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TECHNICAL REPORT 9

3rd International Workshop on *Migration and Survival Mechanisms of Juvenile Salmon and Steelhead in Ocean Ecosystems*

Technical Editors: Nancy D. Davis and Claudia Chan

Vancouver, Canada, 2013

3rd International Workshop on *Migration and Survival Mechanisms of Juvenile Salmon and Steelhead in Ocean Ecosystems*

Honolulu, Hawaii, USA, April 25-26, 2013

ORGANIZING COMMITTEE

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Kwan Eui Hong: Yangyang Salmon Station, Republic of Korea

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Preface

In recognition of the importance of understanding juvenile Pacific salmonid production in ocean environments, on April 25-26, 2013, the North Pacific Anadromous Fish Commission (NPAFC) hosted an International Workshop on “Migration and Survival Mechanisms of Juvenile Salmon and Steelhead in Ocean Ecosystems” at the Sheraton Princess Kaiulani Hotel, Honolulu, HI, USA.

The workshop was the third in a series of workshops NPAFC has held on the topic of juvenile salmon in marine ecosystems. The first workshop was held in Tokyo, Japan, in 2000 (see NPAFC Technical Report No. 2 and NPAFC Bulletin No. 3) and the second took place in Sapporo, Japan, in 2006 (see NPAFC Technical Report No. 7).

Convening the 2013 workshop and producing this volume serves as partial fulfillment of the NPAFC Science Plan 2011-2015 (NPAFC Document 1255). The Science Plan identified research on juvenile salmon ocean migration and survival as important to developing an improved understanding of common mechanisms that regulate production and to explaining and forecasting annual variation in salmon production.

The workshop was attended by over 95 international experts and scientists. Workshop participants presented 33 oral presentations and 40 posters addressing the following topics related to juvenile salmon:

1. Seasonal distribution and migration route and timing
2. Hydrological characteristics, primary production, and prey resources
3. Trophic linkages, growth rates, and predation rates
4. Ecological interactions among species and populations
5. Survival rate and survival mechanisms
6. Survival and salmonid ecology during the first winter at sea

At the workshop researchers shared and reviewed significant new research results. Many presenters suggested the initial period after juvenile salmon migrate to sea and the following first winter are critical phases with respect to ocean survival of anadromous populations. Researchers indicated there is considerable inter-annual variation in abundance, growth, and survival rates of juvenile salmon in the ocean. Potential ecological interactions affecting marine survival of juvenile salmon were identified. Salmon production could be affected by expected climate or ecosystem change at several spatial and time scales. Innovative studies using genetic and morphological techniques continue to provide new information on the migration and distribution of salmon stock groups.

The Workshop Organizing Committee consisted of Joseph Orsi (Chairperson; Auke Bay Laboratories, USA), Kwan Eui Hong and Ju Kyoung Kim (Yangyang Salmon Station, Republic of Korea), Marc Trudel (Pacific Biological Station, Canada), Shigehiko Urawa (Hokkaido National Fisheries Research Institute, Japan), Alexander Zavolokin (Pacific Scientific Research Fisheries Center, Russia), and Nancy Davis (NPAFC Secretariat). Arrangements for the workshop were made by the NPAFC Secretariat. Sujuan Situ and Lara Ouchi volunteered to provide support at the workshop, and we thank them for their help.

On behalf of the Workshop Organizing Committee, we thank participants for sharing information and ideas on juvenile salmon migration and survival mechanisms at the meeting and for submitting materials for this volume.

Technical Report 9 is a compilation of extended abstracts submitted by workshop presenters, and it concludes with a workshop synopsis. Material in this report has not been peer-reviewed and does not necessarily reflect the views of NPAFC, member countries, or authors' agencies. Additionally, some of the investigations included here are preliminary. Abstracts have been edited for clarity and publication purposes.

Nancy D. Davis and Claudia Chan
Technical Editors, NPAFC

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Review of Studies on Asian Juvenile Pacific Salmon Stocks, 2006-2012

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Keywords: juvenile Pacific salmon, growth, survival, migration timing, food supply, ration, feeding habits

Studies of Asian juvenile Pacific salmon stocks have been conducted by the national research programs of Korea, Japan, and Russia towards achieving the NPAFC Science Plan objectives (Fig. 1). They have primarily focused on salmon growth and survival rates under different hydrological conditions (water temperature, salinity, and circulation dynamics), spatial distribution and migration patterns, food supply, feeding habits and trophic relationships, and bioenergetic balance of fish. Estuarine and coastal studies have been investigated for the practical purpose of specifying optimal marine conditions for releasing salmon from hatcheries. In offshore waters, data were collected for studies of stock assessment and population dynamics based on stock identification.

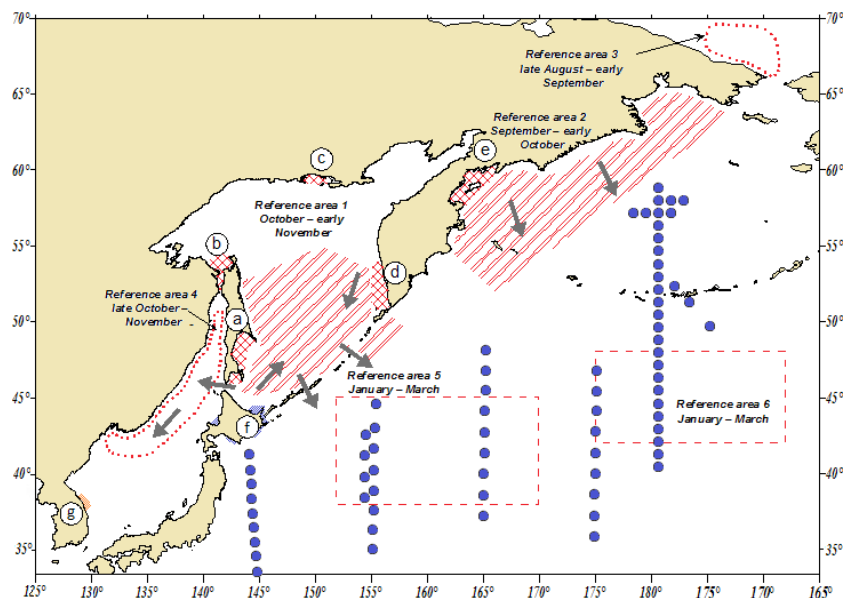


Fig. 1. Reference regions for integrated surveys of estuarine-coastal and marine periods of life for juvenile salmon in the northwestern Pacific Ocean, 2006-2012 (compiled after Nagata et al. 2007; Fukuwaka et al. 2010; Shuntov 2010; Kasugai et al. 2012; Kim et al. 2013; Sasaki et al. 2013).

Freshwater residence and downstream migration

Biological parameters and survival of juvenile salmon entering the marine environment depend on seasonal processes affected by inshore conditions at the time of freshwater residence and downstream migration. On Sakhalin and Iturup islands, gradual intensification of pink salmon downstream migration proceeds against a background of in-river water heating and water level lowering (Kaev et al. 2012). From 75% to 90% of the migrants leave three relatively short rivers in a two-week period. Migration rates change more gradually in larger streams. Four peaks of migration intensity occur in the Rybatskaya River (Iturup Island), where water conditions do not change so sharply. On the northern Sea of Okhotsk coast, juvenile salmon downstream migrations intensify with the seasonal rise of flood waters (Volobuev and Marchenko 2011). In-river water temperatures are 7-8°C at the time of migration peaks in early to mid-June. Migration duration is also longer in larger streams, where it lasts until mid-July. Juvenile chum salmon migrate from the Ol'ga and Avvakumovka rivers (southern Primorie) more intensively in mid-May with water temperatures of 8.8-14.9°C (Kolpakov et al. 2012). In conclusion, juvenile salmon downstream migration dynamics is notably affected by water temperature, level, and discharge rate, but this dependence is different by region and in small and large river basins. For methodological reasons, this variability requires expansion of reference river networks to encompass different types of spawning streams.

In the northern-most Asian regions, long-term exposure of salmon roe and larvae to cold waters during 5-7 months leads to worsening of progeny condition and increased mortality rates after entering the sea. The possibility of utilizing local watersheds for placing net pens for juvenile chum salmon growth to increase their viability has been considered (Khovanskaya et al. 2008, 2009). Ando et al. (2011) reported promising results in vertebral number variation in naturally spawning chum salmon as a response to incubation water temperature. A vertebral number index may be a useful parameter for estimating environmental conditions during ontogenesis.

During the course of the downstream migration, juvenile salmon food spectra usually expand and diet ration changes from nektonic crustacean and insect larvae to zooplankton (Kolpakov et al. 2012). Chironomid larvae and pupae were a preferable food for most salmon species in the Bolshaya River basin (western Kamchatka coast) in April-October 2012. For sockeye salmon, chironomids contributed 87.5-96.0% of total food consumed (Yarosh 2013). Salmon fry do not suffer a food deficit and feed and grow intensively.

In the Meiny-Pylgino River-Lake system (northwestern Bering Sea coast), the food spectrum of pink salmon was mostly composed of insects in July 2012. In the coastal zone adjacent to the river mouth, pink salmon mainly fed on capelin eggs and larvae, which contributed 68-90% of the total weight of stomach contents (Golub and Golub 2012). At this northern periphery for pink salmon spawning, abundance of migrants was the highest and duration of the out-migration was the longest for the whole period of observations conducted since the late 1990s. Food and hydrological conditions for the 2012 pink salmon year-class was favorable.

Coastal zone residence

The first days in the coastal zone are usually considered a critical period of life for juvenile salmon (Beamish and Mahnken 2001). Survival depends on ambient water temperatures that determine metabolic rates of salmon fry and their prey and predators. Thermal conditions in the early marine period depend on downstream migration timing as was shown for wild masu salmon smolts from the Shokanbetsu River on the western coast of Hokkaido (Miyakoshi and Saitoh 2011). In northern areas, temperature shock can occur if juveniles enter the sea at notably lower marine water temperatures in comparison with river thermal conditions. In southern waters around Hokkaido, colder waters usually support a more favorable food supply for juveniles that are represented by high-calorie copepods of the boreal faunistic complex (Seki et al. 2006; Asami et al. 2007; Saito et al. 2009). The optimal sea water temperature (SST) varied between 7-11°C for juvenile salmon out-migrating into coastal Hokkaido waters (Miyakoshi et al. 2007; Nagata et al. 2007). In the coastal zones of Sakhalin and Iturup islands, optimal SST for juvenile chum release was assessed at 6-7°C (Shershneva et al. 2007). On the western Kamchatka shelf, maximal trawl catches of juvenile salmon occurred at 8-9°C in mid-July and 10-13°C in late July – early August (Kolomeitsev 2009; Koval et al. 2011).

In Nemuro Bay (eastern Hokkaido), marked chum salmon were released and re-captured by nets and trawls in the littoral zone and inshore waters between late April and mid-July (Kasugai et al. 2012). As it was found, environmental variability in coastal areas might influence growth of marked fish released in mid-April more strongly than those released after mid-April. Delayed migration to inshore areas from the river or littoral zone due to low SSTs may result in high mortality. It was recommended to reduce releases of juvenile chum salmon into Nemuro Bay by late April–mid May. Size at release of chum salmon from hatcheries, early marine growth of juveniles, and adult returns for five Hokkaido stocks were investigated in relation to SST using path analyses (Saito et al. 2011). Direct linkage between size at release and return rates was found in three stocks—Ishikari, Shari, and Nishibetsu. Results confirmed that juvenile salmon mortality occurred in two phases, including during coastal residency, and the relative importance of both phases varied by stock, region, and downstream migration timing.

Correlations between estimated juvenile sockeye salmon abundance during the downstream migration and assessment by pelagic trawl surveys in the 12-mile coastal zone along the western Kamchatka coast were found in 2005-2011 (Koval and Kolomeitsev 2011). Juvenile sockeye salmon initially migrated northwards in the eastern Sea of Okhotsk like pink and chum salmon in the main spawning regions of the Russian Far East and like chum salmon in the coastal waters of the Korean Peninsula (Kim et al. 2013). Maximal sockeye salmon juvenile catches were 409 fish per 15-min haul northward from the mouth of the Ozernaya River.

Large numbers of juvenile salmon leave the coastal zone for offshore waters when SSTs are above 13°-15°C (Radchenko et al. 2007; Koval et al. 2010; Miyakoshi and Saitoh 2011). These observations agree with experimental results of juvenile sockeye salmon swimming performance that notably declines at temperatures above the optimum 15°C (Brett 1971). The optimum temperature for juvenile salmon changes during the marine phase of the life cycle, and the whole range of thermal conditions in salmon marine habitat significantly exceeds optimal temperature values (Shuntov and Temnykh 2008).

Water mass dynamics, ice conditions in the previous winter, and salinity are listed among the main hydrological factors effecting forage zooplankton abundance and species composition in the coastal zone of the Kamchatka Peninsula (Morozova 2013). Juvenile salmon growth and survival are also affected by feeding interactions with other fish species. Abundant herring in the common feeding areas with juvenile salmon can also serve as a factor to start the migration of salmon juveniles

from the inshore zone near the mouth of the Kamchatka River (Koval et al. 2010). Phytoplankton blooms also begin to develop in the well-heated inshore zone, and juvenile salmon migrations can be temporally related to this seasonal event. Potentially toxic algae species *Alexandrium tamarense complex* present along the western Kamchatka coast (Lepskaya et al. 2009) may prompt juvenile salmon to start migrating further offshore.

An impressive observation of pink salmon intraspecific relations was made in the northern Sea of Okhotsk coastal zone. In the Taui Inlet, which has one of the earliest pink salmon adult returns in the Sea of Okhotsk basin, two adult pink salmon were observed to have consumed pink salmon fingerlings in mid-June 2008 (Izergin et al. 2008). However, this form of intraspecific competition is not likely a significant factor affecting pink salmon populations. In most spawning regions, the overlap in timing of adult pink salmon returns and downstream migration of juveniles is not typical, and rapid early growth of juveniles rather quickly puts them beyond the optimal prey size for adult salmon.

Deep sea residence

Juvenile salmon surveys in the offshore area of the Sea of Okhotsk have been conducted annually. Juvenile pink salmon were widely distributed through the deep sea zone in 2009-2012, so the trawl survey area was expanded in the last two years to 750,000-900,000 from 260,000-400,000 km². In autumn 2011, juvenile salmon abundance was estimated at 950 million fish with mean body weight at 101 g, and 262,000 metric tons of pink salmon were harvested in the Sea of Okhotsk basin in 2012. In autumn 2012, pink salmon juvenile abundance was assessed at 1.128 billion fish. Mean weight was almost 2-times higher—188 g—than in 2011. These assessments imply an even higher catch level in the coming salmon fishery season there in 2013. In 2011 and 2012, juvenile pink salmon aggregations occurred northward of 47°-48° N. In the previous three years, pink salmon occurred across the whole deep-sea basin in the southern Sea of Okhotsk, and in 2010 aggregations even partially extended into the Pacific Ocean. It was concluded that a slow growth rate was related to slower migration velocity from the shelf zone to open waters of the Sea of Okhotsk and then to the Pacific Ocean. However, it must be taken into account that juvenile pink salmon from the northern Sea of Okhotsk usually have smaller average size and leave for the Pacific Ocean earlier than other populations.

In 2012 juvenile chum salmon abundance attained the highest level observed since the previous six years—550 million fish. Since 2005 chum salmon approaching the Russian far-eastern coasts have followed the general trend of increasing stock abundance. Older immature chum salmon have expanded their feeding area and residence time in the Sea of Okhotsk. In autumn 2012, their biomass increased to 100,000 metric tons.

Interspecific relationships of salmon sharing the same feeding area are often considered as an additional factor effecting survival and growth. Researchers have hypothesized that pink salmon in years of high abundance can exhaust the food supply and lead to enhanced mortality of chum and sockeye salmon, which compete for the same zooplankton resources (Kaga et al. 2013). Our 15 years of surveys do not support the idea that a similar situation occurs universally throughout the North Pacific Ocean. For example, in autumn in the Sea of Okhotsk, juvenile pink and chum salmon behave as complementary species with similar patterns of abundance dynamics and body weight (Fig. 2).

Spatial, seasonal, and daily changes in zooplankton communities affect juvenile salmon feeding. As a rule, the copepod portion of the diet decreases and the portion of amphipods, euphausiids, fish egg and larvae increases as the juvenile salmon move seaward (Koval et al. 2007; Nagata et al. 2007; Morozova 2010). The relation between the daily rhythm of juvenile salmon feeding intensity and zooplankton vertical migrations has been investigated (Karpenko and Koval 2007; Koval 2007). Correspondingly, the general pattern of feeding intensity is similar for the planktivorous salmon species (Volkov and Kosenok 2007). The daily food ration and energetic expenditure for growth decrease for all salmon species from summer to late autumn (Karpenko et al. 2007; Erokhin and Shershneva 2007). This reduction is related to the seasonal lowering of feeding intensity and growth that is an adaptation to lower ambient temperatures and less favorable food supplies in winter. Among salmon species, pink salmon have the highest rate of food consumption (relative to body weight) and gross growth efficiency compared to other salmon species (Erokhin and Shershneva 2007). Distinctions in behavioral and biochemical adaptations were found among juvenile pink, chum, and sockeye salmon in the Okhotsk Sea (Klimov et al. 2013).

Monitoring juvenile salmon in the Russian far-eastern seas is conducted from the viewpoint of the ecosystem (Shuntov and Temnykh 2008). This means the structure and dynamics of nektonic communities, place and role of salmon in the ecosystem, their food supply and feeding habits, trophic relationships and degree of potential competition for food with other pelagic animals, and predation pressure are investigated.

Increasing juvenile salmon stock abundance has been followed by increased total nekton biomass in the upper epipelagic layer of the Sea of Okhotsk. The percentage of salmon within the total pelagic fish and squid biomass in the southern Sea of Okhotsk decreased to below 39% on average. These significant changes have occurred in nekton community composition due to the increase in biomass of mesopelagic fish, which undertake diurnal vertical migrations. The portion of the composition comprising mesopelagic fish increased to almost twice, in comparison with the previous eight-year period, and attained 29% of total nekton biomass.

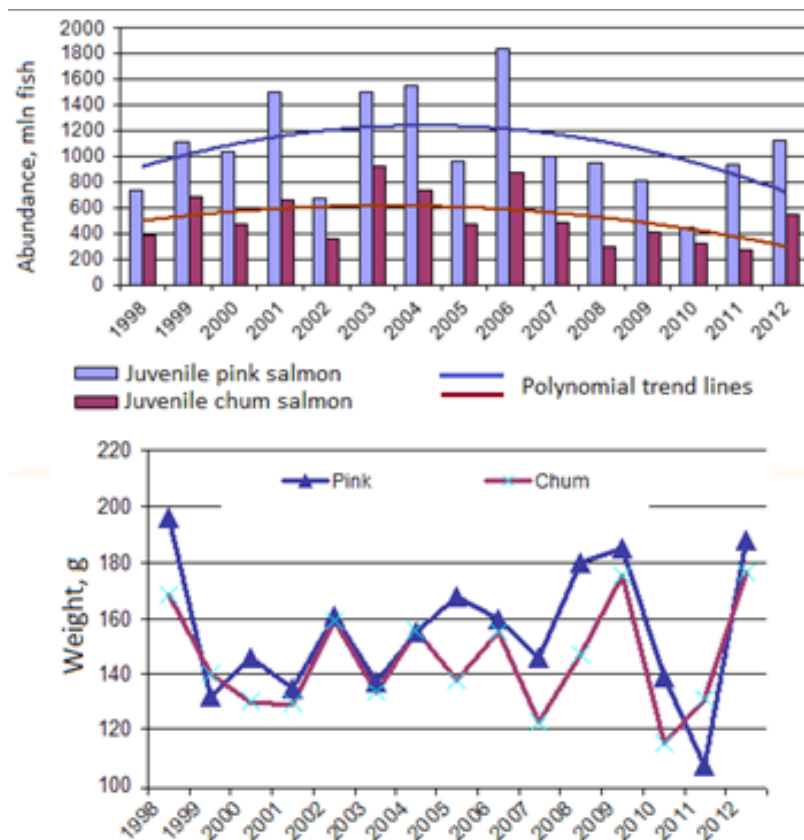


Fig. 2. Abundance dynamics of juvenile pink and chum salmon (upper panel) and interannual changes in body weights (lower panel) in the Sea of Okhotsk in autumn, 1998-2012.

During the last seven years, significant changes also occurred in the composition and structure of epipelagic nektonic communities in the western Bering Sea. The average total nekton biomass decreased by half in autumn 2006-2012 in comparison with the previous four years due to a reduction in walleye pollock abundance. The salmon component in the epipelagic nektonic community increased to 43%, even when the absolute value of salmon biomass slightly decreased. The juvenile pink salmon portion of total nekton biomass increased in even years. Exceptionally high yields of juvenile pink salmon year-classes entered the western Bering Sea in 2008 and 2010 (Glebov et al. 2008; Temnykh 2009; Shuntov and Temnykh 2011). The total number of pink salmon outmigrants from eastern Kamchatka exceeded 1.0 billion fish and were on the same level as the Sea of Okhotsk stocks. Despite relatively low mean weight in 2008, these year-classes have ensured the all-time maximum pink salmon harvest on the eastern Kamchatka coast: first in 2009 and then again in 2011. Pink salmon daily food ration was positively correlated with the abundance of preferred prey, which is similar to the conditions in the Sea of Okhotsk.

Changes in total salmon biomass in the western Bering Sea were related to decreases in stock abundance of immature chum and sockeye salmon. They were less abundant there in 2006-2011 in comparison with previous years of the BASIS program. Along the eastern Bering Sea coast, gradual decreases in juvenile salmon abundance also occurred since 2006 (Farley 2010). This suggests there was shrinkage of the feeding migration area. Immature chum and sockeye salmon abundance indices increased again in 2012, but the future trend remains unclear because the number of out-migrants in the western Bering Sea was low.

These fluctuations occurred against a background of surface water cooling in the Bering Sea, especially in the eastern area, which has continued to the present time (Khen et al. 2013). Periods of warm and cold temperature regimes were relatively short in 1980-2000: not longer than three years. The recent warm period in 2001-2006, and the cold period in 2007 to the present time have been longer and more strongly expressed. We are expecting a stronger effect on planktonic and nektonic communities. The immature ratio-at-age of chum salmon in the Bering Sea has increased (Watanabe et al. 2013), and the average body weight of chum salmon is lower in the central Bering Sea in 2011 as compared to 2007-2009 (Morita et al. 2011). This can also be related to lower ambient water temperature in salmon habitats.

Climate-oceanographic changes in the far-eastern seas are accompanied by clear changes in the quantitative composition of planktonic communities that are the food supply of salmon. Regional features of multiyear zooplankton dynamics were revealed by integrated surveys conducted by researchers aboard Russian, American, and Japanese research vessels (Volkov et al. 2007; Shuntov and Temnykh 2008; Volkov 2008a, b; Shuntov et al. 2010; Shuntov and Temnykh 2011; Volkov 2012a, b, c). Variability in zooplankton composition excites corresponding changes in the diets of nekton, including juvenile salmon. In the western Bering Sea, salmon food spectra varied slightly. Three main prey components—amphipods, euphausiids, and pteropods—have contributed from 78% to 96% of food consumed by juvenile salmon. The portions of these prey varied 5-10% in smaller (15-20 cm) and larger (20-30 cm) size salmon. In the eastern Bering Sea, composition of juvenile salmon diets varied sharply from year to year. Fish larvae and fry formed the basis of prey composition in 2003-2005, and euphausiids and amphipods were the predominant food components in 2006-2007. Since 2008, the hyperiid amphipod, *Themisto libellula*, occurred more abundantly in the ration of planktivorous salmon. Well-expressed changes in the diet of juvenile salmon can strongly affect stock conditions. The western Bering Sea may offer more stable forage conditions, which seems to be more favorable for salmon feeding.

Creation of the TINRO-Center zooplankton database allows for analysis of forage plankton distribution and abundance throughout the far-eastern seas and adjacent waters in all seasons. Large zooplankton standing crop is mainly aggregated in the deepwater basins, while higher biomass of small and middle-sized planktonic animals is observed on the shelf and continental slope zones. Total zooplankton abundance slightly differs in the northwestern and northeastern Pacific. Four taxonomic groups usually predominate in subarctic zooplankton, but only two—euphausiids and amphipods—can be defined as preferred salmon food components in areas beyond coastal waters. Considering the distribution of euphausiids and amphipods, it has been hypothesized that salmon food supply is more plentiful and forage conditions more favorable in the western part of the subarctic North Pacific, especially in Russian waters. In this area, the food supply is supplemented by pteropods and appendicularians, which are readily consumed by planktivorous salmon.

Despite well-expressed seasonal variability, zooplankton resources in the open North Pacific Ocean are sufficient to ensure the food requirements of salmon (Shuntov and Temnykh 2011). There is a seasonal decline, but zooplankton biomass does not decrease sharply in winter. In the northwestern Pacific Ocean zooplankton biomass in winter remains relatively high—averaging more than 300 mg/m³. Our estimates of zooplankton biomass in the open North Pacific are an order of magnitude higher than those published by Nagasawa (2000). According to our calculations, zooplankton biomass does not fall below a critical level that would contribute to salmon natural mortality due to insufficient food. In addition to zooplankton, the biomass of small-size nekton is an additional component of the food supply for salmon, and it is several times higher in the open waters of the North Pacific Ocean than in the deep-water regions of the Okhotsk and Bering seas.

Multiyear dynamics of average zooplankton abundance in the upper epipelagic layer displayed contrary trends in the far-eastern seas and northwestern Pacific Ocean. There were maximal abundances of juvenile salmon in the northwestern Pacific Ocean in 2009-2012 despite a significant decrease in zooplankton abundance in the open areas in the Sea of Okhotsk. Comparison of juvenile salmon food spectra with composition of planktonic communities demonstrated well-expressed salmon prey selectivity (Naydenko et al. 2007; Volkov et al. 2007; Zavolokin et al. 2007; Naydenko et al. 2008; Shuntov and Temnykh, 2008; Shuntov et al. 2010; Zavolokin 2011). Salmon prey selectivity supports the existence of a significant reserve of secondary food that enables salmon to mitigate trophic competition in times of preferred prey shortages.

Chiba et al. (2012) examined the long-term change in the trophic link between *Neocalanus* copepods and pink salmon in the western subarctic North Pacific based on nitrogen stable isotope ($\delta^{15}\text{N}$) analysis. They observed that *Neocalanus* biomass and pink salmon catch increased in the 1990s and related these increases to pelagic food web dynamics. It was hypothesized that *Neocalanus* production/survival benefited from favorable food conditions rich in phytoplankton, which secondarily enhanced pink salmon production. Our data on juvenile salmon feeding do not support the idea that large copepods hold particular significance for salmon nutrition. However, Chiba et al. (2012) undoubtedly emphasized a tight connectivity in the trophic structure of subarctic pelagic ecosystems.

Estimations of zooplankton consumption by salmon in comparison with other nektonic species show that consumption is modest, even in years of high salmon abundance (Naydenko et al. 2007, 2008; Shuntov and Temnykh 2008; Shuntov et al. 2010). In the warm season, total zooplankton consumption by common nekton species does not exceed 15% of prey biomass. For the whole year, zooplankton consumption by nekton ranges from 3% to 20% and varies significantly among the northwestern Pacific regions. Juvenile salmon consumed no more than 1-2% of the total large zooplankton biomass. In the western Bering Sea salmon prey consumption does not exceed 8% of the total food consumed by nekton. In the southern Sea of Okhotsk, juvenile salmon can eat 50-60% of the total consumed by epipelagic nekton.

Data from juvenile pink salmon autumn surveys are used to improve annual adult run forecasts. The forecast is usually generated in two steps: estimation of overall abundance of juvenile salmon in offshore waters of the Okhotsk and Bering seas and regional stock-group identification of the mixed marine aggregations. The stock identification analyses are based upon scale pattern, otolith analysis, and genetic methods. Baseline information of otolith microstructure phenotypes of pink and

chum salmon have been obtained from regions of the Okhotsk Sea, including West Kamchatka, Sakhalin, and the northern coast (Chistyakova et al. 2013). Otoliths were collected in the Sea of Okhotsk northward of 49°N in October-November of 2011. About 72% of total juvenile pink salmon and more than 75% of juvenile chum salmon abundance are represented in the baseline by western Kamchatka wild stocks. Genetic methods of identification referred 54.4% of juvenile pink salmon to the “northern populations”, which was close to the 57% identified in the total pink salmon harvest the following year (Shevlyakov et al. 2012). Among juveniles released from hatcheries, pink salmon from the Kuril’sky hatchery (60%) and chum salmon from Japanese hatcheries (71%) have predominated. More detailed information on otolith marking and genetic stock identification is presented in several extended abstracts in this volume (Saito et al. 2013; Sasaki et al. 2013; Sato et al. 2013; Yoon et al. 2013).

Survival rates of the parental generation must be taken into account when analyzing abundance indices of juvenile salmon. Marine survival of pink salmon from Sea of Okhotsk populations decreased in the first decade of the current century and then began to stabilize (Radchenko 2012). However, marine survival did not attain the values observed for less abundant year-classes of the 1990s. Therefore, we are expecting adult pink salmon returns to the Sea of Okhotsk of about 25% of estimated out-migrant abundance, or 282 million fish. This forecast will be updated after the pelagic trawl surveys of maturing salmon in the ocean waters off eastern Kamchatka and the Kuril Islands in June-July of this year, one month before the fishery begins.

Deviations in the pink salmon catch on the Russian coast (1956-2012) varied similarly to the annual world ocean heat content for the 0-700 meter depth layer (Levitus et al. 2005, with additions from http://www.nodc.noaa.gov/OC5/3M_HEAT_CONTENT/). The relation between catch dynamics and general ocean heat content is stable and remains significant since 2005, when this relationship was first observed. Ocean heat content is determined by climate and synoptic conditions in previous years. It is also correlated with the short-term data series on zooplankton biomass in the upper epipelagic layer of the northwestern Pacific, i.e., throughout the region, which keeps more heat in the upper layer than adjacent layers.

There has been promising parasitological and ichthyopathological studies conducted on different salmon stocks in Korea and Japan (Setyobudi et al. 2010; Suebsing et al. 2011; Urawa 2013). In Russia, advanced ichthyopathological salmon studies are conducted at research institutes in Kamchatka and Sakhalin. They focus on problems of viral and fungal diseases, sea lice outbreaks, and monitoring of hatchery and wild stocks (Vyalova and Shkurina 2005; Rudakova 2008).

Conclusions

1. Most research conducted in 2006-2012 proved the importance of juvenile salmon body size for survival in early marine life. Nevertheless, notable variability of adult salmon return rates despite a stable weight of released juveniles supposes the existence of other important factors driving salmon survival. Thermal conditions, timing of juvenile release, and growth rates are listed among such significant factors for salmon survival. The significance of these factors varies by region and life stage of salmon.
2. Analysis of abundance dynamics indicates that oceanographic and feeding conditions throughout Asian juvenile salmon habitats during the first marine summer and autumn are generally favorable for salmon. A tendency for acceleration of first marine year growth was observed for many Asian chum salmon stocks. Favorable feeding conditions likely play the most important factor during the coastal residence of salmon juveniles, and the thermal regime is the most important factor during the offshore residence period.
3. Studies of trophic relationships and potential competition for food in pelagic nekton communities have provided the understanding that carrying capacity of marine and ocean ecosystems can support the current high level of salmon abundance. The relatively low significance of salmon prey consumption compared to total zooplankton resources suggests good prospects for further hatchery program development in the western North Pacific, at least before there is a new wave of Japanese sardine production.
4. Juvenile pink and chum salmon abundance monitoring in the open sea waters provides a useful tool for predicting the magnitude of adult salmon returns to fisheries.
5. Results from studies on the early marine life period of salmon emphasize the necessity to expand salmon research programs on their status, and their physical and biological surroundings in subsequent life periods, especially during the winter in the North Pacific Ocean. Based on freshwater and coastal studies using varied approaches and the voluminous efforts by NPAFC-member countries, there has been clear progress in understanding salmon stock dynamics. If we work together on research related to the offshore life period of salmon at the same level of cooperation, we can expect the same high degree of advancement in our knowledge of ocean salmon.

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Recent Advances in Marine Juvenile Pacific Salmon Research in North America

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Pacific salmon sustain heavy and highly variable losses in the ocean, with natural mortality rates generally exceeding 90-95% during their marine life (Bradford 1995). Most of this mortality is thought to occur during two critical periods: an early predation-based mortality that occurs within the first few weeks to months following ocean entry, and a starvation-based mortality that occurs following their first winter at sea (Pearcy 1992; Beamish and Manhken 2001). Hence, studies that investigate the processes affecting the survival of Pacific salmon during the juvenile phase of their marine life are critically needed to understand the recruitment variability of Pacific salmon. Here, we provide a brief overview of the progress that has been made in North America on the marine ecology of juvenile Pacific salmon since the “Second NPAFC International Workshop on Factors Affecting Production of Juvenile Salmon” held in Sapporo, Japan, in 2006. We focused our effort on primary publications in peer-reviewed journals as well as NPAFC publications (i.e., Documents, Technical Reports, and Bulletins) and present selected key findings due to the large number of publications that had to be covered as part of this overview (Fig. 1).

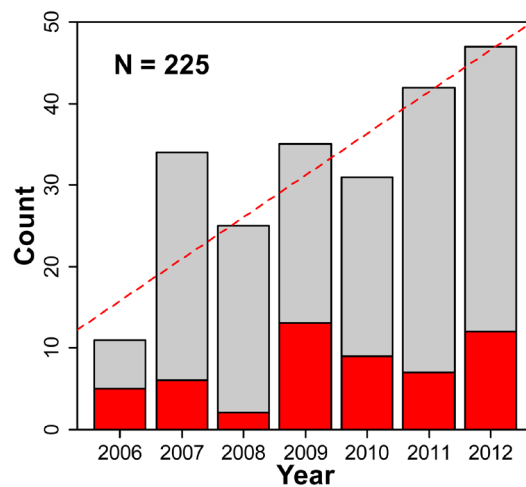


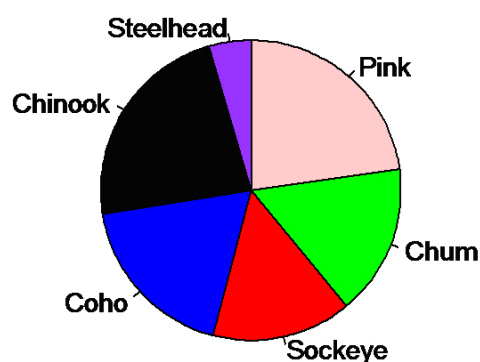
Fig. 1. Number of NPAFC publications (red bars) and peer-reviewed journal articles (grey bars) published between 2006 and 2012 in North America pertaining to marine ecology of juvenile Pacific salmon. The dotted red line represents the trend in the number of publications that are produced each year, excluding seven papers that appeared in a special issue of the American Fisheries Society Symposium Series focusing on juvenile salmon in 2007.

We compiled 225 studies that investigated different aspects of the marine ecology of juvenile Pacific salmon in North America, including survival rates and mechanisms, ocean and climate effects, distribution and migration, bioenergetics and physiology, diet and trophic interactions (Table 1; Fig. 1). Overall, the number of publications has increased steadily by approximately five papers each year since 2006 (Fig. 1). On average, 25% of the papers that have been published during that time period were contributed through NPAFC (Fig. 1). The majority of these studies focused on one (60%) or two (21%) salmon species at a time. Chinook salmon and pink salmon were the two most frequently studied species (Fig. 2).

Table 1. Focus of juvenile Pacific salmon research conducted in North America (2006-2012).

Topic	N
Distribution & Migration	59
Climate & Physical Oceanography	87
Bioenergetics, Growth & Physiology	41
Diet & Trophic Interactions	58
Ecological Interactions	33
Pathogens & Disease	50
Winter Ecology & Survival	4
Survival Rates & Mechanisms	100

For Chinook salmon, this was possibly because of concerns over their decline over a broad geographic area (Tompkins et al. 2011). In the case of pink salmon, this is probably due to the fact that they are the most abundant species of salmon in North America (Irvine and Fukuwaka 2011). Steelhead was the least studied species, possibly because they rapidly move to offshore waters of the North Pacific Ocean (Hartt and Dell 1986).

**Fig. 2.** Proportional representation by species of the number of juvenile Pacific salmon studies investigated in North America (2006-2012).

Survival rates

In North America, considerable effort has been devoted since 2006 to estimate the early marine survival of juvenile salmon (Table 2). However, few of these studies have been performed on juvenile pink and chum salmon compared to other species probably because their small size precludes the utilization of acoustic tags to estimate their survival rate (Table 3). Similarly, few studies have investigated the extent of overwinter mortality in juvenile salmon, probably due to the difficulty of sampling the marine environment during the winter months (Trudel et al. 2007b; Farley et al. 2011). Until acoustic tags became available for relatively small fish, marine survival estimates of salmon also included a freshwater component associated with the downstream migration of smolts and the upstream migration of adults. The application of acoustic tags revealed that significant and variable portion of this “marine mortality” actually occurred in freshwater (Welch et al. 2008; Chittenden et al. 2010a, b; Melnychuk et al. 2012; Moore et al. 2012; Melnychuk et al. 2013). Overall, early marine and winter survival can be quite low (Table 2), though the proximate causes for their low survival remain, for the most part, elusive.

Table 2. Estimates of early marine and first winter marine survival of juvenile Pacific salmon.

Species	Survival	Sources
Pink salmon	--	--
Chum salmon	20-50%	1
Sockeye salmon	20-50%	2-3
Coho salmon	2-20%	4-5
Chinook salmon	2-30%	6-7
Chinook salmon*	10-40%	8
Steelhead salmon	10-80%	9-11

*Winter

Sources: 1. Wertheimer and Thrower (2007); 2. Welch et al. (2009); 3. Wood et al. (2012); 4. Beamish et al. (2010c); 5. Melnychuk et al. (2013); 6. Beamish et al. (2012b); 7. Rechisky et al. (2013); 8. Trudel et al. (2012); 9. Moore et al. (2010b, 2012); 10. Melnychuk et al. (2007); 11. Welch et al. (2004).

Climate effects

The potential effects of climate on salmon production have long been recognized (Beamish 1993; Beamish and Bouillon 1993; Mantua et al. 1997). However, the intermediate steps linking salmon to climate have generally been poorly studied (Baumann 1998). Recent studies conducted in North America suggest that the effects of climate on salmon are largely species, stock, or region-specific (Wells et al. 2008; LaCroix et al. 2009; Malick et al. 2009). In the California Current System and Strait of Georgia, climate effects on salmon survival may be mediated through bottom-up processes that affect juvenile salmon feeding and growth (Beamish et al. 2006b; Wells et al. 2007, 2008; Beamish et al. 2010c; Wells et al. 2012; Daly et al. 2013). Climate may also affect survival in a top-down manner by altering the abundance and distribution of predators and alternative prey (i.e., forage fish) (Emmett et al. 2006; Emmett and Sampson 2007; Emmett and Krutzikowsky 2008), though few salmon have been reported in the stomachs of predators (Emmett et al. 2006; Sturdevant et al. 2009, 2012b). In contrast, no consistent patterns have been observed in Alaska, with both positive and negative effects of temperature on salmon production (Malick et al. 2009; Sharma and Liermann 2010; Sharma et al. 2013). Finally, in addition to large scale climatic effects, local scale processes can also be important and affect salmon survival (Beamish et al. 2010c; Borstad et al. 2011; Sharma et al. 2013).

Table 3. Number of juvenile salmon recovered or tagged to investigate their migration behaviour. HD86: Hartt and Dell (1986); CWT: coded-wire-tags; DNA: genetic stock identification; AT: acoustic tags.

Species	HD86	CWT	DNA	AT
Pink salmon	56	--	--	--
Chum salmon	6	--	1625	--
Sockeye salmon	41	3	8942	1275*
Coho salmon	244	914	2344	417
Chinook salmon	12	2456	8688	3125
Steelhead salmon	1	--	--	1863

*Includes 96 kokanee

Data compiled from Balfry et al. (2011); Beamish et al. (2010a, b, 2012a, b); Chamberlin et al. (2011); Chittenden et al. (2008, 2009, 2010a, b); Farley et al. (2011); Hartt and Dell (1986); Kondzela et al. (2009); McCraney et al. (2010); Melnychuk et al. (2007, 2010, 2013); Moore et al. (2010a, b, 2012); Morris et al. (2007); Murphy et al. (2009); Neville et al. (2010); Preikshot et al. (2012); Quinn et al. (2011); Rechisky et al. (2009, 2012); Rice et al. (2011); Seeb et al. (2011); Thomson et al. (2012); Trudel et al. (2009, 2011); Tucker et al. (2009, 2011, 2012); Van Doornik et al. (2007); Welch et al. (2004, 2009, 2011); Wood et al. (2012).

Distribution and migration

To assess the effects of climate change and ocean conditions on Pacific salmon, we must first determine where they migrate to and how much time they reside in different regions of the ocean (Trudel et al. 2009). Significant progress has been made during the last seven years to understand stock-specific migration behaviour of juvenile Chinook, coho, and sockeye salmon, and steelhead using DNA analyses and tags (Tables 2 and 3). However, little effort has been directed in North America to investigate the migration behaviour of the two most abundant species, pink and chum salmon (Table 2; but see Kondzela et al. 2009). Overall, migration behaviour has been shown to vary among species, stocks, and life-histories, with slow and fast migrants, residents, and southward migrants (Morris et al. 2007; Trudel et al. 2009; Tucker et al. 2009; Beamish et al. 2010a, c). Migration routes may also be genetically programmed (Weitkamp 2010; Sharma and Quinn 2012; Tucker et al. 2012; Burke et al. 2013), but juvenile salmon distribution along their migration trajectory may be affected by size (Tucker et al. 2009; Beacham et al. 2012) and local conditions (Bi et al. 2007, 2008; Farley and Trudel 2009; Bi et al. 2011; Burke et al. 2013). Furthermore, migration behaviour of hatchery and wild fish appear to be different at small scales during the early marine life (Chittenden et al. 2010a; Moore et al. 2012), but similar over larger scales (Tucker et al. 2011). In general, the rapid northward and counterclock-wise migration of juvenile salmon that has been hypothesized by Hartt and Dell (1986) along the continental shelf of the west coast of North America has been supported through the application of coded-wire tags, DNA analyses, and acoustic tags (Morris et al. 2007; Trudel et al. 2009; Tucker et al. 2009, Welch et al. 2009; Tucker et al. 2011, 2012;), though there are some exceptions such as Harrison River sockeye salmon that remain in the Strait of Georgia for an extended period of time before migrating north (Tucker et al. 2009; Beamish et al. 2010a, 2012a).

Growth, bioenergetics, and diet

Although a number of factors may be affecting the survival of juvenile Pacific salmon along their migratory corridor such as prey availability (Tanasichuk and Routledge 2011; Wells et al. 2012) and predator abundance (Emmett and Sampson 2007), it is generally believed that large and fast growing fish have higher survival, either because large fish are less vulnerable to gape-limited predators or can sustain starvation (i.e., winter) for longer periods of time (Beamish and Mahnken 2001). However, it should be noted that while large and fast-growing juvenile salmon have been found to have a survival advantage over small and slow-growing salmon (Beamish et al. 2006a; Duffy and Beauchamp 2011; Farley et al. 2011; Tomaro et al. 2012), size-selective mortality has not always been apparent during summer or winter in juvenile salmon (Welch et al. 2011; Trudel et al. 2012).

Bioenergetics models have been particularly useful for understanding the processes affecting juvenile salmon growth. In particular, they showed that prey quality and quantity may be more important for juvenile salmon growth and survival than temperature itself, and that the effect of temperature on growth is likely indirect and mediated by changes in prey quality and quantity (Beauchamp 2009; Farley and Trudel 2009; Moss et al. 2009). As stomach contents is expected to integrate the variability in prey availability and preferences, diet may also be a key indicator for salmon growth and survival in the marine environment (Armstrong et al. 2008; Kline et al. 2008; Kline 2010; Daly et al. 2013). Recent studies show that juvenile salmon diet is highly variable in space and time, and that diet variability is linked to changes in ocean conditions and climate (Brodeur et al. 2007a, b; Sweeting and Beamish 2009; Daly et al. 2013). In particular, although pink, chum, and sockeye salmon are generally considered planktivorous species, fish may contribute significantly to their diet in the Bering Sea during warm years (Andrews et al. 2009; Farley and Moss 2009; Farley and Trudel 2009). Prey availability may also be influenced by competition with wild and hatchery fish, though competition may be asymmetrical and affect wild and hatchery fish differently (Beamish et al. 2008, 2010d). Competition between hatchery and wild fish is likely more intense in offshore waters as recent studies also indicate that hatchery and wild salmon often feed on different prey in the nearshore environment but on similar prey offshore (Sweeting and Beamish 2009; Daly et al. 2012; Sturdevant et al. 2012a).

Pathogens and disease

Parasites have received the most attention as a mortality agent for salmon, especially in British Columbia, due to a polarized debate over the role of disease transfer from open net pens to juvenile salmon (Brooks and Jones 2008; Krkošek et al. 2008a, b; Riddell et al. 2008). In contrast to other topics, most of this research has focused on pink and chum salmon. The salmon louse (*Lepeophtheirus salmonis*) has been the primary parasite of concern in North America, though other species of lice such as *Caligus clemensi* commonly occur on juvenile salmon and have not always been differentiated from *L. salmonis* during the attached stages in field studies (e.g. Krkošek et al. 2006, 2009). In British Columbia, lice species on farmed and wild salmon varies by location and year: *L. salmonis* and *C. clemensi* are the dominant louse species in the Broughton Archipelago and Discovery Islands, respectively (Jones et al. 2006; Marty et al. 2010; Price et al. 2010, 2011). Laboratory studies have been particularly useful for assessing the susceptibility of different species of salmon to lice infection (Jones et al. 2007, 2008; Sutherland et al. 2011; Braden et al. 2012) and at understanding the lethal and sublethal effects of the salmon louse on juvenile salmon (Webster et al. 2007; Sackville et al. 2011; Tang et al. 2011; Brauner et al. 2012). Field and modeling studies indicate that adult wild salmon can contribute lice to farmed salmon and that farmed salmon can contribute lice to wild juvenile salmon (Krkošek et al. 2006, 2009; Marty et al. 2010), though other fish species contribute lice as well (Jones et al. 2006) and natural infections also occur in areas without salmon farms (Trudel et al. 2007a; Beamish et al. 2009). However, the impacts of disease transmission from aquaculture to wild salmon remain equivocal at this point (Krkošek et al. 2007, Marty et al. 2010; Jones and Beamish 2011; Krkošek and Hilborn 2011; Krkošek et al. 2011).

Future considerations

Despite this recent progress on understanding the marine biology of juvenile salmon, little is known of the causes of mortality of salmon during their marine life. Most of this progress has been achieved by correlating marine survival to one or more factors at a time. It should be kept in mind that correlation does not equal causation (Peters 1991), though correlations are an important step to identify potential mechanisms and generate testable hypotheses in fisheries science (Francis and Hare 1994). Wherever possible, experimental work should be conducted to test these hypotheses. Future effort should aim at quantifying where and when significant mortality occurs in the marine environment, its causes, as well as its contribution to recruitment variability of Pacific salmon.

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The Dispersal Pattern of Juvenile Chum Salmon in the Pacific Ocean Off the Coast of Hokkaido, Japan

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Keywords: otolith microstructure, date of sea entry, fork length at sea entry, migration, brood year strength, early marine survival

Coastal residency of juvenile chum salmon, *Oncorhynchus keta*, is thought to be the period when mass mortality takes place, which often influences their brood year strength (Saito et al. 2011). Predation and/or oceanic conditions may be the main factors causing mortality, but detailed mortality processes are still unclear (Nagasawa 1998; Saito and Nagasawa 2009). Widespread dispersion of juveniles after sea entry and unknown origin of fish after mixing with other stocks after sea entry have impeded further understanding of mortality processes during the early marine period. Otolith thermal marking is a useful tool for determining the origin of juvenile salmon after they leave freshwater. In eastern Hokkaido, otolith-marked juvenile chum salmon have been released into two rivers, the Kushiro River and the Tokachi River, since 2003 and 2005, respectively. Every year, these fish are recaptured in juvenile salmon surveys carried out in coastal waters near the Shiraoi and Konbumori coasts, which are more than 300 km apart. The recapture of marked fish revealed that some juvenile salmon out-migrating from rivers in eastern Hokkaido extend their coastal distribution westward to the vicinity of Shiraoi, which was opposite to the expected eastward direction of migration (Irie 1990; Ohkuma 2007). Comparison of the movement of juveniles originating from the same river (i.e., either Kushiro or Tokachi rivers), but recaptured at either of two distant coastal areas (i.e., Shiraoi [westward] or Konbumori [eastward]) would provide new insights on the early ocean dispersal pattern of juvenile salmon and its consequences. In this study, we examined recapture data of otolith-marked juvenile chum salmon collected in coastal waters of the Shiraoi and Konbumori coasts in April-July, 2005-2010.

At both Shiraoi and Konbumori, a transect line was set and four sampling stations were located along the line from 0.4 km to 8.0 km offshore for capture of juvenile chum salmon. Juvenile salmon were collected with a two-boat surface trawl net. The net used at Konbumori was 20 m in length, 2 m in depth, and a 3-m bag in the middle section. The net used at Shiraoi was 24.3 m in length, 2.25 m in depth, and a 13.3-m bag in the middle section. Both nets were constructed using 4–38 mm mesh sizes. The protocol for net-hauling operations included a 30 min tow at each station at a speed of 2 kts. However, this procedure was not always completed for every operation because of the existence of commercial fishing boats and other fishing gear in the vicinity that had to be avoided. To adjust for the difference in sampling effort among operations, the net-hauling distance was monitored at every operation. Juvenile salmon were collected at both transects four to eight times each year. Consequently, a total of 230 net-hauls, 143 hauls at Shiraoi and 87 hauls at Konbumori, was conducted in 2005–2010. Juvenile salmon samples were stored at -18°C or less until further analyses could be conducted.

In the laboratory, naturally thawed juveniles were measured for fork length and body weight, and otoliths were collected to check for thermal marks. If a Tokachi River or Kushiro River chum salmon was identified based on the thermal mark on an otolith, the second of the paired otoliths from that fish was utilized for microstructure analysis. In the microstructure analysis, the otolith check formed at the time of sea entry (SEC) was detected under a microscope, then (i) the radius from the otolith core to the SEC, (ii) the number of growth increments from the SEC to the otolith edge, and (iii) the spacing of each growth increment from the SEC to the edge were measured using an otolith measurement system (ARP/W+RI version 5.30, Ratoc System Engineering Co. Ltd, Tokyo). From these measurements, the back-calculated fork length at sea entry (mm), date of sea entry, and average daily growth (mm) within the first week after sea entry were estimated for each marked juvenile salmon. The details of the otolith microstructure analysis were reported by Saito et al. (2007, 2009).

The recapture location (Shiraoi or Konbumori) was analyzed using the binomial GLM. The dependent variable was absence-presence data at Shiraoi, in which fish recaptured at Shiraoi and Konbumori were assigned to “1” and “0”, respectively. Possible explanatory variables included year, river of release, number of released fish, date of sea entry, fork length at sea entry, and average daily growth (mm) within the first week after sea entry. To adjust for the difference in sampling effort among years and between locations, the net-hauling distance was used as an offset variable. Model selection was made using the Akaike Information Criteria.

A total of 351 juvenile chum salmon released from the Tokachi or Kushiro rivers was recaptured during 2005–2010. During the study period, 96 fish from the Tokachi River and six fish from the Kushiro River were collected at Shiraoi, and 185 fish from the Tokachi River and 64 fish from the Kushiro River were caught at Konbumori. Year, date of sea entry, and fork length at sea entry were selected as the explanatory variables of the final GLM model. When the fork length at

sea entry was set to 59.5 mm, which was the average value for all juveniles estimated in this study, the model predicted that out-migrants with an earlier date of sea entry have a higher probability of movement to Shiraoi. In addition, year-to-year variability in the probability of arrival at Shiraoi was also evident. When the 50% probability point of the model was compared among the years, the timing of sea entry varied from late April in 2008 and 2009 to mid-May in 2005 and 2010. The average date of sea entry of fish going to Shiraoi with a 50% probability was estimated to be 6 May. When the date of sea entry was fixed at 6 May, the fork length at sea entry showed remarkable annual variability. For instance, at a 50% probability of fish moving to Shiraoi, the model predicted that in 2005 and 2010 fish would need to be 45 mm fork length at sea entry. In 2008 and 2009, the fish would need to be 80 mm fork length at sea entry to be found at Shiraoi at the same level of probability. When the date of sea entry was assumed to be 6 May across years, results indicated the larger a fish was at the time of sea entry, the higher the probability of it going to Shiraoi. The year effect of the model, based on the condition that the date of sea entry was 6 May and the fork length at sea entry was 59.5 mm, predicted probabilities from 12% to 86% of fish moving to Shiraoi. These probabilities correlated with the number of adult returns (sum of age-0.1 and -0.2 adults) of the corresponding brood years in the Tokachi River (Spearman's rank correlation: $r_s = 0.89$, $n = 6$, $p < 0.05$). A similar correlation was observed for returns to the Kushiro River, but the coefficient was not statistically significant (Spearman's rank correlation: $r_s = 0.71$, $n = 6$, $p > 0.05$). These findings indicated that a chum salmon brood year having a higher probability of going to the Shiraoi coast showed relatively higher ocean survival.

In this study, we demonstrated that out-migrants with an earlier date of sea entry, or fish having a larger fork length at sea entry, had a higher probability of westward dispersion after sea entry, which was a direction of movement opposite to what was previously thought. In addition, a brood year having a higher probability of westward dispersion showed higher adult returns to their natal rivers. This implies that wide dispersion during early ocean life may give juvenile salmon opportunities to exploit various habitats and plays an important role in reducing mass mortality of salmon during early marine life.

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Stock Origins of Juvenile Chum Salmon Migrating Along the Eastern Pacific Coast of Hokkaido During Early Summer

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Keywords: migration route, juvenile chum salmon, otolith marking, genetic stock identification

Japanese juvenile chum salmon migrate from their natal river to the Okhotsk Sea during their first summer (Urawa et al. 2001). They remain in the Okhotsk Sea for feeding and growth before moving to the western North Pacific for their first winter. A previous study has suggested coastal migration routes of juvenile chum salmon (Irie 1990), but their stock-specific migration route and timing are unclear. In this study, we estimated stock origins of juvenile chum salmon from the eastern Pacific coast of Hokkaido by analysis of otolith thermal marks and genetic stock identification (GSI) using single nucleotide polymorphism (SNP) markers to collect basic information on the migration route and timing of each regional stock.

Surveys were conducted at the Konbumori coast (42° 57'N, 144° 31'E), eastern Hokkaido, almost weekly from early June to mid-July, 2011 and 2012. Fish samples were collected at four or five stations (0.4-12.0 km from the shore) by a seine net towed by two boats. Otolith and tissue samples were collected from each juvenile chum salmon after recording fork length (FL) and body weight. Otoliths were examined for the presence of thermal marks; marking patterns were detected at the Tokachi and Nemuro Field Stations, Hokkaido National Fisheries Research Institute (HNFRI). DNA was extracted from chum salmon tissue samples at the Sapporo Laboratory of HNFRI. Each sample was assayed for 45 SNP loci using TaqMan chemistry. Five regional stock contributions (Hokkaido: Japan Sea coast, Okhotsk Sea/Nemuro Strait, and Pacific coast; Honshu: Pacific coast and Japan Sea coast) were estimated using a conditional maximum likelihood algorithm and a SNP baseline dataset from 57 Japanese populations.

A total of 622 and 384 juvenile chum salmon was collected in 2011 and 2012, respectively. Juvenile chum salmon were observed when sea surface temperature (SST) was over 8°C at the Konbumori sampling sites. The mean FL of juvenile chum salmon caught in 2011 (7.68 ± 1.55 cm) was significantly smaller than in 2012 (10.26 ± 1.29 cm). In 2011, otolith marks were detected in 68 fish out of 622 juvenile chum salmon. The otolith-marked juveniles (5.6-11.4 cm FL) were found between mid-June and early July, all of which originated from hatcheries located along the Nemuro Strait and Pacific coast of Hokkaido. In 2012, 43 out of 384 samples were otolith-marked fish of which 31 (6.3-11.0 cm FL) were released from hatcheries in Hokkaido and 12 (9.9-12.5 cm FL) were from hatcheries located on the Pacific coast of Honshu.

GSI-estimated stock composition of small juveniles (less than 10 cm FL) caught in 2011 was 96.7% Hokkaido stocks (6.8% Japan Sea coast, 3.0% Nemuro Strait/Okhotsk Sea, and 86.9% Pacific coast) and 3.3% Pacific coast of Honshu stocks. The estimated stock composition of large fish (more than 10 cm FL) caught in 2011 was 55.0% Hokkaido stocks (11.4% Japan Sea coast, 1.2% Nemuro Strait/Okhotsk Sea, and 42.4% Pacific coast), 16.3% Pacific coast of Honshu stocks, and 28.7% Japan Sea coast of Honshu stocks.

In 2012, the estimated stock composition of small fish was 67.5% Hokkaido stocks (5.7% Japan Sea coast, 18.1% Nemuro/Okhotsk Sea, and 43.7% Pacific coast), 25.7% Pacific coast of Honshu stocks, and 6.9% Japan Sea coast of Honshu stocks. The estimated stock composition of large juvenile chum salmon was 30% Hokkaido stocks (4.2% Japan Sea coast, 3.8% Nemuro/Okhotsk Sea, and 22.0% Pacific coast), 67.3% Pacific coast of Honshu stocks, and 2.8% Japan Sea coast of Honshu stocks.

Hasegawa et al. (2013) indicated that the eastern Pacific coast of Hokkaido is a community of juvenile chum salmon originating from rivers on the Pacific coast of Hokkaido and Honshu. Our results indicate that juvenile chum salmon released from hatcheries located on the Pacific coast of Honshu migrate along the eastern Pacific coast of Hokkaido between mid-June and early July, maybe heading for the Okhotsk Sea. Our results also indicate that large juvenile chum salmon (over 10 cm FL) includes a higher percentage of Pacific coast of Honshu stocks than small fish. The mean body size of juvenile chum salmon in 2011 was significantly smaller than in 2012, and the estimated percentage of Honshu stocks in 2011 was lower than in 2012. In addition, otolith marked juveniles from the Pacific coast of Honshu were not recovered in 2011. All results suggest that the 2010 chum salmon brood-year originating from the Pacific coast of Honshu were adversely affected by the big earthquake and tsunami that occurred on March 11, 2011, in Tohoku.

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Linking Abundance, Distribution, and Size of Juvenile Yukon River Chinook Salmon to Survival in the Northern Bering Sea

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Keywords: Chinook salmon, Yukon River, juvenile abundance, migration, size selective mortality

Significant harvest restrictions, including the closure of commercial fisheries and reductions in subsistence fisheries, have been implemented in response to declining production levels of Yukon River Chinook salmon stocks. Causes of their production decline are unclear; however concurrent declines throughout the Yukon River drainage (JTC 2013), production declines in other regions of Alaska (ADFG 2012), declines in marine survival in southeast Alaska Chinook salmon stocks (Guyon et al. 2013), and the presence of bycatch in marine fisheries (Stram and Ianelli 2009) emphasize the importance of ocean conditions and the marine life-history stage of Chinook salmon.

Yukon River Chinook salmon utilize marine habitats adjacent to or on the eastern Bering Sea shelf throughout most of their marine life-history stage (Myers, et al. 2009). Sea ice and its impact on ecosystem level processes on the shelf is an important feature in the marine ecology of western Alaska salmon populations (Farley and Trudel 2009; Moss et al. 2009). Although the principal change in Arctic sea ice has occurred during the summer melt season through the loss of multi-year ice levels, sea ice primarily impacts the Bering Sea through winter/spring ice extent and seasonal ice levels. Winter/spring ice extent has not declined in a manner similar to summer ice and has actually increased in recent years, resulting in recent cooling of the Bering Sea (Stabeno et al. 2012). We review information on juvenile abundance, distribution, and size in relation to survival of Yukon River Chinook salmon and describe how they are connected to sea ice and broad-scale temperature changes in the eastern Bering Sea.

A Canadian-origin juvenile abundance index constructed from surface trawl catch, stock composition, and mixed layer depth data was used to describe juvenile abundance. Juvenile data were provided by the Alaska Fisheries Science Center as part of the US Bering-Aleutian Salmon International Survey (NPAFC 2001) and similar ecosystem-based projects in the northern Bering Sea. Surface trawl operations are described in Murphy et al. (2003) and Farley et al. (2009).

Average juvenile Chinook salmon CPUE (catch/km²) was expanded to an abundance index by the survey area, sampling grid area, and number of stations. The northern Bering Sea was divided into four spatial strata: 60°-62°N, 62°-64°N, Norton Sound, and Bering Strait, and corrections were used to adjust for inconsistent survey effort in the Norton Sound and Bering Strait strata over time. A single nucleotide polymorphism (SNP) genetic baseline (Templin et al. 2011b) was used to estimate stock mixtures of juvenile Chinook salmon through genetic mixed stock analysis (Pella and Masuda 2001). Canadian-origin stock proportions in the northern Bering Sea were reported in Murphy et al. (2009), Templin et al. (2011a), and Guthrie et al. (2013).

Mixed layer depth (MLD) corrections were applied to juvenile catch data to adjust for variation in trawl depth and vertical distribution of juvenile Chinook salmon by assuming a uniform distribution of juvenile Chinook salmon within the surface mixed layer. The MLD was defined as the depth where seawater density increased by 0.10 kg/m³ relative to the surface (Danielson et al. 2011). The MLD correction to trawl catch, θ_y , was estimated as:

$$\theta_y = \sum_j \frac{MLD_{j,y}}{TD_{j,y}} C_{j,y}.$$

where $MLD_{j,y}$, $TD_{j,y}$, and $C_{j,y}$ are the mixed layer depth, trawl depth, and catch, respectively, at stations, j , where trawl depth is above the mixed layer, and year, y . MLD trawl catchability correction, q_y , was estimated by:

$$q_y = \frac{\theta_y}{\sum_i C_{i,y}}.$$

where $C_{i,y}$ is the catch at the i^{th} station in year, y .

Brood year returns of Canadian-origin Chinook salmon to the Yukon River (JTC 2013) and the Canadian-origin juvenile index were used to define the relationship between juvenile and adult abundance. Brood year returns were rescaled to juvenile year based on the assumption that all juveniles were freshwater age-1. Although freshwater age-0 and age-2 Chinook salmon are present in the juvenile population, their numbers are low relative to the number of freshwater age-1 juveniles.

Juvenile scales and body size in the northern Bering Sea (2002-2007), and age structure and scales of adult Chinook salmon returning to the Yukon River (2004-2011) were used to model size-selective mortality. A subsample of 150 scales from Pilot Station in the lower Yukon River was digitized for each juvenile year proportional to age structure. The average (22) and standard deviation (1.98) of juvenile scale circuli counts after the last freshwater annulus were used as the sampling distribution of adult scale circuli. Adult scale measurements were converted to juvenile length (mm) from the juvenile scale radius (mm) model ($\text{length} = 149.98 \times \text{radius} + 49.367$) and reconstructed juvenile lengths (mm) were converted to weight (g) with the length-weight relationship for juvenile Chinook ($\ln(\text{weight}) = 3.0816 \times \ln(\text{length}) - 11.735$). Weight models were used to describe size-selective mortality as size-selective mortality at this life-history stage is believed to be primarily a function of energy storage (Beamish and Mahnken 2001). Due to the underlying energy allocation patterns of juvenile Chinook salmon in the northern Bering Sea, energy density is primarily a function of size and is linear with juvenile weight (Fig. 1). Size selective mortality probabilities, ρ_i , were estimated from the proportion of juvenile, j_i , and surviving adults, a_i , within each weight interval, i , as:

$$\rho_i = \frac{\frac{j_i}{a_i}}{\left(\frac{j_i}{a_i} + 1\right)}.$$

Generalized additive models (Chambers and Hastie 1992) were fit to mortality probabilities and used to describe size-selective mortality in juvenile Chinook salmon.

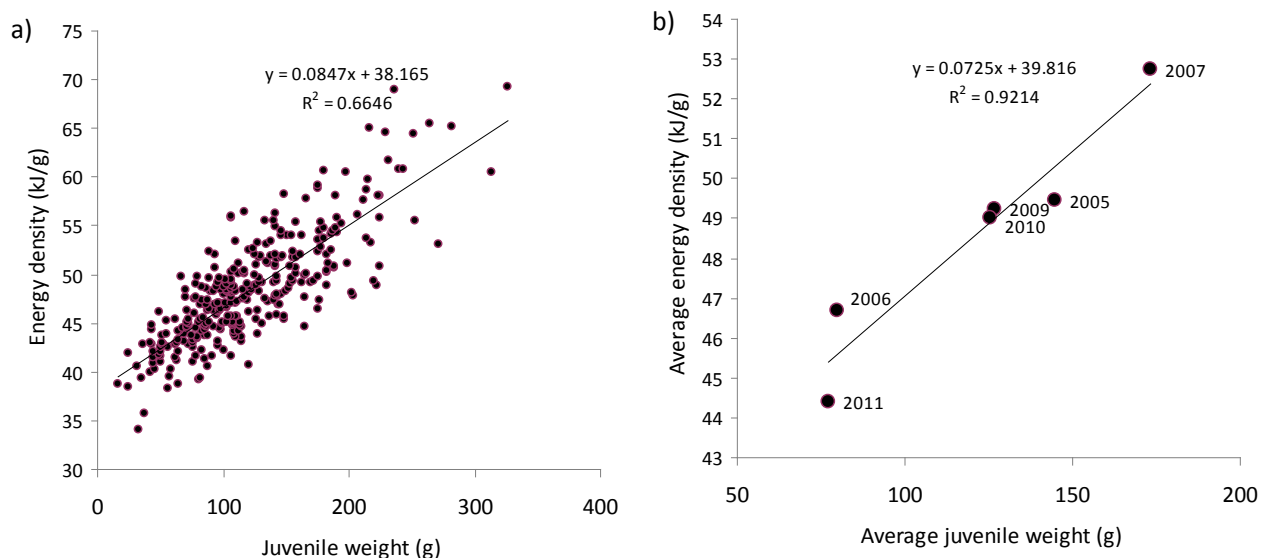


Fig. 1. The relationship between weight (g) and energy density (kJ per gram) of juvenile Chinook salmon in the northern Bering Sea for individual fish (a) and by year (b).

Average seawater temperature within the mixed layer from the BASIS surface trawl surveys were used to define inter-annual variability in seawater temperature of the northern Bering Sea shelf. Significant differences in juvenile abundance, distribution, and size between warm (2003-2007) and cold (2009-2011) years were evaluated with a Student's t-test.

Juvenile abundance of the Canadian-origin stock group was positively correlated with adult returns ($r = 0.89$, $p = 0.04$, $r^2 = 0.62$, $n = 5$; Fig. 2) indicating that juvenile abundance explains a significant ($p < 0.05$) amount of the variability present in recent adult returns. This emphasizes the importance of freshwater and estuarine (early marine) life history stages to inter-annual variability in adult returns. However, the average juvenile survival index is low (0.06; Table 1) and, therefore, mortality after the juvenile stage is important to their overall production; ecosystem and fishery effects on survival after the juvenile stage are needed to adequately address production dynamics of Yukon River Chinook salmon.

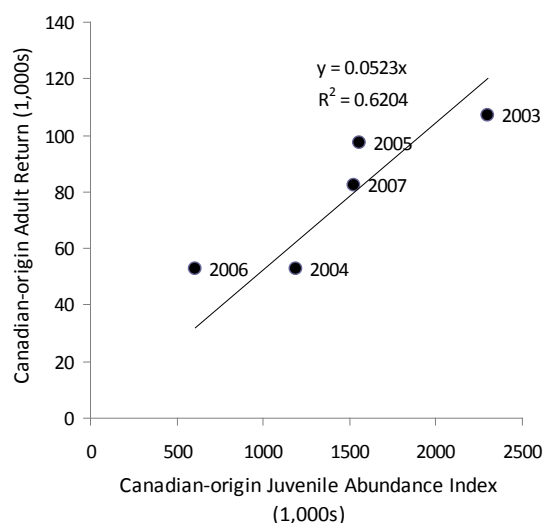


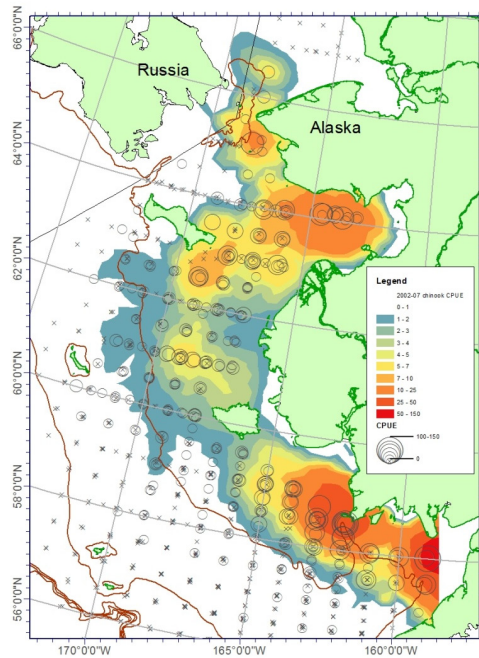
Fig. 2. The relationship between the Canadian-origin juvenile Chinook salmon abundance index and adult returns by juvenile year (2003-2007). Juvenile year is added to each data point.

Temperature limitations in the northern Bering introduce important constraints on juvenile migration. Juveniles are unlikely to survive in the northern Bering Sea once sea ice forms, and quite possibly prior to the formation of sea ice. Sea ice begins to form in coastal habitats utilized by juvenile Chinook in early November and the entire northern shelf is ice covered by early January. Sea water freezes at approximately -1.7°C in the northern Bering Sea as its salinity is in the range of 30-31 PSU (practical salinity unit). Due to shallow water depths in the northern Bering Sea, the entire water column drops below zero as sea ice forms (under ice temperatures reported in Danielson et al. 2006). Salmon lose metabolic function and cannot survive in temperatures near zero for any length of time (Brett and Alderdice 1958). The southern Bering Sea is believed to be the closest suitable overwinter habitat for Yukon River Chinook salmon. Northward dispersal/migration of juveniles through increased current speeds or northward migration behavior will displace juveniles away from winter habitats and may impact their survival (Fig. 3). Average latitude position of juveniles was negatively correlated with survival ($r = -0.68$, $n = 5$, $p = 0.21$; Table 1), and provides support (but not significant ($p < 0.05$) support) for the linkage between juvenile migration and survival.

Table 1. Juvenile abundance index, mixed layer depth (MLD) corrections, Canadian-origin stock proportions in northern Bering Sea juveniles, adult returns, and survival index for Canadian-origin Yukon River Chinook salmon from surface trawl surveys in the northern Bering Sea (2003-2011). Average length, weight, and latitude position of juvenile Chinook in the northern Bering Sea, and average seawater temperatures above the mixed layer depth from surface trawl surveys in the Bering Sea. T-test probabilities of significant differences in abundance, length, weight, latitude, and temperature between warm (2003-2007) and cold (2009-2011) years.

Juvenile Year	Juvenile Index (1,000s)	MLD correction	Canadian Stock Proportion	Canadian Juvenile Index (1,000s)	Canadian Return (1,000s)	Canadian Survival Index	Length (mm)	Weight (g)	Latitude ($^{\circ}$)	MLD Temp. ($^{\circ}\text{C}$)
2003	4,728	0.14	0.43	2,302	107	0.05	201	102	63.18	10.15
2004	2,064	0.12	0.52	1,189	53	0.04	218	130	62.93	10.88
2005	2,563	0.29	0.47	1,556	97	0.06	217	125	62.33	9.37
2006	1,179	0.13	0.46	608	53	0.09	194	87	62.52	9.16
2007	2,748	0.16	0.48	1,523	82	0.05	231	155	63.17	8.96
2008										
2009	1,846	0.01	0.45	842			223	136	61.95	8.03
2010	1,558	0.05	0.43	702			206	108	61.96	8.34
2011	3,209	0.16	0.46	1,701			195	89	62.02	7.90
2003-2007	2,656	0.17	0.47	1,436			212	120	62.83	9.70
2009-2011	2,204	0.07	0.45	1,082			208	111	61.98	8.09
$p(T \leq t, \alpha = .05)$				0.43			0.66	0.56	<0.01	<0.01

a) 2002-2007



b) 2009-2011

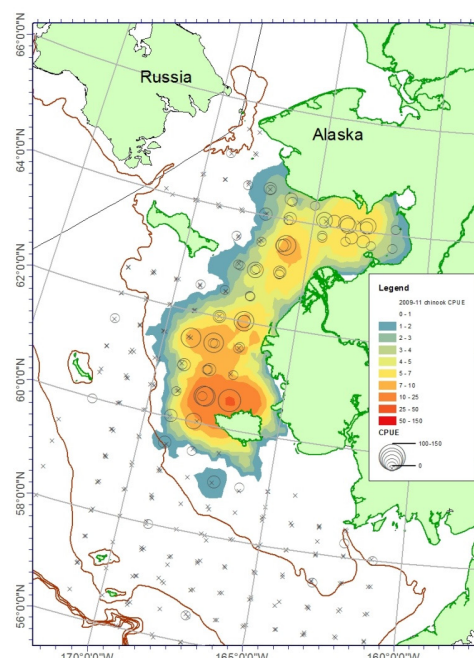


Fig. 3. Distribution of juvenile Chinook salmon catch-per-unit-effort (CPUE, catch/km²) from surface trawl surveys on the eastern Bering Sea Shelf, August-September (2002-2011). Circles are CPUE data at each sample location and average CPUE is shaded from low to high with hues from blue to red. Distributions are shown for two time periods (a) 2002-2007 and (b) 2009-2011. Bering Sea temperatures were warmer during 2002-2007 than 2009-2011.

Size-selective mortality is evident in size distribution differences between juveniles and survivor reconstruction from adult scales (Fig. 4). Juveniles had a lower average weight (141 g) and minimum weight (18 g) than survivors (average weight of 169 g and minimum weight of 62 g). The mortality model for Yukon River Chinook salmon indicates that mortality is very high for the smallest juveniles (these are primarily late out-migrating freshwater age-0 Chinook salmon, distinguishable from age-1 Chinook by the presence of freshwater parr marks), but rapidly declines to the point of neutral selection (mortality probability of 0.5) at approximately 138 g (Fig. 5). Size-selective mortality is believed to introduce important constraints on juvenile life-history through selection against late out-migration of freshwater age-0 juveniles in Yukon River Chinook salmon. Due to the presence of size-selective mortality, faster growth rates and larger juvenile sizes will improve survival.

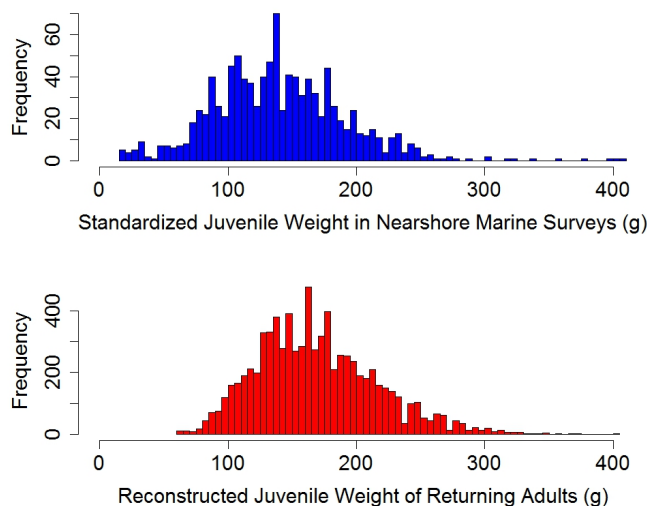


Fig. 4. Distribution of juvenile Chinook salmon weights (g) during September (2002-2007) in the northern Bering Sea and survivor weights reconstructed from adult scales collected at Pilot Station in the lower Yukon River.

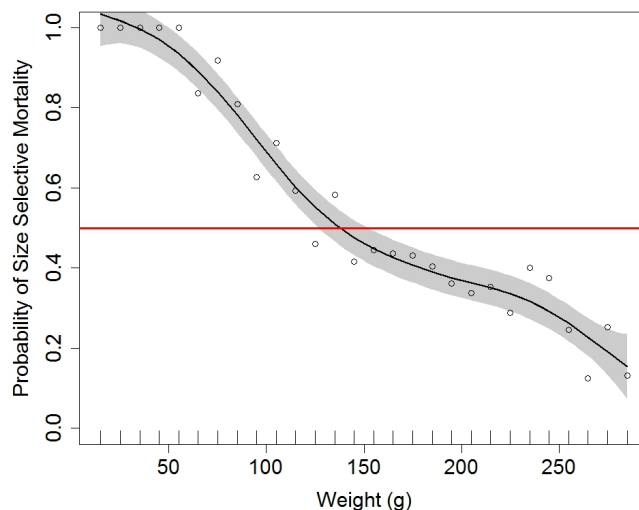


Fig. 5. A generalized additive model fit to size-selective mortality probability of juveniles collected during September (2002-2007) in the northern Bering Sea.

Although juvenile abundance and size were lower in colder years, juvenile distribution (average latitude) was the only feature of the juvenile population that differed significantly (Student's t -test $p = 0.01$, $\alpha = 0.05$) between warm and cold years (Table 1). The absence of significance may reflect a greater dependency of juvenile abundance and size on freshwater and estuarine (local) processes not linked to broad-scale temperature patterns of the eastern Bering Sea. Marine distribution patterns of juveniles appear to have a closer linkage to broad-scale ecosystem patterns of the Bering Sea ecosystem and emphasize the potential negative impact that the loss of sea ice and warming of the Bering Sea could have on juvenile migration and survival. Although adult returns appear to be primarily a function of juvenile abundance and not juvenile survival, juvenile survival impacts the ability to use juvenile abundance as a leading indicator of future returns to the Yukon River.

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Stock-specific Migration Pathways and Size of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) in Nearshore Waters and in the Gulf of Alaska

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Keywords: juvenile migration route, Fraser River, sockeye salmon, genetic stock identification

Individual identification of sockeye salmon (*Oncorhynchus nerka*) caught in Washington, coastal British Columbia, southeast Alaska, and Gulf of Alaska sampling sites during 1996-2011 was estimated through an analysis of microsatellite variation. Variation at 14 microsatellites was analyzed for over 10,000 juvenile sockeye salmon obtained from coastal and Gulf of Alaska surveys. A 387-population baseline spanning Japan, Russia, Alaska, Canada, and Washington State was used to determine the individual identification of the fish sampled, with individuals identified to approximately 35 stocks of origin. We outlined the migration paths and size variation of juvenile sockeye salmon ranging from the Columbia River to southeast Alaska. The study extends the results initially reported by Tucker et al. (2011), by increasing the number of populations or stocks identified from 14 regional stocks to 50 populations or stocks, and by increasing the number of juvenile sockeye sampled from 4,062 individuals to 10,500 individuals.

Determination of juvenile sockeye salmon migration routes was dependent upon accurate identification of individuals to specific populations or stocks of origin. Analysis of a known-origin sample indicated that individuals from 50 populations or stocks of sockeye salmon were estimated with a high degree of accuracy, indicative of little error in the estimated stock compositions. Therefore, reported differences in juvenile fork length and migration routes among populations should accurately reflect differences in juvenile size and migration behaviour among stocks.

Stock compositions of the mixtures analyzed increased in diversity of origin in more northern sampling locations, indicative of a general northward movement of juveniles. The primary migration route of Columbia River and Washington stocks was northward along the west coast of Vancouver Island, with a majority of the juveniles subsequently migrating through Queen Charlotte Sound and Dixon Entrance. During the same sampling month and location, Columbia River and Washington juveniles were consistently larger than those from British Columbia and Alaska. Fraser River stocks migrated principally through the Strait of Georgia and Johnstone Strait. Some Fraser River populations, such as Cultus Lake, appeared to have spent little time rearing in the Strait of Georgia, as individuals from this population were primarily observed in July samples from Hecate Strait, Dixon Entrance, and southeast Alaska. Other Fraser River populations, such as Chilko Lake and Quesnel Lake, were widely distributed in July surveys, being observed from the Gulf of Alaska to the Strait of Georgia. In a population or stock, juveniles of larger body size were observed in more northern sampling regions compared to those sampled in more southern regions, and this trend was consistent across all seasons of sampling. For example, larger individuals from the Chilko River stock in the Fraser River drainage were observed in more northerly locations compared with those in the Strait of Georgia, and mean juvenile body length increased over time during the first year in the ocean (Fig. 1).

There was substantial diversity in body size and juvenile migration pattern displayed by populations and stocks within the Fraser River drainage. There may be a relationship between timing of northward migration from the Strait of Georgia and juvenile body size, with larger-sized individuals migrating earlier than smaller-sized individuals. Body size can influence timing of juvenile northward migration, and the degree to which juveniles utilize coastal waters for rearing during the fall and winter of their first year in the ocean, forgoing rearing in the Gulf of Alaska or the North Pacific Ocean. There was considerable variation among Fraser River populations and stocks in location and timing of capture of juveniles. Some populations moved rapidly through the Strait of Georgia to begin their northward migration. Conversely, some populations or stocks reared for a period of time in the Strait of Georgia before beginning their northward migration. For example, individuals from the South Thompson River stock were abundant in the Strait of Georgia in June (n = 411) and July (n = 85), and this stock constituted 31.3% of all individuals sampled in the Strait of Georgia during summer. Although individuals from this stock were widespread geographically in summer, ranging from the Strait of Georgia to off Kodiak Island, summer captures of this stock were concentrated in more southern sampling regions

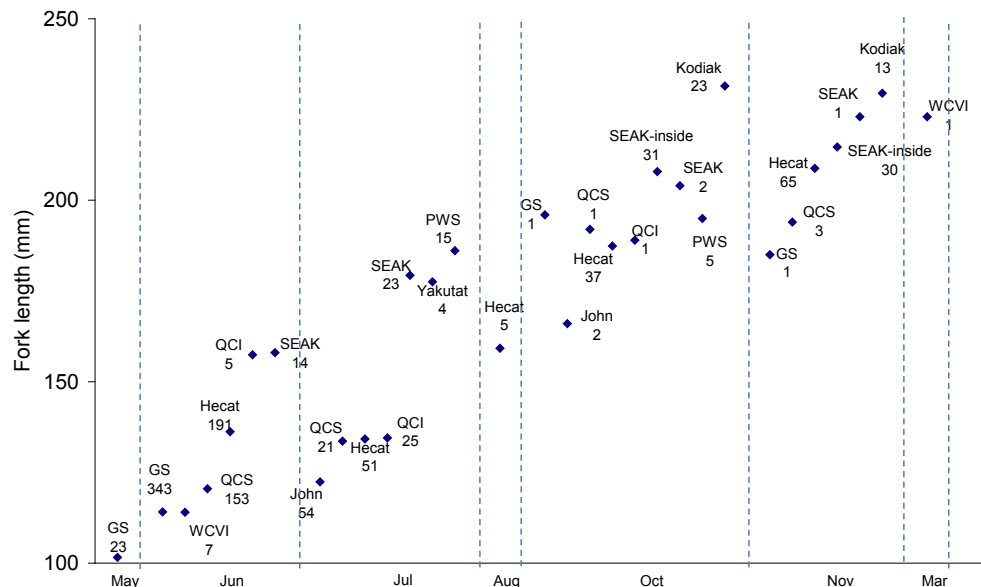


Fig. 1. Mean fork length (mm) by month of juvenile Chilko Lake sockeye salmon from the Fraser River drainage caught in 11 regions during their first year of ocean residence. Region codes are listed, along with sample size for the regional mean length. Region codes are GS (Strait of Georgia), WC (West coast Vancouver Island), JS (Johnstone Strait), QCS (Queen Charlotte Sound), Hecat (Hecate Strait and Dixon Entrance), QCI (Haida Gwaii), Inside (Southeast Alaska inside), SEAK (Southeast Alaska), Yakutat (Yakutat), PWS (Prince William Sound), and Kodiak (Kodiak Island).

Juveniles from Great Central Lake stock on the west coast of Vancouver Island were consistently smaller than those from other west coast of Vancouver Island stocks. For British Columbia central coast and Owikeno Lake stocks, not all individuals migrated northward in the summer, with some individuals still present in local areas in the fall and winter after spring entry into the marine environment. Juvenile Fraser River sockeye salmon dominated the catch of juveniles in the Yakutat, Prince William Sound, Kodiak Island, and Alaska Peninsula sampling locations. Not all Fraser River stocks displayed the same trends in relative abundance with respect to coastal Gulf of Alaska sampling groups, perhaps indicative of differential initial rearing environments. Overall, there was a wide divergence among stocks in juvenile size and dispersion among sampling locations.

Determination of stock-specific winter rearing areas, such as reported by Farley et al. (2011), may prove to be very useful in understanding the migration routes and rearing areas of sockeye salmon, perhaps being of predictive value for subsequent juvenile survival. Determination of the location and timing of specific stocks of sockeye salmon in the Gulf of Alaska and North Pacific Ocean can be obtained through the application of DNA technology.

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Evidence for Navigational Sensory Capabilities of Yearling Chinook Salmon

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Keywords: yearling Chinook salmon, migration behavior, ocean distribution, simulation, individual-based model

Yearling Chinook salmon (*Oncorhynchus tshawytscha*) from the Columbia River enter the ocean after one year in freshwater and quickly migrate north (Peterson et al. 2010). Although general migration patterns have been suggested (Weitkamp 2010; Tucker et al. 2011) and several environmental correlates determined (Bi et al. 2007; Burla et al. 2010a; Peterson et al. 2010; Burke et al. 2013; Miller et al. 2013), we do not have a comprehensive understanding of the early ocean ecology of these juvenile salmon. One of the more difficult aspects of studying juvenile salmon ocean ecology is the behavioral responses to environmental stimuli. For example, what cues do salmon use to orient during migration? If fish make decisions so as to maximize their growth rate (a logical objective, given that mortality is size-dependent (Arendt 1997)), would this strategy result in the growth rates and spatial distributions we observed empirically? Although waters off of Alaska tend to be more productive than areas near Oregon and Washington, fish leaving the Columbia River have no cognitive knowledge of this fact. Is a northward migration therefore an evolved strategy? If so, what role does local environmental variability play in migration?

As a first step towards addressing these complex questions, we created an individual-based model in a coupled Eulerian-Lagrangian framework to simulate fish movement through a virtual environment (Willis 2011; Burke et al. In Review). Specifically, we used the output from a Eulerian hydrodynamic model as the virtual environment and created a Lagrangian individual-based model (IBM) that allowed individual fish movements and behaviors. This model is intended to (1) distinguish between feasible and unrealistic behaviors, under constraints of coastal currents, outmigration timing, and fish size and (2) evaluate various feasible migration behaviors by comparing simulated spatial distributions to observed distributions.

The model was driven by environmental and individual fish-level variables. Environmental input data (three-dimensional flow, temperature, salinity, bathymetry) were obtained from the Virtual Columbia River modeling system (Baptista et al. 2008), which is based on the 3D finite element circulation code SELFE (Zhang and Baptista 2008) run with realistic bathymetry and river, ocean, and atmospheric forcing (Burla et al. 2010b). Chlorophyll *a* concentration was obtained from a satellite via the NOAA CoastWatch Program and NASA's Goddard Space Flight Center, OceanColor Web (<http://coastwatch.pfsl.noaa.gov>, "Chlorophyll-a, Aqua MODIS, NPP, 0.05 degrees, Global, Science Quality*" downloaded March 13, 2012).

Mortality was high in this stage of the salmon life cycle, but we had insufficient information to parameterize mortality mechanistically. Therefore, all simulated fish are survivors of the first three months in the marine environment.

Each simulation started 12:15 am on April 1 and ran through midnight on July 1. At the start of a simulation, we generated 10,000 virtual fish and assigned initial values for outmigration date and a three dimensional location. Fish sizes ($\mu = 155$ mm, SD = 15 mm) and outmigration dates ($\mu =$ May 15, SD = 10 days) were drawn randomly from normal distributions, roughly matching data collected in the Columbia River estuary (Weitkamp et al. 2012). Starting locations were just inside the Columbia River mouth (46.2482 °N, 124.0759 °E) at randomly and uniformly assigned depths within the top 10 m. The model time step was 15 min.

We defined five distinct behavioral rules (Table 1) to determine whether simple and efficient behaviors were sufficient to match simulated fish distributions with empirical data or whether more complex and energetically costly behaviors were required. The null behavior, PP, assumes fish are passive (Willis and Hobday 2007; Brochier et al. 2008) and serves as a particle tracer of ocean currents. Two behaviors allow for vertical migration: OT maintains fish at the depth closest to their optimum temperature for growth (we used 12°C, which was the upper range found by Hinke et al. (2005)) and OF allows fish to selectively adjust depth within the top 20 m to maximize passive northward movement. To tests results from similarly coupled oceanographic and IBM models that showed swimming with or against the currents could be a successful strategy (Booker et al. 2008; Mork et al. 2012), we tested rheotaxis (RP). Although we report results for just positive rheotaxis, we also ran simulations using negative rheotaxis. However, ocean currents in this region are predominantly southern in the springtime and negative rheotaxis was obviously not a viable strategy. Finally, behavior SX simulates active northward swimming (three swim speeds were simulated: 0.3, 0.5, and 0.9 bl·s⁻¹) independent of the local environmental conditions.

Table 1. Simulated movement behaviors.

Behavior ID	Behavior	Description
PP	Passive Particle	No active swimming, passively drift with ocean currents
OT	Optimize Temperature	Migrate vertically each time step to the depth closest to 12°C. Optimal temperature during the first summer at sea is probably between river temperatures (~ 15°C) and temperatures observed for subadults (8 - 12°C, Hinke et al. 2005)
OF	Optimize Flow	Similar to selective tidal transport; migrate vertically each time step to depth of greatest northward flow within the top 20 m
RP	Rheotaxis (positive)	Swim at a constant rate (0.5 bl·s ⁻¹) each time step in the same horizontal direction as the ocean current
SX	Active Northward Biased Migration	Actively swim northward along the coast. Separate simulations were run where using swim speeds of X = 0.3, 0.5, or 0.9 bl·s ⁻¹ . Mean swim direction was 8° west of north. An Ornstein-Uhlenbeck process was used to alter the swim angle each time step to bring fish back towards the 28.5 km-from-shore migration route.

Yearling Chinook salmon from the Columbia River are consistently captured in a longitudinal band less than 0.5° wide along the Washington coast, but our efforts to mechanistically model such a narrow migration corridor were unsuccessful. As the northward migration was our primary focus, we simplified the model by creating an attraction to a specific east-west location (28.5 km from shore) using an Ornstein-Uhlenbeck process. In this framework, fish swam at a mean angle of 8° west of north (approximately along the coastline), but this angle was adjusted at each time step back towards the attraction location.

We used yearling Chinook salmon catch data from an ongoing NOAA Fisheries survey (Peterson et al. 2010) to test the model. This survey is conducted annually in May, June, and September. Few yearling Chinook salmon are caught in September, so we compared simulated spatial distributions to survey data from May 26th and June 26th (the midpoints of survey cruises). We calculated a kernel density of simulated fish locations using the kde2d function in the MASS package of R (Venables and Ripley 2002; R Development Core Team 2011) to summarize model results. Due to limitations of the time to run simulations and the quantity and quality of data on juvenile salmon distribution, we restricted the analysis to migration years 2003, 2004, and 2008, which represent a range of both salmon survival and oceanographic conditions (Tomaro et al. 2012). Details on survey methods and gears used to obtain the fish distributions are available in Brodeur et al. (2005).

Out of five biologically possible migration behaviors for yearling Chinook salmon during their first three months at sea, our analysis indicates only one or two are plausible. Ocean currents off the coast of Washington in spring, which are predominantly from the north, prevent fish with most of the behaviors from heading north. In fact, most behaviors resulted in fish moving south and far offshore of the Oregon coastline in a large offshore eddy, with very few able to counter the strong southward flows.

The behavior sets that produced spatial distributions most similar to observed distributions were month-specific. For May, OF (optimize flow) and SX (active northward biased migration) fit the observed distributions equally well (Fig. 1), suggesting that salmon modified depth to avoid the strongest southerly ocean currents. For June, only active swimming produced a reasonable spatial overlap with observed distributions (Fig. 1); the OF strategy could not maintain northward movement in June. Interestingly, for a given year, the best swim speed was the same in both months.

The swim speed required to match empirical distributions varied among years. In 2004, when southward currents were relatively mild, swimming at 0.3 bl·s⁻¹ matched quite well the observed distributions. In contrast, swimming 0.9 and 0.5 bl·s⁻¹ was required to match observed distributions in 2003 and 2008. The consistent distributions of juvenile salmon along the coast of Washington in spring and summer can only be achieved if using year-specific, northward-biased migration behaviors. This suggests that in addition to a compass sense, salmon have a map sense of location and adjust their speed to achieve a consistent migration rate independent of the ocean current speed.

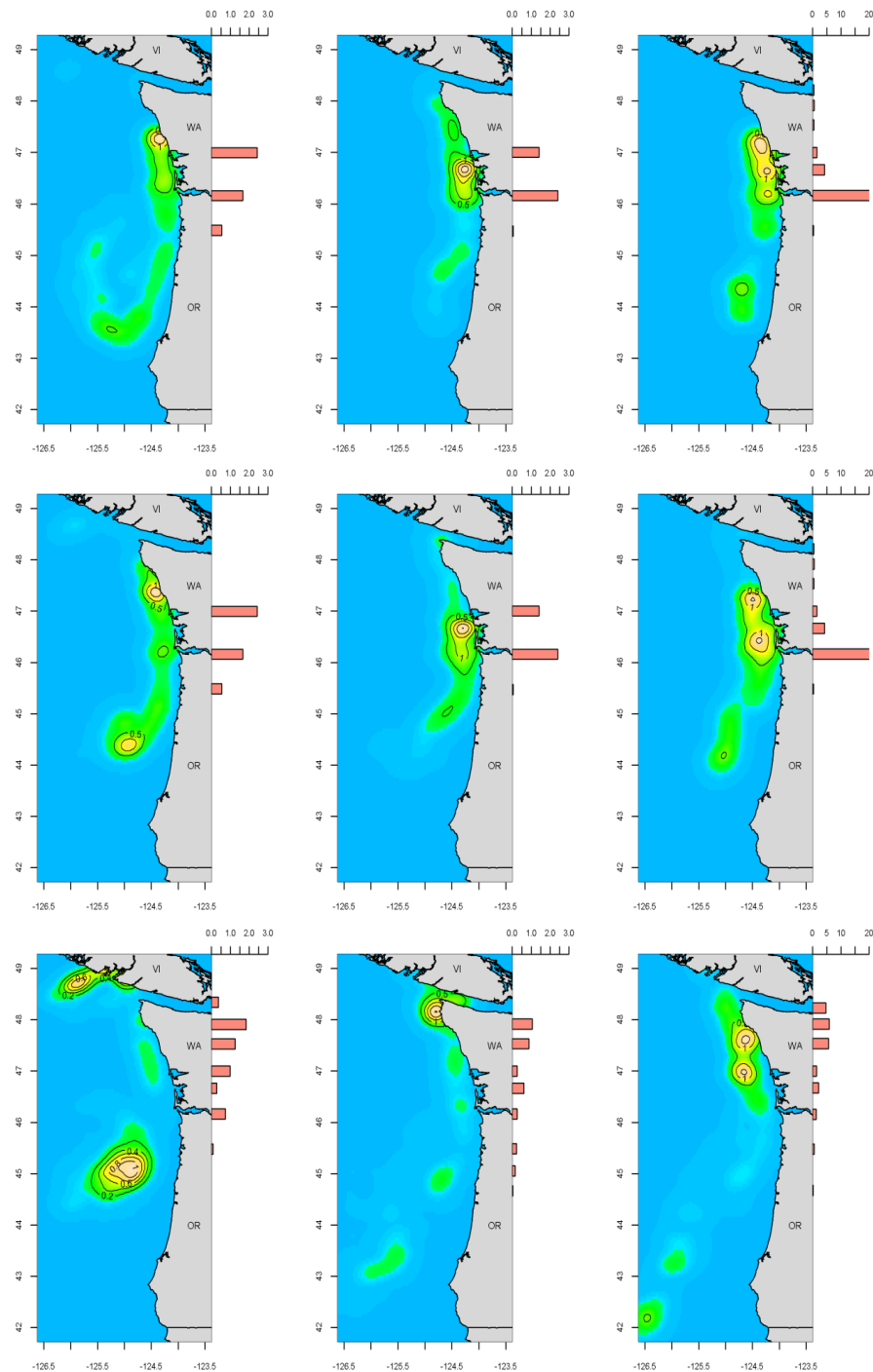


Fig. 1. Best models for May (top row, middle row) and June (bottom row) for 2003 (left column), 2004 (middle column), and 2008 (right column). Black bars represent the mean catch of yearling Chinook salmon in our surveys.

The spatial variance of the simulated fish was higher than for the observed fish (data not shown) suggesting actual fish have greater control of their migration behavior than expressed in our model. For example, simulated fish caught in an eddy south of the Columbia River were quickly transported south and offshore, yet it is quite rare to find yearling Chinook salmon from the Columbia River south of the river mouth (Peterson et al. 2010). This suggests that fish out-migrating from the Columbia River make location-specific behavioral adjustments to avoid entrapment in such eddies. Additionally, yearling Chinook salmon may increase their swim speed through time (Tomaro et al. 2012), reducing overall variance in location as later migrants catch up to early migrants (a behavior not in the model).

We did not test an exhaustive list of behaviors. For example, simulating positive rheotaxis with much higher swim speeds may bring simulated fish further north. Nor did we combine behaviors. It is plausible that salmon minimize southward movement through vertical migrations (avoiding the highly dynamic surface water when it flows south strongly) as a minor component of their migration strategy. Combining behaviors would not change our conclusion that salmon must swim north, but it could alter the swim speeds required to match observed spatial distributions. It is also likely that fish optimize local conditions to some extent, such as thermoregulation via vertical migrations. Studies conclusively show yearling Chinook salmon associated with certain environmental characteristics, which indicates some level of behavioral adjustment to local conditions (Bi et al. 2007; Yu et al. 2012; Burke et al. 2013). However, we did not test for combinations of behaviors and cannot currently estimate the impact of multiple behaviors on spatial distributions.

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Late Ocean Entry Timing Provides Resilience to Populations of Chinook and Sockeye Salmon in the Fraser River

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Keywords: Chinook salmon, sockeye salmon, ocean entry, resilience, Fraser River, South Thompson River, Harrison River, Strait of Georgia

Most sockeye salmon *Oncorhynchus nerka* from the Fraser River enter the Strait of Georgia by early May and most Chinook salmon *O. tshawytscha* by mid-May. There are, however, populations of Chinook salmon from the South Thompson River area and one population of sockeye salmon from the Harrison River that enter the Strait of Georgia almost two months later. The productivity of populations of both of these species with a late ocean entry life history strategy has been exceptional in recent years. The reasons for the recent improved productivity are not known, but the success identifies the importance of a temporal spread in ocean entry times for the aggregate of populations. The recent success also reminds us that the range of ocean entry timing of the aggregate of populations has evolved to be able to adapt to long-term changes in the timing of prey production in the early marine period.

Introduction

The timing of the return of mature Pacific salmon to their natal rivers has been studied extensively because this is when most fishing occurs. For example, the populations of sockeye salmon return to the Fraser River from as early as late June to as late as mid-October, with most returning in mid- to late August. Less studied is the average ocean entry time of the smolts from these populations. This report describes the early marine residence in the Strait of Georgia of sockeye and Chinook salmon that have a late-ocean-entry life history type. Smolts from these populations enter the strait six to eight weeks later than most of the other populations. The survival of these late-ocean-entry fish in recent years has been much higher than individuals from most other populations that enter the Strait of Georgia earlier. Smolts with the late-ocean-entry life history type are smaller and they enter the Strait of Georgia when the surface waters are warmer and lower in salinity. Understanding why Harrison River sockeye salmon and South Thompson River watershed Chinook salmon survive better in recent years is a key to understanding the mechanistic linkage between productivity and a changing Strait of Georgia ecosystem.

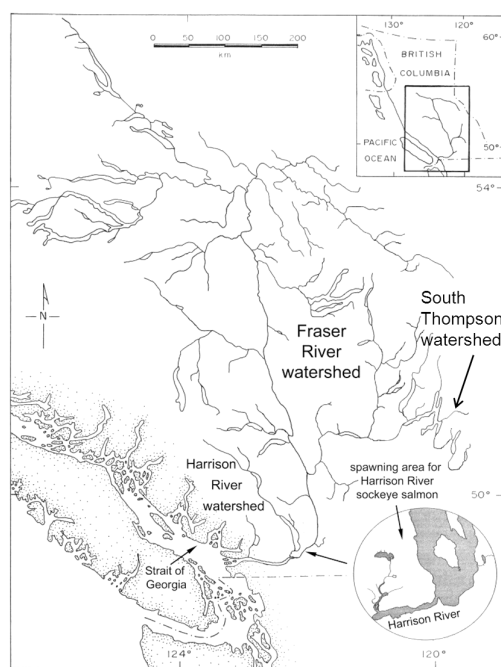


Fig. 1. Map of the Fraser River showing the Harrison River and South Thompson watersheds.

Background

Harrison River Sockeye Salmon

Harrison River sockeye salmon stocks originate from the Harrison River system, a tributary of the Fraser River (Fig. 1). Several key Fraser River sockeye salmon stocks originate from this system including Birkenhead and Weaver Creek. The juveniles of these stocks spend at least one winter in a lake before migrating to the ocean. The Harrison River sockeye salmon, however, do not spend a winter in fresh water but migrate in their first year to the ocean. This sea-type life history type was first discovered in the Fraser River by Gilbert (1914). They were identified as a separate population due to the absence of a freshwater annulus on the scales of returning adults. Although this life history type is found in other rivers, it is generally rare (Schaefer 1951). Gustafson et al. (1997) and Gustafson and Winans (1999) provide tables, which list the sea-type sockeye salmon stocks from the Harrison River in the Fraser River drainage through to Kamchatka. Many of the populations are in trans-boundary rivers (Stikine and Taku river basins) and the Harrison River population is the most southerly late-ocean-entry population known.

The Harrison River sockeye salmon spawn in the Harrison River area below the Harrison rapids. It is believed that the rapids provide a barrier to the movement of the juveniles into Harrison Lake (Gilbert 1920, 1922, 1923; Schaefer 1951). The age-0 Harrison River sockeye salmon juveniles move downstream and feed and grow in tidewater sloughs of the Fraser River estuary (Dunford 1975; Levy and Northcote 1982; Macdonald 1984; Birtwell et al. 1987). Birtwell et al. (1987) identified the Deas Slough and Ladner Reach areas on the lower river as rearing areas for juvenile Harrison River, but very little is known about these sockeye salmon after they leave the estuary. It is known that the population has been very productive in recent years (Fig. 2).

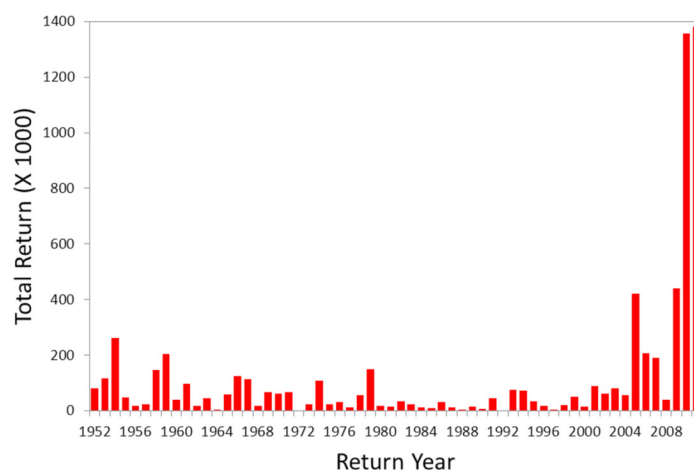


Fig. 2. Total return of sockeye salmon to the Harrison River, 1952-2012.

South Thompson Chinook Salmon

There are 14 populations of Chinook salmon that make up the South Thompson summer Chinook salmon DNA baseline (Fig. 1). Juvenile Chinook salmon from these populations remain in fresh water longer in the spring than most other ocean-type Chinook salmon. Adults return to spawn in the summer and are referred to as summer Chinook salmon.

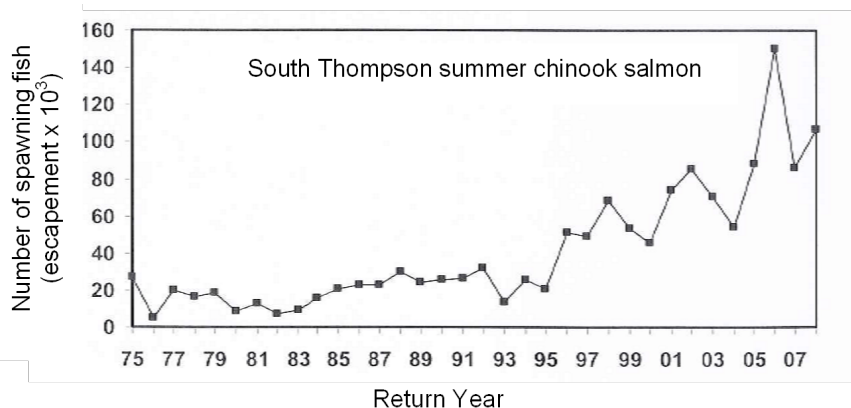


Fig. 3. Number of spawning fish from the South Thompson summer-run Chinook populations, 1975-2008.

In general, South Thompson summer Chinook salmon stocks have been very productive in recent years as indicated by the increasing escapements since the mid-1990s (Fig. 3). Six stocks (Lower Adams, Little River, Lower Shuswap/Upper Adams, Lower Shuswap, Middle Shuswap and South Thompson River) have been particularly productive (PSC 2009). This contrasts with the general escapement trends of almost all of the 133 populations (DFO 2009) that return to the Fraser River (PSC 2009).

Methods

The catch and escapement data for all sockeye and Chinook salmon from the Fraser River are from the Pacific Salmon Commission. Juvenile sockeye and Chinook salmon in the Strait of Georgia are captured during the standard trawl surveys that started in 1998. Survey dates varied slightly, depending on the availability of ship time. All trawl surveys followed a standardized track line (Beamish et al. 2012) and took between seven and nine days to complete. The net design and survey methodology have been reported in Beamish et al. (2000) and Sweeting et al. (2003). Virtually all (98%) sockeye salmon were caught in the top 30 m. Juvenile chinook salmon are caught at deeper depths than other Pacific salmon (Beamish et al. 2011). Catches are reported for 30-min sets. Catches may also be standardized to a catch per unit effort (CPUE), which was the average catch in 1 hr of fishing. Fork lengths were measured from either the total catch or from randomly collected samples. DNA stock identification was determined using the procedures in Beacham et al. (2010), by the Molecular Genetics Laboratory at the Pacific Biological Station.

Results and Discussion

Harrison River Sockeye Salmon

The total production of sockeye salmon from the Harrison River was larger in the 1950s to late 1970s, declined in the 1980s, increased in the 1990s, and increased substantially in the 2000s (Fig. 2). The total returns in 2010 and in 2011 were over 1 million fish and represented 4.8% and 27.6%, respectively, of the total production of all Fraser River sockeye salmon. Juvenile sockeye from the Harrison River were rarely caught in the open Strait of Georgia in the July trawl surveys, although they were abundant in Howe Sound (Figs. 4A-B). In contrast, virtually all of the juvenile sockeye salmon in the Strait of Georgia in the September trawl surveys were from the Harrison River (Fig. 4C). In July, Harrison River sockeye salmon were readily distinguished by their small size that in 2008 averaged 69 mm (Fig. 5). There was one survey in November 2008 that captured Harrison River sockeye salmon (Fig. 4D), indicating that some probably remained within the open strait from about mid-July to mid-November. Harrison River sockeye salmon returned as age-3 and age-4 adults (Fig. 6). In general, more adults return at age-4, similar to the average age of the more abundant adult, lake-type sockeye salmon in the Fraser River. There is an alternating pattern of age-4 adults that is related to the ocean entry year. In even-numbered ocean entry years, the percent of 4-year-old fish is higher. This does not occur in all even-numbered years, but since 1990, this occurs in seven of the ten possible years. It is in even-numbered years that there are large abundances of juvenile pink salmon *O. gorbuscha* in the Strait of Georgia. It is possible that there is a competitive relationship between the pink salmon and the juvenile sockeye salmon. The almost cyclic variations are not large, but they appear real.

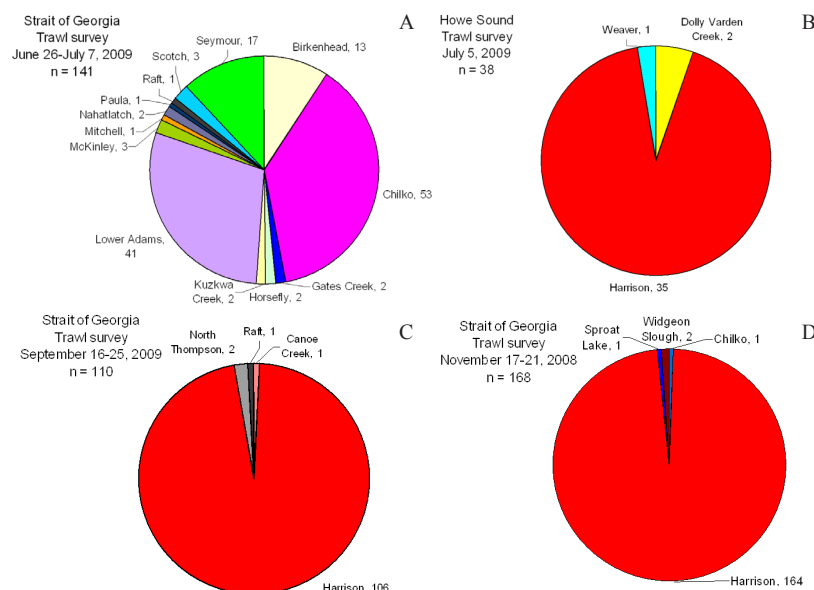


Fig. 4. DNA analysis of juvenile sockeye salmon captured in (A) the Strait of Georgia in July 2009; (B) Howe Sound in July 2009; (C) the Strait of Georgia in September 2009; and (D) the Strait of Georgia in November 2008.

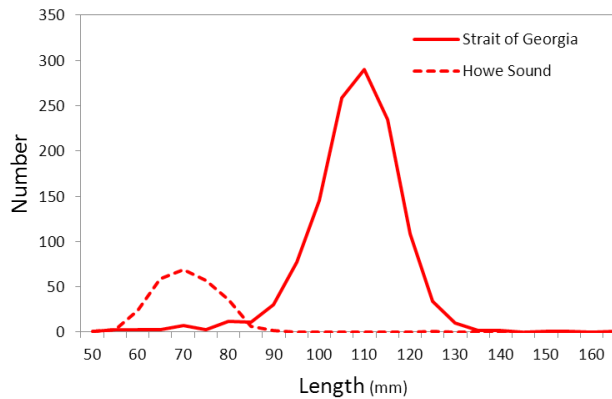


Fig. 5. The lengths of juvenile sockeye salmon captured in the Strait of Georgia (solid line) and Howe Sound (dashed line) in the July 2008 trawl survey.

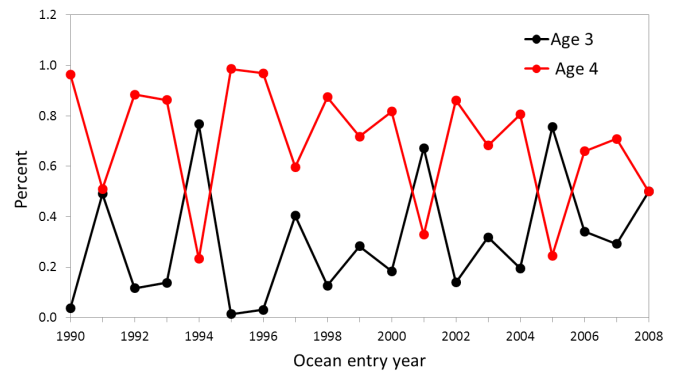


Fig. 6. The percentage of Harrison River sockeye salmon returning as age-3 (black line) and age-4 (red line) fish, 1990-2008 ocean entry year.

One interpretation is that the rate of growth of some juvenile Harrison River sockeye salmon is affected by the competition for prey and that this results in a rate of growth that is not compensated in the offshore areas. As a consequence, a larger percentage of fish remain in the ocean for an extra year. If this interpretation is correct, it is of interest that the age at return could be affected by growth patterns in the early marine period. Support for this interpretation is found in the response of the juvenile Harrison River sockeye salmon in 2007 (Fig. 6). This was an odd-numbered year, when there were relatively few juvenile pink salmon in the Strait of Georgia and when the percent of 3-year-old adults for that ocean entry year should increase. However, the percent actually declined. In the spring of 2007, there was a synchronous failure in production of all juvenile Pacific salmon and Pacific herring *Clupea pallasii* in the Strait of Georgia (Beamish and Sweeting 2012; Beamish et al. 2012; Thomson et al. 2012). The failure was attributed to a major reduction in prey as a consequence of extremely unfavourable climate and ocean conditions (Thomson et al. 2012). The juvenile sockeye salmon were relatively abundant in the Strait of Georgia in September, 2007, but it appears that something in their environment was anomalous in the strait, resulting in an anomalously larger percentage of age-4 adults.

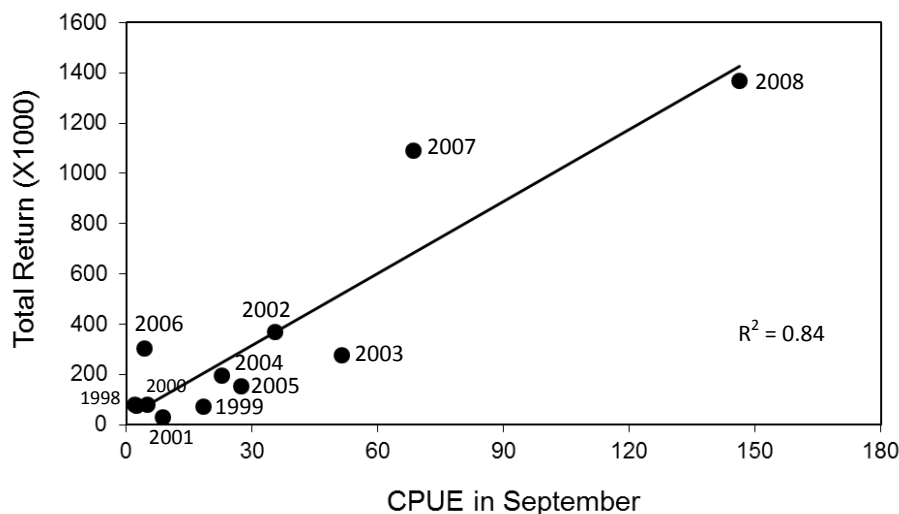


Fig. 7. The relationship between total return of Harrison River sockeye salmon and the CPUE of juveniles in their first ocean year in September. The total return includes fish that return as age-3 and age-4.

In September, the CPUE of juvenile sockeye salmon in the trawl surveys varied among years with the highest of 146.2/hr in 2008 and the lowest of 0.6/hr in 2010. When this CPUE is compared to the total return for a brood year (the sum of catch, escapement and mortalities in the river), there is a strong relationship ($R^2 \leq 0.84$; Fig. 7). This relationship was influenced by the large returns in 2007 and 2008; nevertheless, it appears that brood year strength of the Harrison River sockeye salmon is strongly related to the conditions within the Strait of Georgia during the early marine residence. (There was no relationship between escapement and the CPUE of juveniles in the Strait of Georgia in the next year ($R^2 = 0.01$) or escapement and the

total return in the resulting brood year ($R^2 = 0.23$.) According to this relationship, the total returns for the 2010 brood year (in 2013 and 2014) could be large relative to the historic pattern, and the returns of the 2011 brood year (in 2014 and 2015) could be about average for the past decade.

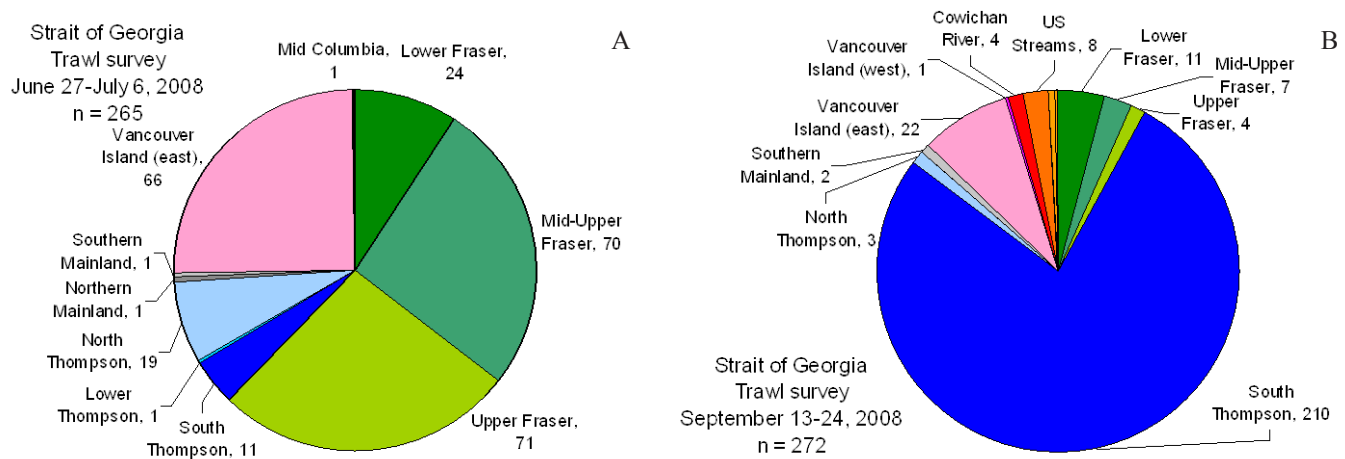


Fig. 8. DNA analysis of juvenile Chinook salmon captured in the Strait of Georgia in (A) July and (B) September 2008.

South Thompson Chinook Salmon

In the July trawl surveys, very few of the juvenile Chinook salmon were from the South Thompson River populations (Fig. 8). However, by September, a large percentage was from these populations. There are two reasons for the major change in the population composition. The juvenile Chinook salmon that entered earlier are dead or have left the strait and there has been a new influx of the late-ocean-entry juveniles into the Strait of Georgia. These late-ocean-entry life history types are small relative to the size distribution of juvenile Chinook salmon that entered the Strait of Georgia in May (Fig. 9), and by September, they can be about the same size as the average size in the July surveys (Table 1). These late-ocean-entry juveniles were not common in a trawl survey in late November, 2008, (Fig. 10) indicating that most also had died or left the Strait of Georgia.

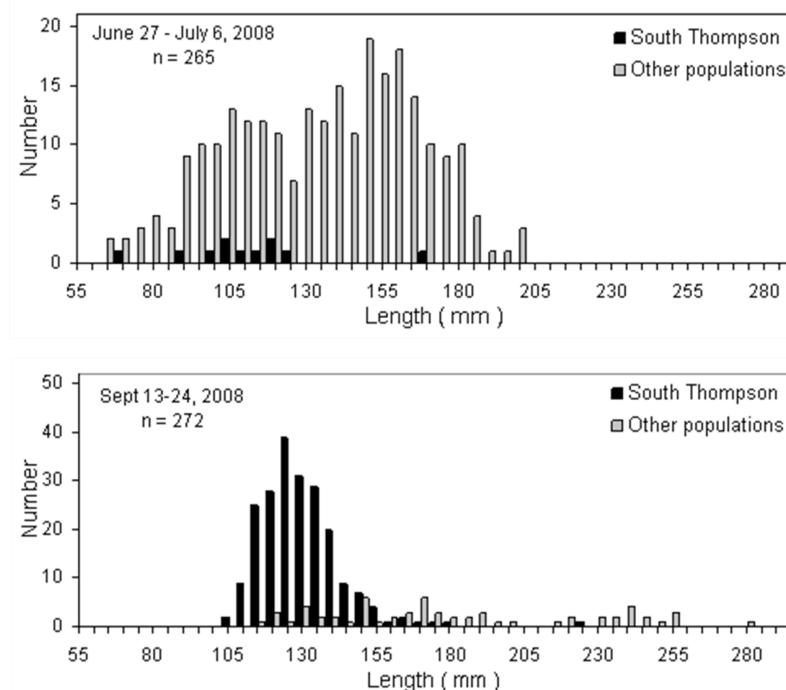
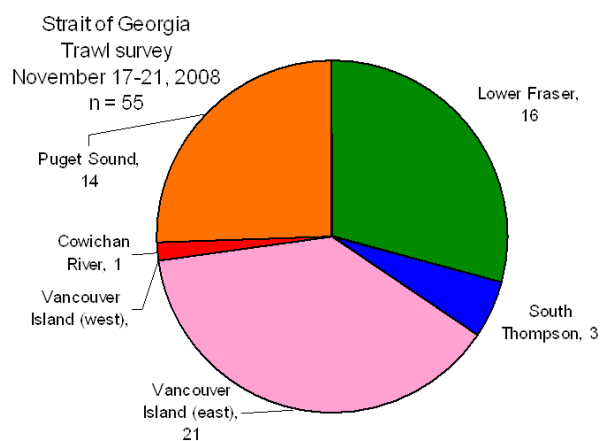
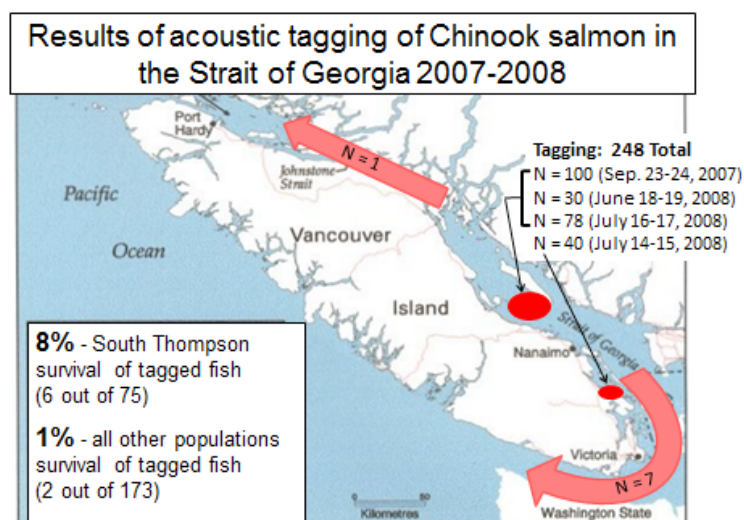


Fig. 9. Fork lengths of South Thompson summer and other populations of Chinook salmon captured in the June-July and September Strait of Georgia trawl surveys.

Table 1. Average lengths of juvenile Chinook salmon sampled in the July and September trawl surveys in the Strait of Georgia 2007-2009.

Year	Average length (SD) in the July survey	Average length (SD) in the September survey
2007	107 (20.0) n = 1,809	152 (18.2) n = 1,124
2008	128 (30.9) n = 1,674	128 (26.4) n = 1,476
2009	133 (27.2) n = 1,845	147 (31.4) n = 1,393

An acoustic tagging study in 2007 and 2008 placed 248 tags in juvenile Chinook salmon captured by purse seine in the central Strait of Georgia. Of the 248 tagged in the strait, only eight were detected leaving the Strait of Georgia. There were six from the South Thompson River populations and two from all other populations. The survival of these tagged fish as indicated by those that were detected leaving the Strait of Georgia was 8% for the South Thompson River fish and 1% for the other populations (Fig. 11). Because very few juvenile Chinook salmon remain in the Strait of Georgia over the winter, as indicated by the winter trawl surveys, the acoustic tagging study showed a higher survival for the late-ocean-entry juvenile South Thompson River Chinook salmon compared to the large abundances of juveniles that enter the Strait of Georgia in May.

**Fig. 10.** DNA analysis of juvenile Chinook salmon captured in the Strait of Georgia trawl survey in November 2008.**Fig. 11.** Detections of acoustically tagged Chinook salmon in 2007-2008 showing the larger percentage of detections of the late-ocean-entry South Thompson population.

Conclusion

The sea-type juvenile sockeye salmon from the Fraser River that enter the Strait of Georgia six to eight weeks later than the dominant lake-type juveniles were very productive in recent years, including years in which the lake-type sockeye salmon had poor survival. Juvenile Chinook salmon entering the Strait of Georgia from the South Thompson River watershed six to eight weeks later than most other juveniles also had improved productivity. The different survival between the early- and late-ocean entry life history types identifies the importance of managing to protect biodiversity. It also indicates that an understanding of the ocean, climate, and ecosystem differences over the entire ocean entry period provides clues to the fundamental processes that regulate brood year strength.

The migration timing of populations of sockeye salmon returning to the Fraser River is known to differ among populations resulting, in some cases, in distinct genetic patterns that are used in management. It might seem logical that if the timing of adults returning to fresh water resulted in a survival advantage at some period in the past, that ocean entry times may also differ among populations as a consequence of past climate and ocean changes that benefited a particular behaviour. If this is correct, we are in a period when the extreme behaviour of late ocean entry is providing a survival advantage to the aggregate of all populations of sockeye and Chinook salmon that enter the Strait of Georgia.

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Genetic Identification of Okhotsk Sea Juvenile Pink Salmon Mixed-Stock Aggregations in the Course of Their Early Marine Period of Life

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Keywords: pink salmon, mitochondrial DNA, haplotypes, genetic identification

Pink salmon is the most abundant Pacific salmon species and one of the most important components of the North Pacific and Bering Sea ecosystem. Post-catadromous juvenile pink salmon leave coastal waters for winter foraging areas after a short stay near the coast. In this paper we identify the region of origin of juvenile pink salmon using RFLP (restriction fragment length polymorphism) analysis of the mtDNA Cytb/D-loop region. Identification was aimed at making quantitative estimates of the contributions of juvenile pink salmon originating from different spawning regions to mixed-stock foraging aggregations in the Okhotsk Sea.

The quantitative evaluation was based of analysis of genetic marker frequencies in samples collected in three autumn trawl surveys in the Okhotsk Sea. Samples were collected by researchers aboard the R/V *Professor Kaganovsky* (TINRO-Center) and the STR *Uzon* (KamchatNIRO) surveys in 2011 and the R/V *TINRO* (TINRO-Center) survey in 2012. Samples were collected at 19 locations in 2011 (Table 1). Regional identification of pink salmon in the mixed-stock aggregation was determined for the total sample, but some data, including September 20–28 and October 18–30 samples, required separate analysis. In 2012 samples were collected at 11 locations (Table 2).

Table 1. Location, period of sample collection, and number (N) of juvenile pink salmon samples collected during cruises in September and October 2011.

Latitude/Longitude	N
20–28 September 2011	
53°01′/152°60′	50
53°00′/154°02′ and 53°02′/155°19′	47
54°04′/153°56′ and 53°60′/152°59′	46
54°00′/152°01′ and 53°60′/151°03′	45
54°00′/150°16′ and 54°00′/148°38′	50
54°60′/148°31′ and 55°00′/149°59′	49
55°00′/150°59′ and 55°00′/152°02′	49
55°00′/152°60′ and 55°02′/153°60′	49
55°01′/155°05′ and 56°01′/154°57′	50
56°33′/153°02′	48
51°04′/153°57′	49
Σ	532
13–30 October 2011	
52°22′/151°08′	35
49°53′/151°06′	50
49°34′/149°13′	50
50°54′/150°39′	50
50°26′/148°55′	50
54°43′/147°39′	47
52°14′/147°47′	50
50°14′/145°39′	50
Σ	382
Total	914

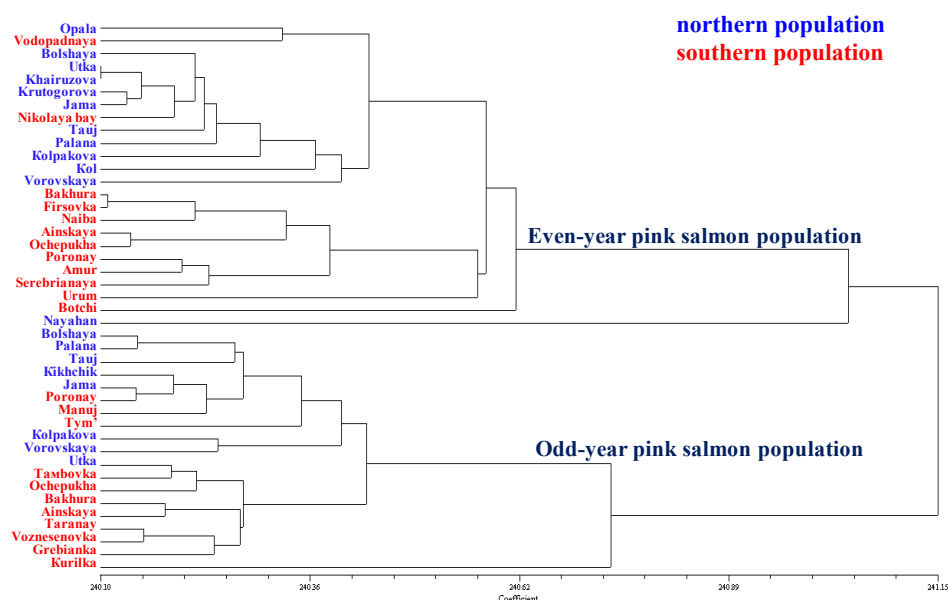
Table 2. Location, period of sample collection, and number (N) of juvenile pink salmon samples collected 7 October – 5 November, 2012.

№	Latitude/Longitude	N
1	53°13'/154°16'	47
2	51°22'/154°51'	50
3	49°41'/151°09'	50
4	55°17'/152°19'	50
5	54°52'/151°05'	49
6	51°08'/149°36'	48
7	48°45'/148°11'	46
8	50°58'/147°44'	50
9	52°37'/148°40'	47
10	52°39'/146°26'	48
11	48°35'/146°04'	48
Total		533

Juvenile pink salmon mixed-stock aggregations collected in 2011 represent fish that would return to native regions for spawning in 2012. Estimation of the error of our method was based on comparing our composition estimates for juveniles collected in 2011 with the magnitude of 2012 adult pink salmon commercial catches obtained in fishing districts located near the natal rivers.

The mtDNA haplotype diversity of the even-year pink salmon brood-line (spawn in even-numbered years) was determined from a baseline comprising 24 local populations of West Kamchatka, Sakhalin, the continental shore of the Okhotsk Sea, and Primorye. Regional identification of fish from the odd-year brood-line (spawn in odd-numbered years) was provided by analysis of a baseline comprising 19 rivers of West Kamchatka, Sakhalin, the continental shore of the Okhotsk Sea, and Kuril Islands. In total, we analyzed the mtDNA haplotype frequencies for approximately 2,500 individuals.

Results revealed 61 haplotype variants (38 composite haplotypes in the even-year brood-line, 32 in the odd-year brood-line, and 9 in both brood-lines) in mature odd- and even-year pink salmon. These data on population diversity of both even- and odd-year pink salmon indicate genetic heterogeneity was expressed clearly and has regional characteristics (Fig. 1). The statistical heterogeneity of the regional groups was visibly higher than the heterogeneity of the populations.

**Fig. 1.** The unweighted pair-group method with arithmetic mean (UPGMA) dendrogram created using genetic chord distances and based on the frequencies of composite haplotypes of even- and odd-year Asian pink salmon (43 rivers).

Identification accuracy was evaluated using maximum likelihood estimates for individuals based on different frequencies of composite haplotypes from rivers of West Kamchatka and the northern part of the continental shore of the Okhotsk Sea (northern populations) and from Sakhalin, Kuril Islands and Primorye (southern populations; Table 3). Identification accuracy was 92% for northern and 88% for southern populations of even-year pink salmon. For odd-year fish, the accuracy

was lower, 79% for northern and 84% for southern populations, which could indicate lower regional differentiation for this brood-line. Judging on these results, there is no doubt that differentiation of the even-year brood-line is sufficient for genetic analysis at a regional level. As for odd-year pink salmon, differentiation requires further clarification based on analysis of the maximum number of samples available from watersheds representing principal spawning areas.

Table 3. Average percent (standard deviation) correct and incorrect allocations (read vertically) by region for simulated mixtures based on the number of even-year pink salmon regional groups. Expected value for estimates shown in bold is 100%.

№	Region	1	2
Even-year pink salmon			
1	Northern populations	92.0 _(4.45)	11.8
2	Southern populations	7.4	87.8 _(6.72)
	Unknown	0.6	0.4
	Σ	100	100
Odd-year pink salmon			
1	Northern populations	78.6 _(13.06)	15.0
2	Southern populations	20.8	84.2 _(10.86)
	Unknown	0.6	0.8
	Σ	100	100

The RFLP analysis of mtDNA from all the mixed-stock marine samples of juvenile pink salmon revealed 21 composite haplotypes. According to the principle of maximum similarity of composite haplotypes, the frequency distribution in the baseline samples from the two populations was used to estimate the percent regional contribution of the mixed-stock samples.

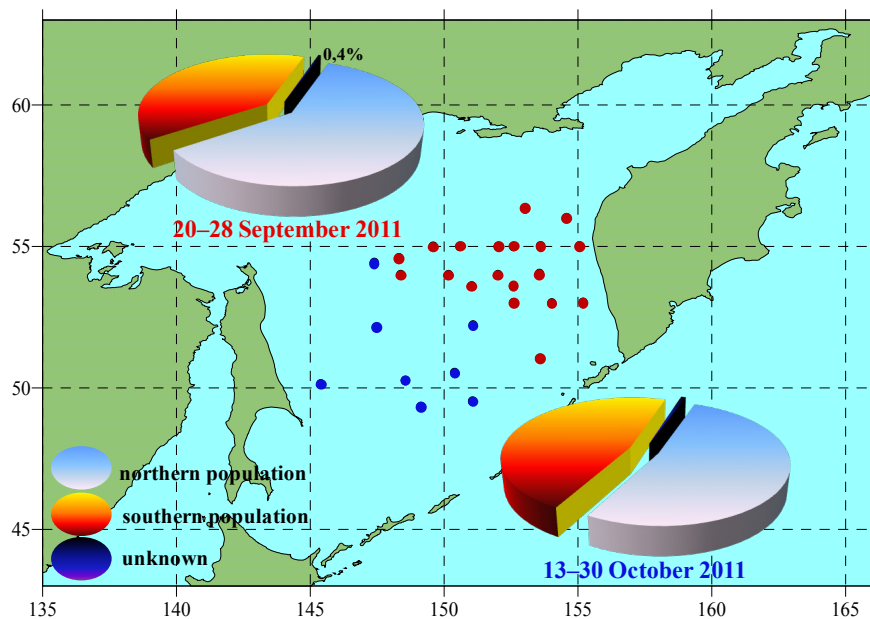


Fig. 2. Regional estimates for pink salmon based on genetic analysis of juveniles in marine feeding aggregations in autumn 2011. Sample location by sampling period is indicated by dot color (September: red, October: blue).

Genetic differentiation of pink salmon allowed for regional identification of the mixed-stock marine samples of juvenile pink salmon (Figs. 2 and 3). Results were obtained from two groups of samples: one group collected in September in the more northerly area and stations close to the Kamchatka Peninsula, and the second group collected in October in the central part of the Okhotsk Sea. In general, the estimated percentage originating from southern populations was less (39.6% in the September samples and 46.9% in the October samples) than the proportion originating from northern populations (Fig. 2). The difference in estimates between the September and October sample groups can result from the different time and area of sampling, but it can also illustrate when juvenile fish emigrate from their native regions and start to leave coastal areas to feed at sea.

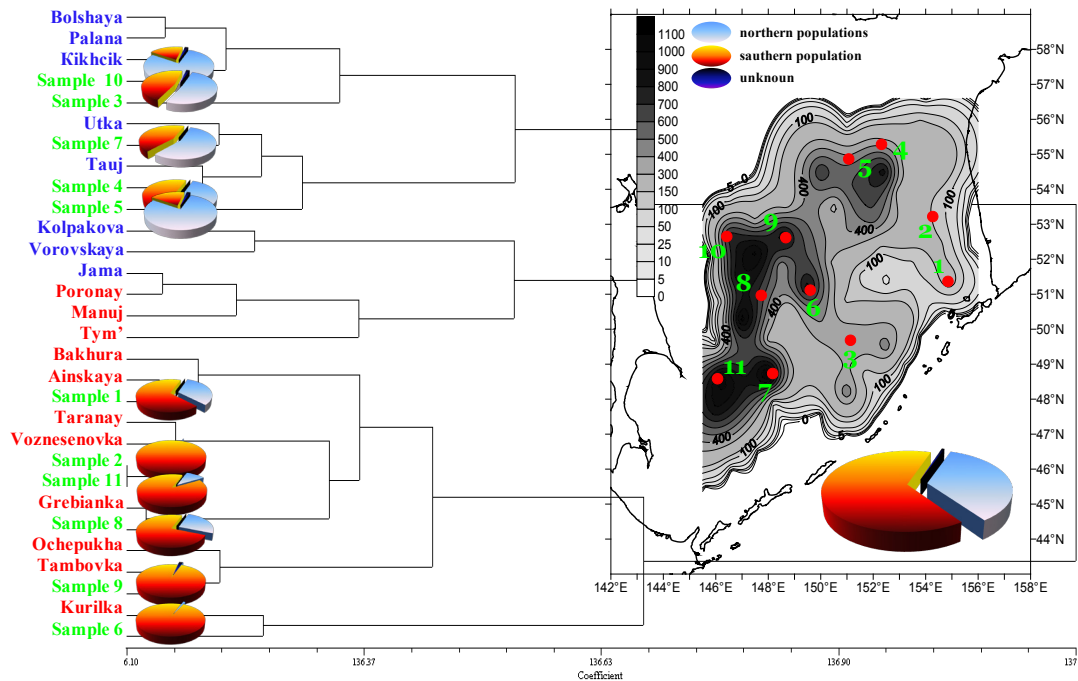


Fig. 3. The unweighted pair-group method with arithmetic mean (UPGMA) dendrogram was created using genetic chord distances and based on the frequencies of composite haplotypes of odd-year Asian pink salmon and samples of juveniles in mixed-stock aggregations.

Estimation of the error of our method was based on comparing our mixing proportion estimates of juvenile pink salmon samples to catches of adults the following year caught in fishing districts in the Okhotsk Sea basin. In a preliminary assessment, the percentage of northern pink salmon populations from West Kamchatka and Magadan Region in the total commercial catch was 57.3%, and the percentage of southern pink salmon populations from Sakhalin, Khabarovsk, and Primorye was 42.7%. These percentages were similar enough to our genetic analysis of juveniles to suggest there is potential for this technique to assess the abundance of juvenile pink salmon stocks in mixed-stock marine aggregations in the early phase of marine foraging.

We analyzed the regional composition of mixed-stock marine aggregations of odd-year juvenile pink salmon collected during the autumn trawl survey in 2012 (Fig. 3). These results showed the portion that was represented by northern populations was rather impressive, > 30% (standard deviation 9%).

In our view, assessment of mixed-stock aggregations of juvenile pink salmon abundance can be done under the following circumstances:

- regional identification accuracy of the odd-year brood-line that is relatively lower than the accuracy of the even-year brood-line;
- sampling time period is strongly influencing composition estimates because the timing of juvenile emergence from rivers and seaward migration varies by region in the Okhotsk Sea basin. The change to an earlier or later sampling period can cause an increase of northern or southern populations in the mixture.

Genetic Stock Composition of Juvenile Chinook Salmon Collected off the Mouth of the Yukon River: Are These Yukon River Fish?

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Keywords: genetic stock composition, Chinook salmon, Yukon River

Numerous federal and state commercial fisheries disaster declarations have been issued for Yukon River Chinook over the last 20 years and low Alaska returns statewide have prompted calls for research to help ascertain potential causes for Chinook salmon declines. As part of annual BASIS research surveys conducted by the United States National Marine Fisheries Service, juvenile Chinook salmon were collected off the mouth of the Yukon River between 2002 and 2011. These samples were genotyped for the genetic markers represented in the Alaska Department of Fish and Game Chinook salmon genetic baseline and preliminary estimates of the stock composition of these samples are presented. Initial results suggest that these juvenile Chinook salmon predominantly originated from coastal western Alaska (includes the lower Yukon), middle Yukon, and the upper Yukon stocks. While the sample numbers in this study were relatively small, these results suggest that research cruises positioned offshore Alaska between 60° and 65°N latitude could be used to collect Yukon-origin juvenile Chinook salmon for other analyses potentially including future models to predict relative abundance of returns.

A Novel Method to Identify Key Factors of the Gene Regulatory Network Behind Salmonids Reproductive Behavior Using Directed Graphical Modeling

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Keywords: salmonid life stage, gene expression, microarray, gene network, graphical modeling

Aquaculture and hatchery supplementation of salmonids is a common practice for both commercial and conservation purposes. However, evidence for lower genetic diversity, survival, and reproductive success of captive-reared fish relative to wild fish has accumulated in recent years. Skaala et al. (2004) genotyped microsatellite markers of wild and domesticated Atlantic salmon (*Salmo salar*) and found that domesticated salmon have 40% lower allele richness than wild fish. McGinnity et al. (2003) released micro-tagged smolts of wild, domesticated, and hybrid Atlantic salmon and found that the number of mature individuals returning to the river was severely reduced in domesticated and hybrid fish as compared to wild fish. Araki et al. (2007) measured relative reproductive success (RRS) of captive-reared steelhead trout (*Oncorhynchus mykiss*), and estimated the effects of domestication reduce subsequent reproductive capabilities by 40% per captive-reared generation. Recent studies of reproductive performance using parentage assignment methods provide deeper insights on effects of captive rearing on wild populations. However, RRS varies widely among crosses, years of release, and environmental conditions (Kitada et al. 2011), and mechanisms underlying reduced RRS are still unclear (Araki et al. 2008). We may need different approaches to elucidate the mechanism of fitness decline, which would be useful for development of sustainable aquaculture and stock enhancement technologies.

The change in reproductive behavior may be caused by changes in the endocrine system and gene expressions. Roberge et al. (2008) observed that over 6% of the cDNA clones exhibited significantly different transcription levels between farmed and wild Atlantic salmon. By directly comparing gene expression in wild-type, domestic, and growth hormone (GH) transgenic strains of coho salmon (*O. kisutch*), Devlin et al. (2009) found that domestication and GH transgenesis are modifying similar genetic pathways. Moreau et al. (2011) reported that wild anadromous males outperformed captive-reared transgenic counterparts in reproductive behavior. Despite recent progress in studies of gene expression between wild and captive-reared fish, the systematic molecular mechanisms are still unclear.

To address this issue, we propose a likelihood-based directed graphical modeling of gene expression profile and phenotypic traits to get the system-biological ground view of molecular mechanisms. Correlated gene expression is well described by a graph. It consists of the set of nodes V and the set of edges E that connect the nodes. The structure of a graph is represented by the adjacent matrix that specifies the presence or absence of edges between the nodes (Fig. 1). Significant edges can be selected by minimizing the Akaike information criterion (AIC; Akaike 1973). Because of the high dimensionality of microarray data compared with the sample size, it is important to control the signal-to-noise ratio. Instead of estimating the interaction among whole genes, we focus on a maximal connected subgraph that includes the target phenotypes or the core pathway (Fig. 2). The chronological order of temporal variation is used as a constraint on the direction of the graph. The maximal connected subgraph may quantify the biological mechanism that generates the diversity of the target phenotypes.

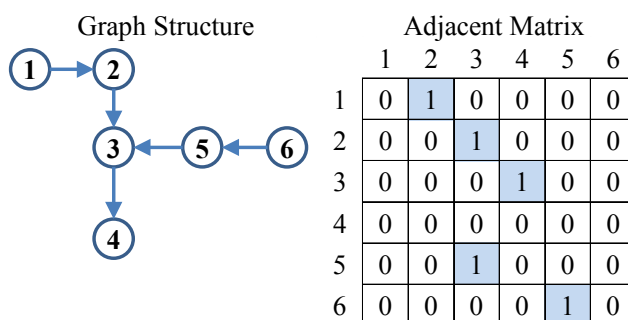


Fig. 1. Graph structure and adjacent matrix used to illustrate gene expression and phenotypic traits. Correlated gene expression is described by the graph. The structure of the graph is represented by the adjacent matrix, which specifies the presence or absence of edges between nodes. Row/column of the matrix represents the upstream/downstream direction of the graph structure.

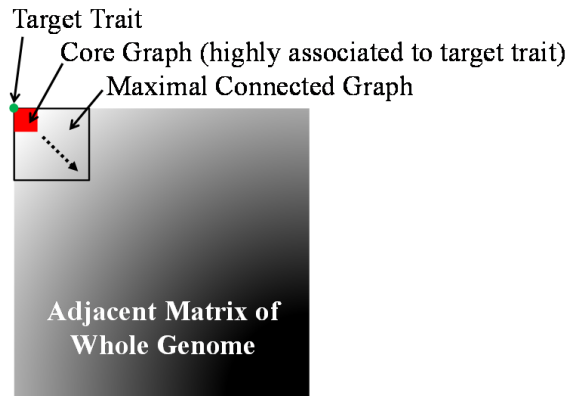


Fig. 2. Maximal connected subgraph including the core set (red block) and the target trait (green dot). Gradation represents the intensity of the association to the target trait.

Assuming a directed acyclic graph as a first approximation, the likelihood of the expression profile $\{X_v: v \in V\}$ given the graph structure (V, E) is

$$L = \prod_{v \in V} P(X_v | \{X_{v'}: v' \in \text{parent}(v)\})$$

Here, $\text{parent}(v)$ is the set of v 's parental nodes. Starting with the core subgraph, we expand the graph as far as the additional edges have significant mutual information. We developed a genetic algorithm with the fitness measure of AIC to construct the maximal connected subgraph. It consists of moving an edge (mutation), adding an edge to a terminal node (insertion), removing an edge (deletion), and crossover of edges among parent graphs.

We analyzed public data sets of sockeye salmon (*O. nerka*) (Miller et al. 2009, Accession GSE13657) and Atlantic salmon (Jantzen et al. 2011, Accession GSE25938) available from the National Center for Biotechnology Information (NCBI) Gene Expression Omnibus (GEO) to estimate the gene expression network. These data sets reflect the starting and the last stages of salmonid life.

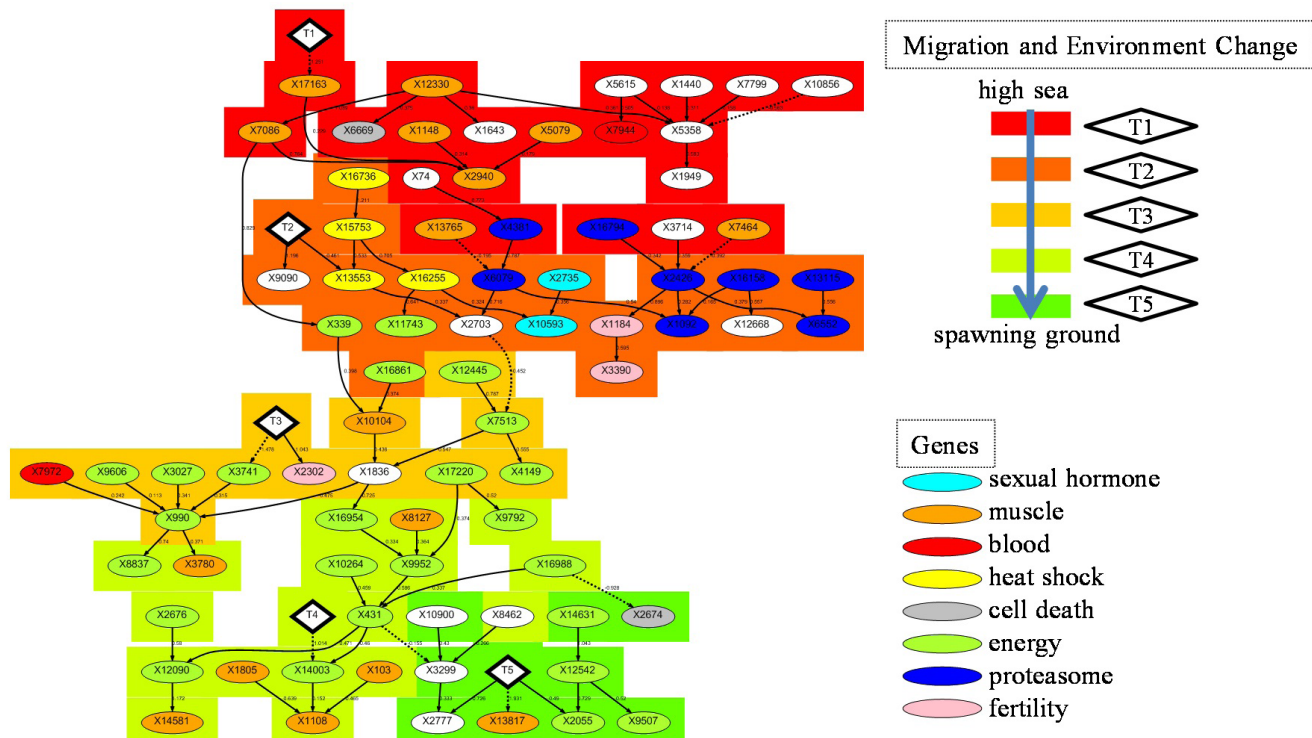


Fig. 3. Gene expression network of maturing sockeye salmon as the fish migrates from the high seas to the spawning grounds.

The first data set consists of 80 sockeye salmon individuals during the spawning migration. Samples were captured at six stages of their migration, that is, (1) high seas, (2) inland sea, (3) river mouth (salt water), (4) river mouth (fresh water), (5) midpoint to the spawning grounds, and (6) upriver spawning grounds. Expressions of 16,006 genes were measured using white muscle tissues. As an initial core subgraph, we selected 25 genes that are significantly correlated with the stages of migration ($p < 10^{-16}$). Our method estimated an expression network of 79 genes related to migration behavior (Fig. 3). Activity of muscle synthesis and energy metabolism was high for high-seas sockeye salmon. Upon entering the river mouth, osmotic shock induced heat-shock proteins that in turn activate sexual hormone receptors and gonads. Finally, fish moving from the river mouth to the spawning grounds exhibited decrease in activity of both muscle synthesis and energy metabolism.

The second data set consists of 51 individuals of Atlantic salmon in early development after fertilization. Samples were taken at ten developmental stages from 2 to 89 days post-fertilization. Expressions of 43,689 genes were measured using the whole body. In total, 45 genes were significantly correlated with the developmental stage ($p < 10^{-26}$). Starting with the subgraph of these genes, our method estimated an expression network of 147 genes working in early development (Fig. 4). Soon after fertilization, genes controlling transcription regulation, energy metabolism, and cell growth began to function. Because these genes are suggested to have a relation with oncogenes, there was concordant activity in tumor suppression. Prior to hatching, genes that generate bone, muscle, and blood were highly activated. After hatching, the immune system was activated in response to exposure to the out-of-egg environment.

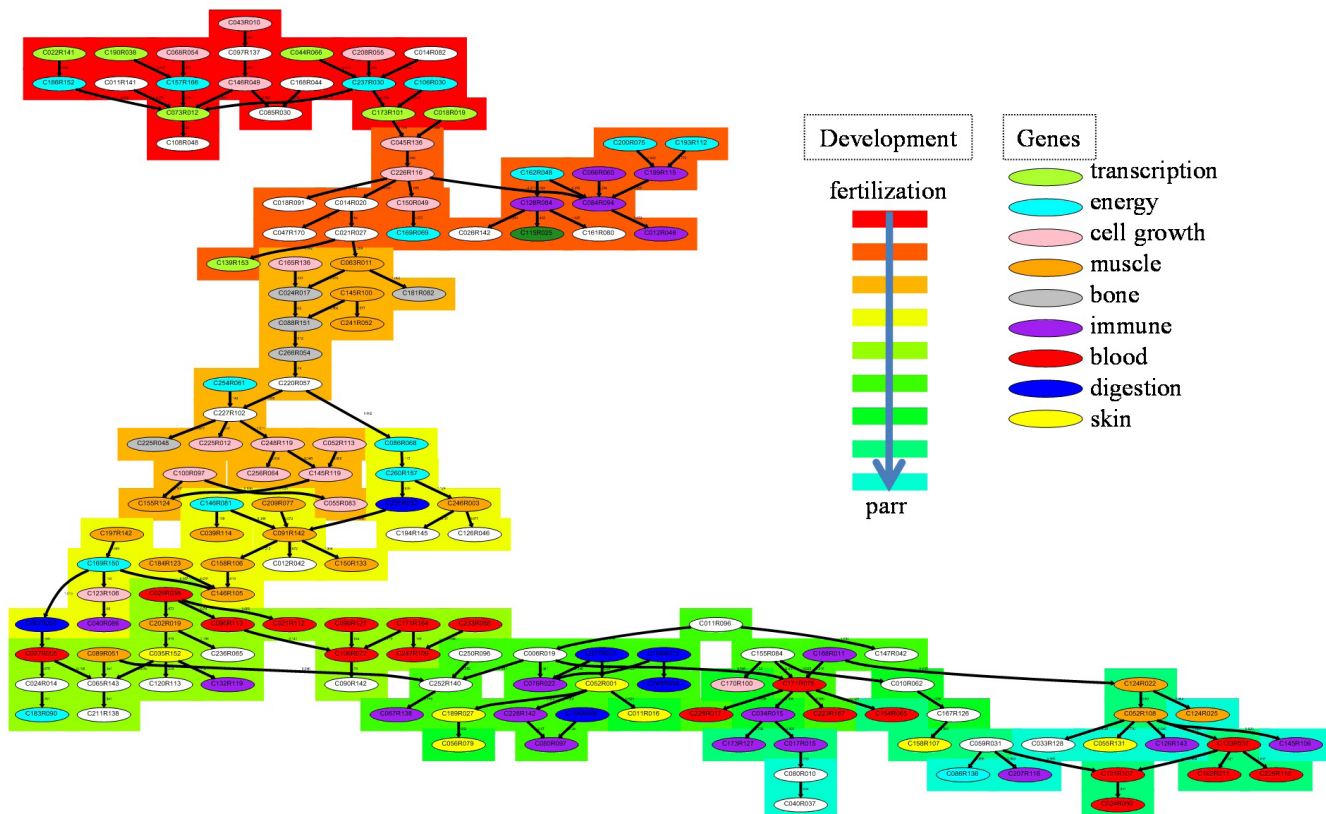


Fig. 4. Gene expression network of developing Atlantic salmon from fertilization to the parr stage.

Our method may help in understanding the gene network mechanism that is the foundation of complicated traits. From the local structure around the phenotype-node, it is possible to estimate the genes and their direct effects in determining phenotype. By tracing a series of hubs from the phenotype-node towards the center of the graph, it is possible to estimate the hierarchical module structure controlling phenotype. Our method not only gives the association among genes, but also provides the directions and effects of cascading gene expression.

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Use of the Otolith Complex Method for Stock Identification of Juvenile Pink and Chum Salmon in the Offshore Waters of the Okhotsk Sea During Post-catadromous Migrations

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Keywords: otolith, stock composition, juvenile pink salmon, juvenile chum salmon, Okhotsk Sea

There is no doubt that identification of the regional stock origin of Pacific salmon in mixed-stock ocean feeding aggregations is a challenge, especially if the stocks have overlapping migration routes. However, the challenge should be answered because the composition of catch, when correctly identified, can enhance the reliability of abundance forecasts for certain species. It is particularly informative when these techniques can be successfully applied to estimating juvenile salmon abundance in the early marine period because this period basically sets the strength of the year-class.

Scientific experience indicates that using morphological differences in otolith structure is promising for stock identification. The otolith, as one of fish's record-keeping structures, has attracted scientific interest for a long time. The formation rate of the otolith's structural elements, influenced in Pacific salmon by environment and genetics, can capture microstructural differences between populations. Normally, individuals from different populations demonstrate different otolith microstructures and relative sizes (Bugaev et al. 2012; Chistyakova et al. 2012). Examination of otolith structural variations in juvenile pink and chum salmon of Kamchatka, Sakhalin, and the northern coast of the Okhotsk Sea has demonstrated reliable differences among stocks. However, if regional variation in otolith microstructure can be used to answer practical questions, this needs to be clarified.

Otolith marking has been used widely in salmon hatcheries of the North Pacific Rim for quite a long time. The North Pacific Anadromous Fish Commission (NPAFC) has a database of all the otolith marks used by hatcheries of the North Pacific that allows for identification of marked hatchery fish in marine catches with almost complete accuracy.

Additional options for salmon stock identification are available by combining analysis of otolith structure collected from wild populations with results of otolith marking of hatchery stocks. We call such approach to analyzing otolith structural diversity as the "otolith complex method". The possibility of identifying juvenile salmon during trawl surveys makes this method particularly timely because otoliths can always be retrieved from fish in the catch, whereas fish scales can be lost in the process of trawling.

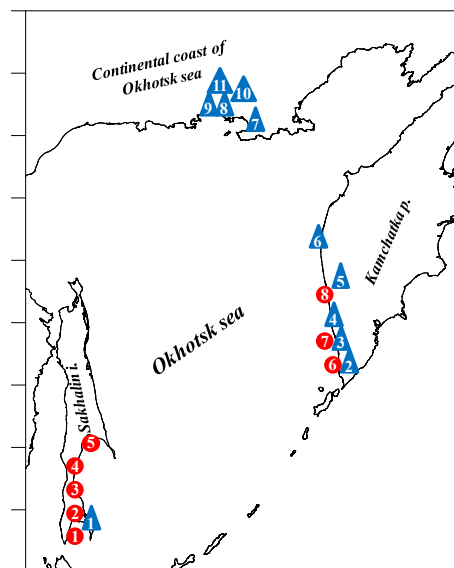


Fig. 1. Locations where baseline otolith samples of pink and chum salmon were collected from rivers of Kamchatka, Sakhalin, and the north coast of the Okhotsk Sea. Pink salmon (red color): Sakhalin: Kura R. (1), Lutoga R. (2), Voznesenka R. (3), Dudinka R. (4), and Poronai R. (5). West Kamchatka: Opala R. (6), Bolshaya R. (7), and Kikhchik R. (8). Chum salmon (blue color): Sakhalin: Ochepukha R. (1). West Kamchatka: Opala R. (2), Bolshaya R. (3), Kikhchik R. (4), Vorovskaya R. (5), and Icha R. (6). The north coast of the Okhotsk Sea: Armansky Hatchery (7), Tauy R. (8), Kava R. (9), Chelomdzha R. (10), and Tauysky Hatchery (11).

Our purpose was to check how well the otolith complex method works in identifying mixed marine aggregations of juvenile pink and chum salmon during autumn migrations in the Okhotsk Sea.

Materials and Methods

Otolith baseline samples were collected by scientists from the fisheries research institutes of KamchatNIRO, SakhNIRO, MagadanNIRO, and researchers from the Kikhchinsky area, Sevvostrybvod. The baseline pool included mostly otoliths collected from juvenile pink and chum salmon. In some cases, when in-river collection of juvenile fish otoliths was not possible, we used otoliths collected from adult fish. The sampling scheme for otolith samples collected from fish in West Kamchatka, Sakhalin, and the north coast of the Okhotsk Sea is shown in Figure 1. The otolith baseline samples consisted of 735 pink and 819 chum salmon.

Mixed-stock samples of juvenile pink and chum salmon otoliths were collected during the complex trawl survey of the R/V *Professor Kaganovsky* in September-October 2011 in the Okhotsk Sea.

Otoliths were processed in the laboratory where they were set in thermoplastic cement onto glass slides and then polished with fine-grit grinding discs until the central part of the otolith was visible. Otolith images were scanned using the visual-analytic complex LEICA DM 1000 device with 900 pixels/mm resolution.

To determine the character and level of otolith structural variety in native stocks of chum salmon, we used signal wavelet-analysis, which is a version of classical spectral analysis (Astafyeva 1998; Dobeshi 2001; Kuznetsova et al. 2004).

In the course of our analysis, we examined the otolith for the presence of a potential otolith hatchery mark. All potential marks were compared with the NPAFC database of known otolith marks to determine the source populations of the marked fish (NPAFC 2013).

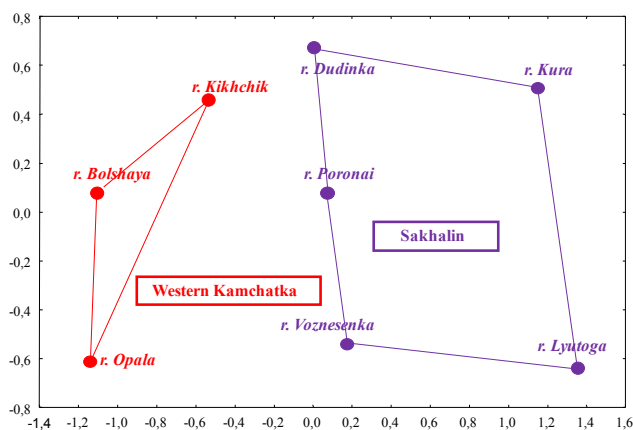


Fig. 2. Centroid plot of populations of pink salmon from West Kamchatka and Sakhalin using multidimensional scaling of otolith characteristics.

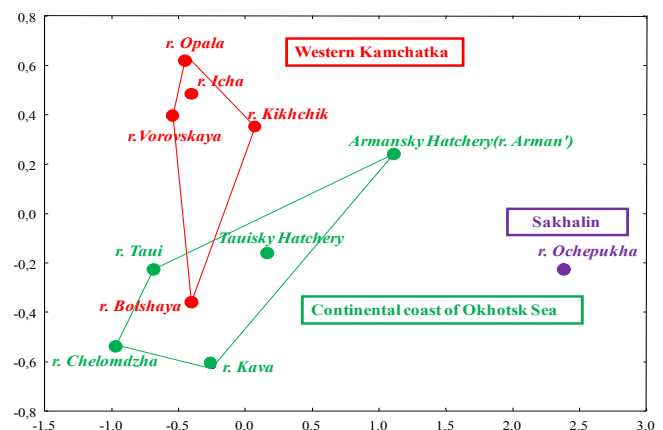


Fig. 3. Centroid plot of populations of chum salmon populations from West Kamchatka, Sakhalin, and the north coast of the Okhotsk Sea using multidimensional scaling of otolith characteristics.

Creation of baselines

Creation of the baselines for analyzing the phenotypic variety of the otoliths was based on principle components analysis. Taking into account the tight geographical connectivity of the Okhotsk Sea sampling area, we assembled baselines only for stocks of three “hot spots” of reproduction for pink and chum salmon, West Kamchatka, Sakhalin, and northern coast of the Okhotsk Sea. The baseline did not include Japan. Later in this paper, we provide results of recaptured otolith-marked fish that is helpful to determine Japanese fish in the mixed samples. This approach works well to provide more accurate estimation of juvenile salmon composition in the catches from the Okhotsk Sea. We determined the regional complexes of pink and chum salmon that were not otolith-marked solely on the basis of otolith structure. Centroid plots of pink and chum salmon otolith baselines based on their geography are shown in Figs. 2 and 3.

Based on Figs 2 and 3, we created two regional complexes of pink salmon stocks: West Kamchatka and Sakhalin and three regional complexes of chum salmon stocks: West Kamchatka, Sakhalin, and the north coast of the Okhotsk Sea.

The next step was to estimate the ability of the baseline models to resolve the components. The method we used was dependent simulation (Tables 1 and 2). The estimated resolution of the baselines was 90.43% for pink and 77.70% for chum salmon.

Table 1. Resolution of the pink salmon otolith baseline estimated using dependent simulation.

Region	MLE	SD	CI \pm 95%	
			Lower	Upper
West Kamchatka	0.9226	0.0577	0.8509	0.9943
Sakhalin	0.8860	0.0706	0.8182	0.9547

Note. The resolution ability is 90.43%.

Table 2. Resolution of the chum salmon otolith baseline estimated using dependent simulation.

Region	MLE	SD	CI \pm 95%	
			Lower	Upper
West Kamchatka	0.7201	0.0874	0.5123	0.7721
Sakhalin	0.9300	0.0648	0.6992	0.9403
North coast of the Okhotsk Sea	0.6810	0.0804	0.5265	0.7930

Note. The resolution ability is 77.70%.

We know, of course, that the baselines cannot illustrate completely the phenotypic diversity in otolith structure of wild pink and chum salmon populations originating from the whole Okhotsk Sea basin. However, it is very difficult to collect otolith samples on a scale as large as the Okhotsk Sea basin.

Identification of regional stock complexes based on otolith structure

Identification of principle regional complexes of juvenile pink and chum salmon in the trawl catches of R/V *Professor Kaganovsky* during post-catadromous migrations in the Okhotsk Sea in 2011 are presented in Table 3. Results showed the dominant stock complex of pink salmon originated from West Kamchatka (72.45%). The contribution of Sakhalin stocks was 27.55%. In the case of chum salmon, the principle stock component originated from West Kamchatka (79.83%). Chum salmon stocks from the north coast of the Okhotsk Sea were secondary (20.02%). The percentage of Sakhalin chum salmon was identified at the level of the statistical error. It is clear that at this stage, these results generally reflect the mixing proportions of wild stocks in the basin.

Recovery of otolith-marked fish

Besides wild populations of pink and chum salmon, the Okhotsk Sea also provides a feeding area for juvenile fish released from a number of salmon hatcheries in the Russian Far East and Japan. Most hatcheries are currently otolith-marking salmon that provide for almost absolute likelihood of correctly identifying mixed-stock catches of fish to region of origin (Munk et al. 1993; Akinicheva and Rogatnykh 1996; Akinicheva et al. 1998; Munk and Geiger 1998; Safronov et al.

Table 3. Identification of the regional stock complexes of juvenile pink and chum salmon collected from trawl catches of the R/V *Professor Kaganovsky* in the Okhotsk Sea, September-October 2011.

Species	No. of Specimens	Parameter	West Kamchatka	Sakhalin	North coast of the Okhotsk Sea
Pink salmon	735	MLE	0.7245	0.2755	—
		SD	0.0348	0.0366	—
Chum salmon	861	MLE	0.7983	0.0015	0.2002
		SD	0.0498	0.0000	0.0520

al. 1999; Akinicheva 2001; Akinicheva et al. 2004; Akinicheva 2006;).

Juvenile pink and chum salmon with otolith marks from Russian Far East hatcheries (West Kamchatka, Sakhalin, South Kuril Islands, and continental coast of the Okhotsk Sea) and Japan (Hokkaido and Honshu) feed in the Okhotsk Sea during their post-catadromous migration. This is why the next step in our work was to determine the origin of the otolith-marked hatchery juvenile pink and chum salmon in the trawl catches.

Analysis of pink and chum salmon otoliths collected in September-October 2011 trawl catches revealed marks from Russian and Japanese salmon hatcheries. The percentage of otolith-marked individuals was 4.08% of total pink salmon examined and 4.88% of chum salmon examined. The percentage of marked juvenile pink and chum salmon by hatchery origin is shown in Figs. 4 and 5.

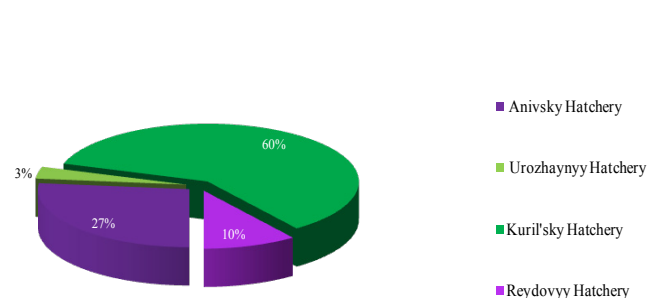


Fig. 4. Percent contribution by hatchery of otolith-marked juvenile pink salmon collected in the trawl catches of the R/V *Professor Kaganovsky* in the Okhotsk Sea, September-October 2011.

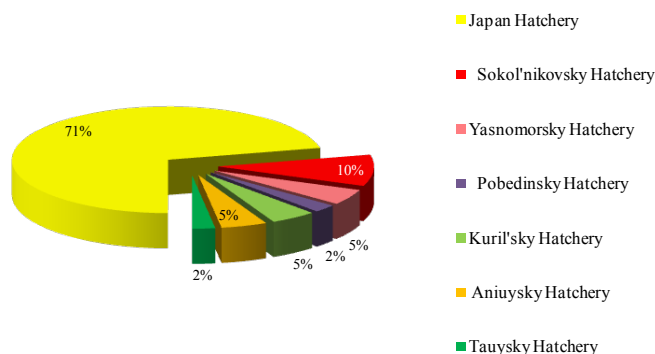


Fig. 5. Percent contribution by hatchery of otolith-marked juvenile chum salmon collected in the trawl catches of the R/V *Professor Kaganovsky* in the Okhotsk Sea, September-October 2011.

Results demonstrate a high percentage (70%) of juvenile pink salmon caught in autumn 2011 originated from Kuril Island hatcheries (Fig. 4). Pink salmon from Sakhalin hatcheries occupy the secondary position (30%). Among chum salmon caught in mixed-stock trawl catches, most otolith-marked fish originated from Japanese hatcheries (71%; Fig. 5). Other otolith-marked chum salmon originated from Russian hatcheries in Sakhalin (17%), Kuril Islands (5%), and the continental coast of the Okhotsk Sea (7%). Because identification of otolith-marked fish is a very accurate method to determine origin of juvenile fish reared in hatcheries, we decided to consolidate results of the theoretical assessment based on regional variation of otolith structure with recovery of otolith-marked juveniles into one “otolith complex method”.

Identification of regional stock complexes by the otolith complex method

Identification of juvenile pink salmon stocks in the autumn 2011 trawl catches in the Okhotsk Sea obtained by the otolith complex method is demonstrated in Fig. 6. West Kamchatkan juvenile pink salmon dominated (72.0%) and Sakhalin fish were the secondary component (24.0%) in the catch.

Identification of juvenile chum salmon stocks in the autumn 2011 trawl catches in the Okhotsk Sea obtained by the otolith complex method is demonstrated in Fig. 7. West Kamchatkan juvenile chum salmon dominated (75.0%), as was the case with juvenile pink salmon (Fig. 6). Chum salmon stocks from the continental coast of the Okhotsk Sea (20.8%) was a secondary component, and the percentage of chum salmon originating from Japan was 3.5% (Fig. 7).

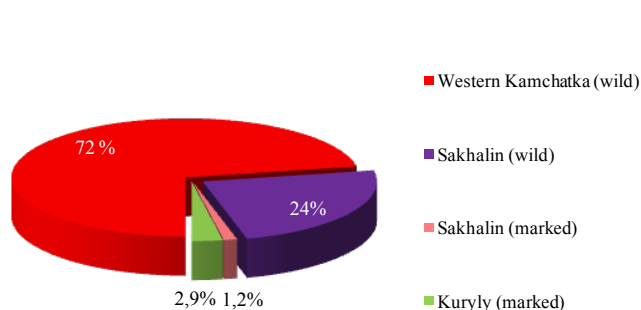


Fig. 6. Stock complex (percentage) of juvenile pink salmon caught in the autumn 2011 trawl catches of R/V *Professor Kaganovsky* in the Okhotsk Sea. Results obtained by the otolith complex method.

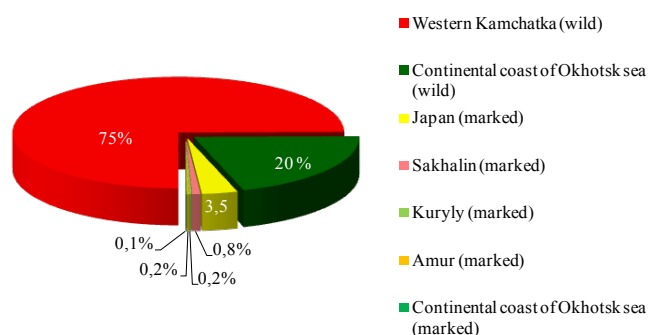


Fig. 7. Stock complex (percentage) of juvenile chum salmon caught in the autumn 2011 trawl catches of R/V *Professor Kaganovsky* in the Okhotsk Sea. Results obtained by the otolith complex method.

In conclusion, we add that we are not proposing to immediately use these results in practice. This investigation is a trial application of a new approach to determine if the stock structure of pink and chum salmon can be determined for mixed marine catches by examining otoliths. In summary, we think this method is promising, especially if used in regions where the abundance of hatchery stocks is significant. Accurate results with the otolith complex method can only be obtained by standardizing and extending baseline sampling sites to encompass all the phenotypic diversity in otolith structure in pink and chum salmon native stocks.

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Juvenile Pink Salmon Distribution in the Coastal Area of Taii Bay in the Sea of Okhotsk

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Keywords: juvenile pink salmon, Taii Bay, migration, estuarine habitat, survival

The Ola River is one of the largest of all river basins that produce runs of pink salmon and drain the continental shore of the Sea of Okhotsk. During odd-numbered years, the number of pink salmon in the spawning run ranges up to 11 million fish, and during even-numbered years the run can be 21 million fish. Downstream migration of juvenile pink salmon takes place from the end of April until the middle of July. The major portion of downstream migrants enter the coastal area by the middle of June.

From the 1980s until the 2008, the Ola River drained into a large estuary of 37.8 km². The estuary was characterized by a high degree of fresh and seawater mixing, shallow depths, and warm temperatures. The combination of these factors had a positive effect on juvenile pink salmon survival because conditions favored the fish's adaptation to a saline environment and provided favorable feeding conditions for the early marine period of life (Fig. 1).

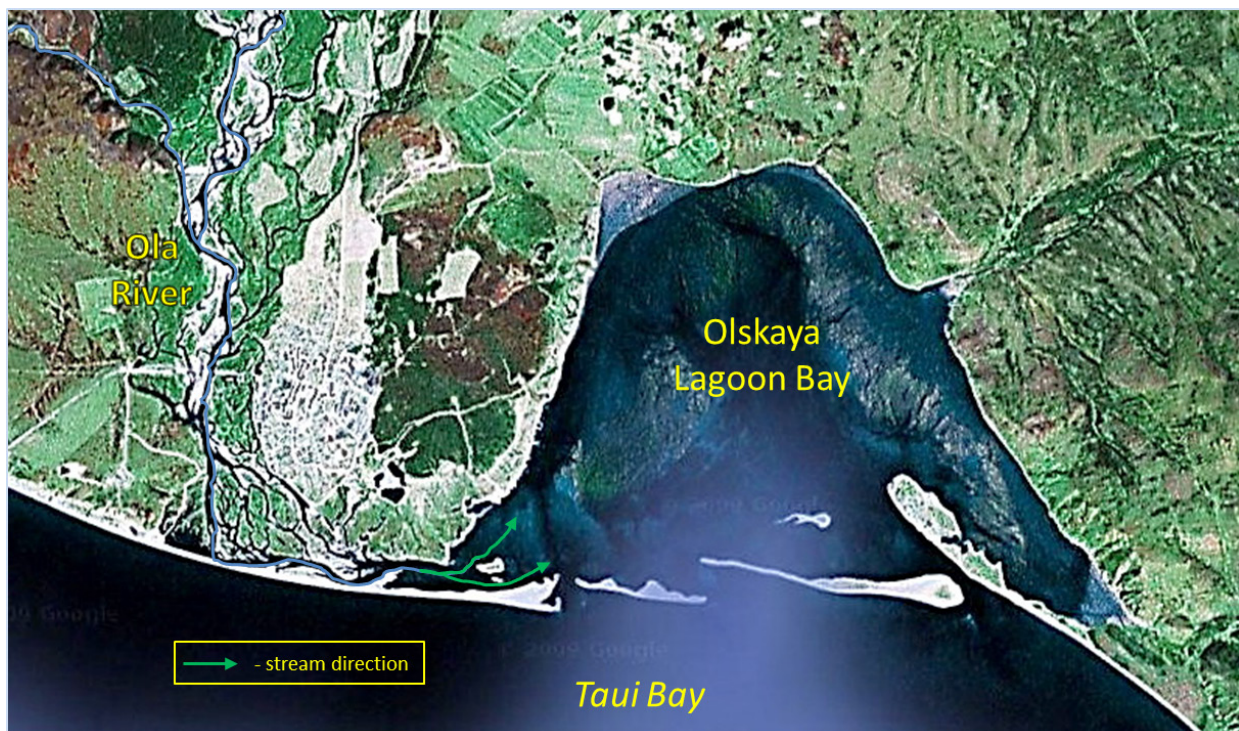
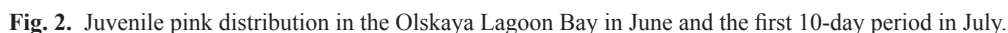


Fig. 1. Map showing the lower Ola River, stream direction, and estuary of Olskaya Lagoon Bay.

In general, the timing of movement of pink salmon into the estuary was such that as they adapted to salt water, major aggregation of juvenile pink gradually shifted to warming shallow waters during the first 10 days in June (Fig. 2). The fish moved progressively to deeper waters of the northern part of the estuary in the second 10-day period in June. Juvenile pink salmon migrated towards the exit of the estuary in the third 10-day period in June, and they left the estuary and moved into Taii Bay in the first 10 days in July. By the beginning of July, density of juvenile pink salmon in the estuary was low. In 2007, the abundance of pink salmon making these movements was 0.36 million fish in the first 10-day period in June, 69.1 million fish in the second 10-day period in June, 54.3 million in the third 10-day period in June, and 0.36 million in the first 10-day period in July. Observations from 2002 to 2008 indicated the abundance of even-year juvenile pink salmon was



A map of Taui Bay area, labeled "© ГИМС «ChartMaster»". The map shows several geographical features: Gertner Bay, Voznyy Pt., Versholaye Bay, Vorobochnyy Pt., Spoil ground, Olsky Pt., Wyuklye Pt., Sakharovskaya Pt., Ota Golofia, Otskayn Lagoon Bay, Alargala, Ust-Lugovoy Drying Sh., Olsky Roads, Gr Pt., and Severny Pt. A blue arrow indicates a route starting from the top right, passing through Otskayn Lagoon Bay, Ust-Lugovoy Drying Sh., and Olsky Roads, then curving south along the coast towards Severny Pt.

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In 2008 a sharp change in the hydrologic regime of the Ola River was associated with the washout of a dike that had separated the river from direct connection with the sea. As a result, the Ola River began to flow directly into Taui Bay, by-passing Olskaya Lagoon Bay. Disconnected from the freshwater input of the Ola River, salinity in the lagoon increased. With the change in the outlet of the river, juvenile pink salmon began to migrate directly to the sea, where they were exposed to high salinity (25-33‰) rather than rearing in the estuary in conditions of high food capacity and variable lower salinity (3-18‰).

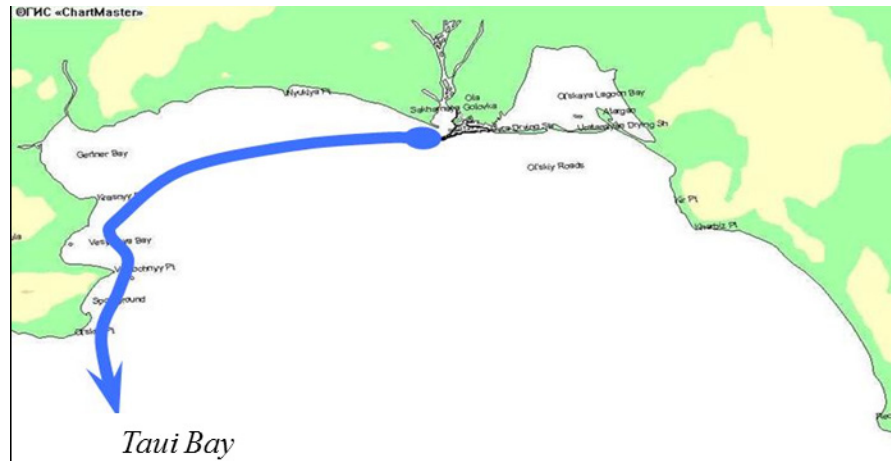


Fig. 4. After 2008 the Ola River had a direct connection to the sea and the migration scheme of juvenile pink salmon changed. Fish moved in a westerly direction towards the Krasni Cape of the Staritzki Peninsula.

In compliance with these hydrographic changes, the distribution of juvenile pink salmon changed. Juvenile pink salmon pushed downstream by flash floods of the Ola River were caught in a branch of coastal cyclonic current and the fish moved in a westerly direction towards the Krasni Cape of the Staritzki Peninsula. The pink salmon aggregated in Batareinaya Bay and Staraya Veselaya Bay, which were favorable areas for initial feeding and for smoltification (Figs. 4 and 5). Near the shore, major aggregations of juveniles were noted in zones that were not strongly affected by currents. Large groups of fish have been observed in shallow warm sandy bottom areas during low tide and near streams outflows. During the period of observation, it was noted that juvenile pink salmon preferred habitats with water temperatures of 6-8°C and salinities of 31-32‰.

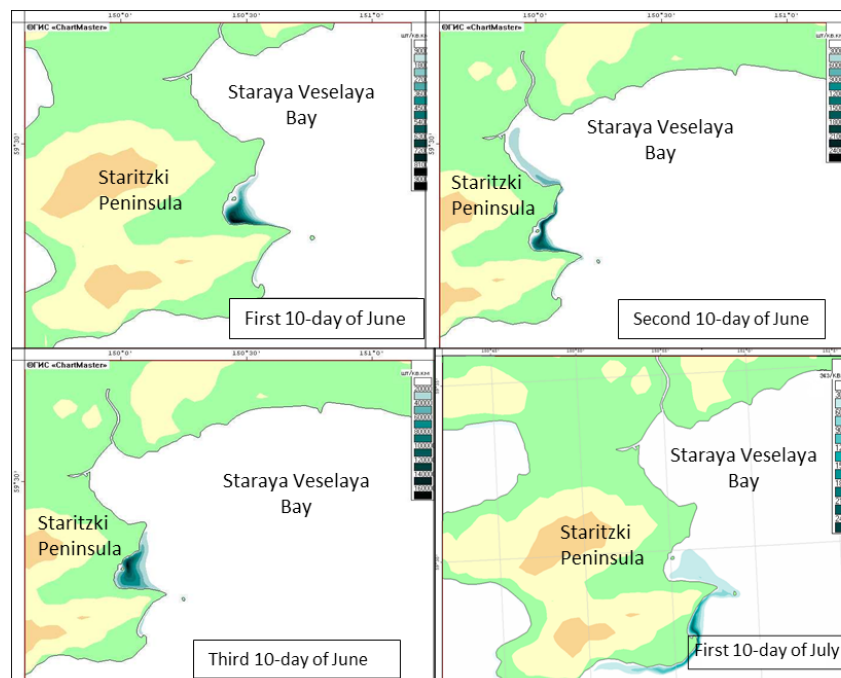


Fig. 5. Juvenile pink distribution along the eastern part of the Staritzki Peninsula during June and the first 10-day period in July.

The number of pink salmon gathering along the eastern shore of the Staritzki Peninsula in odd-numbered years changed in the following way: 45.0 million fish in the first 10-day period in June, 27.0 million fish in the second 10-day period in June, 31.5 million fish in the third 10-day period in June, and 0.24 million fish in the first 10-day period in July. The abundance of juvenile pink salmon gathering at the same location in even-numbered years was much lower: 0.063 million fish in the third 10-day period in May, 0.727 million fish in the first 10-day period in June, 0.346 million fish in the second 10-day period in June, 0.241 million fish in the third 10-day period in June, and 0.104 million fish in the first 10-day period in July.

To compare habitat conditions and biological indices of juvenile pink salmon before and after 2008, it is necessary to mention the following. After 2008, the conditions for juvenile pink salmon feeding became worse. Salmon feeding in the Olskaya Lagoon Bay took place at average water temperatures of 11.3°C and salinity of 18.9‰. However, under present conditions pink salmon appear to be feeding in habitats that are cooler (5.4°C) and typical for a polyhaline basin with an average salinity of 29.5‰ (Figs. 6 and 7). The number of feeding aggregations has decreased by two times, and size and weight indices of juvenile pink salmon have decreased as well. For example, for the time period that juveniles were feeding in Olskaya Lagoon Bay, the length and weight of pink salmon increased to 60-70 mm and to 1.5-2.0 g, respectively. However during the time period that juveniles were feeding along the eastern shore of the Staritzki Peninsula, they attained only 58.5 mm in length and 1.49 g in weight.

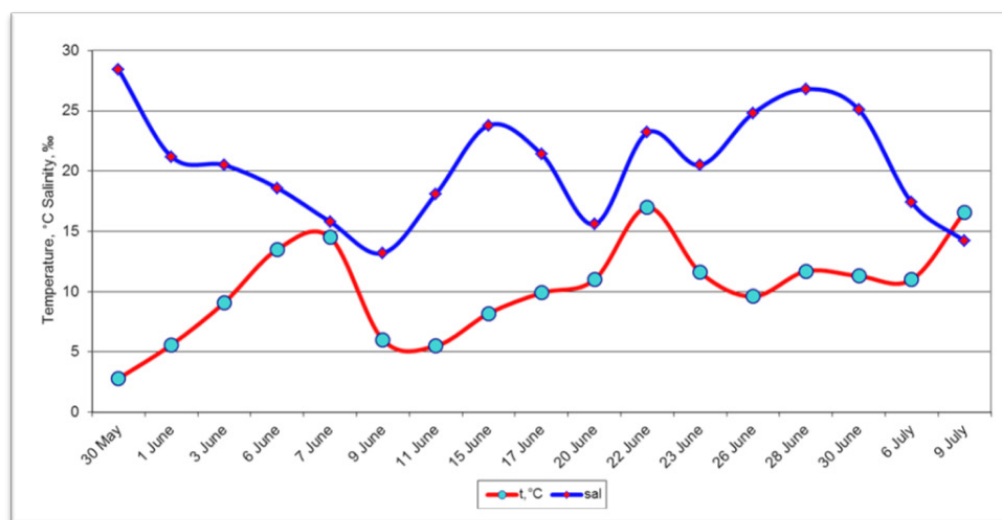


Fig. 6. Average indices of temperature and salinity in Olskaya Lagoon Bay during the time when juvenile pink salmon would be residing in the estuary.

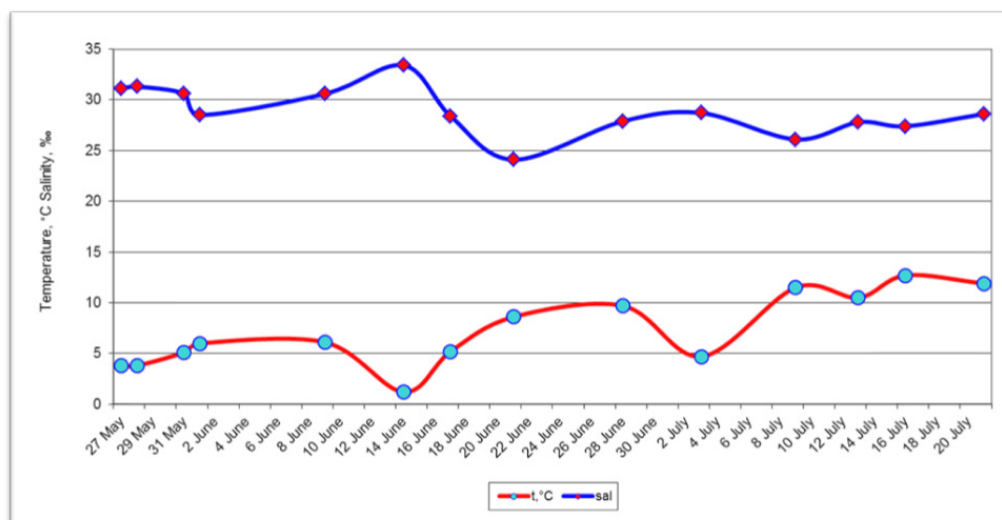


Fig. 7. Average indices of temperature and salinity of water in Batareinaya Bay during the time when juvenile pink salmon would be residing in the area.

To estimate survival of juvenile pink salmon exposed to abruptly changing salinity conditions, halinic tolerance of juvenile fish were experimentally evaluated. Study of the physiologic status of juvenile pink salmon, taking into consideration the level of erythropoiesis, the leukocytic formula, and indices of thrombocytes and leukocytes in peripheral blood, showed fish are rather resistant to sharp salinity changes. Mortality during the experiment did not exceed 10% (Izergina and Izergin 2009).

We note that hydrological changes in the outflow of the Ola River affected qualitative indices of juvenile pink salmon and their survival in the early sea period. However, the high salinity tolerance of pink salmon enables them to maintain a high level of abundance, as compared to other salmon species in rivers of the Magadan region.

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Evidence for Geomagnetic Imprinting as a Homing Mechanism in Pacific Salmon

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Keywords: geomagnetic imprinting, homing, Pacific salmon

In the final phase of their spawning migration, Pacific salmon use chemical cues to identify their home river, but how they navigate from the open ocean to the correct coastal area has remained enigmatic. To test the hypothesis that salmon imprint on the magnetic field that exists where they first enter the sea and later seek the same field upon return, we analyzed a 56-year fisheries dataset on Fraser River sockeye salmon, which must detour around Vancouver Island to approach the river through either a north or south passageway. We found that the proportion of salmon using each route could be predicted by geomagnetic field drift (secular variation); the more the field at a passage entrance diverged from the field at the river mouth, the fewer fish used the passage. Secular variation accounted for as much as 44% of the variability in the migratory route used; including an interactive effect of sea surface temperature we could account for 66% of the variability in the route used by returning salmon. These results provide the first empirical evidence of geomagnetic imprinting in any animal, imply that forecasting salmon movements may be possible using geomagnetic models, and identify a likely homing mechanism for salmon and other marine migrants.

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The Early Marine Distribution of Juvenile Sockeye Salmon Produced from the Extreme Low Return in 2009 and the Extreme High Return in 2010

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Keywords: Sockeye salmon, ocean entry, early marine distribution, Fraser River, Strait of Georgia

Returns of sockeye salmon (*Oncorhynchus nerka*) to the Fraser River in British Columbia are highly variable. Since 1990, there has been a general decline in the returns for all run cycles with three of the four lowest returns on record occurring in 2007, 2008, and 2009. The extremely low 2009 return of 1.6 million sockeye salmon (escapement of 1.1 million fish) led, on the recommendation of the Prime Minister of Canada, to an Order in Council that established a Commission of Inquiry into the decline of sockeye salmon in the Fraser River (Cohen Commission). In 2010, shortly after the Cohen Commission was initiated, a total return of 28.4 million sockeye salmon or spawning escapement of 13.6 million sockeye salmon returned to the Fraser River. This was the largest return in recorded history demonstrating the resiliency of this species. In addition, neither of the extreme returns had been forecasted, indicating our relatively poor understanding of the factors that regulate their production and survival.

The extreme variation in escapement between these two years gave us the opportunity to examine differences in habitat use (residence timing and migration patterns) of juvenile sockeye salmon under conditions of low (2011) and high (2012) juvenile abundance in the Strait of Georgia. Preikshot et al. (2012) showed that the average residence period for juvenile sockeye salmon in the Strait of Georgia was 43-54 days. We are currently examining how the extreme differences in abundance of juvenile sockeye salmon impact their distribution during this residency period in the Strait of Georgia. The data reported in this abstract is part of a larger study funded in part by Department of Fisheries and Oceans' Program for Aquaculture Regulatory Research, the Pacific Salmon Commission, and the Pacific Salmon Foundation to examine the ecology and health of juvenile Fraser River sockeye salmon in the Lower Fraser River and Strait of Georgia.

Table 1. Sampling dates and gear used to collect juvenile sockeye salmon in the Strait of Georgia and Johnstone Strait/Discovery Islands.

Year	Area	Gear	Date	N Sets	Vessel
2011	1-6	Purse seine ²	18-31 May	91	<i>Ocean Venture</i>
	1-6	Purse seine ²	11-25 June	92	<i>Ocean Venture</i>
	1-6 ¹	Rope trawl ³	22 June-6 July	91	<i>WE Ricker</i>
2012	1-6	Purse seine ²	19 May- 1 June	96	<i>Ocean Venture</i>
	1-6	Purse seine ²	11-25 June	97	<i>Ocean Venture</i>
	1-6 ¹	Rope trawl ³	20 June-2 July	98	<i>WE Ricker</i>

¹Area 6 was not fully surveyed by trawl survey due to limited number of fishing days.

²Purse seine was modified with a small mesh bunt for sampling juvenile salmon.

³Survey design and protocol for trawl surveys in Beamish et al. (2000) and Sweeting et al. (2003).

Juvenile sockeye salmon were captured in the Strait of Georgia and Discovery Islands/lower Johnstone Strait from mid-May to early July 2011 and 2012 using a modified purse seine and surface trawl (Tables 1 and 2; Fig. 1). Each year the catch-per-unit-effort (CPUE) in the purse seine survey increased from May to June being 4.5 and 2.0 times larger in June 2011 and 2012, respectively. Between the two years the CPUE in the purse seine surveys was 12.3 and 5.4 times larger in the May and June 2012, compared to May and June 2011, respectively (Table 2; Fig. 2). The CPUE in the June trawl surveys was 11.4 times larger in 2012 than 2011.

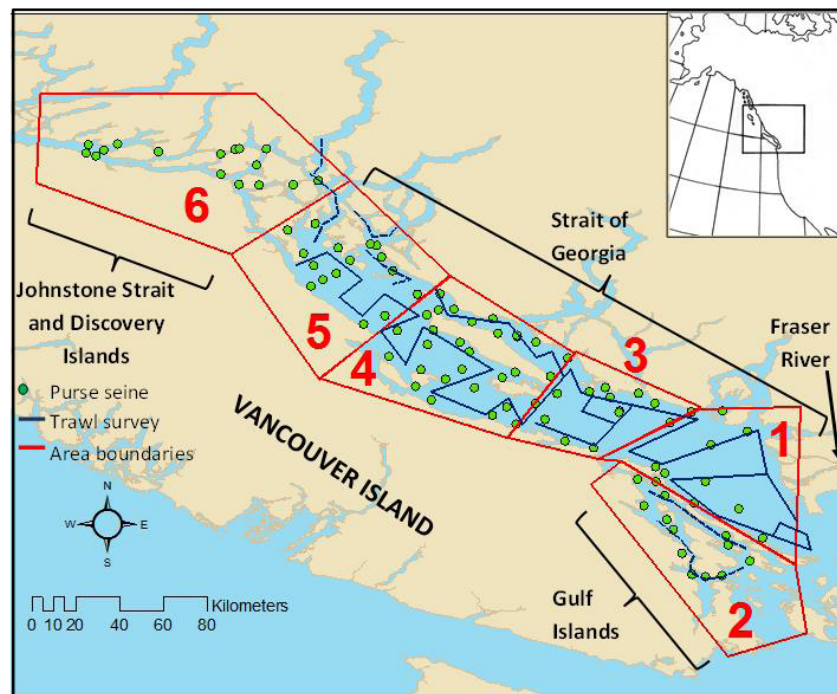


Fig. 1. Locations of surveys for juvenile sockeye salmon in the Strait of Georgia and Johnstone Strait/Discovery Island region in May–July, 2011 and 2012. Location of purse seine sets (green dots), and trawl sets (blue lines) are shown. The study region was divided into six areas (1-6, red polygons) to aid in examination of CPUE data. These areas are based on a combination of physical and biological factors and on researchers' knowledge of region.

In the May 2011 purse seine survey, sockeye salmon were captured primarily in Areas 1-4 with the highest CPUEs of 59.2 (47.4% of total CPUE) and 40.9 (32.7% of total CPUE) reported for Areas 3 and 1, respectively (Fig 2A). In the May 2012 purse seine survey, sockeye salmon were caught in all areas and in much higher numbers (Fig 2B). Similar to 2011, the highest CPUEs of 733.6 (45.3% of total CPUE) and 584.1 (36.1% of total CPUE) were reported for Areas 3 and 1, respectively. Sockeye salmon were more broadly distributed in May 2012 when compared to 2011 with more fish present in Area 5 (11.4% of total CPUE) in 2012.

Based on DNA analysis (Beacham et al. 2010), the few sockeye salmon caught in Area 6 in the May 2012 purse seine survey were southern British Columbia mainland fish from Heydon, Phillips and Sakinaw rivers. There was no evidence of Fraser River sockeye salmon leaving the Strait of Georgia prior to the end of May in either year.

Table 2. Catch-per-unit-effort (CPUE) and average fork length of juvenile sockeye salmon collected in the Strait of Georgia and Johnstone Strait/Discovery Islands in May–July, 2011 and 2012.

Year	Survey	Total catch	CPUE	Length (mm)		
				\bar{x}	SD	<i>n</i>
2011	May purse seine	1,578	17.3	103.6	14.1	345
	June purse seine	7,226	78.5	119.9	12.5	463
	June trawl	509	13.1 ¹	119.6	11.8	465
2012	May purse seine	20,533	211.7	95.2	18.0	1083
	June purse seine	40,912	421.8	94.9	14.8	1616
	June trawl	4,235	148.7 ¹	97.7	12.8	2126

¹CPUE for trawl survey is standardized to hour sets. It is not directly comparable to the CPUE from the purse seine survey.

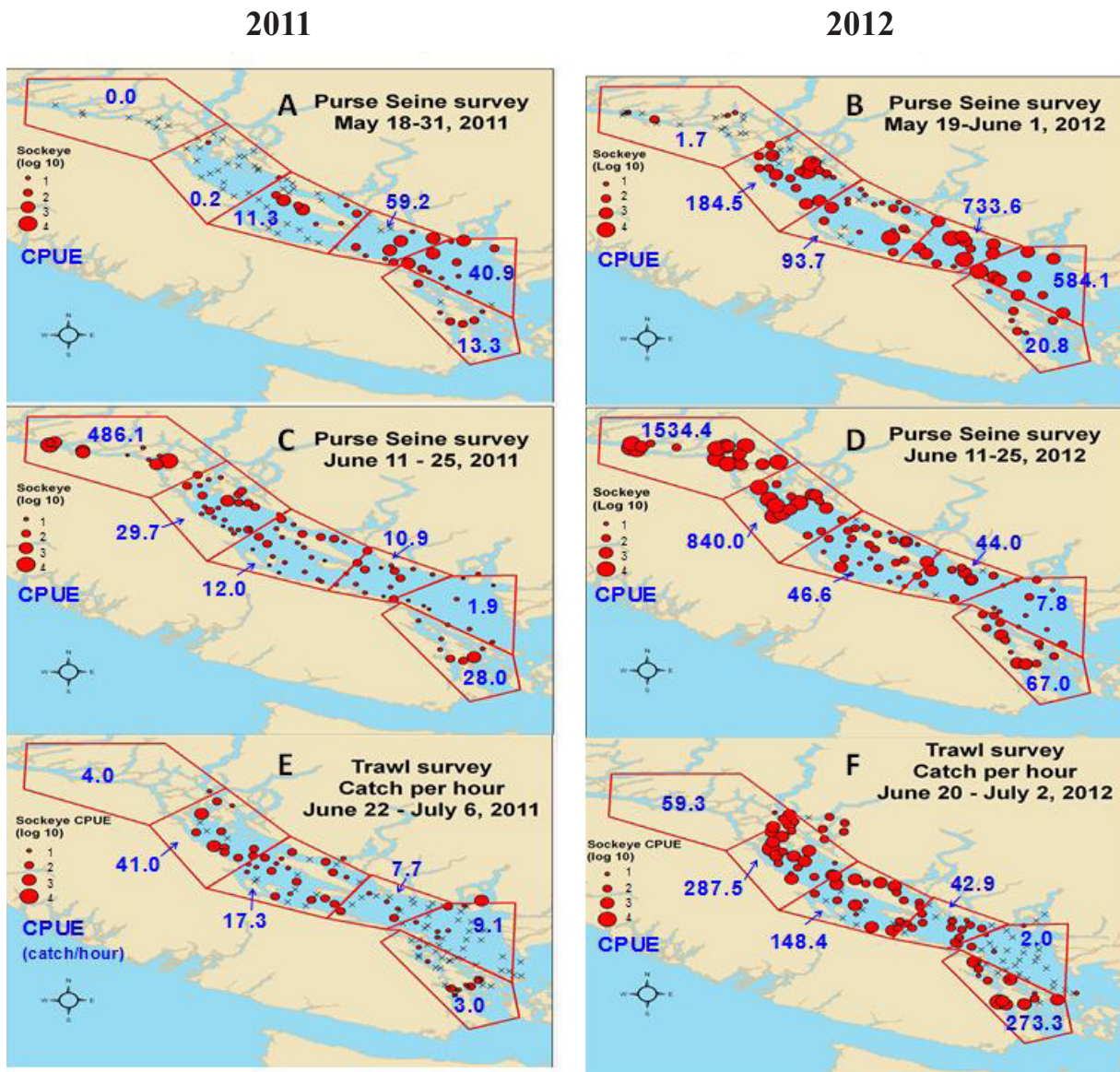


Fig. 2. Distribution and average catch-per-unit-effort of juvenile sockeye salmon in the Strait of Georgia, Gulf Islands, and Johnstone Strait/Discovery Islands by area and survey in May and June in 2011 (left panel) and 2012 (right panel).

In both years the distribution of sockeye salmon shifted northwards by the June purse seine survey with the majority of sockeye salmon captured in Areas 5 and 6 (Fig. 2C and D). Relatively large numbers of juvenile sockeye salmon were present in Area 2 (Gulf Islands) at this time in both years. A similar trend is seen in both years for the June trawl surveys with exception of the high catch of sockeye salmon (33.6% of the total CPUE) in Area 2 in 2012 (Fig. 2E and F). Limitation of ship time restricted the sampling by trawl in Area 6 in both years and therefore distribution in this region remains unknown during late June and early July (Fig. 2C and D), although some juvenile Fraser River sockeye salmon were recovered farther north (M. Trudel, unpublished data).

In both the purse seine and trawl surveys the average length of juvenile sockeye salmon in 2011 was significantly larger than in 2012 ($p < 0.05$, Table 2). The absolute size of the fish did not appear to limit distribution; however, there was an indication of larger fish in both the Gulf Islands (Area 2) and in the northern Strait of Georgia and Discovery Islands area (Areas 5 and 6) in both years. It is not known if this is due to either growth during residence, or variability in distribution patterns within the study area based on size, or both.

There are many factors that cumulatively contribute to the survival, growth, and health of Pacific salmon during their marine residence. However, there is increasing evidence for Pacific salmon that significant mortality occurs during the first few months in the ocean and it is thought that brood year strength may be determined during this time (Beamish et al. 2004, 2010; Farley et al. 2007, MacFarlane 2010). A focus of our program is to determine when and how Fraser River sockeye salmon utilize the Strait of Georgia and the factors that are effecting their growth and survival in this region, so as to assist in determining the relative importance of this early marine period in overall Fraser River sockeye salmon production. Results from this preliminary analysis indicate that the total number of juvenile sockeye salmon entering the Strait of Georgia does not impact their general distribution during their first four to six weeks in the ocean and that the Strait of Georgia is an important rearing area during this critical period, regardless of the numbers of juvenile sockeye salmon entering the ocean.

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Oceanic Distribution of Chinook Salmon Inferred from Age-Specific Arrival Timing

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Keywords: Chinook salmon, ocean migration, arrival order, age

While Columbia River spring–summer Chinook salmon *Oncorhynchus tshawytscha* are known to proceed northwards along the North American coast during their first summer and autumn at sea, their subsequent oceanic distribution is essentially unknown, until they are again detected in the fishery at the mouth of the river or at Bonneville Dam, located 235 km upstream of the river mouth. In addition to the known arrival time ordering of the distinct populations comprising this run, our analysis of returning tagged adults shows that within populations, the oldest fish (ocean age-3) arrive first, the ocean age-2 fish next, and the ocean age-1 fish last (Bracis and Anderson 2013). To explore possible mechanisms underlying this persistent age-dependent ordering of arrival time, we simulated the fish's return migration using a model based on a geomagnetic homing mechanism with age-specific swimming speeds (Bracis and Anderson 2012). To reproduce the observed age-dependent differences in arrival times with the model, within a population, the ocean age-2 and -3 fish needed to initiate migration from the same location and time. On the other hand, ocean age-1 fish may initiate homeward migration from a more consistent location in the northern Gulf of Alaska with some delay (Bracis and Anderson 2013). This would suggest these populations overwinter near the Alaskan coast during their first year at sea before dispersing more broadly during subsequent years of ocean residence. Arrival timing patterns have valuable information that can be used to infer the features of homing migrations, which in turn may be useful for considering potential responses to climate change.

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Ocean Habitat of Juvenile Chinook Salmon at the Southern End of Their Range

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Keywords: habitat, juvenile Chinook salmon, south

Characterizing the ocean habitat of Chinook salmon is important for understanding the mechanisms affecting movement and survival. We sampled juvenile Chinook salmon during summer and fall of 1999 to 2011 from Monterey, California (36.57°N), to Newport, Oregon (44.67°N). Chinook salmon juveniles (< 250 mm fork length [FL]) were present in 46% of the 463 total hauls and sub-adults (250–400 mm FL) were present in 17% of hauls. Catch per unit effort (CPUE) was modeled using season (summer or fall), year, bottom depth, distance from shore, latitude, temperature, salinity, and chlorophyll-*a* concentration as candidate predictors. The relationships between Chinook salmon CPUE and the covariates were assessed using both generalized linear models and generalized additive models. There were significant relationships between salmon CPUE and year sampled, bottom depth, chlorophyll-*a* concentration, and either latitude or distance to shore. The relative contribution of each variable differed with season and fork length, demonstrating that salmon occupy different habitats seasonally and throughout their ocean life. While some patterns appear to be common across the Chinook salmon range, the regional influence of narrow shelf breaks, strong upwelling, and small river plumes influenced the distribution in ways that were regionally specific to the southern part of their range.

Oceanographic and Ecological Indicators for Salmon Returns in the Northern California Current

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Keywords: Pacific Decadal Oscillation, copepods, transport, marine ecosystem indicators, stoplight chart

Estimates of the number of salmonids returning to spawn in the Columbia River basin are needed by managers to set harvest quotas, to determine the efficacy of improvements to fish passage through the hydropower system, and to determine if there are measurable improvements in returns due to freshwater habitat restoration efforts. These efforts are focused primarily on four species: *Oncorhynchus tshawytscha* (Chinook, both stream-type and ocean-type), *O. kisutch* (coho), *O. nerka* (sockeye) and *O. mykiss* (steelhead). Estimates of the number of adult salmonids returning to spawn are derived from sibling regression (jack) models and age-structured cohort models. The same types of models are used for harvest management for salmonids from coastal rivers and streams.

Missing from the harvest models is any consideration of environmental variability during the time that fish reside in the ocean. Three notable attempts have been made and each has proven capable of providing hindcasts of either the number of adults returning to spawn or recruits-per-spawner, but when used in forecast mode, each has failed soon after results were published. Nickelson (1986) showed a significant relationship between coho returns and interannual variations in coastal upwelling. Logerwell et al. (2003) expanded upon these results and showed that three variables could explain coho salmon returns: ocean temperatures the winter before juveniles entered the sea, the timing of the spring transition (the date when upwelling was initiated each year), and the strength of upwelling in April-May when juveniles first enter the sea. Rupp et al. (2012) continued the work on coho salmon and showed that including the Pacific Decadal Oscillation (PDO) into a statistical model provided a reasonable estimate of adult returns (in hindcast mode) but failed in forecast mode. We suggest here that these models failed in forecast mode because the prediction problem is inherently multivariate, that is, no single factor controls growth or sets survival and also because correlation is not causation: we do not understand the mechanisms that link physical forcing (upwelling and the PDO) with a biological response (salmon returns).

Here we report on two issues: first, our attempts to describe a mechanistic link between the PDO and the food chain upon which salmon feed and second, our attempts to use multiple indicators to provide forecasts of the number of adult salmon returning to spawn. The idea for looking at links between the PDO and salmon came from Francis and Hare (1994) who showed that salmon landings were correlated with the North Pacific Index and from Mantua et al. (1997) who showed that salmon landing around the northeast Pacific were correlated with the PDO. Recently, Peterson and Schwing (2003) showed that Columbia River Chinook were correlated with the PDO and that the survival of coho salmon was correlated with the biomass of “cold water copepods” (we expand on this idea later).

At first glance, one could conclude that it would be difficult to study the effects of the PDO on food chain structure using data from an in situ observational program because historically, the PDO only changes phase every 20-30 years. However, since 1998, the PDO has been changing phase every five years, thus these high frequency changes have provided a natural experiment, which has allowed study of the mechanisms by which PDO signals are transmitted to food chains. We have learned that changes in the sign of the PDO are followed closely by changes in copepod community structure: during the negative (“cool”) phase of the PDO, a “cold water community” dominates, whereas during the positive (“warm”) phase a “warm water community” dominates (Fig. 1). The copepods which are key players during the cool phase are *Calanus marshallae* and *Pseudocalanus mimus*, both of which are large lipid-rich species, whereas key players during the warm phase are small lipid-poor species such as *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus spp.* and *Calanus pacificus*. None of these species store large quantities of lipids as compared to *C. marshallae* and *Pseudocalanus sp.* (Lee et al. 2006) with the possible exception of *Calanus pacificus*, which does store some wax esters but in lesser quantities per unit body mass than their more northern congeners (Håkanson 1987; Lee et al. 2006). Thus, we suggest that the mechanism that links the PDO with salmon growth and survival is as follows: when the PDO is persistently negative, waters which upwell are cold, salty, and have higher nutrient content (Chhak and Di Lorenzo 2007), and the source waters which feed the northern California Current (NCC) are sub-arctic in character. When the PDO is positive, a subtropical water type dominates coastal waters in the Pacific Northwest (Fig. 1). Source waters from the north bring the “cold water community” to the NCC, which

results in a food chain anchored by large sub-arctic cold water lipid-rich copepods, whereas source water from the south or offshore bring sub-tropical lipid-depleted copepods to the NCC (Fig. 2). Thus a negative PDO equates to a food chain with a high bioenergetic content favored by salmon, which need to accumulate vast amounts of body fat both to survive their first winter at sea (Beamish and Mahnken 2001) and fuel their metabolic demands while migrating back to, and up, their natal streams to spawn.

Copepod Dynamics: Two Different Source Waters

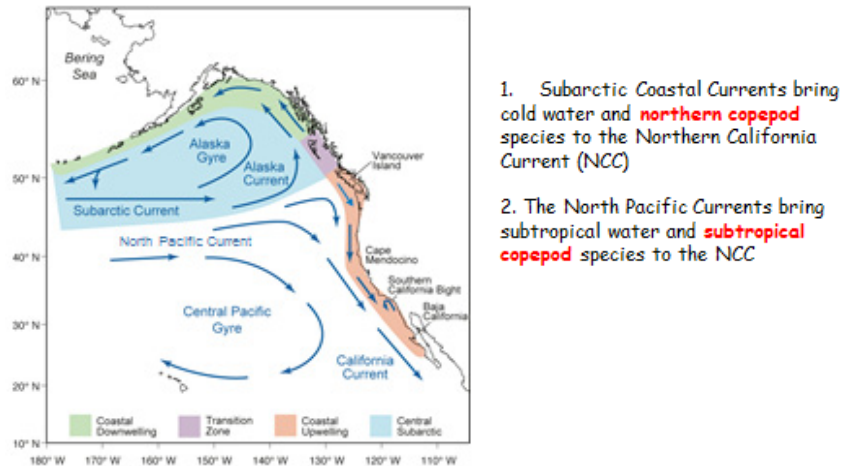


Fig. 1. Chart showing circulation patterns in the eastern North Pacific. The coastal currents transport northern copepods southward from southern British Columbia coastal waters; the North Pacific Current transports subtropical species to the northern California Current. The strength of these currents varies as a function of the sign of the PDO: a negative PDO results in strong southward coastal flows, whereas a positive PDO results in very weak coastal flows and onshore transport of offshore waters from the North Pacific Current to the Oregon coast.

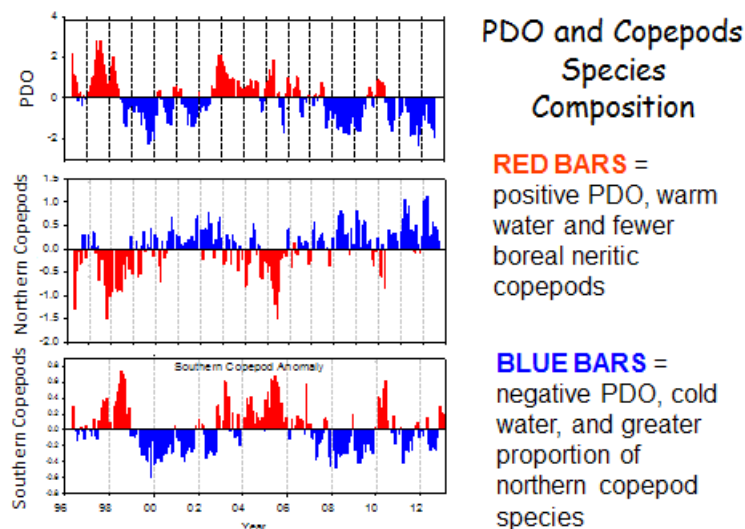


Fig. 2. Time series of the PDO, northern copepods, and southern copepods showing that when the PDO is positive, fewer “northern copepods” are found off Oregon, and vice versa.

The idea that transport is what links the PDO with local food chains was first suggested by Peterson and Hooff (2005) and Hooff and Peterson (2006). This idea was examined rigorously and elegantly by Keister et al. (2011) who used a ROMS model to show that during positive phases of the PDO current anomalies were northward and onshore resulting in transport of warmer waters and warm water copepod species to the coastal waters off central Oregon. During negative phase of the PDO, equatorward current anomalies led to a copepod community dominated by cold water species. Further, Bi et al. (2011) used satellite altimeter and coastal sea level (tide gauge) data to calculate geostrophic transport between the coast and the first offshore altimeter grid point (~ 50 km from shore) and found that alongshore currents and biomass of cold neritic copepods (*P. mimus*, *C. marshallae*, and *Acartia longiremis*) exhibited a strong seasonal pattern that fluctuated in opposite phase: positive alongshore currents (from the south) lead to low biomass of these species in winter and negative alongshore currents (from the north) lead to high biomass in summer (Fig. 3).

Alongshore transport and cold neritic subarctic copepods

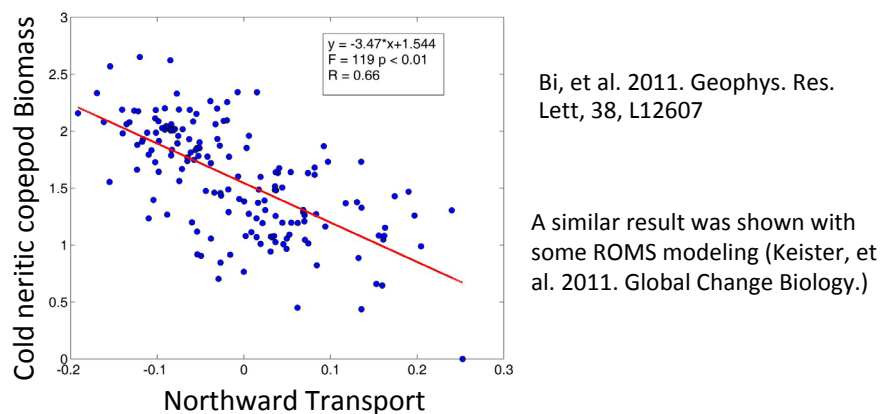


Fig. 3. Scattergram of “cold water” copepod biomass and northward transport. The weaker the northward transport (which is the same thing as strong southward transport), the lower the biomass of cold water lipid-rich copepods.

With these ideas in mind, we have developed a number of physical and ecological indicators, set in the context of an ecosystem approach to management, that have proven useful for providing both management advice as well as forecasts of salmon returns. All data and indicators are publically available on our Center’s website: <http://www.nwafc.noaa.gov> and by clicking on the “Salmon Forecasts” button. The indicators are of three types: those that capture basin-scale physical forcing (the PDO and ENSO) and local-scale physical forcing (upwelling), and those that demonstrate the biological response—primarily bottom-up forcing of food chain structure. Some of the indicators are from web-based sources (SST, upwelling, and the PDO) whereas others are from two long-term at-sea monitoring programs. Data on in situ physical and biological oceanographic variables come from the Newport Hydrographic Line, a line that was sampled intensively by oceanographers from Oregon State University in the 1960s and early 1970s. Sampling along this line languished for a quarter century until 1996 when the line was re-opened and thereafter, sampled biweekly, yielding (now) a 17+ year biological oceanographic time series. Variables monitored include temperature, salinity, oxygen and chlorophyll fluorescence profiles, nutrients, chlorophyll-*a*, and abundance and biomass of copepods, krill, and ichthyoplankton. Data also originate from a long-term study of the distribution and abundance of juvenile salmonids resulting from survey cruises in May, June, and September from 1998 to present. Biological data that are used in the forecasting include biomass of northern and southern copepods, abundance of the fish larvae in winter (using only those larvae that salmon will consume as juveniles in spring), and catches of Chinook salmon in June and coho in September.

Values for each variable are listed in an excel table, ranked across years from 1998 to present (Table 1), and analyzed using principal component (PC) analysis. PC scores are listed in the table as well. An additional analysis uses values from the table along with a set of fish and food chain attributes (growth, salmon diets, estimated numbers of anchovy [as prey] and hake, as well as zooplankton sampled during salmon surveys) that are analyzed using maximum covariance analysis (Burke et al. 2013).

Table 1. List of physical and ecological indicators which summarize ocean conditions in a given year. Green = good, yellow = average, and red = poor. The value of the “mean rank” and the value of the “first principal component--P1” is used to estimate adult salmon returns (see Fig. 4).

<i>Ecosystem Indicators</i>	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
PDO (December-March)	14	6	3	10	7	15	9	13	11	8	5	1	12	4	2
PDO (May-September)	9	4	6	5	10	14	13	15	11	12	2	8	7	3	1
ONI Jan-June	15	1	1	6	11	12	10	13	7	9	3	8	14	4	5
46050 SST (May-Sept)	13	8	3	4	1	7	15	12	5	14	2	9	6	10	11
NH 05 Upper 20 m T winter prior (Nov-Mar)	15	9	6	8	5	12	13	10	11	4	1	7	14	3	2
NH 05 Upper 20 m T (May-Sept)	13	10	12	4	1	3	15	14	7	8	2	5	11	9	6
NH 05 Deep Temperature	15	4	8	3	1	11	12	13	14	5	2	10	9	6	7
NH 05 Deep Salinity	15	3	6	2	5	13	14	9	7	1	4	11	12	8	10
Copepod Richness Anomaly	15	2	1	6	5	11	10	14	12	9	7	8	13	3	4
N. Copepod Biomass Anomaly	14	10	6	7	4	13	12	15	11	9	3	8	5	1	2
S. Copepod Biomass Anomaly	15	3	5	4	2	10	12	14	11	9	1	7	13	8	6
Biological Transition	14	10	6	5	7	13	9	15	12	2	1	4	11	3	8
Winter Ichthyoplankton	16	8	2	4	6	15	14	10	13	12	1	9	3	11	7
Chinook Juv Catches (June)	14	3	4	12	8	10	13	15	9	7	1	5	6	11	2
Coho Juv Catches (Sept)	11	2	1	4	3	6	12	14	8	9	7	15	13	5	10
Mean of Ranks	13.9	5.5	4.7	5.6	5.1	11.0	12.2	13.1	9.9	7.9	2.8	7.7	9.9	5.9	5.5
RANK of the Mean Rank	15	4	2	6	3	12	13	14	10	9	1	8	10	7	4
Principle Component Scores (PC1)	6.56	-2.22	-2.95	-1.60	-2.12	2.08	3.12	4.21	1.10	-0.30	-4.39	-0.91	1.13	-1.76	-1.96
Principle Component Scores (PC2)	-0.51	0.04	-0.24	-0.76	-1.96	-1.53	2.55	-0.43	-0.66	1.07	-0.50	0.96	-0.74	1.36	1.35
<i>Ecosystem Indicators not included in the mean of ranks or statistical analyses</i>															
Physical Spring Trans (UI Based)	3	6	14	12	4	9	11	15	9	1	5	2	7	8	13
Upwelling Anomaly (Apr-May)	7	1	13	3	6	10	9	15	7	2	4	5	11	13	11
Length of Upwelling Season (UI Based)	6	2	14	9	1	10	8	15	5	3	7	3	11	13	11
NH 05 SST (May-Sept)	10	6	5	4	1	3	15	13	8	12	2	14	9	7	11
Copepod Community Structure	15	3	5	7	2	12	11	14	13	8	1	6	10	9	4

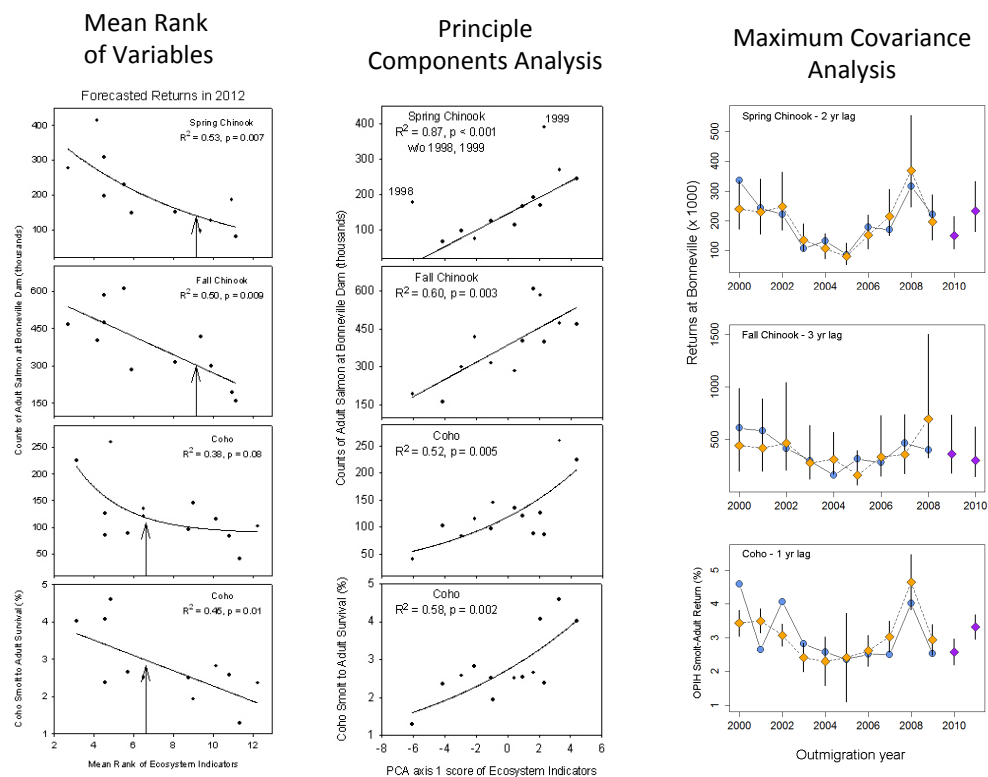


Fig. 4. Examples of the correlations of counts of adult salmon at Bonneville Dam and the mean rank of variables listed in Table 1 (left); correlations with the first principal component of the variables listed in Table 1 (PC1) (center); and the time series of expected versus observed sounds of salmon at Bonneville Dam using maximum covariance analysis (right).

Results of each of these analyses are used to produce three separate “outlooks” using simple correlation analysis (Fig. 4) with each yielding a similar result. To date our efforts have not been adopted by managers, although most are aware of our work. The chief obstacle to the wide-spread use of our indicators is that there is (and always be) uncertainty in our ability to continue to collect oceanographic data during monitoring cruises, due to vagaries associated with funding such work. Regardless, our results are popular because they provide plausible explanations for why salmon runs succeed or fail and clearly show the powerful influence that the ocean has on salmon growth, survival, and returns.

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Coastal Association of Juvenile Chinook Salmon and Krill in the Northern California Current

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Keywords: juvenile Chinook salmon, krill, northern California Current

Understanding predator-prey spatial associations provides key information for ecosystem-based fisheries management. The recent collapse and subsequent closure of the western U.S. Chinook salmon fisheries was ascribed to ocean conditions and variation in prey availability thought to influence young-of-the-year salmon during their initial time at sea. Krill (crustaceans of the family Euphausiidae) have been hypothesized to be critical prey for post-smolt Chinook salmon (*Onchorhynchus tshawytscha*), but until recently data were not available to examine spatial associations. Here, we use hydroacoustic surveys of krill and net samples of juvenile salmon from the central-northern California Current region (San Francisco, CA to Newport, OR) to investigate predator-prey spatial associations over three summers, 2010-2012. Krill were distributed throughout the shelf region, with clear aggregations of abundance at the head of submarine canyons, offshore of major estuary outlets, and adjacent to points or headlands associated with strong Ekman transport. Over 95% of the juvenile salmon were caught in waters < 150 m, which overlapped with some locations of high krill abundance. Negative binomial regression revealed that while juveniles were caught throughout the study area, numbers were concentrated near the Klamath River and San Francisco Bay, indicating that juveniles remain near points of ocean entry. After accounting for distance from points of ocean entry, krill abundance was the only significant predictor of salmon abundance in areas where salmon were caught (presence only). Our findings indicate that shelf habitats in proximity to points of ocean entry as well as prey (krill) abundance in these areas are important determinants of juvenile Chinook salmon distribution and may be used to describe important salmon habitats in the region.

Benefits of Living Life on the Edge: Enhanced Growth and Foraging Opportunities for Juvenile Salmon Inhabiting the Margins of the Sitka Eddy

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Keywords: juvenile salmon, Gulf of Alaska, growth rate, insulin-like growth factor, energetic condition, marine survival, Sitka eddy

Salmon stocks from Alaska, British Columbia, and the Pacific Northwest use the Gulf of Alaska (GOA) as a migratory corridor, which creates potential for inter- and intra-specific competition during periods of high density or spatial overlap. Mesoscale, anticyclonic eddies propagate westward through the Gulf of Alaska from their formation regions along the eastern and northern continental margins (Crawford and Whitney 1999). Most eddies form in late winter and early spring; almost all rotate anticyclonically with typical diameters of 100 to 300 km (Crawford 2002). Juvenile pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon migrating through the coastal GOA during 2010 were distributed throughout the Sitka eddy during the month of July. This study is a basic investigation into how these often large, prominent, and dynamic oceanographic features may influence the health and ultimately the survival of salmon during early ocean residence.

Field sampling efforts began in the coastal waters north of the Southeast Alaska Archipelago in early July and moved south terminating in at the southern tip of Baranof Island in late July. Juvenile salmon were collected with a 184-m long Nordic 264 rope trawl that was fished at the water surface (Orsi et al. 2011) aboard a 49-m chartered fishing vessel. The Nordic 264 rope trawl is comprised of hexagonal mesh wings with a 1.2-cm mesh codend liner and a mouth opening of 24 m deep by 20 m wide (Sturdevant et al. 2011). Insulin-like growth factor 1 (IGF1) was measured from blood collected from juvenile chum, pink, and sockeye salmon in order to provide an index of short-term growth rate for fish at each survey station. Plankton and chlorophyll samples were also collected aboard the vessel at each survey station. Short-term growth rate, energetic condition, and prey quality of juvenile pink, chum, and sockeye salmon were contrasted with geographic position of fish within the eddy as measured by sea surface height.

Fish caught at locations along the eddy perimeter displayed the highest levels of insulin-like growth factor (Fig. 1),

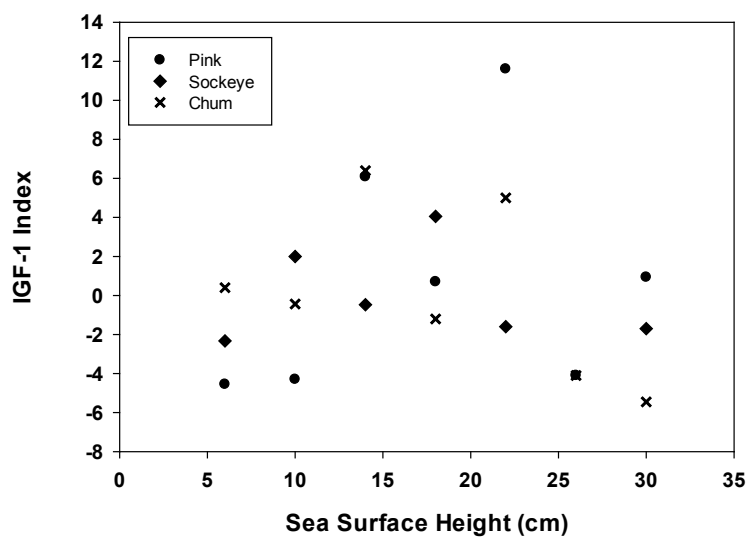


Fig. 1. IGF-1 (insulin like growth factor-1) index values of pink, sockeye, and chum salmon plotted against the location of fish within the Sitka eddy as measured by sea surface height (cm).

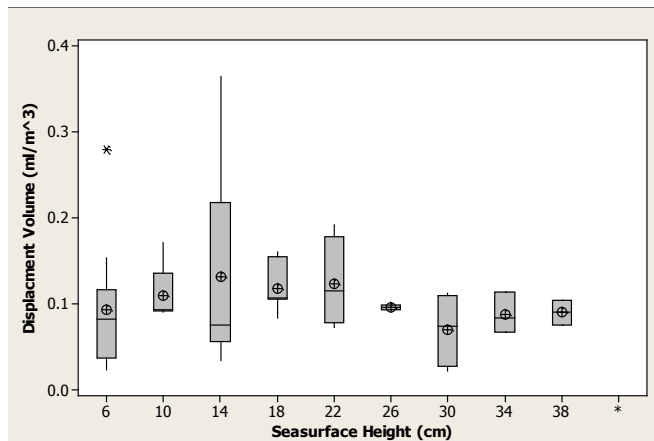


Fig. 2. Zooplankton displacement volume (ml/m³) plotted against the location of samples within the Sitka eddy as measured by sea surface height (cm).

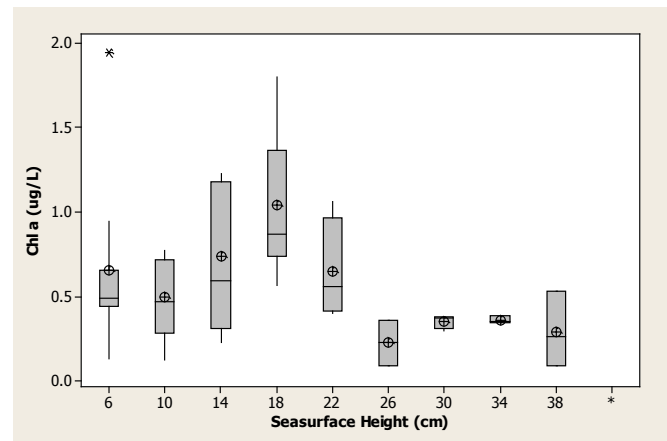


Fig. 3. Chlorophyll-*a* concentration (µg/L) plotted against the location of samples within the Sitka eddy as measured by sea surface height (cm).

indicating that juvenile salmon located in this ocean habitat experienced elevated short-term growth rates. Zooplankton and phytoplankton density was also greatest around the eddy perimeter (Figs. 2 and 3). The position, timing, and strength of the Sitka eddy combined with juvenile salmon outmigration timing may positively affect growth through increased foraging opportunities. Years in which the three primary eddy features in the eastern GOA (Haida, Sitka, and Yakutat eddies) are located close to shore during early summer months, when juvenile salmon are migrating north, enhanced production along the eddy perimeters and should lessen inter- and intra-specific competition and could result in increased survival for certain stocks.

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Assessment and Management of Environmental and Health Factors Affecting Early Marine Survival of Hatchery Reared Coho Salmon in the Strait of Georgia, British Columbia

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Keywords: juvenile coho survival, zooplankton, nearshore environment, fish health, Strait of Georgia

Salmon enhancement program (SEP) hatcheries operated by Fisheries and Oceans Canada (DFO) that are located in the Strait of Georgia target annual releases of 12.4 million coho salmon (*Oncorhynchus kisutch*). However, since the 1980s coho smolt-to-adult survival from facilities bordering the Strait of Georgia has diminished from 8-10% to a present value of around 1% (Beamish et al. 2008). One of the reasons for this shift may be that temporal patterns of productivity in the Strait of Georgia have changed and reduced survival is a consequence of a mismatch between spring zooplankton blooms and the standard single release date still used by most hatcheries. In the early 1980s, survival rates for coho salmon were highest when fish were released near the third week of May at a size of 20-25 g (Bilton et al. 1984). In 2004, the Quinsam Hatchery, located in Campbell River (the town), switched to a staggered release strategy for coho salmon from a single strategy in response to poor adult returns and to address the possibility of mismatched timing between release of juveniles and marine food availability.

The diet of coho salmon during early marine development changes both monthly and interannually depending on the availability of their preferred prey items (Daly et al. 2009). Juvenile salmon are highly selective for prey items regardless of the abundance and composition of available zooplankton (Schabetsberger et al. 2003). Since development of the original plankton monitoring protocol nearly three decades ago, several factors have likely influenced the availability of juvenile salmon food resources, including oceanographic changes, declines in groundfish stocks (source of larval fish prey) and changes to plankton communities (Emmett and Brodeur 2000; Daly et al. 2009).

Changes in the magnitude and timing of ocean productivity in the Strait of Georgia (Beamish et al. 2004) have likely resulted in a mismatch between the timing of smolt release and the occurrence of spring plankton blooms that coho salmon rely on as a primary food source. However, there is a lack of data monitoring the abundance of juvenile salmon prey in plankton communities (Daly et al. 2009). There seems to be a strong correlation between the abundance of coho salmon juveniles in the Strait of Georgia in early summer and the corresponding return of this population as adults (Beamish and Neville 1999; Beamish et al. 2010). Survival of juvenile coho salmon is likely associated with fish reaching a critical size (snout to fork length) by the summer solstice (Beamish and Mahnken 2001). A study conducted on the west coast of Vancouver Island suggests that feed type, particularly zooplankton, and abundance during spring play a primary role in ensuring early marine growth (Tanasichuk 2002).

Discovery Passage is a channel that forms part of the Inside Passage between Vancouver Island and the Discovery Islands off the north end of the Strait of Georgia. The passage is 25 km long and about 2 km wide. The constricted passages in the area create rapid tidal streams and the water is well mixed from top to bottom. This prevents stratification that is typical in the Strait of Georgia and its inlets. Campbell River (the river, not the town) is located in the city limits and registers flows that are the third largest on Vancouver Island. Five species of salmon (Chinook, coho, pink, chum, and sockeye) as well as sea-run trout are distributed in the river. The Quinsam River is a tributary of the Campbell River and joins it 3 km inland. The Quinsam Hatchery is located approximately 2 km upstream on the Quinsam River.

In 2007 a 5-year pilot project was initiated with the objective of developing a monitoring program that could best determine an optimum time frame to release coho salmon to coincide with favourable marine food availability. For this study, we collected juvenile coho salmon during the early spring outmigration to analyze growth, diet, and health. Fish-specific information was related back to plankton data to establish what the juveniles were eating when they exited the estuary and entered the near-shore marine environment. The success of this program was measured by monitoring survival of returning adult coho salmon to the hatchery and assessed by the retrieval of coded-wire tags (CWT).

Early in the project it was determined that estuary conditions as well as ocean conditions made it difficult to make in-season predictions for the best timing for releases from the hatchery. Zooplankton data could be useful, however, in establishing the conditions at release of coho salmon and, along with other studies done in the Strait of Georgia, potentially provide additional information for fishery management, broodstock collection, and establishing escapement targets when the fish returned as adults.

Plankton sampling began each year in late February and continued weekly through to end of June. Zooplankton sampling was conducted using vertical tows from near bottom (20 m depth) to the surface with a 350 µm dark-mesh Bongo net, and chlorophyll *a* levels were determined from analysis of filtered water samples. Chlorophyll-*a* samples collected in 2007-2009 were compared to phytoplankton abundance. The correlation between phytoplankton concentration and chlorophyll *a* was good ($r=0.65$ $p=0.0002$), so we discontinued phytoplankton sampling and continued collecting the filtered water samples after the second year. Water turbidity estimates were added in 2010 and evaluated using a Secchi disk. Water temperature, salinity, and dissolved oxygen profiles were recorded from 0 to 20 m depth, and we observed that water in Discovery Passage was well mixed with temperature and salinity values uniform throughout the water column.

Beach seining to sample juvenile salmonids in the nearshore marine habitat and the Campbell River estuary was initiated about one week after coho salmon were released from Quinsam Hatchery and continued weekly or bi-weekly until the end of June. Tissue samples of kidney, gill, liver, spleen and pyloric caeca were collected from coho for fish health analysis, specifically for *Renibacterium salmoninarum* the causative agent of Bacterial Kidney Disease (BKD) and a significant disease of Pacific salmon. Coho salmon production groups were released from Quinsam Hatchery with clipped adipose-fin patterns and CWTs that allowed for later comparison of release date and adult return.

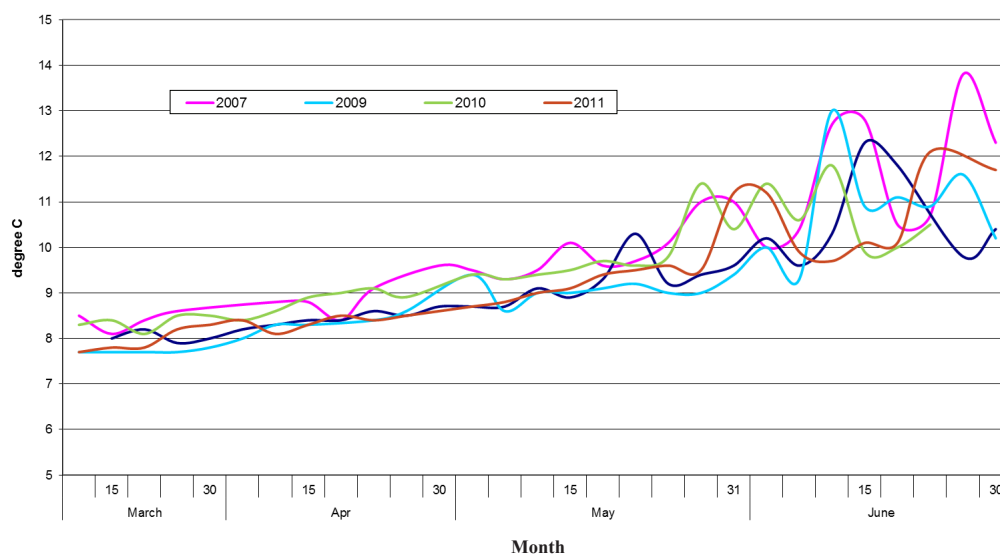


Fig. 1. Water temperature at 5 m depth in the Strait of Georgia, 2007-2011.

The first year of the project occurred near the end of a warming cycle in the Strait of Georgia, which was reflected in the slightly elevated water temperatures compared to the next four years (Fig. 1). Salinity was lowest during 2007. Zooplankton density (count/m³) varied year to year, but 2007 was distinct because densities were substantially lower than those seen during the next four years. Density in 2008 proved to be the highest, and density in 2010 was high as well. For all years of the project, except the 2007, zooplankton densities attained high levels in late April to mid/late May.

As the Campbell River estuary freshwater flows are regulated by BC Hydro, conditions in the estuary vary from year to year. These conditions have an impact on how quickly coho salmon migrate to the ocean. Adult coho salmon returning to the hatchery over the four years of the project (Fig. 2a-d; brood-year 2005-2008) showed that returns were highest for mid-May releases (brood-year 2008 data are not yet compiled). These data are based only on release numbers of tagged smolts and escapement, not expanded to unmarked fish, and do not include other sources of CWT data in fisheries. Quinsam Hatchery now plans releases of the majority of their coho salmon by mid-May to take advantage of the zooplankton blooms. An early release group is still monitored (late April) to determine if there is a shift in the environment that favours earlier release timing. The change to a May 10-15 release for the majority of the Quinsam Hatchery coho salmon, which is based on consistently higher zooplankton density at this time, has resulted in cost savings at the hatchery (mainly from decreased fish feed). It is important to recognize that shifts in the productivity of the marine environment/ecosystem are dynamic; localized conditions as well as larger decadal ocean cycles require continuous repetitive/annual monitoring that also provides information for flexible decision making by management at the individual hatchery level.

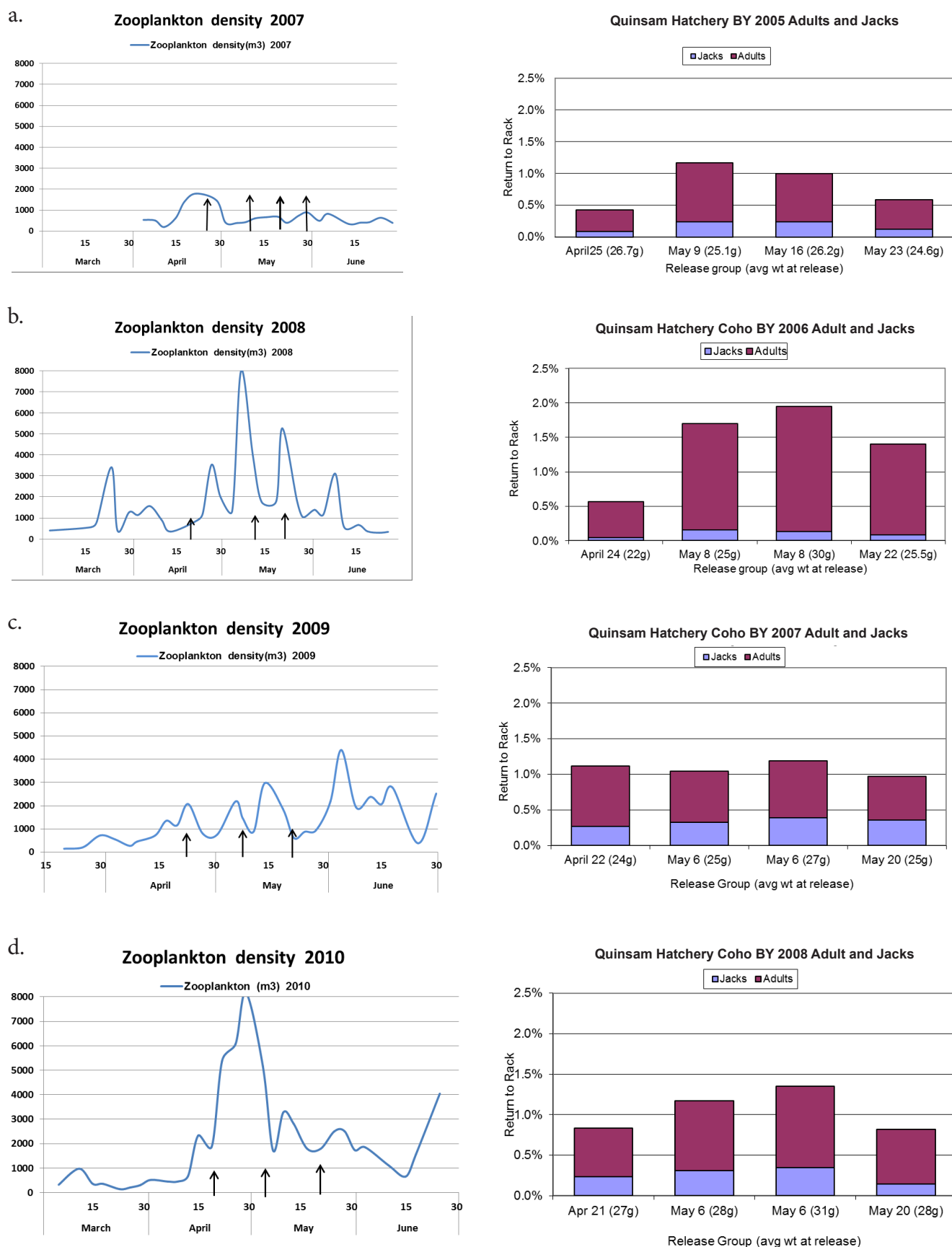


Fig. 2. Annual (2007-2010) zooplankton density (count/m³) in the Strait of Georgia in the spring when marked coho salmon juveniles from brood-year 2005-2008 entered the marine environment (arrows; left column), and the same brood-year returns (2005-2008) of adult and jack coho salmon to the Quinsam Hatchery (right column).

We examined stomach contents of captured fish collected during the first three years of the study (during the following two years, we were unable to collect enough coho salmon in our beach seines for stomach analysis). The hatchery coho salmon appeared to have a slightly more varied diet than the wild fish we retrieved in the beach seine. This may indicate that hatchery coho salmon have a learning curve in selecting optimum prey.

Coho salmon kidneys were tested for *R. salmoninarum* using ELISA (Enzyme-linked Immunosorbent Assay), and the presence of the bacteria was found to be very low.

We continue to assess the data. Beach seine catch data will be analyzed to establish trends in diversity and abundance of species caught over the five years that will be compared to ocean conditions existing at the time when sampling was conducted. In the future we will take a closer look at the zooplankton data to see how community composition varies over the spring of each year and between years.

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How do Oceanographic Characteristics in the Northern Bering Sea Relate to Juvenile Salmon Biomass?

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Keywords: oceanography, North Bering Sea, juvenile salmon, temperature, salinity, zooplankton abundance

The oceanography and shelf dynamics of the southern East Bering Sea (EBS) have been well-studied, while less attention has been given to the northern EBS, although commercially important fisheries are present in both the south and the north. Sea ice extent and duration, and freshwater inputs from the Yukon River are substantially higher in the north compared to the south, resulting in large variations in oceanography between the northern and southern EBS and between regions within the northern EBS. Our goal is to describe spatial and inter-annual variations in oceanographic characteristics (currents, salinity, temperature, and zooplankton abundance) for pre-defined regions (Ortiz et al. in press), and compare these characteristics to juvenile salmon biomass (all species combined) in the northern EBS. Initial findings indicate that, depending on region, juvenile salmon biomass varies with small and large zooplankton abundance, bottom temperature, and salinity.

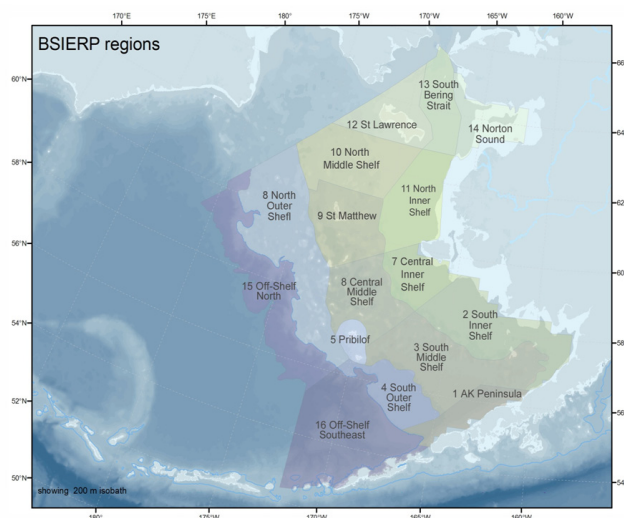


Fig. 1. Bering Sea Integrated Ecosystem Research Program (BSIERP) regions of the northern and southern East Bering Sea (from Ortiz, et al. in press).

Sampling was conducted on a station grid using a CTD (SBE 19, 25 or 9-11) equipped with a Wet Labs fluorometer and beam transmissometer. The survey grid (60 km station spacing) encompassed areas between 60°N and 65°N latitude over the EBS shelf. Sampling occurred from August to October 2002-2011. Data were also collected from multiple University of Alaska Fairbanks (UAF) moorings outfitted with an Acoustic Doppler Current Profiler (ADCP) for velocity measurements and an assortment of temperature (T), T/conductivity (C), and T/C/pressure (P) data loggers. Data from the World Ocean Database (WOD) was used to extend the model area output. Zooplankton was collected over the water column: large taxa with oblique bongo-net tows (505 µm) and small taxa with a vertical Juday-net tow (168 µm). Samples were preserved in 5% formalin and enumerated at shore-based facilities. Juvenile salmon were caught with a surface rope trawl (Can trawl model 400-580; spread 60 m [width] by 15 m [depth]) towed for 30 min at 3.5 to 5 kts. Salmon weights were measured for each species (chum, pink, Chinook, coho, sockeye), and the multispecies biomass catch per unit effort (CPUE) was estimated for all species combined. Bering Sea Integrated Ecosystem Research Program (BSIERP) region delineations were drawn by consensus across researchers based on observed oceanography, bathymetry, benthic fauna, fish, seabird and marine mammal distribution (Ortiz et al. in press). Data were stratified by BSIERP region (Fig. 1) and year and analyzed graphically. Data from moorings (currents, temperature, and salinity) were modeled using MATLAB.

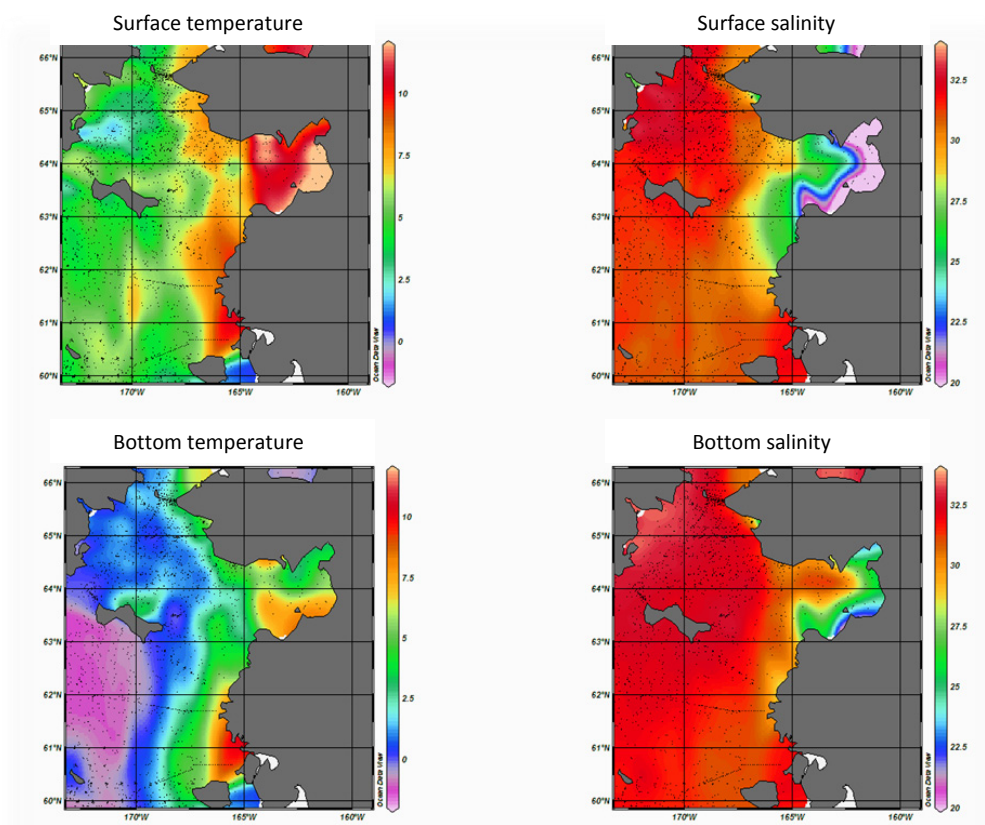


Fig. 2. Northern Bering Sea shelf surface and bottom temperature (left panels) and salinity (right panels) for May-July, 1975-present.

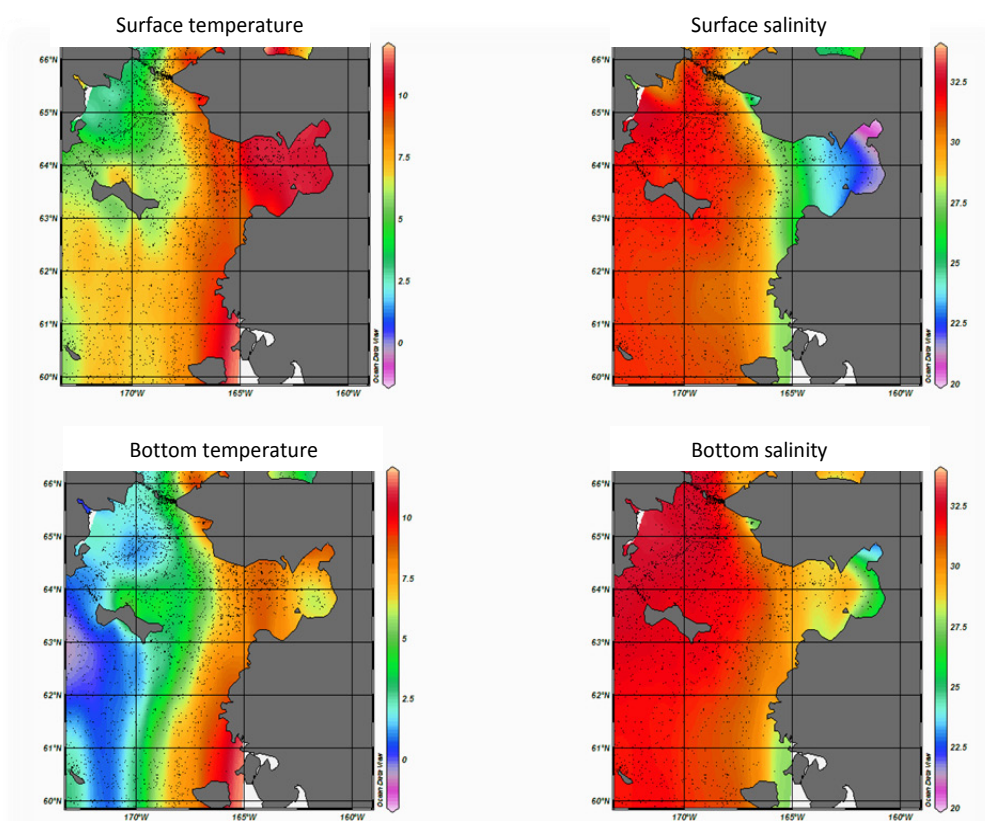


Fig. 3. Northern Bering Sea shelf surface and bottom temperature (left panels) and salinity (right panels) for August-October, 1975-present.

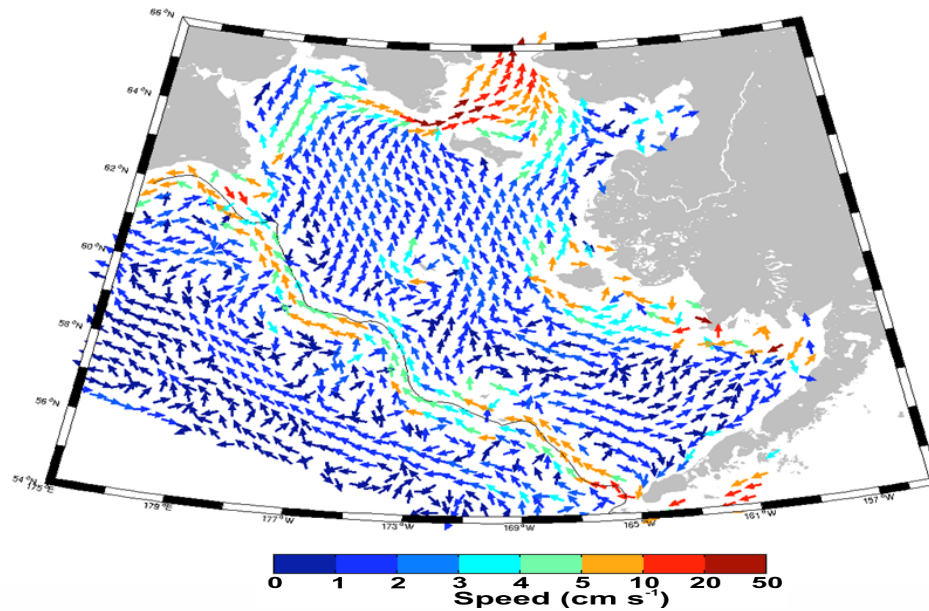


Fig. 4. Mean value for Bering Sea surface currents, 1987-2007.

Salinity increases and temperature decreases from east to west across the northern Bering Sea shelf (Figs. 2 and 3). Low bottom temperatures observed southwards of St. Lawrence Island show the cold pool location (water temperature $< 2^{\circ}\text{C}$ that is formed during previous winter freezing). Temperature varies between domains with distinctly cooler surface temperatures over the St. Lawrence and South Bering Strait domains. Temperatures are considerably higher for both surface and bottom waters in August-October than in May-July. Currents are generally northward, moving at about $2\text{--}3\text{ cm}\cdot\text{s}^{-1}$ near St. Lawrence Island, and increase through the Bering Strait (Fig. 4). Norton Sound stands out as a distinct region characterized by high surface and bottom water temperatures and low surface and bottom salinities (Figs. 2 and 3; Table 1) due to ice breakup and high fresh water run-off. Beam (light) transmission is lower than average due to high particulate suspension (Table 1). There is no predominant current direction in Norton Sound and speeds vary from < 1 to $> 3\text{ cm}\cdot\text{s}^{-1}$ (Fig. 4). The South Bering Strait and North Inner regions are areas of high juvenile salmon biomass, as well as high numbers of large zooplankton (South Bering Strait) and high numbers of small zooplankton (North Inner; Table 1). Highest light transmission values are observed with high bottom and surface salinity in the St. Lawrence region, and low transmission values are found with low bottom and surface salinity in Norton Sound (Table 1).

Table 1. Oceanographic parameters, large and small zooplankton abundance, and juvenile salmon biomass stratified by BSIERP region. Red indicates high/maximum values and blue indicates minimum values.

BSIERP region	Temp Top ($^{\circ}\text{C}$)	Temp Bottom ($^{\circ}\text{C}$)	Salinity Top	Salinity Bottom	Transmission (% light trans)	Large zoo abund. (# m-3)	Small zoo abund. (# m-3)	Juvenile salmon biomass (kg km-2)
North Inner	8.25	6.53	30.63	30.92	82	84	104127	3706
North Middle	7.83	1.26	31.15	31.57	83	90	54969	819
Norton Sound	9.70	8.92	27.00	28.29	65	41	13037	575
South Bering Strait	7.51	5.15	31.11	31.59	82	2418	10399	2287
St. Lawrence	7.65	2.97	31.80	32.20	89	183	13108	194
St. Matthews	7.61	1.33	31.32	31.74	84	67	5941	930

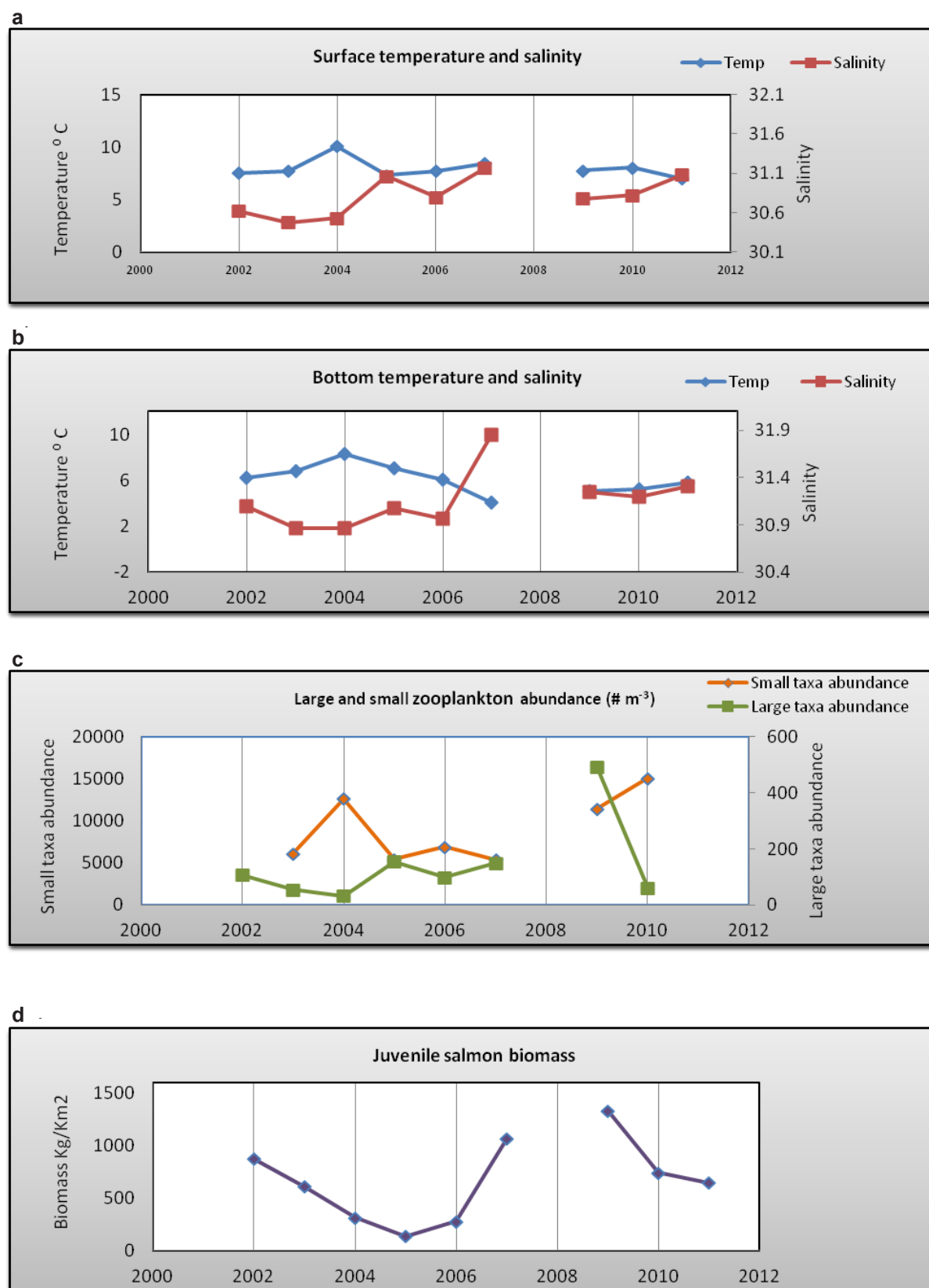


Fig. 5. Temperature and salinity (a, b), large and small zooplankton abundance (c) and juvenile salmon biomass (d) for combined BSIERP regions, 2002-2011. Regions: North Inner and South Bering Strait (NI-SBS).

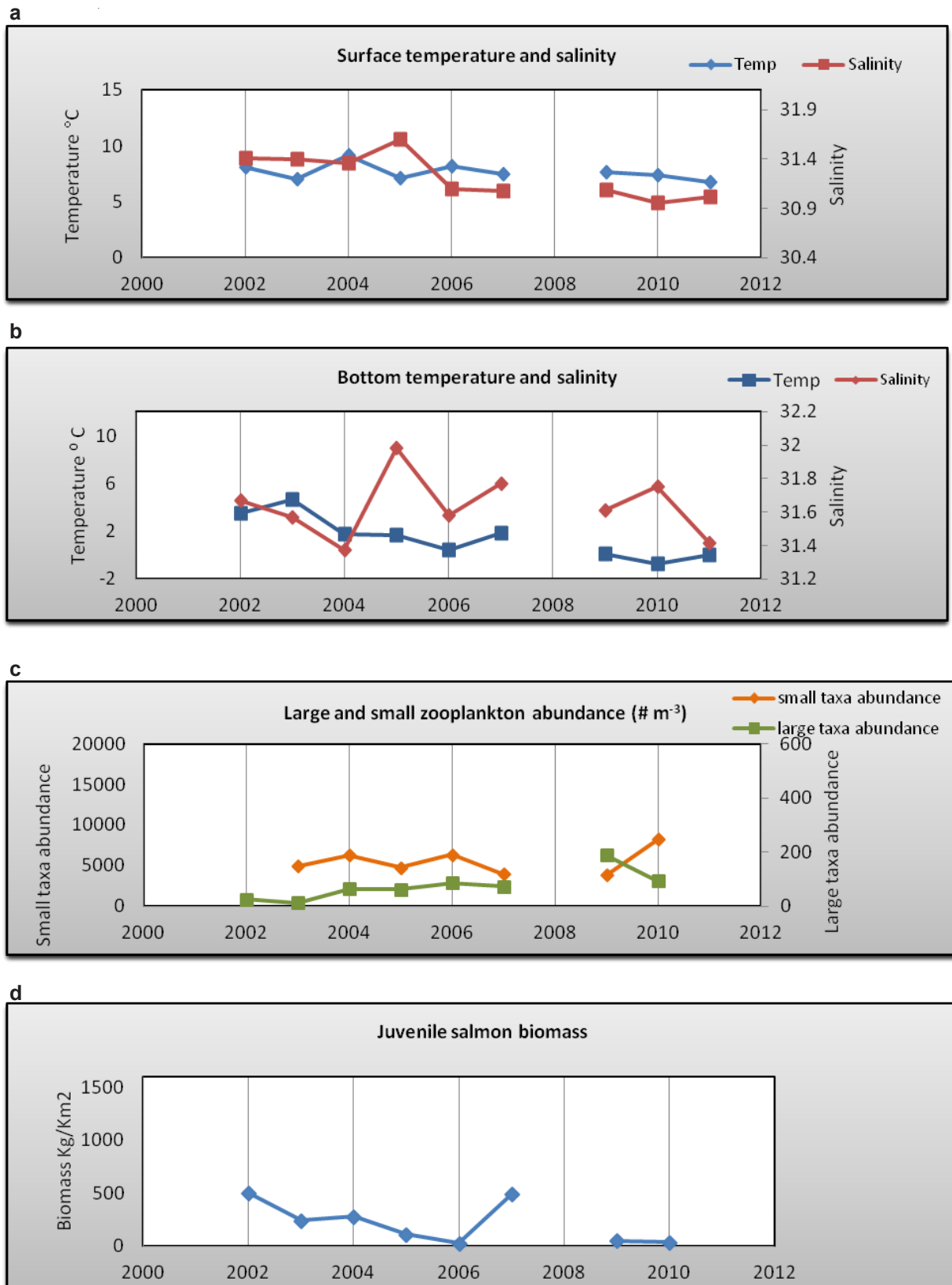


Fig. 6. Temperature and salinity (a, b), large and small zooplankton abundance (c) and juvenile salmon biomass (d) for combined BSIERP regions, 2002-2011. Regions: North Middle and St. Matthews regions (NM-SM).

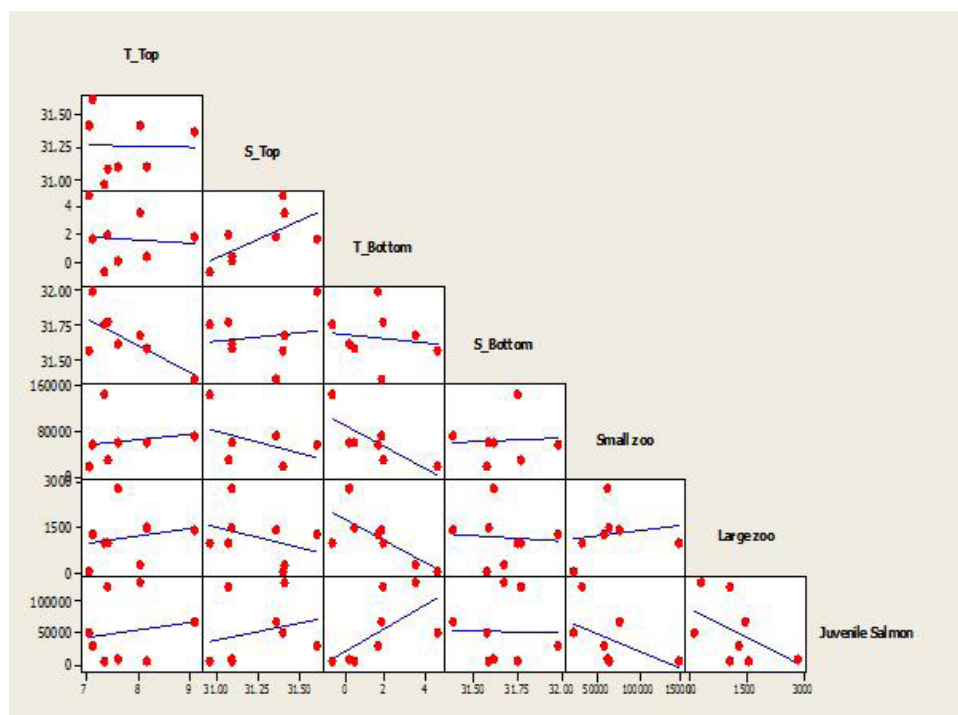


Fig. 7. Matrix plot for of surface (Top) and bottom (Bottom) temperature (T) and salinity (S), large (Large zoo) and small zooplankton (Small zoo) abundance, and juvenile salmon biomass for North Middle and St. Matthews (NM-SM) combined BSIERP regions.

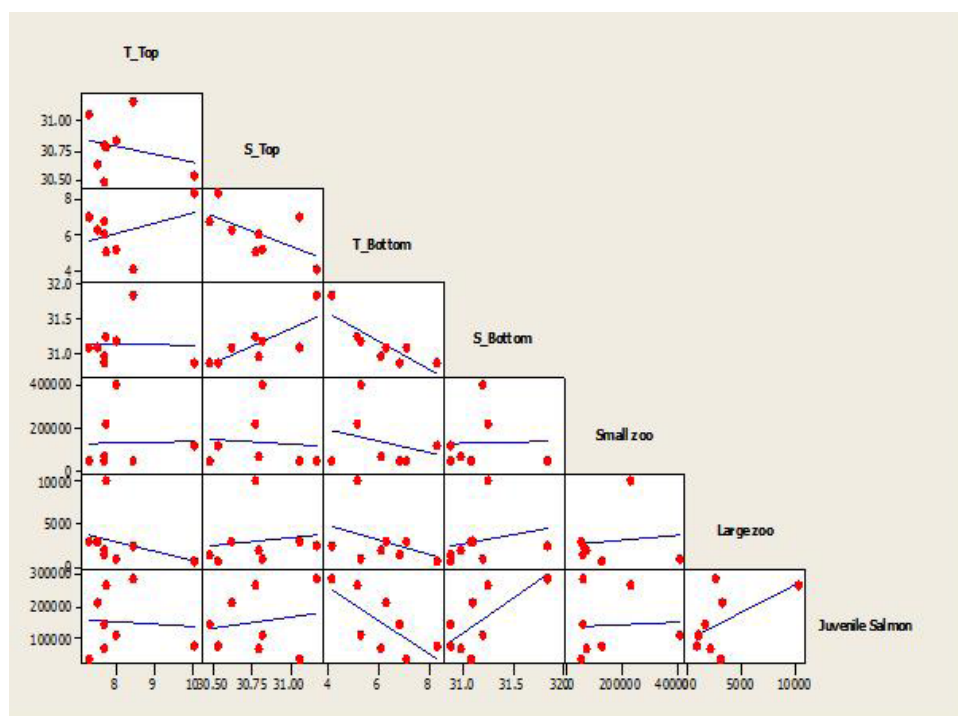


Fig. 8. Matrix plot for of surface (Top) and bottom (Bottom) temperature (T) and salinity (S), large (Large zoo) and small (Small zoo) zooplankton abundance, and juvenile salmon biomass for North Inner and South Bering Strait (NI-SBS) combined BSIERP regions.

BSIERP regions were combined to investigate temporal trends (2002-2011) in parameters (salinity, temperature, large and small zooplankton abundance, and juvenile salmon biomass) by combining North Inner and South Bering Strait regions (NI-SBS; Fig. 5a-d), and North Middle and St. Mathews regions (NM-SM; Fig. 6a-d). Analysis of yearly trends revealed a positive relationship between surface salinity and large zooplankton abundance (NI-SBS) until 2009-2010 (Fig. 5a and c). There is a negative relationship between large and small zooplankton in NI-SBS, and a positive relationship is seen in NM-SM (Figs. 5c and 6c). Juvenile salmon biomass in NI-SBS increased in years with colder, saltier bottom waters (Fig. 5d). In contrast, salmon biomass in NM-SM increased in years with warmer bottom temperatures (Fig. 6d). A matrix plot confirmed the relationships described above (Figs. 7 and 8).

Initial findings reveal connections between juvenile salmon and bottom temperature, bottom salinity, and large and small zooplankton, depending on the region. Surface temperature and salinity changes over the northern EBS can change considerably from season to season and from nearshore to offshore. Norton Sound is a distinct area oceanographically, with relatively low juvenile salmon biomass during late summer/early fall, and the highest juvenile salmon biomass is found in South Bering Strait and North Inner regions. Because the highest abundances of large and small zooplankton were seen in the South Bering Strait and North Inner regions, respectively, large zooplankton could be important prey for juvenile salmon in the South Bering Strait region, and small zooplankton could be important prey for juvenile salmon in the North Inner region. Future analysis will focus on individual salmon species by investigating salmon spatial and temporal relationships with oceanographic parameters.

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Summer Energetic Condition of Juvenile Sockeye Salmon in the Gulf of Alaska

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Keywords: energetic condition, juvenile sockeye salmon, Gulf of Alaska

This study investigates the interannual differences in juvenile salmon diet, energetic content, size, and migration patterns in the Gulf of Alaska (GOA) with regard to the El Nino-Southern Oscillation (ENSO) cycle, which changed from a positive to negative anomaly during 2010 and 2011. Variability in the ENSO cycle has been shown to influence physical and biological characteristics of the surface waters in the GOA that may control marine food habits, growth, and condition of juvenile salmon inhabiting coastal surface waters. The GOA also experienced variability in sea level pressure, sea surface temperature, surface water nutrient concentration, and the Pacific Decadal Oscillation index during our study years that added to the contrast in ocean conditions. All juvenile salmon for this study were collected with a surface rope trawl and analyzed in NOAA's Fishery Ecology Diet and Zooplankton (FEDZ) laboratory in Juneau for food habits and determination of energetic status. This study observes marine conditions during early ocean residence and the influence on recruitment to local fisheries using the record high (2011) and below average returns (2012) of pink salmon to Southeast GOA as an example. The sampling area and duration was extended in 2011 to include Central and Southeast Alaska during summer and fall to observe seasonal and regional differences in juvenile salmon migration timing, community structure, marine food habits, and energetic content. The Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP) fisheries oceanography surveys has created a unique opportunity for observing juvenile salmon abundance, community structure, energetic content, and diet relative variability in ocean conditions and recruitment strength to the fishery. Preliminary results for pink salmon in Southeast GOA collected in July show a decrease in size and weight from 2010 to 2011 indicating that condition during the first year at sea may be correlated with recruitment to the fishery.

Interannual Variation in Prey Resources During the Early Ocean Life of Juvenile Chum Salmon in Four Coastal Areas Around Hokkaido, Northern Japan

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Keywords: zooplankton abundance, species composition, interannual variation, juvenile chum salmon, Hokkaido

The early ocean life of juvenile chum salmon is a critical phase in their life history. It is thought that high mortality occurs in this initial phase, which may be an important determinant of subsequent salmon population size. Previous studies suggested the survival of juvenile chum salmon is affected by both physical factors (e.g., temperature) and biological factors (e.g., prey environment; Irie 1990; Asami et al. 2005). The state of the prey environment, such as zooplankton abundance and species composition, is important for the growth and survival of juvenile chum salmon during their early ocean life.

In order to evaluate the prey environment during the early ocean life of juvenile chum salmon, we conducted a long-term monitoring study of zooplankton from March to July 1998-2010 in four different coastal environments around Hokkaido: Atsuta along the Japan Sea coast, Shiraoi along the western Pacific coast, Konbumori along the eastern Pacific coast, and Shari along the Okhotsk Sea coast. Zooplankton samples were collected with vertical tows (0 - 20 m) by a NORPAC net (0.45 m opening diameter, 0.33 mm mesh) during daytime. If water depth was less than 20 m, the net was towed from 3 m above sea bottom.

Common zooplankton types observed in all areas were hydrozoans, cladocerans, copepods, euphausiids, chaetognaths and appendicularians. Zooplankton types observed occasionally included meroplanktonic larvae, such as gastropods, polychaetes, decapods and echinoderms. Trends of interannual variation of zooplankton abundance and species composition were different among the four areas. Dominant zooplankton were small-size copepods less than 2 mm in body length, such as *Pseudocalanus newmani* collected in the Japan Sea and Okhotsk Sea coast samples, and *Acartia longiremis* in the Pacific coast samples. However, juvenile chum salmon fed on zooplankton larger than 2 mm in body length, and zooplankton species found in chum salmon stomach samples were different among areas (unpublished data). Our results suggest that variation in large-size zooplankton abundance may affect the growth and survival of juvenile chum salmon.

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Coastal Feeding Patterns Based on Spatial Distribution of Released Korean Chum Salmon, *Oncorhynchus keta*, Fingerings

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Keywords: Korean chum salmon, juvenile, stomach contents, feeding strategy, zooplankton distribution

In this study, we conducted a survey to examine the ecological feeding strategy of Korean chum salmon, *Oncorhynchus keta*, juveniles released in March from the Namdaechun Stream and caught in coastal waters during April to May in 2010 and 2011 (Fig. 1). We investigated the feeding patterns of salmon juveniles moving northwards along and away from the coast. The fork lengths and body weights of the salmon releases were not significantly different from one another and ranged 5.2-7.8 cm and 1.5-5.1 g, respectively. In zooplankton samples, the dominant taxonomic group was copepods. The stomach contents of juvenile chum salmon differed by sampling station, but most of the salmon were consuming amphipods. Dipteran terrestrial insects were commonly observed in chum salmon stomach samples, and the occurrence of insects was not related to the distance of the survey site from land. Results showed the most suitable prey items of juvenile chum salmon were dipterans and amphipods in the coastal survey area of the East Sea of Korea. Therefore, we suggest these results become part of the basic data by which to identify the migration pathway of juvenile chum salmon moving away from the release area.

In 2010, zooplankton samples were collected at 16 sites 1 km away from the juvenile chum salmon release site. Samples indicated copepods were the dominant group and accounted for more than 50% of the zooplankters counted, except for survey transect (ST) 3. At ST 3, amphipods accounted for 50.3% (11.7 individuals/ton) and copepods were 47.7% (11.1 individuals/ton) of the items in the samples. Amphipod abundance ranged from 3.0% to 50.3% (0.5 to 11.7 individuals/ton) at the sites 1 km away from the coastal sites, except for five locations. However, the location of macroplankton abundances, including chaetognaths and arthropods, did not show a clear trend.

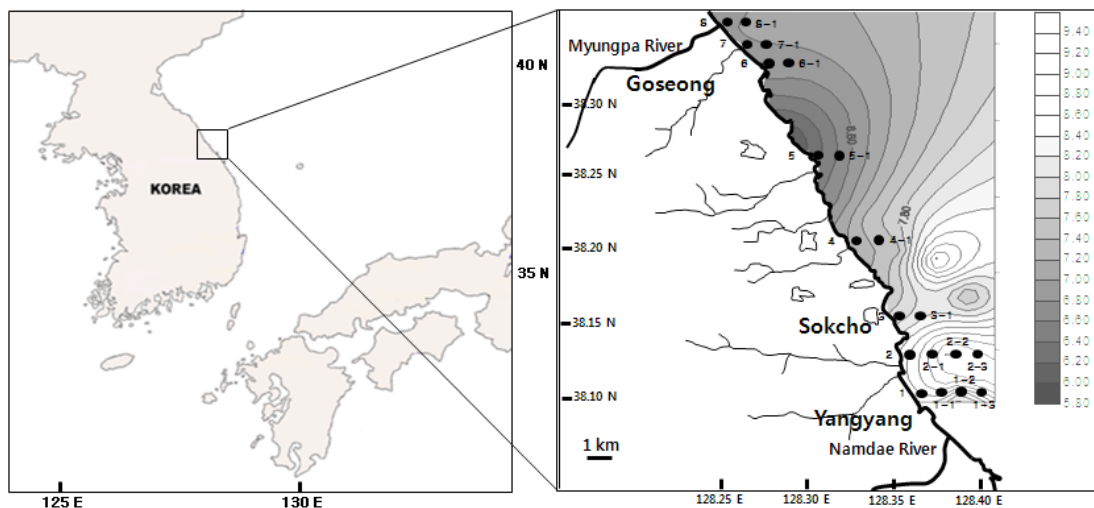


Fig. 1. Location of survey stations in the East Sea off the coast of the Republic of Korea sampled in April-May, 2010-2011.

Analysis of juvenile chum salmon stomach contents collected at the same sites are shown in Fig. 2. Considering coastal sites 1 km away from the juvenile chum salmon release location, copepods were dominant in the stomach samples collected at ST 2-1 and amphipods were dominant at most of the other sampling sites. In addition, diptera were dominant in stomach contents collected at ST 1 and ST 8-1.

In 2011 zooplankton samples collected at ST 1 and ST 2, copepods were the dominant group and accounted for 75% to 100% (5.8 to 892.7 individuals/ton) of the items in the samples, except for those collected at ST 2-2. Amphipods were usually a subdominant group and were present at six of eight transects, but this group accounted for 54.8% (46.6 individuals/ton) of the items in zooplankton samples only at ST 2-2.

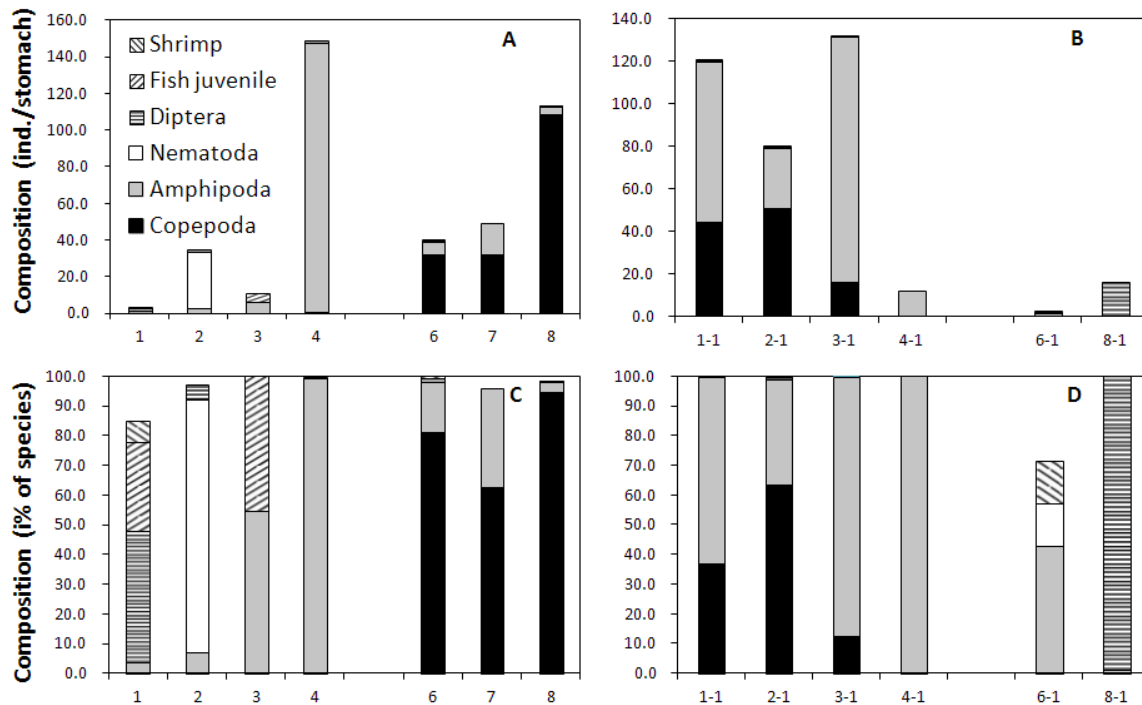


Fig. 2. Juvenile chum salmon stomach contents (count of prey individuals/stomach) collected in spring (April to June) 2010. Other minor categories include decapods, euphausiids, pteropods, fish egg, crab larvae and hydrolysate.

Stomach contents of the juvenile chum salmon varied by site according to the distance the sample was collected from the coast (Fig. 3). Copepods accounted for 81.2% (32.3 individuals/stomach) and 62.7% (108.8 individuals/stomach) of stomach contents at ST 1-3 and ST 2, respectively. Amphipods accounted for 54.5% (6 individuals/stomach), 61.7% (75.5 individuals/stomach) and 62.6% (75.5 individuals/stomach) of stomach contents at ST 1-2, ST 2-1 and ST 2-2, respectively. Nematodes accounted for 84.8% (30.6 individuals/stomach) and 44.5% (1.5 individuals/stomach) of stomach contents at ST 1-1, and ST 1, respectively. Fish prey were consumed only at ST 1, ST 1-2, and ST 1-3, and shrimp were observed in stomach samples collected at ST 1 and ST 2-1. Diptera were observed in stomach contents of juvenile chum salmon caught at most sampling sites, regardless of the distance from the coast.

Terrestrial insects, diptera, observed in juvenile Korean chum salmon stomach samples were generally consumed in the river. The tendency to consume a high proportion of insects was also observed in juvenile Chinook salmon (Rondorf et al. 1990). In coastal waters, amphipods were easy to capture because, among the arthropods, they are relatively slow moving. Diptera and amphipods are excellent sources of nutrients, such as DHA and EPA (docosahexaenoic acid and eicosapentaenoic acid, both omega-3 fatty acids). Consequently, the best food for juvenile Korean chum salmon entering the marine waters of the coastal region is amphipods.

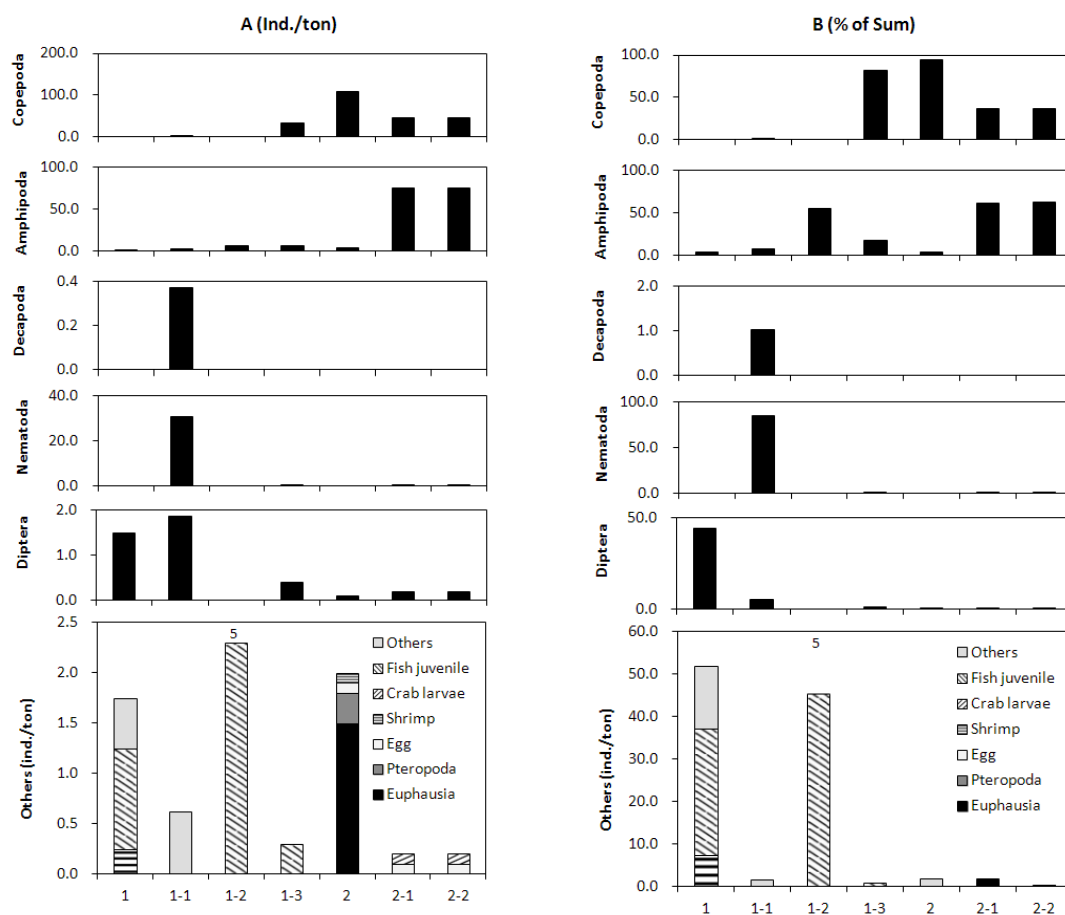


Fig. 3. Stomach contents (individuals/stomach) of juvenile chum salmon collected in spring (April to June) 2011.

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Stock-Specific Predation of Rhinoceros Auklets (*Cerorhinca monocerata*) on Juvenile Salmon in Coastal British Columbia

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Keywords: pink salmon, chum salmon, sockeye salmon, rhinoceros auklets, size-selective predation, condition-based predation susceptibility, DNA stock identification

Mortality rates of Pacific salmon (*Oncorhynchus spp.*) generally exceed 90% during their marine life. Much of this mortality is thought to occur in coastal waters during the first few weeks to months after ocean entry due to predation. Selection of prey in poor body condition is a widespread phenomenon in terrestrial systems (e.g. Murray 2002; Husseman et al. 2003). Similar patterns of prey selection are often assumed to operate in aquatic realms (Burke et al. 2013). However, condition-based susceptibility remains untested given that predator-prey interactions are difficult, if not impossible, to observe. The tendency for terrestrial predators to take substandard prey is linked to a hunting strategy where predators that chase their prey are more likely to take individuals in poorer condition compared to those with ambush tactics (e.g. Fitzgibbon and Fansha 1989).

The timing of the seaward migration of pink, chum, and sockeye salmon coincides with the chick provisioning period of the rhinoceros auklet, a pursuit-diving avian predator known to feed on them. The vast majority of juvenile salmon from southern and central British Columbia (BC) funnel past aggregations of breeding auklets totalling hundreds of thousands of individuals nesting at key points along coastal migration pathways in central and northern BC. The component of juvenile salmon in chick provisioning diets typically ranges between 0-20%, representing 1-5 individual salmon delivered whole to chicks.

We investigated factors that influenced vulnerability of wild juvenile pink, chum, and sockeye salmon to rhinoceros auklet predation by sampling at three bird colonies in BC and concurrent coast-wide trawl surveys. Critically, we were able to evaluate stock specific predation and control for any stock differences in size through molecular-genetic stock-identification techniques (Beacham et al. 2005).

We observed previously unseen amounts of salmon in the diets, and in many cases, diets were exclusively salmon. While pink and chum salmon were more abundant than sockeye salmon, their distribution was patchier in survey catches. However, the majority of salmon in provisioning diets were sockeye (51% sockeye, 31% pink, and 18% chum salmon), suggesting that the more evenly distributed prey was selected. DNA stock identification revealed a full 98% of sockeye salmon originated from the Fraser River system at all colonies; for pink, southern colonies were dominated by Puget Sound stocks (93-99%) and the northern colony was split between Puget Sound and north coast stocks. For chum salmon, colonies were split between salmon originating from the Fraser River and Vancouver Island. The pronounced differences between colonies in the specific stock composition of the salmon consumed suggest there are important spatial-temporal patterns in juvenile salmon migration.

For all species and specific stocks, size and condition were significantly lower for predated salmon at each colony relative to respective salmon caught in survey cruises, providing direct evidence for size-selective and condition-based predation susceptibility. The proportion of salmon in poor condition varies substantially between years due to prevailing ocean and feeding conditions.

We anticipate that our results will be a starting point to evaluate how predation might interact with external factors and consequently influence or structure marine fish populations.

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Interannual and Spatial Variability in the Feeding Ecology of Juvenile Chinook Salmon and Effects on Survival and Growth

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Keywords: stable isotopes, Vancouver Island, Southeast Alaska, trophic level, juvenile Chinook salmon

Chinook salmon are important to the ecology, economy, and culture of British Columbia but are declining in abundance. The drivers underlying these declines are generally poorly understood, but they are thought to occur primarily in the marine environment. The mortality of juvenile salmon during early marine life has been shown to be important for determining year-class strength (Pearcy 1992) and is expected to be size-selective. As such, factors that reduce early marine growth may also reduce subsequent return rates.

Early marine growth rates are largely affected by prey quality and quantity (Beauchamp 2009); higher quality and greater prey abundance can lead to higher growth rates. Here, we use stable isotopes to assess relative changes in prey quality and quantity to determine the potential ways these factors affect growth and survival rates of two groups of Chinook salmon.

Stable isotopes of nitrogen and carbon are commonly used to assess the time-integrated feeding ecology of organisms. $\delta^{15}\text{N}$ is an indicator of trophic level where higher $\delta^{15}\text{N}$ generally relates to higher trophic level. However, differences between regions or years can be obscured by the variability in the $\delta^{15}\text{N}$ values of organisms at the base of the food web (primary consumers). To facilitate further comparisons, a relative trophic level can be calculated using the $\delta^{15}\text{N}$ of zooplankton and a known trophic enrichment factor. In general, larger prey items are more energy dense, they require less energy to capture, and they contain more digestible material. Thus we expect that salmon growth and survival will be enhanced in years with high $\delta^{15}\text{N}$ and high trophic level of juvenile salmon.

There is a relationship between $\delta^{13}\text{C}$ and onshore/offshore productivity (Perry et al. 1999). Onshore areas are more productive and have correspondingly higher $\delta^{13}\text{C}$ values (Miller et al. 2008) and years with greater productivity may also have higher $\delta^{13}\text{C}$. We expect that salmon growth and survival will be positively related to $\delta^{13}\text{C}$.

Juvenile Chinook salmon were sampled by rope trawl in October-November in two regions: west coast of Vancouver Island (WCVI) and Southeast Alaska (SEAK) as part of the High Seas Salmon Program (Fisheries and Oceans Canada) from 2000 to 2009 (Table 1; Trudel et al. 2012). Samples were frozen on-board the research vessel at -20°C . In the laboratory at the University of Victoria, samples were dried, ground to a fine powder, packed into tin capsules, and analyzed using a mass spectrometer. A sample of skin tissue was also run for DNA stock assignment. Linear regressions between yearly average isotope values and yearly growth (change in fork length over time) and survival rates were performed.

Table 1. Summary of sample size, average fork length (FL), and average weight of juvenile Chinook salmon collected from surveys in Southeast Alaska (SEAK) and west coast of Vancouver Island (WCVI).

Year	SEAK			WCVI		
	n	FL (mm)	Weight (g)	n	FL (mm)	Weight (g)
2000	34	279.2	309.1	11	201.1	99.3
2001	41	256.5	231.8	49	160.2	50.4
2002	43	274.5	279.3	38	186.5	91.6
2003	10	236.1	172.0	18	200.7	108.1
2004	6	258.0	238.5	14	187.1	84.6
2005	34	226.9	151.4	40	183.8	74.5
2006	29	255.2	221.2	43	191.1	97.9
2007	60	240.9	197.0	299	162.5	53.3
2008	26	240.3	198.7	39	163.9	50.0
2009	15	249.7	197.6	27	159.0	46.1
Total	297	252.7	224.0	577	169.8	63.0

In samples collected from WCVI, positive relationships between $\delta^{15}\text{N}$ in the tissue of juvenile Chinook salmon and growth and between tissue- $\delta^{15}\text{N}$ and survival were observed (growth: $t = 2.7$, $df = 8$, $p = 0.02$; survival: $t = 2.4$, $df = 8$, $p = 0.04$; Table 2). We did not observe significant relationships between $\delta^{15}\text{N}$ and growth or survival for samples obtained in SEAK (growth: $t = -1.2$, $df = 8$, $p = 0.3$; survival: $t = -0.5$, $df = 8$, $p = 0.6$). In WCVI samples, the trophic level of juvenile Chinook salmon showed a strong positive relationship with survival ($t = 2.6$, $df = 8$, $p = 0.03$) but not with growth ($t = 0.9$, $df = 8$, $p = 0.4$). There was no relationship between trophic level and growth or survival in SEAK samples (growth: $t = -0.2$, $df = 8$, $p = 0.8$; survival: $t = 0.4$, $df = 8$, $p = 0.7$). $\delta^{13}\text{C}$ showed a strong positive relationship with growth and survival in WCVI samples (growth: $t = 3.1$, $df = 8$, $p = 0.01$; survival: $t = 3.1$, $df = 8$, $p = 0.01$) and no relationship in SEAK samples (growth: $t = 2.0$, $df = 8$, $p = 0.08$; survival: $t = 0.7$, $df = 8$, $p = 0.5$).

Table 2. Adjusted R^2 values for the correlations between isotopic ratios and growth and survival rates of juvenile Chinook salmon obtained from surveys along the west coast of Vancouver Island (WCVI) and in Southeast Alaska (SEAK). Significant ($p < 0.05$) correlations are displayed in bold type.

	WCVI			SEAK		
	$\delta^{15}\text{N}$	TL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL	$\delta^{13}\text{C}$
Growth	0.43	-0.03	0.49	0.05	-0.12	0.26
Survival	0.34	0.39	0.50	-0.09	-0.11	-0.06

In samples collected from SEAK, the feeding ecology of juvenile Chinook is not driving differences in growth or survival rates. However, in WCVI samples, shifts in feeding ecology have implications for growth and survival rates. The reasons for regional differences may be related to differences in size or oceanography between regions.

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Continental-Scale Comparative Analyses of Feeding and Resource Ecology of Juvenile Chinook Salmon Along the Pacific Coast of North America

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Keywords: feeding, stable isotope, juvenile Chinook salmon, North America

During the last two to three decades, the adult return of Chinook salmon has been declining for several stocks, which might be linked to large-scale changes in ocean conditions associated with variability in temperature, nutrients, quantity and quality of habitat and food, and predator assemblages. Understanding and modeling the feeding and resource ecology of juvenile Chinook salmon on a continental scale have never been done because of the challenges in collecting and integrating samples and following consistent protocols. To achieve this scale of comparative analysis, we collected zooplankton, salmon, and forage fish from eight cruises along the coastal regions off northern California, Oregon/Washington, Vancouver Island, Southeast Alaska, eastern Bering Sea, and Chukchi Sea during August through October 2007. We examined stable isotope signatures of nitrogen and carbon and concentrations of mercury in the tissue and stomach contents to understand the continental-scale variability in foodweb dynamics, trophic interactions, and resource base of juvenile Chinook salmon. We found large gradients in the $\delta^{13}\text{C}$ signatures along a continental spatial scale that corresponded to regional variability in the diet. Juvenile Chinook salmon up to 200 mm in length showed an ontogenetic niche shift in most regions and then stabilized. Mercury concentrations in juvenile Chinook salmon tissue appear to be linked to growth patterns, not to large-scale loading or mobilization. Finally, we used the zooplankton and forage fish data from the different regions to estimate baseline isotope signatures to compare regional differences in trophic shifts as a function of body size.

Feeding Habits, Consumption Rates, and Growth of Juvenile Salmon in Relation to Fluctuations of the Forage Base and Salmon Abundance

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Keywords: pink salmon, chum salmon, diet, daily ration, food supply, Sea of Okhotsk, Bering Sea

Total salmon abundance in the North Pacific has increased over the last thirty years. In the 1990s, there was some evidence of density-dependent effects in salmon populations that led researchers to conclude there were shortages of food resources and an overpopulation of the North Pacific by Pacific salmon (Ishida et al. 1993; Bigler et al. 1996; Kaeriyama 2003; Klovach 2003). Over the past decade, Pacific salmon abundance has continued increasing. This might cause intensification of competitive interactions between and among Pacific salmon species. This study aims to determine whether feeding habits, consumption rates, growth, and food supply (degree of satisfaction of the feeding requirements of the fish) of juvenile pink and chum salmon changed in 2001-2010, and how this was related to salmon abundance and their forage base.

This study is based on findings of 18 complex epipelagic surveys conducted in the Sea of Okhotsk and western Bering Sea by TINRO-Center in September-November from 2001 to 2010. The surveys included biomass estimation of salmon, ecologically-related plankton and nekton species, and fish diet analysis. Fish were sampled with pelagic trawls (vertical opening 25–45 m, horizontal opening 35-50 m) equipped with a small-size mesh (1 cm) lining the cod end. Zooplankton samples were obtained using a Jedy net (0.1 m² mouth opening and 0.168-mm mesh). Stomach contents were analyzed aboard the vessel using the method described by Volkov and Chuchukalo (1986). For more details see Glebov et al. (2005) and Zavolokin et al. (2007).

Due to the large number of trophic indices used, such as daily ration, stomach fullness, diel feeding rhythm, trophic niche breadth, number of prey, diet overlap, and share of minor food, their interpretation in terms of forage conditions and food supply is potentially biased. I suggest the food supply index (FSI) as a quantitative measure of food supply. The FSI is the average of values (k) for all indirect indices (i): $FSI = \sum k_i / n$. k assumes the values -1, 0 and 1, which means unfavorable, normal, or favorable conditions of the food supply, respectively. The FSI allows for the quantitative measure of food supply and makes statistical analysis possible.

In the Sea of Okhotsk, relatively low salmon food supply occurred in 2001, 2002, 2004 and 2006 (Table 1). In 2002 and 2004, this was indicated by low feeding intensity and a high share of minor food items in salmon stomach contents. In 2001, there was high diet overlap between pink and chum salmon associated with consumption of copepods and chaetognaths. Due to the increase in the share of pteropods in the pink salmon diet and chaetognaths in the chum salmon diet in 2006, a broad feeding spectrum and divergence in salmon feeding testified to a relative decrease in the salmon food supply. High FSI values observed in 2003 and 2007 resulted from high consumption rates and a low proportion of minor food items.

Table 1. Trophic characteristics and food supply index of juvenile pink and chum salmon in the Sea of Okhotsk in 2001-2010.

Trophic feature	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Daily ration	0	-1	1	-1	0	0	1	0	0	0
Stomach fullness	0	-1	1	-1	0	0	1	0	0	0
Diel feeding rhythm	0	0	0	0	0	0	0	0	0	0
Trophic niche breadth	0	0	0	0	0	-1	0	0	0	0
Number of prey	0	0	1	0	0	-1	0	0	0	0
Diet overlap	-1	0	0	0	0	-1	0	1	0	-1
Share of minor food	-1	-1	1	0	0	0	0	0	1	0
Food Supply Index	-0.3	-0.4	0.6	-0.3	0	-0.4	0.3	0.1	0.1	-0.1

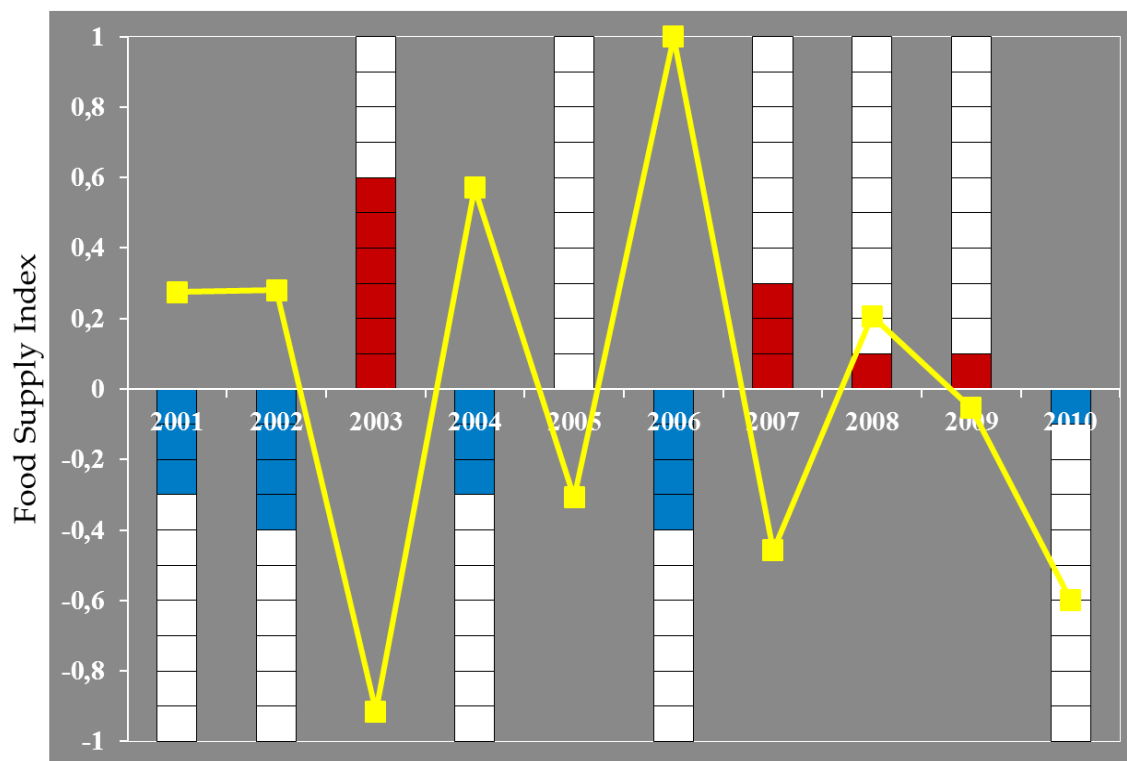
In the Bering Sea, relatively low food supplies occurred in 2006, 2008 and 2010 (Table 2), when food consumption rates decreased. The role of copepods and chaetognaths in salmon diets was insignificant, diet overlap was low, and relatively high daily rations were observed in samples collected during those years.

Table 2. Trophic characteristics and food supply index of juvenile pink and chum salmon in the western Bering Sea in 2002-2004 and 2006-2010.

Trophic feature	2002	2003	2004	2006	2007	2008	2009	2010
Daily ration	1	0	1	0	-1	-1	0	0
Stomach fullness	1	1	-1	-1	0	0	0	0
Diel feeding rhythm	0	0	0	0	0	0	0	0
Trophic niche breadth	0	1	1	0	0	0	0	0
Number of prey	-1	0	0	0	0	-1	0	-1
Diet overlap	0	1	1	-1	0	0	0	0
Share of minor food	-1	1	1	0	0	0	0	-1
Food Supply Index	0	0.6	0.4	-0.3	-0.1	-0.3	0	-0.3

The FSI correlated negatively with juvenile salmon biomass both in the Sea of Okhotsk ($r = -0.78$, $p = 0.008$, $N = 10$; Fig. 1) and the western Bering Sea ($r = -0.56$, $p = 0.150$, $N = 8$; Fig. 2). This means that increases in juvenile salmon biomass were accompanied by changes in feeding habits that resulted in the switch to minor food items (copepods, chaetognaths), widening of trophic niche breadth, change in diet overlap, and/or decrease in feeding intensity, i.e., a density-dependent effect. The question is what does this mean for salmon populations?

Feeding habits of juvenile pink and chum salmon changed in years when there was a high salmon biomass. However, these changes were not pronounced (Tables 1 and 2).

**Fig. 1.** Changes in the food supply index in relation to normalized juvenile salmon biomass in samples collected in the Sea of Okhotsk, 2001-2010.

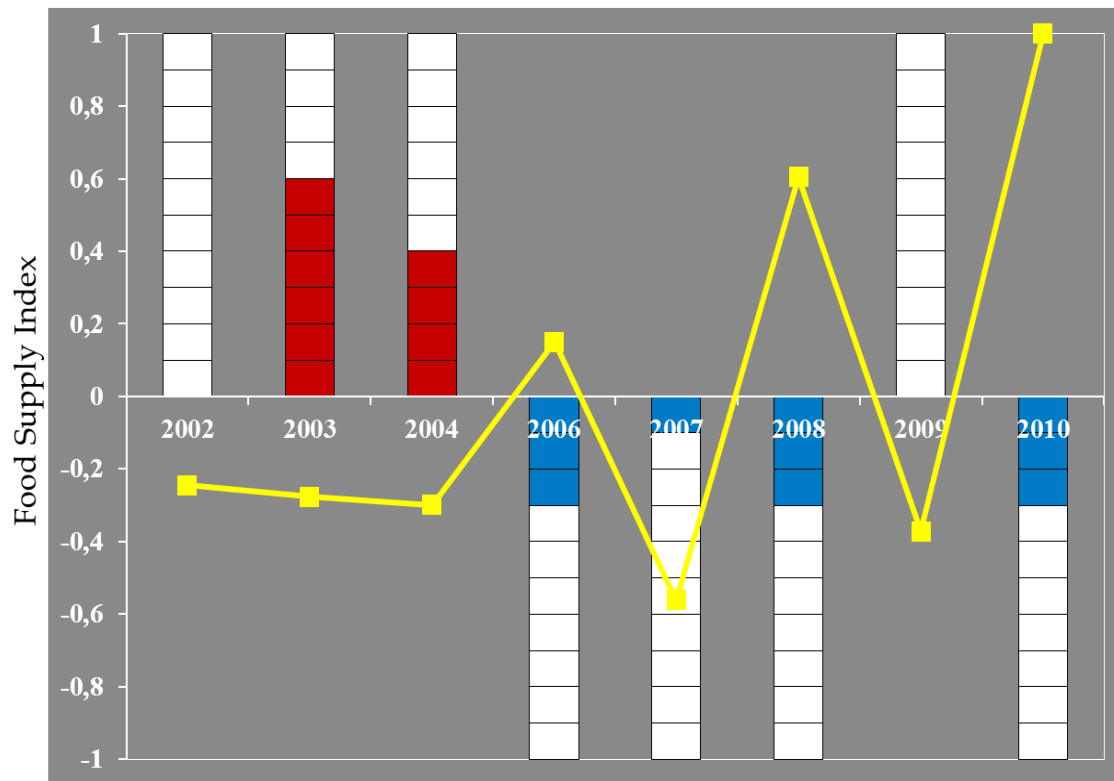


Fig. 2. Changes in the food supply index in relation to normalized juvenile salmon biomass in samples collected in the western Bering Sea, 2002-2004 and 2006-2010.

Daily ration of juvenile salmon was lower in years with a relatively low food supply as compared with other years. The daily ration decreased by 14% in the Sea of Okhotsk and by 9% in the Bering Sea, though these differences in daily ration between years of low and “normal” FSI were insignificant ($p = 0.05$).

Changes in feeding habits and consumption rates did not seem to negatively affect juvenile salmon growth. Body size of juvenile salmon did not significantly correlate either to their abundance or to the relative biomass of the forage base (Shuntov and Temnykh 2008, 2011). On the contrary, growth of juvenile chum salmon, as estimated by scale analysis, tended to be enhanced in the last decades of high salmon abundance (Kaeriyama et al. 2007; Seo et al. 2009; Agler et al. 2012; Zavolokin et al. 2012).

Thus, despite increased salmon abundance there were no strong negative consequences for juvenile salmon in the Sea of Okhotsk and western Bering Sea in 2001-2010. Possible strengthening of competition among salmon populations was compensated by adaptive changes in their feeding habits.

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Exposure to Elevated Temperature During Early Development Affects Sexual Development in *Oncorhynchus mykiss*

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Keywords: alternate life history, sexual phenotype, climate change, wild, hatchery, steelhead

Conditions experienced during early development can have a significant impact on phenotypic variation and subsequent life history options, particularly among species that normally express multiple phenotypes. In *Oncorhynchus mykiss*, known as steelhead and rainbow trout in anadromous and freshwater resident forms respectively, the expression of one or the other of these two forms is determined in part by environmental conditions and in part by genetic architecture (Thrower et al. 2004, Hecht et al. 2012, 2013). However, our understanding of how environmental changes can affect the biology and life history of species having diverse life histories is limited. We do know that sexual development and sexual phenotype among some fishes can be strongly influenced by environmental factors (Ospina-Alvarez and Piferrer 2008; Wedekind et al. 2012). Among salmonids, *O. nerka* (sockeye salmon) show altered sex ratios following embryonic exposure to elevated temperature (Craig et al. 1996; Azuma et al. 2004). Similar studies of *O. mykiss* have had mixed results, from no apparent effect (Van den Hurk and Lambert 1982; Baroiller et al. 1999), to partial effects dependent on the type of temperature application treatment and parental lineage (Magerhans et al. 2009). Current projections are for continued warming of aquatic environments associated with climate change (Meehl et al. 2007), a phenomenon that is likely to have significant impact on temperate fishes occupying temperature-sensitive freshwater habitats. We undertook a comparative study of wild and hatchery sourced *O. mykiss*, using a number of steelhead pairs as a parental source of embryos, to evaluate to what extent genotype (stock source and parental line) and differing temperatures may interact to influence phenotypic sex.

The experiment was conducted at the Oregon Hatchery Research Center (OHRC) located on Fall Creek. Wild and hatchery stocks of *O. mykiss* were collected from returning mature steelhead at the OHRC fish ladder on Fall Creek. Family lines were established by single-pair matings of adults following standard procedures (Noakes and Corrarino 2010) to create five wild family lines and four hatchery family lines. The resulting embryos of these matings resulted in five wild and four hatchery families. These sibling groups were held at either ambient or elevated (+5°C above ambient) temperatures (two replicates for each experimental condition) for a total of 36 (9 families by two temperatures by two replicates) experimental groups. The time of exposure to elevated temperature extended from the beginning of the experimental period at fertilization until swim-up, after which all fish were maintained at ambient temperatures until termination of the experiment. At the end of the experiment all surviving fish were humanely euthanized and processed for taking length/weight data and DNA tissue samples for ongoing studies. In addition, gonadal tissue was removed from 16 fish from each experimental group and processed histologically to determine phenotypic sex.

Assessment of phenotypic sex was based on microscopic examination of histologically-processed gonadal tissue, which was characterized as either ovariform or testiform based on features of gonadal architecture and gonial cell type (Fig. 1), using previously described techniques and criteria (Cole 2010).

Data were analyzed using a mixed generalized linear model with a binomial family distribution. The model assessed was $y = \text{source} + \text{thermal regime} + \text{random (treatment replicate number nested in source replicate number)}$. The ‘glme’ function in the R statistical package, lme4, was used (Bates et al. 2012) and fixed effects generalized linear models were also assessed. In comparing the phenotypic responses of sibling embryos collected from multiple families (spawning pairs) from both hatchery and wild stocks, our data analysis took into account the difference in experimental group sizes resulting from differential mortality.

Based on the fish analyzed histologically, the frequency of occurrence of phenotypic females among heated groups was significantly less than expected (i.e., 50%) and also significantly less than the frequency of occurrence of phenotypic females among ambient temperature groups.

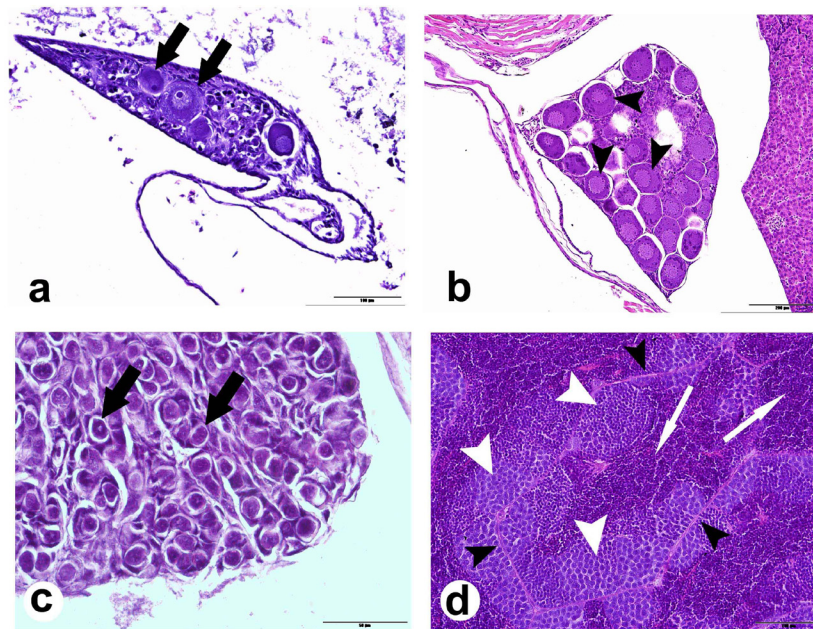


Fig. 1. Gonadal morphology of experimental *Oncorhynchus mykiss*. a. Early-stage ovary showing chromatin nucleolus stage oocytes (black arrow). Scale bar is 100 μm . b. Differentiated immature ovary with perinucleolar stage oocytes (black arrowhead). Scale bar is 200 μm . c. Early stage testis showing cord and cluster organization of spermatogonia and primary spermatocytes (black arrow). Scale bar is 50 μm . d. Mature (precocious) testis with seminiferous lobules made up primarily of spermatocysts (white arrowhead) containing same-stage germ cells (mostly spermatocytes) surrounding a central lumen filled with free spermatozoa (white arrow) and bounded peripherally by connective tissue (black arrowheads). Scale bar is 100 μm .

These findings indicate that increased temperature exposure during early development influences sexual development in *O. mykiss*. The increased temperature (+5°C above ambient) applied here is within the currently predicted range for temperature increases that could be experienced by the end of this century, taking in to account assumptions of greatest surface air temperature warming occurring over land and at higher northern latitudes (Meehl et al. 2007). Moreover, the exposure time was relatively short, lasting only from fertilization to swim-up, before significant gonad development starts to occur. Longer term exposure to elevated temperatures, for example throughout the full period of early gonad development, may result in an even greater male bias in the resulting phenotypic sex ratio.

The prospect of altered sex ratios in *O. mykiss* in response to increased climatic temperatures associated with a reduction in numbers of phenotypic females has significant implications on a number of levels. Both population management plans and conservation strategies are usually developed on an assumption of balanced sex ratios. A significant reduction in either sex is likely to have significant negative impacts on population sustainability. Of greater critical concern, a persistent loss of females brings into question the ability of a species to survive. The objectives of hatchery managers, conservation biologists and fisheries harvesters are quite different, but it is vitally important for all to understand both the mechanisms that regulate development and life history in this species, and the environmental factors that may significantly influence the outcomes of altered developmental patterns.

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Prey Selectivity of Juvenile Salmon on Neustonic Meso zooplankton in the Northern California Current

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Keywords: diet, prey availability, selection, neuston, Chinook salmon, coho salmon, chum salmon, steelhead

Various factors could play a role in influencing early marine survival of juvenile salmon. One factor is availability of prey that salmon consume. Off the coast of Washington and Oregon, juvenile salmon tends to reside in the upper 20 m of the water column (Emmett et al. 2004) and previous studies have indicated that juvenile coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) may be feeding in the neustonic layer (Brodeur et al. 1987, Brodeur 1989). In this study, we examined prey selectivity for four species of salmon (Chinook salmon (both subyearling and yearling), coho salmon, chum salmon (*O. keta*) and steelhead (*O. mykiss*)) by comparing stomach contents to concurrently sampled neustonic prey.

We collected juvenile salmon and neuston samples during four cruises off southern Oregon and northern California. The cruises were conducted in June and August of 2000 and 2002 as part of a GLOBEC salmon distribution study (Pool et al. 2012). To capture juvenile salmon, a Nordic 264 rope trawl constructed by Nor'Eastern Trawl Systems, Inc. was towed at the surface at 1.5 m/s for 30 min. Stomach contents were removed and then identified, measured, and enumerated to the lowest possible taxon (Baldwin et al. 2008). At stations where more than 30 individuals of a salmon species and age class were captured, at least 30 stomachs were processed. To collect potential prey of salmon, a neuston net was towed out of the ship's wake for 5 min at approximately 1.0 m/s. The neuston net had a 1-m wide x 0.3-m high mouth opening and contained 333- μ m mesh (see Pool and Brodeur 2006).

The Johnson Selectivity Index was chosen to examine prey selectivity of juvenile salmon (Johnson 1980). This index has the capability of using numeric proportion (%N), samples with zero counts, and exclusion of certain taxa such as digested fish tissue. The proportions were calculated from counts in stomach samples and concentrations in neuston samples. Next, prey in each stomach (i.e., usage) was ranked according to their %N and ranks were also assigned to prey in each neuston sample (i.e., availability). The index number ranges from negative for the most preferred prey to positive for the least preferred prey. For the purpose of our analysis, only those stations with at least one salmonid stomach and a neuston net tow were examined. The indices were examined with all cruises combined and then calculated for each cruise for temporal trends.

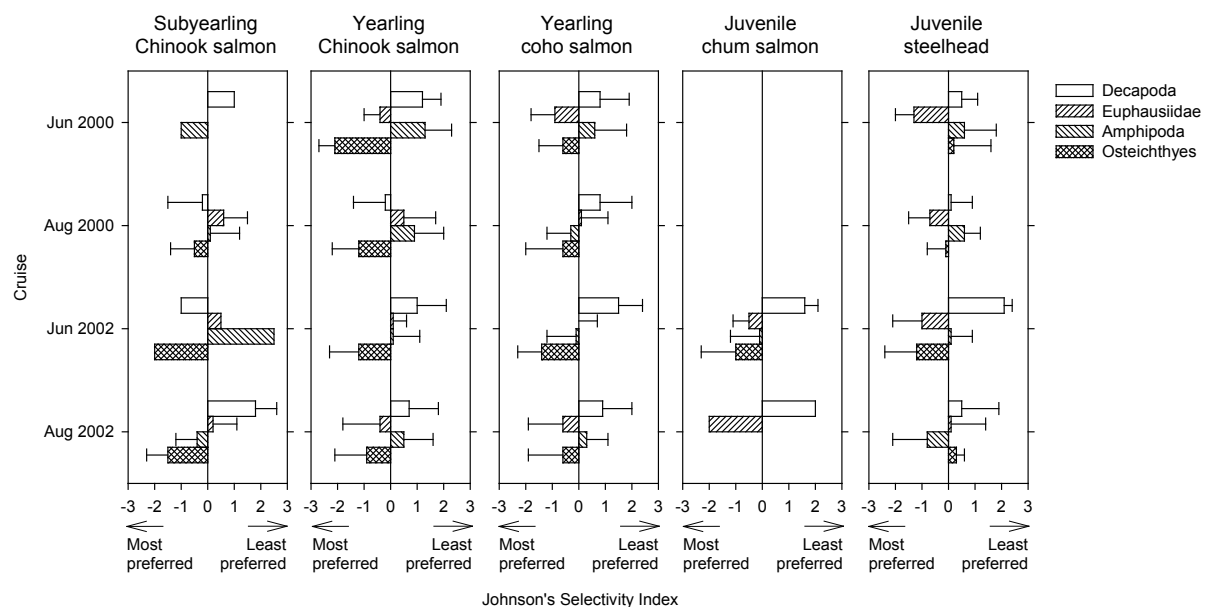


Fig. 1. Johnson's selectivity indices for contents of salmonid stomachs and neuston net tows by the major prey categories collected for each cruise in 2000 and 2002. Values shown are means (bars) and standard errors (error bars).

To examine feeding selectivity, the twenty most dominant taxa by total %N were selected for each salmon species. Of the four major prey groups found in the diets, we found that euphausiids and fishes tended to be positively selected relative to their abundance in the neuston and decapods and amphipods were generally not consumed in the same proportions as their availability in the neuston (Fig. 1). Commonly preferred prey species included sculpins, rockfishes, sand lance, and offshore euphausiid species and the less preferred species included decapod larvae and hyperiid amphipods.

The dominant taxa consumed by subyearling Chinook salmon by %N were hyperiid amphipods, crangonids, fish, caprellids, mysids, insects, and euphausiids (Fig. 2). Subyearling Chinook salmon preferred *Hyperia medusarum* (hyperiid amphipod) and crangonids over *Thysanoessa spinifera* (euphausiid) and *Hyperoche medusarum* (hyperiid amphipod). Fish consumed included *Engraulis mordax* (northern anchovy), Cottidae, Osmeridae, and *Sebastes* spp. (rockfish).

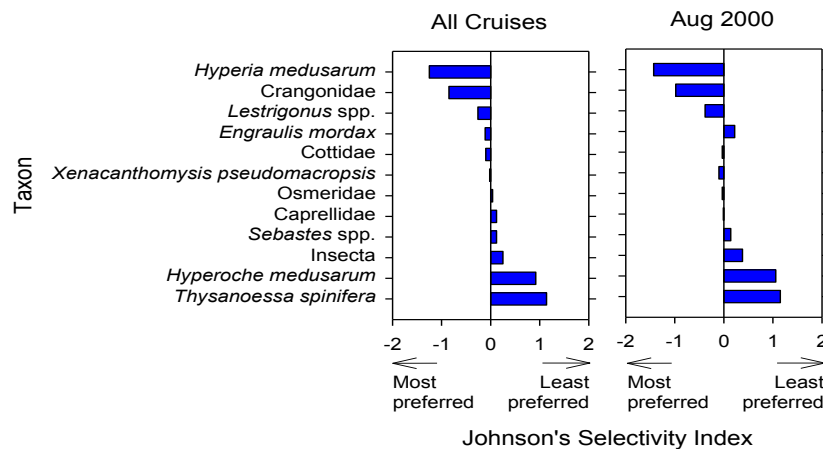


Fig. 2. Subyearling Chinook salmon selectivities for dominant prey and neuston taxa for the August 2000 cruise and all cruises combined. Taxa are ordered in terms of decreasing selectivity in the left panel.

For yearling Chinook salmon, the dominant prey taxa by %N included fish, decapods, hyperiid amphipods, and euphausiids. The first three taxa were fish, *Ammodytes hexapterus* (sand lance), *Hemilepidotus* spp. (Irish lords), and *E. mordax* (Fig. 3). *Cancer* spp. were least preferred. Other fish prey included *Sebastes* spp. and *Glyptocephalus zachirus* (rex sole). Trends in prey preference were somewhat similar in June 2000, August 2000, and June 2002. In August 2002, *G. zachirus*, *Euphausia pacifica* (euphausiid), and *Hyperia medusarum* were more preferred over other taxa.

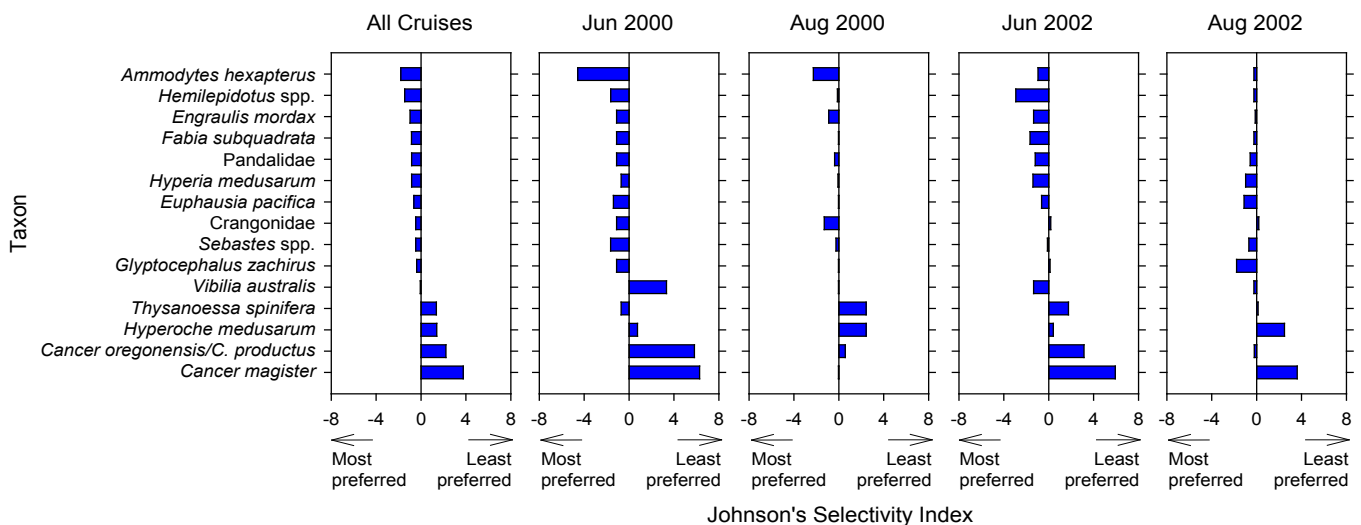


Fig. 3. Yearling Chinook salmon selectivities for dominant prey and neuston taxa by cruise and all cruises combined. Taxa are ordered in terms of decreasing selectivity in the left panel.

For juvenile coho salmon, the dominant taxa by %N included fish, decapods, amphipods, euphausiids, insects, and pteropods. It appears that yearling coho salmon preferred *Hemilepidotus* spp. and *Themisto pacifica* (hyperiid amphipod) over *Cancer* spp. (Fig. 4). Other dominant fish prey were *Sebastes* spp. and *A. hexapterus*. Trends in prey preference were somewhat similar in June 2000, August 2000, and June 2002. Though *T. spinifera* (euphausiid) was the most preferred prey in June 2000. This preference was repeated in August 2002 when *Cancer oregonensis*/*Cancer productus*, *Sebastes* spp., and *A. hexapterus* also were more preferred over other dominant prey taxa.

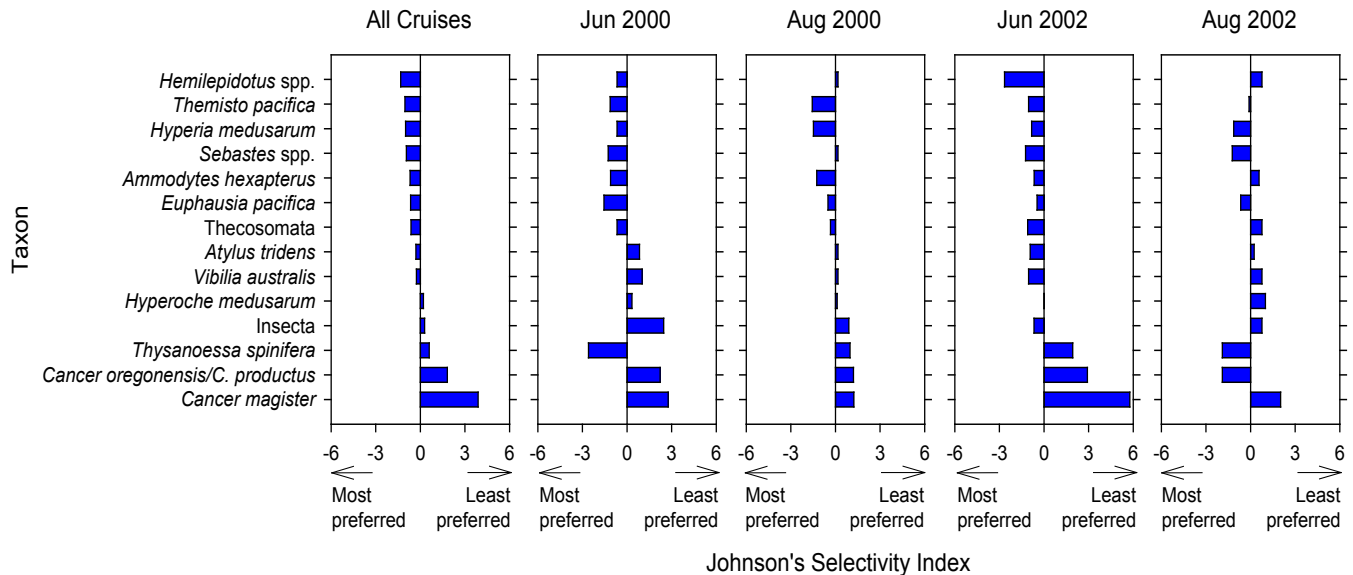


Fig. 4. Juvenile coho salmon selectivities for dominant prey and neuston taxa by cruise and all cruises combined. Taxa are ordered in terms of decreasing selectivity in the left panel.

Juvenile chum salmon were captured in June 2002 only. Dominant prey taxa included copepods, polychaetes, decapods, mysids, amphipods, euphausiids, and chaetognaths. *Epilabidocera* sp. (copepod), polychaetes, and *Fabia subquadrata* (crab) were more preferred than Chaetognatha, *T. spinifera*, and *Hyperoche medusarum* (Fig. 5). The dominant fish prey was *A. hexapterus*.

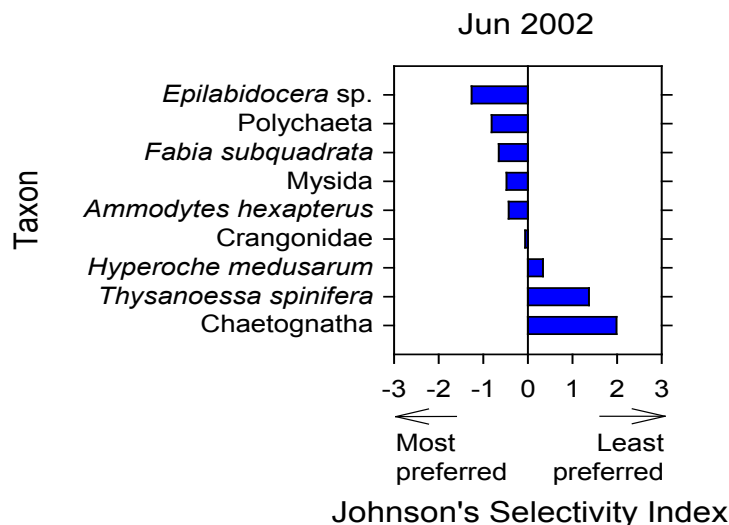


Fig. 5. Juvenile chum salmon selectivities for dominant prey and neuston taxa for the June 2002 cruise. Taxa are ordered in terms of decreasing selectivity in the left panel.

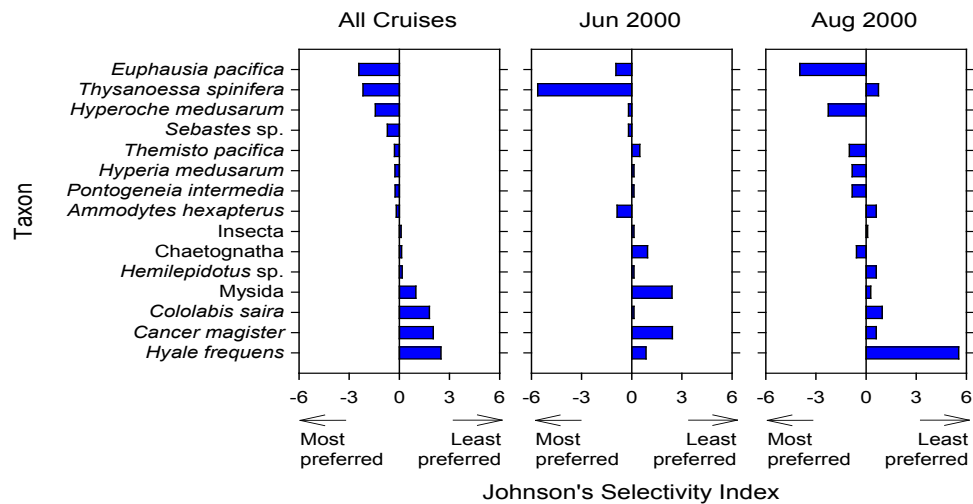


Fig. 6. Juvenile steelhead selectivities for dominant prey and neuston taxa by cruise and all cruises combined. Taxa are ordered in terms of decreasing selectivity in the left panel.

Juvenile steelhead were captured during all cruises but combined for both cruises in 2002 due to the small sample size. Dominant prey taxa included euphausiids, amphipods, fish, insects, mysids, chaetognaths, and decapods. *E. pacifica*, *T. spinifera*, and *Hyperoche medusarum* were more preferred than *Cololabis saira* (Pacific saury), *Cancer magister* (Dungeness crab), and *Hyale frequens* (gammarid amphipod) (Fig. 6). In June 2000, *T. spinifera* was strongly preferred over other prey. Dominant fish prey included *Sebastes* sp., *A. hexapterus*, *Hemilepidotus* sp., and *C. saira*.

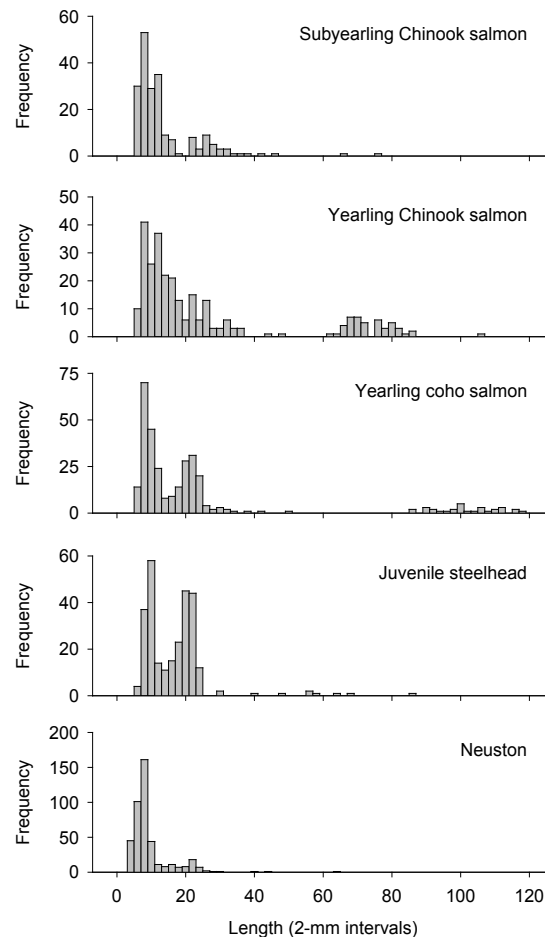


Fig. 7. Comparison of lengths of all prey consumed by juvenile salmon and available in the neuston.

We also compared lengths of prey in stomachs with those in the neuston to determine whether prey size selection was occurring. Most salmon showed a similar bimodal distribution of prey lengths as found in the neuston sampler but yearling Chinook and coho salmon also consumed a larger mode of mostly fish prey that were not sampled by the neuston net, possibly due to their avoidance of the small mouth opening of the net (Fig. 7).

Although the neuston samples do not represent the full range of prey resources available to juvenile salmon as some prey are found only in subsurface layers, there has been a better correspondence between the neuston taxa and diets, especially for juvenile coho and Chinook salmon and steelhead, than with integrated bongo tows (Brodeur 1989, unpublished data). Neuston prey biomass is as important a determinant of salmon habitat as any abiotic variable measured (Pool et al. 2012). Based on the results of our analysis, prey is consumed in the following preference order: Osteichthyes > Euphausiidae > Amphipoda > Decapoda for most species and life history types. Sand lance and sculpins appear to be particularly selected for and *Cancer* crab larvae selected against relative to their abundance in the neuston.

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Trophic Relationships Among Juvenile Salmon During a 16-Year Time Series of Climate Variability in Southeast Alaska

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Keywords: juvenile salmon, pink, sockeye, coho, nutritional condition, feeding intensity, climate change, diet, energy density

Early marine survival of juvenile Pacific salmon (*Oncorhynchus* spp.) has been linked to growth related to marine temperatures and feeding conditions during the first few months in the ocean (Mortensen et al. 2000; Farley et al. 2007; Saito et al. 2009). These relationships for juvenile salmon have been contrasted among coastal regions (Brodeur et al. 2007) and variable environmental conditions in the coastal waters of the Bering Sea (Karpenko et al. 2007; Andrews et al. 2009; Moss et al. 2009), Prince William Sound (Armstrong et al. 2008; Cross et al. 2008), and Southeast Alaska (Landingham et al. 1998; Mortensen et al. 2000; Weitkamp and Sturdevant 2008; Sturdevant et al. 2012c). However, less is known about these relationships for most juvenile salmon over an extended time series characterized by climate change (Miller et al. 2013; Orsi et al. 2013).

To address how trophic linkages and nutritional condition may shift over long-term periods of environmental change, we examined a 16-year time series in groups of warm and cold years for juvenile pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), and coho (*O. kisutch*) salmon. Trophic data included July diet composition and feeding intensity, and nutritional condition (energy density and body size) from Icy Strait (58°N, 135°W), Southeast Alaska. Typically, an $n \leq 10$ diet and $n \leq 20$ energy subsamples of average-size fish per species and year were selected from annual Southeast Coastal Monitoring (SECM) project trawl sampling in Icy Strait during daylight hours (0700-1900) between 21-31 July, 1997-2012 (Orsi et al. 2012). However, to meet sample size criteria, a few coho salmon diet and energy samples were collected from inshore and coastal stations in 1997, but no coho salmon energy samples were available in 1999. A few pink and chum salmon diet samples were supplemented from night trawls in 2004. Warm and cold years were defined by annual deviations from the long-term average of the Icy Strait Temperature Index (ISTI, mean °C, 20-m integrated water column) calculated across the months of May, June, July, and August at $n = 8$ SECM stations in Icy Strait (Fig. 1). The ISTI is significantly correlated with the climate Multivariate ENSO Index (MEI, averaged from November to March, lagged by one year; Sturdevant et al. 2012a; Orsi et al. 2013a), indicating that broad scale climate patterns can be detected in regional signals. We identified nine warm years (mean 9.6°C; range 9.3–10.3°C) and seven cold years (mean 8.8°C; range 8.3–9.0°C) in the 16-year time series (Fig. 1), although monthly anomalies were variable (Sturdevant et al. 2012b).

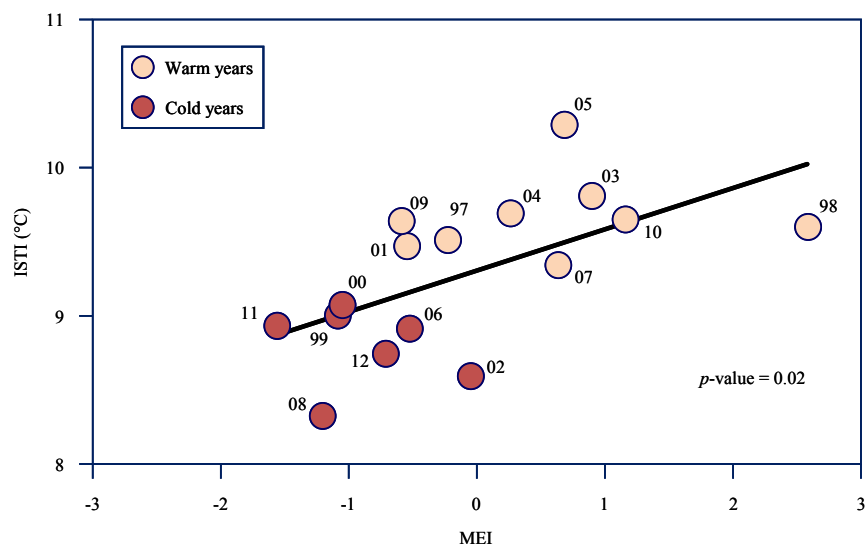


Fig. 1. Warm and cold years were categorized by anomalies of the Icy Strait Temperature Index (ISTI, °C) and correlated with the Multivariate ENSO Index (MEI, averaged from November to March, lagged by one year).

In the laboratory, individual fish examined for diet and feeding intensity were also analyzed for nutritional condition. After the length and weight were measured (fork length, FL, mm; wet weight, g), stomach contents were removed and examined microscopically to identify prey into groups by taxa, species, and stages, when possible. Each prey group was weighed and enumerated, when possible, and the percent weight composition (% weight) was summarized by eight prey categories. Feeding intensity was described by a gut fullness index and percent body weight (% body weight = total prey wt / (fish weight – prey weight) X 100). Energy density was determined as (small) cal/g dry weight (DW) by calorimetry. We tested for species differences in feeding intensity and nutritional condition between warm and cold years using one-way analysis of variance (ANOVA), followed by Tukey's paired comparison tests when significant differences were detected. To identify trophic relationships, overall diet composition was compared among the species between warm and cold years using a multivariate ordination routine (nMDS) based on the Bray-Curtis similarities from square-root transformed percent weight data.

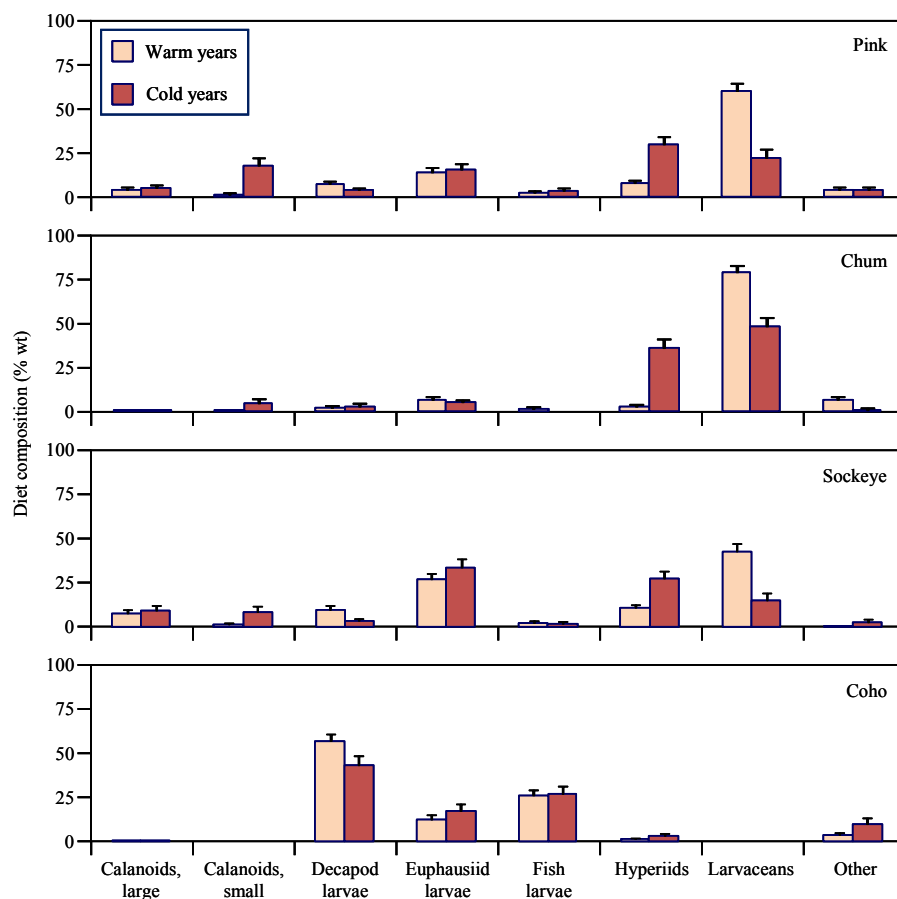


Fig. 2. Mean diet composition (percent weight, % wt) of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

Overall, juvenile pink, chum, and sockeye salmon were planktivorous, whereas juvenile coho salmon consumed a mixed diet of crab larvae and fish larvae (Figs. 2 and 3). Diets differed between warm and cold years only for the planktivorous species. These diets were diverse and consisted of large (≥ 2.5 mm) and small copepod (< 2.5 mm) taxa, decapod, euphausiid, fish larvae, hyperiid amphipods, and larvaceans. From warm years to cold years, planktivore prey utilization shifted from larvaceans to hyperiids and from large to small copepods, with an overall decrease in consumption of decapod larvae. Diets of the more piscivorous juvenile coho salmon consisted of fish, decapod, and euphausiid larvae. Fish and decapod larvae were prominent prey in both warm and cold years, and only minor shifts ($\leq 13\%$ weight) in prey utilization were evident; however, we did not examine fish prey species, which could vary between warm and cold years. Predation on decapod and euphausiid larvae by juvenile coho salmon is common throughout much of its range along the coasts of Washington, British Columbia, and Alaska (Brodeur et al. 2007; Sweeting and Beamish 2009; Cook and Sturdevant 2013).

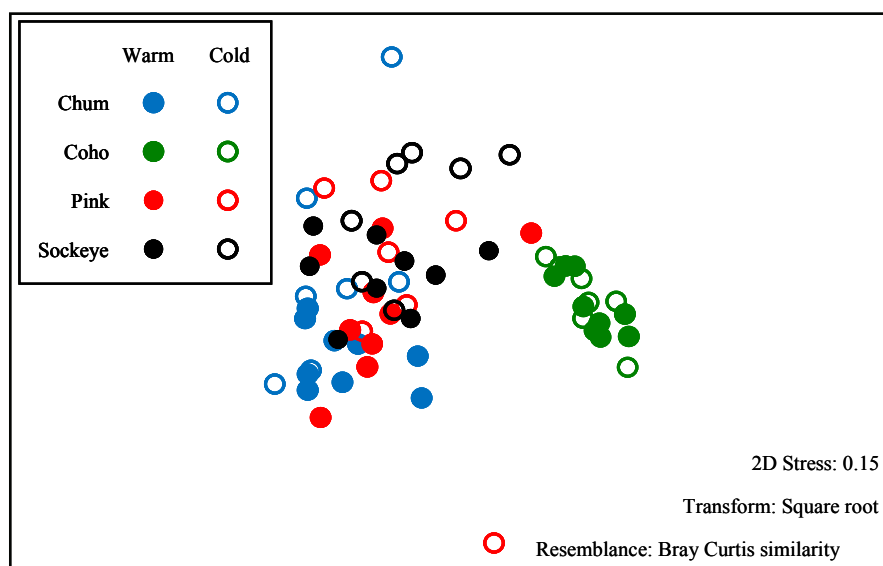


Fig. 3. Multivariate ordination of total diet composition of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012. Each symbol represents one year.

Overall, the nMDS indicated that diet differences between planktivorous pink, chum, and sockeye salmon and piscivorous coho salmon were stronger than diet differences between warm and cold years. Similarly, Sturdevant et al. (2012a) did not find a significant climate effect on adult fish predator diets between warm and cold years. Juvenile planktivorous-fish diet composition was similar to diets of juvenile salmon in the Bering Sea, Gulf of Alaska, and Puget Sound; however, fish prey was typically a much lower proportion of the diets in our samples (Boldt and Haldorson 2003; Brodeur et al. 2007; Farley et al. 2007; Bollens et al. 2010; Cook and Sturdevant 2013). A notable difference is that pteropods, a taxon linked to growth and survival for Gulf of Alaska juvenile pink salmon (Armstrong et al. 2008), contributed little to Southeast Alaska juvenile pink summer diets despite being prominent in adult pink salmon diets (Sturdevant et al. 2012a). This shift in prey composition in planktivorous juvenile salmon diets coincides with strong seasonal patterns of zooplankton composition and abundance that are related to climate in both the Gulf of Alaska and Southeast Alaska. For example, in warm years as compared to cold years in the Bering Sea, abundance of both euphausiids and the large copepod *Calanus marshallae* increased, while both hyperiid amphipods and the small copepod *Acartia sp.* (the predominant small copepod in Southeast Alaska juvenile salmon diets) decreased (Coyle et al. 2011). Similarly, climate-related monthly and interannual shifts in the timing of predominant zooplankton were suggested for conditions in Southeast Alaska (Sturdevant et al. 2012b). These shifts in predominant prey abundance suggest that planktivorous fish diets will also shift in response to changes in climate (Coyle et al. 2011) and likely explains the gradient in diet composition that we observed between warm and cold years in the nMDS results.

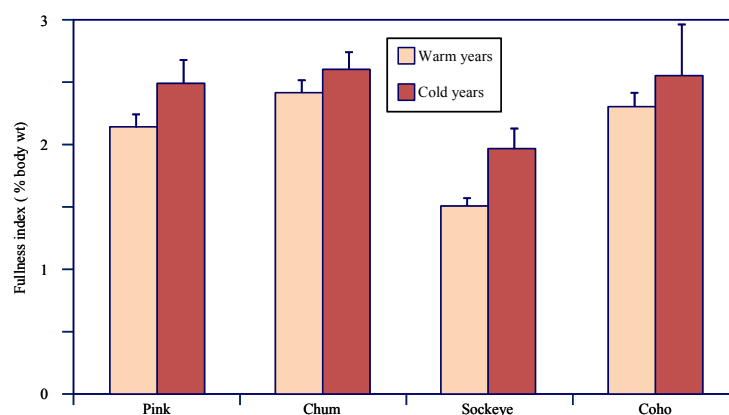


Fig. 4. Mean feeding intensity (stomach fullness index, % body weight) of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

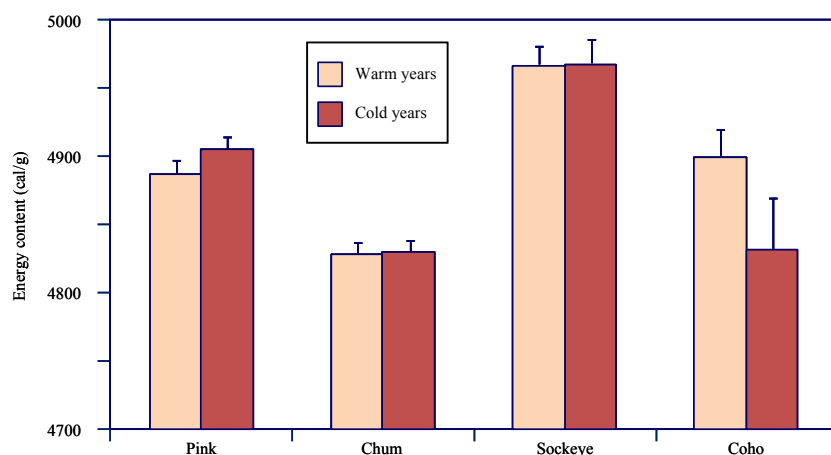


Fig. 5. Mean energy density (cal/g dry weight) determinations of juvenile pink, chum, sockeye, and coho salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

Like diet composition, differences in feeding intensity and juvenile salmon nutritional condition were more common between species than between warm and cold years (Figs. 4–6). Feeding intensity and energy density differed significantly ($p < 0.001$) between salmon species, but only species size differed between warm and cold years. Sockeye salmon had the lowest prey percentage of salmon body weight and chum salmon had the highest. This might have resulted from differences in their primary prey species (euphausiids vs. oikopleurans; Fig. 2) or from differences in salmon body size, as prey percentage of body weight decreases with size (Fig. 6; Sturdevant et al. 2008). The percent body weight for all species increased slightly from warm to cold years. Energy density was lowest in chum salmon and highest in sockeye salmon, and only coho showed a decreasing trend from warm to cold years. These species-specific inverse patterns of feeding intensity, size, and energy density may reflect differences in trophic linkages; low energy, rapidly-digested larvaceans predominated in chum salmon diets in July compared to high energy crustaceans, such as euphausiids, observed in sockeye salmon diets (Landingham et al. 1998; Boldt and Haldorson 2003; Sturdevant et al. 2008). In addition, species differences in diel feeding periodicity and prey-specific evacuation rates have been shown for juvenile salmon in Southeast Alaska. Pink salmon fed intensively on euphausiid larvae mainly early and late in the day in August and September, coinciding with the diel migration of euphausiids, whereas chum salmon fed on oikopleurans throughout the day (Sturdevant et al. 2004). Nonetheless, chum salmon maintained a high daily ration by feeding on this low-energy prey due to rapid digestion and intensive feeding (Sturdevant et al. 2004, 2008). These differences suggest that salmon feeding intensity is affected not only by prey availability but by prey type, prey digestibility, and the salmon's diel feeding rhythms (Benkwitt et al. 2009; Bollens et al. 2010).

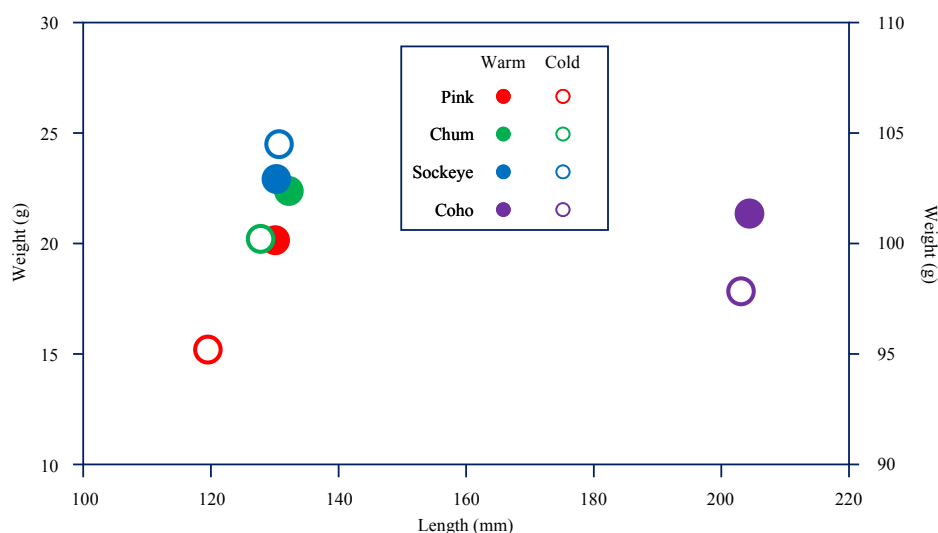


Fig. 6. Mean size (weight, g, and fork length, mm) of juvenile pink, chum, sockeye (left axis), and coho (right axis) salmon collected in warm and cold years. Fish samples were collected in July during annual Southeast Coastal Monitoring project trawling in Icy Strait, northern Southeast Alaska, 1997-2012.

For juvenile pink, chum, and coho salmon, both length and weight were significantly ($p < 0.01$) greater in warm years; in contrast, sockeye salmon were significantly ($p < 0.01$) smaller in warm years (Fig. 6). This counter-intuitive result may be caused by an influx of high numbers of earlier-emigrating, small (age-0) sockeye in warm years (Heard et al. 2013). As size is directly influenced by growth related to water temperature, size could also be indirectly driven by prey availability (delayed plankton bloom in cold years), size-selective predation (smaller fish more likely to be eaten; Mortensen et al. 2000; Farley et al. 2007; Moss et al. 2009; Sturdevant et al. 2013), and differences in life history patterns.

In summary, juvenile salmon adapt their feeding to regional and local prey conditions mediated by habitat, physical environment, climate, and competitive interactions (Brodeur et al. 2007). While comparisons of the breadth and scope of salmon diet and condition among seasons and locales are important, the utility of our time series lies in the systematically-collected samples from a single migratory corridor in northern Southeast Alaska that is being comprehensively examined for biophysical, trophic, and climate linkages (Orsi et al. 2004, Fergusson et al. 2010; Orsi et al. 2012; Sturdevant et al. 2012a, b, c; Orsi et al. 2013). Our preliminary analysis of long-term juvenile salmon feeding ecology indicates a stable feeding gradient among the species with relatively little effect of climate on nutritional condition, and thus these co-occurring juvenile salmon are adapted for the current level of climate change experienced at this locale (on average, a 1°C temperature difference in the upper 20-m water column between warm and cold years). In Southeast Alaska, climate change may be more likely to affect life history parameters such as out-migration timing (Orsi et al. 2013; Sturdevant et al. 2013). Further analysis with this data set will include (1) adding additional years to the dataset as they become available, (2) analysis of interannual feeding patterns to identify years of particularly high influence, (3) examining prey selection from zooplankton prey suites, and (4) addition of juvenile Chinook salmon results to the time series.

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Diet Composition and Feeding Behavior of Juvenile Salmonids Collected in the Northern Bering Sea from August to October, 2009–2011

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An understanding of the feeding habits and prey composition of juvenile Pacific salmon species in the northern Bering Sea is essential for assessing the growth and stock productivity of salmonids confronted with a short growing season, population changes, and changing oceanic conditions (Farley et al. 2007; Irvine and Fukuwaka 2011). Juvenile salmon food habits were examined from samples collected during BASIS (Bering-Aleutian Salmon International Survey) surface trawl operations in the northern Bering Sea in August-October, 2009-2011 (Farley et al. 2005; Moss et al. 2009). This study describes juvenile salmon diet composition, identifies important salmon prey taxa, and relates feeding patterns and behavior to diel periodicity for juvenile Chinook, pink, chum, coho, and sockeye salmon in the northern Bering Sea.

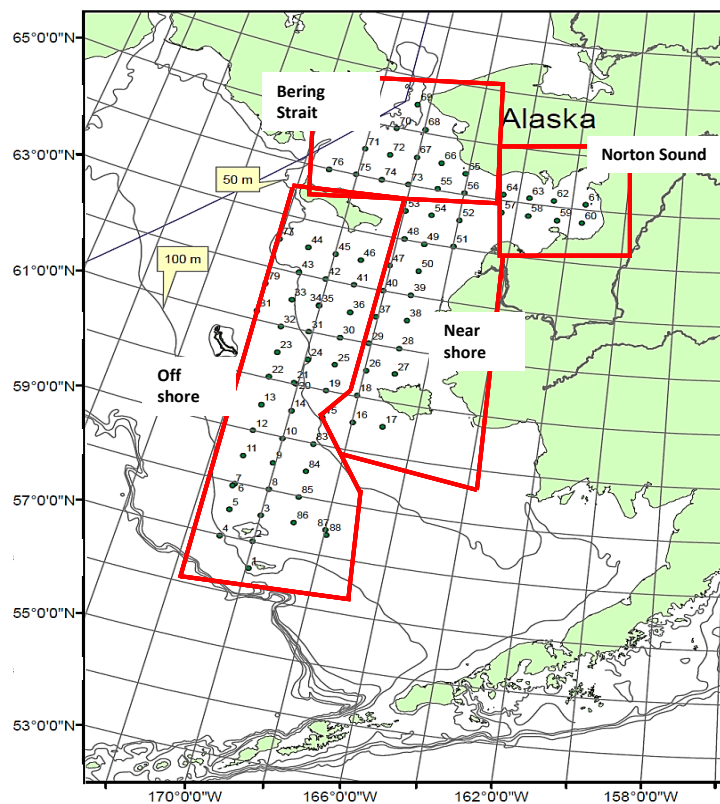


Fig. 1. Regions of the Bering Sea sampled by the BASIS (Bering-Aleutian Salmon International Survey) Program for juvenile salmon diet analysis in August-October, 2009-2011. Regions of the sampling grid are identified by the areas indicated by red lines.

Diets of 1,145 juvenile salmon were examined on board the research vessel from samples collected from four regions of the northern Bering Sea (near shore, Norton Sound, Bering Strait, and off shore; Fig. 1) in August to October, 2009-2011. Feeding intensity was assessed by both volume and weight of prey. The volumetric fullness index (% volume) was determined by visually ranking the total volume of food consumed relative to stomach size based on a scale of 1-4

(where 1 = empty, 2 = less than 25%, 3 = 50-75%, and 4 = 100% full to distended stomachs). Diet composition was then determined by sorting, enumerating, and identifying prey to the lowest possible taxonomic category. Individual prey were pooled and weighed by category, or assigned a percentage of total contents when weights could not be obtained. General diet composition was characterized as the percentage of total prey weight comprising seven prey categories (Fig. 2). Prey encountered infrequently (chaetognaths, insects, ctenophores, and pteropods) were grouped and categorized as “other.” The index of fullness (percent body weight: %BW) for $i = 1$ to n prey taxa was computed as follows:

$$\%BW = [\sum(x_i)(w_i)/(BW - \sum(x_i)(w_i))] * 100$$

where w_i is the weight for $i = 1$ to n prey taxa and BW is fish body weight. Specific diet composition by prey taxa (e.g., *Ammodytes hexapterus*) was computed as the stomach content index (SCI; Hyslop 1980; Orlova et al. 2005).

$$SCI = (w_i/BW * 10^4)$$

The SCI values sum to the total stomach fullness index (SFI; Starovoytov 2007a). Diet similarity between species pairs was calculated as the percent similarity index (PSI; Hurlbert 1978) based on percent weight, and diel feeding periodicity was calculated as percent of stomach volume for 3-hour increments.

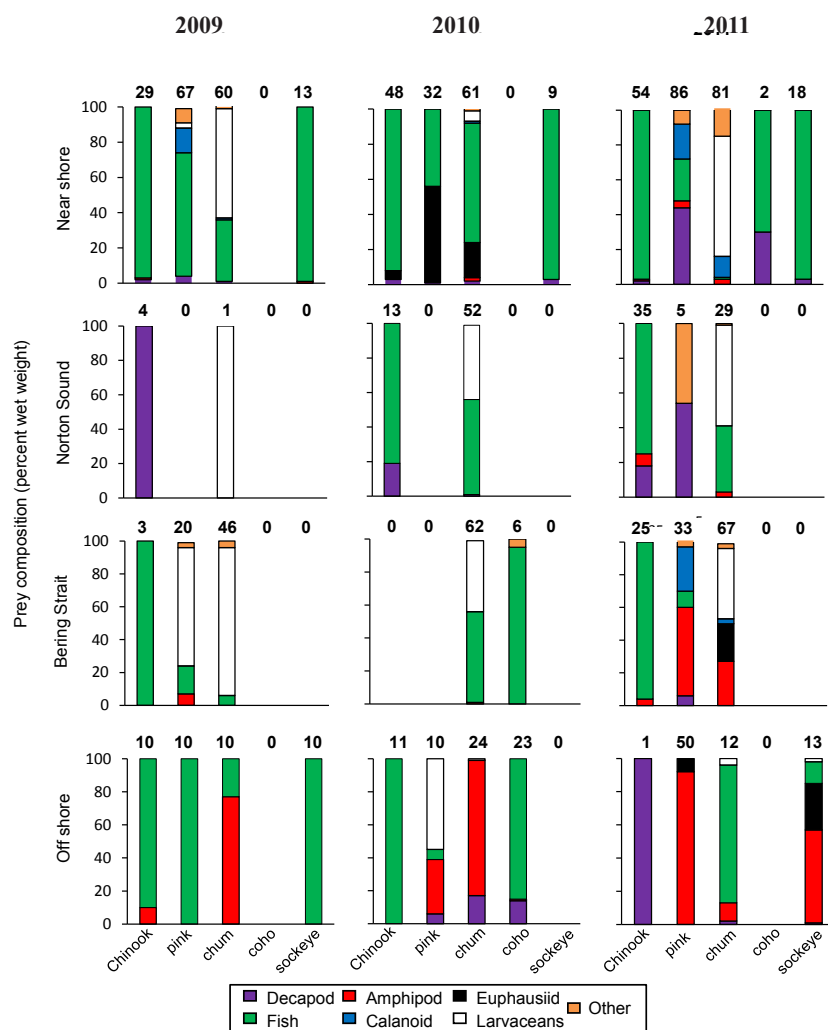


Fig. 2. Prey composition (percent wet weight) of juvenile Chinook, pink, chum, coho, and sockeye salmon stomach contents collected in August-October in four regions of the northern Bering Sea, 2009-2011. Fish sample size is indicated above the bars.

Juvenile salmon diets were summarized by region, year, and diel feeding period to assess potential prey differences and feeding patterns among the species. Most salmon species were sampled in the nearshore, strait, and offshore regions (Fig. 1). Catches in the Norton Sound region were limited and catches of coho salmon were mainly in the nearshore region (Murphy et al. 2009). Diets differed among the regions and years and included both fish and plankton (Landingham 1998; Boldt and Haldorson 2003; Davis et al. 2009). Prey was diverse for piscivorous Chinook and coho salmon and for planktivorous pink, chum, and sockeye salmon (Brodeur et al. 2007). Fish were the primary prey in the nearshore region each year, especially for Chinook and coho salmon (Fig. 2). The larger body size of these salmon requires larger high-energy prey for growth (Schabetsberger et al. 2003), although intensive feeding on alternative, lower-quality prey can also enhance survival (Weitkamp and Sturdevant 2008). The most common fish prey included sand lance (*A. hexapterus*; 40-50 mm) and capelin (*Mallotus villosus*; 60-80 mm), taxa rich in lipids necessary for growth and development (Litzow et al. 2006). Chum and pink salmon diets varied in odd- and even-numbered years, a strategy that may reduce competition (Wilson et al. 2006) and be related to the lower lipid content of chum salmon observed in years when pink salmon are abundant (Kaga et al. 2013). Chum salmon consumed more larvaceans (*Oikopleura* spp.) in samples collected in odd-numbered years and switched to consuming more fish in 2010, whereas pink salmon consumed more crustaceans in odd-numbered years as compared to consumption of more euphausiids and fish in 2010 (Fig. 2). Sockeye salmon diets included fish and brachyuran megalopae in samples collected near shore as compared to diets including hyperiid amphipods and euphausiids (*Thysanoessa* spp.) in offshore samples.

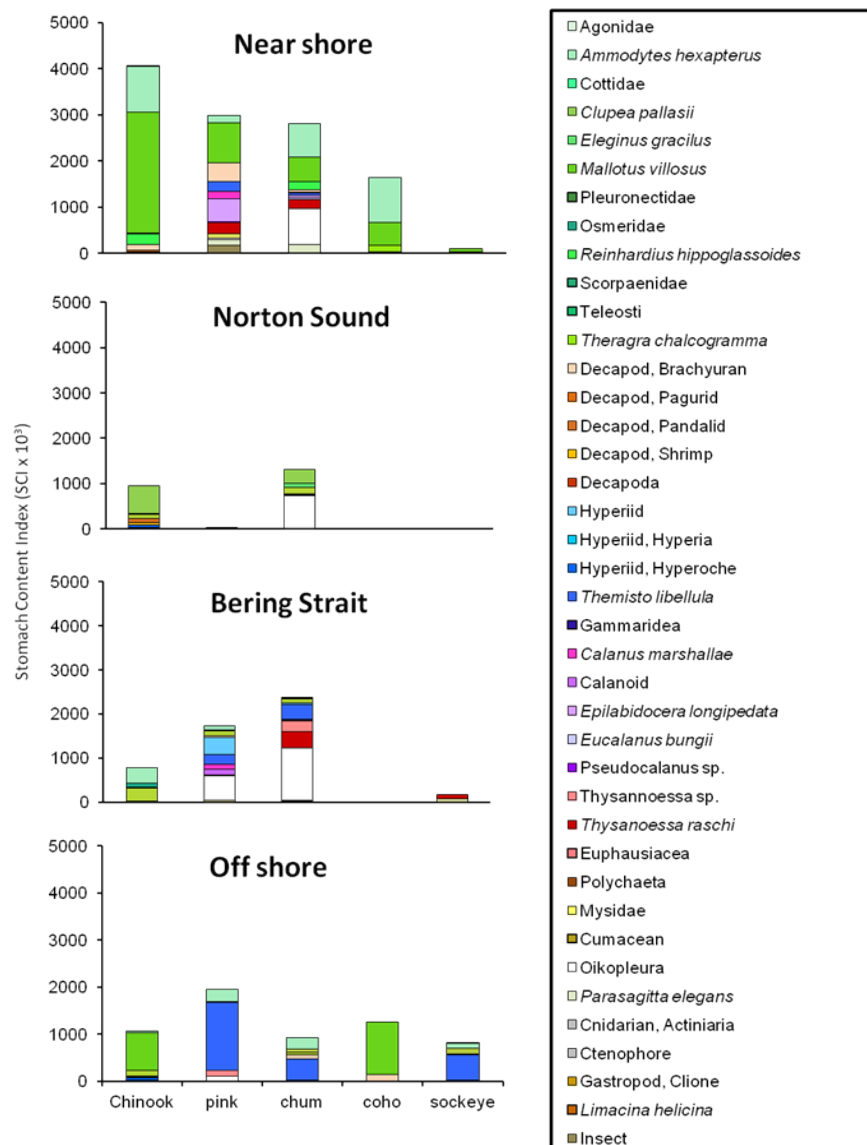


Fig. 3. Stomach content indices (SCI) of juvenile Chinook, pink, chum coho, and sockeye salmon collected in the northern Bering Sea in August-October, 2009-2011. The SCI values are based upon individual prey types.

In the Norton Sound region, Pacific herring (*Clupea pallasii*; 30-40 mm) were the primary foods of juvenile Chinook and chum salmon. Local populations of herring over-winter north of the sound and can be an important prey for piscivorous juvenile salmon (Funk 2001; Tojo 2007). Larvaceans and hyperiid amphipods (*Hyperoche* sp. and *Themisto libellula*) were consumed by juvenile chum salmon (Fig. 2). Juvenile chum salmon preference for rapidly-digested gelatinous prey (Boldt and Haldorson 2003) has been described throughout its range (Brodeur et al. 2007; Karpenko and Koval 2012). Reports of pink salmon feeding on larvaceans are also common (Purcell et al. 2005), however, insects and brachyuran megalopae were the common pink salmon prey in this study (Fig. 2).

Catches of juvenile salmon other than chum salmon were patchy in the Bering Strait. In contrast to samples from Norton Sound, fish prey from the strait region included rainbow smelt (*Osmerus mordax*), Pleuronectidae, and sand lance consumed by Chinook salmon, Pleuronectidae consumed by pink salmon, and Pleuronectidae and Cottidae consumed by chum salmon (Fig. 3). In 2011, pink and chum salmon diets principally comprised of the amphipod *T. libellula*. Chum salmon also consumed euphausiids and larvaceans, while pink salmon consumed more of the large calanoid copepod *Calanus marshallae* (Fig. 2). Since *C. marshallae* is also important in the diet of *T. libellula* (Auel and Werner 2003; Pinchuk et al. 2013), the carrying capacity of the Bering Strait could be affected by interactions between juvenile salmon and carnivorous macrozooplankton if climate change impacts the availability of these prey (Coyle et al. 2011). These amphipods and calanoids are substantial sources of fatty acids that juvenile salmon require during cold periods (Scott et al. 2002; Persson and Vrede 2006).

In the offshore region, hyperiid amphipods, *Themisto* spp., were important prey and contributed a high percentage of the diets of juvenile salmon diets in 2010 and 2011 (Starovoytov 2007b; Temnykh et al. 2010). Fish, such as sand lance (35-45 mm), capelin (60-80mm), Cottidae (16-20 mm), Scorpaenidae (15-25 mm), and Agonidae (20-27mm), were also a high percentage of the diet. The SCI values indicated that hyperiid amphipods were important prey to all species except coho and Chinook salmon (Fig. 3), which consumed large percentages of capelin in this region. Capelin located along the continental shelf provide substantial food to migrating salmon (Vilhjalmsson et al. 2005). Larvaceans contributed a substantial percentage to the diets of pink salmon in 2010 (Fig. 2), but overall SCI values for hyperiid amphipods were higher for pink salmon caught off shore in all three years (Fig. 3).

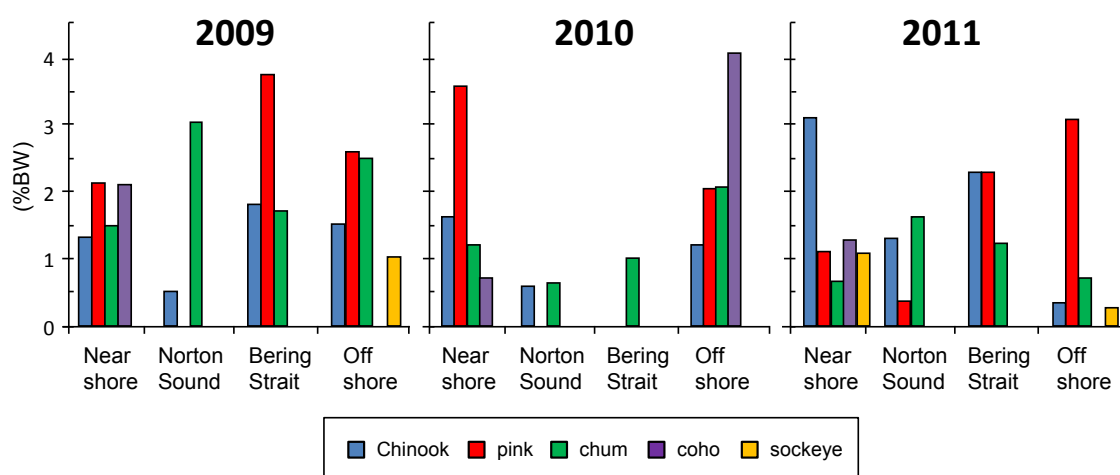


Fig. 4. Percent of salmon body weight (% BW) comprising prey and observed in salmon stomach contents of juvenile Chinook, pink, chum coho, and sockeye salmon collected in four regions of the northern Bering Sea in August-October, 2009-2011.

The amount of prey as a percentage of salmon body weight is a size-related index of feeding intensity and prey availability (Graeb and Dettmers 2004). The percent body weight of prey in stomach contents of Chinook salmon was highest (> 1%) in samples from the nearshore and strait regions, whereas coho salmon fed most intensively in the offshore region (> 4 %BW; Fig. 4). The percentage of Chinook salmon body weight represented by prey in samples collected near shore was unusually high in 2011, despite similar sizes across years in this region (Fig. 5). Pink salmon tended to have the highest percent body weight comprising prey among the salmon species, but their annual body size varied in both the near-shore and off-shore regions where it was often highest. Percent body weight of prey observed in Chinook and chum salmon stomach contents collected off shore decreased over the study period, and pink salmon values increased overall. Small sample sizes and differences in salmon distributions (Sturdevant et al. 2012) may have contributed to some of the feeding differences observed.

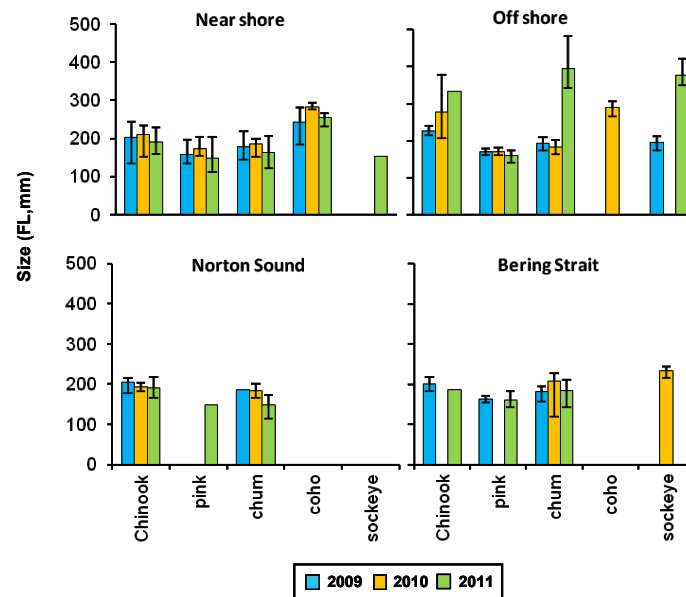


Fig. 5. Average fork length (FL, mm) of juvenile Chinook, pink, chum coho, and sockeye salmon collected in four regions of the northern Bering Sea and pooled over the three-year period, 2009-2011.

Diet overlap (PSI) was calculated for 44 co-occurring species-pairs collected from nearshore and offshore regions (Table 1), but samples were limited to 12 species-pairs in the Norton Sound and Bering Strait regions. Diet overlap of coho and Chinook salmon was consistently > 95% PSI in nearshore regions each year and was based on consumption of fish prey, whereas overlap between other species-pairs varied from year-to-year and was usually low (< 60%; Brodeur et al. 2007). Differential annual movement patterns of juvenile salmon to offshore regions affect their spatial overlap and therefore could affect diet similarity measures (Farley et al. 2007). By contrast, the PSI was significant (81%) only for pink and chum salmon in 2009 in samples collected from the Bering Strait (Table 1; Fig. 2). Diet overlap between piscivorous Chinook and coho salmon is commonly reported (Bollens et al. 2010), but can be overestimated if fish prey taxa differ (Rindorf and Lewy 2004). In this study, both species consumed capelin and sand lance, however, coho fed on pollock (*Theragra chalcogramma*) more than the other salmon species, perhaps alleviating competition for food (Bollens et al. 2010) or indicating different habitat utilization patterns (Weitkamp and Sturdevant 2008).

Table 1. Diet overlap (percent similarity index: PSI) by region and year based on examination of juvenile Chinook, pink, chum, coho and sockeye salmon stomach samples collected in the northern Bering Sea in August-October, 2009-2011.

2009				2010				2011			
				Near shore							
	Chinook	pink	chum	Chinook	pink	chum		Chinook	pink	chum	
pink	72.5	-	-	49.3	-	-		27.4	-	-	
chum	100	41.5	-	74.1	64.6	-		2.6	24.1	-	
coho	100	70.8	35.0	95.2	44.7	69.6		98.6	26.9	1.2	
sockeye								72.2	53.8	1.2	
				Norton Sound							
	Chinook			Chinook				Chinook	pink		
pink	-			-				17.8	-		
chum	-			55.8				46.0	1.0		
				Bering Strait							
	Chinook	pink		chum				Chinook	pink		
pink	17.2	-		-				14.5	-		
chum	5.7	81.6		-				5.0	35.7		
sockeye	-	-		0.8							
				Off shore							
	Chinook	pink	chum	Chinook	pink	chum		Chinook	pink	chum	
pink	90.5	-	-	5.6	-	-		0.2	-	-	
chum	32.3	22.8	-	0.0	39.7	-		2.2	11.3	-	
coho	-	-	-	85.8	11.8	14.2		-	-	-	
sockeye	90.5	100	22.8	-	-	-		1.5	64.4	26.2	

Variation in capelin biomass has been linked to climatic changes and abundance of other pelagic species such as herring and pollock (Benson and Trites 2002; Vilhjalmsen et al. 2005). Similarly, changes in oceanic conditions can limit production of some prey and lead to shifts in planktivorous feeding (Aydin and Mueter 2007; Andrews et al. 2009). Diets of highly piscivorous juvenile salmon species overlapped with planktivorous juvenile salmon species only when the latter ate fish. Thus, diet overlap based on preferred prey is expected to be low when alternate prey is available, but diet quality may differ as a result (Davis et al 2005; Karpenko et al. 2007; Weitkamp and Sturdevant 2008).

A diel feeding rhythm was observed for all juvenile salmon in the northern Bering Sea (Fig. 6). Morning was the period observed with the highest percentage of stomachs that were empty or contained only trace amounts of food. Stomach fullness increased between 09:00 and mid-day hours, dipped in early afternoon, and then remained high until the final sampling period at 21:00 (Temnykh et al. 2010). The afternoon decrease in feeding we observed was similar to sockeye and chum salmon feeding rhythms reported for samples collected in the Bering Sea in summer (Azuma 1992), but rhythms differed with those of pink and chum collected in Southeast Alaska (Sturdevant et al. 2004). Feeding behavior, feeding intensity, and diel prey composition of salmon could be influenced by latitudinal differences in light cycles that affect visual feeding (Schabetsberger et al. 2003; Bieber 2005).

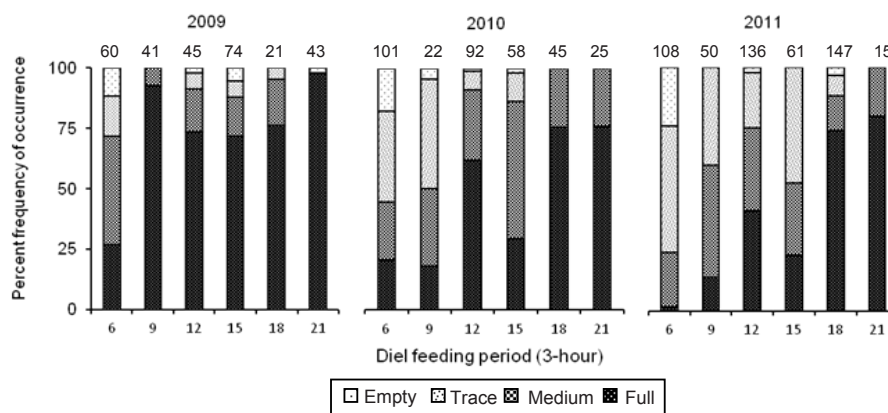


Fig. 6. Juvenile salmon diel feeding rhythm per three-hour period measured as the percent frequency of occurrence of empty, trace, medium, and full stomach volume. Data are grouped for juvenile Chinook, pink, chum, coho, and sockeye salmon collected in all regions of the northern Bering Sea in August-October, 2009-2011. Fish sample size is indicated above the bars.

We examined multivariate trophic relationships among the species and regions using the SCI prey data. Values were square root-transformed and Bray-Curtis similarity matrices were derived. The nonmetric multi-dimensional scaling procedure (nMDS) was used to produce a 2-dimensional ordination plot (PRIMER-E; Plymouth Routines in Multivariate Ecological Research, v6; Clarke and Warwick 2001). The stress value of 0.13 indicates moderately strong relationships among the groups, with species gradients evident in each region except Norton Sound (Fig. 7). The trophic position of sockeye salmon was shown to be distinct from the other species.

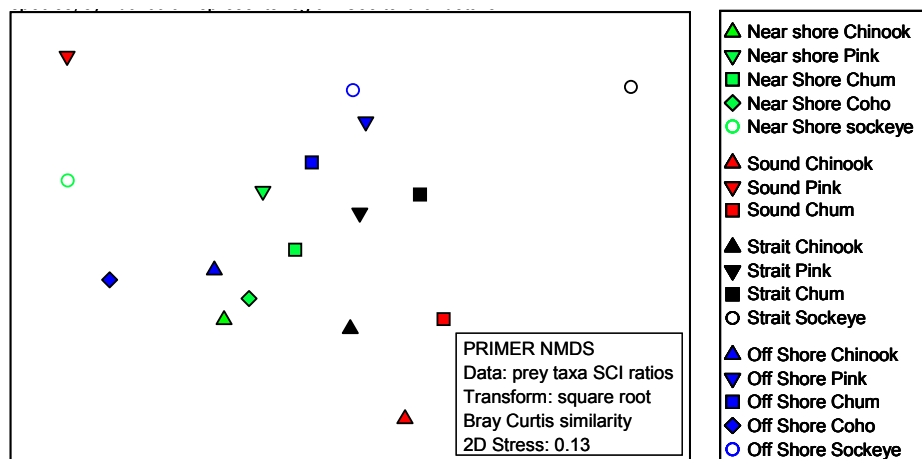


Fig. 7. Multivariate trophic relationships among juvenile Chinook, pink, chum coho, and sockeye collected in the four regions in the northern Bering Sea in August-October, 2009-2011. Diet data are stomach content indices for 40 prey taxa averaged across the three years. Symbol shape represents species; symbol color represents region.

We documented regional and inter-annual differences in juvenile salmon diets for the northern Bering Sea and corroborated previous reports of trophic niches for Chinook, pink, chum, coho, and sockeye salmon and high overlap in the diets of piscivorous Chinook and coho salmon.

As prey fish and invertebrate populations adapt to climate change in the Bering Sea (Overland and Stabeno 2004; Coyle et al. 2011), availability of important pelagic salmon prey resources that can fill the nutritional requirements of juvenile salmon is a concern (Miller et al. 2013), particularly in the face of salmon stock collapses (Orsi et al. 2013). The feeding patterns of migrating juvenile salmon in the Bering Sea suggest that flexibility in feeding on a diverse spectrum of prey types alleviates competition for preferred food types among co-occurring species (Benson and Trites 2002). In the current period of climate and cyclic changes (Andrews et al. 2009; Chittenden et al. 2009; Coyle et al. 2011), information from this and other diet studies contributes to a clearer understanding of the trophic patterns important to the early marine survival of juvenile Pacific salmon in the northern Bering Sea.

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Feeding Interactions of Juvenile Pacific Salmon and Other Fish Species in the Coastal Epipelagic Zone of Kamchatka

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Keywords: juvenile chum salmon, pink salmon, sockeye salmon, Chinook salmon, coho salmon, masu salmon, prey composition, competition, coastal habitat, West Kamchatka, East Kamchatka, Kamchatsky Gulf

This study was based on data collected from trawl surveys conducted on board the RV *MRTK-316* (ship-owner: KamchatNIRO) from June to July 2005-2011 in the coastal waters of Southwest Kamchatka and in August 2007 and 2010 in the Kamchatsky Gulf (East Kamchatka; Fig. 1).

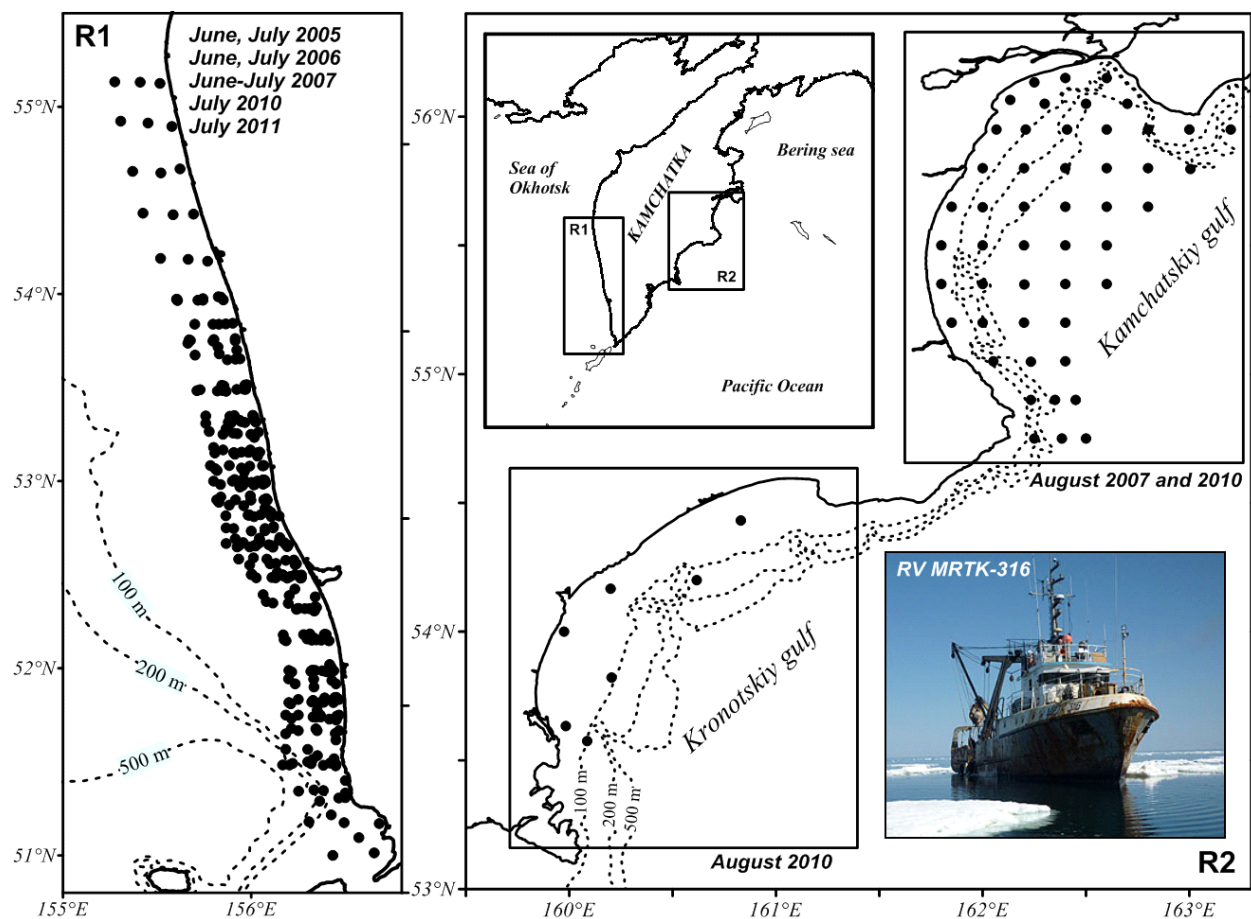


Fig. 1. The scheme of trawl stations used by researchers aboard the R/V *MRTK-316* in the coastal waters of West and East Kamchatka from June to August, 2005-2011.

Pacific salmon and up to 25 other fish species were recorded in the summer trawl catches for the period 2005-2011 in the coastal waters of West Kamchatka as permanent inhabitants of the pelagic zone and members of coastal biocenotic communities. Pacific sand lance, capelin, sandfish, yellowfin sole, starry flounder, and juvenile greenlings were distributed in the survey area. High abundance was typical for Pacific sand lance, capelin and sandfish. In contrast, the most frequently caught species in surveys off East Kamchatka was Pacific herring (Koval et al. 2011).

Mechanisms allow predators to feed maximally on the forage base within an area and to minimize competition among species. These mechanisms are spatial separation of predators and divergence in the spectrum of forage organisms (size and species composition) consumed by the predator. Our analysis revealed that both mechanisms are operating, even from the very early period of Pacific salmon residence in marine waters.

In the waters of West Kamchatka, the maximum similarity in prey composition was observed in predators, including juvenile coho, Chinook, and masu salmon, and adult Pacific sandfish (Fig. 2). Nevertheless, the ration of these predators was different. Juvenile coho salmon typically consumed juvenile walleye pollock, adult capelin, and sand lance. Chinook salmon consumed juvenile sand lance, sculpins, or pricklebacks. Moreover, coho salmon migrated during summer and autumn to the outer edge of the shelf zone to feed on juvenile walleye pollock aggregations—the most preferable forage for coho salmon (Erokhin 1987). Chinook salmon and Pacific sandfish remained on the inner shelf illustrating a spatial divergence from coho salmon. The most abundant group of plankton-eating fish species included juvenile chum, pink, and sockeye salmon, Pacific sandlance, capelin, juvenile Pacific sandfish, and walleye pollock. However, similarity in the prey composition of these fish species was low. The ration generally consisted of organisms of the neritic complex—coastal species of copepods (*Epilabidocera amphitrites*), euphausiids (*Thysanoessa raschii*, *Th. inermis*), mysids, and others. By the end of summer, exploitation of the food web in coastal areas became less intense because pink and chum salmon left these waters, thereby creating spatial divergence among these predators. A characteristic of the West Kamchatka shelf is that typical plankton consumers, such as pink, chum, and sockeye salmon, often consume juvenile and larval fish (> 50 % of prey weight). This can be explained by the mass emergence and early feeding of larval fish of the neritic species complex in summer.

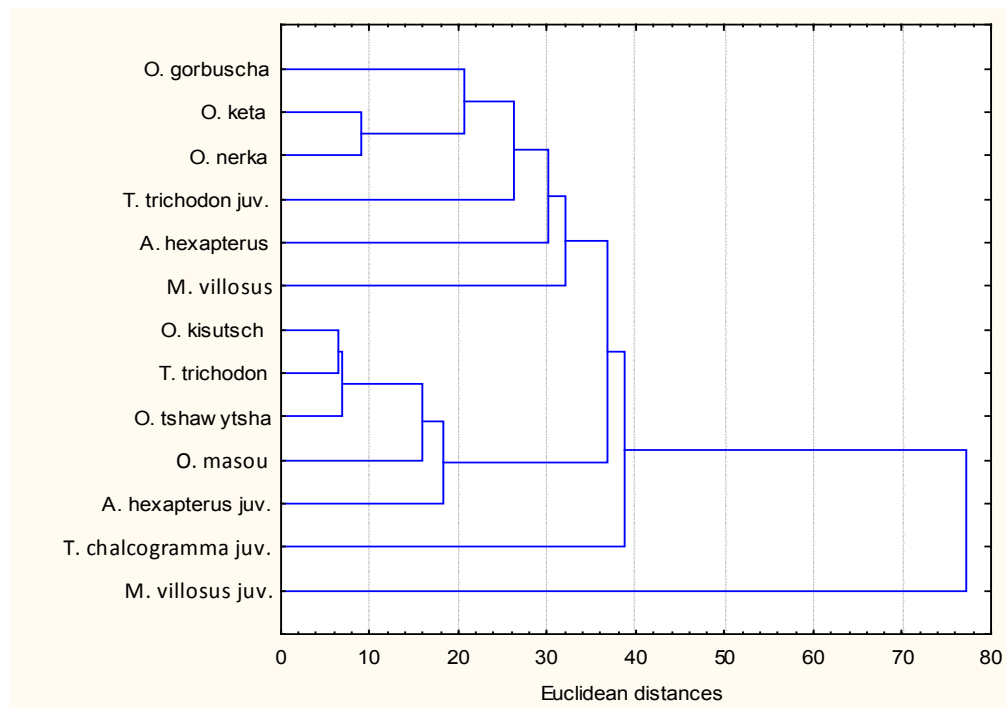


Fig. 2. Food similarity (Euclidean distance) among juvenile Pacific salmon and the other fish species collected in the coastal waters of West Kamchatka in June-July, 2005-2007 and 2010-2011 (all data combined).

Observations of juvenile salmon food habits from the east coast of Kamchatka also demonstrated there are two feeding types: fish predators and plankton consumers (Fig. 3). In the Kamchatsky Gulf, salmon prey included not only neritic organisms, but a number of planktonic organisms (mostly Copepoda) brought into the gulf by water circulation. Thereby the ration of all fish, including fish predators that typically do not feed on zooplankton, can consists mostly of zooplankton (Morozova 2011). An important component of the stomach contents of plankton-eating juvenile salmon was oceanic copepods, *Eucalanus bungii* and *Neocalanus cristatus*. This relates to the narrow area of shallow water on the shelf. In some places in the northern gulf, the outer shelf and slope is as close as 5-10 miles from the shoreline. Therefore, the nearshore habitat of the Kamchatsky Gulf in East Kamchatka provides less stable feeding conditions as compared to conditions in the Okhotsk Sea. Another important characteristic of the northwestern area of the gulf is the run of Pacific herring to coastal

waters during the last half of August (Koval and Morozova 2012). This is probably one of the most important drivers of juvenile salmon early emigration from the Kamchatky Gulf to the ocean. The herring run is important for juvenile sockeye, chum, and pink salmon because the prey of juvenile salmon is very similar to that of herring, and when juvenile salmon and herring are both present competition for the food increases (Koval et al. 2011).

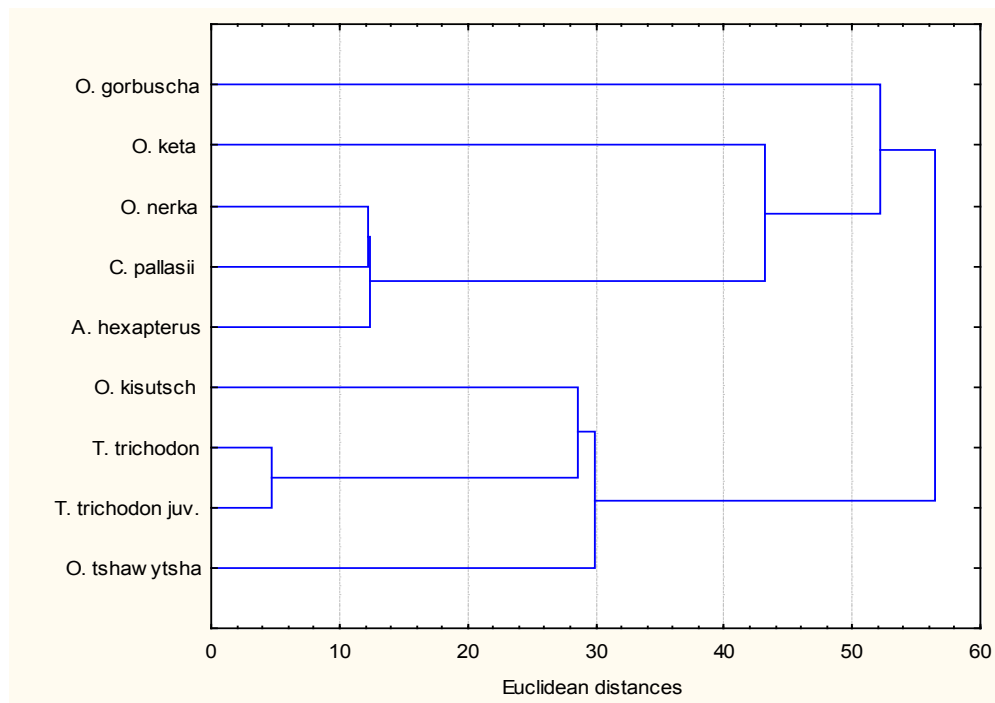


Fig. 3. Food similarity (Euclidean distance) among juvenile Pacific salmon and the other fish species collected in the Kamchatky Gulf (East Kamchatka) in August 2007 and 2010 (all data combined).

Regarding the regional character of early marine feeding by juvenile salmon, the difference between East and West Kamchatka is the duration of juvenile salmon residence in near shore habitats. In the waters of West Kamchatka, species such as sockeye, Chinook, and coho salmon stay in the coastal waters until autumn (sockeye and Chinook salmon remain up to 5-7 months, coho salmon remain about two months). The duration of juvenile salmon residence in the Kamchatky Gulf is 2.5-3 months. Juvenile salmon leave the rivers in June and July (when there is prolonged ice cover) and leave the gulf in late August.

West Kamchatka has a highly productive, developed shelf. In summer the coastal habitat provides a favorable environment for mass emergence of various fish larvae and for feeding during early ontogenesis. This feature of the habitat explains the presence of fish prey in the diet of all species of juvenile salmon. Forage resources in coastal habitats are more fully exploited by juvenile salmon because they remain in these habitats for a long feeding period.

The Kamchatky Gulf has a narrow shelf and less forage production as compared to West Kamchatka. In late August, myriads of Pacific herring move into the gulf and compete for the same prey items as juvenile salmon. Therefore, young salmon strive to adapt and explore oceanic forage resources quickly and move relatively swiftly from the gulf to ocean feeding areas.

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Behavioral and Biochemical Adaptations of Juvenile Pacific Salmon in the Okhotsk Sea and Northwestern Pacific Ocean

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Keywords: juvenile salmon, lipid, protein, calorie content, adaptations, migration, Okhotsk Sea, northwestern Pacific Ocean

Within their phenotype, salmon are a very flexible group of fish with highly variable life histories (Pavlov 1994; Pavlov et al. 2010). Throughout life they periodically move between ecosystems, and in response to these changes there is an adaptation to different abiotic and biotic environments. A distinctive feature of the habitat adaptation period that is different from the other stages of ontogeny is the transition of the energy budget from surplus to deficit, expressed in the intensive use of food reserves, mainly triacylglycerols (Sidorov 1983). Our objective was to identify fluctuations of total lipid and protein content in juvenile salmon and to relate these variations to critical stages in the life of Pacific salmon.

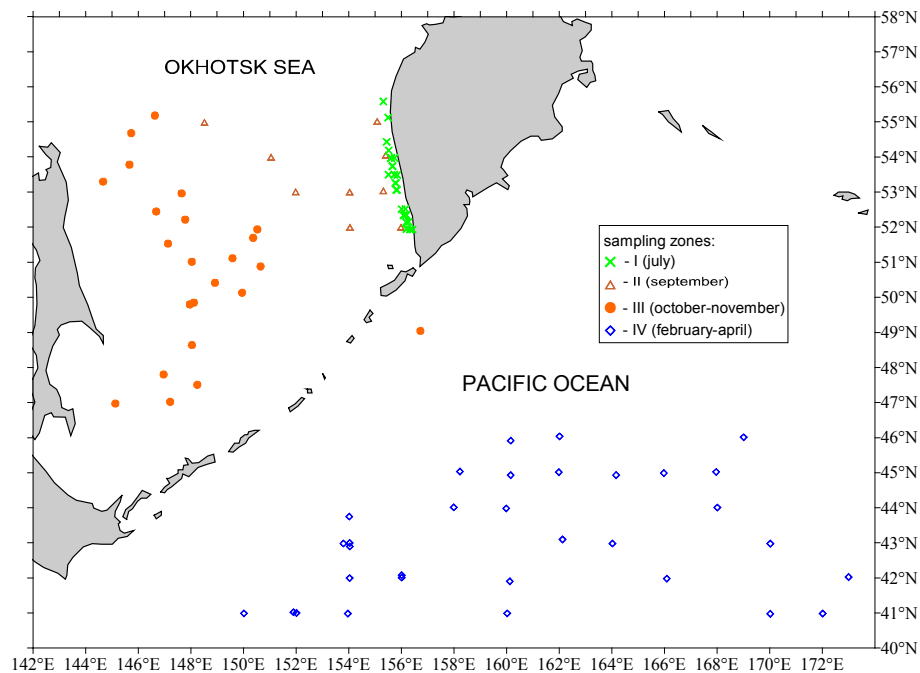


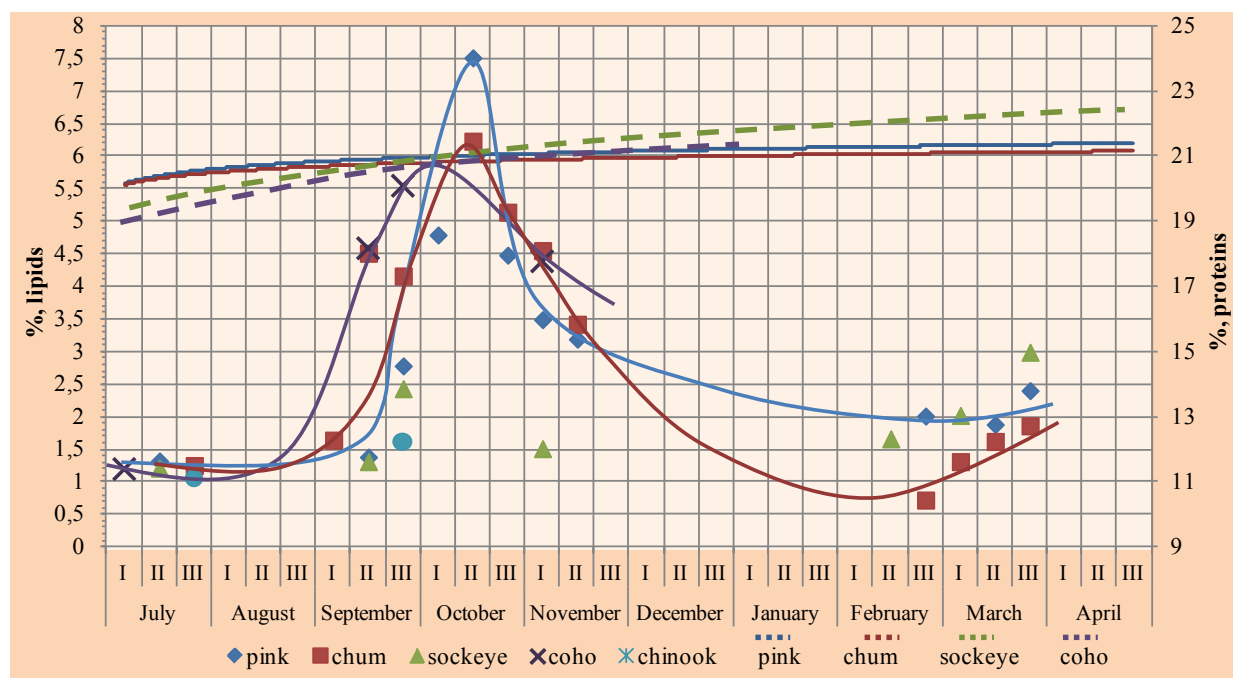
Fig. 1. Location of survey stations and sampling zones in the Okhotsk Sea and northwestern Pacific Ocean where chum, pink, and sockeye salmon tissue samples were collected for biochemical analysis of lipid and protein content.

Samples for biochemical analysis were collected during trawl operations conducted in four geographic zones that included coastal and offshore waters of western Kamchatka, Okhotsk Sea, and northwestern Pacific Ocean (Table 1; Fig. 1). From each trawl operation, 50-100 salmon were examined for full biological analysis that included measurement of body size and weight, gonad weight, determination of sex, and collection of scales and otoliths. For biochemical analysis, 5-30 fish were collected at selected trawl sites. A piece of muscle tissue was collected from near the dorsal fin, along the body from the top of the back to the lateral line. Muscle tissue was excised together with subcutaneous fat. Individual sample weights ranged from 15 to 20 g. Muscle tissue collected during the expeditions was stored at -20°C. In the laboratory, samples were homogenized in a solution of chloroform-ethanol (2:1) and stored at -20°C until analysis was completed. The lipids were extracted by chloroform-ethanol (2:1; Folch et al. 1957). The total lipid content was determined by the gravimetric method (Kates 1975). Weight of non-fat solids (IDS) was collected to determine the protein content of muscle tissue, which is known to consist of more than 90% protein in fish (Shulman and Love 1999). In total, 209 pink, 192 chum, and 110 sockeye salmon were analyzed for lipid and protein content.

Table 1. Sampling areas of the Okhotsk Sea and northwestern Pacific Ocean and months when chum, pink, and sockeye salmon tissue samples were collected for biochemical analysis.

Zone	Time	Place
I	July 2010, 2011	Coastal waters of the western Kamchatka
II	September 2011	Coastal waters of the western Kamchatka and free waters of the Sea of Okhotsk
III	October–November 2010, 2011	Northern and southern part of the free waters of the Sea of Okhotsk, Kuril Pacific Ocean
IV	February–April 2010, 2011	Pacific Ocean in the area of the subarctic front

Results from the July 2010 and 2011 samples showed there was a trawl take of juveniles in the coastal waters of western Kamchatka. Analysis of muscle tissue in all species showed low lipid content of not more than 1.6% on average (Fig. 2). Such lipid levels are observed annually at all stations located in zone I (Fig. 1; Tables 2-4). This period in the development of Pacific salmon continues all summer, and we have identified this as an adaptation period to the sea. During the period of adaptation to marine habitats, juveniles remain mainly in coastal waters (Shuntov and Temnykh 2008).

**Fig. 2.** Seasonal dynamics of total lipid (left y-axis) and protein content (right y-axis) of muscle tissue collected from juvenile salmon during postcatadromous migrations in the Okhotsk Sea.

After completion of the adjustment period of pink and chum salmon, amid the mass migration to the open waters of the Sea of Okhotsk, there is a transition of the energy budget from deficit to surplus. This is accompanied by an increase in the growth rate recorded by accumulation of proteins and active deposition of fat (Tables 2 and 3). Sockeye salmon completing the adaptation period migrate northwards along the coast of western Kamchatka (Erokhin and Shershneva 2007). In sockeye salmon we have not observed rapid changes in the accumulation of nutrients at this time. Such change in behavior in Pacific salmon occurs in early autumn (Table 4).

Table 2. Juvenile pink salmon size and protein (% wet weight) and lipid content (% wet weight) determined from fish caught in the Sea of Okhotsk in 2010 and 2011. Numerator is the average value, denominator is the range.

Years	2011						2010		2011	
Period	July	September		October			November		February–April	
Body length	<u>7.4</u>	<u>16.4</u>	<u>19.9</u>	<u>23.9</u>	<u>22</u>	<u>23.6</u>	<u>24</u>	<u>26</u>	<u>29</u>	<u>35</u>
AC, cm	6.5–8	14.5–17.5	18–22	23–25	20–22	23–25	21–25	25–28	24.4–32	32.6–40.2
Weight, g	<u>7</u>	<u>40</u>	<u>80</u>	<u>133</u>	<u>103</u>	<u>136</u>	<u>128</u>	<u>187</u>	<u>244</u>	<u>428</u>
	6–8	25–58	49–120	105–156	65–122	102–192	85–148	152–252	140–335	332–684
Protein, %	<u>22.28</u>	<u>20.21</u>	<u>19.84</u>	<u>20.24</u>	<u>19.62</u>	<u>19.83</u>	<u>21.45</u>	<u>21.91</u>	<u>19.85</u>	<u>20.49</u>
wet weight	19.09–23.42	18.3–22.38	19.79–21.05	16.92–22.3	16.73–21.73	20.77–22.2	20.49–22.82	15.17–26.94	17.44–24.59	
Lipids, %	<u>1.33</u>	<u>1.8</u>	<u>1.88</u>	<u>2.12</u>	<u>4.8</u>	<u>5.16</u>	<u>3.48</u>	<u>3.99</u>	<u>1.84</u>	<u>2.61</u>
wet weight	1.18–2.43	1.2–2.97	1.46–2.49	2.09–8.92	2.63–9.6	1.52–5.74	2.49–5.89	1.34–2.19	1.55–4.18	

Table 3. Juvenile chum salmon size and protein (% wet weight) and lipid content (% wet weight) determined from fish caught in the Sea of Okhotsk in 2010 and 2011. Numerator is the average value, denominator is the range.

Years	2010		2011						2010	2011
Period	July	July	September		October				November	February–April
Body length	<u>7</u>	<u>8</u>	<u>16</u>	<u>19</u>	<u>22.5</u>	<u>27</u>	<u>22.4</u>	<u>26</u>	<u>22</u>	<u>25</u>
AC, cm	6–8.7	5–11	13–17.5	18.0–20	20.5–24.5	25–30	20–25	25–27	21–23	22.8–28.7
Weight, g	<u>3</u>	<u>6</u>	<u>44.7</u>	<u>77.3</u>	<u>129.6</u>	<u>222.1</u>	<u>121</u>	<u>196</u>	<u>124</u>	<u>158</u>
	2–6	2–14	28–62	58–109	88–188	186–340	84–178	162–232	102–215	112–217
protein, %	<u>20.22</u>	<u>19.97</u>	<u>19.97</u>	<u>20.97</u>	<u>21.50</u>	<u>22.01</u>	<u>20.16</u>	<u>20.48</u>	<u>22.36</u>	<u>21.28</u>
wet weight	18.80–22.13	19.3–20.65	17.09–21.53	19.14–22.97	19.37–23.12	20.81–23.87	17.45–22.53	19.13–21.23	21.79–23.29	18.84–25.08
lipids, %	<u>1.56</u>	<u>1.26</u>	<u>1.38</u>	<u>1.93</u>	<u>3.15</u>	<u>5.01</u>	<u>4.02</u>	<u>5.52</u>	<u>4.01</u>	<u>1.71</u>
wet weight	0.96–2.25	1.04–1.59	1.04–1.88	1.2–3.52	1.37–5.91	2.74–7.97	1.54–7.34	3.31–8.5	2.22–6.09	0.95–3.12

In October, juvenile pink and chum salmon caught in the Okhotsk Sea were characterized by the highest deposition of fat (Fig. 2). High physical activity compensated for by excessive food supply and optimal temperatures for juveniles in the northern Sea of Okhotsk together supply a surplus energy budget, which in turn is reflected in the deposition of nutrients in the tissues, including fat in the muscle (Sidorov 1983; Shulman and Love 1999; Erokhin and Klimov 2010; Tables 2 and 3). Sockeye salmon sized 36–42.5 cm and caught in October near the southern tip of the Kamchatka Peninsula and the northern Kuril Islands on the Pacific side also exhibited high lipid levels (Fig. 1). The lipid status of these sockeye salmon ranged from 1.06–3.20% and averaged 1.81% (Table 4). Judging by the body size, these sockeye salmon were in their second ocean year.

Table 4. Juvenile sockeye salmon size and protein (% wet weight) and lipid content (% wet weight) determined from fish caught in the Sea of Okhotsk in 2010 and 2011. Numerator is the average value, denominator is the range.

Years	2010		2011				2010		2011	
Period	July	July	September		November		February–April			
Body length	<u>10</u>	<u>16</u>	<u>10</u>	<u>14</u>	<u>18.5</u>	<u>21.2</u>	<u>25</u>	<u>37</u>	<u>28</u>	<u>48</u>
AC, cm	6.7–13.9	14.6–18.2	7.9–12.5	13–15.7	17–19.5	20–23.5	24–26	33–42	21.5–30.4	35.3–40
Weight, g	<u>13</u>	<u>43</u>	<u>12</u>	<u>32</u>	<u>74</u>	<u>111</u>	<u>166</u>	<u>571</u>	<u>226</u>	<u>634</u>
	3–34	32–66	5–22	23–44	50–87	87–145	146–192	384–848	92–308	498–787
protein, %	<u>20.30</u>	<u>20.30</u>	<u>20.40</u>	<u>20.41</u>	<u>19.98</u>	<u>20.29</u>	<u>23.08</u>	<u>23.15</u>	<u>23.94</u>	<u>21.55</u>
wet weight	19.02–21.30	18.18–23.12	18.62–22.04	19.08–21.87	19.26–22.10	19.59–21.41	22.54–23.53	22.19–24.44	22.25–25.62	20.77–22.46
lipids, %	<u>1.17</u>	<u>1.53</u>	<u>1.18</u>	<u>1.22</u>	<u>1.43</u>	<u>1.77</u>	<u>1.52</u>	<u>1.81</u>	<u>1.67</u>	<u>2.5</u>
wet weight	0.49–1.81	0.48–2.12	0.64–1.79	0.78–1.66	1.01–2.75	1.04–2.85	1.12–1.84	1.06–3.20	0.62–2.08	1.1–4.57

In November during the migration of pink and chum salmon to the southern Okhotsk Sea, the proportion of lipids in muscle tissue declined. The same was true for sockeye salmon. In the southwestern part of the Okhotsk Sea, juvenile sockeye salmon collected in November had lower lipid levels than in the previous month as levels ranged from 1.12 to 1.84% and averaged 1.52%.

From November to December, juvenile Pacific salmon migrate to the northwestern Pacific Ocean (Shuntov and Temnykh 2008). Passing through the Kuril straits, young pink and chum salmon begin adapting to the ocean. Over the three to four months in the ocean, young fish lose up to 80% of the lipids they accumulated during autumn feeding (Tables 2 and 3). The total lipid content in juvenile sockeye salmon did not decrease, but increased on average up to 9% (1.67%) in comparison with young fish caught in November (1.52%). We suggest that fish size groups of 35–40 cm (498–787 g) and 41.5–53 cm (793–1751 g) as the sizes of salmon that start feeding again in the ocean in the spring (Table 4).

The protein component of muscle tissue was static in comparison with total lipids levels. In the developmental interval between fertilization and when the fish they reach the ocean, the protein level in the muscle tissue undergoes two major changes. First, when the energy needs during embryonic development has expended up to 40% of the protein, then protein levels are restored by in-river feeding (Sidorov 1983). The second change concerns with adaptation by young fish to sea life (Fig. 2). As metabolism of lipids and carbohydrates of juveniles in the sea is dominated by catabolic processes, protein metabolism is predominately an anabolic process, requiring energy for biosynthetic transformations (Varnavskiy 1991).

To review, the first year of life of juvenile salmon in the sea has been divided into three stages: (1) early life and adaptation in the sea (June–August), (2) intensive autumn feeding (September–October), and (3) movement and adaptation to the open ocean (November ~April). The process of migration for juvenile salmon causes a significant expenditure of energy, with a corresponding reduction of the primary energy source—lipids—from the fish's body by a level of three times or more. Adaptation to new habitat conditions by juveniles is also accompanied by increased utilization of ingested energy during the early stages of coastal foraging. At the same time, much of the energy is used for protein synthesis to quickly out-grow the prey size range of various predators, which are a new significant threat in such an environment. In connection with this, we did not observe a decline in the content of proteins during the transition to sea life or during the sea stage.

According to the available data set, the duration of the adaptation of juvenile salmon to the marine period includes all summer months. Apparently, the time boundary when fish start to actively replenish their fat reserves and energy potential is August. Following this time, there is a strong increase in total calories and lipid content in pink and chum, but not sockeye salmon. When foraging at the coast, juvenile sockeye salmon exhibit few changes in muscle lipid content and levels remain low in comparison with chum and pink salmon. The reduced lipid level (to 80%) of juvenile chum and pink salmon indicates the migration out to sea plays an important role in ontogeny, comparable with the early marine adaptation period. However, this is not true for sockeye salmon because the lipid content does not fall as lipid levels increase on average 9%.

Based on analysis of the information presented here, we conclude there are two different strategies for developing offshore feeding areas and biochemical adaptation. On the one hand, juvenile pink and chum salmon, which migrate over vast sea areas, actively put on weight and then spend most of the accumulated nutrients during their migration to the ocean. On the other hand, juvenile sockeye salmon put on weight only in coastal waters and maintain a low lipid level from the time of their initial migration to marine waters through to their movement to the open ocean.

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Density-Dependent Trophic Interactions Between Juvenile Pink (*Oncorhynchus gorbuscha*) and Chum Salmon (*O. keta*) in Coastal Marine Ecosystems of British Columbia and Southeast Alaska

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Keywords: juvenile pink salmon, juvenile chum salmon, stable isotope analysis, density, dietary niche, trophic position

Pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) are the two most abundant salmon species in the North Pacific. After emerging from the freshwater environment, juvenile pink and chum salmon enter the coastal marine environment of the North Pacific Ocean, where their numbers are further augmented by the release of billions of fry from hatcheries (Ruggerone et al. 2010). It is unclear the degree to which the trophic niches of these two species overlap during their early marine life, and how trophic interactions might change according to conditions in the coastal marine environment, such as temperature, density of juvenile salmon, and prey abundance.

Stable isotope analysis is an excellent tool for studying the feeding ecology of a population because isotopes offer a robust approximation of niche characteristics, such as food source and trophic level (Peterson and Fry 1987). Stable isotopes of carbon ($\delta^{13}\text{C}$) reflect the source of production (Post 2002), while the trophic position of a consumer can be inferred from stable isotopes of nitrogen ($\delta^{15}\text{N}$; Peterson and Fry 1987).

The purpose of this study was to determine the degree to which the dietary niches of juvenile pink and chum salmon overlap, and how this is affected by temperature, juvenile salmon abundance, and the availability of prey resources. Because increased competition would result in fewer prey choices for juvenile salmon, we expected that the trophic niche (based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of juvenile pink and chum would overlap more when the abundance of juvenile salmon is high and the abundance of zooplankton is low.

Table 1. Mean trophic position (based on $\delta^{15}\text{N}$), $\delta^{13}\text{C}$ (lipid and trophic corrected), and length (mm) of juvenile pink salmon and chum salmon in the Alaska Coastal Current (ACC/northern region) and the Transition Domain (TD/southern region) in 2000/2001 (cooler years) and 2004/2005 (warmer years).

Year	Region	Species	$\delta^{13}\text{C}$	SD	Trophic Position	SD	Length (mm)	SD
2000	ACC	chum	-19.57	0.58	2.62	0.15	217.0	18.0
		pink	-19.41	0.27	2.47	0.10	238.3	23.2
	TD	chum	-19.09	0.58	2.93	0.14	221.0	16.3
		pink	-19.43	0.56	2.83	0.13	210.7	15.8
2001	ACC	chum	-18.77	0.41	2.48	0.16	217.6	19.5
		pink	-18.62	0.39	2.39	0.13	218.0	26.7
	TD	chum	-18.89	0.59	2.73	0.16	211.6	20.1
		pink	-19.09	0.63	2.60	0.22	198.3	16.9
2004	ACC	chum	-19.89	0.49	2.59	0.20	227.8	8.1
		pink	-18.80	0.51	2.57	0.13	242.1	19.6
	TD	chum	-19.03	0.55	2.98	0.09	218.6	16.4
		pink	-18.88	0.36	2.89	0.06	215.3	11.3
2005	ACC	chum	-18.68	0.51	2.55	0.10	222.8	12.8
		pink	-19.12	0.36	2.59	0.10	233.9	25.7
	TD	chum	-19.09	0.57	2.80	0.17	236.9	14.8
		pink	-18.51	0.43	2.60	0.14	218.2	32.0

The study area for this research extended northward from the northern tip of Vancouver Island to the southern end of Southeast Alaska. This area represents the southern portion of the downwelling domain of the Alaska Coastal Current (ACC) and also the transitional domain (TD) between the ACC and the upwelling domain of the California Current system (Ware and McFarlane 1989). Juvenile salmon were collected in the fall of 2000, 2001, 2004, and 2005. The average sea surface temperatures in the study area in the months leading up to the sampling time were relatively cool in 2000 and 2001 and relatively warm in 2004 and 2005. Due to the dominance of odd-year spawners in the Fraser River, we expected that a greater abundance of juvenile pink salmon would be entering the Strait of Georgia and migrating northward (and into the study area) in 2000 and 2004. By selecting warmer and cooler years we intended to cover a range of feeding conditions, and by selecting odd- and even-numbered years we hoped to observe a range of salmon densities.

Juvenile salmon and zooplankton were collected in October and November; zooplankton density was used to indicate prey availability and as an isotopic baseline signature to estimate the trophic position of juvenile salmon (Post 2002). The CPUE for both species combined was used as an indicator of the overall juvenile salmon density. Similarities between the isotopic compositions (i.e. dietary niches) of juvenile pink and chum salmon were calculated using Euclidean distance. Regression analyses were performed to explore the relationships between the Euclidean distance and CPUE, zooplankton density, SST, and differences in species' mean lengths.

Table 2. Similarity of isotopic composition of juvenile pink and chum salmon as measured by Euclidean distance (‰) and calculated using the baseline corrected $\delta^{15}\text{N}$ and trophic corrected $\delta^{13}\text{C}$. Smaller distance indicates greater niche overlap. Difference in the mean lengths between species of juvenile salmon, catch per unit effort (for both species combined), and the mean density of zooplankton ($\text{g} \cdot 1000 \text{ m}^{-3}$ dry weight) provide information on habitat conditions. ACC: Alaska Coastal Current; TD: transition domain.

Year	Region	Euclidean distance (‰)	Difference in mean length between species (mm)	CPUE (both species combined)	Zooplankton density ($\text{g} \cdot 1000 \text{ m}^{-3}$)
2000	ACC	0.53	21.3	13.9	1.6
	TD	0.46	10.3	53.2	1.5
2001	ACC	0.33	0.4	15.5	2.1
	TD	0.48	13.2	10.7	1.4
2004	ACC	1.09	14.3	1.1	2.4
	TD	0.36	3.3	25.3	0.7
2005	ACC	0.47	11.1	10.8	1.3
	TD	0.89	18.7	5.9	2.1

The combined trophic position and $\delta^{13}\text{C}$ of salmon showed that the trophic niches of juvenile pink and chum tend to overlap, though the degree of overlap varied significantly (Table 1). We expected that the niches of juvenile pink and chum would overlap more when salmon abundance was high and prey availability was low (Table 2). This hypothesis was supported by our results as the distance between their niches decreased with increasing \log_e CPUE ($R^2 = 0.73$, $p = 0.007$) and was positively correlated with zooplankton density ($R^2 = 0.51$, $p = 0.05$). The isotopic niche difference did not appear to be simply the result of a size difference between the two species as this was not significantly correlated with the degree of niche overlap ($R^2 = 0.34$, $p = 0.13$). Nor was there a significant relationship between mean Euclidean distance and mean sea surface temperature ($R^2 = 0.25$, $p = 0.21$). It appeared that when competition was greater for fewer prey items, both species became less selective and incorporated a wider range of prey items into their diets; thus creating more dietary overlap between them.

Although trophic interactions between juvenile pink and chum varied among years, their niches seemed to remain similar to each other, and they most likely competed for the same resources and were affected similarly by changing ocean conditions. In conclusion, the dynamic niche shifts for the two species suggest that they are capable of modifying their diet to compete within and among salmon species for available resources, and that the greater numbers of juvenile pink and chum salmon in the coastal marine environment due to hatchery stocking may thus increase competition for prey resources.

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Potential for Competition Among Herring and Juvenile Salmon Species in Puget Sound, Washington

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Keywords: spatial-temporal overlap, diet composition, diet overlap, feeding rate, consumption, competition, juvenile Pacific salmon, Pacific herring, Puget Sound

The importance of early marine life to the survival of Pacific salmon (*Oncorhynchus* spp.) is well-known (Simenstad et al. 1982, Beamish and Mahnken 2001, Beamish et al. 2004). Growth during the summer rearing period strongly influences salmon survival; juveniles must accumulate sufficient energy stores to reduce size-selective mortality processes. Faster early marine growth is associated with higher marine survival for Chinook salmon (*O. tshawytscha*; Tovey 1999, Duffy and Beauchamp 2011, Tomaro et al. 2012), coho salmon (*O. kisutch*; Beamish et al. 2004), and pink salmon (*O. gorbuscha*; Moss et al. 2005, Cross et al. 2009). However, competition among salmon species and other forage fishes has been linked to reduced growth (Cooney et al. 2001), likely because it limits availability of food resources that already vary naturally.

Puget Sound, Washington State, provides an essential early marine growth environment for Pacific salmon, including Endangered Species Act-listed Chinook salmon (NMFS 1999). Juvenile Chinook salmon that grow bigger by July of their summer in Puget Sound experience significantly higher smolt-to-adult survival (Duffy and Beauchamp 2011). Much of this growth is achieved by feeding in the offshore epipelagic zone of Puget Sound. Variability in offshore growth within Puget Sound can be ascribed to variation in feeding rate (Duffy 2009). Therefore, factors which affect feeding success, such as competition, during this critical period could influence marine survival.

We used midwater trawl data from the main basin of Puget Sound (Central Puget Sound and Admiralty Inlet) to assess spatial-temporal overlap and dietary overlap between Pacific herring (*Clupea pallasii*) and juvenile salmon. We then used bioenergetics model simulations to calculate feeding rates (proportion of the theoretical maximum consumption) for each species.

Midwater trawl operations were conducted by Department of Fisheries and Oceans Canada (DFO) on the CCGS *W.E. Ricker* during July and September/October, 2001-2011 (except in 2003 and 2010, when no trawls were conducted). The trawl net deployed by DFO (model 250/350/14 midwater rope trawl; Cantrawl Pacific Ltd., Richmond, British Columbia) was approximately 14 m deep by 30 m wide when open at depth, it had a 10-cm mesh cod-end with a 1-cm liner for the hindmost 7.6 m of the cod-end, and the towing speed was 2.6 m/s (Beamish et al. 2000). Trawl operations were conducted during daylight at pre-determined, randomly varying 15-m depth increments with the greatest amount of effort at the surface layer (0-15 m).

Counts of all fish in the trawl catch were recorded by species. Hatchery-origin salmon were identified by the presence of coded-wire tags (CWTs) or adipose-fin clips, which comprised about 80% of the total juvenile Chinook catch. Unmarked salmon (no CWT, no clip) were assumed to be wild-origin. However, a low but unknown proportion of unmarked fish were likely of hatchery origin due to incomplete marking. Fork lengths were measured to the nearest 1 mm, and wet weights (WWs) were recorded to the nearest 0.1 g for sub-samples of up to 60 fish per species.

Stomach contents for subsamples of all salmon species were identified by DFO researchers. Herring samples were frozen whole for later analysis. Invertebrate prey items for each sample were separated into broad taxonomic categories (e.g., copepods, crab larvae, euphausiids, gammarid and hyperiid amphipods). Proportional volumetric (cm³) contribution of prey was estimated using each non-empty fish stomach as an individual sampling unit. Stomach contents of frozen herring were analyzed at the University of Washington using dissecting microscopes and following the DFO taxonomic categories. Blotted wet weights of prey categories were measured using an electronic scale and recorded to the nearest 0.0001 g. Proportional wet weight (g) contribution of prey was calculated using each non-empty fish stomach as an individual sampling unit. Diet overlap between species was calculated using the Schoener index (Wallace 1981).

We used the Wisconsin bioenergetics model to estimate feeding rates for salmon species and herring over the July-September/October period. This model uses an energy-balance approach, where consumption over a period is fitted to observed growth, while accounting for time-varying thermal, allometric, and dietary effects on metabolic costs, and waste losses over the same period. Model inputs include the thermal experience, diet, prey and predator energy densities, and growth of the consumer. We used default physiological parameters for Chinook and coho salmon, and substituted pink salmon parameters for chum salmon. Atlantic herring model parameters were used for Pacific herring. We used water temperatures at the top of the trawl net as thermal inputs, average proportional diet composition, literature values for prey energy densities, and apparent growth (Δ WW of the mean individual from July to September).

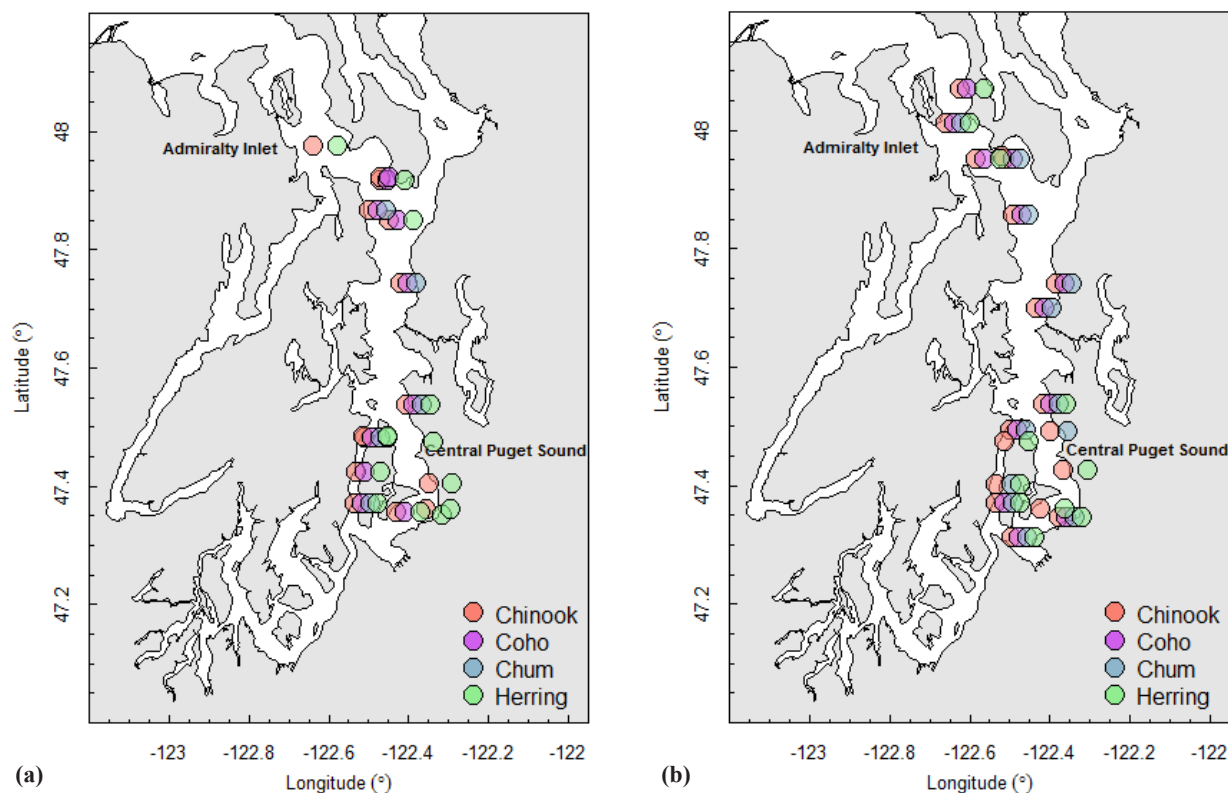


Fig. 1. Presence of Chinook, coho, and chum salmon and herring in 2011 July (a) and September (b) trawl operations conducted in the main basin of Puget Sound, Washington. Each set of dots represents one trawl operation.

Pacific herring dominated the biomass of the shallow pelagic planktivorous fish community and exhibited varying degrees of spatial and dietary overlap with juvenile Chinook, coho, and chum salmon during this critical period, thus creating potential for competition. Salmon species and herring consistently composed the majority of the catch, and they were often found together in trawl catches (e.g., 2011; Fig. 1). Over the years sampled, all four species co-occurred in 44% of trawls conducted in July, and juvenile Chinook salmon and herring occurred concurrently in 70% of trawls in July. In September/October, 23% of trawls contained all four species, and Chinook salmon and herring occurred concurrently in 42% of trawls. Most salmon and herring were found in the upper layers of the water column (0-30 m), particularly in July (Fig. 2).

Proportional diet compositions of juvenile salmon and herring species in July and September/October show similarity among species. Diets of Chinook and coho salmon were most similar, followed by herring, and least similar was chum salmon (Figs. 3 and 4). In July, Chinook and coho salmon and herring consumed diets consisting of large proportions of crab larvae. In September, Chinook salmon tended to eat more fish, although the overall diet composition remained diverse. Coho salmon diets in September relied on gammarid amphipods. Copepods (mainly calanoid) were important prey for herring. The post-analytically grouped “other” category was periodically important prey for chum salmon and herring. In the case of herring, this category was mainly barnacles, ostracods, polychaetes, and unidentified material. For chum salmon, this category consisted mostly of larvaceans (*Oikopleura* sp.), ctenophores, ostracods, chaetognaths, and unidentified material.

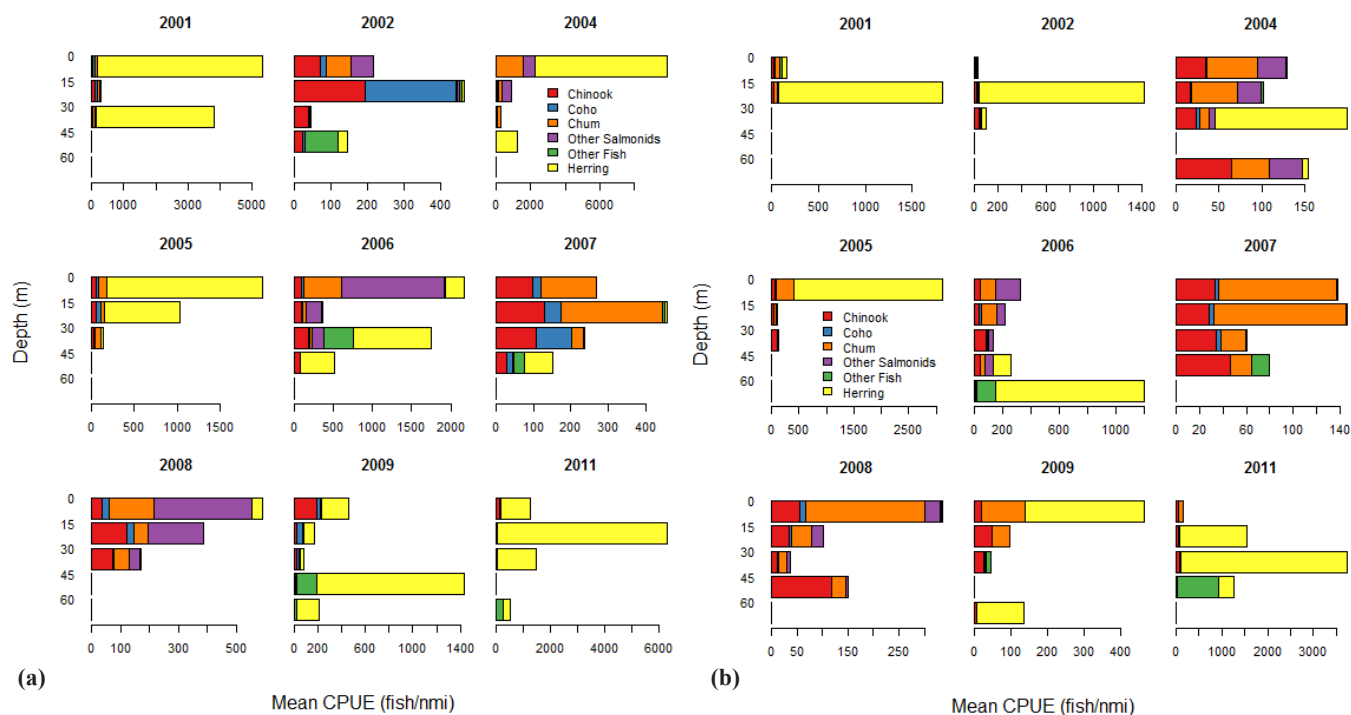


Fig. 2. Annual mean catch per unit of effort (fish/nmi) at depth strata in the water column in July (a) and September/October (b). Trawl operations conducted in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted). The category “other salmonids” includes 24 sockeye salmon (*O. nerka*), 1 steelhead (*O. mykiss*), and 112 pink salmon (*O. gorbuscha*). Note that x-axes are not constant, reflecting the large variability in catches (particularly herring) among years.

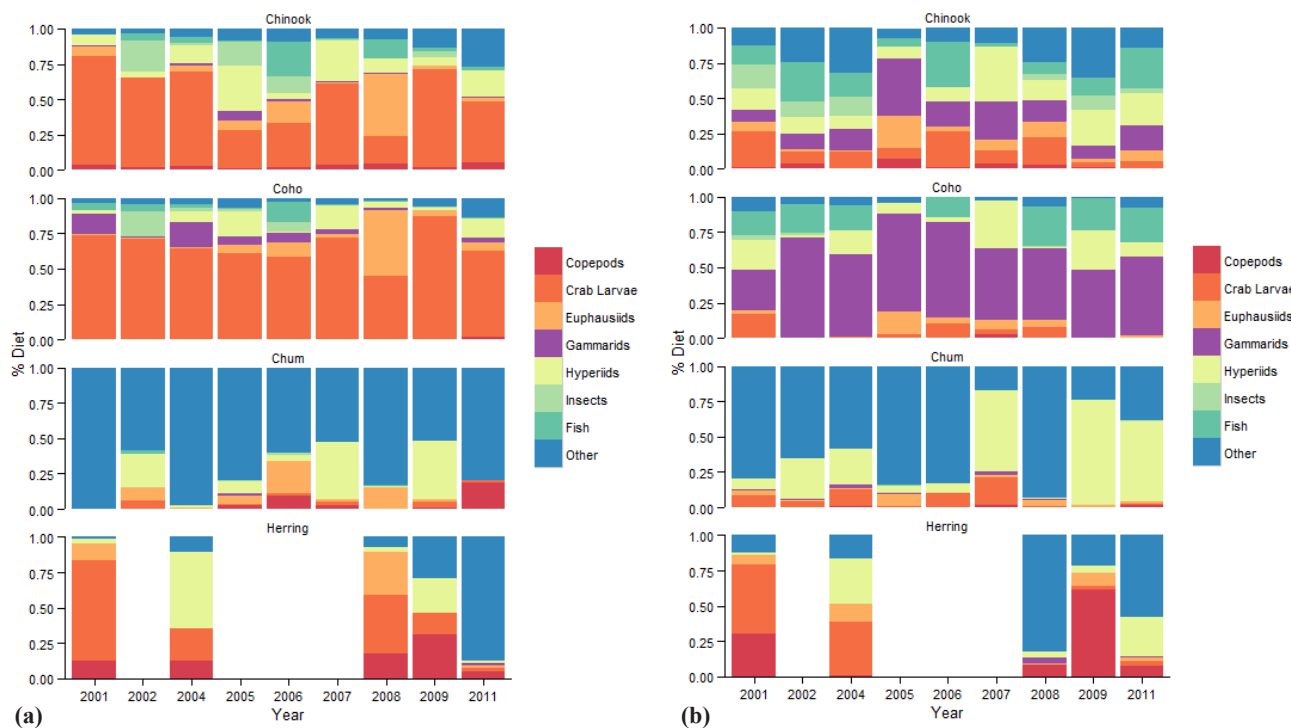


Fig. 3. Interannual comparison of the proportional diet composition by mass or volume for Chinook, coho, and chum salmon and herring in July (a) and September/October (b). Samples collected in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted).

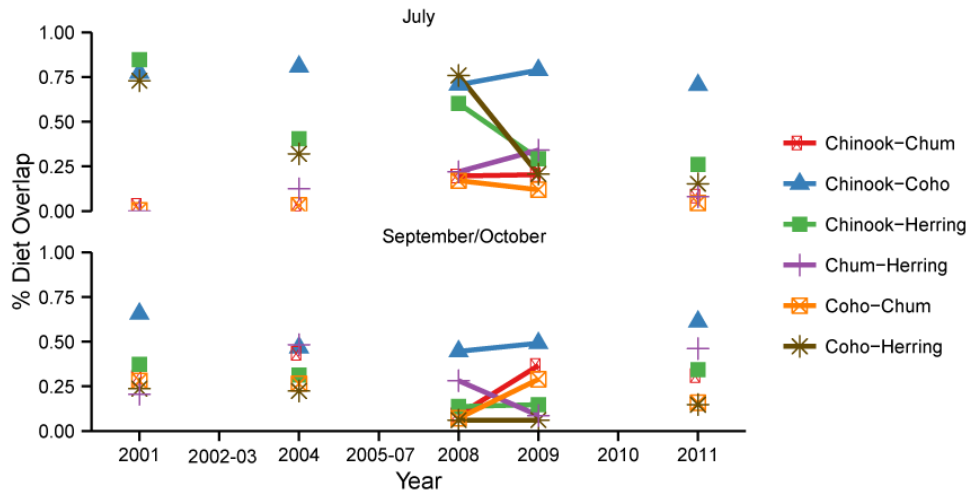


Fig. 4. Seasonal and interannual variation in diet overlap for each species pair in July (top panel) and September/October (bottom panel). Samples collected in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted).

In general, diet overlap between species was higher in July than in September (Fig. 4). Chinook and coho salmon had the greatest amount of diet overlap for both months and across years. Additionally, Chinook and coho salmon diet relationships with the other species appeared similar. Feeding rates varied interannually for all salmon species (Fig. 5). Interannual variability in herring feeding is more difficult to assess, given the lack of a consistent time series. Herring were separated into approximate age classes by size; age-1 herring was the only age-class that we were able to sample consistently over the years from July to September.

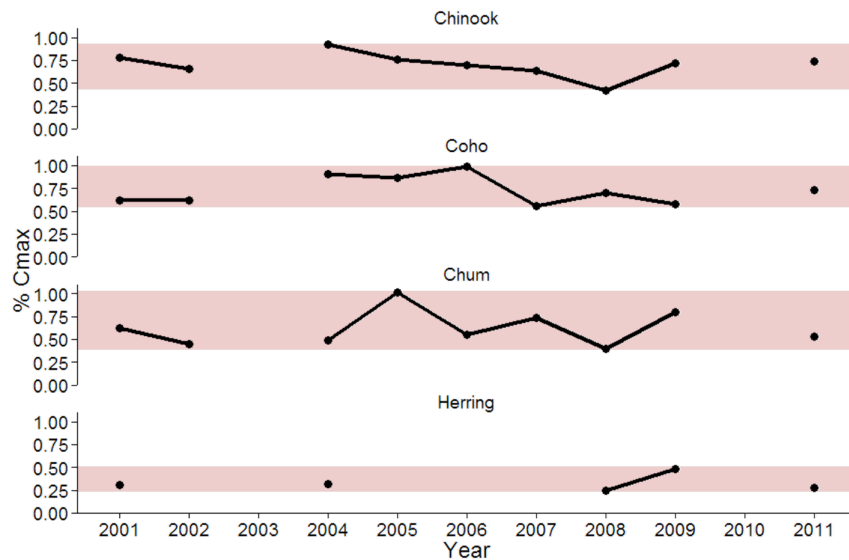


Fig. 5. Interannual variability in feeding rates of age-0 Chinook, coho, and chum salmon, and age-1 herring collected in Puget Sound in 2001-2011 (except in 2003 and 2010, when no trawls were conducted). Feeding rate (%C_{max}) is expressed as the percentage of the theoretical maximum consumption based on bioenergetics simulations for each species.

During the summer growth period in Puget Sound, juvenile salmon and herring exhibit generally high spatial-temporal overlap and variable but often high dietary overlap. Because of their greater population biomass, herring have the potential to remove substantially more of the prey base than do salmon. These observations, paired with previous research linking variable feeding rates and growth to variable survival for Chinook salmon (Beauchamp and Duffy 2011), are consistent with

the hypothesis that competition influences feeding over the summer growth period, thereby affecting marine survival rates of Puget Sound Chinook salmon. Our results suggest that any assessment of marine carrying capacity will need to account for the population and feeding dynamics of all major daylight planktivores in Puget Sound.

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Population Structuring of Chum Salmon, *Oncorhynchus keta*, Populations in Far East Asia

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Keywords: chum salmon, microsatellite DNA, population structure

Chum salmon, *Oncorhynchus keta*, is the most widely distributed species among all the Pacific salmon, ranging from Korea and Japan, northward to the Arctic coast of Russia and North America, and southward to the Oregon coast.

The significant genetic differentiation among and within regions for Pacific Rim chum salmon reflects contemporary restrictions on gene flow (Yoon et al. 2008). In the northeastern Pacific, genetic data have been used to define the evolutionarily significant units (ESUs) and the conservation unit under the Endangered Species Act for chum salmon. However, the historical events and processing of chum salmon genetic structure in the northwestern Pacific still remain unclear.

In the present study, microsatellite DNA (msDNA) was analyzed to estimate the genetic structure of chum salmon populations in Far East Asia. Analyses using four polymorphic loci (OKM4, OKM5, OKM7 and OKM8) were performed using 1,000 fish from 31 populations from Korea, Japan, and Russia (Fig. 1). The assignment tests of individuals was based on an admixture model ($K = 2$) set of baseline samples, and the neighbor-joining phonogram of chum salmon populations was based on the allelic frequencies between populations.

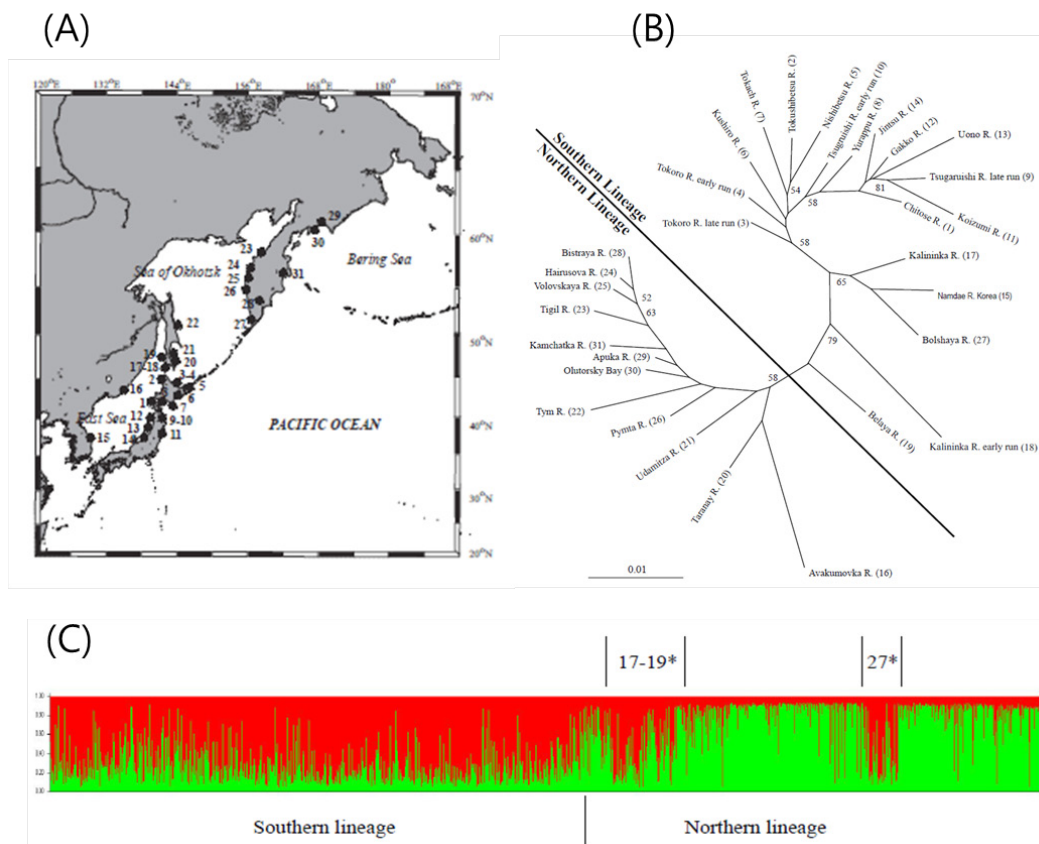


Fig. 1. Map of Far East Asia showing river locations where chum salmon were sampled (A), neighbor-joining phonogram based on allelic frequencies of microsatellite DNA (B), Bayesian analysis of the admixture structure; the optimal cluster number (K) was determined to be two.

The msDNA data reveal clear geographic structuring in the Far East Asian chum salmon among regions (Fig. 1). The analyses showed differentiation between groups of Korean and Japanese populations and Russian populations. In an earlier study, five Russian populations were grouped together with other local populations within the rim of the Okhotsk Sea and West Bering Sea (ROWB) region for management purposes (Yoon et al. 2008). In terms of genetic differentiation, our results suggest that some Russian populations may be intermediate between Korean, Japanese, and other Russian populations. Russian populations shown to be genetically grouped with the Korean and Japanese populations by msDNA data suggests that separate management consideration may be needed for this region. Our results suggest that the observed geographic pattern of the two regions is congruent with patterns obtained in earlier allozyme and mtDNA studies of the same populations (Yoon et al. 2008). Hence, msDNA analysis will be useful for population genetic studies of chum salmon.

Our analyses (msDNA) and an earlier study (mtDNA Yoon et al. 2008) provide differentiation between two regions for effective population size. These findings together might suggest that long-term historical events, such as postglacial re-colonization from different glacial refuges, may influence genetic population structure. Perhaps the Pleistocene ice ages influenced not only historical demographic evidence, glacial population extinctions, and interglacial colonization, but also influenced the contemporary populations of phylogroups of chum salmon along the coasts of Far East Asia.

In conclusion, based on the high degree of chum salmon genetic divergence among geographical groups of populations revealed by msDNA, the genetic markers used in this study will be applicable to identifying the origin of mixture samples collected from salmon aggregations on the high seas, and can be used to further evaluate the discriminative genetic stock identification potential in chum salmon.

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The Population of Chum Salmon (*Oncorhynchus keta*) in the Anadyr River Basin, Chukotka AO, Russia

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Keywords: chum salmon, abundance, Anadyr River, life history

The Anadyr basin of Chukotka is the largest producer of chum salmon in the Russian Northeast Pacific coast (Korotaev et al. 2002). On average, the proportion of chum salmon catches in the Anadyr basin is 75.3% of the catches of all other Pacific salmon in Chukotka. This represents up to 12% of the biomass for the total annual catch of chum salmon in the Russian Far East (Fig. 1). In addition, the chum salmon fishery plays an important role in the traditional life of the native population in Chukotka.

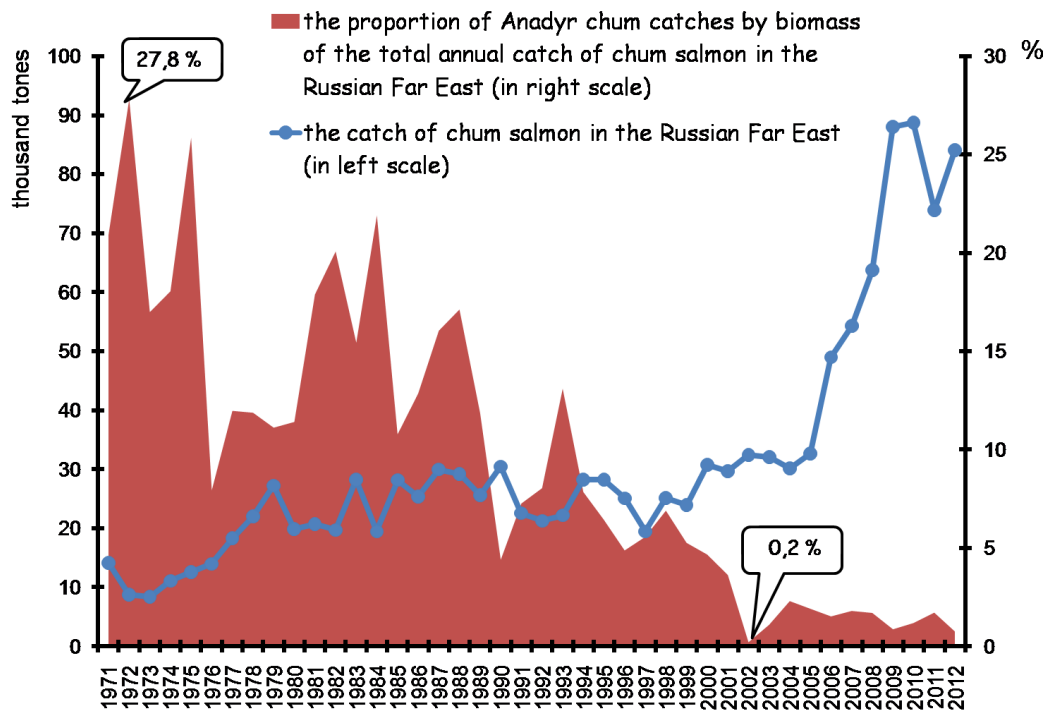


Fig. 1. Proportion of Anadyr basin chum salmon catches by biomass of the total annual catch of chum salmon in the Russian Far East (right y-axis) and the catch (thousand tons) of chum salmon in the Russian Far East (left y-axis), 1971-2012.

The annual monitoring of the Anadyr chum salmon stock includes recording of commercial and non-commercial catches and biological data sampling from adult migrants. The harvest of Anadyr chum salmon began about 100 years ago and has been ongoing since 1910 (Fig. 2). The data collected from monitoring programs are essential for accurate estimations of population size and quota limits for chum salmon. In the recent period, the low numbers of adult migrants was observed in 1968 (0.7 million), 1991 (0.7 million), and 2002 (0.8 million; Fig. 3). The maximum number chum salmon migrants to the Anadyr basin was observed in 1983 (7.3 million), and the annual average is 2.8 million fish (Chereshnev 2008).

The main chum salmon spawning grounds are concentrated in the middle and upper rivers of the Anadyr basin, principally the Anadyr, Velikaya, and Kanchalan rivers (Putivkin 1994). The quantity of chum salmon on spawning grounds fluctuates over a wide range from 0.234 to 2.81 million fish with an annual average (optimum) of 1.5-2.0 million fish. The number of smolts varies from 34 million in 1992 up to 495 million in 1990, and the average annual catch is 265 million fish (Putivkin 1999; Korotaev et al. 2002; Chereshnev 2008).

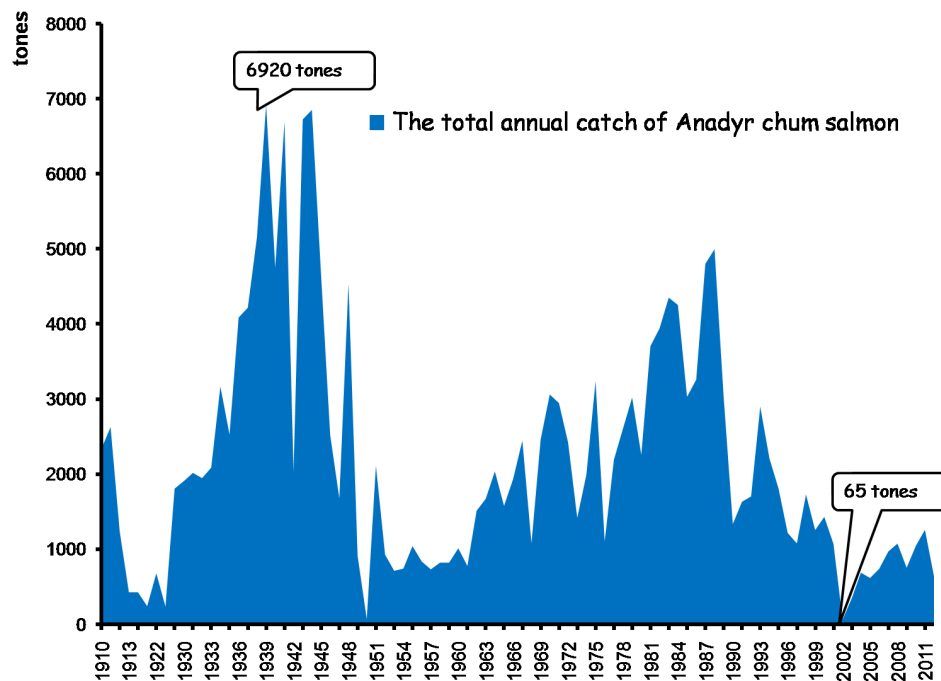


Fig. 2. The total annual catch (tonnes) of Anadyr basin chum salmon, 1910-2011.

Anadyr chum salmon reproduction occurs under extreme conditions for this species. The water level on the spawning grounds decreases to a minimum, causing the destruction of eggs by frost penetration. Juveniles develop in freshwater habitats at low temperatures for about 7-9 months and then migrate to the sea under ice during the April-June period. Inconsistencies in the time periods when fry leave the redds, the various periods of downstream migrations, variable length of the migration routes, and differences in the hydrological conditions among the rivers are the major causes of growth fluctuations of Anadyr chum juveniles both in freshwater and marine life stages (Shtundyk 1982; Korotaev 1997; Putivkin 1999; Korotaev et al. 2002; Chereshevnev 2008). Although smolts differ in length and weight during their migration down to the sea, their sizes become equalized after entering the marine environment for a period (Shuntov and Temnykh 2008).

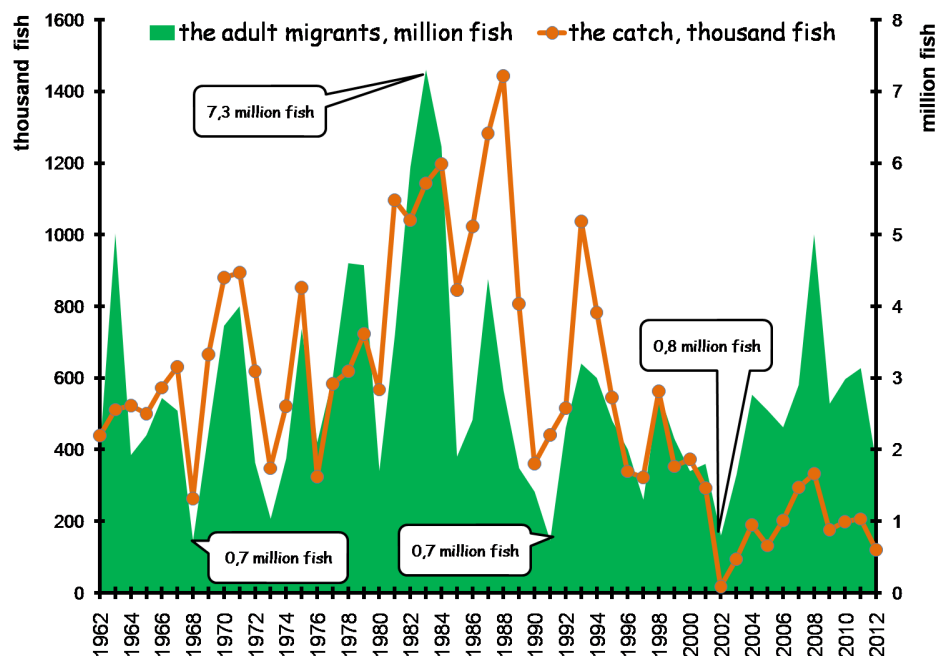


Fig. 3. Number of adult chum salmon migrants to the Anadyr basin (millions of fish; right y-axis) and the catch (thousands of fish; left y-axis), 1962-2012.

The oceanic feeding grounds are located south and southeast of the central part of Aleutian Island chain (Ostroumov 1967; Gritsenko 2002; Chereshevnev 2008; Fig. 4). Implicitly, it is assumed there is a high level of food availability for chum salmon during the marine feeding period.

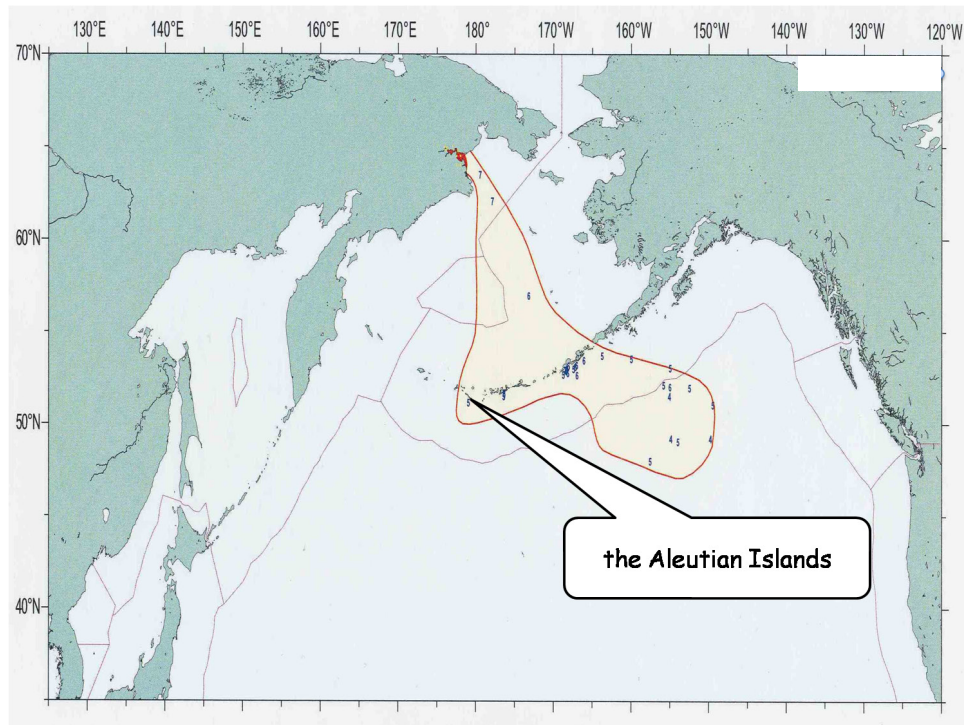


Fig. 4. Spring-summer ocean distribution of Anadyr chum salmon (Gritsenko 2002).

Extreme conditions of egg incubation and larval growth during the first months of the life cycle, including the considerable length of downstream migration, together with some other factors may contribute to larger body length and mass of adult chum salmon migrants in comparison with populations from other regions. In particular, Anadyr chum salmon compete more actively for food with other stocks in the sea and; although low in number, this stock is more viable.

Anadyr chum salmon is affected by predation from other fishes and animals at different stages of its life cycle. Grayling and char consumption of Anadyr chum salmon eggs is significant on the spawning grounds. In the river, jack pike prey on chum salmon juveniles. Anadromous fish species (chars, toothed smelt) eat chum salmon juveniles in the coastal zone. On average, it is estimated that during the adult spawning migration Largha (spotted) seals feed on 260.5 thousand Anadyr chum salmon, and beluga whales consume 77.5 thousand fish. At sea, some fish species have been observed to prey on chum salmon (e.g., daggertooth and longnose lancetfish), and the injury rate of occurrence caused from predation is less than 1%.

An expert estimate of the chum salmon illegal catch is equal to the official statistics in Chukotka. According to fishing data, the portion of chum salmon caught with coastal driftnets is about 1.5%.

In conclusion, the Anadyr basin chum salmon population plays an important role in gene pool preservation as a source stock of wild chum salmon in the North Pacific.

Acknowledgments—I am grateful to the scientific staff of ChukotTINRO for collecting field data.

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Early Marine Growth as an Indicator for Chum Salmon Production

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Keywords: growth, survival, chum salmon

Faster early marine growth rates have been linked to higher marine survival rates in salmon (Mortensen et al. 2000). Ecological interactions with pink salmon that influence chum salmon growth may influence the production of chum salmon. For example, density-dependent reductions in the growth of juvenile pink salmon, due to higher adult pink salmon abundances, were shown to reduce the marine survival of pink salmon (Blackbourn and Tsaka 1990; Beamish 2012). Adult and juvenile pink salmon also consume similar prey items as juvenile chum salmon, such as euphausiids, pteropods, amphipods, and other zooplankton. Therefore, the relationship between early marine growth and returns of chum salmon may differ during years of higher and lower pink salmon abundances. The possible mechanism is the density-dependent effects of adult and juvenile pink salmon on the feeding and growth of juvenile chum salmon. The main goal of this project was to develop a time series for forecasting chum salmon returns. The specific objectives were to (1) evaluate the early marine growth of juvenile chum as an indicator for the returns of chum salmon three years later and (2) evaluate the influence of juvenile and adult pink abundances on the early marine growth and returns of chum salmon.

Scales were collected from chum salmon carcasses at Fish Creek near Hyder, Southeast Alaska. Samples were collected by the National Marine Fisheries Service and the Alaska Department of Fish and Game during the peak of the chum salmon run in mid-August, 1980–1996. Early marine growth was measured on the scales of age-0.3 male chum salmon. The acetate impressions of the scales were projected and measured using an Eberbach scale projector at a magnification of 80x. Early marine growth (1977–1993) was estimated as the distance from the 1st to the 9th circulus in the juvenile growth zone (Fig. 1). Juvenile salmon form approximately one circulus every seven to ten days (Clutter and Whitesel 1956). The early marine growth period for this study estimates growth during the first two to three months at sea.

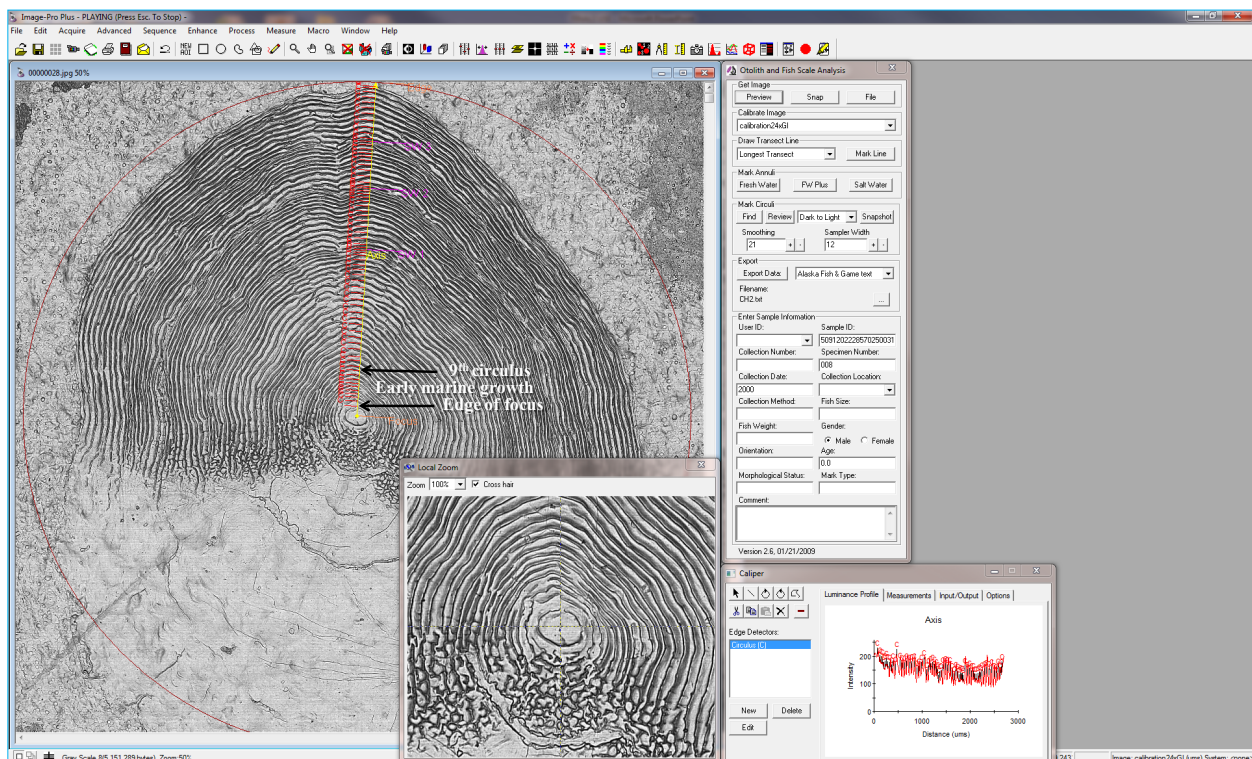


Fig. 1. Scale image from an age-0.3 male chum salmon showing the early marine growth measurement area.

Peak counts of live adult chum salmon in the river were determined by the Alaska Department of Fish and Game (Piston and Heintz 2011) and used as an index of chum salmon returns (1980–1996). Juvenile and adult pink salmon abundances (1977–1993) were back-calculated using mortality schedules (Parker 1968) and the harvest information for pink salmon from the southern Southeast Alaska management region.

Time plots were used to show the relationship between juvenile growth ($t-3$) and the adult chum salmon return index (t). A linear regression model was used to describe the peak counts of chum salmon as a function of the early marine growth of chum salmon, and the estimated abundances of juvenile and adult pink salmon during the year of growth. The Pearson product-moment correlation coefficient was used to assess the relationship between early marine growth and pink salmon abundances. Analyses were conducted in SigmaPlot (Systat software Inc., version 12.0).

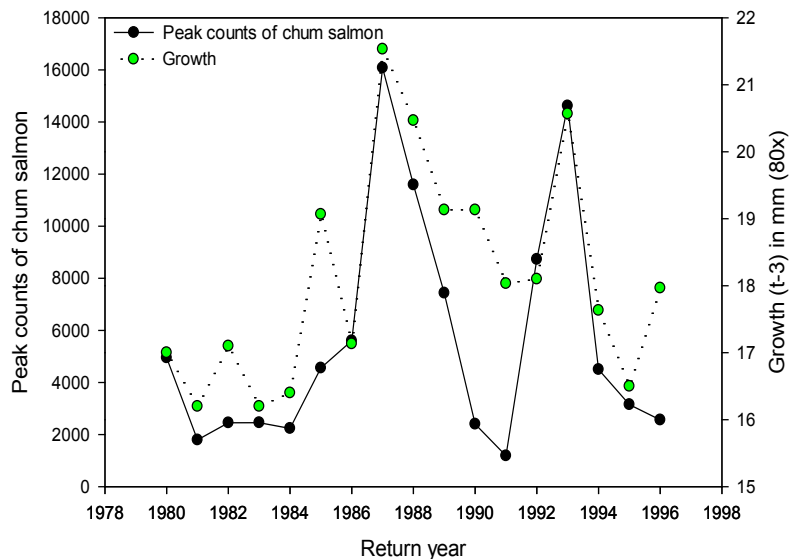


Fig. 2. Early marine growth ($t-3$) estimated from scale patterns of adult age-0.3 male chum salmon that returned to Fish Creek (t) and peak counts of live adult chum salmon (t) in Fish Creek near Hyder, Southeast Alaska.

Results indicated that time trends of early marine growth and chum salmon returns show synchronous patterns from 1980 to 1996 (return year; Fig. 2). In the linear regression model, early marine growth was a positive predictor of chum salmon returns to Fish Creek three years later ($R^2 = 0.675$; $p < 0.001$; Fig. 3). However, estimated abundance of juvenile and adult pink salmon was not significant in the model. In addition, there were no significant correlations between the early marine growth of chum salmon and the estimated abundances of juvenile and adult pink salmon from southeast Alaska.

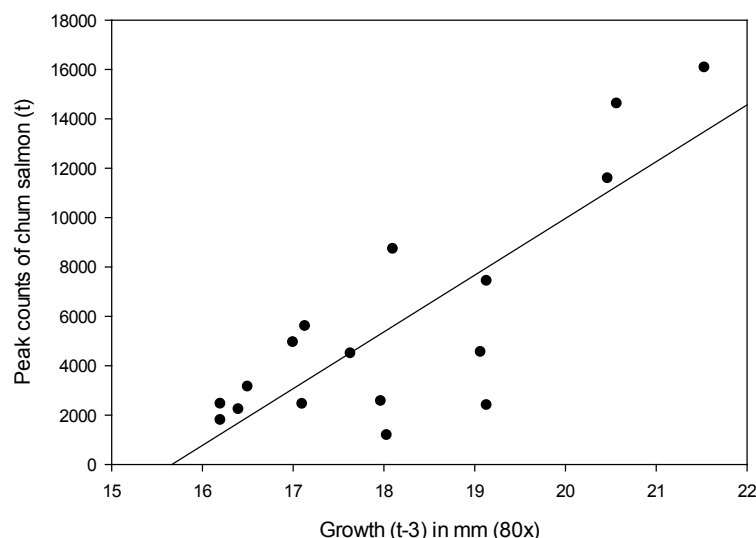


Fig. 3. Relationship between growth ($t-3$) and peak counts of chum salmon (t) at Fish Creek, Hyder, Southeast Alaska ($R^2 = 0.675$; $p < 0.001$).

In conclusion, the early marine growth of chum salmon was a good indicator for strong returns of chum salmon three years later. This relationship needs to be assessed using early marine growth patterns on scales collected from juvenile chum salmon captured at sea. This would provide a pre-season indicator for year-class strength of chum salmon three years prior to returning to the fishery and the natal stream.

Acknowledgments—I appreciate the efforts of Dr. John (Jack) Helle, staff at the Alaska Department of Fish and Game in Ketchikan, and the numerous individuals that collected scales for this project.

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The recommendations and general content presented in this abstract do not necessarily represent the views or official position of the Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Does Predation by Returning Adult Pink Salmon Regulate Pink Salmon or Herring Abundance?

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Keywords: predation impact, trophic interactions, match-mismatch, Pacific salmon, Pacific herring, climate effects

Processes of early marine predation are poorly understood despite the acknowledged role of predation in regulating recruitment (Beamish and Neville 2001; Farley et al. 2007a). Marine predation on juvenile Pacific salmon (*Oncorhynchus* spp.) and Pacific herring (*Clupea pallasii*) by adult salmon and other fish species is often observed (e.g., Prakash 1962; Healey 1976; Livingston 1993; Orlov and Moiseev 2001; Duffy and Beauchamp 2008; Willette 2008; Beamish et al. 2012; Sturdevant et al. 2012); however, assessments of predation impact on survival are often ambiguous (Ware and McFarlane 1986; Beamish et al. 2001; Deriso et al. 2008; Emmett and Krutzikowsky 2008; Sturdevant et al. 2009). Cannibalism by adult pink salmon (*O. gorbuscha*) has long been proposed as a potential mechanism that causes oscillation of odd- and even-year abundance cycles (Ricker 1962; Barber 1979; Dudiak et al. 1984; Krkošek et al. 2011). Similarly, predation by salmon and other fish species has been linked to poor recruitment to herring fisheries (Beamish et al. 2001; Schweigert et al. 2010; Pearson et al. 2012). In Prince William Sound (PWS), a recent shift in pink salmon odd-even brood line dominance (Helle 1964; Heard and Wertheimer 2012) and the continued depression of herring populations (Deriso et al. 2008; Pearson et al. 2012) led to this investigation of pink salmon cannibalism and predation on herring by homing adult pink salmon as potential mechanisms that maintain these conditions.

Homebound adult pink salmon from the ocean often do overlap in space and time with out-migrating juvenile pink salmon and transient herring. Pink salmon are the most abundant salmon species in both PWS and Southeast Alaska (SEAK), where hatchery and wild stocks predominate, respectively (Heard and Wertheimer 2012). Adult pink salmon are usually described as planktivorous (Ishida 1966; Takagi et al. 1981; Davis 2005; Koval 2006; Karpenko et al. 2007), but juvenile pink salmon and herring have been among the prey fish reported in their diets (Beacham 1986; Karpenko and Maksimenkov 1991; Izergin et al. 2008; Sturdevant et al. 2012). In contrast, coho (*O. kisutch*) and Chinook (*O. tshawytscha*) salmon are considered to be the most piscivorous *Oncorhynchus* species, preying extensively on forage fish including both pink salmon and herring (Prakash 1962; Beacham 1986; Karpenko and Maksimenkov 1991; Beamish et al. 2012). Adult pink salmon cannibalism and predation on herring could vary depending on the extent of their spatial and temporal overlap. Climate could determine their overlap by shifting their abundance and behavior, leading to match-mismatched conditions in different years and locations (Cooney et al. 2001; Healey 2011; Beamish et al. 2012), and thus predation interactions may partially depend on migration patterns, distribution, and timing that are affected by climate (Willette et al. 1999; Durant et al. 2007; Willette 2008; Radchenko 2012). Monitoring potential predation events is important because climate and salmon production changes are altering migration patterns, distribution, and timing traits for many salmon species and stocks (Kaeriyama et al. 2004; Kaev and Rudnev 2007; Andrews et al. 2009; Chittenden et al. 2009; Moss et al. 2009; Ruggerone and Nielsen 2009; Beamish et al. 2010; Coyle et al. 2011; Fukuwaka et al. 2011; Beamish et al. 2012; Kaev 2012).

Our objectives in this report were to assess potential salmon predation impact on juvenile salmon and herring by: (1) comparing diets of adult pink salmon during their homing migrations using samples taken from surface trawls in SEAK straits and purse seines in SEAK and PWS; (2) contrasting predation incidence of these abundant pink salmon with the less abundant, more piscivorous adult coho and immature (age-1+) Chinook salmon in SEAK straits; and (3) examining potential climate mechanisms that could influence predator-prey match-mismatch by altering life history patterns of growth, migration timing, or stock-specific characteristics.

Salmon stomach samples were examined shipboard during NOAA surface trawling research in northern SEAK and in the laboratory from frozen samples collected during Alaska Department of Fish and Game (ADFG) purse seine test fisheries (TF) in SEAK and PWS (Fig. 1). Adult pink and coho salmon and immature (age-1+) Chinook salmon were sampled during Southeast Coastal Monitoring (SECM) project annual trawling at eight stations in the vicinity of Icy Strait, SEAK, from June-August or September, 1997-2012 (n ~ 20 trawl operations per month). Adult pink salmon stomachs were sampled more intensively during June and July TFs at alongshore locations in 2009-2011 in PWS and in 2011 in SEAK. In PWS, TFs typically sampled all early-returning adult pink salmon captured in June at eleven stations in the vicinity of Knight Island Passage (Fig. 1) using a small-mesh anchovy seine, whereas adult pink salmon were subsampled in July at three stations

fished with a commercial purse seine at the southwest entrance to PWS. However, in 2011, sampling gear and schedules were altered compared to the other years, and no adults were captured in June. In SEAK, TFs used a commercial purse seine during four weekly samplings beginning in mid-June (~ ADFG Statistical Week 26) at Hawk Inlet (four stations) in the northern region and at Point Gardner and Kingsmill Point in the central region (Fig. 1). Overall, monthly samples were collected approximately concurrently from each locality and gear.

During sample processing, fish were measured for length (mm FL or SL), weighed (kg; trawl samples only), and

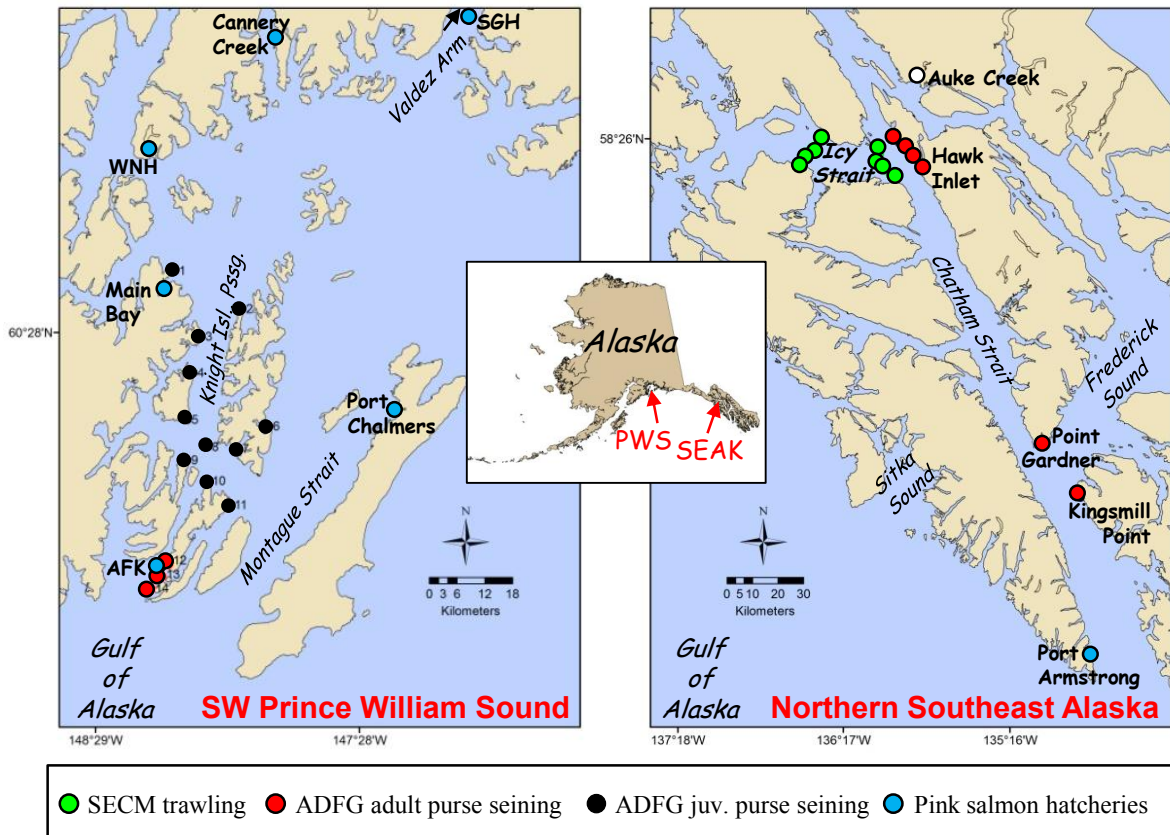


Fig. 1. Locations of pink salmon purse seine test fisheries (TF) in Prince William Sound (PWS; left panel) and Southeast Alaska (SEAK; right panel; black and red circles). Southeast Coastal Monitoring project (SECM) surface trawling in northern SEAK (green circles), and pink salmon hatcheries (blue circles; Solomon Gulch Hatchery, SGH; Wally Noerenberg Hatchery, WNH; Armin F. Koenig Hatchery, AFK). In PWS, numbered sites for June TF (black circles) are: 1-Main Bay, 2-Herring Bay, 3-Point Nowell, 4-North Chenega, 5-Chenega Point, 6-Snug Harbor, 7-Mummy Bay, 8-Squire Island, 9-Bainbridge Point, 10-Shelter Bay, and 11-Bishop Rock. Numbered sites in PWS for July TF (red circles) are: 12-Squirrel Bay, 13-Fox Farm, and 14-Middle Cape. Pink salmon are primarily hatchery-origin in PWS and wild-origin in SEAK.

stomachs were excised. Guts were assigned a volumetric index of fullness (empty, < 25%, 50-75%, and > 75% full). Total contents were weighed, and then prey were sorted, identified to species when possible, and assigned a percentage volume for calculation of weights. Intact prey items were counted and measured (mm, TL or FL). Diets were summarized as percent weight (% W; weight of prey as a percentage of predator body weight) of juvenile salmon, herring, other fish, fish remains (digested), and zooplankton in the stomach contents. Incidence of juvenile salmon and herring was summarized by percent frequency of occurrence (% FO). Predation impact (PI) was calculated as $PI = (\% FO) \cdot (\text{mean number} \cdot \text{gut}^{-1}) \cdot \text{adult harvest}$ (Orsi et al. 2013a). Adult pink salmon otoliths and juvenile salmon prey otoliths from PWS were examined for stock-specific thermal marks to assess stock interactions.

To illustrate potential impacts of climate on predator-prey match-mismatch conditions, we examined 16 years of SECM

trawl salmon diets by years categorized as warm and cold based on annual temperature anomalies in Icy Strait (Sturdevant et al. 2012). We then selected examples of juvenile pink salmon, herring, and adult pink salmon life history metrics from the SECM time series and from local and regional fisheries data to explore how climate-mediated interannual, regional, and stock-specific shifts in timing behavior could influence predation impact on these prey. Additional metrics and ecosystem correlations are reported in Fergusson et al. (2013) and Orsi et al. (2013a).

Diets differed between the salmon predator species, regions, and years (Fig. 2). In SEAK straits, pink salmon were largely planktivorous, whereas coho and Chinook salmon were highly piscivorous. Overall, diet %W differed minimally between warm and cold years in straits. Herring and salmon were uncommon in pink salmon diets, contributed nearly 50% W to coho salmon diets, and only herring contributed to Chinook salmon diets. In alongshore locations, pink salmon clearly consumed large percentages of fish. In PWS alongshore samples, pink salmon diets showed large monthly and interannual differences. Only juvenile salmon were consumed by pink salmon in both June and July in 2009, herring dominated diets in June 2010, but neither species was consumed in July 2010. Neither prey species occurred in pink salmon diets in 2011. In SEAK alongshore samples, no salmon and few herring were consumed by pink salmon in either location in 2011.

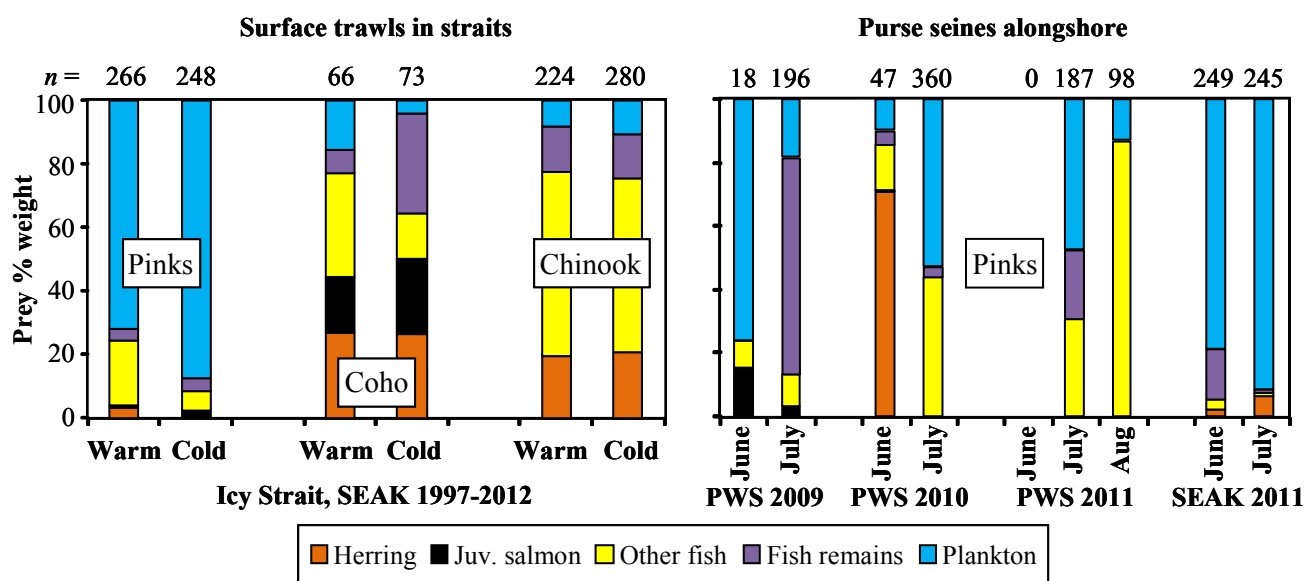


Fig. 2. Diet composition (prey percent weight) for adult pink and coho and immature Chinook salmon captured in Southeast Alaska Coastal Monitoring (SECM) project surface trawls in northern Southeast Alaska (SEAK) in nine warm vs. seven cold years (left panel) and for adult pink salmon captured in purse seine test fisheries alongshore in Prince William Sound (PWS) and SEAK (right panel). Sample size is indicated above the bars.

Overall, pink salmon cannibalism was not common in either PWS or SEAK, with incidence of predation on juvenile salmon and herring generally < 1.1% FO (Fig. 3). Predation on juvenile salmon and herring occurred both in years with low adult/high juvenile salmon abundance and in years with high adult/low juvenile salmon abundance. However, in PWS, rates of cannibalism were out-of-sync with subsequent adult returns: predation impact was approximately twice as high in 2009 (a low return year) as it was in 2010 (a high return year), with a higher incidence and average number of salmon consumed (Table 1). Thus, the hypothesis of oscillating brood-line control was not supported by cannibalism of juvenile pink salmon by adult pink salmon. Conversely, alongshore predation on herring was greatest in PWS in June 2010, when returning adult pink salmon were earlier, larger in size, and more abundant (Fig. 5D). Incidents were observed at four locations, but occurred mainly at Herring Bay (Fig. 1), where 69% of adult pink salmon sampled averaged four herring in their gut. Pink salmon impact on herring in PWS in 2010 was nearly 20 times greater than the impact on juvenile salmon in PWS in 2009, and 20 times greater than the impact on herring in SEAK in 2011 (Table 1). Therefore, localized predation impact on herring in PWS was possible in some years.

Table 1. Estimated predation impact (PI) on juvenile salmon and herring by adult pink salmon from alongshore purse seine samples in Prince William Sound (PWS) and Southeast Alaska (SEAK) and estimated PI by coho salmon from trawl samples in SEAK calculated from diet observations and harvest data. The PI of pink salmon and immature Chinook salmon sampled by trawl in SEAK could not be compared due to sample limitations.

Area	Return year	Harvest (millions of fish)	Number of guts	Empty guts (%FO)	Salmon incidence (%FO)	Mean number in guts	PI (millions eaten)	Herring incidence (%FO)	Mean number in guts	PI (millions eaten)
Pink salmon PI from purse seine samples										
PWS	2009	19.0	214	55.6	1.40	1.3	0.35	0.00	0.0	0.0
	2010	71.3	407	78.6	0.25	1.0	0.18	2.90	3.1	6.41
	2011	32.8	400	19.6	0.00	0.0	0.0	0.00	0.0	0.0
SEAK	2011	47.7	494	63.8	0.00	0.0	0.0	0.80	1.0	0.38
Coho salmon PI from trawl samples*										
SEAK	Warm	1.49	66	10.8	12.4	0.6	0.31	24.4	1.4	0.58
	Cold	1.49	73	17.8	13.2	1.5	0.38	8.5	1.0	0.19

*averages for 8 warm and 7 cold years, 1998-2012

We contrasted these results for adult pink salmon with the incidence of juvenile salmon and herring in diets of coho and Chinook salmon from SEAK trawl surveys. Overall, coho salmon had the most consistent annual predation and the highest % FO of both prey species (up to 50% FO; Fig. 3). In the nine warm years, coho salmon predation on herring was more common and % FO was greater than in the seven cold years, while in cold years predation on juvenile salmon was more common. In contrast, Chinook salmon preyed on herring similarly in warm and cold years at lower % FO than coho salmon, and in more years overall than for pink salmon (Fig. 3). The magnitude of potential predation impact by coho salmon on both juvenile salmon and herring in SEAK trawl samples was similar to that of adult pink salmon in PWS purse seine samples (Table 1), even though annual coho salmon harvests average only ~15% of pink salmon harvests (Orsi et al. 2013a). Coho salmon predation impact was approximately 19% greater on juvenile salmon in cold years and approximately 67% greater on herring in warm years, suggesting shifts in trophic linkages related to climate (Durant et al. 2007; Coyle et al. 2011). In contrast, no significant impact on adult herring abundance was attributed to adult coho or Chinook salmon predation in British Columbia waters (Beamish et al. 2001; Schweigert et al. 2010).

Reports of climate effects on salmon and herring production, migration, timing, and trophic dynamics have increased in recent years (Farley et al. 2007b; Kaev and Rudnev 2007; Tojo et al. 2007; Taylor 2008; Chittenden et al. 2009; Healey 2011; Beamish et al. 2012). One outcome of these climate effects and ecosystem changes is expansion of salmon trophic linkages (Brodeur and Pearcy 1992; Kaeriyama et al. 2004; Coyle et al. 2011; Sturdevant et al. 2012), which could alter typically low patterns of pink salmon cannibalism and piscivory (Durant et al. 2007; Ruggerone and Nielsen 2009; Fukuwaka et al. 2011). For example, oceanographic conditions in coastal British Columbia were related to increased predation pressure on herring from Pacific salmon and other potential predators, to failed year-class strength for herring and salmon (Ware and McFarlane 1986; Hay et al. 2008; Schweigert et al. 2010; Beamish et al. 2012), and cumulative negative climate effects for sockeye salmon (*O. nerka*; Healey 2011).

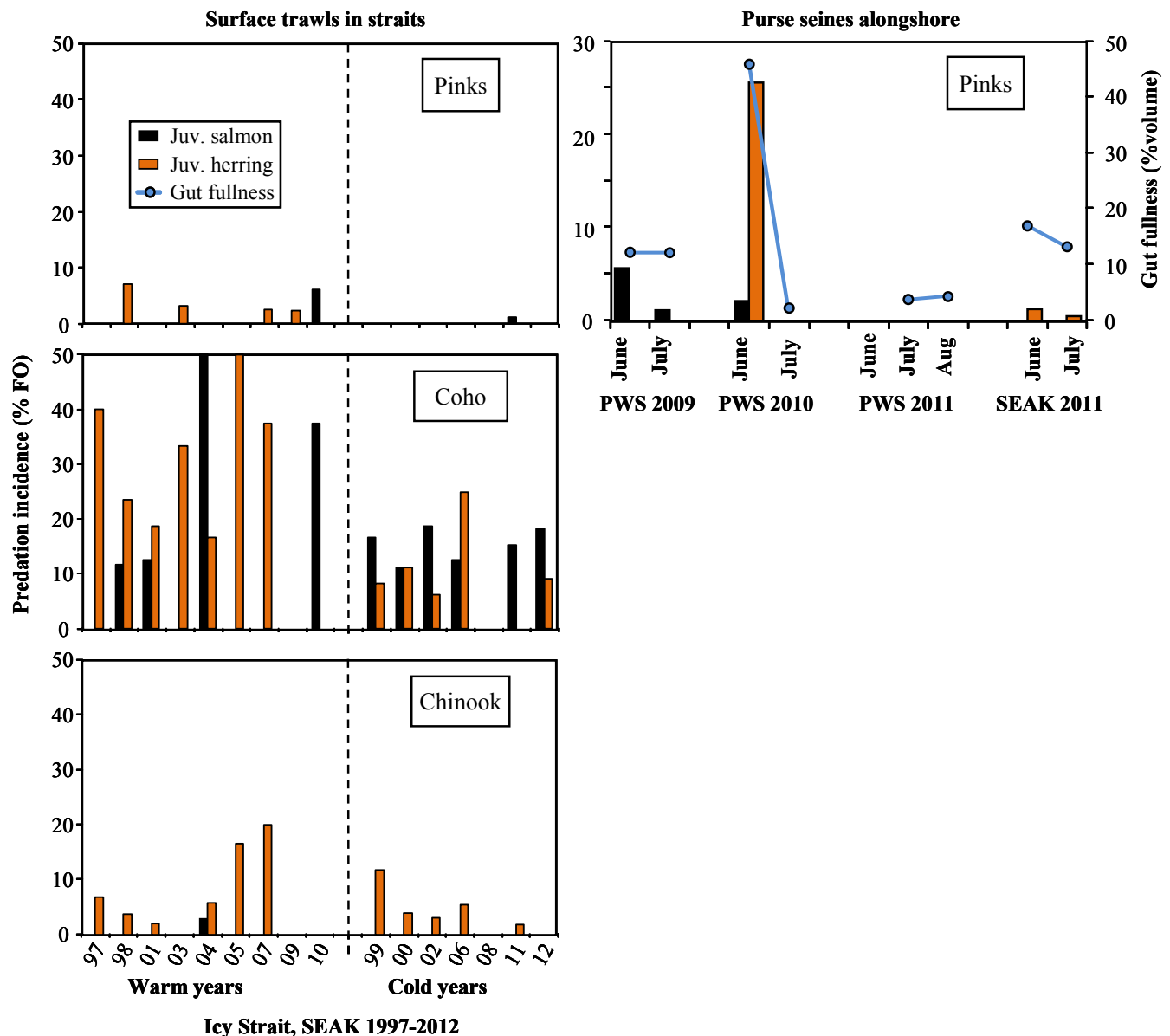


Fig. 3. Incidence of predation (percent frequency of occurrence, %FO) on juvenile salmon and herring by adult pink and coho and immature Chinook salmon captured in Southeast Alaska Coastal Monitoring (SECM) project surface trawls in straits in northern Southeast Alaska (SEAK) in nine warm vs. seven cold years, and by adult pink salmon captured in purse seine test fisheries alongshore in Prince William Sound (PWS) and SEAK. Note the difference in scales of the y-axes.

Climate may influence predation intensity by affecting both predator and prey life history metrics through temperature, hydrography, and feeding/growth environments (Kaeriyama et al. 2004; Durant et al. 2007; Beamish et al. 2012). Climate has been shown to affect salmon and herring phenology and behavior in many locations and life history stages (Farley et al. 2007b; Tojo et al. 2007; Hay et al. 2008; Taylor 2008; Schweigert et al. 2010; Healey 2011; Krkošek et al. 2011; Heard and Wertheimer 2012; Kaev 2012; Orsi et al. 2013a), but effects can differ within small spatial scales (Zheng 1996; Mueter et al. 2002; Hay et al. 2008; Fukuwaka et al. 2011; Beamish et al. 2012). The potentially climate-sensitive prey metrics we considered for the SEAK and PWS regions included juvenile salmon out-migration and epipelagic timing and herring size-at-age (Fig. 4A-C). The predator metrics included pink salmon seasonality of occurrence, body size, stock-specific and brood-line specific abundance and timing, and interannual abundance and timing (Fig. 5A-D). Juvenile salmon migration timing is related to annual temperatures (Mortensen et al. 2000; Cooney et al. 2001; Taylor 2008; Krkošek et al. 2011). Over our study period from 1997-2012, the peak out-migration date of wild pink salmon fry from Auke Creek in northern SEAK varied annually by 26 days and was earlier in warm than in cold years (Fig. 4A). Similarly, adult pink salmon body size, run

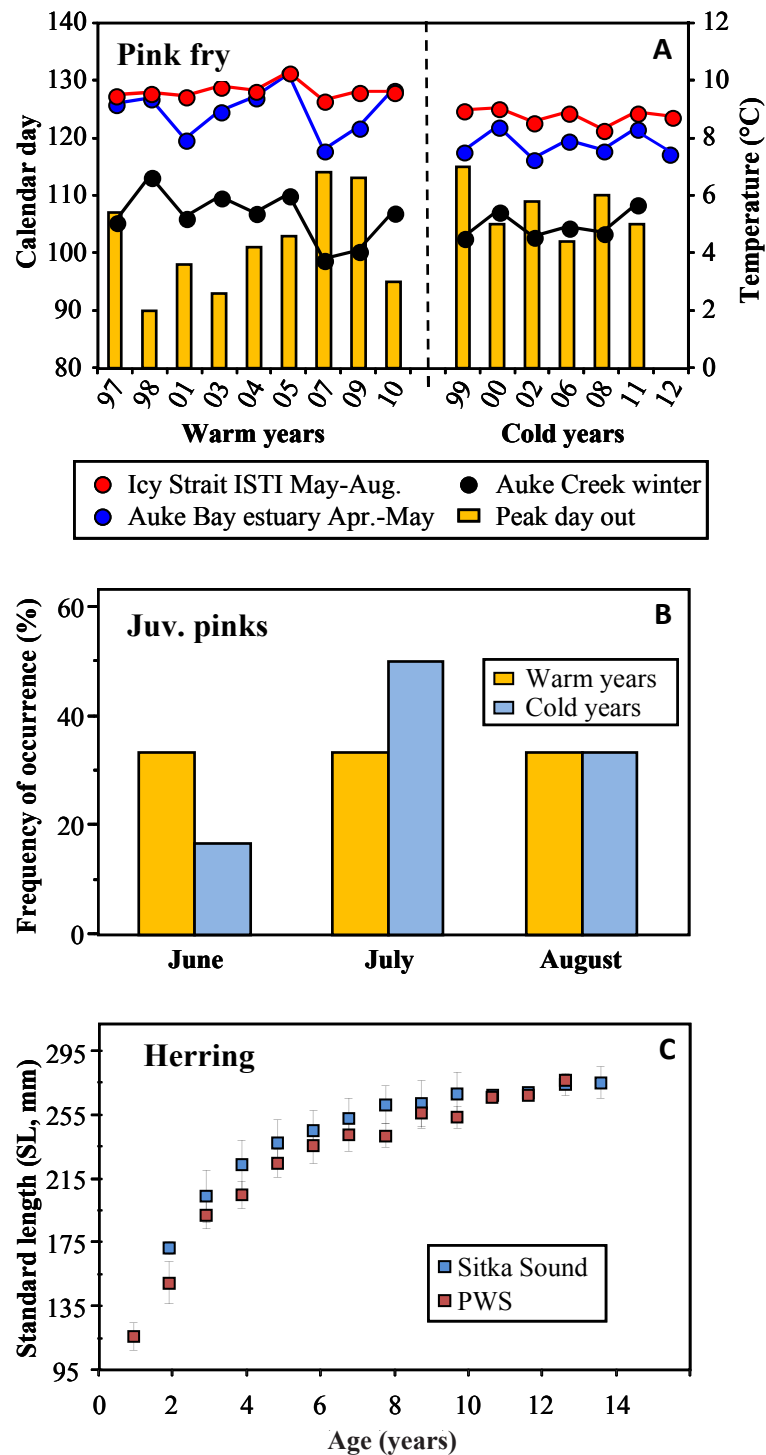


Fig. 4. Examples of climate-sensitive juvenile salmon and herring prey metrics that could impact predator-prey match-mismatch conditions. A. Temperature response of wild pink salmon fry peak out-migration timing (bars; data courtesy J. Joyce, NOAA) from Auke Creek by daily creek overwinter, daily estuarine surface in April-May, and Icy Strait ISTI temperatures (colored lines) for nine warm and seven cold years, 1997-2012. B. Shift in juvenile pink salmon month of peak abundance for warm vs. cold years in Icy Strait, 1997-2012. C. Pacific herring stock-specific size-at-age for Sitka Sound, Southeast Alaska (SEAK), and Prince William Sound (PWS; data courtesy D. Buetner, ADFG).

timing, and abundance varied between stocks and brood lines in SEAK and between years in Southwest PWS (Fig 5B-D). For SEAK, the northern SEAK stocks returning through the Icy Strait corridor arrive earlier than the central SEAK stocks that return using both northern and southern routes (Fig. 5C, D; Davidson and Vaughn 1941; Hoffman 1982). The Icy Strait corridor is also utilized by juveniles exiting from throughout SEAK (Orsi et al. 2012). Stock proportions using alternate routes could also vary with climate. For PWS, mixed-stock adult pink salmon bound for many locations return through the southwest entrance (Sharp et al. 1994), timing varies for early and late and odd-even brood lines (Helle 1964), and adults may intersect with multiple stocks of out-migrating fry (Willette 1996). Thus, the match-mismatch between these predators and prey could vary greatly between years and locations in response to potential climate effects on migration and timing traits (Durant et al. 2007; Chittenden et al. 2009).

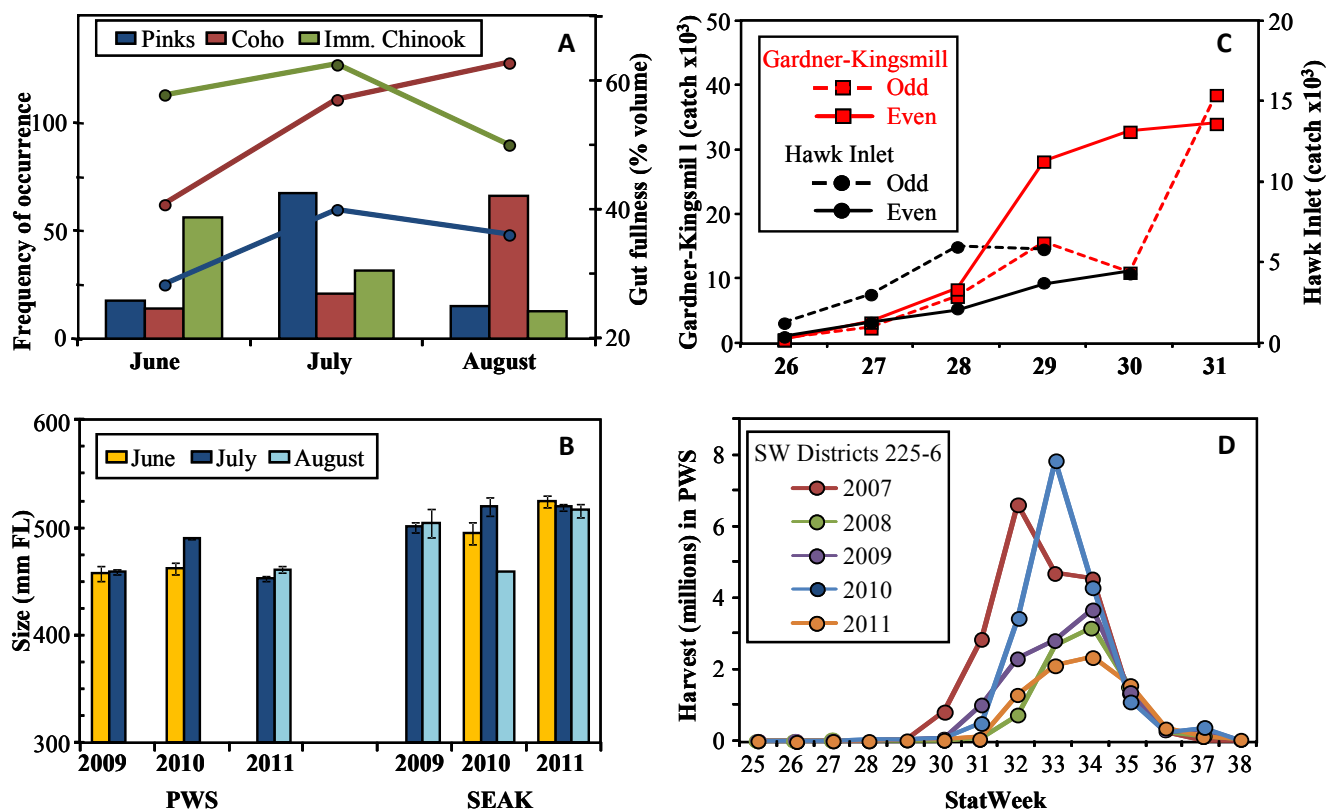


Fig. 5. Examples of climate-sensitive adult salmon predator metrics that could impact predator-prey match-mismatch conditions. A. Seasonality of adult pink and coho and immature Chinook salmon in Southeast Coastal Monitoring (SECM) project trawls in Icy Strait (percent monthly catch frequency, % FO [colored bars], and feeding intensity, % gut fullness [lines]). B. Size of adult pink salmon (FL, mm) between regions, months, and years in Prince William Sound (PWS) purse seine test fisheries (TF) alongshore and SECM trawls in 2009-2011 (size information not available for SEAK TF). C. Adult pink salmon run timing and abundance for stock-specific mean TF catches for odd-even brood lines in northern and central SEAK by statistical week (StatWeek 26 begins approximately 21 June; data courtesy D. Harris, ADFG) during the 16-year SECM time series, 1997-2012. D. Annual commercial harvests (millions of fish) in southwestern PWS, 2007-2011 (data courtesy S. Mofitt, ADFG).

Pink salmon lack of predation on herring in PWS in 2009 contrasted sharply with the intensive predation observed in 2010, suggesting that either predator or prey timing is a factor. Adult pink salmon timing was clearly later and abundance was clearly lower in 2009 commercial catches than in 2010 (Fig. 5D). Our catch data for adult pink salmon and juvenile pink salmon and herring from the June TFs in PWS allowed us to compare the co-occurrence of the early-returning adults with these prey in neritic waters (data not shown). Only 26% of these hauls caught adult pink salmon in 2009, whereas 48% of the hauls did in 2010. For prey species, only herring occurrence differed between the years (Cooney et al. 2001; Norcross et al. 2001; Willette 2008). Herring were present in 37% of hauls in 2009 compared to 91% of hauls in 2010, whereas juvenile pink salmon occurred in > 81% of these hauls in both years. Despite the consistent presence of juvenile salmon, predation on them occurred only at Chenega Point and Squirrel Bay in 2009 and at Shelter Bay in 2010; more herring were consumed at Herring Bay, Main Bay, Bainbridge Point, and Shelter Bay in 2010 (Fig. 1). Overlap of pink salmon adults with migrating

juvenile pink salmon and herring could extend into late summer (Cooney et al. 2001; Norcross et al. 2001; Moss et al. 2005), but we did not observe predation in August 2011 samples.

Our findings also indicate that coho predation on juvenile salmon in SEAK is climate-related, and occurs more often in cold years, when out-migration and peak abundance of juvenile pink salmon occurs later (Fig. 5A, B; Mortensen et al. 2000; Orsi et al. 2013a) and juvenile size is smaller (Fergusson et al. 2013). Juvenile size is correlated with estuarine and strait temperatures and with local river discharge (Beamish et al. 2012; Fergusson et al. 2013; Orsi et al. 2013a); their abundance is correlated with overwinter creek temperature and earlier outmigration (Orsi et al. 2013a). Thus, our predation data suggest that piscivorous coho salmon overlap more temporally with these small and late juvenile salmon in cold years than in warm years (Figs. 4B, 5A), or could indicate size-selectivity (Beacham 1986). All coho salmon predation on juvenile salmon occurred in July or August (one in September, sampled in only 5 of 16 years) on prey ranging in size from 95–195 mm FL.

Similarly, our observation of higher incidence of coho predation on herring in nine warm years vs. seven cold years suggests an effect of climate on timing (Cooney et al. 2001; Norcross et al. 2001). Predation on herring by coho salmon was most common during coho peak abundance in the strait in August. In contrast, predation on herring was most common for Chinook salmon in June and July, concurrent with Chinook salmon increasing size and departure from Icy Strait (Fig. 5A; Orsi et al. 2013b). However, for both of these predators, herring prey size ranged from young-of-the-year (YOY) to adults (60–260 mm FL) and overlapped with size of herring eaten by pink salmon in straits (60 mm maximum FL) and alongshore habitats (35–180 mm FL; average 113 mm). Aggregations of mixed-age herring are common throughout the water column in marine bays and corridors, but are spatially and temporally variable (Norcross et al. 2001; Csepp et al. 2011). Our data indicate mixed ages of herring are vulnerable to salmon predation (Fig. 5C) (Hebert 2012), but vulnerability was not clearly related to predator size. Instead, climate effects on timing and movement patterns determine whether predation occurs. We speculate that in warm years, earlier spawning by adult herring (Norcross et al. 2001; Tojo et al. 2008; Hebert 2011); higher survival, greater YOY abundance, or larger size (Norcross et al. 2001); earlier departure from nursery bays (Beamish et al. 2012); or different migration patterns and areas of concentration (Tojo et al. 2007) could induce greater spatial and temporal overlap of coho and other salmon predators with these prey (Willette 2008). These temperature/hydrography-related traits could be confounded with stock-specific and geographic differences in herring size (Fig. 4C), age of recruitment, and spawning time associated with latitude (Hay et al. 2008; Schweigert et al. 2010; Beamish et al. 2012; Hebert 2012). Thus, as climate effects are not spatially uniform across the North Pacific (Zheng 1996; Mueter et al. 2002; Hay et al. 2008), overlap of large salmon predators with herring prey could shift in different directions or variously affect age classes in discrete locations.

Salmon predation interactions could also differ geographically by region and among stocks through a climate effect on migration routes and feeding motivation (Dyagilev and Markevich 1979; Burgner 1980; Takagi et al. 1981; Kaev and Rudnev 2007; Tojo et al. 2007; Taylor 2008;). Continued feeding during the homing migration is influenced by climate-mediated size, ocean growth, and maturity (Ishida 1966; Dyagilev and Markevich 1979; Takagi et al. 1981; Morita and Fukuwaka 2007; Kaev 2012). The SEAK northern and southern stocks of pink salmon differ by odd-even dominance patterns (Fig. 5C), annual abundance (Fig. 5D), and timing. These brood-line dominance patterns in SEAK also coincided with climate differences because seven of nine odd-year broods returned in warm years, and five of seven even-year broods returned in cold years (Fig. 5C). Odd- and even-year brood line maturation times can differ by 2–3 weeks (Davidson and Vaughn 1941; Dyagilev and Markevich 1979). Coupled with a 2–3 week difference in timing of peak abundance (Fig. 5C), this range in maturation timing suggests that feeding motivation may be reduced for late arriving adults during any remaining period of overlap with migrating prey (Fig. 4A,B), thus reducing predation potential.

A final way that climate could affect stock-specific pink salmon predation is through the length of the migration corridor from the Gulf of Alaska (GOA) to natal sites. In PWS, for example, the corridor length determines the duration of out-migrant vulnerability to predation inside PWS and the duration of adult feeding upon return to PWS (Fig. 1; Ishida 1966). We observed from recovery of otolith marks that ten pink salmon predators on juvenile salmon and herring originated from the most distant enhancement facility, Solomon Gulch Hatchery (SGH); two additional predators originated from the Armin F. Koenig (AFK) hatchery near the southwest entrance to the sound and six were unmarked wild fish. The high percentage of predators from SGH could indicate both earlier return timing and longer continued feeding after entering southwestern PWS than stocks with closer natal sites (Davidson et al. 1943; Takagi 1981). Overall, 1/3 of adult pink salmon consuming juvenile pink salmon and herring were wild fish. Their salmon prey originated from four different hatcheries, and no wild salmon prey was identified. Predation on multiple salmon stocks in southwestern PWS confirmed a common route of out-migration from the sound (Willette 2008), while lack of salmon prey originating from AFK suggests limited predation vulnerability of that stock inside the sound. This difference in juvenile salmon stock vulnerability to predation is supported by higher rates of survival for hatchery stocks released closer to the exit from PWS (Moss et al. 2005; Heard and Wertheimer 2012). We have no information on the effects of residency or feeding duration on predation impact.

Our study provides new information on sources and consistency of predation on juvenile salmon and herring during the final life history stage of homing larger salmon. We conclude that adult pink salmon predation impacts juvenile salmon minimally, but may locally impact herring in some years. We identified a warm-versus-cold year climate effect on coho salmon predation rates, but limited data prevented such a conclusion for pink salmon. Interacting climate effects could determine the spatial and temporal overlap between salmon predators and their prey. Thus the degree of cannibalism and predation on herring by larger salmon depends on their phenology, timing, movements, migration patterns, and feeding motivation. Time series such as ours will be important for apportioning climate effects on regional differences in predation (Mueter et al. 2002; Hay et al. 2008; Schweigert et al. 2010; Healey 2011; Beamish et al. 2012) in the midst of changing ecosystem dynamics and salmon behavior.

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Are Smolts Healthier in Years of Good Ocean Productivity?

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Keywords: microarray, functional genomics, salmon, smolts, infectious, disease, health

Pacific salmon entering the Strait of Georgia in British Columbia (BC) experience profound annual variance in ocean survival. Ocean productivity in the early marine environment is hypothesized to be a key driver of this variation, with other biological stressors such as harmful algal blooms (HABs) and pathogens potentially acting as secondary factors. The question is what do we really know about the cumulative nature of these stressors on the health of salmon? We have developed a program that applies genomic technologies to assess the health and condition of out-migrating smolts and the biological agents to which they are exposed. Additional metrics associated with growth, feeding, energy, hormones, and ion regulation are also collected. These studies not only reveal the variance in salmon condition within and between years, environments, stocks, and species, but can be used to discover the key stressors that may impact salmon performance.

Extensive sampling programs were initiated in 2008 to support this research program, starting with sampling at natal rearing areas in the Fraser River and involving extensive ocean sampling over the first 6-9 months of ocean residence for sockeye, Chinook, and coho salmon. Our collections have included sampling of smolts over an area up to 2,000 km of migration. Individual genetic stock identification has been applied to each fish so that genomic assessments can track the physiological progression of individual stocks over time and space. Contrasts in the physiological variation among stocks, species, hatchery versus wild fish, life-history types, environments, seasons, and years were of interest. Variations associated with growth (IGF-I was used as a measure of instantaneous growth), size, hematocrit values, and other variables were measured (Fig. 1). Importantly, we were also interested in the elucidation of physiological variation among fish using approaches such as principle components analysis to identify the major physiological trajectories in the data (that may or may not correlate with measured variables) to contrast levels of variation between environments and years of good and poor ocean productivity.

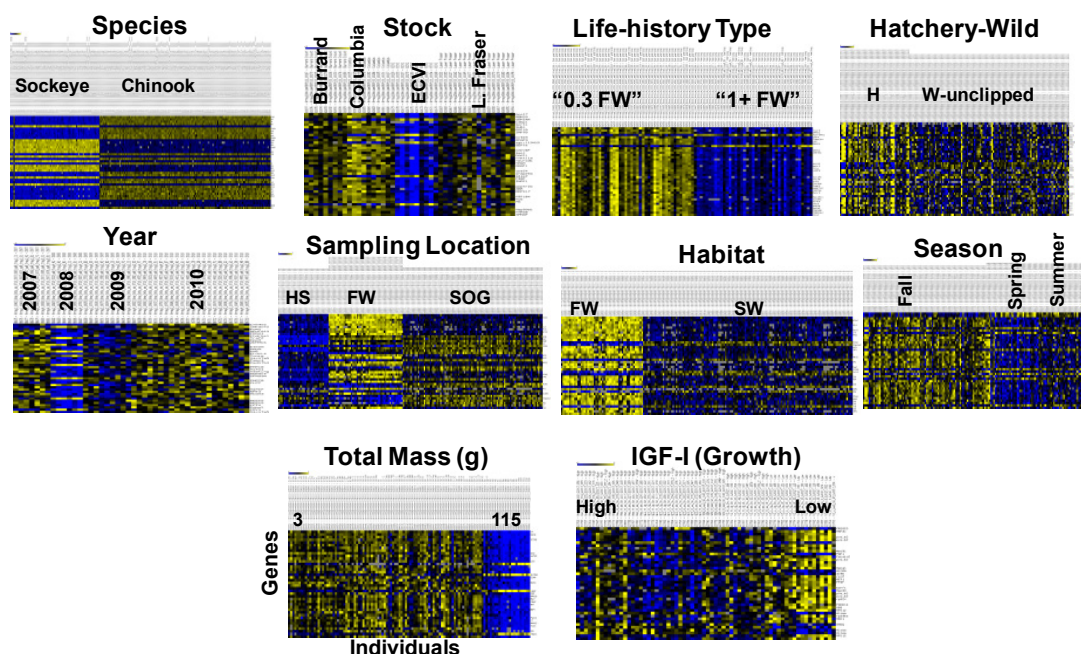


Fig. 1. Heatmaps showing gene expression signatures associated with specific measured variables of interest. Genes are differentiated on the y-axis, individuals on the x-axis, with up-regulated genes in yellow and down-regulated genes in blue. In each heatmap, the top 100 differentially regulated genes are shown.

In our functional genomics studies, microarrays, which are slides that have printed on their surface tens of thousands of salmon gene probes, were applied to assess the activity of the genes in each of four key tissues: brain, liver, gill and white muscle. As the expression (transcription) of genes to make proteins depends upon the physiological function of a given tissue, by surveying multiple tissues with distinct functions we are able to gain a snapshot of the genome-wide physiology of the fish.

Activity of genes expressed in the brain is important for controlling a wide range of behavioural and physiological processes. The most profound shift in the brain transcriptome (expressed genes) over migration occurred in the fall in all three species assessed (sockeye, coho, and Chinook salmon). The signature observed in Chinook and coho salmon showed strong loading of the same genes, suggesting a high functional correlation in these two species. Moreover, this shift was even stronger, and perhaps earlier in hatchery coho than wild coho salmon. Among the most affected physiological processes was the histamine H2 receptor mediated signaling pathway, which was highly up-regulated in the fall. In mammals, this pathway controls feeding and motor activity. Given that we know many Chinook and coho salmon stocks maintain residence in the Strait of Georgia during the summer and begin migrating northward in the fall, we hypothesize that this signature could relate to a signal for continued migration. If this were the case, our data may suggest that hatchery fish may undergo this behavioural migratory shift earlier than wild fish, a hypothesis we plan to test in future.

There is a growing body of literature that suggests that survival of hatchery fish in the early marine environment is lower than that of wild fish, especially when environmental conditions are stressful (e.g. poor ocean productivity; Beamish et al. 2012). If this were the case, we would expect that hatchery fish may retain a degree of physiological distinction from wild fish in the common ocean rearing environment, or at least may respond to environmental stressors differently. Our studies show that while hatchery fish do not remain phenotypically distinct from wild fish, brain and liver profiles show strong differentiation in prevalence of common signatures. Given the functions of these tissues, these data suggest that behavior, metabolism, and feeding may be the most differentially affected processes between hatchery and wild fish.

One of the most important questions we were interested in addressing was the variance in physiology associated with years of good and poor ocean productivity. We were fortunate to sample at least a small number of sockeye smolts leaving the Fraser River in 2007, a year-class that was associated with the lowest returns in over 75 years and resulted in the formation of the Cohen Commission of Inquiry. More extensive sampling was conducted in 2008, an out-migrant year-class that brought back record numbers of sockeye salmon to the Fraser River. We contrasted annual variation in gene expression in all four tissues from 2007 through 2010 (and 2011 for brain) and found that the two out-migrant years with the lowest (2007) and highest (2008) returns were the most physiologically distinct across multiple tissues collected from fish in the ocean. Importantly, this distinction was not limited to the marine environment. Gill tissue collected from migrating smolts in freshwater in 2007 showed the highest variance of all, with a powerful signature associated with differential signaling of immune cells of the gill that affected all sampled Chilko smolts, but the signature was absent six weeks later when the smolts were in the ocean (Fig. 2). This same signature was observed only sporadically in other years, and in sockeye and coho salmon sampled both in the freshwater and marine environments. Contrasts between 2007 and 2008 fish in freshwater and saltwater across multiple tissues revealed that annual variances in gene expression in fish collected from freshwater were often times as great as those observed in fish in the marine environment. Similar patterns of freshwater and saltwater variance across years were observed in coho salmon. These data suggest that the potential for conditional difference among fish entering the ocean should not be discounted as a factor that could undermine the ability of salmon smolts to adapt and respond effectively to stressors in the marine environment.

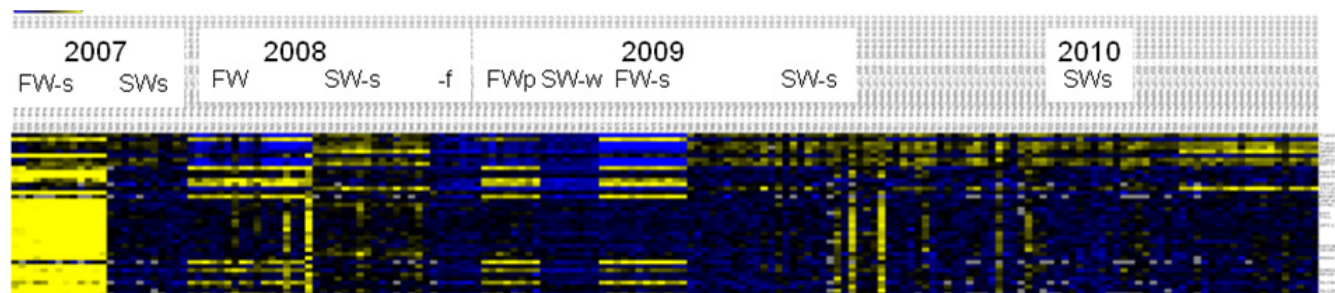


Fig. 2. Heatmap showing the top 100 genes significantly associated with annual variance in gill tissue of sockeye salmon. Note that 2007 fish in freshwater (FW) were highly distinctive from all other years and freshwater samples, as well as the 2007 samples taken in saltwater (SW) six weeks later.

As a whole, the genomic data indicated a poor conditional state of the 2007 out-migrant year-class from the Fraser River, with signs of enhanced anti-viral activity, immunosuppression, hypoxia (potential for harmful algal bloom exposure in the ocean), unusual osmoregulatory shifts in freshwater (potentially prepared for freshwater too early), and signatures in liver and muscle consistent with poor feeding and growth, but not outright starvation.

Chinook salmon populations that migrate to the ocean as yearlings are generally experiencing lower productivity than sub-yearling stocks. Genomic profiling showed that unlike hatchery and wild fish, yearling and sub-yearling smolts are highly distinctive well into ocean residence and across brain, liver and muscle tissues. Brain profiles were consistent with potential differences in feeding behavior, stress response, motility-activity, emotional reactivity, regulation of pain sensation, and learning. In fact, one of the most differentially-affected signaling pathways was that of endogenous cannabinoid signaling, which was highly stimulated in yearling stocks in the ocean. In mammals, this pathway is the same as that stimulated by exogenous cannabis intake, with profound effects on feeding, stress, and pain thresholds. Finally, and perhaps most importantly, annual variance within seasons was almost exclusively observed in yearling populations, consistent with the hypothesis that the yearling life history type is more susceptible to or possibly more exposed to environmental stressors.

Differential immune stimulation was commonly observed among the principal components explaining the highest sources of variation between co-migrating salmon in contrasts between years or stocks with low and high productivity and in adults dying prematurely in the river. We hypothesize that some of these signals may be associated with infectious diseases. To test this hypothesis, we began undertaking research aimed to identify which profiles may be associated with infectious agents. We first conducted a small suite of quantitative PCR analyses using published assays to known infectious agents to elucidate infectious agents associated with key profiles. Using this approach, we found that one signature profoundly affecting fish in the marine environment was associated with the presence and load of a gill microsporidian parasite, *Paranucleospora theridion*. This parasite, associated with proliferative gill disease in Europe, is known to be transmitted through sea lice, but was only recently identified in BC (Nylund et al. 2011; Jones et al. 2012). By combining acoustic tracking and genomic profiling, we also identified an association between infection with IHNv, a virus endemic to BC, and down-stream migration mortality. A strong interferon-type response was also correlated with load of this virus and with fate of fish in the river. Finally, we identified the piscine reovirus (PRV) in both Chinook and sockeye salmon, with virus load increasing in the fall and winter months. Unfortunately, this virus was not prevalent enough in individuals from our microarray studies to identify a unique genomic signature using existing arrays.

We also undertook next generation sequencing to determine if there were any novel viruses associated with our genomic signatures. We obtained a full genome sequence of a novel salmon parvovirus—the first parvovirus to be identified in a fish species. This virus is present in a high load in sockeye salmon smolts migrating to the ocean, with load and prevalence generally declining from summer to fall in the ocean. Prevalence of this virus varies greatly among stocks and years, but we do not yet have data to determine whether it is associated with disease. A full genome sequence of the PRV in BC salmon was also uncovered through next generation sequencing. The PRV was not previously known to be present in BC, and it is suspected to be causative of heart and skeletal muscle inflammatory (HSMI) syndrome in Europe (Palacios et al. 2010). Associations with disease in BC are unknown.

Recently, we have embarked on a new project that aims to develop and validate a high-throughput microfluidics platform to simultaneously conduct quantitative analysis of 45 microbes across 96 samples. Once developed, this platform will be applied across thousands of fish to determine what microbes associated with salmon diseases worldwide are carried by BC salmon. We anticipate retrospective mining of microarray data will facilitate the identification of genomic signatures correlated with the loads of specific microbes, information that could be used to assess their potential to associate with tissue damage and disease. With this approach, we will continue to determine which signatures that we have already identified as showing strong differential immune stimulation may be associated with infectious diseases. Ultimately, by merging data from gene expression profiling, physiological biomarker monitoring (for stress hormones, growth, osmoregulation, and energy), and quantitative microbe assays, we can elucidate patterns of microbe exposure and response across environments, seasons, stocks, species, and life-history types, and the interactions between microbe exposure and signatures potentially associated with differences in feeding, growth, and behaviour. This will allow us to begin to assess cumulative impacts of infectious disease and other stressors on performance of wild salmon in the ocean.

We show that in some years, smolt condition can be compromised before they enter the ocean, potentially exacerbating their ability to survive the additional stressors encountered when ocean feeding conditions are poor. In the marine environment, the condition of salmon is highly divergent between extreme years of good and poor ocean productivity. We show that wild and hatchery salmon are exposed to and potentially impacted by HABs in some years. Finally, we find that differential immune stimulation is a key driver of many of the most powerful conditional signatures both within and between years and hypothesize that at least some of these are in response to infectious agents. Preliminary data from a new microbe surveillance program is revealing a broad range of infectious agents carried by smolts in the ocean, some of which are present in high load and associated with strong immune stimulation in the early marine environment, and some decrease precipitously over time. We hypothesize that biological stressors may be less tolerated and associated with higher levels of mortality in years of poor ocean productivity.

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Potential Mechanisms of Ocean Mortality of Juvenile Salmon and Steelhead Due to Ingestion of Plastic Marine Debris

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Keywords: ingestion, juvenile, mechanisms, mortality, plastic marine debris, salmon, steelhead

Is man-made plastic debris a potential cause of ocean mortality of juvenile salmon and steelhead? Plastic debris is a well-known and increasing pollution problem, affecting aquatic food webs worldwide (Derraik 2002). Decomposing plastic debris can leach potentially toxic chemicals such as BPA (bisphenol A), PCBs (polychlorinated biphenyls), and derivatives of polystyrene (Teuten et al. 2009). Plastic debris can also absorb organic pollutants from seawater, e.g., PCBs, DDT (dichlorodiphenyltrichloroethane), and PAHs (polycyclic aromatic hydrocarbons) (Teuten et al. 2009). Chemicals leached and absorbed by plastic debris can bioaccumulate in fish, and anadromous fish can transport these chemicals back to freshwater habitats (Ewald et al. 1998). Some chemicals leached from plastics, e.g., BPA, mimic estrogen, causing endocrine disruption and reproductive effects such as inhibition of testicular growth (Kang et al. 2007). Surfactants used in plastics can also disrupt pituitary functions in fish, thus affecting their ability to osmoregulate (Björnsson et al. 2011). In this paper we reviewed what is known about the ingestion of plastic debris by Pacific salmon and steelhead, presented field data on ingestion of plastic by salmon and steelhead in international waters (high seas) of the North Pacific Ocean and Bering Sea, and discussed potential mechanisms of ocean mortality of juvenile salmon and steelhead due to ingestion of plastic debris. To our knowledge, this issue has never been the focus of directed marine studies on salmon and steelhead, and all available field data were collected incidental to other research. Analyses of available time-series (1990s-2000s) of high-seas food habits data indicated that salmon and steelhead consume a variety of types and forms of plastic, e.g. pellets, foam, sheets (Fig. 1). The occurrence of plastic debris in stomach contents varied by species, age and maturity group, time, and area.

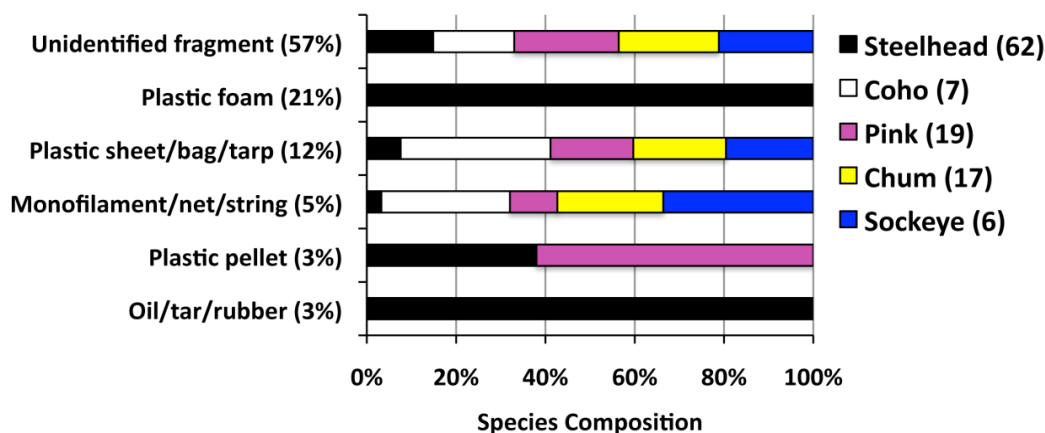


Fig. 1. Percent frequency of occurrence of different types of plastic in the stomach contents of Pacific salmon and steelhead for available time-series (1990s-2000s) of high-seas food habits data. Species key shows sample size (number of fish).

Potential mechanisms of marine mortality of juvenile salmon and steelhead due to ingestion of marine plastic debris may be direct, e.g., lethal mechanical injury or toxicity, or delayed, e.g., heritable alterations in gene expression (epigenetic) affecting early marine survival of progeny (Fig. 2). Our results emphasize the need for directed field and laboratory process studies on this important issue.

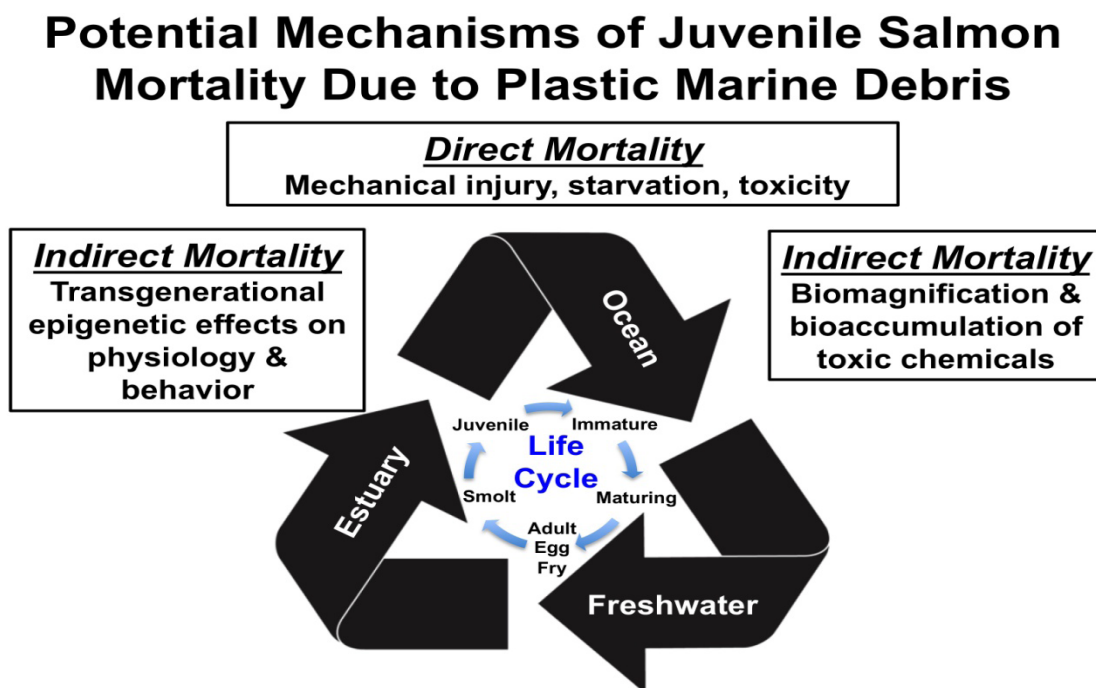


Fig. 2. Potential mechanisms of juvenile salmon mortality due to plastic marine debris.

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Using Bayesian Networks to Link Climate Variability, Ocean Processes, and Coho Salmon Marine Survival

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Keywords: Bayesian networks, climate, coho salmon, marine survival

We used Bayesian networks, which are a class of graphical probabilistic models, to examine the effects of the marine environment on coho salmon survival in the northern California Current region. This novel method extends previous research by (1) explicitly accounting for uncertainties in the links between large-scale climate patterns and salmon survival, (2) explicitly and intuitively representing the ecological causal network that underlies variability in salmon survival, and (3) explicitly accounting for indirect effects of climate and ocean processes on salmon survival. Our results indicated that large-scale climate patterns, such as the Pacific Decadal Oscillation and North Pacific Gyre Oscillation, can have a strong influence on the physical and biological components of the ecosystem, however, the uncertainties tended to increase as you moved further down the casual chains within the network. In general, this propagation of uncertainties within the network dampened the effect of large-scale climate patterns on coho salmon survival in the northern California Current region.

Ecological Predictors of Marine Survival for Coho Salmon in Washington State

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Keywords: coho salmon, marine survival, ecological indicator, spatial scale, Washington State

Annual marine survival rates of coho salmon can vary by an order of magnitude, resulting in a challenge for fishery management in the Pacific Northwest. In Washington State, run size forecasts rely on predictions of marine survival. Hatchery coho run sizes are predicted from recent-year average marine survival rates, and wild coho salmon run sizes have been predicted from historical average ratios of jack (age-2) to adult (age-3) returns. A framework is needed to expand wild coho salmon marine survival predictions to non-monitored systems where jack returns are unknown. In addition, the correlation between jack and adult returns has degraded in recent years requiring further exploration of factors useful for predicting coho salmon marine survival.

The goal of this study is to improve understanding of the marine ecological factors that explain coho salmon marine survival. Our approach considers the marine environment to be heterogeneous at different scales. For example, previous studies suggest that the combination of coastwide (Hare et al. 1999), regional (Beetz 2009), and local (Babson et al. 2006; Moore et al. 2008) scales should contribute to the marine ecology of salmon in general. In this study, we first identify the appropriate spatial scale for explaining trends in Washington State coho salmon stocks and then ask what ecological indicators and scale are the best predictors of marine survival.

We included a total of 17 hatchery and 8 wild coho salmon stocks. Stocks were geographically representative of three major regions in Washington State—Puget Sound, Coastal Washington, and the Lower Columbia River. Marine survival (pre-fishing) was estimated from releases and recoveries of coded-wire tagged hatchery and wild coho salmon for the 1983 to 2011 return years. Hatchery and wild coho survival in the same basin were considered separately because, although they were generally correlated, correlations differed from a slope of one suggesting that wild coho salmon were better able to take advantage of good marine conditions.

A correlation matrix of stock-specific marine survival supported the regional distinctiveness of Puget Sound, Coastal Washington, and Lower Columbia stocks, which was consistent with a previous study that included a subset of these stocks (Beetz 2009). Within the Puget Sound region, marine survival was not synchronous across the oceanographic sub-basins for either hatchery or wild coho salmon. We considered Puget Sound sub-basins (North Sound, Whidbey Basin, Central Sound, South Sound, Hood Canal, and Juan de Fuca) to be the appropriate scale to investigate factors contributing to marine survival. Within the Coastal Washington region, marine survival was not synchronous between north-coast and south-coast stocks. We concluded that the appropriate scale for coho salmon stocks on the Washington Coast was a division between the south coast (Grays Harbor to Willapa River) and the north coast (Quillayute River to Quinault River). Within the Lower Columbia region, coho salmon marine survival was well correlated among stocks and we considered a single average marine survival to be representative of fish from this region.

We selected indicators at three spatial scales. Atmospheric indicators were representative of global climate of the North Pacific. Regional indicators represented marine productivity in the areas of interest (coastal shelf for Lower Columbia and Washington Coast and Strait of Juan de Fuca for Puget Sound). Local indicators were associated with the smolt transition between freshwater and the immediate marine environment. Ecological indicator data were provided by a number of long-term monitoring studies (see Acknowledgments). Multiple linear regression was used to test the contribution of each indicator variable to coho salmon marine survival. An Akaike information criterion (AIC) model selection process was used to determine which combination of indicators best explained the marine survival data. The relative weight was calculated for each indicator using models with a cumulative AIC weight of 0.95.

The best models explained between 12 and 83% of the variation in coho salmon marine survival. The selected indicators did not significantly predict survival in two areas (Central Sound wild- and South Sound hatchery-origin fish). These results should improve forecasts over current methods; however, predictions of marine survival for some stocks still involve considerable uncertainty. Ecological indicators from all spatial scales were included in the best-fit models. Results for the Lower Columbia indicated regional and local indicators had higher relative weights than atmospheric indicators, and indicators for hatchery and wild coho salmon differed from each other. In the coastal Washington model, atmospheric indicators had a high relative weight for the wild coho, whereas regional indicators had the highest relative weight for hatchery coho salmon. Indicators also differed between north- and south-coast hatchery coho salmon that was consistent

with the survival trends between these areas. In the model for Puget Sound, regional and local indicators had higher relative weights than atmospheric indicators across all sub-basins, with the exception that the regional indicators selected were not good predictors of North Sound hatchery coho salmon survival. Prediction of North Sound coho salmon survival might be improved by selecting a regional productivity indicator from the Strait of Georgia. The relative weights of the selected indicators differed among Puget Sound sub-basins and between wild and hatchery coho salmon from the same sub-basin, which was consistent with the different survival trends observed by area and origin.

In conclusion, marine survival of coho salmon stocks in Washington State is best understood by variation at a fairly localized scale (river mouth distances 50 to 140 km), which suggests that local factors (either freshwater or marine) are making a substantial contribution to cumulative marine survival over the 18-month ocean residency of coho salmon.

Acknowledgments—We thank the people who have put long hours of labor and thought into the long-term data sets used for this study. The Washington wild coho salmon research program was initiated by Dave Seiler and Washington Department of Fish and Wildlife (WDFW) in 1978. Coho salmon coded-wire tag data were available due to a coast-wide effort among US and Canadian management agencies. Ecological indicators were made possible due to the information provided by the Northwest Fisheries Science Center Ecosystem Indicator Research Program (B. Peterson). Bakun upwelling indices were derived by the Pacific Fisheries Environmental Laboratory. Puget Sound environmental data were made available by the Washington Department of Ecology Marine Waters Monitoring Program. Stream flow data were made available by the United State Geological Survey. Jeff Haymes (WDFW) provided guidance on the use of hatchery coho salmon coded-wire tag datasets.

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Beyond the Estuary: An Extension of the Nomad Life History Strategy in Coho Salmon

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Keywords: coho salmon, nomad, estuary, marine, rearing, growth, life history, otolith, micro-chemistry, Southeast Alaska

Displaced coho salmon fry known as “nomads” (Chapman 1962) enter estuaries and saltwater where early observers assumed they perished without contributing to the adult population (Chapman 1966; Crone and Bond 1976). However, a substantial body of evidence, summarized by Koski (2009), indicates that many nomads likely survive and grow in the estuary, returning to overwinter before migrating as smolts the following spring. Recorded movement of coded-wire tagged fish among streams separated by saltwater distances of 56–113 km in Lynn Canal and Stephens Passage, Southeast Alaska (Table 1) indicates that presmolts are able to overcome osmoregulatory challenges to achieve much to their growth in marine as well as estuarine waters before they re-enter freshwater in the fall to overwinter and move to the sea in the spring. Of a total of 13 recovered tags, two were from fish migrating upstream in Auke Creek in fall (September–October). The other tagged fish were captured in downstream migrant smolt traps in the spring, including 10 fish from the Berners River and one from Jordan Creek (Lum and Glynn 2007; Table 1).

Table 1. Inter-system movement of tagged presmolt coho salmon in Lynn Canal and Stephens Passage, Southeast Alaska, showing minimum saltwater distances traveled.

Number Recovered	Tagging Location	Tagging Date(s)	Recovery Location	Recovery Date(s)	Recovery Fork Length (mm)	Distance (km)
1	Berners R.	June 22–30, 1988	Auke Cr.	October 11, 1988	125	56
1	Chilkat R.	April 7–June 2, 1999	Berners R.	May 17, 2000	126	67
1	Chilkat R.	June 1–6, 1999	Berners R.	May 26, 2000	127	67
1	Chilkat R.	May 12–29, 2004	Auke Cr.	September 10, 2004	147	109
1	Chilkat R.	May 14–22, 2001	Jordan Cr.	May 13, 2002	—	113
8	Burro Cr. Hatchery	June 13, 2000	Berners R.	May 11–29, 2001	114–142	90

Otoliths from 11 of the fish listed in Table 1, including all 10 fish recovered from the Berners River and one fish from Jordan Creek (Lum and Glynn 2007), were microprobed along a transect from the primordium to the otolith margin to measure the Sr:Ca ratio, an indicator of exposure to freshwater, estuarine, and saltwater habitats (Campana 1999; Zimmerman 2005). Features evident in the growth history of the otolith were matched with the microprobe transect to pinpoint transitional movement between habitats. All of the samples showed elevated Sr:Ca ratios, marking the fish’s exposure to estuarine and marine waters of Lynn Canal and Stephens Passage prior to smolting. However, one of the two wild Chilkat-Berners migrants was of particular interest because it displayed evidence of extended exposure to saline water during two periods, comprising 36% and 15%, respectively, of the smolt’s total growth history as indicated by the distance from the primordium to the margin of the otolith (Fig. 1). A check was evident at emergence, with an apparent winter annulus appearing at the point where the Sr:Ca ratio began to decline in fall 1998, indicating a return to freshwater prior to initial capture and tagging in a section of the Chilkat River 5–26 km upstream from the mouth in spring 1999 (Ericksen 2001). A second marine-rearing period marked by an elevated Sr:Ca ratio is evident as the fish moved 67 km across Lynn Canal before swimming 8 km up the Berners River, where it was captured in May 2000 as a 126 mm migrant in a beaver pond. This was the only sample that displayed evidence of early departure from the river as a typical “nomad” fry, as defined by Chapman (1962), while otolith transects from the other fish indicated exposure to marine waters only after they were tagged as age-1 presmolts during the second spring period after emergence.

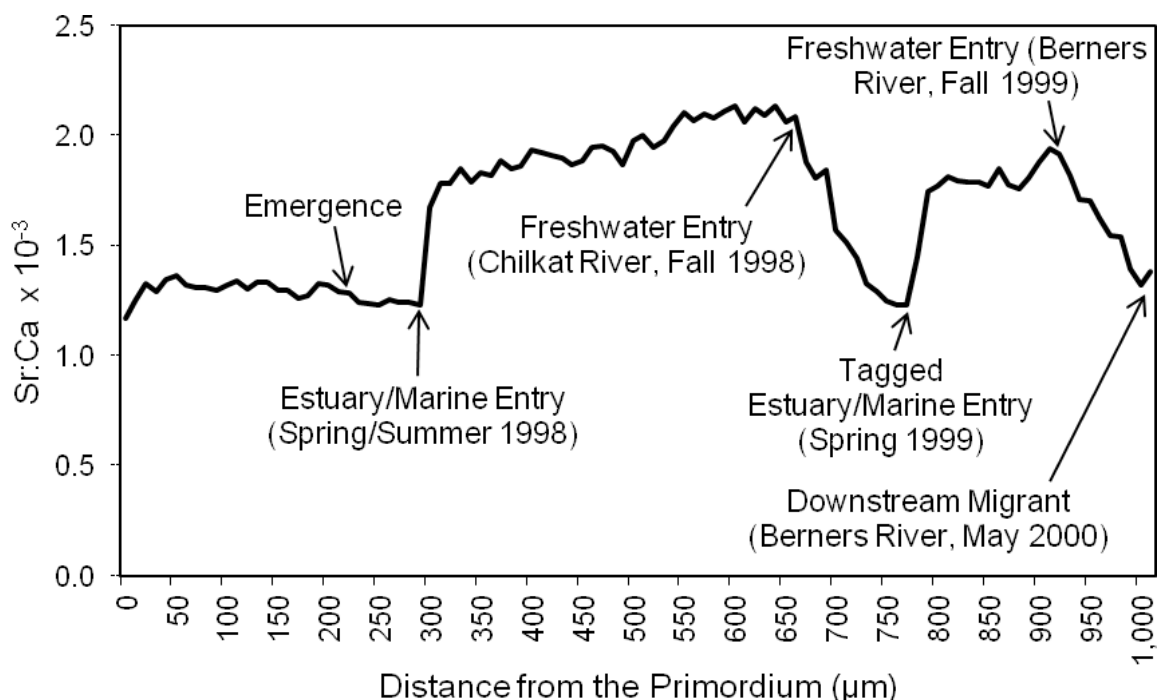


Fig. 1. Changes in the Sr:Ca ratio measured across an otolith from a coho salmon tagged in the Chilkat River between April 7 and June 2, 1999 (Ericksen 2001) and recaptured from the Berners River at a length of 126 mm on May 17, 2000.

In addition to freshwater, there is evidence that some juvenile coho salmon in Alaska over-winter in estuarine habitat (Hoem Neher 2012). An otolith Sr:Ca transect from a fish tagged in the Chilkat River in May 2001 (Ericksen 2003) and captured the following May in a downstream migrant trap located on Jordan Creek, situated at the margin of the estuarine Mendenhall wetlands (Lum and Glynn 2007), shows evidence of overwinter exposure to brackish water until just prior to capture (Fig. 2; Table 1).

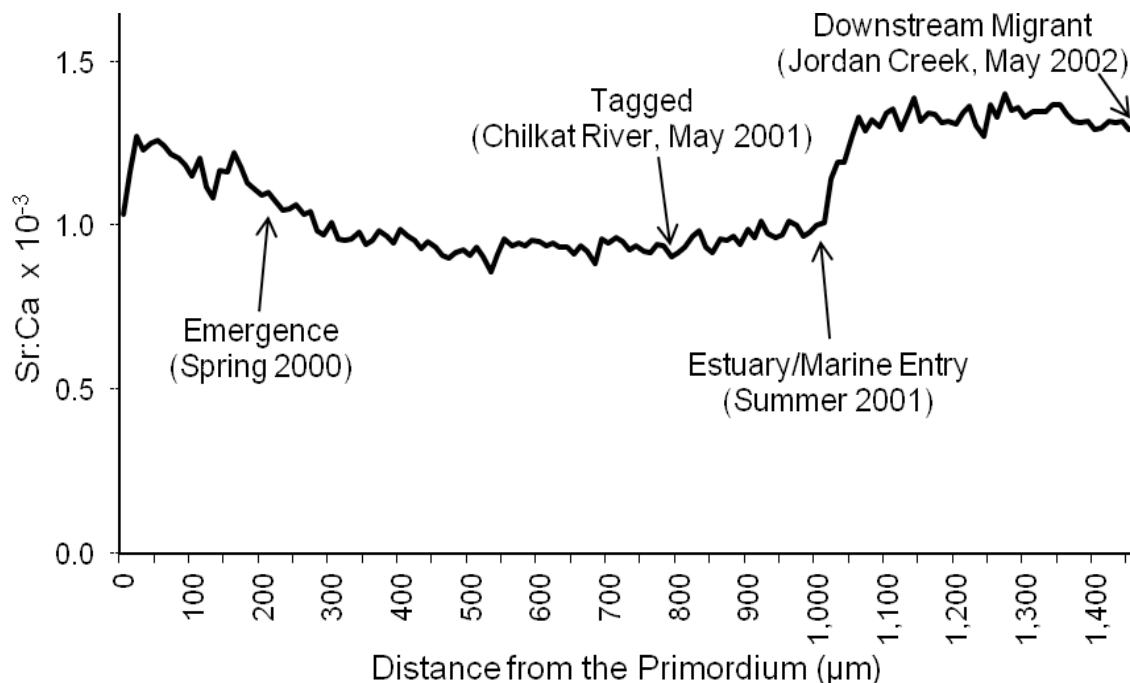


Fig. 2. Changes in the Sr:Ca ratio measured across an otolith from a coho salmon tagged in the Chilkat River between May 14 and May 23, 2001 (Ericksen 2003) and recaptured from Jordan Creek on May 13, 2002 (Lum and Glynn 2007).

Although seldom documented, a fall upstream migration of immature coho salmon juveniles returning to streams from estuaries and marine waters appears to be a common occurrence in Southeast Alaska. These migrations begin as early as mid-summer, peak from mid-September to mid-October during the return of adult spawners, and can continue at least until early November (Harding 1993; Shaul et al. 2011). Harding (1993) found fall immigrants varied widely in fork length from 38 to 235 mm (average 83 mm) with most resembling migrating smolts in color and some with attached sea lice (*Caligus* spp.), suggesting recent immigration from marine water. Several of the largest immigrants (> 200 mm) were dissected and confirmed not to be precocious males. The weir at Auke Creek was modified to capture small immigrants during four years (Taylor and Lum 2003, 2004, 2005; Taylor 2006). Minimum seasonal counts (through late-October) of immigrant juveniles comprised 12.5%, 6.8%, 2.1%, and 6.8% (average 7.0%), respectively, of subsequent downstream smolt migrations from the system the following spring (Taylor and Lum 2004, 2005; Taylor 2006, 2007; Shaul et al. 2011).

Do nomadic juveniles that overwinter in distant freshwater systems and estuaries imprint on the streams from which they eventually smolt, or do they return to spawn in their natal stream? The latter possibility is supported by recovery of four adult spawners in the Chilkat River that had been tagged in the Berners River (3) and Jordan Creek (1) and had moved in the opposite direction between the smolt and adult stages. These recoveries were compared with four fish tagged as apparent presmolts in the Chilkat River that were later recaptured as smolts migrating from the Berners River (2) and Jordan Creek (1) and as a fall immigrant into Auke Creek (Shaul et al. 2011; Table 1). Although imprinting is commonly associated with the parr-smolt transformation, a surge in production of plasma thyroxine associated with imprinting has also been documented in coho salmon during earlier stages involving migration (Dittman et al. 1996), supporting the possibility of imprinting on a natal stream despite subsequent prolonged exposure to a non-natal water source prior to smolting.

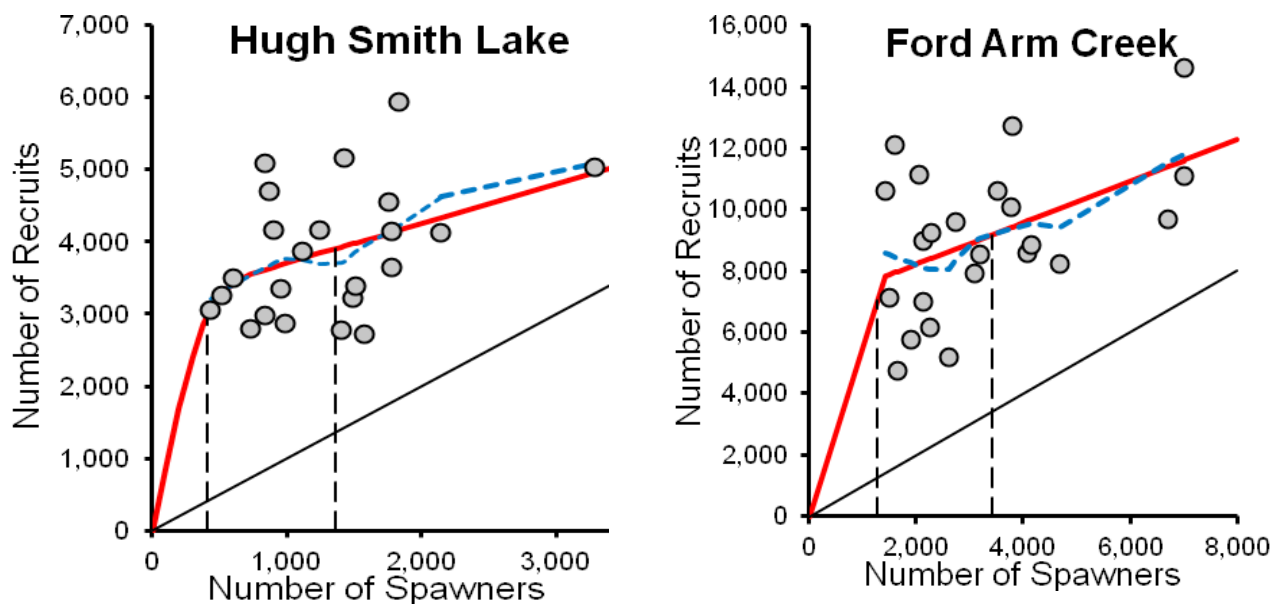


Fig. 3. Bent hockey stock (BHS) spawner–recruit relationships for Hugh Smith Lake coho (1982–2004 brood years) and Ford Arm Lake coho salmon (1982, 1983, and 1985–2005 brood years) showing a 0.75 LOESS trend (blue dashed line), the replacement line (black solid), and the escapement range estimated to produce 90% or more of maximum sustained yield (black dashed lines).

The marine-rearing strategy allows fish that are surplus to the summer carrying capacity of freshwater habitat to attain a high growth rate on estuarine and marine food resources (Murphy et al. 1984; Tschaplinski 1988) before returning in the fall to suitable overwintering habitat. Although estuarine and marine waters present osmoregulatory challenges and increased predation risk, growth and survival in those environments appears to be far less compensatory than in freshwater (Tschaplinski 1988). The successful contribution by nomads to coho salmon smolt and adult populations provides a plausible explanation for the significant positive linear slope observed in the spawner–recruit relationships (parent escapement versus smolts \times average marine survival) for Southeast Alaska coho populations in Hugh Smith Lake (slope = 0.60, $p = 0.04$) and Ford Arm Creek (slope = 0.68, $p = 0.02$; Fig 3). We propose a modification to the logistic hockey stick (LHS) model (Barrowman and Myers 2000; Bradford et al. 2000) in which nomads entering estuarine and marine waters contribute to

smolt and adult production at a constant proportion of the increase in the number of spawners, at escapements above the level needed to maximize smolt production from freshwater habitat (K_F). A conceptual representation, the bent hockey stick (BHS) model, is depicted in Fig. 4 with an initial slope (α), smoothness parameter (θ), and the secondary slope (representing the nomad contribution within and above in the inflection region), based on average parameter estimates for the populations in Hugh Smith Lake and Ford Arm Creek. Although the indicated lower escapement goal bound (13% of K_F) and escapement at maximum sustained yield (E_{msy} ; 17% of K_F) differ very little from the LHS model, the escapement range predicted to produce 90% or more of MSY based on the BHS model encompasses a 74% broader range with an upper bound at 38% of K_F instead of 27% of K_F for the LHS model. A positive population response to increasing escapement allows imprecisely but conservatively managed mixed-stock fisheries to achieve a high percentage of theoretical MSY, with a low yield penalty for variable escapements above E_{msy} (Shaul et al. 2011).

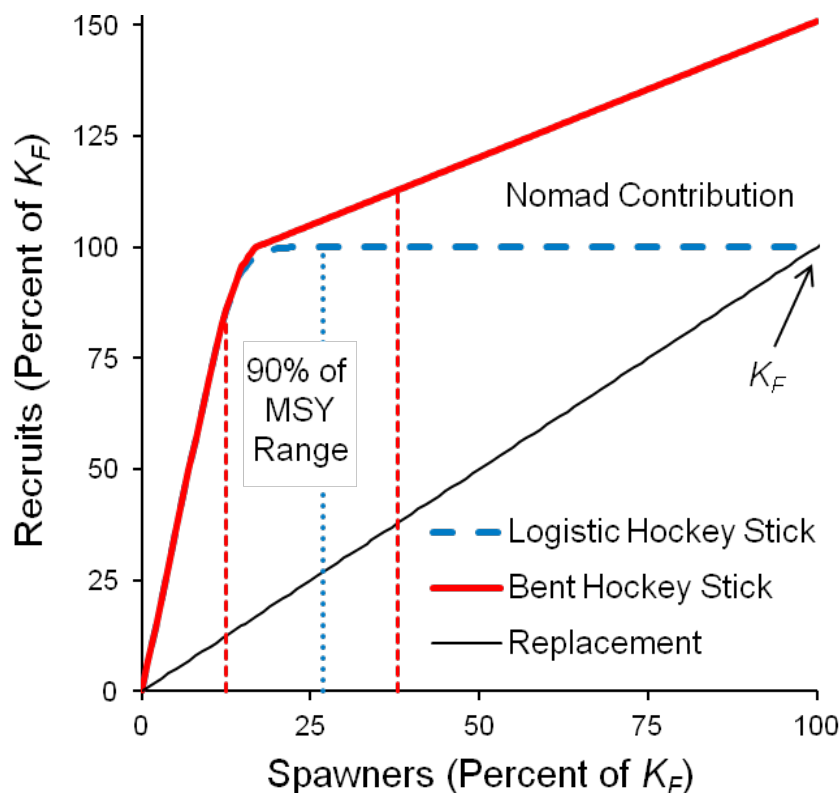


Fig. 4. Conceptual bent hockey stick (BHS) model based on average spawner-recruit parameters (including α , θ , and secondary slope) for the Ford Arm Creek stock and the Hugh Smith Lake stock compared with the logistic hockey stick (LHS) model. Axis scales are shown as a percent of freshwater carrying capacity (K_F) indicated by the LHS model.

If we attribute the slope of the BHS relationship above estimated E_{msy} entirely to nomad production, then the contribution by nomads to adult returns from average brood year escapements of 1,305 spawners at Hugh Smith Lake and 3,275 spawners in Ford Arm Creek is predicted at 12% and 14%, respectively, of combined total production (Shaul et al. 2011). These theoretical proportionate contributions by nomads are similar to the highest minimum count of immature fall coho salmon immigrants into Auke Creek as a percent of the smolt migration the following spring (12.5%), and somewhat above the average for four years (7.0%). While we hypothesize that growth and survival in estuarine and marine waters has an important influence on the spawner-recruit relationship (and optimal fishery management strategy), it is clearly secondary in importance to production of smolts reared entirely in freshwater. Although their survival may be low on average and variable, nomads' use of a different, less density-limiting environment for summer growth benefits populations with life history diversification and a potential population buffer. The strategy enables populations in wet coastal regions like Southeast Alaska to efficiently access diverse habitats for growth and overwinter refuge, connecting thousands of small anadromous streams where coho salmon populations would otherwise remain isolated and vulnerable to population shocks.

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Critical Periods in the Marine Life History of Pacific Salmon?

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Keywords: critical period, smolt survival, acoustic tag

It is now exactly one century since the great Norwegian fisheries biologist Johan Hjort proposed his “critical period” hypothesis: That very early in the life history of marine fish such as cod, a single short period largely determined the major fluctuations in recruitment evident in fish populations (Hjort 1913). Hjort was an excellent scientist, and his original conjecture was that such a critical period might exist just after cod hatched from their eggs, when he viewed the larvae as particularly frail and thus especially vulnerable to environmental variability. However, Hjort also made clear in his writings that he viewed this hypothesis as merely a simple working theory and that research would have to move on to look at later phases in the life history if this initial simplifying theory was not supported. Unfortunately, such was rarely the case and many biologists came to state Hjort’s theory as a fact, and used it as a powerful rationale to justify focussing research efforts on the earliest life history phases, which were typically viewed as more tractable subjects for study than the later life history stages. For salmon populations, this typically meant proposing that the “salmon problem” (poor smolt to adult survival rates) was determined either in freshwater or in the first few days or weeks of life in the ocean. Although a second “critical period” has been proposed to occur in the first winter at sea (Beamish and Mahnken 2001) for salmon, the issue of whether specific critical periods actually exist (and thus make the recruitment problem potentially more tractable) has never been formally examined. After a century of research, there continues to be a persistent effort to simplify research on salmon by assuming that there is a critical period in the freshwater or early marine life history (and to propose large-scale research programs to study it) before actually establishing its existence. The consequences are important because, if the early marine phase is simply studied to assess the drivers of salmon returns without formally testing the theory that this life history period has the dominant role in determining recruitment, research programs may potentially continue for decades without ever establishing that they are studying the “wrong” period, wasting both intellectual and financial resources—and the opportunity to actually identify where the recruitment problem actually lies.

The advent of prototype large-scale freshwater and marine telemetry systems, such as the POST array, now provides an opportunity to formally assess the critical period theory as it applies to Pacific salmon, as a large number of populations have now been tagged and their freshwater and marine survival followed for 1-2 months after release. A 10-fold decline in survival of many Pacific salmon populations occurred over the last three decades, with smolt-to-adult return rates dropping from >10% to ~1%. Using the POST telemetry array we tested whether mortality in the earliest life history phases is large enough to form the primary driver of adult recruitment rates, and whether the survival measured during the early marine period is now small enough to explain a ten-fold decline in smolt-to-adult recruitment.

Size-related effects on smolt survival

Until very recently, current telemetry tags were too large to be implanted into the entire size range of salmon smolts, raising the question of whether telemetry-based survival measurements are representative. Welch et al. 2011 found that in British Columbia studies of sockeye, Chinook, coho salmon, and steelhead, no distortion in the size spectrum of initially tagged smolts relative to that of the survivors 1-2 months later was evident. A similar result is found in our studies of tagged yearling Chinook salmon smolts from the Columbia River (Fig. 1).

It is also possible to compare downriver survival to Bonneville Dam of acoustically tagged smolts with that of smolts tagged with PIT tags, a much smaller tag that is applicable to the entire size range of migrating smolts in the Columbia River (Fig. 2). Survival with distance is indistinguishable, suggesting that neither the larger size of acoustically tagged smolts or higher tag burdens are major contributory factors to survival where it can be compared. This result fits with the one survival study we have conducted where we directly measured the survival to adult return (SAR) of Cultus Lake sockeye using specially programmed acoustic tags (Welch et al. 2011); the resulting survival of the tagged smolts ($2/200=1\% \pm 1.4\%$; mean $\pm 2SE$) compared very favourably with the survival rate of wild (1.5%) smolts.

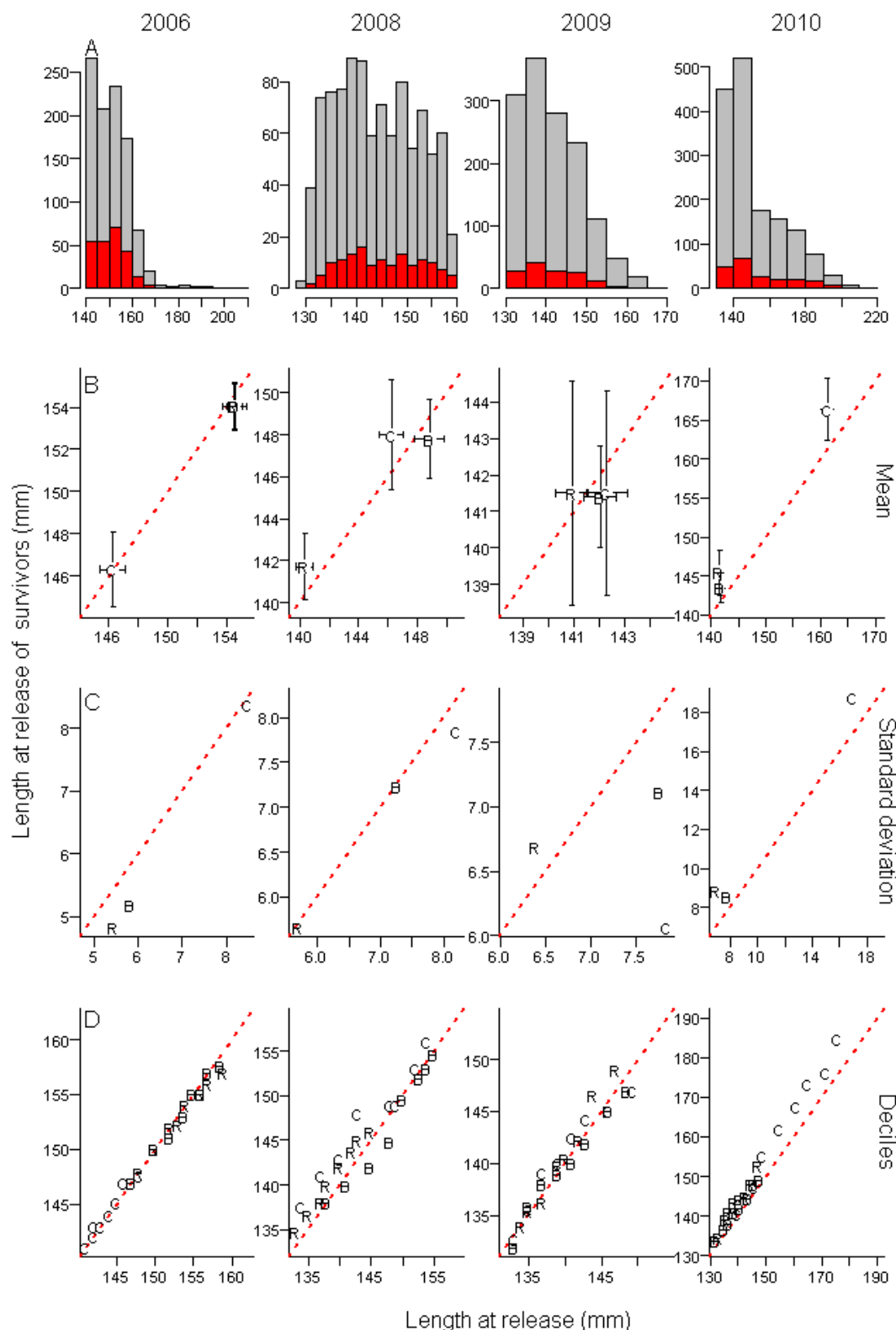


Fig. 1. (Top) Comparison of the size-at-release of all Columbia River tagged spring Chinook smolts released at their hatchery with the size-at-release of those tagged animals surviving to reach Willapa Bay ca. one month later. The middle two rows compare the mean size of smolts at release and of the survivors ($\pm 95\%$ CI) and the variance around the mean; the bottom row shows the QQ plot. In each case there are no departures from 1:1 (dashed red line), indicating that over the size range of fish tagged significant distortions due to differential survival with size are not evident.

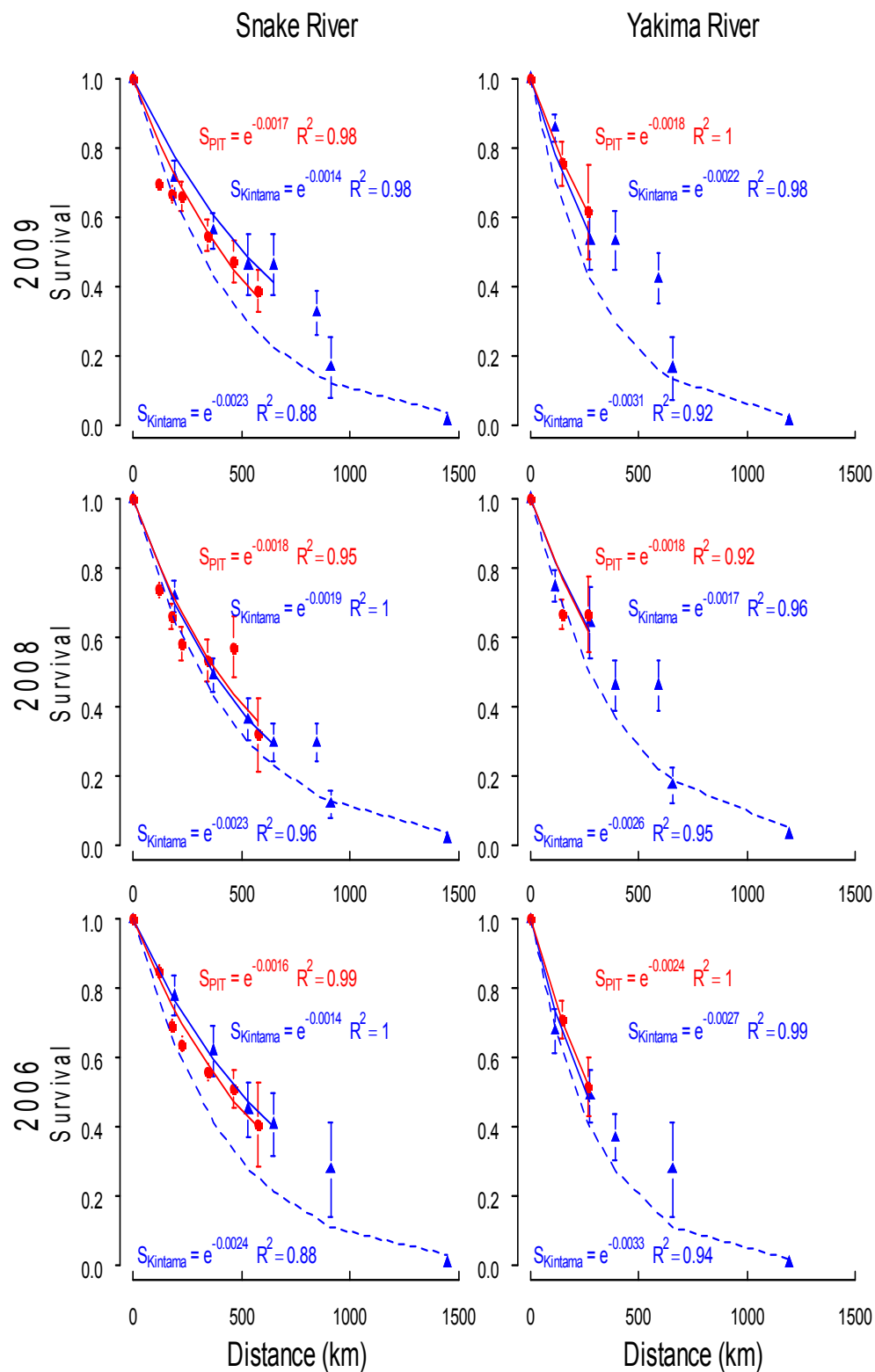


Fig. 2. Comparison of survival with distance from release for PIT and acoustically tagged smolts for two Columbia River spring Chinook stocks. Survival to Bonneville Dam (the last location where survival of PIT tagged fish can be measured) is indistinguishable.

Survival in the early vs later phase of salmon migration

Smolt to adult survival is now down to ca. 1% in many stocks of salmon in both southern British Columbia and the US Pacific Northwest region. The various survival studies conducted using the prototype POST array and reported in Welch et al. (2011) for British Columbia and in Porter et al. (2012a, b) for the Columbia River can be used to compare the magnitude of survival in the early and later phases of the migration. Although direct estimates of survival in the later marine phase are currently lacking, apart from the Cultus Lake study cited above, it is possible to compare the ratio of early to later survival necessary to achieve observed SARs.

We report (Table 1) British Columbia steelhead and sockeye salmon survival to the exit from the Salish Sea (Queen Charlotte Strait/Juan de Fuca Strait sub-arrays) as these two species consistently migrated out of the Salish Sea, while for coho and Chinook salmon stocks (primarily Fraser River) we report survival to the river mouth because these two species ceased migration after entering the ocean and remained resident in the Salish Sea for the remainder of the tag's lifespan. Migration to the river mouth after release typically takes one week in the Fraser River and in the Columbia River takes three weeks to reach Astoria (near the river mouth) and four weeks to reach Willapa Bay, which encompasses the Columbia River plume region.

Table 1. Summary of survival values by species using the prototype POST array. Values in the table are simple means of estimated “critical period” survival across all stocks of a given species. The final column compares survival in the first period to survival over the remainder of the life history necessary to achieve currently observed smolt-to adult return survival (SAR) of ca. 1%. Although the survival ratio is sensitive to the exact value of the SAR, it demonstrates that in all cases early phase survival is much higher and therefore the majority of overall survival to adult return is determined sometime after the first 1-2 months of smolt migration.

Species	“Critical Period” Survival	Current SAR Rates	Survival Ratio (Early/Late)
Southern British Columbia Stocks			
Steelhead	25%	~1%	~6X
Sockeye	15%	~1%	~2X
Coho (River only)	62%	~1%	~100X
Chinook (River only)	27%	~1%	~6X
Columbia R Spring Chinook			
Release to River Mouth (Astoria)	42%	0.5%~1%	100X~200X
Release To Willapa Bay	22%	“	9X~17X
Plume Only (Astoria-Willapa Bay)	49%	“	50X~100X

In each case, survival in the first month of migration is much higher than the survival in the later phase necessary to result in the observed 1% overall SAR. (Note that freshwater survival to the mouth of the Fraser and Columbia rivers is particularly high compared to marine-phase survival).

Discussion

In all populations examined, survival beyond the current extent of the POST array must be substantially lower than survival within the geographic extent of the array. Two counterbalancing effects on survival during the early phases of salmon migration may occur in our telemetry studies that could potentially distort this conclusion: (1) Surgical implantation of tags may reduce survival in the earliest phases (“tagging effects”) and thus inflate estimates of the importance of survival in the early phase; (2) use of larger hatchery smolts in many (but not all) of the studies may result in survival estimates higher than might be experienced by smolts currently too small to tag, deflating estimates of the magnitude of early phase survival.

To date, we have found little evidence that either process is likely to have a substantial influence on survival in the early phase. Overall, our results point to the majority of salmon survival being determined after the first 1-2 months of migration. Of particular importance, our direct measurements of survival in the early phase of the migration are too high to largely account for the 10-fold decline in SARs seen over the past 2-3 decades. Although we do not have direct measurements of survival for periods when survival was formerly much better, even the elimination of all possible sources of mortality in the early marine phase (i.e., raising survival to 100%) would be insufficient to increase SARs by a factor of ten. At best, elimination of all sources of mortality would raise SARs by a factor of 2-5 fold.

It may be appropriate to retire the concept of a single “critical” period and to consider all phases of the life history of salmon as important, rather than to start from the simplifying assumption that one period is of overriding importance and then build research programs on the basis of this assumption. From this perspective, the first phase of a scientific research program should be to evaluate whether a particular life history period is really “critically” important, rather than to simply assume it to be true. Our results using surgically implanted salmon smolts to date have found little evidence that there is sufficient mortality occurring in the first 1-2 months of migration to account for the very large declines in adult survival that have been observed, and there is good evidence that much of the determinants of recruitment occur later in the marine phase.

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A Model Linking Ocean Survival to Smolt Length

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Keywords: Chinook salmon, size selective survival, juvenile survival, adult survival Columbia River, model

The survival of juvenile salmon in their freshwater environment and first year in the ocean depends on their size, such that bigger fish generally survive better. However, studies contradict each other about the importance of this relationship and the form it takes, while others find equivocal or negative results (Sogard 1997). Previous work on Pacific salmon (*Oncorhynchus* spp.) focused on the presence or absence of a length effect on recruitment, but only recently have attempts been made to develop a mathematical form of the relationship (Satterthwaite et al. 2009; Hunsicker et al. 2011). Koenings et al. (1993) used non-parametric Loess smoothing to find common patterns in survival with respect to length, but no general theory has emerged. Although a size-selective survival effect is generally acknowledged and is found in data (Henderson and Cass 1991; Saloniemi et al. 2004), it is sometimes not observed (Rechisky 2010), or the effect is negative, i.e., larger fish having poorer survival (Ewing and Ewing 2002). Understanding the factors that determine size-dependent survival in salmon is important because the ecology of size links closely with recruitment and raises the question of whether large releases of hatchery salmon smolts limits the growth rate of both wild and hatchery fish and thus reduces their survival to adult stages.

As a step in characterizing this linkage, we developed a 4-parameter model relating the survival of juvenile salmonids to their size based on susceptibility to predation. The model is parameterized to test the hypothesis that there is a critical size beyond which smolts experience significantly lower mortality due to a reduction in gape-limited predation. The model was tested with spring-run Chinook salmon (*O. tshawytscha*) tagged in the Columbia River Basin. We apply the model to characterize juvenile survival during river migration and survival from juvenile release to adult return.

Dividing prey mortality into size-dependent and size-independent causes, a differential equation can express the mortality rate experienced by salmon of a certain size as

$$\frac{dN_x}{dt} = -c_1 N_x - c_2 N_x P_x$$

where N_x is the number of smolts of size x , and P_x is the fraction of the total predator population capable of consuming smolts up to size x . The rate of change in number of fish has one part independent of predators (first term) and one part dependent on the number of predators (second term). Parameters c_1 and c_2 are constants assumed to be independent of fish size but may vary from fish stock and by year. The solution of the equation expressing size-specific survival is $S_x = N_x(t)/N_x(0) = c_3 \exp(-c_4 P_x)$ where the size independent mortality is contained in the constant c_3 . Using a Taylor expansion of the exponential, $e^{-y} = 1 - y + y^2/2! - y^3/3! + \dots$, and truncating at the first power because $c_4 P_x < 1$, then the survival is approximated as $S_x \approx k_0 + k_1(1 - P_x)$ where k_0 is the base survival of the smallest fish and k_1 is the maximum survival improvement such that $k_0 + k_1$ is the survival of fish that are too large for the predators.

We assume predators have a normal size distribution and express their density in terms the size of prey they are able to consume as

$$S_x \approx k_0 + k_1 \Phi\left(\frac{x - x_c}{\sigma}\right)$$

Where Φ is the cumulative distribution of predator size expressed in terms of the smolt size susceptible to 50% of the predators, x_c , and the standard deviation of the distribution is σ .

To test the model, three distinct data sets were used in which out-migrating spring Chinook salmon from the Columbia River basin were tagged with Passive Integrated Transponder (PIT) tags. For freshwater survival, PIT-tagged salmon smolts were released at Sawtooth and Rapid River hatcheries on the Salmon River and detected at Lower Granite Dam or farther downstream (Fig. 1). At Sawtooth Hatchery (747 km upstream of Lower Granite Dam; Fig. 1) in 1998, 7039 smolts were tagged and 15.7% reached the dam. In 1991, 7081 fish were tagged and 6.6% reached the dam. At Rapid River Hatchery (283 km above the dam) the number of fish released over the years 1993-2008 varied and survival to the dam ranged between 6.6 and 54.7% (Table 1).

Table 1. Summary of spring Chinook salmon tagged at Rapid River Hatchery and survival to Lower Granite Dam.

Year	Number tagged	Survival (%)	Mean length (mm)
1994	2910	35.12	119.2
1995	1961	61.45	120.8
1996	19072	43.73	124.4
1998	48339	59.62	117.5
1999	45409	61.65	120.8
2000	47577	54.69	119.6
2001	54915	67.11	119.0
2002	182913	60.26	122.7
2003	135717	47.43	120.1
2005	5277	70.21	123.9
2006	49871	61.63	122.0
2007	55584	55.33	115.2
2008	70711	65.61	122.8

The survival of fish released as smolts at Lower Granite Dam and then detected as adults at Bonneville Dam one to three years later was determined for years 1998–2009 (Fig. 1). For this third data set, fish were distinguished by hatchery- or wild-origin and whether they passed through the hydrosystem (Lower Granite Dam to Bonneville Dam) as run-of-river migrants or were collected in barges at Lower Granite Dam and released below Bonneville Dam. Numbers tagged and survival from smolt release to adult return (SAR) are given in Table 2.

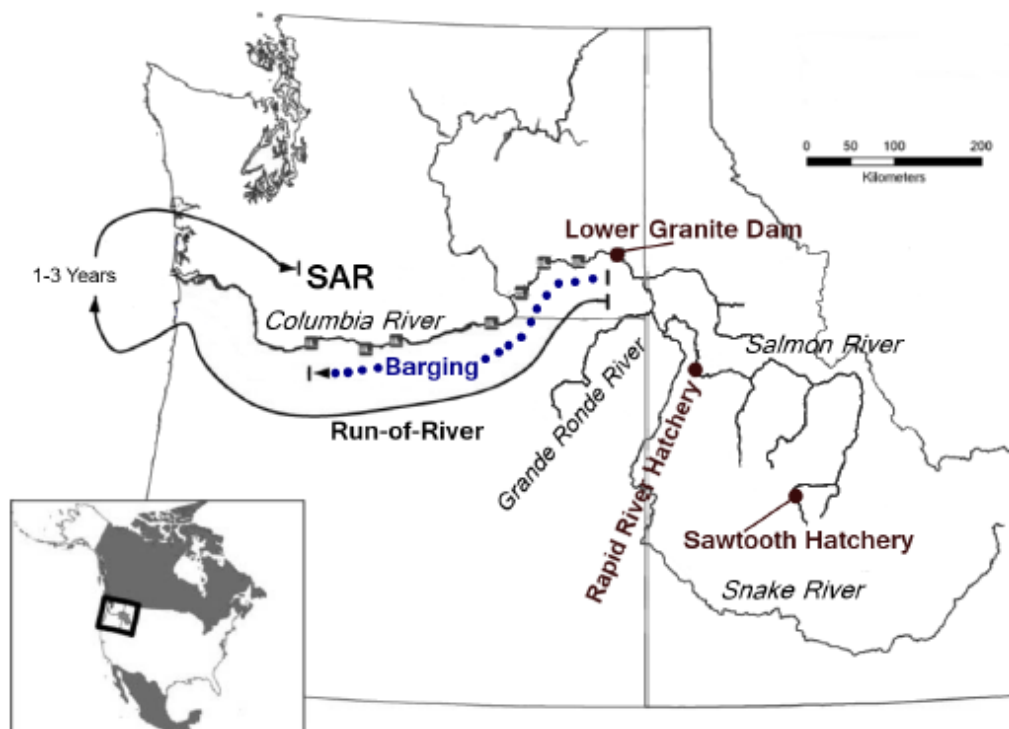


Fig. 1. Spring Chinook salmon freshwater survival calculated as movement from Sawtooth and Rapid River hatcheries to detection at Lower Granite Dam. Ocean survival (SAR) calculated from fish detected as juveniles at Lower Granite Dam and as adults returning to Bonneville Dam 1 to 3 years later. Ocean survival was estimated for fish passing through the hydrosystem in barges or in the river.

Table 2. Spring Chinook salmon PIT-tagged at Lower Granite Dam as juveniles and recovered as adults at Bonneville Dam.

	Wild Fish				Hatchery Fish			
	Barge #	SAR(%)	River #	SAR(%)	Barge #	SAR(%)	River #	SAR(%)
1999	8119	2.35	11829	1.39	43169	2.16	61478	1.49
2000	0		58496	1.77	0		0	
2001	17506	1.01	0		0		0	
2002	4899	1.47	33935	1.03	0		0	
2003	7101	0.42	43051	0.17	0		0	
2004	11194	0.54	0		0		0	
2005	12668	0.31	0		0		36094	0.09
2006	19505	0.91	10095	0.77	33935	0.81	148258	0.57
2007	16752	1.10	14513	0.68	23935	1.02	78111	0.24
2008	19022	3.25	9412	1.77	42452	2.36	98288	1.22
2009	13315	0.98	13815	0.43	0		91253	0.41

The model parameters k_0 , k_1 , x_c , and σ were estimated for individual years using the binary return data with a maximum likelihood estimator (mle2 function in the bbmle package in R; <http://cran.us.r-project.org/>). The survival curves were generated by parameters estimated from the binary data (Figs. 2-6). Survivals calculated by binning data over length increments were plotted on the figures for comparison purposes.

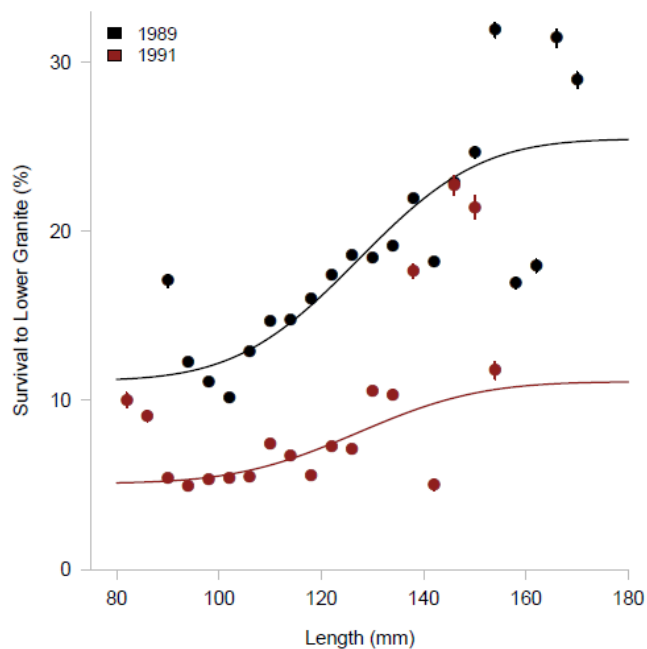


Fig. 2. Sawtooth Hatchery spring Chinook salmon survival for 1989 and 1991. Each point represents survival estimated by length bins. Curves were determined with the maximum likelihood estimator (mle2 function) of the binary data.

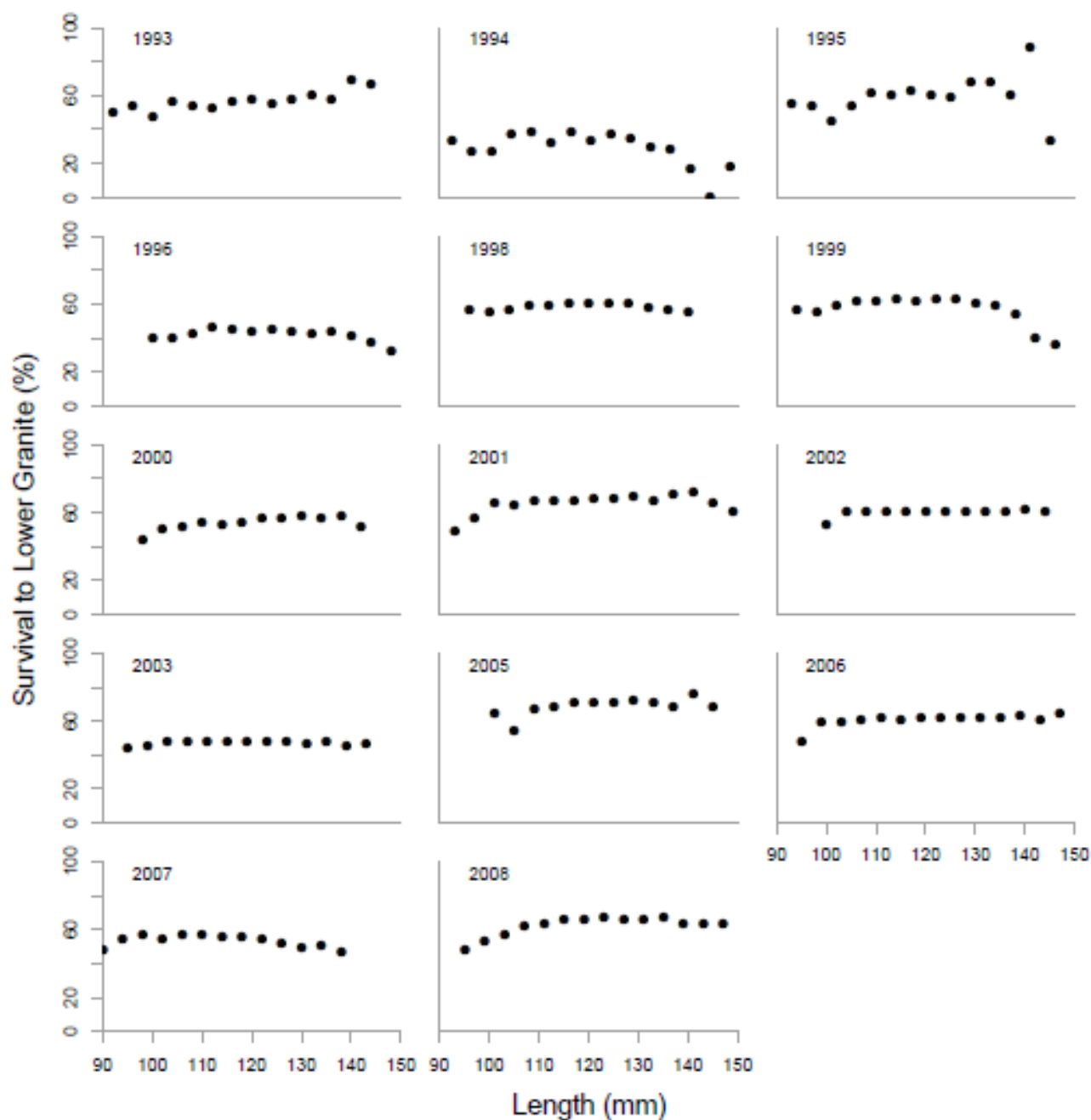


Fig. 3. Survival of Rapid River Hatchery juvenile spring Chinook salmon to Lower Granite Dam versus fish length.

Survival of Sawtooth Hatchery juvenile fish to Lower Granite Dam exhibited a clear size-dependent pattern but the level of mortality was different between years (Fig. 2). Survival of Rapid River Hatchery juvenile fish to Lower Granite Dam did not exhibit a clear size-dependent pattern (Fig. 3).

Size frequency distributions of fish PIT tagged for ocean survival varied between tagging years and were significantly different for the wild and hatchery fish. Wild fish mean length was about 110 mm while hatchery fish length was about 140 mm (Fig. 4).

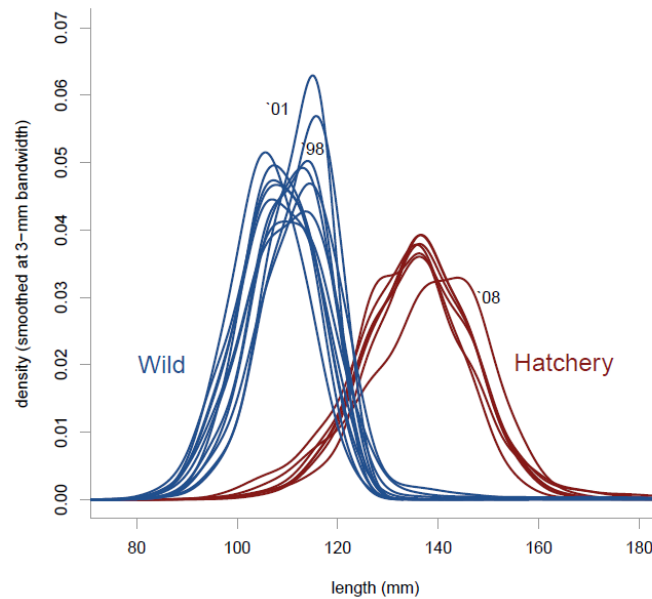


Fig. 4. Length distributions of wild and hatchery spring Chinook salmon tagged at Lower Granite Dam (1999–2009). A 3-mm bandwidth smoother was applied to eliminate extraneous noise.

In general for the ocean group, a strong size-dependent survival pattern was observed for all stocks. Figure 5 illustrates the survival pattern for the 2008 release year. For hatchery fish, which were longer than wild fish, the mean size of susceptibility was larger ($x_c \sim 140$ mm) than for the wild fish ($x_c \sim 100$ mm). Additionally, the barged fish exhibited a larger range of size variability than did the run-of-river fish.

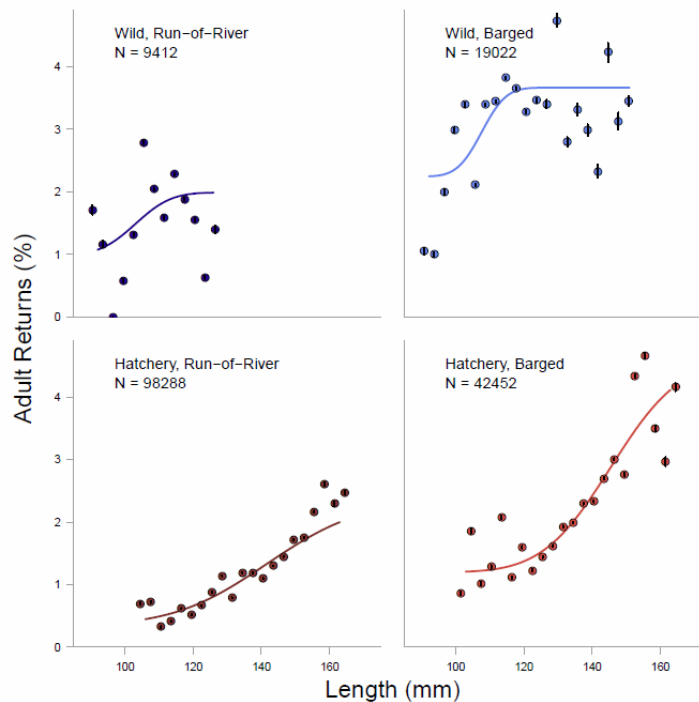


Fig. 5. Model fit of adult returns (%) to body length of the ocean group of hatchery and wild spring Chinook salmon released at Lower Granite Dam in 2008. Chinook salmon were either barged or swam in-river through the hydrosystem.

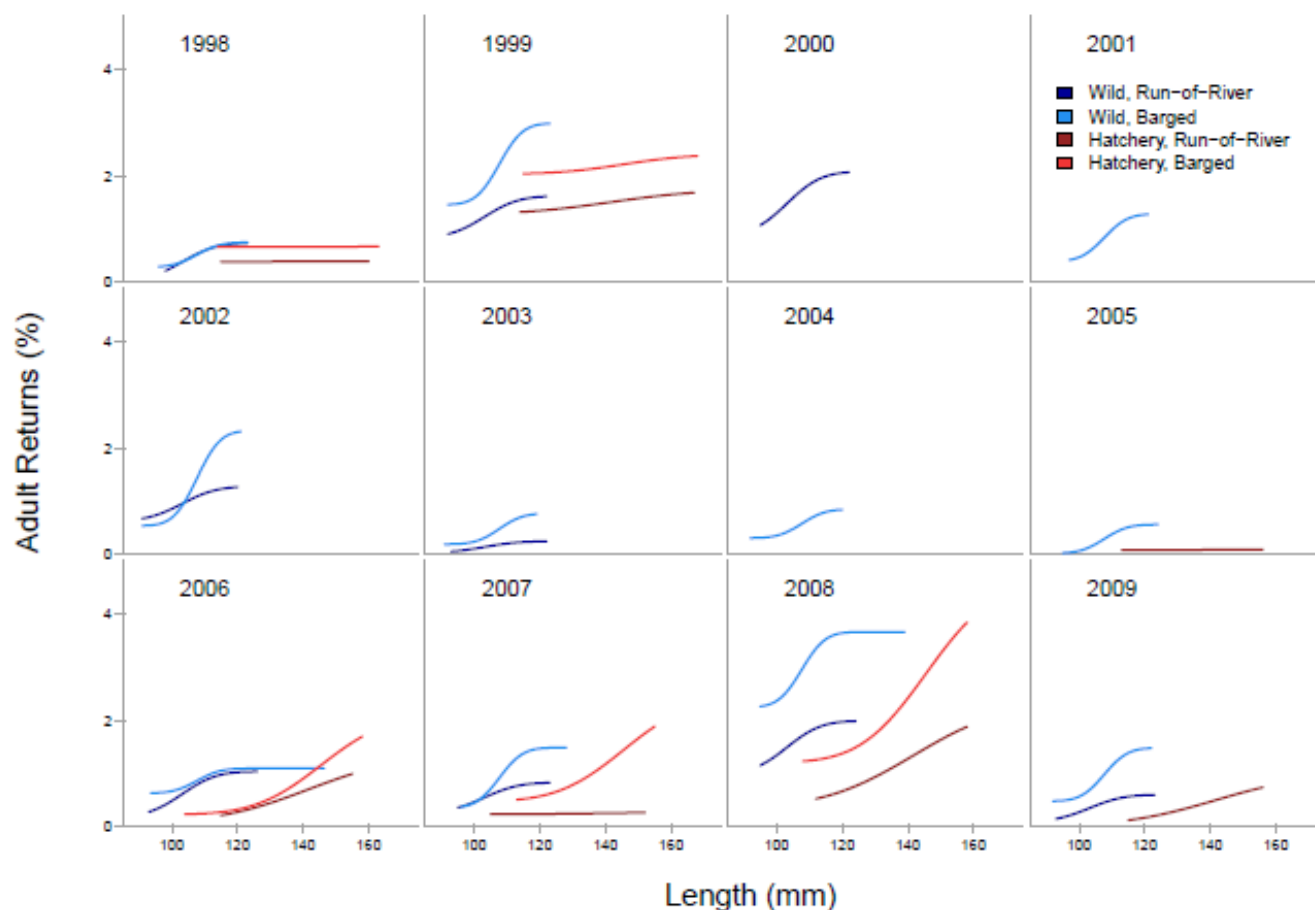


Fig. 6. Model fit of adult returns (%) to releases at Lower Granite Dam, 1998-2009. The model was fit to each run type, k_0 and k_1 allowed to vary by year, and the x_c and σ parameters were constant within each group across years.

Effect of size on ocean survival over all years of data is illustrated in Fig. 6 for wild and hatchery fish traveling by run-of-river and barged passage routes through the hydrosystem. A size effect is prevalent in most datasets, especially in wild fish that are barged.

Table 3. Summary of spring Chinook salmon parameter estimates for Lower Granite Dam data.

Run type	River passage	Mean length (mm)	x_c	x_c lower 95%	x_c upper 95%	σ	σ lower 95%	σ upper 95%
Wild	Barge	110.5	107.6	106.3	109.0	5.6	4.2	7.6
Wild	Run-of-river	109.1	103.1	101.0	105.2	8.2	5.9	11.5
Hatchery	Barge	136.2	145.5	141.0	150.2	15.7	12.6	19.6
Hatchery	Run-of-river	135.6	141.6	138.0	145.3	21.4	18.3	24.9

Summary statistics of model parameters x_c and σ for the ocean group are given in Table 3. The mean lengths of wild fish are slightly larger than the mean critical length estimates, falling outside the 95% confidence interval. The mean lengths of hatchery fish fall below the x_c confidence interval. In general, the size selection of wild and hatchery fish were different and corresponded with the mean size of the respective groups.

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Assessing the Relative Importance of Local and Regional Processes on the Survival of Snake River Spring/Summer Chinook Salmon

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Keywords: Columbia River, Snake River spring/summer Chinook salmon, early marine residence, survival, growth-mortality hypothesis

Snake River spring/summer Chinook salmon was listed as “threatened” under the US Endangered Species Act in 1992. The current management unit, identified as an Evolutionarily Significant Unit, includes all naturally spawned spring/summer Chinook salmon in the mainstem Snake River and the Tucannon, Grande Ronde, Imnaha, and Snake River sub-basins as well as numerous artificial propagation units. An estimated population of >1,000,000 fish in the late 1800s declined to <5,000 in the 1990s, and the current recovery goal is for smolt-to-adult return rates (SARs) in the 2-6% range with an average of 4%. However, from 1998 to 2010, Snake River spring/summer Chinook salmon SARs were well below the targeted recovery goal (<0.5 to 3.2%).

The vast majority of juvenile spring/summer Snake River Chinook salmon migrate to the ocean in spring and early summer as yearlings. Prior research indicates that in-river juvenile survival is positively related to body size (Zabel and Achord 2004; Achord et al. 2011) and that earlier emigrants tend to survive at higher rates than later emigrants (Scheuerell et al. 2009). However, a lack of clarity on the relative importance of freshwater, estuarine, and marine factors in the survival of Snake River spring/summer Chinook salmon continues to impede recovery efforts. We combined eight years of ocean collections off of Washington and Oregon with genetic stock identification and otolith structural and chemical analyses to examine key biological attributes of Snake River spring/summer Chinook salmon, including juvenile size and timing of marine entry and early marine growth rate. First, we characterized individual and interannual variation in these biological attributes and compared them with estimates of SARs to evaluate the growth-mortality hypothesis, i.e., that survival is positively related to body size. Second, to identify likely mechanisms of mortality, we determined which local and regional indicators of river, estuary, and ocean conditions accounted for the most variation in the relevant juvenile attributes, i.e., those related to survival. Finally, we used multi-model inference to evaluate the relative importance of river, estuary, and ocean indices in relation to variation in SARs from 1999 to 2008.

We examined data from surveys that occurred during late May and late June from 1999 to 2008 (Fig. 1). A Nordic 264 rope trawl was towed in surface waters (Daly et al. 2009), and trawl catches were standardized to density (fish km⁻¹) based on trawl width and distance towed. On board, fish were identified, measured (fork length (FL), mm), and frozen. In the laboratory, fish were re-measured and weighed (± 0.1 g). We combined genetic stock identification with otolith structure and chemistry to reconstruct juvenile size at and timing of marine entry and marine growth rates (% d⁻¹, mm) for the spring/summer Snake River stock group. Juvenile Chinook salmon were genotyped at 13 microsatellite DNA loci (Teel et al. 2009) and assigned to stock group using a standardized genetic database (Seeb et al. 2007; Barnett-Johnson et al. 2010). Stock assignments were made with the program ONCOR (Kalinowski et al. 2007) and the likelihood model of Rannala and Mountain (1997). We then determined size at and timing of marine entry based on variation in otolith Sr:Ca. Sagittal otoliths were polished using wet-or-dry paper (240-2500 grit) and lapping film (1- 30 μ m) to expose the dorsal-ventral growth axis using standard procedures for elemental analysis (Miller 2009). Otolith Sr and Ca were measured along the dorsal-ventral growth axis using laser ablation-inductively coupled plasma mass spectrometry. Image analysis was combined with Sr:Ca data to determine otolith width at freshwater emigration and to estimate the date of freshwater emigration. For each individual, the otolith width at the time of freshwater emigration was determined by the initial and abrupt increase in otolith Sr:Ca, which indicates exit from freshwaters, prior to stabilizing at marine values (Miller et al. 2010, 2011).

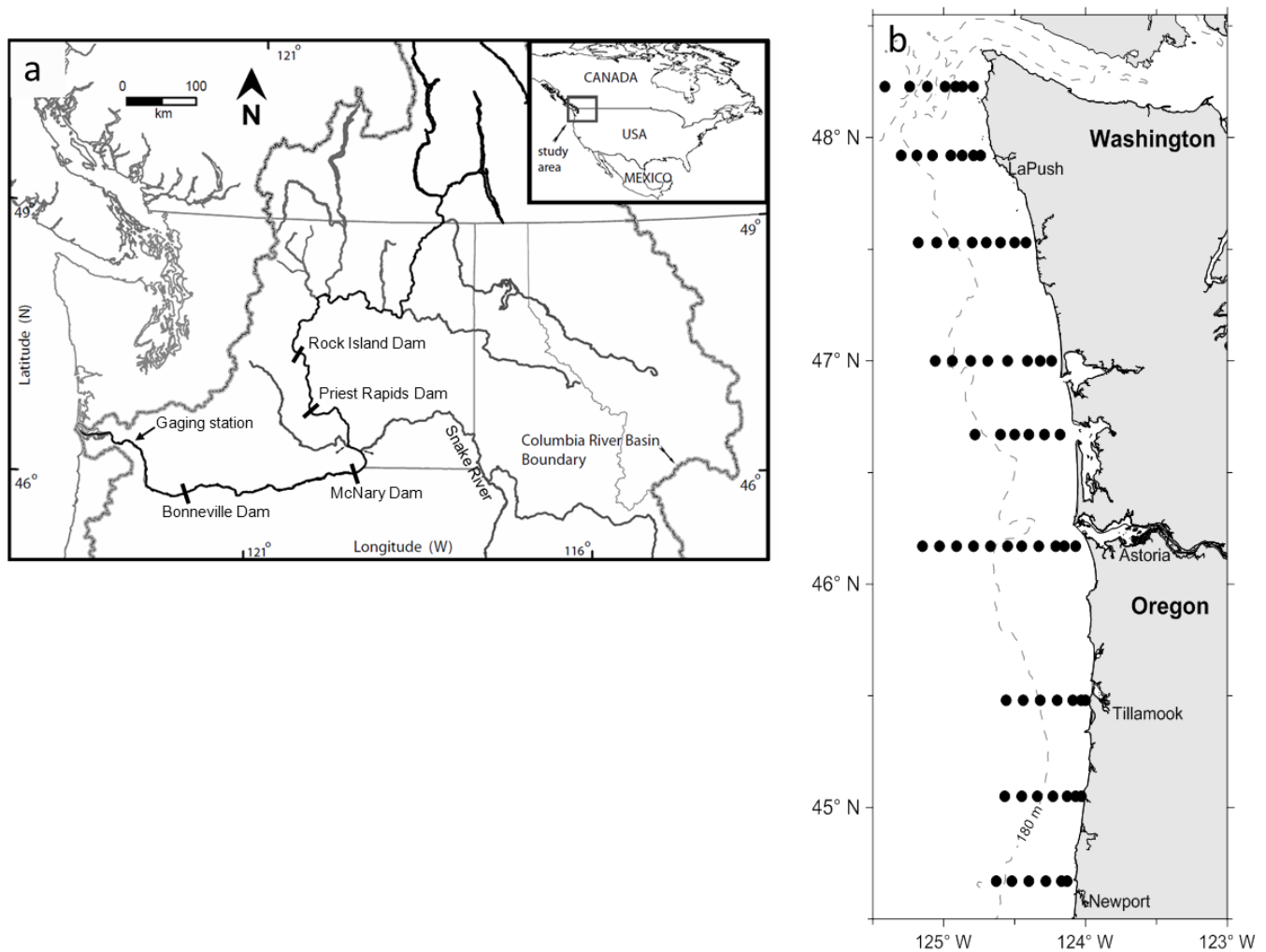


Fig. 1. (a) Columbia River watershed with locations of the mainstem dams and gaging station referred to in text. (b) Transect and station locations for ocean collections used in this study.

We used various indicators of river, estuary, and ocean climate during juvenile emigration for comparison with juvenile attributes and overall survival, including river discharge, metrics of the Columbia River plume environment, and two basin-scale ocean indices—the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO). Data on daily discharge in the lower river were obtained from the United States Geological Survey (Site 14246900 at 46°N, 123°W). For plume metrics, we used the output of simulation databases to characterize the variability in plume size (area of the plume surface and volume of the 3D plume) and location (expressed in terms of coordinates of the centroid of the surface plume; Zhang et al. 2004; Zhang and Baptist 2008). We defined the plume using a cutoff salinity of 28 psu. The simulation databases are a component of a modeling system, known as the “Virtual Columbia River” (www.stccmop.org/datamart/virtualcolumbiariver), which is anchored by 3D unstructured-grid numerical models of water circulation. Burlap et al. (2010) demonstrated that the majority of variation in the coastal surface salinity field is accounted for by variation in river discharge (43%) and prevailing winds (21%).

To provide an indication of interannual variation in coastal productivity, we used the Copepod Community Index (CCI). The CCI is a numerical representation of all copepod species that are present in more than 5% of the samples collected biweekly 9 km offshore of Newport, Oregon, using a 50-cm diameter, 202- μ m mesh ring net towed vertically from 5 m above the sea floor to the surface. The values are rotated Axis 1 scores of a non-metric multidimensional scaling ordination of species abundance by sample date from 1996 to 2010 (Morgan et al. 2003; Hoof and Peterson 2006). During spring and summer, negative CCI values indicate the presence of a “northern community” comprised of cold-water neritic taxa that are large and lipid-rich, whereas positive values indicate the presence of an “offshore or southern community” comprised of

smaller, relatively lipid-poor species (Keister et al. 2011). The CCI may be indicative of the nutritional quality of the food web supporting juvenile salmon and their prey. Therefore, we determined if juvenile Chinook salmon marine growth rates and size at capture were related to the CCI. Finally, we used a multi-model inference approach to assess the ability of the physical and biological variables to account for variation in juvenile attributes during early marine residence and interannual variation in SARs. Survival rates were obtained from the Fish Passage Center (<http://www.fpc.org/>). For analyses that included juvenile Chinook salmon, we included eight years (1999-2000, 2002-2004, and 2006-2008). The years 2001 and 2005 were removed from analysis due to low number of yearlings collected ($n < 10$). For comparisons between SARs and physical (river discharge, plume size and position, PDO, and NPGO) and biological (CCI) metrics, we included data from 1999 to 2008 ($n = 10$ years).

Overall, mean annual timing of juvenile emigration ranged from 6 May to 18 May and all juveniles emigrated between 20 April and 19 June with a shift toward later emigration in 2006-2008. Individual residence in coastal waters prior to capture ranged from 1 to 81 days. Mean annual marine growth rate mean ranged from $0.47\% \text{ day}^{-1}$ in 2002 to $0.83\% \text{ day}^{-1}$ in 2000. We determined that estimated size at marine entry displayed negative, non-significant trends with survival. However, marine growth and length and mass at capture, which occurred an average of 20 days after marine entry, were strongly, positively related to survival ($r > 0.73$). Yearlings grew faster and attained larger sizes during early marine residence in years in which the plume was larger, the NPGO index was more positive, the PDO index more negative, and the copepod community was dominated by northern, boreal species. In terms of accounting for interannual variation in juvenile size after early marine residence, the model that incorporated a local index (plume area) was 1.4 to 2.5 times more likely than the models with basin-scale indices (NPGO and PDO), given the data and family of models. For emigration years 1999 to 2008, interannual variation in SARs was well-described by physical and biological conditions during emigration, including yearling marine density, NPGO, PDO, and the CCI. The most parsimonious hindcast model included NPGO and yearling marine density ($R^2 = 0.85$, $n = 10$). A comparison of the relative importance of model parameters indicated the yearling marine density in June, which represents cohort abundance after an average of 20 days in the ocean, was generally the most important variable in accounting for variation in SARs. The relatively high survival of the cohort that emigrated in 2001, a year with extremely low river discharge and a relatively small plume, may have been due to very good survival conditions in the ocean as indicated by the NPGO and PDO. These data indicate that ocean conditions favorable for survival may modulate poor river conditions.

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Change in Mean Body Size: Growth or Predation?

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Keywords: size-selective mortality, apparent growth, mathematical model

In their freshwater and early ocean life stages salmonids experience rapid growth. Accurate measures of that growth can be important for comparison of habitats, bioenergetics models, and other applications. Growth can be measured as the difference of the mean of the size-frequency distribution at two times. Because smaller individuals tend to experience greater mortality than larger individuals, the apparent growth for the population is larger than the actual growth of individuals in the population. I describe a simple model of simultaneous growth and size-selective predation and use this model to explore the relationship between model parameters for size-selective predation and actual and apparent growth. I explore a method for estimating the mean actual growth of individuals in a population given the mean apparent growth of the population.

The model used is very similar to that of Munch et al. (2003). We assumed that growth and mortality were governed by two ordinary differential equations. The first is a size-dependent growth equation,

$$\frac{dx}{dt} = g(x) \quad (1)$$

where $x(t)$ is the size of an individual at time t and $g(x)$ is the instantaneous growth rate of an individual of size x .

The second is a size-dependent mortality equation,

$$\frac{dN(x, t)}{dt} = -m(x)N(x, t) \quad (2)$$

where $N(x, t)$ is the density of individuals of size x at time t and $m(x)$ is the instantaneous mortality rate for individuals of size x . The second equation is separable and can be solved for $m(x)$, or survival at time t .

$$S(t) = \exp\left(-\int_0^t m(x_t) dt\right) \quad (3)$$

Equation (1) can be solved explicitly for x_t , given x_0 , as long as $g(x)$ is strictly positive. This allows us to change variables from time to size:

$$S(x_0) = \exp\left(-\int_{x_0}^{x_t} \frac{m(x)}{g(x)} dx\right) \quad (4)$$

Given an initial size-frequency distribution, f_0 , the distribution at time t is

$$f_t(x_t) = f_0(x_0) \frac{S(x_0)}{\int_{-\infty}^{+\infty} S(x) dx}$$

I defined the mean apparent growth to be the difference in the means of the two distributions: f_0 and f_t . I defined the mean actual growth to be the mean growth rate computed with respect to the final distribution, f_t .

I used simple growth and mortality models in order to minimize the number of parameters requiring estimation: constant growth and linear mortality.

$$g(x) \equiv g_1 \quad (5)$$

$$m(x) \equiv \begin{cases} (m_1 - x)m_2 & x \leq m_1 \\ 0 & x > m_1 \end{cases} \quad (6)$$

The m_1 parameter can be thought of as the critical size beyond which size-selective mortality no longer applies. The m_2 parameter can be thought of as the strength of size-selection—the larger the m_2 parameter, the greater the difference in mortality rates across size.

I non-dimensionalized the system by focusing on the size-frequency initial distribution. I assumed the initial distribution was normal, with mean μ and standard deviation σ . All measures of size were then standardized against the mean and standard deviation of that distribution:

$$\tilde{f}_0(x) = \frac{f_0(x + \mu)}{\sigma} = N(0,1)$$

$$\tilde{g}_1 = \frac{g_1}{\sigma}$$

$$\tilde{m}_1 = \frac{m_1 - \mu}{\sigma}$$

$$\tilde{m}_2 = \sigma m_2$$

$$\tilde{f}_t(x_0 + \tilde{g}_1) = \frac{\tilde{f}_0(x_0) (\tilde{S}(x_0))}{\int_{-\infty}^{+\infty} \tilde{S}(x) dx}$$

Mean actual growth was \tilde{g}_1 . Mean apparent growth was the mean of the \tilde{f}_t distribution.

I mapped the magnitude of the bias in apparent growth with respect to a fixed amount of actual growth, allowing \tilde{m}_1 to vary between -1 and 12, \tilde{m}_2 to vary between 0 and 5, and \tilde{g}_1 to vary between 1 and 6. I also mapped the magnitude of the bias in apparent growth with respect to a fixed amount of apparent growth, allowing the mortality parameters to vary in the same way.

I performed model fitting on data from the Columbia Basin Fish and Wildlife Program (CBFWP) passive integrated transponder (PIT) tagging of wild-reared Chinook salmon from the Snake River Basin. The data for six years in particular were found to have a substantial number of recaptures at Lower Granite or Little Goose dams. Using the recapture data, I had a direct measure of actual growth against which I could compare the g_1 parameter from the fitted model. The model was first fitted with the g_1 parameter fixed at the value determined from the direct measure of growth in order to get best estimates for the mortality parameters. I then fitted the model using the lengths at tagging as the initial sample and the lengths at recapture as the final sample. I used a technique similar to that outlined by Munch et al. (2003)—with modifications to account for the differences in time between tagging and recapture among individuals. I repeated this process three further times, restricting the possible range of the m_1 and m_2 parameters to within 20%, 10%, and 1% of the best estimates determined using the direct measure of the growth. The apparent growth and the fitted values for g_1 were compared with the growth from the direct measure.

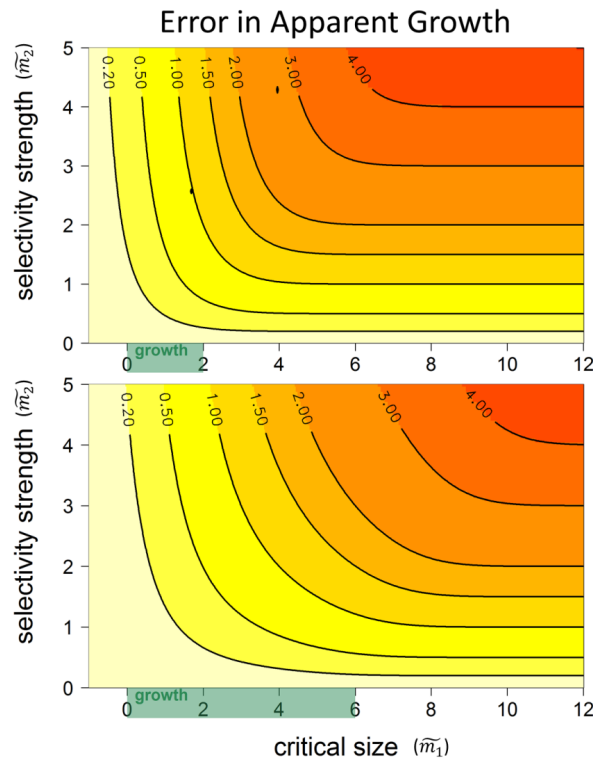


Fig. 1. Map of error in apparent growth. The x-axis shows the \tilde{m}_1 parameter (critical size) and displays the amount of actual growth used in the figure (\tilde{g}_1 , in green). The y-axis shows the \tilde{m}_2 parameter (strength of selectivity). The contours (and shading) indicate the absolute magnitude of the error for an actual growth of 2 (a) and 6 (b) in non-dimensionalized units.

The model exploration revealed behavior in keeping with the simple nature of the model. For large values of m_1 (critical size), only a tiny fraction of the population escapes predation and the magnitude of the apparent growth bias is determined solely by m_2 (strength of selectivity). As the critical size decreases, it can mitigate the effects of selectivity as a greater portion of the population escapes size-selective predation—the greater the strength of selectivity, the more a small change in the fraction of survivors can matter (Fig. 1). The nature of the error in apparent growth is similar when considered from the point-of-view of a fixed amount of apparent growth (Fig. 2).

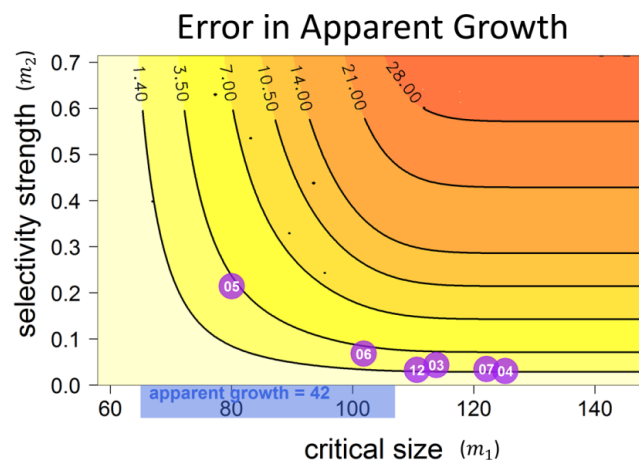


Fig. 2. Map of error in apparent growth for a fixed value of apparent growth. This map is shown in actual units in order to best display the fitted values for the data used (years 2003-2007 and 2012). Mean initial size (65mm) and mean apparent growth (42mm) were computed as averages across years.

Table 1. For each year of PIT tag data with substantial recaptures, the distribution of initial size and directly measured growth are characterized by mean and standard deviation. The absolute error with respect to the actual (directly measured) mean growth is listed in subsequent columns. “Apparent growth” refers to the difference in mean for the two populations. “Unrestricted Model” refers to the fitted model with no restrictions on the growth or mortality parameters. “Restricted (X%)” refers to a fitted model in which the growth parameter was unrestricted, but the mortality parameters were constrained to fall within X% of the “best fit” mortality parameters. The “best fit” mortality parameters were computed by fitting the model while constraining the growth parameter to the directly measured value.

Year	Initial Size		Actual Growth		Apparent Growth Error	Unrestricted Model Error	Restricted (20%) Error	Restricted (10%) Error	Restricted (1%) Error
	Mean	SD	Mean	SD					
2003	63.2	7.0	42.5	10.3	+1.8	-8.5	-3.0	-3.0	-0.4
2004	63.2	6.4	41.3	8.9	+2.1	-7.0	0.3	0.3	0.3
2005	62.9	7.0	44.5	9.4	+2.6	-5.0	-5.0	-3.0	-0.1
2006	66.2	7.1	35.1	9.1	+3.1	-3.6	-3.6	-3.6	-0.4
2007	65.6	6.4	43.7	8.6	+0.9	-8.2	-4.0	-3.2	-0.4
2012	63.4	6.4	36.0	8.8	+1.5	-6.5	-1.5	-1.5	-0.4

The first phase of the model fitting exercise produced best fit mortality parameters consistent with weak selectivity, except in the case of 2005 which suggested much greater selectivity focused on smaller individuals (Fig. 2). The error in the apparent growth measures were less than 10% of the actual growth in all cases and were about one quarter of the standard deviation in the directly measured growth (Table 1). The fitting methodology applied without restrictions to the mortality model parameters produced estimates that were more negatively biased than the apparent growth measures were positively biased. This improved substantially when restricting the fitting algorithm to mortality parameters within 20% of the “best fit” parameters. Further restricting mortality parameters to within 10% of the best fit parameters did not result in corresponding improvement in the estimate of actual growth. Only the restriction within 1% of the best fit mortality parameters produced estimates of growth that were better than the apparent growth estimate. Full details are shown in Fig. 3 and Table 1.

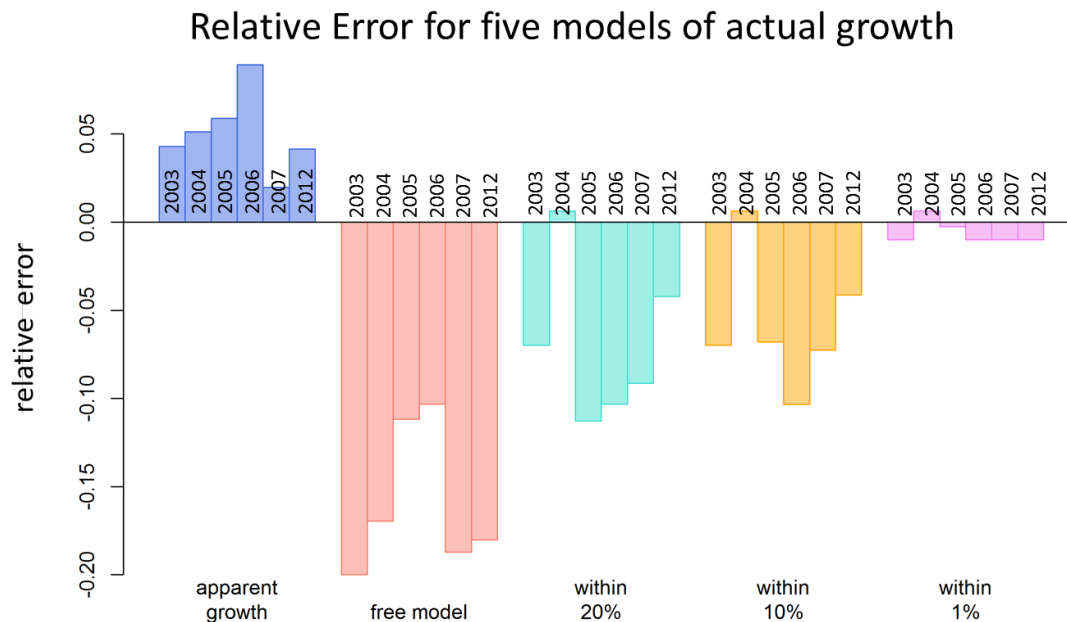


Fig. 3. Relative error in growth measure with respect to directly measured mean growth. For “apparent growth” this is the computed difference in the mean size for samples 1 and 2. For the other models, it is the fitted value for g_1 . For the “free model”, m_1 and m_2 were unconstrained. For the “within X%” models, m_1 and m_2 were constrained to be within X% of the “best fit” model (parameterized using g_1 equal to the directly measured mean growth).

The model characterizes the behavior of a system involving size-selective predation well. Based on the behavior of the fitting algorithms with the overall model and PIT tag data, some changes are needed if this process is to be useful for characterizing the magnitude of the bias when apparent growth is used in place of directly measured growth. Accurately characterizing the predator field to within 1% of the effective mortality model parameters is at least as difficult a goal as directly measuring the growth of the population of interest. There is, however, some hope that further investigation will reveal models that will allow this process to function more accurately.

Future work includes investigation of different mortality models. A simple modification to the existing model—adding a baseline of size-independent mortality—may yield a much better fit to the data. Additionally, a more complex model which is mechanistically linked to the distribution of the size of predators may be able to provide a better fit to the data. A more realistic growth model may also be useful, but simple linear models have not worked well (results not shown). Once the best performing mortality and/or growth models are found, I will explore the kind of priors on the mortality model parameters that best facilitate accurate reconstruction of the mean actual growth.

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Juvenile Yearling Chinook Salmon Survival in the Columbia River Plume (USA): An Information-theoretic Evaluation of Environmental Factors with Telemetry Data

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Pearcy (1992) suggested that the number of juvenile salmon that return as adults may be established during a ‘critical period’ of early marine survival. To best identify the processes directly affecting early marine survival, it is necessary to first measure juvenile survival directly, which is now possible with acoustic telemetry technology (Rechisky et al. 2009; Moore et al. 2010; Melnychuk et al. 2011; Welch et al. 2011; Thorstad et al. 2012). Our first objective was to evaluate the ability of a simple exponential decay model to describe survival data for tagged yearling Chinook salmon in the Columbia River plume. Our second objective was to evaluate the influence of environmental processes and we used model residuals to examine whether measures of biological productivity or total dissolved gas levels in the river would add additional predictive power to the exponential decay model (Kutner et al. 2005). Finally, given the interest in manipulating the dynamics of the Columbia River plume (through flow-controlled river discharge) to benefit juvenile salmon, we used the Akaike information criterion (AIC) for model selection to examine three factors that may affect plume residence time, including sea surface temperature, which may influence the timing and speed of migration, and upwelling and river discharge, which are related to plume orientation and local currents encountered by migrating salmon (Brett et al. 1958; Burnham and Anderson 2002; Sykes and Shrimpton 2010; Burla et al. 2010a, b; Jacobson et al. 2012; Martin et al. 2012).

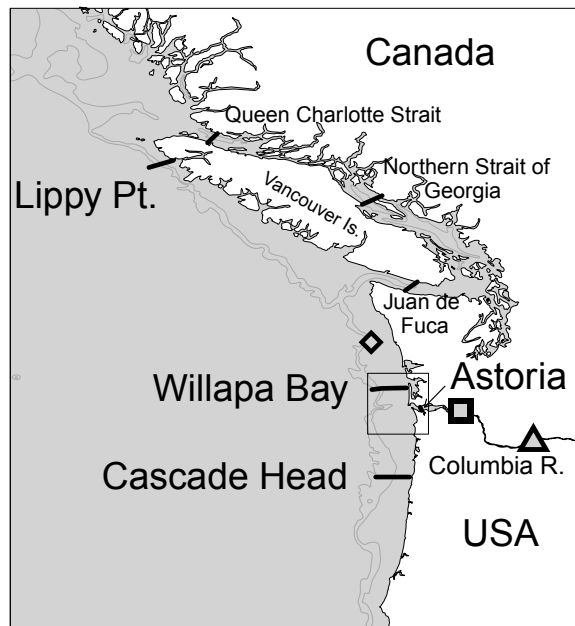


Fig. 1. Map of the study region; the box encompassing the Willapa and Astoria sub-arrays delineates the Columbia River plume area. The black lines mark the named telemetry sub-arrays. Data collection sites include NOAA buoy 46041 (diamond), Beaver Army Terminal at Quincy, OR (square), and Bonneville Dam/Camas Washougal (triangle).

Between 2008 and 2011, 4,646 yearling Chinook salmon from the Columbia River basin were surgically implanted with uniquely coded acoustic transmitters and then tracked as they migrated down the Columbia River and north along the continental shelf (Fig. 1). Tagged fish were grouped according to their origin and handling and included Columbia River run-of-the-river (CR) groups, Snake River run-of-the-river (SR) groups, and Snake River Transport (ST) groups. Detection data from lines of acoustic receivers (sub-arrays) that bisected the river and continental shelf at locations extending from

the Snake River to Lippy Point, British Columbia, Canada (Fig. 1), were used to estimate apparent survival for each group to each detection line in each year in a special case of the Cormack-Jolly-Seber (CJS) live-recapture modeling framework (Lebreton et al. 1992). Modeling was implemented in program MARK (White and Burnham 1999). The complete details of methods, surgical protocols, release locations and timing, tag effect studies, and array efficiency can be found in Porter et al. (2009a, b, 2010, 2011, 2012a and 2012b) and Rechisky and Welch (2010). We excluded a group of transported fish released in early-April 2009 that was released much earlier in the season than the remaining groups, displayed very different migratory behaviors, and likely entered the plume before predators became abundant (Porter et al. 2009b; Collis et al. 2002; Emmett et al. 2006).

Survival data for the Columbia River plume region between the lines of receivers at the Astoria Bridge and Willapa Bay were fit to a simple exponential decay model using the nls function in R (R Development Core Team 2011),

$$S_p = e^{-k \cdot T_p}$$

where S_p is plume survival, k is the mortality rate constant, e^{-k} is the apparent daily survival rate, and T_p is median plume residence time. T_p was determined by subtracting the median individual final detections at Astoria (i.e., plume entry time) from the median of the final detections at Willapa Bay (plume departure). We also estimated plume survival in 2006, when there was no sub-array at Astoria, by dividing the 2006 estimates of combined lower river/plume survival (Bonneville Dam to Willapa Bay) by the average lower river survival (Bonneville Dam to Astoria) in 2008-2011 (average=0.85) and used the range of lower river survival from 2008-2011 (0.71 to 0.99; Porter et al. 2012a) to estimate a 2006 maximum and minimum plume survival.

We plotted logit-transformed survival and residuals from the exponential decay model against the timing of the biological spring transition, two- and four-week cumulative upwelling, and gas supersaturation in the lower river to evaluate the potential role of biological productivity and river conditions on plume survival (Kutner et al. 2005). We also calculated the coefficients of determination (R-squared) between logit-transformed survival and each of the variables.

Environmental data were obtained from public databases. Upwelling index values at 48°N (cubic meters/second/100 meters coastline) were obtained from the NOAA Pacific Fisheries Environmental Laboratory at <http://www.pfeg.noaa.gov/>. Biological spring transition dates for 2008-2011 and lower river gas saturation data were obtained through the Columbia River data access in real time (DART) site at <http://www.cbr.washington.edu/dart/>. Transition dates were used with the permission of Dr. William T. Peterson (NOAA Northwest Fisheries Science Center). Sea surface temperature (SST °C) data from NOAA data buoy 46041 (Fig. 1), which had a complete data set for periods when tagged juvenile salmon were transiting the plume, were obtained from <http://www.ndbc.noaa.gov/>. River discharge recorded at Beaver Army Terminal was extracted from the USACE National Water Information System at <http://waterdata.usgs.gov/>.

We evaluated the environmental factors potentially governing plume residence time by comparing the AIC weights and evidence ratios of a global model of plume residence time, $T_p \sim SST + UP + DIS + UP \cdot DIS$, and its 8 sub-model combinations (Table 1), where T_p is plume residence time, SST is sea surface temperature, UP is upwelling, and DIS is river discharge. Modeling was conducted in R with package MuMIn (Burnham and Anderson 2002; Johnson and Omland 2004; Kutner et al. 2005; Bartoń 2012).

Table 1. Summary of model selection statistics. Evidence is a measure of how many times less likely the model is the best model relative to the top ranked model.

Model	Intercept Parameter	SST Parameter	Upwelling Parameter	Discharge Parameter	Disch:Up Parameter	AICc	$\Delta AICc$	Model Weight	Evidence
SST	29.06	-1.735	-	-	-	41.77295	0	.92	1.0
SST+Dis	27.83	-1.716	-	0.0007817	-	48.80734	7.034388	.027	33.7
SST+Up	29.12	-1.740	0.0009444	-	-	48.97223	7.199273	.025	36.6
Up	8.228	-	-0.0531	-	-	50.24660	8.473644	.013	69.2
Dis	5.966	-	-	0.0001642	-	51.00925	9.236294	.0091	101.3
Up+Dis	1.838	-	-0.1010	0.0005078	-	55.36579	13.592843	.0010	894.6
SST+Up+Dis	25.89	-1.615	-0.01588	0.0001372	-	60.69276	18.919811	.000071	12834.7
Up*Dis	-2.11	-	-0.6625	0.0006881	0.00005825	65.05639	23.283434	.0000081	113745.3
SST+Up*Dis	22.15	-1.447	-0.2014	0.0002325	0.00001833	84.37098	42.598007	.0000000052	1778441824.7

Results showed there was no evidence of any violation of non-linear model assumptions in the exponential decay model, but the model performed better for run-of-the-river migrant groups than groups transported and released below Bonneville Dam (Fig. 2). Derived survival data from 2006 matches the model pattern and refitting the exponential decay model with the 2006 data only changed the decay constant (daily mortality) slightly, from 0.12 to 0.11. In-river migrants entered the plume in a more continuous fashion than transported fish; the median absolute deviation from the median plume entry date of transported juveniles was less than one day (mean=0.56 day), but ranged from 1-7 days (mean=3.39 days) for the in-river migrants. Due to the high variability in transport group survival, we evaluated environmental influences and plume residence time models using the in-river groups only. There were no strong patterns in the plots of the model residuals against biological spring transition dates, two- and four-week cumulative upwelling, or gas supersaturation to suggest that incorporating them would improve the model, nor was there any apparent relationship with survival (R-squared values were 0.14, 0.02, 0.01, and 0.13, respectively). Among the nine candidate models for predicting plume residence time, the model containing only sea surface temperature outperformed all others, as measured by AICc distance and model weights (weight = 92%; Table 1). There was no evidence in diagnostic plots that the SST model violated any standard linear model assumptions.

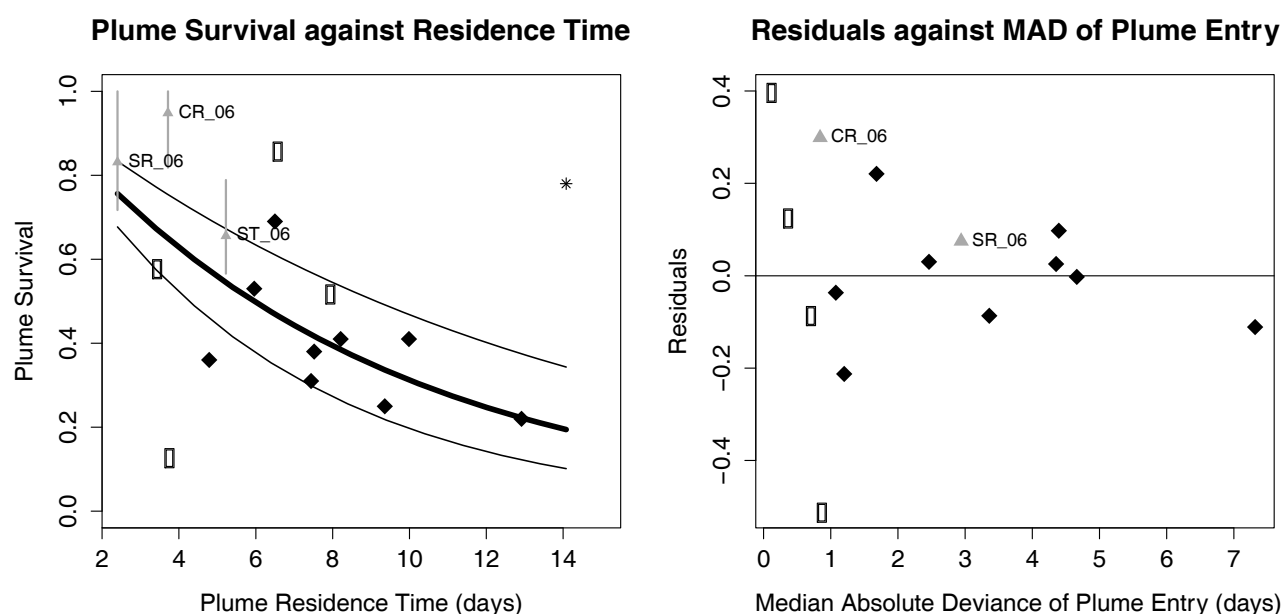


Fig. 2. (Left panel) Comparison of Columbia River plume survival with plume residence time showing the regression curve (thick line) and 95% confidence intervals (thin lines). The model clearly fits the in-river migrant groups (diamonds) better than transported groups (open rectangles). Derived estimates of 2006 plume survival and residence time (triangles; vertical lines show maximum and minimum estimates) also fit the pattern of a simple exponential decline in survival with residence time. The excluded 2009 early-release transport group is also shown (star). (Right panel) Residuals from the regression relationship exhibit greater variance when the spread in plume entry times is low (measured by median absolute deviation), as is also the case for all of the transported groups (open rectangles) in this study. Median absolute deviation at the Bonneville dam sub-array is shown for 2006 (triangles); there are no data for the 2006 transport group as they were released in the vicinity of Bonneville sub-array.

In conclusion, a simple exponential decay model describes juvenile yearling Chinook salmon plume survival well, although the model performs best when analysis is restricted to groups of fish whose individuals enter the plume over a longer time period (Fig. 2). Cohesion in the timing of plume entry in transport groups may mean that a chance encounter with aggregated predators would disproportionately affect overall survival relative to more dispersed groups. This may explain the greater variability in the survival of transported groups and thus the poorer model fit (Fig. 2). The derived estimates of 2006 plume survival lend additional support to the idea that plume survival is negatively related to travel time. We believe that plume residence times (average 7.3 days) were too short for starvation to have had an effect and that predation was the most likely cause of plume mortality (Methot and Dorn 1995; Collis et al. 2002; Lyons et al. 2005; Agostini et al. 2006; Emmett et al. 2006). Plume survival does not appear to be related to biological productivity measures, but there may be a weak effect of exposure to total dissolved gas levels near 125% in the lower Columbia River (a possibility we are exploring in a separate analysis).

While it appears that higher yearling Chinook salmon plume survival could be obtained by reducing residence time, the best model of plume residence time includes only sea surface temperature, which suggests that improving plume survival is beyond management control. Models that included upwelling or river discharge (which can be influenced by management action) had little weight, which is consistent with Burla et al. (2010a) who found that the physical dynamics of the plume at the time of ocean entry do not affect fish survival.

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Mesoscale Eddies as a Climate-Linked Mechanism for Driving Inter-Annual Variability in Ocean Survival of Pink Salmon

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Keywords: pink salmon, ocean survival, hatcheries, eddies, climate change, stable isotopes, Prince William Sound, Alaska

The short two-year life history of pink salmon (*Oncorhynchus gorbuscha*), the most abundant of the Pacific salmon, lends itself to better understanding of processes occurring during early marine life history, which might drive the species' considerable ocean survival variation.

Hypotheses that pink salmon ocean survival is determined during their early marine life history date at least as far back as the work of Parker (1968). More recently, Pyper et al. (2001) hypothesized that pink salmon ocean survival is driven during the coastal early marine stage because of spatial co-variation among local (within 10² km) stocks. Kline et al. (2008) and Kline (2010) found strong stable isotope correlations with ocean survival rate of those Prince William Sound (PWS), Alaska, pink salmon hatchery stocks that Pyper et al. (2001) found to spatially co-vary. Mesoscale eddies can drive isotopic variation and hence PWS pink salmon ocean survival (Kline 2010). These eddies are a dominant oceanographic and ecological feature in the northeastern Pacific Ocean because they may contain 80% of the primary production during spring months (Crawford et al. 2007).

It is possible to accurately assess pink salmon ocean survival from relatively recent hatchery production. Because hatchery output of pink salmon (number of fry released) is given following the freshwater stage, the relationship between this value and the returning population size potentially provides a more accurate assessment of ocean survival compared to estimates based on natural spawning in streams. For example, ocean survival of natural spawning populations may be assessed by using the ratio of number of returning adults to number of adults in the previous generation or R/S. The R/S necessarily includes mortality taking place during the freshwater stages, such as eggs and alevins that are subject to mortality caused by flooding and de-watering, for example. Hatchery output is also relatively constant from year to year eliminating the number of spawners as a driver of even- and odd-year survival differences that one could have in streams (Table 1). Since the late 1990's all pink salmon hatchery production from PWS has been thermally marked (otoliths) enabling accurate estimation of hatchery production caught in the fishery and in other sampling. Hatchery-specific issues may be reduced by merging production across multiple hatcheries.

Table 1. Prince William Sound pink salmon hatchery production, ocean survival, stable isotope values, and categorization of high, low, and intermediate ocean survival rates based on a combination of $\delta^{13}\text{C}$ value and ocean survival are summarized. Red and green colors used to emphasize, respectively, low and high values. Hatchery abbreviations: CCH = Cannery Creek hatchery, WNH = Wally Noerenberg hatchery, and SGH = Solomon Gultch hatchery. The $\delta^{13}\text{C}$ values are based on analyses of NLF = northern lampfish juveniles (length < 50 mm) and *Neocalanus cristatus* stage-5 copepodites.

Ocean entry year	CCH fry released	CCH fry return	WNH fry released	WNH fry return	SGH fry released	SGH fry return	Total fry released	Total fry return	Ocean survival	$\delta^{13}\text{C}$		Category
millions of salmon										NLF	<i>Neocalanus</i>	
1998	138	8.1	104	9.5	195	14.9	436	32.5	7.4%	-21.4	-23.4	Intermediate
1999	131	6.5	127	8.4	214	12.4	472	27.2	5.8%	-21.4	-20.9	Intermediate
2000	132	2.1	116	7.2	196	16.1	444	25.4	5.7%	-22.2	-23.2	Intermediate
2001	139	1.6	128	5.6	204	5.3	471	12.5	2.6%	-22.9	-25.5	Low
2002	139	8.3	106	17.8	203	17.3	447	43.5	9.7%	-21.3	-19.1	High
2003	136	2.8	120	2.7	206	11.1	462	16.6	3.6%	-22.1	-24.6	Low
2004	136	13.5	110	9.2	222	18.1	468	40.8	8.7%	-20.6	-18.3	High
2005	127	2.9	84	4.1	222	9.1	433	16.0	3.7%	-21.6	-22.3	Intermediate
2006	138	7.4	85	7.5	217	23.9	440	38.9	8.8%	-20.8	-19.6	High

Survival rates of three of the four pink salmon hatcheries located in PWS have historically co-varied along with those spawning naturally in streams (Pyper et al. 2001). The one hatchery that has not co-varied is located closer to the open sea than the others (Fig. 1). A goal of this paper is to posit a mechanism that may explain the stable isotope as well as survival observations.



Fig. 1. Sampling location, in red, and locations of Prince William Sound pink salmon hatcheries. Hatchery abbreviations: CCH = Cannery Creek hatchery, WNH = Wally Noerenberg hatchery, SGH = Solomon Gultch hatchery, and AFK = Armin F. Koernig hatchery. Base map from Google.

Sampling took place on long-term observational program oceanographic cruises that began as part of the Northeast Pacific Global Ocean Ecosystem (GLOBEC) research effort (Weingartner et al. 2002). Sampling stations included a transect line known as the Seward Line. Stable isotope data from samples consisting of multiple whole organisms were collected at the set of four stations (GAK 10 to GAK13) that were part of the Seward Line located over the continental slope (Fig. 1). Stage copepodite-5 (*Neocalanus cristatus*) copepods and juvenile (length < 50 mm) northern lampfish (*Stenobranchius leucopsarus*) were sampled systematically (5 copepods per station and 100% of the *Stenobranchius* per station) during May in continental shelf waters during the nine-year time series, 1998 to 2009. Carbon stable isotope values are reported by convention as delta units. The delta unit, which is expressed as $\delta^{13}\text{C}$ for $^{13}\text{C}/^{12}\text{C}$, is the per mil deviation (parts per thousand) from the internationally recognized isotope standard for carbon, Vienna Pee Dee Belemnite (VPDB). Because VPDB is relatively enriched in ^{13}C , organic matter generally has a negative value. Measurement precision is 0.1 per mil. The $\delta^{13}\text{C}$ values were corrected for lipid content as described by Kline (2010). Relatively high and low $\delta^{13}\text{C}$ values are indicated in Table 1 by, respectively, green and red colors. Positive significant ($p < 0.05$) correlations ($r^2 \sim 0.7$) were found between pink salmon ocean survival and $\delta^{13}\text{C}$ values confirming the hypothesis that early marine processes can drive their ocean survival (Kline et al. 2010).

Ocean survival (Table 1) was based on hatchery production data provided by the hatchery operators, the Prince William Sound Aquaculture Corporation and the Valdez Fisheries Development Association (Kline et al. 2008). Relatively high and low ocean survival rates are indicated in Table 1 by, respectively, green and red. Years were categorized as “High”, “Low”, and “Intermediate” using a combination of $\delta^{13}\text{C}$ value and ocean survival (Table 1). In 2003, the year with second lowest ocean survival (although not very low) during the observation period is indicated as low in order to have $N = 2$ and also because of the low $\delta^{13}\text{C}$. Samples collected in 2001 had both the lowest ocean survival and lowest $\delta^{13}\text{C}$ values. Samples collected in 2002, 2004, and 2006 were categorized as high years due to a combination of high ocean survival ($\geq 8.7\%$) and relatively high (> -21) $\delta^{13}\text{C}$ values for one or both organisms. Samples collected in 1998, 1999, 2000, and 2005 were designated intermediate years. Intermediate $\delta^{13}\text{C}$ values of *Neocalanus* were $\sim -23 \pm 1$, other than in 1999.

Mesoscale eddies were identified using sea-surface height anomaly maps generated through the Colorado Center of Atmospheric Research web page (Kline 2009). These maps are shown aggregated by year-category in Fig. 2. Mesoscale eddies have an anticyclonic flow pattern: when they approach the continental shelf near the Seward Line they entrain coastal waters and have an on-shore flow on their leading (western) edge while propagating westward (Okkonen et al. 2003).

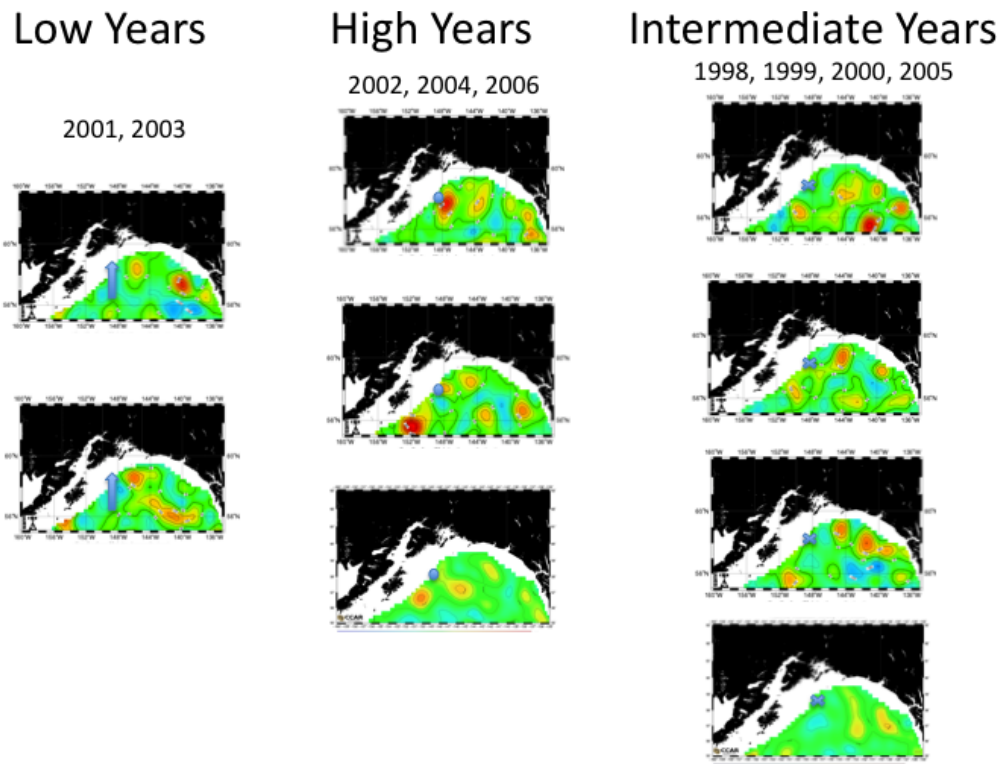


Fig. 2. Sea-surface height anomaly data in May at the time of sampling stable isotopes (Table 1) and interpreted flow pattern by year. Low years, 2001 and 2003, were characterized by eddies immediately east of the sampling area and on-shore flow (blue arrow). High years, 2002, 2004, and 2006, were characterized by eddies present in the sampling area and offshore movement of coastal water (blue circle). Intermediate years, 1998, 1999, 2000, and 2005, were characterized by no eddy in the sampling area or immediately east of the sampling area and thus no cross-shelf flow (blue X).

Anti-cyclonic mesoscale eddies can explain the stable isotope observations (Table 1; Fig. 2). Ocean survival was low for those cohorts when an eddy was located just east of the sampling area in May. The on-shore circulation pattern likely drove the low carbon isotope values observed. Low carbon isotope values were posited to reflect Fe-limited oceanic production (Kline 2010). Conversely, ocean survival was high in years when the May sampling area was located within an eddy and isotope values were high. Eddies entrain and retain coastal waters with their properties and biological constituents (Batten and Crawford 2005). Consequently, oceanic biota in eddies took on high values similar to those more typical of coastal habitats (Kline 2010). No eddy was present in the sampling area in May of years with intermediate ocean survival and intermediate isotope values. These observations suggest that location and presence of mesoscale eddies in May are important factors for driving both ocean survival and isotope value and thus the correlation between isotope value and survival. The multi 100-km spatial scale of eddies is also similar to the spatial scale of co-variation observed of pink salmon populations (Pyper et al. 2001). There is, however, a spatial disconnection between eddies and ocean survival because salmon are not yet in the ocean environment in May. Eddies may thus be important for “setting the stage” for in-coming salmon. Eddies may form a “hot spot” that draw predators away from coastal habitats to the open ocean increasing survival while salmon are still inshore. Eddies thus may “shelter” salmon by providing alternate prey for salmon predators.

Predators heading towards an eddy may exit PWS by passing near the Armin F. Koernig (AFK) hatchery (Fig. 1) providing a potential opportunity for predation. This is a further potential source of variability given that there are multiple pathways between PWS and the open sea; predators may not necessarily pass near AFK and may not be present when pink salmon juvenile are abundant. Stochastic aspects of this hypothetical process may explain the lack of any relationship in the pink salmon ocean survival between AFK and the other hatcheries.

Eddies represent a process that is likely influenced by climate change through the hydrological cycle because they entrain and transport fresher water into the Gulf of Alaska (Crawford 2005). Hydrology (e.g., precipitation) is an important climate variable. Yakutat eddies, in particular, entrain coastal water when they form and retain it as they propagate westward in the northern Gulf of Alaska (Janout et al. 2009). As well, eddies are temporally variable; inter-annual variation has been observed thus far (Henson and Thomas 2008). Eddies should be important components of models that link physical and biological conditions with climatic implications.

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Is Declining Sockeye Salmon Survival the Result of Competition at Sea and Declining Carrying Capacity?

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Keywords: sockeye salmon, marine survival, competition, carrying capacity

Many sockeye salmon (*Oncorhynchus nerka*) populations in the eastern North Pacific experienced significant productivity declines that began about 1990, but there is no consensus on the mechanisms responsible. We examined the 50-year time series for two age classes of sockeye salmon smolts from Chilko Lake in central British Columbia, Canada. Our new survival time series shows a clear pattern break in smolt survival ~1991, when a trend of increasing survival in 1960-1990 changed to a lower and declining survival trend in 1992-2008. We present a simple model to illustrate how increased competition at sea, related in part to the release of large numbers of hatchery salmon in conjunction with changes in ocean productivity, may have played a significant role in improving sockeye salmon survival while reducing their growth before 1991, and reducing survival while the growth of survivors showed no effect afterwards.

Size-Selective Mortality of Bristol Bay Sockeye Smolts in Relation to Smolt Characteristics, Ocean Conditions, and Sockeye Salmon Productivity

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Keywords: sockeye salmon, pollock, scale growth, smolt size, size-selective mortality, density-dependence, Kvichak River, Bering Sea

Mortality of salmon in the ocean is generally believed to be size-selective in which smaller, slower growing fish are less likely to survive (e.g., Moss et al. 2005); however, relatively little is known about the degree to which size-selective mortality varies over decades and is related to ocean conditions, climate shifts, and salmon smolt characteristics. We are currently investigating size-selective mortality of Bristol Bay sockeye salmon, and here we present preliminary findings on Kvichak sockeye salmon. Kvichak River sockeye salmon is the most abundant sockeye stock in the North Pacific (producing annual runs up to 48 million fish), and in some peak-cycle years the Kvichak watershed produced more than 50% of the North Pacific's sockeye salmon (Eggers and Rogers 1987; Ruggerone and Link 2006). Beginning with the 1991 brood year and the adult return in 1995, however, productivity of the Kvichak stock averaged less than one return per spawner (R/S), leading the State of Alaska to classify Kvichak sockeye salmon as a Stock of Concern, even though the habitat was relatively pristine and managers eliminated direct harvests and reduced incidental harvests. The stock has begun to recover in recent years (Morstad and Brazil 2012).

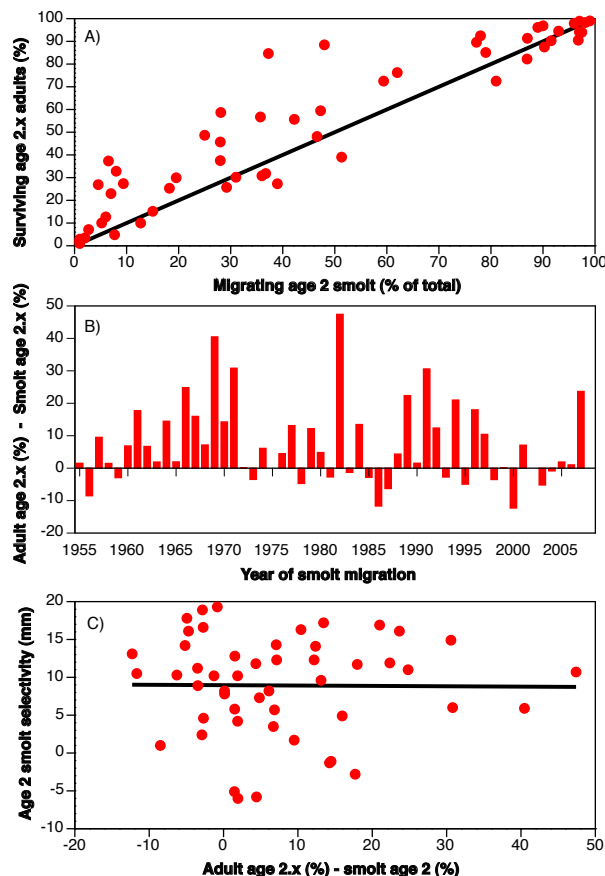


Fig. 1. Tests to examine whether there was significant avoidance of the fyke net by larger age-2 sockeye salmon smolts in the Kvichak River, Bristol Bay, Alaska. All values are aligned by year of smolt migration. For panel C, a positive slope is expected if selectivity of age-2 smolts was significantly affected by avoidance of the net by large smolts. Tests show that age-2 smolts have higher survival than age-1 smolts, as expected, but there was no evidence of significant net avoidance.

We estimated the degree of size-selective mortality of age-1 and age-2 smolts as follows:

$$(1) \text{ Selectivity (mm)} = \text{Length of surviving smolts (mm)} - \text{Length of migrating smolts (mm)}.$$

Mean lengths of age-1 and age-2 sockeye salmon smolts migrating in the Kvichak River from 1955 to 2008 were obtained from annual smolt reports produced by the Alaska Department of Fish and Game and other agencies (e.g., Kerns 1961; Paulus and Parker 1974; Wade et al. 2013). Smolt sampling methods using a fyke net in the Kvichak River have remained largely unchanged over the years (Crawford and Tilly 1995). Net avoidance studies were conducted in the 1960s to minimize net avoidance by larger smolts (e.g., age-2 fish; Kerns 1961). Field crews consistently placed the net in the fastest water possible without losing the net (> 0.9 m/s). We re-examined potential net avoidance by larger age-2 smolts during the past five decades but found little evidence that avoidance might bias the patterns of size-selective mortality (Fig. 1).

To estimate the size of Kvichak sockeye salmon smolts that survived two or three years at sea, we developed a smolt length/scale radius regression and back-calculated size of age-1 and age-2 smolts from adult sockeye scales collected from 1957 to 2010. Smolt scales were collected using scrapes from the preferred scale area (versus single scales from the preferred area among adults); therefore, a small correction (3%) was made to the smolt scale measurements based on analysis of scrape versus individual scale data provided by Clutter and Whitesel (1956). Analysis of covariance and visual plots did not indicate different relationships with respect to sockeye salmon stock (five stocks) or year of smolt migration (five years). Length-at-age of surviving sockeye salmon smolts was calculated from the weighted mean of 50 freshwater scale measurements from each major adult age group per year (up to 200 scales per year).

Mean length of emigrating age-1 and age-2 sockeye salmon smolts averaged 87 mm and 107 mm, respectively, during smolt years 1955-2008. Mean length of migrating smolts were smaller and less variable after the mid-1970s. Mean length of surviving age-1 and age-2 smolts (back-calculated from adult scales) after two or three years at sea was 101 mm and 116 mm, respectively. Length of survivors was variable from year to year, but we observed no clear trend over time. Length of surviving smolts increased with length of the migrating smolts, but the slope was less than one indicating less benefit of greater size at the higher end of both smolt age groups.

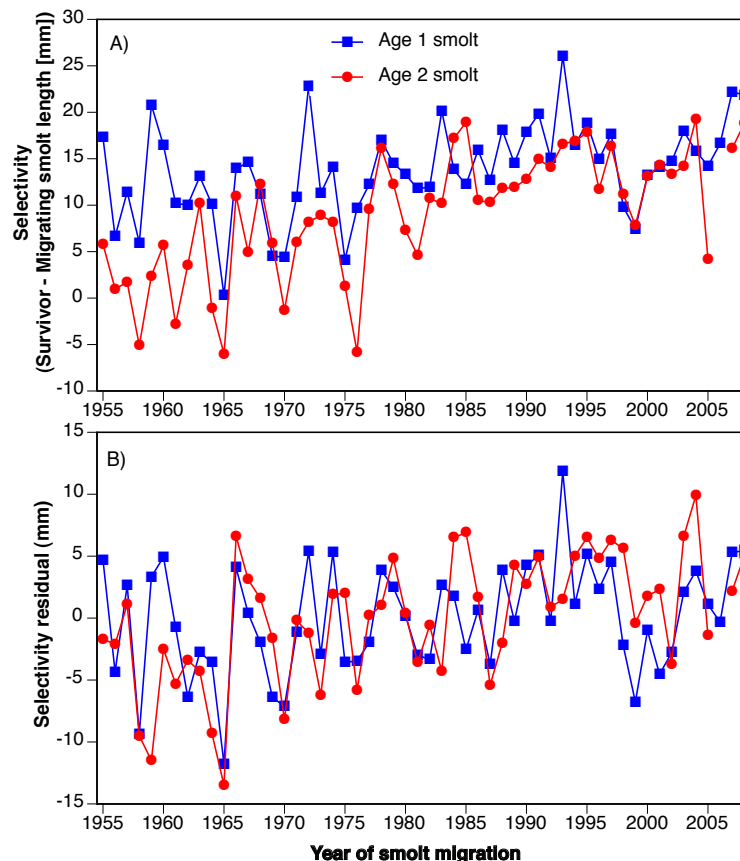


Fig. 2. Selectivity (A) and selectivity standardized for length of emigrating Kvichak River sockeye salmon smolts (B), 1955-2008. Panel (B) values are the residuals of the regressions shown in Fig. 3.

Selectivity of the sockeye salmon smolt age groups was correlated over the 54-year period, and it was consistently higher for age-1 smolts (average 14 mm) versus age-2 smolts (9 mm), as expected, because younger smaller fish are likely to experience greater size-selective mortality. Selectivity tended to be somewhat low and highly variable during the 1950s to early 1970s, then increased after the mid-1970s and became somewhat less variable (Fig. 2A). The high variability in the early period reflects, in part, the high variability in parent spawning escapement, juvenile abundance in the lakes, and length-at-age.

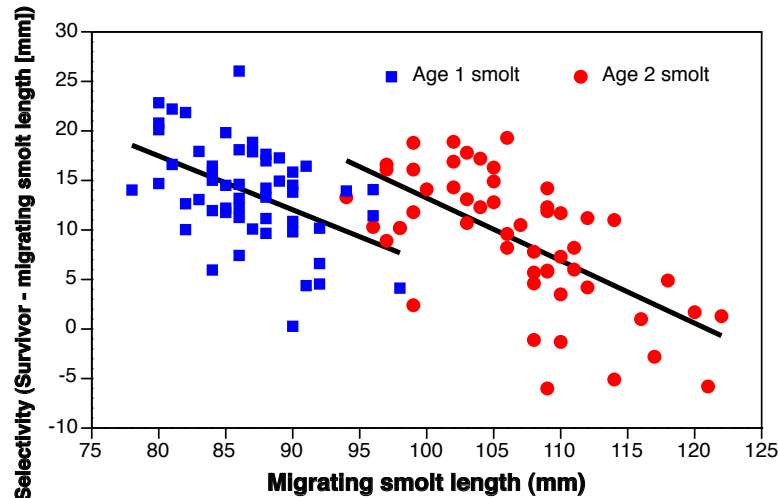


Fig. 3. Selectivity of age-1 and age-2 Kvichak River sockeye salmon smolts in relation to length of migrating smolts.

Selectivity of age-1 and age-2 sockeye salmon smolts declined with mean length of emigrating smolts, as expected (Fig. 3). However, when mean length of age-1 and age-2 migrating smolts overlapped, selectivity was less for age-1 versus age-2 smolts, perhaps reflecting the greater fitness of rapidly growing age-1 smolts versus slower growing age-2 smolts of the same body size. Using the regressions in Fig. 3, we standardized selectivity for length of migrating smolts (i.e., residual of the regressions). Standardized selectivity tended to be low and variable during the early period followed by somewhat higher selectivity after the mid-1970s and lower selectivity during 1998 to 2002, i.e., the years immediately following the strong 1997/1998 El Niño (Fig. 2B).

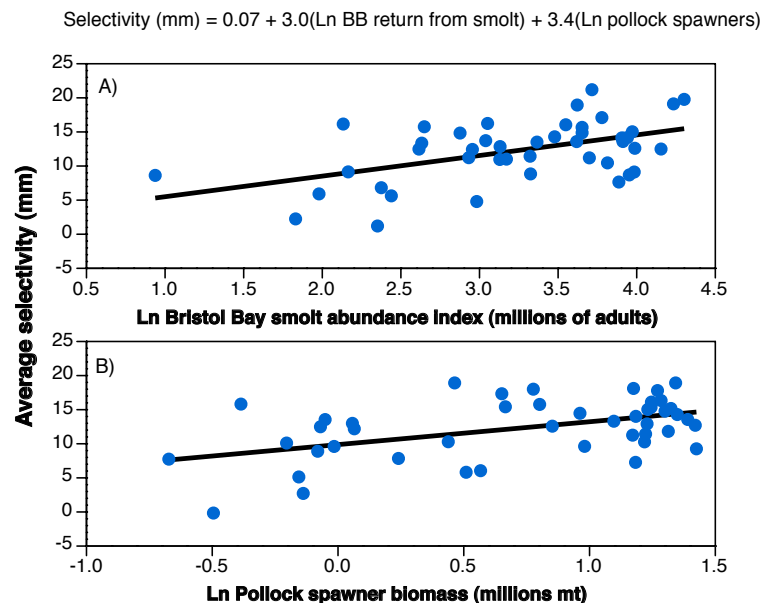


Fig. 4. Multi-variate relationship between average selectivity of age-1 and age-2 Kvichak River sockeye salmon smolts in relation to (A) an index of total sockeye salmon smolts entering the southeastern Bering Sea (based on adult returns from each smolt year) and to (B) an index of age-0 pollock (sockeye prey) during the year of smolt migration, 1964-2008. Both independent variables were significant ($p < 0.05$); overall variability explained by smolt abundance and pollock was 45% (adjusted R^2). Serial autocorrelation of model residuals (0.12) was non-significant.

We plan to conduct additional tests to further examine factors affecting selectivity and how the selectivity index may be related to sockeye salmon productivity. Initial preliminary analyses indicated selectivity of Kvichak sockeye was higher during years of high total sockeye smolt abundance entering the southeastern Bering Sea (Fig. 4A), perhaps reflecting early marine density-dependent growth and survival of sockeye salmon, as indicated by a recent study in the Bering Sea (Farley et al. 2011). Selectivity was also correlated with an index of age-0 pollock abundance in the southeastern Bering Sea in a multivariate regression that included abundance of Bristol Bay sockeye salmon smolts as an independent variable (Fig. 4B). This relationship might reflect an advantage for larger sockeye smolts when juvenile pollock are abundant because larger sockeye salmon eat larger, more energetic juvenile pollock which can be a highly important prey in warm water years (Farley et al. 2004; Farley and Trudel 2009; Farley et al. 2009, 2011).

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Control of the Parasitic Flagellate *Ichthyobodo salmonis*, a Causative Agent of Marine Mortalities of Juvenile Chum Salmon

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Keywords: juvenile chum salmon, marine mortality, parasitic flagellate, *Ichthyobodo salmonis*, control

Survival of juvenile salmon in the ocean is affected by various factors including diseases caused by infectious organisms. *Ichthyobodo salmonis* is an ectoparasitic flagellate infecting the skin and gills of salmonid fishes such as Atlantic salmon (Isaksen et al. 2011). In Japan, the parasite has been recorded as *I. necator* from juvenile chum salmon at hatcheries (Urawa 1992a; and others). Infection experiments have indicated that heavy parasite infections cause severe erosion of the skin epidermis of juvenile chum salmon (Fig. 1), resulting in high mortality of anadromous hosts due to osmoregulatory failure when they migrate into the coastal ocean (Urawa 1993). The parasitic infections commonly occur at salmon hatcheries (Urawa 1992a, 1996). A bath with a dilute formalin solution is the most effective way to treat infected fish (Fig. 2A). In Japan, however, the use of formalin on hatchery fish is restricted because of revision of the Pharmaceutical Affairs Law in 2003. Alternative effective treatment methods are currently not available for hatchery salmon, and some hatchery managers believe that the recent decrease of chum salmon returns in Japan might be partly caused by parasite infections.

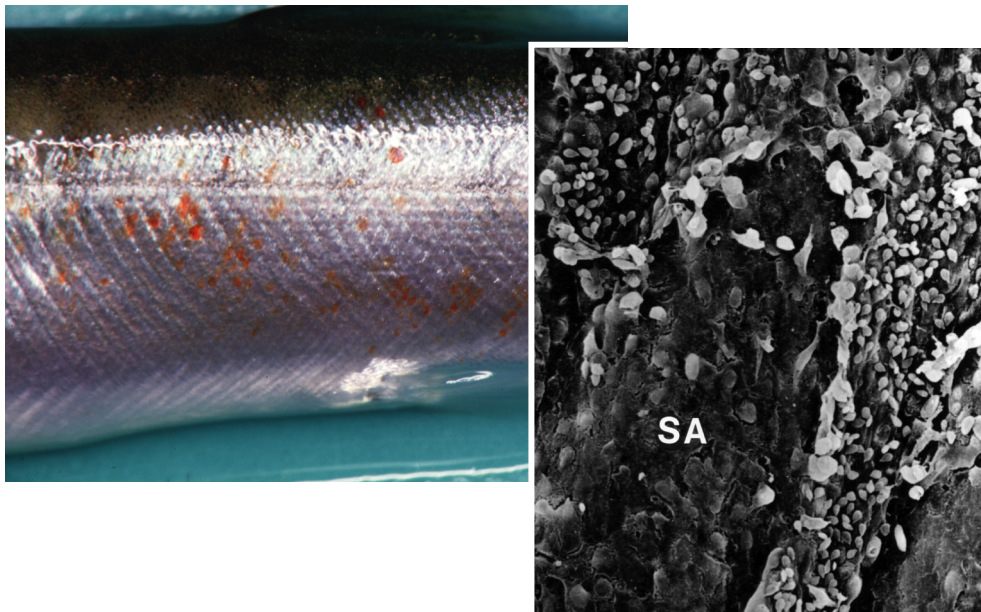


Fig. 1. Heavy parasitic infection caused severe erosion and hemorrhage in the skin epidermis of juvenile chum salmon, and a large area of the epidermal upper layer (SA) was sloughed off. The right image was observed by a scanning electron microscopy (cited from Urawa 1992b).

The present study aimed to develop a safe method to control *I. salmonis* infections of juvenile chum salmon. Various concentrations of salt and vinegar solutions were tested on juvenile chum salmon heavily infected with *I. salmonis*. A 10-min bath with a high concentration (5%) of salt water decreased parasite density (Fig. 2B), but also had a high risk of killing the juvenile fish because the parasite infections reduced the fish's tolerance to salt water (Urawa 1993). Because *I. salmonis* on anadromous salmon can survive even in sea water (Urawa and Kusakari 1990), low concentrations of salt water were not effective to control the parasite infections. A bath containing 0.4-1.0% corn vinegar could control the parasite, but exposure to a 1% corn vinegar (pH 3.9) bath over 15 minutes weakened or killed the treated fish (Fig. 2D). The present treatment study suggested that a one-hour exposure in a bath of low concentration (0.4%, pH 4.5) of corn vinegar is a safe method to control *I. salmonis* infections on juvenile chum salmon at hatcheries (Fig. 2C).

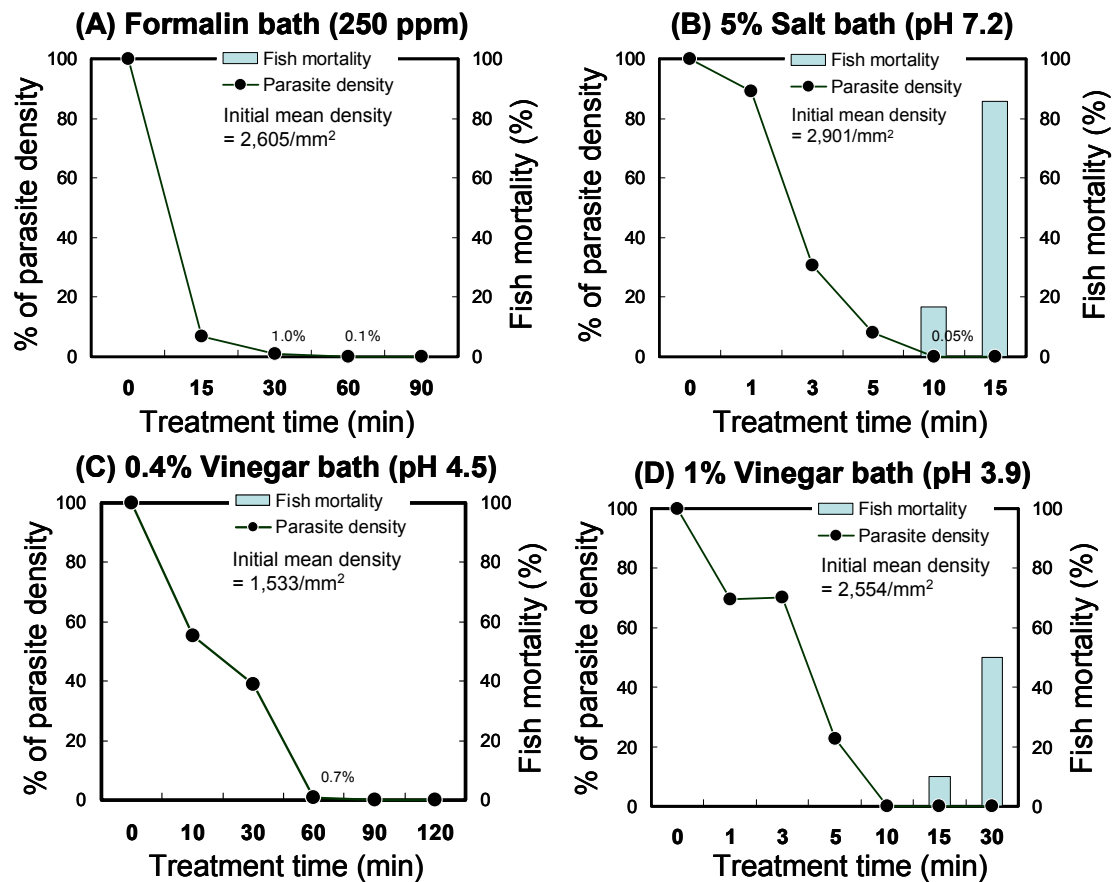


Fig. 2. Effects of various bath treatments on the density of *Ichthyobodo salmonis* on the skin of juvenile chum salmon. Blue bars indicate fish mortality (%) during the treatment.

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Coastal Residence of Juvenile Chum Salmon and Their Adult Returns to the Ishikari River, Hokkaido

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Keywords: juvenile chum salmon, coastal residence, catch per unit effort, otolith analysis

Based on coastal and river catch sizes, the number of chum salmon returning to Hokkaido rivers draining into the Sea of Japan (SJ) region have fluctuated at levels lower than fish returning to rivers draining into the Pacific Ocean and the Sea of Okhotsk. The Ishikari River stock is one of the largest in the SJ region; ~30 million otolith-marked chum fry are released annually from the Chitose Hatchery, which is the only hatchery producing chum salmon fry in the river. Despite the constant number of fry released from the Chitose hatchery, there are large fluctuations in the return of adults to both the Ishikari River (river catch) and SJ region (coastal catch and river catch) stocks.

Improving the number of adult returns to the SJ region would contribute to developing effective strategies for recovering salmon stocks in the region. The early period of marine residence is a critical period for juvenile salmon survival (e.g., Bax 1983; Fukuwaka and Suzuki 2000; Saito et al 2011). Identification of factors that affect juvenile survival during periods of coastal residence is essential for developing salmon propagation techniques aimed towards improved survival of released fish.

We analyzed data for juvenile chum salmon caught in surface trawl surveys conducted in March–July during 2003–2009 in the coastal waters off Atsuta, which is located on the coast near the mouth of the Ishikari River. Atsuta is on the main northward migration route of juveniles originating from the Ishikari River (Mayama and Ishida 2003). Catch per unit effort for otolith-marked juveniles was positively correlated with the return rates of adult salmon to the Ishikari River, suggesting that the abundance of marked fish recaptured at Atsuta is an indicator of survival during early marine residence.

Based on samples obtained from the trawl surveys, we investigated daily growth, sea entry timing, and days of residence in the river and in the sea for three groups of mark-recaptured juvenile chum salmon released at different times (mid-March, late-March, and mid-April) by analyzing otolith daily growth increments. The earlier the fish were released, the earlier they entered the sea; early-released fish spent protracted periods in both the river and the sea. The daily growth of chum salmon after entering the sea was unaffected by the date of entry into the sea. However, adult return rates differed among juveniles released at different times. Chum salmon in the late-March release group had the highest return rate of adults. In the coastal waters off Atsuta, the temperature at 3-m depth during the peak period when juvenile chum salmon appear ranges from 7° to 10°C. The date when water temperatures first warmed to 7°C following the winter period varied by about 20 days from 2003 through 2009. The number of the adult chum salmon returning to the river was negatively related to the number of days after March 1 that water temperatures were below 7°C off Atsuta. Thus, appropriate timing of the seaward migration is an essential component of improved juvenile survival.

The combined effects of seaward migration timing and temperature conditions in the coastal ocean probably strongly affect the survival of Ishikari River juvenile chum salmon.

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Effects of Salinity on Haematological Biochemistry and Structure of Liver Tissue in Young Chum Salmon (*Oncorhynchus keta* Walbaum)

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Keywords: juvenile chum salmon, salinity, biochemical indicators, histology, Heilongjiang River

Salinity is an important factor in the environmental condition of fish by influencing osmotic pressure and metabolism (Jiang et al. 2005; Mustafayev and Mekhtiev 2008); causing changes to the activity, structure, and physiological function of fish digestive enzymes; and affecting development, habits, and survival of fish (Chen et al. 1998; Wang and Zhu 2002). Studies of marine fish, such as the olive flounder (*Paralichthys olivaceus*) and cobia (*Rachycentron canadum*), have shown a common relationship between osmotic pressure and salinity changes; under conditions of acute salinity stress Na⁺, K⁺, and Cl⁻ ions have a regulating effect (Kiyashco et al. 2006; Pan et al. 2006). Fish, such as ayu (*Plecoglossus altivelis*) and Chinese sturgeon (*Acipenser sinensis*), that migrate between life stages in freshwater and marine environments have a two-way ion-regulating conversion mechanism (Saruwatari 1995; Xu et al. 2008). There are very interesting ecological evolutionary phenomena of some halophilic fish, such as the herring (*Clupeonella cultriventris*), which have formed populations in the upper reaches of the Volga River (Yang et al. 2005). Clearly, fish osmoregulation has been highly plastic in adapting to salinity changes.

Most salmon (*Oncorhynchus* spp.) are euryhaline and have a strong migratory adaptation. The catadromous migration of juveniles is a critical period that constrains populations and regression rates (Dong et al. 1999; Zhan et al. 2002). Juvenile salmon migration to the sea is mainly caused by genetics, ecological factors, and food availability (Kaeriyama 1986; Makismovich 2008). Environment affects their physiology, growth, and living conditions (Uchida et al. 1996; Liu et al. 2006; Zhi et al. 2009). Although many scholars have reported on the proliferation of salmon resources, population structure, and ecological protection (Altinok et al. 1998; Vander Linden et al. 1999), few studies have reported on salmon eco-physiology during early stages of life.

Changes to the physiological and biochemical structure and function of Heilongjiang River fall-run juvenile chum salmon (*O. keta*) from long-term exposure to low salinity environments have not been reported previously. Our study simulated the salinity environments of out-migrating juvenile chum salmon. The study focused on serum osmolality, ion content, and liver function and structural changes that occurred during the growth process. We identified problems in salinity adaptation and tolerance of freshwater by chum salmon juveniles.

An experimental study was conducted on haematological biochemistry and structure of liver tissue in young chum salmon (body weight: 26.57±6.32 g, total length: 14.44±1.05 cm). Five different salinity (ppt) treatment groups were tested including 0‰ (freshwater), 5‰, 10‰, 15‰, and 20‰, respectively. Fish in freshwater served as the control. The acute salinity exposure experiments lasted for 130 days, and there were triplicates in each treatment.

Table 1. Change in juvenile chum salmon serum concentration (mg/L) of metals and inorganic ions of fish reared in different salinity treatment groups (0‰ [freshwater], 5‰, 10‰, 15‰, and 20‰) over the period from 1 day (1 d) to 10 days (10 d).

S ‰	Fe		Mn		Na		K		Ca		Mg		Cl ⁻		Ca ²⁺	
	1 d	10 d	1 d	10 d	1 d	10 d	1 d	10 d	1 d	10 d	1 d	10 d	1 d	10 d	1 d	10 d
0	<0.03	<0.03	0.015	0.011	105	108	16.8	18.6	280.7	307.1	48.1	51.4	4805	5285	1348.3	201.4
5	<0.03	<0.03	0.062	0.044	1153	1100	49.1	59.6	363.0	416.9	138.0	140.0	3800	3965	1766.7	443.08
10	<0.03	0.034	0.052	0.026	2332	2298	85.7	99.6	411.3	461.8	276.0	266.0	9610	7688	1952.7	322.24
15	<0.03	<0.03	0.117	0.043	3245	3446	127.3	136.3	508.1	543.2	396.0	394.0	10571	11532	1766.7	281.96
20	<0.03	0.034	0.042	0.025	4573	5074	174.7	171.9	586.2	620.0	557.0	522.0	12380	13454	1813.2	281.96

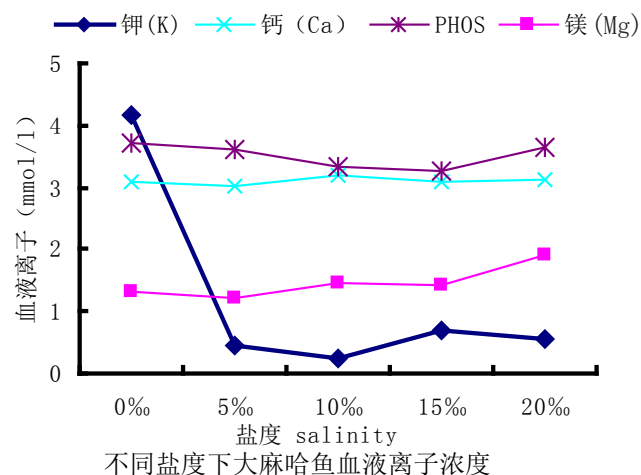


Fig. 1. Serum osmotic pressure and electrolyte concentration in juvenile chum salmon reared in different salinity treatment groups (0‰ [freshwater], 5‰, 10‰, 15‰, and 20‰) for 130 days.

Results showed that osmolality and Na^+ and Cl^- content of serum collected from juvenile chum salmon increased with increasing salinity (Table 1). Osmolality and the serum content of Na^+ in the 15‰ and 20‰ salinity treatment groups were significantly different than in other groups ($p < 0.05$). The concentration of serum Cl^- was significantly different in fish in the freshwater treatment group compared to the 15‰ and 20‰ salinity treatment groups ($p < 0.05$). The content of serum magnesium (Mg^{2+}) in fish in the 20‰ salinity treatment group was significantly higher than in sera collected from fish exposed to 0‰ and 5‰ salinity concentrations ($p < 0.05$). The content of serum potassium (K^+) among the different salinity treatment was significantly different ($p < 0.05$; Fig. 1).

The effect of salinity on juvenile chum salmon serum glucose was relatively significant; the content of blood glucose was highest in juvenile chum salmon exposed to the 10‰ salinity treatment group and was significantly different than concentrations in fish in the 5‰ and 20‰ salinity treatment groups ($p < 0.05$).

The impact of salinity exposure on blood lipid content was smaller. With the exception of total bile acids, other lipid indicators showed no significant differences among all the treatment groups ($p > 0.05$).

There was an overall downward trend in the content total protein (TP), albumin (ALB), and globulin (GLB) content of the sera of fish reared in the higher salinity treatment groups. The TP and GLB content in the sera of fish exposed to freshwater was significantly higher than found in sera collected from fish in the 15‰ and 20‰ salinity treatment groups ($p < 0.05$).

Alanine aminotransferase (ALT) and alkaline phosphatase (ALP) activity in sera collected from fish in the freshwater treatment group were significantly higher than in fish exposed to the other salinity treatment groups ($p < 0.05$; Fig. 2). Aspartate aminotransferase (AST) content of sera collected from fish in the 0‰ and 15‰ salinity treatment groups were significantly different ($p < 0.05$).

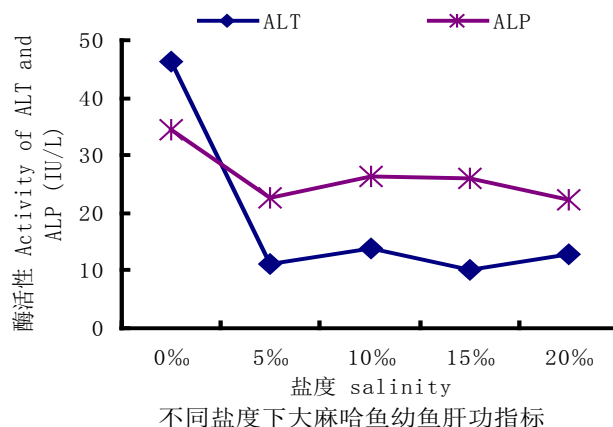


Fig. 2. Serum protein and enzyme activity of alanine aminotransferase (ALT) and alkaline phosphatase (ALP) in juvenile chum salmon reared in different salinity treatment groups (0‰ [freshwater], 5‰, 10‰, 15‰, and 20‰) for 130 days.

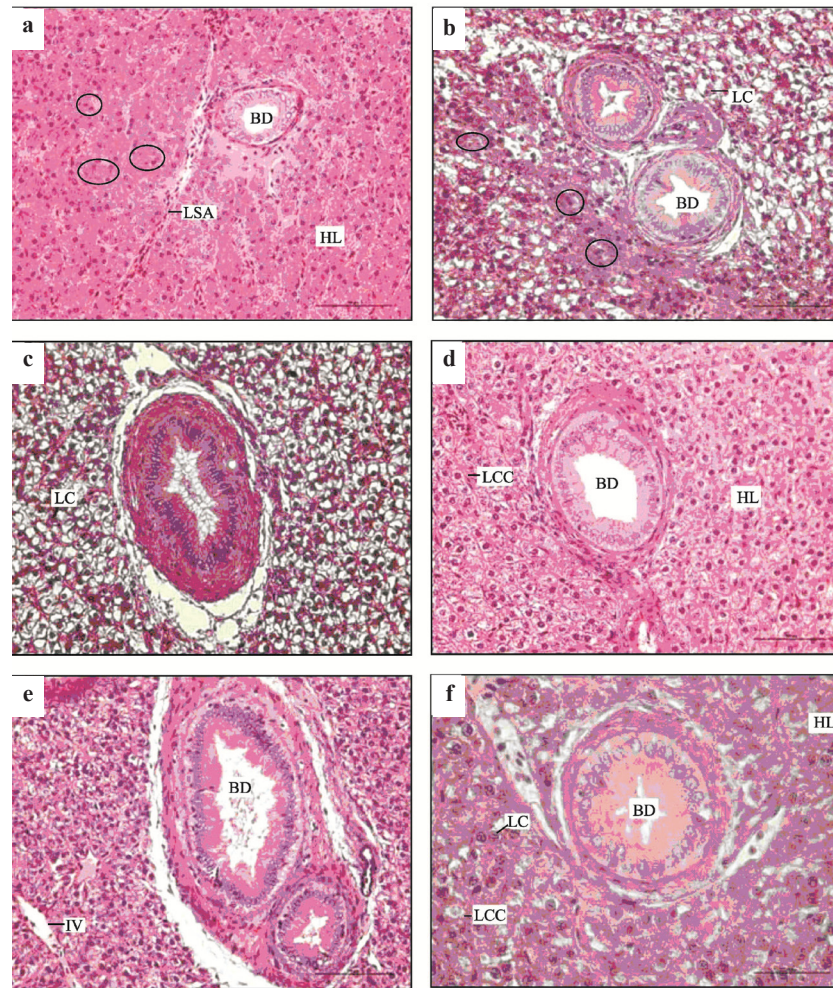


Fig. 3. Histological sections showing structural changes in liver tissue of juvenile chum salmon after exposure to different salinity treatment groups (0‰ [freshwater], 5‰, 10‰, 15‰, and 20‰) for 130 days. BD: bile duct; LSA: liver small artery; HL: hepatic lobule; LCC: liver cell cord; IV: interlobular vein; LC: liver cell. a. freshwater exposure, 20× magnification, bar=100 μm, “○” indicates a liver cells with large vacuoles and karyon showing atrophy and dissolution; b. 5‰ salinity exposure, 20× magnification, bar=100 μm; c. 10‰ salinity exposure, 20× magnification, bar=100 μm; d. 15‰ salinity exposure, 20× magnification, bar=100 μm; e. 20‰ salinity exposure, 20× magnification, bar=100 μm; f. 20‰ salinity exposure, 40× magnification, bar=50 μm.

The impact of salinity on the liver tissue of juvenile chum salmon was high; exposure to low salinity caused some liver cells to breakdown leading to serious vacuolization of the tissue (Fig. 3).

In summary, after rearing chum salmon juveniles for 130 days in different salinity treatment groups, fish blood osmotic pressure stabilized in the normal range, achieving an adaptive physiological balance. But osmotic pressure from salinity ions and elevated serum ion concentration increased, so osmotic pressure was closely related to changes both inside and outside the environment of the fish's body. Ion concentration and serum osmotic pressure in fish reared in the 15‰ and 20‰ salinity treatment groups were significantly higher than in fish reared in the other treatment groups. This affected permeability and indicated that juvenile chum salmon can quickly adapt and prefer high salinity conditions.

Juvenile chum salmon reared in the freshwater treatment group showed symptoms of high serum potassium. Potassium concentration increased to a level 18 times that of concentrations in fish reared in the 10‰ salinity treatment group, indicating that by maintaining osmotic pressure inside and outside the cell there were large loses of potassium into the extracellular fluid. This condition was mainly due to long exposure at the isotonic point of freshwater that causes damage to the myocardial cell membrane. Myocardial potassium entered into the blood and serum K⁺ concentration increased. At

the same time, serum AST also appeared to be at a higher value, further indicating myocardial membrane damage. It is worth noting that increased environmental salinity had no apparent influence of serum K^+ concentration because the average remained in the 0.23 ~ 0.69 range.

In general, Gregory et al. (1988) suggested increasing concentrations of serum Na^+ and Cl^- ions will decrease the concentration of K^+ ions in *Acipenser fulvescens*. This phenomenon was not obvious in our experiment perhaps because we used a different fish species. Our results also suggest that juvenile chum salmon may have a wide adaptative range for salinity. For salinities between 5‰ and 20‰, juvenile chum salmon can adjust to an osmotic balance. Our results are basically similar to those demonstrated by Hirai et al. (1999) and Rodriguez et al. (2002).

In the freshwater treatment group, juvenile chum salmon serum ALT enzyme activity was higher than in the other salinity groups by a factor of two to five times. Total bile acid content of fish in the freshwater treatment group increased to about three times over that of fish in the other salinity treatment groups.

Long-term exposure to freshwater caused varying degrees of injury to the liver and other organs. Histological observations confirmed that liver cells ruptured. In the freshwater and low-salinity treatment groups (0‰ and 5‰), a large number of vacuoles appeared at the same time in liver tissue. This suggested that at low salinity it is beyond the ability of juvenile chum salmon to make physiological adjustments, which results in pathological changes to the structure and function of liver tissue.

Juvenile chum salmon reared at salinities > 10‰ grew well. Biochemical indices were relatively stable, most histological examinations of liver cell structure were normal, and only some cells showed the appearance of small vacuoles.

In the natural environment, juvenile chum salmon migrating from the river to the ocean might be exposed to a range of salinities from 16‰ to 35.5‰. In general, the life habit of the fish is decided by heredity and cannot be changed. The effect of salinity exposure on visceral function is an important parameter to determine the readiness of juvenile chum salmon to adapt to the saline environment. There is a certain degree of adaptability and plasticity in juvenile chum salmon during their migratory period, but prolonged exposure to low salinity can cause various physical reactions and reduce survival time (Wang and Zhu 2002; Jiang et al. 2005).

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Influence of the Conditions in the Hairuzova and Belogolovaya Estuaries (Western Kamchatka) on Total Pacific Salmon Abundance

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Keywords: Hairuzova River, Belogolovaya River, West Kamchatka, estuary, hydrological and morphological conditions, Pacific salmon, juvenile salmon, abundance, mortality

According to the classification provided by Mikhailov and Gorin (2012), the estuaries of the Hairuzova and Belogolovaya rivers are considered as channel estuaries with mouth widening. Such estuaries occur in Kamchatka only on the northwest coast, northward from the Moroshechnaya River (Fig. 1).

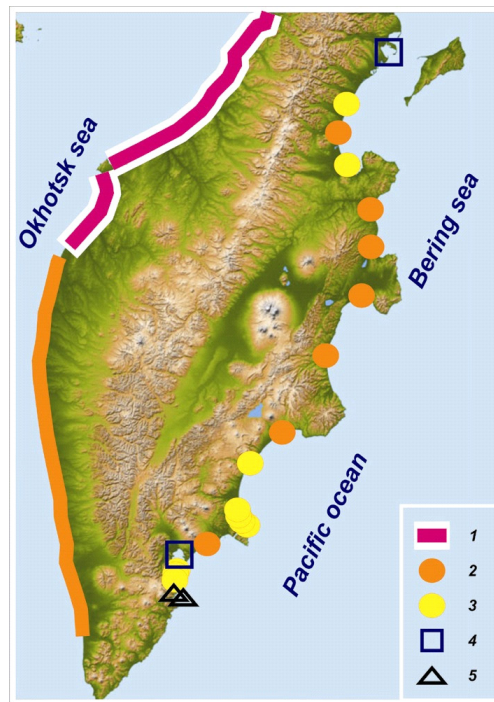


Fig. 1. Types of Kamchatka estuaries classified by Mikhailov and Gorin 2012. 1: channel estuaries with mouth widening; 2: lagoon-channel estuaries; 3: lagoon-lacustrine estuaries; 4: fjord estuaries; 5: marine proper estuaries.

A complex study of the Hairuzova and Belogolovaya estuaries was conducted in October 2011 and June–August 2012. The goals of this study were to determine the local hydrological and morphological conditions and to investigate juvenile Pacific salmon ecology during their downstream migration and early marine period of life (Gorin et al. 2012; Koval et al. 2012).

During our field study it was determined that the morphological and hydrological regime of the Hairuzova and Belogolovaya estuaries separates them into two parts—river and marine (Fig. 2). The boundary between the estuary and the sea is 1–2 km seaward from the outer (marine) edge of the tidal flats where the 25‰ isohaline during the spring ebb tide separates sea water from mixed water masses on the surface. The boundary between the estuary and the river is along the extreme trajectory of the 1‰ isohaline. During the autumnal equinox ebb tides (September–October), the boundary is 14–15 km upriver from the marine edge of the tidal flats (5–6 km upriver from the river-mouth corridor walls of the river channels). During high tropic tides (June–July), the boundary moves 10 km upriver. Thus, the total length of both estuaries can be about 15 km in September–October and 25 km in June–July.

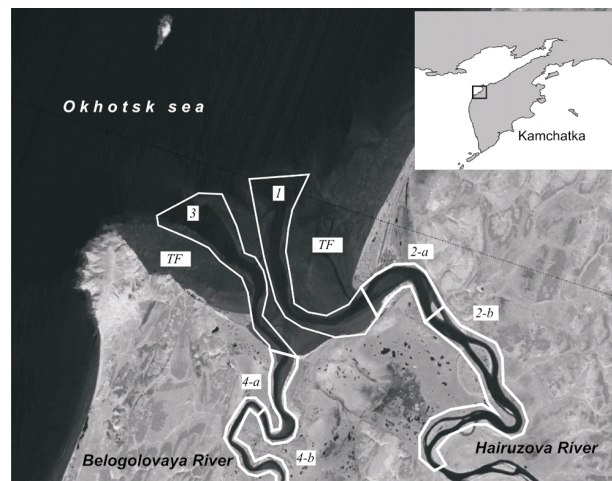


Fig. 2. The scheme of Hairuzova and Belogolovaya estuaries based on field research in October 2011 and June-August 2012.

1—marine part of the Hairuzova estuary (length is 9.3 km);

2—river part of the Hairuzova estuary (a—in ebb equinoctial tide in October; b—in high tropic tide in June);

3—marine part of the Belogolovaya Estuary (length is 9.3 km);

4—river part of the Belogolovaya Estuary (a – in ebb equinoctial tide in October; b – in high tropic tide in June);

TF—tidal flats (covered by marine waters at high tide; dried in ebb tide).

Several key zones with specific abiotic conditions and hydrobiont communities have been determined from examining the species composition and ecology of the Hairuzova and Belogolovaya estuaries. These zones include the freshwater zone (river channels out to the zone of periodic tidal influence), mixing zone (within the river and marine areas of the estuaries), and marine zone (coastal waters of the Okhotsk Sea outside the freshwater zone; Fig. 3). Principal inhabitants of the pelagic and benthic areas in the freshwater zone were juvenile Pacific salmon (sockeye *Oncorhynchus nerka*, chum *O. keta*, pink *O. gorbuscha*, Chinook *O. tshawytscha*, coho *O. kisutch*, and masu *O. masu*); juvenile chars (*Salvelinus alpinus* complex and *Salvelinus leucomaenis*); juvenile trout (*Parasalmo mykiss*); nine-spined stickleback (*Pungitius pungitius*); three-spined stickleback (*Gasterosteus aculeatus*); juvenile starry flounder (*Platichthys stellatus*); and Asiatic brook lamprey (*Lethenteron camtschaticum*). The dominant inhabitants in the mixing zone were fish, including starry flounder and arctic flounder (*Liopsetta glacialis*), pond smelt (*Hypomesus olidus*), toothed smelt (*Osmerus mordax dentex*), three-spined and nine-spined stickleback, juvenile salmon and chars, saffron cod (*Eleginus gracilis*), sculpins (*Cottidae* gen. sp.), blackline prickleback (*Acantholumpenus mackayi*), tube-nosed poacher (*Pallasina aix*), and invertebrate species, including mysids *Neomysis* sp., shrimps *Crangon* sp. and juvenile jellyfish. In the pelagic area of the marine zone the aquatic fauna included pond and toothed smelts, juvenile salmon, greenling (*Hexagrammidae* gen. sp.), and jellyfish.

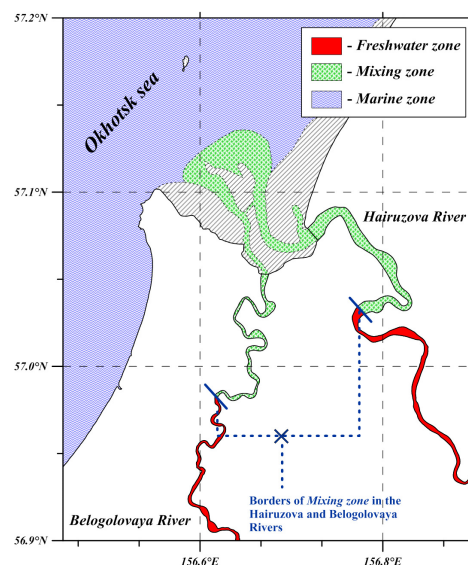


Fig. 3. Location of several key zones that illustrate different abiotic conditions and structure of the hydrobiont communities in the Hairuzova and Belogolovaya rivers and adjacent waters of the Okhotsk Sea in July-August, 2012.

In summary, the relative abundance of the total juvenile fish in the Hairuzova River was 284.0 thousand fish/km². In the Belogolovaya River, juvenile fish abundance was about half—134.7 thousand fishes/km². Maximum density of juvenile fish (919 thousand fish/km²) was observed in the lower part of the Hairuzova River during high tide, where the majority of fish consisted of juvenile and adult smelts (Fig. 4).

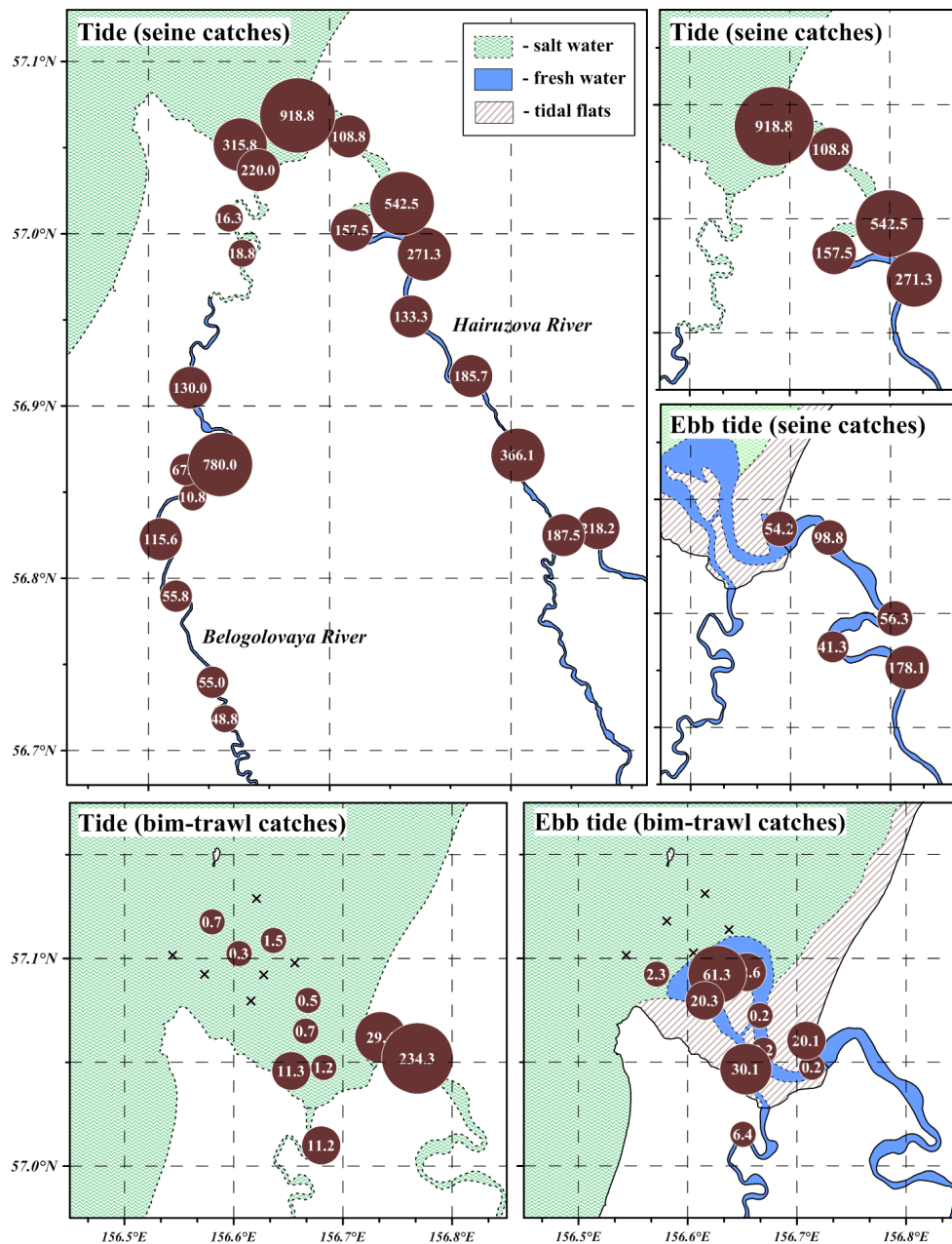


Fig. 4. Distribution total juvenile fish density (thousand fishes/km²) in the rivers Hairuzova, Belogolovaya and adjacent waters of the Okhotsk Sea during various phases of a high and ebb tidal cycle in July-August, 2012. Data collected by seine and beam-trawl; x indicates no catch).

Abundance, distribution, and species composition of juvenile fish in the estuaries demonstrated diurnal cycles, associated with phases of the tide. Juvenile marine fish (mostly smelts) entered the estuaries and lower parts of the rivers in rising tides. At ebb tide, juvenile salmon and sticklebacks were distributed in the estuaries and coastal waters. During the course of the diurnal tidal cycle, first juvenile migrants and next the elder and larger individuals moved into the estuaries (Fig. 5).

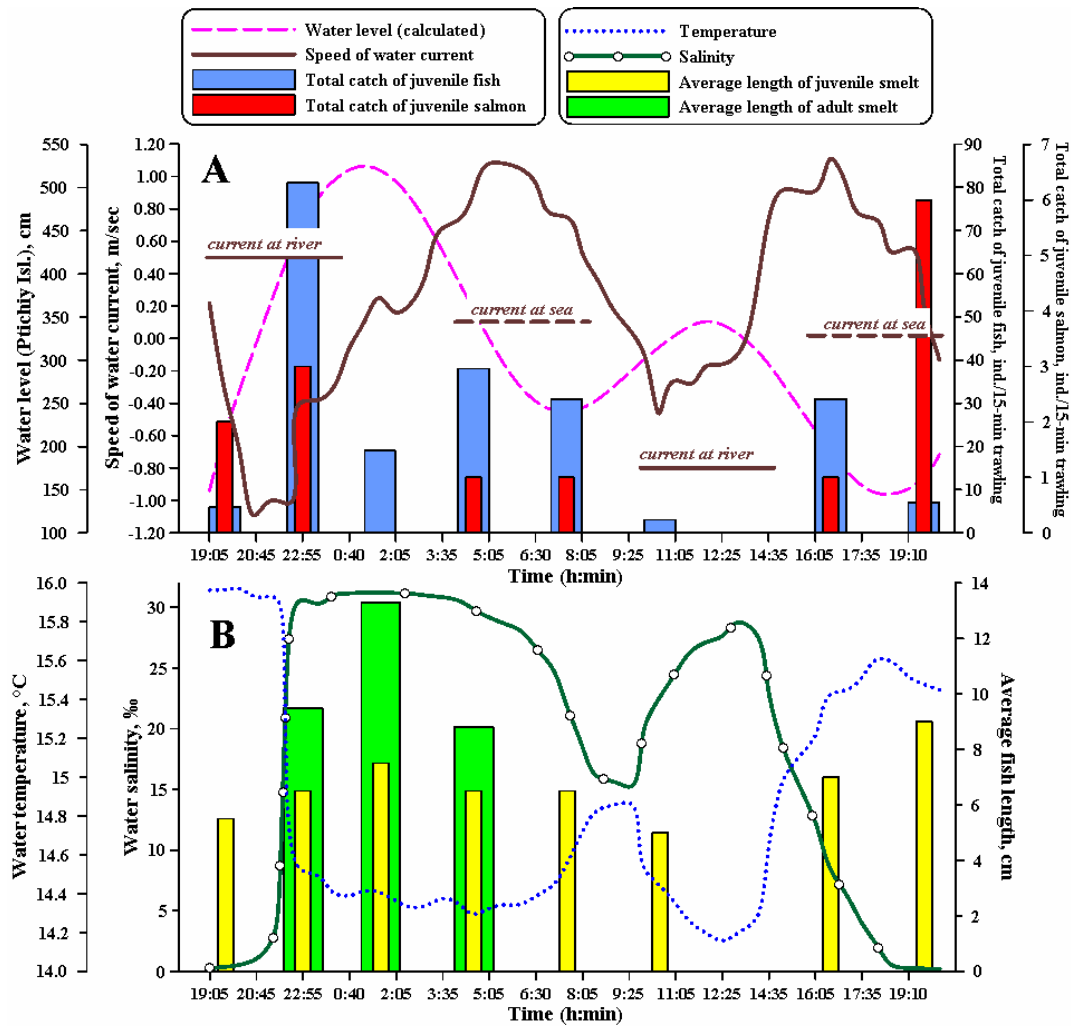


Fig. 5. Changes of the basic hydrological characteristics, juvenile fish abundance (A), and the average body length of smelts (B) in beam trawl catches at a station located at the mouth of the Belogolovaya River that was surveyed throughout the day, July 22–23, 2012.

One of the purposes of our study was an assessment of the role played by the Hairuzova and Belogolovaya rivers in Pacific salmon production. Making this assessment required published field observations and baseline data collected by the federal hydro-meteorological agency (Anonymous 1966; 1977) and archived data collected by KamchatNIRO on the production of salmon populations in Kamchatka.

The Hairuzova and Belogolovaya rivers both have huge drainage systems (basins), but these rivers are minor producers of Pacific salmon compared the other watersheds in the region (Shevlyakov and Maslov 2011). For the period of observations since the 1930s, the annual catch of salmon in these two river systems usually did not exceed 1 thousand tons and averaged 435.1 tons in the Hairuzova R. (1931–2011) and 101.4 tons in the Belogolovaya R. (1962–2011; Table 1). Total abundance (from 1957) of all Pacific salmon species on the spawning grounds of the Hairuzova River averaged 221.5 thousand individuals and averaged 116.9 thousand fish in the Belogolovaya River (Table 1). Hence, the average annual abundance of mature adult Pacific salmon spawning in the two systems every year is estimated at 400–600 thousand individuals. In comparison, the spawning stock of pink salmon in the Bolshaya River system (opens to the Okhotsk Sea 4.5° of latitude southward from the Hairuzova and Belogolovaya rivers) can be 5.5 million individuals. Although the three rivers are similar in length and basin area (Table 1), the Pacific salmon spawning stock in the Bolshaya River system can be 6 million individuals at a minimum, which is 10 times as much as the other two river systems.

Table 1. General morphological and hydrological characteristics, average salmon annual catch (tons), and average salmon density on spawning grounds (thousands of individuals) of the Hairuzova, Belogolovaya, and Bolshaya River systems.

River	General characteristics*			Salmon species**					Total
	Length (km)	Area of basin (km ²)	Average discharge (m ³ /s)	Pink	Chum	Sockeye	Coho	Chinook	
Hairuzova	265	11,600	181***	<u>72.7</u>	<u>263.3</u>	<u>24.2</u>	<u>72.6</u>	<u>2.4</u>	<u>435.1</u>
				151.0	51.5	4.3	9.9	4.7	221.5
Belogolovaya	226	4,000	63***	<u>21.2</u>	<u>55.7</u>	<u>6.6</u>	<u>17.6</u>	<u>0.2</u>	<u>101.4</u>
				91.1	15.8	1.8	6.3	1.9	116.9
Bolshaya	275	10,800	317***	<u>4877.3</u>	<u>398.4</u>	<u>240.2</u>	<u>292.1</u>	<u>93.8</u>	<u>5901.8</u>
				2773.5	42.8	90.2	53.6	18.9	2978.9

*source: Anonymous 1966, 1977.

**source: KamchatNIRO data archive. Bold number above the line is average annual catch. Number below the line is average annual density on the spawning grounds.

***authors' calculations.

What might be the reason for relatively low Pacific salmon production in the Hairuzova and Belogolovaya rivers systems?

According to our observations, the substrates in the estuaries of these rivers (and lower parts of channels) are silty and unfavorable for salmon to use as spawning gravel. This is a well-known characteristic of river mouths affected by tides and can be explained by avalanche-type sedimentation of particles from the river in the mixing zone and regular stagnation of water currents when the tide phase changes. As a result the total area of suitable spawning grounds in the Hairuzova and Belogolovaya rivers is substantially less than in the Bolshaya River (Shevlyakov and Maslov 2011).

Our field observations demonstrated movement of the zone of river and sea water mixing in both estuaries during the 24-hour period that slides from the sea edge to the top of the mixing zone and back. In summer the movement can be up to 15-30 km within the estuary channel, and the maximum water current speed there can reach 1.0-1.5 m/sec (see Fig. 5). Juvenile Pacific salmon are required to transit across the sliding mixing zone during their movement out of the river to the Okhotsk Sea. The juvenile migrants (especially pink and chum salmon that are migrating as underyearlings) cannot actively resist strong currents and are extremely vulnerable to piscine, avian, and mammalian predators (Karpenko 1998). Moreover, the silty substrate in the lower river and estuary reduces availability of benthic attaching organisms, which play a role (like drift and zooplankton) in feeding and shelter of juvenile salmon (Maximenkov 2007). We suggest that juvenile salmon mortality from a complex of limiting factors is higher in the Hairuzova and Belogolovaya river systems than in the other rivers of West Kamchatka.

Another important factor contributing to poor natural salmon production in the Hairuzova and Belogolovaya river systems is predation pressure on adult salmon during anadromous migrations. The principal active predators are marine mammals, including killer whales *Delphinapterus leucas* and large seals *Phoca largha*. During the intense period of the pink salmon spawning run, which normally occurs in this area in early August, the number of killer whales and large seals within the estuaries during high tide can reach several hundred animals. On the rising tide, the mammals can pursue salmon many kilometers up-river to feed on them (Shulezhko et al. 2011). We believe that aggregations of marine mammals are accentuated by the morphology of the Hairuzova and Belogolovaya river-estuaries in summer. Whales don't seem to be afraid to enter estuaries with a wide and deep entrance to the sea. Extensive sandbars visible at low tide can increase effective hunting by whales and seals in such sites.

Thus, it is our view that low abundance of Pacific salmon in the Hairuzova and Belogolovaya rivers is a result of the hydrological and morphological specifics of the estuaries, including:

- (1) silty substrate making the lower parts of the rivers useless for salmon spawning;
- (2) long length of the estuary and extremely strong tidal effects that cause high mortality of juvenile salmon during downstream migration;
- (3) aggregation of predators (especially marine mammals) that increase mortality of adult salmon during upstream migration.

Acknowledgments—Our study was partially supported by the Russian Foundation for Basic Research (RFBR), research project No. 12-05-31453/12, and also supported by the “White Whale Program” (Russian Academy of Sciences and Russian Geographical Society).

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Verification of the Immature Ratio at Age of Chum Salmon in the Bering Sea and Central North Pacific Ocean, 1971–2010

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Keywords: chum salmon, immature, experimental survey, growth rate, Bering Sea, central North Pacific Ocean

The mean age at return of Japanese chum salmon populations, as with other Pacific salmon, increased from the 1970s–2000s, which could be associated with variability of the immature ratio (IMR) at age. Nominal IMRs calculated from Japanese offshore surveys and returns at age given by fishery data will be subject to uncertainty due to biases. To estimate reliable annual IMRs of Japanese chum salmon, we evaluated the IMRs at ages 3–4 by using fishery independent and fishery dependent data separately: (i) Japanese experimental chum salmon survey data (sex, age, gonad weight, and fork length) collected in the Bering Sea and central North Pacific Ocean, July–August, 1971–2010, and (ii) Japanese chum salmon return at age. For data (i) examined using generalized linear mixed models (GLMM), annual means of male and female IMR at age 4 ranged from 0.2–0.8 and 0.1–0.9, respectively, fluctuated in parallel, and increased on a long-term basis. For data (ii) investigated by virtual population analysis (VPA), the sex-combined IMR at age 4 ranged from 0.1–0.5, i.e., was relatively low compared to the GLMM-IMR. All correlations among the VPA- and GLMM-IMRs were positive and significant, thereby supporting the reliability of both the types of relative IMR. As a result of testing factors on IMR variability, the growth rate of immature ages 2–3 chum salmon and the mean sea surface temperature in the Bering Sea were significant indices common to VPA- and GLMM-IMRs. We provide a probable cause whereby the immature ratio of age 4 chum is affected mainly by the growth rate of ages 2–3 chum salmon and environmental conditions.

Freshwater Growth and Recruitment in Two Western Alaskan Populations of Chinook Salmon

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Keywords: Chinook salmon, retrospective analysis, recruitment, growth, scale increments

The importance of Chinook salmon *Oncorhynchus tshawytscha* to western Alaskan communities along the Yukon and Kuskokwim rivers is difficult to overstate. Recent years have seen a decline in total harvest of Chinook salmon in Alaskan fisheries (commercial, subsistence, test, and sport) from these two rivers (Fig. 1). Although both economic and biological factors have contributed to reduced landings (Linderman and Bergstrom 2009), a series of fisheries and economic disaster declarations (beginning in 1997 and including 2012) underscore a sense of fear and uncertainty about the future of Chinook salmon in the region.

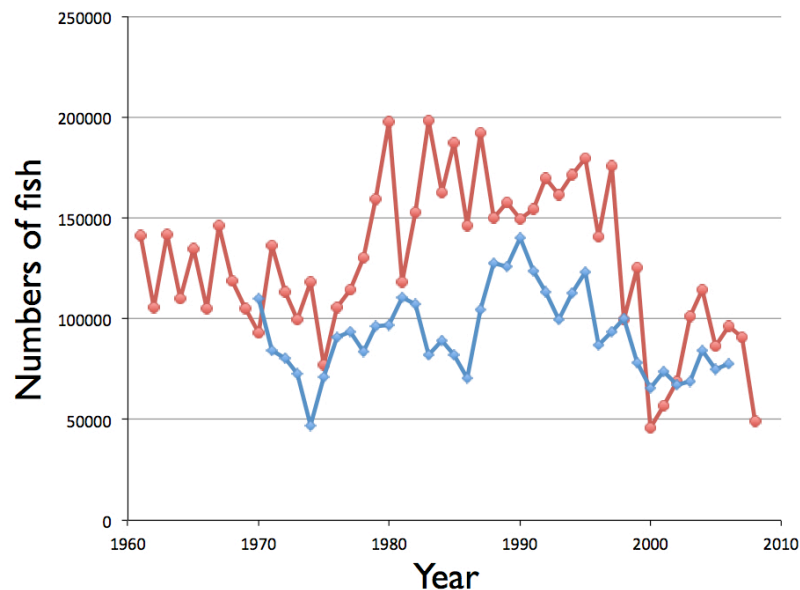


Fig. 1. Total Alaskan harvest (commercial, subsistence, test and sport fisheries) from Yukon (red circles) and Kuskokwim (blue diamonds) rivers by year. Data sources: Yukon River—Evenson et al. (2009); Kuskokwim River—Linderman and Bergstrom (2009).

The objective of this research was to examine the role that freshwater growth might play in declines in Chinook salmon populations in western Alaska. The critical-size/critical-period hypothesis (Beamish and Mahnken 2001) suggests that size-dependent mortality soon after salmon smolts reach the nearshore marine environment has a strong influence on recruitment. For stream-type Chinook salmon such as those in western Alaska (Taylor 1990), freshwater growth could influence early marine survival through its effect on smolt size.

Relatively long time series of escapement and age/sex composition data, as well as archived scale samples, were available from the Alaska Department of Fish and Game (ADFG) for two Chinook salmon escapement monitoring sites in western Alaska: the Andreafsky River weir (Yukon drainage) and the Kogruklu River weir (Holitna River, Kuskokwim drainage; Fig. 2). We used these data and scale collections to (1) reconstruct time series of freshwater and marine growth

increments from the 1970s to 2000s, and (2) test correlations between stock productivity and freshwater and marine growth increments. We analyzed only growth of females, as the fitness effects of large body size are more straightforward than they are in males (reviewed in Quinn 2005), and females likely influence recruitment to a greater extent than do males via their direct effect on total amount of egg deposition.

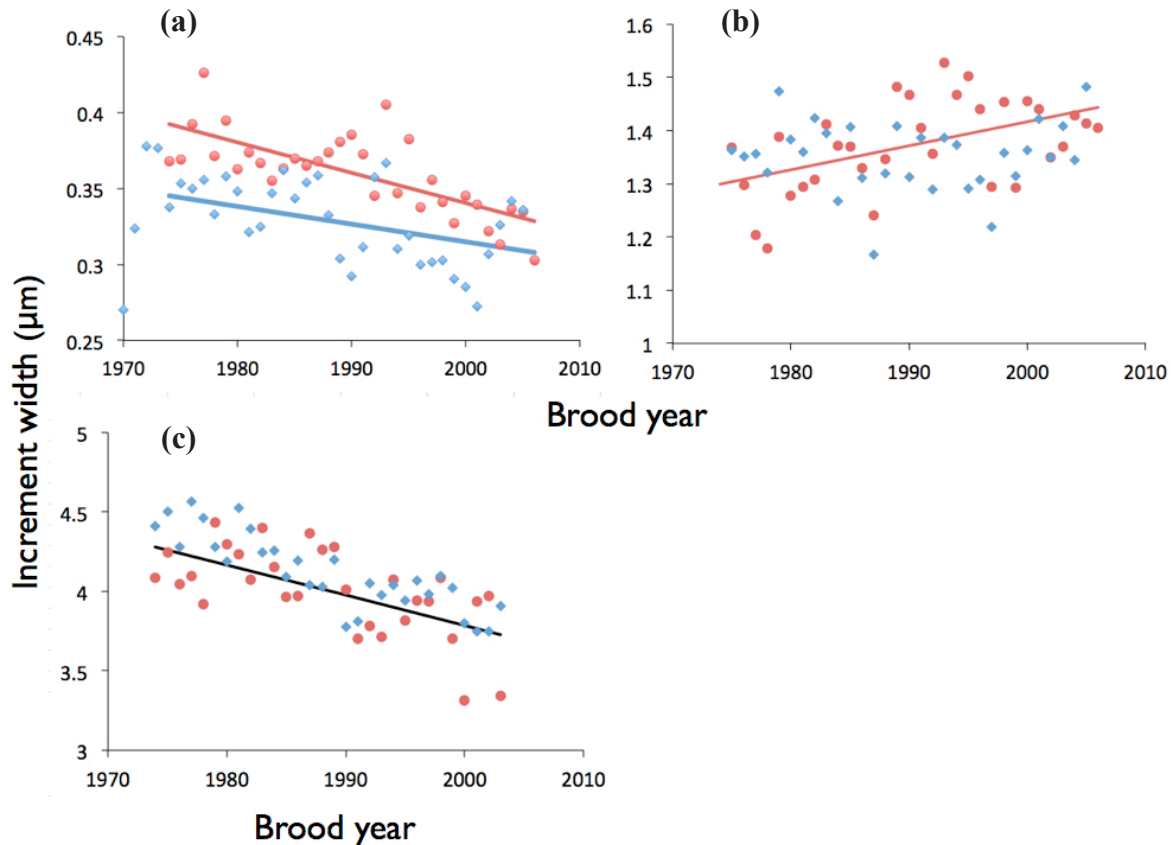


Fig. 2. Average growth increments of female Chinook salmon by brood year: (a) FW1, (b) SW1, and (c) total marine growth. Red circles: Andreafsky River; blue diamonds: Kogruklu River.

Scales were collected at each weir from the preferred body area for salmonids, placed on gum cards, and readings were conducted on acetate impressions following the methods described in Hagen et al. (2001). Up to 25 females per age class were analyzed per year and system, although sample sizes were lower in the less common age-classes. For each readable scale, the number of circuli and total increment width were measured for the following growth zones: first year in fresh water (FW1), additional freshwater growth after the first year (FW+), first year in saltwater (SW1), second year in saltwater (SW2), and so on, up to additional marine growth after last winter at sea (SW+). Analyses reported herein were restricted to increment width data for FW1, SW1, and total marine growth (SW1 through SW+).

Scale data were available for brood years 1974-2006 for the Andreafsky River and brood years 1970-2005 for the Kogruklu River. Simple linear regressions between increment widths and brood year were used to test for temporal trends in growth. Freshwater growth (FW1) declined significantly with brood year (Andreafsky: $p < 0.001$, $R^2 = 0.51$; Kogruklu: $p < 0.01$, $R^2 = 0.16$; Fig. 2a). The SW1 increased slightly with brood year in Andreafsky samples ($p < 0.005$, $R^2 = 0.22$), but did not change significantly with brood year in Kogruklu samples ($p = 0.094$; Fig. 2b). Total marine growth also declined over time ($p < 0.001$, $R^2 = 0.50$; Fig. 2c).

Estimates of escapement, age, sex composition, and harvest were used to estimate stock productivity as recruits per female spawner, or (escapement + harvest)/females, for both Andreafsky and Kogruklu stocks. Details of these calculations are given in Leon (2013). Spearman rank correlation coefficients were then calculated for each stock between productivity (transformed by natural logarithm) and three brood-year growth increments: FW1, SW1, and total marine growth. Exact tests indicated that none of these correlations were statistically significant (Table 1).

Table 1. Spearman rank correlation coefficients (and P-values for exact tests) between growth increments (brood year means) and stock productivity (recruits/female spawner, ln-transformed).

Growth increment	Andreafsky River	Kogrukluk River
FW1	0.005 ($p = 0.99$)	0.044 ($p = 0.87$)
SW1	-0.35 ($p = 0.15$)	0.15 ($p = 0.56$)
SW-all	0.22 ($p = 0.37$)	0.11 ($p = 0.68$)

To summarize, we found declines in freshwater (FW1) and total marine growth over time in both Andreafsky and Kogrukluk escapement samples of Chinook salmon. Declines in total marine growth were due largely to a lower proportion of older females represented in more recent scale samples (data not shown); this is consistent with reports from local fishermen of fewer older, larger females returning to these rivers (A. Bassich, abassich@gmail.com, personal communication). Although environmental change could be driving declines in FW1, we hypothesize that a decrease in FW1 might also be attributed to smaller average size of female spawners, as egg size is often correlated with body size in Chinook salmon (Beacham 2010).

Despite these declines in growth, we detected no significant correlations between growth increments (freshwater or marine) and stock productivity. We had limited power to detect such correlations, however. First, the long lifespan of Chinook salmon (up to 7 years in these stocks) restricted our analysis of productivity to brood years 2006 and earlier. Second, our estimates of stock productivity compounded uncertainty in spawner number, escapement, and harvest (which was a particularly coarse estimate). Therefore, we cannot confidently rule out declines in growth as contributing to population declines in western Alaska.

Finally, we urge caution in interpreting the results presented here. First, growth increments were estimated from escapement samples, which represented the individuals that survived periods of freshwater, marine, and fishing mortality, thus obscuring episodes of size-related mortality. Second, although scale sampling was designed to minimize bias (Leon 2013 and references therein), logistical constraints can result in field sampling that deviates slightly from sampling protocols; this potential bias was not fully evaluated here. Finally, autocorrelation between growth zones can also obscure results (e.g., Ruggerone et al. 2009a, b), making retrospective analyses of growth and abundance difficult to interpret. However, the temporal trends we observed in freshwater and total marine growth suggest that the demographic consequences of these changes in western Alaskan Chinook salmon deserve further attention.

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Implications for Research From the Widespread Decrease in Productivity of Sockeye Salmon Populations in Western North America

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Keywords: sockeye salmon, large-scale drivers of decreasing productivity, western North America, climate change

Researchers of Pacific salmon (*Oncorhynchus* spp.) have begun to understand how environmental factors such as freshwater and ocean conditions cause changes in abundance and productivity (the latter reflects adults produced per spawner). However, there are still many gaps in that knowledge. One key source of evidence of potential causal mechanisms comes from studies across numerous salmon populations that identify the spatial extent of occurrence of similar temporal variation in productivity (e.g., Botsford and Paulsen 2000). That is, where several salmon populations have positively correlated time trends in productivity, it is likely that they share one or more drivers of those changes (e.g., Myers et al. 1997; Mueter et al. 2002a). Furthermore, environmental variables that vary temporally on similar or larger spatial scales compared to those of salmon productivity are likely to be the most important drivers of changes in that productivity (e.g., Mueter et al. 2002b).

Thus, to extend previous research that applied this multi-population approach, we examined data series as far back as 1950 for 64 mostly-wild populations of sockeye salmon (*O. nerka*) from British Columbia (BC), Washington, and Alaska. We also sought to determine whether the decreases in abundance and productivity observed, especially since the early 1990s for Fraser River, BC, sockeye salmon, have occurred more widely or are restricted to those populations. We examined two measures of productivity that reflect survival processes between spawners and their resulting adult returns (i.e., recruits, which are the offspring that return to the coast prior to fishing). Our first indicator of productivity was \log_e (recruits per spawner) residuals from the best-fit “stationary” spawner-to-recruit model, as explained below. These residuals represent the change in \log_e (recruits per spawner) that is attributable to factors other than within-stock density-dependence as spawner abundance changes. For each stock, we estimated a time series of these residuals, v_p , first by fitting the Ricker (1975) spawner-recruit model. That model was $\log_e(R_t/S_t) = a + bS_t + v_p$, where S_t is abundance of spawners in brood year t , R_t is abundance of adult recruits of all ages resulting from those spawners, a is the productivity parameter (in units of $\log_e(R_t/S_t)$) at very low spawner abundance, parameter b reflects within-stock density-dependent effects, and $v_t \sim N(0, \sigma_v^2)$. We refer to this Ricker model as “stationary” because it assumes that a is constant across the entire time series of spawner and recruit data. Our second measure of productivity came from fitting a “non-stationary” version of the Ricker model in which the a parameter in equation 1 is replaced with a time-varying parameter, a_t . To estimate a_t , we used a Kalman filter, assuming that a_t follows a random walk, i.e., $a_t = a_{t-1} + w_t$, and $w_t \sim N(0, \sigma_w^2)$; Chatfield 1989). Previous simulations (Peterman et al. 2000) and empirical analyses (Peterman et al. 2003) show that this Kalman filter method gave the most reliable parameter estimates, compared to the standard regression method, when applied to salmon populations in which there was an underlying time trend in productivity. A fixed-interval smoother applied to the time series of a_t estimates produced the maximum likelihood values of a_t (Harvey 1989) and also drastically reduced the random high-frequency year-to-year variation that tends to obscure underlying long-term trends. These smoothed time series of Kalman-filter-estimated a_t values constituted our second measure of productivity. We used this Kalman filter approach to account for observation error in the data as well as natural variability.

Three main findings emerged. First, the declining productivity of Fraser River sockeye has occurred in numerous other sockeye salmon stocks from western North America. Specifically, relatively rapid and consistent decreases in productivity occurred since the late 1990s, and in many cases since the late 1980s or early 1990s, in 24 of the 37 “southern” sockeye salmon stocks. Those “southern” stocks include Puget Sound (Washington), Fraser River, Barkley Sound, BC, Central Coast of BC, North Coast of BC, Southeast Alaska, and Alaska’s Yakutat peninsula (inside the ellipse in Fig. 1). In contrast, such decreases have generally not occurred in central or western Alaska (stocks 38-64), where productivity tended to either increase over time or vary around a stable mean. For the stocks that show such decreases in productivity, time trends are qualitatively similar, even though starting dates may differ. Furthermore, a period of temporary increase in productivity through the late 1990s is pronounced in a few stocks.

The widespread downward time trend in sockeye salmon productivity is also reflected in the among-stock correlation analysis and Principal Components Analysis (see Peterman and Dorner 2012 for more details). Because the productivity of most central and western Alaskan sockeye salmon populations generally either increased or remained stable instead of decreasing, their correlations with productivity of southern stocks were mostly negative or near zero.

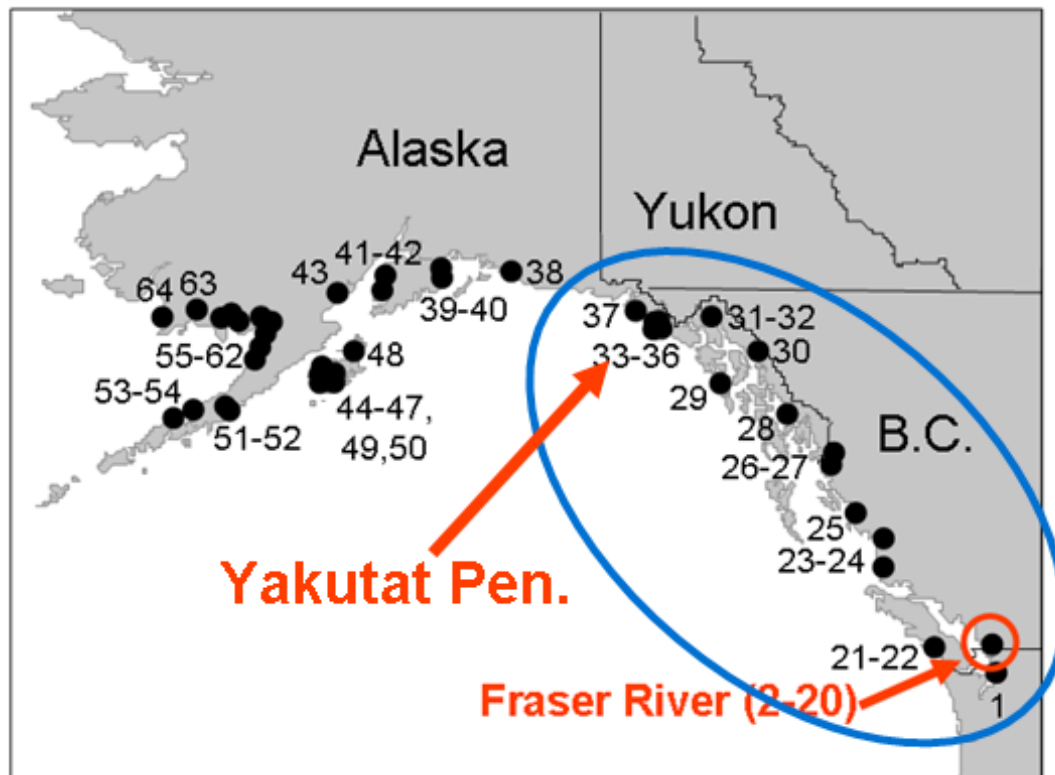


Fig. 1. Locations of ocean entry for seaward-migrating juveniles of the 64 sockeye salmon stocks analyzed here that had lengthy time series data on annual abundances of spawners and their resulting adult recruits. Stock names for each number are given in the Supplementary Information of Table S1 in Peterman and Dorner (2012). Regional groups of stocks include Puget Sound, Washington (1), Fraser River, BC (2-20), Barkley Sound, BC (21-22), Central Coast of BC (23-25), North Coast of BC (26-27), and the following Alaskan stocks: Southeast Alaska (28-32), Yakutat peninsula (33-37), Prince William Sound (38-40), Upper Cook Inlet (41-43), Kodiak (44-50), Chignik (51-52), Alaska Peninsula (53,54), Bristol Bay (55-63), and Arctic-Yukon-Kuskokwim (AYK, 64).

It is conceivable that the decreasing time trends in productivity that appeared across the southern sockeye salmon stocks resulted from a coincidental combination of simultaneous processes related to freshwater habitat degradation, contaminants, pathogens, predators, and/or food supply that have each independently affected particular stocks. However, the large spatial scale of similar time trends in productivity for 24 of the “southern” stocks occurred across a wide range of habitats, ranging from relatively pristine to heavily disturbed areas. This observation suggests that a more likely explanation of the widespread decrease in productivity is that there are shared causal mechanisms across Washington, British Columbia, Southeast Alaska, and the Yakutat region of Alaska.

Our second main finding was that although the positively correlated temporal patterns across numerous “southern” stocks were present in the past (1950-1985 brood years), correlation coefficients have increased since then, especially in the 1995-2004 period. These results indicate that productivity trends have become more synchronized across populations.

Third, and perhaps most importantly, we found that the extent of the positively correlated “southern” area appears to have spread further north over time. This observation suggests that ongoing climate-driven changes may be an important driver of the widespread decreases in productivity.

Our finding of a large spatial extent of changes in productivity of sockeye salmon populations has important implications for research into potential causes of the declines in productivity. Based on our findings, further research into the decreasing productivity of west coast sockeye salmon should look for mechanisms that have three characteristics. (1) The mechanisms should operate at large, multi-regional spatial scales, and/or in marine areas where a large number of the correlated sockeye salmon stocks overlap. (2) The mechanisms should be likely to affect stocks in the geographic range from Puget Sound to Southeast Alaska in a similar way, but may have an inverse effect on stocks from central and western Alaska. (3) The mechanisms should have been present historically, but have intensified in recent years.

Mechanisms consistent with these three criteria include climate-driven increases in freshwater and/or marine mortality induced by pathogens, as well as increases in predation and/or reduced food availability due to oceanographic changes. However, we did not analyze data reflecting those processes. Instead, we leave that to other researchers. We emphasize, though, that the greatest progress in understanding mechanisms will come from coordinated research programs that simultaneously examine numerous stocks with contrasting levels of exposure to these multiple mechanisms. At least some of those mechanisms should be ones that operate at large, multi-regional spatial scales.

The large-scale pattern of decreasing productivity also has implications for management agencies. Managers should be cautious about taking management actions based on studies that only examine small-scale local factors that potentially affect salmon productivity. That caution is justified because similar, broader-scale trends in other nearby salmon populations may indicate that such locally-driven efforts may be relatively ineffective, and that resources could be better spent addressing larger-scale processes.

More complete descriptions of methods, results, and implications of this analysis are reported in Peterman and Dorner (2012).

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Survival and Early Marine Migration of Enhanced Age-0 Sockeye Salmon Smolts Raised in Freshwater and Seawater at Auke Creek, Southeast Alaska

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Keywords: age-0 smolt, release size, survival, residency and migration timing

The adult sockeye salmon, *Oncorhynchus nerka*, population in Auke Creek in Southeast Alaska reached record low levels when 240 fish returned in 1985 and runs were less than a thousand fish for three consecutive years. To help rebuild this depressed population, a restoration project included research on hatchery production and releases of age-0 or sea-type smolts over a five year period, 1988-1992. The study included use of an experimental hatchery and two-way counting weir at the stream mouth to monitor survival and estuarine sampling of juveniles during their early marine period to examine residency in Auke Bay and migration timing.

Table 1. Marine survival for seven groups of age-0 sockeye salmon cultured only in freshwater and eighteen groups of age-0 sockeye salmon with additional culture in seawater released May through August, 1988 to 1992.

Release		Culture days in seawater	Size of smolts		Number of Smolts	Ocean Age of Adults				Total Adults	% Survival
Year	Date		mm	gm		1	2	3	4		
1988	21-Jun	—	75	4.4	16,400	21	14	765	73	873	5.32
1989	21-Jun	—	65	2.7	15,900	0	42	208	8	258	1.61
1990	21-Jun	—	67	2.8	12,599	0	44	659	0	703	5.58
1990	6-Jul	—	76	4.3	12,077	0	22	647	11	680	5.60
1991	5-Jun	—	49	1.2	15,527	0	0	5	0	5	0.03
1991	21-Jun	—	56	2.0	15,500	0	0	139	0	139	0.90
1991	19-Jul	—	71	3.6	15,500	0	0	81	8	89	0.57
					103,503	21	122	2,504	100	2,747	2.65
1988	21-Jun	22	84	6.2	19,888	0	16	1,168	51	1,235	6.21
1989	21-Jun	46	78	4.8	18,300	11	34	538	8	591	3.23
1990	21-Jun	28	85	6.2	13,618	0	58	1,267	4	1,329	9.76
1990	6-Jul	43	103	11.9	11,655	0	51	1,267	15	1,333	11.44
1991	28-May	6	49	1.3	10,172	0	0	19	0	19	0.19
1991	5-Jun	14	46	1.7	11,605	0	0	30	0	30	0.26
1991	21-Jun	10	62	2.6	14,069	0	0	316	8	324	2.30
1991	5-Jul	24	86	6.9	14,794	0	30	864	17	911	6.16
1991	19-Jul	43	104	11.2	15,510	0	60	836	17	913	5.89
1991	19-Jul	9	70	3.6	15,310	0	10	201	0	211	1.38
1991	8-Aug	65	125	19.4	10,020	0	124	689	13	826	8.25
1992	8-Jun	7	52	1.5	6,596	0	0	70	0	70	1.06
1992	8-Jun	16	65	2.9	5,286	0	11	117	0	128	2.42
1992	21-Jun	11	67	3.1	8,112	0	8	194	0	202	2.49
1992	21-Jun	29	88	6.2	8,370	0	23	519	1	543	6.49
1992	6-Jul	11	67	3.2	8,122	0	11	161	1	173	2.13
1992	6-Jul	26	88	6.2	8,209	0	30	384	1	415	5.06
1992	6-Jul	44	102	11.8	9,382	0	11	533	1	545	5.81
					209,018	11	477	9,173	137	9,798	4.69

Fry were initially raised in freshwater (FW) until large enough to become moderately salinity tolerant, generally from 1.0 to 1.5 g (Clark et al. 1978; Rice et al. 1994). Some were transferred to marine net pens in Auke Bay for additional growth in seawater (SW), while others were retained in freshwater rearing containers. Although not known to occur naturally in the Auke Creek population, age-0 sockeye salmon smolts are not uncommon in other nearby regional stocks (McPherson, 1987; Murphy et al. 1988; Heifetz et al. 1989). Gametes from mature Auke Lake spawners were collected from five brood years (1987-1991) from the spawning grounds in Lake Creek, the main tributary to Auke Lake, or its confluence with the lake where adults were held in net pens in the lake until ripe. Dual water sources, from Auke Creek surface water and deep lake water, for incubation and rearing in the hatchery allowed for using favorable water temperatures to accelerate embryo development and initial fry rearing. Debris filtered and ultraviolet sterilized water was used for all incubation and rearing in the hatchery to destroy bacteria and viruses (Taylor 1989; Taylor et al. 1992; Taylor and Heard 1994).

A total of 25 age-0 smolt groups were released: 7 FW groups and 18 SW groups (Table 1). All groups were adipose fin clipped and tagged with half-length coded-wire tags (CWT). From 1989-1996 all sockeye salmon adults entering Auke Creek weir were examined for fin clips and were subsampled to recover wire tags. Other tags were recovered from spawning ground carcasses in Lake Creek. Estimated numbers of adult returns from age-0 sockeye salmon smolts made important contributions to Auke Creek weir counts over a five year period, 1991-1995 (Fig. 1).

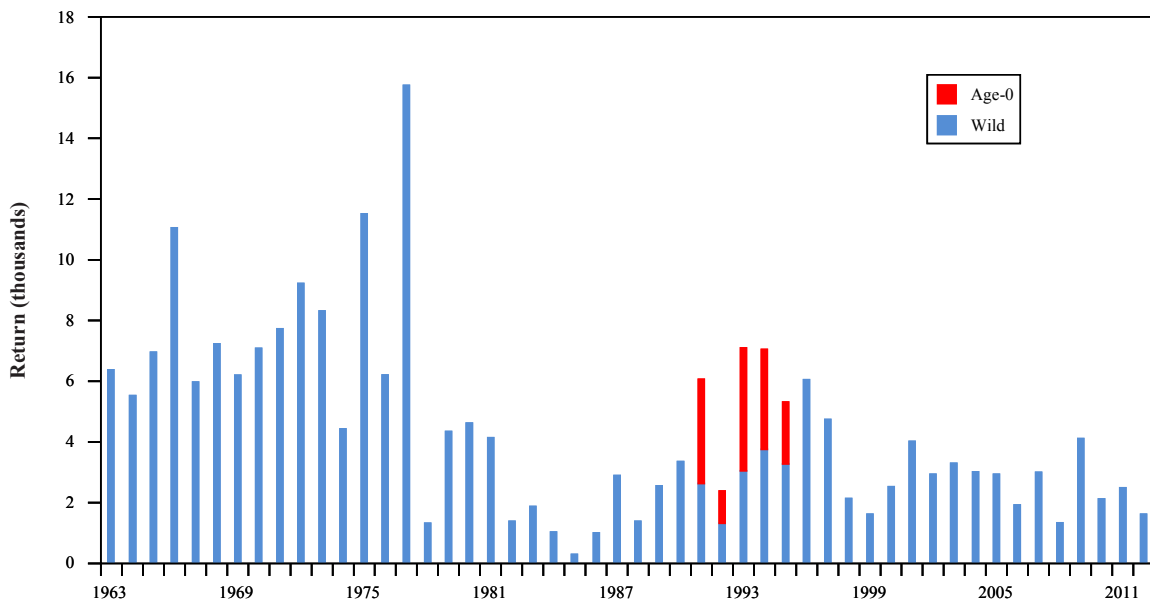


Fig. 1. Adult sockeye salmon returns to Auke Creek from wild and age-0 hatchery smolts, 1963-2012.

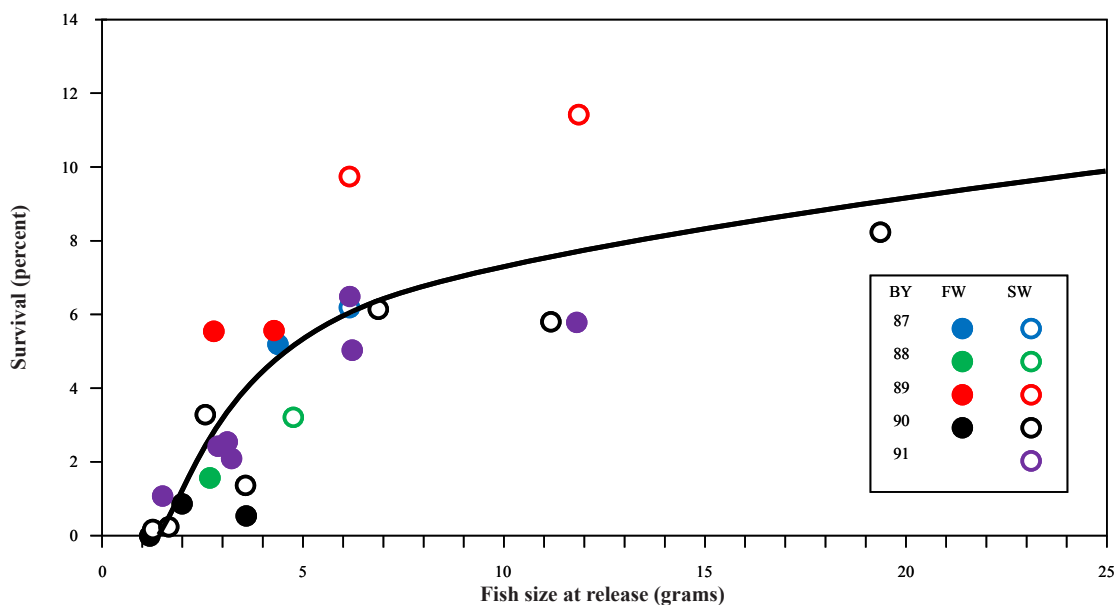
Age-0 smolts were released as early as May 28 and as late as August 2 (Table 1). Nine groups including both FW and SW groups were released on the summer solstice (~ 21 June) over a five year period (Table 2) to examine any temporal significance of this photoperiod event compared with other release dates. Sizes of age-0 smolts ranged from 49 mm and 1.3 g to 125 mm and 19 g. Growth rates in FW during the April through June period ranged from 2% to 4% per day while SW growth rates in May and June often exceeded 5% per day (Taylor et al. 1992; Taylor and Heard 1994).

Marine survival of SW age-0 smolts averaged 4.7% (range 0.2-11.4%) and was significantly greater ($p = 0.05$) than FW-raised smolts (average 2.7%, range 0.03-5.6%; Table 1). Higher SW group survival (Fig. 2) likely was due to larger smolts and greater growth rates in SW (5-7%/day) than in FW (2-4%/day) for juveniles reared during the same time periods. Higher growth rates in SW was the result of warmer temperatures and possibly because sockeye salmon smolts may experience more rapid growth in seawater even if temperatures are similar.

Adult sockeye salmon from age-0 SW smolts returned mostly at ocean age-3 (93.6%). While age-0 FW smolts also returned primarily as ocean age-3 adults, they returned at a slightly lower rate (91.2%, Table 1). This age at return is consistent with wild FW age-1 and age-2 sockeye salmon smolts from Auke Creek that also return mostly as ocean age-3 adults.

Table 2. Marine survival for nine groups of age-0 sockeye salmon smolts all released on June 21, 1988 to 1992, including groups cultured only in freshwater and groups cultured with additional days in seawater (SW).

Release year	Freshwater or seawater culture	SW days	Size		Number of smolts	Ocean age of adults				Total adults	% Survival
			mm	g		1	2	3	4		
1988	FW		75	4.4	16,400	21	14	765	73	873	5.32
1988	SW	22	84	6.2	19,888	0	16	1,168	51	1,235	6.21
1989	FW		65	2.7	15,990	0	42	208	8	258	1.61
1989	SW	46	78	4.8	18,300	11	34	538	8	591	3.23
1990	FW		67	2.8	12,599	0	44	659	0	703	5.58
1990	SW	28	85	6.2	13,618	0	58	1,267	4	1,329	9.76
1991	FW		56	2	15,500	0	0	139	0	139	0.90
1991	SW	11	67	3.1	8,112	0	8	194	0	202	2.49
1992	FW				0						
1992	SW	29	88	6.2	8,370	0	23	519	1	543	6.49
					128,777					5,873	4.56



recoveries of age-0 smolts in both years revealed smaller fish utilized littoral habitats first and then move offshore as they grew larger. In 1990 the 557 sockeye salmon smolts with readable scales revealed the following age structures: 54% age-0 (including 28% hatchery reared with CWT and 26% wild), 40% age-1, and 6% age-2. The longest residency of age-0 hatchery smolts was 41 and 59 days in 1990 and 1991, respectively. Few CWT fish over 100 mm fork length were recovered, suggesting most migrate out of Auke Bay before reaching this size.

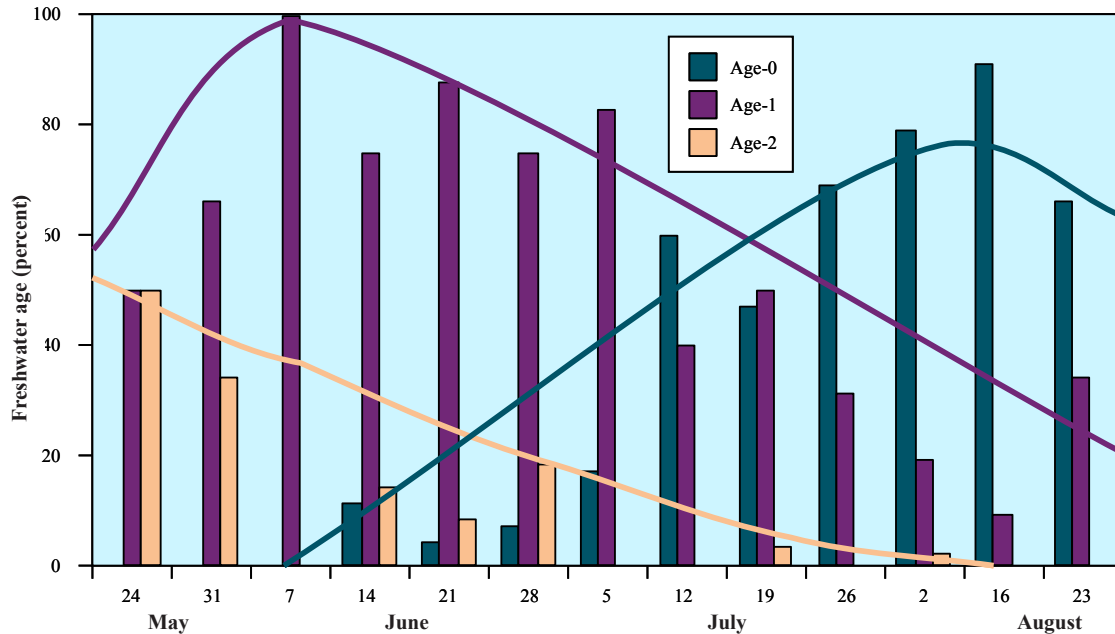


Fig. 3. Smoothed temporal distribution of freshwater age composition of juvenile sockeye salmon caught in Auke Bay with seines and trawls, May 24-August 23, 1990. N = 403 fish

In conclusion, this study demonstrated that sockeye salmon can be successfully cultured and released as age-0 smolts with marine survival averaging 4.7% and 2.7%, respectively, for SW- and FW- raised smolts. Littoral and offshore migration was size dependent with most smolts migrating out of Auke Bay before reaching 100 mm fork length.

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Long Term Ocean Survival Trends of Chinook Salmon Released at the Little Port Walter Marine Station in Southeast Alaska

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Keywords: ocean survival, Chinook salmon, Southeast Alaska

Chinook salmon have been cultured at the National Marine Fisheries Service's Little Port Walter Marine Station since 1976 when broodstock were obtained from Southeast Alaska's Chickamin and Unuk Rivers and spawned. Through 2012, both lines were uniquely maintained by marking every salmon smolt with a coded-wire tag prior to release. These marks were used to positively identify the stock of returning adults for subsequent egg collection and used to identify Little Port Walter origin Chinook salmon caught in (1) Southeast Alaska commercial and recreational fisheries and (2) the salmon bycatch of the Alaska trawl fisheries. Since the 1970s, almost 21 million Chinook salmon eggs were collected at Little Port Walter and most were subsequently cultured for release. This 35-year hatchery data series represents one of the most complete known sources of Alaska stock-specific information regarding the release, survival, and capture of Chinook salmon, a species whose abundance has been declining in Alaska and the subject of various federal and state disaster declarations, including another by the Department of Commerce in 2012. Decreasing trends in survival and age at maturity will be presented and compared with changes in environmental and release conditions to develop correlations that may provide insight into future trends.

Chinook Salmon Marine Migration and Production Mechanisms in Alaska

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Keywords: Chinook salmon, production, marine, Southeast Alaska, migration, survival, forecast

Reduced catches in commercial fisheries indicate that Chinook salmon (*Oncorhynchus tshawytscha*) production has declined throughout Alaska in recent decades. In fact, the Alaska commercial harvest of Chinook salmon in 2012 was the lowest on record in the past 100 years (ADFG 2012; Fig. 1). In September 2012, low Chinook salmon harvest led the U.S. Government to declare under the Magnuson-Stevens Fishery Conservation and Management Act of 1976 (NOAA 2012) “a commercial fishery failure due to a fishery resource disaster exists for three regions of the Alaska Chinook salmon fishery.” To address this problem, the Alaska Department of Fish and Game (ADFG) conducted a series of regional meetings for researchers studying Chinook salmon in the ocean, which culminated in a larger Chinook Salmon Symposium held in Anchorage, Alaska in October 2012 (ADFG 2013). Declining trends of Chinook salmon production in Alaska were presented in terms of weakened spawner/recruit relationships, marine survival, and harvest. Although no single mechanism responsible for the Alaska Chinook salmon production decline was identified at the symposium, the early ocean migration and conditions encountered by juveniles were implicated as a critical period for establishing year class strength.

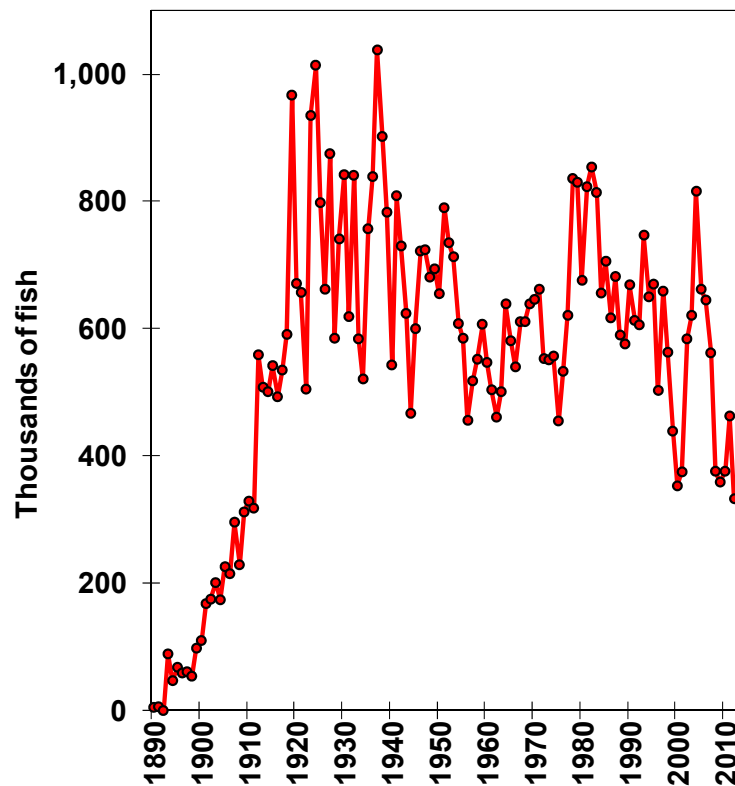


Fig. 1. Alaska Commercial Catches of Chinook salmon: 1890-2012*. Data courtesy of the Alaska Department of Fish and Game (*preliminary).

Understanding marine migration and production mechanisms of Chinook salmon in Alaska is challenging because long-term data sets of seaward-migrating juvenile salmon and associated metrics are rare, and Chinook salmon are the least abundant salmon species along the eastern Pacific Rim. The Auke Bay Laboratories has conducted annual ocean surveys via the Southeast Alaska Coastal Monitoring (SECM) project since 1997 along Icy Strait (58°N, 135W), a principal seaward

migration corridor for salmon in the northern region of Southeast Alaska (SEAK; Orsi et al. 2000, 2012). Salmon catch data were available from monthly epipelagic surface trawling at eight stations sampled annually in June (except 2009), July, and August over the past 16 years.

Chinook salmon sampled from the SECM surveys are predominately immature and of two distinct age groups: juvenile (age -0 fish in their initial seaward migration year) and older (age -1 fish in their second year at sea after one ocean winter). Age data available from fish captured with coded-wire tags (CWTs) provided a sample to validate information on origin and maturity stage. Of the 48 coded-wire tagged Chinook salmon, 96% originated in Southeast Alaska and consisted of the following five ocean age groups: age -0 (35.4 %), age -1 (50.0 %), age -2 (10.4 %), age -3 (2.1%), and age -4 (2.1 %). Mature Chinook salmon were seldom found, furthermore, by virtue of their relatively old, sex-specific age at maturity, all females younger than age -3 are immature in Alaska. Because not all fish caught were coded-wire tagged, size-at-age categories (based on CWT fish) were used to classify fish < 30-cm fork length as age -0, and all larger fish as age -1+.

Catches of age -0 and -1+ Chinook salmon from individual trawl hauls were standardized to an average monthly catch-per-unit-effort (CPUE) metric ($\text{Ln}[\text{catch per 20-min trawl haul} + 1]$).

Objectives for this study were to examine Chinook salmon CPUE data of two age groups (age -0 and -1+) from the SECM surveys to describe: (1) age-specific migrations in Icy Strait and (2) potential connections to Chinook salmon production metrics of wild and hatchery stocks in SEAK. This information is necessary to improve the understanding of mechanisms related to Chinook salmon migration and production in Alaska over periods of climate change, and also to help foster sustainable fisheries for the benefit of resource stakeholders.

Marine migration patterns differed between the immature Chinook salmon age groups. A combined total of 439 age -0 and -1+ Chinook salmon were sampled from 517 trawl hauls in Icy Strait over the 16 years. Overall, age -0 Chinook salmon were less abundant ($n = 177$) than age -1+ ($n = 262$) fish (Fig. 2). Furthermore, the average overall CPUE of age -0 Chinook salmon did not change by month (0.16 in June, 0.16 in July, and 0.19 in August), suggesting a tendency for localized and non-migratory behavior in summer, or continuous low influx of mixed stocks of this age group from throughout the area. In contrast, average CPUE of the more abundant age -1+ Chinook salmon declined by month (0.42 in June, 0.22 in July, and 0.13 in August), suggesting an emigration of this age group from Icy Strait during summer. Our data suggest that seaward-migrating juvenile Chinook salmon from SEAK likely overwinter in Icy Strait and then emigrate elsewhere during their second summer at sea. This protracted migration in the early marine life history of Chinook salmon is important to consider when assessing sources of natural and fishing mortality for modeling age-specific ocean migration patterns (Sharma and Quinn 2012; Miller et al. 2013) and for defining local habitat use and trophic dynamics (Echave et al. 2012, Sturdevant et al. 2012).

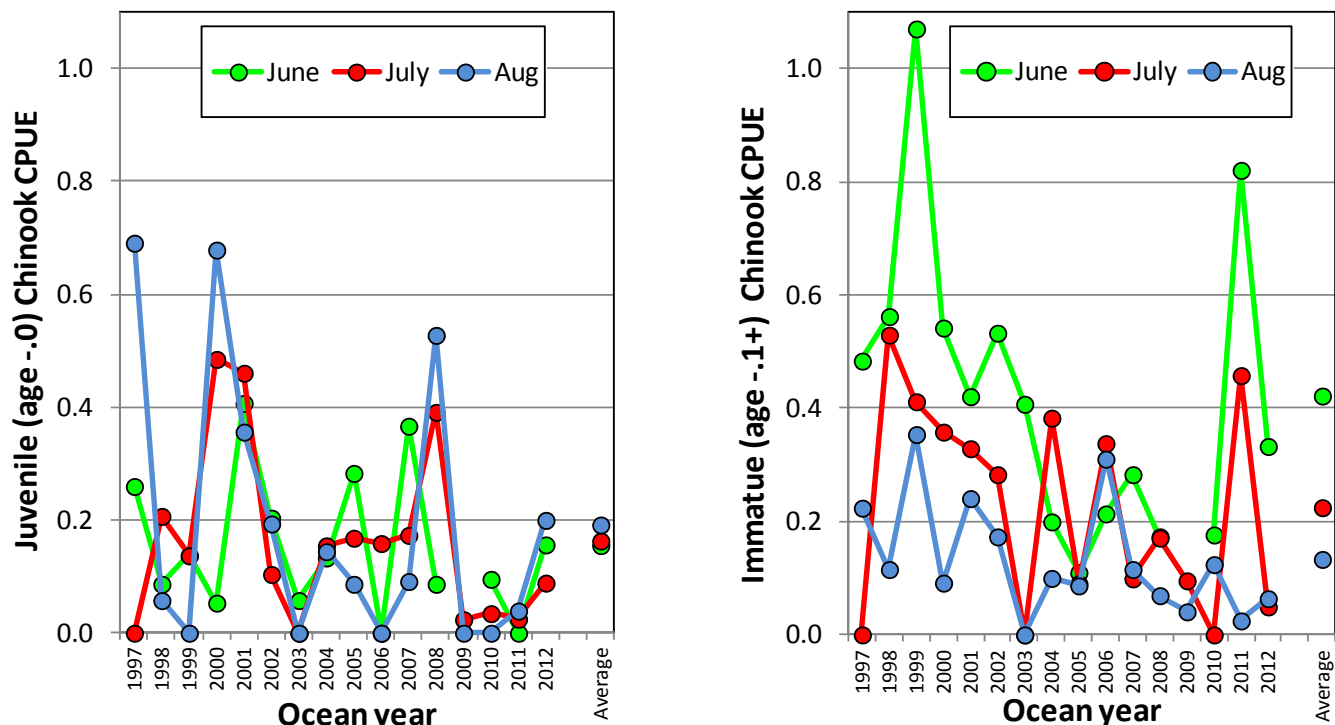


Fig. 2. Monthly CPUE (average LN [catch + 1]) of juvenile (age -0) and older (age -1+) Chinook salmon from the SECM time series in the northern region of Southeast Alaska, June, July, and August of 1997-2012. .

The age-specific Chinook salmon catch data from the SECM surveys were compared to Chinook salmon production metrics for representative wild and hatchery stocks from SEAK. Although both catch and CWT survival data are available for SEAK, survival is a superior production metric because the Chinook salmon fishery harvest in SEAK is quota-capped and thus catches do not indicate year-class strength. In addition, SEAK harvests, particularly on the outer coast, are composed of a diverse mixture of stocks that includes many non-Alaskan Chinook salmon and multiple age classes of intermingling immature and mature fish. Survival information based on CWTs was obtained for three wild stocks (Stikine River, Chilkat River, and Taku River) and three hatchery stocks (Little Port Walter, Hidden Falls, and Douglas Island Pink and Chum) in SEAK (Table 1). For each stock group, marine survival was estimated using data from completed brood cycles through ocean age -5 fish. Survival data were available for up to 11 brood cycles for each stock group, although fewer cycles were typically available for wild stocks (5-10 cycles). For the SECM surveys, CPUEs of juvenile and age -1+ fish were available for each month and year up to the 2006 ocean year and were lagged to the corresponding ocean entry time of the brood year. For example, monthly juvenile Chinook salmon CPUE in Icy Strait in the 2000 ocean year were compared to 1998 brood year survival; similarly, the monthly age -1+ Chinook salmon CPUE in 2000 was compared to the 1997 brood year survival. The year lag is appropriate since SEAK Chinook salmon are virtually all stream-type, with brood and smolt years separated by two years.

Table 1. Correlations of juvenile and immature Chinook salmon CPUE from SECM surveys with wild (W) and hatchery (H) brood year (BY) survival (1995-2005) available from selected Southeast Alaska stocks. Asterisks denotes significant differences in Person correlation coefficients (r), where $*p < 0.05$ or $**p < 0.01$.

Chinook salmon stock-group	Brood years	Number of years in comparisons	Age -0 (BY+2) CPUE June	Age -0 (BY+2) CPUE July	Age -0 (BY+2) CPUE August	Age -1+ (BY+3) CPUE June	Age -1+ (BY+3) CPUE July	Age -1+ (BY+3) CPUE August
Stikine River (W)	1998-2002	5	0.54	0.19	0.19	0.51	-0.80	-0.40
Taku River (W)	1995-2005	11	0.44	0.40	0.53	0.53	0.19	0.12
Chilkat River (W)	1998-2003	6	0.23	0.25	0.31	0.84*	0.00	-0.24
Little Port Walter (H)	1995-1999 2001-2005	10	0.05	0.14	-0.09	-0.12	0.10	0.51
Hidden Falls (H)	1995-2005	11	-0.14	0.34	0.11	0.70*	0.20	0.55
Douglas Island Pink & Chum (H)	1996-2005	10	0.13	0.38	0.03	0.86**	0.47	0.40

Abundance of Chinook salmon sampled during the annual SECM surveys was significantly correlated with the brood year survival of some stocks. Specifically, CPUEs of age -1+ Chinook salmon sampled during June were significantly ($p < 0.05$) correlated with survivals of two hatchery stocks and one wild stock (Table 1). These three stock groups also originated closest to the Icy Strait sampling locality. Analysis of the SECM time series supports the hypothesis that a critical period for Chinook salmon production occurs prior to their second ocean summer and indicates that inshore marine habitat conditions are important areas to investigate in order to understand Chinook salmon production mechanisms in Alaska.

Protracted marine migrations of Chinook salmon in SEAK also allow future ecosystem indicators to be identified, particularly for developing forecast models. For example, the strong age -1+ Chinook salmon component identified by the high CPUE in June 2011 may indicate future strong returns of age -3 fish from the same cohort returning in 2013. Thus, strong returns of Chinook salmon from the 2008 brood year in 2013 will support the use of the age -1+ CPUE metric as a leading ecosystem indicator of year class strength. Time series data, such as we present for SEAK Chinook salmon during recent periods of climate change, are increasingly important to fill knowledge gaps needed to evaluate changing ecosystem dynamics, trophic linkages, and migration patterns (Chittenden et al. 2009; Ruggerone and Nielsen 2009; Coyle et al. 2011; Beamish et al. 2012; Cook and Sturdevant 2013; Miller et al. 2013). For example, extending the time series of food habits among age groups (Weitkamp and Sturdevant 2008; unpublished data on file, Auke Bay Laboratories) could provide insight into trophic niche differences between juvenile and older age groups. Although exact mechanisms responsible for the Chinook salmon production decline in Alaska remain unclear, examining new ecosystem indicators and critical periods of migration may provide insight for future forecast models needed to help foster sustainable fisheries.

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Variation in Abundance and Condition of Juvenile Chum Salmon (*Oncorhynchus keta*) in the Eastern Gulf of Alaska in Relation to Environmental Variables

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Keywords: juvenile chum salmon, Gulf of Alaska, survival, condition, environmental

Commercial ex-vessel value of the chum salmon harvest in Southeast Alaska (SEAK) has increased 64% in the past five years to an annual harvest value close to 83 million dollars in 2012 (ADFG 2013), making it the most valuable commercial salmon fishery (in terms of ex-vessel price) in the region. Harvest of chum salmon has increased since the early 1990s due to the increase in hatchery production, which accounts for 73% of the region's commercial catch on average (Piston and Heintz 2011). However, a recent downward trend in wild chum salmon escapement indices (Piston and Heintz 2011) and the high variation in brood-year survival of hatchery chum salmon releases (Wertheimer and Thrower 2007) highlight the importance of trying to better understand the mechanisms affecting marine survival of chum salmon stocks in SEAK.

The mechanisms affecting marine survival of chum salmon are most influential during early marine residency when juvenile salmon experience high growth (Healey 1982a; Mortensen et al. 2000) and high mortality (Parker 1962). Juvenile chum salmon are highly dependent upon their early marine environment due to a short residence in freshwater rearing streams (Healey 1982b). After a rapid growth period, juvenile chum salmon in northern SEAK predominantly take a seaward migration corridor travelling from inshore waters through Icy Strait and out into the eastern Gulf of Alaska (EGOA; Orsi et al. 2000, 2004). In the EGOA, salmon distribution, abundance, and survival are presumably influenced by inter-annual variability in ocean physical processes.

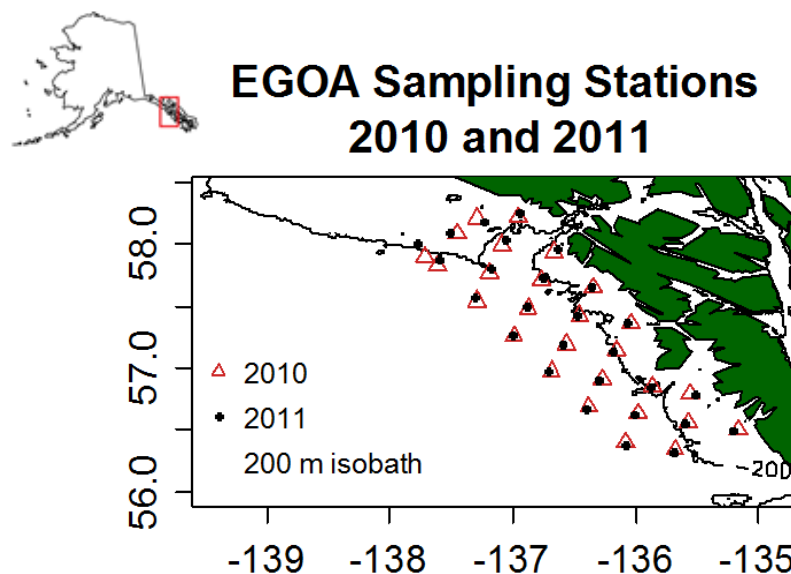


Fig. 1. Location of stations sampled in the eastern Gulf of Alaska (EGOA) in July, 2010 and 2011. Open triangles represent stations sampled in 2010 and black circles represent stations sampled in 2011.

Variability in ocean processes in the EGOA is affected by the Aleutian Low pressure system, a dominant feature of the atmospheric pressure system during the winter in the North Pacific Ocean. Multi-decadal variability in the Aleutian Low affects the abundance of Pacific salmon in the EGOA (Beamish and Bouillon 1993). Inter-annual variability in ocean processes in the GOA is affected by basin-scale processes such as the El Niño Southern Oscillation (ENSO) reflected in the

variation of sea surface temperature (SST). The Multivariate ENSO Index (MEI) is a basin-scale variable that integrates El Niño and La Niña events with longer-term variations in the coupled ocean-atmosphere system, including variability in the Aleutian Low (Wolter 1987). Indirectly, climate variability can constrain early marine growth in chum salmon by altering the distribution and abundance of prey communities and by increasing residence time in shallow littoral zones, thus delaying offshore migration timing and increasing vulnerability to nearshore predators. Faster growing individuals avoid being prey to gape-limited predators (Sogard 1997) resulting in higher marine survival (Healy 1982a; Beamish and Mahnken 2001; Ruggerone et al. 2003; Ruggerone and Goetz 2004).

Directly, thermal conditions can constrain growth by influencing metabolic responses and subsequent allocation of energy in a juvenile salmon. The metabolic response to the thermal condition determines if energy is allocated to basal or active metabolism rather than somatic growth or lipid storage (Beauchamp et al. 2007).

This study examined variation in juvenile chum salmon abundance and condition in relation to marine factors in the EGOA. Specifically, the objectives of this study were to (1) examine differences in abundance and condition of juvenile chum salmon between stocks of different origin, (2) describe the spatial and temporal variability in abundance (CPUE) and condition of juvenile chum salmon, and (3) examine the relationship between abundance and condition of juvenile chum salmon and marine environmental factors.

Twenty-seven stations on a grid were sampled off the coast of northern SEAK during July, 2010 and 2011 (Fig. 1). In 2010 stations were sampled from north to south, and in 2011 stations were sampled from south to north. At each station, juvenile salmon samples were collected with 30-minute surface trawls targeting the top 20 meters. Associated oceanographic variables were also collected, including vertical profiles of conductivity and temperature.

Surface water temperatures in the upper 3 m were significantly different between years (ANOVA, $p = 0.001$) averaging 11.70°C (SD = 0.39) in 2010 and 12.59°C (SD = 1.25) in 2011. In both years, stations sampled in early July (northern stations in 2010 and southern stations in 2011) had lower temperatures than stations sampled later in the month (Fig. 2; ANOVA, $p < 0.001$). Sea surface salinities (SSS) and Chl-*a* values were not found to differ significantly between sampling year or station location.

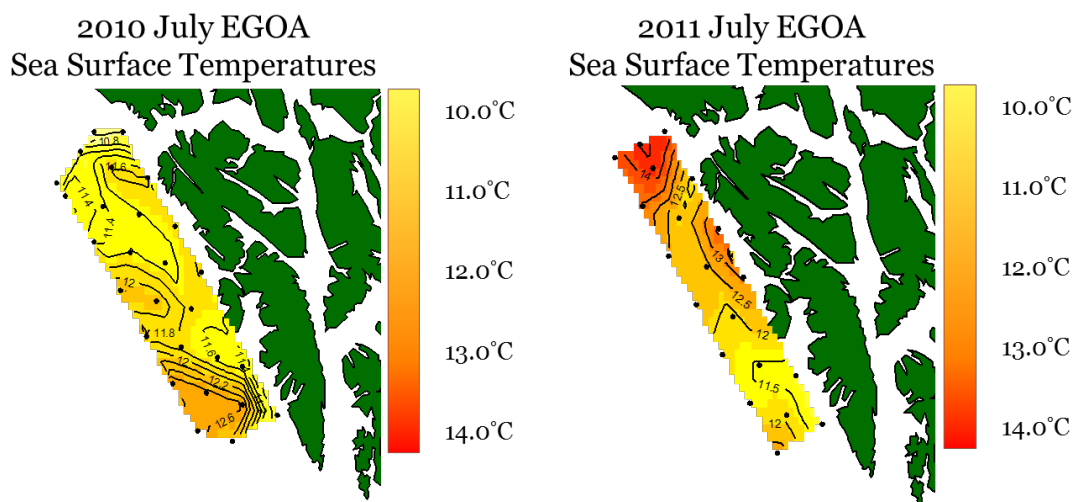


Fig. 2. Interpolated sea surface temperatures (SST) in the vicinity of the survey area in the eastern Gulf of Alaska (EGOA) in July, 2010 and 2011. Black circles represent stations sampled for SST in 2010 ($n = 27$, left panel) and 2011 ($n = 20$, right panel). Contour lines depict temperature gradients.

On average, juvenile chum salmon of the pooled stock groups were larger in 2011 (mean FL = 124.09 mm, SE = 2.26) than in 2010 (mean FL = 121.6 mm, SE = 2.03). Wild juvenile chum salmon had a larger mean length than those originating from hatcheries for both sampling years combined (ANOVA, $p < 0.001$). However, within sampling years, wild stocks were only significantly larger than hatchery stocks in 2011 (ANOVA: 2011 $p < 0.001$; 2010 $p = 0.309$; Table 1).

Two measures of condition were used in comparing the physiological status of juvenile chum salmon in the EGOA: whole-body energy density and weight-at-length residuals. Energy density values and residuals from a regression of ln-transformed weight on ln-transformed length were pooled for both years of sampling. Energy density was higher in chum samples collected in 2011 (4892.97 J/g, SE = 64.27) than in fish collected in 2010 (4688.22 J/g, SE = 75.93).

Table 1. Stock, sample size, and average fish length (mm) for juvenile chum salmon collected in the eastern Gulf of Alaska (EGOA) in July, 2010 and 2011. Stock identified as wild or originating from regional hatcheries in Southeast Alaska (SEAK).

Year	Stock	Sample Size	Min Length (mm)	Max Length (mm)	Length (mm)	Standard Error
2010	WILD	36	85	145	124.22	3.58
2010	NSRAA	19	87	191	128.74	4.12
2010	DIPAC	33	101	126	111.82	1.22
2010	SSRAA	2	152	178	171.5	0.5
2011	WILD	35	96	189	137.6	4.96
2011	NSRAA	71	109	188	115	1.70
2011	DIPAC	5	98	125	109	4.51
2011	SSRAA	5	171	172	168.2	4.45

NSRAA: Northern Southeast Regional Aquaculture Association.

DIPAC: Douglas Island Pink and Chum.

SSRAA: Southern Southeast Regional Aquaculture Association.

The weight-at-length residuals representing the condition of juvenile salmon varied between stations and stocks, but without a clear spatial or temporal trend. While we found significant between-station variability, there was no evidence that the variability in abundance or condition of juvenile chum salmon in the EGOA was related to variability in SST, SSS, or Julian day (linear mixed-effects model, $p > 0.05$).

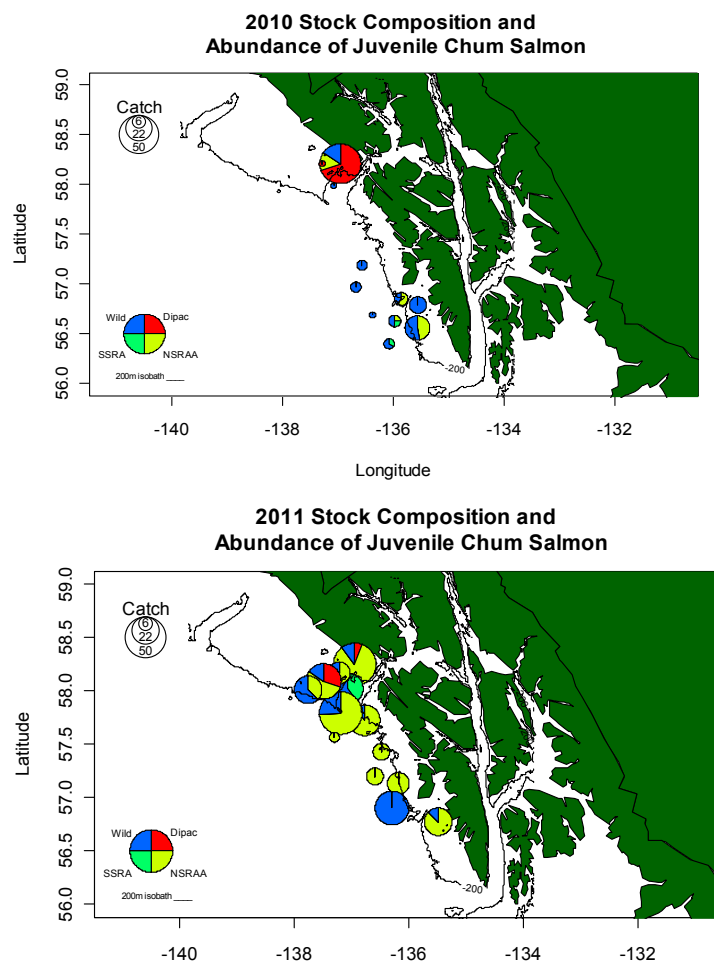


Fig. 3. Wild-hatchery chum salmon stock composition and abundance by station in the eastern Gulf of Alaska (EGOA) surveys conducted in July, 2010 and 2011. Circle radius indicates sample size (up to 50 juvenile chum salmon per station). Stocks are identified in Table 1.

In both years, juvenile chum salmon caught in the EGOA in July originated predominantly from three regional hatcheries in SEAK: Northern Southeast Regional Aquaculture Association (NSRAA), Douglas Island Pink and Chum (DIPAC), and Southern Southeast Regional Aquaculture Association (SSRAA; Fig. 3). For the unmarked wild chum salmon stocks, CPUE was higher in 2011 than 2010. The DIPAC was the only stock with fewer fish in the catch in 2011 than 2010. However, differences in catch composition could be due to temporal and spatial differences in the sampling design between the two years.

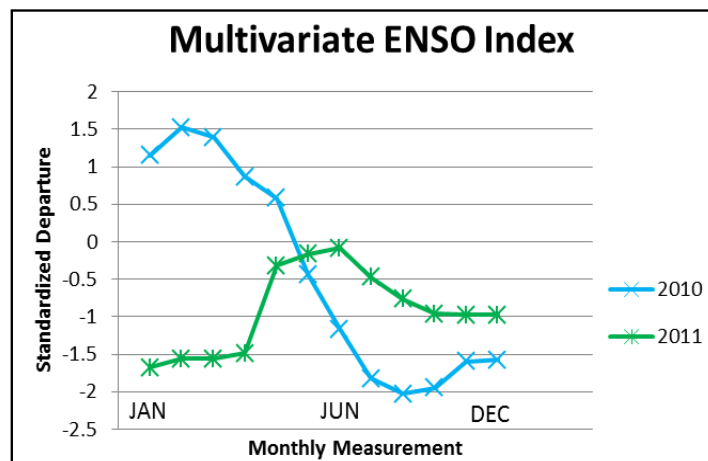


Fig. 4. Comparison of the standardized departures from the mean monthly measurements of the multivariate ENSO index for 2010 and 2011 in the eastern Gulf of Alaska (EGOA; Wolter 2013).

Physical climate indices in the marine environment differed between years. Both the Aleutian Low Pressure Index, measuring the Aleutian Low pressure system, and the MEI characterized 2010 as a weak El Niño year, whereas 2011 was characterized as a weak La Niña year with an anomalously cold winter (Beamish et al. 1997). These measurements of large-scale environmental processes identify 2010 and 2011 as being contrasting years, with high values of the MEI in 2010 corresponding to a warm winter and followed by a drastic decline through the summer to a cold fall and subsequent winter (low MEI values, Fig. 4).

As the thermal regime shifted from 2010 to 2011, so did the abundance and condition of juvenile chum salmon. In general, juvenile chum salmon were less abundant but had higher energy content and were larger in size in 2011, following an anomalously cold winter in the EGOA. A weak Aleutian Low in the EGOA in the winter of 2011 resulted in colder winter/spring SSTs, relaxed downwelling, and reduced onshore transport of prey species in the coastal habitat (Wickett 1967).

Differences in juvenile chum salmon condition and abundance in 2010 and 2011 coincided with years representing positive and negative anomalies of the coupled ocean-atmosphere system. This suggests that previous winter environmental conditions at both the basin and regional scale have potential to be used as predictive tools for forecasting juvenile chum salmon year class strength in SEAK. Future work will use regression models to examine the relationship between juvenile chum salmon condition and associated ecosystem metrics over the years 1997-2011 in northern SEAK.

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The Effects of Post-smolt Growth and Thermal Regime on the Marine Survival of Steelhead Trout (*Oncorhynchus mykiss*) From the Keogh River, British Columbia

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Keywords: steelhead trout, post-smolt growth, marine survival, North Pacific, Keogh River

The population of anadromous steelhead trout *Oncorhynchus mykiss* in the Keogh River has been studied intensively in part because of its pattern of declining recruitment attributed to marine survival conditions (Ward 2000). Climate variability has changed the productivity of salmonid species in all regions of the North Pacific (Atcheson et al. 2012), with areas alternately shifting between periods of enhanced and depressed productivity (Irvine and Fukuwaka 2011). An interest in the mechanisms governing marine survival and adult recruitment are central to contemporary concerns related to resource management, but they are also of concern in regard to the long-term prospects of managing biodiversity (Young et al. 2007). As climate change signals superimpose upon climate variation signals, our assessments of population viability are without historical analogy.

Size at ocean entry appeared to affect the recruitment pattern of many salmonid species (Holtby et al. 1990; Henderson and Cass 1991) and was considered to be a main factor in patterning marine survival in Keogh River steelhead (Ward and Slaney 1988). The survival pattern of this population has since changed without a concomitant change in smolt size at ocean entry (Welch et al. 2000), which prompted our consideration of other factors that may be affecting marine survival.

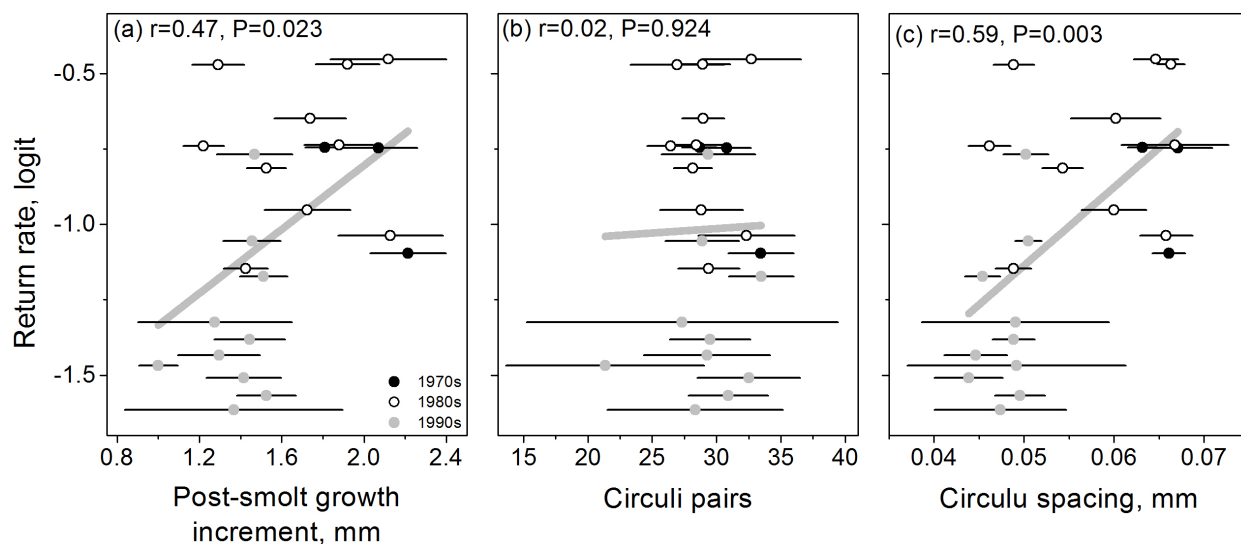


Fig. 1. The relationship between logit transformed return rate of Keogh steelhead and post-smolt growth increment (a), number of circuli pairs in the post-smolt growth increment (b), and average circuli spacing in the post-smolt growth increment (c). Independent variables are plotted with 95% confidence intervals with markers coded to decade of smolt year.

We found that post-smolt growth correlated with the pattern of marine survival of Keogh River steelhead. We measured the circuli spacing of the scales of 425 returning salmon to the Keogh River. Our samples were drawn from both wild (64%) and hatchery (36%) origin fish, which we found provided equivalent estimates of scale growth during the post-smolt phase. We measured the circuli spacing in the post-smolt growth zone, which starts at the end of the freshwater zone and goes to the first winter annulus. We utilized three scale growth parameters from these measurements: post-smolt growth increment, which is the total lineal growth of the scale within the growth zone; the number of circuli pairs deposited in the

zone; and, the mean spacing of circuli pairs within the zone. Post-smolt growth increment and circuli spacing were found to be correlated with return rate of Keogh River steelhead (Figs. 1a and c, respectively). These data suggest that when post-smolts accumulated higher growth during the post-smolt year, they tended to survive better. Although the sample size used in this study is small, we found that the error structure in the data (plotted as 95% confidence intervals around the growth data) support the contention that the decadal differences in the time series are real. The number of circuli pairs deposited does not correlate with the return rate, suggesting this scale characteristic does not respond to growth variation over the range of growth observed (Fig. 1b). Further, proportional allocation of the scale growth characteristics to month of the post-smolt growth season (June through December of the first year at sea) suggests that the initial growth of the fish when they first go to sea is not as important as the sustained growth experienced during the summer and fall of the post-smolt year.

We think it is important to consider how much time growth-related mortality effects have, and for that matter need, to produce a measurable effect on the annual survival rate of juvenile salmon. Both size at ocean entry and post-smolt growth are taken as indicators of the potential for size-related mortality to shape survival patterns. Size at ocean entry likely affects mortality to some degree, but the rapid growth of post-smolts after entering the ocean may ameliorate any initial size differences among and within smolt classes, making the time window associated with the effect of size of ocean entry quite limited. Unless there is an over-riding critical period that exists in the very early life history of the species, post-smolt growth patterns that develop over longer seasonal periods would provide the time for size-related mortalities to accumulate and thus dominate the survival pattern.

The distribution of sea surface temperature (SST) in the ocean thought to provide post-smolt nursery habitat for steelhead show that return rate has been negatively correlated with increasing SST, suggesting that growth is either directly affected by ocean warming or that warming affects the food web steelhead depend upon (Nickelson 1986; Atcheson et al. 2012). Steelhead occupy relatively narrow thermal ranges when at sea (Welch et al. 1998), which have been associated with specific isotherms (Burgner et al. 1992). We correlated the Keogh River return rate to the SST field from the Extended Reconstruction (ERSST) database for the corresponding smolt year. The monthly locations of the 12.5°C isotherm are plotted over the correlation fields to place into context the potential overlap with the assumed distribution of the steelhead post-smolt nursery. There is little correlative density for the first three months at sea, June through August (Figs. 2a-c, respectively). Correlations between SST and return rate develop in September and were highest in October (Figs. 2d and e, respectively), followed by declining correlation in November and December (Figs. 2f and g, respectively). The correlations are negative and the region of highly significant correlation in October is proximate to the 12.5°C isotherm.

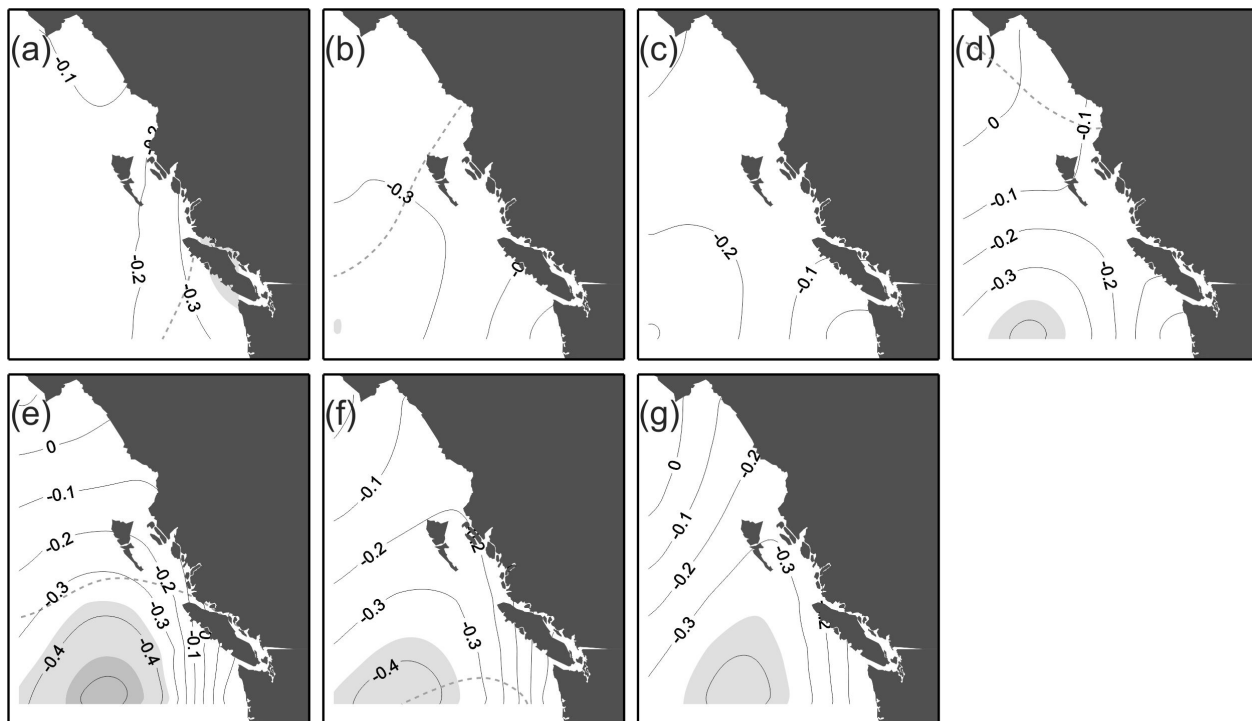


Fig. 2. Contour plots of correlation between the logit transformed return rate of Keogh steelhead and smolt-year sea surface temperatures for the months June through December, panels (a) through (h), respectively. Light grey shading marks approximate regions where correlations are significant at $p = 0.05$, and dark grey shading represents approximate regions significant at $p = 0.01$. Dashed lines mark average position of the 12.5°C isotherm, when present within the map area.

Steelhead appear to be responding to changing climate and growth regimes in the same way as their analog in the North Atlantic, Atlantic salmon *Salmo salar*. Comparative data show that eastern basin populations of Atlantic salmon are also negatively affected by increasing temperature during the post-smolt year (Friedland et al. 2013) and a cause and effect relationship between post-smolt growth and survival has been observed (Friedland et al. 2009). An interesting test would be to see if western Pacific basin steelhead populations also show the same contrasting pattern seen in northwest Atlantic salmon populations of an independence between post-smolt growth and survival and a dependence on thermal regime associated with ocean entry (Friedland et al. 2012).

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The Complexity of Chinook Salmon in the Early Marine Environment

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Keywords: juvenile Chinook salmon, life history pattern, survival

Chinook salmon (*Oncorhynchus tshawytscha*) in the Pacific Northwest exhibit a wide range of life history patterns, with variability in many phenotypic characteristics, that have important impacts in brood year survival rates. This complexity is continued during their early marine rearing phase in the Strait of Georgia, with alternate life-history types occupying different strata within the water column and displaying differences in size and diet. These aspects are discussed in the context of current marine survival trends for the different life history strategies.

Food Supply of Juvenile Pink Salmon in the Subarctic Frontal Zone of the Western North Pacific Ocean in the Winter and Spring

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Keywords: juvenile pink salmon, food supply, activity, lipid content, winter, spring, subarctic frontal zone, northwestern North Pacific

The offshore waters of the North Pacific Ocean are the main areas inhabited by pink and other Pacific salmon in winter and spring. The winter period of marine life of Pacific salmon has been studied insufficiently. Ecosystem studies and research began in 1986-1992 and significantly increased the available information on salmonid ecology during the winter and spring in the open ocean. In 2009-2011 the Pacific Research Fisheries Center (TINRO, Russia) conducted another series of complex research surveys of winter-spring salmon habitat conditions in the Subarctic frontal zone of the western North Pacific Ocean.

Asian pink salmon in the winter-spring period are mainly distributed in the Subarctic frontal zone and in neighboring waters to the north in habitats exhibiting a wide range of temperature, 0.5°-12°C, and salinity, 32.7‰ to 34.9‰. Analysis of 1986-1992 and 2009-2011 data has provided for the determination that spatial distribution of pink salmon depends on the western Subarctic cyclonic macrocirculation state and on the position of the frontal zone of the East Kamchatka Current ocean branch. The state of the western Subarctic cyclonic macrocirculation pattern can be described as “stretched”, “compressed”, or “normal”. These states are distinguished by heightened intensity of the Subarctic Current and intensity of the progression of the Aleutian and ocean branch of the East Kamchatka currents.

When the western Subarctic circulation was in a “stretched” state, pink salmon were distributed more evenly and over a wider area, including in areas to the southeast and eastwards where pink salmon catches were reported between 38°N and 45°N. When the western Subarctic circulation was in a “compressed” state, pink salmon were located in areas further northwards, and the main pink salmon catches were located between 41°N and 45–46°N, closer to the Kuril Ridge (Naydenko in press).

As the epipelagic zone of the northwestern Pacific Ocean is a biotope with clearly expressed dynamics of water circulation and a wide range of temperature and salinity values, salmon habitat conditions differ with regard to these conditions through the season and on an interannual basis.

One index of food supply for salmon is the total biomass of consumers of fodder zooplankton in areas inhabited by salmon. In 2009-2011 it was established that the main biomass of these consumers in the upper epipelagic zone consisted of Pacific salmon, mezopelagic fish, and squids. These nekton groups were the main consumers of fodder resources in the central and western parts of Subarctic frontal zone in winter-spring. The survey in 2010 was unusual because there was a high biomass of Japanese anchovy (*Engraulis japonicus*) caught. But anchovy were present in trawl catches conducted only in transitional subtropical waters. Pink salmon catches were low in transitional subtropical water masses. The nekton density in the research area ranged from 0.37 to 0.65 ton/km² in different years, which were very low values for such a huge area.

The basic trophic relationships among juvenile pink salmon (and other fish and squid) and major zooplankton groups were investigated and daily consumption of forage resources by nekton in the upper epipelagic zone was estimated. Our results showed that the trophic linkages of juvenile pink salmon in winter were directed upon consuming copepods, euphausiids, chaetognaths, hyperiid amphipods, and pteropods (other prey groups had smaller values). The daily consumption of these zooplankton groups by juvenile pink salmon varied depending on salmon abundance and did not exceed 2-14 thousand tons. The daily consumption of zooplankton by all nekton in the upper epipelagic zone was not high either—5 to 20 thousand tons. Our estimates for the total biomass of zooplankton in the western Subarctic frontal zone in these years were 84-158 million tons, significantly higher than consumption estimates. The ratio of the biomass of fodder plankton and nekton varied from 134 to 315 thousand tons in 2009-2011. The ratio was lower in 2009 when abundance of pink salmon, squids, and mezopelagic fish was high. But this index was high in comparison with other areas and seasons. These estimates show that winter is not a period of fasting when food resources are scarce.

The feeding activity of juvenile pink salmon in 2009-2011 was not low; the index of stomach filling (ISF) changed from 5‰₀₀₀ to 460‰₀₀₀ (averaging 54-140‰₀₀₀ in different years), but the ISF in winter was lower than ISF in fall. Pink salmon lipid content was depleted in the winter compared to the level in the fall.

Data on abundance and availability of zooplankton, abundance of nekton, the ratio of the biomass of fodder plankton and nekton, and daily consumption estimates by all nekton on zooplankton prey testify there is sufficient fodder zooplankton for juvenile pink salmon and other nekton in the northwestern Pacific Ocean in the winter and spring. However, there is a marked decrease in feeding activity and lipid content of pink salmon in winter. We do not consider the decrease of these parameters from fall to winter as evidence of unfavorable ambient winter conditions. It can be an expression of an internal rhythm related to pink salmon physiological cycles, adaptation to dwelling in cooler waters, and winter residence in waters with feeding conditions less favorable than summer conditions.

Implications of a Warming Bering Sea for Bristol Bay Sockeye Salmon

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Keywords: sockeye salmon, Bering Sea, Bristol Bay, over-winter survival, energetic status

The eastern Bering Sea shelf is an important nursery ground for juvenile Bristol Bay sockeye salmon (*Oncorhynchus nerka*; Farley et al. 2009) and the mechanism regulating size and condition of juvenile salmon is believed to be bottom-up control of the trophic structure (Farley et al. 2007b). A leading hypothesis for ocean productivity on the eastern Bering Sea shelf suggests that the southern extent and duration of sea ice in spring affects whether the benthic or pelagic communities benefit from spring and summer production (Hunt et al. 2002). Warmer winters with less sea ice are believed to favor pelagic productivity, potentially benefitting salmon growth and early marine survival. Changes in size, survival, distribution, diet, and growth rate potential for western Alaska salmon in response to changing spring and summer sea surface temperatures have been noted (Farley et al. 2005; Farley et al. 2007b; Farley and Moss 2009; Farley and Trudel 2009). While there is evidence that reduced size of juvenile pink (*O. gorbuscha*) and coho (*O. kisutch*) salmon leads to higher over-winter mortality (Beamish et al. 2004; Moss et al. 2005), direct evidence that the first winter at sea is the critical period for Pacific salmon that spend more than one year in the ocean has not been fully documented (i.e. sockeye salmon; Farley et al. 2007a).

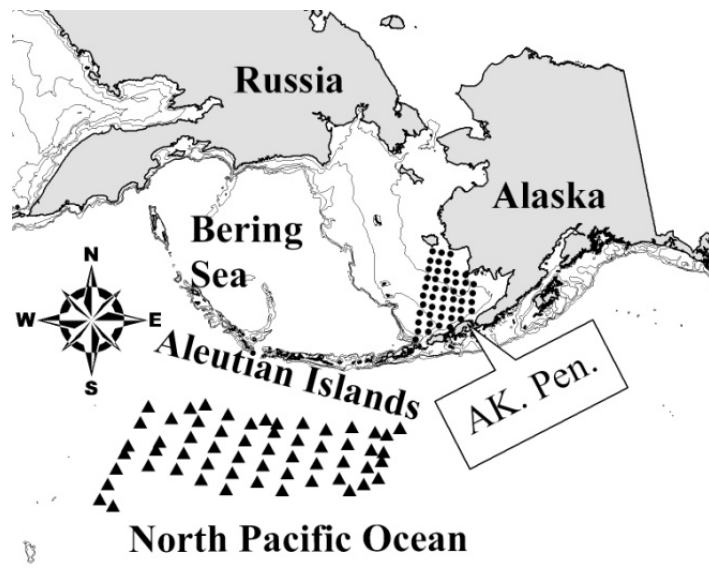


Fig. 1. Map providing examples of stations sampled by scientists with the Alaska Fisheries Science Center, Bering Aleutian Salmon International Survey project during mid August-September, 2002 to 2008 (black dots) and stations sampled by scientists with the TINRO-Center during February-March 2009 (black triangles).

Over-winter survival of Pacific salmon is believed to be a function of size and energetic status they gain during their first summer at sea. We tested this notion for Bristol Bay sockeye salmon utilizing data from large-scale fisheries and oceanographic surveys conducted during mid-August to September 2002 to 2008 by scientists with the Alaska Fisheries Science Center and during February to March 2009 by scientists with TINRO Center (Fig. 1). Genetic analysis indicated

Table 1. Bootstrap estimates of relative abundance (\widehat{RA} , millions) and marine survival index (\widehat{MSI}) with upper and lower confidence bounds (95% confidence intervals, LCI and UCI) for juvenile sockeye salmon collected during Fall 2002 to 2007 in the eastern Bering Sea and subsequent number of adult sockeye salmon returns to Bristol Bay (millions) 2 and 3 years later. The dash (-) indicates that the LCI was below 0%.

Year	\widehat{RA}			Adult Returns	\widehat{MSI}		
	LCI	Est	UCI		LCI	Est	UCI
2002	64.2	136.9	209.6	59.2	21.1%	46.4%	71.7%
2003	98.4	181.6	264.7	33.0	8.9%	19.3%	29.6%
2004	36.3	65.8	95.4	98.4	31.6%	61.5%	91.4%
2005	160.8	338.3	515.8	49.2	7.5%	15.5%	23.6%
2006	27.2	83.4	139.5	38.6	9.6%	52.7%	95.9%
2007	46.3	359.4	672.6	41.0	-%	14.8%	36.2%

that roughly 60% of the ocean age-1 salmon captured in the North Pacific Ocean during February to March 2009 were from Bristol Bay (Table 1). The size frequency data for juvenile and ocean age-1 sockeye salmon indicates that size-selective mortality occurs for Bristol Bay sockeye salmon between fall and their first winter at sea (Fig. 2). Differences in the seasonal energetic signatures for lipid and protein suggest that these fish are not starving but instead the larger fish captured during winter appear to be utilizing energy stores to minimize predation (Fig. 3). Energetic status of juvenile sockeye salmon was also strongly related to marine survival indices (Fig. 4), and years with lower energetic status appear to be a function of density-dependent processes associated with high juvenile sockeye salmon abundance.

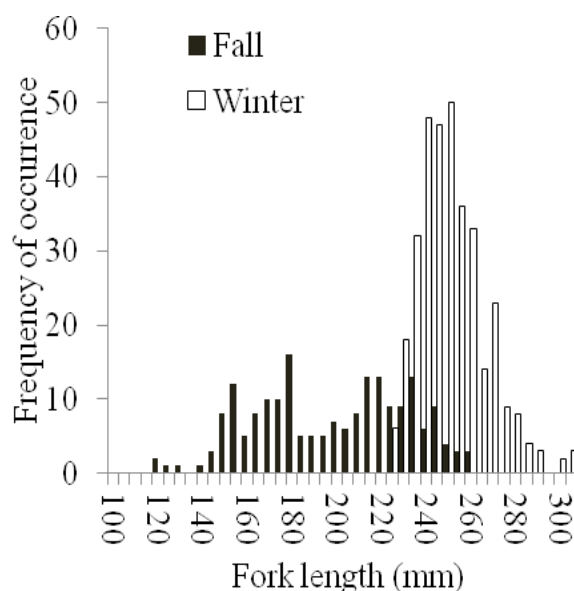


Fig. 2. Fork length frequency for juvenile sockeye salmon captured during fall 2008 (dark bar) in the eastern Bering Sea and ocean age-1 sockeye salmon captured during winter 2009 (clear bar) in the North Pacific Ocean.

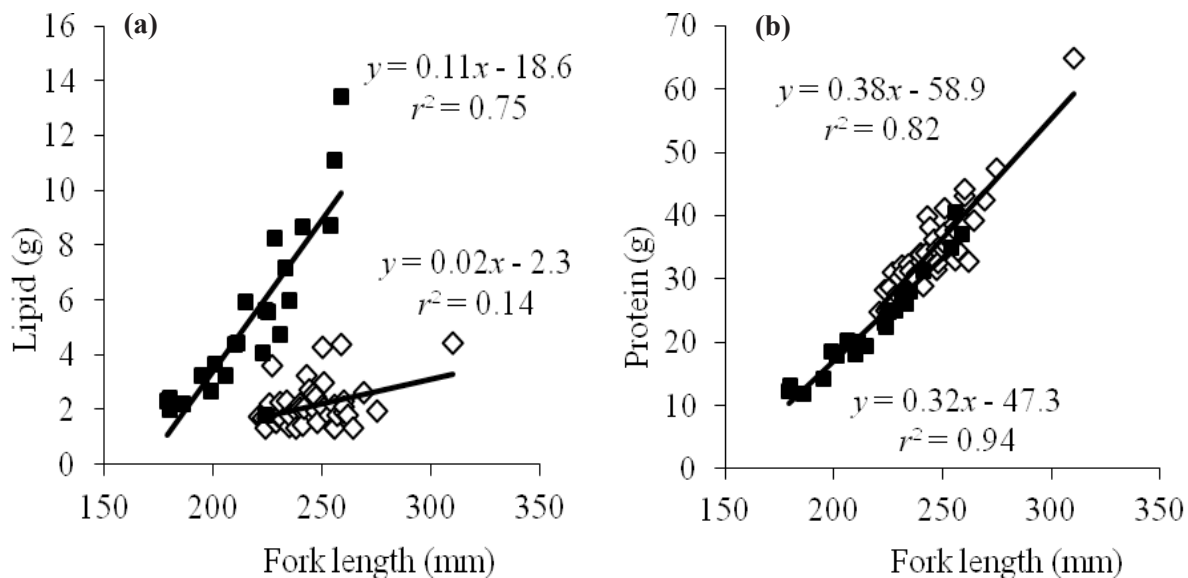


Fig. 3. The relationship between fork length (mm) and (a) lipid (g) and (b) protein (g) for juvenile (squares) and ocean age-1 (triangles) sockeye salmon collected during fall 2008 in the eastern Bering Sea and winter 2009 in the North Pacific Ocean, respectively.

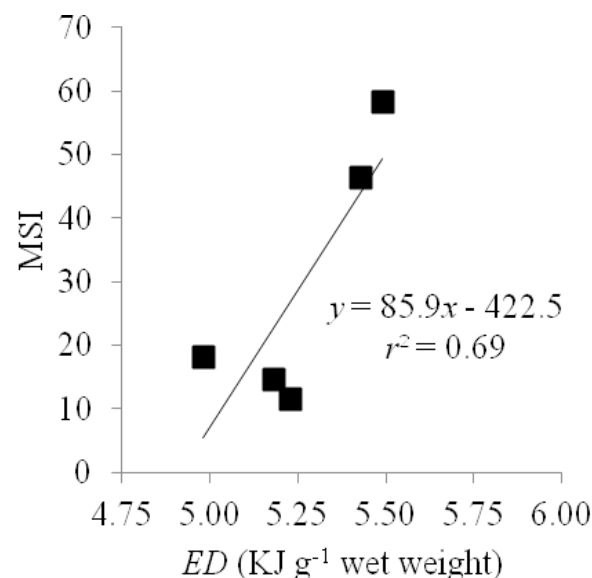


Fig. 4. The relationship between marine survival index (MSI) and energy density (ED; KJ g⁻¹ wet weight) for juvenile salmon captured during fall 2003 to 2007 in the eastern Bering Sea.

It is generally agreed that the Bering Sea will continue to warm up (Christensen et al. 2007), thus there is an expectation for continued healthy returns of sockeye salmon to Bristol Bay watersheds (e.g. Farley et al. 2007b; Farley et al. 2007c). Many juvenile salmon and, in particular, juvenile sockeye salmon relied heavily on age-0 walleye pollock for prey during years with anomalously warm sea temperatures (Farley et al. 2009). However, there is new evidence that extended periods of warming may reduce the availability of lipid-rich crustacean zooplankton, negatively impacting walleye pollock recruitment (Hunt et al. 2011). This result suggests that continued high sea temperatures could reduce the availability of age-0 pollock, causing juvenile sockeye salmon to seek other, potentially lipid-poor prey items. In addition, a previous analysis suggested that if summer sea temperatures were increased by 5°C, the largest decrease in growth rate potential for juvenile Bristol Bay sockeye salmon would occur during years where observed sea temperatures (2000 to 2006) were already anomalously

warm (Farley and Trudel 2009). Thus, under a climate warming scenario, we hypothesize that sustained increases in sea temperatures above those observed during 2002 to 2005 may impact the energetic status and growth rate potential for juvenile Bristol Bay sockeye salmon, potentially leading to increased overwinter mortality.

Note—The full article for this extended abstract was published in ICES Journal of Marine Science—Farley et al. 2011 doi:10.1093/fsr021.

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Marine Survival and Interspecific Interactions of Coho Salmon in Southeast Alaska

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Keywords: marine survival, coho salmon, Southeast Alaska

We examined physical and biotic factors potentially affecting marine survival of coho salmon in Auke Creek, Alaska, where activities conducted at a weir has produced a long time series of smolt and adult abundance. Marine survival was positively related to nearby releases of hatchery-produced pink and chum salmon. Strong correlation of jack and adult coho returns suggested survival was determined in the first summer at sea. Early marine growth was positively related to both the jack return rate and the survival of both male and female coho.

When we expanded this study to 14 coho salmon stocks situated throughout Southeast Alaska, abundance of hatchery produced chum and wild pink salmon was often correlated with coho survival, but the effect was sometimes positive and sometimes negative. Models that best explained coho salmon marine survival varied from place to place, both in the factors included and the direction of their effect. Only the North Pacific Index had a consistent (positive) effect. However, despite the disparity in explanatory models, productivities of the 14 coho salmon stocks were highly correlated.

Connecting the “Dots” Among Coastal Ocean Metrics and Pacific Salmon Production in Southeast Alaska, 1997-2012

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Keywords: pink salmon, coho salmon, production, ocean, ecosystem, forecast, Southeast Alaska

Complex ocean ecosystem dynamics could be better understood in the context of climate change if relationships among coastal ocean metrics and Pacific salmon (*Oncorhynchus* spp.) production could be identified. We examined annual time series of ecosystem metrics during critical periods of salmon ocean life history to establish these connections and to help foster sustainable fisheries management. One critical period is the early ocean migration of juvenile salmon, which has been recognized as a strong determinant of year class strength for many salmon species (Parker 1968; Heard 1991; Pearcy 1992; Karpenko 1998; Quinn 2005). During this early period, important coastal ocean metrics for consideration include physical factors such as stream flow, coastal temperatures, ocean-basin indices, and biological indicators of juvenile salmon prey, growth, condition, and abundance during their seaward migration. In this study, prior year class strength was purposely excluded in order to isolate the predictive power of coastal ecosystem metrics on salmon production.

The selection of salmon production response variables associated with coastal ocean metrics must capture the appropriate spatial and temporal scales. These variables commonly include commercial harvest and marine survival. Because marine survival of salmon operates on spatial scales within 500 km (Mueter et al. 2002a; Pyper et al. 2005; Malick et al. 2009; Sharma et al. 2013), salmon production response variables should be region-specific as opposed to broad-scale in geographic distribution. These variables should also be time-specific because long term production trends of salmon can alternate between southern and northern domains along the west coast of North America, a pattern attributed to long term climate signals such as the Pacific Decadal Oscillation (PDO; Hare and Francis 1995; Mantua et al. 1997; Mueter et al. 2002b). Therefore, disentangling relationships between coastal ocean metrics and salmon production is most tenable by focusing on spatially-explicit regional production response variables over an intermediate temporal scale.

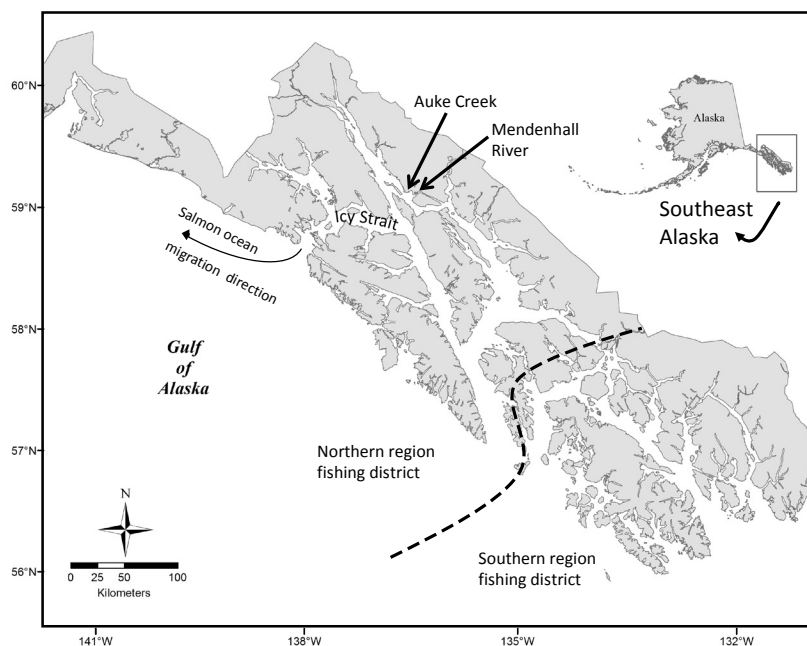


Fig. 1. Localities for sampling regional coastal ocean metrics (from Icy Strait), the estuarine entry point of wild pink and coho salmon (Auke Creek), the freshwater discharge measurement site from the Mendenhall River, and northern and southern commercial salmon harvest regions in Southeast Alaska.

Making solid connections between annual coastal ocean metrics and salmon production is challenging because some species have long brood-year cycles that extend across multiple ocean years, thus confounding annual ocean signals. This is certainly true with species that spend two to five winters in the ocean before returning to spawn, such as sockeye (*O. nerka*), chum (*O. keta*), and Chinook (*O. tshawytscha*) salmon (Groot and Margolis 1991). However, pink (*O. gorbuscha*) and coho (*O. kisutch*) salmon exclusively spend one winter at sea, and thus are more suitable candidates for exploring connections among annual coastal ocean metrics and regional salmon productivity. These species, notwithstanding returns of precocious male coho salmon (“jacks”), also lack important leading indicator year class information from younger siblings for use as a forecasting tool. Consequently, stock assessments prior to pink and coho salmon fisheries is problematic because valuable input parameters for pre-season forecasting models are largely lacking (Haeseker et al. 2005; Wertheimer et al. 2011).

In this study, coastal ocean ecosystem metrics were examined in the context of pink and coho salmon production in Southeast Alaska (SEAK). Over two thousand anadromous salmon streams are located throughout the SEAK Archipelago, with pink and coho salmon occurring in most streams. Ongoing ocean research through the Southeast Coastal Monitoring (SECM) project has accrued a 15-yr time series of biophysical metrics associated with seaward-migrating juvenile salmon (Orsi et al. 2012). The study locality is centered in the vicinity of Icy Strait (58°N, 135°W) in the northern region of SEAK, where both species are harvested commercially. Regional salmon harvest data are available annually from the Alaska Department of Fish and Game (ADFG), and wild stock marine survival data are available from the Auke Creek research station (Fig. 1).

Table 1. Chronology of annual, physical, and biological coastal ocean metrics related to salmon production response variables in Southeast Alaska, 1997-2012. The temporal context of each metric is shown in relation to months from ocean entry times of pink salmon fry and coho salmon smolts.

Metric	Category	Ocean entry time	Period	Narrative	Abbreviation
Coastal ocean					
Multivariate El Niño / Southern Oscillation (MEI) index	Physical	-6	Nov-Mar	Southern Pacific: temperature, wind, pressure, teleconnection with Icy Strait temperatures (Wolter and Timlin 1993)	MEI-W(Nov-Mar)
Pacific Decadal Oscillation (PDO) index	Physical	-6	Nov-Mar	North Pacific sea surface temperature anomaly (Mantua et al. 1997)	PDO-W(Nov-Mar)
Auke Creek stream temperature	Physical	-3	Sep-May	In stream water temperature, warmer temperatures faster hatching and outmigration	Temp AC Sep-May
Mendenhall River discharge	Physical	-1	Mar-May	Freshwater influx to estuaries, faster juvenile transport offshore of littoral zone (USGS 2011)	MRD-Mar-May
Fry/smolt timing	Biological	0	Apr-May	Julian day of peak outmigration: pink fry in April and coho smolts in May	P-pk outmigr day C-pk outmigr day
Auke Bay dock sea surface temp	Physical	0	Apr-May	Littoral zone sea surface temperatures that fry and smolts are exposed to	SST AB Apr-May
Preferred salmon prey fields	Biological	+1	June	Biomass of integrated zooplankton when juveniles are most abundant	Jun-pref bio
Juvenile salmon peak catches	Biological	+1.5	Jun/Jul	Catch per trawl haul of juveniles in peak month	P-CPUE-pk C-CPUE-pk
Icy Strait temperature	Physical	+2	May-Aug	Integrated 1-20 water temp throughout seaward migration period for juveniles	ISTI-Avg20mMJJA
NP Index	Physical	+2	Jun-Aug	Inverse of Aleutian Low, relaxes coastal downwelling, broadens Alaska Coastal Current (Trenberth and Hurrell 1994)	NPI-jja
PDO	Physical	+2	Jun-Aug	North Pacific sea surface temperature anomaly	PDO(sumJJA)
Preferred salmon prey fields	Biological	+2	May-Aug	Numerical abundance of preferred prey items	MJJA-pref bio

Table 1. Continued.

Metric	Category	Ocean entry time	Period	Narrative	Abbreviation
Juvenile salmon energy density	Biological	+2	Jul	Whole body energy content of fish	P-Energy C-Energy
Prey wt/ body wt	Biological	+2	Jul	Percentage of prey wt divided by whole body weight.	P-prey%bw C-prey%bw
Juvenile salmon condition	Biological	+2	Jun-Aug	Length weight conditional residuals	P-CondR C-CondR
Juvenile size at time	Biological	+2	Jul	Size on the 24 th of July (growth proxy) in Icy Strait	P-SzAtT C-SzAtT
Juvenile timing	Biological	+2	Jun-Aug	Peak month of migration along the Icy Strait seaward migration corridor	P-Season C-Season
Predator index	Biological	+3	Jul-Aug	Adult coho abundance and predation rate in Icy Strait (Adult CPUE * predation intensity)	PredIndex
Production response					
Marine survival of Auke Creek jacks	Production response	+4	Sep	Coho salmon (age -0) precocious male jacks that return after a brief coastal residence	COHOjk%ms
Commercial harvest in Southeast AK	Production response	+14	Aug	Pink salmon from purse seine fishery and coho salmon from commercial troll fishery: Both from the northern and entire region of SEAK	PINKharNSE COHOharNSE PINKharSEAK COHOharSEAK
Marine survival of Auke Creek adults	Production response	+16	Oct	Adult pink salmon age -.1 arrive during August and Adult coho salmon arrive in Sep	PINK%ms COHOadult%ms

Ecosystem metrics were chosen to reflect biophysical conditions in the early marine life history phase of pink and coho salmon (Table 1). We examined annual region-specific coastal ocean metrics including overwinter freshwater stream temperatures, spring freshwater discharge, and spring and summer metrics associated with seaward-migrating juvenile salmon (marine water temperature, zooplankton standing stock, salmon migration phenology, abundance, growth-condition-energy, and an associated predation index). Additional annual metrics representing larger basin-scale physical oceanographic conditions included the overwinter Multivariate El Niño/Southern Oscillation Index (MEI), the summer Pacific Index (NPI), and the overwinter and summer Pacific Decadal Oscillation Index (PDO).

The production response variables chosen for pink and coho salmon were the annual commercial harvests of these species in SEAK (northern region and throughout) and stock-specific marine survival from Auke Creek. Salmon harvest data have been used as a historical index of regional productivity (Jaenicke 1995; Jaenicke et al. 1998) and were obtained from ADFG (ADFG 2012). Harvest data from the northern region were examined separately because it encompasses Icy Strait, the locality where most of the coastal ocean metrics were collected (Fig. 1). Fishery harvest data were the number (millions) of fish caught, representing predominantly wild unmarked stocks that fluctuate widely over the time series (Fig. 2). Wild salmon stock survival data were obtained from pink salmon (unmarked) and coho salmon (coded wire tagged, CWT) returning to Auke Creek, where both species are monitored via counting weirs installed for spring downstream migrants and fall upstream returning adults (Fig. 3). The Auke Creek facility is cooperatively managed by NOAA, ADFG, and the University of Alaska to study out migrants and returns of four species of wild salmon fry, smolt, precocious males (jacks), and adults (Taylor 1980; Mortensen et al. 2000; Briscoe et al. 2005; Taylor 2008; Kovach et al. 2013). Coho salmon CWTs allow monitoring of both jacks that return in the same year and adults that are either intercepted in commercial fisheries or return the following year to the system. Thus, marine percent survival data included adults returning after one year at sea (pink salmon age 0.1, coho salmon age -.1), and coho salmon jacks that returned to spawn after 3-4 months at sea (age -.0; Table 1). Coho salmon adult marine survival includes contributions of Auke Creek fish in SEAK commercial fisheries, whereas pink salmon marine survival does not include fishery harvest information.

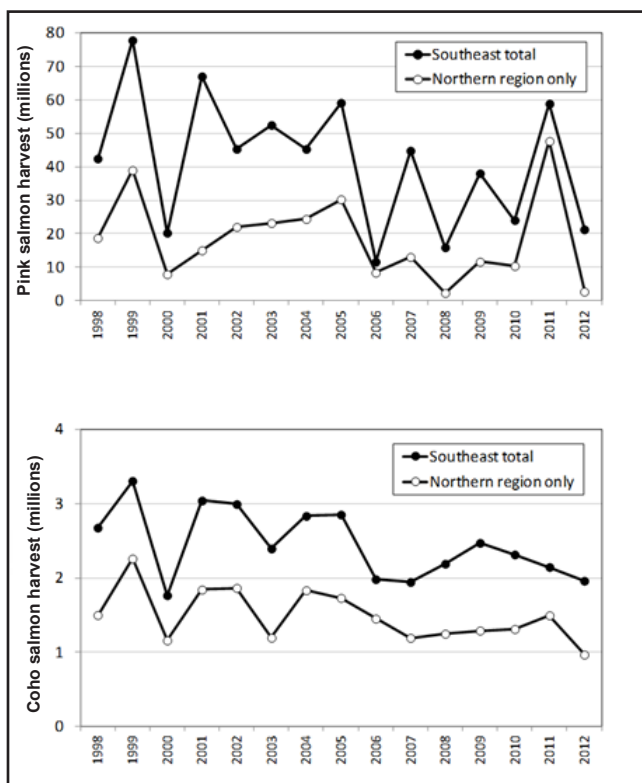


Fig. 2. Commercial harvest patterns of pink and coho salmon in the northern and entire region of Southeast Alaska, 1998-2012.

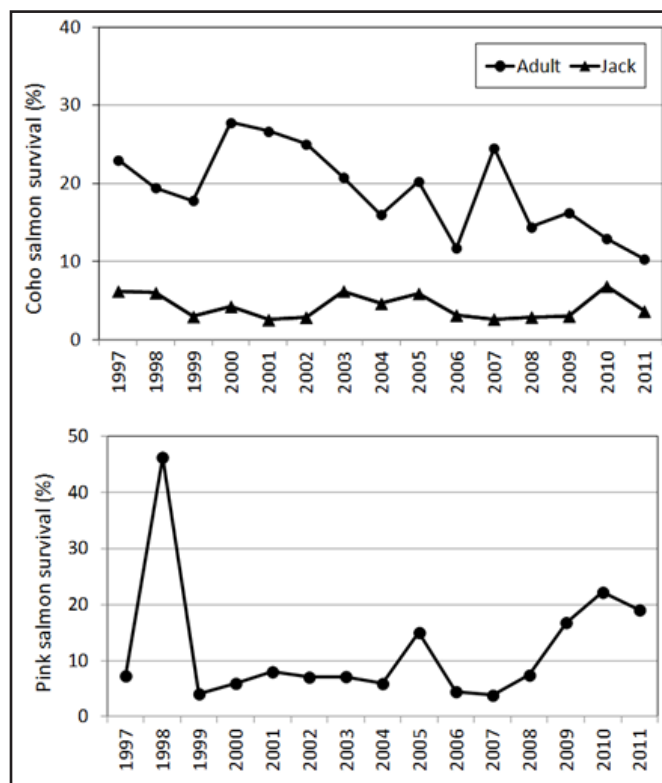


Fig. 3. Wild stock survival of pink and coho salmon from Auke Creek in the northern region of Southeast Alaska, over the 1997-2011 ocean entry years. Pink salmon survival is estimated from unmarked wild fry counted from the downstream trap and subsequent weir counts of returning adults the following year. Coho salmon survival is based on near 100% wild smolt marking and subsequent returns. Coho salmon survival includes jacks returning to Auke Creek the same ocean year as outmigration and of adults returning the following year in addition to fishery harvest estimates.

Our study objective was to examine connections among coastal ocean metrics associated with seaward-migrating juvenile salmon (1997-2011) and adult salmon production response variables for pink and coho salmon (1998-2012). One potential outcome of this study is improved insight into mechanisms operating through ecosystem dynamics or climate change that could influence salmon production in SEAK. Consequently, connecting the dots among coastal ocean metrics and production of pink and coho salmon would provide an opportunity to improve understanding of coastal ecosystem functions and to foster sustainable fisheries through the development of forecast models to benefit resource stakeholders.

A multivariate approach was used to identify and define the relationships among coastal ocean metrics and salmon production response variables for the 15-year time series. First, we used dendrograms from cluster analysis (Fig. 4) based on Spearman rank correlation coefficient resemblances of the normalized data matrix per the average linkage method to define relationship distances (Primer v6 software; Clarke and Gorley 2006). Of the production response metrics, clusters were evident for (a) marine survival of adult pink salmon and coho salmon jacks, and (b) regional harvests of pink and coho salmon (Fig. 4). The clustering of these survival metrics suggests the importance of early marine conditions for both species, as coho salmon jacks return after only four months at sea (Table 1; Fig. 4). In contrast, lack of clustering for adult coho salmon marine survival suggests lack of association with any single coastal ocean metric, which implies that a different factor(s) influences survival of Auke Creek coho salmon beyond their seaward migration phase.

Second, a BEST analysis (Clarke and Gorley 2006) was used to identify a subset of coastal ocean ecosystem metrics having the highest correlation with salmon production response variables. A matrix of production response variables was constructed using Euclidean distances, and then an iterative process was used to choose a subset of coastal ocean variables that it best matched based on Spearman rank correlation coefficients between the two matrices. Results from the BEST analysis indicated that the MEI_{winter} and PeakPinkCPUE variables were closely related ($r = 0.67$) to subsequent salmon production, suggesting that both a lagged, long-distance climate signal and localized, early marine conditions may influence pink and coho salmon production in SEAK.

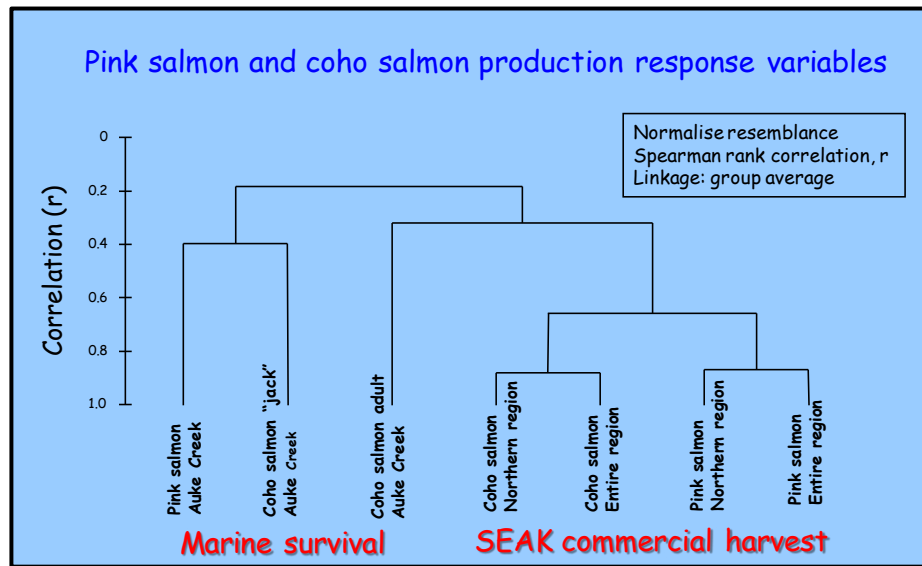


Fig. 4. Spearman rank correlation dendrogram of production response metrics of pink salmon and coho salmon. These represent survival of pink and coho salmon (adult and jack) from Auke Creek in the northern region of Southeast Alaska, as well as commercial fishery harvest in the northern and entire Southeast Alaska region over the 1997-2011 ocean entry years.

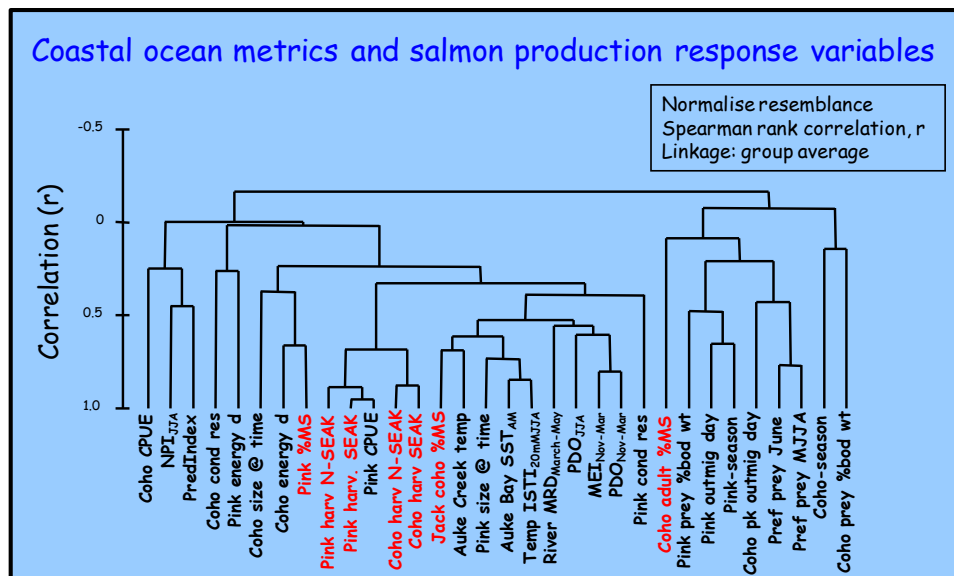


Fig. 5. Spearman rank correlation dendrogram of all normalized coastal ocean metrics associated with seaward migrating pink and coho salmon and response production metrics in Southeast Alaska over the 1997-2011 ocean entry years. Definitions of the metrics are shown in Table 1.

Third, in order to identify similarities among the coastal ocean and salmon production variables in the time series, a second dendrogram was constructed from a matrix of Spearman rank correlation coefficient resemblances for all 32 coastal ocean and salmon production variables (Fig. 5). All of the salmon production response variables except coho salmon adult marine survival grouped into clusters strongly associated ($\rho > 0.6$) with coastal ocean metrics. The strongest associations were for: (1) pink salmon harvest and peakPinkCPUE; (2) coho salmon harvest and peakPinkCPUE; (3) coho salmon jack marine survival and stream temperature in Auke Creek_{Sept-Apr}; and (4) pink salmon marine survival and juvenile coho salmon energy density. No survival response except coho salmon jacks was linked with local stream temperatures. The unusual connection between adult pink salmon survival and juvenile coho salmon energy density could be explained by a common trophic linkage driven by temperature.

Table 2. Forecast models constructed for each of the salmon production response variables, using a forward-backwards stepwise regression and considering all coastal ocean metrics associated with juvenile salmon seaward migration to the Gulf of Alaska, 1997-2011. The metrics shown in the models include: the Multivariate El Niño/Southern Oscillation Index (MEI, November-March), juvenile salmon peak abundance (CPUE_{peak}, average catch [Ln +1] in June or July), Mendenhall River freshwater discharge (MRD, March-May), Auke Bay sea surface temperature (AB-SST, April-May), Icy Strait monthly 1-20 m temperature index (ISTI, May-August), the Pacific Decadal Oscillation (PDO, November-March prior to ocean entry of juvenile salmon), and an Adult Predator index (API, July-August).

Species	Production response metric	Terms in best model	Probability
Pink salmon	Marine survival Auke Creek	MEI _{winter}	$p = 0.014$
Pink salmon	Harvest Northern Southeast only	PDO _{winter} + CPUE _{peak} Pink + API	$p < 0.0001$
Pink salmon	Harvest Southeast	CPUE _{peak} Pink + MRD	$p < 0.0001$
Coho salmon – Adult	Marine survival Auke Creek	%Prey/Coho body wt.	$p = 0.075$
Coho salmon – Jack	Marine survival Auke Creek	AB-SST	$p < 0.0001$
Coho salmon	Harvest Northern Southeast only	CPUE _{peak} Pink + API + ISTI	$p < 0.0001$
Coho salmon	Harvest Southeast	CPUE _{peak} Pink + API	$p = 0.001$

Finally, forecast models were constructed for each of the salmon production response variables, using a forward-backwards stepwise regression approach (General Linear Model, GLM). Of these seven different production response metric models, all models but one (Auke Creek coho survival) were significant ($p < 0.05$; Table 2). Coastal ocean metrics identified as terms in these models included PeakPinkCPUE (four models), API (three models), and MEI_{winter}, PDO_{winter}, MRD, ISTI, and AC stream temperature (one model each). Two of these metrics in the GLM models were also identified in the BEST analysis (PeakPinkCPUE and MEI) and two were identified by Spearman rank correlation coefficient resemblances (PeakPinkCPUE and AC stream temperature).

This study identified coastal ocean metrics associated with juvenile salmon as important leading ecological and performance indicators suitable for forecasting pink and coho salmon production in SEAK, and also links distant ocean basin climate signals such as the MEI_{winter} and PDO_{winter} to subsequent salmon production.

Acknowledgments—We thank Ed Neal of the U.S. Geological Survey for providing data on freshwater discharge used to characterize the Southeast region. We also thank Alex Wertheimer for support in data assimilation. Finally, we appreciate the many biologists and vessel crews who assisted with field and laboratory work over the years.

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Overwintering Ability of Juvenile Ocean-type Chinook Salmon: Effect of Water Temperature and Food Deprivation on Growth, Energetics, and Survival

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Keywords: juvenile Chinook salmon, survival, growth, winter marine temperature, food

In ectothermic animals, metabolic rates are driven by variability in the ambient temperature, and thus influence growth rates and bioenergetics. During winter, many ectothermic fishes can reduce metabolic demands considerably by initiating periods of little or no activity, but pelagic fishes continually swim to maintain position in the water column (Brodersen et al. 2011). As a result, pelagic fishes must consume resources during winter to fuel the metabolic demands associated with sustained activity. Metabolic demands typically increase with temperature and thus, warm winter water temperature, particularly those projected under the current global ocean warming regime, could negatively affect cool water fishes if food resources are not available or abundant enough to meet the increased physiological demands.

The North Pacific region has experienced long-term sea surface warming over the last several decades (Sherman et al. 2009). Long-term ocean warming has been associated with altered timing and magnitude of phytoplankton production in the Strait of Georgia (SOG), thus driving variability in the prey field encountered by migrating Pacific salmon during early marine life (Mackas et al. 2007). Large-scale changes in climate have been implicated in the variable early marine survival exhibited by Pacific salmon populations (Holt 2010) and in the recent declines of southern British Columbia Chinook salmon (*Oncorhynchus tshawytscha*) returns (Tompkins et al. 2011), but the mechanisms remain unclear. Our objectives were to experimentally evaluate how juvenile ocean-type Chinook salmon responded to climate and food variability during early marine life. By controlling water temperature and food for six weeks during the winter 2013, we simulated match/mismatch dynamics in prey abundance associated with regional winter thermal regimes and assessed overwinter survival, growth, and behavior.

Juvenile sub-yearling Chinook salmon were obtained from a local hatchery and transported in an aerated live well by a University of Victoria (UVic) aquatic transport vehicle to the UVic Aquatic Research Facility. At the beginning of the experimental period, eleven fish were transferred into one of sixteen experimental 240-L aquaria. The experimental aquaria were assigned to treatments with one of two temperatures (6.5°C and 10.5° ±0.5°C) simulating the 1940-1970 winter average (hereafter termed cool) sea surface temperature (SST) recorded from the SOG, and a 50-year projected average winter (hereafter termed warm) SST, respectively. Fish were also subjected to three feeding regimes (fed once daily to satiation continuously throughout the entire study period, food deprived for two weeks from the beginning of the experimental period, and food deprived for four weeks from the beginning of the experimental period) to create the factorial design (temperature x feeding regime) with single replicates per treatment combination. The six-week experimental period was divided into three phases consisting of two weeks per phase. During phase one, both of the experimental treatments were food deprived. During phase two, feeding was restored to the two-week food deprived treatment while food deprivation continued in the four-week food deprived treatment. During phase three, feeding was restored to the four-week food deprived treatment. The control groups were fed to satiation once daily during all three phases.

All treatment tanks were monitored at least three times per day (morning, afternoon, and evening). During each monitoring event, water quality and quantity, and treatment parameters were maintained and all tanks were checked for mortalities. Survival was examined graphically for each treatment level using cumulative survival curves. Growth was estimated from randomly sampling six fish for length (TL) and weight (g) from each tank at the beginning of each two-week study phase. Respiration rate (number of buccal cycles per minute) was recorded three times per week from direct observation of one focal fish per tank. Activity was measured three times per week as the proportion of fish in each tank that crossed the vertical and/or horizontal midlines over a one-minute direct observation period. Aggression was measured three times per week as the number of nips, charges, and chases in each tank over a one minute direct observation period.

Preliminary results showed that survival of the juvenile Chinook salmon was high throughout the study period (> 85%). Overall survival was similar between warm (89%) and cool (85%) temperature treatments irrespective of feeding regime. The warm temperature/continuously fed and cool temperature/two-week food deprived treatments experienced 100% survival (Fig. 1) throughout the experimental period. Fish in the cool water temperature/continuously fed treatment suffered the highest mortality (40%) by the end of phase three. The majority of the fish in this treatment died during the initial three weeks of the study and no mortality was observed during phase three (Fig. 1). Survival of fish in the warm water treatments declined the greatest in those deprived of food for two weeks.

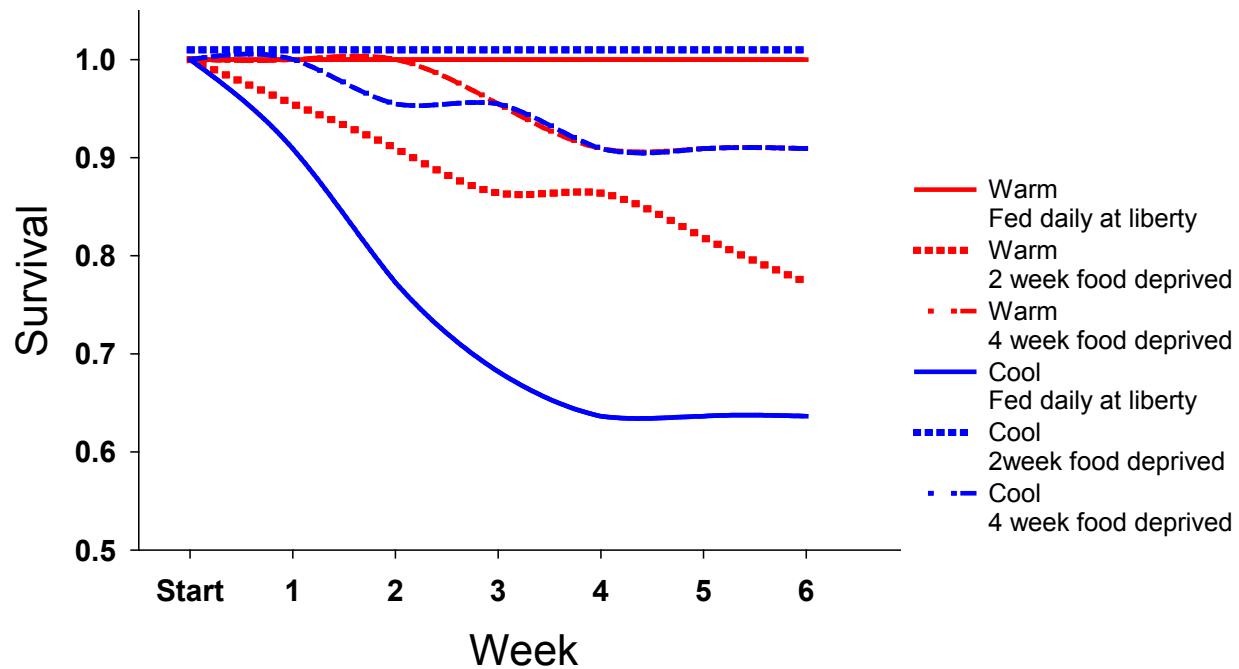


Fig. 1. Cumulative survival curves for juvenile ocean-type Chinook salmon over the six-week experimental period.

The weight of juvenile Chinook salmon was similar among all but one of the treatment combinations during phases one and two. Fish in the warm/four-week food deprived treatment (mean weight = 88 g) were smaller than fish in all other treatments (Fig. 2). The fish in the warm water/four-week food deprived treatment combination lost approximately 1% body weight per day during the two-week period of phase two. Food deprivation did not lead to significant weight loss in any of the cool water food deprived treatments. Compensatory growth was evident only in the cool water/two-week food deprived treatment as fish growth was greatest in this treatment between phase one and phase two of the experiment (Fig. 2).

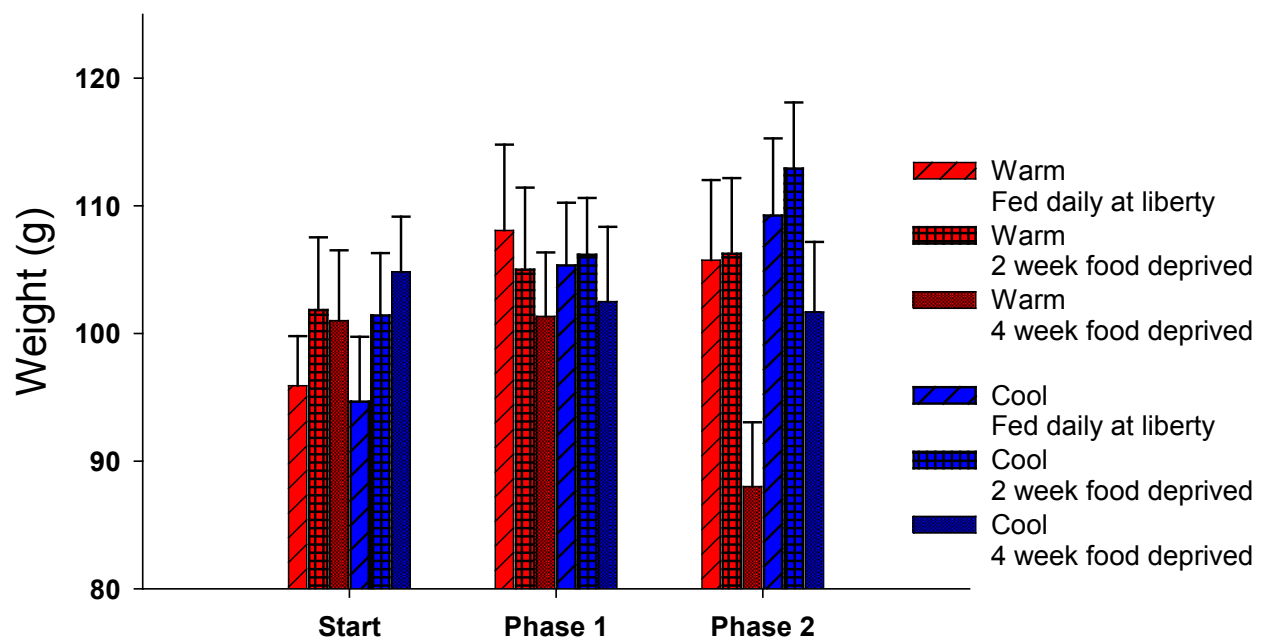


Fig. 2. Weight (g) of juvenile ocean-type Chinook salmon during bi-weekly sampling periods. Phases represent the two- and four-week food deprivation periods (phases one and two) and the re-feeding period for the two-week food deprived treatment (phase two).

The respiration rate of juvenile Chinook was consistently higher in the warm water treatments than in the cool water tanks (Fig. 3). Overall, the respiration rate of fish in the warm treatments (mean = 74 respirations/min) was 30% greater than fish in the cool treatments (mean = 53 respirations/min) combined across all combinations. Within the warm temperature treatment, the respiration rate of continuously-fed juvenile Chinook was higher than both food deprivation treatments during phases one and two, but by the end of phase three, fish in the three feeding regimes exhibited similar respiratory activity (Fig. 3). The respiration rate of juvenile Chinook salmon in both of the warm temperature food deprived treatments declined over the initial two weeks of the study, but increased in two-week food deprived fish during the subsequent re-feeding in phase two. Respiratory activity remained low in the four-week food deprived treatment during phase two, increased immediately upon re-feeding at the beginning of phase 3, and reached equivalent levels of the other warm temperature treatments by the end of the study period (Fig. 3). The respiration rate of juvenile Chinook salmon in the cool temperature feeding regimes varied less than in the warm temperature treatments over the study period, but similar trends in respiratory activity were observed among fish in the three cool water feeding regimes as in the warm temperature treatments (Fig. 3).

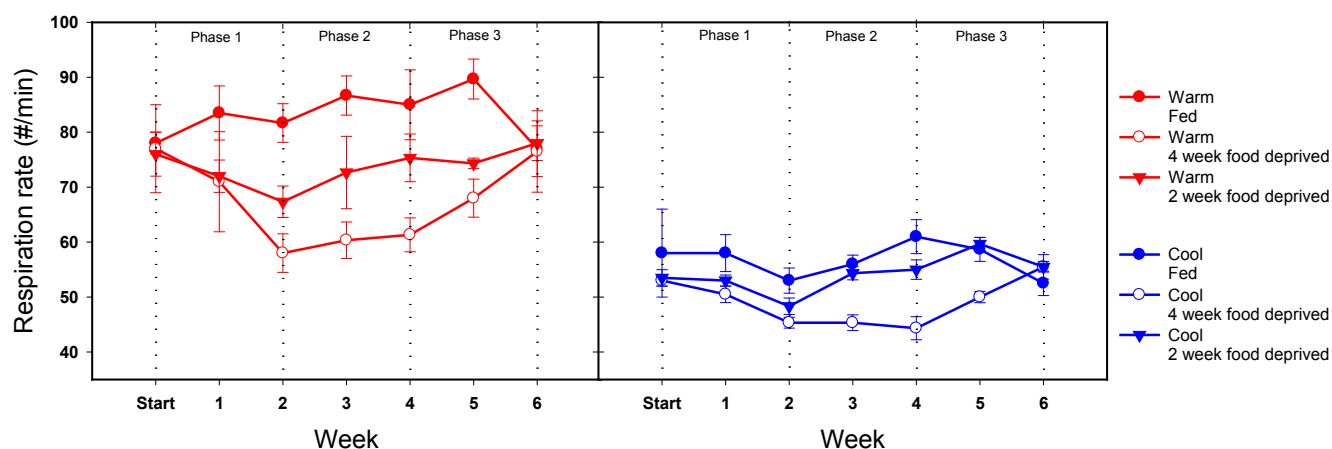


Fig. 3. Respiration rate of juvenile ocean-type Chinook salmon measured as the number of buccal cycles in one minute of one focal fish per aquarium. Phases represent the two-week food deprivation periods (phases one and two) and the re-feeding periods (phases two and three).

Juvenile Chinook salmon were most active in the warm water treatments across all feeding regimes. Within the warm temperature treatment, 50-75% of warm/continuously fed fish were active throughout the study period. However, activity declined in both warm temperature/food deprived treatments during the food deprivation phases and remained at or below 50% during the re-feeding phases. An opposite trend was exhibited by juvenile Chinook in cool water treatments whereby fish in all cool temperature feeding regimes were sedentary (< 25% active) during phase one, while activity increased in two-week food deprived fish (25-50% active) during phase two and in four-week food deprived fish (25-50%) during phase three. Aggression was also higher in fish residing in all warm temperature treatments except for the warm/continuously fed treatment where aggressive behaviors were consistently below one behavior/min throughout the study period. Aggressive behaviors increased within two days after food was withheld from fish in warm/food deprived treatments, declined after feeding was resumed in two-week food deprived fish and just prior to re-feeding in the four-week food deprived treatment. No aggressive behaviors were observed in juvenile Chinook in the cool/continuously fed treatment, and aggression in the cool/food deprived treatments was consistently less than 30% of aggressive behaviors observed in the warm temperature counterparts.

The water temperatures and feeding regimes simulated in this study were likely neither extreme nor extensive enough to reveal a treatment effect on the survival of juvenile ocean-type Chinook salmon. Overall, survival was similar between temperature treatments and among feeding regimes. The mortality observed in the cool temperature/continuously fed treatment is difficult to explain, but may have been the result of the location of the aquaria. All of the fish that died in this treatment had external symptoms of disease. These replicate aquaria were located nearest to the entryway of the building and routine ingress and egress by animal care staff could have induced increased stress on the fish in these treatments. It is still noteworthy that the simulated warm winter water temperature used in the present investigation did not have a direct positive or negative effect on the survival of juvenile Chinook deprived of food for up to one month. Future efforts should take advantage of a longer time scale than conducted here to evaluate whether an increase in water temperatures during an entire winter in the range predicted due to climate change may have consequences for juvenile Chinook early marine survival.

Our results show that temperature is only of minor importance to growth when food availability is not taken into account. The effect of food deprivation for one month on juvenile Chinook was a significant reduction in weight of fish inhabiting only the warm water aquaria. Thus, winter SSTs approaching those simulated in the warm temperature treatments of this study could have a negative impact on the growth of juvenile ocean-type Chinook salmon during prolonged periods of poor resource availability. Further, warmer water temperature did not confer a growth advantage to juvenile Chinook in a simulated environment of abundant food, as the weight of continuously fed fish was similar between the warm and cool temperature treatments. Compensatory growth following the recommencement of feeding was evident only in the cool/two-week food deprived fish. So, even when food becomes available, the capacity for compensatory growth may be limited during winters with the elevated water temperatures predicted over the next several decades. Phase three results of this study have not yet been summarized so we cannot draw conclusions concerning the capacity for compensatory growth in the fish deprived of food for one month.

Metabolic activity was clearly higher and considerably more variable in juvenile Chinook salmon inhabiting the warm water treatments across feeding regimes. The respiration rate of fish deprived of food for four weeks held at 10.5°C was greater than continually fed fish in 6.5°C water. Consequently, even the complete removal of food could not reduce the basic metabolic rate of juvenile Chinook salmon in warm water to that of fish fed daily to satiation in cool water. This finding coupled with the dramatic reduction in weight of phase-two fish in the warm/four-week food deprived treatment suggest that temperature plays a critical role in mediating the bioenergetics of juvenile Chinook salmon during times when food is scarce. In addition, the behavior of juvenile Chinook salmon was altered by water temperature such that fish were more active and aggressive in the warm water treatments than in cool water, and the possibility of temperature-induced abnormal behavior influencing anti-predator and foraging ability warrants further investigation. Together, these results indicate that the potential risks from increased winter ocean temperature may be greater than the potential benefits.

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Wrap-Up Presentation Given at the Conclusion of the Workshop

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Keywords: juvenile salmon, juvenile steelhead, migration, distribution, abundance, production, growth, marine survival, critical period, ecological interaction

I think it is only fitting to start this wrap-up session by first expressing gratitude and thanks to each of the presenters, both oral and poster, for the wide range of excellent presentations focused on migrations and survival mechanisms of juvenile salmon and steelhead in ocean ecosystems. Such presentations are not easy, and what sometimes seems a thankless task involving long hours, weeks, months, even years of research, analysis, and focused effort is needed to make such good presentations. I think it is appropriate that we extend our sincere thanks to all those who have worked so long and hard to make this workshop a success.

This is the third NPAFC workshop on juvenile salmon, and the first to include a focus on steelhead. The first workshop held in Tokyo in 2000 was followed by an in-depth research review of the early marine period of Pacific salmon by Canada, Japan, Russia, and the United States, which was published in 2003 as NPAFC Bulletin 3. The second workshop on juvenile salmon was held in 2006 in Sapporo. And, given the amount of research completed since then, the timing of this workshop is very appropriate as evidenced by the breadth of significant new information we have heard over the past two days. While it is impossible for me to cover all the new findings and insights presented at this workshop, not to mention new insights into some older concepts, I will try to summarize some salient issues covered by keynote presentations from Asia and North America, and touch on a few key ideas covered under the six workshop topics.

My head is still spinning over the extent of information Vladimir Radchenko presented about new Asian research on juvenile salmon. Among other things, he reviewed Russian trawl surveys that described concentrations and migration patterns of juveniles for many stock groups of Asian salmon in the Okhotsk and Bering seas. Those surveys were especially effective for Asian pink salmon stocks by providing a strong basis for making annual forecasts of adult returns to Kamchatka and Sakhalin rivers. Russian surveys in winter and early spring have expanded our knowledge of juvenile and immature salmon biology during these periods, and additional surveys in late spring and summer have provided data for differentiation of stock groups and forecasting updates. Increased abundance of pink salmon from eastern Kamchatka has not changed the role of salmon in the trophic structure of epipelagic nekton communities in the western Bering Sea. Some changes in prey were noted in years of high salmon abundance, but this did not influence growth and survival of juvenile salmon. The food supply for juvenile salmon and micronekton in waters of far-eastern seas and the northwestern Pacific is much higher than the total food consumed by all epipelagic nekton. Food resources consumed by juvenile salmon represent a minor part (1-2%) of the total macro-zooplankton biomass.

I sense that our Russian colleagues, based on their research in the western Pacific involving extensive year-round ocean surveys documenting high standing crops of macro-zooplankton and other micronekton foods of salmon, pretty much hold in abeyance any current concerns about carrying capacity of salmon in these waters. This doesn't mean, however, it can't change in the future.

Marc Trudel's survey of North American research since the 2006 workshop indicated that Chinook and coho salmon have received the most attention. This also turns out to be true for many North American presentations and posters at this workshop, a reflection of increasing concern over population and stock declines of these species over broad geographic regions, including Alaska. Marc reported progress in understanding stock-specific migration behavior of juveniles, and showed how DNA analyses, tags, and biophysical attributes provide tools for studying ocean distribution and behavior. In British Columbia, the role of sea lice parasites transferred from salmon farms to wild fish has received much attention as potential mortality agents on juvenile salmon. Unlike the western Pacific, few studies have been conducted in the eastern Pacific during winter periods. This leaves a huge gap in our understanding of North American salmon ecology during this critical life history period.

An important and continuing theme under the topic of distribution was the application of multiple technologies identifying stock-specific migratory patterns in juvenile salmon. Two Japanese papers using otolith marks and single nucleotide polymorphism markers documented dispersal and migration patterns of specific stocks of chum salmon on the Pacific coast of Hokkaido. North American scientists using variations of 14 DNA microsatellites followed individual Fraser River and central British Columbia (BC) sockeye salmon stocks migrating out of BC and tracked them northwestward throughout much of Gulf of Alaska. Russian scientists identified mixed-stock aggregations of 24 Okhotsk Sea even-year pink

salmon stocks using restriction fragment length polymorphism analysis and found by September most juveniles originating from the southern part of the basin had migrated into the northern Okhotsk Sea. Otolith microstructure was used in another Russian study to identify mixed stock groups of Okhotsk Sea pink and chum salmon.

Migration behavior was another important theme. In the northern Bering Sea, juvenile Chinook salmon from western Alaska rivers migrated in opposite directions along the coast during a series of warm and cold years, affecting survival. Late migration timing and ocean entry were shown to have significant beneficial effects on populations of Fraser River Chinook and sockeye salmon. And a study on persistent age-specific homing and return timing of Columbia River Chinook salmon provided a basis for inferring different ocean distribution patterns in age groups of fish.

A presentation related to homing behavior was the first empirical evidence of geomagnetic imprinting in any animal determined from analyzing divergences in geomagnetic field drift at the mouth of Fraser River. Geomagnetic imprinting could account for the two different entry routes of returning sockeye salmon migrating around Vancouver Island.

Presentations on the physical and biotic environments of salmon habitats covered a range of eastern Pacific regions. In the Strait of Georgia, survival of hatchery coho salmon has decreased from 8-10% to 1% over a 30-year period, leading to new research focused on staggered smolt release dates along with plankton monitoring to assess food quality and availability. The study also has a fish health component to test if a marine bacterium is affecting survival. Increased primary and secondary production indicated favorable conditions for juvenile salmon.

In the northern California Current, a study on spatial associations from shipboard acoustic surveys of distribution and abundance of krill, satellite-derived indices of Chlorophyll-*a*, and occurrences of juvenile Chinook salmon showed persistent high krill and salmon abundance associated with Chlorophyll-*a* hot spots.

A study conducted along the Gulf of Alaska coast demonstrated juvenile salmon migrating through the perimeter of the Sitka Eddy have increased foraging opportunities and elevated growth rates that could mitigate for increased competition in years with high salmon abundance.

The session on trophic linkage, growth rates, and predation rates produced new information. A California Current study demonstrated a strong positive relationship between growth and survival in coho salmon during the first summer at sea with little mortality occurring during the following winter period. Researchers conducting a study along coastal British Columbia reported stock-specific predation on juvenile salmon by rhinoceros auklets at different nesting colonies, indicating there are important spatial-temporal salmon migration patterns. Concurrent coast-wide trawl surveys for juvenile salmon supplied evidence for size-selective predation, as the salmon consumed at each auklet colony were smaller than salmon caught in the surveys.

To better understand coast-wide declines in Chinook salmon, a continental-scale analysis of juvenile salmon feeding ecology from northern California to the eastern Bering and Chukchi seas found large gradients in carbon isotopic data corresponding to regional variations in zooplankton and forage fish in diets, especially in smaller Chinook salmon up to 200 mm in body length.

A presentation described results by utilizing a food supply index to examine relationships among biomass of nekton species, zooplankton, and juvenile salmon in the western Bering and Okhotsk seas. Diets changed somewhat during years of high salmon abundance, but there were no strong negative consequences for juvenile salmon in those years.

Several presentations related ecological interactions among pink salmon and other species. A Southeast Alaska study examined interactions between pink and chum salmon and suggested high brood-line returns of adult pink salmon influenced feeding and growth of juvenile chum salmon. To investigate the possibility that cannibalism by returning adult pink salmon contributes to brood-line oscillations in pink salmon abundance, a study in Southeast Alaska and Prince William Sound examined adult pink salmon predation on juvenile pink salmon and herring. Results indicated that over the 16-year data set, cannibalism rarely occurred, i.e., in less than 1.1% of more than 2000 adult pink salmon stomachs analyzed. I note, however, that Vladimir Radchenko showed an interesting photo of an adult pink with a large number of juvenile pink salmon in its stomach. A study conducted in Puget Sound found likely competition between juvenile salmon and Pacific herring due to similarities in their diets and to greater population biomass of herring.

The topic session with the most number of presentations was related to juvenile salmon survival rates and survival mechanisms. Researchers conducting a Strait of Georgia study reported that years of poor ocean productivity and biological stressors, such as harmful algal blooms and pathogens, may weaken the immune systems of juvenile salmon, which is associated with higher levels of mortality.

An analysis of high-seas food habits revealed salmon and steelhead consume a variety of types and forms of plastic debris. The study explored potential mechanisms of marine mortality due to ingestion of plastic debris and emphasized the need for field and laboratory process studies on this issue.

Two separate modeling studies considered the influence of large-scale climatic patterns such as the Pacific Decadal Oscillation and North Pacific Gyre Oscillation on survival rates of Pacific Northwest coho salmon. Both studies found large-

scale events have strong influence on physical and biological components of ecosystems, but effects were more uncertain at local and regional levels. For example, in one case spatial comparisons of large scale events and ocean sea surface temperatures were better predictors for survival of coastal populations than temperatures inside Puget Sound.

Two other studies took a salmon life-history perspective. The life-history of Southeast Alaskan juvenile coho salmon “nomads” was highlighted as providing substantial life history diversification for efficient use of discontinuous freshwater habitats and a population buffer against survival shocks. The nomad coho salmon life history is one where pre-smolts rear in estuaries and return to natal or non-natal streams to overwinter before smolting in the spring and migrating to the ocean. Another presentation examined critical periods in the marine life history of Pacific salmon and argued for the need to consider all phases of the life history rather than focusing on the assumption that one “critical” period is of overriding importance.

In a study examining fish scales of out-migrating smolts and returning adult Bristol Bay sockeye salmon, authors concluded size-selected mortality was dependent on ocean conditions and biological characteristics of the smolts, and that productivity of these stocks was largely dependent on the degree of size-selective ocean mortality.

In a Gulf of Alaska study, mesoscale eddies were shown to be drivers of stable carbon isotopes in oceanic copepods and it appears these eddies can account for some of the interannual variability of Prince William Sound pink salmon survival.

Another presentation suggested that increased competition at sea, in part related to continued release of large numbers of hatchery salmon (here read pink and chum), may have played a significant role in reduced BC sockeye salmon survival since 1991.

There were several presentations related to salmon survival and salmonid ecology during the first winter at sea. Russian studies on the food supply of pink salmon during winter and spring of 2009-2011 in the upper epipelagic layer of the western Subarctic frontal zone estimated the total biomass of nekton along with the consumption of various zooplankton groups by pink salmon and other organisms. Estimates showed that consumption of zooplankton by pink salmon and all nekton was a minor fraction of the available food in the upper epipelagic zone. Feeding by pink salmon during winter and spring was not low, as was previously reported.

In summary, from my perspective these were some of the highlights of the workshop:

- Major new and continuing improvements in discerning stock-specific migration routes of juvenile salmon based on genetic stock identification techniques, otolith microstructure, otolith marking, and other stock identification technologies.
- Growing evidence regarding the importance of early marine growth in juvenile salmon and the significance of size-selective mortality in marine life stages as a key determinate of overall survival and a cornerstone of the critical size hypothesis. We even learned that rhinoceros auklets can be added to the list of juvenile salmon predators, and the birds seem to target the smaller fish. Looking at this from the salmon’s point of view, I guess we might summarize this whole concept as “getting bigger quicker is better”.
- Possible mismatch of juvenile salmon migration timing and production of suitable marine prey resources from changes in freshwater and marine environments due to global warming and differential climatic effects.
- New insights into salmon homing migratory behavior based on empirical evidence of geomagnetic imprinting.
- Potential deleterious impacts of marine debris on salmon ecology and survival.

In conclusion, I would like to add a comment regarding a future research direction involving Pacific salmon. Because we are in a period of fairly rapid climatic changes, it is important for us to collectively do whatever we can to maintain important long-term data sets, marine surveys, and long-standing observations that give us critical tools to help us better understand what is going on. I know this is tough in times of budget shortfalls and sequesters, but we must persevere and strive to keep the need for these valuable long-term data sets front and center in the minds of administrators and others.

I thank you for your attention and apologize for the many subjects and issues from both oral and poster presentations I was unable to touch on during this wrap-up.

Migration and Survival Mechanisms of Juvenile Salmon and Steelhead in Ocean Ecosystems: The Workshop Synopsis

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The North Pacific Anadromous Fish Commission (NPAFC) hosted the 3rd International Workshop on juvenile salmon in Honolulu, Hawaii, on 25-26 April 2013. The purpose of this workshop was to share, review, and summarize new research results pertaining to the “Migration and Survival Mechanisms of Juvenile Salmon and Steelhead in Ocean Ecosystems.” The Workshop included two full days of oral and poster presentations and was attended by over 95 participants from Canada, China, Japan, Korea, Russia, and the United States.

Since the 2nd International Workshop on juvenile salmon convened in 2006, numerous ocean surveys and subsequent studies have occurred along the North Pacific Rim of Asia and North America. Much of this research focused on the initial period of salmon migration and subsequent overwinter period because of the prevailing paradigm that early ocean periods are highly influential to the survival and production of salmon. Consequently, to gain a better understanding of mechanisms or processes influencing the production of anadromous populations, additional information was needed on inter-annual variations in abundance, growth, and survival rates of juvenile salmon migrating in ocean ecosystems over both regional and basin scales. To accomplish this end, the NPAFC organized the 3rd International Workshop in 2013.

To condense results from the workshop, this synopsis is presented in several sections: (1) the two North Pacific Rim salmon reviews, (2) five themes summarizing most workshop presentations, (3) a Workshop “Wrap Up” overview, and (4) some implications of juvenile salmon marine research for salmon management.

The references cited in this synopsis refer to abstracts compiled in this volume (NPAFC Technical Report 9).

Review of studies from Asia and North America, 2006-2013

Radchenko et al. and Trudel and Hertz summarized advances in marine research on juvenile Pacific salmon made since the previous NPAFC Workshop. Both contributions provided excellent summaries of the extensive research by NPAFC member countries in Asia and North America.

Radchenko et al. reported on studies conducted on the Asian coast (Korea, Japan, and Russia) showing the effects of climate and oceanography on the feeding and migration of juvenile salmon. A high degree of annual variability in salmon diet occurred in ocean regions such as the Bering Sea. It was also reported that in comparison with other nekton, estimates of large zooplankton consumption by Pacific salmon is modest, even in years of high salmon abundance. As for top-down control mechanisms, an example study of con-specific pink salmon predation was noted for controlling brood-line dominance, but concluded it was unlikely because intraspecific interaction is minimal due to the narrow window of spatial overlap between juveniles and adults, and the rapid growth of juveniles quickly puts them beyond the optimum prey size of adults. Low ocean sea surface temperatures were cited as delaying migration and reducing growth and thus contributing to high mortality, which was validated by studies on early marine chum salmon scale growth.

Trudel and Hertz reviewed extensive research conducted by investigators working along the North American coast (Canada and the United States). They reported that the actual causes of juvenile salmon ocean mortality are still poorly known. Furthermore, evidence remains inconsistent regarding effects of hatchery releases on wild salmon production in the marine environment, regardless of the similarity in their diets. Inter-specific interactions of highly abundant pink salmon with other salmon may be context dependent: juvenile pink salmon may be competitors in one region (Strait of Georgia) and a buffer to predation in another (Southeast Alaska). Much work on pathogens off British Columbia have linked sea lice transfers from adult wild salmon to farmed pen-reared salmon and back to wild juvenile salmon with negative consequences. Impacts of predators on juvenile salmon may be modulated by the availability of alternate prey, such as forage fish, but predation events on juvenile salmon are seldom reported. Changes in salmon prey availability and quality have been linked to changes in ocean currents, winds, and climate.

Theme 1. Critical periods or size of juvenile salmon related to production

Many studies support the hypotheses that increased survival for juvenile salmonids in ocean ecosystems is predicated on two critical ocean mortality periods: early marine (high growth minimizing vulnerability to size-selective predation) and winter (high overwinter energy and size needed for survival/growth and predation avoidance). In a study on the Sea of Japan side of Hokkaido, the early marine critical period was validated by sampling otolith-marked chum salmon and comparing the catch per effort in surface trawls to subsequent adult returns (Sasaki et al.). Off the coast of British Columbia in summer, size-selective and stock-specific predation of juvenile salmon by rhinoceros auklets (*Cerorhinca monocerata*) was documented by Tucker et al., thus validating the concept of a critical early marine period of mortality and the importance of the link between fish condition and susceptibility to predation. In the northern California Current, high krill and chlorophyll-*a* abundance was related to the spatial distribution of Chinook salmon, which may aid ecosystem-based assessments by identifying critical marine habitat for juveniles during their early marine residence (Hassrick et al.).

Presentations on modeling and hatchery releases reinforced the importance of growth and size for positively influencing survival. Results from a 4-parameter model relating ocean survival of juvenile salmon to their size, based on susceptibility to predation, supported a critical-size hypothesis (Passolt and Anderson). Rutter and Anderson presented information on a model estimating the growth rate of salmonids by accounting for the effects of size-dependant culling in the frequency distribution of populations. From experimental release times and sizes of age-0 sockeye salmon smolts in Auke Bay, Alaska, Heard et al. demonstrated that release of larger fish produced shorter residence times and higher subsequent marine survivals than release of smaller fish, thus supporting the critical early marine period hypothesis and size-dependant offshore migration. Abundance of juvenile and immature Chinook salmon caught in rope trawls in Southeast Alaska were significantly correlated with brood year survival of wild and hatchery stocks when linked to ocean entry year, thus suggesting critical marine periods both in spring and during the over-wintering period (Orsi et al. Chinook salmon abstract). Farley et al. presented information on Bristol Bay sockeye salmon energetic condition related to marine survival in 2002-2008 and demonstrated size-selective mortality of fish between fall and their first winter at sea was due to inadequate lipid stores to avoid predation. Leon and McPhee did not find a significant relationship between freshwater growth and recruitment of two western Alaskan Chinook salmon populations, but they did report growth in a given year was correlated to growth in the previous year. Ruggerone et al. examined a long-term data set to determine the role of size-selective mortality on sockeye salmon smolts based on scales from adults originating from five watersheds in Bristol Bay. Stormer and Juanes proposed a study on ocean-type Chinook salmon in the laboratory to measure growth and lipids after periods of fasting for subsequent modeling of the conditions during their early marine critical period.

Theme 2. Inter-annual variation in abundance, growth, and survival of salmon

Several studies highlighted the importance of maintaining long-term time series of ocean metrics to enable researchers to detect interannual factors influencing salmon production. By sampling nearshore conditions in the Strait of Georgia, Downey et al. found high annual differences in the timing, abundance, and composition of plankton prey for outmigrating juvenile salmon. They suggested the policy of a standard time of release for hatchery-reared juvenile coho salmon may contribute to low marine survival because juvenile releases may not coincide with the timing of abundant prey. From a 35-yr data set of hatchery releases of Chinook salmon from Little Port Walter, Southeast Alaska, Guyon et al. found a decreasing trend in survival and age at maturity possibly linked to environmental variation. Models that explained marine survival of 14 coho salmon stocks in Southeast Alaska varied by locality, but only the North Pacific Index had a consistent (positive) effect (Adkison et al.). Coastal ocean metrics associated with juvenile salmon were identified as important leading indicators of pink and coho salmon production in Southeast Alaska (Orsi et al. Connecting the “Dots” abstract). Sampling off the coast of British Columbia, Friedland et al. found that initial marine growth of Keogh River steelhead was not as important as sustained growth conditions in the summer and fall of the post-smolt year.

Annual variation in survival of salmon may also be related to hatchery practices. Liu et al. described adverse impacts of low salinity on liver cells of juvenile chum, and Urawa indicated a parasitic flagellate (*Ichthyobodo salmonis*) may cause marine mortality in juvenile chum salmon and described a treatment study using corn vinegar to control the parasite in hatcheries.

Theme 3. Ecological interactions of juvenile salmon in the context of marine survival

Examining the marine ecology of juvenile salmon migrating in the ocean provided insight to possible mechanisms influencing salmon distribution and production due to interactions with prey, competitors, or predators. Primary prey organisms and migration pathways were identified for juvenile chum salmon during their early ocean critical period in coastal waters off northern Japan (T. Sato et al.) and Korea (Kim et al.). In the northern and southern Bering Sea, Gann et al. noted differences in the abundance and taxonomic composition of zooplankton that may have implications for the distribution

of juvenile salmon and other forage fishes. Of four major prey types consumed by juvenile Chinook, coho, chum salmon, and steelhead in the California Current, Brodeur et al. found euphausiids and fish were positively selected relative to their abundance in the neuston, and the opposite was true for decapods and amphipods.

There were many presentations discussing the role of competition as a potential influence on juvenile salmon marine survival. In examining feeding rates and growth of juvenile Pacific salmon in the North Pacific, Zavolokin concluded that salmon abundance in the past 30 years had increased, but adaptive changes in feeding habitats compensated for competition and there were no negative consequences of increased salmon abundance on juvenile salmon in the Okhotsk Sea and western Bering Sea. By examining the diets of five species of Pacific salmon in the Bering Sea in fall, Auburn and Sturdevant found that feeding behavior was related to diel period and sampling localities, thus giving insight to migration strategies for juveniles confronted with a short growing season. Jenkins et al. examined diet overlap of juvenile pink and chum salmon in warm and cold years off British Columbia and Southeast Alaska and concluded that niche overlap increased with high salmon abundance and was not related to fish size. Naydenko and Kuznetsova reported on food supply of pink salmon and other fish and squid in the subarctic frontal zone of the North Pacific Ocean in winter and spring of 2009-2011. She concluded that a decrease in stomach fullness of salmon in winter was not evidence of unfavorable winter feeding conditions, but it was related to the fish's physiological cycle in the winter due to cooler environmental conditions. Regional shifts in annual Chinook feeding ecology were found by Hertz et al. and may be related to declining stocks in North America because years with higher growth and survival indicated fish were feeding at a higher trophic level.

Several researchers reported on competitive interactions between juvenile pink salmon and Pacific herring. Morozova indicated juvenile Pacific salmon interactions occur in the coastal epipelagic zone of Kamchatka. She noted that spatial variability was found among the salmon species, and Pacific herring migrated into salmon habitat in late August and overlapped juvenile salmon diet, which may have displaced them seaward. Spatial overlap was found between Pacific herring and juvenile Chinook and coho salmon in Puget Sound, Washington, by Kemp et al. They suggested the greater biomass of herring impacted zooplankton more than juvenile salmon, but competition for prey could negatively influence growth and survival of juvenile Chinook salmon during their early critical marine period. In Prince William Sound, zooplankton predation by pink salmon was shown to likely influence herring production (Studevant et al.).

Scales collected from adult salmon were used to estimate growth of juvenile stages. Martinson used the early marine growth on scales of adult chum from Southeast Alaska to show that adult pink salmon did not influence chum growth and that early marine growth was a positive predictor of chum salmon production three years later.

Several authors reviewed the role of predation on juvenile salmon marine survival. From data sets of adult pink salmon diets off Southeast and Prince William Sound, Alaska, Sturdevant et al. reported that pink salmon cannibalism by adult fish on juveniles was not a large contributor to alternate brood-year oscillations in pink salmon. Tucker et al. identified the stock-specific consumption of juvenile sockeye, pink, and chum salmon migrating past colonies of chick-provisioning rhinoceros auklets in areas of coastal British Columbia. In samples collected from the coastal zone near the Anadyr River, Baranov identified predation on juvenile chum salmon by char and toothed smelt. Koval and Gorin suggested the strong hydrographic features and tidal influences in western Kamchatka estuaries negatively affected seaward migrating juvenile salmon and they identified negative ecological interactions of marine mammal predators on adult salmon in summer.

Theme 4. Climate or ecosystem change at several scales related to salmon production

The influences of local, regional, and basin scale factors in marine ecosystems on salmon production were identified in many studies. At the local scale, juvenile pink, chum, and sockeye salmon exhibited higher levels of growth, as measured by insulin-like growth factor in the blood, and plankton density was similarly high along the perimeter of the Sitka Eddy in the Gulf of Alaska (Moss et al.). Kline found mesoscale eddies forming in May in the Alaska Coastal Current were influenced by the hydrological cycle and that climate was a critical factor for driving ocean survival for pink salmon because it "set the stage" for the arrival of salmon migrating into the area. Beamish et al. indicated that recently improved productivity of selected stocks of sockeye salmon from the Fraser River appear related to later ocean entry time of sea-type stocks matching long-term changes in the timing of prey populations. Short-term exposure to increased temperatures during early development (from fertilization to swim up) was found to influence the sexual development of steelhead (Cole et al.).

At the regional scale, influences of climate or ecosystem change on salmon production were presented from studies in the Northeast Pacific. J. Miller et al. suggested both local and regional processes positively affect survival of Snake River Chinook salmon. Such conditions include a negative Pacific Decadal Oscillation (PDO), a large size of fish at marine entry, a copepod community dominated by northern boreal species, and increased river discharge (Columbia River plume). Using survival data from hatchery and wild coho salmon releases from coastal and inshore marine waters of Washington State, Zimmerman et al. found that the marine survival of stocks in distinct geographic regions responded differently to ocean conditions. For example, ocean indicators like the PDO and surface temperatures were better predictors of marine survival for coastal populations than for interior stocks in Puget Sound. Fergusson et al. examined trophic relationships among pink,

chum, sockeye, and coho salmon with climate over a 16-yr time series in Southeast Alaska and reported that during relatively warm years fish were larger, diets were more diverse, but energetic conditions of the fish were similar to those in cold years. From 2010 to 2012 off the coast of Southeast Alaska, marine spatial variation in the abundance and condition of juvenile chum salmon was highly influenced by changes in temperatures (Kohan et al.). Juvenile Chinook salmon from the Yukon River were found to disperse northward in warm years, southward in cold years, and average catch latitude was negatively correlated with marine survival, suggesting the northern Bering Sea is not good overwintering habitat for juveniles (Murphy et al.).

At the basin scale, the influences of climate or ecosystem change on juvenile salmon metrics or adult production was identified. Mazumder et al. examined carbon isotope signatures of juvenile Chinook salmon from the west coast of North America and suggested that in most regions there is an ontogenetic shift in diet of fish after growing to a body length of 200 mm. Peterman and Dorner reported that declining trends in sockeye salmon productivity have been synchronous among stocks from Washington to Southeast Alaska, while opposite trends were seen in western Alaska, thus implicating a large-scale influence of climate on salmon productivity. Long term monitoring of ocean indicators off the northern California Current suggest linkages of basin-scale forcing (PDO) and circulation patterns, which in turn affect transport of a lipid-rich food chain (copepods) favorable to juvenile coho and Chinook salmon survival, and this can be used to develop forecast models for adult production (Peterson et al.). By using Bayesian networks, Malick et al. found large-scale climate influences on biophysical components of the ecosystem, but uncertainties increased down the causal chain in the network, thus dampening the effect of large-scale climate patterns on coho salmon survival. In samples collected in 2010 and 2011 as the El Niño Southern Oscillation (ENSO) conditions shifted from positive to negative, Fournier observed reduced size and weight of the fish in the Gulf of Alaska, which suggested poorer conditions in a negative ENSO year. Irvine and Akenhead reported that sustained releases of hatchery salmon after 1990 corresponded with the hypothesis that the North Pacific Ocean entered into a period of low productivity for salmonids and contributed to reduced survival of sockeye salmon.

The question of “What do we really know about the cumulative effect of environmental stressors on the health of salmon?” was posed by K. Miller et al. They suggested a broad range of infectious agents carried by smolts in the ocean and biological stressors may be less tolerated and associated with higher levels of mortality in years of poor ocean productivity.

Theme 5. Migration and distribution of salmon stock groups

It is important to know the spatial and temporal distribution of stock groups to adequately understand ecological interactions or to model habitat utilization patterns. Several studies based on genetics and phenotypic differences indicated the migration and distribution of salmon stock groups. Juvenile sockeye salmon from 35 stocks were identified from ocean sampling off North America and larger body-sized individuals within populations were distributed further northwards in the ocean than smaller fish (Beacham et al.). Extreme annual shifts in abundance of juvenile sockeye salmon in the Strait of Georgia in 2011 (low) and 2012 (high) were documented by Neville et al. S. Sato et al. used single nucleotide polymorphism (SNP) markers to determine migrations of Japanese chum salmon stocks to the Okhotsk Sea from mid-June to early July and reported the Great 2011 Earthquake and Tsunami in Tohoku adversely affected chum salmon releases from Honshu hatcheries along the Pacific coast. T. Saito et al. reported thermal marks were used to determine new unrecognized migration patterns for Hokkaido chum salmon migrating to sea. Guthrie et al. used genetic markers to validate the presence of juvenile Yukon Chinook salmon stocks collected off the river mouth. Yoon et al. described genetic structure of contemporary populations of Far East Asian chum salmon from microsatellite and mitochondrial DNA analysis. Genetic analysis of mixed-stock aggregations of juvenile pink salmon collected in autumn in the Okhotsk Sea showed that stocks could be separated to northern and southern regional stocks and that accuracy of the odd-year brood-line is relatively lower than the even-year line (Shpigalskaya et al.). As a potential method to assess fitness decline, a graphical method was presented to help understand correlated gene expression that provides the basis of complicated traits, and thus making it possible to estimate direct genetic effects in determining phenotype (Nakamichi et al.). Chistyakova et al. observed otolith microstructure and identified mixed stocks of pink and chum salmon in the Okhotsk Sea and regional origins of major Asian stock groups. Izergin et al. reported on pink salmon migrations from Taui Bay to the Sea of Okhotsk from May to July.

Other techniques for examining juvenile salmon migration and distribution employed modeling, observational, and telemetry. Burke et al. described simulation modeling of the initial ocean migration of juvenile stream-type Chinook salmon and suggested that directed swimming by fish aided by a sense of space and time was the most likely model scenario to describe observed movement. Watanabe et al. examined the increasing age at maturity through immature ratios of chum salmon in the Bering Sea and central North Pacific Ocean to see if poorly understood ocean mortality could be attributed to these changes. A modeling study of Fraser River sockeye salmon concluded that the fish use magnetic cues to navigate across the open ocean (Putman et al.). Bracis and Anderson found that spring-summer Chinook salmon display age-specific differences when they arrive at the river mouth as older fish arrive earlier. Chinook salmon in the southern part of their range partitioned habitat use by season and age of fish (Ammann et al.). Kilmov et al. reported that juvenile pink, chum,

and sockeye salmon migrating in the Okhotsk Sea had different foraging strategies. Pink and chum salmon widely explored marine areas, foraged intensively, and then migrated seaward, whereas sockeye salmon foraged for extensive periods within coastal waters and moved offshore later. Another study suggested that the complexity of life history, diet, and size-dependant rearing strategies of Chinook salmon in the Strait of Georgia may be related to marine survival trends (Sweeting). Brosnan et al. used acoustic telemetry data of yearling Chinook salmon in the Columbia River estuary to estimate survival as influenced by predation, ocean productivity, plume dynamics, and prior river experience.

The Workshop “Wrap Up”

Heard presented a Workshop “Wrap Up” to highlight important findings and insights with respect to migration and survival of juvenile salmonids in ocean ecosystems. He summarized the major new information on stock-specific migration gathered using multiple technologies and homing migration behavior based on empirical evidence and validated geomagnetic imprinting. He mentioned that the concept of rapid early marine growth to avoid size-selective mortality was reinforced by many studies and is a cornerstone of the critical-size hypothesis of “getting bigger quicker is better.” He pointed to new information presented on the potential deleterious impacts of marine debris on the ecology and survival of salmon that provided insights to anthropogenic effects on salmon production. Heard reviewed evidence that phenology of salmon migration mis-matched to suitable marine prey resources may be linked to climate. He emphasized the importance of maintaining long-term time series and ocean surveys during the recent periods of climate change and said these metrics are critical tools to help determine what is really happening in salmon habitats.

Implications of juvenile salmon marine research for salmon management

Marine research on juvenile salmon has expanded in many respects with advances in our knowledge of migration and survival mechanisms of salmonids in ocean ecosystems and towards improved understanding of the processes required for sustainable conservation and management. Here are some new (or reinforced) insights on juvenile salmon marine migrations, and how these insights might inform salmon management.

Survival and production estimates. The paradigm of two marine critical periods for juvenile salmon rang true as a central message of many workshop contributors: an early marine nearshore coastal period predicated on size-selective mortality, and a second period over the first marine winter related to both size and energy. This information, coupled with ocean survey data and large-scale ecosystem indicators associated with juvenile salmon, can be used to assess abundance of salmon “survivors” to develop pre-season salmon forecast models to benefit fishery managers and resource stakeholders.

Autumn estuarine migrations of salmon. New insights on salmon life history strategies and migration of several species were discussed, namely age-0 sockeye and coho salmon juveniles in fall. For these two species in the fall, sea-type sockeye reared extensively inshore (Beamish et al.) and coho fry migrated inshore along the coast and reinvaded distant freshwater habitats to overwinter (Shaul et al.). Thus, the later and protracted estuarine migrations of these species emphasize the importance of maintaining intact networks of continuous anadromous habitats. As estuaries serve as conduits to adjacent habitats and neighboring stream systems, applying this knowledge to land use practices concerning estuaries will enable managers to better sustain healthy salmon populations.

Maintaining a diversity of out-migration times. For migrating juvenile salmon, stock-specific migration information indicated that the largest fish within a cohort were located furthest north, suggesting one survival strategy of migrating fast and early. In contrast, late-fall migrating sockeye (sea-type) actually have fared better in recent years than the earlier spring-migrating fish of adjacent stocks, suggesting salmon have a wide spectrum of outmigration timing to ensure an optimal survival window is available each year for a particular stock group. This has implications for the release strategies of hatchery projects because enhancement programs often constrain release periods that may mis-match timing with estuarine productivity during some years. Thus, salmon production may prove more sustainable if a wide spectrum of salmon outmigration times of wild and hatchery stock groups are maintained.

Influences of marine debris in the open ocean. The potential bioaccumulation of chemicals from marine debris ingested by juvenile and immature salmon and steelhead was proposed by Myers et al. as a possible cause of ocean mortality. Evidence was presented that ingestion of marine debris was most prevalent in steelhead and was observed in other salmon species. Moreover, the highest incidence of plastic ingestion occurred closest to the Subarctic Current. Thus, reducing our “garbage footprint” in the ocean will contribute to healthier salmon stocks and help maintain sustainable fisheries.

Validation of salmon migration routes and “critical” periods. Welch et al. suggested that multiple periods may be critical to survival throughout the marine life history of Pacific salmon, rather than only during early marine and overwintering periods. Tucker et al. observed seabird predation on specific salmon stocks and showed the later coastal migration period was a cause of marine mortality by avian predators. K. Miller et al. suggested that there were a broad range of infectious agents carried by smolts during ocean migration and in years of poor ocean productivity these agents may be less tolerated and could be associated with higher mortality. A better understanding of the cumulative interactions of migrating salmonids in ocean ecosystems will better inform managers as to the most appropriate pre-season indicators of salmon productivity.

Future collaboration, coordination, and compilation of coastal ocean time series. Additional data sharing among national researchers is needed—both on regional and Pacific Rim scales—to better inform managers with suitable ecosystem metrics to anticipate future salmonid production. This could be accomplished by developing a standard suite of ecosystem metrics shared and applied over a large spatial scale during critical periods of the salmon life history. Thus it is important for researchers to identify key metrics and time periods for particular species that are related to salmon production (i.e., abundance, growth, size-at-time, energy density, prey fields, diet, temperature, etc.). Such information is vitally important if we are to successfully develop forecasts for salmon stocks that are at historically high levels of abundance as well as stocks that have shown large-scale declines.

List of Participants

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