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Long-term fluctuations of soft-bottom intertidal community structure affected by ice cover at two small sea bights in the Chupa Inlet (Kandalaksha Bay) of the White Sea

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Abstract The effect on bottom organisms of periodic freezing of the upper layer of intertidal sediments during abnormal cold winters has been studied for a long time in seas of a moderate climatic zone. However, the effect of ice cover every year on intertidal communities in polar seas is still poorly investigated. Seasonal and long-term variation in the structure of intertidal soft-bottom communities in two small bights in the White Sea with annual ice cover was studied for over two decades. Sampling was carried out four times a year, in the hydrological spring, summer, autumn, and winter. It was found that bottom macrobenthic communities at upper and lower horizons of the intertidal distinctly differed in the studied sites. Periodic changes caused by the effect of abnormal ice conditions, including the partial removal by ice of sediment with in situ organisms, were discovered. Recovery of communities after disturbance normally took less than half a year. Communities at the lower and upper horizons of the intertidal zone were more stable than intermediate communities, which led to periodic shifts of the biological border between lower and upper intertidal assemblages.

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Introduction

Long-term studies of intertidal communities based on regular annual sampling are relatively few (Dörjes et al., 1986; Ibanez & Dauvin, 1988; Beukema, 1992a, b; Beukema et al., 2001; Maximovich & Guerassimova, 2003; Naumov, 2007; Naumov et al., 2009; Petraitis et al., 2009, and references therein). Most of these studies have focused on seasonal and long-term fluctuation of abundant species.

Although the periodic effect of low and high air temperature in winter (Beukema, 1985, 1992b) and ice-scour (McCook & Chapman, 1991; Petraitis et al., 2009) on intertidal benthic organisms in temperate seas has been discussed in the literature, long-term investigations of intertidal communities, including regular seasonal sampling in polar seas with stable annual ice cover are virtually absent. It is clear, however, that such assemblages in tidal polar seas are strongly affected by near-coast ice during a substantial part of the year (Kuznetzov, 1960; Naumov, 2007). However, no long-term data are available on the effect of regular annual ice cover on macrobenthic community structure in polar seas.

In the White Sea, intertidal ice lying on rocky bars can protect bottom organisms against frost during low tide (Kuznetzov, 1960). The same phenomenon can be found in other seas (Scrosati & Eckersley, 2007). On the other hand, on sandy and muddy tidal flats, ice cover can make contact with sediment containing animals, algae, and plants at spring-tide low water. This can lead to their freezing on to the lower surface of the ice, resulting in possible mortality, or removal by wind-induced drift during ice melting (Kuznetzov, 1960; Naumov, 2007). Both phenomena and their effect on the dynamics of communities remain poorly studied (Naumov, 2007), but it is obvious that such phenomena may result in modification or even complete destruction of intertidal macrozoobenthic communities. Such events sometimes occur in the White Sea under severe wind conditions during ice melting (Naumov, 2007). Data on the recovery of intertidal bottom assemblages after ice induced mortality, and removal during abnormal ice melting in polar tidal seas, are not available, yet information of this kind is essential for understanding the functioning of, and long-term changes in, Arctic intertidal communities.

Elucidation of the level of possible reorganizations in intertidal soft-bottom communities induced by moving ice during melting periods, and the rate of their recovery, are the main objectives of this research. This study analyzes data from seasonal monitoring of sea-floor communities in muddy and sandy–muddy intertidal areas conducted at the White Sea Biological Station over the past 25 years. In this paper, the structure of sea-bottom communities and their typical variations (modifications) in time as a result of abnormal ice are discussed; long-term dynamics of individual species and species interactions are topics for future publications (for example Varfolomeeva & Naumov, 2012).

Materials and methods

Sampling area

To compare the effect of different abiotic conditions, e.g., type of sediment, exposure to wave action, and the effect of ice, sampling was conducted in the intertidal zone of two small bights near the White Sea Biological Station *Kartesh*, namely the Seldyanaya Bight and the Medvezhya Bight (Fig. 1). The average tidal amplitude, as it is common for the White Sea, is approximately 1.5 m at both sites.

Seldyanaya Bight is a long (400 m) narrow bay on the northern coast of the Chupa Inlet. The maximum width at its mouth is approximately 100 m, and it opens to the southeast. The bight is sheltered by the large Keret' Island situated about 2 km to the south. A small stream flows into the head of the bay, and during ebbing tides fresh water runs over the tidal flats. Boulders line the shore at the mouth of the bay, giving way to clay sediment at the head. The tidal flat is covered with a thick layer of semi-liquid silt.

Medvezhya Bight is almost rectangular in shape and opens to the northeast. It is approximately 200 m long and 300 m wide. It is sheltered by a small peninsula approximately 1 km to the north, and from the northeast by a few small islands approximately 3.5 km offshore. Two streams flow into the bight. The larger stream, which has a relatively stable streambed, flows into the southeastern part of the bay. The shores of Medvezhya Bight are largely mixed rocky–sandy ground. The tidal flat deposits are sand with some mud.

The particle-size composition of the intertidal sediments in both bights is presented in Table 1. In the Seldyanaya Bight, aleurite and pelite fractions make up the main part of the sediment. The percentage of sand increases from hydrographic datum level shoreward. The percentage of pelite has the opposite tendency. The water content of the sediment is very high. A large amount of decaying plant material of marine and terrestrial origin results in a pronounced smell of hydrogen sulfide.

In the Medvezhya Bight, well-washed sandy fractions mixed with aleurite prevail. There is no gradient in the distribution of different fraction sizes in the tidal flat compared with those in the Seldyanaya Bight. The water content of the sediment is moderate.

Salinity in the upper 5 m layer is almost evenly distributed in the White Sea (data for the studied bights are given below) because of intense wind-induced turbulence (Babkov, 1982; Naumov, 2011). Therefore, strong intertidal salinity changes in summer, caused by deep water coming in on flooding tides, are not typical, although they depend upon tidal phase and local runoff conditions.

Surface salinity in the Seldyanaya Bight usually depends on weather conditions, and less on the tidal cycle. On rainy summer days during ebb tide, it can

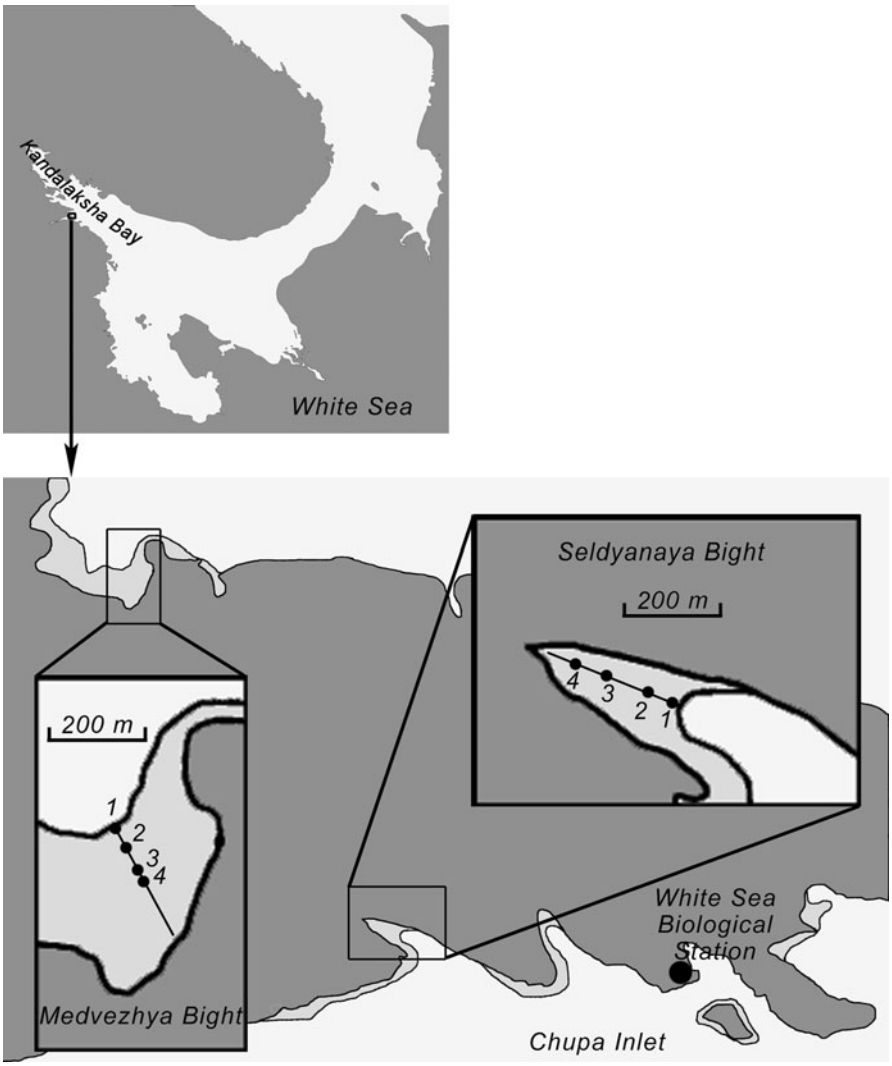

Fig. 1 Location of sampling areas in the studied bights. The intertidal zone is marked *light grey*. *Lines* crossing the intertidal zone are transects, and *dots with numbers* are sampling stations

fall to 10 ppt; during floods, it can increase to 16 ppt. Surface salinity reaches 18 and 23–25 ppt at low and high tides, respectively, on dry days. In contrast, the tidal cycle has a strong effect on the salinity of the upper layer in the Medvezhya Bight. At low tide, freshwater runs over the surface water layer, reducing salinity to 11 ppt on dry days and 9 ppt on rainy days. At high tide surface salinity can increase to 22–24 ppt because of the ponding of fresh water by tidal waves (Fedyakov & Sheremetevsky, 1991).

In winter, the salinity of the upper layer can drop to 5 ppt because of accumulation of fresh water runoff under the ice in both bights. This brackish layer normally does not exceed 0.5 m depth, and water of higher salinity covers the intertidal zone at high tide. Its salinity varies in different years from 10 to 20 ppt (our observations).

Seawater surface temperature is approximately 14–16°C in summer, and decreases to −0.9°C in winter as in the whole area of Chupa Inlet (Babkov, 1982; Babkov & Lukanin, 1985).

Because of the lower average salinity, in the Medvezhya Bight freezing begins about a week earlier than in the Seldyanaya Bight. The time of formation of the first ice varies from year to year. The earliest freezing was observed in October whereas the latest was in February. Ice melting starts in May. The whole ice-period lasts from 3 to 7 months, approximately 6 months on average. The thickness of the ice cover was different in different winters but did not diverge

Table 1 Bottom sediments in the studied bights (mean values ± standard error are presented) (modified from Fedyakov & Sheremetevsky, 1991, with the permission of the Zoological Institute RAS)

Parameter	Seldyanaya Bight	Medvezhya Bight
Specific gravity (g/cm^3)	2.48 ± 0.06	2.70 ± 0.10
Pebbles (10–100 mm) (vol%)	0.75 ± 0.48	1.00 ± 1.00
Gravel (1–10 mm) (vol%)	5.00 ± 1.00	4.50 + 2.22
Sand (0.1–1.0 mm) (vol%)	23.25 ± 2.07	54.25 ± 3.68
Aleurite (0.01–0.1 mm) (vol%)	46.00 ± 7.57	38.00 ± 2.48
Pelite (<0.01 mm) (vol%)	25.00 ± 12.34	2.25 ± 1.65
Median size (mm)	0.04 ± 0.02	0.13 ± 0.01
Water content (vol%)	70.50 ± 7.10	43.00 ± 3.03
Pore water salinity (ppt)	24.28 ± 0.43	24.05 ± 0.41

Fig. 2 Under-ice view of sandy intertidal sediment during low tide in the Medvezhya Bight. Fresh cones of lugworm *A. marina* can be seen (Photo: A. Naumov)

substantially; its mean value was approximately 0.5 m. Sea-bottom organisms remain active during the whole ice-period (Fig. 2).

There is no rock bar in either bight, hence at low tide, ice lies directly on the surface of the sediment. This may lead to freezing of the upper layer of sediment into the ice cover (Fig. 3). Sometimes, if the weather during ice melting is abnormally windy, ice containing a thick layer of frozen sediment with in situ benthic organisms can be removed from the bight, which results in substantial modifications of sea bottom communities (see below). Such events were observed in the Seldyanaya Bight in 1988, 1994, 1998, 2002, 2005, 2006 (Naumov, 2007), and in 2007.

Fig. 3 Frozen-in-ice bottom sediment containing different seafloor organisms in the Seldyanaya Bight. *Z. marina* and *C. sericea* are perfectly visible in different layers formed during spring tides. Ice thickness is approximately 40 cm; the ice block lies on the snow upside down (Photo: A. Naumov)

Neither incorporation of sediment into the ice nor abnormal ice melting were recorded in the Medvezhya Bight during the whole period of observation.

Sampling

Data obtained in the years 1987–2008 (21 complete years) are analyzed in this paper.

Sampling was conducted four times a year in every season: during hydrological spring (end of May/beginning of June), summer (end of July/beginning of August), autumn (end of October/beginning of November), and winter (end of March/beginning of April).

Samples were taken along a transect in each bight. In the Seldyanaya Bight, the transect was made along the bed of the stream whereas in the Medvezhya Bight the transect was made alongside the streambed in the eastern part of intertidal flat. Three samples at each of the four benthic stations on both transects (Fig. 1) were obtained during each survey. Points of sampling were marked with an accuracy of approximately 1 m^2 by use of beach leading beacons constructed especially for this purpose. Numeration of stations in both bights started at hydrographical datum and increased in the direction of the upper horizons. Coordinates of sampling points are given in Table 2.

Two spring surveys (1989 and 1997) were missed completely for logistic reasons, one survey (winter

Table 2 Coordinates of sampling points (map datum: WGS 84)

Station no.	Seldyanaya Bight			Medvezhya Bight		
	Latitude	Longitude	Depth (m)[a]	Latitude	Longitude	Depth (m)[a]
1	66°20.277′N	33°37.310′E	0.0	66°21.085′N	33°35.782′E	0.0
2	66°20.290′N	33°37.274′E	−0.5	66°21.082′N	33°35.811′E	−0.4
3	66°20.277′N	33°37.278′E	−0.9	66°21.081′N	33°35.831′E	−1.0
4	66°20.303′N	33°37.186′E	−1.6	66°21.081′N	33°35.841′E	−0.9[b]

[a] Depths are denoted as negative values, when higher than the hydrographic datum

[b] Station number 4 is located in an intertidal pool in the Medvezhya Bight

2001) was missed in the Medvezhya Bight because of unfavorable ice conditions and three times in different years autumn sampling at station number 1 was missed in the same bight because of adverse weather and tide conditions. Sometimes, for different reasons, fewer than three samples were obtained at individual stations, mainly in the Seldyanaya Bight. Altogether, 82 surveys were conducted, and 672 benthic stations containing 1826 samples were sampled.

Three tube corers (working area 4×10^{-3} m^2, 7.6×10^{-3} m^2, and 1.53×10^{-2} m^2) inserted one into another were used for sampling, to avoid collection of too many juveniles and abundant small organisms. The system of corers was pressed into sediment to a depth of 10–15 cm. Sample washing was performed through a set of sieves (0.5 mm mesh size, 1.0 and 3.0 mm, with round perforations) (Fig. 4). By this method, organisms 0.5–1.0 mm in size were recorded from the smallest corer, those of 1.0–3.0 mm from the smallest and middle corers, and those larger than 3.0 mm from all three corers. The number and weight of all organisms from the three subsamples were recalculated to 1 m^2 and summarized.

All sampled organisms were identified to species level, except for species of the genus *Gammarus*, Nemertini, some species of Algae, Oligochaeta, Opistobranchia, and insect larvae, whose taxonomies were obscure. Species of genus *Monoculodes* were not identified because of the very small size of sampled juvenile specimens.

All organisms were counted and weighed (wet weight) by use of a spring balance, with an accuracy of 0.001 g if their weight did not exceed 1 g and with an accuracy of 0.01 g in other cases. Mollusks were weighed with the shell and mantle fluid, polychaetes without their tubes.

All samples from each station were pooled and considered in this paper as a primary description of the community.

Mathematical processing

All data were processed statistically. In all cases, a standard error follows mean values. Averaged values were compared by use of Student's t statistics. The null hypothesis was rejected at $P_1 = 0.05$ significance level in all cases. However, in two figures (Figs. 5, 6), no standard error bars are presented because of the mode of averaging data, which combined samples obtained during four seasons. During sampling for one

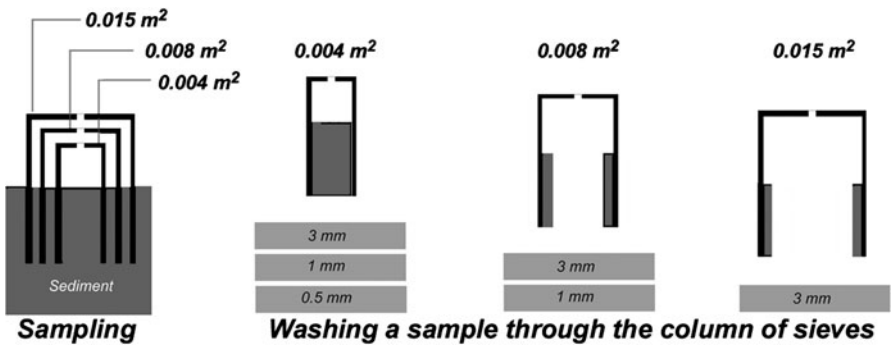

Fig. 4 Sampling and sample washing method. See text for explanations

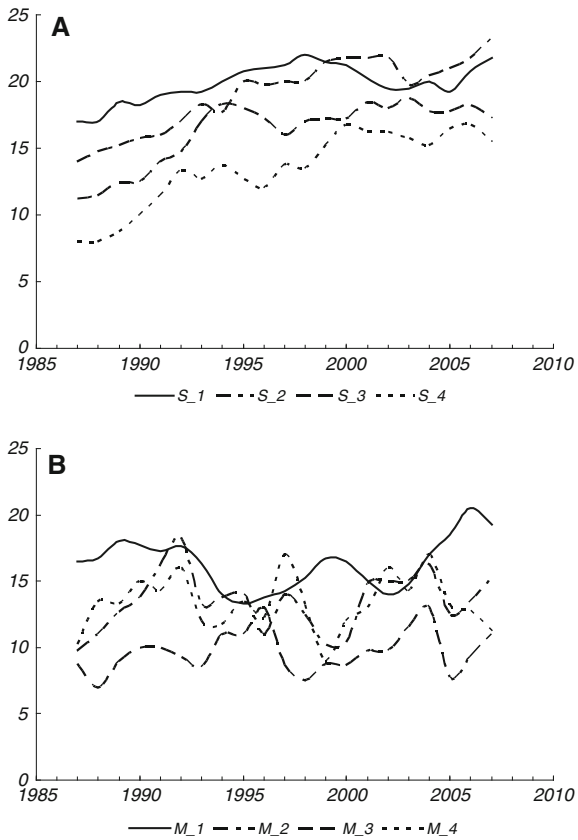

Fig. 5 Long-term dynamics of species number in Seldyanaya Bight (**A**) and in Medvezhya Bight (**B**). Averaged data for four seasons in each year. *X* axis, time (years); *Y* axis, number of species. In the legends, *letters* are abbreviations of the bights and *digits* are station numbers

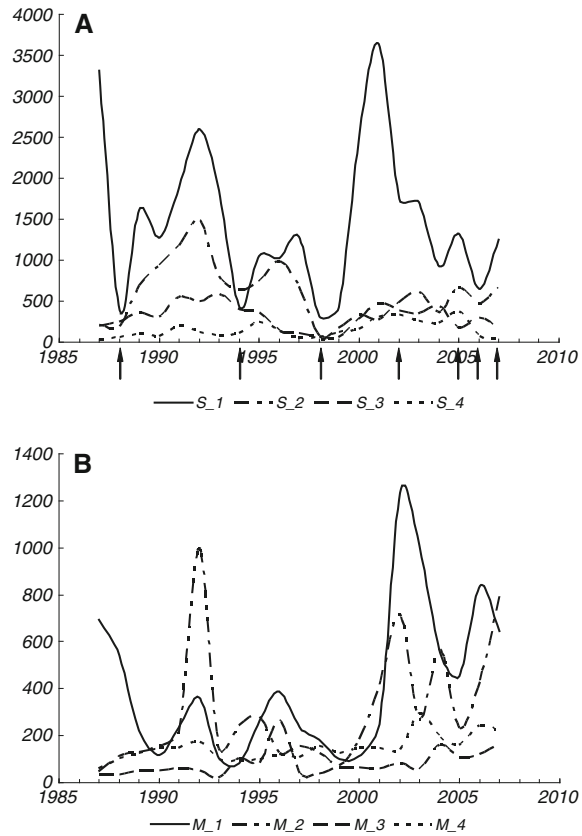

Fig. 6 Long-term dynamics of total biomass in Seldyanaya Bight (**A**) and in Medvezhya Bight (**B**). Averaged data for four seasons in every year. *X* axis, time (years); *Y* axis, total biomass (g/m^2). In the legends, *letters* are abbreviations of the two bights, *digits* are station numbers, and *arrows* denote the years when incorporation of sediment into ice occurred

season, variation is random, which makes it possible to compare different years by individual seasons using methods of linear statistics. When averaging four seasons, the variation is not random, depending on seasonal cyclical dynamics. Combining these two different types of variation does not enable calculation of a year's standard errors correctly, or between-years comparison.

Besides standard methods of linear statistics, the following mathematical treatments were used. Shannon's diversity index (Shannon, 1948), the proportion of species from different biogeographic origin, trophic groups, and life-forms (all in terms of biomass) were calculated to define intertidal communities. To find and generalize similar samples, community structure was described in terms of fractions of logarithmically transformed species biomasses; ln $(x + 1)$ was used for transformation. The Czekanowski–Sørensen index[1] (I_{CzS}) was used to assess the similarity between individual stations:

$$I_{\mathrm{CzS}} = \sum_{i=1}^{S} \mathrm{Min}(p_{i,j}, p_{i,k}),$$

where S is the number of species at two stations and p is the fraction (%) of logarithmically transformed biomass of the ith species at the jth and kth station (Pesenko, 1982).

The square similarity matrices obtained were rearranged by interchanging rows and columns to create Czekanowski's diagrams, where maximum resemblances lie along the main diagonal. Square submatrices of the similarity matrix lying on the main

[1] Recently, this index is often referred to as the Bray–Curtis similarity.

diagonal with an average value of Czekanowski's index of more than 50 and of size more than 5 × 5 were regarded as arrays of identical primary descriptions of community structure. Few remaining stations were rejected from the analysis. Hierarchical cluster analysis was not used for this purpose because of contradictory results from different clustering algorithms.

Primary descriptions included in the sections described above were averaged and the results were regarded as secondary descriptions (the generalized species lists for initial stations) of communities. Secondary descriptions were compared by using the same procedure as for individual stations, and the similarity matrix obtained was used for hierarchical cluster analysis by means of a weighted average linking algorithm.

Estimation of the stability of communities was based on the ideas of Denisenko (2006) who, while investigating *k*-dominance curves (*ABC*) analysis (Warwick, 1986; Warwick et al., 1987), noticed that the more uniform *k*-dominance curve lies on the plot above the less uniform curve. Under stable conditions, *K*-selection prevails in a biotope, which leads to relatively small number of large individuals for most species, and a *k*-dominance curve of biomass lies above a *k*-dominance curve of density. If a biotope is disturbed or a succession process is in progress, *r*-selection prevails. As a result, a relatively large number of small individuals in most species can be found in a community, and a *k*-dominance curve of biomass lies below a *k*-dominance curve of density (Denisenko, 2006). This enabled Denisenko to introduce a measure of community stability, which he called *a difference of evenness* calculated as:

$$D'_{\mathrm{E}} = \frac{H'_{\mathrm{B}} - H'_{\mathrm{N}}}{\log_2 S},$$

where (in my notation) D_{E} is a difference of the specific evenness, H'_{B} is Shannon's diversity index (Shannon, 1948) calculated in terms of biomass, H'_{N} is Shannon's diversity index calculated in terms of density, and S is the number of species in the community. Negative values of D_{E} correspond to the stable state of an undisturbed community. Positive values indicate a level of disturbance or a succession process and an intermediate state gives values close to zero (Denisenko, 2006).

Shannon's diversity index was introduced to compare messages passing through a noisy channel (Shannon, 1948), and is very useful for comparison of nucleotide sequences in genetic investigations, but its biological meaning in synecology is not so clear. For this reason, in this research, the statistical measure of evenness is preferable to the informational one. I have, therefore, used the index of oligomixness (Naumov, 1991) instead of Shannon's diversity index in Denisenko's formula.

The index of oligomixness is the ratio of the standard deviation of the analyzed series to its theoretical maximum. It can be calculated as:

$$I_{\mathrm{O}} = 100 \frac{\sigma_{\mathrm{A}}}{\sum_{i=1}^{S} A_i} \sqrt{S},$$

and its standard error as

$$m_{I_{\mathrm{O}}} = \frac{I_{\mathrm{O}}}{\sqrt{2S}},$$

where I_{O} is an index of oligomixness, A is an abundance value for a species in a community, and σ is the standard deviation in a series of these abundance values. Its definitional domain is $0 \leq I_{\mathrm{O}} \leq 100$. The first limit value indicates the absolute evenness and, therefore, the maximum possible diversity, which means that all species are of equal abundance. The highest limit value indicates the complete absence of evenness and the minimum possible diversity in cases when the entire abundance of a community is concentrated in a singe dominant species and other species have zero abundance. The index depends linearly upon community structure (Naumov, 1991) and can be used as a measure of dominance.

Therefore, the measure of stability of community used in this paper can be called *a difference of oligomixness* (D_{O}) and is calculated as:

$$D_{\mathrm{O}} = I_{\mathrm{OB}} - I_{\mathrm{ON}},$$

and its standard error as

$$m_{D_{\mathrm{O}}} = \sqrt{m_{\mathrm{OB}}^2 + m_{\mathrm{ON}}^2},$$

where indices B and N denote that I_{O} and its standard error are calculated in terms of biomass or density.

The definitional domain of this index is $-100 \leq D_{\mathrm{O}} \leq +100$. Stable state of a community is described by positive values of D_{O} in this analysis.

It is important that none of the methods mentioned take into account modular organisms, the density of which cannot be estimated correctly. Therefore, neither plant nor algae species nor colonial animals can be included into analysis. This limitation of such an approach, in common with *ABC* analysis, should be borne in mind.

Results

Approximately 100 taxa at species and genera level were found in the studied sites, and the species composition of communities in both bights was almost identical. Some rare taxa were only encountered a few times during the whole period of observation: 16 species in Seldyanaya Bight and 18 species in Medvezhya Bight. These species were excluded from subsequent analysis.

Despite broadly similar species lists, the distribution of most of the separate taxa differed noticeably in the studied bights. Only three species: *Hydrobia ulvae* (Pennant, 1777), *Macoma balthica* (Linnaeus, 1758), and *Tubificoides benedeni* (Udekem, 1855) were equally common at both sites. Their occurrence was in the range 75–95 and differences between the bights were not significant. Occurrence of all other species mentioned below differed in both sites at least at $P_2 = 0.01$.

Nine species, *Pygospio elegans* Claparède, 1863, *Littorina saxatilis* (Olivi, 1792), *Tubifex costatus* (Claparède, 1863), *Mya arenaria* Linnaeus, 1758, *Chironomus salinarius* (Kieffer, 1921), *Halocladius vitripennis* (Meigen, 1818), *Fabricia sabella* (Ehrenberg, 1836), *Cladophora sericea* (Hudson) Kützing 1843, and *Zostera marina* Linnaeus, 1753 (listed in descending order of occurrence from 79 to 49%), were common in the Seldyanaya Bight and were relatively rare in the Medvezhya Bight. Four other species, *Scoloplos armiger* (O.F. Müller, 1776), *Mytilus edulis* Linnaeus, 1758, *Capitella capitata* (Fabricius, 1780), and *Phyllodoce maculata* (Linnaeus, 1767) (in descending order from 91 to 51%) were typical of the Medvezhya Bight and were rare in the Seldyanaya Bight.

A similar pattern was observed for other species. Relatively sparse species in the Seldyanaya Bight (occurrence between 48 and 15%), for example *Limnodrilus* sp., *Eteone longa* (Fabricius, 1780), *Jaera albifrons* Leach, 1914, *Ruppia maritima* Linnaeus, 1753, *Halicryptus spinulosus* Siebold, 1849, *Alitta virens* (M. Sars, 1835), Dolichopodidae larvae, and *Polydora quadrilobata* Jacobi, 1883, did not usually exceed 10% occurrence in the Medvezhya Bight. Species whose occurrence in the Medvezhya Bight lay in the range 45–12%, for example *Monoculodes* sp., *Spio theeli* Søderstrøm, 1920, *Arenicola marina* (Linnaeus, 1758), *Clitellio arenarius* (O.F. Müller, 1776), and *Crangon crangon* (Linnaeus, 1758), were rare in the Seldyanaya Bight. Therefore, the general patterns of both intertidal communities were distinctly different, despite the presence of 26 rare species, whose occurrence in the studied bights did not differ significantly.

All the differences between species composition and occurrence of leading forms mentioned can be explained by the different wave exposure and the peculiar properties of bottom sediments.

The number of species decreased on average in both bights at the higher intertidal horizons (Table 3). This decease was significant in all cases, excluding the difference between the number of species at Stations 1 and 2 in the Seldyanaya Bight.

The same tendency was recorded for average biomass (Table 3). Differences between biomass at all stations was significant for both the Seldyanaya and the Medvezhya bights, except for differences between Stations 1 and 2 in the latter bight.

Table 3 Some general features of benthos in the studied bights (mean values ± standard error are presented)

Bight	Characteristic	Station number			
		1	2	3	4
Seldyanaya	Species number	19.86 ± 0.31	19.12 ± 0.59	16.23 ± 0.53	13.43 ± 0.62
	Biomass (g/m^2)	1486.81 ± 202.04	600.56 ± 77.22	308.96 ± 33.64	154.20 ± 22.53
Medvezhya	Species number	16.34 ± 0.42	13.48 ± 0.48	9.67 ± 0.35	13.36 ± 0.45
	Biomass (g/m^2)	410.76 ± 70.06	306.20 ± 56.51	82.16 ± 12.76	148.41 ± 11.86

There was a weak tendency for an increase in species number at all four stations in the Seldyanaya Bight over the entire sampling period (Fig. 5A). In the Medvezhya Bight, the number of species oscillated irregularly around the mean value (Fig. 5B).

Annual average total biomass fluctuated in the Seldyanaya Bight from 500 to 3500 g/m^2 at Station 1 (Fig. 6A). Minimum values were recorded in 1988, 1994, 1998, and 2006, which corresponded to the years when freezing of bottom sediment and abnormal ice melting occurred (for other details see "Discussion"). However, although similar ice conditions occurred in 2002 and 2005, significant biomass reduction in those years was not observed. The inter-annual average of total biomass was lower in the Medvezhya Bight (Fig. 6B). Biomass increased three times over the mean value in 2002 at Station 1, and in 1992 at Station 2. In the first case, this was caused by unusually high biomass of *Myt. edulis*, *H. ulvae*, *C. sericea*, and *Z. marina* in the summer and autumn; in the second case, it was caused by very high biomass of *Myt. edulis* during the whole year and *Fucus vesiculosus* in summer and autumn.

A similar community structure was found in most cases at each sampling station. This structure is referred to as *normal* in subsequent text. During other surveys, different community structure was encountered; this structure is referred to as *modified*.

Nine main types of community (four normal and five modified) were recorded in the Seldyanaya Bight, and six (four normal and two modified) in the Medvezhya Bight, using the methods described above. At each station, excluding Stations 3 and 4 in the Medvezhya Bight, at least two modifications of bottom assemblages were encountered in different years. In the text, tables, and figures below, normal types of assemblage are marked with the letter "*a*" whereas modified assemblages are marked with the letters "*b*" and "*c*".

Some general characteristics distinguishing the types of intertidal bottom community in the Seldyanaya Bight are given in Table 4, and the most abundant species are presented in Table 5. The same information on the Medvezhya Bight communities is given in Tables 6 and 7.

Discussion

Communities altered by the effect of abnormal ice melting in 1998, 2006, and 2007 in the Seldyanaya Bight changed in a similar way in almost all cases. The same modification were noticed in this bight in 1995, when abnormal ice events were not observed, and in the Medvezhya Bight in 1987, 1988, 1996, 1997, and 1998 despite moderate ice conditions during the whole time of sampling. In modified communities, the number of species, total biomass, and fraction of epibenthic forms (in terms of biomass) underwent a substantial reduction (Tables 4, 5, 6, 7). Autotrophic organisms gave way to deposit feeders, and boreal species to arctic-boreal ones. The fraction of vagile species increased substantially (Tables 4, 6).

All these changes were induced, first of all, by a dramatic drop in the abundance of leading species, mainly *Z. marina*, *H. ulvae*, and *M. arenaria*. Different oligochaetes, predominantly *T. benedeni,* became key forms in modified assemblages. Neither biomass, nor density of *Mac. balthica* changed significantly during the described modification of the studied communities (Tables 5, 7).

Hierarchical cluster analysis divided all secondary descriptions of communities' structure into two main clusters (Fig. 7), corresponding to assemblages in the Seldyanaya Bight and in the Medvezhya Bight, connected at a similarity level of 30.26%. Both clusters consisted of groups of communities from the lower and upper intertidal horizons. These groups were connected at a similarity level of 42.64% in the Seldyanaya Bight and 45.77% in the Medvezhya Bight. Different modifications of bottom assemblages described above closely resembled each other at every station except Stations 2 in both bights. Modifications marked with the letter "*a*" were included in a lower horizons cluster whereas those marked with the letter "*b*" were included in an upper one (Fig. 7).

This phenomenon indicates periodic shifting of the border between communities on the lower and upper horizons and relatively stable assemblages near the hydrographic datum and at higher intertidal levels. In the Seldyanaya Bight, such shifts sometimes followed abnormal conditions of ice melting (in 1998, 2006, and 2007) and once (in 1995) without it at Stations 1 and 2. However, no changes in community structure were found in other abnormal years (1988, 1994, 2002, and 2005). The border between lower and upper intertidal assemblages after 1998 remained shifted until 2001 inclusive.

In the Seldyanaya Bight, there was a change in the bottom community at Station 1, with a dramatic

Table 4 Main characteristics of communities in the Seldyanaya Bight in terms of biomass (mean values ± standard error are presented)

Characteristic	S_1a	S_1b	S_2a	S_2b	S_3a	S_3b	S_3c	S_4a	S_4b
Number of stations (samples)	70 (206)	9 (23)	74 (208)	8 (18)	64 (215)	8 (15)	6 (12)	36 (94)	23 (59)
Average similarity (%)	64.87 ± 0.17	58.03 ± 2.75	62.26 ± 0.20	57.68 ± 2.29	59.90 ± 0.20	57.55 ± 1.95	55.4 ± 2.60	58.06 ± 0.35	53.39 ± 061
Community features									
Total number of recorded species	64	26	54	23	69	18	31	44	34
Total biomass (g/m^2)	2107.975	278.252	654.899	216.379	399.611	116.012	105.721	221.490	129.408
Shannon's diversity (bit/g)	1.982	2.544	2.680	2.335	2.752	2.126	2.783	2.990	2.596
Biogeographic composition (%)									
Boreal	50.94 ± 6.20	48.83 ± 19.60	46.20 ± 6.42		17.33 ± 4.95	40.68 ± 18.67	29.75 ± 18.66	14.64 ± 5.67	21.80 ± 9.23
Atlantic-boreal	29.81 ± 5.47	19.59 ± 13.23	33.31 ± 5.48	20.41 ± 14.25	56.29 ± 6.20	58.10 ± 17.44	15.62 ± 14.82	34.21 ± 7.50	57.95 ± 11.04
Arctic-boreal	19.08 ± 4.70	31.01 ± 15.42	17.17 ± 4.38	45.11 ± 17.59	15.05 ± 4.47		27.74 ± 18.28	30.16 ± 7.26	8.95 ± 6.38
Unknown					11.32 ± 3.96			20.99 ± 6.44	
Trophic composition (%)									
Autotrophic	66.30 ± 5.65	49.71 ± 16.67	55.35 ± 5.78		27.91 ± 5.61		47.74 ± 20.39	48.43 ± 7.90	
Filter feeders			21.02 ± 4.74		42.58 ± 6.18	34.24 ± 16.78		9.46 ± 4.63	40.96 ± 11.00
Deposit feeders	29.78 ± 5.47	48.67 ± 16.66	21.19 ± 4.75	74.40 ± 15.43	27.89 ± 5.61	63.02 ± 17.07	48.30 ± 20.40	39.16 ± 7.72	40.82 ± 10.99
Ecological forms (%)									
Epibenthic	95.90 ± 2.37	69.31 ± 15.37	68.93 ± 5.38		42.12 ± 6.17	24.27 ± 15.16	63.25 ± 19.68	73.89 ± 6.94	30.41 ± 10.29
Infaunal				71.05 ± 16.03					
Vagile	31.53 ± 5.55	50.04 ± 16.67	43.44 ± 5.76	83.88 ± 13.00	71.75 ± 5.63	99.66 ± 2.06	51.95 ± 20.40	51.42 ± 7.90	86.70 ± 7.59

Only values different from zero at $P < 0.05$ are displayed. The letter "S" is an abbreviation for Seldyanaya Bight; digits indicate communities at the corresponding station numbers; letters "a", "b", and "c" indicate their modifications

Table 5 Leading species in distinguished communities from the Seldyanaya Bight (mean values ± standard error are presented)

Community/number of stations (samples)	Species	Biomass (g/m^2)	Density (ind./m^2)	Occurrence
S_1a/70 (206)	*Z. marina*	1032.200 ± 183.323		98.57 ± 1.42
	H. ulvae	545.305 ± 373.049	53326.64 ± 9808.69	100.00 ± 0.00
	C. sericea	361.861 ± 64.464		92.86 ± 3.08
	Myt. edulis	45.713 ± 16.424	778.41 ± 242.31	80.00 ± 4.78
	Mac. balthica	40.690 ± 7.086	892.63 ± 173.81	100.00 ± 0.00
S_1b/9 (23)	*Z. marina*	97.899 ± 92.903		44.44 ± 16.56
	H. ulvae	50.180 ± 26.567	11566.11 ± 5479.00	100.00 ± 0.00
	C. sericea	40.424 ± 29.751		55.56 ± 16.56
	Mac. balthica	37.654 ± 15.225	808.00 ± 413.82	100.00 ± 0.00
	T. benedeni	35.673 ± 17.903	22057.56 ± 9429.90	100.00 ± 0.00
S_2a/74 (208)	*Z. marina*	254.140 ± 48.952		74.32 ± 5.08
	M. arenaria	129.560 ± 29.230	1057.00 ± 277.38	95.95 ± 2.29
	C. sericea	87.827 ± 21.921		66.22 ± 5.50
	H. ulvae	68.869 ± 9.755	18271.70 ± 2736.80	100.00 ± 0.00
	Mac. balthica	43.506 ± 7.048	1114.01 ± 219.07	98.65 ± 1.34
S_2b/8 (18)	*T. benedeni*	93.890 ± 93.676	6387.25 ± 4472.36	100.00 ± 0.00
	Mac. balthica	34.790 ± 20.730	546.50 ± 291.11	100.00 ± 0.00
	H. ulvae	27.457 ± 16.318	7430.50 ± 4428.20	100.00 ± 0.00
	M. arenaria	16.458 ± 10.108	1898.50 ± 1570.57	62.50 ± 17.12
	Ch. salinarius	0.837 ± 0.407	633.13 ± 375.68	100.00 ± 0.00
S_3a/64 (215)	*M. arenaria*	168.723 ± 38.054	315.75 ± 86.42	95.31 ± 2.64
	H. ulvae	52.321 ± 9.563	10821.09 ± 1936.77	100.00 ± 0.00
	R. maritima	43.128 ± 12.081		39.06 ± 6.10
	Mac. balthica	40.029 ± 5.995	340.14 ± 84.84	100.00 ± 0.00
S_3b/8 (15)	*H. ulvae*	24.721 ± 20.295	4874.13 ± 4302.47	87.50 ± 11.69
	T. benedeni	2.818 ± 1.624	2024.75 ± 1089.40	87.50 ± 11.69
	Ch. salinarius	2.528 ± 2.039	1006.25 ± 735.12	75.00 ± 15.31
	Tub. costatus	0.898 ± 0.471	1379.88 ± 663.67	87.50 ± 11.69
	P. elegans	0.298 ± 0.154	467.25 ± 227.67	75.00 ± 15.31
S_3c/6 (12)	*Mac. balthica*	28.649 ± 15.784	593.83 ± 333.31	100.00 ± 0.00
	R. maritima	24.824 ± 24.193		50.00 ± 20.41
	C. sericea	22.316 ± 13.382		83.33 ± 15.21
	H. ulvae	14.899 ± 7.623	6809.50 ± 4881.73	83.33 ± 15.21
S_4a/36 (94)	*C. sericea*	52.869 ± 15.675		82.50 ± 6.01
	H. ulvae	51.229 ± 11.193	10406.40 ± 2195.79	100.00 ± 0.00
	R. maritima	43.994 ± 15.530		62.50 ± 7.65
	Ch. salinarius	5.094 ± 1.303	3698.20 ± 911.33	92.50 ± 4.16
	Sal. pojarkovi	3.113 ± 1.786		20.00 ± 6.32
S_4b/23 (59)	*H. ulvae*	21.158 ± 6.389	4146.30 ± 1266.34	100.00 ± 0.00
	Ch. salinarius	4.679 ± 1.879	3153.15 ± 1342.53	85.00 ± 7.98
	Tub. costatus	1.761 ± 0.795	3011.70 ± 1281.89	100.00 ± 0.00
	Limnodrillus sp.	0.314 ± 0.263	800.25 ± 666.85	40.00 ± 10.95
	P. elegans	0.225 ± 0.082	480.50 ± 231.47	70.00 ± 10.25

The five most abundant species are displayed for each community. The letter "S" is an abbreviation for Seldyanaya Bight; digits indicate communities at the corresponding station numbers; letters "a", "b", and "c" indicate their modifications

Table 6 Main characteristics of communities in the Medvezhya Bight in terms of biomass (mean values ± standard error are presented)

Characteristic	M_1a	M_1b	M_2a	M_2b	S_3	S_4
Number of stations (samples)	65 (178)	12 (32)	67 (178)	8 (17)	64 (172)	76 (166)
Average similarity (% ± standard error)	61.96 ± 0.20	54.76 ± 1.04	60.60 ± 0.19	59.73 ± 1.57	60.27 ± 0.21	62.05 ± 0.17
Community features						
Total number of recorded species	63	34	50	21	35	48
Total biomass (g/m^2)	435.800	110.445	302.003	50.862	76.372	139.774
Shannon's diversity (bit/g)	2.382	2.543	2.446	2.484	2.663	2.712
Biogeographic composition (%)						
Boreal	47.69 ± 6.43	53.26 ± 17.38	20.81 ± 5.17	30.08 ± 16.21	23.56 ± 5.35	21.79 ± 4.76
Atlantic-boreal	35.39 ± 5.93	33.54 ± 13.63	66.08 ± 5.78	29.37 ± 16.1	58.45 ± 6.21	57.54 ± 5.67
Arctic-boreal	16.12 ± 4.56		12.7 ± 4.07	39.19 ± 17.26	17.19 ± 4.75	19.5 ± 4.54
Trophic composition (%)						
Autotrophic	56.41 ± 6.15	39.00 ± 14.08	25.69 ± 5.34			
Filter feeders	22.97 ± 5.22		53.29 ± 6.10	10.33 ± 10.76	27.67 ± 5.64	16.91 ± 4.30
Deposit feeders	18.69 ± 4.84	53.64 ± 14.40	20.12 ± 4.90	87.78 ± 11.58	69.07 ± 5.82	77.56 ± 4.79
Ecological forms (%)						
Epibenthic	91.81 ± 3.40	70.89 ± 13.11	86.39 ± 4.19		57.39 ± 6.23	56.61 ± 5.69
Infaunal				69.32 ± 16.30	42.48 ± 6.23	43.21 ± 5.68
Vagile	21.07 ± 5.06	60.73 ± 14.10	23.03 ± 5.14	89.49 ± 10.84	73.87 ± 5.54	84.09 ± 4.20

Only values different from zero at $P < 0.05$ are displayed. The letter "M" is an abbreviation for Medvezhya Bight; digits indicate communities at the corresponding station numbers; letters "a" and b" indicate their modifications

decrease in the number of species, and in the abundance of *Z. marina*, *H. ulvae*, and *C. sericea*. This was accompanied by an increase in *T. benedeni*. Strong changes in biogeographic and trophic composition and in the percentage of different ecological forms and their occurrence were observed (Tables 4, 5). Almost complete replacement of dominant species was recorded at Station 2 after freezing of the sediment (Table 5). Formation of an alternative community started in winter or in spring in all cases. At Station 1 recovery of community structure occurred during the time between consecutive surveys, taking from 2 to 4 months in all cases, whereas at Station 2, after abnormal ice conditions in 1998, the normal sea-floor assemblage was restored only after 4 years, in 2002. Total biomass often remained at a low level for one or two years after the event.

Periodic changes of community structure at Stations 3 and 4 in the Seldyanaya Bight were usually not connected with abnormal ice conditions, with the exception of 1998. Neither abnormal freezing of the sediment, nor changes of community structure in the upper intertidal horizons in the Medvezhya Bight were observed.

The years when abnormal ice melting occurred did not fit oscillations of temperature in adjacent waters, or Arctic Oscillations (for the corresponding data see: Naumov, 2007; Naumov et al., 2009).

Two modifications of the intertidal communities were distinguished at the lower horizons in the Medvezhya Bight. The reason of disturbance is not known for this site. It may be abnormal wave action, or sporadic increasing of fresh run-off, or something else. Nevertheless, the changes in community structure closely resembled those in the Seldyanaya Bight in all cases (Tables 6, 7). Restoration of normal community structure took approximately 4 months in 1988, 1994, 1996, 1997, 2005, and 2008. In almost all cases, shifts from one modification to another were not synchronized with modifications of communities in the Seldyanaya Bight induced by abnormal ice conditions. The exception was simultaneous recovery of

Table 7 Leading species in distinguished communities from the Medvezhya Bight (mean values ± standard error are presented)

Community/number of stations (samples)	Species	Biomass (g/m^2)	Density (ind./m^2)	Occurrence
M_1a/65 (178)	*Z. marina*	198.448 ± 41.891		72.31 ± 5.55
	Myt. edulis	98.152 ± 24.789	1962.31 ± 480.74	89.23 ± 3.84
	H. ulvae	47.908 ± 9.900	20477.62 ± 4170.37	90.77 ± 3.59
	C. sericea	45.547 ± 17.889		64.62 ± 5.93
	Mac. balthica	8.382 ± 1.525	369.97 ± 65.74	90.77 ± 3.59
M_1b/12 (32)	*Z. marina*	42.453 ± 29.883		33.33 ± 13.61
	H. ulvae	30.411 ± 11.229	12221.17 ± 4419.22	100.00 ± 0.00
	Mac. balthica	14.474 ± 4.872	1096.00 ± 429.14	100.00 ± 0.00
	S. armiger	6.724 ± 2.581	491.83 ± 280.33	100.00 ± 0.00
	T. benedeni	4.062 ± 2.314	3150.42 ± 1876.03	91.67 ± 7.98
M_2a/67 (178)	*Myt. edulis*	154.865 ± 32.233	1160.22 ± 404.50	94.03 ± 2.89
	Z. marina	49.917 ± 16.123		32.84 ± 5.74
	H. ulvae	26.010 ± 4.100	11666.72 ± 1940.11	97.01 ± 2.08
	C. sericea	14.799 ± 3.935		65.67 ± 5.80
	Mac. balthica	12.147 ± 2.001	321.76 ± 55.54	98.51 ± 1.48
M_2b/8 (17)	*Mac. balthica*	14.802 ± 8.401	462.75 ± 320.69	100.00 ± 0.00
	H. ulvae	9.663 ± 4.262	4167.25 ± 2179.96	100.00 ± 0.00
	S. armiger	8.092 ± 3.605	281.25 ± 113.24	100.00 ± 0.00
	P. elegans	0.386 ± 0.236	721.75 ± 506.77	100.00 ± 0.00
	A. marina	11.413 ± 9.418	25.88 ± 17.87	62.50 ± 17.12
M_3/64 (172)	*H. ulvae*	21.923 ± 3.858	11021.09 ± 1932.43	96.92 ± 2.14
	Mac. balthica	16.732 ± 2.703	506.08 ± 107.25	96.92 ± 2.14
	Sp. theeli	0.969 ± 0.275	1638.97 ± 587.71	53.85 ± 6.18
	Myt. edulis	17.315 ± 6.792	113.63 ± 48.29	49.23 ± 6.20
	M. arenaria	6.507 ± 4.324	110.69 ± 32.83	44.62 ± 6.17
M_4/76 (166)	*H. ulvae*	56.003 ± 7.631	26271.57 ± 4009.53	97.37 ± 1.84
	Mac. balthica	28.742 ± 4.270	662.00 ± 141.69	97.37 ± 1.84
	S. armiger	7.912 ± 1.299	387.96 ± 60.63	96.05 ± 2.23
	C. sericea	5.164 ± 1.855		48.68 ± 5.73
	T. benedeni	3.723 ± 0.749	3453.83 ± 666.63	97.37 ± 1.84

The five most abundant species are displayed for each community. The letter "M" is an abbreviation for Medvezhya Bight; digits indicate communities at the corresponding station numbers; letters "a" and b" indicate their modifications

community structure in 1998 in both bights, except at the upper horizons in the Medvezhya Bight. All assemblages returned to a normal state only in 2002.

The reasons for such strong synchronous changes are not known. All attempts to find any common abiotic effect failed, and it is difficult to build a biotic model explaining concurrent processes in remote and different communities. Probably, it was just an accidental coincidence.

Despite the changes described, in almost all cases differences between oligomixness indices were not indicative of strong decreases of the stability of modified communities. Normally, they were merely indicative of random and statistically not significant oscillations around the zero level during the whole period of observations. The only exception was noticed at sampling Station 1 in the Seldyanaya Bight, where a very weak succession process in 1998–2003 indicated by lower values of D_O could be supposed. Although the decrease of D_O was not statistically significant in this case also, it was marked by six consecutive values lying on a smooth curve (Fig. 8).

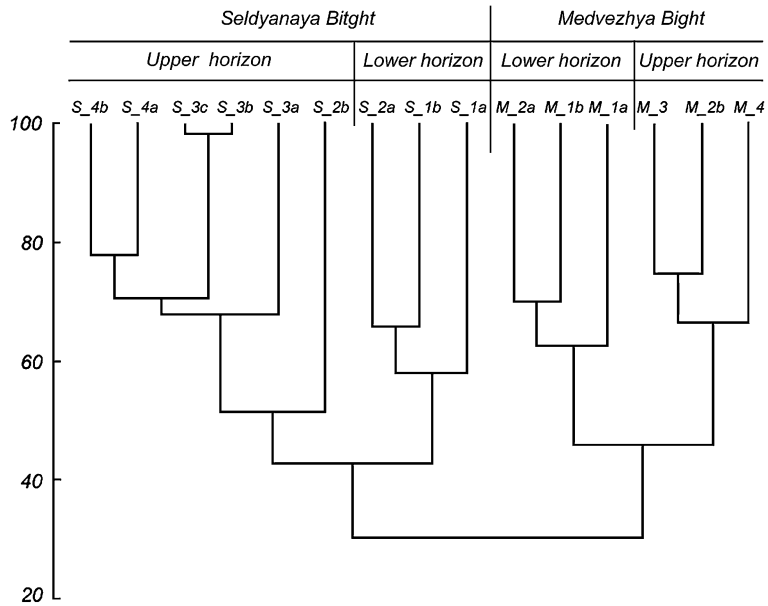

Fig. 7 Cladogram of similarity of distinguished communities. *Y* axis, Czekanowski–Sørensen index. In the legend, the letters *S* and *M* are abbreviations of the bights; *digits* indicate communities at the corresponding station numbers; letters *a*, *b*, and *c* indicate their modifications

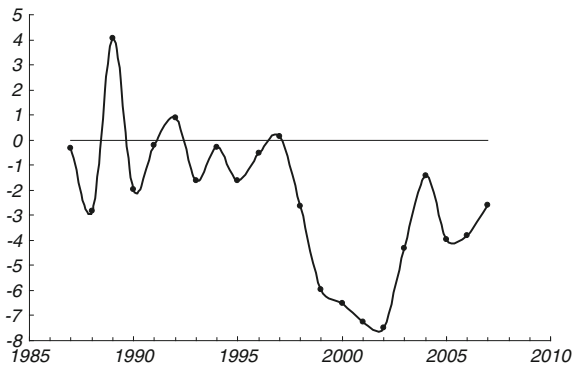

Fig. 8 Long-term changes of difference of oligomixness (D_O) at Station 1 in the Seldyanaya Bight. The *horizontal line* marks the zero level, the *X* axis is time (years), and the *Y* axis is difference of oligomixness (%)

Weak and not periodical fluctuations of the index suggest that investigated disturbance events resulted in modification of communities, but not in their replacement.

Conclusions

Analysis of data from a long-term monitoring survey in two small bights revealed a relatively stable community structure at each of the eight intertidal sampling stations. Disturbance caused by incorporation of the bottom sediment into the ice cover was recorded only three times in the Seldyanaya Bight. The effect of ice cover led to significant changes in community structure and species composition. Nevertheless, in most cases a comparatively short time was needed for intertidal assemblages to return to a stable state.

There was no visible effect of ice cover on intertidal communities in the Medvezhya Bight. However, periodic changes in structure and species composition, resembling those in the Seldyanaya Bight, were observed.

In most cases, communities at the lower and upper horizons remained more stable than those at the intermediate level. This led to a shifting of the biological border between lower and upper intertidal assemblages during disturbances in both bights.

Different kinds of disturbance may result in similar response of intertidal communities.

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