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Bathymetric distribution patterns of Southern Ocean macrofaunal taxa: Bivalvia, Gastropoda, Isopoda and Polychaeta

Angelika Brandt [a,*], Katrin Linse [b], Myriam Schüller [c]

[a] Zoological Institute and Zoological Museum, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany
[b] British Antarctic Survey, Natural Environmental Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK
[c] Lehrstuhl für Evolutionsökologie und Biodiversität der Tiere, Ruhr-Universität Bochum, Universitätsstr. 150, D44780 Bochum, Germany

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A B S T R A C T

The aim of this study is to compare the depth distributions of four major Southern Ocean macrobenthic epi- and infaunal taxa, the Bivalvia, Gastropoda, Isopoda, and Polychaeta, from subtidal to abyssal depth. All literature data up to summer 2008, as well as the unpublished data from the most recent ANDEEP I–III (Antarctic benthic deep-sea biodiversity: colonisation history and recent community patterns) expeditions to the Southern Ocean deep sea are included in the analysis. Benthic invertebrates in the Southern Ocean are known for their wide bathymetric ranges. We analysed the distributions of four of the most abundant and species-rich taxa from intertidal to abyssal (5200 m) depths in depth zones of 100 m. The depth distributions of three macrofaunal classes (Bivalvia, Gastropoda, Polychaeta) and one order (Isopoda) showed distinct differences. In the case of bivalves, gastropods and polychaetes, the number of species per depth zone decreased from the shelf to the slope at around 1000 m depth and then showed stable low numbers. The isopods showed the opposite trend; they were less species rich in the upper 1000 m but increased in species numbers from the slope to bathyal and abyssal depths. Depth ranges of families of the studied taxa (Bivalvia: 31 families, Gastropoda: 60, Isopoda: 32, and Polychaeta: 46 families) were compiled and illustrated. At present vast areas of the deep sea in the Southern Ocean remain unexplored and species accumulation curves showed that only a fraction of the species have been discovered to date. We anticipate that further investigations will greatly increase the number of species known in the Southern Ocean deep sea.

1. Introduction

The last expedition circumnavigating the World's oceans was the Galathea expedition in 1950–52 (Bruun, 1956). It was designed explicitly to sample "deep waters", which at that time were defined as starting at 400 m. The unexpected presence of life even in the deepest trenches was documented, but the methods used did not allow sampling all size classes of the benthic fauna. The common notion at that time was still that species richness declined drastically with depth, and abyssal plains were considered devoid of life or, at best, the realm of large echinoderms (Gage and Tyler, 1991). Later, improved sampling methods began to provide a more accurate picture of how animals were distributed in the oceans.

The history of benthic ecology in Antarctica, from the shelf to the deep sea, started in the nineteenth century (Headland, 1989; Fogg, 1992). The main products of the early scientific expeditions of the heroic era were systematic accounts of different animal groups. Inevitably, they were largely descriptive but served as the basis for

* Corresponding author.
E-mail addresses: abrandt@zoologie.uni-hamburg.de (A. Brandt), kl@bas.ac.uk (K. Linse), myriam.schueller@freenet.de (M. Schüller).

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subsequent ecological studies. In the last three decades international science programmes in Antarctica increased our knowledge of faunal distributions. These included European *Polarstern* Studies (EPOS), Ecology of the Antarctic Sea-Ice Zone (EASIZ) (e.g. Arntz and Clarke, 2002; Clarke et al., 2006), BENTART (San Vincente et al., 2006) as well as the Ross Sea Projects performed from the RV *Italica* (Cattaneo-Vietti et al., 2000; Schiaparelli et al., 2006) and RV *Tangaroa. T*he BIOROSS Programme at NIWA focussed on the communities and faunas of shelf and upper slope (http://www.biodiversity.govt.nz/seas/biodiversity/programmes/bioross.html). The expeditions of the RV *Eltanin* (Landrum, 1975, 1981) collected comprehensive samples from the continental shelves and deep-sea areas from 120°E to 30°W, but identification of the taxa is still ongoing and unpublished. The works of these programmes and many national projects have extended our knowledge of Antarctic marine benthic diversity significantly (e.g. Arntz et al., 1997; Gray, 2001; Clarke and Johnston, 2003). Most of the publications dealing with benthic ecology referred to the Antarctic continental shelf and only a few concerned the deep sea (Clarke and Johnston, 2003). However, it was apparent that benthic species occurred over wide depth ranges and that eurybathy was common (e.g. Brey et al., 1994, 1996), although the lower ends of the depth distributions were unknown. One of the most comprehensive programmes dedicated to the Antarctic deep sea, Antarctic Benthic Deep-Sea Biodiversity (ANDEEP), aimed to broaden our knowledge and understanding of benthic deep-sea ecology. The three expeditions (two in 2002 and one in 2005) sampled large number of new species and extended the depth ranges of known species (Brandt, 2000; Brandt et al., 2007a–c). With more than 90% of the material in most taxa belonging to undescribed species, ANDEEP gave explicit recognition to systematic research, the fundamental documentation of biological diversity through basic descriptive taxonomy followed by the phylogenetic analyses of selected taxa.

The ANDEEP project has increased greatly our knowledge in the Southern Ocean deep sea and yielded first insights into the biodiversity and biogeography of this remote environment from meio- to megafauna (Brandt et al., 2007a–c). Based on comprehensive data collated by taxonomists and ecologists over decades, the present paper describes the general bathymetric distribution patterns of the macrobenthic taxa bivalves, gastropods, isopods, and polychaetes. The main question addressed is whether the contrasting reproduction modes and dispersal abilities of the different taxa are reflected in the distribution with depth of species richness.

2. Material and methods

Data on bathymetric distributions of the macrofaunal taxa were obtained from original literature, the authors' unpublished expedition material and web-based databases.

Because data are pooled from a variety of sources, not all taxa will necessarily occur together within one depth zone. However, they have at least been reported at a single location within a particular depth interval. For the Isopoda, in addition to original literature, the isopod world list (Schotte et al., 1995) http://www.nmnh.si.edu/iz/isopod/) was used. Distributional data on bivalves and gastropods were based on SOMBASE (e.g. Griffiths et al., 2003, 2009; Linse et al., 2006, Clarke et al., 2007). Data for the polychaetes were acquired from the literature (Blake, 1981; Hartman, 1964, 1966, 1978; Hartmann-Schröder and Rosenfeldt, 1988, 1989, 1990, 1991, 1992; Hilbig, 2004; Knox and Cameron, 1998; Maciolek and Blake, 2006; Schüller and Hilbig, 2007; Schüller, 2008), and the ANDEEP I-III expeditions (www.cedamar.org).

For all taxa the majority of bathyal and abyssal data points are based on collections from the ANDEEP I-III expeditions (Brandt and Hilbig, 2004; Brandt et al., 2004; Brandt and Ebbe, 2007; Brandt et al., 2007a–c). Macrofaunal species were sorted and identified partly on board or later in the laboratories in Hamburg, Bochum and Cambridge. Species names are only known for a small fraction of the material. Therefore, morphospecies were provisionally numbered and characterised until taxonomic descriptions can be completed. However, these species are included in the analysis of bathymetric distribution.

Most of the Southern Ocean is deep sea (Fig. 1). For the analysis of bathymetric distribution patterns, water depth was divided into 100-m-wide depth intervals. The descriptions of the distribution of species numbers with depth was based on the number of species found in each depth interval. For comparisons between the four taxa the analysed depth range is 0–5000 m. For the assessment of the depth range at family level, the presence at each depth interval of species of the selected family was taken. When breaks occurred in the depth distributions of two or more

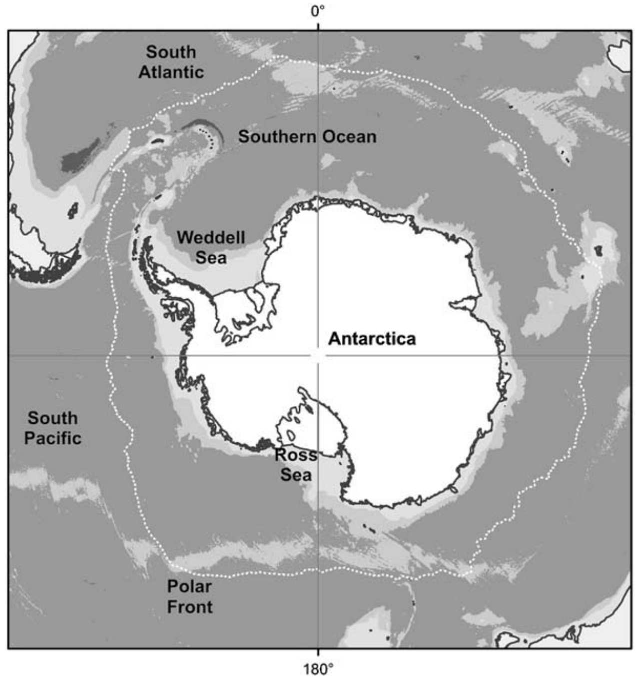

Fig. 1. The bathymetric zones of the Southern Ocean and adjacent seas. Bathymetric ranges: 0–1000 m, 1000–3000 m, 3000–6000 m, >6000 m.

species within a family, they were recorded in the results. The term bathyal was used for stations ranging from ~1000 m down to 3000 m, abyssal from ~3000 to 6000 m where the hadal region starts (Brandt et al., 2007c).

Assessment of the number of samples taken at different depths in the Southern Ocean was based on SOMBASE records of the number of stations with gastropods present per depth interval.

3. Results

In this study depth ranges of 160 species of bivalves, 566 species of gastropods, 903 species of isopods and 657 species of polychaetes were analysed.

The bathymetric distribution patterns from 0 to 5000 m for the four studied taxa are shown in Fig. 2(a–d). The general patterns are similar for bivalves, gastropods and polychaetes, with the highest species numbers per depth interval on the shelf, constantly dropping species numbers on the upper slope (roughly around 1000 m) and then more or less constant species numbers at bathyal and abyssal depths. The pattern in the isopods showed an opposite trend; species numbers are lower on the shelf and upper slope and then increase at bathyal and abyssal depths.

The bivalves have the lowest species richness of the taxa considered in this study (Fig. 2a). In shallow, near-shore waters (0–100 m), bivalve richness is lower (~60 species) than on the shelf (~80 species). Almost 50% of the Antarctic bivalve species occurred on the shelf and upper slope. At depths below 1200 m, the species richness dropped to around 20 species per depth interval and continued at this level down to 5000 m.

The gastropods, a speciose taxon, with almost 600 analysed species, showed a steep decrease in species numbers from the shelf to bathyal depth (Fig. 2b). The 200–300 m depth interval yielded more than 260 gastropod species while at 900–1000 m depth only 80 species were found. Below 1000 m the species numbers were no higher than 40 and below 4000 m no more than 20 species were collected. The numbers of samples obtained within the analysed depth intervals in are shown in Fig. 3. More samples were taken in near-shore waters and on the shelf than on the slope and in the deep basins and trenches.

There are not more than 95 isopod species in any 100 m depth interval between 1 and 1000 m. Isopod species richness per 100-m layer is highest around 3000 m with 241 species and generally high between 3000 and 4000 m (146–241 species). The numbers of species are still fairly high (133–154) between 4500 and 4700 m, but then decrease to 99, and 76 in the following two 100 m intervals. At 5000 m depth, only 14 species were recorded so far (Fig. 2c).

Polychaete (Fig. 2d) species richness is highest on the Antarctic shelf, especially at the shallowest stations

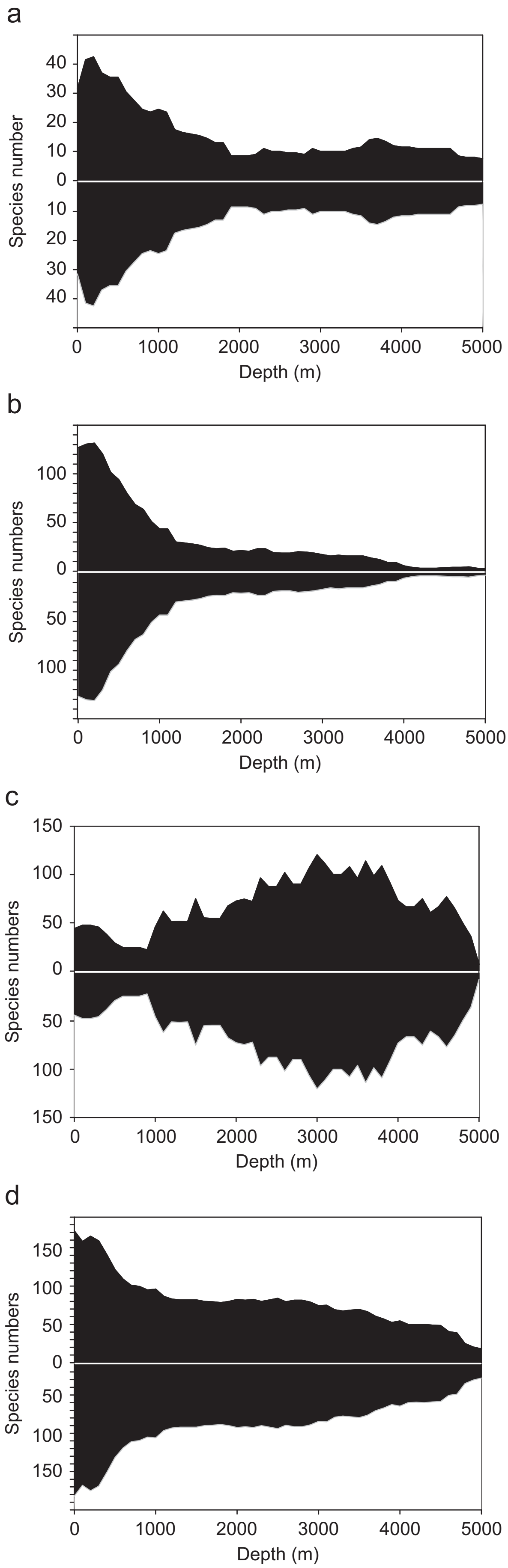

Fig. 2. Species numbers per depth. The abscissa divides the total number of species in half, thus the maximum richness of bivalves in the top panel is just over 80 species in Fig. 2a. (a) Bivalvia, (b) Gastropoda, (c) Isopoda, (d) Polychaeta.

between 0 and 100 m (344 species), and rapidly decreases to about 190 species at 1000 m depth. Species richness appears more stable between 1000 and 2000 m with 160 species at 2000 m depth. At bathyal depths between 3000 m (149 species) and 4000 m (109 species), species numbers per depth interval only slightly decrease, with a more rapid decrease to 36 species at 5000 m.

At the family level, four depth range patterns can be found among the studied taxa: (1) on the shelf only, (2) on the shelf and upper slope, (3) from the shallow-water to abyssal depths, (4) at bathyal and abyssal depth only (Figs. 4–7). Some families showed wide distribution ranges (>1000 m) while others were restricted to narrow ranges (100–300 m).

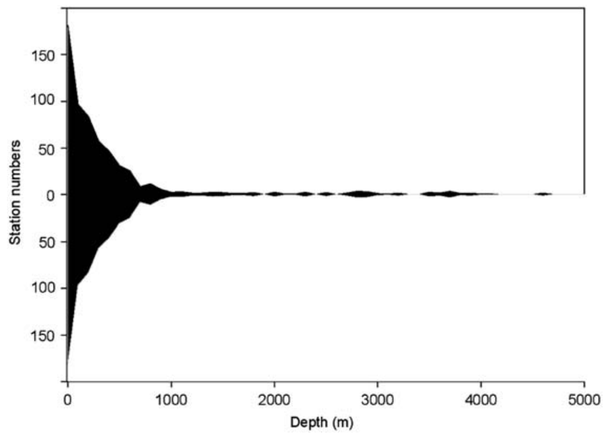

Fig. 3. Sampling efforts per depth. The data show the numbers of samples taken in the Southern Ocean that contained Gastropoda.

A total of 31 bivalve families was analysed (Fig. 4). The Condylocardiidae, Erycinidae, Gaimardiidae, Hiatellidae and Nuculidae are examples of families with a narrow, shelf-bound depth range. Most analysed families occur from the shelf to the upper slope, e.g. Astartidae, Kelliidae and Philobryidae. The Arcidae, Cuspidariidae, Limidae, Limopsidae, Mytilidae, Propeamussiidae, Sareptiidae and Thyasiridae occur from the shelf to abyssal depth.

Of the studied 60 gastropod families the majority were representatives of the first pattern, i.e., they occurred only on the shelf (Fig. 5). The Buccinidae, Cyclostrematidae, Diaphanidae, Eulimidae, Naticidae, Omalogyridae, Philinidae, Scissurellidae, Trochidae, Volutidae, and Zerotulidae are examples of wide-ranging families occurring from near-shore waters to abyssal depth. Members of the families Choristellidae, Conidae, Propolidiidae have only been found at bathyal or abyssal depths in Antarctic waters.

Of the 32 isopod taxa studied, most members of the Scutocoxifera occur on the shelf and the upper slope as well as at depths >3000 m (Fig. 6). The families Anuropidae, Holognathidae, Protognathiidae, Sphaeromatidae and some Asellota (e.g. Vermectiadidae, Santiidae) are restricted to the shelf. The asellote families Janiridae, and Joeropsidae occur on the shelf and upper slope. Species of the Acanthaspidiidae, Antarcturidae, Australarcturellidae, Cirolanidae, Dendrotionidae, Desmosomatidae, Gnathiidae, Haploniscidae, Ischnomesidae, Munnidae, Munnopsidae, Paramunnidae, Pseudidotheidae, Serolidae and Strenetriidae, and those belonging to the suborder Anthuroidea, occur from shallow to abyssal depths. Members of the families Acanthomunnopsidae,

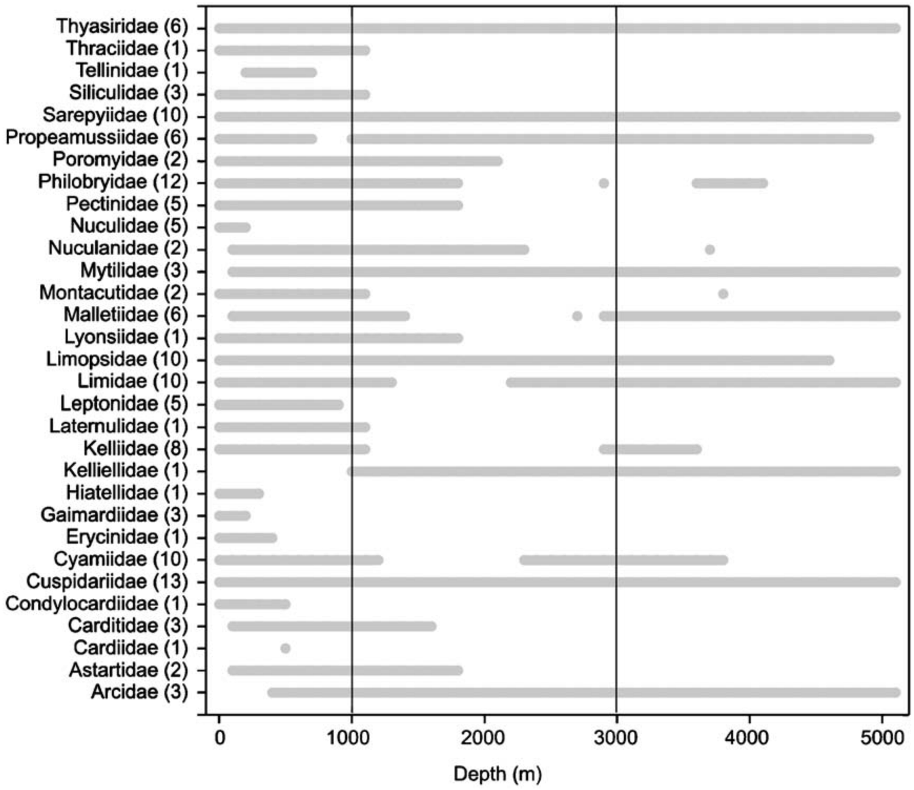

Fig. 4. Bathymetric ranges of bivalve families. In brackets are the numbers of species per family.

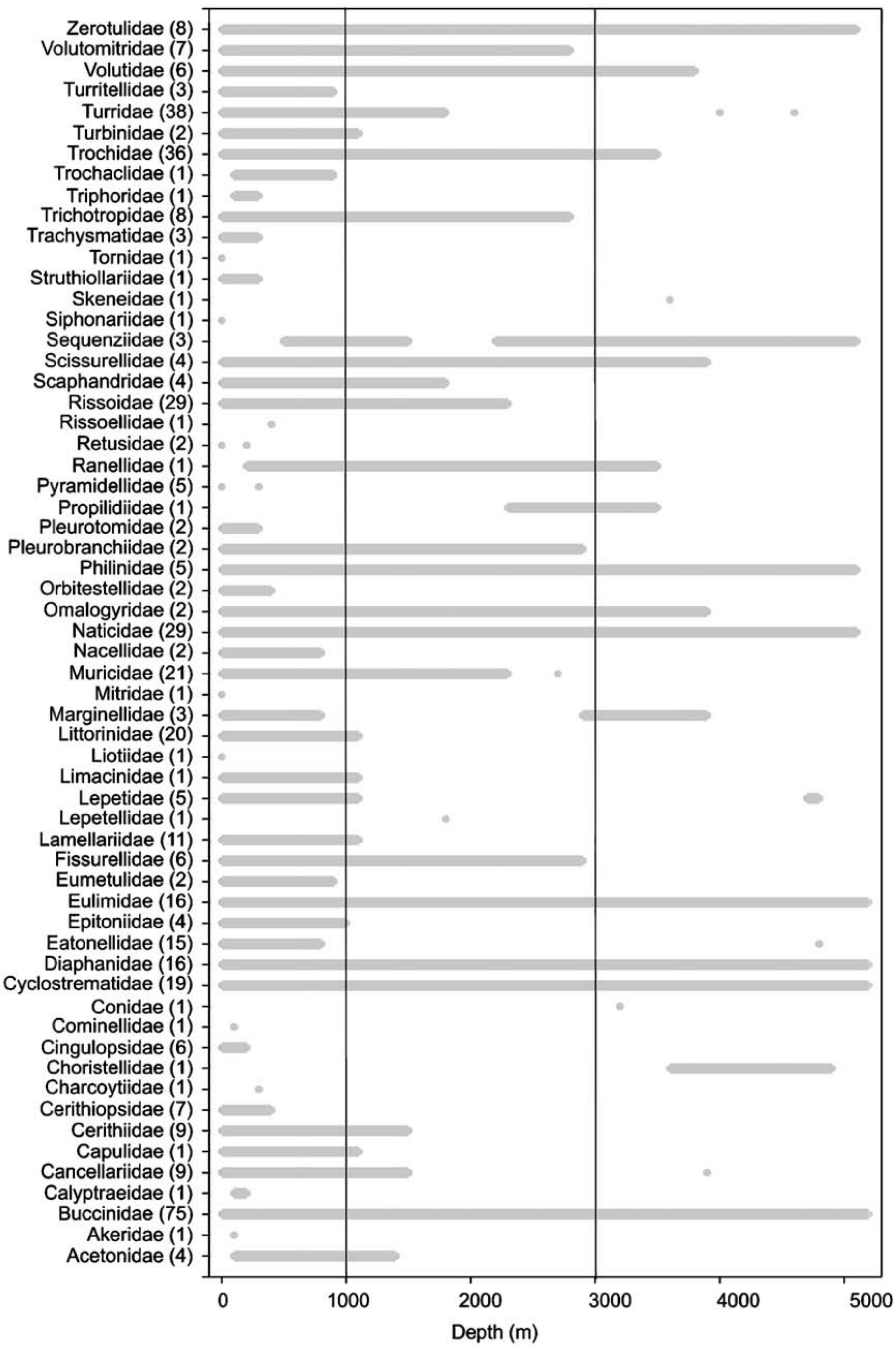

Fig. 5. Bathymetric ranges of gastropod families. In brackets are the numbers of species per family.

Haplomunnidae, Macrostylidae, and Thambematidae have been sampled at bathyal and abyssal depths only.

With rather few exceptions, most of the 46 polychaete families found in the SO occur at depths from the shelf to the abyss regardless of their ecology and lifestyle (Fig. 7). Scaleworms (e.g., Polyonidae and Sigalioidae) are recorded from wide depth ranges that are similar to those of other vagile forms (e.g., Nereididae and Phyllodocidae), sessile forms (e.g., Sabellidae and Serpulidae), and burrowers (e.g., Maldanidae and Opheliidae). Families limited to the shelf are the Arenicolidae, Lacydoniidae, and Spintheridae. To date, no named species of the Arabellidae, Apistobranchidae, Chaetopteridae, Dorvilleidae, Pholoididae, and Sternaspididae have been recorded below the upper shelf, although members of these families have but been observed in unsorted deep-sea samples. Members of the families Cossuridae and Pilargiidae have been reported for bathyal and abyssal depths.

4. Discussion

4.1. Bathymetric patterns of species richness in the Southern Ocean

In recent years the distribution and bathymetric zonation of Antarctic bivalves and gastropods has been

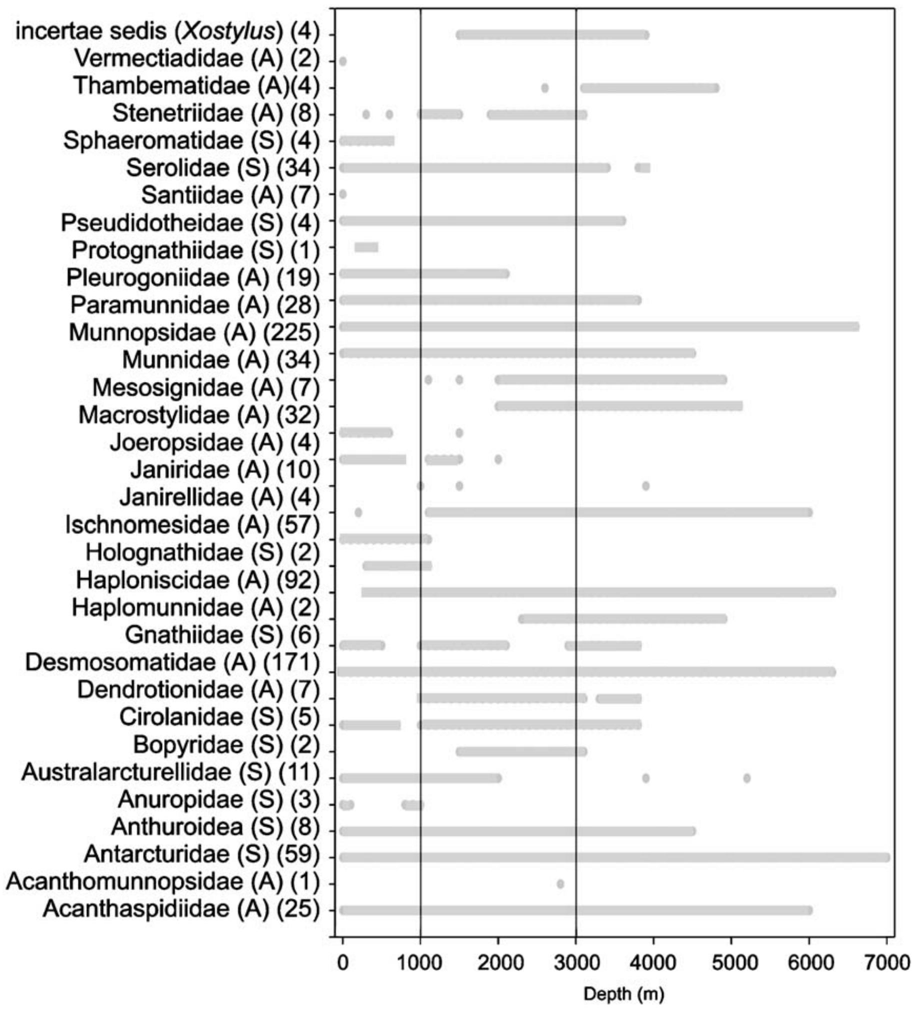

Fig. 6. Bathymetric ranges of isopod families. In brackets are the numbers of species per family, and the suborder: Asellota (A) and Scutocoxifera (S).

the subject of several studies following expeditions to formerly unexplored areas (e.g. Linse, 2004, 2006; Linse et al., 2006; Schwabe et al., 2007; Aldea et al., 2008). These studies focussed on the results from a specific area, but they also gave new insights into the general depth distributions of species and their data therefore are included in our data set.

4.1.1. *Bivalves and gastropods*

In the Southern Ocean the numbers of bivalve species decreases with increasing depth and below 1200 m only about half the number of species are present compared with the number on the shelf. This pattern is the opposite of those found in North Atlantic studies. The bathymetric zonation of bivalves in the Porcupine Seabight and Porcupine Abyssal Plain (NW Atlantic) showed an increase of species numbers from 500 to 1800 m and a slight decrease down to about 5000 m depth (Allen, 2008; Olabarria, 2005). It should be noted that Olabarria (2005) analysed 76 bivalve species collected in 126 trawl samples from 500 to 4866 m depth and not the entire species' depth distribution ranges, potentially biassing the results. Rex et al. (2005) found similar patterns, with the species richness maximum around 2000 m depth, in their analysis of protobranch bivalves in the NW (37 species) and NE (45 species) Atlantic based on the data of Allen and Sanders (1996). The depth of the shelf break in the North Atlantic lies at around ~200 m (Rex et al., 2005). In the Antarctic, the shelf-slope break is much deeper at around ~1000 m as a result of large mass of the ice-sheet depressing the Antarctic continent and the scouring action of previous extensions of the ice-sheet (Clarke and Johnston, 2003).

The number of Antarctic gastropod species per depth zone shows a steep decrease with increasing depth after the shelf-slope break is reached, from ~260 species to ~50 species. The study by Rex et al. (2005) of gastropods in the NW Atlantic (82 prosobranch species) and NE Atlantic (191 neogastropod species) showed that species numbers were highest in the 1000–2000 m zone and decreased towards greater depths. In both areas the depth zone between 4000 and 5000 m still had 22/32 species while in the same depth zone ~40 species were found in the Southern Ocean. Rex et al. (2005) focussed on deep-sea gastropods and excluded the numerous shallow-water and shelf species that do not extend into the deep sea. Therefore, it can be expected that the general pattern for the entire gastropod fauna in the North Atlantic is similar to that in the Southern Ocean. Moreover, we have to consider that the various studies of deep-sea marine

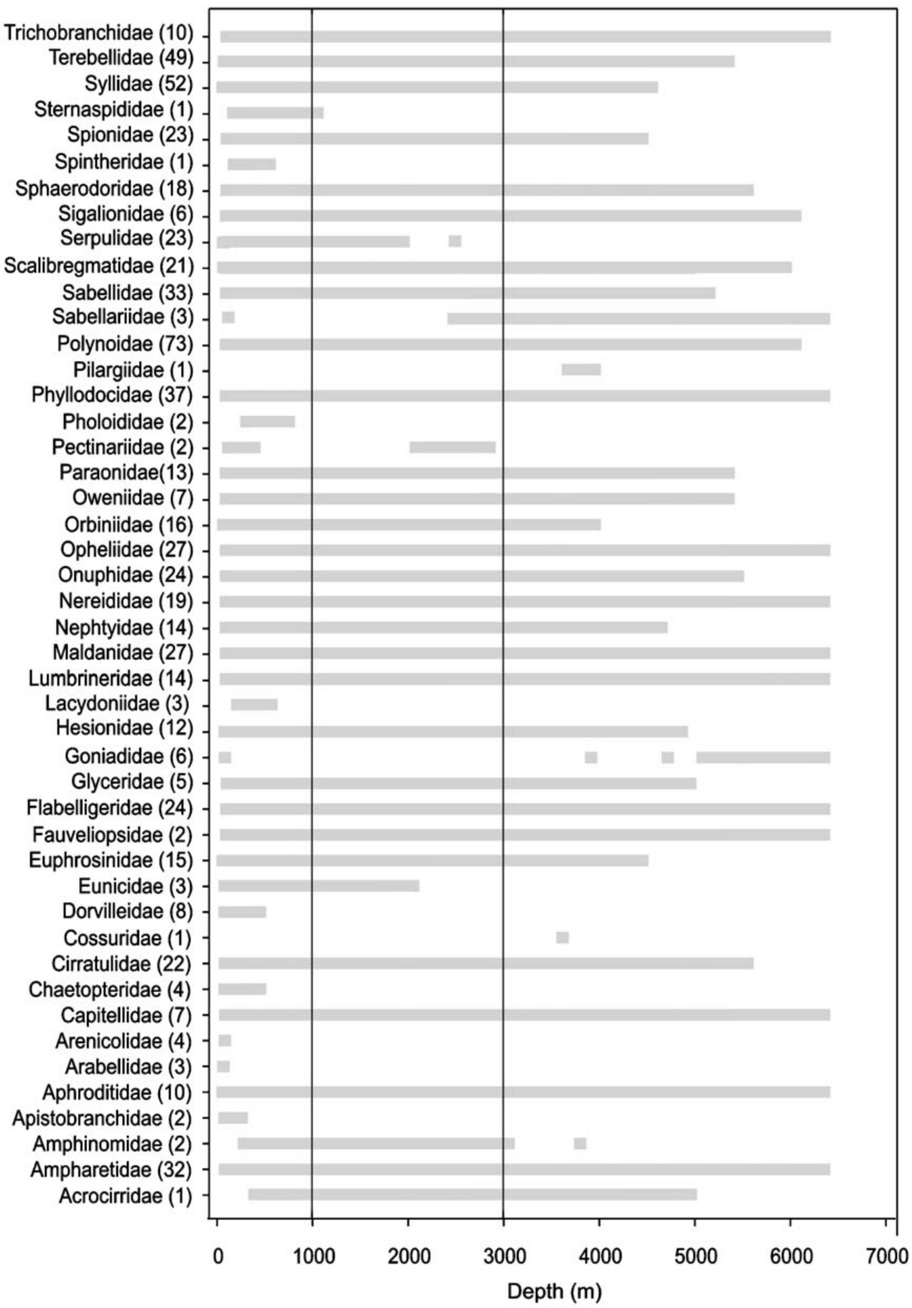

Fig. 7. Bathymetric ranges of polychaete families. In brackets are the numbers of species per family.

diversity did not always utilise comparable data. Here a truly comparable analysis was undertaken, looking at the Southern Ocean data in the same way as Rex et al. (2005) had looked at the North Atlantic data. However, these authors excluded the shelf taxa. Olabarria (2006) studied the depth distributions of 88 gastropod species in the Porcupine Seabight and Porcupine Abyssal Plain (NW Atlantic). The analysed depth range (100–5000 m) is comparable to the data presented here for the Southern Ocean. The results showed first a decrease in species richness from 250 to 1600 m, then an increase towards 4000 m followed by another decrease towards 5000 m (Olabarria, 2006). At a local scale, the species richness can reach a maximum value at varying depths, even in the deep sea, but when global or larger regional scales are analysed, the species numbers drop from shallow to deep water.

4.1.2. Isopods

The Isopoda have either colonised lower bathyal and abyssal depths in the Southern Ocean from shallow water or radiated in situ. The present data support hypotheses that marine biodiversity may be higher in the deep sea than on the shelf or on the continental slope (e.g. Sanders and Hessler, 1969). The depth distribution pattern for the isopods might be related to the fact that, unlike communities on the Antarctic shelf, the Southern Ocean deep-sea fauna is not isolated. The long isolation of the Antarctic shelf faunas caused a high degree of endemism (*in situ* evolved species) due to adaptive radiations of some faunal groups, such as the Antarcturidae and the Serolidae (Isopoda) on the Antarctic shelf (Brandt, 1991, 1999), or the Munnopsidae in the Southern Ocean deep sea (Malyutina and Brandt, 2007). High biodiversity was reported for both macrofaunal and megafaunal taxa in the Southern Ocean deep sea, including isopods (e.g. Brandt et al., 2007b). This is the most eurybathic macrofaunal taxon in the Southern Ocean (Kaiser et al., in prep.), supporting the theory of enhanced SO eurybathy (Brey et al., 1996). Studies based on molecular mitochondrial and nuclear gene sequences show that some of the circumantarctic isopod "species" are in fact cryptic species, presently undergoing speciation, e.g. *Ceratoserolis trilobitoides* and *Glyptonotus antarcticus* (Held, 2003). Further highly diverse species flocks in the Southern Ocean were discovered within the munnopsoid deep-sea isopod *Betamorpha fusiformis* (Raupach et al., 2007) and the acanthaspidid *Acanthaspidia drygalskii* (Raupach and Wägele, 2006). These data imply that our present knowledge of the biodiversity of the Southern Ocean deep-sea Isopoda will increase in future.

The higher species richness of isopods at greater depths compared to the shelf might be related to glacial periods and to the fact that isopods are brooders. Isopods have a reduced gene flow due to brooding. They would have been eradicated under the ice shelf in glacial periods unless they were able to migrate to deeper environments. While the species on the shelf were forced to migrate to deeper water, the species from the deep sea might have successively reached shallower depths due to greater food availability. Migrations like these might be a reason why the bathyal zone is so rich in species today and eurybathy is typical for many species. After the glacial retreat, some isopod species possibly recolonised the shelf from the slope. However, due to the isolation of the Antarctic continental shelf, few species had the chance to reach the shelf in the recent past unlike the Southern Ocean deep sea, which is not isolated to the north and could have been colonised throughout the Neogene. Nevertheless, for this taxon we cannot claim a direct correlation between glacial history and brooding because all Peracarida develop a brood pouch. Certainly, the Southern Ocean generally contains many brooding groups, but there is also the observation that the common taxa in shallow water are typically broadcasters (Pearse et al., 2009 and references therein).

Kussakin (1973) studied the depth distribution of the isopod fauna in all world oceans. He showed that Haploniscidae, Ischnomesidae, Macrostylidae and Desmosomatidae, as well as Munnopsidae, occur at the greatest depths. According to Svavarsson et al. (1990) species richness is highest on the upper continental slope (800–1000 m) in the deep Norwegian and Greenland Seas. In a later study, Svavarsson et al. (1993) analysed the distribution of 106 deep-sea asellote isopod species from the Northern Seas. They found that the Munnopsidae (32 species) and Desmosomatidae (33 species) were the most speciose and occur down to bathyal depth. Unlike depth distributions in the Southern Ocean, only 15 of the 106 species occurred deeper than 1000 m and more than half (70 species) occurred in the upper 500 m. Brandt (1997) reported 67 isopod species from three expeditions to the Arctic Ocean. Their and the depth distributions support the findings of Svavarsson et al. (1993). Later, Svavarsson (1997) reported that in the Arctic the diversity of isopods increased with increased depth to a maximum at about 320–1100 m, but then declined towards deeper waters.

4.1.3. *Polychaetes*

Polychaetes are often among the most abundant and speciose invertebrates in benthic samples from of all depths and different parts of the world (Alongi, 1992; Brandt and Schnack, 1999; Hessler and Jumars, 1974; Hessler and Sanders, 1967). On the Atlantic slope off North Carolina polychaetes contributed 45% of all benthic species collected in 16 box-corer samples at depths between 600 and 3500 m (Blake and Grassle, 1994). Species diversity and the total number of benthic species were highest at depths between 800 and 1500 m with a second peak around 2000 m depth, below which species numbers decreased with increasing depth. Estimates from abyssal sites were not presented by Blake and Grassle (1994), making a comparison of their results with ours difficult. In Clarke and Johnston's (2003) review of Antarctic marine biodiversity, polychaetes were also among the top three most species-rich taxa in the benthos. They stated that their results were mainly based on shelf and upper slope samples and commented on the poverty of deep-sea samples. Within the Polychaeta many of the species found at bathyal and abyssal depth during the ANDEEP expeditions had been reported from the Southern Ocean before, but were thought to be limited to the shelf and upper slope. This indicates that the Southern Ocean deep-sea benthos in general, and especially the infauna (including polychaetes), is still greatly undersampled. A continuation of the identification of ANDEEP polychaetes will therefore further increase the amount of new information at bathyal and abyssal depths.

Compared to the Isopoda, the Southern Ocean polychaetes are characterised by a lower proportion of endemic species in the deep sea. While about 50% of species recorded from depths below 2000 m in the Southern Ocean are only known for Antarctic waters, many species show wide ranges that approach cosmopolitan distributions (www.cedamar.org). However, there are apparent differences between families and a general conclusion is hardly possible. Endemism seems to be common in some speciose families, such as the Nephtyidae, Nereididae, Phyllodocidae, and the Polynoidae. Others, such as the Ampharetidae, Maldanidae, and Onuphidae, include species with very wide global distribution ranges. The latter support the idea that the Southern Ocean deep sea might not be as isolated as the shelf. Moreover, a high degree of eurybathy is reported (Brandt et al., 2007a–c; Hilbig, 2004). Rapid speciation and radiation events due to the Southern Ocean's history and isolation might explain the enhanced species richness of the shelf fauna, but possibly not of the deep-sea fauna.

A decrease in species richness with increasing depth might not be explained simply by visible geographical barriers. Ecological and physiological changes might also be involved. An increase in pressure and a decrease in the heterogeneity of the environment with depth, the dominance of soft bottoms in bathyal waters together with a decrease in food availability, lower densities of macrofaunal elements and thus potential prey are all likely explanations for the lower species number at bathyal and abyssal depths.

4.1.4. Comparison of patterns between taxa

A comparison of the depth distribution patterns between the four studied taxa showed that the patterns for bivalves, gastropods and polychaetes are similar to each other while the isopods show a different overall distribution. The biggest contrast concerns the number of species on the Antarctic continental shelf. While the first three taxa are most speciose on the shelf, the Isopoda are most speciose at bathyal depths (241 species at 3000 m). As species in all four taxa are known to have extreme eurybathic depth ranges in the Southern Ocean, different species depth ranges cannot explain the contrasting trends in species numbers with increasing depth. A potential explanation can be found in the combination of glaciation events and reproduction or species mobility. After the glacial maxima, taxa with free-spawning larvae, including many species of bivalves and some polychaetes, may have recolonised the Antarctic continental shelf from slope or deep-sea sites more easily than isopods. Polychaetes are also obviously able to cross the barrier between the Southern Ocean and adjacent oceans more easily, as many of them have a wider zoogeographical and bathymetrical distribution than isopods (Hilbig, 2004; Brandt et al., 2007b; Schüller and Ebbe, 2007).

4.2. Depth ranges of families in the Southern Ocean

4.2.1. Bivalves and gastropods

The 160 species of bivalves recognised in this study belong to 31 families. The most speciose families were the Philobryidae with 17 species and the Cuspidariidae with 10 species. It was expected that the more species-rich families would have a wide bathymetric range and indeed this pattern was observed. On the other hand families like the Kelliellidae, Mytilidae and Arcidae, which were only represented by a single or a few species, also occurred over a wide bathymetric range. Members of these families occur worldwide in the deep sea (e.g. Allen and Sanders, 1996; Allen, 1998, 2001) and in the Southern Ocean (Linse, 2004; Aldea et al., 2008). Olabarria's study (2005) of 76 bivalve species belonging to 24 families from the NE Atlantic showed a similar suite of deep-water bivalve families as in our study but different families were species rich. In non-Antarctic waters the Philobryidae occur on the shelf, especially at shallow depths, and on the uppermost slope (Powell, 1979), but in the Southern Ocean species of the philobryid genus *Adacnarca* can be found at or lower than 3500 m depth. The characteristic phenomenon of the Antarctic benthos, eurybathy (Brey et al., 1996), is common in Antarctic bivalve species and could explain why many families have depth distributions that extend below 1000 m.

An obvious feature of the depth ranges of gastropod families around Antarctica is that most show species ranges that are restricted to the shelf-slope break and only a third range into deep water. This latter group comprises the speciose families Buccinidae, Turridae, Naticidae, which are common gastropods not only in the Antarctic deep sea (Harasewych and Kantor, 2004; Schwabe et al., 2007; Aldea et al., 2008) but also in the deep sea worldwide (Olabarria, 2006). Gastropod families with only a few species in Antarctic waters exhibit narrow depth ranges. For example, among the Capulidae, *Capulus subcompressus* occurs only on the shelf in Antarctica while *Capulus simplex* occurs at 2800 m depth in the NE Atlantic (Olabarria, 2006).

4.2.2. Isopods

At the end of the last century 365 species of Isopoda were described from the Southern Ocean including the Subantarctic (Brandt, 1999). Most of these records, however, came from shelf and slope rather than deep-sea stations. The ANDEEP expeditions in 2002 and 2005 have increased the species numbers known, especially at bathyal and abyssal sites (Brandt et al., 2007a–c). The most speciose Southern Ocean isopod family is the Munnopsidae, this is represented by 226 species in the Southern Ocean where it is more speciose than in the northern deep Pacific or Atlantic oceans (Malyutina and Brandt, 2007). The munnopsids are followed in order of species richness in the Southern Ocean by the Desmosomatidae (170 species), Haploniscidae (97 species), Ischnomesidae (56 species) and Antarcturidae (49 species). All other families include fewer species. The Desmosomatidae are very speciose throughout the World's oceans, but according to the World List of Marine Isopoda (Schotte et al., 1995), most of the species have been reported from the Atlantic Ocean, Arctic to the Southern Ocean. Most species of the Haploniscidae are known from the Atlantic Ocean, but a considerable number also occur in the Pacific Ocean. The Ischnomesidae are recorded with comparable species numbers from both the Atlantic and Pacific Oceans, while the Antarcturidae clearly radiated on the Antarctic continental shelf and only few species occur in the deep sea or north of 60°S (Brandt, 1991, 1999; Brandt et al., 2007a, b). The general depth distribution of the isopod families reported in the present study corresponds with results of Svavarsson et al. (1990, 1993) and Kussakin (1973).

4.2.3. Polychaetes

The depth distribution patterns for polychaete families shows that those with high species numbers, such as Ampharetidae, Maldanidae, and Polynoidae, have large depth ranges, while rare families with only a few species records in the Southern Ocean, such as Arabellidae, Pholoididae, and Sternaspididae, have a narrower depth range. This pattern, however, may be the result of low sample numbers in the SO. For example, before the ANDEEP project, only 5 species of Opheliidae were recorded for depths below 2000 m around Antarctica (a.o. Hartman, 1966, 1978; Maciolek and Blake, 2006) compared with the total of 14 species now recorded in the

Southern Ocean deep sea (Schüller, in prep.). Specimens of the Arabellidae, Dorvilleidae, and Chaetopteridae have already been observed in unsorted ANDEEP samples and will expand the vertical distribution record for these families in the near future. A similar effect can be expected for other polychaete families. Ongoing efforts to explore the Southern Ocean benthos will improve our knowledge of the bathymetric distribution of polychaete families.

The most speciose polychaete families are the Polynoidae (73 species) and Syllidae (52 species), followed by the Terebellidae (49 species), Phyllodocidae (37 species), and Sabellidae (33 species). These are also among the most species rich polychaete families in shallow waters worldwide (Fauchald, 1977). In the Southern Ocean they are characterised by high species richness on the shelf and upper slope and with only few species in the abyss. In contrast, the next most speciose family, the Ampharetidae (32 species), shows the highest species richness on the continental slope down to the abyss. Ampharetidae have been reported to be one of the most abundant polychaete families in deep-sea communities in the North Atlantic (Cosso-Sarradin et al., 1998; Glover et al., 2001; Thistle et al., 1985). The high species richness in the bathyal Southern Ocean provides further evidence that this family can be considered a deep-sea taxon.

Polychaetes are known to show a great tendency towards eurybathy that is not enhanced in the Southern Ocean compared to other oceans (Brey et al., 1996). Therefore, it is not surprising that most families show very wide vertical distribution ranges. The few families that are limited to the shelf or the abyss are all characterised by low species number with less than 5 species described for the Southern Ocean to date. The lack of reports of these families at other depths therefore might be a result of the low number of samples in the Southern Ocean rather than of true absence. However, of the eleven families that are known across the entire depth range in this study, 50% include less than 15 species, only two in the case of the Fauveliopsidae. This shows that wide depths ranges are not necessarily connected to high species richness.

4.2.4. Comparison of patterns between taxa

Comparing family depth ranges between the four investigated taxa reveals that most of those with wide bathymetric ranges in the Southern Ocean also have wide bathymetric ranges globally. The species-rich families in the deep Southern Ocean are mostly typical deep-sea families that are speciose worldwide, for example the Cuspidariidae (Bivalvia), Buccinidae and Turridae (Gastropda), Munnopsidae and Desmosomatidae (Isopoda) and Ampharetidae (Polychaeta). Exceptions to this pattern are the Philobryidae (Bivalvia) and the Polynoidae, Syllidae and Terebellidae (all Polychaeta), which are characterised as shelf and upper slope taxa outside the Southern Ocean, but are common in the Southern Ocean from shallow- to deep-water.

The global distribution of benthic invertebrate families that occur on the Antarctic shelf and deep sea is not surprising when considering the oceanography of the Southern Ocean. The Antarctic deep waters are linked with the deep waters of the adjacent abyssal plains. The Weddell Sea Bottom Water (WSBW) flows northwards out of the Weddell Sea and the Southern Ocean into the deep basins of the South Atlantic and can be traced even further north (e.g. Fahrbach et al., 2001). Marine taxa, e.g. meiofaunal groups like foraminiferans or macrofaunal groups like bivalves, polychaetes or isopods, or their larval stages, could leave the Southern Ocean with deep-water currents, settle in new areas and radiate into new species. Antarctic deep-sea areas, like the Weddell and Ross Seas, are thought to be cradles for taxa presently living in the Atlantic or Pacific deep oceans (Clarke and Crame, 1992; Brandt et al., 2007a–c). The fact that almost all water masses surrounding the Antarctic continent and its adjacent deep sea are isothermal (Orsi et al., 1993) provides the possibility for the migration of shallow-water species into the Southern Ocean deep sea and hence further north. For this reason, it has been suggested that the Antarctic shelf serves as a "biodiversity pump" of organisms or developmental stages from shallow to deeper areas of the SO (Clarke and Crame, 1989, 1992). Therefore, not only Antarctic deep sea but also shelf taxa could be transported northwards with the current systems and colonise lower latitude areas. Data on the gene flow of bipolar protists (Foraminifera) from the south to the north support this hypothesis (Pawlowski et al., 2007; Brandt et al., 2007b).

Globally most marine invertebrates reproduce by means of planktotrophic or lecithotrophic larvae, which have great dispersal potential, while brooding restricts the dispersal of offspring (Pearse et al., 2009). In the Southern Ocean, the percentage of brooding species is higher than elsewhere. Thus, peracarid crustaceans, a brooding taxon, underwent an extremely successful adaptive radiation and speciation (Brandt, 1999, 2000, 2005), while species of taxa that globally have free-dispersing larvae have developed brooding in Antarctica (e.g. Pearse and Lockhart, 2004; Pearse et al., 2009). Thorson (1936) hypothesized that the polar environmental conditions, which were established in the Eocene or Miocene, affected especially the sensitive early life-history stages and favoured brooding.

Our study shows that the brooding isopods are the most speciose taxon of the four and are represented by more species in the deep sea than on the continental shelf. Interestingly, the isopods have fewer families with an uninterrupted depth range from shallow to deep water than the bivalves, gastropods and polychaetes. This raises the question of why the group that includes species with narrower depth ranges has been particularly successful in colonising the deep sea. Good dispersal ability is of great benefit in the generally oligotrophic deep sea (Lockhart, 2006). Isopods as brooders have poor dispersal capabilities and hence a reduced gene flow (Raupach et al., 2007), making restricted species distributions more plausible. On the other hand they are one of the taxa that underwent a successful adaptive radiation around Antarctica. However, it is difficult to prove in the Southern Ocean deep sea that this reduced gene flow also influences the rate of speciation. Whatever the case, isopods are highly diverse in the Southern Ocean deep sea (Brandt et al., 2007a–c) and species occur with one to few specimens at local scales (Kaiser et al., 2007).

Polychaete families range from shallow to deep water and many species have wide bathymetric ranges (Hilbig, 2004). Schüller and Ebbe (2007) tried to relate global distribution patterns of Southern Ocean polychaetes to larval dispersal. Although reproduction in the Southern Ocean deep sea is documented (Blake and Narayanaswamy, 2004), most data on polychaete larval development originate from tropic to boreal shelf species (e.g., Wilson, 1991; Rouse and Pleijel, 2006). The few data available on SO or deep-sea polychaetes strongly suggests a higher proportion of brooders and species with lecithotrophic larvae compared to free-spawning planktotrophic larvae (Blake, 1993; Hartman, 1967). It is therefore questionable if the developmental mode of polychaetes accounts for a generally enhanced dispersal potential in comparison to exclusive brooders such as isopods.

In general, relatively little is known about the reproductive mode or ecology of species in the Southern Ocean, when compared to the world oceans. Investigations of the metabolism and development of pelagic larvae of Antarctic gastropods showed that oxygen consumption rates for *Marseniopsis mollis* and *Torellia mirabilis* veligers are ~10 times lower than those of comparable temperate gastropod and bivalve veligers (Peck et al., 2006). Investigations on pressure tolerance of early larval stages of the sea urchin *Sterechinus neumayeri* have demonstrated that these stages might be able to persist deeper than in 2000 m depth (Tyler et al., 2000). More studies of reproductive biology are needed to enhance our understanding of why some species have wide, eurybathic distribution ranges while other occur only locally.

5. Conclusions

Species richness of bivalves, gastropods and polychaetes is highest on the Antarctic continental shelf, while isopods species are more numerous at depths around 3000 m in the deep sea. Potential explanations can be found in the reproduction strategy and mobility of taxa. Brooders, including all peracarid isopods, probably have a reduced gene flow and species are distributed on local rather than regional scales (Kaiser et al., 2007; Raupach et al., 2007). Species with planktotrophic larval development, like many polychaetes and bivalves, are more likely to disperse vertically and horizontally and have an enhanced gene flow and larger species ranges, but less pressure to radiate into species complexes.

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References

Aldea, C., Olabarria, C., Troncoso, J., 2008. Bathymetric zonation and diversity gradient of gastropods and bivalves in West Antarctica from the South Shetland Islands to the Bellingshausen Sea. Deep Sea Research Part I: Oceanographic Research Papers 55, 350–368.

Allen, J.A., 1998. The deep-water species of *Dacrydium Torell*, 1859 (Dacrydiinae: Mytilidae: Bivalvia), of the Atlantic. Malacologia 40, 1–36.

Allen, J.A., 2001. The family *Kelliellidae* (Bivalvia: Heterodonta) from the deep Atlantic and its relationship with the family Vesicomyidae. Zoological Journal of the Linnean Society of London 131, 199–226.

Allen, J.A., Sanders, H.L., 1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic the epilogue. Progress in Oceanography 38, 95–153.

Allen, J.A., 2008. Bivalvia of the Deep Atlantic. Malacologia 50, 57–174.

Alongi, D.M., 1992. Bathymetric patterns of deep-sea benthic communities from bathyal to abyssal depths in the western South Pacific (Solomon and Coral Seas). Deep-Sea Research 39 (3/4), 549–565.

Arntz, A., Gutt, J., Klages, M., 1997. Antarctic marine biodiversity: an overview. In: Battaglia, B., Valencia, J., Walton, D.W.H. (Eds.), Antarctic Communities. Species, Structure and Survival. Cambridge University Press, Cambridge, pp. 3–14.

Arntz, W.E., Clarke, A. (Eds.), 2002. Ecological Studies in the Antarctic Sea Ice Zone. Results of EASIZ Midterm Symposium. Springer, Heidelberg, pp. 1–277.

Blake, J.A., 1981. The Scalibregmatidae (Annelida:Polychaeta) from South America and Antarctica collected chiefly during the cruises of the R/V/ Anton Bruun, R.V. Hero and USNS Eltanin. Proceedings of the Biological Society of Washington 94 (4), 1131–1160.

Blake, J.A., 1993. Life history analysis of five dominant infaunal polychaete species from the continental slope off North Carolina. Journal of the Marine Biological Association of the United Kingdom 73, 123–141.

Blake, J.A., Grassle, J.F., 1994. Benthic community structure on the US South Atlantic Slope off the Carolinas: Spatial heterogeneity in a current-dominated system. Deep-Sea Research 41, 835–874.

Blake, J.A., Narayanaswamy, B.E., 2004. Benthic infaunal communities across the Weddell Sea Basin and South Sandwich Slope, Antarctica. Deep-Sea Research II 51, 1797–1815.

Brandt, A., 1991. Zur Besiedlungsgeschichte des antarktischen Schelfes am Beispiel der Isopoda (Crustacea, Malacostraca). Berichte zur Polarforschung 98, 1–240.

Brandt, A., 1997. Biodiversity of peracarid crustaceans (Malacostraca) from the shelf down to the deep Arctic Ocean. Biodiversity and Conservation 6, 1533–1556.

Brandt, A., 1999. On the origin and evolution of Antarctic Peracarida (Crustacea, Malacostraca). Scientia Marina 63 (1), 261–274.

Brandt, A., Schnack, K., 1999. Macrofaunal abundance at 79°N off East Greenland: opposing data from epibenthic-sledge and box-corer samples. Polar Biology 22, 75–81.

Brandt, A., 2000. Hypotheses on Southern Ocean peracarid evolution and radiation (Crustacea, Malacostrasca). Antarctic Science 12 (3), 269–275.

Brandt, A., Hilbig, B., 2004. ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns)—a tribute to Howard L. Sanders. Deep-Sea Research II 51 (14–16), 1457–1919.

Brandt, A., Brökeland, W., Brix, S., Malyutina, M., 2004. Diversity of Antarctic deep-sea Isopoda (Crustacea, Malacostraca) – a comparison with shelf data. Deep-Sea Research II 51 (14–16), 1753–1769.

Brandt, A., 2005. Evolution of Antarctic biodiversity in the context of the past: the importance of the Southern Ocean deep sea. Antarctic Science 17 (4), 509–521.

Brandt, A., De Broyer, C., De Mesel, I., Ellingsen, K.E., Gooday, A., Hilbig, B., Linse, K., Thomson, M., Tyler, P., 2007a. The deep benthos. In: Rogers, A. (Ed.), Antarctic Ecology: From Genes to Ecosystems, Royal Society, London. Philasophical Transactions of the Royal Society B 362, pp. 39–66.

Brandt, A., Gooday, A.J., Brix, S.B., Brökeland, W., Cedhagen, T., Choudhury, M., Cornelius, N., Danis, B., De Mesel, I., Diaz, R.J., Gillan, D.C., Ebbe, B., Howe, J., Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Brandao, S., Pawlowski, J., Raupach, M., 2007b. The Southern Ocean deep sea: first insights into biodiversity and biogeography. Nature 447, 307–311.

Brandt, A., Brökeland, W., Choudhury, M., Brix, S., Kaiser, S., Malyutina, M., 2007c. Deep-sea isopod biodiversity, abundance and endemism in the Atlantic sector of the Southern Ocean – results from the ANDEEP I-III expeditions. Deep-Sea Research II 54 (16–17), 1760–1775.

Brandt, A., Ebbe, B., 2007. ANDEEP III ANtarctic benthic DEEP-sea biodiversity: colonisation history and recent community patterns. Deep-Sea Research II 54 (16–17), 1645–1904.

Brey, T., Klages, M., Dahm, C., Gorny, M., Gutt, J., Hain, S., Stiller, M., Arntz, W.E., 1994. Antarctic benthic diversity. Nature 368, 297.

Brey, T., Dahm, C., Gorny, M., Klages, M., Stiller, M., Arntz, W.E., 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? Antarctic Science 8, 3–6.

Bruun, A.F., 1956. The abyssal fauna: its ecology, distribution and origin. Nature 177, 1105–1108.

Cattaneo-Vietti, R., Chiantore, M., Schiaparelli, S., Albertelli, G., 2000. Shallow- and deep-water mollusc distribution at Terra Nova Bay (Ross Sea, Antarctica). Polar Biology 23, 173–182.

Clarke, A., Crame, J.A., 1989. The origin of the Southern Ocean marine fauna. In: Crame, J.A. (Ed.), Origins and Evolution of the Antarctic Biota. Geological Society of London (Special Publication 47), London, pp. 253–268.

Clarke, A., Crame, J.A., 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. Philosophical Transactions of the Royal Society of London B 339, 299–309.

Clarke, A., Arntz, W.E., Smith, C.R., 2006. EASIZ: ecology of the Antarctic Sea Ice Zone. Deep-Sea Research II 53 (8–10), 803–1140.

Clarke, A., Johnston, N.M., 2003. Antarctic marine benthic diversity. Oceanography and Marine Biology: an Annual Review 41, 47–114.

Clarke, A., Griffiths, H.J., Linse, K., Barnes, D.K.A., Crame, J.A., 2007. How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographic patterns in Southern Ocean gastropod and bivalve molluscs. Diversity and Distributions 13 (5), 620–632(13).

Cosso-Sarradin, N., Sibuet, M., Paterson, G.L.J., Vangriesheim, A., 1998. Polychaete diversity at tropical Atlantic deep-sea sites: environmental effects. Marine Ecology Progress Series 165, 173–185.

Fahrbach, E., Harms, A., Rohard, G., 2001. Flow of bottom water in the northwestern Weddell Sea. Journal of Geophysical Research – Oceans 106 (C2), 2761–2778.

Fauchald, K., 1977. The Polychaete worms. Definitions and keys to the Orders, Families and Genera. Natural History Museum of Los Angeles County Science Series 28, 1–188.

Fogg, G.E., 1992. A History of Antarctic Science. (Studies in Polar Research) Cambridge University Press, Cambridge, UK, 483pp.

Gage, J.D., Tyler, P.A., 1991. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, Cambridge.

Glover, A., Paterson, G., Bett, B., Gage, J., Sibuet, M., Sheader, M., Hawkins, L., 2001. Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic. Deep-Sea Research I 48, 217–236.

Gray, J.S., 2001. Antarctic marine benthic biodiversity in a world-wide latitudinal context. Polar Biology 24, 633–641.

Griffiths, H.J., Linse, K., Crame, J.A., 2003. SOMBASE – Southern Ocean Mollusc Database: a tool for biogeographic analysis in diversity and ecology. Organisms Diversity & Evolution 3, 207–213.

Griffiths, H.J., Barnes, D.K.A., Linse, K., 2009. Towards a generalized biogeography of the Southern Ocean benthos. Journal of Biogeography 36, 162–177.

Harasewych, M.G., Kantor, Yu.I., 2004. The Deep-Sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and Adjacent Abyssal Plains and Trenches. The Nautilus 118 (1), 1–42.

Hartman, O., 1964. Polychaeta Errantia of Antarctica. Antarctic Research Series 3, 1–131.

Hartman, O., 1966. Polychaeta Myzostomidae and Sedentaria of Antarctica. Antarctic Research Series 7, 1–158.

Hartman, O., 1967. Larval development of benthic invertebrates in Antarctic Seas: early development of *Nothria notialis* (Monro) and *Paronuphis antarctica* in Bransfield Strait, Antarctic Peninsula. In: Proceedings of the Symposium on Pacific-Antarctic sciences, JARE Scientific Reports, Special Issue No. 1, pp. 205–208.

Hartman, O., 1978. Polychaeta from the Weddell Sea Quadrant, Antarctica. Biology of the Antarctic Seas VI. Antarctic Research Series 26, 125–223.

Hartmann-Schröder, G., Rosenfeldt, P., 1988. Die Polychaeten der Polarstern-Reise ANT III/2 in die Antarktis 1984 Teil 1: Euphrosinidae bis Chaetopteridae. Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 85, 25–72.

Hartmann-Schröder, G., Rosenfeldt, P., 1989. Die Polychaeten der Polarstern-Reise ANT III/2 in die Antarktis 1984. Teil 2: Cirratulidae bis Serpulidae. Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 86, 65–106.

Hartmann-Schröder, G., Rosenfeldt, P., 1990. Die Polychaeten der Walther Herwig-Reise 68/1 nach Elephant Island (Antarktis) 1985 Teil 1: Aphroditidae bis Cirratulidae. Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 87, 89–122.

Hartmann-Schröder, G., Rosenfeldt, P., 1991. Die Polychaeten der 'Walther Herwig'-Reisen 68/1 nach Elephant Island (Antarkis) 1985. Teil 2: Acrocirridae bis Sabellidae. Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 88, 73–96.

Hartmann-Schröder, G., Rosenfeldt, P., 1991. Zoogeography and ecology of the polychaetes from ANT III/2 of R/V 'Polarstern' to Antarctica in 1984. Bulletin of Marine Science 48 (2), 588.

Hartmann-Schröder, G., Rosenfeldt, P., 1992. Die Polychaeten der 'Polarstern'-Reise ANT V/1 in die Antarktis 1986. Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 89, 85–124.

Headland, R.K., 1989. Chronological List of Antarctic Expeditions and Related Historical Events. (Studies in Polar Research) Cambridge University Press, Cambridge, UK, 740pp.

Held, C., 2003. Molecular evidence for cryptic speciation within the widespread Antarctic crustacean *Ceratoserolis trilobitoides* (Crustacea, Isopoda). In: Huiskes, A.H.K., Giekes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolv, W.J. (Eds.), Antarctic Biology in a Global Context. Backhuys, Leiden, The Netherlands, pp. 135–139.

Hessler, R.R., Jumars, P.A., 1974. Abyssal community analysis from replicate box cores in the central north Pacific. Deep-Sea Research I 21, 185–209.

Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep-sea. Deep-Sea Research I 14, 65–78.

Hilbig, B., 2004. Polychaetes of the deep Weddell and Scotia Seas-composition and zoogeographical links. Deep-Sea Research II 51, 1817–1825.

Kaiser, S., Barnes, D.K.A., Brandt, A., 2007. Slope and deep-sea abundance across scales: Southern Ocean isopods show how complex the deep sea can be. Deep-Sea Research II 54, 1776–1789.

Knox, G.A., Cameron, D.B., 1998. The Marina Fauna of the Ross Sea: Polychaeta. NIWA Biodiversity Memoir 108, 1–125.

Kussakin, O.G., 1973. Peculiarities of the geographical and vertical distribution of marine isopods and the problem of the deep-sea fauna origin. Marine Biology 23, 19–34.

Landrum, B.J., 1975. Technical support for systematic biology. Antarctic Journal of the US 10 (1), 313–315.

Landrum, B.J., 1981. Antarctic biological collections. Antarctic Journal of the US 16 (5), 231.

Linse, K., 2004. Scotia Arc deep-water bivalves: composition, distribution and relationship to the Antarctic shelf fauna. Deep Sea Research II, Special volume 51, 1827–1837.

Linse, K., Griffiths, H.J., Barnes, D.K.A., Clarke, A., 2006. Biodiversity and biogeography of Antarctic and sub-Antarctic Mollusca. Deep-Sea Research II 53, 985–1008.

Lockhart, S.J., 2006. Molecular evolution, phylogenetics, and parasitism in Antarctic cidaroid echinoids. Doctoral Dissertation. University of California, Santa Cruz, 151pp.

Maciolek, N., Blake, J.A., 2006. Opheliidae (Polychaeta) collected by the R/V Hero and the USNS Eltanin cruises from the Southern Ocean and South America. Scientia Marina 70 (3), 101–113.
Malyutina, M., Brandt, A., 2007. Diversity and zoogeography of Antarctic deep-sea Munnopsidae (Crustacea, Isopoda, Asellota). Deep-Sea Research II 54, 1790–1805.
Olabarria, C., 2005. Patterns of bathymetric zonation of bivalves from Porcupine Seabight and adjacent Abyssal Plain, N.E. Atlantic. Deep-Sea Research I 52, 15–31.
Olabarria, C., 2006. Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from Northeastern Atlantic. Biodiversity and Conservation 15, 3685–3702.
Orsi, A.H., Nowlin, W.D., Withworth, T., 1993. On the circulation and stratification of the Weddell Gyre. Deep-Sea Research 40, 169–203.
Pawlowski, J., Fahrni, J., Lecroq, B., Longet, D., Cornelius, N., Excoffier, L., Cedhagen, T., Gooday, A.J., 2007. Bipolar gene flow in deep-sea benthic foraminifera. Molecular Ecology 16 (19), 4089–4096.
Pearse, J.S., Lockhart, S.J., 2004. Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. Deep-Sea Research II 51, 1533–1549.
Pearse, John S., Richard, Mooi, Lockhart, Susanne J., Brandt, Angelika, 2009. Brooding and Species Diversity in the Southern Ocean: Selection for Brooders or Speciation within Brooding Clades? In: Igor Krupnik, Lang, Michael A., Miller, Scott E. (Eds.), Smithsonian at the Poles: Contributions to International Polar Year Science. Proceedings of Smithsonian at the Poles Symposium, Smithsonian Institution, Washington, DC, 3–4 May 2007. Smithsonian Institution Scholarly Press, Washington, DC, pp. 181–196.
Powell, A.W.B., 1979. New Zealand Mollusca. William Collins Publishers Ltd., Auckland, New Zealand.
Peck, L., Clarke, A., Chapman, A.L., 2006. Metabolism and development in pelagic larvae of Antarctic gastropods with mixed reproductive strategies. Marine Ecology Progress Series 318, 213–220.
Raupach, M.J., Wägele, J.W., 2006. Distinguishing cryptic species in Antarctic Asellota (Crustacea: Isopoda)—a preliminary study of mitochondrial DNA in *Acanthaspidia drygalskii*. Antarctic Science 18, 191–198.
Raupach, M.J., Malyutina, M., Brandt, A., Wägele, J.W., 2007. Molecular data reveal a highly diverse species flock within the deep-sea isopod *Betamorpha fusiformis* (Crustacea: Isopoda: Asellota) in the Southern Ocean. Deep-Sea Research II 54, 1820–1830.
Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P., Waren, A., 2005. A source-sink hypothesis for abyssal biodiversity. The American Naturalist 165, 163–178.
Rouse, G., Pleijel, F. (Eds.), 2006. Reproductive Biology and Phylogeny of *Annelida*. Science Publishers, Enfeld, NH, USA, p. 688p.
Sanders, H.L., Hessler, R.R., 1969. Ecology of the deep-sea benthos. Science 163, 1419–1424.
Schiaparelli, S., Lörz, A.-N., Cattaneo-Vietti, R., 2006. Diversity and distribution of mollusc assemblages on the Victoria Land coast and the Balleny Islands, Ross Sea, Antarctica. Antarctic Science 18 (4), 615–631.
Schüller, M., 2008. *Polychaeta* (*Annelida*) of the Deep Southern Ocean – Biodiversity and Zoogeography. VDM Verlag Dr. Müller Aktiengesellschaft & Co. KG, Saarbrücken, pp. 1–209.
Schüller, M., Ebbe, B., 2007. Global distributional patterns of selected deep-sea Polychaeta (Annelida) from the Southern Ocean. Deep-Sea Research II 54, 1737–1751.
Schotte, M., Kensley, B.F., Shilling, S., 1995 onwards. World list of Marine, Freshwater and Terrestrial *Crustacea Isopoda*. National Museum of Natural History Smithsonian Institution, Washington, DC, USA. 〈http://www.nmnh.si.edu/iz/isopod/〉.
Svavarsson, J., 1997. Diversity of isopods (Crustacea): new data from the Arctic and Atlantic Oceans. Biodiversity and Conservation 6, 1571–1579.
Svavarsson, J., Strömberg, J.-O., Brattegard, T., 1990. Distribution and diversity patterns of asellote isopods (Crustacea) in the deep Norwegian and Greenland Seas. Progress in Oceanography 24, 297–310.
Svavarsson, J., Strömberg, J.-O., Brattegard, T., 1993. The deep-sea asellote (Isopoda, Crustacea) fauna of the Northern Seas: species composition, distributional patterns and origin. Journal of Biogeography 20, 537–555.
Schwabe, E., Bohn, J.M., Engl, W., Linse, K., Schroedl, M., 2007. Rich and rare – first insights into species diversity and abundance of Antarctic abyssal Gastropoda (Mollusca). Deep-Sea Research II 54, 1831–1847.
Thistle, D., Yingst, J.Y., Fauchald, K., 1985. A deep-sea benthic community exposed to strong bottom currents on the Scotia Rise (Western Atlantic). Marine Geology 66, 91–112.
Thorson, G., 1936. The larval development, growth, and metabolism of arctic marine bottom invertebrates compared with those of other seas. Meddelelser om Grønland 100 (6), 1–155.
Tyler, P.A., Young, C.M., Clarke, A., 2000. Temperature and pressure tolerances of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri* (Echinodermata: Echinoidea): potential for deep-sea invasion from high latitudes. Marine Ecology Progress Series 192, 173–180.
Wilson, W.H., 1991. Sexual reproductive modes in polychaetes: classification and diversity. Bulletin of Marine Science 48, 500–516.