# BERING SEA SALMON FOOD HABITS: DIET OVERLAP IN FALL AND POTENTIAL FOR INTERACTIONS AMONG SALMON

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**December 2003**

**Amendment to Contract NOAA 2002-01: Extension of Stock Origins of Chinook Salmon in Incidental Catches to include Bering Sea Salmon Food Habits**

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# Bering Sea salmon food habits:
## Diet overlap in fall and potential for interactions among salmon

## Study History

The Yukon River Drainage Fisheries Association (YRDFA) funded this study in spring, 2003, by extending a contract investigating the stock origins of chinook salmon in incidental catches in the Bering Sea (contract number 2002-01 extension). The extension of funding provided for analysis of Bering Sea salmon food habits from samples collected during high-seas trawl survey operations in fall 2002 to show the potential for inter- and intra-specific interactions among salmon in offshore habitats where Yukon River salmon are known to migrate. Analysis of fall samples is important, as there is little information available on food habits of salmon migrating in the Bering Sea at this time of year.

## Abstract

Laboratory analysis and compilation of food habits data from Pacific salmon (*Oncorhynchus* spp.) collected in fall 2002 from the Bering Sea were completed. Samples collected in summer 1991-2002 were analyzed for seasonal (summer-fall 2002) and long-term comparisons of salmon diets. Samples were grouped into three major habitats, representative of the distribution of Yukon River salmon: (1) eastern Bering Sea shelf (<200-m depth contour), (2) central Bering Sea basin (>200-m depth contour), and (3) Aleutian Islands. In fall diet overlap values (modified Schoener's index) were low to moderate for sockeye (*O. nerka*) and chum (*O. keta*) salmon (49%, basin), sockeye and chinook (*O. tshawytscha*, 21%, basin), and chum and chinook (28% basin, 30% shelf). Diet overlap between sockeye and chum salmon was very high (80%) in the Aleutian Islands, where both species consumed macro-zooplankton (crustaceans and pteropods), and was reduced when chum salmon consumed gelatinous zooplankton (medusae and ctenophores). In contrast, chinook salmon consumed predominately small nekton (squid and fish). Shifts in prey composition of sockeye, chum, and chinook salmon between seasons, habitats, and salmon age groups were likely due to changes in prey availability. If prey availability is reduced by poor ocean conditions, then increased food competition could decrease growth and survival of Yukon River salmon in the Bering Sea and Aleutian Islands.

## Key Words

Aleutian, Bering Sea, chinook, chum, diet overlap, food habits, pink, salmon, sockeye.

## Project Data

Project data result from the analysis of salmon stomach content samples collected during the Bering Sea surveys of the R/V *Kaiyo maru* (September 2002) and the F/V *Northwest Explorer* (September-October 2002), and include environmental (sample location and date, sea surface temperature), salmon biological (species, size, sex, age), and food habits data. Data are formatted as Microsoft Excel spreadsheets. Project data are archived by the High Seas Salmon

Research Program, Fisheries Research Institute, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA, USA 98195-5020 (contact: N.D. Davis, ncdd@u.washington.edu, tel. 206-543-7280). There are no access limitations to the project data, but costs associated with filling sample and data requests (staff salaries, data storage media, shipping costs) must be paid by the person(s) or agency requesting the data.

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# Executive Summary

With funding from the Yukon River Drainage Fisheries Association (YRDFA; contract no. 2002-01 extension), we analyzed salmon food habits data from samples collected in fall 2002 in the Aleutian Islands and Bering Sea. Few studies have reported on the ocean food habits of salmon in this region during seasons other than summer. Analysis of fall samples, however, is critical for assessing salmon nutritional status and growth throughout the year. We used salmon food habits data collected in fall and summer to examine seasonal changes in 2002, and compared these results with data collected in summer during odd- and even-numbered years (1991-2001) from salmon collected in the Bering Sea basin. The objectives of this study were to: (1) analyze overlap in salmon food habits by species and habitat in fall 2002, (2) compare results of summer and fall 2002 data with an existing time series of summer Bering Sea salmon food habits (1991-2001), and (3) discuss inter- and intra-specific overlap in salmon food habits in the Bering Sea and speculate on the potential effect of competition on marine growth and survival of Yukon River salmon.

Samples of salmon stomach contents were collected during the September 2002 cruise of the Japanese research vessel *Kaiyo maru*, which conducted a salmon survey in the Bering Sea basin (>200-m depth contour) and the central Aleutian Islands. Stomach contents data were collected during the September-October 2002 salmon survey of the US vessel *Northwest Explorer*, which conducted operations in the Bering Sea basin, western and central Aleutian Islands, and eastern Bering Sea shelf (<200-m depth contour). Examination of the food habits samples collected during the *Northwest Explorer* survey was completed onboard the vessel, however, the development of a food habits database for the *Kaiyo maru* and *Northwest Explorer* samples was completed under this contract. Other data sources included samples collected during the central Bering Sea survey of the *Wakatake maru* (June-July 1991-2002), which were included for seasonal (summer-fall 2002) and long-term comparison (odd-numbered years, 1991-2001 and even-numbered years, 1992-2000) of salmon food habits in the Bering Sea. The *Wakatake maru* data were separated into odd- and even-numbered years because in summer there is a strong cycle with catches showing a 30- to 50-fold increase in pink salmon abundance during odd-numbered years. Biennial fluctuations in pink salmon abundance potentially provide alternating periods of increased (odd-numbered year) and decreased (even-numbered year) pressure from inter- and intra-specific competition for food. Data were stratified into three habitats in the Bering Sea, including basin, Aleutian Islands, and eastern shelf that are representative of the known distribution of Yukon River salmon in this region. Diet overlap was estimated for fall samples using a modified Schoener's index (PSI, percent similarity index), where 0% indicates no diet overlap and 100% indicates complete overlap in diet of two predators. In addition, prey composition was compared graphically by species and habitat for summer and fall 2002 data, and by species, salmon ocean age, and time period for basin data only.

A total of 349 salmon stomachs was analyzed from the fall 2002 cruise of the *Kaiyo maru*, and an additional 467 stomach samples were analyzed from the fall 2002 cruise of the *Northwest Explorer*. The fall results include three pair-wise estimates of diet overlap for the basin (sockeye, chum, and chinook), and one estimate each for the

Aleutian Islands (sockeye and chum) and shelf (chum and chinook salmon). In the Bering Sea basin, diet overlap between sockeye and chum salmon was moderate (PSI=49%), and sockeye and chum salmon consumed the same species and sizes of prey within prey categories having the greatest overlap (euphausiids 17%, fish 17%, amphipods 12%). High consumption of gelatinous zooplankton was unique to chum salmon, and may decrease food competition with sockeye salmon. Diet overlap of sockeye and chinook salmon was low (21%), with overlap mainly in fish prey (17%). Diet overlap between chum and chinook salmon was somewhat higher (28%) because chum salmon consumed more fish prey than did sockeye salmon. Diet overlap between sockeye and chum salmon in the Aleutian Islands was very high (80%), because both salmon consumed large volumes of identical species of euphausiids (44%) and amphipods (27%). Diet overlap between chum and chinook salmon on the shelf was moderate (30%), and fish prey contributed most to the overlap (23%).

There were seasonal and spatial shifts in prey composition within and among salmon species collected in the three habitats. In summer, sockeye salmon in the basin consumed primarily amphipods, followed by euphausiids, squid, and fish, while sockeye salmon collected in the Aleutians Islands ate mostly amphipods and gelatinous zooplankton. In fall, sockeye salmon collected from all three habitats consumed a higher proportion of euphausiids than in summer. Fish were more common in sockeye salmon diets in the basin than in other habitats, and pteropods were more common in their diets on the shelf. Chum consumed a more varied diet than sockeye salmon in summer and fall. In summer, chum salmon in the basin consumed mainly euphausiids and pteropods, and lesser volumes of amphipods, squid, fish, and gelatinous zooplankton, while in the Aleutian Islands, they consumed large volumes of gelatinous zooplankton. In fall pteropods were a very large component of chum salmon diets on the shelf, while their diets in the Aleutian Islands included a large proportion of euphausiids and amphipods. Gelatinous zooplankton were a significant component of the prey of chum salmon in both basin and shelf habitats in fall. Fish consumed by chum salmon in the basin were composed of different species than those consumed on the shelf. Chinook salmon were more specialized consumers. In summer, chinook salmon stomachs collected in the basin contained high volumes of euphausiids, squid, and fish, while in fall they contained relatively low volumes of euphausiids.

Further stratification of data by salmon ocean age showed a seasonal reduction in the diversity of diets of sockeye, chum, and chinook salmon in the basin in fall. Squid was reduced or eliminated from diets of sockeye and chum salmon, and chinook salmon consumption of euphausiids was dramatically reduced in fall. Conversely, fish increased in the diets of sockeye and chum salmon, and squid consumption by chinook salmon increased in fall. Reduction in the diversity of prey groups in fall could be caused by changes in prey availability due to shifts in prey distribution, abundance, or progression of prey life-history stages resulting from seasonal environmental changes. Trends in prey composition by ocean age of salmon also changed between summer and fall. For example, in summer the proportion of euphausiids increased with ocean age of sockeye and chum salmon, however, there was a decrease of euphausiids in older salmon in fall. Ocean age-.1 sockeye and chum salmon in summer consumed a larger proportion of amphipods than older fish, while in fall the amount of amphipods was not related to ocean age. In summer, gelatinous zooplankton increased in the diets of older (ocean age-.3 and -.4) chum salmon, however, in fall less gelatinous zooplankton was consumed by older fish. In summer, fish predominated in the diets of young (ocean age-.1) chinook salmon, while in fall fish consumption was not related to chinook salmon ocean age.

Previous studies have suggested that there are inter- and intra-specific competitive interactions for food among immature and maturing sockeye and chum salmon in the Bering Sea. Although chum salmon have a diverse diet, competition for food within and among stocks may occur when chum salmon are locally abundant. Published analyses indicated that intra-specific competition can cause a reduction in the body size of Japanese chum salmon during their third year of life. Although shifts in the proportions of several prey groups may reduce diet overlap among salmon, these shifts are not without cost. Previous studies have shown dramatic increases in the weight of low energy-density prey in salmon stomach contents in odd-numbered years, when pink salmon were abundant in the central Bering Sea. In addition, bioenergetic models have shown that over relatively short time periods small decreases in daily ration caused by competition, or other causes, could significantly decrease growth.

While previous studies have focused on the inter- and intra-specific interactions among pink, sockeye, or chum salmon, there is no information about these types of interactions for chinook salmon in the Bering Sea. Our estimates of diet overlap suggest there is a relatively low level of inter-specific food competition between immature chinook and immature sockeye or chum salmon. Compared to other salmon species, the low abundance of immature chinook salmon may serve to reduce intra-specific competition at sea. Consumption of nektonic organisms (fish and squid) may be efficient because they are relatively large and have a higher caloric density than zooplankton, such as pteropods and amphipods. However, there is an energetic investment required of chinook salmon to capture actively swimming prey. If nekton abundance is reduced and chinook foraging effort becomes less efficient, then a smaller proportion of ingested energy would be available for chinook salmon growth.

We hypothesize that if salmon prey availability is reduced by predation from abundant stocks of pink and chum salmon, or in combination with adverse climatic and oceanographic changes in the Bering Sea, then increased inter- and intra-specific competition could decrease growth of Yukon River salmon. Furthermore, reduced growth could negatively affect Yukon River salmon survival.

Future studies should focus on determining the season(s), location(s), and salmon life history stage(s) when inter- and intra-specific competition for food is likely to have the greatest impact on growth. This research should include food habits data from all species, age groups (including juvenile (ocean age-.0), immature, and maturing salmon), and seasons. Studies that integrate salmon food habits, prey availability, and bioenergetics are needed, and would substantially increase our understanding of the relationship between inter- and intra-specific competition for food and the ocean growth and survival of salmon.

# Introduction

In 1998, a major economic disaster was declared in western Alaska because of very low salmon (*Oncorhynchus* spp.) returns to commercial and subsistence fisheries (Anonymous 1998). The cause of salmon run failures was linked to changes in marine environmental conditions in the Bering Sea, such as the early retreat of sea ice, decreased winds, and weak water column stratification, that might have shifted plankton community structure and produced feeding conditions less favorable to salmon production (Kruse 1998).

There is increasing evidence that western Alaska stocks of salmon are food limited during their offshore migrations in the North Pacific Ocean and Bering Sea (Rogers 1980, Rogers and Ruggerone 1993, Aydin et al. 2000, Kaeriyama et al. 2000, Ruggerone et al. 2003). A large increase in the abundance of Asian and North American salmon since the mid-to late 1970s corresponded with a decrease in the body size of adult salmon returning to both continents, indicating a limit to the carrying capacity of salmon in the ocean (Kaeriyama 1989, Ishida et al. 1993, Helle and Hoffman 1995, Bigler et al. 1996). During this period, U.S. marine research on salmon carrying capacity focused largely on the early (juvenile) life-history phase, when salmon are migrating in waters over the continental shelf during their first summer at sea (Brodeur et al. 2003). Results of international cooperative high seas salmon research suggest that inter- and intra-specific competition for food and density-dependent growth effects occur primarily among older age groups of salmon, when stocks originating from all geographic regions around the Pacific Rim mix and feed in offshore waters (Ishida et al. 1993, Ishida et al. 1995, Tadokoro et al. 1996, Walker et al. 1998, Azumaya and Ishida 2000, Bugaev et al. 2001, Davis 2003).

A new time-series analysis of scale pattern and abundance data shows a substantial decrease in marine survival of western Alaska salmon during years of peak abundance of Asian salmon (Ruggerone et al. 2003). The period of overlap when marine survival was affected seemed to be from winter of the first year at sea, when western Alaska salmon move off the continental shelf, through at least summer of the second year at sea, when they are distributed across broad regions of the North Pacific Ocean and Bering Sea (Ruggerone et al. 2003). At present there are few data on the food habits of salmon migrating in the Bering Sea in fall, which is probably a critical period for density-dependent growth and survival effects (Nomura et al. 2002).

With funding from the Yukon River Drainage Fisheries Association (YRDFA; contract no. 2002-01 extension), we analyzed salmon food habits data from samples collected in the Bering Sea in fall 2002. The stomach contents data from these collections would be representative of the food habits of all salmon stocks (including Yukon River salmon) migrating in the study area. We compared our fall 2002 data with samples collected in summer 2002, and with data collected in summer during odd- and even-numbered years (1991-2001) from regions representative of the distribution of Yukon River salmon. Diet overlap between sockeye (*O. nerka*) and chum (*O. keta*) increased when chum salmon consumed a high proportion of euphausiids and a lower proportion of gelatinous zooplankton. Diet overlap between chinook (*O. tshawytscha*) salmon and either sockeye or chum salmon was low because chinook salmon were specialized consumers of fish and squid. Samples of stomach contents collected in fall were less diverse in salmon prey composition than samples collected during summer, likely due to changes in prey availability. We hypothesize that if salmon prey availability is reduced, then increased inter- and intra-specific competition could decrease growth and negatively affect Yukon River salmon survival.

## Objectives

Our objectives are those originally defined in the contract's work statement, as follows: (1) analyze overlap in salmon food habits by species and geographic region in fall 2002, (2) compare results of summer and fall 2002 data with an existing time series of summer Bering Sea salmon food habits (1991-2001), and (3) discuss inter-and intra-specific overlap in salmon food habits in the Bering Sea and speculate on the potential for competitive effects on marine growth and survival of Yukon River salmon.

## Methods

### Study Area and Fishing Methods

Station locations were categorized according to three geographic habitats: Bering Sea basin, shelf, and Aleutian Islands. The basin is located north of the Aleutian Islands and west of the shelf. Stations in the basin were located in water depths ranging from 480 m to greater than 1000 m. The Aleutian Islands stations were located in the immediate vicinity of islands (approximately 15 nm north or south or in passes between islands). The depth of Aleutian Islands stations ranged from 85 m to greater than 1000 m. The shelf is the shallow area of the eastern Bering Sea, and stations were located over bottom depths ranging from 39 m to 188 m.

Samples of salmon stomach contents were collected during the September 2002 cruise of the Japanese research vessel *Kaiyo maru*, which conducted a salmon survey in the Bering Sea basin (>200-m depth contour) and the central Aleutian Islands (Fig. 1). In addition, stomach contents data were collected during the September-October 2002 salmon survey of the US vessel *Northwest Explorer*, which conducted operations in the Bering Sea basin, western and central Aleutian Islands, and eastern Bering Sea shelf (<200-m depth contour). Salmon food habits data collected during the central Bering Sea survey of the *Wakatake maru* (June-July 1991-2002) were included for seasonal (summer, 2002) and long-term comparisons (odd-numbered years, 1991-2001, and even-numbered years, 1992-2000) with salmon food habits in 2002. Stations sampled during the *Wakatake maru* 1991-2001 cruises were in essentially the same locations as those sampled in 2002.

Salmon were caught using trawls, gillnets, and longlines. The *Northwest Explorer* and the *Kaiyo maru* caught fish using a surface trawl, however the size of the trawls differed (Azumaya et al. 2003, Murphy et al. 2003a, b). The *Northwest Explorer* used a smaller net, which fished from the surface to an average depth of 17 m, while the *Kaiyo maru* towed a larger net, which fished from the surface to an average depth of 50 m (Murphy et al. 2003b). Both vessels towed the trawl for one hour and, except for one location sampled by the *Northwest Explorer,* all fishing operations were conducted during daylight (Azumaya et al. 2003, Murphy et al. 2003a). The *Wakatake maru* caught fish using a gillnet and a longline (Tanaka et al. 2002). The gillnet was allowed to soak for 12 hours through the late afternoon and night, fished from the surface to approximately 3-m depth, and consisted of 11 different mesh sizes, ranging from 48 m to 158 mm. The longline floated at the surface and baited hooks hung at approximately 1-m depth. The longline was set 30 minutes before sunset and allowed to soak for one hour (Tanaka et al. 2002). Scientists on board the three vessels sorted the salmon catch by species, and a variety of biological data, such as fork length, body weight, sex, gonad weight, and a scale sample for age determination, were collected (Tanaka et al. 2002, Azumaya et al. 2003, Murphy et al. 2003a). Salmon representing a range of body sizes from each species were set aside for food habits analysis.

### Analysis of salmon stomach contents

On board the *Kaiyo maru,* salmon stomach samples were placed individually in labeled bags and stored frozen until they were examined in the laboratory. In the laboratory, each salmon stomach sample was thawed, blotted, and weighed (±0.1 g). The stomach was opened, and the fullness was estimated visually. Stomach contents were removed, the empty stomach was weighed again, and the weight of stomach contents obtained by subtraction. An average digestion stage of stomach contents was estimated, and the stomach contents were sorted to the lowest possible taxonomic group using a binocular dissecting microscope. Life history stage, degree of digestion, and percent volume of each prey group was estimated visually. If the number of prey items in a taxonomic group was less than 100 individuals, then the group was weighed and the number of individuals was counted. In cases where the number of individuals was greater than 100, a subsample was weighed and counted and extrapolated to the whole group. Relatively fresh squid (mantle length, ML) and fish (standard length, SL) prey were measured (± 1 mm). Salmon stomachs collected during the cruise of the *Northwest Explorer* and the *Wakatake maru* were examined by scientists on board the research vessels and followed the same general procedure used in the laboratory. Exceptions to this procedure included the use of scales measuring to ±1 g (rather than 0.1 g), individual prey items were not counted, and the degree of digestion of individual prey groups was not noted.

### Data Analysis

For the fall 2002 samples a modified Schoener's index, called the Percent Similarity Index (PSI), was used to calculate diet overlap between pairwise combinations of sockeye, chum, and chinook salmon in habitats where the sample sizes of both species were each greater than or equal to 15. The PSI is the sum of the proportional volumes of individual prey categories in common between two predators and is calculated according to the formula (Buckley et al. 1999):

$$PSI = \Sigma\ [\min (p_{xi}, p_{yi})]$$

where p is the percentage (or proportion) of prey i in predators x and y. The PSI ranges from 0 to 100%, where 0% indicates no overlap and 100% indicates complete overlap in diet of the two predators.

To examine shifts in prey composition from summer to fall 2002, samples collected in the basin, shelf, and Aleutian Islands were compared graphically. Data were stratified by salmon age, and results from summer and fall 2002 were compared to results of previous data collected in odd- (1991-2001) and even-numbered years (1992-2000) in the Bering Sea basin.

## Results

A total of 349 salmon stomachs was analyzed, including 47 sockeye, 238 chum, 1 pink (*O. gorbuscha*), and 63 chinook salmon, from the fall 2002 cruise of the *Kaiyo maru* (sample dates September 3-18). In addition 467 stomach samples, including 90 sockeye, 302 chum, 1 coho (*O. kisutch*), and 73 chinook salmon and 1 steelhead trout (*O. mykiss*), were analyzed from the fall 2002 cruise of the *Northwest Explorer* (sample dates September 8-October 6). For the seasonal comparison, we used 523 samples, including 141 sockeye, 249 chum, 40 pink, 4 coho, and 89 chinook salmon, from the summer 2002 cruise of the *Wakatake maru* (sample dates June 27-July 14).

In summer and fall 2002, the greatest overlap in station locations occurred in the Bering Sea basin (Fig. 1). The *Wakatake maru* and *Kaiyo maru* each had one station located in the Aleutian Islands, and did not conduct any sampling on the shelf. In contrast, the *Northwest Explorer* surveyed stations in all three habitats. As would be expected from the large number of stations located in the basin, most of the stomach samples (1,125 or 84% of the total) were collected in this area (Table 1). Within the basin, most of the samples were collected from chum (22% summer, 36% fall), followed by sockeye (12% summer, 9% fall), chinook (8% summer, 10% fall), and pink (3% summer, <1% fall) salmon. On the shelf, a relatively small number (99) of stomach samples was collected by researchers on the *Northwest Explorer* in the fall, of which 72% were from chum, 23% from chinook, and 5% from sockeye salmon (Table 2). The total number of stomach samples from the Aleutian Islands was 109 (Table 3). Most of the samples were collected from chum (6% summer, 60% fall), and sockeye (2% summer, 32% fall) salmon.

### Sockeye Salmon Samples

Sockeye salmon stomach samples were collected from June to October, and the largest component of samples came from ocean age-.1 (47%) and -.2 (34%) fish with broad coverage in the basin and Aleutian Islands (grand total=278, Fig. 2). Older ocean age-.3 and -.4 sockeye salmon stomach samples were less numerous and came from fish caught almost entirely in the basin.

In summer, sockeye salmon in the basin consumed primarily amphipods, followed by euphausiids, squid, and fish, while those in the Aleutians Islands ate amphipods and gelatinous zooplankton (Fig. 3). In fall, sockeye salmon in all three habitats consumed a higher proportion of euphausiids than in summer. Sockeye salmon in the basin and Aleutian Islands consumed fish. The fish consumed by sockeye salmon in the basin included northern lampfish (*Stenobrachius leucopsarus*), and juvenile fish, such as Irish lord sculpins (*Hemilepidotus* spp.) and flatfish (Table 4). Sockeye salmon on the shelf did not eat fish. Instead, they ate a high proportion of pteropods and "other" prey (crab larvae and shrimp, Fig. 3).

The large number of samples from the basin allowed us to stratify prey composition by salmon ocean age. Sockeye salmon prey composition showed subtle changes in diet with increasing ocean age (Fig. 4). In summer, the proportion of euphausiids increased with ocean age of the fish. However, in fall the proportion of euphausiids decreased with increasing age. Age-.1 sockeye salmon collected in summer had a larger proportion of amphipods in their stomach contents than was found in older fish. In fall, the proportion of amphipods in stomach contents was not related to ocean age. Squid, which was consumed by all ages of sockeye salmon, disappeared from their diets in the fall. Comparison of prey composition collected during odd-numbered (abundant pink salmon) and even-numbered (scarce pink salmon) years indicated that the proportion of euphausiids was lower and the proportion of pteropods was higher in sockeye salmon stomach contents, when pink salmon were abundant.

## Chum Salmon Samples

Chum salmon stomach samples were collected from June to October, and most samples were from ocean age-.2 fish (34%) collected in the basin (grand total=789, Fig. 5). In addition to wide coverage in the basin, ocean age-.1, -2, and -.3 chum salmon samples were distributed broadly across station locations on the shelf and in the Aleutian Islands. Ocean age-.4 chum salmon were collected predominantly from the basin, with spotty coverage of the shelf and Aleutian Islands. Only three samples were collected from ocean age-.5 chum salmon, all from the basin.

In summer, chum salmon in the basin consumed mainly euphausiids and pteropods, and lesser volumes of amphipods, squid, fish and gelatinous zooplankton (Fig. 3). In the Aleutian Islands, chum salmon consumed large volumes of gelatinous zooplankton and "other" prey (appendicularia and chaetognaths). In general, chum salmon consumed many of the same prey groups in the three habitats in fall (i.e., euphausiids, amphipods, fish, and gelatinous zooplankton). However, pteropods were a large component of the prey observed in chum salmon stomach contents from the shelf. Fall samples of chum salmon collected in the Aleutian Islands contained a large proportion of euphausiids and amphipods, while fish and gelatinous zooplankton were a large component of the prey found in chum salmon collected from the basin and shelf. Fish prey species consumed in the basin (northern lampfish, and juvenile fish including Atka mackerel *Pleurogrammus monopterygius*, sculpins, and flatfish) were different species than fish prey observed in chum salmon stomach contents on the shelf (juvenile rockfish *Sebastes* spp., walleye pollock *Theragra chalcogramma*, and sablefish *Anoplopoma fimbria*, Table 4).

For chum salmon collected in the summer, the proportion of euphausiids increased with ocean age of the fish (Fig. 4). However, in fall samples the proportion of euphausiids decreased with age. Like sockeye salmon, age-.1 chum salmon collected in summer ate more amphipods than age-.3 and -.4 fish. However, in fall samples, the proportion of amphipods in stomach contents was not related to ocean age. The amount of gelatinous zooplankton (medusae, ctenophores, salps), increased with ocean age of chum salmon in summer, however, in fall a higher proportion of gelatinous zooplankton was consumed by younger (ocean age-.1 and -.2) than by older (ocean age-.4) fish. In fall older chum salmon consumed a large proportion of fish. Comparison of prey composition collected during odd- and even-numbered years indicated that the proportion of euphausiids was lower and the proportion of pteropods and gelatinous zooplankton was higher in chum salmon stomach contents, when pink salmon were abundant.

### Chinook Salmon Samples

Stomach samples from ocean age-.1 and -.2 chinook salmon were collected primarily in the basin and on the shelf (grand total=225, Fig. 6). The most northerly samples included a few young chinook salmon collected on the shelf near St. Lawrence Island. Few ocean age-.3 and -.4 chinook salmon samples were collected, and they were located predominantly in the basin.

The prey composition of chinook salmon diets was more limited than either sockeye or chum salmon (Fig. 3). In summer chinook salmon stomach samples from the basin contained high volumes of euphausiids, squid, and fish. In comparison, fall samples of chinook salmon prey in this area were primarily composed of squid and a lesser amount of fish with relatively low volumes of euphausiids. On the shelf, fish were the primary prey and squid contributed a lower proportion to stomach contents. The suite of fish prey species consumed by chinook in the basin (adult northern lampfish, and juvenile rockfish, Atka mackerel, walleye pollock, sculpin, and flatfish) was somewhat different than the fish prey consumed by chinook salmon sampled on the shelf (young herring *Clupea pallasii*, capelin *Mallotus villosus*, walleye pollock, rockfish, and sablefish, Table 4).

Squid was an important prey for ocean age-.1, -.2, and -.3 chinook salmon in summer and fall (Fig. 4). Fish was a large component of the stomach contents of ocean age-.1 chinook salmon in summer, however, the proportion of fish in the stomach contents of young fish was comparatively less in the fall. Euphausiids were an important prey of ocean age-.1, -.2, and -.3 chinook salmon during summer, however, in fall euphausiids were found only in stomach contents of ocean age-.1 fish. The proportion of squid in chinook salmon stomach contents was larger during the summer in even-numbered years, when there was a scarcity of pink salmon in the basin.

### Pink Salmon Samples

Pink salmon provided few samples, and all were (maturing) ocean age-.1 fish collected in the basin (grand total=41, Fig. 7). All samples, with the exception of one, were collected during June-July in the vicinity of 180° longitude, while the remaining pink salmon stomach sample was collected in September in the southeastern area of the basin. In the summer, pink salmon consumed a high proportion of fish and euphausiids, with lesser amounts of amphipods and squid contributing to the diet (Table 1). The one pink salmon caught in the fall consumed exclusively euphausiids.

### Salmon diet overlap in fall 2002

Fall samples sizes were sufficient (n ≥ 15 fish) for three pair-wise estimates of diet overlap in the basin (sockeye, chum, and chinook), and one estimate each for the Aleutian Islands (sockeye and chum) and shelf (chum and chinook salmon; Table 5).

#### *Bering Sea Basin*

In the basin, diet overlap between sockeye and chum salmon was moderate (PSI=49%; Table 5), with both sockeye and chum salmon feeding on euphausiids (17%), amphipods (12%) and fish (17%). Based on material that could be identified from stomach contents, both salmon predators consumed the same prey species and size ranges within these general categories. For example, both sockeye and chum salmon consumed one genus of euphausiid (*Thysanoessa*), and identical species of hyperiid amphipods (*Hyperia medusarum*, *Themisto pacifica*, and *Primno abyssalis*) and fish (northern lampfish, 64-120 mm SL) and juvenile Irish lord sculpin (9-22 mm SL). Diet overlap of sockeye and chinook salmon was low (21%), with overlap mainly in the fish prey category (17%). Northern lampfish in the same size range were identified from both sockeye and chinook salmon stomach contents, however, chinook salmon stomach contents also contained juvenile Atka mackerel (105-143 mm SL). Diet overlap between chum and chinook salmon was slightly higher (28%) because chum salmon consumed more fish prey than sockeye salmon. Northern lampfish and Atka mackerel of approximately the same size range (30-145 mm SL) were identified from the stomach contents of chum and chinook salmon. However, chum salmon caught in the basin consumed a higher diversity of fish prey including juvenile stages of rockfish (19-52 mm SL), walleye pollock (63-77 mm SL), and sculpin (9-22 mm SL).

#### *Aleutian Islands*

In the Aleutian Islands, diet overlap in fall 2002 between sockeye and chum salmon was very high (80%; Table 5), with both consuming large volumes of identical species of euphausiids (44%) and amphipods (27%). In contrast, fish prey was a smaller component of diet overlap in this area than in the basin (Aleutian Islands 5%).

#### *Bering Sea Shelf*

On the shelf, diet overlap during fall 2002 between chum and chinook salmon was moderate (30%), with fish (23%) constituting the largest prey category (Table 5). These results were similar to the overlap value calculated for chum and chinook salmon in the basin. On the shelf, both chum and chinook salmon consumed juvenile walleye pollock. However, the walleye pollock consumed by chinook salmon were somewhat larger (60-190 mm SL) than those consumed by chum salmon (45-95 mm SL). Other fish consumed by chinook salmon included herring (190 mm SL) and capelin (90-115 mm SL), while other fish identified from chum stomach contents included juvenile sablefish (100 mm SL) and juvenile rockfish (48-58 mm SL).

# Discussion

Salmon stock origins and seasonal runs are unknown in our samples. Previous high seas tagging and scale pattern research have shown that fish in the survey area include stocks originating from western and central Alaska, Russia, and Japan (Myers et al. 1987, Myers and Rogers 1988, Davis 1990, Myers et al. 1996, Patton et al. 1998, Myers et al. 2001). We assume the food habits reported in this study are representative of salmon originating from those areas, including Yukon River fish. Although some maturing chum salmon were present in our summer samples from the basin, the late sample date (early July) and large distance from the coast makes it unlikely that these maturing chum are summer-run fish (return by July 15). Fall stomach samples were collected almost exclusively from immature chum salmon, making it impossible to separate summer- and fall-run chum salmon in those samples.

For our comparison of seasonal diet composition, we assume that the stomach contents data describe salmon feeding throughout the day. Seasonal changes in prey composition are possibly confounded with changes in the time of day the salmon were sampled because summer samples were collected from salmon caught during the evening and nighttime, and fall samples were collected from fish caught during the daytime. This difference in the time of day the fish were caught could underestimate the consumption of crustaceans, fish, and squid in samples collected in the fall because salmon consumption of diel migrating prey has been observed to change throughout the day (Pearcy et al. 1984, Davis et al. 2000). However, at present, our data are the only information available regarding summer and fall diets of salmon in these habitats in the Bering Sea. In the future, diel and seasonal changes in salmon food habits will be clarified when samples are collected seasonally, throughout the diel period or consistently at the same period of the day.

No diet overlap could be estimated for fall samples of ocean age-.1 pink salmon because of inadequate sample sizes. By September, maturing pink salmon have returned to freshwater for spawning. In summer, sockeye, chum, and pink salmon consumed a similar diet of predominately euphausiids, amphipods, and fish (Table 1).

Our results reconfirm the observations of earlier Bering Sea salmon food habits studies which showed that immature sockeye and chum are primarily predators of macro-zooplankton (euphausiids, amphipods, pteropods, and gelatinous zooplankton), and chinook salmon are primarily consumers of small nektonic prey, such as fish and squid (Andrievskaya 1966, Sobolevskiy et al. 1994, Davis et al. 1998, Temnykh et al. 2003). Our results showed there were shifts in prey composition among species and between seasons in the three habitats. In addition, our results indicate that there is a seasonal (summer to fall) reduction in the diversity of the diets of Bering Sea sockeye, chum, and chinook salmon (Fig. 4). Squid was reduced or eliminated from diets of sockeye and chum salmon, and chinook salmon consumption of euphausiids was dramatically reduced in fall. In contrast, fish prey increased in the diets of sockeye and chum, and chinook salmon consumption of squid increased in the fall. Reduction in the diversity of prey groups in fall could be caused by changes in prey availability due to shifts in their distribution, abundance, or progression of life-history stages, resulting from the seasonal shift in environmental factors (decreasing water temperatures, deepening thermocline depth, etc.).

Our results showed that in fall sockeye and chum salmon had a very high level of diet overlap (80%) in the Aleutian Islands (Table 5), where they consumed predominately euphausiids and amphipods. In the basin, however, diet similarity between sockeye and chum salmon was reduced to a moderate level (49%) because chum salmon consumed a high proportion of gelatinous zooplankton (Table 1). Diet switching to alternative prey may decrease competition between chum and other macro-zooplanktivorous salmon (Tadokoro et al. 1996, Davis 2003). Dulepova and Dulepov (2003) speculated that consumption of gelatinous zooplankton is advantageous to chum salmon in the final stages of ocean migration because medusae and ctenophores are more easily digested than prey with higher lipid content.

In summer in the central Bering Sea there is a strong biennial pink salmon abundance cycle with summer catches showing a 30- to 50-fold increase in odd-numbered years (Azumaya and Ishida 2000). Evidence from tagging indicates pink salmon in this area are primarily wild stocks from the Karaginsky region of eastern Kamchatka, Russia (Myers et al. 1996). Because of the large similarity in the diets of sockeye, chum, and pink salmon, widely fluctuating pink salmon abundance seems to be the force driving alternating periods of increased (odd-numbered year) and reduced (even-numbered year) inter- and intra-specific competition for food. Shifts in prey composition of salmon stomach contents in odd- and even-numbered years have been observed among sockeye, chum, and pink salmon (Ito 1964, Andrievskaya 1966, Tadokoro et al. 1996, Davis 2003). Decreased size and abundance of Bristol Bay sockeye salmon appears to be linked to feeding competition with odd-year pink salmon from eastern Kamchatka (Ruggerone et al. 2003).

Previous scale growth, ocean distribution, and food habits studies have indicated that immature and maturing chum salmon compete with maturing pink salmon in the Bering Sea and North Pacific Ocean. For example, Walker et al. (1998) observed that edge-of-scale growth was negatively correlated with Asian pink and chum salmon abundance. In years when pink salmon were abundant, Azumaya and Ishida (2000) suggested the summer distribution of chum salmon shifts southeastward in the Bering Sea, away from the coastward migration route of Asian pink salmon, to reduce inter-specific competition.

Although chum salmon have a diverse diet, it is likely that competition for food within and between stocks of chum salmon could occur, particularly when chum salmon are locally abundant. Analyses of scale patterns have suggested that intra-specific competition may cause a reduction in body size of high-seas and Japanese chum salmon, which occurs in the third year of ocean life (Kaeriyama 1989; Ishida et al. 1993; Walker et al. 1998; Azumaya and Ishida 2000). Significant negative relationships have been observed between the population sizes of high-seas and Japanese chum salmon and mean fish size (Ishida et al. 1993, Kaeriyama 1996), and density-dependent factors explained

35% of the decrease in average size of chum salmon in the central North Pacific Ocean (Ishida et al. 1993). We speculate that when large numbers of Asian and western Alaskan chum salmon intermingle in the Bering Sea in summer (Urawa, In press), growth reduction of Yukon River salmon could occur from intra-specific competition for food.

Although shifts in the proportion of several prey groups may reduce diet overlap among salmon, these shifts may not be without cost. Davis (2003) observed dramatic increases (13% in sockeye, 19% in chum, 72% in pink salmon) in the weight of low energy-density prey (pteropods, amphipods, or gelatinous zooplankton) in salmon stomach contents collected during odd-numbered years, when pink salmon were abundant in the central Bering Sea. Estimates of daily ration based on field observations of high seas salmon food habits have shown that fish are feeding at rates close to their physiological maximum, and over relatively short time periods small decreases in daily ration caused by competition, or other causes, could significantly decrease growth (Davis et al. 1998). Under conditions of reduced growth, salmon may not attain a size large enough to feed on larger prey, thereby developing a trophic feedback. In this scenario, salmon relinquish the growth potential afforded by a diet of larger, more energy-dense prey, and remain competitors for consumption of zooplankton (Aydin 2000).

Competition for food among several stocks of Asian and North American pink and sockeye salmon is a likely mechanism for density-dependent reduction of ocean growth (Takagi et al. 1981, Heard 1991, Bugaev et al. 2001). Ishida et al. (1995) compared pink salmon scale growth and pink salmon abundance in the Bering Sea and western North Pacific and observed a density-dependent effect on growth that occurred in the second year of ocean life. Length and weight of Ozernaya River (western Kamchatka) sockeye salmon were substantially reduced in years when marine abundance of Kamchatka pink salmon was high (Bugaev et al. 2001). Intra-specific density-dependent growth of maturing Bristol Bay sockeye salmon has been shown to be affected by food abundance and other factors in their final weeks at sea (Rogers 1980; Rogers and Ruggerone 1993).

Inter-specific food competition may also regulate population abundance. Ruggerone et al. (2003) observed that abundance of wild stocks of pink salmon originating in eastern Kamchatka was inversely related to growth and survival of immature Bristol Bay sockeye salmon. They reasoned that if inter-specific feeding competition (direct or indirect) reduces prey availability and subsequent growth of immature sockeye salmon, then increased predation on sockeye salmon would occur from a larger number of predators able to consume small-bodied fish. During their final summer at sea, competition between maturing Bristol Bay sockeye and maturing Asian pink salmon could be minimized by a separation in their distribution and run timing. Maturing Bristol Bay sockeye salmon are distributed in the North Pacific, eastwards of most maturing Asian pink salmon, and their migrations to coastal areas start earlier than those of pink salmon (Burgner 1991). After examining stomach contents collected in summer and fall in the western Bering Sea, Andrievskaya (1966) concluded the largest degree of diet overlap occurred between sockeye and pink salmon during the summer. An analysis of sockeye salmon food habits data observed a 36% reduction in sockeye stomach fullness in odd-numbered years when pink salmon were abundant (Davis 2003).

While previous studies have focused on inter- and intra-specific interactions among pink, sockeye, and chum salmon, they do not provide any information about chinook salmon competitive interactions in the Bering Sea. Our estimates of diet overlap between chinook and sockeye salmon and chinook and chum salmon were lower than the estimates obtained for sockeye and chum salmon (Table 5). These results suggest a relatively low level of inter-specific food competition between immature chinook and immature sockeye or chum salmon in the Bering Sea because chinook salmon were more specialized consumers. In addition, the relatively low abundance of immature chinook salmon compared to other species may serve to reduce intra-specific competition at sea. Consumption of nektonic organisms (fish and squid) may be efficient because they are relatively large bodied and contain a higher caloric density than zooplankton, such as pteropods and amphipods (Tadokoro et al. 1996, Davis et al. 1998). However, the energetic investment required of chinook to capture actively swimming prey is large, and if fish and squid prey abundance are reduced, a smaller proportion of ingested energy will be available for salmon growth (Davis et al. 1998).

We hypothesize that inter- and intra-specific competition in the Bering Sea could negatively affect the growth of Yukon River chum and chinook salmon, particularly during spring and summer in odd-numbered years, when Yukon River fish overlap to a large extent with Asian and other North American salmon stocks. Decreased growth could lead to reduction in Yukon River salmon survival by increasing predation (Ruggerone et al. 2003), decreasing lipid storage to the point of insufficiency to sustain the salmon through winter when consumption rates are low (Nomura et al. 2002), and increasing susceptibility to parasites and disease due to poor salmon nutritional condition.

## Conclusions

There were inter-specific, inter-seasonal, and inter-regional differences in the prey composition of sockeye, chum, and chinook salmon caught in the Bering Sea in summer and fall. Immature sockeye and chum salmon were primarily predators of zooplankton (euphausiids, amphipods, pteropods, and gelatinous zooplankton), and chinook salmon consumed predominately small nektonic prey (fish and squid). Shifts in prey composition between summer and fall and among habitats likely resulted from changes in salmon prey availability.

Diet overlap between sockeye and chum was high, and was lower between chinook and sockeye salmon, and between chinook and chum salmon. Consumption of gelatinous zooplankton by chum salmon may decrease feeding competition with other zooplanktivorous salmon, but may also result in decreased growth from lower levels of ingested energy. If prey availability is reduced by predation from abundant stocks of pink and chum salmon, or in combination with adverse climatic and oceanographic changes in the Bering Sea, then increased inter- and intra-specific competition could decrease growth of Yukon River chum and chinook salmon. Furthermore, reduced growth, causing increased predation on salmon, poor salmon nutritional condition, insufficient lipid storage, and greater susceptibility to parasites and disease, could negatively affect Yukon River salmon survival.

Future investigations of salmon food habits should include all major salmon species of the Bering Sea (sockeye, chum, pink, and chinook salmon). These studies should be expanded to include all age groups, including juveniles and maturing fish. In addition, samples collected during the winter and spring seasons are needed to help determine if there is a time of the year and life history stage when inter- and intra-specific competition is likely to have the greatest impact on salmon growth. Zooplankton samples have been collected simultaneously with salmon sampling for food habits, and these surveys have employed gear specifically designed to catch salmon prey. Analysis of salmon prey availability together with new and existing salmon food habits data, and bioenergetics studies will substantially increase our capacity to evaluate the relationship between inter- and intra-specific competition for food among salmon and salmon ocean growth.

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Table 1. Mean percent prey composition in salmon stomach contents from fish caught in the Bering Sea basin in summer (*Wakatake maru*, June-July) and fall (*Kaiyo maru*, September and *Northwest Explorer*, September-October) 2002. Ocean age=unk means ocean age could not be determined because the fish's scale was damaged. No. is the total number of samples examined (including empty stomachs). Percent empty stomachs are the percentage of the total number of samples examined that did not contain stomach contents. Empty stomachs were not included in other table entries. SCI=prey weight*100/body weight. Prey composition based on visual estimates. Gel. Zoop.=gelatinous zooplankton (medusae and ctenophores).

**Bering Sea Basin**

| | | | | | | Prey Weight | | SCI | | Mean Percentage Prey Composition by Volume | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | Species | Ocean Age | No. | Percent at Age | % Empty Stomachs | mean | sd | mean | sd | Euphausiids | Copepods | Amphipods | Crab larvae | Squid | Pteropods | Fish | Polychaetes | Chaetognaths | Gel. zoop. | Other prey | Unidentified |
| Summer | Sockeye | 1 | 49 | 35 | 14 | 3.5 | 3.4 | 0.98 | 0.93 | 12 | 4 | 69 | 0 | 3 | 1 | 10 | 0 | 1 | 0 | 0 | 0 |
| | | 2 | 52 | 37 | 8 | 11.0 | 11.5 | 0.82 | 0.87 | 21 | 13 | 23 | 0 | 21 | 7 | 15 | 0 | 0 | 0 | 0 | 0 |
| | | 3 | 29 | 21 | 14 | 21.0 | 20.8 | 0.77 | 0.78 | 26 | 11 | 4 | 0 | 40 | 4 | 15 | 0 | 0 | 0 | 0 | 0 |
| | | 4 | 8 | 6 | 25 | 30.2 | 26.2 | 1.02 | 1.01 | 17 | 14 | 0 | 0 | 38 | 0 | 28 | 0 | 0 | 0 | 3 | 0 |
| | | unk | 1 | 1 | 0 | | | | | | | | | | | | | | | | |
| | | Total | 139 | 100 | 12 | 11.3 | 15.1 | 0.87 | 0.87 | 19 | 10 | 34 | 0 | 19 | 4 | 14 | 0 | 0 | 0 | 0 | 0 |
| Fall | Sockeye | 1 | 56 | 58 | 23 | 3.5 | 3.0 | 0.61 | 0.50 | 56 | 1 | 28 | 0 | 0 | 3 | 9 | 0 | 0 | 1 | 0 | 2 |
| | | 2 | 31 | 32 | 19 | 5.1 | 5.7 | 0.37 | 0.44 | 29 | 1 | 36 | 2 | 1 | 0 | 31 | 0 | 0 | 0 | 0 | 0 |
| | | 3 | 1 | 1 | 0 | 4.0 | | 0.26 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 90 | 0 | 10 |
| | | unk | 9 | 9 | 0 | | | | | | | | | | | | | | | | |
| | | Total | 97 | 100 | 20 | 4.0 | 4.1 | 0.50 | 0.50 | 48 | 1 | 29 | 1 | 0 | 2 | 16 | 0 | 0 | 2 | 0 | 1 |
| Summer | Chum | 1 | 34 | 14 | 6 | 5.9 | 4.8 | 1.37 | 1.13 | 18 | 1 | 59 | 0 | 6 | 5 | 4 | 0 | 1 | 3 | 0 | 3 |
| | | 2 | 64 | 27 | 5 | 12.8 | 10.0 | 1.28 | 0.92 | 36 | 4 | 16 | 0 | 6 | 19 | 5 | 0 | 1 | 7 | 6 | 0 |
| | | 3 | 89 | 37 | 5 | 18.7 | 15.0 | 0.89 | 0.75 | 34 | 6 | 3 | 0 | 8 | 25 | 6 | 0 | 0 | 12 | 6 | 0 |
| | | 4 | 50 | 21 | 2 | 17.9 | 16.2 | 0.66 | 0.64 | 29 | 3 | 2 | 0 | 6 | 23 | 11 | 0 | 1 | 23 | 0 | 2 |
| | | 5 | 3 | 1 | 33 | 14.5 | 0.7 | 0.51 | 0.10 | 32 | 0 | 0 | 0 | 5 | 39 | 22 | 0 | 0 | 2 | 0 | 0 |
| | | unk | 2 | 1 | 0 | | | | | | | | | | | | | | | | |
| | | Total | 242 | 100 | 5 | 15.2 | 13.7 | 1.01 | 0.87 | 31 | 4 | 14 | 0 | 7 | 20 | 6 | 0 | 1 | 12 | 4 | 1 |
| Fall | Chum | 1 | 106 | 26 | 9 | 5.1 | 6.8 | 0.87 | 1.03 | 21 | 0 | 11 | 1 | 1 | 0 | 19 | 0 | 4 | 42 | 0 | 1 |
| | | 2 | 232 | 57 | 9 | 8.0 | 8.3 | 0.69 | 0.75 | 16 | 1 | 13 | 0 | 2 | 0 | 18 | 0 | 1 | 47 | 2 | 0 |
| | | 3 | 47 | 12 | 17 | 12.1 | 14.1 | 0.64 | 0.74 | 13 | 0 | 14 | 0 | 2 | 0 | 42 | 0 | 1 | 26 | 2 | 0 |
| | | 4 | 13 | 3 | 54 | 11.6 | 10.6 | 0.42 | 0.44 | 10 | 0 | 11 | 0 | 0 | 0 | 61 | 0 | 0 | 11 | 0 | 7 |
| | | unk | 6 | 2 | 0 | | | | | | | | | | | | | | | | |
| | | Total | 404 | 100 | 11 | 7.7 | 8.9 | 0.73 | 0.83 | 17 | 0 | 12 | 1 | 2 | 0 | 22 | 0 | 2 | 42 | 2 | 0 |

Table 1. (cont.) Mean percent prey composition in salmon stomach contents from fish caught in the Bering Sea basin in summer (*Wakatake maru*, June-July) and fall (*Kaiyo maru*, September and *Northwest Explorer*, September-October) 2002. Ocean age=unk means ocean age could not be determined because the fish's scale was damaged. No. is the total number of samples examined (including empty stomachs). Percent empty stomachs is the percentage of the total number of samples examined that did not contain stomach contents. Empty stomachs were not included in other table entries. SCI=prey weight*100/body weight. Prey composition based on visual estimates. Gel. Zoop.=gelatinous zooplankton (medusae and ctenophores).

**Bering Sea Basin**

| | | | | | | Prey Weight | | SCI | | Mean Percentage Prey Composition by Volume | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | Species | Ocean Age | No. | Percent at Age | % Empty Stomachs | mean | sd | mean | sd | Euphausiids | Copepods | Amphipods | Crab larvae | Squid | Pteropods | Fish | Polychaetes | Chaetognaths | Gel. zoop. | Other prey | Unidentified |
| Summer | Pink | 1 | 40 | 100 | 10 | 13.9 | 12.0 | 1.23 | 1.00 | 33 | 8 | 10 | 0 | 10 | 2 | 37 | 0 | 0 | 0 | 0 | 0 |
| | | Total | 40 | 100 | 10 | 13.9 | 12.0 | 1.23 | 1.00 | 33 | 8 | 10 | 0 | 10 | 2 | 37 | 0 | 0 | 0 | 0 | 0 |
| Fall | Pink | 1 | 1 | 100 | 0 | 1.0 | | 0.05 | | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | Total | 1 | 100 | 0 | 1.0 | | 0.05 | | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Summer | Chinook | 1 | 10 | 11 | 30 | 4.3 | 4.5 | 0.84 | 0.86 | 16 | 0 | 0 | 0 | 27 | 0 | 57 | 0 | 0 | 0 | 0 | 0 |
| | | 2 | 44 | 49 | 30 | 16.0 | 17.4 | 0.72 | 0.79 | 48 | 0 | 0 | 0 | 35 | 0 | 17 | 0 | 0 | 0 | 0 | 0 |
| | | 3 | 29 | 32 | 31 | 32.5 | 41.0 | 0.70 | 0.81 | 18 | 4 | 0 | 0 | 60 | 0 | 18 | 0 | 0 | 0 | 0 | 0 |
| | | 4 | 1 | 1 | 0 | 190.0 | | 2.18 | | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | unk | 6 | 7 | 33 | | | | | | | | | | | | | | | | |
| | | Total | 90 | 100 | 30 | 22.4 | 34.9 | 0.73 | 0.79 | 33 | 1 | 0 | 0 | 45 | 0 | 21 | 0 | 0 | 0 | 0 | 0 |
| Fall | Chinook | 1 | 82 | 73 | 27 | 18.2 | 16.4 | 1.66 | 1.47 | 6 | 0 | 0 | 0 | 65 | 0 | 29 | 0 | 0 | 0 | 0 | 0 |
| | | 2 | 22 | 20 | 18 | 23.3 | 24.9 | 0.75 | 0.73 | 0 | 0 | 0 | 0 | 69 | 0 | 31 | 0 | 0 | 0 | 0 | 0 |
| | | 3 | 2 | 2 | 0 | 33.0 | 24.0 | 0.67 | 0.33 | 0 | 0 | 0 | 0 | 50 | 0 | 50 | 0 | 0 | 0 | 0 | 0 |
| | | unk | 6 | 5 | 33 | | | | | | | | | | | | | | | | |
| | | Total | 112 | 100 | 25 | 19.5 | 18.4 | 1.43 | 1.37 | 5 | 0 | 0 | 0 | 66 | 0 | 29 | 0 | 0 | 0 | 0 | 0 |

Table 2. Mean percent prey composition in salmon stomach contents from fish caught on the Bering Sea shelf in fall 2002 (*Northwest Explorer*, September-October). Ocean age=unk means ocean age could not be determined because the fish's scale was damaged. No. is the total number of samples examined (including empty stomachs). Percent empty stomachs are the percentage of the total number of samples examined that did not contain stomach contents. Empty stomachs were not included in other table entries. SCI=prey weight*100/body weight. Prey composition based on visual estimates. Gel. Zoop.=gelatinous zooplankton (medusae and ctenophores).

**Bering Sea Shelf**

| | | | | | % | Prey Weight | | SCI | | Mean Percentage Prey Composition by Volume | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | Species | Ocean Age | No. | Percent at Age | Empty Stomachs | mean | sd | mean | sd | Euphausiids | Copepods | Amphipods | Crab larvae | Squid | Pteropods | Fish | Polychaetes | Chaetognaths | Gel. zoop. | Other prey | Unidentified |
| Fall | Sockeye | 1 | 3 | 60 | 33 | 1.0 | 0.0 | 0.21 | 0.01 | 0 | 0 | 48 | 40 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 2 | 2 | 40 | 0 | 3.0 | 2.8 | 0.20 | 0.24 | 38 | 0 | 7 | 0 | 0 | 50 | 0 | 0 | 0 | 0 | 5 | 0 |
| | | Total | 5 | 100 | 20 | 2.0 | 2.0 | 0.21 | 0.14 | 19 | 0 | 28 | 20 | 0 | 31 | 0 | 0 | 0 | 0 | 2 | 0 |
| Fall | Chum | 1 | 15 | 21 | 27 | 3.7 | 2.1 | 0.56 | 0.26 | 16 | 0 | 15 | 27 | 0 | 12 | 13 | 0 | 0 | 17 | 0 | 0 |
| | | 2 | 33 | 47 | 15 | 25.1 | 25.7 | 1.36 | 1.25 | 12 | 0 | 2 | 7 | 4 | 18 | 30 | 0 | 3 | 23 | 0 | 1 |
| | | 3 | 17 | 24 | 35 | 37.2 | 27.2 | 1.32 | 0.93 | 2 | 0 | 0 | 3 | 0 | 55 | 18 | 0 | 0 | 22 | 0 | 0 |
| | | 4 | 4 | 6 | 25 | 25.3 | 12.7 | 0.61 | 0.66 | 3 | 0 | 0 | 0 | 0 | 31 | 33 | 0 | 23 | 10 | 0 | 0 |
| | | unk | 2 | 3 | 50 | | | | | | | | | | | | | | | | |
| | | Total | 71 | 100 | 24 | 22.8 | 24.7 | 1.12 | 1.06 | 10 | 0 | 4 | 10 | 2 | 26 | 24 | 0 | 3 | 21 | 0 | 0 |
| Fall | Chinook | 1 | 12 | 52 | 33 | 15.4 | 14.9 | 1.63 | 0.89 | 10 | 0 | 0 | 0 | 12 | 0 | 78 | 0 | 0 | 0 | 0 | 0 |
| | | 2 | 7 | 30 | 14 | 31.5 | 31.6 | 0.89 | 0.83 | 0 | 0 | 0 | 0 | 50 | 0 | 50 | 0 | 0 | 0 | 0 | 0 |
| | | 3 | 2 | 9 | 100 | | | | | | | | | | | | | | | | |
| | | 4 | 1 | 4 | 0 | 111.0 | | 0.80 | | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 |
| | | unk | 1 | 4 | 0 | | | | | | | | | | | | | | | | |
| | | Total | 23 | 100 | 30 | 28.6 | 31.4 | 1.26 | 0.86 | 5 | 0 | 0 | 0 | 31 | 0 | 64 | 0 | 0 | 0 | 0 | 0 |

Table 3. Mean percent prey composition in salmon stomach contents from fish caught in the Aleutian Islands in summer (*Wakatake maru*, June-July) and fall (*Kaiyo maru*, September and *Northwest Explorer,* September-October) 2002. Ocean age=unk means ocean age could not be determined because the fish's scale was damaged. No. is the total number of samples examined (including empty stomachs). Percent empty stomachs are the percentage of the total number of samples examined that did not contain stomach contents. Empty stomachs were not included in other table entries. SCI=prey weight*100/body weight. Prey composition based on visual estimates. Gel. Zoop.=gelatinous zooplankton (medusae and ctenophores).

**Aleutian Islands**

| | | | | | % | Prey Weight | | SCI | | Mean Percentage Prey Composition by Volume | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | Species | Ocean Age | No. | Percent at Age | Empty Stomachs | mean | sd | mean | sd | Euphausiids | Copepods | Amphipods | Crab larvae | Squid | Pteropods | Fish | Polychaetes | Chaetognaths | Gel. zoop. | Other prey | Unidentified |
| Summer | Sockeye | 2 | 2 | 100 | 0 | 2.0 | 1.4 | 0.15 | 0.10 | 0 | 0 | 73 | 0 | 0 | 0 | 2 | 0 | 0 | 21 | 4 | 0 |
| | | Total | 2 | 100 | 0 | 2.0 | 1.4 | 0.15 | 0.10 | 0 | 0 | 73 | 0 | 0 | 0 | 2 | 0 | 0 | 21 | 4 | 0 |
| Fall | Sockeye | 1 | 24 | 69 | 8 | 4.3 | 3.5 | 0.69 | 0.51 | 68 | 0 | 26 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 2 |
| | | 2 | 7 | 20 | 0 | 5.4 | 3.4 | 0.33 | 0.16 | 32 | 7 | 31 | 6 | 0 | 0 | 23 | 0 | 1 | 0 | 0 | 0 |
| | | 3 | 1 | 3 | 0 | 2.0 | | 0.15 | | 45 | 10 | 35 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 |
| | | unk | 3 | 9 | 33 | | | | | | | | | | | | | | | | |
| | | Total | 35 | 100 | 9 | 5.7 | 6.3 | 0.68 | 0.60 | 60 | 2 | 27 | 1 | 0 | 2 | 5 | 0 | 1 | 0 | 0 | 2 |
| Summer | Chum | 2 | 3 | 43 | 0 | 11.3 | 5.0 | 1.29 | 0.57 | 0 | 2 | 3 | 0 | 0 | 1 | 0 | 0 | 8 | 61 | 25 | 0 |
| | | 3 | 3 | 43 | 0 | 26.7 | 7.6 | 1.38 | 0.22 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 7 | 67 | 22 | 0 |
| | | 4 | 1 | 14 | 0 | 65.0 | | 1.88 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 |
| | | Total | 7 | 100 | 0 | 25.6 | 19.7 | 1.41 | 0.41 | 0 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 6 | 69 | 20 | 0 |
| Fall | Chum | 1 | 14 | 22 | 14 | 3.9 | 4.8 | 0.55 | 0.54 | 63 | 0 | 22 | 1 | 0 | 0 | 8 | 0 | 2 | 4 | 0 | 0 |
| | | 2 | 35 | 54 | 11 | 7.4 | 8.0 | 0.61 | 0.59 | 38 | 3 | 36 | 5 | 1 | 0 | 8 | 0 | 1 | 7 | 1 | 0 |
| | | 3 | 14 | 22 | 0 | 14.5 | 24.4 | 0.80 | 1.28 | 39 | 7 | 19 | 6 | 1 | 0 | 14 | 0 | 1 | 13 | 0 | 0 |
| | | 4 | 1 | 2 | 100 | | | | | | | | | | | | | | | | |
| | | unk | 1 | 2 | 0 | | | | | | | | | | | | | | | | |
| | | Total | 65 | 11 | 11 | 8.3 | 13.7 | 0.64 | 0.79 | 44 | 4 | 29 | 4 | 1 | 0 | 10 | 0 | 1 | 7 | 0 | 0 |

Table 4. Prey organisms observed in the stomach contents of sockeye, chum, pink, and chinook salmon collected in the Bering Sea in July-October 2002. Major prey groups are indicated by bold font. Prey groups: values in parentheses are approximate size (mm) of squid (mantle length, ML) and fish (standard length, SL) found in stomach contents. X indicates a prey item identified in samples of a particular salmon species. Samples collected from three habitats including B= Bering Sea basin, S= Bering Sea shelf, and A= Aleutian Islands.

| Prey groups | Sockeye | | | Chum | | | Pink | | | Chinook | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | S | A | B | S | A | B | S | A | B | S | A |
| **Cnidaria** | | | | | | | | | | | | |
| *Aglantha* | | | | X | | X | | | | | | |
| | | | | | | | | | | | | |
| **Ctenophora** | | | | | | | | | | | | |
| *Beroe* sp. | | | | X | | X | | | | | | |
| | | | | | | | | | | | | |
| **Polychaetes** | | | | | | | | | | | | |
| *Tomopterus* spp. | | | | X | | | | | | | | |
| *Rhynchonerella* spp. | | | | X | | | | | | | | |
| | | | | | | | | | | | | |
| **Copepods** | | | | | | | | | | | | |
| *Neocalanus cristatus* | X | | | X | | X | | | | | | |
| *Candacia columbiae* | | | | | | X | | | | | | |
| | | | | | | | | | | | | |
| **Euphausiids** | | | | | | | | | | | | |
| *Thysanoessa longipes* | | | | X | | | | | | | | |
| *Thysanoessa spinifera* | X | | | X | | | | | | | | |
| *Thysanoessa inermis* | | | | | | | | | | X | | |
| | | | | | | | | | | | | |
| **Hyperiid Amphipods** | | | | | | | | | | | | |
| *Themisto pacifica* | X | X | X | X | X | X | X | | | | | |
| *Phronima sedentaria* | | | | X | | | | | | | | |
| *Primno abyssalis* | X | X | X | X | X | X | X | | | | | |
| *Hyperia medusarum* | X | | X | X | | X | X | | | | | |
| *Paraphronima* spp. | | | | X | | X | | | | | | |

Table 4. Continued.

| Prey groups | Sockeye | | | Chum | | | Pink | | | Chinook | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | S | A | B | S | A | B | S | A | B | S | A |
| **Gammarid Amphipods** | | | | | | | | | | | | |
| Lysianassidae | X | | | X | | | X | | | | | |
| unknown gammarid | X | | | X | | | | | | | | |
| | | | | | | | | | | | | |
| **Shrimps** | | | | | | | | | | | | |
| *Hymendora frontalis* | X | | | X | | | | | | | | |
| Glyphocrangon | | | | X | | X | | | | | | |
| Pandalids | | | | X | | X | | | | | | |
| Crangonids | | | | X | | | | | | | | |
| Pasiphaeids | | | | X | | X | | | | | | |
| | | | | | | | | | | | | |
| **Crabs** | | | | | | | | | | | | |
| Anomuran zoea and megalops | X | | | X | X | X | | | | | | |
| Brachyuran zoea and megalops | X | X | X | X | X | X | | | | | | |
| | | | | | | | | | | | | |
| **Insects** | X | | | X | | X | | | | | | |
| | | | | | | | | | | | | |
| **Gastropods** | | | | | | | | | | | | |
| *Limacina* | X | X | X | X | X | X | X | | | | | |
| *Clione limacina* | X | | | X | X | X | | | | | | |
| | | | | | | | | | | | | |
| **Cephalopods** | | | | | | | | | | | | |
| *Berryteuthis anonychus* (40-105 ) | X | | | | | | X | | | X | | |
| Small squids (5-30) | X | | X | X | X | X | X | | | X | | |
| *Gonatus kamtchaticus* (50-159) | | | | | | | | | | X | X | X |
| *Gonatopsis borealis* (110) | | | | | | | | | | X | | |
| unknown gonatid squid | | | | X | | | | | | | | |
| | | | | | | | | | | | | |
| **Chaetognaths** | | | | | | | | | | | | |
| *Sagitta* spp. | | | | X | | | | | | | | |
| | | | | | | | | | | | | |
| **Urochordates** | | | | | | | | | | | | |
| *Oikopleura* sp. | | | | X | | X | | | | | | |

Table 4. Continued.

| Prey groups | Sockeye | | | Chum | | | Pink | | | Chinook | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | S | A | B | S | A | B | S | A | B | S | A |
| **Pisces** | | | | | | | | | | | | |
| *Clupea pallasii* herring (190) | | | | | | | | | | | X | |
| *Mallotus villosus* capelin (90-115) | | | | | | | | | | | X | |
| *Stenobrachius leucopsarus* lampfish (40-120) | X | | X | X | | X | X | | | X | | |
| *Sebastes* spp. rockfish (20-58) | | | | X | X | | X | | | | | |
| *Pleurogrammus monopterygius* Atka mackerel (53-145) | X | | | X | | | X | | | X | | |
| *Hexagrammos* sp. greenling | | | | | | | | | | X | | |
| *Theragra chalcogramma* walleye pollock (60-190) | | | | X | X | | | | | | X | |
| *Anoplopoma fimbria* sablefish (100) | | | | | X | | | | | | | |
| *Hemilepidotus* spp. Irish lord (9-30) | X | | | X | | | X | | | X | | |
| *Psychrolutes phrictus* giant blob sculpin | | | | X | | | | | | | | |
| Cyclopteridae lumpsucker | | | | | | X | | | | | | |
| *Hippoglossus stenolepis* P. halibut (20-30) | X | | | X | | | X | | | X | | |
| *Atheresthes* sp. flounder (20) | X | | | X | | | X | | | X | | |
| Unk. flatfish | | | | | X | X | X | | | | | |
| Unknown juvenile fish | X | | X | X | | X | | | | X | | |

Table 5. Percent diet overlap of sockeye, chum, and chinook salmon collected in the Bering Sea basin, shelf, and Aleutian Islands in fall 2002. Empty stomachs are not included in calculation of overlap values. Bold values highlight prey groups representing a major component of diet overlap. Overlap values calculated for salmon species for which sample size is > 15.

| Percent overlap: | | | |
|---|---|---|---|
| | low | 1-24% | □ |
| | moderate | 25-49% | ░ |
| | high | 50-74% | ▓ |
| | very high | 75-100% | ■ |

## BASIN

| Prey Group | Pairwise Comparison | | |
|---|---|---|---|
| | sockeye-chum | sockeye-chinook | chum-chinook |
| Euphausiids | **17** | 4 | 4 |
| Copepods | 0 | 0 | 0 |
| Amphipods | **12** | 0 | 0 |
| Squid | 0 | 0 | 2 |
| Pteropods | 0 | 0 | 0 |
| Fish | **17** | **17** | **22** |
| Gelatinous | 2 | 0 | 0 |
| Other | 1 | 0 | 0 |
| Total | **49** | **21** | **28** |

| | sockeye | chum | chinook |
|---|---|---|---|
| sockeye | ╲ | 49 | 21 |
| chum | ░ | ╲ | 28 |
| chinook | □ | ░ | ╲ |

## ALEUTIAN ISLANDS

| Prey Group | Pairwise Comparison |
|---|---|
| | sockeye-chum |
| Euphausiids | **44** |
| Copepods | 2 |
| Amphipods | **27** |
| Squid | 0 |
| Pteropods | 0 |
| Fish | 5 |
| Gelatinous | 0 |
| Other | 2 |
| Total | **80** |

| | sockeye | chum |
|---|---|---|
| sockeye | ╲ | 80 |
| chum | ■ | ╲ |

## SHELF

| Prey Group | Pairwise Comparison |
|---|---|
| | chum-chinook |
| Euphausiids | 5 |
| Copepods | 0 |
| Amphipods | 0 |
| Squid | 2 |
| Pteropods | 0 |
| Fish | **23** |
| Gelatinous | 0 |
| Other | 0 |
| Total | **30** |

| | chum | chinook |
|---|---|---|
| chum | ╲ | 30 |
| chinook | ░ | ╲ |

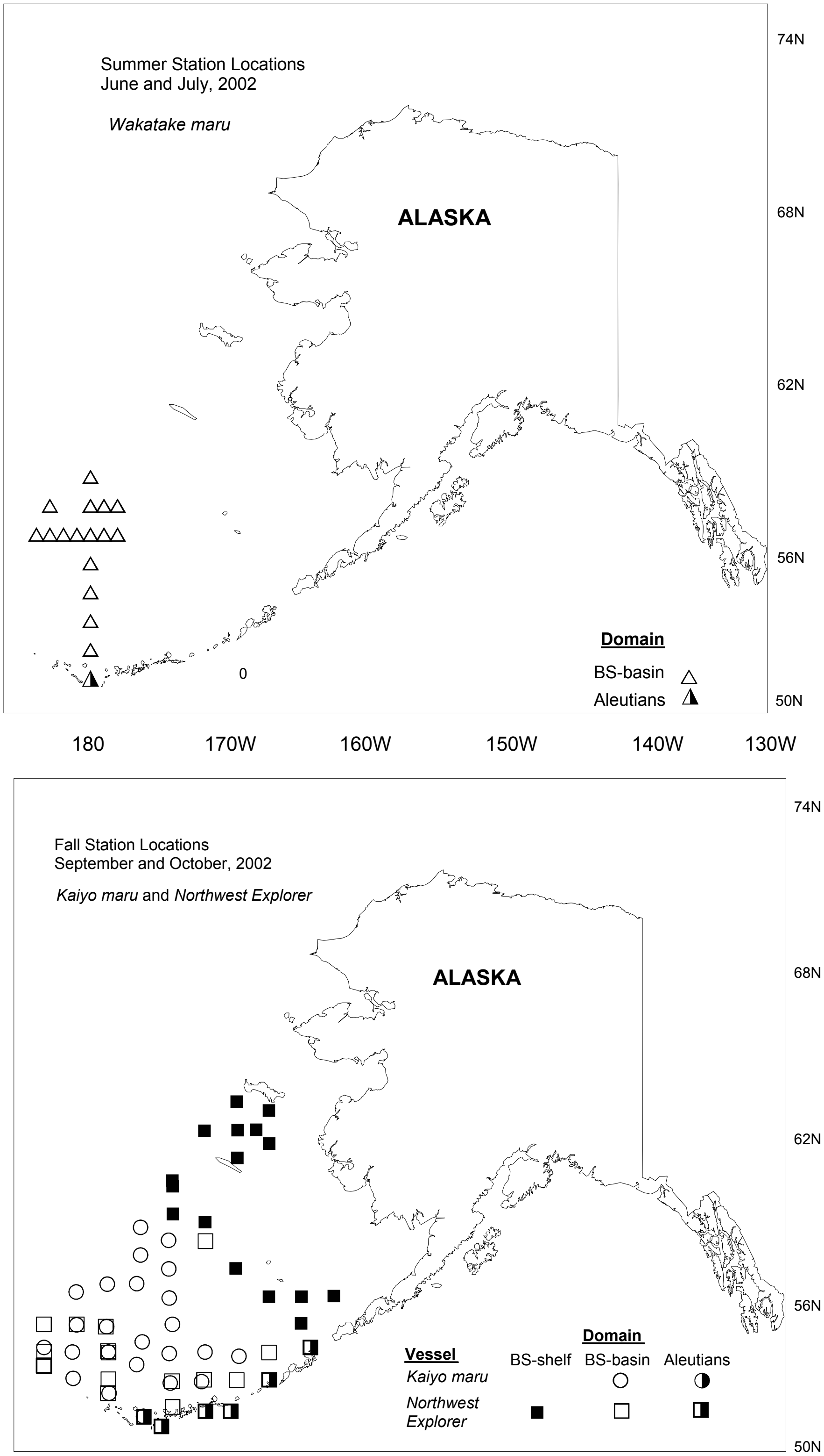

Figure 1. Station locations in summer (upper panel) and fall (lower panel) 2002 where samples were collected for food habits analysis. Shapes depict station locations for each research vessel. Triangles = *Wakatake maru*, circles = *Kaiyo maru*, and squares = *Northwest Explorer*. Geographical habitats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

## Sockeye salmon

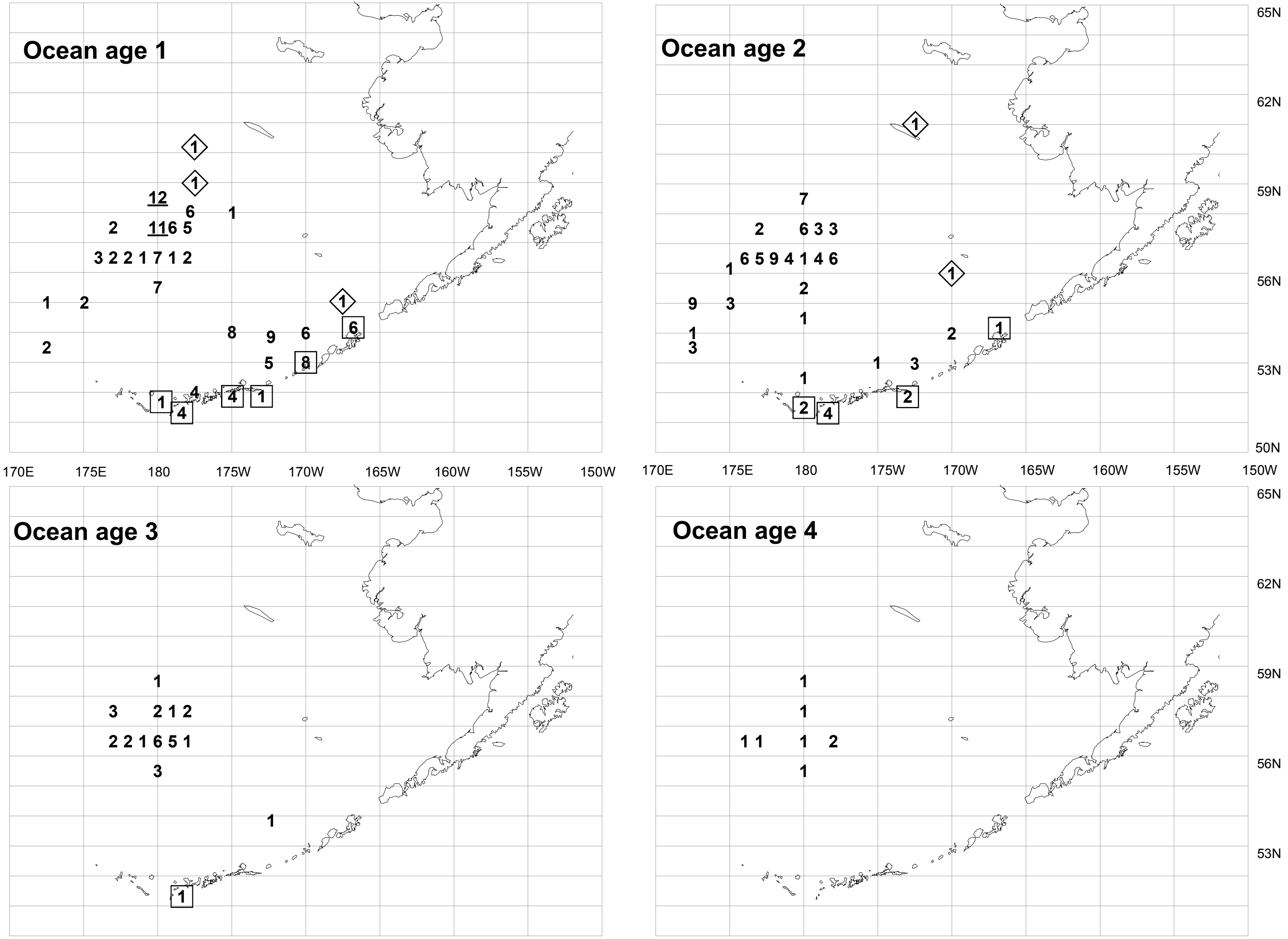

Figure 2. Sample number and location in summer and fall 2002 where sockeye salmon stomach contents were collected by habitat and sockeye salmon ocean age (number of winters spent in the ocean). Shape of the symbol indicates habitat; Bering Sea basin = no symbol, shelf = diamond, and Aleutian Islands = square. Underlined numbers show values ≥ 10.

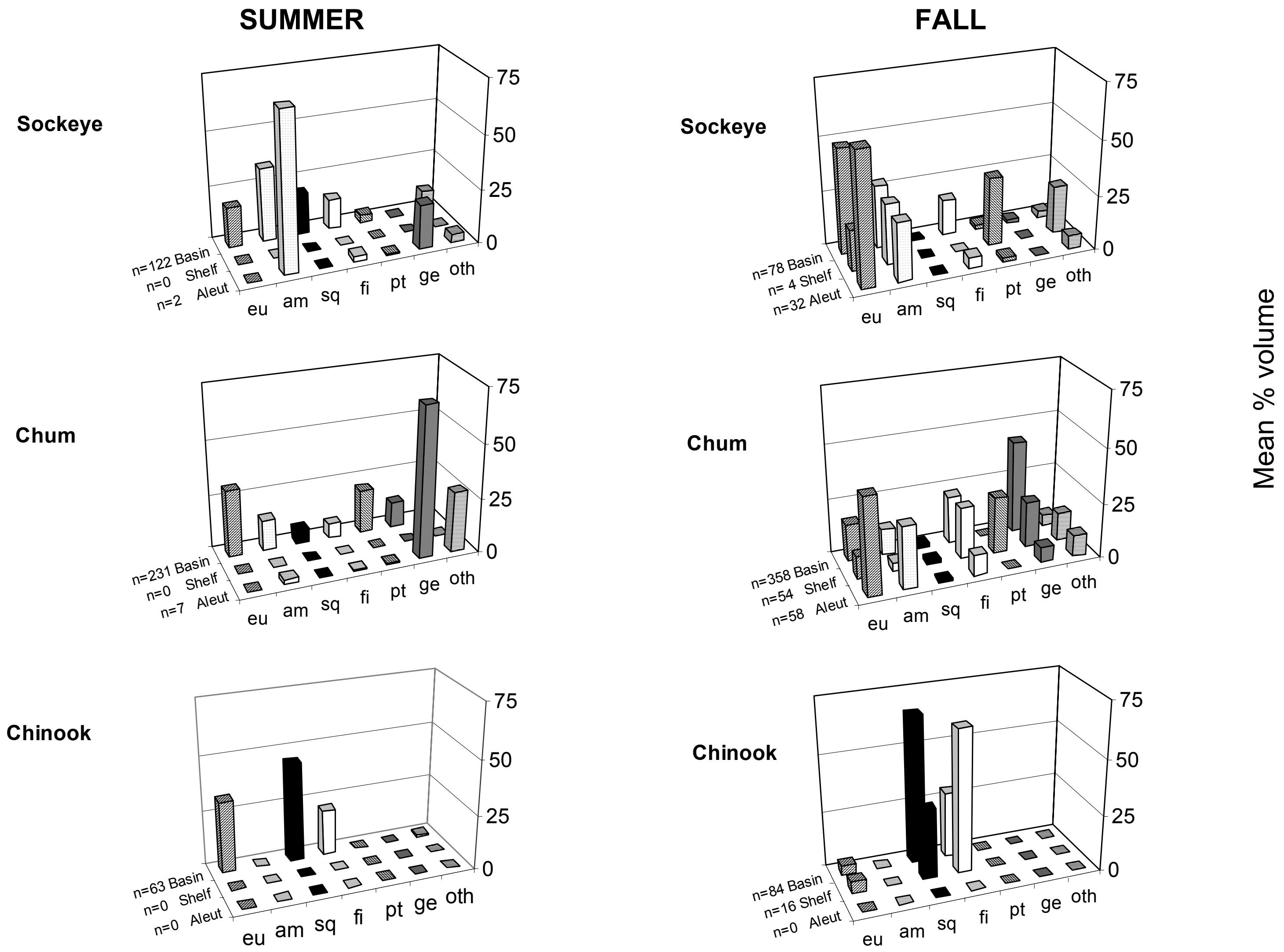

Figure 3. Diet composition (mean percent volume) of sockeye, chum, and chinook salmon collected in the basin, shelf, and Aleutian Islands during summer and fall 2002. Prey categories include; eu = euphausiids, am = amphipods, sq = squid, fi = fish, pt = pteropods, ge = gelatinous zooplankton (medusae and ctenophores), and oth = other. Sample size (n) shown for each habitat.

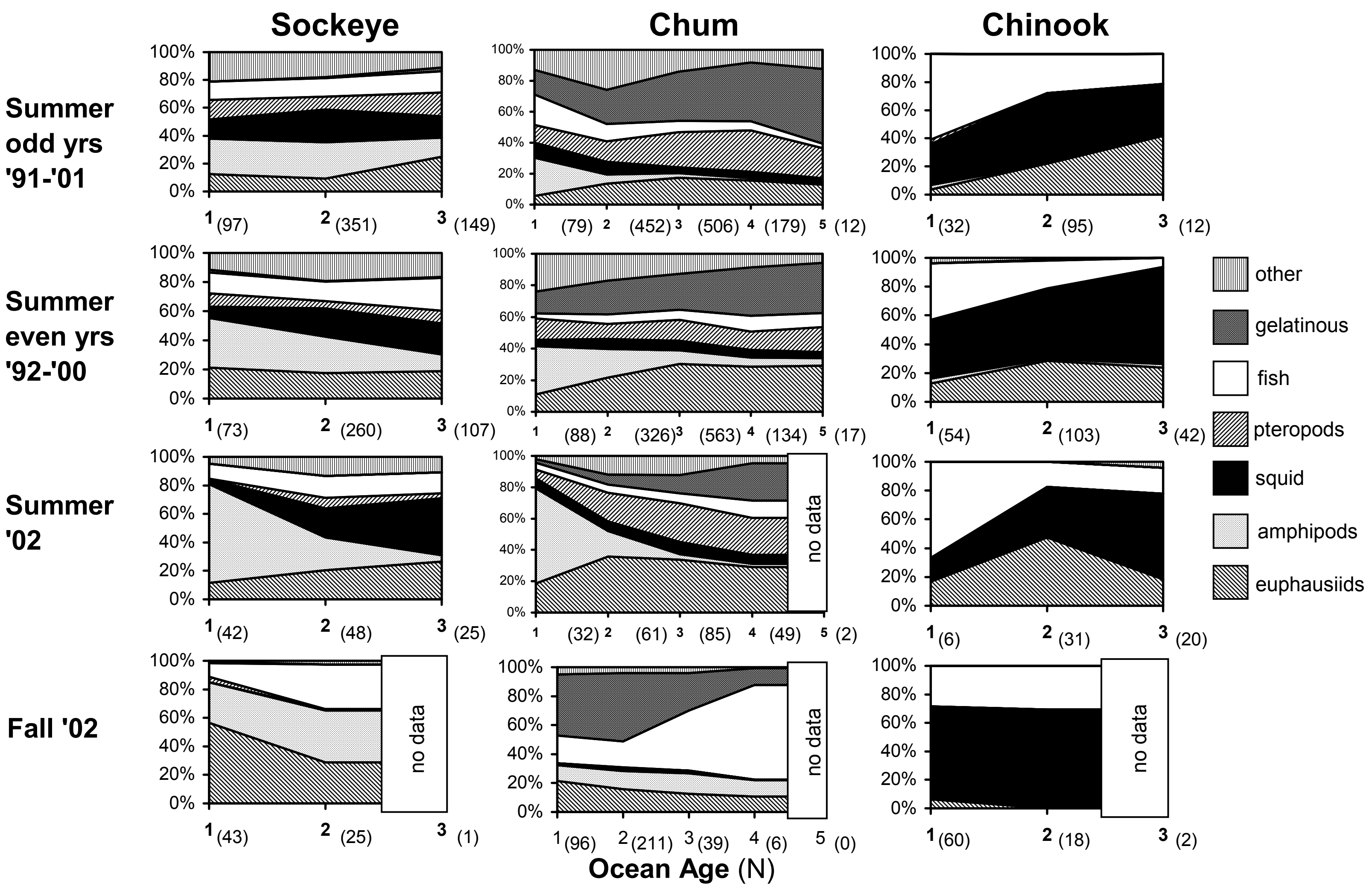

Figure 4. Diet composition (mean percent volume) of sockeye, chum, and chinook salmon collected in the Bering Sea basin stratified by season and ocean age of fish. Sample sources include data for summer in odd-numbered years (1991-2001), summer in even-numbered years (1992-2000), summer 2002, and fall 2002. Ocean age followed by number of salmon stomachs in each age group containing prey is shown on the x-axis. Age groups labeled with "no data" indicate sample sizes too small to characterize stomach contents (n ≤ 5).

**Chum Salmon**

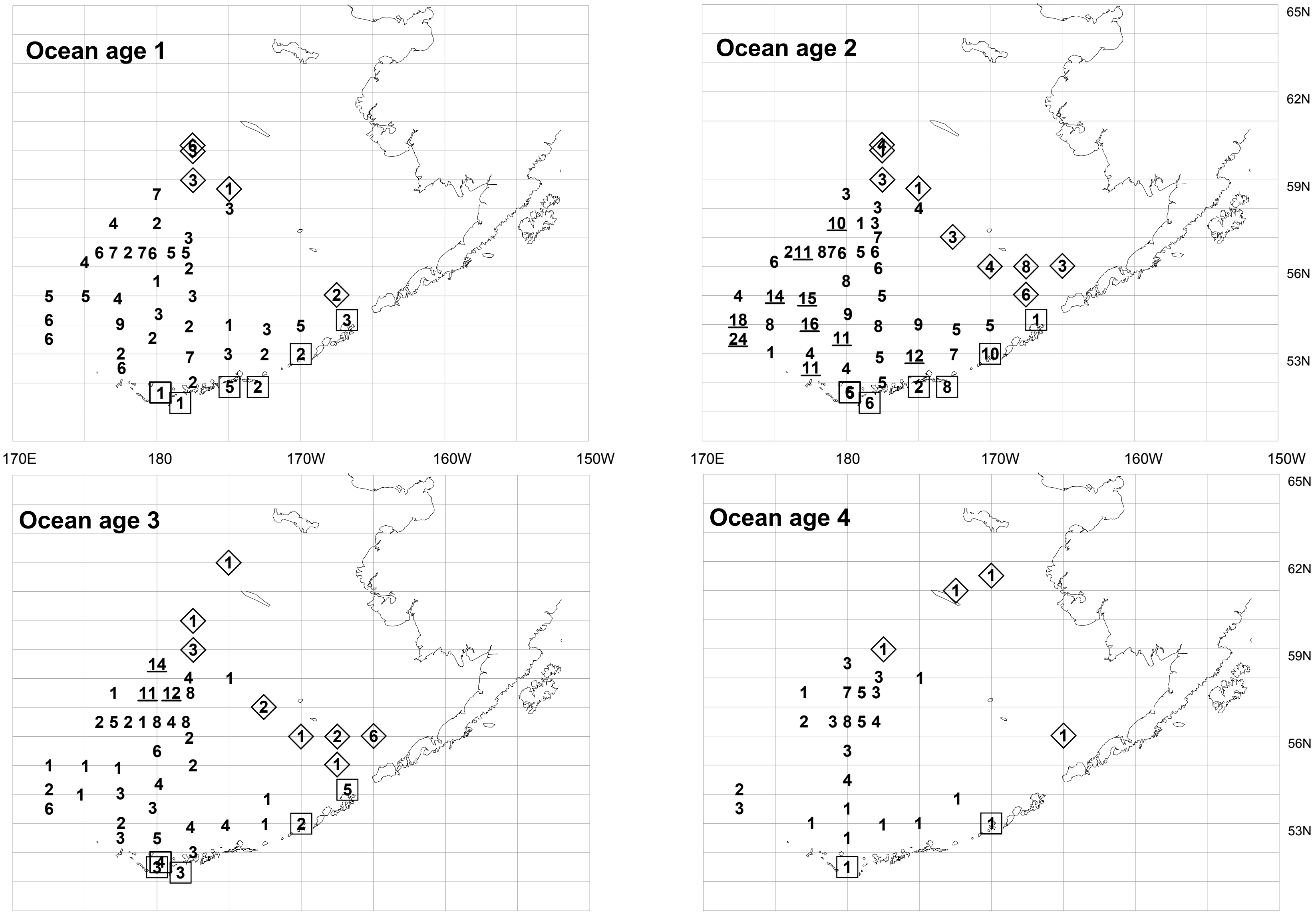

Figure 5. Sample number and location in summer and fall 2002 where chum salmon stomach contents were collected by habitat and chum salmon ocean age (number of winters spent in the ocean). Shape of the symbol indicates habitat; Bering Sea basin = no symbol, shelf = diamond, and Aleutian Islands = square. Underlined numbers show values ≥ 10.

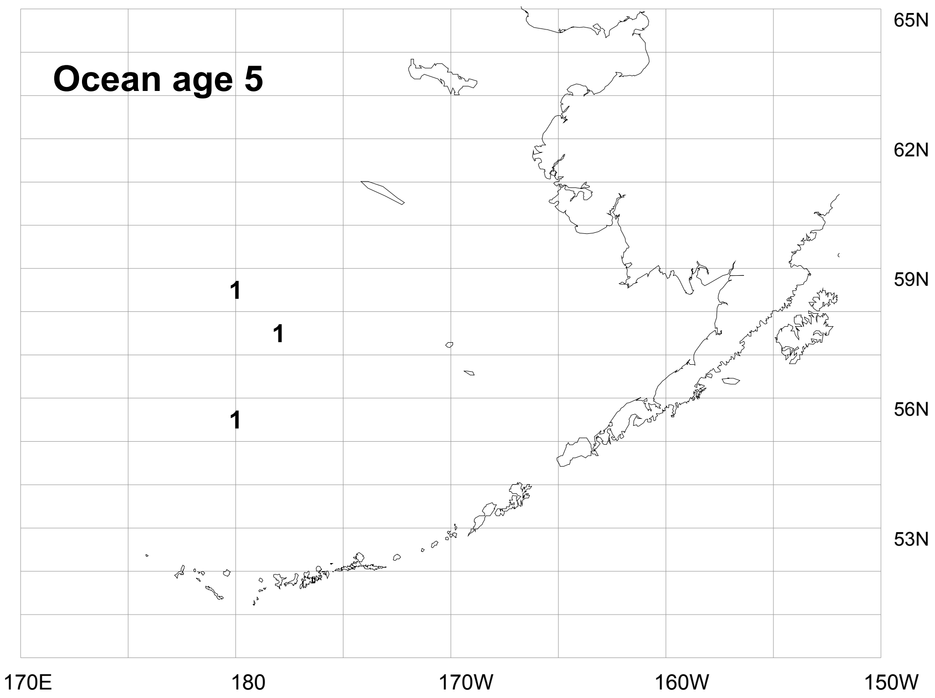
Chum Salmon

Figure 5 (cont.) Sample number and location in summer and fall 2002 where chum salmon stomach contents were collected by habitat and chum salmon ocean age (number of winters spent in the ocean). Shape of the symbol indicates habitat; basin = no symbol, shelf = diamond, and Aleutian Islands = square. Underlined numbers show values ≥ 10.

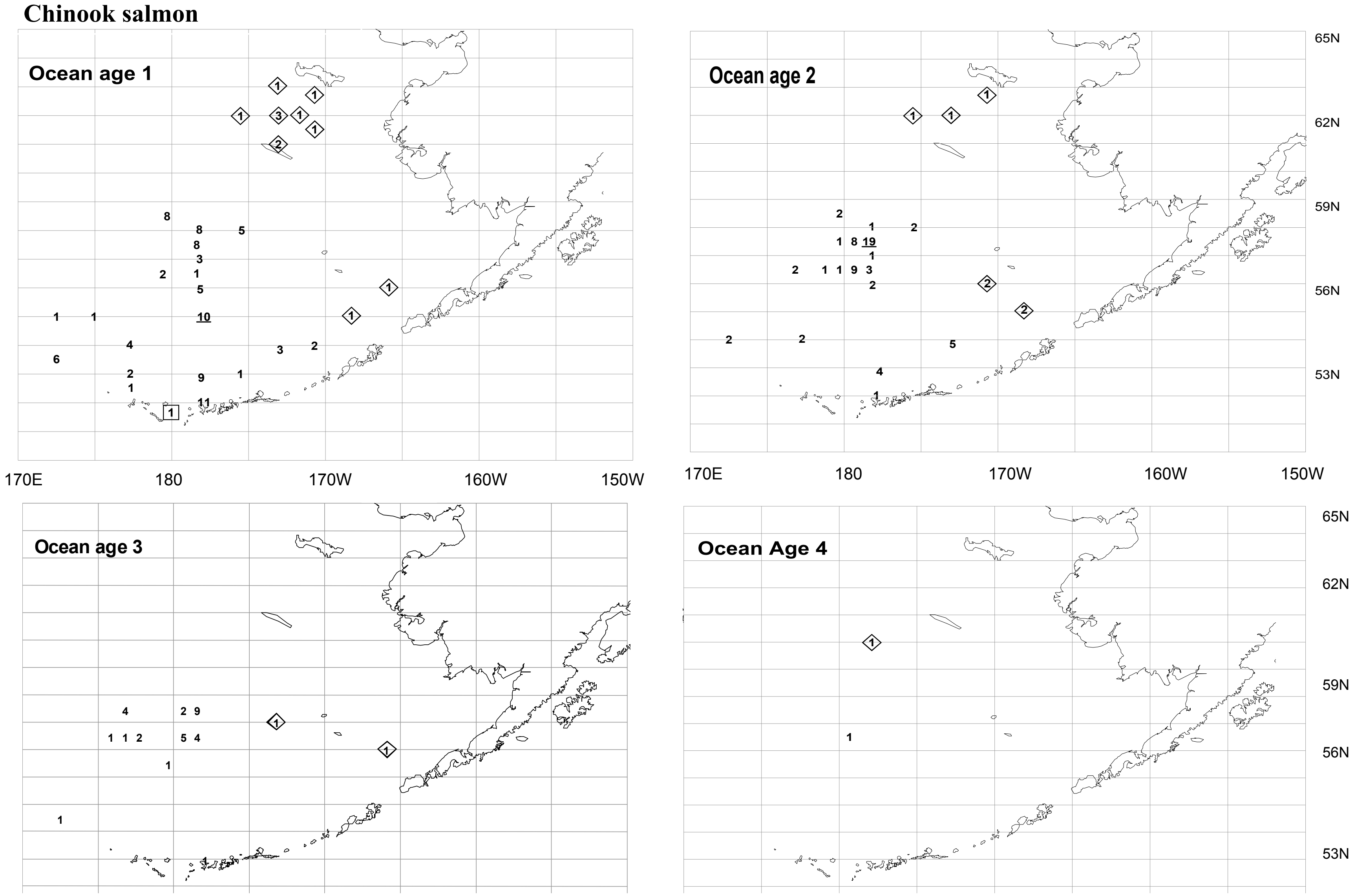

Figure 6. Sample number and location in summer and fall 2002 where chinook salmon stomach contents were collected by habitat and chinook salmon ocean age (number of winters spent in the ocean). Shape of the symbol indicates habitat; Bering Sea basin = no symbol, shelf = diamond, and Aleutian Islands = square. Underlined numbers ≥ 10.

**Pink Salmon**

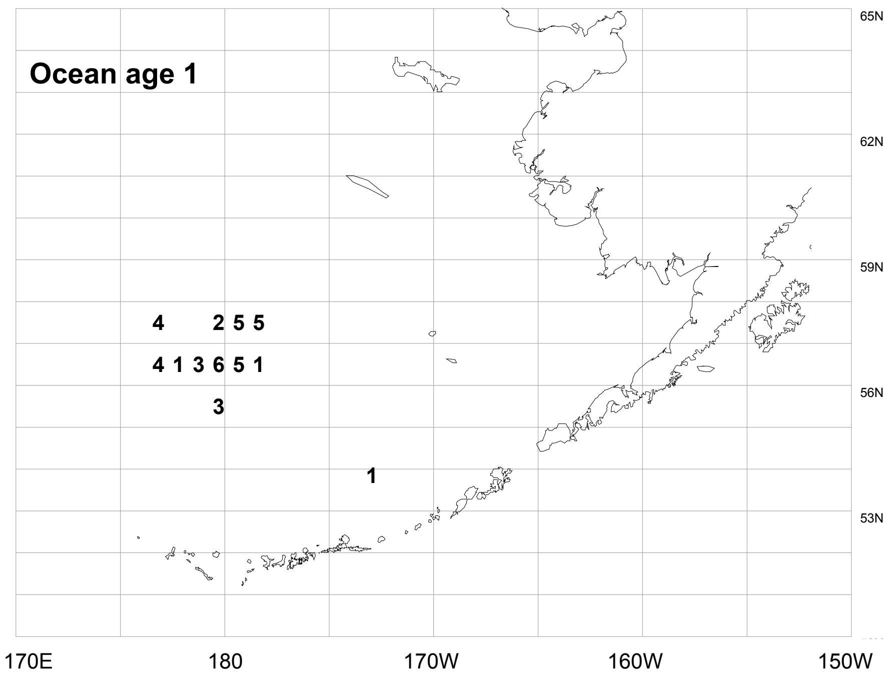

Figure 7. Sample number and location in summer and fall 2002 where pink salmon stomach contents were collected by habitat and pink salmon ocean age (number of winters spent in the ocean). Shape of the symbol indicates habitat; Bering Sea basin = no symbol, shelf = diamond, and Aleutian Islands = square. Underlined numbers show values ≥ 10.