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The Biochemical Composition and Calorie Density of the Walleye Pollock *Theragra chalcogramma* in the Sea of Okhotsk

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Abstract—In tissues of the walleye pollock *Theragra chalcogramma* the dry matter content averages 18.5%. The lipid content of the raw material is 0.7%, the protein content is 15.3%, carbohydrates are 0.6%, and ash is 1.3%. The average calorie density is 940 cal/g wet weight and 5080 cal/g dry weight. The dry matter content of gonads varies within 14.9–28.0% in females and 14.5–17.0% in males. The lipid content of the raw material is 0.9–3.0% in females and 1.3–1.8% in males; the protein content is 10.2–21.5% and 10.7–13.4%, respectively. The calorie density of female gonads is 702–1537 cal/g wet weight and 4426–5482 cal/g dry weight; for the male gonads it is 760–960 cal/g wet weight and 4952–5641 cal/g dry weight. The dry matter content of the liver varies within 42.2–62.2% for females and 34.4–62.4 for males. The lipid content of the raw material is 25.6–44.5% for females and 16.6–41.3% for males; the protein content is 6.3–9.8% and 8.1–12.3%, respectively. The calorie density of the liver in females varies within 2918–4601 cal/g wet weight and 6370–7395 cal/g dry weight; in males it is 2291–4357 cal/g wet weight and 6392–7492 cal/g dry weight. The minimum calorie density of the liver is observed in juvenile pollock: 963 cal/g wet weight and 2045 cal/g dry weight. The dry-matter content of feces in different size groups varies within 15.0–18.4%. Values of the average lipid content of raw material range from 1.1 to 1.6%; the protein content is from 1.8 to 3.8% and carbohydrates are from 0.9 to 1.4%. The calorie density of feces from variously-sized walleye pollock varies within a narrow range, from 308 to 362 cal/g wet weight. The energy equivalent ranges, depending on body size, from 259 to 2377 cal. The share of energy concentrated in the somatic (muscle) tissue of variously-sized walleye pollock during ontogenesis constitutes 56.5–93.9%; in female gonads it is 0.9–26.6%; in male gonads it is 0.4–7.3%, in the female liver it is 7.9–27.2%, and in the male liver it is 5.7–26.9%. The amount of energy (cal), concentrated in the female liver and gonads is on average 1.5 and 3 times as high as that in the male liver and gonads, respectively. The maximum total energy loss (15–30%) in mature walleye pollock of various-sizes occurs in the spawning period, during the transition from the maturity stage 5 to stage 6. The total amount of energy accumulated during the lifecycle from small juveniles (<17 cm) to very large individuals (>60 cm) averages 1964 kcal for females and 1465 kcal for males. The difference in the amount of energy is explained by the fact that oogenesis requires more energy than spermatogenesis.

Keywords: walleye pollock, gonads, liver, somatic tissue, calorie density, energy equivalent

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INTRODUCTION

A study of lifecycles of fish should necessarily include analysis of the dynamics of their physiological status [10]. Among physiological methods, the most effective one is the study of dynamics of the accumulated fat in connection with the biological status of fish. In fish, like in most animals, energy reserves are accumulated in form of neutral (simple) fats, triglycerides. In walleye pollock, a major portion of fat reserve is concentrated in the liver [4], where triglycerides constitute the bulk of total lipids [7]. The studies conducted by the Pacific Research Institute of Fisheries and Oceanography (TINRO) in the Far Eastern seas in the 1990s revealed a dependence of the liver weight and the fat content of the liver on the biological status of fish [1, 8, 9]. As was established, walleye pollock, like many other fishes, does not forage intensively during the spawning period; the post-spawning feeding, which starts almost immediately after spawning, is characterized by the maximum feeding intensity and high stomach fullness, sometimes exceeding 500‰. As fat reserves are accumulated and deposited, mainly in the liver, walleye pollock decreases its feeding intensity, switching to the supporting mode of feeding in the winter. The studies also showed that the fat content of walleye pollock liver is not only related to its biological status, but also manifests clearly pronounced spatial and seasonal dynamics [8]. The fat level of pollock, as discussed by Shvydky and Vdovin in [8], is characterized by a single

parameter: the percentage content of the liver-deposited fat, which was obtained by vaporization method [6].

The goal of our work was to determine the biochemical composition and calorie density of the muscle tissues, liver, and gonads in walleye pollock, taking its stages of differentiation and physiological status into account. Another goal was to measure the amount of energy (energy equivalent) concentrated in muscles, liver, and gonads, also depending on the physiological status of fish. The energy equivalent is calculated as a multiplication of the weight (muscles, liver, and gonads) by the calorie density (cal/g).

MATERIALS AND METHODS

The material was collected during complex expeditions conducted by the Pacific Research Fisheries Center (TINRO Center) in the Sea of Okhotsk in 2003–2013. Primary processing and preparation of walleye pollock specimens for biochemical analysis was performed in field conditions as well. Samples of muscle tissues, gonads, and liver weighing from 20 to 30 g were cut from the fish. The samples were placed into sealed plastic bags and stored under a temperature not higher than −18°C. The body length, sex, maturity stage, and stomach contents of individuals were determined. Muscle tissues, liver, and gonads of each fish were weighed.

The energy value was assessed by determining the total content of proteins, lipids, carbohydrates, ash, and moisture. The analysis of calorie density of aquatic organisms by their chemical composition has some advantages as compared to other methods, such as direct calorimetry, iodate and dichromate oxidation. The use of the latter methods allows sufficiently precise measurement of calorie density of an organism, however, without determining the proportions of certain organic components such as lipids, proteins, and carbohydrates. Studying the chemical composition provides an opportunity to reveal species-specific biochemical features at various stages of the lifecycle [4].

The weight percentages of moisture and ash were determined according to the standard methods [3]. Protein content was determined using the Kjeldahl method, by measuring the amount of nitrogen of protein compounds with a Kjeltec 2300 analyzer (Japan), the carbohydrate content was determined by photocolorimetric measurements using the anthrone reagent [5], and the lipid content was determined by gravimetric measurements after extraction of lipids from tissues using the Folch method [11]. Calorie density (cal/g) and biochemical composition were calculated both for raw and dry matter. The term "somatic tissue" refers to muscles. A total of 163 samples of muscle tissue, 112 gonad samples, 150 liver samples, and 12 samples of feces from intestines were collected and processed for the analysis of the biochemical composition.

RESULTS AND DISCUSSION

The weight of somatic tissue, liver, and gonads is one of the characteristics of the physiological status of walleye pollock. As studies have shown, males exhibit the same tendencies in the dynamics of their liver and gonad weight as females do, but the values of their parameters are lower (Table 1). The weight of the liver and gonads varies cyclically in the course of generative growth, depending on the maturity stage in size groups of adult fish. Variously-sized mature individuals at the gonad maturity stages 3–4 and 4 show the maximum values of the liver weight, which subsequently decrease. Gonads gain the maximum weight in prespawn and spawning fish (maturity stages 4–5 and 5). The most noticeable difference in gonad weight (three- to four-fold) was observed between stages 3 and 4. According to the personal communication by A.M. Privalikhin (All-Russia Research Institute of Fisheries and Oceanography, VNIRO), the transition from the maturity stage 3 to stage 4 in walleye pollock lasts for approximately 1 year. Females at the transitional stage 3–4 are registered mainly in the autumn, after intensive feeding in the summer [2], when they reach stage 4 and become ready for spawning, which in the Sea of Okhotsk occurs in the winter and spring. The lowest values of the liver and gonad weight are recorded from post-spawning fish (gonad stages 6 and 6–2).

Muscle Tissue

No significant differences in biochemical composition and calorie density between male and female pollock of various sizes were found. For this reason, only the averaged data on the biochemical composition of the muscle tissue by maturity stages are provided in Table 2.

The dry-matter content of muscle tissues in walleye pollock at various maturity stages was within the range of 17.2–20.2%. Higher values of the dry-matter content were observed in juveniles. The protein content of raw material varied from 13.9 to 16.8%. The total amount of lipids in walleye pollock tissues showed the smallest variations, from 0.6 to 1.1%. The carbohydrate content in the studied fish was the lowest and varied from 0.4 to 1.0%. The calorie density of walleye pollock varied within a narrow range: from 854 to 1041 cal/g wet weight and from 4921 to 5322 cal/g dry weight. Thus, the dynamics of the main biochemical parameters and the overall calorie density of walleye pollock muscles indicate that variations during ontogenesis are pronounced weakly in them and do not go beyond the error range.

Gonads

The noticeable sex-based differences recorded during the analysis of walleye pollock gonads (Table 3) are also manifested in their biochemical composition and calorie density.

Table 1. The weight of the muscle tissue, liver, and gonads in walleye pollock of various sizes by maturity stages

Size group, cm	Mean size, cm	Mean weight of muscle tissue, g	Sex	Gonad maturity stage	Gonad weight, g	Liver weight, g	Sample size, fish
<17	13.0	14	J	juv	–	2.1	235
17–30	23.7	76	F	2	–	3.2	387
			M	2	–	2.9	362
31–40	35.3	239	F	2	–	8.8	244
			F	2–3	7.0	10.1	30
			F	3	11.5	16.2	6
			F	3–4	25.4	22.4	6
			F	4	27.5	18.5	33
			F	4–5	37.8	17.5	44
			F	5	46.7	9.8	11
			F	6	9.3	10.3	12
			F	6–2	5.2	13.0	2
			M	2	0.0	7.0	57
			M	3	2.5	10.5	33
			M	4	17.1	14.1	36
			M	5	14.5	9.5	81
			M	6	5.5	7.5	16
			M	6–2	2.2	9.9	3
40–50	44.8	455	F	6–3	8.4	17.5	4
			F	3	12.8	27.1	4
			F	3–4	40.1	32.8	24
			F	4	64.7	28.9	57
			F	4–5	117.1	30.1	57
			F	5	151.1	21.5	12
			F	6	22.5	14.8	33
			F	6–2	8.2	12.9	3
			M	2	0.0	13.5	2
			M	3	8.1	17.3	1
			M	4	42.1	20.1	69
			M	5	43.6	18.9	35
			M	6	6.7	17.5	3
			M	6–2	2.5	8.0	2
50–60	53.9	787	F	3	50.7	47.7	3
			F	3–4	121.2	84.2	21
			F	4	144.1	82.5	56
			F	4–5	204.0	65.1	81
			F	5	217.2	52.4	24
			F	6	36.0	41.1	14
			F	6–2	17.1	21.5	2
			M	4	87.2	61.7	22
			M	5	77.2	39.1	35
			M	6	6.9	32.5	2

Table 1. (Contd.)

Size group, cm	Mean size, cm	Mean weight of muscle tissue, g	Sex	Gonad maturity stage	Gonad weight, g	Liver weight, g	Sample size, fish
>60	64.8	1445	F	3	70.0	78.0	2
			F	3–4	232.5	155.4	31
			F	4	310.3	152.3	33
			F	4–5	405.0	126.2	58
			F	5	432.5	102.5	13
			F	6	155.1	78.0	6
			F	6–2	18.7	39.8	2
			M	4	139.0	67.2	8
			M	5	143.5	69.8	6
			M	6	32.2	52.1	2

The dry matter content of female gonads varied within 14.9–28.0%; in males, the amount of dry matter almost did not change, viz., 14.5–17.0%. The ash content of the raw material in females varied from 1 to 1.6%; in males, this was within 1.2–1.5% (Table 3). The lowest ash content was observed in spawning females, 1%.

The contents of the organic matter components in gonads, viz., the lipids, proteins, and carbohydrates, also varied within a broad range in females. The range of the mean values of lipids in the raw material of female gonads was from 0.9 to 3.0%; in male milt was from 1.2 to 1.8% (Table 3). The lowest values were observed in post-spawning individuals. The highest lipid content of the gonads was recorded from females at the maturity stages 3–4 and 4.

The protein content of the raw material of female gonads at various maturity stages varied from 10.2 to 21.5%; for male gonads it varied within a narrower range, 10.7–13.4%. The highest protein content, as well as the highest values of dry matter and lipid contents, were observed in females at maturity stage 3–4.

The resulting parameter of biochemical composition is the energy value (calorie density). In females, the calorie density of the gonads varied from 702 to 1537 cal/g wet weight and from 4426 to 5482 cal/g dry weight; in males it varied from 760 to 960 cal/g wet weight and from 4952 to 5641 cal/g dry weight. The highest calorie density was observed in females at maturity stage 3–4; the overall calorie density of gonads then decreased due to hydration of eggs. The lowest calorie density was observed in post-spawning females due to the decline in the amount of both proteins and lipids.

The Liver

Data on the biochemical composition and calorie density of the liver were obtained for males and females at each stage of ontogenesis. Noticeable sex-based differences were revealed as a result of analysis of the liver weight (Table 4). The sex-based differences in the dynamics of the liver fat level in walleye pollock are explained by the fact that oogenesis requires more energy than spermatogenesis does [10].

The dry matter content of the liver varied from 42.2 to 62.2% in females and from 34.4 to 62.4% in males; in juveniles, it amounted to 47.0%. The lipid content of the liver was the lowest, 5.1% wet weight, in juvenile individuals. The range of mean values of lipids in the raw material varied from 25.6 to 44.5% for females and from 16.6 to 41.3% for males. The lowest values of lipids were recorded from post-spawning individuals: at stage 6–2 in females and immediately after spawning, stage 6, in males.

The highest content of accumulated fat was observed in fish with gonads at maturity stage 2–3 (6–3), most of which were individuals that had already participated in spawning (stage 6–3). Individuals at this stage occurred in catches from September to November, when fat reserves in the liver had restored due to the intensive feeding in summer. At maturity stage 6, the amount of lipids in raw material was 16.6%; at stage 2–3 (6–3), 44.2%, i.e., in fact three times as high (Table 4).

The gonad maturity stage 3 lasts for quite a long time (from April–June to August–September). Despite the fact that the lipid content of the liver during this period declined, the weight of accumulated fat increased by one-third due to the growth of the liver weight (Table 1). At stage 3–4, the content of accumulated fat increased, and the registered concentration of energy in the liver became the highest for the entire ontogenesis period. At stage 4, an abrupt reduction of fat reserves was observed; this unambiguously indicates substantial energy consumption by maturing gonads, as walleye pollock does not change its foraging intensity at this stage [1]. When the weight of female

Table 2. The biochemical composition and calorie density of muscle tissue in walleye pollock from the Sea of Okhotsk by maturity stages

Maturity stage	Percentage of dry matter, %	±SE	Lipids, %	±SE	Protein, %	±SE	Carbohydrates, %	±SE	Ash, %	±SE	Calorie density, cal/g wet weight	±SE	Number of samples
In raw material													
juv	20.2	0.32	1.1	0.10	16.5	0.46	0.4	0.05	1.7	0.20	**1041**	28	12
2	18.9	0.20	0.7	0.03	15.9	0.27	0.6	0.03	1.3	0.05	**970**	16	34
2–3 (6–3)	19.1	0.39	0.7	0.08	16.8	0.34	0.4	0.01	1.1	0.08	**1016**	20	7
3	19.0	0.25	0.6	0.03	16.0	0.36	1.0	0.01	1.1	0.03	**970**	21	22
4	18.7	0.36	0.7	0.04	15.2	0.57	0.5	0.07	1.2	0.03	**930**	31	29
4–5	17.4	0.54	0.8	0.13	14.1	0.48	0.7	0.14	1.3	0.08	**889**	42	10
5	17.8	0.35	0.6	0.04	14.4	0.36	0.4	0.07	1.2	0.04	**878**	22	19
6	17.2	0.33	0.6	0.05	13.9	0.33	0.7	0.12	1.2	0.02	**854**	23	17
6–2	17.9	0.42	0.6	0.04	15.1	0.53	0.4	0.06	1.2	0.06	**912**	31	13
In dry matter													
juv	20.2	0.32	5.3	0.47	81.7	1.79	2.0	0.23	8.6	1.05	**5143**	101	12
2	18.9	0.20	3.7	0.16	84.2	0.86	3.2	0.19	6.8	0.22	**5131**	48	34
2–3 (6–3)	19.1	0.39	3.7	0.44	87.9	0.89	1.5	0.00	5.9	0.46	**5322**	43	7
3	19.0	0.25	3.3	0.16	84.4	1.20	5.1	0.18	5.9	0.21	**5103**	70	22
4	18.7	0.36	3.6	0.21	81.2	2.38	2.8	0.38	6.5	0.28	**4959**	125	29
4–5	17.4	0.54	4.5	0.59	81.1	1.12	3.8	0.73	7.4	0.51	**5101**	122	10
5	17.8	0.35	3.5	0.22	80.8	1.43	2.2	0.35	6.7	0.20	**4921**	85	19
6	17.2	0.33	3.7	0.26	80.7	0.94	3.7	0.57	6.9	0.19	**4952**	65	17
6–2	17.9	0.42	3.3	0.23	84.1	1.37	2.5	0.37	6.7	0.40	**5087**	88	13

Table 3. The biochemical composition and calorie density of gonads in walleye pollock from the Sea of Okhotsk by maturity stages

Sex	Maturity stage	Percentage of dry matter, %	±SE	Lipids, %	±SE	Protein, %	±SE	Carbohydrates, %	±SE	Ash, %	±SE	Calorie density, cal/g	±SE	Number of samples
In raw material														
F	2	16.2	2.76	1.1	0.20	12.0	2.90	0.9	0.10	1.5	0.20	**827**	174	6
	2–3 (6–3)	17.8	0.45	1.5	0.30	13.5	0.60	0.7	0.10	1.6	0.10	**933**	120	7
	3	24.4	1.07	2.6	0.30	18.4	1.20	0.8	0.10	1.5	0.20	**1321**	90	6
	3–4	28.0	0.95	3.0	0.20	21.5	0.80	1.0	0.10	1.5	0.20	**1537**	68	8
	4	24.0	2.20	3.0	0.40	17.5	1.90	0.8	0.00	1.4	0.10	**1307**	136	12
	4–5	21.8	1.64	2.4	0.30	15.1	1.50	0.9	0.10	1.2	0.20	**1114**	112	8
	5	16.9	2.40	1.3	0.20	10.8	2.30	0.8	0.10	1.0	0.20	**765**	135	8
	6	14.9	0.56	1.0	0.10	10.2	0.50	0.8	0.00	1.5	0.10	**702**	34	9
	6–2	15.0	0.64	0.9	0.10	10.8	0.70	0.8	0.10	1.5	0.10	**731**	40	7
M	2	16.9	–	1.2	–	12.3	–	0.8	–	1.5	–	**841**	–	1
	3	15.9	0.50	1.6	0.10	12.0	0.60	0.9	0.10	1.5	0.10	**868**	33	14
	4	16.8	1.47	1.7	0.10	11.5	1.20	0.9	0.10	1.6	0.00	**848**	69	9
	5	15.5	0.54	1.7	0.20	11.0	0.40	0.8	0.10	1.4	0.10	**820**	26	8
	6	14.5	1.61	1.3	0.20	10.7	1.30	0.7	0.10	1.4	0.10	**760**	94	5
	6–2	17.0	0.31	1.8	0.20	13.4	0.20	0.8	0.10	1.3	0.10	**960**	20	4
In dry matter														
F	2	16.2	2.76	8.6	2.50	67.8	8.90	6.3	1.30	8.2	1.30	**4899**	323	6
	2–3 (6–3)	17.8	0.45	8.3	1.30	76.1	3.90	3.9	0.30	9.0	0.30	**5248**	550	6
	3	24.4	1.07	10.6	0.70	75.3	1.80	3.4	0.40	6.2	0.60	**5394**	150	6
	3–4	28.0	0.95	10.7	0.60	76.5	1.00	3.5	0.40	5.4	0.70	**5482**	107	8
	4	24.0	2.20	12.7	1.30	71.2	1.90	4.1	0.60	7.0	1.40	**5387**	181	12
	4–5	21.8	1.64	10.8	1.10	68.4	2.10	4.2	0.60	6.0	1.00	**5056**	208	8
	5	16.9	2.40	8.6	1.20	60.3	4.70	5.0	0.60	7.3	1.90	**4426**	260	8
	6	14.9	0.56	6.7	0.60	68.3	2.00	5.4	0.20	10.3	0.70	**4672**	144	9
	6–2	15.0	0.64	6.4	0.50	71.5	2.00	5.3	0.50	10.1	0.30	**4865**	98	7
M	2	16.9	–	7.1	–	72.4	–	4.7	–	9.0	–	**4952**	–	1
	3	15.9	0.50	10.3	0.50	75.2	2.00	5.6	0.80	9.5	0.70	**5453**	104	14
	4	16.8	1.47	10.4	0.80	68.4	2.20	5.4	0.50	10.0	0.80	**5072**	71	9
	5	15.5	0.54	11.3	1.30	71.1	1.40	5.1	0.50	9.3	0.30	**5291**	128	8
	6	14.5	1.61	9.0	0.70	73.4	1.40	5.4	1.10	9.9	0.80	**5220**	114	5
	6–2	17.0	0.31	10.4	1.10	79.0	1.70	4.8	0.40	7.4	0.90	**5641**	18	4

Table 4. The biochemical composition and calorie density of the liver in walleye pollock from the Sea of Okhotsk by maturity stages

Sex	Maturity stage	Percentage of dry matter, %	±SE	Lipids, %	±SE	Protein, %	±SE	Carbohydrates, %	±SE	Ash, %	±SE	Calorie density, cal/g	±SE	Number of samples
In raw material														
j	juv	47.0	–	5.1	–	8.0	–	0.7	–	1.9	–	**961**	–	1
F	2	51.8	3.9	32.9	3.0	8.3	1.0	0.7	0.1	0.9	0.1	**3655**	286	18
	2–3 (6–3)	62.2	3.7	44.5	3.9	6.4	1.0	0.7	0.1	0.6	0.1	**4601**	324	7
	3	54.6	5.4	34.4	6.0	8.5	0.7	0.8	0.2	1.0	0.2	**3763**	531	7
	3–4	58.1	3.5	39.1	2.3	6.5	0.7	0.7	0.1	0.8	0.1	**4094**	196	9
	4	51.4	3.0	29.4	3.6	8.4	1.0	1.0	0.3	1.1	0.1	**3297**	319	13
	4–5	48.4	3.7	32.8	4.2	8.9	1.0	0.6	0.1	1.0	0.1	**3628**	346	10
	5	48.5	5.3	26.3	4.2	9.8	1.7	0.7	0.1	1.2	0.1	**3071**	312	9
	6	54.1	4.2	38.4	4.6	6.3	1.2	0.8	0.1	0.9	0.1	**4022**	383	10
	6–2	42.2	2.8	25.6	3.7	8.4	0.7	0.6	0.1	1.1	0.1	**2918**	328	8
M	2	50.5	5.4	31.5	3.8	8.8	0.9	0.7	0.1	0.8	0.1	**3502**	443	12
	3	62.4	3.3	40.2	3.7	8.2	0.8	0.6	0.0	0.7	0.1	**4289**	303	14
	4	61.1	3.1	41.3	3.7	7.6	1.4	0.8	0.1	0.9	0.1	**4357**	285	10
	5	53.4	3.7	37.1	3.4	8.1	0.7	0.7	0.1	0.8	0.1	**3992**	292	10
	6	34.4	4.6	16.6	5.4	12.3	1.7	0.7	0.1	1.1	0.1	**2291**	422	7
	6–2	50.9	5.1	28.9	4.9	9.0	1.1	1.7	1.1	0.9	0.1	**3305**	441	5
In dry matter														
j	juv	47.0	–	10.8	–	17.0	–	1.5	–	4.0	–	**2045**	–	1
F	2	51.8	3.9	62.5	3.2	19.3	3.7	1.5	0.2	2.0	0.2	**7060**	208	18
	2–3 (6–3)	62.2	3.7	71.0	4.0	11.2	2.7	1.1	0.1	1.1	0.2	**7383**	507	7
	3	54.6	5.4	59.3	7.3	17.4	3.0	1.9	0.9	2.3	0.8	**6664**	285	7
	3–4	58.1	3.5	67.5	1.4	11.9	1.7	1.3	0.2	1.5	0.2	**7103**	191	9
	4	51.4	3.0	55.8	4.8	17.9	2.7	2.1	0.7	2.3	0.3	**6370**	423	13
	4–5	48.4	3.7	64.8	5.6	21.4	4.9	1.5	0.3	2.3	0.5	**7395**	291	10
	5	48.5	5.3	52.0	4.5	24.9	6.0	1.6	0.3	3.0	0.6	**6391**	237	9
	6	54.1	4.2	67.9	7.1	14.6	4.7	1.5	0.3	2.0	0.6	**7299**	468	10
	6–2	42.2	2.8	58.1	7.0	20.9	2.6	1.5	0.1	2.9	0.8	**6739**	513	8
M	2	50.5	5.4	60.3	4.5	19.4	3.5	1.5	0.2	1.8	0.3	**6859**	314	12
	3	62.4	3.3	62.9	3.5	15.1	3.2	1.1	0.1	1.4	0.3	**6846**	244	14
	4	61.1	3.1	66.5	3.6	13.7	3.1	1.2	0.2	1.6	0.2	**7107**	242	10
	5	53.4	3.7	68.9	2.5	16.4	2.3	1.3	0.3	1.7	0.4	**7492**	219	10
	6	34.4	4.6	41.2	9.9	42.8	9.4	2.2	0.3	3.9	0.8	**6400**	434	7
	6–2	50.9	5.1	54.9	4.5	18.9	4.0	3.2	1.9	2.0	0.3	**6392**	294	5

Table 5. The biochemical composition, calorie density (wet weight), and energy equivalent of the feces in walleye pollock from the Sea of Okhotsk

Body size, cm	Percentage of dry matter, %	Lipids, %	±SE	Protein, %	±SE	Carbo-hydrates, %	±SE	Ash, %	±SE	Calorie density, cal/g (wet weight)	Weight of feces, g	Energy equivalent, cal	Number of samples
<17	18.4	1.1	0.1	3.8	0.2	1.1	0.1	1.4	0.1	362	0.7	259	3
17–30	18.1	1.2	0.3	3.6	0.4	1.0	0.1	1.5	0.2	356	1.2	427	3
30–60	17.7	1.3	0.5	3.3	0.6	0.9	0.1	1.6	0.3	350	3.1	1072	3
60–80	15.0	1.6	0.3	1.8	0.9	1.4	0.1	1.4	0.2	308	7.7	2377	3

gonads at the maturity stage 4 increased by 1.5 times (Table 1) and the oocytes reached the definitive size, the level of accumulated fat in the liver also declined by 1.5 times.

A significant decrease in fat level and calorie density of female liver was also recorded at maturity stage 5, when gonads manifest the highest weight values (Table 1), and hydration of eggs occurs [9]. The egg-hydration process takes place in conditions of dense spawning aggregations, when walleye pollock almost ceases feeding [1], i.e., the energy intake with food is reduced substantially or temporally discontinued.

An insignificant increase in fat level and calorie density of the liver was observed in post-spawning females at stage 6 (Table 4). This can be probably caused by resorption of residual reproductive products, which results in the increase of amount of lipids in the liver (according to a personal communication by S.S. Ponomarev (TINRO Center, Pollock and Herring Laboratory). Females at stage 6–2, which were caught immediately after their spawning (April to June), manifested the lowest lipid content of the liver in spite of their intensive post-spawning feeding. Thus, we suppose that accumulation of fat lasts for quite a long time, apparently from 1 to 2 months, depending on feeding intensity. This supposition is confirmed by a substantial increase in the level of accumulated fat in the liver at early stages of vitellogenesis (6–3). The data on dynamics of the liver fat level in female walleye pollock from the Sea of Okhotsk agree with the values of the main parameters obtained earlier for Sea of Japan walleye pollock [9].

Dynamics of the liver fat level in males, unlike those in females, earlier were not considered separately. An increase in the level of fat in the liver during maturation (development) of gonads was observed during transition from maturity stage 2 to stage 3, with the maximum of fat level and calorie density registered at maturity stage 4. In spawning males at stage 5, the fat level and calorie density decreased. Males caught immediately after spawning (stage 6) showed the lowest values of all the considered parameters of the liver; the energy reserves were then actively restored (stage 6–2), and the fat level and calorie density values increased 1.5 times.

The protein content of the liver at different maturity stages varied from 6.3 to 9.8% in the raw material of females and from 8.1 to 12.3% in that of males (Table 4). The maximum protein content was recorded from post-spawning males at stage 6, when the amounts of dry matter and lipids were the lowest.

The amount of carbohydrates in walleye pollock liver was low and varied from 0.7 to 1.7% in the raw material.

The calorie density of the liver in females varied from 2918 to 4601 cal/g wet weight and from 6370 to 7395 cal/g dry weight; in males it varied from 2291 to 4357 cal/g wet weight and from 6392 to 7492 cal/g dry weight. The highest calorie density was observed in females at stage 2–3 (6–3) and males at stage 4. In juveniles, the calorie density of the liver was the lowest: 963 cal/g wet weight and 2045 cal/g dry weight.

Based on the above data, we can conclude that the dynamics of the accumulated fat in the liver of walleye pollock from the Sea of Okhotsk have a pronounced cyclic pattern and are associated with processes of generative growth.

The Feces

To measure the amount of energy in the undigested food we determined the biochemical composition and calorie density of food residues in the intestine (feces). The dry matter content of the feces in different size groups of walleye pollock varied from 15.0 to 18.4% (Table 5). The range of the average values of lipids in the raw material varied from 1.1 to 1.6%; proteins varied from 1.8 to 3.8%, while carbohydrates varied from 0.9 to 1.4%.

The calorie density of the feces in walleye pollock of various sizes was low and varied within a narrow range, from 308 to 362 cal/g wet weight. To determine the energy losses (the proportion of undigested food) through the utilization of undigested residues for all

Table 6. The distribution of energy (energy equivalent, kcal) in the muscle tissue, liver, and gonads in walleye pollock of various sizes by maturity stages

Sex	Size group, cm	Gonad maturity stage	Energy in muscle tissue, kcal	Energy in gonads, kcal	Energy in the liver, kcal	Total	Percentage, %		
							including		
							muscle tissue	gonads	liver
juv	<17	juv	14.6	–	2.0	16.6	87.8	–	12.2
F	17–30	2	73.7	–	11.7	85.4	86.3	–	13.7
	31–40	2	231.8	–	32.2	264.0	87.8	–	12.2
		2–3	242.8	5.8	46.5	295.1	82.3	2.0	15.7
		3–0	231.8	10.7	61.0	303.5	76.4	3.5	20.1
		3–4	231.8	30.7	86.8	349.3	66.3	8.8	**24.9**
		4	222.3	42.3	61.0	325.5	68.3	13.0	18.7
		4–5	212.5	49.4	63.5	325.4	65.3	15.2	19.5
		5	209.8	52.0	30.1	292.0	71.9	**17.8**	10.3
		6	204.1	7.1	41.4	252.6	80.8	2.8	16.4
		6–2	218.0	3.7	37.9	259.6	84.0	1.4	14.6
	40–50	2	441.4	–	51.9	493.3	89.5	–	10.5
		2–3(6–3)	462.3	7.0	80.5	549.7	84.1	1.3	14.6
		3	441.4	11.9	102.0	555.3	79.4	2.2	18.4
		3–4	441.4	53.0	134.3	628.6	70.2	8.4	**21.4**
		4	423.2	99.5	95.3	617.9	68.5	16.1	15.4
		4–5	404.5	153.0	109.2	666.7	60.6	23.0	16.4
		5	399.5	168.3	66.0	633.8	63.0	**26.6**	10.4
		6	388.6	17.2	59.5	465.3	83.5	3.7	12.8
		6–2	415.0	5.8	37.6	458.4	90.5	1.3	8.2
	50–60	3	763.4	46.9	179.5	989.8	77.2	4.7	18.1
		3–4	763.4	160.1	344.8	1268.3	60.2	12.6	**27.2**
		4	731.9	221.5	272.0	1225.4	59.7	18.1	22.2
		4–5	699.6	266.6	236.2	1202.4	58.2	22.2	19.6
		5	691.0	241.9	160.9	1093.8	63.2	**22.1**	14.7
		6	672.1	27.5	165.3	864.9	77.7	3.2	19.1
		6–2	717.7	12.0	62.7	792.5	90.6	1.5	7.9
	>60	3	1401.7	51.1	293.5	1746.2	80.3	2.9	16.8
		3–4	1401.7	307.2	636.3	2345.1	59.8	13.1	**27.1**
		4	1343.9	477.0	502.1	2322.9	57.9	20.5	21.6
		4–5	1284.6	529.2	457.8	2271.7	56.5	23.3	20.2
		5	1268.7	481.8	314.7	2065.2	61.5	**23.3**	15.2
		6	1234.0	118.6	313.7	1666.3	74.1	7.1	18.8
		6–2	1317.8	13.1	116.1	1447.1	91.1	0.9	8.0
M	17–30	2	73.7	0.0	10.6	84.3	87.4	0.0	12.6
	31–40	2	232.2	0.0	24.5	256.8	90.5	0.0	9.5
		3	207.4	2.3	45.0	254.7	81.4	0.9	17.7
		4	202.7	14.3	61.4	278.5	72.8	5.1	**22.1**
		5	195.9	11.9	37.9	245.8	79.7	4.9	15.4
		6	181.5	4.0	17.2	202.7	89.5	2.0	8.5
		6–2	229.4	2.0	32.7	264.1	86.8	0.8	12.4
	40–50	2	442.1	0.0	47.3	489.4	90.3	0.0	9.7
		3	394.8	7.6	74.2	476.6	82.8	1.6	15.6
		4	385.9	35.3	87.6	508.7	75.9	6.9	**17.2**
		5	373.0	35.9	75.4	484.3	77.0	7.4	15.6
		6	345.6	5.4	40.1	391.1	88.3	1.4	10.3
		6–2	436.7	1.8	26.4	465.0	93.9	0.4	5.7
	50–60	4	667.4	63.8	268.8	1000.0	66.7	6.4	**26.9**
		5	645.2	63.5	156.1	864.8	74.7	7.3	18.0
		6	597.8	5.5	74.5	677.8	88.2	0.8	11.0
	>60	4	1225.4	101.7	292.8	1619.9	75.6	6.3	**18.1**
		5	1184.7	118.0	278.6	1581.3	74.9	7.5	17.6
		6	1097.6	25.8	119.4	1242.8	88.3	2.1	9.6

Table 7. The distribution of energy (energy equivalent, kcal) in the muscle tissue, liver, and gonads in walleye pollock of various sizes

Sex	Size group, cm	Energy in muscle tissue, kcal	Energy in gonads, kcal	Energy in the liver, kcal	Total energy, kcal	Percentage, %		
						in muscle tissues	in gonads	in the liver
juv	<17	14.6	0.0	2.0	16.6	87.8	0.0	12.2
F	17–30	73.7	0.0	11.7	85.4	86.3	0.0	13.7
	31–40	222.8	22.4	51.1	296.3	75.9	7.2	16.9
	40–50	424.1	57.3	81.8	563.2	76.6	9.2	14.2
	50–60	719.9	139.5	203.0	1062.4	69.5	12.1	18.4
	>60	1321.8	282.6	376.3	1980.7	68.7	13.0	18.3
M	17–30	73.7	0.0	10.6	84.3	87.4	0.0	12.6
	31–40	208.2	5.8	36.5	250.4	83.4	2.3	14.3
	40–50	396.3	14.3	58.5	469.2	84.7	3.0	12.3
	50–60	636.8	44.3	166.5	847.5	76.6	4.8	18.6
	>60	1169.2	81.8	230.3	1481.3	79.6	5.3	15.1

the size and age groups of walleye pollock, we calculated the energy equivalent, which varied from 259 to 2377 cal depending on the fish size.

The Energy Equivalent

The accumulation of energy (energy equivalent) during the lifecycle of animals is an indicator that is used for the evaluation of the efficiency of physiological functions, as it takes all of the parameters of the studied object into account.

The estimated energy equivalent of somatic tissues in groups of various sizes of walleye pollock remained almost at the same level throughout the lifecycle, while that of the liver and gonads varied substantially (Table 6). Thus, the amount of energy in somatic tissues is a constant value for a certain considered size-age group during the lifecycle; in the liver and gonads, this value is variable. In spite of the common trends in the course of development, the energy equivalent of the liver and gonads was higher in females.

In juvenile (<17 cm) and immature (17–30 cm) walleye pollock, 87.8 and 86.3% of the energy, respectively, was concentrated in the somatic tissue. At this age, gonads are not developed and the remaining energy is concentrated in the liver: 12.2% in juveniles and 13.7% in immature fish (Table 6). In adult individuals at maturity stage 2, the energy was also concentrated in somatic tissues and the liver: in females, 87.8–89.5% and 12.2–10.5%; in males, 90.3–90.4% and 9.6–9.7%, respectively.

In somatic tissues, the amount of energy in walleye pollock of various sizes decreased from 84.1% to 56.5% from stage 2–3 (6–3) to stage 4–5 due to the energy increase in gonads and liver. The amount of energy in somatic tissues then increased to the maximum at stage 6–2.

In female gonads, a gradual accumulation of energy occurs during ontogenesis; the maximum amount of energy (17.6–26.3%) was recorded from spawning females at maturity stage 5. After spawning, at maturity stage 6, the amount of energy declined strongly (2.7–6.8%). The total amount of energy concentrated in female gonads was 3–5 times as high as that in male gonads.

In the liver, energy accumulation (mainly deposited fat, triglycerides) depends on the feeding intensity and gonad development. The level of fat in the liver and energy rises along with the maturation of gonads.

In female walleye pollock, the maximum concentration of energy in the liver is observed at stage 3–4 (21.4–27.2%), which is related, as is indicated above, to intensive feeding, due to which the synthesis of fat in the liver exceeds its mobilization for gonad maturation (Table 6). Starting from stage 4, females manifest a decrease in the amount of fat in the liver, which is related to the intensive energy consumption for maturing gonads. The minimum values of energy parameters in the liver were observed in post-spawning females at stage 6–2.

In males, the values of the energy parameters of the liver were higher than those of the gonads at all the maturity stages; the maximum amount of energy was observed at stage 4. With transition from stage 3 to stage 4, the calorie density of the liver almost did not change (Table 4), while its weight increased substantially (Table 1). Thus, the intensive accumulation of energy in the liver that is spent for gonad maturation and spawning occurs in this period of ontogenesis.

In mature walleye pollock of various sizes, the maximum total loss of energy (15–30%) concentrated

in the somatic tissues, gonads, and liver, is recorded during transition from maturity stage 5 to stage 6.

In Table 7, we provide the averaged data of accumulation and distribution of energy in the somatic tissues, liver, and gonads for different size groups, without ranking them by maturity stages.

The total amount of energy in female somatic tissues, gonads, and liver is higher than that in males (Table 7) for all size groups; this is explained by the fact that oogenesis requires more energy than spermatogenesis [10]. The total amount of energy accumulated by walleye pollock during its lifecycle, from juvenile (<17 cm) to very large (>60 cm) individuals, constitutes on average 1964 kcal for females and 1465 kcal for males.

CONCLUSIONS

The dynamics of the main biological parameters and the total calorie density of the muscle tissue in walleye pollock show that changes during the ontogenesis process are insignificantly pronounced and remain within the error range.

The components of the organic matter in gonads, viz., lipids, proteins, and carbohydrates, vary within a wide range in females during the maturation process; in males, the dynamics of biochemical composition during ontogenesis are expressed to a much lower extent. The highest level of lipids and protein in gonads is observed in females at maturity stage 3–4.

The noticeable differences in biochemical composition and calorie density of the liver between sexes that were found as a result of the liver weight analysis, occur due to the fact that larger amounts of energy are consumed to provide oogenesis than is required for spermatogenesis. The maximum level of deposited fat was observed in females whose reproductive products were at maturity stage 2–3 (6–3), when the fat reserves in the liver had been restored after the intensive summer feeding. An abrupt decrease of the fat reserve was observed at maturity stage 4, which unambiguously indicates substantial energy consumption for gonad maturation. A remarkable decline of the liver fat level in females was also registered at maturity stage 5, when the gonads have their maximum weight values, the process of egg hydration is completed, and spawning occurs. The minimum level of lipids in the liver was recorded from females at stage 6–2.

The estimated energy equivalent remains almost at the same level in somatic tissues throughout the lifecycle in various size groups of walleye pollock, and substantially varies in the liver and gonads. Thus, the amount of energy in somatic tissues is a constant value during ontogenesis for a certain size-age group; in the liver and gonads, it is a variable value. In spite of the common trends during development, the energy equivalent of the liver and gonads is higher in females. The maximum total loss of energy (15–30%), which is concentrated in the somatic tissues, gonads, and liver of mature walleye pollock of various sizes, is registered during transition from maturity stage 5 to stage 6.

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