Feeding and Energy Characteristics of Juvenile Pink Salmon During Fall Marine Migrations

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Abstract: Spatial distribution and energy metabolism of juvenile pink salmon (*Oncorhynchus gorbuscha*) feeding in the east part of the Sea of Okhotsk during September–October 1980–1990 were studied. In inshore waters caloric density of 40–100 g individuals increases rapidly, reaching a plateau at an average of 1,100–1,200 cal/g for fish with body weight about 120–150 g. In September juvenile pink salmon on the open Sea of Okhotsk feeding grounds begin their migration to wintering grounds. Body caloric content, daily rations (8.6–9.5% of total body caloric content), energy expenditures for growth (3.2–3.6%) and metabolism peak during this period when water temperature (11–12°C) is most favorable. By October, with the decrease in water temperature to 8–9°C, body calloric density declines to 900–1000 cal/g, daily rations to 6.0–8.5%, and energy expenditures for growth to 1.5–1.9%. At the same time, energy expenditures for swimming increase from 3.6–4.0% of total caloric content in September to 5% in October. These increased expenditures for active metabolism are caused by increased swimming of juveniles migrating to the southern areas of the Sea and to the Pacific Ocean.

INTRODUCTION

Juvenile pink salmon (*Oncorhynchus gorbuscha*) disperse widely from their reproductive areas to feeding grounds in the Sea of Okhotsk by fall of the year in which they hatch. For example, in 1995 pink salmon fingerlings from the South Kuril Islands reached 55°N by September of that year (Varnavskaya et al. 1998), and juveniles from the northern rivers arrived in waters above the South Kuril basin by the end of fall and beginning of winter (Shuntov 1989).

Abundance forecasts of Western Kamchatka pink salmon returning to spawn from the ocean are made from catches of juveniles caught by trawl in the Sea of Okhotsk. The reliability of these forecasts depends on the sampling of the stocks of feeding juveniles. They must be sampled at a stage of migration along the coast when they have left the shoal waters, where it is difficult or impossible to operate the trawl, but before they have had time to mix with stocks from other areas. Among physiological indicators of stages of feeding migration, energy content of the fish is especially important. Our study examines the energy content of juvenile pink salmon and its use in swimming and growth during fall migrations in the Sea of Okhotsk.

METHODS

Juvenile pink salmon were caught with a pelagic trawl in summer and fall in the eastern Sea of Okhotsk (51–58°N, from the coast of Kamchatka to 148°E) from August to October in 1982, 1986, 1989, 1990, 1991, 1995 and 1997. They were also caught using purse seines and beach seines along a 160 km coastal zone between 51–58°N in July to September, 1984, and June to August, 1987 and 1988. Fish growth in some stocks was estimated from catches separated by several days up to half a month according to the formulae:

$$\Delta W = (W_t - W_0)/t \quad \text{and} \qquad (1)$$
$$\Delta L = (L_t - L_0)/t \qquad (2)$$

where ΔW and ΔL are the daily increments in weight and length (fork length), respectively, W_t and L_t are weight and length of fish at time t, and W_0 and L_0 are weight and length of fish in the earlier catch.

To evaluate the cost of migration, we calculated a value we called migration intensity (i) as a fish's real length increment (ΔL) divided by the difference between average lengths of fish in a group with larger fish (L_{max}) and a comparable group with a smaller average length (L_{min}) at two stations where capture of the groups was separated by an interval of time (t):

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$$i = \Delta L/(L_{max}-L_{min})/t \quad \text{or} \quad (3)$$
$$i = \Delta Lt/(L_{max}-L_{min}) \quad (4)$$

Values of "i" range between 0 and 1. The further the values deviate from 1, the more heterogeneous the groups. Migration vectors are directed from stations with smaller average fish length towards stations with average larger fish.

Food consumption by fish was estimated from indices of stomach fullness, calculated as the ratio of weight of food in the stomach to body weight ($^{o}/_{ooo}$). We calculated daily rations according to the method of Romanova and Kogan (Kogan 1963), which is based on calculation of speed of digestion as it varies with feeding intensity. Standard basal metabolism was calculated using the following equations suggested by Vinberg (1956):

$$Q = (0.498/q)W^{0.76} \quad (5)$$
$$R = 24k4.86Q10^{-3}C^{-1} \quad (6)$$

where Q is oxygen consumed in ml/sample per hour, q is temperature coefficient for metabolism up to 20°C, W is body weight (g), R is metabolic expenditure (g/sample per day), k is a coefficient of activity equal to 1 for standard metabolism, and C is total caloric content of the body, kcal/g of wet weight.

Energy expenditures for metabolism and growth where rations and growth increments were observed were calculated using the basic equation of balance (Vinberg 1956):

$$0.8\, r = \Delta W + R \quad (7)$$
$$K_2 = 100\Delta W/0.8\, r \quad (8)$$

where r is ration (g/samples per day), ΔW is weight increment (g/samples per day), and K_2 is coefficient of use, or expenditure of assimilation, of the physiologically useful portion of food for growth. We used caloric content of various food organisms as given in the literature (Table 1). Fish food caloric content was assumed to be 1.0 kcal/g.

RESULTS AND DISCUSSION

Migration Routes and Sizes of Juvenile Pink Salmon

After emigrating to sea in April–May, and while adapting to the new habitat conditions, juveniles from the rivers of the western Kamchatka remain for a time in the inshore zone within 24–32 km of the shore. Catches made with a beach seine near river mouths in 1987 and 1988, and with a purse seine within 8–160 km of the coast revealed that only in June–July are juvenile pink salmon, chum salmon (*O. keta*) and sockeye salmon (*O. nerka*) observed in inshore waters. No juvenile salmon were caught beyond the 32 km zone. The narrow coastal zone of low salinity (29–30$^{o}/_{oo}$) surface water, resulting from river outflow, stretches along the complete west coast of Kamchatka. Thirty-two to 100km offshore salinities reach 33$^{o}/_{oo}$ (Davidov 1975). The inshore surface layer is characterized not only by low salinity, but by higher temperature (6–8°C) than offshore (4–6°C). By the beginning of August, water temperatures offshore increase to 8–10°C, while those inshore remain at 6–8°C.

The change in offshore water temperatures through July into August is associated with a redistribution of foraging juveniles of the various salmonid species present. Fingerling pink salmon begin to migrate towards open waters, assembling 160–192 km off the coast of Kamchatka in August (Yerokhin 1998). There are no juvenile salmon in the open Sea of Okhotsk during this period. In September, however, pink and chum salmon feed extensively throughout this Sea, while juvenile sockeye salmon continue to forage in inshore waters.

The September–October feeding migrations of juvenile pink salmon in the eastern Sea of Okhotsk follow two main routes, a long one and a short one (Varnavskaya et al. 1998). The longer route has two branches. An inshore branch proceeds north along the coast of Kamchatka to 58°N, swings westward

Table 1. Plankton caloric content (cal/g wet weight). OS = Sea of Okhotsk, AO = Atlantic Ocean, NPO = North Pacific Ocean.

Groups of organisms	Caloric density (kcal/g wet weight)	Area	Reference
Copepoda	1.5	OS	Shershneva 1991
Euphausiacea	1.39	OS	Shershneva 1991
Amfhipoda, hyperiidea	1.31	OS	Shershneva 1991
Amfhipoda, gammaridea	1.409	AO	Davis 1993
Chaetognatha	0.69	OS	Shershneva 1991
Appendicularia	0.86	AO	Davis 1993
Pteropoda	0.624	NPO	Davis et al. 1998
Cephalopoda	1.125	NPO	Davis et al. 1998

before entering Shelikhov Bay, and then moves southward along meridians 151–152°E. Juveniles following this inshore branch are fingerlings from rivers of western Kamchatka. The offshore branch of the long route proceeds southward. Fish using this offshore branch are from Kamchatka and Shelikov Bay, and also from the southern Okhotsk Sea, and Sakhalin. Fish in this offshore branch therefore have mixed origins.

The shorter migration route proceeds northward to 53–54°N, then westward to 149–150°E, then southward along 147–156°E. The largest juvenile pink salmon from the shorter route mix with juveniles from the longer route, and together they migrate towards the southern Kuril basin along the western periphery of this region. The smaller fish on this shorter route continue feeding in the area 51–53°N, 150–153°E until their body weight is sufficient for further migration southward.

Size groups of pink salmon in September–October coincide with these migration routes. The direction and relative intensity of migrations were determined using equation 4. Indices of "i" coincide in direction and value with fish united in separate areas (Fig. 1). The pink migrations along the coast of Kamchatka run in a northerly direction. Fish following this route are mostly small, and their abundance in inshore waters in September is higher than that of large fish (Fig. 2). Migrations along the western periphery with a southerly trajectory consist mainly of large salmon. Local migrations of low intensity ("i" from 0.1 to 0.3) occur in the southern part of this area between 150–154°E during the fall period of feeding migrations (of both large and small fish), and appear circular around the limits of food accumulation.

The intensity of migration to the warmer southern part of the sea is insignificant in September, but begins to increase by the end of the month, and continues doing so through October and November. Large fish that emigrated earlier are the first arrivals. In the western part of the Sea of Okhotsk, migrations are concluded by late migrating pink salmon from the northwest of Kamchatka, with schools of fish from Shelikhov Bay and the Magadan coast. These fish are characterized by slow growth, smaller sizes, and poor nutritional condition. These fish migrate southward in conjunction with the 6–7°C isotherm, and leave the northern part of the sea at the end of October and early November (Shuntov 1989; Karpenko et al. 1996, 1998). The migrations of juvenile pink salmon are closely related to processes of energy accumulation through food consumption, and its expenditure for growth, metabolism and swimming.

Daily Rhythm of Feeding by Juvenile Pink Salmon

The peak in stomach contents occurred between 17:00 and 21:00 hrs, when the index reached $100^0/_{000}$, but at other times of day it was lower or near this level (Figs. 3–5). Maximum stomach fullness indicates either that this is the most intensive feeding period, or that feeding was reduced or even stopped, and only digestion and removal of the food from the stomach continued. Some researchers have shown that the speed of food evacuation from the stomach (speed of digestion) is directly proportional to stomach fullness (Brett and Glass 1973; Hoar et al. 1983; Amineva and Jarzombek 1984; Smith 1986; Jarzombek 1996). The occurrence of individuals with extremely full stomachs is rare in nature. While the

Fig. 1. Size distribution (cm), and direction and intensity (i) of migrations of "small" (A) and "large" (B) juvenile pink salmon in September 1995, and of large juveniles in September 1997 (C).

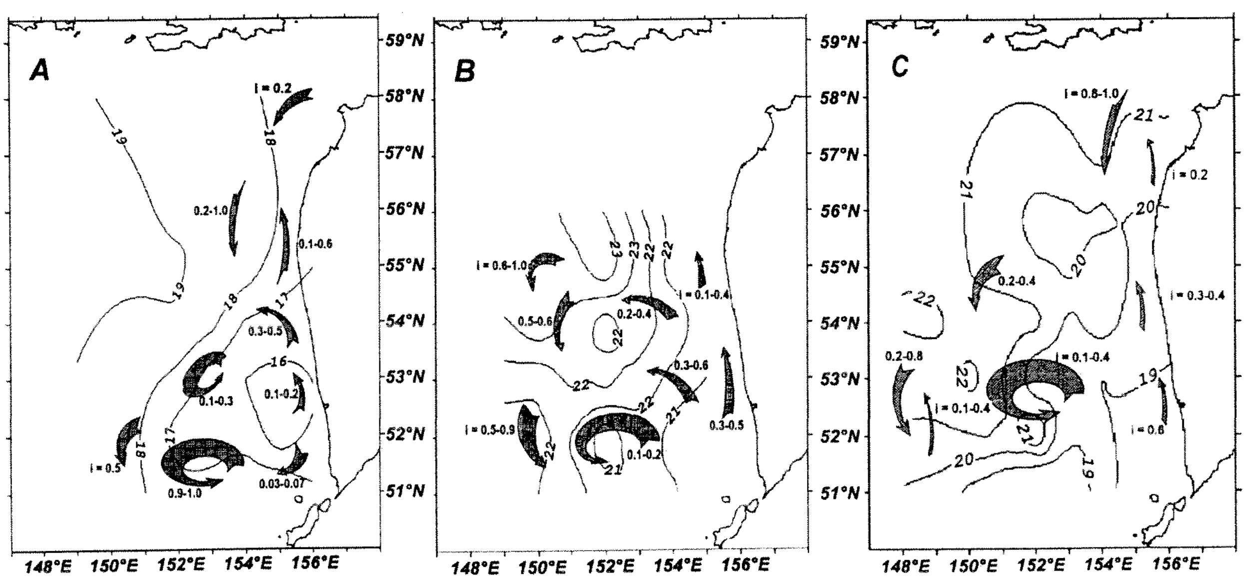


Fig. 2. Percentage of "large" pink salmon of all juvenile. A-1995, B-1997.

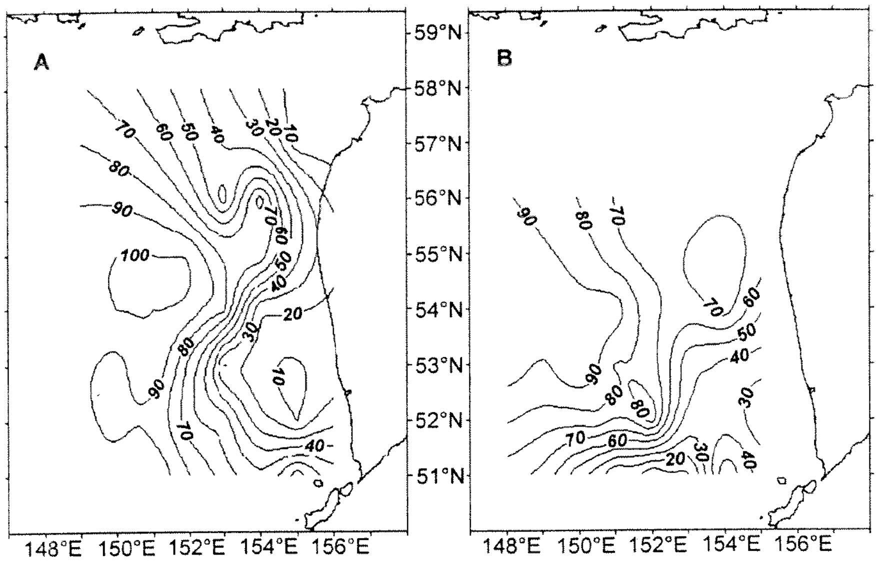


Fig. 3. Daily dynamics of feeding juvenile pink salmon in Sea of Okhotsk. October 1982 (A), September 1986 (B), October 1991 (C).

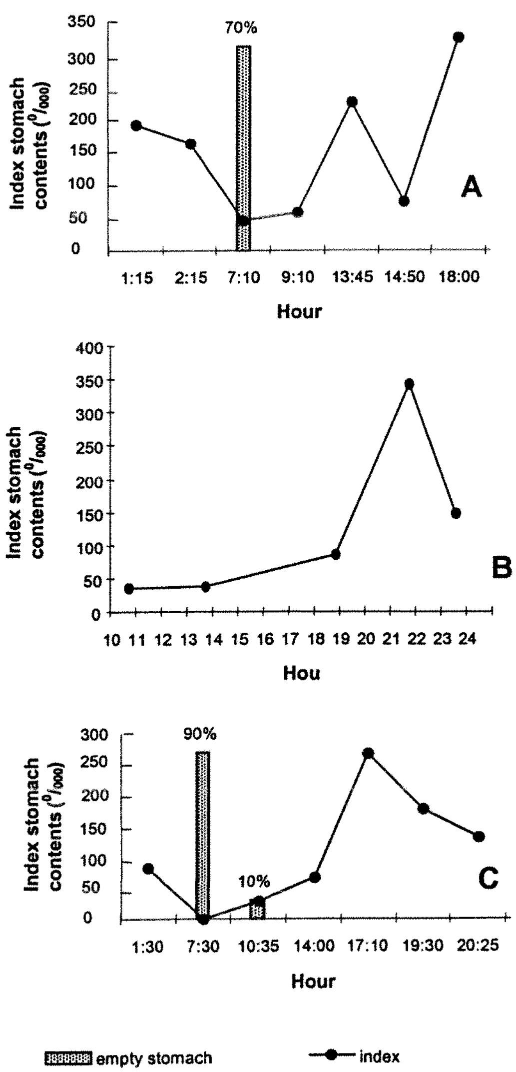


Fig. 4. The degree of pink salmon stomach fullness (0-empty, 4-full) in the Sea of Okhotsk. September 1997.

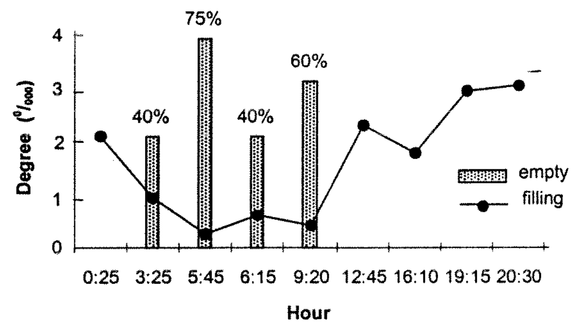


Fig. 5. Daily dynamics of juvenile pink salmon feeding in the Sea of Okhotsk. September to the beginning of October 1991.

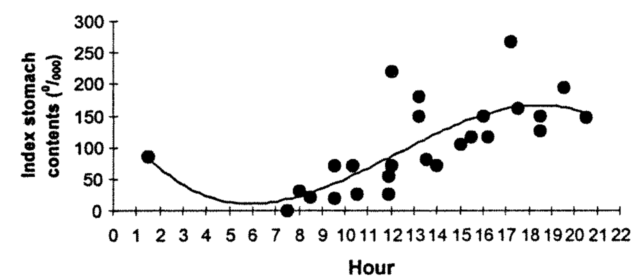


Table 2. Daily dynamics of feeding juvenile pink salmon in the Sea of Okhotsk, September 1995. *Limits: 0- empty, 4-full.*

Period	Empty stomach (%)	Degree of stomach fullness	
		Average	Range
morning	24	1.48	0–3
afternoon	0	2.10	1–4
evening	0	2.53	1–4

range in stomach fullness of individual fish was 25–450$^{o}/_{ooo}$, the range in average indices was much less (150–250$^{o}/_{ooo}$). We reasoned that the variability in speed of digestion was limited in comparison to range in individual speeds of digestion, and in calculating speed of digestion we assumed it was constant for the fish we sampled during the day. Generally 70–90% of fish had empty stomachs in the morning (Table 2, Figs. 3 and 4). We concluded that fish only began feeding in the morning after a pause during the night. From 07:00–13:00 hrs, speed of stomach evacuation was about 0.3% of average weight of fish per hour. We calculated rate of digestion during the evening assuming that when stomachs reached maximum fullness, fish stopped feeding. In one case, speed of digestion between 17:00 and 21:00 hrs was 0.40–0.48% of average body weight per hour (Fig. 3C). Analysis of the daily rhythm of feeding by juvenile pink salmon in 1982 and 1986, and at different periods in 1991 showed that speeds of stomach evacuation ranged from 0.3–0.5% of body weight per hour.

The hourly rate of feeding, as a percentage of full daily ration, clearly shows that the predawn pause in consumption lasts 3–4 hrs (Fig. 6). At this time, fish have empty stomachs, but digestion continues in the pyloric appendage and bowel. There is another pause in feeding in the evening between 17:00 and 20:00 hrs, after the period of maximum stomach fullness. Food digestion and evacuation of the stomach continue at this time.

Daily rations of food consumed by juvenile pink salmon were estimated for different years and locations using the observed diurnal feeding rhythm. Overall, fish caught in September and October throughout our sampling area weighed between 70 and 140 g, and consumed from 5–12 g of food a day, or 5.9–9.5% of their body weight (Table 3).

Energy Accumulation

In September, the caloric content of pink salmon fingerlings increased with length, at least up to 25 cm (Table 4). Differences in caloric content of fish inshore and offshore were not consistent. The relation between body weight and caloric content varied among years and locations (Figs. 7–9), but showed a consistent pattern of first increasing and then decreasing with weight at any one time or place. Between

Fig. 6. Hourly rations of juvenile pink salmon as a percentage of total daily ration.

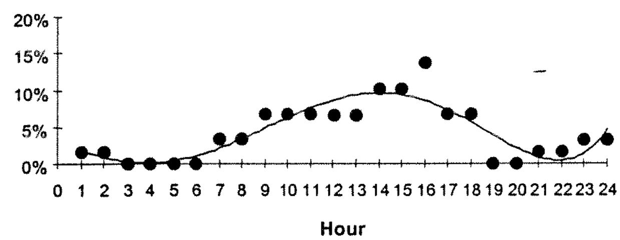


Table 3. Energy metabolism of juvenile pink salmon in the Sea of Okhotsk.

Date & location	Prey caloric density (kcal/g wet weight)	Predator caloric density (kcal/g wet weight)	Average body weight of fish (g)	Daily ration (g)	Daily ration (prey's caloric density converted to predator's) g	Daily ration ratio of body weight (%)	T° C water	Expenditure for body growth g	Expenditure for body growth ratio of body weight (%)	Expenditure for active metabolism g	Expenditure for active metabolism ratio of body weight (%)	Number of fish
1982, October 53° N, 154°30′ E	0.898	1.030	74.80	5.064	4.415	5.90	8°	1.419	1.90	2.113	2.82	62
1986, September, 14–19 52–54° N, 150°30′–152°30′ I	1.316	1.439	125.13	11.77	10.764	8.60	12°	4.014	3.21	4.597	3.67	50
1991, September, 20–25 South-west	1.271	1.103	130.18	10.747	12.387	9.52	11°	4.66	3.58	5.250	4.03	72
1991, October, 2–5 North-west	1.119	0.916	104.86	7.019	8.582	8.18	8°	1.604	1.53	5.262	5.02	50
1991, October, 11 54°N; 152°E	1.004	0.916	138.83	10.74	11.772	8.48	9°	2.291	1.65	7.127	5.13	70

Table 4. Average caloric content (cal/g) over years 1982, 1986, 1989, 1990, 1991, 1995 of juvenile pink salmon in the Sea of Okhotsk.

Location	Body length (cm)	September		October		Number of fish
		offshore	inshore	offshore	inshore	
"North"	below 19	-	-	817.1	879.4	20
	19–25	1376	1175	1033.4	864.5	78
	above 25	971.1	994.5	1004.9	-	29
"South"	below 19	1047	1021	1030	-	67
	19–25	1219.2	1194.6	1591	-	77

Fig. 7. Pink salmon caloric density in the Sea of Okhotsk, 1989: September, 52–53°N; 153–154°E (A); September 1991, 54°N (B); beginning October 1991, 56–57°N, 149–154°E (C).

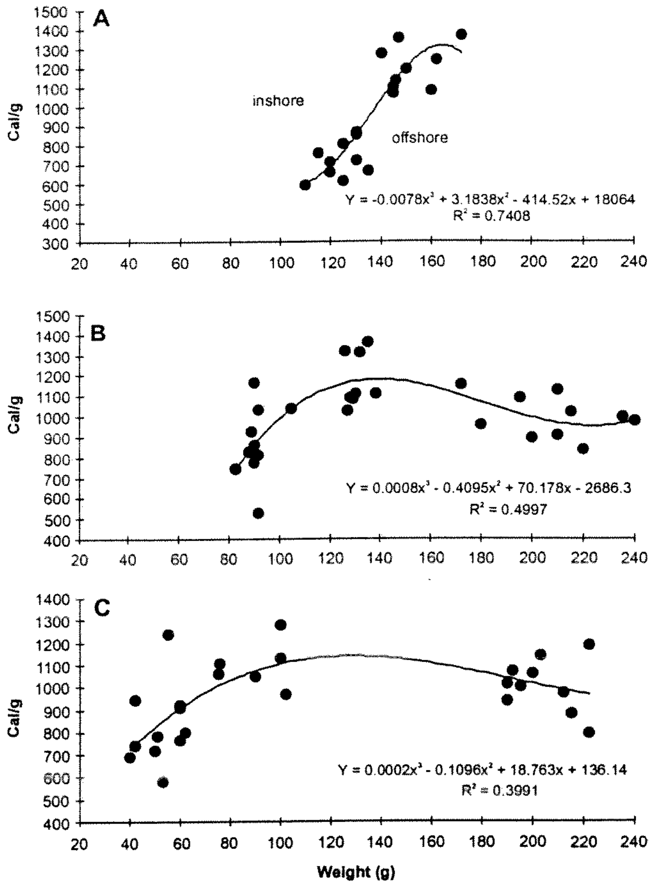


Fig. 8. Pink salmon caloric density in Sea of Okhotsk. September 1990, 51–54° N, 153–154° E (A); September 1991, 54° N (B); beginning October 1991, 56–57° N, 149–154° E (C).

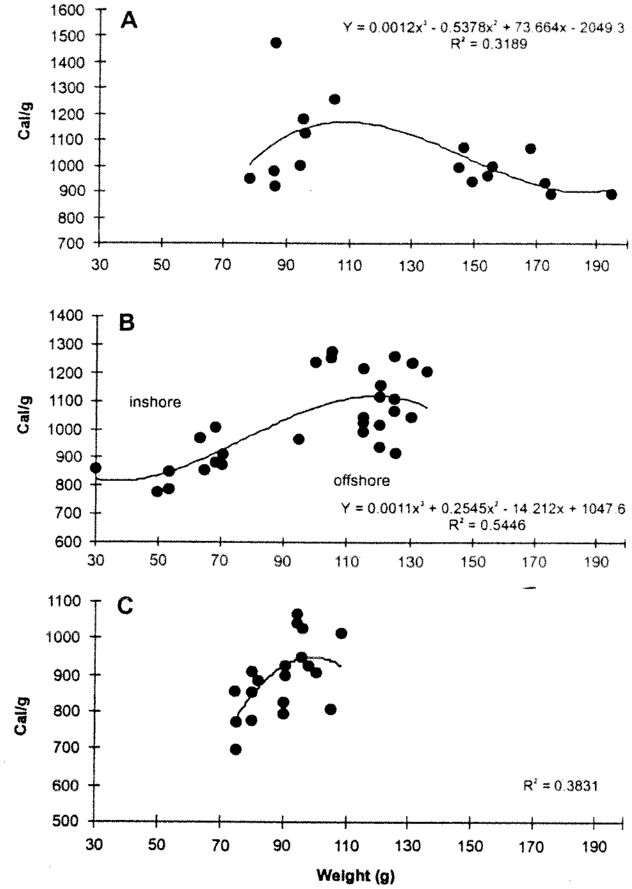
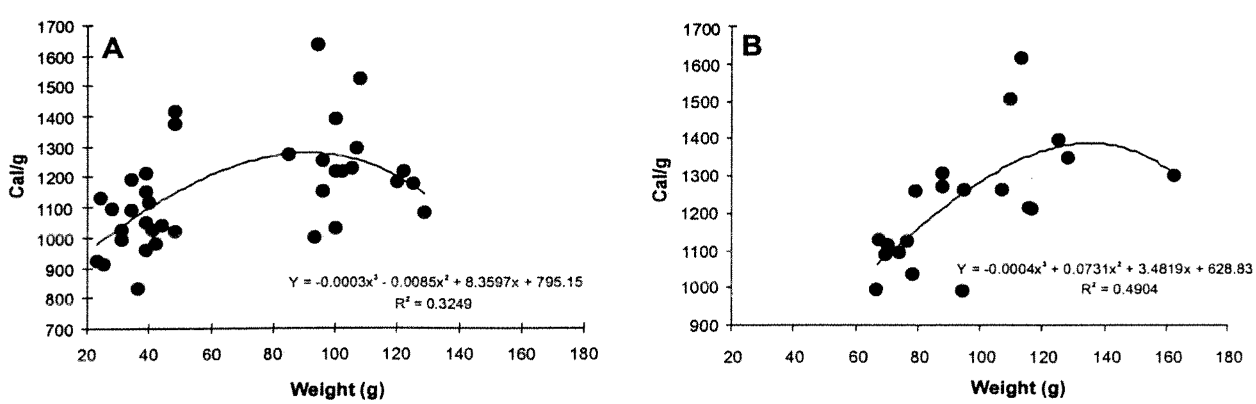


Fig. 9. Pink salmon caloric density in Sea of Okhotsk. September 1995, 52° N, 150–155° E (A); September 1997, 52–53° N, 148–154° E (B).



40 and 100 g, caloric content of fish rose rapidly, reaching a peak at around 1,100–1,200 cal./g for fish weighing 100–140 g in inshore waters, and for 120–160 g fish offshore in the Sea of Okhotsk. With further growth, caloric density (cal./g) declined.

Energy Expenditures by Juvenile Pink Salmon

Daily energy expenditures for fish growth range from 3.2–3.6% of body weight, and expenditures for metabolism 3.7–4.0% when temperatures are around 11° and 12°C (Table 3). Daily ration at this time is 9.0–9.5% of body weight (Table 3).

According to Vinberg (1956), energy lost in urine and excrement is 20% of food consumed, the physiologically useful portion of energy in food being, on average, 80% (= r_{phys}). In September, juvenile salmon expend 46–47% of this physiologically useful energy in food (r_{phys}) on growth, and 53% on active metabolism. With the decrease in temperature in October, ration is reduced by up to 6.0–8.5%, and growth increment is reduced by up to 1.7–1.9% of body weight per day. As a result, energy expenditure of assimilation (K_2) is reduced by 29–40%, while energy expenditure for active metabolism is simultaneously increased up to 60–70% of r_{phys}. Active swimming and intensification of migration by juveniles to the southern part of the Sea of Okhotsk and further to the Pacific Ocean cause the increase in expenditure for active metabolism. The reduction in growth and simultaneous increase in active metabolism are especially obvious in the northern part of the Sea of Okhotsk. In northern regions (56–57°N) during the first ten days of October 1991, the coefficient of expenditure of assimilation (K_2) of juvenile pink salmon decreased by 23.4%, but expenditures for active metabolism increased up to 76.6% of r_{hfys}. From here juvenile pink salmon must migrate south to wintering grounds, while fish located south of 55°N need only make low intensity local feeding migrations. Energy expenditures for active metabolism are higher than those for resting basal metabolism calculated by the formula of Vinberg (1965) (Table 5). Depending on the stage of feeding migration and physiological state, expenditures for active metabolism are 6–8 times higher than the level of basal metabolism in September–October.

CONCLUSIONS

From the beginning of August, pink and chum salmon start to leave the inshore waters for warmer offshore waters. In September, aggregations of juvenile pink and chum salmon form, as a result of localized migrations, where food is plentiful. Favorable temperatures allow indices of caloric body content, daily rations, energy expenditures for growth and metabolism to reach maximum values, marking the completion of this stage of short range feeding migrations, and readiness for prolonged migration. By the end of September and in October, juvenile pink salmon reach lengths of 24–26 cm and weights of 130–180 g earliest in the outer western regions of the sea. Large fish are the first to begin migration to wintering grounds.

With the commencement of prolonged migrations, behavioural strategy of juvenile fish changes. Movement is unidirectional and extends beyond feeding grounds, and consequently feeding is diminished. Food intake (ration) is reduced. The classical description of the positive dependency of feeding efficiency on food density, suggested by V.S. Ivlev (1977) is apparent. As intake of food energy is reduced, the balance of its use is altered toward a reduction for growth, and an increase for swimming.

Table 5. Basal metabolism of juvenile pink salmon calculated by formula $R=24kQ4.86 \cdot 10^{-3}C^{-1}$ (Vinberg 1956)

Date & location	Average body weight of fish (g)	Value «k» for fish at rest	Expenditure for basal metabolism		Real value «k» (the relation of active to basal metabolism)
			g	ratio of body weight (%)	
October 1982. 53° N, 154°30′ E	74.80	1	0.430	0.57	4.9
14–19 September 1986. 52–54° N, 150°30′–152°30′ E	125.13	1	0.754	0.60	6.1
September 20–25 1991. South-west	130.18	1	0.888	0.68	5.9
October 2–5 1991. North-west	104.86	1	0.625	0.60	8.4
October 11 1991. 54°N, 152°E	138.83	1	0.883	0.64	8.1

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