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# Forage Base of Pacific Salmon in the Western Bering Sea and Adjacent Pacific Waters in 2002-2006

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Abstract: The objective of this study was to estimate the total relative biomass of the forage base (zooplankton + nekton) of Pacific salmon (*Oncorhynchus* spp.) in the upper epipelagic zone of the western Bering Sea and adjacent Pacific waters in summer and fall 2002–2006. Zooplankton biomass was estimated from plankton survey data, and nekton biomass was estimated from salmon diet data using a mathematical model of selective feeding. In 2002–2006, estimated total relative biomass of the salmon forage base varied from 690–1590 mg/m$^3$. Biomass was lowest in fall 2004, and was highest in fall 2002. Copepods and chaetognaths dominated the potential forage base. Squids and fishes were 15–22% (average 19%) of the overall biomass. The biomass of fish was highest in the continental shelf area (Anadyr Bay). Squids were more abundant in deep-water regions of the Bering Sea and adjacent Pacific waters. Walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and Pacific sand lance *Ammodytes hexapterus* were the dominant nekton species in the northwestern shelf region. Shortarm gonate squid *Gonatus kamtschaticus*, boreopacific gonate squid *Gonatopsis borealis*, Atka mackerel *Pleurogrammus monopterygius*, and myctophids were prevalent items in the salmon forage base in deep-water areas. In general, the results indicated that immature salmon in both summer and fall were concentrated within deep-water regions of the western Bering Sea, where their forage (overall and preferred prey items) was also concentrated, and were much less numerous in the Pacific waters off the Commander Islands and in the western Bering Sea shelf zone, where their forage was less concentrated.

Keywords: micronekton, plankton, forage base, model of selective feeding, Pacific salmon, Bering Sea

## INTRODUCTION

Estimation of salmon prey abundance is an important objective of research for understanding how ocean conditions affect the marine survival and production of Pacific salmon. As a rule, researchers use plankton sampling to estimate the Pacific salmon forage base. However not only plankton, but also micronekton, constitute a significant part of Pacific salmon diets. Small nekton species dominate chinook and coho salmon diets, and are important in sockeye, chum, and pink salmon diets, especially for adult fish (Andrievskaya 1966; Pearcy et al. 1988; Volkov et al. 1997; Davis et al. 2000; Kaeriyama et al. 2000; Chuchukalo 2006; Karpenko et al. 2007; and many others).

Total estimation of the abundance of the forage base of fish can be performed using several types of gear. Small plankton species are caught by relatively small nets whereas micronekton species are caught with either larger nets or small trawls (see, e.g., Viitasalo et al. 2001; Schabetsberger et al. 2003). However in this case researchers need to use compensatory coefficients for combining the data from different types of gear. In our work, we used a standard approach (plankton net) for zooplankton sampling combined with a mathematical model of fish selective feeding for estimating small-size nekton species biomass.

The purpose of this work was the assessment of the overall salmon forage base using data from plankton sampling and modeled estimates of micronekton (small-size fishes and squids) biomass. The composition of the Pacific salmon forage base and its year-to-year variability and spatial distribution are described.

## MATERIALS AND METHODS

### Study Area

The study was based on data collected as part of the Bering-Aleutian Salmon International Survey (BASIS) by TINRO-Centre in the upper epipelagic zone of the western Bering Sea and adjacent Pacific waters. Surveys were conducted in September–October 2002, July–August and September–October 2003, September–October 2004, June–July 2005, and August–October 2006. The study area included four large districts (Fig. 1). One district was located primarily in the shelf zone (Anadyr Bay and adjacent waters), and other districts were located in deep-water areas of

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the Bering Sea and in adjacent Pacific waters (Commander Basin, western Aleutian Basin, and Pacific waters).

## Forage Base Estimation

The forage base was defined as all plankton and nekton species that are prey of Pacific salmon. The Pacific salmon forage base included two parts: zooplankton and small-size nekton species (micronekton) with body lengths that do not exceed 15 cm.

### *Zooplankton data*

The published data of A.F. Volkov (Volkov et al. 2007) were used to describe the plankton component of the Pacific salmon forage base in the western Bering Sea in summer and fall of 2002–2006. Plankton were sampled and analysed by a unified approach, accepted at the TINRO-Centre (Volkov 1996). Zooplankton samples were obtained with a Juday net (0.1 m$^2$ mouth opening; 0.168-mm mesh net). The Juday net was towed in the upper 50 m of the water column. Because Pacific salmon ingested primarily large zooplankton prey (> 3 mm), zooplankton biomass was evaluated only for items > 3 mm. The total number of plankton stations sampled is shown in Table 1.

### *Micronekton data*

That Pacific salmon have high trophic plasticity is well known (Andrievskaya 1966; Pearcy et al. 1988; Volkov et al. 1997; Davis et al. 2000; Kaeriyama et al. 2000; Efimkin 2003; Temnykh et al. 2004; Kuznetsova 2005; Chuchukalo 2006; Karpenko et al. 2007; Naydenko et al. 2007; and others). Their ration composition changes depending on the forage base. Therefore, the relative biomass of the unknown components of the Pacific salmon forage base can be estimated using data on their diets.

This task was accomplished by a mathematical model of selective feeding. Firstly, this model included trophological circulation from Krogius et al. (1969):

$$q_i = \varepsilon_i p_i \Big/ \sum\nolimits_{j=1}^{n} \varepsilon_j p_j \ , \ i = 1,...,n, \qquad (1)$$

where $q_i$, is the fraction of i-th food species in the predator's ration, $p_i$ is the fraction of the same species in the total biomass of forage base, and $\varepsilon_i$ represents feeding electivities. Values $q_i$, $p_i$, $\varepsilon_i$ are probabilities (fractions), so the sum over all i = 1,…, n foraging objects must be equal to 1 for every one of these variables.

Numerical values of electivities $\varepsilon_i$ can be obtained by solving the next system of *n* linear equations (Sukhanov 1988):

$$\left.\begin{array}{l}
\varepsilon_1 + \varepsilon_2 + ... + \varepsilon_{n-1} + \varepsilon_n = 1 \\
q_2 p_1 \varepsilon_1 + (q_2 - 1) p_2 \varepsilon_2 + ... + q_2 p_{n-1} \varepsilon_{n-1} + q_2 p_n \varepsilon_n = 0 \\
q_3 p_1 \varepsilon_1 + q_3 p_2 \varepsilon_2 + (q_3 - 1) p_3 \varepsilon_3 + ... + q_3 p_{n-1} \varepsilon_{n-1} + q_3 p_n \varepsilon_n = 0 \\
\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots \\
q_n p_1 \varepsilon_1 + q_n p_2 \varepsilon_2 + ... + q_n p_{n-1} \varepsilon_{n-1} + (q_n - 1) p_n \varepsilon_n = 0
\end{array}\right\} (2)$$

If some *j*-th food species were not caught by gear and therefore not included in the forage base, but it was considered prey, then not only electivities $\varepsilon_1$ , $\varepsilon_2$ , …, $\varepsilon_n$ but also fractions of this food species in the total biomass of forage base ($p_j$) must be estimated. So the model (1) becomes nonlinear. Parameter estimation needs to be performed not by solving system equation (2), but by using a special gradient algorithm, that fits model (1) into our data. To accomplish this, the Marquardt method was used (Bard 1979). To uphold the restrictions for model parameters (it must be in the range of 0 and 1), a penalty function (Bunday 1984) was added to the model algorithm. The program for parameter estimation was performed using the algorithmic language TMT-Pascal 3.90.

The algorithm scheme of the model used to evaluate the unknown components of the Pacific salmon forage base is shown in Fig. 2. Input data for this model are the Pacific

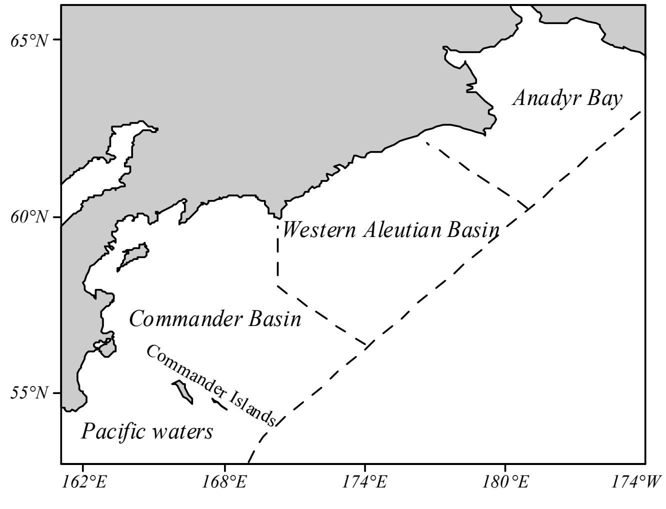

**Fig. 1.** Map of the study area for planktonic and trophological samples.

**Table 1.** Survey date (day.month.year) and total number of plankton stations and analyzed stomachs of Pacific salmon.

| Survey date | Total number of | |
|---|---|---|
| | Plankton stations | Analyzed stomachs |
| Aug 31 – Oct 9, 2002 | 82 | 1,721 |
| July 15 – Aug 24, 2003 | 86 | 2,816 |
| Sep 14 – Oct 25, 2003 | 86 | 2,545 |
| Sep 11 – Oct 23, 2004 | 70 | 3,121 |
| June 17 – July 21, 2005 | 93 | 2,341 |
| Aug 24 – Oct 12, 2006 | 110 | 4,109 |

salmon feeding spectra, zooplankton species composition, and the initial values of parameters. The base of the program includes a model of fish selective feeding, a restriction procedure, and an algorithm that fits parameters by the Marquardt method. Output data are the feeding electivities and the required fractions of small fishes and squids in the total biomass of the forage base. For more detailed information see Sukhanov and Zavolokin (2006).

Table 2 shows an example of input data for the estimation of unknown fractions of small-size fishes and squids. It includes feeding habits of five predators $q_i$ (pink, chum, sockeye, coho, and chinook salmon) and zooplankton species composition $p_i$. Initial values of electivities are calculated based on feeding spectra and zooplankton data using equation (1). Each unknown fraction (fish larvae $p_1$, Pacific sand lance $p_2$ and squid larvae $p_3$) in the total biomass of the forage base was assigned an initial value of 0.05.

Estimated fractions (mean ± standard error) of small-size nekton in the total biomass of the Pacific salmon forage base were: $p_1 = 0.099 \pm 0.018$, $p_2 = 0.076 \pm 0.018$ and $p_3 = 0.033 \pm 0.017$. Based on the biomass of the planktonic component of the salmon forage base (1,424 mg/m$^3$ – Table 2) and estimated values of parameters, the relative biomass of each unknown component of the Pacific salmon forage base was calculated.

Stomach contents that were used for modeled estimates of micronekton biomass were analyzed aboard the vessel using the method described by Chuchukalo and Volkov (1986). Stomachs were removed from up to 25 fish of each size-class (10–30, 31–40, 41–50, 51–60 cm) at each station. Stomach contents of each size-class of fish were mixed and weighed. Prey composition was determined to the lowest possible taxonomic category and the percentage of each prey item was estimated visually. The total number of stations and stomachs analyzed is shown in Table 1.

## RESULTS AND DISCUSSION

### Pacific Salmon Forage Base Composition

Zooplankton dominated the Pacific salmon forage base in the western Bering Sea (Fig. 3). Micronekton were approximately 20% of the forage base. In the northwestern shelf region, the majority of micronekton consisted of small-size fishes. In the deep-water areas, the percentages of fishes and squids were approximately equal.

In the shelf region, the plankton component of the Pacific salmon forage base was dominated by copepods (mainly *Calanus glacialis*) and chaetognaths (Fig. 3). Furthermore, the fraction of euphausiids (mainly *Thysanoessa inermis* and

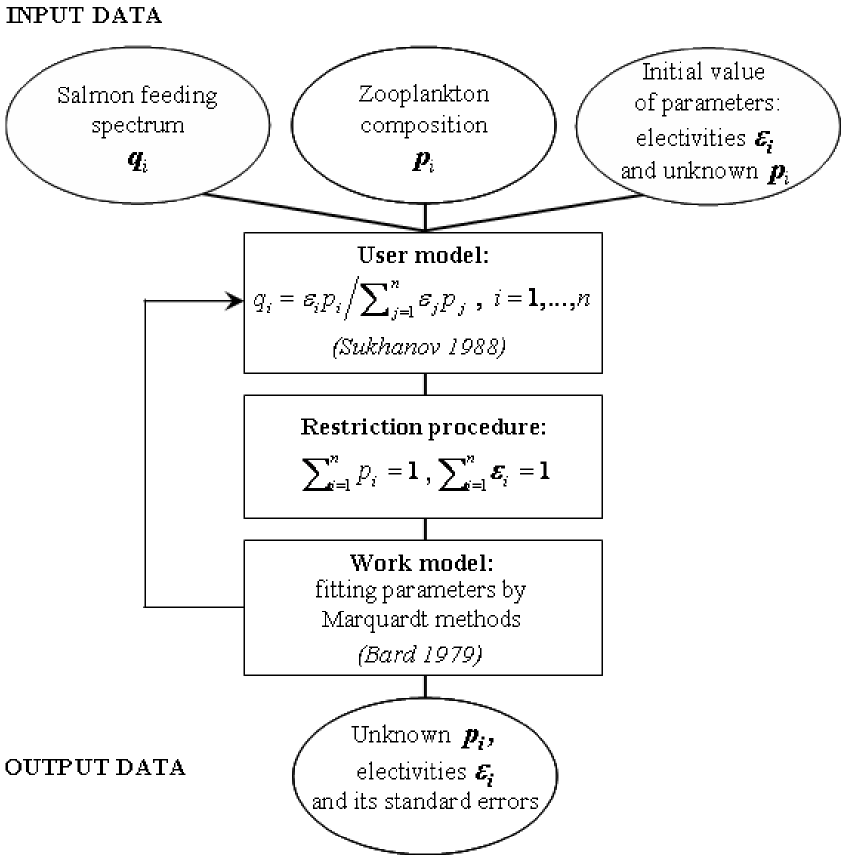

**Fig. 2.** Scheme of the model used to estimate the fraction of squid and fish from the total zooplankton biomass.

**Table 2.** Feeding habits of Pacific salmon of size group 10-30 cm and zooplankton composition in the deep-water basins of the western Bering Sea in fall 2002.

| Species | Pink | Chum | Sockeye | Coho | Chinook | Plankton |
|---|---|---|---|---|---|---|
| **Copepods** | | | | | | |
| *Neocalanus plumchrus* | 0.120 | 0.084 | 0.073 | - | - | 0.493 |
| *N. cristatus* | 0.005 | 0.013 | 0.085 | - | - | 0.010 |
| *Eucalanus bungii* | - | - | - | - | - | 0.025 |
| **Euphausiids** | | | | | | |
| *Thysanoessa longipes* | 0.377 | 0.166 | 0.428 | - | - | 0.041 |
| **Amphipods** | | | | | | |
| *Themisto pacifica* | 0.438 | 0.574 | 0.186 | 0.002 | - | 0.008 |
| *Primno macropa* | 0.018 | 0.014 | 0.006 | - | - | 0.001 |
| **Decapods** | | | | | | |
| Zoea | - | 0.010 | 0.042 | - | - | 0.001 |
| Megalopa | 0.017 | 0.002 | 0.009 | 0.030 | 0.010 | 0.001 |
| **Chaetognaths** | 0.024 | 0.116 | 0.171 | - | - | 0.420 |
| **Fishes** | | | | | | |
| Larvae | - | 0.004 | - | 0.870 | 0.698 | - |
| *Ammodytes hexapterus* | - | 0.017 | - | 0.092 | 0.284 | - |
| **Squid larvae** | 0.001 | - | - | 0.006 | 0.008 | - |
| **Total zooplankton biomass, mg/m$^3$** | | | | | | 1424 |

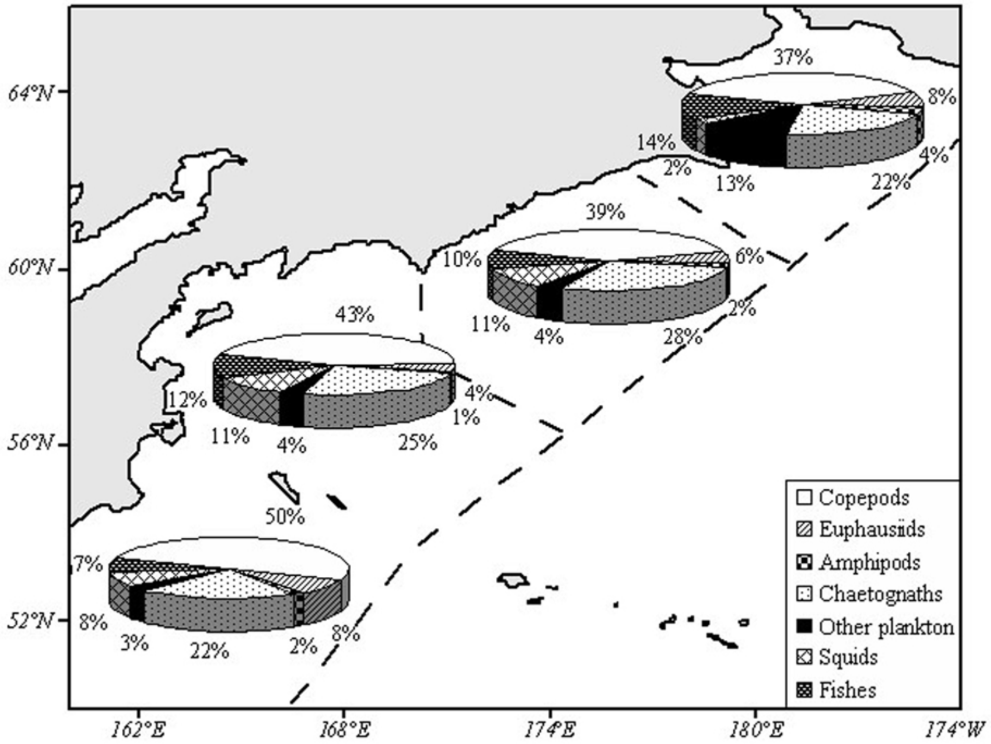

**Fig. 3.** Salmon forage base composition in the western Bering Sea and adjacent Pacific waters in 2002–2006.

*Th. raschii*) was relatively high. The dominant species of the nekton component of the Pacific salmon forage base were walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and Pacific sand lance *Ammodytes hexapterus*. The percentage of fish larvae was substantial as well.

Within the deep-water regions, most of the plankton component of the Pacific salmon forage base consisted of copepods (mainly *Neocalanus plumchrus*) and chaetognaths (Fig. 3). The fraction of euphausiids in deep-water regions was lower than that in the shelf region. The prevalent species of euphausiid was *Thysanoessa longipes*. The nekton component of the Pacific salmon forage base was dominated by two species of gonatid squids (boreopacific gonate squid *Gonatopsis borealis* and shortarm gonate squid *Gonatus kamtschaticus*), small mesopelagic fishes (primarily, northern lampfish *Stenobrachius leucopsarus*), and juvenile Atka mackerel *Pleurogrammus monopterygius*.

The percentage of the most preferred prey items of Pacific salmon such as amphipods and pteropods was very low. In 2002–2006, they contributed about 3.5% and 1.1% of the total forage base in Anadyr Bay and deep-water regions, respectively.

## Inter-annual dynamic of Pacific Salmon Forage Base

The cumulative values for relative biomass estimates of the components of the Pacific salmon forage base varied greatly from year to year. In the shelf region, these values were highest (1,380 mg/m$^3$) in 2002 and lowest in 2003 and 2004 (440–520 mg/m$^3$) (Fig. 4a). Inter-annual dynamics of the cumulative values of the relative biomass of plankton species exhibited a similar pattern (Fig. 4b). Fish biomass was relatively stable and varied from 70 to 120 mg/m$^3$, except for 2006 (Fig. 4c). Relative biomass values for squid were very low in the shelf region, particularly in fall. Squid were abundant only in summer 2003 (Fig. 4d).

Within deep-water regions, cumulative values for relative biomass estimates of the Pacific salmon forage base were highest in summer of 2003 (1,600 mg/m$^3$) and lowest in fall of 2004 (600 mg/m$^3$) (Fig. 5a). Dynamics of the cumulative values of relative abundance estimates of zooplankton were similar to those of the entire forage base of Pacific salmon (Fig. 5b). Fish biomass varied greatly from 40 mg/m$^3$ in fall 2004 up to 190 mg/m$^3$ in fall 2002 (Fig. 5c). Squid biomass was more stable (90–140 mg/m$^3$), and did not vary substantially during these years (Fig. 5d).

In 2002–2006, relative biomass of the preferred prey of Pacific salmon (amphipods, pteropods, euphausiids, small-size fishes and squids) varied from 130–300 mg/m$^3$ in Anadyr Bay (Fig. 4e) and from 220–430 mg/m$^3$ in the basins and Pacific waters (Fig. 5e). In the shelf region, relative biomass of the preferred prey was lowest in fall 2004 and summer 2005 and the highest in fall 2006. In the deep-water regions, minimum relative biomass of the preferred prey of Pacific salmon occurred in fall 2004, and maximum relative

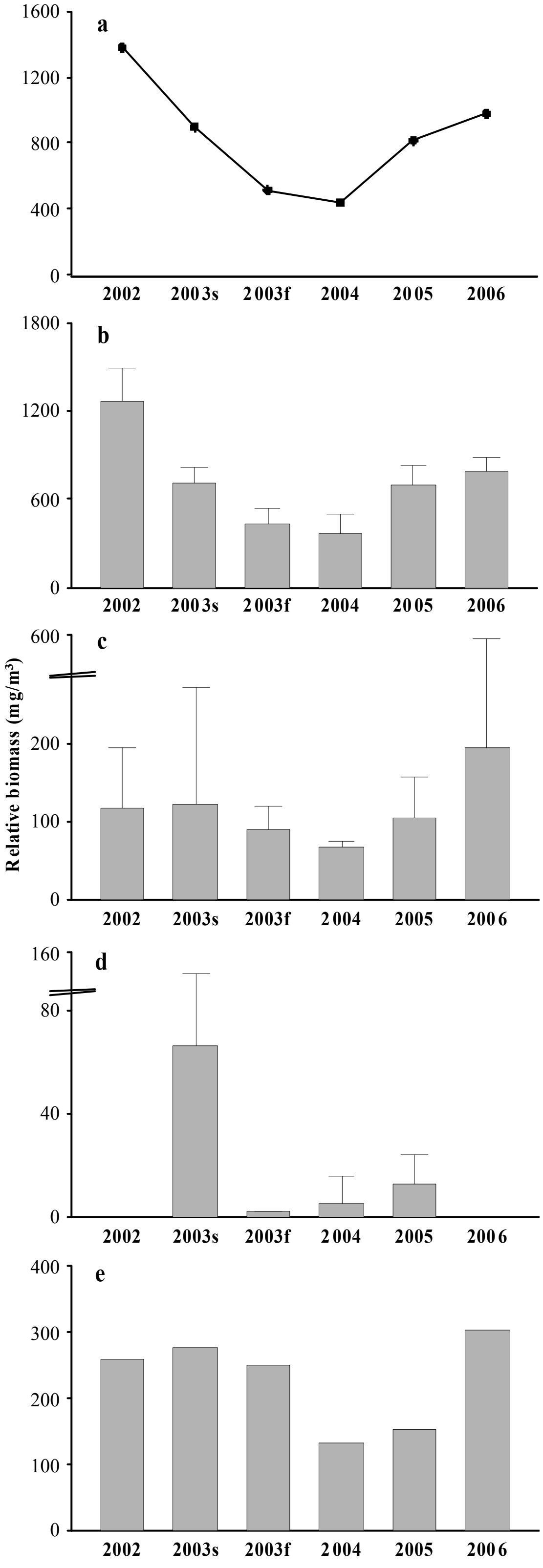

**Fig. 4.** Trends in relative biomass (mg/m$^3$) of the Pacific salmon forage base in Anadyr Bay in 2002-2006. a = Total forage base, b = zooplankton, c = fishes, d = squids, e = preferred salmon prey (amphipods, euphausiids, pteropods, micronekton), 2003s = summer 2003, 2003f = fall 2003.

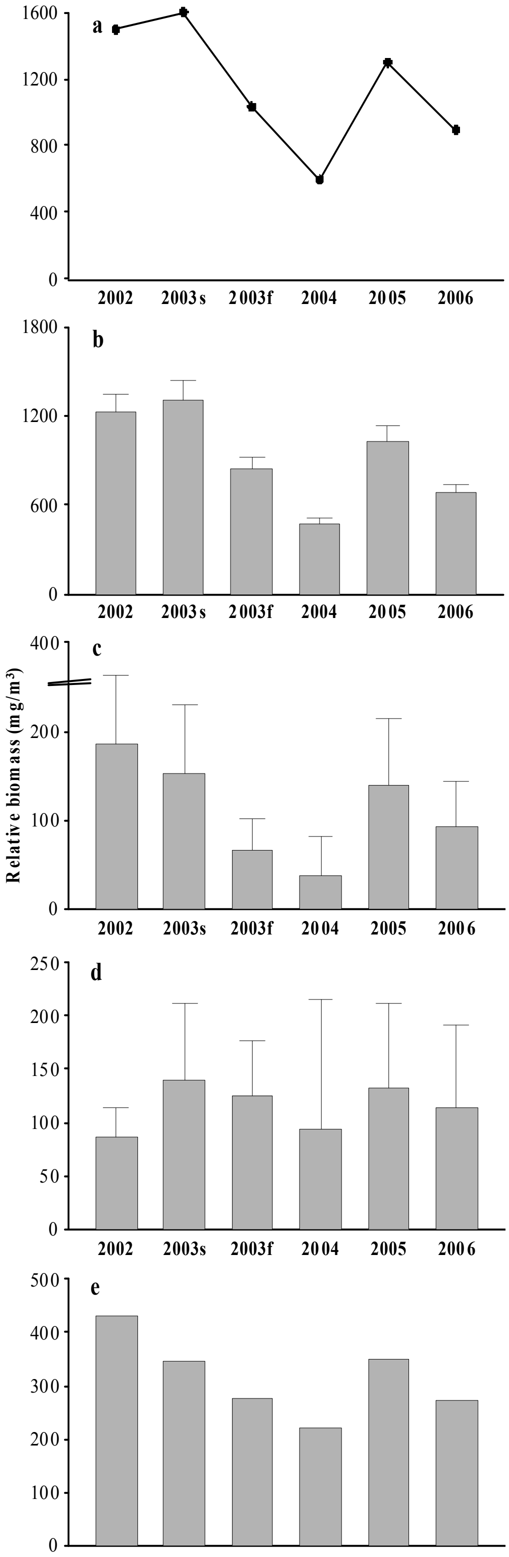

**Fig. 5.** Trends in relative biomass (mg/m$^3$) of the Pacific salmon forage base in deep-water regions of the western Bering Sea and adjacent Pacific waters in 2002-2006. a = Total forage base, b = zooplankton, c = fishes, d = squids, e = preferred salmon prey (amphipods, euphausiids, pteropods, micronekton), 2003s = summer 2003, 2003f = fall 2003.

biomass was in fall 2002.

## Spatial Distribution of Pacific Salmon Forage Base Relative Biomass

The highest concentrations of zooplankton were confined mainly to the deep-water regions – the Commander and Aleutian basins. Zooplankton relative biomass estimates were slightly lower in the Pacific waters and Anadyr Bay (Table 3).

Small-size fishes were located primarily within the Commander Basin area. Furthermore, their relatively high concentrations were observed in the north-western shelf and in the Aleutian Basin. Small-size squids were abundant only in the deep-water basins and Pacific waters. In the shelf zone they were rare (Table 3).

For the entire forage base biomass, the maximum values were in the Commander and Aleutian basins and the minimum values were in Anadyr Bay. That the preferred prey items of Pacific salmon showed a similar pattern of distribution is interesting to note. Their relative biomass estimates were highest in the deep-water regions of the Bering Sea (Table 3).

High concentrations of the Pacific salmon forage base (overall and preferred prey items) in the basin areas may be the cause of observed distributions of immature Pacific salmon, that is, in both summer and fall immature Pacific salmon were concentrated primarily within deep-water regions of the western Bering Sea, and were much less numerous in the Pacific waters off the Commander Islands and in the shelf zone (Fig. 6).

## CONCLUSION

In 2002–2006, cumulative values for relative biomass estimates of the Pacific salmon forage base varied significantly (from 600 to 1,600 mg/m$^3$ in deep-water regions and from 400–1400 mg/m$^3$ in the shelf zone). Relative biomass estimates were the lowest during fall 2004 and the highest in fall 2002 and summer 2003.

The highest cumulative values for relative biomass estimates of the Pacific salmon forage base were observed in the Commander and Aleutian basins of the western Bering Sea. This result provides evidence that deep-basin areas are the most favorable for Pacific salmon feeding. The lowest relative biomass estimates of the forage base were in the shelf region.

The potential forage base of Pacific salmon was dominated by planktonic organisms (copepods, chaetognaths, and euphausiids). The fraction of micronekton comprised about 20% of the potential forage base. In the shelf zone (Anadyr Bay) prevalent micronekton species were walleye pollock, capelin, Pacific sand lance, and fish larvae. Within the deep-water regions, the micronekton community was dominated by gonatid squids, small mesopelagic fishes, and juvenile

**Table 3.** Relative biomass (mg/m$^3$) of the Pacific salmon forage base in the western Bering Sea and adjacent North Pacific waters in 2002-2006. Mean values and standard errors are shown. Preferred prey include amphipods, pteropods, euphausiids, small-size fishes and squids.

| Group | Pacific waters | Commander Basin | Aleutian Basin | Anadyr Bay |
|---|---|---|---|---|
| Zooplankton | 897±144 | 986±160 | 892±125 | 708±130 |
| Fish | 75±18 | 152±27 | 111±40 | 115±18 |
| Squid | 83±13 | 143±33 | 119±28 | 14±11 |
| Preferred prey | 268±74 | 370±39 | 325±49 | 231±25 |
| Overall | 1,055±153 | 1,281±197 | 1,122±170 | 837±139 |

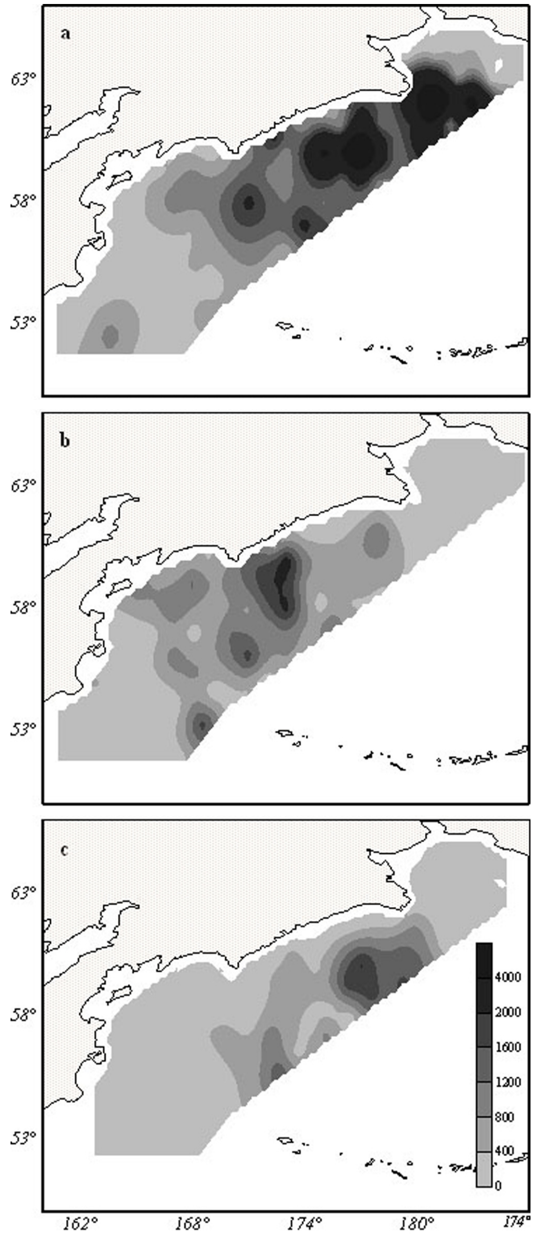

**Fig. 6.** Spatial distribution of immature Pacific salmon relative abundance (number of fish/km$^2$) in the western Bering Sea and adjacent Pacific waters in July-August 2003 (a), September-October 2003 (b), and June-July 2005 (c).

Atka mackerel.

The method used for estimation of small-size nekton biomass has some restrictions. Firstly, estimated values rely on the planktonic component of the forage base. Therefore, inaccuracies and uncertainties in plankton sampling, processing and calculating may affect micronekton biomass estimates. Secondly, this method requires data on feeding habits for all large predatory fish in the epipelagic ecosystem. Further, it is important to note that feeding habits of fish used for estimation of small-size nekton biomass must differ. The more the feeding spectra of predators differ, the higher the accuracy of estimates.

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## REFERENCES

Andriyevskaya, L.D. 1966. Food relations of Pacific salmon in the sea. Vopr. Ichthiologii 6: 84–90. (In Russian).

Bunday, B.D. 1984. Basic optimisation methods. Edward Arnold, London. 128 pp.

Bard, Y. 1979. Nonlinear parameter estimation. Moscow: Statistica. 349 pp. (In Russian).

Chuchukalo, V.I. 2006. Feeding and trophic relationships of nekton and nektobenthos in the Far Eastern Seas. TINRO-Centre, Vladivostok. 511 pp. (In Russian).

Chuchukalo, V.I., and A.F. Volkov. 1986. Guide book of fish feeding study. TINRO, Vladivostok. 32 pp. (In Russian).

Davis, N.D., K.Y. Aydin, and Y. Ishida. 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the Central Bering Sea in summer. N. Pac. Anadr. Fish Comm. Bull. 2: 99-109. (Available at www.npafc.org).

Efimkin, A.Y. 2003. Salmons feeding in the western Bering Sea in summer-fall of 2002. Izv. TINRO 134: 120–134. (In Russian with English abstract).

Kaeriyama, M., M. Nakamura, M. Yamaguchi, H. Ueda, G. Anma, S. Takagi, K.Y. Aydin, R.V. Walker, and K.W.

Myers. 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. N. Pac. Anadr. Fish Comm. Bull. 2: 55-63. (Available at www.npafc.org).

Karpenko, V.I., A.F. Volkov, and M.V. Koval. 2007. Diets of Pacific salmon in the Sea of Okhotsk, Bering Sea, and Northwest Pacific Ocean. N. Pac. Anadr. Fish Comm. Bull. 4: 105–116. (Available at www.npafc.org).

Krogius, F.V., E.M. Krokhin, and B.B. Menshutkin. 1969. Community of pelagic fish of lake Dalnee. Experience of cybernetic modeling. Nauka, Leningrad. 87 pp. (In Russian).

Kuznetsova, N.A. 2005. Feeding and trophic relationships of epipelagic nekton in the north Okhotsk Sea. TINRO-Centre, Vladivistok. 236 pp. (In Russian).

Naydenko, S.V., A.Y. Efimkin, and A.E. Lazhentsev. 2007. Regional diversity of juvenile pink salmon diet in autumn in the Bering, Okhotsk and Japan seas. N. Pac. Anadr. Fish Comm. Bull. 4: 117-126. (Available at www.npafc.org).

Pearcy, W.G., R.D. Brodeur, J. Shenker, W. Smoker, and Y. Endo. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches, and oceanographic conditions in the Gulf of Alaska, 1980–1985. Bull. Ocean Res. Inst. 26: 29–78.

Schabetsberger, R., C.A. Morgan, R.D. Brodeur, C.L. Potts, W.T. Peterson, and R.L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fish. Oceanogr. 12: 523–540.

Sukhanov, V.V. 1988. Modeling of stationary polyphagy. Vopr. Ichthiologii 28: 790–801. (In Russian).

Sukhanov, V.V., and A.V. Zavolokin. 2006. Assessment of fish feeding selectivity parameters in the case of incomplete data. J. Ichthyol. 46(9): 815–818.

Temnykh, O.S., I.I. Glebov, S.V. Naydenko, A.N. Starovoitov, A.Y. Efimkin, V.V. Sviridov, O.A. Rassadnikov, and N.A. Kuznetsova. 2004. Contemporary status of Pacific salmon in the pelagic communities of the Far Eastern Seas. Izv. TINRO 137: 28–44. (In Russian with English abstract).

Viitasalo, M., J. Flinkman, and M. Viherluoto. 2001. Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Mar. Ecol. Prog. Ser. 216: 191–200.

Volkov, A.F. 1996. Zooplankton in the epipelagic zone of the Far Eastern Seas: composition, inter-annual dynamic, role in nekton feeding. TINRO-Centre, Vladivistok. 70 pp. (In Russian).

Volkov, A.F., A.Y. Efimkin, and N.A. Kuznetsova. 2007. Plankton communities in the Bering Sea and some areas of the North Pacific in 2002-2006. Izv. TINRO 151: 338–364. (In Russian with English abstract).

Volkov, A.F., A.Y. Efimkin, and V.I. Chuchukalo. 1997. Regional features of Pacific salmon feeding in summer. Izv. TINRO 122: 324–341. (In Russian).