With the acidification expected in Arctic waters, populations of a key Arctic pelagic mollusc – the pteropod *Limacina helicina* – can be severely threatened due to hampering of the calcification processes. The Greenlandic name, Tulukkaasaq (the one that looks like a raven) refers to the winged 'flight' of this abundant small black sea snail. Photo: Kevin Lee (see also Michel, Chapter 14).

Chapter 8

Marine Invertebrates

Lead Authors

Alf B. Josefson and Vadim Mokievsky

Contributing Authors

Melanie Bergmann, Martin E. Blicher, Bodil Bluhm, Sabine Cochrane, Nina V. Denisenko, Christiane Hasemann, Lis L. Jørgensen, Michael Klages, Ingo Schewe, Mikael K. Sejr, Thomas Soltwedel, Jan Marcin Węsławski and Maria Włodarska-Kowalczuk

Contents

Summary **278**

8.1. Introduction **279**

8.2. Status of knowledge **280**

- 8.2.1. Regional inventories 281
- 8.2.2. Diversity of species rich and better-investigated taxonomic groups 283
  - 8.2.2.1. Crustaceans (Crustacea) 283
  - 8.2.2.2. Molluscs (Mollusca) 284
  - 8.2.2.3. Annelids (Annelida) 285
  - 8.2.2.4. Moss animals (Bryozoa) 286
  - 8.2.2.5. Echinoderms (Echinodermata) 287
- 8.2.3. The realms – diversity patterns and conspicuous taxa 287
  - 8.2.3.1. Sympagic realm 287
  - 8.2.3.2. The pelagic realm 287
  - 8.2.3.3. The benthic realm 288
- 8.2.4. Biogeography 295

8.3. Temporal trends **298**

- 8.3.1. Observations of trends 298
  - 8.3.1.1. Studies that did not show trends 299
  - 8.3.1.2. Studies showing trends where the causes may be other in addition to climate 299
  - 8.3.1.3. Studies showing trends likely due to climate change including borealization 299
- 8.3.2. Predictions 301

8.4. Conclusions and recommendations **302**

- 8.4.1. Conclusions 302
- 8.4.2. Recommendations 303

Acknowledgements **303**

References **304**

> **There are areas where the salmon is expanding north to the high Arctic as the waters are getting warmer which is the case in the Inuvialuit Home Settlement area of the Northwest Territories of Canada. Similar reports are heard from the Kolyma River in the Russian Arctic where local Indigenous fishermen have caught sea medusae in their nets.**
>
> Mustonen 2007.

SUMMARY

This chapter brings together baseline information on the diversity of marine invertebrates in the Arctic Ocean and discusses the importance of factors that have shaped patterns of biodiversity.

The Arctic Ocean is here defined as the areas north of the Bering Strait on the Pacific side and areas with consistent seasonal sea ice cover on the Atlantic side. The known marine invertebrate fauna of this area comprises c. 5,000 species, representing at least 24 phyla with representatives in all three marine realms: sea ice, pelagic and benthic. About 50% of the Arctic Ocean overlays continental shelf areas at water depths ranging from 0-500 m. This Arctic Shelf constitutes 31% of the total shelf area of the world. More than 90% of the known Arctic invertebrate species occur in the benthic realm. As for terrestrial environments, the most species rich taxon in all realms is Arthropoda, with most species among crustaceans, i.e. >1,500 species according to a recent estimate. Other species-rich taxonomic groups are Annelida, mainly bristle worms (Polychaeta), moss animals (Bryozoa) and Mollusca, including bivalves (Bivalvia) and snails (Gastropoda). Among the meiobenthos (small-sized benthic metazoans, < 1 mm) the predominant groups are free-living nematodes (Nematoda), followed by harpacticoids (Copepoda: Harpacticoida). In terms of abundance and biomass, nematodes and harpacticoid copepods typically dominate the meiofauna (as they do elsewhere), while polychaetes, bivalves and amphipods typically dominate the macrofauna, and echinoderms and crustaceans dominate the megafauna.

The number of known marine invertebrate species in the Arctic Ocean is very likely to increase in the future, because vast areas, particularly the deep-sea basins, are under-sampled. For example, a recent estimate suggests that several thousand benthic species have been missed to date. Contrary to paradigms of an impoverished Arctic fauna due to a harsh environment, as seen in the terrestrial realm, the Arctic shelf fauna is not particularly poor, but considered to be of intermediate richness, similar in overall species richness to some other shelf faunas, such as the Norwegian shelf. The pattern of declining species richness with increasing latitude, obvious in the terrestrial realm, is controversial among marine invertebrates and conclusions depend on the taxon and geographic scale studied. A latitudinal decline from the tropics to the Arctic was seen in shelf molluscs, while arthropods seem to show higher diversity in some Arctic areas compared with some non-Arctic areas.

Due to the turbulent geological history with repeated glaciation events over the last 3.5 million years, together with in ineffective isolation from adjacent oceans, *in situ* evolution of species has been hampered, and as a consequence there are few Arctic endemics, at least on the continental shelves. However, bryozoans contain more endemics than many other groups, possibly partly related to poor dispersal in this group.The present-day invertebrate fauna in the Arctic is a mixture of species with different origins, where the majority have distributions reaching outside the Arctic, i.e. the boreal parts of the adjacent oceans. By and large the Arctic Ocean is a sea of immigrants that have dispersed from adjacent oceans both in historical and in recent time.

Today's biogeographic drivers of Arctic diversity are clearly seen in the distributions of origins in relation to the two major gateways into the Arctic, i.e. from the Atlantic Ocean and the Pacific Ocean. On the continental shelves, the proportions of present-day Pacific and Atlantic species decrease with increasing distance from the Bering Strait and the NE Atlantic, respectively. Current inventories indicate that the Barents Sea has the highest species richness, being 'enriched' by sub-Arctic and boreal species. Today's Arctic deep-sea floor fauna is most closely related to the present North Atlantic fauna, which in a geological time perspective contains a strong Pacific influence.

Like other faunal elements in the Arctic, marine invertebrates are affected by climate warming. The most obvious effects will be on the fauna of the permanent ice (sympagic fauna) which will lose its habitat. However, detecting effects in the other realms is difficult, mainly because there are only few time series data available. It is expected that the fauna with strong boreal influence may show (perhaps temporarily) increased diversity, due to a combination of anticipated increased food availability for the benthos and immigration of species adapted to warmer waters. Signs of borealization are already seen in marginal areas of the Actic Ocean. Long-term estimates of climate change effects on diversity are challenging because of the complex interactions of changes on multiple levels of the Arctic system.

It is recommended that conservation actions are targeted towards whole systems rather than individual species. Since system-focused conservation efforts typically focus on limited regions, we need to know more about diversity patterns at a high spatial resolution, in particular the distribution of Arctic endemics in order to conserve as many unique species as possible. Also we need to identify the 'biodiversity hotspots' – the areas which harbor high numbers of unique species due to habitat complexity and other factors.There is a demand for research to get a better understanding of the factors and processes that affect diversity. To achieve this, regional and taxonomic gaps need to be closed, and time series are needed to address temporal dynamics and changes in biodiversity. However, since time is probably short before severe effects of climate change will appear, we cannot wait for a high frequency mapping of the whole Arctic. Instead we suggest the establishment, or in some cases continuation, of time series monitoring at selected sites in species rich Arctic areas close to the major gateways, as well as in some areas distant from the gateways into the Arctic. We also suggest protection of areas with the highest proportion of Arctic endemic species, as well as the productive polynyas where pelagic-benthic coupling

is strong and that are of high importance for higher taxonomic life.

8.1. INTRODUCTION

In this chapter, we consider the diversity of invertebrates from the entire benthic, pelagic and sea-ice realms of the Arctic Ocean, broadly defined as areas north of the Bering Strait on the Pacific side and areas with consistent seasonal sea ice cover on the Atlantic side (Bluhm *et al.* 2011a). This corresponds broadly to the delineation of the Arctic waters made in Fig. 6.4 in the fish chapter (Christiansen & Reist, Chapter 6), but excluding the Bering and Norwegian Seas. We recognize, however, that the literature cited below does not always follow this delineation.

The present invertebrate diversity in the Arctic Ocean area is the net result of many factors acting both in historical and recent time. Like in other systems on Earth, species diversity in the Arctic is influenced by niche-based factors, such as adaptation to different environmental conditions and by dispersal based factors, such as immigration from species pools. The relative importance of these two types of factors is not always easy to disentangle and may vary with scale and the degree of connectivity to other ecosystems.

Niche-based factors like adaptation to different environmental conditions are likely to account for a significant part of biodiversity in the Arctic because it is far from homogeneous. In each of the three realms, invertebrate species inhabit a multitude of different habitats. The pelagic realm contains downwelling or upwelling areas, frontal zones and polynyas with a varying degree of coupling with the benthic realm below. The recent permanent ice-cover in the Central Arctic and seasonal ice in the rest of Arctic act as a specific habitat for sea-ice associated life, and within the ice realm habitats vary from highly productive ice edge areas to more oligotrophic zones in brine channels in the ice, as well as the ice-water interface on the underside of the ice.

The sea floor contains considerable large scale topographic heterogeneity, for instance intertidal coastal areas, semi-enclosed fjords with fjord basins, estuaries of different sizes, an expanded shelf zone with a number of canyons (Voronin, St. Anna) and inner isolated depressions (like Novaya Zemlya Trench), and the deep sea with several basins separated by deep-sea ridges. At smaller scales, benthic areas contain different sediment habitats such as sand and mud as well as harder substrata like boulders and bedrocks. The Arctic Ocean covers a large area, of which about 50% overlays shelf zones, which in turn constitute 31% of the total shelf area of the world (Jakobsson *et al.* 2004). It is well known that diversity generally increases with the extent of an area (MacArthur & Wilson 1967). If so, we would expect a high total diversity in particular of Arctic shelf fauna relative to deep sea areas.

A conspicuous feature of the sea areas of the Arctic is the strong gradient in salinity, both horizontally from river mouths out into the open sea as well as vertically, from close to fresh near the surface to fully marine at depth. Hence, in addition to seasonal ice melt, salinity gradients are highly influenced by freshwater inputs from mainly the Russian rivers, but also the MacKenzie and Yukon rivers in the western part of the Arctic Ocean. These large rivers together with smaller ones create estuarine systems of different spatial sizes which often harbor a peculiar set of species adapted to cold water of low salinity. The area of most intensive fresh water impact is regarded as a specific zoogeographical unit (Siberian brackish shallow province by Filatova 1957). A consequence of high freshwater inputs is also the permanent stratification of the central Arctic Ocean with a surface salinity of less than 32‰ and a deep water salinity of 34‰ (Gradinger *et al.* 2010a), thus providing different habitats for planktonic invertebrates, because pelagic organisms, like benthic ones, have differerent tolerances for low salinity.

Furthermore, different parts of the Arctic have different levels of productivity (Michel, Chapter 14), which also may affect diversity (Currie 1991). Productive areas often have more species than unproductive areas, but the causal relationships are still unclear (Currie *et al.* 2004) and firm evidence is also lacking for such effects on marine benthic diversity, although hump-shaped relationships have been reported between chlorophyll *a* and Arctic benthos richness (Witman *et al.* 2008). An example of an oligotrophic area is the Beaufort Gyre, as compared with a productive area in the Chukchi Sea shelf (Gradinger 2009) or Barents Sea shelf (Sakshaug 1997, Denisenko & Titov 2003).

The Arctic Ocean may be regarded as an open system where the strength of the connections with adjacent oceans has changed over the last 4 million years. Water currents facilitate dispersal from sub-Arctic and boreal parts of adjacent oceans, through the Fram Strait and the Barents Sea from the Atlantic, and the Bering Strait from the Pacific Ocean (e.g. Węsławski *et al.* 2011). While the connection with the Pacific has opened and closed over time due to varying sea levels, the deep Atlantic entrance has been widely open. At present, there is some 10 times more Atlantic water than Pacific water flowing into the Arctic Ocean (Loeng *et al.* 2005).

In addition to habitat complexity and the importance of recent dispersal from adjacent oceans, the turbulent geological history has also been important in shaping present day diversity of Arctic invertebrates. In the comparatively young Arctic Ocean, the evolutionary origin of marine invertebrates reflects a Pacific origin dating back to the opening of the Bering Strait 3.5 million years ago (Adey *et al.* 2008). Throughout most of the Tertiary, the Arctic Ocean region supported a temperate biota, and fully Arctic conditions developed only during the latest part of this period. Sea ice cover formed c. 3-5 million years ago (Briggs 2003). Over the last 3-5 million years, a series of glaciation periods with intermittent de-glaciations has created an unstable environment with a series of extinction and immigration events shaping present day diversity. These extinction events are thought to have precluded extensive local evolution or endemism on the shelves (Dunton 1992). Furthermore, events during the last 3.5 million years have allowed great re-distributions of species in the boreal part of the northern hemisphere likely still affecting Arctic diversity today. The most pervasive change occurred during the late ice-free Pliocene, after the opening of the Bering Strait, when extensive transgressions of invertebrates species across the Arctic occurred (Vermeij 1989, 1991, Mironov & Dilman 2010), mainly from the species-rich Pacific center of diversity (Briggs 2003) to the Northern Atlantic, an event called 'The Great Trans-Arctic Biotic Interchange' (Briggs 1995). As contended by Briggs (2007), there is little evidence from the marine realm that invasions have decreased native diversity, but rather that they have added to the native diversity, resulting in an overall increased diversity. A result of this major transfer was therefore likely an enrichment of the Northern Atlantic pool of species with Pacific species. This pool of species may be the source of immigration into the Arctic Ocean in recent time.

Against this background we expect that invertebrate diversity in the Arctic Ocean has been shaped to a high degree by dispersal based factors like immigration and a low degree of endemism. We expect the Arctic Ocean to be dominated by wide-range boreal species. In this respect, it is interesting to compare the degrees of endemism in the Arctic with those in the Antarctic, another cold region with similar glaciation history (Krylov *et al.* 2008), but which has been much more isolated from adjacent oceans by the strong Antarctic Circumpolar Current (ACC). The ACC, formed in the Miocene, is the only current on Earth extending from the sea surface to the sea floor, unimpeded by any landmasses (Hassold *et al.* 2009). We certainly would predict a much higher degree of endemism in the Antarctic, which as we will see is in fact the case. Furthermore, given that connectivity is strong between the Arctic Ocean and the boreal parts of the Pacific and the Atlantic oceans, we would not expect a markedly lower richness in the Arctic, but fairly similar levels of species richness as in the other oceans, at least in proximity to the two gateways.

In addition to the natural structuring factors, diversity patterns in the Arctic Ocean likely are influenced by variation in sampling methods as well as sampling frequency. For instance, some areas have been extensively investigated for more than a century (Barents Sea), while other less accessible areas (deep Arctic basins) have been relatively poorly studied. This creates a challenge when estimating total numbers of species in the Arctic.

The main questions addressed in this review are:

- Is the marine invertebrate diversity in the Arctic Ocean impoverished compared with adjacent areas?
- Are there large scale diversity patterns within the AO area that can be attributed to dispersal rather than niche adaptation?
- Is the turbulent geological history and openness to adjacent oceans mirrored by a low degree of endemism?
- Are there 'hotspot' areas that by virtue of their species diversity should be protected?
- Can we predict what the effects of global warming on invertebrate species diversity will be?

8.2. STATUS OF KNOWLEDGE

Estimating total species richness in the Arctic is problematic mainly due to different levels of sampling effort among various regions. Furthermore, the sampling methods are selective and often only one or a few methods have been used at the same time and place. For instance, benthic infauna and mobile epifauna demand different gear to be sampled adequately. The seabed is mostly sampled by the traditional 'grab' method, but as grabs sample a limited area of the seabed, large sporadically occurring and patchily distributed epifauna species are poorly represented using this approach. For epifauna gear like trawls, sampling large areas of the seabed are needed. For example, more than 337 megafauna species have been collected by trawl sampling in the Barents Sea (Anisimova *et al.* 2011). Echinoderms, sponges and crustaceans were the dominant groups in this trawl study, in contrast to polychaetes, crustaceans and molluscs dominating grab samples (Zenkevitch 1963, Cochrane *et al.* 2009, Anisimova *et al.* 2011). This shows the importance of using both gear types (Jørgensen *et al.* 2011) to obtain a more complete estimate of the species richness of a given locality. Only very few studies also included the hyperfauna, i.e. the fauna primarily dwelling in the near-bottom water (but see MAREANO 2009). Along the Norwegian coast (Tromsø Flake) of the southern Barents Sea, 834 taxa were recorded using grab, trawl and sledge gear together at the same locality. Of this number, only 128 (15%) of the taxa were sampled with more than one of the gear types (Mortensen *et al.* 2009). Also, the meiofauna from the soft bottom sediments could only be collected correctly with the use of multicorers and boxcorers, while grabs underestimated the abundance of small-sized benthic biota. There are obvious differences in sampling efforts among the different Arctic sub-areas: the Barents Sea has a long history of studies lasting over one hundred years, while the western Arctic had been poorly sampled until the last few decades. A west-east declining gradient in sampling effort is also apparent in the Russian Arctic from the Barents to Laptev Seas. Several research campains undertaken in the last decades improved the situation, to a certain extent equalizing the distribution of sampling effort across the Arctic shelf (Sirenko 2004). This has led to a significant increase in our knowledge of the spatial patterns of biodiversity in Arctic seas (Gradinger *et al.* 2010a).

There have been several attempts to estimate total invertebrate diversity both for the whole Arctic marine environment and for certain areas. Despite methodological shortcomings, such efforts are important and can provide conservative estimates. With this possible bias

Table 8.1. Overview of free-living invertebrate taxa in the Arctic Ocean area as defined in Fig. 6.4 in Christiansen & Reist, Chapter 6, but excluding the Bering and Norwegian Seas. Estimates based on Sirenko (2001) and updates of ArcOD researchers (from Gradinger *et al.* 2010a).

* Includes Bryozoa, ** Includes Nematoda, *** Synonymous with Tunicata.

Taxon	Species numbers	Sea ice realm	Pelagic realm	Benthic realm
Porifera	163			163
Cnidaria	227	3	83	161
Ctenophora	7		7	
Tentaculata*	341			341
Sipuncula	12			12
Platyhelminthes	137	>1		134
Gnathostomulida	1			1
Nemertea	80		2	78
Aschelminthes**	422	>11	16	403
Mollusca	487		5	482
Annelida	571	4	6	565
Tardigrada	7			7
Arthropoda	1,547	>20	214	1,317
Chaetognatha	5		5	
Hemichordata	1			1
Echinodermata	151			151
Urochordata***	60		3	57
Total	4,219	>39	341	3,873

due to different use and selectivity of sampling gears, under-sampling of large areas and different taxonomic specificity in mind, marine invertebrates in the Arctic, excluding the Bering Sea, comprise about 5,000 free living species (Sirenko 2001, Gradinger *et al.* 2010a, Sirenko *et al.* 2010, Bluhm *et al.* 2011a). This comprises c. 8% in pelagic taxa and some connected to the sea ice (c. 1%), while the major proportion, (c. 90%), are benthic organisms living on or in the sea floor. Over 1,000 of these species live in the central Arctic Ocean of which c. 60% also occur on the continental shelves (Bluhm *et al.* 2011a, 2011b). About 75% of the known bottom-dwelling species are macrofauna – organisms larger than 1 mm. However, this high proportion is likely influenced by the higher taxonomic and sampling effort in this group. Comparatively, the microscopic metazoans are still under-studied. This may be a bias in particular when comparing biodiversity of shallow and deep areas, because individual sizes often decrease below shelf depths (Thiel 1975, Udalov *et al.* 2005).

The estimate by Gradinger *et al.* (2010a) arrived at c. 4,200 invertebrate species representing 17 phyla in the three Arctic marine realms (Tab. 8.1). The most species rich group in all three realms is the Arthropoda, mainly crustaceans, accounting for more than a third of all species (37%), followed by Annelida (14%), Mollusca (12%), Nematoda (10%) and Bryozoa, Phoronida and Ectoprocta (together 8%).

8.2.1. Regional inventories

The first complete survey of marine biodiversity in the Russian Arctic was published by Zenkevich (1963). The figures provided therein reflected both real trends in diversity along the eastern Arctic shelf and artifacts of the sampling effort. Zenkevich's review covered a half-century of studies concentrated in the western part of the Eurasian Arctic. The Barents Sea displayed the highest species diversity – with 1,851 species of free-living invertebrates, due both to the longer history of research (beginning in the late 19th century) and the significant contribution of boreal species in the fauna. The number of species was found to decrease eastward to 522 species in the Kara Sea and to increase in the Chukchi Sea (820 species) again because of the influence of the Pacific fauna (Tab. 10.1 in Gradinger *et al.* 2010a). Zenkevitch (1963) did not provide any information for the East Siberian Sea due to lack of data.

This pattern on the Eurasian shelf was still apparent in recent reviews of the macro- and megazoobenthic fauna as a whole (Fig. 8.1; Piepenburg *et al.* 2011), as well as for particular taxonomic groups (e.g Bryozoa; Fig. 8.2, see also Tab. 8.3). An increased sampling effort in the Siberian Arctic in the second half of the 20th century modified the W-E Eurasian shelf pattern to some extent. The number of known species increased drastically in the Laptev Sea from 1932 to 2004, likely a consequence of increased sampling effort (Fig. 8.3; Sirenko 2004). The results of the surveys up to the last decade of the 20th century were summarized by Sirenko (2001). The total number for taxa increased over the last two decades for selected seas by as much as twice or more (Tab. 10.1 in Gradinger *et al.* 2010a). For instance, the total diversity for the Arctic including the central Arctic Basin, but excluding the Canadian Arctic, was 4,784 species (Sirenko 2001). However, vast areas are still under-sampled, and recent estimates of hitherto missed benthic species amount to several thousands (Bluhm *et al.* 2011a, Piepenburg *et al.* 2011).

Nevertheless, these recent compilations show outstandingly high richness in the Barents Sea compared with the other Arctic regions (Fig. 8.1 and 8.2; see also Tab. 8.3). Species richness in the Chukchi Sea is comparable to that in the Laptev, East Siberian and Kara Seas.

The large-scale Arctic Ocean Diversity project (ArcOD), completed during the last decade in the framework of the Census of Marine Life, provided new species records, which have been incorporated in the worldwide on-line catalogs (OBIS 2012) and have generated new analyses of Arctic biodiversity patterns (Gradinger *et al.* 2010a, Sirenko *et al.* 2010, Bluhm *et al.* 2011a, Piepenburg *et al.* 2011). Regional species lists were erected for the Russian Arctic (Sirenko 2001), Svalbard archipelago (Prestrud *et al.* 2004), and on a smaller scale for the fjord Hornsund in Svalbard (European Marine Biodiversity All taxa Inventory site 2009), and for the White Sea at the vicinity of the White Sea Biological Station of Moscow State University (Tchesunov *et al.* 2008).

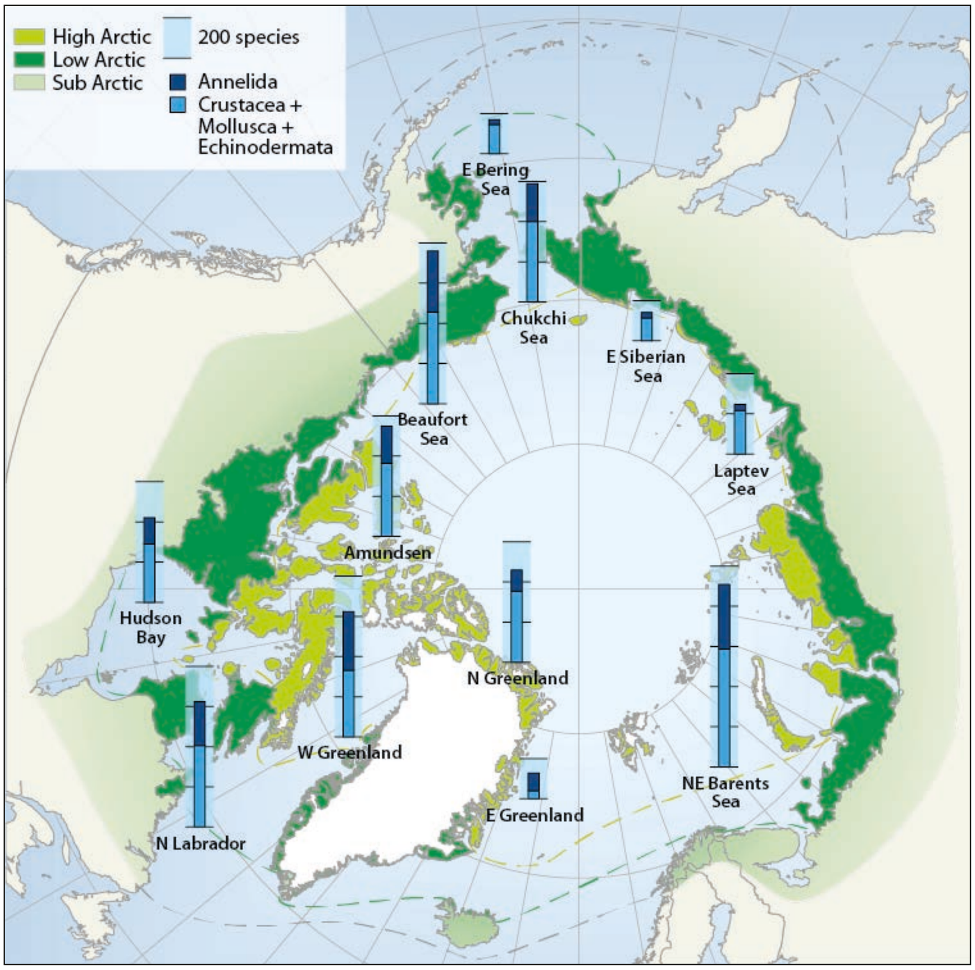

Figure 8.1. Map of the Arctic Ocean with superimposed stacked bars representing species numbers of macrozoobenthos from different shelf sea areas: Crustacea+Mollusca+Echinodermata (blue) and Annelida (black). Compiled by Piepenburg *et al.* (2011).

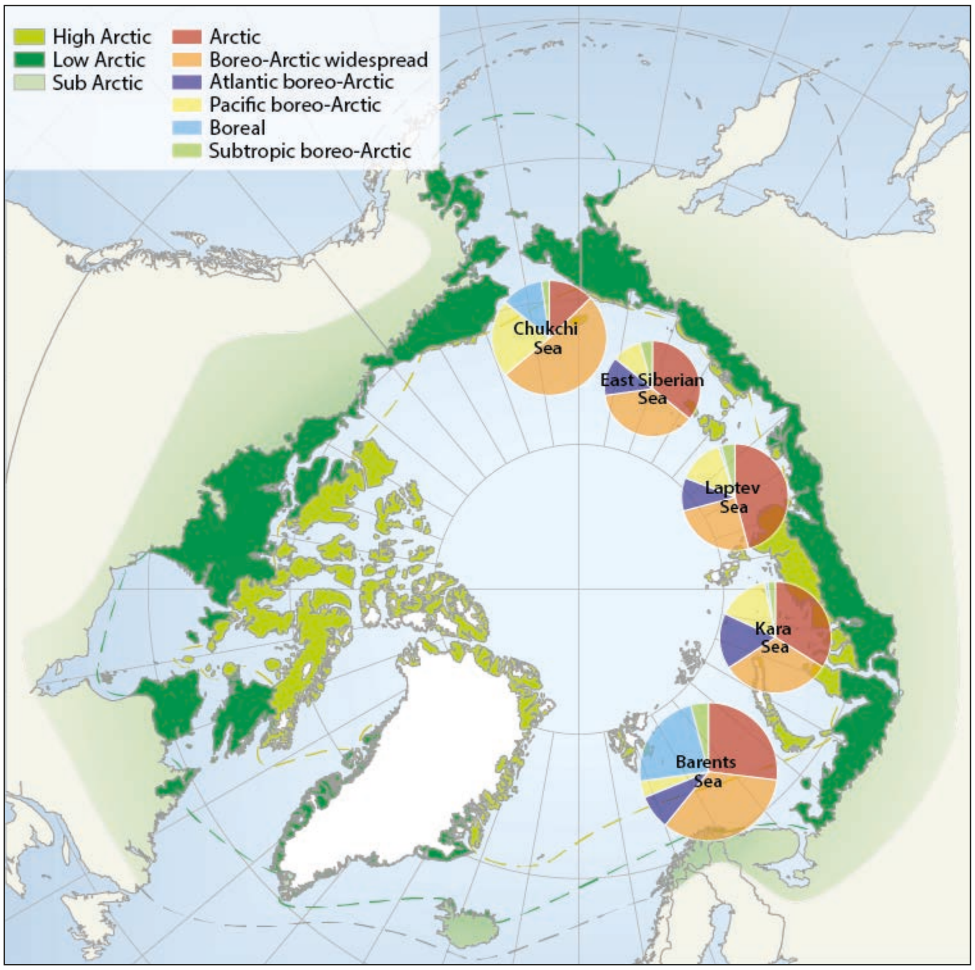

Figure 8.2. Map of the Arctic Ocean showing the distribution of species richness of Bryozoa for different shelf seas along the Eurasian continental shelf. Diameters of circles are proportional to the number of bryozoan species given in Tab. 8.3. Species numbers partitioned into six zoogeographical affinities are shown from the: Barents Sea (Denisenko 1990), Kara Sea (Gontar & Denisenko 1989); Laptev Sea (Gontar 2004), East Siberian Sea (Denisenko 2010), Chukchi Sea (Denisenko 2008).

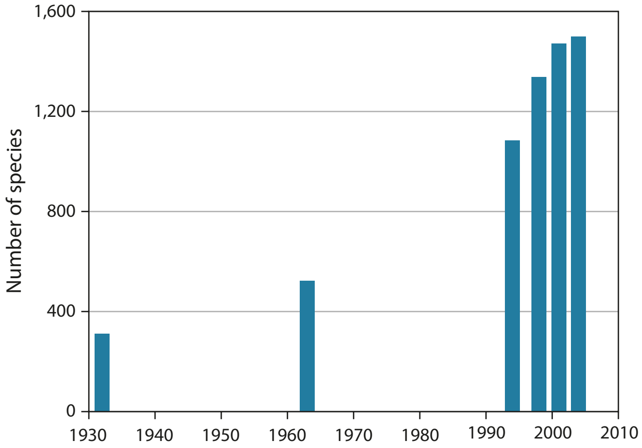

Figure 8.3. The number of macrofauna species in the Laptev Sea over time, likely illustrating effects of increased sampling effort.

In terms of species records, the most significant additions occurred for the Laptev Sea, the Central Arctic Basin and the Canadian Arctic. In the last of these, the Lincoln Sea is the least studied large marine area in the Arctic. The processing and analysis of this new information is still in progress, but a preliminary estimate gives a total of c. 4,600 species of benthic invertebrates (Bluhm *et al.* 2011a). The new records also enabled cell-by-cell area calculation of species diversity with a grid of 5° × 5° (Bluhm *et al.* 2011a). This indicates that the southwestern part of the Barents Sea remains among the most species rich areas. However, a second area of high diversity both in terms of observed and expected numbers of taxa was apparent within the outer shelf and slope of the Laptev Sea.

In an attempt to estimate total species richness of the macro- and megazoobenthic fauna on the Arctic Shelf, Piepenburg *et al.* (2011) compiled richness data for the groups Mollusca, Arthropoda, Echinodermata and Annelida. The total expected numbers of these four major taxa range between 2,596 and 3,116 (2,856±260) species. Assuming that these four taxa comprise 2/3 of total diversity (using calculations based on Sirenko (2001)), the authors concluded that about 3,894-4,674 (4,284 ± 390) macro- and megabenthic species can be expected to inhabit the Arctic shelf regions (Piepenburg *et al.* 2011). This was in reasonable agreement with previous findings of Sirenko (2001) who reported c. 3,000 taxa for the above-mentioned four groups.

An estimate of the total number of benthic invertebrate taxa in the Arctic deep sea by Bluhm *et al.* (2011b) was 1,125. However, as pointed out by the authors, this was a very conservative estimate, because the deep sea is still severely under-sampled. Hence it also is no surprise that over half of all benthic species listed for the deep Arctic have so far only been recorded in that area once or twice.

Another approach in estimating total species diversity is based on the All-Taxa-Biodiversity-Inventory first performed in terrestrial ecosystems (Sharkey 2001, Nichols & Langdon 2007). The first complete survey of this kind in the Arctic was done at the White Sea Biological Station situated on the Arctic Circle on the western White Sea shore (Tchesunov *et al.* 2008). The 50-year-long survey, summarized by 71 specialists, reported 6,008 extant species from an area of 40 km^2 that included both marine and terrestrial environments (Tchesunov 2008). Among the metazoans, 43% of the species were marine, 9% from freshwater and 48% inhabiting terrestrial biotopes. Among the marine metazoans, Arthropoda (Crustacea and Pantopoda) were the most diverse group comprising 335 species, followed by Annelida (Polychaeta, Oligochaeta and Hirudinea) with 136 species, Nematoda (mainly free-living) with 131 species, Mollusca with 113 species, Ectoprocta with 66 species and Cnidaria with 53 species. This small marine area of c. 30 km^2, with water depths ranging from 0 to 100 m, contained 61% of the total number of species known in the White Sea so far (Sirenko 2001, Tchesunov 2008). The macrobenthic fauna of the White Sea is close to being completely described, as species accumulation curves are close to the plateau for the whole sea and for its parts (Berger *et al.* 2001). The list of marine invertebrates is also close to being complete (Sirenko 2001).

A second ongoing program towards a complete inventory of local marine fauna is in Hornsund, Svalbard, an area of c. 50 km^2 from the intertidal to 280 m depth (European Marine Biodiversity All taxa Inventory site 2009). As of January 2012 more than 1,400 marine taxa have been recorded in this area, which has been regularly sampled over recent decades. The data allow extrapolations based on species accumulation curves which forecast over 2,000 metazoan species to occur in that region.

Altogether, despite differences among the different studies of sampling effort and methods, there is fair agreement among the authors with regard to the species number estimates. The existing conservative estimations for the Arctic Ocean area are approaching 5,000 metazoan species, and further increase is expected mainly in less investigated taxonomic groups (primarly meiobenthic) and areas (deep sea basins, E Eurasian and Canadian Arctic).

8.2.2. Diversity of species rich and better-investigated taxonomic groups

8.2.2.1. Crustaceans (Crustacea)

Crustaceans is probably the most species rich invertebrate group in the Arctic Ocean area, dominating the pelagic, benthic and sympagic realms. Species richness of this group in the Arctic seems to be even higher than in adjacent oceans areas of similar size (Archambault *et al.* 2010). Altogether, a recent inventory (Tab. 8.1; Gradinger *et al.* 2010a) estimated over 1,470 crustacean species in the Arctic, representing 95% of all Arctic marine arthropods. Among Crustacea the Amphipoda represents the most species rich sub-group (Tab. 8.2). However, small-sized, infaunal organisms like Harpactiocoida, Ostracoda or some families of minute Amphipoda, are little understood and every year brings discoveries of new species. Also, the number of known harpacticoid species nearly doubled from 110 in 2000 (P. Rybnikov in Sirenko 2001) to 213 in 2010 (Chertoprud *et al*. 2010). Even in the better known large epibenthic and hyperbenthic crustaceans groups like decapods, more species may be expected to be discovered in the future. The regional diversity of harpacticoids varied greatly: 179 species had been reported from the central Arctic Basin, 185 and 153 from the White and Barents Seas, respectively, and from 40-50 species for the Siberian and Canadian Seas (Chertoprud *et al*. 2010).

Table 8.2. Summary of the Arctic crustacean fauna inventory (based on Sirenko 2001 list) updated with new descriptions and distribution records from the Census of Marine Life (Bluhm *et al.* 2011a). Crustacea represent the largest component of the Arthropoda, which is the most speciose phylum in the Arctic.

Class	Order	Number of species in the Arctic marine area
Branchiopoda	Cladocera	4
Malacostraca	Stomatopoda	0
	Nebaliacea	1
	Amphipoda	577
	Decapoda	72
	Amphionidacea	0
	Euphausiacea	7
	Cumacea	59
	Isopoda	102
	Lophogastrida	0
	Mysida	33
	Tanaidacea	11
	Mictacea	0
	Bochusacea	0
	Spelaeogriphacea	0
	Anaspidacea	0
	Bathynellacea	0
Maxillopoda	Calanoida	114
	Cyclopoida	4
	Siphonostomastoida	1
	Mormonilloida	1
	Poecilostomatoida	14
	Monstrilloida	2
	Platycopioida	1
	Harpacticoida	207
Cirripedia	Thoracica	13
Ostracoda	Halocyprida	28
	Myodocopida	8
	Palaeocopida	0
	Platycopida	1
	Podocopida	210
Remipedia	Nectiopoda	0
Pentastomida	Cephalobaenida	0
	Porocephalida	0
Total		1,470

Crustaceans play a key role in the pelagic and sea ice domains (Michel, Chapter 14), where copepods and amphipods, respectively, are the dominant metazoan taxa in terms of biomass and energy flow through the Arctic system's realms (Iken *et al*. 2005, Węsławski *et al*. 2007). Soft sediments, especially in the deep sea, contain considerable numbers of crustacean species, yet polychaete worms and bivalve molluscs are more important here than crustaceans in terms of biomass and carbon remineralization. The cold water of the Arctic generally results in slow growth and high longevity among invertebrates and seasonally abundant, but otherwise sparse, food sources. This combination has permitted several herbivores to attain record sizes within their group, namely Copepoda, Amphipoda and Mysida. High lipid content, in particular for the large pelagic copepods *Calanus hyperboreus* and *C. glacialis*, makes large crustacean herbivores a rich source of energy and high quality prey for top predators, such as whales and seabirds. A limited number of crustaceans are commercially and/or subsistence-harvested in the Arctic. Examples include fisheries of the northern shrimp *Pandalus borealis*, which brings substantial income to Greenland and Norway, and the red king crab *Paralithodes camtschaticus* fishery in the Barents Sea. In the 1960s, the red king crab was first introduced to the Russian part of the Barents Sea, and then spread naturally to the Norwegian sectors. Another crab of economic importance, the snow crab *Chionoecetes opilio,* was observed in 1969 in the Russian Barents Sea, and in 2001 in the Norwegian part of the Barents Sea. Similar to the red king crab, this species seems to be permanently established in the Barents Sea and may be a potential species for harvest in the future (Pavlov & Sundet 2011).

8.2.2.2. Molluscs (Mollusca)

Sirenko's (2001) compilation of invertebrates from the Eurasian Arctic seas lists 485 species of Mollusca, including 304 species of Gastropoda, 140 Bivalvia, 23 Aplacophora, two Scaphopoda, eight Polyplacophora and eight Cephalopoda. No representatives of Monoplacophora have been recorded from the Arctic seas. The majority of the mollusc species live on the sea bottom. A recent review of the macro- and megabenthic fauna of Arctic shelf seas, undertaken within the ArcOD framework by Piepenburg *et al.* (2011), yielded a total of 392 species of Mollusca, with 205 species of Gastropoda and 156 Bivalvia. These numbers represent a very small fraction of the global species richness of marine molluscs, estimated to be about 52,000 (Bouchet 2006). The clear decline of mollusc diversity in the Arctic seas compared with lower latitudes has been reported in studies of different molluscan groups at different spatial scales. Roy *et al*. (1998) reported a clear latitudinal decline from the tropics to the Arctic in species numbers of prosobranch gastropods occurring along the

Pacific and Atlantic coasts of North America. A similar pattern was described for bivalves of the North Pacific continental shelf (Jablonski *et al.* 2000). The substantial differences between Arctic and tropical mollusc diversity has also been detected on a local scale. A comprehensive assessment of shelled benthic molluscs in Kongsfjorden, W Svalbard (Włodarska-Kowalczuk 2007) reported 87 species, while a species inventory of a tropical coastal site of similar area in New Caledonia recorded as many as 2,738 species (Bouchet *et al.* 2002). Clarke (1992) noticed that widely accepted paradigms of latitudinal clines in the seas are based mostly on patterns described for taxonomic groups producing calcareous skeletons, i.e. Mollusca and Foraminifera. He hypothesized that the sharp decrease of richness of these taxa in polar waters may be at least partly explained by the high costs of calcification at low temperatures. The diversity of the Mollusca is especially low in Arctic Ocean deep basins. Bluhm *et al.* (2011b) reviewed the macrobenthic data from Arctic bottoms deeper than 500 m, resulting in a total of only 70 species of molluscs. Bouchet & Waren (1979) explained the low diversity and high endemism of molluscan fauna in northern deep-sea basins by several factors, including the young age of present-day environmental conditions, isolation from the Atlantic and Pacific pools of species, habitat homogeneity and absence of geographic isolating barriers in the Arctic abyssal area.

8.2.2.3. Annelids (Annelida)

Annelida is the second most species rich phylum in the Arctic, after the Arthropoda (Tab. 8.1). Most annelids in the marine realm are Polychaeta, or bristle-worms, with the remainder among the Clitellata, representing leeches and oligochaetes, with few or no bristles. The family Siboglinidae, previously treated as the phyla Pogonophora and Vestimentifera, also known as beard worms, is now recognized within the Polychaeta (Rouse 2001). Therefore, updated compilations using older species lists should take care to include these taxa within the Annelida.

Sirenko (2001) recorded 517 species of Annelida (Polychaeta, Oligochaeta and Pogonophora) for Eurasian seas and the Central Arctic Basin, updated to 571 by Gradinger *et al.* (2010a) for the whole Arctic north from Fram Strait and including the Barents Sea. Zhirkov (2001) reported 670 polychaete species in the Arctic delimited by the Faroe-Iceland Ridge from the Atlantic, accounting for c. 4.5% of the world's bristle-worm fauna. Of the species listed by Gradinger *et al.* (2010a), four species are ice-associated and six have a pelagic lifestyle, with *Tomopteris* being perhaps the most familiar of the pelagic genera. The remaining annelids are benthic, with an important role in seafloor functioning, especially in soft sediments, where their burrowing activities enhance important processes such as irrigation, oxygenation and remineralisation. On hard substrates, encrusting and suspension-feeders predominate. Areas of mixed substrates often support a high species richness, both in terms of numbers of species and functional traits (Cochrane *et al.* 2012 and references therein).

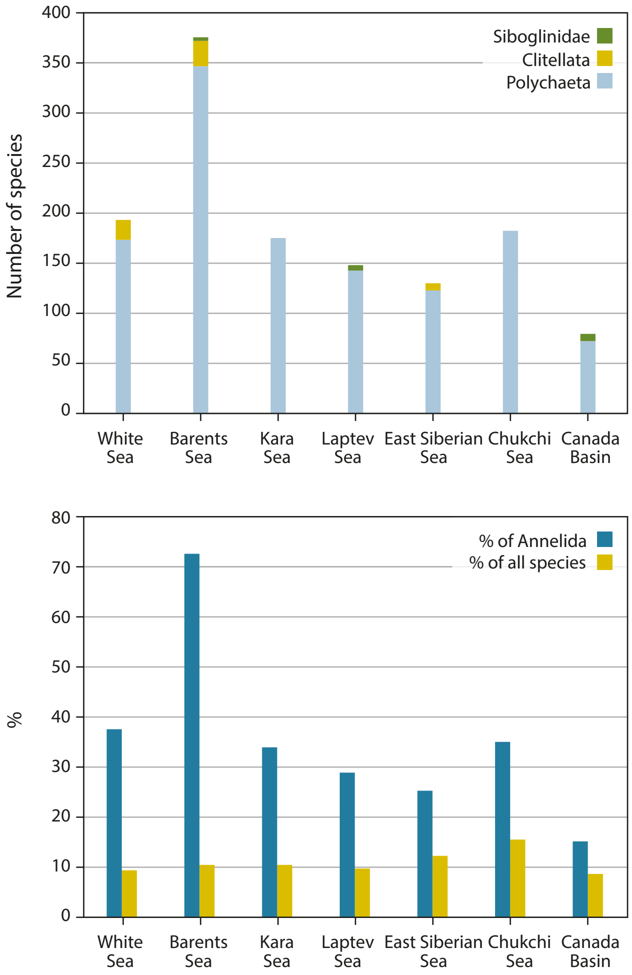

Figure 8.4. Upper panel: Numbers of annelid species recorded from each of seven regional Arctic seas (Sirenko 2001). Note: current values are expected to be somewhat higher, but updated records in this format are not available at this time. Lower panel: Proportions of annelid species numbers from each of seven regional Arctic seas and of the total number of all species recorded from the Arctic seas. Data source as for panel above.

Various reviews of circumpolar annelid species richness show high richness in the Barents, Beaufort and Chukchi seas, with far fewer species recorded from the East Siberian and Laptev shelf seas (Fig. 8.1, 8.4; Sirenko 2001, Piepenburg *et al.* 2011).

A decline in polychaete species richness was found along a transect with a minimum in the central Arctic basin (Renaud *et al.* 2006), but no such trend was evident between the Norwegian and Barents Seas (Renaud *et al.* 2009). Polychaete diversity (but not necessarily species richness) in the Barents Sea was highest in the northernmost, heavily ice-influenced areas, but equivalent trends were not seen in a comparative study off Greenland (Ambrose *et al.* 2009). Generally, annelids comprise about 10% of all species recorded across the study area, with the least in the central basin (9%) and most in the Chukchi Sea (16%). In the majority of areas, fewer than 40% of the total number of annelid species recorded from Arctic seas were present, whereas more than 70%

of all species were represented in the Barents Sea (Ambrose *et al.* 2009). Habitat complexity is likely to influence the number of species present in a given area, but in the case of the Barents Sea, a range of biogeographical affinities (Zenkevich 1963) most certainly also contributes to its high species richness. Examples of particularly species-rich taxa in the Barents Sea are the scaleworms of the genus *Harmothoe* and the spionid genus *Spio,* which have six and seven species occurring in the Barents Sea, respectively, but maximally two and three species, respectively in the other Arctic seas.

In a comparison of the diversity of soft-bottom polychaete assemblages in an Antarctic and two Arctic fjord localities of similar environmental settings, the total number of species and ES(50) were not significantly different, nor were the shapes of the species accumulation curves (Włodarska-Kowalczuk *et al.* 2007a). At both poles, the same families (Terebellidae, Ampharetidae, Maldanidae, Spionidae and Polynoidae) also dominated species numbers.

As in other areas, Arctic polychaetes include a diverse array of feeding types with many in the guild of deposit feeders (e.g. Iken *et al.* 2010). An interesting example of habitat adaptation is the spionid *Scolelepis squamata*, whose juveniles inhabit the seasonal fast ice to feed on the early ice algal bloom rather than spending that life stage in the water column, as elsewhere (Bluhm *et al.* 2010).

8.2.2.4. Moss animals (Bryozoa)

Bryozoans are colonial suspension-feeding species attached to firm substrates such as stones, macroalgae, shells etc. They are one of the most diverse systematic groups of benthic invertebrates in the Arctic seas. Early estimates arrived at c. 340 species in the Arctic region (Gontar & Denisenko 1989). However, reviews of older literature, not previously accessible, e.g. by Osburn (1955), recent field investigations and taxonomic harmonization (Denisenko 1990, 2008, 2010, 2011, Gontar 2004, Denisenko & Kuklinski 2008), as well as descriptions of species new to science (Gontar 1996, Kuklinski & Taylor 2006, Denisenko 2009), have increased the total bryozoan species number to 370 partitioned among two classes, three orders, 42 families and 94 genera. We believe, however, that the actual species number will be higher still, as some regions in the Arctic seas are understudied due to intensive ice-cover, such as the East Siberian Sea and the Canadian Arctic Archipelago. It is also likely that identification using scanning electron microscopy will reveal new taxa of bryozoans. We selected the Bryozoa to demonstrate how species richness for an individual taxon may differ among regions of the Arctic (Tab. 8.3) and how similarities in the faunal communities can illustrate regional patterns.

As is the case for several other groups, the highest species richness is recorded in the Barents and Chukchi Seas, likely resulting from the influence of relatively warm water currents entering the Arctic Ocean from the Atlantic and Pacific Oceans (Gontar & Denisenko 1989, Denisenko 1990, 2008). The share of Arctic species is relatively high in the Laptev and East Siberian Seas (Fig. 8.2), and in the western part of the Chukchi Sea.

Gontar & Denisenko (1989), using presence-absence data, showed that the bryozoan fauna of the southwestern part of the Barents Sea differed strongly from the Siberian and adjacent seas (Kara, Laptev, East Siberian and Chukchi Seas). In another study using data with relative dominance, Denisenko (1990) demonstrated segregation of bryozoan fauna of the Laptev and East Siberian Seas from that of the Barents and Kara Seas. The bryozoan fauna of the southwestern part of the Barents Sea is closely related to that of the northern coast of Norway, and the bryozoan fauna of the Chukchi Sea had a stronger relationship (similarity) with Bering Sea fauna than with bryozoans of the East Siberian Sea (Denisenko 1990). The latter had a fauna similar to the Laptev Sea, and the Canadian Arctic Archipelago bryozoan fauna was dissimilar to the other faunas (Denisenko 2010). Visual inspections of species lists appear to show that the composition of Canadian bryozoans is similar to the bryozoan fauna of the eastern and northwestern parts of the Barents Sea and the Kara Sea. The degree of bryozoan endemism in the Arctic seems higher than in most other groups, and endemism of bryozoans is globally high, which has been attributed to restricted dispersal in this group, having demersal larvae and sessile adults (e.g. Barnes & Griffiths 2008). Compared with another cold environment, the Antarctic, endemism in the Arctic is considerably lower, maybe half of the percentage in the Antarctic (c. 60%; Barnes & Griffiths 2008). This may result from the fact that during the cold period the Antarctic has been much more isolated than the Arctic with the strong Antarctic Circumpolar Current as a dispersal barrier. The cold periods in the two polar regions seem to be of approximately the same duration (Krylov *et al.* 2008).

Sea or area	Number of species	Source
Chukchi Sea	197	Denisenko 2008, Denisenko & Kuklinski 2008
East Siberian Sea	137	Denisenko 2010, 2011
Laptev Sea	170	Gontar 2004
Kara Sea	186	Gontar & Denisenko 1989
Barents Sea	284	Denisenko 1990, 2009, Gontar 1996, Kuklinski & Taylor 2006
Canadian Arctic Archipelago	98	Powell 1968

Table 8.3. Species richness estimates of the bryozoan fauna in the Eurasian seas of the Arctic and in the Canadian Arctic Archipelago (Denisenko 2011).

8.2.2.5. Echinoderms (Echinodermata)

Echinodermata is probably the best known phylum in the Arctic, likely because of relatively large body size and use of primarily epifaunal habitat. The current echinoderm species inventory holds a total of c. 160 species in all five living classes (Sirenko 2001, Sirenko *et al.* 2010), but depends on how the Arctic area[1] is defined. The number of sea stars is highest (c. 80), followed by brittle stars (c. 34), sea cucumbers (c. 32), and a few sea urchins (c. 13) and feather stars (4). Considering a larger undefined Arctic area, Smirnov (1994) listed 183 echinoderm species. In contrast to many other Arctic taxa, the echinoderm fauna is relatively well known, although a new species of sea cucumber, *Elpidia belyaevi*, was recently described (Rogacheva 2007).

Echinoderms typically dominate Artic epifaunal communities in abundance and often also in biomass. These are slow growing animals with usually long life cycles (Bluhm *et al.* 1998, Blicher *et al.* 2007). They represent a variety of feeding habits – many sea stars are predators, scavengers or omnivores; the basket stars *Gorgonocephalus* spp. and the Arctic feather stars are filter-feeders; *Ophiura sarsi* and other brittle stars, the mud star *Ctenodiscus crispatus*, the deep-sea urchin *Pourtalesia jeffreysii* and several sea cucumbers, such as *Kolga hyaline*, are deposit feeders (Iken *et al.* 2005). Echinoids and ophiuroids contribute greatly to benthic remineralization in coastal areas and on Arctic shelves (Ambrose *et al.* 2001, Blicher *et al.* 2009, Blicher & Sejr 2011),

Echinoids can be very abundant in coastal areas (Blicher *et al.* 2007, 2009, Gundersen *et al.* 2010), and ophiuroids can form dense beds attaining densities of > 100/m^2 and biomass of > 1 g C/m^2 on shelves and in the deep-sea (Piepenburg 2000, MacDonald *et al.* 2010, Blicher & Sejr 2011). Often one particular species contributes the majority of this dominance in a region, for example the brittle star *Ophiura sarsi* on the Chukchi and Beaufort Sea shelves (Bluhm *et al.* 2009, Rand & Logerwell 2010), *Ophiocten sericeum* on Eurasian shelves and *Ophiopleura borealis* on continental slopes (Piepenburg 2000).

8.2.3. The realms – diversity patterns and conspicuous taxa

8.2.3.1. Sympagic realm

The sympagic realm, or the system connected to permanent sea ice, provides habitats for both macrofaunal invertebrates and meiofaunal organisms that live in brine-filled networks and pores in the ice or at the ice-water interface. Meiofauna are dominated by acoels, nematodes, harpacticoid copepods and rotifers. In coastal ice, polychaete and other larvae may be a temporary part of the fauna (Gradinger 2002). The ice-water interface under the ice provides microhabitats for endemic macrofauna, mainly gammaridean amphipods (Bluhm *et al.* 2010). Biodiversity in sea ice is low relative to water column fauna and benthic interstitial fauna, with only a few species per higher taxonomic group (Gradinger 2002). This is in part related to the extreme conditions in sea ice, with temperatures dropping below –10 °C and salinities higher than 100‰ during winter and early spring. Also, in terms of body size, organisms are constrained by the diameters of the brine channels (Krembs *et al.* 2000).

Across the entire Arctic, the most common amphipod species occurring under the ice are *Apherusa glacialis*, *Onisimus glacialis*, *O. nanseni* and *Gammarus wilkitzkii* (e.g. Gradinger *et al.* 2010b). These ice-associated crustaceans are key prey species for the macroscopic food web of the ice pack, in particular the polar cod *Boreogadus saida*, which in turn provides primary prey for ice seals. Gradinger *et al.* (2010b) suggested that sea ice pressure ridges may function as refuges for ice fauna during the summer melt period.

Ice faunal abundances vary widely in time and space and with ice thickness, with peak densities typically found in the bottom 10 cm of the cores, where environmental conditions are most favorable. Generally, densities are much higher in coastal fast ice (during peak season up to c. 250,000 individuals/m^2) than offshore pack ice (typically < 10,000 individuals/m^2) and during the spring compared with other seasons (Bluhm *et al.* 2010). A suite of grazing species takes advantage of the early ice algal bloom at times when the pelagic blooms have not yet developed.

8.2.3.2. The pelagic realm

A conspicuous element of Arctic zooplankton includes large herbivorous copepods, such as *Calanus glacialis* and *C. hyperboreus*, which may occur in high abundance and biomass. While these large species have received most of the attention, there are over 100 other mostly smaller species of copepods (Kosobokova 1980). Among non-copepod groups, larvaceans may be abundant in polynyas and in the central Arctic (Kosobokova *et al.* 2011). According to Sirenko (2001) and Sirenko *et al.* (2010), the multicellular holoplankton in the Arctic consists of about 300 species, of which half are copepods, with the remainder including 50 species of cnidarians.

A zooplankton survey of the upper 100 m of the water column in the Arctic Canadian Basin (Hopcroft *et al.* 2005) showed that abundance was dominated by the small copepods *Oithona similis*, *Oncaea borealis* and *Microcalanus pygmaeus* and the larvacean *Fritillaria borealis typica*. Biomass was dominated by the large copepods *Calanus hyperboreus*, *Calanus glacialis* and *Paraeuchaeta glacialis* and the chaetognath *Eukrohnia hamata*. Later, Kosobokova & Hopcroft (2010) surveyed the mesozooplankton in the same area down to 3,000 m depth and found a diverse fauna of 111 species of which c. 50% were copepods. While most of the diversity occurred deeper

---

[1] Southern boundary roughly used here: Bering Strait, Fram Strait, western border of Barents Sea, Baffin Bay.

than 100 m, c. 50% of the biomass was concentrated in the upper 0-100 m layer. Depth preferences were found to be species specific, with different species dominating in different depth layers. Zooplankton diversity in the Canadian, Nansen, Amundsen and Makarov Basins was recently reviewed by Kosobokova *et al.* (2011). They reported a total of 174 species representing the Cnidaria, Ctenophora, Mollusca, Annelida, Nemertea, Crustacea, Chaetognatha and Larvacea; 70% of the species were crustaceans, with copepods as the most diverse group. They also found a great number of unrecorded and undescribed species in the bathypelagic layers, several of them endemic to the Arctic Ocean, but distributed across the different basins, suggesting low efficiency of topographic dispersal barriers between the basins.

Ctenophores and jellyfish are understudied groups in the Arctic and yet likely important invertebrate predators in the pelagic realm. Purcell *et al.* (2010) studied the distribution of these groups in the western Arctic Ocean and found an abundant ctenophore fauna shallower than 35 m water depth. Here the characteristic species are *Dryodora glandula*, *Beroe cucumis* and *Bolinopsis infundibulum*, occurring over a stratum with the large scyphomedusae *Chrysaora melanaster*, introduced into the Arctic with warm Pacific water. Some molluscs are important in the pelagic realm. The pteropod gastropods, especially *Limacina helicina*, are a trophic link between plankton and higher trophic levels, as is the squid *Gonatus fabricii*, feeding on a variety of fish and marine invertebrates and preyed upon by sperm whales *Physeter macrocephalus*, seals, porpoises and birds (Gardiner & Dick 2010).

8.2.3.3. The benthic realm

More than 90% of the invertebrate species described from the Arctic are benthic, and most of these are macrofauna (Sirenko 2001, Gradinger *et al.* 2010a). The highest number of species has been recorded from the Barents Sea, partly because it has been intensively studied in the past, and partly because of enrichment by boreo-Atlantic species (Cochrane *et al.* 2009, Węsławski *et al.* 2011). Sediments are mostly muddy on the outer shelves and in the central basins, as well as in some fjord basins. This provides extensive habitats for soft sediment fauna, including infauna and some epifauna. Coarser substrates like sand and gravel dominate the inner shelves (c.f. Bluhm *et al.* 2011a and references therein). Larger and/or more extensive hard substrate occurs in some localities with strong currents, such as the Bering Strait and Barrow Canyon, where suspension-feeders occur in high numbers. Nearshore locations are often affected by ice scouring, often resulting in a relatively impoverished fauna (Conlan *et al.* 2008). Examples of benthic habitats in eastern Baffin Bay are shown in Fig. 8.5. Solid substrates like rocks, boulder fields etc. have less spatial extension than accumulation bottoms.

While the diversity of macro- and megafauna is dominated by the phyla Annelida, Arthropoda, Mollusca, Echinodermata, Bryozoa, Cnidaria and Porifera, the smaller sized meiofauna (< 0.5 mm) is dominated by Nematoda and harpacticoid Copepoda. Less common are Kinohyncha, Tardigrada, Rotifera, Gastrotricha and Tantulocarida (Mokievsky 2009a, Gradinger *et al.* 2010a).

Because of the comparatively high number of benthic invertebrate species and habitats, the benthic realm has been subdivided into the following sub-realms or major habitats: glacial fjords, intertidal zones, shelves to shelf break at c. 500 m depth, and the deep-sea.

Glacial fjords

Glacial fjords are deep marine inlets carved out by glacial scouring, usually longer than wide, with a restricted water circulation in deeper parts due to sills at the fjord mouth (Syvitski *et al.* 1989). The fjord basins are filled with sediments, often loose muds, while hard bottom – gravel and rocks – can be found on steep sides of the fjords and at outer banks. Tidal glaciers are often located at the heads of the fjords, such that inner basins can be heavily influenced by glacial or glaciofluvial sedimentation. The soft-bottom fauna responds to the gradients of glacial sedimentation by clear changes in species composition, diversity and functional complexity (Włodarska-Kowalczuk *et al.* 2005). Glacial bays are inhabited by the communities dominated by small, mobile, surface-detritus-feeding polychaetes and bivalves (Włodarska-Kowalczuk *et al.* 1998). Suspension feeders, sedentary and tube-dwelling animals are eliminated from glacial bays by heavy mineral sedimentation, instability of sediments and low supply of organic matter. Protobranch bivalves (*Portlandia*, *Yoldiella*) are the most common dominants near glacier areas (e.g. Syvitsky *et al.* 1989, Aitken & Fournier 1993, Renaud *et al.* 2007, Włodarska-Kowalczuk 2007). Central basins of Arctic fjords host much more diverse macrobenthic communities with tube-dwelling polychaetes (the genera *Prionospio*, *Maldane*, *Spiochaetopterus*, *Heteromastus*) and suspension-feeding bivalves (*Bathyarca*, *Astarte*) among the dominants (Holte & Gulliksen 1998, Sejr *et al.* 2000, 2010, 2011, Włodarska-Kowalczuk & Pearson 2004, Glahder *et al.* 2005, Renaud *et al.* 2007, Josefson *et al.* 2008).

Both species richness and diversity usually decrease as one move from shelf toward the fjord heads, as reported from Svalbard fjords (e.g. Holthe & Gulliksen 1998, Włodarska-Kowalczuk *et al.* 2005, Renaud *et al.* 2007, Włodarska-Kowalczuk *et al.* 2012), Greenland (Schmid & Piepenburg 1993, Sejr *et al.* 2000) and the Canadian Arctic (Farrow *et al.* 1983). These patterns are stable in time (Renaud *et al.* 2007, Kedra *et al.* 2010) and are also apparent at lower taxonomic resolution (Włodarska-Kowalczuk & Kedra 2007). The tendency of decreasing species diversity in inner fjord basins is accompanied by simplification in the composition of functional groups (Włodarska-Kowalczuk *et al.* 2005, Somerfield *et al.* 2006, Włodarska-Kowalczuk & Węsławski 2008) and a decrease in spatial heterogeneity in species distribution (Kendall *et al.* 2003, Włodarska-Kowalczuk & Węsławski 2008).

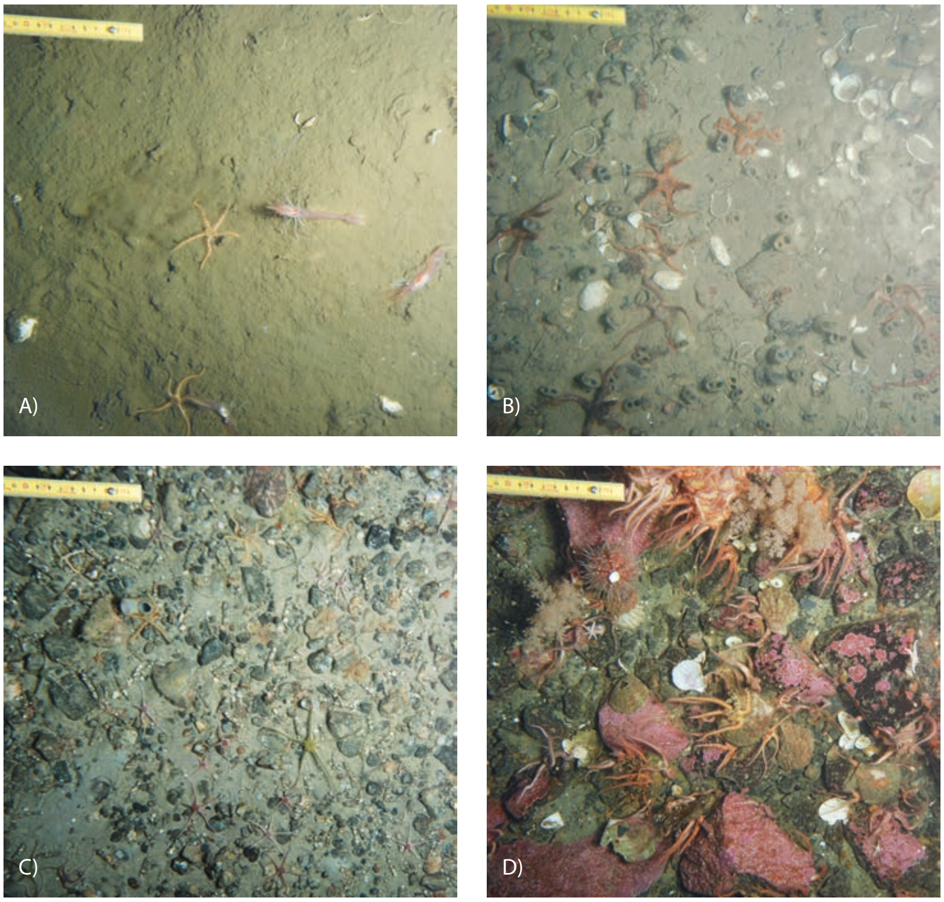

Figure 8.5. Photographs of the sea floor from eastern Baffin Bay in W Greenland, showing different benthic habitats. (A) soft mud, (B) soft sediment with shells and stones, (C) gravelly bottom and (D) boulder bottom (from Sejr *et al.* 2011).

Meiofauna in fjords has attained much less attention than macrofauna. The few published studies show that the glacial or glacio-fluvial inflows in inner fjord basins result in changes similar to those observed for macrozoobenthos, i.e. a decrease in diversity and standing stocks (Somerfield *et al.* 2006, Włodarska-Kowalczuk *et al.* 2007b, Grzelak & Kotwicki 2012).

Several species have a wide depth distribution, e.g. the annelids *Prionospio steenstrupi*, *Chaetozone setosa* (or *Chaetozone* complex) and *Maldane sarsi* that were among the dominating species on the Beaufort Sea shelf (Bilyard & Carey 1979) and the shelf and slope west of Svalbard (Włodarska -Kowalzcuk *et al.* 2004). Sejr *et al.* (2010) found that the total macrofaunal species richness in Godthaabsfjord and in an area offshore in W Greenland was in the upper range of values reported from the Canadian Arctic and the Norwegian shelf. The work of Curtis (1972) suggested a diverse polychaete fauna in Canadian Arctic fjords. Aitken & Fournier (1993) described the macrofauna inhabiting three fjords of eastern Baffin Island and compared it with earlier studies of Syvitski *et al.* (1989). Aitken & Fournier (1993) found that the macrobenthos communities in the fjords were comparable in composition to the fauna on the Baffin Island continental shelf and in E Greenland fjords, and that there was a consistent sequence of communities going from the head to the mouth of the fjords. Conspicuous species of the head community were the bivalve *Portlandia arctica*, followed by the polychaete *Onuphis conchylega*, and at the fjord mouth the maldanid polychaete *Asychis biceps*.

Arctic shallows and littoral zone

In shallow coastal areas below the inter-tidal zone, with suitable benthic substrate and moderate ice scouring, the bottoms are covered by macro-algal forests, so-called kelp beds. These beds may support a diverse and productive benthic invertebrate fauna. In a study of kelp-associated fauna in the Hornsund fjord in W Svalbard, Włodarska-Kowalczuk *et al.* (2009) found an invertebrate species richness of 11.5 species per individual algal plant that was consistent among different algal species. Among 403 plant specimens, a total of 208 invertebrate species were found with the highest number of species found in the Bryozoa (70), Polychaeta (52) and Hydrozoa (37). The most common species were the bryozoans *Tricellaria ternata*, *Celleporella hyalina*, *Eucratea loricata*, *Cibrilina annulata* and *Crisia eburnea*; the gastropod *Margarites helicinus* and the barnacle *Balanus balanus*. Estimating the total number of species using an extrapolation method yielded 259 species, considered lower than for similar assemblages at lower latitudes. In a shallow sound (2-10 m) in W Greenland, dominated by soft bottom and partial ice cover during winter, Blicher *et al.* (2011) found macrozoobenthos in high abundance (> 7,000/m^2), with a total of 120 species at 15 stations. The most common taxa were the polychaetes *Cistenides granulata*, *Owenia fusiformis*, *Ampharete acutifrons*, species of *Pholoe* and *Polydora*, and the bivalves *Macoma calcarea*, *Mya neoovata* and *Crenella decussata*.

While the substrate of kelp beds as well as deeper (> 20 m) shelf bottoms may support a high diversity of invertebrates, the intertidal bottoms generally contain an impoverished fauna, likely due to ice scouring (Węsławski *et al.* 2011). In comparison, littoral zones without ice souring such as the non-Arctic Holandsfjord in northern Norway and Kachemak Bay in S Alaska have high species richness. In contrast, more ice scour at littoral zones like the Beaufort Sea shores or the Godhåbsfjord, W Greenland, yields richness up to two orders of magnitude lower than the sites in Norway and Alaska (Węsławski *et al.* 2011).

Also the intertidal benthic communities tend to move downward to upper subtidal with latitude, as clearly seen along the western coast of Novaya Zemlia (Zenkevich 1963). The same occurs along the Eurasian coast from west to the east. The reduction of tidal amplitude eastwards from the Barents Sea and severe ice conditions force macrobenthic species to avoid the uppermost meters of the shelf zone. However, this zone is severely under-sampled, as most studies in the Arctic shallows were done by research vessels with depth restrictions. Only a few studies describe the fauna and communities between 0 and 10 meters in the area from the SE Barents Sea to the Chukchi Sea. Using SCUBA equipment, such studies were done in the Baydara Gulf of the Kara Sea (Kucheruck *et al.* 1998), Franz Joseph Land, Novosibirsk Islands and Chauna Bay (Golikov 1990, 1994a, 1994b, 1994c, Golikov *et al.* 1994). Work in the eastern Arctic confirmed that the high Arctic intertidal almost lacks macrobenthos eastwards from the Barents Sea. Benthic communities, which are quite species rich close to the shore in the western Kara Sea, tend to shift to deeper water eastwards, where the upper depth limit of permanent macrofauna is reported to be at several meters, below the zone of ice scouring (Golikov *et al.* 1994). Although being devoid of macrofauna, the intertidal and upper subtidal zone is inhabited by meiofauna, which is rich in abundance (Sheremetevsky 1897) and assumedly also diverse. This may also be the case for macrofauna where the effects of ice conditions are relatively mild, even at very high latitudes (79° N at Svalbard), with an intertidal zone that can harbor over 40 macrofauna species that also contribute considerable biomass (e.g. Węsławski *et al.* 2011).

Open shelf

About half of the Arctic Ocean area overlays shelf zones, i.e. areas at water depths down to 200-500 m. There have been great differences in investigation effort between the eastern and western Arctic. The wide open shelf of the Eurasian Arctic is covered much more densely by sampling points than the shelves of the North American Arctic. This could possibly be explained by differences in ice conditions, which has allowed exploration of most parts of Eurasian shelves without icebreakers. However, significant progress was achieved in exploration of the western Arctic during the last decades, and now the total sampling effort is more equal (Bluhm *et al.* 2011a and Fig. 1 therein).

In reviewing historical and recent benthic records, Cusson *et al.* (2007) found higher species richness in eastern than in central and western parts of the Canadian Arctic shelf. The total number of taxa of macrozoobenthos reached c. 1,000 in the Canadian Arctic Archipelago. Using the same data as Cusson *et al.* (2007), Witman *et al.* (2008) searched for general relationships between productivity and benthic species richness in the Canadian Arctic. They found that the shape of the relationships varied with community type, with negative linear relations restricted to sessile epifauna, while hump shaped relations occurred in Arctic macrobenthos (mixed epifauna, infauna). Furthermore, significant effects of chlorophyll *a* co-varied with the effects of salinity, suggesting that environmental stress as well as productivity influences diversity in the Canadian Arctic.

Conlan *et al.* (2008) studied spatial distribution of macrozoobenthos on the Canadian Beaufort shelf in relation to different habitats and reported a total of c. 500 taxa. These taxa occurred in varying densities in four different types of communities: (1) a community from the fast ice and flaw lead regions of the Beaufort shelf, dominated by the polychaete *Micronepthys minuta* and the bivalve *Portlandia arctica* and some amphipods, (2) a shelf slope community dominated by the polychaetes *Maldane sarsi*, *Lumbrineris impatiens* and *Tharyx* sp., a sipunculid and the bivalves *Bathyarca* sp. and *Yoldiella* sp., (3) a shallow-water community in an upwelling area dominated by the amphipods *Ampelisca macrocephala* and *Photis* sp., two species of ostracods and the polychaete *Barantolla Americana*, and (4) a community from the Cape Bathurst polynya, dominated by burrowing polychaetes such as *Maldane sarsi*, and the sediment-surface-feeding polychaetes *Terebellides stroemi*, *Melinna cristata* and *Tharyx* sp., together with the brittle star *Ophiocten sericeum*.

The large scale patterns in community distribution along the Eurasian coasts was summarized by Spiridonov *et al.* (2011), and it was shown that there was a shift from patchily distributed diverse communities in the western part of the area (Barents Sea) to more homogeneous distributions of main community types in the Siberian Arctic. The communities closer to the coast were dominated by bivalves (notably the genus *Tridonta,Macoma calcarea*, several nuculids, *Portlandia* species, *Astarte crenata*, *Yoldia hyperborea*, *Ciliatocardium ciliatum*) and were substituted seawards by ophiuroids (e.g. *Ophiocten sericeum*, *Ophiocantha bidentata* and *Ophiopleura borealis*) (map 2.4B in Spiridonov *et al.* 2011).

The 'Boreo-Arctic *Macoma* community' sampled by grab and described by Thorson (1957) was dominated by the bivalve species of the genera *Macoma* and *Astarte*. This is a common macrobenthic community of Arctic shelf sediments (Longhurst 2007). Of the shelf macrofauna reviewed by Piepenburg *et al.* (2011), the most widely distributed polychaetes were *Onuphis conchylega*, *Aglaophamus malmgreni*, *Eteone longa*, *Lumbrineris fragilis*, *Nicomache lumbricalis*, *Pholoe minuta* and *Scalibregma inflatum*. The most common molluscs were, in addition to the two above mentioned bivalve genera, *Musculus niger*, *Serripes groenlandicus* and *Yoldiella lenticula*. The most common crustaceans were the amphipods *Ampelisca eschrichti*, *Anonyx nugax*, *Arrhis phyllonyx*, *Byblis gaimardi* and *Haploops tubicola*, and the cumaceans *Diastylis* spp. and *Leucon nasica*. In echinoderms, the most common species were *Ophiocten sericeum*, *Ophiura robusta* and *Ophiacantha bidentata* (Piepenburg *et al.* 2011). All of these species are common also in boreal areas outside the Arctic.

The large standing stocks of widespread bivalves that dominate biomass in some shelf areas sustain the populations of gray whales *Eschrichtius robustus* and walrus *Odobenus rosmarus* (Longhurst 2007). For instance, in the *Macoma calcarea* community in the central Chukchi Sea, the greatest biomass of benthos was 4,232 g/m^2, with an average of 1,382 g/m^2 for the investigated areas (Sirenko & Gagaev 2007). Likewise, bivalves in the shallow coastal areas and banks off the Greenland coast provide important feeding items for walrus and the two eiders, common *Somateria mollissima borealis* and king eider *S. spectabilis* (Born *et al.* 2003, Boertmann *et al.* 2004, Blicher *et al.* 2011).

A study of the benthic fauna of the southern part of the Kara Sea (Jørgensen *et al.* 1999) reported nearly 500 taxa, consisting mainly of Crustacea (28%), Polychaeta (26.5%) and Mollusca (21.5%). There was a strong dominance of species with a Boreal-Arctic distribution (70.6%). However, there also was a clear increase in the proportion of Artic species going from marine to estuarine conditions and in a west to east direction, in agreement with the findings of Denisenko *et al.* (2003b). The most conspicuous species, proceeding from marine to estuarine conditions, were the polychaete *Spiochaetopterus typicus*, the bivalves *Tridonta borealis*, *Serripe*s *groenlandicus*, *Portlandia arctica* and, in the area with lowest salinity, the Arctic bivalve *Portlandia estuariorum* and the polychaete *Marenzelleria arctia*. The last of these has recently emmigrated into the Baltic Sea (Bastrop & Blank 2006). The megafauna and hyperfauna of the Kara Sea were not sampled at these locations, but if sampled they would most likely have resulted in a higher total number of taxa for the area. Similarly, Denisenko *et al.* (2003b) studying the macrozoobenthos of the Pechora Sea (SE Barents Sea) reported > 500 species consisting of Polychaeta, Mollusca, Crustacea, Echinodermata, Bryozoa and Cnidaria. Most species (69%) had a wide boreal-Arctic distribution, while only 15% were restricted to the Arctic.

Studies on macrofauna and productivity in the Barents Sea and on the influence of Arctic and Atlantic waters were conducted by Cochrane *et al.* (2009). While they showed a different faunal composition under the two water masses, they found no typical Arctic fauna under the Arctic water mass. Instead many species, many of them with a southerly boreal distribution, occurred under both water masses. These results led the authors to predict that a potential northern shift in the border of the Arctic water body would make the two water mass communities more similar in composition. Nearly 15 dominant species and taxa form about 90% of the biomass of macrozoobenthos in the Barents Sea. Conspicuous species are the bivalves *Tridonta borealis*, *Serripes groenlandicus*, *Macoma calcarea*, the polychaete *Spiochaetopterus typicus*, the sipunculoid *Golfingia margaritacea*, the sea star *Ctenodiscus crispatus* and several sponges (Denisenko 2004).

Sirenko *et al.* (1996) sampled the supra-benthic fauna, i.e. the fauna on the sediment and in near- bottom water in the Laptev Sea, from shelf depths down to the deep sea. They found 139 species in total, consisting of cnidarians, annelids, molluscs and arthropods, and species that are considered pelagic or benthic. Of these species 51 were recorded for the first time in the Laptev Sea area.

Compared with the shelf macrozoobenthos, the meiobenthos, including the protozoan Foraminifera, has received much less attention. Metazoan meiobenthos includes a wide range of higher taxa among about half of the known phyla (Giere 2009, Mokievsky 2009a). The most abundant and diverse metazoan meiofaunal taxa on the shelf are Nematoda, Harpacticoida and Turbellaria. There are more or less complete species lists for the White Sea area, where the small-sized biota represent the most significant component of newly described species. Among the 104 species new to science described from the vicinity of the White Sea Biological Station, 25 were free-living nematodes and 23 were crustaceans, mainly harpacticoid copepods (Tchesunov 2008).

The total species number of Arctic metazoan meiofauna represents c. 25% of the total number of known metazoan species (Mokievsky 2009a). In local Arctic sea faunas, this value varied from 6% to 20%, reflecting mostly differences in sampling effort rather than true differences in diversity. Very preliminary observations of overall meiobenthic diversity in the Russian Arctic seas are given in Spiridonov *et al.* (2011) (Fig. 8.6). Nematodes and harpacticoid copepods were the most diverse groups. The diversity of harpacticoid copepods was reviewed by Chertoprud *et al.* (2010).

Exept for the White and Barents Seas, the diversity of meiobenthos is likely underestimated in Arctic sub-areas. An almost overlooked meiofaunal group, likely due to inadequate sampling methods, is the free-living acoelomate flatworms (Turbellaria). Recent studies also show that this group plays an important role in sea-ice communities (Gradinger *et al.* 2010b). From what is known, the species diversity of turbellarians in the Arctic appears quite low, although the total number of species reported for the Barents Sea exceeds 100 (Sirenko 2001), or slightly less than half the number of nematode species in that area. Nearly the same figures were reported from ArcOD data, 134 species of benthic plathelminths compared with 403 species of benthic Aschelminths, which includes Nematoda (Tab. 8.1; Gradinger *et al.* 2010a). However, in the well studied areas outside the Arctic, the proportion of turbellarians is higher. For the North Sea, the list of species includes 735 species of nematodes, 515 species of harpacticoids (Heip *et al.* 1983) and 400 species of turbellarians (Martens & Schockaert

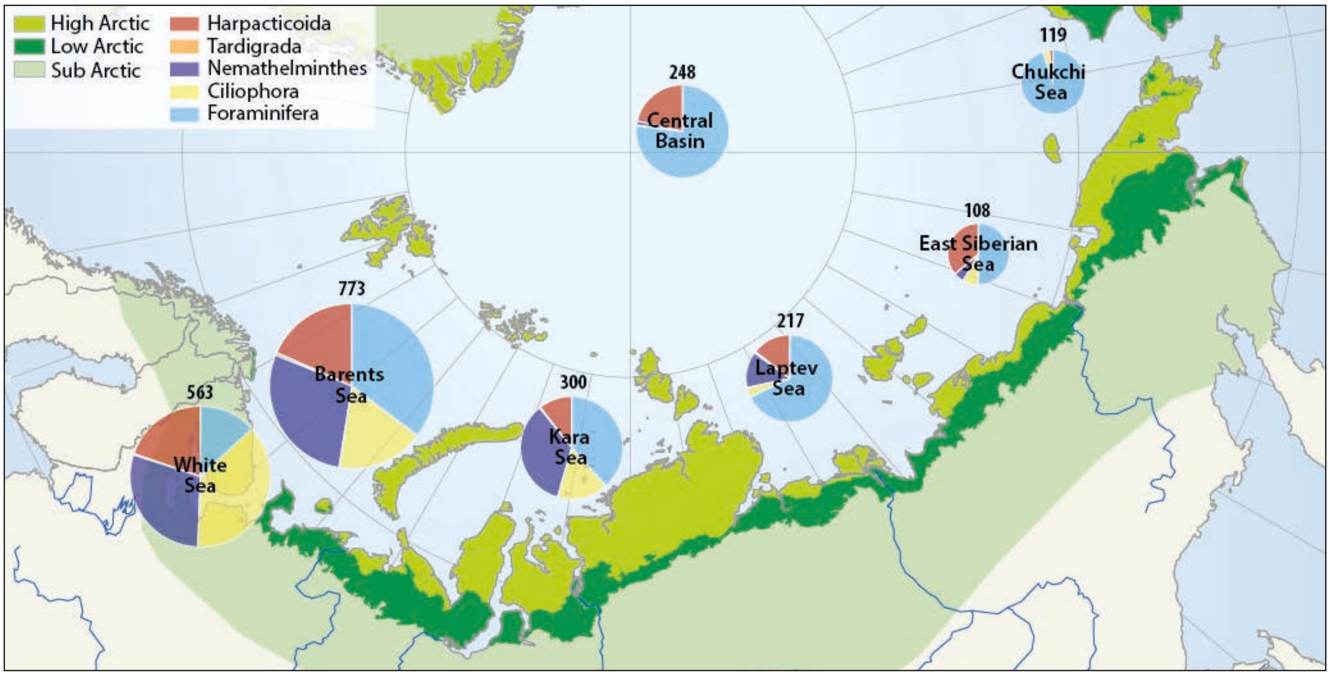

Figure 8.6. Map of the Russian Arctic showing the distribution of meiofauna diversity for different areas (from Spiridonov *et al.* 2011). Sizes of the cakes relates to total number of taxa are indicated above each cake.

1986). The German Wadden See, one of the best investigated areas in the world in terms of meiofauna, is home to 364 species of turbellarians, 333 of nematodes and and 119 of harpacticoids (Gerlach 2004). Therefore, at present it remains to be seen whether or not the relatively low proportion of turbellarians in the Arctic is related to poor knowledge or represents a true phenomenon.

The diversity of the less-studied meiofaunal taxa, such as Gastrotricha, Loricifera, Kinorhyncha and Tardigrada, is almost unknown from the eastern Arctic and Arctic deep-sea. While all these groups were reported from the Arctic (e.g. Mokievsky 1992, Soltwedel & Schewe 1998, Soltwedel *et al.* 2000, 2009b, Vanreusel *et al.* 2000), most were not identified to the species level.

Deep-sea

The deep-sea invertebrate fauna is the least studied faunal component in the Arctic Ocean (Piepenburg 2005). The macrofauna was sampled on the continental margin down into the deep-sea (3,000 m) west of Svalbard by Włhodarska-Kowalzcuk *et al.* (2004). Contrary to the general parabolic bathymetric pattern of benthic diversity in the temperate North Atlantic outside the Arctic, they found a decreasing species richness with increasing water depth, and the diversity at depths lower than 1,000 m was much lower than in comparable temperate areas. They concluded that this was due to geographic isolation of the Greenland-Icelandic-Norwegian Seas from the Atlantic pool of species, rather than to differences in productivity, as the macrobenthic biomasses on the continental margin off Svalbard were comparable to those recorded at lower latitudes.

Kröncke (1994) studied macrozoobenthos in the area between Svalbard and the Makarov Basin, reporting low species abundance, biomass and species number (42 species from 30 sites and a total sampled area of 7.5 m^2, 500 µm mesh). The most common species was the amphipod *Jassa marmorata*. Four years later, using the same methodology, Kröncke (1998) described the macrofauna of the western Eurasian Arctic Ocean on a transect from the North Pole across the Amundsen Basin and Gakkel Ridge, towards the Morris Jesup Rise and the Yermak Plateau. The species richness found this time was higher, 108 taxa from 17 sites, and it was concluded that the findings contradicted the hypothesis of declining species richness with increasing latitude, with richness comparable to levels in Antarctic and even tropical regions. The most species rich groups in this study were Polychaeta and Crustacea, the latter represented by mainly Cumacea, Isopoda and Amphipoda. The macro- and megabenthic fauna in the Arctic Canada Basin was investigated by Bluhm *et al.* (2005). Based on samples sieved through a 250 µm mesh, they reported a total of 90 benthic invertebrate taxa from six sites at the 640-3,250 m depth interval, representing four different biogeographic affinities and at least three isopod species new to science. The identified species were dominated by cosmopolitan boreo-Arctic and boreo-Atlantic species. The former was exemplified by the bivalves *Cuspidaria glacialis* and *Dacrydium vitreum*, the amphipod *Aceroides latipes* and the polychaetes *Maldane sarsi*, *Terebellides stroemi* and *Lumbrineris fragilis*. The latter was characterized by the bivalves *Yoldiella frigida* and *Bathyarca frielei*. An example of the very small group of Arctic endemics was the bivalve *Nucula zophos*. A scaphopod, *Siphonodentalium lobatum*, was reported as the most common mollusc species in Arctic deep-sea basins (Bluhm *et al.* 2005).

The larger free-living nematodes in the deep-sea Canada Basin were studied by Sharma & Bluhm (2011). The study considered individuals larger than 250 µm, of a group that in benthic surveys is often categorized as meiofauna (≥ 32 µm to 1 mm). At the 640-3,848 m depth range they found 84 genera among 25 families, with total abundance varying from 0 to 6,800 ind./m^2. Dominant families were Comesomatidae and Oncholaimidae and dominant genera *Sabatieria* and *Viscosia*. Deubel (2000) studied macrofauna on the Lomonossov Ridge, northern Laptev Sea, at 500-4,170 m, finding 474 taxa from a sampled area of 20.5 m^2 using a 250 µm mesh.

In comparison with macrofauna, the deep sea meiofauna (< 0.5 mm) has received very little attention. For example, a study in the Fram Strait yielded 180 nematode genera (Fonseca *et al*. 2010). The number of putative species found in one locality at about 2,300 m in Fram Strait was 367 (Hasemann & Soltwedel 2011). The repeated survey on the Yermak Plateu (north of Spitsbergen, Svalbard, at the depths 700-1,200 m) gave the figure of 200 putative species distributed within 89 genera (Soltwedel *et al.* 2009b). Elsewhere, on a single transect in the central Arctic Ocean, more than 110 genera of nematodes were found (Vanreusel *et al.* 2000). Even less is known about other meiofaunal groups, which are represented in the Arctic deep-sea by a relatively long list of high taxa. For example, beside nematodes and harpacticoids, the Yermak Plateau also has polychaetes, ostracods, kinorhynchs, bivalves, gastropods, tanaidaceans and tardigrades (Soltwedel *et al.* 2000). The meiofauna of the area west of Svalbard was predominantly nematodes and harpacticoids, but also included polychaetes, gastrotrichs, kinorhynchs, tardigrades, rotifers and tantulocarids. Very few species from all these groups have yet been described from the Arctic. Even for nematodes, the number of known species is low if compared with the potential diversity in the deep sea (Miljutin *et al.* 2010). More detailed studies in eastern Arctic seas will surely increase the known figures for Arctic meiofauna.

Recently, in a circumpolar review, Bluhm *et al*. (2011b) assessed biodiversity of the benthic deep-sea fauna occurring deeper than the shelf break at 500 m. They reported 1,125 taxa from the deep-sea area bounded to the Atlantic by Fram Strait. Dominant species groups in decreasing order of species numbers were Arthropoda, Foraminifera, Annelida and Nematoda. The highest abundances, up to c. 10,000 ind/m^2, were generally found on the shelf slopes. Many of the deep-sea species (61%) also occurred on the shelf, such as the polychaete *Myriochele heeri*, the tanaid *Pseudotanais affinis* and the sea star *Pontaster tenuispinus*, suggesting a shelf origin of these species. Similarly, Bilyard & Carey (1979) reported maximum diversity and abundance of polychaetes at the outer shelf and upper continental slope in the western Beaufort Sea. Abundant species in this area were the widespread boreal polychaetes *Maldane sarsi*, *Heteromastus filiformis* and *Terbellides stroemi*. Other major findings in this review were that species composition of polychaetes indicated a strong influence from the Atlantic, that modern Pacific elements were lacking, and that there was no barrier effect of the mid-Arctic ridges. As in several other habitats and realms, the Arthropoda was the most species-rich phylum.

The HAUSGARTEN case study

The recognition in the recent past that oceans are highly dynamic systems has led to new strategies in studying marine ecosystems, with the goals of achieving a more comprehensive understanding of marine processes and of developing predictions of potential system changes. Snapshot observations are no longer considered sufficient, as only long-term investigations allow the assessment of environmental factors that determine the dynamics, structure and complexity of marine communities. This is particularly obvious for the rapidly changing Arctic systems. Thus, in 1999 the German Alfred Wegener Institute for Polar and Marine Research (AWI) established the first and only Arctic deep-sea long-term observatory to detect and track the impact of large-scale environmental changes in the transition zone between the northern North Atlantic and the central Arctic Ocean (Soltwedel *et al.* 2005). The HAUSGARTEN observatory is located in Fram Strait, the only deep water connection between the central Arctic Ocean and the Nordic Seas, where exchange of intermediate and deep waters takes place. Hydrographic conditions in the area are characterized by the inflow of relatively warm and nutrient-rich Atlantic Water into the central Arctic Ocean (Rudels *et al.* 2000). Advection and the physical properties of these waters primarily control the climate of the Nordic seas and the entire Arctic Ocean (Karcher *et al.* 2011). Multidisciplinary research activities at HAUSGARTEN cover almost all compartments of the marine ecosystem, from the pelagic zone to the benthic realm, with the main emphasis on benthic processes.

The observatory currently comprises 17 sampling sites along a bathymetric transect (1,250-5,500 m water depth) and along a latitudinal transect of c. 150 km, following the 2,500 m isobath. The central HAUSGARTEN station, at 2,500 m, serves as an experimental area for unique biological short- and long-term experiments to determine the factors controlling biodiversity on the deep seafloor (Premke *et al.* 2006, Gallucci *et al.* 2008a, 2008b, Kanzog *et al.* 2009, Guilini *et al.* 2011). Work on the small benthic biota (size range: bacteria to meiofauna) focuses on *in situ* experimental work. Short-term study aspects include investigating the effects of sporadic food supplies, the reduction/prevention of food/energy supply, and the effects of physical disturbances. These experiments are intended to elucidate how the small benthic biotas interact with each other and with their changing environment. Benthic long-term studies at Hausgarten comprise biochemical analyses to estimate the input of phytodetrital matter and to assess activities and biomasses of the small sediment-inhabiting biota. Covering all size classes from bacteria to megafauna, a temporal assessment of the distribution patterns of benthic organisms is a major goal of these studies.

The metazoan meiobenthic studies at HAUSGARTEN between 2000 and 2004 revealed densities ranging on average from 149 to 3,409 ind./10 cm^2 (Hoste *et al.* 2007). Nematodes dominated at every depth and sampling year (85-99%), followed by harpacticoid copepods

(0-4.6%). Based on density of individuals, the bathymetric transect could be roughly subdivided into a shallow part between c. 1,000 and c. 2,000 m water depth, with equally high nematode and copepod densities (c. 2,000 nematodes and 50 copepods/10 cm^2), and a deeper part between c. 3,000 and c. 5,500 m, with clearly lower nematode and copepod densities (c. 600 nematodes and 11 copepods/10 cm^2).

Compared with deep-sea studies from the North Atlantic, the nematode community at HAUSGARTEN was characterized by very high species numbers, even though the number of genera was in the same order of magnitude (Hoste 2006). In the Arctic, there were relatively more rare genera and more species representing less than 1% of the overall nematode abundance. However, the overall nematode community structure at HAUSGARTEN was similar to other typical deep-sea communities, with dominant genera such as *Amphimonhystrella*, *Acantholaimus*, *Halalaimus* and members of the Desmoscolecidae and Monhysteridae. The nematode community composition changed gradually with water depth (Fig. 8.7). Differences were mainly due to variations in the relative abundance of genera rather than the presence/absence of genera. Some indicator species were found at most water depths, especially within the groups Monhysteridae, Xyalidae and Desmoscolecidae. Totaly, 640 morphotypes belonging to 152 genera and 33 families were recorded there with a prominent gradient in species richness: 432 putative species were found at 1,200 m depth, 361 at 2,500 m and 264 at 4,000 m (Hoste 2006).

Aside from water depth as the main factor accounting for differences in nematode communities, inter-annual variability in nematode community structure was apparent, with high relative abundances of *Dichromadora*, *Microliamus* and *Tricoma*. This was found to be related to high food availability (Hoste 2006).

Harpacticoid copepods, the second dominant group within the meiobenthos at HAUSGARTEN, comprised 89 species (Hoste 2006). Dominant families of copepod species numbers included the Ectinosomatidae (23.5%), Cletodidae (15.5%), Danielsseniidae (14.0%), Miraciidae (12.0%), Argestidae (7.5%), Ameiriidae (7.5%) and Huntamaniidae (5.0%). The female to male ratio was approximately 2.5:1. The copepod community comprised a wide range of body shapes, with members of each of the three ecotypes: endobenthic, epibenthic and interstitial. The bathymetric distribution of harpacticoid copepods could be divided into two depth ranges: 1,200-2,000 m and 2,500-5,000 m. according to the relative proportion of general body shapes or ‘living forms’: at the shallower part of the transect, the relative proportion of burrowing species was higher, whereas interstitial species, determined by body shape, were dominant at the deeper sites (2,500-5,000 m water depth). As with nematodes, harpacticoid diversity was higher at the upper part of the transect (Hoste 2006). Other meiobenthic groups found there were polychaetes, gastrotrichs, kinorhynchs, tardigrades, rotifers and tantulocarids. These groups were found in very low abundances, less than 2% of the total (Hoste *et al.* 2007).

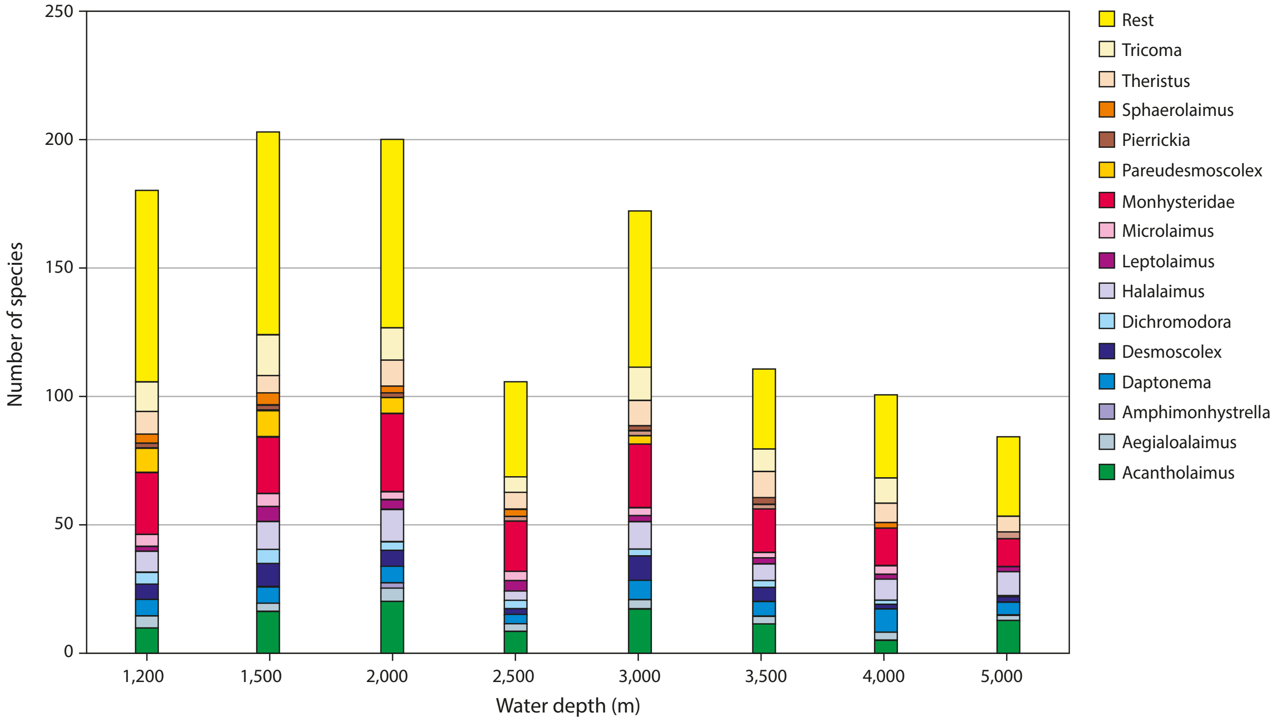

Figure 8.7. Stacked bar plot showing the number of nematode species for each dominant genus at different water depths along the bathymetric HAUSGARTEN transect (Hoste 2006).

Macrofauna in the HAUSGARTEN area was sampled twice during summer, for a bathymetric study along a depth gradient from 200 to 3,000 m in 2000 (Węsławski *et al.* 2003, Włodarska-Kowalczuk *et al.* 2004), and to study horizontal distribution patterns along an isobath at approximately 2,500 m in 2003 (Budaeva *et al.* 2008). Macrofaunal sample species richness decreased with water depth. There was, however, no clear bathymetric pattern in diversity measures; the classic increase of species richness and diversity at mid-slope depths was not observed. According to Włodarska-Kowalczuk *et al.* (2004), Shannon-Wiener diversity was the highest at 525 m ($H'_{(\log e)} = 3.54$) and lowest at 2,025 m depth ($H'_{(\log e)} = 1.46$). Species richness and diversity at the deep stations were much lower than in comparable studies from the temperate North Atlantic. Włodarska-Kowalczuk *et al.* (2004) related this finding to the geographic isolation of the Greenland-Icelandic-Norwegian Seas from the Atlantic pool of species.

Budaeva *et al.* (2008) sampled three sites along a 26 km transect along the 2,500 m isobath. Three box corers (0.25 m^2) were taken at each site, yielding a total of 3,714 specimens, belonging to 59 taxa. Total biomass ranged from 2.31 g ww/m^2 to 6.41 g ww/m^2. Dominant taxa of the macrofauna were the sponge *Tetractinomorpha* sp., the bristle worms *Myriochele heeri* and *Galathowenia fragilis*, the cumacean crustacean *Diastylis polaris*, the sipunculid *Sipunculus* sp., the snail *Mohnia mohni* and the bivalves *Bathyarca frielei* and *Tindaria derjugini*. Budaeva *et al.* (2008) discussed their findings in the context of results published by Włodarska-Kowalczuk *et al.* (2004) and suggested that the macrobenthos in the HAUSGARTEN region is organized at three spatial scales: communities that replace each other along the depth gradients, species assemblages that contribute to the heterogeneity within each vertical zone, and single-species patches that create variability at the local scale.

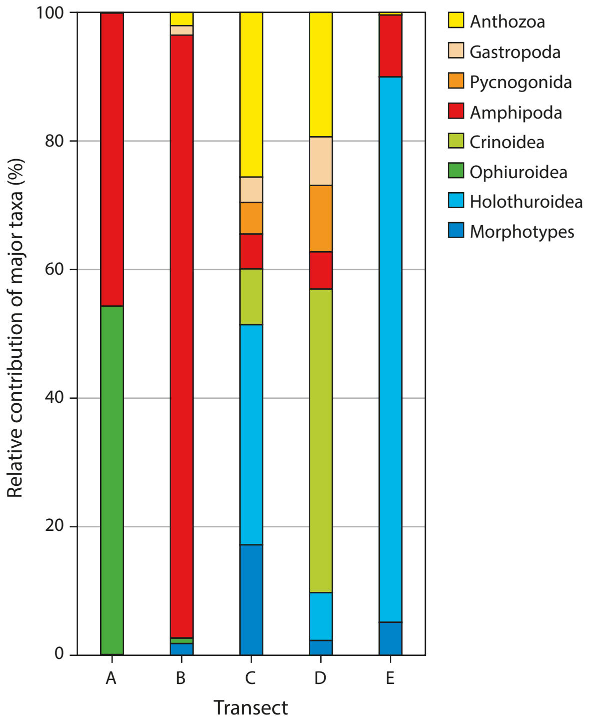

Figure 8.8. Taxonomic composition of the epi-/megafauna at the HAUSGARTEN observatory from photographic transects covering different water depth ranges (A: 1,313-1,316 m; B: 1,642-1,688 m; C: 2,432-2,629 m; D: 2,965-3,907 m; E: 5,333-5,404 m) (Soltwedel *et al.* 2009a). 'Morphotypes' denote unrecognised organisms.

Large-scale distribution patterns of epi/megafauna organisms were assessed using a towed photo/video system (Ocean Floor Observation System). As many megafaunal organisms from deep-sea environments are characterized by rare occurrence, it is advantageous that camera systems can survey transects at the scale of kilometers without causing disturbance or altering the habitat (Thistle 2003, Soltwedel *et al.* 2009a, Bergmann *et al.* 2011).

As elsewhere, megafaunal assemblages along the bathymetric transect of the HAUSGARTEN observatory are characterized by zonation, and the structure of benthic assemblages from different depths varies in terms of species composition, diversity and functional ecology (Soltwedel *et al.* 2009a). At HAUSGARTEN, megafaunal densities ranged between 11 and 38 ind./m^2, with highest densities at 1,650 m and lowest at 3,000 m depth. The number of taxa ranged from four at 5,500 m to 27 at 1,650 m water depth. The Shannon-Wiener diversity index ($H'_{(\log 2)}$), ranged from 0.34 at c. 1,700 m to 2.58 at c. 2,600 m.

The deposit-feeding boreo-Arctic brittle star, *Ophiocten cf. hastatu*, dominated the continental margins up to depths of c. 1,300m (Fig. 8.8), at mean densities of 17 ind./m^2. In contrast, at a nearby station, only some 300 m deeper, small amphipods dominated the fauna (37 ind./m^2). Deeper, at c. 2,500 m water depth, the deposit-feeding Arctic-boreal sea cucumber, *Kolga hyaline*, and suspension-feeding sea anemones accounted for the majority of megafaunal organisms, at densities of four and three ind./m^2, respectively. The suspension-feeding boreo-Arctic crinoid, *Bathycrinus carpenterii*, (5 ind./m^2) and sea anemones (2 ind./m^2) were the most abundant groups seen at c. 3,000 m water depth. The sea cucumber (*Elpidia heckeri*, 30 ind. / m^2) dominated the Molloy Hole. The zonation patterns appear to be controlled primarily by food availability (Soltwedel *et al.* 2009a).

8.2.4. Biogeography

Biogeography is generally understood as the study of broad-scale distribution patterns of species and their derivation in both a short- and long-term perspective. In recent time, this field forms an important component of the discipline macroecology together with ecology (Briggs 2007). Biogeography may help us to understand how some of the species diversity patterns we see today in the Arctic Ocean have been generated.

The Arctic invertebrate fauna on the seafloor is characterized by species with several different biogeographic affinities, with origins inside and outside the Arctic.

Considering the post Pliocene period, there are essentially four main groups with different affinities, although the groupings may vary somewhat among authors and taxonomic groups:

1. Widespread boreo-Arctic species found all over the Arctic and in sub-Arctic seas. There are, for instance, many representatives of this group among annelids.
2. Boreo-Arctic species of Atlantic origin. This is the largest group among echinoderms and the speciose crustaceans, accounting for c. 85% of the crustacean species in today's Arctic.
3. Boreo-Arctic species of Pacific origin. This is a smaller group in echinoderms restricted to the Chukchi Sea area (Sirenko 2001) and accounting for less than 10% of the crustaceans.
4. True Arctic species, including endemics only found in the Arctic. The number in this group is generally small but varies among taxonomic groups and accounts for instance for some 10% of the crustacean species and up to 30% of all bryozoan species.

The distribution patterns of species within these categories reflect the recent geological history of the Arctic but likely also reflect current dispersal barriers. In general, the true Arctic group is a minority, with relatively few endemic species. This is in contrast to the Antarctic which harbors many more endemics, attributed to the long history of geographic isolation by the Antarctic Circumpolar Current (e.g. Clarke *et al.* 2004, Hassold *et al.* 2009). The openness of the Arctic Ocean to the Pacific and the Atlantic Oceans during the last c. 4 million years probably has precluded extensive *in situ* evolution of species here.

Historical redistributions

The origin of a species is to some extent also related to the time period being considered. When we look only at the post-Pliocene period, a major part of the fauna is related to that of the North Atlantic, but when including a longer time period, the picture changes. In the later part of the Pliocene, extensive transgressions of species between the Pacific Ocean and high latitudes of the Atlantic Ocean, via the Arctic Ocean, are thought to have taken place c. 3.5 million years ago, with the direction primarily from the Pacific to the Atlantic (Golikov & Scarlato 1989, Vermeij 1989, Briggs 2003, Vermeij & Roopnarine 2008). Consequently, many of the boreal species found in the northern Atlantic since the Pleistocene and now regressing towards the Pacific on the Eurasian side of the Arctic are possibly expatriated Pacific species that have evolved further to become secondary Atlantic species. This is for instance seen in the asteroid echinoderms (Mironov & Dilman 2010), where several Atlantic taxa have closely related congeners in the Pacific, such as the species pairs of *Pteraster obscurus – P. ornatus* (Asteroidea) and *Gorgonocephalus arcticus – G. eucnemis* (Ophiuroidea) (Smirnov 1994). The hypothetical schemes of these redistributions (Mironov & Dilman 2010), based on species distribution maps, are supported now by the first gene-geographical studies on Arctic marine invertebrates (Addison & Hart 2005, Nikula *et al.* 2007, Hardy *et al.* 2011, Carr *et al.* 2011). Since the Pliocene, some echinoderms endemic to the Arctic may also have evolved (Smirnov 1994), such as the echinoid *Pourtalesia jeffreysii*. The importance of this 'The Great Trans-Arctic Biotic Interchange' (Briggs 1995) may have been an 'enrichment' of the North Atlantic species pool, because as pointed out by Briggs (2007), there is little evidence from the marine realm that invasions have decreased native diversity, but have instead resulted in an overall increased diversity. This pool of species may be a great source of immigration into the Arctic Ocean through the Atlantic gateway in recent time.

Historical extinctions

Later, in the Pleistocene Quarternary period, starting c. 2 million years ago, glaciation periods nearly eradicated the shelf fauna (Dunton 1992), e.g. via ice standing on the shelf sea floor in glacial periods. Moreover, during maximal glaciation, the sea level was c. 100 m lower than today (Hopkins 1973, Fairbanks 1989), and large emergent areas of the shelf were dry or not covered by ice (Chukchi, Beaufort and East Siberian Seas). During that time, the submersed ice-free parts in these areas may have acted as a refugium for some shelf species. If this was the case, the Beringian refugium was important both for marine and terrestrial species. The effects of these historical extinctions are likely seen in the bristle worms (Polychaeta), with littoral and shelf areas down to 300 m dominated by boreal-widespread species and a corresponding near absence of endemic species (Bilyard & Carey 1980). This, and relatively low species richness, was attributed to invasions in inter-glacial periods during the Quarternary (Bilyard & Carey 1980). The changing relative influence of the Pacific on the littoral fauna correlates well with distance from the Bering Strait, with highest proportion of Pacific species in the Chukchi Sea (Fig. 3 in Dunton 1992). The development of population genetic analyses will provide more opportunities to trace the species redistribution on a geological time scale and to evaluate cryptic species diversity in light of historical isolation (Carr *et al.* 2011).

Present patterns

There are several different biogeographic schemes for the Arctic (Zenkevitch 1963, Larsen *et al.* 2003, Spalding *et al.* 2007, Zhirkov 2010), all of them dividing the Arctic Ocean into a deep-sea region with its own fauna and a number of shallow water (shelf) sub-divisions. One of the most prominent boundaries, separating the Arctic from the sub-Arctic, crosses the Barents Sea, from NW to SE (Fig. 8.9; Denisenko 1990). Although the exact positions of the boundaries may vary depending on taxonomic group, they broadly reflect the hydrological and climatic influence on the distribution of species with different biogeographic affinities. A second zoogeographical border in the Arctic is situated in the East Siberian and Chukchi Sea areas. However, the exact position of the border is still unclear (Mironov & Dilman 2010). There are also gaps in knowledge of species distributions in this region, many of which have eastern or western distribution limits. This applies to shallow-water and deep-water

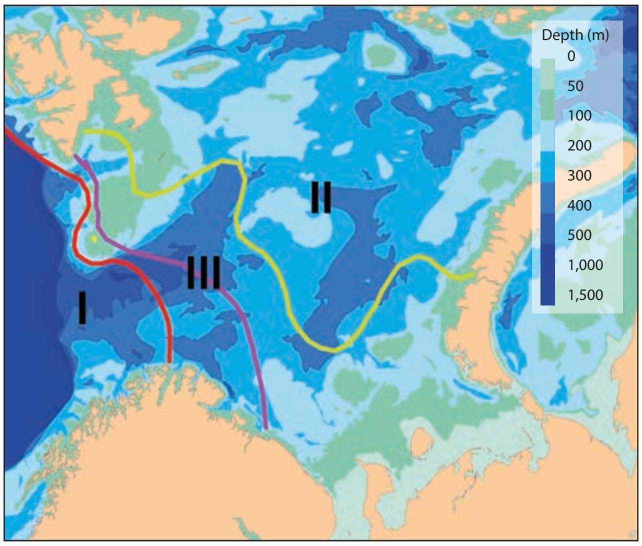

Figure 8.9. Biogeographic borders in the Barents Sea based on species distributions of bryozoans. Average position of the border with 50:50% of Atlantic boreal and Arctic species numbers is indicated by the purple line, and the red and yellow lines indicate the extreme positions of the border in cold and warm periods, respectively. Area III between them is the transitional zone between the Atlantic boreal and the Arctic regions. Thus, area I always has > 50% Atlantic boreal species, and area II always > 50% Arctic species (after Denisenko 1990).

species. The boundary in this region likely reflects the meeting of waters with Arctic and Pacific origin.

Differences in affinity composition among regions

The Atlantic boreal influence is apparent in zoobenthic assemblages of the Barents Sea, a shelf sea at the entrance of the Atlantic, where boreo-Atlantic species dominate in areas influenced by Atlantic and Arctic water masses, and only few species can be characterized as truly Arctic (Cochrane *et al.* 2009). In the adjacent more easterly Kara Sea shelf, Jorgensen *et al.* (1999) and Denisenko *et al.* (2003a) reported c. 20% true Arctic species, c. 70% widely distributed boreal species, with the rest dominated by Atlantic boreal species and only few of Pacific boreal origin.

Biogeographical zonation in the Russian Arctic, recently reviewed by Spiridonov *et al.* (2011), is strongly influenced by freshwater outputs from the large Siberian rivers. The cold brackish shallow zone along the Russian Arctic coast harbors a number of relict species: the isopod *Saduria sibirica*, the bivalves *Cyrtodaria kurriana* and *Portlandia aestuariorum* and some others (Filatova 1957, Gurjanova 1970). Most of these species are not true endemics of the Arctic. During historical changes in their distributional ranges, many of the shallow water species found refuges in the Baltic Sea and North Pacific Ocean.

The deep sea areas (below 300 m) have a different long-term history than shallower areas, as Pliocene glaciations affected these habitats differently. The bathyal parts of the Arctic Ocean have likely not been affected by ice groundings during glacial periods and have a long history of relative isolation from other oceans, in particular from the Pacific due to the shallowness of the Bering Strait (70 m). As a result, the bathyal contains a more endemic fauna with few Pacific elements, as seen in the Polychaeta (Bilyard & Carey 1980) and several other groups (Vinogradova 1997). Examples of deep-sea endemism include sea cucumbers (Holothuroidea) of the genera *Elpidia* and *Kolga,* occurring with four other endemic species in the Arctic, at that time considered endemic (Rogacheva 2007). However, two of these species, *Elpidia glacialis* and *Kolga hyalina*, were later recorded at 2,700 m depth in the sub-Arctic Norwegian Sea (MAREANO 2009, Mortensen *et al.* 2009), indicating that they were not true Arctic endemics.

The differential effects of glaciation history on shelf and deep-sea areas are now also seen in the bathymetric distributions of species and differences in endemism between thes areas. There are probably more endemic species in the deep sea areas of the Arctic Ocean than on the shelf. While glaciation likely eradicated the fauna on large parts of the shelf, the deep-sea was not directly affected in this manner. For example, the Pacific boreo-Arctic echinoderms have a limited bathymetric range in the Arctic (often < 100 m), while the Atlantic boreo-Arctic species are mostly eurybathic. This is believed to be the result of substantial shelf glaciation on the Atlantic side that caused primarily eurybathic species to escape to great depths for survival, and later re-invade the shelves when conditions changed (Nesis 1983). In contrast, the Pacific side of the Arctic lacked significant shelf glaciation. As a consequence, only about two dozen echinoderm species occur deeper than 1,000 m in the Arctic Basin (Anisimova 1989).

The latitudinal gradient

A strong spatial pattern in biogeography (macroecology) is the relationship between species richness and climate, and because climate changes with latitude, there is often a relationship between richness and latitude. Warm and wet areas often harbor more species than cold and dry areas (Currie *et al.* 2004). Broadscale richness patterns of several terrestrial and freshwater organism groups in the Arctic agree with this pattern, showing decreased richness with increasing latitude (see Fig. 2.1 in Payer *et al.*, Chapter 2). It is not clear, however, if richness of marine invertebrates follows this pattern.

Indeed, this general idea of lower diversity in the Arctic due to a harsh climate, but also in relation to the Antarctic, has recently been questioned regarding marine invertebrates (Kendall & Aschan 1993, Kendall 1996, Ellingsen & Gray 2002, Piepenburg 2005, Włodarska-Kowalczuk *et al.* 2007a). As more biodiversity investigations in the Arctic are accumulating, indications are that the Arctic harbors a higher diversity of invertebrate fauna than previously thought. The Arctic shelf fauna is similar in overall species richness to other shelf faunas, such as that of the Antarctic shelf (Piepenburg *et al.* 2011) or the Norwegian shelf (Ellingsen & Gray 2002), and intermediate on a global scale.

However, changes in diversity with latitude may differ depending on taxonomic groups and the geographic extent of the analysis conducted. The decline in diversity with increasing latitude, going from tropical to high Arctic conditions, obvious in the terrestrial realm, was seen in molluscs (Roy *et al.* 1998, Jablonski *et al.* 2000). In contrast, arthropods, by far the most species-rich group in the Arctic, showed high species richness in the Arctic compared with some adjacent non-Arctic areas (e.g. Archambault *et al.* 2010), and earlier studies of the speciose arthropod group Peracarida did not find a latitudinal gradient in species richness (Brandt 1997), nor was there a latitudinal gradient in nematode richness in the worlds oceans (Mokievsky & Azovsky 2002). An explanation of the relatively high species diversity in parts of the Arctic could, as described above, be the extensive immigration of species from the large species pools in the adjacent oceans, from the Pacific to a great extent in late Pliocene and from the Atlantic afterwards until recent time.

A conspicuous feature of Arctic marine invertebrate biodiversity in general, is the strong influence from faunas in adjacent sub-Arctic and boreal parts of the Atlantic and Pacific Oceans. To a large extent, the Arctic Ocean is populated by widespread amphi-boreal species together with a great proportion of species of post-Pliocene Atlantic origin and to a lesser extent of only recent Pacific origin or true Arctic species. Thus the Arctic Ocean is largely a sea of immigrants with only few endemic species. The dramatic geological history of the Arctic Ocean in conjunction with the low degree of isolation from adjacent oceans has probably precluded *in situ* evolution of species, and the species pool in the Arctic Ocean has been differentially affected by immigration through the two major marine gateways into the Arctic Ocean. Thus, the stronger Atlantic influence compared with the Pacific may have partly resulted from the closed Bering Strait prior to the opening 3.5 million years ago. During this same time, the much wider Atlantic gateway was open, allowing an influx of species into the Arctic.

Hotspots – or just species-rich areas

One recent popular conservation strategy, mainly based on terrestrial experience, is to protect as many unique or endemic species as possible, by protecting so-called biodiversity hotspot areas. Such areas should contain "exceptional concentrations of endemic species that are undergoing exceptional loss of habitat" (Myers *et al.* 2000). As seen above, there are relatively few endemic marine invertebrate species in the Arctic, based on our present state of knowledge. Therefore it is doubtful if hotspots, in terms of endemic marine invertebrates, exist at all in the Arctic. A major exception may be species within the ice realm, and particularly so the unique millennia-old ice shelves (see Michel, Chapter 14). Furthermore, there are areas in the Arctic that contain high numbers of both widespread and true Arctic species, which are very likely to undergo rapid habitat change due to climate warming. The most obvious area of this kind is the Barents Sea (including the Kara Sea) area. This area, with its distinct zoogeographical border, may be the region with the highest number of species within the Arctic (e.g. Gradinger *et al.* 2010a). Although this can partly be explained by relatively higher investigation efforts compared with other regions, the elevated richness is also seen to be due to high production and species enrichment from the Atlantic Ocean (Denisenko & Titov 2003, Cochrane *et al.* 2009, Węsławski *et al.* 2011).

Unlike the Barents Sea area, the East Siberian Sea does not show a particularly high species diversity. However, it is also the least studied of all Arctic shelves. Based on present-day knowledge, species richness is higher in the adjacent productive Chukchi Sea (Grebmeier & Barry 1991), at least for groups such as shelf macro- and megazoobenthos (Piepenburg *et al.* 2011) and bryozoans (Tab. 8.3). However, relatively high species diversity is also known on the outer shelf and slope of the Laptev Sea, investigated during recent decades (Bluhm *et al.* 2011b). Similar to the Barents Sea area, the Chukchi Sea region is enriched by species from the adjacent Pacific Ocean. The Labrador-Baffin Bay-W Greenland area, which is very much influenced by the Atlantic, also shows high species richness (Piepenburg *et al.* 2011). This leads to the conclusion that areas close to entrances of the two major gateways into the Arctic may be considered species rich because they are enriched from the large species pools in the adjacent Atlantic and Pacific Oceans. These areas correspond to the 'areas of advection' proposed by Węsławski *et al.* (2011). This means that many of these species here are not unique to the Arctic, but common further south.

Other hotspot-like areas may be polynyas, i.e. productive ice-free areas within the sea ice with rich pelagic life and strong pelagic-benthic coupling (e.g. Brandt 1995, Ambrose & Renaud 1995, see also Michel, Chapter 14). A high diversity of benthic peracarida crustaceans has been reported from such areas (Brandt 1995). It is not clear if Arctic endemics are also more speciose in such areas. Polynyas are certainly of conservation relevance because of high benthic biomass, often molluscs, supporting many bird/mammal stocks (see also Michel, Chapter 14).

8.3. TEMPORAL TRENDS

8.3.1. Observations of trends

To date only a few time series of biological parameters have been collected in the Arctic and only for a limited number of taxa and regions (e.g. Wassmann *et al.* 2011). Nonetheless, some show substantial change in both pelagic and benthic habitats, although examples are most common from the benthic realm. These changes include shifts in distribution ranges as well as levels of abundance and biomass. Most of the observed changes are near the Arctic margins rather than in the central Arctic. Some of these series did not show clear trends, while some temporal studies do show trends that can be explained by climate change, particularly by the borealization of Arctic marginal sea areas.

8.3.1.1. Studies that did not show trends

Studies of macrobenthos in Onega Bay in the White Sea showed no major changes in dominant species between the 1950s and the 1990s (Solyanko *et al.* 2011a), and studies in the adjacent Gorlo Strait showed a similar result, i.e. no change in the biogeographic structure covering the period from 1920s to 2004. Also, there was no addition of North Atlantic species in the 2000s to those previously recorded in the area, leading to the conclusion that current climatic changes have not yet influenced the Gorlo Strait area (Solyanko *et al.* 2011b).

Berge *et al.* (2009) described changes in the community structure of decapods in Isfjord, Svalbard and found increases over the first half of the century for the spider crab *Hyas araneneus* and the hermit crab *Pagurus pubescens*, considered generalist species, while the specialist shrimps, *Lebbeus polaris* and *Spirontocaris spinus*, decreased in abundance. There was no change, however, in decapod species composition over the last 50 years.

Feder *et al.* (2005) studied the epibenthic fauna in the southeastern Chukchi Sea in 1976 and found that large crustaceans dominated abundance, while echinoderms, mainly composed of sea stars, dominated biomass. An investigation of the same area more than 20 years later (1998) did not show significant changes in biodiversity, while abundance and biomass had increased for the most dominant taxa such as the snow crab and the echinoderms *Ophiura sarsi* and *Stongylocentrotus droebachiensis*.

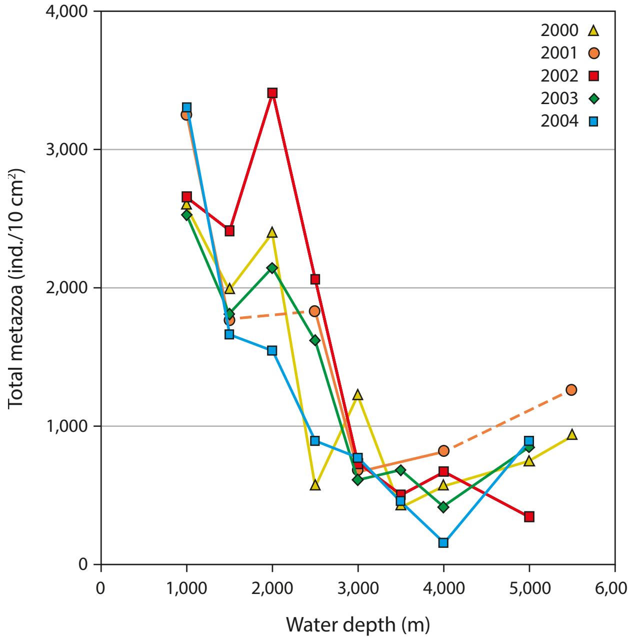

Figure 8.10. Metazoan meiofauna densities along the bathymetric HAUSGARTEN transect from 2000 to 2004 (redrawn from Hoste *et al.* 2007).

Renaud *et al.* (2007) reported high temporal stability of benthic community structure over decades in Van Mijenfjord, Svalbard, and the apparent absence of response to climate change was attributed to characteristics of semi-enclosed fjords counteracting the influence from the adjacent open sea.

No clear trends of change were found in abundance and composition of meiobenthos on the Yermak Plateau north of Svalbard during the ten year period 1997-2006 (Soltwedel *et al.* 2009b), or for meiofauna abundance from 2000 to 2004 in the eastern part of Fram Strait (Fig. 8.10; Hoste *et al.* 2007) .

8.3.1.2. Studies showing trends where the causes may be other in addition to climate

The benthos survey in 1968-1970 (Antipova 1975) showed a large decline in total biomass almost throughout the Barents Sea compared with previous surveys in 1924-1935. A considerable alteration in the distribution of boreal and Arctic species was observed, and the decline in biomass was mainly at the expense of boreo-Arctic species. The decline in the benthos biomass was suggested to be related to climate changes (Fig. 8.11). However, intensive bottom trawling started early in the 20th century and might be the most compelling reason for biomass decline. Thus, while the distribution ranges of species could be affected by changes of water temperature, the total benthos biomass is likely mostly a consequence of disturbance caused by bottom gear (Denisenko & Titov 2003), an impact well established, for example, for the North or Irish Seas (Kaiser & Spencer 1996, Hill *et al.* 1999). While a single trawling event affects an area not exceeding several thousand square meters, the result of continuous trawling affects the entire ecosystem of the sea. Thus, small-scale impacts, repeated many times over a long period, result in changes affecting an entire marine basin (Mokievsky 2009b).

Blanchard *et al.* (2010) described temporal variability in macrobenthic communities over > 35 years (1971-2007) in an Alaskan glacial fjord on the southern border of the sub-Arctic, where they found a lack in long-term stability. Apart from a readjustment after a major earthquake in 1964, long-term climatic trends, in particular in the period 1989-2007, were seen as the major factors affecting stability of community structure.

8.3.1.3. Studies showing trends likely due to climate change including borealization

Within the invertebrates, documented distribution shifts are more numerous in the benthic than pelagic realm, because benthos are easier to quantify due to their sessile habits, and the typically longer benthic life spans result in less seasonally modulated abundance and distribution that better integrate changes over longer time periods (e.g. Blacker 1957). Temporal studies are mainly available from areas close to the two major gateways into the Arctic, the Atlantic and the Pacific gateways.

The Atlantic gateway

In the deep Fram Strait, seafloor photographs taken at c. 2,500 m water depth in 2002 and 2004 indicated a striking decline in megafaunal densities and a decrease in trophic diversity (Bergmann *et al.* 2011). Inclusion of more recent footage from 2011, however, indicates a return to 2002 levels (M. Bergmann, unpubl. data). The rise of bottom water temperatures at HAUSGARTEN and the increased importance of Atlantic water masses in recent years could lead to severe changes in the production in the water column. The 'Atlantification' scenario, which is currently often suggested as the most likely outcome of global change in Fram Strait, may lead to retention of particles in the upper water column and less food reaching the seafloor, such that the benthic communities will be impoverished in the long run (Forest *et al.* 2010). Only continued observation will allow us to judge if the interannual changes witnessed are tied to climatic fluctuations such as the Arctic oscillation or are instead a consequence of the effects of global warming.

In the North Atlantic, a general warming of the ocean was observed in the 1920s and 1930s which resulted in a northward range expansion of several temperate fish species and benthic invertebrates, like the sea star *Asterias rubens*, the polychaete *Nereis virens* and the sea urchin *Echinus esculentus* along the coasts of Greenland and Iceland (Jensen 1939). In the Barents Sea, the warming resulted in a northward expansion of Atlantic species along the west coast of Svalbard (Drinkwater 2006). In the same area, several quantitative surveys (Denisenko 2001, Denisenko & Titov 2003) have also made it possible to evaluate the state of the benthos in the Barents Sea in specific climatic or historical periods. The benthos survey in 1924-1935 (see Zenkevitch 1963 for a review) was important as it probably represented the 'near-natural' state of that community before the increasing anthropogenic impacts on the Barents Sea, including impacts from intensive bottom trawling. The survey was made in a climatic period with temperatures close to long-term means (Fig. 8.11).

On a more local scale, decadal time series exists from several fjords. Glacial fjords are marine environments sensitive to natural and anthropogenic impacts – in particular the deep basin components with stratified salinity and restricted water exchange (e.g. Blanchard *et al.* 2010). Several studies have described temporal trends of invertebrates in such environments (Renaud *et al.* 2007, Blanchard *et al.* 2010). As reviewed by Węsławski *et al.* (2011), there are observations of different trends in macrofauna diversity in different parts of the Svalbard fjords – increasing trends of species richness at the mouth due to immigration with intruding Atlantic water and stable numbers in the inner parts, as in the Van Mijenfjord example.

Beuchel *et al.* (2006) studied the temporal variability of hard bottom macrobenthic diversity and composition on rocky banks of Kongsfjorden (Svalbard) over a period of 23 years (1980-2003). They reported a correlation between benthic diversity and the North Atlantic Oscillation (NAO) index (and related temperature of the West Svalbard Current), as well as a clear change in the composition of dominants that followed the shift of the NAO index from positive to negative mode. Similarly, in the Arctic rocky littoral zone at Svalbard, Węsławski *et al.* (2010) observed a change in diversity over 20 years with increasing temperatures. They reported a twofold increase in intertidal diversity, with an upward shift in algal occurrence on the coast. Sub-Arctic boreal species colonized new areas, while Arctic species retreated. The newcomers to the intertidal zone were present in 1988 in the subtidal zone. In the same fjord, Kedra *et al.* (2010) showed long-term changes in species composition in relation to Atlantic influence of soft sediment benthos. Most recently, a climate-driven regime shift was suggested to explain the abrupt changes in macroal-

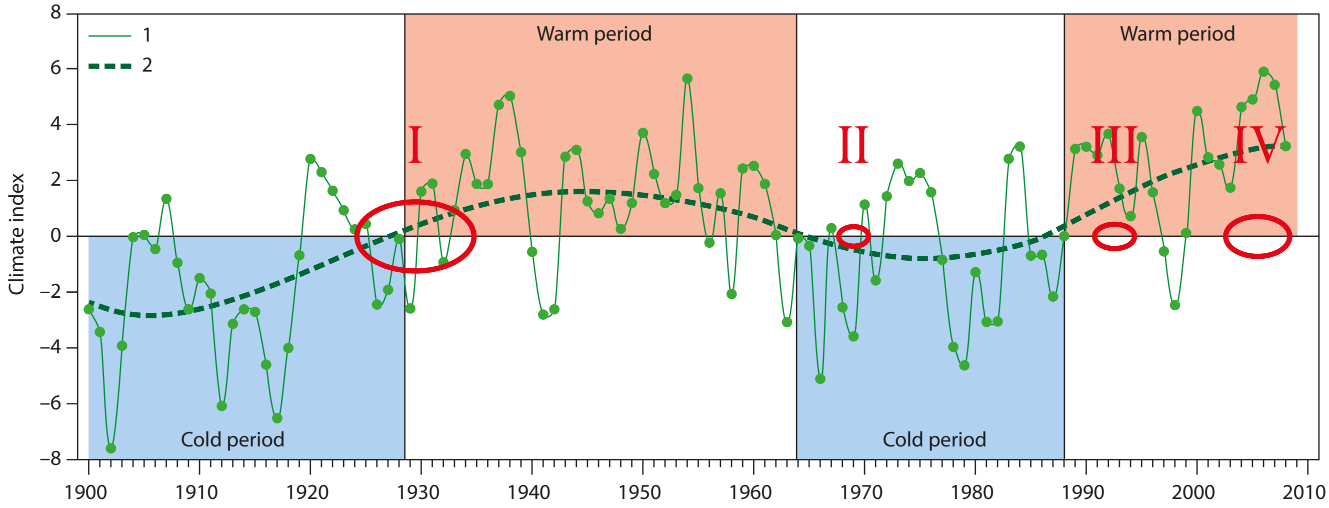

Figure 8.11. Interannual changes in the climatic index of the Barents Sea (1), with running mean curve (2), reflecting the cumulative variability of major indicators of climate (such as sea and air temperature and ice coverage), with warm periods marked in red and cold periods in blue). The periods of main quantitative benthos surveys are shown as red ellipses in the chart (modified from Anisimova *et al.* 2011).

gal cover in the rocky intertidal of two Svalbard fjords, one of them being Kongsfjorden (Kortsch *et al.* 2012). These changes occurred in the period 1995-2000 and had significant impacts on invertebrate abundances. The ecological processes thought to drive the observed regime shifts were suggested to be likely to promote the borealization of these Arctic marine communities in the coming years. Hence, a shift from long-lived, slow-growing Arctic benthic species to faster-growing temperate species on Svalbard reflects increasing water temperatures (e.g. Węsławski *et al.* 2010).

The main observed changes in crustacean diversity attributed to climate warming in the past decades are shifts in species distribution, with increasingly more boreal species advancing north with the West Svalbard Current and with Pacific waters into the Arctic basin (Węsławski *et al.* 2011). For the moment, this results in an increase in species count, as the species pool in lower latitudes is richer than in the Arctic. The fast shrinking multi-year pack ice cover that houses unique ice-associated species results in a diminished space for these species, which will consequently diminish their population size.

Climate change has also resulted in increased growth rates of mollusc species on the coast of NE Greenland (Sejr *et al.* 2009) and in species shifts of molluscs in Svalbard (Berge *et al.* 2005). Of five species of bivalves found in deposits of the Holocene Thermal Optimum in Svalbard and subsequently went extinct, the blue mussel *Mytilus edulis* was again recorded here in 2004 (Berge *et al.* 2005). This change agrees with Salvigsen *et al.* (1992), who predicted that in the course of climate warming, the populations dwelling at lower latitudes will recolonize theArctic coasts. The settlement of *Mytilus edulis*, which occurred in the outer part of the Isfjord, was possibly due to the elevated water temperatures and unusually high Atlantic water transport from the West Svalbard Current in 2002 (Berge *et al.* 2005).

The Pacific gateway

In the Bering and Chukchi Seas, data spanning several decades indicate that ocean warming has induced a shift in the species dominating biomass (Grebmeier 2012). Similarly, there have been northern range extensions in some epifaunal crabs, chitons and bivalves in the Chukchi Sea (Sirenko & Gagaev 2007). The change in distribution of female snow crab to the north in the Bering Sea (Orensantz *et al.* 2004) and a probable increase of that species in the Chukchi Sea (Bluhm *et al.* 2009) may also be related to climate change. However, observed trends in terms of benthic invertebrate biomass are not coherent and include (1) decreasing infaunal and/or amphipod biomass in the northern Bering Sea (Moore *et al.* 2003, Dunton *et al.* 2005, Grebmeier *et al.* 2006, Coyle *et al.* 2007), and (2) increased epifaunal biomass in the northern Bering and southern Chukchi Seas (Feder *et al.* 2005, Hamazaki *et al.* 2005, Bluhm *et al.* 2009). The example of biomass decrease could perhaps be interpreted in support of the prediction that the current benthos-favoring pelagic-benthic coupling will shift toward a pelagic-dominated system (e.g. Carroll & Carroll 2003, Grebmeier *et al.* 2006; see also Michel, Chapter 14). On a regional scale, biomass changes could also result from spatial community-wide shifts, specifically a northward displacement as documented in the Bering Sea (Mueter & Litzow 2008).

While changes in the ranges of species distribution appear primarily tied to water temperatures, changes in biomass, other than those related to harvests, result from a combination of shifts in energy flow or benthic-pelagic coupling and environmental conditions. For example, the increase in biomass of jellyfish in the Bering Sea throughout the 1990s was followed by a biomass collapse in 2000, with subsequent stabilization (Brodeur *et al.* 2008). These dynamics were linked to a number of factors, including ice cover, wind mixing, and sea surface temperatures, as well as prey availability, specifically juvenile Alaska pollock *Gadus chalcogrammus* and zooplankton.

8.3.2. Predictions

Like other organisms in the Arctic, marine invertebrates are likely affected by climate warming, and as described above some effects are already documented from the margins of the Arctic Ocean. However, major effects of warming are anticipated on the sympagic fauna which will lose its habitat as the ice disappears. We do not, however, expect major reductions of invertebrate species diversity due to global warming as large shelf areas in the Arctic Ocean area are already populated by species with more southerly origin, and because there are few endemic Arctic species. On the contrary, the Arctic faunal component with strong boreal influence may show increased diversity due to immigration of species adapted to warmer waters (e.g. Węsławski *et al.* 2011). From a long-term perspective there is concern that, due to the retreat of ice cover, we will see a new Pacific-Atlantic trans-Arctic interchange of species, as probably occurred 3.5 million years ago in the warm Pliocene period (Vermeij 1989). Vermeij & Roopnarine (2008) have made such predictions for present-day Arctic molluscs.

As a consequence of increased temperatures and increased advection, Węsławski *et al.* (2011) predicted a northward spreading of boreal species through the gateways to the Pacific and the Atlantic, thereby increasing diversity in the 'advective areas' on the Arctic side of the gateways.

Little is known about the time scale over which the immigration of species into the Arctic Ocean has taken place. Some immigration certainly took place immediately after termination of glaciation, but it is most likely that immigration, and local extinction inside the Arctic, is an ongoing process. In fact, the proportions of recently immigrated species from the Atlantic and Pacific at least qualitatively mirrors the current differences in water flows from the two oceans, with Atlantic flow many times that of flow from the Pacific (ACIA 2005). This indicates that, today, the potential for import of propagules to the Arctic would be far greater from the Atlantic than from the Pacific.

Furthermore, according to some authors (e.g. Denisenko 2007, Cochrane *et al*. 2009), due to less ice cover, production will increase in these areas, such as the Barents Sea, and consequently have the potential to support higher diversity. However, in other areas such as the Beaufort Sea, ice retreat will occur from shallow to deep sea areas and less production will reach the benthos there.

Whether increased production will result in increased species richness will depend on the productivity level in the hump-shaped relationship between productivity and richness (Witman *et al.* 2008). Some work has described increased benthic richness in productive areas (Brandt 1995 in a polynya, Carroll *et al.* 2008 under a polar front). There are, however, few studies supporting that such changes have taken place.

The temporal changes are multi-scale and include processes with different characteristic time scales from decades to thousands of years. Short-term fluctuations mostly affect species distribution ranges and abundances, while long-time changes are responsible for significant recombination in faunal composition. The time scale should be taken into account in any attempt to forecast future changes in Arctic biota.

Consequently, an important question is the extent to which the invasions of boreal and otherwise widespread species into the Arctic have affected native diversity. This is difficult to assess at this point, but species with Arctic and other origins to some extent do co-exist in the same local areas. Nevertheless, there is concern that human-induced invasions of alien species, such as the introduction of red king-crab in the Barents Sea (Sokolov & Miljutin 2008), could alter the composition of bottom communities (Frolova *et al*. 2003, Rzhavsky *et al*. 2004, Oug *et al*. 2011). The impact by the red king-crab would then be an impoverishment of the native fauna, because it consumes a wide spectrum of prey (Oug *et al.* 2011).

Another threat following climate change is the acidification of the sea with detrimental effects on species with calcareous skeletons or shells like molluscs. Comeau *et al.* (2012) predicted that, with the acidification expected in Arctic waters, populations of a key Arctic pelagic mollusc – the pteropod *Limacina helicina* – could be severely threatened due to hampering of the calcification processes (see also Michel, Chapter 14).

Thus, several studies refer to temperature rise resulting from climate change as the most important factor contributing to changes in biodiversity. However, change in temperature is not the only factor directly affecting marine invertebrate diversity in the Arctic Ocean. Different types of human activities, made increasingly possible by retreat in ice cover as consequence of climate change, have potentially important consequences for Arctic biodiversity. Some of them are not specific to the Arctic but are common for every type of marine systems of any latitude (Mokievsky 2009a). These activities include trawling of the bottom of the ice-free sea, other types of sediment disturbance such as from pipeline construction, dumping, development of port infrastructure, as well as pollution from various sources such as increased shipping and offshore oil and gas drilling. All of these could seriously affect Arctic invertebrate diversity at different geographic scales.

8.4. CONCLUSIONS AND RECOMMENDATIONS

8.4.1. Conclusions

The Arctic Ocean area hosts c. 5,000 species of marine invertebrates, which is a similar level as is found in the other polar environment, Antarctica, and is considered intermediate on a global scale. Arthropoda, mainly crustaceans, is the most speciose group and does not exhibit the decreasing richness with increasing latitude as found in Mollusca.

Although the Arctic contains great morphological heterogeneity and a vast number of environmental gradients, giving the opportunity for extensive niche adaptation, Arctic diversity seems largely a result of extinctions and dispersal events over the last c. 4 million years. Most species have origins from outside the Arctic, and overall there are few species endemic to the Arctic. The degree of endemism varies greatly among different taxonomic groups, where bryozoans for example seem to have a relatively high degree of endemism possibly partly due to their sessile habits and, maybe more importantly, poor dispersal ability.

The glaciation history of the two polar oceans seems fairly similar, but unlike the Antarctic which has a long history of geographic isolation, the Arctic has been, and is, open towards the two major oceans, the Pacific and the Atlantic, although the strength of the connections have varied over the last c. 4 million years. This is a likely explanation for the very low degree of endemism in the Arctic compared with the Antarctic. Today's biogeographic drivers of Arctic diversity are clearly seen in the distributions of origins in relation to the two major gateways into the Arctic, i.e. from the Atlantic and Pacific Oceans, respectively. On the continental shelves, the proportions of present-day Pacific and Atlantic species decrease with increasing distance from the Bering Strait and the NE Atlantic, respectively. Current inventories indicate that the Barents Sea has the highest species richness, being 'enriched' by boreal and sub-Arctic species. Today's Arctic deep-sea floor is most closely related to the present North Atlantic fauna, which in a geological time perspective contains a strong Pacific influence. The regional species richness is highest in Arctic regions close to the two gateways, the Chukchi

Sea for the Pacific and, even higher, the Barents Sea/Kara Sea for the Atlantic. These observations together with the distribution patterns of zoogeographical affinities indicate the importance of dispersal through the gateways into the Arctic Ocean.

While areas within the Arctic with high species richness have been identified, such as the Barents Sea, it is uncertain if there are real 'hotspots' of diversity, i.e. areas with high diversity of unique or endemic species in the Arctic. This is because many of these species may be abundant in waters to the south and thus not unique. The polynyas, ice-free areas within the area of sea ice, may be hotspots in terms of energy flow (Michel, Chapter 14), where benthic and pelagic invertebrates provide food for dense aggregations of birds and mammals.

There are already clear signs of global warming effects on invertebrates, for instance northward expansion of several boreal species. As would be predicted, this borealization has so far occurred in the margins of the Arctic Ocean, primarily at the two major gateways to the boreal parts of the Atlantic and Pacific. The rapidly melting sea ice means loss of habitat for sympagic fauna.

In addition to temperature rise, global change will acidify the oceans, and there is a great concern that this will negatively affect calciferous invertebrates like several benthic as well as pelagic molluscs. Experimental work shows that acidification hampers shell formation in wing snails.

8.4.2. Recommendations

It is recommended that conservation measures are targeted towards whole systems rather than individual species. Specifically, there are urgent needs to document and understand Arctic biodiversity patterns and processes to be able to prioritize conservation efforts.

We need more inventories

- This includes the need to know where the highest diversity occurs in the Arctic, particularly for endemic species, in order to conserve as many unique species as possible. Hence, there is a need for:
- Detailed surveys of diversity in hitherto understudied areas like the East Siberian Sea and the Canadian Arctic, together with deep-sea areas of the Central Arctic Basin and at the Arctic-Atlantic frontier. Studies are also needed in the shallow subtidal to 12 meters, which still is an understudied area.
- Increased sampling and taxonomic effort on poorly investigated groups, including several among the meiofauna.
- Establishing and continuing several observation sites for long-term monitoring of marine ecosystems in different parts of the Arctic proper to obtain a more holistic view of the changing Arctic. The existing biological stations together with marine protected areas could serve as a base for such long-term observations.
- A priority focus on consistent time series monitoring at sites in the species-rich Arctic areas close to the major gateways, as well as in some areas distant from the gateways. Given the likelihood of little time before more severe climate change effects will be manifested, this entails both the establishment of some new sites and the continuation of monitoring at existing sites such as the White Sea Biological Station, the Greenland Ecosystem Monitoring in Godthåbsfjorden in W Greenland and Young Sund in NE Greenland, and the HAUSGARTEN observatory west of Svalbard. The number of observatories in both deep and shallow waters has to be increased to include a wide spectrum of testing areas and communities. Repeated sampling should be conducted in the places of former studies, like those of Golikov (1990, 1994a, 1994b, 1994c) in the Laptev and West Siberian Seas. These studies provide a sufficient background to evaluate any changes in recent community structure and composition.

We need research to understand maintenance of diversity so it is recommended:

- To quantify immigration rates of boreal species into the Arctic and investigate the possible influence of global warming on these rates.
- To investigate whether or not immigration of boreal species 'enriches' native diversity, and whether immigrants have a negative influence on the native fauna.
- To further implement molecular taxonomy to discover the likely presence of sibling species and to reveal historical migration patterns. The most optimistic estimates predict a diversity of 'molecular operational taxonomic units' as much as three times the number of described morphological species, even in such well studied groups as the Polychaeta (Carr *et al*. 2011).
- To investigate how increased primary production, which may be one consequence of shrinking ice cover, affects species diversity both in the pelagic and the benthic systems. This could be performed in connection with polar fronts and productive polynyas.
- To investigate how climate change influences changes in biogeographic distributions, specifically the borealization process, habitat loss for sympagic fauna and the distribution of calciferous fauna.

Based on present knowledge we recommend protection of the following areas:

- Polynyas which are areas known to be important for maintaining seabird and mammal populations. These areas should be closed for fishing as well as petroleum extraction. The latter is necessary because it is virtually impossible to clean up oil in waters with broken ice.
- Large estuaries, which harbor several of the unique Arctic species.

ACKNOWLEDGEMENTS

We acknowledge the helpful comments from G. Pohle, P. Renaud and three anonymous reviewers.

REFERENCES

ACIA 2005. Arctic climate impact assessment. Cambridge University Press, New York.

Adey, W.H., Lindstrom, S.C., Hommersand, M.H. & Müller, K.M. 2008. The biogeographic origin of arctic endemic seaweeds: a thermogeographic view. J. Phycol. 44: 1384-1394.

Addison, J.A. & Hart, M.V. 2005. Colonization, dispersal and hybridization influence phylogeography of North Atlantic sea urchins (*Strongylocentrotus droebachiensis*). Evolution 59: 532-543.

Aitken, A.E. & Fournier, J. 1993. Macrobenthos communities of Cambridge, McBeth and Itirbilung Fjords, Baffin Island, Northwest Territories, Canada. Arctic 46: 60-71.

Ambrose, W.G. & Renaud, P.E. 1995. Benthic response to water column productivity patterns: Evidence for benthic-pelagic coupling in the Northeast Water Polynya. J. Geophys. Res. 100: 4411-4421.

Ambrose, W.G., Clough, L., Tilney, P. & Beer, L. 2001. Role of echinoderms in the benthic remineralization in the Chukchi Sea. Mar. Biol. 139: 937-949.

Ambrose., W.G. Jr, Renaud, P.E., Cochrane, S.K.J., Denisenko, S.G. & Skarðhamar, J. 2009. Polychaete diversity patterns on two Arctic shelves: impacts of ice and primary production? Zoosymposia 2: 457-485.

Anisimova, N.A. 1989. Distributional patterns of echinoderms in the Eurasian sector of the Arctic. In: Y. Herman (ed.). The Arctic seas. Climatology, oceanography, geology and biology, pp 281-301. Van Nostrand Reinhold Company, New York.

Anisimova, N.A., Jørgensen, L.L., Lubin, P. & Manushin, I. 2011. Benthos. In: T. Jakobsen & V.K. Ozhigin (eds.). The Barents Sea. Ecosystem, resources, management. Half a century of Russian-Norwegian cooperation, pp 315-328. Tapir Academic Press, Trondheim.

Antipova, T.V. 1975. Distribution of the Barents Sea benthos biomass. Trudy PINRO 35: 121-124. [in Russian]

Archambault, P., Snelgrove, P.V., Fisher, J.A.D., Gagnon, J.-M., Garbary, D.J., Harvey, M. *et al*. 2010. From sea to sea: Canada's three oceans of biodiversity. PLoS ONE 5(8): 1-26.

Barnes, D.K.A. & Griffiths, H.J. 2008. Biodiversity and biogeography of southern temperate and polar bryozoans. Glob. Ecol. Biogeogr. 17: 84-99.

Bastrop, R. & Blank, M. 2006. Multiple invasions – a polychaete genus enters the Baltic Sea. Biological Invasions 8: 1195-1200.

Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B. & Slagstad, D. 2005. Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar. Ecol. Prog. Ser. 303: 167-175.

Berge, J., Renaud, P.E., Eiane, K., Gulliksen, B., Cottier, F.R., Varpe, Ø. & Brattegaard, T. 2009. Changes in the decapod fauna of an Arctic fjord during the last 100 years (1908-2007). Polar Biol. 32: 953-961.

Berger, V., Dahle, S., Galaktionov, K., Kosobokova, X., Naumov, A., Rat'kova, T. *et al.*. 2001. White sea. Ecology and environment. Derzavets Publ. St. Petersburg-Tromso.

Bergmann, M., Soltwedel, T. & Klages, M. 2011. The interannual variability of megafaunal assemblages in the Arctic deep sea: Preliminary results from the HAUSGARTEN observatory (79°N). Deep-Sea Res. I 58: 711-723.

Beuchel, F., Gulliksen, B. & Carroll, M.L. 2006. Long-term patterns of rocky bottom macrobenthic community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate variability (1980-2003). J. Mar. Sys. 63: 35-48.

Bilyard, G.R. & Carey, A.G. Jr. 1979. Distribution of western Beaufort Sea polychaetous annelids. Mar. Biol. 54: 329-339.

Bilyard, G.R. & Carey, A.G. 1980. Zoogeography of western Beaufort Sea Polychaeta (Annelida). Sarsia 65: 19-26.

Blacker, R. 1957. Benthic animals as indicators of hydrographical conditions and climatic change in Svalbard waters. Fishery Investigations, series 2, 20(10): 1-59.

Blanchard, A.L., Feder, H.M. & Hoberg, M.K. 2010. Temporal variability of benthic communities in an Alaskan glacial fjord, 1971-2007. Mar. Environ. Res. 69: 95-107.

Blicher, M.E. & Sejr, M.E. 2011. Abundance, oxygen consumption and carbon demand of brittle stars in Young Sound and the NE Greenland shelf. Mar. Ecol. Prog. Ser. 422: 139-144.

Blicher, M.E., Rysgaard, S. & Sejr, M.K. 2007. Growth and production of sea urchin *Strongylocentrotus droebachiensis* in a high-Arctic fjord, and growth along a climatic gradient (64-77N). Mar. Ecol. Prog. Ser. 341: 89-102.

Blicher, M. E., Sejr,M.K. & Rysgaard, S. 2009. High carbon demand of dominant macrozoobenthic species indicates their central role in ecosystem carbon flow in a sub-Arctic fjord. Mar. Ecol. Prog. Ser. 383: 127-140.

Blicher, M.E., Rasmussen, L.M., Sejr, M.K., Merkel, F.R. & Rysgaard, S. 2011. Abundance and energy requirements of eiders (*Somateria* spp.) suggest high predation pressure on macrobenthic fauna in a key wintering habitat in SW Greenland. Polar Biol. 34: 1105-1116.

Bluhm, B.A., Piepenburg, D. & Juterzenka, K. 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Bering Sea. Polar Biol. 20: 325-334.

Bluhm, B.A., MacDonald, I.R., Debenham, C. & Iken, K. 2005. Macro- and megabenthic communities in the high Arctic Canada Basin: initial findings. Polar Biol. 28: 218-231.

Bluhm, B.A., Iken, K., Mincks, S.L., Sirenko, B.I. & Holladay, B.A. 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquat. Biol. 7: 269-293.

Bluhm, B., Gradinger, R. & Schnack-Shiel, S. 2010 . Sea ice meio- and macrofauna. In: D. Thomas and D. Diechmann (eds.). Sea Ice, pp 357-393. Wiley-Blackwell, New York.

Bluhm, B.A., Gebruk, A.V., Gradinger, R., Hopcroft, R.R., Huettmann, F., Kosobokova, K.N. *et al*. 2011a. Arctic marine biodiversity: An update of species richness and examples of biodiversity change. Oceanography 24: 232-248.

Bluhm, B.A., Ambrose, W.G. Jr., Bergmann, M., Clough, L.M., Gebruk, A.V., Hasemann, C. *et al*. 2011b. Diversity of the arctic deep-sea benthos. Mar. Biodiv. 41: 87-107.

Boertmann, D., Lyngs, P., Merkel, F.R. & Mosbech, A. 2004. The significance of Southwest Greenland as winter quarters for seabirds. Bird Conserv. Int. 14: 87-112.

Born, E., Rysgaard, S., Ehlmé, G., Sejr, M., Acquarone, M. & Levermann, N. 2003. Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus*) and estimates of their food consumption. Polar Biol. 26: 348-357.

Bouchet, P. 2006. The magnitude of marine biodiversity. In: C. Duarte (ed.). The exploration of marine biodiversity. The scientific and technological challenges, pp 33-64. Fundacion BBVA, Bilbao.

Bouchet, P. & Waren, A. 1979. The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. Sarsia 64: 211-243.

Bouchet, P., Louzet, P., Maestrati, P. & Heros, V. 2002. Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. Biol. J. Lin. Soc. 75: 421-436.

Brandt, A. 1995. Peracarid fauna (Crustacea, Malacostraca) of the Northeast Water Polynya off Greenland: documenting close benthic-pelagic coupling in the Westwind Trough. Mar. Ecol. Prog. Ser. 121: 39-51.

Brandt, A. 1997. Biodiversity of peracarid crustaceans (Malacostraca) from the shelf down
to the deep Arctic Ocean. Biodiv. Conserv. 6: 1533-1556.

Briggs, J.C. 1995. Global biogeography. Elsevier, Amsterdam.

Briggs, J.C. 2003. Marine centres of origin as evolutionary engines. J. Biogeogr. 30: 1-18

Briggs, J.C. 2007. Marine biogeography and ecology: invasions and introduction. J. Biogeogr. 34: 193-198.

Brodeur, R.D., Decker, M.B., Ciannelli, I., Purcell, J.E., Bond, N.A., Stabeno, P.J. *et al.* 2008. Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Prog. Oceanog. 77: 103-111.

Budaeva, N.E., Mokievsky, V., Soltwedel, T. & Gebruk A.V. 2008. Horizontal distribution patterns in Arctic deep-sea macrobenthic communities. Deep-Sea Res. Part I 55: 1167-1178.

Carr, C.M., Hardy, S.M., Brown, T.M., Macdonald, T.A. & Hebert, P.D.N. 2011. A Tri-Oceanic Perspective: DNA Barcoding Reveals Geographic Structure and Cryptic Diversity in Canadian Polychaetes. PLoS ONE 6(7): e22232. doi: 10.1371/journal.pone.0022232

Carroll, M.L. & Carroll, J. 2003. The Arctic Seas. In: K.D. Black & G.B. Shimmield (eds.). Biogeochemistry of Marine Systems, pp 127-156. CRC Press, Boca Raton.

Carroll, M.L., Denisenko, S.G., Renaud, P.E. & Ambrose, W.G. 2008. Benthic infauna of the seasonally ice-covered western Barents Sea: Patterns and relationships to environmental forcing. Deep-Sea Res. II 55: 2340-2351.

Chertoprud, E.S., Garlitska, L.A. & Azovsky, A.I. 2010. Large-scale patterns in marine harpacticoid (Crustacea, Copepoda) diversity and distribution. Mar. Biodiv. 40: 301-315.

Clarke, A. 1992. Is there a latitudinal diversity cline in the sea? Trends Ecol. Evol. 7: 286-287.

Clarke, A., Aronson, R.B., Crame, J.A., Gili, J.-M. & Blake, D.B. 2004. Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf. Antarctic Sci. 16: 559-568.

Cochrane, S.K.J., Denisenko, S.G., Renaud, P.E., Emblow, C.S., Ambrose Jr., W.G., Ellingsen, I.H. & Skardhamar, J. 2009. Benthic macrofauna and productivity regimes in the Barents Sea – Ecological implications in a changing Arctic. J. Sea Res. 61: 222-233.

Cochrane, S.K.J., Pearson, T.H., Greenacre, M., Costelloe, J., Ellingsen, I.H., Dahle, S. & Gulliksen, B. 2012. Benthic fauna and functional traits along a Polar Front transect in the Barents Sea – Advancing tools for ecosystem-scale assessments. J. Mar. Sys. 94: 204-217.

Comeau, S., Gattuso, J.P., Nisumaa, A.M. & Orr, J. 2012. Impact of aragonite saturation state changes on migratory pteropods. Proc. Roy. Soc. B. 279: 732-738.

Conlan, K., Aitken, A., Hendrycks, E., McClelland, C. & Melling, H. 2008. Distribution patterns of Canadian Beaufort Shelf macrobenthos. J. Mar. Sys. 74: 864-886.

Coyle, K.O., Bluhm, B.A., Konar, B., Blanchard, A. & Highsmith, R.C. 2007. Amphipod prey of gray whales in the northern Bering Sea: Comparison of biomass and distribution between the 1980s and 2002-2003. Deep-Sea Res. Part II 54: 2906-2918.

Currie, D.J. 1991. Energy and large-scale patterns of animal and plant-species richness. Am. Nat. 137: 27-49.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.-F., Hawkins, B.A. *et al*. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol. Lett. 7: 1121-1134.

Curtis, M.A. 1972. Depth distribution of benthic polychaetes in two fjords on Ellesmere Island, N.W.T. J. Fish. Res. Bd Canada 29: 1319-1327.

Cusson, M., Archambault, P. & Aitken, A. 2007. Biodiversity of benthic assemblages on the Arctic continental shelf: historical data from Canada. Mar. Ecol. Prog. Ser. 331: 291-304.

Denisenko, N.V. 1990. Occurrence and ecology of bryozoans in the Barents Sea. Apatity: Kola Sci. Centre RAS Press.

Denisenko, N.V. 2008. Bryozoans (Bryozoa) of the Chukchi Sea and Bering Strait. In: B.I. Sirenko & S.V. Vasilenko (eds.). Fauna and zoogeography of the Chukchi Sea. Explorations of fauna of seas, 64 (70). ZIN RAS Press, St. Petersburg.

Denisenko, N.V. 2009. New species and new records of rare ctenostome bryozoans of the genus *Alcyonidium* in the Russian Arctic Seas. Proc. Zool. Inst. Russ. Acad. Sci. 313: 419-426.

Denisenko, N.V. 2010. Bryozoans (Bryozoa) of the East Siberian Sea. In: B.I. Sirenko & S.G. Denisenko (eds.). Fauna of the East Siberian Sea, distribution patterns and community structure. Explorations of fauna of seas, 66 (74), pp 89-129. ZIN RAS Press, St. Petersburg.

Denisenko, N.V. 2011. Bryozoans of the East Siberian Sea: history of research and current knowledge of diversity. In: P.N.W. Jackson & M.E.S. Jones (eds.). Annals of bryozoology 3, pp 1-15. International Bryozoology Association, Dublin.

Denisenko, N.V. & Kuklinski, P. 2008. Historical development of research and current state of bryozoan diversity in the Chukchi Sea. In: P.N.W. Jackson & M.E.S. Jones (eds.). Annals of bryozoology 2: aspects of the history of research on bryozoans, pp 97-116. International Bryozoology Association, Dublin.

Denisenko, N.V., Rachor, E. & Denisenko, S.G. 2003a. Benthic fauna of the southern Kara Sea. In: R.Stain, K. Fahld, D.K.Futterer, E.M.Galimov & O.V. Stepanetz (eds.). Sibirian River Runoff in the Kara Sea: Characterization, quantification variability and environmental significance, pp 213-236. Proceedings in marine science, Elsevier, Amsterdam.

Denisenko, S.G., 2001. Long-term changes of zoobenthos biomass in the Barents Sea. Proc. Zool. Inst. Russ. Acad. Sci. 289: 59-66.

Denisenko, S.G. 2004. Structurally-functional characteristics of the Barents Sea. Zoobenthos. Proc. Zool. Inst. Russ. Acad. Sci. 300: 43-52.

Denisenko, S.G. 2007. Zoobenthos of the Barents Sea under influence of changing climate and anthropogenic impact. In: C. Dal'Nauka (ed.). Dynamic of marine ecosystems and conditions of forming of the biological porencial of seas, pp 418-511. Vladivostok.

Denisenko, S.G. & Titov, O.V. 2003. Zoobenthos distribution and primary production of the Barents Sea. Oceanologia 43: 78-88.

Denisenko, S.G., Denisenko, N.V., Lehtonen, K.K., Andersin, A.-B. & Laine, A.O. 2003b. Macrozoobenthos of the Pechora Sea (SE Barents Sea): community structure and spatial distribution in relation to environmental conditions. Mar. Ecol. Prog. Ser. 258: 109-123.

Deubel, H. 2000. Structures and nutrition requirements of marine macrozoobenthic communities in the area of the Lomonossov Ridge in the Arctic Ocean. Ber. Polarforsch. 370: 1-147. [in German]

Drinkwater, K.F. 2006. The regime shift of the 1920s and 1930s in the North Atlantic. Prog. Oceanog. 68: 134–151.

Dunton, K. 1992. Arctic biogeography: The paradox of the marine benthic fauna and flora. Trends Ecol. Evol. 7: 183-189.

Dunton, K.H., Godall, J.L., Schonberg, S.V., Grebmeier, J.M. & Maidment, D.R. 2005. Multi-decadal synthesis of benthic-pelagic coupling in the western Arctic: Role of cross-shelf advective processes. Deep-Sea Res. Part II 52: 3462-3477.

Ellingsen, K. & Gray, J.S. 2002. Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? J. Anim. Ecol. 71: 373-389.

European Marine Biodiversity All taxa Inventory site 2009: www.iopan.gda.pl/projects/biodaff [accessed 26 September 2012]

Fairbanks, R.G. 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature 342: 637-642.

Farrow, G.E., Syvitski, J.P.M. & Tunnicliffe, V. 1983. Suspended particulate loading on the macrobenthos in a highly turbid fjord: Knight Inlet, British Columbia. Can. J. Fish. Aquat. Sci. 40: 273-288.

Feder, H.M., Jewett, S.C. & Blanchard, A. 2005. Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol. 28: 402-421.

Filatova, Z.A. 1957. Zoogeographical regionalization of northern seas based on bivalve distribution. Proceedings of Institute of Oceanology, USSR Academy of Sciences 23: 195-215. [in Russian]

Fonseca, G., Soltwedel, T., Vanreusel, A. & Lindegarth, M. 2010. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanog. 84: 174-184.

Forest, A., Wassmann, P., Slagstadt, D., Bauerfeind, E., Nöthig, E. & Klages, M. 2010. Relationships between primary production and vertical particle export at the Atlantic-Arctic boundary (Fram Strait, HAUSGARTEN). Polar Biol. 33: 1733-1746.

Frolova, E.A., Anisimova, N.A., Frolov, A.A., Liubina, O.S., Garbul, E.A. & Gudimov, A.V. 2003. Bottom fauna of the Motovskoy Bay. The invertebrate fauna of the Kara, Barents and the White seas (informatics, ecology, biogeography). Apatity. Kola Scientific Ceneter RAS. [in Russian]

Gallucci, F., Fonseca, G. & Soltwedel, T. 2008a. Effects of megafauna exclusion on nematode assemblages at a deep-sea site. Deep-Sea Res. I 55: 332-349.

Gallucci, F., Sauter, E., Sachs, O., Klages, M. & Soltwedel, T. 2008b. Caging experiment in the deep sea: efficiency and artefacts from a case study at the Arctic long-term observatory HAUSGARTEN. J. Exp. Mar. Biol. Ecol. 354: 39-55.

Gardiner, K. & Dick, T.A. 2010. Arctic cephalopod distributions and their associated predators. Polar Res. 29: 209-227.

Gerlach, S.A. 2004. Checkliste der Mikro- und Meiofauna im schleswig-holsteinischen und dänischen Wattenmeer. In: Bundesanstalt für Gewässerkunde (Hrsg.), Die Biodiversität in der deutschen Nord- und Ostsee, Band 2, Bericht BfG-1397, Koblenz.

Giere, O. 2009. Meiobenthology: the microscopic motile fauna of aquatic sediments. Springer.

Glahder, C.M., Asmund, G., Josefson, A., Burmeister, A.D. & Jespersen, M. 2005. Nalunaq environmental baseline study 1998-2001. NERI-Technical report No. 562.

Golikov, A.N. (ed.) 1990. Ecosystems of Noivosibirsk shallows and the fauna of Laptev Sea and adjacent waters. Issled. Fauny Morei 37(45). [in Russian]

Golikov, A.N. (ed.) 1994a. Ecosystems and fauna of Chauna Bay of East Siberian sea. Issled. Fauny Morei 47(55). [in Russian]

Golikov, A.N. (ed.) 1994b. Ecosystems and fauna of Chauna Bay and adjacent waters of East Siberian sea. Issled. Fauny Morei 48(56). [in Russian]

Golikov, A.N. (ed.) 1994c. Fauna of East Siberian sea. Issled. Fauny Morei 49(57). [in Russian]

Golikov, A.N. & Scarlato, O.A. 1989. Evolution of Arctic ecosystems during the Neogene period. In: Y. Herman (ed.) The Arctic seas. Climatology, oceanography, geology and biology, pp 257-279. Van Nostrand Reinhold Company, New York.

Golikov, A.N., Gagaev, S.Y., Galtsova, V.V., Golikov, A.A., Dunton, K., Menshutkina, T.V. *et al.* 1994. Ecosystems and the flora and fauna of the Chaun Bay of the East-Siberian Sea. Exploration of the Fauna of the seas 47(55): 4-110. [in Russian]

Gontar, V.I. 1996. Bryozoa collected by the "Polarstern" expedition in 1991 and 1993. Zoosystematica Rossica 4(1): 45-47.

Gontar, V.I. 2004. List of bryozoan species of the Laptev Sea. In: B.I. Sirenko (ed.). Fauna and ecosystems of the Laptev sea and adjacent deep waters of the Arctic basin. Explorations of fauna of seas, 54(62), pp 151-156. ZIN RAS Press, St. Petersburg.

Gontar, V.I. & Denisenko, N.V. 1989. Arctic Ocean Bryozoa. In: Y. Herman (ed.). The Arctic Seas. Climatology, oceanography, geology and biology, pp 341-371. Van Nostrand Reinhold Company, New York.

Gradinger, R. 2002. Sea ice microorganisms. In: G.E. Bitten (ed.). Encyclopedia of Environmental Microbiology, pp 2833-2844. Wiley, New York.

Gradinger, R. 2009. Sea ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Sea during May/June 2002. Deep-Sea Res. II 56: 1201-1212.

Gradinger, R., Bluhm, B.A., Hopcroft, R.R., Gebruk, A.V., Kosobokova, K., Sirenko, B. & Węsławski, J.M. 2010a. Marine life in the Arctic. In: A.D. McIntyre (ed.). Life in the world's oceans, pp 183-202. Blackwell Ltd.

Gradinger, R., Bluhm, B. & Iken, K. 2010b. Arctic sea-ice ridges – Safe heavens for sea-ice fauna during periods of extreme ice melt? Deep-Sea Res. II 57: 86-95.

Grebmeier, J.M. 2012. Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas. Annu. Rev. Mar. Sci. 2012. 4: 63-78.

Grebmeier, J.M. & Barry, J.P. 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. J. Mar. Sys. 2: 495-518.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W. *et al*. 2006. A major ecosystem shift in the Northern Bering Sea. Science 311: 1461-1464.

Grzelak, K. & Kotwicki, L. 2012. Meiofaunal distribution in Hornsund fjord, Spitsbergen. Polar Biol. 35: 269-280.

Guilini, K., Soltwedel, T., van Oevelen, D. & Vanreusel, A. 2011. Deep-sea Nematodes Actively Colonise Sediments, Irrespective of the Presence of a Pulse of Organic Matter: Results from an In Situ Experiment. PLoS One 6(4), e18912.

Gundersen, H., Christie, H. & Rinde, E. 2010. Sea urchins – from problem to commercial resource. Estimates of sea urchins as a resource and and evaluation of ecological gains by sea urchin exploration. Norwegian Institute for Water Research.

Gurjanova, Y.F. 1970. Peculiarities of the Arctic Ocean fauna and their importance for understanding of formation history. In: Arctic Ocean and its coast in Cainozoe, pp 126-161. Gidrometeoizdat , Leningrad. [in Russian]

Hamazaki, T., Fair, L. Watson, L. & Brennan, E. 2005. Analysis of Bering Sea bottom-trawl surveys in Norton Sound: Absence of regime shift effect on epifauna and demersal fish. ICES J. Mar. Sci. 62: 1597-1602.

Hardy, S.M., Carr, C.M., Hardman, M., Steinke, D., Corstorphine, E. & Mah, C. 2011. Biodiversity and phylogeography of Arctic marine fauna: insights from molecular tools. Mar. Biodiv. 41: 195-210.

Hasemann, C. & Soltwedel, T. 2011. Small-scale heterogeneity in deep-sea nematode communities around biogenic structures. PLoS One 6(12): 1-13.

Hassold, N.J.C., Rea, D.K., van der Pluijm, B.A. & Parés, J.M. 2009. A physical record of the Antarctic Circumpolar Current: Late Miocene to recent slowing of abyssal circulation. Palaeogeography, Palaeoclimatology, Palaeoecology 275: 28–36.

Heip, C., Herman, R. & Vincx, M. 1983. The present state of knowledge on North Sea subtidal meiofauna. In: ICES Council Meeting 1983 Collected Papers. ICES, Copenhagen.

Hill, A.S., Veale, L.O., Pennington, D., Whyte, S.G., Brand, A.R. & Hartnoll, R.G. 1999. Changes in Irish Sea benthos: bossible effects of 40 years of dredging. Estuar. Coast. Shelf Sci. 48: 739-750.

Holte, B. & Gulliksen, B. 1998. Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. Polar Biol. 19: 375-382.

Hopcroft, R.R., Clarke, C., Nelson, R.J. & Raskoff, K.A. 2005. Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. Polar Biol. 28: 198-206.

Hopkins, D.M. 1973. Sea level history in Beringia during the past 250,000 years. Quarternary Res. 3: 520-540.

Hoste, E. 2006. Temporal and spatial variability in the deep-sea meiobenthic communities from the Arctic Marginal Ice Zone. PhD thesis, University Gent.

Hoste, E., Vanhove, S., Schewe, I., Soltwedel, T. & Vanreusel, A. 2007. Spatial and temporal variations in deep-sea meiofauna assemblages in the Marginal Ice Zone of the Arctic Ocean. Deep-Sea Res. I 54: 109-129.

Iken, K., Bluhm, B.A. & Gradinger, R. 2005. Food web structure in the high Arctic Canada Basin. Polar Biol. 28: 238-249.

Iken, K., Bluhm, B.A. & Dunton, K. 2010. Benthic food web structure serves as indicator of water mass properties in the southern Chukchi Sea. Deep-Sea Research II 57: 71-85.

Jablonski, D., Roy, K. & Valentine, J.W. 2000. Analysing the latitudinal diversity gradient in marine bivalves. Geological Society, London, Special Publication 177: 361-365.

Jakobsson, M., Grantz, A., Kristoffersen, Y. & Macnab, R. 2004. Physiography and bathymetry of the Arctic Ocean. In: R. Stein & R. MacDonald (eds.). The organic carbon cycle in the Arctic Ocean, pp 1-6. Spinger, Berlin.

Jensen, A.S. 1939. Concerning a change of climate during recent decades in the Arctic and subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical change. Royal Danish Academy of Science. Biol. Medd. 14, 8.

Josefson, A.B., Hansen, J.L.S., Asmund, G. & Johansen, P. 2008. Threshold response of benthic macrofauna integrity to metal contamination in West Greenland. Mar. Poll. Bull. 56: 1265-1274.

Jørgensen, L.L., Pearson, T.H., Anisimova, N.A., Gulliksen, B., Dahle, S., Denisenko, S.G. & Matishov, G.G. 1999. Environmental influences on benthic fauna associations of the Kara Sea (Arctic Russia). Polar Biol. 22: 395-416.

Jørgensen, L.L., Renaud, P. & Cochrane, S. 2011. Improving benthic monitoring by combining trawl and grab surveys. Mar. Poll. Bull. 62: 1183-1190.

Kaiser, M.J. & Spencer, B.E. 1996. The effects of beam trawl disturbance on infaunal communities in different habitats. J. Anim. Ecol. 65: 348-359.

Kanzog, C., Ramette, A., Quéric, N.V. & Klages, M. 2009. Response of benthic microbial communities to chitin enrichment: an in situ study in the deep Arctic Ocean. Polar Biol. 32: 105-112.

Karcher, M., Beszczynska-Möller, A., Kauker, F., Gerdes, R., Heyen, S., Rudels, B. & Schauer, U. 2011. Arctic Ocean warming and its consequences for the Denmark Strait overflow. J. Geophys. Res. 116: C02037

Kedra, M., Włodarska-Kowalczuk, M. & Węsławski, J.M. 2010. Decadal change in macrobenthic soft-bottom community structure in a high Arctic fjord (Kongsfjorden, Svalbard). Polar Biol. 33: 1-11.

Kendall, M.A. 1996. Are Arctic soft-sediment macrobenthic communities impoverished? Polar Biol. 16: 393-399.

Kendall, M.A. & Aschan, M. 1993. Latitudinal gradients in the structure of macrobenthic communities: a comparison of arctic, temperate and tropical sites. J. Exp. Mar. Biol. Ecol. 172: 157-169.

Kendall, M.A., Widdicombe, S. & Węsławski, J.M. 2003. A multiscale study of the biodiversity of the benthic infauna of the high-latitude Kongsfjord, Svalbard. Polar Biol. 26: 383-388.

Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigues, J., Lønne, O.J. & Gulliksen, B. 2012. Climate-driven regime shifts in Arctic marine benthos. Proc. Natl. Acad. Sci. 109: 14052-14057.

Kosobokova, K.N. 1980. Seasonal variations in the vertical distribution and age composition of Microcalanus pygmaeus, Oithona similis, Oncaea borealis and O. notopus populations in the central Arctic Basin. Biologiya Tsentral'nogo Arkicheskogo Basseyna, pp 167-182. Nauka, Moscow.

Kosobokova, K.N. & Hopcroft, R.R. 2010. Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. Deep-Sea Res. II 57: 96-110.

Kosobokova, K.N., Hopcroft, R.R. & Hirche, H.-J. 2011. Patterns of zooplankton diversity through the depths of the Arctic's central basins. Mar. Biodiv. 41: 29-50.

Krembs, C., Gradinger, R. & Spindler, M. 2000. Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. J. Exp. Mar. Biol. Ecol. 243: 55-80.

Kröncke, I. 1994. Macrobenthos composition, abundance and biomass in the Arctic Ocean along a transect between Svalbard and the Makarov Basin. Polar Biol. 14: 519-529.

Kröncke, I. 1998. Macrofauna communities in the Amundsen Basin, at the Morris Jesup Rise and at the Yermak Plateau (Eurasian Arctic Ocean). Polar Biol. 19: 383-392.

Krylov, A.A., Andreeva, I.A., Vogt, C., Backman, J., Krupskaya, V.V., Grikurov, G.E. *et al*. 2008. A shift in heavy and clay mineral provenance indicates a middle Miocene onset of a perennial sea ice cover in the Arctic Ocean. Paleoceanography 23: PA1S06, 1-10.

Kuklinski, P. & Taylor, P.D. 2006. A new genus and some cryptic species of Arctic and boreal calloporid cheilostome bryozoans. J. Mar. Biol. Ass. U.K. 86: 1035-1046.

Larsen, T., Nagoda, D. & Andersen J.R. (eds.) 2003. A biodiversity assessment of the Barents Sea Ecoregion. Contribution of the St. Petersburg Biodiversity workshop 12-13 May 2001. WWF Barents Sea Ecoregion Programme, Oslo.

Loeng, H., Brander, K., Carmack, E., Denisenko, S., Drinkwater, K., Hansen, B. *et al.* 2005. Marine systems. In: Arctic Climate Impact Assessment, pp 451-538. Cambridge University Press, New York.

Longhurst, A.R. 2007. Ecological geography of the sea. 2nd ed. Elsevier.

MacArthur, R.H. & Wilson, E.O. 1967. The theory if island biogeography. Princeton Univ. Press, Princeton.

MacDonald, I.R., Bluhm, B., Iken, K., Gagaev, S. & Strong, S. 2010. Benthic macrofaunal and megafaunal assemblages in the Arctic deep-sea Canada Basin. Deep-Sea Res. II 57: 136-152.

MAREANO 2009. www.MAREANO.no [accessed 26 September 2012]

Martens, P.M. & Schockaert, E.R. 1986. The importance of turbellarians in the marine meiobenthos: a review. Hydrobiologia 132: 95-303.

Miljutin, D.M., Gad, G., Miljutina, M.A., Mokievsky, V.O., Fonseca-Genevois, V. & Esteves, A.M. 2010. A recent overview and outlook on the state of knowledge on deep-sea nematodes: how many species are known down there? Mar. Biodiv. 40: 143-159.

Mironov, A.N. & Dilman, A.B. 2010. Effect of the East Siberian Barrier on the Echinoderm Dispersal in the Arctic Ocean. Oceanology 50: 342-355.

Mokievsky, V.O. 1992. Composition and Distribution of the Intertidal Meiofauna on West Spitsbergen. Polish Polar Research. Vol. 13, No. 1: 31-40.

Mokievsky, V.O. 2009a. Ecology of Marine Meiobenthos. KMK Ltd., Moscow. [in Russian] (available on-line at www.rfbr.ru/rffi/ru/books/o_17993#1)

Mokievsky, V.O. 2009b. Marine protected areas: theoretical background for design and operation. Rus. J. Mar. Biol. 35: 504-514.

Mokievsky, V. & Azovsky, A. 2002. Re-evaluation of species diversity patterns of free living marine nematodes. Mar. Ecol. Prog. Ser. 238: 101-108.

Moore, S.E., Grebmeier, J.M. & Davies, J.R. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: Current conditions and retrospective summary. J. Zool. 81: 734-742.

Mortensen, L.B., Hodnesdal, H. & Thorsnes, T. 2009. Til Bunns i Barentshavet og havområdene utenfor Lofoten. MAREANO 2011, 2 opplag. [in Norwegian]

Mueter, F.J. & Litzov, M.A. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol. Appl. 18: 309-320.

Mustonen, T. 2007. Report on the Biodiversity Observations of the Indigenous Communities of the ECORA Model Area Lower Kolyma River, Sakha-Yakutia, Russia. A Conference Speech in Snowchange 2007: Traditions of the North, held in April 2007 in Neriungri and Iengra, Sakha-Yakutia, Russia.

Myers, N., Mittemeier, R.A., Mittemeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Nesis, K.N. 1983. A hypothesis of the origin of western and eastern Arctic ranges of marine bottom animals. Biologiya Morya 5: 3-13. [in Russian with English summary]

Nichols, B.J. & Langdon, K.R. 2007. The Smokies All Taxa Biodiversity Inventory: History and Progress Southeastern Naturalist 6: 27-34.

Nikula, R., Strelkov, P. & Väinölä, R. 2007. Diversity and trans-Arctic invasion history of mitochondrial lineages in the North Atlantic *Macoma balthica* complex (Bivalvia: Tellinidae). Evolution 61: 928-941.

OBIS 2012. Ocean Biogeographic Information System. www.iobis.org [accessed 29 November 2012]

Orensantz, J.B., Ernst, D.A., Armstrong, P., Stabeno, P.J. & Livingston, P. 2004. Contraction of the geographic range of distribution of snow crab (*Chionocetes opilio*) in the Eastern Bering Sea: An environmental ratchet? CalCOFI Report 45: 65-79.

Osburn, R.C. 1955. The circumpolar distribution of arctic-Alaskan Bryozoa. In: Essays in the natural sciences in honor of Captain Allan Hancock, pp 29-38. The University of Southern California Press, Los Angeles.

Oug, E., Cochrane, S.K.J., Sundet, J.H., Norling, K. & Nilsson, H.C. 2011. Effects of invasive red king crab (*Paralithodes camtschaticus*) on soft-bottom fauna in Varangerfjorden, northern Norway. Mar. Biodiv. 41: 467-479.

Pavlov, V.A. & Sundet, J.H. 2011. Snow crab. In: T. Jakobsen & V.K. Ozhigin (eds.). The Barents Sea. Ecosystem, resources, management. Half a century of Russian-Norwegian cooperation, pp 315-328. Tapir Academic Press, Trondheim.

Piepenburg, D. 2000. Arctic brittle stars (Echinodermata: Ophiuroidea). Oceanogr. Mar. Biol. Ann. Rev. 38: 189-256.

Piepenburg, D. 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol. 28: 733-755.

Piepenburg, D., Archambault, P., Ambrose, W.G. Jr., Blanchard, A.L., Bluhm, B.A., Carroll, M.L. *et al*. 2011. Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. Mar. Biodiv. 41: 51-70.

Powell, N.A. 1968. Bryozoa (Polyzoa) of the Arctic Canada. J. Fish. Res. Bd. Canada. 25: 2269-2320.

Premke, K., Klages, M. & Arntz, W.E. 2006. Aggregations of Arctic deep-sea scavengers at large food falls: temporal distribution, consumption rates and population structure. Mar. Ecol. Prog. Ser. 325: 121-135.

Prestrud, P., Strøm, H. & Goldman, H.V. (eds.) 2004. A catalogue of the terrestrial and marine animals of Svalbard. Skrifter Norsk Polar Institutt no. 201, Tromsø.

Purcell, J.E., Hopcroft, R.R., Kosobokova, K.N. & Whitledge, T.E. 2010. Distribution, abundance, and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean. Deep-Sea Res. II: 127-135.

Rand, K.M. & Logerwell, E.A. 2010. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol. 34: 475-488.

Renaud, P.E., Ambrose, W.G. Jr., Vanreusel, A. & Clough, L. 2006. Nematode and macrofaunal diversity in central Arctic Ocean benthos. J. Exp. Mar. Biol. Ecol. 330: 297-306.

Renaud, P.E., Włodarska -Kowalczuk, M., Trannum, H., Holthe, B., Węsławski, J.M., Cochrane, S. *et al*. 2007. Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitsbergen). Polar Biol. 30: 295-305.

Renaud, P.E., Webb, T.J., Bjorgesaeter, A., Karakassis, I., Kedra, M., Kendall, M.A. *et al*. 2009. Continental-scale patterns in benthic invertebrate diversity: insights from the MacroBen database. Mar. Ecol. Prog. Ser. 382: 239-252.

Rogacheva, A.V. 2007. Revision of the Arctic group of species of the family Elpidiidae (Elasipodida, Holothuroidea). Mar. Biol. Res. 3: 367-396.

Rouse, G.W. 2001. A cladistic analysis of Siboglinidae Caullery, 1914 (Polychaeta, Annelida): formerly the phyla Pogonophora and Vestimentifera. Zool. J. Linn. Soc. 132: 55-80.

Roy, K., Jablonski, D., Valentine, J.W. & Rosenberg, G. 1998. Marine latitudinal diversity gradients; tests of casual hypotheses. Proc. Natl. Acad. Sci. USA 95: 3699-3702.

Rudels, B., Meyer, R., Fahrbach, E., Ivanov, V.V., Østerhus, S., Quadfasel, D. *et al*. 2000. Water mass distribution in Fram Strait and over the Yermak Plateau in summer 1997. Ann. Geophys. 18: 687-705.

Rzhavsky, A.V., Britaev, T.A., Pavlova, L.V., Kuzmin, S.A. & Kulikova, V.I. 2004. On the distribution of several species of macrozoobenthos in Dalnezelenetskaya Bay (Barents sea) after the invasion of king crab. In: G.G. Matishov (ed.). Investigation of zoobenthos of the shelf. Information support of ecosystems studies. Apatity, Kola Scientific Center RAS, pp 105-116. [in Russian]

Sakshaug, E. 1997. Biomass and productivity distributions and their variability in the Barents Sea. ICES J. Mar. Sci. 54: 341-350.

Salvigsen, O., Forman, S.L. & Miller, G.H. 1992. Thermophilous molluscs on Svalbard during the Holocene and their paleoclimatic implications. Polar Res. 11: 1-10.

Schmid, M.K. & Piepenburg, D. 1993. The benthos zonation of the Disko Fjord, West Greenland. Meddr. Grønland, Biosci. 37: 1-21.

Sejr, M.K., Jensen, K.T. & Rysgaard, S. 2000. Macrozoobenthic community structure in a high-arctic East Greenland fjord. Polar Biol. 23: 792-801.

Sejr, M.K., Blicher, M.E. & Rysgaard S. 2009. Sea ice cover affects inter-annual and geographic variation in growth of the Arctic cockle Clinocardium ciliatum (Bivalvia) in Greenland. Mar. Ecol. Prog. Ser. 389: 149-158.

Sejr, M.K., Włodarska -Kowalczuk, M., Legezyinska, J. & Blicher, M.E. 2010. Macrobenthic species composition and diversity in the Godthaabsfjord system, SW Greenland. Polar Biol. 33: 421-431.

Sejr, M.K., Batty, P., Josefson, A., Blicher, M.E., Hansen, J. & Rysgaard, S. 2011. Survey of macrobenthic invertebrates in the eastern Baffin Bay including estimates of biogeochemical activity and PAH levels of the sediment. In: D. Boertmann & A. Mosbech (eds.). Eastern Baffin Bay – A strategic environmental impact assessment of hydrocarbon activities. Scientific Report from DCE – Danish Centre for Environment and Energy no. 9.

Sharkey, M.J. 2001. The All Taxa Biological Inventory of the Great Smoky Mountains National Park. The Florida Entomologist 84, No. 4: 556-564.

Sharma, J. & Bluhm, B.A. 2011. Diversity of larger free-living nematodes from macrobenthos (>250 um) in the Arctic deep-sea Canada Basin. Mar. Biodiv. 41: 455-465.

Sheremetevsky, A.M. 1897. The role of meibenthos in biocoenosis of south Sachalin, east Kamchantka and Novosibirsk Shallows. Issled. Fauny Morei 35. [in Russian]

Sirenko, B.I. 2001. List of species of free-living invertebrates of Eurasian Arctic seas and adjacent deep waters. Russian Academy of Sciences, Explorations of the fauna of the seas (Zoological Institute, St Petersburg) 51(59): 1-76.

Sirenko, B.I. 2004. On the Study of the Fauna of the Laptev Sea and Adjacent Water Areas. Issled. Fauny Morei 54(62): 5-8. [in Russian]

Sirenko, B.I. & Gagaev, S.Y. 2007. Unusual abundance of macrobenthos and biological invasions in the Chukchi Sea. Rus. J. Mar. Biol. 33: 355-364.

Sirenko, B.I., Markhaseva, E.L., Buzhinskaya, G.N., Golikov, A.A., Menshutkina, T.V., Petryashov, V.V. *et al*. 1996. Preliminary data on suprabenthic invertebrates collected during the *RV Polarstern* cruise in the Laptev Sea. Polar Biol. 16: 345-352.

Sirenko, B.I., Clarke, C., Hopcroft, R.R., Huettmann, F., Bluhm, B.A. & Gradinger, R. 2010. The Arctic Register of Marine Species (ARMS) compiled by the Arctic Ocean Diversity (ArcOD) project. www.marinespecies.org/arms [assessed 4 January 2012]

Smirnov, A.V. 1994. Arctic echinoderms: composition, distribution and history of the fauna. In: B. David, A. Guille, J.P. Feral & M. Roux (eds.). Echinoderms through Time, Proceedings of the 8th International Echinoderms Conference, pp 135-143. Balkema, Rotterdam.

Sokolov, V.I. & Miljutin, D.M. 2008. Recent state of the population of king crab (*Paralithodes camtschaticus*, Decapoda, Lithodidae) in Barents sea. Zoologicheskii Zhurnal. 87: 141-155. [in Russian]

Soltwedel, T. & Schewe, I. 1998. Activity and biomass of the small benthic biota under permanent ice coverage in the central Arctic Ocean. Polar Biol. 19: 52-62.

Soltwedel, T., Mokievsky, V. & Schewe, I. 2000. Benthic activity and biomass on the Yermak Plateau and in adjacent deep-sea regions northwest of Svalbard. Deep-Sea Res. Part I Oceanographic Research Papers 47: 1761-1785.

Soltwedel, T., Bauerfeind, E., Bergmann, M., Budaeva, N., Hoste, E., Jaeckisch, N. *et al*. 2005. HAUSGARTEN: multidisciplinary investigations at a deep-sea, long-term observatory in the Arctic Ocean. Oceanography 18(3): 46-61.

Soltwedel, T., Jaeckisch, N., Ritter, N., Hasemann, C., Bergmann, M. & Klages, M. 2009a. Bathymetric patterns of megafaunal assemblages from the arctic deep-sea observatory HAUSGARTEN. Deep-Sea Res. I 56 (10): 1856-1872.

Soltwedel, T., Mokievsky, V., Schewe, I. & Hasemann, C. 2009b. Yermak Plateau revisited: spatial and temporal patterns of meiofaunal assemblages under permanent ice-coverage. Polar Biol. 32: 1159-1176.

Solyanko, K., Spiridonov, V. & Naumov, A. 2011a. Biomass, commonly occurring and dominant species of macrobenthos in Onega Bay (White Sea, Russia): data from three different decades. Marine Ecology 32 (suppl. 1): 36-48.

Solyanko, K., Spiridonov, V. & Naumov, A. 2011b. Benthic fauna of the Gorlo Strait, White Sea: a first species inventory based on data from three different decades from the 1920s to 2000s. Mar. Biodiv. 41: 441-453.

Somerfield, P.J., Cochrane, S.J., Dahle, S. & Pearson, T.H. 2006. Free-living nematodes and macrobenthos in a high-latitude glacial fjord. J. Exp. Mar. Biol. Ecol. 330: 284-296.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M. *et al*. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. BioScience 57: 573-583.

Spiridonov, V.A., Gavrilo, M.V., Krasnova, E.D. & Nikolaeva, N.G. (eds.) 2011. Atlas of marine and coastal biological diversity of the Russian Arctic. WWF Russia, Moscow.

Syvitski, J.P.M., Farrow, G.E., Atkinson, R.G.A., Moore, P.G. & Andrews, J.T. 1989. Baffin Island fjord macrobenthos: Bottom communities and environmental significance. Arctic 42: 232-247.

Tchesunov, A.V. 2008. Biota of the White Sea Biological Station of Moscow State University. In: M.P. Kirpichnikov (ed.). Scientific conference dedicated to 70th anniversary of the White Sea biological station, pp 42-46. Moscow. [in Russian]

Tchesunov, A.V., Kaljakina, N.M. & Bubnova, E.N. 2008. A Catalogues of the Biota of the White Sea Biological Station of the Moscow State University. KMK Scientific Press Ltd., Moscow. [in Russian]

Thiel, H. 1975. The size structure of deep-sea benthos. Int. Rev. Gesamt. Hydrobiol. 60: 575-606.

Thistle, D. 2003. The Deep-Sea Floor: An Overview. In: P.A. Tyler (ed.). Ecosystems of the Deep Oceans, Ecosystems of the World 28, pp 5-38. Elsevier, London.

Thorson, G. 1957. Bottom Communities (sublittoral or shallow shelf). In: J.W. Hedgepth (ed.). Treatise on marine ecology and paleoecology. Mem. Geol. Soc. Amer. 1.

Udalov, A.A., Mokievsky, V.O. & Azovsky, A.I. 2005. Depth-related pattern in nematode size: Does the depth itself really mean? Progr. Oceanogr. 67(1-2): 1-23.

Vanreusel, A., Clough, L., Jacobsen, K., Ambrose, W., Jivaluk, J., Ryheul, V. *et al*. 2000. Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. Deep-Sea Research I 47: 1855-1879.

Vermeij, G. 1989. Invasion and extinction: The last three million years of North Sea pelecypod history. Conserv. Biol. 3: 274-281.

Vermeij, G. 1991. Anatomy of an invasion: the trans-Arctic interchange. Paleobiology 17: 281-307.

Vermeij, G.J. & Roopnarine, P.D. 2008. The coming Arctic invasion. Science 321: 780-781.

Vinogradova, N.G. 1997. Zoogeography of the abyssal and hadal zones. Adv. Mar. Biol. 32: 326-387.

Wassmann, P., Duarte, C.M., Agusti, S. & Sejr, M.K. 2011. Footprints of climate change in the Arctic marine ecosystem. Global Change Biol. 17: 1235-1249.

Węsławski, J.M., Włodarska-Kowalczuk, M. & Legezynska, J. 2003. Occurrence of soft bottom macrofauna along the depth gradient in High Arctic, 79°N. Polish Polar Res. 24: 73-78.

Węsławski, J.M., Kwasniewski, S., Stempniewicz, L. & Blachowiak- Samolyk, K. 2007. Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. Polish Polar Res. 27: 259-278.

Węsławski, J.M., Wictor, J. Jr. & Kotwicki, L. 2010. Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. Mar. Biodiv. 40: 123-130.

Węsławski, J.M., Kendall, M.A., Włodarska-Kowalcsuk, M., Iken, K., Kedra, M., Legezynska, J. & Sejr, M.K. 2011. Climate change effects on Arctic fjord and coastal macrobenthic diversity – observations and predictions. Mar. Biodiv. 41: 71-85.

Witman, J.D., Cusson, M., Archambault, P., Pershing, A. & Mieszkowska, N. 2008. The relation between productivity and species diversity in Temperate-Arctic marine ecosystems. Ecology 89(11), Supplement: 66-80.

Włodarska-Kowalczuk, M. 2007. Molluscs in Kongsfjorden (Spitsbergen, Svalbard): a Species List and Patterns of Distribution and Diversity. Polar Res. 26: 48-63.

Włodarska-Kowalczuk, M. & Kedra, M. 2007. Surrogacy in natural patterns of benthic distribution and diversity: selected taxa versus lower taxonomic resolution. Mar. Ecol. Prog. Ser. 351: 53-63.

Włodarska-Kowalczuk, M. & Pearson, T. 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). Polar Biol. 27: 155-167.

Włodarska-Kowalczuk, M. & Węsławski, J.M. 2008. Mesoscale spatial structures of soft-bottom macrozoobenthos: physically controlled/impoverished versus biologically accommodated/ diverse communities. Mar. Ecol. Prog. Ser. 356: 215-224.

Włodarska-Kowalczuk, M., Węsławski, J.M. & Kotwicki, L. 1998. Spitsbergen glacial bays macrofauna – a comparative study. Polar Biol. 20: 66-73.

Włodarska-Kowalczuk, M., Kendall, M.A., Węsławski, J.M., Klages, M. & Soltwedel, T. 2004. Depth gradients of benthic standing stock and diversity on the continental margin at a high-latitude ice-free site (off Spitsbergen, 70º N). Deep-Sea Res. I 51: 1903-1914.

Włodarska-Kowalczuk, M., Pearson, T.H. & Kendall, M.A. 2005. Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. Mar. Ecol. Prog. Ser. 303: 31-41.

Włodarska-Kowalczuk, M., Sicinski, J., Gromisz, S., Kendall, M.A. & Dahle, S. 2007a. Similar soft-bottom polychaete diversity in Arctic and Antarctic marine inlets. Mar. Biol. 151: 607-616.

Włodarska-Kowalczuk, M., Szymelfenig, M. & Zajaczkowski M. 2007b. Dynamic sedimentary environments of an Arctic glacier-fed river estuary (Adventfjorden, Svalbard). II. Meio- and macrobenthic fauna. Estuar. Coast. Shelf. Sci. 74: 274-284.

Włodarska-Kowalczuk, M., Kuklinski, P., Ronowicz, M., Legezynska, J. & Gromisz, S. 2009. Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). Polar Biol. 32: 897-905.

Włodarska-Kowalczuk, M., Renaud, P.E., Węsławski, J.M., Cochrane, S.K.J. & Denisenko, S.G. 2012. Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. Mar. Ecol. Prog. Ser. 463: 73-87.

Zenkevitch, L. 1963. Biology of the Seas of the U.S.S.R. George Allen and Unwin, London.

Zhirkov, I.A. 2001. Polychaetes of the Arctic Ocean. Yanus-K, Moscow.

Zhirkov, I.A. 2010. The Life on the Bottom. Bio-ecology and Biogeography of Benthos. KMK Scientific Press Ltd, Moscow. www.evolbiol.ru/large_files/zhirkov2010.pdf [in Russian].