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Benthic fauna of the Gorlo Strait, White Sea: a first species inventory based on data from three different decades from the 1920s to 2000s

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Abstract This study presents an inventory of the sublittoral macrobenthic fauna of the Gorlo Strait, based on historical surveys (1922, 1980s) and an investigation carried out in 2004. A comparison of the species lists was carried out, giving particular attention to current nomenclature, synonymies and biogeographical affinity. Differences in species lists can be explained by differences in sampling gear and design, but generally species lists are complementary. The total number of species in all surveys amounts to 322, with an additional 39 taxa unidentified to species level. All the species identified represent 254 genera and 166 families. The macrobenthic fauna of the Gorlo is thus generally rich but mostly consists of rarely occurring species. This is discussed in the light of specific environmental conditions of the Gorlo, in particular low primary productivity in the water column, strong tidal currents and the unstable lithodynamics. The combined species list was characterised by high taxonomic distinctness index (96) sensu Clarke and Warwick (1998); the indices calculated for particular surveys showed only slight and mostly statistically non-significant differences from this value. The biogeographic structure of species composition of Gorlo does not differ between years, with the Arctic-boreal species constituting the majority (about 60%) and the Boreal and Arctic species having nearly equal shares (about 15%). Although our study revealed few North Atlantic species not hitherto recorded in the White Sea, stable shares of species with particular biogeographical affinity at the decadal scale, stability of the taxonomic distinctness indices and small differences in the composition of the core of most commonly occurring species indicate the absence of major shifts in the faunal composition: current climatic changes most probably have not yet significantly affected specific oceanographical conditions and benthic habitats of the Gorlo which shape the local macrobenthic fauna.

Keywords Arctic and subarctic · Macrobenthos · Historical data · Species list · Taxonomic distinctness · Biogeographical affinity · Climate change

Introduction

Analysis of marine biodiversity patterns across various scales (Godfray and Lawton 2001; Gray 2001) requires detailed species inventories of naturally bordered marine regions. Furthermore, such inventories are required for

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monitoring of the impact of ongoing changes in climatic and oceanographical conditions on marine biodiversity, which are particularly evident in the Arctic (Anisimov et al. 2007; Frolov et al. 2009). For Arctic marine macrobenthic invertebrates, the available general species inventories are mostly specific to particular Russian Arctic seas (Sirenko 2001; Petryashov et al. 2004) and for some seas of the Canadian sector (Cusson et al. 2007). Finer-scale assessments, based on more than one survey, have been sporadically undertaken (Kudersky 1966; Golikov 1994; Gulliksen et al. 1999; Grishankov et al. 2000; Cusson et al. 2007; Renaud et al. 2007; Dahle et al. 2009).

The present study focuses on the Gorlo Strait of the White Sea, the internal sea crossed by the Arctic Circle, but retaining many characteristic features of Arctic seas (Derjugin 1928; Berger and Naumov 2001; Filatov et al. 2005). Specific conditions of the Gorlo Strait, including strong seasonal variation in bottom temperature (Anonymous 1968; Kosobokova et al. 2004; Filatov et al. 2005), appear to form suboptimal conditions for stenothermic taxa, but on the other hand enable the maintenance of some characteristic North-East Atlantic species within the Gorlo Strait macrobenthos (Spiridonov et al. 2008).The history of exploration of the Gorlo Strait extends over 85 years from K.M. Derjugin's expedition on R/V *Murman* (ex *Andrew Pervozvanny*) in 1922 and 1923. As a result of this expedition, the first data on the sublittoral fauna of the Gorlo Strait were published (Derjugin 1928). Subsequently, however, this area was not frequently studied (Lukanin et al. 1995; Spiridonov et al. 2005) with other surveys being based on a limited number of sampling stations (Denisenko et al. 2006; Lyubina et al. 2007). Until now, there have been no attempts made to merge the various existing datasets and compile a species checklist for the Gorlo Strait area, with recent reports of benthic fauna of the Gorlo area only being compiled for specific taxa (Naumov 2006).

This study aims at compilation of a full list of the benthic fauna of the Gorlo, which is necessary for comparative analyses of the Arctic seas fauna, for testing the hypothesis of the role of the Gorlo Strait as a biogeographical barrier (Naumov 2006), and for using the faunal inventory data as a basis for monitoring changes in benthic biodiversity under the influence of global climate change. The present species inventory faces several challenges. Firstly, it is based on surveys carried out during different times, spanning several decades (diachronic surveys). Secondly, the different surveys used different sampling methodologies, ranging from grabs to epibenthic trawls, such that different components of the benthos were selectively sampled. Thirdly, and perhaps most importantly, the taxonomic nomenclature has changed, and much species synonymies and splitting of new species has occurred since the first survey by Derjugin in the 1920s. Because the collections from Derjugin's expedition and most of the material collected in the 1980s are no longer available for re-identification, compiling a joint species list involves a lot of harmonization of the taxonomic names used, and there will always be some remaining uncertainties within the data set. We attempted to make the taxonomic lists comparable by consulting experts in particular groups and checking synonymy and possible validity of identification. To overcome difficulties caused by different sampling methodologies and survey coverage, our analyses used general descriptors based on the presence/absence of species, measures of taxonomic distinctness (Clarke and Warwick 1999) and the proportions of species of different biogeographical affinity. The taxonomic distinctness index is not dependent, on average, on the degree of sampling effort involved in the data collection and this index can be used to compare its values for species lists over different periods of time, which usually involved collection and analysis by different people, using disparate sample sizes (Clarke and Warwick 1999, 2001).

Material and methods

Study area

The Gorlo Strait (Fig. 1) is a comparatively small, shallow basin (10,200 km^2) with a maximal width of 45–50 km and depths up to 100 m, but generally not exceeding ~50 m (Berger and Naumov 2001). The Strait connects the inner part of the White Sea (the Basin, the Kandalaksha Onega and the Dvina Bays) with its outer parts (Voronka and the Mezen' Bay) and through these, with the Barents Sea. Specific conditions of the Gorlo Strait include frontal zones, separating the Gorlo waters in the North and in the South, strong and changing tidal currents, the absence of water column stratification, deep winter convection (Timonov 1950; Naumov and Fedyakov 1991; Pantyulin 2003; Kosobokova et al. 2004; Filatov et al. 2005), predominance of sand and coarse deposits (Nevessky et al. 1977; Rybalko et al. 1989), low primary production in the water column (Rat'kova and Savinov 2001; Romankevich and Vetrov 2001), and may result in a barrier preventing the penetration of Barents Sea fauna into the White Sea (Naumov and Fedyakov 1991; Naumov 2006).

Data sources and nomenclature

Data from three different benthic surveys, carried out in the Gorlo Strait, were used (Table 1; Fig. 1). During Derjugin's expeditions, ten benthic stations were taken; five stations in 1922 and another five in 1923. In 1922, the samples were taken by a dredge and an Agassiz trawl (3 m), whilst in 1923 only the Agassiz trawl was used (Table 1; Fig. 1). In the 1980s benthic surveys, 21 sublittoral benthic stations

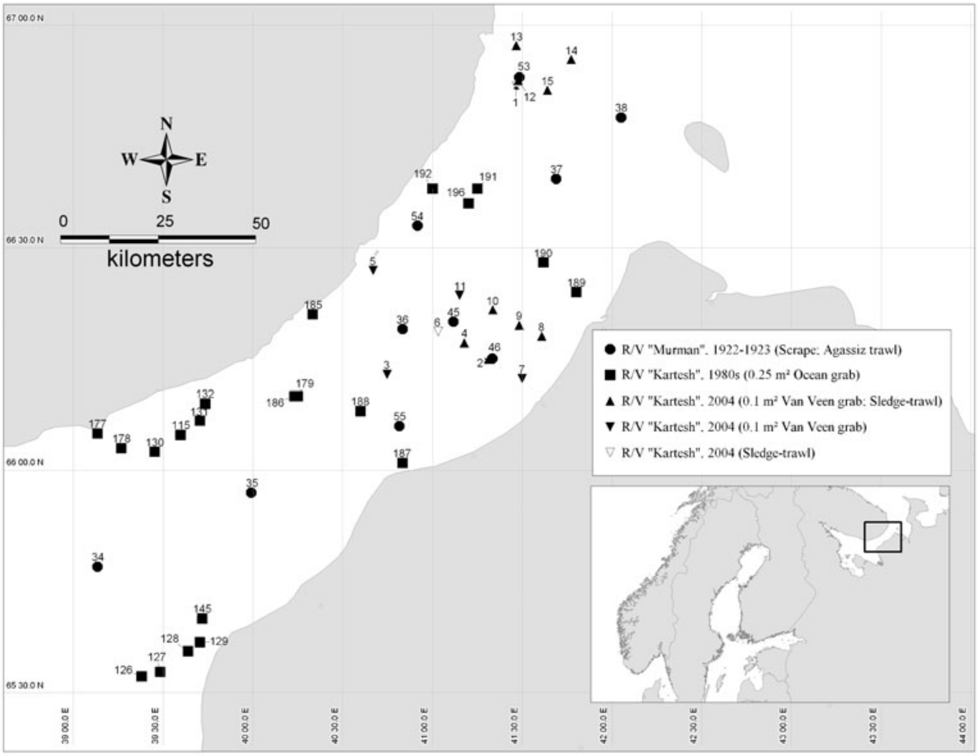

Fig. 1 Location of the Gorlo Strait in the White Sea and location of sampling stations included in the present study

were taken by an Ocean-50 grab (0.25 m^2 sampling area), and in the 2004 benthic survey, 13 van Veen grab stations (74 samples) and 11 epibenthic trawl stations were taken (Table 1; Fig. 1). Authors of the present study took part in the 1980s surveys and the 2004 survey.

The data from the 1920s survey contained descriptions of the stations, and species lists were given per station, partly giving the number of specimens for each qualitative sample, but mostly simply recorded as present. The data from the 1980s comprises species lists with abundance and biomass information (Lukanin et al. 1995). The data from the 2004 survey included species lists with abundance and biomass data (Spiridonov et al., in preparation). It is self explaining that data from the 1920s and trawl data from 2004 can be used only for qualitative analysis of benthic fauna; furthermore, as different grab types show different efficiency with regard to the Arctic benthos (Dahle et al. 2009), results of their sampling are also used qualitatively. The level of taxonomic recognition was high, with over 90% of the material being identified to species level in all of the survey data sets.

All species, recorded in different years, were merged into a single data set. Most of the species names were standardised according to current taxonomic nomenclature, using specialist consultations and nomenclatural checklists (Gulliksen et al. 1999; Sirenko 2001; Tchesunov et al. 2008; Dahle et al. 2009; World register of marine species, http://www.marinespecies.org/; ZOOlogical INTegrated retrieval system, http://www.zin.ru/projects/zooint/index.html). For data standardisation, the frequency of occurrence index was used (percentage of the stations where the species occurred against the whole number of stations). Index of frequency of occurrence describes the commonness of species in each survey recorded as a percentage (ESM Online Resource 1).

Data analysis

Multivariate analysis was undertaken based on the presence/absence of the 15 most frequently recorded species using the PRIMER v.6 package (Clarke and Warwick 2001). Non-parametric multi dimensional scaling (nMDS) was carried out based on Bray-Curtis similarity index. Analysis of similarities (ANOSIM, Clarke and Warwick 1994) was then used to determine the significance of the differences between each survey. The species list for this analysis included 15 species: two species of hydroids, two species of barnacles, two species of polychaetes, four species of bivalves, three species of echinoderms and one species of gastropods and brachiopods. Presumably, all of these species can be represented adequately in all surveys.

The expected number of species in the surveys of different years was calculated using second-order Jacknife estimator; these algorithms are non-parametric methods for estimating theoretically possible species number data, on the basis of permutations of the original sets, and can be used for data with a small number of stations based on a presence/absence matrix (Smith and Van Belle 1984).

Table 1 Surveys included in the present study, with summary data

Characteristics	K.M. Derjugin expedition	White Sea Biological Station of ZISP	IO RAS, project "Population biology of *Crangon allmanni*"	
Year	1922-1923	1980s	2004	
Vessel	R/V *Murman*	R/V *Kartesh*	R/V *Kartesh*	
Gear	Scrape; Agassiz trawl (3 m)	0.25 m^2 Ocean-50 grab	0.1 m^2 Van Veen grab	Epibenthic sledge-trawl
Number of stations	10	21	13	11
Depth range (m)	22–87	8–155	15–50	15–47
Total number of species recorded	196	160	95	85
Unidentified to species level taxa	7	14	26	12

For comparison of taxonomic diversity of benthic fauna, using data from the 1920s, 1980s and 2004, indices of taxonomic distinctness (Clarke and Warwick 1999) were calculated. Taxonomic distinctness index calculates the average distance between all pairs of species, where the distance is defined as the path length through a classification tree connecting these species (Clarke and Warwick 1999). The taxonomic levels used for each phylum were species, genus, family, order and class, i.e. five steps each measured by constant step weigh one (Clarke and Warwick 1998, 2001).

Biogeographical characteristics

For each species, a biogeographical characterisation was assigned on the basis of literature sources (Gaevskaya 1948; Gur'yanova 1951; Starobogatov and Naumov 1987; Naumov 2006; Denisenko 2008; World register of marine species, http://www.marinespecies.org/). For some taxa (mainly Porifera, Polychaeta and Hydroidea), information on species distribution is scarce, and often the species are classed as Arctic, Boreal, or Arctic-boreal without explanation of the criteria. This made it difficult to categorise all the species within a detailed biogeographical classification, resembling that proposed by Sirenko and Vasilenko (2008). For this reason, we use a simplified approach where all species are categorised within one of five latitudinal biogeographical groups:

Arctic—species, which are widely distributed on the shelf and continental slope of all or most of the marginal seas of the Arctic Ocean. These species are not widely distributed in northern parts of the Atlantic and/or Pacific oceans.

Arctic-boreal—species, which are widely distributed on the shelf and continental slope in the North Atlantic and/or the North Pacific waters and in the Arctic Ocean adjacent to the frontier seas (Barents, White, Greenland and Chukchi Seas) and straits.

Boreal—species, which are widely distributed in Northern parts of Atlantic and/or Pacific Ocean. These species can be found in the Arctic Ocean, but only in its marginal seas with the Atlantic or Pacific Oceans.

Subtropical-Arctic—species, which occur in single seas of the Arctic Ocean and the Atlantic Ocean (southern border of this areal goes from the western part of the Ocean near the shore of Morocco, including the Mediterranean Sea); and/or Pacific Ocean (in the north-western part of the Ocean up to northern part of Yellow Sea and Kyusu Island, in the north-eastern part of the Ocean—as far as the southern end of California Peninsula).

Conventionally cosmopolitan (pan-oceanic)—species, recorded in different, widespread regions of the Ocean.

Results

Benthic faunal composition

A merged species list comprising the data from the Gorlo Strait, including frequencies of occurrence, is presented in ESM Online Resource 1. The number of species within particular taxonomic groups (of the order or higher rank) is given in ESM Online Resource 2. Polychaetes were the most species rich group (20%) followed by amphipods (14%), gastropods (11%), cnidarians (mostly Hydrozoa, 10%), bryozoans (11%), and bivalves (8%). For a few of the groups, such as the Nemertini, the taxonomy is poorly studied, and their species numbers cannot be assessed with certainty. However, it is unlikely that these groups, which were only recorded during some of the surveys, are comparable in species number to the dominant taxa listed above.

The total number of species in all surveys amounts to 322, with an additional 39 taxa unidentified to species level. All species represent 254 genera and 166 families. Figure 2 shows that the results of the computation of the

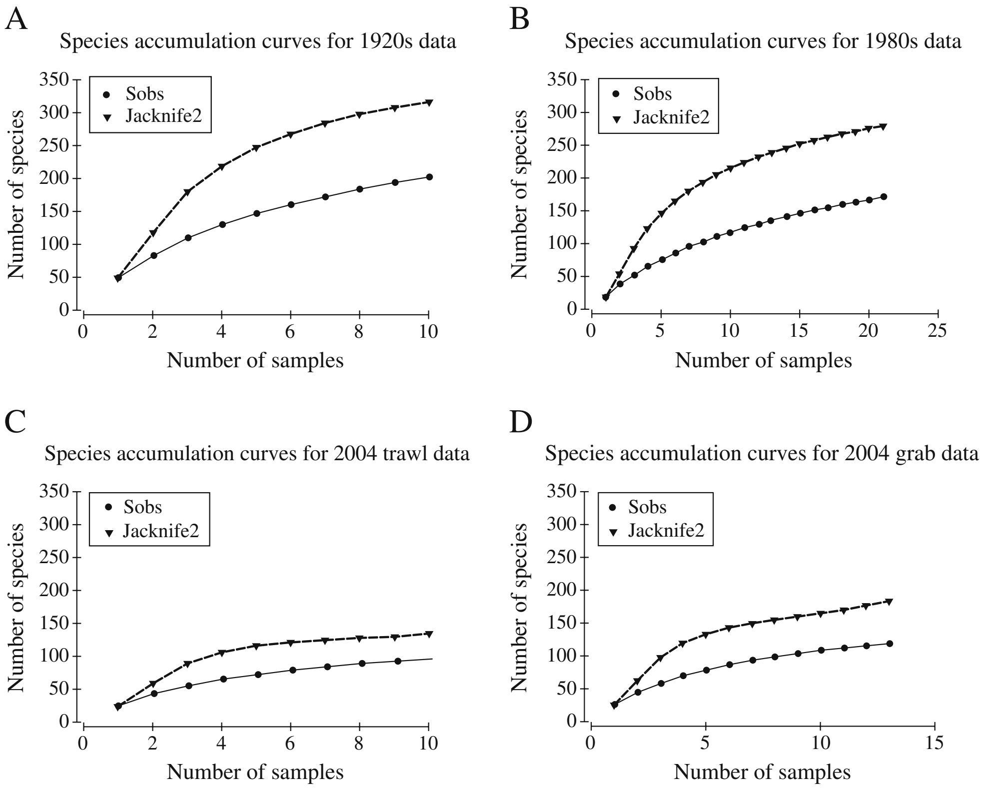

Fig. 2 Species accumulation curves for **a** 1920s, **b** 1980s, **c** 2004 trawl, and **d** 2004 grab. *Sobs* observed number of species, *Jacknife 2* species richness estimator

theoretically possible number of species found in particular surveys on the basis of permutations of the observed values and using the Jacknife 2 algorithm. This figure indicates that the number of species in a particular survey may be underestimated by 25-30% and may in reality be in the range of 247–316 species.

Most of sponges, bryozoans and ascidians were recorded only in the 1922-1923 survey; only a few of these taxa were found during the later studies. This is not surprising because the Agassiz trawl used in the former expeditions collected large boulders and stones encrusted with these epifaunal taxa (Derjugin 1928), whereas the gears used during the later surveys sampled little of this faunal component. Within these groups, between 50 and 90% of species were recorded from a single survey. There were no new species records for the Gorlo Strait fauna recorded from the 2004 survey and only the ascidian *Dendrodoa grossularia* was found in all surveys (Fig. 3a; ESM Online Resource 2).

Similarly, members of the Cnidaria, Polychaeta, Gastropoda, and Amphipoda comprise mostly species found only in a single survey (55–70% of species). However, within these groups, there were both greater number of species found for the first time in 2004, and those recorded in all surveys (Table 2; Fig. 3b, c; ESM Online Resource 2). This was also the pattern characteristic for all taxa taken together (Fig. 3c). Six species of Cnidaria were found in all surveys (Table 2). With respect to polychaetes, seven species were found in all years, with *Harmothoe imbricata* and *Ophelia limacina* occurring more frequently (>25%) in all the surveys (Table 2). In the Gastropoda, the most common species for all surveys comprised of *Boreotrophon clathratus* and *Margarites groenlandicus*, the latter occurring with frequency >25% in most surveys. Only three species of amphipods, *Anonyx nugax*, *Paroediceros lynceus* and *Halirages fulvocinctus*, were common for all of the surveys.

The relatively species poor groups of cumaceans, isopods, and pantopods showed another pattern of occurrence. Although more than 60% of species in these groups were also found in a single survey, and usually with low frequency (ESM Online Resource 1), there were no common species between surveys, and the survey of 2004 brought significant number of new species for the area, just under half of the total number (Table 2; Fig. 3d; ESM Online Resources 1, 2).

Finally, the frequency of occurrence of the decapod and ophiuran species demonstrates a principally different pattern. Most of species were recorded in all the surveys and there were either no (ophiuran) or one (decapod) new species for the area in 2004 (Fig. 3e; ESM Online Resource 2). This caridean shrimp species, for the first time found not only in the Gorlo but also in the White Sea in general, *Spirontocaris lilljeborgii* (Danielssen 1859), has been previously recorded mostly in the western Barents Sea (Sokolov 2003). The most common (occurring also with moderate-to-high, >25% frequency within a single survey)

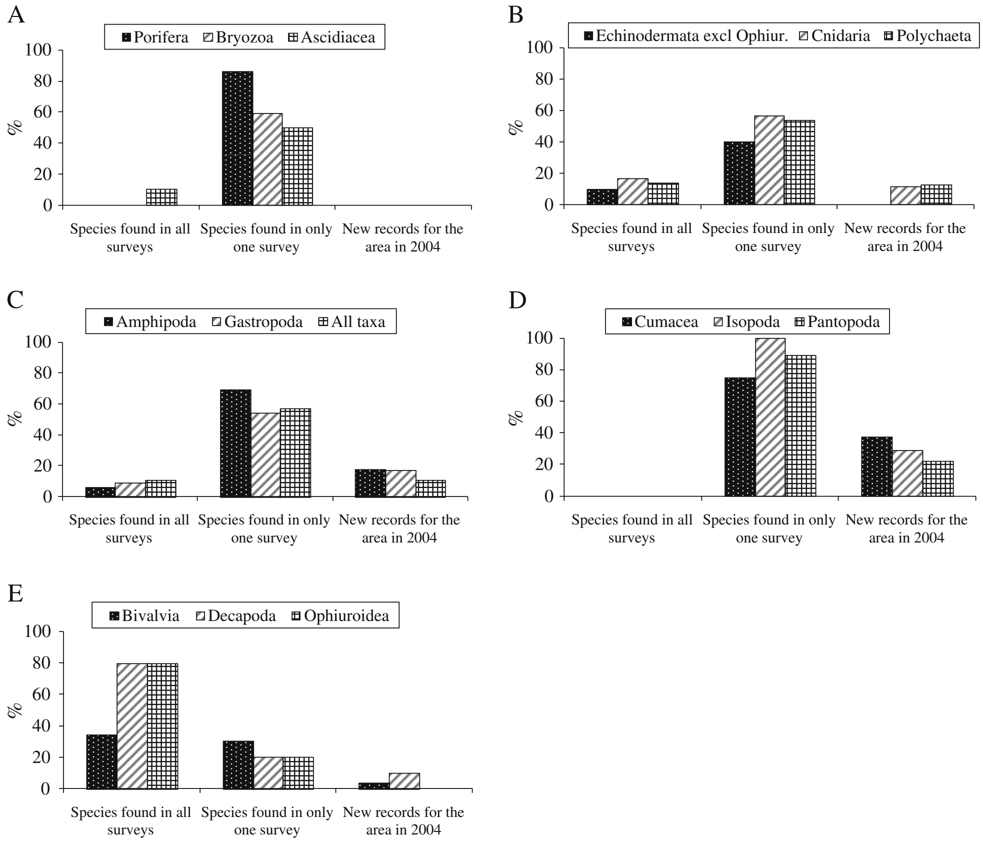

Fig. 3 a–**e** Contributions of species recorded from all surveys, in one survey only or which are new records from 2004, assessed for each of the major taxonomic groups. See explanations in the text

species of the decapods, crustaceans and ophiurans were *Crangon almanni*, *Hyas araneus* and *Sclerocrangon boreas*, and *Ophiacantha bidentata*, *Ophiura robusta* and *Stegophiura nodosa*, respectively (ESM Online Resource 1). Other echinoderms included a higher proportion of rarely occurring species, but similarly to ophiurans, no new species for the area were found in 2004 (Fig. 3b; ESM Online Resource 2). Only *Crossaster papposus* was found in all surveys with notable frequency (ESM Online Resource 1).

The bivalve species showed the most unusual pattern of occurrence. Both the species occurring in all surveys and the species found in a single survey comprised about one-third of the total number of species, and still some new species for the area were observed in 2004 (Table 2; Fig. 3e; ESM Online Resource 2). Ten species of bivalves were recorded in all surveys with the most common (occurring in all surveys with frequency above 25%) species including *Nuculana minuta*, *Elliptica elliptica* and *Hiatella arctica* [or *Hiatella* sp. considering that more than one species of the genus may occur in the White Sea (Naumov 2006)].

Other groups with smaller numbers of species, such as Cirripedia and Brachiopoda (ESM Online Resource 2), also include species found in all surveys with a notable frequency of occurrence, i.e. *Balanus balanus*, *Verruca stroemia* and *Hemithyris psittacea*.

Analysis of similarities

MDS and analysis of similarities (ANOSIM) was undertaken based on a presence/absence matrix. In the case when all species were taken into account there was clear separation between the 2004 grab data, 2004 trawl data and the 1980s data. This indicated a degree of separation between the benthic assemblages, and also differences in the sampling gear applied. This result was highly predictable, so for the analysis we included the 15 species with highest frequency of occurrence throughout all surveys. MDS shows the concentration of the samples from different years in the middle (Fig. 4), and the rest of the samples somewhat separated, mostly due to low numbers of species recorded and the variety of habitats presented. ANOSIM indicates the difference between the 1920s survey and the 2004 grab survey ($R = 0.198$; $p < 0.01$) and between the 1980s survey and the 2004 grab survey ($R = 0.219$; $p < 0.01$), however no significant differences between other groups was observed.

Taxonomic distinctness

Values of average taxonomic distinctness ($\Delta+$) are shown in Fig. 5 and ESM Online Resource 3. It is only for the 2004 grab survey data that $\Delta+$ falls slightly below statistical expectation, while the 1920s survey species stays slightly above the 95% confidence limit. However, all

Table 2 Species of Cnidaria, Annelida, Mollusca, Malacostraca and Pantopoda recorded in the Gorlo in all years and new records for the area in 2004. For details and authors of species see ESM Online Resource 1

Taxon	Consistently recorded species (recorded in all years)	Species recorded for the Gorlo for the first time in 2004
Cnidaria	*Rhizocaulus verticillatis*; *Abietinaria abietina*; *Hydrallmania falcata*; *Sertularia albimaris*; *Sertularia tenera*; *Thuiaria laxa*	*Bougainvillia* sp.; *Coryne lovenii*; *Obelia longissima*; *Abietinaria filicula*
Polychaeta	*Eulalia viridis*; *Harmothoe imbricata*; *Sphaerodorum gracilis*; *Ophelia limacina*; *Amphitrite cirrata*; *Terebellides stroemi*; *Chone infundibuliformis*; *Spirorbis* sp.	*Eteone barbata*; *Eunoe oerstedi*; *Marenzelleria wireni*; *Spio* cf. *theeli*; *Aricidea nolani*; *Ophelina acuminata*; *Scalibregma inflatum*; *Capitella capitata*; *Nicomache minor*; *Praxillella praetermissa*; *Rhodine gracilior*; *Chone duneri*
Loricata	*Stenosemus albus*	None
Gastropoda	*Margarites groenlandicus groenlandicus*; *Boreotrophon clathratus*	*Erginus* cf. *rubellus*; *Moelleria costulata*; *Margarites groenlandicus umbilicalis*; *Margarites* cf. *vahlii*; *Buccinum ciliatum*; *Amaura candida*; *Neptunea* sp.[b]
Bivalvia	*Leionucula belotti*; *Nuculana minuta*; *Modiolus modiolus*; *Mytilus edulis*; *Crenella decussata*; *Elliptica elliptica*; *Nicania montagui*; *Hiatella* sp.; *Macoma calcarea*; *Mya truncata*	*Axinopsida orbiculata*
Amphipoda	*Anonyx nugax*; *Paroediceros lynceus*; *Halirages fulvocinctus*	*Hippomedon propinquus* [c];*Onisimus edwardsi*; *Phoxocephalus holbolli*; *Acanthonotozoma inflatum*; *Arrhis phyllonyx*; *Monoculodes borealis*; *Oediceros* sp.; *Parapleustes assimilis*; *Pleusymtes glaber*; *Dulichia spinosissima*
Cumacea	None	*Lamprops fuscatus*; *Campylaspis costata*; *Pseudocuma longicornis*[c]
Isopoda	None	*Munna* sp., *Pleurogonium spinosissimum*[c]; *Pleurogonium inerme*
Decapoda	*Sclerocrangon boreas*; *Hyas araneus*[a]	*Spirontocaris lilljeborgii* (Danielssen, 1859)
Pantopoda	None	*Achelia laevis*; *Eurycyde hispida*; *Nymphon micronyx*

[a] These species were found in the two trawl surveys and were also recorded (although with low frequency) by grab sampling in the 1980s. In terms of frequency of occurrence in two trawl survey *Crangon allmanni* and *Pandalus montagui* should be added to the list as common species

[b] The species of Neptunea were not recorded in the Gorlo earlier. According to Yu.I. Kantor's opinion this species is close to *Neptunea denselirata* Brögger, 1901; since the above species was never previously recorded from the White Sea we keep some reservation with regard to including it in the present list. The shell of this Neptunea whelk is deposited in the Zoological Museum of the Moscow University

[c] First record for the White Sea

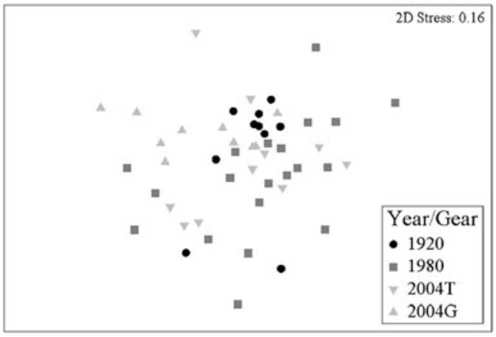

Fig. 4 Non-metric MDS ordination of Bray–Curtis similarities based on presence/absence of the most frequent species (top 15 species included). *T* epibenthic trawl samples, *G* grab survey. Only the 15 most frequently occurring species in each survey were included in the analysis: *Hydrallmania falcata*, *Abietinaria abietina*, *Harmothoe imbricata*, *Ophelia limacina*, *Margarites groenlandicus groenlandicus*, *Nicania montagui*, *Nuculana minuta*, *Modiolus modiolus*, *Verruca stroemia*, *Balanus crenatus*, *Ophiura robusta*, *Ophiacantha bidentata*, *Henricia* sp., *Hemithyris psittacea*

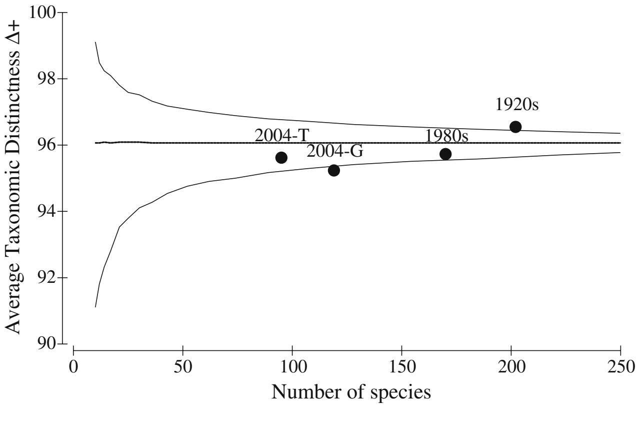

Fig. 5 Average taxonomic distinctness for constant step weighting, for all species lists from the different surveys, plotted against the numbers of species in each list. Also shown is the taxonomic distinctness indices for the full list of fauna of Gorlo (*fat line*) and the 95% confidence limits for indices (*thin line*), for random selections of subsets of number of species from the full list. *T* epibenthic trawl samples, *G* grab survey

estimates, including the combined species list, group around the value of 96. Despite the differences between species lists, the taxonomic distinctness indices show only slight, if any, statistical differences. We can conclude thus that the obtained estimates of taxonomic distinctness are realistic and consistent over time.

Taxonomic distinctness values calculated for particular groups are shown in ESM Online Resource 3. The Echinodermata and the Mollusca have highest Δ+ values (within the range 85.7–92.4 and 87.3–89.1, respectively), while the figures for the Hydrozoa (44–62.2) and the Arthropoda (60.2–66.7) are clearly lower. The Annelida hold an intermediate position (72.9–76.4).

Latitudinal-biogeographical affinity of species

The biogeographical composition of macrozoobenthos of the Gorlo Strait is characterised by having a strong dominance of species with an Arctic-boreal distribution. This group comprises 63% of all the recorded species. Proportions of Arctic and Boreal forms were similar (14%). Subtropical-Arctic and pan-oceanic species made up 5% and 4% of the populations, respectively. Shares of species belonging to particular types of latitudinal distribution in each survey varied between 1 and 4% (Fig. 6). As was the case with the taxonomic distinctness indices, despite the differences between the species lists, the biogeographical composition was markedly consistent between the surveys from the different years.

Discussion

Comparison between the species lists collected during the different surveys

The present data set comprises of the material obtained using different gears in differently designed surveys, and within a time frame of more than 80 years. One can ask a general question as to whether such data can be consistently compared. As we are looking first and foremost at the presence or absence of particular species, comparability would be problematic only in the case when grabs and trawls collect non-overlapping or nearly so sets of species. But the reality is different. Trawls, of course can provide better representation for several groups of epifauna and for large mobile forms of benthos, while grab samples are necessary for better assessment of smaller organisms of infauna. However, there is a group of species belonging both to epi- and infauna which is present in the material of all surveys in the Gorlo regardless of the gear used. Furthermore, trawl and grab samples do not show (in most cases) statistically significant differences in the composition of most common species (Fig. 4 and the results of the ANOSIM test are explained in the text). Another concern may be raised with regard to differences in the depth of sampling. The depth in the Gorlo usually does not exceed 50 m, and our stations are mostly grouped within the range 20-50, with few stations taken in 1922 and the 1980s which fall over a deep (up to 155 m) and narrow trench in the southern part of the strait (Table 1). Taken together, the stations well cover a mosaic of sandy and coarse substrates which is characteristic for the Gorlo (Nevessky et al. 1977; Rybalko et al. 1989). Thus, our combined list is most probably a reliable assessment of the macrobenthic species which occur or may occur in the Gorlo.

Taxa which appear in both trawl and grab samples demonstrate a certain level of similarity between surveys. A group of common species for all surveys has been found among polychaetes and molluscs but especially among hydroids, cirripeds, and ophiurans, i.e. the groups belonging to the epifauna. It is of interest that it is not the predominant bivalves which are characteristic of the Gorlo benthic macrofauna, like in many other parts of the White Sea (Kudersky 1966; Golikov et al. 1985; Lukanin et al. 1995; Naumov 2001). Furthermore, a small set of most commonly occurring species appears to persist through decades and their composition at the stations of different surveys is not markedly different (Table 2; Fig. 6).

Integral characteristics of the taxonomic composition of the Gorlo's macrobenthic communities may be illustrated by taxonomic distinctness indices. These indices do not differ significantly between surveys and are generally the same for most groups sampled at different times (Table 2; ESM Online Resource 3). The data from different surveys in many respects complement each other and a combined list captures important characteristics of sublittoral benthic macrofauna of the Gorlo Strait. Relatively high values of taxonomic distinctness (about 96) appear to be an important characteristic of the macrobenthic fauna of the Gorlo. Such values are obtained when species occurring in the area are distantly related, i.e. the orders include few families, the families are represented by few genera and most of genera have only one

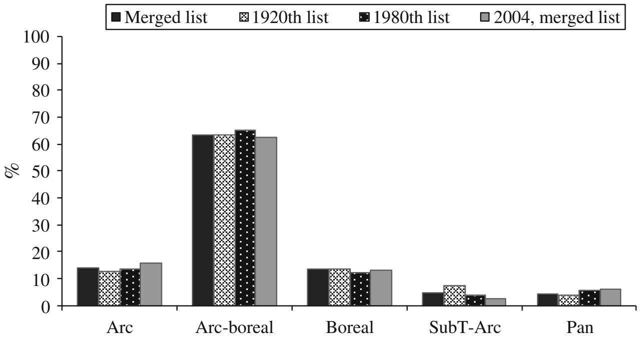

Fig. 6 Composition of species having particular type of zonal-biogeographical affinity in the sublittoral macrobenthic fauna of the Gorlo, White Sea

species in the local fauna. The situation within particular high ranking taxa, however, differs. Molluscs and echinoderms have the highest indices approaching those for the entire fauna, while the indices for hydrozoans and arthropods are considerably lower (ESM Online Resource 3). This may be explained by the fact that most of the Hydrozoa genera have from two to four species in the Gorlo fauna (that is not the case for other groups), while the majority of the Arthropoda species belong to a single order, Amphipoda. However, the question as to whether the taxonomic distinctness measures are affected by various taxonomic concepts (i.e. different placing of families into orders) needs a special investigation.

Despite harmonisation of the taxonomic nomenclature used, the species lists obtained from the three surveys differ. Likely reasons include, firstly, the species identification were carried out by different specialists and historical material is no longer available for re-examination (up to now traces of Derjugin's collection were found neither in the Zoological Institute of the Russian Academy of Sciences nor at St. Petersburg University where they could potentially be deposited). However, the share of possible synonyms, i.e. different species of same genus indicated in different surveys in the absence of common species of the genus does not exceed 14% and in most cases is lower (ESM Online Resource 2), the proportion of taxa not identified to species level is relatively low in each of the surveys and most of the species identifications from the 1920s, which were not recorded in the subsequent surveys, cause little doubt after consulting the relevant taxonomic experts. Furthermore, the publication of the complete list in ESM Online Resource 1 provides the possibility for further discussion and assessment of reliability of identification in specific cases.

A second likely reason for differences between the species lists is the variation in survey gear and sampling effort. In an ideal situation one could compare the historical data, based on similar sampling gear, but in most cases this is impossible. As noted earlier, the most evident reasons for differences in representation of Porifera, Bryozoa, and Ascidiacea between the survey of 1922–23 and later investigations are related to differences in sampling gear, the large Agassiz trawl, which effectively collects boulders and stones with epifauna versus grabs. Using a trawl as well as a grab in the 2004 survey provided better representation for several taxonomic groups, but still the light epibenthic trawl used in 2004 apparently was not as efficient for collecting the epifauna of hard substrates as was the Agassiz trawl used in the 1920s. Important characteristics of the 1980s survey was the location of several stations at shallow depths (Table 1) and thus the presence of intertidal–shallow subtidal species [such as *Tubularia larynx* Ellis and Solander, 1786, *Amphithoe rubricata* (Montagu 1808), *Caprella* spp.; see Marfenin (2006) and Tchesunov et al. (2008) for references] were not recorded by other surveys simply because of the lack of sampling at the relevant depths.

The total number of known macrobenthic species (excluding obligatory intertidal forms) in the Gorlo is about 350. The number obtained is a higher estimate than the one (210 species) published earlier (Naumov 2001). Furthermore, this is very similar to the figures for better studied areas of the White Sea: 310 species in the Kandalaksha Bay, 348 in the central Basin (348 species), and 310 species in the Dvina Bay (Naumov 2001). Only the Onega Bay is currently known to house greater numbers of sublittoral macrobenthic species; 547 according to Kudersky (1966). As expected, the number of species obtained in the surveys using the Jacknife 2 algorithm falls within 280–350 species; only the estimate for the grab survey of 2004 (which included many stations taken in relatively species poor sandy biotopes—see Spiridonov et al. 2005) is lower (Fig. 2). Since all surveys underestimate species belonging to particular taxonomic groups and inhabiting particular biotopes, we may expect that the predicted number of species which may occur in the Gorlo is greater, being likely not less than 400.

The species composition, with regard to the types of biogeographical affinity, indicates a considerable specificity of the Gorlo fauna. In general, there were practically no differences observed in the proportion of the Boreal, Arctic-boreal and the Arctic species in the macrobenthic fauna of the Gorlo between surveys of different years. Most of the species were represented by the Arctic-boreal forms, possibly tolerating a wide range of conditions, while the typical Arctic and Boreal species constitute equal minorities. The most comprehensive analysis for better studied parts of the White Sea was provided by Golikov et al. (1985). Despite some methodological differences with the present approach, it clearly indicates that both the Basin of the White Sea and Onega Bay host a lower percentage of the Arctic species (4% and 1%, respectively) and a higher percentage of the Boreal species (36% and 35%, respectively), while the share of the Arctic-boreal species is similar to that in the Gorlo (60% and 64%, respectively). The Boreal species are probably intolerant to long periods of reduced temperature: negative and close to negative temperature from December to June (Anonymous 1968); the Arctic species possibly cannot tolerate summer warming in August up to and above 8°C (Anonymous 1968).

Environmental conditions at the Gorlo Strait and implications for benthic communities

The environmental conditions in the Gorlo require further discussion. Along with contrasts in temperature, Gorlo is the area dominated by very strong tidal currents (with velocity up to 2.5 m s^{-1}), which change their direction, form local circulations, create high turbulence and mix the water column generally down to the seabed (Timonov 1950; Naumov and Fedyakov 1991; Pantyulin 2003; Kosobokova et al. 2004). This leads to the transport of sand along the bottom in the form of travelling sand bands with ripples, instability of lithodynamic processes and transformation of the sediment structure with the changing current direction. A complex glacial relief complicates the facial structure of the seabed and makes the patchy seascape very dynamic (Nevessky et al. 1977; Rybalko et al. 1989). Pelagic production and accumulation of organic matter in the sediments is low and most of the particulate organic matter is of allochtonous origin and is transported by currents (Romankevich and Vetrov 2001). In such a biotope, stability and connectivity of benthic species populations is permanently under threat. Sessile suspension feeders (such as mussels and cirripeds) and sessile or anchored micropredators (such as hydroids or ophiurans) living on coarse substrates have advantages over mobile deposit or suspension feeders, burying deposit feeders and actively moving predators, but even they may be buried under the moving sand front. Furthermore, these unstable environmental conditions may cause problems for pelagic larvae of benthic invertebrates to settle at appropriate habitats.

One can suppose that most of the benthic species in the Gorlo are associated with small-scale habitat mosaics and only a limited number of species form extensively distributed populations and may be thus frequently found in all surveys. Such a common species of polychaetes as *Ophelia limacina* apparently tolerates organically poor sand deposits, whilst the hydroid *Hydrallmania falcata* is adapted to living in environments with strong currents and can use a broad range of substrata for attaching (Marfenin 2006). Common species of ophiuroids and decapods, i.e. *Crangon allmanni* and are actively moving forms and are generalist predators capable of living in various biotopes and assemblages (Anisimova 2000; Burukovsky 2009). In contrast to these taxa, many rarely occurring species may not form stable populations in the Gorlo. This spatial-temporal variation is thought to be one of the most important contributors to overall relatively high species diversity associated with low frequency of occurrence of the majority of species. Furthermore, it may also influence the differences between the species lists of different surveys.

A seemingly similar case of higher macrobenthic taxa species richness in the areas with heavier sea ice cover and lower phytoplankton production was reported by Ambrose et al. (2009) and Cochrane et al. (2009) for the Barents Sea. Ambrose et al. (2009) suggest that low resource levels may prevent a few species from becoming very abundant and outcompeting rare species. Such an explanation also stands as a complementary one for relatively high species number found in the Gorlo.

Potential for change

The present data, which demonstrate that the macrobenthic fauna of the Gorlo is generally rich but mostly consists of rarely occurring species, provide an additional interpretation for the hypothesis that the Gorlo may act as a barrier for penetration/establishment of particular species in the White Sea, excluding its outer part, the Voronka (Naumov 2006). These rarely occurring species may not have a sufficient potential for dispersal into the inner part of the sea across its central part, the Basin, where depth reaches 300 m.

In the past, during the Holocene temperature maximum, 6-7 thousand years B.P., the Gorlo Strait was somewhat deeper, the water column probably warmer in the upper part and not completely mixed in summer, and sedimentological conditions could have been more favourable for benthic animals than now. This probably provided opportunities for dispersal through the Gorlo into the inner White Sea for those species which are now absent or rarely occurring in the former area (Naumov 2006).

It is of interest to discuss if any changes can be detected, using the present data, in the benthic fauna composition in Gorlo which can be related to changes in climate and/or oceanographic conditions, as has been recently observed in the Arctic (Anisimov et al. 2007). The early 1920s belonged to a colder epoch, the 1980s to the transition epoch (Galkin 1998; Filatov et al. 2005), while the 2000s were characterised by warmer conditions and the significant inflow of Atlantic waters into the Barents Sea (Arneberg et al. 2009) and possible eastward expansion of the Boreal Atlantic species along the coast of the Kola Peninsula in the Barents Sea (Sokolov 2003; Kantor et al. 2008).

Our study in 2004 discovered some species which have not been recorded in the White Sea before. The amphipod *Hippomedon propinquus* and the isopod *Pleurogonium spinosissimum* occur in seas of the Siberian shelf and are characteristic widely distributed Arctic-boreal species (Sirenko 2001). At the same time, the discovery of Boreal species of Cumacea *Pseudocuma longicorne*, not reported in the Barents Sea (Sirenko 2001), but present in the North Sea, the Baltic Sea and other seas of temperate zone of Northern-East Atlantic (http://www.marinespecies.org/aphia.php?p=taxdetails&id=148680) is of note and requires further investigation. The discovery of the shrimp species, which previously has not even been recorded in the adjoining White Sea waters of the Barents Sea (Sokolov 2003), may be interpreted as an example of expansion of the Boreal Atlantic species to polar waters. However, these few examples do not make possible any generalization yet, as it is not clear whether such species can tolerate the conditions of the Gorlo in the longer run, establish populations there and spread further to the internal White Sea. In other aspects the faunal composition of the Decapoda (which are not a species-rich group in the Arctic but may play important role in the ecosystem) show remarkable similarity through the decades. This is in accordance with findings by Berge et al. (2009) in Isfjord of Spitzbergen.

Furthermore, stable shares of species with particular biogeographical affinity at the decadal scale, stability of the taxonomic distinctness indices and small differences in the composition of the core of most commonly occurring species suggest that climatic changes have not yet significantly affected specific oceanographical conditions and benthic habitats of the Gorlo shaping the local macrobenthic fauna. However, to demonstrate multi-decadal stability in benthic communities (as for example was done for a glacial fjord at Spitzbergen, see Renaud et al. 2007) one needs to conduct comparably designed quantitative surveys.

Conclusions

Both integral descriptors of the macrobenthic fauna used in the present study, the proportion of the species of different biogeographical affinity and the index of taxonomic distinctness, appear to be conservative characteristics. At the same time, composition of species of different biogeographical affinity is well known to vary from area to area, and taxonomic distinctness shows considerable spatial variation in and around the Canadian Arctic Archipelago (Cusson et al. 2007). Changes of the above characteristics, in such an area as the Gorlo, would suggest significant shifts in the faunal composition and the governing environmental regime. Obtaining the taxonomic distinctness index and proportions of species with different biogeographical affinity do not depend much on sampling methodology; these characteristics allow statistical comparison and may be highly relevant for monitoring biota changes under the influence of climate change. It is important to explore the applicability of these descriptors further using species inventories of the other frontier regions of the Arctic Ocean. Our case study of the Gorlo Strait suggests that even diachronic surveys, with different sampling protocols, are suitable for biogeographical characterization of the biota and the analysis based on taxonomic distinctness indices.

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