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Energy Consumption and Expenditure of Juvenile Salmon during Post-Catadromous Feeding Migrations in the Okhotsk Sea

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External environment influences on rapidity of all vital processes changing intensity of metabolism. Dynamics of feeding conditions can be analyzed by balancing the elements of metabolism in a particular data series. Classical equation of "standard" metabolism (Equation 1) is not suitable for this comparison. Values of "standard" metabolism were tested on fish at the state of minimum activity (nearly motionless state) in the laboratory: $Q_{st} = (a/q)W^k$ (equation 1), where Q_{st}, consumed oxygen, ml/sample an hour; a, speed of oxygen consumption ml/hour by fish with a weight of 1g (for salmon = 0.498 ml/hour); *q*, temperature correction to adjust metabolism indexes to real temperature according to Krog's normal curve; *W*, weight of fish, g; *k*, coefficient, for salmon = 0.76 (Winberg 1956). Thus, it is necessary to operate values of metabolism for fish in natural conditions.

The main aim of this work was to determine real level of metabolism and its elements in natural habitat conditions of fish. One of the research tasks is calculation of transient coefficient from standard to active metobolism (coefficient "Winberg-2") (Mann 1965; Shulman and Urdenko 1989): $k_{V2} = Q/Q_{st} = A/a$ (Equation 2), where Q, consumed oxygen, ml/sample. an hour in conditions of natural activity, *A*, speed of oxygen consumption ml/hour by fish with a weight of 1g in conditions of natural activity.

Contents of 1500 stomachs were taken for quantitive and qualitative analysis of feeding, 3,342 fish samples were weighted to calculate daily increments, 238 fish samples were taken for calculating calorie content.

Calculations of fish increments: Growth diagrams were built to obtain values of daily increments (coefficient of "x") of regression line $y = ax + в$ (Equation 3).

Calculations of daily rations: Calculations of daily rations were based on stomach contents of fish caught at daily stations (series of trawling were done every 2–3 hours during the day at one area "point"). An example of daily ration calculation of is given in Table 1.

The column I—remainder (index of fullness) includes food mass in stomachs in grams per sample. Calculation of average speed of food digestion from a stomach (*v*) in g/hour/sample is based on food intensity drops (Romanova 1958; Kogan 1963; Yerokhin and Shershneva 2000).

Weight of educed food (g/samples) for each sampling from daily series is calculated according to the formula $ef = v\Delta T_i$ (Equation 4), and weight of consumed food is calculated as $cf_i = ef_i + I_i - I_{(i-1)}$ (Equation 5).

Table 1. Dynamics of feeding and daily ration of juvenile pink salmon based on the data of daily station in the south-western waters of Kamchatka on October 2–3, 1997.

Interval between stations in a series, hr:min	∆T–Interval between stations, hour	Average food weight per sample, g		
		cf—consumed	*ef*—educed	*I*—remainder
00:35–3:35	2.50	0.327	0.893	0.340
3:35–5:55	2.84	0.822	1.014	0.148
5:55–6:25	0.50	0.084	0.179	0.053
6:25–9:30	3.08	1.326	1.100	0.279
9:30–12:55	3.42	1.450	1.221	0.508
12:55–16:15	3.33	1.376	1.189	0.695
16:15–19:25	3.17	2.073	1.132	1.636
19:25–20:45	1.33	0	0.567	1.069
20:45–00:35	3.83	1.204	1.367	0.906
∑ = daily ration:		8.660	8.660	

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Table 2. Balance of energy metabolism of juvenile pink salmon in the Okhotsk Sea.

Year	Period and location	Temperature of water layer (C°)	Caloric content of food (kcal/g of wet weight)	Caloric content of fish (kcal/g of wet weight)	Total caloric content (kcal)	Total caloric content of daily ration (kcal)		Real expenditure for metabolism							k$_{V2}$	Number of fish
								total		body growth		K$_2$	active metabolism			
						kcal	%	kcal	%	kcal	%		kcal	%		
1986	September, 14–19 52–54°N; 150°30–152°30°E	12	1.214	1.439	180.062	14.313	7.95	11.450	6.36	5.776	3.21	50.44	5.674	3.15	5.40	40
1991	September, 20–25 South-west	11	1.204	1.103	143.589	12.943	9.01	10.354	7.21	5.140	3.58	49.64	5.214	3.63	5.30	72
1999	September, 11–19 52°–53°N; 148°–150°E	13	1.184	1.202	79.920	10.517	13.16	8.414	10.53	4.532	5.67	53.86	3.882	4.86	5.30	102
1999	September, 24–30 56°–57°N; 153°–156°E	11	1.075	1.225	100.217	9.405	9.38	7.524	7.51	3.598	3.59	47.82	3.926	3.92	5.70	94
Average data for September (intensive feeding):		11.8	1.169	1.242			9.88		7.90		4.01	50.44		3.89	5.43	308
2001	September, 27–28 53°N–155°30'E	9	1.281	1.072	87.315	6.620	7.58	5.296	6.07	1.738	1.99	32.81	3.559	4.08	6.60	51
1997	October, 2 52°N; 155°E	9	1.054	1.159	118.366	9.128	7.71	7.302	6.17	2.277	1.92	31.19	5.025	4.25	7.80	80
Average data at the end of September and beginning of October (feeding, beginning migration):		9.0	1.168	1.116			7.65		6.12		1.96	32.00		4.16	7.20	131
1982	October, 2–8 53°N; 154°30`E	8	0.898	1.030	77.044	4.548	5.90	3.639	4.72	0.917	1.19	25.19	2.722	3.53	6.10	62
1991	October, 2–5 North-west	8	0.984	0.916	96.052	6.907	7.19	5.525	5.75	1.469	1.53	26.59	4.056	4.22	7.10	50
1991	October, 11 54°N; 152°E	9	0.968	0.916	127.168	10.396	8.18	8.317	6.54	2.099	1.65	25.23	6.219	4.89	7.70	60
Average data for October (active migration):		8.3	0.950	0.954			7.09		5.67		1.46	25.67		4.22	6.97	172

Table 3. Balance of energy metabolism of juvenile chum salmon in the Okhotsk Sea.

Year	Period and location	Temperature of water layer (C°)	Caloric content of food (kcal/g of wet weight)	Caloric content of fish (kcal/g of wet weight)	Total caloric content (kcal)	Total caloric content of daily ration (kcal)		Real expenditure for metabolism							k$_{V2}$	Number of fish
								total		body growth		K$_2$	active metabolism			
						kcal	%	kcal	%	kcal	%		kcal	%		
1999	September, 12–19 52–53°N; 148°–150°E	13	1.028	1.228	102.77	9.181	8.93	7.345	7.15	3.663	3.56	49.9	3.682	3.58	4.3	69
1999	September, 14–16 52–53°N; 154–156°E	11.5	1.126	1.203	96.76	10.188	10.53	8.150	8.42	3.473	3.59	42.6	4.677	4.83	6.4	73
1991	September, 20–25 South-west	11	1.144	1.078	154.05	12.039	7.82	9.632	6.25	5.004	3.25	52.0	4.627	3.00	4.5	69
Average data for September (intensive feeding):		11.8	1.099	1.170			9.09		7.27		3.47	48.1		3.81	5.07	211
1999	September, 25–30 56–57°N; 153–155°E	10.2	0.703	1.219	122.46	5.946	4.86	4.757	3.88	1,445	1,18	30.4	3.312	2.70	4.5	73
2001	September, 27–28 53°N; 155°30´E	9.2	1.266	1.122	99.51	7.866	7.90	6,293	6.32	2.765	2.78	43.9	3.528	3.55	6.1	82
Average data at the end of September (feeding, beginning migration):		9.7	0.985	1.171			6.38		5.10		1.98	37.2		3.12	5.30	155
1991	October, 11 54°N; 152°E	9	0.769	1.033	152.93	9,052	5.92	7,242	4.74	2.922	1.91	40.4	4.319	2.82	5.1	56

Daily sum of consumed (educed) food is equal to daily ration. Calculation of caloric content of food consumed by salmon is based on the data (Shershneva and Koval 2004).

Calculation of energy expenditures: Value of expenditures on real metabolism was determined using the equations of balanced equality: $R = 0.8r - \Delta W$ (Equation 6), where R, expenditures on real metabolism, kcal/sample per day; r, daily ration, kcal; ΔW, daily weight increment, kcal (Ivlev 1939). Daily expenditures on standard metabolism were calculated using Equations 1, 7, and 8: in g/sample per day: $R = 24 \cdot 4.86 \cdot 10^{-3} Q_{st} C^{-1}$ (Equation 7), kcal/sample per day; $R = 24 \cdot 4.86 \cdot 10^{-3} Q_{st}$ (Equation 8), where 4.86, oxy calorie coefficient, cal./ml; C, total calorie content of fish body, kcal/g of wet weight (Winberg 1956; Anon 1986). Coefficients of physiologically useful part of food for growth were calculated as $K_2 = 100\,\Delta W/0.8\,r$ (Equation 9) (Ivlev 1939).

Juvenile salmon metabolism in conditions of active mode of life in marine habitat is 4.3–7.8 times higher than standard one (coefficient values "Winberg-2") (Tables 2, 5). Maximum values of total calorie content, level of total metabolism, increment expenditures, and maximum daily rations of juvenile salmon during August–October were observed at maximum thermal saturation of the upper water layer (11–13°C) in September. Among all the species pink and coho are the most active ones. In some cases their metabolism level at this period is 10.5 and 9.7% (on the average 7.9 and 7.7%), respectively, consumption of total organism energy is 12.1 and 13.2% (on the average, 9.9 and 9.6%) (Table 2, 5). Sockeye is the least active species (Table 4). Chum is closer to the first group (Table 3). Expenditures on fish growth are determined according to intensity of total metabolism and consumption. In September the average level of expenditures for pink, coho and chum is 4.0, 3.9 and 3.5% of total organism energy, respectively, that is much higher than for sockeye (2.1%).

Total metabolism intensity regularly reduces with drop of water temperature in October. Intensity of energy expenditures on growth is nearly equal for all the species by this period (1.6–1.9% of total energy balance). However, rate of decrease of particular elements of metabolism are synchronous only for sockeye (in October elements of total, active metabolism and metabolism associated with muscular activity are 1.2 times lower than in September). Expenditures on growth reduce rapidly for chum and coho: 1.9 times for chum (total—1.5 times, active—1.3 times), 2.1 times for coho (total—1.6, active—1.3 times). Dynamics of metabolism of juvenile pink salmon differs from all the species. Having more gradual decline of total metabolism—1.3 times, the level of metabolism associated with muscular activity decreases rapidly—2.7 times (from 4.1% in September to 1.5% in October), but the level of active metabolism increases (from 3.9% to 4.2%). Consequently, pink has the highest level of food consumption among four species. A sharp drop of metabolism associated with muscular activity for pink at the end of feeding migration in Kamchatka waters indicates an important role of the factors making juvenile intensify active expenditures. One of these is the density factor. By October pink, like chum, migrating from the north in the Sea of Okhotsk flows into aggregations in the south 55–56° N, noticeably increasing their density. Consuming secondary food objects, juvenile has more diversified food composition. It is sustained by declining caloric content of rations (Table 2). Deficit of energy consumed with food increases its payment. Thus, searching

Table 4. Balance of energy metabolism of juvenile sockeye salmon in the Okhotsk Sea.

Year	Period and location	Temperature of water layer (C°)	Caloric content of food (kcal/g of wet weight)	Caloric content of fish (kcal/g of wet weight)	Total caloric content (kcal)	Total caloric content of daily ration (kcal)		Real expenditure for metabolism							k_{V2}	Number of fish
								total		body growth		K_2	active metabolism			
						kcal	%	kcal	%	kcal	%		kcal	%		
1999	September, 21–30 56°–57°N; 153°–156°E	10.8	0.989	1.167	144.957	9.536	6.58	7.629	5.26	2.682	1.85	35.2	4.947	3.41	5.4	98
2001	September, 27–28 53°N–155°30'E	9	1.243	1.143	149.952	11.577	7.72	9.262	6.18	3.453	2.30	37.3	5.809	3.87	7.5	78
Average data for September (intensive feeding):		9.9	1.116	1.155			7.150		5.720		2.076	36.2		3.643	6.45	176
1997	October, 2 52°N; 155°E	9	1.226	1.234	179.304	10.791	6.02	8.633	4.81	3.150	1.76	36.5	5.483	3.06	6.5	58

Table 5. Balance of energy metabolism of juvenile coho salmon in the Okhotsk Sea.

Year	Period and location	Temperature of water layer (C°)	Calorific value of food (kcal/g of wet weight)	Calorific value of fish (kcal/g of wet weight)	Aggregate calorific capacity of fish (kcal)	Aggregate calorific capacity of daily ration (kcal)		Real expenditure for metabolism							k_{V2}	Number of fish
								aggregate		body growth		K_2	active metabolism			
						kcal	%	kcal	%	kcal	%		kcal	%		
1986	28.8–4.9 52°–54°30 N	12.6	0.988	1.271	372.36	31.098	8.35	24.879	6.68	11.431	3.07	45.95	13.447	3.61	6.3	70
1999	September,14–21 52°–55°N;154°–156°E	11.2	1.110	1.148	226.88	27.439	12.09	21.951	9.68	11.457	5.05	52.19	10.494	4.63	7.6	62
2001	September, 27–28 53°N, 155°30 E	9	1.118	1.130	298.13	24.777	8.31	19.822	6.65	10.494	3.52	52.94	9.327	3.13	7.1	47
Average data for September (intensive feeding):		10.9	1.07	1.18			9.59		7.67		3.88	50.36		3.79	7.00	179
1997	October, 2 52°N; 155°E	9	1.015	1.216	347.12	20.843	6.00	16.674	4.80	6.526	1.88	39.14	10.148	2.92	7.3	44

and catching activities are intensified. Increase of motional activity leads to the growth of active expenditures in the balance of energy distribution. But the energy of obtained food is insufficient for growing motional expenditures and for preservation of previous level of somatic growth.

However, in October only the northern part of total aggregation is observed in the waters of Kamchatka, as it inhabits cooling southern part of the Sea of Okhotsk more slowly (Shuntov 1989, 1994). Consequently, it is reasonable to submit that this situation can indicate decrease of food sufficiency, but it does not characterize production characteristics of the whole complex of stocks of the given period. Apparently, for dominant majority of pink and chum fingerlings, feeding in the waters of Kamchatka in September, temperature and feeding conditions are satisfactory with movement to the southern areas. And possibly, high rates of metabolism associated with muscular activity can occur in October.

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