

ORIGINAL ARTICLE

Biomass, commonly occurring and dominant species of macrobenthos in Onega Bay (White Sea, Russia): data from three different decades

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Abstract

Onega Bay is the largest bay in the White Sea, characterised by shallow depth, a range of sediment types and strong tidal currents. All these factors provide conditions for high species richness and biomass. This study reviews data from three surveys of sublittoral macrobenthos undertaken by Russian institutes: the benthic survey covering the entire Onega Bay in 1952; the survey performed in the northern part of the area in 1981/90, and a study carried out in 2006 in the eastern part of the bay. In total, data from 107 stations were analysed. The data in different surveys were collected by different grab types. The datasets of both 1981/90 and 2006 overlap the 1952 survey area. The pattern of biomass distribution was consistent between the years of survey and was characterised by the low biomass at the northern periphery of the bay and the highest biomass observed in the coastal waters of the Solovetsky Islands. Bivalves and cirripeds (mostly *Modiolus modiolus*, *Arctica islandica*, *Balanus balanus* and *Verucca stroemia*) dominated in biomass. Neither the biomass share of dominant species nor the frequency of occurrence of several common species in these groups changed markedly between 1952 and 1981/90. Although the results of the 2006 survey appear somewhat different from the patterns of previous years, this does not indicate major changes in the benthic communities, because the survey in 2006 was designed in a different way and its overlap with the 1952 survey was minimal. However, the dominant species (by biomass) – *A. islandica*, *M. modiolus* and *V. stroemia* – held their leading positions. Results of the multidimensional scaling analysis based on the biomass data for all taxa encountered in the 1952 survey indicate considerable mixing of the samples from all surveys. This may be interpreted as the absence of major shifts in the sublittoral communities of the macrobenthos of Onega Bay at decadal scale. This kind of stability may be explained by an oceanographical regime resilient to climate variation and a relatively low anthropogenic environmental impact when compared to other shallow European seas.

Introduction

Studies conducted in most European seas have shown that the composition of macrobenthic communities,

species frequency of occurrence, population density and biomass often show considerable changes over time. Sometimes sudden inter-annual changes are detected, but changes are more likely across decades. Drastic shifts in

species composition and structure of communities detected in the Black Sea were found to be due to eutrophication, fishing and the introduction of alien species (Chikina & Kucheruk 2005). Reduced biomass and number of species was found in the Kattegat and Skagerrak due to direct effects of trawling, long-term temperature fluctuations and eutrophication of the area (Pearson *et al.* 1985; Rosenberg *et al.* 1987). Considerable changes in benthic communities were detected in the North Sea and the Irish Sea due to eutrophication, bottom trawling, dredging, oil drilling operations and climate variation (Frid *et al.* 1999, 2009; Bradshaw *et al.* 2002; Wieking & Krönke 2003; Krönke *et al.* 2004). In the Barents Sea, changes were associated with bottom trawling pressure and climate variation (Galkin 1998; Brown *et al.* 2005; Denisenko 2008; Carroll *et al.* 2008). These studies indicate the role of anthropogenic effects on the composition of macrobenthic communities.

In the White Sea, the 'youngest' sea of Europe (existing only since the beginning of the Holocene), belonging to both the Northeast Atlantic and Arctic realms and characterised by a very peculiar oceanographical regime (Berger & Naumov 2001; Filatov *et al.* 2005a,b), there has been no attempt to analyse historical datasets on subtidal benthic communities. The emphasis of previous studies has been on identifying spatial patterns (Derjugin 1928; Kudersky 1966; Beklemishev *et al.* 1980; Golikov *et al.* 1985; Lukanin *et al.* 1995; Berger & Naumov 2001); long-term temporal trends in benthic communities have received relatively little attention. Nevertheless, there has been a long tradition of benthic research associated with marine

biological stations (Kudersky 1966; Fokin *et al.* 2006; Naumov 2006). The main objective of the present study was to analyse data from three different decades with regard to the composition, occurrence and biomass of dominant and common macrobenthic species and discuss if any temporal pattern is revealed by these historical datasets.

Study area

Onega Bay is the largest bay in the White Sea, with an area of 12,800 km². The depth of the bay is generally <50 m, with the exception of northern parts, where depths can reach 87 m. The bottom relief is uneven, especially along the coastline. Particularly complex bathymetry is observed along the bay's western coast, where numerous islands are concentrated. A broad range of sediment types characterises Onega Bay, but coarse and hard sediments with a small percentage of silt are the dominant substrata (Berger & Naumov 2001). Onega Bay is connected to the central part of the sea by the Western and the Eastern Solovetsky Salma, or strait (Fig. 1). Deep waters of the Salmas enable large volumes of water to enter the bay, generating strong tidal currents exacerbated by the shallow depths in the Bay. The maximum speed of a spring tide is 1.5–2.0 m s⁻¹ in the Eastern Salma, and 1.5–1.7 m s⁻¹ in the Western Salma (Babkov 1998; Filatov *et al.* 2005a). Strong tidal currents increase the turbidity of the water, leading to vertical homothermy and homohalinity in many parts of the bay. A developed thermocline is largely absent in most areas of the Northern and

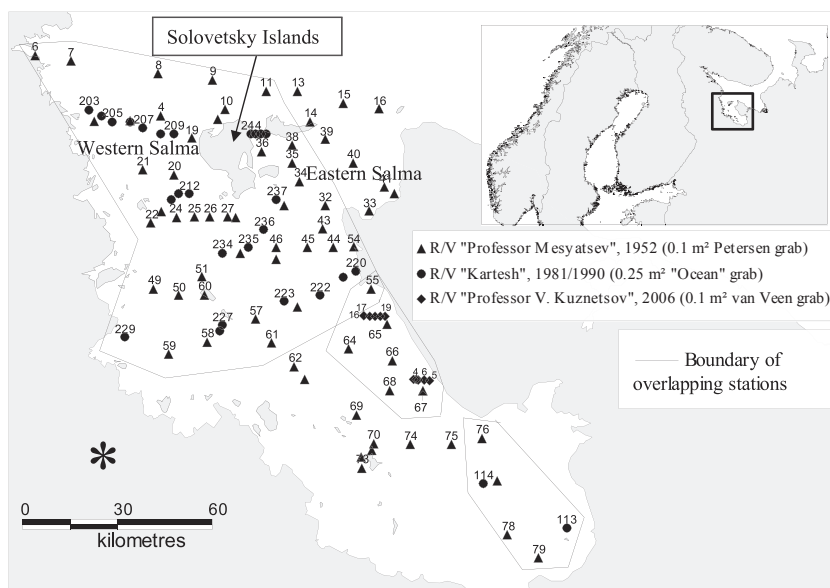


Fig. 1. Location of benthic sampling stations of surveys of Onega Bay in 1952, 1981/90 and 2006 showing overlapping station boundaries.

Central Onega Bay (personal observations in July 2006 and June 2010). Onega Bay is the most species-rich area of the entire White Sea, with around 500 species of invertebrates and a high benthic biomass (Golikov *et al.* 1985; Lukanin *et al.* 1995). The area may be regarded as being exposed to lower anthropogenic impacts than many other Northeast Atlantic seas, as the industrial activity in the area has never been particularly high and has decreased recently (Terzhevik *et al.* 2005).

Methods

This study is based on the data from three benthic surveys conducted respectively in 1952, 1981/90 and 2006 (Fig. 1, Table 1). The data in the different surveys were collected using a Petersen (0.1 m²), a Petersen Ocean-50 (0.25 m²) and a Van Veen (0.1 m²) grab. Table 1 shows the dates of the surveys, vessels, number of stations, samples at a station, depth of sampling, and on-deck processing protocol.

The 1952 survey data pooled with other material collected in Onega Bay were described by Ivanova (1957) and Kudersky (1966), but our re-analysis of these data is based on the original protocols of sample examination. The 1952 survey was processed incompletely: Mollusca, Cirripedia, Brachiopoda, Echinodermata and other taxa were identified to species level by S. S. Ivanova and L. A. Kudersky. Other groups were recorded as higher taxa and the total abundance and biomass of Porifera, Hydrozoa, Polychaeta, Pantopoda, Bryozoa, Tunicata and several orders of Crustacea, *i.e.* Amphipoda, Cumacea and Mysidacea, were calculated. The original station data and the protocols for processing the benthic collections by the

White Sea Biological Station of the Karelian–Finnish Branch of the Academy of Sciences of USSR (WSBS KFB) are deposited in the Archive of the Karelian Science Centre of the Russian Academy of Sciences (KSC RAS) in Petrozavodsk (Anonymous 1952a,b). They were digitised in Microsoft EXCEL format suitable for further use in electronic databases. Material on Porifera, Hydrozoa, Polychaeta, Pantopoda and Bryozoa from this survey was transferred to the Zoological Institute of the then Academy of Sciences of USSR (now Russian Academy of Sciences) in Leningrad, now St. Petersburg (ZIN RAN) (Ivanova 1957). The fate of the material on other groups remains unknown.

Material from the 1981/90 surveys was identified mostly to species level, with the exception of Nemertini, Oligochaeta and some families of Porifera, Hydrozoa and Bryozoa, which were identified by A. D. Naumov, V. V. Fedyakov and V. V. Lukanin in consultation with specialists at ZISP on some faunal groups. The data are maintained in the information system 'Benthos of the White Sea' implemented in CLIPPER 5.0 algorithmic language (Naumov 2006).

Benthic collections from the 2006 survey were processed with methods and taxonomic resolution similar to the one used in 1981/90. Most of the identification was done by A. Rogacheva and K. Solyanko in consultation with other specialists. The material is stored in the Zoological Museum of the Moscow University. Due to the unclear status of the taxon usually identified as *Hiattella arctica* (L., 1867), namely, the possible presence of another, yet unidentified species of the genus (Naumov 2006), the bivalve was listed as *Hiattella* sp. for all surveys.

Table 1. Basic data for surveys in Onega Bay used in the study.

Characteristics	Survey			Notes
	KFB	ZIN RAS	IO RAS	
Dates	10 August – 10 September 1952	26 September 1981 – 2 September 1981; 2 July 1990	15 July – 17 July 2006	Stations 113 and 114 were sampled in 1990
Vessel	<i>Professor Mesyatsev</i>	<i>Kartesh</i>	<i>Professor Vladimir Kuznetsov</i>	
Gear	Petersen grab – 0.1-m ² sampling area	Petersen grab Ocean 50 – 0.25-m ² sampling area	van Veen grab – 0.1-m ² sampling area	
No. of stations	70	28	10	
No. of casts per station	2	1	3–5	
Total no. of grab samples	134	27	38	
Finest mesh size in process of rinsing samples, mm	0.75	1	1	
Depth range, m	7–53	5–70	6–36	
Mean depth, m	26	24	19	

KFB = Karelian–Finnish Branch of the Academy of Sciences of USSR; ZIN RAS = Zoological Institute of the Russian Academy of Sciences, St. Petersburg; IO RAS = Institute of Oceanology of the Russian Academy of Sciences.

To test for differences between surveys in the biomass of 11 biomass-predominant and common bivalve species in 1952 and 2006, univariate techniques were applied such as ANOVA, the Mann–Whitney *U*-test, median test and Kolmogorov–Smirnov test (Hammer *et al.* 2001). Species composition and biomass data for these areas were compared using multivariate techniques (Clarke & Warwick 2001). The one-way ANOSIM test (PRIMER v6) was used to determine the differences in species composition and biomass between the studied years (overlapping stations), using 17 species of bivalves and seven species of echinoderms. Only species from the 1952 (mean values) and the 1981/90 surveys were compared. ANOSIM is analogous to analysis of variance (ANOVA) in univariate statistics. The 1952 data were not compared to the 2006 data because of the small number of overlapping stations. In the ANOSIM procedure, the probability of *a priori* groupings of samples was estimated by repeated permutations of data (*i.e.* repeated random relabelling of samples in the matrix). Initially, a global *R* statistic was calculated to determine whether significant differences exist between all groups (analogous to the global *F* test in ANOVA). If differences were significant at a global level, then pairwise comparisons between sample groups were conducted to test for differences between pairs. In global tests, the null hypothesis (*i.e.* ‘no difference between groups’) was rejected at a significance level of $P < 0.05$.

Possible changes in the community structure in terms of abundance and biomass were measured by the ABC (abundance/biomass comparison, statistics *W*) curves method. This method was applied only for stations where the biomass and abundance had been recorded adequately. The abundance–biomass comparison (ABC) curves were conducted using the PRIMER v.6.0 software package.

Non-metric multidimensional scaling (nMDS) based on Bray–Curtis similarity was carried out using logarithm-transformed biomass data (all replicates included). The data of different years were pooled into one dataset. The list of taxa contained species from the 1952 survey: 20 species of bivalves were included (other species of bivalves appearing in later surveys were pooled into group ‘Other bivalves’), 13 species of gastropods (plus ‘Other gastropods’ group), seven species of echinoderms (plus ‘Other echinoderms’ group), three species of cirripeds and one species of brachiopod. The rest of the taxa were entered as higher taxonomic groups (Porifera, Cnidaria, Polychaeta, Amphipoda, Cumacea, Decapoda, Pantopoda, Bryozoa and Ascidiacea). Although the list of taxa did not include information about all species, the taxa identified to species level were the most important in terms of biomass.

Results

Biomass and abundance of macrobenthos

Biomass distribution in the Northern Onega Bay showed a consistent pattern in 1952 and 1981/90 (Fig. 2). This consistency was also found in the eastern part of the bay when the 1952 and 2006 data were compared. In the northern periphery of the bay, and generally in the Western and the Eastern Salma, the biomass was relatively low and this zone of low biomass extended to the coastal areas in the northwestern part (Fig. 2). The lowest biomass ($5.5 \text{ g} \cdot \text{m}^{-2}$) was recorded at Station 4 near River Zolotitsa in 1952. In the coastal zone of the Solovetsky Islands, biomass varied greatly; however, most stations with biomass exceeding $1000 \text{ g} \cdot \text{m}^{-2}$ were concentrated in this area. The highest biomass recorded was $9200 \text{ g} \cdot \text{m}^{-2}$ at Station 237 in 1981/90 south of Bolshoi Solovetsky Island. In the central part of Onega Bay and off the Onega Peninsula coast the biomass was generally lower than around the islands (in most cases $< 500 \text{ g} \cdot \text{m}^{-2}$) but greater than in the north of the bay (Fig. 2). In general, the macrobenthic biomass in Onega Bay can be considered significant: it exceeded $100 \text{ g} \cdot \text{m}^{-2}$ at more than 60% of all stations.

Among large taxonomic groups, bivalves made a major contribution to total benthic biomass, constituting at least 40% of the biomass of each survey (Fig. 2). Horse mussel *Modiolus modiolus* and quahog *Arctica islandica* together with barnacles *Balanus crenatus* and *Verruca stroemia* constituted the greatest biomass within all surveys. Cirripeds were the next most important contributors to the total benthic biomass (above 20%) in 1952 and 1981/90, followed by polychaetes. However, this was not the case in

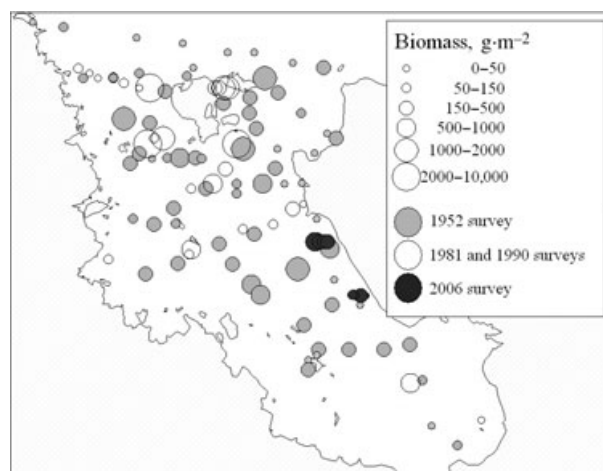


Fig. 2. Distribution of macrozoobenthos biomass ($\text{g} \cdot \text{m}^{-2}$) in Onega Bay in the years 1952, 1981/90 and 2006.

the Southeastern Onega Bay in 2006, where the positions of these two groups were reversed (Fig. 3). Sponges, hydroids, brachiopods, bryozoans and echinoderms contributed to similar fractions of the total macrobenthic biomass (averaging 3–9%) in 1952 and 1981/90 (Fig. 3).

Median biomass values in the surveys were in the range 114–151 g·m⁻² and rather similar (Table 2). However, comparison of biomass values (using a non-parametric Mann–Whitney *U*-test) showed statistically significant differences between all stations in 1952 and in 1981/90 ($P < 0.05$) and between the 1981/90 and the 2006 stations ($P < 0.01$). This was due to some exceptionally high values (>2000 g·m⁻²) in 1981/90 (several stations around the Solovetsky Islands). No statistically significant differences in biomass were found between the 1952 and 2006 data (Table 2). No significant difference was detected between the 1952 stations and the overlapping 1981/90 stations.

Benthic abundance varied considerably between surveys from 10 to 43,604 ind·m⁻² (Table 2). Abundance in 1981/90 was notably higher (mean of 5182 ind·m⁻²) compared to the 1952 survey (mean of 2029 ind·m⁻²) and 2006 survey (mean of 2407 ind·m⁻²). The biomass/abundances ratio (B/A), or a mean mass of a specimen, was remarkably similar (Table 2) and was not significantly different between the 1952 and the 1981/90 surveys. The B/A ratio of the 2006 survey was lower than in the other two surveys (Mann–Whitney *U*-test, $P < 0.01$ for the 1952 and 2006 comparison and $P < 0.05$ for the 1981/90 and 2006 comparison). However, there was no significant difference in the B/A values for the 1952 stations overlapping with the 2006 survey (Table 2). In terms of abundance–biomass comparison (ABC curves)

there was no significant difference between the 1952 survey (taking all stations or overlapped stations) and 1981/90 surveys.

Frequency of occurrence and biomass of particular taxa

Most of the bivalve species which were listed as dominant and subdominant in benthic communities of Onega Bay in 1952 (Ivanova 1957; Kudersky 1966) and the 1980s (Golikov *et al.* 1985; Lukanin *et al.* 1995; Naumov 2001) occurred with similar frequency in 1952 and 1981/90 (Table 3). Furthermore, *Heteranomia* spp., *Nicania montagui*, *Nuculana* sp., *Modiolus modiolus* and *Mytilus edulis* showed nearly the same values. Only *Leionucula bellotii*, *Clinocardium ciliatum*, *Macoma calcaria* occurred 1.6–2.1 times more frequently in 1981/90 compared to 1952, whereas *Thyasira gouldi* was about five times more common in this year (Table 3). Correlation between frequencies of occurrence of the bivalve species listed in Table 3 (without *T. gouldi*, which was the most dissimilar in this respect) in the 1952 and the 1981/90 surveys was high and statistically significant ($r = 0.73$, $P < 0.005$, $n = 13$).

In the 2006 survey area some of the bivalve species were found at a higher frequency than at the overlapping stations in 1952 (Table 3). In contrast, *Heteranomia* spp. was much rarer in 2006 than in 1952. *Mytilus edulis* and *Chlamys islandica* were found only in 1952. Furthermore, both absolute biomass and the biomass shares of particular species in 1952 and 1981/90 were also similar in many cases (Tables 3 and 4). Non-parametric tests indicate statistically significant differences in absolute biomass only for *Elliptica elliptica*, *Heteranomia squamula*, *M. calcaria*

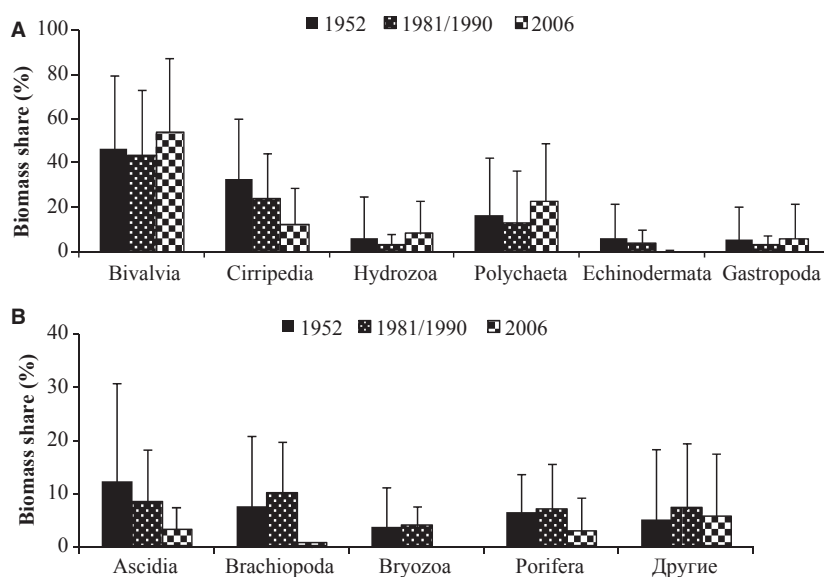


Fig. 3. Percentage of contribution to the total biomass (mean for stations + SD): for taxonomic groups with a high relative contribution (A) and other groups with lower relative contribution (B).

Table 2. Comparison of the macrobenthic biomass and abundance. For mean biomass, mean abundance and mean biomass ratio, the standard deviation is presented in brackets.

Parameters	1952 – all stations	1981/90 – all stations	2006 – all stations	1952 – stations in the area overlapping with 1981/90 survey	1952 – stations in the area overlapping with 2006 survey
No. of stations	70	27	10	41	6
Benthic biomass (B) range, g·m ⁻²	6–2188	11–9210	5–1195	2–2188	14–1706
Mean B, g·m ⁻² (SD)	273 (371)	959 (2008)	190 (254)	332 (408)	374 (504)
Median B, g·m ⁻²	151	142	114	188	68
Benthic abundance (A) range, ind·m ⁻²	10–22,310	60–43,604	250–19,020	10–22,310	230–8630
Mean A, ind·m ⁻² (SD)	2029 (3685)	5182 (9528)	2407 (3540)	2452 (4182)	2928 (2956)
Median A, ind·m ⁻²	595	1332	1170	890	1985
B/A, range, g·m ⁻²	0.02–1.62	0.01–1.24	0.01–0.58	0.02–1.62	0.02–0.53
Mean B/A, g·m ⁻² (SD)	0.28 (0.32)	0.26 (0.35)	0.1 (0.12)	0.26 (0.32)	0.13 (0.15)
Median B/A, g·m ⁻²	0.14	0.11	0.06	0.13	0.07

Table 3. Frequency of occurrence and mean contribution to the total biomass of common bivalves, cirripeds, echinoderms, gastropods, and brachiopods (in descending order of frequency of occurrence for the 1952 survey).

Species	1952 – all stations		1981/90 – all stations		2006 – all stations		1952 – stations overlapping with 1981/90 survey		1952 – stations overlapping with 2006 survey	
	FO ± SE	BS ± SE	FO ± SE	BS ± SE	FO ± SE	BS ± SE	FO ± SE	BS ± SE	FO ± SE	BS ± SE
Bivalvia										
<i>Arctica islandica</i>	18 ± 3	49 ± 17	26 ± 8	30 ± 13	26 ± 7	62 ± 10	15 ± 74	38 ± 11	17 ± 11	35
<i>Chlamys islandica</i>	10 ± 3	16 ± 6	22 ± 8	11 ± 5			15 ± 4	11 ± 4	17 ± 11	30 ± 3
<i>Clinocardium ciliatum</i>	16 ± 3	24 ± 6	52 ± 10	11 ± 4	24 ± 7	25 ± 6	22 ± 5	24 ± 6	8	1
<i>Elliptica elliptica</i>	43 ± 4	13 ± 2	52 ± 10	5 ± 3	37 ± 8	1	49 ± 6	12 ± 3	58 ± 14	14 ± 7
<i>Heteranomia</i> spp.	47 ± 4	4 ± 1	56 ± 10	1 ± 1	8 ± 4	1 ± 1	59 ± 5	4 ± 1	83 ± 11	9 ± 5
<i>Hiatella</i> sp.	27 ± 4	1 ± 1	56 ± 10	1 ± 1	13 ± 5	1 ± 1	33 ± 5	1 ± 1	33 ± 14	3 ± 1
<i>Leionucula bellotii</i>	18 ± 3	1 ± 1	52 ± 10	1 ± 1	58 ± 8	2 ± 1	20 ± 4	2 ± 1	33 ± 14	1 ± 1
<i>Macoma calcarea</i>	9 ± 2	8 ± 4	33 ± 9	7 ± 4	55 ± 8	20 ± 6	12 ± 4	5 ± 2	25 ± 13	1 ± 1
<i>Modiolus modiolus</i>	24 ± 4	46 ± 5	26 ± 8	46 ± 10	53 ± 8	4 ± 2	28 ± 5	51 ± 6	50 ± 14	35 ± 11
<i>Mytilus edulis</i>	8 ± 2	18 ± 4	15 ± 7	12 ± 6			6 ± 3	18 ± 3	8	1
<i>Nicania montagui</i>	31 ± 4	5 ± 2	44 ± 10	1 ± 1	50 ± 8	4 ± 2	30 ± 5	3 ± 1	8	1
<i>Nuculana</i> sp.	52 ± 4	6 ± 1	67 ± 9	2 ± 1	42 ± 8	9 ± 4	56 ± 5	3 ± 1	58 ± 14	6 ± 2
<i>Thyasira gouldi</i>	10 ± 3	2 ± 1	63 ± 9	1 ± 1	37 ± 8	1 ± 1	7 ± 3	1 ± 1	8	1
Cirripedia										
<i>Balanus balanus</i>	37 ± 4	22 ± 4	4	5	3	2	44 ± 5	21 ± 4	33 ± 14	10 ± 2
<i>Balanus crenatus</i>	13 ± 3	31 ± 6	56 ± 10	21 ± 6	37 ± 8	7 ± 3	17 ± 4	36 ± 7	8	6
<i>Verruca stroemia</i>	55 ± 4	15 ± 2	56 ± 10	8 ± 2	21 ± 7	19 ± 8	72 ± 5	15 ± 3	67 ± 14	19 ± 6
Echinodermata										
<i>Henricia</i> sp.	27 ± 4	1 ± 1	26 ± 8	1 ± 1	3	1 ± 1				
<i>Ophiopholis aculeata</i>	4 ± 2	2 ± 1	22 ± 8	2 ± 2			5 ± 2	2 ± 1		
<i>Ophiura robusta</i>	27 ± 4	2 ± 1	59 ± 9	1 ± 1	5	1	23 ± 5	1 ± 1	17 ± 11	1 ± 1
<i>Stegophiura nodosa</i>	12 ± 3	4 ± 3	26 ± 8	3 ± 2	18 ± 6	1 ± 1	13 ± 4	6 ± 5		
Gastropoda										
<i>Margarites g. groenlandicus</i>	4 ± 2	1 ± 1	15 ± 7	1 ± 1			7 ± 3	2 ± 1		
<i>Puncturella noachina</i>	4 ± 2	1 ± 1	7 ± 5	1 ± 1	3	1	6 ± 3	1 ± 1	8	1
<i>Buccinum undatum</i>	4 ± 2	6 ± 2	19 ± 7	1 ± 1	16 ± 6	9 ± 4	5 ± 2	6 ± 2		
Brachiopoda										
<i>Hemithiris psittacea</i>	33 ± 4	8 ± 2	37 ± 9	10 ± 3	5	1 ± 1	43 ± 5	6 ± 1	58 ± 14	11 ± 5

FO = frequency of occurrence (%); BS = biomass share (%); SE = standard error.

Table 4. Differences in biomass and statistical comparison of biomass data for dominant bivalve species at the stations in the overlapping area between the surveys in 1952 and 1981/90 in Onega Bay.

Species	Biomass, g·m ⁻²		Mann–Whitney <i>U</i> -test (P)	Test of median (P)	Kolmogorov–Smirnov test K (P)
	1952 (<i>n</i> = 36) Mean (SE)	1981/90 (<i>n</i> = 27) Mean (SE)			
Species which may be dominant in the benthic communities (Kudersky 1966; Golikov <i>et al.</i> 1985; Lukanin <i>et al.</i> 1995)					
<i>Arctica islandica</i>	14.41 ± 7.98	39.34 ± 27.58	468.00 (0.56)	0.92	0.70 (0.70)
<i>Chlamys islandica</i>	25.54 ± 14.09	95.91 ± 70.33	461.50 (0.51)	0.54	0.55 (0.92)
<i>Clinocardium ciliatum</i>	15.97 ± 4.48	12.62 ± 5.49	470.50 (0.66)	0.39	0.63 (0.82)
<i>Elliptica elliptica</i>	30.08 ± 7.20	12.71 ± 7.13	242.50 (0.001)**	0.01*	1.91 (0.001)**
<i>Modiolus modiolus</i>	203.48 ± 70.89	466.97 ± 253.78	453.00 (0.45)	0.46	0.62 (0.84)
<i>Nicania montagui</i>	1.85 ± 0.55	1.43 ± 0.44	419.50 (0.25)	0.61	0.76 (0.60)
<i>Nuculana</i> spp.	1.89 ± 0.83	1.43 ± 0.44	474.50 (0.73)	0.91	0.50 (0.97)
Other common species					
<i>Heteranomia squamula</i>	13.87 ± 3.18	3.42 ± 1.48	233.50 (0.001)**	0.001**	1.97 (0.001)**
<i>Hiatella arctica</i>	1.94 ± 0.52	4.93 ± 2.32	469.00 (0.86)	0.51	0.61 (0.85)
<i>Macoma calcarea</i>	0.19 ± 0.15	2.29 ± 1.4	381.00 (0.02)*	0.06	0.92 (0.37)
<i>Tyasira gouldi</i>	0.06 ± 0.03	0.45 ± 0.14	251.50 (0.001)**	0.001**	1.95 (0.001)**

*Different levels of statistical significance of differences. SE = standard error; P = probability of belonging to the same general set of variables.

and *T. gouldi* (Table 4). Biomass data for these and other common bivalves (17 species) for 49 overlapping stations were also tested for differences using a one-way ANOSIM test. No significant difference between the studied years was found (Table 5).

The 2006 survey indicated a greater contribution (averaged to nearly 67%) of *A. islandica*. In 1952 the contribution was lower but the species still made the greatest contribution to total benthic biomass (Table 3). Nonetheless, one should bear in mind that the 1952 and 2006 data allow little direct comparison due to the small number of widely scattered stations in the earlier survey versus much more closely set stations along the shoreward transects in 2006.

Amongst common cirripeds *Verucca stroemia* occurred at a very similar rate and made similar contributions to biomass in 1952 and 1981/90, whereas *Balanus balanus*, which occurred twice as frequently in 1952 compared to

B. crenatus, was not common in 1981/90 or 2006. *Verucca stroemia* and *B. crenatus* occurred much more frequently than *B. balanus* in the 1981/90 and 2006 survey areas (Table 3).

The most common echinoderms in the 1952 and the 1981/90 surveys were (in descending order) *Ophiura robusta*, *Stegophiura nodosa*, *Ophiopholis aculeata* and *Henricia* sp. The frequencies of occurrence and average contributions to biomass were higher in 1981/90 for all species, although *S. nodosa* showed higher occurrence in 1952 in the area which overlapped with the 1981/90 survey. Again, the one-way ANOSIM test for seven species of relatively common echinoderms for 34 overlapping stations did not show a significant difference in biomass between the studied years (Table 4). In the overlapping area of the 2006 and 1952 surveys, *O. aculeata* did not occur in either year and other three species were not found in 1952 (Table 3).

Table 5. Comparison of the biomasses of common bivalves (17 species) and echinoderms (seven species) for all overlapping stations between the 1952 and the 1981/90 surveys using a one-way ANOSIM test.

Taxa	Species	No. of species	No. of stations	Global R	P-value
Bivalvia	<i>Arctica islandica</i> ; <i>Chlamys islandicus</i> ; <i>Clinocardium ciliatum</i> ; <i>Elliptica elliptica</i> ; <i>Heteranomia squamula</i> ; <i>Hiatella arctica</i> ; <i>Leionucula bellotii</i> ; <i>Macoma calcarea</i> ; <i>Modiolus modiolus</i> ; <i>Mya truncata</i> ; <i>Mytilus edulis</i> ; <i>Nicania montagui</i> ; <i>Nuculana minuta</i> ; <i>Nuculana pernula</i> ; <i>Pandora glacialis</i> ; <i>Serripes groenlandicus</i> ; <i>Thyasira gouldi</i>	17	49	0.039	0.08
Echinodermata	<i>Asterias rubens</i> ; <i>Henricia sanguinolenta</i> ; <i>Ophiacantha bidentata</i> ; <i>Ophiopholis aculeata</i> ; <i>Ophiura robusta</i> ; <i>Stegophiura nodosa</i> ; <i>Strongylocentrotus pallidus</i>	7	34	0.08	0.06

Gastropods were not commonly found in the 1952 survey; only three species occurred with a frequency above 5%: *Margarites groenlandicus groenlandicus*, *Puncturella noachina* and *Buccinum undatum*. In 1981/90 these three were also the most frequently occurring species, with *P. noachina* occurring with a similar rate, whereas in 1952 the two other species were found more frequently (Table 3).

Hemithyris psittacea, the only brachiopod species living in the White Sea, showed a very similar occurrence rate and average contribution to total benthic biomass in 1952 and 1981/90. In 2006 the species was not as common as in the 1952 survey area overlapping with the 2006 survey (Table 3).

Comparison at the assemblage level

Results of the MDS analysis based on the biomass data for all taxa accounted for in the 1952 survey indicate considerable mixing of the samples of all surveys: variation between samples of the 1981/90 and the 2006 surveys is largely inside the variation of the 1952 survey performed at a wider spatial scale (Fig. 4). A pairwise ANOSIM test revealed no statistically significant differences between the 1952 and the 1981/90 data. However, differences at a statistically significant level ($P < 0.05$) were found between these surveys and the 2006 survey.

To compare the communities at a smaller scale, the study area was divided into sub-areas (Fig. 5). Comparison of the dominant pattern in particular sub-areas between the stations of the 1952 survey and the 1981/91 survey also did not indicate major shifts (Table 6). Sub-area F covered the northern stations of the 2006 survey. These stations were located near Station 65 of the 1952 survey, which had a similar species composition with

Stations 16–19 of the 2006 survey. However, the biomass of *Modiolus modiolus* in 1952 was somewhat higher than in 2006 (Fig. 5, sub-area F). In Southeastern Onega Bay (Fig. 5, sub-area G) the community was also dominated by *Arctica islandica* in both 1952 and 2006.

Discussion

The benthic surveys considered in the present study were not designed to study inter-annual variation in benthic communities. When planning the 2006 survey the stations were intentionally set in the area which was covered the least by the surveys in earlier years. Furthermore, the methods of sampling and gears differed between surveys. Bearing this in mind, we expected to find greater differences between the surveys from three different decades. Median benthic biomass was very similar in all years of investigation and clearly different from other areas of the White Sea with similar depth and bottom topography. In particular, in the Gorlo (the shallow strait separating the outer part of the White Sea from its deep basin) and in the Dvina Bay the median biomass was one order of magnitude lower (Naumov 2001).

Neither the biomass of dominant bivalves and cirripeds nor the frequency of occurrence of the most common species showed any considerable changes between 1952 and 1981/90. The contribution to the total biomass of some bivalves and cirripeds (*Modiolus modiolus*, *Arctica islandica*, *Chlamys islandica*, *Mytilus edulis*, *Elliptica elliptica*, *Balanus balanus*, *Verucca stroemia* and, to lesser extent, *Clinocardium ciliatum*) did not change between 1952 and 1981/90. All these species were described as dominant in various benthic communities identified using different methods in the 1950s and the 1980s (Kudersky 1966; Golikov *et al.* 1985; Lukanin *et al.* 1995). *Nuculana pernula* and *Nuculana minuta* may be added to this list but it is possible that these morphologically similar species were poorly distinguished (Naumov 2006) in earlier surveys and so their presence cannot be confirmed with certainty. Furthermore, the frequency of occurrence and biomass of other common species (*Heteranomia squamula*, *Hiattella* sp., *Nicania montagui*, *Hemithyris psittacea* and common echinoderms) did not show much variation. At the assemblage level, few differences were revealed using multivariate statistics and direct comparison of the closely located stations from different surveys. The stability of the ABC curves and the average mass of a specimen also indicate the absence of shifts in benthic communities similar to those observed in some areas under the influence of eutrophication (Rosenberg 1987). Although the results of the 2006 survey appear somewhat different from the patterns of previous years this does not indicate major

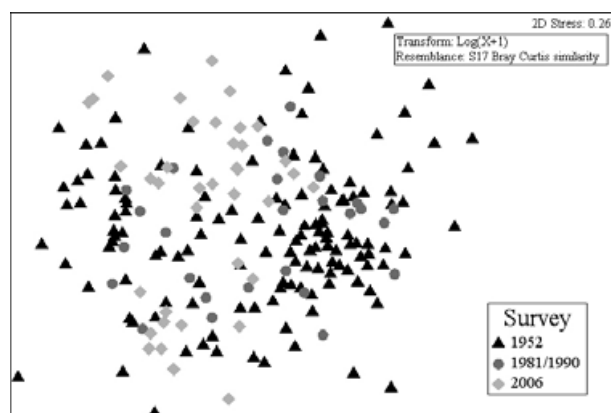


Fig. 4. Results of multidimensional scaling (MDS) analysis of the samples of surveys in Onega Bay conducted in 1952, 1981/90 and 2006. Explanations are given in the text.

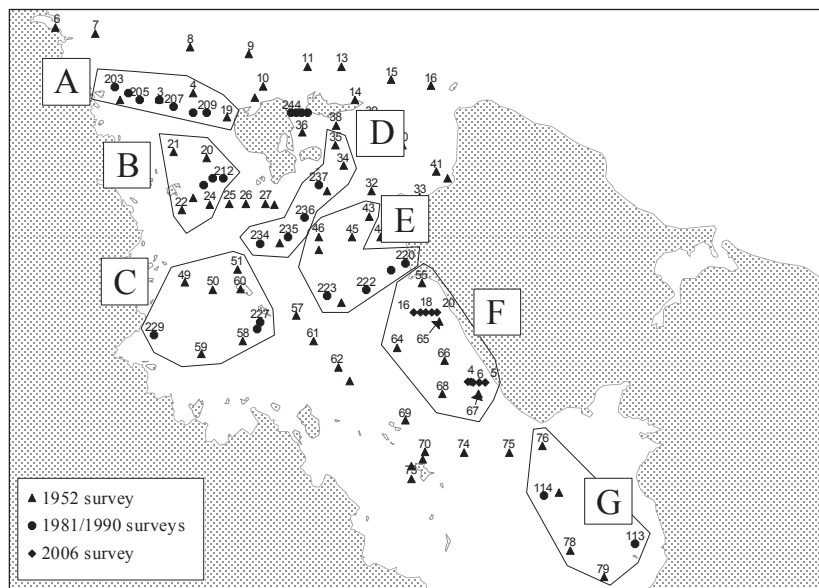


Fig. 5. Sub-areas of detailed comparison at the assemblage level. Explanations are given in the text.

Table 6. Benthic taxa composition (in terms of biomass) at stations of the 1952 and the 1981/90 surveys performed for sub-areas in Onega Bay.

Survey	Subarea (see Fig. 5)	No. of samples	Dominant taxa	One-way ANOSIM test result
1952	A	9	<i>Hemithyris psittacea</i> , Cirripedia, <i>Nuculana minuta</i> , <i>Elliptica elliptica</i> and other bivalves	$R = 0.176$; $P > 0.05$
1981/90		7	<i>Hemithyris psittacea</i> , Cirripedia, <i>Elliptica elliptica</i> and other bivalves	No significant differences
1952	B	7	<i>Modiolus modiolus</i> , Cirripedia, <i>Heteranomia squamula</i> , Hydrozoa	$R = 0.385$; $P > 0.05$
1981/90		3	<i>Modiolus modiolus</i> , Cirripedia, <i>Heteranomia squamula</i> , Ascidia	No significant differences
1952	C	10	<i>Clinocardium ciliatum</i> , <i>Elliptica elliptica</i> , Cirripedia, Ascidia	$R = 0.634$; $P < 0.05$
1981/90		3	<i>Arctica islandica</i> , <i>Clinocardium ciliatum</i> , <i>Serripes groenlandicus</i> , Ascidia, Cirripedia	Significantly different
1952	D	7	Cirripedia, <i>Modiolus modiolus</i> , <i>Chlamys islandicus</i> , <i>Hiatella</i> sp., Bryozoa, Hydrozoa	$R = 0.138$; $P > 0.05$
1981/90		4	Cirripedia, <i>Hemithyris psittacea</i> , <i>Modiolus modiolus</i> , <i>Chlamys islandicus</i> , <i>Hiatella</i> sp., Bryozoa, Hydrozoa	No significant differences
1952	E	8	<i>Modiolus modiolus</i> , Cirripedia, Ascidia, <i>Hiatella</i> sp., <i>Hemithyris psittacea</i>	$R = 0.323$; $P < 0.05$
1981/90		4	Ascidia, Cirripedia, <i>Hemithyris psittacea</i> , <i>Nuculana minuta</i> and other bivalves	Significantly different
1952	G	9	<i>Arctica islandica</i> , <i>Nicania montagui</i> , <i>Nuculana</i> spp., <i>Elliptica elliptica</i>	ANOSIM test failed
1981/90		2	<i>Arctica islandica</i> , <i>Elliptica elliptica</i> , <i>Clinocardium ciliatum</i> , <i>Nuculana minuta</i>	

changes in the benthic communities because the survey in 2006 was designed in a different way and its overlap with the 1952 survey was minimal. However, even in this case, the dominant species *A. islandica*, *M. modiolus* and *V. stroemia* held their positions.

In spite of a similarity overall, there are apparent differences between the surveys which need to be discussed. First, the maximum and the average biomass of keystone species such as *M. modiolus*, *C. islandica* and *A. islandica* were higher in 1981/90 than in 1952. This may reflect population dynamics related to cohort growth and turnover. In clams and mussels, long-term population cycles have been known since the second half of the 20th cen-

tury (Stephen 1938; Parsons *et al.* 1977; Lukanin *et al.* 1989); these are not necessarily related to environmental variation (Naumov 2006). In the White Sea, a patch of benthic assemblages with a strong dominance of *A. islandica* (population density of about 15,000 ind·m⁻²) has been monitored in Chupa Inlet for more than 25 years. The structure and quantitative characteristics of this clam population at depths >10 m remained stable for 23 years, before the fraction of large (30–40 mm) specimens declined owing to a drastic natural elimination. In subsequent years, restoration of the population structure was observed, probably as a result of the re-distribution of the clams (Guerassimova *et al.* 2008).

A lower biomass of dominant bivalves in 1952 may also be explained by the use of different sampling methods. The Ocean-50 grab used in 1981/90 has a slightly larger sampling area (0.25 m²) than two casts of a Petersen grab (0.2 m²). It is possible that large sessile species with aggregated distribution were underestimated by taking two replicate samples of smaller size *versus* the one of larger size. Furthermore, an Ocean-50 grab is much heavier than a Petersen grab because their mass is proportional to L³, where L is a linear dimension of the open grab. A heavy grab is probably more effective in penetrating the dense coverage of large bivalves than a lighter one. Further studies using both theoretical models and field experiments are needed to check these hypotheses.

Some species which were not dominant in their biomass but are relatively common in Onega Bay showed an apparent increase in the frequency of occurrence and biomass between 1952 and 1981/90. These species include small clam *Thyasira gouldi*, echinoderms *Ophiura robusta* and *Ophiopholis aculeata*, and whelk *Buccinum undatum*. In 2006, *T. gouldi* was also common and *B. undatum* occurred with much higher frequency than found in previous surveys. In this case the differences in sampling methodology may also have biased estimates for these species. For example, one may suppose that such mobile and probably aggregating species such as ophiuran and whelks are underestimated by taking only two replicate samples of the Petersen grab. However, it is questionable whether this explanation also holds for *T. gouldi*. Alternative explanations would be trends for extension and/or increasing abundance in the aforementioned species. Regardless of whether these changes or trends are real or artefacts of sampling design, they are not essential in comparison with the apparent absence of shift in the dominance pattern in benthic communities and the relative stability of biomass characteristics of most common species at a decadal scale. Taking into account high spatial variability and methodological constraints of surveys, we may also speculate that such shifts could be potentially overlooked. However, the consistency of the dominance pattern in benthic assemblages in small sub-areas (Fig. 5) over decades suggests that this is not the case. Indeed, in the dynamics of the environmental conditions in the White Sea region we see hardly any major changes that could drive shifts in the dominance pattern in benthic communities.

The period from the early 1940s until the first half of the 1980s was characterised by general cooling, but from the mid-1980s onwards, temperatures increased (Tolstikov *et al.* 2004; Filatov *et al.* 2005b). For water temperature, the data from a permanent station at the entrance of the low-shore fjord in the Kandalaksha Bay, Chupa Inlet, which has unrestricted water exchange with the off-

shore part of the White Sea (Babkov 1998; Howland *et al.* 1999), shows neither strong positive nor negative anomalies since the late 1950s. The average temperature for the 50–65 m layer indicates particularly little inter-annual variation; the anomalies do not significantly exceed 0.5 °C and show a weak correlation with the anomalies in the upper 15-m layer (Berger *et al.* 2003). As Onega Bay is open to the influence of the deep part of the White Sea, owing to tidal wave propagation and an anti-clockwise system of permanent currents (Babkov 1998; Filatov *et al.* 2005a), the pattern of inter-annual variation of thermal regime is not expected to be very different from that in the entrance of Chupa Inlet. River discharge, which can potentially strongly affect benthic communities in the coastal zone, also shows no well expressed trends or major changes (Filatov *et al.* 2005b).

Modelling of yearly average primary production based on satellite chlorophyll data indicates that Onega Bay is one of the most productive areas in the White Sea (Romankevich & Vetrov 2004). A considerable part of the phytoplankton production and allochthonous organic matter supplied by river run-off is consumed by seston-feeding bivalves (*M. modiolus*, *A. islandica*, *C. islandica*, and *M. edulis*) and cirripeds, which constitute the majority of the biomass in Onega Bay. These bivalve species are long-living (Naumov 2006) and have few consumers – mostly flatfish, which do not predate on older age groups of *M. modiolus*, large clams and scallops (Ivanova 1957), and eiders, which are highly abundant in the area. Eiders use the area for breeding, moulting and wintering in the polynyas but mostly concentrate for feeding close to the shore, in particular on blue mussels, *M. edulis* (Bianki 1991; Galaktionov 2001; Makarevich & Krasnov 2005). It is therefore unlikely that predators have a strong impact on the population dynamics of dominant sessile benthic species at the scale of the entire Onega Bay. Due to their role in filtration of organic particles, influencing near-bottom hydrodynamics and producing shell material as substrate for epibenthos (Naumov 2006), the dominant bivalves and cirripeds may be considered keystone species-modifiers (Mills *et al.* 1993) in seabed biotopes. Thus the stability or quasi-periodic changes in their populations contribute to the relative stability of the subtidal macrobenthic communities in Onega Bay.

The characterisation of Onega Bay would be incomplete without mentioning that the anthropogenic influence on its marine ecosystem was low to moderate in the 20th century. Although the trend for eutrophication of the marine waters was seen in the White Sea in the 1980s compared to the 1950s (Maksimova 1991), the White Sea watershed area was not an area of intensive agriculture and pulp production in the second half of the 20th century (Terzhevskiy *et al.* 2005), and natural organic matter

input from river run-off was always considerable (Romankevich & Vetrov 2004). Although there is pollutant transport with river run-off, much of the pollution is entrapped by so-called marginal filters in estuaries (Ivanov & Brizgalo 2005). In Onega Bay, background pollution with hydrocarbons and organochlorides is low; the trace metal concentrations in bivalve tissues may be somewhat higher than in the neighbouring Kandalaksha Bay but they are still not high compared with seas surrounded by areas of high population and industrial density (Savinov *et al.* 2001). Onega Bay has always been an important area for herring and navaga fishing for local and regional markets, but fishermen mostly used passive gears and there was practically no impact of bottom trawling and dredging on seabed habitats. Apart from pink salmon, which was introduced in the late 1950s–1960s, there are no alien species established in the region (Berger 2001).

It is of interest to compare the presumed stability of benthic communities in Onega Bay to examples known from the other shelf areas of similar scale. In the neighbouring Southwestern Barents Sea the response of zoobenthos to long-term fluctuations of temperature and the inflow of Atlantic waters is relatively rapid and manifests itself in changes of occurrence of the arctic and the boreal species (Galkin 1998; Denisenko 2008). However, the principal factor influencing variation of quantitative characteristics of infaunal benthic communities has been the bottom trawl fishery (Denisenko 2001; Carroll *et al.* 2009). In the 20th century, Skagerrak, Kattegat, the North and the Irish Seas show examples of significant changes in benthic (mostly infaunal) communities that are likely caused by eutrophication (Pearson *et al.* 1985; Rosenberg *et al.* 1987), bottom trawling, background pollution (Krönke 1990; Wieking & Krönke 2003; Türkay & Krönke 2004) and scallop dredging (Bradshaw *et al.* 2002). Beginning from the 1980s an increasing impact of climatic trends on benthic communities of the southern part of the North Sea can be traced (Beukema & Dekker 2003; Sonnewald 2008). The studies on the Black Sea benthos indicated that changes in the structure of bottom communities manifesting in the change of dominant species and the high magnitude of variation in abundance and biomass of common species may happen within a few years under the cumulative influence of the consequences of eutrophication and introduction of alien species. The misbalanced benthic communities are continuing to experience rapid changes in their quantitative species composition (Chikina & Kucheruk 2005; Kucheruk *et al.* 2009).

Amongst the seas around Europe, the White Sea and particularly Onega Bay may represent a rare case of a shallow-water benthic ecosystem which has not yet been

modified by human impact. The specific oceanographical regime of the White Sea has possibly also made it resilient to climate variation in the past decades. Taking this into account, Onega Bay with its largely boreal and in several respects similar characteristics to the North Sea and the Western Baltic biota (Zenkevich 1963; Naumov 2001) is a prospective area for studies of natural variation in benthic communities and possible future climate-forcing in this yet undisturbed ecosystem belonging to the Northeast Atlantic realm.

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