

Is Winter the Critical Period in the Marine Life History of Pacific Salmon?

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Abstract: Winter conditions experienced by Pacific salmon in the North Pacific Ocean have been investigated based on data collected in winter–spring, 1986–1992 and 2009–2011, and in summer, 2004–2014. Although forage zooplankton biomass in the western Subarctic Frontal Zone was 40–70% lower in February–March than in April and June–July, the availability of preferred prey items was likely sufficient to satisfy the trophic demands of wintering salmon. Pink, chum, and coho salmon 10–30 and 30–50 cm in fork length foraged intensively in winter. While feeding intensity was higher in autumn than in winter, it was not significantly different among seasons. Distinctions in the seasonal dynamics of feeding rates for different salmon species and sizes seem to provide evidence for a species-specific life strategy rather than to signal the onset of poor food conditions. The rare occurrence of predatory fish in salmon winter habitat also suggests a low rate of salmon mortality. Estimated ocean winter mortality of pink salmon was 36–80% from September–November to June–early-July, which is not higher than mortality experienced during the freshwater, estuarine, or early marine phases of their life history. We conclude that winter is an important period in salmon marine life history, but may not be more critical than earlier life-history periods in fresh water and the ocean.

Keywords: Subarctic Front, Pacific salmon, survival, mortality, spatial distribution, abundance, sea surface temperature, landscape zone, food supply

INTRODUCTION

Although insufficiently studied, winter and spring are very important seasons in the marine life history of Pacific salmon. This has led to contradictory statements being made about winter conditions experienced by salmon rearing on the high seas. Most researchers consider that winter in the North Pacific Ocean is a critical period for Pacific salmon populations. It is thought that the forage zooplankton biomass is very low throughout salmon wintering areas in the ocean, and that salmon could even starve. A decrease in the total lipid content in salmon muscle has been attributed to a poor food supply in winter that affects salmon survival (Nagasawa et al. 1997, 1999; Nagasawa 1999, 2000; Nomura et al. 1999, 2000; Ishida et al. 2000; Nomura and Kaga 2007).

An alternative point of view is that the food resources of the North Pacific in winter are sufficient to meet salmon's needs (Shuntov and Temnykh 2004, 2008, 2011; Shuntov et al. 2010; Naydenko and Kuznetsova 2011, 2013).

There is significant variability in mortality rates during the ocean phase of Pacific salmon life history. Based on TINRO-Center's marine survey data, mortality of pink salmon was thought to range from 48% to 91% during different life stages. This was normally attributed to such

factors as predation and, especially over the last decades, to climate-oceanographic reconstructions that change North Pacific ecosystems (Shuntov, 1994; Radchenko and Rassadnikov, 1997; Radchenko 2001, 2012).

The TINRO-Center has conducted regular pelagic trawl surveys to study salmon ecology in the Sea of Okhotsk in fall and Pacific waters of the Kuril Islands in summer. In 1986–1992 and 2009–2011, the Subarctic Frontal Zone was also surveyed in the winter and spring. Data on salmon abundance allowed the calculation of salmon mortality rates (e.g., pink salmon) at different stages of marine life. Based on the data collected, we estimated the effect(s) of some factors that may contribute to salmon mortality and concluded whether winter is the critical period for Pacific salmon. The results of these studies are presented below.

MATERIALS AND METHODS

Study Area

The epipelagic layer of Subarctic Frontal Zone (hereafter SAF) and adjacent subarctic waters were surveyed in February–April of 1986–1992 and 2009–2011. The survey

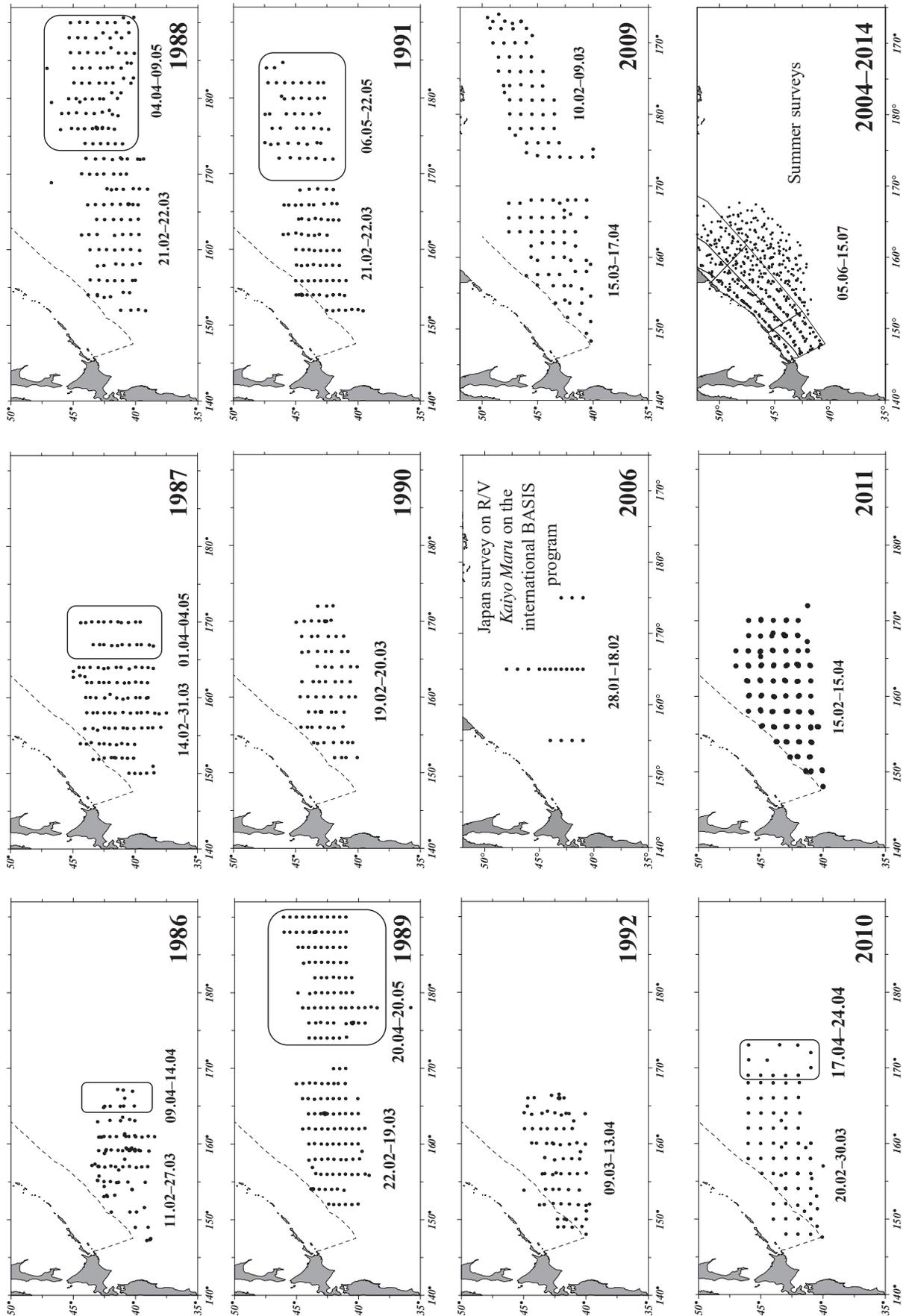


Fig. 1. The area of Russian surveys in the northwest Pacific Ocean in winter to spring 1986–1992 and 2009–2011, and in summer 2004–2014. The borders of biostatistical areas and the 200-mile economic zone of Russia are shown (dashed lines). The surveys conducted in spring are shown inside rectangles.

area was bounded on the north by latitude 37°N to 50°N and on the east by longitude 152°E to 172°E. Additional areas in the central North Pacific—between 174°E and 170°W—were surveyed in 1988, 1989, 1991, and 2009. Survey dates and grids varied slightly in different years. We also used data collected during Japanese surveys on R/V *Kaiyo maru* as part of the international BASIS program in winter 2006, and Russian surveys in Pacific waters of Kuril Islands and southeast Kamchatka in summer 2004–2014 (Fig. 1).

Nekton Data

Salmon and other epipelagic nekton were sampled by pelagic rope trawls with an average vertical net opening of 50 m in 1980s and 30.8 m in 2009–2011. Trawl hauls were conducted round-the-clock and lasted one hour. The trawl towing direction was adjusted for weather and hydrological conditions. The upper epipelagic layer (0–50 m) was swept by trawl net. Vertical and horizontal net openings were measured by a Simrad FS20/25 trawl sonar. In 2009–2011, test trawl hauls were performed in different layers down to a depth of 120 m to describe the vertical distribution of Pacific salmon. The trawl sampling method is published in Temnykh et al. (2002).

Because of differences in trawl net modifications used in the 1980s and 2000s, we plot relative values of Pacific salmon abundance on graphs of their catch distribution. Salmon catches relative to water temperature are expressed as a percentage of their total catch during the survey analyzed. It absorbs the differences related to the different parameters of the trawl nets used, as well as to different Pacific salmon abundances in compared years.

The abundance (N) and biomass (B) of Pacific salmon and other epipelagic nekton per unit of survey area—square kilometer (ind./km² and kg/km²)—for each trawling operation were determined as:

$$\frac{N \cdot p}{A \cdot k} = \frac{N \cdot p}{1.852 \cdot v \cdot t \cdot 0.001 \cdot a \cdot k}$$

and

$$\frac{M \cdot p}{A \cdot k} = \frac{M \cdot p}{1.852 \cdot v \cdot t \cdot 0.001 \cdot a \cdot k},$$

where N is number of fish in the catch (individuals), M is fish biomass in the catch (kg), A is area covered by the trawl (km²), v is trawling velocity (kts), t is trawl duration (hr), a is horizontal opening of the trawl net (m), p , k are correction coefficients, p is capacity coefficient, applied to compensate for stepped trawling at several depths ($p \geq 1$), k is catchability coefficient of the trawl net, 1.852 is number of kilometers in one nautical mile, and 0.001 is the conversion from kilometers to meters.

The average density of distribution of each nekton species within the survey area was determined as the arithmetic

mean of species distribution densities at each trawling operation:

$$Q = n(b)/s,$$

where Q is the arithmetic mean of species distribution densities at each trawling operation, n is the number of fish of each nekton species in the catch (or b is weight of each nekton species in the catch), s is the squared area that is swept during 1 hr of trawling, which is calculated from the horizontal opening and average towing speed of the trawl.

The total abundance (N) and biomass (B) of Pacific salmon and other epipelagic nekton were determined as:

$$N(B) = Q \cdot S / 1,000,000,$$

where $N(B)$ is abundance (biomass in thousands of fish or tons), Q is mean species distribution density within the studied area (kg/km²), and S is the surveyed area (km²).

Oceanographic Data

All trawl surveys were followed by oceanographic observations including temperature and salinity measurements at least down to the 500-m layer. The upper water column was well mixed and practically homogenous in the late winter. Temperature and salinity did not change significantly down to 60–110 m throughout the area of distribution of subarctic waters, and down to 180–200 m within the transitional areas, where the subarctic waters were considerably transformed. Pacific salmon rarely dive below the upper 100-m water layer (Starovoytov 2003; Shuntov and Temnykh 2008, 2011; Starovoytov et al. 2010a, b). Therefore, data collected from the research vessel combined with SST data from satellite images entirely characterized the thermal conditions throughout the salmon distribution in the winter period. Using these data, we identified the location of the discrete Subarctic Frontal Zone and the Western Subarctic Cyclonic Gyre (WSG) elements and boundaries between different water masses. As the SST data were analyzed to a significantly higher extent than is usual for a standard surveyed area, it became a key starting point to explain the specific features of salmon distribution in the vicinity of the SAF.

Plankton Data

Plankton samples were collected with a nylon Juday net with mesh size 0.168 mm and mouth area 0.1 m². Net hauls were performed in 0–50 (upper epipelagic) and in 0–200 m (epipelagic) layers both during day and night prior to the trawling operation. We separated net samples into three size fractions: small (animals < 1.2 mm in length), medium (1.2–3.2 mm), and large (> 3.2 mm). Species composition, weight (as displaced volume), size, and developmental stage by species were determined for each fraction. In biomass calculations, we used Juday net catchability coefficients

(CC), which were established by Volkov (1996): for small-size plankton—1.5; for medium-size plankton—2.0; for large-size plankton: euphausiids < 10 mm—2.0, euphausiids 10–20 mm—5.0, euphausiids > 20 mm—10.0, chaetognaths < 10 mm—2.0, chaetognaths 10–20 mm—5.0, chaetognaths > 20 mm—10.0, hyperiids < 5 mm—1.5, hyperiids 5–10 mm—5.0, copepods < 5 mm—2.0, and copepods > 5 mm—3.0. The methods of sampling and processing of zooplankton are described in detail in Koval (2003).

Feeding Study

The stomach contents were analyzed using the method described by Volkov and Chuchukalo (1986). From each trawl catch, the food lump from fish stomachs of the same species and similar fish size were combined into one sample. Prey items were then identified and total prey weight and weights of all prey components were measured.

The index of stomach fullness (ISF) was determined as:

$$ISF = (m_1/m_2) \cdot 10,000,$$

where m_1 is weight of food and m_2 is weight of fish. To show seasonal dynamics in salmon feeding intensity, we used TINRO-Center’s data collected in the southern Sea of Okhotsk and the western part of the Bering Sea in fall, and in the Pacific waters of the Kuril Islands in summer, 2004–2014.

Daily food ration (R) for different species of nekton was calculated using the methods of Novikova (1949), Yurovitsky (1962), Kogan (1963), and Gorbatenko (1996).

Total daily nekton consumption was determined as:

$$B = b \cdot R,$$

where B is weight of the food consumed by nekton (tons), b is mean nekton biomass over a certain period (tons), and R is daily food ration. Size, age, and seasonal, year-to-year, and regional differences were taken into account in the calculations.

Mortality Rate

Mortality rates of pink salmon for aggregated Okhotsk Sea stocks were assessed as an estimated abundance loss at different stages of the marine life cycle. For example, the estimated mortality rate of pink salmon in winter and spring is a percentage (%) of the ratio of pink salmon abundance in June in the Pacific waters along the Kuril Islands and the abundance of pink salmon juveniles in the southern part of the Sea of Okhotsk in September–November of the previous year. The estimated mortality rate of maturing pink salmon in summer is a percentage (%) of the ratio of total abundance of pink salmon approaching spawning rivers (catch and escapement) and pink salmon abundance in June in the Pacific waters along the Kuril Islands.

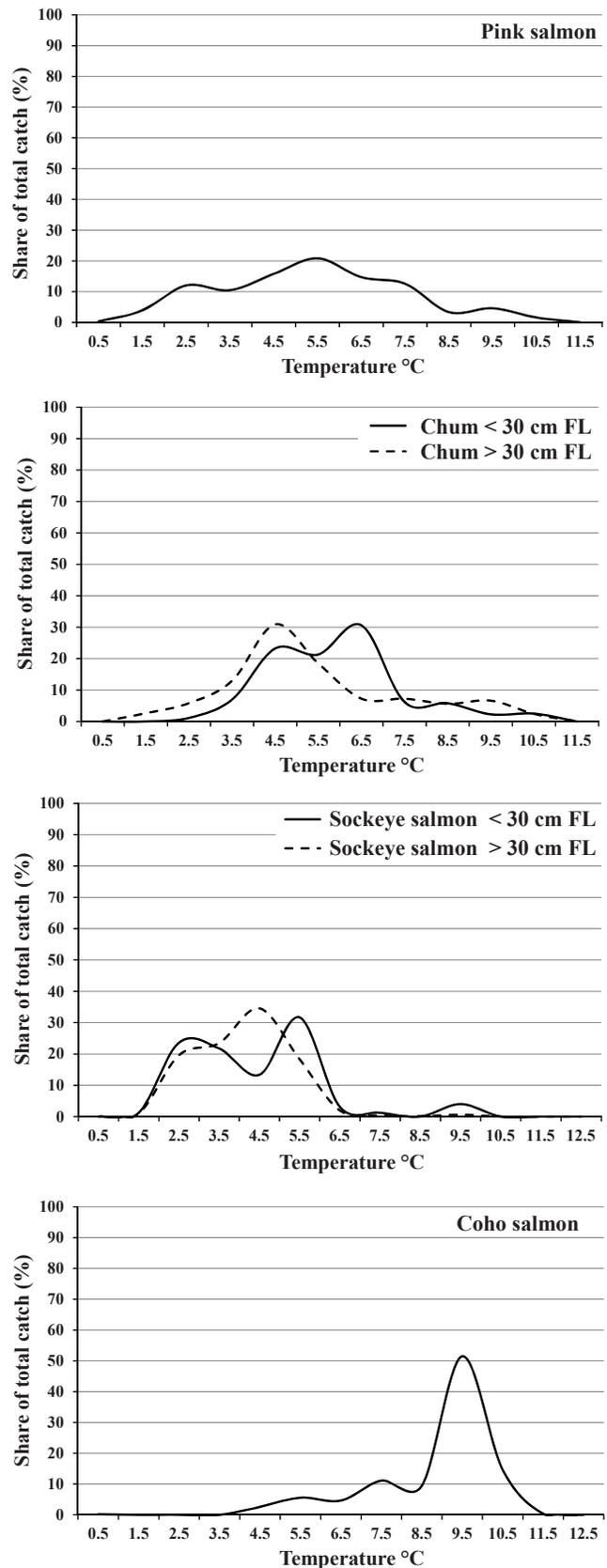


Fig. 2. Distribution of Pacific salmon catches at various temperatures (°C) in winter-spring 1986–1992 and 2009–2011 (from Figurkin and Naydenko 2013, with modifications).

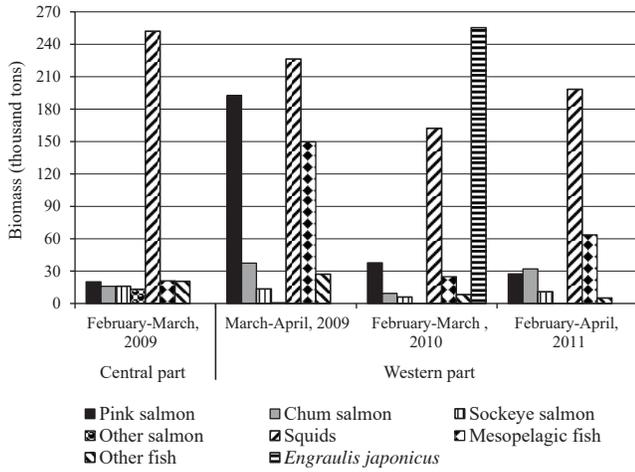


Fig. 3. Biomass (thousand tons) of nekton species and groups in the upper epipelagic (0–50 m) in the central and western parts of the Subarctic Frontal Zone and adjacent subarctic waters in winter-spring 2009–2011 (based on Starovoytov et al. 2010a, b; Naydenko et al. 2010a, b, 2011; Glebov et al. 2011).

RESULTS

Salmon Catches in Relation to Oceanographic Features

Five species of Pacific salmon (pink, chum, sockeye, coho, and Chinook salmon) were caught during the winter-spring cruises in the SAF. In winter, Pacific salmon were distributed across a wide temperature range (0.5–12.0°C), especially pink salmon, whereas sockeye and coho salmon tended to occupy cooler and warmer waters, respectively (Fig. 2). Most small chum salmon (< 30 cm FL) were distributed between 3°C and 8°C, while larger chum salmon shifted to cooler water with a peak temperature at 4.5°C.

Composition and Density of Nekton in Winter and Spring

Squids (mainly *Gonatopsis borealis* and *Watasenia scintillans*), Pacific salmon, mesopelagic fish and anchovy (*Engraulis japonicus*) dominated the nekton community in the upper epipelagic layer in SAF in winter and spring. The percentage of salmon in the total nekton biomass varied from 10 to 27% in different years (Fig. 3).

The average nekton density was 435 ± 106 and 470 ± 126 kg/km² in the central and western parts of the SAF, respectively. A high nekton density was noted in transitional subtropical waters in the western part of the SAF, where mainly anchovy, mesopelagic fish, and squid were caught (Fig. 3). The salmon catches in these waters were not high.

Abundance of Predators

We considered marine mammals and birds, and predatory fish, such as daggertooth (*Anotopterus nikparini*), lancetfish (*Alepisaurus ferox*), and salmon shark (*Lamna ditropis*) as the main predators of salmon during winter in the open ocean. Lampreys are important salmon predators in coastal areas. The predatory fish abundance in the SAF was low and few predatory fish specimens were captured during trawl surveys in winter. The percentage of salmon specimens bitten by predators was lower (0.1–1.5%) in open ocean waters in winter than in coastal areas along the Kuril Islands in summer (1.8–2.6%; Table 1).

Biomass and Composition of Zooplankton Prey Resources

Zooplankton biomass varied among sampling locations, water layers, seasons, and time of day. The large-size zooplankton (animals > 3.2 mm) formed the basis of the forage zooplankton biomass.

Mean winter biomass (in February–March) of large-size zooplankton was 451.2 and 479.7 mg/m³ in daylight and night-time, respectively, in the epipelagic (0–200 m) layer in the western part of the SAF. In the central part of the SAF,

Table 1. The number of fish traumatized by predators caught during research in the Subarctic Frontal Zone and adjacent subarctic waters in February to April 2009–2011 and in Pacific waters of the Kuril Islands in June to July 2010–2012.

	Winter-Spring				Summer		
	Subarctic Frontal Zone				Pacific waters of Kuril Islands		
	Central		Western		2010	2011	2012
2009	2009	2010	2011				
Marine Mammals	0	0	0	1	14	21	7
Daggertooth fish (<i>Anotopterus nikparini</i>)	3	5	2	0	66	4	41
Lamprey	5	0	0	0	7	27	3
Lancetfish (<i>Alepisaurus ferox</i>)	4	0	0	0	11	4	28
Unidentified traumas	10	2	2	0	2	11	35
Number of analysed fish	1656	1387	1003	1628	3838	3658	4244
Share of traumatized fish (%)	1.3	0.5	0.4	0.1	2.6	1.8	2.7

Table 2. Biomass of zooplankton in the epipelagic (0–200 m) layer in western and central parts of the Subarctic Frontal Zone (SAF) and adjacent subarctic waters at different times of day and seasons.

Time of the day	SAF Zone	Season	Number of stations	Biomass \pm standard error of mean (mg/m ³)		
				Large size (> 3.2 mm)	Medium size (1.2–3.2 mm)	Small size (< 1.2 mm)
Daylight	Western	Winter	70	451.21 \pm 35.92	65.13 \pm 10.18	112.12 \pm 7.0
Daylight	Western	Spring	38	714.35 \pm 72.18	109.32 \pm 17.13	110.52 \pm 11.26
Daylight	Western	Summer	123	722.39 \pm 45.59	19.0 \pm 1.8	25.66 \pm 2.45
Daylight	Central	Winter	31	401.57 \pm 53.11	117.85 \pm 29.77	49.94 \pm 7.84
Night-time	Western	Winter	67	479.68 \pm 47.04	83.55 \pm 8.72	94.13 \pm 6.81
Night-time	Western	Spring	23	900.47 \pm 178.14	153.64 \pm 32.58	110.68 \pm 18.19
Night-time	Western	Summer	58	667.82 \pm 66.07	24.8 \pm 3.03	34.22 \pm 5.55
Night-time	Central	Winter	25	463.73 \pm 70.06	94.91 \pm 19.98	48.09 \pm 9.69

mean estimates were practically the same: 401.6 and 463.7 mg/m³ in daylight and night-time, respectively (Table 2).

Euphausiids, copepods, chaetognaths, and gelatinous zooplankton (jellyfishes and salps) were the most abundant large-size zooplankton. The estimated biomass of euphausiids and copepods in the upper epipelagic layer was the highest at night and reached 7,818.5 and 4,602.5 mg/m³, respectively, in some samples. The mean biomass of euphausiids in the western and central parts of the SAF was 537.5 and 388.4 mg/m³, respectively; the mean biomass of copepods in these areas was 635.2 and 341.2 mg/m³, respectively.

Seasonal Changes in Zooplankton Biomass

The mean biomass of large-size zooplankton in spring (April) was higher than in winter by 1.6 and 1.9 times during daylight and night-time, respectively, in the epipelagic layer and by 2.0 times in the upper epipelagic layer in the western part of the SAF.

The mean summer biomass (in June–July) of large-size zooplankton was also higher than in winter by 1.4 to 2.3 times in different water layers (Tables 2 and 3).

The highest mean biomass of medium- and small-size zooplankton was recorded in spring, which was related to breeding and growth cycles of the great majority of zooplankton species (Tables 2 and 3).

There are no data on the seasonal dynamics of zooplankton biomass in the central part of the SAF because plankton research in spring and summer in this area has not been conducted.

Winter and Spring Feeding Intensity

Pink Salmon

We examined 1,587 pink salmon stomachs in February–March, and 1% of them were empty, 46.6% were partially filled (ISF below 50 ‰), 41.5% were full, and 10.9% of fish had excessively full stomachs (Fig. 4). The estimated mean winter ISF was 92.9 and 107.9 ‰ for salmon 10–30 cm and 30–50 cm FL, respectively (Table 4).

Seven hundred pink salmon stomachs were examined in April. The proportion of partially filled stomachs decreased to 20.2%, and the proportion of full stomachs increased up to 65.0% in April. The proportion of excessively full stomachs

Table 3. Biomass of zooplankton in the upper epipelagic (0–50 m) layer in western and central parts of the Subarctic Frontal Zone (SAF) and adjacent subarctic waters in different times of day and seasons.

Time of the day	SAF Zone	Season	Number of stations	Biomass \pm standard error of mean (mg/m ³)		
				Large size (> 3.2 mm)	Medium size (1.2–3.2 mm)	Small size (< 1.2 mm)
Daylight	Western	Winter	70	596.98 \pm 92.45	97.62 \pm 15.84	183.68 \pm 14.87
Daylight	Western	Spring	29	1223.61 \pm 166.44	236.83 \pm 48.43	213.34 \pm 29.09
Daylight	Western	Summer	120	1376.73 \pm 109.61	32.00 \pm 2.97	50.08 \pm 4.32
Daylight	Central	Winter	31	1430.17 \pm 312.22	236.66 \pm 49.28	111.29 \pm 20.46
Night-time	Western	Winter	65	1593.30 \pm 344.54	116.20 \pm 22.31	220.68 \pm 16.96
Night-time	Western	Spring	15	3129.35 \pm 861.47	499.17 \pm 210.69	339.54 \pm 63.66
Night-time	Western	Summer	57	1422.95 \pm 154.19	57.89 \pm 9.48	73.43 \pm 10.66
Night-time	Central	Winter	25	999.41 \pm 159.48	138.17 \pm 31.69	77.41 \pm 13.32

increased up to 14.4% (Fig. 4). Mean spring ISF were 104.4 and 127.4‰ for pink salmon 10–30 and 30–50 cm FL, respectively (Table 4).

Chum Salmon

A total of 985 chum salmon stomachs was examined in February–March and April. Mean winter ISF for chum salmon 10–30 cm FL was at the same level as for pink salmon—99.3‰. The ISF estimated for chum salmon sized 30–50 and > 50 cm FL was lower (69.9 and 24.9‰, respectively). In spring, the feeding intensity of chum salmon was higher than that in winter, but lower in comparison with pink salmon (Table 4).

Sockeye Salmon

A total of 777 sockeye salmon stomachs was investigated. The feeding intensity of sockeye salmon sized 10–30 and 30–50 cm FL was lower in comparison with both pink and chum salmon in February–March and April. The ISF estimated for large-size fish was at the same level as for chum salmon (Table 4).

Coho Salmon

The ISF for coho salmon < 50 cm FL was 93.7±21.7‰ in February–March.

Seasonal Changes in Salmon Feeding Intensity

Pink Salmon

Monthly variations in pink salmon stomach fullness indices revealed that the highest ISF values occurred in salmon < 30 cm FL in September and in fish 30–50 cm FL in April (Fig. 5). A one-way ANOVA showed significant ($p < 0.50$) differences between mean ISF of pink salmon juveniles in September and ISF estimated for all pink salmon size groups in other months. It also showed no significant difference in the ISF of fish < 30 cm FL in September and the ISF of fish 30–50 cm FL in April. Comparison of significant differences between samples is presented in Table 5. The feeding intensity of juvenile pink salmon decreased from September to February–March. However, no statistically significant difference was found between feeding intensity

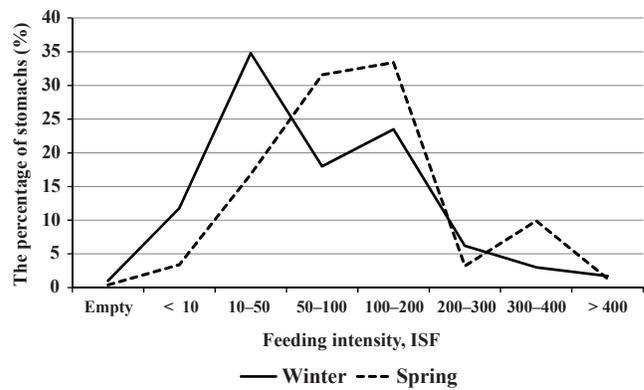


Fig. 4 . The feeding intensity of pink salmon in the Subarctic Frontal Zone and adjacent subarctic waters in winter and spring of 2009–2011.

of pink salmon < 30 cm FL in February and fish 30–50 cm FL in June–July.

Chum Salmon

The highest feeding intensity of chum salmon was observed for fish < 30 cm FL in August and September; in October–November, their feeding intensity decreased and persisted at this level until February (Fig. 6). There was no significant difference found between ISF indices in October–November and February (Table 6). As for fish 30–50 cm FL, the feeding intensity increased in April, remained high in summer, and decreased from September to November. The ISF index decrease was also noted for fish > 50 cm FL from September to October–November, and the lowest ISF was estimated in February. In April, the feeding intensity of this chum salmon size group increased.

Sockeye Salmon

Monthly variations in feeding intensity of small-size sockeye salmon (< 30 cm FL) were similar to those for pink and chum salmon (Fig. 7; Table 7). No significant difference was found between the winter ISF index for fish < 30 cm FL and the summer ISF for fish 30–50 cm FL (Table 6). However, in summer and fall, the ISF estimated for sockeye

Table 4. The feeding intensity of Pacific salmon in the Subarctic Front Zone and adjacent subarctic waters in February–April of 2009–2011.

Species	Month	Mean ISF ± SE of mean		
		10–30 cm	30–50 cm	> 50 cm
Pink	February–March	92.85 ± 11.46	107.91 ± 20.06	
Pink	April	104.35 ± 28.99	127.36 ± 11.45	
Chum	February–March	1593.30 ± 344.54	116.20 ± 22.31	220.68 ± 16.96
Chum	April	3129.35 ± 861.47	499.17 ± 210.69	339.54 ± 63.66
Sockeye	February–March	1422.95 ± 154.19	57.89 ± 9.48	73.43 ± 10.66
Sockeye	April	999.41 ± 159.48	138.17 ± 31.69	77.41 ± 13.32

Abbreviations: ISF—index of stomach fullness (‰); SE—standard error of mean.

salmon was lower in comparison to pink and chum salmon. The feeding intensity of fish 30–50 and > 50 cm FL was low in winter but increased in April. The lowest ISF value was estimated for fish > 50 cm FL in winter.

DISCUSSION

Winter is generally considered as a critical period for salmon because of low temperatures and limited food availability, as inferred from low lipid contents in their muscle. This is thought to jeopardize salmon survival on the high seas during winter.

However, some arguments do not support this hypothesis. First, there is significant variability in salmon mortality during the wintering period in the open ocean. Pink salmon mortality from fall to the next year’s pre-spawning approaches to the coast can vary from 75 to 91% depending on the year (Radchenko 2012). According to 2004–2013 data, mortality of pink salmon in the Sea of Okhotsk integrated stock totaled 36–80% (mean 60%) over six months from September–November to June–early-July (Fig. 8). Second, salmon mortality over winter is not higher than their mortality during freshwater, estuarine, or early marine phases of their life history. During the freshwater and estuarine phases, about 99% (and even more) of the total abundance of a pink salmon year class may be eliminated (Radchenko and Rassadnikov 1997; Shuntov and Temnykh 2008, 2011). Trudel et al. (2012) estimated that from 61 to 99% of the juvenile Marble River Chinook salmon died over the winter months in different years. Previous studies (e.g. Karpenko 1998; Wertheimer and Thrower 2007; Beamish et al. 2012)

also indicate that early marine mortality can be substantial in juvenile salmon. Third, low temperatures, variable food availability, predators and other factors affect salmon during all phases of their life history. Below, we consider the impact of each of these factors on the overwintering survival of salmon (mainly pink salmon as an example) to define whether winter is the critical period.

Hydrological Conditions

It is well known that hydrological conditions, as a factor affecting salmon mortality (both directly and indirectly through variability in the food supply), is mainly important during the freshwater, estuarine, or early marine phases of the salmon life cycle. Despite highly variable ocean conditions, no extreme SST changes were observed throughout

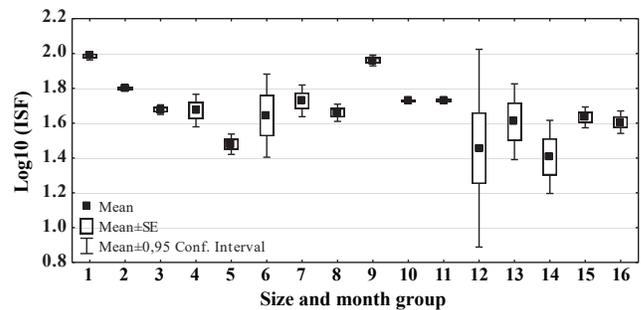


Fig. 5. Dynamics of feeding intensity (ISF, ‰) of pink salmon in the Far Eastern Seas and the central and western parts of the Subarctic Frontal Zone and adjacent subarctic waters in 2000–2014. Pink salmon size group and month as described in Table 5.

Table 5. The levels of statistically significant differences (*p*-level) of average pink salmon feeding intensity for different size-groups in different months. Bold values indicate differences between size and month groups are significant at *p* < 0.05.

Size and Month Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 10–30 cm Sep																
2 10–30 cm Oct	0.0															
3 10–30 cm Nov	0.0	0.0														
4 10–30 cm Feb	0.0	0.0	0.9													
5 10–30 cm Mar	0.0	0.0	0.0	0.0												
6 10–30 cm Apr	0.0	0.1	0.7	0.8	0.1											
7 30–50 cm Oct	0.0	0.0	0.4	0.5	0.1	0.8										
8 30–50 cm Nov	0.0	0.0	0.0	0.0	0.3	0.0	0.0									
9 30–50 cm Feb	0.0	0.1	0.3	0.4	0.0	0.4	0.2	0.0								
10 30–50 cm Mar	0.0	0.0	0.5	0.8	0.0	0.9	0.5	0.0	0.1							
11 30–50 cm Apr	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0						
12 30–50 cm Jun	0.0	0.0	0.0	0.2	0.0	0.4	0.1	0.0	1.0	0.0	0.0					
13 30–50 cm Jul	0.0	0.0	0.0	0.2	0.0	0.4	0.1	0.0	1.0	0.0	0.0	0.9				
14 30–50 cm Aug	0.0	0.2	0.4	0.4	0.9	0.5	0.6	0.9	0.3	0.4	0.1	0.3	0.3			
15 >50 cm Jun	0.0	0.0	0.2	0.5	0.0	0.9	0.8	0.0	0.1	0.5	0.0	0.0	0.0	0.5		
16 >50 cm Jul	0.0	0.0	0.1	0.2	0.0	0.7	1.0	0.0	0.0	0.2	0.0	0.0	0.0	0.6	0.5	

salmon wintering areas in the SAF. Pacific salmon have evolved to live in the open ocean through the development of various species-specific adaptations including dwelling in specific ranges of winter temperatures.

In 1986–1992 and 2009–2011, 87% of pink salmon and 83% of large chum salmon were captured within a 2.5–7.5°C SST range. Between 90 and 97% of small and large sockeye salmon, respectively, were caught in colder waters with SST of 2.5–5.5°C. In contrast, 87% of coho salmon were captured in warmer waters (with SST of 7–10°C; Fig. 2). Thus, in winter each salmon species is distributed in its “comfort zone”, i.e., within water masses with a certain thermohaline structure which is suitable for their wintering. The temperature conditions preferred by each salmon species determine their metabolic and growth rates, etc. This is the subject of separate study and is not discussed here. Radchenko (2012) defined the strength of this factor’s influence (the hydrological regime in a wintering zone in Pacific Ocean), which can affect mortality rates of salmon, as “moderate”.

Predation Mortality

Predator pressure that can limit salmon survival is a “top-down” control factor. Based on data from 2009–2011, we consider that “top-down” control was weaker in the open Pacific Ocean due to the low abundance of predators in salmon overwintering areas (Table 1).

Food Supply

The food supply factor supporting salmon survival and production is very important at all periods in their life cycle. Indicators such as biomass, composition and energy content of forage zooplankton resources, and salmon feeding intensity indices define this term. Food supply conditions are usually considered as a density-dependent factor, so we can estimate its strength by the abundance of food consumers (salmon and other nekton groups), i.e., by the density of nekton distribution.

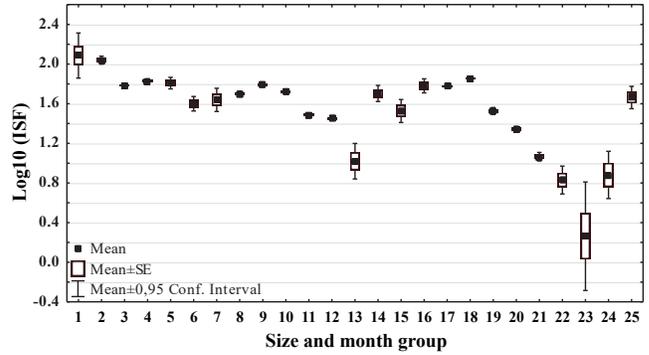


Fig. 6. Dynamics of feeding intensity (ISF, ‰) of chum salmon in the Far Eastern Seas and the central and western parts of the Subarctic Frontal Zone and adjacent subarctic waters in 2000-2014. Chum Salmon size group and month as described in Table 6.

Table 6. The levels of statistically significant differences (*p*-level) of average chum salmon feeding intensity for different size-groups in different months. Bold values indicate differences between size and month groups are significant at *p* < 0.05.

Size and Month Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 10–30 cm Aug																									
2 10–30 cm Sep	0.8																								
3 10–30 cm Oct	0.1	0.0																							
4 10–30 cm Nov	0.2	0.0	0.0																						
5 10–30 cm Feb	0.1	0.0	0.7	0.7																					
6 10–30 cm Mar	0.0	0.0	0.0	0.0	0.0																				
7 10–30 cm Apr	0.0	0.0	0.0	0.0	0.0	0.6																			
8 30–50 cm Jun	0.0	0.0	0.0	0.0	0.1	0.0	0.3																		
9 30–50 cm Jul	0.1	0.0	0.9	0.0	0.7	0.0	0.0	0.0																	
10 30–50 cm Aug	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.5	0.0																
11 30–50 cm Sep	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0															
12 30–50 cm Oct	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0														
13 30–50 cm Nov	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0													
14 30–50 cm Feb	0.1	0.0	0.2	0.1	0.3	0.2	0.5	1.0	0.2	0.8	0.0	0.0	0.0												
15 30–50 cm Mar	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.0	0.0	0.0	0.2	0.0	0.0	0.1											
16 30–50 cm Apr	0.1	0.0	0.9	0.3	0.7	0.0	0.1	0.1	0.8	0.2	0.0	0.0	0.0	0.4	0.0										
17 >50 cm Jun	0.1	0.0	0.4	0.0	0.6	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.3	0.0	1.0									
18 >50 cm Jul	0.2	0.0	0.0	0.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0								
19 >50 cm Aug	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.6	0.0	0.0	0.0							
20 >50 cm Sep	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0						
21 >50 cm Oct	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0					
22 >50 cm Nov	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
23 >50 cm Feb	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
24 >50 cm Mar	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
25 >50 cm Apr	0.0	0.0	0.0	0.0	0.1	0.1	0.5	0.7	0.0	0.5	0.0	0.0	0.0	0.8	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Some studies suggest that the winter biomass of forage zooplankton in the subarctic Pacific is quite low, about 10% of the summer biomass (Sugimoto and Tadokoro 1998; Nagasawa 1999, 2000). Such poor food conditions (with salmon starvation as a result) in the open ocean are considered a cause of low lipid contents in salmon muscle, leading to increased mortality in winter (Ishida et al. 2000; Nomura et al. 2000; Nomura and Kaga 2007). It was suggested that salmonids remain in cold waters in order to reduce their metabolic consumption (Nagasawa 2000).

According to our study, the forage zooplankton biomass is 40–70% lower in the western SAF in February–March compared with April and June–July (Tables 2, 3). However, a large percentage of preferred zooplankton prey (such as hyperiids, pteropods, euphausiids, and copepods) in salmon diets suggests that food availability may be sufficient to satisfy the food demands of wintering salmon. Thus, we believe the winter decline in forage zooplankton biomass could not potentially lead to salmon starvation. In winter 2009–2011, the pink, chum and coho salmon 10–30 and 30–50 cm FL foraged intensively, although their feeding intensity was not as high as in fall. Distinctions in their feeding intensity could be the result of early life-history discrepancies. Survival and growth of juvenile pink and chum salmon with the shortest freshwater period required more energy resources in the fall and winter in comparison with sockeye salmon that have a longer freshwater residence period. Pink salmon spend only one winter and spring in the ocean with active somatic and gonadal growth beginning in spring. Therefore,

pink salmon feeding intensity is the highest among salmon in spring (Figs. 5, 6, and 7). The food supply in the western SAF during winter is presumably sufficient to support pink salmon metabolism while spring feeding intensity indicates the formation of an adequate forage zooplankton crop that supports rapid salmon somatic and gonadal growth, and migration. Coho salmon also spend one winter and spring in the ocean and have individual growth dynamics similar to those of pink salmon (Karpenko et al. 2013). Coho feeding was also active in winter and spring. Feeding intensity of sockeye salmon with body sizes 30–50 and > 50 cm FL are

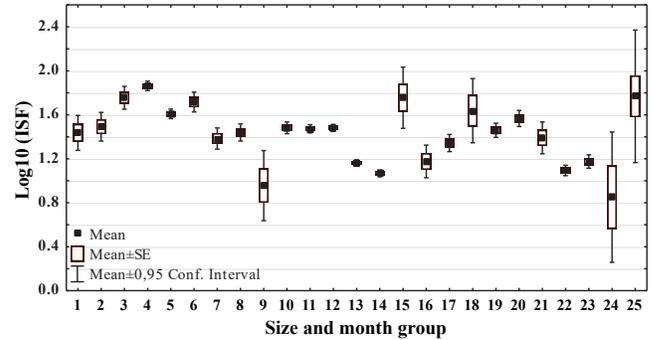


Fig. 7. Dynamics of feeding intensity (ISF, o/ooo) of sockeye salmon in the Far Eastern Seas and the central and western parts of the Subarctic Frontal Zone and adjacent subarctic waters in 2000-2014. Sockeye salmon size group and month as described in Table 7.

Table 7. The levels of statistically significant differences (*p*-level) of average sockeye salmon feeding intensity for different size-groups in different months. Bold values indicate differences between size and month groups are significant at *p* < 0.050.

Size and Month Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 10–30 cm Jun																									
2 10–30 cm Jul	0.6																								
3 10–30 cm Aug	0.0	0.0																							
4 10–30 cm Sep	0.0	0.0	0.3																						
5 10–30 cm Oct	0.0	0.1	0.1	0.0																					
6 10–30 cm Nov	0.0	0.0	0.7	0.0	0.1																				
7 10–30 cm Feb	0.6	0.2	0.0	0.0	0.0	0.0	0.0																		
8 10–30 cm Mar	1.0	0.5	0.0	0.0	0.0	0.0	0.5																		
9 10–30 cm Apr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0																	
10 30–50 cm Jun	0.6	0.9	0.0	0.0	0.0	0.0	0.2	0.4	0.0																
11 30–50 cm Jul	0.6	0.8	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.9															
12 30–50 cm Aug	0.6	0.9	0.0	0.0	0.0	0.0	0.2	0.4	0.0	1.0	0.9														
13 30–50 cm Sep	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0													
14 30–50 cm Oct	0.0	0.0	0.4	0.0	0.0	0.0	0.0																		
15 30–50 cm Nov	0.1	0.2	1.0	0.6	0.5	0.8	0.1	0.1	0.0	0.2	0.2	0.2	0.0	0.0											
16 30–50 cm Feb	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.9	0.1	0.0										
17 30–50 cm Mar	0.4	0.1	0.0	0.0	0.0	0.0	0.8	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0									
18 30–50 cm Apr	0.2	0.3	0.5	0.1	0.8	0.6	0.1	0.1	0.0	0.2	0.2	0.2	0.0	0.0	0.6	0.0	0.0								
19 >50 cm Jun	0.8	0.7	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.7	0.7	0.7	0.0	0.0	0.1	0.0	0.1	0.2							
20 >50 cm Jul	0.2	0.3	0.1	0.0	0.4	0.1	0.0	0.0	0.0	0.2	0.1	0.1	0.0	0.0	0.4	0.0	0.0	0.6	0.1						
21 >50 cm Aug	0.7	0.4	0.0	0.0	0.0	0.0	1.0	0.6	0.0	0.4	0.4	0.4	0.0	0.0	0.1	0.1	0.8	0.1	0.5	0.1					
22 >50 cm Sep	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0					
23 >50 cm Oct	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.8	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.1				
24 >50 cm Mar	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.7	0.8	0.0	0.7	0.1	0.0	0.0	0.0	0.1	0.9	0.6		
25 >50 cm Apr	0.3	0.4	1.0	0.8	0.6	0.9	0.3	0.3	0.0	0.4	0.4	0.4	0.1	0.0	1.0	0.1	0.2	0.7	0.4	0.5	0.3	0.0	0.1	0.1	

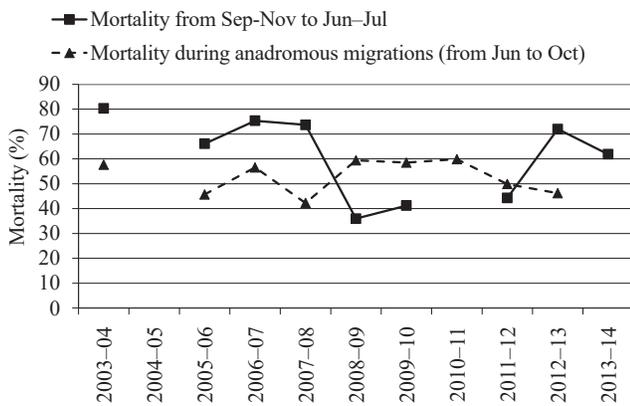


Fig. 8. The mortality (%) of pink salmon from the Sea of Okhotsk at various stages in their marine life history (data from 2003–2014). No surveys were conducted in 2004 and 2010.

defined as 'moderate' and 'low' in winter while the feeding intensity of smaller fish was higher. Different Pacific salmon species and size groups have different feeding intensities in winter and early spring. Differences in feeding intensity of salmon species may be a feature of their species-specific life strategy.

The decrease in the lipid content of salmon muscle tissue could also be explained by biochemical adaptations that are characteristic for species-specific life strategies of Pacific salmon. According to different studies (Nomura et al. 1999, 2000; Ishida et al. 2000; Kaga et al. 2006; Eerokhin and Klimov 2011; Kalchenko et al. 2013; Klimov et al. 2013; Lazhentsev and Maznikova 2014), the lipid content of juvenile pink and chum salmon muscle tissue decreases to 0.2–2.6% and 0.3–2.4%, respectively, from fall to winter (on average, by 4–12 times). The sockeye salmon life strategy differs from that of pink and chum salmon. In fall, the lipid content of sockeye salmon muscle tissue was lower than the lipid content of juvenile pink and chum salmon muscle. Consequently, the difference between lipid content in fall and winter was not considerable (Klimov et al. 2013; Eerokhin and Klimov 2011). Farley et al. (2011) found differences in the seasonal energetic signatures for lipid and protein of juvenile Bristol Bay sockeye salmon and assumed that these fish were not starving, but rather the larger sockeye were apparently utilizing energy stores to minimize predation in winter. Fasting may be a strategy to avoid predation, whereas feeding during winter may increase predation risk.

Changes in feeding intensity, lipid accumulation, and somatic growth rates from fall to spring reflect seasonal cyclic changes in salmon metabolism (Shvydkii and Vdovin 1999; Gorbatenko et al. 2008; Shuntov and Temnykh 2008). We also consider that the winter feeding and growth of salmon may be affected by their habitat temperature, but not by a poor food supply and/or prey availability in winter.

The abundance and density of planktivorous fish and squid are low in areas of salmon wintering. Therefore, the forage zooplankton grazing rate is not high. In general,

common nekton species (squid, salmon, mesopelagic fish, and anchovy) consume a small fraction of the forage zooplankton biomass available in winter. In 2009–2011, daily consumption of euphausiids, copepods and amphipods by these nekton groups did not exceed 0.07% of these zooplankton groups' biomass in areas where salmon live (Naydenko and Kuznetsova 2011, 2013). In comparison, planktivorous fish and squid consumed about 0.2% of these zooplankton groups' biomass daily in Pacific waters of Kuril Islands in summer 2004–2014 because the nekton density in this area was higher ($1,085 \pm 437$ to $4,636 \pm 1,898$ kg/km²) than in winter in the SAF (Khoruzhiy and Naydenko 2014; Naydenko and Khoruzhiy 2014). Thus, low food abundance cannot explain the high salmon mortality rates that are thought to occur during winter.

Critical Size and Critical Period Hypothesis

The mortality of young salmon in the first year of their life is believed to be related to their size to a high degree (Percy 1992; Willette et al. 1999; Kaev 2003; Moss et al. 2005). According to the critical size and critical period hypothesis (Beamish and Mahnken 2001; Farley et al. 2007), small, slower growing fish that accumulated fewer reserves in summer and fall are largely eliminated during their subsequent winter. Zavolokin and Strezhneva (2013) studied the size-selective mortality of pink salmon through measurements of scale increments in juvenile pink salmon that were caught in the southern Sea of Okhotsk in the fall of 2007 and 2008 and in fish of these year classes returning to spawn. The fish of the 2007 and 2008 generations had similar abundance in fall—1,003 and 950 million individuals, respectively, but different growth rates and different survival in winter. Smaller (mean weight (MW) 146 g) and likely slowly growing fish of the 2007 generation had lower winter survival (26%) because they depleted their own energy reserves in fall and winter faster than the larger fish. On the contrary, the larger (MW 180 g) and rapidly growing fish of the 2008 generation had good survival at 64%.

This hypothesis was applied to the Okhotsk Sea pink salmon of the 2011 and 2012 generations (with abundance of 939 and 1,128 million individuals, respectively). Survival of smaller fish (MW 107 g) of the 2011 generation reached 56% from fall to summer (in 6 months) while the survival of larger fish (MW 188 g) was low (28%). This suggests that size-selective mortality may be mediated by environmental conditions experienced prior to, during, and after winter, such as lipid accumulation, cold season duration, abundance and quality of prey, and predator distribution and abundance. The impact of these factors could compensate or strengthen the effects of body size and individual growth rate. There is no relationship between body size of juvenile east Kamchatka pink salmon and their winter mortality rate. Thus, the various combinations of initial (fall) and oceanic (winter) conditions define the mortality rate of salmon in the open ocean. Therefore, conclusions about overwinter size-selective mortality are

equivocal with data both consistent (e.g., Farley et al. 2011; Zavolokin and Strezhneva 2013) and inconsistent with this hypothesis (e.g., Middleton 2011; Trudel et al. 2012).

CONCLUSION

Many factors affect salmon marine survival in winter to varying degrees. However, it is difficult to determine the principal factor affecting winter mortality of salmon because there are too few estimates of mortality based on direct observations. Pacific salmon survival is likely determined by a complex interaction of abiotic and biotic factors.

The mortality of pink salmon ranged from 36–80% from September–November to June–early–July (in 6 months); it was not higher than the mortality during either the freshwater, estuarine, or early marine phases of their life history. Our conclusion is that the winter is a very important period for salmon, but may not be more critical than their early life periods in either fresh water or the ocean.

This study reviews the general problem of salmon survival in winter in the open ocean. For a more comprehensive explanation, it is necessary to broaden the range of data in the following areas: (1) studies of monthly dynamics of zooplankton biomass in areas where salmon live; (2) studies of the caloric content of oceanic zooplankton species in different seasons; (3) establish a data series on salmon energy contents at different stages of Pacific salmon life histories; (4) establish a data series on growth rates of different species of Pacific salmon at different stages of their life histories; and (5) studies of interactions between feeding activity and growth rates for different Pacific salmon species during winter.

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