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Feeding Ecology of Pacific Salmon (*Oncorhynchus* spp.) in the Central North Pacific Ocean and Central Bering Sea, 1991-2000

A Dissertation
Presented to Hokkaido University, Hakodate, Japan

by

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Feeding Ecology of Pacific Salmon (*Oncorhynchus* spp.) in the Central North Pacific Ocean and Central Bering Sea, 1991-2000

Abstract

by Nancy Catherine Drummond Davis

This study describes the food habits and feeding ecology of Pacific salmon (*Oncorhynchus* spp.) in the central North Pacific and Bering Sea during June and July, 1991-2000. Studies of ocean-dwelling salmon feeding ecology and energetics are essential because this is the period in their life history when substantial growth occurs.

gillnet and longline gear were used to catch salmonids. Most of the catches consisted of immature sockeye (*O. nerka*), chum (*O. keta*), and chinook (*O. tshawytscha*) salmon, and maturing coho (O. kisutch) and pink (*O. gorbuscha*) salmon. Common ages were 1.1, 2.1, 1.2, 2.2 (sockeye); 0.1, 0.2, 0.3 (chum); and 1.1, 1.2, 1.3 (chinook salmon). All pink and coho salmon were maturing ocean age .1, and steelhead trout (*O. mykiss)* were a mixture of immature and maturing ocean age .1 and .2 fish. There was a strong biennial cycle of East Kamchatka pink salmon in the survey area, which provided a natural experiment in which to examine inter- and intra-specific feeding interactions.

Pacific Ocean (45°-51°N) indicated mean prey weight was 12.9 g (0.66% body weight). Major prey groups included euphausiids (*Euphausia pacifica*), copepods (*Neocalanus cristatus* CV), hyperiid amphipods (primarily *Parathemisto pacifica*), and squid (*Berryteuthis anonychus*). Squid consumed by sockeye salmon were large-sized *B. anonychus* (approximately 50-100 mm mantle length). Small sockeye salmon (<500 g) fed on a high percentage (70%) of amphipods and pteropods. As sockeye salmon body size increased, the percentage of squid in the stomach contents increased to more than 33% in fish larger than 2000 g.

Analysis of sockeye salmon stomach contents collected from the central Bering Sea (52°-58°N) indicated mean prey weight was 10.4 g (0.66% body weight). Prey weight increased from 8.2 g to 12.9 g in even-numbered years when pink salmon abundance was low. Major prey items included euphausiids (*Thysanoessa longipes*), hyperiid amphipods, copepods (*N. cristatus* CV), squid and fish. Sockeye salmon fed on many small squid (20 to 30 mm in ML). Fish consumption of juvenile *Hemilepidotus* spp., *Pleurogrammus monopterygius*, and adult *Stenobrachius leucopsarus* was substantially greater in the central Bering Sea than south of the Aleutian Islands. There was a 36% reduction in stomach fullness in odd-numbered years when pink salmon were abundant. Likewise, there was a 53% reduction in the weight of high-quality prey and a 13% increase in the weight of low-quality prey in odd-numbered years. As sockeye body weight increased from less than 1000 g to greater than 2500 g, the percentage of amphipods in the stomach contents decreased from 34% to 11% and squid increased from 18% to approximately 30%.

Analysis of chum salmon stomach contents collected from the central North Pacific Ocean indicated prey weight averaged 9.8 g (1.00% body weight; 41°-44°N) and 9.35 g (0.90% body weight; 45°-51°N). Chum salmon consumed a wider variety of prey than other salmon species including euphausiids (*E. pacifica*), hyperiid amphipods (*P. pacifica, Phronima sedentaria),* squid (*B. anonychus*), pteropods (*Limacina helicina, Clione limacina*), fish (*P. monopterygius*), appendicularians (likely *Oikopleura labradoriensis*), ostracods (*Conchoecia magna*), and heteropods (*Carinaria* sp.), and a large proportion of gelatinous zooplankton (medusae, *Aglantha digitale*, ctenophores *Beroe* sp., and salps). Salps were the most common gelatinous zooplankton consumed in this area, including salp "barrels" hollowed-out by resident hyperiid amphipods, *P. sedentaria*. Fish prey was consumed by chum salmon larger than 2500 g.

Analysis of chum salmon stomach contents collected from the central Bering Sea (52°-58°N) indicated mean prey weight was 15.5 g (1.10% body weight). Chum salmon fed on more non-gelatinous zooplankton than farther south. Chum salmon consumed euphausiids (*T. longipes*), copepods (*N. cristatus* CV), amphipods (*P. pacifica*, *Primno*

abyssalis, *Hyperia medusarum*, and *Hyperoche medusarum*), squid (juveniles), pteropods (*L. helicina*, and *C. limacina*), and fish (*P. monopterygius*, *S. leucopsarus*, juvenile *Hemilepidotus* sp., and post-larval *Aptocyclus* spp., *Psychrolutes phrictus*, and *Hippoglossus stenolepis*). Chum salmon abundance was positively correlated, and pink salmon abundance was negatively correlated, with the amount of copepods and amphipods in chum salmon stomach contents. There was no difference in stomach fullness of chum salmon between years of high and low pink salmon abundance. However, there was a 38% reduction in weight of high-quality prey and a 19% increase in weight of low-quality prey when pink salmon were abundant. Differences in prey weight of high- and low-quality prey during odd- and even-numbered years were highly significant ($p<0.01$) and indicated a shift to different prey composition when pink salmon were abundant. Chum salmon weighing less than 500 g fed on a higher percentage of amphipods than chum salmon weighing greater than 1000 g. Although euphausiids were consumed by all sizes of chum salmon, a higher percentage (>20%) was observed in fish weighing greater than 1000 g than in small chum salmon (8% in fish <500 g). All sizes of chum salmon consumed gelatinous zooplankton increasing from 12% in small chum salmon (<500 g) to 36% in larger fish (>3000 g). The percentage of prey composed of juvenile fish, pteropods, and small squid was stable across weight classes.

Analysis of pink salmon stomach contents collected from the central North Pacific Ocean (45°-51°N) indicated prey weight averaged 14.8 g (1.37% body weight). Samples from pink salmon were characterized by sporadic high consumption of large squid (*B. anonychus*). There was a dramatic shift towards increasing percentages of large squid and euphausiids in the stomachs of pink salmon of larger size. In contrast, the percentage of copepods and pteropods decreased from 29% and 17% in the stomach contents of small pink salmon (<1000 g) to 6% and 9% in larger fish (>1500 g).

Analysis of pink salmon stomach contents collected from the central Bering Sea (52°-58°N) indicated mean prey weight was 15.2 g (1.29% body weight). Pink salmon consumed small squid, perhaps *B. anonychus* juveniles. Pink salmon also fed heavily on fish, including juvenile flat fish, juvenile *P. monopterygius*, *Hemilepidotus* sp. and adult

S. leucopsaurus. Pink salmon abundance was negatively correlated with pink salmon stomach fullness and the amount of euphausiids, copepods, squid, and fish in their stomach contents. There was a 23% decrease in stomach fullness, a 32% reduction in the proportion of high-quality prey in the stomach contents, and a 72% increase in the proportion of low-quality prey observed when pink salmon were abundant. The interaction of prey quality and year on stomach fullness indicates when pink salmon are abundant intra-specific competition may reduce prey availability and growth during their final summer at sea. Pink salmon (<500 g) consumed a high percentage of juvenile fish (64%), however, did not consume juvenile squid. For larger pink salmon (>500 g), the proportion of fish and squid consumed prey was relatively constant. The proportion of euphausiids was low (1%) in stomach contents of small pink salmon (<500 g), however, increased to 17% in larger fish (>1500 g).

Analysis of coho salmon stomach contents collected from the central North Pacific Ocean (41°-44°N) indicated prey weight averaged 17.3 g (0.97% body weight; 41°-44°N) and 44.1 g (2.17% body weight; 45°-51°N). Coho salmon consumed a high proportion of large *B. anonychus*. In the southern area hyperiid amphipods (*Phronima sedentaria* in salp barrels) and pteropods (*Clio recurva*) were an alternative prey to squid. At 45°-51°N, large amounts of large *B. anonychus*, in addition to euphausiids, *E. pacifica*, and fish, including *Gasterosteus aculeatus*, *P. monopterygius*, *Cololabis saira*, *Hemilepidotus* spp., *T. crenularis* and *Engraulis japonica* were consumed. Squid was the primary prey for coho salmon of all sizes. The proportion of pteropods (19%) in small coho (<1000 g) decreased to 10% in large coho salmon (>3000 g), while the percentage of fish increased from 9% in the stomach contents of small coho (<1000 g) to 24% in large coho salmon (>3000 g).

Analysis of chinook salmon stomach contents collected from the central North Pacific Ocean (45-51°N) indicated mean prey weight was 31.8 g (0.86% body weight). Chinook salmon (1500 to ≥4000 g) consumed predominately large *B. anonychus*. Large chinook salmon (>2000 g) occasionally consumed large prey fish such as *C. saira* (175

mm SL), *E. japonicus* (125-135 mm SL), *L. schmidti* (114-123 mm SL), and *A. pharao* (140-315 mm SL).

Analysis of chinook salmon stomach contents collected from the central Bering Sea (52°-58°N) indicated mean prey weight was 14.81 g (0.59% body weight). Total prey weight increased from 9.53 g (0.42% body weight) to 21.6 g (0.74% body weight) in even-numbered years when pink salmon abundance was low. There was a 56% reduction in stomach fullness and a 68% reduction in the weight of fish and squid consumed in odd-numbered years. Major prey included squid (predominantly large *B. anonychus*), euphausiids (*T. longipes*), and fish (*P. monopterygius* and *S. leucopsarus*). Chinook salmon caught in the central Bering Sea fed on fish and euphausiids substantially more than those caught in the central North Pacific Ocean. As chinook salmon body weight increased from less than 500 g to 1500 g, the percentage of juvenile fish in stomach contents decreased from 48% to 21%.

Analysis of steelhead stomach contents collected from the central North Pacific Ocean indicated prey weight averaged 14.2 g (0.79% body weight; 41°-44°N), however, was higher to the north where stomach fullness ranged from 33.5 g (1.02% body weight) to 72.1 g (1.85% body weight; 45°-51°N). Steelhead were characterized by a dominance of squid, *B. anonychus*, and fish, including *Gasterosteus aculeatus*, *A. pharao*, *P. monopterygius*, and myctophids in the diet. Other prey occasionally found in high abundance was polychaetes (*Tomopterus* and *Rynchonerella* sp.). The percentage of squid in steelhead stomach contents increased from 40% in smaller fish (<1000 g) to 67% in larger fish (>4000 g), and the proportion of polychaetes decreased from 10% in smaller fish (>1000 g) to less than 1% in larger steelhead (>4000 g).

Results showed regional differences in salmon food habits between areas in the central North Pacific Ocean and the central Bering Sea. The southern area (41°-44°N) was characterized by lower stomach fullness and lower consumption of *B. anonychus* than further to the north (45-51°N). In the southern area, chum and coho salmon consumed salp barrels containing hyperiid amphipods, and steelhead consumed

polychaetes and often ate floating debris (plastic sheet, bits of wood). This area was the poorest for salmon feeding based on prey abundance and prey quality. High levels of stomach fullness in salmon characterized the northern area of the central North Pacific Ocean (45°-51°N). Large (>1000 g) immature and maturing sockeye, pink, coho, and chinook salmon, and steelhead consumed a high proportion of *B. anonychus* (40-125 mm ML), making this region particularly favorable for feeding of maturing salmonids, and large immature chinook salmon.

The central Bering Sea was characterized by young (<1000 g body weight; ocean age .1) sockeye, chum, and chinook salmon ingesting a diverse diet with relatively high proportions of juvenile fish and squid, in addition to euphausiids and other large zooplankton. Stomach fullness and consumption of small fish and squid by young sockeye, chum, and chinook salmon was substantially higher in the central Bering Sea and suggests the summertime feeding environment was critical for young (ocean-age .1) salmon.

I suggest the shift in prey composition observed in chum, sockeye, and pink salmon was due primarily to resource limitation stemming from feeding competition among chum, sockeye, and pink salmon when pink salmon were abundant. Results showed substantial reductions in the proportion of high quality prey in sockeye, chum, and pink salmon with concomitant increases in the amount of low energy-dense prey. These density-dependent interactions negatively affect the feeding of sockeye, chum, and pink salmon and could reduce growth when abundant maturing pink salmon migrate through the central Bering Sea in the summer in odd-numbered years on their return to the rivers of eastern Kamchatka.

Diel catches and food habits analysis of sockeye, pink, and chum salmon were investigated between 57°33´N, 178°41´W and 57°27´N, 178°20´W in the central Bering Sea. Eight operations were conducted in a 24-hour period using a surface gillnet. Sockeye, chum, and pink salmon were caught at the surface during each of the six

daylight gillnet operations, evidence these species spent some time at the surface during daylight periods.

More sockeye salmon were caught during daylight and less during the night than would have been expected had catches been equal in every time period. Pink salmon catches were also small in the afternoon and early evening but increased dramatically after sunset and remained at a high level until after sunrise. Chum catches increased shortly after sunrise and after noon, however, catches were independent of daytime or nighttime. Diel food habits of sockeye salmon illustrated a diel pattern where stomach fullness was significantly greater during the night than during the day ($p<0.001$). However, stomach fullness of pink and chum salmon was not significantly different between day and night ($p=0.07$; $p=0.90$). There was a distinct change in the prey composition in sockeye and pink salmon stomach contents over the diel period, as euphausiids and copepods were consumed at night and fish was consumed during the day. Chum salmon consumed euphausiids during nighttime and fish during daylight, however, gelatinous zooplankton were consumed throughout the diel period. At night, competition for euphausiids may be intense when pink salmon are abundant and the period of darkness is short during summer at high latitudes. Therefore, a daytime switch to feeding on fish by sockeye, pink, and chum salmon may be a mechanism to decrease food competition.

Caloric density determinations were performed by bomb calorimetry on a variety of salmonids, salmon prey organisms, and salmon stomach contents. Caloric density ranged from 470 to approximately 1000 calories per g wet weight for pteropods, hyperiid amphipods, small flat fish juveniles (approximately 20 mm SL), and small squid (<20 mm ML). Slightly larger fish (21-44 mm SL), and middle-sized squid (40 mm ML) had caloric densities ranging from approximately 1100 to 1500 calories per g wet weight. Prey containing the highest caloric density (>1500 calories per g wet weight) included large *B. anonychus* (80-90 mm ML), deep sea smelt, and northern lampfish (43-112 mm SL). Caloric values were reported for the first time for small squid (13-22 mm ML; 850-1010 calories per g wet weight) and juvenile flatfish including *Atheresthes* sp. (20 mm

SL; 624 calories per g wet weight) and *H. stenolepis* (19 mm SL; 853 calories per g wet weight), which were important prey of sockeye, chum, pink, and chinook salmon in the central Bering Sea.

Bomb calorimetry indicated juvenile chum (age 0.0) and pink salmon (age 0.0), and young steelhead (age 2.0) had lower energy density than older steelhead (age 3.0) and sockeye spending one year at sea (age 1.1). Calorimetric determinations of stomach contents collected from similar-sized sockeye, chum, and pink salmon showed caloric density was lowest in chum salmon (270 to 739 calories per g wet weight). A comprehensive table of energy densities determined by bomb calorimetry was compiled for species ecologically-related to Pacific salmon. Caloric values were listed for cnidarians (n=14), ctenophorans (n=14), polychaetes (n=7), pteropods (n=8), squids (n=22), copepods (n=20), euphausiids (n=34), amphipods (n=12), ostracods (n=1), mysids (n=5), decapods (n=11), chaetognaths (n=6), salps (n=3), appendicularia (n=1), and fish (n=122). This table is useful because caloric density can change with location, season, and maturity stage. Tabulated caloric values increase the accessibility of this information to researchers involved in studies of bioenergetics and feeding ecology of salmonids and other animals inhabiting the North Pacific and Bering Sea.

Salmon growth and prey consumption were estimated for a two month summer period using field observations on sea surface temperatures, salmon food habits in the central North Pacific Ocean and central Bering Sea, data on caloric density of salmon and salmon prey, and a published fish bioenergetic model. Growth estimates from the model were compared with summer monthly mean weights of high-seas caught salmon to evaluate daily ration.

Model consumption estimates indicated an ocean age .1 sockeye needed to consume 16-19 g of prey per day, the equivalent of 3.57 to 4.09% body weight per day, depending on temperature (5°-9°C). The specific energy requirements for small sockeye salmon were the first available for young ocean age .1 sockeye in the Bering Sea. Simulation results showed an immature chum salmon required a daily consumption rate

of 42 to 49 g prey per day (3.28-3.86% body weight per day) and a daily prey consumption of 30-35 g per day for a maturing pink salmon (2.73-3.14% body weight per day), depending on temperature (5°-9°C). A maturing coho salmon would require 63-68 g of prey (2.64-2.86% body weight per day) at 9° to 11°C. My estimates of daily ration for maturing coho salmon were the first determined for adult coho in offshore marine habitats.

Model results suggested salmon feeding rate was close to their physiological maximum (85 to 93% of the maximum for immature sockeye and chum, 86 to 96% of maturing pink and coho salmon). Therefore, small decreases in the daily ration can cause significant decreases in growth over a relatively short time period, and prey consumption was more important than temperature for determining salmon growth at summertime temperatures. I speculate when salmon prey is abundant, an upper thermal limit favorable for salmon growth may be bounded by large metabolic requirements at high temperatures, and a lower limit favorable for salmon growth may be bounded by decreased capacity for prey consumption at low temperatures.

My results have shown the summer in the central Bering Sea is critical habitat for salmon because of its role as a nursery area for juvenile and post-larval fish and squid, which provides a rich forage base for feeding Asian and North American stocks of young sockeye, chum, and chinook, and maturing chum and pink salmon. Recent reductions in productivity suggest important environmental changes may be occurring in the Bering Sea. Therefore, monitoring year-round conditions in salmon prey availability and salmon feeding and growth is advised so we may best manage the future of our salmon resources.

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Introduction

"The life history strategy and migration pattern of *Oncorhynchus* reflect an evolution of anadromous fish which have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in freshwater" (Kaeriyama 1996a). Pacific salmon (*Oncorhynchus* spp.) undergoing their ocean feeding migrations dominate the epipelagial waters of the subarctic North Pacific Ocean. Study of salmon feeding and energetics in the ocean is essential because this is the period in their life history when substantial growth in body size occurs. For example, the biomass of returning sockeye salmon (*O. nerka*) adults can be 25 times greater than the biomass of out-migrating smolts (Brett 1986).

A climatic regime shift in 1976-77 may have led to favorable environmental conditions for northern salmon stocks resulting in an increase in abundance of sockeye, pink (*O. gorbuscha*), and chum (*O. keta)* salmon in those areas (Trenberth 1990; Beamish and Bouillon 1993; Miller et al. 1994; Hare and Francis 1995). Concomitant with the increase in population size in the last decade, there has been a gradual decrease in size of Asian and North American stocks of chum and pink salmon (Kaeriyama 1989, 1998; Kaeriyama and Urawa 1992; Ishida et al. 1993; Helle and Hoffman 1995, 1998; Bigler et al. 1996). The relationship between increase in salmon abundance and decrease in body size throughout the North Pacific Ocean have led scientists to hypothesize that salmon may be showing evidence of density-dependent growth. Inter-specific interactions can cause shifts in distribution and changes in growth (Azumaya and Ishida 2000).

Feeding ecology of immature and maturing salmon in offshore waters has been investigated extensively by researchers in the Gulf of Alaska (LeBrasseur 1966, Manzer 1968, Pearcy et al. 1988, Aydin et al. 2000, Kaeriyama et al. 2000, Myers et al. 2000b), the Bering Sea (Nishiyama 1970, 1974, 1977, Kanno and Hamai 1972, Myers et al. 2000b), the North Pacific Ocean (Allen and Aron, 1958, Andrievskaya 1957, 1966, Ito 1964, Takeuchi 1972, Sobolevskiy and Senchenko 1996, Tadokoro et al. 1996, Myers et al. 2000b), and the Okhotsk Sea (Gorbatenko and Chuchukalo 1989). Brodeur (1990)

summarized marine food habits and feeding ecology of salmon by species and life-history type, and concluded that despite differences in prey organisms salmon may be non-selective feeders within a preferred prey size range. Studies have indicated that the prey composition of chum salmon can change in response to the abundance of pink salmon (Andrievskaya 1966, 1970, Shuntov et al. 1993, Tadokoro et al. 1996). Tadokoro et al. (1996) observed that when pink salmon abundance was low, chum salmon fed on a diet similar to the prey ingested by sockeye and pink salmon, however, when pink salmon abundance was high, chum salmon increased the proportion of gelatinous zooplankton and reduced the proportion of crustacean prey in their diet.

My study describes the food habits and feeding ecology of sockeye, chum, pink, coho (*O. kisutch*), and chinook salmon (*O. tshawytscha*), and steelhead trout (*O. mykiss*) in the central North Pacific Ocean and central Bering Sea. Data were collected in a consistent manner over a 10-year time series. Trends in feeding ecology are discussed with respect to annual variation in diet, inter-species effects, regional differences, life-history stage, and diel changes in prey composition. I also provide new laboratory determinations of caloric density for salmon and salmon prey organisms, and estimate prey consumption for young sockeye and chum, and maturing pink and coho salmon in the ocean. My results supply researchers with important input values for bioenergetic (Hewett and Johnson 1992) and ecosystem models (Christensen and Pauly 1992). Information on energy densities, diet composition specific to ocean production areas, and estimates of consumption are provided for individual- and ecosystem-based models.

Chapter 1 summarizes the food habits and feeding ecology of Pacific salmon and steelhead in the central North Pacific Ocean and central Bering Sea from 1991-2000. The summary includes identification of prey organisms, mean and maximum stomach contents weight by species, and feeding salmon based on salmon body size for three oceanographically distinct areas (41°-44°N, 45°-51°N, and 52°-58°N at 180° longitude). Changes in feeding patterns occur against the backdrop of a natural experiment whereby widely fluctuating abundance of maturing pink salmon occurs because of their strong odd-year dominance in the central Bering Sea.

Chapter 2 presents results of a diel study of food habits of sockeye, chum, and pink salmon in the central Bering Sea. The data show there is a shift in the dominant prey organisms observed in daytime versus nighttime sampling. Diel changes in prey composition suggest that studies of salmon food habits relying on sampling at one time of day may fall short in assessing the full spectrum of prey species taken by salmon and, therefore, may hamper a fuller understanding of the overall strategy of salmon feeding ecology.

Chapter 3 provides results of laboratory determinations of caloric density of salmon prey organisms, and young sockeye, chum, and pink salmon and steelhead collected from the central North Pacific, Gulf of Alaska, and Bering Sea. In addition, a tabulation of caloric density values of salmonids and their prey organisms is presented in a format useful for studies of salmonid feeding ecology and salmon bioenergetics.

Chapter 4 presents estimates of daily prey consumption for young high-seas caught sockeye and chum, and maturing pink and coho salmon for a range of summertime temperatures using a published bioenergetics model. The relationship between temperature and prey consumption is examined. Consumption estimates are compared with growth estimates observed from Japanese salmon research vessel data to assess if salmon are feeding at their physiological maximum.

Chapter 5 relates density-dependent growth to salmon species-specific feeding patterns. Concepts are outlined regarding how salmon have unique feeding-related adaptations that can reduce competitive interactions. The relationship between salmon lipid storage and feeding strategy on an annual basis is reviewed. In conclusion, the characteristics of the central North Pacific Ocean and central Being Sea are compared from the viewpoint of salmon feeding.

Chapter 6 is a point-by-point summary of the findings and conclusions made in each of the previous chapters and provides a detailed synopsis of all the material presented.

Chapter 1.0 Salmonid food habits in the central North Pacific Ocean and central Bering Sea, 1991-2000

1.1. Introduction

Recent decreases in chum salmon body size and increases in age of maturity (Kaeriyama, 1989, Ishida et al. 1993, Helle and Hoffman 1995, Bigler et al. 1996), have led to an interest in factors affecting salmon feeding conditions during their migrations at sea. Low lipid levels in pink and chum salmon in the winter suggest salmon may starve in winter due to prey limitation (Nomura et al. 2000, 2001, 2002), and prey availability of squid is a significant factor influencing growth of post-juvenile pink, sockeye, and coho salmon in the Gulf of Alaska (Aydin et al. 2000). To obtain the data required to evaluate the physical and biological factors affecting salmon condition, a long-term monitoring program was initaited in summer of 1991, which continues to the present time in the central North Pacific and central Bering Sea. This research program has generated an important time series on salmon biological characteristics at sea.

In the central Bering Sea there is a fluctuation in the abundance of pink salmon such that there is a 30- to 50-fold increase in odd-numbered years over even-numbered years. This annual switch between high and low abundance of pink salmon provides a natural experiment to examine the inter- and intra-specific effects of changes in pink salmon abundance on salmon feeding. Inter-specific interactions between chum and pink salmon have been observed on the basis of food habits (Ito 1964; Andrievskaya 1966; Tadokoro et al. 1996). The purpose of this analysis was to summarize patterns in the food habits and feeding ecology of sockeye, chum, pink, coho, and chinook salmon, and steelhead caught in the central North Pacific and cental Bering Sea from summertime surveys over the decade from 1991 to 2000. Inter-annual variation in salmon diet, inter- and intra-specific effects, spatial differences, and salmon body size are examined with respect to salmon food habits.

1.2. Methods

Gillnet and longline gear were used in experimental fishing to collect salmonids for biological examination in the central North Pacific and central Bering Sea during June and July from 1991 to 2000 aboard the *Wakatake maru*. Surveys were conducted along a south to north transect located at 179°30'W (1991 to 1996) and 180° longitude (1997-2000; Fig. 1.1). The southernmost station was located at 38°30'N and fishing operations were conducted at stations one degree of latitude apart, northwards across the Aleutian Island chain and into the Bering Sea, where the northernmost station was located at 58°30'N. Additional stations were located at 57°30'N and 56°30'N between 177°30'W and 177°30'E in the international waters of the Bering Sea. Stations were sampled at approximately the same date of the month every year. Routine data collection included oceanographic conditions, surface chlorophyll-*a* concentration, zooplankton biomass, salmon abundance, and salmon biological characteristics. Salmon biological data collection included measurement of body length, body and gonad weight, scale sampling for age determination, and examination of salmon stomach contents.

The cruise track of the *Wakatake maru* crossed several oceanographic areas as the ship moved northward from 38°N (Fig. 1.2). Based on general oceanographic characteristics and salmon catches, data were grouped by latitude into four areas: 38°-40°N, 41°-44°N, 45°-51°N and 52°-58°N. The area furthest to the south, 38°-40° N, was in the vicinity of the Transition Zone. The Transition Zone was south of the Subarctic Boundary, where subarctic and subtropical waters mixed. Generally, the Transition Zone was located south of salmon distribution (Dodimead et al. 1963, Favorite et al. 1976). The area 41°-44°N was located in the Transition Domain, where water temperature was cooler and less saline than further south, and chum and coho salmon dominated catches. The area 45°-51°N included the Subarctic Current, Ridge Domain, and Alaska Stream, and extended north to the Aleutians Islands. Sockeye, chum, pink, coho, and chinook salmon, and steelhead were caught in the cool, dilute waters of this area. The fourth area was located from 52° to 58°N in the central Bering Sea. Stations in the central Bering Sea typically had a shallow thermocline formed by a temperature minimum (<2°C; cold intermediate layer; Luchin et al. 1999) underlying a seasonally-warmed superficial layer.

Sockeye, chum, and pink salmon were abundant, and relatively large catches of chinook salmon were caught in this area.

1.2.1. Oceanographic, chlorophyll-*a*, and zooplankton sampling

Temperature and salinity data were collected using a CTD to a depth of approximately 500 m (1991-1996), or 1000 m (1997-2000) at locations where fishing operations were conducted (Fig. 1.1). Chlorophyll-*a* and zooplankton samples were collected at locations between 38°30'N and 58°30'N, but not at stations east and west of 180° in the central Bering Sea. To estimate chlorophyll-*a* concentration, surface water samples were collected at noon, filtered (Whatman GF/F), then frozen for later laboratory analysis. Chlorophyll-*a* analyses for samples collected from 1991 to 1997 were reported by Shiomoto et al. (1999) and used in this summary. Zooplankton samples were collected at midnight using a vertical tow from 150 m to the surface with a Norpac net (0.45 m diameter opening, 1.95 m length, and 0.335 mm mesh size; Motoda 1994) equipped with a flow meter and preserved in 5% buffered formalin. Zooplankton biomass estimates for 1991-1998 reported by Tadokoro et al. (1995), Nagasawa and Ishida (1997, 1998) and Nagasawa and Ueno (1999) were used in this analysis.

1.2.2. Fishing operations

Fishing operations were conducted using a surface gillnet and longline. The gillnet consisted of 30 tans (one tan=50 m) of 10 mesh sizes (3 tans each of 48, 55, 63, 72, 82, 93, 106, 121, 138, and 158 mm; research mesh) and 17 tans of 115 mm mesh (commercial mesh). The gillnet was set at 16:00 in the afternoon (Local Mean Time, GMT+12 hrs) and retrieved at 04:00 the following morning. Gillnet operations were conducted in international waters in the central North Pacific Ocean between 38°30'N and 47°30'N and in the central Bering Sea between 55°30'N and 58°30'N (Fig. 1.1). The catch per unit of effort (CPUE) was calculated using the number of salmon by species caught in 30-tans of the research-mesh. The CPUEs were calculated from the catch of salmonids in research meshes of the gillnet, which was fished outside of the U.S. 200-mile EEZ. The abundance of salmon in the central North Pacific was estimated from catches south of 48°N, and the abundance of salmon in the Bering Sea was estimated

from catches north of 55°N. There was no abundance data available from the Aleutian Islands vicinity. Fishing operations were also conducted using a surface longline, which comprised 30 hachi (overall length 3.32 km; 1 hachi is 110.68 m long and has 49 hooks) baited with salted Japanese anchovy (*Engraulis japonicus*). This gear was used primarily to catch live salmon for tagging experiments. However, longline mortalities also provided fish samples for stomach content analysis. The longline was set 30 minutes before sunset and hauled 30 minutes after sunset, and was used at all stations (inside and outside the U.S. 200-mile EEZ) in the survey area.

Salmonids were processed soon after removal from the fishing gear. The catch was sorted by mesh size and counted. Biological data included fork length (mm), body weight (g) sex, and gonad weight (g). Scales were collected for age determination.

1.2.3. Food habits data collection

I collected salmon and steelhead stomach samples from a maximum of 10 fish per species from longline mortalities (1991-2000), and a maximum of five fish per species per mesh size from a range of mesh sizes (1997-2000). Usually, I examined the stomach samples on board the vessel immediately after the catch was processed. However, in 1999, stomach samples were frozen and later examined in the laboratory. Fish stomachs were weighed to the nearest gram before and after removal of the contents, and the weight of the contents obtained by subtraction. The weight of stomach contents was used as a measure of stomach fullness, therefore, the two terms are synonymous in this report. When longline bait was present in the stomach, the bait was counted and the weight of the bait was not included in the stomach content weight. The stomach contents were examined using a binocular microscope and separated into the following general prey categories: euphausiids, copepods, amphipods, crab larvae, squid, pteropods, fish, polychaetes, chaetognaths, and gelatinous zooplankton (medusae, ctenophores, and salps). The percent volume of each prey category in stomach contents was estimated visually following the method of Pearcy et al. (1984). When I could identify the prey to finer detail, this information was also recorded. Additional information was occasionally recorded including the count and size of individual prey items, and if the prey were

positioned head-first or tail-first in the stomach. A stomach content index (SCI) was calculated by standardizing prey weight (stomach fullness) with fish body weight (prey weight/body weight *100).

I summarized food habits data individually for sockeye, chum, pink, coho, and chinook salmon, and steelhead trout. For each species, the prey weight, SCI, and percent volume of each prey group was averaged for each station including empty stomachs and these values plotted by year in the areas 41°-44°N, 45°-51°N, and 52°-58°N. To examine the contribution of particular prey groups, the prey weight of major categories was estimated by multiplying the mean percent volume of each group by the mean prey weight (not including empty stomachs). This assumes the density of each prey group was similar. Associations among water temperature, salinity, salmon abundance, total prey weight, and prey weight of major prey groups were explored using correlations. Correlations were calculated for all years combined.

To examine the data for the existence of inter- and intra- specific effects on food habits, data collected were separated into two groups: odd-numbered years when pink salmon were abundant and even-numbered years when pink salmon were scarce. The prey composition was categorized into prey of high quality, such as euphausiids, copepods, squid, and fish (for sockeye, chum, and pink salmon), and low quality, such as amphipods pteropods (for sockeye, chum, and pink salmon), gelatinous zooplankton, and unidentified material (for chum salmon) on the basis of caloric density (see Chapter 3.0.) Chinook salmon consumed a more limited number of prey organisms: fish, squid, and euphausiids. In the case of chinook salmon, squid and fish prey were categorized as high-quality, and euphausiids were considered relatively low-quality in order to compare the food habits in odd- and even-numbered years. Two-way ANOVAs were used to determine if there were significant interactions between year (odd, even) and prey quality (high, low).

To examine trends in prey composition with respect to salmon body size, food habits data for individual salmon were pooled together and summarized by location (41-44°N, 45°-51°N, and 52°-58°N) and salmon body-weight size class. Average prey weight (stomach fullness), SCI, and the proportion of the major prey groups were calculated. Data for particular fish containing the maximum stomach fullness and SCI observed in each size class and area were listed as an example of the maximum stomach fullness observed for each size of salmon.

1.3. Results

In the following sections I summarize the oceanographic conditions, chlorophyll-*a* concentrations, zooplankton biomass, and salmon catches observed during the sampling period. Following this summary, I describe the results of stomach content analysis for sockeye, chum, pink, coho, and chinook salmon, and steelhead trout for the central North Pacific and central Bering Sea.

1.3.1. Oceanographic conditions, chlorophyll-*a* concentrations, and zooplankton biomass

Mean annual water temperature and salinity in the four areas (38°-40°N, 41°-44°N, 45°-51°N, and 52°-58°N) show little overlap among the areas, indicating temperature and salinity characteristics of the four areas were distinctive (Figs. 1.3 and 1.4). Stations located at 38°-40°N were generally south of salmon distribution at this time of year. Water in this area was warmer than 12°C and salinities were greater than 34.0 psu in the upper 30 m (Fig. 1.3). From 1993 to 1995, salinities at 41°-44°N were relatively high because the Subarctic Boundary (identified by the vertical 34.0 isohaline) was located further north in those years, probably due to an intrusion of higher-salinity Transition Zone waters into higher latitudes (41°-44°N). Since 1996 water temperatures at 45° to 51°N showed a cooling trend in the upper 100 m. Water temperatures in the central North Pacific area did not show the dramatic warming that occurred on the east side of the Pacific during the strong El Niño of 1997. Water temperature gradually decreased with depth, while salinity was relatively stable from five to 100 m depth in this area.

In the central Bering Sea, water cooled during the previous winter was present below the surface layer (2.5°C approximately 20-100 m depth). Luchin et al. (1999) identified this cold water mass as the cold intermediate layer. The cold layer results from cooling of the entire active layer in the autumn and winter, followed by surface warming in the spring and summer. The cold intermediate layer was well-developed in the water column at locations sampled in the basin. The unusually calm weather during the summer in 1997 led to warmer than normal conditions in surface waters, probably from decreased wind stress (Fig 1.4). Since 1997, there has been a return to cooler temperatures, with the exception of 2000 when there was a slight deepening of seasonally warmed waters to below 30 m. Temperature at 5 m was not statistically related to temperatures at 30 m or 100 m because wintertime conditions generally affect temperature conditions at 30 and 100 m, while summertime conditions affect primarily the uppermost 10 m (Table 1.1).

Chlorophyll-*a* concentration at 41°-44°N and net zooplankton biomass at 38°-40°N were lower than other areas (Fig. 1.5). In the central North Pacific, net zooplankton were composed primarily of copepods, although there was an unusually large catch of amphipods and pteropods in 1991 at 41°-44° N (Fig. 1.6). At 45°-51°N there was a significant inverse correlation between zooplankton biomass and chlorophyll-*a* not shown in areas to the north or south (Shiomoto et al. 1997; Nagasawa et al. 1999; Table 1.1; Fig. 1.5).

In the central Bering Sea phytoplankton and zoopankton biomass was markedly different than in the central North Pacific Ocean (Fig. 1.7; Table 1.1). I observed no correlation between chlorophyll-*a* concentrations and zooplankton biomass in the Bering Sea data, unlike the inverse relationship observed at 45°-51°N. Copepods represented the majority of the biomass in net zooplankton. However, unlike samples from the North Pacific, Bering Sea NORPAC samples were more diverse in species composition and contained more chaetognaths and euphausiids (Fig. 1.8). The oceanic domain of the Bering Sea basin is characterized by surface waters containing sufficient nitrogen for

phytoplankton growth, however phytoplankton biomass is low (Shiomoto 1999). The pycnocline produced by the cold intermediate layer slows sinking of large phytoplankton, which in turn can be consumed by large herbivorous copepods (e.g. *Neocalanus* and *Eucalanus*, Shiomoto 1999). In a study of chlorophyll-*a* concentrations at these stations from 1991-2000, phytoplankton biomass was considered stable over the decade and was not appreciably influenced by the El Niños of 1991-93 and 1997-98 (Shiomoto et al. 2002). In that study, maximum chlorophyll-*a* concentrations were observed along the transect north of 56°30 N (Fig. 1.1). Shiomoto et al. (2002) attributed higher phytoplankton concentrations at northerly stations to contributions from the "green belt" (Springer et al. 1996) by circulation of the Bering Slope Current.

1.3.2. Salmon catches

Based on CPUEs of salmonids caught in the research-mesh portion of the gillnet, salmon abundance was approximately ten times more abundant in the central Bering Sea than in the central North Pacific south of 48°N (Table 1.2). Abundance of sockeye in 1999 in the central North Pacific was the highest level observed during the ten-year period. In 2000, the abundance of sockeye salmon in this area was lower and more like the level observed in 1998, however sockeye was somewhat more abundant than the earlier 1991 through 1997 levels. This remarkable increase in the abundance of sockeye in the central North Pacific Ocean in 1999 may have resulted from a southward shift in summertime sockeye salmon distribution that year. Sockeye in this area during the summer are predominantly a mixture of stocks from eastern Kamchatka, Bristol Bay, and Aleutian stocks (Myers et al. 1996). In the central Bering Sea, sockeye salmon were approximately 25 times more abundant than in the central North Pacific. Catches of sockeye salmon in the central Bering Sea show a four-year abundance cycle with maximum values in 1993, 1997, and 2001 (Table 1.2; 2001 data not shown). Common age groups for sockeye salmon in the catches were 1.1, 2.1, 1.2, and 2.2 (number before the period is the number of freshwater annuli and the number after the period is the number of ocean annuli observed on scales). Most of the sockeye caught were immature, although there were some maturing fish caught in the central Bering Sea (Myers et al.

2000). The stock mixture in the central Bering Sea in summer originates predominately from Bristol Bay and Aleutian stocks (Myers et al. 1996).

In the central North Pacific the largest catch of chum salmon was 1993 and the lowest was 1998. There was no consistent pattern in chum salmon abundance in this area (Table 1.2). Chum salmon caught in the central North Pacific Ocean during the summer are a mixture of Russian, western Alaskan and Japanese stocks (Myers et al. 1996, Urawa et al. 1998; Winans et al. 1998). There was a significant negative relationship between zooplankton biomass and chum abundance at 45°-51°N (Table 1.1). Chum salmon are the most abundant zooplanktivorous salmon distributed in this area, and when chum salmon are abundant, their consumption of zooplankton could reduce the abundance of zooplankton in this area. In the central Bering Sea, a cycle in chum salmon abundance was evident with approximately twice as many chum salmon caught in even-numbered years than in odd-numbered years when pink salmon were abundant (Azumaya and Ishida 2000; Table 1.2). The inverse relationship between chum and pink salmon was statistically significant (Table 1.1). In the central Bering Sea, chum salmon abundance decreased to particularly low levels every fourth year (1991, 1995, 1999). The common age groups of chum salmon were 0.1, 0.2, and 0.3, and there were increased numbers of older, maturing fish caught in the Bering Sea than further to the south (Myers et al. 2000). Chum salmon in the central Bering Sea originate predominately from stocks in Japan, Russia and western Alaska (Myers et al. 1996; Urawa et al. 1998; Winans et al. 1998).

Pink salmon abundance in the central North Pacific was unusually high in 1999, as it was for sockeye salmon (Table 1.2). On average, pink salmon abundance was substantially higher (35 times greater) in the central Bering Sea than the North Pacific. In the central Bering Sea, there was a strong odd-numbered year dominance cycle in pink salmon abundance. All pink salmon in the catches were maturing ocean-age .1 fish. Pink salmon caught in this area originate primarily from eastern Kamchatka (Karaginsky) stocks, but also include fish from western Alaska (Myers et al. 1996).

Coho salmon were abundant in the central North Pacific, but caught infrequently in the central Bering Sea (Table 1.2). Coho salmon abundance exhibited a pattern where one year of low abundance (1993, 1996, 1999) was followed by two years of high abundance. However, in 2000 coho salmon abundance decreased to the lowest point in the 10-year record. All coho salmon caught were maturing ocean-age .1 (Myers et al. 2000). Coho salmon caught in the central North Pacific Ocean in summer are a mixture of Russian, and western and central Alaskan stocks (Myers et al. 1996. Coho salmon abundance was positively correlated with higher salinity at 30 m depth. This suggests that coho salmon, among the most southerly distributed of the salmon species caught in this area, may be more tolerant of high salinity intrusions from the Transition Domain than either pink or sockeye salmon (Table 1.1). Coho salmon are infrequently caught in the central Bering Sea in June and July. Coho salmon stocks originating from western Alaska may return to their natal rivers by a coastal migration pathway, and therefore do not frequent the Bering Sea basin in July.

Chinook salmon abundance in the central North Pacific was considerably lower than all the other species caught in the central North Pacific Ocean (Table 1.2). The majority of chinook salmon caught in the central North Pacific were immature age 1.2. Chinook origins in the central North Pacific Ocean include contributions from Kamachatka, southeast Alaska and Columbia River stocks (Myers et al. 1996). However, in the central Bering Sea, chinook salmon were relatively abundant. Chinook salmon were particularly abundant in 1998 and 2000 when young ocean age .1 fish were frequently found in the catch. The chinook salmon caught in the central Bering Sea were a mixture of immature age 1.1, 1.2, and 1.3 (Myers et al. 2000). Chinook salmon origins in the central Bering Sea are composed primarily of western Alaskan stocks (Myers et al. 1996).

Steelhead abundance in the central North Pacific Ocean was low (Table 1.2). There was no pattern in catches over the ten-year time period. Immature and maturing ocean age .1 and maturing ocean age .2 fish were the common age-maturity groups in the catches (Myers et al. 2000). The presence of both adipose fin-clipped and non-fin

clipped steelhead in the catches indicate there was a mixture of hatchery and wild fish in the survey area. Steelhead caught in the central North Pacific Ocean are a mixture of stocks predominately from the U.S. Pacific northwest (Washington, Oregon, and Columbia River; Myers et al. 1996). Steelhead were not caught in the central Bering Sea, which reflects the absence of spawning grounds in rivers emptying into the Bering Sea (Sutherland 1973).

1.3.3. Salmonid food habits

The following sections summarize results of food habits analysis of chum and coho salmon, and steelhead caught at 41°-44°N in the central North Pacific Ocean and results of sockeye, pink, and chinook salmon at 45°-51°N in the central North Pacific and at 52°-58°N in the central Bering Sea.

1.3.3.1. Sockeye salmon food habits in the central North Pacific Ocean (45°-51°N)

The number of stations sampled for stomach content analysis ranged from a low of two to a maximum of six at 45°-51°N (Fig. 1.9). Mean prey weights were determined annually from examination of 6 to 37 sockeye salmon stomachs. The overall mean prey weight was 12.9 g (0.66% body weight). Annual values for mean prey weight ranged from 1.6 g (0.1% body weight) to 34.4 g (1.4% of body weight).

Major sockeye salmon prey groups in this area included euphausiids (*Euphausia pacifica*), copepods (*Neocalanus cristatus* CV), hyperiid amphipods (primarily *Parathemisto pacifica*), and squid (*Berryteuthis anonychus*), and the proportions of these organisms in stomach contents varied among years (Table 1.3; Fig. 1.10). The squid eaten by sockeye salmon in this area was large-sized *B. anonychus* subadults and adults (approximately 50-100 mm mantle length; Table 1.3). Sockeye, chum, pink, or coho salmon abundance was uncorrelated with stomach fullness in sockeye salmon (Table 1.4). Significant positive correlations between the amount of euphausiids, copepods, and squid in sockeye stomach contents and stomach fullness indicated the importance these prey groups had in determining overall stomach fullness. Zooplankton biomass was negatively associated with weight of "other" prey, primarily shrimp (*Hymendora*

frontalis), indicating that when copepod abundance was lower, more of the uncommon alternative prey groups were consumed. Effect of prey quality (high quality=euphausiids, copepods, squid and fish; low quality= pterpods and amphipods) on stomach fullness by odd- and even-numbered year was not significant in samples collected in the central North Pacific (2-way ANOVA; F=0.009, p=0.92, residual df=242; year: odd-even, prey value: high-low)

Prey weight increased with body weight of sockeye salmon from 0.82 g (0.231% body weight) for sockeye weighing less than 500 g to 26.3 g (0.80% body weight) for fish weighting 3000 g or more (Fig. 1.11). The number of fish included in each body size class ranged from 19 to 40 (Table 1.5). Maximum SCI values observed in sockeye salmon ranged from 2.3% body weight for ocean age .1 fish to a maximum of 5.2% body weight for ocean age .2 fish. As sockeye body size increased, the percentage of amphipods in the stomach contents decreased from 45% in fish weighing less than 500 g to approximately 9% in sockeye salmon weighing greater than 2500 g. Small sockeye salmon, less than 500 g, fed on a high percentage (70%) of amphipods and pteropods (Fig. 1.11). As sockeye salmon body size increased, the percentage of squid in the stomach contents increased to more than 33% in fish larger than 2000 g. Higher mean prey weight and SCI were associated with sockeye salmon larger than 1500 g feeding on large *B. anonychus*.

1.3.3.2. Sockeye salmon food habits in the central Bering Sea (52°-58°N)

Sample sizes were substantially larger in the central Bering Sea than in the central North Pacific (Fig. 1.9). Annually, the number of stations from which sockeye stomach samples were collected ranged from 9 to 14, and the number of stomachs examined ranged from 33 to 144 annually. The overall mean prey weight was 10.4 g (0.66% body weight) and annual mean values ranged from 6.0 g (0.05% body weight) to 24.2 g (1.1% body weight). Prey weight increased from 8.2 g to 12.9 g in even-numbered years when pink salmon abundance was low.

Major sockeye salmon prey items in the central Bering Sea included euphausiids (*Thysanoessa longipes*), hyperiid amphipods, copepods (*N. cristatus* CV), squid and fish (Fig. 1.10). Sockeye salmon in this area fed on small squid that may be juvenile *B. anonychus*, 20 to 30 mm in mantle length (Table 1.3). Consumption of fish, which included juvenile *Hemilepidotus* spp., *Pleurogrammus monopterygius*, and adult *Stenobrachius leucopsarus* was substantially greater in the central Bering Sea than in the central North Pacific. These fish are abundant in the Bering Sea basin; *S. leucopsarus* maybe the most abundant epipelagic fish species in the area (Sinclair et al. 1999). At night, *S. leucopsarus* migrate vertically from upper mesopelagic waters into the epipelagic zone (Willis and Pearcy 1982). *Pleurogrammus monopterygius* juveniles are also abundant and dominant collections in eastern Bering Sea trawl surverys (Brodeur et al. 1999). Sockeye stomach fullness, or weight of individual prey categories were not correlated with sockeye salmon abundance (Table 1.4). The amount of squid and copepods in sockeye stomach contents was positively associated with stomach fullness. Copepods and squid were important contributors to the prey of sockeye salmon in this area. Zooplankton biomass was positively related to weight of amphipods in sockeye stomach samples, therefore net zooplankton may provide a signal when hyperiid amphipods, particularly the abundant *P. pacifica*, is forming dense aggregations at the surface. The amount of squid in sockeye salmon stomachs was the only prey item to have an association with the physical parameters of temperature or salinity. The amount of juvenile squid in sockeye stomach contents was negatively correlated with water temperature at 5 m and positively related with salinity at 100 m. This correlation may indicate that conditions at the bottom of the cold intermediate layer (100 m) affect juvenile squid abundance or distribution and therefore their availability to salmon as prey.

Comparison of the prey quality in sockeye stomachs by odd- and even-numbered years showed a 36% reduction in stomach fullness when pink salmon were abundant. In odd-numbered years, there was a 53% reduction in the weight of high-quality prey (euphausiids, copepods, squid, and fish) and a 13% increase of in the weight of low-quality prey (pteropods and amphipods; Table 1.6). However, this change was not

statistically significant at p=0.05 (2-way ANOVA; F=2.457, p=0.12, residual df=734; year:odd-even; prey quality: high-low).

Prey weight increased with body weight of sockeye salmon from 2.4 g (0.81% body weight) for fish weighing less than 500 g to 18.3 g (0.52% body weight) for large fish weighing 3000 g, or more (Fig. 1.11). Maximum SCI observed ranged from 5.9-6.9% body weight for ocean age .1 to .3 fish (Table 1.5). As the body weight of sockeye increased from less than 1000 g to greater than 2500 g, the percentage of amphipods in the stomach contents decreased from 34% to 11% and the percentage of squid increased from 18% to approximately 30% (Fig. 1.11). All sizes of sockeye salmon fed upon euphausiids, copepods, fish, pteropods, and fish. The SCI for small sockeye salmon less than 1500 g was consistently higher in the central Bering Sea than in the central North Pacific Ocean, suggesting the feeding environment in the Bering Sea is particularly favorable for small sockeye salmon in the summer.

1.3.3.3. Chum salmon food habits in the central North Pacific Ocean (41°-44°N and 45°-51°N)

At 41°-44°N the number of stations sampled annually for chum salmon stomach contents ranged from 1 to 4 and the number of fish examined each year ranged from 2 to 24 chum salmon (Fig. 1.12). Overall, prey weight averaged 9.8 g (1.00% body weight) and annual mean prey weights ranged from a low of 4.8 g (0.57% body weight) to a maximum of 17.3 g (2.08% body weight).

At 45°-51°N the number of stations sampled for chum salmon ranged from 6 to 8 and the number of chum salmon stomachs sampled each year ranged from 37 to 117 stomachs (Fig. 1.12). Overall prey weight was 9.35 g (0.90% body weight) and annual mean prey weights ranged from 6.8 g (0.65% body weight) to 12.2 g (1.39% body weight).

Chum salmon consumed a wider variety of prey than other salmon species. Chum salmon fed on euphausiids (*E. pacifica*), hyperiid amphipods (*P. pacifica, Phronima sedentaria),* squid (*B. anonychus*), pteropods (*Limacina helicina, Clione limacina*), fish (*P. monopterygius*), appendicularians (likely *Oikopleura labradoriensis*), ostracods (*Conchoecia magna*), and heteropods (*Carinaria* sp.), and a large proportion of gelatinous zooplankton (medusae, *Aglantha digitale*, ctenophore *Beroe* sp. and salps; Table 1.3 and Fig. 1.13). In 1991 and 1992, particularly large amounts of stomach contents were classified as "unidentified material." It was likely, however, that most if not all of this material was digested gelatinous zooplankton. Occasionally, chum fed heavily on appendicularia ("other" category), suggesting that appendicularia may have a patchy distribution and when abundant can be an important prey for chum salmon.

At 41°-44°N chum, coho salmon, or steelhead abundance was not correlated with chum salmon stomach fullness or the weight of any particular prey groups found in the stomach contents (Table 1.7). Positive correlations were observed between the amount of euphausiids, hyperiid amphipods and gelatinous zooplankton in chum salmon stomachs. Salps were the most common gelatinous zooplankton consumed in this area, and many of the salps consumed by chum salmon were "barrels" hollowed-out by resident hyperiid amphipods, *P. sedentaria*. These amphipods and their salp barrels were a common prey item of chum salmon in southern area of the transect. Alternatively, squid and "other" prey (mostly heteropods) were positively associated. Perhaps these groups were more abundant in the same preferred habitats. Fish prey (mostly *Tarletonbeania crenularis*) was significantly positively related to warmer water temperatures at 30 m and 100 m, thus suggesting this myctophid may be more abundant in warmer water habitats.

At 45°-51°N the abundance of sockeye, pink, and coho salmon was not correlated with chum salmon stomach fullness. However, the amount of fish and squid in chum salmon stomachs was positively correlated with chum abundance (Table 1.7). This would occur if chum salmon were distributing themselves according to favorable feeding conditions. Levels of fish and squid in chum salmon stomachs were positively correlated

with stomach fullness. At this location, zooplankton biomass was negatively associated with stomach fullness and may indicate chum salmon feeding can reduce zooplankton abundance (Fig. 1.13 and Table 1.7). Comparison of prey quality (high-quality=euphausiids, copepods, squid, and fish; low-quality=amphipods and pteropods) by year was not significant in samples collected in the central North Pacific (2-way ANOVA; F=0.165, p=0.68, residual df=703; year: odd-even; prey: high-low).

As chum salmon body size increased, the weight of stomach contents increased from 3.13 g (0.88% body weight) for fish weighing less than 500 g to 24.01 (0.70% body weight) for fish weighting at least 2500 g (Fig. 1.14). The number of chum salmon examined in each body size class ranged from 17 to 423 (Table 1.8). Maximum SCI values of 4.3-4.6% body weight were observed for ocean age .1 and .2 fish and values decreased to less than 2.9% body weight for ocean age .5 chum salmon. In the central North Pacific Ocean, mean SCI was stable at approximately 1.0%, particularly for chum less than 2500 g (Fig. 1.14). Gelatinous zooplankton, pteropods, and amphipods were a common prey for all sizes of chum salmon. Chum salmon larger than 1000 g contained a low percentage of copepods in their stomach contents (1%), and those weighing between 1000 g and 2500 g contained a higher percentage of euphausiids (approximately 14%) and squid (9%) than smaller fish. Fish prey was found only in chum salmon larger than 2500 g (9%).

1.3.3.4. Chum salmon food habits in the central Bering Sea (52°-58°N)

In the central Bering Sea the number of stations sampled yearly ranged from 12 to 15 and the number of individual chum salmon stomachs sampled ranged from 169 to 316 (Fig. 1.12). The overall mean prey weight was 15.5 g (1.10% body weight) and mean annual values ranged from 12.1 g (0.71% body weight) to 23.0 g (1.52% body weight). Mean annual prey weight was higher in early 1990s, lower through the mid-1990s, and increased in 2000.

In the central Bering Sea chum salmon fed more commonly on non-gelatinous zooplankton than in the central North Pacific Ocean. Chum salmon consumed euphausiids (*T. longipes*), copepods (*N. cristatus* CV), amphipods (*P. pacifica*, *Primno abyssalis*, *Hyperia medusarum*, and *Hyperoche medusarum*), squid (juveniles), pteropods (*L. helicina*, and *C. limacina*), and fish (*P. monopterygius*, *S. leucopsarus*, juvenile *Hemilepidotus* sp., and post-larval *Aptocyclus* spp., *Psychrolutes phrictus*, and *Hippoglossus stenolepis*) in the central Bering Sea (Figure 1.13; Table 1.3). Chum salmon stomach fullness was not associated with the abundance of chum, sockeye, pink, or chinook salmon (Table 1.7). However, chum and pink abundance were correlated with the amounts of particular prey categories contained in chum stomachs. In particular, abundance of chum was positively associated and abundance of pink salmon was negatively associated with the amount of copepods and amphipods in chum salmon stomach contents. These are common prey items important to the diets of both chum and pink salmon. Chlorophyll-*a* concentrations were inversely associated with the amount of euphausiids in chum salmon stomachs. If the abundance of euphausiids in the stomachs of chum salmon is a measure of euphausiid abundance, then higher abundance of euphausiids could have a depressing effect on phytoplankton standing stock. Warmer water and lower salinity at 5 m and 100 m was positively related to the weight of pteropods (mostly *Limacina*) in chum salmon stomachs and may signify their propensity to form dense swarms in warmer areas of the Bering Sea (pers. comm. W. Lew, Icicle Seafoods, Inc., Seattle).

Mean prey weight and SCI were similar in odd- and even-numbered years indicating no difference in stomach fullness of chum salmon stomach samples between years of high and low pink salmon abundance. However, there were shifts in the amount of particular prey items. The weight of euphausiids and copepods in the stomach contents of chum salmon increased in even-numbered years when pink salmon abundance was low, and the weight of pteropods, fish, and gelatinous zooplankton decreased when pink salmon abundance was low (Table 1.6). There was a 38% reduction in weight of high-quality prey (euphausiids, copepods, squid, and fish) and a 19% increase in weight of low-quality prey (amphipods, pteropods, medusae, and

ctenophores) when pink salmon were abundant. Differences in prey weight of high- and low-quality prey during odd- and even-numbered years were highly significant in samples collected in the central Bering Sea (2-way ANOVA; $F=8.337$, $p<0.01$, residual df=962 year: odd-even, prey value: high-low).

In the central Bering Sea, mean prey weight in chum salmon increased from 5.6 g (1.39% body weight) in fish weighing less than 500 g to 27.3 g (0.62% body weight) in fish weighing 4000 g, or more (Fig. 1.14). Mean SCI values were larger for small chum salmon, weighing less than 1000 g, than for similar-sized chum salmon in the central North Pacific Ocean. Maximum SCI for ocean age .1, .2, and .3 fish ranged from 5.2 to 6.4% body weight, however, decreased to 1.9% body weight in fish ocean aged 0.5 (Table 1.8). Chum salmon weighing less than 500 g fed on a higher percentage of amphipods (25%) than chum salmon weighing greater than 1000 g (<7%; Fig. 1.14). The percentage of copepods, a minor portion of stomach contents, decreased from 6% in chum salmon weighing less than 500 g to 2% in fish weighing more than 2500 g. Euphausiids were consumed by all sizes of chum salmon. However, a higher percentage (>20%) was observed in fish greater than 1000 g than in small chum salmon (8% in fish weighing less than 500 g). All sizes of chum salmon consumed a substantial percentage of gelatinous zooplankton, increasing from 12% in small chum salmon weighing less than 500 g to 36% in fish larger than 3000 g. The percentage of prey composed of juvenile fish, pteropods, and small squid was relatively unchanged across weight classes of chum salmon (Fig. 1.14). The proportion of euphausiids and fish in the stomach contents was higher in the central Bering Sea than in the central North Pacific Ocean.

1.3.3.5. Pink salmon food habits in the central North Pacific Ocean (45°-51°N)

The number of stations sampled for pink salmon stomach contents ranged from 2 to 8 stations and the number of stomachs sampled annually ranged from 2 to 94 (Fig. 1.15). Over the whole period, prey weight averaged 14.8 g (1.37% body weight) and the annual mean prey weight ranged from 4.0 g (0.4% body weight) to 42.0 g (3.0% body weight).

Samples from pink salmon caught in the central North Pacific Ocean were characterized by sporadic high consumption of large squid (*B. anonychu*s, approximately 80-100 mm mantle length), particularly in 1994, 1998, and 2000 (Fig. 1.16, Table 1.3). Abundance of pink, sockeye, chum, or coho salmon were not associated with stomach fullness, or weight of particular prey items in pink salmon stomach contents. Weight of squid in pink salmon stomachs was positively related to total prey weight and indicated the importance of squid to overall stomach fullness (Table 1.9). The effect on stomach fullness of weight of high- and low-quality prey (high quality: euphausiids, copepods, squid, and fish; low quality: amphipods and pteropods) by odd- and even-numbered year was not significant (2-way ANOVA; F=2.55, p=0.11, residual df=386, year: odd-even; prey value: high-low).

The range of pink salmon size categories was small because all fish were the same age (maturing age 0.1). Mean prey weight increased with body weight of pink salmon from 9.9 g (1.18% body weight) for fish weighing 500-999 g to 22.8 g (1.39% body weight) for fish weighing 1500 g, or more (Fig. 1.17). Maximum SCI ranged from 7.6 to 4.5% body weight (Table 1.9). There was a dramatic shift towards increased percentages of large squid and euphausiids in the stomachs of larger pink salmon. The percentage of squid and euphausiids increased from 9% and 14% in the stomach contents of pink salmon weighing less than 1000 g to 38% and 28% in fish weighing more than 1500 g (Fig. 1.17). In contrast, the percentage of copepods and pteropods decreased from 29% and 17% in the stomach contents of pink salmon weighing less than 1000 g to 6% and 9% in those weighing more than 1500 g. The percentage of amphipods was stable in the stomach contents of all size classes of pink salmon.

1.3.3.6. Pink salmon food habits in the central Bering Sea (52°-58°N)

In the central Bering Sea, the number of stations sampled ranged from 3 to 15 stations (Fig. 1.15). The number of pink salmon sampled annually ranged from 5 to 300 fish. The overall mean prey weight was 15.2 g (1.29% body weight) and the annual mean prey weights ranged from 8.1 (0.76% body weight) to 28.8 g (2.47% body weight).

In the central Bering Sea, pink salmon consumed small squid, perhaps *B. anonychus* juveniles, approximately 10-30 mm mantle length (Table 1.3). Squid were a relatively large component of the samples in the earlier half of the 1990's. However, squid was a smaller component through the later part of the decade until 2000, when the samples contained almost exclusively squid and fish (Fig. 1.16). Pink salmon also fed heavily on fish, including primarily juvenile flat fish, juvenile *P. monopterygius*, *Hemilepidotus* sp. and adult *S. leucopsaurus*. The abundance of pink salmon was negatively associated with pink salmon stomach fullness and the amount of euphausiides, copepods, squid, and fish in pink salmon stomach contents (Table 1.9). The weight of squid had a strong positive correlation with the total prey weight and indicated the importance of squid consumption to total stomach fullness. As was the case for squid in the stomachs of sockeye and chum salmon, the weight of squid in the stomachs of pink salmon was negatively related to the water temperature at 5 m, and positively related to salinity at 30 and 100 m.

There was a decrease of 23% in the stomach fullness of pink salmon in odd- as compared with even-numbered years. In addition, there was a 32% reduction in the proportion of high-quality prey in the stomach contents (euphausiids, copepods, squid, and fish) and an increase of 72% in the proportion of low-quality prey (amphipods and pteropods) when pink salmon were abundant (Table 1.6). The interaction of prey quality and year on prey weight was statistically significant (2-way ANOVA; F=5.050, p=0.03, residual df=662; years: even-odd, prey: high-low quality).

Prey weight increased with body weight of pink salmon from 4.4 g (1.10% body weight) in fish weighing less than 500 g to 28.8 g (1.29% body weight) for fish weighing 2000 g, or more (Fig. 1.17). Maximum SCI observed increased from 2.4% body weight to 6.0% for pink salmon weighing up to 1500 g, and decreased in fish heavier than 1500 g (Table 1.10). Fish was a more substantial portion of the diet of pink salmon in the central Bering Sea, as compared to the catches in the central North Pacific Ocean. Samples collected from pink salmon smaller than 500 g body weight contained a high percentage of juvenile fish (64%), however these small fish did not consume juvenile

squid (Fig. 1.17). For pink salmon weighing more than 500 g BW, the percentage of fish and squid prey was relatively constant in stomach contents. The percentage of euphausiids was low (1%) in small pink salmon (weighing less than 500 g), and increased to 17% in pink salmon weighing more than 1500 g.

1.3.3.7. Coho salmon food habits in the central North Pacific Ocean (41°-44°N and 45°-51°N)

At 41°-44°N the number of stations sampled each year for coho salmon stomach contents ranged from 2 to 4 stations (Fig. 1.18). The number of fish examined annually ranged from 14 to 63 coho salmon. Over the whole period, prey weight averaged 17.3 g (0.97% body weight), and annual mean prey weight ranged from 0.92 g (0.05% body weight) to 34.3 g (1.77% body weight).

At 45°-51°N the number of stations sampled for coho salmon stomach contents ranged from 1 to 8 and the number of fish examined each year ranged from 3 to 68 (Fig. 1.18). The overall mean prey weight was 44.1 g (2.17% body weight) and the annual mean prey weights ranged from 28.4 (1.39% body weight) to 69.7 g (3.48% body weight).

Coho salmon caught in the central North Pacific Ocean were characterized by an almost exclusive consumption of large sub- and adult squid, *B. anonychus* (Fig 1.19, Table 1.3). The weight of stomach contents was substantially higher further to the north (45°-51°N) than at 41°-44°N. In the southern area, hyperiid amphipods (*Phronima sedentaria* in salp barrels) and pteropods (*Clio recurva*) comprised an alternative prey source to squid. At 41°-44°N the abundance of coho, chum, or steelhead were not closely associated with stomach fullness of coho salmon (Table. 1.11). The weight of amphipods and squid in the stomach contents was positively correlated with overall prey weight emphasizing the importance of *P. sedentaria* and *B. anonychus* in the diet of coho salmon (Table 1.11). The weight of pteropods in the stomach contents of coho salmon was positively correlated with the abundance of chum salmon. At 45°-51°N the abundance of coho, sockeye, chum, pink, and chinook salmon, or steelhead was not significantly correlated with coho stomach fullness or amount of any particular prey

(Table 1.11). In this area squid was the most important prey and was the only component highly correlated with stomach fullness. In both areas, euphausiids, *E. pacifica*, and fish, including *Gasterosteus aculeatus*, *P. monopterygius*, *Cololabis saira*, *Hemilepidotus* spp., *T. crenularis* and *Engraulis japonica* (Nagasawa and Davis 1998), were consumed by coho salmon (Table 1.3).

Prey weight increased with body weight of coho salmon from 5.8 g (0.71% body weight) to 72.6 g (2.17% body weight) for coho weighting 3000 g, or more, and the maximum SCI ranged from 1.6% to 7.6% (body weight; Fig. 1.20, Table 1.12). Squid was the primary prey item for coho salmon of all sizes (all coho salmon were maturing ocean age .1 fish), ranging from 50% in coho weighing 500 g to 55% squid in fish weighing more than 3000 g (Fig. 1.20). The percentage of pteropods (19%) in small coho weighing less than 1000 g, decreased to 10% in coho weighing more than 3000 g. In contrast, the percentage of fish increased from 9% in the stomach contents of coho salmon less than 1000 g to 24% in coho weighing more than 3000 g. Coho salmon feeding in the summertime in the central North Pacific Ocean increased their SCI at larger body sizes (Table 1.12). As coho salmon increase in size, they can catch larger squid, thus affording coho an increased capacity for growth.

1.3.3.8. Chinook salmon food habits in the central North Pacific Ocean (45°-51°N)

Relatively few samples of chinook salmon stomach samples were obtained from the central North Pacific Ocean. No data was available in 1992, otherwise, from 1 to 5 stations were sampled in this area, and annually between 2 to 26 stomachs were examined (Fig. 1.21). The overall mean prey weight was 31.8 g (0.86% body weight), and annual values ranged from 14.0 g (0.3% body weight) to 69.3 g (1.8% body weight). Chinook salmon preyed almost exclusively on large *B. anonychus*, except in 1999, when a daggertooth, *Anotopterus pharao*, was found in chinook stomach contents (Fig. 1.22; Table 1.3). The exclusive dominance of squid in chinook salmon stomach contents in odd- and even-numbered years indicated there were no shifts in diet in this area on a biennial basis. The abundance of chinook, sockeye, chum, pink, and coho salmon, and steelhead was not significantly correlated with chinook stomach fullness (Table 1.13).

Prey weight increased with body weight of chinook salmon from 11.5 g (0.65% body weight) for chinook salmon weighing 1500 to 1999 g, to 39.0 g (0.69% body weight) for chinook salmon weighing 4000 g or more (Fig. 1.23). Sample sizes for body weight classes ranged from 4 to 17 (Table 1.14). The maximum SCI was 4.2% body weight for age .2 chinook salmon. Squid was the dominant prey for all sizes of chinook salmon sampled in the central North Pacific Ocean ranging from 100% for chinook weighing 1500 to 1999 g to 88% for chinook salmon weighing more than 4000 g (Fig. 1.23). Fish prey was not found in stomachs of chinook salmon weighing less than 2500 g. The fish prey in the central North Pacific Ocean were relatively large-bodied prey items (*C. saira* 175 mm [standard length] SL, *E. japonicus* 125-135 mm SL, *L. schmidti* 114-123 mm SL, *A. pharao* 140-315 mm SL; Table 1.3).

1.3.3.9. Chinook salmon food habits in the central Bering Sea (52°-58°N)

The number of stations from which chinook salmon stomach samples were examined ranged from 6 to 12 and the number of stomachs examined ranged from 12 to 96 (Fig. 1.21). The overall mean prey weight was 14.81 g (0.59% body weight) and annual prey weights ranged from 2.6 g (0.2% body weight) to 49.6 g (1.3% body weight). Abundance of chinook salmon was not significantly correlated with stomach fullness of chinook salmon (Table 1.13). Like the central North Pacific Ocean, the amount of squid was highly correlated with stomach fullness, showing the importance of squid in this area. Total prey weight increased from 9.53 g (0.42% body weight) to 21.6 g (0.74% body weight) in even-numbered years when pink salmon abundance was low (Fig. 1.22). There was a 56% reduction in stomach fullness in odd-numbered years, a 68% reduction in the weight of fish and squid consumed by chinook salmon, and a 44% increase in the weight of euphausiids consumed by chinook salmon when pink salmon were abundant. The effect of prey quality (high-quality=fish and squid, low-quality=euphausiids) and year on prey weight was significant (Table 1.6; 2-way ANOVA; $F=4.042$, $p=0.02$, residual df=252; year=odd-even; prey=high-low quality).

Major chinook salmon prey groups in the central Bering Sea included squid (predominantly large *B. anonychus*), euphausiids (*T. longipes*), and fish (*P. monopterygius* and *S. leucopsarus*; Fig. 1.22; Table 1.3). Chinook salmon fed on fish and euphausiids substantially more in the central Bering Sea than those caught in the central North Pacific. The amount of squid consumed by chinook salmon was not associated with the salinity structure at the bottom of the active layer, unlike the juvenile squid consumed by sockeye, chum, and pink salmon. This suggests that the distribution of larger, older squid may be responding differently to the physical structure of the active layer than juvenile squid.

Prey weight increased with body weight of chinook salmon from 2.4 g (0.72% body weight) for small chinook weighing less than 500 g to 48.9 g (0.98% body weight) for fish weighing 4000 g, or more (Fig. 1.23). The maximum SCI ranged from 3.9% body weight for ocean age .1 to 8.4% body weight for ocean age .3 chinook salmon (Table 1.14). As the body weight of chinook salmon increased from less than 500 g to 1500 g, the percentage of juvenile fish in stomach contents decreased from 48% to 21% (Fig. 1.23). Squid were consumed by chinook of all sizes. The SCI in the central Bering Sea was stable across size classes, except for an abrupt increase in the largest chinook size class (greater or equal to 4000 g). The high SCI value for small chinook salmon indicates the central Bering Sea is an important area for small chinook consumption of small fish prey.

1.3.3.10. Steelhead trout food habits in the central North Pacific Ocean (41°-44°N and 45°-51°N)

At 41°-44°N the number of stations each year from which steelhead stomach contents were examined ranged from 1 to 3 stations (Fig. 1.24). The number of fish examined annually ranged from 1 to 15 steelhead. Over the whole period prey weight averaged 14.2 g (0.79% body weight), and annual mean prey weight ranged from a low of 2.5 g (0.13% body weight) to 42.7 g (2.32% body weight; Fig. 1.24).

At 45°-51°N, the number of stations sampled for steelhead stomach contents was larger and ranged from 3 to 6 stations and the number of stomachs examined annually ranged from 3 to 40 (Fig. 1.24). The overall mean prey weight was higher than the area to the south and ranged from 33.5 g (1.02% body weight) to 72.1 g (1.85% body weight).

Steelhead caught in the central North Pacific Ocean were characterized by a dominance of squid, *B. anonychus*, and fish, including *Gasterosteus aculeatus*, *A. pharao*, *P. monopterygius*, and myctophids in the diet (Figure 1.25; Table 1.3). Other prey that was occasionally found in high abundance were polychaetes (*Tomopterus* and *Rynchonerella* sp.). Abundance of steelhead, chum, or coho salmon was not significantly correlated with stomach fullness, or the abundance of any particular prey group in steelhead stomach contents (Table 1.15). The amount of fish and squid in stomach contents was highly correlated with stomach fullness and indicates the importance of these groups as prey for steelhead.

Prey weight increased with body weight of steelhead from 6.9 g (0.51% body weight) for fish weighing 1000-1499 g to 65.0 g (1.47% body weight) for fish weighing 4000 g or more (Fig. 1.20). Maximum SCI values decreased with ocean age of steelhead from 6.3% in ocean age .1 to 3.5% in ocean age .3 fish (Table 1.16). The percentage of squid in steelhead stomach contents increased from 40% in fish weighing 1000 g to 67% in fish weighing more than 4000 g (Fig. 1.20). The proportion of polychaetes decreased from 10% in fish weighing 1000 g to less than 1% in fish weighing more than 4000 g. All sizes of steelhead were feeding on large squid.

1.4. Discussion

This analysis represents the first decadal-long study of immature and maturing salmonid feeding ecology in the central North Pacific Ocean and central Bering Sea. Previous studies (e.g., Andrievskaya 1966; LeBrasseur 1966; Pearcy et al. 1988; Sobolevskiy et al. 1994; Tadokoro et al. 1996) were more limited in spatial or temporal scales. I presented new information regarding regional and life-history related shifts in

dominance of major salmon prey and expanded findings providing evidence of competition among salmon during the marine phase of life.

My results showed the food habits of salmon were different among the two areas of the central North Pacific Ocean and the third area in central Bering Sea. In the southern area (41°-44°N) of the central North Pacific Ocean, salmonid catches consisted of chum and coho salmon, and steelhead. This area was characterized by low stomach fullness and lower consumption of large *B. anonychus* than the area further to the north (45-51°N; Figs. 1.12; 1.18; 1.24). There was an occasional large fish consumed by chum and coho salmon, and steelhead in this area (*L. schmidti*, *C. saira*, and *E. japonicus*). Chum consumed gelatinous zooplankton including intact salps. This information expands the role of salps in salmon diets further than originally suggested by Birman (1960), who concluded salps were consumed by chum only during their last summer at sea. I observed chum salmon in their first summer at sea, as well as maturing ocean age .4 chum salmon consuming salps. In fact, both chum and coho salmon fed upon salp barrels containing the hyperiid amphipod, *P. sedentaria*. Ingestion of the salp barrel and amphipod together enriched the nutritive value compared to consuming the salp by itself (see Chapter 3.0). Steelhead consumed polychaetes and often ate floating debris (plastic sheet, bits of wood). The southern area of the central North Pacific Ocean (41-44°N) was the poorest from the viewpoint of salmon feeding of the three areas studied.

The northern area of the central North Pacific (45°-51°N) was characterized by high levels of stomach fullness. Large (>1000 g body weight) immature and maturing sockeye, pink, coho, and chinook salmon, and steelhead consumed a high proportion of large-sized *B. anonychus* (40-125 mm [mantle length] ML), a calorically-rich prey item (see Chapter 3.0; Figs. 1.11; 1.17; 1.20; 1.23; 1.20; Table 1.3). In addition, fish prey such as *G. aculeatus*, *P. monopterygius*, and *T. crenularis* (30-85 mm SL) were consumed by large coho and chinook salmon, and steelhead (Table 1.3). Feeding conditions in this area were so favorable due to ingestion of squid that coho salmon stomach fullness standardized to body weight (SCI) was heavier at larger coho sizes. This contradicts the expectation of the SCI to stabilize or decrease with increasing body weight (Brett 1986;

Table 1.20). In this area, chum salmon, greater than 1000 g body weight, occasionally fed on large *B. anonychus*, in addition to the more common gelatinous zooplankton, pteropods, "other" prey (heteropods, appendicularia, and ostracods) found in their stomach contents (Fig. 1.14). Due to this relatively high consumption of large *B. anonychus* by salmon in the northern area of the central North Pacific Ocean (45°-51°N), this region was a particularly favorable feeding area for large immature and maturing salmon.

Alternatively, summer conditions in the central Bering Sea were characterized by young sockeye, chum, pink, and chinook salmon (<1000 g body weight) ingesting a diverse diet with relatively high proportions of juvenile fish and juvenile squid, in addition to euphausiids and other large zooplankton (Figs. 1.11, 1.14, 1.17, 1.23). The juvenile fish prey consumed by small salmon were approximately 12-30 mm SL, and the juvenile squid were in the 9-30 mm ML size range (Table 1.3). In addition to the many small fish and squid prey available for consumption, the SCI for sockeye, chum, and chinook salmon weighing less than 1500 g was substantially higher in the central Bering Sea than in the central North Pacific Ocean (Fig. 1.11, 1.14, 1.23). Thus, the summertime feeding environment in the central Bering Sea was critically important to small, young (at least ocean-age .1) immature sockeye, chum, and chinook salmon.

I observed a gradual change in the feeding patterns of salmon and steelhead from small ocean age .1 fish to larger individuals. Previous analyses reported no change in the types of prey consumed by salmon older than ocean age .1 during their ocean residency (Andrievskaya 1957; Ito 1964). A characteristic of the stomach contents of small sockeye and chum salmon (<1000 g BW) was the high percentage of small hyperiid amphipods, *P. pacifica* and pteropods, *L. helicina*, present (2-3 mm maximum size; Table 1.3; Figs. 11.1, 1.14). In addition, copepods (7-8 mm body length) were more commonly found in the stomachs of small chum and pink salmon. Small fish prey (12-20 mm SL) was particularly important in the diets of small pink salmon (<500 g body weight; Fig 1.17). Gelatinous zooplankton was an important food of chum of all sizes and the percentage of gelatinous prey actually increased as chum salmon body size increased

(>1500 g body weight). As salmon increased in size, they consumed larger-bodied prey. The 1000 g body weight appeared to be a minimum size for pink salmon to include a substantial percentage of large squid (*B. anonychus*) in their diet. Aydin et al. (2000) hypothesized that 1000 g body weight was a minimum size for pink salmon to consume large squid and suggested there was a trophic feedback, whereby small pink salmon could not feed successfully on large squid, thus forgoing the larger growth potential afforded by a squid diet, and remaining competitors of squid for zooplankton prey.

The predilection of immature and maturing chum salmon to feed on gelatinous zooplankton is a fascinating aspect of their food habits, and makes them unique among Pacific salmon in this regard. Medusae and ctenophores have been recognized as prey of immature and maturing chum salmon across a large expanse of their oceanic range including the western North Pacific gyre (Andrievskaya 1957; Ito 1964), central North Pacific Ocean (this study), western (Radchenko and Chigirinsky 1995) and central Bering Sea (Azuma 1992, this study), and Gulf of Alaska (Pearcy et al. 1988). Medusae and ctenophores are not the only gelatinous prey consumed by chum salmon. Intact salps and salp barrel shelters for large hyperiid amphipods were consumed by chum and coho salmon in the central North Pacific Ocean (Table 1.3). Although salps have a high water content and a tunic membrane composed of mucopolysaccharides that can not be assimilated by salmon, the intact salp stomach is nutritive because it contains microzooplankton collected and concentrated by the salp's filtering activity (Kashkina 1986). In addition, a salp barrel containing a large hyperiid amphipod is a considerably more calorically-dense ration than ingestion of the intact salp alone (see Chapter 3.0).

Chum salmon have developed special physiological adaptations that enable them to utilize gelatinous zooplankton and, therefore, consume a more diverse suite of prey organisms than other species of Pacific salmon. The digestive tract of chum salmon is unique among Pacific salmon because it is particularly well adapted for heavy consumption of gelatinous prey (Arai et al. 2000). The stomach of a chum salmon produces a higher stomach acidity than other salmon (Azuma 1995), and the esophageal villi and extensive vascularization in the stomach wall increases the stomach's surface

area and therefore speeds the digestion rate (Welch 1997). These attributes are particularly helpful for efficient digestion of gelatinous prey, which contains a large amount of water. Chum salmon also have a muscular esophageal sphincter (Azuma 1992, Arai et al. 2000) and a stomach considerably less muscular than other salmon (Welch 1997), which helps to prevent regurgitation of large soft-bodied gelatinous prey. The posterior section of the stomach is longer than other salmonids of equivalent body length and the whole stomach is capable of holding approximately 3.5 times the prey volume compared to other salmon of the same body size (Arai et al. 2000). By utilizing gelatinous zooplankton in their diet, chum salmon may reduce direct trophic competition with other salmon (Welch and Parsons 1993).

An earlier analysis of food habits in the same survey area in 1991 and 1992 showed shifts to lower-quality prey by pink, sockeye, and chum salmon when pink salmon were abundant and concluded this shift occurred in both the central North Pacific and Bering Sea (Tadokoro et al. 1996). Both the above cited earlier study and this one show there was a shift in food habits due to intra-specific feeding competition among pink salmon and inter-specific competition between pink and other zooplanktivorous salmon, namely sockeye and chum salmon, when there is a high concentration of maturing pink salmon in an area. The examination of five cycles of pink salmon abundance rather than one has afforded the sample sizes necessary to indicate that the shifts in diet when pink salmon were abundant occurs during the summer in the central Bering Sea, and not in the central North Pacific Ocean.

Reductions in the quantity of high quality prey in the stomach contents of sockeye, chum, and pink salmon were substantial when pink salmon were abundant in the central Bering Sea. The odd-numbered year dominance of pink salmon in the Bering Sea occurred in 1989 and has persisted since that time (Azumaya and Ishida 2000). Results showed reductions in the proportion of high quality prey was 53% in sockeye, 50% in chum, and 33% in pink salmon during odd-numbered years. In samples from *Wakatake maru* cruises in 1991 and 1992, Tadokoro et al. (1996) observed shifts in pink salmon diet, with a drop in gelatinous zooplankton from 17% to 0% and an increase in

micronecton (fish and squid) from 26% to 45% when pink salmon abundance was low. However, they reported only a small reduction (from 57% to 55%) in the proportion of crustaceans in pink salmon stomach contents between odd- and even-numbered years. In this study, there were substantial decreases in the weight of euphausiids, a high caloric-density prey (see Chapter 3.0) and increases in pteropods and hyperiid amphipods, a lower caloric-density prey, in the stomach contents of sockeye, chum, and pinks when pink salmon were abundant. Tadokoro et al. (1996) documented a reduction in the proportion of gelatinous prey from 81% to 25% and an increase in crustaceans (16% to 58%) and micronecton (2% to 18%) in chum salmon stomachs when pink salmon were scarce in 1992. Examination of the decade-long trend shows chum salmon stomachs contained a relatively constant proportion of squid in odd- and even-numbered years. Inter-specific competition may be reduced by chum salmon consumption of lower caloric-density gelatinous zooplankton (Azuma 1992, 1995; Tadokoro et al. 1996).

My analysis extends considerably the time series of the earlier study and supplements previous summaries of the observed changes in salmon food habits that occurred when pink salmon were abundant (Andrievskaya 1957; Ito 1964; Tadokoro et al. 1996). This dramatic fluctuation in pink salmon abundance may affect the feeding of pinks and other salmon in this area because all the pink salmon in the catches were maturing ocean age .1, which were feeding heavily in preparation for their return to coastal waters. To more clearly resolve issues of inter- and intra-species interactions in the central Bering Sea, where fish from many stocks intermingle, more information on stock-specific growth rates and distribution is required.

In the central Bering Sea, weight of small squid (post-larvae or juveniles) in the stomach contents of sockeye, chum, and pink salmon was negatively associated with water temperature in the upper 5 m and positively associated with salinity at 100 m (Tables 1.4; 1.7; 1.9). The distribution of juvenile squid may be influenced by the hydrological condition of the active layer. Additional research is required to determine if the correlation between the level of small squid consumption and these environmental variables was biologically meaningful, and to determine how the structure of the active

layer could affect squid spawning, distribution of juveniles, and developmental rates of young squid. Preserved samples of juvenile squids have been provided to experts for species identification. Further elucidation of the squid life history and patterns of distribution will be important in supplementing studies of salmon feeding ecology in the central Bering Sea.

Trophic dynamics in the salmon-dominated waters of the central North Pacific Ocean and Bering Sea involve complex relationships. There can be a reversal in the role of prey and predator of salmon based on the life-history stage of the fishes involved. For example, the daggertooth (*A. pharao*) is considered an important predator of salmon and a major cause of slash marks on their bodies (Welch et al. 1991; Balanov and Radchenko 1988). However, my observation of small daggertooth (140-315 mm SL; Table 1.3) in chinook salmon stomach contents indicates the role of predator and prey reverses depending upon the respective sizes of the fishes involved. Small daggertooth is prey of piscivorous salmon, like chinook. At an intermediate size, daggertooth probably escape predation by salmon and grow to become a predator and major source of mortality of Pacific salmon. Complexities such as these role reversals should be incorporated as feed-back mechanisms into future ecosystem models.

In the basin of the Bering Sea, salmon feeding in the epipelagic zone consumed many juvenile fish that at a larger size will take up a demersal life-style. These juvenile fish included cottids, stichaeids, poachers, snail fishes, *P. monopterygius*, *Sebastes* sp., and flatfishes including halibut, *H. stenolepis*, and *Reinhardtiius hippoglossoides* and *Atheresthes* sp. Consumption of these juvenile fish by Pacific salmon provides evidence that the deep basin epipelagic community is inextricably linked to demersal fish communities. The demersal fish communities, particularly of the Bering Sea shelf, are well studied with systematic trawl surveys, whereas the basin is not well surveyed. Perhaps it is time to expand pelagic surveys in the Bering Sea basin. “Give the basin a little respect- it is an integral part of the larger ecosystem, but is virtually ignored” (Springer 1999).

Table. 1.1 Correlation coefficents among environmental variables, chlorophyll-*a* concentration, zooplankton biomass, and salmon CPUE. Boxes indicate correlations significant at $p \leq 0.05$. t5m, t30m, t100m=temperature (°C) at 5, 30, and 100 m depth; s5m, s30m, s100m=salinity (psu) at 5, 30, and 100 m depth; chla= chlorophyll-*a* concentration (µg/l); zoop=ln(zooplankton biomass [mg/m^3]); sock=sockeye salmon CPUE (number per 30-tans of research-mesh gillnet); chum=chum salmon CPUE, pink=pink salmon CPUE, coho=coho salmon CPUE; chin=chinook salmon CPUE; sthd=steelhead trout CPUE.

41-44° N latitude

	t5m	t30m	t100m	s5m	s30m	s100m	chla	zoop	chum	coho	sthd
t5m	1.000										
t30m	0.777	1.000									
t100m	0.484	0.735	1.000								
s5m	0.635	0.870	0.830	1.000							
s30m	0.670	0.895	0.831	0.997	1.000						
s100m	0.629	0.883	0.898	0.966	0.972	1.000					
chla	0.587	0.207	-0.348	0.000	0.056	-0.099	1.000				
zoop	0.452	0.426	-0.231	0.201	0.238	0.022	0.716	1.000			
chum	0.325	0.510	0.503	0.609	0.599	0.602	0.248	-0.089	1.000		
coho	-0.322	-0.525	-0.133	-0.198	-0.252	-0.282	-0.452	-0.554	-0.157	1.000	
sthd	-0.103	-0.182	0.165	0.001	-0.038	-0.069	-0.627	-0.366	-0.141	0.626	1.000

45-51°N latitude

	t5m	t30m	t100m	s5m	s30m	s100m	chla	zoop	sock	chum	pink	coho	chin	sthd
t5m	1.000													
t30m	0.809	1.000												
t100m	0.764	0.409	1.000											
s5m	-0.110	0.099	0.029	1.000										
s30m	-0.014	0.133	0.171	0.930	1.000									
s100m	-0.380	0.075	-0.307	0.723	0.622	1.000								
chla	0.055	0.130	0.066	-0.083	-0.147	0.081	1.000							
zoop	-0.293	-0.151	-0.305	-0.078	0.078	-0.050	-0.863	1.000						
sock	-0.458	-0.594	-0.215	-0.475	-0.467	-0.143	-0.157	0.449	1.000					
chum	0.341	0.375	0.073	-0.107	-0.222	0.019	0.613	-0.749	0.052	1.000				
pink	-0.405	-0.668	-0.199	-0.646	-0.721	-0.412	-0.323	0.139	0.787	-0.110	1.000			
coho	0.181	0.269	0.507	0.517	0.649	0.396	0.130	0.060	-0.466	-0.404	-0.559	1.000		
chin	0.206	-0.115	0.351	-0.703	-0.483	-0.573	-0.336	0.375	0.468	-0.338	0.503	-0.016	1.000	
sthd	-0.338	-0.218	-0.270	-0.332	-0.337	-0.098	0.325	0.129	-0.067	-0.428	0.152	0.230	0.188	1.000

52-58°N latitude

	t5m	t30m	t100m	s5m	s30m	s100m	chla	zoop	sock	chum	pink	chin
t5m	1.000											
t30m	0.574	1.000										
t100m	0.526	0.302	1.000									
s5m	-0.190	0.158	-0.539	1.000								
s30m	-0.679	-0.137	-0.781	0.634	1.000							
s100m	-0.660	0.029	-0.517	0.590	0.871	1.000						
chla	0.084	-0.561	-0.300	-0.236	-0.028	-0.245	1.000					
zoop	0.139	-0.436	-0.272	-0.248	-0.288	-0.496	0.600	1.000				
sock	0.577	0.341	0.270	-0.185	-0.526	-0.384	0.489	0.203	1.000			
chum	-0.255	0.009	0.285	-0.371	-0.184	0.008	-0.214	-0.425	0.201	1.000		
pink	0.344	-0.124	0.260	0.190	-0.156	-0.212	0.213	0.190	-0.153	-0.748	1.000	
chin	-0.086	-0.041	0.108	-0.721	-0.048	-0.168	-0.170	0.128	-0.284	0.215	-0.328	1.000

Table 1.2. Mean catch (number of salmonids) per unit (30-tans, 1500 m) of effort by research-mesh gillnet caught by the *Wakatake maru,* 1991-2000. Research-mesh gillnet is composed of three tans each of the following mesh sizes: 48, 55, 63, 72, 82, 93, 106, 121, 138, and 157 mm.

Year	Sampling Dates	Number of Stations	Mean Catch per 30 tans						
			Sock-eye	Chum	Pink	Coho	Chi-nook	Steel-head	Total
Central North Pacific (38°N-47°N, 180°)									
1991	12-21 Jun	10	0.2	11.4	2.3	19.6	0.2	1.9	35.6
1992	17-25 Jun	10	0.0	10.8	0.2	10.3	0.1	0.6	22.0
1993	17-28 Jun	10	0.0	29.7	0.8	6.6	0.1	1.7	25.4
1994	18-27 Jun	10	0.4	8.2	7.1	11.9	0.3	3.7	31.6
1995	18-27 Jun	10	0.2	11.1	2.6	11.2	0.2	2.4	26.9
1996	15-27 Jun	10	0.0	22.7	0.5	8.0	0.3	0.6	32.1
1997	19-28 Jun	10	0.3	16.8	8.1	13.1	0.7	1.7	40.7
1998	17-28 Jun	10	1.8	7.4	0.8	19.3	0.7	2.7	32.8
1999	16-26 Jun	10	10.8	17.1	15.9	6.1	0.6	1.8	52.3
2000	12-22 Jun	10	1.6	17.3	4.7	3.7	0.1	1.4	28.8
Central Bering Sea (55°-58°N, 177°W-177°E)									
1991	1-8 Jul	8	22.9	53.9	365.5	0.0	9.9	0.0	452.1
1992	4-14 Jul	11	22.8	257.5	9.0	0.3	5.4	0.0	295.5
1993	6-16 Jul	11	58.2	111.6	141.2	0.8	1.4	0.0	313.2
1994	5-15 Jul	11	50.3	224.0	13.1	0.0	5.2	0.0	292.7
1995	5-15 Jul	11	37.8	63.8	174.5	0.5	6.5	0.0	283.3
1996	4-14 Jul	9	55.1	200.7	4.8	0.1	6.8	0.0	267.7
1997	6-17 Jul	10	57.0	143.9	379.7	0.3	3.5	0.0	584.5
1998	6-16 Jul	11	37.7	209.6	5.6	0.4	22.7	0.0	281.1
1999	4-14 Jul	11	25.5	64.1	357.3	0.0	4.1	0.0	450.9
2000	30 Jun-12 Ju	11	36.1	141.5	2.2	0.0	10.2	0.0	189.9

Table 1.3. Observations on salmon and steelhead prey characteristics including the approximate size and orientation of prey observed in stomach samples. Size=size of prey observed in stomach samples (maximum body size for zooplankton, mantle length for squid, and standard length for fish). Obs.=X indicates a prey item present in the stomach samples of a particular salmonid species. Hf=prey swallowed head first, tf=prey swallowed tail first. Evidence of bait stealing by longline-caught salmon and steelhead is shown at the bottom of the table.

Prey groups	Approximate	Sockeye		Chum		Pink		Coho		Chinook		Steelhead	
	prey size (mm)	Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment
Cnidaria													
medusae *Aglantha digitale* (proba	5-25	X		X		X		X		X			
Ctenophora													
Beroe sp.	15-58	X		X									
Polychaetes													
Tomopterus sepcentrionalis	15	X		X		X						X	
Rhynchonerella spp.	70-140	X		X								X	
Ostracods													
Conchoecia magna	2-3	X		X		X		X					
Copepods													
Neocalanus cristatus	7-8	X		X		X		X		X		X	
Eucalanus bungii	8					X							
Euphausiids													
Euphausia pacifica	10-15	X		X		X		X		X		X	
Thysanoessa longipes	15-23	X		X		X				X			
Tessarobrachion occulatum	18			X									
Hyperiid amphipods													
Parathemisto pacifica	2-8	X		X		X							
Phronima sedentaria	9-30	X		X		X		X					
Primno abyssalis	7-15	X		X		X							
Hyperia medusarum	7-8	X		X		X						X	
Hyperoche medusarum	7-8	X											
Paraphronima spp.	8			X									
Hyperiid amphipods (unidentified)	6-20	X		X		X		X		X		X	
Gammarid Amphipods													
Lysianassidae	14-18	X				X						X	
Rhacotropis	10			X									
Shrimps													
Hymendora frontalis	40-46	X		X		X							
juvenile shrimp	12-14	X		X		X							
Shrimps (unidentified)	8-42	X		X		X		X		X		X	
Crab zoea	3-4	X		X		X				X			

Table 1.3. Continued.

Prey groups	Approximate prey size (mm)	Sockeye		Chum		Pink		Coho		Chinook		Steelhead	
		Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment
Insects													
Lepidoptera (Moths)						X		X					
Gastropods													
Limacina helicina	2-3	X		X		X		X		X			
Clione limacina	10-26	X		X		X							
Clio pyramidata	11			X		X		X				X	
Clio recurva	23							X					
Heteropods													
Carinaria sp.	30			X		X							
Cephalopods													
Berryteuthis anonychus	40-124	X	count of individuals per salmon stomach=1-10; squid feeding on copepods, euphausiids, chaetognaths, polychaetes, hyperiid amphipods	X	count of individuals per salmon stomach=1-2	X	count of individuals per salmon stomach=1-4	X	count of individuals per salmon stomach=1-14; 60% hf, 40% tf in 10 observations; when stomach is distended with squid, they are packed head to tail in the stomach; squid	X	count of individuals per salmon stomach=1-14; 68% hf, 32% tf in 38 observations; squid feeding on Limacina	X	count of individuals per salmon stomach=1-8; 78% hf, 22% tf in 9 observations; when stomach is distended with squid, they are packed head to tail in the stomach
Small squids	9-30	X	count of individuals per salmon stomach=1-35	X	count of individuals per salmon stomach=1-5	X	count of individuals per salmon stomach=1-10	X	count of individuals per salmon stomach=6-13	X	count of individuals per salmon stomach=1-35; squid feeding on euphausiids		
unknown gonatid squid	53-210							X		X	count of individuals per salmon stomach=1	X	
Chaetognaths													
Sagitta scripsae	15-28	X		X		X		X		X			
Urochordates													
Oikopleura labradoriensis	3	X		X		X							
Salpa spp.	19-25			X				X					

Table 1.3. Continued.

Prey groups	Approximate prey size (mm)	Sockeye		Chum		Pink		Coho		Chinook		Steelhead	
		Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment	Obs.	Comment
Pisces													
Ammodytes hexapterus	26-42	X		X		X							
Hypsagonus quadricornis	13					X							
Cololabis saira	175							X					
Gasterosteus aculeatus	32-60					X		X	count of individuals per salmon stomach=1-8			X	count of individuals per salmon stomach=1-7
Engraulis japonicus	125-135							X	count of individuals per salmon stomach=1-3				
Anotopterus pharao	140-315									X	count of individuals per salmon stomach=1-2; largest one bent in half in the stomach	X	
Pleurogrammus monopterygius	34-85	X	count of individuals per salmon stomach=1-15; 81% hf, 19% tf in 26 observations; Pleurogrammus feeding on copepods and Limacina, hyperiid amphipods	X	count of individuals per salmon stomach=1-39; 36% hf, 64% tf in 11 observations	X	count of individuals per salmon stomach=1-16; 32% hf, 68% tf in 115 observations, Pleurogrammus feeding on Limacina	X	count of individuals per salmon stomach=1-8	X	count of individuals per salmon stomach=1-14; 100% hf in 14 observations	X	count of individuals per salmon stomach=1-15; 100% hf in 4 observations; when stomach is distended the Pleurogrammus are randomized head to tail
Sebastes spp.	9-13	X				X							
Stenobrachius leucopsarus	43-125	X	count of individuals per salmon stomach=1; 50% hf, 50% tf in 4 observations; Stenobrachius feeding on copepods, ostracods	X	count of individuals per salmon stomach=1; 100% tf in 1 observation	X	count of individuals per salmon stomach=1			X	count of individuals per salmon stomach=1; 100% hf in 1 observation		
Tarletonbeania crenularis	35-43			X				X					
Unknown myctophids				X		X				X		X	count of individuals per salmon stomach=1-2

Table 1.3. Continued.

Prey groups	Approximate prey size (mm)	Sockeye Obs.	Sockeye Comment	Chum Obs.	Chum Comment	Pink Obs.	Pink Comment	Coho Obs.	Coho Comment	Chinook Obs.	Chinook Comment	Steelhead Obs.	Steelhead Comment
Trachipteridae juvenile (ribbonfish)	70					X							
Leuroglossus schmidti	114-123			X	count of individuals per salmon stomach=3-4								
Hemilepidotus spp.	12-21	X	count of individuals per salmon stomach=1-5; Hemilepidotus feeding on Limacina, larval shrimp zoea, hyperiid amphipods, calanoid amphipods	X	count of individuals per salmon stomach=1-4	X	count of individuals per salmon stomach=1-50	X		X		X	
Aptocyclus spp.	7			X		X							
Liparis sp.	12					X							
Psychrolutes phrictus	10			X		X							
Hippoglossus stenolepis	15-19	X		X		X							
Reinhardtius hippoglossoides	28-31	X				X							
Atheresthes sp.	17-20	X				X							
Unknown juvenile fish	18-23	X		X		X	count of individuals per salmon stomach=1-19			X			
Other Items													
Floating debris (including plastic sheet, foam, and wood)	5-70	X		X		X		X				X	
feather	20-40	X		X									
Number of bait fish[1] in stomach samples		No. of Obs.		No. of Obs.		No. of Obs		No. of Obs		No. of Obs.		No. of Obs	
1		130		220		98		108		38		21	
2		3		48		12		14		6		4	
3		0		9		6		3		1		0	
4		2		1		0		2		0		0	
5		0		0		0		3		0		0	
6		0		1		0		0		0		0	
>6		0		0		0		1		0		0	
proportion[2]		0.04		0.21		###		###		0.16		0.16	

[1]bait fish is salted anchovy (*Engraulis japonicus*)

[2] proportion=(total number of salmonids with >1 bait fish present in their stomach samples)/(total number with ≥1bait fish present)

Table. 1.4. Correlation coefficents among sockeye salmon prey groups (mean prey weight), salmon CPUE, and environmental variables. Boxes indicate correlations significant at $p \leq 0.05$. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, other=other prey, totprey=total prey weight, sock=sockeye salmon CPUE (number per 30 tans of research-mesh gillnet), chum=chum salmon CPUE, pink=pink salmon CPUE, coho=coho salmon CPUE, chin= chinook salmon CPUE, chla=chlorophyll-*a* concentration (µg/l), zoop=ln(zooplankton biomass [mg/m^3]); t5m, t30m, t100m=temperature (°C) at 5, 30, 100 m depth; s5m, s30m, s100m= salinity (psu) at 5, 30, 100 m depth.

45-51°N latitude Sockeye Salmon

	eu	co	am	sq	pt	fi	other	totprey
eu	1.000							
co	0.952	1.000						
am	0.459	0.296	1.000					
sq	0.394	0.396	0.094	1.000				
pt	0.310	0.164	0.221	0.054	1.000			
fi	-0.189	-0.127	-0.292	-0.134	-0.331	1.000		
other	0.242	0.345	0.133	-0.329	-0.102	-0.206	1.000	
totprey	0.839	0.822	0.387	0.737	0.156	0.084	0.003	1.000
sock	-0.261	-0.249	-0.495	-0.271	0.032	0.013	-0.386	-0.415
chum	0.036	-0.133	0.275	-0.291	0.278	-0.361	0.070	-0.227
pink	-0.085	0.029	-0.361	-0.025	0.142	-0.300	-0.162	-0.217
coho	0.028	0.018	0.056	-0.203	0.167	0.467	0.337	0.110
chla	0.345	0.208	0.337	-0.123	0.231	0.056	0.485	0.219
zoop	-0.237	-0.156	-0.139	0.367	-0.325	0.404	-0.708	0.094
t5m	0.363	0.366	0.236	-0.225	0.200	0.177	0.233	0.213
t30m	0.234	0.129	0.625	-0.271	0.078	0.194	0.123	0.153
t100m	0.264	0.299	-0.158	-0.330	0.463	0.241	0.305	0.077
s5m	-0.127	-0.218	0.047	-0.078	-0.080	-0.139	0.235	-0.155
s30m	-0.240	-0.294	-0.151	-0.090	-0.155	0.197	0.126	-0.153
s100m	-0.452	-0.572	0.209	-0.431	-0.187	-0.059	0.176	-0.501

52-58°N latitude Sockeye Salmon

	eu	co	am	sq	pt	fi	other	totprey
eu	1.000							
co	0.006	1.000						
am	0.067	-0.171	1.000					
sq	-0.188	0.768	-0.053	1.000				
pt	0.673	-0.439	0.042	-0.553	1.000			
fi	-0.073	-0.267	0.125	0.022	-0.219	1.000		
other	-0.126	-0.388	-0.050	-0.313	0.581	-0.111	1.000	
totprey	0.083	0.662	0.135	0.908	-0.358	0.285	-0.291	1.000
sock	0.104	-0.046	-0.121	-0.479	-0.018	0.093	-0.142	-0.420
chum	0.209	0.813	-0.289	0.472	-0.387	-0.048	-0.596	0.455
pink	-0.340	-0.428	-0.094	-0.353	0.322	-0.351	0.734	-0.505
chin	0.269	-0.167	-0.014	-0.138	0.204	0.033	-0.016	-0.065
chla	-0.324	-0.411	0.064	-0.683	0.080	0.154	0.208	-0.789
zoop	-0.026	-0.510	0.766	-0.628	0.227	-0.265	0.120	-0.584
t5m	0.476	-0.385	-0.128	-0.646	0.625	-0.015	0.405	-0.481
t30m	0.310	-0.059	-0.095	0.054	0.154	0.451	0.182	0.268
t100m	0.141	0.296	-0.443	-0.046	0.114	-0.480	0.193	-0.169
s5m	-0.266	0.004	0.163	0.350	-0.120	0.392	0.191	0.416
s30m	-0.384	-0.071	0.053	0.426	-0.263	0.468	0.028	0.434
s100m	-0.404	0.206	-0.104	0.638	-0.390	0.236	-0.036	0.547

Table 1.5. Listing of biological characteristics of sockeye salmon containing the maximum SCI (prey weight/body weight*100) observed in each weight or ocean age class in the central North Pacific Ocean and central Bering Sea. Fage=freshwater age, Oage=ocean age, PW=prey weight (g), eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, other= crab larvae, polychaetes, chaetognaths, gelatinous zooplankton (medusae, ctenophores, and salps), and unidentifed material. X=freshwater age could not be determined because the scale was regenerated or otherwise unreadable, im=immature, and mt=maturing.

Sockeye Salmon

Weight (g) or Ocean age class	N	Maximum SCI	Fork Length (mm)	Body Weight (g)	Sex	Gonad Weight (g)	Fage	Oage	Maturity	PW	EU	CO	AM	SQ	PT	FI	Other
Central North Pacific Ocean (45-51° N latitude)																	
<500	21	2.3	334	420	f	3	1	1	im	10	2	2	96	0	0	0	0
500-999	34	2.3	460	960	m	4	1	2	mt	22	88	0	10	0	1	0	1
1000-1499	40	1.6	472	1100	m	2	1	2	im	17	0	0	50	50	0	0	0
1500-1999	19	5.2	515	1800	m	2	1	2	im	93	0	0	0	100	0	0	0
2000-2499	19	4.3	590	2400	m	10	1	2	mt	103	0	0	0	100	0	0	0
2500-2999	36	4.4	595	2520	m	15	2	2	mt	112	100	0	0	0	0	0	0
≥3000	23	2.6	625	3100	f	80	x	3	mt	79	30	0	0	70	0	0	0
Age .1	23	2.3	334	420	f	3	1	1	im	10	2	2	96	0	0	0	0
Age .2	107	5.2	515	1800	m	2	1	2	im	93	0	0	0	100	0	0	0
Age .3	56	3.1	604	2990	m	21	1	3	mt	93	95	0	0	5	0	0	0
Central Bering Sea (52-58°N latitude)																	
<500	120	5.9	327	410	m	1	1	1	im	24	85	0	15	0	0	0	0
500-999	83	4.4	382	520	m	2	2	1	im	23	93	5	0	2	0	0	0
1000-1499	439	6.9	466	1160	f	7	1	2	im	80	100	0	0	0	0	0	0
1500-1999	200	5.7	491	1540	m	2	x	2	im	87	0	0	0	100	0	0	0
2000-2499	75	3.2	550	2160	m	2	1	3	im	70	0	0	0	60	0	40	0
2500-2999	46	6.0	604	2500	m	35	1	3	mt	151	0	0	0	100	0	0	0
≥3000	94	5.1	652	4550	m	82	x	3	mt	234	0	0	0	95	0	5	0
Age .1	130	5.9	327	410	m	1	1	1	im	24	85	0	15	0	0	0	0
Age .2	676	6.9	466	1160	f	7	1	2	im	80	100	0	0	0	0	0	0
Age .3	203	6.0	604	2500	m	35	1	3	mt	151	0	0	0	100	0	0	0

Table 1.6. Mean weight (g) and proportions of prey groups and total mean prey weight of sockeye, chum, pink, and chinook salmon sampled in odd- and even-numbered years in the Bering Sea (52-58°N), 1991-2000. Gelatinous zooplankton=meduae, ctenophores, salps, and unidentified material. Pink salmon were abundant in odd years in this area and season. Empty stomach were not included. N= number of estimates (stations) used to calculate values. Change in weight shown where negative values represent reduction of prey weight in odd-numbered as compared to even-numbered years.

Salmon Predator	Prey Group	Odd Years weight	Odd Years proportion	Even Years weight	Even Years proportion	% change weight
Sockeye n=46	euphausiids	1.21	0.15	2.22	0.17	-45.3
	copepods	0.69	0.08	1.39	0.11	-50.5
	amphipods	1.95	0.24	1.78	0.14	10.0
	squid	2.05	0.25	4.85	0.38	-57.7
	pteropods	0.62	0.08	0.50	0.04	24.9
	fish	0.97	0.12	1.97	0.15	-50.6
	other	0.66	0.08	0.19	0.01	245.8
	total mean prey weight (g)	8.17	1.00	12.89	1.00	-36.7
Chum n=70	euphausiids	1.98	0.12	4.15	0.28	-52.4
	copepods	0.30	0.02	1.03	0.07	-71.0
	amphipods	0.75	0.05	1.54	0.10	-51.5
	squid	0.81	0.05	0.88	0.06	-9.0
	pteropods	1.93	0.12	1.48	0.10	30.4
	fish	1.20	0.08	0.85	0.06	41.1
	gelatinous zooplankton	6.10	0.37	4.35	0.30	40.2
	other	3.04	0.19	0.54	0.03	461.4
	total mean prey weight (g)	16.10	1.00	14.83	10.00	8.6
Pink n=57	euphausiids	1.87	0.14	2.96	0.17	-36.6
	copepods	1.16	0.08	2.21	0.12	-47.6
	amphipods	1.36	0.10	1.02	0.06	33.8
	squid	3.78	0.28	5.52	0.31	-31.6
	pteropods	0.86	0.06	0.27	0.01	214.2
	fish	4.12	0.30	5.49	0.31	-24.9
	other	0.53	0.04	0.38	0.02	41.9
	total mean prey weight (g)	13.69	100.00	17.85	100.00	-23.3
Chinook n=41	euphausiids	3.45	0.36	2.39	0.11	44.5
	squid	4.68	0.49	17.03	0.79	-72.5
	fish	1.29	0.14	1.81	0.08	-28.7
	other	0.11	0.01	0.38	0.02	-69.9
	total mean prey weight (g)	9.53	100.00	21.60	100.00	-55.9

Table. 1.7. Correlation coefficents among chum salmon prey groups (mean prey weight), salmon CPUE research-mesh gillnet), and environmental variables. Boxes indicate correlations significant at p≤0.05. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, ge=gelatinous zooplankton (medusae, ctenophores, and salps), other=other prey, totprey=total prey weight, sock=sockeye salmon CPU (number per 30-tans of research-mesh gillnet), chum=chum salmon CPUE, pink=pink salmon CPUE, coho=coho salmon CPUE, chin=chinook salmon CPUE, sthd=steelhead CPUE, chla=chlorophyll-*a* concentration (μg/l); zoop=ln(zooplankton biomass[mg/m^3]); t5m, t30m, t100m=temperature (C°) at 5, 30, 100 m depth; s5m, s30m, s100m=salinity (psu) at 5, 30, 100 m depth.

41-44° N latitude Chum Salmon

	eu	co	am	sq	pt	fi	ge	other	totprey
eu	1.000								
co	-0.444	1.000							
am	0.817	-0.540	1.000						
sq	-0.364	-0.089	-0.274	1.000					
pt	-0.444	-0.157	-0.161	0.436	1.000				
fi	-0.455	0.511	-0.337	-0.281	0.129	1.000			
ge	0.404	-0.569	0.680	-0.222	-0.025	-0.065	1.000		
other	-0.404	0.525	-0.329	0.699	0.062	0.066	-0.406	1.000	
totprey	0.274	-0.171	0.586	0.229	-0.010	-0.005	0.703	0.326	1.000
chum	0.059	0.309	0.070	0.065	0.074	0.561	-0.219	0.397	0.234
coho	0.282	0.099	0.165	-0.334	-0.280	-0.237	-0.075	-0.234	-0.206
sthd	0.223	-0.222	0.419	0.224	-0.146	-0.497	0.206	0.193	0.359
chla	-0.631	0.909	-0.748	0.122	0.191	0.488	-0.520	0.531	-0.236
zoop	-0.863	0.576	-0.761	0.407	0.110	0.335	-0.506	0.503	-0.303
t5m	-0.092	0.465	-0.026	-0.076	-0.494	0.435	0.188	0.475	0.540
t30m	-0.217	0.190	-0.002	0.054	-0.199	0.637	0.211	0.350	0.475
t100m	0.130	-0.040	0.353	0.121	-0.073	0.436	0.483	0.200	0.701
s5m	-0.012	0.269	0.085	0.040	-0.342	0.550	0.056	0.354	0.386
s30m	-0.032	0.271	0.065	0.057	-0.337	0.559	0.072	0.369	0.406
s100m	0.100	0.103	0.192	0.012	-0.306	0.539	0.243	0.233	0.489

45-51°N latitude Chum Salmon

	eu	co	am	sq	pt	fi	ge	other	totprey
eu	1.000								
co	0.369	1.000							
am	-0.065	0.629	1.000						
sq	0.064	0.433	0.425	1.000					
pt	-0.078	-0.395	-0.167	0.177	1.000				
fi	0.104	0.269	0.604	0.745	0.382	1.000			
ge	-0.267	-0.090	-0.198	-0.010	-0.543	-0.277	1.000		
other	-0.105	-0.264	-0.251	-0.272	0.726	-0.118	-0.741	1.000	
totprey	0.110	-0.102	-0.341	0.141	0.700	0.089	-0.088	0.489	1.000
sock	-0.262	-0.199	-0.352	-0.251	-0.234	-0.354	0.533	-0.286	-0.104
chum	-0.025	0.410	0.164	0.481	0.487	0.428	-0.171	0.316	0.680
pink	0.016	-0.235	-0.457	-0.274	-0.248	-0.235	0.513	-0.368	-0.104
coho	-0.091	-0.196	0.272	-0.130	-0.086	0.027	0.123	-0.157	-0.098
chla	0.200	-0.080	-0.400	0.135	0.542	-0.065	0.072	0.339	0.925
zoop	-0.155	-0.242	0.178	-0.147	-0.317	-0.078	-0.144	-0.239	-0.836
t5m	0.397	0.286	0.416	0.251	0.296	0.661	-0.557	0.191	0.091
t30m	0.208	0.316	0.660	0.327	0.481	0.689	-0.723	0.363	0.150
t100m	0.234	0.124	0.283	0.089	-0.092	0.424	0.050	-0.259	-0.045
s5m	-0.250	0.421	0.456	0.022	-0.408	-0.195	0.089	-0.072	-0.181
s30m	-0.355	0.203	0.389	-0.003	-0.342	-0.173	0.042	-0.031	-0.280
s100m	-0.579	0.076	0.368	-0.165	-0.037	-0.241	0.105	0.154	0.056

52-58°N latitude Chum Salmon

	eu	co	am	sq	pt	fi	ge	other	totprey
eu	1.000								
co	0.395	1.000							
am	0.470	0.794	1.000						
sq	0.177	0.809	0.575	1.000					
pt	-0.068	-0.457	-0.469	-0.567	1.000				
fi	0.054	-0.133	0.113	0.302	-0.252	1.000			
ge	-0.253	-0.126	-0.294	-0.111	-0.456	-0.291	1.000		
other	-0.431	-0.298	-0.460	-0.004	0.123	-0.180	0.335	1.000	
totprey	0.259	0.262	0.047	0.343	-0.367	-0.167	0.631	0.529	1.000
sock	-0.084	-0.447	-0.334	-0.228	0.360	0.266	-0.570	0.123	-0.501
chum	0.455	0.646	0.658	0.334	-0.113	-0.228	-0.554	-0.427	-0.263
pink	-0.521	-0.400	-0.641	-0.190	0.384	-0.199	0.360	0.624	0.265
chin	0.077	0.061	0.366	-0.267	0.174	-0.225	-0.112	-0.077	-0.062
chla	-0.782	-0.618	-0.606	-0.640	0.157	-0.254	0.241	0.274	-0.427
zoop	-0.521	-0.626	-0.203	-0.624	0.204	0.228	-0.032	-0.139	-0.553
t5m	0.145	-0.638	-0.516	-0.487	0.691	0.062	-0.325	0.395	-0.041
t30m	0.572	-0.044	0.019	0.177	0.150	0.415	-0.282	0.256	0.391
t100m	0.109	0.142	0.046	0.108	0.656	-0.227	-0.636	0.295	-0.079
s5m	0.117	0.062	-0.184	0.311	-0.554	0.207	0.614	0.111	0.569
s30m	-0.053	0.263	0.105	0.304	-0.769	0.027	0.774	0.030	0.550
s100m	-0.020	0.495	0.277	0.689	-0.851	0.210	0.506	0.131	0.561

Table 1.8. Listing of biological characteristics of chum salmon containing the maximum SCI (prey weight/body weight*100) observed in each weight or ocean age class in the central North Pacific Ocean and central Bering Sea. Oage=ocean age, PW=prey weight (g), eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, ge=gelatinous zooplankton (medusae, ctenophores, and salps), other= crab larvae, polychaetes, chaetognaths, and appendicularia, and unid=unidentified material. X=age could not be determined because the scale was regenerated or otherwise unreadable, im=immature, and mt=maturing.

Chum Salmon

Weight (g) or Ocean age class	N	Maximum SCI	Fork Length (mm)	Body Weight (g)	Sex	Gonad Weight (g)	Oage	Maturity	PW	EU	CO	AM	SQ	PT	FI	GE	Other	Unid
Central North Pacific Ocean (45-51° N latitude)																		
<500	140	4.3	307	280	f	1	1	im	12	0	85	0	0	5	0	0	0	10
500-999	423	4.7	402	660	m	1	x	im	31	0	0	10	0	10	0	0	10	70
1000-1499	283	4.6	472	1320	f	24	2	mt	61	100	0	0	0	0	0	0	0	0
1500-1999	70	3.1	523	1500	f	23	2	mt	47	0	0	0	25	65	5	0	5	0
2000-2499	25	3.5	581	2300	m	35	3	mt	80	0	0	1	20	0	0	20	0	59
≥2500	17	2.8	664	3150	m	5	5	mt	87	0	0	2	0	3	2	20	73	0
Age .1	146	4.3	307	280	f	1	1	im	12	0	85	0	0	5	0	0	0	10
Age .2	487	4.6	472	1320	f	24	2	mt	61	100	0	0	0	0	0	0	0	0
Age .3	236	3.5	581	2300	m	35	3	mt	80	0	0	1	20	0	0	20	0	59
Age .4	22	1.8	560	2120	m	110	4	mt	38	38	0	5	0	4	0	48	5	0
Age .5	3	2.8	664	3150	m	5	5	mt	87	0	0	2	0	3	2	20	73	0
Central Bering Sea (52-58°N latitude)																		
<500	110	5.2	358	420	m	1	1	im	22	10	10	0	60	0	20	0	0	0
500-999	576	6.4	460	700	m	1	2	im	45	65	0	25	5	0	5	0	0	0
1000-1499	597	5.4	544	1120	m	2	3	im	60	100	0	0	0	0	0	0	0	0
1500-1999	506	4.3	570	1890	f	33	3	mt	82	95	0	0	5	0	0	0	0	0
2000-2499	307	3.6	572	2100	f	53	3	mt	76	80	0	0	0	10	0	10	0	0
2500-2999	152	3.0	584	2510	m	6	4	mt	76	0	10	10	0	0	0	20	20	40
3000-3999	144	2.5	650	3350	f	70	4	mt	85	100	0	0	0	0	0	0	0	0
≥4000	31	1.9	676	4850	m	110	4	mt	90	0	0	0	0	0	0	50	0	50
Age .1	164	5.2	358	420	m	1	1	im	22	10	10	0	60	0	20	0	0	0
Age .2	768	6.4	460	700	m	1	2	im	45	65	0	25	5	0	5	0	0	0
Age .3	###	5.4	544	1120	m	2	3	im	60	100	0	0	0	0	0	0	0	0
Age .4	276	3.8	499	1620	f	12	4	im	62	0	5	0	0	0	60	35	0	0
Age .5	25	1.9	583	1960	f	23	5	im	38	98	0	0	2	0	0	0	0	0

Table 1.9. Correlation coefficents among pink salmon prey groups (mean prey weight), salmon CPUE and environmental variables. Boxes indicate correlations significant at $p \leq 0.05$. Eu= euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, other=other prey, totprey=total prey weight; sock=sockeye salmon CPUE (number per 30-tans of research-mesh gillnet), chum=chum salmon CPUE, pink=pink salmon CPUE, coho=coho salmon CPUE, chla=chlorophyll-*a* concentration (µg/l), zoop=ln(zooplankton biomass [mg/m^3]); t5m, t30m, t100m=temperature (C°) at 5, 30, 100 m depth; s5m, s30m s100m=salinity (psu) at 5, 30, 100 m depth.

45-51°N latitude Pink Salmon

	eu	co	am	sq	pt	fi	other	totprey
eu	1.000							
co	0.402	1.000						
am	-0.206	-0.470	1.000					
sq	-0.387	-0.206	-0.478	1.000				
pt	0.224	-0.204	0.027	-0.383	1.000			
fi	0.006	-0.546	-0.371	0.540	0.032	1.000		
other	-0.250	-0.092	-0.473	0.940	-0.316	0.399	1.000	
totprey	-0.167	-0.080	-0.599	0.969	-0.298	0.550	0.952	1.000
sock	-0.238	0.446	-0.492	-0.004	-0.179	-0.123	-0.016	-0.040
chum	-0.117	-0.283	0.086	-0.219	0.324	0.127	-0.138	-0.257
pink	0.192	0.551	-0.521	-0.067	0.013	-0.107	0.047	0.014
coho	-0.040	-0.089	0.444	-0.125	0.092	-0.460	-0.134	-0.149
chla	0.122	-0.274	-0.294	-0.121	0.613	0.364	0.049	0.015
zoop	-0.277	0.264	0.126	0.532	-0.701	-0.208	0.243	0.347
t5m	0.380	0.282	0.303	-0.422	-0.055	-0.446	-0.292	-0.362
t30m	0.053	-0.110	0.643	-0.460	0.045	-0.336	-0.417	-0.491
t100m	0.345	0.412	0.206	-0.372	-0.074	-0.682	-0.215	-0.314
s5m	-0.262	-0.714	0.526	0.008	0.049	0.189	-0.183	-0.111
s30m	-0.367	-0.539	0.428	0.168	-0.122	0.051	-0.027	0.042
s100m	-0.563	-0.666	0.528	-0.160	0.366	0.041	-0.352	-0.320

52-58°N latitude Pink Salmon

	eu	co	am	sq	pt	fi	other	totprey
eu	1.000							
co	0.137	1.000						
am	0.267	0.200	1.000					
sq	0.036	0.621	0.046	1.000				
pt	-0.080	-0.136	0.507	-0.504	1.000			
fi	-0.456	-0.466	-0.550	0.113	-0.473	1.000		
other	0.127	0.663	0.533	0.560	0.043	-0.547	1.000	
totprey	-0.016	0.357	-0.100	0.890	-0.609	0.497	0.249	1.000
sock	-0.030	-0.415	-0.162	-0.527	-0.215	0.177	-0.373	-0.366
chum	0.216	0.566	-0.201	0.312	-0.641	0.001	0.108	0.320
pink	-0.074	-0.250	0.245	-0.305	0.550	-0.453	0.318	-0.534
chin	-0.216	0.020	0.126	-0.107	0.093	0.070	-0.245	-0.061
chla	0.068	-0.613	-0.530	-0.608	0.058	-0.072	-0.654	-0.733
zoop	-0.009	-0.506	0.226	-0.608	0.770	-0.305	-0.384	-0.669
t5m	0.047	-0.608	0.267	-0.631	0.170	0.044	-0.114	-0.467
t30m	-0.309	-0.264	0.190	0.127	-0.319	0.538	0.100	0.365
t100m	-0.050	0.254	0.362	-0.217	0.055	-0.450	0.496	-0.371
s5m	0.088	-0.117	-0.182	0.504	-0.253	0.315	0.172	0.542
s30m	-0.127	0.046	-0.340	0.633	-0.334	0.417	-0.116	0.643
s100m	-0.114	0.335	-0.114	0.790	-0.429	0.248	0.160	0.717

Table 1.10. Listing of biological characteristics of pink salmon containing the maximum SCI (prey weight/body weight*100) observed in each weight class in the central North Pacific Ocean and central Bering Sea. All pink salmon are ocean age .1 maturing fish. PW=prey weight (g), eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, other= crab larvae, polychaetes, chaetognaths, gelatinous zooplankton (medusae, ctenophores, and salps), and unidentified material.

Pink Salmon

Weight class (g)	N	Maximum SCI	Fork Length (mm)	Body Weight (g)	Sex	Gonad Weight (g)	PW	EU	CO	AM	SQ	PT	FI	Other
Central North Pacific Ocean (45-51° N latitude)														
500-999	201	7.6	436	970	f	92	74	20	20	5	10	44	0	1
1000-1499	173	7.1	482	1400	m	14	100	0	0	0	100	0	0	0
1500-1999	8	4.5	524	1720	m	42	77	0	0	0	70	0	20	10
Central Bering Sea (52-58°N latitude)														
<500	7	2.4	368	490	m	18	12	0	0	0	0	0	100	0
500-999	269	5.7	420	926	m	56	53	50	5	5	20	0	20	0
1000-1499	784	6.0	460	1200	m	40	72	0	15	20	65	0	0	0
1500-1999	129	5.6	498	1680	m	100	94	70	0	10	10	0	10	0
2000-2499	10	3.5	568	2450	m	130	86	90	0	0	5	0	5	0

Table 1.11. Correlation coefficents among coho salmon prey groups (mean prey weight), salmon CPUE, and environmental variables. Boxes indicate correlations significant at $p \leq 0.05$. Eu=euphausiids, am=amphipods, sq=squid, pt=pteropods, fi=fish, other=other prey, totprey=total prey weight, sock=sockeye salmon CPUE (number per 30-tans of research-mesh gillnet), chum=chum salmon CPUE, pink=pink salmon CPUE, coho=coho salmon CPUE, chin=chinook salmon CPUE, sthd=steelhead CPUE, chla=chlorophyll-*a* concentration (µg/l); zoop=ln(zooplankton biomass[mg/m^3]); t5m, t30m, t100m=temperature (C°) at 5, 30, and 100 m depth; s5m, s30m, s100m=salinity (psu) at 5, 30, and 100 m depth.

41-44°N latitude Coho Salmon

	eu	am	sq	pt	fi	other	totprey
eu	1.000						
am	-0.079	1.000					
sq	0.204	0.700	1.000				
pt	0.109	-0.140	-0.205	1.000			
fi	0.420	-0.063	-0.221	-0.013	1.000		
other	0.225	0.060	-0.068	0.224	0.086	1.000	
totprey	0.378	0.718	0.954	-0.093	0.047	0.014	1.000
chum	0.013	-0.043	-0.150	0.886	-0.206	0.464	-0.094
coho	0.545	0.159	-0.185	-0.034	0.430	0.100	-0.020
sthd	0.133	0.598	0.196	-0.111	0.029	-0.337	0.242
chla	0.245	-0.733	0.008	0.398	-0.040	-0.180	-0.004
zoop	-0.357	-0.310	0.076	0.009	-0.208	-0.455	-0.048
t5m	0.065	0.326	0.617	0.505	-0.186	-0.124	0.628
t30m	-0.476	0.349	0.303	0.558	-0.276	0.022	0.275
t100m	-0.309	0.616	0.244	0.485	0.037	0.169	0.322
s5m	-0.264	0.542	0.314	0.571	-0.060	0.311	0.373
s30m	-0.273	0.527	0.336	0.570	-0.064	0.285	0.391
s100m	-0.290	0.541	0.310	0.564	-0.032	0.351	0.373

45-51°N latitude Coho Salmon

	eu	am	sq	pt	fi	other	totprey
eu	1.000						
am	-0.037	1.000					
sq	-0.545	-0.417	1.000				
pt	0.075	0.378	-0.368	1.000			
fi	0.538	-0.163	-0.505	-0.164	1.000		
other	0.423	0.192	-0.299	0.244	0.589	1.000	
totprey	-0.366	-0.485	0.971	-0.417	-0.325	-0.150	1.000
sock	-0.258	-0.494	0.540	-0.285	-0.177	-0.285	0.535
chum	-0.145	-0.200	0.199	0.370	-0.076	0.307	0.199
pink	0.058	-0.123	0.333	-0.297	0.075	-0.064	0.407
coho	0.033	0.351	-0.320	0.493	-0.308	-0.133	-0.408
chin	0.172	-0.302	0.064	-0.269	0.426	0.204	0.170
sthd	0.123	0.049	0.060	-0.271	-0.166	-0.548	0.054
chla	0.082	-0.571	0.158	0.425	-0.262	-0.300	0.131
zoop	-0.261	0.117	0.174	-0.750	0.043	-0.168	0.144
t5m	0.409	0.061	-0.332	0.310	0.461	0.853	-0.221
t30m	0.046	0.229	-0.296	0.219	0.114	0.532	-0.304
t100m	0.422	0.083	-0.231	0.569	0.197	0.657	-0.143
s5m	-0.068	0.341	-0.383	0.447	-0.337	-0.170	-0.508
s30m	-0.143	0.202	-0.325	0.406	-0.237	-0.140	-0.440
s100m	-0.513	0.381	-0.212	0.373	-0.589	-0.500	-0.434

Table 1.12 Listing of biological characteristics of coho salmon containing the maximum SCI (prey weight/body weight*100) observed in each weight class in the central North Pacific Ocean. All coho salmon are ocean age .1 maturing fish. Fage=freshwater age, Oage=ocean age, PW=prey weight (g), eu=euphausiids, am=amphipods, sq=squid, pt=pteropods, fi=fish, other=copepods, chaetognaths, gelatinous zooplankton (medusae, ctenophores, and salps), and unidentified material. X=freshwater age could not be determined because the scale was regenerated or otherwise unreadable.

Coho Salmon

Weight class (g)	N	Maximum SCI	Fork Length (mm)	Body Weight (g)	Sex	Gonad Weight (g)	Fage	Oage	PW	EU	AM	SQ	PT	FI	Other
Central North Pacific Ocean (40-51° N latitude)															
500-999	16	1.6	384	680	m	5	2	1	11	0	0	100	0	0	0
1000-1499	156	7.5	464	1100	m	5	2	1	82	0	0	100	0	0	0
1500-1999	258	6.7	520	1840	m	13	2	1	123	0	0	100	0	0	0
2000-2499	145	7.6	528	2150	m	9	2	1	163	0	0	100	0	0	0
2500-2999	26	6.5	572	2600	m	15	x	1	168	0	0	100	0	0	0
≥3000	11	7.0	617	3450	m	29	x	1	240	0	0	100	0	0	0

Table 1.13. Correlation coefficents among chinook salmon prey groups (mean prey weight), salmon CPUE, and environmental variables. Boxes indicate correlations significant at $p \leq 0.05$. Eu=euphausiids, sq=squid, fi=fish, other=other prey, totprey=total prey weight, sock=sockeye salmon CPUE, chum=chum salmmon CPUE, pink=pink salmon CPUE, coho=coho salmon CPUE, chinook=chinook salmon CPUE, sthd=steelhead CPUE, chla=chlorophyll-*a* concentration (µg/l); zoop=ln(zooplankton biomass [mg/m^3]); at 5, 30, and 100 m depth; s5m, s30m, s100m=salinity (psu) at 5, 30, and 100 m depth.

45-51°N latitude Chinook Salmon

	eu	sq	fi	other	totprey
eu	1.000				
sq	-0.288	1.000			
fi	-0.098	-0.381	1.000		
other	-0.125	-0.182	-0.129	1.000	
totprey	-0.313	0.981	-0.196	-0.212	1.000
sock	-0.155	-0.329	0.980	-0.158	-0.038
chum	-0.104	0.174	0.099	-0.161	0.323
pink	0.204	-0.638	0.819	-0.138	-0.265
coho	-0.345	0.159	-0.494	0.633	0.000
chin	0.397	-0.351	0.409	-0.179	-0.050
sthd	-0.301	0.220	-0.162	-0.178	0.337
chla	-0.674	0.801	-0.674	0.052	0.794
zoop	0.146	-0.232	0.146	-0.428	-0.467
t5m	0.495	-0.076	-0.421	-0.007	-0.072
t30m	0.138	0.262	-0.512	-0.178	0.039
t100m	0.268	-0.368	-0.228	0.520	-0.226
s5m	-0.341	0.339	-0.490	0.742	-0.113
s30m	-0.309	0.356	-0.529	0.670	-0.051
s100m	-0.679	0.529	-0.061	0.452	0.118

52-58°N latitude Chinook Salmon

	eu	sq	fi	other	totprey
eu	1.000				
sq	-0.257	1.000			
fi	-0.068	0.240	1.000		
other	0.056	-0.128	-0.139	1.000	
totprey	-0.120	0.984	0.343	-0.120	1.000
sock	-0.101	-0.193	0.430	-0.237	-0.161
chum	-0.295	0.204	0.063	0.603	0.177
pink	0.337	-0.460	-0.363	-0.504	-0.460
chin	-0.093	0.308	-0.091	0.629	0.292
chla	0.179	-0.769	-0.310	-0.112	-0.678
zoop	0.043	-0.700	-0.256	-0.049	-0.669
t5m	0.222	-0.127	0.542	-0.328	-0.037
t30m	0.083	0.429	0.670	-0.420	0.509
t100m	-0.023	-0.282	-0.020	0.096	-0.285
s5m	0.269	0.206	0.089	-0.626	0.244
s30m	0.138	0.405	-0.164	-0.113	0.402
s100m	0.187	0.190	-0.115	-0.068	0.202

Table 1.14. Listing of biological characteristics of chinook salmon containing the maximum SCI (prey weight/body weight*100) observed in each weight or ocean age class in the central North Pacific Ocean and central Bering Sea. Fage=freshwater age, Oage=ocean age, PW=prey weight (g), eu=euphausiids, sq=squid, fi=fish, other=copepods, amphipods, crab larvae, pteropods, chaetognaths, gelatinous zooplankton (medusae, ctenophores, and salps), and unidentifed material. X=freshwater age could not be determined because the scale was regenerated, or otherwise unreadable, im=immature, and mt=maturing.

Chinook Salmon

Weight (g) or Ocean age class	N	Maximum SCI	Fork Length (mm)	Body Weight (g)	Sex	Gonad Weight (g)	Fage	Oage	Maturity	PW	SQ	FI	Other
Central North Pacific Ocean (45-51° N latitude)													
1500-1999	4	2.1	489	1750	f	30	x	2	im	37	100	0	0
2000-2499	13	3.0	560	2200	m	5	x	2	mt	66	100	0	0
2500-2999	17	4.2	594	2550	m	2	1	2	im	108	100	0	0
3000-3999	13	3.3	664	3950	f	26	1	2	mt	130	100	0	0
≥4000	9	1.6	760	7200	f	45	1	3	im	115	100	0	0
Age .2	48	4.2	594	2550	m	2	1	2	im	108	100	0	0
Age .3	6	1.6	760	7200	f	45	1	3	im	115	100	0	0
Central Bering Sea (52-58°N latitude)													
<500	37	3.9	315	330	f	3	1	1	im	13	0	100	0
500-999	51	2.6	361	580	m	1	1	1	im	15	45	50	5
1000-1499	40	3.2	446	1050	f	4	1	2	im	34	100	0	0
1500-1999	90	4.1	520	1820	m	1	x	2	im	74	100	0	0
2000-2499	98	4.3	570	2350	m	2	1	2	im	101	100	0	0
2500-2999	46	2.7	586	2550	f	10	1	2	im	68	100	0	0
3000-3999	43	3.0	682	3800	f	33	1	3	im	115	100	0	0
≥4000	48	8.4	672	4000	f	27	1	3	im	337	100	0	0
Age .1	88	3.9	315	330	f	3	1	1	im	13	0	100	0
Age .2	263	4.3	570	2350	m	2	1	2	im	101	100	0	0
Age .3	75	8.4	672	4000	f	27	1	3	im	337	100	0	0

Table 1.15. Correlation coefficents among steelhead trout prey groups (mean prey weight), salmon CPUE, and environmental variables. Boxes indicate correlations significant at $p \leq 0.05$. Am=amphipods, sq=squid, fi=fish, po=polychaetes, other=other prey, totprey=total prey weight, sock=sockeye salmon CPUE (number per 30-tans of research-mesh gillnet), chum=chum salmon CPUE, pink=pink salmon CPUE, coho=coho salmon CPUE, chin=chinook salmon CPUE, sthd=steelhead CPUE, chla=chlorophyll-*a* concentration (µg/l), zoop=ln(zooplankton biomass [mg/m^3]); t5m, t30m, t100m=temperature (C°) at 5, 30, and 100 m depth; s5m, s30m, s100m=salinity(psu) at 5, 30, 100 m depth.

41-44°N latitude Steelhead Trout

	am	sq	fi	po	other	totprey
am	1.000					
sq	0.099	1.000				
fi	-0.215	0.665	1.000			
po	-0.185	-0.210	-0.082	1.000		
other	0.031	-0.232	-0.671	-0.214	1.000	
totprey	0.069	0.981	0.723	-0.041	-0.319	1.000
chum	0.159	0.195	-0.334	-0.145	0.193	0.108
coho	0.296	-0.331	-0.266	-0.385	0.083	-0.400
sthd	0.614	-0.252	-0.290	-0.125	-0.030	-0.274
chla	-0.697	0.535	0.635	-0.030	-0.366	0.537
zoop	-0.754	0.029	0.344	-0.368	-0.054	0.043
t5m	0.177	0.608	0.477	-0.416	-0.187	0.560
t30m	0.150	0.171	0.028	-0.255	-0.013	0.120
t100m	0.528	-0.011	-0.140	-0.119	-0.301	-0.045
s5m	0.184	0.051	-0.177	-0.375	-0.030	-0.047
s30m	0.169	0.086	-0.131	-0.347	-0.053	-0.004
s100m	0.300	0.090	-0.171	-0.266	-0.044	0.015

45-51°N latitude Steelhead Trout

	am	sq	fi	po	other	totprey
am	1.000					
sq	-0.065	1.000				
fi	-0.237	0.669	1.000			
po	-0.057	-0.520	-0.164	1.000		
other	0.834	-0.155	-0.284	0.373	1.000	
totprey	-0.032	0.987	0.764	-0.452	-0.110	1.000
sock	-0.318	-0.136	-0.166	-0.143	-0.350	-0.183
chum	0.135	-0.356	-0.190	-0.031	-0.097	-0.348
pink	-0.313	-0.168	-0.185	0.214	-0.210	-0.202
coho	0.506	0.187	-0.092	-0.355	0.485	0.178
chin	-0.367	-0.478	-0.463	0.404	0.011	-0.516
sthd	-0.305	0.389	-0.211	-0.262	-0.205	0.267
chla	0.178	0.241	-0.493	-0.387	0.055	0.141
zoop	-0.554	0.092	0.466	0.022	-0.457	0.117
t5m	0.136	-0.636	-0.258	0.537	0.361	-0.573
t30m	0.122	-0.531	-0.283	0.147	0.102	-0.507
t100m	0.386	-0.415	-0.196	0.311	0.602	-0.352
s5m	0.672	0.424	0.390	-0.349	0.433	0.487
s30m	0.576	0.388	0.389	-0.328	0.420	0.452
s100m	0.573	0.206	-0.089	-0.640	0.135	0.175

Table 1.16. Listing of biological characteristics of steelhead trout containing the maximum SCI (prey weight/body weight*100) observed in each weight or age class in the central North Pacific Ocean. Fage=freshwater age, Oage=ocean age, PW= prey weight (g), am=amphipods, sq=squid, fi=fish, po=polychaetes, other=euphausiids, copepods, pteropods, polychaetes, floating debris, andunidentified material. X=freshwater age could not be determined because the scale was regenerated or otherwise unreadable, im=immature, and mt=maturing.

Steelhead

Weight (g) or Ocean age class	N	Maximum SCI	Fork Length (mm)	Body Weight (g)	Sex	Gonad Weight (g)	Fage	Oage	Maturity	PW	AM	SQ	FI	Other
Central North Pacific Ocean (40-51° N latitude)														
1000-1499	23	2.3	526	1450	m	2	2	1	im	33	5	80	15	0
1500-1999	73	6.3	522	1540	f	2	2	1	im	97	2	96	0	2
2000-2499	25	3.0	576	2100	f	15	1	1	mt	62	0	65	35	0
2500-2999	13	4.2	668	2720	f	12	x	x	im	115	0	90	10	0
3000-3999	28	4.4	730	3450	m	6	x	x	mt	153	0	100	0	0
≥4000	26	3.9	763	5000	m	5	x	2	mt	194	0	90	10	0
Age .1	103	6.3	522	1540	f	2	2	1	im	97	2	96	0	2
Age .2	58	3.9	763	5000	m	5	x	2	mt	194	0	90	10	0
Age .3	11	3.5	732	4250	m	2	3	3	mt	149	0	100	0	0

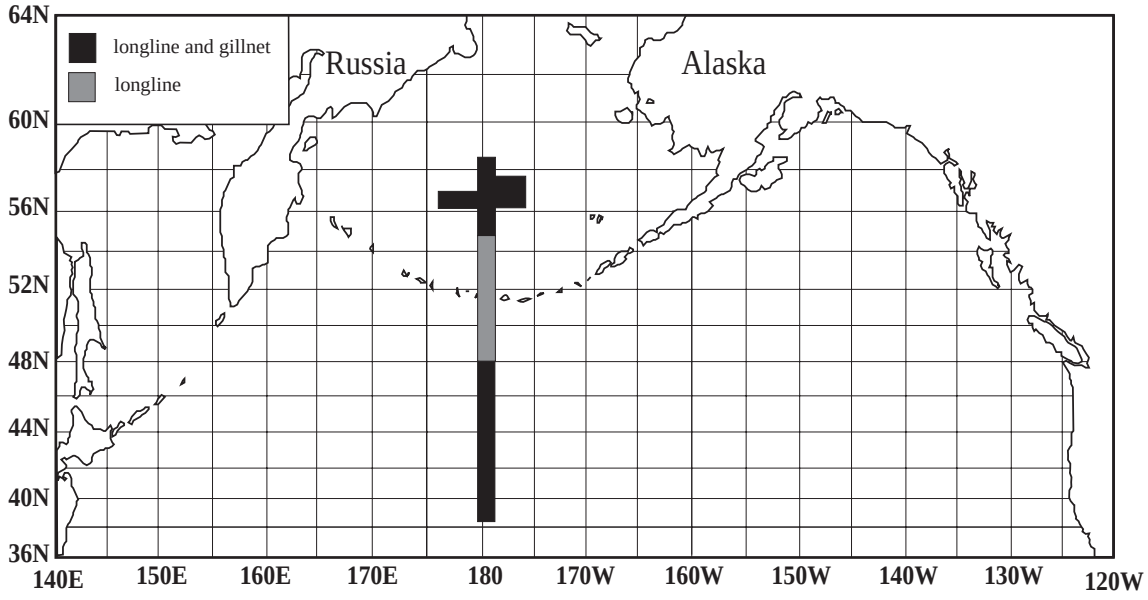

Figure 1.1. Survey area in the central North Pacific and the central Bering Sea where longline and gillnet fishing operations were conducted by the *Wakatake maru* in June and July, 1991-2000.

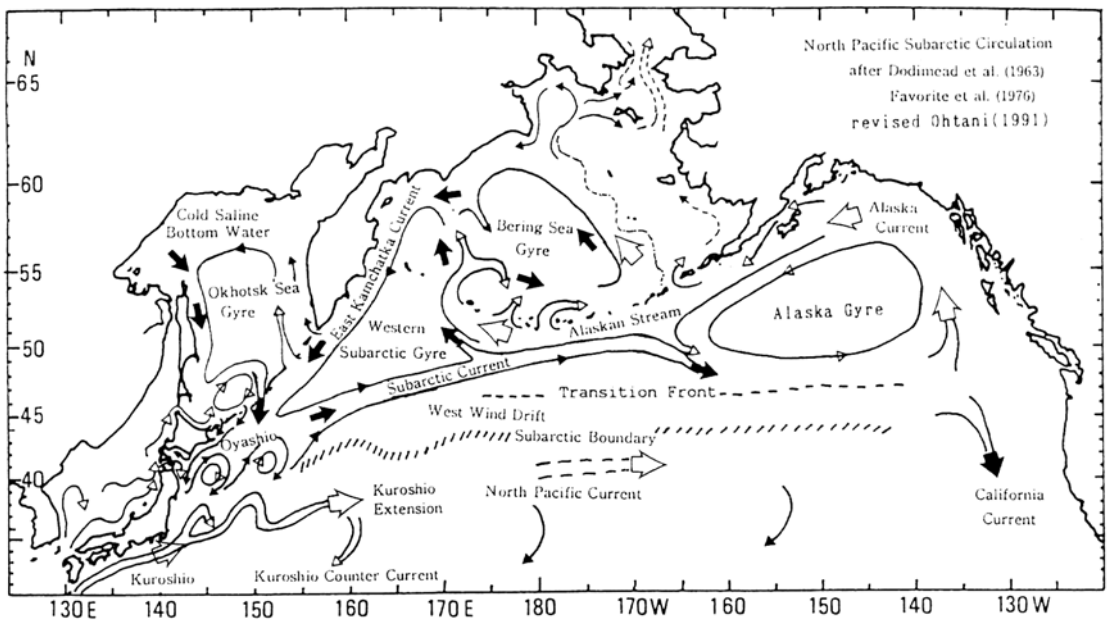

Figure 1.2. Subarctic North Pacific Ocean surface circulation patterns as revised and drawn by Ohtani (1994).

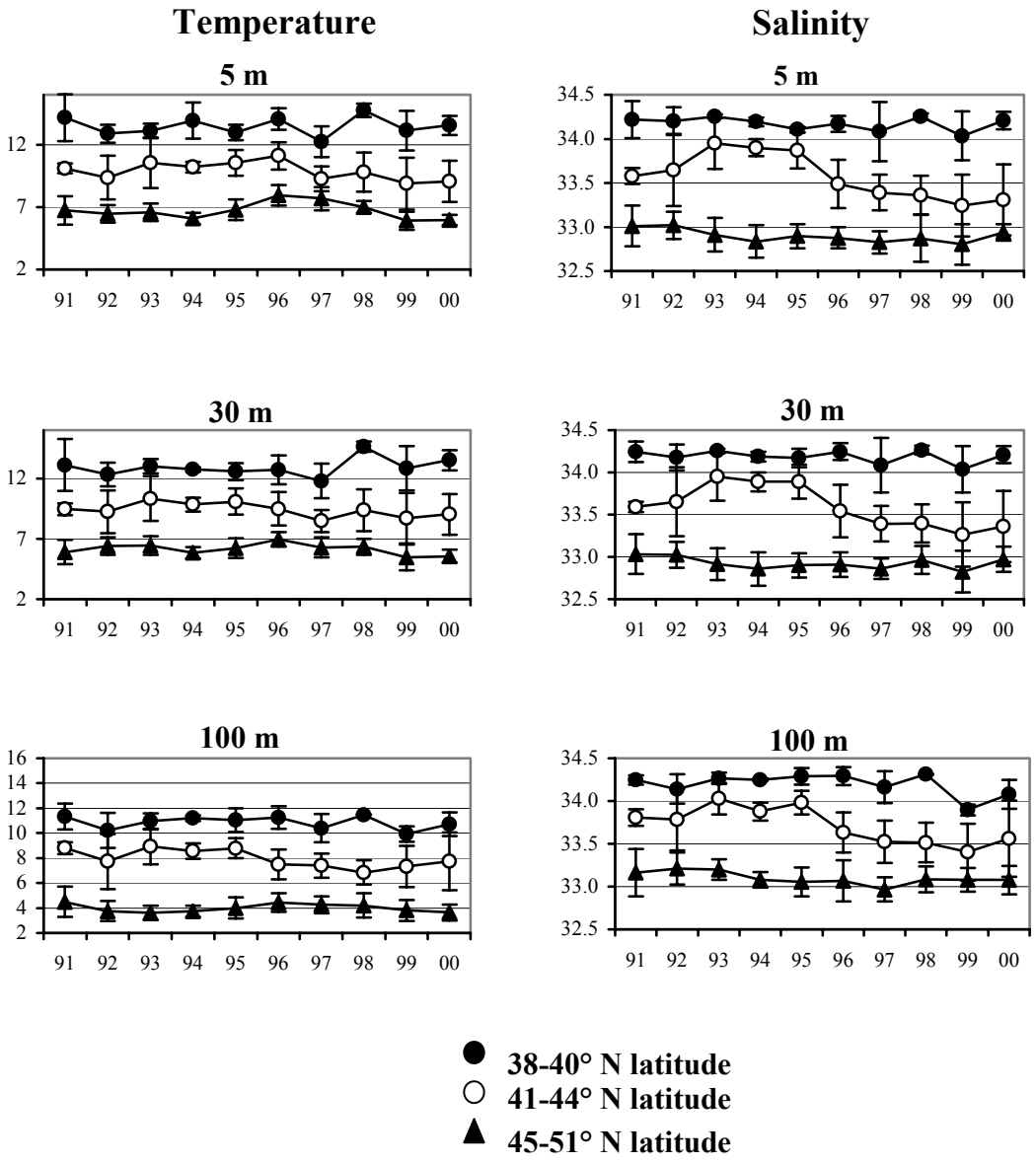

Figure 1.3. Seawater temperature (°C, left) and salinity (psu, right) at three depths along the transect at 180° longitude in the central North Pacific Ocean, 1991-2000. Plotted values are the mean and ± one standard deviation, grouped by latitude. Latitudes correspond to oceanographic domains: Transition Zone (38-40°); Transition Domain (41-44°); Subarctic Current, Ridge Domain, and Alaska Current (45-51°).

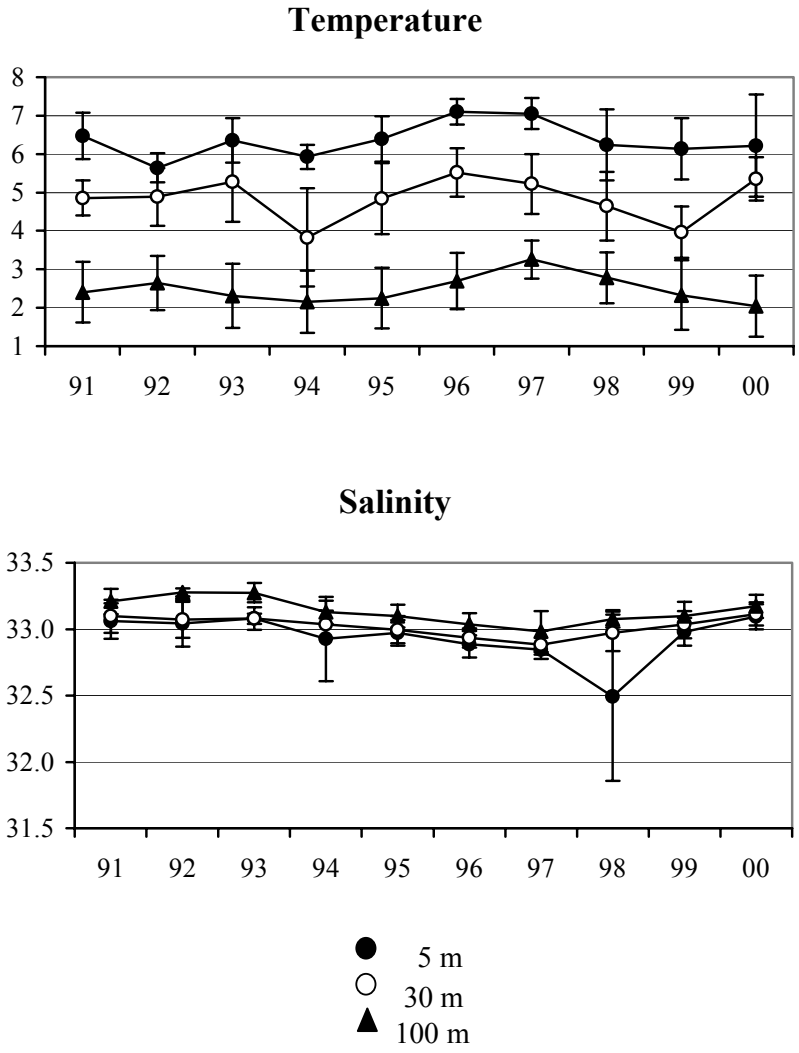

Figure 1.4. Seawater temperature (°C, upper panel) and salinity (psu, lower panel) at three depths along the transect at 180° longitude in the central Bering Sea, 1991-2000. Plotted values are the mean and ± one standard deviation for data collected from 52-58°N latitude.

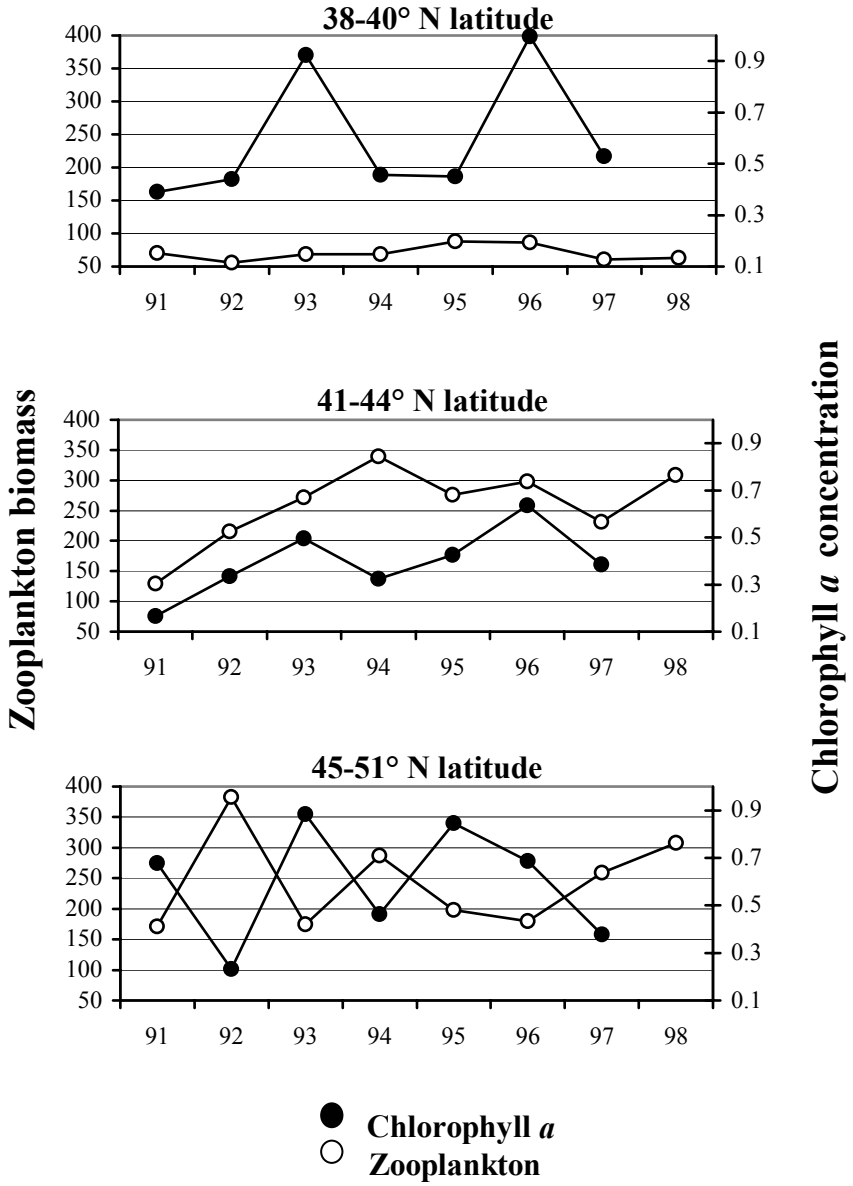

Figure 1.5. Comparison of mean chlorophyll *a* concentration (µg/l; 1991-1997) and mean zooplankton biomass (mg/m3; 1991-1998) grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean. Chlorophyll *a* data from Shiomoto et al. (1999), and zooplankton data from Tadokoro et al. (1995), Nagasawa and Ishida (1997, 1998), and Nagasawa and Ueno (1999).

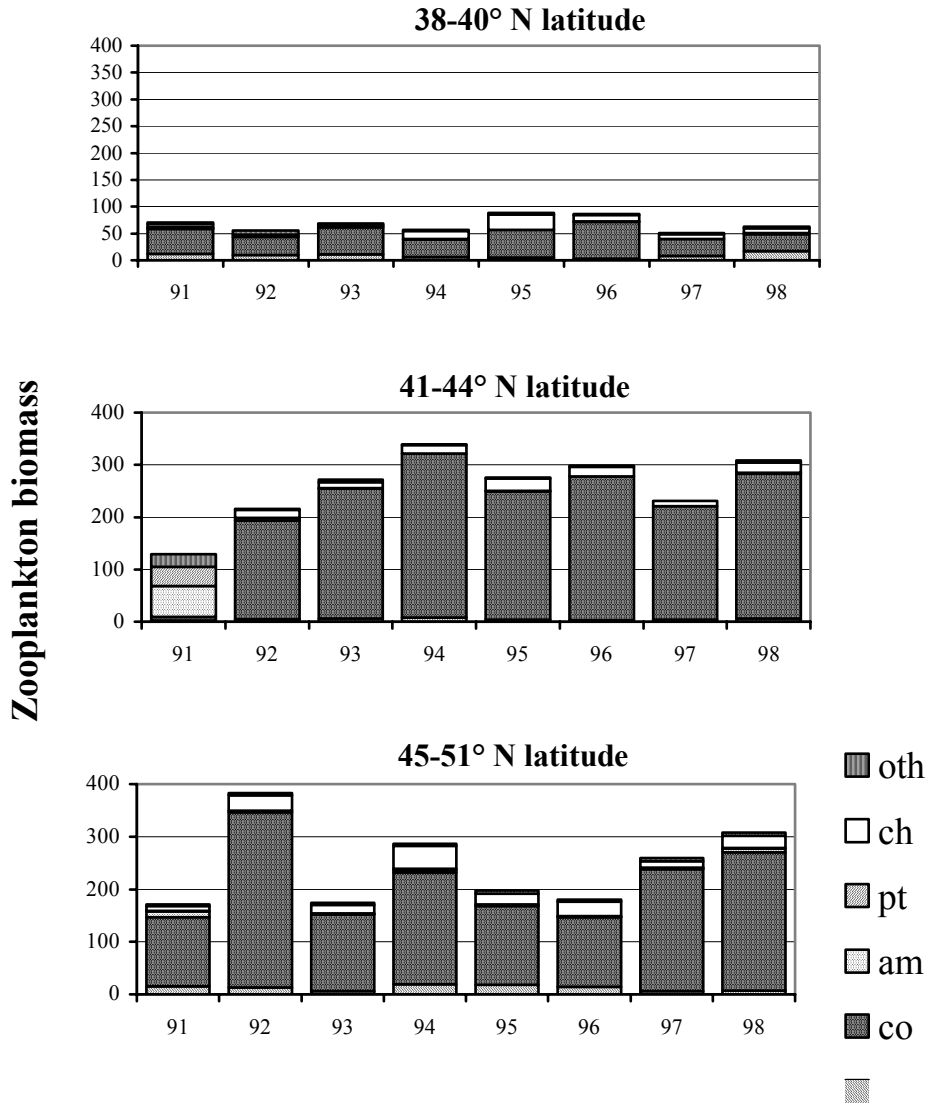

Figure 1.6 Mean biomass (mg/m3) of taxonomic categories of zooplankton for samples collected along a transect at 180° longitude in the central North Pacific Ocean, grouped by latitude, 1991-2000. Eu=euphausiids, co=copepods, am=amphipods, pt=pteropods, ch=chaetognaths, oth=others (ostracods, mysids, decapods, and polychaetes). Jellyfish (medusae, ctenopores, and salps) are not included in these categories. Data from Tadokoro et al. (1995), Nagasawa and Ishida (1997, 1998), and Nagasawa and Ueno (1999).

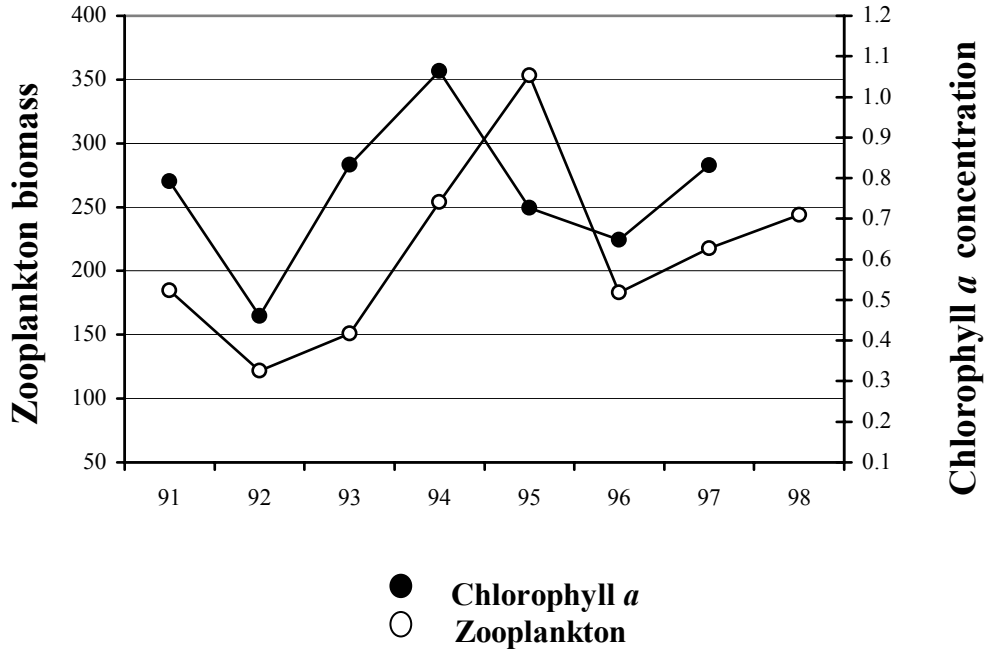

Figure 1.7. Comparison of mean chlorophyll-*a* concentration (µg/l; 1991-1997) and mean zooplankton biomass (mg/m3; 1991-1998) along a transect at 180° longitude in the central Bering Sea. Chlorophyll-*a* data from Shiomoto et al. (1999), and zooplankton data from Tadokoro et al. (1995), Nagasawa and Ishida (1997, 1998), and Nagasawa and Ueno (1999).

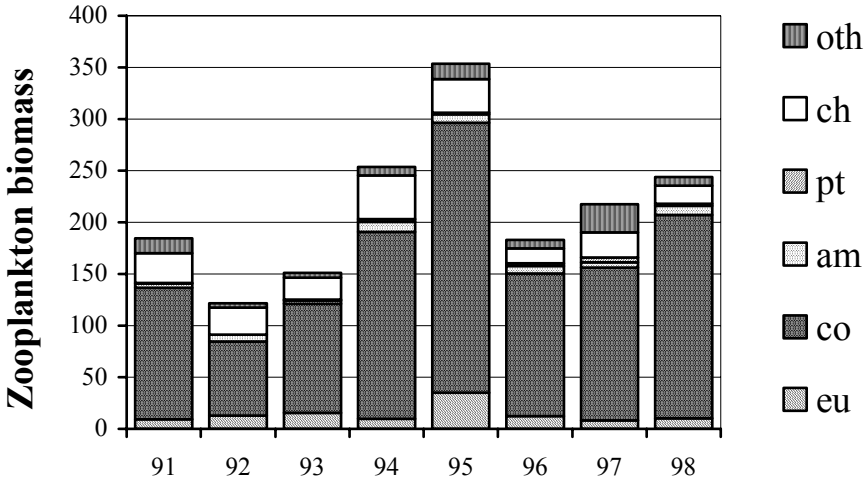

Figure 1.8 Mean biomass (mg/m3) of taxonomic categories of zooplankton for samples collected along a transect at 180° longitude in the central Bering Sea, 1991-1998. Eu=euphausiids, co=copepods, am=amphipods, pt=pteropods, ch=chaetognaths, oth=others (ostracods, mysids, decapods, and polychaetes). Jellyfish (medusae, ctenophores, and salps) are not included in these categories. Data from Tadokoro et al. (1995), Nagasawa and Ishida (1997, 1998), and Nagasawa and Ueno (1999).

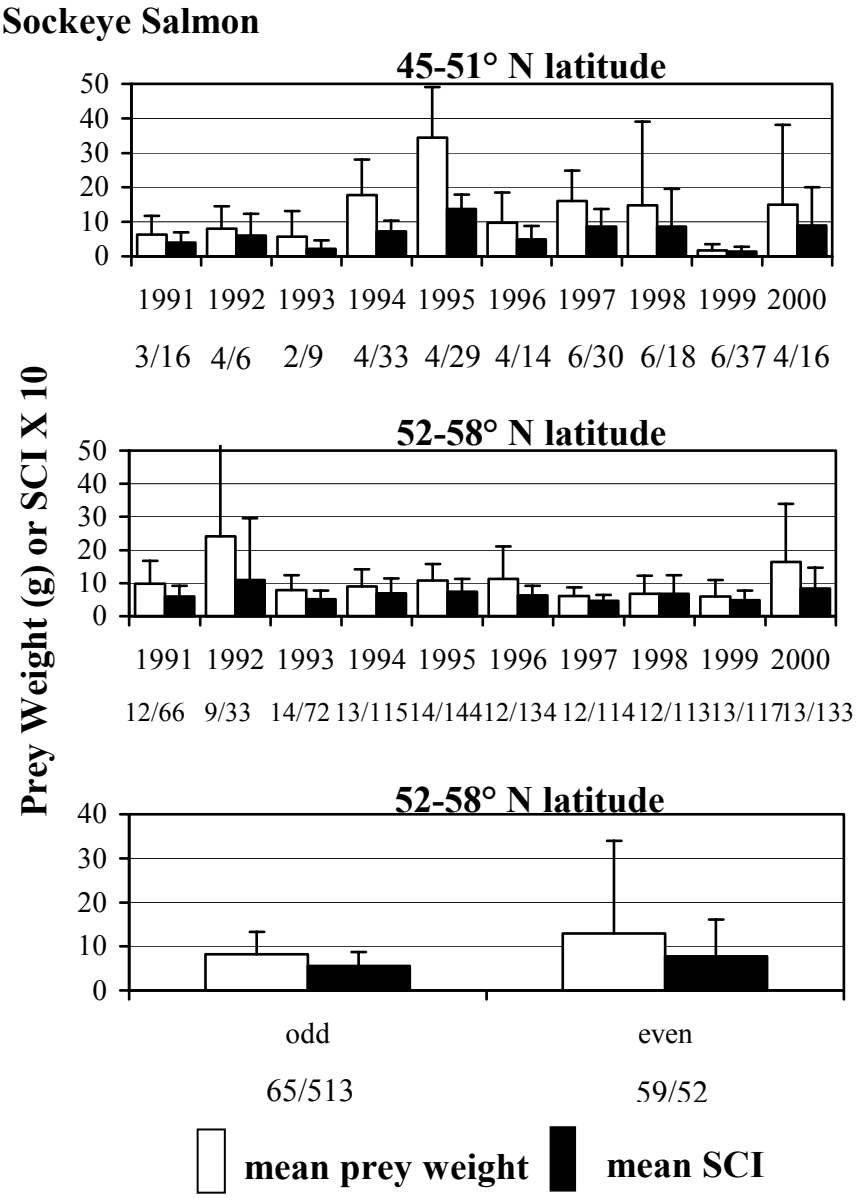

Figure 1.9. Comparison of mean prey weight (g) and SCI (prey weight/body weight*100) sampled annually from sockeye salmon, grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (45-51°N) and the central Bering Sea (52-58°N), 1991-2000. Bottom panel shows data combined odd- and even-numbered years. Error bars indicate one standard deviation. Values below the x-axis: the number of stations sampled followed by a slash mark and the total number of sockeye salmon stomachs sampled.

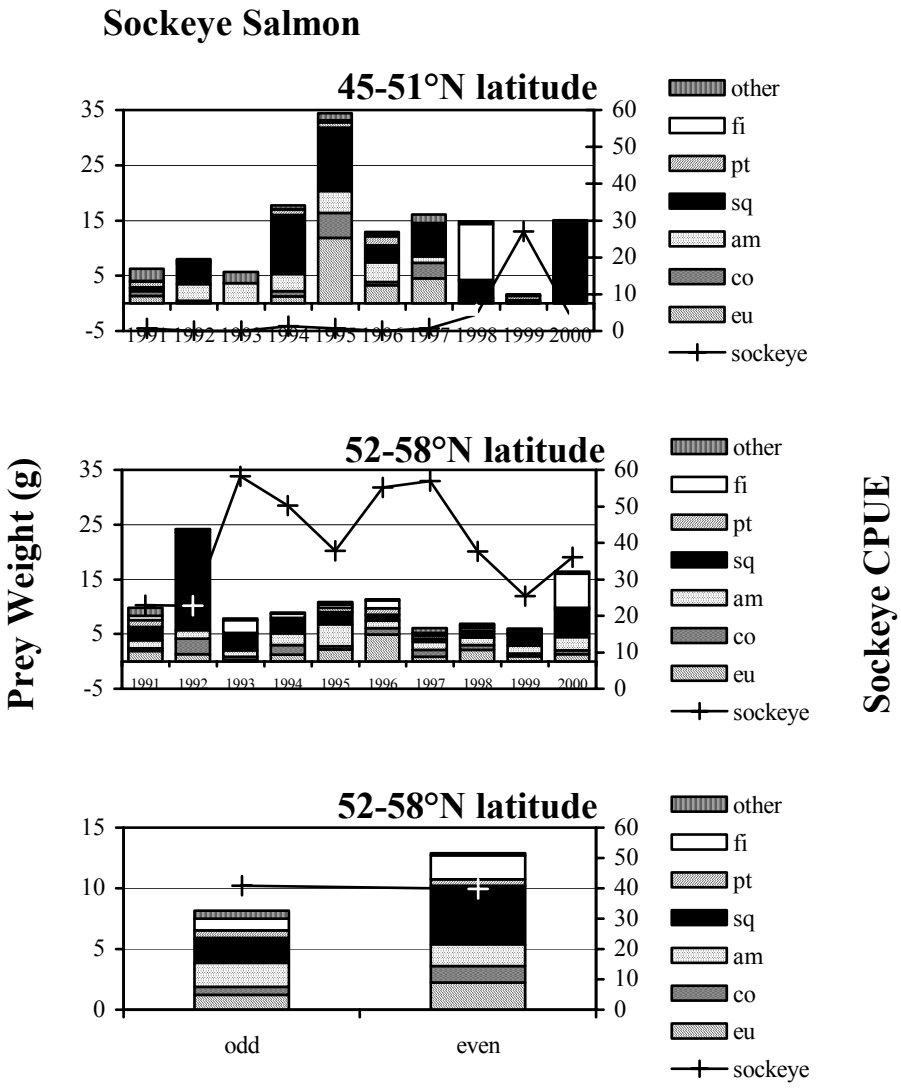

Figure 1.10. Mean weight (g) of each prey category observed in stomach contents of sockeye salmon (primary y-axis) and mean sockeye CPUE (secondary y-axis) grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (45-51°N) and the central Bering Sea (52-58°), 1991-2000. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, and other=crab larvae, polychaetes, chaetognaths, gelationous zooplankton (medusae, ctenophores, and salps), and unidentified material. CPUE is the number of salmon caught in 30 tans of research-mesh gillnet.

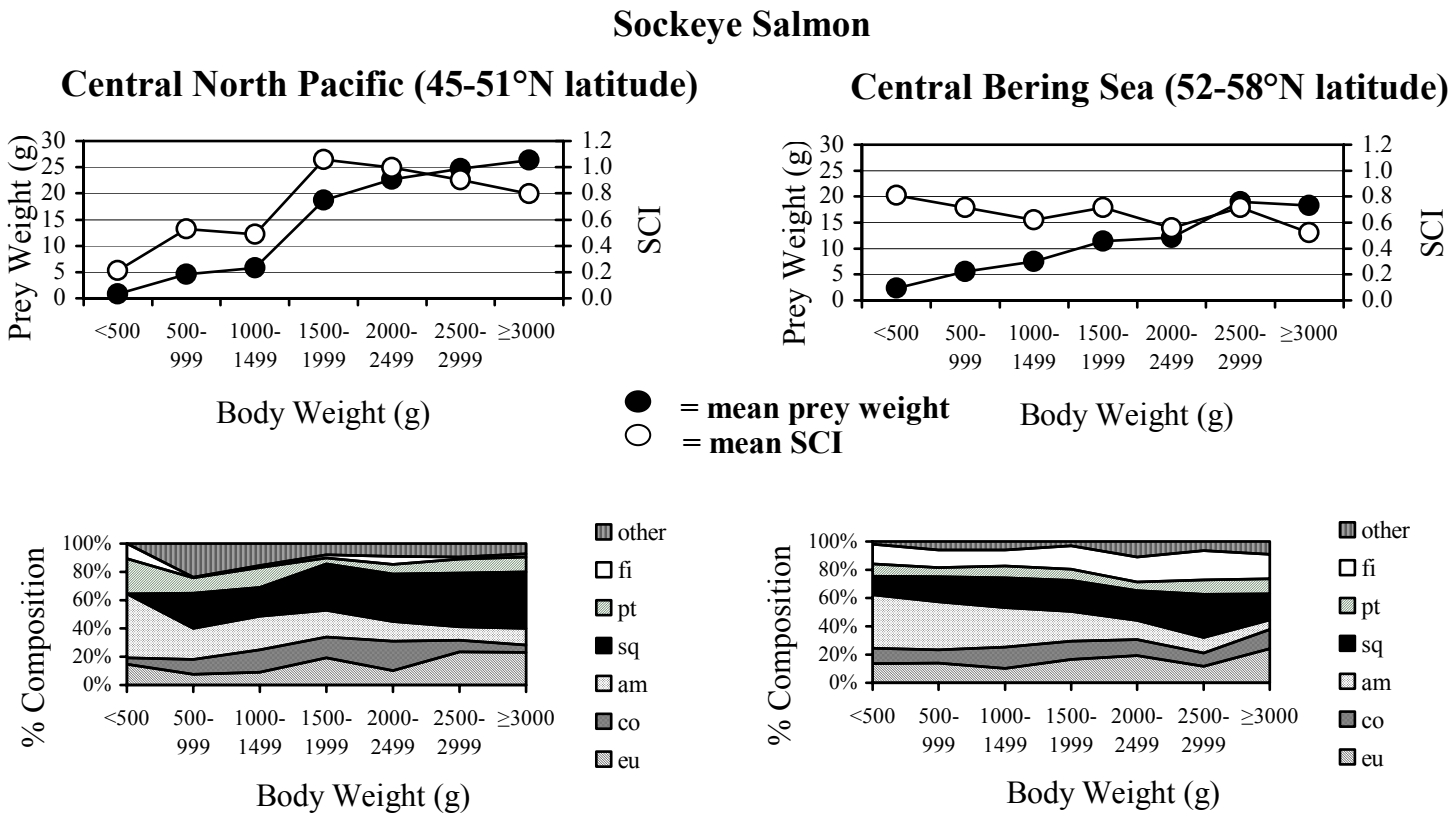

Fig. 1.11. Comparison of mean prey weight, SCI (prey weight/body weight*100), and percent composition of major prey categories collected from stomach samples of sockeye salmon caught in the central North Pacific (left panels) and the central Bering Sea (right panels), grouped by body weight of sockeye salmon. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, and other=crab larvae, polychaetes, chaetognaths, gelatinous zooplankton (medusae, ctenophores and salps), and unidentified material.

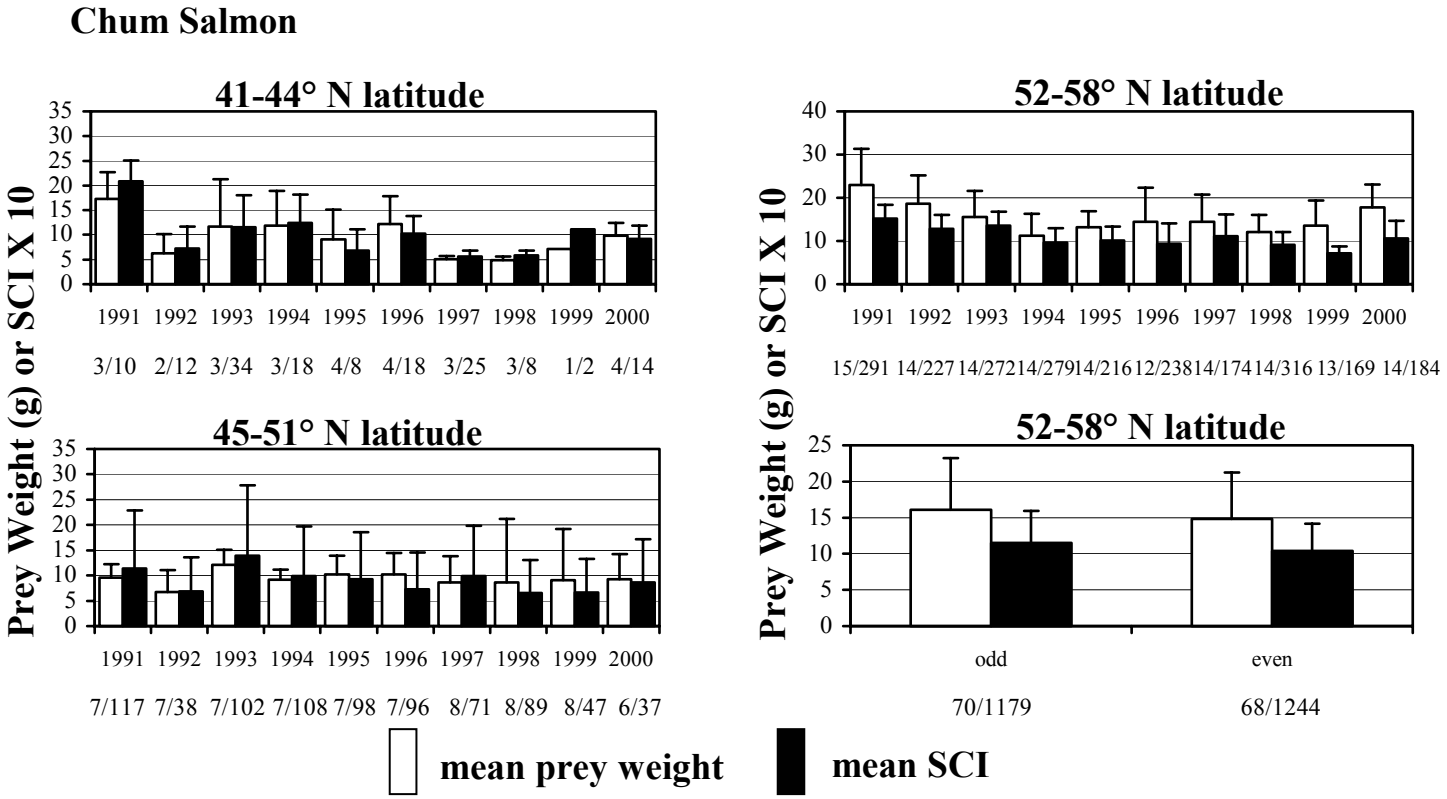

Figure 1.12. Comparison of mean prey weight (g) and SCI (prey weight/body weight*100) sampled annually from chum salmon, grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (41-44° N, 45-51°N) and the central Bering Sea (52-58°N), 1991-2000. Lower right panel shows data combined for odd- and even-numbered years. Error bars indicate one standard deviation. Values below the x-axis: the number of stations sampled followed by a slash mark and the total number of chum salmon stomachs sampled.

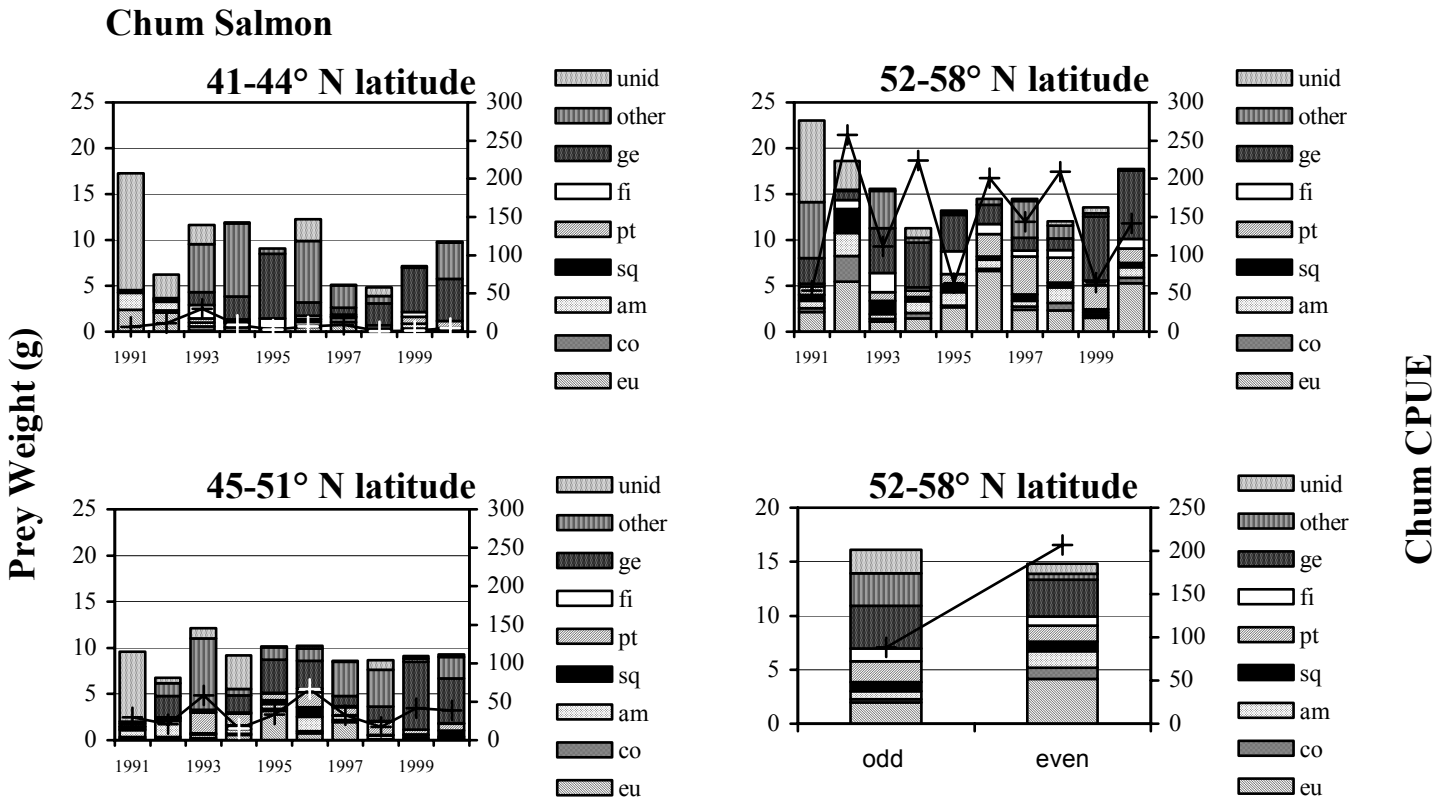

Figure 1.13. Mean weight (g) of each prey category observed in stomach contents of chum salmon (primary y-axis) and mean chum CPUE (secondary y-axis) grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (41-44°N, 45-51°N) and the central Bering Sea (52-58°N), 1991-2000. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, ge=gelatinous zooplankton (medusae, ctenophores, and salps), other=crab larvae, polychaetes, chaetognaths, and appendicularia, and unid=unidentified material. CPUE is the number of chum salmon caught in 30 tans of research-mesh gillnet.

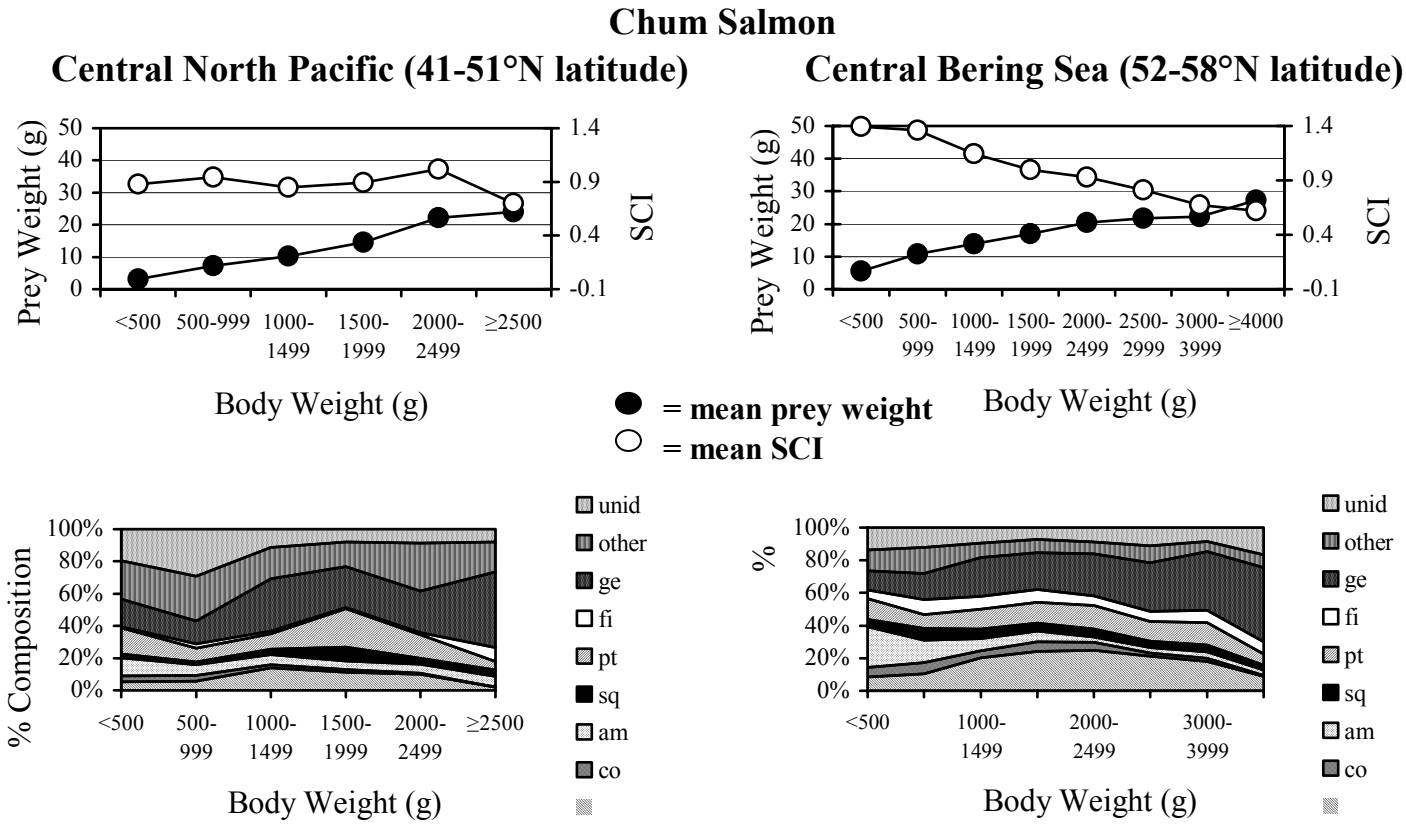

Fig. 1.14. Comparison of mean prey weight, SCI (prey weight/body weight*100), and percent composition of major prey categories collected from stomach samples of chum salmon caught in the central North Pacific (left panels) and the central Bering Sea (right panels), grouped by body weight of chum salmon. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, ge=gelatinous zooplankton (medusae, ctenophores, and salps), other=crab larvae, polychaetes, chaetognaths, appendicularia, mysides, ostracods, and heteropods, and unid=unidentified material.

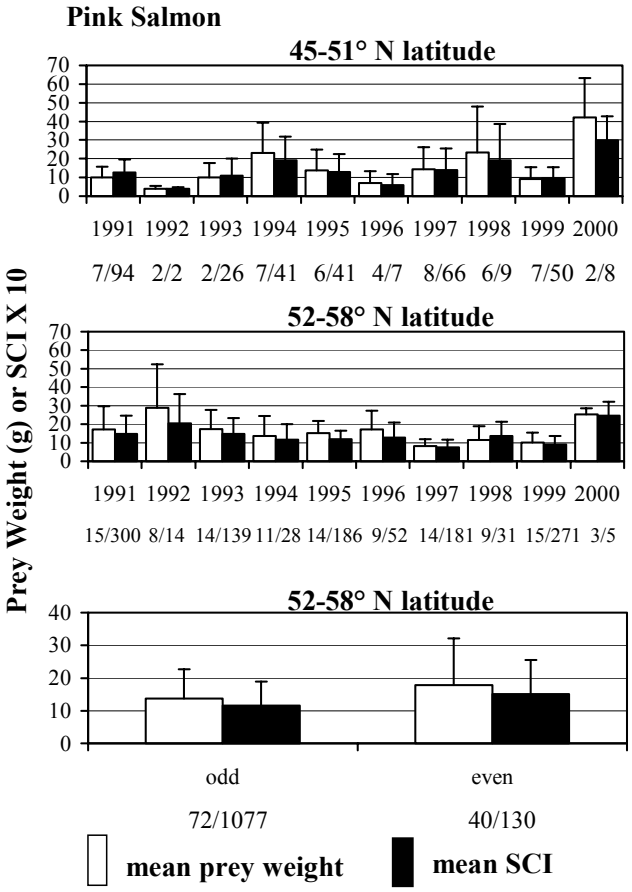

Figure 1.15. Comparison of mean prey weight (g) and SCI (prey weight/body weight*100) sampled annually from pink salmon, grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (45-51°N) and the central Bering Sea (52-58°N), 1991-2000. Bottom panel shows data combined for odd- and even-numbered years. Error bars indicate one standard deviation. Values below the x-axis: the number of stations sampled followed by a slash mark and the total number of pink salmon stomachs sampled.

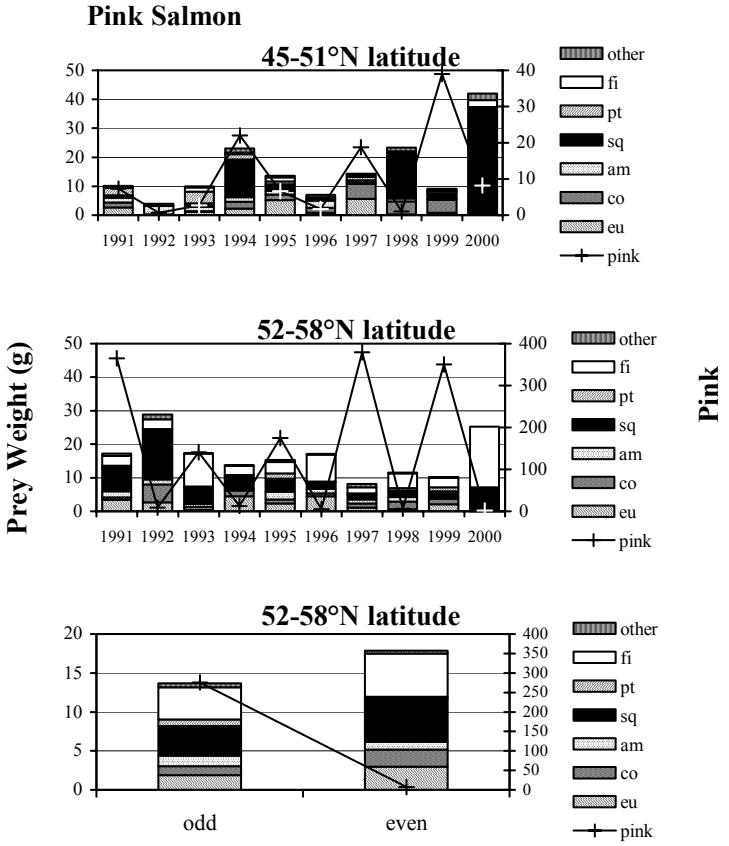

Figure 1.16. Mean weight (g) of each prey category observed in stomach contents of pink salmon (primary y-axis) and mean pink CPUE (secondary y-axis) grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (45-51°N) and the central Bering Sea (52-58°), 1991-2000. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, and other=crab larvae, polychaetes, chaetognaths, gelatinous zooplankton (medusae, ctenophores, and salps), and unidentified material. CPUE is the number of salmon caught in 30 tans of research-mesh gillnet.

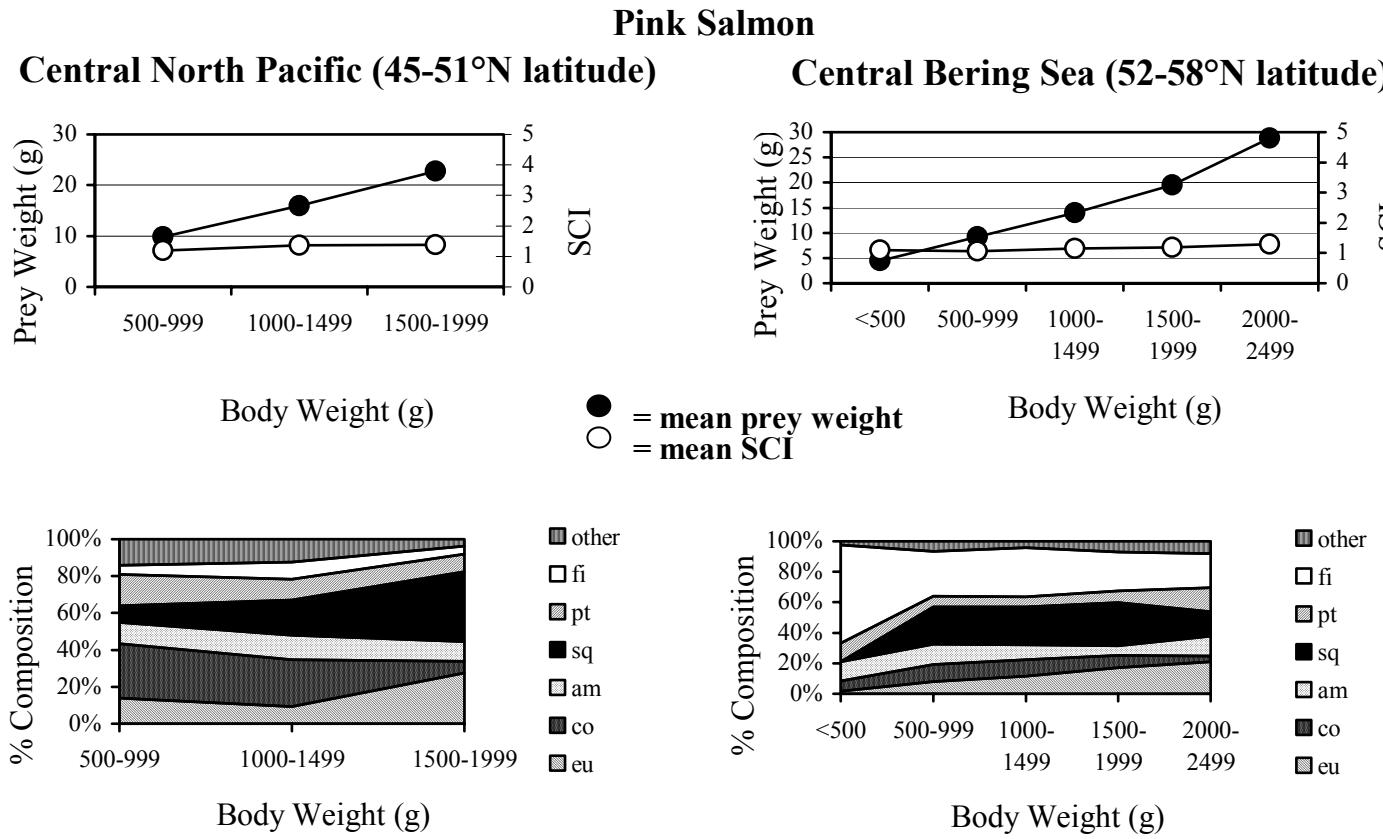

Fig. 1.17. Comparison of mean prey weight, SCI (prey weight/body weight*100), and percent composition of major prey categories collected from stomach samples of pink salmon caught in the central North Pacific (left panels) and the central Bering Sea (right panels), grouped by body weight of pink salmon. Eu=euphausiids, co=copepods, am=amphipods, sq=squid, pt=pteropods, fi=fish, and other=crab larvae, polychaetes, chaetognaths, gelatinous zooplankton (medusae, ctenophores and salps), and unidentified material.

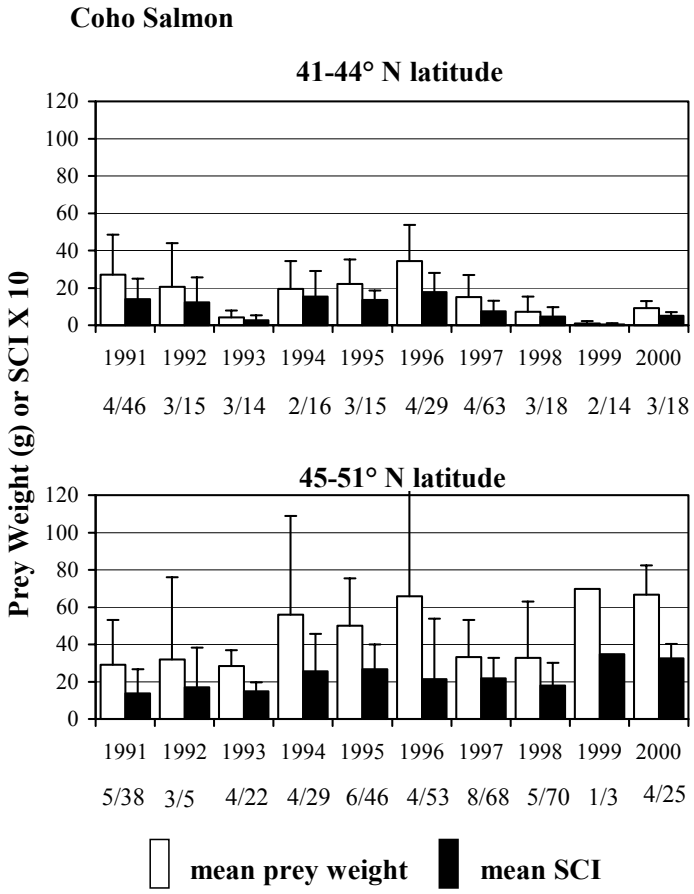

Figure 1.18. Comparison of mean prey weight (g) and SCI (prey weight/body weight*100) sampled annually from coho salmon, grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean, 1991-2000. Error bars indicate one standard deviation. Values below the x-axis: the number of stations sampled followed by a slash mark and the total number of coho salmon stomachs sampled.

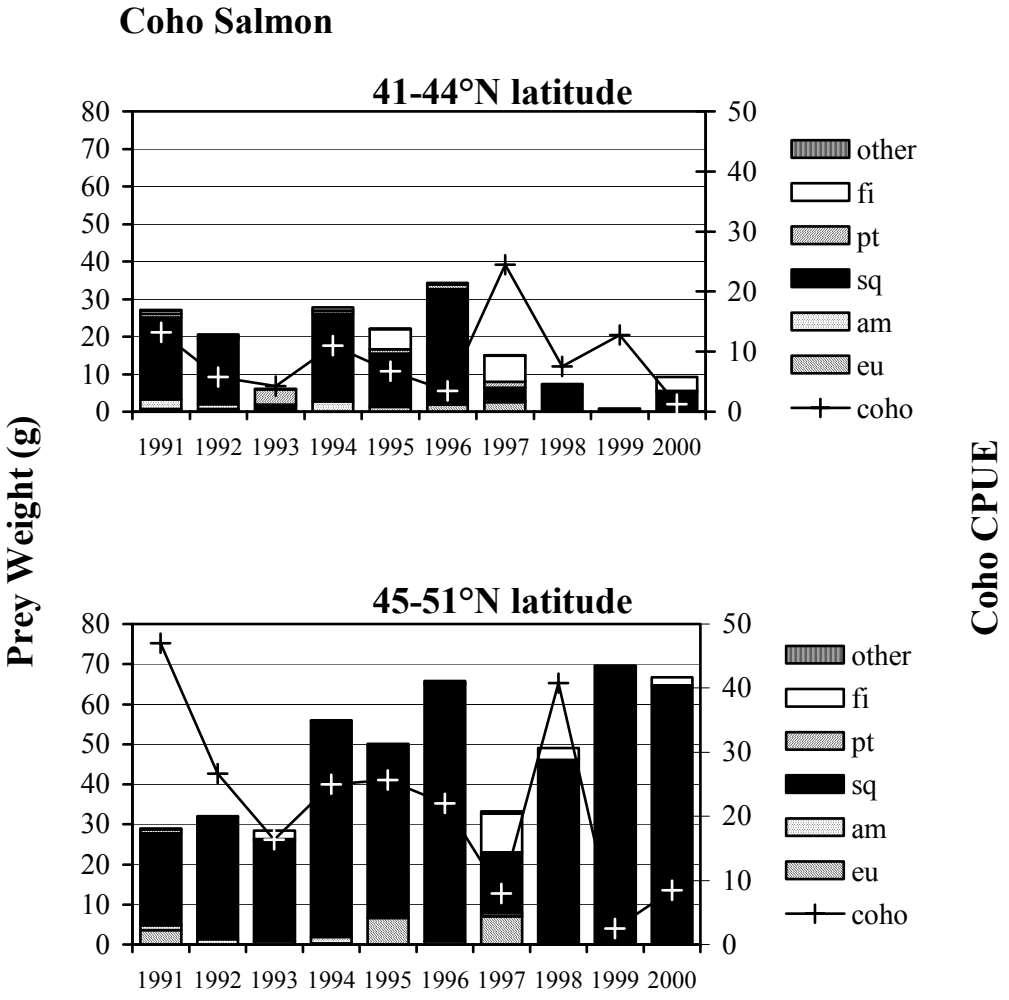

Figure 1.19. Mean weight (g) of each prey category observed in stomach contents of coho salmon (primary y-axis) and mean coho CPUE (secondary y-axis) grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean, 1991-2000. Eu=euphausiids, am=amphipods, sq=squid, pt=pteropods, fi=fish, and other=copepods, chaetognaths, gelatinous zooplankton (medusae, ctenopohores, and salps), and unidentified material. CPUE is the number of salmon caught in 30 tans of research-mesh gillnet.

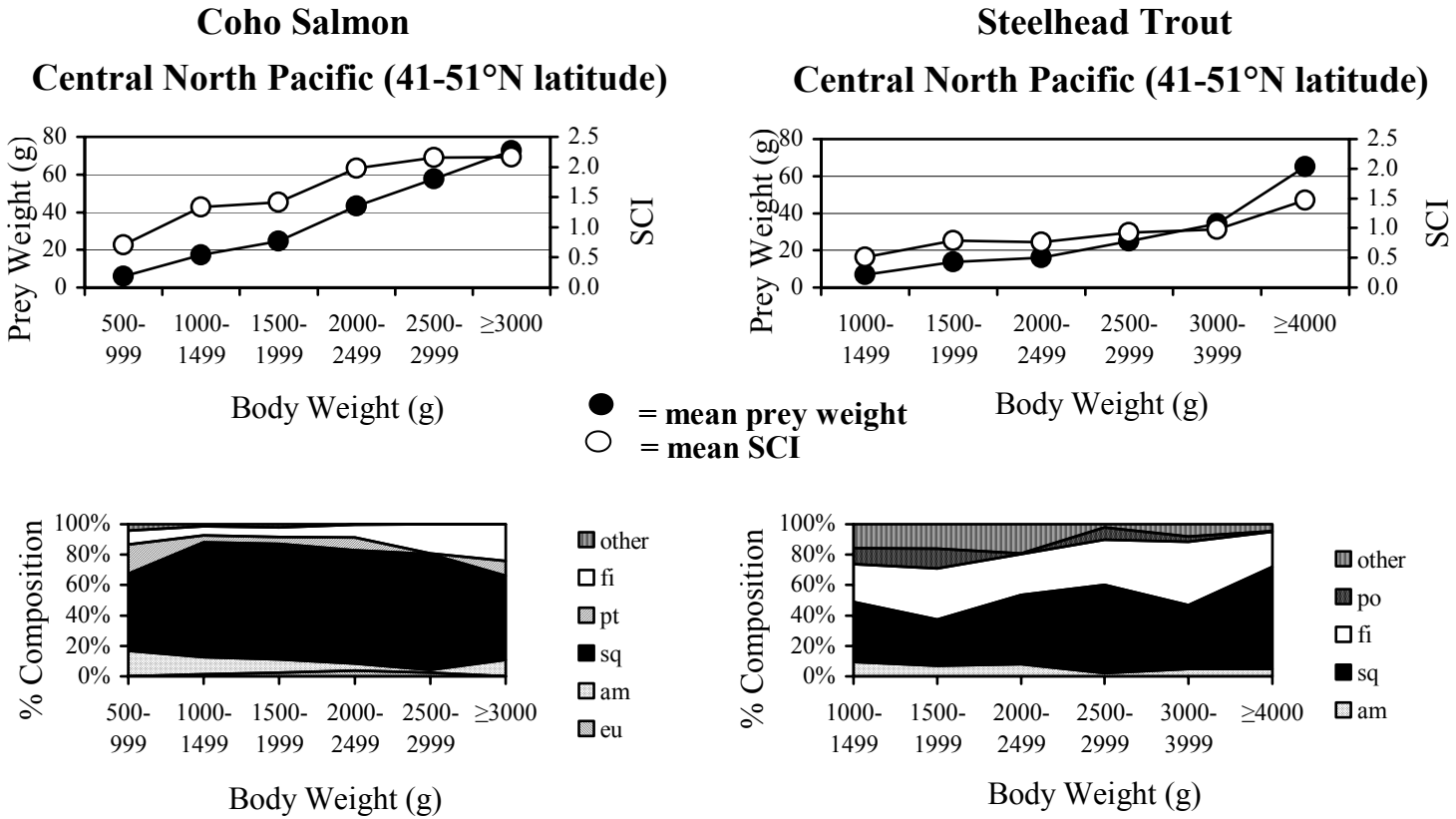

Fig. 1.20. Comparison of mean prey weight, SCI (prey weight/body weight*100), and percent composition of major prey categories collected from stomach samples of coho salmon (left panels) and steelhead trout (right panels) caught in the central North Pacific Ocean, grouped by coho or steelhead body weight. Eu=euphausiids, am=amphipods, sq=squid, pt=pteropods, fi=fish, po=polychaetes, and other (coho)=copepods, chaetognaths, gelatinous zooplankton (medusae, ctenophores and salps), and unidentified material. Other (steelhead)=euphausiids, copepods, pteropods, floating debris, and unidentified material.

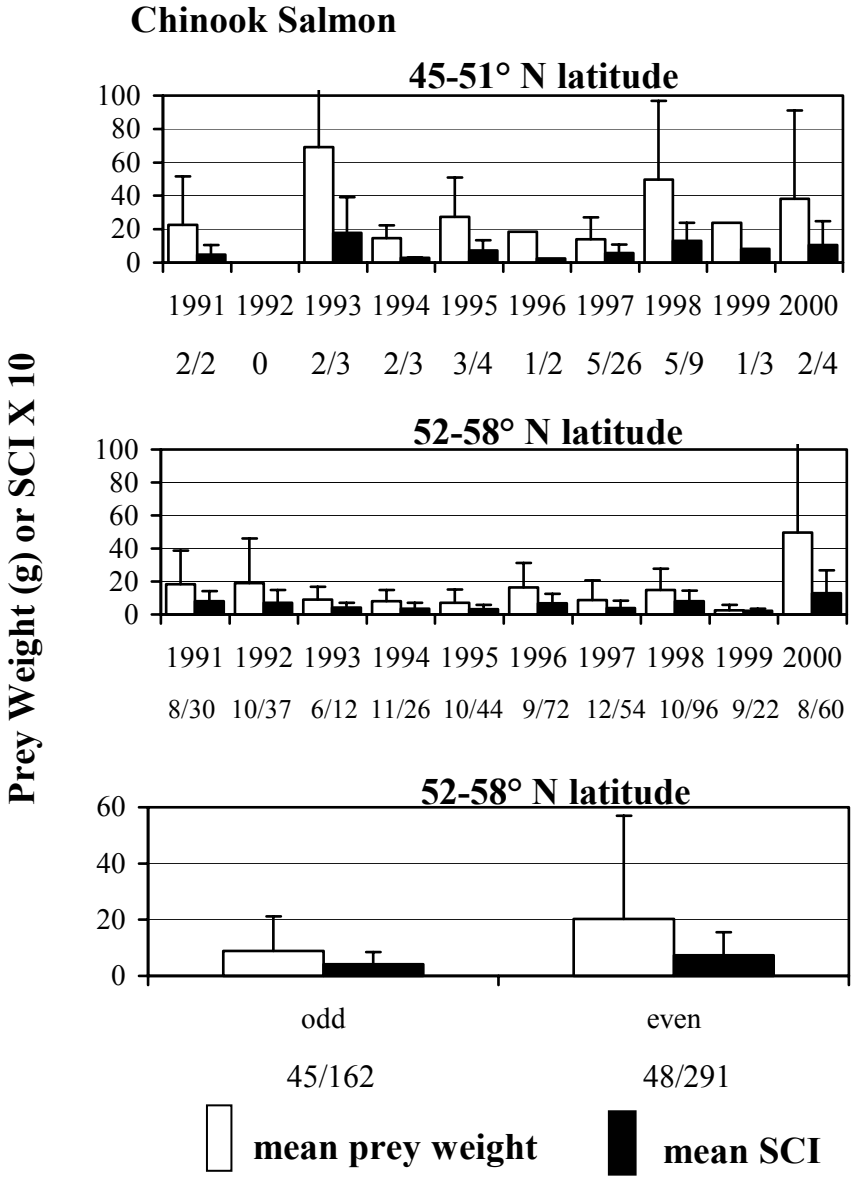

Figure 1.21. Comparison of mean prey weight (g) and SCI (prey weight/body weight*100) sampled annually from chinook salmon, grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (45-51°N) and the central Bering Sea (52-58°N), 1991-2000. Bottom panel shows data combined for odd- and even-numbered years. Error bars indicate one standard deviation. Values below the x-axis: the number of stations sampled followed by a slash mark and the total number of chinook salmon stomachs sampled.

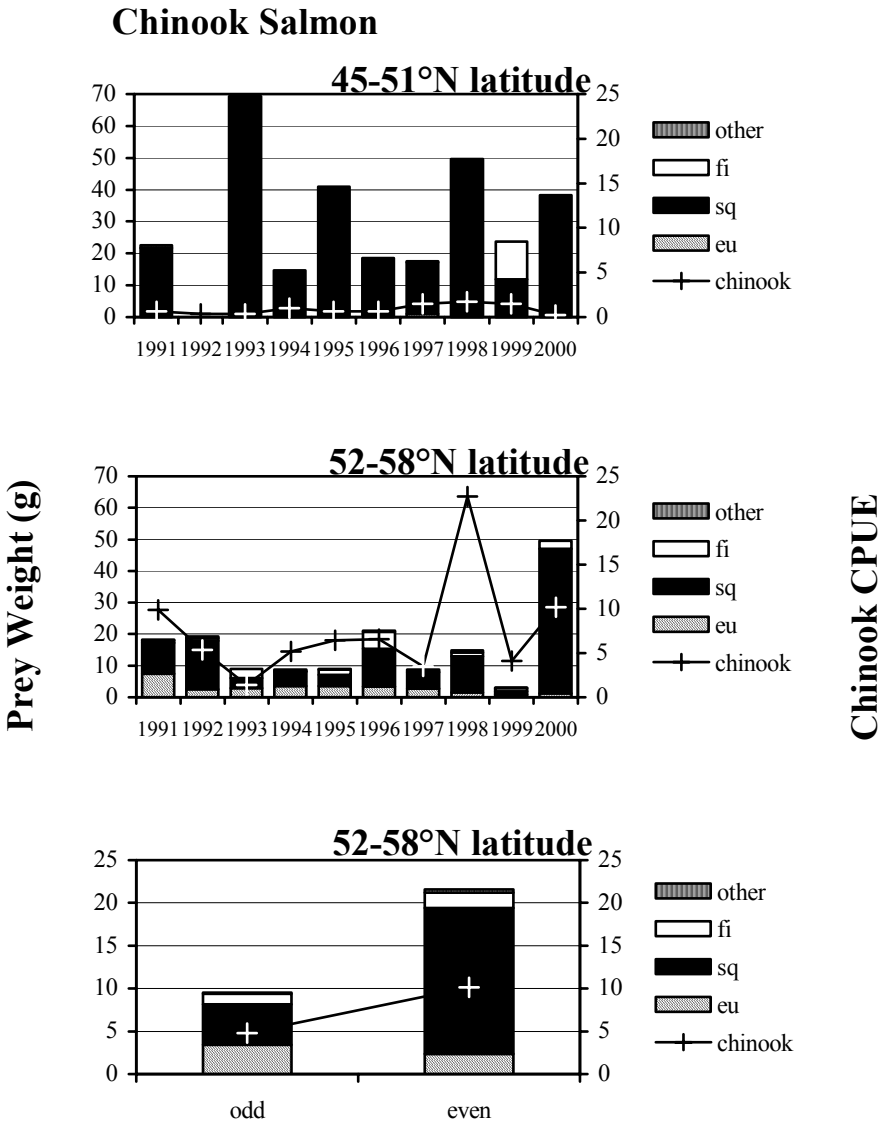

Figure 1.22. Mean weight (g) of each prey category observed in stomach contents of chinook salmon (primary y-axis) and mean chinook CPUE (secondary y-axis), grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean (45-51°N) and the central Bering Sea (52-58°), 1991-2000. Eu=euphausiids, sq=squid, fi=fish, and other=copepods, amphipods, crab larvae, pteropods, chaetognaths, gelatinous zooplankton (medusae, ctenophores, and salps), and unidentified material. CPUE is the number of salmon caught in 30 tans of research-mesh gillnet.

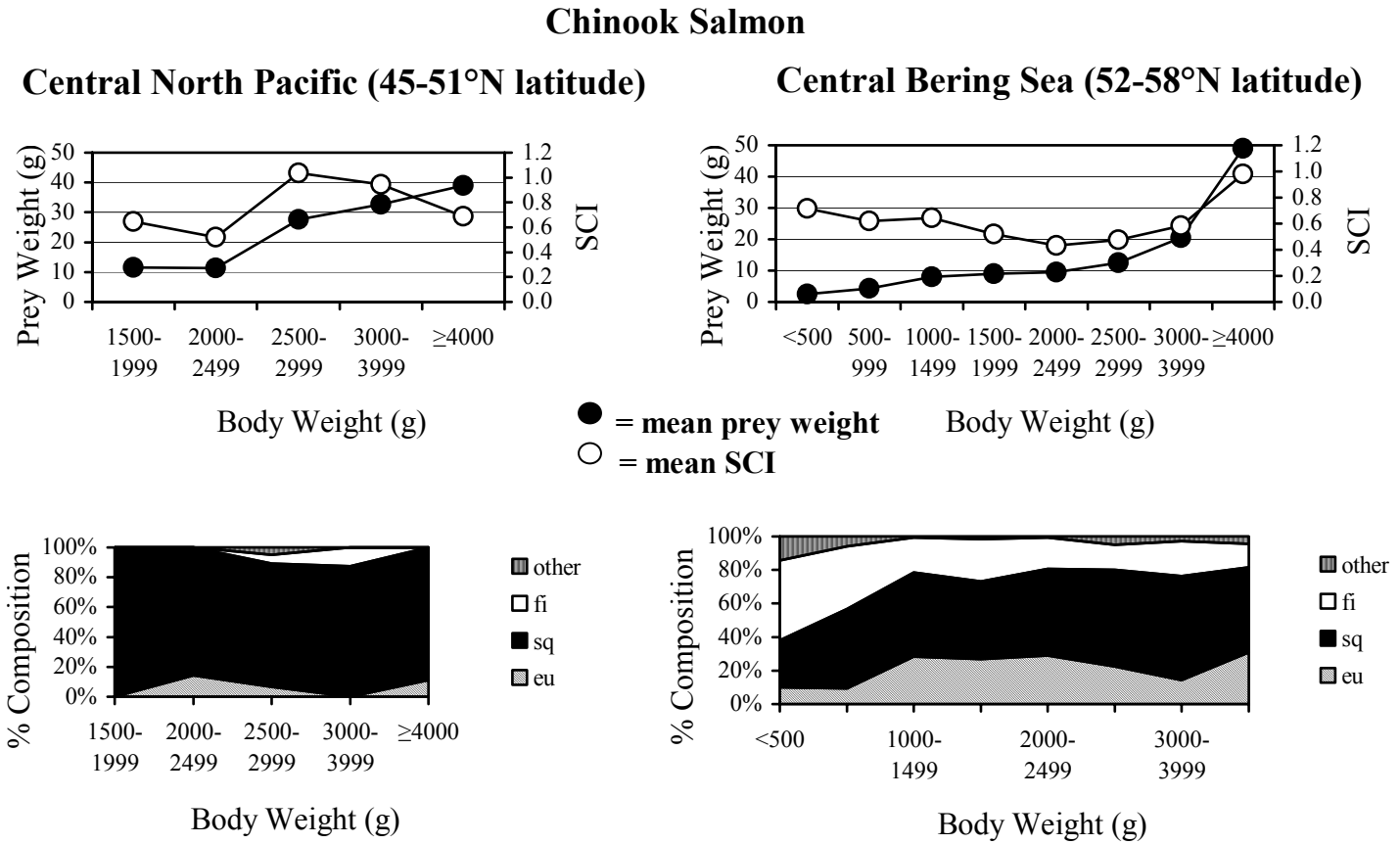

Fig. 1.23. Comparison of mean prey weight, SCI (prey weight/body weight*100), and percent composition of major prey categories collected from stomach samples of chinook salmon caught in the central North Pacific (left panels) and the central Bering Sea (right panels), grouped by body weight of chinook salmon. Eu=euphausiids, sq=squid, fi=fish, other=copepods, amphipods, crab larvae, pteropods, chaetognaths, gelatinous zooplankton (medusae, ctenophores and salps), and unidentified material.

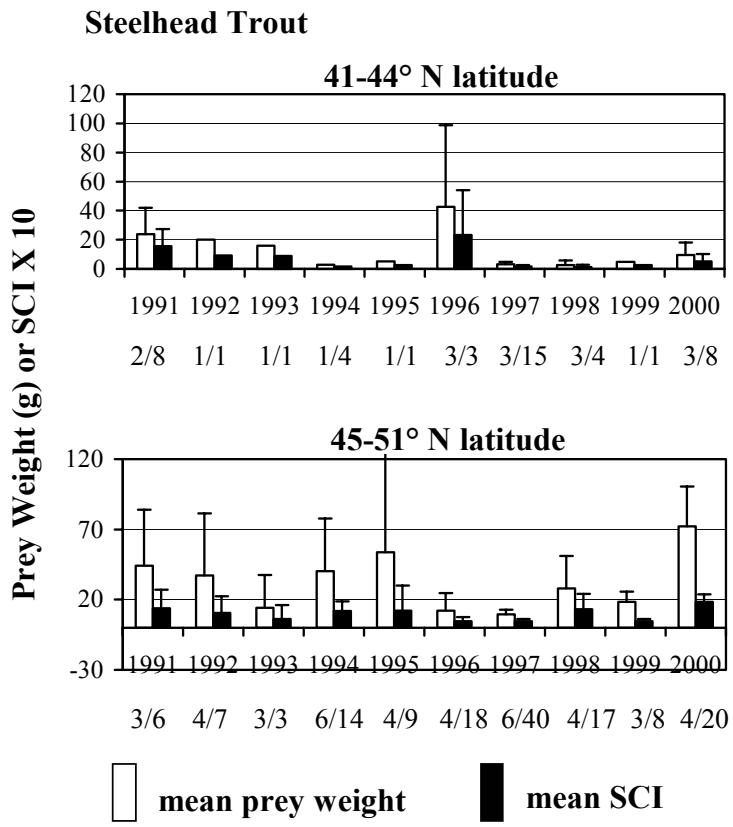

Figure 1.24. Comparison of mean prey weight (g) and SCI (prey weight/body weight*100) sampled annually from steelhead trout, grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean, 1991-2000. Error bars indicate one standard deviation. Values below the x-axis: the number of stations sampled followed by a slash mark and the total number of steelhead trout stomachs sampled.

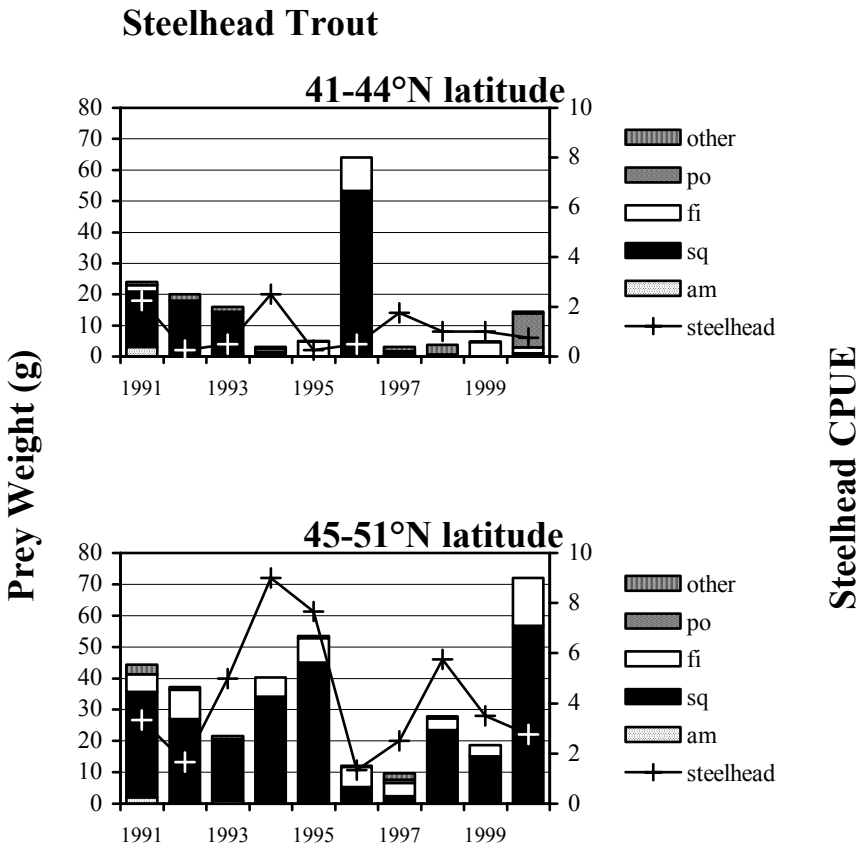

Figure 1.25. Mean weight (g) of each prey category observed in stomach contents of steelhead trout (primary y-axis) and mean steelhead CPUE (secondary y-axis) grouped by latitude along a transect at 180° longitude in the central North Pacific Ocean, 1991-2000. Am=amphipods, sq=squid, fi=fish, po=polychaetes, other=euphausiids, copepods, pteropods, floating debris, and unidentied material. CPUE is the number of trout caught in 30 tans of research-mesh gillnet.

Chapter 2.0. Diel catches and food habits of sockeye, pink, and chum salmon in the central Bering Sea in summer

2.1. Introduction

Previous studies of diel changes in immature and maturing salmon food habits in the North Pacific Ocean have included trawling and serial sampling with gillnets in the waters off eastern Kamchatka (Machidori 1968; Ueno et al. 1969; Chuchukalo et al. 1995; Volkov et al. 1995a,b), the Okhotsk Sea (Shimazaki and Mishima 1969; Gorbatenko and Chuchukalo 1989; Chuchukalo et al. 1995; Volkov et al. 1995a, b), Gulf of Alaska (Pearcy et al. 1984), and the Bering Sea (Azuma 1992; Chuchukalo et al. 1995; Radchenko and Chigirinsky 1995). Machidori (1968) reported on experiments using gillnets and concluded that feeding activity of immature and maturing sockeye and chum salmon was greater during the day than at night and that light was necessary for salmon feeding. Other studies using shorter sampling intervals have concluded that sockeye salmon feed most actively in late afternoon until midnight (Ueno et al. 1969), and that by morning, sockeye salmon stomachs are empty (Chuchukalo et al. 1995). Alternatively, sockeye salmon have been reported to feed after sunset and continue through the night (Pearcy et al. 1984; Azuma 1992). Results for maturing pink salmon were more varied. Experiments indicated intensive feeding immediately after sunrise and sunset (Shimazaki and Mishima 1969), in the evening and shortly after midnight (Ueno et al. 1969), and a somewhat less active feeding period in the mid-morning (Pearcy et al. 1984). In coastal areas off western Kamchatka, maturing pink salmon fed actively during the day and ceased feeding at night (Gorbatenko and Chuchukalo 1989). From earlier studies of immature and maturing chum salmon, active feeding periods have been found immediately after sunrise and sunset (Shimazaki and Mishima 1969; Ueno et al. 1969), and alternatively, chum salmon have been observed to show little or no diel variation in their feeding activity (Pearcy et al. 1984; Azuma 1992). Inconsistency in results suggest that feeding periods of immature and maturing salmon at sea may change in response to several factors including day length, physical characteristics of the water column, and prey availability. For salmon food habit surveys to be useful in estimating prey

consumption, sampling must be conducted to reflect the shifts that might occur in diel feeding activities (Davis et al. 1998).

In odd-numbered years, maturing pink salmon are abundant in the central Bering Sea in the summer. This may contribute to shifts in chum distribution and may also indirectly influence the growth of chum salmon (Azumaya and Ishida 2000). Increased consumption of gelatinous zooplankton by chum salmon has been observed when pink salmon abundance was high in the central Bering Sea (see Chapter 1.0; Tadokoro et al. 1996). However, no previous study in the central Bering Sea has reported salmon food habits over a 24-hour period for sockeye, pink, and chum salmon. In this study, I conducted gillnet operations throughout the diel period and examined changes in catch, stomach content weight, and prey composition of sockeye, chum, and pink salmon.

2.2. Methods

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

Gillnet operations were conducted between 57°33′N, 178°41′W and 57°27′N, 178°20′W in the central Bering Sea (Nagasawa et al. 1997a). Eight operations were conducted in a 24-hour period starting at 0600 hrs and ending at 0500 hrs the following day using a surface gillnet (length=950 m, fishing depth=0-6 m, mesh size=115 mm; Table 2.1). The gillnet set locations were 7.0 to 9.2 km apart. Setting the gillnet required five to six minutes after which it was allowed to soak for two hours. The duration of gillnet retrieval ranged from 16 to 23 min. Although vertical movements of high-seas salmon are different between daylight and dark periods, they spend a portion of time at the surface during all periods of the day (Walker et al. 1999, 2000b), thereby making it possible for gillnets to catch salmon at the surface throughout the diel cycle. To catch salmon from a narrow range of sizes, a single mesh size was used. The mesh size (115

mm) was selected because it is efficient at catching immature and maturing salmon in the Bering Sea in summer.

After each gillnet retrieval, the catch was sorted by species and counted. If the number of individuals per species was greater than 50, the catch was subsampled due to logistical constraints (Table 2.1). Fork length, and body and gonad weight were measured and a scale sample was collected. The salmon stomachs were removed, frozen individually, and sent back to the laboratory for examination. After thawing, the stomach samples were weighed before and after removal of the stomach contents, and the weight of the contents obtained by subtraction. An index of stomach content (SCI; see Chapter 1.0) was calculated by standardizing prey weight as a function of body weight (prey weight/body weight*100), and differences in day and night catches and mean weight of stomach contents compared using the chi-square and one-way ANOVA.

Prey composition of stomach contents was separated into twelve prey categories (euphausiids, copepods, amphipods, crab larvae, squid, pteropods, fish, polychaetes, chaetognaths, and gelatinous zooplankton, other, and unidentified). I visually estimated the percent volume of each category following the method of Pearcy et al. (1984; see Chapter 1.0). Combining less important groups reduced the number of prey categories to eight and the weight of these major prey categories was estimated by multiplying the percent volume of each group by the total measured stomach content weight, assuming the density of all prey was similar.

2.3. Results

In the following sections I briefly summarize the environmental conditions and salmon catches that occurred over the diel period. Following these sections, I summarize the results of stomach content analysis by salmon species for the eight time periods.

2.3.1 Environmental conditions

The duration of daylight was approximately 17 hours when these operations were conducted (sunrise = 0311 hrs, sunset time = 2047 hrs). The moon phase was waxing to

the first quarter and a continuous 100% cloud cover persisted during the diel period, which included drizzling rain between 2300 and 0200 hrs. Hourly sea surface temperatures ranged from 8.3° to 8.6°C (Table 2.1). Maximum seawater temperature was located at the surface and temperatures decreased to 4.48°C at 100 m (Fig. 2.1). The temperature minimum was located at 80 m (3.36°C), and a shallow thermocline was located between 10 and 20 m, where temperatures decreased rapidly from 7.90° to 5.11°C and continued to decrease to 4.23°C at 30 m.

2.3.2. Diel salmon catch

A total of 1,753 salmon was caught in eight gillnet operations (Table 2.1). Pink salmon were the most abundant salmon in the catch (81%), followed by sockeye (13%), chum (5%), chinook (1%), and coho salmon (<1%). Sockeye, chum, and pink salmon were caught in all eight time periods, but coho (n = 1) and chinook (n = 8) salmon were caught only in the morning and afternoon. A relatively large catch of pink, chum, and sockeye salmon was obtained immediately after sunrise (0300-0500 hrs; Table 2.1). The smallest catch of sockeye salmon occurred in late afternoon (1500-1700 hrs). Sockeye salmon catches were not independent of day and nighttime gillnet sets (χ^2; p=0.03; df=1). More sockeye salmon were caught during daylight and less during the night than would have been expected if catches had been equal in every time period. Pink salmon catches were also small in the afternoon and early evening (1500-2000 hrs) but increased dramatically immediately after sunset, and remained at a high level until after sunrise (0300-0500 hrs). Pink salmon catches were not independent of day and night gillnet sets, as less salmon were caught during the day and more at night than would have been expected with equal catches in each time period (χ^2; p=<0.001; df=1). Chum catches increased shortly after sunrise (0300-0500 hrs) and after noon (1200-1400 hrs), however, catches were independent of daytime or nighttime gillnet sets (χ^2; p=0.19; df=1). Unfortunately, chum salmon catches were relatively small throughout the sampling period.

2.3.3. Salmon biological characteristics

Sockeye salmon in gillnet catches were 62% male, predominantly immature (92%), and mostly ocean age .2 (94%) fish (Table 2.2). A few ocean age .3 sockeye salmon were caught and there was no catch of ocean age .1 fish. The mean fork length of sockeye salmon was significantly different among time periods (ANOVA; $p< 0.001$; df=7). Although the Tukey multiple comparisons test did not detect which means were significantly different from one another ($p>0.50$), the greatest difference in mean fork length was in the time interval before and after sunset (1500-1700 hrs, mean=517 mm; 1800-2000 hrs, mean=470 mm). However, a comparison of fork lengths of sockeye salmon caught in daytime versus nighttime sets was not significantly different ($p=0.66$; df=1). Two-thirds (66%) of the pink salmon were males, and all the fish were maturing ocean age .1 (Table 2.2). There was no significant difference in mean fork lengths among time periods ($p=0.27$; df= 7), or between catches in daytime and nighttime gillnet sets ($p=0.21$; df=1). Half (51%) of the chum salmon were female and approximately half (53%) were maturing (Table 2.2). Ocean age .2, .3, and .4 chum salmon were caught, however ocean age .3 was the most abundant age group (61%). The mean fork lengths of chum salmon caught during each time period was not significantly different, either among time periods ($p=0.68$; df=7), or between daytime and nighttime catches ($p=0.81$; df=1). The food habits data were not stratified for predator size because the fork length among individuals of each salmon species was similar between day and nighttime periods.

2.3.4. Diel food habits of sockeye salmon

Stomach contents of sockeye salmon illustrated a diel pattern where prey weight was significantly greater among fish caught during the night than during the day (ANOVA; $p<0.001$; df=1; Fig. 2.2). There was one peak in stomach contents weight immediately after sunset (2100-2300 hrs; Table 2.3). The proportion of stomach contents in a fresh state of digestion was higher during the sunset to early morning hours than in the mid- to late afternoon. Mean stomach content weight decreased from mid-to late afternoon and was at a minimum before sunset (1800-2000 hrs). Few empty stomachs (n=3) were collected from sockeye salmon, regardless of the sampling period, indicating that sockeye were able to find prey during all periods. Sockeye salmon shifted from

nighttime consumption of euphausiids and copepods to daytime consumption of fish and crab larvae (Table 2.3).

2.3.5. Diel food habits of pink salmon

Stomach fullness of pink salmon caught during the day and night were not significantly different from one another (ANOVA; p=0.07; df=1; Fig. 2.2), although there was increased feeding activity after noon (1200-1400) and immediately after sunset (2100-2300 hrs; Table 2.4). Empty stomachs (n=22) were collected from midnight until late afternoon and the number of empty stomachs collected from pink salmon was higher than for sockeye and chum salmon. Pink salmon fed on fish during all time periods. During the night, euphausiids and copepods were important prey and during the day fish and crab larvae were the predominant prey.

2.3.6. Diel food habits of chum salmon

There was no significant difference between day and nighttime stomach fullness of chum salmon (ANOVA; p=0.90; df=1; Fig. 2.2). In every sampling period, chum had more prey in their stomachs than either pink or sockeye salmon (Table 2.5). Unlike diel feeding of sockeye and pink salmon, chum salmon had an increase of stomach content weight in the middle to late afternoon (1500-1700), when fish were a major component of the diet, and showed no peak in prey weight after sunset. The afternoon period when stomach content weight was at a maximum (1500-1700) was also the time interval with the smallest sample size (n=5) and, therefore, may not have been representative. Chum salmon, like sockeye salmon, had few empty stomachs (n=2), suggesting chum salmon were able to find food at all times of the day. The proportion of fish in chum stomachs increased dramatically from noon until 1700 hrs and then decreased through the night. Similar to feeding patterns of sockeye and pink salmon, crustaceans, particularly euphausiids, were a major component of the prey consumed by chum salmon during nighttime gillnet sets (2100-0200). Chum salmon fed on gelatinous zooplankton during the day and night, although it was a more important component of the diet during the late morning (0900-1100).

2.4. Discussion

I caught sockeye, chum, and pink salmon at the surface (0-6 m) during each of the six daylight gillnet operations, providing evidence that these species spent some portion of their time at the surface during daylight periods. Previous gillnet studies have generally shown that catches were usually higher during the night than during the day (Taguchi 1963; Manzer 1964; Takagi 1971; Pearcy et al. 1984; Azuma 1991). Based on these studies, it was hypothesized that perhaps salmon remained at depth during the day (Taguchi 1963; Manzer 1964). Although no consistent diel pattern was shown for short duration tracking of sockeye, pink, and chum using ultrasonic tags (Ogura and Ishida 1995), recent archival tag data recovered from salmon released on the high seas and recovered after many days in the coastal areas of Alaska and Japan have corroborated that salmon generally remain at the surface (<10 m) during the night and, therefore, are susceptible to capture by gillnets (Wada and Ueno 1999; Walker et al. 2000b). During the day, these data have shown that salmon swimming behavior by depth is highly variable because the fish are making continuous dives and ascents from the surface to a depth of approximately 50 m, or more (Walker et al. 2000b). This behavior makes them vulnerable to capture by gillnets in the daytime when salmon return to the surface between dives.

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

(1995) observed that sockeye salmon fed primarily on euphausiids and squid at night and the proportion of copepods, hyperiid amphipods, and pteropods increased during the day.

I observed a pattern in pink salmon food habits characterized by two peaks in feeding intensity, one at night after sunset, and another at mid-day. Earlier studies have observed that pink salmon have a diel rhythm to their food habits, and feeding activity increased immediately after sunset and continued through the night (Shimazaki and Mishima 1969; Ueno et al. 1969; Pearcy et al. 1984). In the Bering Sea, I observed that at night pink salmon decreased the proportion of fish and increased the proportion of euphausiids and copepods in their stomach contents. Shimazaki and Mishima (1969) saw no evidence of a switch in prey types between day and night in the Okhotsk Sea. However, in the Gulf of Alaska there was a clear increase in feeding on euphausiids during the night (Pearcy et al. 1984).

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

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

My results emphasize that daily periods of increased feeding activities are different for each salmon species and that the prey composition shifts between day and night feeding periods. Although studies of salmon food habits that rely on sampling at one time of day highlight the difference in prey composition between salmon species, this type of study may fall short of examining the full spectrum of prey species taken by salmon predation. Therefore, sampling salmon throughout the diel cycle is required to provide an accurate assessment of salmon feeding ecology.

Table 2.1. Salmon catches from eight consecutive gillnet sets on 11-12 July 1997 in the Bering Sea are summarized. Sample is the number of salmon sampled for stomach contents. Gillnet set and retrieval time is the local time (GMT+12) when setting and retrieval of the net began. Sunrise time is 03:11 (local) and sunset time is 20:47 on 11 July. Sunrise time is 03:12 on 12 July. Shading indicates periods in darkness.

Set	SST	Gillnet set and	Sockeye		Pink		Chum		Coho		Chinook		Total	
number	(°C)	retrieval time	Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample	Catch	Sample
1	8.3	0600-0800	25	25	140	67	6	6	1	1	0	0	172	99
2	8.5	0859-1100	29	29	145	35	10	10	0	0	0	0	184	74
3	8.5	1159-1400	24	24	129	21	26	26	0	0	5	5	184	76
4	8.6	1459-1700	16	16	114	51	5	5	0	0	3	3	138	75
5	8.6	1758-1959	27	27	117	39	9	9	0	0	0	0	153	75
6	8.6	2100-2259	23	23	221	50	9	9	0	0	0	0	253	82
7	8.4	0000-0202	21	21	278	50	9	9	0	0	0	0	308	80
8	8.3	0300-0500	68	50	273	20	20	20	0	0	0	0	361	90
Total			233	215	1417	333	94	94	1	1	8	8	1753	651
% Sampled				92		24		100		100		100		37

Table 2.2. Fork length (mm; sd=standard deviation), body weight (g), sex and maturity ratios, and age composition of sockeye, pink, and chum salmon are described for fish caught in consecutive gillnet sets. Totals are data combined for all time periods. Shading indicates periods in darkness.

Species	Time period	Sample size	Fork length		Body weight		Percent female	Percent immature	Percent ocean age			
			mean	sd	mean	sd			1	2	3	4
Sockeye	0600-0800	25	485	29	1435	316	24	96	0	96	4	0
	0900-1100	29	478	26	1272	218	34	97	0	96	4	0
	1200-1400	24	494	45	1448	444	21	79	0	88	12	0
	1500-1700	16	517	50	1652	702	31	38	0	81	19	0
	1800-2000	27	470	21	1179	143	67	100	0	100	0	0
	2100-2300	23	492	26	1371	272	57	100	0	100	0	0
	0000-0200	21	480	26	1290	264	19	95	0	100	0	0
	0300-0500	50	478	22	1244	181	40	100	0	90	10	0
	Total	215	484	32	1333	336	38	92	0	94	6	0
Pink	0600-0800	67	455	19	1198	154	30	0	100	0	0	0
	0900-1100	35	460	22	1234	167	31	0	100	0	0	0
	1200-1400	21	458	17	1209	134	43	0	100	0	0	0
	1500-1700	51	460	24	1268	190	27	0	100	0	0	0
	1800-2000	39	451	17	1153	135	49	0	100	0	0	0
	2100-2300	50	453	22	1186	169	34	0	100	0	0	0
	0000-0200	50	455	21	1170	166	34	0	100	0	0	0
	0300-0500	20	460	16	1201	153	35	0	100	0	0	0
	Total	333	456	20	1202	165	34	0	100	0	0	0
Chum	0600-0800	6	531	55	1845	592	50	50	0	33	67	0
	0900-1100	10	546	77	2149	1125	50	30	0	40	30	30
	1200-1400	26	526	50	1784	515	42	39	0	24	64	12
	1500-1700	5	569	48	2104	559	40	0	0	20	40	40
	1800-2000	9	533	60	1898	1032	44	67	0	22	67	11
	2100-2300	9	524	38	1629	494	67	67	0	33	56	11
	0000-0200	9	547	50	1862	389	44	44	0	22	78	0
	0300-0500	20	526	43	1667	394	65	60	0	21	68	11
	Total	94	533	52	1822	640	51	47	0	26	61	13

Table 2.3. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of sockeye salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

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

[1]includes amphipods, pteropods, polychaetes, chaetognaths, appendicularians, mysids, and unidentified prey
[2]includes medusae, ctenophores, and salps
[3] includes appendicularians and mysids

Table 2.4. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of pink salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

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

[1]includes amphipods, pterpods, polychaetes, chaetognaths, appendicularians, mysids, and unidentified prey
[2]includes medusae, ctenophores, and salps
[3]includes appendicularians and mysids

Table 2.5. Percent of empty stomachs, mean and standard deviation (sd) for stomach content weight (g) and stomach content index (SCI), and prey composition by weight and volume resulting from stomach content analysis of chum salmon. Time period is the time of day when the fish was caught. SCI is the ratio of stomach content weight to salmon body weight times 100. Values for stomach content weight, SCI, and mean prey composition are calculated using all fish including those with empty stomachs. Shading indicates periods in darkness.

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

[1]includes medusae, ctenophores, and salps
[2]includes amphipods, crab larvae, polychaetes, chaetognaths, mysids, and unidentified prey
[3]includes appendicularians and mysids

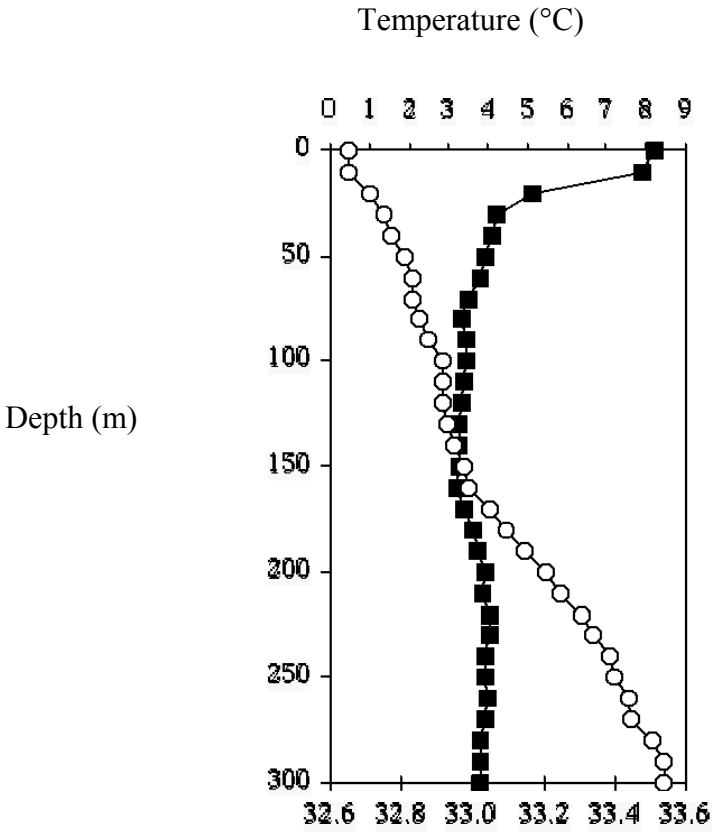

Figure 2.1. Upper water layer profile of temperature (closed box) and salinity (open circle) in the central Bering Sea at 57°30'N, 178°30'W on 10 July 1997 compiled from conductivity-temperature-depth probe data. Temperature decreased rapidly from 8.3°C at the surface to 4.2°C at 30 m depth.

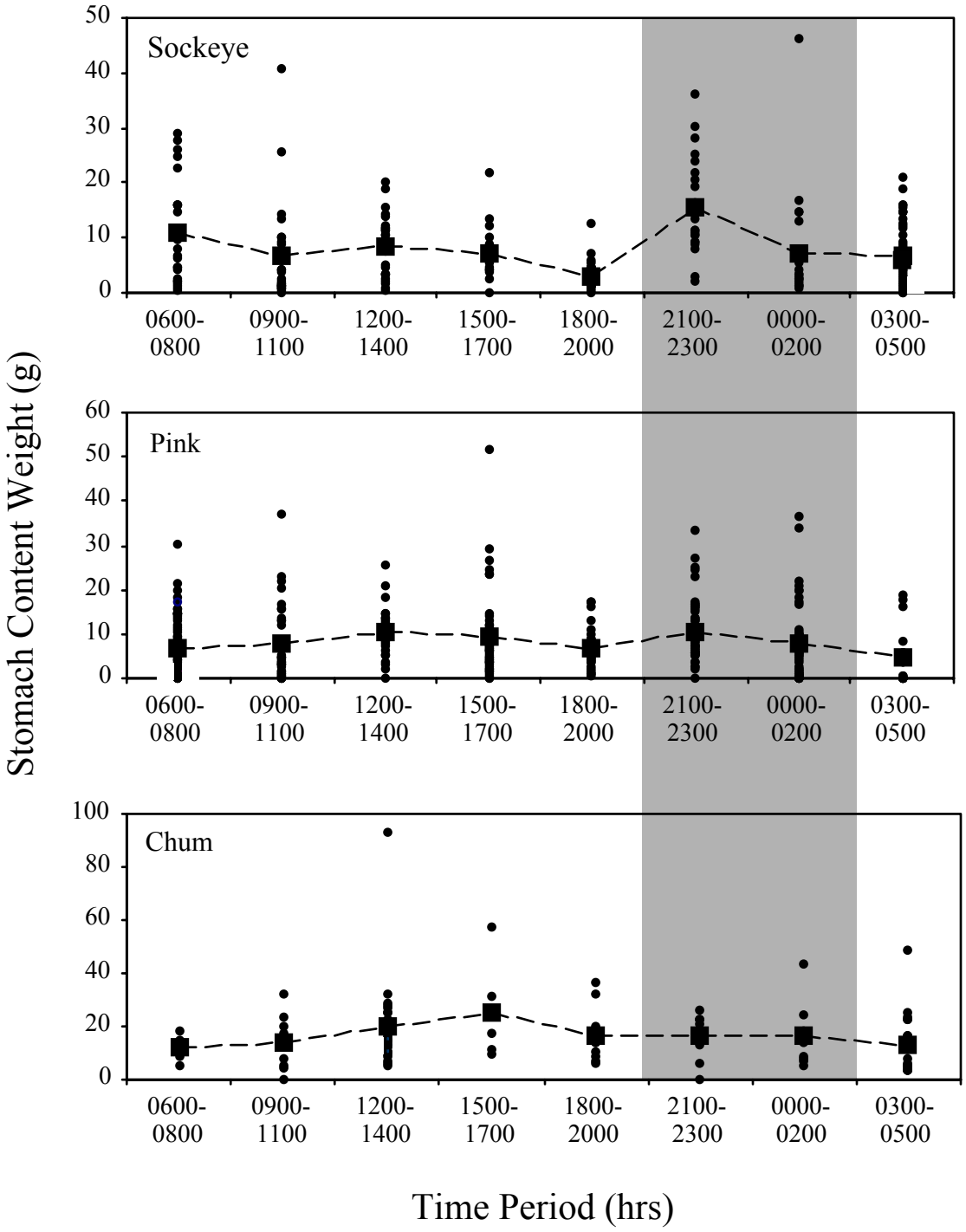

Figure 2.2. Stomach content weight of sockeye, pink, and chum salmon. Time period is the time of day when the fish was caught. The solid square and dashed line indicate the mean stomach content weight for each time period. Solid circles indicate the stomach content weight of each fish examined. Shading indicates periods in darkness.

Chapter 3.0 Caloric density estimates of salmonids and their prey

3.1. Introduction

Analysis of oceanic Pacific salmonid stomach contents have shown a variety of zooplankton, squid, and fish species compose their prey (for example, Andrievskaya 1957, Ito 1964, LeBrasseur 1966, Pearcy et al. 1988, Higgs et al. 1995, see Chapter 1.0). Researchers have used stomach evacuation rates (Gorbatenko and Chuchukalo 1989; Chuchukalo et al. 1995; Hiramatsu et al. 1996), or bioenergetic models (Brodeur and Pearcy 1987; Beauchamp et al. 1989) to estimate prey consumption based on food habits analysis. The bioenergetic model is based on an energy balance equation in which energy available from consumption must balance energy used for metabolism, waste elimination, activity, and growth (see Chapter 4.0). In order to use a bioenergetic model, the caloric density of prey and predator must be obtained because the calorie (or joule) is the basis in which energy consumed and expended is calculated. Caloric density provides a framework by which to evaluate and compare the quality of particular prey items (see Chapter 1.0). Since the 1970s, many researchers have determined the caloric density of marine organisms (for example, Cummins and Wuycheck 1971; Perez 1994). However, not all salmonids or their prey organisms have had their caloric content measured. My objective for this analysis was to create a collection of caloric density values for zooplankton and fish from the subarctic Pacific relevant to studies of salmonid feeding ecology. To achieve this goal, I conducted calorimetry experiments to determine new values for species in which there is little, or no caloric density information available, and I produced a comprehensive tabulation of energy density values for species ecologically-related to Pacific salmon.

3.2. Methods

Energy density values were determined for salmonids, salmon prey, and stomach contents of salmon by bomb calorimetry. My determinations were added to a compilation of energy densities available from previous studies and presented as source material for researchers of Pacific salmon feeding ecology, growth, and prey consumption.

3.2.1. Bomb calorimetry

Salmon prey organisms, including hyperiid amphipods, euphausiids, pteropods, and cephalopods were obtained for determination of caloric density. These specimens were collected in a fresh condition from net tows and salmon stomachs during salmon research cruises in the central North Pacific Ocean, central Bering Sea (*Wakatake maru*), and Gulf of Alaska (*Oshoro maru* and *Pandalus*) in 2000-2001. In addition, fresh stomach content samples were collected from sockeye, chum, pink, and chinook salmon to determine the range of caloric densities in fresh samples of stomach contents from fish caught in the central Bering Sea during the summer. The stomach contents were identified using a binocular microscope and the percent composition (by volume) was estimated by eye during ship-board examination. Juvenile (ocean age .0) pink and chum salmon were collected in Prince William Sound, Alaska in 2001, and juvenile steelhead (ocean age .0) and immature sockeye salmon (ocean age .1) were collected in the central Gulf of Alaska in 2000. All samples were frozen at sea (approximately -20°C) and brought to the laboratory, where samples were thawed and blotted to determine wet weight.

Samples were dried in an oven at 55°C for several days until a constant weight was attained (change in weight < 3%), after which the samples were ground to a powder using a commercial blender. Approximately 0.20 g per sample was pressed into a pellet and used to determine the gross energy content by bomb calorimetry. After charging the combustion vessel to 35 atm with ultra-high purity oxygen, the pellet was burned in a Parr semimicro-bomb calorimeter (Model 1425, Parr Corp., Moline, IL). The unit of heat reported was the (chemical) calorie, the amount of heat required to raise the temperature of 1 g of water from 14.5°C to 15.5°C (4.184 joules). Formation of acids following combustion produces heat, although the heat is expected to be small for marine animal species (<2%; Paine, 1964, 1971). Therefore, a one-calorie correction was assumed for the formation of nitric acid (recommended by Parr Corp.) and the sulfur content was assumed to be 0.6% (mean value for eight fish species, Jenifer McIntyre, pers. comm. SAFS, Univ. Washington, Seattle). A correction factor was used to compensate for the

spike generated by fuse wire combustion. Most of the samples of prey species, stomach contents, and salmon provided a dry weight sufficient for two to four combustions from which the mean and standard deviation were calculated. Conversion of caloric density of the dry sample to wet weight was accomplished by multiplying the proportion of dry material (1.00 minus the proportion of water in the sample) by the caloric density of the dry sample, which provided a point estimate of energy density on a wet-weight basis. Results were summarized graphically and the numerical values were listed in the comprehensive tabulation of energy-density values.

3.2.2. Compilation of energy density values

I compiled caloric density values reported in previous studies for organisms known to be prey of Pacific salmonids during the oceanic phase of their life history. However, not all prey items have had their caloric densities determined. Therefore, I included results from taxonomically-related groups and from organisms from other geographical areas. Values from previous studies included those estimated by direct methods, most often by bomb calorimetry. Estimates of energy content based on proximate analysis were not included in my tabulation because these estimates can over-estimate caloric density relative to values obtained by direct methods (Craig et al. 1978). When available, the season when the organism was collected, the body part or maturity stage used in the energy density determinations, and the location where the organism was obtained were included because energy density may vary significantly with age or maturity of the organism under consideration (Cummins and Wuycheck 1971). Water content was listed as supplementary information in the tabulation because this value is required for conversion of energy densities between wet and dry weight. In addition, the water content can be used as a lipid index because it is inversely related to lipid content and, therefore, energy density of the organism (Hartman and Brandt 1995).

3.3. Results

In the following sections I summarize my energy-density determinations for salmonids, salmon prey, and salmon stomach contents, and present the energy densities I compiled into a comprehensive tabulation based on a review of the literature.

3.3.1. Calorific determinations of zooplankton, squid, and fish

Results from calorific determinations showed energy density on a dry-weight basis were approximately four times the density on a wet-weight basis. Caloric densities ranging from 470 to approximately 1000 calories per gram wet weight were obtained from *C. limacina*, *L. helicina*, (pteropods), *P. pacifica* (hyperiid amphipods), small flat fish juveniles (*Atheresthes* sp. and *H. stenolepis* approximately 20 mm SL), and small squid (<20 mm ML; Fig 3.1). Slightly larger fish including *Hemilepidotus* sp. (21 mm SL), *T. crenularis* (43 mm SL), and *P. monopterygius* (44 mm SL), and middle-sized squid, *B. anonychus* (40 mm ML), had caloric densities ranging from approximately 1100 to 1500 calories per gram wet weight. Prey containing the highest caloric density (>1500 calories per gram wet weight) included larger *B. anonychus* squid (80-90 mm ML), deep sea smelt *L. schmidti* (117 mm SL), and northern lampfish, *S. leucopsarus* (43-112 mm SL; Fig. 3.1). The high caloric density of squid, smelt, and lampfish was obvious during sample preparation because oil exuded from the squid liver and the fish's muscle tissue during the grinding process prior to combustion.

Bomb calorimetry of salmonids indicated that juvenile chum (age 0.0; 117 mm FL) and pink salmon (age 0.0; 111 mm FL), and young steelhead (age 2.0; 228 mm FL) had lower energy density (less than 1200 calories per gram wet weight) than older steelhead (age 3.0; 351 mm FL) and sockeye salmon that had spent one year at sea (age 1.1; 294 mm FL; Fig. 3.2).

The caloric density of five samples of stomach contents collected from large sockeye salmon (520-620 mm FL) showed a wide range in caloric densities (Fig. 3.3). A caloric density of 838 calories per gram (wet weight) was obtained for a sockeye stomach sample containing small squid (43%, percent volume), *P. monopterygius* (40%), *L. helicina* (15%) and *N. cristatus* (2%) and another sample containing a higher proportion of small squid (85%), in addition to *T. longipes* (10%), *N. cristatus* (3%), and *L. helicina* (2%) was 862 calories per gram (wet weight). Slightly higher caloric values (1117 and 1243 calories per gram wet weight) were obtained from sockeye stomach samples

containing high proportions of *T. longipes* (95% and 98%). The maximum caloric density of 1405 calories was estimated from a stomach sample containing *S. leucopsarus* (64%), *T. longipes* (25%), *N. cristatus* (5%), *P. pacifica* (3%), and chaetognaths (3%; Fig. 3.3).

The energy density of stomach contents collected from large chum salmon (542-642 mm FL) was lower than stomach contents samples collected from sockeye, pink, and chinook salmon (Fig. 3.4). Caloric density was lowest for a stomach containing *Beroe* sp. and medusae (95%), *C. limacina* (4%), and *L. helicina* (1%; 270 calories per gram wet weight). A stomach containing *L. helicina* (96%) and fish larvae (4%) had a higher caloric value (507 calories per gram wet weight). The highest caloric density for chum salmon stomach contents (739 calories per gram wet weight) was obtained from a sample containing a large diversity of prey including *L. helicina* (35%), *Beroe* sp. and medusae (29%), *T. longipes* (25%), *H. frontalis* (5%), *C. limacina* (3%), and small squid (3%; Fig. 3.4).

The three stomach samples collected from large pink salmon (440-642 mm FL) had a narrow range of caloric density and all contained similar prey organisms (Fig. 3.5). The lowest density was 991 calories per gram wet weight for a sample containing several types of fish (65%), small squid (20%), *T. longipes* (10%), *L. helicina* (3%), and *N. cristatus* (2%). A higher energy density (1269 calories per gram wet weight) was obtained from a stomach sample containing more euphausiids (*T. longipes* 77%, *N. cristatus* 10%, *P. monopterygius* 10%, and small squid 3%; Fig. 3.5).

Two stomach content samples were collected from relatively small immature chinook salmon (age 1.1 and 1.2; 331 to 530 mm FL). There was a narrow range of caloric densities determined from these samples (Fig. 3.6). A lower density of 1098 calories per gram wet weight was obtained from a sample containing mostly small squid (95%) and a few fish (5%). A higher caloric density (1145 caloric per gram wet weight) was determined from a stomach sample containing mostly fish, *P. monopterygius* (97%) and a few copepods, *N. cristatus* (3%; Fig. 3.6).

3.3.2. Comprehensive tabulation of energy density values

The tabulation of energy density values included the caloric density values determined in this study and those of earlier studies of zooplankton, squid, and fish (Table 3.1). Numerical values resulting from my analysis included point estimates for caloric density on a wet-weight basis, mean and standard deviation of caloric density (dry weight), number of combustions per sample, and percent water contained in the sample.

A range of 30 to 290 calories per gram wet weight was the lowest range of values obtained for a taxonomic group. These low values were determined for cnidaria, ctenophores, and salps, which contained a high percentage of water (93.9-97.2 % water; Table 3.1). Pteropods, copepods, hyperiid amphipods, and chaetognaths had a slightly higher caloric density ranging from 250-1089 calories per gram wet weight, and the percent water contained in these organisms ranged from 77.6-93.2%. Euphausiids, particularly *E. pacifica* and *Thysanoessa* spp., had caloric densities ranging from approximately 1000 calories per gram to a maximum of 1567 calories per gram wet weight. Large squids had caloric densities among the highest of the invertebrates ranging from 920 to 1877 calories per gram wet weight (Table 3.1).

Estimates of the caloric density of fish indicated those with the lowest density, (less than 1000 calories per gram wet weight) included the juveniles of *Theragra chalogramma*, *Sebastes* sp., flatfish, and *Gadus macrocephalus*, and the cottids (of unknown life-history stage)*, Malacocottus kincaidi and Gymnocanthus galeatus* (Table 3.1). Juvenile *P. monopterygius*, *Anoplopoma fimbria*, *Atheresthes* sp., and *Hemilepidotus* spp., and adult *Ammodytes* spp., *T. chalogramma, Sebastes* spp., *T. crenularis*, *Bathymaster signatus*, *C. saira,* and *Mallotus villosus* had higher caloric densities, ranging from 1000 to 2000 calories per gram wet weight. Fish prey common in the stomach contents of Pacific salmon containing the highest caloric density included *Clupea pallasi*, *Thaleichthys pacificus*, *S. leucopsarus,* and *L. schmidti* (approximately 2000-2600 calories per gram wet weight; Table 3.1)

Caloric densities for salmonids ranged from 1000-2000 calories per gram wet weight (Table 3.1). Sockeye, chum, and pink salmon caloric densities increased with increasing fish body size from juveniles to maturing adults. The percent water contained in sockeye, chum, and pink salmon decreased from 75% to 69% as they increased in size. Caloric density of large-bodied coho salmon collected in the ocean ranged from 1287-2083 calories per gram wet weight. Caloric content of chinook salmon was 1363 calories per gram wet weight for mature fish. Mature masou salmon had a relatively high caloric density that ranged from 1566-1719 calories per gram wet weight (Table 3.1).

3.4. Discussion

My results contributed substantially to the information available on caloric densities by supplying new information on major salmon prey items such as squid and fish, in addition to caloric values of salmonids. Specifically, this study provided caloric values for *B. anonychus*, an important prey item for larger immature and maturing salmonids in the central North Pacific Ocean (see Chapter 1.0) and Gulf of Alaska (Aydin et al. 2000), for the size range of squid (40-90 mm ML; 1307-1737 cal/g wet weight) commonly found in salmonid stomach contents. In addition, caloric determinations were reported for the first time for small squid (13-22 mm ML; 850-1010 cal/ g wet weight) and juvenile flatfish including *Atheresthes* sp. (20 mm SL; 624 cal/g wet weight) and *H. stenolepis* (19 mm SL; 853 cal/g wet weight), which were important prey of sockeye, chum, pink, and chinook salmon in the central Bering Sea (see Chapter 1.0; Table 3.1).

There is a paucity of information available on caloric densities of juvenile salmonids during their early marine life. To help remedy this situation, I reported caloric densities for juvenile chum (117 mm FL; 1113 cal/g wet weight) and pink salmon (111 mm FL; 1174 cal/g wet weight) caught shortly after entering the marine environment in the northern Gulf of Alaska. In addition, caloric density was estimated from analysis of juvenile steelhead (351 mm FL; 1228 cal/g wet weight; Table 3.1) spending their first summer in the central Gulf of Alaska. Future analyses should focus on obtaining caloric values of juvenile salmonids, and immature and maturing steelhead caught in the ocean

because there are few caloric density values reported from these groups, and this information will be critical for estimating prey consumption and growth at sea using bioenergetic approaches.

There are two methodological aspects of caloric determinations that can cause serious variability in density estimates: the accurate estimate of percent water contained in the thawed sample, and production of a representative sample of the organism for combustion. The difficulty in determining fresh weight arises from collection of samples at sea, where obtaining an accurate fresh weight for small sample weights is difficult. If the sample is frozen, for later weighing and processing in the laboratory, there can be a loss of fluid from the organism when the sample is thawed. If the wet weight is underestimated, then the percent moisture is underestimated and the resulting caloric density on a wet weight basis is overestimated. Therefore, I have reported caloric density determinations on a wet and dry weight basis. If required, researchers can use their own values for percent water and the caloric density on a dry weight basis that I have supplied to calculate their own caloric densities for wet or fresh material (Table 3.1). Another aspect that contributes to large variation in density estimates is combustion of a sample that may not be representative of the whole body of the organism. Therefore, careful grinding must proceed long enough for complete sample homogenization. Drying and grinding large-bodied organisms, such as immature and maturing salmon can be troublesome, therefore, I recommend samples be dried first then ground, rather than grinding the sample prior to drying in an oven.

Sockeye, chum, and pink salmon caloric densities increased with increasing fish body size (Table 3.1). This is expected because the amount of stored energy (lipid) increases with body weight (Nomura et al. 2001). In high-seas caught ocean age .1 pink salmon, the amount of total (polar and non-polar) lipid contained in the muscle was positively correlated to body weight (Nomura et al. 2000). In a detailed analysis of total lipid content of summer-caught high-seas chum salmon, Nomura et al. (2001) showed lipid content increased with body weight for fish weighing less than 2000 g, however, there was no correlation in chum salmon ocean age .4 and older. Low lipid levels in

young chum salmon suggest growth occurs at the expense of lipid storage during the summer (Nomura et al. 2002).

There was a wide range of caloric densities in the stomach contents of chum salmon (Fig. 3.4). The stomach contents with the lowest caloric density consisted of medusae, ctenophores, salps, and pteropods (Table 3.1). Indeed, chum salmon stomach contents, which contained gelatinous zooplankton, had the lowest caloric density and did not overlap with the values for other salmon species (chum range 270-739, next lowest value was 838 for sockeye salmon; Table 3.1). Alternatively, euphausiids had a high caloric density relative to other crustaceans and small squids common in the stomach contents of sockeye, chum, and pink salmon in the central Bering Sea. As expected, chum salmon stomachs, as well as those of sockeye and pink salmon containing high proportions of euphausiids were higher in caloric density than stomach contents containing less euphausiids (Figs 3.3; 3.4; 3.5). The amount of high-caloric density euphausiids decreased in the stomach contents of chum, sockeye and pink salmon when pink salmon were abundant (see Chapter 1.0). Therefore, the amount of euphausiids in the stomach contents of immature and maturing sockeye, chum, and maturing pink salmon is a sensitive indicator of the overall quality of salmon feeding ecology in the Bering Sea during summer.

The mesopelagic fishes, *S. leucopsarus* and *L. schmidti*, contained extremely high caloric densities (>2000 cal/g wet weight). Of these two species, *S. leucopsarus* is particularly abundant and widely distributed in the basin of the Bering Sea, where migratory individuals can be collected by trawls as shallow as 20 m (Nagasawa et al. 1997b). In the Bering Sea during summer, *S. leucopsarus* is an abundant and rich energy source for sockeye, chum, pink, and chinook salmon. Studies to determine population dynamics, distribution, and migration of *S. leucopsarus* have important implications for studies of salmon feeding ecology in the Bering Sea because this myctophid is a plentiful salmon prey of high quality due to its high energy content.

Tadokoro et al. (1996) suggested that micronekton, such as fish and squid, were the most efficient prey group for salmon to feed upon because of their relatively large size when compared to the small-sized crustaceans such as amphipods and copepods frequently found in salmon stomach contents. Fish and squid were the most calorically-dense salmon prey organisms among those analyzed (Table 3.1). Micronekton are active swimmers making them more demanding for salmon to catch, but the energetic cost of pursuing and capturing fish and squid is probably offset by consumption of this energy-rich prey. However, when fish and squid abundance is low, as might occur when the abundance of maturing pink salmon in an area is high, the time and energy required to search for and capture these rarer prey increases, with the result that a smaller proportion of ingested energy is available for salmon growth.

Table 3.1. Summary of the caloric content of zooplankton, squid, and fish relevant to the studies of salmonid food habits and bioenergetics. Values are collected from previous studies and include new values determined in this study. WW=wet weight; DW= dry weight; AFDW=ash free dry weight; and % Ash= percent of dry weight

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
CNIDARIA									
Aglantha digitale	88	1990	4890	58.5	95.6	Aug-Sep	whole	Arctic	Percy & Fife 1981; mean value
A. digitale		2710	4449			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984; mean value
A. digitale	110	2720	6360		96.0				Bamstedt 1981 (from Arai 1988); mean value
Sarsia princeps	60	1390	3920	63.3	95.6	Aug-Sep	whole	Arctic	Percy & Fife 1981; mean value
Hybocodon prolifera	170	3400	6210	45.4	94.9	Aug-Sep	whole	Arctic	Percy & Fife 1981; mean value
Eutonuna indicans		1140	4250				whole	NE Atlantic	Norrbin & Bamstedt 1984; mean value
Aurelia aurita	30								Shuskina and Musayeva 1982 (from Arai 1988)
Hydromedusae	160								Musayeva and Sokolova 1979, 1980 (from Arai 1988)
Hydromedusae	105								Shuskina and Musayeva 1982 (from Arai 1988)
small medusae	136	2231			93.9	Jun-Jul	whole; 10-13 mm TL	N Pacific & Bering Sea	Davis et al. 1998
medusae	60		4513				whole	NW Atlantic	Steimle & Terranova 1985
Physalia physalis		3740	4150						Wissing et al. 1973 (from Arai 1988)
siphonophores		3775	4100						Wissing et al. 1973 (from Arai 1988)
siphonophores	160								Musayeva & Sokolova 1979, 1980 (from Arai 1988
CTENOPHORA									
Beroe cucumis	46	1350	4590		96.6	Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
B. cucumis	45	1360	3855	66.3	96.7	Aug-Sep	whole	Arctic	Percy & Fife 1981
Beroe sp.	47	1061			95.6	Jun	whole; 100 mm TL	N Pacific	This study; specimens collected by plankton net; mean values
Beroe sp.		3515	3760						Wissing et al. 1973 (from Arai 1988)
Bolinopsis infundibulum		780	3510			May	whole	NE Atlantic	Norrbin & Bamstedt 1984
Mertensia ovum	88	1920	4430	56.2	95.5	Aug-Sep	whole		Percy & Fife 1981
Pleurobrachia pileus		680	3240			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
CTENOPHORA (continued)									
P. pileus	48	2000			97.6				Petipa et al.1970 (from Arai 1988)
P. pileus	45	2560	4585		98.2				Vinogradova et al. 1962 (from Arai 1988)
P. pileus		1150	6020						Bamstedt 1981 (from Arai 1988)
Ctenophores	49	1324	4003	68.3	97.2	Dec-Mar	whole	NW Atlantic	Thayer et al.1973; average value for mixed species; Class Tentaculata
Ctenophores	290								Shuskina and Musayeva 1982 (from Arai 1988)
Coelenterates	494	2886	5882		82.9		whole		Cummins & Wuycheck 1971; grand mean
Coelenterates		3481	4109						Griffiths 1977
POLYCHAETES									
Tomopteris helgolandica		5278	7518			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
T. helgolandica		4083	5816			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
T. helgolandica		4407	6278			Apr	whole	NE Atlantic	Norrbin & Bamstedt 1984
Polychaetes	1094	3792	5239	28.0	70.0		whole	NW Atlantic	Steimle & Terranova 1985; average value for 11 mostly epibenthic species
Polychaetes	673	3388			80.0			NW Atlantic	Tyler 1973 (from Steimle and Terranova 1985)
Polychaetes	849	4798	6070	21.1	79.3		whole	NW Atlantic	Thayer et al. 1973; average value for 3 species
Polychaetes		3641							Griffiths 1977
PTEROPODA									
Clione limacina	472	5016			90.6	Jun	whole; mean 16 mm TL	N Pacific	This study; specimens collected by plankton net; mean values
C. limacina	583	5349	5878	9.0	89.1	Jun-Jul	whole	Bering Sea	Nishiyama 1977
C. limacina	250	3680	6030	38.2	93.2	Aug-Sep	whole	Arctic	Percy & Fife 1981; mean value
C. limacina		4613	6481			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
Limacina helicina	940	4331			78.3	Jun	whole; 2-3 mm TL	N Pacific	This study; specimens collected from sockeye salmon stomach contents, some shell missing; mean value
L. helicina	958	4585	5006	8.4	79.1	Jun-Jul	whole	Bering Sea	Nishiyama 1977
Limacina spp.	624	3547			82.4	Jun-Jul	whole; 3 mm TL	N Pacific, Gulf of Alaska, Bering Sea	Davis et al. 1998

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
PTEROPODA (continued)									
Pteropods	490	4969	5442	8.7	84.1	Jun-Jul	whole	Bering Sea	Nishiyama 1977; mean value
TEUTHOIDA									
Berryteuthis anonychus	1307	5732			77.2	Jul	whole; mean 40 mm TL	Gulf of Alaska	This study; specimenscollected from coho salmon stomach contents; mean values
B. anonychus	1737	6269			72.3	Jul	whole; mean 82 mm ML	Gulf of Alaska	This study; specimenscollected from coho salmon stomach contents; mean values
B. anonychus	1562	6127			74.5	Jul	whole; mean 86 mm ML	Gulf of Alaska	This study; specimenscollected from coho salmon stomach contents; mean values
B. anonychus	1636	6392			74.4	Jul	whole; 90 mm ML	Gulf of Alaska	This study; specimenscollected from coho salmon stomach contents; mean values
B. magister	1320	6120	6610	7.3	78.5	Feb	whole; males & females 202-867 g BW	Gulf of Alaska	Perez 1994; mean value
Berryteuthis sp.	920	5100	5560	8.3	82.0	Jul	whole	Bering Sea	Perez 1994; mean value
Berryteuthis spp.	978	5147			81.0	Jun-Jul	whole; 28-38 mm ML	N Pacific & Bering Sea	Davis et al. 1998
Berryteuthis spp.	1550	5983			74.1	Jun-Jul	whole; 66-100 mm ML	N Pacific and Gulf of Alaska	Davis et al. 1998
Gonatopsis borealis	1125	5259			78.6	Jun-Jul	whole; 42-59 mm ML	N Pacific & Bering Sea	Davis et al. 1998
G. borealis	1155	5224			77.9	Nov-Dec	whole; 62 mm ML	N Pacific	Davis et al. 1998
G. borealis	1120	6200	6520	5.0	82.0	Jun	whole; female 262 mm ML	N Pacific	Perez 1994; mean value
Gonatus spp.	1877	6680			71.9	Jun-Jul	whole; 57-71 mm ML	Bering Sea	Davis et al. 1998
Onychoteuthis borealijaponica	1201	5046			76.2	Jun, Nov-Dec	whole; 45-61 mm ML	N Pacific	Davis et al. 1998
O. borealijaponica	1290	5730	6040	5.3	77.5	Jun-Jul	whole; males & females 186-320 mm ML	N Pacific	Perez 1994; mean value
Ommastrephes bartrami	1560	6000	6380	6.2	74.0	Jun	whole; female 382 mm ML	N Pacific	Perez 1994; mean value
Illex illecebrosus	1695	5254	5636	7.0	69.0		whole	NW Atlantic	Steimle & Terranova 1985
Loligo pealei	1337	4872	5110	8.0	72.0		whole	NW Atlantic	Steimle & Terranova 1985
Loligo brevis	1051	5743	6342	9.4	81.7	Dec		NW Atlantic	Thayer et al. 1972
Squids	1010	5461			81.5	Jul	whole; mean 13 mm ML	Bering Sea	This study; specimenscollected from pink salmon stomach contents; mean values
Squids	982	5426			81.9	Jul	whole; mean 17 mm ML	Bering Sea	This study; specimenscollected from pink salmon stomach contents; mean values

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
TEUTHOIDA (continued)									
Squids	850	5212			83.7	Jul	whole; mean 22 mm ML	Bering Sea	collected from salmon stomach contents; mean values
Squids	749	5065	5578	9.2	85.2	Jun-Jul	whole	Bering Sea	Nishiyama 1977; mean value
COPEPODA									
Neocalanus cristatus	748	4858	5428	10.5	84.6	Jun-Jul	whole	Bering Sea	Nishiyama 1977; mean value
N. cristatus	627	5504			88.6	Jun-Jul	whole; 7-8 mm TL	N Pacific & Bering Sea	Davis et al.1998
N. plumchrus	995	5180	5680	8.8	80.8	Jun-Jul	whole	Bering Sea	Nishiyama 1977
Calanus finmarchicus		6437	7020			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
Metridia longa		6489	7030			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
M. longa		7151	7559			Apr	whole	NE Atlantic	Norrbin & Bamstedt 1984
Euchaeta norvegica		6464	6950			Dec	whole, stage C5	NE Atlantic	Norrbin & Bamstedt 1984
E. norvegica		6299	6651			Dec	males	NE Atlantic	Norrbin & Bamstedt 1984
E. norvegica		6898	7494			Dec	females	NE Atlantic	Norrbin & Bamstedt 1984
E. norvegica		6927				Apr	egg sack	NE Atlantic	Norrbin & Bamstedt 1984
E. norvegica		6566	7060			Apr	stage C5	NE Atlantic	Norrbin & Bamstedt 1984
E. norvegica		7020	7565			Apr	females with eggs	NE Atlantic	Norrbin & Bamstedt 1984
E. norvegica		6595	7107			Apr	females	NE Atlantic	Norrbin & Bamstedt 1984
Chiridius armatus		7175	7698			Dec	females	NE Atlantic	Norrbin & Bamstedt 1984
C. armatus		5980	6550			Apr	females	NE Atlantic	Norrbin & Bamstedt 1984
C. armatus		6127	6674			Apr	females	NE Atlantic	Norrbin & Bamstedt 1984
Diaptomus siciloides		5605	5849	4.3		Aug-Nov	nonreproductive females		Moshiri & Cummins 1969 (from Cummins &Wuycheck 1971)
D. siciloides		5877	6149	4.6		Aug-Nov	females with eggs		Moshiri & Cummins 1969 (from Cummins &Wuycheck 1971)
Diaptomidae	550	5741	5883		90.4		whole		Cummins & Wuycheck 1971
Copepods	965	5027	5512	8.8	80.8	Jun-Jul	whole	Bering Sea	Nishiyama 1977; mean value

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
EUPHAUSIACEA									
Euphausia pacifica	1138	4904	5592	12.3	76.8	Jun-Jul	whole	Bering Sea	Nishiyama 1977
E. pacifica		4280					whole		Small 1967 (from Mauchline & Fisher 1969)
E. pacifica		4530					whole		Small 1967 (from Mauchline & Fisher 1969)
E. pacifica		5160					whole		Small 1967 (from Mauchline & Fisher 1969)
E. pacifica	1050						whole		Childress & Nygaard 1974 (from Mauchline 1980)
E. pacifica		4710				Oct	whole	Gulf of Alaska	Mooney 1999
E. pacifica		4878				Jul	whole	Gulf of Alaska	Mooney 1999
E. superba		4390							Vinogradova 1962 (from Mauchline and Fisher 1969) mean value
E. superba	1100								Chekunova and Rynkova 1974 (from Mauchline 1980)
Thysanoessa longipes	1265	6083			79.2	Jul	whole; mean 23 mm TL	Bering Sea	collected from pink salmon stomach contents; mean values
T. longipes	1020	5454			81.3	Jun	whole; mean 19 mm TL	Bering Sea	collected from pink salmon stomach contents; mean values
T. longipes		6632				Jul	whole	Gulf of Alaska	Mooney 1999
T. longipes		6491				Jul	whole	Gulf of Alaska	Mooney 1999
T. spinifera	840	5217			83.9	Jul	whole; mean 23 mm TL	Gulf of Alaska	collected from coho salmon stomach contents; mean values
T. spinifera		5301				Jul	whole	Gulf of Alaska	Mooney 1999
T. spinifera		5651				Oct	whole	Gulf of Alaska	Mooney 1999
T. spinifera		4709				Jul	whole	Gulf of Alaska	Mooney 1999
T. inermis	1567	6005	6430	6.7	73.9	Aug-Sept	whole	Arctic	Percy and Fife 1981; mean value
T. inermis	927								Hopkins et al. 1978 (from Mauchline1980)
T. inermis		6634				Jul	whole	Gulf of Alaska	Mooney 1999
T. inermis		6444				Jul	whole	Gulf of Alaska	Mooney 1999
T. raschi	652								Hopkins et al. 1978 (from Mauchline1980)
Thysanoessa spp.	1197	4927	5414	9.0	75.7	Jun-Jul	whole	Bering Sea	Nishiyama 1977
Thysanoessa spp.	743	4675			84.1	Jun-Jul	whole; 11-26 mm TL	N Pacific & Bering Sea	Davis et al. 1998

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
EUPHAUSIACEA (continued)									
Meganyctiphanes norvegica	940	4945			81.0	Feb-Dec	whole	NW Atlantic	Tyler 1973
M. norvegica	958	5040			81.0	Jan-Dec	whole	NW Atlantic	Tyler 1973
M. norvegica	812	4633	5946	22.0	82.0		whole	NW Atlantic	Steimle and Terranova 1985; Atlantic species
M. norvegica		7562	8574			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
M. norvegica		6181	6861			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
M. norvegica		5913	6563			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
M. norvegica	788								Hopkins et al. 1978 (from Mauchline1980)
M. norvegica	1100					Winter			Brattelid & Mathews 1978 (from Mauchline 1980); maximum value
M. norvegica	950					Spring			Brattelid & Mathews 1978 (from Mauchline 1980); minimum value
Euphausiids	1173	4949	5554	10.9	76.3	Jun-Jul	whole	Bering Sea	Nishiyama 1977; mean value
HYPERIIDEA									
Parathemisto (Themisto) pacifica	1010	5126			80.3	Jun	whole; females brooding young; mean 8 mm TL	N Pacific	This study; specimens collected from sockeye salmon stomach contents; mean values
P. pacifica	852	5013			83.0	Jun	whole; mixed females, males, and young	N Pacific	This study; specimens collected from sockeye salmon stomach contents; mean values
P. pacifica		4455				Jun	whole males; mean 7 mm TL	N Pacific	This study; specimens collected from sockeye salmon stomach contents; mean value
P. pacifica	887	4958			82.1	Jul	whole; mean 4 mm TL	Gulf of Alaska	This study; specimens collected from sockeye salmon stomach contents; mean values
P. pacifica	621	3608	4556	20.8	82.8	Jun-Jul	whole	Bering Sea	Nishiyama 1977
P. libellula	652	3415	4458	23.4	80.9	Jun-Jul	whole	Bering Sea	Nishiyama 1977
P. libellula	1102	4920	5915	18.0	77.6	Aug-Sep	whole	Arctic	Percy &Fife 1981
P. abyssorum		4733	5815			Apr	whole	NE Atlantic	Norrbin & Bamstedt 1984
Hyperoche medusarum	1089	5420	6345	14.8	79.9	Aug-Sep	whole	Arctic	Percy & Fife 1981
Hyperia galba	860	4442	5898	26.0	80.0		whole	NW Atlantic	Steimle and Terranova 1976
Hyperiid amphipods	589	3952			85.1	July	whole; 3-6 mm TL	Bering Sea	Davis et al. 1998

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
HYPERIIDEA (continued)									
Amphipods	661	3713	4517	17.8	82.2	Jun-Jul	whole		Nishiyama 1977; mean value
OSTRACODA									
Conchoecia elegans		6180				Apr	females with eggs	NE Atlantic	Norrbin & Bamstedt 1984
MYSIDACEA									
Boreomysis arctica		6201	7618			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
B. arctica		7391	8525			Apr	females with eggs	NE Atlantic	Norrbin & Bamstedt 1984
B. arctica		5922	6830			Apr	whole	NE Atlantic	Norrbin & Bamstedt 1984
Mysis stenolepis	990	4714			79.0	Fall-Winter	whole	NW Atlantic	Tyler 1973
Neomysis americana		3845					whole	NW Atlantic	Steimle & Terranova 1985
DECAPODA									
Hymendora frontalis		5484				Jul	whole; mean 46 mm TL	Bering Sea	collected from salmon stomach contents; mean values
Argis dentata	1158	4878			76.0	Jun-Oct	female with eggs	NW Atlantic	Brawn et al. 1968
A. dentata	1081	4549			76.0	Jun-Oct	adults, mixed sexes	NW Atlantic	Brawn et al. 1968
Crangon septemspinosa	1111	4272			74.0	Jan-Apr	whole	NW Atlantic	Tyler 1973
C. septemspinosa	981	4088			76.0	Nov	whole	NW Atlantic	Tyler 1973
Pasiphaea multidentata		5007	5822			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
Pandalus montagui	1291	4610			72.0	Aug-Dec	whole	NW Atlantic	Tyler 1973
P. montagui	1320	4740			72.0	Jun-Oct	whole, mixed sizes and sexes	NW Atlantic	Brawn et al. 1968
P. montagui	1329	4747	5924	24.0	72.0	summer	nonreproduc-tive females		Cummins & Wuycheck 1971
P. montagui	1288	4442	5634	26.0	71.0	summer	reproductive male		Cummins & Wuycheck 1971
Crab Zoea	712	3709	5032	26.3	80.8	Jun-Jul	whole	Bering Sea	Nishiyama 1977
CHAETOGNATHA									
Sagitta elegans		5860	6814			Dec	whole	NE Atlantic	Norrbin & Bamstedt 1984
S. elegans		6716	7546			Apr	whole	NE Atlantic	Norrbin & Bamstedt 1984
S. elegans		4272	4800			Apr	whole	NE Atlantic	Norrbin & Bamstedt 1984
S. elegans	488	5035	6210	18.2	90.3	Aug-Sep	whole	Arctic	Percy & Fife 1981; mean value

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
CHAETOGNATHA (continued)									
Eukrohnia hamata		5789	7218			Apr	whole	NE Atlantic	Norrbin & Bamstedt 1984
Chaetognaths	455	4599	5032	8.6	90.1	Jun-Jul	whole	Bering Sea	Nishiyama 1977
THALIACEA									
Salpa sp.	36	856			95.8	Jun	whole mean 35 mm TL	N Pacific	This study; specimens collected by plankton net and are the same species as seen in chum salmon stomachs; mean values
Salps				73.4			adult		Madin et al. 1981; overall mean
Salpidae	96	2125	4346	51.0	95.0		whole	NW Atlantic	Steimle & Terranova 1985
APPENDICULARIA									
Appendicularia	759	4414			82.8	Jun	whole	N Pacific	Davis et al. 1998
PISCES									
Gasterosteus aculeatus	1172	4155			71.8	Jun	whole; 32 mm SL	N Pacific	This study; specimen collected from salmon stomach contents; mean value
G. aculeatus	1166	4049			71.2	Oct	whole; 32-44 mm SL	Gulf of Alaska	Davis et al. 1998
G. aculeatus	1533	4367			64.9	Oct	whole; 56-62 mm SL	Gulf of Alaska	Davis et al. 1998
Ammodytes hexapterus		4915	5598	12.2		Jun-Jul	larvae	Bering Sea	Nishiyama 1977
A. americanus	1624	5182	5922	12.0	69.0		adult	NW Atlantic	Steimle & Terranova 1985
Tautogolabrus asapersus	1058	4880				Jun-Oct	whole	NW Atlantic	Brawn et al. 1968
Clupea harengus	1927	6360				Jun-Oct	whole	NW Atlantic	Brawn et al. 1968
C. harengus	2532	5995	6497	8.0	57.0		whole	NW Atlantic	Steimle & Terranova 1985
C. pallasi	2050	6210	6790	8.8	68.3	Jul -Aug	whole	Gulf of Alaska & Bering Sea	Perez 1994; mean value
C. pallasi	1914	5907			67.6	Oct	whole; 97-104 mm SL	Gulf of Alaska	Davis et al. 1998
Mallotus villosus	1680	6060	6550	7.5	72.5	Jul-Aug	whole	Gulf of Alaska & Bering Sea	Perez 1994; mean value
M. villosus	1277	5277			75.8	Oct	whole; 63-71 mm SL	Gulf of Alaska	Davis et al. 1998
Thaleichthys pacificus	2630	7350	7660	4.1	64.2	Mar & Aug	whole	Gulf of Alaska	Perez 1994; mean value
Gadus macrocephalus	940	4540	5470	16.9	79.4	Jul-Aug	whole	Gulf of Alaska & Bering Sea	Perez 1994; mean value

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
PISCES (continued)									
Theragra chalcogramma	1011	4554			77.8	Oct	whole; 75-95 mm ML	Gulf of Alaska	Davis et al. 1998
T. chalcogramma	1110	4940	5700	13.4	77.5	Mar & Jul-Aug	whole; males & females 430-530 mm SL	Gulf of Alaska & Bering Sea	Perez 1994; mean value
T. chalcogramma	908	4875		13.6	81.4	Summer	whole, mean 52 mm SL	Gulf of Alaska	Boldt 1997; mean value
T. chalcogramma	927	4906		13.4	81.1	Summer	whole; mean 55 mm SL	Gulf of Alaska	Boldt 1997; mean values
T. chalcogramma	934	4942		12.9	81.1	Summer	whole; mean 53 mm SL	Gulf of Alaska	Boldt 1997; mean values
Sebastes alutus	1470	5410	6430	16.0	72.9	Feb	whole	Gulf of Alaska	Perez 1994; mean values
S. ciliatus	1460	5500	6550	16.0	73.4	Aug	whole	Gulf of Alaska	Perez 1994; mean values
S. polyspinis	1490	5230	6140	14.9	71.6	Feb & Jul	whole; males & females 275-411 g BW	Gulf of Alaska & Bering Sea	Perez 1994; mean values
Sebastes sp.	660	6057			89.1	Jul	whole juveniles; mean 11 mm SL	Bering Sea	This study; specimens collected from pink salmon stomach contents; mean value
Sebastes sp.	1380	5220	6260	16.6	73.8	Feb	whole	Gulf of Alaska	Perez 1994; mean values
Stenobrachius leucopsarus	2226	6397			65.2	Jul	whole; 43 mm SL	Bering Sea	collected from pink salmon stomach contents; mean values
S. leucopsarus	2168	6775			68.0	Jul	whole; 64 mm SL	Bering Sea	collected from salmon stomach contents; mean values
S. leucopsarus	2365	7367			67.9	Jul	whole; 112 mm SL	Bering Sea	collected from salmon stomach contents; mean values
S. leucopsarus	2041	6398			68.1	Jun-Jul	whole; 32-90 mm SL	N Pacific & Bering Sea	Davis et al. 1998
Tarletonbeania crenularis	1199	4814			75.1	Jun	whole; mean 43 mm SL	N Pacific	This study; specimen collected by plankton net; mean values
T. crenularis	1075	4335	5204	16.7	75.2	Jun-Jul	larvae	Bering Sea	Nishiyama 1977
T. crenularis	896	4435			79.8	Jun	whole; 24-50 mm SL	N Pacific	Davis et al. 1998
T. crenularis	1283	4771			73.1	Jun	whole; 65-75 mm SL	N Pacific	Davis et al. 1998
Leuroglossus schmidti	2024	7029			71.2	Jun	whole; mean 117 mm SL	Bering Sea	This study; specimens collected from chum stomach contents; mean values
Pleurogrammus monopterygius	1240	5414			77.1	Jul	whole juveniles; mean 44 mm SL	Bering Sea	This study; specimens collected by plankton net; mean values
P. monopterygius	1186	4841			75.5	Jun-Jul	whole; 42-70 mm SL	N Pacific, Gulf of Alaska & Bering Sea	Davis et al. 1998

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
PISCES (continued)									
P. monopterygius	1074	3347	5049	10.8	67.9	Jun-Jul	larvae	Bering Sea	Nishiyama 1977
Anoplopoma fimbria	1300	5640	6260	9.9	77.2	Feb & Aug	whole; males 184-258 g BW	Gulf of Alaska	Perez 1994; mean values
Gymnocanthus galeatus	910	4130	540	23.6	77.9	Jul	whole	Bering Sea	Perez 1994; mean values
Malacocottus kincaidi	840	4100	5360	23.1	79.7	Feb	females 50-59 g BW	Gulf of Alaska	Perez 1994; mean values
Hemilepidotus hemilepidotus	1561	4923			68.3	Jul	whole juveniles; mean 21 mm SL	Gulf of Alaska	This study; specimens collected from pink salmon stomach contents; mean value
Hemilepidotus sp.	1412	5430			74.0	Jul	whole juveniles; mean 21 mm SL	Bering Sea	This study; specimens collected from sockeye and pink salmon stomach contents; mean values
Hemilepidotus sp.	1184	4520			73.8	Jul	whole; 18-31 mm SL	N Pacific & Bering Sea	Davis et al. 1998
Triglops sp.	1240	4760	5610	14.6	74.0	Jul	whole	Bering Sea	Perez 1994; mean values
Liparis sp.		4699	5395	12.9		Jun-Jul	larvae	Bering Sea	Nishiyama 1977
Liparis sp.	910	4100	4100		78.0	Jul	whole	Bering Sea	Perez 1994; mean values
Bathymaster signatus	1320	5130	5930	13.5	74.3	Feb & Jul	whole;females 285-297 g BW	Gulf of Alaska & Bering Sea	Perez 1994; mean values
Trichodon trichodon	1170	5280	6070	13.0	78.0	Aug	whole	Gulf of Alaska	Perez 1994; mean values
Atheresthes stomias	1230	5170	5830	11.4	76.3	Feb & Jul-Aug	whole; males & females 181-324 g BW	Gulf of Alaska & Bering Sea	Perez 1994; mean values
Atheresthes sp.	624	5425			88.5	Jul	whole juveniles; mean 20 mm SL	Bering Sea	collected from pink salmon stomach contents; mean values
Hippoglossus stenolepis	853	4961			82.8	Jul	whole juveniles; mean 19 mm SL	Bering Sea	This study; specimens collected from pink and sockeye salmon stomach contents; mean values
Hippoglossoides sp.	1087	4748	5329	10.9	77.1	Jun-Jul	larvae	Bering Sea	Nishiyama 1977
Sardinella aurita	1433	4752	5516	14.0	70.0		whole	NW Atlantic	Steimle & Terranova 1985
Anchoa hepsetus	1385	4752	5637	16.0	71.0		whole	NW Atlantic	Steimle & Terranova 1985
Scomberesox saurus	2030	5325	5874	9.0	62.0		whole	NW Atlantic	Steimle & Terranova 1985
Scomber japonicus	1481	5158	5827	12.0	71.0		whole	NW Atlantic	Steimle & Terranova 1985
Thunnus albacares		5588					muscle	NW Atlantic	Steimle & Terranova 1985
Cololabis saira	1536	5224			70.6	Oct	whole; 177 mm SL	Gulf of Alaska	Davis et al. 1998

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
PISCES (continued)									
Salvelinus namaycush	2674	7103		4.5	62.4	Apr-Nov	whole male 584 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	2576	6999		4.9	63.3	Apr-Nov	whole female 619 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	2059	6486		5.1	68.6	Apr-Nov	whole immatures mean 507 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	2458	6885		5.1	64.6	Apr-Nov	all samples; mean 570 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	1247	5421		9.3	76.9	Apr-Nov	age 1	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	1637	6101		6.7	73.3	Apr-Nov	age 2 mean 304 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	2235	6721		6.5	69.9	Apr-Nov	age 3 mean 510 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	2652	7050		4.6	62.4	Apr-Nov	age 4 mean 566 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	2569	7014		4.9	63.5	Apr-Nov	age 5 mean 607 mm FL	Lake Michegan	Rottiers & Tucker 1982
S. namaycush	2739	7140		4.8	62.5	Apr-Nov	age 6 mean 644 mm FL	Lake Michegan	Rottiers & Tucker 1982
Oncorhynchus nerka	1254	5162			75.7	Jul	female immature; 294 mm FL; 145 g BW; age 1.1; gut not included	Gulf of Alaska	This study; mean values
O. nerka	1342	5326			74.8	Nov-Dec	female immature 413 mm FL; 693g BW	N Pacific	Davis et al. 1998
O. nerka	1920	5926			67.6	Nov-Dec	male immature 426 mm FL; 854 g BW	N Pacific	Davis et al. 1998
O. nerka	2330	6420			63.7	Nov-Dec	500 mm FL; 1366 g BW	N Pacific	Davis et al. 1998
O. nerka	1369	3446	3580	3.7	60.3	Aug-Sep	breeding females	Kamchatka	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. nerka	1943					Jun-Jul	muscle tissue, maturing female >300 mm FL	Bering Sea	Nishiyama 1977
O. nerka	1881					Jun-Jul	muscle tissue, maturing male >300 mm FL	Bering Sea	Nishiyama 1977
O. nerka	2910					Jun-Jul	maturing ovary from sockeye >300 mm FL	Bering Sea	Nishiyama 1977
O. nerka	1150					Jun-Jul	maturing testes fom sockeye >300 mm FL	Bering Sea	Nishiyama 1977
O. nerka (kokanee)	1291	3345	3479	3.8	61.4	Oct	breeding females	Kamchatka	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. keta	1113	4798			76.8	Jul	whole juvenile; mean 117 mm FL	Gulf of Alaska	This study; mean values

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
PISCES (continued)									
O. keta	1212	5203			76.7	Jan	female immature 217 mm FL; 112 g BW	N Pacific	Davis et al. 1998
O. keta	1188	5186			77.1	Nov-Dec	female immature 355 mm FL; 362 g BW	N Pacific	Davis et al. 1998
O. keta	1854	6100			69.6	Nov-Dec	female immature 420 mm FL; 701 g BW	N Pacific	Davis et al. 1998
O. keta	1249	5205			76.0	Nov-Dec	male immature 513 mm FL; 1215 g BW	N Pacific	Davis et al. 1998
O. keta	1597	3606	3745	3.7	55.7	Aug-Sep	breeding females	Kamchatka	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. gorbuscha	1174	4890			76.0	Jul	whole juvenile; mean 111 mm FL	Gulf of Alaska	This study; mean values
O. gorbuscha	1300	5307			75.5	Jan	female immature 242 mm FL; 137 g BW	N Pacific	Davis et al. 1998
O. gorbuscha	1796	5986			70.0	Jul	male maturing 473 mm FL; 1122 g BW	Gulf of Alaska	Davis et al. 1998
O. gorbuscha	1785	5833			69.4	Jul	female maturing 532 mm FL; 1838 g BW	Gulf of Alaska	Davis et al. 1998
O. gorbuscha	1687	4043	4187	3.4	58.3	Aug-Sep	breeding females	Kamchatka	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. gorbuscha	1565	3599	3732	3.6	56.5	Sep	breeding females	Murmansk	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. gorbuscha	980					May	juveniles; mean 34 mm FL	Gulf of Alaska	Boldt 2001
O. gorbuscha	927					Jul	juveniles; 92 mm FL	Gulf of Alaska	Boldt 2001
O. gorbuscha	1040					Aug	juveniles; 130 mm FL	Gulf of Alaska	Boldt 2001
O. kisutch	1381	3446	3592	4.1	59.9	Oct	breeding females	Kamchatka	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. kisutch	1931	6227		6.6	69.5	Apr-Nov	whole male 602 mm FL	Lake Michegan	Rottiers & Tucker 1982
O. kisutch	1866	6157		6.4	70.4	Apr-Nov	whole female 576 mm FL	Lake Michegan	Rottiers & Tucker 1982
O. kisutch	1664	6003		6.9	72.4	Apr-Nov	whole immature 503 mm FL	Lake Michegan	Rottiers & Tucker 1982

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
PISCES (continued)									
O. kisutch	1818	6123		6.5	70.8	Apr-Nov	all samples mean 560 mm FL	Lake Michegan	Rottiers & Tucker 1982
O. kisutch	2083	5917			64.8	Jul	male maturing 548 mm FL; 2656 g BW	Gulf of Alaska	Davis et al. 1998
O. kisutch	1287	5046			74.5	Jul	male maturing 630 mm FL; 2134 g BW	Gulf of Alaska	Davis et al. 1998
O. tshawytscha	1363	3649	3740	2.5	62.6	Aug	breeding females	Kamchatka	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. masou	1719	3767	3905	3.6	54.4	Aug-Sep	breeding females	Kamchatka	Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. masou	1566	3464	3588	3.5	54.8	Aug-Sep	breeding females		Smirnov, Kamyshnaya, & Kalashnikova 1968 (from Cummins & Wuycheck 1971)
O. mykiss	1228	4910			75.0	Jul	whole juvenile; 351 mm FL; 390 BW; age 3.0	Gulf of Alaska	This study; mean values
O. mykiss	1120	4889			77.1	Jul	juvenile; 288 mm FL; 105 BW; age 2.0; gut not included	Gulf of Alaska	This study; mean values
Centrarchidae		4677	5130				whole, mixed sizes & sexes		Cummins & Wuycheck 1971; grand mean
Gobidae		3880					whole, mixed sizes & sexes		Cummins & Wuycheck 1971; grand mean
Stichaeidae		4628	5332	13.2		Jun-Jul	larvae	Bering Sea	Nishiyama 1977
Bathymasteridae	1153	4487			74.3	Jul	whole; 42-48 mm SL	Bering Sea	Davis et al. 1998
Cyprinidae		5761					whole, mixed sizes & sexes		Cummins & Wuycheck 1971; grand mean
Labridae	1058	4880			78.3		whole, mixed sizes & sexes		Cummins & Wuycheck 1971; grand mean
Clupeidea	1927	6360			69.7		whole, mixed sizes & sexes		Cummins & Wuycheck 1971; grand mean
Cottidae		4620	5102				whole, mixed sizes & sexes		Cummins & Wuycheck 1971; grand mean
Cottidae	1110	4840	5850	17.2	77.0	Aug	whole	Gulf of Alaska	Perez 1994; mean values
Salmonidae	1492	3598	3736		58.5		breeding females		Cummins & Wuycheck 1971; grand mean
Osteichthyes	1493	5086	5296		70.6		whole, mixed sizes and sexes		Cummins & Wuycheck 1971; grand mean
Fish, Pelagic	1504		5784					NW Atlantic	Steimle & Terranova 1985
Fish, Pelagic	1459								Griffiths 1977 (from Steimle & Terranova 1985)

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
PISCES (continued)									
Fish, Pelagic	1925								Cummins & Wuycheck 1971 (from Steimle & Terranova 1985)
Fish Larvae		4241	4960	14.5		Jun-Jul	larvae	Bering Sea	Nishiyama 1977
Fish Larvae	1197	4567	5207	12.3	73.8	Jun-Jul	larvae	Bering Sea	Nishiyama 1977; mean values
Fish		4928							Griffiths 1977 (from Steimle & Terranova 1985)
Fish	1208	4924	5826	16.4	75.3	all		NW Atlantic	Thayer et al. 1973; mean values
OTHER ITEMS									
O. nerka stomach contents	838	5202			83.9	Jul	stomach contents (vol.)=small squid 43%, Pleurogrammus monopterygius 40%, Limacinahelicina 15%, Neocalanus cristatus 2%	Bering Sea	This study; stomach contents collected from maturing female sockeye; 560 mm FL; 2050 g BW; age 2.3; mean values
O. nerka stomach contents	862	5420			84.1	Jul	(vol.)= small squid 85%, Thysanoessa longipes 10%, Neocalanus cristatus 3%, Limacina helicina 2%	Bering Sea	This study; stomach contents collected from a maturing female sockeye; 620 mm FL; 3520 g BW; age 2.4; mean values
O. nerka stomach contents	1117	5639			80.2	Jul	stomach contents (vol.)=Thysanoessa longipes 98%, Neocalanus cristatus 1%, Hemilepidotus sp. 1%	Bering Sea	This study; stomach contents collected from maturing female sockeye; 604 mm FL; 2850 g GW; age 2.3; mean values
O. nerka stomach contents	1243	5864			78.8	Jul	stomach contents (vol.)=Thysaneossa longipes 95%, small squid 5%	Bering Sea	This study; stomach contents collected from immature male sockeye; 520 mm FL; 1440 mm FL; age 2.2; mean values
O. nerka stomach contents	1405	6243			77.5	Jul	(vol.)=Stenobrachius leucopsarus 64%, Thysanoessa longipes 25%, Neocalanus cristatus 5%, Themisto pacifica 3%, chaetognaths 3%	Bering Sea	This study; stomach contents collected from immature male sockeye; 562 mm FL; 1960 g BW; age 1.3; mean values
O. nerka salmon prey	1100					Jun-Jul	whole	Bering Sea	Nishiyama 1977; mean value Bristol Bay

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
OTHER ITEMS (continued)									
O. keta stomach contents	270	4287			93.7	Jul	Stomach contents (vol.)=ctenophores and medusae 95%, Clione limacina 4%, Limacina helicina 1%	Bering Sea	This study; stomach contents collected from maturing female; 606 mm FL; 3700 g BW; age 0.3; mean values
O. keta stomach contents	507	4450			88.6	Jul	Stomach contents (vol.)=Limacina helicina 96%, fish 4%	Bering Sea	This study; stomach contents collected from maturing male; 642 mm FL; 3000 g BW; mean values
O. keta stomach contents	739	5099			85.5	Jul	(vol.)=Limacina helicina 35%, Beroe and medusae 29%, Thysanoessa longipes 25%, Hymendora frontalis 5%, Clione limacina 3%, small squid 3%	Bering Sea	This study; stomach contents collected from maturing male; 542 mm FL; 3600 g BW; age 0.3; mean values
O. gorbuscha stomach contents	991	5161			80.8	Jul	Stomach contents (vol)=Fish 65% (Pleurogrammus monopterygius, Stichaeidae, Hemilepidotus, Bathymasteridae), small squid 20%, Neocalanus cristatus 2%, Limacina helicina 3%, Thysanoessa longipes 10%	Bering Sea	This study; stomach contents collected from maturing male; 462 mm FL, 1080 g BW; age 0.1; mean values
O. gorbuscha stomach contents	1091	5511			80.2	Jul	(vol.)=Thysanoessa longipes 79%, Neocalanus cristatus 10%, small squid 5%, Pleurogrammus monopterygius 5%, Clione limacina 1%	Bering Sea	This study; stomach contents collected from maturing female; 440 mm FL 1050 g BW age 0.1; mean values
O. gorbuscha stomach contents	1269	5768			78.0	Jul	Stomach contents (vol.)=Thysanoessa longipes 77%, Neocalanus cristatus 10%, Pleurogrammus monopterygius 10%, small squid 3%	Bering Sea	This study; stomach contents collected from maturing female; 452 mm FL 1170 g BW; age 0.1; mean values

Table 3.1. Continued.

Organism	cal/g W W	cal/g D W	cal/g AFDW	% Ash	% Water	Sample Month	Stage, Sex, or Body Part	Sample Area	Data Source and Comment
OTHER ITEMS (continued)									
O. tschawytscha stomach contents	1098	5969			81.6	Jul	Stomach contents (vol.)=small squid 95%, fish larvae (unidentified) 5%	Bering Sea	This study; stomach contents collected from male immature; 530 mm FL; 1960 g BW; age 1.2; mean values
O. tschawytscha stomach contents	1145	5425			78.9	Jul	Stomach contents (vol.)=Pleurogrammus monopterygius 97%, Neocalanus cristatus 3%	Bering Sea	This study; stomach contents collected from immature male; 331 mm FL; 430 g BW; age 1.1; mean values

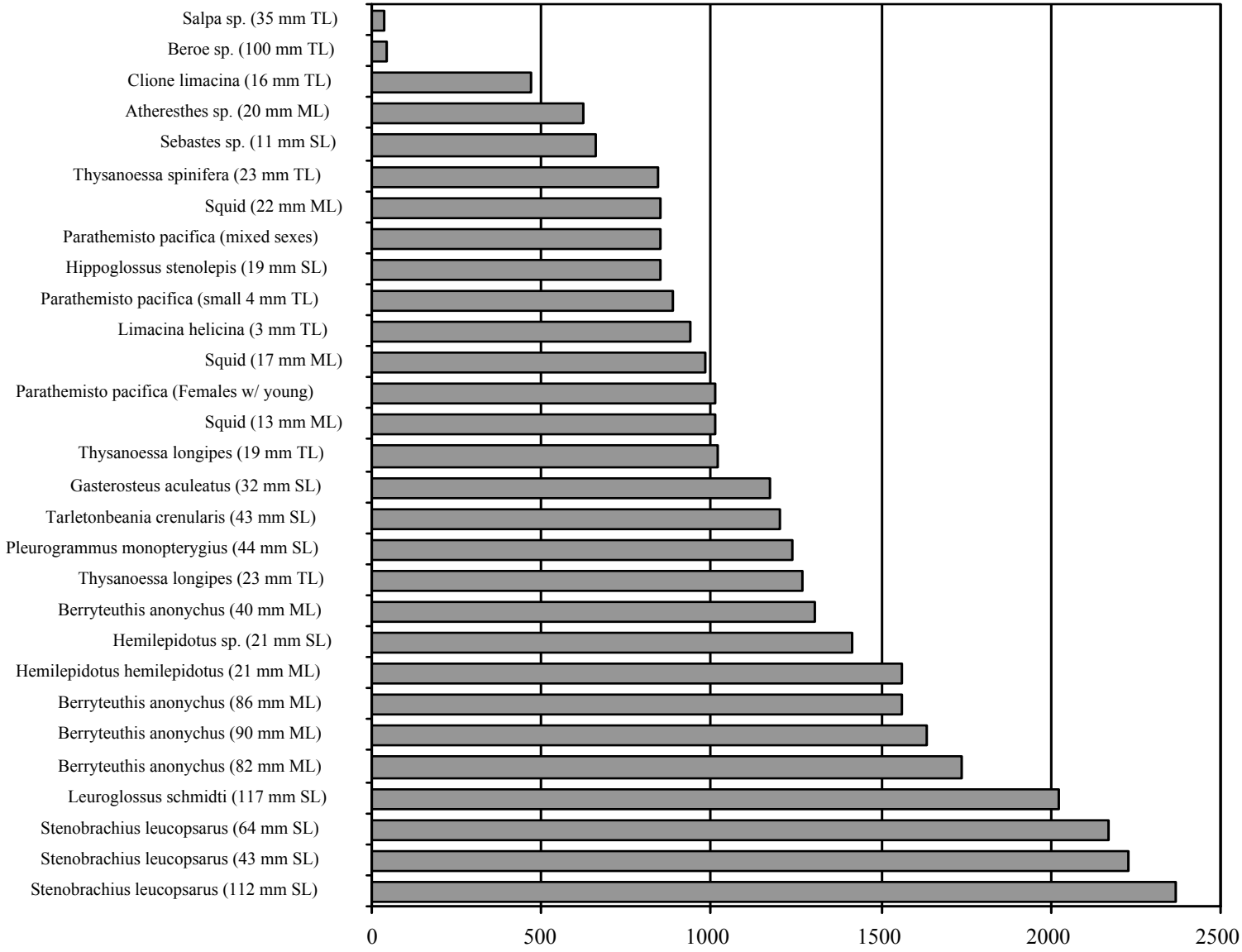

Figure 3.1. Energy density (calorie per gram wet-weight) of zooplankton, squid, and fish estimated from percent water in the sample and bomb calorimetry of the dry sample. Sizes are averages for each sample (SL=standard length, ML=mantle length, TL=total length).

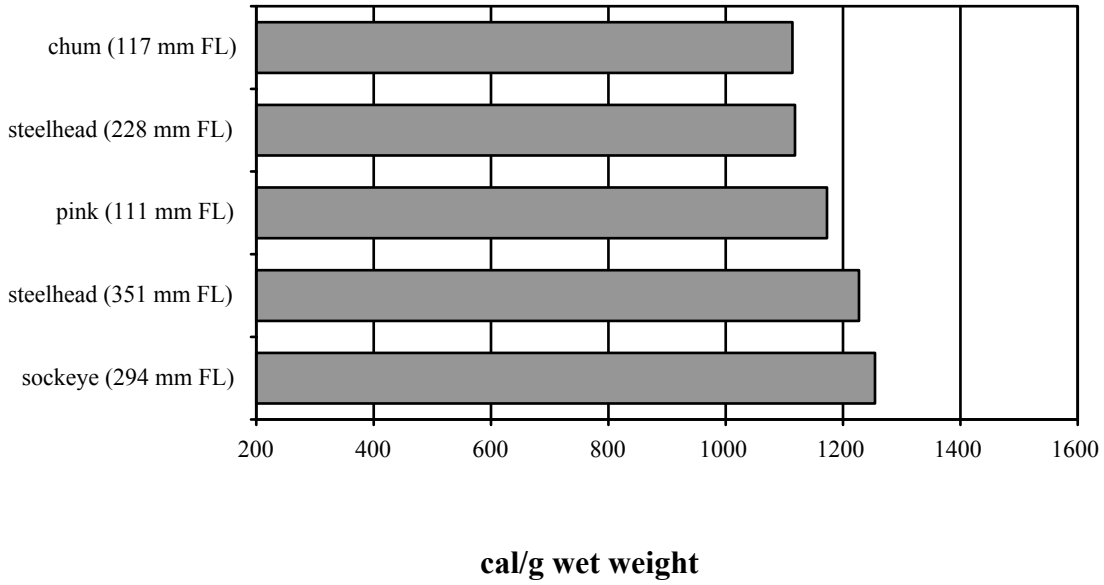

Figure 3.2. Energy density (calorie per gram wet weight) for sockeye (age 1.1), pink (age 0.0), and chum salmon (age 0.0), and steelhead (288 mm FL age 2.0; 351 mm FL age 3.0). Energy density of wet weight estimated from percent water in the sample and the mean calorific determination of two to four combustions of the dry sample. Fork lengths are shown in millimeters.

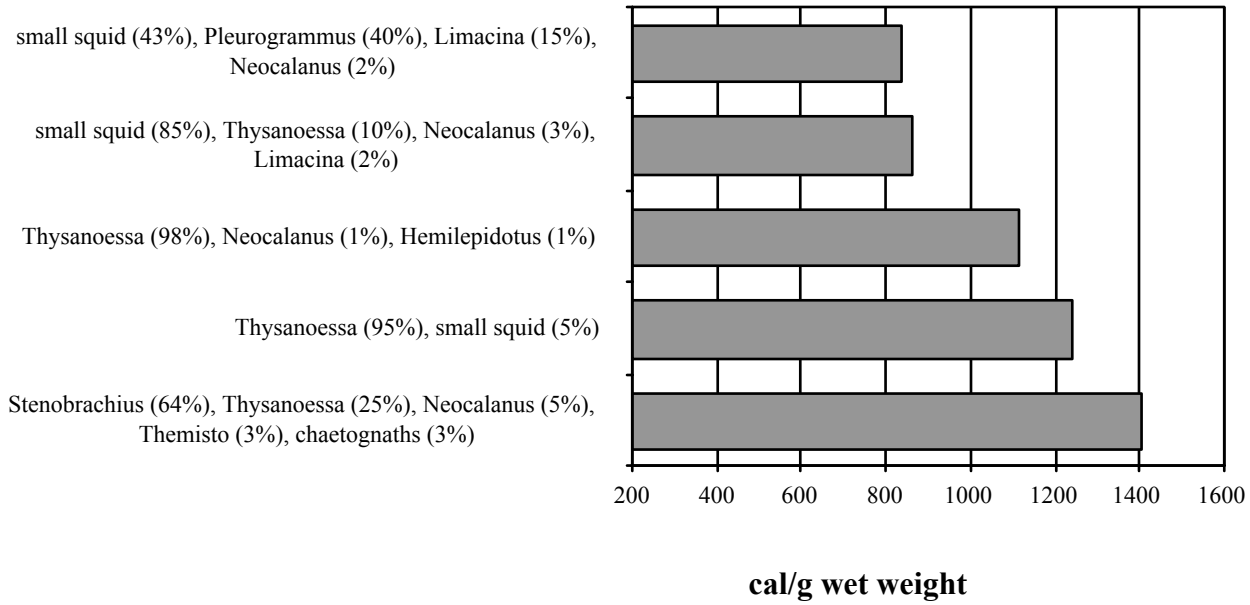

Figure 3.3. Energy density (calorie per gram wet weight) for sockeye salmon (520 to 620 mm FL) stomach contents. Each row represents a stomach sample for which the prey composition (percent volume) is listed. Energy density of wet weight estimated from percent water in the sample and the mean calorific determination of two to three combustions of the dry sample. *Pleurogrammus*= *P. monopterygius*, *Limacina*=*L. helicina*, *Neocalanus*=*N. cristatus* C5, *Thysanoess*a=*T. longipes*, *Stenograchius*=*S. leucopsarus, Themiso*= (*Para)themisto pacifica*.

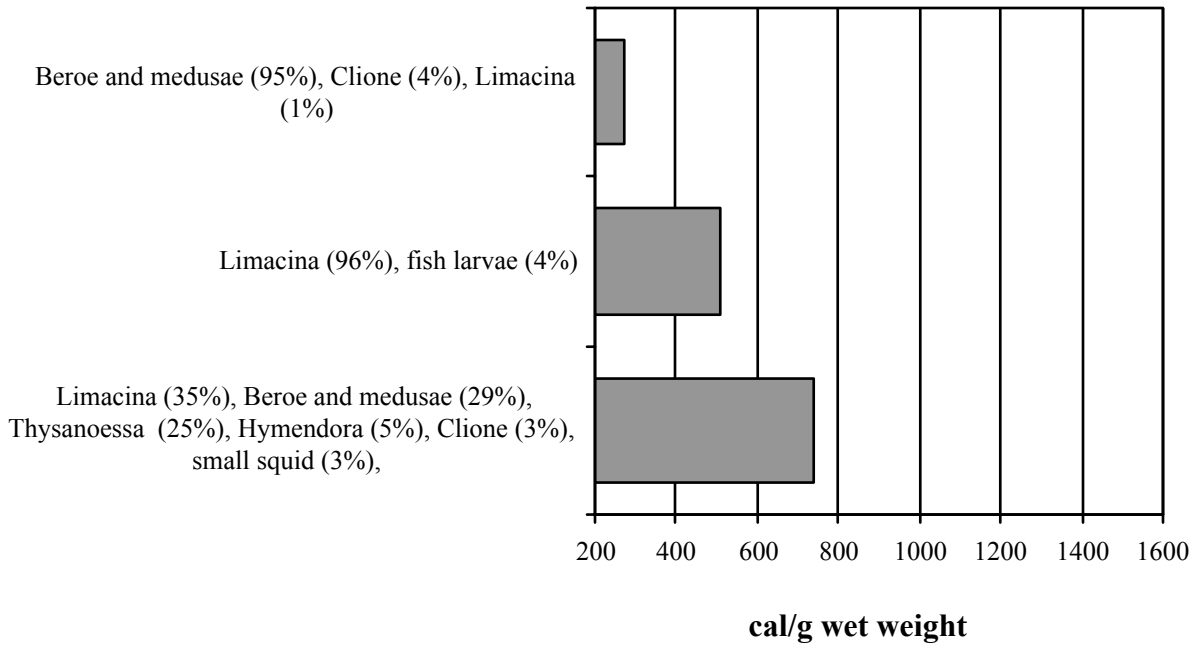

Figure 3.4. Energy density (calorie per gram wet weight) for chum salmon (542 to 642 mm FL) stomach contents. Each row represents a stomach sample for which the prey composition (percent volume) is listed. Energy density of wet weight estimated from percent water in the sample and the mean calorific determination of two to three combustions of the dry sample. *Clione=C. limacina*, *Thysanoessa=T. longipes*, *Hymendora=H. frontalis*.

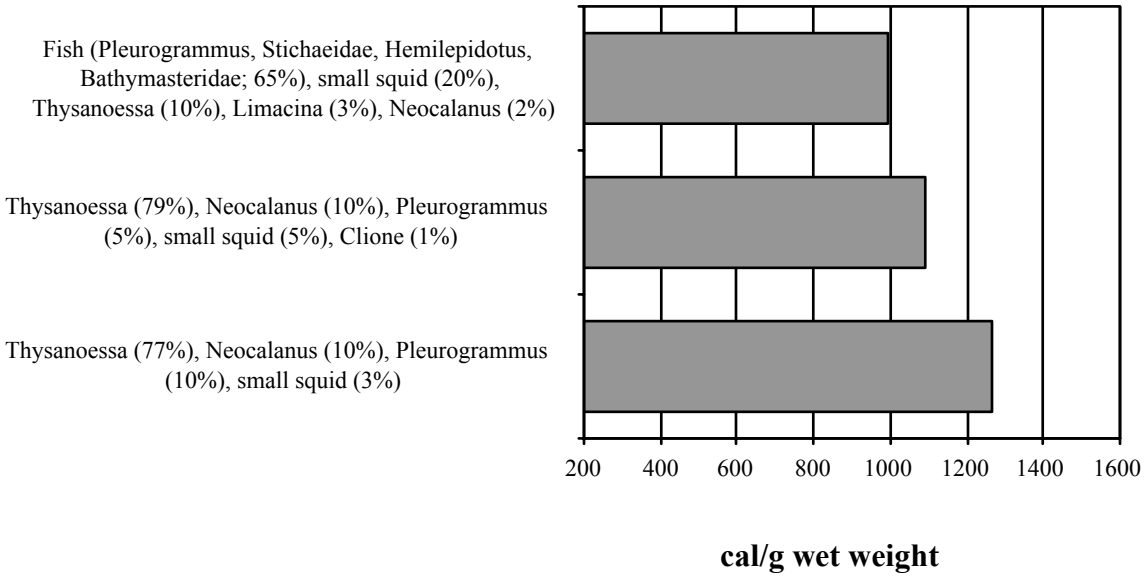

Figure 3.5. Energy density (calorie per gram wet weight) for pink salmon (440 to 642 mm FL) stomach contents. Each row represents a stomach sample for which the prey composition (percent volume) is listed. Energy density of wet weight estimated from percent water in the sample and the mean calorific determination of two to three combustions of the dry sample. *Pleurogrammus=P. monopterygius*, *Thysanoessa=T. longipes*, *Limacina=L. helicina*, *Neocalanus=N. cristatus* C5.

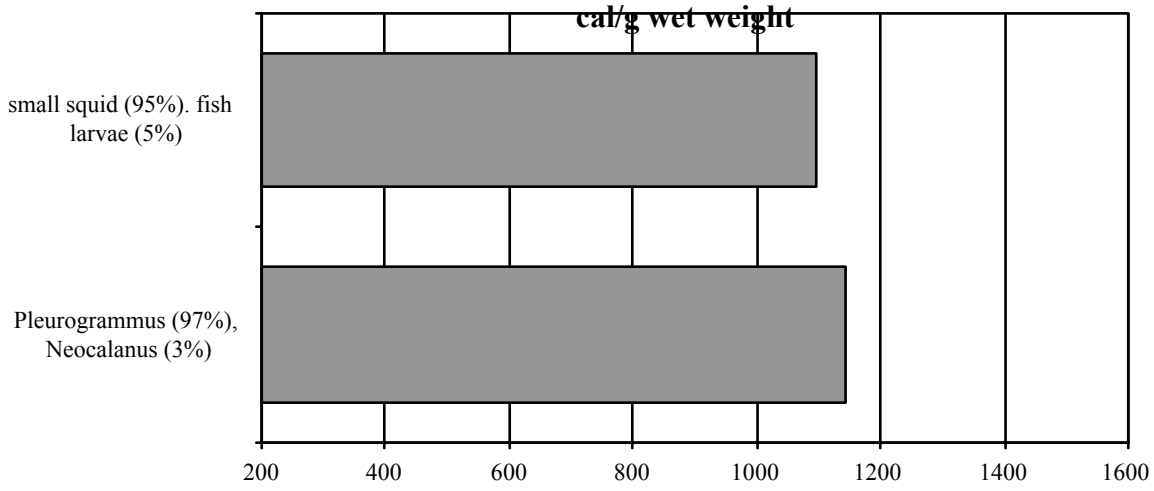

Figure 3.6. Energy density (calorie per gram wet weight) for chinook salmon (331 to 530 mm FL) stomach contents. Each row represents a different stomach sample for which the prey composition (percent volume) is listed. Energy density of wet weight estimated from percent water in the sample and the mean calorific determination of two combustions of the dry sample. *Pleurogrammus=P. monopterygius*, *Neocalanus=N. cristatus* C5.

Chapter 4.0 Estimates of daily food ration for sockeye, chum, pink and coho salmon

4.1. Introduction

Bioenergetic models are useful tools for extrapolating from stomach contents data to estimate prey consumption over time. Two researchers used bioenergetics to investigate the prey rations of adult salmon in offshore waters. Nishiyama (1970, 1974, 1977) examined the bioenergetics of maturing sockeye salmon in the Bering Sea as they migrate into Bristol Bay on their spawning run. He estimated the daily ration required for a 2211-g female was 39 kcal per kg per day and for a 2546-g male was 54 kcal per kg per day (Nishiyama 1970). Brett (1983, 1986) developed a bioenergetic model of the life history of Babine Lake sockeye salmon, and estimated the average daily ration for maturing fish was 41.4 kcal per kg per day. He suggested the ocean growth of salmon was maximal and could exceed those observed under laboratory conditions (Brett 1983).

In this study, I used field observations on sea surface temperatures and salmon food habits in summer in the central North Pacific Ocean and central Bering Sea, data on caloric density of salmon and salmon prey determined from bomb calorimetry, and a published fish bioenergetic model to simulate salmon growth and estimate prey consumption over a 60-day period. A 60-day period was selected because it encompassed a period when consumption rates might be at or near optimal, and the two months approximated the temporal scale of the field data. Growth estimates from the model were compared with summer monthly mean weights of high-seas caught salmon to evaluate daily ration. Gross conversion efficiency (growth/consumption), mean consumption rate (g-prey per day), total consumption by prey category (g), and total energy consumed (kcal) were estimated at the end of the 60-day simulated period.

4.2. Methods

Growth and prey consumption were calculated using the fish bioenergetics Model 2 (Hewett and Johnson, 1992). Model 2 uses a balanced energy equation where energy consumed in the diet equals energy expended for metabolism, waste elimination, and fish

growth. Factors that affect the energy budget are water temperature, fish size, predator and prey energy density, and prey availability. Model 2 input and output values are on a wet-weight basis, computations are specific rates (per unit body weight), and fish weight and consumption are computed on a daily basis in the simulation. Consumption is estimated from an allometric weight function giving the maximum specific consumption rate, modified by a proportionality constant representing prey availability and a temperature function (Table 4.1). The temperature algorithm is the product of two curves: the first curve is the relationship whereby consumption increases with increasing temperature up to a cut-off temperature, and the second is the relationship whereby consumption decreases above the cut-off temperature. This consumption algorithm simulates cold-water fish at low temperatures (Thornton and Lessem 1978). Respiration is determined by calculating the standard (resting) metabolism from an allometric weight function and modifying it for the effect of temperature, an activity factor, and specific dynamic action (metabolic heat loss from digestion of food). Egestion is a function of temperature and ration and includes a correction factor for the indigestible portion of each prey category. Excretion is a function of temperature, ration, and a proportion of consumption minus egestion.

The physiological parameter values provided with Model 2 software included values for pink and sockeye salmon (identical values), and coho salmon (Table 4.2). Because there were no parameter values given for chum salmon, I used the same parameter values given for pink and sockeye salmon and made a modification to the CA parameter (intercept for weight dependence of maximum consumption; Table 4.2). The CA parameter was increased from 0.303 to 0.394 (30%) because preliminary simulations indicated the consumption estimates were too low for chum salmon. This modification of the CA parameter was justified because the specific size of chum stomachs is larger than other salmon, enabling them to have a higher consumption rate (Azuma 1995, Welch 1997).

Pacific salmon are not equally abundant in all areas of the subarctic North Pacific (Pearcy 1992). Summertime gillnet and longline salmon catches in the central Bering

Sea are dominated by sockeye, chum, and, in odd-numbered years, pink salmon (see Chapter 1.0). I attempted to model growth and consumption for sockeye, chum, and pink salmon in conditions that closely resemble the central Bering Sea (52°-58°N, 180°) in summertime. Seawater temperatures frequently encountered in surface waters (0 to 30 m) in the central Bering Sea range from 5° to 9°C. For coho salmon, I modeled summertime conditions in the central North Pacific Ocean (44°-47°N, 180°) because coho salmon are abundant in catches in this area (Davis et al. 1996). Seawater temperature in the surface waters (0 to 40 m) of the central North Pacific Ocean frequently range from 7° to 11°C. Temperature was held constant for each 60-day simulation and separate simulations were run for each 1°C interval across the range of temperatures.

To determine the salmon prey composition for use in the bioenergetics model, salmon stomach contents from fish caught in the central North Pacific Ocean and central Bering Sea were used (see Chapter 1.0). Sockeye and pink salmon in the central Bering Sea have similar prey organisms found in their stomach contents including euphausiids, copepods, amphipods, squid, pteropods, and fish. Chum salmon caught in the central Bering Sea commonly feed on many of the same prey as sockeye and pink salmon, including euphausiids, amphipods, pteropods, and fish, but chum salmon have a broader assortment of prey organisms found in their stomachs because they also feed on gelatinous zooplankton. Coho salmon in the central North Pacific Ocean feed primarily on squid and secondarily on hyperiid amphipods. The prey composition used for the bioenergetics model was the mean percent composition of the common prey categories observed for sockeye, chum, and pink salmon caught in the central Bering Sea, and coho salmon caught in the central North Pacific Ocean normalized to equal 100% (Table 4.3).

The proportion of prey energy content that was indigestible by salmon was calculated based on proximate and moisture content from other studies of the same or closely-related prey species. The gross energy content and the digestible energy content of each prey species were calculated. Gross energy values for protein (5640 cal per g dry weight), lipid (8700 cal per g dry weight), and carbohydrate (4111 cal per g dry weight;

Higgs et al. 1995) were multiplied by the proximate composition determined by other authors (McBride et al. 1959; Ikeda 1972; Nishiyama 1977; Higgs et al. 1995). To determine the digestible energy content, the energy digestible by salmon of protein (5091 cal per g dry weight), lipid (8508 cal per g dry weight) and carbohydrate (3800 cal per g dry weight; Higgs et al. 1995) was multiplied by the proximate composition particular to each prey species. Dividing the digestible energy content by the gross energy content gave the proportion of digestible energy available in each prey organism. The proportion of indigestible energy was calculated by subtracting the proportion of digestible energy from one (Table 4.4).

The caloric density for medusae used in the bioenergetics model was the average of the density determined by Ikeda (1972) for *Aglantha digitale* and for medusae by Davis et al. (1998; Table 4.4). I used the caloric density for squid determined by Nishiyama (1977) for small squid eaten by sockeye and pink salmon in the Bering Sea and the density for large *B. anonychus* squid determined by Davis et al. (1998). Caloric densities for copepods, euphausiids, hyperiids amphipods, pteropods, appendicularians, and fish used in the model were those of Davis et al. (1998). The caloric density of fish prey was the mean value for juvenile *Hemilepidotus* spp. and *P. monopterygius*. The predator energy density for pink and sockeye salmon was defined as a function of weight (following Hewitt and Johnson 1992), and values of 1375 cal per g wet weight and 2083 cal per g wet weight were used for chum and coho salmon (Table 4.3).

The life history stages I selected for the simulations represent common ages and maturity stages of salmon caught in the central Bering Sea and central North Pacific Ocean during summertime cruises of the *Wakatake maru* (see Chapter 1.0). Central Bering Sea salmon catches were primarily composed of sockeye, chum, and pink salmon. Immature ocean age .1 sockeye and ocean age .2 chum salmon were selected because these life history groups were common. All pink and coho salmon caught by the *Wakatake maru* are maturing ocean age .1, the life-history stage for my simulations. Individual salmon weights used in the simulations were the mean weights for June through July (60 days) for immature ocean age .1 sockeye (growing from 361 to 568 g),

immature ocean age .2 chum (growing from 1042 to 1547 g), and maturing pink (growing from 912 to 1313 g) and coho salmon (growing from 1909 to 2975 g) calculated from data collected by researchers on Japanese research vessels operating in the North Pacific Ocean and Bering Sea (1972-1995; Ishida et al. 1998). These weights are an approximation of what the specific age and maturity groups might gain over the summer. The true initial weight and growth of an individual salmon from the Bering Sea and central North Pacific Ocean might be different from these values because the mean values are pooled over a large geographical area and from different salmon stocks. It is possible that an individual salmon feeding and residing in different oceanographic habitats would have significantly different growth rates than the average values used in these simulations.

Daily ration levels used in the simulations included daily maintenance (daily ration resulting in zero growth), daily percent of body weight (1%, 2%, 3%, 4% of wet body weight), and the physiological maximum ration. The physiological maximum is calculated daily and is expressed as a percentage of body weight, decreasing as the fish grows. Over the 60-day period, net production (g), gross conversion efficiency (%; cumulative growth [g]/cumulative consumption [g]), and average consumption rate (total prey consumed g per 60 days) were calculated. Prey consumption was summarized by total weight (g) of each prey category consumed and the total energy consumed (kcal) over the 60-day period.

4.3. Results

The estimated maintenance ration for an immature ocean age .1 sockeye in the central Bering Sea in June and July ranged from 0.8 to 1.3% body weight per day at 5-9°C (Table 4.5). The maintenance ration increased with temperature as the energetic costs of metabolism increased. Likewise, the physiological maximum ration increased from 3.6 to 5.0% body weight per day over the 5-9°C temperature range considered. Net production at each ration level decreased as the temperature increased. For example, at a constant ration of 2% body weight per day, the net production decreased by 43% between 5-9°C. Gross conversion efficiency was highest at the maximum ration and the lowest

temperature (21.5%, 5°C). An ocean age .1 sockeye growing from 361 to 568 g would, therefore, consume an average of 16-19 g of prey per day, the equivalent of 3.57 to 4.09% body weight per day (27-31 cal per g-predator per day), depending on temperature. To achieve this net production (207 g), the sockeye would have to feed at 88 to 93% of its physiological maximum rate. Over two months, the total prey consumption was estimated as 0.975-1.116 kg, the equivalent of 731-837 kcal (Table 4.5).

The estimated maintenance ration for an immature ocean age .2 chum salmon in the central Bering Sea ranged from 0.9 to 1.4% body weight per day and the maximum ration ranged from 3.5 to 4.8% body weight per day at 5-9°C (Table 4.6). At a daily ration of 2% body weight per day, net production decreased by 52% from 5° to 9°C. To grow from 1042 to 1547 g, a mean ration of 3.28-3.86% body weight per day (20-24 cal per g-predator per day) was required, which was a daily consumption rate of 42 to 49 g-prey per day, or 85 to 89% of its physiological maximum consumption rate per day, depending on temperature. Estimated chum salmon cumulative consumption for two months was 2.506-2.949 kg or 1531-1803 kcal (Table 4.6).

The estimated maintenance ration for a maturing ocean age .1 pink salmon in the central Bering Sea ranged from 0.6 to 1.0% body weight per day, and the physiological maximum ration ranged from 2.8 to 3.9% body weight per day at 5-9°C (Table 4.7). At a daily ration of 2% body weight per day, net production decreased by 31% from 5° to 9°C. If a maturing pink salmon grew 912-1313 g, the required ration was estimated as 2.73-3.14% body weight per day (24-27 cal per g-predator per day) and a daily prey consumption of 30-35 g per day, or 86 to 94% of its physiological maximum consumption rate per day, depending on temperature. Over 60 days, 1.800-2.068 kg of prey, or 1552-1783 kcal were estimated to be consumed (Table 4.7).

The estimated maintenance ration for a maturing ocean age .1 coho salmon in the central North Pacific Ocean ranged between 0.7 and 1.1% body weight per day, and the physiological maximum consumption ranged from 2.0 to 3.4% body weight per day at 7-11°C (Table 4.8). At a daily ration of 2% body weight per day, net production decreased

by 33% from 7° to 11°C. A maturing coho salmon growing from 1909 to 2975 g would consume 2.64-2.86% body weight per day (37-40 cal per g-predator per day) and a daily prey consumption of 63-68 g-prey per day at 9° to 11°C, or 91 to 96% of its physiological maximum consumption rate. Over two months, 3.785-4.105 kg of prey, or 5248-5693 kcal of energy would be consumed (Table 4.8).

4.4. Discussion

The bioenergetics approach was helpful in making estimates of consumption and growth using field based observations of salmon food habits and environmental conditions. The bioenergetics Model 2 developed by Hewitt and Johnson (1992) has been used in previous studies to estimate consumption by juvenile sockeye and coho in freshwater and juvenile coho and chinook salmon in coastal waters, and in those cases, the model was in close agreement with laboratory experiments (Beauchamp et al. 1989; Brodeur et al. 1992; Ruggerone and Rogers 1992). Because the model is constrained by the balanced energy equation, it limits error propagation from the numerous parameters used in the model (Hansen et al. 1993). Model parameter estimates could be improved by additional laboratory experiments measuring the metabolic cost of activity at several levels of swimming effort.

The specific energy requirements (27-31 cal per g-predator per day) for small (361-568 g) sockeye salmon determined in this study were the first estimates available for young ocean age .1 sockeye in the Bering Sea (Table 4.5). Nishiyama (1970), also working on sockeye salmon in the Bering Sea, estimated the energy requirements of large (2211 and 2546 g), maturing fish on their spawning migration to Bristol Bay. As expected, Nishiyama's (1970) estimates (39 cal per g-predator per day for females; 54 cal per g-predator per day for males) were higher than mine because he analyzed sockeye salmon undergoing an active spawning migration, and because of large differences in weight, maturity, and age of the fish in the two studies. Specific consumption increase and the ration (as a percentage of body weight) gradually decrease as fish grow. Sockeye salmon gross conversion efficiency in this study was estimated at 18.5-21.2%, slightly less than the lifetime conversion efficiency (26%) estimated for Babine Lake sockeye

salmon (Table 4.5; Brett 1986). The conversion efficiency will likely be higher for older, larger fish, thereby raising the lifetime efficiency for sockeye with two to three years at sea above that determined for the ocean age .1 sockeye salmon in this study. Brett (1983, 1986) hypothesized high conversion efficiency was part of a strategy whereby juvenile sockeye salmon fed heavily in coastal areas, quickly attained a large size and reduced size-dependent mortality, and that sockeye sustained a high growth rate throughout their ocean residence until they return to freshwater for spawning. However, my growth data were pooled, therefore the sockeye salmon were not from a single stock or ocean production area. There may be considerable variation in growth rates among stocks and production areas (Brett 1986).

I estimated the daily maintenance ration (ration for zero growth) required by an ocean age .1 sockeye in the central Bering Sea ranged from 0.8 -1.3% body weight, depending on water temperature (Table 4.5). In comparison, Bilton and Robins (1971) conducted experiments on juvenile sockeye salmon in cold freshwater, and they determined fish could withstand a sustained period of starvation, i. e., zero ration, for 20 weeks with no change in mean weight and low mortality during the starvation period. These results indicate the effect of low temperature depressing the energy demands of metabolism. The water temperature used by Bilton and Robins (1971) was less than 5°C, whereas my estimates were based on temperatures at 5°C or greater. In addition, they were using smaller fish (approximately 7 g body weight) at a different life-history stage (lake-dwelling juveniles) and season than I investigated. Their fish were confined to experimental tanks, whereas I assumed an activity level sufficient for salmon to search for and consume prey. My results showed higher temperatures and higher fish activity levels increase energy demands that results in a small, nonetheless required, energy intake for sockeye salmon to maintain their body weight in the ocean in the summertime.

My estimates of daily ration for an immature ocean age .2 chum salmon (3.3-3.9% body weight; 20-24 cal per g-predator per day) and a maturing pink salmon (2.7-3.1% body weight; 24-27 cal per g-predator per day; Tables 4.6, 4.7) in the central Bering Sea were smaller than the estimates Gorbatenko and Chuchukalo (1989) obtained for pre-

spawning adult chum (7% body weight) and pink salmon (5.8-6.4% body weight) caught on the West Kamchatka shelf in summer. They estimated ration from amount of food consumed and digestion rates. Perhaps my estimates were lower because I assumed a higher prey caloric density and prey digestibility than Gorbatenko and Chuchukalo (1989). However, they did not report the caloric densities or digestibility values used to make their estimates of daily ration, therefore, I cannot determine whether this assumption was correct.

My estimate of 2.6-2.9% body weight (37-40 cal per g-predator per day) daily ration for maturing coho salmon was the first estimate determined for adult coho in offshore marine habitats (Table 4.8). Brodeur and Pearcy (1987) determined daily ration for juvenile coho at 2.4-3.7% body weight for temperatures slightly warmer than those used in this study. At 7° and 8°C, my coho salmon simulations were not able to attain the 1066 g net production indicated from the mean monthly values from the high-seas salmon research vessel data. This indicates either that the model consumption parameters were too low for an offshore maturing coho salmon, or that the mean monthly fish size values were too large. Consumption would have to increase by 18% (increase CA from 0.303 to 0.359) in order for simulated net production to equal 1066 g under conditions of a constant 7° or 8° C thermal habitat. Coho salmon have been caught at 7° and 8° C, so it is not likely that the thermal conditions were unrealistic. Examination of coho salmon stock- and location-specific ocean growth deserves further study.

If estimates of monthly growth during June and July were reasonable, then the most significant result from these simulations was that salmon were feeding at a rate close to their physiological maximum (85 to 93% of the maximum for immature sockeye and chum, and 86 to 96% of the maximum for maturing pink and coho salmon). In addition, my estimates indicate that small decreases in the daily ration can cause significant decreases in growth over a time period as short as two months during the summer, when feeding and growth opportunities should be at or near optimal. Growth estimates used in these simulations were from pooled data, which may not represent the growth rate of a particular stock, or growth condition in a specific ocean production area.

Therefore, stock- and ocean region-specific growth data for particular stocks and time periods are needed for further bioenergetic modeling and to evaluate the recently observed decrease in fish size observed in many Pacific Rim salmon stocks.

The balance between growth and metabolism is affected by temperature (Jobling 1994). As temperature increases, prey consumption and metabolism increase, but the energetic requirements of metabolism increase faster than the energy gained through increasing consumption, thus growth is reduced (Brett et al. 1969). Assuming prey was abundant and that salmon resided in summertime temperatures similar to those used in my simulations (5-9°C in the central Bering Sea and 7-11°C in the central North Pacific Ocean), I speculate that as the energy requirements of metabolism increase with temperature, prey consumption increases and provides sufficient energy for substantial growth. In this temperature range, prey availability rather than metabolic efficiency governs how much the salmon will grow. Welch et al. (1995) observed a step-function response in salmon catch data to upper sea surface temperatures in the northeastern Pacific Ocean in the spring. Perhaps the upper thermal limits Welch et al. (1995) described represent the temperature where energy demands of metabolism begin to rapidly exceed the energy supplied by consumption, even when prey is readily available and the consumption rate is at a maximum. I suggest that there may be lower thermal limits below which, although the energy conversion efficiency for salmon is high because metabolic demands are low, consumption rates are also low, and therefore growth is substantially reduced. For example, hydroacoustic data from a winter trans-Pacific survey showed that salmon were not in sub-surface waters colder than 4°C (Sakai et al. 1996). If true, when salmon prey is abundant, an upper thermal limit favorable for salmon growth may be bounded by large metabolic requirements at high temperatures, and a lower limit favorable for salmon growth may be bounded by decreased capacity for prey consumption at low temperatures.

Characterization of the fish's thermal experience is crucial in bioenergetic modeling because changes in temperatures can have a large effect on energy conversion efficiencies and, therefore, growth of salmon. Movements of salmon during their

summer ocean residence have been detected using transmitters mounted on salmon in conjunction with oceanographic temperature probes to estimate the thermal experience of individual salmon (Ogura and Ishida 1992, 1995, Ogura 1994). More recently, data storage tags recording temperature and depth data have been attached and successfully recovered from Pacific salmon migrating two to three months in the North Pacific Ocean (Walker et al. 1999, 2000a, b; Friedland et al. 2001). Walker et al. (2000a) compared simulated growth and consumption estimates of salmon based on constant temperatures, as used in this study, with results obtained from the temperature information recorded by data storage tags attached to salmon migrating in the ocean. They concluded the average difference in final weight was 1.23% less when information from a data tag was used. This suggests that employing a constant temperature scenario, as I did, may result in an overestimate of daily ration.

Temperature and depth records from data storage tags carried by maturing salmon on the high seas have determined that salmon have a well-developed diurnal vertical migration pattern during the summer and fall (Wada and Ueno 1999; Walker et al. 2000b). During the day, salmon make repeated dives to cooler, deeper water and at night they make few excursions to depth and remain in the warmer surface waters (upper 20 m; Walker et al. 2000b). The nighttime surface orientation is attributed to feeding at the surface on vertically migrating zooplankton and micronekton (Walker et al. 2000b). The frequent up and down movement by salmon during the day may result from salmon following prey descending from the surface, thermoregulation to reduce metabolic costs, developing orientation cues, making greater distance on their homeward migration, or a combination of these purposes (Wada and Ueno 1999, Walker et al. 2000b, Friedland et al. 2001). Diurnal behavior during the oceanic phase of the salmon's homeward migration may be quite different than the behavior exhibited upon approaching inlets and their natal rivers (Walker et al. 2000b, Tanaka et al. 2000, Murphy and Heard 2001), or different from the behavior of immature fish in the ocean during the wintertime. In the future, when data storage tags are recovered from salmon carrying a tag throughout the winter, these data will revolutionize annual estimates of salmon consumption and our understanding of salmon ocean behavior.

Table 4.1. Equations used to calculate consumption, respiration, egestion, and excretion by salmon in the Bering Sea and Subarctic Current. Symbols and equations are those of Hewett and Johnson (1992).

(1) Consumption

$C = CA * W^{CB} * P * f(T)$

where $f(T) = K_A * K_B$

$K_A = (CK1 * L1) / (1 + CK1 * (L1 - 1))$

$L1 = e^{(G1 * (T - CQ)}$

$G1 = (1 / (CTO - CQ)) * LN ((0.98 * (1 - CK1))/(CK1 * 0.02))$

$K_B = (CK4 * L2) / 1 + CK4 * (L2 - 1))$

$L2 = e^{(G2 * (CTL - T))}$

$G2 = (1 / (CTL - CTM)) * LN ((0.98 * (1 - CK4)) / (CK4 * 0.02))$

(2) Respiration

$R = (RA * W^{RB} * f(T) * Activity) + (SDA * (C - F))$

where $f(T) = e^{(RQ * T)}$

$Activity = e^{((RTO - (RTM * T)) * VEL)}$

$VEL = RK1 * W^{(RK4)}$ when temperature is >25°C

$VEL = ACT * e^{(BACT * T)} * W^{(RK4)}$ when temperature is ≤25°C

(3) Egestion

$F = PF * C$

where $PF = ((PE - 0.1) / (1 - 0.1)) * (1 - PFF) + PFF$

$PE = FA * T^{FB} * e^{(FG * P)}$

$PFF = \sum (PREYK[n] * DIET[n]$, for n = 1 to number of prey categories

PREYK[n] = indigestible proportion of the nth prey

DIET[n] = proportion of nth prey in the diet

(4) Excretion

$U = UA * T^{(UB)} * e^{(UG * P)} * (C - F)$

Table 4.2. Fish bioenergetics Model 2 parameter values used to estimate growth and prey consumption by sockeye, chum, pink, and coho salmon given a constant daily food ration (Hewett and Johnson 1992).

Sym-bol	Physiological Parameter Value	Nominal Value		
		Pink/ Sockeye	Chum	Coho
	CONSUMPTION (CON)			
C	Specific feeding rate (g/g/day)			
P	Constant proportion of maximum feeding rate			
W	Fish weight (g)			
CA	Intercept for weight dependence of CON	0.303	0.394	0.303
CB	Slope for weight dependence of CON	-0.275	-0.275	-0.275
CQ	Lower temperature where dependence is CK1	3	3	5
CTO	Higher temperature where dependence is 0.98 of max	20	20	15
CTM	Temp□CTO where dependence is still .98 of max	20	20	18
CTL	Temperature where dependence is CK4	24	24	24
CK1	Temperature dependendence at CQ	0.58	0.58	0.36
CK4	Temperature dependence at CTL	0.50	0.50	0.01
	RESPIRATION (RES)			
R	Specific rate of respiration (g-O2/g/day)			
RA	Intercept for std. matabolism vs weight, temperature, and swimming speed	0.00143	0.00143	0.00264
RB	Slope for weight dependence of standard metabolism	-0.209	-0.209	-0.217
RQ	Coefficient for temperature dependence of metabolism	0.086	0.086	0.06818
RTO	Coefficient for swimming speed dependence of metabolism	0.0234	0.0234	0.0234
RTM	Coefficient for swim speed dependence of temperature	0	0	0
RTL	Cut-off temp	25	25	25
RK1	Intercept for weight dependence of swimming speed when temperatures >RTL	1	1	1
RK4	Slope for weight dependence of swimming speed at all temperatures	0.13	0.13	0.13
ACT	Intercept for swimming speed vs temperature and weight (cm/sec/1-g fish at 0°), when temperature <RTL	9.9	9.9	9.7
BACT	Coefficient for temperature dependence of swimming speed when temperature <RTL	0.0405	0.0405	0.0405
SDA	Proportion of assimilated energy lost to specific dynamic action	0.172	0.172	0.172
	EGESTION (EGES)			
F	Specific rate of egestion (g/g/day)			
FA	Intercept for proportion of consumption EGES vs temperature and ration	0.212	0.212	0.212
FB	Slope for temperature dependence of EGES	-0.222	-0.222	-0.222
FG	Coefficient for feeding level dependence of EGES	0.631	0.631	0.631
	EXCTRETION (EXCR)			
UA	Intercept for proportion of assimilated consumption EXCR vs temperature and ration	0.0314	0.0314	0.0314
UB	Slope for temperature dependence of EXCR	0.58	0.58	0.58
UG	Coefficient for feeding level dependence of EXCR	-0.299	-0.299	-0.299

Table 4.3. Environmental temperatures, salmon,m and prey characteristics used as input values to simulate conditions in the central North Pacific and Bering Sea. Grams are expressed on a wet weight basis. Prey caloric density is the gross energy content, and the mean prey caloric density is weighted by the prey composition.

Salmon predator	Predator caloric density (cal/g)	Region	Temperature range (°C)	Prey category	Prey composition	Prey caloric density (cal/g)	Proportion indigestible
Sockeye	1633-1665*	Bering Sea	5° to 9°	euphausiids	0.14	743	0.1035
				copepods	0.13	627	0.0904
				amphipods	0.24	589	0.1299
				squid	0.25	732	0.0891
				pteropods	0.08	624	0.0907
				fish	0.16	1185	0.0898
				mean		749	
Chum	1376	Bering Sea	5° to 9°	euphausiids	0.26	743	0.1035
				amphipods	0.12	589	0.1299
				pteropods	0.11	624	0.0907
				fish	0.12	1185	0.0898
				medusae	0.27	169	0.1125
				appendicula	0.12	759	0.0926
				mean		611	
Pink	1702-1752*	Bering Sea	5° to 9°	euphausiids	0.15	743	0.1035
				copepods	0.08	627	0.0904
				amphipods	0.09	589	0.1299
				squid	0.30	732	0.0891
				pteropods	0.04	624	0.0907
				fish	0.34	1185	0.0898
				mean		862	
Coho	2083	Subarctic Currrent	7° to 11°	squid	0.83	1550	0.0775
				amphipods	0.17	589	0.1299
				mean		1387	

*predator energy density is a linear function of body weight

Table 4.4. Gross caloric density (cal/g wet weight) for salmon prey organisms, and the estimated proportion of prey that is indigestible for salmon.

Organism or group	cal/g wet weight	Proportion Indigestible	Source
Cnidaria			
Aglantha digitale	202	0.1125	Ikeda 1972
Copepods			
Neocalanus cristatus	717	0.0886	Nishiyama 1977
N. cristatus	910	0.1094	Ikeda 1972
Copepods	1104	0.0731	Higgs et al. 1995
Euphausiids			
Thysanoessa raschii	928	0.1103	Ikeda 1972
Euphausia pacifica	1107	0.1018	Nishiyama 1977
Thysanoessa spp.	1117	0.0966	Nishiyama 1977
Euphausiacea	1130	0.1053	Higgs et al. 1995
Amphipods			
Parathemisto pacifica	665	0.1151	Nishiyama 1977
P. libellula	716	0.1204	Nishiyama 1977
Euthemisto libellula	975	0.1541	Ikeda 1972
Pteropods			
Limacina helicina	636	0.0850	Nishiyama 1977
Clione limacina	563	0.0744	Nishiyama 1977
C. limacina	520	0.1127	Ikeda 1972
Cephalopoda			
Squids	732	0.0891	Nishiyama 1977
Squids	1134	0.0659	Higgs et al. 1995
Pisces			
Clupea pallasi	2341	0.0774	McBride et al. 1959
Mallotus villosus	1179	0.0945	Higgs et al. 1995
Tarletonbeania crenularis	1060	0.1029	Nishiyama 1977
Unidentified Fish	1633	0.0844	Higgs et al. 1995

Table 4.5. Estimated sockeye salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 immature sockeye salmon in the Bering Sea in June and July and an initial weight of 361 g. Main=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross conversion Efficiency (%)=total growth (g)/total weight of prey consumed(g) after 60 days. Prey consumption rate=total prey consumed (g)/ 60 days. Wt=weight (g), BW=body weight, EU=euphausiids, CO=copepods, AM=hyperiid amphipods, SQ= squid, PT=pteropod, FI=fish.

Sockeye Salmon

Temp (°C)	Daily Ration (% BW/day)	Final Wt. (g)	Net Production (g)	Gross Conversion Efficiency	Consumption Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	CO	AM	SQ	PT	FI	Total	
5	maint (0.8%)	361	0	0.0	3.0	25	23	43	44	14	28	177	132.9
	1.0% BW	372	11	5.0	3.7	31	29	53	55	18	35	221	164.7
	2.0% BW	439	78	16.4	8.0	67	62	115	119	38	76	477	358.1
	3.0% BW	518	157	20.1	13.0	109	101	187	195	62	125	779	584.6
	3.57% BW	568	207	21.2	16.2	136	127	234	244	78	156	975	730.6
	max (3.6-4.1%	589	228	21.5	17.7	148	138	254	265	85	170	1060	794.3
6	maint (0.9%)	361	0	0.0	3.3	28	26	48	50	16	32	200	148.9
	1.0% BW	366	5	2.2	3.6	31	28	52	55	17	35	218	163.4
	2.0% BW	432	71	15.0	7.9	66	62	114	118	38	76	474	355.0
	3.0% BW	509	148	19.1	12.9	108	101	186	193	62	124	774	579.5
	3.68% BW	568	207	20.6	16.8	141	131	241	251	80	161	1005	753.4
	max (3.8-4.3%	602	241	21.1	19.0	159	148	273	285	91	182	1138	853.2
7	maint (1.0%)	361	0	0.0	3.7	31	29	54	56	18	36	224	167.4
	2.0% BW	424	63	13.4	7.8	66	61	113	117	38	75	470	351.6
	3.0% BW	499	138	18.1	12.8	107	100	184	191	61	122	765	573.7
	3.8% BW	568	207	20.0	17.3	145	135	249	260	83	166	1038	777.9
	4.0% BW	587	226	20.3	18.5	156	145	267	278	89	178	1113	833.0
	max (4.0-4.6%	611	250	20.7	20.2	169	157	290	302	97	193	1208	906.2
8	maint (1.2%)	361	0	0.0	4.2	35	33	60	63	20	40	251	188.6
	2.0% BW	415	54	11.6	7.7	65	60	111	116	37	74	463	347.8
	3.0% BW	488	127	16.8	12.6	106	98	182	189	61	121	757	567.1
	3.94% BW	568	207	19.3	17.9	151	140	258	269	86	172	1076	806.6
	4.0% BW	574	213	19.4	18.3	154	143	264	275	88	176	1100	823.1
	max (4.1-4.8%	616	255	20.1	21.2	178	165	305	318	##	203	1271	952.5
9	maint (1.3%)	361	0	0.0	4.7	40	37	68	71	23	45	284	212.8
	2.0% BW	405	44	9.5	7.6	64	60	110	115	37	73	459	343.5
	3.0% BW	476	115	15.4	12.5	105	97	179	187	60	120	748	559.8
	4.0% BW	560	199	18.3	18.1	152	141	260	271	87	173	1084	812.1
	4.09% BW	567	206	18.5	18.6	156	145	268	279	89	179	1116	836.8
	max (4.3-5.0%	618	257	19.4	22.1	185	172	318	331	##	212	1324	991.6

* net production estimated for June through July from Japanese research vessel data (Ishida et al. 1998).

Table 4.6. Estimated chum salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .2 immature chum salmon in the Bering Sea in June and July and an initial weight of 1042 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/60 days. Wt=weight (g), BW=body weight, EU=euphausiids, AM=hyperiid amphipods, PT=pteropods, FI=fish, GE= medusae, AP=appendicularia.

Chum Salmon

Temp (°C)	Daily Ration (% BW/day)	Final Wt (g)	Net Production (g)	Gross Conversion Efficiency	Consumption Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	AM	PT	FI	GE	AP	Total	
5	maint (0.9%)	1042	0	0.0	9.2	144	66	61	66	149	66	552	337.8
	1% BW	1061	19	3.0	10.5	164	76	69	76	170	76	631	385.7
	2% BW	1252	210	15.3	22.8	356	164	151	164	370	164	1369	837.7
	3% BW	1477	435	19.4	37.3	581	268	246	268	604	268	2235	1367.0
	3.28% BW	1546	504	20.1	41.7	651	301	276	301	676	301	2506	1531.0
	max (3.5-3.9%	1659	617	21.0	49.0	764	353	323	353	794	353	2940	1798.0
6	maint (1%)	1042	0	0.0	10.4	162	75	68	75	168	75	623	380.5
	2% BW	1229	187	13.8	22.6	353	163	149	163	366	162	1356	829.9
	3% BW	1449	407	18.4	36.9	576	266	244	266	598	266	2216	1354.0
	3.4% BW	1548	506	19.5	43.3	675	312	286	312	701	312	2598	1588.0
	max (3.7-4.2%	1690	648	20.5	52.6	820	379	347	379	852	379	3156	1929.0
7	maint (1.1%)	1042	0	0.0	11.7	183	84	77	84	190	84	702	429.6
	2% BW	1203	161	12.0	22.4	349	161	148	161	363	161	1343	821.0
	3% BW	1418	376	17.2	36.5	569	263	241	263	591	263	2190	1339.0
	3.53% BW	1547	505	18.7	44.9	701	324	297	324	728	324	2698	1648.0
	max (3.9-4.4%	1712	670	20.0	55.8	871	402	368	402	904	402	3349	2047.0
8	maint (1.3%)	1042	0	0.0	13.2	207	95	87	95	215	95	794	486.0
	2% BW	1174	132	10.0	22.1	345	159	146	159	358	159	1326	811.1
	3% BW	1383	341	15.8	36.0	562	259	238	259	584	259	2161	1322.0
	3.68% BW	1546	504	17.9	46.8	731	337	309	337	759	337	2810	1718.0
	4.0% BW	1629	587	18.7	52.3	816	377	345	377	848	377	3140	1919.0
	max (4.1-4.7%	1722	680	19.4	58.6	914	422	387	422	949	422	3516	2149.0
9	maint (1.4%)	1042	0	0.0	15.0	234	108	99	108	243	108	900	550.7
	2% BW	1142	100	7.7	21.8	340	157	144	157	353	157	1308	799.9
	3% BW	1345	303	14.2	35.5	554	256	234	256	575	256	2131	1303.0
	3.86% BW	1547	505	17.1	49.1	767	354	324	354	796	354	2949	1803.0
	4.0% BW	1583	541	17.5	51.5	804	371	340	371	835	371	3092	1890.0
	max (4.2-4.8%	1721	679	18.6	60.9	810	374	343	374	842	374	3117	1906.0

* net production estimated from June through July from Japanese research vessel data (Ishida et al. 1998).

Table 4.7. Estimated pink salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 maturing pink salmon in the Bering Sea in June and July and an initial weight of 912 g. Maint=daily maintenance ration, max=daily physiological maximum consumption. Brams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)= total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/60 days. Wt=weight (g), BW=body weight, EU=euphausiids, CO=copepods, AM=hyperiid amphipods, SQ= squid, PT=pteropdos, FI=fish.

Pink Salmon

Temp (°C)	Daily Ration (% BW/day	Final Wt (g)	Net Pro-duction (g)	Gross Con-version Effi-ciency	Cons sump-tion Rate (g/day)	Total Prey Consumption (g)							Total kcal
						EU	CO	AM	SQ	PT	FI	Total	
5	maint (0.6%)	912	0	0.0	5.7	52	28	31	103	14	117	345	296.7
	1.0% BW	974	62	10.9	9.4	85	45	51	170	23	192	566	487.2
	2.0% BW	1160	248	20.1	20.6	185	99	111	371	49	420	1235	1065.0
	2.73% BW	1314	402	22.3	30.0	270	144	162	540	72	612	1800	1552.0
	max (2.8-3.0%)	1363	451	22.7	33.1	298	159	179	595	79	674	1984	1710.0
6	maint (0.7%)	912	0	0.0	6.5	58	31	35	116	15	132	387	333.9
	1.0% BW	960	48	8.6	9.4	84	45	51	168	22	191	561	483.9
	2.0% BW	1144	232	18.9	20.4	184	98	110	368	49	417	1226	1057.0
	2.81% BW	1313	401	21.7	30.9	278	148	167	556	74	630	1853	1597.0
	3.0% BW	1356	444	22.1	33.5	302	161	181	603	80	684	2011	1734.0
	max (3.0-3.4%)	1394	482	22.3	33.9	323	172	194	647	86	733	2155	1858.0
7	maint (0.8%)	912	0	0.0	7.3	66	35	39	131	17	149	437	376.7
	1.0% BW	945	33	5.9	9.3	84	45	50	167	22	189	557	480.0
	2.0% BW	1125	213	17.6	20.3	182	97	109	365	49	413	1215	1048.0
	2.91% BW	1314	402	21.0	32.0	288	153	173	576	77	652	1919	1654.0
	3.0% BW	1334	422	21.2	33.2	299	159	179	598	80	678	1993	1719.0
	max (3.1-3.5%)	1410	498	21.8	38.1	343	183	206	686	91	777	2286	1971.0
8	maint (0.9%)	912	0	0.0	8.2	74	40	44	148	20	168	494	425.9
	1.0% BW	928	16	2.8	9.2	83	44	50	166	22	188	553	475.7
	2.0% BW	1105	193	16.0	20.1	181	96	108	361	48	410	1204	1039.0
	3.0% BW	1310	398	20.1	32.9	296	158	178	592	79	671	1974	1702.0
	3.02% BW	1314	402	20.2	33.2	299	159	179	597	80	677	1991	1716.0
	max (3.3-3.7%)	1420	508	21.2	40.0	360	192	216	720	96	816	2401	2070.0
9	maint (1.0%)	912	0	0.0	9.3	84	45	50	168	22	190	559	482.4
	2.0% BW	1082	170	14.3	19.9	179	95	107	358	48	405	1192	1027.0
	3.0% BW	1282	370	19.0	32.5	293	156	176	586	78	664	1953	1683.0
	3.14% BW	1313	401	19.4	34.5	310	165	186	621	83	703	2068	1783.0
	max (3.4-3.9%)	1423	511	20.4	41.6	375	200	225	750	##	850	2500	2154.0

* net production estimated from June through July from Japanese research vessel data (Ishida et al. 1998).

Table 4.8. Estimated coho salmon growth and prey consumption over a range of temperatures and daily rations resulting from a 60-day simulation. Model input values represent conditions for an ocean age .1 maturing coho salmon in the central North Pacific Ocean in June and July and an initial weight of 1909 g. Maint=daily maitenance ration, max=daily physiological maximum consumption. Grams are wet weights. Temp=water temperature, Gross Conversion Efficiency (%)=total growth (g)/total weight of prey consumed (g) after 60 days. Prey consumption rate=total prey consumed (g)/60 days. Wt=weight (g), BW=body weight, SQ=sauid, AM=hyperiid amphipods.

Coho Salmon

Temp (°C)	Daily Ration (%BW/day)	Final Wt (g)	Net Pro-duction (g)	Gross Con-version Effi-ciency	Con-sump-tion Rate (g/day)	Total Prey Consumption (g)			Total kcal
						SQ	AM	Total	
7	maint (0.7%)	1909	0	0.0	13.2	657	135	792	1098.0
	1.0% BW	2064	155	13.0	19.8	988	202	1190	1650.0
	2.0% BW	2652	743	27.5	45.1	2244	460	2704	3749.0
	max (2.0-2.2%)	2715	806	28.1	47.8	2381	488	2869	3977.0
8	maint (0.8%)	1909	0	0.0	14.6	728	149	877	1217.0
	1.0% BW	2024	115	9.7	19.6	978	200	1178	1635.0
	2.0% BW	2599	690	25.8	44.6	2221	455	2676	3710.0
	max (2.3-2.6%)	2905	996	28.7	57.9	2881	590	3471	4813.0
9	maint (0.9%)	1909	0	0.0	16.3	810	166	976	1354.0
	1.0% BW	1980	71	6.1	19.4	968	198	1166	1617.0
	2.0% BW	2541	632	23.9	44.1	2195	450	2645	3667.0
	2.64%BW	2976	1067	28.2	63.1	3142	643	3785	5248.0
	max (2.6-2.9%)	3055	1146	28.7	66.6	3319	680	3999	5545.0
10	maint (1.0%)	1909	0	0.0	18.2	904	185	1089	1511.0
	1.0% BW	1932	23	2.0	19.2	956	196	1152	1598.0
	2.0% BW	2477	568	21.8	43.5	2166	444	2610	3619.0
	2.74% BW	2975	1066	27.1	65.5	3264	669	3933	5453.0
	max (2.8-3.0%)	3126	1217	28.1	72.3	3599	737	4336	6013.0
11	maint (1.1%)	1909	0	0.0	20.3	1011	207	1218	1689.0
	2.0% BW	2407	498	19.4	42.9	2135	437	2572	3567.0
	2.86% BW	2976	1067	26.0	68.4	3407	698	4105	5693.0
	3.0% BW	3080	1171	26.7	73.1	3638	745	4383	6078.0
	max (2.9-3.4%)	3197	1288	27.3	78.5	3911	801	4712	6533.0

* net production estimated for June through July from Japanese research vessel data (Ishida et al. 1998).

Chapter 5.0 General Discussion

As Burgner (1991) described it, "inter-specific competition implies an interaction between species that affects natality, survival, and/or individual growth rate in one or both species" and "if food is in short supply, one or other of the competitors, or both may grow more slowly." In this study, direct determination of whether salmon prey were in short supply when feeding interactions occurred in the central Bering Sea has been circumstantial. Hard evidence from independent measures of prey abundance, such as data obtained by collection of plankton and micronekton, is needed. Unfortunately, the catch efficiency of zooplankton nets, like the Norpac net used in this study, is too low to assess the abundance of faster-swimming or micronektonic salmon prey organisms. Salmon are described as opportunistic feeders (Brodeur 1990). Therefore, salmon probably feed on common prey organisms according to their relative abundance in the upper 30 m of the water column where salmon reside during most of their summer-ocean residence (Walker et al. 2000b). In the absence of independent estimates of prey availability, and having observed a decade of biennial shifts in salmon stomach contents, I suggest the shift in prey composition I observed in chum, sockeye, and pink salmon was due primarily to resource limitation stemming from feeding competition.

Density-dependent ocean growth has been observed among several stocks of Asian and North American pink and sockeye salmon, and feeding competition was the mechanism suggested by which salmon growth was negatively impacted (Takagi et al 1981, Heard 1991, Bugaev et al. 2001). Pink salmon undergo large inter-annual production swings, have the shortest lifespan, and are the fastest growing of Pacific salmon (Heard 1991). Therefore, pink salmon size at maturity is a particularly sensitive biological characteristic to measure the effects of feeding competition during their final summer at sea. 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 sockeye 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).

In addition to affecting growth, inter-specific competition has been suggested by Ruggerone et al. (2003) as a regulating mechanism of population abundance. Ruggerone et al. (2003) observed that Asian pink salmon abundance was inversely related to scale growth and smolt-to-adult survival of Bristol Bay sockeye salmon. Ruggerone et al. (2003) reasoned that inter-specific competition caused reduced prey availability, thereby reducing immature sockeye salmon growth. Smaller-sized sockeye salmon would be susceptible to increased predation because their small size makes them available to an increased number of fish predators (Ruggerone et al. 2003). Ruggerone et al. (2003) concluded reduction of sockeye abundance occurred during the second year at sea in odd-numbered years, beginning during the first winter in the central North Pacific and continuing until mid-July in the Bering Sea (Ruggerone et al. 2003). My study of food habits confirmed their conclusion that in July in the Bering Sea feeding competition occurs between immature sockeye and maturing pink salmon in odd-numbered years when pink salmon abundance is high. Later in their ocean migrations, maturing Bristol Bay sockeye salmon may reduce competition with maturing pink salmon by spending their final late spring-early summer season in the North Pacific south of the eastern and central Aleutian Islands, eastwards of most maturing Asian pink salmon, and by starting their return to coastal areas earlier than pink salmon (Burgner 1991).

Density-dependent effects seem to cause the recent growth reduction of chum salmon in the North Pacific Ocean. Recent reductions in the body size of mature chum salmon is thought to occur in the third year of ocean life based on analysis of scale patterns (Kaeriyama 1989; Ishida et al. 1993; Walker et al. 1998; Azumaya and Ishida 2000). Significant negative relationships have been observed between population size of high-seas and Japanese chum salmon and mean fish size (Ishida et al. 1993, Kaeriyama 1996b). Density-dependent factors explained 35% of the decrease in average size of chum salmon in the central North Pacific Ocean (Ishida et al. 1993). After examining

chum salmon scale growth zones, Walker et al. (1998) noted that edge-of-scale growth was negatively correlated with Asian pink and chum salmon abundance, and they concluded that inter-specific competition with abundant pink salmon might influence third-year ocean growth. Analyzing salmon abundance data collected from the Bering Sea and North Pacific Ocean, Azumaya and Ishida (2000) determined that immature chum salmon reduced competition with maturing pink salmon in the summer by moving their distribution southeastwards in the Bering Sea in years when pink salmon were abundant (Azumaya and Ishida 2000).

The remarkable adaptations of chum salmon enabling them to feed efficiently on gelatinous prey are not present in sockeye and pink salmon. Although pink and sockeye salmon reduce their consumption of euphausiids, copepods, squid, and fish, when pink salmon are abundant, sockeye and pink salmon generally do not consume significant quantities of gelatinous prey. Rather, pink and sockeye salmon switch to consuming larger quantities of relatively low-calorie filter-feeding pteropods and small hyperiid amphipods that could lead to reduced growth during periods of severe competition. Chum salmon are unusual because of their heavy consumption of gelatinous zooplankton. Cnidarians, ctenophores, and salps are low in caloric content, so the question remains as to the reason chum salmon consume these gelatinous animals of low nutritive value. Perhaps consumption of this type of prey indicates an evolutionary shift to reduce feeding competition between chum and pink and sockeye salmon, all of which are predominantly zooplanktivorous. The capacity of chum to shift diets by consuming gelatinous zooplankton and thereby reduce dietary overlap with other salmon indicates that chum salmon have a biological elasticity that gives them a capacity to exploit gelatinous forms when abundance of other (crustacean) prey is reduced.

Arai et al. (2000) considered the disadvantage of consuming a diet of low caloric-density gelatinous prey might be offset by the capacity of chum salmon for relatively quick digestion, assimilation, and transport through the gut (Arai 1988). Chum salmon are unique in having a high rate of digestion (Azuma 1995; Hiramatsu et al. 1996; Arai et al. 2000). Arai et al. (2000) conducted experiments on juvenile chum salmon force-fed

ctenophores and estimated the half-life of the weight of gelatinous prey in the stomach to be 6.3 min at 13°C, an astonishingly fast period. In my studies, chum salmon had larger stomach fullness than either pink or sockeye salmon throughout the diel period, and chum salmon maintained a stable level of stomach fullness by increasing the proportion of gelatinous prey when competing for food with abundant maturing pink salmon. Chum salmon, however, did not feed exclusively on gelatinous organisms. For example, in the central Bering Sea chum salmon also consumed the calorically-rich myctophid, *Stenobrachius leucopsarus*, in the early morning hours, which could partially compensate for the potential deficiencies of a diet of predominately gelatinous prey as long as alternative high-calorie prey were available in sufficient quantity.

The use of stomach fullness as a quick and simple measure of prey availability, feeding condition, or feeding competition may not be advisable in analyses involving chum salmon. Andrieveskaya (1966) and this study observed that chum salmon stomach fullness did not change during periods when feeding competition occurred. Chum salmon stomach fullness alone was not sensitive enough to detect feeding interactions between chum and pink salmon. However, the composition of chum salmon prey changed markedly (from less fish, squid, euphausiids, and copepods to more gelatinous zooplankton, hyperiid amphipods, and pteropods) when competing for food with pink salmon. Therefore, I suggest the inclusion of prey composition data is crucial for analysis of effects of feeding competition involving chum salmon.

Recent studies of muscle lipid content in chum salmon have begun to clarify how the balance between energy for growth and storage is accomplished by salmon at sea (Nomura et al. 2000, 2001, 2002). Nomura et al. (2002) observed that chum salmon lipid levels in ocean age .1 fish were unexpectedly low during the summer when prey consumption rates were high. Evidently, during the summer the expenditure of energy for growth in size takes priority over lipid storage, particularly for young chum salmon. Nomura et al. (2002) postulated that energy would be diverted for lipid storage at the expense of growth during the fall to increase survival through the winter. Previous biochemical analysis of juvenile chum salmon suggested there was a build-up of lipid

reserves, rather than protein synthesis just prior to winter, thus slowing growth rates in order to maintain energy reserves (Azuma et al. 1998). This suggests that during the summer consumption rate and prey quality are crucial for growth (length) because the energy consumed over and above what is required for metabolism and movement is put toward growth, rather than lipid storage, thereby reducing the risk of predation. In the fall, priorities change, whereby consumption rate and prey quality are crucial for accumulation of lipid essential for survival through the coming winter when feeding conditions are likely reduced to the minimum.

A consistent pattern has developed from my analysis of a decade of "snapshots" of the summertime feeding conditions for salmon along 180° longitude in the central North Pacific Ocean and central Bering Sea. The central North Pacific Ocean between 41°-44°N (Transition Domain) was a region low in salmon abundance, where immature chum and maturing coho salmon consumed salps and large salp-dwelling hyperiid amphipods of relatively low-caloric value. The central North Pacific Ocean between 45°-51°N (Subarctic Domain) was characterized by medium salmon density, where chinook, large sockeye, and maturing pink and coho salmon (fish greater than 1500 g body weight), consumed large-bodied and calorically-dense prey, particularly squid, *Berryteuthis anonychus,* and occasionally larger fish, such as, *Gasterosteus aculeatus*, *Cololablis saira, Anopterus pharao*, and *Leuroglossus schmidti*. I conclude the southern area (41°-44°N) was a rather unproductive area for salmon feeding, and that is the reason salmon were caught there in low abundance. The northern area, between 45°-51°N was particularly productive for maturing fish spending their final summer weeks at sea, such as maturing pink, sockeye, and coho salmon, and for large immature chinook salmon, which were capable of capturing relatively large-bodied prey.

The central Bering Sea in the summer was characterized by a high abundance of young (ocean age .1) sockeye, chum, and chinook salmon, and maturing pink salmon (in odd-numbered years). Diets of young salmon collected in the central Bering Sea showed a remarkable abundance and diversity of post-larval and juvenile fish, such as *Pleurogrammus monopterygius*, *Hemilepidotus* spp., and flatfishes, adult *Stenobrachius*

leucopsarus, juvenile squids, and particularly the abundant euphausiid, *Thysanoessa longipes*. The large diversity of highly abundant relatively small-bodied prey in the central Bering Sea made this region particularly productive as a feeding area for young ocean age .1 salmon.

In summer the central Bering Sea is critical habitat for salmon because of its role as a nursery area for juvenile and post-larval fish and squid that provide a rich forage base for feeding of Asian and North American stocks of young sockeye, chum, and chinook, and maturing chum and pink salmon. Recently, however, conditions in the Bering Sea suggest there may be an overall reduction in productivity (Schell 1998). Runs of chinook and chum salmon to western Alaska are at low levels (McNair and Geiger 2001). The unusual occurrence of a coccolithophore bloom in 1997 has become routine on the southeastern Bering Sea shelf (Stabeno 2002). Concerns about climate change and changes in salmon production have prompted the international organization responsible for salmon research in the international waters of the North Pacific Ocean (North Pacific Anadromous Fish Commission) to initiate a new five-year research plan in the Bering Sea (Bering-Aleutian Salmon International Survey; NPAFC 2001). The program specifies standardized methods for sampling oceanographic conditions, plankton biomass, salmon, and other fishes using a surface trawl at locations on the continental shelf, slope, and throughout the basin. The proposal recommends sampling throughout spring, summer, fall, and winter to provide a novel synoptic analysis of the region. Studies of salmon food habits and bioenergetics are included among the planned research subjects areas. I hope my study contributes to building the groundwork for future research of ocean salmon ecology.

Chapter 6.0 Summary and Conclusions

1. Gillnet and longline gear were used to collect salmonids for examination of stomach contents in the central North Pacific Ocean and central Bering Sea during June and July from 1991 to 2000 aboard the *Wakatake maru*. Surveys were conducted along a south to north transect located at 179°30'W (1991 to 1996) and 180° longitude (1997-2000). Based on oceanographic characteristics and salmon distribution the transect was divided into four areas: 38°-40°N (south of salmon distribution), 41°-44°N, and 45°-51°N in the central North Pacific Ocean, and 52°-58°N in the central Bering Sea.

2. The common sockeye salmon ages in the catch were 1.1, 2.1, 1.2, and 2.2 (number before the period is the number of freshwater annuli and the number after the period is the number of ocean annuli observed on scales). Most of the sockeye salmon were immature, although there were some maturing fish caught in the central Bering Sea. The common age groups of chum salmon were 0.1, 0.2, 0.3, and there were increased numbers of older, maturing fish caught in the central Bering Sea than further to the south. All the pink and coho salmon in the catches were maturing ocean age .1. Chinook salmon catches were a mixture of predominately immature age 1.1, 1.2, and 1.3 fish. Steelhead catches generally represented immature and maturing ocean age .1 and maturing ocean age .2 fish.

3. Salmon abundance (CPUE: number of salmon caught per 30-tans of gillnet) was ten times more abundant in the central Bering Sea (mean=341 fish) than in the central North Pacific Ocean south of 48°N (mean=33 fish).

4. In the central North Pacific Ocean chum salmon abundance ranged from 7.4 to 29.7 fish and they were the most abundant zooplanktivorous salmon distributed in the area. A negative correlation between zooplankton biomass and chum abundance suggested that when chum salmon were abundant, their consumption of zooplankton could reduce the abundance of zooplankton in that area. Coho salmon abundance ranged

from 3.7 to 19.6 fish and exhibited a pattern where one year of low abundance (1993, 1996, and 1999) was followed by two years of high abundance. However, this pattern changed in 2000 when coho salmon abundance decreased to the lowest point in the 10-year record. Coho salmon abundance was positively correlated with higher salinity at 30 m depth, suggesting that coho salmon, among the most southerly distributed of the salmon species, may be more tolerant of high salinity intrusions from the Transition Domain than other salmon. Sockeye, pink, and chinook salmon abundance was low in the central North Pacific Ocean and ranged from 0.0 to 10.8, 0.2 to 15.9, and 0.1 to 0.7 fish, respectively. Steelhead abundance in the central North Pacific Ocean was low (0.6 to 3.7 fish) and there was no pattern in catches over the ten-year time period. The presence of both adipose fin-clipped and non fin-clipped steelhead in the catches indicate there was a mixture of hatchery and wild fish in the survey area.

5. In the central Bering Sea sockeye salmon abundance (CPUE: number of fish per 30 tans of gillnet) ranged from 22.8 to 58.2 fish. Sockeye salmon abundance reflected a four-year abundance cycle with maximum values in 1993, 1997, and 2001. There was a strong biennial dominance cycle of East Kamchatka pink salmon in the survey area such that pink salmon were approximately 40 times more abundant in odd- than even-numbered years (mean=7 fish in even-numbered years; mean=284 fish in odd-numbered years). Chum salmon abundance in the central Bering Sea reflected a cycle that was inversely related to pink salmon abundance. Approximately twice as many chum salmon were caught in even- than in odd-numbered years (mean=87 fish in odd-numbered years; mean=207 fish in even-numbered years). Chum salmon abundance decreased to particularly low levels every fourth year (1991, 1995, and 1999). Chinook salmon abundance was relatively high in the central Bering Sea, ranging from 1.4 to 22.7 fish. There was a low abundance of coho salmon in the basin area (0.0-0.5 fish) because these maturing fish are probably migrating to their natal rivers by a more coastal route. Steelhead were not caught in the central Bering Sea, which reflects the lack of major spawning stocks draining into that area.

6. In the central North Pacific Ocean (45°-51°N) analysis of sockeye salmon food habits showed overall mean prey weight was 12.9 g (0.66% body weight). Annual values for mean prey weight ranged from 1.6 g (0.1% body weight) to 34.4 g (1.4% of body weight). Major sockeye salmon prey groups included euphausiids (*Euphausia pacifica*), copepods (*Neocalanus cristatus* CV), hyperiid amphipods (primarily *Parathemisto pacifica*), and squid (*Berryteuthis anonychus*). The squid eaten by sockeye salmon in this area was large-sized *B. anonychus* subadults and adults (approximately 50-100 mm mantle length). Effect of prey quality (high quality=euphausiids, copepods, squid and fish; low quality= pterpods and amphipods) on stomach fullness by odd- and even-numbered year was not significant (p=0.92).

7. Samples collected in the central North Pacific Ocean were used to compare changes in sockeye salmon food habits with sockeye body size. Results showed that prey weight increased with body weight of sockeye salmon from 0.82 g (0.231% body weight) for sockeye weighing less than 500 g to 26.3 g (0.80% body weight) for fish weighing 3000 g or more. Maximum SCI values (stomach content index; SCI=prey weight/salmon body weight*100) observed in sockeye salmon ranged from 2.3% body weight for age .1 fish to a maximum of 5.2% body weight for age .2 fish. Small sockeye salmon, less than 500 g, fed on a high percentage (70%) of amphipods and pteropods. As sockeye salmon body size increased, the percentage of squid in the stomach contents increased to more than 33% in fish larger than 2000 g. Higher mean prey weight and SCI were associated with sockeye salmon larger than 1500 g feeding on large *B. anonychus.*

8. In the central Bering Sea (52°-58°N) analysis of sockeye salmon food habits showed overall mean prey weight was 10.4 g (0.66% body weight) and annual values ranged from 6.0 g (0.05% body weight) to 24.2 g (1.1% body weight). Prey weight increased from 8.2 g to 12.9 g in even-numbered years when pink salmon abundance was low. Major sockeye salmon prey items included euphausiids (*Thysanoessa longipes*), hyperiid amphipods, copepods (*N. cristatus* CV), squid and fish. Sockeye salmon in this area fed on many small squid that may be juvenile *B. anonychus* 20 to 30 mm in mantle length. Consumption of fish, which included juvenile *Hemilepidotus* spp.,

Pleurogrammus monopterygius, and adult *Stenobrachius leucopsarus* was substantially greater in the central Bering Sea than in the central North Pacific Ocean. Comparison of the prey quality in sockeye stomachs by odd- and even-numbered years showed a 36% reduction in stomach fullness when pink salmon were abundant. In odd-numbered years, there was a 53% reduction in the weight of high-quality prey (euphausiids, copepods, squid, and fish) and a 13% increase of in the weight of low-quality prey (pteropods and amphipods). However, this change was not statistically significant ($p=0.12$) at the five percent level. I suggest the reductions of high-quality prey in odd-numbered years may be biologically meaningful for sockeye if high abundance of pink salmon causes prey limitation.

9. Samples collected in the central Bering Sea were used to compare changes in sockeye salmon food habits with sockeye body size. Results showed that as body weight increased from less than 1000 g to greater than 2500 g, the percentage of amphipods in the stomach contents decreased from 34% to 11% and the percentage of squid increased from 18% to approximately 30%.

10. In the central North Pacific Ocean at 41°-44°N analysis of chum salmon food habits showed overall prey weight averaged 9.8 g (1.00% body weight) and annual mean prey weights ranged from a low of 4.8 g (0.57% body weight) to a maximum of 17.3 g (2.08% body weight). At 45°-51°N overall mean prey weight was 9.35 g (0.90% body weight) and annual mean prey weights ranged from 6.8 g (0.65% body weight) to 12.2 g (1.39% body weight). Chum salmon consumed a wider variety of prey than other salmon species. Chum salmon fed on euphausiids (*E. pacifica*), hyperiid amphipods (*P. pacifica, Phronima sedentaria),* squid (*B. anonychus*), pteropods (*Limacina helicina, Clione limacina*), fish (*P. monopterygius*), appendicularians (likely *Oikopleura labradoriensis*), ostracods (*Conchoecia magna*), and heteropods (*Carinaria* sp.), and a large proportion of gelatinous zooplankton (medusae, *Aglantha digitale*, ctenophore *Beroe* sp. and salps). Salps were the most common gelatinous zooplankton consumed in this area, and many of the salps consumed by chum salmon were “barrels” hollowed-out by resident hyperiid amphipods, *P. sedentaria*. Comparison of prey quality (high-quality=euphausiids,

copepods, squid, and fish; low-quality=amphipods and pteropods) by year was not significant (p=0.68).

11. Samples collected in the central North Pacific Ocean were used to compare changes in chum salmon food habits with chum body size. Results showed that as chum body size increased, the weight of stomach contents increased from 3.13 g (0.88% body weight) for fish weighing less than 500 g to 24.01 (0.70% body weight) for fish weighing at least 2500 g. Maximum SCI values of 4.3-4.6% body weight were observed for age .1 and .2 fish and values decreased to less than 2.9% body weight for age .5 chum salmon. Fish prey was found only in chum salmon larger than 2500 g.

12. In the central Bering Sea (52°-58°N) analysis of chum salmon food habits indicated overall mean prey weight was 15.5 g (1.10% body weight) and mean annual values ranged from 12.1 g (0.71% body weight) to 23.0 g (1.52% body weight). Chum salmon fed more commonly on non-gelatinous zooplankton than in the North Pacific Ocean. Chum salmon consumed euphausiids (*T. longipes*), copepods (*N. cristatus* CV), amphipods (*P. pacifica*, *Primno abyssalis*, *Hyperia medusarum*, and *Hyperoche medusarum*), squid (juveniles), pteropods (*L. helicina*, and *C. limacina*), and fish (*P. monopterygius*, *S. leucopsarus*, juvenile *Hemilepidotus* sp., and post-larval *Aptocyclus* spp., *Psychrolutes phrictus*, and *Hippoglossus stenolepis*). Abundance of chum salmon was positively correlated, and abundance of pink salmon was negatively correlated, with the amount of copepods and amphipods in chum salmon stomach contents. These are common prey items important to the diets of both chum and pink salmon and may be due to feeding interactions between pink and chum salmon. Mean prey weight and SCI were similar in odd- and even-numbered years indicating no difference in stomach fullness of chum salmon stomach samples between years of high and low pink salmon abundance. However, there was a 38% reduction in weight of high-quality prey (euphausiids, copepods, squid, and fish) and a 19% increase in weight of low-quality prey (amphipods, pteropods, medusae, and ctenophores) when pink salmon were abundant. Differences in prey weight of high- and low-quality prey during odd- and even-numbered years were

highly significant ($p<0.01$) and indicated a shift to different prey composition when pink salmon were abundant.

13. Samples collected in the central Bering Sea were used to compare changes in chum salmon food habits with chum body size. Results showed that mean prey weight in chum salmon increased from 5.6 g (1.39% body weight) in fish weighing less than 500 g to 27.3 g (0.62% body weight) in fish weighing 4000 g, or more. Maximum SCI for ocean age .1, .2, and .3 fish ranged from 5.2 to 6.4% body weight, however, decreased to 1.9% body weight in fish aged 0.5. Chum salmon weighing less than 500 g fed on a higher percentage of amphipods (25%) than chum salmon weighing greater than 1000 g. Euphausiids were consumed by all sizes of chum salmon. However, a higher percentage (>20%) was observed in fish greater than 1000 g than in small chum salmon (8% in fish weighing less than 500 g). All sizes of chum salmon consumed a substantial percentage of gelatinous zooplankton, increasing from 12% in small chum salmon weighing less than 500 g to 36% in fish larger than 3000 g. The percentage of prey composed of juvenile fish, pteropods, and small squid was relatively unchanged across weight classes of chum salmon.

14. In the central North Pacific Ocean (45°-51°N) analysis of pink salmon food habits showed overall prey weight averaged 14.8 g (1.37% body weight) and the annual mean prey weight ranged from 4.0 g (0.4% body weight) to 42.0 g (3.0% body weight). Samples from pink salmon were characterized by sporadic high consumption of large squid (*B. anonychu*s, approximately 80-100 mm mantle length). Effect on stomach fullness of weight of high- and low-quality prey (high quality: euphausiids, copepods, squid, and fish; low quality: amphipods and pteropods) by odd- and even-numbered year was not significant ($p=0.11$) and probably biologically not significant because of the relatively low abundance of pink salmon in this area.

15. Samples collected in the central North Pacific Ocean were used to compare changes in pink salmon food habits with pink body size. Results showed that the mean prey weight increased with body weight of pink salmon from 9.9 g (1.18% body weight)

for fish weighing 500-999 g to 22.8 g (1.39% body weight) for fish weighing 1500 g, or more. Maximum SCI ranged from 7.6 to 4.5% body weight. There was a dramatic shift towards increasing percentages of large squid and euphausiids in the stomachs of pink salmon of larger size. In contrast, the percentage of copepods and pteropods decreased from 29% and 17% in the stomach contents of pink salmon weighing less than 1000 g to 6% and 9% in those weighing more than 1500 g.

16. In the central Bering Sea (52°-58°N) analysis of pink salmon food habits indicated overall mean prey weight was 15.2 g (1.29% body weight) and the annual mean prey weights ranged from 8.1 (0.76% body weight) to 28.8 g (2.47% body weight). Pink salmon consumed small squid, perhaps *B. anonychus* juveniles, approximately 10-30 mm mantle length. Pink salmon also fed heavily on fish, including primarily juvenile flat fish, juvenile *P. monopterygius*, *Hemilepidotus* sp. and adult *S. leucopsaurus*. The abundance of pink salmon was negatively associated with pink salmon stomach fullness and the amount of euphausiids, copepods, squid, and fish in pink salmon stomach contents. There was a decrease of 23% in the stomach fullness of pink salmon in odd- as compared with even-numbered years. A 32% reduction in the proportion of high-quality prey in the stomach contents (euphausiids, copepods, squid, and fish), and an increase of 72% in the proportion of low-quality prey (amphipods and pteropods) was observed when pink salmon were abundant. The interaction of prey quality and year on prey weight was statistically significant ($p=0.03$) and indicates that when pink salmon are abundant intra-specific competition may reduce prey availability and reduce growth during their final summer at sea.

17. Samples collected in the central Bering Sea were used to compare changes in pink salmon food habits with pink body size. Results showed that prey weight increased with body weight of pink salmon from 4.4 g (1.10% body weight) in fish weighing less than 500 g to 28.8 g (1.29% body weight) for fish weighing 2000 g, or more. Maximum SCI increased from 2.4% body weight to 6.0% for pink salmon weighing up to 1500 g, and, decreased in heavier fish. Fish was a more substantial portion of the diet of pink salmon in the central Bering Sea, as compared to the catches in the central North Pacific Ocean.

Pink salmon smaller than 500 g body weight contained a high percentage of juvenile fish (64%), however these small pink salmon did not consume juvenile squid. For pink salmon weighing more than 500 g BW, the percentage of fish and squid prey was relatively constant in stomach contents. The percentage of euphausiids was low (1%) in small pink salmon (weighing less than 500 g), however, it increased to 17% in pink salmon weighing more than 1500 g.

18. In the central North Pacific Ocean (41°-44°N) analysis of coho salmon food habits indicated that prey weight averaged 17.3 g (0.97% body weight), and annual mean prey weight ranged from 0.92 g (0.05% body weight) to 34.3 g (1.77% body weight). Coho salmon were characterized by an almost exclusive consumption of large sub-adult and adult squid, *B. anonychus*. In the southern area (41-44°N hyperiid amphipods (*Phronima sedentaria* in salp barrels) and pteropods (*Clio recurva*) comprised an alternative prey source to squid for coho salmon.

19. In the central North Pacific Ocean (45°-51°N) analysis of coho salmon food habits indicated that overall prey weight was 44.1 g (2.17% body weight), and annual mean prey weights ranged from 28.4 (1.39% body weight) to 69.7 g (3.48% body weight). Coho salmon consumed large amounts of large *B. anonychus*. Occasionally, euphausiids, *E. pacifica*, and fish, including *Gasterosteus aculeatus*, *P. monopterygius*, *Cololabis saira*, *Hemilepidotus* spp., *T. crenularis* and *Engraulis japonica*, were also consumed by coho salmon.

20. Samples collected in the central North Pacific Ocean were used to compare changes in coho salmon food habits with coho body size. Results showed that prey weight increased with body weight of coho salmon from 5.8 g (0.71% body weight) to 72.6 g (2.17% body weight) for coho weighing 3000 g, or more, and the maximum SCI ranged from 1.6% to 7.6% (body weight). Squid was the primary prey item for coho salmon of all sizes (all coho salmon were maturing ocean age .1 fish), ranging from 50% (percentage of weight) in coho weighing 500 g to 55% squid in fish weighing more than 3000 g. The percentage of pteropods (19%) in small coho weighing less than 1000 g,

decreased to 10% in coho weighing more than 3000 g. In contrast, the percentage of fish increased from 9% in the stomach contents of coho salmon less than 1000 g to 24% in coho weighing more than 3000 g. As coho salmon increase in size, they can catch larger squid, thus affording them a larger capacity for growth.

21. In the central North Pacific Ocean (45-51°N) analysis of chinook salmon food habits indicated overall mean prey weight was 31.8 g (0.86% body weight), and annual values ranged from 14.0 g (0.3% body weight) to 69.3 g (1.8% body weight). Chinook salmon consumed predominately large squid, *B. anonychus,* and occasionally large fish such as *C. saira* (175 mm SL), *E. japonicus* (125-135 mm SL), *L. schmidti* (114-123 mm SL), and *A. pharao* (140-315 mm SL).

22. Samples collected in the central North Pacific Ocean were used to compare changes in chinook salmon food habits with chinook body size. Results showed prey weight increased with body weight of chinook salmon from 11.5 g (0.65% body weight) for chinook salmon weighing 1500 to 1999 g, to 39.0 g (0.69% body weight) for chinook salmon weighing 4000 g or more. The maximum SCI was 4.2% body weight for age .2 chinook salmon. The fish prey were relatively large-bodied prey items.

23. In the central Bering Sea (52°-58°N) analysis of chinook salmon food habits indicated overall mean prey weight was 14.81 g (0.59% body weight) and annual prey weights ranged from 2.6 g (0.2% body weight) to 49.6 g (1.3% body weight). Total prey weight increased from 9.53 g (0.42% body weight) to 21.6 g (0.74% body weight) in even-numbered years when pink salmon abundance was low (Fig. 1.22). There was a 56% reduction in stomach fullness in odd-numbered years, a 68% reduction in the weight of fish and squid consumed by chinook salmon, and a 44% increase in the weight of euphausiids consumed by chinook salmon when pink salmon were abundant. Major chinook salmon prey included squid (predominantly large *B. anonychus*), euphausiids (*T. longipes*), and fish (*P. monopterygius* and *S. leucopsarus*). Chinook salmon fed on fish and euphausiids substantially more in the central Bering Sea than those caught in the central North Pacific Ocean.

24. Samples collected in the central Bering Sea were used to compare changes in chinook salmon food habits with chinook body size. Results showed that prey weight increased with body weight of chinook salmon from 2.4 g (0.72% body weight) for small chinook weighing less than 500 g to 48.9 g (0.98% body weight) for fish weighing 4000 g, or more. The maximum SCI ranged from 3.9% body weight for ocean age .1 to 8.4% body weight for ocean age .3 chinook salmon. As the body weight of chinook salmon increased from less than 500 g to 1500 g, the percentage of juvenile fish in stomach contents decreased from 48% to 21%. The high SCI value for small chinook salmon indicates the central Bering Sea is an important feeding area for small chinook consumption of small fish prey.

25. In the central North Pacific Ocean (41°-44°N) steelhead trout food habits analysis indicated that at 41°-44°N, overall prey weight averaged 14.2 g (0.79% body weight), and annual mean prey weight ranged from a low of 2.5 g (0.13% body weight) to 42.7 g (2.32% body weight). At 45°-51°N the overall mean prey weight was higher than the southern area and ranged from 33.5 g (1.02% body weight) to 72.1 g (1.85% body weight). Steelhead caught in the central North Pacific Ocean were characterized by a dominance of squid, *B. anonychus*, and fish, including *Gasterosteus aculeatus*, *A. pharao*, *P. monopterygius*, and myctophids in the diet. Other prey that was occasionally found in high abundance was polychaetes (*Tomopterus* and *Rynchonerella* sp.).

26. Samples collected in the central North Pacific Ocean were used to compare changes in steelhead food habits with steelhead body size. Results showed prey weight increased with body weight of steelhead from 6.9 g (0.51% body weight) for fish weighing 1000-1499 g to 65.0 g (1.47% body weight) for fish weighing 4000 g or more. The percentage of squid in steelhead stomach contents increased from 40% in fish weighing 1000 g to 67% in fish weighing more than 4000 g. The proportion of polychaetes decreased from 10% in fish weighing 1000 g to less than 1% in fish weighing more than 4000 g. All sizes of steelhead examined were capable of consuming large *B. anonychus* squid.

27. Results highlighted regional differences in salmon food habits between areas in the central North Pacific Ocean and the central Bering Sea. The southern area (41°-44°N) was characterized by lower stomach fullness and lower consumption of large *B. anonychus* than further to the north (45-51°N). There was an occasional large fish consumed by chum and coho salmon, and steelhead in this area (*L. schmidti*, *C. saira*, and *E. japonicus*). Both chum and coho salmon fed upon salp barrels containing the hyperiid amphipod, *P. sedentaria*. Steelhead consumed polychaetes and often ate floating debris (plastic sheet, bits of wood). The southern area, 41-44°N, was the poorest from the viewpoint of salmon feeding of the three areas studied based on prey abundance and prey quality.

28. High levels of stomach fullness in salmon characterized the northern area of the central North Pacific Ocean (45°-51°N). Large (>1000 g BW) immature and maturing sockeye, pink, coho, and chinook salmon, and steelhead consumed a high proportion of large-sized *B. anonychus* (40-125 mm ML), a calorically-rich prey item. Due to relatively high consumption of large *B. anonychus* by salmon in the northern area of the central North Pacific Ocean (45°-51°N), this region was a particularly favorable feeding area for maturing salmon, and for large immature chinook salmon capable of capturing relatively large-bodied, quick swimming prey.

29. The central Bering Sea was characterized by young (<1000 g body weight; ocean age .1) sockeye, chum, and chinook salmon ingesting a diverse diet with relatively high proportions of juvenile fish and juvenile squid, in addition to euphausiids and other large zooplankton. In addition to the many small fish and squid prey available for consumption, the SCI for sockeye, chum, and chinook salmon weighing less than 1500 g was substantially higher in the central Bering Sea than in the central North Pacific Ocean. Thus, the summertime feeding environment in the Bering Sea was critically important to small, young (ocean-age .1) immature sockeye, chum, and chinook salmon.

30. Results obtained from analyses of stomach contents showed that during biennial years of high abundance of pink salmon in the central Bering Sea there were changes in the food habits of sockeye, chum, and pink salmon. In the absence of independent estimates of prey availability, and having observed a decade of biennial shifts in salmon stomach contents, I suggest the shift in prey composition I observed in chum, sockeye, and pink salmon was due primarily to resource limitation stemming from feeding competition among chum, sockeye, and pink salmon. Results showed substantial reductions in the proportion of high quality prey (euphausiids, copepods, fish and squid) in sockeye, chum, and pink salmon with concommitant increases in the amount of low energy-dense prey (pteropods in sockeye and pink salmon; pteropods and gelatinous zooplankton in chum salmon). These feeding interactions occur when abundant maturing pink salmon migrate through the central Bering Sea in the summer in odd-numbered years on their return to the rivers of eastern Kamchatka causing density-dependent interactions that negatively affect the feeding of sockeye, chum, and pink salmon. The capacity of chum salmon to shift diets by consuming gelatinous zooplankton and thereby reduce dietary overlap with other salmon indicates that chum salmon have a biological elasticity, which enables them to exploit gelatinous forms when abundance of other (crustacean) prey is reduced.

31. As salmon increased in size, they consumed larger-bodied prey. Small sockeye and chum salmon (<1000 g BW) consumed a high percentage of small hyperiid amphipods, *P. pacifica* and pteropods, *L. helicina*, (2-3 mm maximum size). In addition, copepods (7-8 mm body length) were more commonly found in the stomachs of small chum and pink salmon. Small fish prey (12-20 mm SL) was particularly important in the diets of small pink salmon (<500 g BW). Gelatinous zooplankton was an important food of chum of all sizes and the percentage of gelatinous prey actually increased as chum salmon body size increased (>1500 g BW). The 1000 g body weight appeared to be a minimum size for pink salmon to include a substantial percentage of large squid (*B. anonychus*) in their diet.

32. Diel catches and food habits of sockeye, pink, and chum salmon was investigated between 57°33´N, 178°41´W and 57°27´N, 178°20´W in the central Bering Sea. Eight operations were conducted in a 24-hour period starting at 0600 hrs and ending at 0500 hrs the following day using a surface gillnet. Sockeye, chum, and pink salmon were caught at the surface (0-6 m) during each of the six daylight gillnet operations, providing evidence that these species spent some portion of their time at the surface during daylight periods.

33. More sockeye salmon were caught during daylight and less during the night than would have been expected if catches had been equal in every time period. Pink salmon catches were also small in the afternoon and early evening (1500-2000 hrs) but increased dramatically immediately after sunset and remained at a high level until after sunrise (0300-0500 hrs). Chum catches increased shortly after sunrise (0300-0500 hrs) and after noon (1200-1400 hrs), however, catches were independent of daytime or nighttime gillnet sets.

34. Diel food habits of sockeye salmon illustrated a diel pattern where prey weight was significantly greater among fish caught during the night than during the day ($p<0.001$). There was one peak in stomach fullness immediately after sunset (2100-2300 hrs). Few empty stomachs were collected from sockeye salmon, regardless of the sampling period, indicating that sockeye were able to find prey during all periods. There was a distinct change in the prey composition over the diel period from euphausiids and copepods in sockeye salmon stomachs collected at night to a predominance of fish and crab larvae in stomach contents sampled during the day.

35. Diel food habits of pink salmon indicated that stomach fullness during the day and night was not significantly different from one another, although there was increased feeding activity after noon (1200-1400) and immediately after sunset (2100-2300 hrs). Empty stomachs were collected from midnight until late afternoon and the number of empty stomachs collected from pink salmon was higher than for sockeye and chum

salmon. At night pink salmon decreased the proportion of fish and increased the proportion of euphausiids and copepods in their stomach contents.

36. Diel food habits of chum salmon indicated there was no significant difference between day and nighttime stomach fullness of chum salmon. In every sampling period, chum had more prey in their stomachs than either pink or sockeye salmon. Unlike diel feeding of sockeye and pink salmon, chum salmon had an increase of stomach content weight in the middle to late afternoon (1500-1700), when fish were a major component of the diet, and showed no peak in prey weight after sunset. Chum salmon, like sockeye salmon, had few empty stomachs, suggesting chum salmon were able to find food at all times of the day. Similar to feeding patterns of sockeye and pink salmon, crustaceans, particularly euphausiids, were a major component of the prey consumed by chum salmon during nighttime gillnet sets (2100-0200). Chum salmon fed on gelatinous zooplankton during the day and night, although it was a more important component of the diet during the late morning (0900-1100). Chum salmon consumed the calorically-rich myctophid, *Stenobrachius leucopsarus*, in the early morning hours.

37. These results suggested that salmon were feeding throughout the 24-hour period, whenever prey was available. Salmon shift their feeding between consuming fish during the day and crustaceans at night. Nighttime competition for euphausiids may be intense, particularly when pink salmon are abundant, and when the period of darkness is short during summer at high latitudes. Therefore, a daytime switch to feeding on fish by sockeye, pink, and chum salmon may be a mechanism to decrease competition for food.

38. Caloric density determinations were performed by bomb calorimetry on a variety of salmonids, salmon prey organisms, and salmon stomach contents. Caloric density ranged from 470 to approximately 1000 calories per g wet weight for *C. limacina*, *L. helicina*, (pteropods), *P. pacifica* (hyperiid amphipods), small flat fish juveniles (*Atheresthes* sp. and *H. stenolepis* approximately 20 mm SL), and small squid (<20 mm ML). Slightly larger fish including *Hemilepidotus* sp. (21 mm SL), *T. crenularis* (43 mm SL), and *P. monopterygius* (44 mm SL), and middle-sized squid, *B. anonychus* (40 mm

ML), had caloric densities ranging from approximately 1100 to 1500 calories per g wet weight. Prey containing the highest caloric density (>1500 calories per g wet weight) included larger *B. anonychus* squid (80-90 mm ML), deep sea smelt *L. schmidti* (117 mm SL), and northern lampfish, *S. leucopsarus* (43-112 mm SL). Caloric values were reported for the first time for small squid (13-22 mm ML; 850-1010 calories per g wet weight) and juvenile flatfish including *Atheresthes* sp. (20 mm SL; 624 calories per g wet weight) and *H. stenolepis* (19 mm SL; 853 calories per g wet weight), which were important prey of sockeye, chum, pink, and chinook salmon in the central Bering Sea. The mesopelagic fishes, *S. leucopsarus* and *L. schmidti*, contained extremely high caloric densities (>2000 calories per g wet weight).

39. Bomb calorimetry of salmonids indicated that juvenile chum (age 0.0; 117 mm FL) and pink salmon (age 0.0; 111 mm FL), and young steelhead (age 2.0; 228 mm FL) had lower energy density (less than 1200 calories per g wet weight) than older steelhead (age 3.0; 351 mm FL) and sockeye that had spent one year at sea (age 1.1; 294 mm FL). Caloric densities were determined for juvenile chum (117 mm FL; 1113 calories per g wet weight) and pink salmon (111 mm FL; 1174 calories per g wet weight) caught shortly after entering the marine environment in the northern Gulf of Alaska and juvenile steelhead (351 mm FL; 1228 calories per g wet weight) spending their first summer in the central Gulf of Alaska.

40. The caloric density of stomach contents collected from large sockeye salmon (520-620 mm FL) showed a wide range (838 to 1405 calories per g wet weight). The energy density of stomach contents collected from large chum salmon (542-642 mm FL) ranged from 270 to 739 calories per g wet weight and was lower than stomach contents samples collected from sockeye and pink salmon. The caloric density of pink salmon (440-642 mm FL) stomach contents ranged from 991 to 1269 calories per g wet weight. Generally, sockeye, chum, and pink salmon containing high proportions of euphausiids and/or the northern lampfish, *S. leucopsarus,* were higher in caloric density than stomach contents containing few to none of these organisms.

41. A comprehensive table of energy densities was compiled from literature values for species ecologically-related to Pacific salmon. Results showed the energy density of cnidaria, ctenophores, and salps ranged from 30 to 290 calories per g wet weight, which was the lowest range of values obtained for a taxonomic group.

42. Pteropods, copepods, hyperiid amphipods, and chaetognaths had a slightly higher caloric density ranging from 250-1089 calorie per g wet weight. Euphausiids, particularly *E. pacifica* and *Thysanoessa* spp., had caloric densities ranging from approximately 1000 calories per g to a maximum of 1567 calories per g wet weight. Large squids had caloric densities among the highest of the invertebrates ranging from 920 to 1877 calories per g wet weight.

43. Estimates of the caloric density of fish indicated those with the lowest density, (less than 1000 calorie per g wet weight) included the juveniles of *Theragra chalogramma*, *Sebastes* sp., flatfish, and *Gadus macrocephalus*, and the cottids (of unknown life-history stage)*, Malacocottus kincaidi and Gymnocanthus galeatus*. Juvenile *P. monopterygius*, *Anoplopoma fimbria*, *Atheresthes* sp., and *Hemilepidotus* spp., and adult *Ammodytes* spp., *T. chalogramma, Sebastes* spp., *T. crenularis*, *Bathymaster signatus*, *C. saira,* and *Mallotus villosus* had higher caloric densities, ranging from 1000 to 2000 calories per g wet weight. Fish prey common in the stomach contents of Pacific salmon containing the highest caloric density included *Clupea pallasi*, *Thaleichthys pacificus*, *S. leucopsarus,* and *L. schmidti* (approximately 2000-2600 calories per g wet weight). Caloric densities for salmonids ranged from 1000-2000 calories per g wet weight. Caloric density of large-bodied coho salmon collected in the ocean ranged from 1287-2083 calories per g wet weight. Caloric content of chinook salmon was 1363 calorie per g wet weight for mature fish. Mature masou salmon had a relatively high caloric density that ranged from 1566-1719 calories per g wet weight.

44. Fish and squid prey organisms were the most calorically-dense salmon prey organisms among those analyzed. Micronekton are active swimmers making them more demanding for salmon to catch, but the energetic cost of pursuing and capturing fish and

squid is probably offset by consumption of this energy-rich prey. However, when fish and squid abundance is low, as might occur when the abundance of maturing pink salmon in an area is high, the time and energy required to search for and capture these rarer prey increases, with the result that a smaller proportion of ingested energy is available for salmon growth.

45. Salmon growth and prey consumption were estimated for a 2-month summer period using field observations on sea surface temperatures, salmon food habits in the central North Pacific Ocean and central Bering Sea, data on caloric density of salmon and salmon prey, and a published fish bioenergetic model. Growth estimates from the model were compared with summer monthly mean weights of high-seas caught salmon to evaluate daily ration. Gross conversion efficiency (growth/consumption), mean consumption rate (g-prey per day), total consumption by prey category (g), and total energy consumed (kcal) were estimated at the end of the 60-day simulated period.

46. The estimated maintenance ration for an immature ocean age .1 sockeye in the central Bering Sea in June and July ranged from 0.8 to 1.3% body weight per day at 5-9°C. The maintenance ration increased with temperature as the energetic costs of metabolism increased. Likewise, the physiological maximum ration increased from 3.6 to 5.0% body weight per day over the 5-9°C temperature range considered. Net production at each ration level decreased as the temperature increased. Gross conversion efficiency was highest at the maximum ration and the lowest temperature (21.5%, 5°C). An ocean age .1 sockeye growing from 361 to 568 g would, therefore, consume an average of 16-19 g of prey per day, the equivalent of 3.57 to 4.09% body weight per day (27-31 calories per g-predator per day), depending on temperature. To achieve this net production (207 g), the sockeye would have to feed at 88 to 93% of its physiological maximum rate. Over two months, the total prey consumption was estimated as 0.975-1.116 kg, the equivalent of 731-837 kcal. The specific energy requirements (27-31 calories per g-predator per day) for small (361-568 g) sockeye salmon determined in this study were the first estimates available for young ocean age .1 sockeye in the Bering Sea.

47. The estimated maintenance ration for an immature ocean age .2 chum salmon in the central Bering Sea ranged from 0.9 to 1.4% body weight per day and the maximum ration ranged from 3.5 to 4.8% body weight per day at 5-9°C. At a daily ration of 2% body weight per day, net production decreased by 52% from 5° to 9°C. To grow from 1042 to 1547 g, a mean ration of 3.28-3.86% body weight per day (20-24 calories per g-predator per day) was required, which was a daily consumption rate of 42 to 49 g-prey per day, or 85 to 89% of its physiological maximum consumption rate per day, depending on temperature. Estimated chum salmon cumulative consumption was 2.506-2.949 kg or 1531-1803 kcal.

48. The estimated maintenance ration for a maturing ocean age .1 pink salmon in the central Bering Sea ranged from 0.6 to 1.0% body weight per day, and the physiological maximum ration ranged from 2.8 to 3.9% body weight per day at 5-9°C. At a daily ration of 2% body weight per day, net production decreased by 31% from 5° to 9°C. If a maturing pink salmon grew 912-1313 g, the required ration was estimated as 2.73-3.14% body weight per day (24-27 calories per g-predator per day) and a daily prey consumption of 30-35 g per day, or 86 to 94% of its physiological maximum consumption rate per day, depending on temperature. Over 60 days, an estimated 1.800-2.068 kg of prey, or 1552-1783 kcal were consumed.

49. The estimated maintenance ration for a maturing ocean age .1 coho salmon in the central North Pacific Ocean ranged between 0.7 and 1.1% body weight per day, and the physiological maximum consumption ranged from 2.0 to 3.4% body weight per day at 7-11°C. At a daily ration of 2% body weight per day, net production decreased by 33% from 7° to 11°C. A maturing coho salmon growing from 1909 to 2975 g would consume 2.64-2.86% body weight per day (37-40 calories per g-predator per day) and a daily prey consumption of 63-68 g-prey per day at 9° to 11°C, or 91 to 96% of its physiological maximum consumption rate. Over two months, 3.785-4.105 kg of prey, or 5248-5693 kcal of energy would be consumed. My estimate of 2.6-2.9% body weight (37-40 calories per g-predator per day) daily ration for maturing coho salmon was the first determined for adult coho in offshore marine habitats.

50. Results of the simulations indicated that salmon were feeding at a rate close to their physiological maximum (85 to 93% of the maximum for immature sockeye and chum, and 86 to 96% of the maximum for maturing pink and coho salmon). Therefore, small decreases in the daily ration can cause significant decreases in growth over a time period as short as two months during the summer, when feeding and growth opportunities should be at or near optimal. In addition, at summertime surface temperatures encountered in the central North Pacific Ocean and central Bering Sea, prey consumption was more important than temperature for determining salmon growth. I speculate that as the energy requirements of metabolism increase with temperature, prey consumption increases and provides sufficient energy for substantial growth. In the summertime temperature ranges such as those used in my simulations, prey availability rather than metabolic efficiency governs how much the salmon will grow. I suggest that there may be lower thermal limits below which, although the energy conversion efficiency for salmon is high because metabolic demands are low, consumption rates are also low, and therefore growth is substantially reduced. If true, when salmon prey is abundant, an upper thermal limit favorable for salmon growth may be bounded by large metabolic requirements at high temperatures, and a lower limit favorable for salmon growth may be bounded by decreased capacity for prey consumption at low temperatures.

51. My results have shown that during the summer the central Bering Sea is critical habitat for salmon because of its role as a nursery area for juvenile and post-larval fish and squid, which provides a rich forage base for feeding of Asian and North American stocks of young sockeye, chum, and chinook, and maturing chum and pink salmon. Recently, overall reduction in productivity, small runs of chinook and chum salmon to western Alaska, and unusual coccolithophore blooms suggest that the environment may be changing in the Bering Sea, an area particularly sensitive to conditions brought about by global climate change. These concerns warrant particular attention to monitoring year-round conditions in salmon prey availability and salmon feeding and growth in order that we can best manage the future of our salmon resources.

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