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MARINE BIOLOGY

Feeding of Dominant Zooplankton Species and Their Grazing Impact on Autotrophic Phytoplankton in the Yenisei Estuary in Autumn

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Abstract—Feeding of dominant mesozooplankton species was investigated in freshwater zone, estuarine frontal zone of Yenisei Estuary and adjacent inner shelf area during autumn season. Ingestion rate was estimated based on gut fluorescence measurements. It was shown that in spite on the end of productive season daily ingestion of phytoplankton for the most of the investigated freshwater, brackish and marine zooplankton species was higher than their metabolic requirements. Total phytoplankton consumption by zooplankton differed in different zones. In freshwater zone under high level of autotrophic phytoplankton biomass and primary production zooplankton grazing impact was low: 1.5% of standing stock and 20% of primary production. In the estuarine frontal zone 3.2–14.3% of standing stock and 150–290% of primary production was grazed by zooplankton per day, in adjacent inner shelf: 1.4 –7.0% and 130%, accordingly. Based on comparatively analysis of obtained data and results of investigation of zooplankton feeding in Ob Estuary during the same season some general patterns of the zooplankton role in organic matter biotransformation in the large arctic rivers estuarine areas were revealed.

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INTRODUCTION

The ecosystem of the Yenisei River estuary has been intensively studied over the past two decades and, due to a series of complex scientific expeditions, could be considered as a well-studied Arctic estuarine area [2, 3, 7, 13, 16]. Particular attention has been paid to the study of the zooplankton community, which in estuarine areas plays a key role in the biotransformation of allochthonous material brought by river runoff. The structure of the zooplankton community, seasonal dynamics of its composition and abundance, and distribution pattern of dominant species have been described [2, 8, 9]. The existence of specific complexes of species inhabiting different areas of the estuarine area of the Yenisei River has been shown [2, 9]. A recent study analyzed in detail the connection of species composition and the quantitative distribution of zooplankton in general and dominant species with mesoscale variations in the hydrophysical structure and circulation features of the water mass. It was found that the maximum abundance and biomass of zooplankton are associated with fronts, the latitudinal extent of which is less than 10 km [7]. Despite the fact that structure and patterns of quantitative distribution of zooplankton in the Yenisei River estuary area have been sufficiently studied, there are practically no data about its role in the process of biotransformation of organic matter.

This paper makes the first attempt to quantify the amount of autotrophic phytoplankton consumed by mesozooplankton in the Yenisei River estuary areas that differed by degree of the influence of river runoff.

MATERIAL AND METHODS

The work was carried out as part of multidisciplinary research of the ecosystem of the Kara Sea in September 2011 on board the R/V *Akademik Mstislav Keldysh*. The material was obtained at 11 stations in the Yenisei River estuary and adjacent shelf area (Fig. 1). The feeding rate of zooplankton was evaluated by the fluorescent method in terms of the gut pigment content (*Chl-a* and phaeopigments) and digestion time [22]. For analysis, zooplankton was collected using a Juday net (0.1 m^2 mouth area, 180 μm filter cone mesh) towed vertically from the bottom to the surface. The animals were immediately anesthetized by filtered seawater saturated with carbon dioxide to prevent the release of food from the guts. The immobilized animals were sorted by species and stages and placed in 90% acetone for phytopigment extraction. Depending on the size of zooplankters, from 3 to 20 specimens were selected for each assay. Extraction was carried out at 4°C for 24 h. The fluorescence of the extracts was measured before and after acidification with two drops of 10% HCl using a Trilogy fluorometer (Turner Designs, United States). The device was previously calibrated using pure chlorophyll. The gut pigment content was determined according to [27]:

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

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

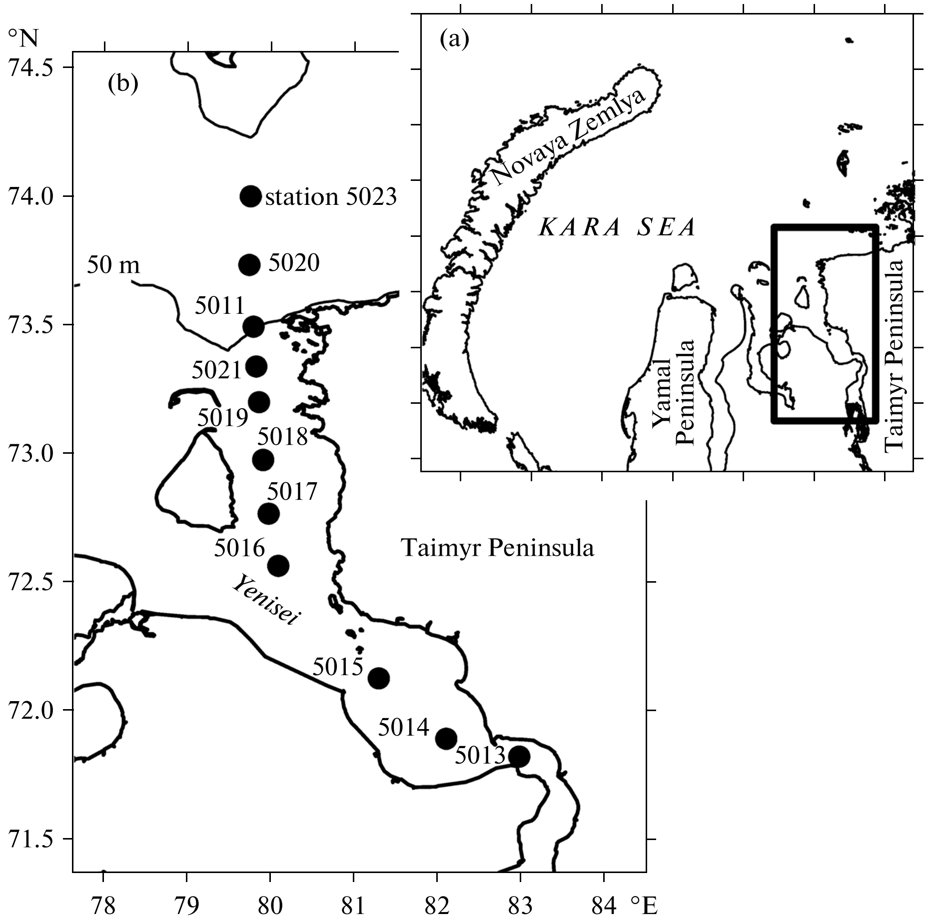

Fig. 1. Map of the study area (a) and location of stations on the transect in the Yenisey River estuary (b).

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

The total pigment content in the guts (G, ng $Chl\text{-}a$/ind.) was calculated by the formula [17]:

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

Table 1. Digestion time (T, h) for different species of zooplankton

Species/stage	T	Source
Bosmina longirostris	0.28	[10]
Daphnia sp.	0.11	[10]
Eurytemora sp., CV-Fem	1.1	[18]
Eudiaptomus sp., CV-Fem	1.23	[12]
Pseudocalanus sp., CV	0.68	[25]
Cyclops sp., CV	1.67	[25]
Drepanopus bungei, CV-Fem	0.68	[25]

Special experiments were carried out to determine the digestion time of phytoplankton in species *Mysis oculata*, *Limnocalanus macrurus*, and *Calanus glacialis*. To minimize the influence of experimental conditions on the digestion process, immediately after capture the crustaceans were placed in vessels with 30–50 mL of unfiltered seawater, and the time interval between the output of the first and second fecal pellet (Δt_{f}, h) was measured. The pellets were collected for subsequent determination of the amount of phytopigments (G_{f}, ng/pcs). Digestion time was calculated as $T = G\Delta t_{\mathrm{f}}/G_{\mathrm{f}}$.

Daily rations of the dominant species were calculated using literature data on digestion time corrected to a temperature of 8°C, taking into account $Q_{10} = 2.2$ [19] (Table 1). For *Cyclops* sp. and *Drepanopus bungei* we were not able to find published data on the digestion time of plant foods, so we used the values obtained in [25] for the marine species of Cyclopoida and Pseudocalanidae, respectively.

The daily consumption of $Chl\text{-}a$ (I, ng $Chl\text{-}a$/ind. per day) was calculated as $I = Gt/T$, where t is a feeding time of 24 h for species that have not revealed any pronounced circadian rhythm of feeding activity. For the

Table 2. Chlorophyll *a* concentration (*Chl-a*, mg/m^2), primary production (PP, mg C/m^2 per day) and the ratio of organic carbon of autotrophic phytoplankton and *Chl-a* (C_{ph}/*Chl-a*, mg C/mg *Chl-a*) at stations in the Yenisei River estuary and the adjacent shelf in September 2011

	Station no.	Date	Time	Depth	*Chl-a*	PP	C_{ph}/*Chl-a*
Freshwater area	5013	18/09	20:30	30	82.7	151	28.2 ± 17.4 (4)
	5014	19/09	02:00	8	23.1	49	
	5015	19/09	15:50	12	42.9	56	
	5016	19/09	21:30	13	17.7	23	
Frontal zone	5017	20/09	03:30	15	10.8	No data	21.5 ± 14.9 (11)
	5018	20/09	05:30	20	14.2	18	
	5019	20/09	10:20	20	17.3	15	
	5021	21/09	09:00	31	29.6	43	
	5011(2)	20/09	17:00	25	26.7	No data	
Inner shelf	5020	20/09	20:20	30	34.6	14	38.4 ± 25.7 (5)
	5023	21/09	18:30	26	16.4	25	

species in which *G* values were significantly different at different times of the day, we used the formula: $I = (G_1t_1 + G_2t_2)/T$, where G_1 and G_2 are the average amount of phytopigments in the gut in the day time and the night time and t_1 and t_2 are durations of the light and dark periods, respectively.

The total consumption of autotrophic phytoplankton by mesozooplankton ($E_{Chl\text{-}a}$, mg *Chl-a*/m^2 per 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 *i* species, N_i is the abundance of the *i* species in the layer (ind./m^2), and *n* is the number of species. Data on the abundance of species are given in [7]. To convert daily food consumption to carbon units (E_c, mg C/m^2 per day), data on the content of organic carbon in the autotrophic algae species (C_{ph}), which were obtained by processing the phytoplankton samples and determining its biomass carbon according to [24] (materials of I.N. Sukhanova and V.M. Sergeeva), were used. Data on the primary production and the concentration of *Chl-a* were provided by A.S. Demidov and S.A. Mosharov.

RESULTS

Regional features. Hydrophysical conditions in the region of research are described in detail in [7]. On the basis of the distribution of surface salinity in the investigated region, these authors allocated three main areas: a freshwater area with surface layer salinity of 0–5 PSU (stations 5013–5016), a mixing zone of river and sea water (estuarine frontal zone area) with a salinity of 5–18 PSU (stations 5017–5019, 5011, and 5021), and an area of the adjacent inner shelf, where the salinity was above 18 PSU (stations 5020 and 5023). The data on the concentration of *Chl-a*, primary production, and the C_{ph}/*Chl-a* ratio at stations located in the mentioned areas are presented in Table 2.

Consumption rate of phytoplankton by zooplankton. The results of measuring the amount of phytopigments in the digestive tract of the dominant zooplankton species in different areas of the investigated region (*G*, ng/ind.) are presented in Table 3.

Among the studied species of zooplankton, two dominant species of copepods *Calanus glacialis* and *Pseudocalanus* sp. revealed a significant variability in the amount of phytopigments in their guts, which is indicated by a high standard deviation, often higher than average values. Differences in the concentration of phytoplankton in different areas may be one of the possible reasons for such a significant variability in feeding activity. However, correlation analysis showed that the amount of phytopigments in the guts of copepods is practically independent of the *Chl-a* concentration in the range from 0.63 to 1.15 μg *Chl-a*/L: $r^2 < 0.18$ for both the species. Differences in the feeding activity at different times of day, which are described for many zooplankton species, are another reason [26]. Therefore, we compared the results of measuring the amount of phytopigments in the guts of these species, caught at different times of the day (Fig. 2). Analysis of these data showed that the *G* values for *Pseudocalanus* sp. and females and CV *C. glacialis* in the dark and day time are significantly different at $p < 0.05$, for CIV *C. glacialis* at $p < 0.1$ (Mann–Whitney U-test).

The results of the experimental determination of the digestion time in the three zooplankton species are presented in Table 4. The amount of phytopigments in one pellet of copepods was 1/3–1/4 of the gut contents, and the digestion time was about 50 min. In mysids, the digestive tract emptied after 10 pellets; the digestion time of phytroplankton was more than three hours.

Based on data on the amount of phytopigments in the guts of the dominant zooplankton species and the food digestion time, the daily consumption of

Table 3. Gut pigment content of dominantzooplankton species (mean ± SD) in different Yenisei estuarine habitats (parentheses indicate the number of replicates)

Species, stage/size	Freshwater area	Frontal zone	Inner shelf
Bosmina longirostris	0.68 ± 0.21 (2)		
Daphnia sp.	1.21 ± 0.41 (7)		
Cyclops sp., CV	3.95 ± 1.20 (3)		
Eudiaptomus gracilis, Fem	1.09 ± 0.19 (2)		
Eurytemora gracilis, Fem	2.33 ± 0.59 (4)		
Limnocalanus macrurus, CVI	2.13 ± 1.42 (13)		
Mysis relicta, 15–20 mm	535.01 ± 205.71 (10)		
Senecella siberica, CV	18.79 ± 1.73 (2)		
Drepanopus bungei, Fem		0.31 ± 0.09 (3)	
Drepanopus bungei, CV		0.81 ± 0.54 (5)	
Calanus glacialis, Fem		18.42 ± 18.77 (4)	23.94 ± 24.76 (10)
Calanus glacialis, CV		8.07 ± 7.09 (13)	21.57 ± 16.90 (21)
Calanus glacialis, CIV		5.83 ± 5.36 (6)	11.25 ± 9.51 (19)
Pseudocalanus sp., Fem			1.52 ± 0.97 (2)
Pseudocalanus sp., CV		1.25 ± 1.34 (8)	2.15 ± 2.25 (19)
Pseudocalanus sp., CIV			0.75 ± 0.74 (8)

Table 4. Amount of phytopigments in the guts (G, ng/ind.) and fecal pellet (G_f, ng/psc), the interval between the successive defecations (Δt_f, h), and digestion time (T, h). Mean values ± SD are given; parentheses show the number of measurements

Species/stage, size	G	G_f	Δt_f	T
Mysis oculata, 15–20 mm	285.37 ± 231.39 (6)	29.9 ± 6.43 (3)	0.33 ± 0.05 (6)	3.3
Limnocalanus macrurus, Fem	3.75 ± 0.93 (3)	1.1	0.25 ± 0.15 (5)	0.85
Calanus glacialis, Fem	9.36 ± 3.06 (5)	3.3	0.29 ± 0.10 (4)	0.84

autotrophic phytoplankton (I) by these species and their daily ration in carbon units (R) were calculated. For the two species of copepods *Pseudocalanus* sp. and *C. glacialis*, the calculations were made, taking into account daily changes in feeding activity (Table 5).

Zooplankton grazing impact on phytoplankton. Based on the data on the amount of phytoplankton daily consumption by the dominant zooplankton species and their abundance, we estimated the total grazing impact on the autotrophic phytoplankton biomass and primary production at different stations (Fig. 3).

Figure 3a shows the absolute and relative values of the grazing impact on phytoplankton in terms of *Chl-a*. In the freshwater area of of the Yenisei River estuary at stations 5013–5015 the total consumption of phytoplankton is minimal (0.17–0.38 mg *Chl-a*/m^2 per day). Zooplankton daily consumes only 0.4–1.5% of the available biomass of autotrophic phytoplankton. At station 5016, which is located in proximity to the contact area of river and sea water, the daily grazing rate increases to 0.78 mg *Chl-a*/m^2 per day (5% of the biomass). In the area of river and seawater mixing, the daily grazing rate is 0.85–2.1 mg *Chl-a*/m^2 per day or 3.2–14.3% of the algal biomass. In the area of the adjacent shelf (stations 5020 and 5023), the zooplankton community daily consumes 1.4–7.0% of phytoplankton biomass.

Figure 3b shows the values of the total zooplankton grazing in organic carbon units and the proportion of the consumed primary production. In general, the variation of these parameters in different areas is similar to that described above for grazing of phytoplankton biomass: relatively low levels (5–12 mg C/m^2 per day or 8–20% PP) in the area of the greatest river runoff influence at stations 5013–5015, an increase to 22 mg C/m^2 per day and 84% PP at station 5016, a marked increase at stations 5017–5019

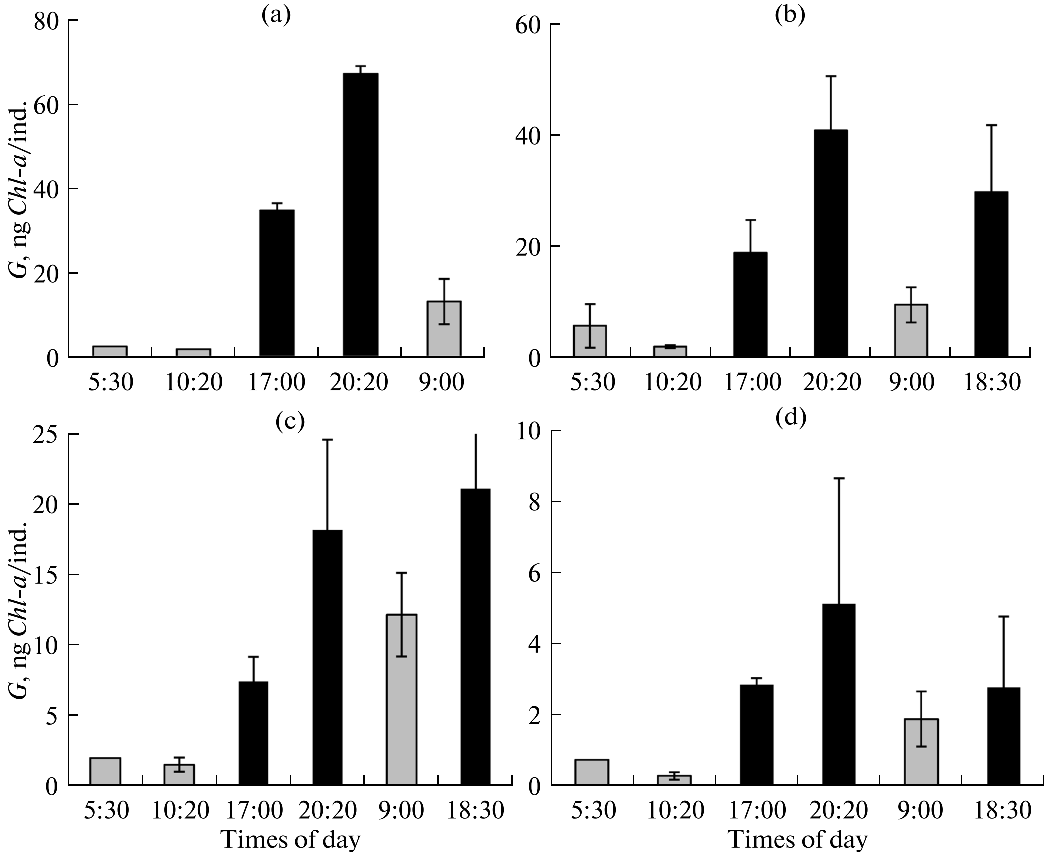

Fig. 2. Gut Pigment content (G) *Calanus glacialis* (a) in a female, (6) CV, (c) CIV, and (d) *Pseudocalanus* sp. CV at different times of the day.

(26–43 mg C/m^2 per day, 150–290% PP) in the mixing area and at station 5023 (44 mg C/m^2 per day, 175% PP) at the adjacent inner shelf. At stations 5021, 5011, and 5020, the total ingestion of the dominant zooplankton species varied within a small range from 18 to 21 mg C/m^2 per day and the proportion of PP consumption from 42 to 130%.

It is of special interest to assess the role of different zooplankton species in the grazing impact on phytoplankton, which can make it possible to reveal complexes of species responsible for the biotransformation of organic matter in different parts of the Yenisei River estuarine area during the study period. Our results show that in the freshwater area a major role in the grazing impact on autotrophic phytoplankton belongs to the freshwater species *Daphnia*, *Bosmina*, and *Cyclops*: the contribution of these species at all stations was more than 50% of the total PP consumption (Fig. 3f). At most stations in this area, mysids contributed 9 to 40% to the total PP consumption; at some stations a significant role belongs to populations of brackish copepods *Limnocalanus macrurus* (40% at station 5015) and *Drepanopus bungei* (15% at station 5016). In the area of fresh and sea water mixing and in the adjacent inner shelf, the grazing impact on the phytoplankton production is almost completely determined by the populations of marine copepod species *Calanus glacialis* and *Pseudocalanus* sp. There, *Pseudocalanus* sp. makes 99% of the total consumption at the interior boundary of the estuarine frontal zone (station 5017), while the population of *Calanus glacialis*, whose contribution amounts to more than 60%, significantly increases its role at the exterior boundary (station 5020).

DISCUSSION

Studies of the functional characteristics of the zooplankton community of the estuarine areas of the major Arctic rivers, are virtually limited to a single paper [1], dedicated to the study of zooplankton feeding and its role in the transformation of organic matter in different areas of the Kara Sea, including the Ob River estuary in autumn. Since the species composition of zooplankton in the Ob and Yenisei estuaries is almost the same, it was interesting to compare our data and the results of this work. Figures for the daily ingestion of autotrophic phytoplankton in terms of *Chl-a* are close for most species inhabiting the freshwater area. According to our estimates, the daily ingestion of phytoplankton by *Eurytemora* sp., *Eudiaptomus* sp., *Cyclops* sp., *Limnocalanus macrurus*, and *Senecella siberica* was 51, 22, 57, 59, and

Table 5. Daily consumption of phytoplankton (*I*, ng *Chl-a*/ind. per day) by dominant zooplankton species, the daily ration (*R*, μg C/ind. per day), and the specific daily ration *R*/*W* (%). *W* is the weight in terms of organic carbon

Species/stage	*W*, μg C	*I*	*R*	*R*/*W*
Bosmina longirostris	1.0*	58.5	1.6	164
Cyclops sp., CV-Fem	4.5**	57.0	1.6	36
Daphnia sp.	13.0***	279.0	31.0	71
Eudiaptomus sp., CV-Fem	3.2*	21.4	0.6	17
Eurytemora sp., CV-Fem	6.0**	50.8	1.4	24
Mysis oculata,15–20 mm	1280****	1326.0	37.1	3
Drepanopus bungei, CVI	6.0****	29.6	0.8	14
Senecella siberica, CV	52.0**	345.2	9.7	19
Limnocalanus macrurus, CVI	99.0*	59.3	1.7	2
Calanus glacialis, Fem	320.0**	581.2	17.4	5
Calanus glacialis, CV	128.0**	432.6	13.0	6
Calanus glacialis, CIV	80.0**	278.2	8.3	10
Pseudocalanus sp., CV	7.0**	52.2	1.6	22
Pseudocalanus sp., CIV	4.0**	22.3	0.7	17

* According to [30].
** According to [1].
*** According to [23].
**** Organic carbon content is taken as 6% wet weight calculated by nomograms [8].

345 ng *Chl-a*/ind. per day, respectively. According to [1], the *I* values for the same species were 53, 23, 54, 38, and 306 ng *Chl-a*/ind. per day. However, the *I* values that we obtained for the marine copepods *Calanus glacialis*, CV (433 ng *Chl-a*/ind. per day) and *Pseudocalanus* sp. (52 ng *Chl-a*/ind. per day) in the Yenisei River estuary and the adjacent shelf considerably exceeded the values measured for these species in the Ob River estuary, 107 and 24 ng *Chl-a*/ind. per day. The range of changes in the abundance of phytoplankton differed slightly (11–35 mg *Chl-a*/m^2 in the Yenisei River estuary and 18–25 mg *Chl-a*/m^2 in the Ob River estuary), so the effect of food concentration on the ingestion rate of these copepods can be excluded. The reason for the significant differences is that our estimates were obtained taking into account the daily variation of feeding activity of the copepods, which is characterized by a manyfold increase in feeding activity in the dark.

According to our calculations, the specific daily ration of the studied species varied from 2 to 160% of the body carbon. The highest values (70–160%) were obtained for cladocerans; the specific daily ration of freshwater copepods was 17–36%. While the level of respiration for all of these species ranges from 5 to 8% of the body carbon, which was calculated according to [21], with $Q_{10} = 2.3$ [5], the amount of energy ingested covers with the excess the respiration energy losses. Among the brackish species inhabiting the freshwater area, the daily intake of algae by copepods *Senecella siberica* and *Drepanopus bungei* (14–17% of the body carbon) also covers organic carbon losses associated with respiration. For other representatives of this complex, *Limnocalanus macrurus* and *Mysis oculata*, the energy derived from phytoplankton is not sufficient to compensate the energy respired, amounting to 2–7% of carbon per day [21]. According to [15, 29], both of these species could actively feed on small zooplankton, which in some cases can serve as a significant additional source of carbon. The relative daily ration of marine copepods (5–10% for different age stages of *Calanus glacialis* and 17–22% in *Pseudocalanus* sp.) was significantly higher than the respiration carbon losses r (2% in *C. glacialis* [11] and 4% in *Pseudocalanus* sp. [20]. Overall, our data suggest that in the Yenisei estuary area, despite the end of the productive season, the trophic conditions for the majority of dominant zooplankton species were favorable and the consumption of autotrophic phytoplankton not only compensated the energy losses, but also provided the growth and/or accumulation of reserve substances.

The total amount of phytoplankton consumed by mesozooplankton considerably varied both in different areas of the Yenisei River estuary and within the same area. In the freshwater area, with high phytoplankton biomass (2.8–3.8 μg *Chl-a*/L) and primary production (50–150 mg C/m^2 per day), the grazing impact of zooplankton on autotrophic phytoplankton is insignificant, not more than 1.5% of the biomass and 20% of the primary production per day. According to [1], in the freshwater area of the Ob River estuary the proportion of the phytoplankton biomass consumed daily by zooplankton was also low, amounting

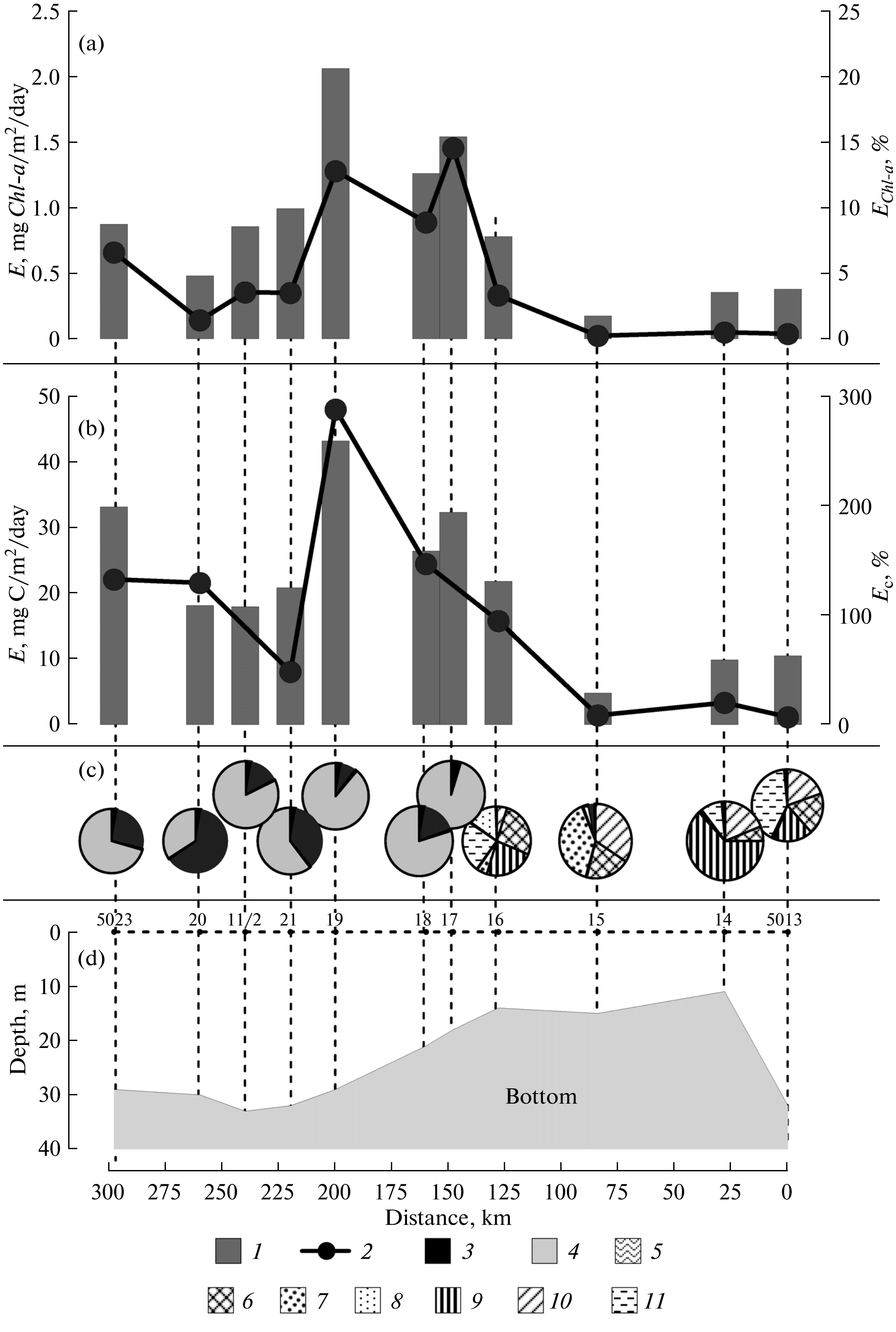

Fig. 3. Zooplankton grazing on phytoplankton in the Yenisei River estuary: (a) grazing of phytoplankton biomass (mg *Chl-a*/m^2/day), (b) grazing of primary production (mg C/m^2/day), (c) contribution of different zooplankters to total grazing of primary production (%), and (d) bottom topography and location of stations. *1*, absolute values; *2*, relative values; *3*, *Calanus glacialis*; *4*, *Pseudocalanus* sp.; *5*, *Limnocalanus macrurus*; *6*, *Cyclops* sp.; *7*, *Eurytemora* sp.; *8*, *Drepanopus bungei*; *9*, *Daphnia* sp.; *10*, *Bosmina longirostris*; *11*, *Mysis oculata*.

to about 1%. At the same time, in contrast to our results, the total daily consumption of zooplankton was 10% higher than PP. Given that PP in this area of the Ob River estuary was not lower than in the freshwater area of of the Yenisei River estuary, the only explanation for such significant differences may be that the authors carried out calculations using a C_{org} particulate matter/*Chl-a* ratio (300 μg C/μg *Chl-a*) of an order of magnitude greater than the value of C_{ph}/*Chl-a* for autotrophic phytoplankton used in this study. In the zone of fresh and seawater mixing of the Yenisei River estuary, zooplankton grazing impact of on phytoplankton increased, accounting for an average of 8% of their biomass and 130% of production. For comparison, it is estimated [1] that in the estuarine frontal area of the Ob River estuary the total amount of phytoplankton consumed by zooplankton averaged about 2% of the biomass and more than 300% PP at the ratio C_{org} of particulate matter/*Chl-a* of more than 100 μg C/μg *Chl-a*. These estimates give an general estimates of the scale of the transformation of primary organic matter by zooplankton in the areas of river and seawater mixing. However, as it was shown in [2, 6, 7], the Ob and Yenisei estuaries are characterized by local zooplankton aggregations associated with the fronts transect, where activity of organic matter utilization may be substantially higher. In the area that we investigated, the maximum concentration of mesozooplankton was observed at station 5017, which is located on the main front separating fresh waters from moderately salt water [7]. The total consumption of phytoplankton (14% of the biomass) at this station is almost twice the average value. Let us note that at this station we recorded a biomass of autotrophic algae, which was the minimum for the entire area in terms of *Chl-a* (see Table 2). A high level of grazing (12% of the biomass and almost 300% PP) was also recorded at station 5019, located on the front, with a gradient in salinity from 6 to 21 PSU over 13 km, which is associated with the meander formation. Since in the Ob River estuarine frontal area the grazing impact of the zooplankton aggregations on autotrophic algae was not estimated, based on the data on the abundance [6] and the ingestion rate of dominant species [1] we calculated a total consumption for station 4997 at which the number of zooplankters was maximal. According to these calculations, about 15% of the phytoplankton biomass of is consumed by zooplankton daily. The main consumers were brackish copepods *Limnocalanus macrurus* and *Senecella siberica*: their total contribution was 80%. In the Yenisei River estuary, grazing on phytoplankton is determined by numerically dominant small marine copepods of genus *Pseudocalanus* (Fig. 3). Outside the estuarine frontal zone, on the inner shelf, the contribution of large marine copepods *C. glacialis* markedly increases. The total consumption of autotrophic algae in this area averaged about 3% of the available biomass and 130% PP and, in fact, was determined by these two species. On the inner shelf adjacent to the Ob River estuary, the zooplankton community grazed 4% of biomass and 90% PP [1].

An important aspect in the study of the biotransformation of organic matter in marine ecosystems is the assessment of the role of zooplankton in the vertical transport of organic matter, as zooplankton fecal pellets are one of the most effective mechanisms of biosedimentation [28]. In shallow estuarine areas, the contribution of zooplankton to the flow of organic carbon to the bottom can be particularly great. Using obtained data on the total ration of zooplankton and taking the phytoplankton assimilation as 0.6, it seemed interesting to estimate in the first approximation the flow of organic carbon contained in fecal pellets (C_f) in different areas of the Yenisei River estuary. Calculations show that C_f varied from 2–4 mg C/m^2 per day in the freshwater area to 8–17 mg C/m^2 and 7–13 mg C/m^2 per day in the estuarine frontal zone and the adjacent shelf, respectively. Measured by sediment traps, the flow of organic carbon in these areas of the Yenisei estuary at the end of the productive season (September) was 368 mg C/m^2 per day, 11–15 mg C/m^2 per day, and 6–7 mg C/m^2 per day, respectively [4]. According to other estimates [14], the flow of organic carbon on the adjacent shelf in September and October was 82–146 mg C/m^2 per day. These data show that in the area of the most pronounced river runoff influence the proportion of C_f in the vertical flow of organic carbon in the average does not exceed 1%, while in the estuarine frontal zone and the shelf the contribution of the pellet material may be much higher.

CONCLUSIONS

Analysis of our results and their comparison with the data obtained in the Ob River estuary [1] makes it possible to identify a number of common patterns of organic matter biotransformation in the estuarine areas of major Arctic rivers.

1. For the majority of dominant zooplankton species trophic conditions were favorable and the consumption of autotrophic phytoplankton not only compensated the energy respired but also provided the opportunity for the growth and/or accumulation of reserve substances. A high biomass of phytoplankton at the end of the productive season is one of the manifestations of the influence of river runoff in the estuarine areas.

2. Zoning of the estuarine areas largely determines quantitative aspects of consumption of newly synthesized organic matter by herbivorous zooplankton, vertical flux of organic matter, and the balance of production and destruction processes (Fig. 4). In the phytoplankton-rich fresh-water area, zooplankton grazing on phytoplankton is low, and the majority of organic matter apparently settles to the bottom in an untransformed state. In the zone of sea and river water mixing, the role of mesozooplankton in utilizing the primary production is markedly increased. Maximum values of grazing are

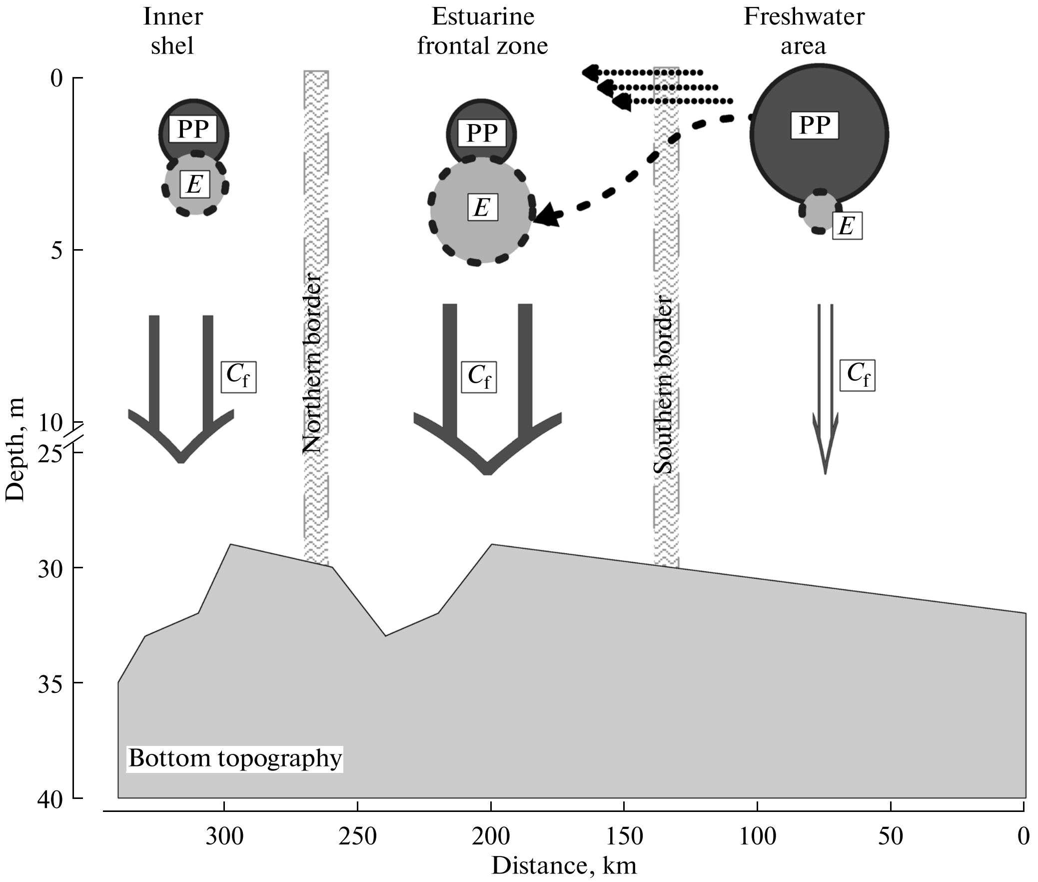

Fig. 4. Diagram illustrating the role of zooplankton in the biotransformation of organic matter in different habitats of the Yenisei River estuary. PP, primary production (mg C/m^2 per day); *E*, total amount of phytoplankton consumed by zooplankton (mg C/m^2 per day), C_f, the flux of carbon contained in fecal pellets (mg C/m^2 per day).

confined to the fronts. According to our estimates, all the available biomass of phytoplankton in these areas can be consumed within several days, and the total ration of zooplankton is almost three times greater the amount of newly synthesized organic carbon. The contribution of zooplankton to sedimentation of organic carbon markedly increases. On the inner shelf adjacent to the estuarine area the level of grazing is reduced, the processes of creation of primary production and its utilizing by zooplankton are more balanced.

3. The complexes of mesozooplankton species responsible for the transformation of newly synthesized organic carbon differed in different areas. Freshwater species, as well as brackish copepods *Limnocalanus macrurus* and mysids, are the main consumers of autotrophic planktonic algae in the freshwater area. One or two dominant species of zooplankton define the grazing of phytoplankton in the estuarine frontal area: small marine copepods of genus *Pseudocalanus* in the Yenisei River estuary and large opportunistic species *L. macrurus* and *Senecella siberica* in the Ob River estuary. The main role in the consumption of phytoplankton on the adjacent inner shelf belongs to marine copepods *Pseudocalanus* sp. and *Calanus glacialis*.

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