

## Changes in the Trophic Structure of an Epipelagic Community in the Western Bering Sea and Western North Pacific Ocean with an Emphasis on Pacific Salmon (*Oncorhynchus* spp.)

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**Abstract:** A comparative analysis of the trophic structure and interactions between Pacific salmon (*Oncorhynchus* spp.) and epipelagic communities in the western Bering Sea and Pacific waters off the Kuril Islands was conducted using the Ecopath modeling approach. In recent decades, the nekton communities in the Bering Sea and western North Pacific Ocean have changed greatly. For each region, we built two models describing the trophic structure of communities (1) in a period of relatively low salmon biomass and high biomass of other nekton species (walleye pollock, *Theragra chalcogramma*, and/or Pacific sardine, *Sardinops melanostictus*) characteristic of the 1980s and early 1990s, and (2) in a period of high salmon biomass and greatly decreased biomass of walleye pollock and/or sardine characteristic of the 2000s. To evaluate possible changes in trophic flows, we also examined hypothetical scenarios in which Pacific salmon biomass was multiplied by 1.5 relative to their highest level in the 2000s. Despite drastic changes in the biomass of several abundant species, the overall trophic structure of epipelagic nekton communities in both the western Bering Sea and Pacific waters off the Kuril Islands has not changed appreciably during the last 30 years. Between the 1980s and 2000s, Pacific salmon biomass increased greatly in the western Bering Sea and Pacific waters off the Kuril Islands resulting in increased food consumption. The increase in total food consumption appears to be associated with decreases in their diet composition from groups occupying relatively high trophic levels (e.g., amphipods and squids) and a rise in prey groups occupying relatively low trophic levels (e.g., euphausiids, copepods, and pteropods). As a result of this diet shift, the estimated trophic level of Pacific salmon in the food web declined between the 1980s and 2000s. In the simulation with salmon biomass expanded 1.5 times relative to the 2000s estimate, the abundance of forage species was sufficient to maintain higher salmon consumption. The ability of Pacific salmon to access a variety of prey species at a variety of trophic levels appears to give them the capacity to satisfy their food requirements even during periods of extremely high biomass.

**Keywords:** Pacific salmon, trophic structure, model, Ecopath, Bering Sea, western North Pacific

### INTRODUCTION

Over the past three decades, Pacific salmon (*Oncorhynchus* spp.) abundance in the North Pacific Ocean has greatly increased. At the same time, there have been wide fluctuations in abundance of other dominant pelagic fish such as walleye pollock (*Theragra chalcogramma*) and Pacific sardine (*Sardinops melanostictus*) (Naumenko 2001; Belyaev 2003; Shuntov et al. 2003; Zverkova 2003; Ivanov 2013).

These large changes in the biomass of dominant fish likely have had profound impacts on associated food webs including trophic linkages to commercially important fish such as Pacific salmon.

Changes in Pacific salmon abundance temporally coincided with large-scale climate trends in the North Pacific Ocean as indicated by climate indices and regime shifts (Beamish and Bouillon 1993; Hollowed et al. 2002, 2013; Mantua and Hare 2002; Kaeriyama 2004; Klyashtorin and

Lyubushin 2005; Ruggerone et al. 2010). Overall salmon production tended to decrease after the climate shift in 1947 and increased after the climate shift in 1977 (Hare and Mantua 2000; Irvine and Fukuwaka 2011).

Several hypotheses have been proposed to explain the increase in the carrying capacity of the North Pacific Ocean by Pacific salmon under changing climatic conditions. They are based on understanding of a limited salmon food supply in their offshore feeding areas, intense competition for food, especially with the high abundance of pink salmon (*O. gorbuscha*) and Japanese hatchery chum salmon (*O. keta*), alteration of trophic webs, and auto-regulation of populations through the dynamics of mortality, growth rate, and age at maturity e.g. (Gritsenko et al. 2000; Gritsenko and Klovach 2002; Helle et al. 2007; Johnson and Schindler 2009; Kaeriyama et al. 2009; Irvine and Akenhead 2013). However, these hypotheses are not supported by factual data on food consumption by Pacific salmon, zooplankton standing crop, and productivity.

Studies conducted by TINRO-Center in the Bering Sea, Okhotsk Sea, and western North Pacific Ocean (Kuznetsova 2005; Chuchukalo 2006; Naydenko 2007, 2010; Shuntov and Temnykh 2008a, 2011; Shuntov et al. 2010) suggest that the trophic role of Pacific salmon in marine and oceanic pelagic communities has been relatively low in years of both low and high abundance. During the last 30 years, their average share of total food consumption by nekton (all non-planktonic stages of fish and squid species) was estimated to be 1–5% in the western Bering Sea, 0.5–1.0% in the Okhotsk Sea, and < 1% in the Pacific waters off the Kuril Islands (Shuntov and Temnykh 2011). However, these studies do not take into account production rates of plankton and nekton. Rather, they focus mostly on the species occupying middle trophic levels—zooplankton, fish and squids.

Ecosystem modeling using the Ecopath model has been used extensively to examine and contrast marine ecosystems in many regions of the world's oceans including the Russian far-eastern seas (Aydin et al. 2002; Radchenko 2011, 2015). Despite limitations related to incomplete biomass and diet data for all components of marine ecosystems (especially those at lower trophic levels), models provide an opportunity to study the marine trophic structure and energy flow. As a complement to prior field studies that targeted Pacific salmon using simple block models (e.g., Naydenko 2010), ecosystem modeling using the Ecopath approach includes estimations of production rates and trophic links among all groups or species in order to provide a deeper understanding of pelagic trophic webs.

Ecopath is a balance model of ecosystem trophic structure that has been widely acknowledged as a methodology for compiling and processing data on trophic relationships in marine ecosystems (Polovina 1985; Christensen and Pauly 1992; Pauly et al. 2000). Its advantage over the block model is the ability to use a large amount of data and to assimilate it into a single logical architec-

ture. It quantifies the dominant trophic links and focuses on the pathways of dominant mass transfer, sorting them by importance to assess the function of the ecosystem as a whole. Progressive model possibilities include a better capability to visualize results, to compare and interpret data, and to take advantage of higher calculation speeds. As this work emphasizes Pacific salmon, Ecopath was used to construct a mass-balance model of marine ecosystems. This modeling system focuses on dynamics of large vertebrates and does not require detailed data on species occupying lower trophic levels (Christensen and Walters 2004; Preikshot 2007).

In this research, we consider Pacific salmon as a group of ecologically similar species to emphasize their importance as one of the core elements of pelagic fish communities. We did not consider individual trends of species and/or regional groups. Such an approach adequately reflects the mixed nature of Pacific salmon aggregations in deep-water regions of the Bering Sea and the subarctic Pacific Ocean, i.e., areas of migration and foraging for numerous regional stocks. In this particular pelagic fish community, pink and chum salmon (species with similar feeding habits; Johnson and Schindler 2009) comprise the largest proportion of the biomass and total abundance. Sockeye salmon (*O. nerka*), another largely planktivorous fish, comprise the third largest biomass (Shuntov and Temnykh 2008a; Ruggerone et al. 2010).

The goal of this study was to compare the trophic structure of epipelagic communities under different Pacific salmon production regimes in both the western Bering Sea and the western North Pacific Ocean, and to determine whether the ecosystem is capable of supporting even higher populations of salmon than were previously observed.

## MATERIALS AND METHODS

An Ecopath mass balance model was developed to construct a trophic structure of pelagic ecosystems of the western Bering Sea and western North Pacific Ocean. An Ecopath model is built by solving a set of linear equations that quantify the biomass and energy moving in and out of each compartment (functional group) in a modeled food web. The master Ecopath equation is, for each functional group (i) with predators (j):

$$B_i \left( \frac{P}{B} \right)_i EE_i + IM_i = \sum_j \left( B_j \left( \frac{Q}{B} \right)_j DC_{ij} \right) + EM_i + C_i,$$

where  $B$  = biomass,  $P/B$  = production/biomass ratio,  $IM$  and  $EM$  = immigration and emigration,  $Q/B$  = consumption/biomass ratio,  $DC$  = full proportional diet matrix,  $C$  = fisheries catch + discards, and  $EE$  = ecotrophic efficiency. Any six of the seven parameters are input for each species group in the Ecopath model. The seventh, unknown parameter can then be calculated. Typically,  $EE$ , the

ecotrophic efficiency of a group, is left unknown due to the difficulty of deriving empirical measurements of this parameter (Christensen et al. 2008). *EE* is the fraction of a species group's production that is consumed by other functional groups. The estimation of *EE* is the primary diagnostic tool for data calibration in Ecopath. Estimates of biomass, consumption and production for modelled species groups often lead to configurations in which species are being preyed upon more than they are being produced ( $EE > 1.0$ ), which is impossible under the mass-balance assumption. In the cases of mesopelagic fish in the Bering Sea model and forage fish in the Kuril Islands model, *EE* was set to 0.95 in order to allow production by these prey species to satisfy consumption by predator groups (Essington 2007).

Models have been developed to emulate pelagic ecosystems in the western Bering Sea and western North Pacific Ocean in "typical" years with an emphasis on upper trophic level species. For the Bering Sea, data from 1986 was used to represent the period of relative abundance of walleye pollock and relatively low Pacific salmon biomass. Conversely, 2006 was chosen to represent the period of low biomass of walleye pollock and high Pacific salmon biomass. In the North Pacific Ocean, analogous models were developed for 1991 and 2009. In 1991, there was a relatively high abundance of Pacific sardine combined with low abundance of Pacific salmon, whereas Pacific sardine biomass was relatively low and abundance of Pacific salmon was relatively high in 2009. To analyze food web changes and the status of forage resources for Pacific salmon, we modeled a hypothetical scenario, in which Pacific salmon biomasses were entered as 50% greater than those used in the 2006 model for the Bering Sea and the 2009 model for the western North Pacific.

Ecosystem models were developed to emulate the marine habitats that provide important Pacific salmon foraging areas. In the Bering Sea, the modeled area included the Commander Basin, the western part of Aleutian Basin, and the Navarin Region (Fig. 1). The western North Pacific Ocean model included Pacific waters off the Kuril Islands within the Russian EEZ excluding coastal waters to 12 nautical miles offshore. The spatial extent of the model was adjusted to Pacific salmon habitat in summer and fall. The vertical extent of the models was 0–50 m depth that is close to the extent of the surface water mass in warm seasons (Rostov et al. 2003). Because the model emphasized Pacific salmon habitat, we ignored the fact that some part of production of species performing diel vertical migrations originates outside of the modeled system. The modeled spring/summer period reflects the duration of salmon occurrence in the studied areas.

We considered Pacific salmon as a single functional group. In the modeled habitats, most of Pacific salmon biomass consisted of three species: pink, chum and sockeye. In fact, the percentages of pink, chum, sockeye, coho (*O. kisutch*) and Chinook (*O. tshawytscha*) comprised 16%, 57%, 24%, 1%, and 2% in the western Bering Sea in 2006.

In western North Pacific Ocean, dominance of the first three species is even more pronounced: in 2009, the share of pink, chum, sockeye, coho and Chinook was about 59%, 35%, 5%, 1% and < 0.1%. While diets of dominant salmon species had some species-specific peculiarities, they fed similarly in these regions consuming mainly zooplankton (euphausiids, amphipods, copepods, and pteropods) and small-sized nekton and therefore can be considered as one group with similar features (Zavolokin et al. 2007).

The high percentage of dominant salmon species with similar diet habits implies that modelling these three species as a single function group is acceptable for evaluating the role of salmon in the epipelagic trophic structure.

Input model parameters are presented in Appendix Tables 1–8. Data used for fish, squid, and plankton biomasses were collected in integrated surveys of TINRO-Center in the Bering Sea (R/V *Babaevsk*, 11 September–12 October 1986, and R/V *TINRO*, 24 August–23 September 2006) and in the western North Pacific Ocean (R/V *Professor Kaganovsky* and R/V *Professor Levanidov*, 18 June–10 August 1991, and R/V *Professor Kaganovsky*, 2–25 June 2009). TINRO-Center's archival information was also used for describing biomass dynamics of walleye pollock and Pacific salmon in the western Bering Sea. It is based on the data from pelagic surveys in summer and fall (from June to October) in 1986–1995 and 2002–2010. During the surveys, trawl tows in the epipelagic layer (0–200 m) were conducted over 24-h periods. The vertical spread of the trawl varied from about 30 to 60 m, depending on the type of trawl. The trawl was usually towed for one hour at about 3.0–4.6 kn. For the western North Pacific Ocean, data on commercial catches of Pacific salmon in the Okhotsk Sea area (www.npafc.org) and Russian catches of Pacific sardine off the Kuril Islands (Zhigalin and Belyaev 1999) were used as indices of their biomass in the studied domain.

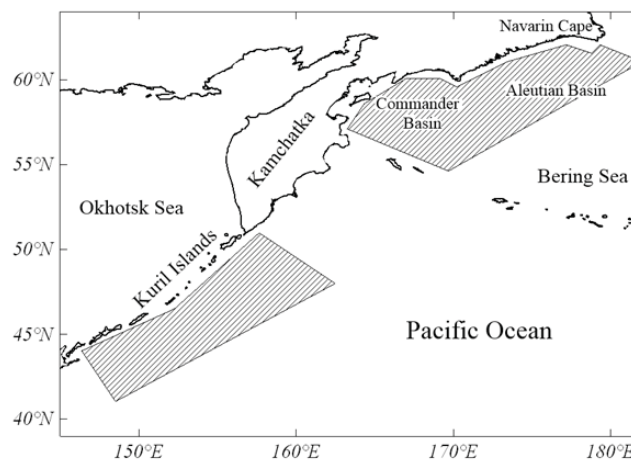
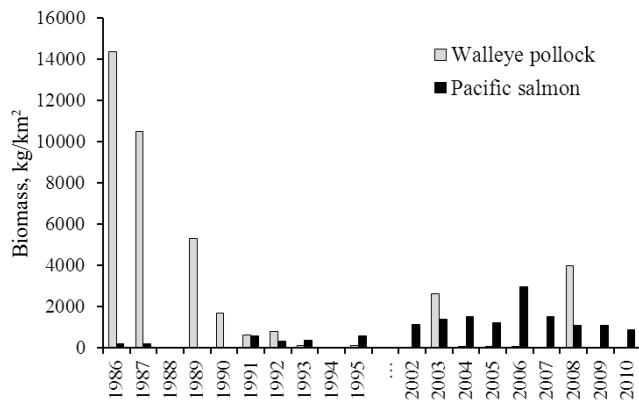


Fig. 1. Map of areas (striped) used to model the trophic structure of epipelagic communities in the western Bering Sea and western North Pacific Ocean.



**Fig. 2.** Changes in biomass (kg/km<sup>2</sup>) of walleye pollock and Pacific salmon in the upper epipelagic layer of the western Bering Sea in summer and fall, 1980s–2000s.

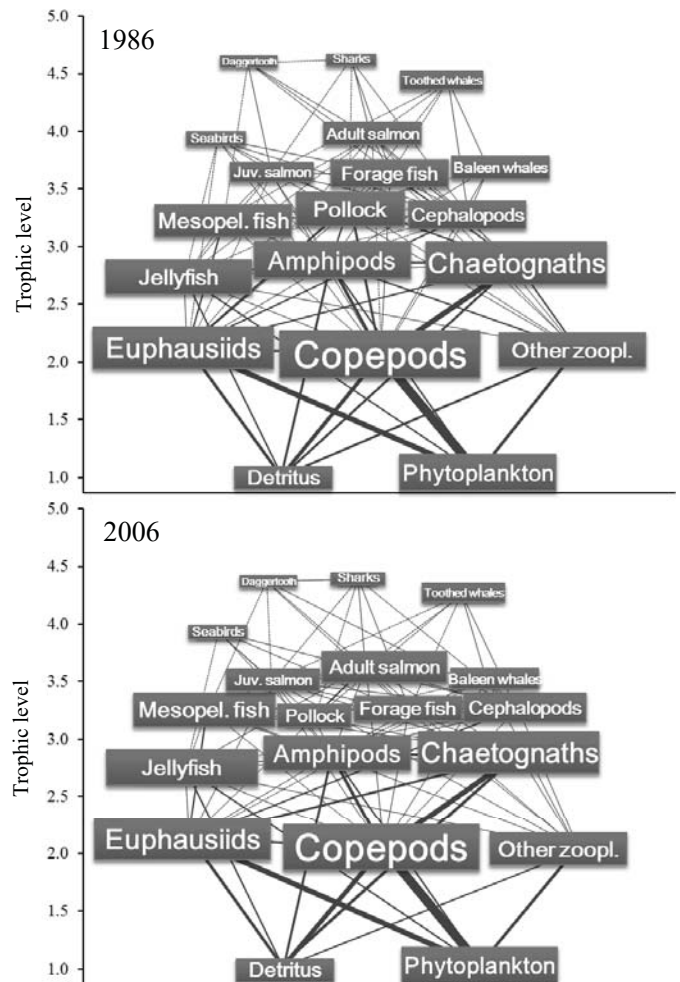
Data on whale biomass in the Bering Sea were from a literature review on marine mammal abundance by Kuzin (2003). Taking into account that the modeled area was restricted mainly by deep-water basins, we totaled the abundance estimations of Dall’s porpoise *Phocoenoides dalli*, orca *Orcinus orca*, and sperm whale *Physeter macrocephalus*, (toothed whales) and humpback whale *Megaptera novaeangliae*, fin whale *Balaenoptera physalus*, and minke whale *Balaenoptera acutorostrata*, (baleen whales). In the western North Pacific Ocean, whale biomass was estimated from data in Vladimirov (1994) with corrections made by Shuntov (2016). Estimations of seabird biomass were based on data presented in summary papers by Shuntov (1988, 1998), Smirnov and Velizhanin (1986), and Artyukhin (1991).

Data on fish diet rations were collected in integrated surveys in the Bering Sea in 1986 and 2006, and in the western North Pacific Ocean in 1991 and 2009. For each functional group in the model, parameters were calculated as a weighted average value of included species, taking into account their biomass ratio within the group. For example, pink, chum and sockeye adults and juveniles are similar to each other in diet composition and feeding rates and are much more abundant than coho, Chinook and cherry salmon. Therefore, the three latter species contributed less to the estimated functional group diet ration.

Feeding spectra and consumption rates of whales and seabirds in the Bering Sea were based on parameters used by Aydin et al. (2002), who compared the eastern and western Bering Sea ecosystems using an Ecopath model. We also used parameters from Aydin et al. (2002) for our model parameter estimates for zooplankton feeding as well as their P/B-coefficients, which were based on earlier zooplankton publications (Beklemishev 1954; Sheader and Evans 1975; Andreeva 1977; Kozhevnikov 1979; Pavlyutin 1987; Raimont 1988; Pogodin 1990; Ponomareva 1990; Dulepova 1993, 2002). Whale diet data were de-

rived from the summary research book on the Kuroshio Current ecosystem by Belyaev (2003). Parameters for daggertooth *Anotopterus pharao* and sharks were based on field research data in Balanov and Radchenko (1998) and Chuchukalo (2006).

Parameters were adjusted to account for particular features of the study area and the seasonal abundance dynamic of different species. In particular, to estimate average biomass of adult Pacific salmon taking into account its seasonal changes, we used archived data accumulated in other surveys conducted in the western Bering Sea and western North Pacific Ocean in summer and fall. Juvenile Pacific salmon and Pacific saury *Cololabis saira* biomass estimates were halved because they spend half the time there compared to other species in the Bering Sea.



**Fig. 3.** Models of the trophic webs of the upper epipelagic layer in the western Bering Sea (deep-water basins and the Navarin region) in 1986 and 2006. Hereafter, box heights are proportional to the eighth root of the biomass (t/km<sup>2</sup>); the width of each predator/prey flow is proportional to the eighth root of the volume of the flow (t/km<sup>2</sup>/year<sup>2</sup>).

## RESULTS AND DISCUSSION

### Western Bering Sea

Compiling the models, we proceed from the concept that the trophic structure of nekton communities in the western Bering Sea epipelagic layer experienced drastic changes between the early 1980s and the 2000s. According to collected background information, walleye pollock was the main consumer of forage resources during the period of its relatively higher abundance in the 1980s (Shuntov et al. 1993). During that period, walleye pollock consumed up to 85% of the food taken by all nekton species (Naydenko 2007). In the 1990s and 2000s, walleye pollock abundance decreased dramatically while the abundance of other nekton species such as Pacific salmon and squids increased (Shuntov and Temnykh 2008b).

Data from summer and fall integrated surveys show that walleye pollock biomass in deep-water regions was high (5–15 t/km<sup>2</sup>) in 1986–1989 and then decreased (Fig. 2). In 1990–2000s, it usually did not exceed 1 t/km<sup>2</sup> excluding a few years (2003 and 2008), when probably large numbers of walleye pollock migrated from the eastern to the western part of the Bering Sea.

From the 1980s to 2000s, Pacific salmon biomass gradually increased and peaked in the mid-2000s. High salmon biomass in the western Bering Sea is related to the growing biomass pool of immature fish (Irvine et al. 2009; Shuntov and Temnykh 2011), which originate from other regions and migrate to the Bering Sea in summer and fall (Groot and Margolis 1991). At the same time, the abundance of local salmon stocks in the western Bering Sea has also increased (Shuntov and Temnykh 2011). In the 2000s, Pacific salmon became one of the main food consumers in the epipelagic zone.

As mentioned above, the highest estimated biomasses of walleye pollock and Pacific salmon occurred in 1986 and 2006, respectively. These years were chosen to contrast the fish communities' composition to analyze changes in trophic flows in the western Bering Sea. Fig. 3 shows the food web model outputs for the upper epipelagic layer in the western Bering Sea (deep basin and the adjacent Navarin region) in 1986 and 2006. These models support the theory that the vast majority of the transportation of matter and energy occurs at low and medium trophic levels. Taking this into account, changes in biomass and consumption of walleye pollock and Pacific salmon look small relative to the total transport of matter through the food web.

According to both models, the largest trophic flow links phytoplankton to copepods, which are the most important functional group of zooplankton (Fig. 3). In addition, consumption of phytoplankton by euphausiids and consumption of copepods by chaetognaths were also pathways with relatively large matter transport.

In summer and fall, food consumption by all squid and fish species decreased by 13 t/km<sup>2</sup> (from 24 to 11 t/km<sup>2</sup>)

in 2006 in comparison to that in 1986. This decline was caused by a decrease in walleye pollock biomass. Food consumption by walleye pollock in the deep-water basin and the Navarin region fell from 17.7 to 0.5 t/km<sup>2</sup> (Table 1) due to the reduction of its biomass in these areas. As adult salmon abundance increased from the 1980s to the 2000s, the amount of food that they consumed increased from 0.4 to 3.6 t/km<sup>2</sup>. Food consumption by squid, mesopelagic fish, and juvenile salmon also rose by 1.8 t/km<sup>2</sup>. However, this compensated for only one-third of the reduction in total food consumption by nekton that resulted from the decrease in walleye pollock abundance.

The role of jellyfish as a consumer of food resources in epipelagic ecosystems has remained minor despite a notable increase in food consumption by this group, from 2.7 to 3.9 t/km<sup>2</sup>, as a result of an increase in their biomass. Our results refute the suggestion that they could cause a food shortage for pelagic fish and particularly for Pacific salmon as concluded by Karpenko et al. (2013). Jellyfish biomass in the western Bering Sea is much smaller in comparison with other regions of the world's oceans suffering from adverse impacts of jellyfish blooms (Uye and Ueta 2004; Lynam et al. 2006; Brodeur et al. 2008; Zavolokin 2011), although in the eastern Bering Sea jellyfish may play significant role in the marine ecosystem (Decker et al. 2014).

Biomass of the "other pelagic fish" group was similar in both 1986 and 2006 but its composition differed greatly. In 1986, Pacific herring *Clupea pallasii* comprised the main part of the group. In 2006, herring biomass was low and saury that migrated to the southwestern Bering Sea from

**Table 1.** Food consumption (t/km<sup>2</sup>) by nekton and zooplankton in the western Bering Sea in summer and fall of 1986 and 2006. d = difference between consumption in 2006 and 1986;  $p < 0.0005$ .

| Species/group     | 1986    | 2006    | d       |
|-------------------|---------|---------|---------|
| Toothed whales    | 0.072   | 0.072   | +       |
| Baleen whales     | 0.565   | 0.293   | -0.272  |
| Daggertooth       | +       | +       | +       |
| Sharks            | 0.001   | 0.002   | 0.001   |
| Walleye pollock   | 17.705  | 0.531   | -17.174 |
| Adult salmon      | 0.353   | 3.613   | 3.260   |
| Juvenile salmon   | 0.157   | 0.543   | 0.385   |
| Cephalopods       | 1.616   | 2.561   | 0.945   |
| Mesopelagic fish  | 2.227   | 2.734   | 0.507   |
| Other forage fish | 2.044   | 1.267   | -0.776  |
| Jellyfish         | 2.670   | 3.878   | 1.208   |
| Chaetognaths      | 64.200  | 58.716  | -5.484  |
| Amphipods         | 23.877  | 14.466  | -9.411  |
| Euphausiids       | 83.461  | 67.974  | -15.487 |
| Copepods          | 309.160 | 265.655 | -43.505 |
| Other zooplankton | 16.125  | 8.250   | -7.875  |

the Pacific Ocean predominated. Three-spined stickleback *Gasterosteus aculeatus* and juvenile Atka mackerel *Pleurogrammus monopterygius* were sub-dominant species in the “other pelagic fish” group in both 1986 and 2006.

The highest quality of parameter data for biomass, production rates, feeding spectra, and consumption rates was for the medium and high trophic level species groups. Figure 4 shows trophic flows linking zooplankton and micronekton with adult Pacific salmon. In 1986, amphipods, squids, euphausiids, and juvenile walleye pollock were the largest food fluxes. In 2006, euphausiids as well as other zooplankton (pteropods and decapod larvae), mesopelagic fish, amphipods, and squids comprised the main prey of adult salmon. From 1986 to 2006, consumption of all these prey groups increased markedly: euphausiids by 1.1 t/km<sup>2</sup> over half a year (summer and fall), mesopelagic fish by 0.7, pteropods and decapod larvae by 0.3, jellyfish by 0.3, amphipods by 0.3, copepods by 0.2, and other groups by 0.5 t/km<sup>2</sup> for half a year.

Figure 4 shows that Pacific salmon can prey on a wide variety of forage species at the second to third trophic levels. Almost all groups of epipelagic micronekton and macropelagic from these trophic levels can occur in their diet rations. Due to high feeding plasticity (Shuntov and Tem-

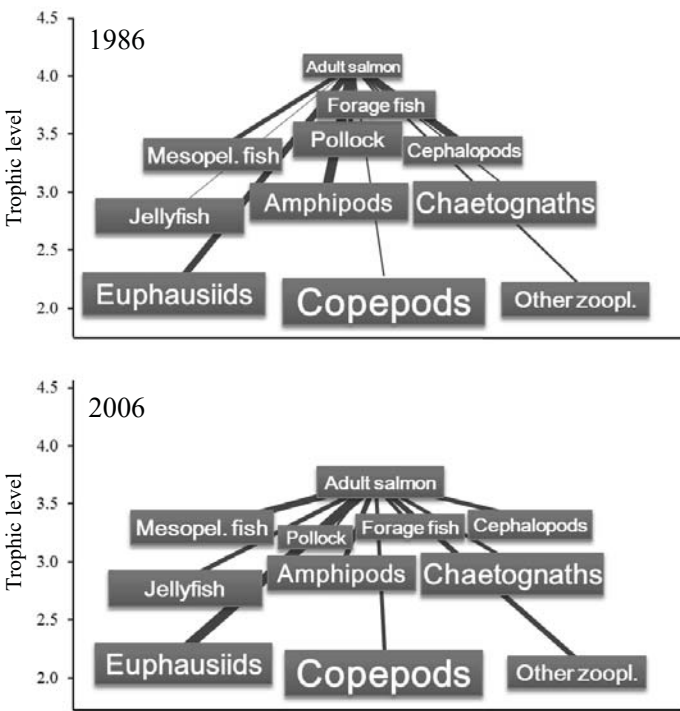


Fig. 4. Trophic flows directed at adult salmon (age-1 and older) in the western Bering Sea in 1986 and 2006.

Table 2. Possible changes in salmon diets (%) to balance the model with an increase in salmon biomass (x 1.5) relative to its level in 2006 in the western Bering Sea. d = difference in salmon diets in 2006 and in the modeled scenario.

| Prey                     | Scenario 1 |       |    | Scenario 2 |       |    |
|--------------------------|------------|-------|----|------------|-------|----|
|                          | 2006       | x 1.5 | d  | 2006       | x 1.5 | d  |
| Copepods                 | 5          | 14    | 9  | 5          | 5     | 0  |
| Euphausiids              | 33         | 33    | 0  | 33         | 41    | 8  |
| Amphipods                | 10         | 10    | 0  | 10         | 10    | 0  |
| Chaetognaths             | 4          | 4     | 0  | 4          | 4     | 0  |
| Jellyfish                | 8          | 8     | 0  | 8          | 8     | 0  |
| Other zooplankton        | 9          | 9     | 0  | 9          | 9     | 0  |
| Juvenile walleye pollock | 1          | 1     | 0  | 1          | 1     | 0  |
| Mesopelagic fish         | 19         | 12    | -7 | 19         | 12    | -7 |
| Other forage fish        | 4          | 2     | -2 | 4          | 3     | -1 |
| Cephalopods              | 7          | 7     | 0  | 7          | 7     | 0  |

nykh 2008a, 2011), Pacific salmon food demand can be accommodated by changing the percentages of different prey items in their diet. Trophic flow charts for 1986 and 2006 reflect that an increase in salmon consumption of lower trophic level prey (copepods, euphausiids, and other zooplankton) resulted in a decline in the apparent trophic level of Pacific salmon. Given the high biomass of copepods and euphausiids, which were able to support highly abundant populations of walleye pollock in the past, a large reserve of forage resources may be available for Pacific salmon.

From 1986 to 2006, Pacific salmon biomass in the western Bering Sea increased 14-fold<sup>1</sup>, up to 400,000 t. Given such a potential for increase, we examined whether larger increases in Pacific salmon abundance would affect the trophic structure of epipelagic communities. To explore this question, we multiplied Pacific salmon biomass in 2006 by 50% (added 200,000 t) and tried to balance the model by varying the salmon diet matrix.

Table 2 illustrates two scenarios of possible changes in the Pacific salmon diet to balance the energetic structure of the model. In the first scenario, the model was balanced by increasing the portion of copepods in the diet composition by 9% and decreasing small mesopelagic (by 7%) and epipelagic (by 2%) fish. Raising the portion of copepods in the salmon diet from 5% to 14% is within the observed natural variability in the occurrence of this zooplankton group in salmon stomachs. For example, average percentage of copepods in pink

<sup>1</sup> Pacific salmon biomass in 1980s was likely underestimated due to sampling not only in the surface layer but also in deeper waters. However, this underestimation was likely negligible because Pacific salmon commercial catches on the Russian coasts, which reflect their abundance level in nearby waters, were notably smaller in the 1980s than in the 2000s.

and chum salmon diets in the western Bering Sea in the 2000s reached 29% and 18%, respectively (Zavolokin 2014).

In the first scenario, the consumption of copepods increased 4 times, from 0.18 to 0.74 t/km<sup>2</sup>. Consumption of copepods, amphipods, chaetognaths, jellyfish, other zooplankton, and squid also became higher than in 2006. The ecotrophic efficiency of copepods rose from 0.88 to 0.89, which implies that a large portion of their production (more than 10%) was not used by predators.

In the second scenario, the portion of copepods in the Pacific salmon diet was fixed at the previous level, and the model was balanced by changing euphausiid consumption. The decline in euphausiid consumption due to the decrease in walleye pollock from the 1980s to the 2000s may be compensated by increased Pacific salmon food demand. In our model-balancing exercise, the percentage of euphausiids in the salmon diet ration was raised from 33% to 41% (Table 2). Similar occurrences of euphausiids in diet rations of pink, chum and sockeye salmon were observed in the Bering Sea in the 1990s and 2000s (Efimkin et al. 2004; Volkov et al. 2007).

In the second scenario, the consumption of euphausiids by Pacific salmon increased by 1.1 t/km<sup>2</sup> (from 1.18 to 2.24). Consumption of amphipods, other zooplankton, jellyfish, and squids also became higher, by 0.19, 0.17, 0.15, and 0.12 t/km<sup>2</sup>, respectively.

In an alternate scenario, the model could also have been balanced by changing the percentage of squid, amphipods, or pteropods in Pacific salmon diet. A high percentage of these groups (up to 50%) has been observed in salmon diets in the Bering Sea (Efimkin 2006). In addition, Pacific salmon could potentially access chaetognath production, which had relatively low ecotrophic efficiency in both the 1986 and 2006 models.

It is important to note that the model was balanced only by adjusting the diet composition of Pacific salmon and not by altering the feeding rate. If the daily ration of individual Pacific salmon decreased, changes in their food spectra could be even smaller. Our results indicate that forage resources will support Pacific salmon food demands in the western Bering Sea even if their biomass increased one and a half times.

### Western North Pacific Ocean

A similar understanding of nekton communities' alternation due to fluctuations in abundance in dominant species over the last three decades was developed by TINRO for the epipelagic zone of the western North Pacific Ocean. In the 1980s, Pacific sardine and walleye pollock were the main consumers of forage resources in the Pacific waters off the Kuril Islands, accounting for approximately 70% of the total annual consumption by all fish and squid species in the epipelagic zone (Ivanov 1998; Chuchukalo 2006). While walleye pollock inhabit the narrow shelf zone off the Kuril Islands, Pacific sardine was the dominant species in offshore waters in summer and fall (Ivanov 2005). The

sardine portion of the total food consumption by nekton comprised 40–70% for a whole year (Ivanov 1998; Belyaev 2003; Ivanov 2005; Chuchukalo 2006) and probably no less than 80% in waters off the Kuril Islands in summer months during periods of high abundance.

In the early 1990s, Pacific sardine abundance sharply decreased (Belyaev 2003). Accordingly, its portion of total food consumption by nekton fell. In 1991–1995, it was about 10% of all food consumed, and by the 2000s it comprised < 1% (Naydenko 2002; Chuchukalo 2006; Naydenko and Khoruzhiy 2014).

In contrast, use of pelagic prey resources by Pacific salmon in Pacific waters off the Kuril Islands increased from the 1990s to the 2000s. Although their portion of the food consumption by all nekton species in the upper epipelagic layer was about 3% in the early 1990s, it reached 9–10% by the mid-1990s, and in the 2000s it increased again to 21% (Naydenko 2002; Naydenko and Khoruzhiy 2014).

Figure 5 shows changes in Russian catches of Pacific sardine off the Kuril Islands (Zhigalin and Belyaev 1999) and the Russian catch of Pacific salmon in the Okhotsk Sea area ([www.npafc.org](http://www.npafc.org)), which were used as indices of their biomass in the domain studied. From the mid-1970s to 1980s, Russian catches of Pacific sardine gradually increased and reached 394,000–418,000 t in the late 1980s. It then sharply declined and the Russian fishery for Pacific sardine was shut down by the mid-1990s. Russian catches of Pacific salmon in the Okhotsk Sea basin have gradually increased over the last decades: from 24,000–48,000 to 295,000–376,000 t from the early 1970s to the 2010s.

As discussed in the methods section, integrated pelagic surveys in the upper epipelagic layer in the western North Pacific Ocean began in 1991, so 1991 and 2009 were chosen as contrast years to model pelagic food webs. In 1991, Pacific sardine biomass was relatively high while Pacific salmon biomass was relatively lower than in the 2000s. In 2009, the Russian catch of Pacific salmon in the Okhotsk Sea area reached its historically highest level (380,000 t) while Pacific sardine biomass was negligible.

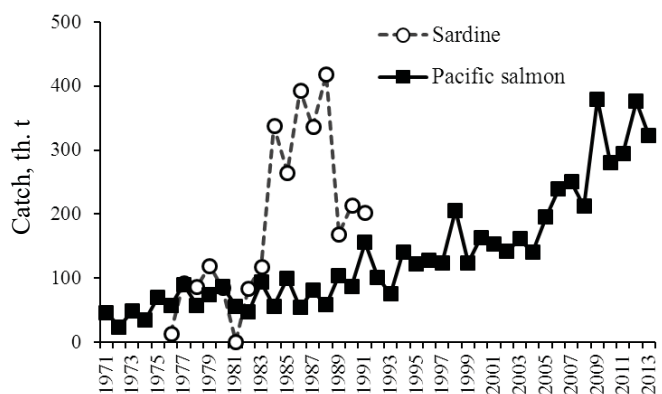


Fig. 5. Russian catch of sardines in Pacific waters off the Kuril Islands and Pacific salmon in the Okhotsk Sea basin.

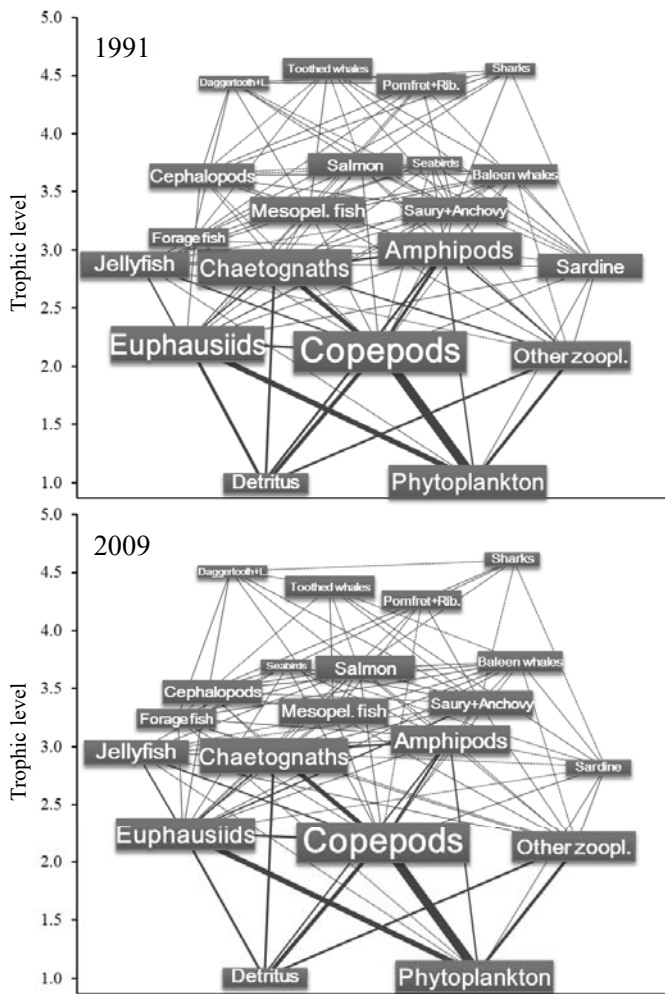


Fig. 6. Models of the trophic webs of the upper epipelagic layer in Pacific waters off the Kuril Islands in 1991 and 2009.

As in the western Bering Sea, no structural changes occurred in the epipelagic food web despite fluctuations in nekton abundance in the Pacific waters off the Kuril Islands (Fig. 6). Major trophic flows linked plankton groups occupying the first three trophic levels both in 1991 and in 2009. The most intensive flow linked phytoplankton to copepods. Phytoplankton consumption by euphausiids and consumption of copepods by chaetognaths were also remarkable.

The total food consumption by all fish and squid species in summer and fall did not change greatly between 1991 and 2009 (Table 3). Food consumption by Pacific sardine decreased from 0.74 to 0.02 t/km<sup>2</sup>. Food intake by squid and mesopelagic fish also decreased (in aggregate, from 4.46 to 3.61 t/km<sup>2</sup>). On the other hand, there was an increase in food consumption by Pacific salmon (from 1.13 to 2.42 t/km<sup>2</sup>) and the saury + Japanese anchovy (*Engraulis japonicus*) group (from 2.62 to 3.17 t/km<sup>2</sup>). In 1991, Japanese anchovy contributed about 60% to the group biomass while Pacific saury comprised about 80% in 2009.

Copepods consumed more in 2009 than in 1991 (Table 3). In the contrast, food consumption by euphausiids and amphipods notably decreased (by 38 and 33.2 t/km<sup>2</sup>, respectively). There was an increase in food consumption by both toothed and baleen whales, the abundance of which rose over the three last decades (Vladimirov 2000). However, these changes are small relative to the scale of trophic flows at lower trophic levels.

Total food consumption by all fish and squid in the Pacific waters off the Kuril Islands (about 10 t/km<sup>2</sup>) was similar to the low level of consumption in the western Bering Sea in the 2000s. In 2006, it was about 11 t/km<sup>2</sup>, while in 1986 it was much higher (24 t/km<sup>2</sup>) due to the high abundance of walleye pollock. However, Pacific sardine biomass had already decreased in the western North Pacific Ocean by 1991. In the mid-1980s, when Pacific sardine were more abundant than in 1991, overall food consumption by nekton was likely much greater.

Similar to the Bering Sea model, more reliable information on biomass, production rates, feeding spectra, and consumption rates was available for the model compartments occupying medium and high trophic levels. This allowed us to examine this part of food web in detail. Figure 7 shows trophic flows going through the Pacific salmon functional group in 1991 and 2009. Pacific salmon biomass in these two years differed two-fold.

Table 3. Food consumption (t/km<sup>2</sup>) by nekton and zooplankton in the Pacific waters off the Kuril Islands in summer and fall of 1991 and 2009. d = difference between consumption in 2009 and 1991; p < 0.0005.

| Species/group            | 1991    | 2009    | d       |
|--------------------------|---------|---------|---------|
| Toothed whales           | 0.363   | 0.452   | 0.089   |
| Baleen whales            | 0.410   | 0.513   | 0.103   |
| Daggertooth + Lancelfish | 0.007   | 0.002   | -0.005  |
| Sharks                   | 0.002   | 0.007   | 0.004   |
| Pacific salmon           | 1.125   | 2.415   | 1.290   |
| Sardine                  | 0.737   | 0.023   | -0.714  |
| Saury + Anchovy          | 2.617   | 3.167   | 0.550   |
| Pomfret + Ribbonfish     | 0.209   | 0.149   | -0.061  |
| Cephalopods              | 2.493   | 2.116   | -0.377  |
| Mesopelagic fish         | 1.962   | 1.495   | -0.468  |
| Other forage fish        | 0.435   | 0.623   | 0.189   |
| Jellyfish                | 1.860   | 2.070   | 0.210   |
| Chaetognaths             | 63.780  | 63.780  | +       |
| Amphipods                | 45.640  | 12.460  | -33.180 |
| Euphausiids              | 90.270  | 52.275  | -37.995 |
| Copepods                 | 360.643 | 447.496 | 86.853  |
| Other zooplankton        | 8.625   | 15.375  | 6.750   |



In 1991, Pacific salmon, as a group, preyed mostly on amphipods and euphausiids. Copepods, jellyfish, other zooplankton, squid, and mesopelagic fish were other prevalent groups in the Pacific salmon diet ration. In 2009, the portion of amphipods in the salmon diet fell, whereas that of copepods, chaetognaths, and jellyfish rose. Total consumption of most prey species groups increased: copepods by 0.5 t/km<sup>2</sup>, euphausiids by 0.3, jellyfish by 0.3, cephalopods by 0.1, mesopelagic fish by 0.06, and other zooplankton by 0.02 t/km<sup>2</sup>.

Modeled changes indicate that, similar to the pattern in the Bering Sea, Pacific salmon movement down the food web, from trophic level 3.7 to 3.6, followed an increase in their biomass.

In 2009, the average salmon biomass for summer and fall in Pacific waters off the Kuril Islands increased two-fold relative to 1991, reaching 300,000 t. According to catch statistics (Fig. 5), the Pacific salmon biomass estimate in 2009 was at an historic high. To analyze possible changes in trophic structure of epipelagic communities, Pacific salmon biomass in the model was multiplied by 1.5.

A 50% increase in Pacific salmon biomass should not affect significantly the trophic structure of the epipelagic communities of the Pacific waters off the Kuril Islands. The increase in consumption above production would occur only for three groups of small-sized forage nekton: squid, mesopelagic fish, and forage fish. Table 4 shows two possible scenarios of changes in the salmon diet to balance the model. In the first scenario, the model was balanced by increasing the portion of copepods in the Pacific salmon diet by 5% and decreasing that of squid, mesopelagic fish, and forage fish. This change is within the range of natural variability of this group (Naydenko and Kuznetsova 2002).

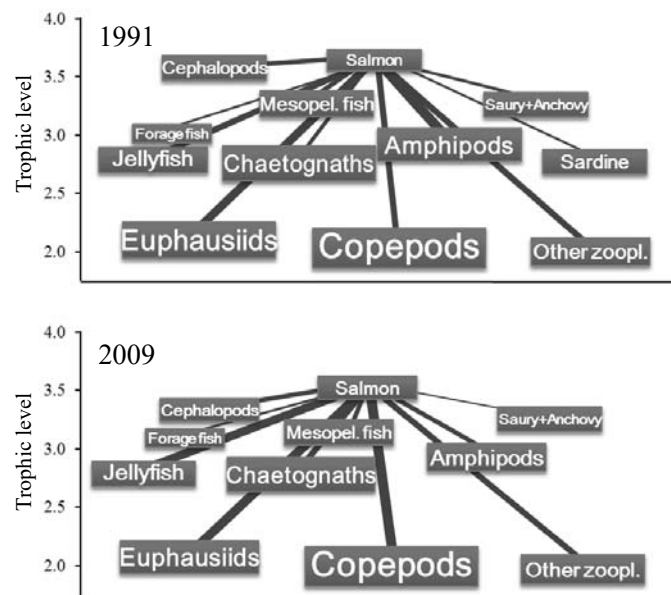


Fig. 7. Trophic flows directed at adult salmon (age-1 and older) in Pacific waters off the Kuril Islands in 1991 and 2009.

Table 4. Possible changes in salmon diets (%) to balance the model with an increase in salmon biomass (x 1.5) relative to its level in 2009 in the Pacific waters off the Kuril Islands. d = difference in salmon diets in 2009 and in the modeled scenario.

| Prey              | Scenario 1 |       |    | Scenario 2 |       |    |
|-------------------|------------|-------|----|------------|-------|----|
|                   | 2009       | x 1.5 | d  | 2009       | x 1.5 | d  |
| Copepods          | 26         | 31    | 5  | 26         | 26    | 0  |
| Euphausiids       | 21         | 21    | 0  | 21         | 26    | 5  |
| Amphipods         | 6          | 6     | 0  | 6          | 6     | 0  |
| Chaetognaths      | 12         | 12    | 0  | 12         | 12    | 0  |
| Jellyfish         | 17.8       | 17.8  | 0  | 17.8       | 17.8  | 0  |
| Other zooplankton | 5          | 5     | 0  | 5          | 5     | 0  |
| Saury + Anchovy   | 0.2        | 0.2   | 0  | 0.2        | 0.2   | 0  |
| Mesopelagic fish  | 5          | 3     | -2 | 5          | 3     | -2 |
| Other forage fish | 1          | 0     | -1 | 1          | 0     | -1 |
| Cephalopods       | 6          | 4     | -2 | 6          | 4     | -2 |

In the first scenario, the largest increase in overall consumption by Pacific salmon was for copepods (from 0.6 to 1.1 t/km<sup>2</sup>). In addition, there was an increase in consumption of euphausiids (by 0.25 t/km<sup>2</sup>), jellyfish (by 0.22 t/km<sup>2</sup>), and chaetognaths (by 0.15 t/km<sup>2</sup>).

In the second scenario, we did not change the portion of copepods in the salmon diet ration. The model was balanced by increasing the portion of euphausiids by 5% and decreasing the portions of cephalopods, mesopelagic fish, and forage fish (Table 4). The percentage of euphausiids increased to 26% and remained at that level for Pacific salmon diets in this region (Naydenko and Kuznetsova 2002; Chuchukalo 2006). Consumption of euphausiids increased from 0.5 to 0.9 t/km<sup>2</sup>, and the consumption of copepods, jellyfish, and chaetognaths also rose (by 0.3, 0.2, and 0.2 t/km<sup>2</sup>, respectively).

Increased consumption of copepods and euphausiids in both modeled scenarios is not excessive as the ecotrophic efficiency of copepods and euphausiids only increased from 0.60 to 0.61 and from 0.76 to 0.80, indicating a large portion of excess production for these groups in the model.

CONCLUSIONS

Our model suggests that the observed changes in biomass of important commercial species in the western Bering Sea and Pacific waters off the Kuril Islands caused relatively minor shifts in the distribution of energy within the trophic webs of these systems. Consequently, the food web structure of epipelagic nekton communities in the western Bering Sea and Pacific waters off the Kuril Islands generally did not change. Major trophic flows persisted within low and

medium trophic levels, irrespective of nekton biomass. As a consequence, Pacific salmon, the biomass of which is relatively low in comparison with other nekton species, played a minor role in marine ecosystems in the 1980s–2000s.

From the 1980s to 2000s, salmon biomass increased greatly in the western Bering Sea and Pacific waters off the Kuril Islands in warm seasons. This caused an increase in their total food consumption and changes in their diet rations with a shift from prey organisms occupying relatively high trophic levels (amphipods, squid) to an increase in the percentage of prey from relatively low trophic levels (euphausiids, copepods, pteropods). As a result, the average estimated trophic level of Pacific salmon in the modeled food webs declined. Modeled scenarios of potential further increases in Pacific salmon biomass reveal that the available forage resources could satisfy the expanded energetic demands. Pacific salmon can prey on a wide variety of food items from the second to the third trophic levels to satisfy their energetic demands on prey species even during periods of extremely high biomass. How such changes would affect individual species of Pacific salmon remains a topic for future investigation.

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**Appendix Table 1.** Ecopath input parameters describing the 19 functional groups in the 1986 western Bering Sea ecosystem model. Biomass ( $B$ ) is in  $t/km^2$ , Production/Biomass ( $P/B$ ) and Consumption/Biomass ( $Q/B$ ) are rates (1/year); Ecotrophic Efficiency ( $EE$ ) is a proportion.

| Species/group     | $B$     | $P/B$ | $Q/B$ | $EE$ |
|-------------------|---------|-------|-------|------|
| Toothed whales    | 0.0173  | 0.01  | 4.15  |      |
| Baleen whales     | 0.0646  | 0.01  | 8.75  |      |
| Seabirds          | 0.0010  | 0.4   | 43.5  |      |
| Daggertooth       | 0.00001 | 0.25  | 2.5   |      |
| Sharks            | 0.0004  | 0.2   | 2     |      |
| Pollock           | 3.5410  | 1.2   | 5     |      |
| Adult salmon      | 0.0775  | 0.9   | 4.55  |      |
| Juvenile salmon   | 0.0172  | 3     | 9.15  |      |
| Cephalopods       | 0.3020  | 1.6   | 5.35  |      |
| Mesopelagic fish  |         | 0.475 | 1.75  | 0.95 |
| Forage fish       | 0.3144  | 1.25  | 6.5   |      |
| Jellyfish         | 1.7800  | 0.75  | 1.5   |      |
| Chaetognaths      | 10.7000 | 3     | 6     |      |
| Amphipods         | 3.4110  | 1.75  | 7     |      |
| Euphausiids       | 9.8190  | 1.55  | 8.5   |      |
| Copepods          | 23.6000 | 4.75  | 13.1  |      |
| Other zooplankton | 2.1500  | 2.5   | 7.5   |      |
| Phytoplankton     | 3.0000  | 117   |       |      |
| Detritus          | 0.1000  |       |       |      |

**Appendix Table 2.** Diet matrix (proportion of prey for each predator) for the 1986 western Bering Sea Ecopath model.

| Prey                  | Predator |       |       |       |       |         |        |        |       |       |       |       |       |       |       |       |       |
|-----------------------|----------|-------|-------|-------|-------|---------|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                       | 1        | 2     | 3     | 4     | 5     | 6       | 7      | 8      | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    | 17    |
| 1. Toothed whales     | -        | -     | -     | -     | -     | -       | -      | -      | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 2. Baleen whales      | 0.001    | -     | -     | -     | -     | -       | -      | -      | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 3. Seabirds           | -        | -     | -     | -     | -     | -       | -      | -      | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 4. Daggertooth        | -        | -     | -     | -     | -     | -       | -      | -      | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 5. Sharks             | -        | -     | -     | 0.001 | -     | -       | -      | -      | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 6. Pollock            | 0.301    | 0.104 | 0.258 | -     | 0.050 | 0.094   | 0.161  | -      | 0.027 | -     | -     | -     | -     | -     | -     | -     | -     |
| 7. Adult salmon       | 0.096    | -     | -     | 0.350 | 0.300 | -       | -      | -      | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 8. Juvenile salmon    | 0.048    | -     | 0.010 | 0.050 | 0.300 | -       | -      | -      | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 9. Cephalopods        | 0.313    | 0.104 | 0.052 | 0.050 | 0.200 | 0.010   | 0.239  | 0.037  | 0.012 | -     | -     | 0.010 | -     | -     | -     | -     | -     |
| 10. Mesopelagic fish  | 0.241    | 0.177 | 0.237 | 0.499 | 0.150 | 0.010   | 0.005  | 0.009  | 0.004 | -     | -     | -     | -     | -     | -     | -     | -     |
| 11. Forage fish       | -        | -     | -     | 0.050 | -     | 0.029   | 0.054  | 0.001  | 0.009 | -     | -     | 0.010 | -     | -     | -     | -     | -     |
| 12. Jellyfish         | -        | -     | 0.031 | -     | -     | 0.00003 | 0.0001 | 0.0004 | -     | -     | -     | -     | -     | -     | 0.050 | -     | -     |
| 13. Other zooplankton | -        | -     | -     | -     | -     | 0.010   | 0.011  | 0.001  | 0.012 | 0.001 | -     | 0.155 | 0.050 | 0.010 | 0.030 | -     | -     |
| 14. Chaetognaths      | -        | -     | -     | -     | -     | 0.070   | 0.002  | 0.015  | -     | 0.365 | -     | 0.098 | -     | -     | 0.110 | -     | -     |
| 15. Amphipods         | -        | 0.073 | 0.052 | -     | -     | 0.115   | 0.353  | 0.575  | 0.006 | 0.214 | 0.064 | 0.025 | -     | 0.030 | 0.015 | -     | -     |
| 16. Euphausiids       | -        | 0.260 | 0.258 | -     | -     | 0.371   | 0.175  | 0.353  | 0.929 | 0.381 | 0.916 | 0.222 | -     | 0.040 | 0.010 | 0.005 | -     |
| 17. Copepods          | -        | 0.281 | 0.103 | -     | -     | 0.292   | 0.002  | 0.009  | 0.001 | 0.038 | 0.021 | 0.111 | -     | 0.780 | 0.551 | 0.200 | 0.060 |
| 18. Phytoplankton     | -        | -     | -     | -     | -     | -       | -      | -      | -     | -     | -     | 0.246 | 0.700 | -     | 0.054 | 0.645 | 0.820 |
| 19. Detritus          | -        | -     | -     | -     | -     | -       | -      | -      | -     | -     | -     | 0.123 | 0.250 | 0.140 | 0.180 | 0.150 | 0.120 |

**Appendix Table 3.** Ecopath input parameters describing the 19 functional groups in the 2006 western Bering Sea ecosystem model. Biomass ( $B$ ) is in  $t/km^2$ , Production/Biomass ( $P/B$ ) and Consumption/Biomass ( $Q/B$ ) are rates (1/year).

| Species/group     | $B$     | $P/B$ | $Q/B$ |
|-------------------|---------|-------|-------|
| Toothed whales    | 0.0173  | 0.01  | 4.15  |
| Baleen whales     | 0.0335  | 0.01  | 8.75  |
| Seabirds          | 0.0010  | 0.4   | 43.5  |
| Daggertooth       | 0.00001 | 0.25  | 2.5   |
| Sharks            | 0.0008  | 0.2   | 2     |
| Pollock           | 0.0850  | 1.2   | 6.25  |
| Adult salmon      | 0.7940  | 0.9   | 4.55  |
| Juvenile salmon   | 0.0593  | 3     | 9.15  |
| Cephalopods       | 0.4787  | 1.6   | 5.35  |
| Mesopelagic fish  | 1.5620  | 0.475 | 1.75  |
| Forage fish       | 0.1950  | 1.25  | 6.5   |
| Jellyfish         | 2.5851  | 0.75  | 1.5   |
| Chaetognaths      | 9.7860  | 3     | 6     |
| Amphipods         | 2.0670  | 1.75  | 7     |
| Euphausiids       | 7.9970  | 1.55  | 8.5   |
| Copepods          | 20.2790 | 4.75  | 13.1  |
| Other zooplankton | 1.1000  | 2.5   | 7.5   |
| Phytoplankton     | 3.0000  | 117   |       |
| Detritus          | 0.1000  |       |       |

**Appendix Table 4.** Diet matrix (proportion of prey for each predator) for the 2006 western Bering Sea Ecopath model.

| Prey                  | Predator |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|-----------------------|----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                       | 1        | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    | 17    |
| 1. Toothed whales     | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 2. Baleen whales      | 0.001    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 3. Seabirds           | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 4. Daggertooth        | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 5. Sharks             | -        | -     | -     | 0.001 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 6. Pollock            | 0.050    | 0.020 | 0.090 | -     | 0.050 | 0.001 | 0.015 | 0.011 | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 7. Adult salmon       | 0.260    | -     | -     | 0.350 | 0.300 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 8. Juvenile salmon    | 0.140    | -     | 0.190 | 0.050 | 0.300 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 9. Cephalopods        | 0.430    | 0.110 | 0.220 | 0.050 | 0.200 | -     | 0.068 | 0.004 | 0.022 | -     | 0.013 | 0.010 | -     | -     | -     | -     | -     |
| 10. Mesopelagic fish  | 0.119    | 0.180 | 0.470 | 0.499 | 0.150 | -     | 0.036 | 0.007 | 0.004 | -     | -     | -     | -     | -     | -     | -     | -     |
| 11. Forage fish       | -        | -     | -     | 0.050 | -     | -     | 0.186 | 0.001 | 0.009 | 0.002 | -     | 0.005 | -     | -     | -     | -     | -     |
| 12. Jellyfish         | -        | -     | 0.020 | -     | -     | -     | 0.082 | -     | -     | -     | -     | -     | -     | -     | 0.060 | -     | -     |
| 13. Other zooplankton | -        | 0.030 | -     | -     | -     | -     | 0.092 | 0.210 | 0.012 | 0.070 | 0.035 | 0.100 | 0.050 | 0.010 | 0.030 | -     | -     |
| 14. Chaetognaths      | -        | -     | -     | -     | -     | 0.002 | 0.041 | 0.038 | -     | 0.013 | 0.010 | 0.101 | -     | -     | 0.110 | -     | -     |
| 15. Amphipods         | -        | 0.070 | 0.010 | -     | -     | 0.080 | 0.103 | 0.360 | 0.006 | 0.210 | 0.180 | 0.020 | -     | 0.030 | 0.005 | -     | -     |
| 16. Euphausiids       | -        | 0.270 | -     | -     | -     | 0.070 | 0.328 | 0.273 | 0.941 | 0.300 | 0.676 | 0.223 | -     | 0.040 | 0.010 | 0.005 | -     |
| 17. Copepods          | -        | 0.320 | -     | -     | -     | 0.847 | 0.050 | 0.096 | 0.006 | 0.405 | 0.086 | 0.111 | -     | 0.780 | 0.551 | 0.200 | 0.060 |
| 18. Phytoplankton     | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | 0.253 | 0.700 | -     | 0.054 | 0.645 | 0.820 |
| 19. Detritus          | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | 0.175 | 0.250 | 0.140 | 0.180 | 0.150 | 0.120 |



**Appendix Table 5.** Ecopath input parameters describing the 20 functional groups for 1991 in the model of the Pacific waters off the Kuril Islands. Biomass (*B*) is in t/km<sup>2</sup>, Production/Biomass (*P/B*) and Consumption/Biomass (*Q/B*) are rates (1/year).

| Species/group            | <i>B</i> | <i>P/B</i> | <i>Q/B</i> |
|--------------------------|----------|------------|------------|
| Toothed whales           | 0.1100   | 0.03       | 3.3        |
| Baleen whales            | 0.0760   | 0.01       | 5.4        |
| Seabirds                 | 0.0020   | 0.4        | 43.5       |
| Daggertooth + Lancetfish | 0.0028   | 0.25       | 2.5        |
| Sharks                   | 0.0011   | 0.2        | 2          |
| Salmon                   | 0.2045   | 1.25       | 5.5        |
| Sardine                  | 0.4910   | 0.2        | 1.5        |
| Saury + Anchovy          | 0.4058   | 0.78       | 6.45       |
| Pomfret + Ribbonfish     | 0.1112   | 0.38       | 1.88       |
| Cephalopods              | 0.4660   | 1.6        | 5.35       |
| Mesopelagic fish         | 1.1214   | 0.475      | 1.75       |
| Forage fish              | 0.0669   | 1.25       | 6.5        |
| Jellyfish                | 0.6200   | 1.5        | 3          |
| Chaetognaths             | 10.6300  | 3          | 6          |
| Amphipods                | 6.5200   | 1.75       | 7          |
| Euphausiids              | 10.6200  | 1.55       | 8.5        |
| Copepods                 | 27.5300  | 4.75       | 13.1       |
| Other zooplankton        | 1.1500   | 2.5        | 7.5        |
| Phytoplankton            | 4.0000   | 117        |            |
| Detritus                 | 0.1000   |            |            |

**Appendix Table 6.** Diet matrix (proportion of prey for each predator) for the 1991 Ecopath model for the Pacific waters off the Kuril Islands.

| Prey                        | Predator |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|-----------------------------|----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                             | 1        | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    | 17    | 18    |
| 1. Toothed whales           | 0.001    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 2. Baleen whales            | 0.001    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 3. Seabirds                 | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 4. Daggertooth + Lancetfish | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 5. Sharks                   | -        | -     | -     | 0.001 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 6. Salmon                   | 0.005    | 0.001 | -     | 0.400 | 0.550 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 7. Sardine                  | 0.032    | 0.002 | 0.050 | 0.120 | 0.100 | 0.010 | -     | -     | 0.060 | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 8. Saury + Anchovy          | 0.021    | 0.002 | 0.025 | 0.080 | 0.100 | 0.020 | -     | -     | 0.220 | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 9. Pomfret + Ribbonfish     | 0.005    | -     | -     | 0.010 | 0.020 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 10. Cephalopods             | 0.687    | 0.050 | 0.063 | 0.070 | 0.200 | 0.040 | -     | 0.030 | 0.510 | 0.073 | -     | -     | -     | -     | -     | -     | -     | -     |
| 11. Mesopelagic fish        | 0.193    | 0.070 | -     | 0.050 | -     | 0.050 | -     | -     | 0.190 | 0.094 | -     | -     | 0.010 | -     | -     | -     | -     | -     |
| 12. Forage fish             | 0.054    | 0.050 | 0.300 | 0.269 | 0.030 | 0.010 | -     | -     | 0.010 | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 13. Jellyfish               | -        | -     | 0.038 | -     | -     | 0.110 | -     | 0.010 | -     | -     | 0.040 | 0.020 | 0.070 | -     | 0.010 | -     | -     | -     |
| 14. Chaetognaths            | -        | 0.240 | -     | -     | -     | 0.040 | 0.010 | 0.020 | -     | 0.042 | 0.035 | 0.040 | 0.050 | -     | 0.140 | -     | -     | -     |
| 15. Amphipods               | -        | 0.050 | 0.063 | -     | -     | 0.300 | 0.050 | 0.160 | -     | 0.272 | 0.070 | 0.020 | 0.030 | 0.030 | 0.015 | -     | -     | -     |
| 16. Euphausiids             | -        | 0.210 | 0.325 | -     | -     | 0.220 | 0.300 | 0.330 | 0.010 | 0.445 | 0.600 | 0.100 | 0.090 | 0.040 | 0.020 | 0.005 | -     | -     |
| 17. Copepods                | -        | 0.280 | 0.138 | -     | -     | 0.110 | 0.306 | 0.440 | -     | 0.073 | 0.250 | 0.810 | 0.450 | 0.780 | 0.551 | 0.200 | 0.060 | -     |
| 18. Other zooplankton       | -        | 0.045 | -     | -     | -     | 0.090 | 0.004 | 0.010 | -     | -     | 0.005 | 0.010 | 0.020 | 0.010 | 0.030 | -     | -     | 0.050 |
| 19. Phytoplankton           | -        | -     | -     | -     | -     | -     | 0.330 | -     | -     | -     | -     | -     | 0.010 | -     | 0.054 | 0.645 | 0.820 | 0.700 |
| 20. Detritus                | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | 0.270 | 0.140 | 0.180 | 0.150 | 0.120 | 0.250 |

**Appendix Table 7.** Ecopath input parameters describing the 20 functional groups in the 2009 ecosystem model for the Pacific waters off the Kuril Islands. Biomass (*B*) is in t/km<sup>2</sup>, Production/Biomass (*P/B*) and Consumption/Biomass (*Q/B*) are rates (1/year).

| Species/group            | <i>B</i> | <i>P/B</i> | <i>Q/B</i> | <i>EE</i> |
|--------------------------|----------|------------|------------|-----------|
| Toothed whales           | 0.1370   | 0.03       | 3.3        |           |
| Baleen whales            | 0.0950   | 0.01       | 5.4        |           |
| Seabirds                 | 0.0020   | 0.4        | 43.5       |           |
| Daggertooth + Lancetfish | 0.0008   | 0.25       | 2.5        |           |
| Sharks                   | 0.0033   | 0.2        | 2          |           |
| Salmon                   | 0.4390   | 1.25       | 5.5        |           |
| Sardine                  | 0.0150   | 0.2        | 1.5        |           |
| Saury + Anchovy          | 0.4910   | 0.78       | 6.45       |           |
| Pomfret + Ribbonfish     | 0.0790   | 0.38       | 1.88       |           |
| Cephalopods              | 0.3956   | 1.6        | 5.35       |           |
| Mesopelagic fish         | 0.8540   | 0.475      | 1.75       |           |
| Forage fish              | –        | 1.25       | 6.5        | 0.95      |
| Jellyfish                | 0.6900   | 1.5        | 3          |           |
| Chaetognaths             | 10.6300  | 3          | 6          |           |
| Amphipods                | 1.7800   | 1.75       | 7          |           |
| Euphausiids              | 6.1500   | 1.55       | 8.5        |           |
| Copepods                 | 34.1600  | 4.75       | 13.1       |           |
| Other zooplankton        | 2.0500   | 2.5        | 7.5        |           |
| Phytoplankton            | 4.0000   | 117        |            |           |
| Detritus                 | 0.1000   |            |            |           |

**Appendix Table 8.** Diet matrix (proportion of prey for each predator) in the 2009 Ecopath model for the Pacific waters off the Kuril Islands.

| Prey                        | Predator |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|-----------------------------|----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                             | 1        | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    | 17    | 18    |
| 1. Toothed whales           | 0.001    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 2. Baleen whales            | 0.001    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 3. Seabirds                 | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 4. Daggertooth + Lancetfish | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 5. Sharks                   | -        | -     | -     | 0.001 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 6. Salmon                   | 0.006    | 0.001 | -     | 0.520 | 0.585 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 7. Sardine                  | 0.002    | 0.001 | 0.001 | -     | 0.011 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 8. Saury + Anchovy          | 0.135    | 0.002 | 0.061 | 0.080 | 0.128 | 0.002 | -     | -     | 0.170 | 0.005 | -     | -     | -     | -     | -     | -     | -     | -     |
| 9. Pomfret + Ribbonfish     | 0.011    | -     | -     | 0.010 | 0.032 | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 10. Cephalopods             | 0.558    | 0.050 | 0.063 | 0.070 | 0.213 | 0.060 | -     | -     | 0.360 | 0.050 | 0.003 | -     | -     | -     | -     | -     | -     | -     |
| 11. Mesopelagic fish        | 0.230    | 0.070 | -     | 0.050 | -     | 0.050 | -     | -     | 0.350 | 0.030 | -     | -     | 0.010 | -     | -     | -     | -     | -     |
| 12. Forage fish             | 0.057    | 0.050 | 0.304 | 0.269 | 0.032 | 0.010 | -     | -     | -     | 0.005 | -     | -     | -     | -     | -     | -     | -     | -     |
| 13. Jellyfish               | -        | -     | 0.038 | -     | -     | 0.178 | -     | 0.010 | -     | -     | -     | -     | 0.070 | -     | 0.010 | -     | -     | -     |
| 14. Chaetognaths            | -        | 0.240 | -     | -     | -     | 0.120 | 0.010 | 0.020 | -     | 0.081 | 0.010 | 0.090 | 0.050 | -     | 0.140 | -     | -     | -     |
| 15. Amphipods               | -        | 0.050 | 0.063 | -     | -     | 0.060 | 0.050 | 0.110 | -     | 0.126 | 0.040 | 0.010 | 0.010 | 0.030 | 0.015 | -     | -     | -     |
| 16. Euphausiids             | -        | 0.210 | 0.330 | -     | -     | 0.210 | 0.300 | 0.510 | 0.100 | 0.388 | 0.480 | 0.210 | 0.090 | 0.040 | 0.020 | 0.005 | -     | -     |
| 17. Copepods                | -        | 0.280 | 0.139 | -     | -     | 0.260 | 0.306 | 0.330 | 0.020 | 0.315 | 0.465 | 0.670 | 0.470 | 0.780 | 0.551 | 0.200 | 0.060 | -     |
| 18. Other zooplankton       | -        | 0.045 | -     | -     | -     | 0.050 | 0.004 | 0.020 | -     | -     | 0.002 | 0.010 | 0.020 | 0.010 | 0.030 | -     | -     | 0.050 |
| 19. Phytoplankton           | -        | -     | -     | -     | -     | -     | 0.330 | -     | -     | -     | -     | 0.010 | 0.010 | -     | 0.054 | 0.645 | 0.820 | 0.700 |
| 20. Detritus                | -        | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | 0.270 | 0.140 | 0.180 | 0.150 | 0.120 | 0.250 |