

**Scientific Cooperation in the Russian Arctic:
Ecology of the White Sea
with Emphasis on its Deep Basin**

Edited by Eike Rachor

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Foreword

The White Sea as an „internal“ Russian water was out of bounds of the majority of western scientists for decades until the early 1990s. Nevertheless, this sea became one of the best investigated in the Soviet Union, although a great part of this knowledge has not been accessible to much of the international scientific community because of linguistic and former political reasons.

In 1993, the Zoological Institute of the Russian Academy of Sciences in St. Petersburg, and the Alfred-Wegener-Institute for Polar and Marine Research in Bremerhaven, initiated cooperative studies in benthic ecology and ecophysiology at the White Sea Biological Station (WSBS) at Cape Kartesh (Chupa Inlet, Kandalaksha Bay). This cooperation has proven very successful, and, by including research groups from Moscow State University, the P.P. Shirshov-Institute of Oceanology as well as from VNIRO, a research proposal was made to INTAS (International Association for the promotion of cooperation with scientists from the New Independent States of the former Soviet Union, Brussels) to investigate the ecology of the the deep basin part of the White Sea, which previously had been poorly studied.

As a baseline for this and other future cooperation, short review papers about the existing, mainly Russian, knowledge have been prepared, which form the bulk of this specific issue of „Berichte zur Polarforschung“. A few more articles deal with the zoobenthos of the basin and results obtained during the new Russian-German cooperation in the White Sea, the majority of which was financed by INTAS.

The editor acknowledges the support given by all Russian partners for this work, but, also the subsistence provided by INTAS and his home institute (AWI). Editing work was partly aided by Ksenia Kossobokova (Moscow), Alina Agatova (Moscow) and most of the authors, to whom I am indebted especially for answering the many exhausting questions I raised after first reading.

During editing I learned that another, more general, review booklet is being prepared by Russian and Norwegian colleagues (eds. Berger & Dahle). I hope that both together will help scientists to plunge more deeply into the ecology of the not-so-blank White Sea.

April 2000

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Fig. 1: The White Sea

A. Reviews

General features of the White Sea

Morphology, sediments, hydrology,
oxygen conditions, nutrients and organic matter

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The White Sea (Beloe Morye) belongs to the marginal seas of the Arctic Ocean. It is connected with the Barents Sea by a 50 km wide and shallow strait, named Gorlo, and the spacious northernmost water area known as Voronka. According to Sailing Manuals, the northern boundary of the White Sea is the line connecting Capes Svyatoy Nos and Kanin Nos (Fig. 1). The area of the White Sea is equal to 89,600 km², its volume is 5,400 km³, the average depth – 60 m and its maximal depth - 343 m (Babkov, Golikov, 1984).

The coast line of the Kandalaksha and Onega Bays is of complicated configuration with a lot of islands and inlets. The western coast is hilly, while the eastern one is mainly lowland. In some places the altitude of the Kandalaksha shore reaches 650 m. The western coasts of the sea are formed mainly by granite cliffs. Clayey flats and sandy beaches dominate on the eastern coast.

In the northern part, the Voronka, the depth reaches 60-70 m (Fig 2). It decreases gradually to the South to 30-40 m. A fairly deep trough approaches Tersky Shore (Bereg) connecting the Voronka with the profound part of the Gorlo. A shallow zone lies along Kanin Shore. Within the Mezen Bay, where the depth rarely exceeds 20 m, extended shallows exist with a hollow-wise descent in the axial region as a continuation of the Mezen river-bed. The average depth of the Gorlo Strait is about 40 m. There are some troughs and ridges that stretch parallel to Tersky Shore in the West and Zimny (Winter) Shore in the East. The bottom relief of the Dvina Bay is relatively smooth. In the southern and south-eastern parts of the bay there are a number of banks. Depths over 100 m lie in the northern part of the bay. The Onega Bay is stretched in north-west to south-east direction, with the largest depth of about 50 to 60 m being localized in its centre.

The deepest part of the White Sea, the Basin, occupies the central part of the sea. Depths exceeding 200 m take up about a half of the total area of the Basin. The bottom relief of this region is characterized by local separate eminences and significant heights at its periphery. The Kandalaksha Bay is closely related to the Basin by its bottom relief. The greatest depth of the sea – 343 m - is recorded just there in the vicinity of Cape Tury. Towards the North-West the depth of Kandalkasha Bay sharply rises up to 100 - 50 m.

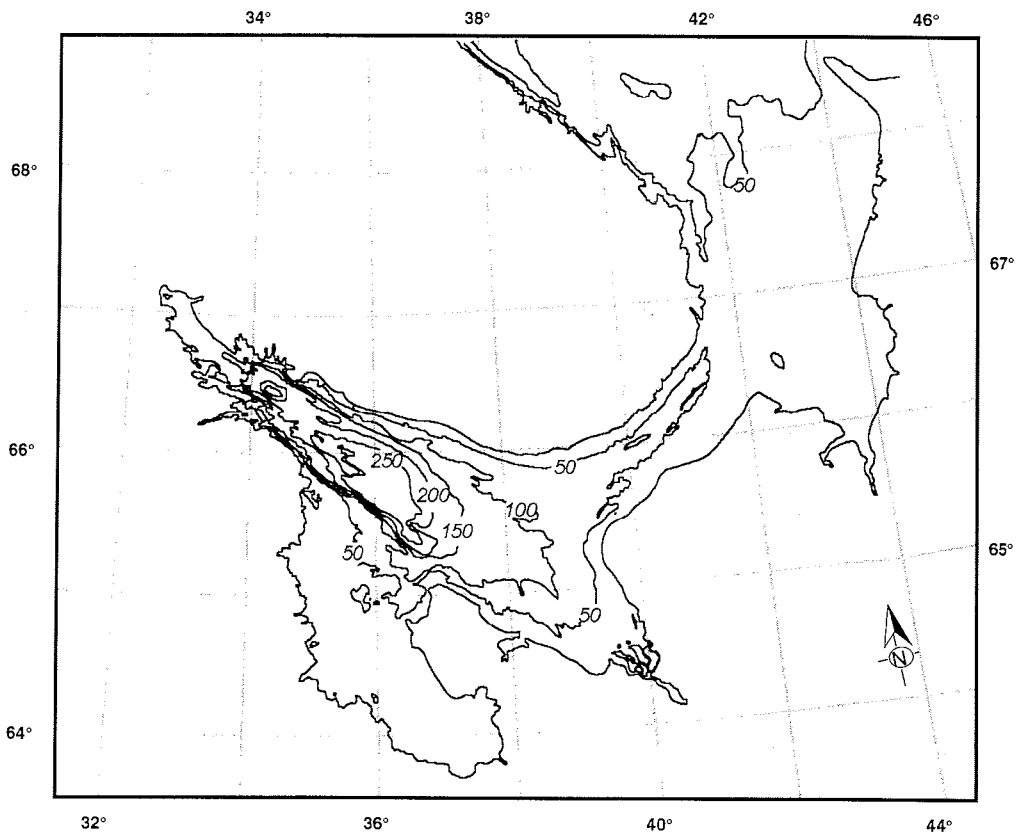


Fig 2: Bathymetric map of the White Sea. Depth contours in metres

Bottom sediments of the White Sea are very different by their mechanical composition (Nevessky et al., 1977). A high content of sandy fractions (about 70%) is characteristic for the northern shoal of the sea and the Gorlo. Only near Cape Kanin Nos the content of sandy fractions decreases considerably (10-30 %), due to the enrichment of the sediments with aleurite (mainly silt) components. Pebble and gravel components are contained in certain regions of the Voronka, Gorlo and Mezen Bay in amounts of about 30-50% and even more. Near Tersky Shore (in the North) sands contain many bivalve and barnacle shells. In the Basin area this coast is framed with a narrow stripe of sediments comprising up to 70% of sand or is built of sandstone cliffs. As the depth increases, the sediments become gradually enriched in fine-grained material. In the deep part of the Basin the amount of pelite (clayey) components reaches 70-90%. This fraction dominates in the deepest parts of the Dvina Bay also, whereas sand is concentrated in the shallow area due the intensive water movements there. In the Kandalaksha Bay pelite sediments lie in the deepest zones while at depths of less than 100 m sand and silt dominate. In the Onega Bay large areas of the bottom are occupied by sands or sandy aleurite fractions. More information, especially about sediment geochemistry, is found in the contribution of Strekopytov (this volume).

In the Voronka and Gorlo the summer temperature of the water at the surface is about 6-8° C. In the Gorlo vertical homothermy is observed due to the strong turbulent water movement caused by the tidal wave. In the Onega Bay one can find a similar situation. The only difference is that in summer the temperature of its water is a little bit higher – about 9-12° C. In the Onega and Kandalaksha Bays, the Basin and the top of the Dvina Bay, in summer, waters are warmed more (up to 15-20° C) than in the Voronka, Gorlo and Mezen Bay. Due to intensive water circulation summer warming is still effective to water layers about 15 m deep. Below that level the water temperature sharply decreases and reaches negative values at the depth of about 50-60 m. The lowest temperature, about –1.5° C, is registered in the deep water hollows of the White Sea (Derjugin, 1928). The temperature of surface water in winter is close to the water freezing point at corresponding salinity.

The salinity of the White Sea is considerably lower than that of the Barents Sea. This is due to a bulk fresh water run-off and limited water exchange with the Barents Sea. The salinity of the surface waters in the Basin and open parts of bays varies from 24 to 27 psu (‰). The salinity of deep water regions of the sea is about 29.5-30 (Derjugin, 1928, and own measurements). However, in the estuaries of large rivers it falls down to 5-8 and even less. In the Gorlo, the water salinity reaches 29 near Tersky Shore, and 24 near Zimny Shore. Further to the North salinity increases up to 32 at the boundary with the Barents Sea (Naumov, Fedyakov, 1991). Sharp seasonal variations of surface water salinity are typical for the White Sea, which can be explained by the dynamics of freshwater inflow. Freshening of surface water begins in winter when the sea is covered with ice. The most prominent

decrease in salinity of the upper layer is observed in April-May just before and during the period of ice-melting (Babkov, Lukanin, 1985).

Like in most seas of the Northern hemisphere, a permanent current circumscribes the White Sea in counter-clockwise direction. Besides, it forms separate gyres. In the insular regions of the sea, particularly in the Onega and Kandalaksha Bays, the pattern of stable currents is extremely complicated. The average velocity of the relatively stable currents is comparably low: not more than 10-20 cm/s.

The tides in the White Sea are regular semi-diurnal (in the Gorlo and near Tersky shore) and shallow (asymmetrical) semi-diurnal in the other parts of the sea. The tidal wave comes from the Barents Sea into the Voronka and Gorlo causing in the mouth of the Mezen River very high tides, reaching 8-9 m. In the Basin and bays the amplitude of the tide decreases and does normally not exceed 2-2.5 m. The speed of tidal currents is rather high and reaches 5 knots in the Gorlo and 2 knots in the Onega Bay (Oceanographic conditions..., 1991).

In the water balance of the White Sea an essential role is played by the river run-off delivering about 95% of net fresh water entering the sea. Evaporation and precipitation practically compensate each other. The river freshet determines seasonal variations of the water exchange between the Barents and White Seas. The spring flood in May-June provides about 50% of the annual delivery of river water. Consequently, at this time the exchange between the seas is intensified. 240 km³ of land runoff waters flowing into the White Sea, after transformation, outflow from it annually. Total annual water outflow is 450-600 km³; accordingly, there is a substantial water renewal from the Barents Sea, 220-390 km³. The theoretical „layer“ of river inflow water in the White Sea amounts to 2.6 m per year, the layer of precipitation – about 37 cm, evaporation – about 24 cm. But, seasonal variations of the sea level do not exceed a few centimetres (Elisov, 1997).

Waters of the White Sea contain a relatively big amount of oxygen, varying from 6.06 to 8.59 ml/l. The most aerated are surface waters of the Onega Bay and Gorlo. Nevertheless, even in bottom layers of water in the Kandalaksha and Dvina Bays and at the maximal depth of the Basin the oxygen content is rather high: 6.6-7.8 ml/l (ca. 75-95 % saturation).

About 2.13×10^6 tons of oxygen per year are advected to the White Sea with the Barents Sea waters. This inflow is approximately equal (Maximova, 1991) to the out-flow to the Barents Sea which makes $2.1-2.2 \times 10^6$ tons per year. Therefore, the oxygen balance of the White Sea is mainly determined by autochthonous processes. Oxygen inflow with river waters and photosynthesis contribute to oxygen input besides absorption from the atmosphere.

Data on the seasonal dynamics of oxygen content in water indicate that the surface waters are most saturated with oxygen in spring. In summer and especially in autumn the amount of

oxygen decreases due to reduction in the photosynthetic activity, warming and intensification of oxidative processes, mainly owing to respiration.

In the water of the White Sea biogenic elements (carbon, nitrogen, phosphorus, silicon and microelements) are present mainly in the form of organic compounds. Besides, they undergo substantial seasonal variations. This occurs due to an intensive consumption of the inorganic forms of these components during the period of spring growth of phytoplankton.

Inorganic nitrogen is present mainly in the maximally oxidized form, e.g. nitrates make about 80% of all nitrogen containing inorganic substances. The average concentration of nitrates in the White Sea varies from 52 mg/m³ at the surface to 70 and more mg/m³ near the bottom. In the photic layer in spring the maximal concentration of nitrates (60 mg/m³) has been discovered in the Onega Bay, the minimal – 20 mg/m³ – in the Basin.

Nitrite nitrogen, the share of which in the total inorganic nitrogen of the White Sea is not more than 10%, does not play any significant role in supplying nitrogen to phytoplankton. In the photic layer its content may be about 1.7 mg/m³. Maximum concentrations of nitrites may occur in different water masses of the White Sea, e.g. sometimes in the Mezen and Onega Bays, but, also in the Kandalaksha Bay and the Basin.

Ammonia nitrogen reaches maximal concentrations of about 20 mg/m³ in autumn after the processes of ammonification are completed. In winter its concentration falls 2-4 times.

Inorganic forms of phosphorus containing compounds are represented in the White Sea water mainly by phosphates. The average concentration of phosphorus over many years is equal approximately to 20 mg/m³. In the photic layer it does not exceed 15 mg/m³.

Though the concentration of phosphorus in the photic layer decreases significantly during the peak of the vegetation period, it should be noted that it is seemingly still not the minimum, limiting factor for the development of phytoplankton.

The content of silicon in the water of the White Sea varies considerably. Its concentration does not reach the analytical zero in the photic layer in the period of extensive blooming of phytoplankton. According to the data recorded during many years (Maximova, 1991) the content of silicon acid in the Mezen and Dvina Bays may not fall below 500 and 400 mg/m³, respectively. The maximal content of silicon was registered in the water of the Dvina Bay – 2000 mg/m³ and even more. In the deep regions the concentration of silicon is more or less stable over the whole sea: 450 mg/m³.

The classical stoichiometric ratio of the main biogenic elements (Si : N : P) in the Ocean water is 20 : 7 : 1. In the photic layer of the White Sea this ratio may sometimes rise to 25 : 2.4 : 1, which indicates a shift towards an increased content of silicon and a decreased content of nitrogen compared to the normal oceanic water. Hence, it can be concluded that nitrogen, when present at minimal concentrations, may become a limiting factor for the growth of phytoplankton and that its recycling may be of great significance for production e.g. in summer.

The content of total organic matter in different water basins is usually estimated by doubling the concentration of organic carbon. On average, 7 mg/l of suspended and dissolved organic compounds are contained in the White Sea waters. Their concentration normally varies within a narrow range: 5-10 mg/l. Higher concentrations of organic substances are usually registered only near the mouths of rivers falling into the White Sea (Maximova, 1991).

The production of phytoplankton amounts to 3-4 Mio. C per year in the total balance of organic matter. About 5.4 Mio. tons C are delivered with the river run-off. These organic substances play a versatile role in energy processes in the sea. The quite labile organic matter produced by phytoplankton is more important, since it is entirely included into the biological energy and substance cycles. A part of the allochthonous organic matter delivered with rivers is utilized only slowly.

One can judge on the extent of the utilization of organic substances by the ratio of biochemical consumption of oxygen to permanganate oxidation (although permanganate reduction is influenced by additional factors). For a labile and easily assimilated organic matter of plankton genesis this ratio is about 1. Lower values of the ratio indicate a greater stability of organic compounds and their lesser capability to be assimilated. According to available data (Maximova, 1991), in the White Sea, this parameter normally varies from 0.5 to 0.75. Near river mouths, where the content of allochthonous organic matter is high, the ratio is much lower: 0.15 - 0.25.

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Geochemical investigations in the White Sea

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It is known that geochemical conditions in marine sediments, especially redox properties of sediments, are very important for the ecology of benthic fauna. This fact explains why the properties of the White Sea sediments have attracted the attention not only of geologists, but also that of biologists (Derjugin, 1928). Geochemical studies of the White Sea sediments were initiated in the 1920s after the expeditions of the Marine Scientific Institute (Plavinornin), during which sediments were sampled from a transect from the Dvina Bay to the Kandalaksha Bay and several cross transects. Contents of major chemical elements were determined, and it was shown that the surface layer of sediments is enriched in Fe, Mn and P. Sediments were divided into two types by color: brown or tan and gray with black spots. First determinations of reduced sulfur in the White Sea sediments have shown that about 0.1% of acid volatile sulfides is a sufficient content for the black coloration of sediment (Gorshkova, 1931). The brown-gray color transition that was found downward the sediment core was explained by reduction processes (Samojloff and Gorshkova, 1924).

The next stage in the geological and geochemical studies of the White Sea were the expeditions of the Shirshov Institute of Oceanology (1964 – 1968). Results of these investigations were presented in a monograph, "The White Sea: Sedimentogenesis and Holocene Development", covering nearly all aspects of marine geology (Nevesky et al., 1977). By now, this book is the most comprehensive source of geological and geochemical data on the White Sea.

The distribution of major chemical elements and forms of iron, as well as contents of carbonate carbon, organic carbon and amorphous silica was studied for all regions of the White Sea. The maxima of contents of C_{org} , Fe, Mn, P, and Ti are located in the deep parts of the White Sea Basin near the boundaries of the Kandalaksha Bay and the Dvina Bay. The location of these maxima corresponds to the central parts of the stationary cyclonic gyres (Nevesky et al., 1977). Content of manganese in the White Sea sediments (up to 2% in the Basin) is higher than that in sediments of the other Arctic seas (Gorshkova, 1966). The high content of manganese can be explained by its transportation from the land in a form bound to humic substances and, then, deposition in deep central parts. Though a comprehensive set of experimental data for the White Sea sediments exists, diagenetic redox transformations in them were poorly

investigated. Contents of reactive iron that reflect to some extent the redox conditions were obtained only for a few horizons of sediments (Kalinenko et al., 1972), and forms of reduced sulfur have never been studied. It was shown that the upper part of the sediment core (0.5–10 cm) is oxidized, and downward the column, the Fe (III) content is decreased down to the limit of detection, while the Mn content is decreased to the lithogenic background (0.04–0.07%) (Kalinenko, 1975). In general, reduction processes in the deep Basin sediments are quite slow in spite of the relatively high content of organic carbon (1–2.5%). Gorshkova (1975) showed that the content of humic substances in the sediments of the White Sea Basin is about 50% of the bulk organic carbon content. The relatively low content of easily metabolizable organic matter (OM) in the central part of the White Sea may lead to the weak diagenetic alterations in sediments, e.g., low scales of sulfate reduction. Oxidized conditions in the surface layer of sediments are supported by high concentrations of dissolved oxygen in deep waters (typically >80% of oxygen saturation).

The rates of production of OM in littoral and sublittoral zones are of great interest because of the input of such OM to the deeper parts of the sea. In some inlets of the Kandalaksha and Dvina bays the sediment content of C_{org} increases up to 4% reflecting the input of macroalgal and terrigenous, poorly metabolizable OM (Gorshkova, 1975). The genesis of sublittoral OM can probably be studied using the composition of humic acids: river-borne OM contains mainly high- and intermediate-molecular fractions of humic acids (Bek et al., 1992). The sublittoral zone may also be subjected to the consequences of human activities: Addition of metabolizable OM, for example from the mariculture of mussels, may deteriorate the oxygen regime at the bottom (Chivilev and Ivanov, 1997).

One of the characteristic features of the White Sea sediments is the formation of ferromanganese concretions. According to the opinion of V.V.Kalinenko (1988), Fe-Mn aggregates are more abundant in the White Sea than in the other Arctic Seas, which is in accordance with the higher content of Mn in sediments. The process of Fe-Mn ore formation begins with thin oxyhydroxide crusts and finishes with the formation of large concretions (10–12 cm in diameter) (Samojloff and Gorshkova, 1924). Comprehensive data on these Fe-Mn aggregates are presented in the papers of Derjugin (1928) and Gorshkova (1931), where flat and round concretions (from several mm to 10–12 cm in diameter) and Fe-Mn crusts on bivalves and polychaete tubes with different Fe/Mn ratio are described. The role of the microbial community in the formation of Fe-Mn aggregates in the White Sea sediments was mentioned for the first time by Butkewitsch (1928) and Perfiljew (1927). The microbiological origin of the Fe-Mn crusts on the shells of bivalves was proved by Zavarzin (1964), who has also shown that the

presence of the live mollusk itself is not necessary for the formation of a crust. The level of Mn accumulation in the sediments of the White Sea and abundance of Fe-Mn concretions in them are similar to those in the Kara Sea and in the semi-closed regions of the Baltic Sea (Gulf of Bothnia and Gulf of Riga). According to Gorshkova (1967), concentration of Mn in sediments depends on the amount of Mn supplied by river runoff and the character of water exchange in the sea.

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Life in the depth of the White Sea - What is known about it

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The scientific investigation of the White Sea was initiated more than 100 years ago. Due to objective difficulties, the deepest parts of the Sea, named Basin, are known much worse than the shallow ones. This basin part of the White Sea is a large depression with a maximum depth of 343 m, situated at the boundary of the Kola and the White Sea platforms. The shape of the Basin is more or less elliptic with apexes in the North-West and South-East; its area is 218 km², and its volume – 27.25 km³.

Since 1882, by the European Northern Marine Biological Station at the Solovki Islands, only Boreal species had been marked in the White Sea waters. N.M. Knipowitsch (1893) was the first who had found the typical Arctic mollusc *Portlandia arctica* in Dolgaya Inlet, Solovetsky Island. At the first time he considered this fact as an amazing exception till he found (1896) real Arctic communities in the deep areas of the Sea. At the same time he had found out stable negative temperatures in water depths below 150 m. He supposed (1906) a stagnation of cold winter water in the Basin, which allowed the species of Arctic origin to survive there since the last glaciation period.

More detailed observations of deep-water bottom communities were made by K.M. Derjugin (1928). They enlarged the species list of Arctic origin and confirmed Knipowitsch's idea that the whole Basin at depths of more than 150 m is occupied by cold-water assemblages.

At the same time V. V. Timonov (1929) studied the hydrological regime of Gorlo Strait, the connection of the White Sea with the Barents Sea. He suggested that the cold winter water of the Gorlo Strait flew down to the Basin causing the water exchange and preventing permanent stagnation. The general scheme of water exchange between the Barents and White Seas was published by V.V. Timonov in 1947.

It should be noticed that neither Gorlo Strait nor Voronka have Arctic species in their sea floor assemblages. Only in the shallow waters of the Kara Sea one can observe similar Arctic communities like in the deep White Sea. So, there is a large gap in the distribution areas of Arctic organisms. The similarity of faunas of the White and Kara Seas is not accidental and comes from the earlier postglacial times when Arctic marine species were distributed along the edge of the glacier (Naumov et al., 1986; see also Ekman, 1953).

A number of cruises of the research vessel of Moscow State University were organized in the 1970-ies. It was nearly the first attempt to get quantitative benthic samples in the area under discussion. The material obtained allowed O.I. Malutin (1980) to make clear the trophical relations of the central part of the White Sea. Deposit feeders form about 95% of

biomass in deep-water communities. The other novelty of the Moscow State University research team work was the analysis of the granulometric composition of bottom sediments. It was found out that the deposits in the deep area consist mainly of clay particles less than 0.001 mm in diameter.

Applying the method of T , S , z -curves to summer hydrological data, A.N. Pantyulin (1974) developed a new model of the White Sea water structure. He suggested three vertically distributed water masses instead of two of previous authors. Later, the Moscow State University research team declared that the boundaries of distribution of different types of sediments and water masses were identical (Beklemishev et al., 1975). Nevertheless, N. L. Semenova (1979) discussing the ecological features of two most common zoobenthos species in the Basin, namely *Portlandia arctica* and *Nuculana pernula*, marked that the occurrence of the former is connected with size of sediment particles and of the latter – with cold water. It is a curious treatment of the subject, because *Portlandia* is a high Arctic species found in cold areas only, while *Nuculana* - an Arctic-Boreal one - occupies the temperate Onega Bay.

Using all-the-year-round data from different parts of the Sea, A. I. Babkov and A. N. Golikov (1984) proposed to return back to the classic Timonov's two water-layers scheme. Their main argument was that, due to huge seasonal changes, the upper water layer had to be excluded from analysis. This was required already by the founders of T , S , z -method (Helland-Hansen and Nansen, 1927).

During the last twenty years the benthic team of the White Sea Biological Station of the Zoological Institute RAS in St. Petersburg have provided ecological investigations overall in the Sea. Unfortunately there were no systematic observations in the deepest part of the Basin, but, the data obtained are quite similar to those got by the authors mentioned above.

Not only the central depression of the White Sea possesses an Arctic fauna (s. Naumov & Fedyakov, this volume). It was not surprising to find *Portlandia arctica* in the Dolgaya Inlet (Solovetsky Island). There are some more or less shallow inlets in Onega and Kandalaksha Bays with a ridge at their mouth, which have a water exchange similar to that of the open deep White Sea. As a result the cold water remains there for all the year round. Among such inlets, Dolgaya (Knipovich, 1893; Livanov 1911; Chudnov, 1926), Babye More (Gurvich, 1934), Lov (Naumov, 1979) and Kolvitsa (Naumov et al., 1986) were studied.

It is interesting to notice that in all this cases the maximum depth is approximately five times more than the depth of the sill, like in the White Sea itself as well. The only exception is the Babye More Inlet where this ratio is more than seven. Only this inlet has a stagnation area which is situated deeper than 25 m. The depth of the ridge of this inlet is about 5 m.

It is well known that bacterial production plays a great role in marine communities. Unfortunately, there were almost no studies carried out in the White Sea till now. We possess almost no data on bacterio-benthos, both of our own or got from scientific literature, at all. As for bacterio-plankton, only desultory and contradictory information of two or three papers is available. There is scarcely a reason to discuss these data before we get new material, although recycling of nutrients (especially N-compounds during summer) may play an important role (s. Berger & Naumov, this volume).

During previous investigations, only 9 quantitative deep-water stations were taken by the White Sea Biological Station (WSBS) of ZISP. The macro-zoobenthos communities found are rather similar, so they can be described all together. The results can well be compared with those of Deubel (1995), who analysed 4 deep basin stations and a 98 m deep one during a joint activity of the WSBS and the AWI Bremerhaven in July 1994. More details, especially about new results, are found in Naumov & Fedyakov (this volume) as well as in a short version Deubel's work (this volume, too).

The list of our previous stations follows (Table 1):

Table 1. *List of stations*

Latitude N	Longitude E	Depth (m)
65°25.00'	38°18.00'	105.0
66°39.00'	34°12.00'	110.0
66°36.00'	33°48.00'	290.0
65°40.00'	39°43.00'	155.0
66°10.00'	40°14.00'	140.0
66°25.30'	33°58.40'	147.0
66°27.40'	33°59.30'	198.0
66°28.20'	33°59.50'	249.0
66°28.90'	34°00.45'	325.0

The temperature at all the stations was about -1.49 °C, salinity oscillated between 28.82 and 30.10 psu. The sediment contained 54 per cent by volume of water.

136 species were found at depths of more than 100 m. The average biomass of the community was 52.9 g/m² (total wet mass, including shells in molluscs). Menhinick's species richness was equal to 5.729, the Shannon's species diversity measured by biomass – 4.2201 bit/g; and polymixness by biomass (Naumov, 1991) was 27.62 ± 1.72 %. Accordingly, we have there a polymixous community rich in species number, poor in biomass and having no forms strongly dominating by biomass.

(„Mixness“ is a measure of evenness with values near zero in case of even biomass distribution amongst species and near 100%, if only one species would make up almost all biomass. „Polymixous“ communities have values < 70%, „oligomixous“ > 85 %; assemblages with intermediate values are termed „mesomixous“.)

The biogeographical composition of White Sea deep-water community differs essentially from those found in other regions. First, one can notice a great percentage of Arctic species, producing almost one third of the total biomass of the deep-water assemblage (Fig. 1).

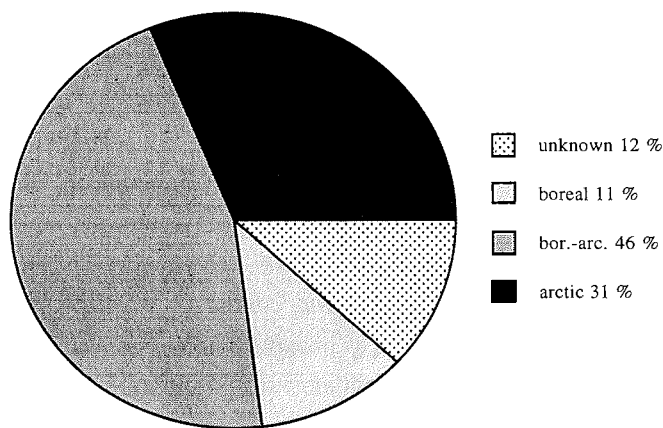


Fig. 1. *Biogeographic composition of the White Sea deep-water community.*

As soft sediments are widely found in the White Sea basin, the role of deposit feeders is extremely great (Fig. 2). The most abundant are epifauna species (63%, both, vagile and sessile), due to the same reason. Vagile burrowing forms produce 60% of total biomass in this community; for, there are very few hard substrata to attach for sessile species.

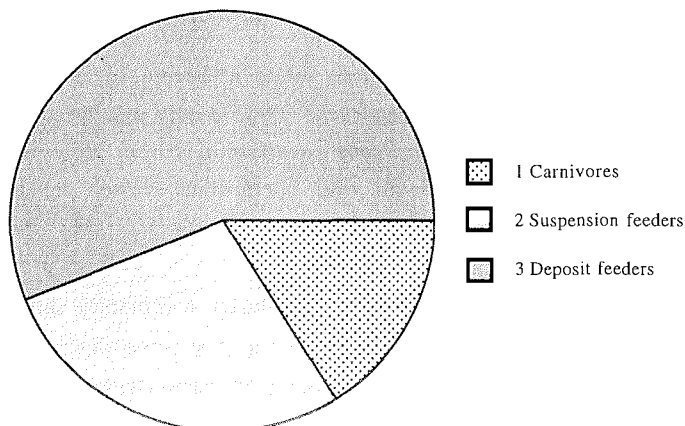


Fig. 2. Trophic composition of the White Sea deep-water community.

Portlandia arctica is the dominating species of the deep-water community, reaching a biomass of $8.9 \pm 4.4 \text{ g/m}^2$. *Gersemia fruticosa*, *Tealia felina* and *Urasterias lincki* (6.7 ± 7.1 , 6.0 ± 6.4 and $5.0 \pm 5.3 \text{ g/m}^2$, respectively) can be considered as subdominants. Their total biomass is 17.7 g/m^2 , and they form the main part of living organic matter together with next group of six species (*Nuculana pernula*, *Buccinum elatior*, *Dysidea fragilis*, *Hemithyris psittacea*, *Chiridota pellucida* and *Edwardsia sp.*), which contribute 15.6 g to the total biomass of the community. *Ophiura robusta*, *Ophiacantha bidentata*, *Pectinaria hyperborea*, *Golfingia sp.*, *Ophiopholis aculeata*, *Modiolus modiolus*, *Halecium beani*, *Flustra seculifrons* and *Lepeta coeca* play less important roles, and their overall biomass is 6.4 g only. The other 85 species contribute not more than 4.2 g/m^2 .

As for density, *Ophiura robusta* and *Portlandia arctica* are the most abundant. Their density is about 90 and 60 ind. per m^2 , respectively. Cirratulidae of several genera, *Myriochele oculata*, *Scoloplos armiger*, *Nuculana pernula*, *Apistobranthus tullbergi*, *Cylichna occulta* and *Maldane sarsi* can be referred as common ones (about 10 individuals per m^2), while *Nephtys malmgreni*, *Nuculana minuta*, *Nicania montagui*, *Dacrydium vitreum*, *Gammaropsis melanops*, *Leionucula belottii*, and *Thelepus cincinatus* are considered to be rare (about 5 individuals per m^2). The other 69 species are distributed with densities of 1 individual per m^2 or even less; accordingly, they were met only occasionally.

First new results of the macrofauna investigations within the INTAS-project about the deep basin ecology are included in this volume (Naumov & Fedyakov, 2000).

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Deep-water meiobenthos research in the White Sea

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During the last few decades the White Sea meiobenthic fauna and communities have been investigated extensively from many points of view. Both taxonomic and ecological continuous investigations have been conducted here at two biological stations and in numbers of expeditions. After twenty years of investigations, the White Sea became a model object for studies on meiobenthos community structures and dynamics including investigations of long-term changes, population structure of dominating species etc. These studies were partly reviewed by V.V. Galtsova (1991) and recently by H.U. Dahms, V.V. Galtsova and V.O. Mokievsky (in prep.). However, most of these studies were conducted in the intertidal and, rather seldom, in the upper subtidal zones.

The deepest part of the Sea still is nearly a „white spot“ of meiobenthic studies even from a taxonomical point of view. Only a few studies were done on material from the central basin of the sea. Several species of Enoplida (Nematoda) were described from there by I.N. Filipjev (1927). Some notes on Foraminifera inhabiting the Central basin were provided by E.I. Kirienko (1973). She supposed that agglutinated foraminiferans prevail there. Quantitative distribution and taxonomic composition of foraminiferans are different in the deep and shallow areas. During a large scale survey of Foraminifera distribution, E.M. Mayer (1977, 1980) collected several samples in the northern part of Central Basin down to a depth of 290 m. Among 161 species which are known for the Sea, only 95 occur in the central basin. The rate of calcareous forms increases with the depth - they constitute about 1% of whole community in the shallow zone, 20% in the intermediate depths and reach up to 50% of total foraminiferan density in the deep part. Total foraminiferan density according to this study reached the highest values (200-300 and more ind/10 cm³ in the uppermost sediment layer) in Kandalaksha Bay in depths ranging from 15 to 110 m. In the deep part (at depths of more than 200 m) the mean density of living forms is less than 51 ind/10 cm³.

The most recent studies covering most meiobenthic taxa were done in the central part of Kandalaksha Bay, where the meiobenthos abundance and composition were investigated along a transect down to a depth of 300 meters (Galtsova, Valdimirov, 1988). Quantitative distribution was there more or less typical for the sea.

Eumeiobenthos was represented by Foraminifera, Nematoda, Harpacticoida, Ostracoda and Halacarida, and pseudomeiobenthos included Polychaeta, Oligochaeta, Bivalvia, Gastropoda, Nemertina, Isopoda, Cumacea and Insecta. The dominance of different taxa changes with the depth: in intertidal and subtidal zones Nematodes prevail over the other, while in the depth of 150 m and more foraminiferans become more abundant. In terms of biomass, foraminifera also predominated in the deep part of the transect. Total density of meiobenthos varied on the transect from 6,300 to 3,168,000 ind/m² and biomass (wet weight) from 0.05 to 91 g/m². The maximal rates occur from the intertidal zone down to the depth of 7-10 meters and then decrease rapidly.

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The White Sea Basin phytoplankton - a review

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History of the phytoplankton investigations in the White Sea

The taxonomic composition of the White Sea phytoplankton has been studied since the 19th century (Goby, 1878; Merezhkovsky, 1878; Zenkovsky, 1881; Reingard, 1882). In the beginning of 20th century, these studies have been continued (Levander, 1916; Kiselev, 1925, 1957; Derjugin, 1928), however, at that early stage they presented only qualitative descriptions of the pelagic flora. First quantitative estimates of numbers of the phytoplankton cells in the water, and phytoplankton biomass were obtained by Voronkov and Krechman (1939) near Umba. The improvement of the sampling and processing methods during the last 30 years allowed to assess phytoplankton biomass, its relative composition (Kokin et al., 1971; Kokin & Koltzova, 1970; Konoplya, 1971; Sergeeva, 1991; Likhacheva, 1991; Sarukhan-Bek et al., 1991; Mordasova & Wentzel, 1994) and to evaluate primary production (Fedorov & Bobrov, 1977; Fedorov et al., 1974; Bobrov & Savinov, 1986; Maksimova, 1990; Naletova et al., 1994). While extensive studies regarding the seasonal dynamics of phytoplankton have been carried out in the coastal zone of the White Sea (the Kandalaksha Bay including the Chupa and Rugozerskaya Inlets, the Mezen and Onega Bays, Gorlo and Voronka) (Khlebovich, 1974; Semina & Sergeeva, 1983; Zhitina & Mikhailovsky, 1990; Lovyagin, 1990; Smirnov et al., 1989; Sarukhan-Bek et al., 1991), astonishing little is known about its dynamics in the Sea Basin. Very few expeditions collected phytoplankton in this area. Therefore, the seasonal variation there may be studied only by the comparison of data obtained in different years. So, the interannual variations may mask the seasonal changes.

In most studies during the last 30 years, plankton nets of different models and sizes have been used for phytoplankton sampling, while water bottles were used relatively rarely (Kokin et al., 1971; Konoplya, 1970; Khlebovich, 1974; Zhitina & Mikhailovsky, 1990). The phytoplankton samples were usually preserved with formaldehyde and then concentrated by filtration (net samples) or settling and decantation (bottle samples). These methods do not permit smaller phytoplankton counting, as small naked algae may be missed during the filtration or decantation and, in addition, may be partly destroyed by formaldehyde. Therefore, the small fragil phytoplankton cells with a diameter <20 μm have been ignored during the most previous investigations in the White Sea, which apparently resulted in considerable underestimations of the phytoplankton abundance. The first evaluations of the

small size phytoplankton abundance in the White Sea were presented by Likhacheva (1991), Mordasova & Wentzel (1994) and Ilyash (1998).

Phytoplankton composition

According to the revision by Semina & Sergeeva (1983), the list of the plankton algae of the White Sea includes 145 species and varieties, among which 92 taxa belong to Bacillariophyta (diatoms), 45 to Pyrrophyta (dinoflagellates), 4 to Chrysophyta (euchryomonads, coccolithophorides and silicoflagellates), 1 to Xanthophyta and 3 to Chlorophyta. In the Basin, 74 taxa were encountered (54 diatoms, 18 dinoflagellates and 2 silicoflagellates).

Among diatoms, the most diverse genera are *Chaetoceros* (33 taxa), *Coscinodiscus* (12 taxa) and *Thalassiosira* (9 taxa). Among dinoflagellates, the most diverse genus is *Peridinium* (23 taxa). From the 145 taxa encountered in the White Sea, 40% are cosmopolitan, 28% arcto-boreal, 5% bipolar, 1% arcto-boreal-tropical, and a few species are tropical (Semina & Sergeeva, 1983). Neritic and ice-neritic species dominate (Kiselev, 1925; Khlebovich, 1974; Semina & Sergeeva, 1983).

The plankton flora of the White Sea is less diverse compared to the Barents Sea, due to low salinity which prevents survival of some of the Barents Sea species. Besides, some of the arcto-boreal species may not survive in the White Sea because of strong seasonal temperature variations from -1.4°C in winter to +24.0°C in summer (Burkovsky, 1976). The Gorlo area seems to be a barrier for the Barents Sea species (Kiselev, 1957). The White Sea flora includes ca. 50% of the Barents Sea species only. According to Makarevich and Larionov (1992) there are 308 phytoplankton species in the Barents Sea, and only 145 species in the White Sea according to Semina and Sergeeva (1983). The high proportion of cosmopolitan species in the White Sea is noteworthy.

Seasonal succession

The most detailed study of the development of the inshore sea-ice flora in the White Sea was presented by Zhitina & Mikhailovsky (1990). They showed that planktonic algae present in the water column in autumn were enclosed into the sea ice during its formation (the diatoms *Chaetoceros* spp., *Skeletonema costatum*, *Thalassiosira nordenskiöldii* and the dinoflagellates *Ceratium fusus*, *Dinophysis norwegica*, *Proto-peridinium pellucidum*). Immediately after ice formation, sea-ice algae were found to develop inside the ice: the diatoms *Amphiprora hyperborea*, *Nitzschia frigida*, *Navicula pelagica* and the dinoflagellate *Peridiniella (Goniaulax) catenata*. The latter were more abundant in the ice than planktonic ones. In December, plankton and ice algae were scarce (less than 5×10^3 cells/l). An increase of the number of cells in the lower layer of ice has been observed since March. By the end of this month, a 13-fold increase of the algal abundance was registered. In April, this

concentration decreased rapidly and became equal to the phytoplankton concentration in the water under the ice. The latter one reached its maximum in April; however, it was lower than the maximum abundance of algae within the ice one month earlier (Zhitina & Mikhailovsky, 1990). The taxonomical composition of the ice algae was similar to that in the water, but abundances were different for the same species. Almost all planktonic „spring“ species developed in the ice in a great advance to their growth in the water.

During the ice melting in spring, the ice-neritic species *Nitzschia frigida* and *Navicula* spp. develop. The spring phytoplankton bloom is dominated by the neritic *Chaetoceros* spp., *Fragilariopsis* spp., *Thalassiosira* spp., *Amphyprora hyperborea* and *Bacterosira bathyomphala (fragilis)* (Kokin et al., 1971; Semina & Sergeeva, 1983). In May the main phytoplankton bloom dominated by *Fragilariopsis oceanica* was observed (Ilyash, 1998). This bloom declined in early June. In July, the bloom of diatoms *Chaetoceros* spp., *Skeletonema costatum*, flagellates and small dinoflagellates was encountered, while *N. frigida* and *Fragilariopsis* spp. were almost absent at the same inshore sites (Khlebovich, 1974; Semina & Sergeeva, 1983). The small flagellates were found to be especially abundant in the Basin (Mordasova & Wentzel, 1994). In June to July, picophytoplankton dominated by single celled cyanobacteria becomes very abundant, as well (Ilyash, 1998). In autumn, the dinoflagellates *Dinophysis norwegica*, *Ceratium fusus*, *Protoberidinium leonis* and *P. pellicidum* become abundant. Some of the planktonic diatoms (*Thalassiosira nordenskioeldii*, *Skeletonema costatum* and *Nitzschia closterium*) develop also (Zhitina & Mikhailovsky, 1990). *Coscinodiscus concinnus* and *Chaetoceros decipiens* dominate in September and early October; however, they are scarce (1 to 5 x 10³ cells/l) and their biomass is low (Khlebovich, 1974; Zhitina & Mikhailovsky, 1990).

Primary production

The primary production undergoes strong seasonal variation in the White Sea. It depends primarily on the light conditions throughout the productive period and the nutrient supply in summer. The highest primary production (up to 302 mg C m⁻² day⁻¹) was recorded in spring, from April to the first decade of June (Fedorov & Bobrov, 1977). In summer, production decreases to 71-117 mg C m⁻² day⁻¹, but in some years, according to Naletova et al. (1994), it may be very high (up to 2.8 g C m⁻² day⁻¹). In autumn, in October, it drops down to 49-98 mg C m⁻² day⁻¹. The highest monthly production to biomass ratio (P/B coefficient) of 0.98 was registered in April, while the lowest one of 0.22 was observed in May (Fedorov & Bobrov, 1977).

The yearly primary production varies between 13 and 52 g C m⁻² in different years, with one or two maxima developing during the season of vegetation. While the most pronounced spring maximum develops from May to June, a second, autumn maximum, may develop in August. However, in some years a second maximum was not observed at all (Fedorov et al.,

1974). Phytoplankton production is much lower in the White Sea compared to the Barents Sea due to unfavourable light conditions during the winter, ice cover and rapid nutrient depletion in the upper layer during the spring phytoplankton bloom.

Phytoplankton abundance and biomass

The phytoplankton abundances were underestimated considerably in previous investigations due to two main reasons. First, when phytoplankton was collected with nets, a considerable portion of smaller diatoms, coccolithophorides and dinoflagellates was missed. Second, small flagellates and single-celled stages of *Phaeocystis*, which contribute up to 99% to the total algae numbers in many northern sites (Verity et al., 1999) were not counted in most of the studies cited above, but a few works (Likhacheva, 1991; Mordasova & Wentzel, 1994; Ilyash, 1998). Therefore, the published absolute numbers of the algal cells have to be used for any comparison with serious restrictions in mind. On the other hand, due to their small cell volume, the mentioned groups of algae contribute less to the total biomass. Therefore, the published data on seasonal trends of the phytoplankton biomass in the White Sea seem to be rather reasonable.

According to the data available, phytoplankton biomass is higher in the inshore sites than in the Basin. The maximum phytoplankton biomass of up to 1 g wet weight m^{-3} and about 1.5 mg Chl a m^{-3} develops in the inshore area in May and early June and then falls down to 200 mg wet weight m^{-3} in July and August (Fedorov & Bobrov, 1977). Thus, in June-July 1991, phytoplankton biomass was as high as 2 mg Chl a m^{-3} (Mordasova & Wentzel, 1994). In April and October, biomass is much lower, 20-30 mg wet weight m^{-3} . Only few cells survive during the winter (Fedorov & Bobrov, 1977). From September to February, phytoplankton biomass is less than 20 mg wet weight m^{-3} with the minimum registered in December (Zhitina & Mikhailovsky, 1990).

There are several aspects of the phytoplankton dynamics and distribution which have not been studied sufficiently in the White Sea so far. Under conditions of a high water column stability in summer, the vertical phytoplankton distribution may be of great importance for a better understanding of the pelagic community structure (Beklemishev et al., 1975). The size structure of phytoplankton, its taxonomical composition, absolute abundance and the relative contribution of the different groups to abundance and biomass during different seasons seem to be also important characteristics of this ecosystem, which are insufficiently known. The evaluation of these parameters using modern methods of the collection, preservation and processing of the phytoplankton samples will allow reasonable assessments of the grazing impact on the phytoplankton and of vertical fluxes in the pelagic realm.

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Zooplankton of the White Sea

History of investigations and the present state of knowledge – a review

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Introduction

Zooplankton studies in the White Sea started in the last century. The first publications mainly deal with morphology, taxonomy and general biology of organisms (Merezhkovsky, 1877; Wagner, 1885; Schlatter, 1891; Linko, 1899; Virketis, 1926; 1928). Some of them presented detailed morphological descriptions with excellent hand drawings of the pelagic organisms (Wagner, 1885; Linko, 1899) missing in later studies. In a later stage the study of zooplankton distribution was intensified (Jaschnov, 1940; Epshtein, 1957, 1963; Pertzova, 1962, 1970, 1971, 1980a; Prynokova, 1967, 1985). Seasonal patterns in distribution were discovered (Epshtein, 1957; Pertzova, 1962, 1970; Prynokova, 1967, 1974) and first population and life cycle studies were carried out (Prynokova, 1968, 1974; Pertzova, 1974a,b, 1980b, 1981).

Understanding of the significance of copepods as secondary producers led to intensified studies of their feeding, physiology and breeding activity, assessment of secondary production of the key-species and the phytoplankton-zooplankton interactions (Perueva 1976, 1977a,b, 1984; Arashkevich & Drits, 1984; Arashkevich & Sergeeva, 1991; Kosobokova, 1979, 1980, 1990, 1993, 1998; Pertzova & Kosobokova, 1996). However, the different areas of the White Sea have not been equally covered by investigations. The Kandalaksha, Dvina and Onega Bays represent the areas of the most extensive work, while the central part including the Sea Basin is less studied. The present review aims to summarize available knowledge on the zooplankton of the White Sea. It is restricted to mesozooplankton organisms in the size range from 0.2 to 30 mm.

Faunal composition of zooplankton

The faunal composition of the zooplankton was studied in a number of early publications (Merezhkovsky, 1877; Wagner, 1885; Schlatter, 1891; Jakobson, 1894; Birula, 1896; Pedashenko, 1897; Linko, 1899). The first most complete list of species was presented by Virketis (1926; 1928). Later studies provided more details on the faunas of particular sea areas (Chmiznikova, 1947; Kamshilov, 1957; Epstein, 1957, 1964; Pertzova, 1962, 1970, 1972, 1983; Ivanova, 1963; Pertzova & Chibisova, 1970; Prygunkova, 1974). According to the recent review by Pertzova & Prygunkova (1995), a total of 142 species have been encountered in the zooplankton of the White Sea until now (Table 1). Among them, 41% are arcto-boreal, 22% - arctic, 20% - widespread, and 17% are boreal species. The first two groups form a cold-water, and the latter two - a warm-water assemblage of the zooplankton, respectively.

Table 1. Taxonomic composition of zooplankton of the White Sea

<u>Taxa</u>	<u>Number of species</u>
Ciliophora, Tintinnina	55
Hydroidea	19
Scyphozoa	2
Ctenophora	5
Rotatoria	5
Cladocera	3
Copepoda	35
Mysidacea	5
Hypeiidae	5
Euphausiacea	2
Pteropoda	2
Chaetognatha	1
Appendicularia	3

The plankton fauna of the White Sea is less diverse compared with the Barents Sea. Several taxonomic groups like Radiolaria, planktonic Foraminifera and Ostracoda are entirely absent. Of the 25 copepod species recorded from the eastern Barents Sea, 16 are not found in the White Sea. Strong tidal currents, intensive mixing of water in the Gorlo and a sharp decrease in salinity are assumed to be major factors preventing dispersal and survival of the Barents Sea species in the White Sea (Derjugin, 1928; Virketis, 1929; Zenkevich, 1947, 1963; Gurjanova, 1948).

The Tintinnina, Copepoda and Hydroidea are the most diverse taxonomic groups of the White Sea zooplankton (Table 1). The Tintinnina are not considered here because their systematics are rather unstable (Laval-Peuto, 1981). Among the Copepoda, 35 species are recorded until now, including 15 Calanoida, 4 Cyclopoida, 15 Harpacticoida and 1 Monstrilloida (Pertzova & Prygunkova, 1995). According to Brotskaja (1962), only 2 of the

harpacticoid species listed for the White Sea, *Microsetella norvegica* and *Parathalestris croni*, are really planktonic. All other harpacticoids are assumed to belong to the suprabenthic fauna, irregularly washed out of mainly macrophytes.

The most diverse plankton fauna is reported for the Kandalaksha Bay (Table 2) which is the best studied area. The high number of species is certainly related to the high diversity of environmental conditions and wide range of depths. The fauna of the Basin is less diverse due to the absence of a number of neritic species, which are more typical inhabitants of the shallow-water areas of the bays (Pertzova & Prygunkova, 1995).

Table 2.

The number of the zooplankton species in the different regions of the White Sea

Region	Number of species	
	Total	Except Tintinnina and Rotatoria
Basin	52	37
Kandalaksha Bay	117	75
Onega Bay	74	53
Dvina Bay	34	27
Mezen Bay	26	19
Gorlo	61	36
Voronka	46	24

General distribution of zooplankton biomass

The distribution of the zooplankton biomass in the White Sea has been studied almost exceptionally in spring and summer. First data on biomass in the Basin, Kandalaksha, Dvina and Onega Bays were obtained in spring, 1929 (Jaschnov, 1940). The summer observations were carried in the same area much later, between 1959 and 1981 (Epstein, 1963; Pertzova, 1980a; Prygunkova et al., 1985). These surveys covered almost all sea regions (Table 3, 4) which made it possible to describe the general pattern of horizontal distribution of zooplankton in summer. The highest mean biomass (mg/m^3) was found in the deep areas with pronounced stratification of the water column (the Basin, Kandalaksha and Dvina Bays, Table 3, 4). In the well-mixed areas, separated from the Basin by hydrographic fronts (Onega Bay, Gorlo, and Voronka), zooplankton biomass was generally lower. This has been confirmed by recent studies.

A plankton survey of the White Sea Biological station (Moscow University) in July, 1972 provided more details on the horizontal and vertical distribution of zooplankton biomass in the central part of the sea including the Basin and adjacent areas. Within this area, the lowest biomass was found in the center of the Basin (Pertzova, 1980a). Areas of increased biomass were confined to the Basin periphery, to the zones of the seasonal thermal

fronts. One of such spots was located close to the southern border of Gorlo, while another was found to the north of the Solovetsky Islands, at the border between the Basin and Onega Bay. The pattern of the zooplankton distribution was strongly related to the circulation pattern with the minimum in the area of a cyclonic and the maximum in the area of an anticyclonic gyre. The maximum biomass was found in the 25-50 m water layer, while in the deeper layers biomass showed a clear decrease.

Table 3. Historical data on the zooplankton biomass (mg dry weight /m³, average for the entire water column) in the different regions of the White Sea in summer. Dry weight (DW) is converted from wet weight (WW) according to DW=0.16 WW

Date	Basin Bay	Kandalaksha Bay	Onega Bay	Dvina Bay	Gorlo	Mezen Bay	Voronka	Source
V-VI.1928	24	24	1.1	24	-	-	-	Jaschnov, 1940
VII.1949	-	-	-	-	-	6.4	-	Kamshilov, 1957
VIII.1950	-	-	-	-	-	-	40	Epshtein, 1957
VI-VII.1951	-	-	25	-	-	-	-	Epshtein, 1957
VIII.1952	-	36	-	-	-	-	-	Kamshilov, 1957
VII-VIII.1959	24	9	6	17	6	-	10	Epshtein, 1963
VIII.1969	-	28	-	-	-	-	-	Pertzova, 1971
VI.1963	-	-	-	-	12	3.8	-	Pertzova, 1983

Table 4. Average zooplankton biomass (mg dry weight/m³) in the upper 0-50 m water layer of the White Sea in summer. Dry weight(DW) is converted from wet weight (WW) according to DW=0.16 WW

Date	Basin Bay	Kandalaksha Bay	Onega Bay	Dvina Bay	Gorlo	Mezen Bay	Voronka	Source
VII.1972	17	29	-	9	-	-	-	Pertzova, 1980b
VII.1981	41	46	16	35	-	1.8	2.6	Prygunkova et al., 1985

Composition of the zooplankton biomass

As in the other arctic seas, the copepods are the most important group in the zooplankton in terms of abundance and biomass. Among them, only few species constitute the bulk of the zooplankton stock. They are the boreal *Centropages hamatus*, *Temora longicornis*, *Acartia longiremis*, the arcto-boreal *Pseudocalanus minutus* and the arctic copepods *Calanus glacialis* and *Metridia longa* (Pertzova & Prygunkova, 1995).

In summer, *Pseudocalanus minutus* ranks first in the zooplankton biomass over all sea regions. In the shallow regions (Onega, Mezen Bay and Gorlo) *P. minutus* dominates along with the small-sized boreal copepods *Centropages hamatus* and *Temora longicornis* (Pertzova, 1980b). The contribution of the boreal species increases there, remarkably, in the

second half of summer (Epstein, 1957). In the deep regions (Basin, Kandalaksha and Dvina Bays), *P. minutus* dominates biomass along with the two arctic species, *C. glacialis* and *M. longa* (Table 5, Pertzova, 1980b). Other copepods, including cyclopoids, built up less than 7% of the total biomass in the deep area. They seem to be rather evenly distributed and do not affect the general pattern of the zooplankton distribution. Among other taxa, the chaetognath *Sagitta elegans* and the appendicularian *Oikopleura vanhoeffeni* contribute up to 11-24% biomass. Their horizontal distribution in the Basin and adjacent areas is similar to that of the cold-water copepod species (Pertzova & Prygunkova, 1995).

Table 5. Relative contribution (%) of the dominant copepod species to the total zooplankton biomass in July, 1972 (from Pertzova, 1980b)

Species	Basin	Kandalaksha Bay	Dvina Bay
water layer 0 - 50 m			
<i>Metridia longa</i>	13.5	8.3	8.8
<i>Calanus glacialis</i>	4.9	16.8	2.5
<i>Pseudocalanus minutus</i>	44.8	30.4	52.2
Total	63.2	55.5	63.5
water layer 50 m - bottom			
<i>Metridia longa</i>	15.8	19.4	22.4
<i>Calanus glacialis</i>	14.6	12.3	7.0
<i>Pseudocalanus minutus</i>	39.7	44.1	53.9
Total	70.1	75.8	83.3

Life cycles and distribution patterns of the dominant copepod species

Life cycle studies carried out on most dominant copepod species in the Kandalaksha Bay revealed striking differences between temperate-boreal (warm-water) and arctic (cold-water) copepod species in relation to their life cycle strategies, generation length, number of generations per year, and seasonal variations of their vertical and horizontal distributions (Prygunkova, 1968, 1974; Pertzova, 1974a,b, 1980b, 1981, 1984).

The dominant boreal copepods *Centropages hamatus* and *Temora longicornis* form a temporal component of zooplankton. They are present in the water column during the warm season, from spring to autumn, and are entirely absent during the winter. Throughout the period of their occurrence, both species are restricted to the warmest surface water layer from 0 to 25-30 m. From May to October three generations develop. The development of the spring and autumn generations takes one and a half month each. The summer generation completes development in one month due to higher temperatures. Females of the autumn generation produce resting eggs, which overwinter in the bottom sediments and give rise to the first generation next spring (Pertzova, 1974a).

In spring, both species appear from their resting eggs at first in the shallow coastal waters, where warming is most pronounced. Their absence from the deep area suggests a low overwintering success for the resting eggs in the deep parts of the sea. In summer, maximum abundance and biomass of both species are also confined to the shallow zone, however, they inhabit a wider area compared to the spring. By mid-summer, surface water movements (tidal and wind-induced currents) spread their populations from the coastal zone almost over the entire sea. By autumn, eggs, nauplii, and young copepodite stages of *Centropages hamatus* and *Temora longicornis* almost disappear from the plankton population. Abundances decrease considerably, and horizontal distribution becomes strictly confined to the narrow coastal zone. From November to May *C. hamatus* and *T. longicornis* are not present in plankton.

The arctic copepods *Calanus glacialis* and *Metridia longa* are present in the plankton throughout the whole year. They are slow-growing, and have long life cycles of one or two years. The herbivorous *C. glacialis* takes two years to mature and reproduce (Prygunkova, 1968; Kosobokova & Pertzova, 1990; Kosobokova, 1998, 1999). The spawning in May and June produces a stock which develops to copepodite stage IV (CIV) during the first summer and overwinters in diapause in the deep water until the next spring. The following year they continue to CV during the spring and summer, mature in autumn and winter and reproduce at the age of two years. The omnivorous *M. longa* produces one generation per year (Pertzova, 1974b). It has a long reproductive period with most active spawning from late summer to autumn (August-October). Young developmental stages of both arctic species are tolerant of seasonal fluctuations of temperature. They inhabit the upper water layers and penetrate with surface currents into the coastal zone in early spring (*C. glacialis*) and autumn (*M. longa*) when boreal species are not abundant there. Thus, the *C. glacialis* offspring appear in the coastal area in May-June, before the spring increase of the boreal species (Pertzova & Kosobokova, 1996). In turn, the recruits of *M. longa* reach their highest abundance in the coastal area in September-October, when the boreal *Centropages hamatus* and *Temora longicornis* almost disappear from plankton. Late copepodite stages of the arctic species strongly prefer waters with negative temperatures; therefore, the “core” of their biomass is confined to the cold-water layer in the deep basin area.

The arcto-boreal copepod *Pseudocalanus minutus* is also present in the plankton throughout the whole year. The females lay eggs from March to October (Pertzova, 1981, 1984; Pertzova & Kosobokova, 1996). By the end of the productive season recruits of the new generation reach copepodite stages CIII, IV and V and enter diapause which lasts until spring (Pertzova, 1981). The overwintering stock continues development during early spring the following year and generally completes its life cycle in one year. A small portion of the population represented by offspring of the females spawned in March may reach maturity by August, resulting in two generations per year (Pertzova, 1981).

Vertical migrations

Seasonal, ontogenetic and diel variations in the vertical distribution of zooplankton have been studied in the White Sea for all the most abundant copepod species (Bogorov, 1941; Prygunkova, 1974; Pertzova, 1974b, 1981, 1984; Kosobokova & Pertzova, 1990). The populations of *Calanus glacialis*, *Metridia longa* and *Pseudocalanus minutus* undergo pronounced seasonal vertical migrations covering the entire water column (Pertzova, 1974b, 1981; Prygunkova, 1979; Kosobokova & Pertzova, 1990). The herbivorous *C. glacialis* and *P. minutus* concentrate near the surface at the beginning of spring for feeding and reproduction and stay in the upper layer during the productive season. In autumn, they descend into the deep layer for overwintering. In contrast to *Calanus* and *Pseudocalanus*, the omnivorous *Metridia* concentrates close to the surface in autumn and winter (Pertzova, 1974). In addition to seasonal migrations, all the three species undergo ontogenetic migrations in summer and autumn with older stages tending to occur deeper than younger ones (Pertzova, 1981, 1983; Kosobokova & Pertzova, 1990). Moreover, *M. longa* and *P. minutus* perform pronounced diel vertical migrations throughout most of the year with the highest intensity between August and October (Pertzova 1974b, 1984). Late copepodite stages C IV - C V and adult females are most active diel migrants. In *C. glacialis* diel migrations were observed during the same period with C IV and C V being the most active migrants (Kosobokova & Pertzova, 1990). In the boreal calanoids *Temora longicornis* and *Centropages hamatus* all variations of the vertical distribution are restricted to the upper water layer. Within this layer, ontogenetic and diel migrations were observed in summer (Pertzova, 1984)

Feeding, physiology and reproduction

Studies of feeding behavior, gut content, daily rations and feeding rhythms have been carried out on two of the larger calanoids of the White Sea, *Metridia longa* and *Calanus glacialis*. Gut content investigations confirmed that *Metridia* ingests a high proportion of animal food, primarily copepod nauplii and invertebrate eggs, in addition to phytoplankton (Perueva, 1984). The greatest feeding activity was registered at night (Perueva, 1983). The daily ration was estimated to be 3-5% of body weight, and defecation rate was approximately one pellet per hour. *Calanus* is usually referred to as a predominantly herbivorous filter-feeder (Arashkevich & Kosobokova, 1988). However, examination of the gut contents of copepodite stage IV revealed that tintinnids and nauplii as well as phytoplankton were ingested, which suggested its successful growth in habitats other than diatom blooms (Perueva, 1977). The study of the ingestion rates and diel feeding rhythms of *Calanus* showed highest feeding intensity at night (Perueva 1976, 1977). The defecation rate of *C.*

glacialis C IV at ambient food concentration was estimated to be 3-4 pellets per hour (Arashkevich & Sergeeva, 1991), and the maximum daily rations on different kinds of phytoplankton food - of 12-17% of body weight (Arashkevich & Drits, 1984).

Energy content of the key zooplankton species including the copepods *Calanus glacialis*, *Pseudocalanus elongatus* and *Metridia longa*, and the chaetognath *Sagitta elegans* in terms of caloric values was studied by Kosobokova (1980). These data indicated pronounced seasonal variations in the energy content of the particular zooplankton organisms related to their growth and lipid accumulation. High lipid contents of the White Sea *Calanus* were initially described by Sushkina (1961, 1962). A detailed quantitative study of the biochemical composition of *Calanus* in terms of protein and lipid body content was conducted during the productive season in the Kandalaksha Bay (Kosobokova, 1990; Kosobokova & Pertzova, 1990). Seasonal variations of the lipid content were observed for all stages older than C III. The spring molting of overwintered C IV to C V was followed by 4- to 6-fold increase of the lipid content. Lipid accumulation during the summer resulted in 1.5 - to 2-fold increase of the C V lipids (Kosobokova 1990). To estimate the metabolic requirements of plankton at ambient temperatures in the White Sea, the respiration rates of *Calanus* and *Metridia* were measured in summer (Kosobokova, 1979) and winter (Arashkevich & Kosobokova, 1988). The daily respiratory losses of the *Calanus* in winter at temperatures of 0 to -1.0°C were estimated to be 0.9-1.0% of body weight, which allowed them to survive from November to March without feeding by consuming the lipids accumulated in summer.

The reproductive biology and egg production rates have been studied for *Calanus glacialis* (Kosobokova & Pertzova, 1990; Kosobokova, 1993, 1998, 1999) and *Pseudocalanus minutus* (Pertzova & Kosobokova, 1996). Average daily egg production of the *Calanus* females corresponded to 2.2% of body carbon. The highest production by a single female during 29 days under experimental conditions was 719 eggs, which corresponded to 128% body carbon. The number of clutches produced by a single *Pseudocalanus* female during its reproductive life was estimated to be between 4-6 at the in situ temperatures (near 0°C), while the total fecundity was estimated to be 80-120 eggs per female or 100-400% female body carbon (Pertzova & Kosobokova, 1996).

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Macroplankton and micronekton

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Pelagic organisms which are relatively large (i.e. normally exceed 8-10 mm in one dimension) and capable to escape small to medium size zooplankton nets are conventionally considered as macroplankton and micronekton. Faunistically, this group in the White Sea consists of species commonly occurring in the Barents Sea and includes two species of Scyphozoa, five species of Ctenophora, two species of Mollusca Pteropoda, one species of Chaetognatha, five species of Mysidacea, five species of Amphipoda Hyperideia, and two species of Euphausiacea (Beloe More, 1995). Of the latter, *Thysanoessa inermis* has been found only occasionally in the deep waters while *Thysanoessa raschii* is rather common, in particular in the Basin and in the deep waters of the Kandalaksha Bay (Derjugin, 1928; Pertzova, unpubl). The larvae of decapod crustaceans and fishes may be assigned to macroplankton as well. Many of these species are characteristic for the Basin but occur also in the shallow water. Since most of zooplankton studies in the White Sea have been done using medium size zooplankton nets, the distribution, life histories of macrozooplankton species in the White Sea remain very poorly studied, so does energy flow through their population. It is worth noting that both vertical and horizontal mesoscale distribution of macroplankton species is subject to rapid changes due to a combined effect of swimming activity of the animals and oceanographical phenomena. For example, vertical migrations and local changes of abundance of pteropod molluscs, *Clione limacina* and *Limacina helicina* may be strongly influenced by stormy weather (Wagner, 1885; Naumov et al., 1987). Euphausiids are known by their wandering schools which are occasionally observed in the coastal areas and are believed to originate from the deep waters. We suggest that macroplankton populations greatly contribute to variation in the pelagic ecosystems both at macro- and at mesoscale and this variation must be a priority subject for future studies.

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B. Original Contributions

On the macro-invertebrate sublittoral bottom fauna in the White Sea – with comments on its zoogeography

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The White Sea is the smallest sea in the northern part of Russia. It is connected with the Barents Sea by an extensive shallow sill. Because of the enclosed situation, the continental climate conditions near the polar circle and influence of some relatively warm Atlantic waters, ZENKEVITCH (1963) characterized this area as „sub-arctic“.

In summer the waters of the main basin of the White Sea are highly stratified and of low productivity (MILEIKOVSKY 1970). In June and August the temperature of the surface layer rises up to 16°C in inshore waters. At a depth of 10m it drops to 10°C, and the 0°C-isotherm is located between 25 to 40 m. Below 100m the water mass is characterized by permanently low temperatures (-1°C to -1.5°C) and higher salinities of approximately 30‰.

Tab. 1: Station data

Station	Date	Latitude	Longitude	Depth	Sediment-Temp.	Water-Temp.	Salinity
	1994	N	E	[m]	[°C]	[°C]	[‰]
Chupa Inlet							
Ch 10	01.07.	66° 16'89	33° 13'80	10	3,5	4,7	24,2
Ch 20	01.07.	66° 16'81	33° 13'62	20	1,6	2,6	25,0
Ch 30	01.07.	66° 16'73	33° 13'42	31	0,6	1,8	25,8
Ch 40	01.07.	66° 16'70	33° 13'55	40	0,4	0,8	26,0
Ch 50	08.07.	66° 16'76	33° 13'70	50	(-)	(-)	(-)
Ch 70	08.07.	66° 16'67	33° 14'06	70	(-)	(-)	(-)
Kandalaksha Bay							
Ka 30	06.07.	66° 20'50	33° 41'00	30	-0,1	0	27,0
Ka 50	06.07.	66° 23'40	33° 57'60	58	-0,9	-0,9	27,6
Ka 100	06.07.	66° 24'80	33° 58'40	98	-1,2	-1,4	29,0
Ka 150	05.07.	66° 25'30	33° 58'60	147	-1,4	-1,4	29,4
Ka 200	05.07.	66° 27'40	33° 59'30	198	-1,4	-1,5	29,6
Ka 250	05.07.	66° 28'20	33° 59'50	249	-1,5	-1,5	28,8
Ka 300	05.07.	66° 28'90	34° 00'45	325	-1,5	-1,5	28,9

The present investigation is based on data from 13 stations in the area of the Chupa Inlet and Kandalaksha Bay in the White Sea. Altogether, the macrofauna of 39 Okean grabs (0,25m²), at each station three replications, were evaluated in two transects covering a depth range of 10 to 325 m. The samples were sieved over a 1-mm screen and preserved in buffered 4%-formalin. The biomass is given as wet weight.

Results

A total of 4640 individuals were identified, which were spread over 146 species (s. Table 2, Annex). Polychaetes (47%), molluscs (27%), crustaceans (12%) and echinoderms (5%) are the most significant macrobenthic taxa.

Based on the abundances of 141 species faunistic similarities were computed for all 13 stations. 4 clusters were classified according to their different stocks of species. The clusters reflected the depth zonation of the macrobenthic invertebrates in the investigation area. The stations of smaller depth of both transects were pooled into two communities. The remaining three resp. four stations of the deep areas of the Chupa Inlet and Kandalaksha Bay were combined in further groups.

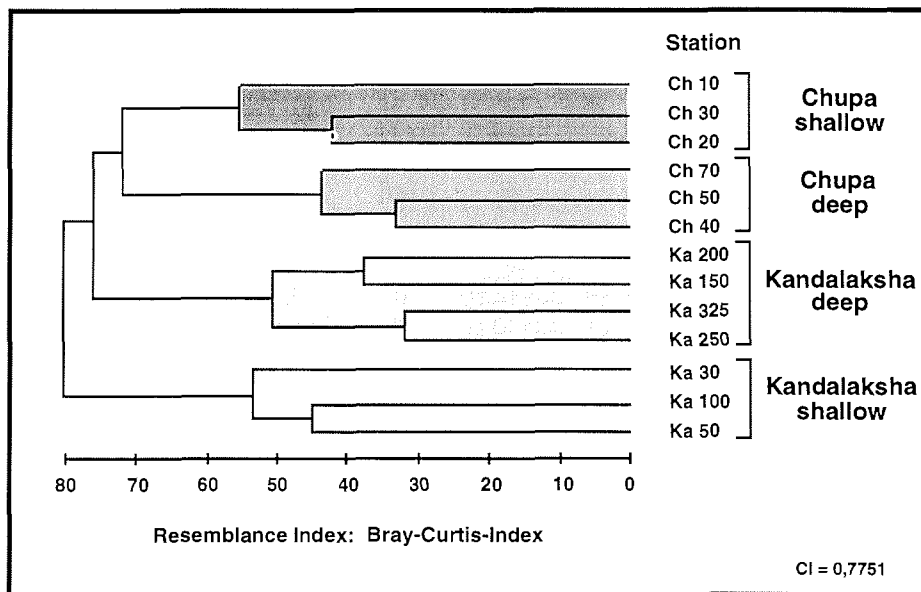


Fig.1: Grouping of stations (Chupa Inlet Ch10 to Ch70, Kandalaksha Bay Ka30 to Ka325) based on a cluster analysis of the Okean grab samples taken in the White Sea in summer 1994.

The „Chupa shallow“ (CS) cluster consisted three stations in water depths between 10 and 30m. This cluster contained 61 of the total 75 species found in the Chupa Inlet. The benthic fauna of „Chupa shallow,, were characterized by the polychaete *Nephtys ciliata*

and the bivalve *Arctica islandica*. The latter species was found only in the samples of CS.

The three stations of „Chupa deep“ (CD) cluster were found in water depth between 40 and 70 m. In contrast to „Chupa shallow“, the numbers of taxa were lower (46), while the abundances (1097) were similar. The character species of CD were two polychaete species, *Cossura longocirrata* and *Owenia fusiformes*. *O. fusiformes* was present only in this macrobenthic association.

The macrobenthic community „Kandalaksha shallow“ (KS) is characterized by a high number of taxa (104) and high abundances (2806). The cluster combined three stations in water depth of 30 to 100m. The key species were the bivalves *Astarte elliptica*, *Dacrydium vitreum* and *Tridonta montagui*, the polychaete *Myriochele oculata* and one ophiuroid, *Ophiacantha bidentata*.

The cluster „Kandalaksha deep“ (KD) consisted of four stations with a total of 56 taxa and 1129 individuals. The stations were located in the deep basin of the Kandalaksha Bay at water depth between 150 and 325 m. In comparison with KS, abundances and species numbers were lower. This cluster was characterized by the dominance of the bivalve *Portlandia arctica*. However, the molluscs *Nucula bellotii* and *Philine lima* and the polychaete *Apistobanchus tullbergii* were additional key species. The bivalve *Nuculana pernula* occurred with higher biomasses in all samples from this community, but does not fulfil the qualifications for character species (after SALZWEDEL et al 1985).

Zoogeographic characteristics

With regard to the zoogeographical distribution of the macrobenthic fauna, five different classes are distinguished: atlantic-boreal, atlantic-boreal-arctic, pacific-boreal-arctic, amphiboreal-arctic, arctic.

In the total investigation area most of the macrobenthic species belong to the amphiboreal-arctic distribution type (71%), followed by the atlantic-boreal-arctic (13%) and the atlantic-boreal species (4%). In this analysis, only 3% of the macrobenthic species belonged to the arctic fauna (*Oenopota novajasemliensis*, *Philine lima*, *Portlandia arctica*, *Urasterias linkii*), whereas the brittle star *Stegophiura nodosa* is the only species with pacific-boreal-arctic zoogeographical distribution.

Concerning the echinodermata, only the atlantic-boreal-arctic species *Ophiura robusta* was found in higher abundances, whereas the arctic seastar *Urasterias linkii*, was found as few single specimens.

A total of 37 molluscs have been identified, of which 24 taxa are amphiboreal-arctic with a wide zoogeographical distribution area. The snails *Philine lima* and *Oenopota novajasem-liensis* and the bivalve *Portlandia arctica* are elements of the arctic fauna.

Concerning the polychaeta, only four species do not belong to the amphiboreal-arctic distribution type. The atlantic-boreal-arctic species *Branchiomma bombyx*, *Neoamphitrite affinis* and *Nicomache trispitana* were found only in few numbers as well as the atlantic-boreal polychaete *Tharyx marioni*.

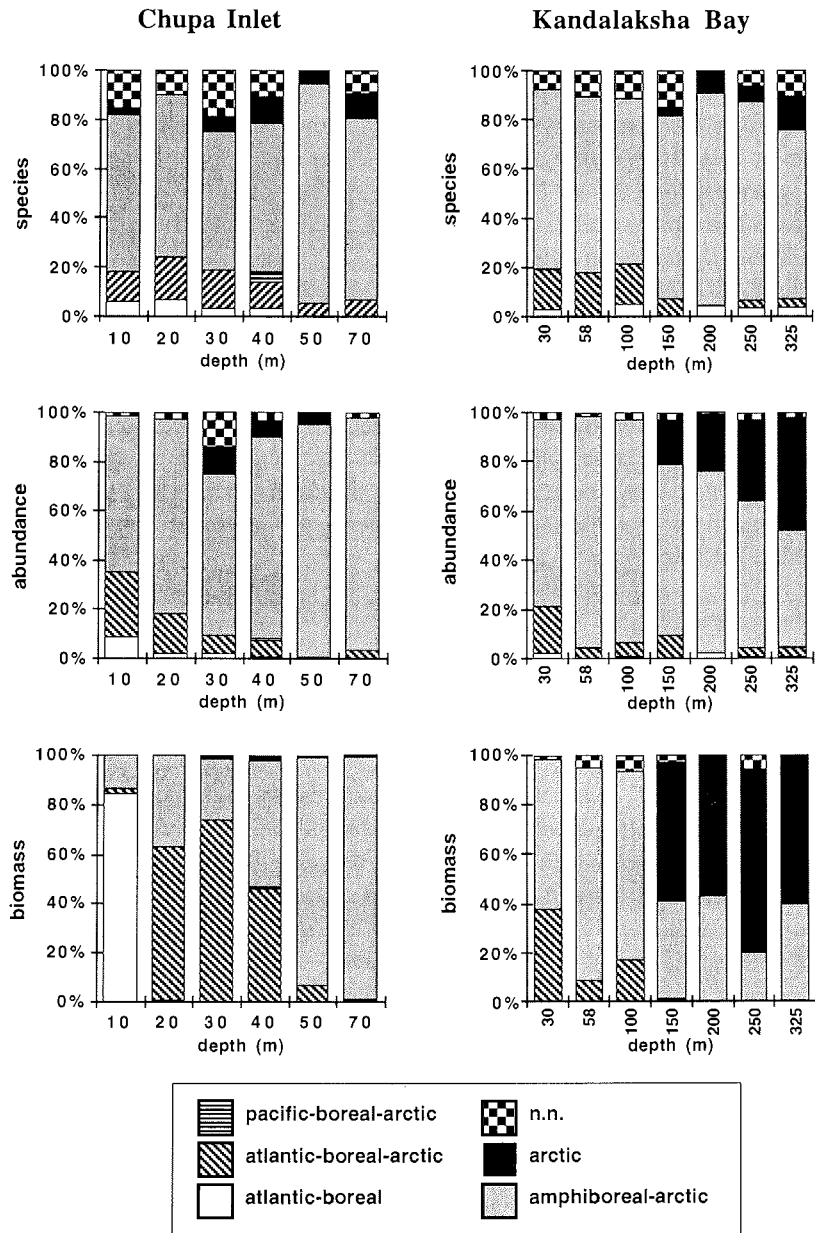


Fig. 2: Different zoogeographical groups in the Chupa Inlet and Kandalaksha Bay

Chupa Inlet

The amphiboreal-arctic taxa set never less than 50% of the species and increased in 50m water depth up to 80% (Fig.2). They accounted in water depth less than 50m for up to 90% of the abundances, but increased by biomass from 15% (10m) to nearly 100% at the 70m station. Together with the atlantic-boreal-arctic species they were the only zoogeographic group, which may be evidenced at all stations. However, atlantic-boreal-arctic species accounted in different water depths only with a maximum of 20% of the species. The larger abundance of the ophiuroid *Ophiura robusta* caused a higher proportion at the 10m-station.

The atlantic-boreal-arctic anthozoan *Cerianthus lloydii* was responsible for the higher biomass in depth between 20 to 40m. Atlantic-boreal species only occurred in water depth less than 40 m. The most important representative was *Arctica islandica*, which accounted for 80% of the local biomass at the 10m-station. Real arctic species were found only as a few individuals (mainly *Portlandia arctica*). Their weight is very small, so that they are uninfluential on the total biomass.

Kandalaksha Bay

Similar to Chupa Inlet in the Kandalaksha Bay most species belong to the amphiboreal-arctic distribution type (Fig.2). The species percentages did not differ very much between the single stations, whereas major variations in abundances and biomass between the different depth zones were more obvious. Atlantic-boreal-arctic species were of less importance of the macrofauna in the Kandalaksha Bay. Their highest abundances were found at the 30m-station, mainly caused by the presence of *Ophiura robusta* and the cumacean *Diastylis scorpioides*. Atlantic-boreal species like *Oenoba jeffreysii* were the minority at the stations of the Kandalaksha Bay. However, excluding the depth of 58m and 150m, atlantic-boreal species were found at all other stations. The real arctic fauna was found in water depth of more than 150 m. The essential element of this distribution type was the bivalve *Portlandia arctica*, with its higher abundance (>40%) at the station in 325m water depth. With respect to its biomass, the percentage ranged from 50 to 70% in depth of more than 150m.

Discussion

The White Sea has never had a marine connection to the Baltic Sea and is strongly influenced from the adjacent Barents Sea and, thus, the northeasternmost Atlantic Ocean. The White Sea as a cold water system is rather young in terms of geological history.

From a hydrographical point of view, ZENKEVITCH (1963) divided the Arctic region in three zones concerning the distribution of benthic organisms. Together with the southern and central Barents Sea, the White Sea belongs to the „lower-arctic shallow sub-region“, whereas the remaining Russian arctic region accounted to the „high-arctic shallow sub-region“. Regarding zoogeography, the White Sea is very heterogeneous. The main part of its macrobenthic species are amphiboreal-arctic and can be found in the Atlantic, Pacific and Arctic Ocean. In this investigation, only 4 species exhibit an arctic distribution, while, by the high total biomass of *Portlandia arctica* in the deep basin, the arctic share in total biomass may be relatively high (s. NAUMOV & FEDYAKOV, this volume). Atlantic and amphiboreal-arctic species occurred mainly in the shallow areas, whereas the arctic fauna is an element of the deeper parts of the White Sea (EKMAN 1953). 38 species of molluscs were identified, 18 bivalvia and 19 snails, accounting for 44% of 41, respectively 17% of 112, species altogether known in the White Sea. Abundance and biomass of gastropoda were low in all samples. Only three species of molluscs can be characterised as arctic. *Portlandia arctica* is the main arctic macrobenthic element in the deeper parts (FEDYAKOV 1979, NAUMOV & FEDYAKOV, this volume), whereas in other arctic regions *P. arctica* lives in water depth between 10 to 50 m (OCKELMANN 1954). It seems that low water and sediment temperatures are important environmental factors for *P. arctica* (GOVBERT 1973, NAUMOV 1977). The arctic snail *Philine lima* is not restricted to greater water depth and is found in shallow zones of the White Sea, too (SCALATO 1987). In this investigation, however, *P. lima* was collected only in the deeper parts of the White Sea basin. The 68 identified polychaeta represent 45% of the 158 species known from the White Sea area. EKMAN (1953) stressed that 28% of the polychaeta are restricted to the arctic region. Similar to other investigations in other arctic seas (CURTIS 1975, HOLTHE 1978, SCHMID & PIEPENBURG 1993) the polychaete fauna of the White Sea is dominated by amphiboreal-arctic species (52 species = 77%, in this investigation). Not any polychaete species found was arctic.

The climate changes during the Pliocene, Pleistocene and Holocene eras are responsible for the immature character of the arctic sublittoral fauna (BILYARD & CAREY 1980). In the White Sea this is confirmed by the large amount of boreal species. A special endemic fauna comparable to the Antarctic one could not evolve, since the evolution of species takes plenty of time (KNOX & LOWRY 1977). Accordingly, the White Sea is inhabited by a very heterogeneous fauna with strong relations to the Atlantic region. During the last glaciation period the original fauna of the White Sea was totally extinguished (GOVBERT 1973). Starting with the reduction of the ice shield, arctic species like *Portlandia arctica* and *Urasterias linkii* immigrated into the White Sea. In continuation of the warming, the arctic species migrated into the deeper parts and can be regarded as an arctic relict fauna. Some time afterwards, the boreal fauna from the Atlantic and partly from the Pacific area spread into the White Sea and settled in shallow water depth. Today, the White Sea accommodates beside its boreal and boreal-arctic a cold-water and a warm-water relict fauna (EKMAN 1953, ZENKEVITCH 1963).

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ANNEX: Table 2: List of Species

Chupa shallow (CS); Chupa deep (CD); Kandalaksha shallow (KS); Kandalaksha deep (KD)

		CS	CD	KS	KD
Porifera	<i>Trichostemma hemisphaericum</i>			X	
Cnidaria	<i>Actinia</i> sp.			X	
	<i>Cerianthus lloydii</i> GOSSE, 1859	X	X		
	<i>Edwardsia</i> sp.1	X			
	<i>Edwardsia</i> sp.2				X
	<i>Gersemia fruticosa</i>	X		X	
Priapulida	<i>Priapulidus caudatus</i> LAMARCK, 1816			X	X
Nemertini	Nemertini spp.	X	X	X	
Annelida					
Errantia	<i>Aglaophamus malgreni</i> THEEL, 1879	X	X	X	X
	<i>Anaitides groenlandica</i> (OERSTED, 1842)				X
	<i>Anaitides maculata</i> (L.)			X	
	<i>Eteone flava</i> FABRICIUS, 1780			X	X
	<i>Eteone longa</i> FABRICIUS, 1780				X
	<i>Exogone</i> sp.			X	
	<i>Gattyana cirrosa</i> (PALLAS, 1766)				X
	<i>Glycera capitata</i> OERSTED, 1843			X	
	<i>Harmothoe nodosa</i> (M. SARS, 1860)				X
	<i>Harmothoe sarsi sarsi</i> (KINGBERG, 1865)				X
	<i>Lagisca extenuata</i> (GRUBE, 1840)	X	X		
	<i>Lumbrineris fragilis</i> (O. F. MÜLLER, 1766)	X		X	X
	<i>Nephtys ciliata</i> (O. F. MÜLLER, 1776)	X	X	X	X
	<i>Nephtys longosetosa</i> OERSTED, 1843	X			
	<i>Nephtys paradoxa</i> MALM, 1874			X	
	<i>Pholoe minuta</i> FABRICIUS, 1780	X		X	X
	<i>Schistomeringos caeca</i>				X
	<i>Sphaeodorum flavum</i> OERSTED, 1843			X	
Sedentaria	<i>Ampharete acutifrons</i> (GRUBE, 1860)			X	X
	<i>Ampharete finmarchica</i> (M. SARS, 1864)		X	X	X
	<i>Amphitrite</i> sp.			X	
	<i>Apistobanchus tullbergii</i> THEEL, 1879				X
	<i>Aricidea jeffreysii</i> (McINTOSH, 1879)	X	X	X	X
	<i>Brada villosa</i> (RATHKE, 1843)	X			X
	<i>Branchiomma bombyx</i> (DALYELL, 1853)			X	
	<i>Chaetozone setosa</i> MALGREN, 1867		X	X	X
	<i>Chitinopoma</i> sp.			X	
	<i>Chone dunerii</i> MALGREN, 1867	X		X	
	<i>Chone infundibuliformes</i> KRÖYER, 1856	X			
	<i>Cirratulus cirratus</i> (O. F. MÜLLER, 1776)			X	
	<i>Clymenura borealis</i> (ARWISSON, 1906)			X	X
	<i>Cossura longocirrata</i> WEBSTER & BEN., 1887	X	X	X	X
	<i>Diplocirrus glauca</i> (MALGREN, 1867)			X	X
	<i>Euchone analis</i> (KRÖYER, 1856)		X	X	X
	<i>Euclymene praetermissa</i> MALGREN, 1865			X	

Fabelligeridae sp.	X			
Fabriciinae sp.	X		X	
<i>Lanassa nordenskiöldi</i> MALM, 1874			X	
<i>Laonice cirrata</i> (M. SARS, 1851)	X		X	
<i>Maldane sarsi</i> (MALGREN, 1876)	X	X	X	X
Maldanidae spp.	X	X	X	X
<i>Manayunkia</i> sp.	X		X	
<i>Meline cristata</i> (M. SARS, 1851)	X			
<i>Myriochele heeri</i> (MALGREN, 1865)				X
<i>Myriochele oculata</i> ZAKS, 1922		X	X	X
<i>Neoamphitrite affinis</i> (HESSLE, 1971)			X	
<i>Nichomache lumbricalis</i> FABRICIUS, 1780			X	
<i>Nichomache personata</i> (JOHNSON, 1901)			X	
<i>Nichomache trispitana</i> (ARWIDSSON, 1906)			X	
<i>Nicolea zostericola</i> (OERSTED, 1844)			X	
<i>Notomastus latericus</i> SARS, 1851			X	
<i>Owenia fusiformes</i> DELLE CHIALE, 1841		X		
<i>Paramphitrite birulai</i> (HOLTJE, 1976)			X	
<i>Paraonis</i> sp.			X	
<i>Pectinaria granulata</i> (L.)			X	
<i>Pectinaria hyperborea</i> MALGREN, 1865	X	X	X	X
<i>Pherusa plumosa</i> (O. F. MÜLLER, 1776)			X	
<i>Polydora quadrolobata</i> JACOBI, 1883				X
<i>Prionospio cirrifera</i> WIREN, 1883	X	X	X	X
<i>Rhodine gracilior</i> TAUBER, 1879			X	
Sabellinae sp.			X	
<i>Scalibregma inflatum</i> RATHKE, 1843			X	X
<i>Scoloplos armiger</i> (O. F. MÜLLER, 1776)	X	X	X	X
<i>Tharxy marioni</i> SAINT-JOSEPH, 1894	X			X
<i>Terebellides stroemi</i> M. SARS, 1853			X	
Sipunculida				
<i>Golfingia margaritaceum</i> (SARS, 1851)		X		
Mollusca				
Bivalvia				
Caudofoveata spp.	X	X	X	X
<i>Arctica islandica</i> (L.)	X			
<i>Astarte elliptica</i> (BROWN, 1827)	X		X	
<i>Ciliatocardium ciliatum</i> (FABRICIUS, 1780)			X	
<i>Crenella decussata</i> (MONTAGU, 1808)	X		X	
<i>Dacrydium vitreum</i> (MOELLER, 1842)		X	X	X
<i>Hiatella arctica</i> (L.)	X	X	X	
<i>Macoma calcarea</i> (GMELIN, 1790)	X	X	X	X
<i>Modiolus modiolus</i> (L.)			X	
<i>Musculus discor</i> (L.)	X	X	X	
<i>Musculus niger</i> (GRAY, 1842)	X			
<i>Nucula bellotii</i> (ADAMS, 1856)			X	X
<i>Nuculana minuta</i> (MÜLLER, 1779)	X			
<i>Nuculana pernula</i> (MÜLLER, 1779)	X	X	X	X
<i>Panomya arctica</i> (LAMARCK, 1818)		X		
<i>Portlandia arctica</i> (GRAY, 1824)	X	X		X
<i>Thyasira gouldi</i> (PHILIPPI, 1846)	X		X	X
<i>Tridonta montagui</i> (DILLARYN)	X		X	
<i>Yoldia amygdalea hyperborea</i> TORELL, 1859	X	X	X	

Gastropoda	<i>Cylichna alba</i> (BROWN, 1827)		X		
	<i>Cylichna occulta</i> (MIGHELS, 1841)		X	X	X
	<i>Diaphane minuta</i> (BROWN IN SMITH, 1839)	X	X	X	
	<i>Hydrobia ulvae</i> (PENNTANT, 1777)	X			
	<i>Lacuna neritoidea</i> GOULD, 1840			X	
	<i>Lepeta coeca</i> (MÜLLER, 1776)			X	
	<i>Littorina obtusata</i> (L.)	X			
	<i>Margarites groenlandicus umbilicalis</i> (BRODERIP & SOWERBY, 1829)			X	
	<i>Moelleria costulata</i> (MOELLER, 1842)			X	
	<i>Oenoba jeffreysii</i> (WALLER, 1864)			X	
	<i>Oenopota novajasemliensis</i> (LECHE, 1878)	X	X		X
	<i>Oenopota trevelyana</i> (TURTON, 1834)	X	X		X
	<i>Philina lima</i> (BROWN, 1827)				X
	<i>Puncturella noachina</i> (L.)			X	
	<i>Retusa pertenuis</i> (MIGHELS, 1843)		X	X	
	<i>Retusa</i> sp.			X	X
	<i>Trichotropsis borealis</i> (BRODERIP & SOWERBY, 1829)	X		X	
<i>Velutina velutina</i> (MÜLLER, 1776)			X		
Arthropoda					
Amphipoda					
<i>Anonyx sarsi</i> (STEEL & BRUNEL)	X				
<i>Arrhis</i> sp.	X	X	X	X	
<i>Harpinia</i> sp.	X		X		
<i>Lembos</i> sp.			X		
<i>Menigrates</i> sp.	X				
<i>Monoculoides</i> sp.	X		X		
<i>Phoxocephalus</i> sp.	X	X	X	X	
<i>Stegocephaloides</i> sp.		X			
<i>Tiron</i> sp.	X		X		
Cumacea					
<i>Diastylis scorpioides</i> (LEPECHIN, 1778)	X	X	X		
<i>Diastylis rathkei</i> (KRÖYER, 1841)	X		X		
<i>Diastylopsis resima</i> SARS, 1900		X	X	X	
<i>Leptostylis ampullacea</i> (LILJEBORG, 1855)			X		
<i>Leptostylis macrura</i> O. G. SARS, 1869			X		
<i>Leucon</i> sp.	X		X		
Mysidacea sp.		X			
Brachiopoda					
<i>Hemithyris psittacea</i> (GMELIN, 1782)			X		
Echinodermata					
Asteroidea sp. juv.	X				
<i>Urasterias linkii</i> (MÜLLER & TROSCHER, 1842)				X	
<i>Strongylocentrotus pallidus</i> (SARS, 1871)			X		
<i>Chiridota pellucida</i> (VAHL, 1806)	X	X			
<i>Ophiacantha bidentata</i> (RETZIUS, 1805)			X	X	
<i>Ophiopholis aculeata</i> (L.)			X		
<i>Ophiura robusta</i> (AYRES, 1851)	X	X	X		
<i>Stegophiura nodosa</i> (LÜTKEN, 1854)		X	X		

New results on the macro-zoobenthos of the White Sea deep basin

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Part 1 Macrobenthos of the White Sea deep basin

1.1. Introduction

In spite of the fact that the White Sea is one of the best studied Russian seas, the life of its deepest part is yet known insufficiently. N.M. Knipowitsch was the first who sampled sea floor organisms in the deep part of the Basin (Knipowitsch, 1896). Twenty five years later the famous studies directed by K.M. Derjugin were organised (Derjugin, 1928). A good knowledge of species composition was a result of these investigations, but there were no data on the quantitative distribution of deep-water bottom animals in the White Sea. The first material of this kind was obtained by L.A. Zenkewitsch (1927). Since that time very few data have been available from the deep-water part of the open basin of the White Sea (Semenova et al., 1995). Taking this into account, it is important to study sea floor assemblages of this area under modern aspects.

In this investigation the deep-water area of the White Sea was considered as the zone situated at approximately 200 m depth and deeper. This zone occupies about 10% of the whole area of the internal part of the sea. It is an ancient depression filled with moraine material covered with clay and a more or less thick layer of muddy sediment on its surface. This mud consists of 70% pelite (clay) and 30% aleurite (silt) in average (Nevessky et al., 1977).

The hydrodynamic conditions of this area are not studied at all; but, the presence of a thick layer of aleurite-pelite sediment, containing a great amount of water and inhabited by fauna, which reaches sometimes up to 20 cm, is an indication that there may not be strong water movements in the White Sea central depression.

The hydrological regime of the deepest part of the White Sea is very stable. The temperature is about -1.5°C there all the year round, and the water salinity of this area is about 30‰. There are no seasonal variations of these hydrological parameters (Babkov, Golikov, 1984; see also Berger & Naumov, this volume).

1.2. Material and methods

Material was sampled on board of research vessels «Kartesh» and «Professor Vladimir Kuznetsov» in summer 1998 (Table 1) in the deep part of the Basin and the Kandalaksha Bay (Fig. 1). Seven benthic stations, with three samples each one, were taken by Petersen's grab („Okean“-type) of a sampling area of 0.25 m^2 . The only exception was station E, where six samples were taken: three in June and three in July. The samples were sieved on board of the research vessel (mesh size 1 mm) and preserved by 4% formalin and then sorted in the laboratory. All species were identified except those belonging to Caudofoveata and Nemertini. In some polychaetes only the family could be identified. Specimens of each species were counted and weighed with an accuracy to 0.001 g (total wet weights, incl. shells). Density and biomass of each species were recalculated for 1 m^2 .

Table 1
Description of stations taken

Station	Date	Depth	N latitude	E longitude
A	12.08.98	170	66°22.00'	34°15.00'
B	30.06.98	270	66°25.50'	34°22.00'
C	26.07.98	240	66°29.00'	34°30.30'
D	26.07.98	190	66°00.00'	35°00.00'
E-1	29.06.98	260	66°06.00'	35°41.40'
E-2	29.07.98	260	66°06.00'	35°41.40'
I	26.07.98	292	65°48.00'	35°44.00'
K	27.07.98	240	66°12.00'	35°00.00'

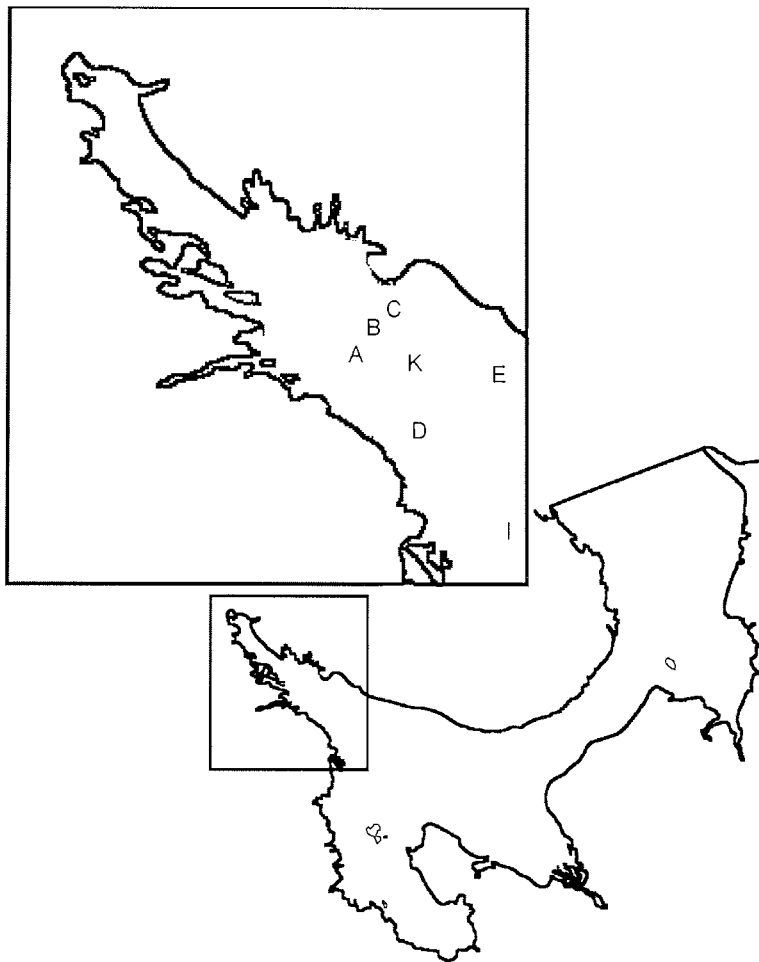


Fig. 1. Location of stations. Stations are marked with corresponding letters

All the data were processed statistically. The confidence level $P < 0.05$ was used as a criterion of significant differences.

A function suggested earlier (Naumov et al., 1986a) was used to estimate whether the species composition was studied sufficiently. It is the function

$$S = S_0 (1 - e^{-kN}), \quad [1]$$

where S is the number of species discovered, S_0 – estimated number of species, e – the base of Napierian logarithm, N – number of samples and k – coefficient. The coefficient k of the function measurably reflects the evenness of species spatial distribution, namely the higher its value is, the faster decreases the value of the first derivative, the more even is the benthos distribution.

An iterative procedure to obtain the empirical curve was used. At each iteration the average number of species for all samples was calculated and a sample possessing the most close species number was selected in the primary matrix. This number was added to the cumulative value, and the chosen sample with all its species was removed from the primary matrix.

The equation [1] in a recurrent form was used to obtain the theoretical curve.

If the local fauna is totally studied the first derivative at the point of the last sample should be equal zero. So its value was calculated for the point N_{\max} in order to estimate whether the list of species was complete enough.

The χ^2 method was used to estimate the correspondence of the empirical and theoretical curves.

The Shannon-Weaver index (Shannon, Weaver, 1949)

$$H' = \sum_{i=1}^S \frac{B_i}{B} \log_2 \frac{B}{B_i} \quad [2]$$

where S is the number of species, B_i – the biomass of i -th species and B – the total biomass of a community, was used to describe the species diversity in assemblages.

The index of oligomixness (Naumov, 1991)

$$I_o = \frac{\sigma_B}{B} \sqrt{S} \quad [3]$$

where S is the number of species, s_B – the standard deviation of species biomass of a community and B – its total biomass, was used to describe the evenness of biomass distribution between the species within an assemblage.

To find out the degree of resemblance of communities, the Jaccard similarity index (Jaccard, 1912) was used,

$$K_j = \frac{\sum_{i=1}^S \min(A_i, B_i)}{\sum_{i=1}^S \max(A_i, B_i)} \quad [4]$$

where S is the overall number of species in communities A and B , with A_i and B_i – the biomass of i -th species in them.

1.3. Results

The matrix of Jaccard similarity index was calculated to find out if there is any difference between stations taken in the Basin. No clearly separable clusters were obtained. The average value of Jaccard index in the matrix was $41 \pm 2\%$. Such a value can be considered as a rather low one; so it can be concluded that all the stations belong to a single assemblage. Average biomass and density of each species in this assemblage are presented in Table 2.¹

¹ Species lists of each station are given in Appendix 1. Main features of communities found are given in Appendix 2.

Table 2: List of species of the deep-water assemblage of the White Sea, ranked by biomass (g total wet weight per m²)

Species	Biomass	Density
<i>Portlandia arctica</i>	8.793±2.023	152.583±54.822
<i>Halcampa arctica</i>	3.885±1.635	1.833±0.742
<i>Tharyx marioni</i>	2.371±0.748	693.708±197.120
<i>Nuculana pernula</i>	1.977±0.730	4.500±1.676
<i>Nephtys</i> sp.	1.434±0.374	2628.875±1153.288
<i>Nephtys ciliata</i>	1.322±0.640	0.833±0.381
<i>Cossura longicirrata</i>	1.280±0.330	4082.250±1117.588
<i>Polychaeta</i> (fragmenta)	0.894±0.244	
<i>Scoloplos armiger</i>	0.813±0.672	98.125±55.967
<i>Chiridota pellucida</i>	0.770±0.787	0.167±0.1708.
<i>Urasterias lincki</i>	0.599±0.426	0.417±0.2482.
<i>Prionospio cirrifera</i>	0.320±0.120	154.958±56.944
<i>Saccoglossus merezhkowskii</i>	0.240±0.122	2.375±1.022
<i>Laonice cirrata</i>	0.228±0.161	211.792±127.817
<i>Caudofoveata</i>	0.156±0.118	0.667±0.417
<i>Ophiacantha bidentata</i>	0.136±0.100	0.333±0.241
<i>Maldane sarsi</i>	0.131±0.055	29.792±18.735
<i>Arrhis phyllonyx</i>	0.130±0.097	32.583±23.534
<i>Diplocirrus longisetosus</i>	0.118±0.083	52.875±37.276
<i>Aceroides latipes</i>	0.114±0.086	65.167±40.761
<i>Nemertini</i>	0.101±0.094	0.500±0.381
<i>Leionucula belotii</i>	0.084±0.061	0.667±0.482
<i>Pholoe minuta</i>	0.082±0.054	40.750±24.968
<i>Tubularia</i> sp.	0.081±0.083	
<i>Thyasira gouldi</i>	0.080±0.027	2.333±0.798
<i>Aricidea</i> sp.	0.072±0.053	53.542±37.315
<i>Nemidia torelli</i>	0.066±0.034	59.083±45.507
<i>Artacama proboscidea</i>	0.055±0.041	24.625±18.767
<i>Pectinaria hyperborea</i>	0.048±0.029	49.542±37.365
<i>Cylichna occulta</i>	0.041±0.034	33.750±33.292
<i>Musculus niger</i>	0.037±0.034	24.458±18.615
<i>Antinoella</i> sp.	0.033±0.019	3.167±1.761
<i>Leptognathia sarsi</i>	0.033±0.024	81.625±68.614
<i>Gammaridea</i>	0.033±0.033	16.292±16.641
<i>Hydractinia allmani</i>	0.033±0.033	
<i>Probeta harpularioides</i>	0.027±0.014	1.167±0.614
<i>Musculus corrugatus</i>	0.022±0.022	0.167±0.170
<i>Chaetozone setosa</i>	0.016±0.017	16.292±16.641
<i>Westwoodilla brevicar</i>	0.016±0.017	16.292±16.641
<i>Monoculodes</i> sp.	0.016±0.017	16.292±16.641
<i>Philine lima</i>	0.011±0.008	0.667±0.482
<i>Sabellidae</i>	0.008±0.008	16.292±16.641
<i>Buccinum elatior</i>	0.008±0.008	0.167±0.170
<i>Pandora glacialis</i>	0.006±0.006	0.167±0.170
<i>Myriochele oculata</i>	0.005±0.004	0.833±0.565
<i>Gersemia fruticosa</i>	0.004±0.004	
<i>Admete couthouyi</i>	0.003±0.003	0.167±0.170
<i>Milnedwardsia polaris</i>	0.002±0.002	0.167±0.170
<i>Lumbrineris fragilis</i>	0.001±0.001	0.833±0.702
<i>Ampharete arctica</i>	0.001±0.001	0.667±0.417
<i>Leiochone polaris</i>	0.001±0.001	0.500±0.295
<i>Eteone longa</i>	0.001±0.001	0.167±0.170
<i>Ampharete</i> sp.	0.001±0.001	0.167±0.170
<i>Capitella capitata</i>	0.000±0.000	0.167±0.170
<i>Perigonimus yoldiaearcticae</i>	+ ¹	

¹ In all the tables (+) character means that the species was registered but not weighted.

The average biomass of this assemblage is 27.094 g/m², 55 species were found in it. The following parameters of the cumulative function [1] of species number for our material were found:

$$S=57.19(1-e^{-0.352N}) \quad [5]$$

See the plot of empirical and theoretical curves at Fig. 2. The χ^2 value was 3.64, number of degrees of freedom being 21, so one can consider these curves to be in good correspondence. The estimated number of species (57.19) is very close to the empirical one (55); the theoretical function reaches the value of 55 at 13-th sample and its first derivative is equal to 0.004 in the point N_{max} . Thus, we can consider that the species composition of the White Sea deep-water assemblage was studied well enough by the sampling method used, and the species found make 96% of expected ones.

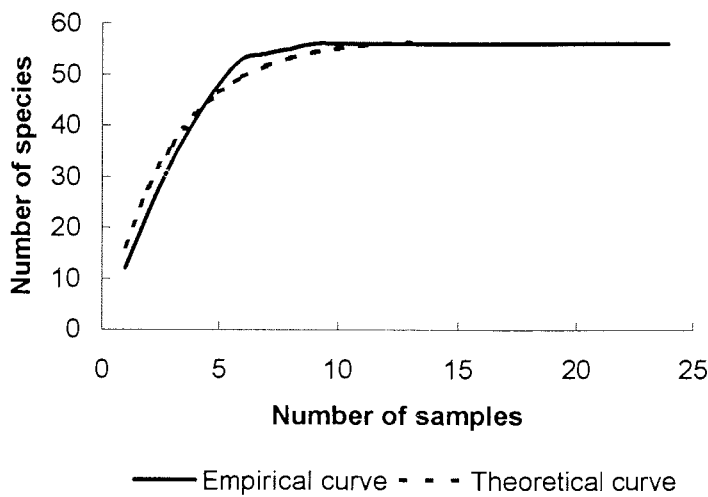


Fig. 2. Dependence of number of species on the number of samples

It is interesting to compare the evenness of benthos distribution in different parts of the White Sea (Table 3). It can be easily seen that the most even spatial distribution of the sea floor animals is observed in the deep-water part of the Basin.

Table 3: The value of k coefficient in different parts of the White Sea

Place	k value	Source of information
Basin	0.352	Present investigation
Kandalaksha Bay	0.138	Data-base of the White Sea Biological Station, ZISP
Onega Bay	0.116	Naumov et al., 1986a
Dvina Bay	0.060	Naumov et al., 1986a
Mezen' Bay	0.109	Naumov et al., 1986a
Gorlo Strait	0.040	Naumov et al., 1986a

Species diversity of the deep-water assemblage of the Basin, estimated by biomass is 3.582 bit/g and by density – 2.326 bit/specimen. Its oligomixness is by biomass 36.68±3.50% and

by density – $55.46 \pm 5.55\%$. Thus, we deal with a diverse polymixous community where Mollusca, represented by 13 species, play the main role in terms of biomass (Fig. 3).

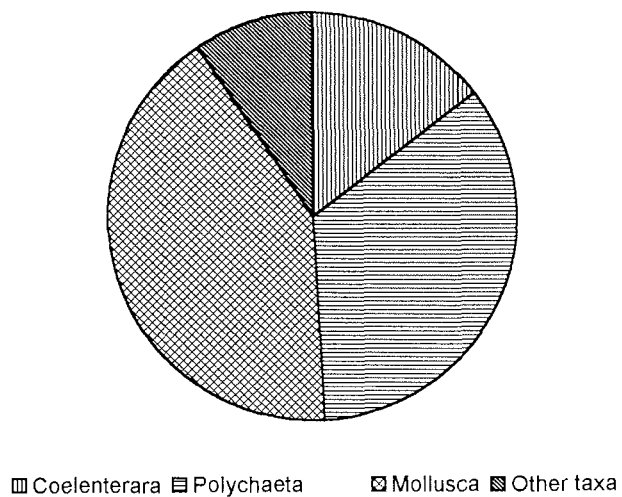


Fig.3. Taxonomic composition of the deep-water assemblage estimated by biomass

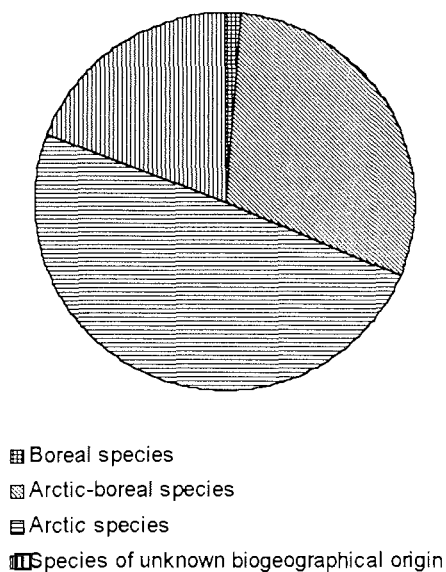
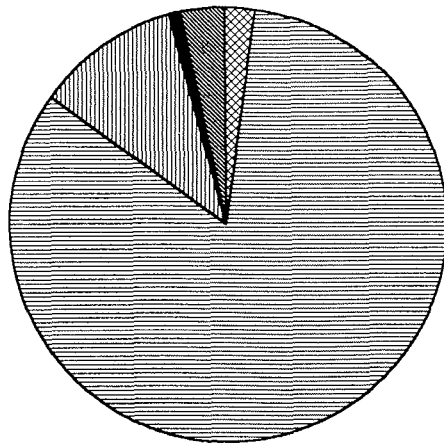


Fig. 4. Biogeographic composition of the deep-water assemblage estimated by biomass



- ☒ Suspension feeders
- ☒ Deposit feeders
- ☒ Carnivorous species
- Omnivorous species
- ☒ Species of unknown mode of feeding

Fig. 5. Trophic composition of the deep-water assemblage estimated by biomass

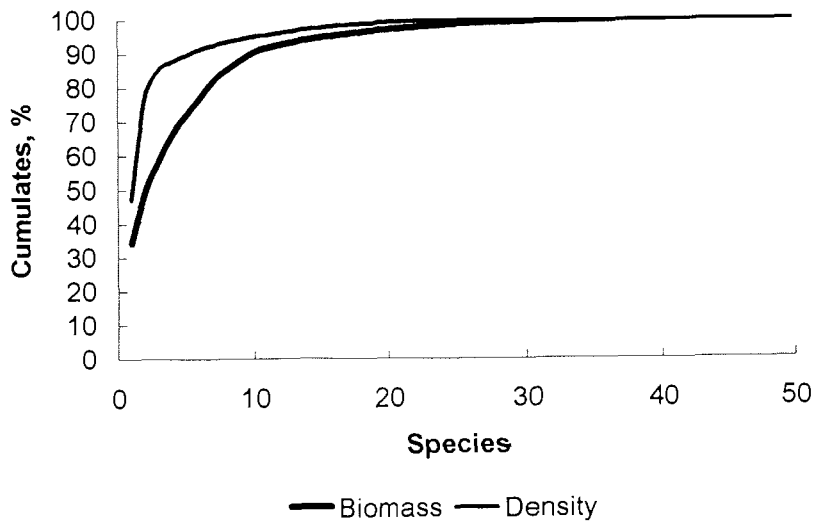


Fig. 6. k-dominant curves for the deep-water assemblage

The second position in these terms is occupied by Polychaeta (25 species). About 30% of biomass of this assemblage are created by arctic-boreal species and about 50% – by arctic ones. For the biogeographic composition see fig. 4. More than 80% of biomass belong to deposit feeders (Fig. 5). Infauna species create about 90% of biomass, and an overwhelming majority of deep-water benthic forms are vagile species (93%). To estimate the succession process in the assemblage, the *k*-dominant curves (Warwick et al., 1987) were plotted (Fig. 6). The *k*-dominant curve of density lies higher than one of biomass. Difference between biomass and density cumulates, verified by Kholmogorov-Smirnov criterion, is of high significance. Since the investigated site is far away from the polluted areas of the White Sea (Naumov, Fedyakov, 1993), the fact may be considered as a reflection of some succession processes according to Warwick's hypothesis.

The frequency of occurrence of species in the assemblage under consideration allows to divide them into three groups: very regular („obligate“), common and rare ones. We considered a species as regular if its occurrence did not differ significantly from 100%. Occurrence of rare species, on the contrary, did not differ from zero. All other species were regarded as common. A significant hiatus can be mentioned between the occurrence of obligate and common species (Fig. 7). In this terms such species as *Portlandia arctica*, *Nephtys* sp., *Cossura longicirrata* and *Tharyx marioni* can be treated as obligate forms for the White Sea deep-water assemblage. Its common species are *Maldane sarsi*, *Prionospio cirrifer*, *Thyasira gouldi*, *Nuculana pernula*, *Scoloplos armiger*, *Halcampa arctica*, *Saccoglossus mereschkowskii*, *Diplocirrus longisetosus*, *Aricidea* sp., *Nemidia torelli*, *Nephtys ciliata*, *Antinoella* sp., *Urasterias lincki*, *Pectinaria hyperborea*, *Cylichna occulta* and *Probebella harpularioides*. At last *Laonice cirrata*, *Caudofoveata* gen. sp., *Aceroides latipes*, *Nemertini* gen. sp., *Pholoe minuta*, *Leptognathia sarsi*, *Myriochele oculata*, *Ampharete arctica*, *Leiochone polaris*, *Ophiacantha bidentata*, *Arrhis phyllonyx*, *Leionucula belotii*, *Artacama proboscidea*, *Musculus niger*, *Philine lima*, *Lumbrinereis fragilis*, *Chiridota pellucida*, *Gammaridea* gen. sp., *Musculus corrugatus*, *Chaetozone setosa*, *Westwoodilla brevicar*, *Monoculodes* sp., *Sabellidae* gen. sp., *Buccinum elatior*, *Pandora glacialis*, *Admete couthouyi*, *Milnedwasia polaris*, *Eteone longa*, *Ampharete* sp., *Capitella capitata*, *Tubularia* sp., *Hydractinia allmani* and *Gersemia fruticosa* can be named as rare species for the deep part of the Basin. All the above mentioned species are listed by their frequency of occurrence in decreasing order. Further in the text only obligate and common species are discussed.

The analysis of species density allows to distinguish some density groups in the assemblage under discussion. A two-fold drop of density in the ranged sequence was taken as criterion for division. In the present material the threshold value was exceeded in three cases. Four density groups were established according to this fact – bountiful species *Cossura longicirrata* and *Nephtys* sp.; abundant species *Tharyx marioni*; numerous species *Prionospio cirrifer*, *Portlandia arctica*, *Scoloplos armiger*, *Nemidia torelli*, *Aricidea* sp., *Diplocirrus longisetosus*, *Pectinaria hyperborea*, *Cylichna occulta* and *Maldane sarsi*; sparse species *Nuculana pernula*, *Antinoella* sp., *Saccoglossus mereschkowskii*, *Thyasira gouldi*, *Halcampa arctica*, *Probebella harpularioides*, *Nephtys ciliata* and *Urasterias lincki* (Fig. 8).

Portlandia arctica is a species, dominant by biomass in the assemblage (Fig. 9). The biomass of the dominant species did not exceed significantly the biomass of the first ordinary species, which is *Halcampa arctica*, and there is no reason to consider it as a subdominant. Such a situation is typical for polymixous communities, where the biomass is distributed more or less even among the species. As it was shown earlier, polymixous communities are common to deep sites in the White Sea (Naumov, 1991).

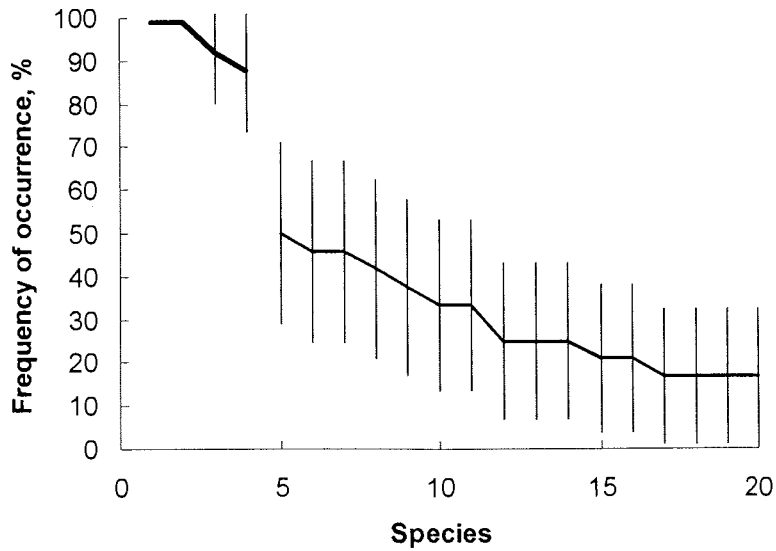


Fig. 7. Frequency of occurrence of obligate (thick line) and common (thin line) species (rare species are truncated), plotted in decreasing order. X axis – number of species in ranged sequence
Vertical bars – confidence intervals

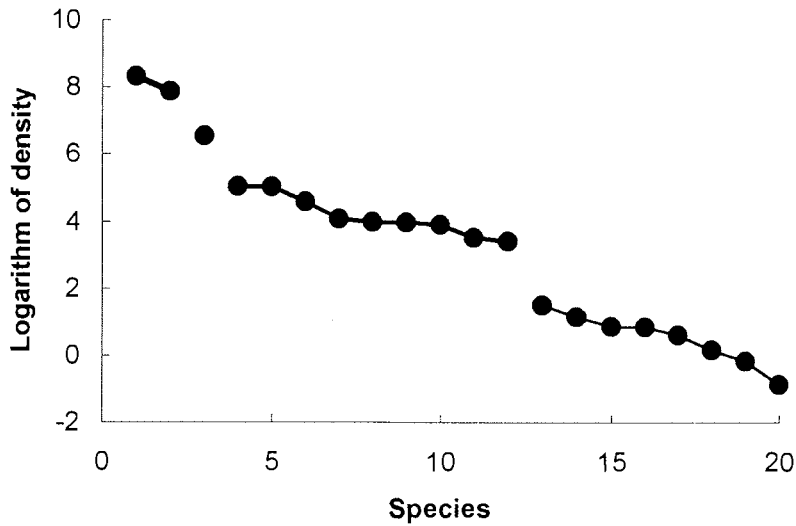


Fig. 8. Density (in logarithm scale) of obligate and common species in the deep-water assemblage (rare species are truncated), plotted in decreasing order. X axis – number of species in ranged sequence
Thick line – bountiful species; single dot – abundant species;
medium line – numerous species; thin line – sparse species

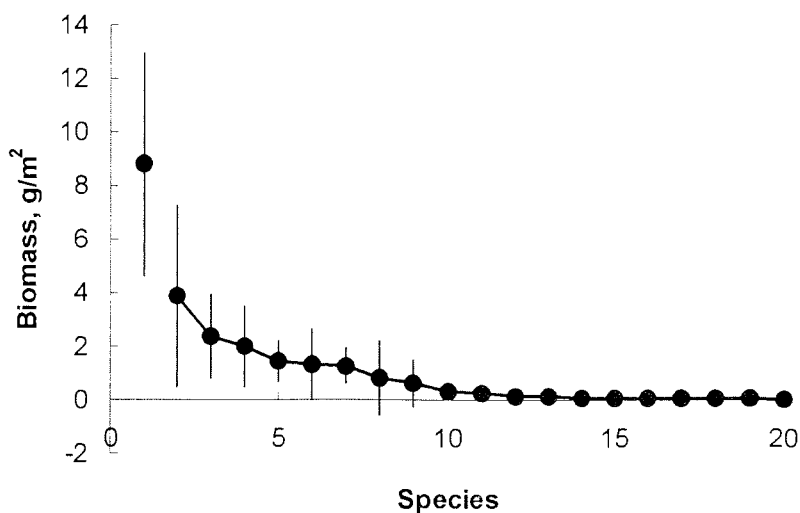


Fig. 9. Biomass of obligate and common species in the deep-water assemblage (rare species are truncated), plotted in decreasing order. X axis – number of species in ranged sequence
Vertical bars – confidence intervals, single dot – dominant species

1.4. Discussion

It is interesting to compare the deep-water assemblage with *Portlandia arctica* as a dominant and characteristic species with some other similar communities from the White Sea. Similar assemblages can be found in different places. First of all it is the open basin of the White Sea. We can compare our material with community found near the Srednie Ludy Archipelago, Kandalaksha Bay (depth 290 m, one station, one sample from 1981, our data, unpublished), in the Velikaya Salma Strait, Kandalaksha Bay (depth 120 m, one station, one sample, our data obtained within the framework of present project, sampled in 1998), at the transection Sharapov Cape – Tury Cape, Kandalaksha Bay (average depth 230 m, four stations, twenty samples, sampled in 1994, Deubel, 1995; see also Deubel, this volume) and Dvina Bay (average depth 96 m, four stations, four samples, our data, sampled in 1981, Lukanin et al., 1995). On the other hand one can find comparable communities in some more or less deep inlets, isolated from the main hollow of the White Sea by a shallow ridge (sill).¹

The temperature in such inlets is rather low, being about zero, or even negative all the year round (Knipowitsch, 1893; Naumov, 1979; Naumov et al., 1986b, Ninburg, 1990). It allows arctic organisms to live there in a shallow area. Normally they cannot survive at corresponding depth in the open parts of the White Sea due to high summer temperature. We have some material of such sites as the Palkina Guba Inlet, Kandalaksha Bay (depth 40 m, one station, three samples, our data, sampled in 1998, unpublished), mouth part of the Kolvitsa Inlet, Kandalaksha Bay (average depth 50 m, four station, four samples, our data, sampled in 1985, Naumov et al., 1986b), head part of the Kolvitsa Inlet, Kandalaksha Bay (depth 40 m, one station, one sample, our data, sampled in 1985, Naumov et al., 1986b), the Voronya Guba Inlet, Kandalaksha Bay (depth 6 m, one station, one sample, data of Laboratory for Marine Benthos Ecology, kindly offered by Dr. E. A. Ninburg, sampled in 1975, unpublished) and the Dolgaya Guba Inlet, Onega Bay (average depth 15 m, ten stations, ten samples, data of

¹ For the main features of these communities see Appendix 3.

Laboratory for Marine Benthos Ecology, kindly offered by Dr. E. A. Ninburg, sampled in 1985, Ninburg, 1990).

All the above mentioned material was collected and processed by methods, similar to those used in our investigation. The average biomass of species was calculated for every site mentioned above. During the first step of our analysis, only regular and common species were used for the comparison with the deep-water assemblage. But, in the cases of the head part of Kolvitsa Inlet, Voronya Inlet, Srednie Ludy Archipelago and Velikaya Salma Strait, where only one sample is available, all the species were used in the analysis. During our second analytical step, only species found in five or more sites were included into the primary matrix to avoid the influences of rare animals. The Jaccard similarity index together with the weighted pair-group average clustering method were used to create a dendrogram of resemblance of the assemblages under investigation (Fig. 10).

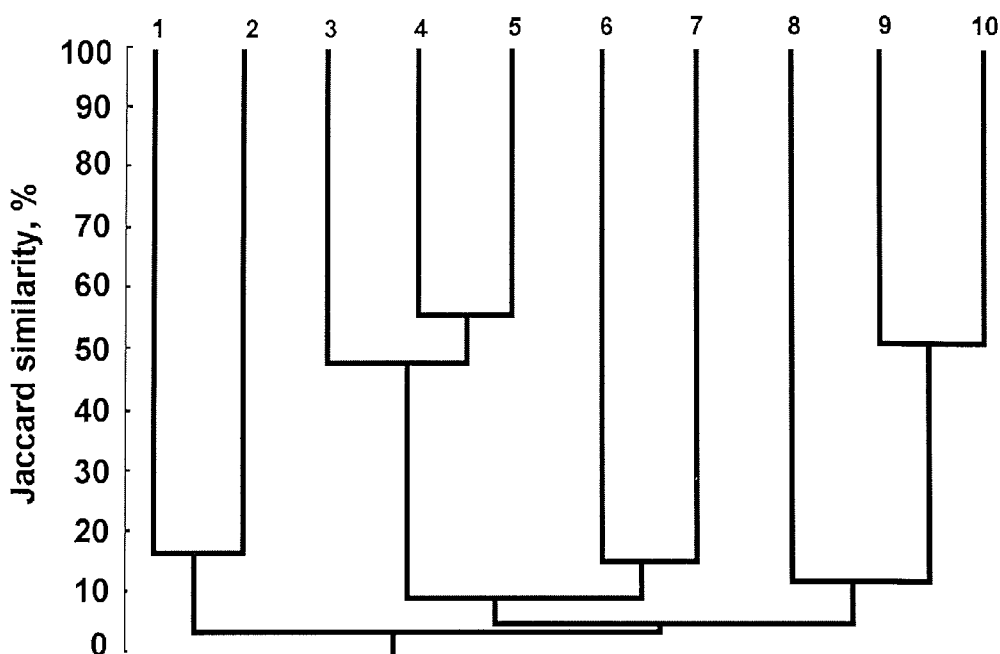


Fig. 10. Cladogram of Jaccard similarity between different assemblages with *Portlandia arctica* as a dominant species calculated by species biomass

Assemblages from:

1 – Dvina Bay (96 m); 2 – Voronya Guba Inlet (6 m); 3 – Palkina Guba Inlet (40 m); 4 – head part of the Kolvitsa Inlet (40 m); 5 – mouth part of the Kolvitsa Inlet (50 m); 6 – Dolgaya Guba Inlet (15 m); 7 – Srednie Ludy Archipelago (290 m); 8 – Velikaya Salma Strait (120 m); 9 – transection Sharapov Cape – Tury Cape (average: 230 m; data from Deubel, 1995); 10 – deep-water part of the Basin

It is easily seen that our material is closely related to that obtained by Deubel (1995). It confirms our suggestion about one single assemblage inhabiting the deepest part of the White Sea hollow. The second good cluster is formed by communities from Palkina Guba Inlet and two sites in the Kolvitsa Inlet, all three located in the head part of the Kandalaksha Bay. Assemblages from other sites form their own clusters. Such a clustering can be easily explained. The deep-water assemblage occupies the main White Sea depression with very stable conditions: all year-round temperature there is about -1.4°C and salinity about 29-30‰. The same conditions are observed in the region of Srednie Ludy Archipelago. At the station under discussion the temperature was -1.4° and salinity 29.5‰. This site is the north-west extremity of the central White Sea depression. So one could expect to find the same community there. Yet we encountered a community of a great difference instead. It should be noticed,

however, that the region of Srednie Ludy Archipelago was already marked as a place with abnormal distribution of benthic species (Fedyakov, Naumov, 1983; Fedyakov, 1986; Naumov, Fedyakov, 1993). The high hydrodynamic activity of this region was mentioned earlier to explain some peculiarities in the distribution of heavy minerals in the White Sea sediments (Nevesky et al., 1977).

The Palkina Guba Inlet and the Kolvitsa Inlet are situated close to each other and have similar hydrological and hydrodynamic conditions (1.6°C and 24.8‰ in the Palkina Guba Inlet, -0.2°C and 28.4‰ in the mouth part of the Kolvitsa Inlet, 0.5°C and 27.2‰ in its head part). So it is no surprise to find similar communities in those sites. Four other sites differ considerably from each other and from localities already discussed. The Velikaya Salma is neither open hollow nor inlet, but a strait with its own hydrodynamic regime. Stations in the Dvina Bay are situated at the very shallow area of distribution of the assemblage under discussion. Though the hydrological conditions there are similar to those in the deepest part of the White Sea (-1.3°C and 29.2‰ in summer), the fraction of sand is in average two times higher in the Dvina Bay (Nevesky et al., 1977). This may influence the bottom species.

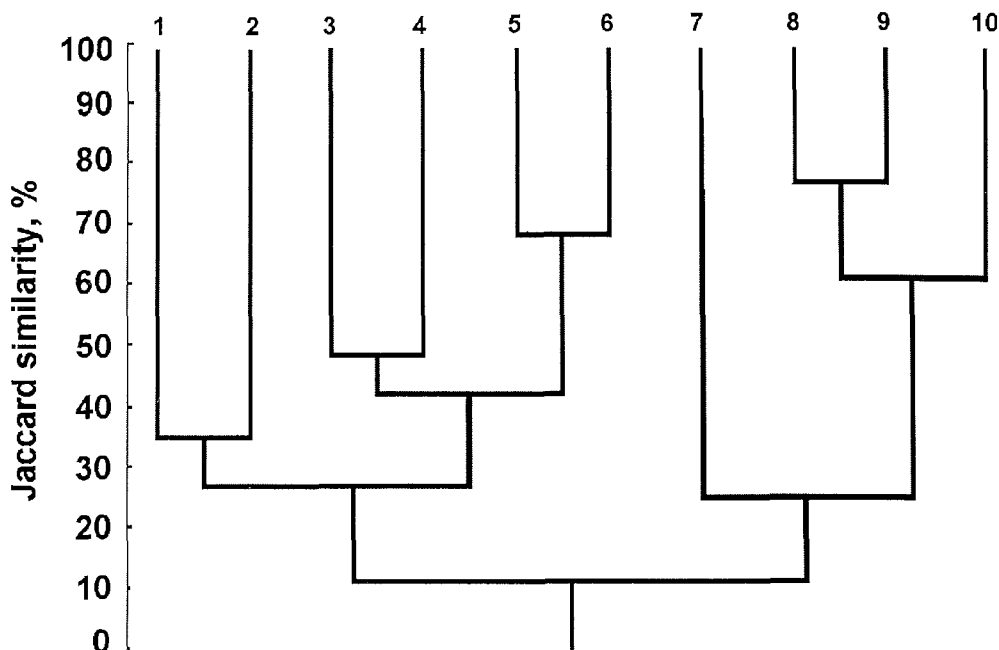


Fig. 11. Cladogram of Jaccard similarity between different assemblages with *Portlandia arctica* as a dominant species calculated by fraction of species biomass

Assemblages from:

- 1 – Dvina Bay; 2 – Voronya Guba Inlet; 3 – Palkina Guba Inlet; 4 – head part of the Kolvitsa Inlet;
- 5 – mouth part of the Kolvitsa Inlet; 6 – Dolgaya Guba Inlet; 7 – Srednie Ludy Archipelago;
- 8 – Velikaya Salma Strait; 9 – transection Sharapov Cape – Tury Cape; 10 – deep-water part of the Basin

The Dolgaya Guba Inlet and the Voronya Inlet are very shallow coves situated in quite different parts of the White Sea (Solovetsky Island, Onega Bay and continental shore, Kandalaksha Bay). Nothing is known about the hydrological and hydrodynamic regimes of the Voronya Inlet. On the contrary, the complicate and very specific water exchange and peculiar temperature and salinity conditions of the Dolgaya Guba Inlet are studied rather well (Knipowitsch, 1893; Ninburg, 1990). So, all the above mentioned sites have their own specific features and possess differing assemblages of arctic species with *Portlandia arctica* as a dominant one.

In order to compare the structure of assemblages under consideration, normalised data were taken in the analysis. The fraction of total biomass of each species was used to normalise the community structure. Jaccard similarity matrix was clustered with weighted pair-group average method as in the previous case.

Two main clusters can be seen in the cladogram (Fig. 11). One cluster includes assemblages of open sea and the other – assemblages of cold-water inlets. The only exception is the open site assemblage from the Dvina Bay, belonging to small inlets cluster. We shall obtain more main clusters if we take the 50% level of similarity as a threshold value. In this case one cluster will combine assemblages of open waters of the Kandalaksha Bay, the second cluster – assemblages of the Dolgaya Guba Inlet and mouth part of the Kolvitsa Inlet. All other communities will form their own clusters.

As the community structure of assemblages in the shallow water inlets differs from that of open parts of the sea, it is interesting to compare the average characteristics in both types of biotopes (Tables 4-7).

Table 4. *General features of assemblages of Portlandia arctica from different biotopes*

Biotop	Depth, m	Number of species	Biomass, g/m ²	Diversity index, bit/g	Index of oligomixness, %
Inlets	30	37	99.637	2.531	52.63
Open hollow	195	43	73.888	2.575	51.03

„(Oligo-)Mixness“ is a measure of evenness with values near zero in case of even biomass distribution amongst species and near 100%, if only one species would make up almost all biomass. „Polymixous“ communities have values < 70%, „oligomixous“ > 85 %; assemblages with intermediate values are termed „mesomixous“)

Table 5. *Zoogeographic composition of assemblages of Portlandia arctica from different biotopes, biomass, %*

Biotope	Boreal species	Arctic-boreal species	Arctic species
Inlets	3.94±2.34	32.73±5.65	54.90±5.99
Open hollow	0.87±1.12	42.65±5.95	46.73±6.01

Table 6. *Trophic composition of assemblages of Portlandia arctica from different biotopes, biomass, %*

Biotop	Suspension feeders	Deposit feeders	Carnivorous species	Omnivorous species
Inlets	12.92±4.04	81.68±4.66	4.81±2.58	0.49±0.84
Open hollow	17.53±4.58	77.37±5.04	3.58±2.24	0.35±0.72

Table 7. *Fraction of infaunal and vagile (incl. infauna) species in the assemblages of Portlandia arctica from different biotopes, biomass, %*

Biotope	Infauna	Vagile species
Inlets	87.38±4.00	94.02±2.85
Open hollow	71.73±5.42	81.54±4.67

There is no significant difference between the general features of the fauna of both types of biotopes except the percentage of vagile animals; so, this cannot account for the division of our material into two big clusters. Neither this fact can be explained by the composition by larger taxa (Table 8), though the biomass of Anthozoa is significantly higher in the open hollow biotopes and such taxa as Sipunculida and Aplacophora were not found at all in shallow inlets. All three taxa mentioned are of low frequency of occurrence; and the two last ones have a very small biomass there. Thus, they can not influence the average community structures so strongly.

Table 8. *Taxonomic composition of the assemblages of Portlandia arctica from different biotopes, biomass, %*

Taxon	Open hollow	Inlets
Porifera	0.26±0.62	0.32±0.68
Hydrozoa	1.26±1.34	0.01±0.13
Anthozoa	17.42±4.57	2.93±2.03
Nemertini	0.10±0.38	3.68±2.27
Priapulida	0.14±0.46	0.27±0.62
Sipunculida	0.06±0.30	0.00±0.00
Polychaeta	12.06±3.92	15.17±4.32
Aplacophora	0.41±0.77	0.00±0.00
Gastropoda	0.88±1.13	2.73±1.96
Bivalvia	56.69±5.97	68.65±5.58
Tanaidacea	0.02±0.19	0.01±0.02
Cumacea	0.07±0.32	1.24±1.33
Amphipoda	0.35±0.71	0.52±0.86
Bryozoa	0.19±0.52	0.05±0.26
Enteropneusta	0.19±0.53	0.02±0.17
Asteroidea	6.27±2.92	2.50±1.88
Holothuroidea	0.57±0.91	1.40±1.42
Ophiuroidea	1.42±1.42	0.46±0.81
Tunicata	1.62±1.52	0.04±0.23

To conclude, the assemblages in the open basin and in the shallow inlets do not differ in general features, but, only by their mere species composition and shares. Five species are regarded responsible for this: *Portlandia arctica* whose biomass in shallow inlets is 25% higher; *Nuculana pernula*, almost totally replaced in the inlets by *Macoma calcarea*; *Lumbrineris fragilis* whose biomass in the open parts of the White Sea is six times lower, and Nemertini, which were very rare in the deep-water assemblage. All the other mentioned species are regular or common and are present at least in five assemblages under discussion (Table 9).

The dependence of some characteristics of assemblages, with *Portlandia arctica* as a dominant form, on the depth is of special interest. The sites where more than one sample is available were taken in the analysis. Each type of biotope – open sea hollow or shallow inlets – are represented with three communities only. Due to the lack of material the tendencies shown below should be considered as preliminary information. The biomass, number of species and fraction in biomass of carnivorous species increase with the depth both in coves and in the open sea. As an example, the number of species plotted against the depth is shown at the Fig. 12.

Another type of depth-dependence was found for the index of oligomixness, fraction in biomass of deposit feeders, species of arctic origin and infauna species. In all these cases a peak is found at the middle class of depth both in inlets and in the open basin. As an example of such a dependence see Fig. 13.

For Shannon-Weaver's diversity index and fraction of arctic-boreal species in the biomass this dependence is vertically inverted. Future investigations are needed to clarify all these results.

Table 9. Species composition of the assemblages of *Portlandia arctica* from different biotopes, biomass, %; (species differing significantly are marked)

Species	Open basin	Inlets
<i>Portlandia arctica</i> *	51.30±6.02	67.38±5.64
<i>Nuculana pernula</i> *	30.42±5.54	1.20±1.31
<i>Nephtys</i> sp.	3.45±2.20	2.14±1.74
<i>Thyasira gouldi</i>	2.51±1.88	0.34±0.70
<i>Pectinaria hyperborea</i>	2.45±1.86	4.65±2.54
<i>Cylichna occulta</i>	2.11±1.73	0.08±0.34
<i>Scoloplos armiger</i>	2.07±1.71	0.47±0.82
<i>Lumbrineris fragilis</i> *	1.43±1.43	8.69±3.39
<i>Aricidea</i> sp.	1.07±1.24	1.02±1.21
<i>Retusa pertenuis</i>	1.06±1.23	0.06±0.29
<i>Chaetozone setosa</i>	0.64±0.96	1.09±1.25
<i>Maldane sarsi</i>	0.53±0.87	0.50±0.85
<i>Leionucula belotii</i>	0.52±0.87	0.84±1.10
<i>Macoma calcarea</i> *	0.46±0.81	8.70±3.39
Nemertini gen. sp.*	0.10±0.38	2.84±2.00

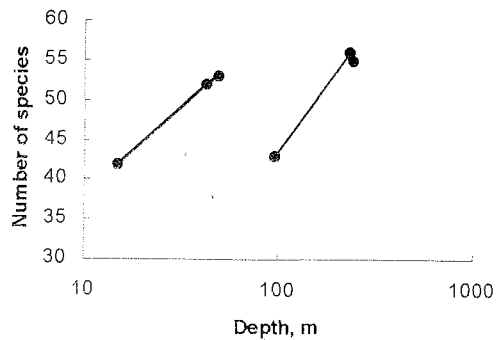


Fig. 12. Dependence of species number on the depth
Thick line – shallow inlets, thin line – open basin

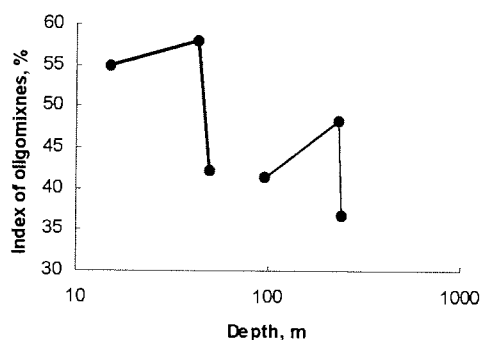


Fig. 13. Dependence of the index of oligomixness on the depth
Thick line – shallow inlets, thin line – open basin

Not only the White Sea is a water-basin where *Portlandia arctica* forms specific communities. One can find such assemblages in the Novaya Zemlya Trough and Spitsbergen area (Barents Sea) as well as in the Kara Sea. The more far to the east, the more intensively this clam is replaced by other species of the genus *Portlandia*. There is very little material in the literature on the Arctic Seas, which could be compared with our data. The paper of V.A. Brotskaja and L.A. Zenkevich (1939) was the only comparable material found. Three stations at the depth of 150-200 m in the Novaya Zemlya Trough, where an assemblage with *Portlandia arctica* as a leading species was found, were sampled by these authors. For species composition (obligate and common species) see Table 10.

Table 10. Species composition of the sea floor assemblage from the Novaya Zemlya Trough (computed after data of V.A. Brotskaja and L.A. Zenkevich, 1939)
Species, common to the White Sea deep-water assemblage are marked

Species	Biomass	Density
<i>Macoma calcarea</i> *	158.30	223
<i>Portlandia arctica</i> *	104.82	129
<i>Golfingia margaritaceum</i>	31.42	4
<i>Ciliatocardium ciliatum</i>	15.07	9
<i>Nuculana pernula</i> *	6.22	11
<i>Leionucula belotii</i> *	5.24	12
<i>Yoldia amygdalea</i>	3.54	6
<i>Pectinaria hyperborea</i> *	3.40	31
<i>Owenia assimilis</i>	1.75	48
Amphipoda	1.34	20
<i>Scalibregma inflatum</i>	1.21	22
<i>Terebellides stroemii</i>	0.66	5
<i>Ophiocten sericeum</i>	0.56	3
<i>Mesidotea sabini</i>	0.37	2
<i>Cylichna alba</i>	0.04	7
<i>Ampharete arctica</i>	0.01	2

It should be noticed first of all that the dominant species of this assemblage is *Macoma calcarea*, *Portlandia arctica* taking rank of a subdominant. There are no *Nephtys* sp., *Scoloplos armiger*, *Lumbrineris fragilis* and some other species, so typical for the White Sea deep-water bottom communities. On the other hand such species as *Ciliatocardium ciliatum*,

Yoldia amygdalea and *Terebellides stroemii* are found in the Novaya Zemlya Trough whereas in the White Sea they are common members of much more shallow-water assemblages. So the species composition of the bottom fauna in these two regions differs rather considerably from each other.

The biomass of the Barents Sea assemblage (about 370 g/m²) is more than ten times higher than the White Sea one. - On the other side, Brotskaja and Zenkevich marked only 30 species in the Novaya Zemlya Trough community, while 55 species were found in our White Sea deep-water material.

If the shallower parts of the White Sea basin, with depths of 105-110 m, are included, the species number rises up to more than 130 (see Galkina et al., this volume). And when the additional 11 species found in our corer samples (see part 2) are taken into account, the total number of species found in 1998-99 is 66. Deubel (1995) found 79 species in depths between 98 and 325 m.

There are very few samples in the material for reliable conclusions, but it should be marked, nevertheless, that in our empirical data the cumulative of species number reaches the value $S=33$ in the third sample, which is similar in the theoretical curve – $S_3=36$ (Fig. 2). If the distribution of benthic species in the Novaya Zemlya Trough is even enough, we can expect a similar number of species as in the White Sea deep-water assemblage. The suggestion of evenness of benthos distribution is more or less reasonable; for, the environmental conditions are alike in both sites. So, at our present level of knowledge we have no reason to suggest a great difference in species numbers of the two assemblages.

The species diversity in the Novaya Zemlya Trough assemblage makes 2.445 bit/g (computed by us on the base of Brotskaja's and Zenkevich's data), which is of about one bit/g lower than in our White Sea material. The index of oligomixness is 50.48%. Accordingly, the assemblage can be treated as polymixous as the communities from the White Sea basin. The fraction of biomass, belonging to deposit feeder is almost the same in both areas: about 86% in the Novaya Zemlya Trough and about 80% in the White Sea hollow. So, one may conclude that by many formal features there is no huge difference between the assemblages under discussion. The main distinction is that in the species composition. This strongly affects the biogeographic composition: The biomass of arctic species makes 28.40% only in the area of Novaya Zemlya, arctic-boreal species forming 69.12%. In the White Sea deep-water community the situation is just contrary.

1.5 Conclusions

1. The deep-water part of the White Sea is inhabited by a single macro-zoobenthos assemblage, *Portlandia arctica* being its dominant species.
2. This deep-water assemblage of the White Sea is diverse and polymixous. 55 species were identified (at depths > 170 m).
But, total species number is even higher (> 130), especially, when the more shallow margins of the basin (100 - 150 m) and other methods than grab sampling (tube coring) are included in evaluations.
3. Infauna species and deposit feeders are predominant in this assemblage.
4. Somehow similar communities inhabit some shallow-water inlets of the White Sea. However, they differ from the deep-water assemblage by their species composition.
5. A similar assemblage found by Brotskaja and Zenkevich in the Barents Sea differs from that of the White Sea by its species and biogeographic composition.
The assemblage in the White Sea basin is of much more arctic nature.

1.6 Acknowledgements

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References: see Part 2

New results on the macro-zoobenthos of the White Sea deep basin

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Part 2

Small benthic organisms and juveniles of macrobenthic species in the White Sea deep-water assemblage

2.1. Introduction

The White Sea deep-water biotope is exceptionally stable. For the short description of this area, see part 1 of our macro-zoobenthos report. The main idea of the present investigation was to find out if there is any seasonal dynamics in density or biomass of macrobenthic species in such a stable environment, where only seasonal changes of sedimentation conditions (including input of food particles) may occur. It is evident that for adult organisms, with more or less long life cycles, the seasonal dynamics, if any, could hardly be discovered owing to the relatively short duration of the project. One way to solve this problem is to investigate the dynamics of juveniles and small species with approximately one-year life cycles. So, in present research, the complex of such organisms belonging to the White Sea deep-water assemblage, described in the first part of this Report, was studied. This complex was considered as a whole and was not divided into juveniles and small adult animals. Macrobenthic, as these species are treated traditionally, they are of size of meiobenthic organisms or hardly exceed it.

The seasonal dynamics of the sea floor communities in the White Sea are not yet studied sufficiently. Some papers deal with shallow-water assemblages (Myagkov, 1975; Golikov et al., 1985), others – with individual species (Kalyakina, 1980). But, there is not a single one on seasonal changes in the White Sea deep-water communities. Accordingly, it was important to examine, whether there is any seasonal dynamics in such specific conditions, and, thus, to contribute the the overall project objective to investigate the intensity of pelagic-benthic coupling and the seasonality of the White Sea deep basin ecosystem.

2.2. Material and methods

The chosen stations were the same as in macrobenthic investigations (see 1.2). In addition, one station named NL near the Ileyky Islands was established at a depth of about 100 m in order to have some information for comparison. Material was sampled on board of research vessels «Kartesh» and «Professor Vladimir Kuznetsov» in the deep part of the Basin and the Kandalaksha Bay (Fig. 14) by minicorer with tubes of a sampling area of 25.5 cm² (sampling time, locations and other information are presented in Table 11). The samples were preserved by 4% formalin on board, then washed out (sieve mesh size 0.25 mm) and sorted in the laboratory. Almost all species were identified except some juveniles of Polychaeta, Crustacea and Bivalvia. Nemertini and some hydrozoan species were not identified.

Specimens of each species were counted. If the specimens were heavy enough, they were weighed with an accuracy 0.001 g, if not, they were measured under a binocular microscope with an accuracy 0.025 mm, and their weights were computed according to the following rules: For worm-like organisms length and diameter were measured, and their volume was approximated by a cylinder; a spherical approximation was used for bivalve juveniles (< 1 mm), the length of their shells being measured. As a first approximation the volume was assumed equal to the weight of these tiny animals. Density and biomass of each species were recalculated for 1 m². All the data were processed statistically. The confidence level $P < 0.05$

was used as a criterion of significant differences. Other mathematical methods used are described in the chapter 1.2 (see Part 1).

Table 11. *Description of sampling stations*

Station	Date	Number of samples	Depth (m)	N Latitude	E Longitude
A	12.08.98	3	170	66°22.00'	34°15.00'
A	01.06.99	3	170	66°22.00'	34°15.00'
A	01.08.99	3	170	66°22.00'	34°15.00'
B	27.06.98	3	270	66°25.00'	34°22.00'
B	15.10.98	3	270	66°25.00'	34°22.00'
B	01.06.99	3	270	66°25.00'	34°22.00'
B	01.08.99	4	270	66°25.00'	34°22.00'
B	24.11.99	1	270	66°25.00'	34°22.00'
C	27.06.98	3	240	66°29.00'	34°30.30'
C	01.06.99	3	240	66°29.00'	34°30.30'
C	01.08.99	4	240	66°29.00'	34°30.30'
D	26.06.98	3	190	66°00.00'	35°00.00'
E	26.06.98	3	260	66°06.00'	35°41.40'
I	26.06.98	3	292	65°48.00'	35°44.00'
K	27.06.98	3	240	66°12.00'	35°00.00'
NL	14.10.98	3	106	66°22.00'	33°48.00'
NL	01.08.99	1	106	66°22.00'	33°48.00'
NL	24.11.99	1	106	66°22.00'	33°48.00'

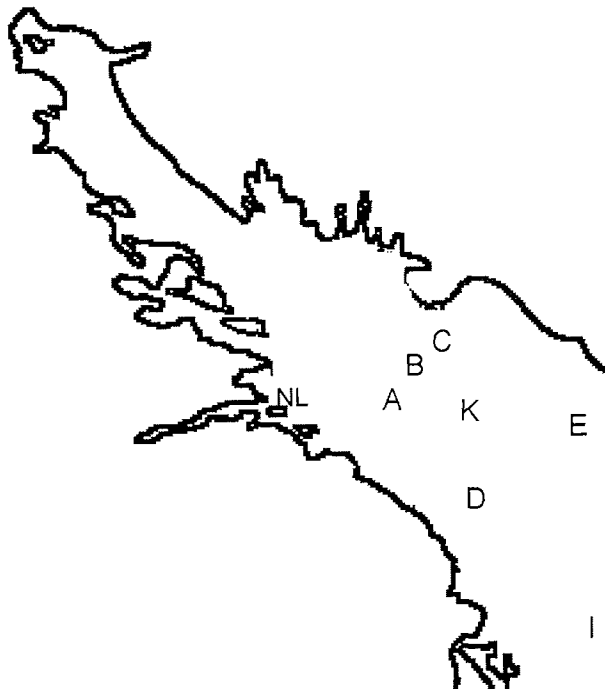


Fig. 14. *Location of stations. Stations are marked with corresponding letters*

2.3. Results

The matrix of Jaccard similarity index was calculated to find out if there is any difference between stations taken in the Basin. No good clusters were obtained. So one may conclude, that all the stations belong to a single assemblage. Nevertheless, the complex at the station near the Ileyky Islands differs somewhat from that of other stations by species composition and biomass. That is why below they are treated as closely related but different complexes. On the other hand the material available does not allow to distinguish any seasonal changes in them. Nevertheless an attempt will be made further to discover some seasonal dynamics for separate species.

Average biomass and density of each species in the complexes under discussion are presented in Table 12.¹

Table 12. *List of species of the complex of small species and juveniles in the deep-water assemblage of the White Sea*

Species	Open hollow		Near Ileyky Islands	
	Biomass	Density	Biomass	Density
<i>Cossura longicirrata</i>	1.219±0.124	3749±408	3.750±0.782	18612±3673
<i>Nephtys</i> sp.	1.612±0.177	2059±121	2.420±0.438	2893±626
<i>Polychaeta fragmenta</i>	0.578±0.110		0.860±0.516	
<i>Prionospio cirrifera</i>	0.322±0.092	130±33	0.586±0.419	156±96
<i>Tharyx marioni</i>	1.470±0.336	556±92	0.156±0.156	78±78
<i>Artacama proboscidea</i>	0.052±0.039	13±10	0.235±0.235	78±78
<i>Saccoglossus mereschkowskii</i>	0.730±0.510	17±12	0.860±0.611	156±96
<i>Portandia arctica</i>	0.226±0.145	113±29	0.000±0.000	0±0
<i>Tubularia regalis</i>	0.043±0.043		0.000±0.000	
<i>Pholoe minuta</i>	0.035±0.027	26±15	0.080±0.062	235±156
<i>Musculus niger</i>	0.009±0.006	9±9	0.000±0.000	0±0
<i>Scoloplos armiger</i>	1.079±0.502	174±44	0.023±0.023	78±78
<i>Maldane sarsi</i>	0.430±0.284	26±15	0.000±0.000	0±0
Oedicerotidae	0.004±0.004	9±9	0.000±0.000	0±0
<i>Laonice cirrata</i>	0.295±0.123	243±107	0.000±0.000	0±0
<i>Leptognathia sarsi</i>	0.019±0.012	52±36	0.000±0.000	0±0
<i>Diplocirrus longisetosus</i>	0.148±0.057	139±42	0.000±0.000	0±0
<i>Aricidea nolani</i>	0.128±0.051	87±27	1.210±0.432	547±199
Sabellidae	0.004±0.004	9±9	0.000±0.000	0±0
<i>Nemidia torelli</i>	0.009±0.006	17±12	0.000±0.000	0±0
<i>Chaetozone setosa</i>	0.218±0.113	78±29	2.260±0.858	704±287
<i>Aceroides latipes</i>	0.217±0.153	52±24	0.469±0.379	156±96
<i>Monoculodes</i> sp.	0.009±0.009	9±9	0.000±0.000	0±0
<i>Cylichna occulta</i>	0.104±0.073	35±21	0.078±0.078	78±78
<i>Arrhis phyllonyx</i>	0.070±0.050	17±12	0.000±0.000	0±0
<i>Westwoodilla brevicealcar</i>	0.009±0.009	9±9	0.547±0.547	156±156
<i>Pseudoma truncatum</i>	0.009±0.009	9±9	0.000±0.000	0±0
<i>Pectinaria hyperborea</i>	0.065±0.044	61±25	1.486±0.746	3050±1486
<i>Hydractinia</i> sp.	0.017±0.017		0.000±0.000	
Bougainvillidae	0.004±0.004		0.000±0.000	
<i>Lumbrinereis fragilis</i>	0.280±0.246	26±15	15.953±15.565	91±76
Athecata	0.004±0.004		0.008±0.008	

¹ Species lists of each station are given in Appendix 4.

Table 12 (continuation). List of species of the complex of small species and juveniles in the deep-water assemblage of the White Sea

Species	Open hollow		Near Ileyky Islands	
	Biomass	Density	Biomass	Density
<i>Yoldia amygdalea</i>	0.000±0.000	0±0	0.899±0.379	2581±1082
Nemertini	0.105±0.073	26±15	0.238±0.234	196±124
<i>Philine lima</i>	0.148±0.148	9±9	0.039±0.039	78±78
<i>Typhlotanais finmarchicus</i>	0.000±0.000	0±0	0.063±0.027	391±175
<i>Brada</i> sp.	0.007±0.007	9±9	0.117±0.078	156±96
Spiomorpha	0.000±0.000	0±0	0.117±0.117	235±235
<i>Capitella capitata</i>	0.000±0.000	0±0	0.078±0.078	156±156
<i>Myriochele oculata</i>	0.000±0.000	0±0	0.156±0.156	78±78
<i>Dacrydium vitreum</i>	0.001±0.000	9±9	0.000±0.000	0±0
Tanaidacea	0.000±0.000	26±19	0.000±0.000	0±0
<i>Limnoria lignorum</i>	0.015±0.007	130±61	0.000±0.000	0±0
Bivalvia	0.008±0.005	148±68	0.009±0.009	547±547
Polychaeta	0.018±0.011	165±50	0.077±0.077	156±156
<i>Mytilus edulis</i>	0.001±0.000	130±39	0.002±0.002	235±235
Syllidae	0.026±0.026	26±19	0.000±0.000	0±0
<i>Leucon nasicoides</i>	0.008±0.008	9±9	0.000±0.000	0±0
Phyllodocidae	0.017±0.017	9±9	0.000±0.000	0±0
<i>Admete couthouyi</i>	0.052±0.052	17±12	0.000±0.000	0±0
Aphroditidae	0.017±0.017	9±9	0.000±0.000	0±0
<i>Syrroe crenulata</i>	0.004±0.004	9±9	0.000±0.000	0±0
<i>Eucratea loricata</i>	0.043±0.043		0.000±0.000	
<i>Paroediceros lynceus</i>	0.035±0.035	9±9	0.000±0.000	0±0
Ampharetidae	0.009±0.009	17±12	0.000±0.000	0±0
Terebellidae	0.017±0.017	9±9	0.000±0.000	0±0
<i>Gersemia fruticosa</i>	0.087±0.087		0.000±0.000	
<i>Harpinia antennaria</i>	0.004±0.004	9±9	0.000±0.000	0±0
<i>Praxillella praetermissa</i>	0.113±0.113	9±9	0.000±0.000	0±0
Maldanidae	0.000±0.000	9±9	0.039±0.039	78±78
<i>Macoma calcarea</i>	0.000±0.000	0±0	0.078±0.078	156±156
<i>Frigidalyvania janmayeni</i>	0.000±0.000	0±0	0.391±0.391	78±78
<i>Retusa pertenuis</i>	0.000±0.000	0±0	0.156±0.156	78±78
<i>Thyasira gouldi</i>	0.000±0.000	0±0	0.156±0.156	156±156
<i>Terebellides stroemi</i>	0.000±0.000	0±0	0.003±0.003	78±78
<i>Flabelligera affinis</i>	0.000±0.000	0±0	0.022±0.022	78±78

The average total biomass of the complex of small species and juveniles in the deep-water assemblage is 10.63 g/m² (which makes 39.22% of the total biomass in it), 49 species were found there. The following parameters of the cumulative function [1, Part 1] of species number for our material were found:

$$S=50.29(1-e^{-0.093N}) \quad [6]$$

See the plot of empirical and theoretical curves at Fig. 15. The χ^2 value was 4.07, number of degrees of freedom being 42; therefore, one can consider these curves to be in good correspondence. The estimated number of species (50.29) is very close to the empirical one (49), the theoretical function reaches the value of 49 at the 40-th sample; and its first derivative is in point $N_{\max}=0.074$. Thus, we can consider that the species composition of small species and juveniles complex, belonging to the White Sea deep-water assemblage, was studied well enough for the sampling method used, and the species found make 97% of expected number. 11 additional small species were found in the corer tubes compared with the grab samples (see

part 1). The total number of species found in the deep basin during the INTAS study in 1998 and 1999, accordingly, is 66.

The 5 samples available at the station near the Ileyky Islands are too few to estimate, whether the species composition was sufficiently studied there. It can only be noted that 36 species were found there and the biomass of the complex was 35.74 g/m² – which exceeds biomass in the deep part of the Basin more than three times.

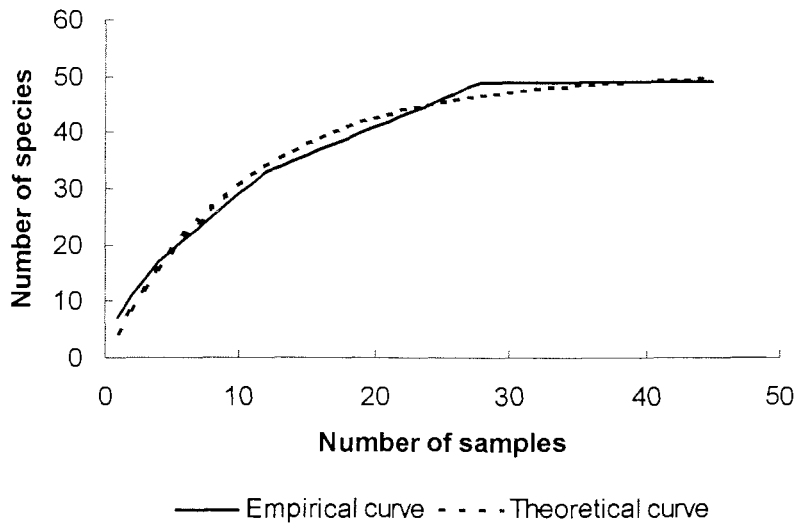


Fig. 15. Dependence of the number of species on the number of samples

The taxonomic composition in both complexes is practically identical, with Polychaeta dominating by biomass (table 13), whereas in the whole assemblage Mollusca prove dominant (see Part 1).

In comparison to the whole assemblage, the fraction of biomass of arctic species is extremely low (Table 14). About a half of biomass of the complex belongs to arctic-boreal species. Thus, the complex in general does not look as arctic as the whole assemblage. The significant difference in the fraction of arctic-boreal small/juvenile species between the communities of the open basin and near the Ileyky Islands should be noted (Table 14).

Deposit feeders make the main part of biomass in the complex as well as in the whole deep-water assemblage. No significant difference of their fraction by biomass was found between the open hollow and near the Ileyky Islands (Table 15).

Four groups of species can be distinguished in the complex by their frequencies of occurrence (Fig. 16). The rules described in the chapter 1.3 of part 1 were used to discriminate them. *Nephtys* sp. and *Cossura longicirata* were considered as very regular (obligate) species, *Tharyx maioni* – as a frequent one, and *Scoloplos armiger*, *Prionospio ciriferi*, *Aricidea nolani*, Polychaeta gen. sp., *Portandia arctica*, *Diplocirrus longisetosus*, *Chaetozone setosa*, Bivalvia gen. sp., *Pectinaria hyperborea*, *Mytilus edulis*, *Laonice cirata*, *Aceroides latipes* and *Limnoria lignorum* – as common species. All these groups are significantly different from each other. It should be especially marked that juveniles of *Mytilus edulis* were found at a great depth in the open hollow of the White Sea. Thus, the larvae of blue mussel can drift far away from the shore and pass metamorphosis under unusual conditions. Obviously these juveniles do not survive; for, not any adult mussel was found in the deep part of the Basin since its investigation started a century ago.

Table 13. *Taxonomic composition of small species and juveniles complex, estimated by biomass*
Fractions of each taxon are given, followed by standard errors

Taxon	Open hollow	Near Ileyky Islands
Coelenterata	1.47±1.76	0.02±0.63
Polycheata	76.88±6.28	82.91±16.8
Bivalvia	2.31±2.24	3.20±7.87
Gastropoda	2.86±2.48	1.86±6.04
Crustacea	3.80±2.85	3.02±7.65
Other taxa	12.69±4.69	8.98±12.78

Table 14. *Biogeographic composition of the complex of small species and juveniles, estimated by biomass; compared with the data on larger macrofauna, taken from Table 5 (part 1)*
Fractions of each biogeographic group followed by standard errors are given

Biogeographic group	Open basin small macrof.	Near Ileyky Islands	Open basin large macrof. (data s. part 1)
Boreal	3.57±2.76	2.52±7.01	0.87±1.1
Arctic-boreal	40.58±7.32	71.33±20.22	42.65±5.9
Arctic	5.57±3.51	2.95±7.57	46.73±6.0
unknown	50.28±7.45	23.19±18.87	ca. 10

Table 15. *Trophic composition of small species and juveniles complex, estimated by biomass*
Fractions of each trophic group followed by standard errors are given

Trophic group	Open hollow	Near Ileyky Islands
Deposit feeders	55.32±7.41	80.73±17.64
Suspension feeders	35.21±7.12	13.63±15.34
Carnivorous	0.33±0.85	0.00±0.00
Omnivorous	3.54±2.75	3.02±7.65

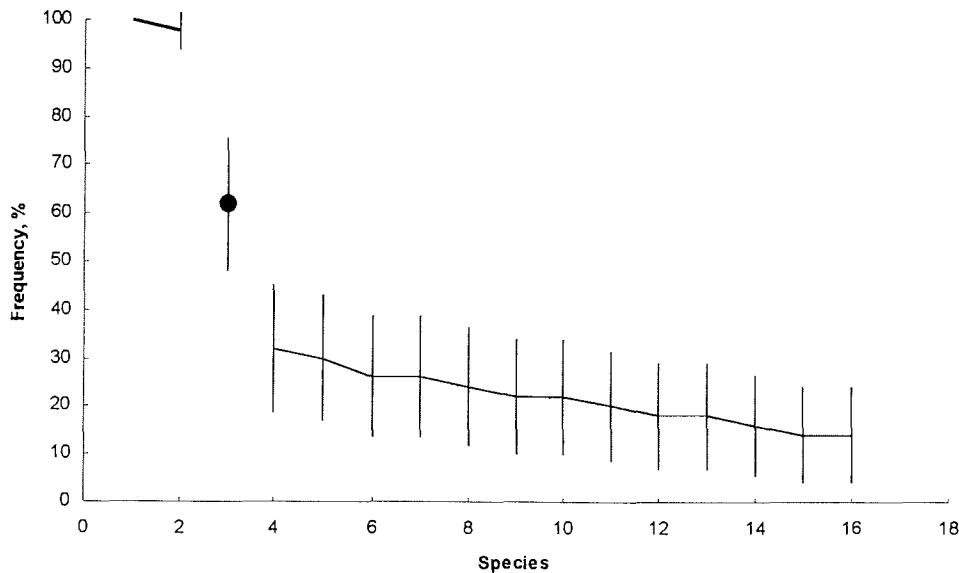


Fig. 16. Frequency of occurrence of regular (thick line), frequent (single dot) and common (thin line) species (rare species are truncated), plotted in decreasing order
X axis – number of species in ranked sequence. Vertical bars – confidence intervals

The group of rare species consists of *Pholoe minuta*, *Lumbrinereis fragilis*, *Nemertini* sp., *Saccoglossus mereschkowskii*, *Cylichna occulta*, *Artacama proboscidea*, *Maldane sarsi*, *Leptognathia sarsi*, *Brada* sp., *Dacrydium vitreum*, *Musculus niger*, *Nemidia torelli*, *Arris phyllonyx*, *Westwoodilla brevicealcar*, *Athecata* sp., *Phyline lima*, *Tubularia regalis*, *Oedicerotidae* sp., *Sabellidae* sp., *Monoculodes* sp., *Pseudoma truncatum*, *Hydractinia* sp., *Bougainvillidae* sp., *Syllidae* sp., *Leucon nasicoideis*, *Phyllodocidae* sp., *Admete couthouyi*, *Aphroditidae* sp., *Syrroe crenulata*, *Eucratea loricata*, *Paroediceros lynceus*, *Ampharetidae* sp., *Terebellidae* sp., *Gersemia fruticosa*, *Harpinia antennaria* and *Praxillella praetermissa*.

All the above mentioned species are listed in decreasing order of their frequency of occurrence. In the further text only regular, frequent and common species are discussed.

The analysis of species density allows to distinguish some density groups in the complex under discussion. The criterion chosen for division was the same as for the whole assemblage, namely a two-fold decrease of density in a ranged sequence. The threshold value was exceeded twice in the material presented. Three density groups were established according to this fact – bountiful species *Cossura longicirrata*, abundant species *Nephtys* sp.; and sparse species *Tharyx marioni*, *Pectinaria hyperborea*, *Laonice cirrata*, *Scoloplos armiger*, *Chaetozone setosa*, *Aricidea nolani*, *Prionospio cirrifera*, *Diplocirrus longisetosus*, *Limnoria lignorum*, *Portandia arctica* and *Aceroides latipes* (Fig. 17).

Three groups of species, differing by biomass, were distinguished in the complex (Fig. 18). A sharp drop in biomass (about 0.5 g/m² in our material) in a ranged sequence was chosen as a criterion for discriminating of the three groups of species. The leading group in the decreasing order of biomass was represented by *Nephtys* sp., *Cossura longicirrata* and *Tharyx marioni*, the group of medium biomass included only one species – *Scoloplos armiger*. Common species such as *Chaetozone setosa*, *Prionospio cirrifera*, *Laonice cirrata*, *Aceroides latipes*, *Aricidea nolani*, *Pectinaria hyperborea*, *Portandia arctica*, *Diplocirrus longisetosus* and *Limnoria lignorum* formed the third group with the lowest biomass.

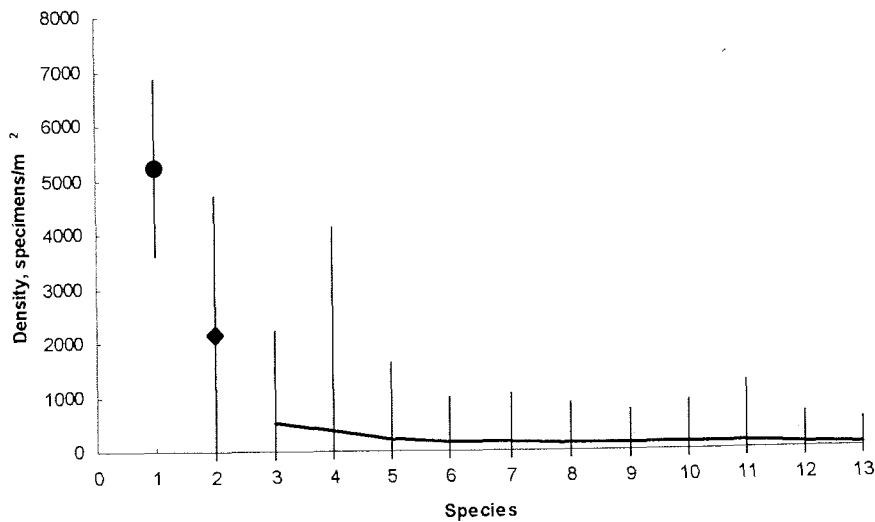


Fig. 17. *Density of regular, frequent and common species, plotted in decreasing order (rare species are truncated)*
 X axis – number of species in ranked sequence
 Vertical bars – confidence intervals; single round dot – bountiful species;
 single rhombic dot – abundant species; line – sparse species

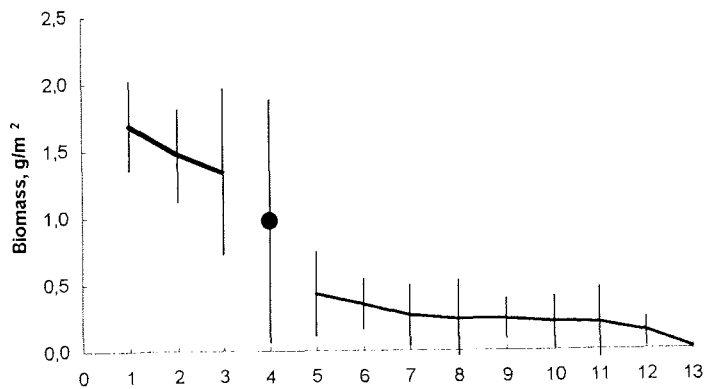


Fig. 18. *Biomass of regular, frequent and common species, plotted in decreasing order (rare species are truncated)*
 X axis – number of species in ranked sequence.
 Vertical bars – confidence intervals; thick line – leading species;
 single dot – species with medium biomass; thin line – common species

2.4. Discussion

No significant changes in total biomass and structure were found in the complex of juveniles and small species belonging to the deep-water assemblage in the present investigation. The question arises if there is any seasonal dynamics in any particular species. Due to a very high dispersion of biomass and density any changes of these properties were not statistically significant for all the species studied. Nevertheless we shall try to trace time variation of density in some deep-water benthic juveniles in order to find out if it is necessary to pay attention to them in future investigations. No other station is discussed but the station B; for, it is the only site where material was obtained five times in different seasons. All the ideas discussed below are not firmly established facts, only suggestions; they are of preliminary nature.

First of all it should be noted that all bivalve juveniles except *Portlandia arctica* were found only in August, when the mass recruitment of clam populations takes place. Thus, not only blue mussel spat can be assumed to drift from coastal waters and pass metamorphosis in the open hollow of the White Sea. It is very probable that all unidentified juveniles of *Bivalvia* in our material are shallow-water ones; and they do not survive the severe conditions of the deep-water biotope.

As the most part of species in the complex under consideration have very low densities, only few of them can be discussed. First of all these are *Cossura longicirrata* and *Nephtys* sp. (Fig. 19). *Cossura longicirrata* is most abundant in the second part of summer, probably, in August. It is difficult to determine the exact time, because of rare sampling. Nevertheless the most probable term of spawning of this species is July. The maximum of its biomass was observed in November 1999 (Fig. 20), while in 1998 no late autumn/winter sampling was done.

As for *Nephtys* sp., there was no change in density found (fig. 19), but its biomass shows the same pattern as *Cossura longicirrata*'s density (Fig. 20). Probably, the spawning in this species take place earlier and the peak of density was not detected due to the fact that sampling was not performed in the proper time.

Fig. 21 presents the density of four other species plotted against the time of observation. The main patterns strongly resemble that of *Cossura longicirrata*; accordingly, the spawning of these species also seems to occur in July.

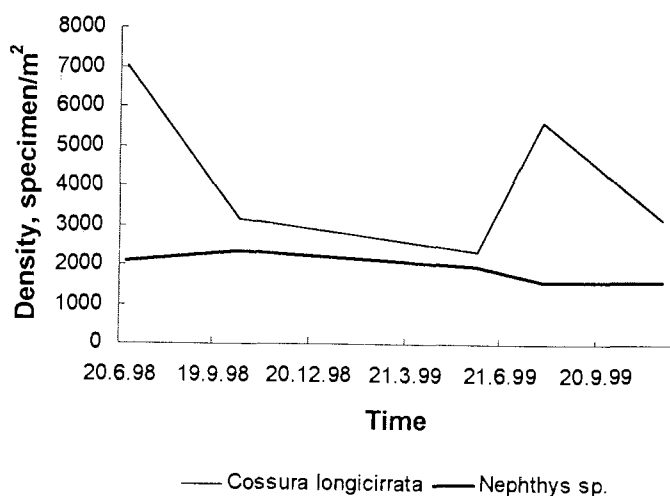


Fig. 19. Dynamics of density of juveniles in bountiful and abundant species during the time of investigation

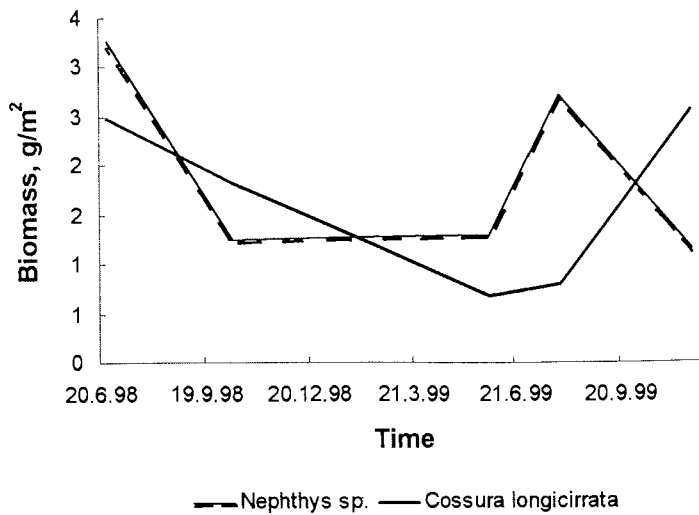


Fig. 20. Dynamics of biomass of juveniles in bountiful and abundant species during the time of investigation

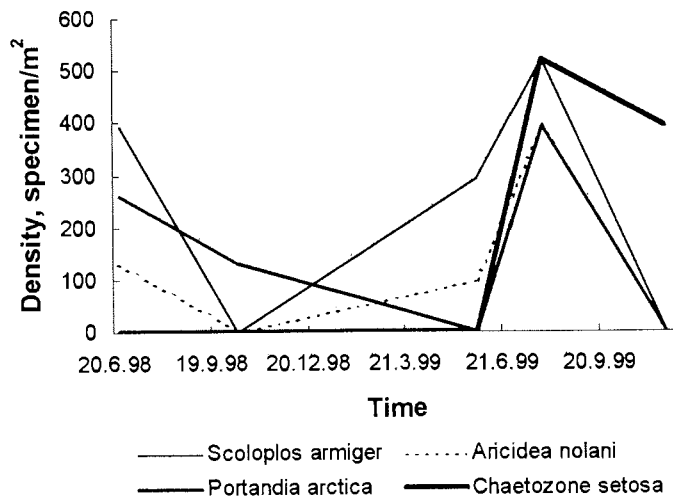


Fig. 21. Dynamics of density of juveniles in four sparse species during the time of investigation

It can be preliminarily concluded from these observations that the most probable time of spawning in the species mentioned is the middle of summer. Additional investigations are needed to confirm this. In future research, if any, more often sampling should be made, once or twice a month at least during the navigation period without ice. On the other hand, in order to compare the annual patterns, at least three years of observations are necessary. However, already now is clear that seasonal dynamics of density can occur in some species belonging to the deep-water assemblage of the White Sea hollow notwithstanding the stable environmental conditions there.

2.5. Conclusions

1. No seasonal dynamics in the deep-water assemblage of the White Sea was found in the total biomass and structure of the complex of juveniles and small species.
2. A preliminary conclusion can be made that particular species, nevertheless, can exhibit seasonal dynamics.

2.6. Acknowledgements

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Appendix 1

Species found at the grab stations in the deep basin area of the White Sea.
Average biomass (g/m² total wet weights) and average densities (specimens/m²)
followed by standard errors are given

Station A

Species	Biomass	Density
<i>Portlandia arctica</i>	5.865±4.85	21.33±16.70
<i>Nuculana pernula</i>	5.707±4.80	12.00±10.58
<i>Nephtys ciliata</i>	4.413±3.73	2.67±2.22
<i>Tharyx marioni</i>	4.040±4.39	521.33±434.44
<i>Nephtys</i> sp.	1.825±1.40	2085.33±1662.85
<i>Cossura longicirrata</i>	1.303±0.88	3388.67±2307.47
<i>Polychaeta</i> (fragmenta)	1.238±0.90	
<i>Caudofoveata</i>	1.187±1.10	4.00±3.53
<i>Ophiacantha bidentata</i>	1.084±0.92	2.67±2.22
<i>Aceroides latipes</i>	0.782±0.79	391.00±344.83
<i>Scoloplos armiger</i>	0.652±0.78	130.33±156.64
<i>Arrhis phyllonyx</i>	0.391±0.47	130.33±156.64
<i>Prionospio cirrifera</i>	0.391±0.47	130.33±156.64
<i>Thyasira gouldi</i>	0.115±0.11	5.33±5.01
<i>Pholoe minuta</i>	0.065±0.08	130.33±156.64
<i>Pectinaria hyperborea</i>	0.065±0.08	130.33±156.64
<i>Pandora glacialis</i>	0.048±0.06	1.33±1.60
<i>Gersemia fruticosa</i>	0.033±0.04	
<i>Myriochele oculata</i>	0.027±0.03	4.00±4.81
<i>Maldane sarsi</i>	0.016±0.02	1.33±1.60

Station B

Species	Biomass	Density
<i>Portlandia arctica</i>	13.80±9.83	129.33±90.99
<i>Scoloplos armiger</i>	5.44±6.26	424.33±469.27
<i>Nephtys</i> sp.	3.27±2.21	2105.33±1505.39
<i>Tharyx marioni</i>	3.16±2.43	1332.67±1047.01
<i>Cossura longicirrata</i>	2.48±1.80	7038.00±5265.21
<i>Urasterias lincki</i>	2.23±2.59	2.67±2.22
<i>Halcampa arctica</i>	1.87±2.24	1.33±1.60
<i>Nephtys ciliata</i>	1.45±1.75	1.33±1.60
<i>Polychaeta</i> (fragmenta)	0.91±1.10	
<i>Prionospio cirrifera</i>	0.69±0.47	545.33±391.93
<i>Arrhis phyllonyx</i>	0.65±0.78	130.33±156.64
<i>Aricidea</i> sp.	0.40±0.47	141.00±156.67
<i>Cylichna occulta</i>	0.33±0.32	268.67±312.99
<i>Saccoglossus mereschkowskii</i>	0.27±0.32	5.33±5.01
<i>Hydractinia allmani</i>	0.26±0.31	
<i>Thyasira gouldi</i>	0.20±0.16	5.33±3.80
<i>Pectinaria hyperborea</i>	0.19±0.23	262.00±314.89
<i>Westwoodilla brevicar</i>	0.13±0.16	130.33±156.64
<i>Probabella harputarioides</i>	0.11±0.10	5.33±4.44
<i>Philina lima</i>	0.05±0.06	2.67±3.21
<i>Antinoella</i> sp.	0.03±0.02	2.67±2.22
<i>Milnedwardsia polaris</i>	0.02±0.02	1.33±1.60
<i>Diplocirrus longisetosus</i>	0.01±0.01	12.00±14.42
<i>Leiochone polaris</i>	0.01±0.01	1.33±1.60
<i>Ampharete arctica</i>	0.01±0.01	2.67±3.21
<i>Eteone longa</i>	0.01±0.01	1.33±1.60
<i>Myriochele oculata</i>	0.01±0.01	1.33±1.60
<i>Lumbrineris fragilis</i>	0.01±0.01	1.33±1.60
<i>Leptognathia sarsi</i>	0.01±0.01	1.33±1.60
<i>Perigonimus yoldiaearcticae</i>	+	

Station C

Species	Biomass	Density
<i>Halcampa arctica</i>	12.89±11.75	6.67±5.67
<i>Portlandia arctica</i>	11.70±7.87	485.67±396.77
<i>Chiridota pellucida</i>	6.160±7.40	1.33±1.60
<i>Nuculana pernula</i>	2.981±2.27	12.00±8.94
<i>Laonice cirrata</i>	1.825±1.49	1694.3±1159.2
<i>Nephtys</i> sp.	1.694±1.26	1955.0±1433.7
<i>Cossura longicirrata</i>	1.173±0.81	1824.7±1452.0
Polychaeta (fragmenta)	1.107±0.74	
<i>Tharyx marioni</i>	0.652±0.56	260.67±217.22
<i>Diplocirrus longisetosus</i>	0.521±0.63	130.33±156.64
<i>Leionucula belottii</i>	0.389±0.47	2.67±3.21
<i>Nemidia torelli</i>	0.365±0.29	338.33±398.36
<i>Prionospio cirrifera</i>	0.261±0.31	130.33±156.64
<i>Leptognathia sarsi</i>	0.261±0.22	651.67±639.98
<i>Aricidea</i> sp.	0.130±0.16	260.67±313.282
Sabellidae	0.065±0.08	130.33±156.64
Nemertini	0.049±0.06	

Station D

Species	Biomass	Density
<i>Portlandia arctica</i>	6.49±5.24	146.33±169.27
<i>Nuculana pernula</i>	5.79±3.92	9.33±6.36
<i>Nephtys ciliata</i>	1.36±1.64	1.33±1.60
<i>Tharyx marioni</i>	0.98±0.73	326.00±226.85
<i>Nephtys</i> sp.	0.587±0.49	9122.00±1018
<i>Pholoe minuta</i>	0.587±0.49	195.67±172.50
<i>Maldane sarsi</i>	0.568±0.44	198.33±172.36
<i>Musculus niger</i>	0.293±0.31	195.67±172.50
Polychaeta (fragmenta)	0.293±0.26	
Gammaridea	0.261±0.31	130.33±156.64
<i>Cossura longicirrata</i>	0.196±0.17	195.67±172.50
<i>Scoloplos armiger</i>	0.196±0.17	195.67±172.50
<i>Thyasira gouldi</i>	0.115±0.10	2.67±2.22
Caudofoveata	0.064±0.08	1.33±1.60

Station E (June)

Species	Biomass	Density
<i>Portlandia arctica</i>	7.19±4.96	60.0±41.05
<i>Saccoglossus mereschkowskii</i>	1.41±1.05	6.67±4.64
<i>Tharyx marioni</i>	0.85±0.59	302.67±206.08
Polychaeta (fragmenta)	0.54±0.37	
<i>Antinoella</i> sp.	0.24±0.17	22.67±15.86
<i>Maldane sarsi</i>	0.22±0.160	20.00±13.53
<i>Scoloplos armiger</i>	0.21±0.154	34.67±24.16
<i>Thyasira gouldi</i>	0.05±0.061	1.33±1.6
<i>Aricidea</i> sp.	0.05±0.041	26.67±22.58
<i>Prionospio cirrifera</i>	0.04±0.031	42.67±29.31
<i>Philine lima</i>	0.04±0.048	2.67±3.21
<i>Nephtys</i> sp.	0.04±0.025	28.00±20.31
<i>Admete couthouyi</i>	0.03±0.032	1.33±1.60
Nemertini	0.03±0.030	1.33±1.60
<i>Diplocirrus longisetosus</i>	0.02±0.013	20.00±14.67
<i>Lumbrineris fragilis</i>	0.01±0.010	5.33±6.41
<i>Cossura longicirrata</i>	0.01±0.004	9.33±7.86
<i>Leiochone polaris</i>	0.01±0.004	2.67±2.22
<i>Capitella capitata</i>	0.001±0.002	1.33±1.60
<i>Cylichna occulta</i>	0.001±0.002	1.33±1.60
<i>Ampharete arctica</i>	0.001±0.002	1.33±1.60

Station E (July)

Species	Biomass	Density
<i>Portlandia arctica</i>	7.59±5.58	42.67±30.03
<i>Tharyx marioni</i>	5.82±4.03	1175.67±815.64
<i>Nephtys</i> sp.	1.72±1.29	1695.0±1264.53
<i>Cossura longicirrata</i>	1.43±1.07	5995.33±4185.80
<i>Polychaeta</i> (fragmenta)	0.72±0.56	
<i>Tubularia</i> sp.	0.65±0.78	
<i>Prionospio cirrifera</i>	0.39±0.47	130.33±156.64
<i>Maldane sarsi</i>	0.20±0.20	14.67±13.12
<i>Thyasira gouldi</i>	0.10±0.09	2.67±2.22
<i>Saccoglossus mereschkowskii</i>	0.09±0.09	1.67±1.64
<i>Pectinaria hyperborea</i>	0.09±0.10	2.67±3.21
<i>Nemidia torelli</i>	0.07±0.08	2.67±3.21
<i>Urasterias lincki</i>	0.02±0.02	0.33±0.40
<i>Myriochele oculata</i>	0.004±0.005	1.33±1.60
<i>Ampharete arctica</i>	0.004±0.005	1.33±1.60

Station I

Species	Biomass	Density
<i>Portlandia arctica</i>	9.81±6.87	40.00±26.77
<i>Halcampa arctica</i>	4.59±3.85	2.67±2.22
<i>Nephtys ciliata</i>	3.35±4.02	1.33±1.60
<i>Cossura longicirrata</i>	1.37±1.14	5604.3±4682.5
<i>Nuculana pernula</i>	0.76±0.91	1.33±1.60
<i>Saccoglossus mereschkowskii</i>	0.76±0.91	2.67±3.21
Nemertini	0.76±0.88	4.00±3.53
<i>Nephtys</i> sp.	0.76±0.63	1440.3±1199.6
<i>Tharyx marioni</i>	0.38±0.32	144.0±120.5
<i>Leionucula belottii</i>	0.28±0.34	2.67±3.21
<i>Polychaeta</i> (fragmenta)	0.28±0.23	
<i>Artacama proboscidea</i>	0.26±0.31	65.33±78.52
<i>Antinoella</i> sp.	0.09±0.10	10.67±12.82
<i>Scoloplos armiger</i>	0.07±0.09	8.00±9.62
<i>Buccinum elatior</i>	0.06±0.07	1.33±1.60
<i>Maldane sarsi</i>	0.06±0.06	6.67±6.55
<i>Pectinaria hyperborea</i>	0.04±0.05	1.33±1.60
<i>Nemidia torelli</i>	0.03±0.04	1.33±1.60
<i>Prionospio cirrifera</i>	0.009±0.01	10.67±12.82
<i>Diplocirrus longisetosus</i>	0.005±0.006	4.00±4.81
<i>Aricidea</i> sp.	0.003±0.003	1.33±1.60
<i>Cylichna occulta</i>	0.001±0.002	1.33±1.60

Station K

Species	Biomass	Density
<i>Portlandia arctica</i>	5.87±4.85	21.33±16.705
<i>Nuculana pernula</i>	5.71±4.80	12.00±10.58
<i>Nephtys ciliata</i>	4.41±3.73	2.67±2.22
<i>Tharyx marioni</i>	4.04±4.39	521.33±434.44
<i>Nephtys</i> sp.	1.83±1.40	2085.33±1662.85
<i>Cossura longicirrata</i>	1.30±0.88	3388.67±2307.47
<i>Polychaeta</i> (fragmenta)	1.24±0.90	
<i>Caudofoveata</i>	1.19±1.10	4.00±3.53
<i>Ophiacantha bidentata</i>	1.08±0.92	2.67±2.22
<i>Aceroides latipes</i>	0.78±0.79	391.0±344.8
<i>Scoloplos armiger</i>	0.65±0.78	130.33±156.64
<i>Arrhis phyllonix</i>	0.39±0.47	130.33±156.64
<i>Prionospio cirrifera</i>	0.39±0.47	130.33±156.64
<i>Thyasira gouldi</i>	0.12±0.11	5.33±5.01
<i>Pholoe minuta</i>	0.07±0.08	130.33±156.64
<i>Pectinaria hyperborea</i>	0.07±0.08	130.33±156.64
<i>Pandora glacialis</i>	0.05±0.06	1.33±1.60
<i>Gersemia fruticosa</i>	0.03±0.04	
<i>Myriochele oculata</i>	0.03±0.03	4.00±4.81
<i>Maldane sarsi</i>	0.02±0.02	1.33±1.60

Appendix 2

Main features of sea floor communities, found on stations A, B, C and D

Feature	Stations			
	A	B	C	D
Number of species	21	31	18	14
Biomass, g/m ²	29.639	38.537	43.526	17.775
Infauna species by biomass, %	86.39±19.80	86.63±19.65	93.02±14.71	91.93±15.73
Vagile species by biomass, %	94.08±13.63	94.53±13.13	94.16±13.54	93.51±14.22
Diversity				
By biomass, bit/g	3.3363	3.2195	2.9192	2.5594
By density, bit/specimen	2.1394	2.1634	2.8517	1.0566
Oligomixness, %				
By biomass	29.26±4.51	38.31±4.95	37.84±6.31	44.16±8.35
By density	53.40±8.90	57.72±7.86	34.33±6.27	83.92±16.46
Biogeographic composition by biomass, %				
Boreal species	1.32±6.59	1.80±7.68	0.60±4.46	
Arctic-boreal species	53.03±28.81	37.51±27.95	20.56±23.33	54.50±28.75
Arctic species	22.52±24.12	46.93±28.81	56.49±28.62	36.52±27.80
Unknown	23.13±24.34	13.77±19.89	22.35±24.05	8.98±16.51
Trophic composition by biomass, %				
Phytofagous species			0.60±4.46	
Suspension feeders	1.59±7.22	2.10±8.28	3.14±10.07	1.65±7.35
Deposit feeders	71.64±26.02	80.75±22.76	88.98±18.08	80.98±22.66
Carnivorous species	21.27±23.63	12.62±19.17	4.73±12.26	14.25±20.18
Omnivorous species	1.32±6.59	2.15±8.37		
Unknown	4.18±11.55	2.37±8.78	2.54±9.08	3.11±10.02
Taxonomic composition by biomass, %				
Hydrozoa		0.676±4.732		
Anthozoa	0.112±1.935	4.882±12.441	29.616±26.360	
Nemertini			0.113±1.943	
Polychaeta	47.357±28.827	46.958±28.814	17.907±22.136	26.798±25.571
Aplacophora	4.004±11.319			0.360±3.458
Gastropoda		1.254±6.425		71.375±26.097
Bivalvia	39.592±28.235	36.339±27.769	34.618±27.467	
Thanaidacea		0.003±0.340	0.599±4.455	
Amphipoda	3.958±11.256	2.029±8.141		1.467±6.940
Ophiuroidea	3.657±10.838			
Asteroidea		5.795±13.490		
Holothuroidea			14.153±20.124	
Enteropneusta		0.709±4.845		

Main features of sea floor communities, found on stations E (June), E (July), I and K

Feature	Stations			
	E (June)	E (July)	I	K
Number of species	21	16	23	21
Biomass, g/m ²	10.957	19.346	23.782	29.639
Infauna species	94.84±12.77	90.15±17.20	98.16±7.76	86.39±19.80
Vagile species	92.61±15.10	89.49±17.71	97.20±9.52	94.08±13.63
Diversity				
By biomass, bit/g	1.8576	2.4432	2.7308	3.3363
By density, bit/specimen	2.6804	1.3853	1.0593	2.1394
Oligomixness, %				
By biomass	65.52±10.11	46.04±8.14	44.79±6.60	29.26±4.51
By density	50.14±7.93	66.84±13.11	77.48±11.96	53.40±8.90
Biogeographic composition by biomass, %				
Boreal species	0.41±3.69	2.02±8.12	1.14±6.13	1.32±6.59
Arctic-boreal species	5.28±12.91	18.69±22.51	28.53±26.07	53.03±28.81
Arctic species	65.96±27.3628	39.33±28.20	60.55±28.22	22.52±24.12
Unknown	28.34±26.02	39.96±28.28	9.78±17.15	23.13±24.34
Trophic composition by biomass, %				
Phytofagous species				
Suspension feeders	2.42±8.87	5.73±13.42	0.63±4.57	1.59±7.22
Deposit feeders	91.99±15.67	81.32±22.50	80.82±22.73	71.64±26.02
Carnivorous species	0.32±3.26	9.25±16.73	17.38±21.88	21.27±23.63
Omnivorous species	0.37±3.51			1.32±6.59
Unknown	4.90±12.46	3.71±10.91	1.16±6.18	4.18±11.55
Taxonomic composition by biomass, %				
Hydrozoa		3.368±10.416		
Anthozoa			19.287±22.779	0.112±1.935
Nemertini	0.231±2.773		3.190±10.146	
Polychaeta	20.236±23.196	53.993±28.775	28.146±25.964	47.357±28.827
Aplacophora				4.004±11.319
Gastropoda	0.621±4.534		0.269±2.991	
Bivalvia	66.050±27.340	39.739±28.253	45.637±28.757	39.592±28.235
Thanaidacea				
Amphipoda				3.958±11.256
Ophiuroidea				3.657±10.838
Asteroidea		0.078±1.607		
Holothuroidea				
Enteropneusta	12.862±19.328	0.465±3.929	3.196±10.155	

Appendix 3

Main features of sea floor assemblages with *Portlandia arctica* as dominant species in open parts of the White Sea

Feature	Site				
	Deep-water part of the Basin	Transection Sharapov Cape – Tury Cape	Srednie Ludy Archipelago	Velikaya Salma Strait	Dvina Bay
Number of samples	24	20	1	1	4
Average depth	240	230	290	120	96
Number of species	55	56	24	39	43
Biomass, g/m ²	27.094	38.764	97.480	186.092	20.008
Infauna species	80.00	66.11	27.39	98.57	86.56
Vagile species	90.00	99.42	32.30	97.34	88.66
Diversity					
By biomass, bit/g	3.582	2.553	1.840	1.836	3.063
By density, bit/specimen	2.326	4.106	2.770	3.568	3.811
Oligomixness, %					
By biomass	36.68	48.31	63.41	65.43	41.34
By density	55.46	30.78	49.43	31.87	32.64
Biogeographic composition by biomass, %					
Boreal species	1.39	0.02	0.10	0.03	2.81
Arctic-boreal species	29.95	20.89	72.76	33.49	56.17
Arctic species	49.59	65.88	21.90	65.00	31.29
Unknown	19.08	13.21	5.95	1.47	9.73
Trophic composition by biomass, %					
Phytophagous species					
Suspension feeders	2.16	0.07	67.27	0.57	17.59
Deposit feeders	82.84	96.86	30.57	98.07	78.50
Carnivorous species	10.82	2.54	1.21	0.57	2.75
Omnivorous species	0.64	0.11	0.55	0.16	0.31
Unknown	3.42	0.42	0.41	0.63	
Taxonomic composition by biomass, %					
Porifera	1.32				
Hydrozoa	0.42		5.72		0.16
Anthozoa	14.36	11.10	61.55		0.07
Nemertini	0.37				0.12
Priapulida		0.68	0.04		
Sipunculida			0.31		
Polychaeta	34.33	5.04	1.64	10.11	9.21
Aplacophora	0.58	1.48			
Gastropoda	0.33	1.71	1.51	0.83	0.04
Bivalvia	40.59	49.84	26.07	88.93	78.05
Tanaidacea	0.12				
Amphipoda	1.14	0.04	0.03	0.05	0.48
Cumacea		0.00		0.00	0.35
Bryozoa			0.22		0.73
Asteroidea	2.21	29.13			
Ophiuroidea	0.50	0.98	2.91	0.01	2.70
Holothuroidea	2.84				
Enteropneusta	0.88			0.08	
Tunicata					8.10

Main features of sea floor assemblages with *Portlandia arctica*
as dominant species of some White Sea inlets

Feature	Site				
	Dolgaya Inlet	Kolvitsa Inlet. mouth	Kolvitsa Inlet. head	Palkina Inlet	Voronya Inlet
Number of samples	10	4	1	3	1
Average depth	15	50	38	42	6
Number of species	42	53	30	52	9
Biomass, g/m ²	21.934	194.504	151.576	112.701	17.470
Infauna species	96.52	63.95	95.20	96.45	84.77
Vagile species	99.30	77.26	94.15	99.38	100.00
Diversity					
By biomass, bit/g	2.726	3.336	2.415	2.201	1.978
By density, bit/specimen	3.460	3.000	3.580	2.536	2.190
Oligomixness, %					
By biomass	54.89	42.07	52.55	57.89	55.77
By density	35.63	50.40	30.30	61.29	43.59
Biogeographic composition by biomass, %					
Boreal species	5.07	2.11	0.23		12.31
Arctic-boreal species	32.03	41.66	47.22	24.06	18.66
Arctic species	55.32	52.57	47.37	59.73	59.53
Unknown	7.59	3.66	5.18	16.20	9.50
Trophic composition by biomass, %					
Phytophagous species	0.05				
Suspension feeders	15.17	23.89	6.16	19.40	
Deposit feeders	80.97	70.39	93.16	79.09	84.77
Carnivorous species	1.35	5.46	0.67	1.36	15.23
Omnivorous species	2.35	0.05		0.04	
Unknown	0.10	0.21	0.01	0.12	
Taxonomic composition by biomass, %					
Porifera	0.64	0.96		0.00	
Hydrozoa		0.06			
Anthozoa		13.21		1.44	
Nemertini	6.53	0.49	2.27	9.12	
Priapulida	1.04		0.29		
Sipunculida					
Polychaeta	28.47	12.29	6.03	1.78	27.30
Aplacophora					
Gastropoda	0.16	3.13	1.52	0.04	8.82
Bivalvia	58.87	57.73	89.43	77.48	59.76
Tanaidacea					
Amphipoda	2.38	0.18	0.01	0.03	
Cumacea	1.77		0.22	0.07	4.12
Bryozoa		0.24			
Asterozoa		9.31		3.21	
Ophiurozoa		2.05	0.24	0.00	
Holothurozoa		0.30		6.71	
Enteropneusta	0.10				
Tunicata	0.06			0.13	

Appendix 4

Small infauna from minicorer stations

Average biomass (g/m² total wet weights) and average density (specimens/m²) followed by standard errors are given

Fauna found at the minicorer station A

Species	12.8.98		1.6.99		1.8.99	
	Biomass	Density	Biomass	Density	Biomass	Density
<i>Cossura longicirrata</i>	1.30±0.13	3389±470	0.61±0.32	2476±652	1.21±0.40	2998±726
<i>Nephtys</i> sp.	1.85±0.69	2085±912	1.07±0.10	1955±451	3.31±0.75	2216±568
<i>Polychaeta fragmenta</i>	1.24±0.36		0.0±0.0		0.0±0.0	0±0
<i>Prionospio cirrifera</i>	0.39±0.39	130±130	0.65±0.65	130±130	0.0±0.0	0±0
<i>Tharyx marioni</i>	4.04±3.47	521±261	0.81±0.58	1173±391	0.0±0.0	0±0
<i>Saccoglossus mereschkowskii</i>	0.0±0.0	0±0	0.0±0.0	0±0	0.0±0.0	0±0
<i>Portandia arctica</i>	0.0±0.0	0±0	0.0±0.0	0±0	0.01±0.01	130±130
<i>Pholoe minuta</i>	0.07±0.07	130±130	0.0±0.0	0±0	0.0±0.0	0±0
<i>Scoloplos armiger</i>	0.65±0.65	130±130	0.08±0.06	261±130	1.33±0.67	521±130
<i>Laonice cirrata</i>	0.0±0.0	0±0	0.26±0.26	130±130	0.52±0.52	130±130
<i>Diplocirrus longisetosus</i>	0.0±0.0	0±0	0.13±0.13	261±261	0.01±0.01	130±130
<i>Aricidea nolani</i>	0.0±0.0	0±0	0.01±0.01	130±130	0.0±0.0	0±0
<i>Chaetozone setosa</i>	0.0±0.0	0±0	0.0±0.0	0±0	0.13±0.13	130±130
<i>Aceroides latipes</i>	0.78±0.60	391±226	0.0±0.0	0±0	0.0±0.0	0±0
<i>Arris phyllonyx</i>	0.39±0.39	130±130	0.0±0.0	0±0	0.0±0.0	0±0
<i>Pectinaria hyperborea</i>	0.07±0.07	130±130	0.65±0.65	130±130	0.0±0.0	0±0
<i>Bougainvillidae</i>	0.07±0.07		0.0±0.0		0.0±0.0	
<i>Anisopoda</i>	0.0±0.0	0±0	0.01±0.003	261±261	0.001±0.001	0±0
<i>Limnoria lignorum</i>	0.0±0.0	0±0	0.05±0.05	261±130	0.01±0.01	261±261
<i>Bivalvia</i>	0.0±0.0	0±0	0.001±0.001	521±345	0.10±0.05	130±130
<i>Polychaeta</i>	0.0±0.0	0±0	0.02±0.01	261±261	0.01±0.01	521±261
<i>Mytilus edulis</i>	0.0±0.0	0±0	0.0±0.0	261±130	0.004±0.002	130±130
<i>Syllidae</i>	0.0±0.0	0±0	0.0±0.0	0±0	0.39±0.39	391±226
<i>Leucon nasicooides</i>	0.0±0.0	0±0	0.0±0.0	0±0	0.12±0.12	130±130

Fauna found at the minicorer station B
Average biomass, g/m² and average density, specimens/m²
followed by standard error are given

Species	27.6.98		15.10.98	
	Biomass	Density	Biomass	Density
<i>Cossura longicirrata</i>	2.476±0.73	7038±2389	1.825±0.69	3128±1129
<i>Nephtys</i> sp.	3.258±0.35	2085±568	1.238±0.24	2346±451
<i>Polychaeta fragmenta</i>	1.955±0.39		0.587±0.30	
<i>Prionospio cirrifera</i>	0.652±0.13	521±130	0.130±0.13	130±130
<i>Tharyx marioni</i>	3.128±1.20	1564±391	1.238±0.17	587±0
<i>Portandia arctica</i>	2.151±2.05	261±130	0.065±0.07	130±130
<i>Scoloplos armiger</i>	5.213±5.21	391±391	0±0	0±0
<i>Maldane sarsi</i>	0±0	0±0	0±0	0±0
<i>Leptognathia sarsi</i>	0±0	0±0	0±0	0±0
<i>Diplocirrus longisetosus</i>	0±0	0±0	0.196±0.20	130±130
<i>Aricidea nolani</i>	0.391±0.39	130±130	0±0	0±0
<i>Chaetozone setosa</i>	0±0	0±0	0±0	0±0
<i>Aceroides latipes</i>	0±0	0±0	2.346±2.15	261±130
<i>Cylichna occulta</i>	1.303±0.94	391±226	0±0	0±0
<i>Arris phyllonx</i>	0.652±0.65	130±130	0±0	0±0
<i>Westwoodilla brevicar</i>	0.130±0.13	130±130	0±0	0±0
<i>Pseudoma truncatum</i>	0.130±0.13	130±130	0±0	0±0
<i>Pectinaria hyperborea</i>	0.130±0.13	261±261	0±0	0±0
<i>Hydractinia</i> sp.	0.261±0.26	0±0	0±0	0±0
<i>Lumbrinereis fargilis</i>	0±0	0±0	0.130±0.13	130±130
Athecata	0±0		0.065±0.07	
Nemertini	0±0	0±0	0±0	0±0
<i>Phyline lima</i>	0±0	0±0	0±0	0±0
<i>Brada</i> sp.	0±0	0±0	0±0	0±0
<i>Dacrydium vitreum</i>	0±0	0±0	0±0	0±0
Anisopoda	0±0	0±0	0±0	0±0
Bivalvia	0±0	0±0	0±0	0±0
Polychaeta	0±0	0±0	0±0	0±0
<i>Mytilus edulis</i>	0±0	0±0	0±0	0±0
Phyllocidae	0±0	0±0	0±0	0±0
<i>Admete couthouyi</i>	0±0	0±0	0±0	0±0
Aphroditidae	0±0	0±0	0±0	0±0
<i>Syrroe crenulata</i>	0±0	0±0	0±0	0±0
<i>Eucratea loricata</i>	0±0		0±0	
<i>Paroediceros lynceus</i>	0±0	0±0	0±0	0±0
Ampharetidae	0±0	0±0	0±0	0±0

Fauna found at the minicorer station B (continuation)

Species	30.5.99,		1.8.99		24.11.99	
	Biomass	Density	Biomass	Density	Biomass	Density
<i>Cossura longicirrata</i>	0.675±0.223	2346±639	0.802±0.388	5604±345	2.558	3128
<i>Nephtys</i> sp.	1.300±0.114	1955±276	2.740±1.745	1564±0	1.157	1564
<i>Polychaeta fragmenta</i>	0±0		0±0		0.000	
<i>Prionospio cirrifera</i>	0.293±0.293	196±196	0±0	0±0	2.764	391
<i>Tharyx marioni</i>	0.733±0.378	391±226	0±0	0±0	0.000	0
<i>Portandia arctica</i>	0±0	0±0	0.263±0.259	391±0	0.000	0
<i>Scoloplos armiger</i>	5.083±3.566	293±187	0.206±0.252	521±261	0.000	0
<i>Maldane sarsi</i>	0±0	0±0	1.760±1.760	0±0	0.000	0
<i>Leptognathia sarsi</i>	0±0	0±0	0±0	0±0	0.094	391
<i>Diplocirrus longisetosus</i>	0±0	0±0	0.250±0.125	391±226	0.303	391
<i>Aricidea nolani</i>	0.293±0.293	98±98	0.576±0.306	391±0	0.000	0
<i>Chaetozone setosa</i>	0±0	0±0	2.229±1.244	521±261	0.003	391
<i>Aceroides latipes</i>	0±0	0±0	0±0	0±0	0.000	0
<i>Cylichna occulta</i>	0±0	0±0	0±0	0±0	0.782	391
<i>Arris phyllonyx</i>	0±0	0±0	0±0	0±0	0.000	0
<i>Westwoodilla brevicar</i>	0±0	0±0	0±0	0±0	0.000	0
<i>Pseudoma truncatum</i>	0±0	0±0	0±0	0±0	0.000	0
<i>Pectinaria hyperborea</i>	0.073±0.051	196±113	0±0	0±0	0.000	0
<i>Hydractinia</i> sp.	0±0	0±0	0±0	0±0	0.000	0
<i>Lumbrinereis fargilis</i>	0±0	0±0	0±0	0±0	11.055	391
Athecata	0±0		0±0		0.000	
Nemertini	0.587±0.587	98±98	0±0	0±0	0.000	0
<i>Phyline lima</i>	1.662±1.662	98±98	0±0	0±0	0.000	0
<i>Brada</i> sp.	0±0	0±0	0±0	0±0	0.332	391
<i>Dacrydium vitreum</i>	0.001±0.001	0±0	0±0	0±0	0.000	0
Anisopoda	0±0	98±98	0±0	0±0	0.000	0
Bivalvia	0.001±0.001	0±0	0.005±0.004	1043±855	0.000	0
Polychaeta	0.007±0.004	98±98	0.021±0.011	391±226	0.017	391
<i>Mytilus edulis</i>	0±0	196±113	0.007±0.002	782±226	0.000	0
Phyllococidae	0.196±0.196	0±0	0±0	0±0	0.000	0
<i>Admete couthouyi</i>	0±0	98±98	0.782±0.782	130±130	0.000	0
Aphroditidae	0±0	0±0	0.261±0.261	130±130	0.000	0
<i>Syrroe crenulata</i>	0±0	0±0	0.065±0.065	130±130	0.000	0
<i>Eucratea loricata</i>	0±0		0.652±0.652		0.000	
<i>Paroediceros lynceus</i>	0±0	0±0	0.521±0.521	130±130	0.000	0
Ampharetidae	0±0	0±0	0±0	130±130	0.000	0

Fauna found at the minicorer station C
Average biomass, g/m² and average density, specimens/m²
followed by standard errors are given

Species	27.6.98		1.6.99		1.8.99	
	Biomass	Density	Biomass	Density	Biomass	Density
<i>Cossura longicirrata</i>	1.173±0.226	2476±345	0.591±0.194	2092±493	0.997±0.128	3324±1282
<i>Nephtys</i> sp.	1.694±0.568	1955±597	0.964±0.333	2385±229	1.474±0.688	2216±345
<i>Polychaeta fragmenta</i>	1.108±0.065		0±0		0.130±0.130	
<i>Prionospio cirrifera</i>	0.261±0.261	130±130	0.196±0.196	78±52	0±0	0±0
<i>Tharyx marioni</i>	0.652±0.345	261±130	0.684±0.293	235±86	0±0	0±0
<i>Portandia arctica</i>	0.717±0.622	391±226	0±0	117±83	0±0	0±0
<i>Scoloplos armiger</i>	0±0	0±0	0.978±0.978	39±39	0±0	0±0
<i>Laonice cirrata</i>	1.825±0.855	1694±261	0.196±0.196	1017±405	1.564±1.195	391±226
<i>Leptognathia sarsi</i>	0.261±0.130	652±470	0±0	196±157	0±0	0±0
<i>Diplocirrus longisetosus</i>	0.521±0.521	130±130	0.463±0.384	235±119	0±0	0±0
<i>Aricidea nolani</i>	0.130±0.130	261±261	0±0	156±86	0.412±0.381	261±130
Sabellidae	0.065±0.065	130±130	0±0	39±39	0±0	0±0
<i>Nemidia torelli</i>	0.065±0.065	130±130	0±0	39±39	0±0	0±0
<i>Chaetozone setosa</i>	0±0	0±0	0±0	78±52	0.782±0.451	261±130
<i>Pectinaria hyperborea</i>	0±0	0±0	0.020±0.020	39±39	0±0	0±0
<i>Lumbrinereis fargilis</i>	0±0	0±0	0±0	39±39	0.391±0.391	130±130
Nemertini	0±0	0±0	0.587±0.587	78±52	0.018±0.018	130±130
<i>Dacrydium vitreum</i>	0±0	0±0	0.003±0.003	39±39	0±0	0±0
<i>Limnoria lignorum</i>	0±0	0±0	0.058±0.034	430±243	0.093±0.084	521±345
Bivalvia	0±0	0±0	0.007±0.006	156±86	0.003±0.003	130±130
Polychaeta	0±0	0±0	0.148±0.111	313±163	0.005±0.005	130±130
<i>Mytilus edulis</i>	0±0	0±0	0±0	156±86	0.004±0.000	521±130

Fauna found at the minicorer stations **D, E, I, K**
Average biomass, g/m² and average density, specimens/m²
followed by standard errors are given

Station D

Species	Biomass	Density
	26.06.98	
<i>Cossura longicirrata</i>	0.261±0.130	261±130
<i>Nephtys</i> sp.	0.782±0.226	1825±793
<i>Polychaeta fragmenta</i>	0.391±0.195	
<i>Tharyx marioni</i>	1.173±0.391	391±0
<i>Portandia arctica</i>	0.065±0.065	130±130
<i>Pholloe minuta</i>	0.456±0.363	261±130
<i>Musculus niger</i>	0.130±0.065	130±130
<i>Scoloplos armiger</i>	0.261±0.130	261±130
<i>Maldane sarsi</i>	4.692±3.526	391±0
<i>Oedicerotidae</i>	0.065±0.065	130±130

Station E

Species	Biomass	Density
	26.06.98	
<i>Cossura longicirrata</i>	1.434±0.470	5995±1243
<i>Nephtys</i> sp.	1.043±0.261	1694±568
<i>Polychaeta fragmenta</i>	0.652±0.235	
<i>Prionospio cirrifera</i>	0.391±0.391	130±130
<i>Tharyx marioni</i>	5.735±1.158	1173±226
<i>Saccoglossus mereschk.</i>	10.948±5.474	261±130
<i>Tubularia regalis</i>	0.652±0.652	

Station I

Species	Biomass	Density
	26.6.98	
<i>Cossura longicirrata</i>	2.151±0.113	8993±677
<i>Nephtys</i> sp.	1.108±0.065	1955±226
<i>Polychaeta fragmenta</i>	0.847±0.284	
<i>Prionospio cirrifera</i>	0.261±0.261	130±130
<i>Tharyx marioni</i>	0.521±0.345	196±113
<i>Artacama proboscidea</i>	0.782±0.451	196±113

Station K

Species	Biomass	Density
	27.6.98	
<i>Cossura longicirrata</i>	1.499±0.363	5213±1503
<i>Nephtys</i> sp.	1.238±0.284	2085±690
<i>Polychaeta fragmenta</i>	1.760±0.517	
<i>Prionospio cirrifera</i>	0.521±0.521	130±130
<i>Tharyx marioni</i>	2.867±1.018	1434±470
<i>Portandia arctica</i>	0.130±0.065	261±130
<i>Diplocirrus longisetosus</i>	0.391±0.391	261±261
<i>Nemidia torelli</i>	0.065±0.065	130±130
<i>Chaetozone setosa</i>	0.130±0.130	130±130
<i>Aceroides latipes</i>	0.130±0.130	130±130
<i>Monoculodes</i> sp.	0.130±0.130	130±130

Fauna found at the minicorer station NL
Average biomass, g/m² and average density, specimens/m²
followed by standard error are given

Species	14.10.98		01.08.99		24.11.99	
	Biomass	Density	Biomass	Density	Biomass	Density
<i>Cossura longicirrata</i>	3.39±1.32	22808±4683	3.68	14076	4.91	10557
<i>Nephtys</i> sp.	2.74±0.60	3780±345	2.63	2346	1.26	782
<i>Polychaeta fragmenta</i>	1.43±0.69		0.0		0.0	
<i>Prionospio cirrifera</i>	0.26±0.26	130±130	0.0	0	2.15	391
<i>Tharyx marioni</i>	0.26±0.26	130±130	0.0	0	0.0	0
<i>Artacama proboscidea</i>	0.39±0.39	130±130	0.0	0	0.0	0
<i>Saccoglossus mereschk.</i>	1.04±1.04	130±130	0.0	0	1.17	391
<i>Pholloe minuta</i>	0.03±0.03	130±130	0.32	782	0.0	0
<i>Scoloplos armiger</i>	0.04±0.04	130±130	0.0	0	0.0	0
<i>Aricidea nolani</i>	0.91±0.57	652±345	2.41	391	0.91	391
<i>Chaetozone setosa</i>	1.43±1.24	261±130	3.91	1564	3.09	1173
<i>Aceroides latipes</i>	0.78±0.60	261±130	0.0	0	0.0	0
<i>Cylichna occulta</i>	0.13±0.13	130±130	0.0	0	0.0	0
<i>Westwoodilla brevicealcar</i>	0.91±0.91	261±261	0.0	0	0.0	0
<i>Pectinaria hyperborea</i>	2.48±0.79	5083±1480	0.0	0	0.0	0
<i>Lumbrinereis fargilis</i>	26.59±25.8	152±121	0.0	0	0.0	0
Athecata	0.01±0.01		0.0		0.0	
<i>Yoldia amygdalea</i>	1.50±0.17	4301±451	0.0	0	0.0	0
Nemertini	0.39±0.39	196±196	0.02	391	0.0	0
<i>Phyline lima</i>	0.07±0.07	130±130	0.0	0	0.0	0
<i>Typhlothanais finmarch.</i>	0.10±0.01	652±130	0.0	0	0.0	0
<i>Brada</i> sp.	0.20±0.11	261±130	0.0	0	0.0	0
Spiomorpha	0.20±0.20	391±391	0.0	0	0.0	0
<i>Capitella capitata</i>	0.13±0.13	261±261	0.0	0	0.0	0
<i>Myriochelle oculata</i>	0.26±0.26	130±130	0.0	0	0.0	0
Bivalvia	0.0±0.0	0±0	0.05	2737	0.0	0
Polychaeta	0.0±0.0	0±0	0.39	782	0.0	0
<i>Mytilus edulis</i>	0.0±0.0	0±0	0.01	1173	0.0	0
Maldanidae	0.0±0.0	0±0	0.20	391	0.0	0
<i>Macoma calcarea</i>	0.0±0.0	0±0	0.39	782	0.0	0
<i>Frigidalvania janmayeni</i>	0.0±0.0	0±0	1.96	391	0.0	0
<i>Retusa pertenuis</i>	0.0±0.0	0±0	0.0	0	0.78	391
<i>Thyasira gouldi</i>	0.0±0.0	0±0	0.0	0	0.78	782
<i>Terebellides stroemi</i>	0.0±0.0	0±0	0.0	0	0.02	391
<i>Flabelligera affinis</i>	0.0±0.0	0±0	0.0	0	0.11	391

Phytoplankton composition in the White Sea Basin in summer - autumn 1998 and 1999.

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Most of the phytoplankton investigations in the White Sea were carried out in inshore sites. And the composition of planktonic microalgae was well studied there (Ratkova, this issue). The central part of the sea, the Basin, was less studied, however. Only a few expeditions were carried out there (Kiselev 1925; Sergeeva 1991; Mordasova, Wentzel 1994). In the course of these investigations 74 species (without flagellates) were found in the Basin (Semina, Sergeeva, 1983). The INTAS project about the ecology of the the White Sea deep basin brought about new insights into its phytoplankton composition, which is presented in this article.

Material and methods

The samples were collected during 6 cruises in the White Sea Basin deep area: May-June 1998; August and October 1998 and June, August and November 1999. Phytoplankton was collected by water bottles from the horizons 0, 10, 20, 30, 50, 100 m and above the bottom. 50 ml aliquots of sea water from each depth were fixed with a glutaraldehyde-Lugol solution (Rousseau et al. 1990). In the laboratory, phytoplankton was analysed and counted with a non-inverted light microscope furnished with a counting stage (Semina 1978). The whole sample was gently mixed; and pico- ($< 2 \mu\text{m}$) and the most abundant nanoplankton (2-20 μm) algae were counted in a Fuchs-Rosenthal counting chamber at 400x magnification. The samples were then allowed to settle for a week and slowly decanted through a glass tube covered with two layers of fine-mesh nylon gauze. After gentle mixing, part of the remaining sample was removed with a glass tube and placed into a 0.05 ml chamber. Microplankton cells ($> 20 \mu\text{m}$) and less abundant nanoplankton algae were counted at 200x magnification. In order to count rare phytoplankton forms, a special 1.0 ml chamber was used. Many algae could be identified only to genus level. Flagellates were „identified“ mainly by their size groups. The bio-volumes of algal cells were calculated from the volumes of appropriate stereometrical bodies (Smayda 1978).

The identification of the species was performed mainly in water mounts, but, additionally, permanent mounts of acid cleaned diatoms were prepared (Hasle, Syvertsen 1997); and some

of the diatoms species were determined in these mounts by light microscope with a magnification of 1350x.

The nomenclature follows "Identifying Marine Phytoplankton" (1997); for the species, absent from this key, the following literature was used: for diatoms, "Polar Marine Diatoms" (1991), Hendey (1964), Quillfeldt (1996), "Diatomovyi Analyz" (1949/50), and for dinoflagellates, Quillfeldt (1996), Okolodkov (1998) and Konovalova (1998).

Biogeographical and ecological classification follows Semina (1974) and Semina & Sergeeva (1983); characteristics given in "Identifying Marine Phytoplankton", "Polar Marine Diatoms", "Diatomovyi Analyz", Hendey (1964), Konovalova (1998), Hsiao (1983), Usachev (1949) and Tuschling (2000) were used as well.

Results

In the White Sea Basin 203 species and varieties of phytoplankton were found. Diatom algae dominated, the number of their species and varieties amounting to 122. Next were dinoflagellates with 59 species. Prymnesiophyceae, Cryptophyceae, Chrysophyceae, Dictyochophyceae, chlorophytes and zoomastigophores accounted to 3, 4, 2, 3, 5 and 5 species, respectively (see annexed Table).

The ecology of the White sea phytoplankton was not well studied yet. For most of the identified species the ecological features were uncertain. Neritic, open-sea-neritic and ice-neritic species dominated the White Sea Basin phytoplankton (43, 25 and 12 species, respectively). Open-sea species were less numerous (31 species). Few benthic and epiphytic species were encountered, too (2 and 1 species). Most of the species were marine (66) or euryhaline (14), and a few - from brackish (3) and fresh waters (6).

Arcto-boreal species dominated the White Sea phytoplankton (68 species); species with wide geographical distribution ranges (cosmopolitans and tropic-arcto-boreal species) were very numerous, too (48 and 23 species, respectively). Bipolar and tropical forms were represented by 10 and 8 species, respectively. The geographical distribution of 46 species remained uncertain. According to Semina and Sergeeva (1983), a high proportion of cosmopolitan species (more than 40%) is noteworthy for the whole White Sea area. Arcto-boreal (28%), bipolar (15%) and a few tropical species were also encountered (Semina, Sergeeva, 1983). The higher abundances of cosmopolitan species in the shallow waters of the White Sea may be due to the stronger variations of water salinity and temperature, compared to the central part of the sea.

Seasonal phytoplankton groups should be mentioned: The spring species *Bacterosira bathyomphala*, *Chaetoceros furcellatus*, *Lauderia annulata* and *Thalassiosira bulbosa*, rather abundant in June, were almost absent from the plankton in August and October-November. Other spring species, especially *Fragilariopsis cylindrus* and *F.oceanica*, *Pseudonitzschia delicatissima*, *P.seriata* var. *obtusa*, *Thalassiosira antarctica* and *T.nordenskioldii* had their maxima in June, but were rather abundant in August and October-November, too. The summer species *Leptocylindrus minimus*, *Scrippsiella trochoideum*, *Chroomonas marina* were most abundant in August. Autumn species like *Thalassionema nitzschioides*, *Ceratium fusus*, *Dictyocha speculum* were almost absent in June, and most abundant in August and October-November. Some of the species had two seasonal maxima: in June and in August and October-November: *Achnanthes delicatula* and *A.minutissima*, *Cyclotella litoralis* and *Thalassiosira anguste-lineata*. Interannual variations and spatial patchiness may have masked the seasonal succession, because only few localities were sampled during each of the activities and as there were only three cruises a year.

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Table: Phytoplankton species,
 encountered in the White Sea Basin in summer-autumn 1998/99.
 Geographical ranges: C-cosmopolitan, A-B - arcto-boreal, BP - bipolar,
 T-A-B - tropic- arcto-boreal, T - tropical, - uncertain range;
 Ecology: E - euryhaline, B - brackish water, F - fresh water, N - neritic,
 M - marine, M-N - open-sea-neritic; I-N - ice-neritic; BOTT - bottom and
 EPIPH - epiphytic species.

	CELL	GEOGR.	ECOLOGY	JUNE	AUGUST	OCTOBER	MAY-JUNE	AUGUST	NOVEMBER
	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ⁻³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
DIVISION CHROMOPHYTA									
Class Bacillariophyceae									
<i>Achnanthes brevipes</i> Agardh	4000	C	B, N	1	0	22	0	15	1
<i>A.delicatula</i> (Kutzing) Grunow	200	A-B?	E, N	228	1	81	404	95	137
<i>A.minutissima</i> Kutzing	250	-	F	179	0	288	0	0	0
<i>A.taeniata</i> Grunow	1000	A-B	E, M-N	162	0	1	1079	0	169
<i>Actinocyclus octonarius</i> Ehrenberg	48000	C	E, M-N	23	0	0	0	0	18
<i>Amphora</i> spp.				1	17	10	12	4	13
<i>Asterionella formosa</i> Hassal	800	C	F	0	0	2	2	0	1
<i>Asterionellopsis glacialis</i> (Castracane) Round	250	C	E, M-N	2	0	0	0	0	0
<i>Attheya septentrionalis</i> (Oestrup) Crawford	150	A-B	M, I-N	3	0	0	1	0	0
<i>Bacillaria paxillifer</i> (O.F.Muller) Hendey	800	-	E, N	0	0	0	0	0	3
<i>Bacterosira bathyomphala</i> (Gran) Syvertsen & Hasle	2200	A-B	N	667	17	7	320	9	0
<i>Cerataulina pelagica</i> (Cleve) Hendey	15000	T-A-B	N	0	0	0	1	0	0
<i>Chaetoceros affinis</i> Lauder	4600	A-B?	N	18	0	0	0	66	0
<i>C.atlanticus</i> Cleve	3400	C	M	0	0	0	5	0	0
<i>C.borealis</i> Bailey	11250	A-B	M	31	21	19	4	149	0
<i>C.compressus</i> Lauder	600	T-A-B	N	105	0	43	94	269	212
<i>C.concavicornis</i> Mangin	2200	A-B	M	424	0	0	0	49	0
<i>C.constrictus</i> Gran	1800	T-A-B	N	4	0	192	0	58	0
<i>C.curvisetus</i> Cleve	900	C	N	0	0	0	0	263	0
<i>C.danicus</i> Cleve	7500	T-A-B	E, N	3	0	0	1	1	0
<i>C.debilis</i> Cleve	600	T-A-B	N	57	0	0	471	341	739
<i>C.decipiens</i> Cleve	13500	C	M	217	0	0	0,2	68	0
<i>C.densus</i> (Cleve) Cleve	2200	C	M	0,3	0	0	1	5	0
<i>C.diadema</i> (Ehrenberg) Gran	3100	A-B	E, N	12	0	4	0	0	0
<i>C.didymus</i> Ehrenberg	1700	T-A-B	N	0	0	0	0,2	48	0
<i>C.furcellatus</i> Bailey	200	A-B	N	82	0	0	159	6	1
<i>C.karianus</i> Grunow	540	A-B	N	306	0	0	0	20	0
<i>C.laciniosus</i> Schutt	400	T-A-B	N	6	0	0	0	5	0

	CELL	GEOGR.	ECOLOGY	JUNE	AUGUST	OCTOBER	MAY-JUNE	AUGUST	NOVEMBER
	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ⁺³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
<i>C.peruvianus</i> Brightwell	3150	T-A-B	M	1	0	0	0	0	0
<i>C.simplex</i> Ostenfeld	200	T-A-B	E, N	11	0	0	0	1	1
<i>C.socialis</i> Lauder	100	C	E, N	27183	9573	5245	200180	465434	65765
<i>C.teres</i> Cleve	18000	A-B	N	3	0	2	0	5	0
<i>C.wighamii</i> Brightwell	600	A-B	E, N	1	0	0	65	23	0
<i>C.sf.perpusillus</i> Cleve	300	T-A-B	N	0	0	0	69	877	0
<i>Cocconeis costata</i> Gregory	4600	A-B?	M	3	0	7	4	53	19
<i>C.pediculus</i> Ehrenberg	1440	-	B, N	1	4	4	6	21	110
<i>Coscinodiscus asteromphalus</i> Ehrenberg	1012500	C	M	2	0	2	1	0	0
<i>C.concinnus</i> W.Smith	1350000	C	E, N	15	1	0	0	0	0
<i>C.radiatus</i> Ehrenberg	42300	C	M	4	0	15	0	0	0
<i>C.wailesii</i> Gran & Angst	1192000	C	M	0	0	0	1	0	0
<i>C. spp.</i>				2	17	3	9	17	4
<i>Ctenophora pulchella</i> (Ralfs & Kutzing) Williams & Round	6370	A-B	E, N	18	1	87	54	98	60
<i>Cyclotella litoralis</i> Lange & Syvertsen	16000	BP	E, N	0	0	22	2	13	0
<i>C.striata</i> (Kutzing) Grunow	3000	A-B?	E, N	16	4	20	4	21	10
<i>Cylindrotheca closterium</i> (Ehrenberg) Lewin & Reimann	450	C	E, N	1	0	21	61	2	30
<i>Dactyliosolen fragilissimus</i> (Bergon) Hasle	5100	C	N	0	1	7	0	0	0
<i>Detonula confervacea</i> (Cleve) Gran	270	A-B	N	1	0	0	0	0	0
<i>Diatoma tenuis</i> Agardh	800	-	F	0	0	15	0	0	0
<i>Diploneis didyma</i> (Ehrenberg) Ehrenberg	10000	A-B?	N	0	0	3	0	0	6
<i>D.interrupta</i> (Kutzing) Cleve	15000	A-B?	N	0	7	2	0	0	0
<i>D.litoralis</i> var. <i>clathrata</i> (Oestrup) Cleve	5300	A-B	I-N	5	7	2	9	0	6
<i>Ditylum brightwellii</i> (West) Grunow	11800	T-A-B	N	0	0	7	2	4	6
<i>Entomoneis alata</i> (Ehrenberg) Ehrenberg	3000	-	E	0,3	0	0	0	0	9
<i>Eucampia groenlandica</i> Cleve	1500	A-B	N	0	0	6	0	1	0
<i>Fallacia forcipata</i> (Greville) Stickle & Mann	23520	C	M	4	0	0	0,4	8	4
<i>Fragilaria striatula</i> Lyngbye	2560	A-B	M	19	0	7	3	652	106
<i>Fragilariopsis cylindrus</i> (Grunow) Krieger	100	BP	M, I-N	6049	2956	2491	5603	392	1647
<i>F.oceanica</i> (Cleve) Hasle	400	A-B	M, I-N	1025	12	46	8108	108	95

	CELL	GEOGR.	ECOLOGY	JUNE	AUGUST	OCTOBER	MAY-JUNE	AUGUST	NOVEMBER
	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ⁴³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
<i>Gomphonemopsis cf. exigua</i> (Simonsen) Medlin	1920	A-B?	I-N	6	0	0	0	0	2
<i>Grammatophora arctica</i> Cleve	12000	A-B?	N	6	17	43	8	1	29
<i>Guinardia delicatula</i> (Cleve) Hasle	7000	C	E, M	0	0	0	1	1	6
<i>Gyrosigma fasciola</i> var. <i>tenuirostris</i> (Grunow) Cleve	7000	A-B?	M-N	1	0	4	0	0	0
<i>G. tenuissimum</i> var. <i>hyperborea</i> (Grunow) Cleve	3400	-	M-N	0	0	0	1	0	4
<i>Hannaea arcus</i> (Ehrenberg) Patrick	3200	-	F	0	0	3	0	0	0
<i>Lauderia annulata</i> Cleve	22800	A-B	N	13	0	0	2	0	0
<i>Leptocylindrus mediterraneus</i> (H. Peragallo) Hasle	25200	C?	M-N	0	0	0	0	0	7
<i>L. minimus</i> Gran	600	T-A-B	E	14	1373	0	0	145	0
<i>Licmophora communis</i> (Heiberg) Grunow	4100	A-B?	M-N	4	0	0	0	3	1
<i>L. gracilis</i> (Ehrenberg) Grunow	18200	-	N	0	0	0	0	1	6
<i>L. hyalina</i> (Kutzing) Grunow	8000	A-B?	N	1	0	0	0	0	0
<i>L. paradoxa</i> (Lyngbye) Agardh	7680	-	M-N	0	0	0	0	3	0
<i>Melosira arctica</i> Dickie	1500	A-B	M, I-N	62	1	0	84	0	28
<i>M. nummuloides</i> Agardh	43500	C	E, N	0	0	2	0	0	27
<i>Navicula delicatula</i> Cleve	2200	-	-	2	0	3	2	0	66
<i>N. directa</i> (W. Smith) Ralfs	9000	A-B	M, I-N	0	0	0	2	2	0
<i>N. distans</i> (W. Smith) Ralfs	56300	A-B?	BOTT	6	7	11	14	7	10
<i>N. monilifera</i> Cleve	10000	A-B?	M	0	0	0	0	0	3
<i>N. pelagica</i> Cleve	1100	A-B	E, N	0	0	0	39	0	0
<i>N. transitans</i> var. <i>derasa</i> (Grunow) Cleve	9600	A-B	M, I-N	2	0	0	17	4	7
<i>N. transitans</i> var. <i>derasa</i> f. <i>delicatula</i> Heimdal	1300	-	-	24	0	27	94	17	26
<i>N. vanhoeffenii</i> Gran	2200	A-B	E, M-N	0	0	0	31	0	0
<i>N. spp.</i>				0	0	0	8	0	0
<i>Nitzschia angularis</i> W. Smith	3200	-	M	0	0	3	0	0	0
<i>N. dissipata</i> (Kutzing) Grunow	2250	-	F	228	1	34	2	1	0
<i>N. frigida</i> Grunow	4500	A-B	E, I-N	0,3	34	0	0	0	2
<i>N. hybrida</i> Grunow	2400	A-B	B, I-N	0	0	0	0	0	3
<i>N. longissima</i> (Brebisson) Ralfs	830	BP	E	0	0	2	0	1	0
<i>N. promare</i> Medlin	560	A-B	M, I-N	0	0	0	21	0	0

	CELL VOLUME	GEOGR. RANGE	ECOLOGY	JUNE 1998		OCTOBER 1998		MAY-JUNE 1999		AUGUST 1999		NOVEMBER 1999	
				MEAN (N=6)		MEAN (N=2)		MEAN (N=5)		MEAN (N=3)		MEAN (N=2)	
N.scabra Cleve	12000	A-B	M	0	0	1	0	0	0	0	0	0	0
Odontella aurita Agardh	10500	A-B	E	3	0	0	0	0	1	1	0	1	1
Paralia sulcata (Ehrenberg) Cleve	3300	C?	BOTT	19	36	24	186	54	54	108	108	108	108
Plagiogramma staurophorum (Gregory) Heiberg	3840	A-B?	M-N	0	0	7	0	0	0	0	0	0	0
Plagiotropis scaligera Grunow	10000	-	-	3	0	3	0	0	0	0	0	0	0
Pleurosigma angulatum (Quekett) Wm.Smith	6000	-	E	0	0	0	1	0	0	0	0	0	0
P.finnarchicum Cleve & Grunow	67500	-	E	2	0	0	28	8	8	6	6	6	6
P.normanii Ralfs	4500	-	M	0,4	2	3	7	5	5	0	0	0	0
P.stuxbergii Cleve & Grunow	28000	A-B	M, I-N	0	0	0	0,4	0	0	0	0	0	0
Porosira glacialis (Grunow) Jorgensen	38800	PB	N	0,1	17	25	93	1	1	1	1	1	1
Pseudonitzschia delicatissima (Cleve) Heiden	200	A-B	M	20	0	0	30	0	0	12	12	12	12
P.granii (Hasle) Hasle	30	A-B?	M	0	0	14	464	57	57	162	162	162	162
P.pseudodelicatissima (Hasle) Hasle	100	A-B	M	1	3	15	6	1	1	0	0	0	0
P.pungens (Grunow & Cleve) Hasle	1400	C	M	0	0	7	0	0	0	0	0	0	0
P.seriata f.obtusa (Hasle) Hasle	2200	A-B	M	33	0	6	62	2	2	5	5	5	5
Rhabdonema arcuatum (Lyngbye) Kutzing	49500	A-P	EPPH	0	0	0	0	0	0	3	3	3	3
Rhizosolenia setigera Brightwell	18000	C	C	8	0	0	0,2	0	0	0	0	0	0
R.styliformis Brightwell	163300	C	N	0,1	0	0	0	0	0	0	0	0	0
Rhoicosphenia curvata (Kutzing) Grunow	4000	-	B	0,3	0	0	1	6	6	0	0	0	0
Skeletonema costatum (Greville) Cleve	200	C	E, N	5962	154	334	1778	42260	42260	507	507	507	507
Stauroneis amphioxys Gregory	24000	A-B?	B, N	0	0	3	0	0	0	0	0	0	0
Tabellaria fenestrata (Lyngbye) Kutzing	3500	-	F	0	0	0	0	2	2	6	6	6	6
Tabularia fasciculata ((Agardh) Williams & Round	7300	A-B?	E	0	0	4	0	2	2	9	9	9	9
Thalassionema nitzschoides (Grunow) Grunow & Hustedt	400	T-A-B	-	69	65	614	180	2514	2514	1562	1562	1562	1562
Thalassiosira angulata (Gregory) Hasle	4300	A-B	-	522	68	121	157	148	148	212	212	212	212
T.anguste-lineata (A.Schmidt) Fryxell & Hasle	12000	T-A-B	N	37	0	10	14	0	0	19	19	19	19
T.antarctica var. borealis Fryxell, Douchett & Hubbard	14580	A-B	-	537	69	99	1996	279	279	264	264	264	264
T.bulbosa Syvertsen	400	A-B	-	30	0	0	11	0	0	0	0	0	0
T.constricta Gaarder	18700	A-B?	-	0	0	37	27	0	0	0	0	0	0
T.eccentrica (Ehrenberg) Cleve	23400	T-A-B	E	35	21	0	5	1	1	6	6	6	6

	CELL	GEOGR.	ECOLOGY	JUNE	AUGUST	OCTOBER	MAY-JUNE	AUGUST	NOVEMBER
	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ⁺³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
<i>T.gravida</i> Cleve	9000	BP	-	8	0	15	3	3	0
<i>T.hyalina</i> (Grunow) Gran	6500	A-B	-	19	0	675	810	64	0
<i>T.hyperborea</i> (Grunow) Hasle & Lange	4500	A-B	B				513		
<i>T.kushirensis</i> Takano	3800	A-B?	-	0	0	0	6	0	0
<i>T.cf.lineoides</i> Herzig & Fryxell	36000	T-A-B?	-	0	7	0	0	0	0
<i>T.nordenskioldii</i> Cleve	2900	A-B	E, N	20607	261	278	552	53	239
<i>T.spp.</i>				214	7	1254	1328	915	615
<i>Trachyneis aspera</i> (Ehrenberg) Cleve	160000	-	M, N	1	0	0	0	0	0
<i>Pennates</i> unidentified				161	38	121	952	11	489
Class Dinophyceae									
<i>Alexandrium ostenfeldii</i> (Paulsen) Balech & Tangen	147000	T-A-B?	E, N	0	0	0	0,2	0	0
<i>A.tamarense</i> (Lebour) Balech	19000	T-A-B?	N?	0,4	0	0	12	1	4
<i>Amylax triacantha</i> (Jorgensen) Sournia	5000	A-B	N	0,3	0	0	0	0	0
<i>Amphidinium crassum</i> Lohmann	5250	T-A-B?	N	0	0	0	3	480	0
<i>A.larvale</i> Lindemann	190	-	E	0	0	0	14086	1149	2295
<i>A.longum</i> Lohmann	1300	C	E, N	34	1905	68	1	0	216
<i>A.sphenoides</i> Wulff	1100	A-B	M-N	198	1051	11	3	3	37
<i>Ceratium fusus</i> (Ehrenberg) Dujardin	91800	C	M-N	0	0	6	0	12	0
<i>C.gravidum</i> Gourret	405500	T	M	0	0	0	0	0	1
<i>C.horridum</i> (Cleve) Gran	85000	T-A-B	M-N	0,1	0	0	0	2	0
<i>C.longipes</i> (Bailey) Gran	92300	A-B	M	0,1	0	0	0	0	0
<i>Dinophysis acuminata</i> Claparede & Lachmann	19000	C	N	2	0	4	1	1	0
<i>D.acuta</i> Ehrenberg	18000	BP	M	3	1	3	0	7	1
<i>D.arctica</i> Mereschkowsky	9000	BP	M-N	5	7	6	1	21	25
<i>D.contracta</i> (Kofoid & Skogsberg) Balech	6000	T-A-B	M	4	0	0	0	0	0
<i>D.norwegica</i> Claparede & Lachmann	35000	A-B	N	1	0	0	0	1	0
<i>D.rotundata</i> Claparede & Lachmann	12000	C	M-N	1	0	7	14	5	0
<i>Diplopeltopsis minor</i> (Paulsen) Pavillard	6000	T-A-B	-	1	0	0	0	0	0
<i>Diplopsalis lenticula</i> Bergh	14000	T	-	3	6	2	7	8	1

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	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
Glenodinium gymnodinium Penard	50000	-	-	0,4	0	0	0	0	0
Gonyaulax digitalis (Pouchet) Kofoid	40000	T	M-N	0,3	0	0	0,3	0	0
G.grindleyi Reinecke	18000	C	N	5	1	2	0,2	0	0
G.spinfifera (Claparede & Lachmann) Diesing	9900	C	N	4	0	0	0	0	0
Gymnodinium arcticum Wulff	4000	A-B	M-N	86	41	27	26	4	136
G.frigidum Balech	13500	BP	N	76	0	0	15	23	7
G.heterostriatum Kofoid & Swezy	4700	T	-	113	706	18	32	121	290
G.japonica Hada	400	-	-	1918	3160	1967	6372	530	2516
G.lebourii Pavillard	108000	-	-	1	0	0	0	0	0
G.veneficum Ballantine	900	-	N	2244	3947	1824	523	674	3819
G.vitiligo Ballantine	1700	-	N	193	613	345	63	357	787
G.simplex (Lohmann) Kofoid & Swezy	190	T-A-B	N	0	0	62	0	0	0
Gyrodinium cf.aureolum Hulburt	24000	BP	E, M-N	7	4	0	12	29	12
G.fusifforme Kofoid & Swezy	1620	T-A-B	M-N	68	5	13	28	66	103
G.lachryma (Meunier) Kofoid & Swezy	36700	BP	M-N	1	0	0	0	1	0
G.prunus (Wulff) Lebour	47000	C	-	17	0	0	12	21	7
G.spirale (Berg) Kofoid & Swezy	17000	C	M-N	13	0	0	20	13	10
Heterocapsa triquedrum(Lohmann) Hansen	6900	C	E, N	0,3	0	0	0	0	6
Katodinium glaucum (lebour) Loeblich	2100	T-A-B	M-N	204	0	0	0	0	0
Katodinium rotundatum (Lohmann) Loeblich	400	T-A-B	N	0	0	0	104167	0	0
Oxytoxum belgicum Meunier	1000	A-B?	-	0	0	0	0	5	0
O.sceptrum (Stein) Schroeder	3000	T	M	0	0	0	6	0	0
O.variabile Schiller	900	T	M	23	0	0	4	4	0
Pronoctiluca acuta (Lohmann) Schiller	1600	-	-	0,3	0	9	1	8	64
Prorocentrum balticum (Lohmann) Loeblich	400	C	M, M-N	7	179	17	0	0	0
P.compressum (Bailey) Abe & Dodge	7000	C	M, M-N	0	0	0	16	0	4
P.micans Ehrenberg	6000	T-A-B	N	1	0	7	3	11	9
P.minimum (Pavillard) Schiller	720	C	E, N	73	1	49	7	3	365
Protoperdinium bipes (Paulsen) Balech	2000	A-B	N	33	0	0	74	32	0
P.breve (Paulsen) Balech	23300	C	-	1	1	0	0	0	0

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	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ⁺³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
<i>P.brevipes</i> (Paulsen) Balech	10100	BP	N	7	4	0	8	17	7
<i>P.conicoides</i> (Paulsen) Balech	37500	A-B	N	0,4	0	0	0	0	0
<i>P.curvipes</i> (Ostenfeld) Balech	13500	BP	-	1	0	0	0	0	0
<i>P.depressum</i> (Bailey) Balech	130000	C	M	1	0	0	1	0	0
<i>P.pallidum</i> (Ostenfeld) Balech	13500	BP	M-N	3	0	0	0	0	0
<i>P.pellucidum</i> Bergh	51800	C	M-N	8	0	1	2	0	0
<i>P.pyriforme</i> (Paulsen) Balech	6000	C	M	2	0	0	0	1	7
<i>P.subinerme</i> (Paulsen) Loeblich III	62500	A-B	E, N	1	0	0	1	0	0
<i>Scrippsiella trochoidea</i> (Stein) Loeblich III	5900	C	E, N	15	39	16	26	1154	12
<i>Warnowia schuetti</i> (Kofoid & Swezy) Shiller	6000	-	-	6	5	3	2	0	3
Armored dinoflagellates unidentified				62	19	10	174	214	18
Unarmored dinoflagellates unidentified				15	1	14	10	1	17
Class Prymnesiophyceae									
<i>Chrysochromulina hirta</i> Manton	260	-	-	0	0	4	0	0	0
<i>Emiliania huxleyi</i> (Lohmann) Hay & Mohler	260	C	-	0	0	4	0	13	1209
<i>Phaeocystis pouchetii</i> (Hariot) Lagerheim	200	BP	M	600133	480813	204016	458311	200977	5080669
Class Cryptophyceae									
<i>Chroomonas marina</i> (Buttner) Butcher	1100	-	-	20393	100236	1117	176	26042	645
<i>Hilea fusiformis</i> (Schiller) Schiller	64	-	-	0	0	0	7514	6509	14744
<i>Leucocryptos marina</i> (Braarud) Butcher	480	-	-	0	0	314	0	0	0
<i>Plagioselmis</i> sp.	750			689	1196	3014	9783	10800	4122
<i>Teleaulax acuta</i> (Butcher) Hill	340	-	-	28059	231975	49750	39439	10112	6684
Class Chrysophyceae									
<i>Dinobryon balticum</i> (Schutt) Lemmermann	800	A-B	M	0	0	166	0	0	0
<i>D.belgica</i> Meunier	600	A-B	-	7812	0	0	73409	12615	0

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	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ⁺³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
Class Dictyochophyceae									
Dictyocha fibula Ehrenberg	5500	T-A-B?	-	0	0	106	2	0	189
D.speculum Ehrenberg	6900	C	E, N	47	16	31	5	13	17
Parapedinella reticulata S.M.Pedersen & Thomsen	4000	-	-	0,3	0	0	3734	1987	43
DIVISION CHLOROPHYTA									
Class Chlorophyceae									
Carteria sp.	100			0,2	3	0	209	3	150
Class Euglenophyceae									
Euglena sp.	12000			0	0	0	13	1	0
Eutreptiella cf.eupharyngea Moestrup & Norris	600	-	-	7867	7	2	5937	10473	1756
Class Prasinophyceae									
Halosphaera viridis Schmitz	171500	C	-	0,3	0	0	0	0	0
Pterosperma marginatum Gaarder	1700	-	-	3	0	0	18503	1713	0
Pyramimonas grossii Parke	140	C?	-	0	0	0	0	0	0
P.nephroidea McFadden	320	-	-	0,1	0,5	0	50	0,3	8
Unidentified flagellates				7619604	7652336	10367327	5352676	3677744	14075577
Unidentified monads				15061963	12454044	13201367	18280819	7632307	30955529
Unidentified cyanobacteria				1261730	197611	104688	763220	91640	0

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	VOLUME	RANGE		1998	1998	1998	1999	1999	1999
	Fk ⁺³			MEAN	MEAN	MEAN	MEAN	MEAN	MEAN
				(N=6)	(N=2)	(N=2)	(N=5)	(N=3)	(N=2)
PHYLUM ZOOMASTIGOPHORA									
Class Kinetoplastida									
Telonema subtilis Griessmann	300	-	-	0	33	2288	0	4	250
Class Choanoflagellidea									
Acanthocorbis unguiculata (Thomsen) Hara & Takahashi	1700	-	-						4
Desmarella moniliformis Kent	108	-	-	0	0	0	193	0	7394
Parvicorbicula socialis (Meunier) Deflandre	2000	-	-	3	0	73	4253	195	0
Class Eбриida									
Ebria tripartita (Schumann) Lemmermann	4500	A-B	M	4	10	46	40	24	52

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