ISSN 0001-4370, Oceanology, 2015, Vol. 55, No. 4, pp. 583–594. © Pleiades Publishing, Inc., 2015.
Original Russian Text © M.V. Flint, S.G. Poyarkov, A.G. Timonin, K.A. Soloviev, 2015, published in Okeanologiya, 2015, Vol. 55, No. 4, pp. 643–655.

MARINE BIOLOGY

The Structure of the Mesoplankton Community in the Area of the Continental Slope of the St. Anna Trough (Kara Sea)

M. V. Flint, S. G. Poyarkov, A. G. Timonin, and K. A. Soloviev

Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, 117218 Russia
e-mail: m_flint@orc.ru

Received June 14, 2014

Abstract—Zooplankton samples and concomitant hydrophysical data have been obtained in the outer Kara shelf over the continental slope and adjacent deepwater region of the western spur of the St. Anna Trough in the last ten days of September in 2007 and 2011. Mesoplankton biomass in the examined regions in 2007, the warmest year of the last three decades, was 1.5–2 times higher than the relatively cold year of 2011. A frontal zone, distinct in temperature, salinity, and chlorophyll fluorescence in the surface sea layer was located over the continental slope. The temperature gradient in the frontal zone reached 0.25–0.67°C/km, and its salinity gradient reached 1.6–4.7 psu/km. An increase in mesoplankton biomass was associated with the frontal zone, which was especially pronounced in the upper layers of the water column. The average biomass content in the upper 50 m in the frontal maximum amounted to 1210 mg/m^3 in 2007 and 972 mg/m^3 in 2011, being two orders of magnitude higher than the outer shelf and the deepwater domain of the basin. The pteropod *Limacina helicina* was dominant at the slope maximum, accounting for up to 80% of mesoplankton biomass. The frontal zone over the slope also represented a distinct boundary separating the shelf mesoplankton community from the deepwater community, which drastically differed in composition and biomass.

DOI: 10.1134/S0001437015040062

The Kara Sea is among the best studied of the Siberian Arctic seas, as is the zooplankton of the basin. The species composition of the mesoplankton in different seas of this region, its biomass, and the spatial variation in quantitative parameters of these communities have been comprehensively described by Yashnov [29, 30], Khmyznikova [24–27], Bernshtein [2], Ponomareva [12], and in more recent studies by Fomin [21–23], Zubova [9], Vinogradov et al. [3], Hirche et al. [36], and Nesterova and Orlova [11]. However, despite the abundance of data relative to other Siberian seas, our knowledge about the structure of the mesoplankton communities in several key regions of the Kara Sea, first and foremost the Ob and Yenisei estuarine regions and the continental slope in the area of the St. Anna and Voronin Troughs in the north of this basin, lacks necessary detail. Characteristic of these regions is the high spatial heterogeneity of the pelagic environment, which significantly influences the composition and, most importantly, the trophic characteristics and productivity of plankton communities [19, 20, 35, 43]. The listed features are most frequently evident on spatial scales of 10–20 km or less, yet they have a tremendous effect on the functioning of marine ecosystems [18, 32, 35]. The discovery of these features requires not only a considerably more comprehensive analysis of the plankton communities as compared with the routinely used surveys, but also a concurrent assay of the physical properties of the pelagic environment, allowing for the assessment of the correlation between environmental features and biota, which determines the unique local properties of the pelagic communities. Studies utilizing this approach have been recently conducted in the Ob and Yenisei estuarine regions. This has made it possible to discover the accumulation of herbivorous mesoplankton with a biomass that exceeds the level in the background region of the Kara Sea shelf by five to ten times and forms unique "biological filters" for allochthonous substances delivered by river runoff as well as suggesting the stable association of these aggregations with certain regions within the estuarine frontal zones [1, 6, 7, 19].

Plankton communities in the area of the continental slope of the St. Anna Trough have remained almost unexamined. Data from individual stations of this region in the Kara Sea [2, 11, 21, 36] only demonstrate a change in zooplankton composition at the interface between the shelf and the deepwater domain of the basin. However, an increase in plankton biomass and productivity is characteristic of slope regions in ocean [15, 18, 31, 32, 35, 43], which has not been found so far in the Kara Sea. According to available data, modified Atlantic water from the north intensively flows into the western spur of the St. Anna Trough [14, 42, 44]. This is also confirmed by zooplankton distribution [24]. Note that certain data suggest that the summer flow in this region has an opposite direction, from southwest to northeast, i.e., from the Kara basin to Arctic [39, 40]. The role of hydrophysical processes on the slope of the St. Anna Trough in the interaction between the Arctic shelf and the deepwater basin eco-

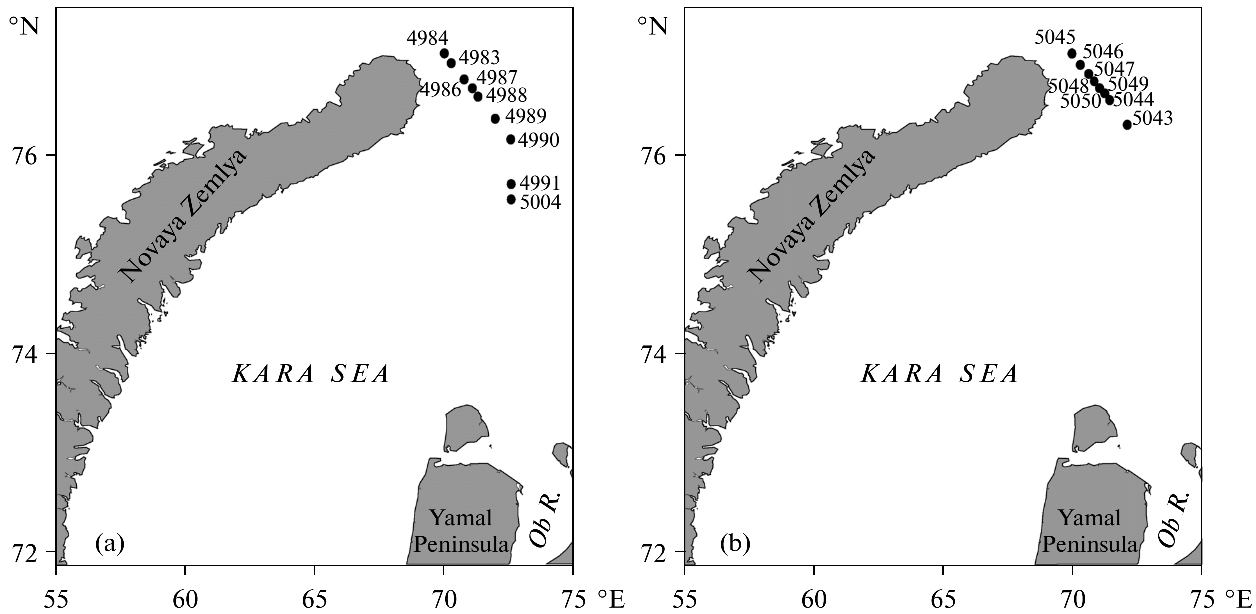

Fig. 1. Location of the transects and stations in (a) 2007 and (b) 2011.

systems and the inflow of the Arctic and Barents Sea plankton fauna to the Kara Sea is still unclear, as is the sharpness of the boundary between the mesoplankton community of the shelf and the deepwater domain. It is also unclear whether processes associated with the continental slope influence biological productivity.

The goal of this work was to study the structure of mesoplankton communities and estimate its connection with the structure of hydrophysical fields and hydrophysical processes over the continental slope in the western spur of the St. Anna Trough.

INVESTIGATED REGION, MATERIALS, AND METHODS

The examined region comprised the continental slope and adjacent shelf and deepwater domains in the western spur of the St. Anna Trough in the north of the Kara Sea (Fig. 1). The material was collected on September 23–30, 2007 and September 28–29, 2011. Depths in the examined area varied from 120–140 m over the outer shelf to 510–545 m in the deepwater domain of the trough. In 2007, the plankton was sampled with a Juday net (mouth area of 0.1 m^2 and 180 μm net mesh), and in 2011, with a MultiNet sampler (mouth area, 0.125 m^2; five nets with 180 μm mesh). Water volume filtered through the net was assessed according to the covered distance in 2007, and in 2011, with a water flow-meter. The sampling covered the overall water column from the surface to bottom by layers of 0–50, 50–100, 100–200, 200–300, 300–400, and 400–500 m (bottom). The samples were fixed with a 4% formaldehyde solution and examined according to a standard protocol in a Bogorov chamber [37] using a binocular microscope with identification to the level of species or genus and body-length measurement. Individual wet weight of the animals for the subsequent calculation of population biomass and total wet biomass of the community was assessed using the correlations between the body length and weight for individual species and groups [5] and Chislenko nomograms [28].

The associated data on temperature and salinity distributions in the water column were obtained from vertical CTD profiling (SBE 911 probe) at the stations [8]. Flow rates were calculated by the geostrophic method. The temperature, salinity, and chlorophyll fluorescence in the surface layer were constantly recorded using a SeaBird SBE911 CTD complex and flow fluorometer.

RESULTS

Oceanographic conditions. We regard the following specific features in the hydrophysical structure and dynamics as important for explaining the specific features in mesoplankton composition and quantitative distribution in the examined region. A significant local decrease in the temperature of the upper mixed layer (UML) was observed over the upper part of the trough over the continental slope. In 2007, the UML temperature over the outer shelf was 3.0–3.5°C, it decreased to 0.4°C over the slope, and it rose again to 2.1–2.7°C over the outer part of the slope (Fig. 2a). The pattern observed in 2011 was similar. The corresponding values were somewhat higher despite the fact that 2011, in its climatic and ice conditions, was in general colder than 2007 [41]. Surface sea temperature in 2011 over the shelf reached 5.6°C and sharply changed over the

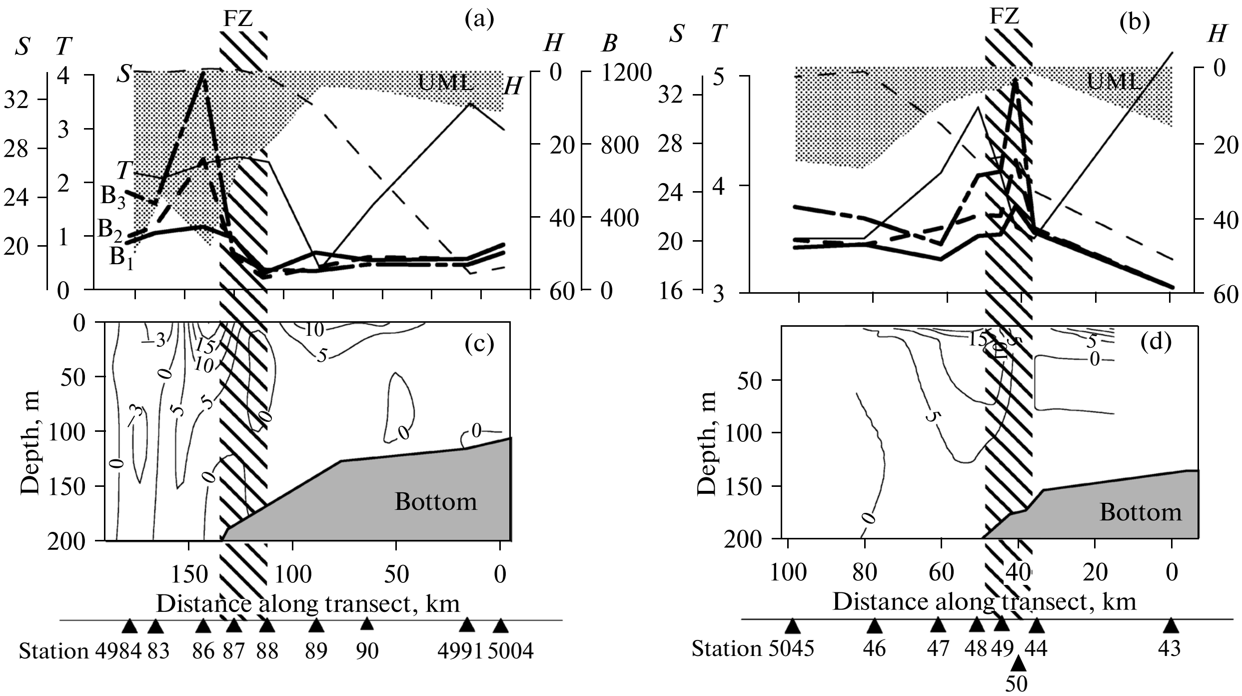

Fig. 2. Distribution of average mesoplankton biomass (B, mg/m^3) in the 0 m–bottom (B_1), 0–100 m (B_2), and 0–50 m (B_3) layers; surface temperature (T, °C); surface salinity (S, psu); and changes in the depth of the upper mixed layer (H, UML) in the transects of (a) 2007 and (b) 2011. Directions and speeds of flow during mesoplankton sampling in (c) 2007 and (d) 2011. FZ, frontal zone.

slope, initially decreasing to 3.1°C and then rising to 4.5–4.7°C 4 km to the north (Fig. 2a). The surface temperature in the deepwater domain of the trough was 3.5–3.6°C. The latitudinal width of the region with a minimum UML temperature was narrow; it was estimated as 20–30 km in 2007 and more precisely as 10–15 km in 2011 on the basis of to a continuous recording of the parameters. In both years, UML depth over the slope was considerably reduced, as compared with the adjacent regions (Figs. 2a, 2b). In 2007, it amounted to 4 m and in 2011, 2–4 m. Note that the UML depth to the south over the outer shelf was 12–16 m and increased to 25–50 m in the deepwater domain to the north of the slope. The salinity in UML over the shelf break and the slope in both years increased gradually from 17.0–18.0 PSU, characteristic of the northern shelf region, to 33.5–34.3 PSU in the adjacent deepwater domains.

The geostrophic flow patterns of 2007 and 2011 were similar (Figs. 2c, 2d). At the surface layer of 0–50 m, a consolidated stream of the northeastern transfer, with a core speed of over 20 cm/s, was observed along the isobath lines of 200–300 m. The flow in the upper (25–50 m) layer over the shelf, with depths of 120–150 m, was also directed to the northeast but had a slower speed of 10–15 cm/s. The flows were separated by a narrow zone with a width of approximately 10–20 km and a southwestern counterflow, more pronounced in 2011 [8].

The distribution of the total mesoplankton biomass in the water column displays a distinct trend of increase with depth from south to north. In 2007, fresh biomass content in the outer shelf varied in the range of 14.0–18.5 g/m^2, increased over the continental slope to 80.5–139 g/m^2, and amounted to 129.6–161.5 g/m^2 in the adjacent deepwater domain (Fig. 3a). The corresponding values for 2011 were somewhat lower. A single observation for the outer shelf gave an amount of 5.3 g/m^2 (Fig. 3b). According to a detailed sampling over the continental slope, the minimum and maximum biomasses were 39.5 and 60.5 g/m^2. Biomass rose to 102–104 g/m^2 in the deepwater domain of the trough.

The distribution pattern for mesoplankton biomass in the upper 100-m layer was quite different. In both years, latitudinal biomass distribution had a distinct maximum over the upper part of the slope, which reached 720 mg/m^3 in 2007, versus a biomass of 71–250 mg/m^3 over the outer shelf and 293–351 mg/m^3 in the deepwater region. In 2011, the biomass at the slope maximum and total biomass in the water column were lower than in 2007, amounting to 580 mg/m^3 over the slope, 40 mg/m^3 in the outer shelf, and 219–240 mg/m^3 in the deepwater region.

The vertical distribution of mesoplankton biomass also had specific features in the region of continental slope. In 2007, mesoplankton biomass over the slope (station 4986, Fig. 4) in the upper 50-m layer reached a

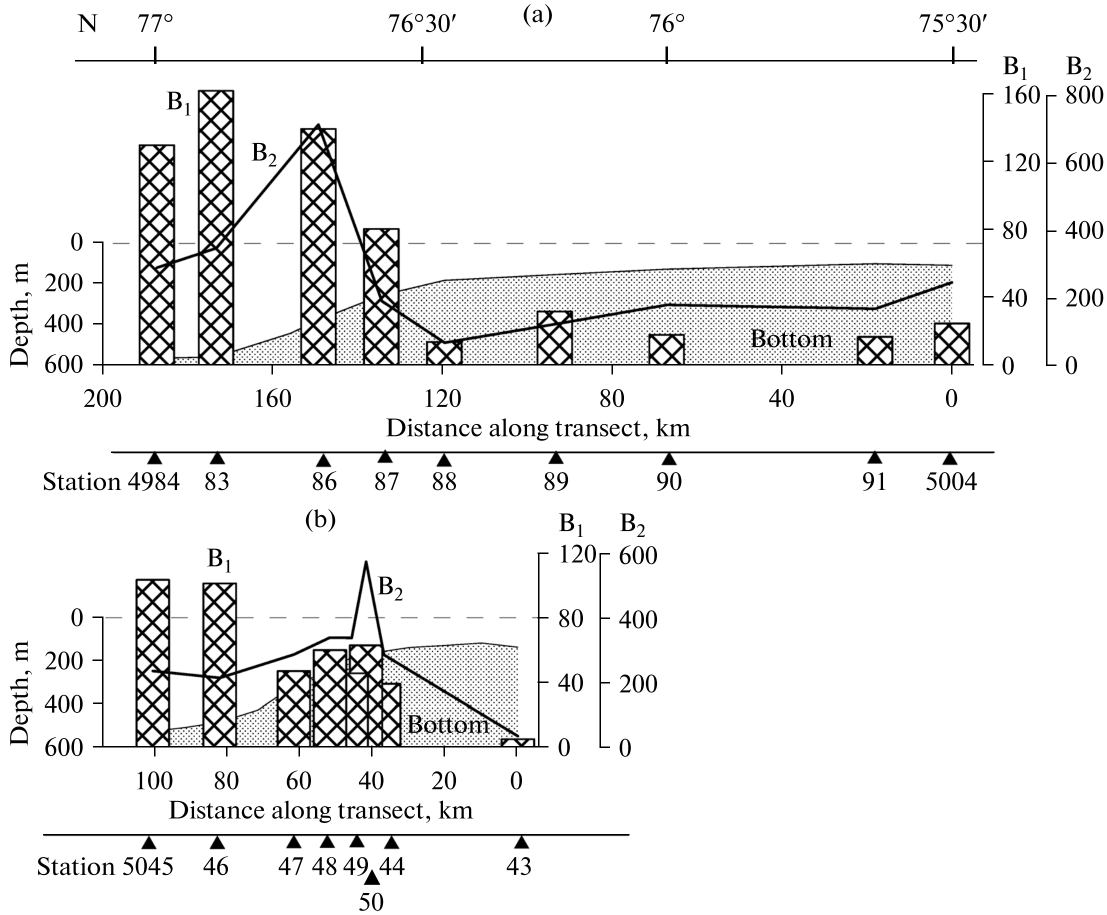

Fig. 3. Distribution of the total biomass of mesoplankton in the water column (B_1, g/m^2) and average biomass in layer 0–100 m (B_2, mg/m^3) over the outer shelf, continental slope, and in adjacent deepwater domain of the western spur of the St. Anna Trough in (a) 2007 and (b) 2011.

maximum value for the examined section, 1190 mg/m^3, but did not exceed 250 mg/m^3 in the deep layers. The outer shelf and deepwater domain displayed the pattern of vertical mesoplankton distribution typical of an early fall, namely, biomass contents in the surface and deep layers of the water column were close or almost equal. Only the upper layers over pycnocline in the southern outer shelf (stations 4991 and 5004, Fig. 4) were extremely poor (less than 15 mg/m^3), while maximum biomass, 200–220 mg/m^3, was observed under the pycnocline. In 2011, at all stations over the slope, the upper 50-m layer was considerably enriched with the mesoplankton as compared with the deepwater layers (stations 5044 and 5048–5050, Fig. 5). Here, maximum values for the transect were observed and biomass varied from 800 to 1260 mg/m^3; however, biomass was only 60 to 120 mg/m^3 at the deep layers. Besides the slope, such a mesoplankton distribution pattern was observed only at one station, the deepest, station 5045 (Fig. 5). The vertical mesoplankton distribution on the shelf (station 5043) was uniform, and the biomass was almost equal in all water layers.

Distribution of dominant mesoplankton species. Most of the mesoplankton biomass (>80%) in the examined Kara Sea area was represented by the copepods *Calanus glacialis*, *C. finmarchicus*, *C. hyperboreus*, *Pseudocalanus* sp., and *Metridia longa*; chaetognaths *Eukrohnia hamata* and *Parasagitta elegans*; appendicularia *Oikopleura vanhoeffeni*; and pteropod *Limacina helicina*. Individual contributions of these species to total biomass in different years varied but their distributions displayed several common features.

Calanus glacialis. In 2007, this species was absolutely predominant in the biomass of the mesoplankton community in the deepwater domain of the St. Anna Trough and over the slope (Fig. 6a). Its total biomass in the water column amounted to 25–60 g/m^2 and sharply decreased to 1.5–4.5 g/m^2 over the outer shelf. In 2011, *C. glacialis* biomass was lower than in 2007, and everywhere it was close to the biomasses of other dominant species of interzonal copepods (*C. finmarchicus* and *C. hyperboreus*. Biomass in the deepwater trough domain was 21–23 g/m^2 in the water column and, similarly to 2007, sharply decreased over the slope and shelf to 1.5–2.5 g/m^2 (Fig. 6d). On the background of this decrease, note the small (11.5 g/m^2) maximum over the upper part of the slope, which, as will be evident below, was to a greater or lesser degree

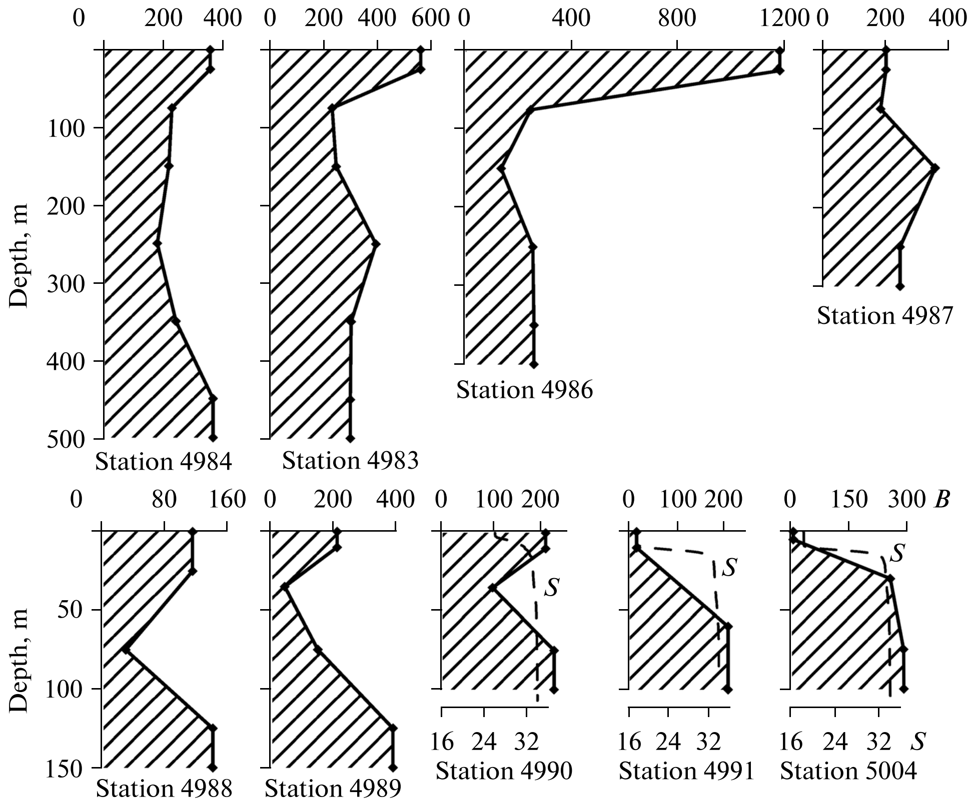

Fig. 4. Vertical distribution of salinity (S, psu) and total mesoplankton biomass (B, mg/m^3) in the water column at the stations of the transect in 2007.

also characteristic of the distributions of other dominant mesoplankton species in 2011.

Calanus finmarchicus. In 2007, the biomass of this species in the deepwater domain and over the lower slope was 14–23 g/m^2 and southward decreased to 0.5–1.0 g/m^2 (Fig. 6a). In 2011, *C. finmarchicus* formed the same distribution pattern with a close level of biomass. Population biomass in deepwater domain was 12–20 g/m^2 and decreased to 5.0–6.0 g/m^2 over the slope and to 0.5 g/m^2 over the shelf (Fig. 6d).

Calanus hyperboreus. In 2007, this species was distributed similarly to *C. finmarchicus.* Its biomass in both the deepwater domain and over the lower slope was 9–14 g/m^2 in the water column and to the south, decreased to 0.5–4.0 g/m^2 (Fig. 6a). In 2011, biomass in the deepwater domain varied from 5.0 to 16.0 g/m^2, and over the shelf it varied from 0.5 to 1.5 g/m^2 (Fig. 6d). Similar to *C. glacialis*, *C. finmarchicus* displayed a maximum (biomass, 7.2 g/m^2) over the upper part of the continental slope over the background of the distinct trend of a decrease in biomass from the deepwater domain to shelf.

Pseudocalanus sp. This group comprised several species (*P. minutes*, *P. acuspes*, and *P. major*), which are hardly distinguishable at IV and younger juvenile stages and were, correspondingly, pooled for mass assays. In 2007, the distribution of this group displayed a distinct peak with a biomass of 13.5 g/m^2 over the lower continental slope; however, biomass drastically decreased to 0.5–1.0 g/m^2 over the outer part of the slope and shelf break (Fig. 6c). Biomass amounted to 6.5–7.5 g/m^2 in the deepwater domain of the trough and to 3.5–7.0 g/m^2 over the outer shelf. In 2011, the *Pseudocalanus* sp. biomass in the deepwater region was 8.0–9.5 g/m^2 and decreased to <2.5 g/m^2 on the outer shelf (Fig. 6f). Similar to many other species, *Pseudocalanus* sp. formed a small but distinct peak (8 g/m^2) in the distribution of its biomass over the upper part of the continental slope. Presumably, we did not observe an increase in the *Pseudocalanus* sp. on the outer shelf in 2011 because of the insufficient southward extension of the transect. The shelf station was at a distance less than 40 km from the shelf break in the region where a distinct minimum of *Pseudocalanus* sp. biomass was observed in 2007. Our observations of 2007, which covered the southern part of the outer shelf and the inner shelf, have demonstrated that *Pseudocalanus* sp. was a significant contributor to the mesoplankton biomass of this region [19].

Metridia longa. This species diurnally migrated during the observation period with insignificant presence on the shelf. In 2007, the *M. longa* biomass in the deepwater trough domain and over the continental slope was 12.0–17.0 g/m^2 and sharply decreased to 0.1–

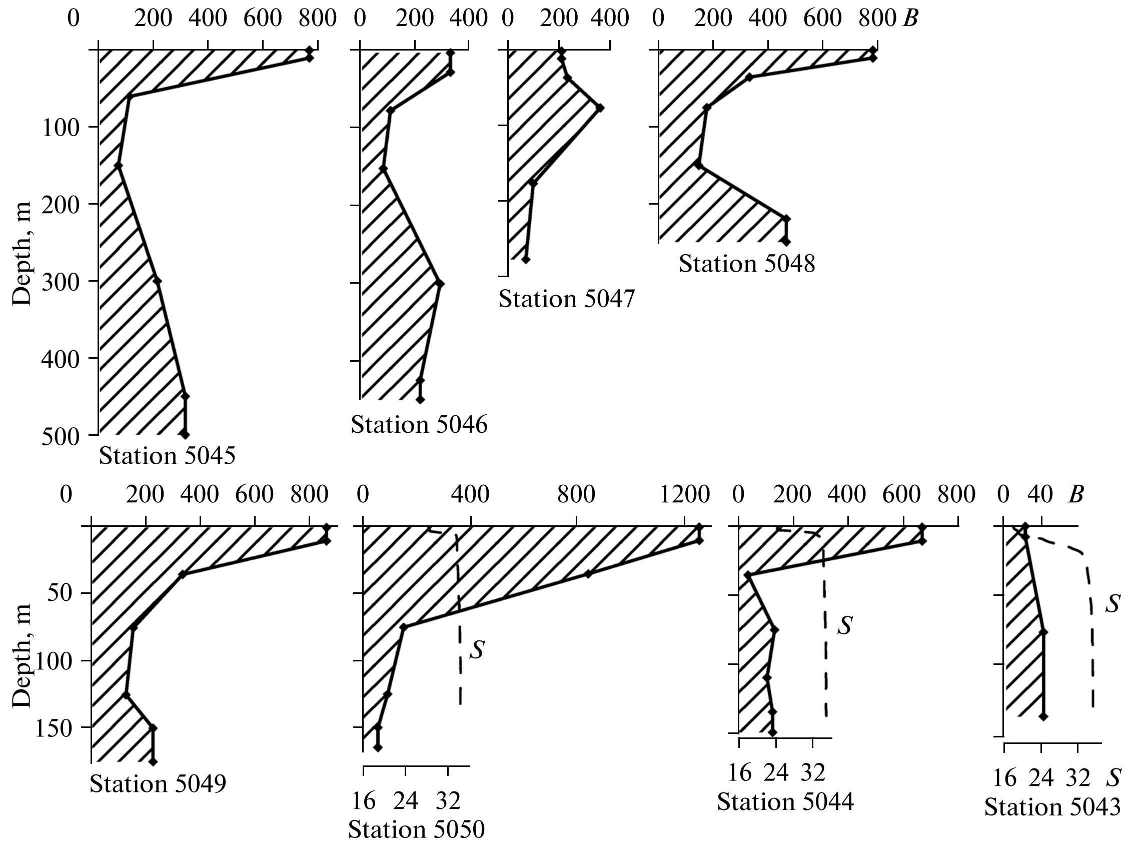

Fig. 5. Vertical distribution of salinity (S, psu) and total mesoplankton biomass (B, mg/m^3) in the water column at the stations of the transect in 2011.

2.0 g/m^2 over the shelf (Fig. 6a). In 2011, its biomass to the north of the slope amounted to 15.5–23.0 m^2; over the slope, to 4.0–9.5 m^2; and over the outer shelf, to 1.5–2.0 m^2 (Fig. 6d).

Eukrohnia hamata. In 2007 and 2011, this species had the same distribution patterns (Figs. 6b, 6e). Its biomass was maximal in the deepwater trough domain (4.0–5.0 g/m^2), decreased over the slope, and attained minimum values (<0.2 g/m^2) at the outer shelf boundary, disappearing to the south.

Parasagitta elegans displayed a different distribution pattern than *E. hamata*. In 2007, maximum biomass (7.0–8.0 g/m^2) was recorded over the lower part of the continental slope and decreased to 3.0–4.0 g/m^2 in the deepwater domain (Fig. 6b). To the south of the slope maximum over the uppermost slope part and the shelf break, *P. elegans* biomass sharply decreased to values minimal for the examined region (0.4–1.0 g/m^2) and again rose to 4.0–5.5 g/m^2 southward. In 2011, its biomass amounted to 2.0–2.5 g/m^2 in the trough and gradually decreased southward to 0.8–0.3 g/m^2 over the outer shelf (Fig. 6e). Over this background, a local biomass maximum (1.9 g/m^2) was present over the upper slope. The very low *P. elegans* biomass over the shelf in 2011 has the same explanation as that for *Pseudocalanus* sp.

Oikopleura vanhoeffeni displayed a similar distribution patterns in both years. Its biomass amounted to 1.5–2.5 g/m^2 in the deepwater domain of the trough and gradually decreased southward to 0.1–0.4 g/m^2 in the outer shelf (Fig. 6b, e).

Limacina helicina was the major contributor to the total mesoplankton biomass in the deepwater trough domain and over the continental slope (20–70%), yielding only to *Calanus glacialis* in 2007. In both years, the distribution of this species exhibited a distinct maximum over the continental slope (Fig. 6c, f). In 2007, the biomass in the slope maximum reached 23 g/m^2. The biomass sharply decreased to the south, reaching 0.1–0.3 g/m^2 over the outer shelf. In the deepwater domain of the trough, *L. helicina* biomass was 12–14 g/m^2. In 2011, the slope maximum in its distribution was even sharper, with biomass there reaching 43 g/m^2, while biomass in the adjacent slope regions was 22–24 g/m^2. In the deepwater domain, biomass varied from 10.0 to 15.0 g/m^2 and decreased to a minimal level of 0.1 g/m^2 over the outer shelf.

DISCUSSION

The considered data on zooplankton were obtained in the same region of the Kara Sea in two years differ-

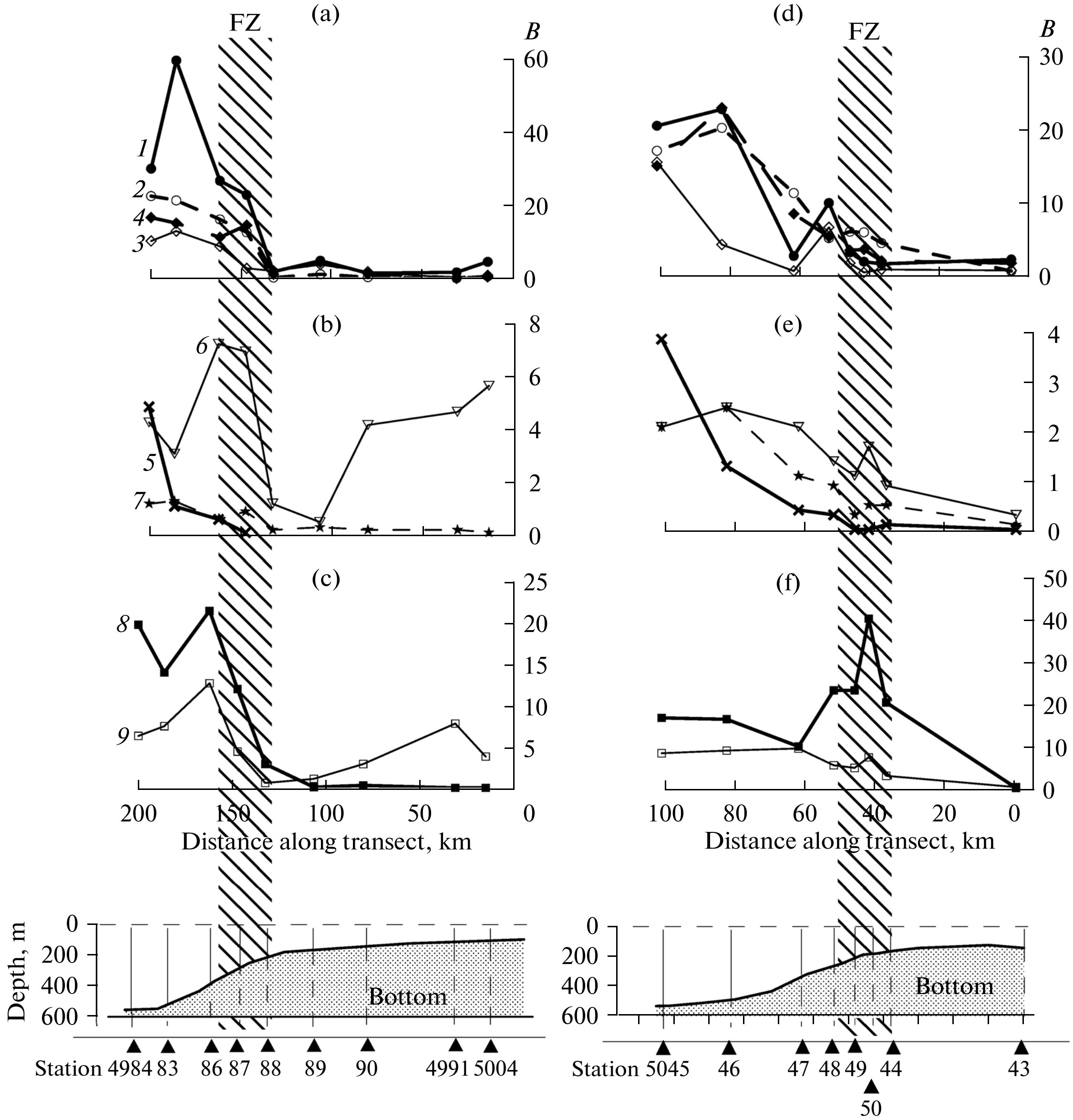

Fig. 6. Distribution of dominant mesoplankton species biomass in the water column (B, g/m^2) over the outer shelf, slope, and in adjacent deepwater domain of the western spur of the St. Anna Trough in (a–c) 2007 and (d–f) 2011: (*1*) *Calanus glacialis*; (*2*) *C. finmarchicus*; (*3*) *C. hyperboreus*; (*4*) *Metridia longa*; (*5*) *Eukrohnia hamata*; (*6*) *Parasagitta elegans*; (*7*) *Oikopleura vanhoeffeni*; (*8*) *Limacina helicina*; and (*9*) *Pseudocalanus* sp. FZ, frontal zone.

ing in their climatic and ice conditions [41]. This gives a unique possibility to assess interannual variation in the biomass and structure of the mesoplankton communities in the context of climate changes in the region. Long-term observations [41] have demonstrated that 2007 was one of the warmest years over the last decade (yielding only to 2012), with an early retreat of the ice edge and a significant shift in its summer boundary to the north, as compared with the long-term average annual position. The climatic conditions of 2011 were close to average for the last decade.

The total mesoplankton biomass in the water column in all three examined biotopes—the outer shelf, continental slope, and adjacent deepwater domain of the St. Anna Trough western spur—was higher in 2007 than in 2011. The average biomasses for these biotopes in 2007 were 21.3, 110.1, and 145.7 g/m^2, respectively, and in 2011, they were 5.3, 51.7, and 103.2 g/m^2. Analogous interannual differences in mesoplankton biomass were also observed in the upper 100-m layer, and amounted, in particular, to 160 mg/m^3 on the outer shelf, 457 mg/m^3 over the slope, and 324 mg/m^3 in the deepwater domain. The corresponding values for 2011 were 39, 373, and 227 mg/m^3. A characteristic feature for both years was maximum biomass over the slope (Figs. 3 and 7a).

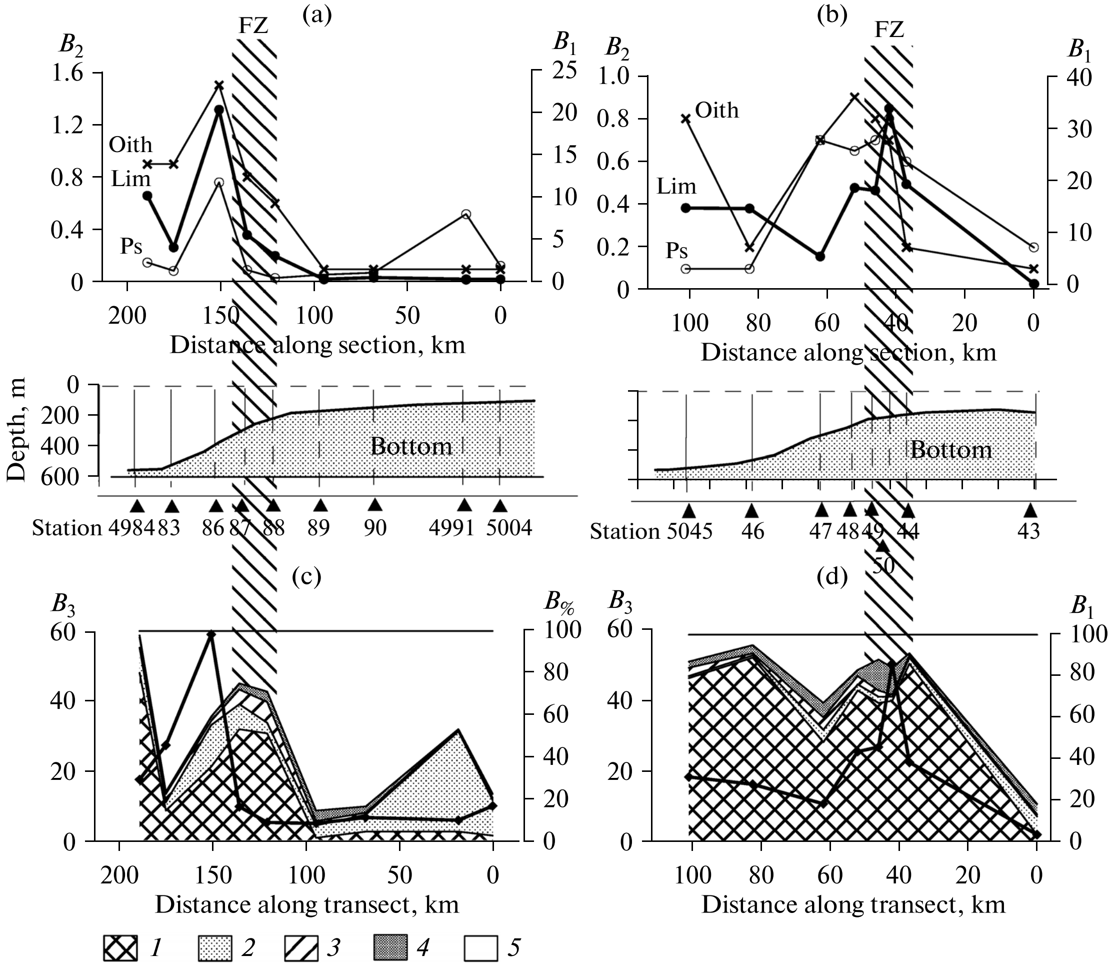

Fig. 7. Distributions of (a and b) for dominant species biomass (g/m^2) and (c and d) total mesoplankton biomass (g/m^2) and the relative contribution of dominant species to the total biomass (%) in layer 0–50 m: Ps, *Pseudocalanus* sp.; Oith, *Oithona* sp.; and Lim, *Limacina helicina*. (a) 2007; B_1, *Pseudocalanus* sp. and B_2, *Oithona* sp.; (b) 2011; B_1, *L. helicina* and B_2, *Pseudocalanus* sp. and *Oithona* sp.; (c) 2007; B_3, total mesoplankton biomass; and (d) 2011; B_3, total mesoplankton biomass: (*1*) *L. helicina*; (*2*) *Pseudocalanus* sp.; (*3*) *Oithona* sp.; (*4*) *Calanus* sp. juv.; and (*5*) the remaining species. FZ, frontal zone.

Mesoplankton composition in general, as well as the groups of species and forms making the largest contributions to the total biomass, was almost the same in the years differing in their climatic conditions. Note that no group of species was dominant in the biomasses. *Calanus glacialis* was the principal contributor to the total mesoplankton biomass in the water column in the relatively warm year of 2007. The population biomass of this species in the region of slope maximum reached 66 g/m^2, accounting for 13% of the total biomass (Fig. 6a). The next contributor was the pteropod *Limacina helicina*, with a biomass of 14.5–20.2 g/m^2, accounting for 8–16% of the total mesoplankton biomass (Fig. 6c). Under the average climatic conditions of 2011, the greatest contribution to the total community biomass was by *L. helicina*. Its biomass in the region of the slope maximum reached 24.2–41.5 g/m^2, accounting for 51–65% of the total mesoplankton biomass (Fig. 6f). Pteropod biomass, amounting to 47.5–52.0 g/m^2 over the slope, was close to the total biomass of three interzonal copepod species in the deepwater trough domain (Fig. 5d). In the upper 50-m layer, *L helicina* dominated in the biomass everywhere except for the outer shelf. This was determined not only by the high biomass of this species, but also because of the seasonal descent of dominant interzonal copepods to deeper layers. The share of *L. helicina* in the total mesoplankton biomass in layer 0–50 m of the deepwater domain and over the slope reached 40–82% in 2007 (Fig. 8c) and 55–87% in 2011 (Fig. 8d). In the observations of 2007, *Pseudocalanus* sp. was the dominant group over the outer shelf, accounting for up to 18–51% (Fig. 8c).

The temperature and salinity distributions in the area of the St. Anna Trough suggested the presence of a distinct frontal zone over the continental slope. This frontal zone is based on the main slope flow with its core observed in 2007 and 2011 in the 0–100-m layer

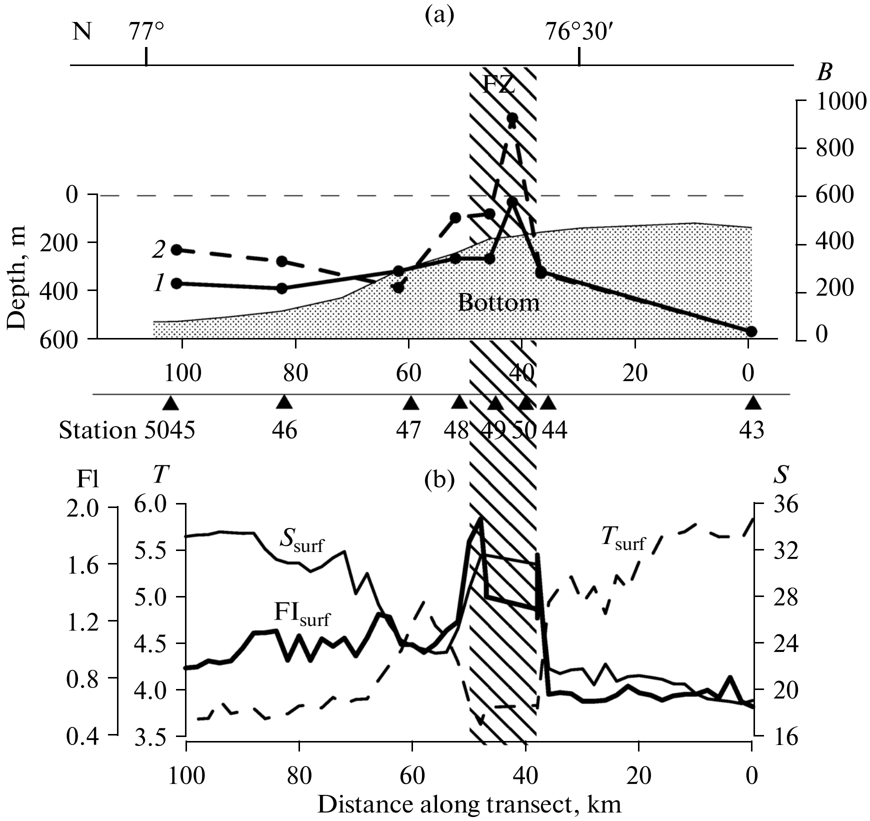

Fig. 8. (a) Distribution of the average mesoplankton biomass (mg/m^3) in layers (*1*) 0–100 m and (*2*) 0–50 m over the outer shelf, slope, and in adjacent deepwater domain of the St. Anna Trough western spur in 2011. (b) Distributions of temperature (*T*, °C), salinity (S, psu) and chlorophyll fluorescence (FL, arbitrary units) in the surface layer during mesoplankton sampling. FZ, frontal zone.

(Fig. 2); the flow itself involved the overall water column down to the bottom [8]. This slope flow is a characteristic feature of the circulation in this trough [39]. According to discrete station-based observations, the horizontal gradients of surface temperature and salinity over the slope in 2007 were 0.1°C/km and 0.37 psu/km, and in 2011, they were 0.1°C/km and 0.61 psu/km, respectively. Evidently, these values are considerably leveled. A continuous recording of surface temperature and salinity in 2011 has shown that the gradients of these parameters in the frontal zone over the slope were considerably more pronounced. They reached 0.25–0.67°C/km for temperature and 1.6–4.7 psu/km for salinity, suggesting hard frontal boundaries in the slope area of the St. Anna Trough. In both years, the UML depth was drastically reduced to 2–6 m in the southern (shelf) periphery of the slope flow, which most likely suggests an upward water flow in this region. This phenomenon is characteristic of main slope flows as well as the accompanying water descent in the northern periphery of the frontal zone [13, 16, 34, 35, 43]. A local increase in salinity (Fig. 7b) and silica concentration is confirmation of the existence of an upward flow in the area of the St. Anna Trough slope as well as an increase in the abundance of the diatom algae in UML [10, 17]. An increase in the primary production in the euphotic layer to 9 mg C/m^3 versus a background level of 2–4 mg C/m^3 (A.B. Demidov, personal communication) was also recorded there. Continuous recording of chlorophyll fluorescence in the surface layer from a sailing vessel also detected a maximum in the concentrations of pigments precisely coinciding with the temperature minimum and salinity maximum in the surface sea layer over the upper continental slope (Fig. 7b).

Discrete observations allow only rough estimates of the width of the slope frontal zone. According to continuous data on surface temperature, salinity, and chlorophyll fluorescence (Fig. 7b), recorded in 2011 concurrently with mesoplankton sampling, the width of the slope frontal zone amounted to 10–15 km, and it was localized to the upper slope.

The data obtained in both years suggest that the frontal slope zone significantly influences the structure of the mesozooplankton communities. This effect appears in two ways, namely, (1) an increased mesoplankton biomass, observable in the frontal zone, and (2) the fact that the frontal zone is the boundary preventing penetration of many mesoplankton species from the deepwater domain of the basin to the shelf and, as a consequence, is the boundary between communities of different composition. This pattern of influence on plankton communities is also characteristic of other types of frontal zones [18, 20, 32, 33, 35, 38].

An increase in mesoplankton biomass was associated with either the very frontal zone over the upper slope of the St. Anna Trough (2011) or the region over the outer part of the slope directly adjacent to the frontal zone from the north (2007) (Fig. 2). The increase in biomass over the slope is the most pronounced in layers 0–50 and 0–100 m (Figs. 2a, 2b, 3, and 7a). Presumably, this results from the fact that the midstream of the boundary flow is associated with the upper layers, making related frontal processes more pronounced (Fig. 2). The 2011 data demonstrate a distinct match of the mesoplankton biomass maxima in layers 0–100 and 0–50 m to the frontal zone region over the slope, evident in the temperature, salinity, and chlorophyll fluorescence distributions in the surface sea layer (Figs. 7a, 7b).

Mesoplankton biomass in the upper 50 m of the water column in the region of the frontal maximum attained record amounts for the Kara Sea, reaching on the average 1210 mg/m^3 in 2007 and 972 mg/m^3 in 2011 (Figs. 2a and 7a). These values exceed by an order of magnitude and more estimates known for the shelf and deepwater domain [19, 21, 36] and are close to the level of mesoplankton biomass in the richest region of this basin, the Ob River estuarine frontal zone (3100 mg/m^3) [19]. It should be emphasized that the observations in both years were made in the fall, when the populations of dominant interzonal species inhabiting deepwater sea domain and slope enter the resting stage of their seasonal cycle and mainly descend from the surface layers. This is also suggested by the vertical distribution pattern of the mesoplankton biomass (Figs. 4 and 5). Enrichment with mesoplankton was also observable in the frontal zone according to the distribution of total biomass in the water column, although to a considerably smaller degree (Fig. 2b).

The most pronounced increase in the biomass over the slope in both years was characteristic of the populations of the species actively functioning in the upper sea layers. The most illustrative example here is the species *Limacina helicina* (Fig. 8). This species was an absolute leader in mesoplankton biomass in the 0–50-m layer both over the slope and in the deepwater domain of the trough immediately adjacent to the slope; the corresponding contributions were up to 50–80% in 2007 and up to 70–90% in 2011. *L. helicina* biomass in the slope maximum reached 22 g/m^2 (440 mg/m^3) in 2007 and 37g/m^2 (740 mg/m^3) in 2011. These values exceed the average level of total mesoplankton biomass in the water column known for the examined Kara Sea area by more than one order of magnitude [36]. The distinct maxima of biomass in the upper 50-m layer associated with the slope frontal zone are also characteristic of other dominant mesoplankton groups, *Pseudocalanus* sp. and *Oithona* sp. (Fig. 8a, b). *Pseudocalanus* sp. biomass in the maximum over the slope in 2007 and 2011 was higher by an order of magnitude than the adjacent regions. The corresponding differences for *Oithona* sp. amounted to two- to tenfold in 2007 and four- to fivefold in 2011.

High biomasses of *Limacina helicina*, *Pseudocalanus* sp., and *Oithona* sp. in the slope frontal zone determined the highest levels of phytoplankton biomass and production consumption by herbivorous zooplankton for the overall examined region. According to Drits et al. [6], they reached 8 and 230%, respectively. Note that the average values characterizing the trophic activity of dominant herbivorous mesoplankton group in both the outer shelf and deepwater region were significantly lower. The grazing rate for the available phytoplankton biomass in the outer shelf was 0.1%, and that of the primary production were 2% versus 2.5 and 20%, respectively, in the deepwater regions.

Our results suggest that the frontal zone formed over the western spur of the St. Anna Trough continental slope is a distinct boundary between the shelf and deepwater pelagic biotopes, which significantly differ in their properties, as well as the boundary between the mesoplankton communities inhabiting these biotopes, which cardinally differ in composition and biomass. This allows us to state that the western spur of the St. Anna Trough, at least in the examined periods, is not a region with intensive inflow of waters and plankton fauna from the deepwater Arctic to the Kara Sea, as was earlier believed [24, 42]. This conclusion is confirmed by detailed studies of the bottom community structures in this region performed during the period of our work [4]. All these data suggest that the frontal zone over the slope of the western spur of the St. Anna Trough may be regarded as an ecosystem boundary. Presumably, water and fauna enter this region of the Kara Sea shelf from the north during the periods of changed circulation, when the frontal zone over the slope is poorly pronounced.

Evidently, the frontal zone of the slope in the western spur of the St. Anna Trough is a region of increased productivity, mesoplankton concentration, and intensive trophic interactions at the basic trophic levels of pelagic ecosystem. These characteristics in the frontal zone may exceed the background level by several orders of magnitude. The richness of the frontal zone is evident even in the fall, when the primary production and plankton biomass decrease and a considerable part of the populations of interzonal copepods, both the major consumers of the primary production and secondary producers, come to the resting phase and descend to deep layers (below 200 m). Presumably, the role of the frontal zone over the slope in the functioning of the Kara Sea pelagic ecosystem is considerably more important during the spring–summer season, becoming comparable to the role of the Ob River estuarine system [1, 19]. Undoubtedly, the frontal zone of the slope in the western spur of the St. Anna Trough is a "hotspot" of the ecosystem and a full estimation of its significance will become clear with the data on the spring–summer season, which is the most biologically active in these latitudes.

ACKNOWLEDGMENTS

The work was supported by the Russian Scientific Foundation, projects nos. 14-50-00095 (processing of hydrophysical data and their general interpretation) and 14-17-00681 (processing of plankton samples).

REFERENCES

1. E. G. Arashkevich, M. V. Flint, A. B. Nikishina, A. F. Pasternak, A. G. Timonin, J. V. Vasilieva, S. A. Mosharov, and K. A. Soloviev, "The role of zooplankton in the transformation of the organic matter in the Ob estuary, on the shelf, and in the deep regions of the Kara Sea," Oceanology (Engl. Transl.) **50** (5), 780–792 (2010).
2. T. P. Bernshtein, "Description of zooplankton from the Kara Sea based on the results of the Arctic Scientific Research Institute expedition of R/V *Sedov* in 1930 and R/V *Lomonosov* in 1931," Tr. Arkt. Nauchno-Issled, Inst. **9**, 3–58 (1934).
3. M. E. Vinogradov, G. M. Vinogradov, G. G. Nikolaeva, et al., "Mesoplankton of the western part of the Kara Sea and Baidratskaya Inlet," Okeanologiya (Moscow) **34** (5), 709-715 (1994).
4. S. V. Galkin, A. A. Vedenin, K. V. Minin, A. V. Rogacheva, T. N. Molodtsova, A. K. Rajskiy, and N. V. Kucheruk, Okeanologiya (Moscow) **55** (4), (2015) (in press).
5. L. N. Gruzov and L. P. Alekseeva, "Ratio of weight and length of body of general groups pf zooplankton in equatorial part of the Atlantic Ocean," Tr. Atlant. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. **37**, 378–400 (1971).
6. A. V. Drits, E. G. Arashkevich, A. V. Nikishina, V. M. Sergeeva, K. A. Solovyev, and A. V. Flint, Okeanologiya (Moscow) **55** (4), (2015) (in press).
7. A. V. Drits, E. G. Arashkevich, A. V. Nikishina, et al., Okeanologiya (Moscow) **55** (4), (2015) (in press)
8. A. G. Zatsepin, S. G. Poyarkov, V. V. Kremenetskiy, A. A. Nedospasov, S. A. Shchuka, V. I. Kondrashov, and A. O. Korzh, Okeanologiya (Moscow) (in press).
9. E. Yu. Zubova, "Composition and distribution of dominant zooplankton species in the Kara Sea," in *Structural and Functional Organization of Kara Sea Ecosystem* (Kola Scientific Center, Academy of Sciences of USSR, Apatity, 1990), pp. 103–120.
10. P. N. Makkaveev, Z. G. Mel'nikova, A. A. Polukhin, et al., Okeanologiya (Moscow) **55** (4), (2015) (in press).
11. V. N. Nesterova and E. L. Orlova, *Ecosystem of the Kara Sea* (Polar Scientific Research Institute of Fishery and Oceanography, Murmansk, 2008), pp. 106–123.
12. L. A. Ponomareva, "Zooplankton of western part of the Kara Sea and Baidaratskaya Inlet," Tr. Inst. Okeanol. im. V.V. Shirshova, Akad. Nauk SSSR **20**, 228–245 (1957).
13. S. G. Poyarkov, "Hydrophysical conditions in the region of Northern Peru," in *Frontal Zones of the Southeastern Pacific*, Ed. by M. E. Vinogradov and K. N. Fedorov (Nauka, Moscow, 1984), pp. 35–51.
14. E. V. Sentyabov, "Physical-geographical characteristics and hydrometeorological conditions of the Kara Sea," in *Ecosystem of the Kara Sea* (Polar Scientific Research Institute of Fishery and Oceanography, Murmansk, 2008), pp. 21–42.
15. V. M. Sergeeva, Candidate's Dissertation in Biology (Shirshov Scientific Research Institute of Oceanology, Moscow, 2013).
16. K. N. Fedorov, *Physical Nature and Structure of Oceanic Fronts* (Gidrometeoizdat, Leningrad, 1983) [in Russian].
17. I. N. Sukhanova, M. V. Flint, E. I. Druzhkova, et al., Okeanologiya (Moscow) **55** (4), (2015) (in press).
18. M. V. Flint, Doctoral Dissertation in Biology (Shirshov Scientific Research Institute of Oceanology, Moscow, 2005).
19. M. V. Flint, T. N. Semenova, E. G. Arashkevich, I. N. Sukhanova, V. I. Gagarin, V. V. Kremenetskiy, M. A. Pivovarov, and K. A. Soloviev, "Structure of the zooplankton communities in the region of the Ob River's estuarine frontal zone," Oceanology (Engl. Transl.) **50** (5), 766–779 (2010).
20. M. V. Flint and I. N. Sukhanova, "Influence of coastal fronts on structure and productivity of phytoplankton," in *Physical, Geological, and Biological Studies of Oceans and Seas* (Nauchnyi Mir, Moscow, 2010), pp. 446–465.
21. O. K. Fomin, "Some structural characteristics of zooplankton," in *Ecology and Bioresources of the Kara Sea* (Kola Scientific Center, Academy of Sciences of USSR, Apatity, 1989), pp. 65–85.
22. O. K. Fomin and V. S. Petrov, "Role of natural factors in distribution of plankton biomass in the Kara Sea," in *Nature and Economics of the North* (Murmansk. Knizhn. Izd., Murmansk, 1985), No. 13, pp. 34–45.
23. O. K. Fomin, V. M. Savinov, and Yu. A. Bobrov, "Spatial distribution of plankton biomass in the Kara Sea," Nauchn. Dokl. Vyssh. Shk., Biol. Nauki, No. 2, 54–59 (1984).
24. V. L. Khmyznikova, "Some data on zooplankton in eastern straits and northern part of the Kara Sea," Tr. Taimyr. Gidrograf. Eksp., No. 2, 175–190 (1935).
25. V. L. Khmyznikova, "Zooplankton of the Kara Sea as the biological indicator of currents," in *Collection of Scientific Papers "Northern Marine Navigation Route"* (Glavsevmorput', Leningrad, 1936), pp. 68–75.
26. V. L. Khmyznikova, "Zooplankton of southern and southeastern part of the Kara Sea," Issled. Morei SSSR, No. 24, 232–259 (1936).
27. V. L. Khmyznikova and M. M. Zabelina, "Plankton of the southwestern part of Kara Sea," Tr. Arkt. Nauchno-Issled. Inst., 3–44 (1946).
28. L. L. Chislenko, *Nomograms for Determination of Weight of Aquatic Organisms by Size and Body Shape* (Nauka, Leningrad, 1968) [in Russian].
29. V. A. Yashnov, "Zooplankton of the Kara Sea," Tr. Plavuch. Morsk. Nauch. Inst. **2** (2), 3–59 (1927).

30. V. A. Yashnov, *Plankton Productivity of the Northern Seas of the Soviet Union* (Moscow Society of Naturalists, Moscow, 1940) [in Russian].
31. M. V. Flint, A. V. Drits, M. V. Emelianov, et al., "Significance of oceanographic and biological processes in the outer and middle shelf domains, at the shelf break and middle fronts for biological productivity of the Pribilof ecosystem, the eastern Bering Sea. Oceanographic conditions and plankton communities in the coastal zones and coastal fronts of the St. Paul and St. George Islands," in *Investigations of the Pribilof marine ecosystem* (Shirshov Inst. Oceanology, Russian Academy of Sciences, Moscow, 1996).
32. M. V. Flint and A. N. Golovkin, "How do planktivorous least auklets (*Aethia pusilla*) use foraging habitats around breeding colonies? Adaptation to mesoscale distribution of zooplankton," Oceanology (Moscow) **42** Suppl. Issue (1), 114–121 (2002).
33. M. V. Flint and I. N. Sukhanova, "The influence of the coastal fronts around the Pribiof Islands (Bering Sea) on the distribution and dynamics of phytoplankton," Oceanology (Moscow) **42** (1), S63–S78 (2003).
34. M. V. Flint, I. N. Sukhanova, E. G. Arashkevich, et al., "Plankton communities in the Eastern Mediterranean coastal waters," in *The Eastern Mediterranean as a Laboratory Basin for the Assessment of Contrasting Ecosystems*, Ser. 2: *Environmental Security*, Ed. by P. Malanotte-Rizzoli, et al. (Kluwer, Dordrecht, 1998), Vol. 51, pp. 141–159.
35. M. V. Flint, I. A. Sukhanova, A. I. Kopylov, et al., "Plankton distribution associated with frontal zones in the vicinity of the Pribilof Islands," Deep Sea Res., Part II **49** (26), 6069–6093 (2002).
36. H.-J. Hirche, K. N. Kosobokova, B. Gaye-Haake, et al., "Structure and function of contemporary food webs on Arctic shelves: a panarctic comparison. The pelagic system of the Kara Sea – communities and components of carbon flow," Progr. Oceanogr. **71**, 288–313 (2006).
37. *ICES Zooplankton Methodology Manual*, Ed. by R. Harris et al. (Academic, London, 2000).
38. J. Le Fevre, "Aspects of the biology of frontal systems," Adv. Mar. Biol. **23**, 163–299 (1986).
39. M. J. Karcher, M. Kulakov, S. Pivovarov, et al., "Arctic water flow to the Kara Sea: comparing model results with observations," in *Siberian River Run-Off in the Kara Sea*, Ed. by R. Stein, et al. (Elsevier, Amsterdam, 2003), pp. 47–72.
40. T. F. McClimans, D. R. Johnson, M. Krosshavn, et al., "Transport in the Kara Sea," J. Geophys. Res., C: Oceans Atmos. **105** (6), 14121–14139 (2000).
41. National Snow and Ice Data Center. http://nsidc.org
42. V. K. Pavlov and S. L. Pfirman, "Hydrographic structure and variability of the Kara Sea: Implications for pollutant distribution," Deep Sea Res., Part II **49** (6), 1369–1390 (1995).
43. A. M. Springer, C. P. McRoy, and M. V. Flint, "The Bering Sea Green Belt: shelf edge processes and ecosystem production," Fish. Oceanogr. **5** (3/4), 205–223 (1996).
44. V. A. Volkov, O. M. Johannessen, V. E. Borodachev, et al., *Polar Seas Oceanography: An Integrated Study of the Kara Sea* (Springer-Verlag, Berlin, 2002).

Translated by G. Chirikova