FORAGE BASE AND FEEDING OF THE SEA OF OKHOTSK PINK SALMON *ONCORHYNCHUS GORBUSCHA* (SALMONIDAE) DURING MARINE MIGRATIONS IN THE SEA OF OKHOTSK AND ADJACENT WATERS OF THE PACIFIC OCEAN

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The forage base of the pink salmon *Oncorhynchus gorbuscha* during its marine migrations in the Sea of Okhotsk (August−December) is sufficient for feeding and migration of juveniles of this species despite significant changes. According to long-term data, the daily ration of juvenile Sea of Okhotsk pink salmon was 7−10 in summer and 4.0−4.5% of the body weight in autumn. At the beginning of the winter period, in December, the biomass of forage plankton in the epipelagic zone in the Sea of Okhotsk and northwestern Pacific waters off the Kuril Islands decreased by an average of 1.5 times, in the upper epipelagic zone, by more than two times. However, the feeding intensity of juvenile pink salmon decreased slightly in December compared to October–November, mainly due to large interzonal copepods (Copepoda) due to their seasonal migrations to the mesopelagic zone for wintering. The minimal biomass of forage plankton (on average 204.1 mg/m^3) and low feeding intensity of pink salmon (daily ration of 3.1%) were observed during the typical winter period, in January. In late February-early April (winter-spring period in most of the studied water area), large interzonal copepods migrate to the epipelagial after wintering, their proportion of the forage plankton was 48.9%, as a result, the average biomass of the latter increased more than twice (up to 459.4 mg/m^3). The feeding intensity of pink salmon also increased (daily ration 3.6%). During spring and summer periods, the biomass of forage plankton in the epipelagial increased significantly to 718.7 and 820.2 mg/m^3, respectively. Pink salmon fed

intensively before the beginning of pre-spawning migrations. In July, despite a favorable forage base, the feeding intensity of migrating pre-spawning pink salmon was minimal: in open waters the daily diet was 3%, closer to the coast, 1−2%.
Keywords: pink salmon, forage base, feeding, Sea of Okhotsk, Northwest Pacific Ocean.

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INTRODUCTION

The ecological role of Pacific salmon (*Oncorhynchus*) is variable, as they transfer energy directly or indirectly at various trophic levels in several ecosystems (freshwater, estuarine, marine, oceanic). Changes in climatic conditions during the salmon life cycle can affect the quantity and quality of downstream juveniles, their survival and development in marine conditions, as well as fish distribution, abundance, growth rates, and food supply at different stages of ontogenesis (Shuntov, Temnykh 2008). Shuntov and Temnykh (2011) indicated that in both seas and oceans, the quantitative and qualitative characteristics of the food supply largely depend on the hydrological background and the intensity of water dynamics. Therefore, to predict the determining catch of Pacific salmon returning to spawning grounds, it is necessary to consider, along with the food supply, changes in oceanological conditions in various biotopes (areas) during marine migrations, which ultimately determine the size and mass characteristics of salmon at different stages of the marine period of life.

Size and weight of juvenile pink salmon *O. gorbuscha* by the end of the marine life period (November-December), at first glance, should determine the success of further migrations (mortality rate) in Pacific waters and the number of fish returning to spawning grounds, that is, serve as a starting point for forecasting the return and catch of pre-spawning individuals of this species. Many authors agree with this concept (Parker, 1971; Willette et al., 1999 ; Beamish, Mahnken, 2001) , with some of them directly linking mortality rates to the size of individuals by the end of the marine life period, before migration to Pacific waters (Pearcy, 1992). However, other researchers (Shuntov, Temnykh, 2008, 2011; Naidenko, Temnykh, 2016) believe that the size of juvenile pink salmon cannot always be used as an indicator of its subsequent returns, as fish survival during the marine life period depends on both the starting conditions during downstream migration and the prevailing conditions in the sea in autumn and in Pacific waters in winter. That is, one factor should not be considered as strictly limiting the pink salmon abundance during the winter period. Probably, the complex impact of biotic and abiotic factors can influence the species survival in the ocean to varying degrees.

The aim of this work is to summarize materials on the composition and abundance of plankton, as well as on the feeding of the Sea of Okhotsk pink salmon throughout its marine life cycle, to identify the complex impact of various factors on pink salmon survival, and based on data on size and weight indicators of fish, to assess their growth during the summer-autumn period in the Sea of Okhotsk and winter-spring and summer periods in the northwestern Pacific Ocean (NWPO).

MATERIAL AND METHODOLOGY

The work was carried out within the framework of the ecosystem research section on biological resources of the Far Eastern seas according to the TINRO thematic plan, and it is based on information obtained during comprehensive expedition macro-surveys. Data for the winter-spring months in the western part of the Subarctic Front are presented based on the results of surveys conducted in December 2021, January 2019, and February-May 2009-2011 (Fig. 1). The work was carried out in various water masses - transformed subarctic, mixing zone, and subtropical. When calculating, data on net plankton in subarctic waters and the mixing zone showed similar values, so they were combined. Summer expeditions (June-July) in Pacific waters near the Kuril Islands and autumn work in the Sea of Okhotsk (October-November) are standardized, performed annually, and station schemes are provided in the cited works (Shuntov, Temnykh, 2008, 2011).

During all expeditions, a standard set of work was performed: trawl macro-surveys, during which the composition and biomass of nekton and large jellyfish were recorded, and hydrobiological stations where data were collected on the composition and quantitative distribution of net plankton and nekton feeding, as well as biostatistical materials characterizing the state and size-age structure of hydrobionts.

Plankton was caught in the 0-200 m layer (0 - bottom at depths less than 200 m) with large Juday nets (entrance area 0.1 m^2, sieve with 0.15 mm mesh) and processed according to a unified methodology adopted at TINRO, with corrections for undercatch (Volkov, 2008). The sampled horizon of 200-0 m was chosen due to the fact that pink salmon individuals in the late autumn and winter-spring periods make vertical migrations in the layer up to 150 m (Shuntov, Temnykh, 2008, 2011).

To assess the food supply in 2009-2011, 2019, and 2021, 448 plankton samples from the Sea of Okhotsk were processed, including 298 samples in autumn (October-November) and 21 samples in winter (December). From the Northwestern Pacific Ocean, 491 samples were processed, including 179 in winter and early spring (December-March), 46 in spring (April-May), and 266 in summer (June-July).

To study the diet of pink salmon, 1328 samples were taken (10254 pink salmon stomachs examined), including 540 samples (3467 stomachs) in the Sea of Okhotsk and 788 samples (6787 stomachs) in the Northwestern Pacific Ocean. Processing of gastrointestinal tracts was carried out in accordance with standard methods adopted at TINRO (Manual for the study..., 1986). Due to the fact that it is not possible to accurately differentiate fish by their belonging to regional stocks, the material was mainly analyzed by average Smith length (*FL*) and body weight of pink salmon at different periods of its life cycle.

The daily ration (DR) of pink salmon of each size group was calculated separately according to generally accepted methods of Yurovitsky (1962) and Kogan (1969), which were applied depending on the observed daily feeding rhythm (Chuchukalo, 2006; Gorbatenko, 2018). Since the diet of pink salmon contained planktonic and nektonic organisms with a wide spectrum of digestibility, we applied a modified Yurovitsky method (1962) for fish of each size group, and the daily ration was calculated as follows: $DR = 2(Pl_{max1} + Pl_{max2}) + fish + squid$, where Pl_{max1} and Pl_{max2} are two peaks of plankton consumption. The calculation of the nekton portion was carried out by summing freshly swallowed portions.

As a result, through the biomass of pink salmon of each size group, we obtained the amount of food consumed per day and then (after summing the data by size groups) - the average daily ration for all individuals in the study area.

RESULTS

Conditionally, the life cycle of pink salmon after its juveniles migrate from rivers can be divided into four stages: 1) initial period of marine feeding in the estuarine-coastal zone (spring-summer period, mainly May-July); 2) feeding and migrations in the deep-water part of the Sea of Okhotsk (late summer-autumn period, mainly October-November); 3) winter (December, January), winter-spring (February-April), and spring (April-June) migrations in the western part of the NWPO; 4) summer pre-anadromous migrations of adult pink salmon in the NWPO and the Sea of Okhotsk (June-August). It is very important that the collection of data on fish was accompanied by mass collection of information on environmental conditions - climatic-oceanological and hydrobiological environment (Shuntov, Temnykh, 2008). Water temperature during salmon surveys in June in the Sea of Okhotsk was 5.5-7.0 (average 6.4), in August 9.0-11.0 (10.2), in September-October 7.0-9.0 (8.3), in October-November 6.0-8.0 (7.3); in the NWPO in February-March 5.0-6.0 (5.9), March-April 4.5-5.5 (5.1)°C.

1st stage is one of the important periods in the life cycle of pink salmon. Downstream migration of juveniles from rivers can occur from mid-April to late July in different parts of the range (Birman, 1985; Karpenko, 1998). In numerous publications, which are summarized in the monograph by Shuntov and Temnykh (2008), it is indicated that the physiological condition of juvenile pink salmon is of crucial importance in the development of the marine coastal area, one indicator of which is size and weight characteristics. However, due to a number of methodological difficulties in collecting adequate information, a clear picture of the dynamics of these indicators does not emerge. Objectively, the main problems in determining the size and weight composition and identifying the growth characteristics of juveniles arise due to imperfect fishing gear, the extended period of fry migration from rivers to coastal marine areas, unequal periods of stay of specific individuals here, as well as the different rate of their departure toward the open sea (Shuntov, Temnykh, 2008).

However, the sizes of pink salmon juveniles in different years can vary up to two times and in the coastal zone depend on the food supply and oceanological conditions (Shuntov, Temnykh, 2008). This is quite consistent with regional water temperature differences important for growth: high in the south (faster growth), low in the north (slower growth). It is important to keep in mind that often, apparently, not the specific temperature values are more significant, but the complex of conditions developing in warm or cold spring-summer seasons.

Summarizing the analysis of ideas about the importance of food supply for juvenile salmon in the estuarine-coastal zone, Shuntov and Temnykh (2008) suggest that at this stage, food availability may be a limiting factor, as the density factor operates most strongly in the coastal zone. However, in most cases, the feeding rate of juvenile pink salmon was high, immediately after downstream migration from the rivers of the SR in certain areas of the Sea of Okhotsk it was 7-15% of body weight (Chuchukalo, 2006; Karpenko et al., 2013). In the diet of early juvenile pink salmon, along with plankton (mainly copepods (Copepoda)), bottom and near-bottom organisms are noted: harpacticoids (Harpacticoida) , chironomids (Chironomidae) , gammarids (Gammaridae).

2nd stage . In the late summer and summer-autumn periods, juvenile pink salmon feed over the deep-water basins of the seas until they enter the ocean (Shuntov, Temnykh, 2008, 2011). Therefore, the habitat conditions (oceanological and feeding) of juvenile pink salmon during this period are of considerable importance for them to achieve such size-weight and bioenergetic indicators that will allow them to migrate to the ocean and survive during the winter-spring period.

To date, expeditions have collected a large amount of data on juvenile pink salmon beyond the neritic zone of the Sea of Okhotsk (Shuntov, Temnykh, 2008, 2011). Long-term studies have shown that in July in the open waters of the Sea of Okhotsk, individuals with *FL* 9.0-15.0 (average 11.2-12.5) predominate, in August - 9.0-16.0 (10.4-14.6) cm. In September, the size of juveniles increases sharply to 16.0-24.0 (18.6-21.4) cm. In all cases, the minimum and maximum sizes differ significantly, which is associated with differences in both growth rate and timing of downstream migration in different regions (Shuntov, Temnykh 2008).

The most important factor in assessing the food supply of fish and squid is the availability and abundance of their food resources. Previously, it was noted that there is no food shortage for juvenile pink salmon in the open waters of the Sea of Okhotsk during the autumn period (Shuntov et al., 1999; Shuntov, Temnykh, 2008, 2011).

Plankton studies in the 2000s in the open waters of the Sea of Okhotsk during the autumn period showed that the total biomass of zooplankton in different years varied by no more than 1.5–2.0 times (Fig. 2). Thus, in the autumn of 2009, the biomass of food plankton was below the multi-year average values, and in two deep-water areas where the main feeding of salmon occurs, it was only 160.1 mg/m^3. However, by the end of the feeding period in November 2009 in the southern part of the Sea of Okhotsk, juvenile pink salmon migrating to Pacific waters had maximum size and weight indicators (Shuntov, Temnykh, 2008). At the same time, the feeding of young-of-the-year pink salmon in open waters was medium to high. In August–September, the daily ration (DR) was 5–10, in October–November – 4–5%. The diet of pink salmon consisted mainly of various species of large-sized zooplankton, numerous juveniles and adults of small-sized fish and squid species (Chuchukalo, 2006; Kuznetsova, 2010; Gorbatenko, Melnikov, 2019).

At the end of summer (August), young-of-the-year pink salmon, migrating from coastal waters, often form aggregations in shelf waters (Gorbatenko, Chuchukalo, 1989). Thus, in August 1986, off the coast of Western Kamchatka on the inner shelf, the diet of juvenile pink salmon *FL* 10–14 cm was dominated by larvae and juveniles of mass nekton species (including walleye pollock *Gadus chalcogrammus* , capelin *Mallotus villosus* and squid), i.e., the young-of-the-year behaved like predators. Their DR was 5–7% of body weight, and the proportion of nekton in the diet was ~90%, while when moving away from the shore, larger pink salmon individuals completely switched to feeding on zooplankton, but feeding intensity remained high (Gorbatenko, Chuchukalo, 1989).

At the end of summer (in August) and autumn (in October) during migrations in open waters, the rates of linear and weight growth decrease, which is mainly associated with protein growth and fat accumulation during feeding (Lazhentsev, Maznikova, 2014). For example, in August 2012, the monthly growth of pink salmon in the open waters of the Sea of Okhotsk was 10.2 cm and 75 g, in October - 2.7 cm and 57 g. In August 2012, in the epipelagic zone of the open waters of the Sea of Okhotsk, the average biomass of food plankton was 542 mg/m^3, in October - 485 mg/m^3, in August the daily ration of pink salmon was estimated at 7-10%, in October it was twice lower - 4.0-4.5%. At the same time, the average weight of fish in August was 24.7 g (*FL* 13.5 cm), and in October - 205.3 g (*FL* 26.6 cm). That is, when recalculated to the mass of an individual, the absolute consumption of food in October increased threefold. Such intensive feeding against the background of decreasing rates of linear growth led to an increase in fat accumulation, mainly triacylglycerols.

Thus, the presented data indicate the absence of a direct dependence of pink salmon juvenile growth rates on the size of the food base in the late summer and autumn periods in the open waters of the Sea of Okhotsk and fully confirm the conclusions of Shuntov and Temnykh (Shuntov, Temnykh, 2008). And the main difference in the size and abundance of juvenile pink salmon migrating to Pacific waters is determined by the timing of downstream migration and conditions of existence of juveniles at the initial stage of ontogenesis.

3rd stage . Pink salmon accumulates most of its biomass during the winter-spring feeding period, the success of which is determined by a complex of various abiotic and biotic factors in the areas of its feeding aggregations (Shuntov, Temnykh, 2008, 2011; Gorbatenko, 2018).

With the onset of winter, in late November-December, the main part of juvenile pink salmon migrates to Pacific waters, while during the winter-spring period it is the main salmon species feeding in the NWPO. The dynamics of abundance, distribution, and conditions of existence of wintering pink salmon for the entire study period, starting from the 1980s, are presented in the work of Shuntov and Temnykh (2011). In general, the boundaries of this species' habitat during the wintering period are similar to the position of the 2-9°C isotherms. Maximum aggregations were observed at surface water temperatures of 3.5-6.5°C (Erokhin, 1990; Temnykh, 2004).

In late autumn-early winter, during the juvenile migration to the ocean, their linear and weight growth rates decrease. In open waters, monthly growth increments of juvenile pink salmon are 1.5-2.5 cm and 34-50 g (Takagi et al., 1981; Erokhin, 1990; Shvydkiy, Vdovin, 1999). According to long-term data, throughout the winter-spring period, the average size and weight of pink salmon increase from 30.0 cm and 287.0 g to 41.3 cm and 970.1 g, that is, by 11.3 cm and 683.1 g (Shuntov, Temnykh, 2011). The monthly increments for late February-first half of March were 2.4 cm and 63 g, then until mid-April - 3.9 cm and 207 g, from mid-April to the first ten days of May - 3.3 cm and 186 g, and further until early June - 3.6 cm and 342 g.

Studies conducted in December 2021 in the near-Kuril Okhotsk Sea and Pacific waters at the initial stage of winter migrations of juvenile pink salmon with a modal size of 27-29 cm and weight of 200-260 g showed that their food base in the upper epipelagic (0-50 m) and epipelagic as a whole (0-200 m) deteriorated compared to data from October 2021 from the Sea of Okhotsk by more than twice (Fig. 2, 3). However, despite the relatively low biomass of food plankton in December, the feeding rate of juvenile pink salmon in the near-Kuril waters of the Sea of Okhotsk and Pacific waters compared to October-November changed insignificantly. In November, the average daily ration was 4.2%, and in December - 3.4% of body weight; the decrease occurred mainly due to copepods, which during this period migrated to winter in the lower layers and were almost absent in the diet of juvenile pink salmon (Fig. 4).

In winter, various stocks of pink salmon feed in the Northwestern Pacific Ocean; their distribution area is limited to the north by the 2°C isotherm and to the south by the 10°C isotherm (Birman 1968; Erokhin, 1990; Shuntov, Temnykh, 2008, 2011). The Okhotsk Sea and Kuril stocks of pink salmon winter mainly in the western part of the Subarctic Front zone (eastward to 170°-175°E).

J a n u a r y . Based on long-term research, in January *FL* of pink salmon is 25-31 cm, and by the end of February-March this indicator increases by 2.1-2.6 cm and reaches 29.8-31.4 cm (Shuntov, Temnykh, 2008). Plankton studies during the typical winter period (January) of 2019 in the western part of the Subarctic Front (Fig. 1) showed that its average biomass in the epipelagic layer of subarctic waters and the mixing zone was 204.1 mg/m^3, while in subtropical waters, where pink salmon was practically absent, it was only 24.0 mg/m^3. In the epipelagic zone as a whole, the biomass of food plankton was on average 1.2 times higher than in the upper epipelagic layer across the area. The stomach fullness indices (SFI) of pink salmon were moderate – 90-100‱, with the main components of the food bolus being hyperiids (Hyperiidae) – 60%, euphausiids (Euphausiacea) – 16%, and sagittas (Sagittae) – 14%. Large interzonal copepods were practically absent in both diet and plankton, as according to Vinogradov (1968), they migrate to mesopelagic waters for wintering.

F e b r u a r y - A p r i l . Feeding conditions for juvenile pink salmon in February-April in the ocean are illustrated using the example of 2009-2011 (Fig. 1). During these years, various states of the Western Subarctic Gyre (WSG) and hydrological water regime ("compressed" and "stretched") were observed in the North Pacific, which affected the distribution of the subarctic water mass. The "stretched" state of the gyre contributed to greater dispersal of pink salmon and expansion of its winter feeding area: it was distributed more evenly across a larger area, actively utilizing southeastern and eastern regions. During the "compressed" state of the WSG (when minimum values of subarctic water distribution were observed in the oceanic branch of the East Kamchatka Current, and its southern boundary shifted to the northwest due to the action of the intense Aleutian Current), the area of pink salmon distribution to the south and east decreases.

In 2009, the state of the WSC was closer to "compressed," excluding the weak intensity of the Aleutian Current (Figurkin, Naydenko, 2013). The year was characterized as very warm in the areas of the Oyashio Current and the mixing zone, from the side of the East Kamchatka and Aleutian Currents. This year saw a more northern position of the mixing zone boundary (southern boundary of the subarctic structure), therefore a significant portion of pink salmon was located north of the Subarctic Front zone – in the Aleutian waters (Nagasawa, 2000; Starovoitov et al., 2010a, 2010b), meaning there was an expansion of the pink salmon feeding area in the northern direction.

In March-April 2009, in the epipelagic layer of subarctic waters and the mixing zone, where the main concentrations of pink salmon were observed (Fig. 5), the biomass of forage plankton was high (averaging 741.6 mg/m^3). At the same time, in March-April 2009 in the upper 50-meter layer, as in December 2009, lower (~300 mg/m^3) concentrations of forage plankton were observed (Naydenko et al., 2009). Copepods dominated in the forage plankton and pink salmon diet, and the daily food consumption rates of pink salmon were relatively high – 121-149‱ (Naydenko et al., 2009). It should also be noted that in the winter period of 2009, pink salmon were dispersed to a depth of 150 m, which was apparently related to food distribution and feeding conditions (Shuntov, Temnykh, 2011).

In 2010, the state of the WSC was "stretched." It was a warm year in the areas of Oyashio and the mixing zone, but cold from the side of the East Kamchatka and Aleutian Currents. This year saw a more southern position of the boundary of the subarctic structure waters , which caused a shift of the main concentrations of pink salmon in the southern direction (Fig. 7a), as the spatial distribution of fish from Russian stocks depends to a certain extent on the state of the WSC (Figurkin, Naydenko, 2013).

In winter and spring of 2010 (February 24–April 30) in the epipelagic zone of subarctic waters and the mixing zone, the average biomass of forage plankton throughout the entire studied area was relatively high – on average 655.3 mg/m^3 (Fig. 6). At the same time, in the western part of the area, where the main concentrations of pink salmon were observed (Fig. 7a), the biomass of forage plankton was 1.5 times higher than in the eastern part – 890 versus 516 mg/m^3. In the western part, large copepods (*Neocalanus cristatus*) predominated, while in the eastern part – copepods, sagittas, and euphausiids.

In the western part of the area in the second half of March, the SCI (stomach content index) of pink salmon were medium – 101–140‱. Large copepods, sagittas, pteropods (Pteropoda), and hyperiids dominated in the diet, while in large pink salmon (*FL* > 40 cm), nekton dominated – 71.3%.

In the eastern part of the area, despite relatively high biomass of forage plankton (516 mg/m^3), minimal SCI of pink salmon were observed (53–54‱), with low-calorie sagittas forming the basis of the diet. Low SCI were associated with the features of horizontal distribution of forage zooplankton. The main concentrations of large copepods, which determined the relatively high average biomass of large plankton, were concentrated on the western periphery of the area, and euphausiids – on the eastern periphery, therefore, the latter were inaccessible to pink salmon in most of the area. In the vast waters of the central part of the area, either low concentrations of large zooplankton were noted (< 100 mg/m^3), or low-calorie sagittas predominated in the large plankton, which were always classified as secondary food for pink salmon.

Thus, in the eastern part of the area, an unfavorable food supply was noted, and pink salmon was forced to migrate to more food-rich areas in the northern or eastern directions, where maximum biomass of food plankton was observed in April (up to 994 mg/m^3) (Fig. 6, 7) with the dominance of large copepods. Therefore, in the winter period of 2010, there was a significant undercount of pink salmon: in March-first half of April, 134 million individuals were counted, and in July in the waters near the Kuril Islands, four times more – 475 million individuals (Naidenko et al., 2010). The main reasons: pink salmon was not counted in areas north of 46° N and east of 168° E, as well as vertical redistribution of pink salmon in the epipelagic zone (migrations beyond the upper 50-meter layer studied during such work into deeper layers).

In the spring period, work in pink salmon distribution areas was conducted from April 17-24, 2010 (Fig. 1). The biomass of food plankton in the studied area was high in subarctic waters and the mixing zone – 781.7 mg/m^3 (Fig. 6). In southern areas with warm subtropical waters (April 25-May 3, 2010), where pink salmon was found only on the northern periphery, the biomass of food plankton in the epipelagic zone was 562.8 mg/m^3 (Fig. 6). Copepods predominated everywhere in the plankton: in subarctic waters and the mixing zone, large copepods *N. cristatus* dominated, while in southern subtropical waters – *N. plumchrus* . The FSI (feeding stomach index) of grown pink salmon *FL* 30-40 (average 37.3) cm was medium – 103‱, and for individuals *FL* > 40 (40.6) cm was high – 194.5‱ (Kuznetsova, 2010). The foundation of the diet for smaller pink salmon was zooplankton – 80.8% (euphausiids, copepods, hyperiids), while in larger individuals, nekton predominated in the diet – 72.9%.

In 2011, the condition of the Western Subarctic Gyre was distinctly "compressed" (Figurkin, Naidenko, 2013). Oceanological conditions in the western section of Oyashio were close to normal, while in all other areas the year was warm and very warm (in terms of absolute temperature values, it was close to the record warm years of 1991 and 2009). Both branches of the East Kamchatka Current were weakly expressed, and a very strong Aleutian Current was observed. In all areas except the western section of Oyashio, the warm year corresponded to a more northern position of the southern boundary of the subarctic structure. During the winter-spring period of research, the year was "warm" not only in hydrological but also in hydrobiological characteristics, which was expressed in the acceleration of spring processes in planktonic communities (Glebov et al., 2011; Kuznetsova et al., 2011).

In the winter-spring period of 2011 (February 22–April 07) in the subarctic waters and mixing zone, where the main concentrations of pink salmon were observed (Fig. 7b), the average biomass of forage plankton was 1.5–2.0 times lower than in 2009 and 2010, and in the epipelagic zone it was only 364.4 mg/m ^{3} (Fig. 6). The decrease in biomass occurred mainly due to copepods (*N. cristatus*) and sagittas (*Sagitta elegans*). The stomach fullness indices (SFI) of pink salmon from the studied area were low to medium – 68–102‱, with euphausiids and copepods forming the basis of their diet. For large pink salmon *FL* > 40 (average 41) cm, SFI varied from 67 to 135‱, and their diet was dominated by large copepods, with nekton, euphausiids, and hyperiids to a lesser extent. In the central part there were extensive areas with low concentrations of forage plankton (50–100 mg/m ^{3}), and the area with favorable food resources occupied only the western part of the studied area (Kuznetsova et al., 2011).

Thus, in 2010 and 2011, extensive areas with low concentrations of forage zooplankton (50–100 mg/m ^{3}) were observed, which determined the low SFI of pink salmon (50–80‱) in these areas and active migrations of fish to more food-rich regions in the north and east.

Stage 4 . With spring warming, salmon begin migrations from their wintering grounds. Pink salmon migrations in the Sea of Okhotsk direction in 2009-2011 were assessed in comprehensive TINRO expeditions in the northwestern Pacific Ocean approaching the Kuril straits. According to literature data, during this period, individuals of the species most intensively increase their weight, with maximum rates of generative growth and fat accumulation (Ricker, 1964; Shvydky, Vdovin, 1999). Long-term studies have shown that the monthly growth of pink salmon from mid-April to the first ten days of May is 3.3 cm and 186 g, and further until early June - 3.6 cm and 342 g (Shuntov, Temnykh, 2011). High growth rates and gonad maturation require intensive feeding.

According to research in the near-Kuril waters of the NWPO in June-July 2009-2011, aggregations with the most significant concentrations of pink salmon after winter-spring migrations were observed in waters with surface temperatures from 5-7 to 11-12°C (Shuntov, Temnykh, 2011). At this time, the average *FL* of grown pink salmon in 2009 was 45.5, in 2010 - 43.4, and in 2011 - 43.6 cm.

Plankton studies in the 2000s in Pacific waters in June-July showed that the total biomass of zooplankton in different years varied from 460.5 to 1301.0 mg/m ^{3}, and the long-term average biomass in the epipelagic zone was 793.1 mg/m ^{3} (Fig. 8), while in autumn in the Sea of Okhotsk, the long-term average biomass of food plankton was twice as low - 365.3 mg/m ^{3} (Fig. 2). In 2009-2011, in the epipelagic zone of the near-Kuril waters of the NWPO, the highest biomass of food plankton was recorded in 2009 - 980 mg/m ^{3}, and the lowest in 2011 - 460.5 mg/m ^{3} (Fig. 8).

The daily ration of pink salmon (all size groups) from the studied area in 2009 was 4.9%. The diet was primarily composed of euphausiids - 39.0%, copepods - 27.7%, and pteropods - 13.7%, with the proportion of nekton not exceeding 6.5% (Table 1).

Table 1. Diet composition and daily ration of pink salmon *Oncorhynchus gorbuscha* in the near-Kuril waters of the NWPO in June-July 2009-2011.

Food component	Component share, % of mass			
	2009	2010	2011	Average
Euphausiids	39.0	27.6	49.6	38.7
Copepods	27.7	33.3	17.0	26.0
Hyperiids	5.5	12.0	14.4	10.6
Sagittae	5.8	6.7	3.7	5.4
Pteropods	13.7	10.8	7.9	10.8
Nekton	6.5	9.5	6.8	7.6
Others	1.8	0.1	0.6	0.9
Daily ration, % of body mass*	4.9	4.9	4.4	4.7

Note. Here and in Tables 3, 4: NWPO - Northwestern Pacific Ocean. *Data on pink salmon feeding of all size groups were used.

In 2010, despite the lower average plankton biomass (Fig. 8), the DR of pink salmon did not change and amounted to 4.9% of body mass. However, the total impact of this species on the biota of the studied area, expressed in the daily consumption of food objects, was 23.4 thousand tons, which is one and a half times lower than in 2009. This is due to the lower biomass of pink salmon (by 1.5 times). The basis of its diet consisted of euphausiids - 27.6%, copepods - 33.3%, and hyperiids - 12.0% (Table 1).

In the summer of 2011, the biomass of food plankton was significantly lower than the long-term average values (Fig. 8), however, the feeding of pink salmon was relatively high, with a DR of 4.4%. As before, euphausiids, copepods, hyperiids, and pteropods formed the basis of the diet (Table 1). Thus, it can be concluded that in summer in the near-Kuril waters of the NWPO, changes in the biomass of food plankton did not significantly affect the feeding of pink salmon, meaning favorable feeding conditions were observed in the pre-anadromous period.

After feeding in the Pacific waters in June-July, in July-August pink salmon migrates to the Sea of Okhotsk towards the rivers to spawning grounds. During pre-anadromous migrations in the Sea of Okhotsk, its feeding rate decreases, reaching minimum values in coastal waters (Chuchukalo, 2006). Studies of pink salmon feeding in the 2000s showed that in general, the daily ration (DR) of mature pink salmon in the Sea of Okhotsk was relatively low (~ 3% of body weight), with the diet mainly consisting of euphausiids, amphipods, and fish (Table 2). When approaching rivers in the coastal zone, pink salmon feeding was even lower, with DR at 1-2% of body weight (Chuchukalo, 2006).

Table 2. Diet composition and daily ration of mature pink salmon *Oncorhynchus gorbuscha* in summer in the Sea of Okhotsk based on multi-year data from 2000-2014 (from: Gorbatenko, 2018, with modifications)

Food component	Component proportion, % by weight

Plankton:	85.4
Euphausiids	29.6
Copepods	0.1
Amphipods	53.9
Sagittas	0.1
Pteropods	1.1
Others	0.6
Nekton:	14.6
Squids	4.9
Fish	9.7
Daily ration, % of body weight	3.0

DISCUSSION

Plankton studies conducted in the epipelagial zone of the Sea of Okhotsk and western part of the Northwestern Pacific Ocean in different periods of the 2000s showed significant changes in the biomass of forage plankton during the period of marine migrations of pink salmon (Fig. 8). The lowest biomass values in the Sea of Okhotsk are observed in early winter (December), in Pacific waters - in December and January, while maximum values occur everywhere during spring and summer months. Throughout the entire study period, the large fraction comprised the bulk of the net plankton (Table 3, Fig. 9).

Table 3. Proportion of size groups (fractions) of net plankton and its dominant taxonomic groups in the open waters of the Sea of Okhotsk and the western part of the NWPO (area A) in subarctic waters and mixing zone in different seasons and on average for the year (2009-2011, 2019, 2021), %

Plankton	Sea of Okhotsk				Western part of NWPO (area A)			
	Summer	Autumn	Winter	Year	Winter	Spring	Summer	Year
Size group, mm								
Small (0.4-1.2)	7.7	11.8	12.0	10.0	14.8	5.8	2.6	6.3
Medium (1.2-3.2)	9.9	10.3	6.5	9.3	7.7	8.2	2.3	5.8
Large (≥ 3.2)	82.4	77.9	81.5	80.7	77.5	86.0	95.1	87.9
Taxon								
Copepods	66.2	48.7	50.5	57.2	54.9	56.1	71.9	64.8
Euphausiids	21.0	22.7	17.6	20.9	12.9	11.7	3.5	7.2
Hyperiids	1.3	5.2	13.1	5.0	2.1	1.8	0.6	1.1

Sagittas	10.8	20.9	16.9	15.4	24.4	22.6	21.6	19.8
Others	0.7	2.5	1.9	1.5	5.7	7.8	2.4	7.1

Net zooplankton consists of four taxonomic groups - copepods, euphausiids, hyperiids, and sagittas (Table 3), which to varying degrees form the food base for pink salmon. Figure 4 shows changes in biomass of the dominant taxonomic groups of zooplankton, where it can be seen that the main changes in food plankton occur due to copepods, which in the Sea of Okhotsk constitute 57.2 (48.7-66.2)%, and in the NWPO 64.8 (54.9-71.9)% of the net plankton mass.

The feeding of differently sized pink salmon during the marine period of life fluctuated greatly (Table 4), which is mainly associated with changes in the food supply and habitat conditions. The maximum and minimum feeding rates were observed in August in the Sea of Okhotsk, at the beginning and end of the marine period of the life cycle, respectively. In pink salmon fingerlings, the average daily ration is 8.5% of body weight, while in pre-spawning fish – 3.0%.

Table 4. Seasonal dynamics of the size of Okhotsk pink salmon *Oncorhynchus gorbuscha* and its daily ration in the Sea of Okhotsk and NWPO

Area	Season	*FL*			Daily ration, % of body weight		
		M	min	max	*M*	min	max
Sea of Okhotsk	Summer (August)	12.0	9.0	16.0	8.5	7.0	10.0
	Autumn (October-November)	25.3	24.0	26.0	4.2	4.0	4.5
NWPO	Winter (December)	28.0	27.0	29.0	3.9	3.7	4.1
	Winter (January)	29.9	29.0	33.0	3.1	2.5	3.2
	Winter-Spring (February-March)	33.0	31.0	36.0	3.6	2.6	4.3
	Spring (April)	39.0	37.4	40.6	4.2	4.0	4.4
	Summer (June-July)	44.1	33.4	45.5	4.8	4.4	5.0
Sea of Okhotsk	Summer (July-August)	45.0	34.1	47.5	3.0	2.4	3.4

Note. *FL* – fork length, mm; *M* , min, max – mean, minimum and maximum values, respectively.

In numerous publications, summarized in the books by Shuntov and Temnykh (2008, 2011), which examine pink salmon feeding in various biotopes during the marine period of life, it is shown that the species is highly adaptable in its consumption of aquatic organisms, however, the preferred food is hyperiids and euphausiids. In the Sea of Okhotsk in August, the diet of fingerlings is primarily composed of copepods, while in shelf areas they consume benthos and fish larvae that are accessible by size (Fig. 10). In autumn, during October-November, and in December, pink salmon clearly prefers hyperiids and to a lesser extent euphausiids.

From the above, it follows that in the Sea of Okhotsk during summer and autumn periods, despite changes in food plankton biomass in different years (Fig. 2), juvenile pink salmon had sufficient food, and this conclusion corresponds to the assertion of Shuntov and Temnykh (2008, 2011). The daily ration in different years for juvenile pink salmon in the Sea of Okhotsk varied from 7 to 10% in summer and from 4.0 to 4.5% of body weight in autumn.

At the beginning of the winter period, in December, the biomass of food plankton decreased on average by half (Fig. 10a), while the concentrations of food zooplankton in the upper epipelagic zone during this period were lower than in the epipelagic zone as a whole. However, the feeding of juvenile pink salmon in December compared to October-November decreased insignificantly (Fig. 10b). This decrease occurred mainly due to large interzonal copepods in connection with their seasonal migrations to winter in the mesopelagic zone (Vinogradov, 1968), and in the plankton, copepods were represented by small and medium-sized species, which were almost absent in the pink salmon diet.

Thus, the feeding level of juvenile pink salmon in December was average, which means the situation with its food supply was far from critical. The decrease in the rate of linear and weight growth in migrating juvenile salmon (Takagi et al., 1981; Erokhin, 1990; Shvydky, Vdovin, 1999) is more related to seasonal changes in abiotic conditions and active migrations. The feeding level of juvenile pink salmon in December was relatively high despite the lowest biomass of forage zooplankton, especially in the upper 50-meter layer. This was facilitated by the fact that in December, juvenile pink salmon make feeding migrations to a depth of 150 m, which naturally increases their food supply. In addition, hyperiids (64.6%) form the basis of their diet during this period, and they concentrate in the surface 5-10 meter layer. During vertical catches, they are poorly accounted for by the Juday net, and the obtained data typically do not reflect their actual biomass in the late autumn period (Zavolokin et al., 2007).

In the typical winter period, in January, the minimum biomass of forage plankton was observed (averaging 204.1 mg/m^3) along with very low feeding of pink salmon (DFI 3.1%) (Fig. 10). Sagittas predominated in the forage plankton, while hyperiids, euphausiids, and sagittas dominated the pink salmon diet; as in December, copepods were absent.

In late February-early April, the winter-spring period was observed throughout most of the studied area: seasonal migrations of large interzonal copepods (mainly *N. cristatus*) from the mesopelagic to the epipelagic began after wintering. The average biomass of forage plankton in February-April in the epipelagic increased more than twofold (459.4 mg/m^3), mainly due to large interzonal copepods, and the proportion of sagittas, which in January amounted to 49.0%, decreased to 24.9% (Fig. 10a). The feeding level of pink salmon also increased, and in the winter-spring period, the DFI already was 3.6% (Fig. 10b). Copepods (35.9%) and euphausiids (23.1%) dominated the pink salmon diet.

In the spring (April) and especially summer (June-July) periods, the biomass of forage plankton in the epipelagic increased significantly and amounted to 718.7 and 820.2 mg/m^3 respectively (Fig. 10a). During this period, pink salmon fed intensively, with an average DFI of 4.2% in spring and 4.8% of body weight in summer (Fig. 10b). The basis of the diet in Pacific waters during spring and summer periods consisted of large copepods and euphausiids. In summer (July), despite favorable food resources (Fig. 10a), feeding intensity of pre-spawning pink salmon was minimal - in open waters, the feeding coefficient was 3.0% (Fig. 10b), and closer to the shore even lower - 1-2%. The minimal feeding intensity of pre-spawning pink salmon in summer in the Sea of Okhotsk is related to active migrations toward rivers and the physiological condition of fish during the pre-spawning period.

CONCLUSION

The food base of pink salmon in the Sea of Okhotsk (August-December), despite significant changes, is sufficient for feeding and migrations of juvenile fish. In Pacific waters, the decrease in plankton biomass during winter-spring months (December-February), especially in the upper epipelagic zone, is partially compensated by daily vertical migrations of pink salmon in a relatively homogeneous 150-meter thermohaline layer. However, due to uneven distribution of food plankton during winter months in the studied area of Pacific waters in 2009-2011, extensive areas with low concentrations (50-100 mg/m^3) of food zooplankton were observed. This determined low values of the stomach fullness index (50-80‱) of pink salmon in these areas and, apparently, natural mortality of some individuals due to food shortage and low energy reserves accumulated during the autumn feeding period in the Sea of Okhotsk, which are necessary for active migrations of wintering pink salmon to more food-rich areas in the north and east. According to preliminary data from biochemical studies, the lipid level in pink salmon bodies in February-April was minimal (varying from 0.4 to 1.1% of wet weight in different years, with a minimum in 2010 - 0.4-0.7%). In autumn, October-November, juvenile pink salmon had lipid content of 2.5-4.1% of wet weight (Gorbatenko et al., 2008), which decreased to 1.6% by December.

In the spring and especially summer periods, due to the migrations of large interzonal copepods from the mesopelagic zone to the upper layers, the maximum concentration of food plankton is observed, and the feeding rate of pink salmon increases. During this time, the consumed food was sufficient not only for active migrations, somatic and generative growth, but also for the accumulation of lipids, mainly reserve triacylglycerols, necessary for successful migrations to spawning grounds. In the Pacific waters, the lipid level in pink salmon (with gonads at stage III–III–IV maturity) in June was 3.4–3.5% of wet weight, in the Sea of Okhotsk (gonads at stage IV maturity) it decreased to 2.7–2.9% of wet weight (Gorbatenko et al., 2008).

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COMPLIANCE WITH ETHICAL STANDARDS

The collection of material and its processing did not contradict international standards for the treatment of animals, corresponding to Directive 2010/63/EU of the European Parliament and the Council of the European Union dated 22.09.2010 on the protection of animals used for scientific purposes (https://ruslasa.ru/wp-content/uploads/2017/06/Directive_201063_rus.pdf).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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FIGURE CAPTIONS

Fig. 1. Material collection sites in the winter-spring months in the western part of the NWPO (area A): a – winter–spring (20.03–17.04.2009); b: *1* – winter–spring (24.02–30.03.2010), *2* – spring (17.04–03.05.2010); c – winter–spring (22.02–07.04.2011); d: *3* – winter (15–31.01.2019), *4* – winter (02–12.12.2021). (★) – January, (●) – February, (✸) – March, (×) – April, (○) – May, (⊕) – December; waters: (▨), (⬚) – subtropical and subarctic structure, respectively; (▥) – mixing zone. Here and in Fig. 4, 6, 8, 9: NWPO – northwestern part of the Pacific Ocean.

Fig. 2. Biomass of forage zooplankton (large fraction, organism size > 3.2 mm) in open waters of the epipelagic zone of the Sea of Okhotsk at depths > 150 m during autumn in the 2000s: (····) – mean multi-year biomass value (365.3 mg/m ^{3})

(▢) – years for which data were used in calculations due to the availability of information for the winter period in the following year.

Fig. 3. Seasonal changes in biomass of forage zooplankton (large fraction, organism size > 3.2 mm) and the ratio of its taxonomic groups (in %) in the upper epipelagic zone (0-50 m) of the Kuril waters of the Sea of Okhotsk (⬚) and Pacific Ocean (▥): (■) – Copepoda, (⬚) – Euphausiacea, (⬚) – Hyperiidae, (▩) – Chaetognatha, (▭) – others; (▨) – Kuril Islands, (⇨) – general direction of pink salmon migrations, (···) – 200 m isobath; *mean value for 2008-2010.

Fig. 4. Changes in biomass of dominant zooplankton groups in the epipelagic zone of the Sea of Okhotsk and western part of NWPO (area A) during the marine period of the pink salmon *Oncorhynchus gorbuscha* life cycle: a – Copepoda, b – Euphausiacea, c – Hyperiidae, d – Chaetognatha. Data used from 2008-2010 for the Sea of Okhotsk; from 2009-2011, December 2021 and January 2019 – for the northwestern Pacific Ocean .

Fig. 5. Distribution density of pink salmon *Oncorhynchus gorbuscha* against the background of surface water temperatures in March-April 2009: (—) – isotherms.

Fig. 6. Average biomass of forage zooplankton (large fraction, organism size > 3.2 mm) in the epipelagic zone of the western part of NWPO (area A) during winter-spring period: a – subarctic + mixed waters, b – subtropical waters; *spring only.

Fig. 7. Distribution of pink salmon *Oncorhynchus gorbuscha* against the background of surface water temperatures in February-April 2010 (a) and 2011 (b): (▨) – area with zooplankton biomass of large fraction (organism size > 3.2 mm) < 100 mg/m^3. See Fig. 5 for other designations.

Fig. 8. Biomass of fodder zooplankton (large fraction, organism size > 3.2 mm) in the epipelagic zone of the Kuril waters of the NWPO in summer (June-July) of the 2000s: (····) – multi-year average biomass value (793.1 mg/m^3), (▢) – years for which data were used in calculations.

Fig. 9. Changes in the biomass of fodder (large fraction, organism size > 3.2 mm) (a) and total net zooplankton (b) in the epipelagic zone of the Sea of Okhotsk and western part of the NWPO (area A) during the marine life cycle of pink salmon *Oncorhynchus gorbuscha* according to data from 2008-2011, 2019, 2021.

Fig. 10. Average biomass of fodder plankton (mg/m^3) in the epipelagic zone of the Sea of Okhotsk and Pacific waters (a), food composition and daily rations (DR, % body weight) of pink salmon *Oncorhynchus gorbuscha* of different sizes (b) during its migrations at different stages of the life cycle in the 2000s: ( ) – Copepoda, ( ) – Euphausiacea, ( ) – Hyperiidae, ( ) – Pteropoda, ( ) – Sagittae, ( ) – nekton, ( ) – others; *FL* – fork length (multi-year average values are given); ( ) – general direction of pink salmon migrations.