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MARINE BIOLOGY

Zooplankton of the White Sea: Features of the Composition and Structure, Seasonal Dynamics, and the Contribution to the Formation of Matter Fluxes

N. M. Pertsova[1] and K. N. Kosobokova[2]

[1] *Biological Faculty, Moscow State University, Moscow, Russia*

[2] *Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia*

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Abstract—The composition, seasonal dynamics, and regional variations in the distribution of zooplankton are studied in the shallow-water coastal and deep-water open areas of the White Sea. In the shallow-water areas, seasonal observations were carried out in the period between 1960 and 1997 from spring to autumn and during several annual cycles. In the deep-water areas, the data was collected in the course of several plankton surveys from early spring to late autumn during the period from 1998 to 2001. The available data shows that the boreal, Arctic, and arctic–boreal taxa comprise most of the zooplankton stock in this subarctic sea. The boreal taxa, together with meroplankton, represent a temporal component of the zooplankton and they dominate the stock of the shallow-water regions during the warm season. The variability of the seasonal biomass is well pronounced in the shallow-water areas. The difference between the minimum winter biomass and the summer maximum is 10- to 20-fold. In contrast, in the deep-water areas, in the period from 1998 to 1999, only a twofold difference was observed from spring to fall. In the deep-water areas, the seasonal variations in the vertical and horizontal distribution of zooplankton are well pronounced. They are identified by a few "key" psychrophil (Arctic and arctic–boreal) species; namely, by the copepods *Calanus glacialis, Metridia longa, Pseudocalanus minutus*, and by the chaetognath *Sagitta elegans*. These species undergo clearly pronounced seasonal vertical migrations, which result in a dramatic vertical replacement of the biomass within the water column over the course of the year. Regional differences in the biomass distribution between different areas and bays of the White Sea are described. These are closely related to the hydrophysical regime, the circulation pattern, and the bottom topography. Possible ways of assessing the contribution of zooplankton to the vertical carbon flux in the White Sea are discussed.

INTRODUCTION

The studies of White Sea zooplankton have more than a century-old history. During this period, for different areas of the sea distinct in their hydrological conditions and bottom topography, the faunistic composition of zooplankton has been studied and the factors which determine it have been described [36]. Thanks to the long-standing observations carried out in the coastal areas of Kandalaksha Bay of the White Sea, by staff members of the Pertsov White Sea Biological Station affiliated with Moscow State University and the White Sea Biological Station affiliated with the Zoological Institute of the Russian Academy of Sciences, the annual dynamics of the abundance and biomass of zooplankton and the ecology and life cycles of mass species, as well as their vertical migrations, have been comprehensively examined [36; 51, 58 and references within them]. Over almost a half-century period, a great amount of data on the interannual biomass variations of Kandalaksha Bay has been accumulated [34].

Up to the present day, the majority of systematic zooplankton observations have been carried out precisely in Kandalaksha Bay. The remaining areas have been examined casually, and often using incomparable methods [34]. Only in recent years have several complex expeditions been performed. Observations were repeatedly carried out using standard methods against the background of hydrophysical, hydrochemical, and geochemical measurements over a vast water area in different seasons [23, 59]. These studies have brought many new views of the structure and seasonal dynamics of the plankton community from the least understood deep-water areas [34, 59], its interaction with the communities from the coastal areas [57], and the biological processes in the zones of influence of major and minor rivers [23, 35], as well as at the boundary between the White Sea Basin and the Gorlo [23, 54].

This study is aimed at the generalization of the new data regarding the White Sea plankton community that has been acquired during recent years, the description of quantitative regularities in the zooplankton distribution over the water area of the sea, and the discussion of the role of zooplankton in the formation of vertical carbon fluxes and sedimentation.

MATERIAL AND METHODS

The materials used in this paper were collected in Kandalaksha and Dvina bays, the White Sea Basin, and the Gorlo during the period from 1998 to 2001. They were collected during a series of multidisciplinary expeditions under the aegis of international programs such as INTAS 96-1359, INTAS 97-1881, INCO-Copernicus ICA2 -CT-2000 -10053, and also during the multidisciplinary cruise 49 of the R/V *Professor Shtokman* of the Shirshov Institute of Oceanology, Russian Academy of Sciences (Fig. 1). In addition, the authors used data not yet published and received by them during seasonal and year-round observations at permanent stations and sections in Kandalaksha Bay (1961–1997).

During all the expeditions, zooplankton was sampled with a Juday net with a mouth opening 37 cm in diameter and a net cone with a mesh size of 180 μm, from the standard depth levels 0–10, 10–25, 25–50, 50–100, 100–150, 150–200 (100–200), and 200 m–bottom. The samples were fixed with a 4% solution of formaldehyde and treated using the standard method [16]. All the copepodite stages of large copepods, hydromedusae and scyphozoans, as well as ctenophores, pteropods, chaetognaths, the eggs and larvae of euphausiids, and other organisms larger than 1.5 mm were counted in the samples to obtain their total numbers. The younger stages of small copepods, along with representatives of meroplankton and Cladocera, were counted in one-twentieth of the sample taken with a stamp-pipette. The biomass (wet weight) was calculated using the tables of the standard weights of plankton animals from the White and Barents seas [6, 26].

RESULTS AND DISCUSSION

1. Environmental Conditions and Zoogeographical Composition of Zooplankton

The White Sea—which directly borders the Arctic area and lies in the subarctic zone, only partially beyond the Polar Circle (a part of Kandalaksha Bay, Mezen' Bay, and the Voronka)—is a frigid Arctic sea in terms of the environmental conditions and the character of fauna and flora. It is even more Arctic than the adjacent southern part of the Barents Sea [4, 11, 12, 47]. The inland location of the sea determines its climate. Every year, for six or seven months, the White Sea is covered by ice. The long and cold winter gives way to a short but warm summer, and the annual temperature amplitude is about 10°C greater than that of the Barents Sea, which is very significant for marine basins [11]. During the summer, the surface layers of the sea are warmed up to 12–15°C and more in some places. How-

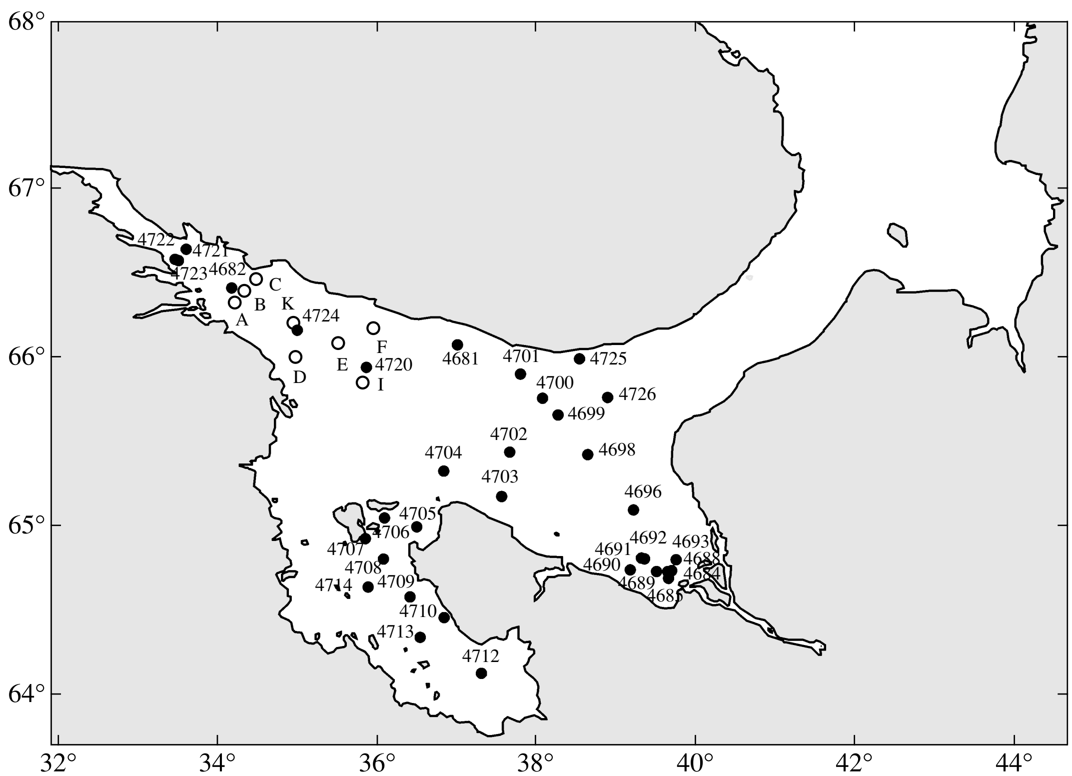

Fig. 1. White Sea. Map of plankton stations. Stations A to I (open circles) were carried out in the period from 1998 to 2001 by the INTAS and INCO-Copernicus programs; stations 4684–4727 (filled circles) were performed during cruise 49 of the R/V *Professor Shtokman* in 2001.

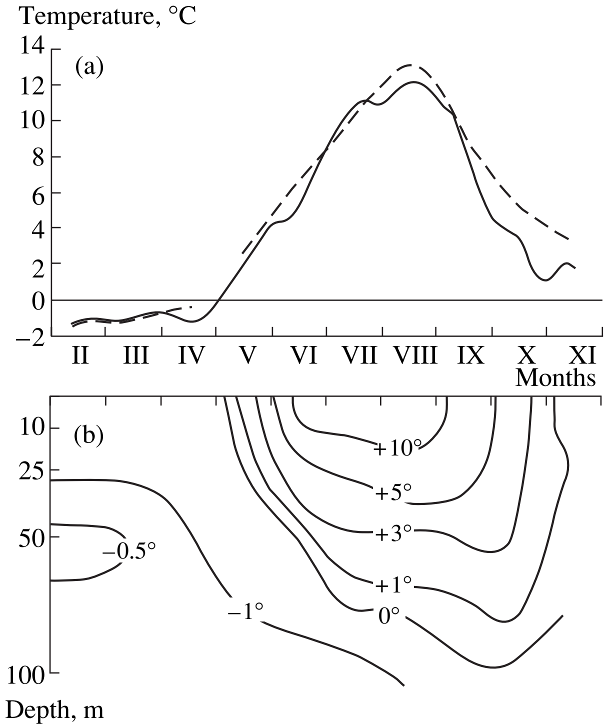

Fig. 2. White Sea. (a) Seasonal changes in the temperature of the surface layer in 1961 (solid line) and 1976 (dashed line). (b) Seasonal curves of isothermals within the water column.

ever, below 50–75 m, the temperature remains negative all year round (Fig. 2).

The bottom topography of the White Sea is very important for the population of the water column. The sea is bucket-shaped, being sort of a vast fjord with a maximum depth of 340 m, and divided from the Barents Sea by the narrow and relatively shallow-water strait called the Gorlo with minimum depths of about 40 m. The three bays—Mezen', Onega, and Dvina—are relatively shallow-water. In Mezen' Bay, the depths seldom exceed 20 m. In Onega Bay, the prevailing depths range from 10 to 40 m, whereas in Dvina Bay, they progressively increase from 10–20 to 100 m, as one moves from its top (internal) part to the external part facing the Basin. The central part of the sea—i.e., the Basin and the external part of Kandalaksha Bay—are the deepest areas (100–340 m). The area with the maximum depths is located at the boundary between Kandalaksha Bay and the Basin. The top part of Kandalaksha Bay is shallow-water.

In terms of species composition, White Sea zooplankton is significantly poorer than that of the adjacent Barents Sea [36]. The hydrological regime of the Gorlo is believed to prevent many of the Barents Sea forms from penetrating into the White Sea [10, 12]. Among the plankton, groups such as ostracods, foraminifers, radiolarians, and siphonophors are completely absent. All the authors who have examined the biogeographical composition of the White Sea fauna [9–12, 58] have noted its mixed nature. In the zooplankton, the Arctic and arctic-boreal species are prevalent, making up 63% of the total, whereas the boreal species comprise 17% [58].

The role of the groups listed is different in terms of the zooplankton abundance and biomass. For example, in June 1998, in Kandalaksha Bay, at station B with a depth of 260 m (Fig. 1), the arctic-boreal species dominated in terms of abundance (more than 70%), while the Arctic species were only about 3%, and the boreal species did not exceed 0.1%. The ratio of these groups was quite different in terms of biomass. The biomass of the arctic-boreal species was only 28%, that of the Arctic species was 69%, and the boreal species did not exceed 0.01%. Thus, even though the abundance of the Arctic species is low compared to that of the arctic-boreal species, they make the greatest contribution to the biomass due to their large body size.

The ratio between the abundance and biomass values of the species of different zoogeographical groups is not constant throughout the year. Wide seasonal variations in these parameters are characteristic of both the shallow-water coastal areas and the surface waters of the open deep-water areas. The great seasonal variations in the zooplankton abundance in the shallow-water areas are caused by the fact that part of the animals populating them are not encountered in the pelagic zone all year round. During the winter, among the plankton, there are no Cladocera or the two most abundant boreal species of Copepoda (*Temora longicornis* and *Centropages hamatus*), which are the heterotropic species that exist for part of their life cycle at the bottom in resting stages [29, 31]. They reach their maximum abundance among the plankton in the shallow-water areas during the summer, in the period of maximum water warming.

2. Seasonal Dynamics of Zooplankton in the Coastal Areas

In the White Sea, like in other subpolar areas, seasonal variations are observed in the composition, abundance, biomass, and distribution of zooplankton related to the presence of clearly pronounced seasons over the year, changes in the intensity of solar radiation, and the cyclic character of phytoplankton vegetation [7]. The curve of the seasonal changes in the plankton community has been most comprehensively examined in the coastal areas of Kandalaksha and Chupa bays, and in the Velikaya Salma Strait, where year-round observations have been carried out for a number of years [14, 25, 27, 37, 39, 42, 44].

According to our data, in the coastal areas, the minimum number of species and the minimum abundance and biomass of zooplankton are observed in the winter. At this time, the shallow-water locations where neritic species prevail are especially poor. According to the observations carried out in Velikaya Salma Inlet (Kandalaksha Bay) at a permanent station with a sea depth of 20 m, in the period from December to March, the biomass of zooplankton ranged from 10 to 50 mg/m^3 and it very seldom reached 100 mg/m^3 in individual samples (Fig. 3a). The same values in the winter were also noted for Onega Bay [15, 48]. At the end of the hydrological winter—in the period from March to April, when the greatest cooling of the water column is noted (Fig. 2)—zooplankton is represented by psychrophil Arctic and arctic–boreal species and their larvae. In this period, in the shallow-water areas, among the Arctic copepods, the species *Metridia longa* is also encountered and reproduces to a small extent. Similarly, the females of *Calanus glacialis* with attached spermatophores are encountered. The psychrophil arctic–boreal copepods *Pseudocalanus minutus* and *Oncaea borealis*, the hydromedusae *Aeginopsis laurentii*, and the ctenophores *Beroe cucumis* and *Bolinopsis infundibulum* are known to reproduce, and the larvae of the pteropod *Clione limacina* are also present.

In April, in the shallow-water areas, the number of species increases mainly due to meroplankton; namely, the larvae of bottom animals such as Cirripedia, Polychaeta, Decapoda, and Bivalvia, although they are still not very numerous. The reproduction of the mass eurythermous copepod species *Oithona similis* begins.

In May, the first month of hydrological spring, the species diversity of zooplankton increases due to the appearance of hydromedusae, the ephyrae of scyphozoans, Cladocera, and larval plankton. In May, following the disappearance of the ice and during the phytoplankton bloom, the abundance of larvae of the barnacles Cirripedia markedly increases. The monthly mean zooplankton biomass reaches 100 mg/m^3 and greater (Fig. 3).

By June, with the beginning of the intensive heating of the surface waters (Fig. 2), the species diversity of zooplankton grows sharply. In June, in Velikaya Salma, the maximum number of plankton species is observed. The number of hydromedusae species is especially large. The larvae of euphausiids and the juveniles of copepods, which spent the winter at the bottom of the basin at the stage of resting eggs, now appear, and the larva diversity rises among the bottom animals such as Polychaeta, Bivalvia, Gastropoda, Decapoda, and Ophiuroidea. The abundance of neritic thermophilic species of Copepoda and Cladocera gradually increases. The older stages of the development of psychrophil Arctic and arctic–boreal species such as *C. glacilis* and *P. minutus*, noted here in the winter, disappear from the shallow-water areas in June, being replaced by their younger stages. In June, the biomass almost doubles in the shallow-water areas.

In July, in the coastal areas, the species composition of zooplankton is still very diverse, but the disappearance of a number of species of hydromedusae is already observed; all the developmental stages of the Arctic copepods—namely, *Calanus* and *Metridia*—are absent; and only the younger developmental stages are noted in the arctic–boreal *Pseudocalanus.* A number of larvae of the bottom animals are not seen in the plankton due to their settlement at the bottom of the basin, but meroplankton is added by the Asteroidea larvae. When the shallow-water areas are progressively warming up, the species of the thermophilic assemblage reach their maximum development; namely, the copepods *Temora longicornis, Centropages hamatus*, and *Acartia longiremis*. The biomass is as large as 200–350 mg/m^3 and more (Fig. 3). In August, during the maximum water heating in the coastal areas, the biomass begins to decrease, although sometimes a second peak is noted [27, 42, 44].

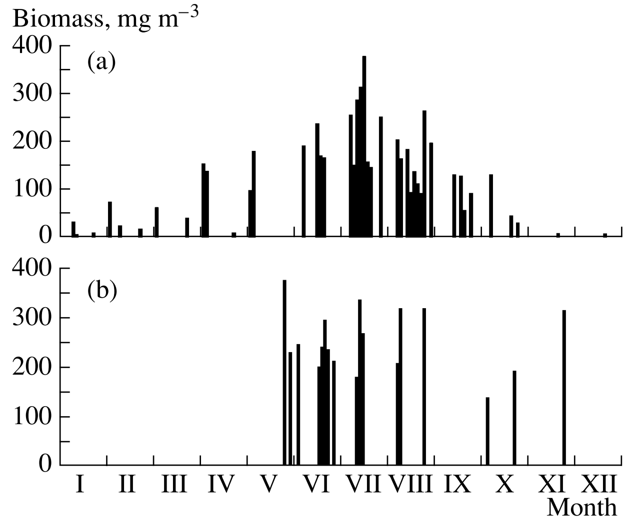

Fig. 3. Seasonal changes in the biomass of zooplankton (mg/m^3, wet weight) (a) in the coastal areas during the period from 1961 to 2001 and (b) in the deep-water part of the White Sea during the period from 1998 to 2001.

In September, the water temperature drops quickly (Fig. 2). The number of pelagic species decreases due to the disappearance of a number of species of hydromedusae and scyphozoans. The abundance of the Cladocera species sharply decreases, and, by the end of the month, they completely disappear from the plankton. When the water temperature decreases, the period of the mass reproduction of the Arctic copepod *M. longa* begins. In the plankton, many representatives of larval plankton appear; namely, Ascidia eggs and larvae. The biomass of zooplankton continues to drop.

In October, the water temperature decreases sharply; the composition of zooplankton becomes comparable to that in March. This means that the Arctic hydromedusa *Aeginopsis laurentii* begins to reproduce again, while the abundance of the species of the thermophilic assemblage markedly decreases. In November, the sea starts to freeze up. The thermophilic heterotopic species of copepods disappear from the plankton [31], while the abundance of other species drops

Table 1. Share (%) of main components in the biomass of zooplankton inhabiting the deep-water part of Kandalaksha Bay, the White Sea, in different seasons of 1988 and 1999

Date	June 25, 1998	July 27, 1998	October 15, 1998	May 30, 1999	August 1, 1999	November 24, 1999
Species, group						
Calanus glacialis	30.6	20.0	17.1	39.5	54.7	34.3
Metridia longa	40.8	21.6	19.9	25.0	20.0	24.2
Pseudocalanus minutus	11.6	14.8	29.2	6.3	9.3	19.7
Other Copepoda	2.3	0.8	2.9	2.7	2.0	2.5
Sagitta elegans	8.4	7.7	9.3	16.7	3.1	6.3
Coelenterata	0.2	8.6	10.1	1.9	3.0	6.1
Mycidacea	1.1	0.1	0.1	2.6	0.6	0.6
Euphausiacea	0.4	0	1.5	0.4	0.3	0.1
Appendicularia	2.5	8.2	3.4	0.2	0.03	0.5
Amphipoda	0.9	1.3	1.8	1.9	1.6	3.9
Others	1.1	17.5	4.7	2.8	6.0	1.8

sharply. During the winter, the number of species is only 30–40% of the total number of the zooplankton species found in the White Sea [17, 27].

3. Seasonal Dynamics of Zooplankton in the Deep-Water Areas of the Sea

In the seaward deep-water areas, the composition of zooplankton is somewhat different. There, the share of the neritic species is much smaller—especially that of the species of the thermophilic assemblage—whereas the share of the psychrophil Arctic species is larger. The seasonal dynamics of zooplankton in the deep-water part of the White Sea has been more poorly understood than that in the shallow-water areas [17, 27, 32, 35, 36]. Only recent observations carried out at the permanent section through the Kandalaksha Depression and in the Basin in different seasons over the period from 1998 to 2001 allowed us to follow its composition and describe the pattern of seasonal changes in its distribution.

From early spring to late fall, in the deep-water area, three species of copepods prevail by biomass; namely, *C. glacialis, M. longa*, and *P. minutus*, as well as the chaetognath *Sagitta elegans* (Table 1), which exist in the plankton all year round. Pronounced annual dynamics are characteristic for the development of each of them. This means that the period of reproduction is confined to a certain season, while the age composition, abundance, and biomass vary from season to season [2, 19, 20, 29, 30, 31, 41, 43, 53]. Over the year, the pattern of the vertical distribution of each of the mass species also markedly changes.

In the early spring, the populations of the psychrophil phytophages–filter feeders *C. glacialis* and *P. minutus* rise toward the surface layers (Figs. 4a, 4b), where they are concentrated up until the end of June and the beginning of July; i.e., until the period when the surface temperature begins to grow sharply (Fig. 2). Beginning at this time, their populations start to sink below the limits of the warmed layer. Starting in August, 80% of the copepods are concentrated at depths greater than 100 m (Figs. 4a, 4b). Over the period from August to November, this pattern of vertical distribution is broken only in the nighttime, since the individuals of the older stages of both species perform their regular daily migrations, rising to the surface layers during the night [20, 33]. In the winter, the bulk of the populations of *C. glacialis* and *P. minutus* exist at depths greater than 100 m. Nevertheless, selected individuals of both species are encountered near the surface during the winter months as well [17, 20, 25, 43]. The third dominant species—namely, the copepod *M. longa*—has another characteristic pattern of seasonal vertical migrations. In the spring and summer, its population inhabits deeper layers than in the fall and winter (Fig. 4c). In addition, this species performs the most active daily vertical migrations [30], the intensity of which [7] is as great as 24–58% in the period from August to October.

The clearly pronounced seasonal migration of the entire mass of zooplankton is a result of the "summation" of the seasonal vertical migrations of individual species (Fig. 5). In 1999 we carried out the earliest observations of the vertical distribution of the total biomass throughout the water column, immediately after the ice removal at the end of May–beginning of June, as well as the latest observations on the eve of complete freezing at the end of November. In the period from the end of May to the beginning of June, the pattern of the biomass distribution over the water column from surface to bottom was very inhomogeneous. Within the 0–10-m layer, 78–90% of the total zooplankton were concentrated, and the biomass markedly decreased with depth (Fig. 5). The mean value of the biomass within the 0–10-m layer, averaged over three stations, was 4284 mg/m^3; at one of these stations, for the first time in the deep-water area of all of Kandalaksha Bay, we observed the highest biomass of zooplankton within this layer in the history of White Sea research—namely, 7256 mg/m^3. Within this surface layer, the copepod–filter feeder *C. glacialis* dominated overwhelmingly (77–92% of zooplankton biomass, Fig. 5). Throughout the entire water column, the three species of copepods *C. glacialis, Metridia longa*, and *P. minutus* comprised from 71 to 84% of the total biomass at different stations, while the share of the predator–chaetognath *S. elegans* varied from 5 to 17%. Hyperiidae, Mysidacea, Euphausiidae, Appendicularia, and Hydromedusae (Trachylida) such as *Aglantha digitale* and *Aeginopsis laurentii* were of lesser importance. The larvae of the bottom animals were also present in insignificant amounts.

In the summer, on August 1, 1999, the pattern of the biomass vertical distribution was almost homogeneous (Fig. 5). The biomass values varied from 238 to 382 mg/m^3 at different depths (Table 2, the mean for three stations). Within the 0–10-m surface layer, it decreased by a factor of 14 compared to the period from May to June, while at depths greater than 100 m, it increased at more than a tenfold rate (Table 2). Within the upper 10-m layer, *C. glacialis* was completely absent, although it was encountered in minor amounts in the 10–25-m layer. By this time, the bulk of *Calanus* had already sunk to depths greater than 100 m (Fig. 5). *P. minutus* was still abundant up to a depth of 100 m, whereas *M. longa* was encountered only deeper than 25 m. Within the 50-m surface layer, representatives of meroplankton and the juveniles of the hydromedusae *A. digitale* were of great importance.

In the fall, at the end of November 1999, the biomass of zooplankton decreased even further within the surface layer (up to a depth of 25 m), to 8–27 mg/m^3 (Fig. 5, Table 2). Its highest values, up to 418 mg/m^3, were observed at depths greater than 100–200 m (Fig. 5), where it increased by a factor of 13 compared to the spring period (Table 2). At depths greater than 100 m, 97% of the *C. glacialis* biomass was concentrated, while it was completely absent in the upper 50-m layer.

In 1998, in the same area, the seasonal observations began three to four weeks later and finished a month earlier than in 1999. The seasonal changes observed in the distribution of zooplankton biomass were similar to those in 1999. At the end of June, a peak in the biomass was also mainly noted in the 0- to 10-m surface layer (Fig. 5); however, the values of this maximum were

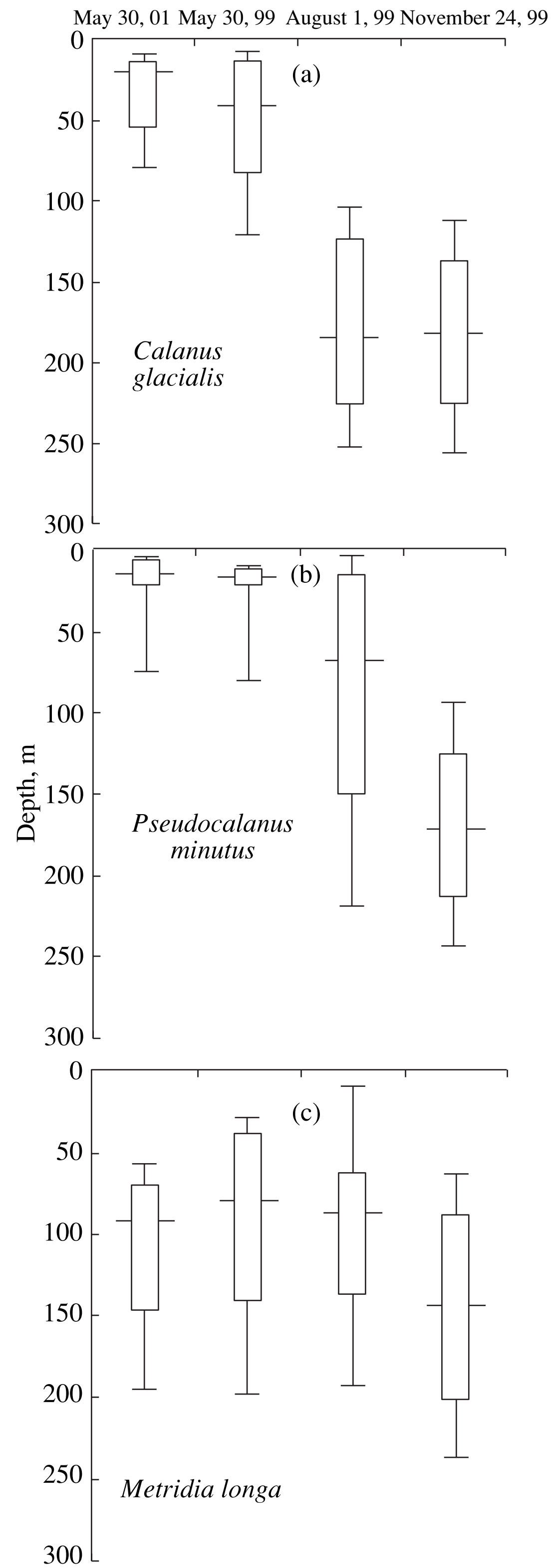

Fig. 4. Seasonal changes in the vertical distribution of the dominant species of zooplankton in the deep-water part of the White Sea. The upper, intermediate, and lower horizontal lines show the location of 10, 50, and 90% levels of the population abundance, respectively; the upper and lower boundaries of the rectangle are the 25 and 75% levels of the abundance.

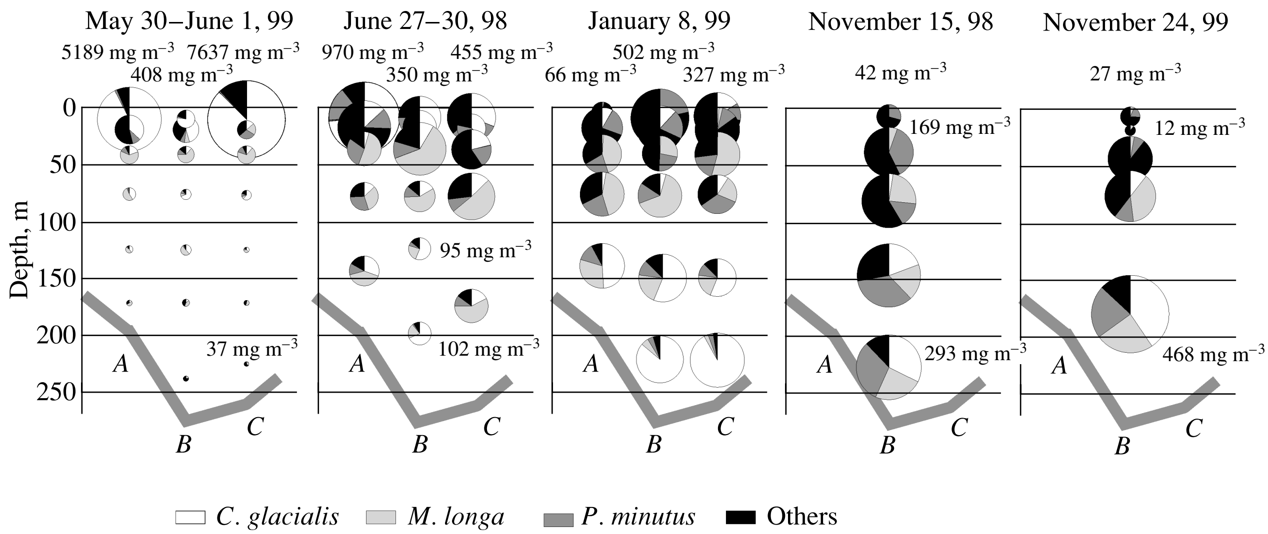

Fig. 5. Seasonal changes in the vertical distribution of the biomass of zooplankton at stations A–B–C in Kandalaksha Bay during the period from 1998 to 1999. The bottom profile is indicated by the broken line.

much lower than in the period from the end of May to the beginning of June 1999 (350–970 mg/m^3, with a mean value of 592 mg/m^3, Table 2). Like in the spring of 1999, three species of copepods—namely, *C. glacialis, M. longa*, and *P. minutus*, along with chaetognaths—dominated over the water column; however, *M. longa* played the leading role (24–43%). On June 27, 1998, the pattern of the vertical distribution of biomass

Table 2. Biomass of zooplankton (mg/m^3, wet weight) at the permanent section A–B–C across the Kandalaksha depression in different seasons in the period from 1998 to 1999 (the mean for three stations), and indexes of the changes in the biomass at selected depths: (*1*) from spring to summer; (*2*) from summer to fall; (*3*) from spring to fall

Date	June 1, 1999	August 1, 1999	November 24, 1999	*1* Early spring/summer	*2* Summer/fall	*3* Spring/fall
Depth, m						
0–10	4294	298	27	14.4	11.1	159.9
10–25	784	287	8	2.7	36.6	100.1
25–50	393	238	139	1.7	1.7	2.8
50–100	155	266	180	0.6	1.5	0.9
100–200	65	283	418	0.23	0.68	0.16
200–bottom	33	382	418	0.09	0.91	0.08
0–bottom	368	289	307	1.3	0.9	1.2
Date	June 25, 1998	July 27, 1998	October 15, 1998	*1* Late spring/summer	*2* Summer/fall	*3* Spring/fall
Depth, m						
0–10	592	180	42	3.3	4.3	14.1
10–25	308	324	42	0.9	7.8	7.4
25–50	356	204	169	1.7	1.2	2.1
50–100	255	101	203	2.5	0.5	1.3
100–200	162	134	180	1.22	0.48	0.58
200–bottom	102	136	293	0.75	0.46	0.35
0–bottom	235	148	241	1.6	0.6	1.0

was quite similar to that of observed by us on August 1, 1999, while in mid-October, the pattern resembled that in the late fall of 1999 (Fig. 5).

Unlike the shallow-water areas, the range of the seasonal changes in zooplankton biomass in the deep-water areas from early spring to late fall was not wide. Both in 1998 and in 1999, during the period from the spring to the summer, the decrease in the mean value of biomass over the water column was very small; namely, it decreased by a factor of 1.6 and 1.3, respectively. This decrease was followed by another very slight increase—by a factor of 1.6 and 1.1, respectively—during the period from the summer to the fall (Table 2). Finally, in the fall of 1998, the biomass was the same as it had been in the spring, whereas by the fall of 1999, it had decreased by a factor of 1.2 from its spring levels (Table 2).

It is difficult to say how much the biomass decreases during the winter period. However, a comparison of the abundance and age composition of one of the most numerous species—namely, *C. glacialis*—at station B in Kandalaksha Bay in the fall of 1998 and in the spring of 1999 gave us the following results (Table 3). The mean *Calanus* abundance over the water column at the latest date of sample collection in 1998 (October 15) was 25 ind./m^3. On the earliest date in the spring of 1999 (May 30), it was almost unchanged at 27 ind./m^3. The shares of females and males over the winter was also practically unchanged, whereas the share of copepodite stage CV in the spring (62.3%) reached almost the same value as that of copepodite stage CIV (68.7%) in the fall of the preceding year (Table 3). It is hardly surprising to see such a change in the population composition, because the transition from copepodite stage CIV to stage CV usually takes place precisely in May. It is likely that this transition had already been completed by the end of May 1999. It was followed by the expected increase in biomass (Table 3), as the size and weight of copepodite stage CV are markedly higher than those of CIV [26]. The example given demonstrates that there are almost no losses in the population of this Arctic species, and thus, the total biomass of plankton in the deep-water area does not decrease during the winter period. One of the reasons for this may be the absence of plankton-feeding fish in the deep layers, where the water temperature is always negative and thus unfavorable for them. Judging from the results, the pressure from other plankton predators is also small at these depths. We can suggest that the deep-water areas of the White Sea serve as a natural reservoir for the conservation of basic parts of the populations of the dominant Arctic and arctic–boreal species during the winter period.

Table 3. Abundance, biomass, and age composition (%) of *Calanus glacialis* at station B (Kandalaksha Bay) in the area of the maximum depths for the White Sea, during fall 1998 and spring 1999

Date	October 15, 1998	May 30, 1999
Abundance, ind./m^3	25	27
Biomass, mg/m^3	41	74
Age composition, %		
CIV	68.5	25.0
CV	17.0	62.3
CVI, females	11.1	12.3
CVI, males	3.3	0.4

4. Seasonal Changes in the Composition of Zooplankton from the Shallow-Water to the Deep-Water Areas

The fact that seasonal changes in the plankton of the coastal and open deep-water areas of the sea are different in nature, and are caused by seasonal changes in the populations of various zoogeographical components of plankton, is well traced in the “axial” section across Kandalaksha Bay (Fig. 6a). In this section, the depths gradually increase from 20 m in the top part of the bay to 300 m in its open part (Fig. 6b). This allows us to consider the role of the main components of plankton both in coastal and deep-water areas in different seasons.

At the end of June, all over the bay, from the shallow waters to the area with the maximum depths, the arctic–boreal species *P. minutus* and the Arctic species *C. glacialis* and *M. longa* dominate in terms of biomass (Fig. 6c). The latter is only encountered in the area with depths greater than 100 m (stations 2–12). At this time, the boreal heterotopic species have just begun to appear in the plankton in the shallow-water areas (stations 18–29), where their share is no greater than 1–2% (Fig. 6c). The share of *C. glacialis* in the plankton inhabiting the shallow-waters areas is lower, while that of *P. minutus* is higher than in the deep-water areas.

In mid-summer, in August, the pattern becomes fundamentally different (Fig. 6d). In the shallow-water areas (stations 15–29), boreal species dominate overwhelmingly, with a small addition of the arctic–boreal species *P. minutus*. As for the areas with greater depths (stations 2–12), there the Arctic species *C. glacialis* and *M. longa* prevail to a large degree, whereas boreal species are quite rare. At all the stations, the contribution of *P. minutus* to the abundance is low, due to the

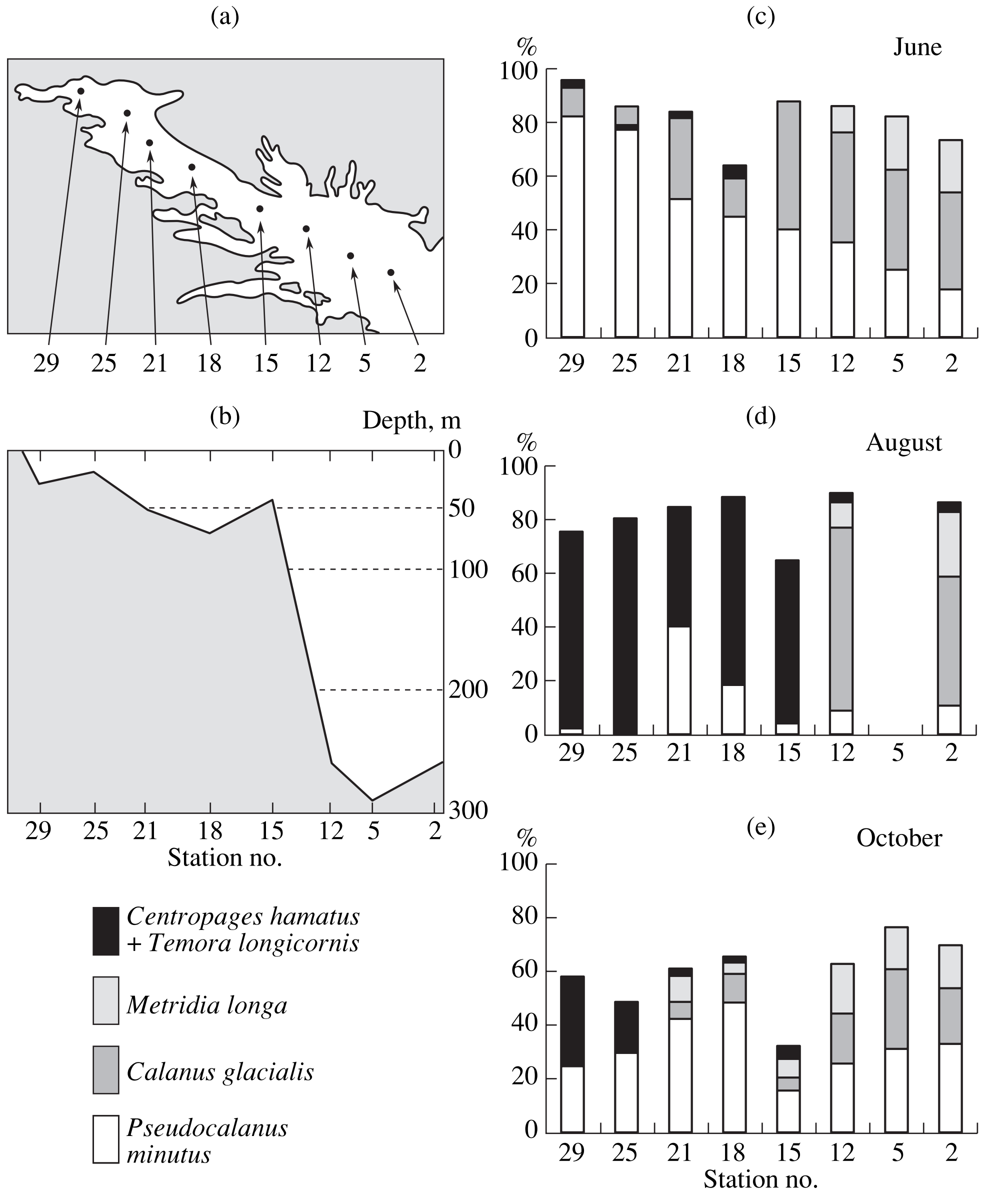

Fig. 6. (a) Location of plankton stations over the section across Kandalaksha Bay, from the collections of 1960–1961; (b) bottom topography along the section; (c), (d), (e) contribution from the dominant species to the biomass of zooplankton at the stations of the section (c) in the spring (May), (d) in the summer (August), and (e) in the fall (October)

extremely high predominance of the boreal species in the shallow-water areas, and that of the Arctic species in the deep-water area.

In the fall, the pattern changes again. By this time, boreal species have almost disappeared from the plankton, and their contribution to the biomass is observed only in the most shallow-water area (Fig. 6e). At the stations with depths smaller than 50 m, the Arctic species are absent. In the areas with depths greater than 50 m, they are present in small amounts, and only in the most deep-water areas, where their share is as great as 40–45% (Fig. 6e). Over the entire section, the share of *P. minutus* ranges from 10 to 25% of the biomass. During the fall period, the share of other groups of plankton grows; namely, that of chaetognaths, amphipods, and the hydromedusae *A. digitale*, comprising 15–85% of the biomass.

5. Horizontal Distribution of Biomass in Different Seasons

Comparing the values of biomass at different stations in the deep-water area during different seasons, one sees that in the spring (late May–June), the biomass is higher at stations located near the coasts (Fig. 7, stations A and C), and lower at the deepest stations, located along the axis of Kandalaksha Bay (Fig. 7, station B). In the summer (early August), the values of biomass decrease by a factor of 1.4, while at the deep-water station, they increase by a factor of 1.7. In the fall, from October to November, the stock of zooplankton is found in the deepest areas of the sea (Fig. 7), which has been noted previously [28]. These changes proceed due to changes in the distribution of the Arctic and arctic–boreal species, which, by Zelikman's expression [13], change "the lace" of their area of distribution when abiotic conditions change.

6. Regional Features of Zooplankton Distribution

The data given above show that the seasonal changes in the plankton community of the White Sea are so great that a well justified study of the differences between individual areas can only be performed on the basis of data acquired in the same season. At present, it is only possible to describe the existing regional differences for the spring–summer period. We combined the results of our own observations and the published data. We grouped the data collected from the end of May to the beginning of June into the spring period, while grouping the data obtained from mid-July to the end of August into the summer period (Table 4). For both periods, most of the data was obtained in Kandalaksha Bay (10 surveys in the spring and 14 surveys in the summer); for the rest of the test areas, the bulk of the data was limited to one or two surveys.

When comparing the mean values of the biomass for the entire water column in the Basin and Kandalaksha, Dvina, Onega, and Mezen' bays, as well as at the boundary with the Gorlo and in the Voronka (Table 4), one can see that—in the spring and summer—the values of the biomass are higher in areas with a so-called "Basin" type of water structure. In the summer, this is characterized by a clearly pronounced stratification of temperature, salinity, and density, and by the relatively slow penetration of heat and freshening into deeper layers. These are the wide-open areas within and between the Basin and Kandalaksha and Dvina bays. The values of the biomass are significantly lower in the shallow-water Onega Bay, in the Gorlo, and in Mezen' Bay (Table 4); i.e., in areas with a homogeneous type of the water structure [45]. Due to mixing, these areas are characterized by a homogeneous and sometimes quite uniform vertical distribution of temperature, salinity, and other hydrological parameters.

According to the data obtained previously, within each area the patterns of the zooplankton biomass distribution are also inhomogeneous. In the Basin, the minimum biomass is observed in its central part, the location of the so-called "warm pole"; i.e., the area with an increased water temperature at its center [22]. The values of the biomass increase at the interface of the Basin with Onega Bay and the Gorlo; i.e., in the areas where the seasonal thermal fronts are located [32]. These fronts are formed at the boundaries of these areas

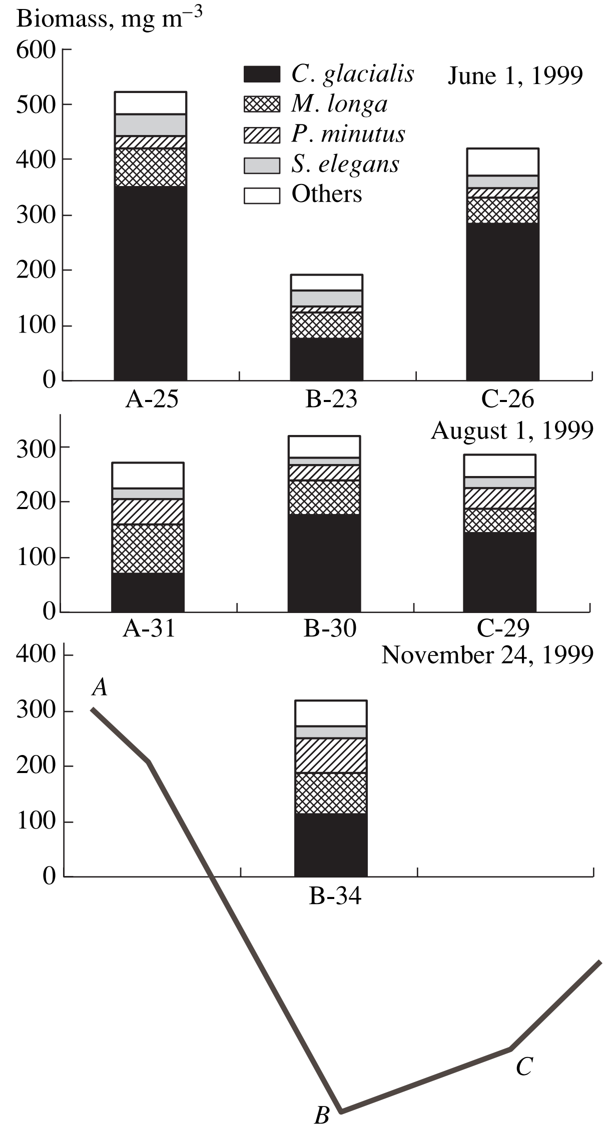

Fig. 7. Seasonal changes in the biomass of zooplankton and the contribution from the dominant species (mg/m^3, wet weight) over section A–B–C through the deep-water part of Kandalaksha Bay. The bottom topography is shown by the polygonal line.

in spring. In one of these areas, tidal currents may mix the waters from surface to bottom, whereas in another area, they may not [22]. An increase in the biomass is also observed in the eastern part of the Basin adjacent to Dvina Bay, in the area of the "cold pole"; i.e., in the area with a reduced water temperature at the center. Near the Terskii, Kandalaksha, and Letnii coasts, as well as toward the shallow-water areas of Kandalaksha Bay, the biomass also increases [32].

7. Role of Zooplankton in Vertical Carbon Fluxes

Vertical fluxes of organic matter in the sea are formed mainly due to primary production ([61] and ref-

Table 4. Biomass of zooplankton (mg/m^3, wet weight) for different areas of the White Sea according to the data from plankton surveys in the period from 1998 to 2001 and the published data

Area	Spring		Number of surveys	Summer		Number of surveys	Author
	average biomass	range		average biomass	range		
Kandalaksha Bay	264	151–577	12	186	57–290	16	Surveys from 1998 to 2001 and [18, 28, 32, 44, 48, 50]
Basin	248	151–335	2	265	179–351	2	Surveys from 1998 to 2001 and [32, 48]
Dvina Bay	134	118–151	2	152	107–196	2	Surveys from 1998 to 2001 and [32, 36, 49]
Onega Bay	7	–	1	133	102–157	2	Surveys from 1998 to 2001 and [36, 48–50]
the Gorlo	77	–	1	39	–	1	[33, 48]
Mezen' Bay	24	–	1	25	11–40	2	[18, 33, 36]
the Voronka	–	–	–	109	16–249	3	[36, 48, 49]

erences within it). However, zooplankton also plays a large role in the formation and modification of the fluxes of organic matter through the water column. On the one hand, by feeding on phytoplankton, zooplankton decreases the amounts of resynthesized organic compounds settling at the bottom of a basin. On the other hand, the phytoplankton consumed by it is converted into faecal pellets in the course of digestion; they sink into the deep layers rather quickly, encouraging the rapid transfer of organic compounds from the surface to the deep layers. The sinking and deteriorating pellets can be a food source for the animals which inhabit the deep layers, leading to the utilization of unassimilated organic matter; or, having reached the bottom, this matter enriches the bottom sediments [52, 55]. The natural dying-off of plankton animals themselves also plays a specific role in the formation of the organic matter flux to the bottom.

In the White Sea, the role of zooplankton in the formation of carbon fluxes remains poorly studied. For this basin, no estimates of phytoplankton grazing or of the balanced states of the cycles of primary and secondary production have been carried out, because of the absence of simultaneous seasonal observations of the dynamics of primary production and variations of the phyto- and zooplankton biomass. There is no agreement in the estimates of the values of primary production among individual specialists [5, 24, 46, 51]. Little is known about the seasonal changes in the phytoplankton biomass and the regularities of its distribution over the water area of the sea [47, 60], or about the factors regulating the intensity of the feeding of the mass representatives of zooplankton. To date, the transformation of organic matter in the stomachs of plankters in the course of digestion, the organic and mineral composition of faecal pellets, the natural rate of their sinking, and the transformation of their matter as they sink have all been poorly studied.

Despite the absence of information about many parameters determining the role of zooplankton in the formation of vertical carbon fluxes, the fluxes of pellet material can still be roughly estimated using calculating techniques based on available data about the structure and seasonal dynamics of the plankton community [32, 36, 58], and other data based on experimental observations of zooplankton feeding [1, 3, 39, 40]. A similar estimate for the shallow-water areas of the White Sea in the period of the summer bloom (August) was first carried out by Arashkevich and Sergeeva [3] on the basis of experimental data. The authors showed that—with a normal level of feeding activity in this season—the amount of wet compounds excreted per day by a population of *C. glacialis* was 180 mg. According to the data of the same authors, the rate of sinking of the *Calanus*' pellets was 84 m day^{-1}. Since in the test area, the depth did not exceed 100 m, the authors came to the conclusion that the life activity of the population of this mass plankton filter-feeder results in a daily sedimentation of 180 mg of organic matter to the bottom [3], which is equivalent to 11.5 mg of carbon (the wet weight to organic carbon ratio was assumed equal to 0.064) [8]. The real daily value of the flux of the suspended biogenic carbon should be higher than the value obtained, because in the calculations, the contributions from all the other species of zooplankton were not taken into account, not to mention the possible settlement of phytoplankton not utilized by filter-feeders, and the corpses of the zooplankters themselves.

We performed a similar calculation of the value of the pellet flux of *C. glacialis* in the deep-water part of the White Sea (stations A, B, C, Fig. 1) during the spring period (late May–early June, 1999 and 2001). We based on our data on the population abundance and structure, as well as on the published data regarding the rates of production and pellet settlement [3]. This showed that at the levels of the maximum spring biomass of *Calanus* known for the White Sea (1999), the daily amount of organic carbon sinking to the bottom can vary from 21 to 83 mg. At the same calendar time of 2001, with smaller values for the biomass and abundance of the large stages of *Calanus* and available individuals of the new generation, the daily value of the flux was 12–40 mg of organic carbon.

For the coastal areas of the sea, one can also estimate the fluxes for the onset of the productive period in the pelagic zone. Our recent studies in Chupa Bay at the end of the winter (on April 6–7, 2002) showed that the development of the ice algae at the lower ice edge begins long before the ice cover starts melting off [21]. The populations of filter-feeders, which are not numerous near the surface at this time, gain the opportunity of being fed under the ice; thus, pellet material appears within the water column [21]. The calculation of the matter amounts reaching the bottom in this period due to the pellets of *C. glacialis* showed that from 0.3 to 1.2 mg of organic carbon can settle there per day.

The given estimates of the contribution to the vertical carbon fluxes from only one mass species of White Sea zooplankton show that, depending on several factors—the season, the population composition of phytophages–filtrators, their abundance, the pattern of their vertical distribution, and the depth of the test area—the amounts of organic matter settling with pellets can vary within three orders of magnitude; i.e., from 0.3 to 83 mg of organic carbon. The values obtained by us are well within the limits of seasonal variations of the values of the pellet fluxes found in other areas [56, 61]. However, to arrive at more exact estimates, it will be necessary to carry out comprehensive examinations of different aspects of feeding of the mass representatives of zooplankton, and the relationships between their actual food requirements and the amounts of the food available.

CONCLUSION

The study of the dynamics of the plankton community in the coastal shallow-water and in the central deep-water areas of the White Sea shows that a clearly pronounced seasonal character of biological processes is typical of both. In the shallow-water areas, the seasonal changes mostly manifest themselves in changes in the composition of zooplankton, its quantitative parameters, and in variations in the contribution of individual biogeographical groups to the abundance and biomass. The variations in the values of abundance and biomass have greater amplitudes, and they take place almost exclusively due to the boreal species of copepods which appear only in the warm period of the year, as well as because of the larvae of bottom animals. The disappearance of plankton from both groups, occurring every year, results in the marked reduction of these parameters. The range of the biomass variations from winter to summer can be 10- and even 20-fold.

The minor contribution of the boreal species and the ongoing predominance of the psychrophil species with long-term (one–two years) life cycles are characteristic of the deep-water areas of the sea. Due to their seasonal migrations, the pattern of the vertical distribution of the total biomass of plankton throughout the water column is subject to seasonal changes. The differences between the seasonal minimum and maximum of biomass within the 10-m surface layer of the sea are even greater in the deep-water areas than they are in the shallow-water areas (by a factor of 150). However, from spring to fall, throughout the entire water column from bottom to surface, the values of the biomass change no more than two-fold (see Table 2).

The seasonal dynamics of the abundance and migration of the boreal species and species of the psychrophil assemblage explains the seasonal changes in the distribution of the total biomass of zooplankton over the area of the sea. The Arctic and arctic–boreal species play a leading role in the biomass of the deep-water plankton all year round, whereas in the shallow-water areas, they only dominate in spring. In the summer, the role of the boreal species increases largely in the coastal shallow-water areas.

Different areas of the sea, characterized by different ranges of depths and by peculiar hydrophysical regimes, differ in the composition of the dominant forms of the thermophilic and psychrophil assemblages and in the quantitative parameters of zooplankton. To a great extent, the latter two factors determine the contribution of zooplankton to vertical carbon fluxes and sedimentation. This contribution itself is also subject to pronounced seasonal changes. The study of the role of zooplankton in the formation of these processes is an urgent challenge for future research in the White Sea.

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REFERENCES

1. Arashkevich, E.G. and Drits, A.V., Influence of the Size of Food Particles on the Parameters of the Dependence of Consumption Rate on Food Concentration for Copepods-Phytophages of the Calanus genus, *Okeanologiya*, 1984, vol. 24, no. 4, pp. 677–683.
2. Arashkevich, E.G. and Kosobokova, K.N., On the Life Strategy of Herbivorous Copepods: Physiology and Biochemical Composition of the Wintering Stock of *Cala-*

nus glacialis under Starvation Conditions, *Okeanologiya*, 1988, vol. 28, no. 4, pp. 657–662.

3. Arashkevich, E.G. and Sergeeva, O.M., Rate of Consumption of Different Phytoplankton Species, Amount of Faecal Pellets Consumed, and Rate of Their Precipitation for the White Sea *Calanus glacialis, Issledovanie fitoplanktona v sisteme monitoringa Baltiiskogo morya i drugikh morei SSSR* (Studies of Phytoplankton in the System of Monitoring in the Baltic Sea and Other Seas of the USSR), Moscow: Gidrometeoizdat, 1991, pp. 285–294.
4. Berger, V.Ya., Naumov, A.D., Lorents, G.K., and Lukin, L.R., Physical–Geographic Characteristic of the White Sea. General Characteristic, *Beloe more. Biologicheskie resursy i problemy ikh ratsional'nogo ispol'zovaniya. Issledovaniya fauny morei* (The White Sea. Biological Resources and Problems of Their Rational Use. Studies of Marine Fauna), 1995, vol. 42 (50), Part I, pp. 47–51.
5. Bobrov, Yu.A., Maksimov, M.P., and Savinov, V.M., Primary Production of Phytoplankton, *Beloe more. Biologicheskie resursy i problemy ikh ratsional'nogo ispol'zovaniya. Issledovaniya fauny morei*, (The White Sea. Biological Resources and Problems of Their Rational Use. Studies of Marine Fauna), 1995, vol. 42 (50), Chapter I, pp. 92–114.
6. Bogorov, V.G., Standardization of Marine Plankton Studies, *Tr. Inst. Okeanol. Akad. Nauk SSSR*, 1957, vol. 24, pp. 205–215.
7. Vinogradov, M.E., *Vertikal'noe raspredelenie okeanicheskogo zooplanktona* (Vertical Distribution of Oceanic Zooplankton), Moscow: Nauka, 1968.
8. Mitropol'skii, A.Yu., Bezborodov, A.A. and Ovsyanyi, E.Yu., *Geokhimiya Chernogo morya* (Geochemistry of the Black Sea), Kiev: Naukova Dumka, 1982.
9. Virketis, M.A., Zooplankton of the White Sea, *Issled. Fauny morei*, 1926, vol. 3, pp. 1–47.
10. Virketis, M.A., On the Zooplankton Distribution in the Gorlo of the White Sea, *Tr. In-ta po izucheniyu Severa*, 1929, no. 40, p. 305.
11. Gur'yanova, E.F., *Beloe more i ego fauna* (The White Sea and Its Fauna), Petrozavodsk: 1948.
12. Deryugin, K.M., Fauna of the White Sea and Conditions of Its Dwelling, *Issledovaniya morei SSSR*, vols. 7–8, 1928.
13. Zelikman, E.A., Arctic Pelagic Communities, *Okeanologiya. Biologiya okeana. T. II. Biologicheskaya produktivnost' okeana* (Oceanology. Ocean Biology: Vol. II. Biological Productivity of the Ocean), Vinogradov, M.E., Ed., Moscow: Nauka, 1977, pp. 43–55.
14. Ivanova, S.S., Zooplankton of Chupa Bay, *Materialy po kompleksnomu izucheniyu Belogo morya* (Materials on Multidisciplinary Studies of the White Sea), Moscow: USSR Academy of Sciences, 1963, no. 2, pp. 17–31.
15. Ivanova, S.S., Qualitative and Quantitative Characteristic of the Benthos in Onega Bay of the White Sea, *Materialy po kompleksnomu izucheniyu Belogo morya* (Materials on Multidisciplinary Studies of the White Sea), Moscow: USSR Academy of Sciences, 1963, no. 1, pp. 355–380.
16. *Instruktsiya po sboru i obrabotke planktona* (Guide for Plankton Collection and Processing), Moscow: Vses. Nauch.-Issl. Inst. Rybn. Khoz. Okeanogr., 1971.
17. Kamshilov, M.M., Winter Zooplankton of the White Sea, *Dokl. Akad. Nauk SSSR*, 1952, vol. 85, no. 6, pp. 1403–1406.
18. Kamshilov, M.M., New Data on the White Sea Plankton, *Materialy po kompleksnomu izucheniyu Belogo morya* (Materials on Multidisciplinary Studies of the White Sea), Moscow: USSR Academy of Sciences, 1957, pp. 305–314.
19. Kosobokova, K.N., New Data on the Life Cycling of *Calanus glacialis* in the White Sea (From Seasonal Observations of the Development of Generative System), *Okeanologiya*, 1998, vol. 38, no. 3, pp. 387–396.
20. Kosobokova, K.N. and Pertsova, N.M., Biology of the Arctic Copepod *Calanus glacialis* in the White Sea, *Biologicheskii monitoring pribrezhnykh vod Belogo morya* (Biological Monitoring of the Coastal Waters of the White Sea), Moscow: Shirshov Inst. Oceanology, Russian Academy of Sciences, 1990, pp. 57–71.
21. Kosobokova, K.N., Rat'kova, T.N., and Sazhin, A.F., Zooplankton Under the Ice of Chupa Bay, the White Sea, in the Summer of 2002, *Okeanologiya* (in press).
22. Kravets, A.G., Features of Formation of the Surface Thermal Inhomogeneities in the White Sea and Their Application to Indicate the Regions with Enhanced Biological Productivity, *Tez. dokl. konf. "Problemy izucheniya, ratsional'nogo ispol'zovaniya i okhrany prirodnykh resursov Belogo morya* (Conference "Problems of Research, Rational Use, and Protection of Natural Resources of the White Sea, Abstracts of Papers), Arkhangel'sk: 1985, pp. 45–46.
23. Lukashin, V.N., Kosobokova, K.N., Shevchenko, V.P., *et al.*, Results of Multidisciplinary Oceanological Studies in the White Sea in June 2000, *Okeanologiya*, 2003, vol. 43, no. 3.
24. Naletova, I.A., Sapozhnikov, V.I., and Metreveli, M.P., Production–Destruction Processes in the White Sea, *Kompleksnye issledovaniya ekosistemy Belogo morya* (Multidisciplinary Studies of the White Sea Ecosystem), Moscow: Vseross. Nauch.-Issl. Inst. Rybn. Khoz. Okeanogr., 1994, pp. 76–82.
25. Pertsova, N.M., Sostav i dinamika biomassy zooplanktona proliva Velikaya Salma Belogo morya, *Tr. Belomorskoi biol. st. Mosk. Gos. Univ.*, Moscow: Mosk. Gos. Univ., 1962, vol. 1, pp. 35–50.
26. Pertsova, N.M., Mean Weights and Sizes of the Mass Zooplankton Species in the White Sea, *Okeanologiya*, 1967, vol. 7, no. 2, pp. 305–313.
27. Pertsova, N.M., Zooplankton of Kandalaksha Bay of the White Sea, *Tr. Belomorskoi biol. st. Mosk. Gos. Univ.*, Moscow: Mosk. Gos. Univ., 1970, vol. 3, pp. 34–45.
28. Pertsova, N.M., On the Quantitative Vertical Distribution of Zooplankton in Kandalaksha Bay of the White Sea, *Kompleksnye issledovaniya prirody okeana* (Multidisciplinary Studies of the Nature of the Ocean), Moscow: Mosk. Gos. Univ., 1971, no. 2, pp. 153–162.
29. Pertsova, N.M., Life Cycle and Ecology of the Warm-Water Copepod *Centropages hamatus* in the White Sea, *Zool. Zh.*, 1974, vol. 53, no. 7, pp. 1013–1022.

30. Pertsova, N.M., Distribution and Life Cycle of *Metridia longa* Lubbock in the White Sea, *Tr. Belomorskoi biol. st. Mosk. Gos. Univ.*, Moscow: Mosk. Gos. Univ., 1974, pp. 14–31.

31. Pertsova, N.M., Features of Life Cycling of Warm-Water Neritic Copepods as a Reason for the Seasonal Changes in the Abundance of Zooplankton in the White Sea, *Kompleksnye issledovaniya prirody okeana* (Multidisciplinary Studies of the Nature of the Ocean), Moscow: Mosk. Gos. Univ., 1980, no. 7, pp. 278–273.

32. Pertsova, N.M., Zooplankton Distribution in the Basin and Kandalaksha Bay of the White Sea, *Tr. Belomorskoi biol. st. Mosk. Gos. Univ.*, Moscow: Mosk. Gos. Univ., 1980, vol. 5, pp. 49–68.

33. Pertsova, N.M., Zooplankton of the Gorlo of the White Sea and Mezen' Bay, *Ekologiya i fiziologif zhivotnykh i rastenii Belogo morya* (Ecology and Physiology of Animals and Plants of the White Sea), Moscow: Mosk. Gos. Univ., 1983, pp. 17–25.

34. Pertsova, N.M. and Kosobokova, K.N., Interannual Changes in the Biomass and Distribution of Zooplankton in Kandalaksha Bay of the White Sea, *Okeanologiya*, 2002, vol. 42, no. 2, pp. 240–248.

35. Pertsova, N.M. and Kosobokova, K.N., Zooplankton of the Estuary of Minor Rivers of Kandalaksha Bay of the White Sea, *Tr. Belomorskoi biol. st. Mosk. Gos. Univ.*, Moscow: Mosk. Gos. Univ., 2002, vol. 8, pp. 175–184.

36. Pertsova, N.M. and Prygunkova, R.V., Zooplankton, *Beloe more. Biologicheskie resursy i problemy ikh ratsional'nogo ispol'zovaniya. Issledovaniya fauny morei* (The White Sea. Biological Resources and Problems of Their Rational Use. Studies of Marine Fauna), 1995, vol. 42 (50), Part I, pp. 115–141.

37. Pertsova, N.M. and Sakharova, M.I., Zooplankton of Velikaya Salma Bay (White Sea) as Related to the Features of the Hydrological Regime in 1966, *Okeanologiya*, 1967, vol. 7, no. 6, pp. 1068–1075.

38. Pertsova, N.M. and Sakharova, M.I., Features of the Zooplankton Development in the Coastal Regions of Kandalaksha Bay (Velikaya Salma) in 1966–1967, *Tr. Belomorskoi biol. st. Mosk. Gos. Univ.*, Moscow: Mosk. Gos. Univ., 1970, vol. 3, pp. 22–33.

39. Perueva, E.G., On the Feeding of Copepodite IV of *Calanus glacialis* Jaschnov from the White Sea on the Colonial Alga *Chaetoceros crinitus* Schutt, *Okeanologiya*, 1976, vol. 16, no. 6, pp. 1087–1091.

40. Perueva, E.G., Daily Feeding Rhythm of Copepodite IV of *Calanus glacialis* Jaschnov, *Okeanologiya*, 1977, vol. 17, no. 6, pp. 1085–1089.

41. Prygunkova, R.V., On the Development Cycle of Calanuses (*Calanus glacialis* Jaschnov) in the White Sea, *Dokl. Akad. Nauk SSSR*, 1968, vol. 182, no. 6, pp. 1447–1450.

42. Prygunkova, R.V., Seasonal and Annual Changes in the Zooplankton of Chupa Bay of the White Sea, *Cand. Sci. (Biol.) Dissertation*, Leningrad: Zool. Inst. Akad. Sci. USSR, 1970.

43. Prygunkova, R.V., Selected Features of Seasonal Development of Zooplankton of Chupa Bay of the White Sea, *Sezonnye yavleniya v zhizni Belogo i Barentseva morei. Issled. fauny morei. T 13 (21)* (Seasonal Phenomena in the Life of the White and the Barents Seas. Studies of Marine Fauna), Leningrad: Nauka, 1974, pp. 4–53.

44. Prygunkova, R.V., Spatiotemporal Changes in the Structure and Abundance of Zooplankton in Kandalaksha Bay of the White Sea in the Summer Period, *Morskoi i presnovodnyi plankton* (Marine and Freshwater Plankton), Leningrad: Zool. Inst. Akad. Nauk SSSR, 1987, pp. 68–82.

45. Timonov, V.V., Principal Features of the Hydrological Regime of the White Sea, *Sb. pamyati Shokal'skogo* (Shokal'skii in Memoriam. Collection of Papers), Moscow, 1950, vol. 2, pp. 206–236.

46. Fedorov, V.D., Zhitina, L.S., Korsak, M.N., and Belaya, T.I., Distribution of Biomass and Production of Phytoplankton in the White Sea Basin, *Biol. Nauki*, 1980, vol. 11, no. 11, pp. 72–75.

47. Fedorov, V.D., Il'yash, L.V., Kol'tsova, T.I., *et al.*, Phytoplankton. Ecological Studies of Phytoplankton, *Beloe more. Biologicheskie resursy i problemy ikh ratsional'nogo ispol'zovaniya. Issledovaniya fauny morei* (The White Sea. Biological Resources and Problems of Their Rational Use. Studies of Marine Fauna), 1995, vol. 42(50), Part. I, pp. 79–91.

48. Epshtein, L.M., Zooplankton of Onega Bay and Its Significance for the Feeding of Herring and Fish Juveniles, *Materialy po kompleksnomu izucheniyu Belogo morya i vnutrennikh vodoemov Karelii* (Materials on Multidisciplinary Studies of the White Sea and Inland Basins of Karelia), Moscow: USSR Academy of Sciences, 1957, vol. 1, pp. 315–349.

49. Epshtein, L.M., Zooplankton of the White Sea and Its Significance for the Feeding of Herring, *Problemy ispol'zovaniya promyslovykh resursov Belogo morya i vnutrennikh vodoemov Karelii* (Problems of the Use of Fishery Resources of the White Sea and Inland Basins of Karelia), Moscow: USSR Academy of Sciences, 1963, no. 1, pp. 98–104.

50. Yashnov, V.A., *Plankticheskaya produktivnost' severnykh morei SSSR* (Planktic Productivity of the Northern Seas of the USSR), Moscow: Mosk. Obshch. Isput. Prirody, 1940.

51. Berger, V., Dahle, S., Galaktionov, K., *et al.*, *White Sea: Ecology and Environment*, St. Petersburg–Tromso: Berger, V. and Dahle, S., Eds., 2001.

52. Fowler, S.W. and Knauer, G.A., Role of Large Particles in the Transport of Elements and Organic Compounds Through the Oceanic Water Column, *Prog. Oceanography*, 1986, vol. 16, pp. 147–194.

53. Kosobokova, K.N., The Reproductive Cycle and Life History of the Arctic Copepod *Calanus glacialis* in the White Sea, *Polar Biology*, 1999, vol. 22, pp. 254–263.

54. Kosobokova, K.N., Zooplankton Investigations in the 49th Cruise of the R/V *Prof. Schtockman* in the White Sea, Summer 2001, *Abstracts of LOIRA*, 2002, Moscow, November 12–15, 2002, p. 58.

55. Lampitt, R.S., Noji, T., and von Bodungen, B., What Happens to Zooplankton Faecal Pellets? Implications for Material Flux, *Marine Biology*, 1990, vol. 104, pp. 15–23.

56. Olli, K., Riser, C.W., Wassmann, P., *et al.*, Seasonal Variation in Vertical Flux of Biogenic Matter in the Marginal

Ice Zone and the Central Barents Sea, *J. Mar. Syst.,* 2002, vol. 38, pp. 189–204.

57. Pertzova, N.M. and Kosobokova, K.N., Comparative Study of Distribution and Life Cycles of the Dominant Copepod Species in the White Sea, *Abstr. 6th Intern. Conf. Copepoda*, Oldenburg: 1996, p. 88.

58. Pertzova, N.M. and Kosobokova, K.N., Zooplankton of the White Sea. History of Investigations and the Present State of Knowledge—A Review, *Berichte zur Polarforschung*, 2000, no. 359, pp. 30–41.

59. Rachor, E., Scientific Cooperation in the Russia Arctic: Ecology of the White Sea with Emphasis on its Deep Basin, *Berichte zur Polarforschung*, 2000, no. 359.

60. Rat'kova, T.N., The White Sea Basin Phytoplankton—A Review, *Berichte zur Polarforschung*, 2000, no. 359, pp. 23–29.

61. Riser, C.W., Wassmann, P., Olli, K., and Arashkevich, E., Production, Retention, and Export of Zooplankton Faecal Pellets on and off the Iberian Shelf, North-West Spain, *Prog. Oceanogr.*, 2001, vol. 51, pp. 423–441.