

Similar soft-bottom polychaete diversity in Arctic and Antarctic marine inlets

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Received: 7 May 2006 / Accepted: 26 September 2006 / Published online: 21 October 2006
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Abstract The diversity of soft-bottom polychaete assemblages in one Antarctic (Admiralty Bay) and two Arctic (Kongsfjord and van Mijenfjord) localities was compared. The data sets included 79 (Admiralty Bay), 80 (Kongsfjord) and 44 (van Mijenfjord) samples collected with use of 0.1 m² van Veen grab. The number of species per sample in Kongsfjord (mean 19.9 ± 8.0 SD) was higher than that in Van Mijenfjord (13.7 ± 8.3) or Admiralty Bay (15.7 ± 9.4). The differences in species numbers reflected differences in numbers of individuals in samples: $310.4 \text{ ind}/0.1 \text{ m}^2 \pm 178.0$ in Kongsfjord, $132.7 \text{ ind}/0.1 \text{ m}^2 \pm 88.7$ in Van Mijenfjord and $138.9 \text{ ind}/0.1 \text{ m}^2 \pm 91.5$ in Admiralty Bay. The Hurlbert diversity for 50 individuals ($ES_{[50]}$) was similar at all sites: 10.7 ± 3.4 in Kongsfjord, 9.7 ± 4.2 in van Mijenfjord, 10.5 ± 4.9 in Admiralty Bay. The shape of

species accumulation curves was also similar for all localities. There was no significant difference (at $P < 0.05$) either in the total number of species or in species richness as estimated by *Chao1* and *Chao2* estimators. The generic and family richness at three sites was also similar. We found no substantial differences in the distribution of species among families. At both poles Terebellidae, Ampharetidae, Maldanidae, Spionidae and Polynoidae were dominant in terms of species numbers. The similarity of infaunal polychaete diversity at the polar sites studied contrasts with the substantial differences reported for epi-megafauna. Our study suggests that the patterns of diversity of polar benthic communities are shaped by patterns of habitat heterogeneity which appears to mask any historical processes.

Communicated by O.Kinne, Oldendorf/Luhe.

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Introduction

For several years the Antarctic biota has been described as being more diverse than that of the Arctic (Knox and Lowry 1977; Dayton 1990; Dunton 1992). The often-cited Knox and Lowry's (1977) review of polar biodiversity reported that the number of species in all major macrobenthic groups in the Antarctic seas was 50–100% higher than that in the same groups in the Arctic. A number of hypotheses have been proposed to explain the origins of this difference. The most common explanations are the harshness and relative homogeneity of habitats in the Arctic (an equilibrium theory) and the differences in geological age of two polar regions (a non-equilibrium one) (Clarke and Crame 1997). The considerable interest in the relative diversity of the Arctic and Antarctic fauna was driven by the challenging ecological

issues of the existence and the origins of global latitudinal gradients in marine diversity. The strength of the latitudinal patterns in two hemispheres is largely shaped by the relative levels of diversity in the polar regions. The latitudinal cline in diversity of deep-sea fauna is far more pronounced in the North Atlantic than that in the southern hemisphere (Gage et al. 2004; Rex et al. 1993). That notable asymmetry in latitudinal patterns was attributed to the difference in the geological history and resulting difference in diversity of two polar regions (Gage et al. 2004; Rex et al. 1993).

Piepenburg (2005) reviewed the recent Arctic benthic literature and questioned the paradigm of the generally higher Antarctic diversity calling it an “undue overgeneralization”. The comparisons of the regional species lists suffer from biases and the inconsistencies in sampling effort, spatial and taxonomic coverage of the limited number of studies accounting for the species inventories. Furthermore, Gutt et al. (2004) attempted to compare the results of recent estimates of regional species richness and found the total number of benthic species in the Antarctic only “slightly higher” than that in the Arctic and intermediate when compared with other large marine regions. The updated checklists of macrobenthic species occurring only in the Eurasian sector of the Arctic seas include 570 species of Amphipoda, 140 species of Bivalvia, 469 species of Polychaeta (Sirenko 2001), while the estimated Antarctic species richness within the same groups are 520, 110 and 645, respectively (Clarke and Johnston 2003). These new reports suggest that the common notion of a diverse Antarctic benthic fauna set against a poor Arctic biota must be revisited. Such a revision requires standardized comparative studies of the fauna in both regions. Piepenburg (2005) points out that the paradigm of higher Antarctic diversity was developed from either literature studies or data sets which were not necessarily methodologically or spatially consistent. Fully comparable data sets on the benthic fauna from both polar regions are sparse (Clarke and Crame 1997). In particular, there are few Antarctic studies that provide comprehensive data on soft-bottom faunal identity and abundance. The recently reported standardized comparisons of benthic diversity in Arctic and Antarctic were conducted with use of dredges (Piepenburg et al. 1997) or underwater video images (Starmans and Gutt 2003) and so were focused on the epifauna. There are no similar comparative studies undertaken of the polar infauna while the evidence from the vast literature on latitudinal gradients in marine benthic diversity suggests that the large-scale patterns might not be uniform across different habitats and taxa. Thorson (1957) described the clear (over tenfold) cline of species richness from tropics to high Arctic sites for

coastal epifauna, while there were more or less the same number of infaunal species in tropical, temperate, boreal and high Arctic shallow seas. Clarke (1992) stated that while the latitudinal cline in diversity was well documented for molluscs and foraminiferans, similar patterns were not observed in other taxa.

The crucial issue in comparative studies of diversity is the scale over which the diversity is to be measured. There are several systems of naming the range of scales in diversity studies (Whittaker 1972; Magurran 2004; Rosenzweig 1995). The various approaches were reviewed by Gray (2000) who proposed a simple unifying terminology for the scales of diversity: (1) point (single sampling unit) species richness, SR_p ; (2) sample (site of defined area) species richness, SR_s ; (3) large area species richness, SR_L ; (4) biogeographical province species richness, SR_B . Gray (2001) has pointed out that most of the comparative studies in diversity have been performed at one of the two extreme spatial scales—at either extremely large scales (regional species lists) or at highly local scales (the comparison of single samples). The regional species lists suffer from all the pitfalls of the compilations of studies varying in sampling methodology, spatial coverage, taxonomic expertise of identifiers, etc. The other approach—the comparison of number of species in single samples—allows a high level of standardization of sampling and taxonomic methods, but has been strongly criticized as unrepresentative of either the size of some theoretical species pool or the rate of species accumulation in a collectors curve. Gray (2001) postulated that a greater emphasis on intermediate scales of data collection and a focus on species/area relationships were needed.

In this paper, our aim is to contribute to the debate on polar diversity by comparing data sets on polychaetes collected at the intermediate scale—the scale of whole marine inlets. The data come from Arctic (Spitsbergen) fjords and an Antarctic (King George Island) inshore bay. We aimed to: (1) compare the species richness at Antarctic and Arctic sites, both at the scale of single samples (SR_p), and at the scale of the whole marine inlets (SR_L); and (2) examine taxonomic patterns within the polychaete fauna to determine if the various locations have different patterns of species allocation between families that might indicate differences in the pattern of speciation.

Materials and methods

Sampling and laboratory analyses

Samples were taken in two Arctic sites: Kongsfjord and van Mijenfjord and one Antarctic site: Admiralty Bay.

Kongsfjord and van Mijenfjord are both situated in west Spitsbergen (Svalbard; Fig. 1). Kongsfjord is an open (no sill) fjord with three tidal glaciers situated toward its head. Its physical and biological characteristics have been reviewed by Svendsen et al. (2002) and Hop et al. (2002). The soft-bottom macrofauna was described by Wlodarska-Kowalczyk and Pearson (2004). Unlike Kongsfjord, van Mijenfjord has a sill; its soft-bottom fauna has been studied by Gulliksen et al. (1985) and Renaud et al. (2006). Admiralty Bay is an irregular fjord-like embayment at King George Island. The physical setting of Admiralty Bay was reviewed by Rakusa-Suszczewski (1993), the soft-bottom macrofauna was described by Jazdzewski et al. (1986) and polychaetes by Sicinski and Janowska (1993) and Sicinski (2000).

In Kongsfjord the material considered in this paper was collected during two cruises of R.V *Oceania*—in July of 1997 and 1998. The samples were taken on soft bottom at depths ranging from 38 to 380 m. The 30 stations were situated haphazardly throughout the fjord. One to three van Veen grabs (0.1 m²) were taken at each station, giving a total of 80 samples. In van Mijenfjord the samples were taken during two cruises of R.V *Oceania* in July 2000 and 2001. Four van Veen samples (0.1 m²) were taken at 11 stations situated along the fjord axis, on a soft bottom, at depths from 64 to 104 m. In Admiralty Bay 79 van Veen samples were taken in austral summer of 1985 at 79 stations situated haphazardly throughout the embayment on soft bottom at depths from 30 to 504 m.

Recovered sediments were sieved using a 0.5 mm (Kongsfjord and Admiralty Bay) or 1 mm (van

Mijenfjord) mesh sieve. Warwick et al. (2006) studied the relation between the benthic diversity estimates and sizes of sieve meshes. They showed that the species diversity of soft-bottom benthic samples did not significantly differ between samples sieved on 1 or 0.5 mm sieves. We have therefore decided to use the material sieved on these two different mesh sizes in our comparative study. The samples were fixed in formalin and in the laboratory all the animals were sorted, identified to the lowest possible taxonomic level and enumerated.

Data analyses

Point-scale diversity was expressed as the number of species (S) per sample and by the Hurlbert rarefaction index ($ES_{[n]}$). $ES_{[n]}$ is an estimate of the number of species in subsample of n individuals, based on the relative abundance of species in original sample (Hurlbert 1971). $ES_{[n]}$ was developed to facilitate the comparisons of diversity of samples comprising differing numbers of individuals. $ES_{[n]}$ was calculated for $n = 50$. The differences in the number of individuals per sample (N), S and $ES_{[50]}$ between sites were tested using the nonparametric Kruskal–Wallis test, as even after data transformation, variances could not be homogenized. Post hoc testing of differences between pairs of sites was carried on with using pairwise Mann–Whitney U tests.

Species accumulation curves describe the number of observed species (S_{obs}) as a function of the number of samples. They allow the comparison of the diversity of faunal assemblages at comparable levels of sampling

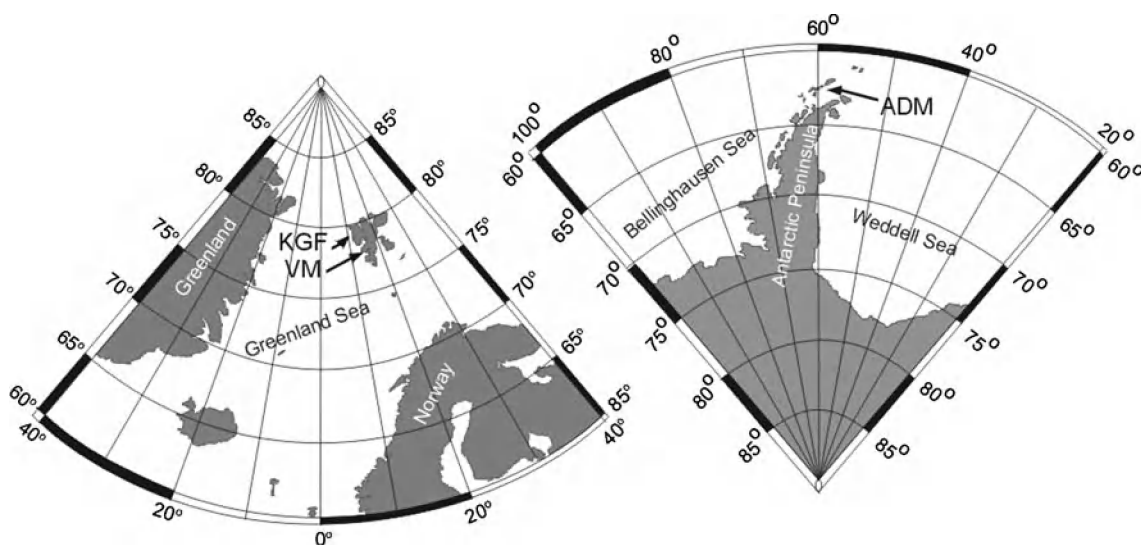


Fig. 1 Location of study areas: Kongsfjord (KGF) and van Mijenfjord (VM) off Spitsbergen (Svalbard) and Admiralty Bay (ADM) off King George Island (South Shetlands)

effort. Species accumulation curves with 95% confidence intervals were computed using the formulae of Colwell et al. (2004). The computation of confidence intervals permits the direct statistical comparison of species richness of two data sets, i.e., the differences are not significant at $P < 0.05$ if the 95% confidence intervals overlap (Colwell et al. 2004).

In the cases where species accumulation curves fail to reach an asymptote, the comparison of total species richness between assemblages requires the use of methods of species richness estimation. Alternative approaches are: (1) extrapolation of the accumulation curve or (2) nonparametric techniques. The Michaelis–Menten (MM) function is the most commonly used method of generating an asymptotic curve fitting the species accumulation curve (Magurran 2004). The predicted asymptote is used as an estimate of total species richness. MM has been shown to produce stable and broadly accurate estimates even at small numbers of samples (Magurran 2004). The MM asymptote estimation was computed for each of the three sites. Alternative methods—the nonparametric *Chao1* and *Chao2* estimators of species richness—are based on the concept that rare and uncommon species carry information about the number of species missing in samples (Chao 2004). $Chao1 = S_{obs} + F_1^2/2F_2$, where F_1 is the number of species represented by single individual (singletons) and F_2 is the number of species represented by exactly two individuals (doubletons). $Chao2 = S_{obs} + Q_1^2/2Q_2$, where Q_1 is the number of species that occur in just one sample (uniques) and Q_2 is the number of species that occur in exactly two samples (duplicates). Foggo et al. (2003) evaluated six nonparametric species richness estimators using marine ecological data sets and recommended the use of *Chao1* due to its better performance at intermediate sampling efforts. *Chao2* provided the least biased estimates of species richness for small numbers of samples in the evaluation of seven estimators performed by Colwell and Coddington (1994). In our study the *Chao1* and *Chao2* are both computed along with log-linear 95% confidence intervals as suggested by Chao (1987).

The patterns of taxonomic domination in the studied sites were illustrated with a plot of hollow curve distributions (HCD). The numbers of species per family were plotted for the three sites studied with families ordered from the most diverse to the least diverse (according to the average number of species per family).

$ES_{[n]}$ was calculated with use of the PRIMER Package. Species accumulation curves, MM, *Chao1* and *Chao2* estimators of species richness were computed with use of EstimateS (Version 7.5, R. K. Colwell, <http://www.purl.oclc.org/estimates>). The statistical analyses

were carried on with use of the Statsoft Inc. software STATISTICA v.6.

Results

The mean number of polychaete individuals in a sample (N) was much higher in Kongsfjord ($310.4 \text{ ind}/0.1 \text{ m}^2 \pm 178.0 \text{ SD}$) than that in either van Mijenfjord ($132.7 \text{ ind}/0.1 \text{ m}^2 \pm 88.7$) or Admiralty Bay ($138.9 \text{ ind}/0.1 \text{ m}^2 \pm 91.5$; Fig. 2). There were significant differences in numbers among sites (Kruskal–Wallis $H = 54.5$ $P < 0.001$): post hoc multiple pairwise testing showed Kongsfjord to have higher numbers of polychaetes than two other sites ($P < 0.05$, Mann–Whitney U test). Similarly, S was significantly higher in Kongsfjord (19.9 ± 8.0) than in either van Mijenfjord (13.7 ± 8.3) or Admiralty Bay (15.7 ± 9.4) [Kruskal–Wallis ($H = 19.4$, $P < 0.001$) followed by post hoc, pairwise Mann–Whitney U tests, $P < 0.05$]. $ES_{[50]}$ was similar at the three studied sites: 10.7 ± 3.4 in Kongsfjord, 9.7 ± 4.2 in van Mijenfjord, 10.5 ± 4.9 in Admiralty Bay. No significant differences in $ES_{[50]}$ between sites were found with use of the Kruskal–Wallis test at $P < 0.05$.

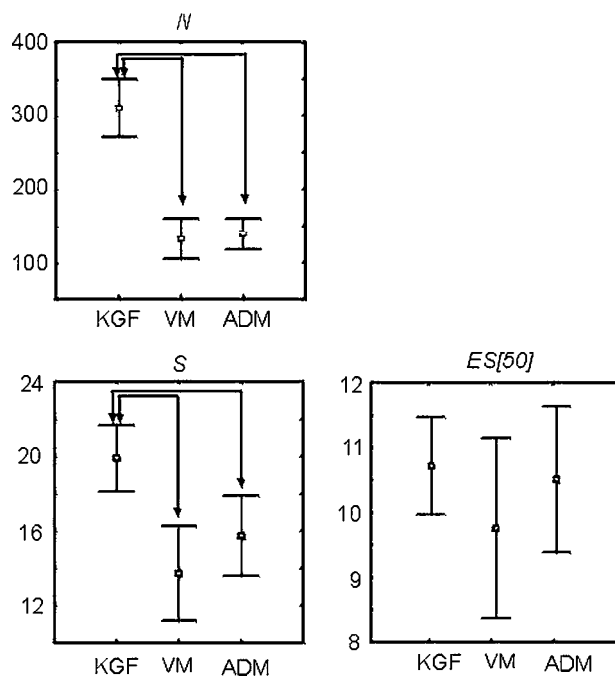


Fig. 2 Polychaeta density (N number of individuals per 0.1 m^2) and alpha diversity (S number of species per sample, $ES_{[50]}$ Hurlbert index for 50 individuals) in studied sites. KGF Kongsfjord, VM Van Mijenfjord, ADM Admiralty Bay. Means and 0.95 confidence intervals are plotted. Arrows indicate significant differences ($P < 0.05$, post hoc multiple U Mann–Whitney tests) between pairs of sites

The shapes of the species accumulation curves were very similar for the three sites (Fig. 3). The 95% confidence intervals for the three curves overlapped for all sample accumulation levels indicating that there were no significant differences between them at $P < 0.05$. The total observed number of polychaete species was 101 in Admiralty Bay, 97 in Kongsfjord and 91 in van Mijenfjord.

Chao1 gave an estimate of 110 species (with 95% confidence intervals from 104 to 133) in Admiralty Bay, 114 species (95% CI from 103 to 138) in Kongsfjord and 99 species (95% CI from 93 to 115) in van Mijenfjord (Fig. 3). The *Chao1* estimate of total rich-

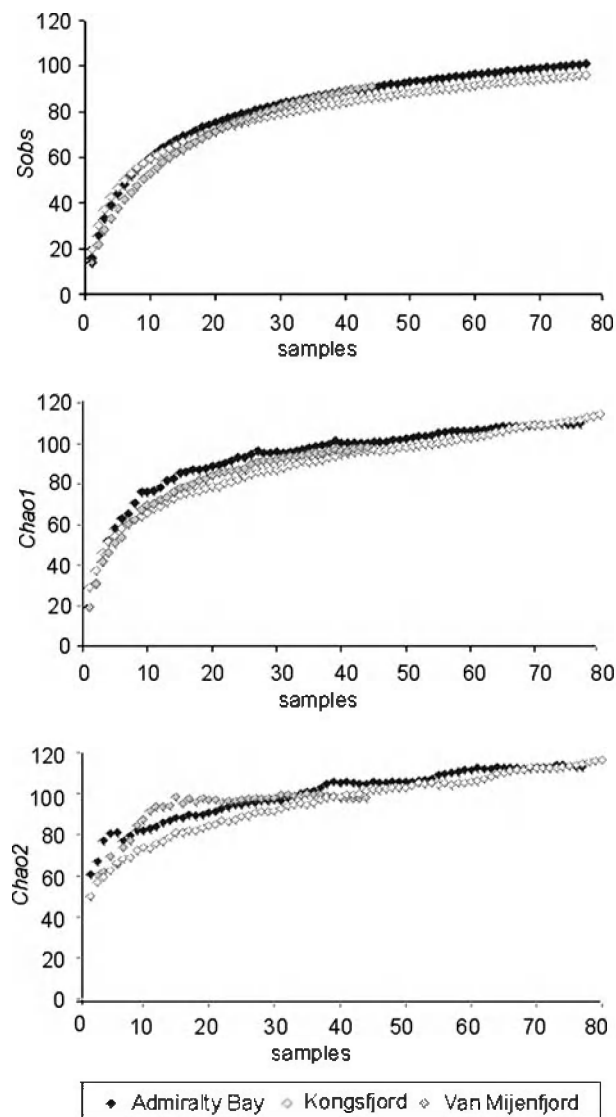


Fig. 3 Species accumulation curves for the three sites. Species richness estimated by the total number of all species (*Sobs*), *Chao1* and *Chao2* estimators. For the clarity of the graph the confidence intervals are not presented

ness was lowest for van Mijenfjord, but the slopes and shapes of the species accumulation curves for *Chao1* were similar for the three sites, and the 95% confidence intervals overlapped. The *Chao1* estimates of total richness calculated for 44 samples (the total number of samples collected in van Mijenfjord) gave mean 100 species (95% CI from 94 to 122) in Admiralty Bay and 97 species (95% CI from 89 to 121) in Kongsfjord.

Chao2 estimate of total richness gave mean 115 species (with 95% confidence intervals from 106 to 139) in Admiralty Bay, 118 species (95% CI from 105 to 152) in Kongsfjord and 99 species (95% CI from 93 to 115) in van Mijenfjord (Fig. 3). The points of the species accumulation curves for *Chao2* were slightly scattered when low numbers of samples were considered (up to about 20 samples). For larger sets of data the points tended to form curves of similar shape for the three sites. The 95% confidence intervals of all the curves overlapped. The *Chao2* estimates of total richness calculated for 44 samples gave mean 106 species (95% CI from 97 to 132) in Admiralty Bay and 103 (95% CI from 92 to 131) in Kongsfjord.

The MM estimator of the asymptotic value of total species richness gave 105 species in Admiralty Bay, 96 species in Kongsfjord and 102 species in van Mijenfjord.

There were 75 genera and 28 families of polychaete in Kongsfjord, 63 genera and 27 families in van Mijenfjord and 86 genera and 28 families in Admiralty Bay. The distribution of species among families was similar at all sites (Fig. 4) and the same families dominated in terms of the number of species. The most speciose families included Terebellidae (7–14 species), Ampharetidae (6–13 species), Maldanidae (7–12 species), Spionidae (4–9 species) and Polynoidae (4–9 species). Nine families were represented by no more than one species in each of the sites: Scalibregmatidae, Chaetopteridae, Pectinaridae, Hesionidae, Cossuridae, Apistobranchidae, Pholoidae, Sternaspidae and Onuphidae.

Discussion

There was no difference in diversity, across a range of measures, between the infaunal polychaetes of the Antarctic Admiralty Bay and the Arctic fjords of Svalbard. There are only a few other polar benthic studies which both: (1) report the polychaete diversities, (2) use sampling methods comparative to ours. The sample and the site species richness of Kongsfjord, van Mijenfjord and Admiralty Bay lay within the same range as a group of other Arctic and Antarctic sites

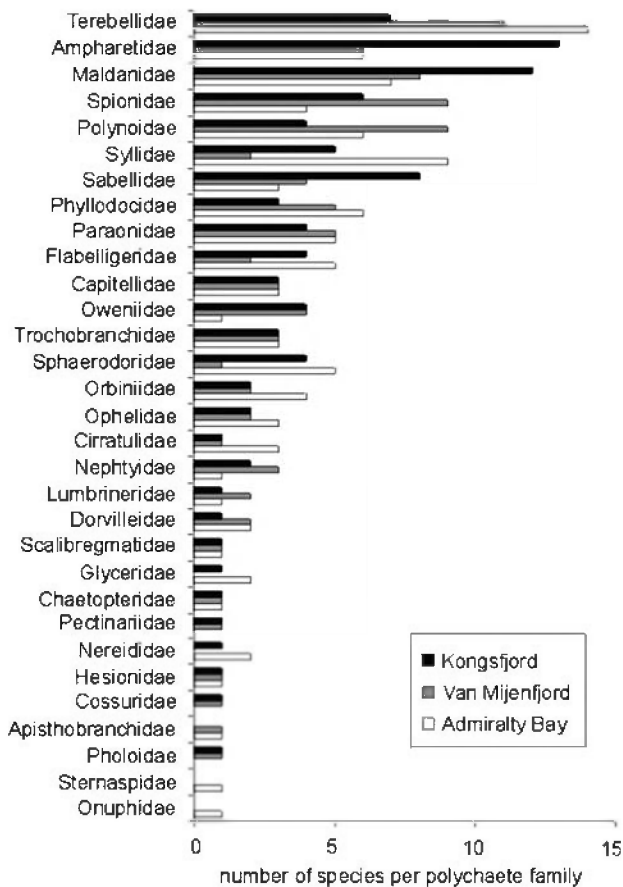


Fig. 4 Hollow curve distribution of the number of species per polychaete families in the studies sites. The families are ordered according to the average number of species

(Table 1). This finding contrasts sharply with the substantial differences in diversity of Arctic and Antarctic epibenthic megafauna. Piepenburg et al. (1997) recorded that the diversity of brittle stars and sea stars dredged from the Weddell Sea was higher than off north-eastern Greenland, and noted that the differences were consistent at different spatial scales (sample, assemblage and regional). Starmans and Gutt (2003) found higher numbers of taxa per sample of epibenthic megafauna in the Weddell Sea and Bellingshausen Sea than off north-eastern Greenland. The lack of a large-scale latitudinal gradient in sediment infaunal assemblages, in contrast to clear patterns observed for hard bottom epifauna, was pointed out in early work of Thorson (1957). Richardson and Hedgepeth (1977) studied soft-bottom fauna at Anvers Island (Antarctic Peninsula) and found diversities (Shannon–Wiener index) comparable to and species richness even higher than values noted for Virginia and North Carolina shelf fauna. Kendall and Aschan (1993) failed to find significant differences in the sample diversity of shallow water soft-bottom infauna of Spitsbergen

(78° N), North Sea (55° N) and Java (7° S). Our study suggests no difference in Arctic/Antarctic infaunal polychaete diversity at the scale of a sample or at the scale of a large area. That contrasts with results of methodologically standardized studies of mega-epifauna (Starmans and Gutt 2003; Piepenburg et al. 1997). Nevertheless, all the polar comparisons mentioned above are based on a small number of sites in a limited geographical area and this raises questions of how well sampling has represented the generality of Arctic and Antarctic faunas. There are possible sources of biases in comparative diversity studies as ours. No two sampling campaigns are alike; samples are collected for many purposes other than making comparisons of diversity, but nevertheless we have little option but to use the data they provide in comparative studies of biodiversity. The generality of the patterns observed in our study will hopefully be tested in the future. If the results of our study are proved to reflect the general pattern, the question emerges: why should there be a pattern of higher Antarctic diversity in megabenthic epifauna but not in the polychaetes or generally in infauna?

A number of hypothesis have been proposed to explain the differences in Arctic and Antarctic biodiversity. Macroecologists argue that diversity patterns at geographical scales are driven by regional rather than local processes (Ricklefs 1987). If this train of argument is followed, the differences in diversity between polar regions are presumed to derive from the longer period of stable conditions in the Antarctic. The Antarctic biota has evolved over the past 20 million years of relatively stable physical conditions pertaining after the isolation of Antarctica by circum-Antarctic current and subsequent massive cooling (Dayton et al. 1994; Dayton 1990). In contrast, during the last glaciation Arctic continental shelves were either exposed or covered with glacial ice resulting in a nearly complete eradication of the benthic fauna (Dunton 1992). The present Arctic benthic fauna is a young biocenosis that has remained in a state of active colonization over the past 6,000–14,000 years (Dayton et al. 1994). An alternative argument for the higher Antarctic diversity relates to the fact that the area of the Arctic Ocean is less than half that of the Southern Ocean (Dayton 1990). According to species richness–area relationships (Rosenzweig 1995) that should result in lower Arctic diversity (Gray 2001).

Do these large-scale evolutionary processes lead to the differences in diversity at local scales? Cornell and Lawton (1992) argued that local species richness is proportional to the size of the regional species pool. Witman et al. (2004) studied the latitudinal patterns of

Table 1 Number of polychaete species recorded in Arctic and Antarctic soft-bottom surveys

| Site | Sieve mesh size (mm) | Sampled area (m ²) | <i>S</i> | <i>TS</i> |
|---|----------------------|--------------------------------|----------------------|-----------|
| Arctic | | | | |
| Kongsfjord, Spitsbergen ^a | 0.5 | 8.0 | 19.9 ± 8.0 | 97 |
| Van Mijenfjord, Spitsbergen ^a | 1 | 4.4 | 13.7 ± 8.3 | 91 |
| Sassenfjord, Spitsbergen ^b | 0.5 | 2.5 | 31 ± 3 | 69 |
| Coastal waters of Kara Sea ^c | 0.5 | 8.0 | 21 ± 11 ^k | 81 |
| Disko Fiord, West Greenland ^d | 1 | 3.2 | – | 48 |
| Barents Sea ^e | 1 | 4.4 | 12.2 ± 5.6 | 95 |
| Pechora Sea ^f | 1 | 6.6 | 12.2 ± 4.3 | 78 |
| Frantz Josef Land ^g | 1 | 4.5 | 14.9 ± 6.0 | 77 |
| Antarctic | | | | |
| Admiralty Bay ^a | 0.5 | 7.9 | 15.7 ± 9.4 | 101 |
| Terra Nova Bay, Ross Sea ^h | 1 | 1.4 | 22.8 ± 13.7 | 77 |
| South Shetland Islands ⁱ | 0.5 | 6.9 | 16.4 ± 6.6 | 89 |
| Arthur Harbor, Anvers Island ^j | 1 | 6.8 | – | 106 |

All studies employed 0.1 m² van Veen grabs to collect samples
S number of polychaete species per sample (mean ± SD); *TS* total number of polychaete species found in a study

^a Present study

^b Kendall (1994)

^c Jorgensen et al. (1999)

^d Schmid and Piepenburg (1993)

^e Dahle et al. (1997)

^f Dahle et al. (1998)

^g Dahle et al. (2006)

^h Gambi et al. (1997)

ⁱ San Martin et al. (2000)

^j Richardson and Hedgepeth (1977)

^k Number of species per station (five replicate grab samples per station, sample data not available)

hard bottom epibenthic diversities at both local and regional scales and showed that latitudinal patterns were much stronger at the regional scale than at the local scale. The variation of local community richness at a global scale apparently reflected both the size of the regional pools of species and the local-scale ecological processes. We do not know the extent to which the ecological and evolutionary mechanisms are reflected in data sets collected at different spatial scales, or if local studies can reveal broad-scale low amplitude drivers. Actually, some mechanisms operating at the ecological temporal and spatial scales were also proposed as possible explanations of observed Arctic/Antarctic diversity differences.

For some time, Arctic benthic habitats have been regarded as environmentally harsher due to regular disturbance by the iceberg scouring, which was supposed to result in low benthic diversity (Dayton 1990). However, iceberg scouring is also a common phenomenon in the

Antarctic and even if it negatively impacts the benthic biota at the local scale, it may increase the regional diversity due to the increase in habitat heterogeneity and prevention of competitive exclusion (Gutt and Piepenburg 2003).

Another explanation for differences in benthic diversity between Arctic and Antarctic was related to differences in bottom heterogeneity (Jazdzewski et al. 1995). Knox and Lowry (1977) assumed that due to the lower sedimentation of terrestrial material the Antarctic bottom is supposed to be covered by larger number of stones and small boulders transported by icebergs. Additionally, numerous sponges, gorgonians, holothurians and other large sessile suspension feeders serve as biogenic substrata for other animals thereby creating the typical Antarctic “multi-storied assemblages” (Gutt and Schickan 1998). Starman and Gutt (2003) observed hot-spots in benthic diversity at sites with mass occurrences of sponges and much lower diversity in habitats lacking the three-dimensional structures. They mentioned that at predominantly soft-bottom Antarctic stations the numbers of taxa recorded fell within the range typical of Arctic sites.

We suppose that the widely accepted paradigm of higher Antarctic diversity first perceived and well documented for the epi-fauna is linked to the differences in three-dimensional heterogeneity of their habitat. The three-dimensional structures created by large drop stones and mass occurrences of large suspension feeders provide extra substrata and increase the structural complexity of the habitat that result in the huge species enrichment of epifauna. Within the sediment fabric there is little heterogeneity of the scale described for the epibenthos. The spatial heterogeneity created by biogenic structures, different sediment sorting, etc., are of a far lesser scale and are probably of the same magnitude in Arctic and Antarctic sedimentary habitats. All the other arguments such as differences in geological age or regional area apply equally to both epifauna and infauna. If such explanations operate they should also generate a difference in the diversity of the infauna of both regions. In the surveys reported above we were unable to document any difference in species richness either on sample or large area scale. We suggest that heterogeneity of habitat has an overwhelming effect on patterns of local diversities and masks the effects of differences in regional history. An interesting point was raised by Ragua-Gil et al. (2004), who studied mega-epibenthos in a few Antarctic localities and found high dissimilarities in faunal composition between them. They failed to find a direct relationship between the strength of faunistic dissimilarities and the distances between the localities, concluding that shallow-water Antarctic com-

munities are shaped by local conditions rather than large-scale processes, and that the circumpolar dispersion is limited by the fragmented distribution of shallow water areas (isolated by grounded or floating ice covering 95% of the coastline in the high Antarctic). The species pool around Antarctic may become compartmentalized by ice that would result, at least for inshore species, in reduced size species pools from which the colonisers of any particular site can be drawn.

Diversity at higher taxonomic levels might be a better indicator of the historical and regional processes that shape contemporary diversity patterns. Ricklefs (1987) noted that families have more ancient origins than genera and species, and patterns of familiar diversity undoubtedly record the evolutionary, historical, and biogeographical settings of local communities more faithfully than do patterns of generic and, especially, specific diversity. In the case of Arctic and Antarctic soft-bottom polychaetes, however, the diversity was similar in all studied sites at the level of species as well as at that of genera and families.

The HCD plots indicate the clades which are the most diverse, and thus probably experienced more rapid speciation and reduced extinction compared with their sister taxa (McHugh and Fong 2002). In our study there was little difference between the identity of the dominant families in the Arctic and those in the Antarctic. The same set of families was reported to be the most diverse by the other polar benthic studies (Table 2) as well as by the all taxa inventories compiled by Sirenko (2001) for the Arctic and by Clarke and Johnston (2003) for the Antarctic. The most speciose families described in polar polychaete studies are among the most diverse families worldwide indicated by the HCD plotted from the complete world polychaete species list by McHugh and Fong (2002). In search for the biological explanation of the similar HCDs across different taxa, several life history traits were proposed as stimulating intensive speciation. Short generation time (early age of first reproduction, short life-spans) and high resource availability (high mobility, trophic status) were found to correlate with high diversity in mammalian and bird assemblages (Marzluff and Dial 1991). Nevertheless, it is difficult to find an association between life history traits and diversity within polychaete families. The most diverse polychaete families (such as Terebellidae, Ampharetidae, Maldanidae, Spionidae or Polynoidae) differ in the age of the first reproduction, life span, body size, fecundity, dispersal, mobility and feeding types (McHugh and Fong 2002).

Our simple comparison of just a few data sets from polar regions give a surprising results of similar local diversity measured at the scale of samples and at the scale of the whole marine inlets. These findings corrob-

Table 2 Most speciose polychaete families in polar benthic studies

| | Arctic | | | | | Antarctic | | | | |
|-----------------|--------|---|---|---|---|-----------|---|---|---|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| Terebellidae | + | + | + | + | + | + | + | + | + | + |
| Ampharetidae | + | + | + | + | + | + | + | + | | |
| Sabellidae | + | | + | + | + | | | + | + | |
| Polynoidae | | + | + | | + | + | | | | + |
| Spionidae | + | + | + | + | + | | | + | + | |
| Maldanidae | + | + | | + | + | + | + | + | + | |
| Phyllodocidae | | | | | + | + | + | + | | + |
| Syllidae | | | | | + | + | + | + | + | + |
| Lumbrineridae | | | | | | | | | | + |
| Dorvilleidae | | | | | | | | | | + |
| Flabelligeridae | | | | | | | | | | + |

+ Indicates family represented by a number of species higher than 5% of all polychaete species recorded in a given study; 1 Kongsfjord (present study); 2 van Mijenfjord (present study); 3 Hare and Tanquary fiords, Ellesmere Island (Curtis 1972); 4 coastal waters of Kara Sea (Jorgensen et al. 1999); 5 all Arctic species inventory (Sirenko 2001); 6 Admiralty Bay (present study); 7 South Shetland Islands (San Martin et al. 2000); 8 Arthur Harbor, Anvers Island (Richardson and Hedgepeth 1977); 9 Terra Nova Bay, Ross Sea (Gambi et al. 1997); 10 all Antarctic species inventory (Clarke and Johnston 2003)

orate Piepenburg's (2005) recent argument that common notion of the generally higher Antarctic diversity should be revisited. How general is the pattern of Antarctic being more diverse than the Arctic? How does this pattern vary across different ecological groups (as infauna/epifauna) or across different taxa? Is it uniform over the range of spatial scales? These questions remain unresolved until the new extensive comparative data on polar biota are available.

Acknowledgments We wish to thank the participants of the R.V *Oceania* cruises who took part in sampling in Kongsfjord and van Mijenfjord. The sampling and analyses of samples from van Mijenfjord were conducted thanks to economical support of coal company Store Norske which is gratefully acknowledged. We would like to thank Dr. P. E. Renaud and Prof. J. M. Weslawski for valuable discussions and comments on the paper. The study has been completed thanks to funds provided by a grant from the Committee of Scientific Research, Poland, no. PBZ-KBN-108/P04/2004. We acknowledge also the support by the MarBEF Network of Excellence "Marine Biodiversity and Ecosystem Functioning" which is funded by the Sustainable Development, Global Change and Ecosystems Programme of the European Community's Sixth Framework Programme (contract no. GOCE-CT-2003-505446). This publication is contribution number MPS-06041 of MarBEF and a contribution to the MarBEF responsive mode program ArctEco.

References

Chao A (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43:783–791

- Chao A (2004) Species richness estimation. In: Balakrishnan N, Read CB, Vidakovic B (eds) Encyclopedia of statistical sciences. Wiley, New York, pp 1–23
- Clarke A (1992) Is there a latitudinal diversity cline in the sea? *Trends Ecol Evol* 7:286–287
- Clarke A, Crame JA (1997) Diversity, latitude and time: patterns in the shallow sea. In: Ormong RFG, Gage JD, Angel MV (eds) Marine biodiversity. patterns and processes. Cambridge University Press, Cambridge, pp 122–147
- Clarke A, Johnston NM (2003) Antarctic marine benthic diversity. *Oceanogr Mar Biol Ann Rev* 41:47–114
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philos Trans R Soc Lond* 345:101–118
- Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85:2717–2727
- Cornell HV, Lawton JH (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J Anim Ecol* 61:1–12
- Curtis MA (1972) Depth distribution of benthic polychaetes in two fiords on Ellesmere Island, N.W.T. *J Fish Res Bd Canada* 29:1319–1327
- Dahle S, Cochrane S, Gulliksen B, Larsen LH, Oug E, Palerud R (1997) The northern Barents Sea: geographical distribution of benthic fauna. Akvaplan-niva report no 421.93.301, Akvaplan-niva, Tromsø
- Dahle S, Denisenko SG, Denisenko NV, Cochrane S (1998) Benthic fauna in the Pechora Sea. *Sarsia* 83:183–210
- Dahle S, Anisimova NA, Pärerud R, Pearson TH, Matishov GG (2006) Macrobenthic fauna of the Frantz Josef land archipelago (in press)
- Dayton PK (1990) Polar Benthos. In: Smith WO (ed) Polar oceanography. Part B: Chemistry, biology and geology. Academic Press, San Diego, pp 631–685
- Dayton PK, Mordida BJ, Bacon F (1994) Polar marine communities. *Am Zool* 34:90–99
- Dunton K (1992) Arctic biogeography: the paradox of the marine benthic fauna and flora. *Trends Ecol Evol* 7:183–189
- Foggo A, Attrill M, Frost MT, Rowden AA (2003) Estimating marine species richness: an evaluation of six extrapolative techniques. *Mar Ecol Prog Ser* 248:15–26
- Gage JD, Lambshhead PJD, Bishop JDD, Stuart CT, Jones NS (2004) Large-scale biodiversity pattern of Cumacea (Peracarida: Crustacea) in the deep Atlantic. *Mar Ecol Prog Ser* 277:181–196
- Gambi MC, Castelli A, Guizzardi M (1997) Polychaete populations of the shallow soft bottoms off Terra Nova Bay (Ross Sea, Antarctica): distribution, diversity and biomass. *Polar Biol* 17:199–210
- Gray JS (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *J Exp Mar Biol Ecol* 250:23–49
- Gray JS (2001) Antarctic marine benthic biodiversity in a world-wide latitudinal context. *Polar Biol* 24:633–641
- Gulliksen B, Holte B, Jakola KJ (1985) The soft-bottom fauna in vanMijenfjord and Raudfjord, Svalbard. In: Gray J, Christiansen ME (eds) Marine biology of polar regions and effects of stress on marine organisms. Wiley, Oslo, pp 199–215
- Gutt J, Piepenburg D (2003) Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Mar Ecol Prog Ser* 253:77–83
- Gutt J, Schickan T (1998) Epibiotic relationships in the Antarctic benthos. *Antarctic Sci* 10:398–405
- Gutt J, Sirenko BI, Smirnov IS, Arntz WE (2004) How many macrozoobenthic species might inhabit the Antarctic shelf? *Antarct Sci* 16:11–16
- Hop H, Pearson TH, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczyk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey R, Lonne OJ, Zajaczkowski M, Falk-Petersen S, Kendall MA, Wängberg S-Å, Bischof K, Voronkov A, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res* 21:167–208
- Hurlbert SH (1971) The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52:577–586
- Jazdzewski K, Jurasz W, Kittel W, Presler E, Presler P, Sicinski J (1986) Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands. *Polar Biol* 6:5–16
- Jazdzewski K, Weslawski JM, de Broyer C (1995) A comparison of the amphipod faunal diversity in two polar fjords: Admiralty Bay, King George Island (Antarctic) and Hornsund, Spitsbergen (Arctic). *Pol Arch Hydrobiol* 42:367–384
- Jorgensen LL, Pearson TH, Anisimova NA, Gulliksen B, Dahle S, Denisenko SG, Matishov GG (1999) Environmental influences on benthic fauna associations of the Kara Sea (Arctic Russia). *Polar Biol* 22:395–416
- Kendall MA (1994) Polychaete assemblages along a depth gradient in a Spitsbergen fjord. *Mem Mus Nat Hist* 162:463–470
- Kendall MA, 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
- Knox GA, Lowry JK (1977) A comparison between the benthos of the southern ocean and the north polar ocean with special reference to the Amphipoda and the Polychaeta. In: Dunbar MJ (ed) Polar ocean conference. McGill University, Montreal, pp 423–461
- Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Malden
- Marzluff JM, Dial KP (1991) Life history correlates of taxonomic diversity. *Ecology* 72:428–439
- McHugh D, Fong PP (2002) Do life history traits account for diversity of polychaete annelids? *Invertebr Biol* 121:325–338
- Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revisited. *Polar Biol* 28:733–755
- Piepenburg D, Voß J, Gutt J (1997) Assemblages of sea stars (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea) in the Weddell Sea (antarctica) and off Northeast Greenland (Arctic): a comparison of diversity and abundance. *Polar Biol* 17:305–322
- Ragua-Gil J, Gutt J, Clarke A, Arntz WE (2004) Antarctic shallow-water mega-epibenthos: shaped by circumpolar dispersion or local conditions? *Mar Biol* 144:829–839
- Rakusa-Suszczewski S (1993) The maritime Antarctic coastal ecosystem of Admiralty Bay. Department of Antarctic Biology, Polish Academy of Sciences, Warsaw
- Renaud PE, Wlodarska-Kowalczyk M, Trannum H, Holte B, Weslawski JM, Cochrane S, Dahle S, Gulliksen B (2006) Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitsbergen). *Polar Biol*. DOI 10.1007/s00300-006-0183-9
- Rex MA, Stuart CT, Hessler RR, Allen JA, Sanders HL, Wilson GDF (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636–639
- Richardson MD, Hedgcock JW (1977) Antarctic soft-bottom, macrobenthic community adaptations to a cold, stable, highly productive glacially affected environment. In: Llano A (ed) Adaptations within Antarctic ecosystems. Proceedings of the third SCAR symposium on Antarctic biology. Smithsonian Institution, Washington DC, pp 181–196

- Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. *Science* 235:167–171
- Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge
- San Martin G, Parapar J, Garcia FJ, Redondo MS (2000) Quantitative analyses of soft bottom infaunal macrobenthic polychaetes from South Shetland Islands (Antarctica). *Bull Mar Sci* 67:83–102
- Schmid MK, Piepenburg D (1993) The benthos zonation of the Disko Fjord, West Greenland. *Meddr Grønland* 37:1–21
- Sicinski J (2000) Polychaeta (Annelida) of Admiralty Bay: species richness, diversity and abundance. *Pol Polar Res* 21:153–169
- Sicinski J, Janowska E (1993) Polychaetes of the shallow sublittoral of Admiralty Bay, King George Island, South Shetland Islands. *Antarctic Sci* 5:161–167
- Sirenko BI (2001) List of species of free-living invertebrates of Eurasian Arctic seas and adjacent waters. *Explor Fauna Seas* 51:1–131
- Starmans A, Gutt J (2003) Mega-epibenthic diversity: a polar comparison. *Mar Ecol Prog Ser* 225:45–52
- Svendsen H, Beszczynska-Moller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Orbaek JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther JG, Dallmann W (2002) The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res* 21:133–166
- Thorson G (1957) Bottom Communities (sublittoral or shallow shelf). In: Hedgpeth, JW (ed) *Treatise on marine ecology and paleoecology*. Mem Geol Soc Am 1:461–534
- Warwick RM, Dashfield SL, Somerfield PJ (2006) The integral structure of a benthic infaunal assemblage. *J Exp Mar Biol Ecol* 330:12–18
- Whittaker R (1972) Evolution and measurement of species diversity. *Taxon* 21:213–251
- Witman JD, Etter RJ, Smith F (2004) The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proc Natl Acad Sci USA* 101:15664–15669
- Wlodarska-Kowalczyk M, Pearson TH (2004) Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biol* 27:155–167