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ORIGINAL PAPERS

The Biochemical Composition and Caloric Content of the Macrozoobenthos of the Western Kamchatka Shelf

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Abstract—Data on the biochemical composition and caloric content of common species of the zoobenthos of the western Kamchatka shelf were estimated for the entire body of an organism together with the integument and separately for muscle tissue. Estimates of the gross biomass of zoobenthos at different trophic levels calculated from bottom trawl and dredge sampling data, taking the isotope composition of benthic invertebrates into account, showed that the proportion of zoobenthos at the second trophic level was approximately 87%, while at the subsequent trophic levels it only slightly exceeded 13%. More than 70% of the energy was concentrated in valuable forage species. The total amount of energy at the second trophic level was 77.8%, while at the third and fourth levels it was 22.2%.

Keywords: zoobenthos, caloric content, trophic levels, energy equivalent, western Kamchatka shelf

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INTRODUCTION

The study of benthic communities includes several main aspects: determination of the species composition, abundance, and biomass of benthic animals, as well as their energy characteristics. The latter information is necessary for assessing the role of benthic animals in the feeding of the predatory benthos, nektobenthos, and nekton. In the Far-Eastern waters of Russia, the western Kamchatka shelf is an important fishing area with considerable stocks of valuable species of fish and invertebrates that feed largely on the zoobenthos [2, 22]. The quantitative and qualitative characteristics of the macrozoobenthos of the western Kamchatka shelf have been studied since the middle of the last century [1, 5, 13–16, 21]. However, without data on the caloric content of marine invertebrates it is impossible to make a representation of the energy value of macrozoobenthos as a forage resource of predatory animals. With this aim, we determined the biochemical composition and caloric content of common zoobenthos species for the entire organism (together with integument tissue) and separately for the muscle tissue (organic compounds) and, in addition, assessed the amount of energy concentrated at different trophic levels of benthic invertebrate communities of the western Kamchatka shelf.

MATERIALS AND METHODS

The material on the zoobenthos of the western Kamchatka shelf was collected in June–August 1986 during bottom grab and trawl surveys of similar-sized groups of animals [9] that were performed by the Pacific Research Institute of Fisheries and Oceanography (PRIFO) on the research/survey vessel *Mys Babushkina*. Intact, non-formalin-fixed organisms were used for analysis. The moisture content was determined by drying to a constant mass at a temperature of 105°C; the fat content was determined by ethyl oxide extraction in a Soxhlet device [12]; nitrogen (for "wet protein" estimation) was determined on an MTN-500 high-speed analyzer (Yanako, Japan). When entire organisms were analyzed, the mineral residue also means, among other issues, the proportion of integument tissue (shell, chitin, etc.). Carbohydrates were disregarded because of their insignificant content in benthic organisms [10]. In calculations of the caloric content (kcal/g) of the wet mass of an organism, the following coefficients were used: 5.65 for protein and 9.45 for fat [18].

In 2004, the caloric content was only estimated for the muscle tissue of benthic organisms based on the total content of proteins, lipids, carbohydrates, ash, and moisture. The proportion of water and ash was determined according to the generally accepted procedure [8]. The content of proteins was measured as the amount of nitrogen in protein compounds by the Kjeldahl method on a Kjeltec 2300 (Japan) nitrogen analyzer; carbohydrates were determined by photocolorimetry using an anthrone reagent [11]; lipids were determined by gravimetry after their extraction by the

Folch method [24]. A total of 62 species of zoobenthos were analyzed in 1986 and 21 species in 2004.

Estimates of the gross biomass of macrozoobenthos were based on materials collected during a dredge survey of the macrozoobenthos of the western Kamchatka shelf that was carried out by the PRIFO on the R/V *Professor Kaganovskiy* in July–August 2004. Sampling was conducted using an Okean-50 grab dredge (capture area, 0.25 m^2) at 117 stations (189 samples) at depths of 19 to 241 m (mainly at 40–180 m). The gross biomass estimated using Voronoi diagrams [19] was 16989000 t [15]. The biomass of invertebrates that cannot be caught with a bottom grab (crabs, shrimps, large ophiuroids, cucumaria, buccinids, and others) was determined from the averaged data on trawl catches for 2008–2011. During that period, four surveys were performed with a BT/TM 27.1/24.4 bottom trawl at a depth of 20 to 204 m. A total of 848 trawl hauls were carried out. Resources of marine organisms were assessed using individual catchability coefficients [23]. The gross biomass was calculated by the spline-approximation method [20] in the GIS CartMaster V4 program. The biomass of amphipods was determined with allowance for grazing on this group during the summer [4].

RESULTS AND DISCUSSION

The biochemical parameters of organisms varied within a wide range due to the markedly different biology of the investigated species of zoobenthos. The dry matter content in 61 taxa of macrozoobenthos varied from 9.1 to 65.8% (Table 1). Due to this, entire animals were taken for analysis, the lowest values of dry matter were found in organisms that lack a thick chitinous integument and shell. These were common sponges, coelenterates, nemerteans, nematodes, annelids, sipunculans, and ascidians, with dry matter contents rarely exceeding 20%. The highest proportion of dry matter (mainly more than 40%) was found in animals with a well-developed chitinous and calcareous protective covering (shell); these were gastropod and bivalves mollusks, sea urchins, ophiuroids, and cirripedes. Crustaceans (isopods, amphipods, and decapods) were in an intermediate position in terms of the amount of dry matter; its proportion varied from 20 to 40% and depended on the thickness of the chitinous carapace.

The content of ash in dry matter varied from 11% in the polychaete *Nereis zonata* to 95.6% in the bivalve *Cyclocardia crebricostata*. As was the case for dry matter, the amount of ash directly depended on the presence and thickness of the coverings (Table 1). The content of lipids and protein in dry matter also varied widely. The relative content of fat and protein (i.e., the caloric content of the dry matter) was largely determined by the proportion of integument tissue in the total mass of the organism. At the same time, the content of fat and protein in tissues of most of the studied marine invertebrates that lack elements of the integument was similar. The average concentration of lipids in dry matter of animals varied from 0.3 (*C. crebricostata*) to 23.6% (sea anemones) (Table 1). On the whole, the studied species were characterized by a low content of lipids. The proportion of lipids in dry matter exceeded 10% only in seven species (some polychaetes, sea anemones, and crustaceans). The content of protein in dry matter varied from 4.3 to 79.2%. Like lipids, the percentage of protein was lowest in *C. crebricostata* (the ash content in this mollusk was 95.6%) and highest in the polychaete *Lumbrineris fragilis* (Table 1).

The resulting index of the biochemical composition of hydrobionts is the energy value, viz., the caloric content. Among the studied zoobenthos, species with a thin integument had the highest caloric content; marine invertebrates with the maximum percentage of the integument tissue had a relatively low caloric content. The caloric content of most species of bivalves, gastropods, echinoderms, and cirripedes was minimal and did not exceed 1000 cal/g. The maximum caloric content (more than 3000 cal/g) was found in most species of polychaetes, decapods, and amphipods (Table 1).

In fisheries research, the energy value is generally expressed as the amount of energy per unit of wet mass. The data obtained on the biochemical composition and caloric content of wet matter for the entire organism (Table 1) allow a direct conversion of biomass to calories. This is necessary for the evaluation of the energy potential of individual species and groups of marine organisms, as well as bottom animals, which are forage items for predatory species of nekton and nektobenthos. In general, the studied species were characterized by low lipid contents. The amount of this component in wet matter exceeded 4% only in some species of polychaetes and crustaceans. The content of protein varied in a wider range: 10–15% of the wet mass in most species of shrimps and polychaetes, and no more than 3% in sponges, cirrepedes, sea urchins, and some species of bivalves. Analysis of the biochemical composition of the muscle tissue showed that the relative content of dry matter varied in a narrow range from 11.1 to 26.2%. The content of protein in the dry matter of the studied species varied from 42.0 to 82.1%; lipids, 1.3 to 15%; and carbohydrates, 2.1 to 15.5% (Table 2).

Comparison of the data on the caloric content of individual species of zoobenthos that were obtained for entire organism and for muscle tissue revealed substantial differences among animals with a thick outer skeleton, primarily gastropods and bivalves (see Fig. 1). At the same time, most of the studied species that lacked such an integument, as well as species in which only muscle tissue was analyzed, had similar caloric contents and biochemical compositions.

Table 1. The biochemical composition and caloric content of the zoobenthos of the western Kamchatka shelf

Taxon	Wet matter					Dry matter				
	moisture, %	proteins, %	lipids, %	ash, %	cal/g	dry matter, %	proteins, %	lipids, %	ash, %	cal/g
Demospongia fam. gen. sp.	87.9	2.4	0.4	9.3	175	12.1	19.9	3.3	76.8	1438
Hydrozoa fam. gen. sp.	86.0	6.8	0.3	7.0	408	14.1	48.5	1.8	49.8	2907
Anthozoa										
Actiniaria fam. gen. sp.	86.9	5.8	3.1	4.2	621	13.1	44.7	23.6	31.8	4751
Calcigorgia spiculifera	64.8	8.4	1.3	25.3	595	35.2	23.7	3.7	71.8	1687
Nemertea fam. gen. sp.	83.4	12.0	1.1	3.6	778	16.7	72.1	6.3	21.6	4671
Priapulida										
Priapulus caudatus	87.7	6.9	0.4	5.1	424	12.3	56.0	2.9	41.1	3440
Polychaeta										
Aphrodita talpa	79.6	10.1	0.5	9.9	611	20.4	49.4	2.2	48.4	3000
Eunoe spinicirris	81.0	12.5	0.6	5.9	761	19.0	65.8	3.1	31.1	4012
Harmathoe imbricata	84.3	10.3	1.1	4.3	687	15.7	65.8	6.9	27.2	4374
Nereis pelagica	76.6	15.4	2.4	5.6	1099	23.4	65.7	10.4	24.0	4689
N. zonata	76.1	16.6	4.7	2.6	1379	23.9	69.5	19.5	11.0	5772
Nephthys paradoxa	79.6	14.6	0.3	5.5	856	20.4	71.4	1.7	26.9	4194
Lumbrineris fragilis	78.3	17.2	1.7	2.8	1135	21.8	79.2	7.9	13.0	5216
Pectinaria hyperborea	81.7	4.6	0.5	13.2	308	18.3	25.1	2.8	72.1	1681
Ampharete longipaleolata	75.7	10.4	3.5	10.4	919	24.3	42.9	14.4	42.6	3789
Sabella sp.	77.2	13.1	0.9	8.9	823	22.9	57.2	3.9	38.9	3600
Chone sp.	75.3	15.0	0.5	9.2	893	24.7	60.6	2.1	37.3	3621
Potamilla reniformis	83.0	9.8	1.1	6.1	660	17.0	57.6	6.6	35.8	3882
P. neglecta	76.3	12.5	0.9	10.4	785	23.7	52.5	3.6	43.9	3308
Echiuroidea fam. gen. sp.	90.9	3.8	0.9	4.5	295	9.1	41.6	9.5	49.0	3244
Sipunculidea fam. gen. sp.	84.0	7.8	0.3	7.9	467	16.0	48.8	1.7	49.6	2914
Cirripedia										
Balanus sp.	37.3	3.4	0.2	59.1	208	62.7	5.4	0.3	94.3	332
Isopoda										
Gnorimosphaeroma sp.	60.7	15.1	0.6	23.6	912	39.3	38.5	1.6	60.0	2320
Arcturus hastiger	73.7	9.2	1.9	15.3	693	26.3	34.8	7.0	58.1	2633
Amphipoda										
Lembos arcticus	71.2	11.3	2.1	15.5	834	28.8	39.2	7.1	53.6	2892
Haploops laevis	71.1	14.7	4.4	9.9	1241	28.9	50.8	15.1	34.1	4294
Decapoda										
Anomura										
Pagurus sp.	77.0	9.3	2.5	11.2	758	23.0	40.5	10.7	48.7	3304
Hapalogaster grebnitzkii	58.9	13.6	4.5	23.1	1187	41.2	33.0	10.8	56.2	2884
Dermaturus mandtii	57.7	14.0	1.8	26.5	962	42.3	33.0	4.3	62.7	2272
Brachyura										
Chionoecetes opilio	74.2	8.8	0.6	16.4	555	25.8	34.2	2.3	63.5	2148
Hyas coarctatus	68.7	9.2	0.8	21.3	598	31.4	29.4	2.6	68.0	1907

Table 1. (Contd.)

Taxon	Wet matter					Dry matter				
	moisture, %	proteins, %	lipids, %	ash, %	cal/g	dry matter, %	proteins, %	lipids, %	ash, %	cal/g
Caridea										
Pandalus goniurus	78.0	15.3	1.2	5.5	978	22.0	69.5	5.5	25.0	4445
P. borealis	77.8	14.4	1.4	6.5	940	22.3	64.5	6.1	29.3	4224
Spirontocaris arcuata	75.1	16.2	1.3	7.4	1038	24.9	65.0	5.2	29.8	4163
Eualus suckleyi	76.6	14.0	1.4	8.2	923	23.4	59.7	6.1	35.2	3944
Crangon dalli	75.1	16.4	0.9	7.7	1008	24.9	65.6	3.6	30.8	4043
Argis ovifer	78.2	14.8	0.6	6.4	890	21.8	68.0	2.6	29.4	4088
A. lar	76.5	13.9	1.3	8.4	906	23.6	58.9	5.5	35.6	3847
Sclerocrangon salebrosa	74.3	13.4	0.9	11.5	840	25.8	52.2	3.3	44.5	3262
S. boreas	74.2	14.9	0.6	10.3	897	25.8	57.9	2.3	39.9	3482
Lebbeus groenlandicus	75.0	13.3	0.7	11.1	813	25.0	53.0	2.7	44.3	3250
Gastropoda										
Margarites sp.	45.2	6.5	0.6	47.7	425	54.8	11.9	1.1	87.0	777
Buccinum bayani	47.7	9.3	0.7	42.3	597	52.4	17.8	1.4	80.8	1141
Bivalvia										
Nucula tenuis	42.4	7.1	0.9	49.7	481	57.6	12.3	1.5	86.2	835
Nuculana sp.	39.7	6.5	1.2	52.6	479	60.3	10.8	1.9	87.2	795
Megayoldia thraciaeformis	60.6	8.1	1.3	30.1	576	39.4	20.4	3.3	76.3	1462
Yoldia hyperborea	52.7	8.2	1.8	37.4	628	47.3	17.3	3.7	79.0	1328
Y. bartschi	63.3	10.2	2.3	24.2	798	36.8	27.8	6.3	65.8	2172
Hiatella arctica	44.2	2.7	0.2	52.9	172	55.8	4.9	0.3	94.8	309
Cyclocardia crebricostata	34.2	2.8	0.2	62.9	178	65.8	4.3	0.3	95.6	270
Serripes groenlandicus	53.1	5.3	0.2	41.5	318	46.9	11.2	0.4	88.3	677
Macoma calcarea	53.9	6.8	2.7	36.7	637	46.2	14.8	5.8	79.5	1380
Bryozoa										
Flustrella gigantea	80.0	8.6	0.2	11.2	508	20.0	43.1	1.1	55.8	2539
Echinodermata										
Asteroidea fam. gen. sp.	72.3	8.5	0.9	18.3	565	27.7	30.7	3.3	66.0	2043
Ctenodiscus crispatus	58.0	6.9	0.8	34.3	470	42.0	16.5	2.0	81.5	1119
Ophiura sarsi	49.3	5.7	0.5	44.5	371	50.7	11.3	1.0	87.7	731
Ophiopenia vicina	54.9	4.5	1.4	39.2	386	45.1	10.0	3.1	86.9	856
Strongylocentrotus pallidus	67.7	2.3	0.1	29.9	138	32.3	7.1	0.3	92.6	427
Echinarachnius parma	47.1	2.7	0.9	49.3	233	52.9	5.1	1.6	93.3	441
Chiridota laevis	81.7	5.8	0.3	12.2	355	18.3	31.7	1.5	66.7	1937
Ascidiacea fam. gen. sp.	85.4	3.6	0.2	10.8	222	14.6	24.3	1.6	74.1	1524

Data from [9] are used in the table.

The averaged data on the caloric content in groups of macrozoobenthos (Table 3), whose biomass was determined based on the 2004 grab survey [15] and 2008–2011 bottom trawl surveys (Table 4), indicated that the caloric content of the marine invertebrates with the highest biomass was low. In particular, sea urchins in aggregations on sandy bottoms [13, 15] had a relatively low energy equivalent, 155 cal/g of wet

Table 2. The biochemical composition and caloric content of the muscle tissue of benthic invertebrates of the western Kamchatka shelf

Taxon	Wet matter						Dry matter					
	moisture,%	proteins, %	lipids, %	carbohydrates, %	ash, %	cal/g	dry matter,%	proteins, %	lipids, %	carbohydrates, %	ash, %	cal/g
Nemertea	83.4	11.0	1.2	0.8	3.6	780	16.6	66.3	7.2	4.8	21.6	4625
Polychaeta												
Nereis pelagica	77.9	13.8	3.3	1.3	3.7	1167	22.1	62.4	15.0	5.9	16.7	5189
Travisia forbesii	85.5	7.4	0.7	0.3	6.1	501	14.5	51.0	4.8	2.1	42.1	3424
Sipunculidea	82.4	6.8	0.2	1.5	9.1	487	17.6	38.4	1.3	8.5	51.8	2634
Amphipoda												
Acanthosthepheia sp.	78.2	12.5	1.5	0.6	11.2	882	25.8	48.4	5.8	2.3	43.4	3382
Anonyx sp.	75.4	10.6	1.4	1.0	11.6	788	24.6	43.1	5.7	4.1	47.2	3139
Decapoda												
Pandalus goniurus	78.9	12.9	1.8	2.2	4.2	1023	21.1	61.1	8.5	10.4	19.9	4688
P. borealis	78.5	12.9	2.4	2.4	3.8	1091	21.5	60.0	11.2	11.2	17.7	4903
Argis ochotensis	75.4	10.1	1.6	2.7	10.2	874	24.6	41.1	6.5	11.0	41.5	3384
Gastropoda												
Buccinum bayani	74.8	13.5	0.8	2.4	8.5	975	25.2	53.4	3.3	9.5	33.7	3723
Neptunea laticostata laticostata	73.8	15.6	1.0	2.2	7.4	1099	26.2	59.7	3.7	8.4	28.2	4065
Bivalvia												
Megayoldia thraciaeformis	76.8	14.0	1.6	1.7	5.09	1037	23.2	60.4	6.8	7.3	25.4	4358
Yoldia bartschi	78.4	12.3	2.5	2.2	4.6	1056	21.6	56.9	11.6	10.2	21.3	4730
Y. myalis	77.1	13.1	1.9	3.0	4.9	1089	22.9	57.2	8.3	13.1	21.4	4553
Keenocardium californiense	77.1	13.7	1.9	3.5	3.8	1149	22.9	59.7	8.3	15.3	16.8	4781
Serripes groenlandicus	77.2	13.4	2.3	3.1	4.0	1150	22.8	58.8	10.1	13.6	17.5	4831
S. notabilis	79.9	16.5	0.5	0.7	2.4	1019	20.1	82.1	2.5	3.5	11.9	5016
Nuculana pernula	76.4	11.6	2.1	1.6	8.3	944	23.6	49.2	8.9	6.8	35.2	3896
Ciliatocardium ciliatum tchuktchense	82.6	7.3	1.8	2.7	5.6	735	17.4	42.0	10.3	15.5	32.2	3984
Ophiuroidea												
*Ophiura sarsi**	46.7	5.2	0.5	0.3	47.3	358	53.3	9.8	0.9	0.6	88.7	663
Holothuroidea												
Chiridota laevis	88.9	6.3	0.5	1.1	3.2	465	11.1	56.8	4.5	9.9	28.8	4039

* For ophiuroids, entire organisms together with coverings were sampled.

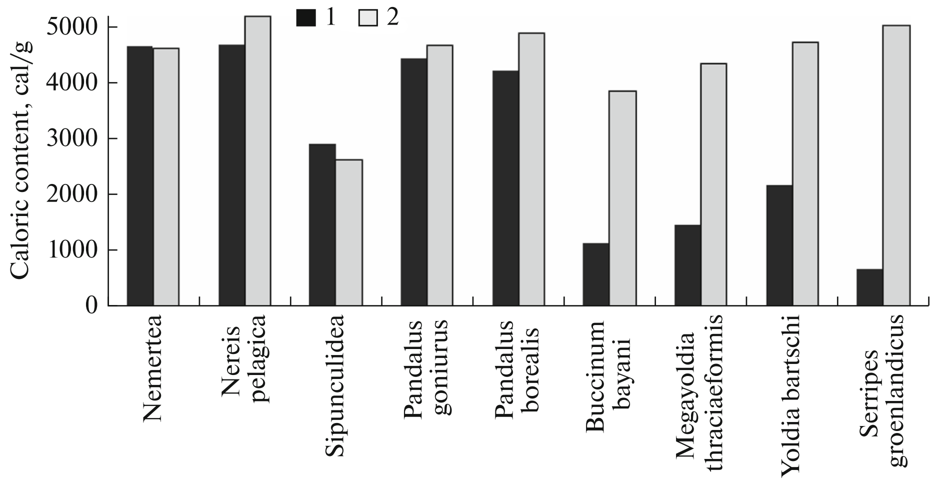

Fig. 1. The caloric content (in dry matter) of some species of the macrozoobenthos. (1) entire organism; (2) muscle tissue.

Table 3. The average values of the caloric content of animals of large taxonomic groups of the benthos of the western Kamchatka shelf

Taxon	Caloric content, cal/g	
	wet matter ± SD	dry matter ± SD
Bivalvia	474 ± 43.6	1025 ± 100.9
Polychaeta	840 ± 31.9	3934 ± 143.5
Echinodermata	360 ± 136.6	1079 ± 446.2
Echinoidea	155 ± 23.3	434 ± 70.3
Holothuroidea	386 ± 11.2	856 ± 28.1
Ophiuroidea	364 ± 14.5	697 ± 28.0
Asteroidea	518 ± 18.1	1581 ± 57.5
Nemertea	778 ± 42.0	4671 ± 214.4
Isopoda	803 ± 12.0	2476 ± 40.4
Amphipoda	1037 ± 38.3	3593 ± 112.8
Decapoda	886 ± 171.9	3418 ± 812.4
Anomura	969 ± 48.4	2820 ± 122.5
Brachyura	576 ± 12.1	2028 ± 46.8
Caridea	923 ± 42.5	3875 ± 185.5
Gastropoda	511 ± 47.0	959 ± 89.1
Others (average)	383 ± 146.9	2395 ± 1032.5
Demospongia	175 ± 8.5	1438 ± 73.5
Hydrozoa	408 ± 18.7	2907 ± 147.7
Anthozoa	608 ± 34.8	3219 ± 160.4
Priapulida	424 ± 37.8	3440 ± 272.6
Echiuroidea	295 ± 32.4	3244 ± 367.5
Sipunculidea	467 ± 46.7	2914 ± 297.2
Cirripedia	208 ± 17.8	332 ± 24.4
Bryozoa	508 ± 23.8	2539 ± 130.9
Ascidiacea	222 ± 37.8	1524 ± 261.6

The values of the caloric content were calculated taking skeletal structures into account. Here and in Table 5, SD signifies the standard deviation.

Table 4. The gross biomass and the ratio of taxonomic groups of macrozoobenthos on the western Kamchatka shelf based on dredge (2004) and trawl (2008–2011) survey data

Taxon	Gross biomass, thousand t	Proportion, %
Echinoidea*	5945	33.17
Bivalvia	3996	22.30
Polychaeta	3062	17.09
Holothuroidea*	1478	8.25
Gammaridea	645	3.60
Ophiuroidea*	441	2.46
Gastropoda*	340	1.90
Porifera	323	1.80
Actiniaria	245	1.37
Foraminifera	173	0.96
Echiurida	156	0.87
Ascidiacea	154	0.86
Asteroidea*	126	0.70
Nemertea	118	0.66
Anomura*	185	1.03
Brachyura*	80	0.45
Caridea*	65	0.36
Bryozoa	99	0.55
Hydroidea	91	0.51
Cirripedia	73	0.41
Sipunculidea	40	0.22
Priapulida	22	0.12
Isopoda	1	0.01
Others**	62	0.35
Total	17920	100

*The resource was calculated taking trawl catches and grab data into account.
**This includes seven taxonomic groups.

Table 5. The energy parameters of the macrozoobenthos of the western Kamchatka shelf

Taxon	Resource, thousand t	Proportion, %	Caloric content, cal/g wet matter ± SD	Energetic equivalent, 10^{12} kcal	Proportion, %
<u>First-order consumers</u>	15567	86.9	398 ± 253	6.19	77.8
Bivalvia	3996	22.3	474 ± 43	1.89	23.8
Polychaeta	2062	11.5	840 ± 31	1.73	21.8
Echinoidea	5945	33.2	155 ± 23	0.92	11.6
Holothuroidea	1478	8.2	386 ± 11	0.57	7.2
Gammaridea	430	2.4	1037 ± 38	0.45	5.6
Ophiuroidea	441	2.5	364 ± 14	0.16	2.0
Others	1215	6.8	383 ± 146	0.L47	5.8
<u>Second-third order consumers</u>	2353	13.1	752 ± 216	1.77	22.2
Nemertea	118	0.7	778 ± 42	0.09	1.1
Polychaeta	1000	5.6	840 ± 31	0.84	10.5
Isopoda	1	0.0	803 ± 12	0.001	0.0
Gammaridea	215	1.2	1037 ± 38	0.22	2.8
Asteroidea	126	0.7	518 ± 18	0.07	0.9
Anomura	185	1.0	969 ± 48	0.18	2.3
Brachyura	80	0.4	576 ± 12	0.05	0.6
Caridea	65	0.4	923 ± 42	0.06	0.8
Gastropoda	340	1.9	511 ± 47	0.17	2.1
Others	223	1.2	383 ± 26	0.09	1.1
Benthos as a whole	17920	100	444 ± 265	7.96	100

mass. The forage value of polychaetes on silty bottoms was fairly high (840 cal/g, wet mass). Approximately 50% of the gross biomass of zoobenthos on the western Kamchatka shelf was contributed by echinoderms, sponges, bryozoans, sea anemones, cirripedes, ascidians, some species of bivalves, and others (Table 4), viz., low-calorie groups made a considerable contribution to the biomass of the zoobenthos. This apparently explains the high selectivity in the feeding of common species of benthivores with respect to high-calorie groups of benthos such as crustaceans, mollusks, and worms, but low selectivity with respect to echinoderms [7].

Studies on the isotope composition of macrobenthos in the trophic web of the western Kamchatka shelf [3] allowed the energy of zoobenthos to be estimated at different trophic levels (Table 5). Almost all bivalves, echinoderms, ophiuroids, holothurians, as well as nonpredatory polychaetes and gammarids, are at the second trophic level (first-order consumers). The animals of these groups are collecting detritivores, nonselective ground-eating detritivores, and mobile suspension feeders; their biomass was up to 86.9% of the total zoobenthos. Carnivores were represented in samples by seven taxonomic groups: predatory polychaetes, sea stars, amphipods, isopods, decapods, nemerteans, and gastropods; their biomass is 13.1%. Despite the fact that species of these groups are omnivorous and eat a wide range of food items (from animal detritus to large invertebrates and fish), the isotope study indicated that almost all these species are at the third–fourth trophic levels, viz., are II–III order consumers.

The gross biomass estimates of macrozoobenthos at different trophic levels, which were calculated based on bottom trawl and grab survey data with account taken of the isotope composition of benthic invertebrates, indicated that the proportion of the zoobenthos at the second trophic level was approximately 87%; it was only slightly greater than 13% at subsequent trophic levels. On the shelf of the Sea of Okhotsk, the biomass of the zoobenthos of the second trophic level was up to 91% [6].

Based on the biomass and caloric content, we calculated the energy equivalent of the biomass of the benthos (10^{12} kcal). In analyzing the amount of energy concentrated in different groups of the zoobenthos, there was a considerable discrepancy with their biomass (Table 5). In terms of biomass, the macrobenthos was dominated by low-calorie sea urchins (33.2%). The proportion of these animals calculated in terms of energy did not exceed 12.3%. The main amount of energy (more than 70%) was concentrated in valuable forage species. The total amount of energy at the second trophic level was 77.8%; at the third and fourth trophic levels it was 22.2%.

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