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MARINE BIOLOGY

Structure of the Zooplankton Communities in the Region of the Ob River's Estuarine Frontal Zone

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Abstract—The studies were carried out on September 27–30, 2007, in the area of the Ob estuarine frontal zone and over the adjacent inner Kara Sea shelf. Based upon the latitudinal changes in the salinity, the 100 nautical mile wide estuarine frontal zone was marked out. The frontal zone was inhabited by a specific zooplankton community dominated by species that occurred outside the frontal zone in only minor amounts. The biomass of the mesozooplankton averaging 984 mg/m^3 in the frontal zone exceeded by 1.5 and 6 times the corresponding values in the inner desalinated area of the estuary and the adjacent areas of the Kara Sea shelf. At the inner southern periphery of the frontal zone, at maximal latitudinal salinity gradients (>2 psu per mile), the maximal development of the mesoplankton with the mean biomass for the water column of 3.1 g/m^3 (37 g/m^2) and up to 5.8 g/m^3 in the subpycnocline layer was observed. The latitudinal extension of the biomass in the maximum zone did not exceed 10 miles. More than 90% of the maximum was composed of herbivorous zooplankton with the strong domination of the copepod *Limnocalanus macrurus*. The daily consumption within the zooplankton maximum area was estimated at 820 mgC/m^2 per day. This value exceeds by two orders of magnitude the local primary production. At that level of consumption, the available phytoplankton biomass was consumed by grazers in less than 8 hours (!). A zooplankton aggregation at the southern periphery of the estuarine front exists due to the advection of phytoplankton from the adjacent river zone. The aggregation forms a natural pelagic biofilter where new allochthonous organic matter delivered by the river flow is accumulated and high secondary production is formed on its basis. An anomalously high concentration of planktic predatory *Parasagitta elegans* with biomass of over 1 g/m^3 (46% of the total zooplankton biomass) was associated with the outer northern periphery of the estuarine frontal zone.

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INTRODUCTION

Estuarine regions of large rivers play a very important role in the regulation of the impact of the continental processes upon the marine ecosystems and the transformation of the allochthonous material delivered by the riverine flux [10, 25[. The zones of mixing of the sea and river waters are characterized by specific environmental conditions and unique geochemical and biological processes. These features determine to a high extent the impact of the freshwater discharge on the adjacent sea regions, the regional biological productivity, and the horizontal and vertical fluxes of mater. Finally, the conditions of the mixing zones form one of the most important properties of the estuarine and precontinental sea regions: the cross shelf zonality in the structure of the pelagic and bottom ecosystems. Such zonality was revealed in some sea regions [29, 30] including the Kara Sea [6, 11, 18, 27]. The river estuaries are affected by the climatic (determining the volume and the regime of the freshwater discharge) and anthropogenic factors (affecting the chemical composition and pollution of the riverine waters as well as the volume of their inflow into the adjacent seas).

In the Arctic regions, the role of the estuarine processes is especially important. This is determined by the fact that majority of the epicontinental Arctic seas receiving riverine discharge are shallow. This discharge plays a key role in the formation of the environmental conditions and the functioning of the ecosystems over vast areas including the shelf, the continental slope, and the deepwater regions of the Arctic basin. In the Kara Sea studied in the present paper, the annual riverine discharge averaging about 1100 km^3 per year conventionally increases the level of the basin by 1 m at its mean depth of 111 m [32, 34]. This value is more than one order higher compared to mean value for the World Ocean, evidencing the principal importance of the processes of the interaction of the riverine and marine waters for the functioning of the basin's ecosystem.

The estuarine zones of the large Arctic rivers and the adjacent shelf regions of the epicontinental seas are the areas in which the freshwater environment actively interacts with the marine one; interaction of the freshwater and marine ecosystems takes place there resulting in the formation of massive frontal

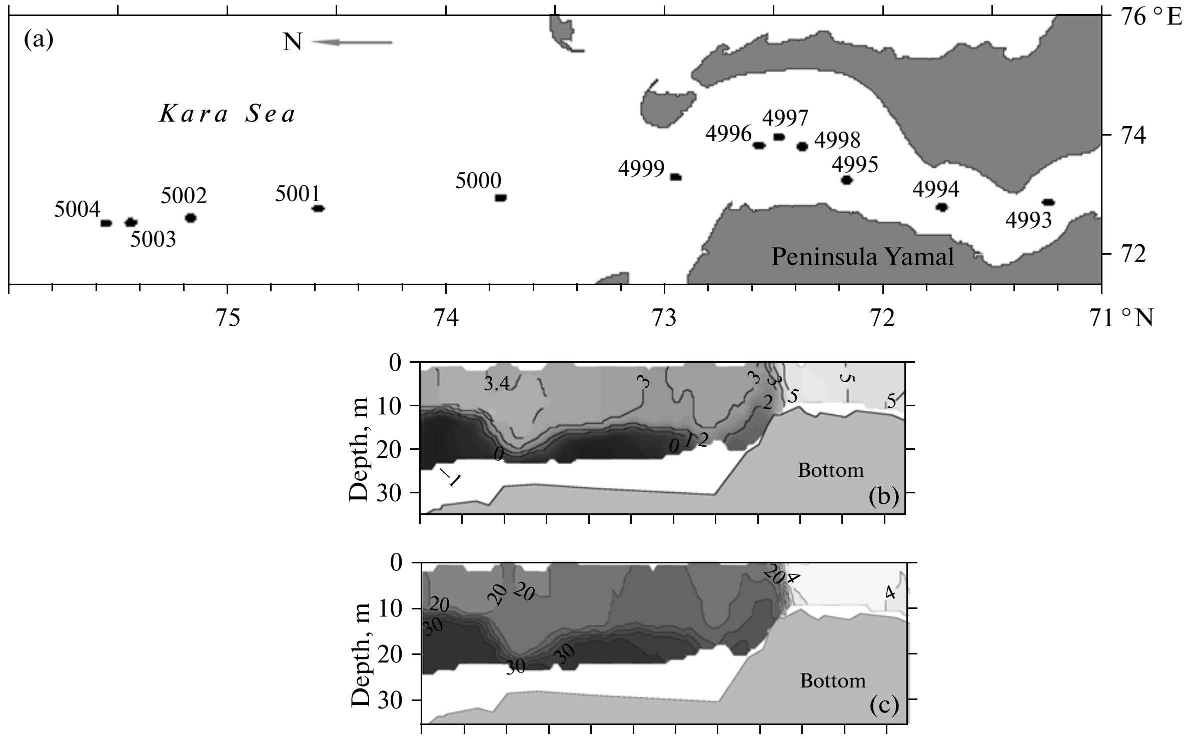

Fig. 1. Scheme of the locations of the stations (a); the distribution of the temperature, °C (b); and the salinity, psu (c), in the Ob estuary and on the adjacent shelf.

zones and borders along with pronounced vertical stratification and associated biological phenomena [5, 10, 30, 33]. These phenomena, as well as their spatial scale, quantitative, and qualitative characteristics are of great interest. They relate to the processes of the transformation of the suspended matter of various nature entering the seas with the riverine flux at amounts reaching 6–16.6 million tons in the large Arctic rivers [24, 25] and the formation of the biological production in the unique gradient biotope of the estuary. At the same time, above mentioned phenomena are the initial link from which the cross shelf zonality of the marginal Arctic seas starts. This zonality determines to a high extent the very important interactions connecting the continent, shelf, and deepwater basin in the Arctic. Finally, the temporal variability of the phenomena related to the estuarine zones of large Arctic rivers may serve as the most sensitive indicator and measure of the climatic and anthropogenic variability of the processes taking place in the river–sea system.

The following goals were set for the present paper: to analyze the spatial structure of the mesoplanktic communities of the Ob River estuarine area and the adjacent Kara Sea shelf; to reveal the relations of this structure with the peculiarities of the highly gradient environment in the zone of the interaction of the Ob River and the sea waters and its separate frontal borders; to assess the potential impact of the frontal phenomena on the biological productivity and matter fluxes in the large Arctic estuary.

MATERIALS AND METHODS

The zooplankton was sampled during the 54th expedition aboard the R/V *Academician Mstislav Keldysh* (27–30 of September 2007) along the transect from the inner part of the Ob estuary to the inner Kara Sea shelf (Fig. 1a).

The zooplankton was collected by vertical sampling using a 37/50 Judy net (the mesh size of the filtering cone was 180 μm) at a 0.6–0.8 m/s towing velocity. The samples were collected in the upper mixed layer and in the layer under the seasonal pycnocline. The location of the latter was preliminary determined based on the vertical CTD probing.

The samples were preserved with 4% neutral formalin and processed in the laboratory according to the standard routine in a Bogorov chamber using a binocular microscope with the identification of the organisms to the species or genus level and the measuring of their body lengths. The individual wet weight of the animals for the further calculations of the population and total community biomass was determined using the body length/weight ratios for various species and groups [7] and Chislenko's nomograms [17].

The relevant data on the water temperature and salinity were obtained by vertical CTD probing at the

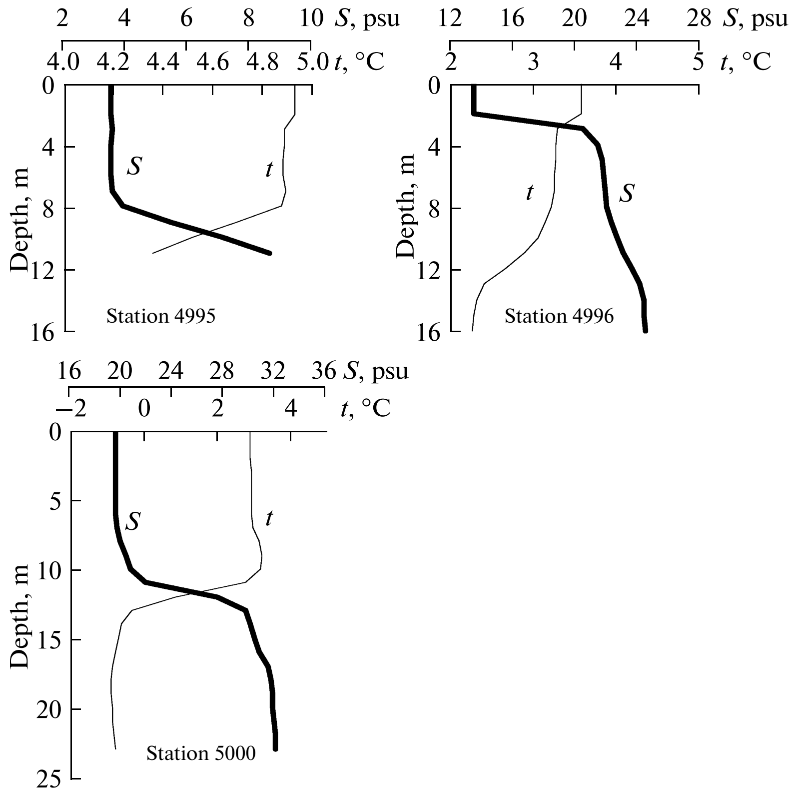

Fig. 2. Vertical profiles of the temperature (*t*, °C) and salinity (*S*, psu) at stations in various parts of the transect.

sampling stations and in the regime of continuous scanning of the water column by the CTD probe during ship's movement [8].

RESULTS

The oceanographic conditions along the transect. The studied region covered the freshwater part of the Ob estuary with water salinity of <0.1 psu with lack of vertical stratification and the region of intensive interaction of the river and sea waters at the outer part of the estuary and the inner Kara Sea shelf adjacent to the estuary where the water column was firmly stratified by salinity and temperature (Figs. 1b, 1c; 2). The latitudinal extension of the studied region was slightly more than 4 degrees or 260 miles. The depths varied from 11–20 m in the southern part of transect and to 110 m in the northern one.

The pronounced changes in the salinity along the latitudinal direction were the most important characteristics of the pelagic environment in the studied region. In the surface water layer, it increased from 0.05 psu at the southern station 4993 to 18.6 psu at the northern station 5004 (Figs. 3a; 4a). The most pronounced horizontal gradients (0.6 psu per mile) were recorded in the narrow four mile wide area between stations 4996 and 4997 (Fig. 4b). In the layer under the pycnocline, the relevant changes in the salinity along the transect were even more pronounced ranging from 0.05 to 34.9 psu. The maximal latitudinal salinity gradients reached 0.6–0.9 psu per mile and were registered between stations 4996 and 4998 (Fig. 4b). The nine mile wide area with the maximal salinity gradients in the layers under the pycnocline had greater latitudinal extension than the respective area in the upper mixed layer. In the area of the maximal latitudinal salinity gradients, the maximal differences between the salinities in the upper mixed and subthermocline layers reaching 19, 16, and 17.5 psu at stations 4997, 4998, and 4999, respectively, were observed. There, at stations 4997 and 4998, the sharpest vertical gradients of the salinity (7.2 and 9.5 psu/m, respectively) were recorded.

The temperature within the studied region ranged from 7.2°C in the south to 2.7°C in the north (Fig. 1 b) in the surface layer and 7.2°C to –1.6°C near the bottom. The latitudinal temperature gradients were less pronounced than the gradients of the salinity. The area with the maximal temperature gradient in the surface layers, 0.25°C per mile, coincided with the area of the maximal salinity gradients and was situated between stations 4996 and 4997. North of station 5000, the temperature in the upper mixed layer did not change, in fact ranging from 2.5 to 2.8°C. Two areas of high latitudinal gradients were observed in the distribution of temperature in the subpycnocline layers: the first one

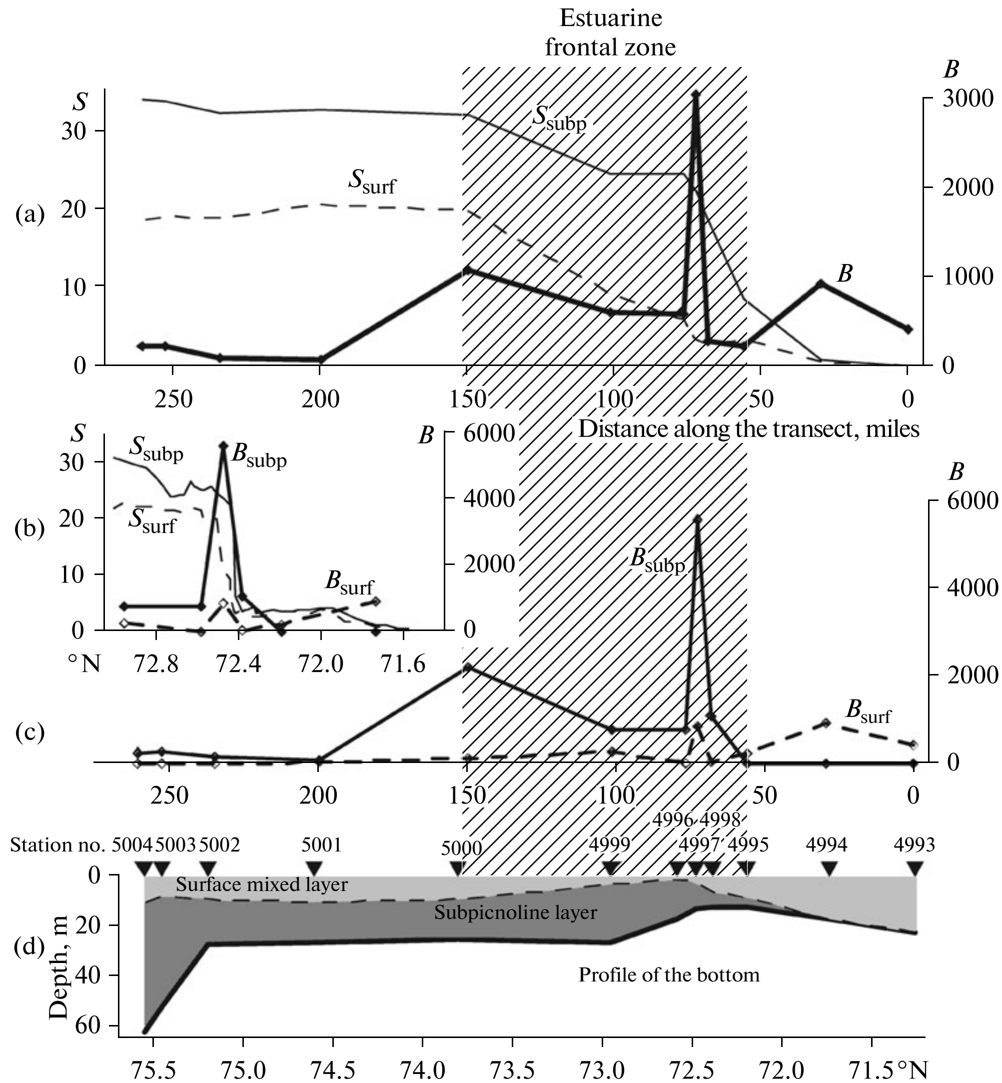

Fig. 3. Distribution of the average for the water column mesoplankton biomass (B, mg/m^3) and the salinity according to the CTD probing data in the surface layer (S_{sur}, psu) and in the layer below the pycnocline (S_{subp}, psu) along the transect (a); the distribution of the average for the water column mesoplankton biomass (B, mg/m^3) and the salinity in the surface layer (S_{sur}, psu) and in the layer below the pycnocline (S_{subp}, psu) according to the CTD probing data in the region of the southern periphery of the estuarine front (b); the distribution of the mesoplankton biomass in the layers above (B_{surf}, mg/m^3) and below (B_{subp}, mg/m^3) the pycnocline along the transect (c); the locations along the stations and the changes in the depth along the upper mixed layer of the transect (d). The cross hatching marks the region of the estuarine frontal zone.

related to the maximal salinity gradients between stations 4995 and 4998 with a gradient of 0.14°C per mile; the second one situated seaward between stations 4996 and 4999 with a gradient of 0.11°C per mile. In this region, the maximal jump of the temperature near the bottom from 2.3°C to 0°C was observed. The vertical jump of the temperature in the pycnocline did not exceed 1.9°C in the southern part of the estuary (south of station 4996), it increased north of station 4999, and it reached a maximum of 3.9–4.0°C above the inner Kara Sea shelf at the northernmost stations 5003 and 5004.

The described and presented in the figures pattern of the latitudinal changes in the salinity and temperature in the Ob estuary was observed over a background of northern water current with an average velocity of 0.5 m/s during the summer and fall [12].

Based on the changes in the main parameters of the pelagic environment described above and following the commonly accepted criteria [14], we marked out the *estuarine frontal zone*. This zone is the area where the interaction of the riverine and sea waters is the most intensive, the environment is characterized by the most pronounced horizontal gradients, and the vertical structure of the property fields undergoes the clearest changes. The southern periphery of the estuarine frontal zone was situated next to station 4995 (Figs. 3 and 4). The first signs of the impact of the sea

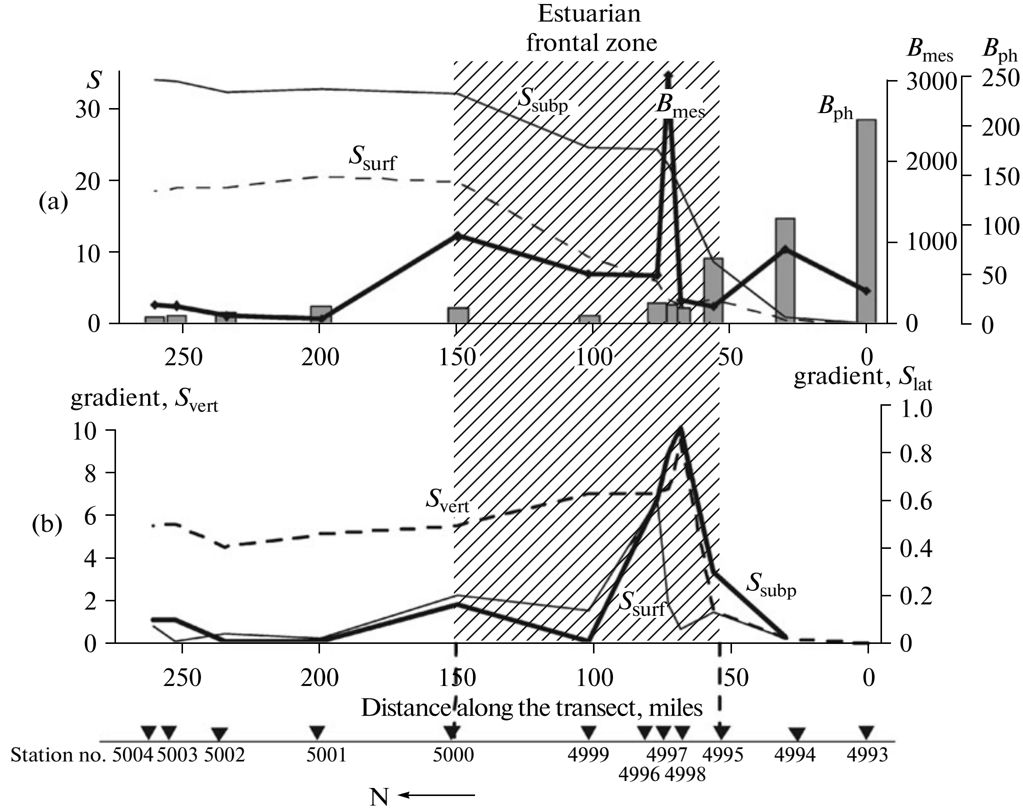

Fig. 4. Distribution of the average for the water column phytoplankton biomass (B_{ph}, mgC/m^3), the mesoplankton biomass (B_{mes}), and the salinity according to the CTD probing data in the surface layer (S_{surf}, psu) and in the layer below the pycnocline (S_{subp}, psu) along the transect (a); the changes in the latitudinal salinity gradients in the upper mixed layer (S_{surf}, psu/mile) and in the layer below the pycnocline (S_{subp}, psu/mile) and the changes in the vertical salinity gradients in the pycnocline (S_{vert}, psu/m) according to the CTD probing data along the transect (b). The cross hatching marks the region of the estuarine frontal zone.

water and of the formation of the stratification of the water column were observed here; the salinity in the surface layer increased to 3.5 psu and to 8.7 psu near the bottom (Figs. 1b, 1c; 2a; 3a; 4b). Further to south, the area of the maximal latitudinal gradients of the salinity and temperature (stations 4996–4999) was situated. In this zone, the depth of the upper mixed layer decreased to 2–6 m, and the vertical salinity gradients in the pycnocline reached 6–9.5 psu (Fig. 2c; 3a; 3d; 4b). South of station 4999, even though the latitudinal gradients of the salinity and temperature were clearly pronounced, they decreased considerably and the lower border of the upper mixed layer gradually deepened. Seawards of station 5000 situated off the Ob estuary on the inner Kara Sea shelf, the latitudinal gradients of the salinity and temperature became relatively small, while the vertical structure of the water column stabilized: the depth of the upper mixed layer up to northern station 5000 of the transect ranged from 8 to 12 m (Figs. 2c; 3a; 3d; 4b). Station 5000 was also the southern point to which the subthermocline sea waters with a temperature below zero (–0.9°C; Fig. 1b) occupying huge areas of the Kara Sea shelf penetrated [8]. All the above mentioned allowed us to mark out the region of station 5000 as the northern periphery of the Ob estuarine front. There, the width of the estuarine frontal zone situated between stations 4995 and 5000 was slightly less than 100 miles or 1°35′ by latitude.

The distribution of the total mesoplankton biomass. The average values of the total mesoplankton biomass in the river zone, the zone of the estuarine front, and on the inner Kara shelf differed considerably (table). The highest biomass was recorded in the estuarine frontal zone. The average for the whole water column values of the biomass characterizing the frontal zone as a whole in fact reached 1 g/m^3 or 15 g/m^2 (here and hereafter, wet weight). The lowest values of 162 mg/m^3 or about 6 g/m^2 were registered on the inner Kara Sea shelf.

The changes in the total biomass of the mesoplankton along the transect are shown in detail in Fig. 3a. The figure illustrates the considerable unevenness of the mesoplankton distribution in the region of the estuarine frontal zone. Two maxima are clearly defined there: the first relates to the southern “riverine” periphery of the frontal zone; the second, with its

The minimal, maximal, and average values of the total biomass of the mesoplankton (B, mg/m^3 in the layer) and the diapasons of the salinity (S, psu) in various biotopes of the studied region

Layer	Inner Kara Sea shelf		Estuarine frontal zone		River desalinated zone*	
	S	B	S	B	S	B
Whole water column		74–236 $x = 162.1 \pm 84.0$; $n - 4$		230–3067 $x = 983.6 \pm 852.3$; $n - 6$	0.05–0.6	420–933 $x = 677$; $n - 2$
Upper mixed layer	18.5–20.6	1–37 $x = 11.9 \pm 14.3$; $n - 4$	2.7–19.8	15–874 $x = 266.0 \pm 251.5$; $n - 6$		
Subthermocline layer	32.7–34.0	103–289 $x = 206.9 \pm 72.4$; $n - 4$	8.7–32.1	774–5775 $x = 2105.2 \pm 1613.1$; $n - 6$		

* Water column mixed vertically.

northern border. In the southern maximum, the biomass reaches values the maximal for the whole studied region: 3.1 g/m^3 on average for the water column or 37 g/m^2. The most peculiar features of this maximum were its small not more than 10 mile latitudinal extension and clear connection with the area of the maximal salinity gradients (Figs. 3a; 4). In the maximum close to the northern seaward border of the estuarine frontal zone, the average for the whole water column biomass of the mesoplankton was lower (1.1 g/m^3), but, at greater depth the total biomass under 1 m^2 reached 31 g.

The obtained data allow for the analysis of the mesoplankton biomass distribution separately for the upper mixed and subthermocline layers and for connecting this distribution with certain salinity and temperature characteristics of the biotope (Figs. 3b, 3c). In the upper mixed layer, along the whole transect, the mesoplankton biomass was relatively low. The maximal values (420–930 mg/m^3) were recorded in the southern desalinated (0.5–0.7 psu) and nonstratified region. In the estuarine frontal zone with a stratified water column (stations 4995–5000) and the salinity above the pycnocline increase from 2.7 to 19.8 psu, the mesoplankton biomass above the pycnocline decreased to 15–130 mg/m^3. The local maximum of 875 mg/m^3 was related to the narrow area of sharp horizontal salinity gradients (Figs. 3b, 3c; 4). According to the materials of the standard hydrophysical observations at the stations, these gradients are 0.65 psu per mile (between 3.5 and 6.0 psu); according to the more detailed data obtained using the scanning CTD probe, the gradients are 2.7 psu per mile (between 3.5 and 16.5 psu) (Fig. 3b). On the inner Kara Sea shelf (north of station 5000), at salinity above 20 psu, in the upper desalinated layer, the biomass varied between 1 to 37 mg/m^3.

The pattern of the quantitative distribution of the mesoplankton in the subpycnocline layer (where at the majority of the transect stations 80 to 99% of the biomass was aggregated) was different and less even. In the estuarine frontal zone, the mesoplankton biomass varied from 0.7 to 5.8 g/m^3. The most clearly pronounced maximum of the biomass, 5.8 g/m^3, was confined to the southern periphery of the estuarine frontal zone (station 4997, Figs. 3b, 3c). The values found at the neighboring stations situated 4.8 miles south and 4.2 miles north of the above station were respectively six and seven times lower. The maximal values of the mesoplankton biomass, as in the layer above the pycnocline, were firmly confined to the narrow area of the highest latitudinal salinity gradients (Figs. 3b, 3c; 4). According to the CTD observations at the stations, these gradients were 0.4 psu per mile (between 8.7 and 22.3 psu) (Fig. 3a), while, according to the data of the scanning CTD probe, these gradients may have reached 3.8 psu per 0.1 mile (!) at the narrow areas within 4–19 psu diapason of salinity changes (Fig. 3b). The second lower maximum of the mesoplankton biomass (2.3 g/m^3) in the subpycnocline layers was related to the northern periphery of the estuarine front (station 5000). This maximum was confined to the area in which ended the considerable latitudinal gradients related to the estuarine frontal zone, and the salinity reached >32 psu (typical for the near bottom water on the inner Kara Sea shelf) (Fig. 3a). In addition, near station 5000 in the subpycnocline zone, changes in the water temperature were observed. The temperature dropped down to below zero, which is also typical for the Kara shelf and is totally different from the estuarine frontal zone, where the temperature below the pycnocline changed from 4.4°C at the southern periphery to 0°C in the north.

The biomass of the mesoplankton at the shelf stations of the transect (stations 5001–5004) in the subpycnocline layers was relatively low, from 103 to 263 g/m^3 (table), and exhibited a trend towards a gradual increase in the direction to the northern border of the inner shelf (Figs. 3a, 3c). The latitudinal increase in the salinity from 32.7 to 34.0 psu and the rise of the near bottom layer with temperatures below zero (from −1.0 to −1.6°C) from 7 m at station 5001 to 90 m at station 5004, along with the increase in depth from 25 m to 110 m, were characteristics of the subthermocline biotope in the above mentioned area.

The dominating species of mesoplankton and their distribution. To analyze the peculiarities of the quantitative distribution of the plankton in the studied region, we selected 12 mass species of mesoplankton belonging to different taxonomic groups. The selected species represent a wide ecological spectrum in terms, first of all, of the relations of their populations to the riverine, estuarine, and shelf biotopes and their salinity preferences [3, 5, 9, 19, 20]. The following species were analyzed: the copepods *Calanus glacialis*, *C. hyperboreus*, *C. finmarchcus*, *Pseudocalanus* spp. (*P. minutus* + *P. acuspes* + *P. major*), *Limnocalanus macrurus*, *Jashnovia tolli*, *Drepanopus bungei*, *Senecella sibirica*, *Metridia longa*; the amphipod *Onisimus birulae*, mysid *Mysis oculata*; and the Chaetognath *Parasagitta elegans*. The representatives of this group of species were dominant by total biomass, accounting together for more than 80% of the total biomass. At many stations (first of all, at the richest ones), this group accounted for more than 90% of the total biomass of the mesoplanktic community.

In terms of the distribution pattern, the mesoplankton species listed above are split into several types.

The first type of the distribution is represented by *Onisimus birulae*. It was found only at the freshwater biotope at station 4993, where it accounted for 90% of the total mesoplankton community biomass at its own biomass of 370 mg/m^3 (Fig. 5a). The vanishing of this species from the plankton marked the southern border of the estuarine frontal zone.

The second rather paradoxical type of distribution was demonstrated by the two species: the copepod *Senecella sibirica* and the mysid *Mysis oculata* (Figs. 5b, 5c). Both species formed a clearly pronounced maximum in the desalinated zone at salinity <0.6 psu at the southern periphery of the estuarine frontal zone (station 4994). The biomass of *S. sibirica* at the maximum reached 300 mg/m^3; that of *M. oculata*, 240 mg/m^3. These species together accounted for more than 60% of the total community's biomass. Mass aggregations of these species were noted in the region of the maximal latitudinal salinity gradients at the southern part of the frontal zone (station 4997). At this location, the aggregations were confined exclusively to the subthermocline layers of the water column with salinity of 22.3 psu (Figs. 5b, 5c). The biomass of *S. sibirica* and *M. oculata* in the region of the maximum reached 170 and 430 mg/m^3, respectively (about 10% of the total mesoplankton biomass). The zone of the maximum stretched in the latitudinal direction for less than 10 miles. Thus, both species considerably contributed to the mesoplanktic community in the region of the sharp border between the biotopes strongly differing in water salinities.

Three mass estuarine copepods, *Limnocalanus macrurus*, *Jashnovia tolli*, and *Drepanopus bungei*, exhibited the third type of distribution: they inhabited predominantly the zone of the estuarine front and occurred in very inconsiderable amounts in the desalinated zone at the southern stations of the transect (Figs. 5d–5f). In the stratified regions of the estuarine frontal zone, *L. macrurus* and *J. tolli* inhabited almost exclusively the water column below pycnocline, while *D. bungei* was also found in the upper mixed layer. The population of *L. macrurus* was characterized by the maximal biomass values and the latitudinal diapason in which this species reached considerable abundance was the narrowest among all the studied species. In the region of the maximal latitudinal salinity gradients at the southern periphery of the estuarine frontal zone, the biomass of *L. macrurus* reached 4.8 g/m^3. Such massive aggregations were observed at the salinity of 22.3 psu, while the maximum had the shape of a sharp peak with latitudinal extension of <10 miles (station 4997; Fig. 5d). Outside the region of the maximal concentrations at the northern part of the estuarine frontal zone, the biomass of *L. macrurus* was two orders lower and the species was absent from the inner shelf. The distribution of *J. tolli* and *D. bungei* was also characterized by a peak of the biomass confined to the subpycnocline layers in the region of high salinity gradients at the southern part of the estuarine frontal zone at station 4997 (Figs. 5e, 5f). Opposite to *L. macrurus*, the species *J. tolli* and *D. bungei* were quite abundant in fact over the whole estuarine frontal zone. At the inner shelf seaward of station 5000, *J. tolli* was not found while *D. bungei* was represented in an inconsiderable amount.

The fourth type of distribution was exhibited by the large-sized copepod *Calanus glacialis*, fine-sized *Pseudocalanus* spp. and the chaetognath *Parasagitta elegans*, which, in the studied, region were mainly aggregated in the subpycnocline layers. They demonstrated very similar distribution patterns with clearly pronounced maximum in the region of the southern border of the estuarine frontal zone with salinity increased from 24.5 to 32 psu (Figs. 5g–5i; station 5000). The biomass of *C. glacialis* in the maximum reached 80 mg/m^3; that of *Pseudocalanus* spp., 550 mg/m^3; and that of *Parasagitta elegans*, 1100 mg/m^3. Together the representatives of this mesoplankton group made up 81% of the total mesoplankton biomass. North of the frontal maximum at the inner Kara Sea shelf and in the region of the estuarine frontal zone, their abundance decreased. An exception to the trend was demonstrated by *C. glacialis*: its biomass increased to 20–50 mg/m^3 at the northern stations of the transect at the region of the transition from the inner to the outer shelf. South of the region with the maximal latitudinal salinity gradients, at the "riverine" periphery of the estuarine frontal zone (stations 4997–4998), at salinity in the subpycnocline layers below 19–22 psu, *C. glacialis*,

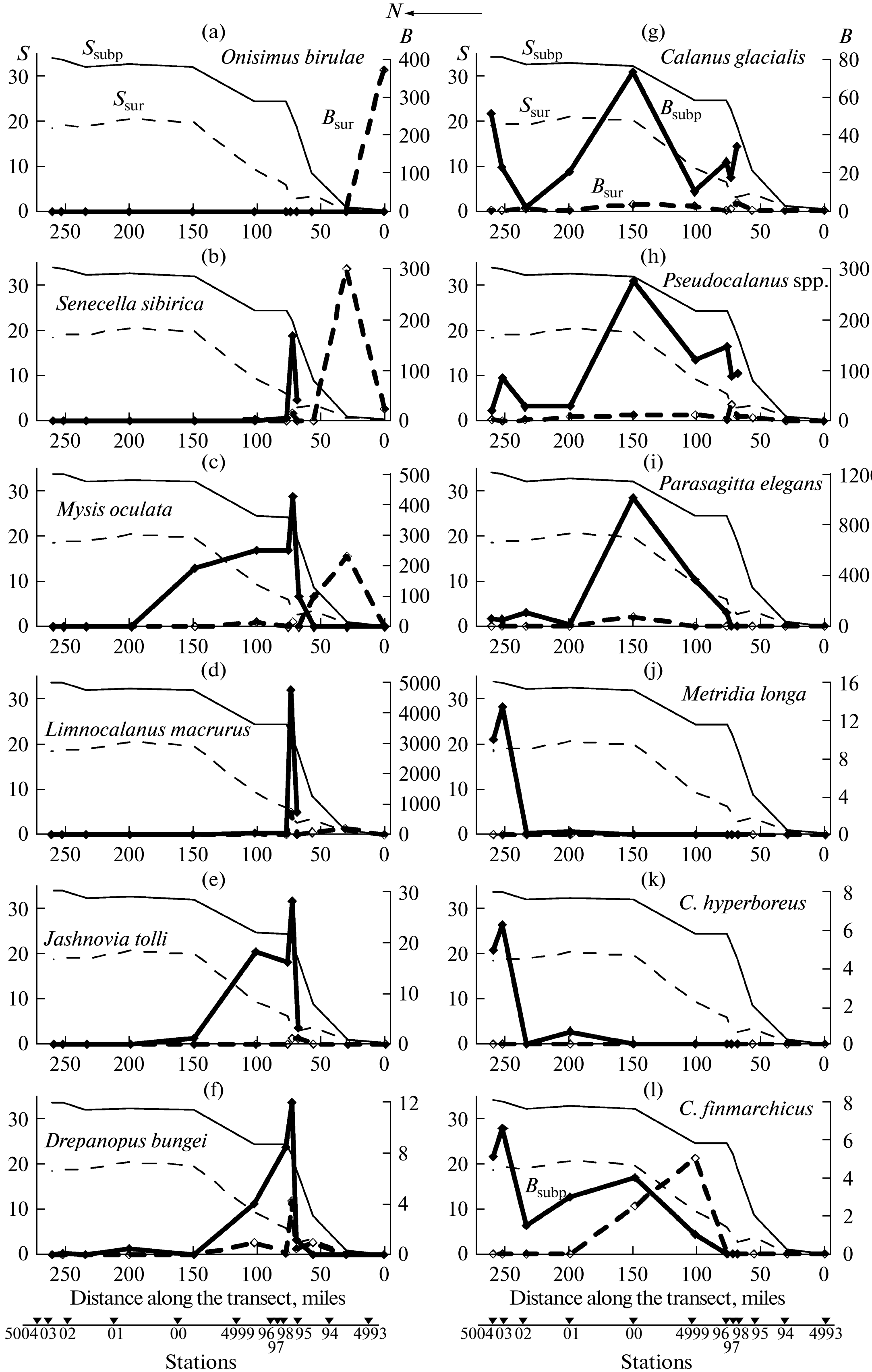

Fig. 5. Distribution of the biomass of the mass mesoplankton species (B, mg/m^3) in the upper mixed layer (dotted line) and below the pycnocline (solid line) and the salinity in the upper mixed layer (S_{sur}, psu) and in the layer below the pycnocline (S_{subp}, psu) along the transect.

Pseudocalanus spp. and *Parasagitta elegans* were not found.

The fifth distribution type included *Calanus hyperboreus* and *Metridia longa* (Figs. 5j–5k). During the studied period, their populations were confined exclusively to the subthermocline layers of the water column. The maxima of these species' biomass were found in the northernmost part of the studied region: seaward of the border of the inner shelf (stations 5003–5004) with the salinity near the bottom ranging from 33.5 to 34.0 psu, while the temperatures declined to −1.3 to −1.5°C. Solitary specimens of *C. hyperboreus* and *M. longa* were found at the inner shelf up to station 5001, while the plankton of the estuarine frontal zone was devoid of these species.

A specific type of distribution differing from that of all the other species was exhibited by *Calanus finmarchicus* (Fig. 5l). This species was found at the inner shelf and the northern part of the estuarine frontal zone. In general, its biomass was low, reaching 6–7 mg/m^3 in the maxima. In the frontal zone, the population of *C. finmarchicus* also dwelled in the upper mixed layer and below the pycnocline; at the shelf, only deeper than pycnocline. The southern border of the distribution of this species was connected in the surface layers with salinity of 6–10 psu; below the pycnocline, 22–24 psu.

DISCUSSION

The data presented here allow for the characterization of the range of the important structural parameters of the Ob estuary mesoplankton community and the adjacent regions of the inner Kara Sea shelf. It is worth noting that these characteristics relate to the fall period of the seasonal succession of the Kara Sea ecosystem, when the stage of intensive reproduction and growth in the majority of the populations of the mass species is over.

Another important feature of the autumn season concerned the sharp decrease in the riverine discharge into the Kara Sea. In the Ob River, at beginning of October, the discharge volume is about 50 km^3/month versus more than 100 km^3/month in June–July [26]. According to the estimates given in [27], the difference in the flow volume between the autumn months and summer maximum is estimated at 1000–1200 and 2800–4200 m^3/s, respectively. The low intensity of the fall discharge determines the seasonal specificity of the most important properties of the pelagic environment: the distribution of the salinity and temperature and their latitudinal gradients in the region of the interaction of the riverine and sea waters in the Ob estuary, the latitudinal extension of the estuarine frontal zone, the positions of their southern and northern borders, the character of the vertical stratification, and the vertical gradients of the properties. In turn, this specificity affects the structure of the planktic communities.

During the studied period, the mesoplankton communities of the estuarine zone and the adjacent shelf region in general had a composition and dominant groups of species typical for this region of the Kara Sea [3, 5, 9, 19, 20]. It is only worth noting that, in our materials, the abundance of the copepod *Drepanopus bungei* was relatively low, while, according to the earlier studies, it was one of the dominant mesoplankton species both in the inner desalinated part of the Ob estuary and in the estuarine frontal zone [5, 19, 20]. Such differences cannot be explained by the different observation times and the seasonal state of the mesoplankton communities. The data referred to above and used for the comparison concern September, i.e., in fact the same time period as ours. Presumably, the low abundance of *D. bungei* in 2007 reflects the possible interannual differences (most important, the changes in the composition of the dominant group of species) in the structure of the mesoplankton communities of the Ob estuary.

The region of the estuarine frontal zone was characterized by relatively high concentrations of mesoplankton. This was also reflected in the mean for the whole water column values of the biomass (table; Fig. 3a) and especially in the distribution of the biomass as assessed separately for the layers above and below the halo/pycnocline (table; Figs. 3b, 3c). The mean values of the biomass in the water column of the frontal zone reached 984 mg/m^3, i.e., were 1.5 times higher than in the desalinated part of the estuary and six times higher than in the adjacent regions of the inner Kara shelf. Even more pronounced differences were observed in the values characterizing the quantitative distribution of the mesoplankton in the layer below the halocline. The mean mesoplankton concentration under the halocline in the frontal zone reached 2.1 g/m^3; i.e., it was three and ten times, respectively, higher than the relevant values in the desalinated region and shelf (table).

The values given above, along with the data presented in the table and in Figs. 3a and 3c, show that, in the region where the vertical salinity stratification of the water column was formed (i.e., north of the southern periphery of the estuarine frontal zone north of station 4995), the main part of the mesoplankton during the studied period was concentrated in the layer under the pycno/halocline. The aggregations of mesoplankton below the jump layer particularly determined the general pattern of the mesoplankton's quantitative distribution, in which the relative richness of the frontal zone was evident.

The values of the mesoplankton's biomass in the estuarine frontal zone revealed in our study are close to those revealed by Vinogradov et al. [5] in September 1993. In this study, the frontal zone was also marked as the richest in the western half of the Kara Sea, and the biomass for the water column on average ranged from 0.99 to 4.3 g/m^3. At the same time, the values for the inner desalinated part of the Ob estuary given in paper [5] were considerably lower than in our own observations (table): 160 mg/m^3; the values for the regions of the inner shelf adjacent to the estuarine zone were slightly higher, 200–350 mg/m^3. The data given in [5] also show that, in fact, everywhere the main mass of the mesoplankton was confined to the water layer below the pycno/halocline. According to the integral assessments [27], the region of the interaction of the riverine and sea waters in the Ob estuary is inhabited by the mesoplankton community richest in biomass among the communities of the southern and central parts of the Kara Sea. Based upon the data averaged for several years, the authors indicate for this region a biomass value of 710 mg/m^3, which is six times higher comparing to the inner desalinated part of the estuary (120 mg/m^3) and three times higher comparing to the Kara shelf (271 mg/m^3).

The biomasses of mesoplankton related to the estuarine frontal zone (first of all, the inner southern periphery) are especially noteworthy. According to our observations, there the biomass's average for the water column reached 3.1 g/m^3 (37 g/m^2), while, in the layer below the pycnocline, it was 5.8 g/m^3 (Fig. 3). The data given in Figs. 3b and 3c shows that the maximum was formed mainly as a result of the local enrichment by mesoplankters of the water layer located deeper than the pycno/halocline, and this maximum had very little latitudinal extension (less than 9 miles). Most likely this assessment is overestimated and was determined by the distance between stations 4996 and 4998, i.e., respectively, north and south of station 4997 where the biomass values were maximal. The mesoplankton biomass in the maximum was five and ten times higher than at the neighboring stations 4996 and 4998. The former value was three, 4.5, and 19 times higher than the average biomass values in the region of the estuarine frontal zone, the desalinated river zone, and the inner shelf, respectively. The projection of the quantitative distribution of the mesoplankton over the structure of the salinity field shows that the biomass maximum was spatially related to the narrow region of the maximal latitudinal salinity gradients at the southern "riverine" periphery of the estuarine frontal zone (Figs. 3 and 4). In the same region, the vertical salinity gradients in the pycnocline reached maximal values (Fig. 4b), indicating the active processes facilitating the stratification of the water column. The main maximum of the mesoplankton biomass at the southern periphery of the frontal zone coincided with the salinity of 22.3 psu in the layer under the pycnocline and 3.4 psu in the upper mixed layer.

The second (having lesser biomass) maximum of the mesoplankton was registered in our study at the northern periphery of the estuarine frontal zone (station 5000). In this maximum, the biomass (1.1 g/m^3 on average for the water column or 25.5 g/m^2 and 2.3 g/m^3 in the subpycnocline layer) was considerably lower than in the "southern" one. This maximum was also connected to the area of increased latitudinal salinity gradients in the surface and near-bottom layers (Fig. 5).

The only earlier study describing the local maximum of the mesoplankton biomass related to the Ob estuarine frontal zone is published in [5]. According to the data of this paper, the average for the water column biomass reached 4.3 g/m^3 (65.3 g/m^2), but, due to the long distance between the stations, the latitudinal extension of the area enriched by the mesoplankton may be roughly assessed as being less than 50 miles. Detailed simultaneous hydrophysical observations were not carried out in this study. However, the given values of the salinity suggest that, as in our study, the main maximum of the biomass was confined to the southern periphery of the frontal zone. The salinity values in the area of the maximum were close to those registered in our the study: 1.3–4.8 psu in the surface layer; 11.4–20.0 psu below the pycnocline.

As we have shown above, the dominant mesoplankton species fall into several groups according to the pattern of the quantitative distribution (Fig. 5). The basis of the community inhabiting the Ob estuarine frontal zone is composed by the biomass of the brackish water species of the copepods *Senecella sibirica*, *Jashnovia tolli*, *Limnocalanus macrurus*, and *Drepanopus bungii* and the mysid *Mysis oculata* possessing different levels of tolerance to dwelling in the fresh and highly saline (sea) waters. These species are well known as mass species in the area of the mixing of the riverine and sea waters in the Kara Sea [3, 5, 19, 20, 27]. However, our study revealed for the first time that, for the vast majority of these species, except for *S. sibirica*, the frontal zone in particular serves as the main biotope (Fig. 5). Thus, our study makes it possible to indicate the presence of the typical for the autumn brackish water community in the Ob estuarine frontal zone. The formation of the specific composition of the mesoplankton in the frontal zone distinguishes it from the phytoplankton community of this area: during the studied period, the later had no brackish water status different from the communities of the areas adjacent to the south and north. The phytoplankton of the frontal zone represented a mixture of freshwater and marine species in ratios changing in the direction from the south to north depending on the specific salinities [13].

In addition to the species listed above, marine species contributed greatly to the community of the estuarine frontal zone. Considerable amounts of such species penetrated into the area with lower salinity. These were the copepods *Calanus gracilis*, *Pseudocalanus* spp. and the chaetognath *Parasagitta elegans*. The species most abundant in the frontal zone played different roles in the formation of the biomass maximum at its southern and northern peripheries.

The maximum with highest values of the mesoplankton biomass at the southern periphery of the estuarine frontal zone was built exclusively by brackish water species (Figs. 5b–5f) that predominantly were herbivorous and detritivorous. The herbivorous copepod *Limnocalanus macrurus* with biomass of 4.8 g/m^3 (83% of the total mesoplankton biomass) played the leading role in the maximum. This maximum was formed in the area directly neighboring the area of high phytoplankton biomass adjacent to the border of the frontal zone to the south (Fig. 4a) [13]. This suggests that the allochthonous phytoplankton delivered by the riverine flux that concentrated at the southern frontal border and penetrated the southern part of the frontal zone [13] most likely served as a main source of food for the animals forming the southern frontal maximum of the biomass. Here, at the southern frontal border of the estuarine frontal zone, the pelagic biofilter is formed. Some part of the allochthonous organic matter carried by the riverine waters accumulates and precipitates in this filter.

The maximum of the mesoplankton situated 80 miles seaward and connected to the northern periphery of the estuarine frontal zone had another structure. This maximum was formed mainly by several mass marine species contributing up to 75% (1.7 g/m^3) to the total biomass (Figs. 5g–5i). The predatory chaetogtnath *Parasagitta elegans* with biomass above 1 g/m^3 and accounting for 46% of the total biomass played the leading role among these species. The small-sized copepods *Pseudocalanus* spp. composed the second group of species with their contribution to the community biomass of 0.55 g/m^3. Thus, in the mesoplankton maximum associated with the northern border of the estuarine frontal zone, the high concentrations of the mass predator and of its potential preys spatially coincided. It is worth noting that, in earlier studies, Chaetognatha were not mentioned as an important component of the mesoplankton communities of the Ob estuarine front [5, 19, 20, 27]. Most likely, this is because aggregations of predators occupy narrow zones and were not revealed in the studies when stations were separated by long distances and lacking preliminary detailed hydrophysical surveys allowing for the location of the planktic stations in the specific areas and frontal borders of the estuarine frontal zone.

What are the mechanisms responsible for the formation of the maxima of the mesoplankton biomass at the southern and northern peripheries of the Ob estuarine frontal zone? Most likely these mechanisms relate to the local specificity of the circulation owing to which the mesoplankton concentrates at the frontal borders, and these aggregations remain for a long time. The presented data on the distribution of the mesoplankton evidence that the peculiarities of the circulation related to the formation of high concentrations of animals are first of all characteristic of the water column below the pycnocline. The detailed hydrophysical survey of the southern periphery of the estuarine frontal zone carried our using the scanning CTD probe revealed the mesoscale anomaly in the structure of the salinity and temperature fields, which most likely relates both to the intensive vertical mixing and the formation of a narrow local quasienclosed circulation cell in the layer from the bottom to the pycno/halocline (Fig. 6). In space, this anomaly coincides with the location of station 4997, at which the maximum of the zooplankton biomass was recorded.

It is obvious that the formation of the high mesoplankton biomass within the narrow area at the southern periphery of the frontal zone was provided not only by the mechanical concentration of the animals. The spatially coinciding maxima of one group of species (e.g., the brackish water copepods *Limnocalanus macrurus* and *Drepanopus bungei* and the mysid *Mysis oculata*; Figs. 5c–5f) are accompanied by the absence of maxima of the other species (e.g., the abundant in the frontal zone mass marine copepods *Paracalanus* spp. and *Calanus gracilis* and the chaetognath *Parasagitta elegans*; Figs. 5g–5i). This indicates that the mechanism of the formation of the high local concentrations also includes behavioral adaptations allowing for the animals to exploit the local specificity of the pelagic environment. This assumption is confirmed by the fact that, in the area of the local mesoplankton maxima, neither the relevant maxima of the components of the passive suspension [2] nor of the phytoplankton [13] were found. To understand in detail the mechanisms responsible for the formation of the patterns of the quantitative distribution of the mesoplankton in the estuarine frontal zone and at its periphery, it is necessary to carry out careful spatial–temporal synchronous studies of the environment and biota in this region.

The structure of the mesoplankton communities in the Ob estuarine frontal zone resembles in many aspects the patterns characteristics to other types of fronts: the coastal tidal front, the front associated with the continental slope, and the front formed in the shelf regions as a result of interaction of quasi-stable currents [4, 15, 16, 22, 23, 31]. The main common feature of these fronts is the presence of a narrow area enriched in the herbivorous zooplankton directly neighboring or partially overlapping the area of the high phytoplankton biomass and production. This determines the constant during the vegetation season high availability of food for the secondary producers and consequently the high local secondary production [15, 22]. The characteristic scales of the zooplankton maxima associated with the front (no more than 5–10 miles wide) are also similar, as well as the 2.5 times to one order higher maximal "frontal" biomass values compared to the background values typical for the adjacent areas. In all the types of fronts listed above, the formation of the maxima of the phytoplankton (primary production) and the zooplankton is determined by the local specificity of the vertical circulation: the close proximity of the zones of divergence (water lifting) associated with the fronts where the euphotic layer is enriched with nutrients and convergence where the plankton concentrates [15, 16, 22, 23].

The plankton community of the southern periphery of the Ob estuarine frontal zone substantially differs from the communities of the types of frontal zones listed above. The difference concerns the fact that the high biomass and production of the phytoplankton in the area of the estuarine front is of allocthonous but not autochthonous origin and is transported to this area with the riverine flux [13]. One more difference concerns the relative position in space of the maxima of the herbivorous and predatory mesoplankton. In the zones of the shelf tidal fronts and slope frontal zones, these maxima always coincide and overlap [15, 21, 22]. In the frontal areas, as a rule, chaetognaths are the mass planktic predators and their local biomass during the second half of the vegetation season is comparable (in some cases higher) to the total biomass of the herbivorous mesoplankton. According to our observations, the maximum of the predators' biomass also composed of Chaetognatha was spatially disconnected with the main maximum of the herbivorous mesoplankton. The former maximum was located 80 miles south lying at the northern periphery of the estuarine frontal zone. However, it was associated with the second in size northern maximum of the biomass of the herbivorous plankton, which was formed by the mass marine herbivorous copepods (Figs. 5h, 5i). Most likely, the reasons of such seaward shifting of the predators' maximum relate to the high latitudinal changes of the salinity within the wide estuarine frontal zone and to the conditions hardly appropriate for the Chaetognatha near its southern border, where the biomass of the herbivorous mesoplankton reaches its maximum due to the species tolerant to low water salinity.

Our data presented here and in [1] allow for the assessment of the grazing of the present phytoplankton biomass and of the primary production by the herbivorous zooplankton within the narrow area of the frontal maximum at the southern part of the Ob estuary. During the studyied period, the biomass of the phytoplankton at station 4997 (Fig. 4a) averaged 262 mgC/m^2 for the water column and the primary production, 11.1 mgC/m^2 per day [13]. The value of $I_{spec.} = 0.328$ [1] calculated for the large-sized species of herbivorous mesoplankton mainly forming the frontal maximum and their total biomass in the area of the maximum (25 g/m^2 wet weight or 2.5 gC/m^2) at using the calculation coefficient [28] give the assessed value of the daily grazing equal to 820 mgC/m^2 day. This value is almost two orders higher than the daily primary production observed during the studied period. The present biomass of phytoplankton at such a rate of consumption would be utilized by the primary consumers in less than eight hours (!). Thus, during the studied period, massive aggregations of herbivo-

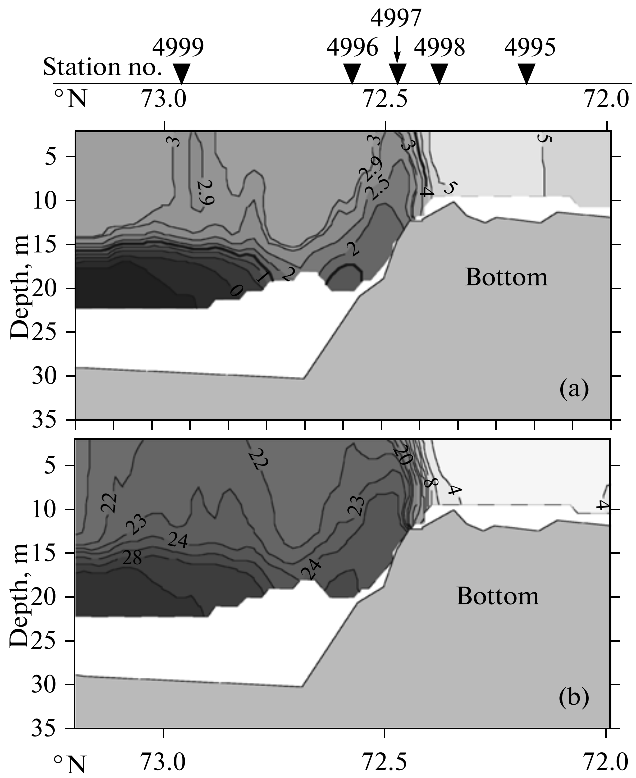

Fig. 6. Distribution of the temperature (a) and salinity (b) in the region of the southern periphery of the estuarine's frontal zone.

rous mesoplankton at the southern periphery of the estuarine frontal zone can not exist without adequate "doping" by organic material appropriate for feeding. Most likely such "doping" originates from the advection of the phytoplankton into the narrow area of the frontal maximum of the mesoplankton from the adjacent riverine zone, where the phytoplankton biomass is more than one order higher reaching 1.92–4.35 gC/m^2 during the studied period [13].

All the facts given above allow for the conclusion that the aggregations of herbivorous mesoplankton form in the Ob estuarine frontal zone a specific pelagic biofilter. This filter accumulates allochthonous organic matter, first of all, the phytoplankton transported by the riverine flux, and produces on its basis high biomass (secondary production), and, at depths of 12–15 m, considerably accelerates the transition through the fecal fluxes of allochthonous organic matter to the sediments. This pelagic biofilter is associated with the area of maximal latitudinal gradients of the salinity at the southern periphery of the estuarine frontal zone. The aggregations of herbivorous mesoplankton near the northern seaward periphery of the estuarine front had six times lower biomass and, hence, played a less important role as a pelagic biofilter. In this region, conditions for the intensive consumption of the secondary production by planktic predators were formed.

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