

The Role of Pacific Salmon in the Trophic Structure of the Upper Epipelagic Layer of the Western Bering Sea during Summer-Autumn 2002–2006

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Abstract: Pacific salmon are among the dominant fish in the epipelagic layer of the subarctic Pacific Ocean and are considered the principle consumers of forage resources. In recent years (1990s and 2000s) most Pacific salmon stocks have increased two-fold in abundance. Many researchers consider that such high abundance may increase interspecific competition for food and influence density-dependent factors during periods of limited food availability and may change salmon characteristics such as length, weight, fecundity, and the average age of populations. Long-term data series on Pacific salmon and their food resources have traditionally been collected during Russian surveys in the pelagic zone of the Far Eastern Seas and adjacent waters of the northwestern North Pacific Ocean. More recently (summer–autumn, 2002–2006) surveys have been conducted by TINRO-Centre in the epipelagic zone of the western Bering Sea as part of the international BASIS program. The integration of the results of these programs make it possible to better understand the status of Pacific salmon and their role in North Pacific pelagic communities.

Keywords: Pacific salmon, competition, forage resources, trophic structure, carrying capacity

INTRODUCTION

Over the last 25 years researchers have documented a significant increase in the abundance of many Pacific salmon populations, including Asian stocks. Based on data collected during anadromous migrations (catch size and value, densities of fish on spawning grounds, e.g.), it is estimated that the abundance of Pacific salmon may be twice as high compared to levels of stocks in the 1950s–1970s (Temnykh et al. 2003, 2004; Shuntov and Temnykh 2004, 2008; Temnykh 2005).

The possible effect(s) of these high population levels on intra- and inter-specific competition among salmon for food resources have been discussed in many scientific publications. There is some consensus among researchers that the North Pacific is now overpopulated by salmon, and that tissue degeneration of salmon (for example, the occurrence of ‘flabby chum’) is possibly caused by limited forage resources on marine feeding grounds (Klovach 2000, 2003; Gritsenko and Klovach 2002; Mikodina et al. 2002). Some studies suggest that density-dependent factors result in changes in some parameters of salmon stocks such as length, weight, age, and fecundity (Ishida et al. 1993, 2000; Bigler et al. 1996; Kaeriyama 1996; Davis et al. 1998; Azumaya and Ishida 2000).

However, the extensive and detailed results on the structure and dynamics of nekton and plankton communi-

ties, including their trophic structuring, obtained during many complex large-scale surveys to the Far Eastern Seas and Northwest Pacific, summarized and published in Russian journals and monographs (Shuntov et al. 1993a,b, 2007; Volkov 1996; Shuntov 2001; Dulepova 2002; Temnykh 2004, 2008; Kuznetsova 2005; Chuchukalo 2006; Shuntov and Temnykh 2008) allow us to create a clearer picture of the status of Pacific salmon and their role in North Pacific pelagic communities.

Long-term data series on Pacific salmon and their food resources have traditionally been collected during Russian surveys in the pelagic zone of the Far Eastern Seas and adjacent waters of the northwestern North Pacific Ocean. More recently (summer–autumn, 2002–2006) surveys have been conducted in the epipelagic zone of the western Bering Sea by TINRO-Centre as part of the international BASIS program. The integration of the results of these programs make it possible to better understand the status of Pacific salmon and their role in North Pacific pelagic communities.

MATERIALS AND METHODS

Data on food habits of Pacific salmon and the distribution and composition of plankton were collected by the research vessel *TINRO* of the Pacific Fisheries Research

Center (TINRO) in the western Bering Sea in summer 2003 and autumn 2002–2006, including surveys that were part of the international research program BASIS (Bering-Aleutian Salmon International Survey).

To sample salmon and other epipelagic nekton a standard midwater rope trawl RT/TM was used. Technical characteristics of the trawl are provided in Table 1. The trawl hydrodynamic plate had floats on the headrope. The trawl had quadrangular mesh in the body and wings and a small-mesh (1 cm) codend. The trawl was fished with 4 bridles, each 112 m long and 1.9 cm thick. One 220-kg chain is attached to the footrope and 2 weights (200 kg each) are attached in front of the footrope to sink the trawl. V-shaped conical midwater trawl doors (6 m² and 1.3 tons each) were used.

Trawls were conducted round-the-clock and lasted one hour. The trawling course was adjusted according to weather and hydrological conditions. The trawl hydrodynamic plate was maintained at 0 m level. The position of the plate was verified by acoustic readings and by sight.

Standard methods, developed by Volkov and Chuchukalo (1986) and widely applied at TINRO-Centre, were used for sampling and processing fish stomach contents. The contents of all stomachs from fish of the same species and

of similar size in each trawl catch were combined into one sample. Prey items were identified and measurements of total prey weight and weights of all prey components were recorded. Daily food rations were calculated by the methods of Novikova (1949), Yurovitsky (1962), Kogan (1963), and Gorbatenko (1996). The total consumption by nektonic consumers was determined as:

$$B = b \cdot R \cdot n$$

where B is the weight of the food consumed by nektonic consumers (tons); b is mean nekton biomass (tons) during a certain period; R is daily ration; n is duration of the period (days (summer = 92, and autumn = 91 days)). Size, age, and seasonal, year-to-year, and regional differences were taken into account in the calculations. The consumption of forage resources by nekton was calculated for the western Bering Sea in summer 2003 and autumn 2002–2006. These calculations were compared with the same calculations for the western Bering Sea in autumn 1986, 1987, and 1990, the southern Okhotsk Sea in summer 1991 and 2003 and autumn 2006, and the Pacific waters of the Kuril Islands in summer 1995, 2004, 2006 and 2007.

Table 1. Specifications of the trawl RT/TM 80/396.

Parameters	Average and its intervals (min-max)
Headrope	80 m
Perimeter of the trawl opening	396 m
Hydrodynamic plate	6 m ² , 0.6x10 m
Length of the trawl	30 m
Vertical opening*	32.2 m (26-40 m)
Horizontal opening*	49.0 (42-61 m)
Speed of trawling	4.8 knots (4.0-5.7 knots)
Length of warps	256 m (245-280 m)
Square of water surface per 1 hour	0.44 km ² (0.34-0.53 km ²)

*vertical and horizontal openings were measured by Simrad FS20/25 vertical and horizontal scanning trawl sonars.

Table 2. Juday net catchability coefficients for certain groups of plankton (from Volkov 1996).

Plankton size group	Catchability coefficient (CC)
Small (< 1.2 mm)	1.5
Medium (1.2–3.2 mm)	2.0
Large (> 3.2 mm):	
euphausiids < 10 mm	2.0
euphausiids 10–20 mm	5.0
euphausiids > 20 mm	10.0
chaetognaths < 10 mm	2.0
chaetognaths 10–20 mm	5.0
chaetognaths > 20 mm	10.0
hyperiid < 5 mm	1.5
hyperiid 5–10 mm	5.0
copepods < 5 mm	2.0
copepods > 5 mm	3.0

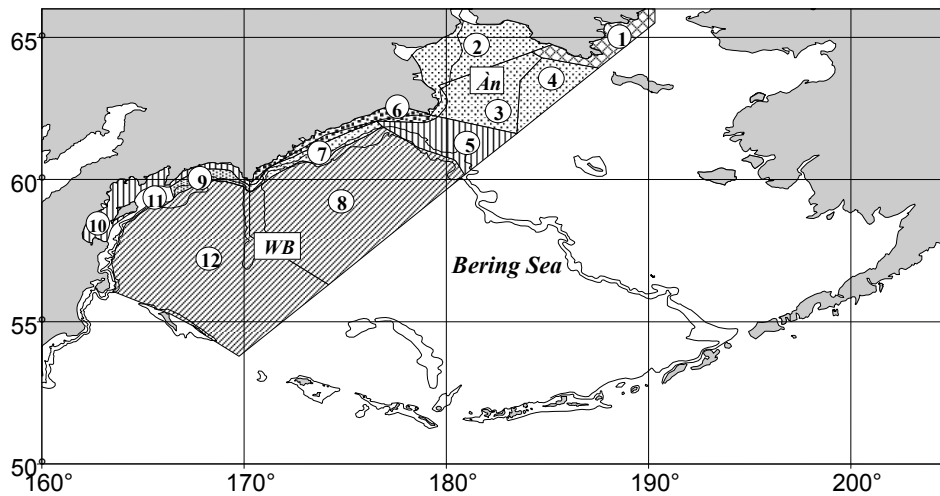


Fig. 1. Map of biostatistical regions covered in 5 surveys by TINRO-Centre on the R/V *TINRO* as part of the international research program BASIS (Bering-Aleutian Salmon International Survey) in the epipelagic layer of the western Bering Sea in 2002–2006. 1, Bering Strait; 2, north-western Anadyr Bay; 3, southeastern Anadyr Bay; 4, eastern Anadyr Bay; 5, Navarin region; 6, Koryak shelf; 7, Koryak slope; 8, western Aleutian Basin; 9, Olutorskiy slope; 10, shelf of Karaginskiy and Olutorskiy bays; 11, Karaginskiy slope; 12, Commander Basin; An, Anadyr Bay; WB, western Bering Sea basins (from Shuntov et al. 1986, 1988a, b).

Plankton samples were collected with a Juday net (nylon, mouth area 0.1 m², mesh size 0.168 mm) from 0–50 and 0–200 m both during the day and at night just before trawling. The samples were divided into three size fractions: small (animals < 1.2 mm in length), medium (1.2–3.2 mm), and large (> 3.2 mm). Species composition was determined for each fraction, and weight (as displaced volume), size, and developmental stage determined for each species. The results on abundance and biomass were multiplied by catchability coefficients (CC) of the Juday net (Table 2).

All data were averaged by standard biostatistical regions proposed for the Russian EEZ by Shuntov et al. (1986,

1988a, b) (Fig. 1).

RESULTS AND DISCUSSION

Composition of the Epipelagic Nekton Community

The epipelagic nekton community of the western Bering Sea in summer–autumn consists of walleye pollock, Pacific salmon, squids and also the mezopelagic fishes, capelin, atka mackerel and Pacific herring (Fig. 2). This nekton community (biomass, physiological condition, distribution, and migration patterns, e.g.) determines the principle trophic rela-

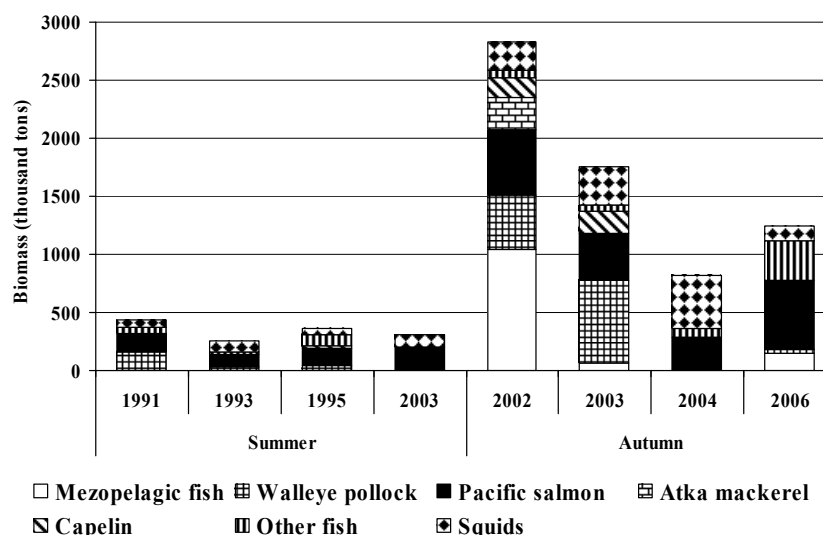


Fig. 2. The biomass (thousand tons) of nekton in the upper epipelagic layer in the western Bering Sea during summer and autumn (from Shuntov et al. 1993b, 2007; Radchenko 1997; Temnykh et al. 2003, 2004; Shuntov and Temnykh 2004, 2005; Shuntov and Sviridov 2005; Temnykh 2005, 2006; Glebov et al. 2006; Starovoytov 2007; with modifications).

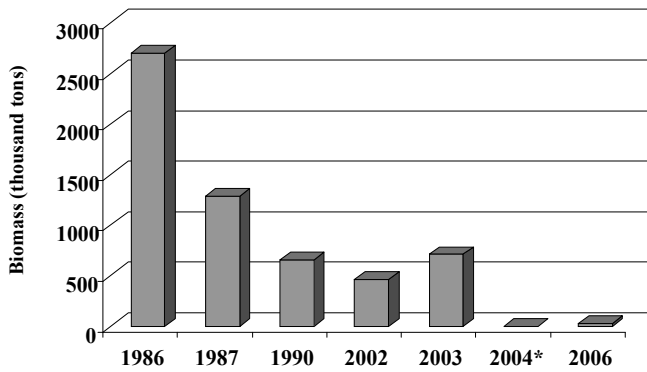


Fig. 3. Walleye pollock biomass in the upper epipelagic layer in the western Bering Sea during autumn 1986–1987, 1990 and 2002–2006. *Only a part of the shelf was surveyed. (Shuntov et al. 1993a; Shuntov and Sviridov 2005; Glebov et al 2006).

tionships within the epipelagic community. Walleye pollock and Pacific salmon are always present in the pelagic community in summer–autumn, and are the most important influence. Pollock distribution in the western Bering Sea is very variable and depends on the stock and environmental conditions (Shuntov et al. 1993b; Stepanenko 1997, 2001; Shuntov and Sviridov 2005; Glebov et al 2006). For example, the relative biomass of adult pollock at the sea floor can be high, while the biomass of juvenile pollock in the epipelagic zone can be low. The migrations of juvenile pollock from the eastern to the northwestern Bering Sea in 2004 and 2006 were reduced considerably, so the relative biomass of pollock in the western Bering Sea in these years was low (Fig. 3) (Nikolaev and Stepanenko 2006). By contrast, salmon biomass has increased 3-fold since the 1980s such that their share of the total fish biomass in the upper pelagic layer of

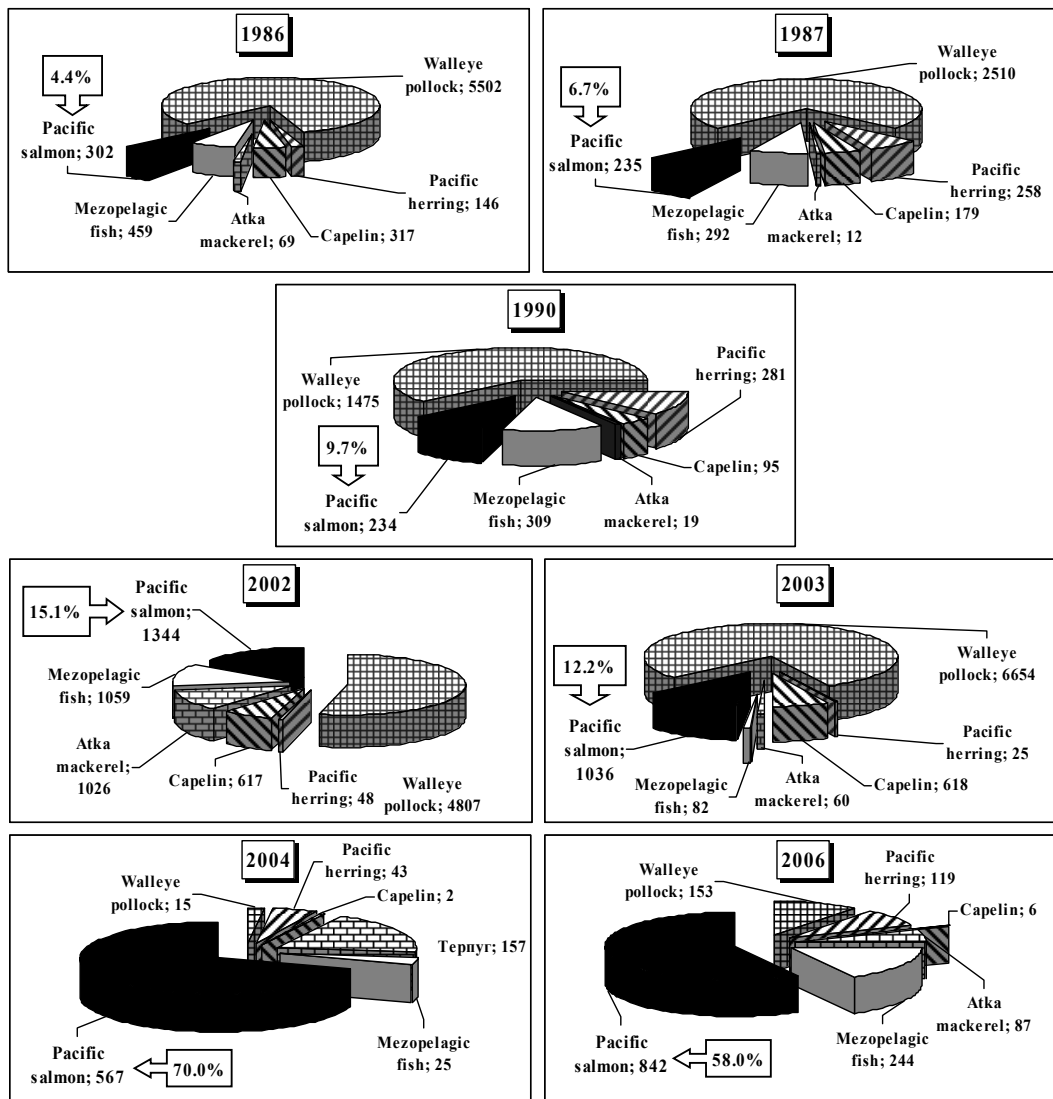


Fig. 4. The consumption (thousand tons) of total forage resources by fish in the upper epipelagic layer in the western Bering Sea during autumn 1986–1987, 1990, and 2002–2006 (Naydenko 2007).

the western Bering Sea increased to 21–53% in 2002–2006 (Shuntov et al. 1993a, 2007; Temnykh et al. 2003; Shuntov and Temnykh 2004, 2005; Glebov et al. 2006; Starovoytov 2007).

Trophic Structure of the Nekton Community

Changes in the abundance and structure of the main consumers have affected the trophic structure of the nekton community. The volumes of consumption, energy flows, and trophic roles of many major species, including salmon, have changed.

In the epipelagic zone of the western Bering Sea the total consumption of resources by fish alone reached from 3.5 to 8.9 million tons in years when pollock biomass was high (for example, in 1986–1987, 1990, and 2002–2003). In 2004 and 2006 consumption decreased to 1 million tons (Fig. 4). Accordingly, the share of pollock in total consumption declined from 80 to 10%, and the share of food consumption by salmon increased from 4.4 to 58–70% (Fig. 4). Pacific salmon consumed 52% of total food consumption by nekton (fishes and squids) in summer 2003, and 39–41% in autumn 2004 and 2006 (Fig. 5). However, the role of salmon in the trophic structure of the upper pelagic layer is still not as important as that of pollock.

For example, in autumn 2002 and 2003, pollock consumed almost 1/3 of the total stock of euphausiids (3.5 and 3.1 million tons, respectively) but their grazing was estimated as 1/30 of the total stock in the autumn of 2004 and 2006, when pollock abundance was low (Naydenko 2007). In the same years (2004 and 2006) grazing on copepods had decreased by 10–20-fold (Table 3), but the decrease in hyperiid grazing was not so dramatic because of active consumption of this group by salmon, atka mackerel and other nekton species (Naydenko 2007).

Despite an increase in abundance, Pacific salmon consumed a much smaller part of forage resources compared to walleye pollock. For example, in autumn 2004 and 2006 salmon consumed 167–179 thousand tons of euphausiids, 87–230 10³ tons of hyperiids, 4–27 thousand tons of copepods, and 6–130 thousand tons of pteropods (Naydenko 2007). Consumption of zooplankton by salmon was higher in summer (for example, up to 1754 thousand tons in summer 2003) (Fig. 6).

Thus in autumn of 2002 and 2003 the predominant path-

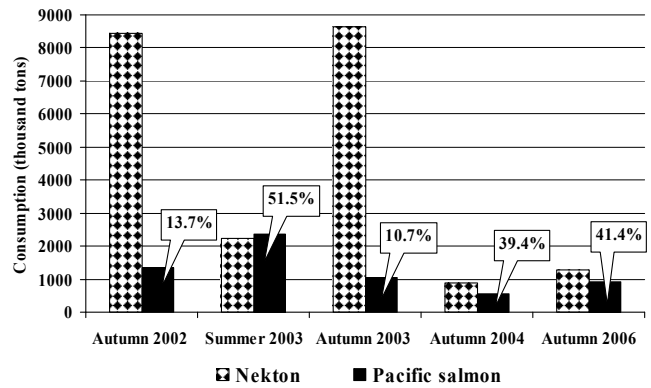


Fig. 5. The consumption (thousand tons) of total forage resources by Pacific salmon and other nektonic consumers in the upper epipelagic layer in the western Bering Sea during summer 2003 and autumn 2002–2006 (Naydenko 2007).

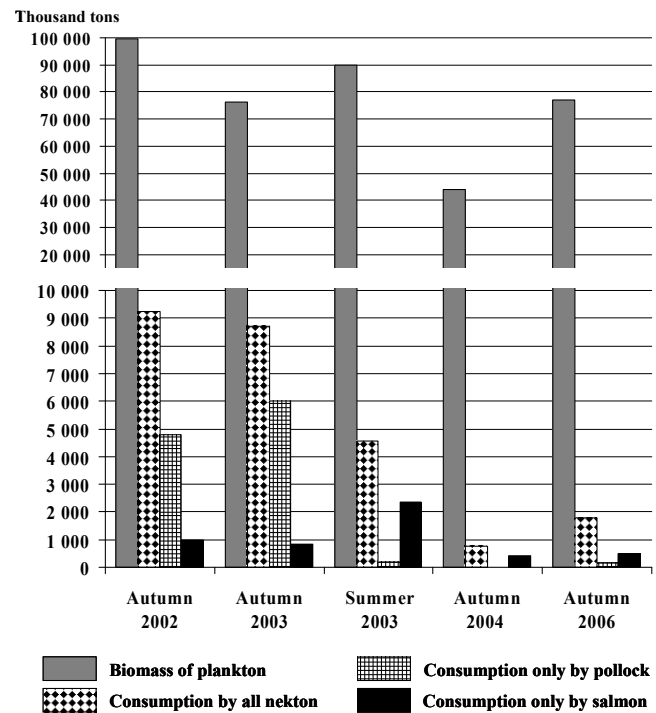


Fig. 6. The biomass of zooplankton and its consumption (thousand tons) by nektonic consumers in the epipelagic layer of the western Bering Sea.

Table 3. The main zooplankton groups (103 tons) in the upper pelagic layer of the western Bering Sea in autumn 2002–2006 and their grazing by nektonic consumers (numerator = consumption by all nektonic consumers, denominator = consumption only by fish) (Naydenko 2007).

Years	Euphausiids		Copepods		Hyperiids	
	Biomass	Consumption	Biomass	Consumption	Biomass	Consumption
2002	9,067	4,082/3,514	43,722	2,337/2,333	2,424	1,047/1,042
2003	10,059	4,141/3,095	80,438	2,075/2,071	1,833	577/569
2004*	14,429	709/222	10,145	120/118	1,796	294/293
2006	8,568	1,089/716	27,035	226/224	1,794	219/209

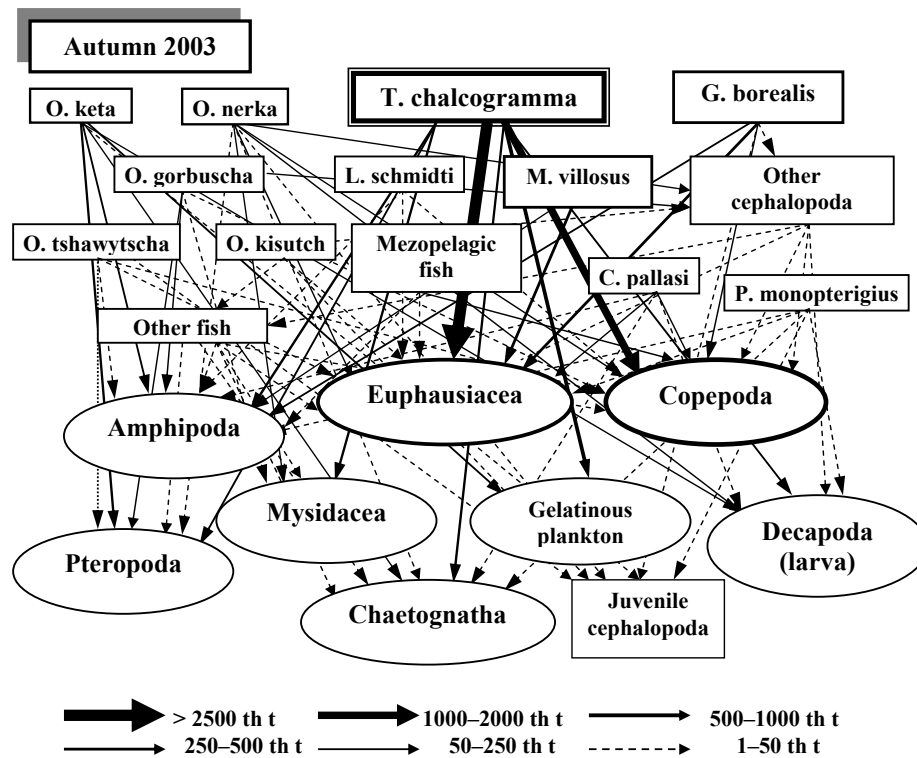


Fig. 7. Schematic of the basic trophic relationships of dominant nektonic species and major zooplankton groups in the upper epipelagic zone of the western Bering Sea in autumn 2003 (thickness of arrows indicates volumes of autumn consumption, thousand tons (th t)).

way of energy flow in pelagic communities of the western Bering Sea led from two zooplankton groups, euphausiids and copepods, toward walleye pollock (Fig. 7). In autumn 2004 and 2006 Pacific salmon and squids (and in some cases atka mackerel, capelin or mezopelagic fishes) were the major consumers, such that the trophic links were directed not only toward euphausiids and copepods but also other zooplankton groups such as hyperiids, pteropods, and larval decapods (Fig. 8). On the whole, the energy flows from zooplankton toward higher trophic levels of the epipelagic community have decreased considerably. Most likely these energy flows switched to plankton predators (jellyfishes, chaetognaths, or other copepods). Unfortunately, the trophic relationships within the pelagic zooplankton community in the western Bering Sea are not well understood. It should be noted that with the substantial increase in the abundance of predatory plankton, serious shifts in trophic relationships and the direction of energy flow in the epipelagic zone of the western Bering Sea in the last 20 years were not observed.

The observed increase in plankton resources, a result of lower consumption rates and high plankton biomass, should contribute to a satisfactory foraging environment for pelagic nekton species, including Pacific salmon.

Based on estimates by Shuntov (2001), Dulepova (2002), Shuntov and Temnykh (2007) and Volkov et al. (2004, 2007a), the total stock of zooplankton in the epipelagic layer of the subarctic northwestern Pacific, including

the Okhotsk and Bering seas, has decreased by 134.5 million tons over two decades (from 722.5 million tons in 1980 to 587.8 million tons in 2000), i.e. approximately 20%. The decrease has been noted everywhere, from inner shelf areas to the deep ocean. However, the large-size fraction of zooplankton, the most important prey for nektonic planktivores, showed other changes: a slight decrease from 1980 to the early 1990s (from 560.8 to 500.5 million tons, or 8%) and a slight increase in succeeding years (up to 520.1 million tons). Generally, despite a decrease in the total abundance of macroplankton, the biomass levels are rather high. In the western Bering Sea macroplankton biomass is estimated at 81.4 million tons, of which about 60% is concentrated in deepwater areas (Shuntov 2001; Dulepova 2002; Shuntov and Temnykh 2007). This conclusion is very important in the estimation of forage resources, because the main feeding grounds for Pacific salmon are located in deepwater areas where the biomass of nekton is usually lower.

Not all zooplankton species are equally consumed by nekton. Only a few species are actively consumed. However, in the epipelagic zone of the western Bering Sea the abundance of these preferred species is sufficient. For example, the total biomass of five species (*Thysanoessa longipes*, *Neocalanus plumchrus*, *Themisto pacifica*, *Clione limacina*, and *Limacina helicina*) which are the most important food items of nekton was estimated at 15–19 million tons, which exceeds the consumption of these species by several times.

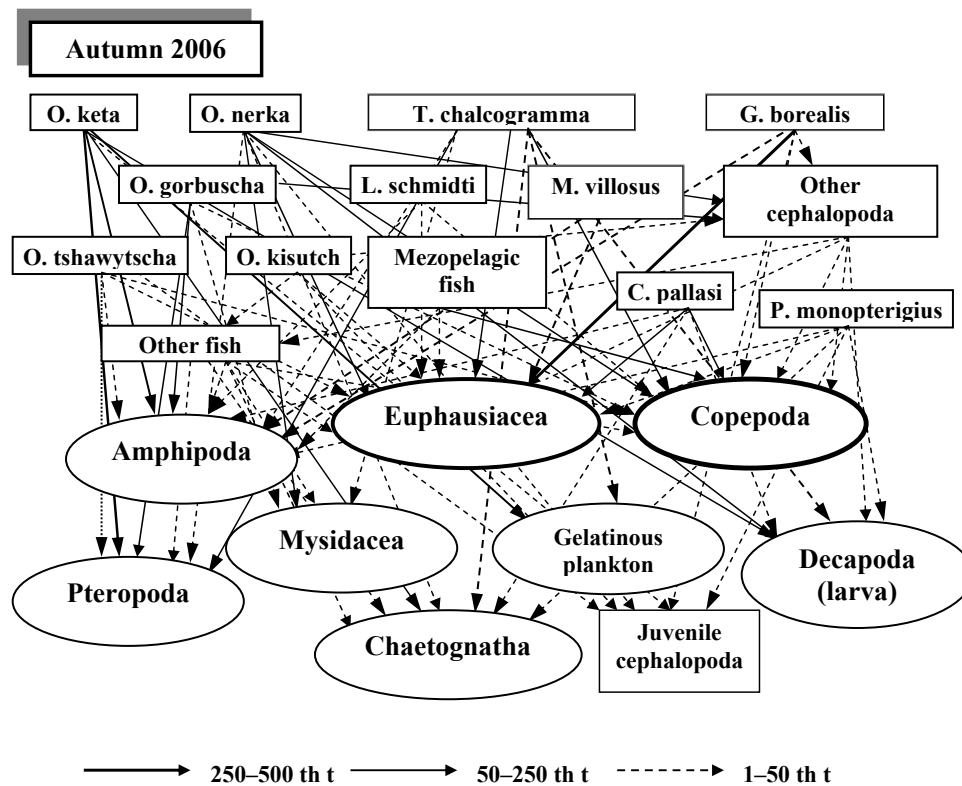


Fig. 8. Schematic of the basic main trophic relationships of dominant nektonic species and major zooplankton groups in the upper epipelagic zone of the western Bering Sea in autumn 2006. (thickness of arrows indicates volumes of autumn consumption, thousand tons (th t)).

If we take zooplankton production into account, the difference between zooplankton biomass and zooplankton consumption by nekton will be even higher. A satisfactory food supply for salmon in the western Bering Sea is also shown by stable and high values of their daily rations, and a permanent preference for feeding on hyperiids, pteropods, and euphausiids.

Besides zooplankton, small fishes and squids also make up a considerable part of the salmon diet. Their mean concentration is estimated to be 0.1–3.9 g/m² depending on the region surveyed (Shuntov and Temnykh 2007), compared with the mean concentrations of preferred macroplankton such as pteropods (1–2 g/m²), hyperiids (2–8 g/m²), and euphausiids (15–25 g/m²). Small pelagic nekton are able to compensate for the lack of zooplankton forage resources, for example, in the eastern Bering Sea where larval fish and bottom-dwelling invertebrates form the base of salmon diet when large-size zooplankton are not abundant (Volkov et al. 2007a, b).

Other important factors that contribute to satisfactory foraging environments for Pacific salmon are the spatial dissociation of the main consumers and the timing of migrations and feeding. Pacific salmon, juvenile atka mackerel, and squids feed mainly in deepwater areas of the western Bering Sea. The forage resources in deepwater areas are affected by these fishes and squids during summer–autumn (especially in summer during salmon migrations and graz-

ing on zooplankton by juvenile atka mackerel). By contrast, the main feeding grounds of pollock, capelin and herring are located in shallow waters of Anadyr Bay and at Cape Navarin. The consumption of zooplankton by these fishes is very high in autumn, especially when pollock are abundant. The example of walleye pollock, atka mackerel, and sockeye and chum salmon distribution in the western Bering Sea in autumn 2003 is shown in Fig. 9. In 2004 and 2006 the consumption of forage resources was highest in deepwater areas (Fig. 10).

Some competition for food among salmon and other abundant nekton species is possible where feeding grounds and/or migration dates overlap, however such situations are mitigated by plasticity and electivity in salmon feeding, as well as by excess forage reserves. All salmon species have a high feeding plasticity and are able to change from one food source to another, depending on the state of forage resources. This ability is well illustrated by the different feeding habits of Pacific salmon in the western and eastern regions of the Bering Sea.

CONCLUSIONS

Any fluctuations in the biomass of major consumers lead to changes in the trophic structure of pelagic communities. However, even multiple variations in highly fluctuating species’ biomass, such as that of walleye pollock, result

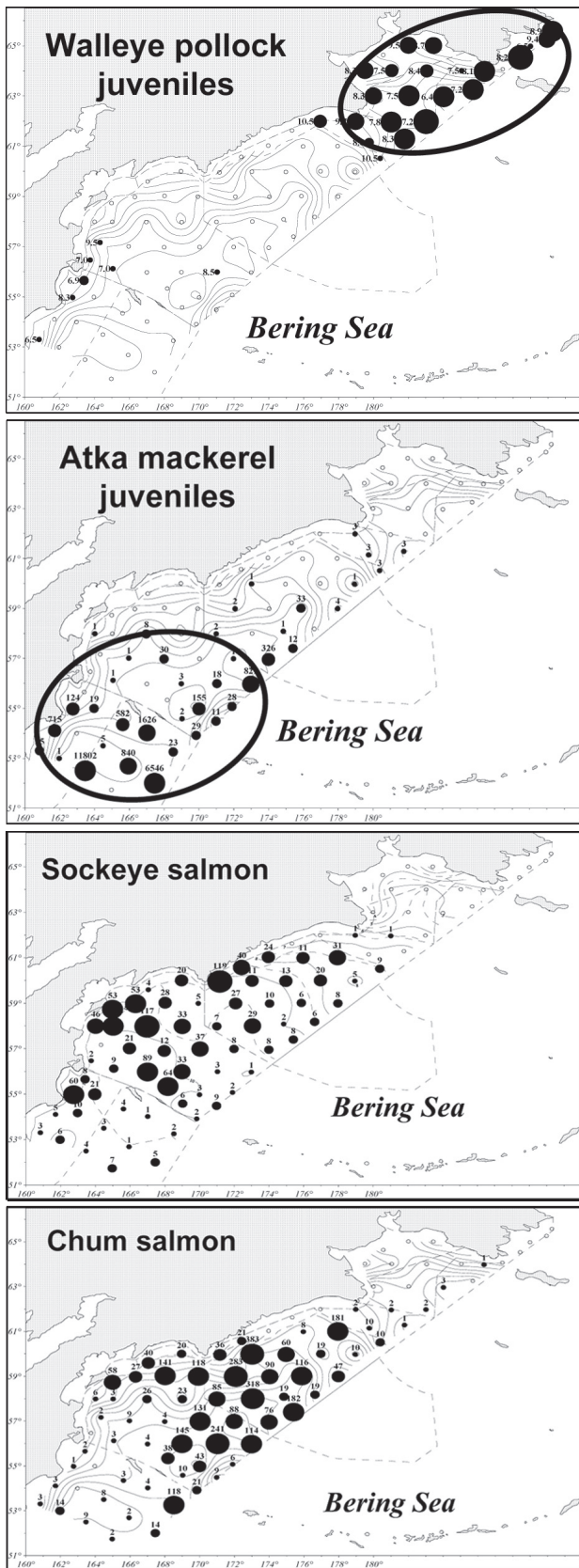


Fig. 9. Distribution of the walleye pollock, atka mackerel, and sockeye, and chum salmon in the western Bering Sea in autumn 2003.

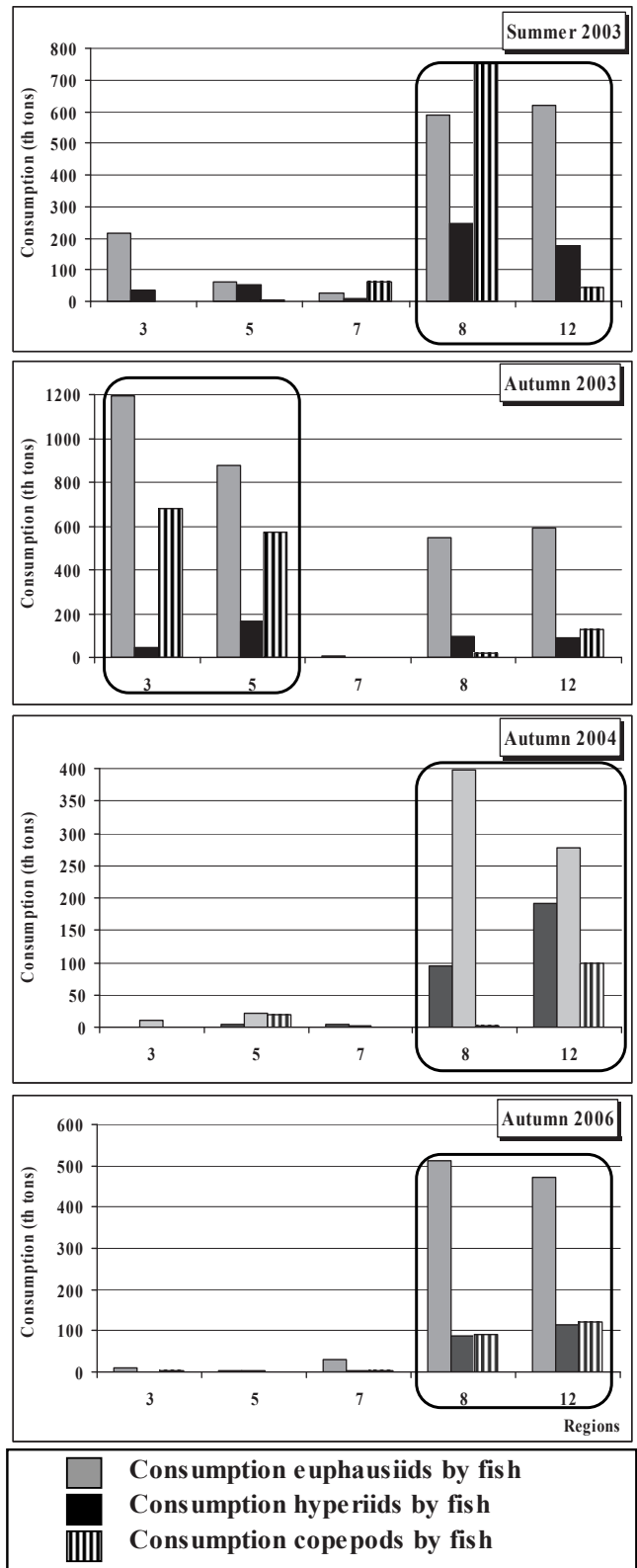


Fig. 10. The consumption (thousand tons) of zooplankton forage groups by nektonic consumers in the upper epipelagic layer in the different regions of western Bering Sea during summer 2003 and autumn 2003, 2004, and 2006 (Naydenko 2007). See Fig. 1 for designation of regions.

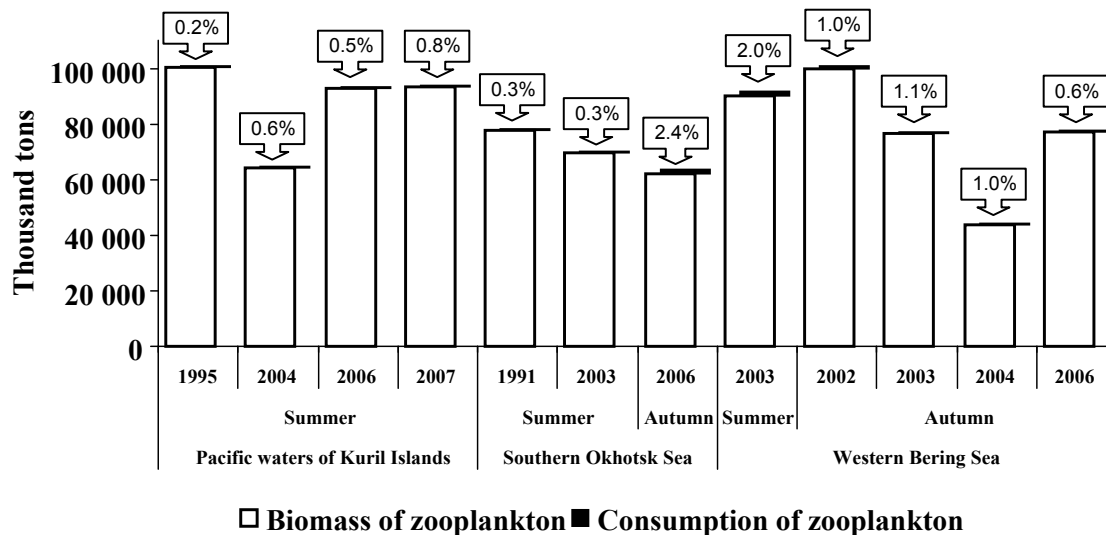


Fig. 11. The biomass of zooplankton (thousand tons — white columns) and its consumption (arrows indicate %) by Pacific salmon in the epipelagic layer of the Okhotsk and Bering seas and Pacific waters of the Kuril Islands (from Naydenko 2007, 2008, with modifications).

only in changes in trophic relationships and the direction of energy flow (namely a change to grazing on euphausiids and copepods by pollock). The contribution of Pacific salmon to the consumption of forage resources in all the areas we investigated is not significant and changes from only 0.2 to 2.4% of total zooplankton biomass (without production), depending on region and year (Fig. 11). It follows that the recent increase in Pacific salmon abundance is unlikely to cause serious shifts in the trophic structure of the upper pelagic zone of the Far Eastern Seas.

The carrying capacity of the pelagic layer for Pacific salmon (in relation to the sufficiency of the forage supply) is not a constant value and depends on multiple factors such as the amount of forage resources, the abundance of major consumers, and the spatial dissociation and migration timing of salmon and other major consumers. According to our data (a high total stock of zooplankton compared with its low consumption by nekton and the spatial dissociation of major consumers), the carrying capacity of the upper epipelagic layer of the Far Eastern Seas and the Pacific waters of eastern Kamchatka and the Kuril Islands in relation to Pacific salmon is high.

Our conclusion that salmon production in the North Pacific is not limited by zooplankton abundance on foraging grounds contradicts the conclusions of Klovach (2003) that large-scale hatchery production and release of chum salmon by the Japanese fishery was impacting salmon returns to the Russian Far East and North America, primarily because of the high abundance of salmon in marine foraging habitats. Klovach (2003) reached these conclusions using indirect production characteristics (changes in length, weight and the physiological state of salmon under conditions of high abundance) and without taking into account quantitative estimates of zooplankton biomass and consumption values of forage resources by salmon and other nekton species.

It is also necessary to note that our conclusions are based on data obtained in the Far Eastern Seas in summer and autumn only. Such calculations cannot be performed for open waters of the North Pacific in winter and spring because of a lack of data. There are vague and contradictory opinions on the feeding conditions for salmon in winter–spring. According to some researchers, zooplankton biomass in the North Pacific in winter is considerably lower compared to summer (Nagasawa 1999, 2000; Ishida et al. 2000) and results in unsatisfactory feeding conditions. Others doubt these estimates and suggest that zooplankton abundance is underestimated because of methodical problems (Shuntov 2001). Quantitative studies of both zooplankton and salmon feeding habits in winter–spring are necessary, including information on daily rhythms of feeding activity, and studies of feeding of other nekton species on common winter feeding grounds. Other important problems in estimating forage reserves are definition of energy values and the biochemical composition of the food necessary to assess trophic relationships in communities and ecosystems. Because many problems are still unsolved it remains tenuous at best to attempt to make realistic estimates of the carrying capacity of pelagic waters over a broad spatial and temporal range.

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