The biodiversity of the deep Southern Ocean benthos

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Our knowledge of the biodiversity of the Southern Ocean (SO) deep benthos is scarce. In this review, we describe the general biodiversity patterns of meio-, macro- and megafaunal taxa, based on historical and recent expeditions, and against the background of the geological events and phylogenetic relationships that have influenced the biodiversity and evolution of the investigated taxa. The relationship of the fauna to environmental parameters, such as water depth, sediment type, food availability and carbonate solubility, as well as species interrelationships, probably have shaped present-day biodiversity patterns as much as evolution. However, different taxa exhibit different large-scale biodiversity and biogeographic patterns. Moreover, there is rarely any clear relationship of biodiversity pattern with depth, latitude or environmental parameters, such as sediment composition or grain size. Similarities and differences between the SO biodiversity and biodiversity of global oceans are outlined. The high percentage (often more than 90%) of new species in almost all taxa, as well as the high degree of endemism of many groups, may reflect undersampling of the area, and it is likely to decrease as more information is gathered about SO deep-sea biodiversity by future expeditions. Indeed, among certain taxa such as the Foraminifera, close links at the species level are already apparent between deep Weddell Sea faunas and those from similar depths in the North Atlantic and Arctic. With regard to the vertical zonation from the shelf edge into deep water, biodiversity patterns among some taxa in the SO might differ from those in other deep-sea areas, due to the deep Antarctic shelf and the evolution of eurybathy in many species, as well as to deep-water production that can fuel the SO deep sea with freshly produced organic matter derived not only from phytoplankton, but also from ice algae.

Keywords: Southern Ocean; biodiversity; benthos; geological history; evolution

1. INTRODUCTION

The deep sea is the largest environment on the planet, the least well known and one of the least studied. It contains extremely large habitats, and millions of square kilometres of continental slopes and abyssal plains. These enclose other geological structures, including canyons, seamounts, reefs, hydrothermal vents, mud volcanoes and faults at active and passive margins, which support unique microbiological and faunal communities. When considering our humble knowledge of deep-sea biodiversity, we assume that it is likely that more species occur in the deep sea than anywhere

else on Earth. In many taxa, far more than 90% of the species collected in a typical abyssal sediment sample are new to science, and many of these are rare. One could argue that the high numbers of new species do not necessarily mean that the deep-sea environment in the SO is more diverse than the shelf, only that these areas are less well studied. Although this is certainly the case, intensive investigations since 2002 at approximately 40 stations in the SO during the ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) expeditions (figure 1) reveal that, for some taxa, almost as many species are known in the deep SO as on the Antarctic continental shelf (Fütterer *et al.* 2003; Brandt & Hilbig 2004). Some authors have demonstrated that the occurrence of rare species in samples is the result of sampling the regional fauna only (Rex *et al.* 2005a). If these species reflect
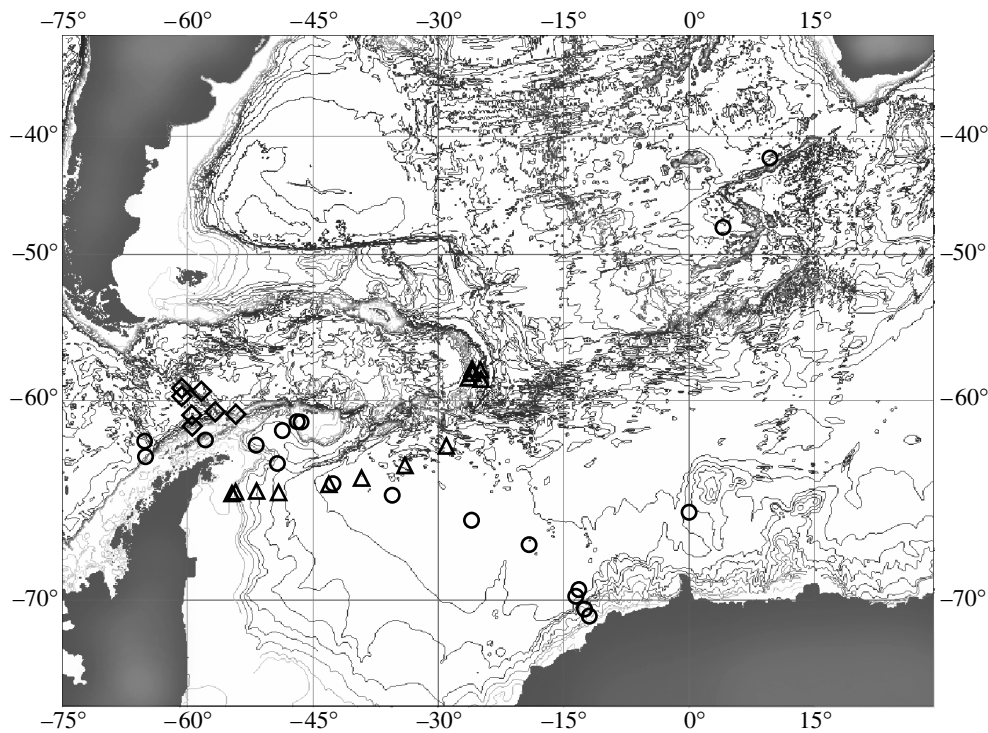
Figure 1. Locations of the ANDEEP expeditions. Diamonds, ANDEEP I (January to February 2002); triangles, ANDEEP II (February to April 2002); circles, ANDEEP III (January to April 2005).

source–sink dynamics of larvae transported from bathyal to abyssal sites, then current views about the hyperdiverse nature of deep-sea environments may need to be moderated. Nevertheless, we do find rather different patterns in the biodiversity and biogeography of SO deep-sea meio-, macro- and megafaunal taxa, which points to the fact that—even if the source–sink hypothesis can be proved for some taxa—large-scale biodiversity and biogeography patterns largely depend on size, biology (feeding mode and reproductive adaptations) and mobility of the taxa investigated (cf. also Rex *et al.* 2005*b*) combined with historical geologic patterns, productivity, predation and the relationship between regional and local species diversity (Witman *et al.* 2004).

In total, the SO covers an area of 34.8 million km². The shelves around Antarctica are on average 450–500 m deep, but exceed 1000 m in places. Of the total SO area, the continental shelf (<1000 m in depth) covers 4.59 million km², the continental slope (1000–3000 m in depth) covers 2.35 million km² and the deep sea (>3000 m in depth) covers approximately 27.9 million km² (Clarke & Johnston 2003). Thus, much of the SO is deep sea. The main purpose of this paper is to present the first review of the benthic organisms which inhabit this vast and little-known area of ocean floor. We first consider the geological background to deep SO biodiversity. We then briefly review biodiversity and biogeographic patterns, phylogenetic relationships and relationships between faunal assemblages and environmental variables. In §9, we compare and contrast Antarctic deep-sea ecosystems with those from other parts of the world ocean. Much remains to be learnt about biodiversity in the deep SO and we hope this review will create a platform on which future studies can build.

2. HISTORY OF ANTARCTIC BIODIVERSITY WORK

A chronological list of all terrestrial and marine Antarctic expeditions and related historical events was published by Headland (1989). The major expeditions at the beginning of deep-sea exploration were organized by European scientists, although these were not devoted to the SO deep sea. The first oceanographic cruise, the *Challenger* Expedition, took place from 1872 to 1876. Further examples are the North Atlantic deep-sea expeditions of the Norwegian RV *Michael Sars* in 1910, the Swedish RV *Albatross* Expedition in 1947–1948 and several others, culminating in the Danish *Galathea* Expedition from 1952 to 1956 (Wolff 1960) that demonstrated the existence of life even at the greatest depths of the oceans.

Many early expeditions to the SO investigated the sediments. These included the German South Polar Expedition (Philippi 1910), the *Discovery* Expeditions, or later the USNS *Eltanin*, RV *Conrad* and USCGC *Glacier* (e.g. Bullivant 1959; Anderson 1990), or Russian and French expeditions (e.g. Dangeard *et al.* 1977). Their results documented that the SO deep seafloor is characterized by soft sediment like other deep-sea basins. However, it is characterized by a high frequency of dropstones, and grain size usually decreases with increasing distance from the continent due to iceberg rafting. The percentage of silicate and carbonate has also been demonstrated to increase to the south of the Polar Front.

Few investigations of deep-sea biology have been carried out in the SO, and none has been devoted exclusively to the deep water. Some data were collected in the years between 1950 and 1960 as part of Russian and US expeditions (*Eltanin, Glacier, Akademik Kurchatov, Akademik D. Mendeleiev*) that mainly
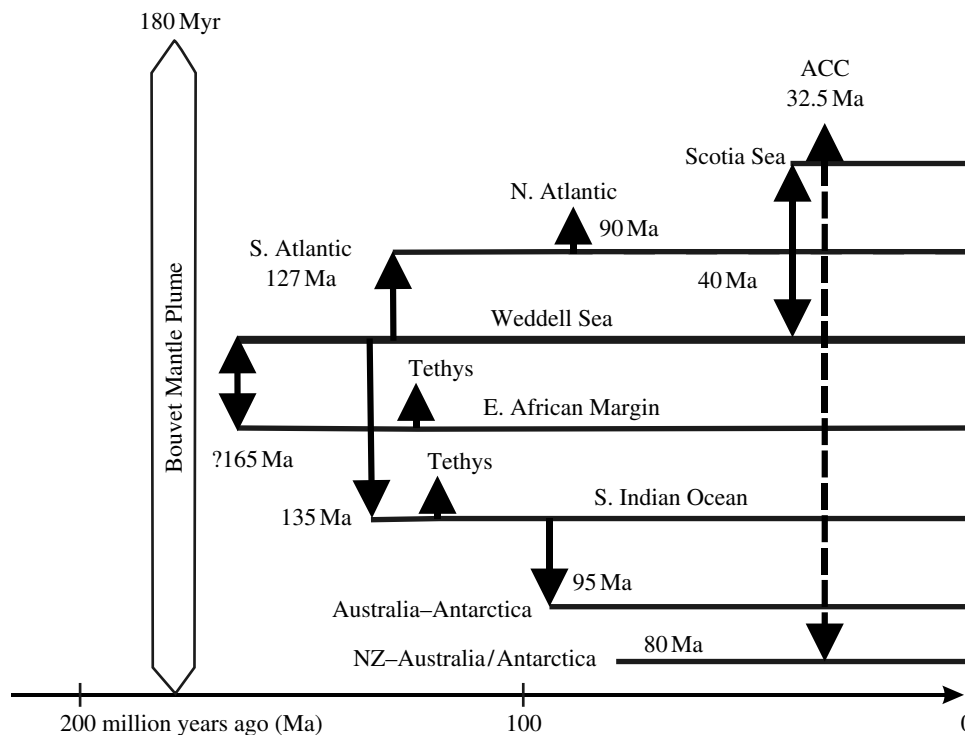
Figure 2. Diagram to show the evolution of deep-marine connections between the Weddell Sea region and the rest of the world's developing oceans as the Gondwana supercontinent broke up. Horizontal lines represent developing oceans through time, with side arrows indicating the initiation of links to other oceans and seas. The timing of events is in millions of years.

focused on the shelf off the South Orkneys and South Sandwich Islands. The Beagle Channel was sampled in 1873–1876 (HMS *Challenger*), including several deep-sea stations, and later during IBMANT (interactions between the Magellan Region and the Antarctic) in 1994 (Arntz & Rios 1999; Arntz *et al.* 1999).

More recent programmes, such as EPOS (European Polarstern Studies) and EASIZ (Ecology of the Antarctic Sea Ice Zone), also included collection of deep-sea data, but again only as additional sampling to that on the shelf to study key ecological processes at the organism and community level. Both have provided a wealth of taxonomic data on the benthos of the high Antarctic Weddell Sea and the Antarctic Peninsula (Arntz *et al.* 1990; Arntz & Gutt 1997; Arntz & Clarke 2002; Arntz & Brey 2003). GLOBEC and JGOFS both concentrated on process studies in the deep pelagic realm. Most information on the benthic deep-sea fauna in the Weddell Sea, available to date, is based on a few stations sampled during EASIZ II in the austral summer of 1998 (Brandt 2001; Arntz & Clarke 2002), and ANDEEP I–III, which was the most recent and extensive biological deep-sea survey in the Antarctic, yielding 40 biological, sedimentological and geological stations in 2002 and 2005 (Brandt & Hilbig 2004). The results from previous Russian deep-sea expeditions were summarized by Malyutina (2004), including a table with all benthic taxa collected during these surveys.

While the biological results from the *Eltanin* expeditions in the deep Atlantic and Pacific show that a high percentage of the shelf fauna can also be found on the slopes and in the deep sea (Menzies *et al.* 1973), data from the RV *Polarstern* ANDEEP campaigns in the

SO demonstrated that a high percentage of the deep-sea fauna is unknown.

3. GEOLOGICAL HISTORY AND EVOLUTION OF THE ANTARCTIC

The focus of ANDEEP investigations has been the deep oceanic basins of the Scotia and Weddell Seas (Brandt *et al.* 2004a,b). The region has a complex tectonic history, being sited close to the point where the break-up of the Gondwana supercontinent began, *ca* 180 Myr ago, close to the Bouvet Mantel Plume (White & McKenzie 1989; Storey 1991, 1995). Thus, the Weddell Sea developed at the focus of radial seaways, spreading out to become the Indian and South Atlantic oceans (figure 2). The Weddell is the older of the two seas under consideration here, with the seafloor dating back to the Middle Jurassic, whereas the Scotia Sea formed much later, during the last *ca* 40 Myr ago (Thomson 2004).

(a) *Indian Ocean*
Probably the first break across the Gondwana super-continent was that between Africa and the Madagascar–India–Antarctica block, forming the Somali and Madagascar basins. Although spreading began *ca* 165 Myr ago, the Madagascar Basin remained 'closed' until some time between 132 and 120 Myr ago (Roeser *et al.* 1996), after which a continuous seaway opened along the coast of eastern Africa and a link to the Tethyan Ocean was initiated. India/Madagascar began to break away from Antarctica/Australia at *ca* 135 Myr ago and had completely separated by 100 Myr ago. Madagascar itself separated from India at *ca* 100 Myr ago. Thus, by Mid-Cretaceous times there were

well-developed marine connections between the southernmost Atlantic/Weddell Sea region and the Tethys Sea. An arm from the southern Indian Ocean began to extend between Australia and Antarctica from *ca* 95 Myr ago, and the complex of continental fragments that now make up the New Caledonia–New Zealand region began to separate from the Australia–West Antarctica margin between 75 and 84 Myr ago.

(b) *South Atlantic*
The South Atlantic began to open from the south at *ca* 127 Myr ago and promulgated northward to join up with the North Atlantic at *ca* 90 Myr ago (Natland 1978; Ryan *et al.* 1978). However, for a considerable time, the Walvis Ridge acted as a barrier, separating the South Atlantic into two basins: Angola–Brazil (northern) and Cape–Argentine (southern). During the Aptian (121–112 Myr ago), the Angola–Brazil Basin was closed to the north and the Walvis Ridge at least partly emergent, forming a more-or-less closed basin and leading to the deposition of evaporate deposits. The Cape–Argentine Basin was also restricted to the south by the Agulhas Fracture Zone sill and largely anoxic conditions prevailed. Sinking of the Walvis Ridge and Agulhas sill through the Albian (112–99 Myr ago) allowed flushing and oxygenation of first the Cape–Argentine Basin and finally the Angola–Brazil Basin in the Turonian (93.5–89 Myr ago) when a connection to the North Atlantic was established.

(c) *Weddell Sea*
The tectonic history of the Weddell Sea is by no means as clear as for the Atlantic and Indian oceans, not least because the pre-break-up configuration of the region has yet to be confirmed, and because of the difficulty in identifying seafloor magnetic anomalies. The whole of what is now West Antarctica is generally believed to have been a mosaic of continental blocks, each of which moved to its present position in Late Mesozoic times. However, there seems to be little agreement as to their precise original positions (cf. Grunow *et al.* 1991; Leitchenkov *et al.* 1996; Storey *et al.* 1996). Further problems are posed by the Falkland Islands. Once widely considered as part of an original fixed extension to the Argentine continental shelf, there is a growing body of geological argument to suggest that they rotated from a position, east of Natal (Mitchell *et al.* 1986; Curtis & Hyam 1998). However, it is uncertain exactly when and how this occurred, and no suture between a supposed Falkland block and continental Argentina has yet been identified.

The opening history is clearer some time after 126 Myr ago when gravity (McAdoo & Laxon 1996) and magnetic anomalies become identifiable in the central and northern Weddell Sea (Livermore & Hunter 1996). By that time, the Falkland Islands block was probably attached to the Argentine continental shelf as the Falkland Plateau, and the Ellsworth–Whitmore mountains, Haag Nunataks and Weddell Sea Embayment blocks had moved close to their present locations; the Antarctic continent had more or less its present configuration back to *ca* 120 Myr ago (Hunter *et al.* 1996; Livermore & Hunter

1996, p. 236). Although identifiable seafloor magnetic anomalies are absent in the southern part of the Weddell Sea, LaBrecque & Barker (1981) reported seafloor *ca* 165 Myr old between 69° and 70° S in the eastern Weddell Sea and suggested that the 'southern Weddell Basin is pre-Late Jurassic to Cretaceous in age'; other authors (e.g. Livermore & Hunter 1996) suggest a younger age, *ca* 150 Myr old. Seafloor in the northern Weddell Sea can be dated to as recent as 10 Myr ago in the vicinity of latitude 60° S.

The possibility for the existence of a 'shallow' marine connection from the Pacific Ocean into the Weddell Sea–South Atlantic area, prior to the opening of Drake Passage (§3*d*), was suggested by Lawver & Gahagan (1998). They envisaged that, in the Early Cenozoic, prior to Antarctic glaciation, a seaway existed between the Pacific and the Atlantic, extending from the Ross Sea, between Marie Byrd Land and the Transantarctic Mountains, and then between Southeastern Antarctic Peninsula and the western end of the Ellsworth Mountains, into the Weddell Sea. While this 'trans-Antarctic seaway' was unlikely to have permitted much water exchange between the proto-Ross and Weddell Seas (Lawver & Gahagan 2003), it could nevertheless have provided a route for the migration of marine animals. They suggested that this seaway may have persisted into the Oligocene, as long as there was no West Antarctic ice sheet, and perhaps even into the Mid-Miocene (*ca* 22.5 Myr ago). This trans-Antarctic seaway could have reopened during the Pliocene (*ca* 4 Myr ago) warming.

(d) *Drake Passage and Scotia Sea*
Owing to its importance to the understanding of the origin of the Antarctic Circumpolar Current (ACC), there have been numerous studies of the tectonic evolution of Drake Passage and the Scotia Sea. Ideas on the time of opening of Drake Passage and the Scotia Sea and their possible effects on the marine biota were reviewed by Thomson (2004, 2005), and the resultant oceanographic changes by Mackensen (2004). There is general agreement that the old continental link between South America and the Antarctic Peninsula began to disintegrate *ca* 40 Myr ago (Lawver & Gahagan 2003) or even 50 Myr ago (Livermore *et al.* 2005), but the detailed history is far from resolved (cf. also Brown *et al.* 2006). A key issue has been the timing of the opening of Drake Passage and the onset of deep-water flow. Livermore *et al.* (2004) argued that the Shackleton Fracture Zone ridge is a relatively recent feature (less than 8 Myr old), and therefore that deep-water flow from the Pacific eastwards was possible in the Early Oligocene and potentially more powerful than that of today. However, it still remains unresolved as to how much of a barrier the dispersing horseshoe of continental fragments of the Scotia arc to the east might have posed (Maldonado *et al.* 2003). The precise relationship between the development of the ACC and the onset of glaciation also awaits clarification. The timing of the two is close, around the Eocene–Oligocene boundary (*ca* 34 Myr ago), but which is the older?

Table 1. Species numbers and endemism rates for selected macro- and megabenthic taxa in the SO. (All numbers are based on the current knowledge of diversity in the SO and are given to the best estimate taken from either article or personal communications. Numbers are given for the total number of species known from the SO and their percentage of endemism. The columns 'shelf (0–1000 m)' and 'deep sea (>1000 m)' give total number of species found at these depth zones. The columns 'shelf only' and 'deep sea only' represent the number of species found only in this depth zone. As for some taxa, no information on their depth distribution of species is given in the article; the numbers presented below do not always add up.)

	Southern Ocean	endemics	shelf (0–1000 m)	shelf only	deep sea (>1000 m)	deep sea only
Porifera (Janussen & Tendal 2005, personal communication)						
Hexactinellida	50	60%	27		~45	~30
Calcarea	20	60%	14		~15	~10
Demospongiae	400	60%	~350		100	~60
Cnidaria (Peno Cantero 2004)						
Hydrozoa	155		148		13	7
Mollusca						
Bivalvia (Linse *et al.* 2003, 2006*b*)	158	57%	122	76	82	36
Gastropoda						
Prosobranchia (Linse *et al.* 2003, 2006*b*)	535	80%	463	365	160	62
Polyplacophora (Linse, personal communication)	8	60%	8	6	2	0
Scaphopoda (Steiner & Kabat 2004)	8	50%	3	3	6	5
Cephalopoda						
Octopoda (Collins & Rodhouse 2006)	36	100%	25	22	11	9
Crustacea						
Malacostraca						
Amphipoda (De Broyer 2005, personal communication)	510	85%	470	427	84	38
Tanaidacea (Guerrero-Kommritz 2005, personal communication)	127	23%	~80		~50	
Cumacea (Mühlenhardt-Siegel 2005, personal communication)	77	95%	72	68	9	5
Isopoda (Brandt 2006, personal communication)	991	87%	371	327	~650	~600
Mysidacea (Brandt *et al.* 1998)	37	51%	37	24	13	0
Natantia (Gorny 1999)	10		10	8	4	
Reptantia (Gorny 1999)	27		27	21	1	
Tentaculata						
Bryozoa (Barnes & De Grave 2001)						
Stenolaemata	35		35		0	
Gymnolaemata	307		~280		~30	
Brachiopoda (Forster 1974)	19	79%	13	6	13	5
Echinodermata						
Echinoidea (David *et al.* 2000)						
Regularia	35	66%	31	19	16	4
Irregularia	39	75%	29	19	20	10

Such profound geographical changes in the past would almost certainly have had a marked influence on the migration, distribution and evolution of marine taxa in general. Given its location close to the point of origin of the Gondwana break-up, it might be expected that the faunas of the Weddell Sea were particularly influenced. To what extent the changes may still be reflected in the benthic marine faunas of the present day remains to be seen, but the tectonic history should be borne in mind when trying to assess the evolutionary history of the faunas.

4. BENTHIC COMPOSITION AND DIVERSITY OF MEIO-, MACRO- AND MEGABENTHOS

The composition and biodiversity of SO marine taxa has been dealt with in many publications (e.g. Dayton 1990; Arntz *et al.* 1997; Brandt 1999; Clarke & Johnston 2003; De Broyer *et al.* 2003). Species richness of the SO marine fauna was published, for example, by

Dell (1972) and White (1984) and recently reviewed by Arntz *et al.* (1997), De Broyer *et al.* (2003) and Clarke & Johnston (2003). The most speciose taxa of the Antarctic benthos are the Polychaeta, Gastropoda, Bryozoa, Amphipoda, Isopoda and Porifera (table 1). The sessile taxa are favoured on the Antarctic shelf as a result of the adequate substrata provided by the poorly sorted glacial–marine sediments and increasing incidence of dropstones towards the shore (Clarke 1996). Polychaetes and molluscs are speciose in the SO, occurring with 800 species or more. Some taxa of Amphipoda and Isopoda (Peracarida) may have radiated owing to the extinction of decapod crustaceans.

In general, the species composition of abyssal deep-sea communities is poorly known in comparison with shelf and upper-slope environments (Gage & Tyler 1991). The SO deep sea differs in faunal composition from the shelf. Contrary to the SO shelf, which is zoogeographically well isolated through the ACC, the SO deep-sea fauna can freely migrate in and out of

the SO abyssal plains. Data from the SO deep sea obtained so far have shown that the fauna does not differ generally in composition at the higher taxonomic level from that of other deep-sea regions of the world oceans. However, at the species level, most of the SO deep-sea meio- and macrofauna are new to science, except for certain well studied groups, notably the hard-shelled, Foraminifera which are well known at the species level.

Large-scale biodiversity in the deep sea exhibits a strong poleward decline in the northern hemisphere (Poore & Wilson 1993; Rex *et al.* 1993; Crame 2000). However, patterns in the southern hemisphere have been shown to be different (Brey *et al.* 1996), and largely reflect a combination of evolutionary processes and environmental gradients that have helped to shape taxonomic diversity gradients (Crame & Clarke 1997; Crame 1999).

(a) *Meiofauna*

The deep-sea meiofauna (protists and metazoans in the 32–1000 µm size range) is usually dominated by Foraminifera and nematodes, followed by harpacticoid copepods, with other groups constituting a minor component (Thiel 1983; Vincx *et al.* 1994). Many studies have excluded the Foraminifera, and data on their contribution to the meiofauna are therefore sparse on a global scale. Published values range from a few per cent to more than 90% of the total meiofaunal abundance (Gooday 2001). However, when the rarely studied soft-shelled taxa are included, the proportion of Foraminifera usually exceeds 50% (Vincx *et al.* 1994; Gooday 2001). Cornelius & Gooday (2004) report the only data on the relative abundance of the foraminiferal and metazoan meiofauna in the same samples from the SO. Foraminifera typically made up 60–78% of the meiofauna in the western Weddell Sea (1100–5000 m water depth).

To a large extent, work on Foraminifera and metazoan meiofauna in the SO has been conducted in different places by different people with different scientific aims. Early taxonomic work on Foraminifera was linked to major national expeditions and based on qualitative samples collected using sounding devices and trawls (Ehrenberg 1844; Pearcey 1914; Heron-Allen & Earland 1922; Wiesner 1931; Earland 1933, 1934, 1936; Chapman & Parr 1937; Parr 1950; Lindenberg & Auras 1984). Much of the subsequent research was carried out by geologists and addressed only the fossilizable hard-shelled Foraminifera. Mcknight (1962) made the earliest quantitative studies, while the first workers to use rose Bengal staining to distinguish live from dead Foraminifera were Herb (1971) and Basov (1974). In recent decades, box corers (Mackensen *et al.* 1990, 1993; Schmiedl & Mackensen 1997) and hydraulically damped multiple corers (Harloff & Mackensen 1997; Cornelius & Gooday 2004) have been the standard equipment used to sample Foraminifera and other meiofauna in the SO. In general terms, foraminiferal assemblages in the deep SO comprise a mixture of calcareous, agglutinata and organic-walled taxa, resembling those found at similar depths in the North Atlantic. Macrofauna-sized komokiacean species that are known from the North Atlantic

are abundant in the central Weddell Sea, as they are on other abyssal plains. However, as discussed below, distinctive, entirely agglutinated assemblages occur in some intrashelf basins around the Antarctic continent. Another notable feature of SO Foraminifera is the prevalence of species attached to hard substrata, mainly dropstones. Taxa such as *Dendrophrya* spp., *Dendronina* spp., *Sorosphaera* spp. and *Tholosina* spp. are abundant at sites on the continental slope around South Georgia, the Antarctic Peninsula and in the Scotia Sea (Earland 1933, 1934). More than two-thirds (69%) of the 852 stained Foraminifera recovered from a box core (above 300 µm fraction, 0–5 cm layer) at 1100 m in the northwestern Weddell Sea (ANDEEP II station 133) by Cornelius (2005) were attached to dropstones. However, many of these species are macrofaunal in size.

Data on the diversity of deep-water foraminiferans have been reported for Antarctica by many authors since the 1960s (Mcknight 1962), but different methodologies have made comparisons between sites difficult. Moreover, the vast majority of studies are confined to hard-shelled taxa, and many earlier investigations concerned 'total' (live plus dead) assemblages. Only Cornelius & Gooday (2004) included soft-shelled species among their live assemblages. They recognized 158 live foraminiferal species in small core samples (above 63 µm fraction) from the western Weddell Sea. Diversity indices were highest, and dominance lowest at 3000 and 4000 m. A notable feature of this dataset was that species numbers, diversity indices and dominance varied considerably between replicate subcores at some stations, largely resulting from variations in the abundance of the dominant species, *Epistominella exigua*.

The first metazoan meiofaunal study in the Antarctic deep sea was by Herman & Dahms (1992), who described higher taxon composition along a depth transect (500–2000 m) across the continental shelf in Halley Bay. Subsequently, the ecology of higher taxa was studied off Kapp Norvegia (Vanhove *et al.* 1995*a*,*b*), along a depth transect at the South Sandwich Trench (Vanhove *et al.* 2004), at abyssal depths near the Shackleton Fracture Zone (Gutzmann *et al.* 2004) and at two sites in the Ross Sea (Fabiano & Danovaro 1999). The last is the only paper on deep-sea meiofauna in a non-Atlantic sector of the SO.

Metazoan meiofauna communities are generally rich in higher taxa. A total of 29 have been reported from the Antarctic, with between 3 (Gutzmann *et al.* 2004) and 22 (Herman & Dahms 1992) coexisting in individual samples. As in most other marine sediment communities, nematodes dominate the meiofauna (excluding Foraminifera) in the Weddell Sea, where they make up between 83 and 97% of the total community compared with 56 and 97% in the Ross Sea (Fabiano & Danovaro 1999). The second most abundant group are the harpacticoid Copepoda (1–9%; 27% are reported in the Ross Sea). Other taxa frequently found in Antarctic marine sediments include the Polychaeta, Kinorhyncha, Ostracoda, Loricifera, Gastrotricha, Tardigrada and Bivalvia, although these are often represented by a few individuals only.
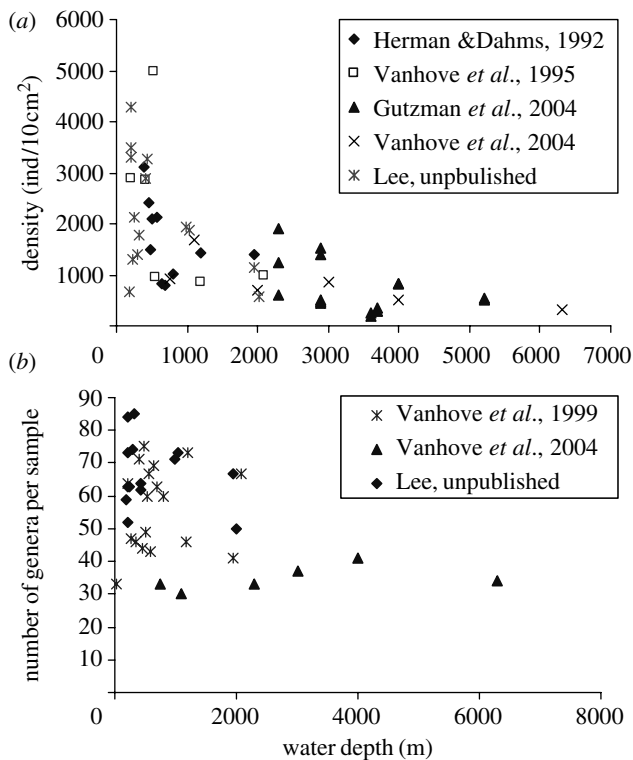
Figure 3. (*a*) Average meiofauna densities versus depth, with symbols referring to the information source. Note that the data points from Gutzman *et al.* (2004) represent median densities, while other data points represent mean densities. (*b*) Average number of genera versus depth, with symbols referring to the information source.

The Nematoda is the only group to have been examined at a lower taxonomic level (genera and species; figure 3*a*,*b*). Nematode genus composition has been studied on the continental slope off Kapp Norvegia and Halley Bay (Vanhove *et al.* 1999), Vestkapp and Bransfield Strait (Lee 2005, unpublished data) and along a bathymetric gradient towards the South Sandwich Trench (Vanhove *et al.* 2004). In total, 194 nematode genera have been recognized, with between 30 (1100 m, South Sandwich Transect) and 73 (1000 m, Drake Passage) occurring at each station. On the trench floor (6300 m), 34 nematode genera were counted. Genus diversity seems to be negatively related to depth (figure 3*b*), although this conclusion is based mainly on data from a single study at depths between 2000 and 6000 m in the South Sandwich Trench (Vanhove *et al.* 2004).

Recently, species diversity has been analysed within a number of selected nematode genera (Vermeeren *et al.* 2004; Fonseca *et al.* 2006; De Mesel *et al.* 2006; Ingels *et al.* in press). These studies suggest very high local and regional species diversity. The highest number of co-occurring species within the same genus was found at 2000 m off Vestkapp, where 23 species of the genus *Acantholaimus* occurred in one sample. At the same site, five *Dichromadora* species and one *Molgolaimus* species were recognized. Thus, 29 species were distinguished among only 3 out of the 68 genera analysed. These genera represented 14% of the total community in terms of numbers. Many species occurred only at one site, indicating high species

turnover between sites (β-diversity) and thus high regional diversity.

(i) *Macrofaunal composition and diversity*

Diversity of macrofaunal taxa is poorly known, but differs tremendously between taxa. For example, high latitude decapod crustaceans are impoverished, probably as a result of physiological constraints since the Tertiary climatic deterioration, and crabs probably became extinct *ca* 15 Myr ago (Arntz *et al.* 2006). Approximately 120 benthic species of shrimp and crab occur in the Subantarctic. In the high Antarctic, only five benthic shrimp species are represented (Arntz & Gorny 1991; Gorny 1999; Thatje *et al.* 2005).

Lithodidae (decapod crabs) were recently found in Antarctica (Thatje *et al.* 2005) and occur in the SO with 15 species. Recolonization of the continental shelf might have occurred via the deep sea and there is evidence of recent speciation among taxa on isolated seamounts and islands (Thatje *et al.* 2006).

Within the Isopoda, 317 species (morphotypes) were discriminated during the first two SO ANDEEP I and II deep-sea surveys to the Atlantic sector of the SO, the Drake Passage, Elephant Island, the South Shetland Islands and trench, the Weddell Sea and the southeastern South Sandwich Islands (Brandt & Hilbig 2004). Ninety-eight per cent of these belong to the suborder Asellota. Species of the suborder Valvifera or the family Serolidae that are typical for shelf stations were much rarer in the SO deep sea. Species richness was documented to be highest in the northwestern Weddell Sea during ANDEEP I and II. Preliminary results from ANDEEP III revealed that the eastern Weddell Sea slope or lower shelf at approximately 1000 m depth is characterized by a very high abundance of isopods, indicating that diversity might also be high. Within the Asellota, the Munnopsididae were the most dominant isopod family, with 61% of the specimens, 118 species and 28 genera. Other important families were the Desmosomatidae with 48 species, Haploniscidae with 42, Ischnomesidae with 34, Nannoniscidae with 14 and Macrostylidae with 7 species (Brandt *et al.* 2004*a*,*b*; Fahrbach 2006). Families such as the Paramunnidae (11 species) and Munnidae (12 species) were less diverse in the deep sea, as were the species of the suborders of the Scutocoxifera (e.g. the Valvifera with six species and the Serolidae—three species in the SO deep sea—of the suborder Sphaeromatoidea).

A very high number of the species, almost 50%, were rare and occurred only at a single station, with only one or a few specimens. The proposed source–sink hypothesis by Rex *et al.* (2005*a*,*b*) is unlikely to apply here owing to the brooding biology of isopods and their feeding mainly on detritus. Moreover, the evolution of many of the rare species in the bathyal or abyssal depths is likely and was hypothesized (Brandt 1991; Raupach 2004). Depth was the most important factor accounting for differences in isopod communities followed by sediment composition and grain size, and there was no clear pattern between isopod communities and geographical area. In the past, the SO deep-sea Isopoda were most extensively investigated by Russian scientists,
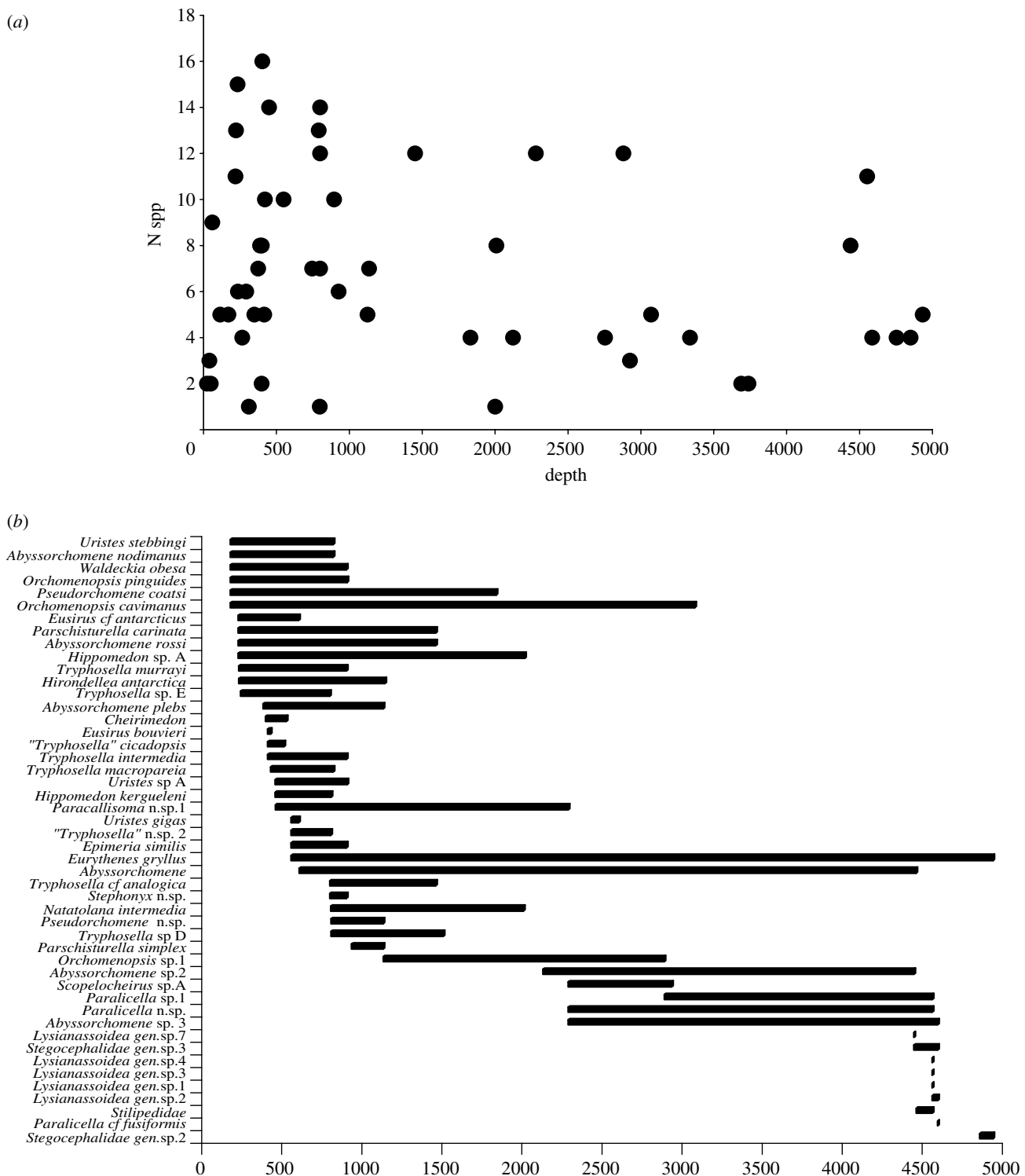
(a)

(b)

Figure 4. (*a*) Bathymetric distribution of amphipod scavengers. (*b*) Depth zonation exemplified on amphipod scavengers.

and the knowledge (mainly the descriptions of new species) is summarized in a table by Malyutina (2003, 2004).

Amphipod crustaceans are known to count among the most speciose animal groups in Antarctic coastal and shelf communities, where 510 benthic and bentho-pelagic species have been recorded (De Broyer & Jazdzewski 1996, updated; Vinogradova 1997). In the Antarctic deep sea, the very limited investigations before the ANDEEP cruises revealed the presence of 72 benthic or benthopelagic species belonging to 33 families below 1000 m. Among these, only 16 species

from 12 families—all primitive and characterized by free-swimming males—were known from the abyssal zone below 3000 m.

More than 10 000 amphipod specimens were collected during the ANDEEP cruises (Brandt & Hilbig 2004), using epibenthic sledge (EBS), baited traps, Agassiz trawl and boxcorers. For the Antarctic deep sea, the ANDEEP results showed that Amphipoda contributed up to 32% of the large material collected by the EBS, ranking second after Isopoda (38%), the usual dominant group in the deep sea. This is in sharp contrast with other deep-sea samples where

amphipods are usually much less abundant (Dahl 1954; Brandt *et al.* 2004*a*,*b*).

Within the amphipods (with an estimated 200 species in the Antarctic deep sea), the scavenger guild has been studied in detail and provided useful information on the composition and distribution of this part of the amphipod taxocoenosis. In the Antarctic deep sea, below 1000 m, 46 scavenger species were collected using baited traps (Takeuchi *et al.* 2001; De Broyer *et al.* 2004, in press). They mostly belong to the Lysianassoidea, including 39 species from 18 genera and 8 families. New species of *Alicella*, *Hirondellea*, *Orchomenopsis*, *Paralicella* and *Tryphosella* were found. In addition to lysianassoids, single species of Epimeriidae and Iphimediidae (the latter accidentally in traps) were also sampled, as well as some Eusiridae and Stegocephalidae.

The Antarctic continental slope (1000–3000 m) appears to be richer in scavenger species than elsewhere in the world at similar depth range (31 *Antarctic* spp. versus maximum 11 elsewhere). On the other hand, in the Antarctic abyssal waters (3000 m or deeper), the species richness of the scavenger guild (17 spp. recorded) appears quite similar to that of the abyssal trap collections elsewhere in the world. Indeed, the largest abyssal trap record outside the SO yielded 15 different species (13 lysianassoids, 1 scopelocheirid, 1 valettiopsid), from 3144 to 5940 m in the northeastern and tropical Atlantic Ocean (Vader 1972; Bowmann 1974; Thurston 1990; Berge & Vader 2001, 2003). The relation between species richness of necrophagous amphipods and depth is shown in figure 4*a*. The figure clearly shows the variability of amphipod richness in coastal and shelf traps, and its relatively limited reduction from the shelf down-slope to the abyssal zone. As the identification process is still in progress, the total number of deep-sea amphipod species collected by ANDEEP is presently unknown, but it can be estimated on the basis of the sorting operations and present identifications to be over 200. A high percentage of unknown species has been detected in most families (De Broyer *et al.* 2004; Berge 2005, personal communication; Thurston 2005, personal communication).

Tanaidacea were known with 127 species from the SO, mostly from shelf depths (Brandt 1999; Schmidt 1999). However, recent descriptions (e.g. Blazewicz-Paszkowycz & Larsen 2004; Guerrero-Kommritz & Blazewicz-Paszkowycz 2004) have raised this number to 173 species according to Guerrero-Kommritz (2005, personal communication). Besides 55 species known from the deep sea, 50 are known from the continental shelf, 34 from the west Antarctic and 34 species from the east Antarctic.

Cumaceans were known with 77 species from the SO, mainly from the shelf, and 73 are endemic for this area. From these 73 species, four species show a wide bathymetric distribution and occur on the shallow shelf deeper than 1000 m, and another five species occur only deeper than 1000 m. Nevertheless, many new species still need to be described from the ANDEEP material, and identification and sorting of these has just started (Mühlenhardt-Siegel, personal communication). Mysidacea are known with 59 SO species

(Brandt *et al.* 1998; Brandt 1999), with 18 species occurring at 1000 m or deeper. *Mysidetes* is the most speciose genus and the species *Eucopia australis* has the widest bathymetric range down to 6000 m (Brandt *et al.* 1998).

Besides Peracarida, the most important macrofaunal taxa are Polychaeta and Mollusca (Bivalvia and Gastropoda). There is very little information on the diversity of deep-sea polychaetes from the SO, as publications resulting from the expeditions to Antarctic waters since the end of last century (e.g. McIntosh 1885; Monro 1930, 1936; Augener 1932; Fauvel 1936; Hartman 1964, 1966, 1967; Hartmann-Schröder & Rosenfeldt 1988, 1989) do not address quantitative questions. Hilbig (2001) published the first quantitative results based on samples from depths greater than 1000 m that yielded approximately 800 individuals belonging to 115 species in 28 families. The most speciose family was the cirratulids with 13 species, followed by ampharetids (11 species), terebellids (9 species), paraonids (8 species) and maldanids (8 species). All of these families are sedentary or discretely motile surface or subsurface deposit feeders that live either at the sediment–water interface (cirratulids, ampharetids, terebellids and paraonids) or deeper in the sediment (maldanids). The only vagile family with a relatively large number of species was the syllids. The opportunistic spionids and capitellids were poorly represented (6 and 2 species, respectively), as well as epibenthic and highly vagile forms, such as polynoids, and motile carnivores, such as nephtyids and glycerids. Thus, while polychaete diversity at the level of families in the Antarctic generally resembles that found elsewhere in the deep sea, several opportunistic families typically dominating temperate slope communities are poorly represented. Reasons for this may be a lesser abundance of patches of organically enriched sediments and opportunist niches being occupied by amphipods rather than polychaetes (Hilbig 2001). Species richness is low if compared with the temperate deep sea (Hilbig & Blake 2006; Hilbig *et al.* in press), but the diversity is high if the extremely low abundances are considered.

Diversity patterns of polychaetes have proved to be complex (Hilbig *et al.* in press) as depth-related trends can be overlain by strong regional differences. For example, if the shelf and upper slope off the Antarctic Peninsula are compared with the Weddell Sea shelf, species richness is about half as high on the Weddell Sea shelf and thus very similar to the adjacent slope region. First quantitative investigations of abyssal plain and trench stations in the Weddell and Scotia seas indicate highly variable abundance and species richness values that on average tend to be about half that of the slope (Ellingsen *et al.* submitted).

Most of the molluscan species found in the Antarctic deep sea belong to the macrofauna. Exceptions are some large-sized turrid, naticid, buccinoid and bathydorid gastropods, scaphopods of the genera *Siphonodentalium* and *Fissidentalium* and cephalopods.

To date, we know approximately 190 molluscan morphospecies of five classes from the deep sea. With 100 morphospecies, gastropods are the dominant group in terms of species numbers, followed by

bivalves. Sixty species of bivalves belonging to 17 families were found during the ANDEEP cruises, and at least seven of these species are new to science. In comparison with the shelf fauna of the Scotia Arc, the deep-water bivalve community showed similar species richness. This indicates that there is no diversity cline with depth in Antarctic bivalves, but it does provide evidence for underestimated species richness in deep water owing to the lack of sampling (Linse 2004). Aplacophoran species are quite common with 6 morphotypes of Caudofoveata and 15 morphotypes of Solenogastres. Seven species of scaphopods and two species of polyplacophorans were found. While most of the bivalve and scaphopod species show a wide distributional range and occur with several specimens in the samples, gastropod species have rare occurrences; often they are found with only one to two specimens at one to two sites (Linse *et al.* 2006b).

The diversity and spatial distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep SO has recently also been compared in Ellingsen *et al.* (submitted), using datasets collected during the EASIZ and ANDEEP cruises. Both the isopods and the polychaetes had a high proportion of unique (species restricted to one single site, 46 and 50%, respectively) and duplicate species (species found at only two sites, 24 and 22%, respectively). However, the bivalves displayed a different distributional pattern, with a higher proportion of the species represented at more sites and only 17% of the species restricted to one site. The proportion of bivalve species found at only one, two or three sites (50%) was lower than that of isopods and polychaetes (Ellingsen *et al.* submitted).

The number of species shared between all pairwise combinations of sites was low for all three taxonomic groups, and the proportion of the average number of shared species of the average total richness for all pairwise combinations of sites was low (7.0% for isopods and polychaetes and 17.6% for bivalves). Using Whittaker's original β-diversity measure and the classical Jaccard similarity coefficient, Ellingsen *et al.* (submitted) showed that the extent of change of community composition among sites was high for all three taxonomic groups, although to a lesser extent for the bivalves.

(ii) *Megafaunal composition and diversity*

More than 26 major taxonomic groups are recognized among the megafauna of the SO deep sea. Echinoderms dominate in terms of abundance, biomass and species richness. Within this taxon, holothurians are more diverse and higher in biomass than ophiuroids, asteroids and echinoids. The dominance of holothurians is typical of many deep-sea communities in the northeast Atlantic Ocean (Billett *et al.* 2001). In terms of abundance and biomass, other taxa, including sponges, anthozoans, malacostracan crustaceans, polychaetes, gastropods and bivalves, were of less importance. When present, both fishes and cephalopods (mainly octopodids) are important components in terms of biomass.

In general, the SO deep-sea megafauna can be divided into three major groups defined by their lifestyles: (i) errant benthopelagic species, (ii) errant benthic species, and (iii) sessile species.

The benthopelagic species comprise large scavenging amphipods, deep-water shrimp-like decapods, octopods and bottom-living fishes. Specimens of these taxa occur frequently in the samples, but often in low numbers. The exceptions are swarm-forming natant shrimps *Nematocarcinus* and the scavenging amphipods that appear in high numbers as soon as food is available. The most common scavenging amphipod in the Antarctic deep sea was found to be the panoceanic eurytheneid *Eurythenes gryllus* (De Broyer *et al.* 2004, 2006). Baited traps deployed in bathyal and abyssal depths attracted several hundreds of individuals. Several species of cirrate octopods occurred in abyssal trawls, often represented by single specimens only. Bottom-living fishes comprise the most important part of the benthopelagic deep-sea fauna in terms of biomass. Most commonly, specimens of the families Macrouridae, Zoarcidae and Liparidae are collected, but also species of the families Oreosomatidae, Muraenolepididae, Moridae and Rajidae are found (Andriashev 1987). The Macrouridae, also called rattails or grenadiers, are among the most abundant and diverse deep-sea fishes worldwide and in Antarctica. The snailfishes or Liparidae are also species rich.

The five classes of the echinoderms, Ophiuroidea, Asteroidea, Echinoidea, Crinoidea and Holothuroidea, are the dominant errant megafaunal taxa in the Antarctic deep sea in terms of abundance and diversity. Although their species richness is higher on the shelf, echinoderms show a rich diversity along the slope and on the deep-sea plains. Large and long-armed ophiuroids can cover the abyssal seafloor in dense beds, and they show biomasses comparable to those on the shelf. In these brittle star associations, several different species occur next to each other. The deep-water asteroids vary little from the morphotypes that can be found on the shelf; cushion-like forms exist next to short- and long-armed forms. Remarkable in trawls from the Antarctic abyssal plains is the high species diversity, as often the number of morphospecies resembles the number of the few collected specimens. The species richness and biogeography of Antarctic Echinoidea, comprising regular and irregular sea urchins, are well studied (David *et al.* 2000). At present, 35 regular sea urchins are known, of which 31 species are reported from the shelf and 16 from the deep sea. Only four of the deep-sea species are endemic to the deep and the other 12 species show eurybathy. For the Irregularia, 29 species are known from the shelf and 20 species from the deep sea; half of them are endemics. An interesting ecological aspect in the Antarctic echinoid fauna is that high numbers of brooding species are observed in both regular cidaroid and irregular sea urchins (Lockart *et al.* 2003). With approximately 30 described species, Crinoidea are the least species-rich class of the Antarctic echinoderms. Most of the species belong to the Comatulida, feather stars, and are common on the shelf and nearshore habitats, but they can also be found on the upper continental slope. These unstalked forms often raise their position by attaching themselves to large

hexactinellid sponges and gorgonians. More remarkable is the occurrence of stalked crinoids, sea lilies, from the upper slope to abyssal depth. Several genera, *Bathycrinus*, *Hyocrinus* and possibly *Rhizocrinus*, are reported (Lockart *et al.* 2003; Bohn 2006). Stalked crinoid densities vary extremely between locations; often only single specimens are collected by trawls or seen on deep-sea videos, while at two slope locations in the eastern Weddell Sea (PS65/231, 1500 m; Gerdes 2004, unpublished data) and Bellingshausen Sea (PS67/154, 3600 m; Bohn 2006; Carpenter 2002, unpublished data), dense aggregations with several specimens per metre square occurred. Holothuroidea of the SO are accounted with just over 100 species (Clarke & Johnston 2003). Most obvious are the large-sized, epibenthic elasipodid holothurians, which occur in almost all deep-water trawls, while the small-sized, mainly infaunal apodid forms are less reported. At present, 13 apodid holothurians are known from the SO, of which nine species are found in the deep sea. Records report approximately 30 elasipodid morphospecies from the SO deep sea. Local species richness can be high, as up to seven morphospecies were found in trawl catches. Conspicuous are species with fused dorsal podia that form shorter or longer 'sails', for example in the genera *Peniagone* and *Scotoplanes*. Deep-sea holothurian species are very widely distributed in various ocean basins; the species *Psychropotes longicauda* and *Oneirophanta mutabilis* are thought to occur from the northeast Atlantic Porcupine Abyssal Plain to the South Atlantic abyssal Weddell Sea.

Molluscs from the shelf of the SO are fairly well known, especially for the gastropods and bivalves, while records from the Antarctic deep sea are scarce. Recent publications (e.g. Allcock *et al.* 2004; Harasewych & Kantor 2004; Linse 2004) enhance the knowledge on the deep-water fauna. All seven molluscan classes with benthic taxa are represented in the deep sea: Aplacophora (Caudofoveata and Solenogastres); Monoplacophora; Polyplacophora; Gastropoda; Scaphopoda; Bivalvia; and Cephalopoda. For all classes, more species are reported from the shelf. Aplacophorans, famous from the Antarctic shelf for their enormous gigantism in genera like *Neomenia* (Salvini-Plawen 1978), are small-sized in the deep sea. The discovery of one of the three Antarctic monoplacophorans, *Laevipilina antarctica*, from the SO abyssal extends the bathymetric range for this species from former 210–644 m to over 3000 m. Polyplacophorans are almost absent in SO deep waters, with only two records for *Leptochiton kerguelensis* and *Stenosemus simplicissimus* from the upper continental slope in the Ross and Weddell seas (Linse *et al.* 2003,2006*b*). Three species of the scaphopod genera *Fissidentalium* and *Siphonodentalium* can grow to a large size (18–54 mm). The deep-sea gastropod fauna is characterized by the dominance of medium-sized (10–40 mm) omnivorous, predatory species of the Buccinoidea, Turridae and Naticidae and the occurrence of many small-sized (1–3 mm) taxa. Analysis of the taxonomic diversity of Antarctic buccinoid genera showed that the abyssal fauna shared no genera with sublittoral or bathyal faunas (Harasewych & Kantor 2004). The deep-sea bivalve fauna is dominated by taxodont taxa, especially

of the Nuculanidae and Limopsidae, but also carnivorous genera like *Cardiomya* and *Cuspidaria* are present. Most of the bivalve species reach final sizes of less than 10 mm, although some species such as *Lyonsiella angelikae*, *Limopsis marionensis* and *Limatula* (*Antarctolima*) can be larger. The comparison of the ratios of gastropod to bivalves species richness from the shelf (1.94–2.94) with the deep sea (1.37–1.66) shows that bivalve richness decreases less with depth than gastropod richness.

While polychaetes, in general, dominate species numbers in the deep sea, the number of megafaunal species in the SO is negligible. Sea spiders, pycnogonida, that are commonly found with large-sized species on the Antarctic shelf are less frequent on the bathyal continental slope and were not found at abyssal depths. Burrowing sipunculids and echinoids are recorded from bathyal and abyssal depths, but little is known of their taxonomy.

Sessile megafauna are often attached to exposed rock outcrops or basaltic rocks of oceanic spreading centres, but as these substrata are rare in the Antarctic deep sea, the fauna here relies on dropstones lost by icebergs or has to attach to the sediment. The most diverse component of the sessile megafauna is anthozoan taxa, including Alcyonaria, Pennatularia and Actinaria, while sponges are important in terms of biomass. Rare in occurrence and biomass are bryozoans, stalked ascidians and stalked crinoids, with the exception of two sites recently discovered in the Weddell and Bellingshausen seas, where dense beds of stalked crinoids were discovered (Bohn 2006).

The phylum Porifera is well represented in the SO by members of the three classes Hexactinellida, Calcarea and Demospongiae. While Demospongiae and Calcarea in temperate and tropical waters displace hexactinellid sponges from the shelf to the deep sea, the latter dominate the south-polar shelf waters. At present, species richness is dominated by species found on the shelf, while records from the Antarctic deep sea are still scarce owing to the undersampling of abyssal depths. The most species-rich group are the Demospongiae, with approximately 400 species followed by the Hexactinellida (approx. 50 spp.) and the Calcarea (approx. 20 spp.; Janussen & Tendal 2005, personal communication). At depths greater than 1000 m, the fauna probably comprises approximately 100 demosponge species, 40–45 hexactinellid (Barthel & Tendal 1992; Janussen *et al.* 2004) and 10–15 calcareous sponge species. The most important uncertain factors concerning this estimate are (i) lack of investigations as mentioned previously, (ii) some collections are still not worked up, (iii) some species are considered circum-Antarctic in distribution, but may in fact represent groups of species very similar in morphological traits, and (iv) small-sized species are easily overlooked. For instance, the Calcarea were undiscovered in the Antarctic deep sea before the ANDEEP II expedition in 2002 (Janussen *et al.* 2003). Recent sampling in the deep Weddell Sea collected 11 species of hexactinellids, 29 species of demosponges and 4 species of Calcarea; 33% of these species were new to Antarctica and 20% new to science (Janussen *et al.* 2004, Janussen in press). Most of the specimens

collected at the slope down to approximately 2000 m depths are representatives of known, eurybathic Antarctic shelf species, although their genera are well known from the global deep sea, like the hexactinellids *Bathydorus*, *Caulophacus* and *Chonelasma*. In depths below 3000 m, members of the typical deep-sea sponge associations can be found. Compared to the sponges on the shelf, most of the deep-water forms are smaller in size and much lower in biomass. In the abyssal environment, soft bottoms dominate and hard substrata like rocks are rare. The surfaces of the latter, mostly dropstones lost by melting icebergs, are often covered by encrusting demospongids similar to *Sphaerotylus*. Sponges inhabiting the soft bottom environments have erect, often vase-shaped bodies that might even sit on slender stalks. In the samples collected at abyssal depths during the ANDEEP expeditions, carnivorous demosponges of the family Cladorhizidae were common. This family are typically deep-sea sponges adapted to a life in waters with poor suspended nutrition (Janussen 2003). Of special interest are the records of several species of Calcarea from the deep Weddell Sea, as this group is extremely rare in Antarctic shelf water and almost unknown from abyssal depths worldwide (Janussen 2003).

Cnidarians, next to sponges, are important parts of the Antarctic benthos in structuring the benthic habitats, especially the hydrozoans and alcyonarian anthozoans. Benthic scyphozoans are of less importance owing to only few records of the genera *Atolla* and *Periphylla* from the shelf and deep sea.

The latest review of benthic hydrozoans recorded 155 species for Antarctica, with most species (142 spp.) inhabiting the shelf (down to 1000 m depths), only six species occurring from the shelf to the upper slope and only seven species being endemic to the deep sea (Peno Cantero 2004). Our current knowledge of the total number of Antarctic anthozoan species is imprecise, and therefore comparisons of species richness between the shelf and the deep sea are impossible. However, recently, the eastern Weddell Sea and Antarctic Peninsula have been sampled from the shelf to the deep sea by several expeditions with RV *Polarstern* (e.g. Gili *et al.* 2005; López-González 2006) and the anthozoan fauna was identified to morphospecies. When the anthozoan species are separated into their subclasses Octocorallia and Hexacorallia, a trend in species richness with depth is seen. While on the shelf Octocorallia comprise approximately 60% of anthozoan fauna, Hexacorallia dominate the deep-sea fauna. Within the Hexacorallia, an increase in the diversity of the order Zoanthidea is observed. The abyssal plains of the Weddell Sea show a nearly constant species/group composition as in the deep sea in other oceans (López-González 2006): *Galatheanthemum profundale*; *Antipatharia* spp.; and *Umbellula* cf. *thomsoni*. *Caryophyllia* and *Fungiacyathus* represent the group of the stony corals, the Scleractinians, in the Antarctic deep sea down to approximately 3500 m depth.

Ascidians are a conspicuous and ecologically important component of the Antarctic continental shelf fauna and comprise approximately 120 species (Clarke & Johnston 2003). Data on their species richness and diversity are unavailable for the SO deep sea. During the ANDEEP expeditions, only few, often single, specimens were found in Agassiz trawl catches, which await taxonomic identifications. In the abyssal depths of the Weddell Sea (2500–4900 m), solitary and colonial stalked ascidians similar to the genera *Octacnemus* and *Megalodicopia*, typical deep-sea ascidians, occurred in most trawls.

5. PHYLOGENETIC RELATIONSHIPS OF SELECTED TAXA

(a) *Foraminifera*

Molecular data on the phylogenetic position of deep-water Antarctic Foraminifera are published for two monothalamous species from the Weddell Sea. *Bathyallogromia weddellensis* branches within a morphologically heterogeneous clade that includes species from a coastal site in Explorers Cove (McMurdo area of the Ross Sea) and shallow-water sites in the northern hemisphere (Pawlowski *et al.* 2002a,b; Gooday *et al.* 2004). Its closest relative is an undescribed allogromiid from Mediterranean caves. The second species, *Conqueria laevis*, constitutes a distinct clade of monothalamous Foraminifera. It forms a sister group to a clade (Clade E of Pawlowski *et al.* 2002a,b) that includes *Vellaria zuchellii* from Terra Nova Bay and *Psammophaga* sp. from Explorers Cove, in addition to two northern hemisphere species (Gooday & Pawlowski 2004). However, the relationship between Clade E and *Conqueria* is very weakly supported.

Pawlowski *et al.* (2005) provide the first report of the diversity of monothalamous Foraminifera and gromiids from under the Ross Ice Shelf (923 m water depth). They recognized 14 allogromiids and 3 morphotypes. Partial small subunit rDNA sequences, including 19 obtained from individual isolates and 17 from environmental DNA samples, revealed the existence of 11 new allogromiid lineages. Molecular phylogenetic analyses suggest the endemic character of this assemblage, although more work is required to confirm this conclusion.

There is preliminary molecular evidence for genetic divergence between morphologically identical Arctic and Antarctic populations of shallow-water foraminiferal morphospecies (Pawlowski *et al.* 2003). Considerable genetic differentiation has occurred in Arctic and Antarctic populations of the planktonic foraminiferan *Neogloboquadrina pachyderma* (Darling *et al.* 2004). Whether deep-water populations of widely distributed benthic morphospecies in Antarctic waters are differentiated genetically from populations of the same morphospecies in the northern hemisphere remains to be tested.

(b) *Isopoda*

On the shelf, many species of isopods possess well-developed eyes and are endemic to the SO (Brandt 1991), while closely related species sampled in the SO deep sea were eyeless or had only rudimentary eyes. The Antarcturidae, for example, occur in the Atlantic deep sea down to >7200 m (Kussakin & Vasina 1993). For this family, we have to conclude that the deep-sea species had ancestors on the continental shelf. For some Janiroidea, like the families Acanthaspidiidae,

Munnidae and Paramunnidae, Brandt (1991) hypothesized polar submergence, because the abundant shelf species possess highly developed eyes. The Asellota, which are typical shallow-water species known to thrive globally on the continental shelves, can also be found at greater depths in the SO deep sea, supporting the theory of enhanced eurybathy of the SO benthic taxa (Brey *et al.* 1996). Kussakin (1973), like Dahl (1954), Wolff (1962) and Menzies *et al.* (1973), was also in favour of the submergence theory of SO Isopoda.

Other opinions are that the Isopoda have developed in the deep sea *in situ*, where they radiated before they emerged onto the continental shelves, especially at higher latitudes (e.g. Zenkevitch & Birstein 1960; Broch 1961; Belyaev 1974; Hessler & Thistle 1975; Hessler & Wilson 1983; Wilson & Hessler 1987). Emergence can be postulated in Antarctica, for example for the Munnopsididae, Haploniscidae, Desmosomatidae, Nannoniscidae and Ischnomesidae (Brandt 1991, 1992; Wilson 1998, 1999; Brandt *et al.* 2004*a*,*b*; Brökeland 2004). Both submergence and emergence do occur within the Isopoda, and the evolution of the shelf taxa cannot be studied in isolation from that of the deep-sea fauna. Hypotheses on the SO deep-sea isopod evolution and radiation were also published by Brandt (1999, 2000); however, the abyssal isopod fauna of the SO deep sea was not investigated in detail until recently (Brandt *et al.* 2004*a*,*b*).

Raupach (2004) corroborated these hypotheses of the evolution of isopod asellote families using molecular methods. He demonstrated the monophyly of the deep-sea families Munnopsididae, Acanthaspidiidae, Desmosomatidae, Haploniscidae, Ischnomesidae and Macrostylidae, as well as the eye-bearing shelf family Joeropsididae (Asellota, Janiroidea) using 18S rDNA sequences. On the contrary, the eye-bearing 'Janiridae' are polyphyletic. Moreover, the author could demonstrate that the deep sea was colonized at least four times independently, by the Acanthaspidiidae, the Haploniscidae, the Dendrotiidae and Haplomunnidae, and by a clade consisting of the Mesosignidae, Janirellidae, Nannoniscidae, Macrostylidae, Ischnomesidae, Desmosomatidae and Munnopsididae (Raupach 2004).

16S rDNA data from the circum-Antarctic species *Acanthaspidia drygalskii* document that this species is a cryptic species complex, consisting at least of three species; two haplotypes were found sympatrically in the western Weddell Sea and another one in the eastern Weddell Sea. Brökeland (2004) described speciation and radiation of deep-sea asellotes on the basis of a *Haploniscus* (Haploniscidae, Asellota, Janiroidea) species complex. She described seven new species within this genus. Whether this speciation process is a similar phenomenon like the adaptive radiations of the shelf isopod families Antarcturidae and Serolidae (Brandt 1991) and amphipod families Epimeriidae and Iphimediidae (Watling & Thurston 1989) is not known. Raupach (2004) discriminated four haplotypes within the *Haploniscus* species complex using 16S rDNA. Cryptic speciation within Isopoda is also known for shelf taxa (e.g. Held 2003). It is likely that these species have also colonized the deep sea several

times independently. The speciation processes culminating in radiations on the shelf or in the deep sea might have been caused by the subsequent changes in the ice-shelf extension, causing fragmentation, reproductive isolation, speciation and secondary contact of populations. It is for this reason that Clarke & Crame (1992) and others (e.g. Briggs 2003) have referred to Antarctica as a diversity pump.

It is unknown to what extent species have migrated up and down the Antarctic continental shelf and slope following ice extensions and retreats during glacial maxima and minima. As a potential consequence of past climate changes, eurybathy can be observed within many taxa today (Brey *et al.* 1996). The Weddell Sea is known to feed the newly formed cold deep water, the so-called Antarctic Bottom Water, into the ACC from where it spreads as part of the global thermohaline circulation into the basins of all three world oceans. By this process, the SO plays a significant role in global climate. The more-or-less isothermal water column of the Weddell Sea and other SO areas provides a perfect conduit for the migration of shallow-water species into the deeper waters. It is therefore possible that the SO deep sea is a centre of evolution for the Isopoda and other taxa, and it has influenced the composition and species richness of the isopod faunas of the world deep oceans. Whether the observed changes in the bottom water with temperature decrease (Fahrbach *et al.* 2005) influence the evolution and migration of any SO species will have to be investigated in the future.

(c) *Tanaidacea*

Sieg (1988) and his last unpublished manuscript postulated that the SO shelf Tanaidacea are descendants from deep-sea ancestors. This is because the Apseudomorpha, which are considered to be an ancient taxon, are missing on the shelf.

(d) *Mollusca*

Molecular studies on Antarctic species of the bivalve genus *Limatula* from the SO shelf revealed evidence of speciation and dispersal across the Polar Front (Page & Linse 2002) and strong support for the subgenera *L.* (*Limatula*) and *L.* (*Antarctolima*). Since this study, several specimens, morphologically belonging to both subgenera, have been found in deep-water samples of ANDEEP I–III and selected specimens have been sequenced. Preliminary analysis of sequences from the two morphotypes showed that the deep-water specimens group within the species of their subgenus but are genetically distinct from these shelf species (Linse 2004, unpublished data). Further molecular work on more specimens of the deep-water limids collected during ANDEEP will show if there is genetic divergence between morphologically identical specimens from the deep Weddell Sea (Atlantic Ocean) and Bellingshausen Sea (Pacific Ocean).

Studies on the molecular relationships of the mytilid *Dacrydium* sp. from a wide geographical range (eastern Weddell Sea to western Antarctic Peninsula, distance >2600 km) showed no significant divergence in the 18S, 16S and 28S sequences (Walsh & Linse 2004, unpublished data).

The Antarctic members of the arcoid *Limopsis* belong to a phylogenetically old group of this genus (Oliver 1981). The molecular results on the Antarctic members of the arcoid genus *Limopsis* show basal positions of deep-sea species (*Limopsis tenella*, *Limopsis* sp. 1 and *Limopsis* sp. 2), from which the shelf species (*L. marionensis*, *L. enderbyensis* and *L. lilliei*) evolved (Linse, unpublished data). The molecular data show evidence against extreme eurybathy and for the existence of cryptic species in the case of *Limopsis marinoensis*, as specimens collected from the shelf to the slope (300–1500 m) differed significantly from morphologically similar specimens collected at the deeper slope (2000–3000 m, *Limopsis* sp. 2) and in the deep-water basins (>3000 m, Limopsis sp. 1; Linse, unpublished data). 18S, 28S and ITS sequences of specimens collected within the three depth ranges varied insignificantly over a wide geographical area, ranging from the Antarctic Peninsula and Weddell Sea over the islands of the South Orkneys, South Sandwichs and South Georgia to the island of Bouvet.

6. BIOGEOGRAPHY AND ENDEMISM
At least for metazoan taxa, only preliminary data are available on the biogeographic relations of the Antarctic deep-sea fauna, because until now only the Atlantic sector of the SO deep sea has been investigated in detail (Brandt & Hilbig 2004).

(a) *Porifera*
For sponges, it is to be expected that the high percentage (more than 60%) of species endemism found on the shelf can be traced down to approximately 2000 m, although probably decreasing with depth (Barthel & Tendal 1989). At abyssal depths, endemism seems to be lower (Janussen 2003). Most Antarctic deep-water sponge species have been found only once or a few times, and this of course gives a high theoretical endemism. Below 2000 m, depending on how the Antarctic region is defined in the deep sea, the endemism may be high in some areas, especially in closed or semiclosed basins, but it is to be expected that faunal connections to areas of the Atlantic, Pacific and Indian Ocean will be found.

(b) *Foraminifera*
Based on his own and other work conducted in the early part of last century, Earland (1934) concluded that Antarctic deep-water Foraminifera are cosmopolitan and have migrated from deep-sea areas adjacent to the SO. Some later studies support this view. For example, Ward *et al.* (1987) found that 23% of species in their samples from 79 to 856 m in McMurdo Sound also occurred at Arctic sites. Many of the deeper-water associations recognized by Murray (1991) from the SO are dominated by widely distributed species, such as *Cyclammina pusilla*, *Epistominella exigua*, *Nuttallides umboniferus* and *Globocassidulina subglobosa*. A preliminary comparison by Cornelius & Gooday (2004) of calcareous foraminiferans in Weddell Sea and Porcupine Abyssal Plain samples suggested that more than 65% of species were common to both the areas. Some deep-water species, however, may be endemic to

Antarctic waters (Mikhalevich 2004). One possible example is *Haplophragmoides umbilicatum* Pearcey 1914, a species reported only from the abyssal Weddell Sea (Cornelius and Whittaker, in preparation). Many specimens of the distinctive monothalamous genus *Vanhoeffenella* from deep Antarctic waters differ from those found at lower latitudes in having a wide agglutinated rim. They may represent a distinct species confined to the SO.

Benthic foraminiferal species ranges in the deep ocean are based almost entirely on test morphology. A recent study by Pawlowski *et al.* (2005) of the morphological and molecular diversity of monothalamous Foraminifera and gromiids (a related group of testate protists), from a site 12 km from the edge of the Ross Ice Shelf (923 m water depth), indicates a high degree of endemism, with approximately 50% of the allogromiid phylotypes being unknown at other localities (McMurdo Sound, Weddell Sea, Arctic Ocean) from which molecular data are available. However, the small number of comparative sites made this conclusion preliminary. It is also possibile that apparently bipolar and cosmopolitan species consist of a number of cryptic species. Mikhalevich (2004) points to the existence of closely related Arctic and Antarctic species that were formerly regarded as representing single bipolar species (see also Schmiedl & Mackensen 1993). Taxonomic studies that combine morphological and molecular genetic approaches may reveal further examples of other apparently bipolar species, which really comprise closely related 'paired species'.

(c) *Metazoan meiofauna*
The generic composition of the deep-sea nematode fauna seems to be very similar worldwide (e.g. Netto *et al.* 2005), including the Antarctic deep sea (Vanhove *et al.* 1999, 2004). However, in addition to the typical deep-sea nematode genera (e.g. *Acantholaimus*, *Microlaimus*, (*Thalasso*) *Monhystera*, *Daptonema*, *Leptolaimus* and *Halalaimus*), other genera that are generally less common for deep water can be rather abundant in the SO. These taxa include *Southerniella*, *Paracanthonchus*, *Pareudesmoscolex* and *Desmodora*. Unlike the macrofauna, however, no endemic nematode genera have been found.

The ecology and distribution of species within five genera (*Acantholaimus*, *Dichromadora*, *Desmodora*, *Desmodorella* and *Molgolaimus*) has been studied on Antarctic shelves and slopes (Vermeeren *et al.* 2004; Fonseca *et al.* 2006; De Mesel *et al.* 2006; Ingels *et al.* in press). Of the 89 species distinguished, 57 occurred in deep-sea sediments. At least 56% of these deep-sea species were new to science, 37% were endemic to one station and 56% were endemic to one region (e.g. Weddell Sea, Antarctic Peninsula, South Sandwich Trench). On the other hand, a number of species had a rather wide distribution. Whether some are circumpolar is presently unknown, because species-level information is only available from the Atlantic Sector of the SO. Owing to our limited knowledge of deep-sea species worldwide, it is too early to draw any general conclusions regarding the biogeography of Antarctic deep-water nematodes.

(d) *Peracarida*

The SO deep-sea isopod fauna is unique, although at the genus level, many taxa are widely distributed and are cosmopolitan or bipolar. Many SO deep-sea species are new to science and of those being recognized, most were known from the South Atlantic (11 species), with others from the North Atlantic (five species), the Pacific (one from the north and three from the south) and one species from the Indian Ocean. However, these numbers are probably influenced by the sample locations in the Atlantic sector of the SO deep sea. Of the SO deep-sea species of Isopoda sampled, approximately 50% were rare and occurred at only one station. Almost 85% of the species known to date are endemic to the SO deep sea, a value similar to that of the shelf (88%; Brandt 1991; Brandt *et al.* 2004*a*,*b*). However, at this stage, it is not clear whether these are true patterns or a result of the undersampling of the SO deep sea. This result is probably an artefact, as the deep basins around the SO deep sea are generally unknown. However, Ellingsen & Gray (2002) also found a high proportion of North Atlantic shelf species to be rare. Thirty-six per cent of the total number of species were restricted to only one or two sites along the Norwegian continental shelf (i.e. 1960 km apart).

With the exception of the benthopelagic amphipod species exhibiting a larger distribution (e.g. *E. gryllus*, *Paralicella similis*, *Paracallisoma* cf. *alberti*, *Parandania boecki*), all but 10 of the strictly benthic deep-sea species are restricted to the SO. The 10 bathyal and abyssal species also occurring outside the SO have been recorded in only one other basin peripheral to the SO (Argentinian, Cape or Eastern Australian Basin).

There are 510 known Antarctic species of Amphipoda, with 85% endemism in the SO. To date, it is not possible to present an estimate of SO deep-sea endemism, because the data are not yet worked up for Amphipoda.

Tanaidacea are represented by 25% of endemic species in the SO, but 29% of the deep-sea species are endemic (Guerrero-Kommritz 2005, personal communication).

Cumaceans show 95% endemism in the SO; 73 out of the 77 known species have only been sampled in the SO, but mainly on the shelf. From the deep sea (>1000 m), five of these species were described to date (Mühlenhardt-Siegel 2005, personal communication) and ANDEEP Cumacea will be worked up by Mühlenhardt-Siegel in due course.

Eighteen per cent of the 59 SO species of Mysidacea are known from the deep sea (Brandt *et al.* 1998).

(e) *Mollusca*

The SO deep-sea bivalves share 90% of their genera with the Antarctic shelf. The remaining 10% of genera are typical deep-sea genera and are, for example, found in the deep South African basins. Within the SO Atlantic sector (Weddell Sea, Scotia Sea), the collected bivalve fauna is homogenous; species and morphospecies different from the SO ones were found during ANDEEP III in the Cape and Aghulas Basins, indicating the existence of a barrier to dispersal between these basins. In the samples taken off Brabant Island (Bellingshausen Sea), two distinct morphotypes of two taxodont species were found that are very different from any other Antarctic taxodont. The species collected on the shelf near Brabant are the same as those commonly found on the Antarctic Peninsula and Weddell Sea. This might indicate that the deep-sea fauna of the Bellingshausen Sea is influenced by Pacific species.

Most of the bivalve species from the Antarctic deep sea are known to have lecithotrophic larvae. This means that their dispersal range is not as wide as in planktotrophic species, but currents can distribute lecithotrophic larvae to a considerable distance.

Most Antarctic deep-sea gastropod species are endemic to the deep sea, especially the brooding and directly developing species of the Buccinoidea, Naticidae and Turridae. Harasewych & Kantor (2004) discuss the high rate of endemism and high proportion of monotypic genera in the Antarctic and Magellanic deep waters.

(f) *Echinodermata*

Within the regular sea urchins 4 out of 16 deep-sea species are endemic, and in the irregular urchins it is 10 out of 20 deep-sea species. Lockart *et al.* (2003) mentioned the high proportion of brooding species in Antarctic irregular urchins.

(g) *Brachiopoda*

Nineteen species are known from the SO, of which 13 species can be found in the deep sea and five of these species are endemic.

(h) *Polychaeta*

Polychaetes, unlike other taxa, apparently have wide geographical ranges. Similarities were found with deep-sea fauna worldwide on the generic level and with adjacent basins at the species level. A few yet undescribed species are already known to occur in the Angola Basin: *Flabelligella* sp. 2DIVA (family Acrociridae); *Brada* sp. 1DIVA; *Pherusa* sp. 2DIVA (family Flabelligeridae); and *Unobranchus* sp. 1DIVA (family Trichobranchidae). Moreover, the abyssal polychaete fauna of the SO includes a number of new species belonging to genera that have not been reported from the area, but could be expected to occur there because their congeners have been reported at least once from the deep sea of the northern hemisphere, e.g. the ampharetids *Egamella* sp. 1, *Mugga* sp. 1, and *Muggoides* sp. 1 (family Ampharetidae). Other genera represented by new species in the abyssal SO are typical faunal elements on continental slopes worldwide, e.g. *Cossura* (family Cossuridae) and *Dysponetus* (family Chrysopetalidae). Noteworthy was the occurrence of two new species of the dorvilleid genus *Ophryotrocha*, as this genus is known to be abundant and speciose on continental slopes worldwide, but highly under-represented in deep waters of the SO (Hilbig 2004).

7. RELATIONSHIP OF SELECTED FAUNAL ASSEMBLAGES TO ENVIRONMENTAL VARIABLES

(a) *Large-scale patterns with depth*

(i) *Meiofauna*

Mikhalevich (2004) noted that wide bathymetric ranges are characteristic of Antarctic Foraminifera,

with some deep-water species emerging into the upper bathyal zone and onto the shelf. Bandy & Echols (1964) established a series of bathymetric zones based on the first appearance of foraminiferal species with depth. A number of species occurred from 200 m to more than 3000 m depth. Faunal boundaries based on Foraminifera have been recognized in the Antarctic by a number of other authors. For example, in the Scotia Sea, Echols (1971) found a rapid turnover among agglutinated Foraminifera at 1200–1300 and 2100–2300 m depth. Like those of Bandy & Echols (1964), however, some of Echol's (1971) species have bathymetric ranges extending from approximately 200 m to several thousands of metres. Murray (1991) distinguished a series of faunal associations in the Antarctic, each characterized by an abundant species and additional common species. Some of these associations span an enormous depth range, e.g. 164–3770 m (*Alabaminella weddellensis* association), 50–4008 m (*Cassidulina crassa* association), 0–2100 m (*Miliammina arenacea* association). Such studies suggest that while many species are confined to shelf depths, some extend across the shelf break into the bathyal or even abyssal deep sea. These patterns, however, are based almost entirely on morphospecies. Molecular data (SSU rRNA gene sequences) from a depth transect are available for only one species, the allogromiid *Bathyallogromia weddellensis*. Sequences were almost identical between 1080 and 6330 m water depth in the Weddell Sea, suggesting a substantial degree of genetic coherence between bathyal and abyssal populations.

For the metazoan meiofauna, most of the available information on bathymetric patterns relate to total densities. In samples from the continental shelf and slope from Kapp Norvegia (Vanhove *et al.* 1995*a*,*b*; Lee, unpublished data), Halley Bay (Herman & Dahms 1992), Vestkapp, Bransfield Strait and Drake Passage (Lee, unpublished), and from two depth transects on the Weddell Sea abyssal plain (Gutzmann *et al.* 2004), there was a clear drop in total densities around 500 m water depth (figure 3*a*). The meiobenthic densities shown in figure 3*a* are situated above the world ocean's regression line of meiobenthic stock against water depth (unpublished data based on Soltwedel 2000). In the Ross Sea, however, densities are two to seven times lower than in similar deep polar regions (Fabiano & Danovaro 1999).

Many taxa (e.g. Copepoda and Tardigrada) follow the same general pattern of decreasing densities with increasing water depth. However, there is no correlation between the depth and the abundance of the Loricifera and Tantulocarida, and there is only a positive correlation of low significance in the case of the Gastrotricha (Gutzmann *et al.* 2004). Absolute nematode densities either decrease with depth or exhibit no correlation (Vanhove *et al.* 1995*a*,*b*; Gutzmann *et al.* 2004).

In the South Sandwich Trench, Vanhove *et al.* (2004) found the same genera between 750 and 6300 m water depth. However, a shift in dominance enabled them to distinguish between a 'shallow' community (750–1100 m), characterized by *Dapto-nema*, *Dichromadora*, *Molgolaimus* and the families
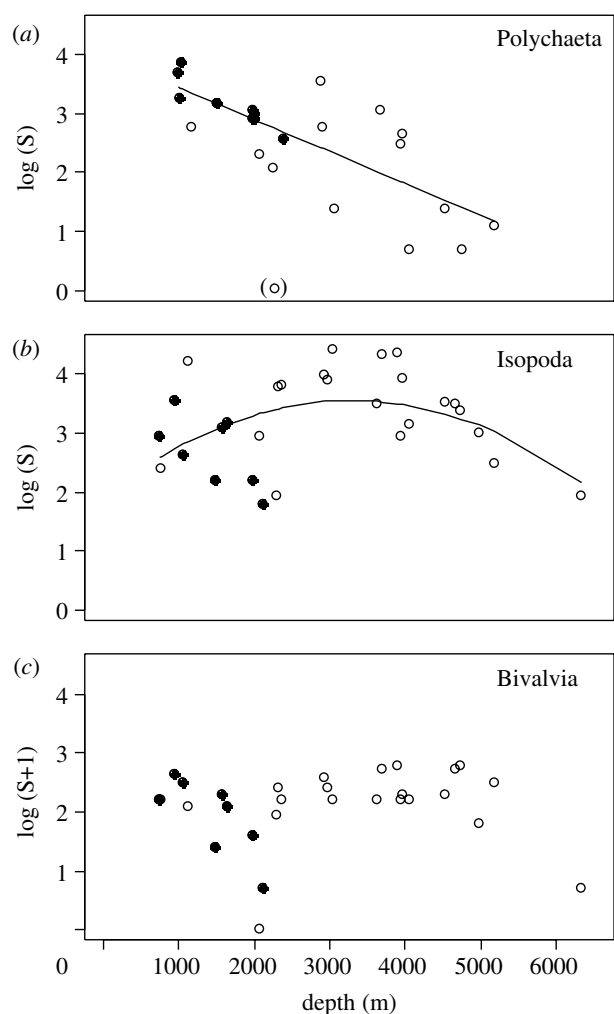

Figure 5. Number of species related to water depth (m). (*a*) Polychaeta, $y = 3.98 - 5.43 \times 10^{-5}x$, $R^2 = 0.59$; (*b*) Isopoda, $y = 1.93 + 9.87 \times 10^{-5}x - 1.50 \times 10^{-8}x^2$, $R^2 = 0.21$; and (*c*) Bivalvia, n.s. Solid circles, EASIZ cruises; open circles, ANDEEP cruises.

Comedomatidae, Cyatholaimidae and Desmodoridae, and a 'deep' community (4000–6300 m) characterized by the genus *Tricoma*. The intermediate stations (2000 and 3000 m) formed a transit between these two assemblages. Along a depth transect from the shelf to the slope at Kapp Norvegia and Halley Bay, there was a distinction between 'upper-slope', 'down-slope', 'Halley shelf', 'Kapp Norvegia shelf' and 'shelf-break' communities. Again, it was the relative abundance of genera, rather than their presence or absence, that defined these communities (Vanhove *et al.* 1995*a*,*b*). Finally, a number of typical deep-sea genera of copepods (*Pseudotachidius*; Veit-Köhler & Willen 1999) and nematodes (*Acantholaimus*; De Mesel *et al.* 2006) have been found in shelf communities, suggesting that the eurybathic distribution patterns reported for certain macrofauna (Arntz *et al.* 1994) and Foraminifera (see above) in the SO also apply to some metazoan meiofaunal taxa.

(ii) *Macrofauna and megafauna*

In very general terms, macro- and megafaunal organisms also show clear differences in patterns with increasing depth and between taxa (e.g. Carney 2005). Within Peracarida, for example, abundances and
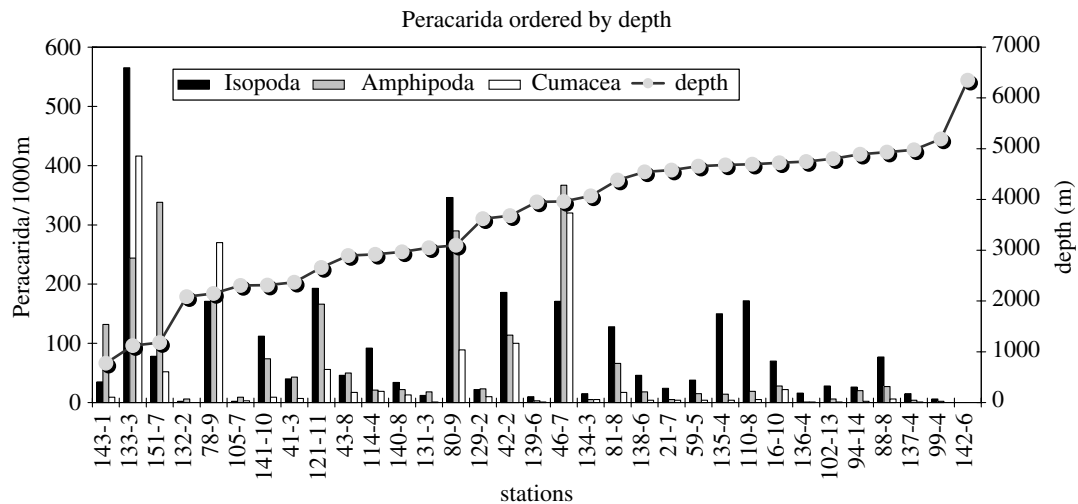
Peracarida ordered by depth

Figure 6. Most abundant Peracarida ordered by depth from ANDEEP I–III stations.

diversity are highest around 3000 m and Isopoda are more abundant deeper than other peracarid taxa (figures 5 and 6).

Kussakin (1973) reported for the Janiroidean asellote isopods, which dominate in the ANDEEP material, that a minor fraction (16%) would exist at shallow depths in boreal areas, whereas 46% occur in polar or deep-sea areas. An investigation of the vertical distribution of the Isopoda revealed that the Acanthaspidiidae were recorded at greatest depths down to 7210 m, followed by the Munnopsididae (6730 m) and the Ischnomesidae (6071 m; Brandt 1991), and some deep samples immediately increased the knowledge on the bathymetric range of taxa (Zimmermann & Brandt 1992).

The SO isopod shelf fauna differs in taxon composition from the SO deep sea. For example, 45 species of Munnopsididae are known from the SO shelf, in the deep-sea 118 species were observed; eight species of the Desmosomatidae are known from the shelf, 48 were found in the deep sea; and six species of Haploniscidae were sampled in the past (Brandt 1991) and until now 36 species could be discriminated (Brandt *et al.* 2004*a,b*). Emergence is likely for these taxa. On the contrary, the Acanthaspidiidae were known to occur with 20 species on the SO shelf, in the deep sea only five species could be discriminated until now. The Serolidae occur with at least 44 species on the SO shelf; however, during the deep-sea investigations only three species were sampled, and while 90 species of Valvifera (mainly Antarcturidae) are known from the shelf, ANDEEP discovered only six species in the area sampled (Brandt *et al.* 2004*a,b*). These findings support the theory that these taxa have evolved and radiated on the shelf and later submerged in the deep sea, where they occur only with a small number of species to date.

Down to approximately 1500 m, we still find a typical shelf fauna within the isopod crustaceans, being composed of higher numbers of Valvifera and Serolidae; on the contrary, the stations deeper than 2000 m are clearly characterized by the deep-sea asellote isopods, which comprise 98% of the Isopoda sampled. Therefore, we expect the change between the shelf/ slope and the true deep-sea fauna somewhere between 1500 and 2000 m depth.

While abundance of Isopoda is generally highest on the shelf around 1000 m (Brandt 2001), species richness increases with depth and is highest at approximately 3053 m depth in the northwestern Weddell Sea; for example, in 3053 m depth, 83 species were recorded (Brandt *et al.* 2004*a,b*; figure 5).

Contrary to the former knowledge of the scarcity of SO deep-sea Isopoda (Brandt 2000), recent expeditions have documented that the deep sea of the SO is characterized by a large number of isopod species. Prior to the ANDEEP cruises, 25 families of SO Isopoda were known, now 27 families are reported. Likewise, the number of known genera increased from 73 to 151 and the number of SO isopod species from 371 to 991 due to the recent ANDEEP investigations, although not many of the recently sampled, newly identified species are as yet described, and not all of them can be described, due to the scarcity of the material (almost approx. 50% of the species sampled at only a single location and often only with one specimen).

Brandt *et al.* (2005) reported that depth explains isopod species richness better than both latitude and longitude. Between 58 and 65° S, the number of species ranged from 9 to 82 (mean 36), while further south in the Weddell Sea, between 73 and 74° S, species richness was found to be lower and the number of species ranged from 6 to 35 (mean 19). When longitude was compared, the highest species richness (up to 82 species) was found between 50° and 60° W in the area of the South Shetland Islands and around the Antarctic Peninsula, whereas numbers did not exceed 50 species in the eastern Weddell Sea.

The Amphipoda collected in the Antarctic deep sea belong to 38 families (De Broyer & Jazdzewski 1993; Thurston 2001; Vader & Berge 2003; De Broyer *et al.* 2004, in press). In comparison, from all oceans, Thurston (2001) recorded 56 amphipod families with representatives occurring deeper than 1000 m. The families particularly well represented in the Antarctic deep sea are the various lysianassoid families, in particular Eurytheneidae, Lysianassidae (Tryphosinae), Scopelocheiridae and Uristidae, as well as Eusiridae, Ischyroceridae and Podoceridae.

The current understanding is that half of the 72 amphipod species occurring below 1000 m are in fact shelf species extending their distribution from a few tens of metres depth to the upper slope at a maximum depth of 1500–2000 m (in one case at 2894 m). Eighteen species (15 Antarctic endemics) are restricted to the bathyal zone (1000–3000 m) and 13 species (nine endemics) to the abyssal zone (>3000 m depth).

A number of scavenger species occurred on both the shelf and the slope, showing in some cases a quite extended level of bathymetry (figure 4*b*, updated from De Broyer *et al.* 2004). In the SO, *E. gryllus* is the only scavenger species found on the shelf, the slope and in the abyssal zone. It is known as a panoceanic bathyal, abyssal and hadal stenothermal species that can occur far above the seafloor (Thurston 1990). It has been found in both polar regions at bathyal and abyssal depths, as well as in bird stomachs (Stoddart & Lowry 2004). Concerning the two other widely eurybathic species (*Orchomenopsis cavimanus* and *Abyssorchomene scotianensis*), small morphological differences have been observed between their shelf and deep-sea populations, and a molecular analysis is required to detect potential cryptic species before confirming this very wide eurybathy.

Polychaetes show a very particular depth zonation, with a 'eurybathic' shelf community reaching down to over 2000 m (Hilbig 2004). Below approximately 1000–1500 m, the fauna becomes increasingly depauperate because there is no replacement of shelf species by a slope and rise community, a typical phenomenon seen on the continental slopes of temperate regions that results in the common diversity peak around 2000 m (Paterson & Lambshead 1995; Cosson-Saradin *et al.* 1998; Hilbig & Blake 2006). A shift to a true deep-sea community does not occur until approximately 2000–2500 m. This community, which is composed of genera considered typical for the deep sea worldwide, may extend down to abyssal plains.

The degree of eurybathy was not found to differ substantially between the deep SO and the other deep-sea areas (Hilbig *et al.* 2006). The wide geographical ranges suggest that polychaetes in the SO, in contrast to other invertebrates such as peracarid crustaceans, have larval stages for dispersal, even though only occasional catches have been made with plankton nets and the EBS. Possibly, they live in low densities within the nepheloid layer that cannot be sampled with either gear. The use of innovative technology may reveal the presence of polychaete larvae, which until now can only be deduced from distributional patterns.

Ellingsen *et al.* (submitted) examined general macrofaunal response to water depth (figure 5) using data on polychaetes, isopods and bivalves collected during the EASIZ and ANDEEP cruises, ranging from 774 to 6348 m water depth. They found that the isopods displayed higher species richness in the middle depth range and lower in the shallower and deeper parts of the area (Brandt *et al.* 2005), as reported for other deep-sea areas (e.g. Gage & Tyler 1991). However, interestingly, the number of polychaete species showed a negative relationship to depth, whereas the bivalves showed no clear relationship to depth (Ellingsen *et al.* submitted). Although the data

were collected over a huge geographical scale (58°14′–74°36′ S, 22°08′–60°44′ W), neither the number of isopod, polychaete nor bivalve species showed any clear relationship to latitude or longitude. However, sample (or small scale) species richness of all taxonomic groups was very variable, a finding that is typical for marine datasets (e.g. Clarke & Lidgard (2000): bryozoans; Ellingsen & Gray (2002): shelf macrobenthos).

According to Peno Cantero (2004), hydroid species show three distinct depth zones in vertical distribution, from the shallow to approximately 500 m, from approximately 500 to 1000 m, and species occurring deeper than 1000 m. Ninety per cent of bryozoans occur on the shelf at depths above 1000 m (Barnes & De Grave 2000); until now not a single cyclostome species was found in waters deeper than 1000 m. In the Bivalvia, samples collected down to 1500 m shared many species and morphospecies with the shelf, while samples from 2000 m and below represented a different species composition only known from the deep sea. In Gastropoda, the shelf to deep-sea break appears to be around 800–1000 m. Brachiopods were reported to shift from the shelf to the deep sea between 1000 and 1200 m in the SO (Forster 1974). Within the Echinoidea, DeRidder (2005, personal communication) found no clear distinction between shelf and deep-sea species, although the various families are known to have different depth preferences.

To summarize, based on the existing datasets from the deep SO, the spatial distribution of species varies between different taxonomic groups, and the impact of depth is not consistent among groups. However, it seems that a common limit at 1500–2000 m for shelf fauna appears in isopods, amphipods and part of the molluscs.

8. PATTERNS INFLUENCED BY OTHER ENVIRONMENTAL OR PHYSICAL FACTORS
(a) *Foraminifera*

On some parts of the Antarctic continental margin, carbonate dissolution leads to major changes in foraminiferal assemblages over relatively small distances. In the Ross Sea (Kennett 1968; Osterman & Kellogg 1979; Ward *et al.* 1987), the Weddell Sea (Anderson 1975) and off the Adelie-George V coast (Milam & Anderson 1981), continental shelf and slope assemblages are predominantly either calcareous or agglutinated. Deep, intrashelf basins are occupied by assemblages that are almost entirely agglutinated. Saidova's (1998) synthesis of foraminiferal distributions in the SO (552 stations covering the depth range 20–5500 m) supports the idea that carbonate dissolution strongly influences foraminiferal assemblage composition on the Antarctic margin. She recognized 40 associations ('communities'), of which 24 were dominated by agglutinated species and the remainder by calcareous species. Saidova concluded that distributions are controlled mainly by the bottom-water temperature and the degree of carbonate undersaturation. However, carbonate undersaturation does not always limit species distributions. Cornelius & Gooday (2004) report substantial numbers of certain

small calcareous species at depths >4000 m in the Weddell Sea, where the carbonate compensation depth (CCD) is located approximately at 4000 m (Mackensen *et al.* 1990). Both Anderson (1975) and Saidova (1998) considered the foraminiferal assemblages from this depth to be entirely agglutinated. The persistence of these opportunistic species below the CCD was attributed by Cornelius and Gooday (2004) to the availability of phytodetritus.

Other factors linked to the well-developed water mass architecture around the Antarctic continent influence foraminiferal species distributions in the SO (Mackensen *et al.* 1995; Mikhalevich 2004). In the eastern Weddell Sea, Mackensen *et al.* (1990) recognized five live assemblages on the shelf and the slope (237–4541 m). A *Trifarina angulosa* assemblage is associated with strong currents and sandy sediments around the shelf break and the upper slope. A *Nonionella iridea* assemblage is associated with high organic carbon fluxes in the outer-shelf, shelf-break and upper-slope area. A *Bulimina aculeata* assemblage is associated with lower current activity, warmer water (above 0°C) and higher organic carbon content on the upper slope. A *Cribrostomoides subglobosus* assemblage occurs from 2000 to 3000 m and at >4500 m depth, the upper limit coinciding with the upper boundary of Antarctic Bottom Water. Ishman & Domack (1994) also emphasize the role of water masses in controlling the distribution of two main foraminiferal assemblages on the western margin of the Antarctic Peninsula. The *B. aculeata* assemblage, although named after a calcareous species, is predominantly agglutinated, while the *Fursenkoina* spp. assemblage is predominantly calcareous. Ishman & Domack (1994) link the distribution of these assemblages to warm Circumpolar Deep Water (CDW; *B. aculeata* assemblage) and cold Weddell Sea Transitional Water (*Fursenkoina* spp. assemblage) rather than to the CCD or the organic carbon content of the sediment.

(b) *Metazoan meiofauna*

Sediment grain size and food availability are considered the most important factors influencing the distribution and community structure of metazoan meiofauna. This was well illustrated by Fabiano & Danovaro (1999), who found significantly higher meiofaunal densities, and a different higher taxon composition, in muddy sediments compared with coarser sands mixed with calcareous debris at 500 m water depth in the Ross Sea. The latter sediment type harboured much higher densities of copepods and nauplii. Ostracods and isopods were also associated with these coarser biogenic sediments, whereas kinorhynchs and loriciferans were present only in the muddy sediments. At each site, meiofaunal distributions were affected by different inputs of utilizable organic material originating from the photic layer. According to the same study, nematodes are the group most sensitive to changes in food availability, a conclusion confirmed by a later study at abyssal depths in the Weddell Sea (Gutzmann *et al.* 2004). Off Kapp Norvegica and in Haley Bay, the distribution of half the nematode genera was significantly correlated with granulometry and/or food (organic matter, CPE and ATP; Vanhove *et al.* 1999).

(c) *Isopoda*

Faunal differences in isopod composition reflect historical processes that influenced the evolution of the species as well as biotic (e.g. competition, coexistence) and abiotic parameters (depth, sediment grain size, salinity, temperature and ocean currents). In the SO deep sea, no clear pattern in isopod composition could be observed with geographical area. The Bransfield Strait, however, seems to be different in terms of lower abundances and values of species richness if compared with the deep Weddell Sea (Brandt 2004).

Rex *et al.* (1997) documented that the variability of large-scale biodiversity patterns depends on both bathymetry and latitude, a result which was also shown for SO deep-sea Isopoda (Brandt *et al.* 2005). Rex *et al.* (1997) found maximum species richness at mid-slope depth, while the species richness declined towards greater depth. However, considering the decreasing abundance with depth, this result might not be astonishing (Gage & Tyler 1991). Species richness of Isopoda was also observed to be generally higher below 1000–1500 m depth (Brandt 2004) and highest at 3053 m in the northeastern Weddell Sea; it then decreased with increasing depth (Brandt *et al.* 2005). This might result from higher food availability in deeper waters owing to deep-water production (Fahrbach *et al.* 1994). In very general terms, the shallower stations were more similar to each other and so were the deeper stations.

Differences between stations were probably not only owing to depth, but also to the nature of the substratum. Grain size of the sediment at different stations does not necessarily depend on depth, but also on the steepness of the slope (e.g. Howe *et al.* 2004). Depth was the most important environmental parameter being responsible for patterns followed by sediment composition and grain size in the Weddell Sea (Brandt *et al.* 2004a,b). Unfortunately, we do not know much about the behaviour and lifestyles of most janiroidean asellote isopods, making it difficult to correlate their distributions with environmental parameters (Hessler & Strömberg 1989).

9. SIMILARITIES AND DIFFERENCES BETWEEN THE ANTARCTIC AND OTHER DEEP-SEA SYSTEMS

(a) *The environment*

The deep SO is a subset of the deep world ocean (Clarke 2003). Above a depth of approximately 3000 m, all the main deep-sea regions are directly connected and thus there should, in theory, be no barrier to dispersal and the establishment of populations, both to and from the SO. Below 3000 m are the major ocean basins that reach depths of 5000–6000 m, requiring a degree of eurybathy in potentially colonizing species.

However, a greater effect on potential dispersal and thus endemism will come from the distribution of water masses in the world ocean. Not only will water masses determine geographical distribution, but also their flow will aid dispersal and may also affect zonation at bathyal depths along the deep ocean margin (Tyler & Zibrowius 1992).

The deep sea around Antarctica is contiguous and bathed in water that forms the Antarctic CDW mass, which circulates in a general west to east direction and may form an effective barrier between the SO deep sea and the rest of the world. A possible connection between the SO deep sea and the rest of the world is the Antarctic Bottom Water. This is a generic term for very dense cold waters formed especially in the Weddell Sea, but also in the other peripheral seas of Antarctica. This water sinks to the deepest seabed and is entrained in the lowest layer of the CDW. As it flows to the east, branches extend into the main oceans, although the extent of penetration varies, being limited by topographic features such as the Walvis Ridge in the Atlantic and the Southwest and Southeast Indian Ridges in the Indian Ocean. However, most of the great abyssal plains of the world ocean are bathed in North Atlantic Deep Water (NADW) formed in the Norwegian Sea and spread at abyssal depths throughout the world ocean (Mantyla & Reid 1983).

A third major variable to consider is the flux of surface production to the seabed. Surface production varies considerably through the surface waters of the ocean, and generally it appears that species diversity and benthic biomass are related to food availability at the seabed, as well as to other factors (Levin *et al.* 2001). One might predict that the generally high production in Antarctica would lead to a species diversity similar to the northeast Atlantic, but greater than the regions of the Pacific and Atlantic underlying surface oligotrophic gyres.

(b) *A direct comparison between the deep sea of the SO and the world ocean*

A comparison such as this is constrained by the sampling effort from different areas. Diversity is reasonably well known for the northeast and northwest Atlantic (Grassle & Maciolek 1992; Gage 1997), in the Central Pacific (Lambshead *et al.* 2002) and the central North Pacific (Hessler & Jumars 1974). Even in these cases, the diversity in detail is limited to specific taxonomic groups. The same applies to the SO, although the ANDEEP programme is possibly one of the most taxonomically comprehensive programmes in the deep sea.

Clarke (2003) summarizes the information on the SO megafauna and compares it with that of the world ocean, and notes that at the generic level there are many similarities. This applies particularly to the holothurians, ophiuroids, some echinoids and the pennatulids. Another similarity is that in all the world's ocean, biomass decreases with depth, although actual values may vary.

Specific diversity differences between the SO and the rest of the world are better known for some taxa. The higher Crustacea, particularly the Decapoda, were believed to be absent in the SO, being replaced by a rich pycnogonid and peracarid fauna. Recently, however, Thatje *et al.* (2005) reported 15 species of lithodid crabs in the SO and discussed the potential reasons for this distribution. The low species numbers of the Decapoda are regarded to be the prime reason for the success of the brooding peracarid crustaceans in the SO.

The high number of isopods in the deep SO is also typical for other deep-sea basins (Menzies 1962; Hessler & Thistle 1975; Gage & Tyler 1991; Hilbig 1994; Gage 1997; Kröncke 1998). In the European Northern Seas, Isopoda were found to dominate deep-sea peracarid composition in EBS samples as well (Brandt 1995, 1997; Brandt & Schnack 1999); however, in the northern areas, samples were characterized by lower isopod species richness but higher abundances (Brandt 2001). It is known that processes regulating species diversity differ at local, regional and global scales (Levin *et al.* 2001; Snelgrove & Smith 2002), and therefore it is difficult to compare data from different areas. A factor of prime importance for biodiversity of taxa in zoogeographic areas is the age of the environment (Gaston & Chown 1999) and the evolutionary time over which species have developed in that particular region (Webb & Gaston 2000). This may explain why we generally find high species richness in many taxonomic groups in the SO compared with northern polar areas (Gaston 2000).

A potential, but as yet, unquantified difference between the SO and the rest of the world ocean is the zonation from the edge of the shelf into deep water. In Antarctica, the deep shelf may contain eurybathic species thus giving rise to wide zones for individual species (Clarke 2003). Conversely, in the northeast Atlantic, the asteroid fauna shows narrow species zonation with depth, with the densest distribution being found over very limited vertical distances (Howell *et al.* 2002), but see the recent review of deep-sea zonation by Carney (2005). A strong zonation was also observed on the steep rocky surfaces in deep water to the west of Ireland, in which the zones were related to water mass structure (Tyler & Zibrowius 1992). The lack of definition in CDW in the SO may allow greater vertical dispersal of larvae and thus reduce constrained zonation.

(c) *Dispersal and recruitment between the SO and the rest of the world*

Most marine invertebrates disperse by means of a planktotrophic or lecithotrophic larva. The accepted paradigm is that planktotrophic development will have the widest dispersal, while lecithotrophy would have limited dispersal. This accepted theory was challenged by Shilling & Manahan (1994), who demonstrated that lecithotrophic larvae had a potentially significantly longer larval life in the plankton than planktotrophic species. Such a dispersal adaptation would be of great benefit for dispersal in the generally oligotrophic deep sea. However, relatively little is known of the reproduction in SO deep-sea species, when compared with the world ocean.

Peracarid crustaceans are brooders and juveniles leave the maternal brood pouch when they can feed themselves after several moults. This brooding biology might have an influence on the gene flow and thus the migration potential of the species, a potential reason why we find such a high degree of endemism, both on the shelf and in the deep sea. The SO deep-sea Peracarida document a high diversity including many rare and new species, and only a minor proportion of the species is known from other deep-sea basins. One might wonder how they find a partner to mate, as most

of the species are not very vagile; they are rather small and many were only found once on roughly 85 000 m² of seafloor covered with the EBS.

In contrast, within the Polychaeta, many more species seem to have crossed the barrier between the SO and adjacent oceans, and these have a much wider zoogeographic and also bathymetric distribution. Although we do not know the reasons for this phenomenon, we might suspect differences in the biology (Hilbig 2004). For example, brooding is, as far as we know, much less common among polychaetes, making larval dispersal via free-swimming trochophorae more common. In addition, polychaetes may exhibit a particularly high physiological flexibility in coping with large temperature and pressure changes. Data on reproductive stages of some polychaetes suggest that species limited to abyssal depths are reproducing there. Other species with broader depth ranges may be receiving recruits from slope depths (Blake & Narayanaswamy 2004; Hilbig 2004). As passive distribution via ocean currents is more likely for larvae than for benthic life forms, the source–sink hypothesis is more likely to apply to polychaete abundance and distribution than to that of the brooding peracarids (Pearce *et al.* 2001).

(d) The special case of chemosynthetically driven deep-sea systems

The discovery of hydrothermal vents in 1977, and the subsequent discovery of cold seeps in 1984, forced marine biologists to assess the energy available for primary production in the deep sea. In the intervening years, there has been a huge effort in determining, *inter alia*, the biogeography of these ecosystems (Van Dover *et al.* 2002; Tyler *et al.* 2003). However, to the south of the Polar Front, such ecosystems were unknown—although expected, as hydrothermal plumes had been detected at the Scotia Ridge (German *et al.* 2000)—until sediment-hosted vents and cold seeps were found in the Bransfield Strait (Klinkhammer *et al.* 2001), and the first Antarctic chemosynthetically hosting metazoan, a siboglinid tube-worm, was described from this area (Sahling *et al.* 2005). As many of the conditions for vent and seep ecosystems are found in Antarctica, it is only a matter of time before a large chemosynthetically driven ecosystem is found. The relationship between the species at such vents or seeps and their relationship with Atlantic or Pacific species will give an interesting guide to the dispersal of larvae of vent and seep organisms.

10. CONCLUSIONS

SO biodiversity is high, although the spatial distribution of species varies between different taxonomic groups, and the impact of depth is not consistent among groups. A common limit for shelf fauna appears at 1500–2000 m in isopods, amphipods and part of the molluscs, probably documenting the depression of the Antarctic continent due to the weight of the overlaying ice shield. This special physical characteristic of the Antarctic continental shelf combined with the isothermic water column might have led to the extended eurybathy documented for several taxa. This, as well as the fact that deep bathyal and abyssal sites can be fuelled with freshly produced organic matter

(phytoplankton, detritus and remains of ice algae) due to deep-water production, makes it unlikely that the source–sink hypothesis of Rex *et al.* (2005*a*) applies to SO abyssal benthic organisms. The high proportion of species new to science, the ongoing speciation of selected taxa (e.g. Haploniscidae, Isopoda), the high degree of endemism as well as the high number of rare species document the fragility of this pristine environment and serve as a sound basis for future conservation. Unlike deep-sea systems in the rest of the world oceans, exploitation of abyssal resources in the SO might result in significant levels of species extinctions because conspecific source populations do not exist on the adjacent continental margins. On the other hand, there is good evidence for strong faunal links among some taxa with other parts of the deep ocean. For example, abyssal foraminiferal assemblages in the deep Atlantic sector of the SO are remarkably similar to faunas occurring at equivalent depths in the North Atlantic.

Carbonate dissolution is an important environmental factor in some parts of the SO. The depth of the CCD is highly variable and sometimes very shallow, as witnessed by the almost entirely agglutinated foraminiferal assemblages that characterize intrashelf basins, such as the Crary Trough in the Weddell Sea. These unusual faunas provide a glimpse of how deep-water benthic communities might respond to acidification of the oceans caused by global climatic changes.

Differences between local and regional biodiversity are already apparent in selected groups, but must be investigated further before hypotheses regarding the taxonomic and ecological characteristics of the SO deep-sea fauna can be formulated and tested statistically. Nevertheless, our recent investigations have improved our knowledge of SO deep-sea biodiversity considerably. We hope the present review will be a springboard for future studies, which will provide a sound scientific basis for policies on environmental conservation. As human impact on deep-sea ecosystems increases, and concerns about the profound implications of climate change grow, the need for further surveys of the fragile and remote SO ecosystems has never been more urgent.

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