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MARINE BIOLOGY

Mesozooplankton Grazing Impact on Phytoplankton in the Northern Regions of the Kara Sea in Autumn

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Abstract—The role of mass zooplankton species, copepods *Pseudocalanus* spp. and *Oithona* spp. and pteropods Limacina helicina, in grazing impact on phytoplankon in the upper 50 m layer was investigated. Material was collected at 14 stations along two sections crossing the outer shelf, continental slope and adjacent deepwater regions in the western and eastern branches of St. Anna trough (Kara Sea) in September 2011. Feeding rate was measured with fluorescence method. It was shown that total grazing impact on phytoplankton varied in a wide range from 0.2 to 8.7% of biomass and from 2 to 230% of daily primary production. The main contribution to phytoplankton grazing was made by small copepods Oithona spp. and juvenile pteropods. Maximum values of grazing were found in the frontal zones over the slope, minimum – over the outer continental shelf. Significant mesoscale spatial heterogeneity in total zooplankton grazing due to the changes in zooplankton composition and abundance was observed.

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INTRODUCTION

The Kara Sea ecosystem has been extensively studied in the past two decades [4, 5, 8, 28, 33, 38]. This is mainly due to its great role in the transformation of the river runoff to the Arctic and in the process of interaction between the shelf and deepwater areas of the Arctic Basin. In addition, such research is needed to understand how the climate processes affect high-latitude ecosystems of epicontinental seas. The prospect of the development of huge hydrocarbon reserves on the shelf of the Kara Sea also requires new data on the environment and biota, which are necessary for the development of regional policy on environmentally sound nature management. These studies have provided a quite detailed understanding of the structural organization of the Kara Sea ecosystems in the western and central parts of the basin, but many highly important aspects of its functioning remained poorly understood until recently. These include processes of the primary transformation of organic matter in the pelagic food chain. Despite the obvious importance of quantifying these processes, study on them in the Kara Sea is limited to a single work [1].

Herbivorous zooplankton is a key component of trophic chains in ecosystems of the Arctic seas, which regulate the transformation of biological production and organic matter flows. In high-latitude planktonic communities, biomass in the upper layer of the sea during the most productive season consists of large interzonal copepods of genus *Calanus*, *C. hyperboreus*, *C. glacialis*, and *C. finmarchicus* [3, 10, 20]. Mass development of the populations of these species is confined to spring phytoplankton bloom accompanied by the active growth, reproduction, and accumulation of reserve substances [24, 36, 37]. At the end of the productive season, these species descend to the deeper layers of the water column and remain in a state of diapause for most of the year [26, 27] and do not participate in the processes of organic matter transformation in the epipelagic zone. The zooplankton community of Arctic marine ecosystems at this time basically consists of species that have no resting phase in their life cycle and inhabit the surface layers throughout the year [15, 29, 31]. In the north of the Kara Sea in the deepwater areas of the St. Anna Trough these are juvenile pteropods *Limacina helicina* of 0.3–0.7 mm and small copepods *Pseudocalanus* spp. and *Oithona* spp. The total contribution of these species to the wet biomass of zooplankton in the upper production 50-m layer in September and October generally exceeds 70%, often reaching as high as 90% [9]. According to the data obtained in September 2007, the small-sized (<0.5 mm) part of zooplankton in the northern regions of the Kara Sea plays a leading role in the utilization of newly formed organic matter by consuming 45–96% of the daily primary production by the end of the growing season [1].

The aim of this work is a detailed estimation of the spatial variability of the consumption of autotrophic phytoplankton by populations of dominant zooplankton species in the north of the Kara basin in the border area between the pelagic ecosystems of the shelf and deepwater Arctic regions.

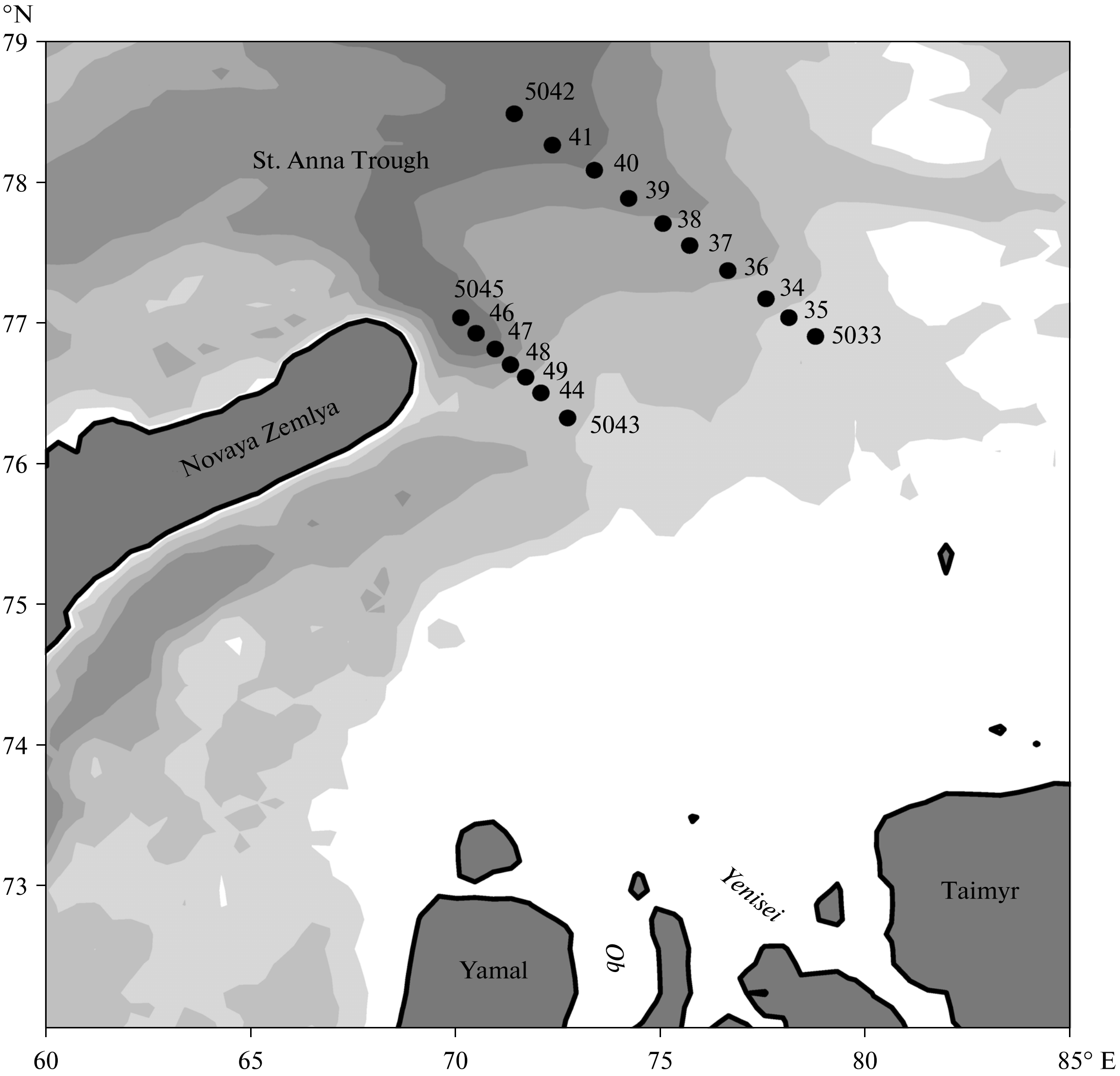

Fig. 1. Locations of studied stations.

MATERIALS AND METHODS

The work was carried out as part of multidisciplinary study of the ecosystem of the Kara Sea in September 2011 during an expedition of the RV *Akademik Mstislav Keldysh*. The material was obtained at 14 stations of two sections crossing the Kara Sea shelf at depths of 135–150 m, the area of the continental slope, and the adjacent deepwater areas in the western and eastern branches of the St. Anna Trough, with depths up to 500 m (Fig. 1).

We considered dominant mesozooplankton species dominating the community of the upper 50-m layer of the water column—copepods *Pseudocalanus* spp. and *Oithona* spp. and juvenile pteropods *Limacina helicina*. They represented a small-sized fraction of zooplankton community, with a body size of 0.3–1.7 mm, and in aggregate formed more than 70% of total mesozooplankton biomass [9].

In order to determine the species composition and abundance, zooplankton was collected using Multinet nets. The method of collecting and processing the plankton samples is described in detail in [9].

The feeding rate of zooplankton was estimated by fluorescence of phytopigments (*Chl-a* and phaeopigments) in the gut and the digestion time [32]. Analyzed zooplankton was collected using a Juday net (0.1 m^2 mouth area, 180 μm filter cone mesh) from the upper 50-m layer. Immediately after sampling, the animals were anesthetized with filtered seawater saturated with carbon dioxide to prevent release of food from the guts. Under a binocular microscope, the immobilized animals were sorted by species and stage and placed in 90% acetone for extraction of phytopigments. Each assay included 30–40 animals. Extraction was carried out at a temperature of 7°C for 24 h. The amount of phytopigments was determined as described in [39]:

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

$$\text{Phaeopigment} = k(RFa - Fb)/(V_{\text{extr}}/n),$$

where k is the calibration coefficient of the device; Fb and Fa are fluorescence of the test solution before and after acidification, respectively; R is the acidification coefficient; V_{extr} is the acetone extract volume, mL; and n is the number of animals in the extract.

The total pigment content in the gut (G, ng *Chl-a*/ind.) was calculated by the formula [12]:

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

The digestion time for copepods was taken from study [35]: 1.67 h for *Oithona* spp., 0.67 h for *Pseudocalanus* spp., and 1.5 h for *Metridia longa*. The digestion time (T, h) for *Limacina helicina* was determined in experimental conditions by two methods. In the first method, we measured the rate of decrease of pigments in the digestive tract (r, h^{-1}) by incubating freshly caught pteropods (600 specimens) in a 100-mL vessel filled with sea water filtered through a glass fiber filter GF/F. After a certain time (1.5–2 h at the beginning of the experiment and 4–8 h at the end of the experiment) some of the animals were collected from the experimental vessel to measure the amount of pigments in their guts. The digestion time was calculated as $T = 1/r$. We used the second method in order to exclude the effect of the lack of food on the digestion time: 250 *Limacina helicina* specimens were incubated for one day in 1-L vessels with unfiltered sea water taken from the horizon of maximum fluorescence. The experiment was carried out in four replicates with four controls (vessels without animals). The daily consumption of pigments (I, ng *Chl-a*/ind./days) was determined by the difference in the initial and final concentrations of *Chla-a*. At the end of the experiment we also measured the pigment content in the animals (G, ng *Chl-a*/ind.). The digestion time was calculated as $T = G24/I$.

The daily ingestion of *Chl-a* (I, ng *Chl-a*/ind. per day) was calculated as:

$$I = Gt/T$$

where t is the feeding time equal to 24 h for *Oithona* spp. and *Pseudocalanus* spp. and juvenile pteropods, all of which permanently inhabit the surface layer, and to 8 h for *M. longa*, which rise to the 0–50-m layer in the dark.

The total consumption of the autotrophic phytoplankton biomass by all the studied mesoplankton species in the 0–50-m layer ($E_{Chl\text{-}a}$, mg *Chl-a*/m^2/day) was calculated using the formula:

$$E_{Chl\text{-}a} = \sum_{i \to 1}^{n} I_i N_i,$$

where I_i is the daily consumption of *Chl-a* for the ith species/group of species, N_i is the number of ith species/group of species in the layer (ind./m^2), n is the number of species/group of species. To convert daily food intake into carbon units (E_c, mg C/m^2/day), we used data on the content of organic carbon in autotrophic algae species (C_{phyt}), obtained by processing the phytoplankton samples from the upper 50-m (materials of I.N. Sukhanova and V.M. Sergeeva). The data on the primary production and *Chl-a* concentration are given in [6].

RESULTS

The data on *Chl-a* concentration, the primary production, the C_{phyt}/*Chl-a* ratio, and the abundance of the dominant zooplankton species at each station in the 0–50-m layer used in our calculations are presented in Table 1 and Fig. 2.

Zooplankton feeding activity. Figure 3 shows data on the gut pigment content of the three studied zooplankton species caught at stations in the eastern and western branches of the St. Anna Trough at different times of the day. The results showed no daily rhythms of feeding activity in any of the studied species (ANOVA, $p > 0.05$). Similarly, the influence of the *Chl-a* concentration on the feeding activity was analyzed (Fig. 4). Given the relatively small range of changes in the phytoplankton concentrations from 0.21 to 0.53 μg *Chl-a*/L, the amount of pigments in the gut of animals did not differ significantly (ANOVA, $p > 0.05$).

For large copepods *Metridia longa*, which rise to the surface layers only at night, the gut pigment content was measured only once, at station 5037. The G values in females and older copepod stages (CV and CIV) in this species were equal to 18.01 ± 1.56, 15.82 ± 2.04, and 9.10 ± 0.56 ng *Chl-a*/ind., respectively.

Digestion time in *Limacina helicina*. The results of experiments to determine the rate of gut pigment content decrease in *Limacina helicina* kept in filtered water are shown in Fig. 5. The resulting relationship is described by the exponential equation $G_t = 0.36e^{-0.052t}$ ($n = 17$, $r^2 = 0.75$), and T is 19.2 hours. Digestion time, calculated based on the results of experiments in which pteropods were incubated in unfiltered seawater, was about 19 h.

Zooplankton grazing Impact on phytoplankton biomass and production. The total consumption of phytoplankton by the dominant zooplankton species on the transect through the western branch of the St. Anna Trough varied in a wide range from 0.01 mg *Chl-a*/m^2/day on the shelf (station 5043) to 1.41 mg *Chl-a*/m^2/day at station 5045, the deepest and farthest from the continental slope station (Fig. 6a). High values of the phytoplankton biomass consumption by all the studied mesozooplankton species in the 0–50-m layer exceeding 1 mg pigments/m^2 per day were obtained at stations 5048 and 5049, located in the area of the continental slope. The proportion of phytoplankton biomass consumed daily by dominant mesozooplankton species was highest at station 5048

Table 1. Amount of *Chl-a** (*Chl-a*, mg/m^2 in the 0–50-m layer), primary production* (PP, mg C/m^2 per day), and the ratio of organic carbon of autotrophic phytoplankton** and *Chl-a* (C_{phyt}/*Chl-a*, mg C/mg *Chl-a*) on transects through the western and eastern branches of the St. Anna Trough in September 2011

Area	Station no.	Date	Time	*Chl-a*	PP	C_{phyt}/ *Chl-a*
			Western branch			
Trough	5045	29/09	3:30	21.9	11	13.0
	5046	29/09	9:00	23.0	21	7.5
Slope	5047	29/09	13:45	11.8	16	15.5
	5048	29/09	16:30	12.5	8	17.0
	5049	29/09	18:20	15.6	8	9.0
Outer shelf	5044	28/09	16:20	19.8	18	35.5
	5043	28/09	9:00	26.5	16	12.6
			Eastern branch			
Trough	5042	26/09	16:40	17.2	10	15.0
	5041	26/09	13:45	11.5	12	25.0
Slope	5039	26/09	5:40	9.6	15	39.0
	5037	25/09	21:40	10.2	21	35.0
	5035	25/09	15:40	22.1	39	26.0
Outer shelf	5034	25/09	10:20	12.8	56	24.5
	5033	25/09	5:50	10.3	48	22.5

* Data from [6].

** Data from [7].

(8.7%) and lowest at the shelf station 5043 (0.05%), which is the farthest from the continental slope (Fig. 6a). Calculations of zooplankton grazing impact on primary production show that the populations of the studied tdominant species *Pseudocalanus* spp., *Oithona* spp., and *Limacina helicina* consumed daily 20–100% 120–230%, 77% of phytoplankton production in the deepwater area, in the slope area and on the outer shelf, respectively (Fig. 6b). A minimum value of 2% was also obtained at shelf station 5043. The contribution of each of these species to the total consumption significantly differed at different stations (Fig. 6c). At the shelf station 5043, copepods of genus *Pseudocalanus* were the main consumers of phytoplankton; their contribution was 70% of the total grazing. At station 5044, a leading role (60%) was played by the juvenile stages (0.3–0.7 mm) of pteropods. The contribution of the copepod of genus *Oithona* increased in the deepwater area, reaching 50–80% of the total phytoplankton consumption.

On the transect through the eastern branch of the St. Anna Trough, the total consumption of phytoplankton by the dominant zooplankton species was significantly lower as compared to the western branch, accounting for 0.15–0.36 mg *Chl-a*/m^2/day (Fig. 7a). The highest value of the grazing impact on the algal biomass (3.6%) was recorded at station 5039; at the other stations this value varied within a narrow range from 1.3 to 2.1%. Expressed in terms of organic carbon, the total amount of phytoplankton consumed by the studied zooplankton species daily was the highest (about 14 mg C/m_2/day) at stations 5039 and 5035. At the other stations of the transect, the E_c value ranged from 3 to 6 mg C/m^2/day (Fig. 7b). Daily consumption of primary production did not exceed 90%. Minimum values (7–9%) were obtained at stations 5033 (the outer shelf) and 5034 (the slope). At station 5035, located between these stations, at a distance of only 10 km from each, zooplankton grazing impact increased by a factor of four up to 34% of primary production. At most of the stations located in the eastern branch of the St. Anna Trough, a pivotal role in grazing of phytoplankton belonged to copepods *Oithona* spp., whose contribution amounted to more than half of the total consumption of primary production (Fig. 7c). Only at stations 5042 and 5041 in the deepwater area of the trough a significant portion (42–45%) of algal production was consumed by the population of *Limacina helicina*.

The grazing impact of the older stages of *Metridia longa* on phytoplankton for the period of their night stay in the 0–50-m layer at station 5037 was equal to 0.21 mg *Chl-a*/m^2 and 7.52 mg C/m^2, which amounted to 2.1 and 36% of the biomass and production of autotrophic algal species, respectively.

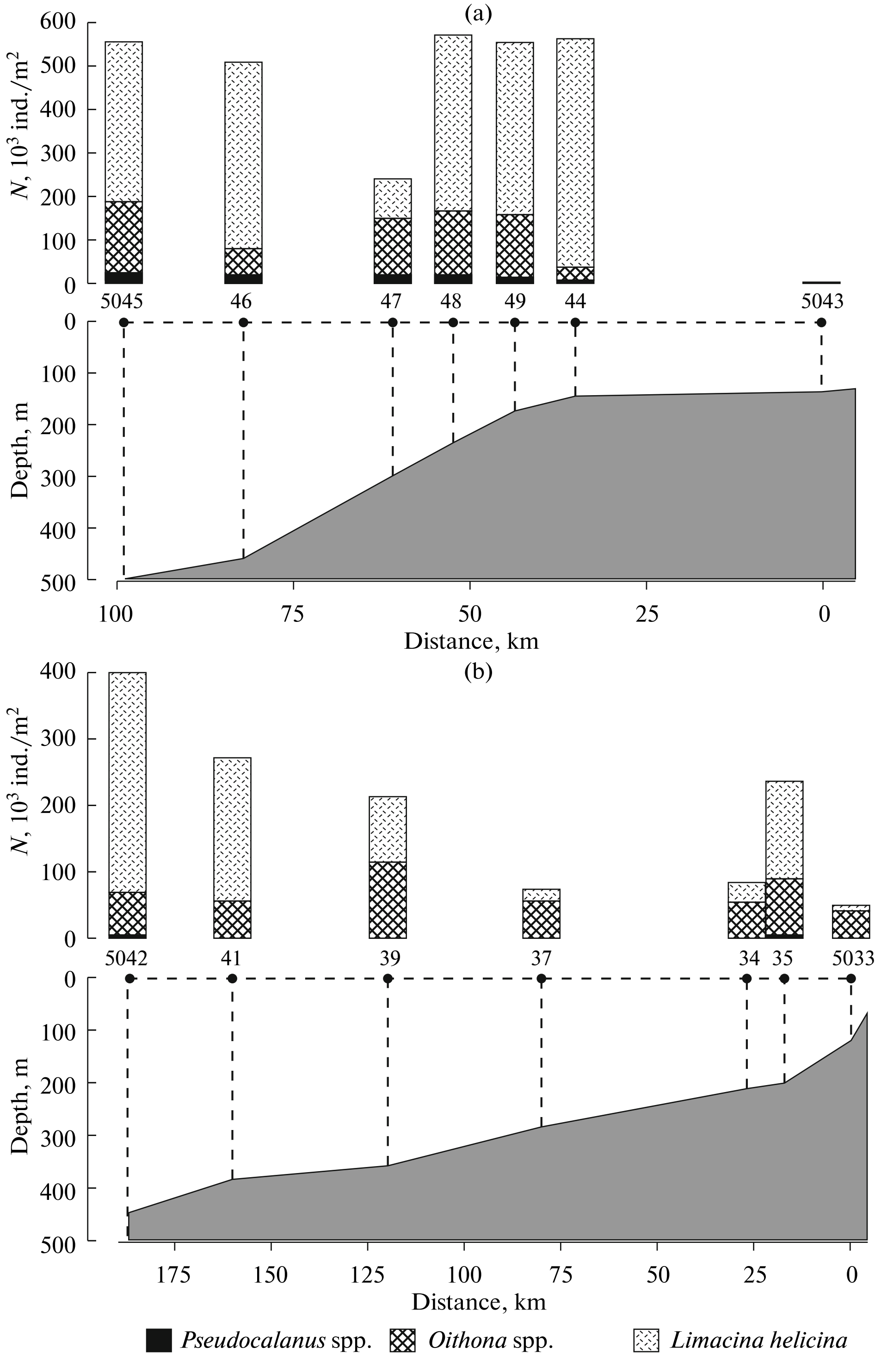

Fig. 2. Abundance of different zooplankton species at stations of the western (a) and eastern (b) transects in the upper 50-m layer.

DISCUSSION

Our research in the Kara Sea was carried out at the end of the productive season, with a relatively low abundance of phytoplankton [7], and a low level of primary production [6]. In the area of the St. Anna Trough, at low values of *Chl-a* and the small range of its spatial variaton, the ingestion rate of the studied species on phytoplankton was almost independent on *Chl-a* concentration (Fig. 4). It indicates, that in autumn, autotrophic phytoplankton is not a major source of food for these species; they could feed on the other resources, such as heterotrophic algae and

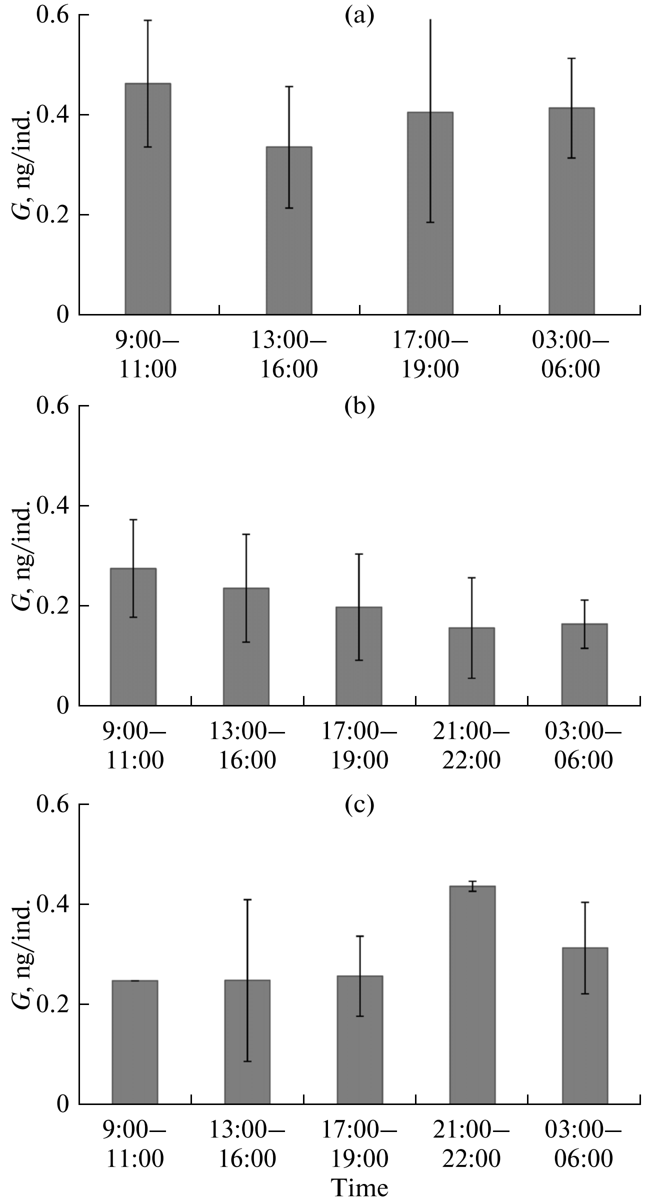

Fig. 3. Daily variability in gut pigment content ts (G, ng/ind.) of (a) *Oithona* spp., (b) *Limacina helicina*, and (c) *Pseudocalanus* spp.

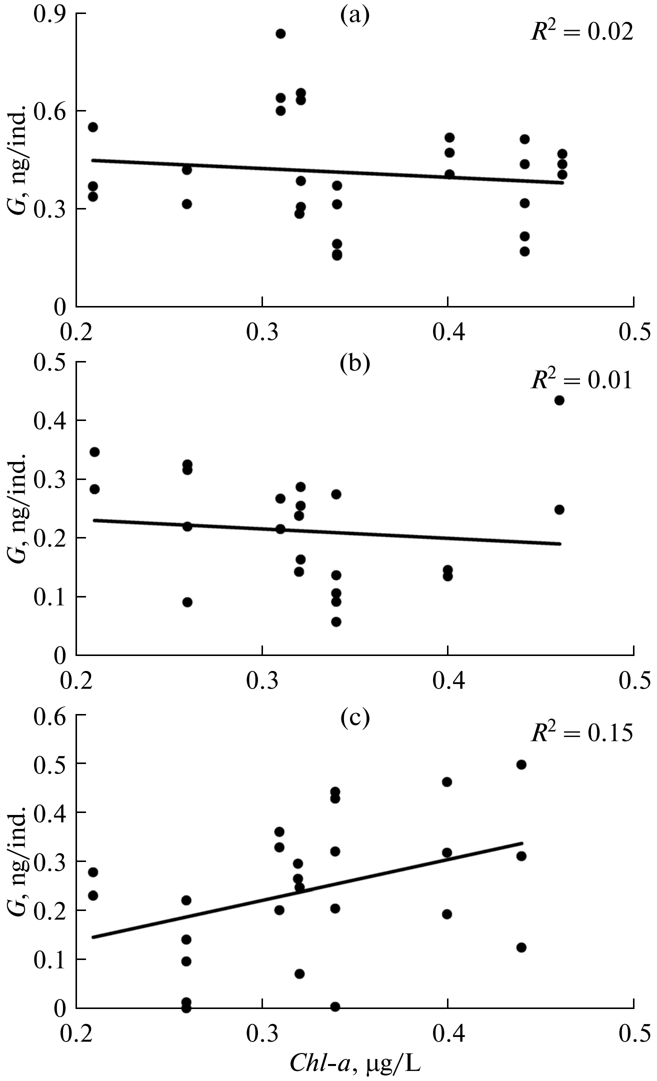

Fig. 4. Gut pigments content at different *Chl-a* concentrations. (a), *Oithona* spp., (b) *Limacina helicina*, and (c) *Pseudocalanus* spp.

flagellates, microzooplankton and detritus with aggregated bacteria. A switch from a predominantly herbivorous feeding to an omnivorous one at the end of the productive season is shown for different zooplankton species in high latitudes, including copepods of genera *Pseudocalanus* and *Oithona* [14, 17, 34, 41] and juvenile stages of *Limacina* [22].

According to our results, no zooplankton species revealed a statistically significant diurnal change in feeding activity. The lack of daily feeding rhythm in *Limacina helicina* juveniles seems quite natural because of a prolongedl digestion time, which, according to our experiments, was only a little less than 24 h. A long digestion time in *L. helicina* (>10 h) was also observed by other authors [18, 23]. Well-defined daily rhythms of feeding with increasing activity at night are described for many species of small copepods, including the genus *Pseudocalanus* [19, 25]. However, according to [16], at low concentrations of phytoplankton the smoothing or almost complete disappearance of the night maximum are observed. It can be assumed that the lack of pronounced daily variation of feeding activity in *Pseudocalanus* and *Oithona* are also associated with the low abundance of phytoplankton.

Being dominant in terms of the abundance and biomass in the upper productive layer, the studied species are responsible for utilization of the most part of the newly synthesized organic matter. According to our estimates, their total grazing impact on the biomass and production of phytoplankton in the western branch of the trough was on average 2.5–5 times higher than in the eastern one. These differences are mainly determined by the high abundance of the dominant species in the western branch (the average for the section 5×10^5 ind./m^2) as compared to the eastern one (the average for the section 2×10^5 ind./m^2).

Each of the studied areas revealed a significant spatial variability in the grazing on phytoplankton, and the pattern of such variability had some common features. In particular, both areas showed an increase in the absolute value of the total consumption of the phytoplankton biomass at stations 5035 (eastern branch) and 5048 (western branch) located over the continental slope. The proportion of primary production consumed by dominant species of zooplankton reached 90% at station 5035 and 230% at station 5048; the latter is a maximum value for the entire investigated area of the Kara Sea. According to [2, 9], these stations are located at the fronts, which is associated with the slope currents and separates the shelf water and deepwater masses of the Kara Sea. Significant spatial variations in the grazing impact in these areas occurred at a distance of 10–15 km.

In the deepsea areas, spatial variation in the grazing impact of are not always directly determined by the total abundance of the dominant species of zooplankton s. For example, station 5039 high grazing (80% of primary production) at low zooplankton abundance was found, while, despite the high abundance of zooplankton at stations 5042 and 5046, the grazing impact on phytoplankton production was 20–40%. The feeding activity of the studied zooplankton species, as we have shown above, was not dependent on the phytoplankton concentration or the time of day, and the marked spatial variations in the grazing impact are likely to be determined by the relative abundance of different species and their contribution to the total consumption. The main contribution to the total consumption belonged to copepods *Oithona* spp. and juvenile pteropods. Correlation analysis showed that the total grazing impact is largely determined by the abundance of *Oithona* spp. ($r^2 = 0.8$) rather than the abundance of pteropods ($r^2 = 0.35$). The significant role of *Oithona* spp. in the biotransformation of organic matter in marine ecosystems in various regions of the World Ocean and, in particular, the Arctic seas, especially in the later stages of the seasonal succession, has been indicated by a number of researchers [15, 21, 30, 40]. There are no data on the role of pteropods of genus *Limacina* in the grazing impact on phytoplankton, except for the single work of [13], which found that the population of the Antarctic species *Limacina retroversa* consumed from 8.4 to 140% (!) of phytoplankton biomass daily. Our results, which for the first time have made it possible to estimate the phytoplankton ingestion by *L. helicina* in the Kara Sea, indicate that in aggregations (station 5044) the juveniles of this species consume more than 40% of the primary production. It should be noted that in our calculations we used the abundance of pteropods which was defined on the basis of processing the plankton samples collected using nets with a mesh size of 180 μm, which led to the underestimation of specimens smaller than 200 μm. At some of the stations we collected zooplankton using an Apstein net with a filter cone mesh size of 60 μm, which allowed rough calculation of the consumption of phytoplankton by part of the *L. helicina* population of size 80–200 μm. We carried out calculations based on the assumption that the specific daily food intake (ng C/mg wet weight) for this size group of juvenile pteropods is the same as that of larger ones, while being aware of the fact that in this case we obtain some underestimations. Small-sized pteropods can consume daily up to 30% of primary production (Table 2). These results once again demonstrate the need to take into account the contribution of small-sized fraction of zooplankton when studying biotransformation processes in marine planktonic ecosystems.

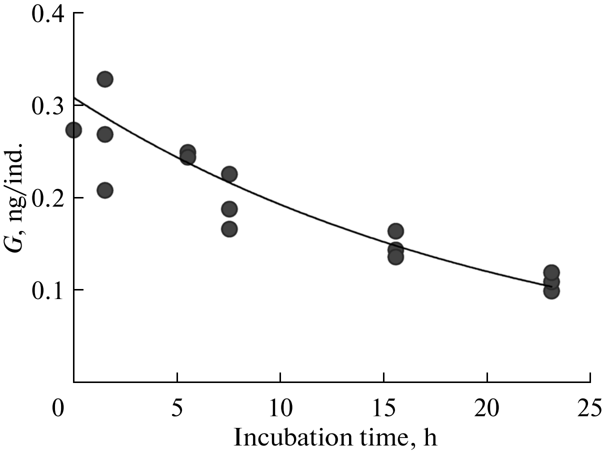

Fig. 5. Changes in gut pigment content (*G*, ng/ind.) of *Limacina helicina* incubated in filtered water.

We have considered the role of the dominant zooplankton species in the grazing impact on phytoplankton; these species permanently inhabit the surface layers and not perform daily vertical migrations of large amplitudes. However, one of the dominant species of mesozooplankton of high latitudes is the copepod *Metridia longa*, older age stages of which perform diur-

Table 2. Abundance (N, 10^3 ind./m^2), daily phytoplankton intake (I_c, ng C/ind. per day), and grazing impact on primary production (E_c, mg C/m^2 per day) of *Limacina helicina* of <0.2 mm size

Station no.	N	I_c	E_c	E_c, %
5042	1200	0.41	0.48	4.5
5039	2800	1.62	4.54	30.3
5034	995	1.37	1.37	2.4

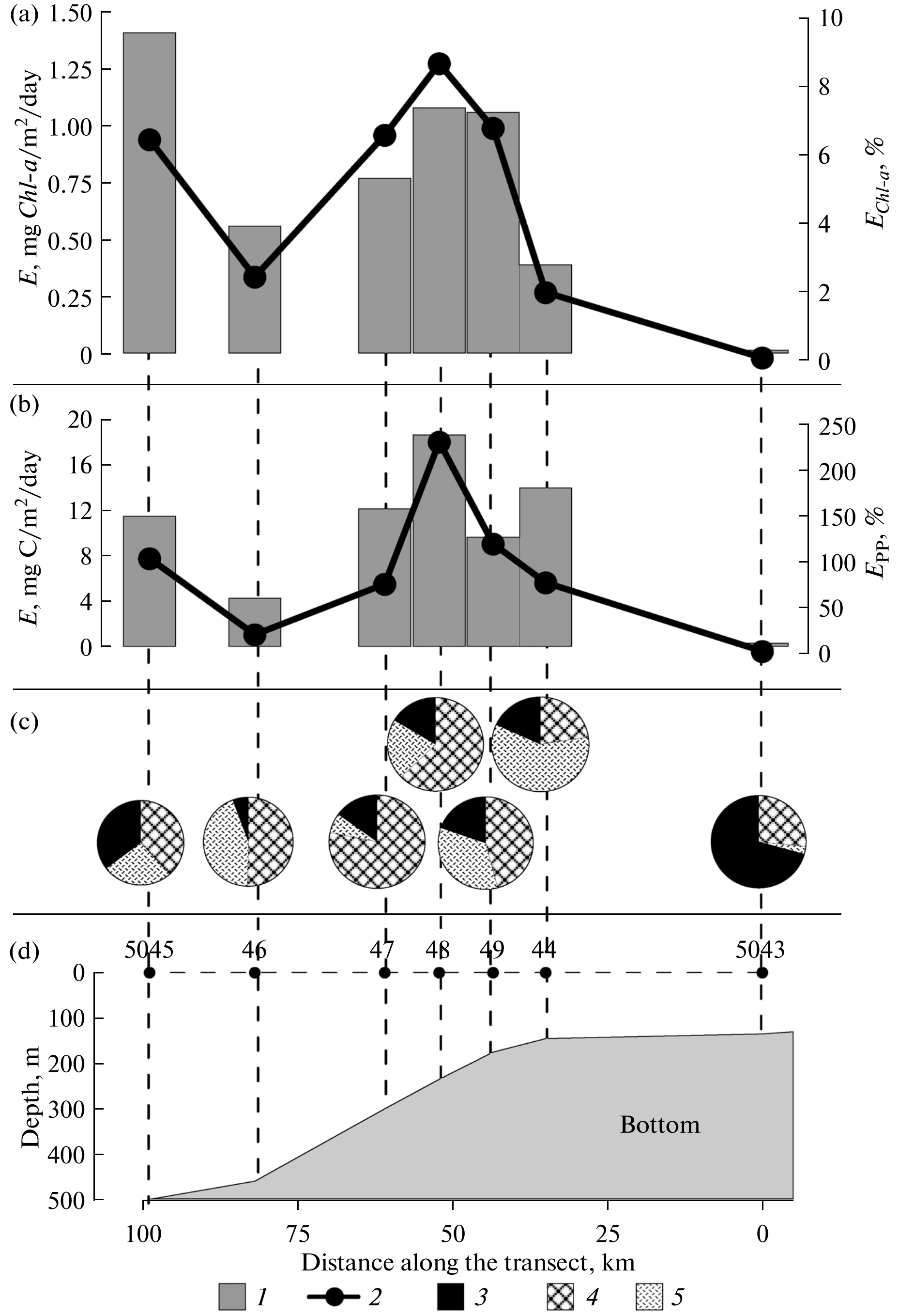

Fig. 6. Zooplankton grazing Impact on phytoplankton on the transect through the western branch of the St. Anna Trough. (a), grazing impact on phytoplankton biomass (mg *Chl-a*/m^2/day), (b) grazing impact on primary production (mg C/m^2/day), (c) contribution of various zooplankters in total grazing impact on primary production (%), (d) bottom topography and locations of stations. *1*, absolute values; *2*, relative values; *3*, *Pseudocalanus* spp.; *4*, *Oithona* spp.; *5*, *Limacina helicina*.

nal migrations of several hudreds meters [20]. *Metridia longa*, unlike other large herbivorous copepods, is active throughout the year. Ascending in the dark to the surface layers, they actively feed [3]. Data obtained during the night at station 5037 showed that the population of *M. longa* in the autumn season consumed about 35% of primary production, which amounted to 60% of the total zooplankton grazing impact on phytoplankton production. It is obvious that without taking into account the contribution of the *M. longa* population, the calculations of the phytoplankton comsumption by the zooplankton community in areas of high

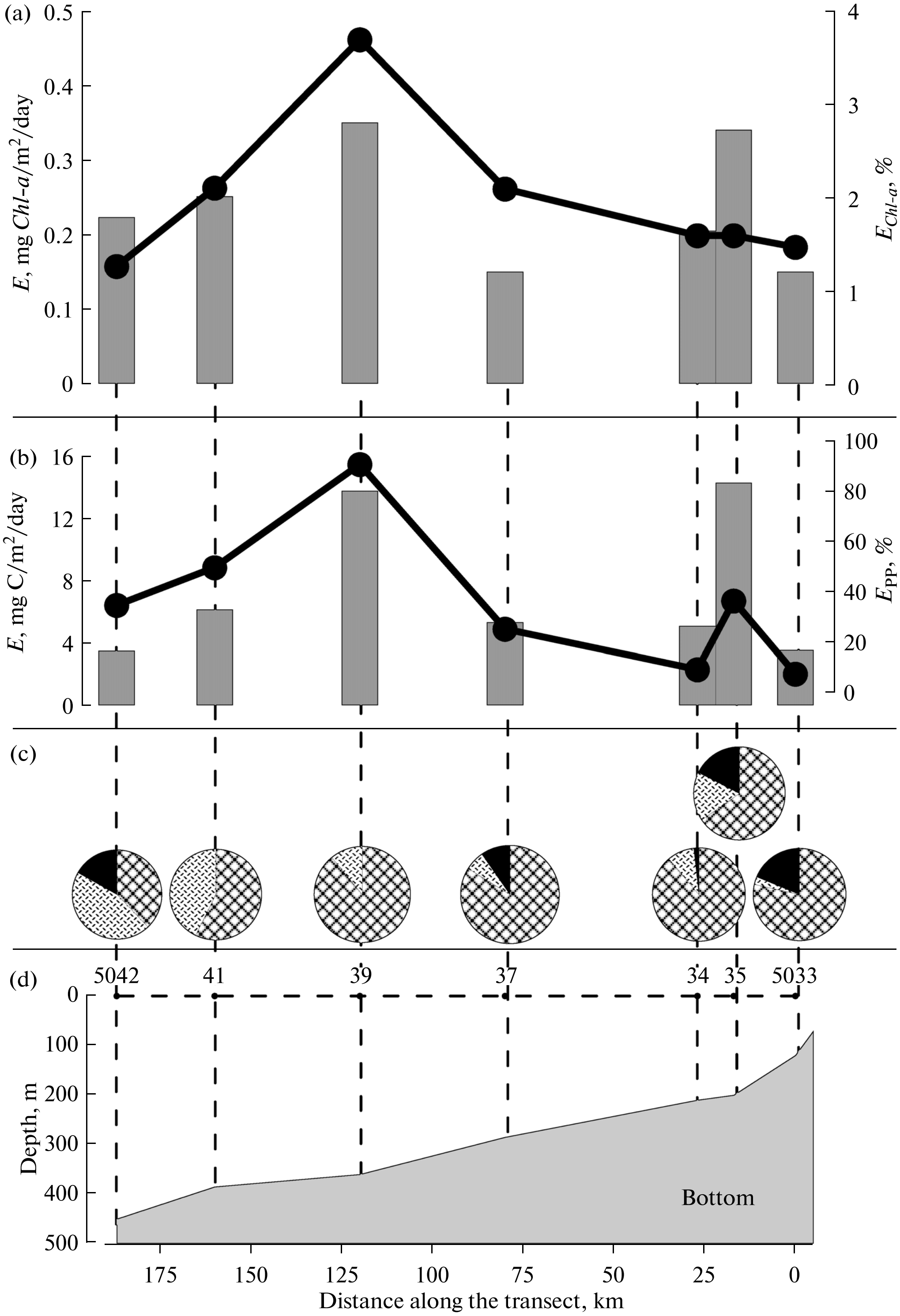

Fig. 7. Zooplankton grazing impact on phytoplankton on the transect across the eastern branch of the St. Anna Trough. (a), grazing impact on phytoplankton biomass (mg Chl-a/m^2/day), (b) grazing impact on primary production (mg C/m^2/day), (c) contribution of various zooplankters in total grazing impact on primary production (%), (d) bottom topography and locations of stations. For symbols, see Fig. 6.

abundance of this species may be significantly underestimated, especially in the absence of other large herbivorous copepods in the upper production layer.

Our estimates of the grazing impact of the dominant zooplankton species on the phytoplankton biomass are comparable with the values given in the paper [1], which is devoted to studying the role of zooplankton in the transformation of organic matter in the Kara Sea. According to these authors, in September 2007, the total grazing impact of the entire zooplankton community on the phytoplankton biomass was 2.6%, 10%, and 5%on the shelf, the continental slope, and the deepwater part of the western branch of the St. Anna Trough, respectively. The estimates for the consumption of primary production were 86, 72, and 114%.

The main conclusions that can be drawn from our research are as follows:

1. In the fall season on the outer shelf, over the continental slope, and in the adjacent deepwater areas of the Kara Sea, small-sized (0.3–1.7 mm) species of zooplankton, which form the basis of the community of the upper 50-m layer, consume daily from 2 to 230% of the newly synthesized organic matter. At the fronts over the continental slope substantial activation of the process of the biotransformation of organic matter was found.

2. In final stages of the productive season, an important role in the phytoplankton utilization belongs to pteropods *Limacina helicina*, the proportion of which in the total grazing impact reaches 60%. Interzonal copepods *Metridia longa* may significantly contribute to phytoplankton utilization (up to 60%) in the area of the continental slope and in the deepwater area of the basin.

3. Zooplankton grazing impact on autotrophic phytoplankton demonstrates significant mesoscale spatial variability. This is due to changes in both the abundance and composition of the zooplankton community.

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