

Diversity and species distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean

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Abstract We examined deep-sea benthic data on polychaetes, isopods and bivalves from the Atlantic sector of the Southern Ocean. Samples were taken during the expeditions EASIZ II (1998), ANDEEP I and II (2002) (depth: 742–6,348 m). The range between sites varies from 3 to 1,900 km. Polychaetes (175 species in total) and isopods (383 species) had a high proportion of species restricted to one or two sites (72 and 70%, respectively). Bivalves (46 species) had a higher proportion of species represented at more sites. Beta diversity (Whittaker and Jaccard) was higher for polychaetes and isopods than for bivalves. The impact of depth on species richness was not consistent among groups; polychaetes showed a negative relationship to depth, isopods displayed highest richness in the middle depth range (2,000–4,000 m), whereas bivalves showed no clear relationship to depth. Species richness was

not related to latitude (58–74°S) or longitude (22–60°W) for any group.

Introduction

The idea that the deep-sea benthic fauna is rich in species was first documented by R. R. Hessler and H. L. Sanders during the 1960s (Hessler and Sanders 1967; Sanders and Hessler 1969). It has repeatedly been corroborated since (Snelgrove and Smith 2002). We have poor knowledge of how many species occur in the seas and how they are distributed, and the knowledge about the benthic species inhabiting deep waters is particularly limited (e.g. Gage and Tyler 1991; Clarke and Johnston 2003; Brandt et al. 2007). According to Grassle and Maciolek (1992), the world's deep-sea fauna might encompass as much as 10 million species of macrobenthos, although there is debate if the deep sea is hyperdiverse (e.g. Lamshead and Boucher 2003). A huge proportion of the species sampled during recent investigations in the deep sea is still new to science (e.g. Glover et al. 2002: 90%; Guerrero-Kommritz and Blazewicz-Paszkowycz 2004: 98%; see also Brandt et al. 2007), and only a small fraction of this habitat has been sampled as yet.

Most marine studies of species richness have been done at small scales, that of alpha diversity. In the deep sea a shift in the emphasis in biodiversity research to studies at both local and larger scales has become important in order to understand patterns of biodiversity at the global scale (Stuart et al. 2003; Gage 2004).

In common with most ecological data sets, many deep-sea species seem to be rare (e.g. Grassle and Maciolek 1992). Rare species can be regarded as those having low

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abundance or small range size (e.g. Brown 1984; Gaston 1994). Quantifying the spatial distribution of species in the deep sea is important for general community and macro-ecological theory that mostly have been based on terrestrial studies (e.g. Brown 1995; Gaston and Blackburn 1996).

Beta diversity or the extent of variation in community composition between sites (Whittaker 1960) is poorly studied in the deep sea (Paterson et al. 1998; Glover et al. 2002). Compared with the knowledge of alpha diversity, beta diversity has been far less studied in marine systems. Beta diversity can be quantified in many different ways (see Koleff et al. 2003; Magurran 2004 for recent overviews), but Whittaker's (1960, 1972) original measure has been one of the most frequently used measures (Koleff et al. 2003). Most studies of beta diversity have focused on a single taxon (e.g. bryozoans: Clarke and Lidgard 2000, polychaetes: Paterson et al. 1998, echinoderms: Price et al. 1999), yet patterns in beta diversity may be expected to vary among taxa (Harrison et al. 1992; Ellingsen and Gray 2002).

A number of studies suggest that species diversity peaks at depths around 2,000 m and then decreases (e.g. Gage and Tyler 1991). Diversity–depth trends have been attributed to a wide range of ecological influences like, for example, grain size heterogeneity (Etter and Grassle 1992) that vary with depth (e.g. Levin et al. 2001; Glover et al. 2002). Unimodal species diversity–depth patterns do not appear to be universal (Rex et al. 1997). Most likely, deep-sea patterns of diversity are controlled by a complex of biological and environmental factors operating at different scales of time and space (Levin et al. 2001; Snelgrove and Smith 2002; Stuart et al. 2003). Rex et al. (2005) suggest that bathyal and abyssal populations may form a source-sink system.

The sparseness of data from the southern hemisphere, particularly the deep Southern Ocean (SO), limits our understanding of deep-sea benthic biodiversity patterns at the global scale. Assessing biodiversity patterns of Antarctica has become increasingly important in the debate on the latitudinal gradient of increasing diversity from the poles to the equator (e.g. Gage 2004).

Although most of the SO is deep water the knowledge of the fauna of the continental slope and abyssal plain of Antarctica is poor (Clarke and Johnston 2003; Brandt et al. 2007). In recent years, the characterisation of benthos in the deep SO has received increased interest. Here, we use data from the EASIZ II expedition (Ecology of the Antarctic Sea-Ice Zone) in 1998 and the ANDEEP I and II expeditions (Antarctic benthic deep-sea biodiversity—colonisation history and recent community patterns) in 2002 in the Atlantic sector of the deep SO. Subsets of the data have previously been described separately for different taxonomic groups (Polychaeta: Hilbig 2001, 2004;

Isopoda: Brandt 2001; Brandt et al. 2004a; Bivalvia: Linse 2004). The objective of this paper is to synoptically compare patterns of polychaetes, isopods and bivalves from the deep SO and to examine specifically (1) the spatial distribution of species, (2) beta diversity or the extent of change of community composition between sites, and (3) the relationship between species richness and water depth, latitude and longitude.

Materials and methods

Study area and sampling

Polychaetes were collected from ten sites with a multi box-corer (Gerdes et al. 1992) during the EASIZ II (ANT XV-3) cruise of *RV Polarstern* from February to March 1998. At each site 4–7 cores, each sampling an area of 0.024 m², were collected. The first 3 cores were washed through a 0.3 mm sieve and the next 1–4 cores were washed through a 0.5 mm sieve. Samples were fixed in 4% buffered formalin in seawater, and later transferred to 70% ethanol (Hilbig 2001). Cores were pooled, thus adding up to 0.096–0.168 m² depending on the number of useable cores. The mesh size used to sieve the samples (0.3 or 0.5 mm) turned out to have no effect on the composition of the polychaetes (Hilbig 2001). This is somewhat atypical for deep-sea samples, which usually consist of mostly small individuals that are lost when the larger mesh size of 0.5 mm is used.

During the ANDEEP I and II (ANT XIX/3/4) expeditions from January to April 2002 polychaetes were collected from 14 additional sites with a 0.25 m² Sandia box-corer with the box divided into 25 10 × 10 cm² sub-cores. Here we used data from ten sub-cores pooled together (i.e. total area from one site: 0.1 m²). Samples were washed through a 0.3 mm sieve, fixed in 4% buffered formalin in seawater, and later transferred to 70% ethanol. Water depth at the 24 sites varied from 994 to 5,194 m (58°14'–74°39'S, 22°09'–60°43'W; Fig. 1, Table 1).

Isopods and bivalves were collected with an epibenthic sledge (Brenke 2005) during the expeditions EASIZ II and ANDEEP I and II of *RV Polarstern*. We used data from 29 sites between 742 and 6,348 m water depth; eight sites from the EASIZ cruise and 21 sites from the ANDEEP cruises (58°14'–74°36'S, 22°08'–60°44'W, see Fig. 1, Table 1). The datasets from these cruises were collected and processed by identical methods.

The epibenthic sledge carries two sampling boxes with an opening of 100 cm width and 33 cm height. A plankton net of 0.5 mm mesh size is attached to the epibenthic sampler (extending 27–60 cm above the seafloor) and to the suprabenthic sampler (100–133 cm above the bottom), and the mesh size for the cod ends is 0.3 mm (see Brandt

Fig. 1 Geographical position of the sampling sites in the Atlantic sector of the Southern Ocean

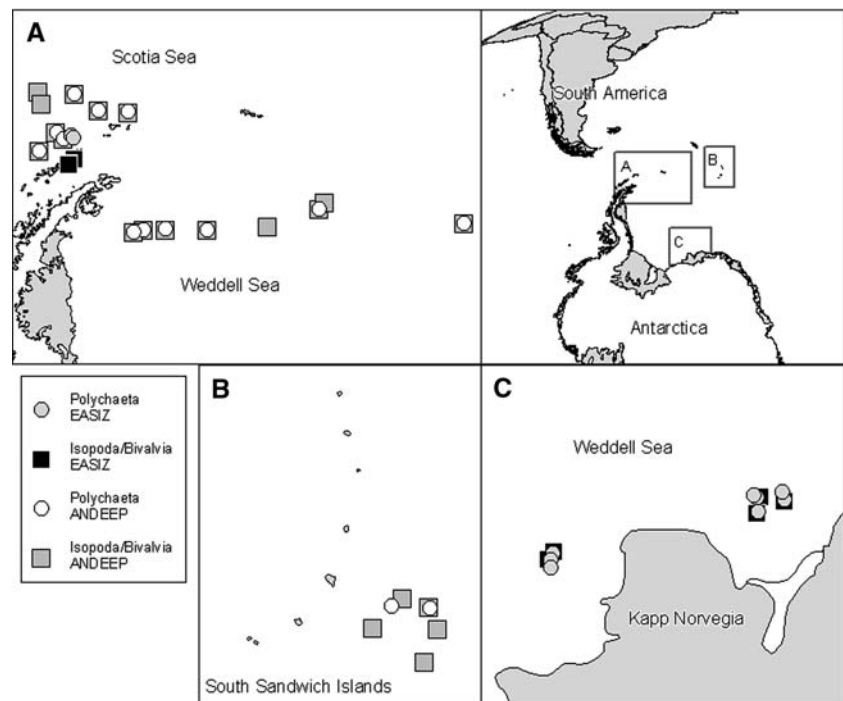


Table 1 Geographic position, water depth (m), number of individuals (N), species richness (S) given as gamma diversity and range of alpha diversity in parenthesis, number of uniques (U : species restricted to 1

site), number of uniques and duplicates (D : species restricted to two sites), given as total and range (in parenthesis)

Taxa	Number of sites	Latitude ($^{\circ}$ S) range	Longitude ($^{\circ}$ W) range	Depth (m) range	N	S	U	$U + D$
Polychaeta	24	58 $^{\circ}$ 14'–74 $^{\circ}$ 39'	22 $^{\circ}$ 09'–60 $^{\circ}$ 43'	994–5,194	1,106 (2–157)	175 (1–47)	88 (0–14)	126 (0–24)
Isopoda	29	58 $^{\circ}$ 14'–74 $^{\circ}$ 36'	22 $^{\circ}$ 08'–60 $^{\circ}$ 44'	742–6,348	7,762 (10–864)	383 (6–83)	177 (0–20)	269 (2–41)
Bivalvia	29	58 $^{\circ}$ 14'–74 $^{\circ}$ 36'	22 $^{\circ}$ 08'–60 $^{\circ}$ 44'	742–6,348	3,363 (0–521)	46 (0–15)	8 (0–2)	19 (0–4)

Polychaetes are from box-corer samples (EASIZ II in 1998: 10 sites; ANDEEP I and ANDEEP II in 2002: 14 sites), isopods and bivalves are from epibenthic sledge samples (EASIZ II in 1998: eight sites; ANDEEP I and ANDEEP II in 2002: 21 sites)

and Barthel 1995). The sledge was hauled over the ground for 10 min at a velocity of 1 knot (1,852 m/h). The calculated haul distances varied from 807 to 6,464 m (see Brandt et al. 2005b for details). Supra- and epibenthic sledge samples were pooled. On deck the samples were transferred into 96% ethanol.

Further details of sampling and analyses are given in Brandt (2001) (EASIZ II: Isopoda), Brandt et al. (2004a) (ANDEEP I and II: Isopoda), Hilbig (2001: EASIZ: Polychaeta, 2004: ANDEEP I and II: Polychaeta) and Linse (2004) (ANDEEP I and II: Bivalvia).

Statistical analyses

It is well known that comparative studies of diversity are problematic due to use of different sampling procedures, varied sampling effort, analyses at different spatial scales and use of different measures of biodiversity (e.g. Arntz

et al. 1997; Clarke 1992). We will therefore first examine patterns of biodiversity for each taxonomic group separately using the same measures of biodiversity, and then compare the results among the groups.

Unidentified species were only included in the analyses if they could not be mistaken for other identified species. We defined the number of species restricted to one single site as uniques, species occurring at two sites only as duplicates, species represented by one single individual as singletons and species represented by two individuals doubletons (cf. Colwell and Coddington 1994). Here, 'range size' is expressed as the number of sites at which a species occurred within the study area; i.e. we do not relate 'range size' to the entire geographical range of species (Gaston et al. 1997).

Here gamma diversity was measured as the total number of species in the entire study area. Alpha diversity was measured as species richness (S) or the number of species

in a sample. Although we have kept the analyses of sledge samples quite separate from box cores, species richness was log-transformed to facilitate a comparison of relative changes among the different taxonomic groups. There was no relationship between the number of polychaete species and the area sampled during the EASIZ II expedition ($\beta = 0.59$ [−9.927, 11.102], $n = 10$, $R^2 = 0.002$). Thus, we combined data on polychaetes from the EASIZ and ANDEEP expeditions in the further analyses.

Beta diversity or the extent of variation in community composition between sites (Koleff et al. 2003; Magurran 2004) was measured with Whittaker's (1960, 1972) original beta diversity measure, $\beta_W = (\gamma/\bar{\alpha}) - 1$, where γ is the total number of species recorded for the area or gamma diversity and $\bar{\alpha}$ is the average number of species per individual site or the average alpha diversity. Thus, it is the proportion by which a given area is richer in species than the average richness of samples within it. In addition, the total richness, the numbers of species shared and the Jaccard similarity (%) were calculated for all possible pairs of sites. The classical Jaccard similarity measure is one of the most widely used ecological measure of similarity (e.g. Chao et al. 2005). It gives the compositional similarity between two sites as $d_J = a/(a+b+c)$, where a is the number of species shared, b the number of species at site 1 that do not occur at site 2 and c is the number of species at site 2 that do not occur at site 1. Thus, it is the proportion of shared species out of the total number of species recorded at the two sites. A low number of shared species or a low-similarity denotes high beta diversity. The above coefficients are included in the ESTIMATES software (Colwell 2004).

For each taxonomic group we regressed sample species richness (S) on depth, depth², latitude and longitude, and selected the most parsimonious model based on Akaike's Information Criterion (AIC) using the step AIC function

implemented in the MASS library (Venables and Ripley 1998) of the R software (R Development Core Team 2004).

Results

The total number of polychaete species (or gamma diversity) observed in the box-corer samples from 24 sites was 175. Species richness at a site (or alpha diversity) ranged from 1 to 47 species (Table 1). Eighty-eight of these species (50%) were only found at one single site (i.e. uniques), 38 species (22%) were only found at two sites (i.e. duplicates), and 85% were only represented at less than four sites (Fig. 2). The number of uniques at a site ranged from 0 to 14 species, and the number of uniques plus duplicates at a site ranged from 0 to 24 (Table 1). The data on polychaetes comprised 1,106 individuals. Of the unique species, 68 (or 72%) were represented by only one individual (i.e. singletons) and seven (8%) by two individuals (i.e. doubletons). The most abundant polychaete species (*Paramphinoe australis*, 110 individuals) was represented at the highest number of sites (13 sites) (Table 2).

Gamma diversity of isopods observed in the epibenthic sledge samples from 29 sites was 383 species, and alpha diversity ranged from 6 to 83 species (Table 1). The isopods showed a similar distributional pattern as the polychaetes (Fig. 2). The uniques comprised 177 species (46%) and 92 species (24%) were duplicates. Eighty-two per cent of the species were only found at less than four sites. The number of uniques at a site ranged from 0 to 20 and the number of uniques plus duplicates ranged from 2 to 41 species (Table 1). The isopods were represented by 7,762 individuals. Of the unique species 63 (or 36%) were singletons and 35 species (20%) were doubletons. The two most widespread isopod species were represented at 16 sites (the 6th and the 18th most abundant species). The

Fig. 2 Distribution of species range sizes, given as the proportion of the total number of species of each taxonomic group. Range size is the number of samples where a species was observed out of a total of 24 sites for polychaetes and 29 sites for isopods and bivalves

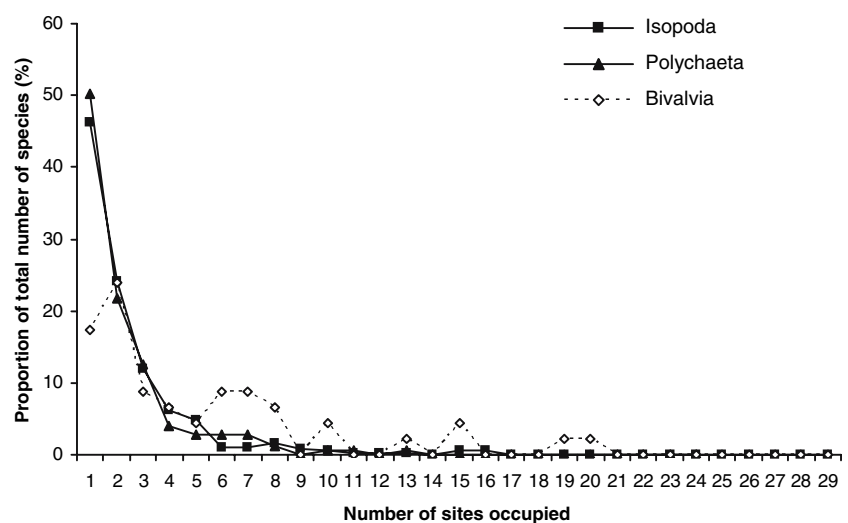


Table 2 Abundance and range size of the most dominant species of each taxonomic group across the whole data set

Taxonomic group	Species	N	Range size
Polychaeta	<i>Paramphinome australis</i>	110	13
	<i>Anobothrus sp. 1</i>	58	10
	<i>Chaetozone sp. 1</i>	43	7
	<i>Monticellina sp. 2</i>	42	6
	<i>Aricidea simplex</i>	41	4
Isopoda	<i>Betamorpha fusiformis</i>	538	15
	<i>Disconectes sp. 1 antarctica</i>	471	9
	<i>Leptanthura glacialis</i>	353	15
	<i>Paramunna cf. n. sp.</i>	306	3
	<i>Eurycope ‘‘comlanata’’ sp. 1</i>	278	12
Bivalvia	<i>Yoldiella cf. vallettei</i>	664	15
	<i>Genaxius cf. bongraini</i>	528	13
	<i>Kelliella sirenkoi</i>	475	20
	<i>Genaxius sp. n. 1</i>	470	19
	<i>Yoldiella cf. ecuadata</i>	233	10

most abundant species, *Betamorpha fusiformis*, which was found at 15 sites (Table 2), proved to be a cryptic species in the meantime (M. J. Raupach et al. submitted).

The number of bivalve species observed in the epibenthic sledge samples from 29 sites was 46, and alpha diversity was ranging from 0 to 15 species (Table 1). The bivalve fauna consisted of a higher proportion of species represented at more sites than the polychaetes and the isopods (Fig. 2). Only eight species (17%) were uniques, ranging from 0 to 2 at a site, and the proportion of species found at less than four sites (50%) was clearly lower than for polychaetes and isopods. The data on bivalves comprised 3,363 individuals. Of the eight uniques, four were singletons and one was a doubleton. The bivalve *Kelliella sirenkoi* was represented at the highest number of sites (20 sites) and was the third most abundant bivalve species (475 individuals). For all taxonomic groups the most abundant species were generally the most widespread (Table 2).

Whittaker’s beta diversity measure (β_w) was 9.6 for polychaetes, 10.9 for isopods and 4.5 for bivalves. The numbers of shared species in all pairwise combinations of sites were low for all three taxonomic groups if compared

to the total species richness between sites (Table 3). The average Jaccard similarity between all possible pairs of sites was low, ranging from $5.9 \pm 2.9\%$ for polychaetes, $6.2 \pm 3.6\%$ for isopods to $17.6 \pm 6.9\%$ for bivalves (Table 3). Thus, the extent of variation in community composition among sites (or beta diversity) was higher for polychaetes and isopods than for bivalves; i.e. highest for those groups with the highest proportion of restricted-range species (Fig. 2).

The number of polychaete species showed a negative relationship to water depth, the isopods displayed highest species richness in the middle depth range (2,000–4,000 m), whereas the bivalves showed no clear relationship to depth (Fig. 3, Table 4). Note that including the outlier marked with brackets in Fig. 3a (i.e. polychaetes) did not alter our results. Species richness was not related to latitude or longitude for any taxonomic group (Table 4).

Discussion

In the Antarctic the lack of thermal structure has been regarded to encourage colonisation into the deep sea from the adjacent shelf (e.g. Menzies et al. 1973; Brandt 1991, 2005; Brandt et al. 2007). Present day benthic species occurring on the isostatically depressed Antarctic continental shelf are discussed to be a product of a complex geologic history (Brandt 1991, 2000, 2005).

In the SO, the long geological and hydrographical isolation, cold climate and high but seasonal primary production may have encouraged the development of high endemism, gigantism and slow rates of individual growth on the Antarctic continental shelf (Lipps and Hickman 1982; Brandt 1991; Brandt et al. 2004b; Gage 2004). Brandt and Hilbig (2004) and Brandt et al. (2007) provide reviews of SO deep-sea biology, species richness, vertical distribution, assemblages, endemism and zoogeography. The Antarctic diversity pump has generated high rates of speciation and endemism not only on the continental shelf, but according to the above mentioned papers, it can be assumed also to operate in the contiguous deep-sea areas of the Scotia and Weddell Seas.

Table 3 Total species richness of all pairwise combinations of samples, number of species shared and the Jaccard similarity (%) between all combinations of samples, given as mean \pm C.I. and range (in parenthesis) for Polychaeta, Isopoda and Bivalvia

Taxa	Number of combinations	Total species richness	Shared species	Jaccard (%)
Polychaeta	276	31.0 ± 2.6 (3–75)	2.2 ± 0.3 (0–17)	5.9 ± 2.9 (0–29.4)
Isopoda	406	59.9 ± 4.0 (13–136)	4.2 ± 0.5 (0–30)	6.2 ± 3.6 (0–34.1)
Bivalvia	406	14.2 ± 0.6 (1–24)	2.5 ± 0.2 (0–8)	17.6 ± 6.9 (0–100)

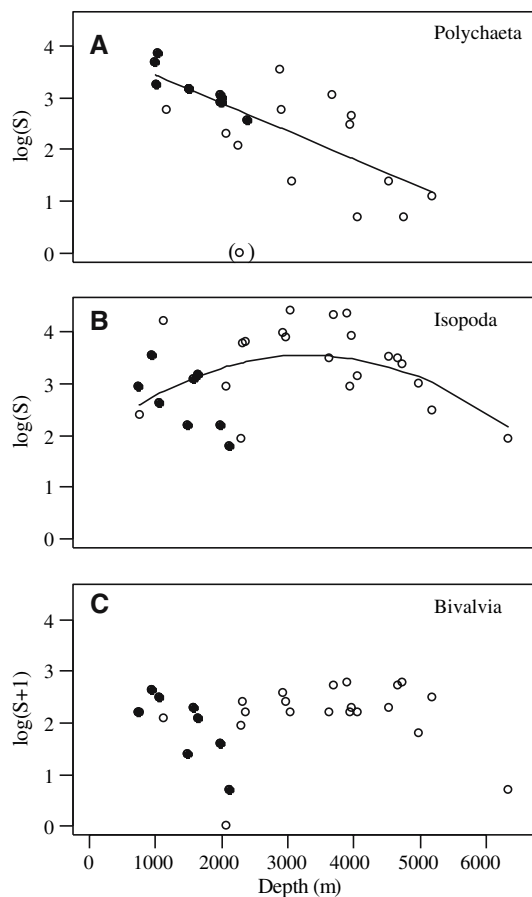


Fig. 3 Species richness (S) in a sample related to water depth (m). **a** Polychaeta, $y = 3.98 - 5.43 \times 10^{-5}x$, $R^2 = 0.59$; **b** Isopoda, $y = 1.93 + 9.87 \times 10^{-5}x - 1.50 \times 10^{-8}x^2$, $R^2 = 0.21$; and **c** Bivalvia, n.s. Solid circles EASIZ cruise; open circles ANDEEP cruises

Unlike the polar basins in the northern hemisphere the Antarctic deep sea is composed of four contiguous and confluent basins surrounding the Antarctic land mass (Clarke and Johnston 2003; Brandt et al. 2004b; Gage 2004). There is open confluence of the Antarctic deep sea with the three other major oceans to provide pathways for evolutionary radiation, which has been postulated and reported for the SO deep sea (Brandt et al. 2004b; Brökeland 2004; Gage 2004; Raupach et al. 2004). This contradicts the theory of Rex et al. (2006) that evolutionary opportunities for adaptive radiations in the bathyal zone (200–4,000 m) are more favourable than in the abyss (>4,000 m).

Our study revealed a very high proportion of unique and duplicate species of polychaetes and isopods (Fig. 2), and a high proportion of the uniques were only represented by one or two individuals. The isopods were collected in sample areas of 807–6,464 m² per site, adding up to more than 100,000 m² of study area (14,050 m² during EASIZ II and 88,363 m² during ANDEEP I and II). Likewise, in a study of peracarid crustaceans from the abyssal plain of the

Angola Basin, Brandt et al. (2005a) found that 49% of the species were restricted to only one site, although again a large area was sampled with the epibenthic sledge (>100,000 m²). Rex et al. (2005) suggest that rare species in deep-sea samples is the result of source-sink dynamics, in which many abyssal populations are maintained by immigration from the bathyal zone. One other possible explanation is that only very tiny samples of the regional diversity are taken into account. The area sampled with the epibenthic sledge is large, but if compared to the 34.8 million km² of SO seafloor (Clarke and Johnston 2003; Brandt 2005) the area sampled is small. The much lower regional diversity of bivalves if compared to the high-regional diversity of isopods and polychaetes (Clarke and Johnston 2003) also reflect the amount of singletons in the samples. Source-sink dynamics was postulated for molluscs (Rex et al. 2005), and it is unlikely for the brooding peracarids. Most probably the peracarids evolved in situ in the SO deep sea, as they were never sampled on the shelves and slopes (Brandt et al. 2007). Raupach et al. (2004) documented that asellote isopods have undergone impressive radiations in the SO deep sea and have colonised the deep sea several times.

In a study of polychaetes in the central Pacific abyss, Glover et al. (2002) found a substantial proportion of unique species, varying from 20 to 50% at a given site. Species with restricted range and/or low abundance also make up a considerable proportion of the total number of species in a given area in shallow water (Schlacher et al. 1998), on the continental shelf (Ellingsen and Gray 2002) as well as in terrestrial ecosystems (e.g. Gaston 1994). Rare species have a low probability of being recorded, and thus their characterisation and observed distribution is directly linked to sampling intensity (e.g. Brown 1984, 1995; Gaston 1994). The present paper includes data from only 29 sites (24 for polychaetes) distributed over a large geographical area, suggesting that a number of the ‘rare’ species most likely occur at more sites (see also Glover et al. 2002).

The finding that the most abundant species were widely spatially distributed (Table 2), whereas species of low abundance had strongly compressed range sizes holds for many different groups of species over a variety of habitat types and spatial scales and appears to be general (Brown 1984).

The high numbers of unique and duplicate species results in low numbers of shared species between sites as well as low levels of faunal similarities between sites (i.e. high beta diversity; Table 3). The problem of under-sampling also means that if sampling intensity increases, more ‘rare’ species are most likely found, and faunal similarity between sites will decrease.

Two different measures of beta diversity used in our study shows that beta diversity was higher for polychaetes

Table 4 Model selection based on Akaike's Information Criterion (AIC) for the analyses of the relation of polychaete ($n = 23$), isopod ($n = 29$) and bivalve ($n = 29$) species richness (S) to potential determinants (depth, latitude and longitude)

Dependent variable	Independent variables					k	AIC	Δ AIC
	Intercept	Depth	Depth ²	Latitude	Longitude			
Polychaeta: log(S)	x	x	x	x	x	5	-17.25	4.4
	x	x	x	x		4	-19.20	2.45
	x	x		x		3	-20.93	0.72
	x	x				2	-21.65	0.00
	x					1	2.43	24.08
Isopoda: log(S)	x	x	x	x	x	5	-14.35	2.5
	x	x	x	x		4	-16.14	0.71
	x	x	x			3	-16.85	0.00
	x	x				2	-12.19	4.66
	x					1	-14.01	2.84
Bivalvia: log(S + 1)	x	x	x	x	x	5	-18.07	5.41
	x	x	x	x		4	-20.07	3.41
	x	x	x			3	-20.90	2.58
	x	x				2	-21.56	1.92
	x					1	-23.48	0.00

The variables included in each model are marked with x. The selected model is in bold, (k) is the number of parameters in the model, and (Δ AIC) is the difference in AIC between the selected model and the given model

and isopods than for bivalves in the deep SO. There are, as yet, few studies that can be used as a comparison, and indeed we do not know enough about beta diversity in the sea to decide what is a high value and what is a low value. A comparison with terrestrial studies is complicated by the different spatial scales at which ecological processes take place (e.g. Levin 1992). Making comparisons of biodiversity patterns between different studies is complicated by differences in sampling equipment used as well as scale of sampling (Arntz et al. 1997; Clarke 1992). The scales describing alpha and gamma diversity vary among authors, and this also means that it is problematic to compare beta diversity among studies. As an example, in a terrestrial study in Britain, Harrison et al. (1992) used $50 \times 50 \text{ km}^2$ as their alpha scale, whereas in other studies this scale is more comparable to gamma diversity (see, e.g. Ellingsen and Gray 2002). In this investigation alpha diversity of polychaetes was described as 0.1 m^2 of the seabed sampled from one single site (or between 0.096 and 0.168 m^2 in the EASIZ dataset). The smallest scale examined for the isopods and bivalves was haul distances ranging from 807 to $6,464 \text{ m}$. In a study of North Atlantic bryozoans Clarke and Lidgard (2000) pooled data into bins of 10 degrees of latitude and found lower values of Whittaker's beta diversity measure (β_w) than what we report for the polychaetes (9.6) and isopods (10.9) in our study (58 – 74°S). Their β_w values were, for example, lower than 4 for the 50 – 60°N and 60 – 70°N bins. The low numbers of shared species and the low similarity values between sites for all

taxonomic groups suggests, however, that beta diversity in the deep SO is high.

Because different gear was used in this study, the datasets include organisms collected from the near-bottom water column (i.e., from about 1 – 2 m over the seabed), from the sediment surface and from within the sediment; some data are quantitative and some are qualitative. Despite the different sampling procedures and spatial scales, polychaetes and isopods displayed similar patterns in species distributions (Fig. 2) and similar values of beta diversity (Whittaker and Jaccard). These findings are interesting since most polychaete species show larval development and isopods are brooders. Conversely, bivalves, collected by identical methods and sampling intensity as isopods, displayed a different species distribution pattern and lower beta diversity than the 2 other taxonomic groups, despite being characterised by free-spawning larvae as well. These findings suggest that our results reflect real differences among groups. Mollusc biodiversity was also found to be very patchy in the SO in the extensive biogeographic analyses of Linse et al. (2006).

Our data revealed that sample species richness (or alpha diversity) of all taxonomic groups was very variable (Fig. 2), a finding that is typical for marine datasets (e.g., Clarke and Lidgard 2000: continental shelf bryozoans; Ellingsen and Gray 2002: continental shelf macrobenthos). When using the epibenthic sledge, the haul length of each sample should ideally be the same, but in the present study the haul lengths varied between 807 and $6,464 \text{ m}$. Analy-

sing almost the same dataset on isopods as in the present study, Brandt et al. (2005b) showed that haul length was positively related with depth, but there was no linear relationship between haul length and species richness. Thus haul length was not an important factor explaining patterns of isopod species richness.

As sedimentary characteristics have been suggested to be influential on diversity (e.g., Etter and Grassle 1992), data on polychaete species richness at stations sampled during ANDEEP I and II (Hilbig 2004) with sediment data derived from SPI photographs (Diaz 2004) were compared. No direct influence of sedimentary characteristics on the number of polychaete species present at any one site was found (Brigitte Ebbe unpublished, not included in this paper). According to Witman et al. (2004) patterns of local diversity in temperate, tropical and high latitude marine benthic communities are influenced by processes operating on larger spatiotemporal scales.

Across the study area, species richness was not related to latitude (ranging from 58 to 74°S) or longitude (22–60°W) for any taxonomic group. One possible explanation for the lack of a latitudinal gradient might be that the scale of the study area is too small. Large-scale trends in benthic diversity may be superimposed upon the variation at a limited geographic range of 10–20°, and only be evident over very large latitudinal spans. Thus, any underlying pattern may be disrupted by variation in diversity with, for example, longitude and depth (Gaston 2000). Over a broader spatial scale, the high species richness of isopods in the deep SO (gamma diversity in the present study was 383 species) is also typical for other deep-sea areas (see Brandt et al. 2007).

Our analyses showed that the isopods displayed highest species richness in the middle depth range (see also Brandt et al. 2005b), as reported for other deep-sea areas (e.g. Gage and Tyler 1991). The number of polychaetes showed a negative relationship to depth, and the bivalves showed no clear relationship to depth. In our study only 29 sites (24 for polychaetes) were visited and only a very small fraction of this deep-sea habitat has been sampled. The statistical power is thus limited. Based on these datasets our results show that taxonomic groups can differ in patterns of biodiversity (see also Ellingsen and Gray 2002; Ellingsen et al. 2005: continental shelf) suggesting to exercise caution in drawing broad conclusions.

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