# Diets of Pacific Salmon in the Sea of Okhotsk, Bering Sea, and Northwest Pacific Ocean

**Vladimir I. Karpenko**[1], **Anatoly F. Volkov**[2], and **Maxim V. Koval**[1]

[1]*Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO), 18 Naberezhnaya Street, Petropavlovsk-Kamchatsky 683602, Russia*
[2]*Pacific Scientific Research Fisheries Centre (TINRO-Centre), 4 Shevchenko Alley, Vladivostok 690950, Russia*

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Abstract: Since the 1950s the food habits of Pacific salmon have been studied from samples representing multiple salmon life-history stages, collected from principal feeding areas (Sea of Okhotsk, Bering Sea, and Northwest Pacific Ocean) within Russia's 200-mile economic zone. Data have been gathered by various types of fishing gear designed to catch juvenile and adult salmon. Using a comparative analysis, we examined feeding habits of pink, chum and sockeye salmon. Our results showed that in the 1950s, in offshore waters, the principal prey of these salmon consisted of energetically valued hyperiids and euphausiids. The basic juvenile salmon diet consisted of copepods, which also contributed substantially to the food of returning adults. Diets were stable until the 1980s, when the contribution of pteropods and juvenile fish to salmon diets became more significant. Since that time, low-energy organisms, including arrow worms, appendicularia, and salps, have appeared in the diets of salmon in relatively high numbers, particularly in the Bering Sea. Chum salmon have the most varied diet, and may be the best indicator of plankton production. Research shows that changes in diet can be associated with changes in plankton and nekton abundance. Regional variables and salmon abundance have also affected salmon diet composition. The composition of salmon diets has affected the size and average age at maturity toward the end of the last century, which has influenced the productivity of salmon stocks and populations.

Keywords: salmon, food spectrum, variability, food similarity, component, survival, production

## INTRODUCTION

Trophic interactions are one of the key factors determining not only the biological characteristics of fish, but also their survival which, in turn, regulates salmon abundance and productivity. The state of the salmon forage base depends on oceanic climate conditions that influence the development of the principal components of zooplankton and nekton in areas where salmon migrate during particular periods in their life cycle. Further, salmon migrations are seasonal, which also influences their food supply and, therefore, the survival of generations.

These interactive processes cannot be explained based on episodic or short-term observations, especially if such observations are based only on a particular unit of a fish stock. Proper analysis requires continuous observations using a common method to create a large database for comparison. Data on Pacific salmon in most regions of the North Pacific Ocean have been collected by KamchatNIRO (since the mid 1950s) and by TINRO-Centre (since the mid 1980s).

The purpose of this paper is to examine and analyze the content, weight, and prey composition by stomach analysis of pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon during different periods of oceanic life to assess of the influence of trophic interactions on the development of biological parameters and the abundance of salmon in the Northwest Pacific Ocean.

## MATERIALS AND METHODS

Archival materials and published long-term datasets, collected by researchers from Russian research institutions, primarily KamchatNIRO, for the first decades of Pacific salmon studies were used for our analyses (Andriyevskaya 1957, 1958, 1964). This period, beginning with the studies of adult salmon at KamchatNIRO, covers over 50 years (from 1954), and for juvenile salmon, about 40 years (from 1965) (Karpenko 2003). Unfortunately, there is no continuous line of observation for any particular area or for any one species. Also, there is no standard method for collecting and processing data because the methodologies have either changed or improved over time. Most of the changes are related to modernization of vessels and techniques for sampling and processing. All data used in this analysis were transformed into a standard format and processed with the same methods. Individual weight measurements for over

All correspondence should be addressed to V. Karpenko.
e-mail: karpenko@kamniro.ru

10,000 adult salmon and over 14,000 juveniles were available. The data from the BASIS program have also been analyzed (Volkov et al. 2005). That analysis included 11,671 stomachs of three species: pink salmon (2,119 specimens), chum (5,617 specimens) and sockeye (3,935 specimens), which were collected throughout the Bering Sea. Our current analysis uses the results of studies of 1,592 juveniles and 3,861 maturing salmon, caught only in the western Bering Sea. We examined 10,000 stomachs of each of the species mentioned. Additionally we used data from the published literature about the feeding habits of these species in particular areas of the Far Eastern seas, and adult salmon biological parameters and abundance.

## RESULTS AND DISCUSSION

### Juvenile Pacific Salmon Diets

The river systems (rivers and lakes) flowing into the Sea of Okhotsk provide spawning areas for all species of Asian Pacific salmon, except chinook. The Sea of Okhotsk is the most important feeding area for juvenile Pacific salmon stocks of Asian origin. In spring, salmon emerge from the rivers and begin feeding in coastal waters, mixing extensively before leaving for the high seas of the North Pacific. The diet of juvenile pink, chum and sockeye salmon consists of approximately 60 species: over 50 species in the diet of pinks, 45 in the chum diet, and 35 in the sockeye diet.

In the Sea of Okhotsk the most abundant species is the juvenile pink salmon, although in some years chum salmon can dominate. The dominance of chum salmon occurred most often in the 1960s and 1970s, two decades of very reduced salmon abundance. Juvenile pink salmon, perhaps because of its abundance and its early and rapid migration to the Okhotsk Sea, has the widest spectrum of food of all the species of salmon. The basic diet consists of hyperiids, euphausiids, copepods, and pteropods. The summary percentage of these organisms is usually over 80% of the total food weight. During all of the years of observation, hyperiids played a dominant role, providing 29 to 67% of food weight (Fig. 1A). In the 1960s and 1970s this taxon dominated at 67 and 51%, respectively, whereas in the 1980s, 1990s and 2000s it made up about one-third of the diet of juvenile pink salmon (ranging from 29% to 35%). The dominant species was *Themisto japonica*. Only in 1969 did another species, *T. libellula*, supply the bulk of food (86%). In the 1960s the second most dominant food source were copepods (13%). The percent of all of the other food components did not exceed 5% of food weight. In the 1970s and 1980s, besides a high percentage of hyperiids, pink salmon also consumed euphausiids (18% and 11%, respectively) and copepods (11% and 18%, respectively). In the 1990s and 2000s, pteropods (22% and 26%, respectively), copepods (16% and 14%, respectively) and euphausiids (12% and 23%, respectively) made up a significant percentage of food weight. Only in the 1970s did juvenile fish provide over 8% of food weight; in the other periods the percentage was lower. A narrow food spectrum for pink salmon was recorded in the 1960s and 1970s (16 and 13 components, respectively). A wide spectrum was seen in the 1990s and 2000s (30 and 24 components, respectively). Average stomach fullness varied extensively, from 56.3 to 312.9$^{o}/_{ooo}$. It was highest in the 1980s (up to 313$^{o}/_{ooo}$), and lowest by the late 1990s and into the 2000s (< 200$^{o}/_{ooo}$). Overall, the dominance of hyperiids in the diet was observed in years of low pink salmon abundance, whereas a high percent of pteropods, copepods and euphausiids was observed in years of high pink salmon abundance.

Chum salmon also consumed mostly hyperiids, contributing 22–64% of food weight (Fig. 1B). Similar to pink salmon, *T. japonica* formed the basis of the juvenile chum salmon diet; *T. libellula* dominated (90.5%) only in 1969. In addition to these species, in the 1960s and 1970s chum salmon consumed juvenile fish (9% and 14%, respectively) and euphausiids ( 9% and 16%, respectively). In the 1980s and 1990s, chum salmon consumed *Oikopleura* sp. (20% and 26%, respectively) and pteropods (12% and 22%, respectively). In recent years the chum salmon diet included a significant percentage of euphausiids (24%), pteropods (16%), copepods (11%) and *Oikopleura* sp. (10%). A narrow food spectrum (up to 16 components), similar to the spectrum of the pink salmon diet, was observed in chum salmon in the 1960s and 1970s, and a wide spectrum (up to 25 components) in the 1990s and 2000s. The stomach fullness of chum salmon was lower (34–220$^{o}/_{ooo}$) compared to values for pink salmon. It was also high in the 1980s (54 to 220$^{o}/_{ooo}$), and low (up to 130$^{o}/_{ooo}$) in the 1960s and recent 2000s. In general, the percentage of hyperiids decreased from 64 to 27%, whereas the percentage of euphausiids increased (to 24%), as well as pteropods (to 22%), *Oikopleura* sp. (to 26%), and copepods (to 11%).

Sockeye salmon have the most narrow food spectrum of all Pacific salmon. In the 1960s, 1970s and 1980s they fed mostly on hyperiids (43%, 48% and 35% of food weight, respectively) (Fig. 1C). Among other plankton, only juvenile fish (34% in the 1960s) and euphausiids (18% in the 1970s, and 20% in the 1980s) played an important role in sockeye diets. During this period (1960s to 1980s) the sockeye food spectrum included only 5–11 components. In the 1990s and 2000s the food spectrum of juvenile sockeye increased to up to 20 components, and an important role was played by pteropods (30% in the 1990s, and 15% in the 2000s) and euphausiids (15% in the 1990s, and 28% in 2000s). Besides these taxa others began to play more important roles, including juvenile fish (14% in the 1990s, and 19% in the 2000s), copepods (16% in the 2000s), larval crabs (8% in the 1990s, and 10% in the 2000s), among others. The stomach fullness of juvenile sockeye was lower, when compared with other species, and did not exceed 100$^{o}/_{ooo}$ (varying from 18 to 98$^{o}/_{ooo}$). During the periods of observation it varied little, showing little evidence of food sustainability for this salmon species.

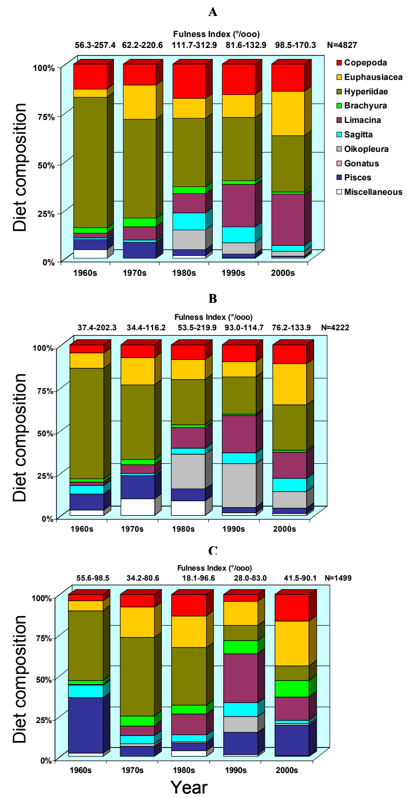


**Fig. 1.** Diet composition of juvenile pink (A), chum (B) and sockeye (C) salmon (1960s–2000s) in the Okhotsk Sea.

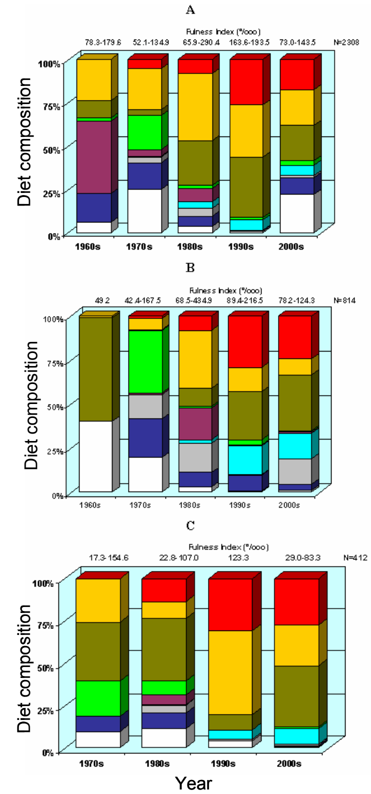


**Fig. 2.** Diet composition of juvenile pink (A), chum (B) and sockeye (C) salmon (1960s–2000s) in the Bering Sea. Key as in Figure 1.

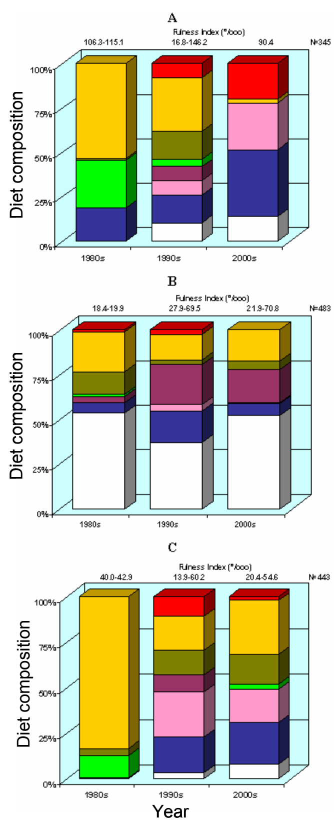


**Fig. 3.** Diet composition of adult pink (A), chum (B) and sockeye (C) salmon (1980s–2000s) in the Bering Sea. Key as in Figure 1.

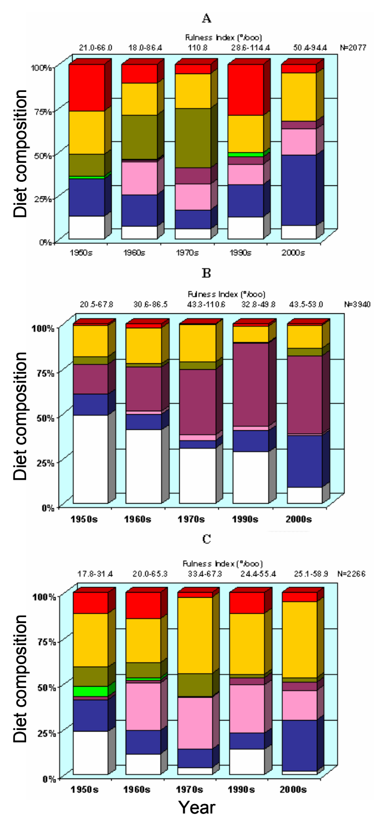


**Fig. 4.** Diet composition of adult pink (A), chum (B) and sockeye (C) salmon (1950s–2000s) in the Northwest Pacific Ocean. Key as in Figure 1.

Among the three species of juvenile Pacific salmon in the Sea of Okhotsk the most consistent consumer of marine crustaceans is the sockeye salmon. Pink salmon also prefer high caloric crustaceans, including hyperiids, euphausiids and copepods (Yerokhin and Shershneva 2000; Shershneva and Koval 2004). Chum salmon consume a varied diet with a wide spectrum of food. When pink salmon are abundant, they consume a larger number of organisms of lower caloric value, including pteropods and *Oikopleura* sp., among others.

In the western Bering Sea, juvenile salmon have a relatively narrow food spectrum, compared to those in the Sea of Okhotsk, and consisting of < 50 components. The diet of juvenile pink salmon includes 43 components, chum salmon includes 39, and sockeye salmon includes 28. The main diets of juvenile sockeye consisted of euphausiids, hyperiids and copepods, and also larval crabs and juvenile fish. Occasionally other plankton began to play an important or even dominant role.

For example, in the 1960s the principal food of juvenile pink salmon were pteropods (42% of food weight). Other plankton were less important, including euphausiids (24%), juvenile fish (17%) and hyperiids (10%) (Fig. 2A). In the 1970s, the most numerous items were euphausiids (24%), *Podon* sp. (21%), larval crabs (20%) and juvenile fish (15%). A more stable but wider food spectrum was observed in juvenile pink salmon during the 1980s and 2000s, when the principal food consisted of crustaceans, including euphausiids (26–39% of food weight), hyperiids (26–35%) and copepods (8–26%). The principal species of Copepoda were *Neocalanus cristatus* and *N. plumchrus*, although in 1990 *Eucalanus bungii* made up 20% of the food weight. The percentage of other organisms was very low: in the 1980s pteropods made up 8% of food weight, and in the 2000s juvenile fish made up 13%. During the periods of observation from 1965 to 2002 the juvenile pink salmon food spectrum increased from 3 to 28 components. The spectrum was the narrowest during the period of low catches in the 1960s and 1970s (3–11 components). However, the stomach fullness was highest in the 1960s (from 78–180$^{o}/_{ooo}$) and in the 1980s (66–290$^{o}/_{ooo}$). The stomach fullness of pink salmon was low in the 1970s (52–135$^{o}/_{ooo}$) and 2000s (73–144$^{o}/_{ooo}$).

The food spectrum of juvenile chum salmon showed the widest seasonal and interannual variations (Fig. 2B). For example, in 1965 the basis of the chum salmon diet consisted of hyperiids (59%) and *Polychaetae* (31%). In the 1970s it consisted of larval crabs (35%) and juvenile fish (22%), and in the 1980s it consisted of euphausiids (33%), pteropods (18%) and *Oikopleura* sp. (17%). In 1978 *Oikopleura* sp. accounted for 30% of food weight. Only in the 1990s and 2000s did crustaceans (including hyperiids (27-31%), copepods (24–29%) and euphausiids (9–14%)) play an important role in chum salmon diets; the role of arrow worms was also important (15% to 16%). In the course of our studies the chum salmon food spectrum increased from 5 to 22 components. Low stomach fullness (42–168$^{o}/_{ooo}$) was observed from 1965 to 1970, and in the 2000s (78–124$^{o}/_{ooo}$). It was the highest (up to 434$^{o}/_{ooo}$) in the 1980s.

Juvenile sockeye had the most consistent food spectrum, consisting of crustaceans, including hyperiids, euphausiids and copepods, that varied by year (Fig. 2C). During the 1970s, 1980s and 2000s hyperiids dominated, making up > 35% of the food weight. Only in the 1990s did this group fall to third place behind euphausiids (49%) and copepods (31%). Among the other plankton only larval crabs in the 1970s (21%) and juvenile squid in the 1980s (11%) played an important role in the sockeye diet. The number of food components varied from 3 to 14 in those decades. The stomach fullness of juvenile sockeye was also relatively stable, varying from 17 to 155$^{o}/_{ooo}$, with an average of approximately 100$^{o}/_{ooo}$. These characteristics suggest that sockeye salmon are the most consistent consumer of crustaceans in the western Bering Sea.

**Adult Pacific Salmon Diets**

The food spectrum of adult salmon was different from that of juveniles. It was significantly wider, consisting of approximately 60 components: 34 components in pink, 45 in chum, and 43 in sockeye salmon. The role of crustaceans was significant only in the spectrum of pink and sockeye salmon, while chum were feeding mostly on other organisms.

The diet of adult pink salmon in the 1980s and 1990s consisted of euphausiids (54% and 30%, respectively) (Fig. 3A). In the 1980s, besides these organisms, there was a high percentage of larval crabs (27%) and juvenile fish (19%), and in the 1990s there was a high percentage of hyperiids and juvenile fish (16% for each). Juvenile fish was the basis of the adult pink salmon diet in the 2000s (38%), when other items in the diet consisted of juvenile squid (26%) and copepods (20%). The average stomach fullness varied by year and was about 100$^{o}/_{ooo}$.

Chum salmon consumed mostly euphausiids (14–22%), pteropods (4–22%) and juvenile fish (6–18%) (Fig. 3B). However, usually up to one-third of the chum salmon diet was difficult to identify because the prey items were rapidly digested. Among crustaceans only euphausiids made up a significant part of the food spectrum (14–22%), while hyperiids and copepods rarely contributed more than 10% of food weight. The stomach fullness of chum salmon usually was low, not over 70$^{o}/_{ooo}$, but the food spectrum was relatively wide in the 1980s, consisting of 24 components.

The sockeye salmon diet in the 1980s and 2000s consisted of euphausiids, which made up 84% and 30%, respectively, of the food weight (Fig. 3C). Besides these groups in the 2000s, there was a significant percentage of juvenile fish (23%), squid (18%) and hyperiids (16%). The widest spectrum of food (23 components) was recorded for sockeye adults in the 1990s, when the principal food items were juvenile squid (25%) and fish (20%), and also euphausiids (19%), hyperiids (14%) and copepods (11%). The stomach fullness of sockeye salmon was the lowest among all salmon and never exceeding 60$^o/_{ooo}$, and averaging slightly > 40$^o/_{ooo}$.

In the western Bering Sea the principal food of both adult and juvenile salmon,was crustaceans, including euphausiids, hyperiids and copepods. Occurrence of other food components was recorded in the cases of increased abundance of consumers or transformations in pelagic plankton or nekton communities when salmon began to consume large amounts of pteropods, juvenile fish and squid, as well as *Chaetognatha* and *Oikopleura* spp. Among three salmon species – pink, chum and sockeye, sockeye salmon had the least variable diet. Chum had the most variable diet. Pink salmon took an intermediate position. However, because of the high abundance of pink salmon, they influence the state of pelagic crustacean communities, which may determine the interannual variations in productivity of particular salmon species.

In the Pacific Ocean waters off Kamchatka the adult salmon returning to spawn in the river systems of the Far East are caught by gillnets. Kapron nets were used until the 1970s, and were later replaced by fibre nets. These nets undoubtedly have different fishing efficiencies. Kapron nets were used mostly for research purposes until the 1980s. The fibre nets were used in the Japanese Pacific salmon fishery, and also for the last ten years on Russian research vessels.

The food composition of salmon diets included approximately 70 components. Chum had the widest food spectrum (69 components), with sockeye having the narrowest spectrum (52 components). Pink salmon had an intermediate position (58 components). The wider food spectrum of chum salmon, compared to the other salmon species, is determined by a larger contribution and number of jelly-bodied organisms and juvenile fish.

Pink salmon adults consumed mostly crustaceans - copepods, hyperiids and euphausiids, and also pteropods, squid and juvenile fish; the percentage of these components showed significant interannual variations (Fig. 4A). In the 1950s the principal components of pink adult diets were: copepods (27%), euphausiids (25%) and juvenile fish (21%); in the 1960s they were hyperiids (24%), juvenile squid (19%) and fish (18%); in the 1970s, hyperiids (34%), euphausiids (20%) and juvenile squid (15%); in the 1990s, copepods (30%), euphausiids (21%) and juvenile fish (19%); and in the 2000s, juvenile fish (40%), euphausiids (28%) and juvenile squid (15%). In some years the basic diet consisted of relatively rare plankton species. For example, *Sagitta elegans* in February–April in 1986 made up 33–45% of the food weight, and squid in 1962 made up 62.6% and in 2000, made up 40.3%. The widest food spectrum (23 components) was shown in pink salmon adults in the mid 1950s and early 2000s; the narrowest spectrum was seen in the early 1960s (8 components). The stomach fullness was relatively low in the 1950s and 1960s (18–86$^o/_{ooo}$) and relatively high in the 1970s. The increase in recent years (over 100$^o/_{ooo}$), is perhaps due to the use of different gillnets. Overall, the dominance of juvenile fish and squid in diets was observed during years of high abundance of pink salmon, whereas the dominance of crustaceans was recorded in years of low abundance of pink salmon.

Chum salmon fed mostly on pteropods, euphausiids and juvenile fish, and sometimes a high percentage of coelenterates (Fig. 4B). The latter dominated (21%) in the 1950s, in particular in 1957 when they made up 72.6%, in 1958 when they made up 49.6% and in 1997 when they made up 27.8% of food weight. Chum salmon also fed on euphausiids (17%) and juvenile fish (12%). In the 1960s the basis of the adult chum diet consisted of pteropods (25%) and euphausiids (20%); in the 1970s, 1990s and 2000s it consisted of pteropods (37–46%), euphausiids (9–21%) and juvenile fish (5–29%). The widest food spectrum (30 components) was shown in adult chum diets, similar to that for pink salmon in the mid 1950s and early 2000s. The narrowest spectrum for adult chum was seen in the mid 1960s and early 1970s. Stomach fullness of adult chum salmon was always lower in comparison to that of the other salmon, and only in the 1970s was it over 100$^o/_{ooo}$. Similar to pink salmon, chum salmon showed a dominance of pteropods and juvenile fish in diets during high salmon abundance, in particular pink salmon.

Sockeye salmon consumed mostly euphausiids, juvenile squid and fish, with a lesser role played by copepods, hyperiids and pteropods (Fig. 4C). In the 1950s the principal components in sockeye diets were euphausiids (30%), juvenile fish (17%), copepods (11%) and hyperiids (11%); in the 1960s the principal components were juvenile squid (26%), fish (13%), euphausiids (25%) and copepods (15%); in the 1970s and 1990s euphausiids ( 42% and 34%, respectively) and juvenile squid (29% and 27%, respectively) were most important; in the 2000s, euphausiids and juvenile squid (41% and 16%, respectively), and also juvenile fish (28%) were most important. Among the other forage organisms, in 1962, *Callizona* sp. supplied 32.9%, and squid supplied 46.8% to 54.6%; in 1964, 59.7% in 1970, 75.7% in 1998 and in 2000, 43.3% of food weight. Sockeye had the widest spectrum of food in the 1950s and 2000s (18 and 26 components, respectively). In the 1950s, stomach fullness was the lowest (18–31$^o/_{ooo}$), whereas in the 1970s it was the highest (33–67$^o/_{ooo}$). Sockeye salmon, as the most active competitor, did not change its principal food item. Only in the 1960s was the percentage of euphausiids nearly equal to that of juvenile squid. We conclude that the most stable and active consumer of crustaceans is sockeye salmon. Pink salmon compete with sockeye salmon, The most flexible consumer of various organisms is chum salmon.

**BASIS Program Studies**

Scientists from TINRO-Centre in three research vessels (Russian, American and Japanese) collected samples from salmon and processed them using the standard method accepted at TINRO-Centre (Chuchukalo and Volkov 1986; Volkov 1996). This method includes mass processing of stomach-enteric tracts immediately after catching without preservation. This method allows scientists to estimate the digestion stage of food, and, more important, to process all materials collected immediately while still at sea. The immediacy allows researchers to gain insights about the features and intensity of salmon feeding in each area surveyed. The basic juvenile salmon diets in the autumn of 2002–2004 consisted of hyperiids, (21.3–98.4% of food weight) (Fig. 5). In 2002 the dominant component was euphausiids (40.5%), but the portion of copepods (19.9%) and of arrow worms (14%) was also significant. In 2003 the sockeye diet also included pteropods (18.3%). The food spectrum of juvenile sockeye salmon was narrow (2–7 components), and stomach fullness was low (99–160$^{o}/_{ooo}$).

Juvenile pink and chum salmon had wider food spectra (6–10 and 4–10 components, respectively). In 2002 the food spectrum of juvenile pink salmon included a high percentage (36.9%) of euphausiids, and in 2003 a high percentage (24.5%) of pteropods. The same species of plankton in the same years contributed a relatively high percentage in juvenile chum diets, 16.6 and 19.3% respectively. The stomach fullness of juvenile pink and chum salmon was also high (174–232$^{o}/_{ooo}$ and 110–288$^{o}/_{ooo}$, respectively).

Maturing chum and sockeye salmon had wider spectra of food than pink salmon (11–17 and 11–13 components, respectively) (Fig. 6). The ratio between spectra varied significantly by year. In 2002 and 2004 the basic chum diet consisted of juvenile fish (40.9% and 37.6%, respectively), hyperiids (25% and 18.2%, respectively) and euphausiids (13.6% and 30%, respectively). In 2003, chum salmon fed on pteropods (32.9%), hyperiids (9.5%) and juvenile fish (8.1%); approximately 40% of the food consisted of an extensively digested component whose composition could not be identified.

The stomach fullness of chum salmon varied from 29 to 59$^{o}/_{ooo}$. Variations in fullness in sockeye salmon were high, from 15 to 70$^{o}/_{ooo}$. The basic sockeye diet in 2002 and 2004 consisted of hyperiids (34.1% and 42%, respectively), euphausiids (15.5% and 25.6%, respectively), larval crabs (16.3% and 13.7%, respectively) and juvenile fish (10.3% and 14.4%, respectively). In 2003 chum fed on juvenile squid (39.4%), hyperiids (21.2%), pteropods (10.7%) and euphausiids (9.3%).

Thus, in the western Bering Sea, the dominant items in the diets of pink, chum and sockeye salmon were hyperiids, pteropods and small squid. The percentage of euphausiids was comparatively small. This could be explained firstly by the abundance of this plankton and secondly by the availability of these animals during the day when salmon feed most actively (Volkov and Kosenok 2005; Koval 2005). Interannual dynamics of the role of pteropods in salmon diets relates first of all to the peculiarities of the biology of this taxon (Volkov 2003). The highly abundant copepods and

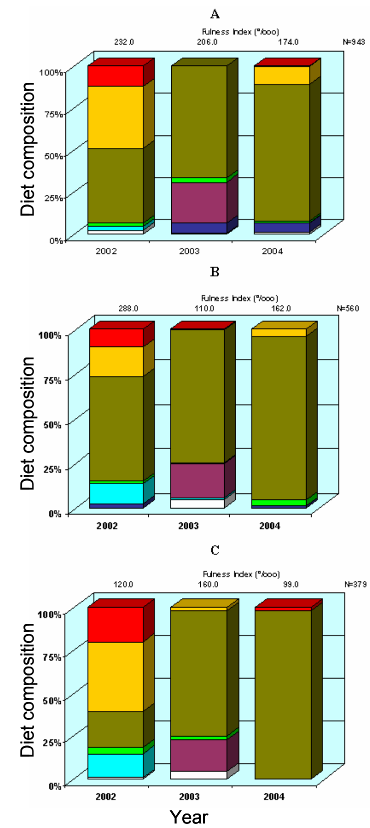


**Fig. 5.** Diet composition of juvenile pink (A), chum (B) and sockeye (C) salmon (2002–2004) from the BASIS program. Key as in Figure 1.

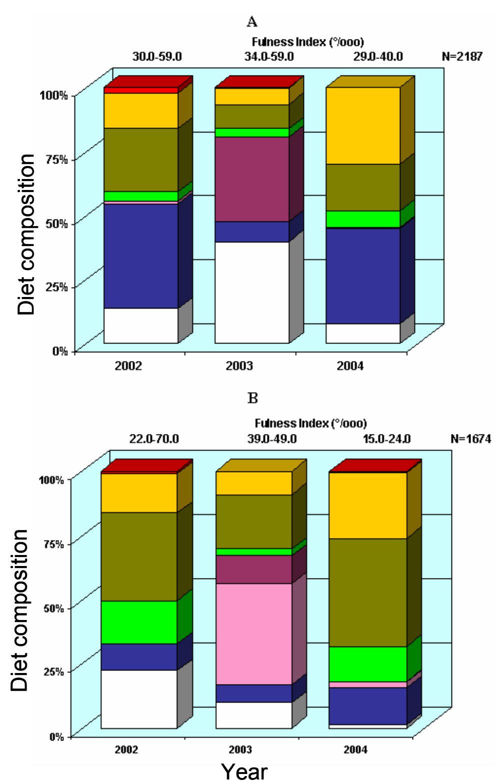


**Fig. 6.** Diet composition of immature chum (A) and sockeye (B) salmon (2002–2004) from the BASIS program. Key as in Figure 1.

*Chaetognatha* made up only a small percentage of salmon food weight.

**Comparison of Plankton Community Structure and Diets**

The data collected during the BASIS program allow us to compare diet composition and plankton biomass in the western Bering Sea (Figs. 7 and 8). Summary characteristics (distribution) of these parameters (plankton biomass and food composition) were similar, on the whole, as fractions–hyperiids, euphausiids, and so on. This is the foundation for our conclusion, that Pacific salmon are the best "plankton and nekton gear," and can be used for estimating the pro-

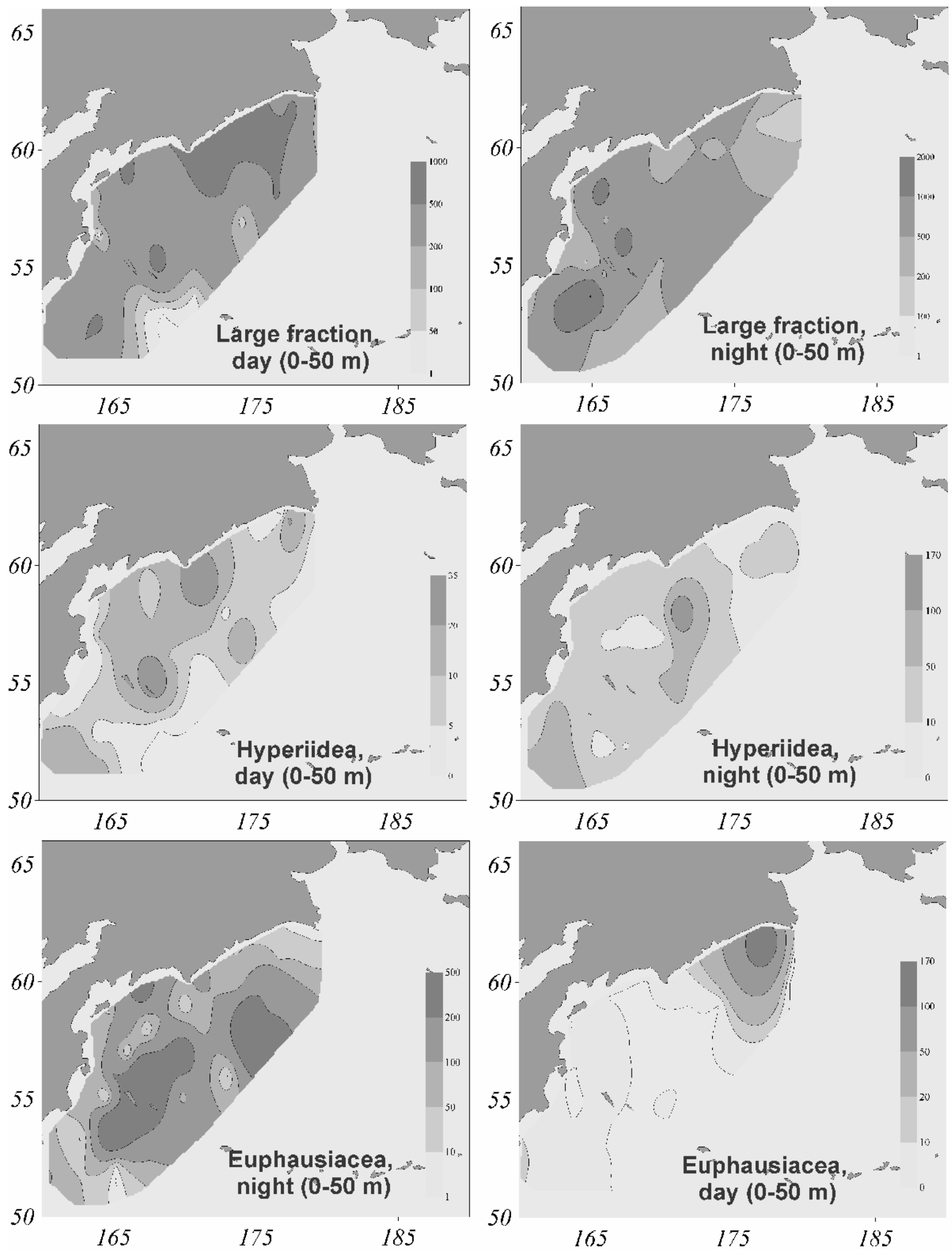


**Fig. 7.** Biomass (mg/m$^3$) of zooplankton at 0–50 m during day and night in the western Bering Sea and North Pacific Ocean (Source: BASIS).

ductivity of these planktonic organisms, for seasonal, intra-annual, and interannual comparisons.

**Salmon Feeding Interactions**

The composition of salmon diets is determined by the abundance of forage organisms in the areas where salmon feed, and the dynamics of inter- and intra-specific feeding interactions. To provide an analysis of the character of salmon feeding interactions we have tried to analyze variations in the number of components and the structural composition of juvenile and adult salmon food in the areas of long-term

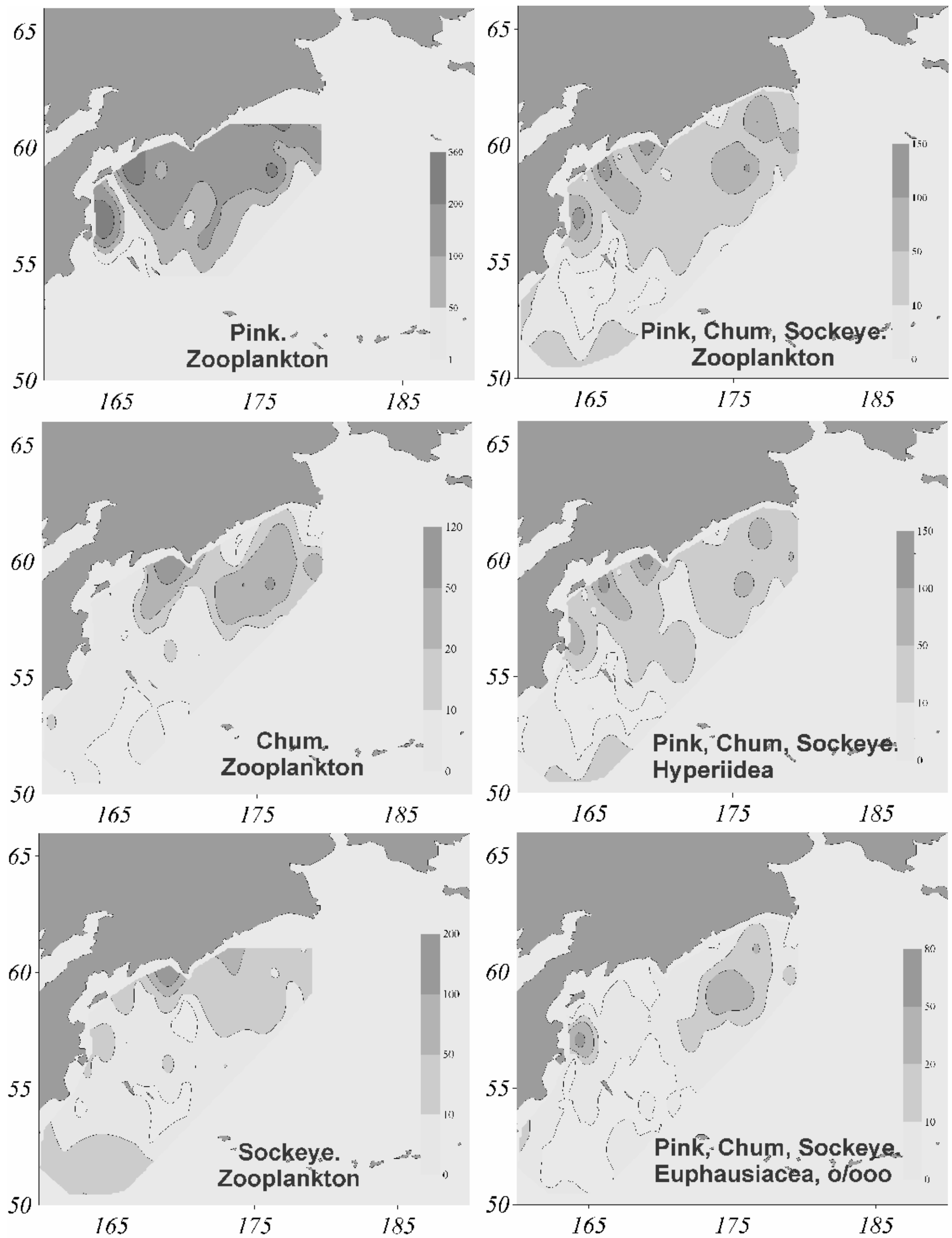


**Fig. 8.** Diet composition ($^{o}/_{ooo}$) of pink, chum and sockeye salmon (both individually and grouped together) in the western Bering Sea and North Pacific Ocean (Source: BASIS).

monitoring programs. We also tried to compare food similarity or food overlap (FS-coefficients).

*Juvenile salmon*

Diets of juvenile pink, chum and sockeye salmon have been recorded for nearly 40 years (1966–2002) in the Sea of Okhotsk (Fig. 9A). The diets of juvenile sockeye salmon had the smallest number of components (from 5 to 11), in comparison with the other species. In the late 1990s and early 2000s (in 1997, 1999 and 2001, specifically) the food spectrum for sockeye increased to up to 20 components. In recent years the widest food spectrum was seen in juvenile chum (up to 25 components) and pink salmon (up to 30 components). Also in recent years the highest abundance of feeding juvenile salmon, pink salmon in particular, was observed. The food spectrum for pink and chum usually included from 9 to 17 components and it did not vary significantly in either species by year.

In the Okhotsk Sea, diets of salmon juveniles of the three species used to show maximum food similarity, which can indicate favorable feeding conditions and a high level of the salmon forage base. For example, average FS-coefficients are usually over 50%, reaching up to 71% in pink and chum salmon; the lowest FS-coefficient (47.2%) was found in chum and sockeye (Fig. 10A). Moreover a higher food similarity was observed in the 1960s (90% to 100%) and 2000s (70% to 76%), and the minimal food similarity was seen in 1974 (33.4%) and 1983 (39%). The diets of pink and sockeye salmon had maximum food similarity in 1967 (75%), 1973 (83.9%) and 1986 (73.4%), and minimum food similarity in 1972 (9.5%). Minimum food similarity was also characteristic of chum and sockeye salmon (FS = 9.5% in 1972). These species had maximum food similarity in 1967 (89%) and 1981 (72.6%).

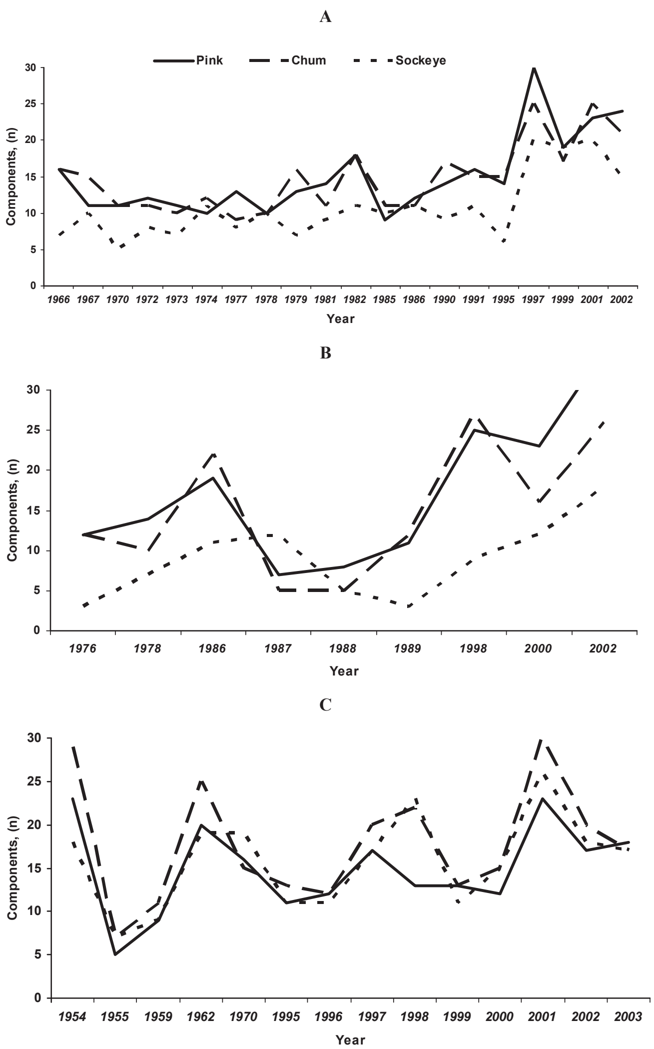


**Fig. 9.** Number of food components in the diets of pink, chum and sockeye salmon. A - juveniles, Okhotsk Sea, 1966–2002; B - juveniles, Bering Sea, 1976–2002; C - adults, North Pacific Ocean, 1954–2003.

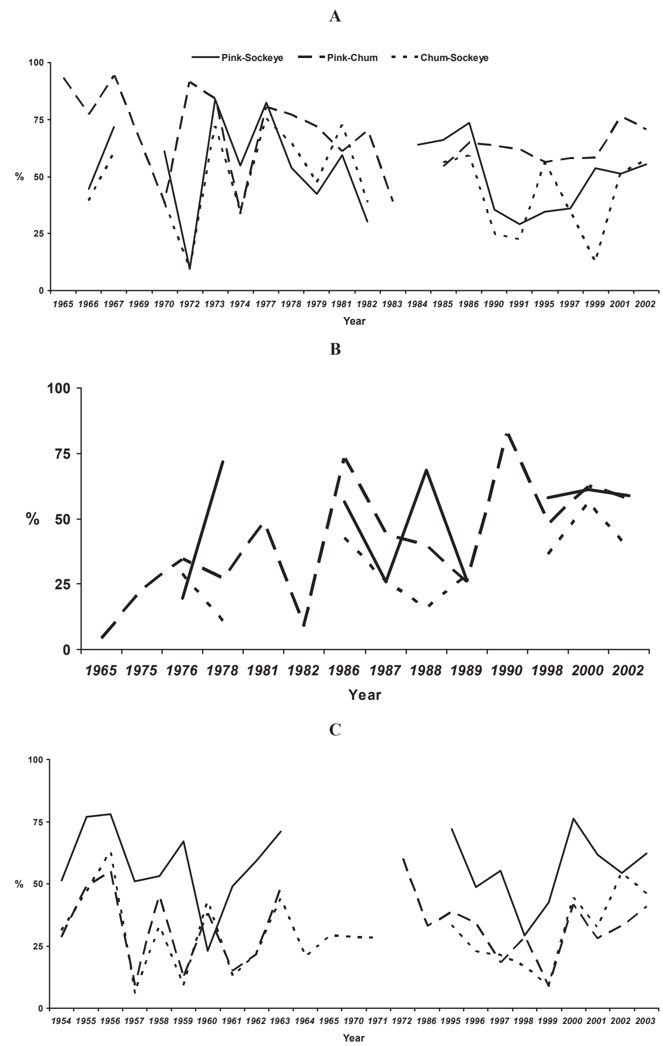


**Fig. 10.** FS-coefficients for pink, chum and sockeye salmon. A - juveniles, .Okhotsk Sea, 1965–2002; B - juveniles, Bering Sea, 1965–2002; C - adults, North Pacific Ocean, 1954–2003.

For the 9-year period of observation in the Bering Sea (BASIS), the narrowest food spectrum (3 to 18 components) was recorded for sockeye salmon (Fig. 9B). The food spectrum of the other two other species was twice as wide (5 to 35 components). Similar to those in the Sea of Okhotsk, the spectra of the two latter species increased substantially in the late 1990s to the early 2000s, coincident with a high abundance of juvenile pink and chum salmon. Comparative analysis of variations in food component number in pink salmon and chum salmon also has indicated this alternation.

Maximum FS-coefficients were observed between juvenile pink and sockeye salmon, averaging 50%. Minimum FS coefficients were seen in 1976: 19.9%; maximum values in 1978: 71.6% (Fig. 10B). The food similarity between pink and chum salmon; and also between chum and sockeye salmon was 5–10% less. In the first case it varied from 4.3% (1965) to 82.2% (1990) and in the second case from 11% (1978) to 56.6% (2000). Low FS-coefficients were observed when crustaceans were least important in the diets of juvenile chum salmon.

*Adult salmon*

In the Bering Sea the number of components in adult salmon diets (a 5-year observation period) was similar, except in 1996 when the number of components in the adult pink salmon diet decreased by half. In odd years the food spectrum was a bit wider in all species, which most likely was related to the high abundance of pink salmon. This occurred even though the diet compositions, as noted above, were very different.

Food similarity among adult salmon was lower when compared with juveniles, rarely exceeding 40%. Also the most similar diets were seen in pink and sockeye salmon – from 41.1% (1997) up to 75% (1983). Pink-chum FS-coefficients varied from 12.8% (2000) to 47.3% (1997). Chum-sockeye FS-coefficients ranged from 13.5% (2000) to 61.2% (1998).

The data record of diets of adults of the three species of salmon in the Pacific Ocean waters off Kamchatka extends from 1954 to 2003. The number of food components varied from 5 to 30, with the food spectrum of chum salmon usually being the widest (Fig. 9C). Recently, the widest food spectra have been seen in the three species of adult salmon. The number of food components was not significantly different among the three salmon species during the period of observation. An exception is 1998 when the pink salmon diet consisted of 13 components only, while chum and sockeye diets consisted, respectively, of 22 and 23 components. Maximum food diversity was seen in chum salmon; the minimum, in pink salmon. Sockeye salmon were intermediate between the two.

Diet comparisons among the three species showed maximum diet similarity between pink and sockeye salmon, and minimum diet similarity between chum and sockeye salmon. The highest FS-coefficients (77%–78%) were found for pink and sockeye in 1955–1956, and the lowest (23% and 29.2%, respectively) in 1960 and 1998 (Fig. 10C). Pink-chum diet similarity ranged from 8.6% (1999) to 60% (1972). Chum-sockeye diet similarity ranged from 6% (1957) to 63% (1956). This is related to a high feeding liability of chum salmon in comparison with the other species. In general, diet similarity between pink and sockeye salmon is almost twice as high as that between pink and chum salmon or between chum and sockeye salmon.

**Influence of Feeding on Biological Parameters of Fish**

Salmon feeding conditions determine the timing of maturation, age composition of spawning fish and biological parameters such as length and weight. Moreover, the conditions often help explain the variations in the timing of salmon spawning runs. The variations range from several weeks early to later-than-normal timing, which, in turn can determine the effectiveness of the fishery for particular salm-

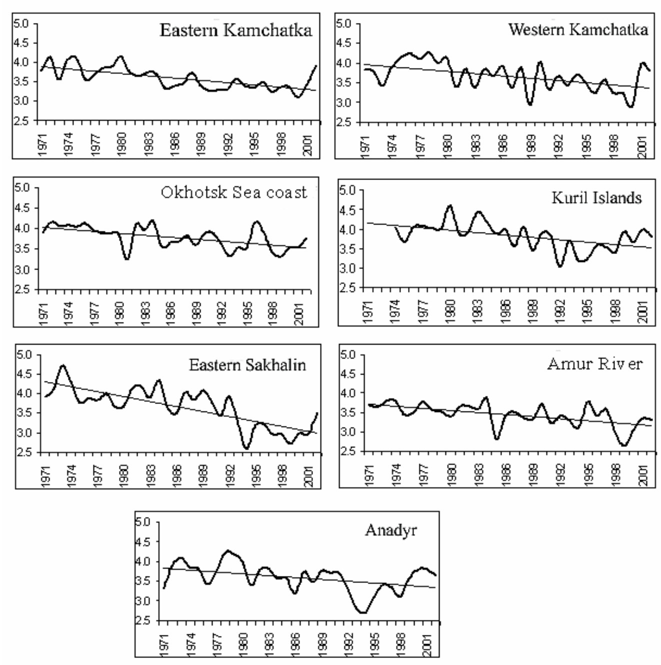


**Fig. 11.** Average weight (kg, on the y-axis) of chum salmon from commercial catches in different areas of the Russian Far Eastern Seas, 1971–2002.

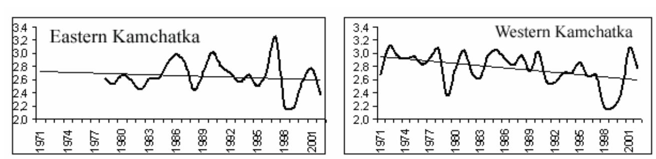


**Fig. 12.** Average weight (kg, on the y-axis) of sockeye salmon from commercial catches in eastern and western Kamchatka, 1971–2002.

on species.

In the course of our analysis of salmon length variations for the years following the period of serious depression in the 1960s–1970s, we noted that different species show different tendencies. For example, in most regions the average weight of pink salmon in spawning runs increased, with the exception of the southwestern Sakhalin pink salmon run. The reason, apparently, is that a principal part of this pink salmon stock feeds in the Sea of Japan, where forage resources are limited. For most other stocks that feed in the high seas areas of the Pacific Ocean, a significant increase in size is characteristic. For example this pattern is seen in the West Kamchatka, East Sakhalin and Kuril pink salmon stocks (Karpenko and Rassadnikov 2004). The average weight of sockeye salmon and of chum salmon, in particular, decreased during the same period (Figs. 11 and 12) (Karpenko and Rassadnikov 2004). Moreover, a maximum decrease was observed particularly in the regions where the maximum growth of pink salmon had been recorded. Since the late 1980s an increase in the percentage of older chum salmon in spawning runs has been recorded, especially for the northeastern Kamchatka populations (Gritsenko et al. 2000; Zavarina 2001, 2003, 2005), the northern coast of the Okhotsk Sea (Volobuev 2000;Volobuev and Volobuev 2000), and also for the North American chum salmon (Bigler et al. 1996; Helle and Hoffman 1995, 1998). In the twenty-first century the average weight of chum salmon has been increasing, which has been shown, in particular, for the fish from East Sakhalin, Kamchatka and Anadyr (Karpenko and Rassadnikov 2004).

Our data indicate, that the maximum influence on the development of biological parameters, including size and age composition of adult fish (sockeye and chum salmon in particular), has been shown by pink salmon, the most abundant salmon species in Asia. Sockeye salmon, as a food competitor, is the next most abundant, with chum salmon being the most vulnerable species. Studying the trophic interactions of pink, chum and sockeye salmon clearly allows us to obtain insights into the state of pelagic ecosystems in the North Pacific Ocean.

## CONCLUSIONS

Our analysis of pink, chum and sockeye diets leads us to suggest the following:

1. The Pacific salmon is the best “plankton gear”. The diets of pink, chum and sockeye salmon are a good indicator of the state of plankton and nekton communities in regions of the North Pacific Ocean, reflecting the development and composition of these communities. The level can be figured out by judging the composition of food and intensity of feeding of the adult fish, and also the migration routes of juvenile fish from the rivers to the sea.

2. Among the three salmon species studied, the best indicator of plankton production and community composition is the chum salmon because it is the most flexible consumer of marine plankton in forage zones of the North Pacific Ocean. In poor forage conditions, chum salmon consume a high percentage of organisms of low caloric value. Such diets are thought to result in lowered growth rates and rates of maturation of returning adults.

3. More accurate assessment of the forage resources in regions of the North Pacific requires intense study of the long-term variations in the pelagic community - the interactions not only between particular salmon species, but between salmon and the structure of plankton, and dynamics of the abundance of other plankton consumers and the volume of food they are consuming.

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## REFERENCES

Andriyevskaya, L.D. 1957. Summer migration and food of Pacific salmon during marine period of life. Izv. TINRO 44: 75–96. (In Russian).

Andriyevskaya, L.D. 1958. Pacific salmon feeding in the Northwestern Pacific Ocean. *In* Materials on the biology of marine period of life of the Pacific salmon. Special publication. VNIRO. Moscow: 64–75. (In Russian).

Andriyevskaya, L.D. 1964. Food relations of Pacific salmon in the sea. Vopr. Ichthiologii 6: 84–90. (In Russian).

Bigler B.S., D.W. Welch, and J.H. Helle. 1996. Decreasing size of North Pacific salmon (*Oncorhynchus* spp.): possible causes and consequences. Can. J. Fish. Aquat. Sci. 53: 455–465.

Cuchukalo, V.I., and A.F. Volkov. 1986. Guidance study of the food of fish. TINRO, Vladivostok. 32 pp. (In Russian).

Gritsenko, O.F., L.O. Zavarina, A.A. Kovtyn, and S.V. Putivkin. 2000. Ecological consequences of the large-scale chum salmon hatchery. *In* Commercial-biology investigations of fishes in the Pacific waters of the Kuril Islands and adjacent regions of the Sea of Okhotsk and Bering Sea 1992–1998. Special publication. VNIRO. Moscow: 241–246. (In Russian).

Helle J.H., and M.S. Hoffman. 1995. Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in western North America, 1972–1992. Can. Sp. Pub. Fish. Aquat. Sci. 121: 245–260.

Helle J.H., and M.S. Hoffman. 1998. Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus keta*) before and after a major regime shift in the North Pacific Ocean. N. Pac. Anadr.

Fish Comm. Bull. 1: 81–89. (Available at http://www.npafc.org).
Karpenko, V.I. 2003. Review of Russian marine investigations of juvenile Pacific salmon. N. Pac. Anadr. Fish Comm. Bull. 3: 69–88. (Available at http://www.npafc.org).
Karpenko, V.I., and O.A. Rassadnikov. 2004. Contemporary state (1971–2002) of the Far East Pacific salmon stocks abundance. *In* Investigation of water biological resources of Kamchatka and northwestern Pacific Ocean. Petropavlovsk-Kamchatskii. Vol. 7. pp. 14–26. (In Russian).
Shershneva, V.I., and M.V. Koval. 2004. Caloric content of mass zooplankton and ichthyoplankton species of Kamchatka water. Izv. TINRO 139: 349–369. (In Russian).
Volkov, A.F. 1996. Epipelagic zooplankton of the Far East seas: community composition, interannual dynamics, status in the nekton food. Dissertation, Doctor Biol. Science. Vladivostok. 70 pp. (In Russian).
Volkov, A.F., and N.S. Kosenok. 2005. Similarity of diurnal rhythms of Pacific salmon genus *Oncorhynchus* feeding. Problems of Fisheries. Moscow. Vol. 6.2(22): 200–210. (In Russian).
Volkov, A.F., N.S. Kosenok, and N.A. Kuznetsova. 2006. Results investigation Pacific salmon food during fall period 2002–2004 on the BASIS program. Izv. TINRO . 144: 198–218. (In Russian).
Volobuev, V.V. 2000. Long-term changes in the biological parameters of chum salmon of the Okhotsk Sea. N. Pac. Anadr. Fish Comm. Bull. 2: 175–180. (Available at http://www.npafc.org).
Volobuev, V.V., and M.V. Volobuev. 2000. Ecology and structure of populations as the main elements of forming life strategy of chum salmon *Oncorhynchus keta* in the continental coast of the Sea of Okhotsk. Vopr. Ichthiologii 4: 516–529. (In Russian).
Yerokhin, V.G., and V.I. Shershneva. 2000. Feeding and energy characteristics of juvenile pink salmon during fall marine migrations. N. Pac. Anadr. Fish Comm. Bull. 2: 123–130. (Available at http://www.npafc.org).
Zavarina, L.O. 2001. Biological and age-specific changes of the mature part of the Kamchatka River chum salmon - *Oncorhynchus keta* (Walbaum). Abstracts PICES X Annual Meeting. Victoria, BC. p. 156.
Zavarina, L.O. 2003. Biological structure of chum salmon *Oncorhynchus keta* in the Northeastern Kamchatka. Special Volume “Memory V.Ya. Levanidova”. Vladivostok. pp. 531–540. (In Russian).
Zavarina, L.O. 2005. Dynamics of biological parameters and of chum salmon *Oncorhynchus keta* (Walbaum) abundance in the north-east coast of Kamchatka and reasons to determine the dynamics. Abstracts of NPAFC-PICES Joint Symposium “The status of Pacific salmon and their role in North Pacific marine ecosystems”. p. 48.