–1997) of ocean growth data. Scale growth rates in the first, second, and third ocean years all declined prior to the late 1950s and early 1960s after which they began to steadily increase until 1970 when the three growth patterns diverged: first year growth continued to increase, but at a lower rate, second year growth showed no further increase, and third year growth began to steadily decrease. Scale growth of sockeye salmon with the same ocean history (but different broods) was highly correlated, illustrating the importance of the environment in affecting growth rates of sockeye salmon, not only in the early marine environment but later in their life history when the sockeye are more dispersed. The importance of sea surface temperature (SST), particularly during the growing season, was noted in many of the regression models. SST had its greatest influence (positive) on scale growth in the first ocean year where sockeye are migrating out of Bristol Bay and into the Aleutian Islands region.

### INTRODUCTION

The past three decades have been characterized by substantial changes in fish populations and climate. One of these changes—decreases in the size of Pacific salmon (*Oncorhynchus* spp.) starting from the 1970s—has raised concerns about the capacity of the northern Pacific Ocean to sustain levels of salmon biomass incurred by concurrent increases in salmon population abundances (Bigler et al. 1996). In particular, despite a two-fold increase in zooplankton production in recent years, the average size in almost all Pacific salmon populations has decreased (Brodeur and Ware 1992, 1995; Rogers 1994), suggesting the possibility of density dependence of salmon in the ocean environment.

Linkages between fish growth and climatic changes may be direct and indirect: for example, changes in atmospheric circulation patterns may affect zooplankton production through changes in the mixed-layer depth and temperatures (Polovina et al. 1995), or they may influence the physiology of fish directly (Evans 1993; Davis et al. 1998). The linkages may also occur through other species, which serve as competitors to sockeye salmon (*O. nerka*). Pink (*O. gorbuscha*), and chum (*O. keta*) salmon are two of these competitors whose abundances have

increased markedly in the past two decades and whose habitat and geographic distribution overlap those of sockeye salmon (Myers et al. 1996). Pink, chum, and sockeye diets not only include the same food items but can also contain similar proportions of the same food (Davis et al. 1998); thus the diminishing size of salmon in the region may be related to increased density of one or more of these salmon species on the feeding grounds.

Scales are easily measurable structures that are useful for reconstructing size and growth patterns of fish. A relationship between the scale radius and body length has been demonstrated in a number of previous studies of salmon (Stone 1976; Bumgarner 1993). Although salmon have been intensively studied and harvested throughout this century and beyond, long-term scale collections are available for few populations. One such population is the Kvichak River, which is also one of the largest sockeye salmon producers in the world (Stone 1976; Eggers and Rogers 1987), and has been exploited since 1884 (Rich and Ball 1928). Scales have been collected since the start of the commercial fishery in the Kvichak River (Mathisen and Poe 1981) and, with the exception of several years, are available from 1914 to the present.

This paper describes the long-term growth history of Kvichak River sockeye salmon based on scale measurements collected since 1914. Effects of age-class, ocean annulus, and year of growth are examined graphically and statistically to determine significant patterns/effects in growth. Scale growth is compared among three time periods: two periods of high abundance 1920–1950, and 1976–1995, and one period of low abundance 1951–1975. Environmental and sockeye population abundance data are also examined to identify possible factors explaining growth patterns observed in the data.

## MATERIALS AND METHODS

### The Kvichak River Sockeye Salmon Stock

The Kvichak is the only major sockeye salmon system in Bristol Bay that has a pronounced cyclic variation in yearly return (Burgner et al. 1969). In peak cycle years, Kvichak sockeye salmon often dominate the overall Bristol Bay run of sockeye salmon, constituting up to 79% of the total run (Stone 1976). Since the early 1980s, about 46% of the Bristol Bay sockeye salmon catch has consisted of Kvichak River fish. Peak spawning typically falls between August 20 and September 5, but varies among age-classes (Blair et al. 1993). Over 98% of males and 99.8% of females consist of four principal age-classes: 1.2, 2.2, 1.3, and 2.3.

### Rearing Grounds

The Kvichak River (90 km long) connects Bristol Bay with the Iliamna/Clark Lakes system (Fig. 1). Iliamna Lake is the largest freshwater basin in Alaska (Burgner et al. 1969), covering 2,622 km<sup>2</sup> of surface area. The Kvichak lake systems provide

extensive spawning habitat for mature sockeye salmon with 71 stream and pond areas and 23 beach areas classified as major spawning grounds (Demory et al. 1964). The Alaska Department of Fish and Game (ADFG) maintains a visual counting station at Igiugig, the outlet of Iliamna Lake. A separate diurnal counting station at the Newhalen River, which connects Lake Clark with Iliamna Lake, is maintained by the Fisheries Research Institute (Jensen and Mathisen 1987).

### Ocean Life-history

Most smolts of freshwater age 1. and 2. migrate to the sea after ice breakup in lakes (Burgner et al. 1969). Upon leaving the Kvichak River, smolts encounter brackish water and mingle with migrants from the east side rivers (Straty 1974; Straty and Jaenicke 1980). Although juvenile sockeye grow little from their point of entry in Inner Bristol Bay until they reach Port Moller (Fig. 1), these growth rates still exceed those in freshwater. In years with warm SSTs, the migration to Port Moller is generally completed by August (Straty 1974). Past Port Moller, the Kvichak sockeye grow quickly as they migrate along the Alaskan Peninsula and Aleutian Islands (Straty 1974). The juvenile sockeye salmon then move south through the Aleutian Islands passages and into the North Pacific Ocean where they progress toward the Alaskan Gyre (French et al. 1976), a highly productive region in the Gulf of Alaska (Brodeur and Ware 1992, 1995). After spending 2 to 3 years in the ocean, the Kvichak sockeye return home along the Alaskan Stream, moving through the Aleutian passages and then through the offshore waters of Bristol Bay.

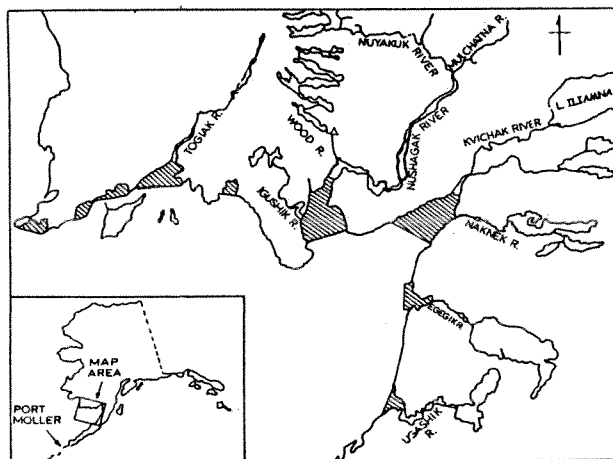
### Scale Measurement Procedures

#### Scale Collections

Scale collections were obtained from the Fisheries Research Institute (FRI) archives (1914, 1919–1953, and 1949–1959) and the Alaska Department of Fish and Game (1960–1997). All four major age-classes, 1.2, 1.3, 2.2, and 2.3, were included in our study. Ages were recorded on sampling forms employing the European notation (Koo 1962). In this notation, the number preceding the decimal point gives the number of freshwater annuli while the number following the decimal gives the number of marine annuli. Summing these two numbers and adding one yields the total life span of returning sockeye salmon.

Prior to 1960, scales were collected from the commercial fishery in different locations near the mouth of the Kvichak River (Table 1 and Fig. 1).

**Fig. 1.** Map of Bristol Bay, showing the Naknek-Kvichak Region. Shaded areas denote fishing regions.





**Table 1.** Detailed summary of the origins and number of Kvichak sockeye salmon digitized from the period 1914 to 1997.

| System <sup>1</sup> | Year | Age-Classes |    |       |     |    |       |     |    |       |     |    |       | Scales<br>Digitized | Scales<br>Available |
|---------------------|------|-------------|----|-------|-----|----|-------|-----|----|-------|-----|----|-------|---------------------|---------------------|
|                     |      | 1.2         |    |       | 1.3 |    |       | 2.2 |    |       | 2.3 |    |       |                     |                     |
|                     |      | M           | F  | total | M   | F  | total | M   | F  | total | M   | F  | total |                     |                     |
| K                   | 1914 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 15    | 15                  | 280                 |
| K                   | 1919 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 40    | 40                  | 360                 |
| N-K                 | 1920 |             |    | 35    |     |    | 0     |     |    | 57    |     |    | 47    | 139                 | 520                 |
|                     | 1921 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 0                   |
|                     | 1922 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 0                   |
| K                   | 1923 |             |    | 0     |     |    | 12    |     |    | 49    |     |    | 57    | 118                 | 1160                |
|                     | 1924 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 0                   |
| K                   | 1925 |             |    | 47    |     |    | 14    |     |    | 0     |     |    | 0     | 61                  | 480                 |
| K                   | 1926 |             |    | 26    |     |    | 53    |     |    | 57    |     |    | 14    | 150                 | 3320                |
| K                   | 1927 |             |    | 7     |     |    | 57    |     |    | 57    |     |    | 57    | 178                 | 1760                |
| K                   | 1928 |             |    | 29    |     |    | 12    |     |    | 57    |     |    | 22    | 120                 | 1680                |
| K                   | 1929 |             |    | 23    |     |    | 57    |     |    | 19    |     |    | 57    | 156                 | 1160                |
| K                   | 1930 |             |    | 32    |     |    | 16    |     |    | 22    |     |    | 18    | 88                  | 800                 |
| K                   | 1931 |             |    | 32    |     |    | 12    |     |    | 57    |     |    | 4     | 105                 | 1320                |
| N-K                 | 1932 |             |    | 6     |     |    | 9     |     |    | 46    |     |    | 12    | 73                  | 320                 |
| N-K                 | 1933 |             |    | 0     |     |    | 0     |     |    | 57    |     |    | 19    | 76                  | 320                 |
| N-K                 | 1934 |             |    | 5     |     |    | 9     |     |    | 15    |     |    | 55    | 84                  | 320                 |
| K                   | 1935 |             |    | 22    |     |    | 20    |     |    | 35    |     |    | 27    | 104                 | 600                 |
| N-K                 | 1936 |             |    | 29    |     |    | 29    |     |    | 57    |     |    | 26    | 141                 | 600                 |
| N-K                 | 1937 |             |    | 33    |     |    | 29    |     |    | 57    |     |    | 42    | 161                 | 720                 |
| N-K                 | 1938 |             |    | 11    |     |    | 0     |     |    | 57    |     |    | 0     | 68                  | 320                 |
| L                   | 1939 |             |    | 0     |     |    | 56    |     |    | 0     |     |    | 47    | 103                 | 2400                |
| N-K(Kog)            | 1940 |             |    | 53    |     |    | 55    |     |    | 32    |     |    | 53    | 193                 | 3280                |
|                     | 1941 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 0                   |
| K                   | 1942 |             |    | 0     |     |    | 0     |     |    | 45    |     |    | 0     | 45                  | 1600                |
| N-K(PAF)            | 1943 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 480                 |
| L-Kog               | 1944 |             |    | 54    |     |    | 44    |     |    | 0     |     |    | 47    | 145                 | 1200                |
| N-K (Kog)           | 1945 |             |    | 38    |     |    | 39    |     |    | 0     |     |    | 0     | 77                  | 800                 |
|                     | 1946 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 0                   |
|                     | 1947 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 0                   |
|                     | 1948 |             |    | 0     |     |    | 0     |     |    | 0     |     |    | 0     | 0                   | 0                   |
| L,G,GS,K,Kog        | 1949 |             |    | 0     |     |    | 0     |     |    | 0     | 27  | 26 | 55    | 55                  | 500                 |
| G,L,M,C             | 1950 | 39          | 18 | 57    | 16  | 13 | 29    | 25  | 28 | 53    | 19  | 32 | 51    | 190                 | 960                 |
| P,L,G,GS            | 1951 | 3           | 3  | 7     | 10  | 8  | 18    | 32  | 23 | 55    | 4   | 11 | 15    | 95                  | 720                 |
| L,K,CC,G,M          | 1952 | 0           | 0  | 5     | 8   | 7  | 15    | 27  | 28 | 55    | 6   | 16 | 22    | 97                  | 1120                |
| L,M,G,GS            | 1953 | 0           | 0  | 0     | 8   | 5  | 13    | 10  | 12 | 22    | 11  | 10 | 21    | 56                  | 880                 |
| K,C,G,L             | 1954 | 6           | 9  | 15    | 2   | 5  | 7     | 0   | 0  | 3     | 11  | 17 | 28    | 53                  | 840                 |
| L,K,H,DMS           | 1955 | 22          | 14 | 38    | 5   | 7  | 12    | 12  | 23 | 35    | 4   | 3  | 7     | 92                  | 560                 |
| WS,M,G,L            | 1956 | 17          | 24 | 41    | 2   | 4  | 6     | 18  | 14 | 32    | 0   | 0  | 3     | 82                  | 400                 |
| L,K                 | 1957 | 0           | 0  | 0     | 26  | 30 | 60    | 35  | 13 | 51    | 9   | 10 | 20    | 131                 | 640                 |
| M,L                 | 1958 | 0           | 0  | 8     | 0   | 0  | 6     | 0   | 0  | 19    | 0   | 0  | 14    | 47                  | 160                 |
|                     | 1959 | 0           | 0  | 0     | 0   | 0  | 0     | 0   | 0  | 0     | 0   | 0  | 0     | 0                   | 0                   |
| K(I)                | 1960 | 34          | 16 | 53    | 0   | 0  | 6     | 2   | 5  | 12    | 0   | 0  | 3     | 74                  | 1640                |
| K                   | 1961 | 0           | 0  | 3     | 20  | 32 | 66    | 15  | 28 | 43    | 0   | 0  | 3     | 115                 | 1000                |
| K                   | 1962 | 0           | 0  | 5     | 0   | 0  | 15    | 28  | 23 | 62    | 8   | 13 | 67    | 149                 | 760                 |
| K                   | 1963 | 25          | 24 | 49    | 6   | 8  | 14    | 24  | 28 | 57    | 30  | 21 | 50    | 170                 | 640                 |
| K                   | 1964 | 0           | 0  | 55    | 0   | 0  | 23    | 0   | 0  | 60    | 0   | 0  | 8     | 146                 | 4200                |
| K                   | 1965 | 0           | 0  | 0     | 0   | 0  | 11    | 11  | 50 | 61    | 0   | 0  | 0     | 72                  | 5880                |
| K                   | 1966 | 9           | 22 | 30    | 8   | 21 | 29    | 15  | 34 | 49    | 20  | 32 | 52    | 160                 | 4760                |
| K                   | 1967 | 10          | 5  | 15    | 20  | 3  | 23    | 26  | 31 | 57    | 34  | 16 | 55    | 149                 | 3520                |
| K                   | 1968 | 29          | 32 | 61    | 2   | 2  | 4     | 25  | 34 | 59    | 16  | 41 | 57    | 180                 | 2640                |
| K                   | 1969 | 29          | 38 | 66    | 5   | 4  | 9     | 23  | 39 | 63    | 6   | 2  | 8     | 146                 | 1800                |
| K                   | 1970 | 0           | 0  | 20    | 0   | 0  | 9     | 0   | 0  | 59    | 0   | 0  | 7     | 95                  | 3680                |
| K                   | 1971 | 12          | 25 | 37    | 23  | 37 | 60    | 21  | 37 | 58    | 34  | 23 | 57    | 212                 | 2480                |
| K                   | 1972 | 24          | 35 | 60    | 17  | 17 | 35    | 34  | 30 | 64    | 19  | 21 | 40    | 199                 | 960                 |
| K                   | 1973 | 27          | 27 | 55    | 23  | 19 | 42    | 27  | 28 | 59    | 28  | 29 | 57    | 213                 | 1440                |
| K                   | 1974 | 4           | 2  | 6     | 22  | 15 | 37    | 30  | 29 | 59    | 4   | 8  | 12    | 114                 | 1760                |
| K                   | 1975 | 4           | 3  | 7     | 0   | 0  | 0     | 33  | 22 | 55    | 16  | 20 | 36    | 98                  | 3120                |
| K                   | 1976 | 25          | 36 | 61    | 2   | 6  | 8     | 30  | 27 | 57    | 21  | 35 | 56    | 182                 | 1800                |
| K                   | 1977 | 30          | 26 | 56    | 7   | 31 | 38    | 27  | 26 | 53    | 13  | 27 | 40    | 187                 | 2200                |

continue...

<sup>1</sup> C, Cutbank; CC, Coffee Cr.; DMS, Dead Man Sands; G, Graveyard; GS, Moon Bay; I, Igiugig; K, Kvichak; Kog, Koggiung; L, Libbyville; M, Middle-Channel; P, Pederson Gravel Spit; H, Half Pt. Source: 1914–1938, Auke Bay Lab; 1939–1953 and 1949–1959–FRI; and 1961–1997, ADF&G. Sex data were available from 1950 to 1997. Sex data for some individuals are missing. In the period from 1950 to 1997 some years did not contain any data on sex.

Table 1. continued.

|        |      | Age-Classes |     |       |     |     |       |     |       |       |     |     |       | Scales<br>Digitized | Scales<br>Available |
|--------|------|-------------|-----|-------|-----|-----|-------|-----|-------|-------|-----|-----|-------|---------------------|---------------------|
| System | Year | 1.2         |     |       | 1.3 |     |       | 2.2 |       |       | 2.3 |     |       |                     |                     |
|        |      | M           | F   | total | M   | F   | total | M   | F     | total | M   | F   | total |                     |                     |
| K      | 1978 | 0           | 0   | 54    | 0   | 0   | 17    | 0   | 0     | 0     | 0   | 0   | 8     | 79                  | Not<br>registered   |
| K      | 1979 | 30          | 28  | 58    | 24  | 32  | 56    | 22  | 32    | 54    | 3   | 3   | 6     | 174                 | 3080                |
| K      | 1980 | 9           | 22  | 33    | 7   | 11  | 19    | 26  | 29    | 55    | 8   | 8   | 17    | 124                 | 2840                |
| K      | 1981 | 27          | 27  | 54    | 23  | 31  | 54    | 17  | 37    | 54    | 16  | 19  | 35    | 197                 | 2120                |
| K      | 1982 | 27          | 27  | 54    | 19  | 35  | 54    | 15  | 39    | 54    | 27  | 16  | 43    | 205                 | 2320                |
| K      | 1983 | 19          | 35  | 54    | 9   | 12  | 21    | 13  | 41    | 54    | 0   | 0   | 3     | 132                 | 2760                |
| K      | 1984 | 23          | 31  | 54    | 20  | 34  | 54    | 20  | 34    | 54    | 9   | 12  | 21    | 183                 | 3520                |
| K      | 1985 | 8           | 15  | 23    | 22  | 32  | 54    | 15  | 39    | 54    | 12  | 42  | 54    | 185                 | 3400                |
| K      | 1986 | 18          | 36  | 54    | 7   | 17  | 24    | 25  | 29    | 54    | 21  | 33  | 54    | 186                 | 1800                |
| K      | 1987 | 20          | 34  | 54    | 8   | 7   | 15    | 18  | 28    | 46    | 3   | 6   | 9     | 124                 | 2480                |
| K      | 1988 | 20          | 34  | 54    | 16  | 38  | 54    | 26  | 28    | 54    | 7   | 8   | 15    | 177                 | 2760                |
| K      | 1989 | 13          | 23  | 36    | 30  | 24  | 54    | 21  | 33    | 54    | 5   | 15  | 21    | 165                 | 3400                |
| K      | 1990 | 9           | 18  | 27    | 1   | 12  | 13    | 21  | 33    | 54    | 23  | 31  | 54    | 148                 | 3480                |
| K      | 1991 | 24          | 29  | 54    | 28  | 23  | 54    | 29  | 21    | 54    | 19  | 30  | 54    | 216                 | 4160                |
| K      | 1992 | 14          | 40  | 54    | 18  | 36  | 54    | 17  | 37    | 54    | 16  | 26  | 42    | 204                 | 3520                |
| K      | 1993 | 27          | 26  | 54    | 21  | 33  | 54    | 20  | 33    | 53    | 25  | 29  | 54    | 215                 | 5880                |
| K      | 1994 | 25          | 29  | 54    | 5   | 17  | 22    | 23  | 31    | 54    | 11  | 6   | 17    | 147                 | 3280                |
| K      | 1995 | 18          | 32  | 54    | 8   | 13  | 22    | 27  | 27    | 54    | 19  | 33  | 54    | 184                 | 4400                |
| K      | 1996 | 18          | 33  | 54    | 17  | 29  | 46    | 22  | 32    | 54    | 19  | 35  | 54    | 208                 | 1760                |
| K      | 1997 | 21          | 30  | 53    | 11  | 14  | 25    | 20  | 31    | 54    | 16  | 11  | 30    | 162                 | 1600                |
| Total  |      | 719         | 908 | 2,276 | 526 | 724 | 1,884 | 927 | 1,226 | 3,106 | 599 | 776 | 2,148 | 9,414               | 135,420             |

Although scales from sampling locations close to the Naknek River were not used in our analyses, it is still possible that some of the scales came from fish destined to rivers other than Kvichak, increasing the variance of scale measurements and distorting the mean value in the early samples. Scales collected after 1959 are not problematic because they came from the sampling station at Igiugig, a half mile below the outlet from Iliamna Lake.

Since 1955, scales were collected from the preferred body area (Anas 1963); the preferred body area is located two rows above the lateral line and intersects with the row of scales descending from the posterior region of the dorsal fin base. Before that date, scales were collected from the side of the fish body, introducing a second additional source of variability in the older data.

#### *Aging Based on Scales*

Although some of the scales had been aged previously by ADFG and FRI employees, all scales were independently aged by the senior author using a microfiche reader with a 48X lens and using criteria established by Mosher (1968).

#### *Aging Precision*

Precision of aging between the senior author and another experienced scale reader (Patricia Nelson, Alaska Dept. of Fish and Game, Kodiak, Alaska) was estimated using a total of 348 scales selected from three different years. Aging differences were few (see Table 4 in Isakov 1998), and a statistical test showed them to be not significant ( $p < 0.01$ ; test from Hoenig et al. 1994).

#### *Sample Size Determination*

The number of available scales for each age-class was constrained by small sample collections in some years, and by variation in age-class composition that resulted in some age-classes either not being represented or existing in very small proportions for particular years. As a result, we randomly selected 50 scales per age-class and year, which was comparable to sample sizes used in similar studies (Zimmermann 1991; Bumgarner 1993).

#### *Male-female Growth Comparisons*

Scale data from males and females were pooled because of sample size restrictions. In fact, sample sizes were often small in number even after pooling male and female samples (Table 1). Nevertheless, significant differences ( $t$ -test,  $p = 0.01$ ) were observed in fork length (yearly means) between males and females for three age-classes: 1.3, 2.2, and 2.3, where the increased size of males ranged from 14.5 mm for the 2.2 age-class to 21.9 mm for both the 1.3 and 2.3 age-classes. Although the test for differences between males and females for the 1.2 age-class was not significant, males were still slightly larger, averaging about 9.8 mm longer than females. In many years, however, confidence intervals of body length for males and females overlapped (Figs. A10–A13 in Isakov 1998), suggesting similar growth between males and females for those years.

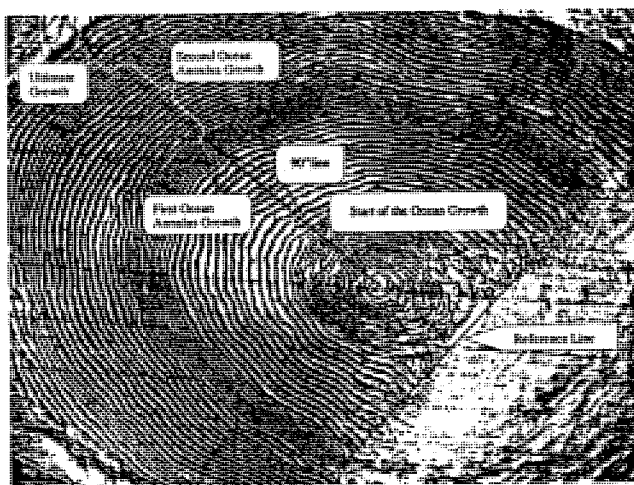
Because scales were selected randomly (except for those year/age-class strata with insufficient numbers of scales), the proportion of males and females in the analyses should reflect the yearly population

ratios; thus introducing increased variance in the data but no inherent bias unless there is a trend in the sex ratio over time. Unfortunately, sex ratio data do not exist prior to 1950 and have not been tabulated since that time.

### Saltwater Scale Measurements

Scales were digitized utilizing OPTIMAS (1993) image analysis software (Fig. 2). Digitizing steps were as follows: 1) a reference line was established along the reticulated region, connecting the first circulus of ocean growth; 2) a line 90° (axis line) to the reference line was drawn from the focus to the edge of the scale; 3) the image was magnified 1.5 times, focusing on the region of marine growth and ensuring that the axis line remained unchanged; 4) a digitizing line was placed along the axis line and the intercirculi and interannular distances extracted; and 5) the data were exported to an Excel 4.0 file. These data were combined into the following measures: growth by ocean annulus, the sum of ocean annulus growth, ultimate growth (distance from the last annulus to the edge of the scale), and total ocean growth (sum of ocean annulus growth plus ultimate growth).

Fig. 2. Scale measurement zones of an age 2.2 Kvichak sockeye salmon.



The 90° axis line was used instead of the longest axis on the scale to ensure consistency between this study and a subsequent study on freshwater growth. The last few circuli are often only measurable along the longest axis; thus using the 90° axis can, on the one hand, result in underestimating total scale growth and introduce a possible bias in using growth measurements from the final few months at sea (ultimate growth). On the other hand, using the longest axis separately for the salt and freshwater parts of the scale introduces other biases because of differences in the direction of scale growth in the

freshwater and the ocean. Since we did not use scale measurements beyond the final annulus, our use of the 90° axis line did not affect any of the analyses.

### Statistical Methods

Histograms of scale measurements revealed non-normalities in distribution. Box-plots of scale measurements showed considerable variability along with many outliers and extreme values (see Figs. A14–A35 in Isakov 1998). In most samples, the distributions were successfully normalized by applying a natural logarithm transformation to the data. As a result, the logtransformed data were used in graphical, correlation, and ANOVA analyses. The median estimate of logtransformed growth (for a particular strata; e.g., age or year) was then exponentiated and used as a dependent variable in the regression analyses.

The growth data were smoothed with a distance-weighted least squares fit algorithm (StatSoft 1996) and plotted to identify long-term patterns in the data. The growth data were either lagged to the same year of growth deposition in the ocean (hereafter called ocean year) or used unlagged (e.g., common year of return) in correlation analyses.

The effects of age-class, ocean year, and year-class (or brood year) on log-transformed growth data were evaluated by an analysis of variance (ANOVA). Differences in growth were tested for three major periods of Alaska salmon abundance and climate. The periods 1920–1950 and 1976–1997 are generally characterized by high salmon abundance and warm temperatures, and the period 1950–1975 is characterized by lower salmon abundances and cooler temperatures (Beamish and Bouillon 1993; Hare and Francis 1995). Stepwise multiple regressions were made to examine the association of growth with annual measures of Bristol Bay sockeye salmon catch, Fraser River sockeye salmon run size, and sea surface temperatures (SST). Several measures of SST were used corresponding to three areas in the North Pacific Ocean (Bristol Bay, Bristol Bay plus the Aleutian Islands, and Gulf of Alaska) and two time periods (January to December, and April to October mean values). All regression variables were lagged to the year in which scale growth occurred.

Annual run data for Fraser River sockeye salmon were provided by Dr. J.C. Woodey (Chief, Fisheries Management Division of Pacific Salmon Commission). Bristol Bay sockeye salmon catch data were taken from the Alaska Dept. of Fish and Game annual reports. Sea Surface Temperature (SST) data were extracted from the comprehensive ocean-atmosphere data set (COADS) provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado at their web site: <http://www.cdc.noaa.gov/>.

For further details, see Isakov (1998) on treatment of environmental data.

## RESULTS

Regression analyses of scale growth versus body length on eight randomly chosen samples showed that body length was more closely related to the sum of ocean annulus growth than the total ocean growth in all four age-classes (Table 2). The percent of variation in body length explained by the sum of ocean annulus growth varied from 11 to 39%, with a median value of 31%.

**Table 2.** Regression of two scale growth measures on body length of Kvichak River sockeye salmon.

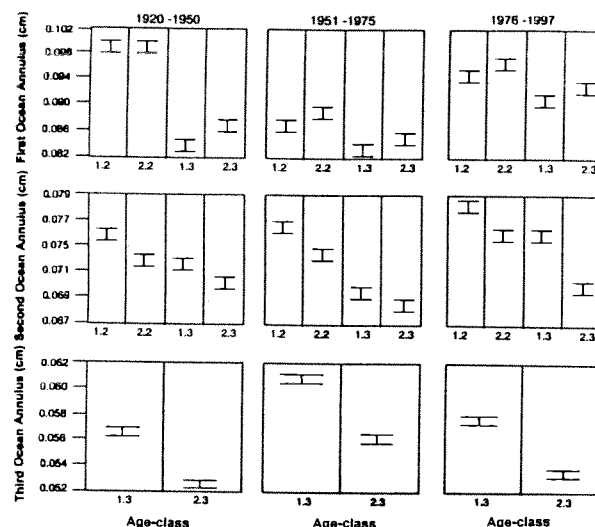
| Regression Model                           | Age-class (Year) | Multiple R | R <sup>2</sup> | SE    | n  |
|--------------------------------------------|------------------|------------|----------------|-------|----|
| Total Ocean Scale Growth vs. Body Length   | 1.2 (1971)       | 0.57       | 0.32           | 0.014 | 37 |
|                                            | 1.3 (1971)       | 0.33       | 0.11           | 0.015 | 60 |
|                                            | 2.2 (1965)       | 0.56       | 0.31           | 0.014 | 61 |
|                                            | 2.3 (1973)       | 0.56       | 0.31           | 0.015 | 57 |
| Sum of Ocean Annuli Growth vs. Body Length | 1.2 (1971)       | 0.62       | 0.39           | 0.013 | 37 |
|                                            | 1.3 (1971)       | 0.43       | 0.19           | 0.013 | 60 |
|                                            | 2.2 (1965)       | 0.56       | 0.31           | 0.014 | 61 |
|                                            | 2.3 (1973)       | 0.59       | 0.35           | 0.014 | 57 |

### Between Period Differences in Scale Growth

Scale growth rates varied extensively within and between years. Although Fig. 3 shows a high level of between-year variation in age 1.2 sockeye salmon prior to 1935, this increase was not always reflected in the other age-class data (see appendices in Isakov 1998). Growth rates also varied on a variety of longer time scales, ranging from an apparent 4–6 year cycle to longer, multi-decadal, trends.

The effects of low-frequency changes in scale growth rates were apparent when data for each ocean annulus were summarized by age-class and time period (Fig. 4). First ocean annulus growth (FOAG) of 1.2 and 2.2 sockeye was significantly greater during

**Fig. 4.** Range in scale growth measurements classified by ocean year, age-class and time period.



the 1920–1950 (1<sup>st</sup>) and 1976–1997 (3<sup>rd</sup>) time periods than the 1951–1975 (2<sup>nd</sup>) time period. FOAG of 1.3 and 2.3 did not differ much between the 1<sup>st</sup> and the 2<sup>nd</sup> periods, but exhibited a large increase in the third period. More generally, first year growth rates were always higher for freshwater age 2 fish, and FOAG of 1.2 and 2.2 age-class sockeye was always greater than FOAG of 1.3 and 2.3 age-class sockeye.

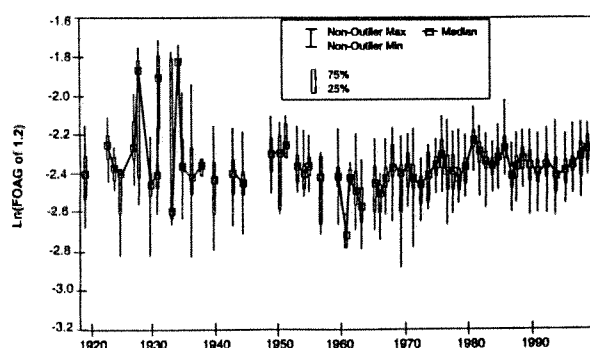
Second year ocean scale growth (also called SOAG) was greatest for fish maturing in their second year; fish staying in the ocean a third year before maturing grew less in their second year than those maturing as age class x.2. Second year growth rates, however, were always higher for freshwater age 1 than for freshwater age 2 fish. Sockeye of all age-classes experienced reduced second year growth between 1951 and 1975; these differences in SOAG were significant for 1.2, 1.3 and 2.3 age-class sockeye, but not significant for 2.2 age-class sockeye.

Scale growth during the third ocean year (also called TOAG) of 1.3 and 2.3 age-classes exhibited an opposite pattern to FOAG and SOAG growth; low scale growth occurred during the 1<sup>st</sup> and 3<sup>rd</sup> periods, whereas high scale growth occurred in the second period. TOAG was also greater for freshwater age 1 fish than freshwater age 2 fish.

### Scale Growth Patterns

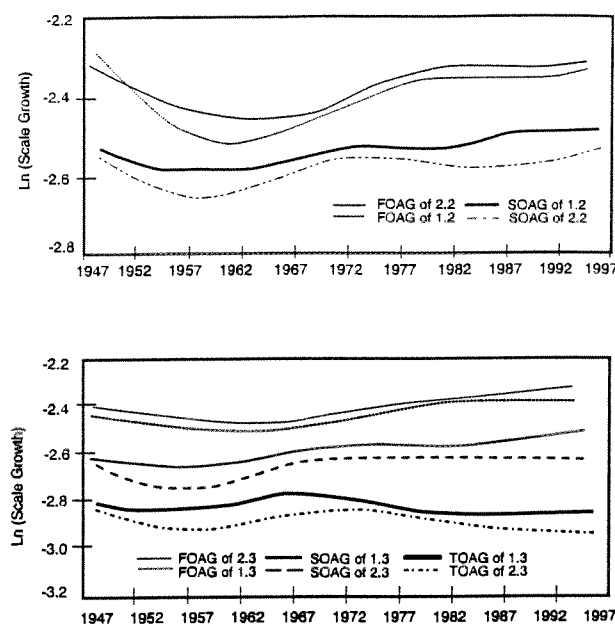
Scale Growth patterns over the study period were evaluated further by plotting smoothed mean values of scale measurements by year and age-class lagged to the same year of growth deposition. Fish with the same ocean life-history (e.g., 1.2 and 2.2 age-class, or 1.3 and 2.3 age-class fish) exhibited nearly identical growth patterns (Fig. 5). Although FOAG was always greater than SOAG, growth dur-

**Fig. 3.** Time-series of annual scale growth statistics (median, upper and lower quartiles, and range) for the first ocean year of age 1.2 Kvichak sockeye salmon.



ing the first two ocean years was still similar over the study period. Growth rates in all ocean years (FOAG, SOAG, and TOAG) declined prior to the late 1950s and early 1960s after which they reversed and began to steadily increase until 1970 when the three growth patterns diverged: FOAG continued to increase, but at a lower rate, SOAG showed no further increase, and TOAG began to steadily decrease. In general, freshwater age 2 sockeye (2.x) grew larger than 1.x sockeye only during the first ocean year. The reverse was true during the second and third ocean years; in both cases, 1.x sockeye outgrew 2.x sockeye during this period.

Fig. 5. Trends in ocean growth rates by age-class and ocean year (1947–1997).



### Correlation between Scale Growth Measurements

When the data were lagged to the year of growth deposition, correlation coefficients were highest for growth zones of sockeye sharing the same ocean history (Table 3). Take, for example, 1.2 and 2.2 age-class salmon returning as adults in a particular year. Although they belong to different broods, they emigrate to sea in the same year sharing the same early ocean environment which was reflected by the FOAG correlation coefficient of  $r = 0.835$ . The correlation dropped a bit during the second year at sea, but still stayed relatively high ( $r = 0.757$ ). Correlations between 1.3 and 2.3 age-class sockeye were also high, but exhibited a reversed pattern, with the lowest correlation occurring during the first year in the ocean ( $r = 0.584$ ) and the highest during the third year ( $r = 0.813$ ).

Second year growth correlations dropped substantially when some combination of ocean history, ocean year, and freshwater history differed. Consider the following four correlations: (1)  $r = 0.757$  when ocean year and ocean life history were similar, but freshwater history differed (SOAG of 1.2 vs. SOAG of 2.2 age-class sockeye salmon); (2)  $r = 0.487$  when freshwater history and ocean year were similar, but ocean life-history differed (SOAG of 1.2 vs. 1.3 age-class sockeye salmon); (3)  $r = 0.41$  when freshwater history was the same, but ocean year and ocean life-history differed (SOAG of 1.2 and TOAG of 1.3 age-class sockeye salmon); and  $r = 0.313$  when ocean life-history was the same, but ocean year and freshwater history differed (SOAG of 2.3 vs. TOAG of 1.3 age-class sockeye salmon).

Data fixed to the year of adult returns showed negative correlations between first and second year growth rates of both 1.2 and 2.2 age-class sockeye.

Table 3. Correlation coefficients between Kvichak scale growth data stratified by age-class and lagged: (A) to the year of growth deposition; and (B) year of adult returns. Abbreviations are: FOAG, first ocean annulus growth; SOAG, second ocean annulus growth; and TOAG, third ocean annulus growth.

| A: Scale Data Lagged to the Year of Growth Deposition in the Ocean |             |             |             |             |             |             |             |             |
|--------------------------------------------------------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
|                                                                    | FOAG of 1.2 | FOAG of 2.2 | FOAG of 1.3 | SOAG of 1.2 | SOAG of 2.2 | SOAG of 1.3 | SOAG of 2.3 | TOAG of 1.3 |
| FOAG of 2.2                                                        | 0.835       |             |             |             |             |             |             |             |
| FOAG of 2.3                                                        |             | 0.299       | 0.584       |             |             |             |             |             |
| SOAG of 2.2                                                        | 0.389       |             |             | 0.757       |             |             |             |             |
| SOAG of 1.3                                                        |             | 0.308       |             | 0.487       | 0.476       |             |             |             |
| SOAG of 2.3                                                        |             |             |             | 0.518       | 0.59        | 0.697       |             |             |
| TOAG of 1.3                                                        |             |             |             | 0.41        | 0.414       |             | 0.313       |             |
| TOAG of 2.3                                                        |             |             |             | 0.425       | 0.396       |             | 0.348       | 0.813       |
| B: Scale Data Lagged to the Year of Adult Returns                  |             |             |             |             |             |             |             |             |
|                                                                    | FOAG of 1.2 | FOAG of 2.2 | FOAG of 1.3 | FOAG of 2.3 | SOAG of 1.2 | SOAG of 2.2 | SOAG of 1.3 | TOAG of 1.3 |
| FOAG of 2.2                                                        | 0.835       |             |             |             |             |             |             |             |
| FOAG of 2.3                                                        | 0.397       | 0.425       | 0.584       |             |             |             |             |             |
| SOAG of 1.2                                                        | -0.495      | -0.266      |             |             |             |             |             |             |
| SOAG of 2.2                                                        | -0.37       | -0.352      |             |             | 0.757       |             |             |             |
| SOAG of 1.3                                                        |             | 0.308       |             |             |             |             |             |             |
| SOAG of 2.3                                                        |             |             |             |             |             | 0.284       | 0.697       |             |
| TOAG of 1.3                                                        |             |             |             |             | 0.41        | 0.414       |             |             |
| TOAG of 2.3                                                        |             |             |             | -0.341      | 0.425       | 0.396       |             | 0.813       |

First and third year growth of the 2.3 age-class was also negatively correlated. Both of these results mean that when first year growth rates were above average, growth in the second and third years was below average. This inverse relationship was not observed between second and third year growth rates where growth correlations were positive.

### ANOVA of Scale Data

Because of the different growth patterns of x.2 and x.3 sockeye, two three-way ANOVAs were performed, one for age-classes 1.2 and 2.2 and the other for age-classes 1.3 and 2.3 (Table 4). The three-way interaction between age-class, ocean year, and year was highly significant in both cases ( $p < 0.001$ ). All two-way interactions as well as main effects were highly significant except for the interaction between age-class and year, which was significant for age-classes 1.2 and 2.2 ( $p < 0.01$ ) but not significant for age-classes 1.3 and 2.3 ( $p = .25$ ). The significant three-way interactions indicate that there were no consistent growth patterns—either across broods or across ocean years—of salmon from different age-classes, and they confirm that differences in growth seen in previous analyses were statistically significant.

### Stepwise Multivariate Regression Analyses

Regression models using data pooled over age-class or ocean year performed less well than models using separate data sets (Table 5). Sea surface temperatures selected in the stepwise regressions generally related to the growing and feeding season (April to October), rather than annual averages. First year ocean growth was significantly associated with Bristol Bay and Aleutian Islands sea surface tempera-

tures. Second year ocean growth was generally not associated with any of our environmental or population abundance variables; the highest correlation ( $r = 0.21$ ) occurred between SOAG of 1.3 age-class sockeye and Fraser River sockeye returns. Third year ocean growth was most highly associated with Gulf of Alaska sea surface temperatures and Bristol Bay sockeye returns. The explanatory power, however, of these stepwise regression models was low, with  $R^2$  values less than 15% across all models (Table 5).

### DISCUSSION

One of the key assumptions behind our study was that scale growth is a suitable proxy for body length. Although the linear relationship between log-transformed scale growth and body length was significant in our study, there was still substantial variability in body length unexplained by scale size. This unexplained variability was due, in part, to: (1) variations in freshwater growth not accounted for in the total scale growth measurements because of a lack of freshwater measurements; (2) not differentiating between sexes in our analyses; and (3) using the 90° (rather than the longest) axis for scale measurements, which made using scale growth data beyond the last annulus problematic.

The relatively low correlation coefficients between body and scale growth in our study are similar (in magnitude) to those obtained in other works dealing with sockeye salmon scale measurements (Bilton 1985; Bumgarner 1993). Bumgarner (1993) used the 90° axis and obtained low values, whereas Bilton (1985) used the longest axis but also obtained low values. Stone (1976), however, reported relatively higher correlation coefficients applying a different axis to the total scale growth of the Kvichak sockeye salmon.

**Table 4.** Analysis of Variance of Kvichak scale growth data with ocean age, year, and age-class as the main effects.

| Summary of all Effects for Age-classes 1.2 and 2.2 |           |           |          |          |        |         |
|----------------------------------------------------|-----------|-----------|----------|----------|--------|---------|
|                                                    | DF Effect | MS Effect | DF Error | MS Error | F      | p-level |
| Age-Class                                          | 1         | 0.1097    | 9580     | 0.0172   | 6.37   | 0.012   |
| Ocean Year                                         | 1         | 60.96     | 9580     | 0.0172   | 3538.5 | <0.001  |
| YEAR                                               | 56        | 0.406     | 9580     | 0.0172   | 23.57  | <0.001  |
| Age-Class x Ocean Year                             | 1         | 0.82      | 9580     | 0.0172   | 47.5   | <0.001  |
| Age-Class x YEAR                                   | 56        | 0.0289    | 9580     | 0.0172   | 1.68   | 0.001   |
| Ocean Year x YEAR                                  | 56        | 0.64      | 9580     | 0.0172   | 37.08  | <0.001  |
| Age-Class x Ocean Year x YEAR                      | 56        | 0.062     | 9580     | 0.0172   | 3.59   | <0.001  |
| Summary of all Effects for Age-classes 1.3 and 2.3 |           |           |          |          |        |         |
|                                                    | DF Effect | MS Effect | DF Error | MS Error | F      | p-level |
| Age-Class                                          | 1         | 1.05      | 10911    | 0.0219   | 48.07  | <0.001  |
| Ocean Year                                         | 2         | 94.04     | 10911    | 0.0219   | 4294.8 | <0.001  |
| YEAR                                               | 59        | 0.204     | 10911    | 0.0219   | 9.3    | <0.001  |
| Age-Class x Ocean Year                             | 2         | 1.414     | 10911    | 0.0219   | 64.59  | <0.001  |
| Age-Class x YEAR                                   | 59        | 0.025     | 10911    | 0.0219   | 1.12   | 0.250   |
| Ocean Year x YEAR                                  | 118       | 0.278     | 10911    | 0.0219   | 12.7   | <0.001  |
| Age-Class x Ocean Year x YEAR                      | 118       | 0.046     | 10911    | 0.0219   | 2.11   | <0.001  |

**Table 5.** Stepwise multiple regression analyses of Kvichak scale growth data on selected sea surface temperature variables and sockeye salmon catch data. Sea surface temperature variables denoting regions and time period of data: BBA = Bristol Bay, annual averages; BBW = Bristol Bay, April to October averages; BAA = Bristol Bay plus Aleutian Islands annual averages; BAW = Bristol Bay plus Aleutian Islands April to October averages; GAA = Gulf of Alaska annual averages; and GAW = Gulf of Alaska, April to October averages. Abbreviations for other variables: BRISTOL = annual catch of Bristol Bay sockeye salmon; and FRASER = yearly run of Fraser River sockeye salmon. FOAG, SOAG and TOAG are defined in Table 3.

| Scale Growth Data                                    | Explanatory Variables list by order of entry in analysis, and final model |      |        |      |         |      |         |      |       |                                    |
|------------------------------------------------------|---------------------------------------------------------------------------|------|--------|------|---------|------|---------|------|-------|------------------------------------|
|                                                      | First                                                                     | R    | Second | R    | Third   | R    | Fourth  | R    | Final | R <sup>2</sup> <sub>adjusted</sub> |
| Pooled Sum of Ocean Annuli (1.2 and 2.2 age-classes) | BBW                                                                       | 0.14 | BAW    | 0.15 | GAW     | 0.16 |         |      | 0.16  | 0.024                              |
| Pooled Sum of Ocean Annuli (1.3 and 2.3 age-classes) | BAW                                                                       | 0.06 | GAW    | 0.09 | BBW     | 0.10 | Bristol | 0.11 | 0.11  | 0.012                              |
| Pooled FOAG (1.2 and 2.2)                            | BBA                                                                       | 0.36 | BAW    | 0.36 | BBW     | 0.37 |         |      | 0.37  | 0.137                              |
| Pooled FOAG (1.3 and 2.3)                            | BAW                                                                       | 0.28 | BBW    | 0.33 | GAW     | 0.36 |         |      | 0.36  | 0.127                              |
| Pooled SOAG (1.2 and 2.2)                            | BAA                                                                       | 0.06 | BAW    | 0.19 | Bristol | 0.21 |         |      | 0.21  | 0.033                              |
| Pooled SOAG (1.3 and 2.3)                            | Fraser                                                                    | 0.14 | BAA    | 0.14 | GAW     | 0.17 |         |      | 0.17  | 0.027                              |
| Pooled TOAG (1.3 and 2.3)                            | Bristol                                                                   | 0.21 | GAW    | 0.22 | BAW     | 0.23 |         |      | 0.23  | 0.052                              |
| Sum of Ocean Annuli of 1.2                           | BBW                                                                       | 0.16 | BAW    | 0.18 |         |      |         |      | 0.18  | 0.033                              |
| Sum of Ocean Annuli of 2.2                           | BAW                                                                       | 0.11 | GAW    | 0.13 |         |      |         |      | 0.13  | 0.015                              |
| Sum of Ocean Annuli of 1.3                           | Bristol                                                                   | 0.11 | BBW    | 0.15 |         |      |         |      | 0.15  | 0.020                              |
| Sum of Ocean Annuli of 2.3                           | BAW                                                                       | 0.08 | GAA    | 0.09 | Bristol | 0.10 | Fraser  | 0.12 | 0.12  | 0.013                              |
| FOAG of 1.2                                          | BBA                                                                       | 0.37 |        |      |         |      |         |      | 0.37  | 0.140                              |
| FOAG of 2.2                                          | BBW                                                                       | 0.33 | BAA    | 0.34 | BAW     | 0.36 |         |      | 0.36  | 0.130                              |
| FOAG of 1.3                                          | BAW                                                                       | 0.28 | GAW    | 0.35 | Fraser  | 0.38 |         |      | 0.38  | 0.145                              |
| FOAG of 2.3                                          | BAW                                                                       | 0.28 | BAA    | 0.34 | GAA     | 0.36 | Bristol | 0.38 | 0.38  | 0.138                              |
| SOAG of 1.2                                          | BBA                                                                       | 0.08 | BAW    | 0.21 |         |      |         |      | 0.21  | 0.040                              |
| SOAG of 2.2                                          | Bristol                                                                   | 0.09 | BAA    | 0.12 | BAW     | 0.20 |         |      | 0.20  | 0.038                              |
| SOAG of 1.3                                          | Fraser                                                                    | 0.21 |        |      |         |      |         |      | 0.21  | 0.042                              |
| SOAG of 2.3                                          | Fraser                                                                    | 0.07 | BBW    | 0.10 |         |      |         |      | 0.10  | 0.008                              |
| TOAG of 1.3                                          | GAA                                                                       | 0.19 | Fraser | 0.24 | Bristol | 0.25 |         |      | 0.25  | 0.060                              |
| TOAG of 2.3                                          | Bristol                                                                   | 0.24 | GAW    | 0.24 | BAW     | 0.27 |         |      | 0.27  | 0.070                              |

Growth differences between the three time periods of low and high sockeye abundance were evident in all age-classes. The largest between-period differences occurred for first year growth rates, suggesting an increased sensitivity to factors affecting growth changes. The consistent pattern among the four age-classes (from 1.2, 2.2, 1.3, and 2.3) of greatest to least in second year scale growth is likely due to: (1) different maturation schedules between age-classes; and (2) growth compensation. Fish maturing after their second year in the ocean show higher growth rates than those maturing after three years, which explains the increased second year growth of x.2 age-class sockeye. Growth compensation occurs when individuals growing most rapidly during their first year at sea exhibit reduced growth rates the following year (in comparison with individuals growing more slowly at first (see, for example Beacham 1981)), and can explain the reversal in growth rate status for 1.2 and 2.2 age-class sockeye between their first and second year at sea. This reversal is also indicated by the negative correlations between first and second year growth in the unlagged data (sockeye returning the same year). Growth compensation may also explain patterns in third year growth rates between time periods. For example, growth rates in the third ocean year are highest during the 2<sup>nd</sup> time period, the period

of time when growth in the first two ocean years is lowest.

The correlation analyses were a variation on the multi-stock approach suggested by Peterman et al. (1998) as a useful tool to identify sources of variability in fish stocks. By correlating salmon with differing life-history type, year of growth deposition, or ocean age, we learn about the commonality of conditions experienced by the different groups of salmon and insight into the processes influencing growth. For example, the high correlation between growth for sockeye with the same ocean history suggests the importance of the environment in affecting growth rates of sockeye salmon, not only in the early marine environment (e.g., 1.2 and 2.2 sockeye lagged to year of growth deposition), but later in their life history when the sockeye may be more dispersed (e.g., third year growth of 2.3 and 1.3 sockeye lagged to year of deposition). The similarity of first year growth between x.2 age-class fish with different freshwater ages also suggests that freshwater growth history has a minor influence on ocean growth for faster growing, early maturing, sockeye salmon.

First year growth correlations, however, drop substantially for x.3 age-class fish with differing freshwater ages, and even more so for sockeye with similar freshwater ages but differing ocean return

times. These results suggest that perhaps fish with differing maturation histories differ in their ocean distribution (consistent with McKinnell (1995)) and that fish maturing after two years remain most closely associated in space and time. These results also complement data from Peterman et al. (1998) who showed that marine survival among groups of Bristol Bay sockeye was correlated highest when the groups shared a common brood year and ocean entry year. When brood years were still aligned, but ocean entry year differed, correlations in survival dropped substantially.

Although the ANOVA showed that differences in growth between age-classes were highly significant statistically (in part due to extremely large sample sizes in the tests), it is striking how all of the age-classes follow similar growth patterns over time (Fig. 5). This similarity suggests several hypotheses that could be tested through field surveys, namely that: (1) sockeye salmon of differing age-classes migrate similarly, and are thus exposed to similar environmental conditions; or (2) if they migrate dissimilarly, then the temporal/spatial variations in ocean habitat (experienced between the migrating groups) are small, and in any event, less than year to year differences in environmental conditions. Data from Fukuhara (1975), showing that fish in 1° X 1° quadrants are homogenous whereas in fish 2° X 5° quadrants are not, support the first hypothesis. So do the reduced correlations when growth by age-class is compared between ocean years (e.g., second and third year growth). Resolution of such questions, however, will be limited until better stock identification methods for sockeye salmon are developed for high seas sampling.

The reverse in growth trends around the late 1950s and early 1960s is one of the most notable results in our analysis. This pattern is not associated with similar patterns in either sockeye abundances or environmental data (Isakov 1998). Moreover, it has little association with recent long-term changes in climate patterns that showed marked changes around 1976. Nor is it likely associated with changes in the gear used to collect fish for scales: before 1960, scales were collected from fish captured in commercial gillnets; since 1960, scales were collected from fish captured in rivers using seines. Gillnets are size-selective and since the 1920s, mesh sizes used in Bristol Bay have been predominantly 140 mm (5.5 inches). This size of mesh selects strongly for larger fish (e.g., ocean age 3 versus ocean age 2), and any differences in catchability before and after 1960 would be greatest for the older, larger, x.3 fish (Mathisen 1971). Thus if the growth changes are due to changes in catchability we should see a bigger signal with the x.3 fish, which we do not.

This lack of association was reflected in the stepwise regression analyses as none of the models

explained much of the variability in growth data. Part of this may be the difficulty in constructing variables that accurately measure the environment encountered by salmon while migrating (in lieu of SST data). Another part may stem from our focus on growth during juvenile and immature life-history stages. Adult body size has been shown to be highly associated with both SST and salmon density (Pyper and Peterman 1999); the bulk of somatic growth, however, occurs during the final year at sea which was not included in our scale measures.

Nevertheless, the influence of SST, particularly during the growing season, was noted in most of the regression models. SST had its greatest influence on growth in the first ocean year when sockeye are migrating out of Bristol Bay and into the Aleutian Islands region. SST was also more associated with first year growth of 1.2 and 2.2 age-class sockeye salmon than with 1.3 and 2.3 age-class salmon. Since our growth measures were year specific, we did not compare growth with SST at any other lag in time (e.g., Adkison et al. 1996) other than those expected by direct, causal, mechanisms.

This early ocean growth-SST relationship has been noted previously by Straty and Jaenicke (1980) who observed increased scale growth of juveniles captured near Port Moller in years with high SSTs. Several mechanisms can account for this relationship. High SSTs increase swimming speed, quickening the migration rate through inner Bristol Bay (an unproductive environment) to Port Moller where zooplankton are more abundant and larger in size (Straty 1981). Warmer SSTs also increase the width of the migration corridor, spreading out the salmon and enlarging the area of feeding.

Peterman et al. (1998) showed that yearly recruitment of Kvichak sockeye salmon was strongly associated with marine survival and that regional rather than basin-scale environmental factors were most influential to sockeye salmon survival. These results point towards survival mechanisms employing environmental factors unique to Bristol Bay sockeye salmon. SST during the early marine migration period is one of the more promising factors and is likely linked to survival through growth.

The persistent yearly increase in first and second year growth beginning around 1960 was not reflected in the third year growth data, which exhibited a decreasing trend from around 1970 to the early 1990s. This period of decline is roughly associated with the declivitous recovery of salmon populations in the North Pacific Ocean (Beamish and Bouillon 1993). The inclusion of Fraser River in second-year ocean growth models lends some support to the influence of other salmon populations on growth of Kvichak River sockeye. Although Fraser River sockeye represent, on average, about 10 percent of the total Alaskan catch of sockeye salmon, they overlap in high-



seas distribution with the Kvichak sockeye where they compete for food on the feeding grounds (Pyper and Peterman 1999).

The decreasing size at return for many salmon populations (Bigler et al. 1996), was not observed in our data, which only showed growth reductions during the last year at sea and not during the early and intermediate ocean periods. This increasing trend in growth since the 1970s has been also observed in sockeye returns to the Chignik River (Bumgarner 1993), which empties into the Gulf of Alaska on the south side of the Alaska Peninsula. The reduction in growth during the final ocean year occurs when fish concentrate in larger groups as they near their spawning grounds. The lack of growth reductions in the second ocean year suggests a more diffused distribution of sockeye salmon then, where they utilize a broad region of the Subarctic Domain. Likewise the reductions in adult size of many pink and chum populations may indicate a more concentrated distribution during their high-seas resident period. It may also reflect differences in ocean distribution patterns where sockeye tend to inhabit the broad region of the Ridge Domain whereas chum, pink and coho are often found further south, feeding in a rather narrow region characterized by subarctic current waters.

## CONCLUSIONS

Our analyses of scale growth data provided several useful insights into marine growth patterns of Kvichak River sockeye salmon since the early 1920s. Low-frequency changes in growth followed, to some degree, some of the overall patterns observed in salmon populations during this century. Growth rates during the first and second year in the ocean were highest during periods of warm temperatures and increased salmon abundance in the North Pacific Ocean. Third year growth rates began a steady decline just several years before the period of salmon population increase in the mid-1970s. Age-classes with the same ocean-history had very similar ocean growth patterns—even if the freshwater life-history and thus brood year differed—which supports the hypothesis that ocean conditions exert a strong influence on salmon populations.

A number of questions still remain, however, particularly with respect to the importance of smolt body size (not measured in this study) and cyclic changes in the Kvichak sockeye population abundance. In particular, the importance of salmon density dependence on growth rate, one of the original questions posed in this study, is still unclear. Although measures of salmon population abundance were not found important in this analysis, Fig. 3 shows an obvious effect of abundance on growth rate which was masked by the stratification of growth data into broad time periods. Perhaps some of these

questions will be addressed by multivariate time-series analyses of these data which are currently underway and designed to yield a more in-depth and comprehensive treatment of growth patterns.

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## Recent Reduction in Chum Salmon (*Oncorhynchus keta*) Growth and its Consequences for Reproduction

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**Abstract:** A statistically significant decrease in body length and fecundity of the Iturup Island chum salmon (*Oncorhynchus keta*) after 1985 coincided with an increase in mean age and decline in adult returns. These changes were accompanied by an increase in ocean mortality, but conditions of fry growth in the coastal zone appeared to be the determining factor in changes in overall chum salmon survival in the sea. The rate of sexual maturation was positively related to age at maturity of parents. Increased age of chum salmon spawners, associated with low spawning numbers, partially compensated for decreasing fecundity. This is an example of reproductive homeostasis.

### INTRODUCTION

Since the middle 1980s uncommonly strong anomalies in ice formation were recorded in the northwestern part of the Pacific Ocean as a consequence of climate changes (Khen 1997). Early in the 1990s water circulation and structure of zooplankton and nekton communities altered in response to global climate change (Shuntov et al. 1996; Radchenko et al. 1997). A decrease in Pacific salmon catches in the second half of the 1990s may be connected with these changes (Klyashtorin and Sidorenkov 1996; Beamish et al. 1997).

If this climate change seriously affects chum salmon (*Oncorhynchus keta*) feeding and growth in the ocean, the consequences should become apparent in various biological indices. An investigation of these indices is the objective of the present study. Long-term changes in growth, fecundity and age at maturation of chum salmon are considered in an attempt to explain changes in population abundance.

### MATERIALS AND METHODS

Chum salmon reproduction has been studied at Iturup Island (Kuril Islands) since 1974. These salmon were from a comparatively isolated group from Kuril Bay and the rivers Kurilka, Rybatskaya and Kitovaya flowing into the Okhotsk Sea. Adults were sampled from commercial catches during chum salmon mass migration every 7–10 days. Fork length (FL), body weight, sex, and female fecundity were

determined. Scales were collected from 2–4 rows above a lateral line behind the dorsal fin. Fish age is denoted by the number of years of life completed (e.g. 0.3: 0 years in freshwater, 3 full sea years and part of the following year). Annual growth was determined by back calculation from scale ring increments. Scales were measured along the longest radius. The numbers of adult fish were determined from commercial catch data in the bay and river mouths, and from visual counting in rivers by foot-survey. The small size and shallow depth of these rivers facilitated this task. Annually in the first half of November, while chum salmon were spawning, the number of live and dead fish were counted in 70–90% of the total area of chum salmon distribution from river mouths to upper reaches. Then the number of chum salmon, calculated per total area, was increased 20% in expectation of later returns (Kaev 1989).

The number of fry migrating down the Rybatskaya River was determined from net traps set at night. A standard method for such studies (Hunter 1959; Volovik 1967) modified for small rivers of the Kuril Islands was used (Kaev 1989). A coefficient of downstream migration was determined from a ratio of number of fry migrants to the total female fecundity (nos. of females  $\times$  average individual fecundity) in the Rybatskaya River. This coefficient from the Rybatskaya River (4,200 m<sup>2</sup> of spawning grounds) was used to estimate numbers of fry migrants in the rivers Kurilka (15,200 m<sup>2</sup>) and Kitovaya (2,300 m<sup>2</sup>). On the basis of estimated numbers of fry migrants, chum

salmon abundance in rivers, and commercial catch data, a return coefficient was calculated as the ratio of returning adult fish to the number of fry migrants. As for the Rybatskaya River, a coefficient of fry downstream migration was determined for the Ilyushin River at Kunashir Island (Kuril Islands), where the author has conducted regular investigations since 1994.

Fry migrants were sampled for body length since 1974, but only since 1977 were fry sampled in numbers proportional to catches throughout the period of downstream migration. In addition, fry were caught every 10 days from Kuril Bay during May, June and July to determine their length, weight, feeding indices, and scale structure. Fry growth could not be determined directly from their body length because of continuous arrival and departure of fish into or out of the bay. Some fry had left the rivers recently and were without scales. Others had been in the bay for some time and had scales with several rings. Sampled fry were divided into groups with equal numbers of scale rings. For each group a bar chart of body length composition was made. Then all bar charts were combined and a coefficient of asymmetry ( $A_s$ ) was determined. This index has been suggested as representing fry condition during early sea life (Kacv 1979).

Between 100 and 400 adult fish were collected in most years for determination of their age, length and fecundity (Table 1). Fry were also sampled both as migrants in the river, and as fry with scales from the bay (Table 1). The author participated in collecting and processing these samples from 1974 to 1988, and from 1989 to 1995 determined age and annual scale increments from samples collected by A.I. Ardavichus.

Significance of the difference between means was assessed using the formula from Plochinsky (1970, p. 296):

$$F_d = [(M_1 - M_2)^2 \sigma_z^{-2}] [n_1 n_2 (n_1 + n_2)^{-1}] \geq F_{st}$$

where  $F_d$  is Fisher's criterion for significant difference;

$M_1 - M_2$  is the difference between means;

$n_1, n_2$  is the number of fish in first and second samples;

$\sigma_z^2 = [(n_1 - 1) \sigma_1^2 + (n_2 - 1) \sigma_2^2] (n_1 + n_2 - 2)^{-1}$ ;  $\sigma$  - means standard deviation;

$F_{st}$  - standard values of Fisher criterion at 95 %, 99 % and 99.9 % significance levels.

**Table 1.** Numbers of adult chum salmon sampled annually for age, length and female fecundity from commercial catches near mouths of rivers in the Kuril Bay area (Iturup Island) 1974–1995, numbers of downstream migrating fry in the Rybatskaya River sampled for length, and numbers of fry sampled in the bay for length, and number of sclerites on their scales.

| Year | Numbers of adult chum salmon |           | Numbers of fry |     |
|------|------------------------------|-----------|----------------|-----|
|      | Age and Length               | Fecundity | River          | Bay |
| 1974 | 300                          | 130       | 263            | 287 |
| 1975 | 300                          | 121       | 93             | 106 |
| 1976 | 400                          | 202       | -              | 143 |
| 1977 | 200                          | 102       | 112            | 188 |
| 1978 | 200                          | 103       | 158            | 274 |
| 1979 | 300                          | 140       | 176            | 276 |
| 1980 | 300                          | 156       | 256            | 323 |
| 1981 | 271                          | 162       | 319            | 163 |
| 1982 | 100                          | 44        | 254            | 144 |
| 1983 | 300                          | 95        | 322            | 274 |
| 1984 | 200                          | 120       | 396            | 461 |
| 1985 | 300                          | 168       | 403            | 323 |
| 1986 | 380                          | 183       | 321            | 260 |
| 1987 | 300                          | 134       | 631            | 329 |
| 1988 | 200                          | 99        | 536            | 225 |
| 1989 | 200                          | 79        | -              | -   |
| 1990 | 188                          | 90        | -              | -   |
| 1991 | 193                          | 36        | -              | -   |
| 1992 | 207                          | -         | -              | -   |
| 1993 | 149                          | 29        | -              | -   |
| 1994 | 193                          | -         | -              | -   |
| 1995 | 197                          | 19        | -              | -   |

## RESULTS

Chum salmon return to spawn in the rivers of Iturup Island at the age of 0.2–0.6. Fish of the most abundant age groups (0.3 and 0.4) were used to follow long-term changes in body length and fecundity. First, anomalies in chum salmon growth were noticed in the second half of the 1980s (Kaev 1994), and therefore data were grouped by year of return before and after 1985. Mean fish length from 1974–1984 was significantly greater ( $p < 0.05$  Fisher test) than from 1985–1995 (Table 2). Annual growth did not decline uniformly at all ages. The growth of age 0.3 fish decreased in the third year of life, and growth of age 0.4 fish decreased in the third and fourth years of life. There were no significant differences in length in both age groups when aged 0.1.

Together with reduced growth, variability in length increased in recent years. This is illustrated by age 0.4 fish, which have growth marks at both age 0.3 and 0.4, that is at both ages at which anomalously low annual growth appears. In the most recent 10 years, annual growth increment for age 0.4 fish has increased compared to 0.3, and the coefficient of variation has also increased (Fig. 1). A significant decrease in female fecundity in this period was also noted (Table 2).

In recent years the proportion of older chum salmon in returns has increased. The proportion of age 0.2 fish declined by half, the proportion of 0.3 also declined, and the proportions of older fish increased respectively (Table 3). The proportions of

age 0.2, 0.5 and 0.6 fish among returns were very small, and therefore to characterize chum salmon age trends, the percentage relationship of age 0.4 fish in the total of age 0.3 and 0.4 fish was used. Not only did the proportion of older fish increase, but also the fluctuation of ages in returns in contiguous years increased (Fig. 2). The increased variability occurred despite a reduction in average abundance of chum salmon. For instance, the returns of chum salmon in 1971–1981 averaged 315,000 individuals, and the difference in numbers between contiguous generations averaged 2.2 times, while returns of 1982–1991 averaged only 48,000 individuals, with contiguous generations differing by a factor of 3.6 times.

Estimated survival from egg to downstream migrant (downstream migration coefficient, Fig. 3), and mean length of fry migrants (Fig. 4) tended to increase as the proportion of parents aged 0.4 increased over the proportion aged 0.3. Fry length in different years was associated with the average age of their parents ( $R^2 = 0.37$ ;  $n = 12$ ;  $p < 0.05$ ) rather than their parents' body length ( $R^2 = 0.04$ ;  $n = 12$ ;  $p > 0.05$ ).

In recent years chum salmon survival at sea declined. Marine survival of brood year classes from 1973–1981 ranged from 0.57 to 1.90%. In later years survival at sea declined, ranging from 0.12 to 0.84% (Fig. 5). Because of the dependence of marine survival on the asymmetry of fry growth, representing condition, in the coastal zone before 1982 and after 1982, one can say that condition appeared to be a factor determining chum salmon survival in the sea.

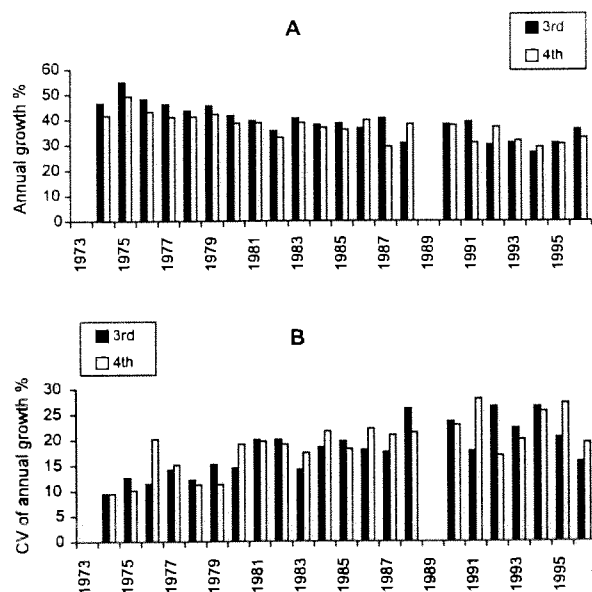
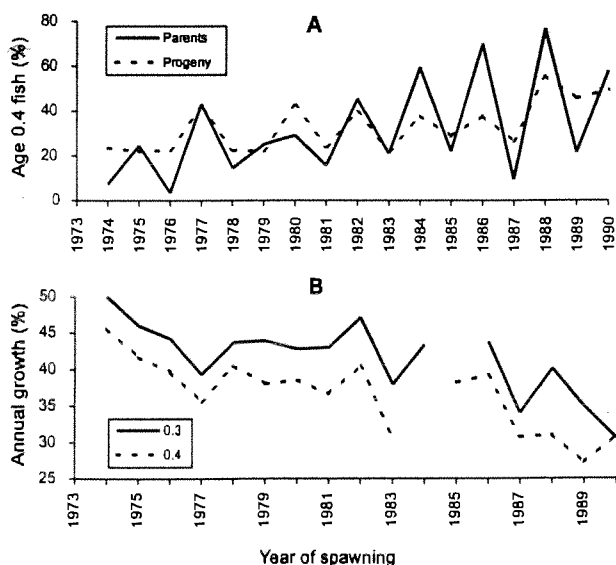
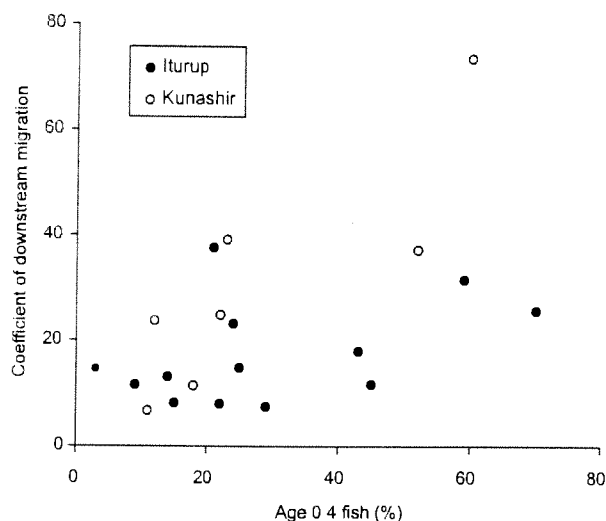
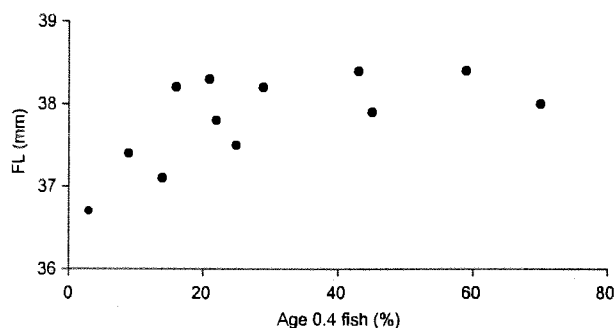
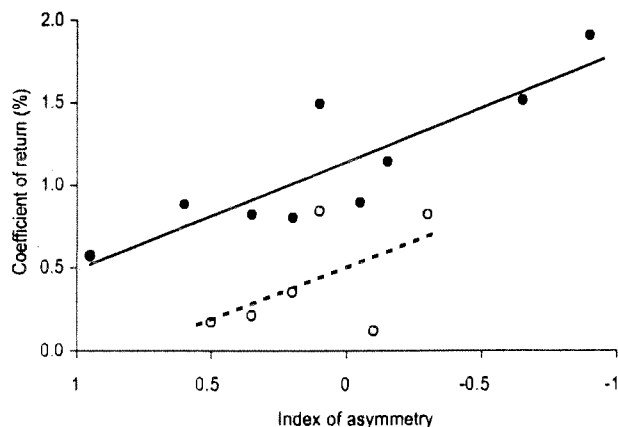
**Table 2.** Absolute fecundity (AF, eggs), fork length (FL, cm) and annual mean length increment (FL<sub>i</sub>, cm) of chum salmon at Iturup Island at the age of 0.3 and 0.4 during two periods.

| Age | Indices         | 1974–1984 |      |          | Fisher criterion | 1985–1995 |      |          |
|-----|-----------------|-----------|------|----------|------------------|-----------|------|----------|
|     |                 | Mean      | S.D. | <i>n</i> |                  | Mean      | S.D. | <i>n</i> |
| 0.3 | AF              | 2550      | 232  | 11       | 12.01**          | 2261      | 101  | 9        |
|     | FL              | 71.22     | 1.16 | 11       | 21.50***         | 68.22     | 1.77 | 10       |
|     | FL <sub>1</sub> | 27.67     | 0.73 | 11       | 0.01             | 27.71     | 1.27 | 10       |
|     | FL <sub>2</sub> | 16.75     | 0.57 | 11       | 0.55             | 16.53     | 0.78 | 10       |
|     | FL <sub>3</sub> | 12.31     | 0.83 | 11       | 14.73**          | 10.75     | 1.03 | 10       |
|     | FL <sub>4</sub> | 14.48     | 0.73 | 11       | 4.53*            | 13.25     | 1.76 | 10       |
| 0.4 | AF              | 2613      | 179  | 11       | 15.12**          | 2294      | 173  | 8        |
|     | FL              | 76.80     | 1.78 | 11       | 24.95***         | 72.67     | 2.01 | 10       |
|     | FL <sub>1</sub> | 26.85     | 0.69 | 11       | 0.75             | 27.25     | 1.35 | 10       |
|     | FL <sub>2</sub> | 16.37     | 0.81 | 11       | 2.39             | 15.82     | 0.82 | 10       |
|     | FL <sub>3</sub> | 11.65     | 1.30 | 11       | 21.70***         | 9.24      | 1.04 | 10       |
|     | FL <sub>4</sub> | 10.81     | 0.94 | 11       | 14.86**          | 9.17      | 1.01 | 10       |
|     | FL <sub>5</sub> | 11.07     | 0.79 | 11       | 0.66             | 11.18     | 1.07 | 10       |

Note: \*symbols, values of Fisher's criterion exceeding the critical values at 95% (\*), 99% (\*\*) and 99.9% (\*\*\*) significance levels comparing means in the two periods; SD, standard deviation; *n*, number of observation years; F<sub>1</sub>, F<sub>2</sub>..., annual mean length increments in 1, 2... and last not full year of life.

**Table 3.** Proportion of different age chum salmon from Kuril Bay (Iturup Island) in 1974–1984 and in 1985–1995.

| Years     | Percentage of chum salmon at age |      |      |     |     |
|-----------|----------------------------------|------|------|-----|-----|
|           | 0.2                              | 0.3  | 0.4  | 0.5 | 0.6 |
| 1974–1984 | 6.1                              | 69.2 | 24.3 | 0.4 | 0   |
| 1985–1995 | 2.8                              | 55.5 | 40.8 | 0.8 | 0.1 |

**Fig. 1.** Average growth in length during the third and fourth year (A), as a percentage of growth during the first year of life, and coefficient of variation (CV) of growth (B) during the third and fourth year of Iturup Island age 0.4 chum salmon maturing in 1974–1996.**Fig. 2.** Proportion of returning age 0.4 chum salmon and the corresponding proportion of age 0.4 fish of their parents (A), and the growth rate in the third year of life of age 0.3 and age 0.4 fish (B).A:  $R^2 = 0.59$ ;  $p < 0.001$ ;  $n = 17$ .**Fig. 3.** Relationship between the coefficient of downstream migration (estimated survival egg to fry) of chum salmon and proportion of older (age 0.4) parents in rivers of Iturup Island (1975–1987) and Kunashir Island (1990–1991, 1994–1998). For Iturup chum salmon:  $R^2 = 0.18$ ;  $p > 0.05$ ;  $n = 13$ .**Fig. 4.** Relationship between fork length of downstream migrating chum salmon fry in the Iturup Island rivers in 1977–1988 and the proportion of age 0.4 fish among their parents.  $R^2 = 0.37$ ;  $p < 0.05$ ;  $n = 12$ .**Fig. 5.** Relation between coefficient of return of chum salmon and index of asymmetry (condition) of fry in the coastal shallows of Iturup Island for broods from 1973–1981 (dark circles, full line) and from 1982–1987 (light circles, dotted line).1973–1981:  $Y = 1.14 - 0.65x$ ;  $R^2 = 0.76$ ;  $p < 0.01$ ;  $n = 9$ .1982–1987:  $Y = 0.50 - 0.63x$ ;  $R^2 = 0.29$ ;  $p > 0.05$ ;  $n = 6$ .



## DISCUSSION

The results of the Iturup Island chum salmon monitoring indicate considerable change in reproductive success in recent years. The reduction in chum salmon length and fecundity, and increasing age of spawners coincided with an increase in survival of fry prior to entering the sea, and a decrease thereafter. The reduction in annual growth at sea has been recorded for different chum salmon populations on Asian coasts (Kaev 1994; Kaeriyama 1996) and American coasts (Helle and Hoffman 1995) of the Northern Pacific Ocean. Moreover the "disruption" of chum salmon growth appeared to be not only in reduction of annual growth, especially after the second year of life in the ocean, during the period 1985–1992 compared to 1976–1980 (Kaeriyama 1996), but in the increased variability of annual growth in the latter period (Kaev 1994).

The reduction in size of returning adults may be caused by a density-dependent factor arising from the doubling of Pacific salmon abundance since the early 1980s (Bigler et al. 1996). But other factors must be taken into account: (a) a documented re-establishment of zooplankton communities in the early 1990s (Shuntov et al. 1996), (b) strong differences in annual growth increments for contiguous years (Fig. 1), (c) no significant changes in chum salmon growth in Sakhalin, Kuril and Hokkaido populations during the first and second year of life, when living in the Okhotsk Sea and adjacent waters of the Pacific Ocean.

Increasing age of chum salmon spawners could be expected as a result of reduced growth in recent years (Gritsenko and Kovtun 1986; Nikolaeva 1987). Older age with slower growth has also been described in chum salmon of American and Asiatic origins (Helle and Hoffman 1995; Kaeriyama 1996). As noted above, the Iturup Island chum salmon have also become older and smaller. However, analyses do not confirm a deceleration in maturity with slow growth.

The increased age of chum salmon spawners in recent years was apparently caused by the interaction of two factors: the rate of sexual maturation and appearance of contiguous generations greatly differing from each other in abundance. That is, at return of age 0.3 chum salmon of a less abundant brood the proportion of age 0.4 fish appears greater in that year because of the return of age 0.4 adults of the preceding much more abundant cohort. As a result not only is the number of spawning fish increased, but also the age and proportion of females is increased (females accounted for 65.7% of age 0.4 fish). Thus, in most cases, the slower growing cohorts of chum salmon matured younger. A strong relationship (Fig. 2) between the age of parents and their progeny was revealed, which speaks in favor of genetic control of chum salmon age at sexual maturation.

The increased proportion of older fish on spawning grounds is also important. Earlier a significant reduction in fecundity and increase in egg weight with age in equally sized females was observed for chum salmon (Kaev and Kaeva 1986). As in single-age populations of pink salmon (*O. gorbuscha*), not only does the number of eggs produced increase with size within an age group of chum salmon, but egg size is also weakly correlated with body length (Kaev and Kaeva 1986). Therefore, fecundity within age groups is subject to both quantitative and qualitative changes with increase in age. In some years older females can be less fecund than young ones, but their average egg size is larger. In this respect the increased age of chum salmon spawning in recent years means not so much a proportional increase in larger and more fecund older females, as an increase in females with larger eggs.

A tendency of migrant fry body length to increase with parental age was shown (Fig. 4). Although fry of smaller length resulted from parents with a wide range of ages, nevertheless the largest fry originated from older parents with potentially large eggs, and the smallest fry from younger parents with potentially small eggs.

Large-sized progeny from large eggs is well known. High survival of progeny from older parents or from larger eggs has also been reported (Wallace and Aasjord 1984; Hislop 1988; Helle 1989; Markovich et al. 1993). Differential survival of progeny may be due to better protection of deeper-buried eggs during embryogenesis (Van den Berghe and Gross 1989), or the selective mortality of different-sized juveniles (West and Larkin 1987; Kaev 1992). Therefore it would be expected that greater survival from the egg to the downstream migrant would be associated with older parents (Fig. 3). Because of many incidental factors (river floods, changes in flow of ground water and so on) the relationship was not significant. However, in all the years with higher proportions of age 0.4 spawners, the ratios of fry migrant numbers to egg numbers were higher than the average long-term ratio. Analogous data for chum salmon from the Ilyushin River (Kunashir Island) show a similar trend (Fig. 3).

## CONCLUSIONS

A reduction of chum salmon length and fecundity in 1985–1995 compared to 1974–1984 was observed in Iturup Island chum salmon. These changes were accompanied by an increase of chum salmon growth variability and an increase in their mortality in the ocean. Fry growth in the coastal zone was positively associated with survival for individual cohorts. In most cases the slower growing cohorts of chum salmon may have matured younger. A strong positive

relationship between the age of parents and their progeny was found, which suggests a genetic influence on chum salmon age of sexual maturation. A mixed chum salmon age composition is an important component in maintaining a stable reproductive potential in a population, not only because interannual fluctuations in numbers of spawners are smoothed over succeeding generations, but also because qualitative differences in spawning fish increase reproductive efficiency. This should be considered as an example of reproductive homeostasis.

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# Wild and Hatchery Production and Recruitment of Autumn Chum Salmon (*Oncorhynchus keta* Walbaum) in the Tym River, Sakhalin, 1960–1998

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**Keywords:** Fishery, return, abundance, chum salmon, wild and hatchery production, differentiation

**Abstract:** The state of the Tym River chum salmon (*Oncorhynchus keta*) stock is assessed by the fishery from the number of fish returning after feeding from two to five years in the Pacific Ocean. Ocean feeding conditions probably generally determine their survival. Chum salmon returns to the Tym River greatly decreased for the recent ten years. A regular annual driftnet fishery in the Pacific Ocean may negatively affect chum salmon abundance. This is supported in part by the analysis of data on chum salmon reproduction and returns to the Tym River for the period 1960–1998. Since the level of chum salmon abundance in the Tym River is maintained by the combined wild and hatchery production, we divided a total fish return into wild and hatchery, and determined the optimal number of spawners entering the Tym River spawning grounds in order to estimate the efficiency of wild spawning and hatchery production. It appeared that chum salmon returns from wild spawning are five times more than hatchery ones. Tendencies of returns to decrease for wild and hatchery chum salmon are identical, which suggests the same factors affect the survival of both wild and hatchery fish.

## INTRODUCTION

Several species of salmonids enter the Tym River to spawn, and the most abundant of them is chum salmon (*Oncorhynchus keta*). Currently chum salmon abundance is depressed (Table 1). Chum salmon returns may have decreased not only because of the regular driftnet salmon fishery in the Pacific Ocean, but also because of poor survival in the ocean due to other factors.

The objective of this work is an analysis of wild and hatchery chum salmon returns to the Tym River for the period 1960–1998 by assessing the mixed chum salmon runs to that river for spawning efficiency of wild and hatchery fish, by comparing the return coefficients (RC) of wild and hatchery chum salmon, including those in the mixed catches from Niysky Bay. Since 1993 only a control catch for research and a catch by a small number of people of the North for their needs have been allowed in Niysky Bay. The average annual capture is 17.1% of a total chum salmon abundance during a six-year fishery closure. I also wanted to determine the optimal spawning numbers for the Tym River spawning

grounds using the Ricker curve in a preliminary analysis of the “spawner-recruit” relationship model.

## MATERIAL AND METHODS

The Tym River is one of the largest Sakhalin rivers. Its length is 325 km, and its basin area 7,850 km<sup>2</sup>. The Tym River can be divided into three sections: fast flowing upper river, from the river-head to the confluence of two branches near the settlement of Kirovskoye; the middle river with medium currents, from the settlement of Kirovskoye to the Nysh River falls; slow flowing lower river, from the mouth of Nysh River to Niysky Bay. During the August–October chum salmon spawning in the upper section containing 60% of total spawning grounds, current ranges from 0.05 to 1.0 m/sec. In February the rate does not exceed 0.7 m/sec, averaging 0.3 m/sec (Gritsenko et al. 1987). According to Rukhlov (1969), the Tym River spawning grounds are 37.1% gravel (0.2–2.0 cm), 40.7% pebble (2.1–10 cm) 14% sand and 8.2% cobble (more than 10 cm). The depth is 0.5–1.0 m, and the river width at low-water ranges from 20 to 30 m. In its middle section the river

**Table 1.** Numbers of chum salmon spawners returning to and fry migrating from the Tym River, and numbers of adults caught in Niysky Bay.

| Year  | Spawners entering the river, thou. ind. |                   | Density on the spawning grounds, ind./100 m <sup>2</sup> | Catch  |            | Taken by fish culturists in Rybovodny Spring |            |
|-------|-----------------------------------------|-------------------|----------------------------------------------------------|--------|------------|----------------------------------------------|------------|
|       | Near Kirovskoye                         | Total river basin |                                                          | Tons   | Thou. ind. | Tons                                         | Thou. ind. |
| 1987  | 530.5                                   | 575.6             | 65.5                                                     | 1227.4 | 323.4      | 180.0                                        | 52.9       |
| 1988  | 318.0                                   | 689.5             | 78.3                                                     | 708.7  | 172.9      | 160.0                                        | 38.8       |
| 1989  | 43.0                                    | 80.2              | 9.1                                                      | 263.3  | 64.2       | 160.0                                        | 44.4       |
| 1990  | 62.3                                    | 135.1             | 15.1                                                     | 347.1  | 102.1      | 260.7                                        | 75.4       |
| 1991  | 50.0                                    | 108.5             | 12.3                                                     | 332.8  | 95.1       | 209.0                                        | 62.8       |
| 1992  | 17.7                                    | 33.5              | 2.0                                                      | 260.0  | 74.3       | 144.0                                        | 45.0       |
| Aver. | 170.2                                   | 270.4             | 30.4                                                     | 523.2  | 138.7      | 185.6                                        | 53.2       |
| 1993  | 58.8                                    | 111.4             | 6.5                                                      | 73.2   | 17.9       | 83.1                                         | 21.5       |
| 1994  | 84.2                                    | 159.6             | 9.3                                                      | 76.2   | 19.6       | 86.4                                         | 15.7+11.0* |
| 1995  | 102.1                                   | 193.3             | 11.2                                                     | 106.9  | 27.4       | 202.8                                        | 28.6+24.0* |
| 1996  | 25.2                                    | 47.8              | 2.8                                                      | 97.3   | 24.3       | 147.9                                        | 27.4+9.6*  |
| 1997  | 100.0                                   | 184.7             | 10.7                                                     | 90.4   | 27.4       | 120.2                                        | 22.7+13.7* |
| 1998  | ind                                     | 10.0              | 0.6                                                      | 76.4   | 21.8       | 88.6                                         | 18.1+7.2*  |
| Aver. | 61.7                                    | 117.8             | 6.9                                                      | 86.7   | 23.1       | 121.5                                        | 21.9+13.1* |

\* Including the catch of spawners in Pilenga River

\*\* Release of fry chum salmon from the hatchery "Pilenga Godo"

continue...

reaches 30–100 m in width. The depths in pools are up to 3 m, in reaches 15–20 cm, with sand and pebble spits often appearing near the banks, especially in the lower river. A tidal bore spreads 25–30 km up the river on spring tides, and on heap tides as far as 20 km (Gritsenko et al. 1987). Water in the Tym River system originates mainly from winter precipitation, and less from summer rains. The spring flood usually starts in the third week of April, and its peak is recorded in mid-May.

I use the term "return coefficient" (RC), which is percent survival at sea from the time chum salmon fry descend downstream to the time of return to spawn, including spawners caught in the local fishery as well as those entering spawning grounds or the hatchery. In 1993, for instance, 45 million fry migrated downstream, and 85,800 adults returned from 1995 to 1998. The percentage of returning adults to fry migrants was 0.191%, the RC. Since 1987 to 1994, the RC of wild and hatchery chum salmon varied from 0.19 to 0.42%, and averaged 0.27% (Table 2).

When estimating the proportions of hatchery and wild chum salmon returning to the Tym River spawning grounds, some assumptions were made:

1. The returns of chum salmon released from the two hatcheries located in the middle section of the

Tym River (Ado-Tymovsky and Pilenga Godo) are fully accounted for by numbers recorded near the hatcheries (Rybovodny Spring, a tributary of Pilenga River).

2. The proportion of hatchery fish taken during fishing in Niysky Bay is assumed to be equal to the proportion of hatchery fish in the total of reproducing fish.

3. Only wild chum salmon arrive at the Tym River spawning grounds.

4. Age structures of chum salmon from the upper sites of spawning grounds, from hatcheries located in the middle section, and from the fishery in the lower section are assumed to be the same at every site, because it was shown earlier from an analysis of scales, that growth of chum salmon from different spawning sites is not significantly different (Kovtun 1981).

Until the early 1990s the area of chum salmon spawning ground in the Tym River was 880,000 m<sup>2</sup>. Of this 60% (528,000 m<sup>2</sup>) fell in the upper river near the settlement of Kirovskoye (Gritsenko et al. 1987). Over several years, after the Tym River ceased being used for timber rafting, spawning grounds began to recover. As a result, new estimates of spawning ground have risen by a factor of almost two. At present the spawning area accounts for 1,723,000 m<sup>2</sup>.

Table 1. continued.

| Total number of<br>chum salmon,<br>thou.ind. | Commercial<br>catch, % of total | Number of downstream migrants, millions |                                       |                            |       | Percentage<br>migrants from<br>hatcheries |
|----------------------------------------------|---------------------------------|-----------------------------------------|---------------------------------------|----------------------------|-------|-------------------------------------------|
|                                              |                                 | Near<br>Kirovskoye                      | From all river<br>spawning<br>grounds | Release from<br>hatcheries | Total |                                           |
| 951.1                                        | 33.9                            | 18.0                                    | 31.0                                  | 53.4                       | 84.4  | 63.2                                      |
| 901.2                                        | 19.2                            | 23.4                                    | 50.4                                  | 53.7                       | 104.1 | 51.6                                      |
| 188.8                                        | 34.0                            | 27.0                                    | 50.5                                  | 49.2                       | 99.1  | 49.3                                      |
| 312.6                                        | 32.7                            | 4.8                                     | 9.0                                   | 47.0+4.3**                 | 60.3  | 85.1                                      |
| 266.4                                        | 35.7                            | 13.9                                    | 29.9                                  | 48.3+29.5**                | 107.7 | 72.3                                      |
| 152.8                                        | 48.6                            | 8.1                                     | 13.5                                  | 40.3+18.8                  | 72.6  | 59.1                                      |
| 462.3                                        | 34.0                            | 15.9                                    | 30.7                                  | 48.7+17.5**                | 88.1  | 63.4                                      |
| 150.8                                        | 11.9                            | 2.6                                     | 4.4                                   | 27.0+13.6**                | 45.0  | 90.2                                      |
| 205.9                                        | 9.5                             | 15.4                                    | 25.7                                  | 25.6+0.17**                | 51.5  | 50.1                                      |
| 272.7                                        | 10.0                            | 9.0                                     | 15.0                                  | 18.5+11.5**                | 45.0  | 66.7                                      |
| 109.1                                        | 22.3                            | 14.6                                    | 24.4                                  | 36.0+14.4**                | 74.8  | 67.4                                      |
| 248.5                                        | 11.0                            | 2.0                                     | 3.3                                   | 27.7+15.5**                | 46.5  | 92.9                                      |
| 57.1                                         | 38.2                            | 15.7                                    | 26.2                                  | 37.2+10.8**                | 74.2  | 64.7                                      |
| 174.0                                        | 17.1                            | 9.9                                     | 16.5                                  | 28.7+11.0**                | 56.2  | 72.0                                      |

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Spawners entering the river and fry migrating downstream annually were counted at the upper section and estimated for the total basin.

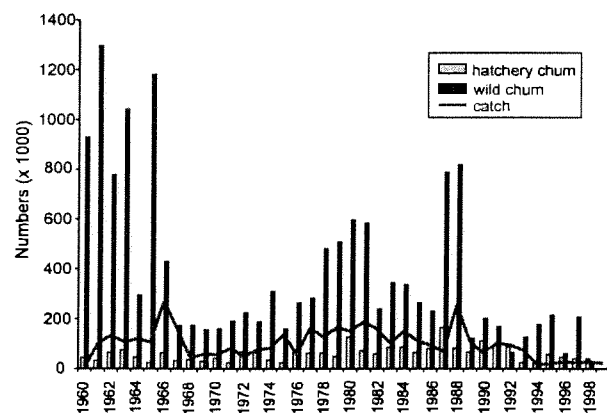
The previous measure of spawning area (880,000 m<sup>2</sup>) was used when estimating optimal spawning escapement during the period 1960–1994, and only in the final estimation of density for optimal spawning grounds was the modern area (1,723,000 m<sup>2</sup>) used.

## RESULTS AND DISCUSSION

Except in 1992 and 1998, hatchery chum salmon returns have been less than returns of wild fish (Fig. 1). For the entire study period the number of hatchery fish returning has been low, 63,100 individuals. The number of wild spawners, 313,600 is almost five times higher. The number of downstream wild migrants from the spawning grounds is only 1.2 times that of hatchery fish, but their survival is higher (Gritsenko et al. 1987) (Table 1).

Low chum salmon returns from hatchery propagation can be explained in part by the unfortunate need to transport eggs for incubation from the upper section of Tym River to Rybovodny Spring (middle section), where the Ado-Tymovsky Hatchery is located. During years of transportation (1976–1986), only fish with mature gonads were observed returning to Rybovodny Spring. Gonad maturation rate for

Fig. 1. Numbers of hatchery and wild Tym River chum salmon and their combined catch in Niysky Bay for the period 1960–1998.



chum salmon spawning in upper section of Tym River is slower than from that in the middle section. Volovik and Landyshevskaya (1968) suggested that the maturation rate was caused by the remoteness of spawning grounds from the sea, and the duration of migrations by fry and mature fish in fresh waters. It had to be considered a hereditary feature.

Ricker (1972), analyzed the results of transport of many salmon eggs and concluded that effects were almost always negative. Returns from transported eggs may be much lower than from local eggs, even

**Table 2.** Numbers of chum salmon (wild and hatchery) from various brood years leaving from and returning to the Tym River, and their percent return (Return Coefficient, RC).

| Year of return (new brood year) | Numbers of adults entering to spawn (thousands) | Numbers of fry migrating (millions) | Numbers of offspring returning |        |        |        |        |        |
|---------------------------------|-------------------------------------------------|-------------------------------------|--------------------------------|--------|--------|--------|--------|--------|
|                                 |                                                 |                                     | 1984                           | 1985   | 1986   | 1987   | 1988   | 1989   |
| 1987                            | 951.9                                           | 84.4                                | 606360                         | 18086  |        |        |        |        |
| 1988                            | 901.9                                           | 104.1                               | 295594                         | 598397 | 7210   |        |        |        |
| 1989                            | 188.8                                           | 99.7                                |                                | 90812  | 92890  | 5098   |        |        |
| 1990                            | 312.6                                           | 60.3                                |                                |        | 114412 | 186935 | 11253  |        |
| 1991                            | 266.4                                           | 107.7                               |                                |        |        | 79121  | 159840 | 27439  |
| 1992                            | 152.8                                           | 72.6                                |                                |        |        |        | 40645  | 103446 |
| 1993                            | 150.8                                           | 45.0                                |                                |        |        |        |        | 48559  |
| 1994                            | 205.8                                           | 51.5                                |                                |        |        |        |        | 5353   |
| 1995                            | 272.7                                           | 45.0                                |                                |        |        |        |        |        |
| 1996                            | 109.1                                           | 74.8                                |                                |        |        |        |        |        |
| 1997                            | 248.5                                           | 46.5                                |                                |        |        |        |        |        |
| 1998                            | 57.1                                            | 74.2                                |                                |        |        |        |        |        |
| Total returns                   |                                                 |                                     |                                | 707296 | 214512 | 271154 | 211738 | 184796 |
| Average percent return:         |                                                 |                                     |                                |        |        |        |        |        |

continue ...

if the transportation is carried out within the same river basin. Transported salmon retain the timing of runs and spawning according to their origin (Okazaki 1982). Ado-Tymovsky Hatchery is located far from natural spawning grounds, to ensure reproductive isolation from wild chum salmon. This helps avoid detrimental genetic mixing between hatchery and wild chum salmon, against which some specialists have warned (Barns 1976; Helle 1976).

Annual fluctuations in wild chum salmon returns ranged from 16,200 to 1,297,200, a factor of 80. The number of returning hatchery chum salmon ranged from 23,400 to 164,700, a factor of 7 (Fig. 1).

Wild chum salmon runs were highest during the early 1960s and late 1970s to early 1980s. The first maximum was about 1.3 million individuals, the second was almost half that (600,000 individuals). Chum salmon returns during 1987–1988, unexpectedly increased to 800,000. They were offspring of adults returning in 1984, that produced high numbers of four-year old chum salmon in 1987, and five-year old fish in 1988. Chum salmon returns in the 1990s decreased in numbers by almost 4 times, and did not rise above 215,000 individuals.

A comparison of the returns of hatchery chum salmon with those of wild fish shows parallel fluctuations in abundance, which suggests the influence the same survival factors during feeding migrations at sea. At present, hatchery and wild chum salmon co-exist as two reproductively independent populations (Gritsenko and Kovtun 1991). Since conditions for marine survival appear to be similar, when forecasting abundance by the method of Bird (1982), the total number of wild and hatchery fry migrants is considered.

After separation of the number of wild and hatchery returns, RCs were calculated for both stocks separately for the period 1960–1992. The average long-term RC for wild chum salmon was 1.006% with a range from 0.152 to 2.864%. For hatchery chum salmon this index was 0.142% with a range from 0.063 to 0.294%. Judging from these data the survival of wild chum salmon from the Tym River basin appears to be about seven times higher than that for hatchery chum salmon (Fig. 2). Fewer hatchery migrants and lower survival at sea resulted in five times more wild fish being caught in the Niysky Bay fishery.

Earlier Gritsenko et al. reported (1987) that survival of larvae in redds increased with numbers of spawners to 450,000–500,000 individuals, then began to decrease as numbers of spawners rose further. The number of fry migrating downstream is positively

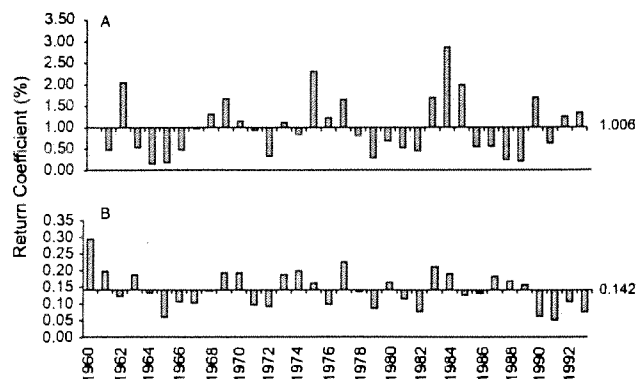
**Fig. 2.** Percent survival (RC) of wild (A) and hatchery (B) Tym River chum salmon from migrating fry to returning adult (+ commercial fishery catch in Niysky Bay) shown for each year as deviation from the average of all years from 1960–1995.



Table 2. continued.

| from previous brood years |        |        |       |        |       |      | Total offspring<br>returning,<br>(thousands) | Percent<br>returning (RC) |
|---------------------------|--------|--------|-------|--------|-------|------|----------------------------------------------|---------------------------|
| 1990                      | 1991   | 1992   | 1993  | 1994   | 1995  | 1996 |                                              |                           |
|                           |        |        |       |        |       |      | 271.1                                        | 0.321                     |
|                           |        |        |       |        |       |      | 211.7                                        | 0.203                     |
|                           |        |        |       |        |       |      | 184.8                                        | 0.186                     |
|                           |        |        |       |        |       |      | 184.9                                        | 0.307                     |
|                           |        |        |       |        |       |      | 228.1                                        | 0.212                     |
| 8710                      |        |        |       |        |       |      | 231.8                                        | 0.319                     |
| 97718                     | 4524   |        |       |        |       |      | 85.8                                         | 0.191                     |
| 76595                     | 120863 | 3089   |       |        |       |      | 216.5                                        | 0.420                     |
| 1909                      | 100899 | 167165 | 2727  |        |       |      |                                              |                           |
|                           | 1855   | 61532  | 44622 | 1091   |       |      |                                              |                           |
|                           |        |        | 37772 | 195073 | 15655 |      |                                              |                           |
|                           |        |        | 628   | 20328  | 34660 | 1484 |                                              |                           |
| 184932                    | 228141 | 231786 | 85749 | 216492 |       |      |                                              |                           |
|                           |        |        |       |        |       |      |                                              | 0.270                     |

...continued

correlated ( $r = 0.53$ ) with the number of spawners entering the Tym River spawning grounds during 1960–1998. This relationship is described as follows:  $X = 23.751 + 0.528Y$  (Fig. 3).

Higher numbers of spawners were observed in the 1960s, as was the maximum number of fry migrants. In the 1990s the return of spawners decreased, and so too did the number of migrating fry. This relationship was described by a parabolic curve, as before (Gritsenko and Kovtun 1991). According to this curve, maximum numbers of spawners (900,000–950,000) result in the greatest numbers of fry migrating downstream (70–75 million).

The relationship between the number of fry per female and the number of spawning females shows, apparently, that the fewer the number of females spawning, the greater the number of downstream migrants per female (Fig. 4). In the 1990s the deviation from the mean long-term value (328.7 fry/female) is significant (150 fry/female) (Fig. 5).

Fig. 3. Relation between the number of fry migrating downstream and the number of spawners entering the Tym River for the period 1960–1998.

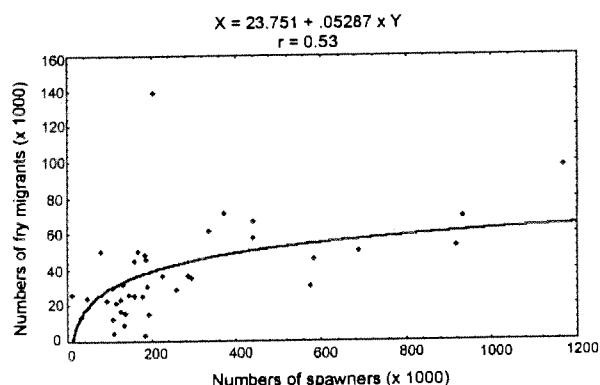


Fig. 4. Relation between numbers of the chum salmon fry migrants per female and numbers of spawning females in Tym River for the period 1960–1998.

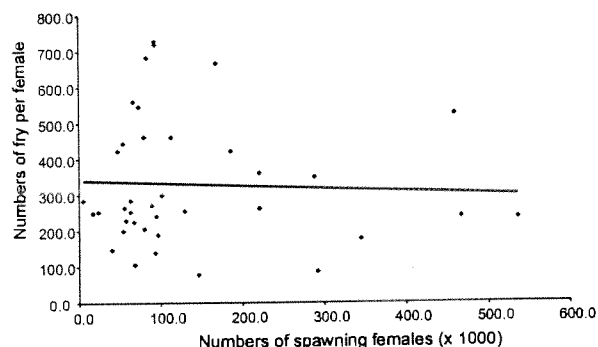


Fig. 5. Numbers of chum fry migrants per female shown as the deviation from the average for the years 1961–1998.



The second form of the Ricker “spawner-recruit” model was chosen for estimation of the optimal number of spawners when parents (P) and recruits (R) were measured in the same units (Ricker 1979). The Ricker model reflects the relationship between the number of spawners entering to spawn (parents)

and the number of their offspring returning (recruits), expressed in thousands of individuals. The second form of this relationship is:

$$R = Pe^{a(1-P/Pe)} \quad (1)$$

where R is the number of recruits; P is the number of parents; a is a dimensionless parameter.

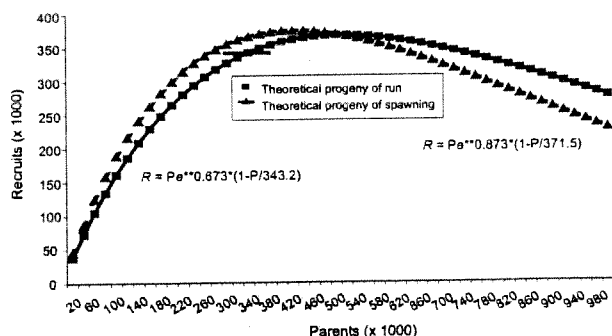
Data from 33 years were used to construct the Ricker curves, and two curves were produced:

1. Return from the spawners' entrance;
2. Return from the total number of chum salmon in the year of spawning (the curve data are not analyzed) (Fig. 6).

The equation for return from the spawners' entrance was:

$$(1) \quad R = Pe^{0.873(1-P/371.5)} \quad (2)$$

**Fig. 6.** Ricker curves showing numbers of recruits returning to spawn as a function of the numbers of parents in the preceding generation, derived from data from the Tym River chum salmon for the period 1960–1998.



The actual number of spawners entering the spawning grounds (in thousands of individuals) in the following years was introduced into formula (1), and the expected number of recruits was calculated. The optimal number of spawners was calculated for the new area of spawning grounds (1,723,000 m<sup>2</sup>). It was 727,000 individuals. Higher numbers of spawners are not effective, because chum salmon returns decrease above this optimum. Optimum density on spawning grounds is 42 individuals per 100 m<sup>2</sup>. The optimum density is assumed to be constant over a given time, and is used as a reference standard to regulate the Tym River chum salmon stock.

## CONCLUSION

Long-term observations on the status of autumn chum salmon in the Tym River permitted a comparative analysis of reproduction of hatchery and wild chum stocks for the period 1960–1998, and a calculation of RC, the percent survival of the number of fry migrating downstream that returned to spawn or be

caught in the local fishery. The average percent survival within the whole period 1960–1994 was 1.006% for wild, and 0.142% for hatchery chum salmon. The smaller number of hatchery fry migrating downstream and their lower survival at sea mean that during the fishery in Nizhny Bay five times fewer hatchery chum salmon were caught than wild ones.

Numbers of wild and hatchery chum salmon returns varied in parallel, suggesting that the same factors were affecting survival during ocean life. The decrease in all reproductive indices occurred in the last decade, when the driftnet fishery was operating in the Pacific Ocean. The closure in 1993 of the Nizhny Bay fishery did not promote the restoration of stocks. A historically minimal chum salmon return was recorded in 1998 (57,100).

Wild chum salmon are more important for maintaining stock abundance, and based on the Ricker "spawner-recruit" model, 727,000 spawners at an average density of 42 fish per 100 m<sup>2</sup> are necessary for optimal use of the spawning grounds of Tym River (1,723,000 m<sup>2</sup>). In the last decade a significant deficit of spawners on the spawning grounds (16.4% of standard), has caused the decrease in returns.

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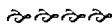


## Application of Microsatellite DNA Variation to Estimation of Stock Composition and Escapement of Skeena River Sockeye Salmon (*Oncorhynchus nerka*)

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**Keywords:** Escapement estimation, microsatellites, sockeye salmon, stock identification

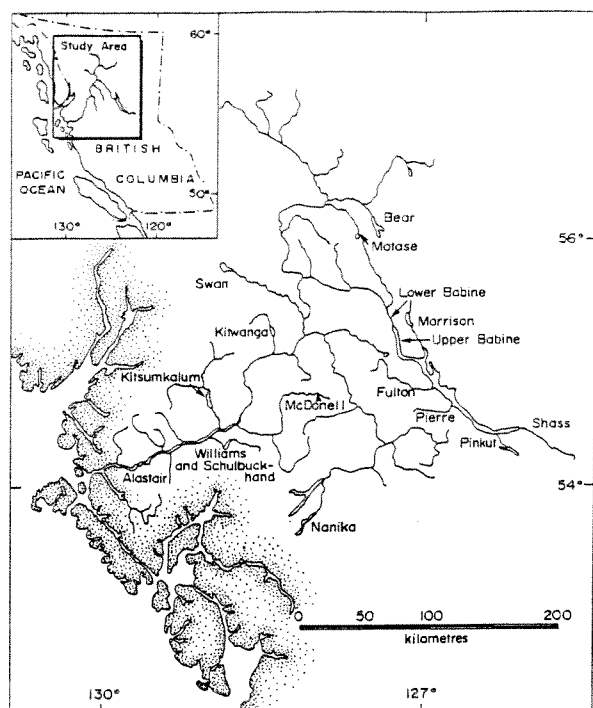
**Abstract:** Microsatellite loci can be used to estimate spawning escapements of individual Pacific salmon populations returning to remote spawning locations throughout large river systems by analysis of appropriately weighted samples from test fisheries near the river mouth. Variation at six microsatellite loci (*Omy77*, *Ots3*, *Ots3*, *Ots3*, *Ots3*, and *Ots3*) was surveyed from approximately 1,700 sockeye salmon (*Oncorhynchus nerka*) from 17 populations in the Skeena River drainage in northern British Columbia, as well as from 1,400 fish in test fisheries conducted in the lower river during 1996–1999. Simulated mixed-stock samples suggested that the six microsatellite DNA loci should enable relatively accurate and precise estimates of stock composition when utilized for fishery management applications within the river. Analysis of the test fishery samples indicated that sockeye salmon from Babine Lake comprised a substantial portion of the returning fish. We also compared population structure of sockeye salmon from both the Skeena and Nass rivers. Simulated and actual mixed-stock samples suggested that accurate estimates of stock composition of sockeye salmon from these two major production areas in northern British Columbia should be obtained in analysis of samples from mixed-stock marine fisheries.

### INTRODUCTION

Sockeye salmon (*Oncorhynchus nerka*) populations returning to the Skeena River in northern British Columbia comprise an important group of populations, second only to those of the Fraser River in British Columbia in terms of sockeye salmon production (Sprout and Kadowaki 1987). The Skeena River drainage contains one very large lake (Babine Lake), and a number of smaller lakes throughout the drainage (Smith and Lucop 1966). Sockeye salmon spawn in over 70 distinct sites and rear in 27 lakes in the watershed, but over 90% of the production has been attributed to Babine Lake and its tributaries (Larkin and McDonald 1968; West and Mason 1987). Production from the Babine Lake system is enhanced by two spawning channels at Fulton River and one at Pinkut Creek. As these facilities can produce over four million returning salmon per year (Wood et al. 1998), fishery managers ideally would target higher exploitation rates on these enhanced populations than on less productive populations within the drainage. However, there is currently no ability to differentiate

enhanced populations from unenhanced populations within the drainage.

Estimation of the number of fish returning to spawn (escapement) is a key aspect of management and assessment of Pacific salmon. In theory, it should be possible to estimate the relative escapements of individual spawning populations by mixed-stock analysis of appropriately weighted samples from test (assessment) fisheries near the river mouth. In practice, the feasibility of this approach has usually been limited by practical difficulties in identifying closely related populations within the same watershed. For the Skeena River, a test fishery has been conducted annually since 1955 near the river mouth at Tyee, and the test fishery provides managers with an index of daily sockeye salmon escapement to the drainage (Jantz et al. 1990). Babine Lake escapement has been estimated at a counting fence since 1949 (Wood et al. 1998), but escapements to other lakes in the system are generally estimated by visual surveys. Previous estimates of stock compositions in the lower river test

**Fig. 1.** Locations of spawning sampling sites in the survey.

fishery derived from analysis of allozymes, age composition, and parasite prevalence characters indicated that Babine Lake populations comprised 70–85% of total drainage escapement during 1987–97 (Rutherford et al. 1999), whereas comparison of escapement surveys suggested that 95% of drainage escapement was derived from Babine Lake populations. It is uncertain whether this discrepancy in the relative abundance of Babine Lake populations is due to errors in stock identification, unrepresentative sampling of the test fishery, or underestimation of the non-Babine component due to visual survey techniques. If representative samples are obtained from the test fishery and an accurate estimate of the Babine Lake stock component is available, then perhaps more accurate estimates of the escapement of the non-Babine Lake component of the returns can be derived than that currently provided by the sum of the visual estimates.

Wood et al. (1994) found that the allozyme variation in the sockeye salmon populations of British Columbia was not strongly regionally structured, and concluded that it would be of limited use for estimation of stock composition in coast-wide mixture problems. However, estimation of stock composition in marine sockeye salmon fisheries remains a continuing area of interest for fisheries managers. Compared with allozyme variation, variation at the more polymorphic, faster-evolving microsatellite loci (Banks et al. 1999) may reveal regional structure in sockeye salmon populations that can be used to provide estimates of stock composition in marine fisheries.

Analysis of microsatellite DNA variation has

improved the ability to identify specific populations of sockeye salmon within major (Beacham and Wood 1999) and minor river systems (Nelson et al. 1998; Beacham et al. 1998, 2000). For Pacific salmonids, microsatellite variation has provided the ability to determine fine-scale population structure (Nielsen et al. 1997; Wenburg et al. 1998) and to provide estimates of stock composition on either a local or regional basis (Small et al. 1998; Beacham et al. 1999; Shaklee et al. 1999). Given the continuing issues in management of the Skeena River sockeye salmon stock complex to which an analysis of microsatellite variation may prove to be beneficial, we initiated a survey of microsatellite variation and evaluated some potential management applications.

Specifically, the objective of the present study was to analyze variation at six microsatellite DNA loci in Skeena River sockeye salmon to describe population structure and evaluate applications for stock identification. We then applied microsatellite DNA technology to estimate stock composition of sockeye salmon sampled during 1996, 1998, and 1999 in a test fishery near the mouth of the Skeena River. We also compared the Skeena River populations with those of the Nass River, another major river system in northern British Columbia, to determine if there was a regional population structure. We evaluated whether microsatellite variation can provide accurate and precise estimates of stock composition for sockeye salmon from the two watersheds when they occur together in marine mixed-stock fisheries.

## MATERIALS AND METHODS

### Collection of DNA Samples and PCR

For the characterization of the baseline populations prior to 1998, DNA was extracted from liver samples of adult sockeye salmon that had been previously collected for protein electrophoretic studies and frozen at  $-20^{\circ}\text{C}$ . The 1998 collections consisted of operculum punches from the Alastair Lake and Kitwanga River populations preserved in ethanol. Approximately 1,700 fish were sampled from 17 populations, with four of the populations sampled in two years (Table 1). Laboratory methods detailing DNA extraction procedures, details of the six loci amplified (*Omy77*, *Ots3*, *Ots100*, *Ots103*, *Ots107*, and *Ots108*), and PCR details were outlined in Beacham and Wood (1999).

### Gel Electrophoresis and Band Analysis

PCR products were size fractionated on 16 cm by 17 cm non-denaturing polyacrylamide gels and visualized by staining with 0.5 mg/ml ethidium bromide

**Table 1.** Population, nursery lake, sample collection years, number of fish sampled per year, and total number of fish sampled for 17 populations of Skeena River sockeye salmon.

| Population          | Nursery Lake | Years      | Number   | Total |
|---------------------|--------------|------------|----------|-------|
| Lower Skeena        |              |            |          |       |
| McDonell Lake       | McDonell     | 1987, 1988 | 81, 75   | 156   |
| Williams Creek      | Lakelse      | 1988       | 98       | 98    |
| Schulbuckhand Creek | Lakelse      | 1988       | 77       | 77    |
| Alastair Lake       | Alastair     | 1988, 1998 | 21, 83   | 104   |
| Kitwanga River      | Kitwanga     | 1998       | 98       | 98    |
| Kitsumkalum River   | Kitsumkalum  | 1994       | 77       | 77    |
| Upper Skeena        |              |            |          |       |
| Motase Lake         | Motase       | 1987       | 50       | 50    |
| Swan Lake           | Swan         | 1988, 1994 | 100, 81  | 181   |
| Bear                | Bear         | 1988       | 71       | 71    |
| Bulkley River       |              |            |          |       |
| Nanika River        | Morice       | 1988       | 75       | 75    |
| Babine Lake         |              |            |          |       |
| Lower Babine River  | Babine       | 1994       | 100      | 100   |
| Upper Babine River  | Babine       | 1987       | 81       | 81    |
| Pinkut Creek        | Babine       | 1990       | 100      | 100   |
| Fulton River        | Babine       | 1990, 1994 | 100, 100 | 200   |
| Morrison River      | Babine       | 1988       | 76       | 76    |
| Shass Creek         | Babine       | 1987       | 78       | 78    |
| Pierre Creek        | Babine       | 1988       | 79       | 79    |

in water and illuminating with ultraviolet light. Nelson et al. (1998) and Beacham and Wood (1999) provided a more complete description of gel electrophoretic conditions. Gels were scanned at a 1024 x 1024 pixel density with a Kodak charge coupled device camera with low light capability and a yellow filter. Images were analyzed using BioImage Whole Band software (Millipore Corp. Imaging Systems, Ann Arbor, Michigan), with the size of the amplified microsatellite alleles reported to the nearest bp based upon the molecular size grid created with 20-bp markers.

As there was some uncertainty in estimation of allele size as determined from the 20-bp grid, we identified alleles on the basis of a binning procedure (Gill et al. 1990). Peaks in the allele frequencies were used to identify main alleles, and bin widths generally corresponding to a repeat unit were set with the main allele occurring in the middle of the bin. Precision of estimation of allele size was evaluated with a standard fish analyzed for each locus.

### Precision of Estimation of Allele Size

Standard deviations of the estimate of allele sizes for the heterozygous standard fish analyzed at each locus ranged from 0.34 to 0.89 with the larger alleles estimated with the least precision (Table 2). For the smaller allele at *Ots3*, 100% of the estimated sizes for the allele spanned a two-bp interval, as did 97%

(35/36) of the size estimates for the larger allele. For the smaller allele at *Omy77*, 100% of the estimated sizes of the allele were in a two-bp interval, as were 89% (51/57) of the estimated sizes of the larger allele. Although *Omy77* is a dinucleotide microsatellite locus, the level of precision of estimated allele sizes for the standard fish indicated that alleles could not be consistently assigned correctly to 2-bp bins. Therefore, *Omy77* alleles were conservatively defined on the basis of 4-bp wide bins, which has the practical effect of pairwise pooling of alleles that differ in size by 2 bp. Estimated sizes of alleles of the standard fish analyzed at the other loci were all estimated within a four-bp bin interval.

**Table 2.** Precision of estimation of allele size (bp) for standard fish analyzed repeatedly at each locus, with the fish run only once on each gel. N is the number of gels where allele sizes for the fish were estimated. Standard deviation is in parentheses.

| Locus         | N  | Allele size  | Range   | Allele size  | Range   |
|---------------|----|--------------|---------|--------------|---------|
| <i>Ots3</i>   | 24 | 93.6 (0.57)  | 93–95   | 74.1 (0.34)  | 74–75   |
|               | 12 | 89.6 (0.51)  | 89–90   | 74.6 (0.51)  | 74–75   |
| <i>Omy77</i>  | 57 | 116.0 (0.58) | 114–117 | 105.3 (0.46) | 105–106 |
| <i>Ots107</i> | 33 | 118.0 (0.56) | 116–119 | 110.3 (0.52) | 109–111 |
| <i>Ots108</i> | 25 | 185.8 (0.84) | 185–187 | 111.8 (0.44) | 111–113 |
| <i>Ots100</i> | 53 | 186.2 (0.57) | 185–187 | 159.4 (0.53) | 158–160 |
| <i>Ots103</i> | 41 | 214.0 (0.65) | 213–215 | 175.8 (0.89) | 175–177 |

### Data Analysis

Each stock at each locus was tested for departure from Hardy-Weinberg equilibrium (HWE) using GENEPOP version 3.1 (Raymond and Rousset 1995), as was temporal stability of allele frequencies. For populations sampled in more than one year, HWE was tested on samples pooled over years if no significant annual variation in allele frequencies was observed. For those populations in which significant annual variation in allele frequencies was detected at any locus, HWE was tested on an annual basis at all loci in the population. In this case, the lowest probability of conformance to HWE in the annual tests was considered. Tests of genetic differentiation utilizing pairwise comparisons between all population pairs at each locus were also conducted using GENEPOP. The dememorization number was set at 1,000, and 50 batches were run for each test with 1,000 iterations/batch. Critical significance levels for simultaneous tests were evaluated using sequential Bonferroni adjustment (Rice 1989). A neighbor-joining analysis illustrating genetic relationships among populations was conducted with PHYLIP (Felsenstein 1993). The allele frequency matrix was resampled 1,000 times and Cavalli-Sforza and Edwards (1967) chord distance was used to estimate

distance among populations.  $\theta$  values for each locus were determined with FSTAT (Goudet 1995). Estimation of variance components in allele frequencies among populations and years was determined with BIOSYS (Swofford and Selander 1981). Identification of individuals to specific populations was done with the DISCRIM procedure in SAS with a jackknife sampling procedure (SAS 1989). Classification functions were developed using all fish sampled except the one to be classified, with each fish tested individually in turn. This procedure should reflect the accuracy expected when applied to new, previously unsampled fish. Identification of individual fish was restricted to those fish for which data were available at all six loci.

### Estimation of Stock Composition

Genotypic frequencies were determined at each locus for each stock, and the model of Fournier et al. (1984) was used to estimate stock composition. Each locus was considered to be in Hardy-Weinberg equilibrium, and expected genotypic frequencies were determined from the observed allele frequencies and used as model inputs. Each baseline population was resampled with replacement in order to simulate random variation involved in the collection of the baseline samples before the estimation of stock composition of each mixture. Two mixture compositions were examined that would be typically expected in returning Skeena River sockeye salmon in order to evaluate accuracy and precision of the estimated stock compositions. Hypothetical fishery samples of 200 fish were generated by randomly resampling with replacement the baseline populations, and adding the appropriate number of fish from each stock to the mixture. Estimated stock composition of the mixture was then determined, with the whole process repeated 100 times to estimate the mean and standard deviation of the individual stock composition estimates. Estimated stock composition of each test fishery was determined as a point estimate of the sample, with standard deviations of individual stock estimates derived from bootstrap resampling of both the baseline populations and the mixture.

### Test Fishery

Samples were collected from sockeye salmon caught in a gillnet test fishery in 1996, 1998, and 1999 near the mouth of the Skeena River (Jantz et al. 1990). We used weekly estimates of sockeye salmon escapement (CPUE) at the test fishery to construct an appropriately weighted random sample of approximately 200 fish representing the entire annual escapement for 1996 and 1998. For example, if 10% of the total run was estimated to have passed by the test

fishery in a particular week, then the annual escapement sample of 200 fish included 20 fish picked randomly from fish sampled in that week. Increased analysis of samples collected during 1999 allowed biweekly estimates of stock composition to be made. The seasonal estimate of stock composition in 1999 was determined from a sample of 550 fish, with sampling based in proportion to weekly run abundance. DNA was derived from either a punch of operculum tissue or a single scale for each fish included in the analysis, and samples within a week were randomly selected from the available pool of samples. Escapement estimates for non-Babine stocks were calculated by using the annual stock composition estimates from the test fishery in conjunction with the Babine fence counts and reported catches in fresh water as outlined by Rutherford et al. (1999).

### Comparison with the Nass River

The use of microsatellite DNA for estimation of stock composition in potential marine applications in northern British Columbia would require separate identification of Skeena River and Nass River sockeye salmon. The ability to discriminate between Skeena River and Nass River sockeye salmon using microsatellite variation was examined first by simulation analysis using mixtures of known proportions of Skeena River fish (0, 50, and 100%). The Nass River baseline populations used in the analysis included those populations for which at least 50 fish had been sampled, with the distribution of allele frequencies outlined by Beacham and Wood (1999). Six Nass River populations were included in the baseline (Meziadin Lake, Damdochax Lake, Bowser Lake, Bonney River, Kwinageese River, and Gingit Creek) along with the 17 populations surveyed in the Skeena River drainage. Test fishery samples from the Skeena River collected in 1996, 1998 and 1999 and the Nass River collected in 1996 (Beacham and Wood 1999) were also analyzed using the combined Skeena/Nass baseline.

## RESULTS

### Variation within Populations

Heterozygosity varied among both loci and populations surveyed. Observed heterozygosity at *Ots3* was 0.44 in the pooled samples (population range 0.12–0.89), *Omy77* 0.60 (0.40–0.87), *Ots100* 0.75 (0.57–0.87), *Ots103* 0.83 (0.53–0.94), *Ots107* 0.41 (0.03–0.67), and *Ots108* 0.76 (0.58–0.92). Mean heterozygosity of the lower Skeena River populations was 0.59, the same as the mean heterozygosity of the Nanika River (Bulkley drainage) population. Mean heterozygosity of upper Skeena River populations



was 0.68, with mean heterozygosity of the Babine Lake populations at 0.66. There was some tendency for more upriver populations to have higher levels of heterozygosity than those in the lower river.

Significant departures from genotypic frequencies expected under Hardy-Weinberg equilibrium were observed at *Omy77* for Williams Creek and Schulbuckhand (Scully) Creek (homozygote excess), at *Ots3* for Motase Lake, Nanika River (homozygote excess), and Pierre Creek (heterozygote excess), at *Ots107* for McDonell Lake and Kitsumkalum River (homozygote excess), and at *Ots108* for McDonell Lake, Bear Lake, Pinkut Creek, and Pierre Creek (homozygote excess). There was no evidence of a consistent null or nonamplifying allele at any of the six loci surveyed.

Significant annual variability in allele frequencies was observed at *Ots3* ( $p = 0.0075$ ) and *Ots108* ( $p = 0.0001$ ) for the Fulton River population, at *Ots3* ( $p = 0.0000$ ) and *Ots107* ( $p = 0.0047$ ) for the Alastair Lake population, and at *Ots3* ( $p = 0.0004$ ) and *Ots108* ( $p = 0.0000$ ) for the McDonell Lake population. No significant differences in allele frequencies were observed in the Swan Lake population (all nominal  $p$  values  $> 0.025$ ).

### Variation among Populations

There was clear genetic differentiation among sockeye salmon populations in the Skeena River drainage. The greatest differentiation at *Omy77* was observed among lower river populations, with the frequency of *Omy77*<sup>94</sup> ranging from 0.02 for Lakelse Lake populations (Williams Creek, Schulbuckhand (Scully) Creek) to 0.69 in Kitsumkalum River (Fig. 2). At *Ots3*, the greatest differentiation was again observed among lower river populations, with the frequency of *Ots3*<sup>88</sup> ranging from 0.18 (Williams Creek) to 0.94 (Kitwanga River). Some regional structuring of allele frequencies within the watershed was observed, with the frequency of *Ots100*<sup>195</sup>  $< 0.05$  in the lower river populations, 0.13–0.30 in the upper river populations, 0.31 in the Bulkley River (Nanika) population, and 0.03–0.12 in the Babine Lake populations. Similar regional structuring was observed at *Ots103*, with the frequency of *Ots103*<sup>198</sup>  $< 0.13$  in the lower river populations, 0.17–0.26 in the upper river populations, 0.20 in the Bulkley River stock, and  $< 0.09$  in the Babine Lake populations. Four main alleles were observed at *Ots107*, with a lower frequency of *Ots107*<sup>113</sup> in the upper river and Bulkley River populations (generally  $< 0.45$ ) compared with higher frequencies in the lower river (generally  $> 0.80$ ) and Babine Lake populations (generally 0.70–0.80)(Fig. 2). At *Ots108*, considerable variation in frequencies of the 122, 126, and 130 alleles was ob-

served among lower river populations, similar to the pattern of variation at *Omy77* and *Ots3*.

Pairwise population comparisons of allele frequencies indicated that there was significant genetic differentiation between populations ( $p < 0.0001$ ) with some exceptions. Non-significant differences were observed among populations in some comparisons between Babine Lake populations at all six loci surveyed. Similarly, in comparisons between the Schulbuckhand Creek and Williams Creek populations, both tributaries of Lakelse Lake, no significant differences were observed at any locus except *Ots3*, where a significant difference was observed ( $p < 0.0001$ ). Other than the similarity between Scully Creek and Williams Creek, all lower river populations were genetically distinct at each locus from all other lower river populations. All three upper river populations were genetically distinct from each other at all loci except for *Ots3* allele frequencies between Motase Lake and Bear Lake ( $p = 0.014$ ).

### Stock Structure

Substantial differentiation was observed among populations within the Skeena River drainage, with  $\theta$  values for the six loci as follows: *Omy77* 0.136 (SD = 0.028), *Ots3* 0.158 (0.045), *Ots100* 0.062 (0.014), *Ots103* 0.082 (0.040), *Ots107* 0.082 (0.025), and *Ots108* 0.086 (0.026). The average  $\theta$  value for all six loci was 0.094 (0.013). Annual variation in allele frequencies within populations was always less than the differences among populations, with the ratios of the variance components for among population differences divided by between years within populations as follows: *Omy77* 6.72, *Ots3* 1.24, *Ots100* 32.80, *Ots103* 29.60, *Ots107* 8.37, and *Ots108* 4.30. The average variance component ratio for all six loci was 4.83. On average, differences among populations were about five times larger than annual variation within populations.

Regional structuring of populations within the Skeena River drainage was evident. The consensus neighbor-joining dendrogram indicated that Babine Lake populations were reasonably distinct and well-defined from other populations in the drainage, clustering together in 76% of the 1,000 trees used to construct the consensus tree (Fig 3). Lower river and upper river/Bulkley River populations formed less cohesive units, as they were grouped together in identifiable clusters about 40% of the time. The diversity observed among the lower river populations (Fig. 2) was reflected in the lower proportion of times that the populations grouped together compared with the more homogeneous Babine Lake populations.

Regional structuring of populations between the Nass River and Skeena River drainages was also ob-

**Fig. 2.** Population or regional allele frequencies of sockeye salmon in Lakelse Lake (Schulbuckhand (Scully) Creek and Williams Creek), Alastair Lake, Kitwanga River, Kitsumkalum River, McDonnell Lake, Bulkley River (Nanika River), upper Skeena River populations, and Babine Lake populations.

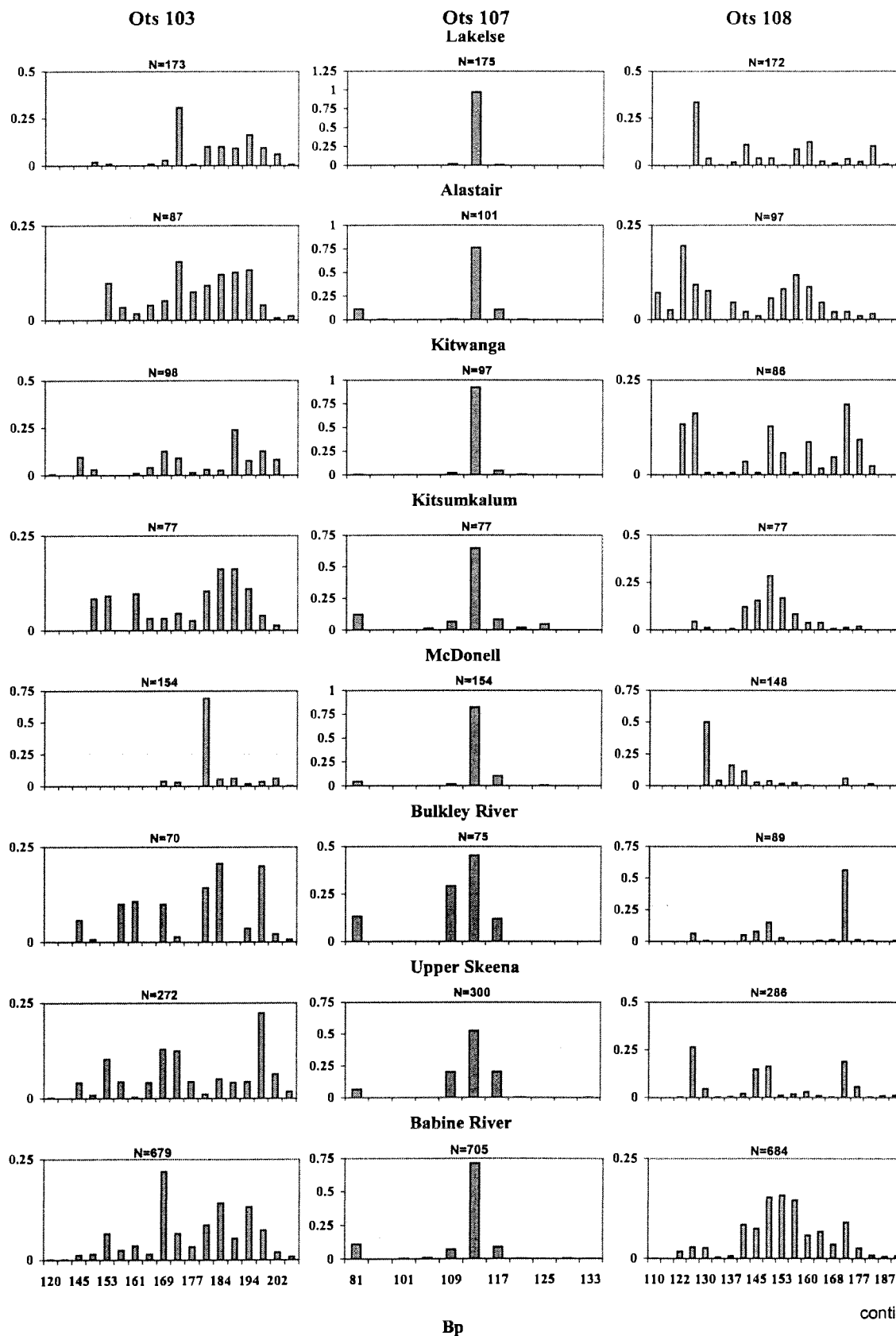
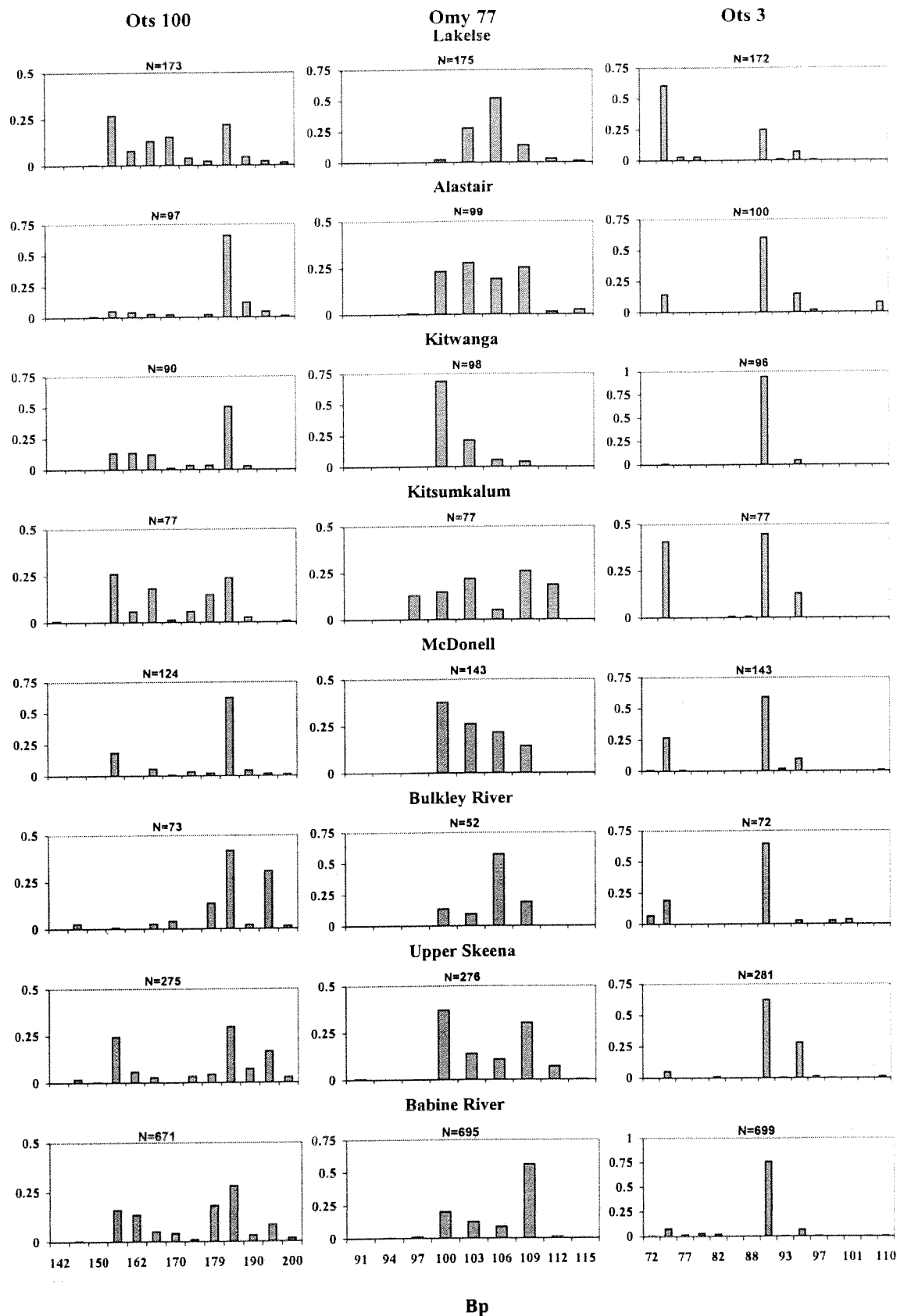
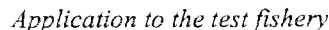


Fig. 2. Continued.



that accurate estimates of regional stock composition should be derived when applied to samples collected from the Skeena River drainage.



served. Populations in the Nass River in which juveniles rear in lakes (Kwinageese, Bonney, Meziadin, Damdochax, Bowser) formed a reasonably distinct group that clustered together in 74% of the 1,000 trees examined. The Nass River population in which juveniles rear in rivers without access to lake habitat (Gingit) was less distinct from the Skeena River populations than the lake-rearing populations. The analysis indicated that there was sufficient genetic differentiation between Nass River and Skeena River sockeye salmon populations to enable their distinction in marine mixed-stock samples.

Increased analysis of sampled sockeye salmon during the 1999 return allowed estimates of stock composition to be made on a biweekly basis and seasonal basis. Sockeye salmon from Lakelse Lake comprised over 30% of the returns prior to June 26, but salmon from this population were virtually absent after July 11 (Table 5). Upper Skeena populations were more prevalent in the early portion of the returns compared with the later portion. Babine Lake sockeye salmon were estimated to have comprised 81% of the total returns in 1999, intermediate in relative abundance compared with returns in 1996 and 1998.

### Simulated mixtures

### Identification of Individuals

Accuracy of estimated stock composition is correlated with the ability to identify individual fish in mixtures to specific stocks. We evaluated the ability of microsatellite variation to identify individual sockeye salmon as originating from either the Nass River or Skeena River drainages, with the individuals tested excluded from the development of the discriminant functions. Correct assignment to river drainage was achieved for 84% ( $n = 1758$ ) of Nass River and 83% ( $n = 1643$ ) Skeena River sockeye salmon. With this relatively accurate classification of individual fish to correct river drainage, estimated stock compositions of mixtures of these fish should also be accurate.

Three simulated samples of Nass River and Skeena River sockeye salmon were constructed and their composition estimated with a 23-stock Nass/Skeena baseline to evaluate the accuracy and precision

**Table 3.** Estimated percentage composition of two mixtures of Skeena River sockeye salmon in simulations using observed variation at six microsatellite DNA loci. Each mixture of 200 fish was generated 100 times. To control stock composition, desired contributions for each stock were resampled with replacement from the baseline data, then combined. Stock composition of the mixture was estimated by resampling each baseline stock with replacement to obtain the original sample size and a new distribution of allele frequencies. The individual estimates for all populations within each geographic area outlined in Table 1 have been summed to provide an estimate for each area. Standard deviation is in parentheses.

| Mixture 1      |         |             | Mixture 2           |         |             |
|----------------|---------|-------------|---------------------|---------|-------------|
| Stock          | Correct | Estimated   | Stock               | Correct | Estimated   |
| Swan           | 5.0     | 4.3 (2.1)   | Σ upper Skeena      | 0.0     | 1.6 (1.4)   |
| Σ upper Skeena | 5.0     | 6.0 (2.7)   | Schulbuckhand Creek | 5.0     | 2.8 (1.7)   |
| Alastair       | 5.0     | 4.2 (2.1)   | Σ lower Skeena      | 5.0     | 6.5 (2.3)   |
| Kitsumkalum    | 5.0     | 1.8 (1.3)   | Σ Bulkley           | 0.0     | 0.3 (0.6)   |
| Σ lower Skeena | 10.0    | 7.2 (2.8)   | Upper Babine        | 5.0     | 4.2 (4.8)   |
| Nanika         | 5.0     | 3.9 (1.8)   | Lower Babine        | 15.0    | 13.3 (9.0)  |
| Σ Bulkley      | 5.0     | 3.9 (1.8)   | Pinkut Creek        | 25.0    | 28.5 (10.0) |
| Pinkut Creek   | 30.0    | 31.7 (10.5) | Fulton River        | 20.0    | 9.2 (7.9)   |
| Fulton River   | 25.0    | 8.3 (6.2)   | Morrison            | 10.0    | 6.8 (5.9)   |
| Pierre Creek   | 25.0    | 27.3 (5.3)  | Pierre              | 20.0    | 23.3 (4.4)  |
| Σ Babine       | 80.0    | 82.8 (3.6)  | Σ Babine            | 95.0    | 91.6 (2.5)  |

**Table 4.** Estimated percentage stock composition of 1996 and 1998 Skeena River test fishery samples and resulting escapement estimate (number of fish) for sockeye salmon in four areas in the Skeena River drainage. Standard deviation is in parentheses. Escapement estimate from Babine Lake is the actual fence count.

| Stock          | 1996          |            | 1998          |            |
|----------------|---------------|------------|---------------|------------|
|                | % Composition | Escapement | % Composition | Escapement |
| N              | 207           |            | 201           |            |
| Motase Lake    | 0.66 (0.76)   |            | 0.00 (0.24)   |            |
| Swan Lake      | 2.12 (1.50)   |            | 2.50 (1.41)   |            |
| Bear           | 0.00 (0.38)   |            | 1.85 (1.48)   |            |
| Σ upper Skeena | 2.78 (1.68)   | 66,400     | 4.35 (1.98)   | 23,300     |
| McDonell       | 0.00 (0.17)   |            | 0.59 (0.77)   |            |
| Lakelse        | 1.75 (1.17)   |            | 3.66 (1.67)   |            |
| Alastair       | 2.12 (1.70)   |            | 5.37 (1.96)   |            |
| Kitwanga       | 0.76 (0.72)   |            | 2.04 (1.62)   |            |
| Kitsumkalum    | 5.37 (3.63)   |            | 11.31 (3.31)  |            |
| Σ lower Skeena | 10.00 (3.76)  | 261,000    | 22.97 (4.18)  | 142,500    |
| Nanika         | 1.44 (1.23)   |            | 0.00 (0.16)   |            |
| Σ Bulkley      | 1.44          | 32,500     | 0.00 (0.16)   | 0          |
| Upper Babine   | 19.45 (8.20)  |            | 16.52 (6.29)  |            |
| Lower Babine   | 0.00 (4.38)   |            | 0.00 (0.16)   |            |
| Pinkut Creek   | 5.78 (6.18)   |            | 9.83 (6.97)   |            |
| Fulton River   | 17.19 (9.49)  |            | 19.22 (10.73) |            |
| Morrison       | 29.37 (9.91)  |            | 18.38 (8.90)  |            |
| Pierre         | 0.00 (0.43)   |            | 0.00 (1.52)   |            |
| Shass          | 13.99 (6.47)  |            | 8.73 (4.21)   |            |
| Σ Babine       | 85.78 (4.40)  | 2,056,205  | 72.68 (4.10)  | 558,873    |

**Table 5.** Estimated percentage stock composition of the 1999 Skeena River Tyee sockeye salmon test fishery samples for 6 periods in 1999. N is number of fish analyzed in each period. Standard deviation is in parentheses. The seasonal estimate of 550 fish is based on sampling in proportion to weekly run abundance.

| Stock          | June 6–26  | June 27–July 10 | July 11–24 | July 25–Aug. 7 | Aug. 8–21  | Aug. 22–Sept. 18 | Seasonal   |
|----------------|------------|-----------------|------------|----------------|------------|------------------|------------|
| N              | 122        | 205             | 200        | 225            | 213        | 62               | 550        |
| Motase         | 0.0 (0.0)  | 1.1 (0.5)       | 0.0 (0.2)  | 0.6 (1.3)      | 1.7 (1.1)  | 1.4 (1.2)        | 0.4 (0.8)  |
| Swan           | 3.3 (3.2)  | 5.5 (3.2)       | 14.2 (3.4) | 2.1 (1.9)      | 0.0 (1.6)  | 0.0 (3.9)        | 5.5 (1.9)  |
| Bear           | 0.0 (1.3)  | 0.9 (2.2)       | 1.9 (1.2)  | 2.3 (2.3)      | 6.2 (2.9)  | 0.0 (1.5)        | 1.3 (0.9)  |
| Σ upper Skeena | 3.3 (3.2)  | 7.5 (3.7)       | 16.1 (3.6) | 5.0 (3.0)      | 7.9 (4.1)  | 1.4 (4.2)        | 7.2 (2.3)  |
| McDonell       | 0.0 (1.2)  | 1.5 (1.7)       | 1.5 (1.6)  | 0.5 (0.3)      | 0.0 (1.1)  | 1.3 (3.5)        | 1.0 (0.6)  |
| Lakelse        | 32.5 (5.5) | 9.5 (2.2)       | 0.0 (1.4)  | 1.6 (1.2)      | 1.2 (0.7)  | 0.0 (4.0)        | 3.3 (0.9)  |
| Alastair       | 1.3 (0.8)  | 6.7 (2.6)       | 0.0 (1.4)  | 4.0 (2.6)      | 4.4 (2.2)  | 7.3 (6.8)        | 2.7 (1.3)  |
| Kitwanga       | 2.8 (2.4)  | 1.0 (1.5)       | 0.0 (1.8)  | 1.7 (0.9)      | 1.7 (1.5)  | 2.7 (2.8)        | 2.0 (0.7)  |
| Kitsumkalum    | 2.1 (3.9)  | 0.8 (2.7)       | 2.8 (2.5)  | 2.0 (1.2)      | 5.1 (2.1)  | 7.4 (6.3)        | 2.8 (1.6)  |
| Σ lower Skeena | 38.7 (7.7) | 19.5 (4.5)      | 4.3 (4.1)  | 9.8 (3.4)      | 12.4 (3.7) | 18.7 (9.9)       | 11.8 (2.7) |
| Nanika         | 0.0 (2.6)  | 0.2 (1.1)       | 0.0 (0.8)  | 0.6 (0.8)      | 0.2 (0.9)  | 0.0 (0.3)        | 0.0 (0.2)  |
| Σ Bulkley      | 0.0 (2.6)  | 0.2 (1.1)       | 0.0 (0.8)  | 0.6 (0.8)      | 0.2 (0.9)  | 0.0 (0.3)        | 0.0 (0.2)  |
| Σ Babine       | 58.0 (8.3) | 72.8 (5.3)      | 79.6 (4.8) | 84.7 (4.3)     | 79.6 (5.0) | 80.0 (10.4)      | 81.0 (3.4) |

of estimated stock compositions for possible marine applications. Mean estimated stock composition of samples of pure (100%) Skeena River sockeye salmon was 97.6% (SD = 2.0%) Skeena origin, and that of samples comprising 50% Skeena River origin fish was 48.9% (SD = 2.0%) Skeena origin (Table 6). Mean estimated stock composition of samples containing no (0%) Skeena River fish was 2.8% (SD = 1.4%) Skeena origin. These simulations demonstrate that the microsatellite loci surveyed could be used to provide relatively accurate and precise estimates of stock composition for mixtures comprising only Skeena River or Nass River sockeye salmon.

#### *Application to test fisheries*

The simulations demonstrated that it should be feasible to obtain accurate estimates of stock composition from actual fishery samples. The validity of the simulations was investigated by estimating stock compositions of sockeye salmon samples from test fisheries conducted at the mouth of the Nass River in 1996 and the mouth of the Skeena River in 1996, 1998, and 1999. The estimated composition of the Nass River sample was 97.6% (SD = 1.5%) Nass-origin fish, and that of the 1996 Skeena River sample was 91.5% (SD = 3.9%), the 1998 Skeena sample 94.4% (SD = 3.5%), and for the 1999 sample used to estimate seasonal stock composition 93.5% (SD = 3.5%) Skeena-origin fish (Table 7). When the 1996

samples from both rivers were combined, creating a sample of 44.9% Skeena-origin fish, the estimated stock contribution of Skeena River was 41.2% (SD = 3.0%). When the 1996 Nass and 1998 Skeena samples were combined, creating a sample of 44.2% Skeena-origin fish, the estimated Skeena River contribution was 42.2% (SD = 2.9%). When the 1996 Nass and 1999 Skeena seasonal samples were combined, creating a sample of 68.4% Skeena-origin fish, the estimated Skeena River contribution was estimated at 65.8% (SD = 2.6%). Thus, accurate estimates of Nass River and Skeena River sockeye salmon were obtained over a wide range of relative proportions in samples from fisheries in which only Nass River and Skeena River sockeye salmon occur.

## DISCUSSION

Microsatellites are becoming an increasingly powerful tool for characterizing population structure in natural populations. In salmonids, microsatellites are generally characterized by high levels of variability and differentiation among spawning populations (Nielsen et al. 1997; Seeb et al. 1998; Small et al. 1998). The high heterozygosities observed at microsatellite loci allows a substantial amount of genetic differentiation to be detected and exploited for stock identification applications, which was the main focus of our current study.

Significant annual variation in allele frequencies

**Table 6.** Estimated percentage composition of three mixtures of Skeena River and Nass River sockeye salmon in simulations using observed variation at six microsatellite DNA loci. Each mixture of 200 fish was generated 100 times with replacement, and stock compositions of the mixtures estimated by resampling each baseline stock with replacement to obtain the original sample size and a new distribution of allele frequencies. Seventeen populations were used in the Skeena River baseline, and six populations in the Nass River baseline. Standard deviation is in parentheses.

| Mixture 1    |         |             | Mixture 2   |         |            | Mixture 3  |         |            |
|--------------|---------|-------------|-------------|---------|------------|------------|---------|------------|
| Stock        | Correct | Estimated   | Stock       | Correct | Estimated  | Stock      | Correct | Estimated  |
| Lakelse      | 5.0     | 2.8 (1.3)   | Gingit      | 10.0    | 10.4 (1.9) | Bonney     | 10.0    | 11.0 (3.1) |
| Upper Babine | 5.0     | 4.4 (4.1)   | Meziadin    | 30.0    | 29.1 (1.2) | Gingit     | 10.0    | 11.1 (1.6) |
| Lower Babine | 15.0    | 12.0 (8.9)  | Damdochax   | 10.0    | 10.4 (1.7) | Kwinageese | 5.0     | 5.6 (3.8)  |
| Pinkut Creek | 25.0    | 27.6 (11.4) | Pinkut      | 25.0    | 17.9 (4.2) | Meziadin   | 50.0    | 48.6 (2.0) |
| Fulton River | 20.0    | 8.3 (7.9)   | Fulton      | 10.0    | 10.5 (4.3) | Damdochax  | 10.0    | 11.1 (2.6) |
| Morrison     | 10.0    | 6.1 (5.7)   | Bear        | 5.0     | 4.0 (1.2)  | Bowser     | 10.0    | 10.0 (1.6) |
| Pierre       | 20.0    | 24.0 (4.9)  | Kitsumkalum | 10      | 9.0 (1.5)  | Brown Bear | 5.0     | 0.0 (0.1)  |
| Σ Skeena     | 100.0   | 97.6 (2.0)  | Σ Skeena    | 50.0    | 48.9 (2.0) | Σ Skeena   | 0.0     | 2.8 (1.4)  |
| Σ Nass       | 0.0     | 2.4 (2.0)   | Σ Nass      | 50.0    | 51.1 (2.0) | Σ Nass     | 100.0   | 97.2 (1.4) |

**Table 7.** Estimated percentage stock composition of the 1996, 1998, and 1999 Skeena River test fishery samples, the 1996 Nass River test fishery sample outlined in Beacham and Wood (1999), and combined test fishery samples derived from the 23 stock baseline used for the simulated mixtures in Table 5. Standard deviation is in parentheses. N is the number of fish sampled in each mixture.

| Sample                   | N   | Skeena River |            | Nass River |            |
|--------------------------|-----|--------------|------------|------------|------------|
|                          |     | Correct      | Estimated  | Correct    | Estimated  |
| 1996 Skeena test fishery | 207 | 100.0        | 91.5 (3.9) | 0.0        | 8.5 (3.9)  |
| 1998 Skeena test fishery | 201 | 100.0        | 94.4 (3.5) | 0.0        | 5.6 (3.5)  |
| 1999 Skeena test fishery | 550 | 100.0        | 93.5 (3.5) | 0.0        | 6.5 (3.5)  |
| 1996 Nass test fishery   | 254 | 0.0          | 2.4 (1.5)  | 100.0      | 97.6 (1.5) |
| 1996 Skeena, 1996 Nass   | 461 | 44.9         | 41.2 (3.0) | 55.1       | 58.8 (3.0) |
| 1998 Skeena, 1996 Nass   | 455 | 44.2         | 42.2 (2.9) | 55.8       | 57.8 (2.9) |
| 1999 Skeena, 1996 Nass   | 804 | 68.4         | 65.8 (2.6) | 31.6       | 34.2 (2.6) |

was observed at some loci in some populations surveyed in the Skeena River drainage, but on average, differences among populations were about five times larger than annual variation within populations. Generally, differentiation among sockeye salmon populations within a region is greater than annual variation within populations. For example, differentiation among Nass River populations was about 11 times greater than annual variation within populations (Beacham and Wood 1999), and about 12 times greater for Barkley Sound populations on the west coast of Vancouver Island (Beacham et al. 2000). Although temporal changes in allele frequencies can affect mixed-stock fishery analysis (Waples 1990), the relative magnitude of population differentiation versus within population variation suggests that annual variation in allele frequencies will have minimal effects on estimates of stock composition. For practical estimation of stock composition, annual sampling of populations contributing to a sockeye salmon fishery is not required, but clearly some level of monitoring of allele frequencies over time is appropriate to ensure that allele frequencies characterizing each population are still relevant.

The value of a particular microsatellite locus in stock identification can differ among regions. Previous analyses of population differentiation at the six microsatellite loci surveyed in this study indicated that *Ots103* provided the least population differentiation for Nass River (Beacham and Wood 1999) and Barkley Sound populations (Beacham et al. 2000). However, in the Skeena River drainage, its value in population differentiation was considerably enhanced, with  $\theta$  values up to seven times larger than in previous studies. Surveys of microsatellite variation in each geographic region of interest will probably be necessary to determine which loci are the most effective in identifying local populations in stock identification applications.

An important aspect of fishery management applications of microsatellite variation within the Skeena River drainage is to be able to identify Babine Lake populations. The counting fence on Babine River provides a direct and presumably reliable count of escapement to Babine Lake. If representative samples from the test fishery at the mouth of the Skeena River and a reliable estimate of the proportion of Babine Lake populations in these samples are obtained, coupled with catch data from fisheries in the drainage, then an estimate of total escapement to the Skeena River drainage is possible.

There has been a continuing discrepancy in the estimated contribution of Babine Lake sockeye salmon in Skeena River drainage escapement between the approaches in which non-Babine escapements are estimated from visual surveys and those in which they are estimated from the test fishery at the mouth of the

Skeena River (Rutherford et al. 1999). The proportion that Babine Lake populations contribute to drainage escapement is always higher when estimated from direct observation than when estimated from test fishery sampling. This discrepancy may arise from (1) stock identification errors made in the determination of the Babine Lake component of samples derived from the test fishery whereby the Babine Lake component is consistently underestimated, (2) the test fishery provides non-representative samples such that Babine Lake sockeye salmon are consistently under-represented, perhaps because of their smaller average size or higher abundance (Cox-Rogers and Jantz 1993), or (3) visual estimates of escapement that seriously underestimate true escapement in rivers other than Babine.

Previous stock identification studies of Skeena River sockeye salmon have utilized variation at allozymes, frequency of occurrence of parasites, and age compositions to estimate the proportion of Babine Lake sockeye salmon (Rutherford et al. 1994, 1999). The estimated proportion of Babine Lake populations in the test fishery has ranged from 70–86% during 1989–1997, and the 1998 estimate derived from microsatellites was 73%, toward the lower end of these estimates. As samples from the 1996 test fishery were analyzed using both allozymes/parasites/scales (Rutherford et al. 1999) and microsatellites (this study), it was possible to compare stock compositions estimated by the two methods. There was a striking concordance in results, with both methods providing estimates of 85.8% Babine-origin fish, and 10% lower-river (downstream from the Skeena/Bulkley confluence) populations. Simulation studies for both stock identification methods indicate that reliable estimates of the proportion of Babine Lake sockeye salmon should be obtained. Since the two methods are independent but give strikingly similar results, the discrepancy in the estimated contribution of Babine Lake to Skeena River drainage escapement is not likely due to a systematic bias or underestimation of the Babine Lake component in the test fishery samples.

Are samples representative of the migrating fish obtained from the test fishery? During times of high abundance of migrating fish, the gillnet sampling gear could be saturated, such that the true abundance of migrating populations would not be adequately represented in the reconstructed sample. If so, the very abundant Babine Lake component would not be adequately represented in the reconstructed sample. One way to evaluate whether the gillnet test gear does become saturated is to compare the abundance index derived from the test fishery with the observed escapement of Babine Lake populations at the counting fence. If indeed the catchability of the gillnet changes, then large returns to Babine Lake should not

necessarily be associated with higher indices of abundance in the lower river test fishery. However, there is clearly a relationship between the lower river test fishery abundance index and the Babine Lake fence count (Rutherford et al. 1999), so the discrepancy in the relative contribution of Babine Lake populations is unlikely due primarily to unrepresentative sampling in the test fishery, although this may have some role.

How accurately do visual surveys of escapement estimate true abundance? Visual surveys in the Skeena River drainage traditionally underestimate abundance when compared with direct fence counts (Brett 1952), and in the case of the Sustut River, a relatively clear tributary in the upper Skeena River drainage, fence counts may be five times higher than visual counts (McKinnell and Rutherford 1994). Possibly a significant portion of the discrepancy between estimated and observed non-Babine Lake escapement is attributable to underestimation of escapement by visual observation in the absence of a fence. If the estimated stock composition of Babine Lake sockeye salmon is accurate and the sampling at the test fishery is representative, then the 1996 estimated escapement of non-Babine Lake sockeye salmon was about 360,000 fish and in 1998 the estimated escapement of non-Babine Lake sockeye salmon was approximately 166,000 fish. The estimate of 166,000 fish for 1998 contrasted with a visual estimate of 22,000 fish. If they are present, where are these "missing" fish? The stock identification analysis suggests that they are largely in the lower river tributaries. A large part of the discrepancy is attributable to the Kitsumkalum River population, which has an estimated escapement of 70,000 fish from stock identification analysis but only 5,000 from visual surveys. The Kitsumkalum River is glacially turbid with limited visibility, and would be a good candidate for more refined escapement estimation procedures. Another would be Alastair Lake (microsatellite estimate 33,000 fish in 1998) which has been historically reported to contain significant populations of sockeye salmon (Shepard and Withler 1958; Aro and Shepard 1967), but for which only 2,500 fish were observed in 1998. In 1999, the data indicate that Lakelse Lake may have had larger escapements than in 1996 or 1998.

Populations originating from Babine Lake were estimated to have comprised 73% of the drainage escapement in 1998, towards the lower end of the range derived from stock identification studies (Rutherford et al. 1999). Populations enhanced in the Babine Lake Development Project (primarily Pinkut Creek and Fulton River) account for most of the fry recruitment into Babine Lake (Wood et al. 1998). However, infection by the "ich" parasite (white spot disease) caused high prespawning mortality at both

enhancement sites in 1994 and 1995 (Traxler et al. 1998), such that enhanced fry production from these two brood years was < 60% of the 1984–93 average (Wood et al. 1998). Total smolt production from the 1994 and 1995 brood years in the Babine Lake system was the lowest observed since production began from the enhancement facilities. Relatively poor returns from Babine Lake populations were thus expected in 1998, and this was reflected in the relatively low estimated proportion of Babine Lake sockeye salmon in the test fishery.

Wood et al. (1994) found that allozyme variation in the sockeye salmon populations of British Columbia was not strongly regionally structured, and concluded that it would be of limited value in coast-wide mixture problems. However, variation at the more polymorphic, faster-evolving microsatellite loci surveyed to date revealed regional structure between Nass and Skeena River sockeye salmon populations that allowed accurate estimates of stock composition when sockeye salmon from both river drainages occurred in mixed-stock samples. Elucidation of regional structure is important because successful application of genetic stock identification to mixed-stock salmon fisheries generally requires that geographically proximate populations share distinctive genetic characteristics. That makes it unnecessary to obtain baseline samples from all the individual populations that might contribute to a fishery. For regionally-structured species, that portion of a mixed-stock sample derived from unsampled populations is usually allocated to sampled populations from the same region, reducing the cost and complexity of establishing a sufficient baseline for mixture analysis. Although only Nass River and Skeena River populations were compared in the current study, additional regional structure exists in British Columbia sockeye salmon populations (Beacham et al. unpublished data), and once a suitable baseline has been established, microsatellites will likely prove very effective in providing estimates of stock composition of samples in high seas applications.

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## Early Summer Movements of Tagged Pink Salmon off Southwestern Sakhalin Island, 1995–1998

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**Keywords:** Pink salmon, migration, tagging, southwestern Sakhalin

**Abstract:** A tagging experiment on mature pink salmon (*Oncorhynchus gorbuscha*) was conducted from small fishing vessels in southwestern Sakhalin coastal waters during June–July from 1995 to 1998 during the period of their feeding migration. In total 17,696 fish were tagged and released, and 1,225 or 6.9% were recaptured. Recaptures were distributed mainly along Sakhalin Island: 1,195 fish along the southwestern coast (95.7%), 21 fish in Aniva Bay (1.7%), 5 fish in the Terpeniya Gulf (0.4%). A few tagged fish were recaptured outside Sakhalin Island in the River of Tumnin, Khabarovsk Territory (1 fish), and near the Soya Cape, Hokkaido, Japan (2 fish). The majority of tagged fish were recaptured in Sakhalin waters. Movements of tagged pink salmon were observed along southwestern Sakhalin coast both northward, and southward to bays Aniva and Terpeniya, and northwestern Hokkaido.

### INTRODUCTION

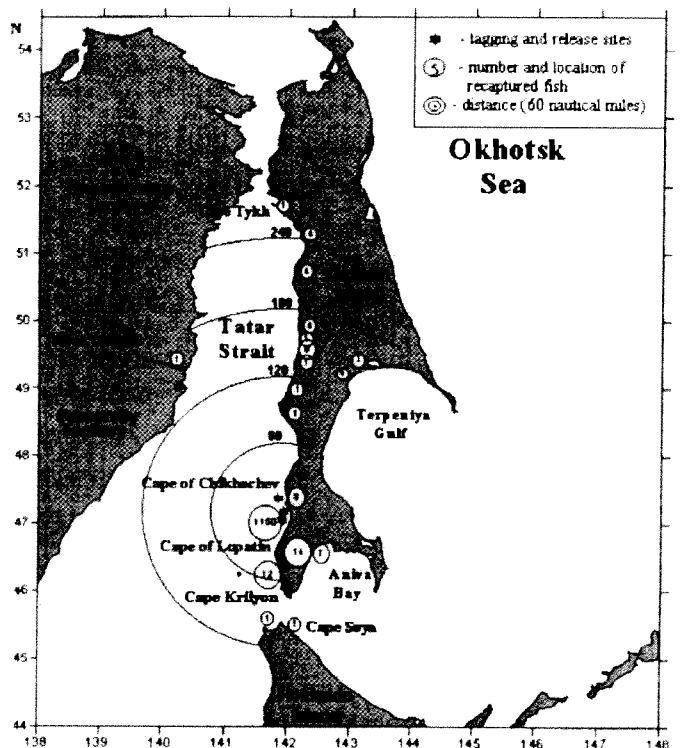
Pink salmon (*Oncorhynchus gorbuscha*) that have over-wintered in the Sea of Japan complete their final summer feeding, as indicated by their distended stomachs, in the coastal waters of southwestern Sakhalin at temperatures of 6–9°C. Pink salmon first arrive in this area in late May. For 1.5–2 months (June to early July) they form commercial aggregations near the southwestern Sakhalin coast (Dvinin 1949, 1950; Landyshevskaya 1962; Landyshevskaya and Volovik 1967). The main aggregations are usually observed in coastal waters north of Cape Lopatin and south of Cape Chikhachev (Fig. 1). Fishing is conducted with traditional gear—gigantic trap nets. For the last 40 years salmon catches here varied from 110 to 16,130 tons (Ivanova 1997).

There are no rivers on this part of the coast with high quality spawning grounds for pink salmon. The main spawning areas are located in rivers of the middle and northern parts of Sakhalin Island. Pink salmon caught off southwestern Sakhalin Island have poorly developed gonads: in May gonads make up 1.2% of body weight of males, and 3.2% of females; in June, mean gonad weight increases to 3.1% for males, and 5.7% for females; in early July it is 4.8% for males and 6.9% for females.

A tagging experiment was conducted to determine the movements of pink salmon and their distribution while feeding in the coastal zone of

southwestern Sakhalin Island. The results are the subject of this work.

**Fig. 1.** Release and recapture sites and numbers of pink salmon tagged in southwestern Sakhalin waters in 1995–1998. Portions of circles show straight-line distances (nautical miles) from the central release site.



## MATERIAL AND METHODS

The tagging experiment on maturing pink salmon was conducted in June–July 1995–1998. Due to differences in time, duration of movement and catches for pink salmon occurring in coastal waters from Cape Lopatin to Cape Chikhachev, we divided this coastal zone into three tagging sites: 47°03'N and 141°58'E (1st southern site), 47°08'N and 141°59'E (2nd central site), 47°23'N and 141°57'E (3rd northern site). In 1995 tagging was carried out at all three sites from 10 June to 15 July, the majority of tagging in June (Table 1). In 1996 because of variable and small salmon runs to coastal waters, tagging was carried out only at two sites (1st and 2nd) from 14 June to 17 July, the majority again in June. In 1997 tagging was carried out at all three sites, but only from 11 to 27 June. In 1998 tagging was carried out only at the 2nd site from 9 June to 6 July.

Pink salmon were caught by trap nets, and transported in live-holds aboard boats to offshore waters a distance of 5–5.5 km, tagged and released. Water in live-holds was aerated for maximum survival. Fresh seawater was pumped under high pressure and sprayed into the holds. Survival during transportation was 98–100% (Ivanova 1997).

Fish were tagged with bright red plastic tags 25 mm long and 5 mm wide. A tag was attached to the flesh in front of the dorsal fin with a 10–12 mm fish-hook. Tags had a number and address, and an appeal to send or report the tag to SakhNIRO or Fishing Inspection. To encourage returns, announcements were made on the radio, TV, and in newspapers.

Posters were distributed in the main regions of pink salmon fishing and processing on Sakhalin Island.

Annual catches, distribution, migrations, biological characteristics (length, body weight, absolute fecundity), of mature pink salmon collected in coastal waters and on spawning grounds of the southwestern Sakhalin rivers (within Cape Tykh in the north, and Cape Krilyon in the south of the western Sakhalin coast) were recorded.

The following biological characteristics were used for analyses: fork length (cm), fish weight (g), gonad weight (g), coefficient of maturity (proportion of gonad weight to total weight of fish, %), absolute fecundity (number of eggs) (Pravdin 1966).

## RESULTS

The proportion of pink salmon recaptured in rivers and coastal zone varied significantly among years ( $\chi^2$  test,  $p < 0.01$ ). Most of this variation arose in 1997 when more tagged fish were recovered in rivers than expected (Table 2).

Recaptures were tabulated by approximate distance north or south of their release site, using the middle site as the starting point (Fig. 1), and by number of days between release and recapture, to look for differences in rate and distance of travel among months (June or July) or years (Table 3–6). This analysis showed no obvious patterns in direction or speed of migration among months or years. Most recaptures occurred within 25 days of release, and rates of travel usually were between 8 and 15 miles per day, with a few individuals travelling much faster (20–60 miles per day over several days). A pink

**Table 1.** Numbers of maturing pink salmon tagged at three sites near the southwestern Sakhalin coast in 1995–1998.

| Year  | Site <sup>1</sup><br>of tagging | Number of<br>operations | Number of fish tagged |      | Total tagged<br>fish |
|-------|---------------------------------|-------------------------|-----------------------|------|----------------------|
|       |                                 |                         | June                  | July |                      |
| 1995  | 1                               | 3                       | 1657                  | 0    | 1657                 |
|       | 2                               | 4                       | 2202                  | 0    | 2202                 |
|       | 3                               | 2                       | 743                   | 432  | 1175                 |
|       | Sub-total                       | 9                       | 4602                  | 432  | 5034                 |
| 1996  | 1                               | 4                       | 1280                  | 780  | 2060                 |
|       | 2                               | 5                       | 3428                  | 400  | 3828                 |
|       | 3                               | 0                       | 0                     | 0    | 0                    |
|       | Sub-total                       | 9                       | 4708                  | 1180 | 5888                 |
| 1997  | 1                               | 1                       | 1099                  | 0    | 1099                 |
|       | 2                               | 3                       | 1949                  | 0    | 1949                 |
|       | 3                               | 1                       | 960                   | 0    | 960                  |
|       | Sub-total                       | 5                       | 4008                  | 0    | 4008                 |
| 1998  | 1                               | 0                       | 0                     | 0    | 0                    |
|       | 2                               | 5                       | 1966                  | 800  | 2766                 |
|       | 3                               | 0                       | 0                     | 0    | 0                    |
|       | Sub-total                       | 5                       | 1966                  | 800  | 2766                 |
| Total |                                 | 28                      | 15284                 | 2412 | 17696                |

<sup>1</sup>Site locations: 1, 47°03'N, 141°58'E  
2, 47°08'N, 141°59'E  
3, 47°23'N, 141°57'E

**Table 2.** Recaptures of tagged pink salmon by regions ( coast and rivers ).

| Return location      | Region          | Year of tagging<br>(Number of recaptured fish) |                |                |                | Total recaptures in region |            |
|----------------------|-----------------|------------------------------------------------|----------------|----------------|----------------|----------------------------|------------|
|                      |                 | 1995<br>(5034)                                 | 1996<br>(5888) | 1997<br>(4008) | 1998<br>(2766) | Number                     | Percentage |
|                      |                 |                                                |                |                |                |                            |            |
| River                | S-W Sakhalin    | 8                                              | 4              | 12             | 9              | 33                         | 62.3       |
|                      | Aniva Bay       | 5                                              | 5              | 4              | 0              | 14                         | 26.4       |
|                      | Terpeniya Gulf  | 1                                              | 4              | 0              | 0              | 5                          | 9.4        |
|                      | Turnin River    | 0                                              | 0              | 0              | 1              | 1                          | 1.9        |
|                      | Okhotsk Sea *   | 0                                              | 0              | 0              | 0              | 0                          | 0          |
|                      | Hokkaido Island | 0                                              | 0              | 0              | 0              | 0                          | 0          |
|                      | Total           | 14                                             | 13             | 16             | 10             | 53                         | 100        |
| Coast                | S-W Sakhalin    | 434                                            | 414            | 246            | 68             | 1162                       | 99.1       |
|                      | Aniva Bay       | 7                                              | 0              | 0              | 0              | 7                          | 0.6        |
|                      | Terpeniya Gulf  | 0                                              | 0              | 0              | 0              | 0                          | 0          |
|                      | Turnin River    | 0                                              | 0              | 0              | 0              | 0                          | 0          |
|                      | Okhotsk Sea *   | 0                                              | 1              | 0              | 0              | 1                          | 0.1        |
|                      | Hokkaido Island | 2                                              | 0              | 0              | 0              | 2                          | 0.2        |
|                      | Total           | 443                                            | 415            | 246            | 68             | 1172                       | 100        |
| Total                | S-W Sakhalin    | 442                                            | 418            | 258            | 77             | 1195                       | 97.5       |
|                      | Aniva Bay       | 12                                             | 5              | 4              | 0              | 21                         | 1.7        |
|                      | Terpeniya Gulf  | 1                                              | 4              | 0              | 0              | 5                          | 0.4        |
|                      | Turnin River    | 0                                              | 0              | 0              | 1              | 1                          | 0.1        |
|                      | Okhotsk Sea *   | 0                                              | 1              | 0              | 0              | 1                          | 0.1        |
|                      | Hokkaido Island | 2                                              | 0              | 0              | 0              | 2                          | 0.2        |
|                      | Total           | 457                                            | 428            | 262            | 78             | 1225                       | 100        |
| Percentage of return |                 | 9.1                                            | 7.3            | 6.5            | 2.8            | 6.9                        | -          |

\*tag was returned without information on date and location of recaptured fish

**Table 3.** Distance and time between release and recapture of pink salmon tagged in 1995, and direction north or south of release site.

| Distance (nautical miles)<br>from release location * |                 | Days after release |      |       |       |       | Average<br>Time | Av. Nautical<br>miles/day |      |
|------------------------------------------------------|-----------------|--------------------|------|-------|-------|-------|-----------------|---------------------------|------|
|                                                      |                 | 0-5                | 6-10 | 11-15 | 16-20 | 21-25 | 26-30           |                           |      |
| June                                                 |                 |                    |      |       |       |       |                 |                           |      |
| North                                                | 241-300         |                    |      | 4     | 1     |       |                 | 14.0                      | 19.3 |
|                                                      | 181-240         |                    |      |       |       |       |                 |                           |      |
|                                                      | 121-180         |                    |      | 1     |       |       |                 | 12.0                      | 12.5 |
|                                                      | 61-120          |                    | 1    |       |       |       |                 | 11.0                      | 8.2  |
|                                                      | within 60 miles | 248                | 65   | 87    | 4     | 6     | 5               | 6.3                       | 4.8  |
| South                                                | 61-120          | 1                  | 1    |       |       |       |                 | 5.2                       | 17.4 |
|                                                      | 121-180         |                    | 2    |       | 7     | 3     |                 | 17.6                      | 8.6  |
|                                                      | 181-240         |                    |      |       |       |       |                 |                           |      |
|                                                      | 241-300         |                    |      |       | 1     |       |                 | 18.0                      | 15.0 |
| July                                                 |                 |                    |      |       |       |       |                 |                           |      |
| North                                                | 241-300         |                    |      |       |       |       |                 |                           |      |
|                                                      | 181-240         |                    | 1    |       |       |       |                 | 7                         | 30.1 |
|                                                      | 121-180         |                    |      |       |       |       |                 |                           |      |
|                                                      | 61-120          |                    |      |       |       |       |                 |                           |      |
|                                                      | within 60 miles | 12                 | 3    | 4     |       |       |                 | 5.6                       | 5.4  |
| South                                                | 61-120          |                    |      |       |       |       |                 |                           |      |
|                                                      | 121-180         |                    |      |       |       |       |                 |                           |      |
|                                                      | 181-240         |                    |      |       |       |       |                 |                           |      |
|                                                      | 241-300         |                    |      |       |       |       |                 |                           |      |
| Total recaptured                                     |                 | 261                | 73   | 96    | 13    | 9     | 5               |                           |      |

\*central tagging and release site ( 2nd ) is assumed starting point for calculating distance.

**Table 4.** Distance and time between release and recapture of pink salmon tagged in 1996, and direction north or south of release site.

Site.

| Distance (nautical miles)<br>from release location * |         | Days after release |      |       |       |       | Average<br>Time | Av. Nautical<br>miles/day |
|------------------------------------------------------|---------|--------------------|------|-------|-------|-------|-----------------|---------------------------|
|                                                      |         | 0-5                | 6-10 | 11-15 | 16-20 | 21-25 | 26-30           |                           |
| June                                                 |         |                    |      |       |       |       |                 |                           |
| North                                                | 241-300 |                    |      |       |       |       |                 |                           |
|                                                      | 181-240 |                    |      |       | 2     | 1     |                 | 19.7                      |
|                                                      | 121-180 |                    |      |       |       |       |                 | 10.7                      |
|                                                      | 61-120  |                    | 1    |       |       |       |                 | 7.5                       |
| within 60 miles                                      |         | 358                |      |       |       |       |                 | 12.1                      |
| South                                                | 61-120  |                    |      |       |       |       |                 | 2.5                       |
|                                                      | 121-180 |                    | 1    |       |       |       |                 | 8.0                       |
|                                                      | 181-240 |                    |      |       |       |       |                 | 18.8                      |
|                                                      | 241-300 | 1                  | 1    |       |       |       |                 | 5.2                       |
| July                                                 |         |                    |      |       |       |       |                 |                           |
| North                                                | 241-300 |                    |      |       |       |       |                 |                           |
|                                                      | 181-240 |                    |      |       |       |       |                 |                           |
|                                                      | 121-180 | 1                  |      |       |       |       |                 | 2.5                       |
|                                                      | 61-120  |                    |      |       |       |       |                 | 60.2                      |
| within 60 miles                                      |         | 56                 |      |       |       |       |                 | 2.5                       |
| South                                                | 61-120  |                    |      |       |       |       |                 | 12.0                      |
|                                                      | 121-180 |                    |      | 2     | 2     |       |                 | 20.5                      |
|                                                      | 181-240 |                    |      |       |       |       |                 | 7.3                       |
|                                                      | 241-300 |                    | 1    |       |       | 1     |                 | 15.1                      |
| Total recaptured                                     |         | 416                | 4    | 2     | 4     | 2     |                 | 17.9                      |

\*central tagging and release site ( 2nd ) is assumed starting point for calculating distance.

**Table 5.** Distance and time between release and recapture of pink salmon tagged in 1997, and direction north or south of release site.

| Distance (nautical miles)<br>from release location * | Days after release |      |       |       |       |       | Average<br>Time | Av. nautical<br>miles/day |
|------------------------------------------------------|--------------------|------|-------|-------|-------|-------|-----------------|---------------------------|
|                                                      | 0-5                | 6-10 | 11-15 | 16-20 | 21-25 | 26-30 |                 |                           |
|                                                      | June               |      |       |       |       |       |                 |                           |
| 241-300                                              |                    |      |       |       |       |       |                 |                           |
| 181-240                                              |                    |      |       |       |       |       |                 |                           |
| 121-180                                              |                    | 7    | 2     |       | 1     |       | 10.5            | 14.3                      |
| 61-120                                               |                    |      |       |       |       |       |                 |                           |
| within 60 miles                                      | 155                | 82   | 3     | 8     |       |       | 4.9             | 6.1                       |
| 61-120                                               |                    |      |       |       |       |       |                 |                           |
| 121-180                                              |                    | 1    | 1     | 1     | 1     |       | 15.5            | 9.7                       |
| 181-240                                              |                    |      |       |       |       |       |                 |                           |
| 241-300                                              |                    |      |       |       |       |       |                 |                           |
| Total recaptured                                     | 155                | 90   | 6     | 9     | 2     |       |                 |                           |

\*central tagging and release site ( 2nd ) is assumed starting point for calculating distance.

**Table 6.** Distance and time between release and recapture of pink salmon tagged in 1998, and direction north or south of release site.

| Distance (nautical miles)<br>from release location * |         | Days after release |      |       |       |       | Average<br>Time | Av. nautical<br>miles/day |
|------------------------------------------------------|---------|--------------------|------|-------|-------|-------|-----------------|---------------------------|
|                                                      |         | 0-5                | 6-10 | 11-15 | 16-20 | 21-25 | 26-30           |                           |
| June                                                 |         |                    |      |       |       |       |                 |                           |
| North                                                | 241-300 |                    |      |       |       |       |                 |                           |
|                                                      | 181-240 |                    |      |       |       |       |                 |                           |
|                                                      | 121-180 |                    |      |       | 1     |       |                 | 19.0                      |
|                                                      | 61-120  |                    |      |       |       |       |                 | 7.9                       |
| within 60 miles                                      | 31      | 6                  | 4    |       |       |       | 4.3             | 7.0                       |
| South                                                | 61-120  |                    |      |       |       |       |                 |                           |
|                                                      | 121-180 |                    |      |       |       |       |                 |                           |
|                                                      | 181-240 |                    |      |       |       |       |                 |                           |
|                                                      | 241-300 |                    |      |       |       |       |                 |                           |

continue...

Table 6. continued.

| Distance (nautical miles)<br>from release location * |                 | Days after release |      |       |       |       |       | Average<br>Time | AV nautical<br>miles/day |
|------------------------------------------------------|-----------------|--------------------|------|-------|-------|-------|-------|-----------------|--------------------------|
|                                                      |                 | 0-5                | 6-10 | 11-15 | 16-20 | 21-25 | 26-30 |                 |                          |
|                                                      |                 | July               |      |       |       |       |       |                 |                          |
| North                                                | 241-300         |                    |      |       |       |       |       |                 |                          |
|                                                      | 181-240         |                    |      |       |       |       |       |                 |                          |
|                                                      | 121-180         |                    |      |       |       |       |       |                 |                          |
|                                                      | 61-120          |                    | 1    |       |       |       |       | 10.0            | 9.1                      |
|                                                      | within 60 miles | 8                  | 27   |       |       |       |       | 6.7             | 0.5                      |
| South                                                | 61-120          |                    |      |       |       |       |       |                 |                          |
|                                                      | 121-180         |                    |      |       |       |       |       |                 |                          |
|                                                      | 181-240         |                    |      |       |       |       |       |                 |                          |
|                                                      | 241-300         |                    |      |       |       |       |       |                 |                          |
| Total recaptured                                     |                 | 39                 | 34   | 4     | 1     |       |       |                 |                          |

\*central tagging and release site ( 2nd ) is assumed starting point for calculating distance.

salmon tagged in July 1998 and recaptured in the River Tumnin 10 days later travelled a distance of more than 160 nautical miles. Another recaptured in the Krasnogorka River (southwest Sakhalin Is.) nine days after release had travelled about 90 nautical miles (Table 6).

Although there was no discernible relation between month or year of release of tagged fish and direction in which they later were recaptured, there was a definite relation among the three release sites and direction of recapture. Of all fish released from the most southerly site (site 1), 45.2% (97 fish) migrated southwards, and 54.7% (117 fish) migrated northwards (direction not significant,  $p > 0.05$ , binomial distribution). At site 2 (middle), 73.1% (629 fish) migrated mainly southwards, and 26.7% (229 fish) migrated northwards (difference in direction significant,  $p < 0.01$ , binomial distribution). One fish migrated in a northwest direction and was recaptured in the River Tumnin. At site 3 (most northerly), 94% (142 fish) migrated southwards, and only 6.0% (9 fish) migrated northwards ( $p < 0.01$ , binomial distribution). The differences in direction from release sites were statistically significant ( $\chi^2 = 100$ ,  $p < 0.001$ ).

The period between release and recapture along the southwestern coast of Sakhalin Island varied among months and years from 2.5 to 20 days on average (Tables 3-6), and for individual fish from a few hours to 30 days. The period between release of the 21 fish recaptured in Aniva Bay was 8 to 20.5 days, and of the seven fish recaptured in Tereniya Gulf 5.2 to 18 days. One tagged pink salmon was recaptured in coastal waters off Hokkaido Island six days after release, and another individual was recovered at Hamasaruhtsu Fish market, Hokkaido Island, four days after release.

## DISCUSSION

The comparison of data collected in June-July 1995-1998 with the results of earlier tagging studies has revealed the general pattern of Japanese Sea pink

salmon migrations at the final stage of feeding along the southwestern Sakhalin coast.

Earlier Russian and Japanese studies have shown that two pink salmon stocks spend the winter in the southwestern part of the Sea of Japan, one in Korean Bay and the other near the southwestern Hokkaido coast (Okushiri Island) (Kaganovsky 1949; Hirano 1951; Dvinin 1952; Enutina 1954; Miyaguchi 1957). Further, pink salmon migrate from the southwestern part of the Sea of Japan northwards, and in May they mix with those wintering near Hokkaido Island and continue migrating to waters of Tatar Strait. In the region of 46°N they distribute by the individual areas: Primorye coast, West Sakhalin and partially through La Perouse Strait to the Okhotsk Sea. North of 47°N pink salmon annually migrate to the Primorye coast (Hirano 1951; Darda 1968). The distribution of tagged fish within the rather wide area near Okushiri Island in 1958, 1960, 1961 and near southwestern Sakhalin Island in 1958, 1962 (Dvinin 1958; Landyshevskaya 1962), 1969, 1973, and 1979 (Efanov and Ivanova 1979—SakhNIRO archives "unpublished data") has been documented through tagging. Tag returns were recovered from the western and eastern Sakhalin coasts, Aniva Bay, Primorsky Territory, Khabarovsk Territory, Sakhalin Bay and the northern coast of the Okhotsk Sea. The main results of our experiment illustrate the distribution of tagged pink salmon towards the regions of their reproduction on Sakhalin Island and Khabarovsk Territory after completion of their feeding migration along southwestern Sakhalin. Unusually, tagged pink salmon were recaptured near Hokkaido Island; this is the first such record.

In addition, the analysis of scale patterns from pink salmon caught at feeding sites and in spawning rivers, allowed us to conclude that mixed pink salmon stocks mainly reproducing on Sakhalin Island, fed along the southwestern Sakhalin coast (Ivanova 1990, 1994, 1997, 1999).

As we have already noted, the pink salmon tagged at different sites migrated mainly in two directions—north and south. Almost 70% of the total

tagged fish migrated to the south, in accordance with the results of tagging in 1947, but in contrast with the distribution of 1962 (Dvinin 1947; Landyshevskaya 1962). In the opinion of A.E. Landyshevskaya, the predominant direction of pink salmon migrations after feeding in the southeastern part of Tatar Strait is determined mainly by their abundance on the feeding grounds.

The results of our long-term attempts to increase the abundance of southwestern Sakhalin pink salmon populations through management provide indirect evidence of mixed stocks growing in southwestern Sakhalin waters. Management by restricting the catch, or the number of trap nets and fishing intervals, and even a full fishery closure in the coastal zone for almost 11 years in the mid 1970s, were not a success. Spawners on spawning grounds of the southwestern Sakhalin rivers did not increase in number.

The recapture of the majority of tagged pink salmon along southwestern Sakhalin Island, and the different directions of their migration from different tagging sites are explained, to a great extent, by the behavior of these pink salmon during feeding and maturation. Favorable temperature and food conditions in the coastal zone allows them to remain in this area until sexually mature, when they migrate to spawning areas.

The method of tagging used in this experiment can also be used for tagging salmon at their final stages of growth or migrations in the sea. Its application does not demand any special equipment or great financial expenditure. A well organized tag collection program in regions of expected catches of tagged fish is the condition required for a successful experiment.

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## Geographic Origin of High-Seas Chum Salmon Determined by Genetic and Thermal Otolith Markers

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**Keywords:** Chum salmon, stock origin, Gulf of Alaska, thermal otolith mark, genetic stock identification

**Abstract:** Genetic stock identification (GSI) and thermal otolith marking techniques were used for determining the stock origin of chum salmon (*Oncorhynchus keta*) caught in two offshore transects (165°W and 145°W) in the Gulf of Alaska during June and July 1998. In the central Gulf of Alaska (49–56°N, 145°W), 49 thermally-marked chum salmon were found (14.5%,  $n = 339$  fish). Most of these marked salmon were immature fish originated from four hatcheries in southeast Alaska (SEAK) and Prince William Sound (PWS), while two immature fish were from Nitinat Hatchery on southwest Vancouver Island, British Columbia (BC). In the western Gulf of Alaska (45–50°N, 165°W), however, we found only two marked chum salmon (1.1%,  $n = 188$  fish) that had been released from the Hidden Falls and Gastineau hatcheries in SEAK. The GSI results indicated that North American chum salmon were common in the central Gulf of Alaska (15% west Alaska, 25% Alaska Peninsula/Kodiak, 28% SEAK/PWS, and 18% BC stocks), and Asian chum salmon were predominant in the western Gulf of Alaska (25% Japan, 53% Russia, and 13% west Alaska stocks). The GSI and thermal mark results suggest that in the central Gulf of Alaska, the contribution of SEAK/PWS hatchery stocks was high among the ocean age .1 group, but decreased with increasing ocean age mainly because other stocks such as west Alaska stocks penetrated these waters after the second year of their ocean life.

### INTRODUCTION

Thermal marking of salmonid otoliths has been well developed as an effective tool to determine the hatchery origin of salmon. This technology has been primarily used for stock management in near-shore interception fisheries (Hagen et al. 1995). Now, large numbers of thermally-marked chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) are annually released from hatcheries in Alaska (U.S.A.), British Columbia (Canada), Washington State (U.S.A.), and Russia. Japan has also started thermal marking, beginning with the 1998 brood year stocks.

Many thermally-marked chum and pink salmon are collected in the eastern Bering Sea (Ignell et al. 1997) and coastal waters of the Gulf of Alaska (Farley and Munk 1997, 1998). In the meantime, a genetic stock identification (GSI) technique has been developed for estimating stock compositions of high-seas chum salmon (Seeb et al. 1995; Urawa et al. 1997, 1998; Wilmot et al. 1998; Winans et al. 1998; Seeb and Crane 1999a, 1999b). By combining both identification techniques, we expect to be able to estimate the stock origins and components of wild and hatchery salmon in the ocean.

In the Gulf of Alaska, chum salmon occur all the

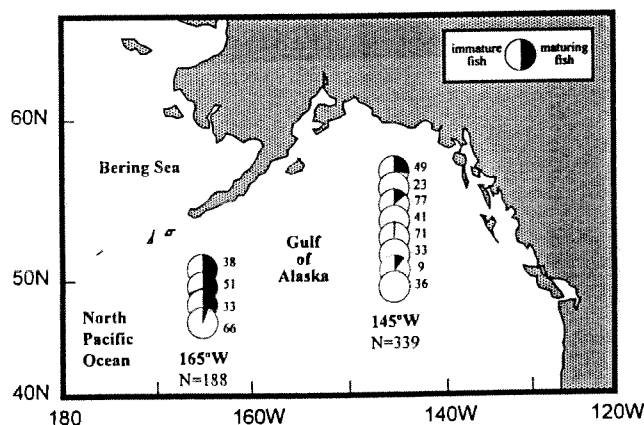
year around. North American juveniles migrate westward along the coast of the Gulf of Alaska during summer and fall (Hartt and Dell 1986), but it is unclear where they disperse in the following winter and spring. Tagging recoveries have indicated that Asian chum salmon migrate into the Gulf of Alaska in addition to North American stocks (Neave et al. 1976; Ogura 1994). However, quantitative analyses have not been applied to the stock components of immature and maturing chum salmon in these waters. The present study was conducted to determine the stock structure of chum salmon in the offshore waters of the Gulf of Alaska during summer by using genetic and thermal marks.

## MATERIALS AND METHODS

### Fish Samples

Chum salmon ( $n = 527$  fish) were captured on two transects ( $165^{\circ}\text{W}$  and  $145^{\circ}\text{W}$ ) in the Gulf of Alaska by research gillnet operations of T/V *Oshoro maru* during June and July 1998 (Fig. 1). The fork length, body weight and gonad weight of each fish were recorded, and scales were removed for age determination. Maturity was determined from gonad weights (Takagi 1961). The sagittal otoliths, muscle, heart, and liver were collected from each fish. The sagittal otoliths were dried and kept in cell well plates until used for detection of otolith marks. The other tissues (muscle, heart, and liver) were immediately frozen at  $-80^{\circ}\text{C}$ , and shipped to the Genetics Section of the National Salmon Resources Center for genetic analysis. The catch per unit effort (CPUE) was calculated:  $\text{CPUE} = \text{total catch (number)}/\text{set of research gillnets (30 tans)}$ .

Fig. 1. Map showing sampling locations with the proportion of maturing and immature chum salmon caught in  $145^{\circ}\text{W}$  and  $165^{\circ}\text{W}$  transects of the Gulf of Alaska during June and July 1998. Numerals indicate the number of fish samples at each sampling location.



### Detection of Thermal Otolith Marks

The left sagittal otoliths were mounted on glass slides using thermoplastic cement (Buehler Co.), and then ground to expose the primordia. If the left sagittal otoliths were not available, the right sagittal otoliths were used. Otolith microstructures were observed under a light microscope, and the microstructure patterns were compared to the thermal mark patterns of voucher specimens collected from hatcheries before releases. All otoliths were read independently by two readers.

### GSI Analysis

Samples were examined for protein electrophoretic variation on horizontal starch gels using standard procedures described by Aebersold et al. (1987). Standard nomenclature for loci and alleles was used as outlined in Shaklee et al. (1990). Alleles were compared and standardized for 20 polymorphic loci (Seeb et al. 1995). We used the simplified baseline data set formulated in Seeb et al. (1995) for 69 stock groups that was augmented by Wilmot et al. (1998) to a 77 stock group/20 locus data set. Our analyses are based on a 19-locus baseline (Table 1). We dropped dipeptidase (PEPA) from our analyses because it was frequently missed in the electrophoretic screening of mixture samples (Winans et al. 1998). Stock contributions were estimated with a conditional maximum likelihood algorithm (Pella and Milner 1987) using the GIRLS program of Masuda et al. (1991). Standard deviations of estimates were estimated by 500 bootstrap resamplings of the baseline and mixture samples. Stock contribution estimates were made of individual stocks and then pooled to regional stock groups used by Seeb et al. (1995) and Wilmot et al. (1998). The regional stock groups are Japan, Russia, west Alaska (summer run), Yukon River (fall run), Alaska Peninsula/Kodiak, southeast Alaska (SEAK) and Prince William Sound (PWS), British Columbia (BC), and Washington. Simulation studies indicated that average stock contribution estimates were greater than 80% accurate when true group contributions were 100% (Wilmot et al. 1998).

## RESULTS

### Thermal Otolith Mark

Thermal otolith marks were detected in 51 chum salmon (9.7% of fish examined; Table 2). All of these marked chum salmon were immature except for one maturing fish caught in the central Gulf of Alaska ( $56^{\circ}\text{N}$ ,  $145^{\circ}\text{W}$ ).

In the central Gulf of Alaska ( $49$ – $56^{\circ}\text{N}$ ,  $145^{\circ}\text{W}$ ), 49 chum salmon with thermally-marked otoliths were found (14.5%,  $n = 339$  fish). Most of these marked

**Table 1.** Protein coding loci of enzymes used for stock identification of high-seas chum salmon and the tissues and buffers in which they were resolved. Enzyme nomenclature and EC numbers follow IUBMBNC (1992). Locus nomenclature follows Shaklee et al. (1990).

| Enzyme                                   | EC No.   | Locus                                | Tissue <sup>1</sup> | Buffer <sup>2</sup>    |
|------------------------------------------|----------|--------------------------------------|---------------------|------------------------|
| Aspartate aminotransferase               | 2.6.1.1  | <i>sAAT-1,2*</i><br><i>mAAT-1*</i>   | H, M<br>H           | ACE7.0, TBE<br>ACE7.0  |
| Aconitase hydratase                      | 4.2.1.3  | <i>mAH-3*</i>                        | H                   | ACE7.0                 |
| Alanine aminotransferase                 | 2.6.1.2  | <i>ALAT*</i>                         | M                   | TBE                    |
| Esterase-D                               | 3.1.-.-  | <i>ESTD*</i>                         | H, M                | TBCLE, TBE             |
| Glyceraldehyde-3-phosphate dehydrogenase | 1.2.1.12 | <i>G3PDH-2*</i>                      | H                   | ACE7.0                 |
| Glucose-6-phosphate isomerase            | 5.3.19   | <i>GPI-B1,2*</i><br><i>GPI-A*</i>    | M<br>M              | TBCLE<br>TBCLE         |
| Isocitrate dehydrogenase (NADP*)         | 1.1.1.42 | <i>mIDHP-1*</i><br><i>sIDHP-2*</i>   | H, M<br>L           | ACE7.0<br>ACE7.0       |
| L-Lactate dehydrogenase                  | 1.1.1.27 | <i>LDH-A1*</i><br><i>LDH-B2*</i>     | M<br>M              | ACE7.0, TBCLE<br>TBCLE |
| Malate dehydrogenase                     | 1.1.1.37 | <i>sMDH-A1*</i><br><i>sMDH-B1,2*</i> | H, L<br>H, M        | ACE7.0, TC4<br>ACE7.0  |
| Malic enzyme (NADP*)                     | 1.1.1.40 | <i>mMEP-2*</i><br><i>sMEP-1*</i>     | M<br>M              | ACE7.0<br>ACE7.0       |
| Mannose-6-phosphate isomerase            | 5.3.1.8  | <i>MP1*</i>                          | H                   | TBE                    |
| Tripeptide aminopeptidase                | 3.4.-.-  | <i>PEPB-1*</i>                       | H, L, M             | ACE7.0, TC4, TBE       |
| Phosphogluconate dehydrogenase           | 1.1.1.44 | <i>PGDH*</i>                         | H, L, M             | ACE7.0                 |

<sup>1</sup>H, heart; L, liver; M, muscle.

<sup>2</sup>Buffers and electrophoretic protocol are from Aebersold et al. (1987).

**Table 2.** Thermally-marked chum salmon caught in the Gulf of Alaska in the summer of 1998. FL, fork length; BW, Body weight; Mat, maturity according to the criteria of Takagi (1961); RBr, Regional band rings showing coding structure of thermal marks (Munk and Geiger 1998); F, female; M, male; IM, immature; MT, maturing; TM ID, thermal mark identification; AFK, Armin F. Koernig Hatchery; DIPAC, Gastineau Hatchery; HF, Hidden Falls Hatchery; NIT, Nitinat Hatchery; PC, Wally H. Noerenberg Hatchery (Port Chalmers); WHN, Wally H. Noerenberg Hatchery.

| No | Date      | Lat (N) | Long (W) | Sex | FL (mm) | BW (g) | Gonad (g) | Mat | Age | RBr       | TM ID   |
|----|-----------|---------|----------|-----|---------|--------|-----------|-----|-----|-----------|---------|
| 1  | 08-Jul-98 | 52°00   | 145°00   | M   | 400     | 780    | 1         | IM  | 0.1 | 1:1.4     | AFK96   |
| 2  | 11-Jul-98 | 49°00   | 145°00   | M   | 401     | 620    | 1         | IM  | 0.1 | 1:1.4     | AFK96   |
| 3  | 06-Jul-98 | 54°00   | 145°00   | M   | 611     | 2420   | 3         | IM  | 0.4 | 2:1.3     | DIPAC93 |
| 4  | 06-Jul-98 | 54°00   | 145°00   | M   | 525     | 1680   | 1         | IM  | 0.3 | 1:1.4     | DIPAC94 |
| 5  | 30-Jun-98 | 45°30   | 165°00   | F   | 456     | 1120   | 7         | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 6  | 05-Jul-98 | 55°00   | 145°00   | M   | 479     | 1220   | 1         | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 7  | 06-Jul-98 | 54°00   | 145°00   | F   | 506     | 1520   | 12        | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 8  | 06-Jul-98 | 54°00   | 145°00   | F   | 506     | 1440   | 11        | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 9  | 07-Jul-98 | 53°00   | 145°00   | F   | 491     | 1480   | 12        | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 10 | 07-Jul-98 | 53°00   | 145°00   | M   | 514     | 1540   | 1         | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 11 | 07-Jul-98 | 53°00   | 145°00   | F   | 497     | 1560   | 10        | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 12 | 07-Jul-98 | 53°00   | 145°00   | F   | 467     | 1220   | 13        | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 13 | 08-Jul-98 | 52°00   | 145°00   | M   | 506     | 1460   | 1         | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 14 | 08-Jul-98 | 52°00   | 145°00   | F   | 512     | 1600   | 14        | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 15 | 08-Jul-98 | 52°00   | 145°00   | F   | 488     | 1340   | 11        | IM  | 0.2 | 1:1.5     | DIPAC95 |
| 16 | 06-Jul-98 | 54°00   | 145°00   | M   | 378     | 560    | 1         | IM  | 0.1 | 1:1.6     | DIPAC96 |
| 17 | 08-Jul-98 | 52°00   | 145°00   | M   | 405     | 740    | 1         | IM  | 0.1 | 1:1.6     | DIPAC96 |
| 18 | 09-Jul-98 | 51°00   | 145°00   | M   | 358     | 520    | 1         | IM  | 0.1 | 1:1.6     | DIPAC96 |
| 19 | 09-Jul-98 | 51°00   | 145°00   | M   | 384     | 680    | 1         | IM  | 0.1 | 1:1.6     | DIPAC96 |
| 20 | 11-Jul-98 | 49°00   | 145°00   | F   | 369     | 540    | 5         | IM  | 0.1 | 1:1.6     | DIPAC96 |
| 21 | 11-Jul-98 | 49°00   | 145°00   | M   | 395     | 620    | 2         | IM  | 0.1 | 1:1.6     | DIPAC96 |
| 22 | 29-Jun-98 | 47°00   | 165°00   | F   | 467     | 1300   | 11        | IM  | 0.2 | 1:1.3,2,3 | HF95    |
| 23 | 04-Jul-98 | 56°00   | 145°00   | F   | 529     | 1820   | 110       | MT  | 0.3 | 1:1.3,2,3 | HF95    |
| 24 | 06-Jul-98 | 54°00   | 145°00   | F   | 477     | 1180   | 14        | IM  | 0.2 | 1:1.3,2,3 | HF95    |

continue...

Table 2. continued.

| No | Date      | Lat (N) | Long (W) | Sex | FL (mm) | BW (g) | Gonad (g) | Mat | Age | RBr       | TM ID  |
|----|-----------|---------|----------|-----|---------|--------|-----------|-----|-----|-----------|--------|
| 25 | 08-Jul-98 | 52°00   | 145°00   | M   | 504     | 1640   | 1         | IM  | 0.2 | 1:1.3,2.3 | HF95   |
| 26 | 08-Jul-98 | 52°00   | 145°00   | M   | 482     | 1280   | 1         | IM  | 0.2 | 1:1.3,2.3 | HF95   |
| 27 | 05-Jul-98 | 55°00   | 145°00   | M   | 368     | 520    | 1         | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 28 | 06-Jul-98 | 54°00   | 145°00   | F   | 382     | 640    | 5         | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 29 | 07-Jul-98 | 53°00   | 145°00   | M   | 336     | 460    | 1         | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 30 | 08-Jul-98 | 52°00   | 145°00   | F   | 388     | 680    | 12        | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 31 | 09-Jul-98 | 51°00   | 145°00   | M   | 418     | 740    | 1         | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 32 | 09-Jul-98 | 51°00   | 145°00   | M   | 376     | 600    | 1         | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 33 | 10-Jul-98 | 50°00   | 145°00   | M   | 392     | 660    | 1         | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 34 | 11-Jul-98 | 49°00   | 145°00   | F   | 333     | 390    | 3         | IM  | 0.1 | 1:1.3,2.4 | HF96   |
| 35 | 05-Jul-98 | 55°00   | 145°00   | F   | 631     | 3000   | 12        | IM  | 0.2 | 1:1.3+2.3 | NIT95  |
| 36 | 08-Jul-98 | 52°00   | 145°00   | F   | 405     | 780    | 3         | IM  | 0.1 | 1:1.4     | NIT96  |
| 37 | 09-Jul-98 | 51°00   | 145°00   | F   | 378     | 620    | 7         | IM  | 0.1 | 1:1.6     | PC96E  |
| 38 | 09-Jul-98 | 51°00   | 145°00   | M   | 368     | 560    | 1         | IM  | 0.1 | 1:1.6     | PC96E  |
| 39 | 11-Jul-98 | 49°00   | 145°00   | F   | 418     | 860    | 8         | IM  | 0.1 | 1:1.6     | PC96E  |
| 40 | 06-Jul-98 | 54°00   | 145°00   | M   | 429     | 820    | 1         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 41 | 08-Jul-98 | 52°00   | 145°00   | M   | 428     | 960    | 1         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 42 | 08-Jul-98 | 52°00   | 145°00   | F   | 407     | 740    | 5         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 43 | 09-Jul-98 | 51°00   | 145°00   | M   | 394     | 600    | 1         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 44 | 09-Jul-98 | 51°00   | 145°00   | F   | 379     | 640    | 7         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 45 | 10-Jul-98 | 50°00   | 145°00   | F   | 354     | 460    | 7         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 46 | 11-Jul-98 | 49°00   | 145°00   | F   | 404     | 780    | 10        | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 47 | 11-Jul-98 | 49°00   | 145°00   | M   | 423     | 820    | 1         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 48 | 11-Jul-98 | 49°00   | 145°00   | M   | 395     | 640    | 1         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 49 | 11-Jul-98 | 49°00   | 145°00   | F   | 385     | 660    | 9         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 50 | 11-Jul-98 | 49°00   | 145°00   | M   | 390     | 640    | 1         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |
| 51 | 11-Jul-98 | 49°00   | 145°00   | M   | 375     | 620    | 1         | IM  | 0.1 | 1:1.3,2.2 | WHN96L |

fish were released from four hatcheries in SEAK and PWS, while two fish were from the Nitinat Hatchery on southwest Vancouver Island, BC. The percentage of thermally-marked fish was higher in southern waters (21.5%, 49–52°N) than in northern waters (8.9%, 53–56°N) (Fig. 2). The CPUE of thermally-marked fish showed a similar trend (Fig. 3). The number of thermally-marked immature chum salmon decreased with increase in ocean age: 31 fish (36.9%) in age 0.1, 15 fish (7.9%) in age 0.2, and one fish (3.6%) in age 0.3 groups (Fig. 4).

In the western Gulf of Alaska (45–50°N, 165°W), thermal marks were found in only two chum salmon (1.1%,  $n = 188$  fish; Fig. 2). These marked fish were released from the Hidden Falls and Gastineau hatcheries in SEAK.

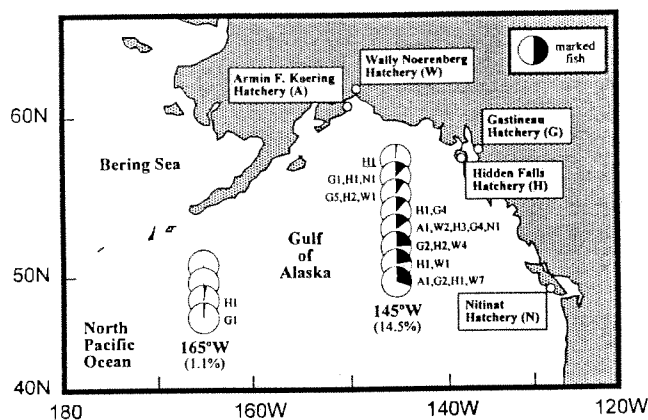
### Genetic Stock Identification

The GSI results indicated that North American chum salmon were common in the central Gulf of Alaska, and Asian chum salmon were predominant in the western Gulf of Alaska (Fig. 5).

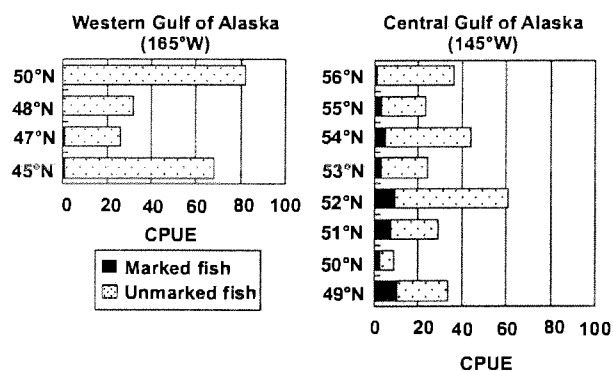
In the central Gulf of Alaska, Alaskan stocks comprised 72% of immature chum salmon, while the proportion of southern North American stocks (BC and Washington) was high (58%) among maturing fish (Fig. 6). A geographical comparison of stock composition in immature chum salmon (Fig. 7) indicated that the percentage of SEAK/PWS stocks was higher in the southern waters (49–52°N) than in northern waters (53–56°N). In the age 0.1 group, SEAK/PWS stocks were dominant (41%), and west Alaskan stocks were rarely present (Fig. 8). However, the proportion of SEAK/PWS stocks decreased with an increase in ocean age, and west Alaskan stocks accounted for 21% and 17% of age 0.2 and 0.3 groups, respectively.

In the western Gulf of Alaska, the proportion of Russian and Japanese stocks was 56% and 18% among immature fish, and 41% and 34% among maturing fish, respectively (Fig. 6). North American stocks were rare except for the west Alaskan stock whose proportion was 15% and 12% in immature and maturing groups, respectively.

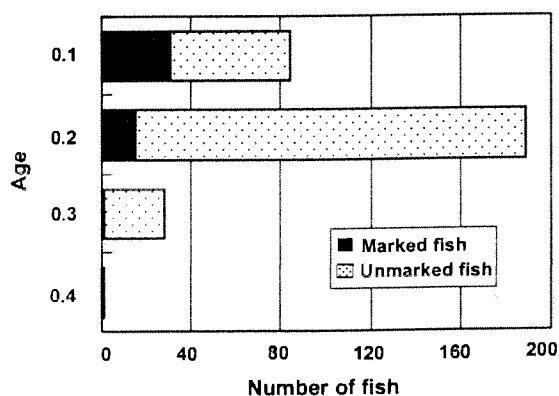
**Fig. 2.** Proportion (%) of chum salmon with thermally-marked otoliths caught on transects at 145°W and 165°W in the Gulf of Alaska during June and July 1998. Numerals following hatchery identification initials indicate number of thermally-marked fish. All marked fish were immature except for one maturing fish (56°N, 145°W) indicated by an underline.



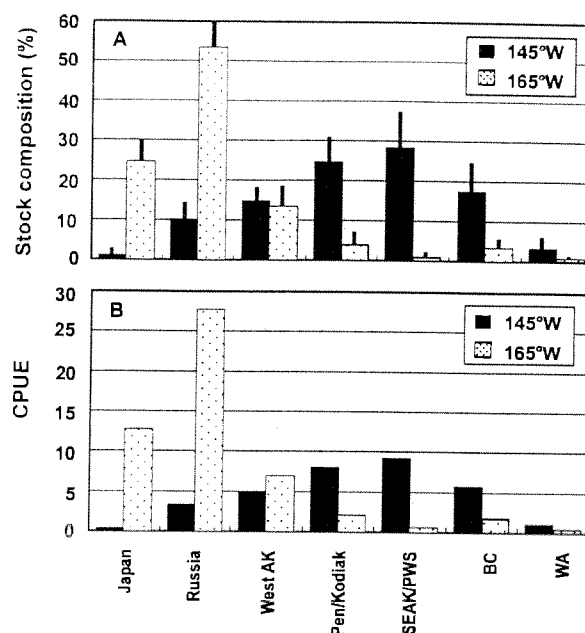
**Fig. 3.** CPUE (fish catch per set of research gillnets) of thermally-marked and unmarked chum salmon on transects at 145°W and 165°W in the Gulf of Alaska in the summer of 1998.



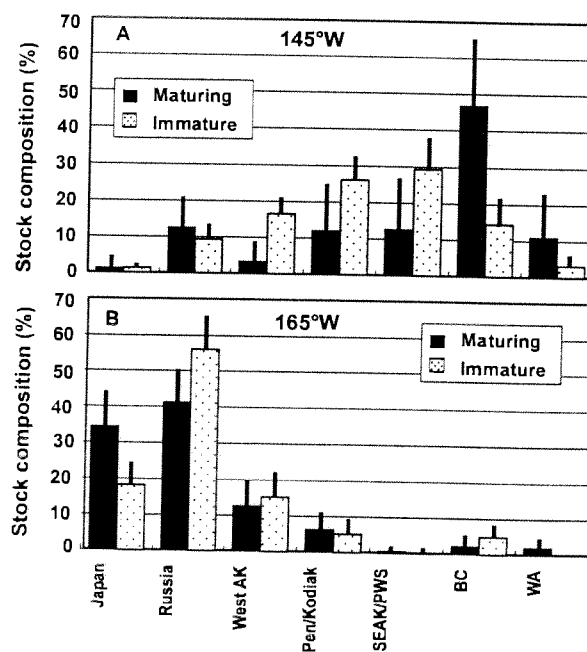
**Fig. 4.** Age composition of thermally-marked fish among immature chum salmon caught at 145°W transect in the Gulf of Alaska in the summer of 1998.



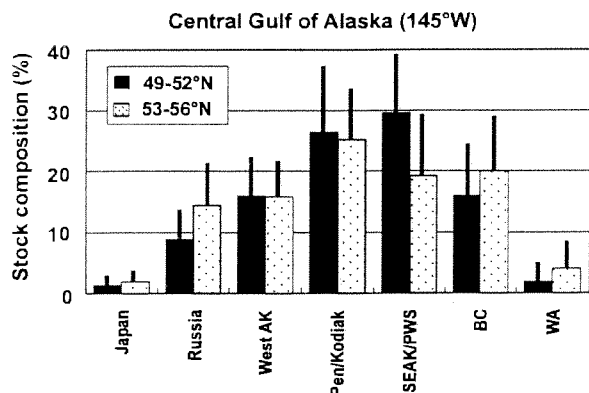
**Fig. 5.** GSI-estimated stock composition (%), A) and CPUE (number of fish per set of research gillnets, B) of chum salmon caught on transects at 145°W and 165°W in the Gulf of Alaska in the summer of 1998. Bars indicate SD of estimates. West AK, West Alaska; Pen/Kodiak, Alaska Peninsula and Kodiak; SEAK/PWS, Southeast Alaska and Prince William Sound; BC, British Columbia, WA, Washington.



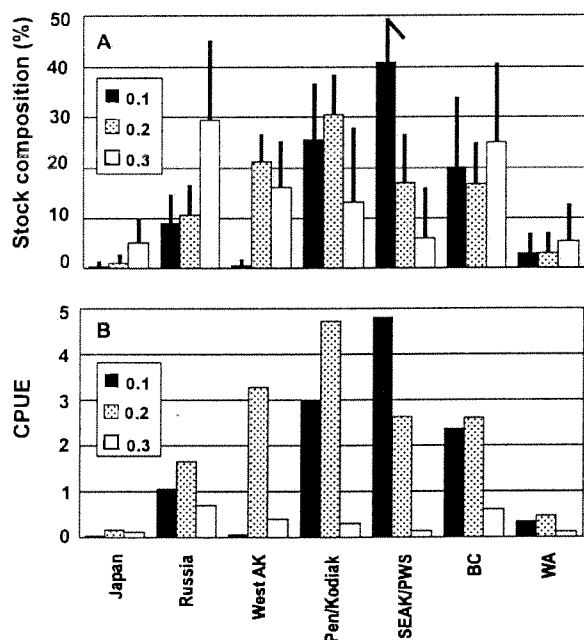
**Fig. 6.** GSI-estimated stock composition (%) of immature and maturing chum salmon caught on transects at 145°W (A) and 165°W (B) in the Gulf of Alaska in the summer of 1998. Bars indicate SD of estimates. West AK, West Alaska; Pen/Kodiak, Alaska Peninsula and Kodiak; SEAK/PWS, Southeast Alaska and Prince William Sound; BC, British Columbia, WA, Washington.



**Fig. 7.** A comparison of GSI-estimated stock composition (%) of immature chum salmon caught in the southern (49–52°N) and northern (53–56°N) waters at 145°W transect in the Gulf of Alaska in the summer of 1998. Bars indicate SD of estimates. West AK, West Alaska; Pen/Kodiak, Alaska Peninsula and Kodiak; SEAK/PWS, Southeast Alaska and Prince William Sound; BC, British Columbia; WA, Washington.



**Fig. 8.** By age stock composition (% A) and CPUE (number of fish per set of research gillnets, B) of immature chum salmon caught at 145°W transect in the Gulf of Alaska in July 1998. The compositions were estimated by genetic stock identification. Bars indicate SD of estimates.



## DISCUSSION

The 1996 winter GSI results showed that various regional stocks of North American and Asian chum salmon intermingled in the central Gulf of Alaska, but Asian stocks were dominant in the western Gulf of Alaska (Urawa and Ueno 1997; Urawa et al. 1997). The present summer GSI results indicated similar stock composition estimates in the western Gulf of Alaska. In the central Gulf of Alaska, however,

North American stocks (central and southeast Alaska, and BC) were common in the summer of 1998.

The GSI results were supported by data of thermal otolith marks showing frequent occurrence of marked chum salmon in the central Gulf of Alaska and rare detection in the western waters. Among these marked fish ( $n = 51$ ), 49 originated from four hatcheries in PWS and SEAK, where about 200 million chum fry were released annually after thermal marking (Fig. 9; Geiger and Munk 1998). Two other marked chum salmon were from Nitinat Hatchery in BC, where about 30 million chum fry were thermally marked annually (Hargreaves et al. 1999). In the Gulf of Alaska, we found no marked chum salmon that were released from Washington (Volk and Hagen 1998) and Russia (Akinitcheva and Rogatnykh 1999).

Ninety-eight percent of thermally-marked chum salmon were immature when they were caught in the Gulf of Alaska during late June and early July. This may reflect their spawning season: by this time maturing fish have already moved to coastal waters for spawning in PWS and SEAK. The GSI results suggested that maturing chum salmon originating from southern North America (BC and Washington) were still distributed in the northern waters of the central Gulf of Alaska in early July. This is possible because the main spawning season of southern stocks is usually between October and December. Thermal mark and GSI results indicated that this biased distribution may be caused partly by entry of northern populations such as Alaska Peninsula and west Alaska stocks.

Contributions of SEAK/PWS stocks to immature chum salmon in the central Gulf of Alaska were estimated by both GSI and thermal marks (Fig. 10). This comparison suggested that most of SEAK/PWS chum salmon in the Gulf of Alaska may be hatchery origin if the survival rate is similar among thermally-marked and unmarked hatchery fish. The number of thermally-marked chum salmon of PWS/SEAK ori-

**Fig. 9.** Annual changes in number of thermally otolith marked chum salmon juveniles released from hatcheries in southeast Alaska and Prince William Sound.

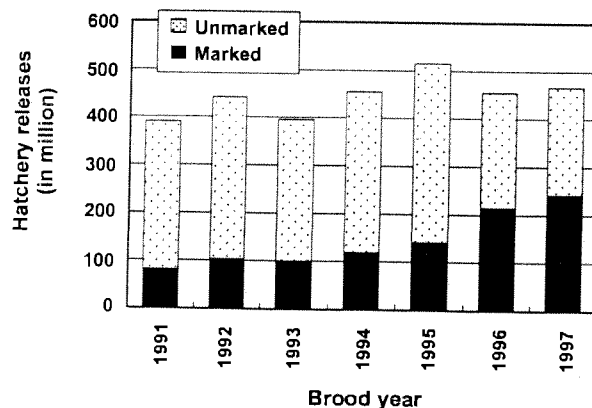
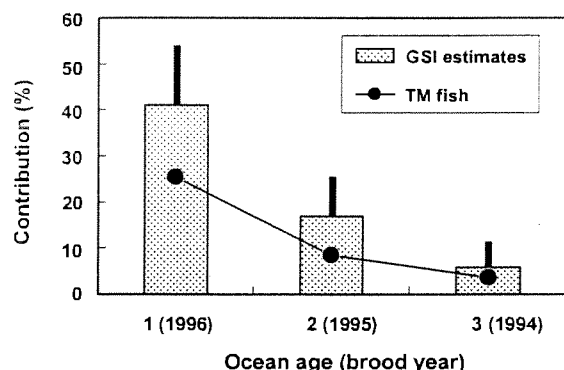


Fig. 10. Contributions of Southeast Alaska (SEAK)/Prince William Sound (PWS) stocks to immature chum salmon caught in the central Gulf of Alaska (145°W) in July 1998. TM fish, thermally-marked fish originating from SEAK/PWS. Bars indicate SD of GSI estimates.



gins decreased as ocean age increased among immature chum salmon in the central Gulf of Alaska (Fig. 4). This decrease may partly reflect annual changes in the number of thermally marked fish released from hatcheries (Fig. 9). However, the GSI analysis also showed a similar trend toward a high proportion of SEAK/PWS stocks (41%) among age 0.1 fish, which decreased to 17% and 6% among age 0.2 and 0.3 fish, respectively (Fig. 10). In contrast, west Alaskan chum salmon rarely appeared in the age 0.1 group, but comprised 17–21% of older age groups. The proportion of Russian chum salmon also increased to 29% in the age 0.3 group. These results suggest that chum salmon stocks along the Gulf of Alaska coasts (SEAK/PWS, Alaska Peninsula and BC) are dominant in early ocean life in the central Gulf of Alaska, but their predominance may decrease because other stocks (such as west Alaska and Russia) enter these waters in after the second year of their ocean life. This influx of other stocks may bias the distribution towards an apparently lower proportion of SEAK/PWS stocks in northern waters and a higher proportion in southern waters where younger fish were more abundant.

Thermal otolith marking is an effective tool for determining hatchery origins of individual salmon in high seas as well as in coastal waters. However, some duplication of codes occurs within or between Alaska, British Columbia and Russia, because of the limited number of thermal marks (Hagen 1999) and poor coordination among agencies. In the present study, these duplications could be resolved by secondary characters. However, duplicated thermal marks are a challenge even for the experienced observer (Munk 1999). Thermal marking has been primarily used for coastal fishery management in Alaska, and coordination of thermal mark coding has not occurred among countries or states. Now there are large numbers of thermally-marked salmon released from hatcheries in North Pacific Rim countries.

This provides a good opportunity to study life histories and population dynamics of hatchery salmon and their relations to wild stocks in the ocean. To reduce duplications of thermal mark patterns, we should consider coordination of marking strategies.

## ACKNOWLEDGMENTS

We thank crews of the T/V *Oshoro maru* for their help in fish sampling, and William R. Heard of Auke Bay Laboratory, Alaska Fisheries Science Center, for providing a data set of hatchery releases in SEAK/PWS.

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# The Use of Thermal Otolith Marks to Determine Stock-Specific Ocean Distribution and Migration Patterns of Alaskan Pink and Chum Salmon in the North Pacific Ocean 1996–1999

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Carlson, H.R., E.V. Farley, Jr., and K.W. Myers. 2000. The use of thermal otolith marks to determine stock-specific ocean distribution and migration patterns of Alaskan pink and chum salmon in the North Pacific Ocean 1996–1999. N. Pac. Anadr. Fish Comm. Bull. No. 2: 291–300.

**Keywords:** Salmon, ocean, distribution, migration, rope-trawl, thermal-otolith-mark

**Abstract:** Off shore distribution of juvenile (ocean age .0) Alaskan pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon with thermal otolith marks caught by midwater trawl in the North Pacific varies by geographic region. This may reflect differences in the width of the continental shelf. A few juvenile southeastern Alaska hatchery chum salmon were caught south of major exit corridors, counter to the predominant northward migration pattern. The northern Shelikof Strait may be an important summer migration corridor for juvenile pink salmon. The ocean range of central Alaska pink salmon extends further to the southwest (to 42°N, 165°W) than shown by high-seas tag experiments, and some maturing chum salmon caught in the coastal waters off Prince William Sound in May, are from an early southeastern Alaska hatchery run (peak harvest in mid-July). We conclude that sufficient numbers of thermally-marked hatchery salmon can be recovered during coastal and offshore salmon surveys to provide significant new stock-specific information on ocean distribution and migration patterns of salmon.

## INTRODUCTION

In 1995, the Ocean Carrying Capacity (OCC) program at the Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, initiated a comprehensive program to describe the role and spatial distribution of salmon in the marine ecosystem, and to test for density dependence in the growth rate of Pacific salmon (*Oncorhynchus* spp.) during various periods of ocean residency (National Marine Fisheries Service 1995). The work is part of an international research effort coordinated through the North Pacific Anadromous Fish Commission (NPAFC) to investigate the physical and biological factors that may be responsible for density-dependent marine growth and survival of salmon (e.g., Kaeriyama 1989, 1996; Helle and Hoffman 1995, 1998; Bigler et al. 1996; Myers et al. this volume).

The primary research emphasis of the OCC program is on the coastal marine phase of juvenile salmon (ocean age .0) in the Alaska Coastal Current (ACC), and a secondary emphasis is on immature and maturing salmon in the Alaska Gyre. From 1996 to 1999, the OCC program focused on broad-scale ship-

board surveys in coastal and offshore waters in spring and summer (Carlson et al. 1996, 1997, 1998a, b, 1999). The major objectives of the surveys were to learn more about the ocean distribution of salmon in the ACC and Gulf of Alaska (GOA), their migration pathways in relation to the continental shelf or slope and distance from shore, the relative abundance and co-occurrence of salmon species, their stock identity or river system of origin, ocean growth, and food habits.

This is the first US program to use large, mid-water rope trawls, towed at high speeds (5.0 kts), to capture salmon at sea, a technique pioneered by Russian researchers and further developed by the OCC program in cooperation with Canadian scientists (e.g., Shuntov et al. 1993; Auke Bay Laboratory, unpublished data). The use of rope trawls greatly enhances our ability to conduct intensive sampling of salmon over broad areas of the North Pacific Ocean in relatively short periods of time, even in moderately rough weather and poor sea conditions.

In recent years, some of the most important scientific advances in ocean salmon research have come through the pioneering, cooperative efforts of the OCC and other NPAFC-related research programs to

† deceased

apply new stock-identification technologies to investigations of distribution, migration, growth, and diet of specific stocks or regional populations of salmon (e.g., thermal otolith marks: Farley and Munk 1997; Farley et al. 1999; Farley and Carlson this volume; Urawa et al. this volume; data storage tags: Walker et al. 2000; genetics: Guthrie et al. this volume; Urawa et al. this volume). Thermal marking of salmon otoliths is a relatively new stock identification technique that is now being used by commercial fisheries managers in Alaska to provide information on the contribution of individual hatchery stocks to commercial and cost recovery salmon fisheries (Hagen et al. 1995). Farley and Munk (1997) reported the first recoveries of thermally marked hatchery salmon caught during OCC salmon surveys in the GOA in July and August 1996.

In this paper, we summarize information on the recoveries of thermally marked Alaskan hatchery pink (*O. gorbuscha*) and chum (*O. keta*) salmon during 1996–1999 OCC field surveys. We report new information on salmon distribution and migration patterns in the ACC and Gulf of Alaska, compare our results to previous conceptual models of ocean distribution and migration patterns of salmon, and briefly discuss the factors that may influence these patterns.

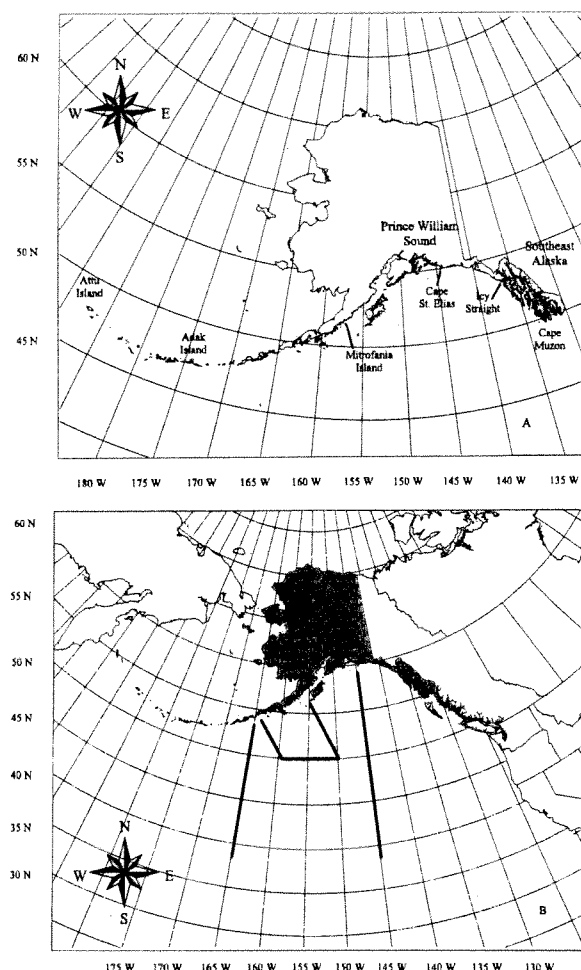
## MATERIALS AND METHODS

### Surveys

During spring (April and May) of 1998 and 1999 and summer (July and August) of 1996–1998, the OCC program conducted five surveys to describe the distribution of juvenile, immature, and maturing salmon in the ACC and GOA. The summer surveys focused on sampling juvenile salmon in coastal waters. During the summers of 1996 and 1998, the coastal surveys began in southern Southeast Alaska (Cape Muzon), and sampled coastal waters to as far west as Adak Island (Carlson et al. 1996; Carlson et al. 1998b; Fig. 1A). During 1997, the survey began at Cape St. Elias, and sampled coastal waters to Attu Island (Carlson et al. 1997). Transects sampled during the summer surveys were perpendicular to the coast and 110–220 km apart. Fish sampling along each transect generally occurred from near shore to at least 185 km off shore.

The spring surveys focused on sampling immature and maturing salmon in offshore waters of the Gulf of Alaska and northeastern North Pacific (Carlson et al. 1998a; Carlson et al. 1999; Fig. 1B). During May 1998, the OCC survey sampled waters south and then east along the 50°N latitude line to 150°W. The survey continued south along the 145°W longi-

**Fig. 1.** Survey area sampled by the OCC program during (A) July–August 1996–1998 (coastal waters of the North Pacific Ocean; Cape Muzon to Attu Island), and transects sampled during (B) April–May 1998 and 1999.



tude line beginning at 59°N and ending at 38°N. During May 1999, the OCC survey sampled waters south along the 165°W longitude line from 52°N to 38°N, then continued north along the 145°W longitude line from 38°N to 59°N. Fish sampling along each of the longitudinal lines generally occurred at every degree latitude.

All surveys were conducted aboard a contracted 38 m stern trawler (F/V *Great Pacific*). The fishing gear was a midwater rope trawl, model 400/580, made by Cantrawl Pacific Ltd.<sup>1</sup> of Richmond, B.C. The net was 198 m long, had hexagonal mesh in the wings and body, and a 1.2 cm mesh liner in the codend. The net was fished with three 60 m, 1.9 cm bridles attached at a single point to steel alloy 5 m midwater trawl doors, each weighing 463 kg. The net was towed at 5 kts at or near surface, with floats on the headrope and 260 m of warp line on each

<sup>1</sup>Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

door. The net was monitored using a Simrad 300 net sounder, which showed a typical spread of 52 m horizontally and 18 m vertically. All tows lasted 30 to 60 minutes and covered 2.8 to 11.1 km. During the summer surveys, all sampling was done during daylight hours; all but 7 tows during the spring surveys were completed during daylight hours.

Catches were brought aboard, and the codend was emptied onto a sorting table. Juvenile (first ocean year; ocean age .0), immature (second or third ocean year; ocean age .1 or older), and maturing salmon were identified and sorted by species. Standard biological measurements including fork length, body weight, and sex as well as scale samples from the preferred area (to document age and growth) were taken from subsamples of all salmon species. Otoliths from pink and chum salmon were saved to identify hatchery origin for salmon with thermally induced otolith marks.

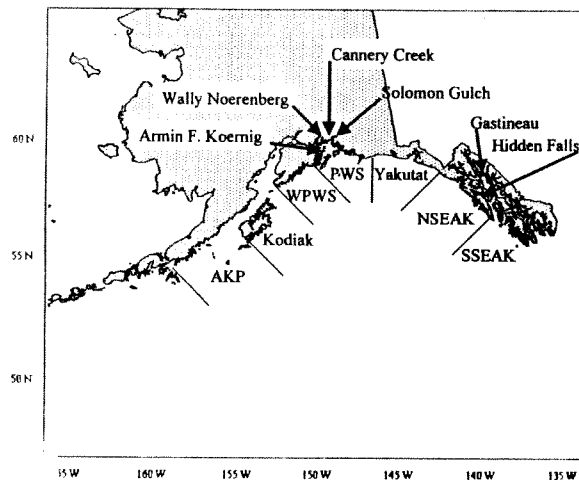
### Stock Identification Techniques

Salmon otoliths were analyzed to determine stock-specific distribution and migration. Left and right sagittal otoliths were removed from salmon heads, and the left sagittal otoliths mounted, using thermal resin, on petrographic slides and then ground to expose the primordia. If left sagittal otoliths were not available or were overground, then the right sagittal otoliths were used. Otolith microstructure was examined under a compound microscope, and the microstructure patterns were compared to thermal mark patterns from voucher specimens collected from hatcheries. For this study, we compared otolith thermal mark patterns from pink and chum salmon collected during the surveys to voucher specimens collected from Gastineau and Hidden Falls hatcheries located in Southeast Alaska and Armin F. Koernig, Cannery Creek, Solomon Gulch, and Wally H. Noerenberg hatcheries located in Prince William Sound (Fig. 2). All otoliths were read independently by a second reader to assure accuracy and confidence in the readings (Hagen et al. 1995). Disagreements between otolith readers were resolved by the most experienced otolith reader.

### Data Analysis

Catches (numbers of fish) were pooled over years for juvenile salmon in summer coastal surveys (1996–1998) and for immature and maturing salmon in spring offshore surveys (1998–1999), and summarized graphically to show variation by species, maturity-group, region, and distance off shore. For graphical displays of juvenile salmon data, we divided the area along the coast into seven regions (Fig. 2). The distributions of thermally marked salmon from Southeast Alaskan and Prince William Sound hatch-

**Fig. 2.** Regions defined for the coastal waters of the Gulf of Alaska sampled by the OCC program during July–August 1996–1998. (Regions include: Southern Southeast Alaska (SSEAK); Northern Southeast Alaska (NSEAK); Yakutat; Prince William Sound (PWS); Western Prince William Sound (WPWS); Kodiak; and Alaska Peninsula (AKP)) and approximate locations of Prince William Sound (Armin F. Koernig, Wally Noerenberg, Cannery Creek, and Solomon Gulch) and Southeast Alaska (Gastineau and Hidden Falls) hatcheries.



eries are represented as percentages of the total catch in each region. Catch per unit effort (CPUE), calculated as catch per 1-hour trawl, was used as a measure of relative abundance of salmon. Information on ocean ranges of thermally marked hatchery salmon stocks was compared to known ranges from high seas tag recovery experiments (1956–present, data archived at the University of Washington, School of Aquatic and Fishery Sciences, Fisheries Research Institute, Seattle).

## RESULTS

### Summer Coastal Surveys

During the summer (1996–1998) surveys, a total of 245 trawl stations were sampled along 54 transects. A total of 47,856 salmon representing five species (and including all life-history stages (juvenile, immature, and maturing) were captured (Table 1). The vast majority of the salmon captured during the summer coastal surveys were juvenile salmon, including pink (50%), chum (12%), sockeye (*O. nerka*; 8%), coho (*O. kisutch*; 5%), and chinook (*O. tshawytscha*; < 1%) salmon. Immature and maturing salmon were also captured during the surveys including immature chum (10%), sockeye (4%), and chinook (< 1%) salmon and maturing pink (5%), chum (1%), sockeye (< 1%), coho (< 1%), and chinook (< 1%) salmon.

Juvenile salmon were distributed along the continental shelf from southern Southeast Alaska (Cape Muzon) to Mitrofanina Island, west of Kodiak Island (Fig. 1). Juvenile pink and chum salmon catches

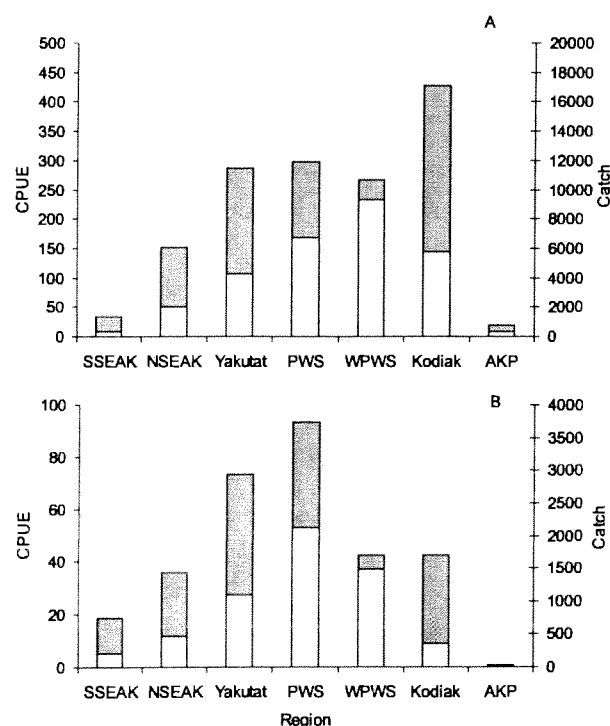
**Table 1.** Number of juvenile (J), immature (I), and maturing (M) salmon captured during summer (1996–1998) in the coastal waters of the North Pacific Ocean.

| Year  | Pink   |       | Chum  |       |     | Sockeye |       |     | Coho  |     | Chinook |     |    |
|-------|--------|-------|-------|-------|-----|---------|-------|-----|-------|-----|---------|-----|----|
|       | J      | M     | J     | I     | M   | J       | I     | M   | J     | M   | J       | I   | M  |
| 1996  | 4,701  | 1,438 | 1,932 | 2,059 | 260 | 1,414   | 411   | 132 | 1,405 | 178 | 31      | 99  | 17 |
| 1997  | 788    | 548   | 323   | 1,802 | 185 | 322     | 698   | 54  | 357   | 49  | 19      | 43  | 13 |
| 1998  | 18,594 | 541   | 3,487 | 1,105 | 128 | 2,296   | 1,019 | 28  | 842   | 120 | 349     | 51  | 18 |
| Total | 24,083 | 2,527 | 5,742 | 4,966 | 573 | 4,032   | 2,128 | 214 | 2,604 | 347 | 399     | 193 | 48 |

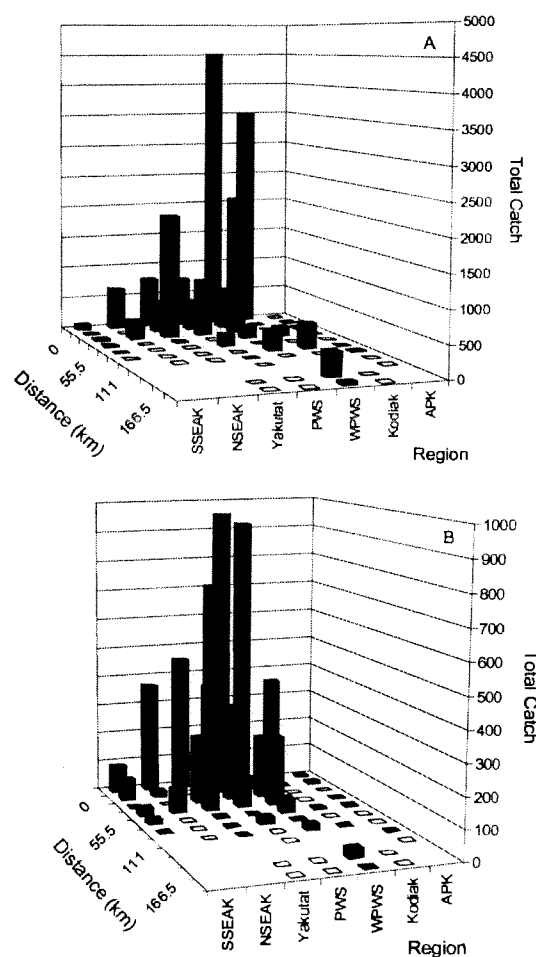
were generally largest in regions west of known exit corridors for juvenile salmon leaving inside waters of southeastern Alaska (Icy Strait) and Prince William Sound (Figs. 3A and B). CPUE for juvenile pink and chum salmon generally followed catch patterns for these fish around the coast except for juvenile pink salmon in the Kodiak Island region where the CPUE was larger (Figs. 3A and B).

Juvenile pink and chum salmon distribution varied by region and by species. Off the coast of Southeast Alaska (southern Southeast Alaska (SSEAK) and northern Southeast Alaska (NSEAK) regions), juvenile pink and chum salmon were distributed from near shore to 93 km off shore (Figs. 4A and B). In the Yakutat region, juvenile pink salmon were generally distributed near shore to 56 km off shore, whereas, juvenile chum salmon were distributed near

**Fig. 3.** Catch per unit effort (CPUE; clear bar) and total catch (gray bar) by region (regions include: Southern Southeast Alaska (SSEAK); Northern Southeast Alaska (NSEAK); Yakutat; Prince William Sound (PWS); Western Prince William Sound (WPWS); Kodiak; and Alaska Peninsula (AKP)) for juvenile (A) pink and (B) chum salmon caught in the coastal waters of the Gulf of Alaska by the OCC program during July–August 1996–1998.



**Fig. 4.** Total catch of juvenile (A) pink and (B) chum salmon by distance offshore and coastal region (regions include: Southern Southeast Alaska (SSEAK); Northern Southeast Alaska (NSEAK); Yakutat; Prince William Sound (PWS); Western Prince William Sound (WPWS); Kodiak; and Alaska Peninsula (AKP)) in the Gulf of Alaska during summer (1996–1998). Dark bars indicate total catch; empty bars indicate area sampled but no juvenile pink salmon were caught.



shore to 111 km off shore. In the western Prince William Sound (WPWS) region, both juvenile pink and chum salmon were distributed from near shore to 185 km off shore. In the Kodiak Island and Alaska Peninsula (AKP) regions, juvenile pink salmon were generally distributed near shore to 111 km off shore, whereas juvenile chum salmon were distributed near shore to 130 km off shore.

The largest catches of juvenile pink and chum salmon varied by distance off shore, region, and species (Figs 4A and B). In the SSEAK and NSEAK regions, the largest catches of juvenile pink and chum salmon occurred near shore. In the Yakutat, Prince William Sound (PWS), and WPWS regions, the largest catches of juvenile pink salmon occurred between near shore and 37 km off shore; whereas, the largest catches of juvenile chum salmon in this area occurred between near shore and 56 km off shore. Juvenile pink and chum salmon catches declined in the Kodiak Island and AKP regions. The largest catches of juvenile pink and chum salmon occurred nearshore in the Kodiak Island region, while in the AKP region there was no particular pattern in juvenile pink or chum salmon catch.

Distribution of juvenile hatchery pink and chum salmon from Southeast Alaska and Prince William Sound varied little between species (Figs. 5A and B). Juvenile hatchery pink salmon from Southeast Alaska were distributed from the Yakutat region to the WPWS region while juvenile chum salmon were distributed from the NSEAK to the WPWS region. Juvenile pink and chum salmon from Prince William Sound hatcheries were distributed from the WPWS region to the AKP region.

The percentage of Southeast Alaska and Prince William Sound hatchery pink and chum salmon in our catch varied between regions (Figs 5A and B). The percentage of Southeast Alaska hatchery pink salmon in our catch ranged from less than 1% in the PWS and WPWS regions to 1% of our catch in the Yakutat region. The percentage of chum salmon from Southeast Alaska hatcheries was larger than that for juvenile hatchery pink salmon from that area, ranging from 1% in the NSEAK region to 28% in the PWS region. The percentage of Prince William Sound hatchery pink and chum salmon in our catch ranged from 17% and 10%, respectively, in the Kodiak Island region to 30% for each species in the WPWS region.

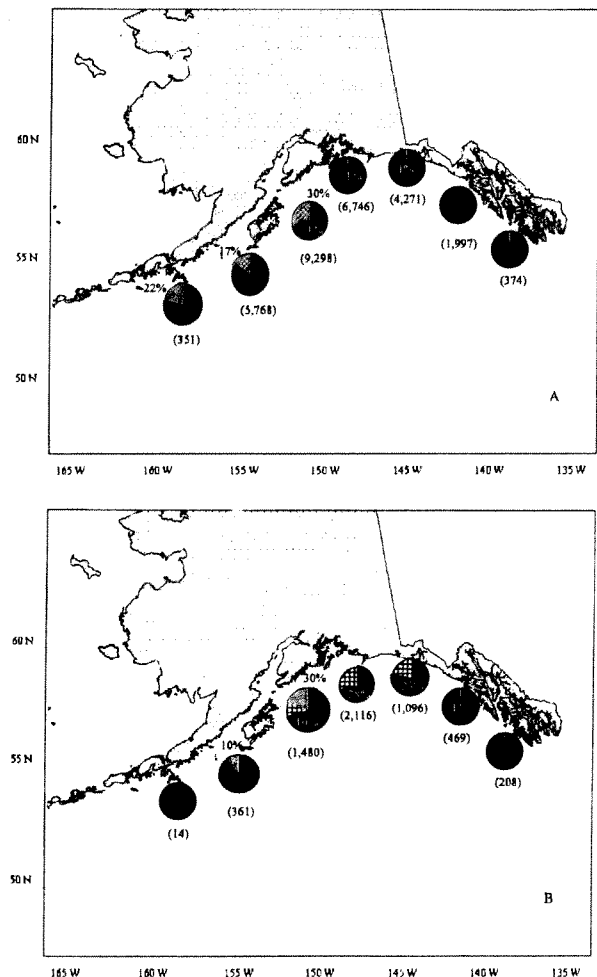
### Spring Offshore Surveys

During the spring (1998 and 1999) surveys, 121 trawl stations were sampled and a total of 2,643 salmon representing five species were captured (Table 2). Salmon captured during the surveys included

immature chum (16%), sockeye (32%), and chinook (4%) and maturing pink (11%), chum (22%), sockeye (13%), coho (2%) and chinook (< 1%) salmon.

Maturing pink salmon were distributed along the 145°W longitude line from 41° N to 55°N and along the 165°W longitude line from 39°N to 48°N (Figs. 6A and B). The largest CPUE of pink salmon occurred between 45°N and 50°N along the 145°W

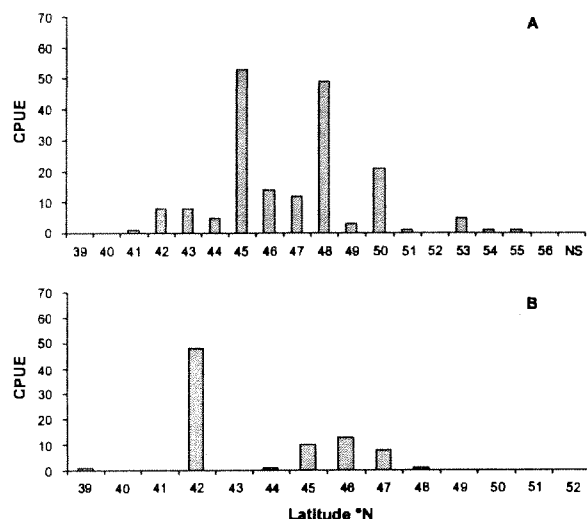
**Fig. 5.** Distribution and percentage of thermally marked juvenile (A) pink and (B) chum salmon (pie chart; solid black area—percentage not marked; solid gray area—percentage (written outside of pie chart) of thermally marked Prince William Sound hatchery pink or chum salmon in our catch; squared area—percentage (written inside solid black area) of thermally marked Southeast Alaska hatchery pink or chum salmon in our catch) by the OCC program during July–August 1996–1998.



**Table 2.** Number of immature (I) and maturing (M) salmon captured during spring (1998–1999) in offshore waters of the North Pacific Ocean.

| Year  | Pink | Chum |     | Sockeye |     | Coho | Chinook |   |
|-------|------|------|-----|---------|-----|------|---------|---|
|       | M    | I    | M   | I       | M   | M    | I       | M |
| 1998  | 109  | 184  | 322 | 602     | 141 | 36   | 84      | 6 |
| 1999  | 183  | 236  | 254 | 247     | 196 | 22   | 19      | 2 |
| Total | 292  | 420  | 576 | 849     | 337 | 58   | 103     | 8 |

**Fig. 6.** Catch per unit effort (CPUE) for maturing pink salmon along the (A) 145°W longitude line and (B) 165°W longitude line during spring 1998 and 1999. (NS is defined as the area sampled from near shore to 100 km offshore.)

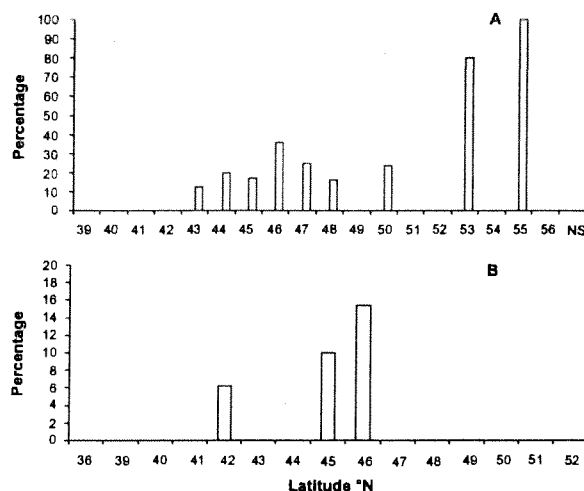


longitude line and at 42°N along the 165°W longitude line. All of the thermally marked maturing pink salmon caught during the spring surveys were from Prince William Sound hatcheries. These fish were distributed between 43°N and 55°N along the 145°W longitude line and from 42°N to 46°N along the 165°W longitude line (Figs. 7A and B). The percentage of Prince William Sound pink salmon in our catch ranged from 11% at 43°N to 100% at 55°N along the 145°W longitude line and from 6% at 42°N to 15% at 46°N along the 165°W longitude line.

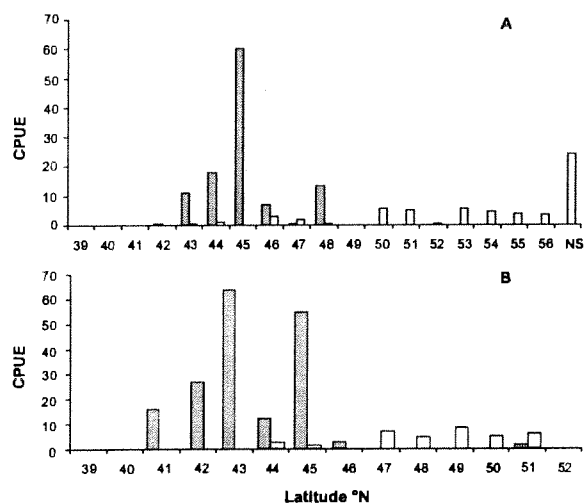
Immature chum salmon were distributed in the southern half of both longitudinal transects while maturing salmon were distributed in the northern half of each longitudinal transect (Figs. 8A and B). Immature chum salmon were distributed along the 145°W longitude line from 42°N to 48°N and along the 165°W longitude line from 41°N to 51°N. The largest CPUE for immature chum salmon occurred at 45°N along the 145°W longitude line and south of 47°N along the 165°W longitude line. Maturing chum salmon were distributed between 43°N and nearshore (NS) with the largest CPUE occurring north of 50°N along the 145°W longitude line. Maturing chum salmon captured along the 165°W longitude line were distributed between 44°N and 51°N with the largest CPUE occurring north of 46°N.

All of the immature and maturing hatchery chum salmon caught during the spring surveys were distributed east of the 165°W longitudinal line. Immature hatchery chum salmon from Southeast Alaska and Prince William Sound hatcheries were distributed between 43°N and 48°N along the 145°W longitude line (Fig. 9). The percentage of immature hatchery chum salmon from Southeast Alaska in our catch along the 145°W longitude line ranged from 23% at 43°N to 7% at 48°N. The percentage of immature

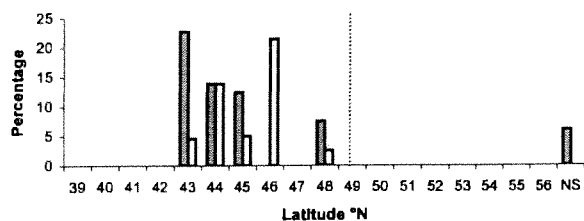
**Fig. 7.** Percentage of thermally marked pink salmon along the (A) 145°W longitude line and (B) 165°W longitude line from Prince William Sound (clear bar) hatcheries in our catch during spring 1998 and 1999. (NS is defined as the area sampled from near shore to 100 km offshore.)



**Fig. 8.** Catch per unit effort (CPUE) for immature (solid bar) and maturing (clear bar) chum salmon along the (A) 145°W longitude line and (B) 165°W longitude line during spring 1998 and 1999. (NS is defined as the area sampled from near shore to 100 km offshore.)



**Fig. 9.** Percentage of thermally marked immature and maturing chum salmon along the 145°W longitude line from Southeast Alaska (solid bar) and Prince William Sound (clear bar) hatcheries in our catch during spring 1998 and 1999. (NS is defined as the area sampled from near shore to 100 km offshore. Dotted line indicates break between immature (left side) and maturing salmon (right side) in our catch.)



hatchery chum salmon from Prince William Sound in our catch along the 145°W longitude line ranged from 21% at 46°N to 3% at 48°N. Almost all of the maturing hatchery chum salmon were from Southeast Alaska hatcheries and were found in the nearshore (NS) waters of the 145°W longitude line.

## DISCUSSION

A conceptual model of oceanic migration patterns of juvenile salmon from Southeast Alaska and Prince William Sound suggests that these stocks migrate in a narrow band around the coastal waters of the Gulf of Alaska (Hartt and Dell 1986). Various ocean surveys in the coastal region of Southeast Alaska estimated the coastal migration corridor of juvenile salmon to be from near shore waters to as far as 74 km off shore (Hartt and Dell 1986; Jaenicke and Celewycz 1994; and Murphy et al. 1999). We found juvenile pink and chum salmon to 93 km off shore in SSEAK but only to 56 km off shore in NSEAK suggesting regional off shore distribution patterns for juvenile pink and chum salmon.

The regional off shore distribution differences for juvenile pink and chum salmon may be influenced by the regional differences in the width of the shelf along the coast. The distance across the shelf in the SSEAK region is approximately 75 km, whereas the distance across the shelf in the NSEAK region is approximately 45 km. The continental shelf broadens to span a distance of nearly 200 km in the region directly west of Prince William Sound. Coincidentally, juvenile pink and chum salmon in our catch were distributed well off shore in the WPWS region, and were found along the entire shelf from near shore to 185 km off shore. However, a variety of factors such as coastal current, sea temperature, food availability, and body size may also affect off shore distribution of juvenile salmon.

A conceptual model of oceanic migrations for Southeast Alaska and Prince William Sound pink and chum salmon stocks also suggests that these stocks migrate in a counter-clockwise direction around the coastal waters of the GOA (Hartt and Dell 1986). Almost all of the thermally marked salmon we collected during the summer surveys were distributed west of major exit corridors for juvenile salmon leaving inside waters of Southeast Alaska (Icy Strait) and Prince William Sound. This suggests a counter-clockwise migration of these stocks around the coastal waters of the Gulf of Alaska. However, there were four thermally marked chum salmon from Southeast Alaska hatcheries located in the coastal waters of the GOA south of Icy Strait. Two possible explanations for this include: (1) these salmon migrated south after entering the coastal waters via Icy Strait; or (2) these salmon migrated south while still

in inside waters and entered the coastal waters via Dixon Entrance.

As mentioned in the previous section, CPUE for juvenile pink and chum salmon generally followed catch patterns for these fish around the coast except for the Kodiak Island region, where CPUE was larger. The large CPUE in the Kodiak Island region is an artifact of our 1998 sampling design. During our 1998 summer survey, we sampled four stations along the northern entrance to Shelikof Strait that were not sampled during the 1996 or 1997 summer surveys. The large juvenile pink and chum salmon CPUE for this region is the result of the large catches of juvenile pink and chum salmon in Shelikof Strait coupled with fewer trawl hauls in the Kodiak Island region when compared to the WPWS region. Overall, 90% of the juvenile pink salmon catch in the coastal region of Kodiak Island occurred in northern Shelikof Strait. The large catches of juvenile pink salmon in northern Shelikof Strait were not expected, and may indicate the importance of this area as a migration corridor for juvenile pink salmon during summer.

The percentage of juvenile Southeast Alaska hatchery pink salmon in our catch seemed low in comparison to the percentage of juvenile Prince William Sound hatchery pink salmon in our catch. Of the two hatcheries thermally marking salmon in Southeast Alaska, only Gastineau Hatchery is thermally marking pink salmon. The low percentage ( $\leq 1\%$ ) of juvenile pink salmon from Southeast Alaska in our catch may be due to the low numbers of thermally marked pink salmon being released from Gastineau Hatchery. For example, during 1998 Gastineau Hatchery released 9 million thermally marked pink salmon, whereas Prince William Sound hatcheries released approximately 543 million thermally marked pink salmon (Kristen Munk, Alaska Department of Fish and Game, P.O. Box 25526, Juneau, Alaska, 99802-5526, personal communication).

All of the maturing pink salmon with thermal otolith marks captured during our spring surveys were from Prince William Sound hatcheries. High seas tag recoveries of maturing pink salmon (1956–present) indicated that central and southwestern Alaska pink salmon stocks were widely distributed in the GOA during spring, and were found as far south as 44°N and as far west as 160°W. Thermally marked pink salmon from Prince William Sound hatcheries caught during our spring surveys were found as far south as 42°N and as far west as 165°W, which is a southwestward range extension for central Alaska pink salmon.

Chum salmon caught during our spring surveys were widely distributed north and south along the central and western GOA transects. Past surveys during May indicated a more southerly distribution of immature chum salmon and a more northerly distribution for maturing chum salmon in the central and

western GOA (Neave et al. 1976). This is consistent with the distribution patterns of immature and maturing chum salmon caught during our spring surveys. Our largest catches of immature chum salmon were located further south in both the central and western GOA than was found in previous studies, while the largest catches of maturing chum salmon were located further north.

High seas tagging experiments conducted during 1956 to 1971 indicated a dominance of Asian stocks in the western GOA and a dominance of North American stocks in the central GOA during spring (Neave et al. 1976). More recently, genetic stock identification techniques (GSI) performed on immature and maturing chum salmon caught in the central and western GOA during winter 1996, indicated that various regional stocks of North American and Asian chum salmon intermingled in the central GOA, while Asian stocks were dominant in the western GOA (Urawa et al. 1997; Urawa and Ueno 1997). The tagging and GSI results are supported by the thermal mark results for chum salmon captured during our spring surveys. All of the thermally marked chum salmon from Prince William Sound and Southeast Alaska hatcheries were located in the central GOA; whereas, none of the chum salmon caught in the western GOA during our spring surveys were from Alaska hatcheries.

Almost all of the maturing hatchery chum salmon caught during our spring surveys were from Southeast Alaska hatcheries, and were located in the coastal waters off Prince William Sound. High-seas tagging experiments of maturing chum salmon in the coastal waters west of Prince William Sound indicated the presence of southeastern Alaska stocks during June; those tagged during May were located in oceanic waters in the central GOA (Neave et al. 1976). In general, the peak nearshore abundance of chum salmon returning to southeastern Alaska occurs during the first two weeks of August, while peak harvest in the northern districts of southeastern Alaska occurs around August 5 (Clark and Weller 1986). However, peak harvest of Gastineau hatchery chum salmon occurs during mid July ([www.alaska.net/~dipac/](http://www.alaska.net/~dipac/)) and may explain the earlier (spring) coastal distribution of these stocks.

## CONCLUSIONS

Our results demonstrate that sufficient numbers of thermally marked hatchery salmon can be recovered during coastal and offshore salmon surveys to provide significant new stock-specific information on their ocean distribution and migration patterns. We plan to continue applying this valuable new tool to international salmon research efforts coordinated through the NPAFC. Because the number of thermal otolith mark patterns available for use is limited, the

NPAFC is playing an important role in coordinating the application and use of these marks for salmon research in international waters (NPAFC 1999). We encourage all agencies planning to use otolith marking techniques for salmon research and management to cooperate in this important international effort.

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## Using Temperatures from Data Storage Tags in Bioenergetic Models of High-Seas Salmon Growth

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**Keywords:** Bioenergetics, data storage tags, Pacific salmon, high-seas migration, growth, temperature

**Abstract:** Data storage tags provide a new technology for acquiring environmental data on salmon movements at sea. In 1998 and 1999, temperature-recording data tags were recovered in Alaska and Japan from salmonids tagged in the Gulf of Alaska and Bering Sea. One use of temperature data records is to improve bioenergetic models of salmon growth in the ocean. Recent bioenergetic models of salmon growth have often used constant, fixed temperatures, because information on actual daily temperature regimes for salmon was lacking. We used actual temperatures in a bioenergetic model to estimate daily ration. We compared simulated salmon marine growth under two temperature conditions: a constant temperature close to sea surface temperature (SST) at the point of release, and actual temperatures. Estimated daily rations were 1.30–1.72% of body weight/day for three chum salmon over migrations of 62 to 98 days from the Bering Sea to Hokkaido. Over a 30-day simulation, final weights of fish at actual temperatures differed from weights of fish at a constant temperature SST by 0.15%–3.46%. Differences were usually negative, because fish migrated from cooler waters, where the constant temperatures used in our analyses were taken, to warmer coastal waters.

### INTRODUCTION

Data storage tags (DSTs) provide a new technology for acquiring environmental data from salmon migrating at sea. In 1998 and 1999, DSTs were recovered in Alaska and Japan from Pacific salmonids (*Oncorhynchus* spp.) tagged in the North Pacific Ocean and Bering Sea (Fukuwaka et al. 1999; Wada and Ueno 1999; Walker et al. 1999, 2000). These tags provide the first detailed records of ambient sea water temperatures encountered by Pacific salmonids. One potential use of these temperature data is to improve bioenergetic models of salmon growth in the ocean. Recent bioenergetic models of ocean salmon growth have often used fixed (Davis et al. 1998) or monthly average (Hinch et al. 1995) sea surface temperatures, as information on actual daily temperature regimes for salmon was lacking. The diel behavior pattern indicated by the DST data, with frequent descents to cooler water during the day, could be feeding behavior, or an indication of a strategy to conserve energy, as proposed by Bevelhimer

and Adams (1993) for kokanee salmon (*O. nerka*). Such a strategy might be detectable as an increase in growth rate (Brett 1971).

We have employed a commonly-used bioenergetic model and data on actual temperatures experienced by migrating salmon for two objectives: 1) to estimate the daily ration or consumption rate of migrating chum salmon, and 2) to evaluate possible differences in growth with respect to temperature by comparing simulated salmon marine growth using actual temperatures and using constant temperatures based on sea surface temperatures.

### MATERIALS AND METHODS

Fish growth was calculated using a published model, Fish Bioenergetics 3.0 for Windows (Hanson et al. 1997). This model uses a balanced energy equation where energy consumed equals energy expended in metabolism, waste elimination, and growth. Users enter data for several factors that affect the energy budget: water temperature, predator

and prey energy density, diet composition, and initial predator weight.

The physiological parameter values provided with the software included values for pink (*O. gorbuscha*) and sockeye (*O. nerka*) salmon (identical values), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*; Appendix Table 1). These parameters were taken from studies on juvenile and adult Pacific salmonids in freshwater lakes. Because no parameter values are given for chum salmon (*O. keta*), we followed the example of Davis et al. (1998) and used the same values as those for pink and sockeye, modifying the intercept for weight dependence of maximum consumption (CA) to accommodate the larger stomach and faster digestion rate of chum (Azuma 1995; Welch 1997).

For initial predator weight and diet composition,

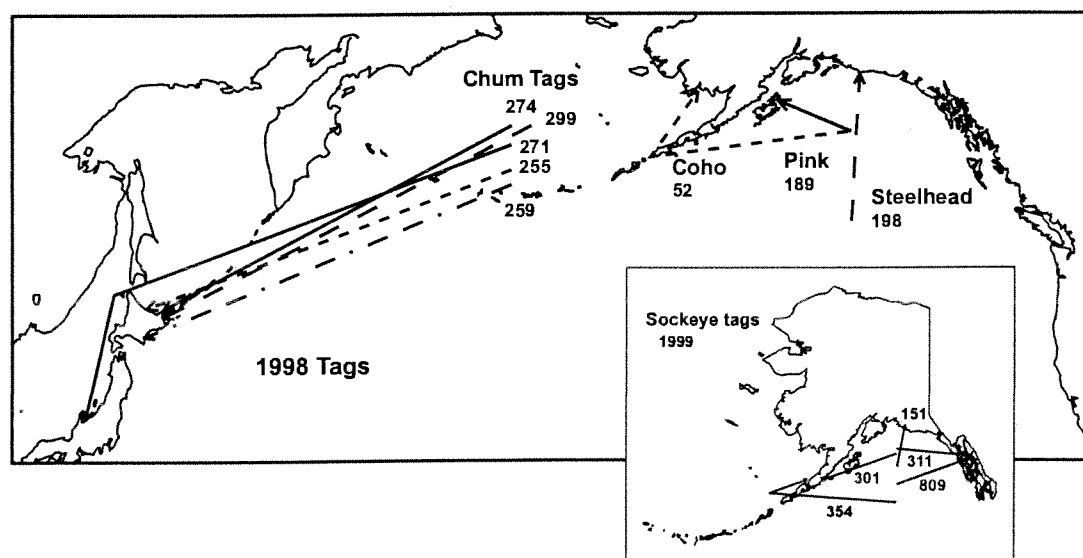
we used average values for each species from catches in the regions where the tagged fish were released (Table 1; Fig. 1). When data from several ocean age classes were available for a species, these parameters were taken from the same age group as the fish in the model, and in the case of chum salmon, weights were calculated from age- and maturity-specific regressions of length and weight of chum caught in the region of tagging. Caloric values for prey were taken from Davis (1993) and Davis et al. (1998). The model allows entry of the fraction of each prey type that is indigestible; these values were also taken from the compilations in Davis et al. (1998). Predator caloric density is a function of body mass for all species except chum salmon. For chum salmon, a value determined by Davis et al. (1998) was used (1376 cal/g).

**Table 1.** Diet composition and prey caloric values used in bioenergetic simulations of salmon tagged with data storage tags. EU, euphausiids; CO, copepods; AM, amphipods; SQ, squid; PT, pteropods; FI, fish; GE, gelatinous zooplankton; PO, polychaetes; AP, appendicularians; CH, chaetognaths. Caloric values taken from Davis et al. (1998).

|             |                         |                |     | Prey            |      |     |     |       |     |      |     |     |     |     |
|-------------|-------------------------|----------------|-----|-----------------|------|-----|-----|-------|-----|------|-----|-----|-----|-----|
|             |                         |                |     | EU              | CO   | AM  | SQ  | PT    | FI  | GE   | PO  | AP  | CH  |     |
|             |                         |                |     | caloric value:  | 743  | 627 | 589 | 1550, | 624 | 1185 | 169 | 814 | 759 | 455 |
| Species     | Data Tag No.            | Region         | Age | (cal/g wet wt.) | 775* |     |     |       |     |      |     |     |     |     |
| Proportions |                         |                |     |                 |      |     |     |       |     |      |     |     |     |     |
| Sockeye     | 151,301,311             | Gulf of Alaska | -.3 | 56              | 12   |     |     | 11    |     | 8    |     | 8   | 5   |     |
|             | 354                     |                | 2.2 | 33              | 16   | 5   |     | 21    | 12  | 5    |     | 5   | 3   |     |
|             | 809                     |                | 1.3 | 19              | 24   | 20  | 11  | 14    | 5   | 2    | 5   |     |     |     |
| Chum        | 255,259,271,<br>274,299 | Bering Sea     |     | 20              | 10   | 15  | 5*  | 20    | 8   | 12   | 10  |     |     |     |
| Pink        | 189                     | Gulf of Alaska | 0.1 |                 | 9    | 10  | 52  | 29    |     |      |     |     |     |     |
| Coho        | 52                      | Gulf of Alaska | 1.1 | 5               |      | 5   | 85  | 5     |     |      |     |     |     |     |
| Steelhead   | 198                     | Gulf of Alaska | 2.3 |                 |      | 2   | 55  | 10    | 33  |      |     |     |     |     |

\* lower caloric value (775) used for larval squid consumed in Bering Sea

**Fig. 1.** Release and recovery locations of thirteen data storage tags placed on Pacific salmonids in the Gulf of Alaska and Bering Sea in 1998 and 1999. Lines connect release and recovery sites and do not indicate actual routes traveled.



Temperature data were taken from thirteen data storage tags placed on five sockeye, five chum, one pink, and one coho salmon and one steelhead trout (Table 2; Fig. 1). Tags were manufactured by Conservation Devices, Inc., and are described more fully in Walker et al. (2000). Temperature data were re-

corded over a range of  $-5^{\circ}\text{C}$  to  $30^{\circ}\text{C}$  with an accuracy of  $\pm 0.2^{\circ}\text{C}$  at intervals of 1.875 to 30 minutes. Fish for tagging were caught by surface longline (chum, pink, coho, steelhead, and sockeye tag 809) or trawl (remaining four sockeye).

**Table 2.** Release and recovery information for 13 salmonids tagged with data storage tags in the North Pacific Ocean and Bering Sea in 1998 and 1999 and recovered in Alaska and Japan. Age determined from scale sample taken at release. Days = number of days fish was at large after tagging. Distance = great circle distance between release and recovery points (for tags 354 and 52, two segments via Unimak Pass; for Tag 271, two segments via Soya Strait). Data points = total temperature data points recorded while the fish was at large and do not include data before release or after recovery.

| Include data before release or after recovery. |         |         |                                       |          |     |          |      |                                                |          |        |                   |        |        |     |
|------------------------------------------------|---------|---------|---------------------------------------|----------|-----|----------|------|------------------------------------------------|----------|--------|-------------------|--------|--------|-----|
| Release                                        |         |         |                                       |          |     | Recovery |      |                                                |          |        |                   |        |        |     |
| Species                                        | Tag No. | Date    | Location                              | Length   | Age | Date     | Days | Location                                       | Distance | Data   | Data              | Length | Weight | Sex |
|                                                |         |         |                                       | (FL; mm) |     |          |      |                                                | (km)     | Points | Interval          | (mm)   | (kg)   |     |
| Sockeye                                        | 151     | 5/21/99 | Gulf of Alaska<br>57°37'N<br>145°00'W | 525      | 2.3 | 7/9/99   | 50   | Copper R.<br>61°29'N<br>144°27'W               | 431      | 4,697  | 15"               |        |        | M   |
| Sockeye                                        | 301     | 5/22/99 | Gulf of Alaska<br>58°26'N<br>145°00'W | 640      | 1.3 | 6/16/99  | 26   | Chignik Lagoon<br>56°20'N<br>158°29'W          | 839      | 4,857  | 7.5"              |        |        |     |
| Sockeye                                        | 311     | 5/22/99 | Gulf of Alaska<br>58°58'N<br>145°00'W | 635      | 1.3 | 7/4/99   | 44   | Taku Inlet<br>58°12'N<br>134°06'W              | 636      | 4,150  | 15"               | 652    |        | M   |
| Sockeye                                        | 354     | 5/20/99 | Gulf of Alaska<br>54°45'N<br>145°00'W | 490      | 2.2 | 7/11/99  | 53   | Port Moller<br>56°31'N<br>159°53'W             | 1,670    | 4,976  | 15"               |        |        |     |
| Sockeye                                        | 809     | 7/14/99 | Gulf of Alaska<br>56°10'N<br>145°04'W | 635      | 1.3 | 8/3/99   | 21   | Taku Inlet<br>58°07'N<br>134°04'W              | 697      | 10,837 | 1.875"<br>& 3.45" |        |        |     |
| Chum                                           | 255     | 7/4/98  | Bering Sea<br>53°30'N<br>179°30'W     | 560      | 0.3 | 10/10/98 | 98   | Yubetsu, Okhotsk<br>44°13'N<br>143°40'E        | 2,845    | 4,680  | 30"               | 610    | 2.1    | M   |
| Chum                                           | 259     | 7/3/98  | Bering Sea<br>52°30'N<br>179°30'W     | 622      | 0.3 | 9/4/98   | 62   | Tokachi R. mouth<br>42°39'N<br>143°37'E        | 2,942    | 6,011  | 15"               | 650    | 3.0    | M   |
| Chum                                           | 271     | 7/6/98  | Bering Sea<br>55°30'N<br>179°30'W     | 592      | 0.3 | 10/31/98 | 117  | Sho R., Hon.,<br>J. Sea<br>36°47'N<br>137°05'E | 3,997    | 5,607  | 30"               | 610    | 1.8    | M   |
| Chum                                           | 274     | 7/7/98  | Bering Sea<br>56°30'N<br>179°30'W     | 680      | 0.4 | 9/24/98  | 79   | Shiretoko<br>Peninsula<br>44°19'N<br>145°21'E  | 2,779    | 3,782  | 30"               | 716    |        | M   |
| Chum                                           | 299     | 7/12/98 | Bering Sea<br>56°30'N<br>177°30'W     | 577      | 0.3 | 10/5/98  | 85   | Shibetsu, Nem. Strt<br>43°41'N<br>145°09'E     | 2,969    | 4,059  | 30"               | 590    | 2.4    | F   |
| Pink                                           | 189     | 7/3/98  | Gulf of Alaska<br>55°59'N<br>145°00'W | 495      | 0.1 | 7/24/98  | 21   | Afognak Island<br>58°06'N<br>152°20'W          | 501      | 4,063  | 7.5"              |        | 1.4    |     |
| Coho                                           | 52      | 7/3/98  | Gulf of Alaska<br>55°59'N<br>145°00'W | 592      | 1.1 | 8/24/98  | 52   | Togiak Bay<br>59°02'N<br>160°20'W              | 1,858    | 5,857  | 15"               |        |        | M   |
| Steelhead                                      | 198     | 7/9/98  | Gulf of Alaska<br>49°58'N<br>144°58'W | 690      | 2.3 | 8/14/98  | 36   | Copper R. Delta<br>60°13'N<br>144°40'W         | 931      | 6,909  | 7.5"              |        | 3.4    | M   |

## Daily Ration

To estimate daily ration, we used initial weights estimated from release lengths and weight-length regressions of appropriate age and maturity classes of chum salmon in the area of release, final weights as reported by fishermen, average diet of chum salmon in the release area, and temperature data recorded from release to recovery. Tagged fish were not weighed prior to release, to avoid additional trauma. Data returned by fishermen with recovered tags usually did not include weight, and when included, weight was often estimated or approximate. We received weights at recovery for six salmon. For two fish (a pink salmon and one chum salmon), initial weights as estimated by length-weight regressions were larger than the final reported weights. For a steelhead trout, there were insufficient data to estimate initial weight. For the remaining three fish, all chum salmon, initial weight estimates were less than recovery weights, and estimation of daily ration was possible.

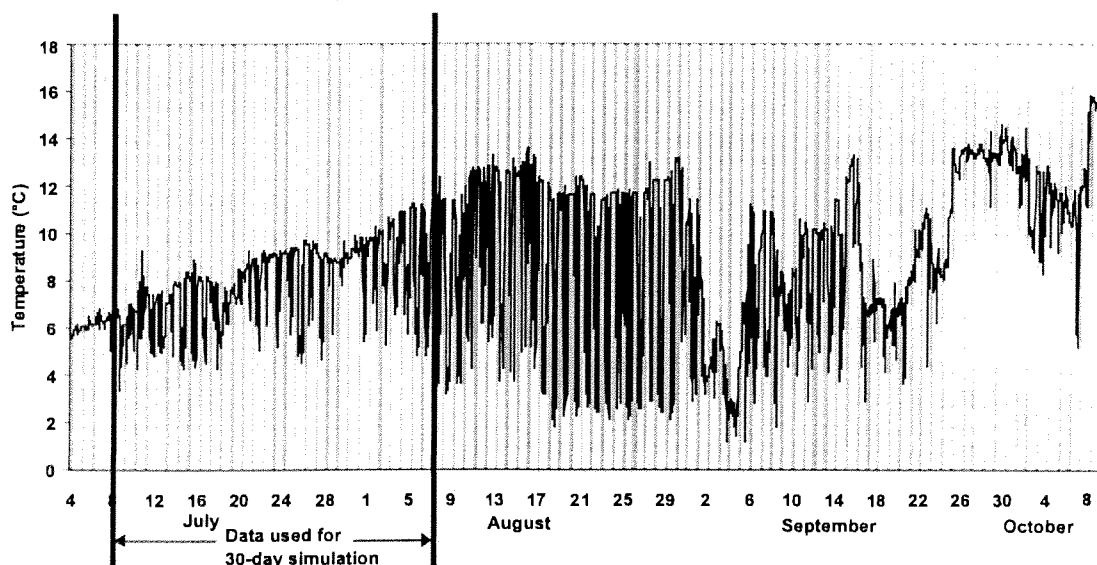
## Temperature Comparison

For each fish in Table 2, a simulation was run at a constant temperature approximating the sea surface temperature (SST) at the release site of the tagged fish, rounded to the nearest integer. A second simulation was run using data from the data storage tags for the first 30 days following recuperation from tagging trauma (Fig. 2). (The recuperation period

was defined as ending when relatively frequent temperature changes began, indicating resumption of diving behavior. The period ranged from 0 to 21 days in the thirteen salmon in this study.) A uniform simulation period of 30 days was chosen to allow comparison between different fish; most fish had at least 30 days of post-recuperation data (for three fish lacking 30 days of data, data were resampled). Final salmon body weights from simulations using temperature data from DSTs were compared to the final weights from simulations using the constant SSTs from the release site.

The model allows two approaches: fit to end weight (which was used in the daily ration estimates) and fit to consumption. As we had no accurate measures of end weight for most fish, we used the fit to consumption method. Prey weights from stomachs of salmon caught at the same times and places as tagged fish were in the range of 0.6%–1.2% of body weight. These are values from one period of the day and are likely very conservative estimates of daily consumption because no corrections were made for digestion. They are also below the range of estimates derived by Davis et al. (1998) to match observed summer growth of immature salmon (2.6–4.1%) and by Aydin (unpublished data) based on prey consumption (2.7–3.3%), but are closer to the daily rations estimated for three chum salmon (1.3–1.72%; see Results below). We chose uniform values of 2% and 3% for our simulations and fit the model to 30 days of consumption at rates of 2% and 3% of body weight per day. The value of 2% was in the range of

**Fig. 2.** Temperature data from chum salmon tagged with data storage tag 255 in the Bering Sea and recovered on the Sea of Okhotsk coast of Hokkaido. Data used for 30-day simulation are indicated between dark vertical lines. Entire data set used for daily ration estimation. Light grey bars indicate hours of darkness.



0.44–0.81 of maximum feeding rate, while 3% was close to or exceeded the maximum rate for sockeye and coho (0.94–1.2 of maximum rate). The 3% rate was 0.64–0.93 of the maximum rate for chum, pink and steelhead.

Computations are based on specific rates and a "daily" time step: grams of oxygen per gram of body weight per day and grams of food per gram of body weight per day at a single temperature. To accommodate simulations using actual temperatures, the model parameters implicitly based on 24 hr (only three: CA, RA, and the daily consumption rate) were divided by 48, 96, or 192, to accommodate data intervals of 30, 15, and 7.5 minutes, respectively.

## RESULTS

Estimated daily rations were 1.30–1.72% of body weight/day for three chum salmon over migrations of 62 to 98 days from the Bering Sea to Hokkaido (Table 3). Weight gains between estimated initial and final weights were 60 to 279 g. Consumption rates were 35% to 48% of possible maximum rates. When the same weight-length regression used to calculate initial weights from initial lengths was applied to lengths reported at recovery, the estimated final weights were close to reported weights for two fish (3058 cf. 3000 g; 2365 cf. 2400 g; Table 3). For the other fish (tag 255), the estimated final weight was much larger than the reported weight (2584 g vs. 2100 g), which suggests the regression may not have provided an accurate estimate for the initial weight.

Final weights from 30-day simulations using actual temperatures differed from weights of fish at a constant temperature by 0.15%–3.46% (Table 4). The average difference was -1.23%, and the average magnitude of difference was 1.42%. Differences were usually negative.

## DISCUSSION

The estimated daily rations for three chum salmon are lower than some other estimates of consumption for salmon. Model simulations by Davis et al. (1998) showed that observed size changes in sockeye, chum, pink, and coho in the Bering Sea and North Pacific in early summer indicated salmon were feeding at rates close to their physiological maxima. Brett (1983) also found that sockeye feeding rates probably approximated maximum intake. There could be several reasons for our lower values. The chum salmon in our study were on homeward migrations. While they may have fed at maximal rates in the Bering Sea, feeding rates probably declined during directed movement toward spawning streams. In warm coastal waters, salmon may not have been feeding at all, and may have lost weight. This could have been especially true for the chum carrying tag 271. After 117 days, including six weeks near the end of its migration where surface temperatures were between 19°C and 22°C, the reported weight at capture for this fish was only 1.8 kg, less than the weight we estimated from the length at tagging.

Our simulations were based on estimated initial values, since the tagged fish were not weighed. If the estimations were not accurate, the daily ration estimates would also be in error. However, when the same method was used to estimate the final weights, for two fish the estimated final weights differed from the observed final weights by less than 2%. For the other fish, the estimated weight differed by 23% from the reported weight.

The differences in simulated salmon growth using actual data and one constant temperature were not large over the short 30-day simulation period, but the differences are not negligible. The fish are actually spending a large portion of the day at the surface (most of the night, and moving between the surface

**Table 3.** Daily rations estimated from estimated initial weights and reported final weights for three chum salmon tagged in the Bering Sea and recovered in Hokkaido, Japan. Daily rations were estimated using average diets of chum salmon in the area of release and actual data storage tag temperature data in Fish Bioenergetics Model 3.0. Initial weights were estimated from age- and maturity-specific regressions of data from chum salmon caught in the region of release. Weights estimated from lengths reported at recovery are provided for comparison with actual reported weight. Days = number of days fish was at large after tagging. FL, fork length; BW, body weight.

| Species | Tag No. | Age | Release            |                       | Days | Recovery                |                                    |                |                       |
|---------|---------|-----|--------------------|-----------------------|------|-------------------------|------------------------------------|----------------|-----------------------|
|         |         |     | Length<br>(FL; mm) | Est.<br>Weight<br>(g) |      | Actual<br>Weight<br>(g) | Est.<br>Daily Ration<br>(% BW/day) | Length<br>(mm) | Est.<br>Weight<br>(g) |
| Chum    | 255     | 0.3 | 560                | 2060                  | 98   | 2100                    | 1.30                               | 610            | 2584                  |
| Chum    | 259     | 0.3 | 622                | 2721                  | 62   | 3000                    | 1.72                               | 650            | 3058                  |
| Chum    | 299     | 0.3 | 577                | 2230                  | 85   | 2400                    | 1.56                               | 590            | 2365                  |

**Table 4.** Results of 30-day bioenergetic simulations of salmon growth using data from data storage tags (DST). Actual SST = sea surface temperature at release site. Actual DST = actual temperatures as recorded by DSTs (minimum and maximum of range are indicated). % difference = difference from final weight using constant temperature.

| Species   | Data Tag No. | Actual SST (°C) | Type of temperature data | Temperature used (°C) | Initial wt. (g) | 2% consumption |              | 3% consumption |              |
|-----------|--------------|-----------------|--------------------------|-----------------------|-----------------|----------------|--------------|----------------|--------------|
|           |              |                 |                          |                       |                 | Final Wt. (g)  | % difference | Final Wt. (g)  | % difference |
| Sockeye   | 151          | 5.1             | Constant                 | 5                     | 2435            | 2613.36        |              | 2659.92        |              |
|           |              |                 | Actual DST               | 4.0–17.2              | 2435            | 2562.90        | -1.93        | 2666.46        | 0.25         |
|           | 301          | 7.2             | Constant                 | 7                     | 2435            | 2586.41        |              | 2674.76        |              |
|           |              |                 | Actual DST               | 4.4–10.11             | 2435            | 2593.30        | 0.27         | 2670.81        | -0.15        |
|           | 311          | 7.3             | Constant                 | 7                     | 2435            | 2586.43        |              | 2674.76        |              |
|           |              |                 | Actual DST               | 5.5–11.9              | 2435            | 2552.90        | -1.30        | 2668.02        | -0.25        |
|           | 354          | 4.9             | Constant                 | 5                     | 1802            | 1959.43        |              | 2021.00        |              |
|           |              |                 | Actual DST               | 4.3–11.5              | 1802            | 1951.82        | -0.39        | 2030.07        | 0.45         |
|           | 809          | 10.2            | Constant                 | 10                    | 3059            | 3228.35        |              | 3386.56        |              |
|           |              |                 | Actual DST               | 7.2–17.3              | 3059            | 3173.83        | -1.69        | 3345.87        | -1.20        |
| Chum      | 255          | 5.9             | Constant                 | 6                     | 2060            | 2290.64        |              | 2478.17        |              |
|           |              |                 | Actual DST               | 3.3–11.4              | 2060            | 2241.28        | -2.15        | 2432.37        | -1.85        |
|           | 259          | 7.4             | Constant                 | 7                     | 2721            | 3002.42        |              | 3249.02        |              |
|           |              |                 | Actual DST               | 1.6–14.8              | 2721            | 2916.29        | -2.87        | 3152.06        | -2.98        |
|           | 271          | 6.3             | Constant                 | 6                     | 2387            | 2655.74        |              | 2869.79        |              |
|           |              |                 | Actual DST               | 1.2–13.6              | 2387            | 2563.73        | -3.46        | 2773.13        | -3.37        |
|           | 274          | 6.9             | Constant                 | 7                     | 3363            | 4046.36        |              | 4368.07        |              |
|           |              |                 | Actual DST               | 0.04–11.8             | 3363            | 4021.26        | -0.62        | 4275.21        | -2.13        |
| Pink      | 189          | 11.0            | Constant                 | 11                    | 1331            | 1490.03        |              | 1649.64        |              |
|           |              |                 | Actual DST               | 5.7–14.4              | 1331            | 1500.88        | 0.73         | 1659.42        | 0.59         |
| Coho      | 52           | 11.0            | Constant                 | 11                    | 3170            | 3572.64        |              | 3913.73        |              |
|           |              |                 | Actual DST               | 6.6–14.4              | 3170            | 3578.38        | 0.16         | 3885.11        | -0.73        |
| Steelhead | 198          | 10.9            | Constant                 | 11                    | 3200            | 3534.50        |              | 3898.77        |              |
|           |              |                 | Actual DST               | 6.4–15.6              | 3200            | 3482.07        | -1.48        | 3839.93        | -1.51        |

and deeper, cooler waters during the day). The percent of time in cooler waters may be too small to have a major effect on simulated growth. The fact that differences were usually negative was perhaps because fish migrated from cooler waters where the constant temperatures used in our analyses were taken, to warmer coastal waters.

The differences are of a similar magnitude to those found by Cianelli et al. (1998), who used the same fish bioenergetics model to study juvenile wall-eye pollock (*Theragra chalcogramma*). Over a one month simulation period, they found a 1.16% difference in final weights between fish modeled at a constant temperature and fish modeled at two different temperatures, simulating vertical migration, on a daily basis. They also found that the model was much more sensitive to consumption parameters than to temperature. In this case, the differences in temperature that salmon experience may have less effect on their growth than availability of food.

Further uses and analyses of the DST data are

planned. For example, the DST data help to clarify some features of 24-hr experiments on salmon feeding (Davis et al. this volume). Sampling with surface gillnets over a 24-hour period indicated that fish may be feeding throughout the day (though on different prey). While fish were found with food in their stomachs throughout the day, it was not clear if all fish were from a population that fed at the same time, or if successive groups of fish were feeding at different times of the day and becoming successively vulnerable to surface gillnets. DST data indicate that all fish recovered so far are moving vertically during the day, so it is likely one population of fish and many of them are feeding throughout the day.

## CONCLUSIONS

Data storage tags are a useful new tool for investigating salmon marine life. Their use and development have been endorsed by the NPAFC Committee on Scientific Research and Statistics, which identified



five areas for future research. Our study is a beginning in one area: swimming behavior and bioenergetics relating to carrying capacity. The data from DSTs have great potential for improving our ability to model more accurately salmon behavior and growth at sea.

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## Appendix

**Appendix Table 1.** Parameter values used to estimate growth and prey consumption by sockeye, pink, chum, and coho salmon and steelhead trout given a constant daily food ration. Parameters are published in Fish Bioenergetics Model 3.0 (Hanson *et al.* 1997), and are taken from values in the literature derived from studies of Pacific salmonids in lakes. Value for CA for chum salmon was estimated by Davis *et al.* (1998).

| Symbol            |                                                                                                       | Physiological Parameter | Nominal Value    |         |         |           |
|-------------------|-------------------------------------------------------------------------------------------------------|-------------------------|------------------|---------|---------|-----------|
|                   |                                                                                                       |                         | Sockeye/<br>Pink | Chum    | Coho    | Steelhead |
| CONSUMPTION (CON) |                                                                                                       |                         |                  |         |         |           |
| CA                | Intercept for weight dependence of CON                                                                | 0.303                   | 0.394            | 0.303   | 0.628   |           |
| CB                | Slope for weight dependence of CON                                                                    | -0.275                  | -0.275           | -0.275  | -0.3    |           |
| CQ                | Lower temperature where dependence is CK1                                                             | 3                       | 3                | 5       | 5       |           |
| CTO               | Higher temperature where dependence is 0.98 of max                                                    | 20                      | 20               | 15      | 20      |           |
| CTM               | Temp≥CTO where dependence is still .98 of max                                                         | 20                      | 20               | 18      | 20      |           |
| CTL               | Temperature where dependence is CK4                                                                   | 24                      | 24               | 24      | 24      |           |
| CK1               | Temperature dependence at CQ                                                                          | 0.58                    | 0.58             | 0.36    | 0.33    |           |
| CK4               | Temperature dependence at CTL                                                                         | 0.50                    | 0.50             | 0.01    | 0.2     |           |
| RESPIRATION (RES) |                                                                                                       |                         |                  |         |         |           |
| RA                | Intercept for std. metabolism vs weight, temperature, and swimming speed                              | 0.00143                 | 0.00143          | 0.00264 | 0.00264 |           |
| RB                | Slope for weight dependence of standard metabolism                                                    | -0.209                  | -0.209           | -0.217  | -0.217  |           |
| RQ                | Coefficient for temperature dependence of metabolism                                                  | 0.086                   | 0.086            | 0.06818 | 0.06818 |           |
| RTO               | Coefficient for swimming speed dependence of metabolism                                               | 0.0234                  | 0.0234           | 0.0234  | 0.0234  |           |
| RTM               | Coefficient for swim speed dependence of temperature                                                  | 0                       | 0                | 0       | 0       |           |
| RTL               | Cut-off temp                                                                                          | 25                      | 25               | 25      | 25      |           |
| RK1               | Intercept for weight dependence of swimming speed when temperatures >RTL                              | 1                       | 1                | 1       | 1       |           |
| RK4               | Slope for weight dependence of swimming speed at all temperatures                                     | 0.13                    | 0.13             | 0.13    | 0.13    |           |
| ACT               | Intercept for swimming speed vs temperature and weight (cm/sec/1-g fish at 0°), when temperature <RTL | 9.9                     | 9.9              | 9.7     | 9.7     |           |
| BACT              | Coefficient for temperature dependence of swimming speed when temperature <RTL                        | 0.0405                  | 0.0405           | 0.0405  | 0.0405  |           |
| SDA               | Proportion of assimilated energy lost to specific dynamic action                                      | 0.172                   | 0.172            | 0.172   | 0.172   |           |
| EGESTION (EGES)   |                                                                                                       |                         |                  |         |         |           |
| FA                | Intercept for proportion of consumption EGES vs temperature and ration                                | 0.212                   | 0.212            | 0.212   | 0.212   |           |
| FB                | Slope for temperature dependence of EGES                                                              | -0.222                  | -0.222           | -0.222  | -0.222  |           |
| FG                | Coefficient for feeding level dependence of EGES                                                      | 0.631                   | 0.631            | 0.631   | 0.631   |           |
| EXCRETION (EXCR)  |                                                                                                       |                         |                  |         |         |           |
| UA                | Intercept for proportion of assimilated consumption EXCR vs temperature and ration                    | 0.0314                  | 0.0314           | 0.0314  | 0.0314  |           |
| UB                | Slope for temperature dependence of EXCR                                                              | 0.58                    | 0.58             | 0.58    | 0.58    |           |
| UG                | Coefficient for feeding level dependence of EXCR                                                      | -0.299                  | -0.299           | -0.299  | -0.299  |           |

## Genetic Stock Identification of Sockeye Salmon Captured in the Coastal Waters of Unalaska Island during April/May and August 1998

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**Keywords:** Migration, protein electrophoresis, El Niño

**Abstract:** This study is part of the Auke Bay Laboratory's Ocean Carrying Capacity (OCC) which has extensively sampled salmon in the North Pacific since 1996 to obtain information on marine life history and migration patterns. Genetic stock identification techniques (protein electrophoresis) indicated that Bristol Bay stocks of immature sockeye salmon (*Oncorhynchus nerka*) made up the largest percentage in two samples taken near Unalaska Island in 1998. The substantial numbers of immature sockeye salmon captured at Cape Cheerful during May 1998 were unexpected, based on current migration models of western Alaska sockeye salmon. Immature sockeye constituted the largest percentage of our immature salmon catch captured at Cape Prominence during August 1998. This was also unexpected since immature chum salmon (*O. keta*) were the predominant catch during August 1996 and 1997 at the same location. These unexpected events may be due to changes in distribution resulting from the strong El Niño event during 1997–1998.

### INTRODUCTION

Scientists from the Auke Bay Laboratory (ABL), Alaska Fisheries Science Center, National Marine Fisheries Service, conducted two surveys of salmon (*Oncorhynchus spp.*) distribution during 1998, one in the eastern Aleutian Islands and North Pacific Ocean during April and May, and one in the Gulf of Alaska during July and August (Carlson et al. 1998a, b). These surveys were part of ABL's OCC study on the dynamics of ocean residence of salmonids (National Marine Fisheries Service 1995). Two large catches of immature sockeye salmon collected north and south of Unalaska Island provided an opportunity to estimate their area of origin using a genetic stock identification technique. Sockeye salmon are a valuable food fish, and their absence in expected numbers in the 1997 and 1998 Bristol Bay fishery created substantial economic disruption (Ocean Carrying Capacity Program 1999). The ability to determine stock origins of the salmon during their early ocean life history phase may be used to forecast drops in abundance of important fisheries and protect smaller stocks from overexploitation. Knowledge of stock location in the ocean may help determine exposure to other factors that could affect abundance, e.g., interception by trawl fisheries or drift-net fisheries, or

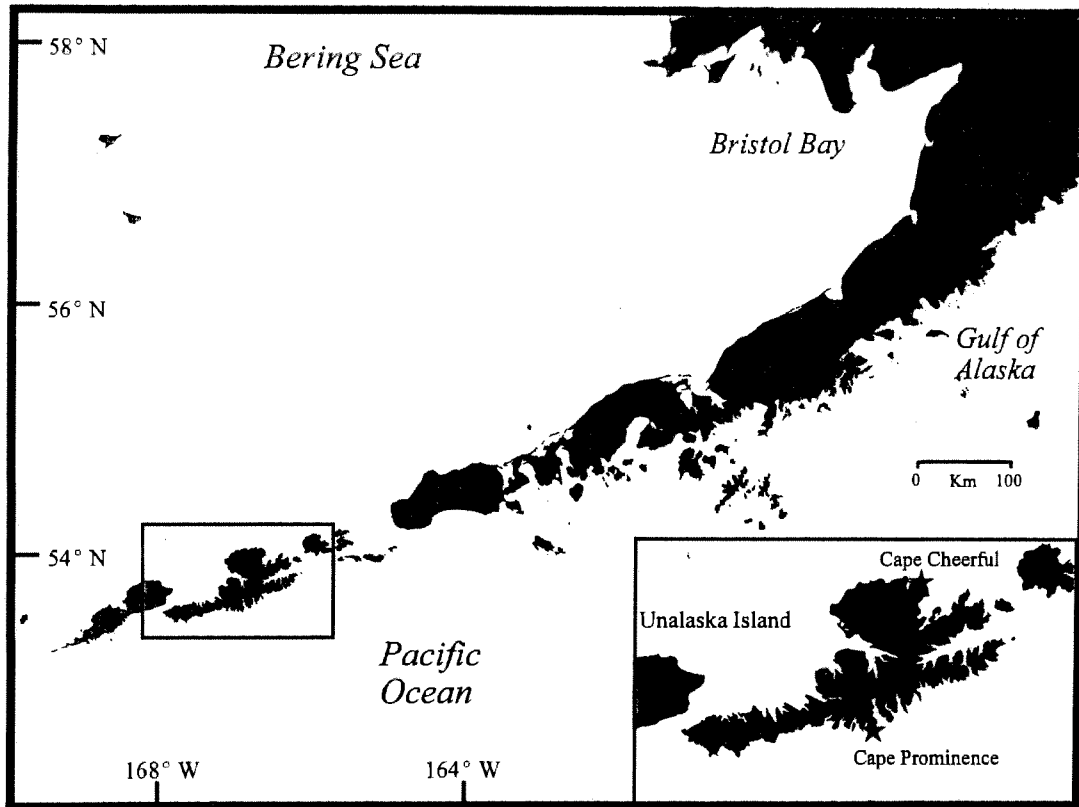
altered marine survival caused by climate changes such as El Niño.

Genetic stock identification relies on genetic differences among stocks in relative allelic frequencies of protein-coding genes (allozymes), or many other types of genetic markers detected by electrophoresis. A sockeye salmon allozyme baseline has recently been constructed from potentially contributing stocks around the North Pacific Ocean, and was used to determine the region of origin of sockeye salmon from a seized high sea's drift net vessel, the *Ying Fa* (Wilmot et al. 1999). Our study used this baseline to identify the region of origin of immature sockeye salmon collected in two samples from the eastern Aleutian Islands in 1998.

### METHODS AND MATERIALS

Immature salmon were collected during two salmon surveys of the North Pacific Ocean by the 38 m stern trawler F/V *Great Pacific*, using a midwater rope trawl (Carlson et al. 1998a, b). At less than 30 nautical miles offshore of Cape Cheerful (Fig. 1) on the Bering Sea side of Unalaska Island (approximately 54°03' N latitude and 166°40' W longitude) 440 immature sockeye salmon were collected on April 30, and May 1, 1998 (Carlson et al. 1998a).

Fig. 1. Map of southwest Alaska and Aleutian Islands. Inset shows Unalaska, ★ indicates areas of fish collection.



Three hundred immature sockeye salmon were collected within 11 nautical miles south of Cape Prominence (Fig. 1) on Unalaska Island (approximately 53°19' N latitude and 166°38' W longitude) on August 11, 1998 (Carlson et al. 1998b).

Immature sockeye salmon collected off of Cape Cheerful were frozen whole. Tissues for genetic analysis (eye, heart, muscle and liver) from immature sockeye salmon collected off of Cape Prominence were dissected on board the F/V *Great Pacific*. The whole fish and tissue samples were stored frozen at -60°C until they were shipped to ABL for further analysis.

At the ABL samples of tissue from the heart, liver, muscle, and eye were placed in individual tubes, and frozen at -80°C until analysis. Starch-gel protein electrophoretic analysis followed procedures described by Aebersold et al. (1987) and results are reported using the genetic nomenclature of the American Fisheries Society (Shaklee et al. 1990). Specific tissues and buffers used to interpret genetic variation at 73 loci for sockeye salmon followed Guthrie et al. (1994). The genotypic frequency of the locus *PGM-1\** could not be determined due to null allele variation and was therefore treated as a phenotypic character. Variation at co-migrating, duplicated loci (termed isoloci, Allendorf and Thorgaard 1984) was treated as if all the variability appeared at one

locus and the other was monomorphic. This is a conservative treatment for isoloci having relatively low allelic variability (Gharrett and Thomason 1987).

A sockeye salmon allozyme baseline was recently constructed (Wilmot et al. 1999) containing data for 165 populations: seven populations from Russia (ABL, unpublished data), 30 from western Alaska (Varnavskaya et al. 1994; Everett and Wilmot, ABL unpublished data; W. Templin, Alaska Department of Fish and Game [ADF&G], 333 Raspberry Rd., Anchorage, Alaska 99518, U.S.A., personal communication), 52 from southcentral Alaska (W. Templin, personal communication; Seeb et al. in press) 37 from southeastern Alaska (Guthrie et al. 1994; ABL unpublished data) 34 from British Columbia (Wood et al. 1994; C. Wood, Pacific Biological Station, Nanaimo BC, Canada V9R5K6, personal communication), and five from Washington (Winans et al. 1996). For this study we modified the sockeye allozyme baseline to include 150 populations to form nine regional groups: Western Alaska, Bristol Bay, Alaska Peninsula, Kodiak, Southcentral Alaska, Eastern Gulf of Alaska, Southeastern Alaska, British Columbia, and Fraser River (Table 1). Washington and Russian populations were omitted since they were not likely to be potential contributors due to geographic distance and were missing data for four loci. In doing so, the number of available loci in-

**Table 1.** Sockeye salmon populations sampled for genetic analysis, and source of the data.

| Site                                 | Source | Site                           | Source* |
|--------------------------------------|--------|--------------------------------|---------|
| <b><u>Western Alaska</u></b>         |        | Talkeetna River Slough         | 4       |
| Stoney River                         | 1      | Stephan Lake                   | 4       |
| Kanektok River                       | 1      | Susitna River Slough           | 4       |
| Kagati River                         | 1      | Red Shirt Lake                 | 4       |
| Goodnews River                       | 1,3    | Birch Creek                    | 4       |
| <b><u>Bristol Bay</u></b>            |        | Byers Lake                     | 4       |
| Togiak River                         | 1      | Larson Lake                    | 4       |
| Igushik River                        | 1      | Chelatna Lake                  | 4       |
| Wood River                           | 1      | WF Yetna River                 | 4       |
| Nushagak River                       | 1      | Hewitt/Whiskey Lake            | 4       |
| Battle Creek                         | 1      | Shell Lake                     | 4       |
| Kulik Creek                          | 1      | Tnnity/Movie Lake              | 4       |
| Belinda Creek                        | 1      | Judd Lake                      | 4       |
| Copper River                         | 1,2    | Sixmile Creek                  | 4       |
| Gibraltar Creek                      | 1,2    | Jim Creek                      | 4       |
| Iliamna River                        | 1,2    | Fish Creek                     | 4       |
| Lower Talarik Creek                  | 1      | Cottonwood Creek               | 4       |
| Fuel Dump Island                     | 2      | Nancy Lake                     | 4       |
| Knutson Creek                        | 2      | Swanson River                  | 4       |
| Woody Island                         | 2      | Bishop Creek                   | 4       |
| Lake Clark                           | 1      | Daniels Lake                   | 4       |
| Margot Creek                         | 1      | Russian River above/Early      | 4       |
| Upatree Creek                        | 1      | Russian River Above/Late       | 4       |
| Bear Creek                           | 1      | Russian River below            | 4       |
| Bible Creek                          | 1      | Kenai River                    | 4       |
| Featherly Creek                      | 1      | Skilak Lake Outlet             | 4       |
| Franks Creek                         | 1      | Quartz Creek                   | 4       |
| Kejulik River                        | 1      | Ptarmigan Creek                | 4       |
| Ruth River                           | 1      | Hidden Creek                   | 4       |
| Ugashik River                        | 1      | Tem Lake                       | 4       |
| <b><u>Alaska Peninsula</u></b>       |        | Moose Creek                    | 4       |
| Bear River                           | 1      | Johnson/Railroad Creek         | 4       |
| Sapsuk Lake                          | 1      | Kasilof River                  | 4       |
| Alec River                           | 3      | Coal Creek                     | 4       |
| Chignik Lake                         | 3      | Chilligan River                | 4       |
| <b><u>Kodiak</u></b>                 |        | Packers Lake                   | 4       |
| Saltery Creek                        | 3      | Crescent Lake                  | 4       |
| Malina Lake                          | 3      | McArthur River                 | 4       |
| Frazer Lake                          | 5      | Wolverine Creek                | 4       |
| Little Kitoi                         | 3      | Delight Lake                   | 3       |
| Afognak Lake                         | 3      | Eshamy Lake                    | 3       |
| <b><u>Southcentral Alaska</u></b>    |        | Coghill Lake                   | 3       |
| Mama/Papa Bear Lake                  | 4      | Eyak Lake                      | 3       |
| Bering Lake                          | 3      | <b><u>British Columbia</u></b> |         |
| <b><u>Eastern Gulf of Alaska</u></b> |        | Lower Taku River               | 6       |
| Situk Lake                           | 5,6    | Upper Taku River               | 6       |
| Old Situk River                      | 5      | Little Trapper                 | 5,6     |
| East Alsek River                     | 5,6    | Little Tatsamenie              | 5,6,7   |
| Klukshu Lake                         | 7      | Tahltan Lake                   | 5,7     |
| <b><u>Southeastern Alaska</u></b>    |        | Bowser Lake                    | 7,8     |
| Sitkoh Lake                          | 6      | Bonney Lake                    | 7,8     |
| Eva Lake                             | 5      | Damdochax Lake                 | 7,8     |
| Kook Lake                            | 5      | Alastair Lake                  | 7,8     |
| Ford Arm Lake                        | 5      | Williams Creek                 | 7,8     |
| Redoubt Lake Beach                   | 5      | McDonnell Lake                 | 7,8     |
| Redoubt Lake Outlet                  | 5      | Bear Lake                      | 7,8     |
| Redfish Lake                         | 5      | Sustat River                   | 7       |

continue...

Table 1. continued.

| Site               | Source | Site                 | Source* |
|--------------------|--------|----------------------|---------|
| Benzeman Lake      | 5      | Johnson Creek        | 7       |
| Chilkoot Lake      | 6      | Nanika River         | 7,8     |
| Chilkat Lake       | 6      | Fulton River Channel | 7       |
| Lace River         | 5      | Pierre Creek         | 7,8,9   |
| Windfall Lake      | 6      | Pinkut River Channel | 7       |
| Auke Lake          | 5,6    | Morrison River       | 7,8     |
| Steep Creek        | 1,5    | Kimsquit Lake        | 7,8     |
| Yehring Creek      | 6      | Tenas Lake           | 7,8     |
| Speel Lake         | 5,6    | Owikeno Lake         | 7,8     |
| Crescent Lake-SEAK | 5      | <b>Fraser River</b>  |         |
| Thoms Lake         | 5,6    | Weaver Channel       | 7       |
| Naha River         | 5,6    | Birkenhead River     | 7       |
| Hugh Smith Lake    | 5,6    | Gates Channel        | 7       |
| McDonald Lake      | 5,6    | Chilko Lake          | 7       |
| Kutlaku Lake       | 5,6    | Stellako River       | 7       |
| Alecks Lake        | 5,6    | Nadina Channel       | 7       |
| Red Bay Lake       | 5,6    | Gluskie Creek        | 7       |
| Salmon Bay Lake    | 5,6    | Dust Creek           | 7       |
| Karta River        | 5,6    | Shale Creek          | 7       |
| Luck Lake          | 6      | Narrows Creek        | 7       |
| Kegan Lake         | 6      | Middle River         | 7       |
| Klakas Lake        | 6      | Adams River          | 7,8     |
|                    |        | Shuswap River        | 7,9     |

## \*Sources:

1 W.J. Spearman, USFWS, Anchorage, AK (personal communication)

2 Varnavskaya et al. (1994)

3 W. Templin, ADF&amp;G, Anchorage, AK (personal communication)

4 Seeb et al. (In Press)

5 C.M. Guthrie, ABL, Juneau, AK, (unpublished data)

6 Guthrie et al. (1994)

7 C. Wood et al. (1994)

8 C. Wood, CDFO, Nanaimo, BC (personal communication)

9 Winans et al. (1996)

creased from 18 (10 loci/4 isoloci) to 22 (14 loci/4 isoloci). The loci used were: *sAAT-1,2\**, *mAAT-1\**, *sAH-1\**, *ALAT\**, *GPIB-1,2\**, *sIDHP-1\**, *sIDHP-2\**, *LDHB-1\**, *LDHB-2\**, *MPI\**, *sMDHA-1,2\**, *sMDHB-1,2\**, *sMEP-1\**, *mMEP-1\**, *PEPLT\**, *PGM-1\**, *PGM-2\**, and *sSOD-1\**. Conditional maximum likelihood estimates (MLE) of stock composition collections were calculated for the two sockeye collections using the Statistics Program for Analyzing Mixtures developed by ADF&G (SPAM ver. 3.2, ADF&G 1997) based on the GIRLS (Masuda et al. 1991) and CONJA-S (Pella et al. 1996) algorithms. Standard errors of stock composition estimates were determined by 500 bootstrap resamplings of baseline and mixture samples (Efron and Tibshirani 1986). The reliability of stock composition estimates was evaluated by conducting simulation studies of the baseline using SPAM (ver. 3.2). Simulated baseline samples of sizes equal to actual baseline samples were generated by 500 bootstrap resamplings. Each simulated mixture ( $n = 300$ ) was composed of 100% of the region under study, with each regional population contributing equally to the mixture. Genotypes of individuals in these hypothetical mixtures of known composition were generated from baseline

allele frequencies assuming independence of loci and Hardy-Weinberg equilibrium. The allocate sum procedure was followed, whereby estimated contributions of the individual populations were first calculated, and then summed into regional groups.

## RESULTS

Ninety-eight percent of all immature salmon captured at Cape Prominence in August of 1998 were sockeye salmon (Carlson et al. 1998b). This was unexpected since immature chum salmon (*O. keta*) constituted the largest percentage of our immature salmon catch at the same location during August in 1996 (77%) and 1997 (66%) (Carlson et al. 1996, 1997).

Seventeen (11 loci/3 isoloci) of the loci used in the baseline were variable in the mixtures: *mAAT-1\**, *sAH-1\**, *ALAT\**, *GPIB-1,2\**, *LDHB-1\**, *LDHB-2\**, *sMDHA-1,2\**, *sMDHB-1,2\**, *sMEP-1\**, *mMEP-1\**, *PEPLT\**, *PGM-1\**, *PGM-2\**, and *sSOD-1\**. The mixture samples were variable at 22 additional loci (16 loci/3 isoloci) that were missing from the following baseline regions: Bristol Bay (*G3PDH-1,2\**, *G3PDH-4\**, *mIDHP-1\**, *LDH-A2\**, *PEPC\**, *MAH-4\**

and *PGDH\**); British Columbia (*GPIA\**, *PEPD-1\**, *TPI-1,2\**, *TPI-3\**, and *TPI-4\**); Bristol Bay and British Columbia (*MAH-1,2*, *MAN\**, *CKA2\**, *CKC2\**, *FDHG\**, *FH\**, and *GAPDH-2\**). *PGK-2\** was also variable, but baseline data were only available from Southeast Alaska.

The correct allocation to region of origin of fish in the simulated mixture samples that contained fish from a single region (100% simulations) ranged from a low of 47.2% for Western Alaska to a high of 94.1% for the Fraser River (Table 2A). Results for the other regions were: Bristol Bay 72.0%, Alaska Peninsula 81.3%, Kodiak 74.1%, Southcentral Alaska 66.4%, Eastern Gulf of Alaska 61.8%, Southeast Alaska 65.7% and non-Fraser River British Columbia 71.8%.

Bristol Bay was the largest component of the estimates of origin by region for the immature sockeye salmon sampled near Cape Cheerful and Cape Prominence at 49.6% and 38.6%, respectively (Table 2B). Cape Cheerful also had statistically significant numbers of fish from the Alaska Peninsula (10.8%), southcentral Alaska (17.7%), and non-Fraser River British Columbia (1.7%). Cape Prominence had statistically significant numbers from Kodiak (10.9%), southcentral Alaska (18.7%), southeast Alaska

(14.0%), and British Columbia non-Fraser River (9.6%).

## DISCUSSION

The largest contributing region to both collections of immature sockeye salmon was Bristol Bay (Table 2). This is not unexpected given Unalaska Island's proximity to Bristol Bay. The collection from Cape Prominence shows a greater contribution from southcentral and southeastern populations, perhaps because this location is closer to more southern populations than those collected from Cape Cheerful.

Simulation studies were conducted with the sockeye salmon baseline to evaluate the reliability of stock composition estimates. Western Alaska had the poorest reliability, while Fraser River had the highest (Table 2). Misallocation of the mixture samples could be caused by the absence of important populations from the baseline (i.e., Karluk and Copper rivers) or by the absence of highly polymorphic loci from the baseline (i.e., *PEPC\**, *MAH1*, *2\**). The majority of misallocation for the 100% simulation of western Alaska went to nearby regions; Bristol Bay (25.5%), and Alaska Peninsula (8.3%), and a surprising amount to southeast Alaska (10.1%). Reliability may be enhanced by using all 62 variable loci found

**Table 2.** (A) Mean estimated proportion of sockeye salmon by region for 500 bootstrap simulations where each region comprises 100% of the mixture ( $n = 300$ ). Boldface numbers are the correct allocation and should equal one. (B) Regional origin estimates of sockeye salmon from Cape Cheerful and Cape Prominence. Standard deviations are in parentheses.

| Estimated Region            | (A) 100% Simulations |                        |                            |                        |                        |                        |  |
|-----------------------------|----------------------|------------------------|----------------------------|------------------------|------------------------|------------------------|--|
|                             | Western Alaska       | Bristol Bay            | Alaska Peninsula Peninsula | Kodiak                 | Southcentral Alaska    | Eastern Gulf of Alaska |  |
| Western Alaska              | 0.4730 (0.1362)      | 0.0371 (0.0690)        | 0.0102 (0.0239)            | 0.0029 (0.0100)        | 0.0284 (0.0354)        | 0.0114 (0.0255)        |  |
| Bristol Bay                 | 0.2554 (0.1280)      | <b>0.7197 (0.1172)</b> | 0.0514 (0.0604)            | 0.0402 (0.0573)        | 0.1523 (0.1021)        | 0.0847 (0.0669)        |  |
| Alaska Peninsula            | 0.0833 (0.0688)      | 0.0293 (0.0389)        | <b>0.8128 (0.0856)</b>     | 0.0054 (0.0138)        | 0.0258 (0.0316)        | 0.0070 (0.0147)        |  |
| Kodiak                      | 0.0133 (0.0265)      | 0.0243 (0.0368)        | 0.0066 (0.0205)            | <b>0.7412 (0.1200)</b> | 0.0277 (0.0407)        | 0.0024 (0.0101)        |  |
| Southcentral Alaska         | 0.1010 (0.0725)      | 0.0890 (0.0620)        | 0.0638 (0.0520)            | 0.1866 (0.1072)        | <b>0.6636 (0.1116)</b> | 0.1144 (0.0791)        |  |
| Eastern Gulf of Alaska      | 0.0043 (0.0116)      | 0.0088 (0.0184)        | 0.0017 (0.0059)            | 0.0010 (0.0038)        | 0.0113 (0.0208)        | <b>0.6184 (0.1068)</b> |  |
| Southeast Alaska            | 0.0398 (0.0395)      | 0.0411 (0.0456)        | 0.0344 (0.0406)            | 0.0123 (0.0196)        | 0.0450 (0.0366)        | 0.0825 (0.0540)        |  |
| British Columbia Non-Fraser | 0.0269 (0.0327)      | 0.0464 (0.0385)        | 0.0173 (0.0212)            | 0.0098 (0.0163)        | 0.0281 (0.0268)        | 0.0426 (0.0368)        |  |
| British Columbia Fraser     | 0.0029 (0.0063)      | 0.0045 (0.0085)        | 0.0018 (0.0052)            | 0.0006 (0.0021)        | 0.0178 (0.0150)        | 0.0365 (0.0374)        |  |

| Estimated Region            | (A) 100% Simulations   |                             |                         | (B) Origin Estimates |                 |
|-----------------------------|------------------------|-----------------------------|-------------------------|----------------------|-----------------|
|                             | Southeast Alaska       | British Columbia Non-Fraser | British Columbia Fraser | Cape Cheerful        | Cape Prominence |
| Western Alaska              | 0.0132 (0.0281)        | 0.0088 (0.0263)             | 0.0004 (0.0022)         | 0.0204 (0.0328)      | 0.0035 (0.0725) |
| Bristol Bay                 | 0.0889 (0.0740)        | 0.1397 (0.0971)             | 0.0030 (0.0068)         | 0.4958 (0.1529)      | 0.3860 (0.1900) |
| Alaska Peninsula            | 0.0785 (0.0708)        | 0.0116 (0.0230)             | 0.0008 (0.0029)         | 0.1057 (0.0983)      | 0.0703 (0.0923) |
| Kodiak                      | 0.0056 (0.0134)        | 0.0047 (0.0136)             | 0.0002 (0.0012)         | 0.0625 (0.1030)      | 0.1088 (0.0539) |
| Southcentral Alaska         | 0.0833 (0.0602)        | 0.0539 (0.0472)             | 0.0191 (0.0197)         | 0.1771 (0.1655)      | 0.1871 (0.1274) |
| Eastern Gulf of Alaska      | 0.0111 (0.0187)        | 0.0038 (0.0113)             | 0.0023 (0.0074)         | 0.0146 (0.0343)      | 0.0099 (0.0422) |
| Southeast Alaska            | <b>0.6569 (0.0980)</b> | 0.0422 (0.0401)             | 0.0244 (0.0228)         | 0.0292 (0.0297)      | 0.1398 (0.0684) |
| British Columbia Non-Fraser | 0.0450 (0.0402)        | <b>0.7182 (0.1025)</b>      | 0.0092 (0.0153)         | 0.0733 (0.0526)      | 0.0760 (0.0748) |
| British Columbia Fraser     | 0.0175 (0.0260)        | 0.0172 (0.0169)             | <b>0.9407 (0.0341)</b>  | 0.0167 (0.0162)      | 0.0086 (0.0122) |

in sockeye salmon that are not currently available for all the baseline populations (Pella and Milner 1987). It was shown in Utter et al. (1992) that additional loci in the chinook salmon (*O. tshawytscha*) baseline allowed previously indistinguishable populations to be genetically separated. Simulation studies for the 36 loci (30 loci, 3 isoloci) 254 population chinook salmon baseline (Teel et al. 1999) showed a high reliability of discrimination for 29 regions (26 > 90%; 3 > 86%).

Genetic differentiation in sockeye salmon populations can resemble a mosaic, rather than a strong regional structure (Wood et al. 1994). For example, populations within a river system can be more easily identified than those among river systems, e.g., Kamchatka River in Russia, and the upper Taku River in British Columbia have high frequencies of the *LDHB2\*115* allele while populations just east and west of the Taku River have a low frequency (Guthrie et al. 1994; Varnavskaya et al. 1994). Complicating matters are the two life histories of sockeye salmon; the "lake-type" and the "river/sea-type" (Gustafson and Winans 1999). A preliminary allozyme study (Gustafson and Winans 1999) has shown that the "river/sea-type" is a genetically cohesive group throughout a 2000 km geographic region relative to the mosaic genetic structure of the "lake-type" sockeye. Preliminary results on ages based on an analysis on preferred scales of immature sockeye salmon taken at both locations showed that the majority the salmon were ages 1.1 (~2/3) and 2.1 (~1/3) indicating these fish were "lake-type". Perhaps incorporating the life history information with the genetic data could improve the mixed fishery analysis; baseline populations with primarily "river/sea-type" age structure could be omitted from the analysis.

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# Spatial Variations in Early Marine Growth and Condition of Thermally Marked Juvenile Pink and Chum Salmon in the Coastal Waters of the Gulf of Alaska

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Keywords: Salmon, ocean, condition, thermal-otolith-mark

**Abstract:** We examined spatial variations in early marine growth and condition factor of juvenile Prince William Sound hatchery pink (*Oncorhynchus gorbuscha*) and Southeast Alaska hatchery chum (*O. keta*) salmon collected in the coastal waters of the Gulf of Alaska (GOA) during July–August 1996. Mean lengths and weights of juvenile Prince William Sound hatchery pink salmon and Southeast Alaska hatchery chum salmon increased as fish migrated westward along the coast; the smallest individuals were found at Cape Spencer and Cape Puget which are near the exit corridors for juvenile chum salmon leaving inside waters of Southeast Alaska and juvenile pink salmon leaving inside waters of Prince William Sound. Condition factor was significantly lower for hatchery origin chum and pink salmon caught at Cape Spencer and Cape Puget, respectively, than at the next transect located further along the migratory pathway for these salmon.

## INTRODUCTION

During 1995, scientists at the Auke Bay Laboratory, National Marine Fisheries Service, Ocean Carrying Capacity (OCC) program initiated a comprehensive study to describe the role and spatial distribution of salmon in the marine ecosystem, and to test for density dependence in the growth rate of Pacific salmon (*Oncorhynchus* spp.) during various periods of ocean residency (National Marine Fisheries Service 1995). One objective of this ongoing study is to collect and analyze otoliths from juvenile pink and chum salmon caught in the coastal waters of the Gulf of Alaska (GOA) and identify hatchery origin of these fish. Since the beginning of our study, recoveries of thermally marked pink (*O. gorbuscha*) and chum (*O. keta*) salmon at sea have provided unique information on stock-specific early marine migration, distribution, and growth of these salmon (Farley and Munk 1997, 1998; Farley et al. 1999).

In this paper, we summarize growth and condition factor of thermally marked pink and chum salmon caught in the coastal waters of the Gulf of Alaska during July and August 1996. We report new information on stock-specific size and condition factor patterns for juvenile pink and chum salmon from Prince William Sound and Southeast Alaska hatcheries, respectively, and briefly discuss the factors that may influence these patterns.

## METHODS

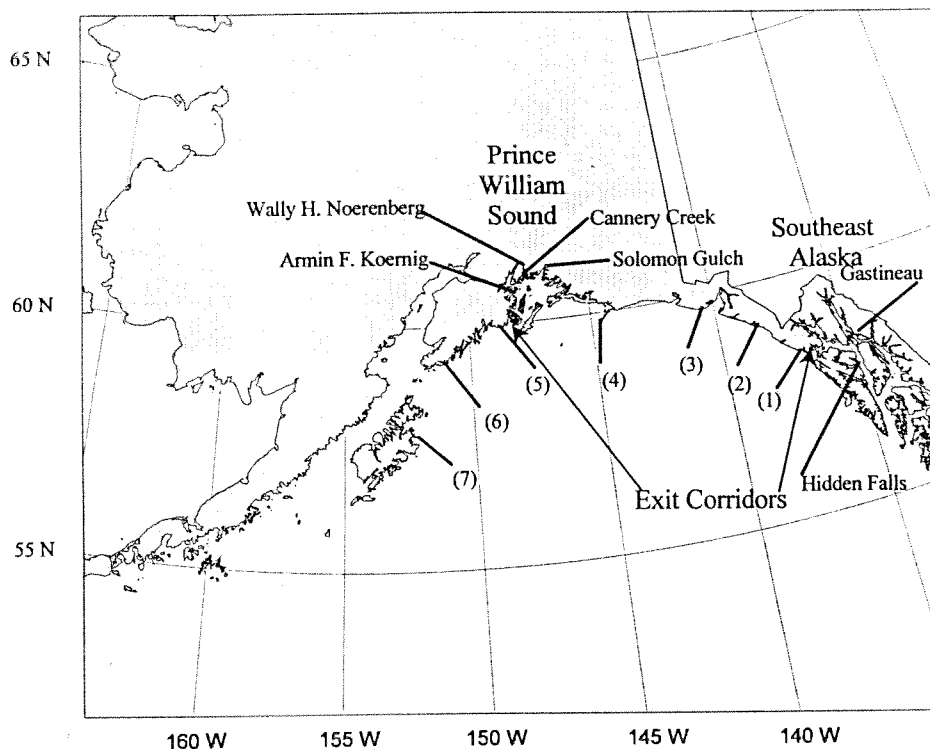
Juvenile pink and chum salmon captured during the July–August 1996 survey (See Carlson et al. this volume for details on sampling methods) were frozen whole and shipped to the laboratory for analysis. In the laboratory, juvenile salmon were thawed and standard length (measured from tip of snout to posterior end of caudal peduncle) and weight were recorded for subsamples of juvenile pink and chum salmon. Left and right sagittal otoliths were removed, and the left sagittal otoliths mounted, using thermal resin, on petrographic slides and then ground to expose the primordia. If left sagittal otoliths were not available or were overground, then the right sagittal otoliths were used.

Otolith microstructure was examined under a compound microscope, and the microstructure patterns were compared to thermal mark patterns from voucher specimens collected from the hatcheries before release. For this study we compared otolith thermal mark patterns from juvenile chum salmon caught during our survey to voucher specimens collected from Gastineau and Hidden Falls hatcheries located in Southeast Alaska (Fig. 1). Otolith thermal mark patterns from juvenile pink salmon caught during the summer survey were compared with voucher specimens collected from Armin F. Koernig, Cannery Creek, Solomon Gulch, and Wally H. Noerenberg

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**Fig. 1.** Transects sampled in the North Pacific Ocean during July–August 1996 by the Ocean Carrying Capacity program and locations of Southeast Alaska and Prince William Sound hatcheries. (1) Cape Spencer; (2) Cape Fairweather; (3) Ocean Cape; (4) Cape St. Elias; (5) Cape Puget; (6) Gore Point; (7) Cape Chiniak.



hatcheries located in Prince William Sound (Fig. 1). We will refer to each of these hatcheries as a separate 'stock' throughout the rest of the paper. All otoliths were read independently by a second reader to minimize reader error and provide confidence in readings (Hagen et al. 1995). When disagreements between otolith readers occurred, they were resolved by the most experienced reader.

Data included standard length ( $L$ , mm) and weight ( $W$ , g) for each hatchery pink and chum salmon stock. We tested for significant differences between length and weight of the four Prince William Sound (PWS) hatchery pink salmon stocks and two Southeast Alaska hatchery chum salmon stocks to determine whether these data could be pooled by species across hatchery stocks. Length and weight for both species were significantly different ( $p < 0.01$ ) between hatchery stocks; therefore, these data were not pooled. A length-weight regression,  $\ln(W_{ij}) = \alpha_0 + \beta \ln(L_{ij})$  where  $i$  represents species and  $j$  represents hatchery stock, was performed for each hatchery pink and chum salmon stock. A condition factor ( $K$ ) was defined as the ratio of the weight of each fish to its expected weight based on the length-weight regressions for that hatchery (Perry et al. 1996). Juvenile pink and chum salmon characteristics ( $L$ ,  $W$ , and  $K$ ) were grouped by transect and differences in salmon characteristics were examined graphically using box-

plots (Cleveland 1993). The Tukey-Kramer multiple comparison method (Kramer 1956) was used to calculate 95% confidence intervals (expressed as Lower Bound (L-Bound) and Upper Bound (U-Bound)) for all pairwise differences between fish characteristic ( $L$ ,  $W$ , and  $K$ ) means at each transect. Confidence intervals that exclude 0 suggest the pairwise difference was significant. Statistical analyses were conducted using the S-Plus 2000 statistical system (MathSoft, Inc. 1999).

## RESULTS

### Thermal Mark/Recoveries

Subsamples of otoliths from the total catch of juvenile pink and chum salmon were analyzed for hatchery thermal marks (see Farley and Munk 1997 for details). Transects sampled along the coastal GOA that contained sufficient numbers ( $\geq 10$ ; but we did use one sample of 3) of thermally marked salmon for statistical analyses included Cape Puget, Gore Point, and Cape Chiniak for PWS hatchery pink salmon stocks and Cape Spencer, Cape Fairweather, Ocean Cape, and Cape St. Elias for Southeast Alaska hatchery chum salmon stocks (see Fig. 1 for transect locations). Numbers of thermally marked salmon by species, hatchery, and transect are given in Table 1.

## Growth and Condition

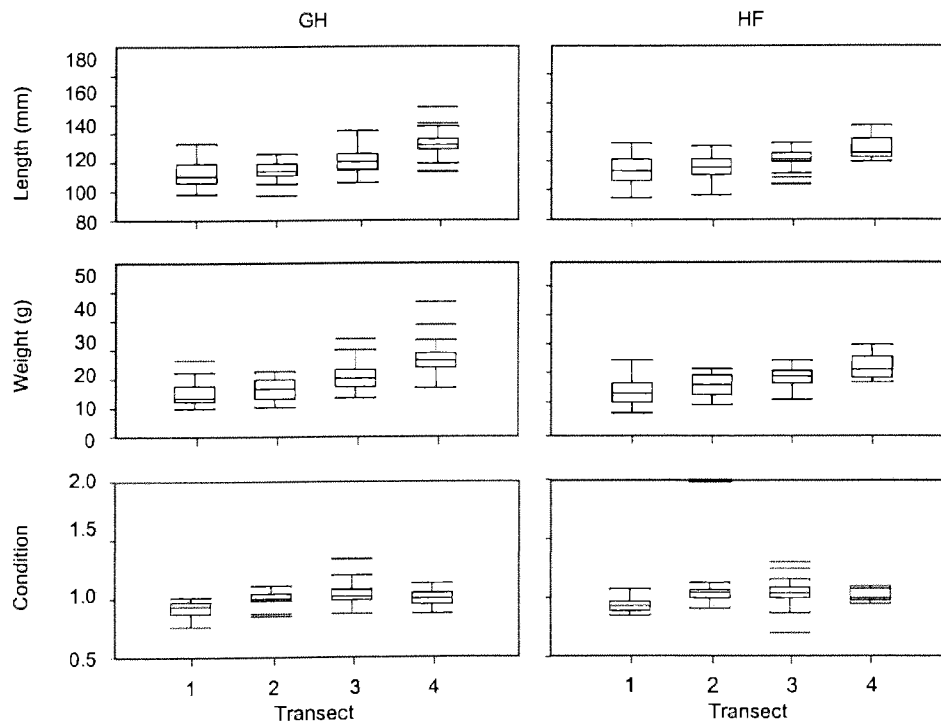
Growth (length and weight) and condition factor of PWS hatchery pink and Southeast Alaska hatchery chum salmon stocks varied among transects (Figs. 2 and 3). Median size of pink and chum salmon increased from east to west along the coast starting at transects near exit corridors (Cape Spencer near Southeast Alaska and Cape Puget near PWS). In general, the multiple comparison procedure showed that differences in length and weight of each of the hatchery pink and chum salmon stocks between tran-

sects were significant ( $p < 0.05$ ; Tables 2 and 3). The length-weight regression indicated that weights were significantly related to lengths for each hatchery pink and chum salmon stock (Table 4). The condition factor based on the ratio of actual Vs expected weight at length for each of the PWS hatchery pink and Southeast Alaska chum salmon stocks was significantly lower at transects near exit corridors (Cape Puget and Cape Spencer, respectively) than at the next transect further east along their migratory path (Tables 2 and 3).

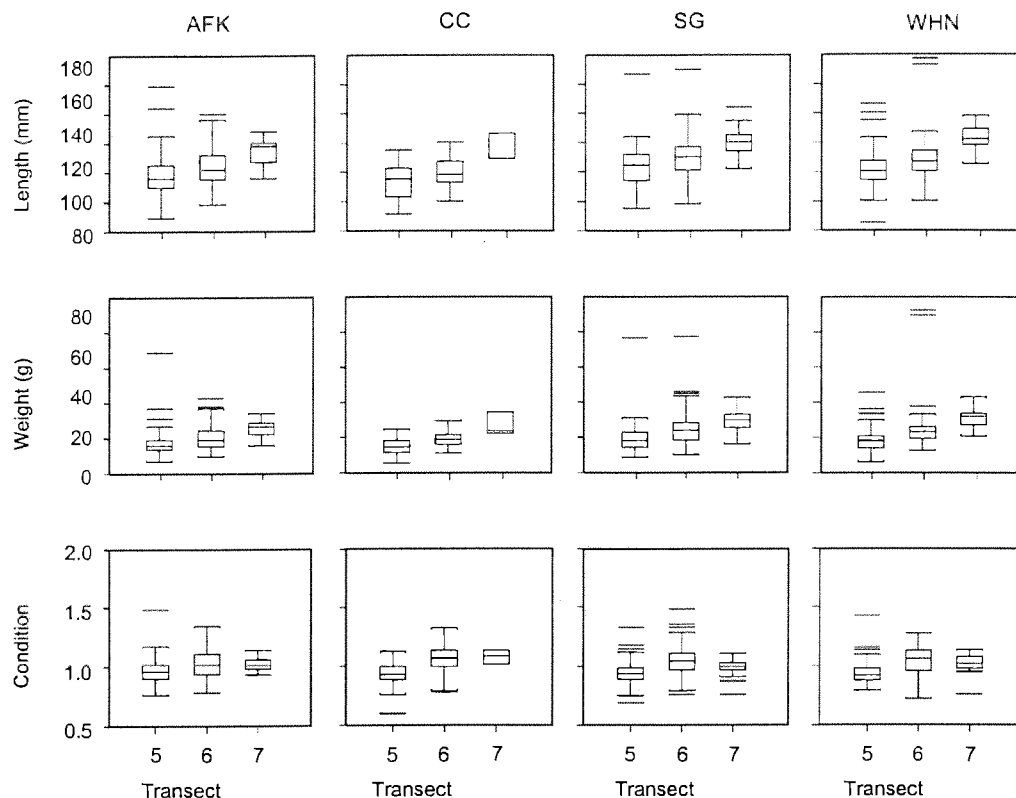
**Table 1.** Number of thermally marked Prince William Sound hatchery pink salmon and Southeast Alaska hatchery chum salmon caught during July and August 1996 at each transect in the coastal waters of the Gulf of Alaska. (Prince William Sound hatcheries include: Armin F. Koerning (AFK), Cannery Creek (CC), Solomon Gulch (SG), and Wally H. Noerenberg (WHN); Southeast Alaska hatcheries include: Gastineau Hatchery (GH) and Hidden Falls (HF).)

|                  | Hatchery |    |     |     |     |     |
|------------------|----------|----|-----|-----|-----|-----|
|                  | AFK      | CC | SG  | WHN | GH  | HF  |
| Pink Salmon      |          |    |     |     |     |     |
| Cape Puget       | 50       | 40 | 96  | 57  |     |     |
| Gore Point       | 80       | 33 | 154 | 86  |     |     |
| Cape Chiniak     | 17       | 3  | 38  | 17  |     |     |
| Totals           | 147      | 76 | 288 | 160 |     |     |
| Chum Salmon      |          |    |     |     |     |     |
| Cape Spencer     |          |    |     |     | 30  | 51  |
| Cape Fairweather |          |    |     |     | 10  | 24  |
| Ocean Cape       |          |    |     |     | 96  | 48  |
| Cape St. Elias   |          |    |     |     | 69  | 11  |
| Total            |          |    |     |     | 205 | 134 |

**Fig. 2.** Box plots of juvenile chum salmon length, weight, and condition factor from Gastineau (GH) and Hidden Falls (HF) hatcheries. Transect numbers correspond to: 1—Cape Spencer; 2—Cape Fairweather; 3—Ocean Cape; and 4—Cape St. Elias. The line within the box represents the median, the upper and lower edges define the 75<sup>th</sup> and 25<sup>th</sup> percentiles (interquartile distance), the whiskers represent values that fall within 1.5 times the interquartile distance, and the separate lines represent outliers.



**Fig. 3.** Box plots of juvenile pink salmon length, weight, and condition factor from Armin F. Koernig (AFK), Cannery Creek (CC), Solomon Gulch (SG), and Wally H. Noerenberg (WHN) hatcheries. Transect numbers correspond to: 5—Cape Puget; 6—Gore Point; and 7—Cape Chiniak. The line within the box represents the median, the upper and lower edges define the 75<sup>th</sup> and 25<sup>th</sup> percentiles (interquartile distance), the whiskers represent values that fall within 1.5 times the interquartile distance, and the separate lines represent outliers.



**Table 2.** Multiple comparison results for length, weight, and condition factor for Prince William Sound hatchery pink salmon caught during July and August 1996 in the coastal waters of the Gulf of Alaska by the OCC program with 95% simultaneous confidence intervals (Lower Bound—L-bound; Upper Bound—U-bound) for specified linear combinations, by the Tukey-Kramer method. (Confidence intervals that exclude 0 (**Bold**) indicate significant differences between transects).

| Transect                  | Armin F. Koernig |              | Cannery Creek |              | Solomon Gulch |               | Wally Noerenberg |               |
|---------------------------|------------------|--------------|---------------|--------------|---------------|---------------|------------------|---------------|
|                           | L-bound          | U-bound      | L-bound       | U-bound      | L-bound       | U-bound       | L-bound          | U-bound       |
| <b>a. Length</b>          |                  |              |               |              |               |               |                  |               |
| Cape Puget - Gore Point   | -11.00           | 0.04         | -11.90        | 0.86         | <b>-9.31</b>  | <b>-1.79</b>  | <b>-12.00</b>    | <b>-0.77</b>  |
| Cape Puget - Cape Chiniak | <b>-24.80</b>    | <b>-7.30</b> | <b>-37.00</b> | <b>-4.40</b> | <b>-22.40</b> | <b>-11.30</b> | <b>-29.70</b>    | <b>-11.50</b> |
| Gore Point - Cape Chiniak | <b>-18.90</b>    | <b>-2.16</b> | -31.60        | 1.26         | <b>-16.50</b> | <b>-6.07</b>  | <b>-22.90</b>    | <b>-5.42</b>  |
| <b>b. Weight</b>          |                  |              |               |              |               |               |                  |               |
| Cape Puget - Gore Point   | <b>-6.60</b>     | <b>-0.16</b> | <b>-6.67</b>  | <b>-1.38</b> | <b>-7.58</b>  | <b>-2.71</b>  | <b>-9.46</b>     | <b>-1.62</b>  |
| Cape Puget - Cape Chiniak | <b>-14.00</b>    | <b>-3.80</b> | <b>-18.50</b> | <b>-5.01</b> | <b>-14.00</b> | <b>-6.81</b>  | <b>-19.00</b>    | <b>-6.33</b>  |
| Gore Point - Cape Chiniak | <b>-10.40</b>    | <b>-0.63</b> | <b>-14.50</b> | <b>-0.94</b> | <b>-8.65</b>  | <b>-1.86</b>  | <b>-13.20</b>    | <b>-1.05</b>  |
| <b>c. Condition</b>       |                  |              |               |              |               |               |                  |               |
| Cape Puget - Gore Point   | <b>-0.10</b>     | <b>-0.01</b> | <b>-0.21</b>  | <b>-0.01</b> | <b>-0.13</b>  | <b>-0.07</b>  | <b>-0.15</b>     | <b>-0.06</b>  |
| Cape Puget - Cape Chiniak | -0.13            | 0.02         | -0.37         | 0.13         | -0.09         | 0.00          | <b>-0.15</b>     | <b>0.00</b>   |
| Gore Point - Cape Chiniak | -0.07            | 0.07         | -0.27         | 0.24         | <b>0.01</b>   | <b>0.10</b>   | -0.04            | 0.10          |

**Table 3.** Multiple comparison results for length, weight, and condition factor for Southeast Alaska hatchery chum salmon caught during July and August 1996 in the coastal waters of the Gulf of Alaska by the OCC program with 95% simultaneous confidence intervals (Lower Bound—L-bound; Upper Bound—U-bound) specified linear combinations, by the Tukey-Kramer method. (Confidence intervals that exclude 0 (**Bold**) indicate significant differences between transects).

| Transect                          | Gastineau Hatchery |               | Hidden Falls Hatchery |              |
|-----------------------------------|--------------------|---------------|-----------------------|--------------|
|                                   | L-bound            | U-bound       | L-bound               | U-bound      |
| <b>a. Length</b>                  |                    |               |                       |              |
| Cape Spencer - Cape Fairweather   | -8.52              | 6.18          | -6.69                 | 3.67         |
| Cape Spencer - Ocean Cape         | <b>-12.40</b>      | <b>-3.96</b>  | <b>-12.00</b>         | <b>-3.55</b> |
| Cape Spencer - Cape St. Elias     | <b>-23.90</b>      | <b>-15.10</b> | <b>-21.90</b>         | <b>-8.02</b> |
| Cape Fairweather - Ocean Cape     | <b>-13.70</b>      | <b>-0.32</b>  | <b>-11.50</b>         | <b>-1.02</b> |
| Cape Fairweather - Cape St. Elias | <b>-25.20</b>      | <b>-11.50</b> | <b>-21.10</b>         | <b>-5.85</b> |
| Ocean Cape - Cape St. Elias       | <b>-14.50</b>      | <b>-8.16</b>  | <b>-14.20</b>         | <b>-0.22</b> |
| <b>b. Weight</b>                  |                    |               |                       |              |
| Cape Spencer - Cape Fairweather   | -5.62              | 2.42          | <b>-4.87</b>          | <b>-0.17</b> |
| Cape Spencer - Ocean Cape         | <b>-8.01</b>       | <b>-3.40</b>  | <b>-7.02</b>          | <b>-3.19</b> |
| Cape Spencer - Cape St. Elias     | <b>-13.90</b>      | <b>-9.07</b>  | <b>-11.80</b>         | <b>-5.47</b> |
| Cape Fairweather - Ocean Cape     | <b>-7.76</b>       | <b>-0.45</b>  | <b>-4.96</b>          | <b>-0.21</b> |
| Cape Fairweather - Cape St. Elias | <b>-13.60</b>      | <b>-6.15</b>  | <b>-9.57</b>          | <b>-2.65</b> |
| Ocean Cape - Cape St. Elias       | <b>-7.51</b>       | <b>-4.03</b>  | <b>-6.69</b>          | <b>-0.34</b> |
| <b>c. Condition</b>               |                    |               |                       |              |
| Cape Spencer - Cape Fairweather   | <b>-0.14</b>       | <b>-0.01</b>  | <b>-0.21</b>          | <b>-0.06</b> |
| Cape Spencer - Ocean Cape         | <b>-0.16</b>       | <b>-0.08</b>  | <b>-0.16</b>          | <b>-0.05</b> |
| Cape Spencer - Cape St. Elias     | <b>-0.12</b>       | <b>-0.04</b>  | <b>-0.17</b>          | 0.02         |
| Cape Fairweather - Ocean Cape     | -0.10              | 0.02          | -0.04                 | 0.10         |
| Cape Fairweather - Cape St. Elias | -0.07              | 0.06          | -0.05                 | 0.16         |
| Ocean Cape - Cape St. Elias       | 0.01               | 0.07          | -0.07                 | 0.12         |

**Table 4.** Regression results for salmon weight versus length, for juvenile Prince William Sound hatchery pink salmon stocks and Southeast Alaska hatchery chum salmon stocks collected during July and August 1996 in the coastal waters of the Gulf of Alaska by the OCC program. Coefficients ( $\alpha_0$ ) and ( $\beta$ ) are from the regression model,  $n$  represents the number of data points,  $r^2$  is the proportion of variance explained by the regression, and  $p$  represents the probability value for the regression.

| Pink Salmon        | $n$ | $r^2$ | $P$     | $\alpha_0$ | $\beta$ |
|--------------------|-----|-------|---------|------------|---------|
| Armin F. Koernig   | 147 | 0.91  | < 0.001 | -12.31     | 3.17    |
| Cannery Creek      | 76  | 0.77  | < 0.001 | -10.31     | 2.75    |
| Solomon Gulch      | 288 | 0.90  | < 0.001 | -12.68     | 3.25    |
| Wally Noerenberg   | 160 | 0.89  | < 0.001 | -11.85     | 3.08    |
| <b>Chum Salmon</b> |     |       |         |            |         |
| Gastineau          | 205 | 0.92  | < 0.001 | -12.27     | 3.18    |
| Hidden Falls       | 134 | 0.92  | < 0.001 | -12.25     | 3.18    |

## DISCUSSION

Prince William Sound hatchery pink salmon stocks and Southeast Alaska chum salmon stocks caught along the coastal waters of the Gulf of Alaska during July and August 1996 displayed spatial variations in growth and condition factor. The smallest PWS hatchery juvenile pink salmon were caught at Cape Puget, while the smallest Southeast Alaska hatchery chum salmon were caught at Cape Spencer. Condition factor for each of the Southeast Alaska hatchery chum salmon and PWS hatchery pink salmon stocks was also significantly lower at these

two transects than at the next transect located further along the migratory pathway for these salmon. This result may be related to reduced growth, feeding intensity, or survival of juvenile hatchery pink and chum salmon while entering the coastal GOA from inside waters.

Condition factor for fishes has been measured differently by different authors (Perry et al. 1996; Lambert and Dutil 1997). Lambert and Dutil (1997) measured condition factor using somatic weight (total weight of fish less stomach and gonad weights) instead of total weight of each fish, since feeding intensity and gonad maturation can vary significantly and

independently of condition within and between stocks. The condition factor used in our study was measured as the ratio of actual weight to expected weight based on the length-weight regressions for each hatchery stock (similar to Perry et al. 1996). The hatchery pink and chum salmon captured during our survey were juveniles, thus differences in gonad weight of individuals could be considered negligible; however, differences in stomach content weights could vary significantly between transects and hatchery stocks. Juvenile pink and chum salmon captured at Cape Puget and Cape Spencer had less food in their stomachs than those fish captured at transects further along the coast (Mary Auburn-Cook, National Marine Fisheries Service, Auke Bay Laboratory, Juneau, AK 99801, personal communication) suggesting that the lower condition factor in our study may be related to feeding intensity.

Feeding intensity of juvenile hatchery pink and chum salmon captured during our survey may be impacted by differences in size and/or species of zooplankton along the coastal GOA. Zooplankton data collected during NMFS Marine Salmon Investigation surveys in inside waters of northern Southeast Alaska (Icy Strait) and in the coastal waters of the GOA near Cape Spencer during July indicated that zooplankton found in inside waters were generally smaller and in some instances of different species than zooplankton in the coastal waters (Joe Orsi, National Marine Fisheries Service, Auke Bay Laboratory, Juneau Alaska 99801, personal communication). As mentioned earlier, Cape Spencer as well as Cape Puget are located near exit corridors for juvenile salmon leaving inside waters of Southeast Alaska and Prince William Sound, respectively. The significantly lower condition factor for juvenile salmon at Cape Spencer, and perhaps Cape Puget may indicate a period of adjustment for juvenile salmon leaving inside waters and entering the oceanic waters of the GOA before they can actively feed on larger and different prey items found in the oceanic waters of the GOA.

Feeding intensity of PWS and Southeast Alaska hatchery pink and chum salmon stocks entering the coastal waters of the GOA may also be related to their hatchery origins. Condition factor was positively related to stomach fullness for juvenile chum salmon captured off the coastal waters of northern Vancouver Island, B.C. during early summer 1992 but negatively related to stomach fullness for those captured off of southern Vancouver Island, B.C. (Perry et al. 1996). The authors speculated that juvenile chum salmon captured on the southern end of Vancouver Island during their survey were most likely from the Nitinat hatchery which had released approximately 40 million chum salmon into the ocean during spring 1992. Pink salmon caught in the same area, however, exhibited a significant positive rela-

tionship between condition factor and stomach fullness, suggesting that Nitinat Hatchery chum salmon, and perhaps other hatchery salmon, may not be as competent at feeding on wild zooplankton as fish that have survived longer in the marine environment (Perry et al. 1996).

Spatial variations in zooplankton abundance may also explain the differences in feeding intensity of Southeast Alaska hatchery chum and PWS hatchery pink salmon stocks entering the GOA. Zooplankton biomass in the coastal waters of the GOA near Cape Spencer (Icy Point) during July was lower than in inside waters (Icy Strait) of northern Southeast Alaska (Murphy et al. 1999). Large numbers of juvenile salmon leaving inside waters of Southeast Alaska and entering the coastal waters near Cape Spencer may exceed the carrying capacity of this area, suggesting the possibility that feeding intensity in the vicinity of Cape Spencer is density dependent.

## CONCLUSIONS

Our study examined spatial variations in size and condition factor for four PWS hatchery pink and two Southeast Alaska hatchery and chum salmon stocks caught in the coastal waters of the GOA during July and August 1996. We have suggested that the significantly lower condition factor for these hatchery pink and chum salmon when they enter the GOA may be related to feeding intensity of these juvenile salmon. We speculate that the lower feeding intensity of juvenile salmon at exit corridors is related to zooplankton abundance, high density, or a transitional period either before juvenile salmon leave inside waters and enter the ocean, or before hatchery raised juvenile salmon actively feed in the marine environment. Testing these hypotheses requires a time series of observations on migration routes, feeding success, condition, and growth (in inside and outside waters along the GOA) for hatchery and wild stocks of salmon.

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## Using the Coordinates of some Character Points of Scales for Differentiation of Pacific Salmon Stocks

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**Keywords:** Stock identification, population, scales, sockeye salmon

**Abstract:** Classification accuracy of adult sockeye salmon (*Oncorhynchus nerka*) from three known populations (one fluvial and two limnobiatic) spawning in the Paratunka River basin (East Kamchatka) was assessed by two methods. The first method used scale structure (spacing of circuli triples and so on), the second method used these characteristics, in conjunction with X and Y coordinates of some typical points at the inner boundary between the fresh-water scale zone and the marine first year scale zone. Discriminate analysis with additional use of two-dimensional parameters revealed a significant increase in average accuracy of classification.

### INTRODUCTION

Fishery management and monitoring of national resources within international waters require a reliable method of identifying origin of salmon stocks. There are many methods used currently, but the most promising is differentiation of adult fish scale structure (Anas and Murai 1969; Tanaka et al. 1969; Cook and Lord 1978; Cook 1982; Nikolayeva and Semennets 1983; Myers 1985; Davis 1987; Millar 1988; Schwartzberg and Fryer 1993; Bernard and Myers 1994; Kayev 1998; Temnykh 1998; and others). Scale characteristics include distances from the scale center to various structures (some circuli, circuli triplets, annual ring, fresh-water growth zone and marine growth zone boundaries and so on) and distances between the structures, and the number of circuli within various zones on the scale.

Usually the scale characteristics are sufficient for identification of large stocks on the basis of representative standard samples. However, in some cases (for example, to differentiate various populations of a species which spawn in closely spaced spawning grounds, or to estimate adult return to different hatcheries within one river) traditional characteristics might be not enough. Therefore, in addition to these characteristics, we also use two-dimensional scale parameters. One of these parameters can be X and Y coordinates of some typical points in relation to the scale center. We have suggested that several edge points delineating the boundary of the first marine year zone might be useful for identification of stocks inhabiting different ecological niches during early life.

Identification of stock origin from scale shape and otholiths, using the Fourie function, has been done (Jarvis et al. 1978; Bird et al. 1986). However, when using the Fourie function the coordinates of a group of edge points in relation to the center of estimation area must be found. We have proposed using the scale center as the center of coordinates, which allows measurement of the vertical and horizontal asymmetry. Scale characteristics may be related to locomotory function of fish. It is possible that scale structures are determined by the level of adaptation of individuals to intense or prolonged swimming.

Two-dimensional parameters of the first year zone on scales were successfully used as additional characteristics for identification of wild and hatchery chum salmon entering spawning grounds of Paratunka River, West Kamchatka (Zaporozhets and Zaporozhets 1999). We decided, therefore, to apply the method to sockeye salmon (*Oncorhynchus nerka*) from different populations inhabiting one river to see if we could improve the separation of two such closely related populations.

In this study we used scale measurement data from fish whose origin was known, in order to estimate potential benefit from using the two-dimensional method.

### MATERIALS AND METHODS

Adult sockeye salmon scale samples from three populations were collected from spawning grounds by scientists working in KamchatNIRO (Eugeny Pogodayev and authors). Spawning grounds were all in the Paratunka River basin: Blidzneye Lake, Dalneye

Lake and upper reaches of Paratunka River. Scales were taken according to NPAFC recommendations (Knudsen 1985; Davis et al. 1990). Age was estimated by Eugene Pogodayev.

The radiuses of all circuli in the first annual zone were measured by one reader, along a long axis of the scale between reference lines connecting the edges of extreme circuli (Fig. 1). These measurements were analyzed using "BioSonics" OPRS (OPRS, BioSonics Inc., Seattle, WA) at the magnification of x82. We also measured X and Y coordinates from the center (focus) of scales to six characteristic points as follows: 1) left lowest termination of the first year growth zone, 2) left extreme of the first year zone, 3) upper extreme of the first year growth zone, 4) maximum radius point at the first year growth zone, 5) right extreme of the first year growth zone, 6) right lowest termination of the first year growth zone.

Fig. 1. Central zone of sockeye salmon scale demonstrating characteristic axes and points: 0, center (focus) of scale; 1, left lowest termination of the first year growth zone; 2, left extreme of the first year zone; 3, upper extreme of the first year growth zone; 4, maximum radius point at the first year growth zone; 5, right extreme of the first year growth zone; 6, right lowest termination of the first year growth zone; 1-6, reference line; 0-4, axis used for making measurements.



Geometrical coordinates are defined as follows:

- $X_0, Y_0$  - focus of scale;
- $X_1 < 0, |Y_1| < 0 \rightarrow \text{Max}$ ,
- $|X_2| < 0 \rightarrow \text{Max}, Y_2$  - any location,
- $X_3$  - any location,  $Y_3 \rightarrow \text{Max}$ ,
- $X_4 \rightarrow \text{Max}, Y_4 \rightarrow \text{Max}$ ,
- $X_5 \rightarrow \text{Max}, Y_5 > 0$ ,
- $X_6 > 0, |Y_6| < 0 \rightarrow \text{Max}$ ;
- $Y_1 \approx Y_6$ ;

#### Scale Variables

Initially OPRS measurement data consisted of radial and coordinate parameters.

I. Radial parameters: distances from the center of the focus to the outer edge of each circulus that was marked on the OPRS monitor. These data were re-formatted into an initial set of 11 variables:

- 1) - R1 - central zone size;
- 2) - NF - total number of fresh-water sclerites;
- 3) - RF - radius of last fresh-water circulus;
- 4) - NR - number of sclerites until first marine year circulus;
- 5-11) - average circulus spacing in seven initial triplets (T1 - T7), assessed from the equation

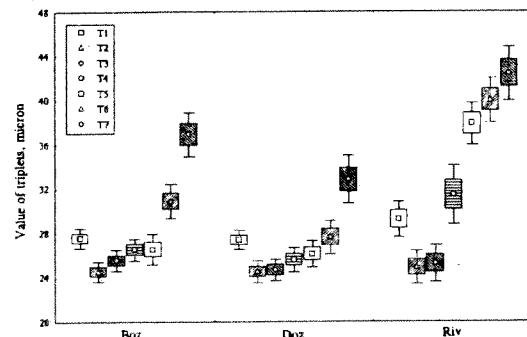
$$T_n = (DR_n + DR_{n+1} + DR_{n+2})/3,$$

Where  $DR_n = R_{n+1} - R_n$ , and  $R_{n+1} \parallel R_n$  - radii of two neighbouring sclerites.

The triplets were assessed as particular sclerites united in groups by three in every group to 'smooth' the individual circulus increments on a particular fish scale and to make characteristics of stocks more certain (Davis 1987; Bernard and Myers 1994). We did not separate the fresh-water triplets from marine triplets because the number of fresh-water sclerites in fluvial sockeye can be very low (Fig. 2). The separation would, therefore, complicate matters.

II. Coordinate parameters: X and Y coordinates of the seven points on the scale mentioned above (including the center) were estimated from the center of the focus to the outer edge of each circulus marked on the OPRS monitor. The system was re-formatted by subtracting coordinates: coordinates of the points ( $X_n, Y_n$ ) minus coordinates of the center ( $X_0, Y_0$ ).

Fig. 2. Dispersion diagrams of seven triplets in three sockeye salmon populations in the Paratunka River basin: BOZ, "Blizhneye Lake"; DOZ, "Dalneye Lake"; RIV, "Fluvial". Central square, diamond, etc., mean; boxes, standard error; whiskers, 95% confidence interval.



#### Variable Selection

Transformed data were tested for missing values, inter-group correlation and normal distribution

through the STATISTICA-5.1 program (StatSoft, Inc. 1998). Variables which failed the tests were excluded from the analysis. Extreme outliers were sought through distribution diagrams (Scatterplot with Box Plot). Extreme mean values were also excluded from the analysis. All individuals having an incomplete set of variables were excluded from the analysis automatically according to the Casewise deletion of missing data option.

Two-factor dispersion analysis ANOVA (origin and year of birth,  $\alpha = 0.05$ ) was used to select further variables. The task was to find sub-sets of variables which were significantly different in different sockeye populations, but similar among different aged individuals.

In final studies we used only four circuli triplets  $T_3$ - $T_6$ , first radius  $R_1$  and coordinates:  $X_1$ ,  $Y_2$ ,  $Y_3$ ,  $Y_4$ ,  $Y_5$ . We analyzed data from measurements of 180 individual scale samples collected in 1996, including 86 scale samples from Blidzneye Lake sockeye (1), 64 samples from Dalneye Lake sockeye (2), and 28 from Paratunka River sockeye (3).

### Tests of Model Performance

Discriminate analysis of data was accomplished using the program STATISTICA 5.1 after preliminary computation. Classification accuracy was tested through the five-fold cross-validation. This kind of validating has been useful when there is no particular test sample.

Classification is repeated five times, each time a sub-sample being excluded in constructing a test-sample for cross-validating. Thus, every sub-sample should act five-1 times as a participant of learning sample and as a test-sample. Cross-validation costs, estimated for five test samples, are averaged to get five time errors for estimation of the cross-validation cost, together with its standard error. The cost is expressed as the percent of mistakenly classified observations. Accordingly, the data were divided into three equal sub-samples, every sub-sample having 48%, 36% and 16% of Blidzneye Lake, Dalneye Lake and Paratunka River sockeye, respectively. Then three-fold classification of learning and test samples was accomplished.

## RESULTS

Two-factor ANOVA (origin and year of birth) showed there was no significant difference ( $p < 0.05$ ) between the three sockeye populations in their average size of initial spacing between circuli triplets ( $T_1$ ,  $T_2$ ). Otherwise, NF and  $T_2$  variables depended significantly on the age of fish ( $p < 0.05$ ). These variables were excluded from the analysis.

The most common significant differences among populations occurred with the following characteristics:  $X_1$ ,  $Y_1$ ,  $X_2$ ,  $Y_3$ ,  $Y_4$ ,  $X_5$ ,  $T_5$ ,  $T_6$ . However, after analysis of correlation matrix and preliminary simulation the following characteristics were selected:  $R_1$ ,  $X_2$ ,  $Y_2$ ,  $Y_3$ ,  $Y_4$ ,  $Y_5$ ,  $T_3$ ,  $T_4$ ,  $T_5$ ,  $T_6$ .

Step-by-step discriminate analysis of three equal data sub-samples using ten selected variables indicated that one of the characteristics ( $Y_4$ ,  $T_3$ ,  $T_4$ ) was surplus and the program did not select that characteristic for the model. Nevertheless, those characteristics were not completely excluded from the analysis because average accuracy of classification would have been decreased.

The model, which included nine variables, obtained from program selection, classified learning samples with an average accuracy of about  $84 \pm 4\%$ , and test sub-samples with average accuracy of  $77 \pm 6\%$  (Table 1). Results with test subsamples were best for Blidzneye Lake sockeye ( $88 \pm 5\%$ ). Dalneye Lake sockeye classification with the model was poor ( $60 \pm 7\%$ ) (Fig. 3). Average cost of classification was  $23 \pm 6\%$ .

Step-by-step discriminate analysis of three equal data sub-samples using 5 radial variables ( $R_1$ ,  $T_3$ ,  $T_4$ ,  $T_5$ ,  $T_6$ ) showed that one of these variables ( $T_3$ ) was surplus in two of three cases.

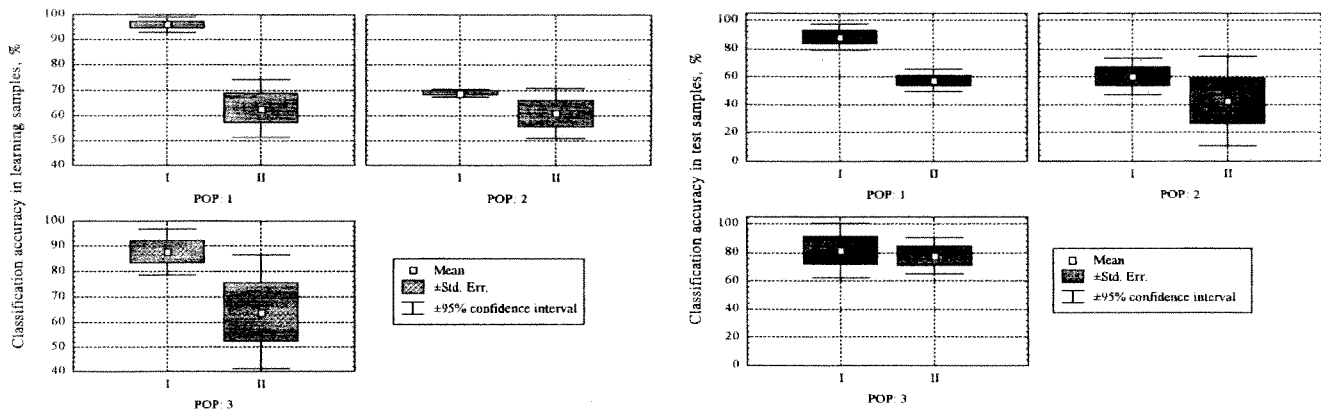
The model, which included four to five variables, selected as a result of simulation, classified learning samples with an average accuracy of about  $63 \pm 4\%$ , and test sub-samples with an accuracy of  $59 \pm 7\%$  (Table 1, Fig. 3). Average cost of classification was increased by 1.4 times ( $32 \pm 7\%$ ) compared to the first method.

Examination of canonical analysis results showed that contribution of coordinate characteristics to differentiation of three sockeye salmon populations in first and second discriminate functions took about 60% and more than 70% respectively (Fig. 4).

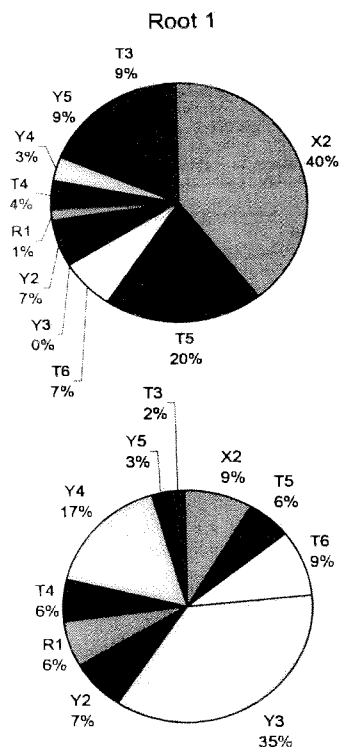
**Table 1.** Classification accuracy (mean %  $\pm$  standard error) of sockeye salmon origin assessed with "coordinate" characteristics (RT+XY) and without these characteristics (RT). BOZ, Blidzneye Lake; DOZ, Dalneye Lake; RIV, Fluvial Stock of Paratunka River.

| Samples               | RT+XY          |                |                |                | RT             |                 |                 |                |
|-----------------------|----------------|----------------|----------------|----------------|----------------|-----------------|-----------------|----------------|
|                       | BOZ            | DOZ            | RIV            | M $\pm$ m      | BOZ            | DOZ             | RIV             | M $\pm$ m      |
| Learning              | 95.9 $\pm$ 1.5 | 69.0 $\pm$ 0.8 | 87.7 $\pm$ 4.6 | 84.2 $\pm$ 4.2 | 62.9 $\pm$ 5.9 | 60.9 $\pm$ 5.1  | 63.9 $\pm$ 11.6 | 62.5 $\pm$ 4.1 |
| Test                  | 88.3 $\pm$ 4.7 | 60.3 $\pm$ 6.7 | 81.7 $\pm$ 9.7 | 76.8 $\pm$ 5.6 | 57.6 $\pm$ 4.1 | 42.8 $\pm$ 16.3 | 77.9 $\pm$ 6.4  | 59.4 $\pm$ 7.3 |
| Classification effort | 11.7 $\pm$ 4.7 | 39.7 $\pm$ 6.7 | 18.3 $\pm$ 9.7 | 23.2 $\pm$ 5.6 | 42.5 $\pm$ 4.1 | 57.0 $\pm$ 16.4 | 22.2 $\pm$ 6.4  | 31.9 $\pm$ 7.3 |

**Fig. 3.** Classification accuracy among three sockeye salmon populations (Pop. 1, Blizhneye Lake; Pop. 2, Dalneye Lake; Pop. 3, Paratunka River) in learning samples (above) and test samples (below), compared by two methods: 1 using coordinate characteristics; 2 without these characteristics.



**Fig. 4.** Reliable contribution of different variables to discrimination of bench-mark sockeye salmon samples from three populations spawned in 1996 in Paratunka River. Above, first canonical function; below, second canonical function.



## DISCUSSION

Statistically reliable differences in scale characteristics of sockeye salmon from three populations (two limnetic and one fluvial) indicated that limnetic growth of fish in these populations during embryogenesis and feeding was different.

There was much more similarity between the two limnetic populations than between them and the fluvial population. This indicates similar conditions for spawning and development during the first fresh-water year in lakes. However, the two lakes differed in geomorphology: Blidzneye Lake is a shallow-water lake, warming quickly in summer; Dalneye Lake is deeper and more stable in water temperature regime (Pogodayev 1995). Feeding of Blidzneye Lake juvenile sockeye salmon is poor compared to that of Dalneye Lake juvenile sockeye: in Blidzneye Lake abundance of competitors for food and predators (juvenile stickleback, *Gasterosteus aculeatus* and coho, *O. kisutch*) is several times greater than abundance of juvenile sockeye salmon (Pogodayev 1995).

Growth conditions for the juvenile sockeye salmon in Paratunka River and its tributaries are different to those in lakes. Rapid flow and powerful spring floods cause these juvenile sockeye salmon to migrate to the sea early. Consequently, only a few narrow fresh-water sclerites occur on the scales. Later, rapid growth of these sockeye in the ocean results in many wide marine sclerites (Fig. 2).

Complicated age structure of sockeye populations makes the discriminate analysis of scale characteristics difficult. Therefore, accuracy of classification of multiple-age samples, despite conducting variable selection procedures, is lower than classification accuracy of mono-age samples. Nevertheless, we were unable to collect enough mono-age samples for this study.

Classification accuracy of test sub-samples made with and without coordinate characteristics (Table 1) spoke in favor of using these additional characteristics. The more complex model, including both types of characteristics, was 1.3 times better at classifying sockeye populations than the radial model, and the cost of classification was 1.4 times lower.

It could be suggested that higher classification accuracy of complex models arises because there are more variables. However, simulations, carried out with the same number of variables, suggest otherwise: classification accuracy of learning samples in the model with five radial variables ( $R_1$ ,  $T_3$ ,  $T_4$ ,  $T_5$ ,  $T_6$ ) was  $62.5 \pm 4.1\%$ , in the model with five coordinate variables ( $X_2$ ,  $Y_2$ ,  $Y_3$ ,  $Y_4$ ,  $Y_5$ ) -  $77.3 \pm 0.5\%$ , and in the model with five complex variables ( $X_2$ ,  $Y_3$ ,  $T_3$ ,  $T_4$ ,  $T_5$ ) -  $82.3 \pm 1\%$ .

Significant contribution of coordinate variables to the total discrimination of groups (Fig. 4) speaks in favor of using the variables as additional parameters for population differentiation.

## ACKNOWLEDGEMENTS

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# Back-Calculated Fish Lengths, Percentages of Scale Growth, and Scale Measurements for Two Scale Measurement Methods used in Studies of Salmon Growth

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**Keywords:** Back-calculation, scale measurement methods, chum salmon, growth

**Abstract:** Scale measurements, percentages of annual scale growth, and back-calculated fish lengths were examined for the INPFC method (75° anterior reference line) and Traditional method (anterior-posterior reference line) on scales of chum salmon (*Oncorhynchus keta*) for three ages, two stocks, and two brood years. Mean measurements of annual increments of scale growth were greater for the INPFC method than the Traditional method. Differences in percentages of scale growth and back-calculated fish lengths for the two methods were tested using the Hotelling one-sample  $T^2$  test. Percentages of annual scale growth differed significantly ( $p \leq 0.003$ ) between the two methods for seven of nine tests. Mean percentage of annual scale growth was greater in the first year for the Traditional method and in the final year for the INPFC method; intermediate years were similar. Back-calculated fish lengths computed by the Fraser-Lee method differed significantly between the INPFC and Traditional method ( $p \leq 0.004$ ) for seven of nine tests. Although differences in back-calculated lengths of the two methods were statistically significant, the biological differences were small (~1 cm).

## INTRODUCTION

Scales from many species of fish are commonly used to estimate age, growth history, spawning history, and racial differences. Also, when the scale radius is proportional to the length of the fish, size at younger ages can be estimated by back-calculation using scale measurements (Van Oosten 1928; Hile 1936). Back-calculations can be used to trace the effects of winter oxygen levels (Casselman and Harvey 1975), fishing pressures (Nicholls 1958), and food consumption (Weatherly 1959) on growth rate.

The number of circuli in the first ocean zone of Pacific salmon (*Oncorhynchus* spp.) scales is often used to identify racial differences. The circuli may be counted along several different orientations on the scale; in back-calculation studies the most commonly used line of measurement is the anterior-posterior line through the focus of the scale (Fig. 1), which we refer to as the Traditional method.

LaLanne (1963) observed in chum salmon (*O. keta*) that the Traditional method circuli were often broken or discontinuous, so he developed an alternative line of count. This line was developed for racial studies on chum salmon for the International North Pacific Fisheries Commission (INPFC). LaLanne (1963) determined that a line that bisects the focus at

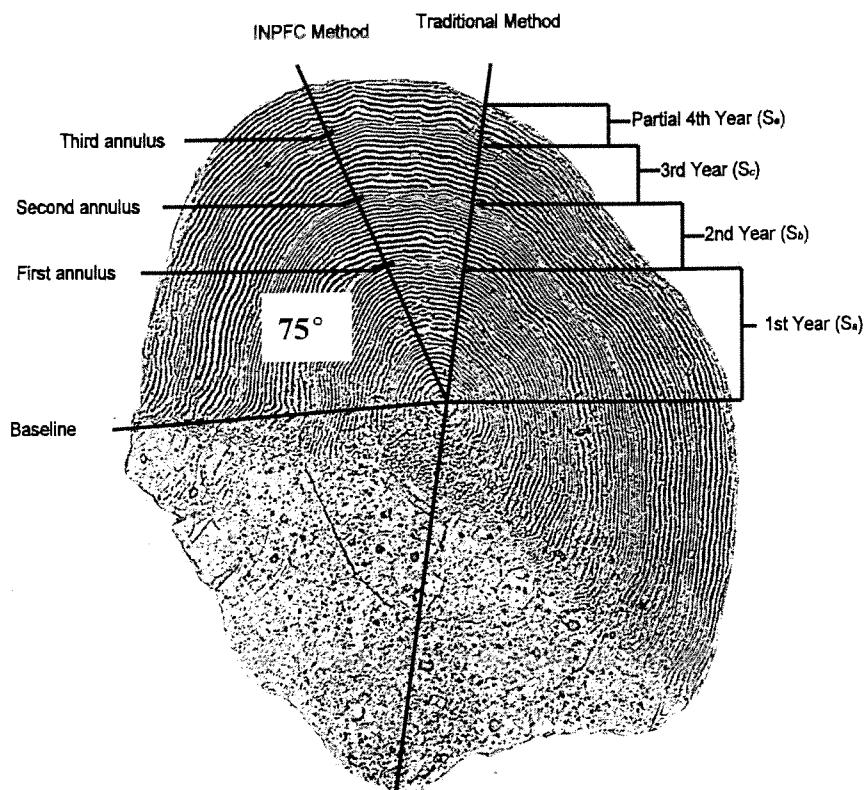
75° from a line drawn between the focus and shortest distance to where the first annulus enters the translucent exposed portion of the scale provided circuli counts with the least variation (Fig. 1); we call this the INPFC method. Both the Traditional and INPFC methods are used in scale growth studies of chum salmon.

To understand the differences between the Traditional and INPFC methods, we compared scale measurements, percentages of annual scale growth, and back-calculated fish lengths. This study presents results for different stocks, brood years, and ages.

## MATERIALS AND METHODS

Length measurements and scales were collected by author Helle from chum salmon in August 1985 and 1992 at Fish Creek, located at the head of Portland Canal in southern southeastern Alaska (U.S.A.) and in December 1985 at Quilcene National Fish Hatchery, in Hood Canal, Washington (U.S.A.). Scales were taken from the "preferred area" of the body (Anas 1963) and placed on gummed cards with the reticulated side facing up. Lengths were taken from the middle of the eye to the end of the hypural plate (MEHP).

Fig. 1. Scale of an ocean-age 3 male chum salmon illustrating the INPFC method (75° reference line) and Traditional method (anterior-posterior reference line), with years of growth.



In the laboratory, scales were pressed onto plastic acetate cards using a heated hydraulic press to produce impressions of the scales (Arnold 1951) and viewed on an Eberbach<sup>1</sup> projector at a magnification of 80x. Ages were designated using the European method, but excluding the number of freshwater years and the decimal point (Koo 1962); therefore we merely present number of winters spent at sea (ocean age). Ocean age was read by counting the number of true annuli on the scale. We examined only scales of ocean-age 2, 3, and 4 male chum salmon. Scales were measured from the focus to the first annulus ( $S_a$ ), first to the second annulus ( $S_b$ ), second to third annulus ( $S_c$ ), third to the fourth annulus ( $S_d$ ), and from the last annulus to the edge ( $S_e$ ) using the INPFC and Traditional methods. Measurements were then converted to actual size by dividing by 80 (the magnification).

#### Back-calculation Method

Back-calculations were based upon a linear regression model developed by Fraser (1916) and Lee (1920), which assumes that fish length is directly pro-

portional to scale radius (Dahl 1909). The model can be written as

$$L_i = c + (L_T - c) * (S_i / S_T),$$

where  $i$  = age at the time of annulus formation,

$c$  = length of fish at the onset of scale formation,

$L_T$  = fish length at capture,

$L_i$  = fish length at time of annulus formation,

$S_T$  = scale radius at capture, and

$S_i$  = scale radius at time of annulus formation (ocean age).

Scale radii at time of annulus formation ( $S_i$ ) were as follows: first annulus or ocean age-1 ( $S_1 = S_a$ ), second annulus or ocean age-2 ( $S_2 = S_a + S_b$ ), third annulus or ocean age-3 ( $S_3 = S_a + S_b + S_c$ ), and fourth annulus or ocean age 4 ( $S_4 = S_a + S_b + S_c + S_d$ ).

In estimating length of fish at time of scale formation ( $c$ ), we used length measurements taken from fry before they developed scale circuli. Helle (1979) reported that chum salmon fry ( $n = 29$ ) in the intertidal zone at Olsen Creek, Prince William Sound, had scales but no circuli. On average, these fish were 46 mm from the tip of the snout to the fork of the tail (TSFT). In the lab we measured TSFT and MEHP of chum salmon fry ( $n = 50$ ) before they were released from Douglas Island Pink and Chum Fish Hatchery,

<sup>1</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Juneau, Alaska in 1999 and developed a regression model:  $MEHP = 0.85 \cdot TSFT - 2.9$ ;  $r = 0.99$ . Using the regression model, TSFT (46 mm) was converted to MEHP (36 mm) and used as common intercept ( $c$ ) for the INPFC and Traditional methods in the back-calculation model.

### Graphical and Statistical Method

Measurements of annual scale growth ( $S_a$ ,  $S_b$ ,  $S_c$ ,  $S_d$ ,  $S_e$ ), percentage scale growth within years ( $S_a/S_T \cdot 100$ ,  $S_b/S_T \cdot 100$ ,  $S_c/S_T \cdot 100$ ,  $S_d/S_T \cdot 100$ ,  $S_e/S_T \cdot 100$ ), and back-calculated lengths at each ocean age ( $L_1$ ,  $L_2$ ,  $L_3$ , and  $L_4$ ) were evaluated using vertical error bar charts showing mean and 95% confidence intervals.

The back-calculated fish lengths for the INPFC method and Traditional method can be considered as two data sets from which we draw inferences. Each data set consists of vectors of several lengths per fish (for example  $L = (L_1, L_2, L_3)'$  for ocean-age 3 fish), where the subscripts represent ocean ages. The data sets themselves are not independent from each other, but are repeated-measures data; that is, back-calculated fish lengths for the two axes are computed from the same fish. Because the lengths calculated at each ocean age (2–4) are probably dependent on each other, the data lend themselves to multivariate analysis. To determine whether the back-calculated lengths computed from the two scale methods differed significantly from each other, we compared the paired vectors of lengths ( $L_I$  and  $L_T$ ) for all the fish, where  $I$  = INPFC method and  $T$  = Traditional method. Differences were computed between paired back-calculated lengths,  $d = L_I - L_T$ . If the  $d$ 's are considered to be sampled from a multivariate normal population with mean  $\delta$ , then  $\bar{d}$  can be compared to  $\delta$ . Specifically, we computed a multivariate likelihood ratio statistic (Mardia et al. 1979) to test the null hypothesis:  $H_0: \delta = \delta_0$ ,  $\Sigma$  unknown, where  $\delta_0 = 0$ . This test is also known as a Hotelling one-sample  $T^2$  test. Assuming the data are multivariate normally distributed, test statistics can be compared to an F distribution to determine significance probability. We used a battery of normality tests (Aitchison 1986) on the data to verify the assumption of multivariate normality.

The sets of percentages of annual scale growth for the two scale methods were analyzed similarly. Each data set consisted of vectors of three percentages (for example  $S = (S_a/S_T \cdot 100, S_b/S_T \cdot 100, S_c/S_T \cdot 100)'$  for ocean-age 3 fish). To determine whether the percentages of scale growth computed from the two scale methods differed significantly, a Hotelling one-sample  $T^2$  test similar to the one described above was performed.

### RESULTS

Mean back-calculated fish lengths for all ages, stocks, and brood years were greater for the Traditional method than for the INPFC method (Fig. 2). Mean calculated lengths for the Traditional method were 229–249 mm at ocean-age 1, 395–405 mm at ocean-age 2, and 501–504 mm at ocean-age 3. Mean calculated lengths from the INPFC method were 217–240 mm at ocean-age 1, 390–402 mm at ocean-age 2, and 495–500 mm at ocean-age 3. Differences in mean back-calculated fish lengths between scale methods were 3–9 mm at ocean-age 1, 1–9 mm at ocean-age 2, 2–10 mm at ocean-age 3, and 0–15 mm at ocean-age 4. Differences in back-calculated length between the scale methods varied more between stocks than between brood year or age of the same stock (Fig. 2).

After performing a battery of normality tests (Aitchison 1986) on the back-calculated lengths, we concluded the data were multivariate normally distributed. We then tested whether the lengths back-calculated from increments using the two scale methods differed significantly, using a Hotelling one-sample  $T^2$  test. Lengths calculated from the two methods differed significantly ( $p \leq 0.004$ ) for all stocks, brood years, and ages except brood-year 1981 ocean-age 4 fish from Fish Creek ( $p = 0.27$ ) and Quilcene National Fish Hatchery ( $p = 0.33$ ).

Mean percentages of annual scale growth were greater for the Traditional method in the first ocean year (~2%) and greater for the INPFC method in the last ocean year (~2%) (Fig. 3). For intermediate years, difference in percentages of annual scale growth varied little between methods. Normality tests were performed similarly on the scale percentages. Because the percentages did not deviate greatly from the multivariate normal distribution, we assumed the data were multivariate normally distributed. Differences in percentages along the two axes were then tested using a Hotelling one-sample  $T^2$  test. Percentages for the two methods differed significantly ( $p \leq 0.003$ ) for all stocks, brood years, and ages except for brood-year 1981 ocean-age 4 fish from Quilcene National Fish Hatchery ( $p = 0.30$ ) and Fish Creek ( $p = 0.28$ ). Note that sample size from Quilcene National Fish Hatchery was small ( $n = 13$ ).

Mean measurements of annual increments of scale growth were greater for the INPFC method: 0.01–0.11 mm in the first year (1–9%), 0.05–0.13 mm in the second year (6–13%), 0.00–0.06 mm in the third year (0–14%), 0.20–0.50 mm in the fourth year (10–14%), and 0.04–0.15 mm in the last year (7–24%). Scales of Quilcene fish had greater differences between scale methods than scales of Fish Creek fish (Fig. 4).

Fig. 2. Fish length at each ocean age, or annulus, calculated from chum salmon scale measurements using the INPFC and Traditional methods. Circles equal means and bars are 95% confidence intervals of the mean. Sample size is in parentheses.

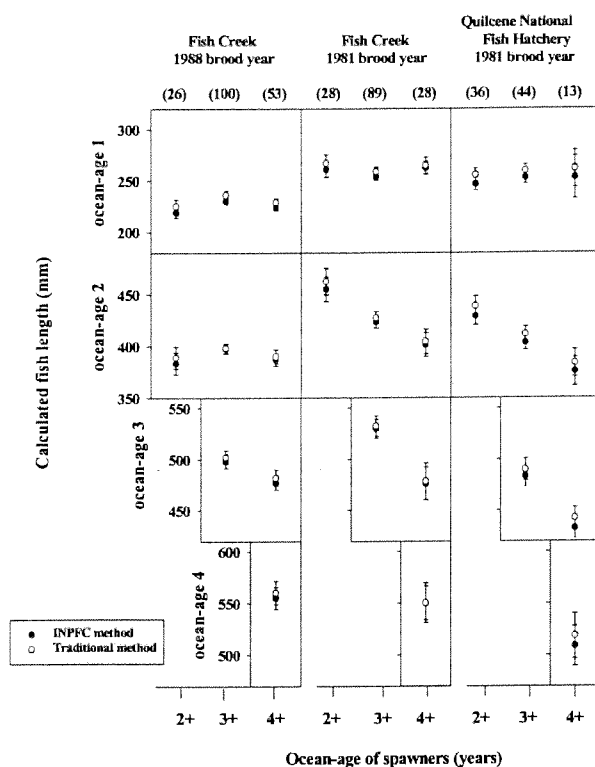


Fig. 3. Percentage of scale growth during each marine year for the INPFC method and Traditional method on scales of chum salmon. Circles are means and bars are 95% confidence interval of the mean. Sample size is in parentheses.

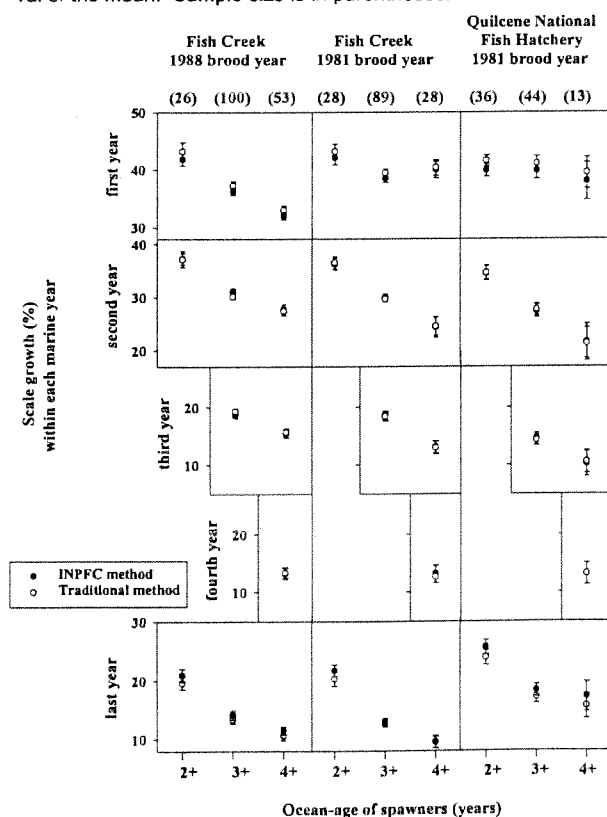
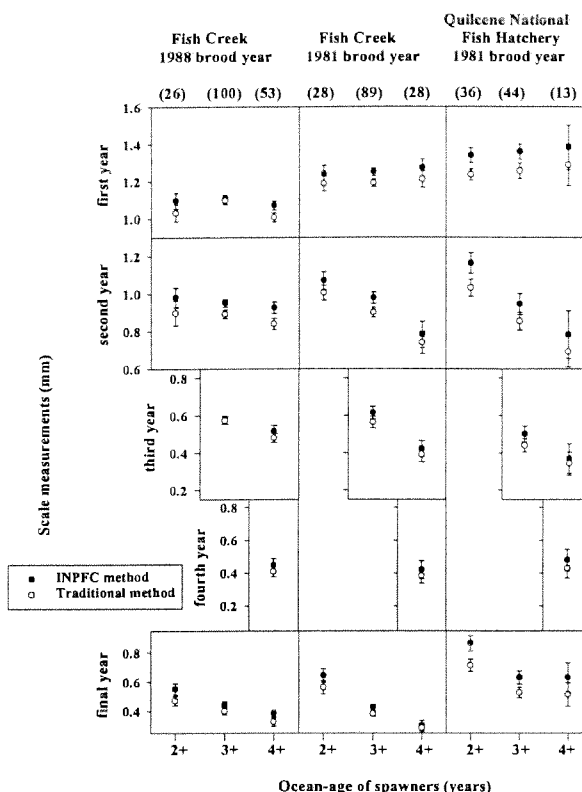


Fig. 4. Measurements of annual increments of growth for INPFC and Traditional methods on scales of chum salmon. Circles are means and bars are 95% confidence intervals of the mean. Sample size is in parentheses.



## DISCUSSION

The choice of scale method (position of the reference line on the scale) influenced the back-calculated fish lengths (BCFLs), percentages of annual scale growth, and scale measurements. Differences in the two methods were greater between stocks than between brood years or ages.

In other species, scale method also influenced scale measurements, circuli counts, and back-calculated fish lengths. For Lake Herring (*Leucichthys artedii*), Van Oosten (1928) found significant differences between BCFLs for the lateral-radial axis and antero-lateral axis (Traditional method), both between and within races. On scales of sockeye salmon smolts, scale radius and circuli counts differed between the longest axis, dorsal 20° radial axis, and ventral 20° radial axis (Clutter and Whitesel 1956). In northern pike (*Esox lucius*), scale radius varied between the anterior axis, lateral axis, and posterior axis (Casselman 1990).

Calculated lengths corresponded well with empirical lengths of immature chum salmon at sea (Carlson et al. 1998), except at ocean-age 1. Calculated lengths at ocean-age 1 were 22–44% shorter than the empirical lengths for both methods. Are larger fish being selected against after the first year at sea, or are we making an invalid comparison? We

question the validity of comparing BCFLs of single-stock fish to measured lengths of mixed-stock fish from the high seas because of variation in growth between stocks (Hile 1970; Helle 1984). Back-calculations could be validated using mark-recapture techniques on the high seas.

In studies validating Fraser-Lee BCFLs, lengths at earlier ages were commonly underestimated. For bluegill (*Lepomis macrochirus*), and bluegill X sunfish (*L. cyanellus*) hybrid, the low estimates of lengths at earlier ages were attributed to difficulties in recognizing the second annulus (Klumb and Bozek 1999). We were able to recognize the location of the annuli in our study. For rainbow trout (*O. mykiss*), the underestimates were attributed to the influence of the intercept as fish length increased (Davies and Sloane 1986). If we had used a larger intercept (*c*), the calculated lengths at ocean-age 1 would have been larger for INPFC and Traditional methods, but the difference between the methods would have decreased by only a few millimeters.

The Traditional method usually provided greater estimates of BCFLs at each ocean age (Fig. 2) than the INPFC method. In most cases, the Traditional method had larger additive percentages of scale growth at each consecutive annulus than the INPFC method. Because Fraser-Lee BCFLs are based on the addition of consecutive percentages of annual scale growth, the BCFLs were larger for the Traditional method at each ocean age.

## CONCLUSION

The selection of a particular scale method (orientation of line of measurement) for analyzing growth of chum salmon may significantly affect BCFLs, measured percentage of scale growth, and scale measurements. Although differences in mean BCFLs between the methods were statistically significant, the biological differences were small (~1 cm). These results support the need for standardization of a scale measurement method.

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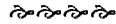
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## Digitized Scale and Otolith Microstructures as Correlates of Juvenile Pink Salmon Size

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Keywords: Pink salmon; Scale; Otolith; Microstructure; Growth

**Abstract:** The purpose of this study was to determine whether scale or otolith microstructures were more strongly related to fish growth. Scales and otoliths were sampled from 231 juvenile pink salmon (*Oncorhynchus gorbuscha*) collected from the marine waters of Southeast Alaska during two periods in 1993 and 1994. A computerized image analysis system was used to measure several periodic and non-periodic scale and otolith microstructures from each specimen. The measurements from each fish were compared with each other and with fish length using non-parametric correlation analysis and parametric regressions. As expected, growth of most scale and otolith microstructures was significantly positively correlated with fish growth. Scales and otoliths also portrayed recent marine growth (growth near the time of capture) more reliably than earlier marine growth (growth more distant from the time of capture). An unexpected result was that the number and width of periodic scale microstructures (circuli) were more strongly related to fish length than were the number and width of periodic otolith microstructures (increments). These results indicate that, at least for pink salmon, there is a tradeoff between the finer temporal resolution available from otolith increments (near daily) and the stronger correlation with fish length available from scale circulus measurements.

### INTRODUCTION

Given approximate proportionality between fish growth and the periodic features in its bony structures, the width of the most recently formed periodic structures should provide a measure of recent growth (Campana and Jones 1992). The use of scale circulus widths as a proxy for fish growth in Pacific salmon (*Oncorhynchus* spp.) has a historical and ongoing precedent; for example, the estimation of variability in natural mortality rates and environmental effects on fish growth (Clutter and Whitesel 1956; Healey 1982; Friedland et al. 1996; Walker et al. 1998). More recently, the collection and interpretation of otolith daily increments has been introduced (e.g., Stevenson and Campana [ed.] 1992). Campana and Neilson (1985) concluded that the width of otolith increments was generally proportional to fish growth. In pink salmon, otolith increment widths have been used as a proxy for growth rates to analyze environmental and experimental effects on fish growth (Mortensen and Carls 1995; Volk et al. 1995).

The availability of microcomputer digitizing technology provides a tool for comparing the proportionality of scale and otolith microstructures in relation to fish length. Microcomputer digitizing archi-

ture allows for the rapid measurement of many features from the microstructure of fish scales and otoliths in addition to the standard periodic microstructures such as scale circuli and otolith increments (Courtney 1997; Courtney and Mortensen in press). Measurements can be obtained from any area or distance of interest and at several different resolutions depending upon the magnification chosen. Once a desired protocol for feature extraction has been established, much of the process can also be automated with image analysis software (Courtney and Mortensen in press). The purpose of this study was to utilize available microcomputer digitizing technology to obtain a variety of periodic and non-periodic scale and otolith microstructure measurements at various resolutions in order to determine which microstructures were most strongly related to fish growth.

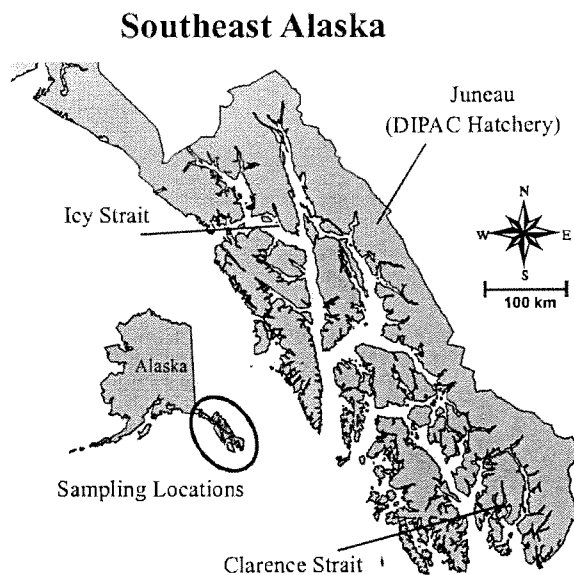
### MATERIALS AND METHODS

#### Field Collections

The National Marine Fisheries Service (NMFS) Auke Bay Laboratory has collected and maintained a time series of juvenile pink salmon scales and otoliths

from the marine waters of Southeast Alaska for the years 1993–1996 (Orsi, NMFS unpublished Cruise Reports 96-05 and 96-08). Juvenile pink salmon (*O. gorbuscha*) used in this study were captured with surface trawl-nets from Clarence Strait and Icy Strait, Alaska in 1993 and 1994 (Fig. 1). Two cruises were conducted each year, the first in early July (early-summer) and the second in early August (late-summer). Each cruise consisted of three to four nights of sampling in Clarence Strait followed by three to four nights of sampling in Icy Strait. In each region, six equally spaced stations were sampled each night along a transect bisecting the strait. Sampling was conducted with a Kodiak FRI pair trawl fished on the surface between the 27.5 m NOAA ship *John N Cobb* and a seine skiff. The surface trawl had a 6 m (horizontal) by 3 m (vertical) opening and was towed at 3.7 km/h (2 kn) for 10 minutes per set. Two sets were made at each station usually perpendicular to the transect line with one set in either direction roughly parallel to shore. Fishing was conducted primarily from dusk to dawn.

Fig. 1. Sampling locations for juvenile pink salmon in Icy Strait and Clarence Strait, Southeast Alaska.



All pink salmon captured were measured for fork length (tip of snout to fork in tail) on an electronic fish measuring board. Up to 50 juveniles per set were sub-sampled for scales and otoliths until as many as 300 fish were sampled from each region for each cruise for each year. A smear of scales was removed from the preferred region, as described by Bilton (1985), of each sub-sampled fish and placed between strips of acetate and stored in individual coin envelopes. The heads of each sub-sampled fish were removed and preserved in vials of 95% ethanol for later otolith retrieval.

## Scale and Otolith Processing

Juvenile pink salmon scales and otoliths selected for this study were further sub-sampled from those collected at sea. Up to 50 scales and otoliths were selected at random from each region (Icy Strait, and Clarence Strait) for each cruise (early-summer and late-summer) for both years (1993 and 1994) for a total of 231 samples.

Scale processing generally followed that of Courtney (1997). For each selected fish, a single scale was selected from among the smear of scales collected. The smear of scales was searched under magnification systematically from top to bottom and left to right. The first scale encountered with a clear first circulus (focus), an unbroken scale edge, and clear circuli from the focus to the edge was digitized (Fig. 2A).

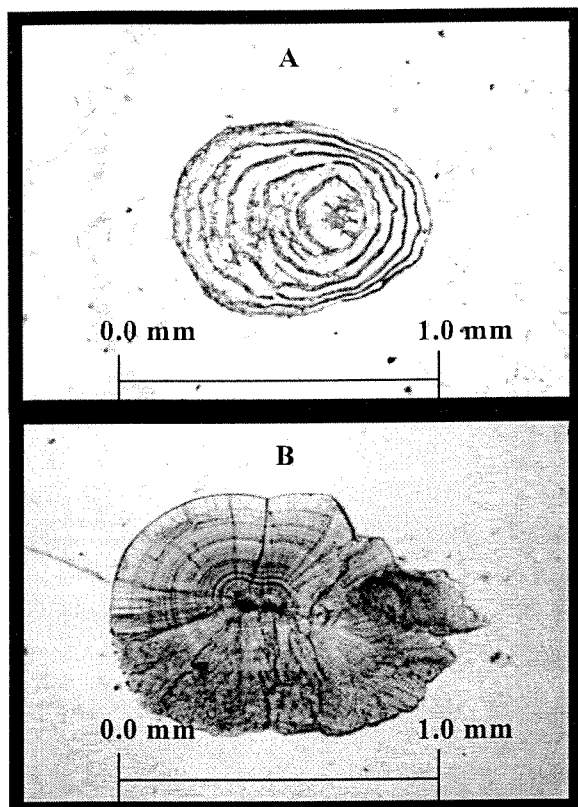
The left sagitta otolith of each selected fish was extracted from the head using the guillotine method described by Secor et al. (1992). The otolith was placed sulcus side down on a glass petrographic slide and partially immersed in a drop of thermoplastic cement (thermal resin) in a manner similar to that described by Secor et al. (1992). When the thermal resin hardened, it affixed the otolith to the slide and provided a bulwark around the otolith for grinding and polishing. Many of the pink salmon otoliths exhibited growth patterns that obscured the fine increments and gave the otolith an uncharacteristic shape. This type of otolith growth was consistent with the anomalous compositional pattern described as vaterite crystalline mineral structures in the otoliths of other species (Brown and Severin 1999). Before grinding, each mounted otolith was visually inspected under magnification for such anomalous growth. If the otolith exhibited this type of anomalous growth it was rejected. The surface of the otolith was rough ground to the primordium on 1,000 grit wet or dry silicon carbide paper on a rotating lap wheel and polished with 12,000 grit paper. The grinding process was repeated on the second side by reheating the thermal resin and flipping the otolith. Each otolith was ground along a plane extending from the primordium to the outside edge of the dorsal posterior quadrant (e.g., see Fig. 1 from Mortensen and Carls 1995). Care was taken to leave the dorsal posterior edge of the otolith intact and not to grind completely through the primordium (Fig. 2B).

Scale and otolith microstructures were digitized with two software specific computer programs (macros) written for image analysis software (Courtney and Mortensen in press.). One macro digitized scales while the other digitized otoliths. The image analysis software utilized a transmitted-light compound microscope, a video camera, and a personal computer equipped with a 486 processor, a 640 x 480 pixel



frame grabber board, a dual video monitor display and an electronic drawing pad and pen. The frame grabber board converted the black and white video input to a calibrated digital image which was output to the dual video monitor screen while the interactive program was run on the computer monitor screen. Scales were digitized at a magnification of 40x and otoliths at magnifications of 40x, 100x and 400x. The digitized measurements were automatically stored on a spreadsheet for analysis.

**Fig. 2.** A scale (A) and the left sagittal otolith (B) from the same 104.0 (mm) fork length juvenile pink salmon.



### Scale and Otolith Comparisons

Similar scale and otolith microstructures were grouped into two categories: non-periodic, and periodic. Non-periodic scale microstructure measurements included the area ( $\text{mm}^2$ ), focus area ( $\text{mm}^2$ ), major axis (mm) and minor axis (mm). Non-periodic otolith microstructure measurements included the area ( $\text{mm}^2$ ), major axis (mm), minor axis (mm), distance from primordium to marine entry (mm) and distance from marine entry to the outside edge of the otolith (mm). Periodic scale microstructure measurements included the number of circuli, the cumulative distance measured between circuli ( $\mu\text{m}$ ), and the mean distance per circulus ( $\mu\text{m}$ ). Periodic otolith microstructure measurements included the number of

increments, the cumulative distance measured between increments ( $\mu\text{m}$ ), and the mean distance per increment ( $\mu\text{m}$ ).

Two obvious outliers were revealed with scatter plots of all variables regressed against each other in SPLUS statistical software and were removed from the sample set. Many of the scale and otolith microstructure measurements had bimodal distributions as a result of sampling for fish during two periods (early-summer and late-summer) each year. Consequently, non-parametric methods were chosen for correlations of the overall growth of microstructures and fish length. The scale, otolith, and length measurements were compared using Spearman Rank non-parametric correlation analysis conducted with SAS statistical software.

Scale circulus counts, otolith increment counts, and cumulative widths between scale circuli and otolith increments were compared with fish length using parametric straight-line regressions. Scale circulus and otolith increment counts were normalized with the square root transformation as suggested by Zar (1984), for normalizing data consisting of counts. An examination of the regression residuals revealed an apparent increase in the magnitude of residuals with an increase in fish length, so the length data were transformed with the natural log to normalize the error. The cumulative widths between scale circuli and otolith increments were not transformed because their distributions were only slightly bimodal and the large sample size ( $n = 231$ ) was assumed to be of sufficient size to approximate a normal distribution. Standard statistical procedures could not be used to test for differences in the regression  $R^2$  values because scale circulus and otolith increment measurements from the same fish were not independent.

### Validation of Otolith Daily Increments

Thermally-induced hatchery otolith marks (thermal marks) were recovered from several of the fish captured from Icy Strait in 1993. The thermal marks identified the pink salmon as hatchery fish and uniquely identified their hatchery of origin (Hagen et al. 1995; Farley and Munk 1997; Courtney et al. 2000). All of the recovered thermal marks originated from Douglas Island Pink and Chum (DIPAC) hatchery in Juneau, Alaska (Fig. 1). Pink salmon start laying down increments after entering marine water and the entry event can be distinguished on the otolith by a distinct check (Volk et al. 1995). For the purposes of age validation, it was assumed that the dates of marine entry were the same for all DIPAC fish. Sampling in 1993 occurred during two periods, early-summer and late-summer, separated by about 30 days. The difference between the mean number of daily increments counted from each group of fish

(early-summer and late-summer) recovered from DIPAC was compared to the mean number of days between capture for each sampling period. The difference between the mean number of scale circuli counted from each group of fish (early-summer and late-summer) recovered from DIPAC was also compared to the mean number of days between capture for each sampling period. However, it was likely that scale formation did not begin at the same time as the marine entry check for fish recovered from DIPAC because scale formation begins at an indeterminate time following marine entry for pink salmon in south-eastern Alaska.

## RESULTS

### Otolith Daily Increment Validation

Sixteen thermally marked DIPAC otoliths were recovered from Icy Strait (Fig. 1): one in 1994, seven from the early-summer sampling period in 1993, and eight from the late-summer sampling period in 1993 (Table 1). The average day of the year of capture was computed for the thermally marked fish recovered from each sampling period in 1993 and the elapsed time between the capture of these two periods was calculated as 33.1 days (Table 1). Increment counts were only obtained from six marked otoliths from the early sampling period and three otoliths from the late sampling period. The difference between the average number of increments counted for each period was 32.2 (Table 1). Therefore, the number of increments added between periods agreed with the number of days between capture for the two groups of marked fish to within one day. The difference between the average number of scale circuli counted for each period was 4.5 (Table 1).

**Table 1.** Mean number of otolith increments, scale circuli, days between capture, and mean fish length of 15 thermally marked juvenile pink salmon recovered in 1993,  $\pm 1$  SD. Sample size is given in parentheses.

| Period       | Otolith increments     | Scale circuli         | Number of days        | Fish length (mm)        |
|--------------|------------------------|-----------------------|-----------------------|-------------------------|
| Early-summer | 47.8 $\pm$ 7.4<br>(6)  | 7.3 $\pm$ 1.1<br>(7)  | 181 $\pm$ 0.38<br>(7) | 113.3 $\pm$ 10.8<br>(7) |
| Late-summer  | 80.0 $\pm$ 16.0<br>(3) | 11.8 $\pm$ 1.9<br>(6) | 214 $\pm$ 1.5 (8)     | 147.0 $\pm$ 16.9<br>(8) |
| Difference   | 32.2                   | 4.5                   | 33.1                  | 33.7                    |

### Scale and Otolith Comparisons

After the beginning of scale formation, both fish length and the number of otolith increments generally increased with the number of scale circuli (Table 2). Fish length and many of the scale and otolith measurements were bimodal. Consequently, the overall growth comparisons were performed non-parametrically. The majority of the non-parametric

**Table 2.** The average number of otolith increments and mean fish length corresponding to the number of scale circuli for 231 juvenile pink salmon.

| Scale circuli | Mean number of increments | Mean length (mm) | Sample size |
|---------------|---------------------------|------------------|-------------|
| 2             | 43                        | 79.0             | 2           |
| 3             | 43                        | 86.0             | 1           |
| 4             | 53                        | 93.4             | 13          |
| 5             | 57                        | 96.6             | 30          |
| 6             | 54                        | 103.8            | 39          |
| 7             | 56                        | 109.9            | 31          |
| 8             | 63                        | 121.1            | 21          |
| 9             | 66                        | 122.3            | 21          |
| 10            | 71                        | 129.7            | 22          |
| 11            | 72                        | 137.0            | 22          |
| 12            | 75                        | 140.9            | 19          |
| 13            | 86                        | 149.3            | 6           |
| 14            | 78                        | 154.7            | 3           |
| 15            | 61                        | 150.0            | 1           |

correlations were either significant ( $p \leq 0.05$ ), or highly significant ( $p \leq 0.001$ ; Tables 3, 4, and 5). However, as a result of the large number of correlations performed, the individual correlations had a higher likelihood of being significant by chance alone than was reported by the  $p$ -values. Therefore, the significant correlation coefficients were used only as a relative measure of the strength of each microstructure's correlation to all of the others. Significant correlation coefficients  $|r| \geq 0.7$  were considered very strong, significant correlation coefficients  $0.5 \leq |r| < 0.7$  were considered moderately strong, and significant correlation coefficients  $|r| < 0.5$ , or non-significant correlations were considered poor.

In general, scale microstructure measurements were more highly correlated with each other and with fish length (Table 3) than were otolith microstructure measurements (Table 4), and non-periodic scale and otolith microstructures were more highly correlated with each other (Table 5A) than were periodic scale and otolith microstructures (Table 5B). In particular, most non-periodic scale and otolith microstructure measurements were strongly correlated ( $r \geq 0.7$ ) with each other, with other scale and otolith microstructure measurements, and with fish length (Tables 3, 4, and 5). Exceptions were microstructures representing the early development of scales (focus area) and otoliths (distance from primordium to marine entry), which were poorly ( $|r| < 0.5$ ) correlated with each other, with other scale and otolith measurements, and with fish length (Tables 3, 4, and 5).

Most periodic scale and otolith microstructure measurements were also strongly ( $r \geq 0.7$ ) or moderately ( $0.5 \leq r < 0.7$ ) correlated with each other, with other scale and otolith measurements, and with fish length (Tables 3, 4, and 5). Exceptions were the mean distance per scale circuli and the mean distance

**Table 3.** Scale microstructure measurements and correlation coefficients from 231 juvenile pink salmon.

A. Mean, standard deviation, and coefficient of variation of fish length and digitized scale measurements from 231 fish.

| Statistic          | Fish length (mm) | Scale area (mm <sup>2</sup> ) | Major axis length (mm) | Minor axis length (mm) | Number of circuli | Cumulative circuli width (μm) | Focus area (μm <sup>2</sup> ) | Distance per circuli (μm) |
|--------------------|------------------|-------------------------------|------------------------|------------------------|-------------------|-------------------------------|-------------------------------|---------------------------|
| Mean               | 117              | 0.661                         | 0.972                  | 0.865                  | 7.97              | 362.2                         | 38.8                          | 47.1                      |
| Standard deviation | 19.1             | 0.301                         | 0.231                  | 0.194                  | 2.70              | 97.6                          | 10.1                          | 7.38                      |
| CV (Percent)       | 16.3             | 45.5                          | 23.8                   | 22.5                   | 33.9              | 26.9                          | 26.1                          | 15.6                      |

B. Spearman rank correlation coefficients (*r*) of fish length and digitized scale measurements from 231 fish.

| Scale Parameters                      | Fish length | Scale area | Major axis length | Minor axis length | Number of circuli | Cumulative circuli width | Focus area | Distance per circuli |
|---------------------------------------|-------------|------------|-------------------|-------------------|-------------------|--------------------------|------------|----------------------|
| Fish length <sup>a</sup>              | 1           |            |                   |                   |                   |                          |            |                      |
| Scale area <sup>a</sup>               | 0.918**     | 1          |                   |                   |                   |                          |            |                      |
| Major axis length <sup>a</sup>        | 0.911**     | 0.989**    | 1                 |                   |                   |                          |            |                      |
| Minor axis length <sup>a</sup>        | 0.900**     | 0.981**    | 0.950**           | 1                 |                   |                          |            |                      |
| Number of circuli <sup>a</sup>        | 0.903**     | 0.912**    | 0.911**           | 0.884**           | 1                 |                          |            |                      |
| Cumulative circuli width <sup>a</sup> | 0.920**     | 0.948**    | 0.951**           | 0.920**           | 0.931**           | 1                        |            |                      |
| Focus area <sup>c</sup>               | 0.204*      | 0.276**    | 0.259**           | 0.283**           | 0.063             | 0.247**                  | 1          |                      |
| Distance per circuli <sup>c</sup>     | -0.491**    | -0.458**   | -0.451**          | -0.447**          | -0.697**          | -0.410**                 | 0.317**    | 1                    |

\* Significant correlation,  $p \leq 0.05$ \*\* Highly significant correlation,  $p \leq 0.001$ <sup>a</sup> Relatively strong correlation,  $|r| \geq 0.7$ <sup>b</sup> Moderately strong correlation,  $0.5 \leq |r| < 0.7$ <sup>c</sup> Poor correlation,  $|r| < 0.5$ , or non-significant.**Table 4.** Otolith microstructure measurements and correlation coefficients from 231 juvenile pink salmon.

A. Mean, standard deviation, and coefficient of variation of fish length and digitized otolith measurements from 231 fish.

| Statistic          | Fish length (mm) | Otolith area (mm <sup>2</sup> ) | Major axis length (mm) | Minor axis length (mm) | Marine entry to edge (mm) | Number of increments | Cumulative increment width (μm) | Distance per increment (μm) | Primordia to marine entry (mm) |
|--------------------|------------------|---------------------------------|------------------------|------------------------|---------------------------|----------------------|---------------------------------|-----------------------------|--------------------------------|
| Mean               | 117              | 0.978                           | 1.22                   | 1.12                   | 0.201                     | 62.6                 | 179                             | 2.92                        | 0.217                          |
| Standard deviation | 19.1             | 0.253                           | 0.170                  | 0.146                  | 0.0566                    | 16.0                 | 50.0                            | 0.430                       | 0.0425                         |
| CV (Percent)       | 16.3             | 25.9                            | 14.0                   | 13.0                   | 28.1                      | 25.6                 | 27.9                            | 14.7                        | 19.6                           |

B. Spearman rank correlation coefficients (*r*) of fish length and digitized otolith measurements from 231 fish.

| Parameter                                 | Fish length | Otolith area | Major axis length | Minor axis length | Marine entry to edge | Number of increments | Cumulative increment width | Distance per increment | Primordia to marine entry |
|-------------------------------------------|-------------|--------------|-------------------|-------------------|----------------------|----------------------|----------------------------|------------------------|---------------------------|
| Fish length                               | 1           |              |                   |                   |                      |                      |                            |                        |                           |
| Otolith area <sup>a</sup>                 | 0.889**     | 1            |                   |                   |                      |                      |                            |                        |                           |
| Major axis length <sup>a</sup>            | 0.879**     | 0.972**      | 1                 |                   |                      |                      |                            |                        |                           |
| Minor axis length <sup>a</sup>            | 0.870**     | 0.966**      | 0.917**           | 1                 |                      |                      |                            |                        |                           |
| Marine entry to edge <sup>a</sup>         | 0.771**     | 0.782**      | 0.786**           | 0.763**           | 1                    |                      |                            |                        |                           |
| Number of increments <sup>b</sup>         | 0.537**     | 0.521**      | 0.510**           | 0.500**           | 0.599**              | 1                    |                            |                        |                           |
| Cumulative increment width <sup>a,b</sup> | 0.701**     | 0.699**      | 0.703**           | 0.678**           | 0.779**              | 0.837**              | 1                          |                        |                           |
| Distance per increment <sup>c</sup>       | 0.364**     | 0.401**      | 0.422**           | 0.405**           | 0.426**              | -0.112               | 0.403**                    | 1                      |                           |
| Primordia to marine entry <sup>c</sup>    | -0.002      | 0.024        | -0.011            | 0.020             | -0.320**             | -0.258**             | -0.309**                   | -0.188*                | 1                         |

\* Significant correlation,  $p \leq 0.05$ \*\* Highly significant correlation,  $p \leq 0.001$ <sup>a</sup> Relatively strong correlation,  $|r| \geq 0.7$ <sup>b</sup> Moderately strong correlation,  $0.5 \leq |r| < 0.7$ <sup>c</sup> Poor correlation,  $|r| < 0.5$ , or non-significant.

**Table 5.** Correlation coefficients of non-periodic and periodic scale and otolith microstructures.**A. Spearman rank correlation coefficients (*r*) of non-periodic scale and otolith microstructures.**

| Scale parameters                 | Otolith parameters          |                                  |                                  |                                     |                                        |
|----------------------------------|-----------------------------|----------------------------------|----------------------------------|-------------------------------------|----------------------------------------|
|                                  | Otolith area <sup>a,c</sup> | Major axis length <sup>a,c</sup> | Minor axis length <sup>a,c</sup> | Marine entry to edge <sup>a,c</sup> | Primordia to marine entry <sup>c</sup> |
| Scale area <sup>a,c</sup>        | 0.854**                     | 0.843**                          | 0.832**                          | 0.731**                             | -0.004                                 |
| Major axis length <sup>a,c</sup> | 0.847**                     | 0.837**                          | 0.825**                          | 0.726**                             | -0.016                                 |
| Minor axis length <sup>a,c</sup> | 0.838**                     | 0.824**                          | 0.819**                          | 0.702**                             | 0.008                                  |
| Focus area <sup>c</sup>          | 0.158*                      | 0.157*                           | 0.185*                           | 0.109                               | 0.098                                  |

**B. Spearman rank correlation coefficients (*r*) of periodic scale and otolith microstructures.**

| Scale parameters                         | Otolith parameters                          |                                             |                                     |
|------------------------------------------|---------------------------------------------|---------------------------------------------|-------------------------------------|
|                                          | Number of otolith increments <sup>b,c</sup> | Cumulative increment width <sup>a,b,c</sup> | Distance per increment <sup>c</sup> |
| Number of scale circuli <sup>a,b,c</sup> | 0.508**                                     | 0.705**                                     | 0.421**                             |
| Cumulative circuli width <sup>b,c</sup>  | 0.481**                                     | 0.662**                                     | 0.391**                             |
| Distance per circuli <sup>c</sup>        | -0.364**                                    | -0.494**                                    | -0.280**                            |

\* Significant correlation,  $p \leq 0.05$ \*\* Highly significant correlation,  $p \leq 0.001$ <sup>a</sup> Relatively strong correlation,  $|r| \geq 0.7$ <sup>b</sup> Moderately strong correlation,  $0.5 \leq |r| < 0.7$ <sup>c</sup> Poor correlation,  $|r| < 0.5$ , or non-significant.

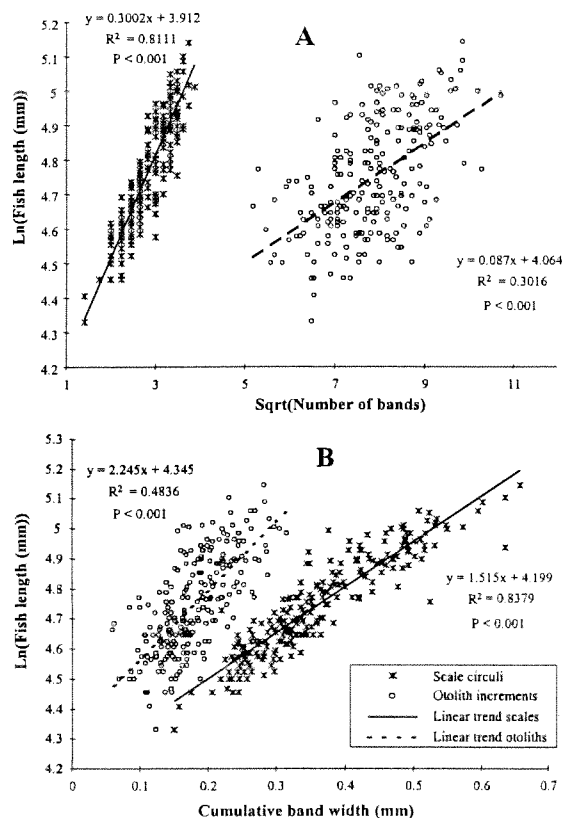
per otolith increment which were poorly correlated ( $|r| < 0.5$ ) with most other scale and otolith measurements, and with fish length (Tables 3, 4, and 5). In addition, the mean distance per scale circuli was strongly negatively correlated ( $r = -0.7$ ) with the number of scale circuli (Table 3).

Parametric regression analysis revealed significant linear relationships ( $p < 0.001$ ) for the natural log of fish length with the square root of both the number of scale circuli and the number of otolith increments. The number of scale circuli explained 81 percent of the variation in fish length ( $R^2 = 81\%$ ), while the number of otolith increments explained only 30 percent of the variation in fish length ( $R^2 = 30\%$ ; Fig. 3A). There was a similar relationship for the cumulative width measurements from scales and otoliths regressed upon the natural log of fish length. Both regressions were significant ( $p < 0.001$ ), but scale circulus widths explained a higher proportion ( $R^2 = 84\%$ ) of the variation in fish length than otolith increment widths ( $R^2 = 48\%$ ; Fig. 3B).

## DISCUSSION

### Scale and Otolith Proportionality

The purpose of this study was to compare scale and otolith microstructures for estimating growth from periodic and non-periodic hard part measurements. In general, the results of this study agree with previous findings in that the width measurements of periodic scale and otolith microstructures were significantly proportional to fish length (Weisberg 1993;

**Fig. 3.** Parametric regressions of (A), number of scale circuli and number of otolith increments on fish length, and (B), cumulative scale circuli and otolith increment width on fish length.

Fukuwaka 1998). In addition, non-periodic structures representing more recent growth (nearer the time of capture) were more highly correlated with each other, with other scale and otolith microstructures, and with fish length than were structures representing earlier growth (growth more distant from the time of capture).

The authors expected that periodic otolith microstructures (increments) would provide better proxies for fish growth than the periodic structures of scales (circuli) because the resolution of otolith increment deposition is higher (near daily) than that of scale circuli (one circulus forms every four to eight days). However, the widths and number of periodic otolith increments in this study were more poorly correlated with each other, with other otolith and scale microstructures and with fish length than were the widths and number of periodic scale circuli (Tables 3, 4, and 5). In particular, cumulative width measurements of scale circuli explained 84 percent of the variation in fish length ( $R^2 = 84$ ,  $p < 0.001$ ; Fig. 3A), while cumulative width measurements of otolith increments explained only 48 percent of the variation in fish length ( $R^2 = 48$ ,  $p < 0.001$ ; Fig. 3B).

On the one hand, the relatively strong relationships found here between periodic scale microstructures and fish length, may imply that somatic growth in pink salmon is more strongly related to periodic scale microstructures than to periodic otolith microstructures. Campana and Jones (1992) and Neilson (1992) have suggested that backcalculation from otolith increments can suffer from a number of logistical and theoretical constraints, including the uncoupling of somatic and otolith growth and the appearance of nondaily increments. The use of periodic boney structures as a proxy for fish growth are necessarily subject to the same constraints. For salmonids in particular, Wright et al. (1990) described the uncoupling of somatic and otolith growth in some Atlantic salmon (*Salmo salar*) parr. Bradford and Geen (1987) suggested that the conservative nature of otolith growth compared to fish growth in juvenile chinook salmon (*O. tshawytscha*) may preclude very detailed analyses of juvenile chinook growth rates based on otolith microstructure. If backcalculation is used, then there are also those additional problems encountered when backcalculating growth from any periodic boney structure (Campana 1990; Pierce et al. 1996).

On the other hand, the relatively weak proportionality of periodic otolith microstructures to fish length may have resulted from resolution-related effects (Neilson 1992). Scale circuli were spaced more widely apart (mean 47.1  $\mu\text{m}$ ; Table 3) than otolith increments (mean 2.92  $\mu\text{m}$ ; Table 4) and were more clearly defined; consequently, a lower magnification (40x) was required to resolve scale circuli, than to

discriminate between otolith increments (400x), and it was relatively less difficult to detect and measure scale circuli than otolith increments. With the scale digitizing macro used in this study, it was possible to repeatedly detect nearly the same number of circuli along a measurement axis (Courtney and Mortensen in press). With the otolith digitizing macro used in this study it was more difficult to consistently detect the same number of increments along a measurement axis (Courtney and Mortensen in press).

Furthermore, the wide spacing of scale circuli made it possible to view a whole image of a juvenile pink salmon scale at a resolution high enough to discriminate between scale circuli on a single video display. This resulted in the establishment of a consistent measurement axis from one scale to the next from which to extract periodic microstructure measurements.

In contrast, the higher magnification required to discriminate between otolith increments made it impossible to view a whole image of a pink salmon otolith at a high enough resolution to resolve between otolith increments on a single video display. Consequently, multiple high resolution images on the video display were required to extract otolith increment measurements from a single otolith and this made it more difficult to establish a consistent digitizing axis from one otolith to the next (Courtney and Mortensen in press). These results occurred despite the authors' use of the latest image analysis technology and their best efforts to develop an otolith digitizing protocol that was comparable with protocols already established for scale digitizing (Courtney 1997; Courtney and Mortensen in press).

### Scale and Otolith Periodicity

The assumptions underlying the use of periodic feature width measurements as a proxy for instantaneous growth rate are the same as those for general growth backcalculation: (a) the frequency of formation of the periodic feature is constant, and (b) the distance between consecutive features is proportional to fish growth (Campana and Jones 1992). For the purposes of this study it has been assumed that the formation of periodic otolith (increments) and scale (circuli) microstructures was constant, but this is a simplifying assumption at best, and needs further investigation. The daily periodicity of otolith increment formation has been documented in over 30 species (e.g., Campana and Neilson 1985). However, Volk et al. (1995) described the presence of indistinguishable daily and sub-daily increments at magnifications as high as 2000x in the sagitta otoliths of juvenile pink salmon and validated these findings with electron scanning microscopy. A magnification of 400x was used in this study in an attempt to coalesce

the sub-daily bands documented by Volk et al. (1995) into daily bands.

Campana (1992) suggests that 400x is an appropriate magnification for the examination of rapidly growing otoliths with width measurements between increments greater than or equal to one to two micrometers. The average width between otolith increments visible at 400x in this study was 2.9  $\mu\text{m}$  (Table 4). The validated periodicity of pink salmon otolith increment deposition (visible at 400x magnification) in this study was near daily when averaged over a one-month period (Table 1). However, the marked fish were only recovered from two sampling periods and average periodicity does not necessarily imply that the daily periodicity of increment formation was constant. Furthermore, the average periodicity reported here might be inaccurate because of the small sample size (a total of 15 thermally marked individuals with only 3 fish in the smallest sample group), and more individuals need to be examined.

The periodicity of scale circulus formation remains unclear. Scale formation in southeastern Alaska pink salmon is thought to occur as juvenile fish leave the near-shore marine environment. In British Columbia, juvenile pink salmon emigration from the near-shore environment occurs approximately 40 days after marine entry (Parker 1964, 1965, 1968), which is consistent with the number of otolith increments (43) found in this study for fish near scale formation (fish with 2 or 3 circuli; Table 1). In the coastal northern Pacific, juvenile pink salmon captured on the surface in seine and trawl nets between June 23 and September 10 during the years 1962–1965 averaged 60 to 80 mm fork length when scale formation began (Pearson 1966) which is also consistent with the lengths (mean length  $\geq 79.0$  mm) found in this study for fish near scale formation (Table 1). In the coastal northern Pacific, Pearson (1966) found that pink salmon scale formation began on or after June 25 and by September 10 averaged 17.4 circuli. That is, the population gained an average of 17.4 circuli in 77 days or approximately 1 circulus every 4.4 days. In this study, the average periodicity of scale circulus deposition, for pink salmon recovered from DIPAC, was 4.5 circuli over an average of 33.1 days, or one circulus every 7.4 days (Table 1). However, recovered DIPAC hatchery pink salmon, like wild pink salmon in southeastern Alaska, begin scale formation at an indeterminate time after marine entry and it is possible that the 16 hatchery fish recovered in this study did not begin scale formation at the same time.

## CONCLUSIONS

The results of this study agree with previous findings in that the width measurements of periodic

scale and otolith microstructures were significantly proportional ( $p < 0.001$ ) to fish length. As expected, non-periodic microstructures representing recent life history (near the time of capture) or that integrated all of a fish's life history were generally more strongly correlated to fish length than were microstructures representing earlier growth (life history more distant from the time of capture). An unexpected result was that the periodic structures of scales were more strongly related to fish length than were the periodic structures of otoliths. We had assumed that the higher resolution available from periodic otolith microstructures would provide for a stronger relationship between periodic otolith microstructures and fish length. This creates an apparent trade-off between the higher resolution available from periodic otolith microstructures, and the higher proportionality with fish length of periodic scale microstructures. This trade-off should be considered before choosing which structure to use as a proxy for recent growth. In addition, the assumption of constant periodicity in periodic pink salmon scale and otolith microstructures required to obtain these results needs further examination.

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## Variations in Muscle Lipid Content of High-Seas Chum and Pink Salmon in Winter

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Key words: Lipid, high-seas salmon, chum salmon, pink salmon, fatty acid, winter, trophic condition

**Abstract:** The potential use of lipids for estimating trophic condition of high-seas chum, *Oncorhynchus keta*, and pink salmon, *O. gorbuscha*, was evaluated by examining variations in total lipid content and lipid classes in the white muscle during the winter. Total lipids of both species were low and the total lipid content of the white muscle of pink salmon varied by capture location. Significant differences were observed in the proportions of 22:6n3 (docosahexaenoic acid) in the neutral lipids, and of 22:6 and 18:1n9 (elaidic acid) in the polar lipids. As the total lipid content decreased, the proportions of 22:6n3 and 18:1n9 increased and decreased respectively. The low lipid levels and the changes in fatty acids profiles suggest that chum and pink salmon are starving in winter.

### INTRODUCTION

All animals require dietary lipids for metabolic energy and the synthesis of cell membranes. In carnivorous fish like salmonids, which have a limited ability to utilize carbohydrates as an energy source, dietary lipids play a more important role in providing energy and in sparing dietary protein (Watanabe 1982). Despite the common use of biochemical techniques to assess growth and nutrition of fish species since the 1980s, particularly salmonids (Idler and Bitners 1958; Fukuda et al. 1986; Nakano 1988; Shearer et al. 1994), surprisingly little is known about lipid changes in high-seas salmon. Azuma et al. (1998) examined growth characteristics of chum, *Oncorhynchus keta*, pink, *O. gorbuscha*, and sockeye, *O. nerka*, salmon caught on the high-seas and reported the content of triacylglycerol in the muscle of the fish.

Winter in the North Pacific Ocean may be stressful for salmon because water temperatures are low and there is little food available. As an energy source for metabolism, lipids play an important role during periods of stress, especially starvation in fish. Yet there is no information on the lipid contents and fatty acid profiles of chum and pink salmon in winter. Therefore, we examined the total lipid content, lipid classes, and fatty acid composition in the white muscle of chum and pink salmon from the high-seas to

gain information on their feeding condition and energy reserves at that season.

### MATERIAL AND METHODS

A total of 80 salmon (10 chum and 70 pink salmon), was captured from the eastern North Pacific Ocean (ENPO; 45°N, 179°W), from two stations in the western North Pacific Ocean (WNPO; 45°N, 165°E and 45°N, 160°E) and from the Gulf of Alaska (46°N, 168°W) by the research vessel *Kaiyo maru* in January 1996 (Ueno et al. 1997) and February 1998 (Nagasawa 1999) (Table 1). For comparative purposes, a total of 53 salmon (25 chum and 28 pink salmon), was captured in the Gulf of Alaska (52°N, 145°W) by the research vessel *Oshoro maru* in July of 1998 for use as summer-season reference samples (Table 1). Fish were caught with gill net or trawl net and measured fork length (cm) and body weight (g) for computation of the condition factor (fork length (cm)<sup>3</sup>/body weight (g) x 1,000). The white muscle tissue for lipid analysis was taken from the lateral part just behind the head. The tissue samples were frozen at -80°C until analyzed. Total lipids in the white muscle were extracted with chloroform/methanol and measured gravimetrically (Bligh and Dryer 1959), separated into polar lipid and neutral lipid fractions with Sep-Pak (Waters Co., MS, U.S.A.), and measured gravimetrically (Juaneda and

**Table 1.** Biological characteristics of chum and pink salmon used in this study. Values are mean and (S.D.).

| Species     | Maturity | Area                        | Location    | Date         | No. of Fish | Fork Length (cm) | Body weight (g) | Condition Factor |
|-------------|----------|-----------------------------|-------------|--------------|-------------|------------------|-----------------|------------------|
| Chum salmon | Immature | Eastern North Pacific Ocean | 45°N, 179°W | 21 Feb. 1998 | 10          | 35.4(1.2)        | 428 (63)        | 9.6 (0.7)        |
|             | Immature | Gulf of Alaska              | 52°N, 145°W | 8 July 1998  | 25          | 51.4 (3.7)       | 1,679 (452)     | 12.1 (0.7)       |
| Pink salmon | Immature | Western North Pacific Ocean | 45°N, 165°E | 10 Feb. 1998 | 10          | 28.9 (1.9)       | 216 (40)        | 9.4 (0.3)        |
|             | Immature | Western North Pacific Ocean | 45°N, 160°E | 11 Jan. 1996 | 20          | 23.8(1.8)        | 123 (32)        | 8.9 (0.7)        |
|             | Immature | Gulf of Alaska              | 46°N, 168°W | 18 Jan. 1996 | 40          | 25.1(1.8)        | 138 (32)        | 8.5 (0.7)        |
|             | Mature   | Gulf of Alaska              | 52°N, 145°W | 8 July 1998  | 28          | 49.3 (2.6)       | 1,602 (368)     | 13.1 (1.5)       |

Condition factor = (Fork length (cm)<sup>3</sup>/Body weight (g)) × 1,000

Rocquelin 1985). Each of the polar and neutral lipids was dissolved in 2 ml of absolute methanol containing 2N of potassium hydroxide and saponified at 80°C for 10 min. The non saponifiable material was then removed by an initial petroleum ether extraction of the alkaline saponification mixture and discarded. Fatty acids were converted to their methyl esters by refluxing for 1 hr in 5% HCl-methanol solution at 100°C and the fatty acid methyl esters were extracted with hexane (Ichihara *et al.* 1996). The fatty acid compositions were analyzed with Hewlett-Packard model 6890 gas chromatography (Hewlett-Packard Co., WA, USA) on PUFA capillary column (Supelco Inc., PA, USA). A flame ionization detector was employed to detect mass peaks, and peak areas were integrated electronically with Hewlett-Packard GC ChemStation Rev. A.03.05 (Hewlett-Packard Co., WA, USA); % by weight was estimated from peak areas of each fatty acid. The resulting values were tested for significant differences using the Student's *t*-test.

A short hand designation for fatty acids was used throughout where the carbon number identified the position of the first double bond counting from the methyl end. The first number identified the number of carbon, the second number, the number of double bonds and last number the position of the double bond.

## RESULTS

### Total Lipid Content

#### *Chum salmon*

Total lipid content in chum salmon captured in February 1998 in the ENPO (45°N, 179°W) was low in white muscle (< 1.7%, mean = 1.1%). Total lipid contents in the white muscle of chum salmon caught in the Gulf of Alaska (52°N, 145°W) in July of 1998 was high (< 18.6%, mean = 12.3%). Polar lipids in the white muscle were unchanged in winter (mean = 0.7%) and summer (mean = 0.9%), but neutral lipids varied (mean = 0.3% in winter and 11.4% in summer) (Table 2, Fig. 1).

#### *Pink salmon*

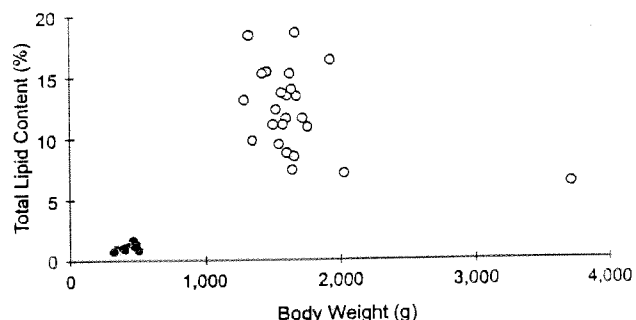
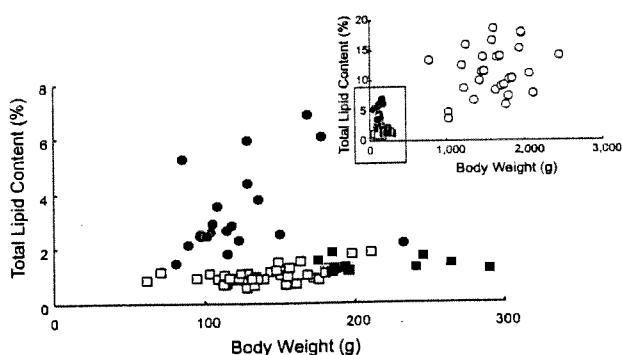
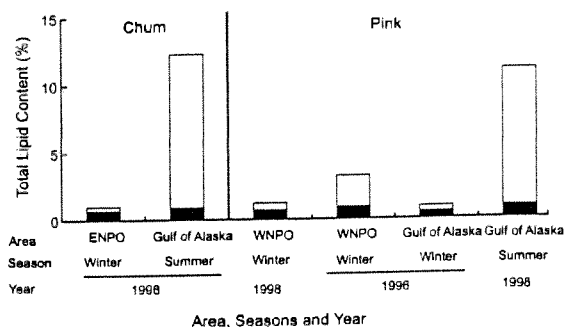
Total lipid content in pink salmon captured in WNPO (45°N, 165°E), was also low in white muscle (< 1.7%, mean = 1.4%) (Table 2). Total white muscle lipid content in pink salmon captured in January 1996 in WNPO (45°N, 160°E) (< 6.9%, mean = 3.3%) was significantly higher ( $p < 0.001$ ) than in pink salmon captured in the Gulf of Alaska (46°N, 168°W) (< 1.8%, mean = 1.0%) in the winter of 1996 (Table 2). The lipid contents were correlated with body weight (Fig. 2). As in chum salmon, total lipid contents in pink salmon captured in July of 1998 in the Gulf of Alaska (52°N, 145°W) was also high in white muscle (< 18.5%, mean = 11.3%). The lipid contents were correlated with body weight (Figs. 2 and 3). Polar lipids in the white muscle were unchanged in winter and summer, but neutral lipids varied seasonally (Table 2, Fig. 3) as in chum salmon.

### *Composition of Fatty Acids*

Eighteen fatty acids were identified in all samples of chum and pink salmon (Tables 3, 4, and 5). In addition, we were able to resolve some minor unidentified fatty acids and an unknown substance. Of the neutral lipids in summer samples of chum and pink salmon, 16:0, 18:1n9, 20:1n11, 20:5n3, 22:1n11 and 22:6n3 were present in significant amounts. Among polar lipids from summer sampled chum and pink salmon, 16:0, 18:1n9, 20:5n3 and 22:6n3 were also present in significant amounts. There was no difference between species in the more abundant fatty acids present in winter and summer samples. However, a significant seasonal difference ( $p < 0.05$ ) was observed in the proportion of 22:6n3 among neutral lipids of chum (Fig. 4), and pink salmon (Fig. 5) and 18:1n9 among polar lipids of chum salmon. As the total lipid content decreased, the proportion of 22:6n3 increased among neutral lipids, and 22:6n3 and 18:1n9 increased and decreased respectively among polar lipids. In pink salmon, significant differences ( $p < 0.05$ ) in the proportion of 22:6n3 were observed in both neutral lipids and polar lipids fatty acid composition between the winter and summer samples (Tables 4 and 5).

**Table 2.** Total lipid (TL), polar lipid (PL) and neutral lipid (NL) contents in the white muscle of chum and pink salmon caught in the North Pacific Ocean in the winter of 1996 and 1998, and the summer of 1998. Values are mean and (S.D.)

| Species     | Maturity | Area                        | Location    | TL(%)      | PL (%)    | NL (%)    |
|-------------|----------|-----------------------------|-------------|------------|-----------|-----------|
| Chum salmon | Immature | Eastern North Pacific Ocean | 45°N, 179°W | 1.1 (0.3)  | 0.7 (0.1) | 0.3 (0.2) |
|             | Immature | Gulf of Alaska              | 52°N, 145°W | 12.3 (3.5) | 0.9 (0.3) | 11.4(3.4) |
| Pink salmon | Immature | Western North Pacific Ocean | 45°N, 165°E | 1.4 (0.2)  | 0.7 (0.1) | 0.5 (0.2) |
|             | Immature | Western North Pacific Ocean | 45°N, 160°E | 3.3(0.3)   | 0.9(0.2)  | 2.3(1.3)  |
|             | Immature | Gulf of Alaska              | 46°N, 168°W | 1.0(0.4)   | 0.5(0.1)  | 0.4(0.2)  |
|             | Mature   | Gulf of Alaska              | 52°N, 145°W | 11.3 (4.1) | 0.9(0.3)  | 10.2(4.0) |

**Fig. 1.** Percentage of total lipid content in the white muscle of chum salmon of various sizes (body wt.) caught in the western North Pacific Ocean in winter (solid circles, 45°N, 179°W) and the Gulf of Alaska in summer, 1998 (open circles, 52°N, 145°W).**Fig. 2.** Percentage of total lipid content in the white muscle of pink salmon of various sizes (body wt.) caught in the western North Pacific Ocean in the winter of 1996 (solid circles, 45°N, 160°E), the western North Pacific Ocean in the winter of 1998 (solid squares, 45°N, 165°E), Gulf of Alaska in the winter of 1996 (open squares; 46°N, 168°W) and Gulf of Alaska in the summer of 1998 (open circles, 52°N, 145°W).**Fig. 3.** Polar lipid (solid bars) and neutral lipid (open bars) content of the muscle in chum and pink salmon caught in the Gulf of Alaska, western North Pacific Ocean (WNPO) and eastern North Pacific Ocean (ENPO) in the winter and summer of 1996 and 1998.

## DISCUSSION

In carnivorous fish like salmonids, which have a limited ability to utilize carbohydrates as an energy source, dietary lipids play an important role in providing energy (Watanabe 1982).

Our current knowledge of lipids in salmonids was based largely on mature fish in freshwater or adult salmon caught in coastal areas. There are few reports of lipid content in high sea salmonids (Azuma et al. 1998). One of the most important findings in this report is that the lipid content in the muscle of pink and chum salmon in winter was low, and among classes of lipids, neutral lipids were much lower in winter than in summer. In general, the polar lipid content, which is a component of the cell membrane, did not vary significantly with species or time of year, and remained approximately at 1% in fish muscle. There was no difference in polar lipid content between winter and summer in either chum or pink salmon muscle. Neutral lipids, which are used by salmon as an energy source, in the muscle of winter salmon were low, about 2.6% of that in summer in chum salmon and 3.9–22.5% of the summer in pink salmon (Table 2). Lipids in the food of fish are digested and absorbed. Following digestion, the free fatty acids in the food are reconstructed as neutral and polar lipids. The low lipid content in the muscle in the winter suggests that chum and pink salmon have inadequate food at that season. Such a low lipid content jeopardizes survival of salmon in high-seas during winter. Nagasawa (this volume) reported that in all of the western and central Pacific, Gulf of Alaska and Bering Sea, the winter zooplankton biomass was low, being, in January or February, about 10% of the summer biomass. Zooplankton biomass was higher in the western Pacific Ocean than in the central Pacific Ocean and Gulf of Alaska in November (Nagasawa this volume). There was a similarity between the regional difference in zooplankton reported by Nagasawa (this volume) and the regional and seasonal variation in lipid content in muscle of pink salmon described in this report (Table 2, Fig. 2).

Sasaki et al. (1989) examined the composition of fatty acids in the total lipids of chum salmon during

**Table 3.** Fatty acid percentage of neutral lipids (NL) and polar lipids (PL) in the muscle of chum salmon caught in the winter and summer of 1998. Values are mean of fatty acids and (S.D.).

| Fatty Acids | NL                |                             | PL                |                             |
|-------------|-------------------|-----------------------------|-------------------|-----------------------------|
|             | Feb. 1998<br>WNPO | July 1998<br>Gulf of Alaska | Feb. 1998<br>WNPO | July 1998<br>Gulf of Alaska |
| 14:0        | 3.37(1.33)        | 7.21(1.03)                  | 0.89(0.25)        | 4.35(1.90)                  |
| 16:0        | 13.33(1.89)       | 15.07(2.06)                 | 23.14(5.09)       | 25.93(5.46)                 |
| 16:1n7      | 4.46( 2.12)       | 4.84(0.88)                  | 1.12(0.14)        | 1.42(0.75)                  |
| 18:0        | 3.90( 0.75)       | 4.50(0.84)                  | 4.62(1.24)        | 5.59(1.32)                  |
| 18:1n9      | 18.39( 6.65)      | 18.85(3.39)                 | 5.04(0.77)        | 10.99(3.52)                 |
| 18:1n7      | 2.97(1.38)        | 1.63(0.29)                  | 1.92(0.53)        | 1.46(0.39)                  |
| 18:1n5      | 0.91(0.39)        | 0.61(0.08)                  | 0.50(0.14)        | 0.47(0.17)                  |
| 18:2n6      | 1.61(0.53)        | 1.56(0.18)                  | 0.43(0.16)        | 0.77(0.10)                  |
| 18:3n3      | 1.30(0.66)        | 1.15(0.24)                  | 0.39(0.08)        | 0.45(0.03)                  |
| 18:4n3      | 1.39(0.96)        | 2.24(0.79)                  | 0.22(0.05)        | 0.55(0.08)                  |
| 20:1n11     | 2.19(1.08)        | 3.97(1.72)                  | 0.21(0.16)        | 1.42(0.83)                  |
| 20:1n9      | 2.95(2.16)        | 1.63(0.30)                  | 0.46(0.49)        | 0.88(0.59)                  |
| 20:4n3      | 1.30(0.58)        | 1.64(0.29)                  | 0.67(0.12)        | 0.94(0.14)                  |
| 20:5n3      | 5.18(2.44)        | 6.25(1.57)                  | 7.26(1.27)        | 7.74(1.84)                  |
| 22:1n11     | 2.65(1.69)        | 4.05(1.58)                  | 0.06(0.05)        | 2.01(1.05)                  |
| 22:1n9      | 1.94(1.09)        | 2.85(1.32)                  | 0.05(0.03)        | 1.03(0.47)                  |
| 22:5n3      | 1.97(0.60)        | 1.54(0.27)                  | 2.25(0.62)        | 2.08(0.32)                  |
| 22:6n3      | 13.39(8.70)       | 10.89(3.09)                 | 41.89(7.02)       | 30.67(12.51)                |

WNPO; Western North Pacific Ocean

**Table 4.** Fatty acid percentage of neutral lipid in the muscle of pink salmon caught in the western North Pacific Ocean (WNPO) and Gulf of Alaska in the winter of 1996 and 1998, and the summer of 1998 in the Gulf of Alaska. Values are mean percentages of fatty acids and (S.D.).

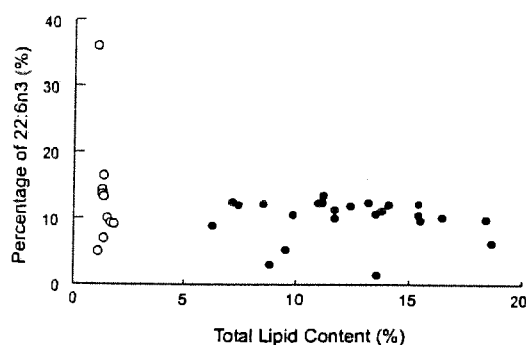
| Fatty Acids | Jan. 1996<br>WNPO | Jan. 1996<br>Gulf of Alaska | Feb. 1998<br>WNPO | Jul. 1998<br>Gulf of Alaska |
|-------------|-------------------|-----------------------------|-------------------|-----------------------------|
|             | WNPO              | Gulf of Alaska              | WNPO              | Gulf of Alaska              |
| 14:0        | 4.93(0.98)        | 1.67(1.09)                  | 2.86(1.34)        | 4.49(0.82)                  |
| 16:0        | 13.53(1.69)       | 19.53(3.28)                 | 12.46(2.95)       | 11.83(1.73)                 |
| 16:1        | 3.73(0.71)        | 2.03(1.11)                  | 3.36(1.62)        | 3.41(0.88)                  |
| 18:0        | 2.06(0.63)        | 4.57(0.96)                  | 4.63(1.30)        | 2.63(0.56)                  |
| 18:1n7      | 1.88(0.55)        | 2.86(0.66)                  | 2.32(0.35)        | 1.04(0.37)                  |
| 18:1n9      | 12.82(3.73)       | 9.67(4.28)                  | 13.87(5.52)       | 10.65(3.25)                 |
| 18:2n6      | 1.48(0.50)        | 0.69(0.23)                  | 1.90(0.45)        | 1.59(0.25)                  |
| 18:3n3      | 1.97(0.38)        | 1.35(0.82)                  | 1.07(0.53)        | 1.04(0.19)                  |
| 18:4n3      | 3.71(1.20)        | 0.74(0.53)                  | 0.99(0.42)        | 1.79(0.44)                  |
| 20:1n11     | 9.25(2.73)        | 2.47(2.52)                  | 5.16(2.94)        | 13.95(2.37)                 |
| 20:1n9      | 2.10(0.27)        | 2.24(1.69)                  | 1.88(0.94)        | 1.45(3.92)                  |
| 20:5n3      | 5.89(1.29)        | 6.68(1.55)                  | 5.67(2.29)        | 5.71(3.92)                  |
| 22:1n11     | 9.04(2.69)        | 2.54(2.65)                  | 4.18(2.02)        | 11.61(2.63)                 |
| 22:5n3      | 1.25(0.25)        | 1.74(0.36)                  | 1.80(0.45)        | 1.59(0.24)                  |
| 22:6n3      | 9.83(2.40)        | 28.72(8.99)                 | 21.64(11.71)      | 9.89(1.62)                  |

**Table 5.** Fatty acid percentage of polar lipid in the muscle of pink salmon caught in the western North Pacific Ocean and Gulf of Alaska in the winter of 1996 and 1998, and the summer of 1998 in the Gulf of Alaska. Values are mean of percentages of fatty acids and (S.D.).

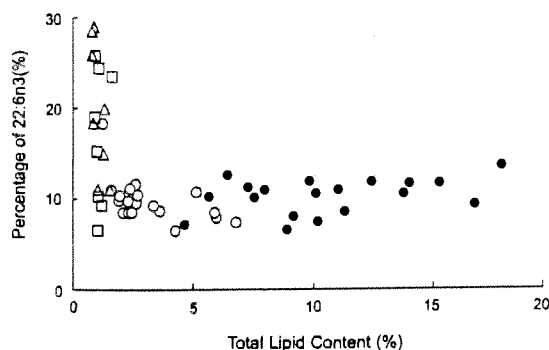
| Fatty Acids | Jan. 1996<br>WNPO | Jan. 1996<br>Gulf of Alaska | Feb. 1998<br>WNPO | Jul. 1998<br>Gulf of Alaska |
|-------------|-------------------|-----------------------------|-------------------|-----------------------------|
| 14:0        | 1.12(0.25)        | 0.59(0.13)                  | 1.13(0.42)        | 1.48(0.22)                  |
| 16:0        | 20.23(2.15)       | 17.61(2.64)                 | 20.40(1.11)       | 16.36(2.32)                 |
| 16:1        | 1.02(0.24)        | 0.71(0.16)                  | 0.9(0.16)         | 1.07(0.26)                  |
| 18:0        | 3.75(0.25)        | 4.49(0.84)                  | 4.59(0.41)        | 4.71(1.34)                  |
| 18:1n9      | 5.10(0.66)        | 5.88(1.18)                  | 4.23(0.28)        | 5.30(1.25)                  |
| 18:1n7      | 1.61(0.23)        | 1.76(0.25)                  | 1.19(0.13)        | 1.41(0.22)                  |
| 18:1n5      | 0.69(0.18)        | 0.35(0.38)                  | 0.37(0.37)        | tr                          |
| 18:2n6      | 0.54(0.12)        | 0.40(0.11)                  | 0.68(0.68)        | 0.58(0.19)                  |
| 18:3n3      | 0.52(0.14)        | 0.25(0.08)                  | 0.44(0.44)        | 0.55(0.21)                  |
| 18:4n3      | 1.00(0.32)        | 0.50(0.41)                  | 0.32(0.32)        | 0.45(0.10)                  |
| 20:1n11     | 0.43(0.13)        | 0.52(0.25)                  | 0.22(0.22)        | 1.49(1.41)                  |
| 20:1n9      | 1.40(2.11)        | 0.73(0.60)                  | 0.50(0.20)        | tr                          |
| 20:5n3      | 7.79(1.88)        | 7.00(1.09)                  | 8.82(1.31)        | 4.74(2.55)                  |
| 22:1n11     | 0.42(0.20)        | 0.17(0.11)                  | tr                | tr                          |
| 22:5n3      | 1.57(0.22)        | 1.76(0.22)                  | 1.76(0.20)        | 1.99(0.28)                  |
| 22:6n3      | 44.57(3.73)       | 47.20(1.55)                 | 47.11(2.00)       | 33.99(7.13)                 |

tr=trace

**Fig. 4.** Proportion of 22:6n3 in the neutral lipid content of chum salmon caught in the winter (open circles) and the summer (solid circles).



**Fig. 5.** Proportion of 22:6n3 in neutral lipid contents of pink salmon caught in the western North Pacific Ocean (open circles, 45°N, 160°E) in the winter of 1996, the western North Pacific Ocean (open squares, 45°N, 165°E) in the winter of 1998, Gulf of Alaska (open triangles, 46°N, 168°W) in the winter of 1996, and Gulf of Alaska (solid circles, 52°N, 145°W) in the summer of 1998.



their coastal spawning migration and reported that the major fatty acids in the muscle were 16:0 (15.3%), 18:1n9 (12.01%), 20:1n11 (7.5%), 20:5n3 (7.0%), 22:1n11 (including n13) (5.8%) and 22:6n3 (20.2%). We found that the fatty acids of both pink and chum salmon caught in summer in the Gulf of Alaska were similar, but in winter, when lipid content was less than 1.1 %, the percentages of some fatty acids were altered from those in summer. The proportion of 22:6n3 was increased in neutral lipids in winter, and reached 30% of total fatty acids in pink salmon neutral lipids (Table 4). Docosahexaenoic acid (22:6n3) is the major n-6 polyunsaturated fatty acid in fish, and plays an important role in metabolism. The increasing proportion of 22:6n3 in the samples occurred for one or both of two reasons: an increase in 22:6n3 acid or a decrease in other major fatty acids. Indeed, the proportion of 16:0 and 18:1n9 decreased. We think that the increasing proportion of 22:6n3 was the result of utilization and depletion of 16:0 and 18:1n9.

The uptake of fatty acids in the fish intestine appears to be non-selective, owing to the presence of lipase capable of hydrolyzing fatty acids from triacylglycerol molecules in the three positions (Patton et al. 1975; Lie and Lambertsens 1985). These fatty acids are transported in the blood to either fat depots or target organs, as in mammals. Similar fatty acid profiles of dietary lipids and triacylglycerol rich organs suggest that fatty acid deposition in fish lipids is a nonselective process. Fatty acids are then specifically mobilized from lipid reserves during periods of

starvation or low food intake as noted in rainbow trout (*O. mykiss*) and chum salmon (Ando et al. 1985; Sasaki et al. 1989). Kiessling and Kiessling (1993) studied the oxidation rate of 10 major fatty acids with CoA of rainbow trout white muscle. Two fatty acids (14:0 and 16:0) were oxidized as rapidly as pyruvate. Another six acids (16:1n7, 18:0, 18:1n9, 20:1n9, 22:1n9 and 22:6n3) were oxidized at about three-quarters to one half the rate of pyruvate. The unsaturated fatty acid 22:6n3 was oxidized at a comparable rate to 22:1n9, which is half the rate of palmitic acid oxidation. The change of fatty acids profile in winter as related to changes in total lipids also suggests that salmon had little food during winter. The low lipid contents and changes in fatty acid profiles in winter suggest that chum and pink salmon are confronted with difficult conditions during this season.

Further study of the seasonal and spatial variation in lipid content among North Pacific salmonids is needed to better estimate changes in feeding conditions of salmon during their high seas residency.

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# Manipulating the Timing of a Chum Salmon (*Oncorhynchus keta*) Run Using Preserved Sperm

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**Abstract:** Run timing for two experimental groups of adult returns to a natal river and adjacent areas was compared for 1991 and 1993 broods of chum salmon (*Oncorhynchus keta*). In the experimental group of the 1991 brood, eggs and sperm were collected from fish returning early in December, and eggs were inseminated immediately. For the second experimental group, eggs were taken from fish returning in early December and inseminated with sperm collected in early November that had been preserved in artificial seminal plasma and antibiotics at 0°C for one month. Adults returning in each group were identified from fin-clips and scale analysis. The fresh sperm group returned mainly in early December over four years from 1994 to 1997; over four years there was a single abundance peak of returns to the natal river and adjacent areas. The preserved sperm group showed two peaks, one in late October and the other in early December. Comparable results were also observed for similar experiments conducted with 1993 brood fish. These results suggest that the return timing to a natal river is influenced by genetic factors that can be manipulated using preserved sperm.

## INTRODUCTION

It is known that the timing of upstream migration and spawning in salmonid fish is different for each river, and that there may be several spawning runs in a river (Mayama 1986). One explanation for these phenomena is that the physical conditions that influence spawning and survival are different for each river. If adults return too early or too late, the river will often not be suitable for spawning or development of their embryos (Smoker et al. in press). Thus, run timing is clearly important to the persistence of populations, and we suspect that run timing is affected genetically (Mayama 1986, Smoker et al. 1998). Mayama (1986) inferred that maturation time of salmonid fish is influenced by the spawning time of the parents. Pink salmon (*Oncorhynchus gorbuscha*) tend to return to spawn at the same time in a run that their parents did (McGregor et al. 1998). However, these reports were based on ordinary propagation; the fish were mated with fish that had matured at the same time.

In our experiment, we focused on the return timing of chum salmon to a natal river, comparing

broods raised from eggs fertilized with preserved sperm and with fresh sperm. The purposes of this experiment were to investigate whether there is any genetic control over season of run timing by using preserved sperm.

## MATERIALS AND METHODS

### 1991 Brood

In 1991, eggs and sperm were obtained from mature chum salmon (*O. keta*) from the Akka River of Iwate prefecture, Japan. There were two different groups in this experiment. In the first group, eggs and sperm were collected from 86 females and 4 males that returned to the river on 4 December; half the eggs from the 86 females were inseminated immediately with fresh sperm (Table 1). For the second group, sperm for insemination was stripped from 4 males that were in the river on 6 November. The sperm was preserved by mixing it with artificial seminal plasma containing antibiotics (streptomycin, penicillin, fungizone). The sperm was stored at about 0°C until 4 December. The other half of the

**Table 1.** Dates and locations where eggs and sperm were collected.

| Brood year | River of origin | Date sperm collected | Date eggs collected | Date of fertilization |
|------------|-----------------|----------------------|---------------------|-----------------------|
| 1991       | Akka R.         | Dec. 4, 1991         | Dec. 4, 1991        | Dec. 4, 1991          |
|            | Akka R.         | Nov. 6, 1991         | Dec. 4, 1991        | Dec. 4, 1991          |
| 1993       | Tsugaruishi R.  | Nov. 26, 1993        | Nov. 26, 1993       | Nov. 26, 1993         |
|            | Tsugaruishi R.  | Oct. 22, 1993        | Nov. 26, 1993       | Nov. 26, 1993         |

eggs collected on 4 December (86 females) were inseminated immediately with the preserved sperm.

The preserved sperm was stored in two kinds of seminal plasmas with different components. The chemical components of one were 130 mM NaCl, 40 mM KCl, 2.5 mM CaCl<sub>2</sub>, 1.5 mM MgCl<sub>2</sub> and 2.5 mM NaHCO<sub>3</sub> in water for cell culture. The other consisted of 80 mM NaCl, 50 mM KCl, 2.5 mM CaCl<sub>2</sub>, 1.5 mM MgCl<sub>2</sub> and 50 mM NaHCO<sub>3</sub>. The chum salmon fry obtained from these experiments were all released at the same location and at the same time into the Osawa River on 13 April 1992 (Table 2). There were 77,700 marked fry from the fresh-sperm group and 45,300 from the preserved-sperm group. Each group was identified by fin clipping and scale analysis. The fry from the fresh-sperm group were marked by clipping both the adipose fin and the left ventral fin. The preserved-sperm group was marked by clipping both the adipose fin and the right ventral fin. From 1993 to 1997, we looked for marked fish from 1991-brood releases in the river and along the coast in Iwate prefecture, Japan.

For the purposes of run timing, we have defined the natal river and adjacent areas as the Osawa River and the Yamada fish market. The Yamada fish

market sells salmon that are caught in set nets from near the mouth of Osawa River.

### 1993 Brood

In 1993, the eggs and sperm of the fresh-sperm group were obtained on 26 November from 58 females and 3 males captured in Tsugaruishi River, Iwate prefecture, Japan. Half the eggs from 58 females were inseminated immediately with fresh sperm (Table 1).

For the preserved-sperm group, the sperm had been stripped from 4 males captured in the Tsugaruishi River on 22 October. Sperm was preserved until 26 November. The other half of the eggs collected from 58 females captured in the river on 26 November were inseminated immediately with preserved sperm. There were 36,400 marked chum salmon fry from the fresh-sperm group, and 51,200 from the preserved sperm group (Table 2). Fry were released into the Osawa River on April 20, 1994. From 1995 to 1998 we looked for marked adults returning from the 1993-releases.

### RESULTS

For the 1991-brood experiment a total of 57 marked fish from the fresh-sperm group and 46 marked fish from the preserved-sperm group were recovered (Table 3). Recovery rates were 0.07% and 0.10% respectively, but were not significantly different ( $\chi^2$ ,  $p > 0.05$ ). Most recoveries in both groups were age 3+ and 4+, and were not statistically different ( $\chi^2$ ,  $p > 0.05$ ) (Table 3).

**Table 2.** Summary of release information on marked chum salmon fry.

| Date of release | No. released | River of release | Fork length mean $\pm$ SD(cm) | Body weight mean $\pm$ SD(g) | Marked fin            | Group <sup>1</sup> |
|-----------------|--------------|------------------|-------------------------------|------------------------------|-----------------------|--------------------|
| Apr. 13, 1992   | 77,700       | Osawa R.         | 6.1 $\pm$ 0.41                | 1.62 $\pm$ 0.32              | Adipose+Left ventral  | F                  |
| Apr. 13, 1992   | 45,300       | Osawa R.         | 6.2 $\pm$ 0.32                | 1.74 $\pm$ 0.26              | Adipose+Right ventral | P                  |
| Apr. 20, 1994   | 36,400       | Osawa R.         | 6.7 $\pm$ 0.35                | 2.54 $\pm$ 0.38              | Adipose+Left ventral  | F                  |
| Apr. 20, 1994   | 51,200       | Osawa R.         | 6.2 $\pm$ 0.31                | 2.16 $\pm$ 0.33              | Adipose+Right ventral | P                  |

<sup>1</sup> F, fresh sperm; P, preserved sperm

**Table 3.** Age, sex, and numbers of marked chum salmon that were recovered in rivers and along the coast of Iwate Prefecture, Japan.

| Brood year | Marked fin            | Group <sup>1</sup> | Number of fish | Age |    |    |    | Male | Female |
|------------|-----------------------|--------------------|----------------|-----|----|----|----|------|--------|
|            |                       |                    |                | 2+  | 3+ | 4+ | 5+ |      |        |
| 1991       | Adipose+Left ventral  | F                  | 57             | 2   | 24 | 31 | 0  | 20   | 37     |
|            | Adipose+Right ventral | P                  | 46             | 3   | 22 | 20 | 1  | 12   | 34     |
| 1993       | Adipose+Left ventral  | F                  | 33             | 3   | 17 | 13 | -  | 7    | 26     |
|            | Adipose+Right ventral | P                  | 37             | 2   | 27 | 8  | -  | 15   | 22     |

<sup>1</sup> F, fresh sperm; P, preserved sperm



For the 1993-brood experiment, 33 fish were recovered from the fresh-sperm group and 37 from the preserved-sperm group (Table 3). Recovery rates were 0.09% and 0.07%, and again were not significantly different ( $\chi^2, p > 0.05$ ). Most fish in both groups were aged 3+ and 4+, and age compositions were not statistically different ( $\chi^2, p > 0.05$ ).

### Timing of Returns

In 1991-brood experiments, the fish that recovered from the Osawa River and Yamada fish market were 33 (fresh-sperm group) and 21 (preserved-sperm group) (Table 4). The adults returned to the area from mid September to mid December; the range was the same for both groups. However, the fresh-sperm group returned mainly in early December and had a single peak; the preserved-sperm group showed two peaks, one in late October and the other in early December. In the fresh-sperm group, about 42% of the recovered fish returned during the peak. In the preserved sperm group, about 24% returned during the first peak and 33% returned during the second. Neither distribution (run timing) was significant (Kolmogorov-Smirnov test,  $p > 0.05$ ) (Fig. 1a).

Similar results were observed in the experiment initiated in 1993. All of the recovered fish (31 from the fresh-sperm group and 32 from the preserved-sperm group) were recovered in the Osawa River and Yamada fish market (Table 4). A single peak in the fresh-sperm group was observed in early December, and the percentage of fish in the return peak was about 29%. There were two peaks in the preserved-sperm group, one in late October and the other in mid November; percentages were about 16% and 38%, respectively (Fig. 1b). Both distributions (run timing) were significant (Kolmogorov-Smirnov test,  $p < 0.01$ ).

### Location of Recoveries

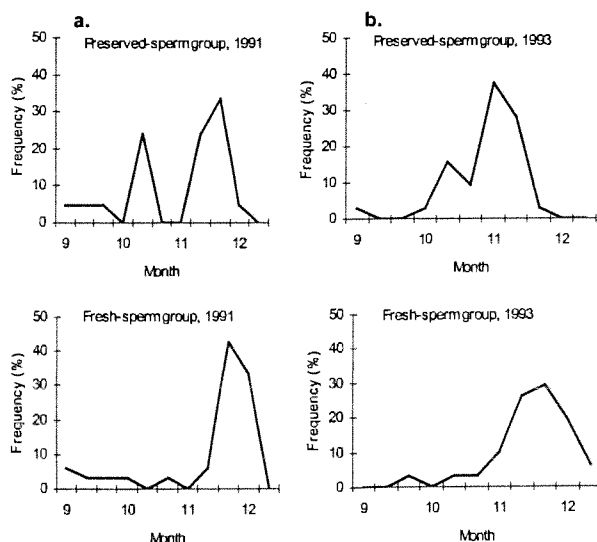
Among the fresh-sperm group in the 1991-brood experiment, 27 adults were recovered from the Osawa River, and 6 adults from Yamada fish market (24 adults were from other areas) (Table 4). The periods of recovery were different in the two areas (Fig. 2a). Most of the 27 fish recovered in the Osawa River were found in the second half of the observation period. By contrast, the 6 fish from adjacent areas were recovered in the first half. Similar results were observed for the preserved-sperm group, i.e., most of

**Table 4.** Summary of marked chum salmon recovered in the Osawa River and in Yamada fish market.

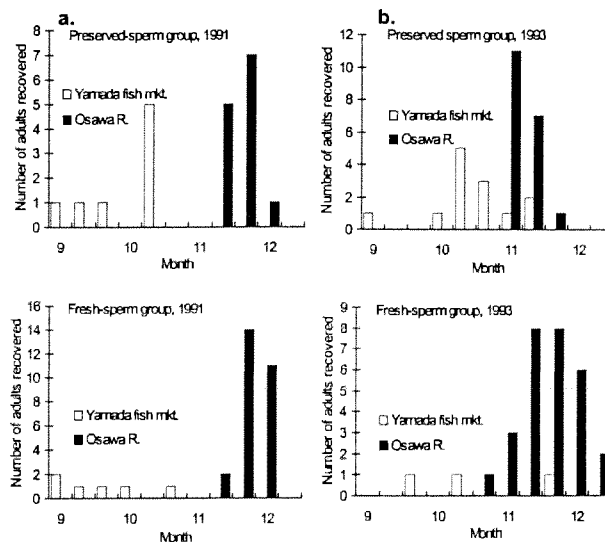
| Brood year | Marked fin            | Group <sup>1</sup> | Total number of fish | Number of fish |        |        | Male | Female |
|------------|-----------------------|--------------------|----------------------|----------------|--------|--------|------|--------|
|            |                       |                    |                      | Osawa          | Yamada | others |      |        |
| 1991       | Adipose+Left ventral  | F                  | 33                   | 27             | 6      | 24     | 10   | 23     |
|            | Adipose+Right ventral | P                  | 21                   | 13             | 8      | 25     | 7    | 14     |
| 1993       | Adipose+Left ventral  | F                  | 31                   | 28             | 3      | 2      | 6    | 25     |
|            | Adipose+Right ventral | P                  | 32                   | 19             | 13     | 5      | 14   | 18     |

<sup>1</sup> F, fresh sperm; P, preserved sperm

**Fig. 1.** Number of marked fish recovered in the Osawa River (the river of release) and Yamada fish market (near Osawa River), Iwate Prefecture, Japan, 1994–1998.



**Fig. 2.** Number of marked adult chum salmon recovered Sept.–Dec. from the Osawa River and from the Yamada fish market, 1994–1998.



the 13 fish that were recovered in the Osawa River were found in the second half of the observation period. The 8 fish that were recovered in coastal areas near the river were found in the first half of the observation period. In these results, few fish were recovered in the Osawa River late in October.

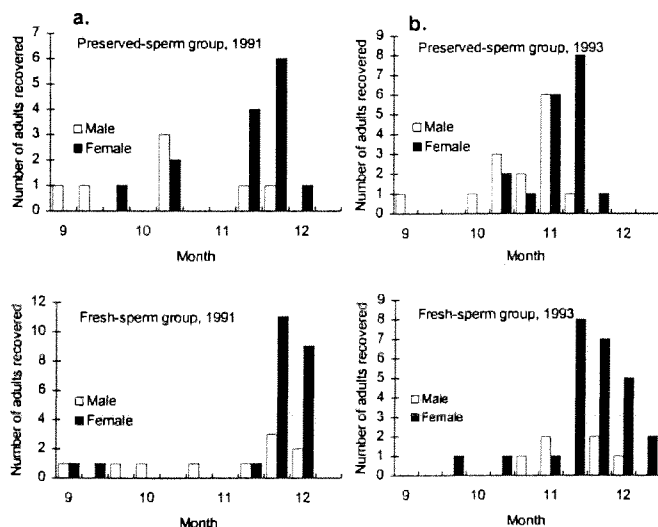
Results were similar in the 1993-brood experiments where few fish were recovered from the Osawa River in late October for either the fresh-sperm group or the preserved-sperm group (Table 4 and Fig. 2b).

### Sex Composition

Sex composition of marked fish from the 1991-brood experiments recovered in the Osawa River and Yamada fish market consisted of 7 males and 14 females for the preserved-sperm group (Table 4). For this group the peak numbers of recovered males was in late October, and for females in early December (Fig. 3a). For the fresh-sperm group, there were 10 males and 23 females from the same areas. The peak in the number of females occurred in early December, but males did not produce an obvious peak.

For the 1993-brood experiments sex composition of adults recovered in the preserved-sperm group was 14 males and 18 females (Table 4). In the case of the males, there were two abundance peaks, one in late October and the other in mid-November. Female abundance peaks appeared in late October and again in late November (Fig. 3b). In the fresh-sperm group, 6 male and 25 female fish were recovered from the same area. Though a single peak for the females occurred in late November, no peak was observed for the males.

Fig. 3. Number of male and female marked adult chum salmon recovered Sept.–Dec., 1994–1998.



### DISCUSSION

It has been known empirically that chum salmon propagated on the same day in the usual way form a unimodal distribution when they return (Kobayashi 1985; Mayama 1986). Moreover, the center of the frequency distribution is the day the parents were spawned; the range is three weeks before and after this date (Kobayashi 1985; Mayama 1986).

In our experiments, we propagated fish from pairs that differed in maturation times by using preserved sperm, and the results show an interesting pattern. When we used preserved sperm we obtained a bimodal distribution, unlike the pattern obtained with fresh sperm. That is, dates of peak returns of chum salmon that were propagated using preserved sperm coincided with the sperm-stripping date and the date eggs were collected and fertilized. However, there was no significant difference in run timing of each group in the 1991 brood experiment. However, the important point is that the date of the return peaks for chum salmon corresponded with the dates of return of their parents.

Miyagi Prefecture (1999) conducted similar experiments using sperm after cryopreservation. However, their results did not agree with ours with regard to the characteristics of the returns (especially run timing). They reported that the date when the peak occurred fell between the sperm stripping date and the date of insemination. In either case, preserved sperm groups were somewhat different from run timing in the fresh sperm group; in other words, it is likely that run timing is under genetic influence.

Mayama (1986), McGregor et al. (1998) and Smoker et al. (1998) reported that the spawning time of salmonids has a genetic component. Moreover, it has been reported for chum salmon that spawning time is closely related to the date the fish return to their natal river. Seki and Shimizu (1996), suggested that the date of return to the natal river for chum salmon is influenced by parental genetic factors. Judging from this and our experiments, run timing is under genetic influence.

Another characteristic that was observed when using preserved sperm was that some fish returned early (similar in time to when the male parent returned). These fish were recovered near the natal river, but had not entered the river. We do not understand the reason for this, but there may have been a difference in the stage of maturity. We did not observe any special trends related to sex composition.

Experimental releases were conducted by transplantation in our experiments. However, transplantation did not seriously influence the run timing of our experiments. This is because the timing of upstream migrations is not easily changed by environmental differences (Okazaki 1982a, b).

In our experiments, the number of recovered fish was not large, and we cannot be certain that the results would apply to the whole population. Therefore, further experiments will be required to clarify the relationship between run timing and genetic factors.

There have been numerous studies on techniques for preserving sperm for use in artificial propagation. Salmonid fish have frequently been used in these studies (Smith and Quistorff 1943; Barrett 1951; Forester 1965; Withler and Humphreys 1967; Hoyle and Idler 1968; Truscott et al. 1968; Withler and Morley 1968; Ott and Hortor 1971; Hiroi 1973). However, the main objectives were to determine storage methods, fertilization techniques, motility and the fertility rates of the sperm. Therefore, the biological characteristics of the adult salmon that contributed the sperm were not described in detail. Our experiments suggest that run timing can be manipulated using preserved sperm. We also suggest that it can be a useful technique for maintaining balanced stocks during artificial propagation, because there are many more male chum salmon than females during the first run. Also, sperm preservation could maintain chum salmon diversity in a river without having to transplant rare stocks of early run fish. Naturally we should be careful using preserved sperm until all features of its use are clear.

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We are sincerely grateful to Mr. Kiyoharu Sakamoto for storing sperm. We would also like to thank the staffs of the Shimoakka Fishery Cooperative Society, the Tsugaruishi Salmon Hatchery and the Osawa River Salmon Hatchery.

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## VI. Closing Remarks

Distinguished Mr. Chairman, Colleagues, Ladies and Gentlemen

Our symposium is coming to an end. This is the third meeting of scientists organized by the NPAFC. The two previous ones were in 1996 and 1998. Similarly, the present symposium was oriented to the discussion of a specific concern to scientists and practical fishermen. The papers presented provide us with a good idea of the state of knowledge of salmon, and identify priorities.

About ten years ago, nearly concurrently with the establishment of NPAFC, salmon research entered a new phase. Previously, the main effort was oriented to the freshwater period. It was expressly for the freshwater period that the main quantitative characteristics had been obtained. Marine research was significant, too. It provided us with a detailed picture of the life of salmon at sea. However, this research was mostly qualitative. It had little relevance to quantitative assessment and to process or mechanism analysis.

The situation changed radically throughout the past decade. The share of marine research has risen considerably whereby quantitative assessments are made which enable us to understand the processes occurring within salmon stocks at sea.

I shall try to list recent achievements which I have memorized well. Naturally, I shall omit something because of my special interest.

Understanding of salmon as a natural phenomenon has become more profound. The same is true of recognition of dependence of salmon on global natural processes. This opens up possibilities for macroscale forecasts in the future.

The structural feature of salmon migration on the high seas was discovered and described. It was found that the migrations in the ocean have a structure that is similar to the structure of spawning runs in rivers, and that this characteristic is established hundreds of miles away from the coast.

Trawling techniques for salmon were developed for projections of returns and possible catch. For several years, this system was applied successfully in Russia to Okhotsk Sea pink salmon stocks.

Previously, salmon research was restricted mostly by the fishing season. At present, studies are conducted the year round, making it possible to get knowledge of

wintering of salmon, and the factors that affect these species during winter.

We have come to understand better the year-round features of growth, sufficiency of food, and food relations. We have begun very promising investigations of lipids. The above factors will allow us to understand better the characteristics of mortality and survival of salmon and, still more important, factors of mortality and survival during wintering. Those data can make it possible to improve significantly the quality of fishing forecasts.

We have raised tagging of salmon, especially with archival tags, to a new level.

The establishment of the international database for genetic identification of stocks can be viewed as a great success.

Several hypotheses of special interest have been put forward recently which show a vector of future research.

The above-mentioned success could be achieved only through international cooperation of scientists. On the other hand, this united effort is augmented significantly by the activities of NPAFC.

In closing, on behalf of all the participants, I would like to thank the Government of the United States for the opportunity to hold this symposium. My thanks go to the State of Alaska and to our colleagues from Juneau for their kind hospitality and for excellent conditions to work and relax in.

I am grateful to the Secretariat of the NPAFC for the excellent organization of the event. I thank the NPAFC for the support which made it possible for several scientists to take part in the symposium. I also thank members of the steering committee for their preparatory work.

I would like to thank Alaskan weather which tied us up closer to this house and allowed us to feel better the warmth of its walls and the warmth of communication.

Thank you all. Happy journey home.

This symposium is adjourned.

Oleg Gritsenko

Chairman

Committee on Scientific Research and Statistics

1997-1999

