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Migration Studies of Salmon in the Bering Sea

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Final Report
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Summary

This is the final report on "Migration Studies of Pacific salmon (*Oncorhynchus* spp.) in the Bering Sea," a contract research project funded by the National Oceanic and Atmospheric Administration in 2002-2006. This contract was an extension of work in support of U.S. commitments to the North Pacific Anadromous Fish Commission (NPAFC), which operates under the NOAA Authorization Act of 1992. Research on migrations of salmon in the Bering Sea has important fishery management implications for the U.S. government. In 1997-2002, reduced runs of salmon to western Alaska resulted in an economic disaster for many people whose livelihoods depend on natural salmon resources. In 1997 the federal government declared a commercial salmon fishery failure in the Kuskokwim and Bristol Bay regions of western Alaska. This was the first time that the U.S. Department of Commerce had used its legislative authority under section 312(a) of the Magnuson-Stevens Act to declare a commercial fishery failure in response to a request from a state governor. Salmon fishermen and other stakeholders continue to be concerned about whether climate-induced changes in ocean conditions or ocean fisheries or both are contributing to unexpected fluctuations in the abundance of adult salmon returns to western Alaska. In 2002, these concerns prompted the U.S. government to lead other NPAFC member nations in the development and implementation of the Bering-Aleutian Salmon International Survey (BASIS). This report summarizes the results of contract work by scientists at the School of Aquatic and Fishery Sciences (SAFS), University of Washington, which included original scientific research, synthesis and review of historical research, research coordination, sample and data exchange, and scientific meeting activities in support of U.S. commitments to BASIS.

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Migration Studies of Salmon in the Bering Sea

Table of Contents

Page No.

List of Figures

Page No.

List of Tables

Page No.

Migration Studies of Salmon in the Bering Sea

Introduction

This is the final report on “Migration Studies of Pacific salmon (*Oncorhynchus* spp.) in the Bering Sea,” a contract research project funded by the National Oceanic and Atmospheric Administration (NOAA Contract No. NA17RJ1232 AM021). This contract was an extension of work in support of U.S. commitments to the North Pacific Anadromous Fish Commission (NPAFC), which operates under the NOAA Authorization Act of 1992 (PL 102-567, Title VII: North Pacific Anadromous Stocks Convention). Declines in runs of several salmon species and changes in oceanographic conditions in the Bering Sea in the late 1990s prompted (then) NPAFC member nations (Canada, Japan, Russia, and United States; Korea joined later) to initiate the Bering-Aleutian Salmon International Survey (BASIS) in 2002 (NPAFC 2001a). The goal of BASIS is to investigate how salmon and their marine ecosystems respond to climate change (NPAFC 2005a). Contract work by scientists at the School of Aquatic and Fishery Sciences (SAFS), University of Washington, involved original scientific research, synthesis and review of historical research, research coordination, sample and data exchange, and scientific meeting activities in support of U.S. commitments to BASIS.

Research on the migrations of salmon in the Bering Sea has important fishery management implications for the U.S. government. In 1997-2002, reduced runs of salmon to western Alaska resulted in an economic disaster for many people whose livelihoods depend on this valuable natural resource (Anonymous 2002). In 1997 the federal government declared a commercial salmon fishery failure in the Kuskokwim and Bristol Bay regions of western Alaska. This was the first time that the U.S. Department of Commerce had used its legislative authority under section 312(a) of the Magnuson-Stevens Act to declare a commercial fishery failure in response to a request from a state governor (Alaska Governor Tony Knowles; NMFS 1997). The Alaska Department of Fish and Game forecasts of salmon returns to Bristol Bay and Kuskokwim watersheds in 1997 were off by 78%, and caused the value of the fishery to drop nearly $100 million from recent averages (NMFS 1997). Approximately 800 small businesses in Alaska suffered substantial economic injury due to the 1997 fishery failure. In addition, the State of Alaska declared economic salmon fishery disasters in the Norton Sound watershed (2000, 2001, 2002), Yukon and Kuskokwim watersheds (1997, 1998, 2000, 2001, and 2002), and the Bristol Bay watershed (1997, 1998, 2001, and 2002) the Yukon River watershed in 1997, 1998, 2000, 2001, and 2002. In 2002, the federal government again declared a salmon fisheries disaster in the Yukon, Kuskokwim, and Norton Sound regions of western Alaska. Since 2002 some western Alaska salmon runs have increased, however, commercial salmon fisheries in the region are still recovering from weak market conditions and limited buying capacity (Eggers 2006). While it is now generally well-accepted that the 1997-2002 declines in western Alaska salmon runs were related to reduced ocean survival, scientists have yet to clearly identify the underlying causal mechanisms, due in large part to the lack of scientific data on salmon migrating in the Bering Sea ecosystem prior to the start of BASIS in 2002.1997

A number of factors, separately or in combination, have been proposed as causes for the declines of Western Alaska salmon during 1997-2002. One leading hypothesis is that climate negatively affected the ocean survival of salmon through changes in benthic and pelagic food webs (Kruse 1998). In 1997-1998 unusual changes in marine nutrients, primary production (cocolithophore blooms), and energy transfer through eastern Bering Sea food chains, may have resulted in poor feeding conditions that reduced growth and survival of juvenile salmon. Late runs and smaller than average body sizes of salmon returning to western Alaska in 1997-1998 indicated that adult salmon may also have been affected by these unusual conditions. In addition, high sea temperatures along adult migration routes in the eastern Bering Sea in 1997 or other factors (increased parasitism, predation, competition, and disease) caused high adult salmon mortalities.

The Bering Sea is undergoing rapid and dramatic changes in environmental and biotic conditions associated with climate warming, including thinning of sea ice and northern movement of subarctic species into the arctic (Hunt et al. 2002, Overland et al. 2004, Grebmeier et al. 2006). Cumulative effects of climate changes may adversely affect the ocean distribution, growth, and survival of immature and maturing western Alaska salmon distributed in the Bering Sea and adjacent areas of the North Pacific Ocean. Ocean migration routes of North American salmon species and stocks may have shifted to the north and west into areas within the 200-mile zones (EEZs) of other nations (Russia and Japan), increasing the potential for competitive interactions between Asian and North American salmon stocks, as well as the risk of interceptions by commercial fisheries in those areas.

Salmon driftnet fisheries operating inside of the Russian EEZ have caught large numbers of salmon in the 1990s (e.g., NPAFC 2001b). Historical studies of salmon distribution and migration, based on research conducted in the 1950s and 1960s, indicated that stocks of western Alaska salmon do not migrate in large numbers through the Russian EEZ in the western Bering Sea. However, changes in oceanographic conditions may have altered historic migration patterns. Historic changes in the migratory habits of immature salmon are poorly known because of a lack of stock-specific research on immature and maturing salmon in the Bering Sea.

To provide scientific information and research planning and coordinating activities needed to address these issues, the work plan for this contract included: (1) participation of SAFS scientists in BASIS and related cooperative high seas salmon research cruises, (2) bioenergetic modeling of salmon in the Bering Sea, (3) salmon tagging, (4) a review of historical data on salmon distribution, migration, and interceptions in the Bering Sea, and (5) participation of SAFS scientists in NPAFC-BASIS and other meetings related to salmon research in the Bering Sea. This document is our final report on these research activities and our research results.

Research Activities and Results

1. Participation in BASIS and related cooperative high seas salmon research cruises

According to the work plan developed by NOAA/NMFS, Alaska Fisheries Science Center, priority was to be given to participating in surveys in the western Bering Sea in 2002 and 2003, especially inside the Russian EEZ with the hope of gaining new data on Alaska salmon that might be migrating through that area. The first cruise was to be onboard the Japanese R/V *Torishima*, which was intended to survey in the Sea of Okhotsk, western North Pacific, and Japanese and Russian EEZs in October-November, 2002. Unfortunately, the *Torishima* sank in an unrelated accident and the planned survey was cancelled. In spring of 2003, two SAFS predoctoral graduate research assistants (GRAs) experienced in both salmon research and Russian language were prepared to board the Russian BASIS cruise of the R/V *TINRO*. However, both GRAs were female, and Russian authorities insisted that females would not be comfortable on this vessel, and Russian approval was not given for their participation. The R/V TINRO cruises are very long (usually 6 months between port calls), and contract funding was not sufficient to hire alternate professional research scientists (males) for a 6-month research vessel survey. Constrained by these conditions, we were unable to provide SAFS participants for the 2003 Russian BASIS survey.

Russian cruises notwithstanding, SAFS scientists were able to participate in U.S. and cooperative Japan-U.S. BASIS cruises during 2002-2004. In 2002 one SAFS research scientist (N. Davis) participated in the U.S. BASIS trawl survey of the F/V *Northwest Explorer* between Sept. 5 –Oct. 8, 2002. Cruise objectives included collaboration with other BASIS programs to define salmon migration routes, investigation of the spatial overlap of stock groups of salmon in the Bering Sea, and to evaluation of the nutritional status, forage availability, and growth of salmon in the Bering Sea (Murphy et al. 2003). The first half of the cruise surveyed locations along the Aleutian Islands and adjacent basin areas from Dutch Harbor westward to Attu Island (Fig. 1). The second half conducted trawl operations along the eastern Bering Sea slope and adjacent shelf areas from Dutch Harbor northwestward to St. Lawrence Island. Forty-four rope trawl operations were conducted including a diel survey and coordinated trawl operations with the research vessels *Kaiyo maru* and *TINRO*. A total of 2,297 salmon was caught including 290 sockeye (*O. nerka*), 1836 chum (*O. keta*), 55 pink (*O. gorbuscha*), 11 coho (*O. Kisutch*), and 105 Chinook (*O. tshawytscha*) salmon (Murphy et al. 2003). No salmon tagging operations were conducted during this cruise because fish did not appear to be viable enough for tagging.

In 2003 one SAFS research scientist (N. Davis; funded in part by this contract and in part by NOAA Contr. 50-ABNF-00002) participated in a BASIS-related cooperative research cruise onboard the Japanese research vessel *Wakatake maru* (Fig. 2). The *Wakatake maru* conducted a gillnet and longline survey at 180° longitude in the central North Pacific and Bering Sea from June 7 to July 22 (Fukuwaka et al. 2003a). The objectives of this cruise were to monitor salmon stock condition and to tag and release salmon. In the Bering Sea and the Aleutian Islands area (north of 50°N) a total of 11,690 salmon (500 sockeye, 2085 chum, 8941 pink, 12 coho and 152 Chinook salmon) was caught and 739 salmon (21 sockeye, 139 chum, 549 pink, 2 coho, and 28 Chinook salmon) were tagged and released. N. Davis coordinated shipboard collection and post-cruise exchanges of salmon genetic tissues and other samples and data requested by U.S. BASIS researchers, as well as analyses of salmon age and diet, plankton, and oceanographic data for bioenergetic models (see section 2).

In 2004 two SAFS scientists participated in BASIS and BASIS-related cooperative research cruises with the Japanese (Fig. 2). One SAFS scientist (Robert Walker) participated in the BASIS research cruise of the *Kaiyo maru* in the central Bering Sea and Aleutian Islands area from June 17 to July 16 (Azumaya et al. 2005b; NPAFC 2005). A total of 3,731 salmon was caught including 365 sockeye, 3048 chum, 123 pink, 7 coho, 188 Chinook salmon. During this cruise 346 salmon, including 29 sockeye, 284 chum, 18 pink, 11 coho, and 4 Chinook salmon, were tagged and released. R. Walker coordinated shipboard salmon tagging operations and collection and post-cruise exchanges of salmon genetic tissues and other samples and data requested by U.S. BASIS researchers. Another SAFS scientist (N. Davis, funded in part by this contract and in part by NOAA Contr. 50-ABNF-00002) participated in the BASIS-related cruise of the *Wakatake maru*.

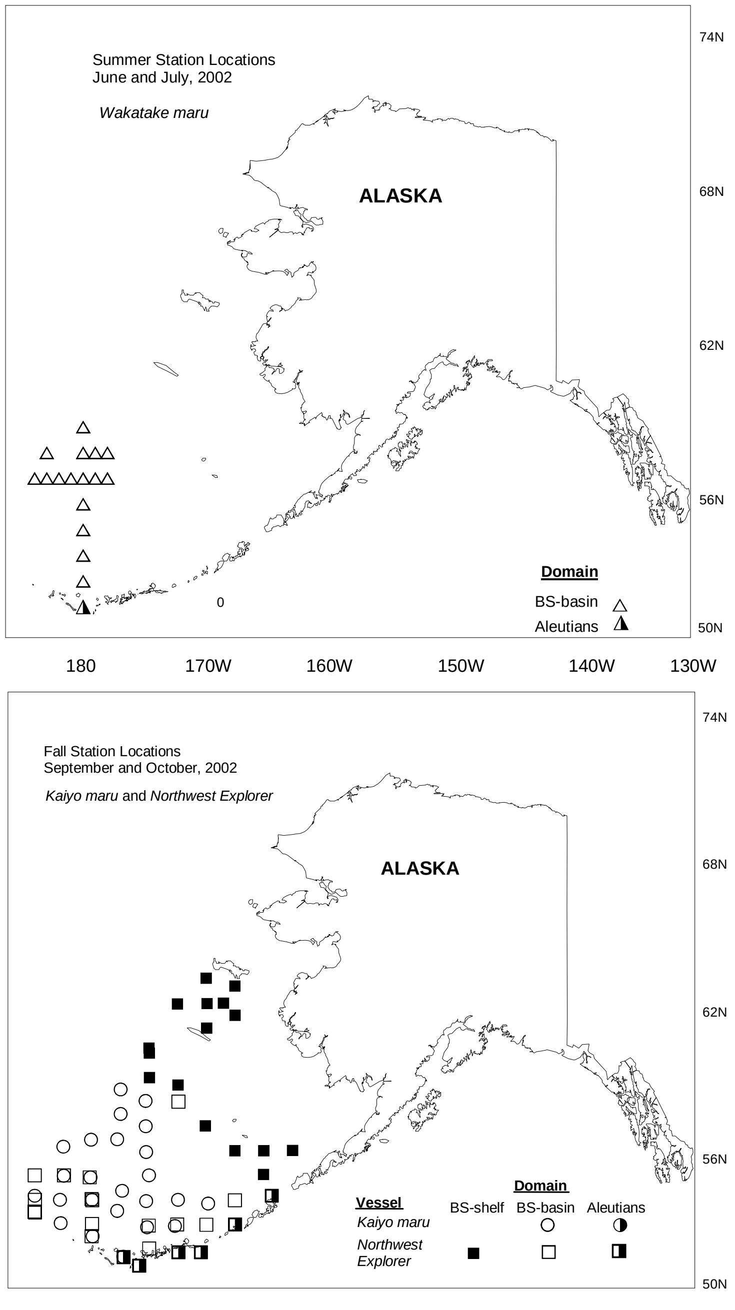


Fig. 1. Station locations in summer (upper panel) and fall (lower panel) 2002 where samples were collected for food habits analysis. Shapes depict station locations for each research vessel. Triangles = *Wakatake maru*, circles = *Kaiyo maru*, and squares = *Northwest Explorer*. Geographical habitats are indicated by fill pattern; basin = no fill, shelf = solid fill, and Aleutian Islands = partial fill.

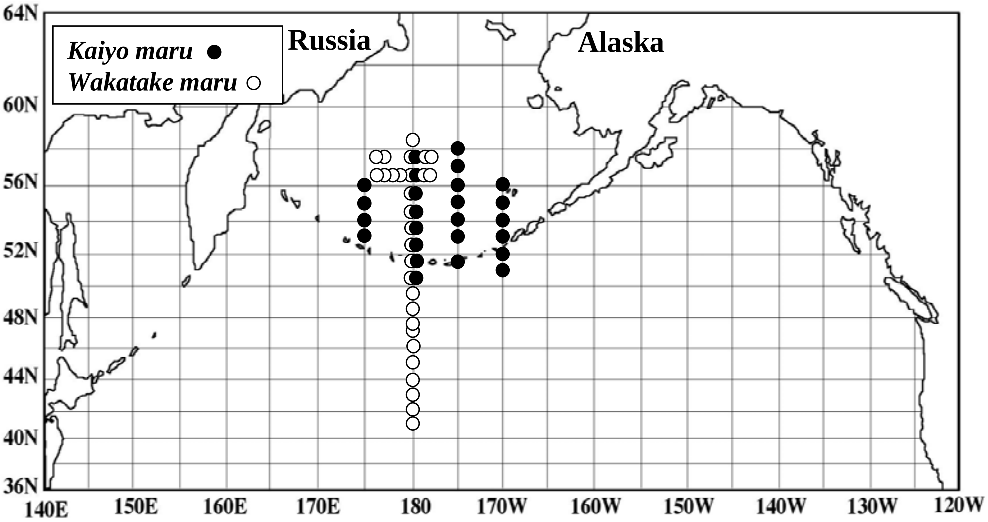


Fig. 2. Sampling areas of BASIS-related international cooperative high seas salmon research cruises. Cruise track of the *Wakatake maru* in 2003-2004 and the *Kaiyo maru* in 2004.

The *Wakatake maru* revisited the same area of the central Bering Sea and North Pacific between June 9 and July 21 the ship had surveyed the previous year (Fig. 2; Morita et al. 2004). In the Bering Sea and the Aleutian Islands area (north of 50°N) a total of 5,876 salmon, including 579 sockeye, 4483 chum, 581 pink, 16 coho, and 217 Chinook salmon, was caught. A total of 623 salmon was tagged and released during the cruise (29 sockeye, 284 chum, 18 pink, 11 coho, and 4 Chinook salmon). N. Davis coordinated shipboard collection and post-cruise exchanges of salmon genetic tissues and other samples and data requested by U.S. BASIS researchers, as well as analyses of salmon age and diet, plankton, and oceanographic data for bioenergetic models (see section 2).

2. Bioenergetic Modeling of Salmon in the Bering Sea

In this section of the report, we review the scientific literature on food habits of salmon in the Bering Sea, and we use diet, plankton, and oceanographic data from *Wakatake maru* and BASIS surveys to explore the potential effects of climate change (warming sea surface temperatures) on the growth and prey consumption of juvenile, immature, and maturing sockeye salmon in the Bering Sea.

Review of Bering Sea salmon food habits

Salmon food habits studies are important because they help identify salmon density-dependent effects on growth and survival and can be used for food web models. Since the 1960s these studies have been conducted in the western Bering Sea (e.g., Ito 1964; Andrievskaya 1966; Machidori 1968; Karpenko 1982a; Karpenko and Maksimenkov 1988; Chuchukalo et al.1995; Klovach et al. 1996; Koval and Karpenko 1998; Bugaev and Shaporev 2002; Karpenko 2003;

Smorodin et al. 2004), eastern Bering Sea (e.g., Nishiyama 1974; Straty 1974; Carlson et al. 1998; Murphy et al. 2003; Davis et al. 2004; Farley et al. 2004), and central Bering Sea f(e.g., Kanno and Hamai 1972; Azuma 1992; Davis et al. 2000; Myers et al. 2004a) Bering Sea.

Salmon distribution during their ocean migration has been linked to prey availability (Nishiyama 1974; Straty 1974; Carlson 1976; Karpenko 1979, 1983; Karpenko and Piskunova 1984; Sobolevskiy et al. 1994; Farley et al. 2004; Klovach and Gruzevich 2004). Bering Sea salmon food habits studies have shown the major prey common to all species of salmon include euphausiids (*Thysanoessa)*, hyperiid amphipods (*Themisto)*, pteropods (*Limacina),* and juvenile squids (*Gonatopsis*, *Gonatus*, and *Berryteuthis*). Important fish prey include *Stenobrachius leucopsarus* and juvenile greenlings (*Pleurogrammus*) in basin habitats, and juvenile walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*), and sand lance (*Ammodytes*) in shelf habitats. Future studies focusing on the distribution and abundance of these major prey species will improve our assessment of prey availability, diet overlap and salmon feeding competition.

In response to the biennial cycle of pink salmon abundance in the Bering Sea, density-dependent shifts in prey composition have been observed in the food habits of pink, chum, and sockeye salmon (Ito 1964; Andrievskaya 1966; Tadokoro et al. 1996; Karpenko et al. 1998; Davis 2003). During even-numbered years (low abundance of maturing pink salmon), total stomach content weight and proportions of euphausiids, copepods, fish, and squid increase in sockeye and pink salmon, and the proportion of euphausiids and other crustaceans increase in chum salmon stomach contents (Fig. 3).

Salmon diet overlaps (percent similarity index) were calculated for sockeye, chum, pink, and Chinook salmon collected in the basin during the summer cruises (1991-2003) of the *Wakatake maru* (Fig. 4). Results showed a very high (> 75%) diet overlap between sockeye and pink salmon in odd- and even- numbered years. In odd-numbered years, however, diet overlaps between chum and sockeye, and chum and pink salmon were reduced. Comparing summer to fall overlaps using data collected onboard the *Northwest Explorer* in 2002 (Davis et al. 2004), indicated seasonal reduction in diet similarity between sockeye and chum salmon, and sockeye and Chinook salmon (Fig. 4). In fall, overlap between sockeye and chum salmon in the Aleutian Islands was very high (> 75%), while overlap between chum and Chinook salmon was moderate (28-30%) in the basin and the eastern shelf.

While previous studies have focused on the inter- and intra-specific interactions among pink, sockeye, or chum salmon, Davis et al. (2004) suggested relatively low level of inter-specific food competition between immature Chinook and immature sockeye or chum salmon. However, if salmon prey availability is reduced by adverse environmental changes in the Bering Sea then increased inter- and intra-specific competition could decrease growth of Bering Sea Chinook salmon.

Seasonal variation in salmon food habits has been observed in the Bering Sea (Takeuchi 1972, Davis et al. 2004). The occurrence of the pteropod *Limacina* decreased from spring to summer in the diets of sockeye, chum and pink salmon (Takeuchi 1972). In fall sockeye salmon collected in the basin of eastern shelf consume a higher proportion of euphausiids than in

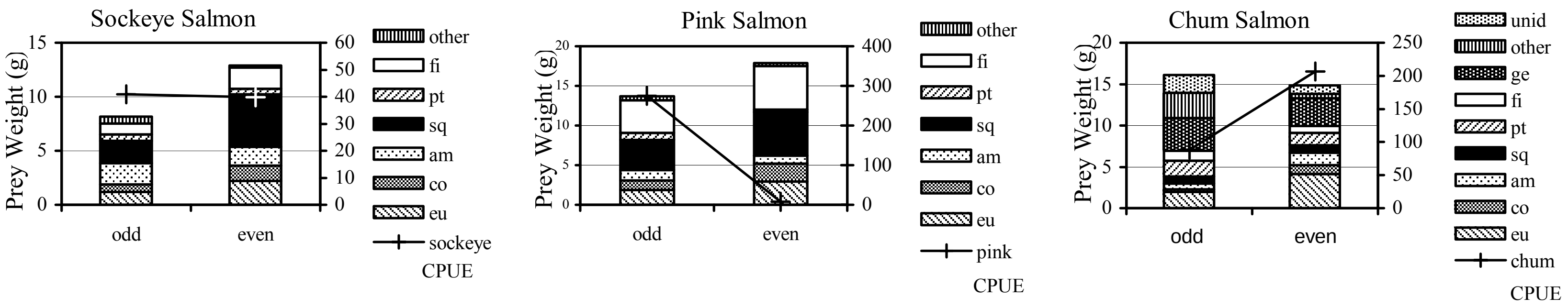
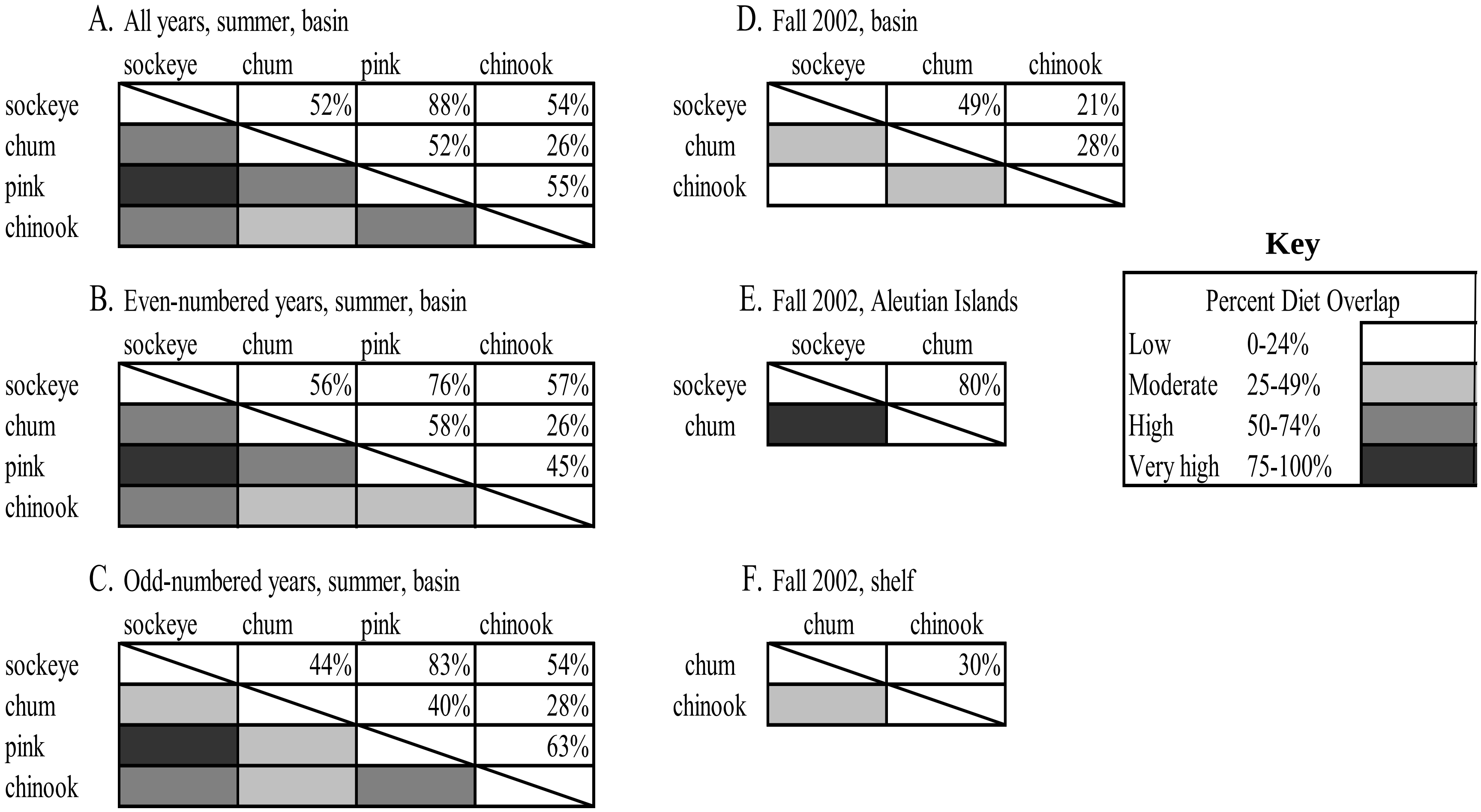


Fig. 3. Mean weight (g) of each prey category observed in the stomach contents of sockeye, pink, and chum salmon and mean CPUE (number of fish/50-m tan of research gillnet) observed during odd- and even-numbered years in the central Bering Sea in July, 1991-2000. eu = euphausiids, co = copepods, am = amphipods, sq = squid, pt = pteropods, fi = fish, ge = gelatinous zooplankton, unid = unidentified.



A. All years, summer, basin

	sockeye	chum	pink	chinook
sockeye		52%	88%	54%
chum	▒		52%	26%
pink	▓	▒		55%
chinook	▒	░	▒	

B. Even-numbered years, summer, basin

	sockeye	chum	pink	chinook
sockeye		56%	76%	57%
chum	▒		58%	26%
pink	▓	▒		45%
chinook	▒	░	░	

C. Odd-numbered years, summer, basin

	sockeye	chum	pink	chinook
sockeye		44%	83%	54%
chum	░		40%	28%
pink	▓	░		63%
chinook	▒	░	▒	

D. Fall 2002, basin

	sockeye	chum	chinook
sockeye		49%	21%
chum	░		28%
chinook	□	░	

E. Fall 2002, Aleutian Islands

	sockeye	chum
sockeye		80%
chum	▓	

F. Fall 2002, shelf

	chum	chinook
chum		30%
chinook	░	

Key

Percent Diet Overlap		
Low	0-24%	□
Moderate	25-49%	░
High	50-74%	▒
Very high	75-100%	▓

Fig. 4. Percent diet overlap of sockeye, chum, pink, and Chinook salmon collected in the Bering Sea Basin, Aleutian Islands, and eastern Bering Sea shelf. Panel A = diet overlap in the basin for all years, summer 1991-2003; Panel B = even-numbered years, basin, summer 1992-2002; Panel C = odd-numbered years, basin, summer 1991-2003; Panel D = fall, 2002, basin; Panel E = fall, 2002, Aleutian Islands; Panel F = fall; 2002, eastern Bering Sea shelf.

summer (Davis et al. 2004). In summer, chum salmon in the basin consumed mainly euphausiids and pteropods and lesser volumes of amphipods, squid, fish and gelatinous zooplankton. In the fall pteropods were a large component of chum salmon diets on the shelf (Davis et al. 2004). Gelatinous zooplankton was a significant component of prey of chum salmon in basin and shelf habitats in fall and summer. Chinook salmon stomachs collected in the basin during summer contained high volumes of euphausiids, squid, and fish. However, in fall they contained relatively low volumes of euphausiids (Davis et al. 2004).

Bering Sea food habits studies have shown that prey composition shifts with salmon body size (Dell 1963; Andrievskaya 1968; Davis 2003; Dulepov and Dulepov 2003; Temnykh et al. 2003). In the basin, smaller sockeye and chum salmon contain a higher proportion of hyperiid amphipods than larger salmon (Fig. 5; Davis 2003). The proportion of squid in sockeye salmon increased with salmon body size, and the proportion of gelatinous zooplankton increased in chum salmon larger than 2500 g. Maturing chum salmon may consume more gelatinous zooplankton because it is easily digestible and widens their feeding niche (Dulepova and Dulepov 2003).

Daily ration estimates should be age- or size-specific, rather than generalized to life history stage because consumption rates shift as the fish grows (Davis et al. 1998). Such estimates will lend more realism to Bering Sea trophic models. Until recently, most consumption estimates for salmon were for fish described only by maturity stage. In addition, reporting ration as a percentage of body weight and energy per gram body weight would improve assessment of salmon diet quality.

Using bomb calorimetry, caloric value of some salmon prey organisms have been determined (Davis 2003). Gelatinous zooplankton (salps, ctenophores) had the lowest caloric value (<100 cal/g wet weight, ww). Pteropods, hyperiid amphipods, smaller euphausiids, and juvenile squid (<2 cm mantle length) had values ranging from 500-1000 cal/g ww. Caloric values of juvenile fishes, small Atka mackerel (*Pleurogrammus monopterygius*), larger euphausiids, and medium-sized squids (approximately 4 cm ML) ranged from approximately 1000 to 1500 cal/g ww, and 1500 to 2000 cal/g ww was measured from larger squid (8-9 cm ML). High values (>2000 cal/g ww) were found in deep sea smelt (*Leuroglossus schmidti*) and *S. leucopsarus*.

Estimation of salmon growth and food consumption are important steps towards addressing larger questions in food web dynamics, predator-prey interactions, and estimates of production potential of fishes in their environment (Brandt and Hartman 1993). Bering Sea salmon daily rations have been estimated from gut fullness and bioenergetics models (Nishiyama 1974; Karpenko 1982b; Karpenko and Nikolaeva 1989; Shuntov et al. 1993; Chuchukalo et al. 1995; Radchenko and Chigirinsky 1995; Volkov et al. 1995; Sobolevskiy and Senchenko 1996; Davis et al. 1998; Glebov 1998; Walker et al. 2000; Temnykh et al. 2003; Radchenko and Mathisen 2004). Gut fullness can be corrected for digestion rate, which is affected by prey composition, prey size, meal size, and water temperature (Windell 1978; Ney 1990). However, this method requires frequent sampling (approximately every 3 hrs) and assumes stomach contents measure food consumed. Because gut evacuation and feeding occur simultaneously, stomach contents at the end of the feeding period can underestimate the amount consumed (Elliott and Persson 1978).

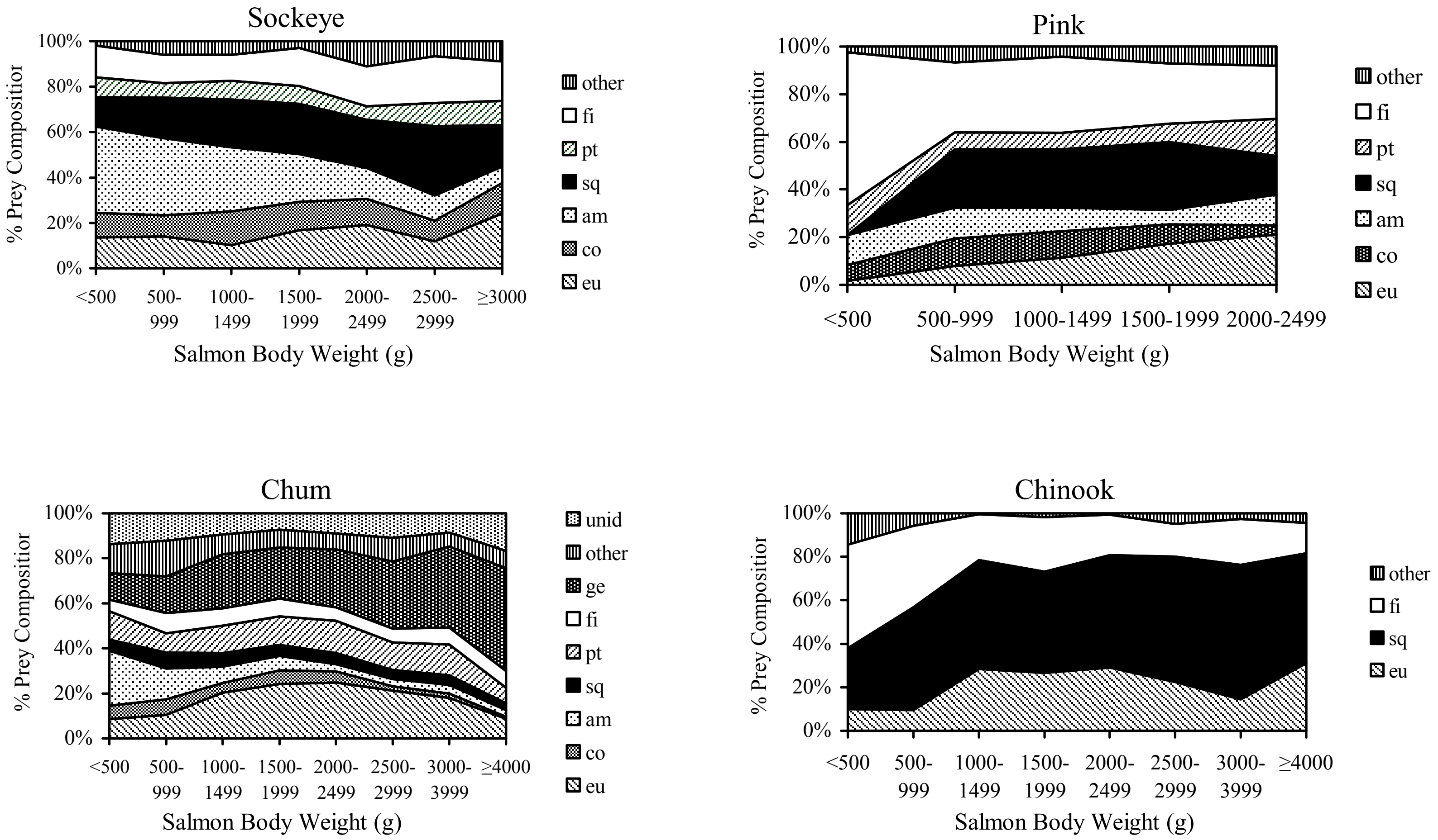


Fig. 5. Percent composition (by weight) of major prey categories collected from sockeye, chum, pink, and Chinook salmon stomach contents for size groups of fish caught in the central Bering Sea basin in July, 1991-2000. Size class < 500 g represents the smallest size group for ocean age-.1 fish. eu = euphausiids, co = copepods, am = amphipods, sq = squid, pt = pteropods, fi = fish, ge = gelatinous zooplankton, and unid = unidentified.

The bioenergetics approach uses a balanced energy budget. The Winberg bioenergetic model (Winberg 1956) assumes waste and food processing costs are fixed proportions of consumption, and active metabolism is a multiple of standard metabolism (Ney 1990). Bioenergetic models using constraints on consumption when salmon growth can be reasonably estimated (e.g., the Wisconsin model) can provide realistic consumption estimates (Hanson et al. 1997). The Wisconsin bioenergetics model estimates consumption as a proportion of maximum consumption of a fish at any weight or temperature and can provide relative consumption or growth estimates under differing conditions of temperature and prey availability (Ney 1990).

Bioenergetic modeling

In 2002-2004, summer and fall oceanographic conditions across the entire Bering Sea during BASIS research vessel cruises were characteristic of warm years and winter cooling was moderate (NPAFC 2005). Current climate model projections indicate that by 2050 mean sea surface temperatures (SSTs) in high latitudes could increase 2°C over 1990 values (IPCC 2001). Japanese research vessel data indicate that the upper thermal limit of salmon distribution in the ocean is 13.3 °C for sockeye, 15.6 °C for chum, 16.6 °C for pink, 15.7 °C for coho and 13.4 °C for Chinook salmon (Azumaya et al., in press). Because sockeye salmon have a lower upper thermal limit than other species, increases in SSTs at high latitudes might initially have the greatest influence on sockeye salmon. We examined potential effects of increasing temperature on Bering Sea salmon by comparing sockeye salmon feeding and growth that might occur during current and future SST warming conditions using a bioenergetic model. Bioenergetic models can simulate growth potential based on temperature predictions and improve our assessment of the potential effects of climate change on salmon food habits and growth.

We were unable to collect new food habits and growth data from surveys in the western Bering Sea because there were no SAFS scientists placed Russian cruises during the contract period. However, food habits data were collected during surveys of the central and eastern Bering Sea (section 1). We used a bioenergetics model to estimate growth and prey consumption for sockeye salmon in the Bering Sea using satellite observations of SST, literature values and field observations of salmon prey composition, and literature values of prey energy. We modeled summer growth and prey consumption for several age-maturity groups of sockeye salmon, including 60-day simulations for juvenile sockeye (ocean age-.0) in the eastern Bering Sea, 90-day simulations for immature sockeye (ocean age-.1 and -.2) in the central Bering Sea, and 60-say simulations for maturing sockeye salmon (ocean age -.2 and -.3) in the central Bering Sea.

Monthly averaged SSTs in 2004 were obtained from the Integrated Global Ocean Service System (IGOSS) database (http://ingrid.ldeo.columbia.edu/SOURCES/.IGOSS/) at a 1° X 1° resolution. The eastern Bering Sea area was delineated by the area 55.5°N to 58.5°N and 160.5°W to 165.5°W from July to September, and the central Bering Sea area was delineated by the area 55.5°N to 59.5°N and 175.5°E to 175.5°W from May to September (Fig. 6).

Prey composition data for juvenile sockeye salmon (>200 mm fork length) were taken from a coastal survey in the eastern Bering Sea by the F/V *Sea Storm* (leg 2; Farley et al. 2004). The prey category named "other" was removed from the prey composition and remaining categories reapportioned to equal 100% (Table 1). Mean prey composition for immature and maturing sockeye salmon in the central Bering Sea were determined from stomach analysis of sockeye

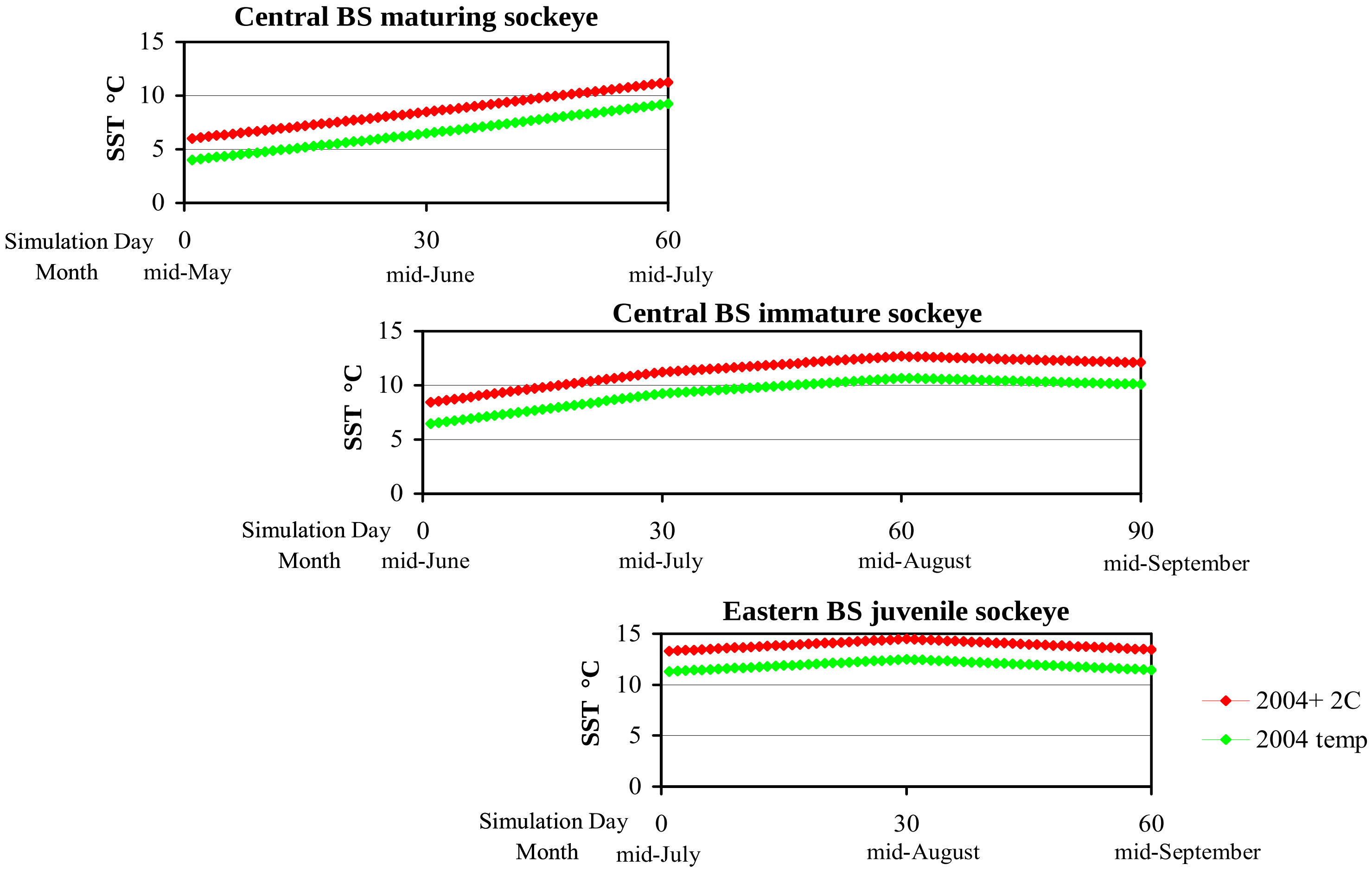


Fig. 6. Sea surface temperatures (°C) used in bioenergetics simulations. Simulations for juvenile sockeye (ocean age-.0) include mid-July to mid-September temperatures in the Eastern Bering Sea in 2004 and a higher temperature scenario with an increase of 2° C. Simulations for immature sockeye (ocean age -.1 and -.2) include mid-June to mid-September temperatures in the central Bering Sea in 2004 and a higher temperature scenario with an increase of 2° C. Simulations for maturing sockeye (ocean age-.2 and -.3) include mid-May to mid-July temperatures in the central Bering Sea in 2004 and a higher temperature scenario with an increase of 2° C.

caught in that area during cruises of the R/V *Wakatake maru* from 1991 to 2003 (e.g., Fukuwaka et al. 2003a). Mean prey composition was determined from fish containing prey; “other” and “unidentified” were removed, and the remaining categories reapportioned to equal 100%. Prey energy densities were obtained from literature values (Table 1).

We used the Wisconsin bioenergetic model, which supplies physiological parameters for sockeye salmon (Hanson et al. 1997). The model can estimate prey consumption based on a given growth increment, or estimate the growth increment based on a given start weight and consumption rate. Estimating consumption is accomplished by giving start and final weights and the model will estimate the proportion of maximum consumption (p-value) required to produce the given growth increment. A p-value of 0.0 means no prey has been consumed during the simulation and a p-value of 1.0 means the fish consumed prey at its maximum consumption rate, given its size and water temperature.

We ran the model both ways: estimating consumption based on a specified growth increment, and estimating the growth increment based on a specified start weight and a maximum p-value (p value=1.0; Hanson et al. 1997). For juvenile sockeye, we used mean lengths of juveniles collected from Aug 21 to Oct 8, 2003 during a coastal eastern Bering Sea salmon survey (start and final weights are 70.0 and 151.4 g; Farley et al. 2004). Start and final weights for immature and maturing sockeye were from data provided by Ishida et al. (1998) based on monthly average body weight-at-age for sockeye salmon caught in offshore Japanese research vessel cruises from 1972 to 1995. These weights included growth of 362.6 to 610.5 g for immature ocean age-.1 fish (Jun to Sep), 1047.1 to 1607.2 g for immature ocean age-.2 fish (Jun to Sep), 1571.0 to 2229.4 g for maturing ocean age-.2 fish (May to Jul), and 2518.5 to 3056.8 g for maturing ocean age-.3 fish (May to Jul; Ishida et al. 1998).

For each maturity and age group simulated, prey composition and prey energy density were constant (Table 1). Five different scenarios of temperature and prey consumption were considered. Scenario 1 represented conditions resembling those during summer 2004 (growth increment given, environmental temperatures were 2004 values, and p-value estimated). Scenario 2 represented conditions when SSTs would be 2°C warmer with the fish attaining the same growth increment as scenario 1 (growth increment given, environmental temperatures were 2004 + 2°C values, and p-value estimated). Scenario 3 represented conditions when SSTs would be 2°C warmer and 10% less prey available for salmon consumption (final fish weight estimated, environmental temperatures were 2004 + 2°C, and p-value set at 10% less than scenario 1). Scenario 4 represented growth potential under 2004 temperature conditions and the fish consumed prey at its physiological maximum (final fish weight estimated, environmental temperatures were 2004 values, and p-value=1.0). Scenario 5 represented growth potential under 2004 + 2°C warmer temperature conditions and the fish consumed prey at its physiological maximum (same as scenario 4, except warm temperatures; i.e, final fish weight is estimated, environmental temperatures were 2004 + 2°C values, and p-value=1.0). Growth estimates (g), gross conversion efficiency (growth/consumption), mean consumption rate (g prey/day), and total prey consumption (g and kJ) were estimated for each of the five scenarios and maturity-age groups for the 60- or 90-day simulations.

Bioenergetic simulations showed conversion efficiencies were lower for all scenarios that included 2°C increased temperatures (scenario 1 vs. 2 and 3; 4 vs. 5; Tables 2-6). This occurs because as environmental temperature increase, energy demands of metabolism and elimination

Table 1. Prey composition and prey energy density values used in a bioenergetics model to simulate growth and prey consumption for juvenile, immature, and maturing sockeye salmon in the Bering Sea.

			Prey				
Maturity	Ocean age	Months Simulated	Items	% Composition	Source	Energy Density (J/g)	Source
juvenile	0	mid-Jul to mid-Sep (60 days)	*Thysanoessa raschii*	0.01	Farley et al. 2004	2729	Mauchline 1980
			Ammodytes hexapterus	0.03	Farley et al. 2004	5392	Nishiyama 1977
			Mallotus villosus	0.04	Farley et al. 2004	5346	Davis et al. 1998
			Theragra chalcogramma	0.87	Farley et al. 2004	3801	Boldt 1997
			Larval fish	0.05	Farley et al. 2004	5011	Nishiyama 1977
immature	1	mid-Jun to mid-Sep (90 days)	euphausiids	0.21	this report	4270	Davis 2003
			copepods	0.09	this report	2625	Davis et al. 1998
			amphipods	0.39	this report	3566	Davis 2003
			crab larvae	0.01	this report	2980	Nishiyama 1977
			squid	0.09	this report	3558	Davis 2003
			pteropods	0.03	this report	3935	Davis 2003
			fish	0.17	this report	5911	Davis 2003
			chaetognaths	0.01	this report	1905	Nishiyama 1977
immature	2	mid-Jun to mid-Sep (90 days)	euphausiids	0.14	this report	4270	Davis 2003
			copepods	0.12	this report	2625	Davis et al. 1998
			amphipods	0.25	this report	3566	Davis 2003
			crab larvae	0.02	this report	2980	Nishiyama 1977
			squid	0.20	this report	3558	Davis 2003
			pteropods	0.08	this report	3935	Davis 2003
			fish	0.19	this report	5911	Davis 2003
maturing	2	mid-May to mid-Jul (60 days)	euphausiids	0.17	this report	4270	Davis 2003
			copepods	0.17	this report	2625	Davis et al. 1998
			amphipods	0.23	this report	3566	Davis 2003
			crab larvae	0.05	this report	2980	Nishiyama 1977
			squid	0.24	this report	3558	Davis 2003
			pteropods	0.05	this report	3935	Davis 2003
			fish	0.07	this report	5911	Davis 2003
			gelatinous zooplankton	0.02	this report	569	Davis et al. 1998
maturing	3	mid-May to mid-Jul (60 days)	euphausiids	0.27	this report	4270	Davis 2003
			copepods	0.10	this report	2625	Davis et al. 1998
			amphipods	0.08	this report	3566	Davis 2003
			crab larvae	0.03	this report	2980	Nishiyama 1977
			squid	0.22	this report	3558	Davis 2003
			pteropods	0.11	this report	3935	Davis 2003
			fish	0.15	this report	5911	Davis 2003
			polychaetes	0.02	this report	3554	Thayer et al. 1973
			chaetognaths	0.01	this report	1905	Nishiyama 1977
			gelatinous zooplankton	0.01	this report	569	Davis et al. 1998

Table 2. Juvenile sockeye salmon growth and prey consumption estimated from a 60-day bioenergetics simulation. Model input values represent conditions for an ocean age-.0 sockeye salmon with an initial weight of 70.0 g in the eastern Bering Sea in mid-July to mid-September. Prey composition and prey energy density were constant for all scenarios. Scenario 1: final fish weight is pre-determined, environmental temperatures are 2004 values, and p-value is estimated. Scenario 2: final fish weight is pre-determined, environmental temperatures are 2004 + 2°C values, and p-value is estimated. Scenario 3: final fish weight is estimated, environmental temperatures are 2004 + 2°C, and p-value is set at 10% less than scenario 1. Scenario 4: final fish weight is estimated, environmental temperatures are 2004 values, and p-value=1.0. Scenario 5: final fish weight is estimated, environmental temperatures are 2004 + 2°C values, and p-value=1.0. The p-value is the proportion of the fish's maximum consumption rate that is consumed by the fish, given its size and water temperature.

Juvenile ocean age-.0 sockeye salmon

Items	Scenario				
	1	2	3	4	5
Start weight (g)	70.0	70.0	70.0	70.0	70.0
Final weight (g)	151.4	151.4	130.0	235.3	227.6
P-value (proportion)	0.649	0.685	0.584	1.000	1.000
Net production (g)	81.4	81.4	60.0	165.3	157.6
Conversion efficiency (%)	26.1	23.8	22.0	28.4	26.5
Mean energy density (J/g)					
predator	6703	6703	6698	6721	6719
prey	3960	3960	3960	3960	3960
Prey Consumption (g)					
Thysanoessa raschii	3.1	3.4	2.7	5.8	6.0
Ammodytes hexapterus	9.4	10.2	8.2	17.5	17.9
Mallotus villosus	12.5	13.7	10.9	23.3	23.8
Theragra chalcogramma	271.4	297.1	237.6	507.0	517.8
Larval fish	15.6	17.1	13.7	29.1	29.8
Total prey consumption (g)	311.9	341.5	273.1	582.7	595.1
Total prey consumption (kJ)	1235	1352	1081	2307	2357
Mean consumption rate (g/d	5.2	5.7	4.6	9.7	9.9

Table 3. Immature sockeye salmon growth and prey consumption estimated from a 90-day bioenergetics simulation. Model input values represent conditions for an ocean age-.1 sockeye salmon with an initial weight of 362.6 g in the central Bering Sea in mid-June to mid-September. Prey composition and prey energy density were constant for all scenarios. Scenario 1: final fish weight is pre-determined, environmental temperatures are 2004 values, and p-value is estimated. Scenario 2: final fish weight is pre-determined, environmental temperatures are 2004 + 2°C values, and p-value is estimated. Scenario 3: final fish weight is estimated, environmental temperatures are 2004 + 2°C, and p-value is set at 10% less than scenario 1. Scenario 4: final fish weight is estimated, environmental temperatures are 2004 values, and p-value=1.0. Scenario 5: final fish weight is estimated, environmental temperatures are 2004 + 2°C values, and p-value=1.0. The p-value is the proportion of the fish's maximum consumption rate that is consumed by the fish, given its size and water temperature.

Immature ocean age-.1 sockeye salmon

Items	Scenario				
	1	2	3	4	5
Start weight (g)	362.6	362.6	362.6	362.6	362.6
Final weight (g)	610.5	610.5	541.1	1051.6	1044.9
P-value (proportion)	0.530	0.558	0.477	1.000	1.000
Net production (g)	247.9	247.9	178.5	689.0	682.3
Conversion efficiency (%)	23.3	20.8	18.4	27.2	25.4
Mean energy density (J/g)					
predator	6899	6901	6884	6995	6996
prey	4016	4016	4016	4016	4016
Prey Consumption (g)					
euphausiids	223.8	250.6	203.9	532.4	564.2
copepods	95.9	107.4	87.4	228.2	241.8
amphipods	415.6	465.4	378.6	988.8	1047.7
crab larvae	10.7	11.9	9.7	25.4	26.9
squid	95.9	107.4	87.4	228.2	241.8
pteropods	32.0	35.8	29.1	76.1	80.6
fish	181.2	202.9	165.0	431.0	456.7
chaetognaths	10.7	11.9	9.7	25.4	26.9
Total prey consumption (g)	1065.8	1193.4	970.7	2535.3	2686.4
Total prey consumption (kJ)	4280	4793	3898	10182	10789
Mean consumption rate (g/d	11.8	13.3	10.8	28.2	29.8

Table 4. Immature sockeye salmon growth and prey consumption estimated from a 90-day bioenergetics simulation. Model input values represent conditions for an ocean age-.2 sockeye salmon with an initial weight of 1047.1 g in the central Bering Sea in mid-June to mid-September. Prey composition and prey energy density were constant for all scenarios. Scenario 1: final fish weight is pre-determined, environmental temperatures are 2004 values, and p-value is estimated. Scenario 2: final fish weight is pre-determined, environmental temperatures are 2004 + 2°C values, and p-value is estimated. Scenario 3: final fish weight is estimated, environmental temperatures are 2004 + 2°C, and p-value is set at 10% less than scenario 1. Scenario 4: final fish weight is estimated, environmental temperatures are 2004 values, and p-value=1.0. Scenario 5: final fish weight is estimated, environmental temperatures are 2004 + 2°C values, and p-value=1.0. The p-value is the proportion of the fish's maximum consumption rate that is consumed by the fish, given its size and water temperature.

Immature ocean age-.2 sockeye salmon

Items	Scenario				
	1	2	3	4	5
Start weight (g)	1047.1	1047.1	1047.1	1047.1	1047.1
Final weight (g)	1607.2	1607.2	1449.3	2197.2	2162.1
P-value (proportion)	0.625	0.663	0.563	1.000	1.000
Net production (g)	560.1	560.1	402.2	1150.1	1115.0
Conversion efficiency (%)	21.4	19.0	16.8	24.2	22.2
Mean energy density (J/g)					
predator	7338	7342	7304	7473	7471
prey	4013	4013	4013	4013	4013
Prey Consumption (g)					
euphausiids	366.3	412.4	335.9	666.1	702.5
copepods	313.9	353.5	287.9	570.9	602.1
amphipods	654.0	736.4	599.9	1189.5	1254.4
crab larvae	52.3	58.9	48.0	95.2	100.4
squid	523.2	589.1	479.9	951.6	1003.6
pteropods	209.3	235.6	192.0	380.6	401.4
fish	497.1	559.6	455.9	904.0	953.4
Total prey consumption (g)	2616.2	2945.5	2399.5	4757.9	5017.8
Total prey consumption (kJ)	10499	11820	9629	19093	20136
Mean consumption rate (g/d	29.1	32.7	26.7	52.9	55.8

Table 5. Maturing sockeye salmon growth and prey consumption estimated from a 60-day bioenergetics simulation. Model input values represent conditions for an ocean age-.2 sockeye salmon with an initial weight of 1571.0 g in the central Bering Sea in mid-May to mid-July. Prey composition and prey energy density were constant for all scenarios. Scenario 1: final fish weight is pre-determined, environmental temperatures are 2004 values, and p-value is estimated. Scenario 2: final fish weight is pre-determined, environmental temperatures are 2004 + 2°C values, and p-value is estimated. Scenario 3: final fish weight is estimated, environmental temperatures are 2004 + 2°C, and p-value is set at 10% less than scenario 1. Scenario 4: final fish weight is estimated, environmental temperatures are 2004 values, and p-value=1.0. Scenario 5: final fish weight is estimated, environmental temperatures are 2004 + 2°C values, and p-value=1.0. The p-value is the proportion of the fish's maximum consumption rate that is consumed by the fish, given its size and water temperature.

Maturing ocean age-.2 sockeye salmon

Items	Scenario				
	1	2	3	4	5
Start weight (g)	1571.0	1571.0	1571.0	1571.0	1571.0
Final weight (g)	2229.4	2229.4	2165.2	2271.5	2305.1
P-value (proportion)	0.950	0.921	0.855	1.000	1.000
Net production (g)	658.4	658.4	594.2	700.5	734.1
Conversion efficiency (%)	21.7	20.4	20.1	21.8	20.7
Mean energy density (J/g)					
predator	7631	7636	7621	7640	7654
prey	3617	3617	3617	3617	3617
Prey Consumption (g)					
euphausiids	515.0	548.6	503.6	546.3	603.7
copepods	515.0	548.6	503.6	546.3	603.7
amphipods	696.8	742.2	681.3	739.1	816.8
crab larvae	151.5	161.3	148.1	160.7	177.6
squid	727.1	774.5	711.0	771.2	852.3
pteropods	151.5	161.3	148.1	160.7	177.6
fish	212.1	225.9	207.4	224.9	248.6
gelatinous zooplankton	60.6	64.5	59.2	64.3	71.0
Total prey consumption (g)	3029.4	3227.0	2962.4	3213.3	3551.3
Total prey consumption (kJ)	10957	11672	10715	11623	12845
Mean consumption rate (g/d	50.5	53.8	49.4	53.6	59.2

Table 6. Maturing sockeye salmon growth and prey consumption estimated from a 60-day bioenergetics simulation. Model input values represent conditions for an ocean age-.3 sockeye salmon with an initial weight of 2518.5 g in the central Bering Sea in mid-May to mid-July. Prey composition and prey energy density were constant for all scenarios. Scenario 1: final fish weight is pre-determined, environmental temperatures are 2004 values, and p-value is estimated. Scenario 2: final fish weight is pre-determined, environmental temperatures are 2004 + 2°C values, and p-value is estimated. Scenario 3: final fish weight is estimated, environmental temperatures are 2004 + 2°C, and p-value is set at 10% less than scenario 1. Scenario 4: final fish weight is estimated, environmental temperatures are 2004 values, and p-value=1.0. Scenario 5: final fish weight is estimated, environmental temperatures are 2004 + 2°C values, and p-value=1.0. The p-value is the proportion of the fish's maximum consumption rate that is consumed by the fish, given its size and water temperature.

Maturing ocean age-.3 sockeye salmon

Items	Scenario				
	1	2	3	4	5
Start weight (g)	2518.5	2518.5	2518.5	2518.5	2518.5
Final weight (g)	3056.8	3056.8	2958.7	3523.5	3570.4
P-value (proportion)	0.625	0.630	0.562	1.000	1.000
Net production (g)	538.3	538.3	440.2	1005.0	1051.9
Conversion efficiency (%)	20.3	18.4	17.0	22.5	21.3
Mean energy density (J/g)					
predator	8104	8110	8086	3000	8232
prey	3988	3988	3988	3988	3988
Prey Consumption (g)					
euphausiids	714.2	791.4	697.4	1206.2	1332.0
copepods	264.5	293.1	258.3	446.7	493.3
amphipods	211.6	234.5	206.7	357.4	394.7
crab larvae	79.4	87.9	77.5	134.0	148.0
squid	582.0	644.9	568.3	982.8	1085.4
pteropods	291.0	322.4	284.1	491.4	542.7
fish	396.8	439.7	387.5	670.1	740.0
polychaetes	52.9	58.6	51.7	89.3	98.7
chaetognaths	26.5	29.3	25.8	44.7	49.3
gelatinous zooplankton	26.5	29.3	25.8	44.7	49.3
Total prey consumption (g)	2645.3	2931.2	2583.1	4467.4	4933.5
Total prey consumption (kJ)	10549	11690	10301	17816	19675
Mean consumption rate (g/d	44.1	48.9	43.1	74.5	82.2

increase faster than prey consumption. Reduction in conversion efficiency was greater in juvenile and immature fish than maturing fish (juveniles=2.3%, immature age-.1 and -.2=2.5 and2.4%, maturing age-.2 and -.3=1.3%, and 1.9%; scenario 1 vs. 2). Higher energy demands associated with a 2°C increase in SSTs lead to an increase in prey consumption of 6 to 11% (g or kJ) to attain the same weight increment. If higher temperatures accompanied a 10% decrease in prey availability (scenarios 1 and 2 vs. 3), then net production (g) decreased by 26 to 28% for juvenile and immature fish or 10-18% for maturing sockeye salmon. To attain the mean monthly weight-at-age reported by Ishida et al. (1998) and Farley et al. (2004) with a thermal experience of 2004 SSTs (scenario 1), p-values ranged from 0.53 to 0.65 for all groups except maturing age-.2s. The p-value for this group was much higher, 0.95 (Table 5), indicating either maturing age.-2 sockeye were the only age group feeding near its maximum consumption rate, or that prey energy density estimates and/or growth increments were incorrect. Growth increments were taken from mean weights pooled over large areas and in some cases combined over several years. Simulation estimates would be improved by using individual growth rates that could be estimated by back calculation from scale measurements.

An increase in mean summer temperatures of 2°C indicated sockeye salmon would experience less growth at all age-maturity stages unless prey availability, or prey energy density increased commensurately. Current indications are that climate warming is linked to ecosystem disturbance (Overland et al. 2004, Grebmeier et al. 2006). Climate change effects on salmon prey abundance, distribution, and energy density requires further study.

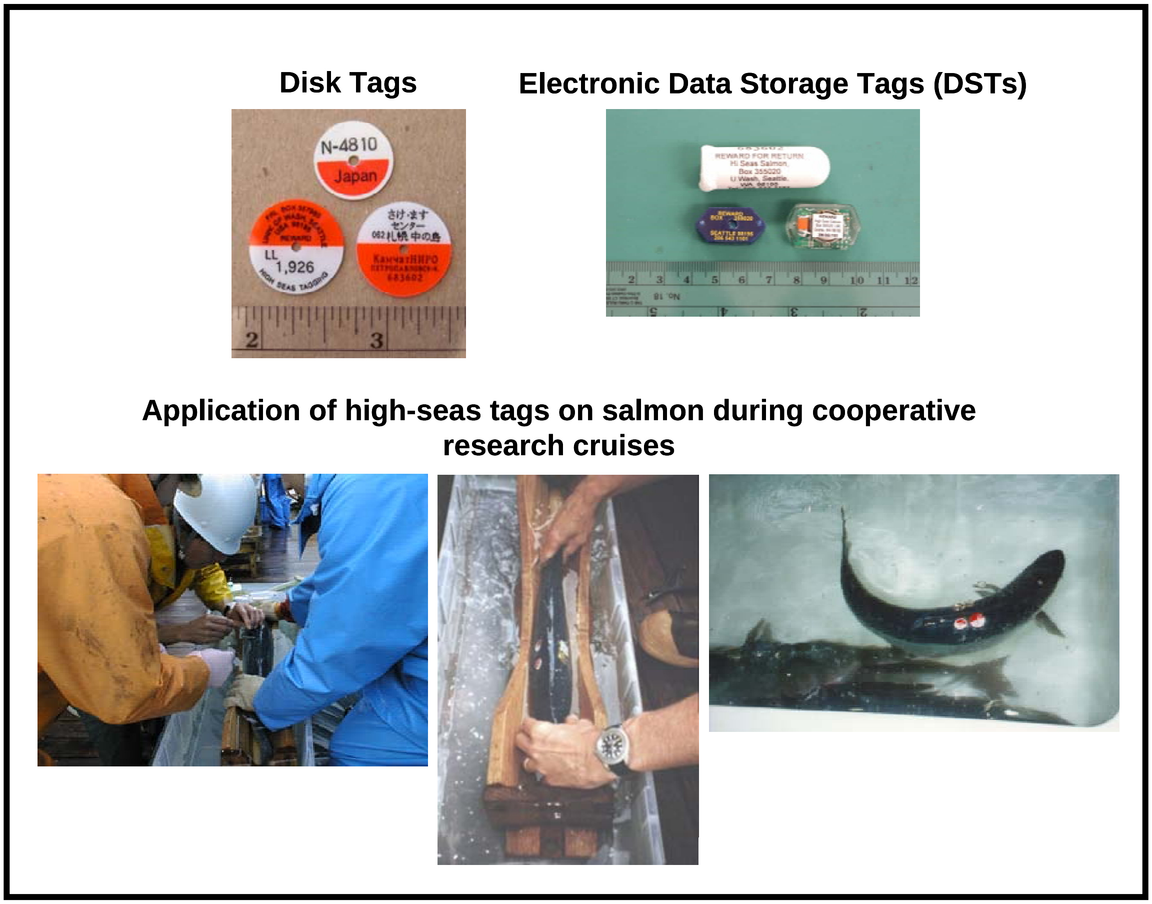
3. Salmon Tagging

Tagging work covered by this contract includes fish tagged during surveys conducted during 2003 and 2004. Support for tagging work was also provided by NOAA Contract 50-ABNF-00002 and funding to NPAFC from the North Pacific Research Board (Walker et al. 2006). Both disk tags and electronic data storage tags (DST) were placed on salmon during that time. U.S. disk tags are 20 mm diameter red-and-white Petersen tags (Fig. 7). Japanese disk tags are a few millimeters smaller and are orange and white in color. Disk tags were mounted externally on the fish with a plastic locking-cinch strap placed in the area immediately anterior to the dorsal fin. The DSTs were placed on a subset of fish tagged with disk tags. The DSTs record one or more environmental conditions (e.g., temperature, depth, and salinity).

In 2003, two types of DSTs were used (Fig. 7). One type is a small circuit board potted in a clear urethane, manufactured by Lotek Marine Technologies (models LTD_1100-300 and LTD_1100-500). These DSTs record temperature and depth and are 27 X16 X 8 mm and weight 5 g. The other DST type records only temperature. These tags are Thermonchron iButton tags (DS-1921H-F5 and DS-1921Z-F5) manufactured by Dallas Semiconductor, Inc. and repackaged in urethane for fish tagging by AlphaMach, Inc. Three models of iButton type tags were used: Model iB4 tags are oval, 24 X 16 X 8 mm, and weigh 3.8 g in air; Model iBLite tags are hexagonal, 26 X 17 X 7 mm, and weigh 3 g; Model iBKrill tags are hexagonal, 25 X 13 X 8 mm, and weigh 3.2 g.

Archival tags were placed just anterior to the dorsal fin using 76 or 64 mm nickel pins, with disk tags placed on the other side of the fish (Fig. 7).

In 2004, three types of DSTs were used including Lotek's model LTD_1100-500 and AlphaMach's iBKrill tags. The third type of DST was the Model DST CTD tag manufactured by Star-Oddi. These tags are housed in a ceramic shell and are bullet-shaped, measure 27 X 13 X 8 mm, and weigh 8 g (Fig. 7). This tag records salinity, temperature, and depth data. The DST CTD tag was attached in the same location, anterior to the dorsal fin, but was affixed with stainless steel wire, with a small oval plastic plate on the opposite side of the fish. Disk tags (U.S. and Japanese) were placed on the wires either underneath the archival tag or over the plate.


Disk Tags

Electronic Data Storage Tags (DSTs)

Application of high-seas tags on salmon during cooperative research cruises

Fig. 7. Images displaying disk tags (inch scale), electronic data storage tags (centimeter scale), and placement of these tags on salmon by SAFS scientists during BASIS-related salmon research cruises.

In June and July, 2003 and 2004, scientists onboard the *Wakatake maru* tagged viable salmon caught by longline (Fukuwaka et al. 2003a,b, Walker et al. 2003, Nagasawa et al. 2004). In June and July 2004, scientists aboard the *Kaiyo maru* tagged viable salmon by hook and line fishing conducted specifically to catch salmon in good condition (Azumaya et al. 2005b). In addition, some salmon removed from trawl catches in good condition were also tagged.

In 2003, in the central Bering Sea and Aleutian Islands area (N of 50°C) a total of 739 disk tags were placed on 21 sockeye, 139 chum, 549 pink, 2 coho, and 28 Chinook salmon (Table 7). Among these fish, a subset of 135 salmon (17 sockeye, 40 chum, 60 pink, and 18 Chinook salmon) was also tagged with DSTs. In 2004, tagging operations increased the number of disk-tagged salmon to 969, including 59 sockeye, 820 chum, 41 pink, 14 coho, and 35 Chinook salmon. Among these fish, 305 DSTs were placed on 43 sockeye, 180 chum, 36 pink, 11 coho and 35 Chinook salmon (Table 7).

Table 7. Number of tagged salmon released during cooperative salmon research surveys in the central Bering Sea and central Aleutian Islands area (north of 50°N) in 2003 and 2004. Tagging operations were conducted during June and July. Salmon tagged with an electronic data storage tag (DST) were also tagged with a (Japanese and U.S.) disk tag. Counts for disk tag releases include those placed on fish with DSTs.

		Number Released					
Tag Type	Year	Sockeye	Chum	Pink	Coho	Chinook	Total
Disk	2003	21	139	549	2	28	739
DST	2003	17	40	60	0	18	135
Disk	2004	59	820	41	14	35	969
DST	2004	43	180	36	11	35	305

Thus far, 33 disk-tagged fish and 39 DST-tagged fish have been recovered from fish that were released in the Bering Sea (north of 50°N) in 2003 and 2004 (Table 8). These recoveries provide valuable data because they are the only direct information available on ocean ranges, seasonal migration patterns, overlaps in distribution, and individual migration and growth rates of Bering Sea salmon.

In 2003 there were 10 reported recoveries in Asia and North America from salmon tagged and released with DSTs and one recovery of a sockeye salmon carrying disk tags only. Three recoveries of high-seas tagged salmon in North America were reported by fishermen in 2003 (Walker et al.2003). All were from sockeye salmon tagged in the Bering Sea in 2003, and all were recovered in the Bristol Bay-north Alaska Peninsula area. One fish carrying a DST recording temperature and depth data was caught in Nelson Lagoon, Alaska Peninsula. Another DST, recording temperature data, was returned from a fish caught in Naknek, Bristol Bay. Plots of temperature and depth recorded from these tags can be found in Walker et al. (2003). A third sockeye salmon, carrying disk tags only, was caught just north of False Pass at the eastern end of the

Alaska Peninsula. In addition, four salmon tagged with iButton tags, which record sea temperature, were recovered in or off of eastern Kamchatka. Asian recoveries of salmon with DSTs that record sea temperature and depth included one in Sakhalin, one off southern Kamchatka, and two in Hokkaido. These recoveries included the first DSTs from Asian pink salmon, the second and third DSTs recovered from Bristol Bay/north Peninsula sockeye salmon, the first DST from a Russian hatchery, the first DST from a Russian chum salmon, the second DST from a Russian sockeye salmon, and a DST from a Japanese chum (Walker et al. 2003).

Table 8. Number of tagged fish released and/or recovered in the Bering Sea from tagging operations 2003 and 2004. Salmon tagged with an electronic data storage tag (DST) were also tagged with a (Japanese and U.S.) disk tag. Counts for disk tag recoveries do not include tags recovered from fish with a DST.

	Number Recovered					
Tag Type	Sockeye	Chum	Pink	Coho	Chinook	Total
Disk	1	24	7	1	0	33
DST	8	24	4	1	2	39

In 2004 there were 25 reported recoveries in Asia and North America from salmon tagged and released with DSTs (Walker et al. 2004). The large number of recoveries was due to the large number of tags deployed that year. Seventeen salmon were recovered in Asia, seven in North America, and one was recovered by the vessel that tagged it seven hours after it was released in the Bering Sea. Important recoveries included the first recovery of a maturing sockeye from the south-central Alaska, which had been tagged in the Bering Sea, and the first DST from a salmon from the north coast of the Sea of Okhotsk (Walker et al. 2004). Plots of the temperature and depth data recorded by these tags are shown in Walker et al. (2004).

These recoveries provided important new time-series data showing the temperature-depth habits of maturing Russian, Japanese, and western Alaska salmon from release sites in July the central Bering Sea. These tags allow BASIS scientists to compare and infer possible differences in migration routes of Japanese and Russian fish (Walker et al. 2005). Additional discussion of tagging results is provided in Section 4 of this report.

4. Review of Historical Data on Salmon Distribution, Migration, and Interceptions in the Bering Sea

An issue of major concern to western Alaska salmon fishermen is whether climate-induced changes in ocean conditions or ocean fisheries or both are contributing to unexpected fluctuations in the abundance of adult salmon returns (e.g., AYK SSI 2006). Climate-induced effects on ocean conditions can have direct effects on salmon survival (e.g., lethal sea temperatures) or indirect effects on their distribution, migration patterns, and trophic interactions (e.g., shifts in the distribution, timing, and peak density or biomass of prey, predators, or competitors) or both. Because ocean distribution and migration patterns (horizontal and vertical) and trophic interactions of salmon vary by life history stage, a single climatic event can have varied or even opposite effects on different size (age) and maturity stages of fish from the same population. In turn, climate-induced ontogenetic effects on population structure and trophic dynamics can be modified by fishing mortality (for example size-selective removals of salmon by non-target fisheries). Ocean interceptions of western Alaska salmon occur in commercial salmon fisheries, e.g., the False Pass Fishery (Area M, South Alaska Peninsula; Seeb et al. 2004), as well as in commercial fisheries targeting other species, e.g., bycatch of western Alaska Chinook and chum salmon by groundfish fisheries in the Bering Sea (e.g., Myers and Rogers 1988; Patton et al. 1998; Wilmot et al. 1998). Since the inception of the NPAFC, interceptions of western Alaska salmon by foreign fisheries in international waters of the North Pacific Ocean and Bering Sea have not been considered a problem. However, new results from BASIS show that distribution and abundance of western Alaska salmon in the northwestern Bering Sea (inside the Russian EEZ) is more extensive than previously known (e.g., Bugaev 2005; Habicht et al. 2005), which underscores the need to continue to evaluate the potential effects of distant water fisheries on western Alaska salmon survival.

To understand the effects of fishing and climate-induced changes in ocean conditions on western Alaska salmon, we first need to know when and where salmon migrate in the ocean. Historical research related to high seas salmon driftnet fisheries and various other ocean interception fisheries has yielded data on the ecology and biology of salmon in the North Pacific Ocean since the mid-1950s. Much of the early research in the mid-1950s by INPFC member nations was simply to ascertain the range limits and migration routes of the different species of Pacific salmon (Jackson and Royce 1986). Since then, many scientific field investigations have provided additional information on ocean distribution, migration patterns, abundance, and stock origins of salmon. Data acquired by numerous researchers pursuing different lines of research have been combined to show oceanic distribution and relative abundance of salmon. However, these data were collected over many years with a variety of different types of fishing gear (e.g., purse seines, gillnets, longlines, surface trawls), and distribution of fishing effort in the Bering Sea has been spotty. The majority of this historical research occurred in summer and fall, and information from other seasons is much less extensive. Additional historical data are limited to the times and areas of intensive coastal and high seas commercial fisheries for salmon and other species.

Accurate methods are needed to identify the natal region or population of origin of salmon in mixed-stock ocean catches. Successful methods have included physical tags (disk, coded wire), thermal marks on otoliths, natural tags (parasites, otolith trace-elements, etc.), and genetics (e.g., Myers et al. 2004c). Among these techniques, genetics is fast becoming the technique of choice. Recent advances in genetic techniques have increased our knowledge of salmon population structure in the Bering Sea. A comprehensive genetic (allozyme) baseline has been developed for chum salmon, and BASIS research is contributing to further development and application of comprehensive DNA baselines to identify of salmon migrating in the Bering Sea.

In this section of our report, we review historical information on salmon distribution, migration, and interceptions in the Bering Sea. Data on salmon distribution and relative abundance were taken from published scientific literature, processed agency reports, and databases maintained and updated annually with new information by the SAFS's High Seas Salmon Research Program. These databases include the high seas tag (1956-present) and coded-wire tag (1981-present) recovery databases and high seas research and fishery catch and effort data files (1955-present). Additional unpublished data on salmon in the Bering Sea have been provided by the Fisheries Agency of Japan, Russia's Pacific Research Institute of Fisheries and Oceanography (TINRO-Center), and the U.S. National Marine Fisheries Service. Material has also been extracted from International North Pacific Fisheries Commission (INPFC) and NPAFC documents submitted by the Contracting Parties (Canada, Japan, Russia, and the United States). Methods for estimating distribution, migration patterns, and stock composition are described in cited references. Freshwater and ocean age designation for salmon follows the European formula (Koo 1962). In this notation, a number preceding a dot is the number of years (winters) that the fish spent in freshwater, and a number following a dot is the number of years spent in the ocean. For example, an age-1.4 Chinook salmon spent one year in freshwater and four years in the ocean. All salmon in the ocean are assigned the same birthday, that is, all fish become one year older on January 1. We followed the definitions for salmon life-history and maturity stage established in previous reviews, that is, a "juvenile" fish is in its first ocean year (ocean age-.0), an "immature" fish is in its second or subsequent ocean year (ocean age-.1 or older) but not its last ocean year, and a "maturing" fish is in its last ocean year. Portions of our review have already been published in the peer-reviewed scientific literature (Brodeur et al. 2003; NRC 2005) or have been accepted for publication.

Overview Distribution and Migration Patterns of Salmon in the Open Ocean

A major premise of our review is that Pacific salmon in the open ocean have stock-specific distribution and migration patterns. This is not a new idea, e.g., Moiseev (1956) may have been one of the first scientists to publish scientific evidence that the marine habitats of individual stocks of salmon are located in specific areas of the open ocean. Recent genetic work has revealed a strong hierarchical geographic structuring of genetic variation in freshwater habitats that descends from the largest scale, i.e., major (ancestral) geographic lineages, to regional geographic subdivisions, to individual subbasins, and to life-history subdivisions within these subbasins (Utter et al. 1989; see review by Williams et al. 2006). Similarly, we hypothesize that distribution patterns of salmon populations in the open ocean also have a hierarchical geographic structure, i.e., stocks that are genetically similar or geographically adjacent to each other in freshwater or both have ocean distribution and migration patterns that are more similar to each other than populations that are genetically or geographically distant. Individual populations or life-history variants within these populations usually occupy only a portion of the entire oceanic range occupied by higher levels, e.g., regional stock complexes.

At the largest spatial scale, Pacific salmon species migrating in open waters are distributed primarily in the region north of the Subarctic boundary (Fig. 8). Pearcy (1992)

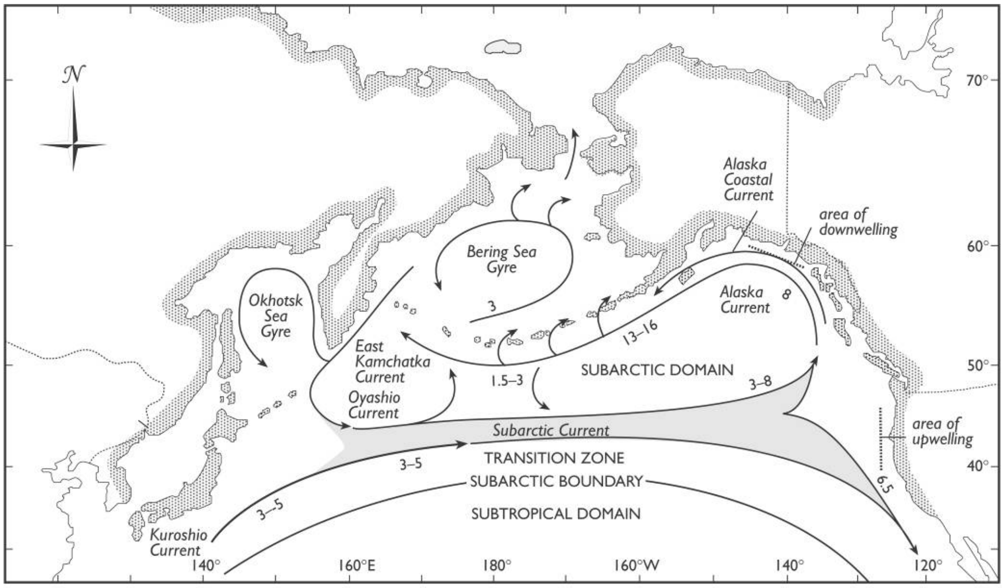


Fig. 8. Map showing ocean domains and major currents in the North Pacific Ocean and Bering Sea (numbers indicate approximate current speeds in km/d). Source: Quinn 2005.

hypothesized that the evolutionary "divergence of North Pacific salmonids and their emergence as successful and abundant fishes is related to the formation of the cold Subarctic Water Mass in the North Pacific." Across this immense marine region, the known ranges of salmon encompass all major oceanic currents and domains (Fig. 8). Marine habitat conditions (e.g., sea temperatures and salinities) within acceptable limits for salmon, however, can sometimes extend south of the Subarctic boundary, which expands their known open ocean range into subtropical waters.

A general seasonal model of the open ocean distribution of immature and maturing Pacific salmon is that in winter and spring they are distributed primarily south of the Commander Islands-Aleutian Islands chain in the North Pacific Ocean, and in summer and fall they are widely distributed throughout the North Pacific Ocean and Bering Sea (Fig. 9). There are major exceptions to this general model, e.g., the Bering Sea is a major winter habitat for populations of Chinook salmon from throughout their freshwater range (e.g., Radchenko and Glebov 1998a,b; Myers and Rogers 1988).

During their first year in the ocean, there is apparently little or no intermingling of juvenile Asian and North American salmon. Although data are limited, most juvenile pink, chum, and sockeye salmon apparently move from relatively shallow, coastal waters to surface waters over the deep ocean basins in late fall or early winter (e.g., Hartt and Dell 1986; see recent national reviews of the early marine period, NPAFC 2003). Possible exceptions are Russian and western Alaskan stocks of juvenile salmon, which may intermingle during their first summer and fall in the northeastern Bering Sea (Farley et al. 2005).

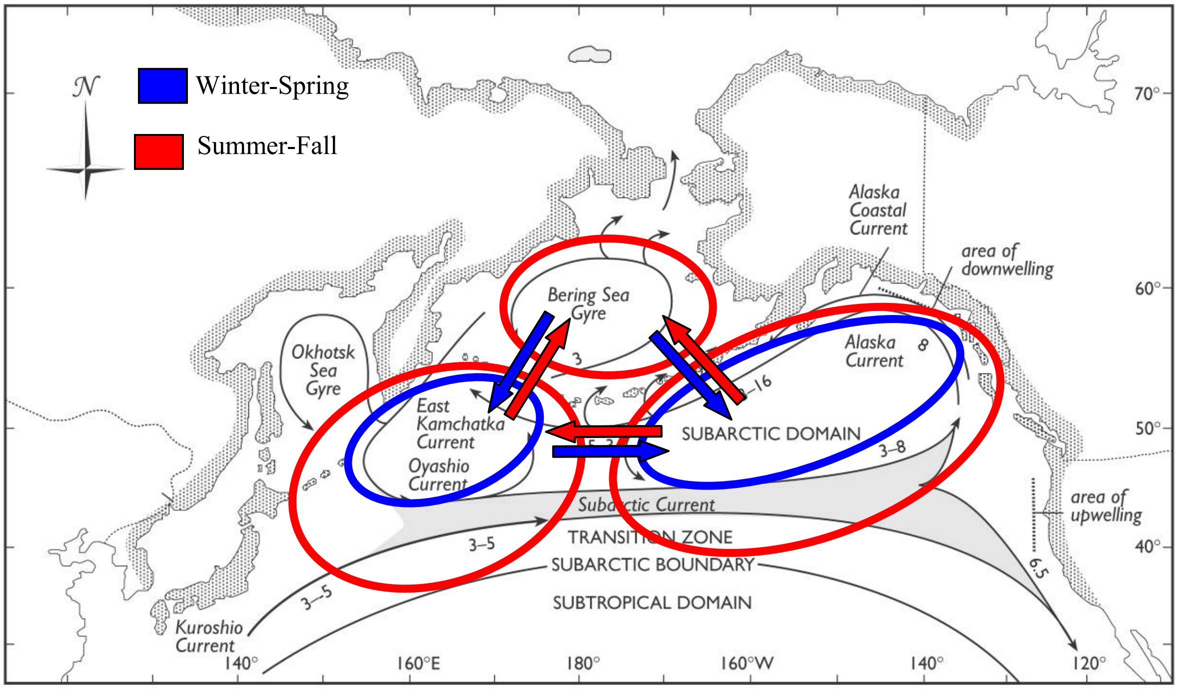


Fig. 9. A general conceptual model of seasonal distribution and movements of Pacific salmon in the open ocean. Salmon are distributed in both the Bering Sea and North Pacific Ocean in summer and primarily in the North Pacific Ocean in winter. The general patterns of movement of immature salmon are to the south or east or both in winter and spring (blue arrows) and to the north or west or both in summer and fall (red arrows). Base map source is Quinn (2005).

At the scale of major geographical lineages or continent-of-origin and regional stock complexes, open ocean distributions of immature and maturing Asian and North American are frequently depicted by composites of recovery data from INPFC/NPAFC-coordinated high seas salmon tagging experiments (e.g., French et al. 1975; Myers et al. 1990, 1996; Klovach et al. 2002; Beamish et al. 2005). These data indicate that Asian stocks are distributed primarily west of 180°, and North American stocks are distributed primarily east of 180°. The apparent areas of mixing of immature and maturing Asian and North American salmon in the open ocean vary by species, and are largest for chum salmon (174°E-140°W, 44°N-61°N), smaller for pink salmon (between 175°E and 160°W, 44°N-57°N), and least for sockeye salmon (165°E-175°W, 45°N-58°N) (Fig. 10). Between-species differences in areas of mixing seem to be positively correlated with their relative abundance in the open ocean. For example, chum salmon spend multiple years in the open ocean (as many as 5 winters), are more abundant, and have a larger area of mixing than pink salmon, which spend only 1 winter in the ocean. Differences in the east-west extent of distribution also seem to be positively correlated with the relative abundance of Asian and North American salmon. For example, Asian pink and chum salmon are more abundant and have a more extensive east-west range than North American pink and chum salmon (Fig. 10). Similarly, North American sockeye salmon

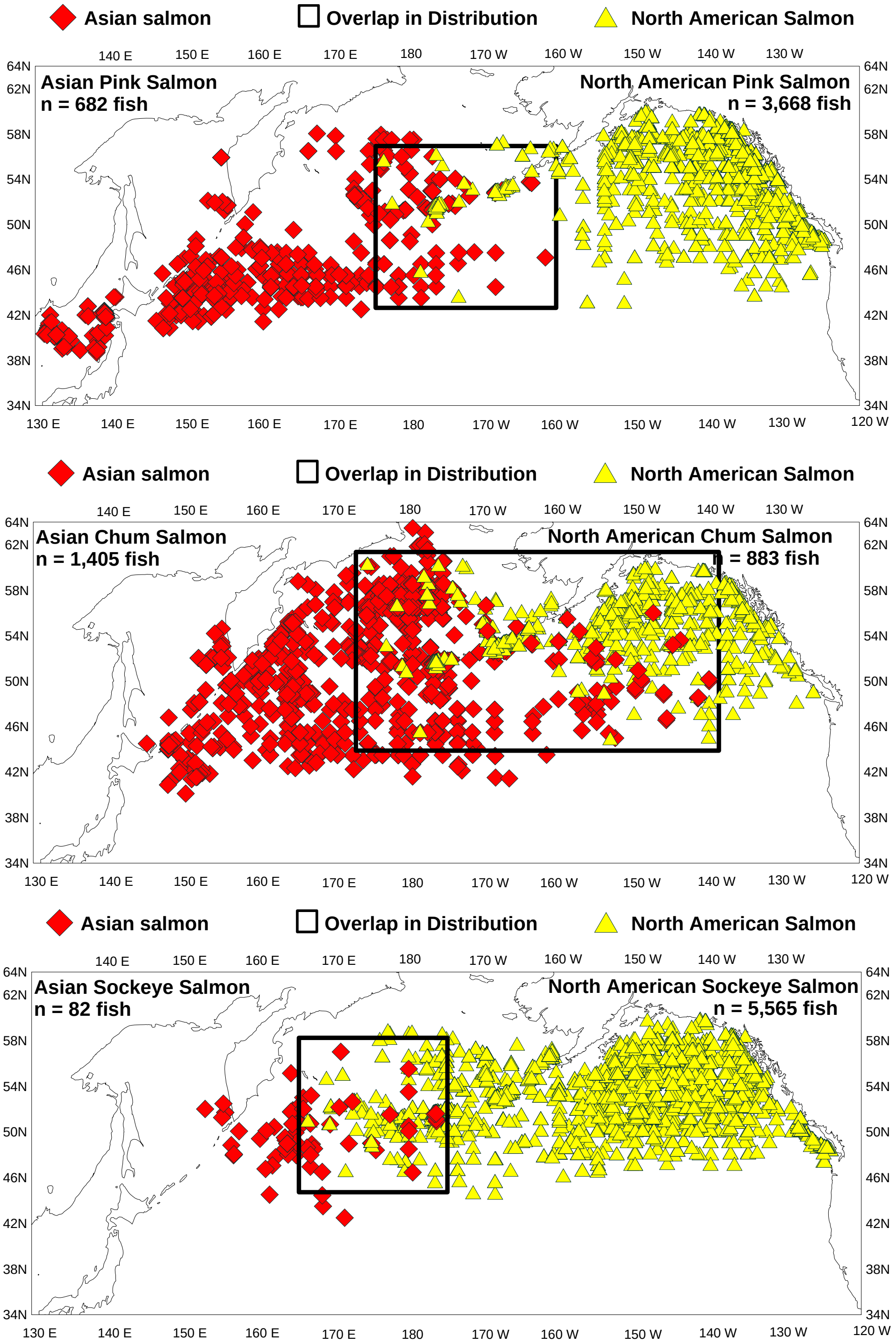


Fig. 10. Composite map showing overlap in open ocean distributions of Asian and North American pink (top), chum (center), and sockeye (bottom) salmon as shown by high seas tagging experiments (1956-2004). Closed (red) diamonds = Asian stocks; Closed (yellow) triangles = North American stocks, open box = region of overlap. Data source: High Seas Salmon Research Program, Univ. Wash.

are more abundant and have a more extensive east-west range than Asian sockeye salmon (Fig. 10).

Asymmetrical distributions of Asian and North American salmon in the open ocean might reflect density-dependent interactions, as explained by the theoretical concept of “ideal free distribution” (Fretwell and Lucas 1970), i.e., as competitive interactions increase with increasing abundance of salmon, their geographic distribution increases until it reaches a new equilibrium. Ogura and Ito (1994) suggested that large-scale releases of hatchery chum salmon in Japan were accompanied by an expansion in their known ocean range. To detect stocks at the limits of their geographic range, however, might simply be easier when they are abundant. Asymmetrical distributions of Asian and North American salmon in the open ocean have also been attributed to physical oceanic factors, such as cold winter sea temperatures in the western North Pacific (e.g., Shepard et al. 1968; Neave et al. 1976) or passive (eastward) transport of immature Asian fish by wind-driven and geostrophic currents (Ueno et al. 1999; Azumaya and Ishida 2004).

Distribution and Migration of Juvenile Salmon on the Eastern Bering Sea

In western Alaska, timing of juvenile salmon movements to coastal marine waters corresponds to spring ice breakup in rivers and peak water temperatures along migration corridors (e.g., Straty 1974). At ocean entry, small juvenile salmon typically are distributed in shallow, littoral habitats (beach areas between low and high tide). As summer progresses and fish grow, juvenile salmon move to neritic habitats (shallow, pelagic areas near shore or over a continental shelf, from low-tide mark down to a depth of about 200 m). The extent of distribution of juvenile salmon over and beyond the continental shelf varies regionally, annually, seasonally, and by species and stock (e.g., Straty 1981; Straty and Jaenicke 1984; Hartt and Dell 1986). Vertical distribution of juvenile salmon in neritic habitats is influenced by biotic (species, age, size, forage location) and abiotic (water temperature, salinity, season, light, turbidity, currents, tides, and bottom topography) factors. Seasonal habitat use is linked to species, stock, water temperature, and zooplankton distribution.

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

In the southeastern Bering Sea, pioneering research in 1956-1970 by the Fisheries Research Institute (FRI), University of Washington, sampled juvenile salmon using purse seine gear (Hartt 1980; Hartt and Dell 1986). Most of the catch was sockeye salmon collected between 18 and 54 km offshore. The Auke Bay Laboratory (ABL), Alaska Fisheries Science Center, U.S. National Marine Fisheries Service (NMFS), conducted research on the distribution and migration of juvenile sockeye salmon in Bristol Bay during 1966-67 and 1969-72 (Straty 1974; Carlson 1976; Straty and Jaenicke 1980; Straty 1981). The surveys were conducted using purse seines and occurred within inner Bristol Bay east of Port Heiden and along the coast of the Alaska Peninsula west of Port Heiden (outer Bristol Bay). In addition to purse seining, some environmental (sea temperature and salinity) and biological (zooplankton) sampling took place at selected stations throughout the survey area.

The results of these early studies indicated that juvenile sockeye salmon from all river systems entering Bristol Bay follow the same southwesterly seaward migration route along the coast of the eastern Bering Sea (Straty 1974; Straty and Jaenicke 1980; Straty 1981; Hartt and Dell 1986; Isakson et al. 1986). Bristol Bay sockeye salmon usually spend 1 or 2 years in freshwater before migrating to the ocean. Sockeye smolts (approximately 4-15 g in weight) leave freshwater rearing areas from mid May to mid July. The seasonal timing of smolt outmigration can be influenced by annual differences in environmental conditions, such as time of ice breakup on lakes and anomalously cold sea temperatures. For example, during 1971, a year characterized by anomalously cold sea temperatures from spring through fall, juvenile sockeye salmon were virtually absent in outer Bristol Bay in early July; whereas, they were abundant in this area during 1967, a year with warm spring through fall sea temperatures. The migration rate of juvenile sockeye salmon through inner Bristol Bay is rapid, whereas their migration rate slows once they entered outer Bristol Bay, presumably due to increased food resources encountered in this region. In general, movements from the river mouths are nearshore along the southeast and south side of Bristol Bay to Port Moller, and offshore beyond Port Moller. Tidal currents influenced direction of movement, which was variable (Hartt and Dell 1986). Migration routes through Bristol Bay corresponded to areas with the steepest salinity gradients (Straty 1974; Straty and Jaenicke 1980; Straty 1981). Juvenile sockeye salmon were most abundant at or near the surface (upper 1 m at night, 2-m depth during the day; Straty 1974), and were scarce or absent in summer (June-October) sampling in neritic waters off the Aleutian Islands (Hartt and Dell 1986).

Historical data indicated that throughout much of the summer juvenile sockeye salmon were concentrated in schools around the perimeter of Bristol Bay and along the north side of the Alaska Peninsula (most within 93-111 km of shore; Hartt and Dell 1986). The southwestward extent of distribution of juvenile sockeye salmon along the north side of the Alaska Peninsula in July, August, and September might be influenced by sea temperatures, with fish moving farther southward (west of Port Moller) earlier in the year in warm years (Straty and Jaenicke 1980; Hartt and Dell 1986; Isakson et al. 1986). In July, juvenile sockeye salmon were caught only in waters with SSTs warmer than 6°C, northeastward of Port Moller. By September, waters had warmed and the largest concentrations of juvenile sockeye salmon were offshore, west of Port Moller.

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

Historical marking studies indicate some separation in major stocks of juvenile Bristol Bay sockeye salmon as far seaward as Port Moller (Straty 1974). Factors that may contribute to stock-specific distributions include differences in time of outmigration, travel distance from the lake system of origin, age, and size. Annual variation in time of outmigration is caused by time of ice breakup, water temperature, and wind action in nursery lakes. All Bristol Bay stocks have early, middle, and late components, but the average time of outmigration is earliest for Ugashik and Egegik smolts intermediate for Kvichak (later in cold than in warm years), and latest for Naknek and Wood River smolts (Rogers 1988). There is substantial annual variation in the abundance and distribution of sockeye salmon juveniles in Bristol Bay on a given date, which is caused by annual variation in smolt production and migration timing in each lake system and spring weather conditions that affect the beginning of outmigration (Rogers 1977). Because of differences in migration timing, the distributions of Egegik and Ugashik smolts may not overlap those of the majority of smolts from the Naknek and Kvichak rivers, and may be well separated from the Nushagak stocks, and the separation may be greater in cold years because of greater delay in Kvichak and Wood River migrations (Rogers 1988). For example, Ugashik or Egegik River smolts may arrive at the outer boundary of Bristol Bay in mid-July, whereas Wood River fish may not arrive at there until the end of September (Bax 1985; Rogers 1988). By the time they reach Port Moller juvenile Bristol Bay sockeye salmon stocks may be well mixed. Estimated travel rates of Bristol Bay sockeye salmon juveniles in the Bering Sea between Port Moller and Unimak Island (3.9-6.7 km d^{-1}) are slower than those of British Columbia stocks migrating northward in the Alaska coastal current (Skeena River - 6.5-13.9 km d^{-1}; Fraser River - 14.1-26.7 km d^{-1}; Hartt and Dell 1986).

Hartt and Dell (1986) provided limited information on the distribution of other species of juvenile salmon in the eastern Bering Sea and Aleutian Islands. Most of their sampling was done from late June to September 1964-1968 in neritic waters beyond the 46-m depth contour with fine-mesh purse seines. Pink and chum salmon fry (less than 1 g in weight) begin to migrate into Bristol Bay in July (Rogers 1977). Hartt and Dell (1986) had only small catches of juvenile chum salmon in July in the eastern Bering Sea and Aleutians, which were probably composed of local stocks, and their catches increased in August in the eastern Bering Sea. Pink salmon juveniles were scarce or absent in their catches throughout the region. Juvenile coho were caught in small numbers in the eastern Bering Sea in July, August, and September. Juvenile Chinook salmon first appeared in eastern Bering Sea catches late June, and were caught in all subsequent time periods. The westernmost catches of juvenile Chinook salmon were south of the central Aleutian Islands during July. Data were inadequate for inferring migration patterns between juvenile and age-.1 stages, but indicated that western Alaskan stocks migrated farther offshore in than stocks from other North American production areas to the south. The mixing of juvenile (age-.0) and immature age-.1 Chinook salmon in both coastal and offshore waters appeared to be unique compared to other Pacific salmon species. There was no evidence of overlap in distribution of Bering Sea and Gulf of Alaska salmon stocks at the juvenile stage for any species. The direction of local movements of all species of salmon juveniles in the eastern Bering Sea was variable, apparently influenced by strong tidal currents and rich feeding conditions. There are no reported catches of steelhead (*O. mykiss*) juveniles in the eastern Bering Sea and Aleutian Islands, although steelhead populations occur in some streams along the north side of the Alaska Peninsula and eastern Aleutian Islands (see review by Burgner et al. 1992).

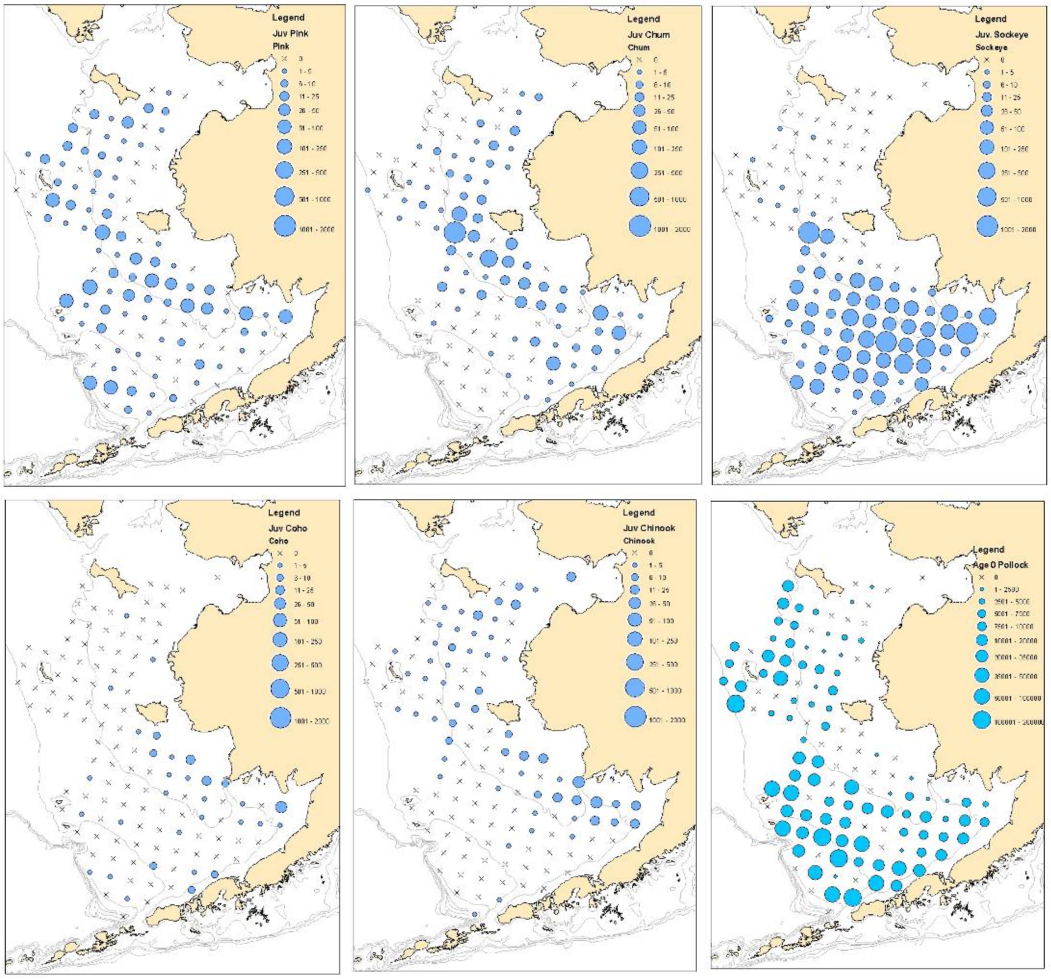


Fig. 11. Distribution of juvenile pink (top left), chum (top center), sockeye (top right), coho (bottom left), and Chinook (bottom center) salmon, and age-0 walleye Pollock, which are a major component of juvenile salmon diets, in research trawl catches in the eastern Bering Sea in fall 2005. Graduated circles show catch per unit effort at trawl stations. Crosses indicate no catch. (Source: Ocean Carrying Capacity program, Auke Bay Laboratory, Alaska Fisheries Science Center, http://www.afsc.noaa.gov/ABL/occ/basis.htm).

The Ocean Carrying Capacity (OCC) program of ABL/NMFS initiated research in 1999 to investigate the effects of climate on growth, migration, and distribution of juvenile salmon in the eastern Bering Sea. Sampling for juvenile salmon by the OCC Program was also conducted during broad-scale coastal surveys of the northeastern North Pacific, Gulf of Alaska, Bering Sea, and Aleutian Islands from 1996-1999. The results of OCC research in the eastern Bering Sea in July-October indicates substantial annual, seasonal, and spatial variation in distribution by species and life history stage of juvenile chum, pink, coho, and Chinook salmon (Farley et al. 1999, 2000a, b, 2001, 2002, 2003, 2004, 2005). In the eastern Bering Sea, juvenile coho and Chinook salmon tend to be distributed nearshore, rather than in deeper offshore waters (Farley et al. 2005; Fig. 11). Farley et al. (2005) hypothesized that juvenile Yukon River Chinook salmon migrate in a southwesterly direction along the western Alaska coastline. In addition, juvenile pink salmon body size and distribution data indicate the presence of Russian pink salmon juveniles in offshore areas of the northeastern Bering Sea region (Farley et al. 2005). No juvenile salmon were caught during extensive research trawl surveys in neritic waters of the Aleutian Islands in July-August 1996-1997 (Carlson et al. 1996; 1997).

There is a strong relation between early marine distribution, growth, and survival of juvenile salmon. Results of both historical and recent studies indicate that distribution patterns of juvenile salmon are closely associated with the distribution of their prey (e.g., Fig. 11). When prey resources are abundant, high growth rates of juvenile salmon are associated with high (non-lethal) sea temperatures. As juvenile salmon grow, they move farther away from shore and the points of ocean entrance; they are better able to avoid fish, bird, and marine mammal predators; and they can feed on a greater diversity and size range of prey. Climate-induced variation in ocean conditions affects the carrying capacity of juvenile salmon in the eastern Bering Sea. Cold spring temperatures in 1999 might have reduced carrying capacity in the eastern Bering Sea, resulting in poorer than expected returns per spawner in subsequent years. Climate-change events are chaotic and cannot be predicted with a high degree of certainty. Thus, long-term field monitoring programs are needed to accurately forecast interannual variation in the early marine survival of juvenile salmon in the eastern Bering Sea.

Distribution and Migration of Juvenile Salmon on the Western Bering Sea

Karpenko (2003) reviewed Russian marine investigations of juvenile Pacific salmon in the western Bering Sea. Fall (August-November) stock assessment surveys of juvenile salmon in the southeastern Bering Sea using small mesh driftnets began in 1960. Since 1981 pelagic trawls have been use at a standard pattern of stations. A special pelagic trawl (54.4/192 m; 25-30 m vertical opening) developed specifically to catch juvenile salmon has been used since 1985. Abundance estimates of juvenile pink salmon from annual trawl surveys are used to correct commercial forecasts 8-9 months prior to fishing.

Karpenko and Smorodin (2001) used the results of surveys from 1981 to 2000 to describe the distribution and migration routes of juvenile pink and chum salmon in the western Bering Sea. The intensity of the East Kamchatka Current and annual water heating budgets (warm years vs. cold years) influence the food supply and distribution of juvenile salmon in this region. Migratory activity is regulated by feeding behavior. In years when the Kamchatka Current is less intense, juvenile pink salmon are distributed farther to the east and begin their offshore feeding migration earlier. Juvenile chum salmon enter the Bering Sea later than pink salmon and are distributed over a less extensive area (within 60 nm of shore). In fall, juvenile pink salmon move offshore from northeastern Kamchatka in wide fronts (Shuntov 1994), migrating along one or two southeastward routes and a third route used by the smallest fish along the east Kamchatka coast (Smorodin et al. 2001). Juvenile chum salmon start their offshore migration later and at cooler water temperatures than pink salmon, and their migration routes are located closer to shore (Karpenko and Smorodin 2001). Migration routes of juvenile chum salmon in the northwestern Bering Sea vary between cold years (southward) and warm years (eastward) (Karpenko and Smorodin 2001).

Distribution and Migration of Immature and Maturing Salmon in the Eastern Bering Sea

Historical research on the distribution and migration patterns of salmon in the eastern Bering Sea focused largely on determining coastal distribution and movements of juvenile and adult Bristol Bay sockeye salmon in spring and summer (see review by Burgner 1991). Data from historical research vessels surveys in the eastern Bering Sea are insufficient to describe seasonal distribution and migration patterns of immature and maturing salmon. Winter and early spring are likely the most critical survival periods. Data from U.S. research in the 1960s indicated that some immature and maturing sockeye salmon overwinter in the Bering Sea, but the main concentrations of salmon in winter are probably in the subarctic North Pacific waters south of the Aleutian Islands and Alaska Peninsula and in the Gulf of Alaska (French et al. 1976). Annual variation in winter conditions in the eastern Bering Sea and Gulf of Alaska might cause substantial shifts the distribution of salmon over this vast oceanic region. Decadal-scale cyclic fluctuations in abundance of salmon returning to different coastal regions are related to large-scale oceanographic and meteorological events (for example, Francis and Hare 1994, Mantua et al. 1997). We do not know if there have been changes in offshore distribution and migration patterns of immature and maturing salmon in the eastern Bering Sea since the well-documented 1976-77 climate regime shift, because there were few Japanese research vessel surveys for salmon in this area after 1978. The geographically extensive Great Pacific salmon surveys (1996-1999) by the OCC Program, ABL/NMFS, focused primarily on learning more about juvenile salmon distribution in areas south of the Aleutian Islands, Alaska Peninsula, and Gulf of Alaska (Carlson et al. 1996, 1997, 1998). However, during one survey in late April-early May 1998, large aggregations of immature (20-30 cm FL, ocean age .1) sockeye salmon were caught within 6 nmi of shore in the southeastern Bering Sea off the north side of Unimak Island, indicating that they might have overwintered in the Bering Sea. The OCC Program trawl surveys in the eastern Bering Sea (1999-present), which also focus on juvenile salmon research, have provided some new data on distribution of immature and maturing salmon on the eastern Bering Sea shelf in summer and fall (Farley et al. 1999; 200a,b; 2001; 2003; 2004; 2005; e.g., Fig. 12).

Since the early 1980s, recoveries of coded-wire tagged salmon, primarily by U.S. groundfish fishery observers, have provided some useful new information on stock-specific distributions of immature and maturing chum, coho, and Chinook salmon in the eastern Bering Sea (e.g., Myers et al. 2005, Fig. 13). Recoveries indicate that juvenile, immature, and maturing western Alaska (Yukon River) Chinook salmon overwinter in the eastern Bering Sea, and that the ocean ranges of British Columbia chum and coho salmon and most southern regional stocks of Chinook salmon also extend into the southeastern Bering Sea.

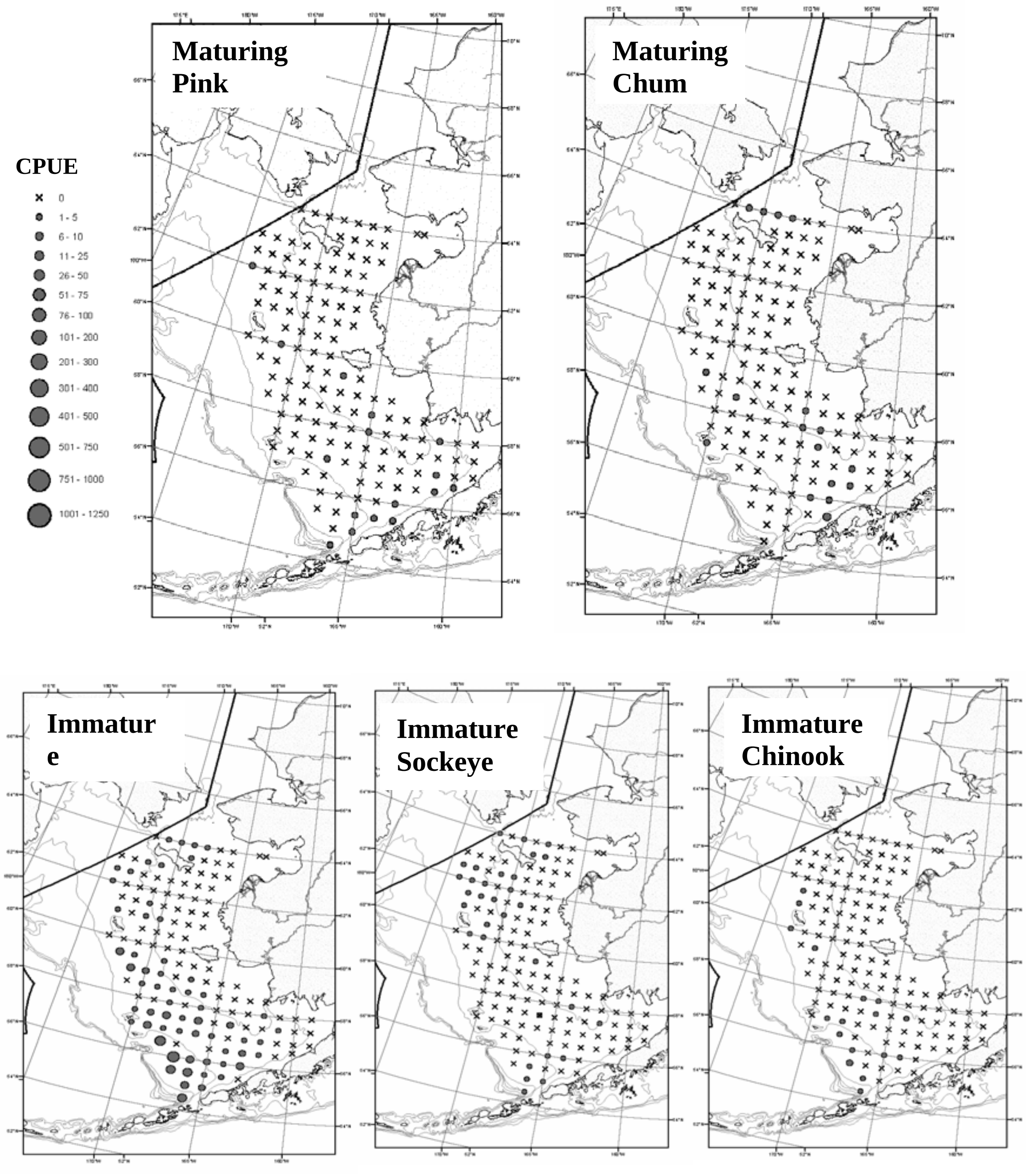


Fig. 12. Distribution (shown by graduated symbol of catch per unit effort) of immature and maturing pink, chum, sockeye, and Chinook salmon during the August 11-October 3, 2004 (OCC/BASIS research trawl cruise in the eastern Bering Sea. Crosses indicate locations sampled, but no fish of this species and maturity group were caught. (Source: Ocean Carrying Capacity program, Auke Bay Laboratory, Alaska Fisheries Science Center, http://www.afsc.noaa.gov/ABL/occ/basis.htm).

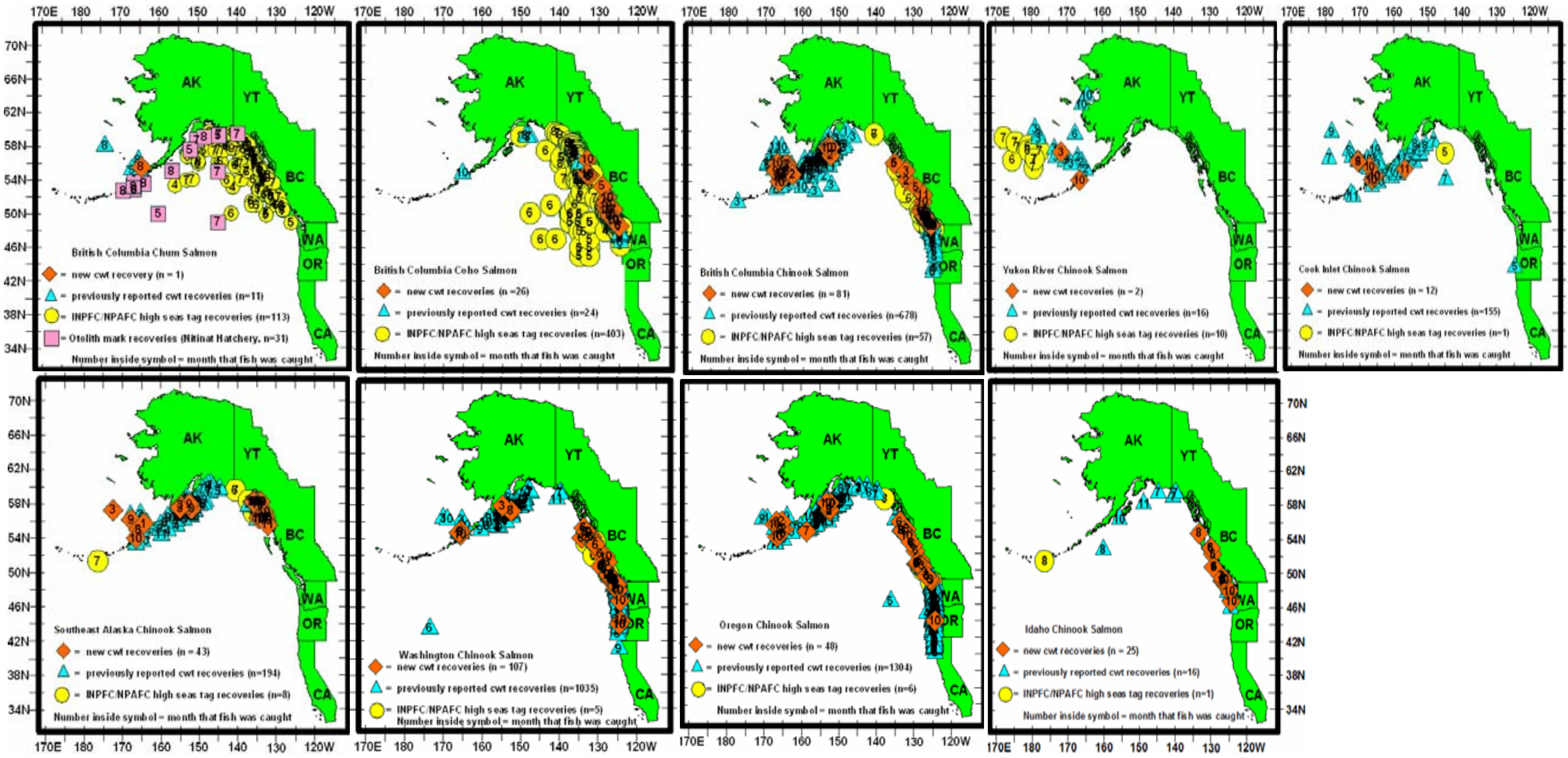


Fig. 13. Stock-specific ocean distribution of immature and maturing salmon in the Bering Sea and North Pacific, as shown by recoveries of coded-wire tags (CWT), high seas tags, and otolith marks, 1956-2005 (Myers et al. 2005). New recoveries in 2005 are indicated by a closed (orange) diamond. Recoveries of otolith-marked immature and maturing British Columbia chum salmon (Nitinat Hatchery, Vancouver Island) in 1997 and 1998 were reported by Farley and Munk (1998), Carlson et al. (2000), and Urawa et al. (2000). An additional 38 recoveries of otolith-marked British Columbia chum salmon in the 1994-1996 Bering Sea walleye pollock (*Theragra chalcogramma*) trawl fishery, reported by Ignell et al. (1997), are not shown. Processing plant recoveries of CWT fish are not shown. AK=Alaska, YT=Yukon Territory, BC=British Columbia, WA=Washington, OR=Oregon, CA=California.

Distribution and Migration of Immature and Maturing Salmon in the Central Bering Sea

Japanese research gillnet surveys provide the most comprehensive historical data on the spatial and temporal distribution of immature and maturing salmon in the central Bering Sea in late spring and summer (Figs. 14-17). In June through August, the average catch per unit effort (CPUE) of maturing pink salmon is highest in the western North Pacific, reflecting the highly abundant populations of Russian pink salmon distributed in this region (Fig. 14). In the central Bering Sea, where the distribution of Asian and North American stocks overlaps (Fig. 10), average CPUEs increase from June to July. By August, most maturing pink salmon have returned to coastal areas (Fig. 14). Chum and sockeye salmon distribution varies by age and maturity group (Figs. 15 and 16). In June older age groups of maturing (ages 0.3 and 0.4) and immature chum salmon (ages 0.2 and 0.3) are distributed in the Bering Sea, while young (age 0.1) immature chum salmon remain in the North Pacific (Fig. 15). In the central Bering Sea, the abundance of young immature chum salmon increases from July to August, as the abundance of maturing fish decreases. By August, the oldest (age 0.4) maturing chum salmon have left the central Bering Sea. In June most immature (ocean ages-1 and -2) sockeye salmon are distributed across a broad region of the North Pacific Ocean (Fig. 16). The abundance of immature sockeye salmon in the central Bering Sea increases in July, and their distribution shifts to the northwest in August. In June and July, the relative abundance of maturing (ocean ages-2 and -3) sockeye salmon is highest in the southeastern Bering Sea (east of 180°), reflecting abundant populations returning to Bristol Bay, Alaska. By August most maturing sockeye salmon have returned to coastal areas. In summer, maturing coho salmon (age 0.1) are distributed across the North Pacific, but they are rarely caught in the Bering Sea (Fig. 17). Chinook salmon are distributed in the Bering Sea in all seasons; however, their abundance is low compared to other species (Fig. 17).

In the 1990s, the Fisheries Agency of Japan (FAJ) occasional winter research trawl surveys in the areas where Japanese hatchery chum salmon were thought to be distributed. The FAJ surveys provided some incidental information on other species of immature and maturing salmon, but stock origins of pink, sockeye, coho, and Chinook salmon in the Japanese research vessel catches are not known except for data from a few tag returns. The February 1998 *Kaiyo maru* survey was the third winter salmon survey conducted by the Fisheries Agency of Japan in the 1990s (previous surveys were in December 1992 and January 1996), and was the first winter salmon survey in the central Bering Sea since 1964. The combined results of the three *Kaiyo maru* surveys indicate that juvenile salmon (fish in their first winter at sea) are distributed well offshore in December, and that in the western North Pacific Ocean, chum and pink salmon are more abundant in offshore waters in February than in December or January. Most of the salmon catch in February 1998 was distributed in a narrow band from 42°-45°N in the western North Pacific Ocean (at 165°E). Chinook salmon was the only species caught in the Bering Sea. There was no catch of sockeye salmon in the central Bering Sea in 1998, unlike the results of earlier studies in the 1960s. Sockeye salmon may have changed their winter distribution, or the sampling effort by the *Kaiyo maru* may have been insufficient to catch sockeye salmon. Chum salmon were not caught in the Bering Sea during the 1998 cruise, but incidental catches of chum and Chinook salmon in commercial

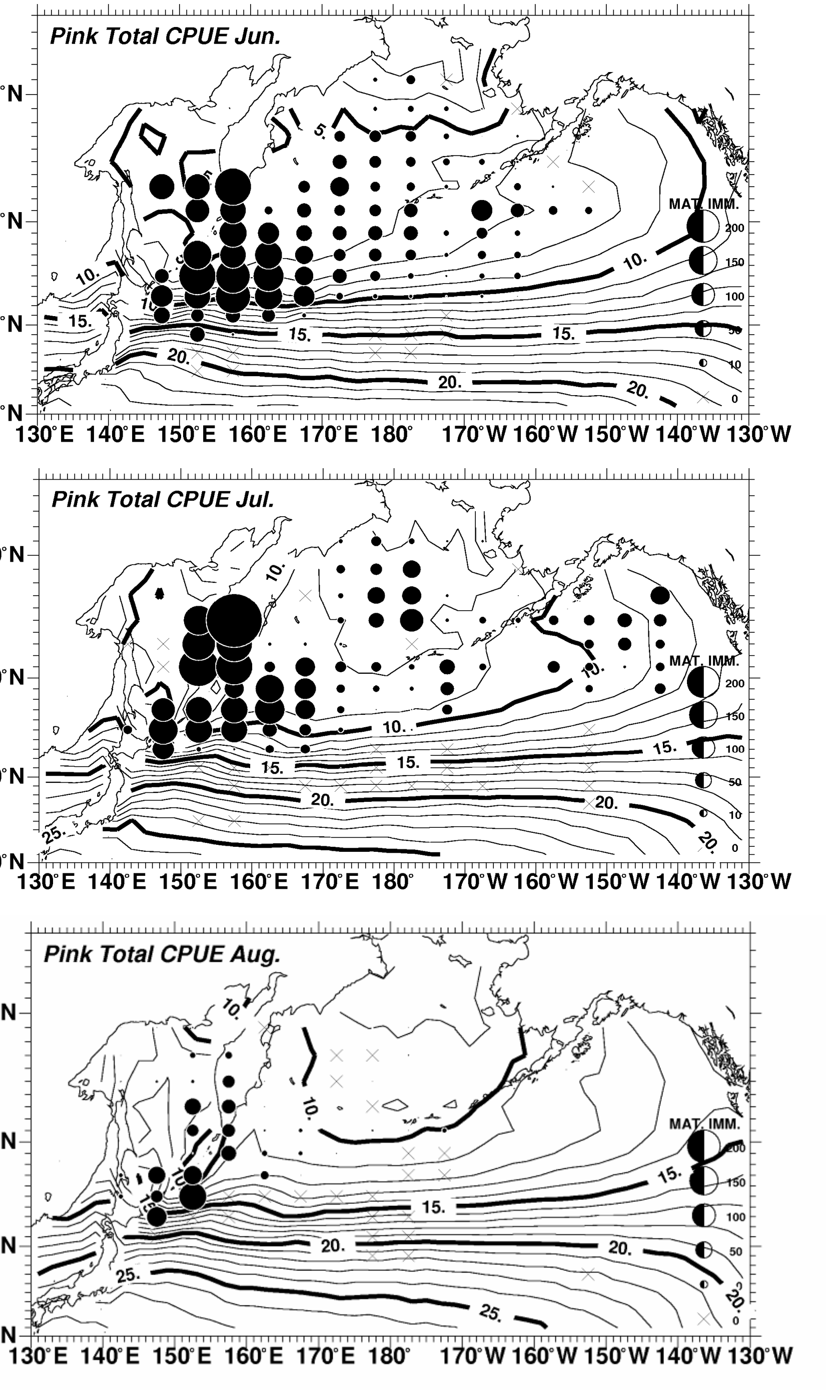


Fig. 14. Horizontal distribution of maturing pink salmon and mean sea surface temperatures (°C) in the Bering Sea and adjacent waters in June-August, 1972-2002. Graduated circles show mean catch per unit effort (CPUE) of pink salmon by Japanese research gillnets in 2° latitude ×5° longitude areas. Crosses indicate no catch. Source: Nagasawa et al. (2005); T. Nagasawa, T. Azumaya and M. Fukuwaka, Hokkaido National Fisheries Research Institute, Kushiro, Japan, pers. comm.

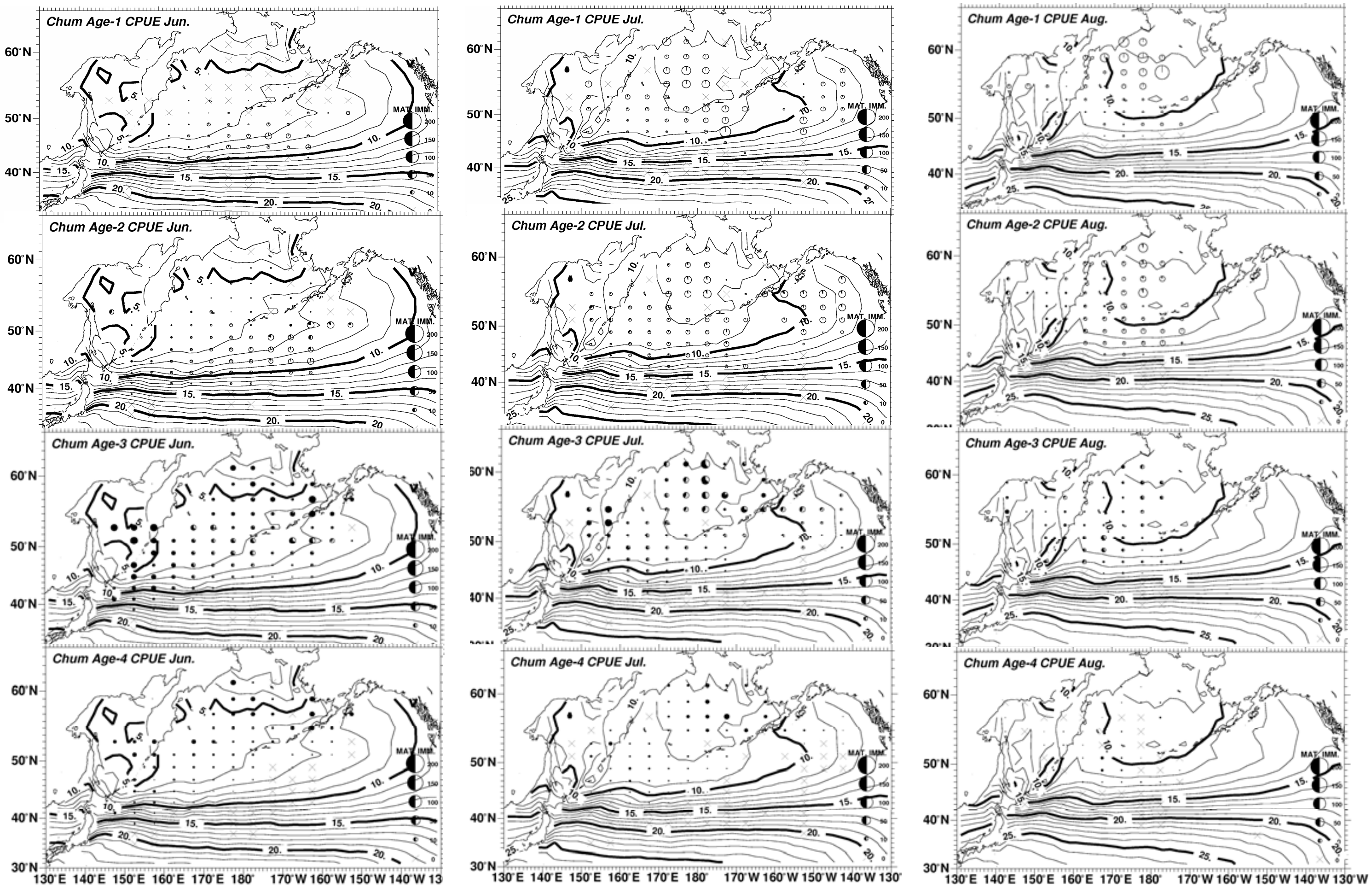
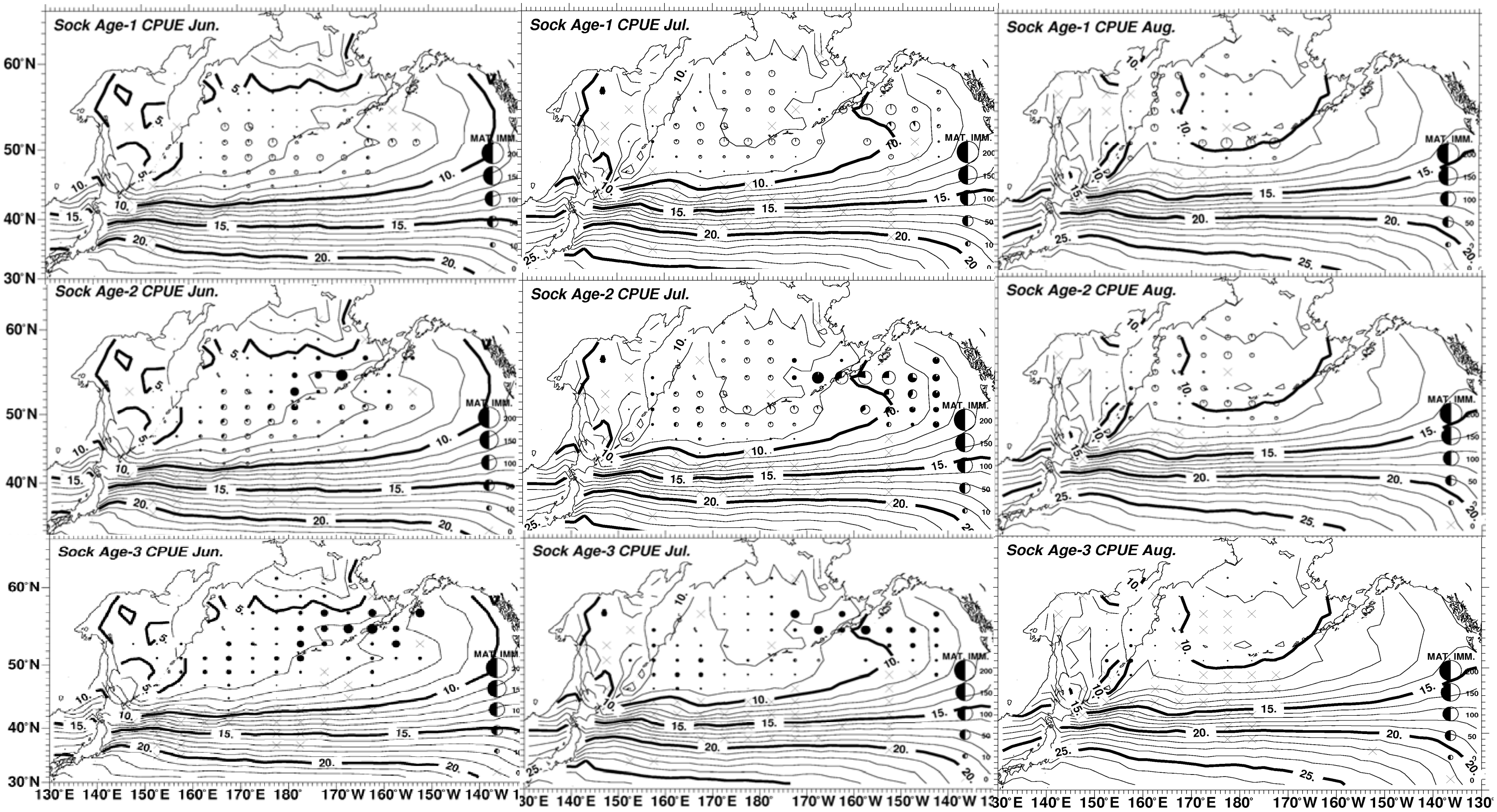


Fig. 15. Horizontal distribution of chum salmon in the Bering Sea and adjacent waters in June-August by ocean age and maturity group. Graduated circles show mean CPUE of chum salmon by Japanese research gillnets in 2° latitude ×5° longitude areas, 1972 to 2002. Crosses indicate no catch. Lines are sea surface temperature (°C) isotherms. Source: Nagasawa et al. (2005); T. Nagasawa, T. Azumaya and M. Fukuwaka, Hokkaido National Fisheries Research Institute, Kushiro, Japan, pers. comm.


Sock Age-1 CPUE Jun.

Sock Age-1 CPUE Jul.

Sock Age-1 CPUE Aug.

Sock Age-2 CPUE Jun.

Sock Age-2 CPUE Jul.

Sock Age-2 CPUE Aug.

Sock Age-3 CPUE Jun.

Sock Age-3 CPUE Jul.

Sock Age-3 CPUE Aug.

Fig. 16. Horizontal distribution of sockeye salmon by ocean age and maturity group and mean sea surface temperatures (°C) in the Bering Sea and adjacent waters in June-August, 1972-2002. Graduated circles show mean CPUE of sockeye salmon by Japanese research gillnets in 2° latitude ×5° longitude areas. Crosses indicate no catch. Source: Nagasawa et al. (2005); T. Nagasawa, T. Azumaya and M. Fukuwaka, Hokkaido National Fisheries Research Institute, Kushiro, Japan, pers. comm.

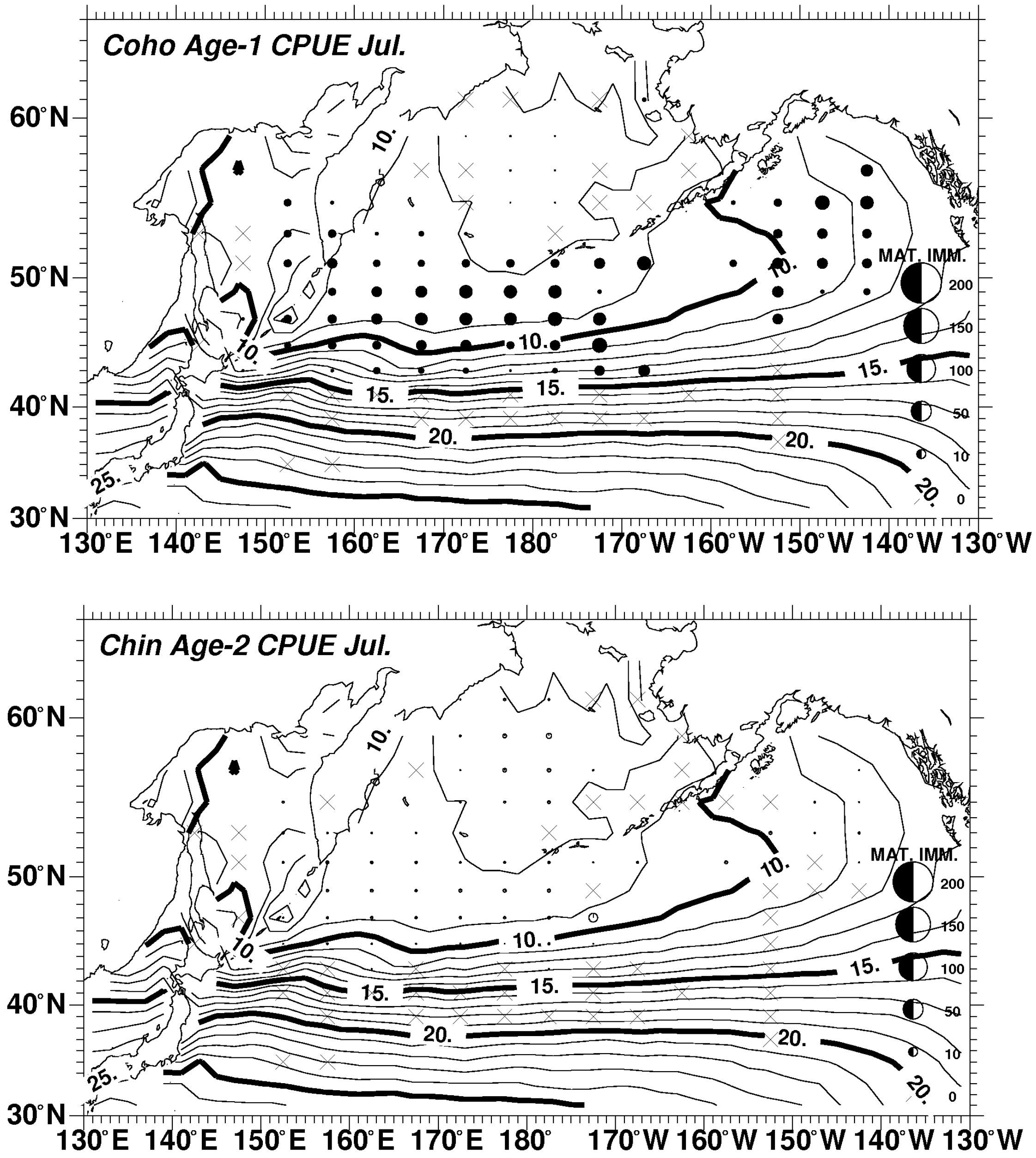


Fig. 17. Horizontal distribution maturing coho salmon (top) and immature and maturing Chinook salmon (bottom) in the Bering Sea and adjacent waters in July. Graduated circles show mean catch per unit effort (CPUE) in Japanese research gillnets in 2° latitude ×5° longitude areas, 1972 to 2002. Crosses indicate no catch. Lines are sea surface temperature (°C) isotherms. (Source: Nagasawa et al. 2005; T. Nagasawa, T. Azumaya and M. Fukuwaka, Hokkaido National Fisheries Research Institute, Kushiro, Japan, pers. comm...).

groundfish fisheries suggest that these species may reside at greater depths than were sampled during the *Kaiyo maru* survey. A detailed wintertime research trawl survey in the Bering Sea would be helpful in updating models of salmon distribution and seasonal movement.

Summer survey data from Japanese salmon research vessels show trends in sea temperatures and salmon abundance in the Bering Sea and North Pacific Ocean from 1992 to 1999 (Fukuwaka et al. 1999). In 1997, mean SSTs in the central Gulf of Alaska (12.2°C) and Bering Sea (8.41°C) were the warmest on record for the 8-year period, while SSTs in the western North Pacific Ocean (9.2°C) were the coldest since 1992 (8. 9°·C). From 1997-1999, there was a cooling trend in summer SSTs in the Gulf of Alaska and the Bering Sea that coincided with a decrease in abundance of sockeye salmon in gillnet catches in these regions and an increase in sockeye abundance in the central North Pacific. Japanese scientists speculate that cold summer SSTs in the Bering Sea and central North Pacific in 1999 might have caused a southward shift in salmon distribution. Sockeye salmon in Bering Sea and central North Pacific catches in summer are predominantly immature ages 1.1, 1.2, 2.1, and 2.2 fish. Relative abundance of immature ocean age 2.1 sockeye salmon in the central Bering Sea was extremely low in 1995, which might reflect the sharp decline in abundance of the 1991 brood year Kvichak sockeye salmon. However, the stock composition of sockeye salmon in Japanese research vessel catches was not known. There are no U.S. data showing trends in spring, fall, or winter salmon distribution in the 1990s.

Japanese research vessel catches of salmon in the Bering Sea show a tremendous amount of inter-annual variation (e.g., Ishida et al. 2002; Ishida et al. 2005; Nagasawa et al. 2005), which likely reflects changes in stock abundance and composition, distribution, migration routes, and migration timing, as well as biological responses to changes in prey abundance or distribution and physical habitat (temperature, salinity, currents, etc.). At present, however, time series of genetic stock identification data are too limited to provide detailed information on interannual variation in stock-specific distribution and migration routes in the open ocean. Perhaps, the best available genetic (allozyme) data time series is for chum salmon caught in research gillnets in the central Bering Sea in July. These data show strong odd-even year variation in research gillnet catch per unit effort (CPUE) of maturing chum salmon. This interannual variation is likely due to a density-dependent change in distribution (not survival) of chum salmon in years of high abundance of maturing eastern Kamchatka pink salmon, which have a dominant odd-year cycle in the Bering Sea in July (Azumaya and Ishida 2000; Ishida et al. 2002). However, there is no apparent relation between genetic (allozyme) estimates of the relative abundance of maturing Japanese and Russian chum salmon in research gillnet catches in the central Bering Sea in July and subsequent adult returns to Asia (commercial catch, e.g., PICES 2004).

Distribution and Migration of Immature and Maturing Salmon in the Western Bering Sea

While not a member of INPFC, the U.S.S.R. implemented an extensive program of high seas salmon research in 1954, including pioneering research on distribution, migration, abundance, stock composition, and ecology of salmon in the western Bering Sea (Birman 1958; 1985). In the early 1980s, TINRO-Center scientists pioneered the use of pelagic trawls for marine salmon surveys, and were also the first to implement integrated studies of pelagic ecosystems in the Bering Sea. TINRO-center studies focusing on the marine life of Pacific salmon began in 1991 as part of integrated pelagic ecosystem research (Shuntov et al. 1993; Radchenko and Chigirinski 1995), and this research continues to present as part of the Russian commitment to NPAFC/BASIS research.

Radchenko and Chigirinsky (1995) provide a comprehensive review of information on the distribution, migration, and trophic ecology of salmon in the western Bering Sea. They estimated that during summer and fall, salmon account for about 60% of the total biomass of epipelagic fish in the Bering Sea. Chum and pink salmon are the most abundant species of salmon in the western Bering Sea, and the relative abundance of sockeye and Chinook salmon is low. Coho salmon are relatively rare in the western Bering Sea. Maturing pink salmon are most abundant in odd-numbered years. Runs of pink salmon to eastern Kamchatka streams begin in late June and continue to mid September. Migration routes of pink salmon between the North Pacific and western Bering Sea are through Near Strait and the western and central Aleutian Islands passes. Chum salmon have the broadest distribution of all salmon species in the western Bering Sea, and are most abundant in even-numbered years. Runs of maturing chum salmon start to enter the western Bering Sea in mid May, while immature chum salmon first appear along their annual feeding migration routes in late-May to early June. By fall most large immature chum (>50 cm) migrate into the shelf zone to complete their feeding migration route, while smaller immature chum (<50 cm) remain in off –shelf waters (deep-sea zone). In fall, maturing chum salmon and the largest immatures are distributed in the coastal zone, older immature chum (age 0.2 and older) and juvenile (age-0.0 chum salmon are distributed over the outside shelf and slope, and young (age 0.1) chum salmon are distributed in offshore (deep basin) waters. Chum salmon leave the western Bering Sea by late November. Sockeye salmon are distributed along migration routes in the western Bering Sea in summer and fall. In winter and early spring (December – April) most immature sockeye salmon leave the western Bering Sea and are distributed in North Pacific waters south of the Aleutians. Runs of maturing Chinook in offshore waters of the western Bering Sea are finished by late June-early July. Immature Chinook salmon are widely distributed throughout the western Bering Sea from mid summer to fall, most frequently in the Aleutian Basin in mid summer and late fall, and near the shelf and continental slope in late summer-early fall. The overall pattern of Chinook salmon migrations is to the northwest in spring and summer and to the southeast in fall.

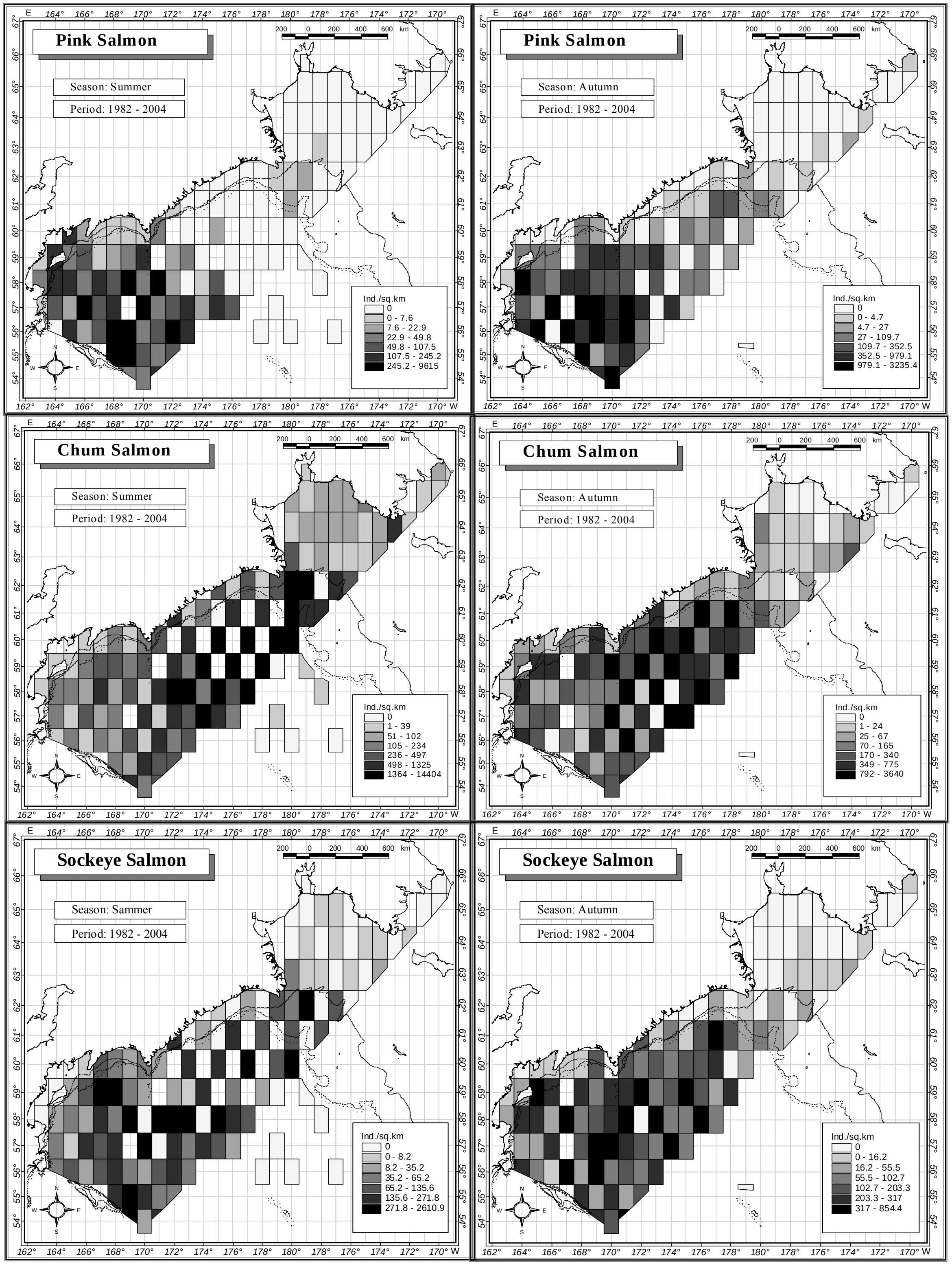


Fig. 18. Estimated density (individuals per km^2) of pink, chum, and sockeye salmon in the western Bering Sea (Russian EEZ) in summer and autumn, 1982-2004. Data are from epipelagic trawl surveys in summer and autumn, 1982-2004. Source: Volvenko (2005).

Volvenko (2005) used a Geographic Information System (GIS) to summarize research trawl survey data collected from 1982 to 2004 (Figs. 18 and 19). In general, densities of all salmon species were low in the far northern area (Cape Navarin through the region north of Cape Chukotski, 62-66°N). Pink salmon densities were highest in the southwestern Bering Sea south of 60°N (Fig. 18), which reflects the high abundance of pink salmon populations in the Karaginsky region of eastern Kamchatka. Chum and sockeye salmon had a broader distribution than pink salmon, and densities of both species tended to be higher offshore from Cape Olyutorskiy to Cape Navarin (60-62°N) than in the Karaginsky region. Densities of coho and Chinook salmon were low (Fig. 19).

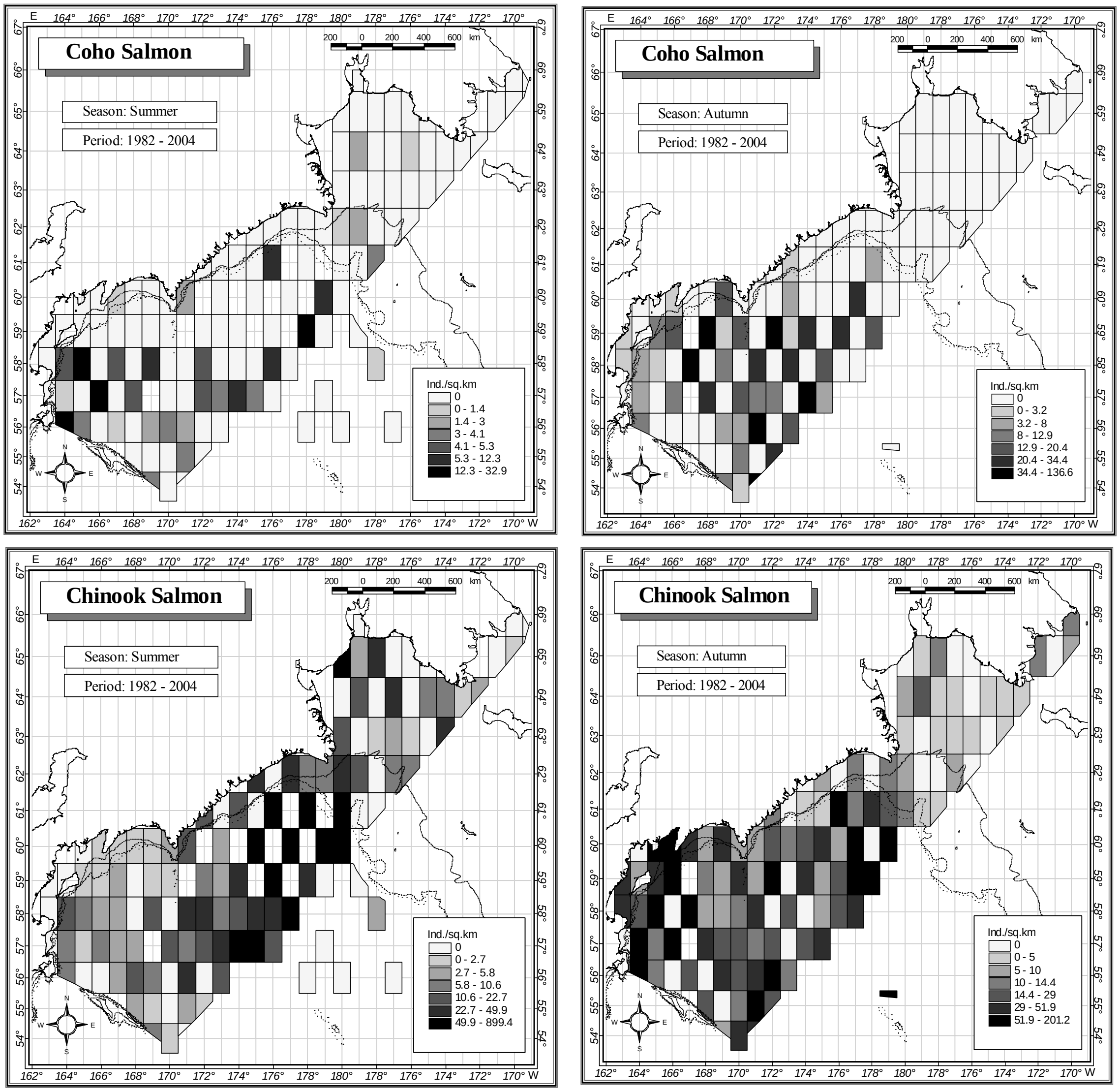


Fig. 19. Estimated density (individuals per km^2) of coho and Chinook salmon in the western Bering Sea (Russian EEZ) from epipelagic trawl surveys in summer and autumn, 1982-2004. Source: Volvenko (2005).

Review of Information on Vertical Distribution of Salmon

Walker et al. (2006) reviewed information on the vertical distribution of salmon. Tracking of fish carrying ultrasonic tags allowed Ogura and Ishida (1992, 1995; Ogura 1999) to gain insights into the detailed behavior of individual salmon in the central Bering Sea and North Pacific. Chum, pink, sockeye, coho, and Chinook salmon were all mostly within the top 50 m, and the first four species were primarily shallower than 20 m. Chinook salmon were deeper (20-50 m) than other species. Coho salmon showed the clearest diurnal pattern of movement. Unfortunately, it was possible to track fish for only a few days (0.6-5.5 days), and tagging or vessel effects may have obscured normal behavior.

Data storage tags have permitted a longer term look at what salmon do at sea. Nine tags on Japanese chum salmon also showed fish usually within the top 60 m and making deeper excursions during the day than at night (Wada and Ueno 1999, Azumaya and Ishida 2005, Tanaka et al. 2005). Depths over 80-100 m generally were not accessed until the fish neared Japan, when they occasionally descended to 150-360 m. These data are very similar to those we have retrieved from data tags on chum salmon returning to Japan and Russia. The short intervals of data collection (every 5 s) on the tag analyzed by Tanaka et al. (2005) also allow an accurate characterization of the daytime dives by chum salmon. They found fish made dives about 8.6 times per hour, with durations of about 5 min and 1.4 min intervals between dives. Fish were presumed to be feeding on prey which had moved deeper during daylight hours.

On the northeastern Bering Sea shelf Russian trawl fisheries took Chinook salmon incidentally at depths to 360 m throughout year and chum salmon in summer and fall (Radchenko and Glebov 1998a,b). The majority (90%) of Chinook was taken at 50-400 m, and fish were slightly deeper August-September. They found more older fish in winter and more younger fish in the summer and fall.

New tagging technologies have provided precise detailed data from individual fish as they migrate. NPAFC scientists cooperated in the deployment of data storage tags (DSTs) for international cooperative high seas tagging programs since 1998. Archival DSTs that recorded temperature or temperature and depth during salmonid ocean migrations have been applied to salmon captured during U.S. and Japanese research cruises. Data storage tag studies have provided new insight into the migratory behavior and habitat utilization of salmon (Walker et al. 2000a, b; Friedland et al. 2001; Walker et al. 2001). These studies have shown that salmon undergo extensive vertical migrations, and that their vertical distribution varies significantly by species and time-of-day. Data from the first recoveries of temperature-recording DSTs from salmon tagged on the high seas showed a clear diel pattern of higher, relatively constant average temperatures at night, with narrower temperature ranges and fewer descents than during the day (Walker et al. 2000a). Alaskan pink and coho salmon and steelhead tagged in the Gulf of Alaska were at higher temperatures on average (10°-12°C) than Japanese chum salmon tagged in the Bering Sea (8°-10°C). Japanese chum salmon were also found at a wider range of temperatures (-1°-22°C vs. 5°-15°C). This is probably related both to the different oceanographic regions through which the fish migrated, as well as species differences in thermal ranges and vertical movements. All species show considerable diurnal and shorter-term variation in ambient temperatures, which suggests that ocean distribution of salmon may be linked more to prey distribution, foraging, and migration than to SSTs. Walker et al. (2000b) used actual temperatures recorded on DSTs in a bioenergetic model to estimate daily ration and compare simulated salmon marine growth under differing temperature conditions. Friedland et al. (2001) used differences in sea surface temperatures between the beginning and end of day and night as indications of progress against thermal gradients, and concluded that chum salmon migrating from the Bering Sea to Japan make more progress in their migration during the day than during the night. Rough migration routes based on sea surface temperatures were also estimated.

Depth data from tags indicates that salmon often remain near the surface at night and move between the surface and greater depths during the day. Simple descriptors of depth, such as "average depth", do not capture some of the variation in salmon behavior. In summarizing the data, Walker et al. (2006) calculated measures of average 'maximum' depths. This entailed finding the maximum depth recorded for each day (24 h), daylight, or nighttime period, and averaging these maximum depths (Fig. 19). Average daily minima were also calculated. Because overall average depths include many nighttime values near the surface, they are relatively shallow. Average daytime depths are deeper, but include both surface and deeper values and are often more reflective of depths salmon move through briefly during movement between the surface and target depths. Average daytime maximum depths are more representative of the deeper waters salmon move to each day.

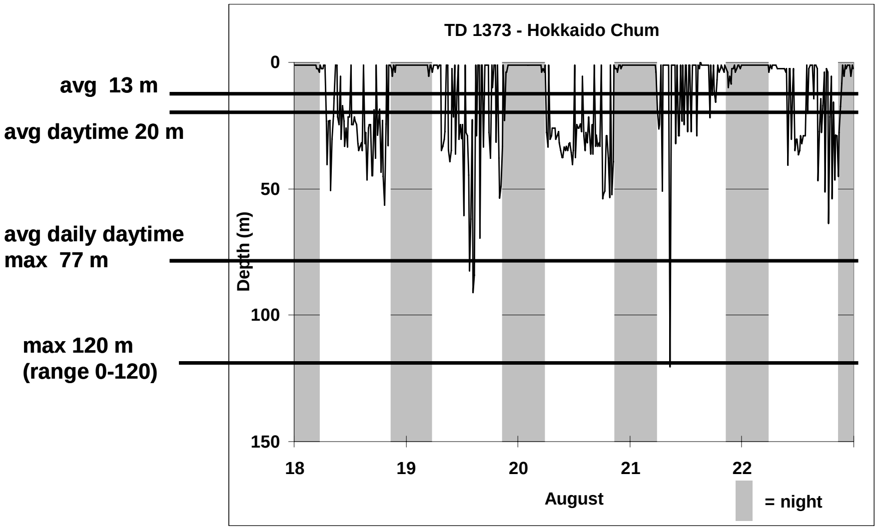


Fig. 19. Example to illustrate differences in calculations of average depth, average daytime depth, average daily maximum depth, and maximum depth. Data are from five days in August 2002 from a chum salmon returning to Hokkaido, Japan, carrying temperature-depth tag 1373. Day/night periods are interpolated estimations from sunrise and sunset times at release and recovery locations. Source: Walker et al. (2006).

Depth data from a limited number of DSTs (n=34) confirm that Chinook and chum salmon have the deepest vertical distributions. Average depths (Chinook: 42 m; chum: 16 m) and average daily maxima (Chinook: 130 m; chum: 58 m) are deeper than those of the other three species (Table 9). Among sockeye, pink, and coho salmon, sockeye have the shallowest vertical distribution (average 4 m, average daily max 22 m), followed by pink (average 10 m, average daily max 37 m) and coho (average 11 m, average daily max 46 m). Most fish displayed a diel pattern of vertical distribution, moving between shallower and deeper waters and near the surface at night (average nighttime depths of 3-8 m), except for Chinook. The diel pattern was strongest in chum and pink salmon, and was variably expressed, even in a single fish. The Chinook data are from two fish. One was tagged as an immature, and the tag has two years of data showing several different patterns of vertical distribution that changed seasonally; the fish remained below 100 m for one winter. Data from all other fish are from maturing fish in summer and fall.

Table 9. Depth data (average, average minimum, maximum, average day and night, average day, night, and daily maxima), by species, from data storage tags, 1999-2006. Source: Walker et al. (2006).

Species	N	Avg Depth	Avg Daily Min	Avg Night	Avg Day	Day-Night Difference	Avg Night Max	Avg Day Max	Avg Daily Max	Max
Sockeye	8	4	0	3	4	1	13	20	22	50
Pink	3	10	1	4	13	8	19	36	37	74
Coho	10	11	0	8	12	5	29	42	46	97
Chum	11	16	1	8	20	13	33	56	58	253
Chinook	2	42	17	40	43	3	84	125	130	344

Temperature ranges varied throughout the period the fish carried the tags for all species. Temperatures are indicative of the temperature profiles of the water masses that the salmon traversed (Fig. 20). Daily maximum depths did not change significantly over time, although temperature ranges experienced at those depths did. This indicates that salmon chose consistent depth ranges and not temperature ranges, and that usual depths may remain relatively constant across water masses and ocean areas.

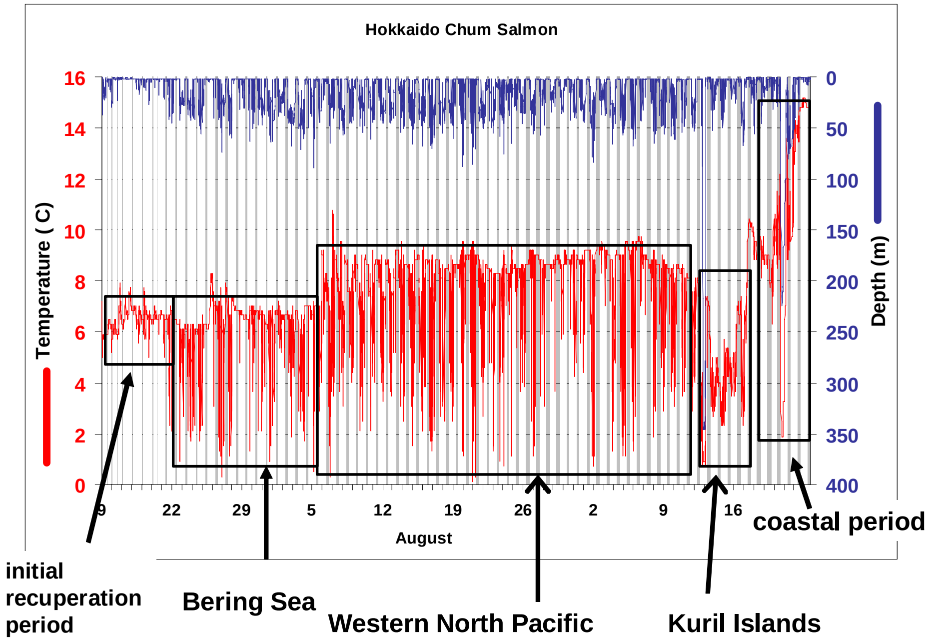


Fig. 20. Example to illustrate variation in temperature ranges during chum salmon migration. Data are from a chum salmon tagged in the Bering Sea and caught near Nemuro, Hokkaido, Japan. Temperature ranges vary across water masses, while depths remain relatively constant. Source: Walker et al. (2006).

The only DST tag with overwintering data recovered to date was from a Chinook salmon, tagged with a temperature-depth tag in the Bering Sea in 2002 and recovered almost two years later in the Yukon River. The data on the tag show a complete record of the temperatures and depths experienced by the fish over two years (Fig. 21). The behavior of the fish differed markedly between the two winters. A diurnal pattern continued through the winters, but in the first winter the fish was moving toward the surface during the day while in the second it moved down. During the first winter, as an immature fish, the Chinook remained below 100 m at temperatures of about 4°C. During the second winter before returning to spawn, the fish was at depths above 50 m at temperatures of 1° to 5°C. The very deep dives this fish undertook in late winter to spring of both years are also puzzling. The maximum depth this tag model could record was 350 m, which the fish often exceeded. The data may provide insight on the wintering areas of different maturity stages of this stock.

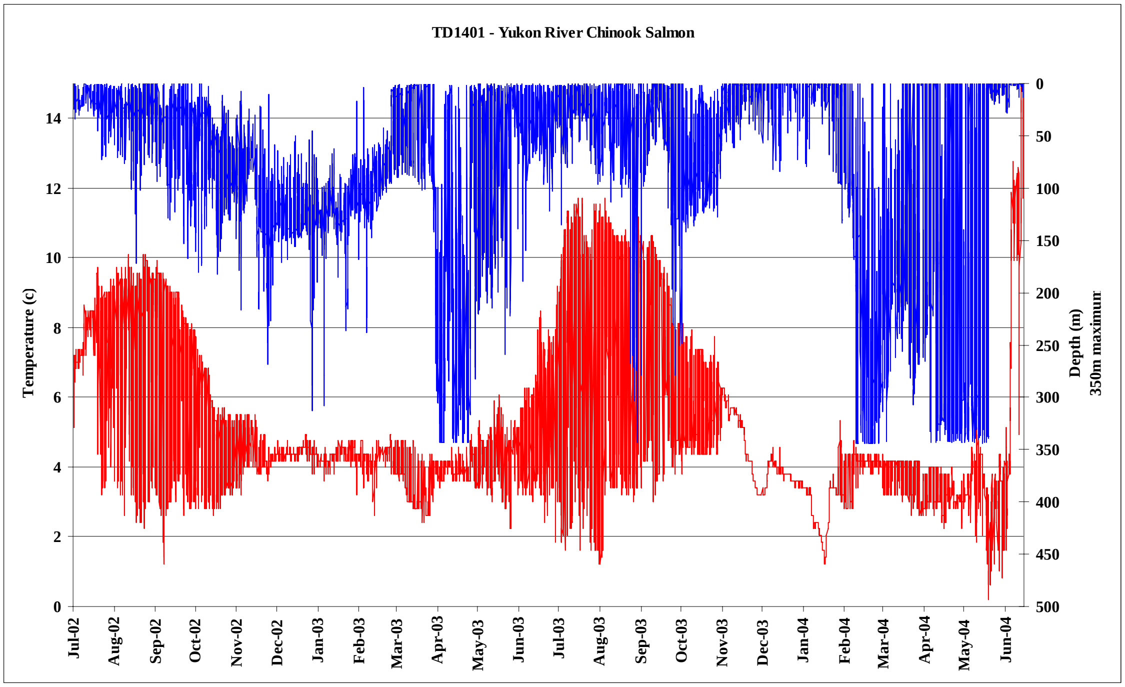


Fig. 21. Data from a Chinook salmon tagged in the Bering Sea in July 2002 and recovered in the Yukon River in June 2004. Data source: High Seas Salmon Research Program, Univ. Washington.

Salinity data from a maturing Yukon River Chinook salmon show the fish moving from oceanic water of 32 psu into brackish water of 24 psu for a day, then back into saltier water (30 psu) for a day or so before finally moving into the fresh water of the Yukon (Fig. 22). The fish was in the top five meters during this period. Such searching and testing is a well-known behavior of Pacific salmon seeking their natal rivers.

The results of Walker et al. (2006) from data tags are generally in line with previously reported information. However, they illuminate some aspects of behavior, such as changes from remaining near the surface at night to movements up and down in the water column during daylight hours. This daytime movement shows that salmon do not move down to a fixed depth and remain there during the day, but are in constant vertical motion, meaning an “average” daytime depth, such as obtained from nets or hooks, may not give a full picture of the overall vertical distribution. Also, it does not seem that individual salmon are “stratified” during the day, with some near the surface and some deeper, but most are moving vertically. Data show nighttime distribution close to the surface in very shallow waters, and this confirms conjectures of why salmon abundance drops at night in surveys which employ gear such as trawls and hydroacoustics which do not fully sample near-surface waters (e.g., Nero and Huster 1996 and unpublished BASIS trawl data).

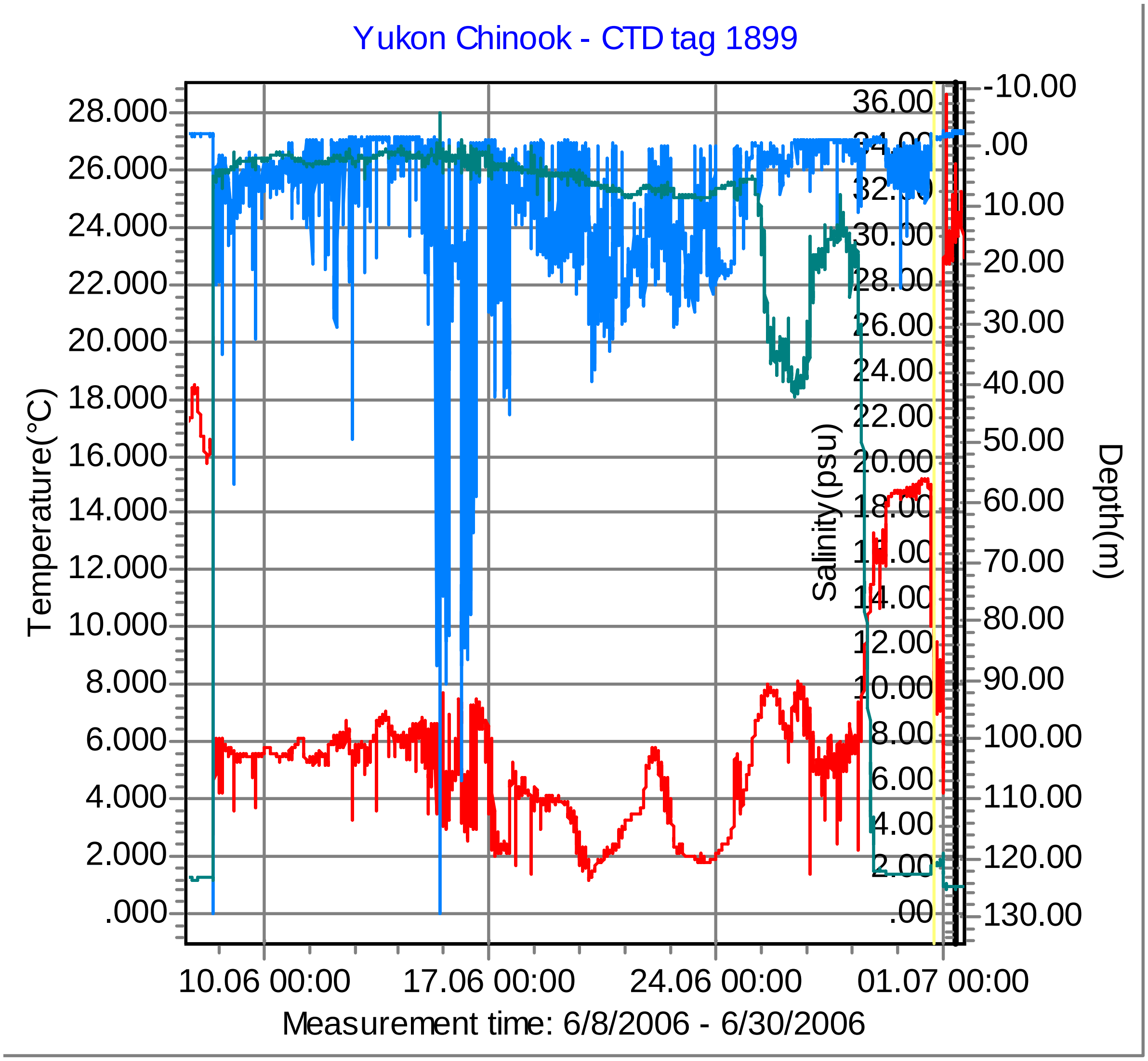


Fig. 22. Salinity, temperature, and depth data from a Chinook salmon tagged in the Bering Sea in June 2006 and recovered three weeks later in the Yukon River. Data source: High Seas Salmon Research Program, Univ. Washington.

Data tags also allow a fuller picture of vertical distributions, with information on occasional or rare excursions to depths deeper than normal. Many other studies have been limited by depths fished, for example only setting nets to depths of 20 m or 40 m. While not common for sockeye, pink, and coho salmon, use of greater depths by salmon of all species show their capabilities. A subtler breakdown of salmon behavior is possible than with coarser sampling gear, such as deep gillnets or trawls with large vertical openings. While knowledge that distribution is within the top 40 or 60 m may be adequate for some purposes, knowledge of movements within that range may also be of use.

DST data might offer some guidance for fishery managers and policy makers (Walker et al. 2006). For example, if a high proportion of salmon are near the surface at night, it might be desirable to operate deepwater trawls at night to avoid bycatch of salmon. Data on vertical distribution can also add a dimension to consideration of the response of salmon to ocean and climate change. If salmon seek relatively uniform depths, warming ocean temperatures within those depths could place higher physiological burdens on them. However, we do not know the reasons for vertical movements. It is likely they are feeding on prey that move deeper during the day. If prey move even deeper in response to warmer temperatures, salmon may follow, but at a greater energetic cost.

In conclusion, DST tag recovery data have provided a much more detailed understanding of vertical distribution and movements of Pacific salmon (Walker et al. 2006). Depth data confirm that Chinook and chum salmon have deeper vertical distributions (average daily maxima: Chinook: 130 m; chum: 58 m) than those of sockeye (22 m), pink (37 m), and coho salmon (46 m). One tag with two years of data from a Chinook salmon shows changing behavior throughout the year and between two successive winters, but a lack of tag returns from any other overwintering fish leaves winter behavior and distribution of salmon as a major unanswered question. Temperature ranges varied widely among water masses traversed by maturing salmon, while maximum daily depths remained fairly uniform. This indicates that salmon choose maximum depths and not temperature ranges, and that usual depths of maturing salmon may remain relatively constant across water masses and ocean areas (Walker et al. 2006). This observation warrants further investigation into the reasons for salmon vertical movements and whether usual depths would increase with warming ocean temperatures and possible increasing depth of prey organisms.

Stock-Specific Models of Salmon Distribution and Migration Patterns

In the late 1960s and 1970s conceptual models of the distribution and migration patterns of major regional stock complexes of Asian and North American salmon were developed by INPFC researchers using composite information from high seas research and commercial fishing catch and effort data, biological data, tag recovery data, and stock-identification results, primarily natural parasite tags and analysis of scale patterns. These historical models were a major breakthrough in our understanding of stock-specific migratory behavior of salmon in the open ocean, and are still frequently cited in the scientific literature.

One of the earliest conceptual models summarized the entire ocean migration of Bristol Bay sockeye salmon as "two or three circuits of an elongated east-west course extending from about 165ºE to 140ºW (Royce et al. 1968; Fig. 23). Royce et al. (1968) hypothesized several outstanding features of salmon migration in the open ocean that most species share in common: (1) navigation is by an inherited series of responses to stumuli; (2) salmon migrate near the ocean surface, mostly in the upper 10 m; (3) salmon migrations cover long distances (1000s of kilometers); (4) migration is not "to and fro, but circular, (5) particular stocks occupy a distinctive but very large part of the ocean; (6) particular stocks have no tendency to school; (7) salmon travel almost continuously (immatures average 18.5 km per day; maturing fish commonly average 46.3-56.6 km per day); (8) migrations terminate on a "remarkably consistent schedule"; (9) migration routes seem unrelated to land or continental shelves and traverse different ocean domains.

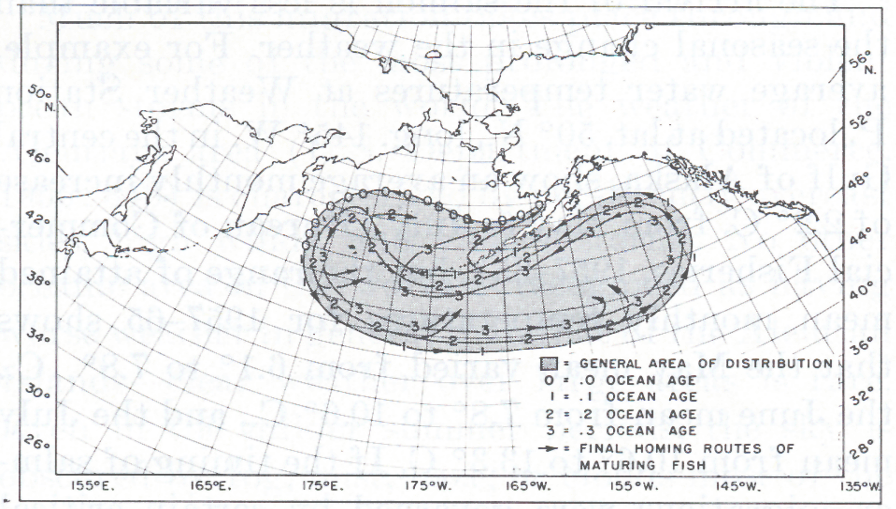


Fig. 23. The first conceptual model of the ocean migrations of Bristol Bay sockeye salmon based on U.S. seine catch data, and of Canadian, Japanese, and U.S. tagging data through 1966 (Royce et al. 1968). For convenience, Royce et al. (1968) showed change in age only at the western extremity of the migration path, however, the authors noted that "undoubtedly each age group is distributed over a considerable part of the migratory path at the time the winter annuli are formed."

In a more detailed diagram, Royce et. al. (1968) used arrows to indicate swimming direction and approximate distribution (Fig. 24). This model depicts the primary features of migration patterns of Bristol Bay sockeye salmon in Bering Sea as determined by catch and high seas tag data. According to this model, juveniles (age-.0) apparently do not migrate out of the Bering Sea during their first summer, and some may overwinter in the western Bering Sea (Fig. 24A; model based on catches of age-.1 sockeye during winter gill netting in 1962 and 1963; French and Mason 1964). In their second summer at sea, migrations of immature (age-.1) fish extend into the far northwestern Bering Sea (Fig. 24B; model based on tag returns from catches by the Japanese high seas fishing fleet in the year of release and the dominance of Bristol Bay stocks in coastal tag returns in the following year). In fall and winter, age-.1 (prior to January 1) and age-.2 (after January 1) fish have a broad distribution in the western Bering Sea (Fig. 24C; model based on limited winter sampling and from distribution and migrations observed in the following spring and summer. In their third or fourth years at sea, maturing fish migrate eastward across the Bering Sea to Bristol Bay from June-August, and immature fish repeat the same migration pathways as immature age-.1 fish in June-August and immature age-.2 fish in September-May (Fig. 24D-F). The Royce et al. (1968) model was updated and revised by French et al. (1976). Burgner (1991) updated the French et al. (1976) sockeye salmon migration models with new data from the results of scale pattern analyses conducted in the 1980s in the open ocean region south of 46°N (Harris 1987; see review by Myers et al. 1993; Fig. 25). Similarly, models were also developed for pink salmon (Takagi et al. 1981; Fig. 26) and chum salmon (Fredin et al. 1977; Fig. 27).

Bristol Bay Sockeye Salmon Migration Model – Royce et al. (1968)

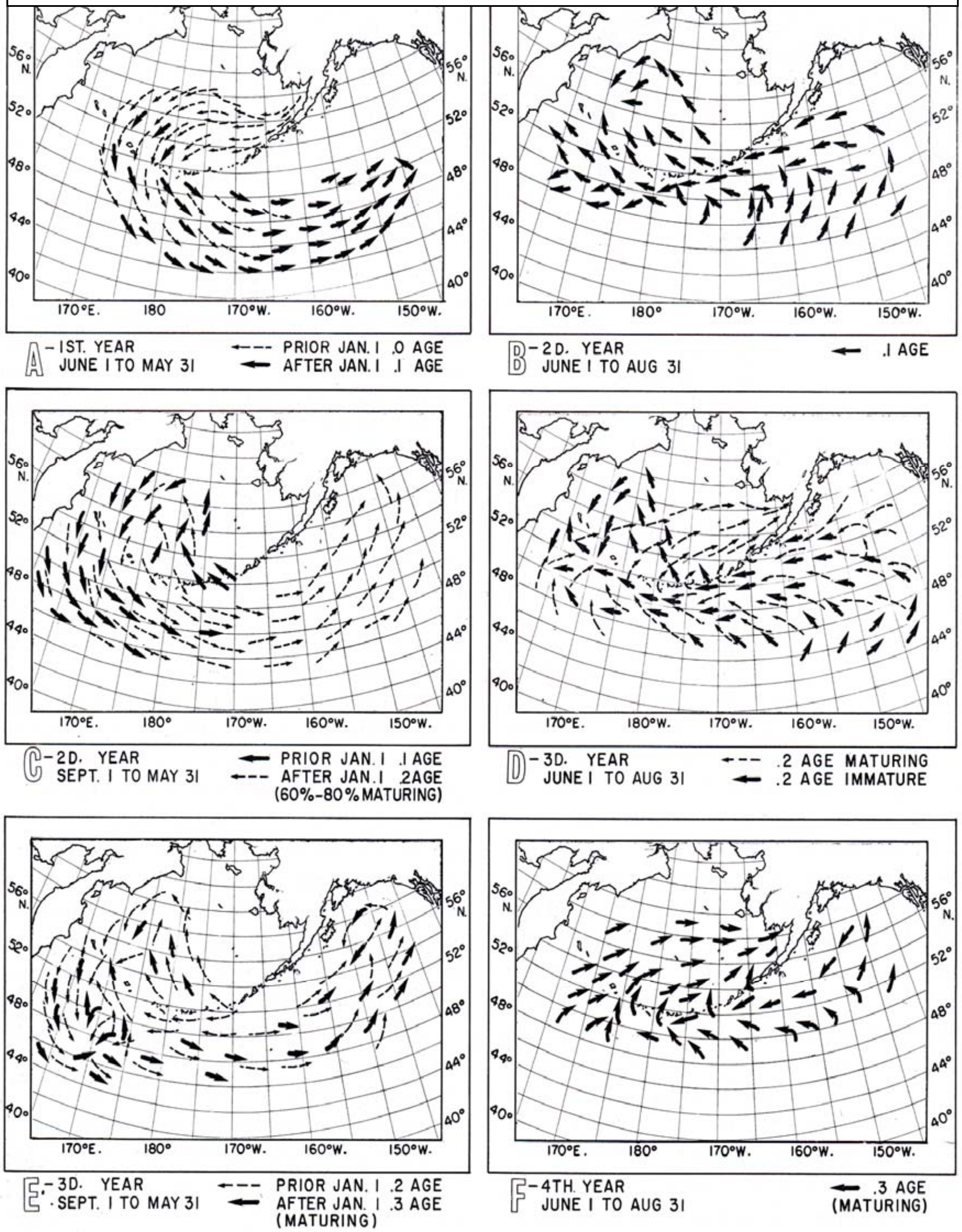


Fig. 24. Model of ocean migrations of Bristol Bay sockeye salmon based on seine catch and tagging data through 1966; arrows indicate direction and approximated distribution. Source: Royce et al. 1968.

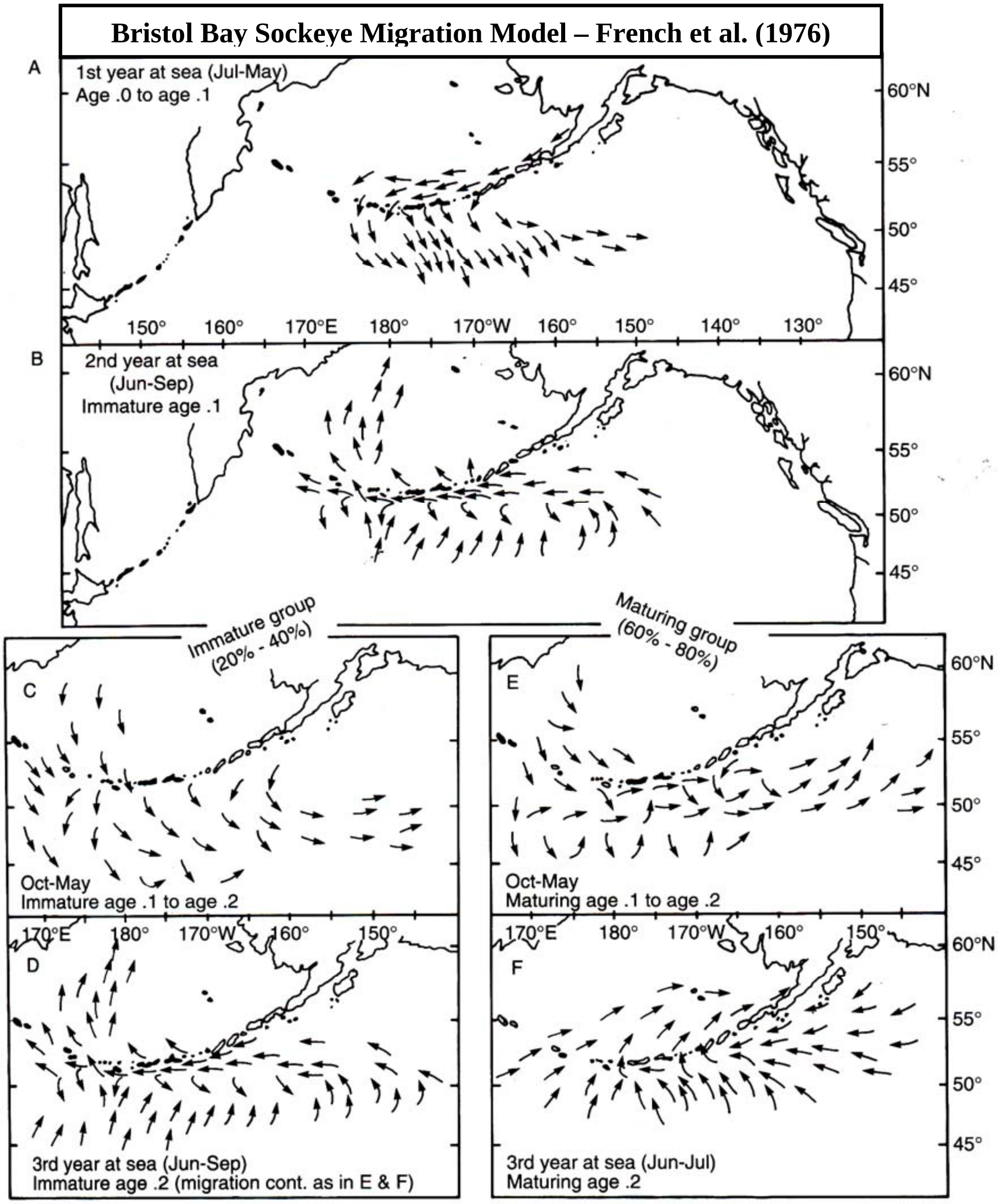


Fig. 25. Model of ocean migrations of Bristol Bay sockeye salmon developed largely from commercial and research vessel catches, tagging, and parasite data collected from 1956-1970 (French et al. 1976) and updated by Burgner (1991) with more recent information from tagging experiments and scale pattern analysis (Harris 1987). Arrows indicate direction of movement and approximated distribution. Source: Burgner 1991.

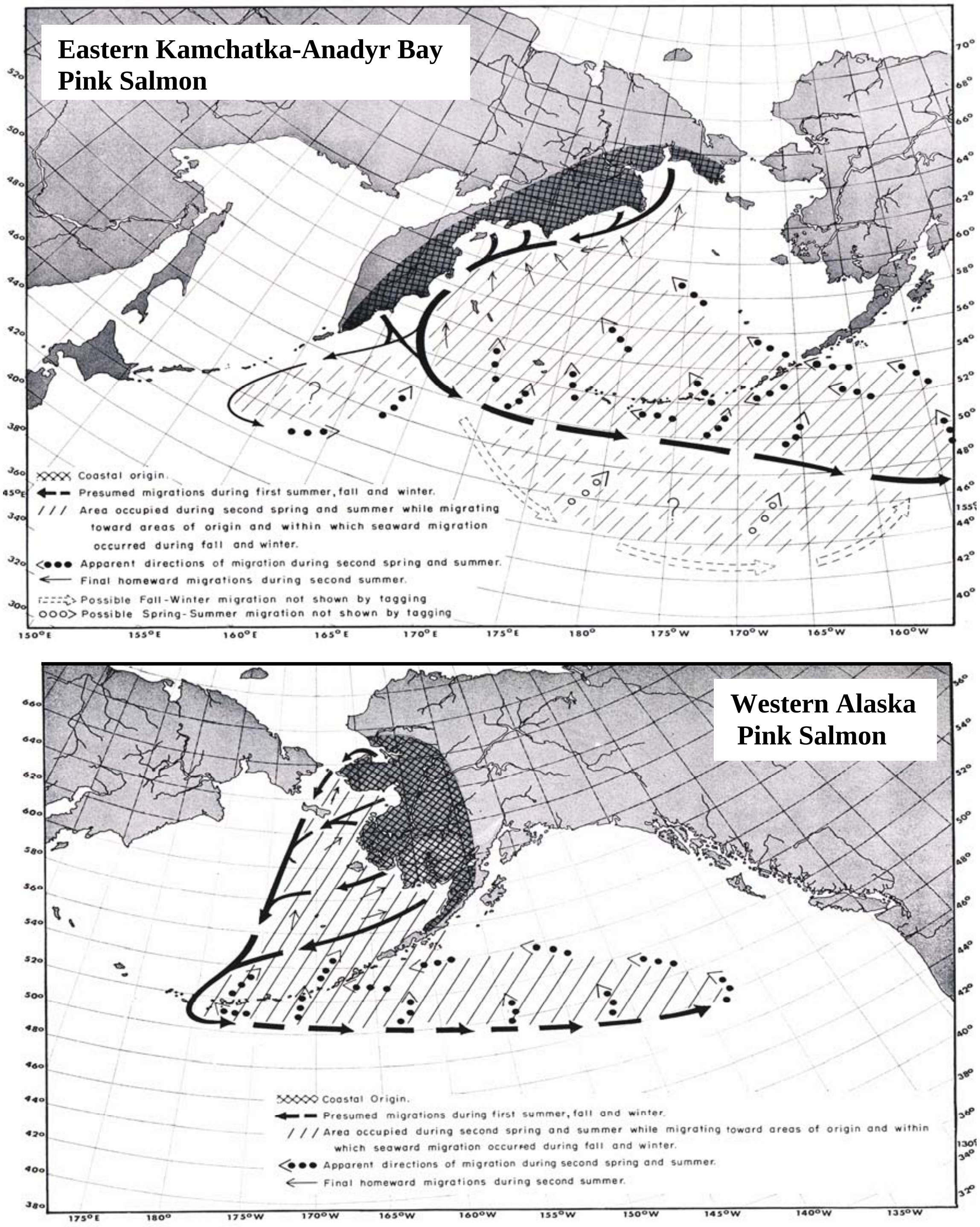


Fig. 26. Models of seasonal ocean migration patterns of pink salmon origination in east Kamchatka and northward to Anadyr Bay (top panel) and western Alaska (north side of Alaska Peninsula to Kotzebue Sound including St. Lawrence Island). Arrows indicate direction of movements. Source: Takagi et al. 1981.

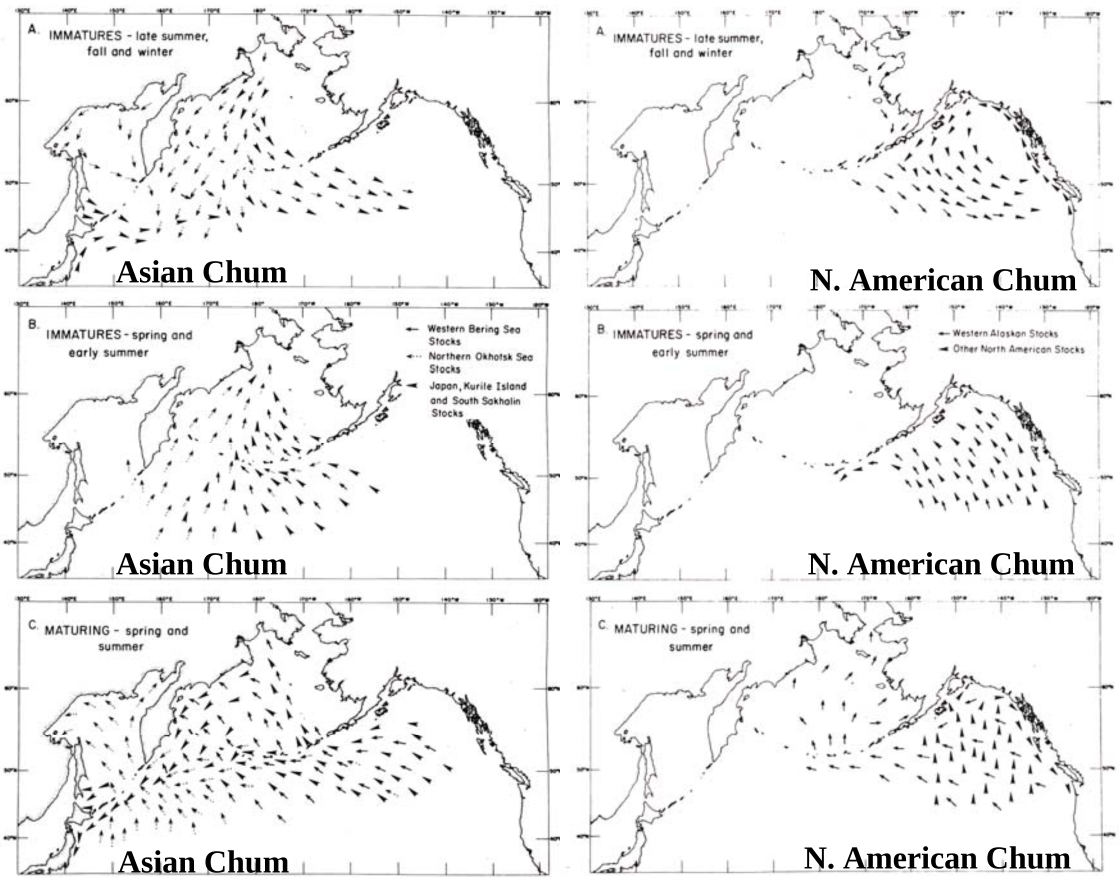


Fig. 27. Models of seasonal ocean migration patterns of Asian and North American chum salmon. Arrows indicate direction of movement of immatures in late summer, fall, and winter (top panels), immatures in spring and early summer (center panels), and maturing fish in spring and summer (bottom panels). Source: Fredin et al. 1977.

More recently many researchers have attempted to develop quantitative models of open ocean distribution and movements of some numerically dominant species and stocks of salmon (e.g., Hiramatsu and Ishida 1989; Thomson et al. 1992, 1994; Dat et al. 1995; Rand et al. 1997; Walter et al. 1997; Azumaya and Ishida 2004). For the most part, these quantitative models have failed to successfully capture relatively clear and simple differences in the open ocean distribution and migratory orientation of Asian and North American salmon stocks. An added difficulty is that existing time series of empirical data are usually not sufficient to validate computer models.

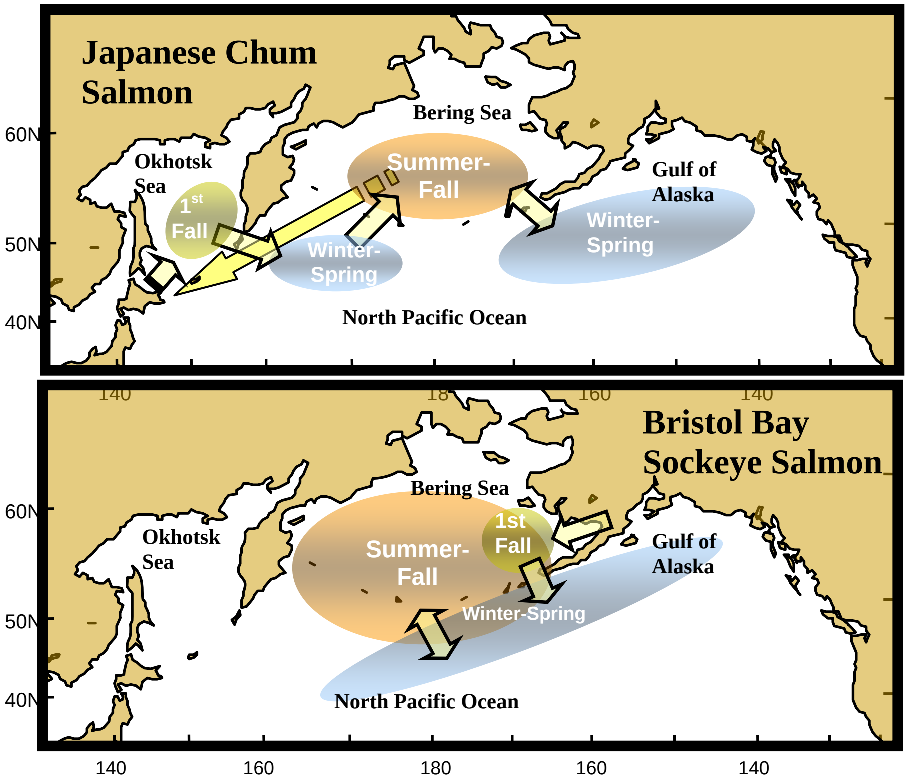


Fig. 28. Examples of seasonal stock-specific migration models of Asian and North American salmon. **Top panel:** Model for Japanese hatchery chum salmon as estimated by genetic stock identification (Urawa 2000, 2003). In their 1st summer-fall, juveniles are distributed in the Okhotsk Sea. In their 1st winter, they are distributed in a narrow region of the western North Pacific. By their 2nd summer-fall they have migrated into the Bering Sea, and in late fall they migrate south and east, and spend their 2nd winter in the Gulf of Alaska. In subsequent years, they migrate between summer/fall feeding grounds in the Bering Sea and winter habitat in the Gulf of Alaska. In their last summer and fall, maturing fish migrate back to Japan through the western Bering Sea and western North Pacific. **Bottom panel:** Migration model for Bristol Bay sockeye salmon as indicated by tag recoveries, scale pattern analysis, parasite tags, (Burgner 1991), genetic (DNA) stock identification (Habicht et al. 2005), and exploratory fishing (Farley et al. 2005). In their 1st ocean summer and fall, juveniles are distributed on the eastern Bering Sea shelf, and by the following spring immatures are distributed across a broad region of the central and eastern North Pacific. In their 2nd summer and fall immature fish migrate to the west in a band along the south side of the Aleutian chain and northward through the Aleutian passes into the Bering Sea. In subsequent years, immature fish migrate between summer/fall feeding grounds in the Aleutians and Bering Sea and winter habitat in the North Pacific. In their last spring maturing fish migrate across a broad east-west front from their winter/spring feeding grounds in the North Pacific, northward through the Aleutian passes into the Bering Sea, and eastward to Bristol Bay.

We are now in the midst of a genetic revolution that is beginning to provide reliable, mid- to small-scale estimates of salmon stock composition needed to develop and validate quantitative models of interannual variation in open ocean distribution and migration patterns of salmon. The focal species for the initial development of a comprehensive Pacific Rim genetic (allozyme) baseline was chum salmon. These data have been used to develop a new conceptual model of the seasonal distribution and migration patterns of Japanese chum salmon (Urawa 2000, 2001, 2004; Fig. 28, top panel). The results of analyses using 20 allozyme loci from 356 chum salmon populations have shown (1) a higher degree of overlap in distribution of Asian and North America stocks in the open ocean than shown by previous methods, (2) substantial intra-annual fluctuations in stock composition over short time periods, and (3) distribution of stocks from throughout the range of chum salmon in the Bering Sea (see review by Seeb et al. 2004). Seeb et al. (2004) also discuss some results which suggest that geographically but not genetically close populations of chum salmon follow similar migration routes.

New comprehensive DNA baselines for chum salmon and other species, which are even more effective than allozyme baselines at identifying individual populations, are being developed and applied to questions about open ocean distribution and migration patterns of salmon (e.g., NPAFC 2004b). Our preliminary conceptual model of the seasonal migrations of Bristol Bay sockeye salmon (Fig. 28, bottom panel), which incorporates recent data from genetic (DNA) analysis (Habicht et al. 2005), scale pattern analysis (Bugaev 2005), and exploratory fishing (Farley et al. 2005), also reflects more extensive distribution of juvenile and immature North American sockeye salmon in the Bering Sea in summer and fall than was indicated by earlier models (Figs. 23-25). However, earlier models might accurately reflect seasonal distributions of salmon in the Bering Sea during “cool” periods, as most of the data were collected during a relatively cool period in the 1950s-60s, while most recent data were collected during a period of warming in the Bering Sea (Khen and Basyuk 2005).

We conclude that historical models of stock-specific distribution and migrations of salmon in the Bering Sea need to be updated because they are based primarily on data collected during the mid to late 1950s and 1960s, when: (1) the North Pacific climate regime was in a different phase (Mantua et al. 1997), (2) there were no large-scale releases of hatchery chum and pink salmon into the North Pacific Ocean (Mahnken et al. 1998), and (3) large-scale high seas driftnet fisheries harvested large percentages of salmon returning to Russia and Alaska (e.g., Fredin et al. 1977; Harris 1987). In addition, these old conceptual models do not tell us anything about interannual variation and the effects of ocean conditions on stock-specific distribution and migration patterns. Unfortunately, the genetic “revolution” in salmon stock identification is happening at a time when the number of salmon research vessel surveys in the open ocean and government support for these surveys is diminishing. Nevertheless, through cooperative research programs coordinated by NPAFC, e.g., BASIS (Bering Aleutian Salmon International Survey, 2002-present), we are rapidly advancing our knowledge of stock-specific distribution and migration patterns of salmon in the Bering Sea (NPAFC 2005).

Ocean Interceptions of Western Alaska Salmon

Brodeur et al. (2003) briefly reviewed the history of salmon fishing and trends in commercial salmon catches in Alaska. Pacific salmon have been fished by native Alaskans for millennia in streams and along a coastal band that was accessible from small vessels. Fishing in more oceanic waters required sturdier vessels. Ocean fishing for salmon increased after development of the gasoline engine and refrigeration in the early 1900s. The coastal Alaskan salmon fisheries were managed by the federal government from 1867 through 1959 although they were virtually unregulated. Since the establishment of the U.S. 200-mile zone, ocean fisheries within 3 miles of shore have been managed by the State of Alaska, and fisheries from 3-200 miles offshore are managed by the federal government (NMFS). Commercial gears for catching salmon in the ocean have included traps, beach seines, purse seines, drag seines, drift gillnets, and set gillnets, among others. Commercial fishing for salmon in Alaska began in the 1880s, and catches peaked in 1936 at 290,000 mt. The decline from that peak to a level below 100,000 mt in the 1950s through early 1970s was largely due to overfishing and unfavorable climate conditions (Brodeur et al. 2003). Conservation measures, favorable climate conditions, and reductions in the Japanese high seas salmon driftnet fisheries, among other factors, resulted in an increasing trend in commercial salmon catches that continued from the late 1970s through the mid 1990s (peak in 1995 at 412,000mt). In the late 1990s and early 2000s poor runs of salmon in many areas of western Alaska combined with low prices due to the glut of farmed salmon on world markets, resulted in an economic disaster for commercial salmon fisheries in western Alaska. There has been some improvement since 2003. For example, the 2003 Yukon River Chinook salmon and fall chum salmon runs were the strongest in recent years, and supported small commercial harvests (NPAFC Working Group on Stock Assessment 2003). In Norton Sound, however, the combination of poor salmon runs and lack of fish buyers in 2003 resulted in the second lowest commercial harvest on record. It is interesting to note that runs of chum salmon to eastern Siberia (Anadyr R.) also experienced ‘unexpected and dramatic’ declines, resulting in a decrease in commercial harvests from an average of 2,000-3,000 mt to 72 mt in 2002 and 349.5 mt in 2003 (NPAFC Working Group on Stock Assessment 2003)

Interceptions of western Alaska salmon by commercial salmon fisheries in other regions of Alaska have been a longstanding concern, particularly interceptions by the South Unimak Island (False Pass) and Shumagin Island fisheries, also called “South Peninsula June fisheries”, and in non-terminal areas by the South Alaska Peninsula Post-June fisheries (Eggers et al. 1991; Shaul et al. 2004a,b). These fisheries are collectively called the “Area M” fisheries. Shaul (2003) reviewed the history of the South Peninsula June fisheries, which began in 1911. These fisheries target maturing sockeye salmon, but also have a large incidental harvest of chum salmon and other species, which are caught along their migration routes from the Gulf of Alaska to the Bering Sea. Harvests of chum salmon by the June fishery averaged 186,000 fish in 1960-1969, 306,000 fish in 1970-1979, and 566,000 fish in 1980-1987, including a record harvest of 1.1 million fish in 1982 (Eggers et al. 1991). From 1994-2003, harvests by the June fishery have averaged 4,370 Chinook, 1,133,297 sockeye, 2,234 coho, 485,308 pink, and 324,163 chum salmon

(Shaul et al. 2003a). To protect western Alaska chum salmon stocks, harvest caps were the primary method used by ADFG during the June fisheries (400,000 fish in 1986; 500,000 fish in 1988-1989; 600,000 fish in 1990-1991; 700,000 fish in 1992-1997; and a "floating cap" of 350,000-650,000 in 1998-2000; Shaul 2003). Since 2001, when the Alaska Board of Fisheries designated Kvichak (Bristol Bay) sockeye salmon and several Arctic-Yukon-Kuskokwim (AYK) chum stocks as 'stocks of concern,' the South Peninsula June fisheries were limited to no more than nine fishing days for seine and drift gillnet gear (with no harvest limits). In non-terminal areas the Post- June (July-October) South Alaska Peninsula fishery also intercepts adult salmon returning to other regions, and, at times, large numbers of immature salmon (Chinook, sockeye, coho, and chum salmon that become gilled in purse seine web; Shaul et al. 2004b). From 1994-2003, annual harvests by the South Peninsula Post-June fishery have averaged 1,847 Chinook, 535,073 sockeye, 200,058 coho, 5,486,201 pink, and 679,770 chum salmon (Shaul et al. 2004b). In 2004, the BOF rescinded a 60,000 cap on coho salmon that had been in effect since 1998 to limit interceptions of AYK salmon by the Post-June fisheries in late July. Tagging studies have shown that chum salmon from many populations in Asia and North America, including AYK, are intercepted by the June fisheries (Eggers et al. 1991). Recent genetic studies of chum salmon in the Shumagin Islands fisheries indicate that AYK stocks are the largest contributors in early June (as high as 69% in early June test fisheries) and decline through June and July to about 5% (Seeb et al. 2004).

Historically, the ocean fisheries of greatest concern to Alaska stakeholders were the Japanese high-seas salmon driftnet fisheries. Harris (1987) reviewed the history of these fisheries and the international agreements that regulated them. The high-seas driftnet fishery for salmon started when the Soviet Union began restricting access to salmon along the Kamchatka Peninsula in the early 1930s, forcing the Japanese to fish elsewhere, including the Bering Sea. World War II curtailed these activities but after the war's end the Japanese began anew to expand the activities of their fishing fleet. Both Canada and the United States were concerned that the Japanese were taking North American salmon in this ocean-intercept fishery. This concern led to the 1952 International Convention for the High Seas Fisheries of the North Pacific Ocean, which established the INPFC and restricted the Japanese to fishing west of 175°W in the North Pacific Ocean and Bering Sea (Jackson and Royce 1986). This restriction and others imposed by the Soviet Union led to a contentious situation as the Japanese continued to expand their high-seas intercept fishery for salmon. The Japanese high-seas driftnet fishery was contentious, in part because it caught immature and maturing salmon of unknown origin. The major goal of INPFC research was to determine the origin of fish taken on the high seas.

Estimates of interceptions of western Alaska salmon by the Japanese salmon driftnet (mothership) fisheries (1956-1975) were reviewed by Fredin et al. (1977). The major North American salmon stocks intercepted by these fisheries were from western Alaska. The effect of these fisheries on returns of salmon to the western Alaska was substantial. For example, Yukon River (immature age 1.2 fish) was estimated to be the major stock contributing to Chinook salmon catches by the Japanese mothership fishery in the Bering Sea (Myers et al. 1987), averaging 36% of the total catch during 1975-1977 and 42% during 1978-1981 (Rogers 1987).

In 1976 the Magnuson Fishery Conservation and Management Act extended U.S. jurisdiction offshore to 200 miles and exerted limitations on ocean fisheries, with the implicit goal of excluding all non-US vessels from the fisheries. Following the lead of the United States, the Soviet Union declared a 200-mile fishery conservation zone in 1977 that further restricted the Japanese fishery. New agreements by INPFC in 1978 eliminated the fishing sector southeast of 56°N, 175°E, and research emphasis in NPAFC shifted to estimating interceptions of North American salmon by the landbased driftnet fisheries operating southwest of 46°N, 175 °W (Myers et al. 1993). An exceptionally large catch of 864,000 Chinook salmon by the Japanese mothership and landbased driftnet salmon fisheries in the Bering Sea and North Pacific Ocean in 1980 included an estimated 229,000 Yukon and 196,000 Kuskokwim Chinook salmon (Rogers 1987). By the late 1980s further restrictions by USSR-Japan and INPFC agreements, had led to substantial reductions in the Japanese high-seas salmon fisheries.

As the Japanese high-seas salmon driftnet fisheries were further reduced, new Asian pelagic squid driftnet fisheries developed rapidly in the North Pacific Ocean in the early 1980s. The squid driftnet fisheries legally intercepted salmon as part of their bycatch, but substantial illegal directed salmon fishing also occurred. Estimates of legal catches by the 1990 Japanese squid driftnet fishery calculated by two different methods were 210,000 fish (plus 21,000 fish that dropped out of the driftnets during retrieval) and 164,000 fish (17,000 dropouts; Pella et al. 1993). Illegal high-seas catches by non-salmon producing (Asian) nations in 1988 were estimated to be at least 10,000 metric tons (5.5 million salmon; Pella et al. 1993). In 1989, the United Nations' General Assembly adopted a resolution that called for a ban on all large-scale high-seas driftnet fishing, unless effective conservation and management measures were taken. In 1991 the high-seas driftnet fishing nations and other nations agreed to a global moratorium on all large-scale pelagic high seas driftnet fishing, effective at the end of 1992. The last year of operation of the legal high-seas salmon driftnet fisheries was in 1991, and the last year of operation of the legal high-seas squid driftnet fisheries was in 1992.

In 1993 the Convention for the Conservation of Anadromous stocks in the North Pacific Ocean established the NPAFC. The NPAFC convention area is the world's largest marine conservation area for salmon (all international waters north of 33°N in the North Pacific Ocean and Bering Sea). Throughout the NPAFC Convention area all directed fishing for six species of Pacific salmon, as well as steelhead trout, is prohibited, and incidental catches of salmon by fisheries targeting other species must be minimized. These conservation measures and fishery regulations are strictly practiced and enforced by the governments that have signed the treaty (Canada, Japan, Russia, Republic of Korea, and the United States).

The salmon conservation and management authority of NPAFC does not extend into the 200-mile zones of member nations. For example, within the Russian 200-mile zone a large-scale Japanese salmon driftnet fishery still operates legally, as well as a Russian salmon driftnet (research) fishery that developed during the 1990s. And within the U.S. 200-mile zone, U.S. groundfish trawl and mixed-stock salmon fisheries are known to intercept Canadian, Russian, and Japanese salmon, as well as fish from all salmon-producing regions of North America (e.g., Seeb et al. 2004). Illegal high seas driftnet fishing and enforcement activities are reported annually to NPAFC, and these reports indicate that illegal high-seas driftnet fishing for salmon is currently at an all-time low. With respect to other types of high seas fishing gear and fisheries, information on salmon bycatch and illegal directed fishing for salmon is largely anecdotal.

The effect of groundfish trawl fisheries operating in the Bering Sea and Gulf of Alaska on returns of Chinook and chum salmon to western Alaska has been a major concern since 1977, when the NMFS scientific observer program began to provide estimates of salmon bycatch by foreign vessels operating in the U.S. 200-mile zone (French et al. 1982). Compared to interceptions by the former Japanese high seas salmon driftnet fisheries, however, the estimated interceptions of Yukon River and Kuskokwim River Chinook salmon by foreign and joint-venture groundfish trawl fisheries in the Bering Sea and Aleutian Islands (BSAI) region of the U.S. 200-mile zone in 1977-1985 were relatively low (15,200 fish in 1977, 13,600 fish in 1978, 43,500 fish in 1979, 40,000 fish in 1980, 11,200 fish in 1981, 5,300 fish in 1982, 3,600 fish in 1983, 3,900 fish in 1984, 3,400 fish in 1985, and 2,000 fish in 1986; Myers and Rogers 1988). The foreign and joint-venture fisheries in the U.S. 200 mile-zone were rapidly phased out as the U.S. groundfish fishing industry reached full capacity. Since then, there have been only a few attempts to quantify the stock composition of salmon bycatch, which is largely chum and Chinook salmon (Berger 2003). Estimates of the stock composition of chum salmon in incidental catches by U.S. trawl fisheries in the Bering Sea in 1994 indicated that 39-55% originated in Asia, 20-35% in western Alaska, and 21-23% in southeastern Alaska, British Columbia or Washington (Wilmot et al. 1998). In 1995, 11% of the chum bycatch by the U.S. Bering Sea trawl fishery was sampled, and an estimated 13-51% originated in Asia, 33-53% in western Alaska, and 9-46 % in southeastern Alaska, British Columbia or Washington (Wilmot et al. 1998). A substantial bycatch of chum and Chinook salmon also occurs in U.S. trawl fisheries in the Gulf of Alaska (Berger 2003), although there are no estimates of the stock composition of the salmon bycatch in this region. Witherell et al. (2002) reviewed available information on salmon bycatch in U.S. groundfish fisheries in from 1990-2001, and estimated that an annual bycatch of 30,000 immature Chinook salmon in the Bering Sea groundfish fisheries equates to an adult equivalent bycatch (fish that would have returned to spawn had they not been intercepted) of 14,581 western Alaska Chinook salmon or a 2.7% reduction in western Alaska Chinook salmon runs (catch and escapement). Witherell et al. discussed problems with estimating salmon bycatch in the U.S. groundfish trawl fisheries, including the lack of recent estimates of stock composition, and recommended that a high priority be given to salmon stock composition research.

Myers et al. (2003) used scale pattern analysis to estimate the bycatch of western Alaska Chinook salmon by the U.S. domestic groundfish fisheries in the BSAI region in 1997-1999. Despite the decline in abundance of western Alaska Chinook salmon during this period, western Alaska was the dominant regional stock (average 56%) in BSAI bycatch samples in 1997-1999. Western Alaska Chinook salmon stocks were 48% of the total bycatch in 1997 and 1998, and 60% of the total in 1999. Similar to the results of Myers and Rogers (1988), Myers et al. (2003) found that: (1) the proportions of the three western Alaskan subregional stocks (Yukon, Kuskokwim, and Bristol Bay) in the BSAI area vary considerably with such factors as brood year, time, and area; (2) Yukon River Chinook salmon are often the dominant stock in the BSAI in winter, particularly among age 1.2 fish in the western BSAI (west of 170ºW) and age 1.4 fish in the eastern BSAI (east of 170ºW); (3) Bristol Bay and Cook Inlet are the dominant stocks of age 1.2 Chinook salmon in the eastern BSAI in fall; and (4) age 1.1 Chinook salmon in the eastern BSAI in fall are largely Gulf of Alaska stocks (Cook Inlet, southeast Alaska-British Columbia). The results of previous scale pattern analyses and tagging studies suggest that in summer immature Yukon River Chinook salmon are distributed farther to the west in the Bering Sea than other North American stocks, which may explain their relatively low percentages in fall 1997-1999 bycatch samples from the eastern BSAI. The estimates of interceptions of Yukon River Chinook salmon by U.S. groundfish fisheries in the BSAI in 1997-1999 were higher than estimated interceptions by the foreign and JV trawl fisheries in the BSAI after 1980. The accuracies of interception estimates, however, depend on the accuracy of the NMFS estimates of Chinook salmon bycatch, which are associated with high levels of uncertainty.

There are also commercial trawl fishing fleets operating inside the Russian 200-mile zone in the Bering Sea, Commander Islands, and western North Pacific Ocean that may intercept at least some western Alaska salmon. Russia does not have a scientific observer program to quantify salmon bycatch by these fleets. Russian estimates based on research trawl data have indicated that salmon bycatch by these trawl fisheries is low (Radchenko and Glebov 1998a,b).

Since the early 1990s, a Japanese salmon driftnet fishery, regulated by a bilateral (Russia-Japan) commission, and a Russian research driftnet fishery have operated in the Russian EEZ. The number of North American salmon intercepted by these fisheries is not known. BASIS is providing new information on the stock composition of salmon migrating in the Bering Sea portions of the Russian EEZ (e.g., Bugaev 2005; Habicht et al. 2005) that can be used to estimate interceptions of North American stocks salmon by commercial and research fishing fleets.

5. Participation in NPAFC meetings

This contract supported the travel of SAFS staff to participate in several contract-related meetings. N. Davis participated in the NPAFC International Workshop "Application of Stock Identification in Defining Marine Distribution and Migration of Salmon" in Honolulu, HI, USA, Nov 1-2, 2003. Davis co-authored two papers for this meeting: (1) "A history of U.S. high seas salmon and steelhead stock identification research" (Myers et al. 2004c) and (2) "Stock origins of Chinook salmon in incidental catches by groundfish fisheries in the eastern Bering Sea 1997-1999" (Myers et al. 2004b). Extended abstracts from these presentations were included in the technical report of the meeting (NPAFC 2004a).

R. Walker attended the 2004 NPAFC Research Planning and Coordination Meeting in Petropavlovsk-Kamchatskii Russia May 6-14, 2004 (NPAFC 2004b). Walker coordinated contract-related tagging work at this meeting.

N. Davis attended the NPAFC International Workshop "BASIS-2004: Salmon and Marine Ecosystems in the Bering Sea and Adjacent Waters" in Sapporo, Hokkaido, Japan, Oct 30-31, 2004. As a part of contract work, Davis presented a paper on food habits and bioenergetics research: "Salmon food habits studies in the Bering Sea, 1960 to present" (Davis et al. 2005). As a part of contract work, SAFS scientists authored or co-authored several other papers at this meeting , as follows: "New information from archival tags from Bering Sea tagging, 1998-2004 (Walker et al. 2005) , "National overview of BASIS research for the United States" (Helle et al. 2005), "Spatial comparison of the feeding ecology of sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) in the ocean during the summer 2003" (Kitagawa et al. 2005), "Lipid and moisture content of salmon prey organisms and stomach contents of chum, pink, and sockeye salmon in the Bering Sea" (Nomura and Davis 2005), "First record of swimming speed of a Pacific salmon undertaking oceanic migration from the central Bering Sea to the Japanese coast" (Tanaka et al. 2005), and "Changes in chum salmon plasma levels of steroid hormones during onset of the spawning migration in the Bering Sea" (Onuma et al. 2005). Extended abstracts from these presentations were included in the technical report of the meeting (Azuma et al. 2005a).

This contract provided partial support for SAFS staff (K. Myers) to participate in NPAFC research planning and coordinating activities with the Alaska Fisheries Science Center in Seattle (Point of Contact: L. Low) and to participate in the drafting of the BASIS research plan (NPAFC 2001a), the 2002 Report of the BASIS Working Group (NPAFC 2002), annual reports of BASIS research results (NPAFC 2003b, 2004c, 2005a), the 2006-2010 NPAFC Science Plan (NPAFC 2005b), and editorial work on NPAFC Technical Report 6 ("BASIS-2004: Salmon and marine ecosystems in the Bering Sea and adjacent waters"; Azumaya et al. 2005a).

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References Cited

Andrievskaya, L.D. 1966. Food relationships of the Pacific salmon in the sea. Preliminary translation by US Joint Publications Res. Serv., Bureau Comm. Fish. 11 p.

Andrievskaya, L.D. 1968. Feeding of Pacific salmon fry in the sea. Fish. Res. Board Can. Transl. Ser. 1423. 16 p.

Anonymous. 2002. Knowles declares Western Alaska fishing a disaster. Assoc. Press. Web posted on AlaskaLegislature.com on Aug 26, 2002. Website: www.alaskalegislature.com/stories/082602/knowles.shtml. Last accessed March 17, 2006.

Arctic Yukon Sustainable Salmon Initiative (AYK SSI). 2006. AYK Salmon Research and Restoration Plan. Bering Sea Fishermen's Association, Anchorage.

Azuma, T. 1992. Diel feeding habits of sockeye and chum salmon in the Bering Sea during the summer. Nippon Suisan Gakkaishi 58(11):2019-2025.

Azumaya, T., and Y. Ishida. 2000. Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. N. Pac. Anadr. Fish Comm. Bull. 2: 165-174.

Azumaya, T., and Y. Ishida. 2004. An evaluation of the potential influence of SST and currents on the oceanic migration of juvenile and immature chum salmon (*Oncorhynchus keta*) by a simulation model. Fish. Oceanogr. 13:10-23.

Azumaya, T., and Y. Ishida. 2005. Mechanism of body cavity temperature regulation of chum salmon (*Oncorhynchus keta*) during homing migration in the North Pacific Ocean. Fish. Oceanogr. 14: 81-96.

Azumaya, T., R. Beamish, J. Helle, S. Kang, V. Karpenko, C.S. Lee, K.W. Myers (and 3 others; eds.). 2005a. Technical Report 6. Workshop "BASIS-2004: Salmon and marine ecosystems in the Bering Sea and adjacent waters." N. Pac. Anadr. Fish Comm., Vancouver, Canada. 127 p.

Azumaya, T., T. Nomura, N. Tanimata, O. Sakai, T. Onuma, and S. Sato. 2005b. Results of the survey in the Bering Sea in 2004. (NPAFC Doc. 843). Hokkaido Nat. Fish. Res. Inst., Fish. Res. Agency, 116 Katsurakoi, Kushiro 085-0802. 13 p.

Azumaya, T., T. Nagasawa, O.S. Temnykh, and G.V. Khen. In press. Spatial and temporal limitation of salmon distribution. NPAFC Bull. 4.

Bax, N.J. 1985. Simulation of the effects of oil spill scenarios on juvenile and adult sockeye salmon (*Oncorhynchus nerka*) migrating through Bristol Bay, Alaska. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest and Alaska Fisheries Science Center, Processed Rept. 85-03, 128 p.

Beamish, R.J., G.A. McFarlane, and J.R. King. 2005. Migratory patterns of pelagic fishes and possible linkages between open ocean and coastal ecosystems off the Pacific coast of North America. Deep-Sea Res. II 52:739-755.

Berger, J.D. 2003. Incidental catches of salmonids by U.S. groundfish fisheries in the Bering Sea/Aleutian Islands, Gulf of Alaska, and the Pacific Coast, 1990-2003. North Pacific Anadromous Fish Commission Doc. 700, Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle. 11 p.

Birman, I.B. 1958. On the occurrence and migration of Kamchatka salmon in the northwestern part of the Pacific Ocean. Pages 31-51 *in* Materialy po biologii morskovo perioda zhizni dalnevostochnykh lososei. Vsesoiuznyi Nauchno-issledovatel'skii Instutut Morskovo Rybnovo Khoziaistvo i Okeanografii, Moscow. (Transl. from Russian; Fish. Res. Board Can. Transl. Ser. 180)

Birman, I.B. 1985. Marine period of life and abundance dynamics of Pacific salmon stock. Moscow, Agropromizdat. 208 pp. (in Russian)

Brandt, S.B., and K.J. Hartman. 1993. Innovative approaches with bioenergetics models: Future applications to fish ecology and management. Trans. Amer. Fish. Soc. 122:731-735.

Brodeur, R.D., K.W. Myers, and J.H. Helle. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. N. Pac. Anadr. Fish. Comm. Bull. 3: 89-131.

Bugaev, A.V. 2005. Identification local stocks of sockeye and Chinook salmon by scale pattern analysis from trawl catches of R/V "TINRO" worked by program of the Bering-Aleutian Salmon International Survey (BASIS) in September-October 2002. N. Pac. Anadr. Fish Comm. Tech. Rep. 6:88-90.

Bugaev, A.V., and R.A. Shaporev. 2002. Results of marine research on the RMS "Moskamalfa" in 2001. (NPAFC Doc. 607.) 20p. Kamchatka Fishery and Oceanography Institute (KamchatNIRO), Russia.

Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1-117 *in* C. Groot and L. Margolis, eds. Pacific salmon life histories. UBC Press, Vancouver.

Burgner, R.L., J.T. Light, L. Margolis, T. Okazaki, A. Tautz, and S. Ito. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 51. 92 p.

Carlson, H.R. 1976. Foods of juvenile sockeye salmon, *Oncorhynchus nerka*, in the inshore coastal waters of Bristol Bay, Alaska, 1966-1967. Fish. Bull. 74:458-462.

Carlson, H.R., K.W. Myers, E.V. Farley, H.W. Jaenicke, R.E. Haight, and C.M. Guthrie III. 1996. Cruise report of the F/V *Great Pacific* survey of young salmon in the North Pacific–Dixon Entrance to western Aleutian Islands–July-August 1996. (NPAFC Doc. 222.) 50 pp. Available from Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 11305 Glacier Highway, Juneau 99801.

Carlson, H.R., E.V. Farley, R.E. Haight, K.W. Myers, and D.W. Welch. 1997. Survey of salmon in the North Pacific Ocean and Southern Bering Sea–Cape St. Elias to Attu Island–July-August 1997. (NPAFC Doc. 254.) Available from Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 11305 Glacier Highway, Juneau, 99801-8626, 24 pp.

Carlson, H.R., E.V. Farley, K.W. Myers, E.C. Martinson, J.E. Pohl, and N.M. Weemes. 1998. Survey of salmon in the southeastern Bering Sea, Gulf of Alaska, and northeastern Pacific Ocean April-May, 1998. (NPAFC Doc. 344.) 33p. Auke Bay Laboratory, Nat. Mar. Fish. Serv., USA.

Carlson, H.R., E.V. Farley, Jr., and K.W. Myers. 2000. The use of thermal otolith marks to determine stock-specific ocean distribution and migration patterns of Alaskan pink and chum salmon in the North Pacific Ocean 1996-1999. N. Pac. Anadr. Fish Comm. Bull. No. 2: 291-3000.

Chuchukalo, V.I., A.F. Volkov, A. Ya. Efimkin, and N.A. Kuznetsova. 1995. Feeding and daily rations of sockeye salmon (Oncorhynchus nerka) during the summer period. NPAFC Doc. 125. Pac. Res. Inst. Fish. and Oceanogr. (TINRO), Vladivostok. 9 p.

Dat, C.G., P.H. LeBlond, K.A. Thomson, and W.J. Ingraham. 1995. Computer simulations of homeward-migrating Fraser River sockeye salmon: is compass orientation a sufficient direction-finding mechanism in the north-east Pacific Ocean? Fish. Oceanogr. 4:209-216.

Davis, N.D. 2003. Feeding ecology of Pacific salmon (*Oncorhynchus* spp.) in the central North Pacific Ocean and central Bering Sea, 1991-2000. Ph.D. Dissertation. Hokkaido University. 190 p.

Davis, N.D., K.W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated ocean growth and prey consumption. N. Pac. Anadr. Fish Comm. Bull. No. 1:146-162.

Davis, N.D., K. Y. Aydin, and Y. Ishida. 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the central Bering Sea in summer. N. Pac. Anadr. Fish Comm. Bull. 2:99-109.

Davis, N.D., J.L. Armstrong, and K.W. Myers. 2004. Bering Sea salmon diet overlap in fall 2002 and potential for interactions among salmon. NPAFC Doc. 779. Sch. Aquat. Fish. Sci., Univ. Washington, Seattle. 30 p.

Davis, N.D., M. Fukuwaka, J.L. Armstrong, and K.W. Myers. 2005. Salmon food habits studies in the Bering Sea, 1960 to present. NPAFC Technical Report No. 6:24-28.

Dell, M.B. 1963. Oceanic feeding habits of the sockeye salmon, *Oncorhynchus nerka* (Walbaum), in Aleutian waters. M.Sc. Thesis, Univ. Michigan, Ann Arbor, USA. 40p.

Dorval, E. 2004. Determination of Essential fish habitat for juvenile spotted seatrout in Chesapeake Bay using trace-element chemistry in surface waters and otoliths. Ph.D. thesis, Old Dominion University, Norfolk, VA 120p.

Dulepova, E.P., and V.I. Dulepov. 2003. Interannual and interregional analysis of chum salmon feeding features in the Bering Sea and adjacent Pacific waters of eastern Kamchatka. (NPAFC Doc. 728). Pac. Res. Fish. Ctr. (TINRO-Centre), Vladivostok. 8 p.

Eggers, D. 2006. Run forecasts and harvest projections for 2006 Alaska salmon fisheries and review of the 2005 season. Special Publication No. 06-07. Alaska Department of Fish and Game.

Eggers, D.M., K. Rowell, and B. Barrett. 1991. Stock composition of sockeye and chum salmon catches in southern Alaska Peninsula fisheries in June. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Research Bulletin No. 91-01. 49 p.

Elliott, J.M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. J. Animal Ecol. 47: 977-991.

Farley, E.V., Jr., and K. Munk. 1998. Incidence of thermally marked pink, chum and sockeye salmon in the coastal waters of the Gulf of Alaska, 1997. NPAFC Doc. 341. Auke Bay Laboratory, Alaska Fisheries Science Center, NMFS, NOAA, 11305 Glacier Highway, Juneau, AK 99801-8626. 18 p.

Farley, E.V., Jr., J.M. Murphy, R.E. Haight, G.M. Guthrie, C.T. Baier, M.D. Adkison, V.I. Radchenko, and F.R. Satterfield. 1999. Eastern Bering Sea (Bristol Bay) coastal research on Bristol Bay juvenile salmon, July and September 1999. N. Pac. Anadr. Fish Comm. Doc. 448. 22 p.

Farley, E.V., Jr., R.E. Haight, B.L. Wing, E.D. Martinson, C.M. Guthrie III, J.H. Helle, and M.D. Adkison. 2000a. Factors affecting distribution, migration, and growth of juvenile sockeye salmon in the Eastern Bering Sea (July and September 1999). NPAFC Tech. Rep. 2, pp. 25-27.

Farley, E.V., Jr., R.E. Haight, C.M. Guthrie III, and J.E. Pohl. 2000b. Eastern Bering Sea (Bristol Bay) coastal research on juvenile salmon, August 2000. N. Pac. Anadr. Fish Comm. Doc. 499. 18 p.

Farley, E.V., Jr., C.M. Guthrie III, S. Katakura, and M. Koval. 2001. Eastern Bering Sea (Bristol Bay) coastal research (August and September 2001) on juvenile salmon. N. Pac. Anadr. Fish Comm. Doc. 560. 19 p.

Farley, E.V., Jr., B. Wing, A. Middleton, J. Pohl, L. Hulbert, J. Moss, M. Trudel, E. Parks, T. Hamilton, C. Lagoudakis, and D. McCallum. 2003. Eastern Bering Sea (BASIS) coastal research (August-October 2002) on juvenile salmon. N. Pac. Anadr. Fish Comm. Doc. 678. 25 p.

Farley, E.V. Jr., J. Murphy, A. Middleton, L. Eisner, J. Moss, J. Pohl, O. Ivanov, N. Kuznetsova, M. Trudel, M. Drew, C. Lagoudakis, and G. Yaska. 2004. Eastern Bering Sea (BASIS) coastal research (Aug-Oct 2003) on juvenile salmon. (NPAFC Doc. 816.) Auke Bay Lab., Nat. Mar. Fish. Serv., Juneau. 29 p.

Farley, E.V., Jr., J.M. Murphy, B.W. Wing, J.H. Moss, and A. Middleton. 2005. Distribution, migration pathways, and size of western Alaska juvenile salmon along the eastern Bering Sea shelf. Alaska Fish. Res. Bull. 11:15-26.

Francis, R.A., and S.R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the northeast Pacific: a case for historical science. Fish. Oceanogr. 3:279-291.

Fredin, R.A., R.L. Major, R.G. Bakkala, and G.K. Tanonaka. 1977. Pacific salmon and the high seas salmon fisheries of Japan. National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Seattle. 324 p. (processed report)

French, R., and J.E. Mason. 1964. Salmon distribution and abundance on the high seas—winter season 1962 and 1963. Int. N. Pac. Fish. Comm. Annu. Rep. 1963: 131-141.

French, R.R., R. Bakkala, and D.F. Sutherland. 1975. Ocean distribution of stocks of Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdnerii*, as shown by tagging experiments: charts of tag recoveries by Canada, Japan, and the United

States, 1956-69. National Oceanic and Atmospheric Administration Tech. Rep NMFS SSRF-689. 89 p.

French, R., H. Bilton, M. Osako, and A. Hartt. 1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. N. Pac. Fish. Comm. Bull. 34.

French, R., R. Nelson, Jr., and J. Wall. 1982. Role of the United States observer program in management of foreign fisheries in the northeast Pacific Ocean and eastern Bering Sea. N North American Journal of Fisheries Management 2:122-131.

Fretwell, S.D., and H.J. Lucas Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor. 19:16-36.

Friedland, K.D., R.V. Walker, N.D. Davis, K.W. Myers, G.W. Boehlert, S. Urawa, and Y. Ueno. 2001. Open-ocean orientation and return migration routes of chum salmon based on temperature data from data storage tags. Mar. Ecol. Prog. Ser. 216: 235-252.

Fukuwaka, M., T. Azumaya, Y. Ishida, T. Meguro, and Y. Kajiwara. 1999. Ocean condition and Pacific salmon stock assessment in the North Pacific Ocean, 1999. NPAFC Doc. 415. Hokkaido National Fisheries Research Institute, Fisheries Agency of Japan, Kushiro.

Fukuwaka, M., N. Davis, T. Onuma, A. Jodo, M. Nomura, amd S. Tsuchiya. 2003a. International salmon research aboard the R/V *Wakatake maru* in the central North Pacific Ocean and Bering Sea during the summer of 2003. NPAFC Doc. 716. Hokkaido Nat. Fish. Res. Inst., Fish. Res. Agency, Kushiro. 21 p.

Fukuwaka, M., S. Urawa, K. Hirasawa, N. Davis, and R. Walker. 2003b. Recoveries of high-seas tags in Japan in 2002, and tag releases and recoveries of fin-clipped salmon from Japanese research vessel surveys in the North Pacific Ocean in fall of 2002 and summer of 2003. NPAFC Doc. 715. Hokkaido Nat. Fish. Res. Inst., Fish. Res. Agency, Kushiro 11 p.

Glebov, I.I. 1998. Chinook and coho salmon feeding habits in the Far Eastern seas in the course of yearly migration cycle. NPAFC Doc. 378. Pac. Res. Fish. Centre (TINRO) Vladivostok. 57 p.

Grebmeier, J.M., J.E. Overland, S.E. Moore, E.V. Farley, E.C. Carmack, L.W. Cooper, K.E. Frey, J.H. Helle, F.A. McLaughlin, S.L. McNutt. 2006. A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464.

Habicht, C., N.V. Varnavskaya, T. Azumaya, S. Urawa, R.L. Wilmot, C.M. Guthrie III, and J.E. Seeb. 2005. Migration patterns of sockeye salmon in the Bering Sea discerned from stock composition estimates of fish captured during BASIS studies. N. Pac. Anadr. Fish Comm. Tech. Rep. 6:41-43.

Hanson, P.C., T.B. Johnson, D.E. Schindler, and J.F. Kitchell. 1997. Fish Bioenergetics 3.0. Software published by University of Wisconsin Sea Grant and Center for Limnology, University of Wisconsin-Madison. WISCU-T-97-001.

Harris, C.K. 1987. Catches of North American sockeye salmon (*Oncorhynchus nerka*) by the Japanese high seas salmon fisheries, 1972-84, p. 458-479. In H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Hartt, A.C. 1980. Juvenile salmonids in the oceanic ecosystem-the first critical summer. In Salmonid ecosystems of the North Pacific, Edited by W. J. McNeil and D.C. Himsworth. Oregon State Univ. Press, Corvallis, OR. pp. 25-37.

Hartt, A.C., and M.B. Dell. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. Int. North Pac. Fish. Comm. Bull. No. 46, 105 p.

Helle, J.H., K.W. Myers, and J.E. Seeb. 2005. National overview of BASIS research for the United States. NPAFC Technical Report No. 6:13-15.

Hiramatsu, K., and Y. Ishida. 1989. Random movement and orientation in pink salmon (*Oncorhynchus gorbuscha*) migrations. Can. J. Fish. Aquat. Sci. 46: 1062-1066.

Hunt, G.L., Jr., P. Stabeno, G. Walters, E. Sinclair, R.D. Brodeur, J.M. Napp, and N.A. Bond. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res. II 49 (26):5821-5853.

Ignell, S.E., C.M. Guthrie III, J.H. Helle, and K. Munk. 1997. Incidence of thermally-marked chum salmon in the 1994-96 Bering Sea Pollock B-season trawl fishery. NPAFC Doc. 246. Auke Bay Laboratory, Alaska Fisheries Science Center, NMFS, NOAA, 11305 Glacier Highway, Juneau, AK 99801-86-26. 16 p.

IPCC (Intergovernmental Panel on Climate Change). 2001. Climate Change 2001: Synthesis Report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. [Watson, R.T., and the Core Writing Team (eds.)] Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA. 398 pp.

Isakson, J.S., J.P. Houghton, D.E. Rogers, and S.S. Parker. 1986. Fish use of inshore habitats north of the Alaska Peninsula June – September 1984 and July-July 1985. Final Report Outer Continental Shelf Environmental Assessment Program Research Unit 659. 380 p.

Ishida, Y., S. Ito, Y. Ueno, and J. Sakai. 1998. Seasonal growth patterns of Pacific salmon (*Oncorhynchus* spp.) in offshore waters of the North Pacific Ocean. N. Pac. Anadr. Fish Comm. Bull. No. 1:66-80.

Ishida, Y., T. Azumaya, M. Fukuwaka, and N. Davis. 2002. Interannual variability in stock abundance and body size of Pacific salmon in the central Bering Sea. Prog. Oceanogr. 55:223-234.

Ishida, Y., T. Azumaya, M. Fukuwaka, and T. Nagasawa. 2005. Density dependent growth of pink salmon *Oncorhynchus gorbuscha* in the Bering Sea. N. Pac. Anadr. Fish Comm. Tech. Rep. 6:47.

Ito, J. 1964. Food and feeding habit of Pacific salmon (Genus *Oncorhynchus*) in their oceanic life. Hokkaido Suisan Shinkenjo Hokoku 29: 85-97. (Translated from Japanese by Fish. Res. Bd. Can. Transl. Ser. No. 1309.)

Jackson, R.I., and W.F. Royce. 1986. Ocean forum: an interpretative history of the International North Pacific Fisheries Commission. Fishing News Books Ltd., Farnham, Surrey, England. 240 pp.

Kanno, Y., and I. Hamai. 1972. Food of salmonid fish in the Bering Sea in summer of 1966. Bull. Fac. Fish. Hokkaido Univ. 22:107-128.

Karpenko, V.I. 1979. Feeding habits of juvenile Pacific salmon in the coastal waters of Kamchatka. Sov. J. of Marine Biology 5(5):398-405.

Karpenko, V.I. 1982a. Diurnal feeding rhythm of young salmon during the initial stage of marine life. J. Ichthyol. 22(2): 131-134.

Karpenko, V.I. 1982b. Biological peculiarities of juvenile coho, sockeye, and Chinook salmon in coastal waters of east Kamchatka. Soviet J. Mar. Biol. 8(6).317-324.

Karpenko, V.I. 1983. Influence of environmental factors on qualitative parameters of juvenile far-eastern salmon of the genus *Oncorhynchus* (Salmonidae) in Kamchatkan waters of the Bering Sea. J. of Ichthyol. 23(5): 93-101.

Karpenko, V.I. 2003. Review of Russian marine investigations of juvenile Pacific salmon. N. Pac. Anadr. Fish Comm. Bull. 3:69-88.

Karpenko, V.I., and V.V. Maksimenkov. 1988. Preliminary data on the interactions between Pacific salmon and herring during early ontogeny. J. Ichthyol. 28(5): 136-147.

Karpenko, V.I., and E.T. Nikolaeva. 1989. Daily feeding rhythm and rations of juvenile chum salmon, Oncorhynchus keta, during river and early marine part of their life cycle. J. of Ichthyol. 29(4):75-82.

Karpenko, V.I., and L.V. Piskunova. 1984. Importance of macroplankton in the diet of young salmons of Genus *Oncorhynchus* (Salmonidae) and their trophic relationships in the southwestern Bering Sea. J. Ichthyology 24(5):98-106.

Karpenko, V.I., and V.P. Smorodin. 2001. Distribution characteristics of pink and chum salmon juveniles in the western Bering Sea. Pages 101-114 *in* K. Neeley, O. Johnson, J. Hard, and K. Myers (eds.) Proceedings of the Northeast Pacific Pink and Chum Salmon Workshop, March 21-31, 2001, Seattle, Washington.

Karpenko, V.I., V.G. Erokhin, and V.P. Smorodin. 1998. Abundance and biology of Kamchatkan salmon during the initial year of ocean residence. N. Pac. Anadr. Fish Comm. Bull. No. 1:352:366.

Khen, G.V., and E. O. Basyuk. 2005. Oceanographic condition of the Bering Sea in BASIS. N. Pac. Anadr. Fish Comm. Tech. Rep. 6:21-23.

Kitagawa, M., T. Azumaya, K.W. Myers, M. Kaeriyama. 2005. Spatial comparison of the feeding ecology of sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) in the ocean during the summer of 2003. NPAFC Tech. Rep. 6:31-34.

Klovach, N., and A. Gruzevich. 2004. Results of 2003 salmon research cruise of the SRTMK "Sovremennik" (NPAFC Doc. 767). 32p. Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), Russia.

Klovach, N.V., L.A. Rzhannikova, S.B. Gorodovskaya. 1996. Biological characteristics of the chum salmon *Oncorhynchus ket*a during the summer period of foraging in the sea. J. Ichthyol. 36(8): 591-599.

Klovach, N.V., V.I. Karpenko, A.E. Bobyrev, A.K. Gruzevich, E.M. Klovach, and S.S. Kozlov. 2002. Atlas of marine distribution of Pacific salmons during the spring-summer feeding and pre-spawning migrations. O.F. Gritsenko (editor). VNIRO Publishing, Moscow.

Koo, T. S. Y. 1962. Age designation in salmon. Pages 41-48 in T. S. Y. Koo, editor. Studies of Alaska red salmon. University of Washington Press, Seattle.

Koval, M.V., and V.I. Karpenko. 1998. Feeding of Pacific salmon during anadromous migrations in the Kamchatkan waters. (NPAFC Doc. 365). 11p. Kamchatka Fishery and Oceanography Research Institute (KamchatNIRO), Russia.

Kruse, G. H. 1998. Salmon run failures in 1997-1998: A link to anomalous ocean conditions? Alaska Fishery Research Bulletin 5(1):55-63.

Machidori, S. 1968. Vertical distribution of salmon (Genus *Oncorhynchus*) in the Northwestern Pacific III. Bull. Hokkaido Reg. Fish. Res. Lab. 34: 1-11. (In Japanese with English summary.)

Mahnken, C., G. Ruggerone, W. Waknitz, and T. Flagg. 1998. A historical perspective on salmonid production from Pacific rim hatcheries. N. Pac. Anadr. Fish Comm. Bull. 1:38-53.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. 78:169-1079.

Martin, D.J., D.R. Glass, C.J. Whitmus, C.S. Simenstad, D.A. Milward, E.C. Volk, M.L. Stevenson, P. Nunes, M. Savoie, and R.A. Grotefendt. 1986. Distribution, seasonal abundance, and feeding dependencies of juvenile salmon and non-salmonid fishes in the Yukon River Delta. U.S. Dep. Commer., NOAA, Outer Continental Shelf Environmental Assessment Program (OCSEAP), Final Rep. 55: 381-770.

Mauchline, J. 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18:1-677.

Moiseev, P.A. 1956. High-seas salmon fisheries in the North Pacific. P. 55-63 *in* Pacific salmon: selected articles from Soviet periodicals. Israel Program for Scientific Translations, Jerusalem 1961. (Translated from Russian, Rybnoe khozyaistvo 32(4):54-59).

Morita, K., N. Davis, A. Urano, M. Abe, and Y. Ito. 2004. The 2004 Japan-U.S. cooperative high-seas salmon research cruise of the R/V *Wakatake maru*. NPAFC Doc. 787. Hokkaido Nat. Fish. Res. Inst., Fish. Res. Agency, Kushiro. 20 p.

Murphy, J., N. Davis, O. Ivanov, M. Rohr, S. Elmajatii, W. Barber. 2003. Cruise report of the 2002 F/V *Norwest Explorer* BASIS survey in the Bering Sea, September-October. NPAFC Doc. 676 Rev. 1. NMFS Auke Bay Lab., Sch. Aquat. Fish. Sci., Univ. Washington, TINRO-Centre, Vladivostok, Alaska Quaternary Ctr., Univ. Alaska Fairbanks, Inst. Mar. Sci., Univ. Alaska Fairbanks. 24 p.

Myers, K.W., and D.E. Rogers. 1988. Stock origins of Chinook salmon in incidental catches by groundfish fisheries in the eastern Bering Sea. North American Journal of Fisheries Management 8:162-171.

Myers, K.W., C.K. Harris, C.M. Knudsen, R.V. Walker, N.D. Davis, and D.E. Rogers. 1987. Stock origins of Chinook salmon in the area of the Japanese mothership salmon fishery. North American Journal of Fisheries Management 7: 459-474.

Myers, K.W., R.V. Walker, S. Fowler, and M.L. Dahlberg. 1990. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956-1989. Int. N. Pac. Fish. Comm. Doc. FRI-UW-9009. Fish. Res. Inst., Univ. Washington, Seattle. 57 p.

Myers, K.W., C.K. Harris, Y. Ishida, L. Margolis, and M. Ogura. 1993. Review of the Japanese landbased driftnet salmon fishery in the western North pacific Ocean and the continent of origin of salmonids in this area. International North Pacific Fisheries Commission Bulletin No. 52.

Myers, K.W., K.Y. Aydin, R.V. Walker, S. Fowler, and M.L. Dahlberg. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956-1995. North Pacific Anadromous Fish Commission Document 192. FRI-UW-9614. Fisheries Research Institute, University of Washington, Seattle.

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

Myers, K.W., R.V. Walker, J.L. Armstrong, and N.D. Davis. 2003. Estimates of the bycatch of Yukon River Chinook salmon in U.S. groundfish fisheries in the eastern Bering Sea, 1997-1999. Final Report to the Yukon River Drainage Fisheries Association, Contr. No. 04-001. SAFS-UW-0312, School of Aquatic and Fishery Sciences, University of Washington, Seattle. 59 p.

Myers, K.W., R.V. Walker, N.D. Davis, and J.L. Armstrong. 2004a. High seas salmon research program, 2003. SAFS-UW-0402, School of Aquatic and Fishery Sciences, University of Washington, Seattle. 93 p.

Myers, K.W., R.V. Walker, J.L. Armstrong, N.D. Davis, and W.S. Patton. 2004b. Stock origins of Chinook salmon in incidental catches by groundfish fisheries in the eastern Bering Sea, 1997-1999. N. Pac. Anadr. Fish Comm. Technical Report 5:74-75.

Myers, K.W., R.V. Walker, N.D. Davis, and R.L. Burgner. 2004c. A history of U.S. high seas salmon and steelhead stock identification research. N. Pac. Anadr. Fish Comm. Tech. Rep. 5:16-17.

Myers, K.W., N.D. Davis, A.G. Celewycz, E.V. Farley, Jr., J. Morris, M. Trudel, M. Fukuwaka, S. Kovalenko, and A. Shubin. 2005. High seas salmonid coded-wire tag recovery data, 2005. (NPAFC Doc. 905.) SAFS-UW-0505, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA. 42 p.

Nagasawa, T., T. Azumaya, and M. Fukuwaka. 2005. Which salmon are using the Bering Sea as their feeding area? NPAFC Tech. Rep. 6:8-10.

Nagasawa, T., M. Fukuwaka, S. Urawa, K. Hirasawa, N. Davis, and R.V. Walker. 2004. Recoveries of high-seas tags in Japan in 2003, and tag releases and recoveries of fin-clipped salmon from Japanese research vessel surveys in the North Pacific Ocean in fall of 2003 and summer of 2004. NPAFC Doc. 786. Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 116 Katsurakoi, Kushiro 085-0802. 13 p.

(NMFS) National Marine Fisheries Service. 1997. NMFS declares commercial fisheries failure in Alaska's Bristol Bay/Kuskokwim salmon fishery, November 6, 1997. NOAA 97-R167. http://www.publicaffairs.noaa.gov/pr97/nov97/noaa97-r167.html

Neave, F., T. Yonemori, and R.G. Bakkala. 1976. Distribution and origin of chum salmon in offshore waters of the North Pacific Ocean. Int. N. Pac. Fish. Comm. Bull. 35.

Nero, R.W., and M.E. Huster. 1996. Low-frequency acoustic imaging of Pacific salmon on the high seas. Can. J. Fish. Aquat. Sci. 53:2513-1523.

Ney, J.J. 1990. Trophic economics in fisheries: Assessment of demand-supply relationships between predators and prey. Rev. Aquat. Sci. 2: 55-81.

Nishiyama, T. 1974. Energy requirement of Bristol Bay sockeye salmon in the central Bering Sea and Bristol Bay. pp. 321-343. In D.W. Hood and E.J. Kelley (eds.). Oceanography of the Bering Sea with emphasis on renewable resources. Occasional Publ. No. 2. Inst. Mar. Sci., Univ. Alaska, Fairbanks.

Nishiyama, T. 1977. Food-energy requirements of Bristol Bay sockeye salmon Oncorhynchus nerka (Walbaum)during the last marine life stage. Res. Inst. N. Pac. Fish. Spec. Vol. 289-320. (In Japanese, English summary).

Nomura, T., and N.D. Davis. 2005. Lipid and moisture content of salmon prey organisms and stomach contents of chum, pink, and sockeye salmon in the Bering Sea. NPAFC Technical Report 6:59-61.

NPAFC (North Pacific Anadromous Fish Commission). 1993. Handbook: Convention for the Conservation of Anadromous Stocks in the North Pacific Ocean. Vancouver, B.C., Canada. 25 pp.

NPAFC (North Pacific Anadromous Fish Commission). 2001a. Plan for NPAFC Bering-Aleutian Salmon International Survey (BASIS), 2002-2006. (NPAFC Doc. 579, Rev. 2). 27p. N. Pac. Anadr. Fish Comm., Canada.

NPAFC (North Pacific Anadromous Fish Commission). 2001b. CD-Rom Statistical Yearbook 2000-2001 and Historical Data. Vancouver, BC.

NPAFC (North Pacific Anadromous Fish Commission). 2002. Report of the Bering-Aleutian Salmon International Survey (BASIS) Working Group Meeting, Vladivostok, Russia. NPAFC Doc. 599. Vancouver, B.C. 11 p.

NPAFC (North Pacific Anadromous Fish Commission). 2003. A review of the research on the early marine period of Pacific salmon by Canada, Japan, Russia, and the United States. N. Pac. Anadr. Fish Comm. Bull. 3.

NPAFC (North Pacific Anadromous Fish Commission). 2003b. Annual report of the Bering-Aleutian Salmon International Survey (BASIS), 2002. (NPAFC Doc. 684, Rev. 1.) 38 p. Vancouver, B.C., Canada.

North Pacific Anadromous Fish Commission (NPAFC). 2004a. Workshop on application of stock identification in defining marine distribution and migration of salmon. N. Pac. Anadr. Fish Comm. Tech. Rep. 5.

NPAFC (North Pacific Anadromous Fish Commission). 2004b. Report of the Research Planning and Coordinating Meeting. NPAFC Doc. 761. North Pacific Anadromous Fish Commission, Vancouver, B.C., Canada.

NPAFC (North Pacific Anadromous Fish Commission). 2004c. Annual report of the Bering-Aleutian Salmon International Survey (BASIS), 2003. (NPAFC Doc. 769.) 78 p. Vancouver, B.C., Canada

NPAFC (North Pacific Anadromous Fish Commission). 2005a. Annual report of the Bering-Aleutian Salmon International Survey (BASIS), 2004. NPAFC Doc. 857. BASIS Working Group, North Pacific Anadromous Fish Commission, Vancouver, B.C., Canada. 105 p.

NPAFC (North Pacific Anadromous Fish Commission). 2005b. North Pacific Anadromous Fish Commission Science Plan 2006-2010. NPAFC Doc. 921. 19 p. Committee on Scientific Research and Statistics (CSRS), North Pacific Anadromous Fish Commission, Vancouver, B.C., Canada.

NPAFC Working Group on Stock Assessment. 2003. A provisional report on the 2003 salmon season. North Pacific Anadromous Fish Commission Document 738. 16 p.

NRC (National Research Council). 2005. Developing a research and restoration plan for Arctic-Yukon-Kuskokwim (Western Alaska) salmon. The National Academies Press, Washington, D.C. 207 pp.

Ogura, M. 1999. Rapid dives and ascents of sockeye salmon *Oncorhynchus nerka* observed by ultrasonic telemetry in the open sea. Fish. Sci. 65: 659-660.

Ogura, M., and Y. Ishida. 1992. Swimming behavior of coho salmon, *Oncorhynchus kisutch*, in the open sea as determined by ultrasonic telemetry. Can. J. Fish. Aquat. Sci. 49: 453-457.

Ogura, M., and Y. Ishida. 1995. Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus* spp.) in the central Bering Sea. Can. J. Fish. Aquat. Sci. 52: 532-540.

Ogura, M., and S. Ito. 1994. Change in the known ocean distribution of Japanese chum salmon, *Oncorhynchus keta*, in relation to the progress of stock enhancement. Can. J. Fish. Aquat. Sci. 51:501-505.

Onuma, T., S. Sato, A. Jodo, N.D. Davis, H. Ando, M. Ban, M. Fukuwaka, and A. Urano. 2005. Changes in chum salmon plasma levels of steroid hormones during onset of the spawning migration in the Bering Sea. NPAFC Technical Report 6:104-106.

Overland, J.E., and P.J. Stabeno. 2004. Is the climate of the Bering Sea warming and affecting the ecosystem. EOS 85(33):309-316.

Patton, W.S., K.W. Myers, and R.V. Walker. 1998. Origins of chum salmon caught incidentally in the Eastern Bering Sea walleye Pollock trawl fishery as estimated from scale pattern analysis. N. Am. J. Fish. Managmt. 18:704-712.

Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids. Univ. Wash. Press, Seattle.

Pella, J., R. Rumbaugh, L. Simon, M. Dahlberg, S. Pennoyer, and M. Rose. 1993. Incidental and illegal catches of salmonids in North Pacific driftnet fisheries. International North Pacific Fisheries Commission Bulletin 53: 325-358.

PICES. 2004. Marine ecosystems of the North Pacific. PICES Special Publication 1. 280 p.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. Univ. Wash. Press, Seattle. 378 pp.

Radchenko, V.I., and A.I. Chigirinsky. 1995. Pacific salmon in the Bering Sea NPAFC Doc. 122. Pac. Res. Inst. Fish. Oceanogr. (TINRO), Vladivostok. 80 p.

Radchenko, V.I., and I.I. Glebov. 1998a. On vertical distribution of Pacific salmon in the Bering Sea, collected by trawling data. J. Ichthyology 38: 603-608.

Radchenko, V.I., and I.I. Glebov. 1998b. Incidental by-catch of Pacific salmon during Russian bottom trawl surveys in the Bering Sea and some remarks on its ecology. N. Pac. Anadr. Fish Comm. Bull. 1: 367-374.

Radchenko, V.I., and O.A. Mathisen. 2004. Distribution, growth, and feeding of sockeye salmon in the western Bering Sea. Trans. Amer. Fish. Soc. 133: 606-621.

Rand, P.S., J.P. Scandol, and E.E. Walter. 1997. NerkaSim: a research and education tool to simulate salmon in a dynamic ocean environment. Fisheries 22(10):6-13.

Rogers, D.E. 1977. Determination and description of knowledge of the distribution, abundance, and timing of salmonids in the Gulf of Alaska and Bering Sea. A supplement to the final report to Outer Continental Shelf Assessment Program (OCEAP) covering salmonids in Bristol Bay (St. George Basin Region). FRI-UW-7736, Fisheries Research Institute, Univ. Wash., Seattle. 29 p.

Rogers, D.E. 1986. Pacific salmon. Pages 461-476. *In* D.W. Hood and S.T. Zimmerman (eds.). The Gulf of Alaska: physical environment and biological resources. U.S, National Ocean Service, Ocean Assessments Div., Alaska Office; U.S. Minerals Management Serv., Alaska OCS Region, Washington, D.C.

Rogers, D.E. 1987. Interceptions of Yukon salmon by high seas fisheries. FRI-UW-8705, Fisheries Research Institute, School of Fisheries, University of Washington, Seattle. 34 pp.

Rogers, D.E. 1988. Bristol Bay smolt migrations, timing and size composition and the effects on distribution and survival at sea. *In* Salmon production, management, and allocation. *Edited by* W.J. McNeil, Oregon State University Press, Corvallis, p. 87-101.

Royce, W.F., L.S. Smith, and A.C. Hartt. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. U.S. Fish Wildl. Serv., Fish. Bull. 66:441-462.

Seeb, L.W., Crane, P.A., Kondzela, C.M., Wilmot , R.L., Urawa, S., Varnavskaya, N.V., and Seeb, J.E. 2004. Migration of Pacific Rim salmon on the high seas: insights from genetic data. Environmental Biol. Fishes 69: 21-36.

Shaul, A.R. 2003. South Unimak and Shumagin Islands June salmon fishery, report to the Alaska Board of Fisheries, 2004. Regional Information Report No. 4K03-65, Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 68 p.

Shaul, A.R., C. Burkey, Jr., J.J. Dinnocenzo, and S. Duesterloh. 2004. South Unimak and Shumagin Islands June salmon fishery management plan, 2003. Regional Information Report No. 4K04-8, Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 10 p.

Shaul, A.R., C. Burkey, Jr., J.J. Dinnocenzo, and S. Duesterloh. 2004b. Post-June salmon management plan for the South Alaska Peninsula, 2004. Regional Information Report No. 4K04-7, Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 22 p.

Shepard, M.P., A.C. Hartt, and T. Yonemori. 1968. Salmon of the North Pacific Ocean-Part VII. Chum salmon in offshore waters. Int. N. Pac. Fish. Comm. Bull. 25:69.

Shuntov, V.P. 1994. New data on marine period of life of Asian pink salmon. Izv. TINRO 116: 3-41. In Russian; as cited by Karpenko (2003).

Shuntov, V.P., V.I. Radchenko, V.V. Lapko, and Yu.N. Poltev. 1993. Distribution of salmon in the western Bering Sea and neighboring Pacific Waters. J. Ichthyology 33(7): 48-62.

Smorodin, V., A. Dekshtein, V. Davydenko, E. Luchinski, and V. Docenko. 2001. Results of 2000 salmon research cruise of the STR “Sajanogorsk”. NPAFC Doc. 524. KamchatNIRO, Petropavlovsk-Kamchatski. 14 p.

Smorodin, V.P., M.V. Koval, O.B. Tepnin, A.V. Morozova. 2004. The results of trawling survey in the southwest Bering Sea during September-October 2002 STR “Koryaksky”. (NPAFC Doc. 782). 48p. Kamchatka Fishery and Oceanography Research Institute (KamchatNIRO), Russia.

Sobolevskiy, E.I., V.I. Radchenko, and A.V. Startsev. 1994. Distribution and diet of chum salmon, *Oncorhynchyus keta*, in the fall-winter period in the western part of the Bering Sea and Pacific Ocean waters of Kamchatka. J. Ichthyology 34(4): 92-101.

Sobolevskiy, E.I., and I.A. Senchenko. 1996. The spatial structure and trophic connections of abundant pelagic fish of eastern Kamchatka in the autumn and winter. J. Ichthyol. 36(1): 30-39.

Straty. R.R. 1974. Ecology and behavior of juvenile sockeye salmon (Oncorhynchus nerka) in Bristol Bay and the eastern Bering Sea. Pp. 285-320. In D.W., Hood and E.J. Kelley (eds.). Oceanography of the Bering Sea With emphasis on renewable resources. Occasional Publ. No. 2. Inst. Mar. Sci. Univ. Alaska, Fairbanks.

Straty, R.R. 1981. Trans-shelf movements of Pacific salmon. In The Eastern Bering Sea: Oceanography and Resources. Edited by D.W. Hood and J.A. Calder. U.S. Dept. Comm. pp. 575-595.

Straty, R.R. and H.W. Jaenicke. 1980. Estuarine influence of salinity, temperature, and food on the behavior, growth, and dynamics of Bristol Bay sockeye salmon. In Salmonid ecosystems of the North Pacific, Edited by W. J. McNeil and D.C. Himsworth. Oregon State Univ. Press, Corvallis, OR. pp. 247-265.

Stevens, T. 2000. Administration declares fisheries disaster for Western Alaska. US Senator Ted Stevens' Home page, August 3, 2000.

Tadokoro, K., Y. Ishida, N.D. Davis, S. Ueyanagi, and T. Sugimoto. 1996. Change in chum salmon (*Oncorhynchus keta*) stomach contents associated with fluctuation of pink salmon (*O. gorbuscha*) abundance in the central subarctic Pacific and Bering Sea. Fish. Oceanogr. 5(2):89-99.

Takeuchi, I. 1972. Food animals collected from the stomachs of three salmonid fishes (*Oncorhynchus*) and their distribution in the natural environments in the northern North Pacific. Bull Hokkaido Reg. Fish. Res. Lab. 38:1-119.

Takagi, K., K.V. Aro, A.C. Hartt, and M.B. Dell. 1981. Distribution and origin of pink salmon (*Oncorhynchus gorbuscha*) in offshore waters of the North Pacific Ocean. Int. N. Pac. Fish. Comm. Bull. 40.

Tanaka, H., Y. Naito, N.D. Davis, S. Urawa, H. Ueda, and M. Fukuwaka. 2005. First record of swimming speed of a Pacific salmon undertaking oceanic migration from the central Bering Sea to the Japanese coast. NPAFC Technical Report 6:65-66.

Temnykh, O.S., A.N. Starovoytov, I.I. Glebov, G.V. Khen, A.Ya. Efimkin, A.M. Slabinsky, and V.V. Sviridov. 2003. The results of trawling survey in the epipelagic layer of the Russian economic zone in the Bering Sea during September-October, 2002. (NPAFC Doc. 682 Rev. 2). 39p. Pacific Scientific Research Fisheries Center (TINRO-Center), Russia.

Thayer, G.W., W.E. Schaff, J.W. Angelovic, and M.W. LaCroix. 1973. Caloric measurements for some estuarine organisms. Fish. Bull., U.S., 71:289-296.

Thomson, K.A., W.J. Ingraham, M.C. Healey, P.H. LeBlond, C. Groot, and C.G. Healey. 1992. The influence of ocean currents on latitude of landfall and migration speed of sockeye salmon returning to the Fraser River. Fish. Oceanogr. 1:163-179.

Thomson, K.A., W.J. Ingraham, M.C. Healey, P.H. LeBlond, C. Groot, and C.G. Healey. 1994. Computer simulations of the influence of ocean currents on Fraser River sockeye salmon (*Oncorhynchus nerka*) return times. Can. J. Fish. Aquat. Sci. 51: 441-449.

Ueno, Y., Y. Ishida, K. Nagasawa, and T. Watanabe. 1999. Winter distribution and migration of Pacific salmon. Salmon Rep. Ser. 48:59-82.

Urawa, S. 2000. Ocean migration route of Japanese chum salmon with a reference to future salmon research. National Salmon Resources Center, Newsletter 5:3-9.

Urawa, S., M. Kawana, G. Anma, Y. Kamei, T. Shoji, M. Fukuwaka, K.M. Munk, K.W. Myers, and E.V. Farley, Jr. 2000. Geographic origin of high-seas chum salmon determined by genetic and thermal otolith markers. NPAFC Bull. No. 2:283-290.

Urawa, S., Y. Ueno, Y. Ishida, L.W. Seeb, P.A. Crane, S. Abe, and N.D. Davis. 2001. A migration model of Japanese chum salmon during early ocean life. N. Pac. Anadr. Fish Comm. Tech. Rep. 2:1-2.

Urawa, S. 2004. Stock identification studies of high seas salmon in Japan: a review and future plan. N. Pac. Anadr. Fish Comm. Tech. Rep. Tech. Rep. 5: 9-10.

Utter, F., G. Milner, G. Stahl, and D. Teel. 1989. Genetic population structure of Chinook salmon, *Oncorhynchus tshawytscha*, in the Pacific Northwest. Fish. Bull. 87:239-264.

Volkov, A.F., V.I. Chuchukalo, and A. Ya. Efimkin. 1995. Feeding of Chinook and coho salmon in the northwestern Pacific Ocean. NPAFC Doc. 124. Pac. Res. Inst. Fish. and Oceangr. Vladivostok. 12 p.

Volvenko, I.V. 2005. GIS and atlas of salmons spatial-temporal distribution in the western part of the Bering Sea. N. Pac. Anadr. Fish. Comm. Doc. 880. Pacific Research Fisheries Centre (TINRO-center), Vladivostok. 23 p.

Wada, K., and Y. Ueno. 1999. Homing behavior of chum salmon determined by an archival tag. (NPAFC Doc. 425.) Hokkaido Natl. Fish. Res. Inst., Hokkaido. 29 p.

Walker, R.V., K.W. Myers, N.D. Davis, K.Y. Aydin, K.D. Friedland, H.R. Carlson, G.W. Boehlert, S. Urawa, Y. Ueno, and G. Anma. 2000a. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fish. Oceanogr. 9: 171–186.

Walker, R.V., K.W. Myers, N.D. Davis, K.Y. Aydin, and K.D. Friedland. 2000b. Using temperatures from data storage tags in bioenergetic models of high-seas salmon growth. N. Pac. Anadr. Fish. Comm. Bull. 2: 301-308.

Walker, R.V., N.D. Davis, K.W. Myers, J.M. Murphy, and M. Fukuwaka. 2001. Releases and recoveries of U.S. salmonid data storage tags, and recoveries of high seas tags in North America, 2001. (NPAFC Doc. 556.) AFS-UW-0112. School of Aquatic and Fishery Sciences, University of Washington, Seattle. 11 p.

Walker, R., N. Davis, K. Myers, and M. Fukuwaka. 2003. Releases and recoveries of U.S. salmonid data storage tags, and recoveries of high seas tags in North America, 2003. NPAFC Doc. 722. SAFS-UW-0308. Sch. Aquat. Fish. Sci., Univ. Washington, Seattle. 14 p.

Walker, R.V., N.D., Davis, K.W. Myers, S. Urawa, and K. Hirasawa. 2004. Releases and recoveries of U.S. and NPRB salmonid data storage tags, and recoveries of high seas in North America, 2004. NPAFC Doc. 806. SAFS-UW-0406. Sch. Aquat. Fish. Sci., Univ. Washington, Seattle. 23 p.

Walker, R.V., N.D. Davis, K.W. Myers, and J. H. Helle. 2005. New information from archival tags from Bering Sea tagging, 1998-2004. NPAFC Technical Report 6:38-40.

Walker, R.V., J.H. Helle, K.W. Myers, N.D. Davis, J.M. Murphy, S. Urawa, O.S. Temnykh, V.V. Sviridov, and V.G. Fedorenko. 2006. NPAFC Salmon Tagging. Project no. 204, Final Report to the North Pacific Research Board, Anchorage. 37 p.

Walter, E.E., J.P. Scandol, and M.C. Healey. 1997. A reappraisal of the ocean migration patterns of Fraser River sockeye salmon (*Oncorhynchus nerka*) by individual-based modeling. Can. J. Fish. Aquat. Sci. 54(4):847-858.

Williams, R.N., J.A. Lichatowich, and M.A. Powell. 2006. Diversity, structure, and status of salmon populations. P. 99-171 in R.N. Williams (ed.). Return to the river: restoring salmon to the Columbia River. Elsevier Academic Press, Amsterdam.

Wilmot, R.L., C.M. Kondzela, C.M. Guthrie, and M.S. Masuda. 1998. Genetic stock identification of chum salmon harvested incidentally in the 1994 and 1995 Bering Sea trawl fishery. N. Pac. Anadr. Fish Comm. Bull. 1:285-299.

Winberg, G.G. 1956. Rate of metabolism and food requirements of fish. Fish. Res. Board Can. Transl. Ser. 194. 251 pp.

Windell, J. T. 1978. Digestion and the daily ration of fishes. In Ecology of freshwater fish production. Edited by S.D. Gerking. Blackwell, Oxford. pp. 159-183.

Witherell, D., D. Ackley, and C. Coon. 2002. An overview of salmon bycatch in Alaska groundfish fisheries. Alaska Fishery Research Bulletin 9:53-64.