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MARINE BIOLOGY

The Role of Zooplankton in the Transformation of the Organic Matter in the Ob Estuary, on the Shelf, and in the Deep Regions of the Kara Sea

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Abstract—The data for the present study were collected at 20 sampling stations in the Kara Sea along the transect from the Ob estuary to the deep sea St. Anna Trough in September 2007. Based on the hydrophysical features, the distribution of the *Chl a*, and the primary production, we distinguished six habitats: the river, estuary, inner and outer shelf, continental slope, and trough. The impact of the small-size (<0.5 mm) and large-size (>0.5 mm) fractions of the zooplankton on the phytoplankton's organic carbon in the different regions of the Kara Sea was estimated. The ingestion rate was assessed using the analysis of the gut fluorescence content and the gut evacuation rate. The zooplankton grazed 1–2% of the phytoplankton biomass in the river and estuary; 3.5% over the shelf; and 6 and 10% in the regions of the trough and slope, respectively. The grazing impact of the small-sized zooplankton increased from the river zone to the deep regions (from 1 to 90%) along with their share in the total zooplankton abundance (from 18 to 95%). From 72 to 86% of the primary production was grazed over the shelf and slope. The primary production did not cover the feeding requirements of the zooplankton in the estuarine regions and St. Anna Trough in the autumn. In the estuarine regions, the major portion of the organic matter settles on the bottom due to the strong inflow of the allochthonous matter and the relatively low zooplankton grazing.

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INTRODUCTION

The Kara Sea is a shallow marginal Arctic basin. The shelf with depths of less than 100 m occupies 90% of the total Kara Sea area, while the areas less than 50 m deep occupy slightly more than 40% [33]. For the most part of the year, the sea is covered with ice. The seasonal ice melting usually starts at the end of May–June depending on the geographical latitude of the location. The ice cover is established at the end of September to the beginning of October.

The most characteristic feature of the Kara Sea is that it receives the Arctic's biggest river discharge. The annual discharge volume averages 1200 km^3 with most of the volume being contributed by the Ob and the Yenisei rivers [8, 23]. About 220 million tons of suspended and dissolved matter enter the Kara Sea shelf with the riverine water [23], strongly affecting the biological productivity and biogeochemical cycles of the sea's ecosystem. The riverine discharge accelerates the ice's breaking up in the spring time, enriches the shelf waters with allochthonous nutrients, and determines the formation over the most part of the sea area of the firm density stratification of the water column with the depth of the upper mixed layer being about 10 m. The northern parts of the sea are influenced by the Barents Sea and by the transformed Arctic waters.

The oceanographic features of the Kara Sea listed above determine the specificity of the structure and the functioning of the regional plankton communities. The spring phytoplankton blooms are related to the start of the ice's melting and, according to the data available, it continues for about 4.5 months [21, 22]. During this short period, in particular, the main part of the organic matter synthesized (the *de novo*) is utilized by the herbivorous zooplankton. The quantitative parameters of the utilization of the newly synthesized organic matter are determined by the seasonal dynamics of the phytoplankton community and the state of the populations of the mass herbivorous organisms.

One of the most important features of the spatial structure of the Kara Sea's plankton communities is the clear cross shelf zonality present from the estuarine regions in the south to the deepwater parts in the north. The evidence of such zonality was reported in earlier published papers [4, 6, 20, 24]. The spatial structure of the phyto- and zooplankton communities is analyzed in detail elsewhere [12, 15, 17]. The processes of the water exchange at the basin's north determine the inflow of the Barents Sea and Arctic faunas and, hence, their impact upon the structure of the zooplankton communities in this region.

Table 1. Characteristics of the defined regions: *T*, °C is the temperature of the surface layer, *S* is the salinity of the surface layer, *Chl a* is the concentration of chlorophyll in the 0–50 m layer (bottom), and PP is the primary production in 0–50 m layer (bottom)

Region	No. of the station	Depth, m	*T*, °C (1 m)	*S*, psu (1 m)	*Chl a*, mg/m^2	PP, mg C/m^2 per day
River	4993	21	7.7	0.05	92.7	59.0
Estuary	4994–4998	11–17	4–6	0.6–5.9	25.4 ± 21.1	11.0
Inner shelf	4999–5002	24–29	2.7–3.5	9.3–20.6	18.1 ± 7.7	72.5
Outer shelf	1991, 5003–5004	60–110	2.7–3.5	17.9–19	12.5 ± 3.7	56.5
Slope	4988–4990	125–175	0.3–2.6	26.2–33.9	7.1 ± 3.2	47.2
Trough	4983–4987	260–550	2.2–2.7	34.1–35.1	28.2 ± 1.7	60.7

The inflow of the allochthonous nutrients plays an important role in the processes of the formation of the biological productivity in the estuaries of the large rivers and in the shelf regions affected by the freshwater discharge. The highest values of the *Chl a* concentration and the primary production are recorded in the inner desalinated part of the Ob and Yenisey estuaries [4, 14]. Relatively high values of the primary production are observed by the end of the vegetation season in the shelf region adjacent to the Ob estuary [14]. It was assumed that the high biomass of the phytoplankton in the estuarine regions of the Kara Sea is considerably underutilized by the pelagic community, and the most part of the newly formed organic matter sediments on the bottom [10, 11, 21]. However, the utilization of the primary production and the phytoplankton biomass either by the zooplankton community as a whole or by its components has not yet been assessed in the various biotopes of the Kara Sea. This data gap does not allow even for the very general assessment of the share of newly synthesized organic matter that is involved in the pelagic trophic chains or directly settles in the bottom sediments providing food for the bottom dwellers. It is also unclear how such a ratio relates to the zonality of the Kara Sea's ecosystem.

The main goal of the present research was to study the role of the zooplankton and its small and large size fractions in the utilization and transfer of the newly synthesized organic matter during the autumn period. The studied region covered various pelagic biotopes of the Kara Sea: from the desalinated inner part of the Ob estuary to the deepwater St. Anna Trough inhabited by plankton communities differing in their structures and patterns of functioning.

To achieve our goal, the following parameters of the plankton communities were analyzed:

1. The distribution of the *Chl a* and the values of the primary production.
2. The ratio of the number and biomass of the large and small fractions of the herbivorous zooplankton.
3. The intensity of the feeding of the mass species of large- and small-sized herbivorous zooplankton.
4. The role of the zooplankton in the ingestion of the phytoplankton biomass and primary production.

MATERIAL AND METHODS

The studies were carried out in September 2007 aboard the *Akademik Mstislav Keldysh* along the transect from the Ob River to the St. Anna Trough (Fig. 1; Table 1).

The sampling of the zooplankton. The large-sized fraction of the mesozooplankton (>5 mm) was sampled using a Juday net (the diameter of the mouth was 37 cm; the mesh size of the filtering cone was 180 μm), while the small-sized fraction (<0.5 mm) using a modified Apshtein net (the diameter was 16 cm; the mesh size of the filtering cone was 60 μm). The zooplankton was sampled by vertical catches with net lifting speeds of 0.6–0.8 m/s. The samples were collected either in the upper 50 m layer or the layer of 0 m to the bottom at the lesser depths. The samples were preserved with 4% neutral formalin. The taxonomic and size compositions of the zooplankton were determined using a binocular microscope at ×40 magnification.

The individual wet weight (WW) of the animals was determined using nomograms [18]; to transform the wet biomass weight to carbon units (C), the coefficient C/ WW = 0.1 recommended in [25] was applied.

The determination of the *Chl a* and the pheopigments. The samples for the determination of the concentrations of the phytopigments were collected using a Niskin bottle of the Rosett complex. The layers for

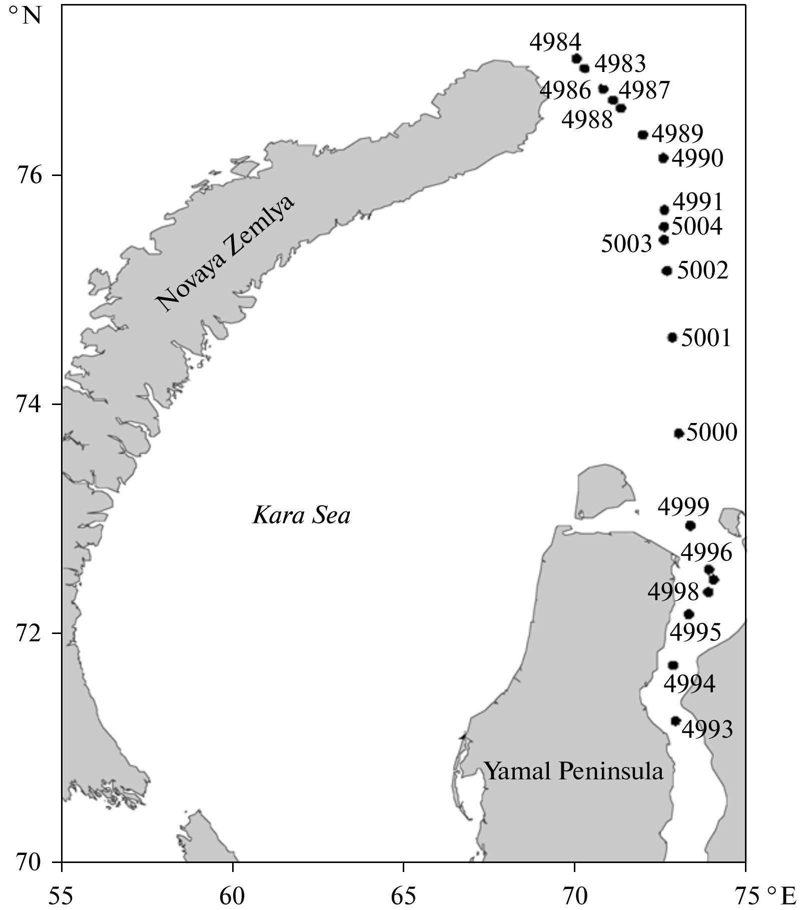

Fig. 1. Map of the studied region and the location of the sampling stations along the Ob–St. Anna Trough transect.

the sampling were chosen based on the probing with a CTD probe equipped with the relevant detectors. If the vertical stratification was absent at the sampling station, the samples were collected from three water layers evenly distributed in the water column. At the presence of stratification, the samples were collected from two to three depths in the upper mixed layer, one to two depths in the zone of the density jump and/or in the layer of the maximal fluorescence, and one to two depths in the zone below the pycnocline. The water (0.5–1 l) was filtered through glass fiber GF/F filters at a vacuum level of not more than 0.3 atm. The extraction was performed with 90% acetone at a temperature of +4°C in darkness for 24 h.

Before and after acidification the extracts with two drops of 10% HCl, the fluorescence was measured using a Trilogy Turner Designs (USA) fluorometer. The device was calibrated using pure chlorophyll prior to the determinations. The concentrations of *Chl a* and pheopigments (mg/m^3) were calculated using the equation given in paper [32] for *in vitro* flourimetry:

$$Chl\ a = k(Fb - Fa)(V_{\text{extr}}/V_{\text{water}})$$

$$\text{Pheopigment} = k(R\ Fa - Fb)\ (V_{\text{extr}}/V_{\text{water}}),$$

where k stands for the device's calibration coefficient; Fb and Fa, the fluorescences of the sample solution before and after acidification, respectively; R is the acidification coefficient; V_{extr} is the volume of the acetone extract; and V_{water} is the water volume.

The primary production was determined using a radio-carbon analysis according to [5] at the simulation of the illumination conditions in the on-deck incubator. The experiments are described in detail in [14].

The feeding of the zooplankton was assessed using the fluorescence technique using the contents of the phytopigments (the *Chl a* and the pheopigments) in the stomachs and by the rate of the food passage through the guts [26]. For the analysis, the zooplankton was sampled using a Juday net from the upper 50 m layer. To prevent the excretion of food from the intestines, the animals were immediately narcotized using filtered marine water saturated with carbon dioxide. The immobilized animals were sorted to the species and developmental stages under a binocular microscope and placed in 90% acetone for the extraction of the phytopigments. The extraction was performed at a temperature of 7°C for 24 h. The amount of the pigments was determined using the method described in [32]:

$$Chl\ a = k(Fb - Fa)(V_{\text{extr}}/n)$$

$$\text{Pheopigments} = k(R\,Fa - Fb)/(V_{\text{extr}}/n),$$

where k stands for the device's calibration coefficient; Fb and Fa, the fluorescences of the sample solution before and after the acidification, respectively; R is the acidification coefficient; V_{extr} is the volume of the acetone extract; and n is the number of animals in the extract.

The total content of pigments in the stomachs (G, ng was calculated using equation [25]:

$$G = (Chl\ a + 1.51\ \text{pheopigment}).$$

The daily ingestions of chlorophyll for each species (I, ng pigments/ind. per day) was calculated according to [26]: $I = (G/T)\ 24$, where G stands for the content of the pigments in the stomach (ng/ind.), and T is the rate of the food digestion (h). The values of the digestion rates in the various zooplankton species were taken according to published data [1, 2, 29].

The total ingestion of the phytoplankton biomass by all the herbivorous species in the water column of 0–50 m (bottom) (I_{tot}, mg of pigments/m^2 per day) was calculated using the following equation:

$$I_{tot} = \sum_{i \to 1}^{n} I_i Z_i,$$

where I_i designates the daily rate of the chlorophyll ingestion by the i species (I, mg/pigments/ind. per day), Z_i is the number of the i species/stage in the layer (ind./m^2), and n is the number of species and stages. The specific food ingestion (I_{sp}, mg of C for the phytoplankton/mg of C for the zooplankton per day) by all the zooplankton in the water column was determined as

$$I_{sp} = I_{tot}/B_{tot},$$

where B_{tot} is the zooplankton biomass in the organic carbon units (mg of C/m^2).

For the expression of the daily food ingestion in the carbon units, the data on the concentration of the suspended organic carbon (C_{org}) for the upper 50 m water layer at the same sampling stations [3] were used.

RESULTS

The characteristics of the region. The studied region of the Kara Sea covered the zone stretching in the latitudinal direction for six degrees (71°N to 77°N) (Fig. 1). The region includes the pelagic biotopes from the Ob River's mouth to the deepwater regions of the St. Anna Trough differing in the environmental conditions and compositions of the phyto- and zooplankton communities. The sampling stations were combined into groups based upon the following parameters: the water salinity and temperature in the upper mixed layer, the depth, the *Chl a* concentration, and the value of the primary production. Based upon these combinations of parameters, six zones were distinguished: the river, estuary, inner shelf (<50 m), outer shelf (>50 m), continental slope, and deepwater trough (Table 1). In the river with water salinity not exceeding 0.05 psu, the *Chl a* concentration averaged 92.7 mg/m^2 and the primary production, 59 mg of C/m^2 per day. In the estuarine zone, the chlorophyll content decreased with approaching the sea (Fig. 2), while averaging 25.4 mg/m^2; the mean primary production was only 11 mg of C/m^2 per day. Above the shelf, the chlorophyll content ranged from 12 to 18 mg/m^2. The lowest chlorophyll content (7.1 mg/m^2) was recorded in the zone of the continental slope. At the northernmost stations in the St. Anna Trough, the chlorophyll content increased to 28.2 mg/m^2. In the sea part of the transect, the maximal value of the primary production was observed at the inner shelf (72.5 mg of C/m^2 per day), while the minimal (47.2 mg of C/m^2), above the slope (Table 1).

The pattern of the vertical distribution of the *Chl a* changed along the transect as shown in Fig. 2. In the river and estuarine zone, the chlorophyll was evenly distributed from the surface to the bottom, while, on the inner and outer shelf, considerable vertical stratification was observed according to the density stratification of the water column. The relatively high chlorophyll concentrations (1–2 mg/m^3) were confined to the upper mixed ~10 m deep layer; deeper, the concentration sharply decreased to 0.2–0.4 mg/m^3. In the region of the slope and the St. Anna Trough, the chlorophyll content ranged from 0.2 to 0.6 mg/m^3, and its vertical distribution in the whole 50 m layer was even.

The ratio of the suspended organic matter (C_{org}) to the *Chl a* also changed with increasing distance from the river (Fig. 3). The values of this index were maximal in the river and estuary (Fig. 3a). Presumably, this is due to the high content of terrigenic organic matter in the riverine water. On the shelf, the C_{org}/*Chl a* ratio dropped down to the values typical for the autumn (Fig. 3b) [30]. The lowest values were recorded in the deepwater regions above the slope and trough (Fig. 3c). This assumes that the major part of the suspended organic matter in all the regions situated north of the estuary consisted of phytoplankton.

The distribution of the zooplankton. The minimal total number (16.6×10^3 ind./m^2) of mesozooplankton was recorded at the stations within the river zone. In the northward direction along the transect, the number gradually increased and reached its maximum (1540×10^3 ind./m^2) at the St. Anna Trough (Fig. 4a). Especially noticeable was the increase in the amount of the small-sized fraction of the plankton animals. Their number was the highest in the region of the continental slope and the St. Anna Trough (268 thousand

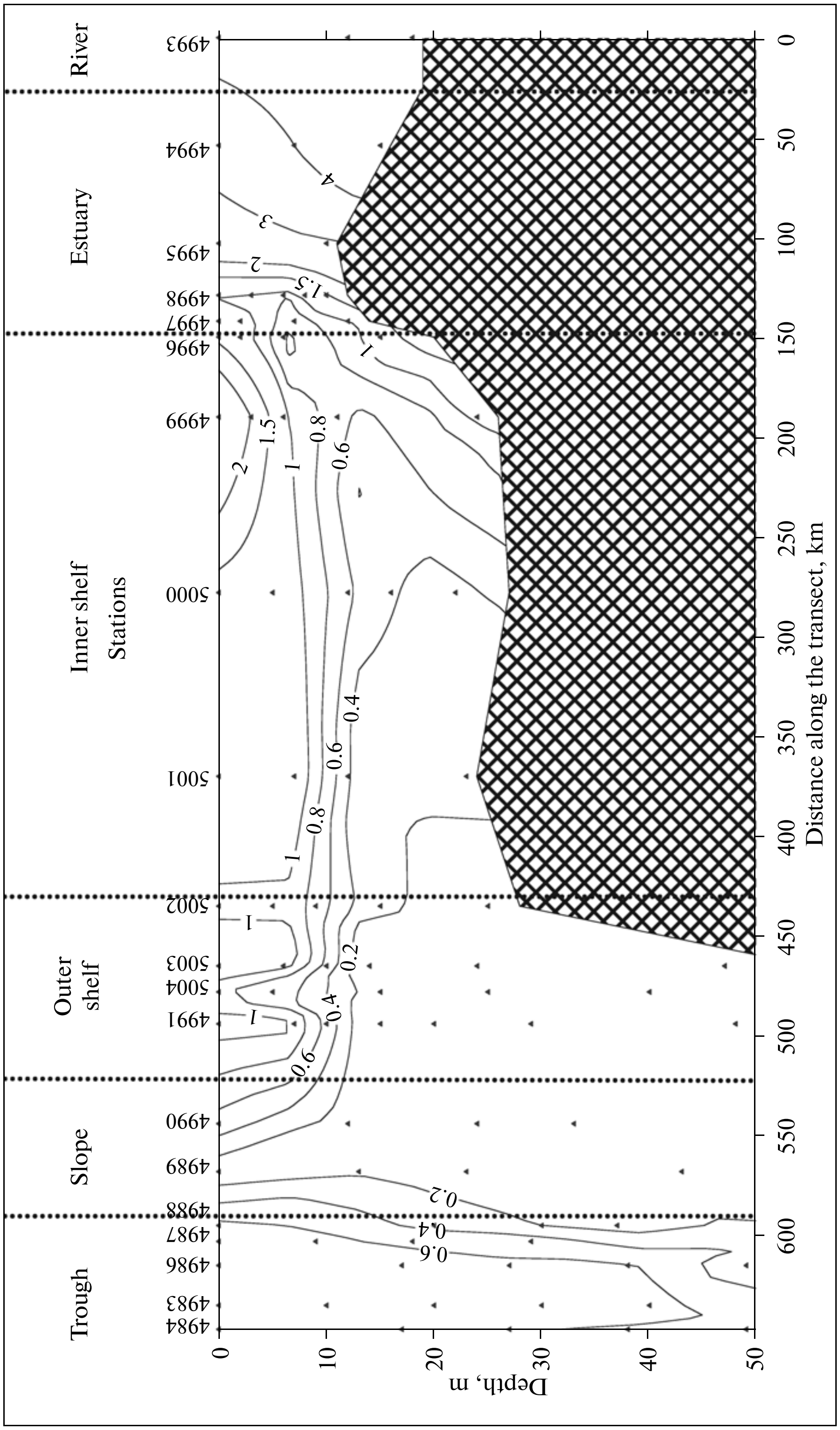

Fig. 2. Distribution of the *Chl a* along the Ob–St. Anna Trough transect.

and 1540 thousand ind./m^2, respectively) accounting for 95% of the total mesozooplankton number. In these regions, the small forms dominated: *Oithona similis*, *Limacina* sp., and the copepod nauplii. In the river zone and estuary, the large forms of zooplankton dominated in the community (Fig. 4a): the brackish water species *Senecella siberica* and *Limnocalanus macrurus*.

Considerable latitudinal changes in the total zooplankton biomass were recorded along the transect (Fig. 4b). The maximal values of the biomass were recorded in the estuarine zone and in the region of the St. Anna Trough (10.2 and 13.1 g/m^2, respectively), while the minimal (0.9 and 1.6 g/m^2), in the river zone and above the slope. At all the stations, large zooplankton dominated in the biomass. The biomass of small animals (as their number) increased along the direction from the river and the estuarine zones to the trough, where it reached the maximum of 3.9 g/m^2 (Fig. 4b). The share of the small fraction in the zooplankton biomass varied within <1% limits in the river and estuary to 30–49% in the deepwater part of the transect.

The intensity of the zooplankton feeding. The values of the daily ingestion of phytopigments by the mass herbivorous species determined experimentally are shown in Table 2; Table 3 presents the relevant calculated values of the mean daily rations expressed in carbon units and percent of the body weight. The data in Table 3 illustrate the higher intensity of the feeding of the small zooplankton species compared to the larger ones for each of the separated zones. For instance, the specific rations (% of the body weight) of the small animals (*Eurytemora lacustis* and *Cyclops strenuus*) in the river reach 38–70%, while, for the large species (*Senecella sibirica*), these values reach only 30 % (Table 3). In the estuarine zone, such differences are more pronounced: the rations of the small-sized *Cyclops stenuus* and *Pseudocalanus* spp. reached 27–35%, while, for *Limnocalanus macrurus*, the ration was 3–4%. A good example is the population of one of the dominant species of the marine community (St. Anna Trough), *Calanus finmarchicus*: the specific rations of the younger copepodit stages are an order higher than for the elder CIV and CV stages (Table 3).

The higher feeding activity of the small-sized fraction of the zooplankton in general is illustrated by Fig. 5. The specific consumption of phytoplankton carbon by the small animals was considerably higher than for the large animals in all the biotopes. Everywhere, except for the river zone, the ingestion by the small zooplankton was 4–9 times higher. Only in the river zone was the specific consumption of the phytoplankton approximately the same in both size groups.

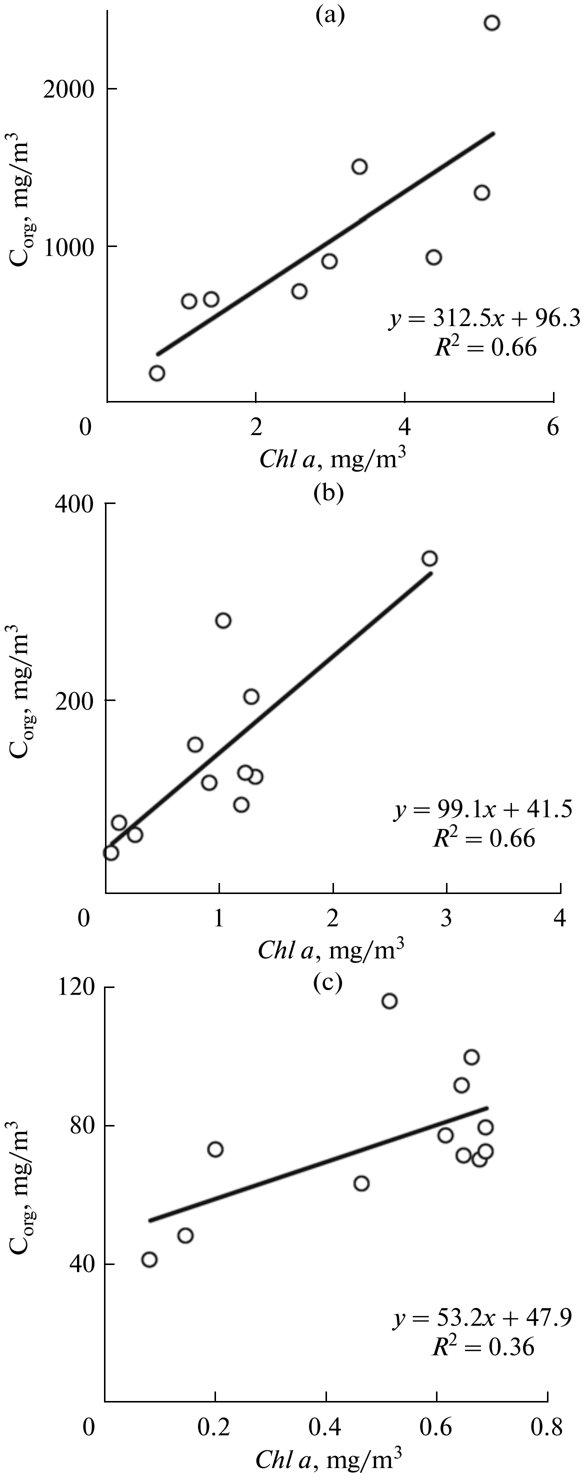

Fig. 3. Ratio of the concentration of suspended organic matter (C_{org}) to the concentration of chlorophyll (*Chl a*) (a) in the Ob River and estuary, (b) in the inner and outer shelves, and (c) above the continental slope and in the St. Anna Trough region.

A pronounced tendency for a decrease in the specific ingestion of phytoplankton by both the small-sized and large-sized zooplankters in the direction from the estuarine zone to the northern deepwater sea regions is also shown in Fig. 5. The maximal differences (more than two-fold) in the specific consumption of algae by the zooplankton of the studied regions

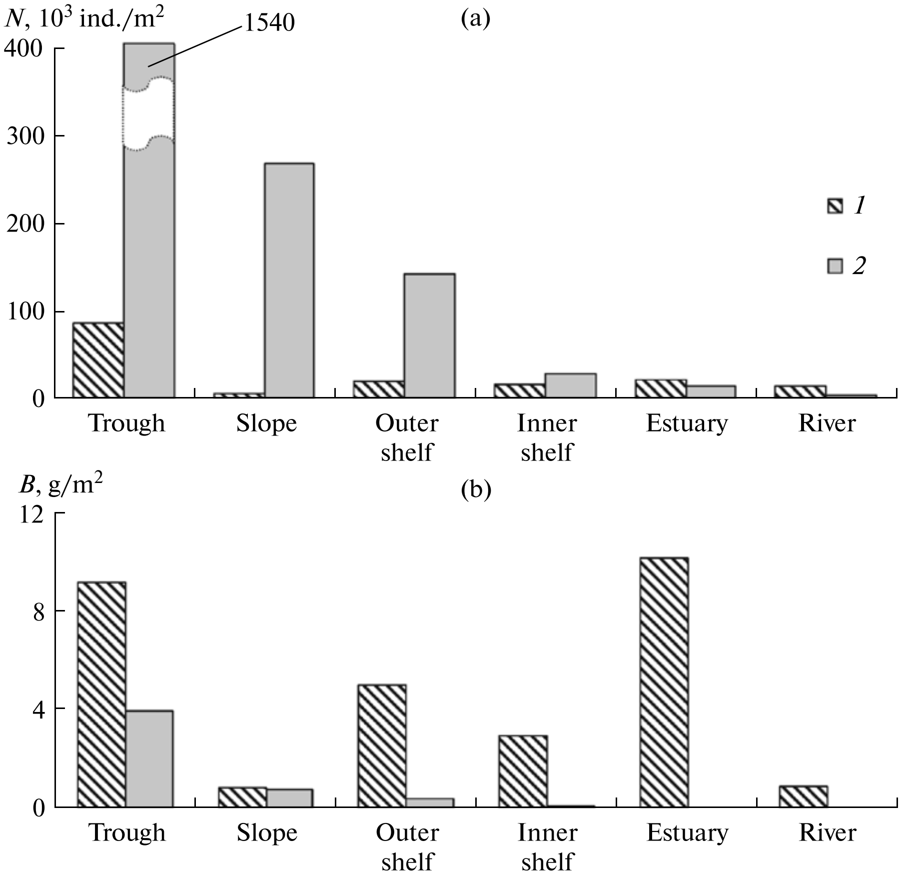

Fig. 4. Distribution along the transect of the (a) number and (b) biomass of the small (body size < 0.5 mm) and large (body size > 0.5 mm) fractions of the zooplankton in the layer of 0–50 m (bottom).
1—large fraction; 2—small fraction.

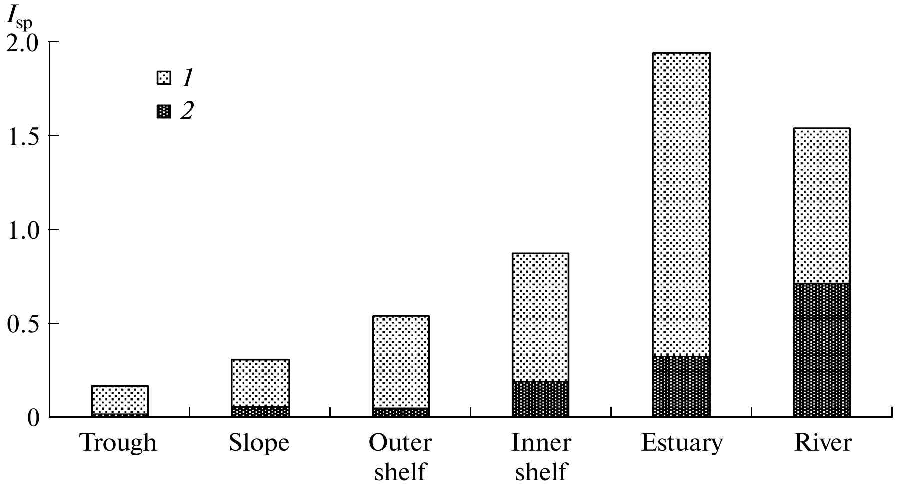

Fig. 5. The specific ingestion (I_{sp}, mg of C of the phytoplankton/mg of C of the zooplankton) by the different size fractions in the layer of 0–50 m (bottom) along the Ob–St. Anna Trough transect. *1*—small fraction; *2*—large fraction.

were noted at the comparison of the Ob estuarine zone and the inner shelf region. The general decrease in the zooplankton feeding activity in the deepwater regions compared to the estuarine zone reached 11 times in the small-sized fraction and 33 times in the large-sized group.

Table 2. Daily consumption of phytopigments (ng of pigment/ind. per day) by the mass species of herbivorous zooplankton in various sea regions (the mean ± the standard deviation)

Type and stage of progress/size	River	Estuary	Inner shelf	Outer shelf	Continental slope	St. Anna Trough
Eurytemora lacustris, fem	26.3 ± 9.4					
Eudiaptomus sp., fem	23.2 ± 3	45.5 ± 11.3				
Eudiaptomus sp., male	16.9					
Cyclops strenuus, fem	47.2					
Cyclops strenuus, CV	21.6 ± 17.1	8.5 ± 2.5				
Senecella siberica, fem	267.4 ± 67.5	305.7 ± 47.5				
Senecella siberica, CV		177.2 ± 40.2				
Limnocalanus macrurus, fem		37.5 ± 28.2	10.4 ± 2.5			
Limnocalanus macrurus, male		39.2 ± 27.1	20.3 ± 16.8			
Jaschnovia tolli, CV		51.0 ± 8.7	46.8 ± 35.6			
Pseudocalanidae, CV		24.3 ± 4.9	19.5 ± 13.2	6.3 ± 1.7	21.8 ± 3.9	25.9 ± 14.2
Pseudocalanidae, CIII					8.9 ± 6.2	11.7
Pseudocalanus major, CV				9.8 ± 3.1		
Calanus glacialis, fem				23.2		
Calanus glacialis, CV		46.6	106.8	36.6 ± 16.4		
Calanus glacialis, CIV			31.3	47.7 ± 28.1		
Calanus glacialis, CIII				13.6 ± 8.5		
Calanus finmarchicus, CV			214.9	25.0 ± 6.7		122.0
Calanus finmarchicus, CIV					82.2	14.1
Calanus finmarchicus, CIII					19.8 ± 9.5	38.6 ± 19.4
Calanus finmarchicus, CII					9.6 ± 1.2	22.8 ± 10.7
Calanus finmarchicus, CI						9.3 ± 0.3
Metridia longa, fem				4.72 ± 0.45		
Metridia longa, CV					80.2	
Metridia longa, CIV					71.4 ± 18	
Oithona similis, CV-CVI			2.1		3.81	3.8 ± 0.8
Oikopleura vanhoeffeni, 0.5–1.0 mm			42.55	31.68 ± 6.06	28.0	45.7 ± 9.3
Oikopleura vanhoeffeni, 1.0–1.5 mm			94.67 ± 36.62			60.3 ± 38.0
Limacina helicina, juv						8.5

Table 3. Values of the mean daily ration in the units of organic carbon (*I*, μg of C/ind. per day) and in percent (%) of the body weight (*W*, μg of C/ind.) of the mass species of herbivorous zooplankton in various sea regions

Type and stage of progress/size	*W*	River		Estuary		Inner shelf		Outer shelf		Slope		St. Anna Trough	
		I	%	*I*	%	*I*	%	*I*	%	*I*	%	*I*	%
Eurytemora lacustris, fem	6	2.6	43										
Eudiaptomus sp., fem	6	2.3	38	4.5	75								
Eudiaptomus sp., male	5	1.7	33										
Cyclops strenuus, fem	7	4.7	67										
Cyclops strenuus, CV	3	2.1	70	0.8	27								
Senecella siberica, fem	87	26.5	30	30.3	35								
Senecella siberica, CV	52			17.6	33								
Limnocalanus macrurus, fem	110			3.7	3	1.0	1						
Limnocalanus macrurus, male	88			3.9	4	2.0	2						
Jaschnovia tolli, CV	55			5.1	9	4.6	8						
Pseudocalanidae, CV	7			2.4	34	1.9	28	0.6	9	1.2	17	1.4	20
Pseudocalanidae, CIII	4									0.5	12	0.6	16
Pseudocalanus major, CV	35							1.0	3				
Calanus glacialis, fem	320							2.3	0.7				
Calanus glacialis, CV	215			4.6	2	10.6	5	3.6	2				
Calanus glacialis, CIV	80					3.1	4	4.7	6				
Calanus glacialis, CIII	22							1.3	6				
Calanus finmarchicus, CV	115					21.3	18	2.5	2			6.5	6
Calanus finmarchicus, CIV	45									4.4	10	0.8	2
Calanus finmarchicus, CIII	12									1.1	9	2.1	17
Calanus finmarchicus, CII	3.5									0.5	15	1.2	35
Calanus finmarchicus, CI	0.7											0.45	64
Metridia longa, fem	193							0.5	0.2				
Metridia longa, CV	75									4.3	6		
Metridia longa, CIV	25									3.8	15		
Oithona similis, CV-CVI	0.5					0.2	40			0.2	40	0.2	40
Oikopleura vanhoeffeni, 0.5–1.0 mm	6					4.2	70	3.1	52	1.5	25	2.4	40
Oikopleura vanhoeffeni, 1.0–1.5 mm	15					9.4	62					3.2	22
Limacina helicina, juv	8											0.5	6

The role of zooplankton in the utilization and vertical transport of the organic matter. Our assessment of the feeding rate for the herbivorous zooplankton, along with the data on its quantitative distribution and the data on the *Chl a* distribution, allow for the estimation of the amount of phytoplankton grazed by the two size groups of zooplankton in the various Kara Sea regions.

The share of chlorophyll (the index of the present phytoplankton biomass) consumed by the zooplankton per day considerably differed in the various pelagic biotopes (Fig. 6). In the river zone and in the estuary, the sum of the grazing was only 1–2% of the total amount of *Chl a* in the water column. Above the shelf, this value rose to 3.5 %; in the region of the slope and trough, it was ~10% and 6%, respectively. At that, the contribution of the small-sized zooplankton in the total daily grazing of the chlorophyll drastically increased from 1% to 74% in the direction from the river zone to the deepwater regions (Fig. 6).

The assessment of the consumption of the primary production by the zooplankton revealed that not in all the defined regions does the newly synthesized organic matter cover the demand of the whole mesozooplankton community for carbon (Fig. 7).

DISCUSSION

High levels of the spatial and temporal variability are characteristics of the Kara Sea's pelagic ecosystem. The annual and regional differences in the zooplankton biomass may reach an order of magnitude [6, 20, 24], thus determining the relevant differences in the productivity and material flows at the base trophic levels of the ecosystem. Two components of the temporal variability, the seasonal and the interannual, are the most important for understanding the regularities of the functioning of the pelagic communities in the Kara Sea.

As in any other high-latitude basin, the seasonal changes in the biological processes are clearly pronounced in the Kara Sea. The maximal primary production over the majority of the basin area relates to the spring blooming of the phytoplankton in the end of May to June continuing for no longer than two weeks [24, 27]. The herbivorous zooplankton partially utilizes the spring peak. During most of the summer and fall, its development is determined by the considerably lower values of the primary production and phytoplankton biomass typical for the second half of the vegetation season. Our data allow for the characterization of the processes of the phytoplankton consump-

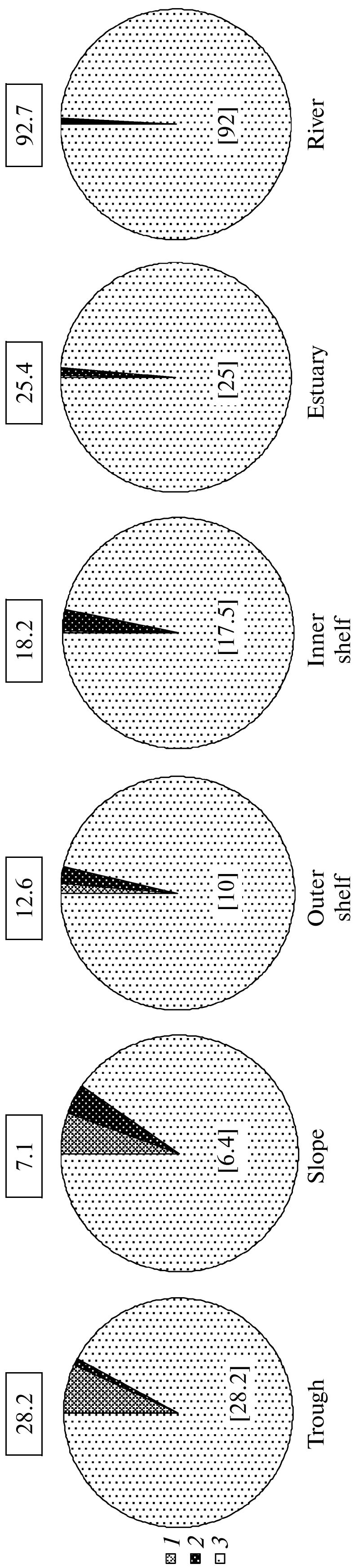

Fig. 6. Share of the daily grazing of *Chl a* by the zooplankton in the layer of 0–50 m (bottom) along the Ob–St. Anna Trough transect. The mean regional *Chl a* (mg/m^2) concentration is given in the boxes. *1*—grazing by small zooplankton; *2*—grazing by large zooplankton; *3*—the underused part of the chlorophyll.

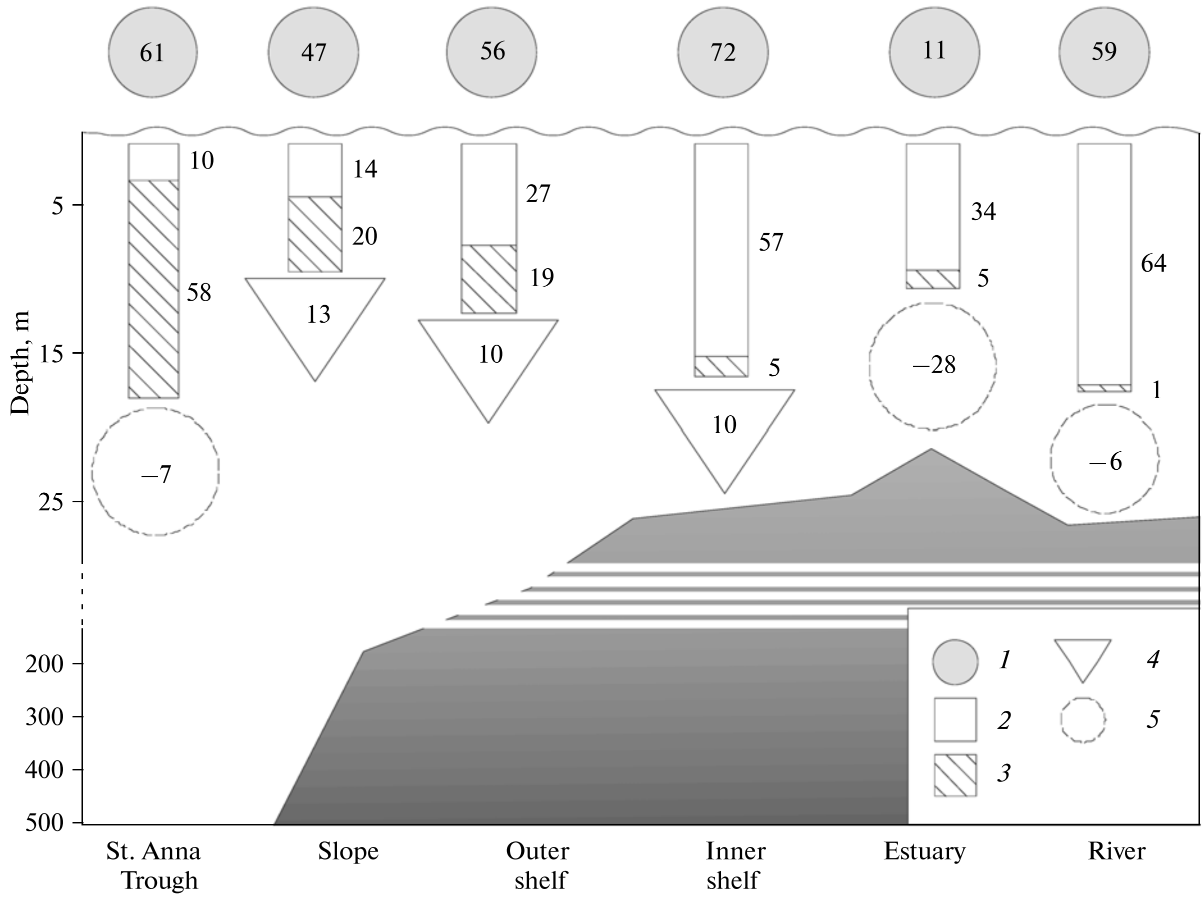

Fig. 7. The sum total consumption of organic carbon and the extent of the use of the primary production by the zooplankton in various regions of the Kara Sea. *1*—values of the primary production (mg of C/m^2 per day); *2*—consumption of carbon by large (>0.5 mm) zooplankton (mg of C/m^2 per day); *3*—consumption of carbon by small (<0.5 mm) zooplankton (mg of C/m^2 per day); *4*—the unused primary production (mg of C/m^2 per day); *5*—the deficit of the primary production concerning meeting the feeding demands of the zooplankton (mg of C/m^2 per day).

tion by the phytovirous plankton (which accounts for up to 90% of the whole plankton community's biomass in the Kara Sea) and of the flows of organic matter in the various biotopes in the autumn.

The total consumption of the plankton algae by the herbivorous zooplankton in the studied regions of the Kara Sea varied from 0.4 to 2.6 mg of *Chl a*/m^2 per day, accounting for 1% to 10% of the present phytoplankton biomass (Fig. 6). The level of the primary production during the studied season in the all biotopes was not sufficient for covering the daily rations of the herbivorous mesoplankton (Fig. 7). In the shelf and continental slope regions, the zooplankton grazed 72% to 86% of the daily phytoplankton production. In the river zone and the deepwater regions, the daily grazing of the zooplankton was 10% higher than the level of the primary production. The maximal excess of the grazing over the daily phytoplankton production was observed in the estuarine zone and reached 28 mg of C/m^2 per day; i.e., in this biotope, the grazing was three times higher than the amount of newly synthesized organic matter. This shows that, in the autumn, a deficiency of the production for the support of the functioning of the herbivorous zooplankton community was characteristic of vast areas of the Kara Sea and not only all the newly synthesized during organic matter but also a part of the present phytoplankton biomass (reaching the maximal values in the whole studied region) was consumed (Fig. 5). The specific features of the structure of the phytoplankton community [15] presume that, both in the river and estuarine zones, the herbivorous zooplankton depended to a high extent on the allochthonous food resources—the phytoplankton entering these zones with the riverine flux. In the deepwater region, the deficit of the primary production for covering the daily nutritional demands of the zooplankton may be a characteristic of the end of the vegetation season. By the end of this season, some herbivorous species move to the deep waters and cease feeding while lapsing into their diapauses, while others turn to the consumption of heterotrophic organisms, as was shown for the Barents Sea plankton community [34].

The relatively important role of the small-sized fraction of the zooplankton (<0.5 mm) in the consumption of the plankton algae on the outer shelf, above the continental slope, and in the northern deepwater regions of the basin was another characteristic feature of the trophic relations in the Kara Sea's plankton communities during the fall succession. These values reached 41%, 58% and 85% of the total grazing by the zooplankton, respectively, while accounting for 32–96% of the primary production. This was determined by the large number of small crustaceans, their aggregation in the upper mixed layer, and the higher specific rate of the food consumption. In addition, the seasonal state of the populations of the mass large-sized herbivorous species of zooplankton during the studied period was characterized by the domination of the elder developmental stages, the descending of crustaceans from the euphotic zone, and turning to the resting wintering state. With the increasing distance from the river to the St. Anna Trough, the share of small (<10 μm) algae [15] serving as more available food for the small-sized zooplankters increased. The important role of the small-sized zooplankton in the consumption of the plankton algae is a characteristic feature of the autumn period of the seasonal succession of the Arctic seas' communities [19, 28, 29, 34].

We obtained data on the grazing of the herbivorous zooplankton on the phytoplankton in the Kara Sea for the first time. This is why it is impossible to present even very general assessments of the interannual and climatic variability of this parameter of the pelagic ecosystem. It is worth noting that the values presented here characterize the regional specificity of the transformation of the newly synthesized organic matter in the anomalously warm year at the minimal (for last 30 years) area of the ice cover in the Arctic basin [16].

Our assessment shows that, in the biotopes rich in phytoplankton, the river zone and estuary, the herbivorous zooplankton, despite its high concentrations, consumes during the autumn 0.8–1.6% of the present algal biomass. The main part of the organic matter in these regions precipitates on the bottom in the nontransformed form and may provide favorable feeding conditions for the bottom communities. In some cases, such precipitation forms anaerobic conditions in the bottom sediments. With the increasing distance from the estuary to the sea, the phytoplankton biomass decreases with a concomitant increase in the values of its consumption by the herbivorous community. These results are in accord with the data obtained by the analysis of sedimentation traps [7, 11, 21, 22, 31]. According to this analysis, the strong accumulation of sediments occurs in the estuarine regions, while the vertical flow of the organic matter decreases in the direction to the outer shelf and the deepwater parts of the basin. The considerable contribution of the small zooplankton to the consumption of the plankton algae in the regions situated seawards of the outer shelf also facilitated a decrease in the vertical transfer of the organic matter related to the pellet transport in these regions. This was determined by the relatively small size of the fecal pellets of the small-sized crustaceans and by their decomposition in the upper water layers due to the low rate of the sedimentation and retention on the seasonal pycnocline.

The latitudinal zonality of the Kara Sea's ecosystem is clearly manifested in the physical and chemical properties of the pelagic environment [9, 13], the productivity and structure of the phytocenosis [4, 14, 15, 20], and the structure of the zooplankton community [6, 17]. Our study revealed that this zonality also determines, to a high extent, the quantitative aspects of the consumption of the newly synthesized organic matter by the community of herbivorous zooplankton and the vertical flows of organic matter in the various biotopes.

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