Depth-related gradients in community structure and relatedness of bivalves and isopods in the Southern Ocean

Angelika Brandt1, Katrin Linse², Kari E. Ellingsen³, Paul J. Somerfield4

1 Zoological Museum, Centre of Natural History, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany, E-mail: abrandt@zoologie.uni-hamburg.de

² British Antarctic Survey, Natural Environmental Research Council, High Cross, Madlingley Road, Cambridge CB3 OET, U.K., E-mail: kl@bas.ac.uk

³ Norwegian Institute for Nature Research, Fram Centre, P.O. Box 6606 Langnes, 9296 Tromsø, Norway, E-mail: kari.ellingsen@nina.no

4 Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, U.K., E-mail: pjso@pml.ac.uk

**Abstract**

Despite increased research over the last decade, diversity patterns in Antarctic deep-sea benthic taxa and their driving forces are only marginally known. Depth-related patterns of diversity and distribution of isopods and bivalves collected in the Atlantic sector of the Southern Ocean are analysed. The data, sampled by epibenthic sledge at 40 deep-sea stations from the upper continental slope to the hadal zone (774 – 6348 m) over a wide area of the Southern Ocean, comprises 619 species of isopods and 81 species of bivalves. There were more species of isopods than bivalves in all samples, and species per station varied from 2 to 85 for isopods and from 0 to 18 for bivalves. Most species were rare, with 72% of isopod species restricted to one or two stations, and 45% of bivalves. Among less-rare species bivalves tended to have wider distributions than isopods. The species richness of isopods varied with depth, showing a weak unimodal curve with a peak at 2000 – 4000 m, while the richness of bivalves did not. Multivariate analyses indicate that there are two main assemblages in the Southern Ocean, one shallow and one deep. These overlap over a large depth-range (2000 – 4000 m). Comparing analyses based on the Sørensen resemblance measure and Γ+ (incorporating relatedness among species) indicates that rare species tend to have other closely related species within the same depth band. Analysis of relatedness among species indicates that the taxonomic variety of bivalves tends to decline at depth, whereas that of isopods is maintained. This, it is speculated, may indicate that the available energy at depth is insufficient to maintain a range of bivalve life-history strategies.

**Highlights**

* Species richness of isopods varied with depth, richness of bivalves did not
* Different shallow and deep communities overlap from 2000 to 4000 m
* There is no evidence of a specialised slope fauna of either isopods or bivalves
* Most species are rare, but each has closely-related species in the same depth range

**Keywords**

Deep ocean floor; Ecological distribution; Water depth; Isopods; Bivalves; Southern Ocean Weddell Sea

1. Introduction

Studies on the spatial patterns of diversity and distribution of species in the deep sea are as important for general community and macroecological theory as terrestrial studies (Brown, 1995; Gaston and Blackburn, 1996, 1997; Rex et al., 1997, 2005 a, b, Levin and Dayton 2009). On the background of increasing pressure based on future mining activities, it is important to study deep-sea benthos (Levin & Le Bris, 2015). High species richness in the benthic faunas of the deep sea was first described in the 1960s (Hessler and Sanders, 1967; Sanders and Hessler, 1969), and the importance of depth for species richness has been stressed in many publications, suggesting diversity peaks at depths around 3000 m (e.g. Etter and Grassle, 1992; Brandt et al., 2007 a, b; Ellingsen et al., 2007). However, patterns of deep-sea benthic diversity are complicated and diverse (Rex et al., 1997; Brandt et al., 2012; McClain et al., 2012; Brault et al., 2013) and differ between taxa (Ellingsen et al., 2007; see also Ellingsen et al., 2005 and Somerfield et al. 2009a for continental shelf macrobenthos).

Such studies are rare for the Southern Ocean (SO) deep sea (Ellingsen et al., 2007) where high species richness has been documented within many faunal groups (Brandt and Hilbig, 2004; Brandt and Ebbe, 2007, Brandt et al., 2007b, 2012) for the ANDEEP I and II expeditions (Antarctic benthic deep-sea biodiversity - colonization history and recent community patterns) based on 21 stations, about half of the deep-sea stations analysed here. From this area totals of more than 500 species of sponges, 750 species of molluscs, 1500 species of malacostracan crustaceans and 670 species of polychaetes, almost 500 species of tentaculates and many more in other groups were recorded, all with apparently complex biogeography (Brandt et al., 2012). Gutt et al. (2013a, b) presented a circumpolar overview of Antarctic macrobenthic communities and their spatial heterogeneity. De Broyer et al. (2014) summarized the current state of SO benthic biogeography, indicating gaps in biogeographic coverage.

We focus on two taxonomic groups, peracarid isopods and bivalves, which are common in deep-sea environments (Young, 2003) and which are the only invertebrate taxa which have been identified to species level from the 40 deep-sea stations analysed. Latitudinal gradients in bivalve and isopod species richness pattern have been described for the northern hemisphere (Rex et al., 1993) and for the SO deep sea (Ellingsen et al., 2007). These groups have been chosen as model taxa in studies on which ecological theory has been built (e.g. Brandt et al., 2005a, 2007a-c, 2009, 2012; Ellingsen et al., 2007; Linse, 2004, Rex et al., 1993; Rex and Etter, 2010) and because of their contrasting reproductive modes and life histories (Pearse et al., 2009). Deep-sea isopods are generally direct developers which brood their offspring in a marsupium until juvenile stages are released to feed by themselves. They do not have free-living larval stages. Species in this group live within (e.g. Macrostylidae and Ischnomesidae) or on sediments, as well as suprabenthically (Munnopsidae). In contrast, deep-sea bivalves are mostly infaunal and reproduce with lecitotrophic or planktotrophic larvae. An epibenthic habit or brooding of larvae is rare.

Isopod species richness is generally higher than that of bivalves (Brandt et al, 2007b, 2012). Patterns in species richness have been related to depth, latitude and longitude (Brandt et al., 2005a, Linse, 2004). Ellingsen et al. (2007) illustrated differences in diversity and spatial distribution of isopods and bivalves (and polychaetes) in the Atlantic sector of the deep SO using data from the ANDEEP I and II expeditions, as well as an earlier expedition (EASIZ II in 1998). The 19 stations sampled during the ANDEEP III expedition were not included in previous studies. Species richness was not related to latitude or longitude for isopods or bivalves, though highest species richness was reported in the area of the South Shetland Islands and around the Antarctic Peninsula. The relationship of species richness with depth was not consistent among taxa. While isopods displayed the highest richness at mid-depth ranges (2000–4000 m), bivalve richness showed no clear relationship with depth.

Although the drivers of variation in deep-sea biodiversity are undoubtedly multivariate (Rex and Etter, 2010; Tittensor et al., 2011; Brault et al., 2013), Witman et al. (2004) emphasized the importance of geologic processes (evolution of taxa), productivity, predation and the relationship between regional and local species diversity as drivers of abyssal species richness. While the focus of the majority of these studies is on species richness, this is known to be a problematic measure of diversity, especially because of the strong relationship between observed richness and sampling effort. This is likely to be especially the case in deep-sea studies, where samples are generally extremely small compared to the areas they are intended to represent, and widely scattered owing to the difficulties of quantitative work in the open ocean. Studies of differences (or variability) in species composition among sites (i.e., beta diversity, Whittaker, 1972; Koleff et al., 2003; Magurran, 2004) are also rare (e.g. Paterson et al., 1998; Glover et al., 2002).

This study builds on the findings of Ellingsen et al. (2007) by including additional data from the ANDEEP III expedition. Patterns in isopod and bivalve community structure and relatedness are contrasted. The analyses go beyond describing basic patterns in species richness by using methods appropriate for detecting patterns in species composition in both univariate and multivariate contexts and, in particular, to examine relationships between taxonomic composition and depth in the SO.

2. Material and methods

Model organisms used in this study are Isopoda (Crustacea, Peracarida) which brood their offspring in a brood pouch, the marsupium, and Bivalvia (Mollusca) which reproduce via planktotrophic or lecitothrophic larvae. The supplementary Table 1 illustrates the categories of the different modes of reproduction of Isopoda and Bivalvia as well as their life-styles (inbenthic, epibenthic, or suprabenthic occurrence).

2.1. Study area and sampling

The data used here are from 40 stations from between 774 and 6348 m water depth distributed over a wide geographic scale (Fig. 1) including the Bellingshausen Sea, Cape Basin, Drake Passage, Powell Basin, South Shetland Islands, South Sandwich Islands and the Weddell Sea. The stations were visited by the RV *Polarstern* during ANDEEP I and II in 2002, and ANDEEP III in 2005 (Brandt et al., 2007 a). For additional information see Supplementary Information in Brandt et al. (2007a at http://www.nature.com/nature/journal/v447/n7142/extref/nature05827-s1.pdf) and references therein.

Specimens of isopods and bivalves were collected with an epibenthic sledge (Brenke, 2005) that carries two sampling boxes, an epibenthic sampler (deployed 27 to 60 cm above the seafloor) and a suprabenthic sampler (deployed 100 to 133 cm above the bottom) with openings 100 cm wide and 33 cm high (Brandt and Barthel, 1995). A plankton net of 0.5 mm mesh size with a 0.3 mm cod end is attached to each box. Although the aim was to haul the sledge over the ground for 10 minutes at a velocity of 1 knot (1852 m.h-1), calculated haul distances varied from 711 to 6464 m (Table 1). Samples collected by both samplers at each station were pooled. On deck, the complete samples were immediately fixed in pre-cooled 96% ethanol and kept at least for 48 hours at -20°C. Specimens were sorted on board or later in the laboratory at the Zoological Museum of the University of Hamburg (working group of A. Brandt) or at the British Antarctic Survey (K. Linse) where the material is currently stored. All species of macrobenthic Isopoda and Bivalvia were determined. As the sledge was 1 m wide total numbers of individuals were converted to density (individuals.1000 m-2) by dividing by the haul length.

Sampling stations span a depth range from the upper continental slope (5 stations, 774-1584 m), through the bathyal (14 stations, 1984-3405 m) and abyssal (20 stations, 3640-5191 m) zones to the hadal zone (1 station, 6348 m). As the focus of this study is to examine relationships with depth the allocation of stations to predefined ecological zones with uneven coverage was not used. Instead stations were assigned to depth bands so as to give a more even sampling effort per band, namely a) < 2000 m, 7 stations; b) 2000-3000 m, 9 stations; c) 3000-4000 m, 9 stations; and d) > 4000 m, 15 stations.

2.2. Univariate measures of diversity and distribution of species

The number of species (S) of isopods and bivalves in each sample was determined. Species density (S\*) was calculated by dividing S by local density. Average taxonomic distinctness (Δ+) was calculated for isopods and bivalves in each sample. Average taxonomic distinctness is defined as: Δ+ = [ΣΣi<jωij]/[s(s - 1)/2], where s is the number of species present, the double summation is over {i = 1,…s; j = 1,…s, such that i<j}, and ωij is the ‘distinctness weight’ given to the path length linking species i and j in a hierarchical classification (Clarke and Warwick, 1998). This is a measure of the average relatedness of species in a sample, being the average distance between every pair of species. Here distances between species are defined using a taxonomic hierarchy, and the path length between species *i* and *j* is denoted by *ωij*, where the steps from species to genus, genus to family, etc. are regarded as equal. The maximum path length is set at 100. All species of isopods belong to one order, and bivalves belong to one class.

Unlike most measures of diversity, Δ+ is generally independent of sampling effort and associated variation in species richness, and requires only species lists (and a description of relationships among species) for its calculation (Clarke and Warwick, 1998; Warwick and Clarke, 2001). Clarke and Warwick (1998) devised a randomization test to compare the observed value of Δ+ against an ‘expected’ value derived from the master list of species from all samples (the species pool). The null expectation is that the species present at any one place or time behave like a random selection from the species pool or, in other words, every species in the pool has an equal probability to exist at all locations or times. Random sub-samples (typically 1000) of a fixed number of species drawn from the species pool are used to calculate the distribution of Δ+ values. If the procedure is repeated for differing numbers of species, the expected values can be plotted as a probability funnel, against which the observed Δ+ values from real samples may be plotted. Plotting a ‘significance level’ (formally a probability value) onto the funnel, normally at the 5% level, addresses the question of whether a sample has a ‘lower (or higher) than expected’ taxonomic spread (Clarke and Warwick, 1998). Somerfield et al. (2008) considered the hypothesis in more detail, arguing that because some species are common and tend to occur everywhere, while others are relatively rare and do not, an alternative null hypothesis is that the composition of assemblages in samples behaves as though species are assembled at random from the ‘master list’, but the probability of species occurring is dependent on their frequency of occurrence across all samples. To address this hypothesis, the simulation of random draws from the ‘master list’ is constrained to match the probabilities of occurrence of each species, as defined by their frequency of occurrence in the complete dataset. Thus, certain species are picked more often in the random subsets because they are observed more often (are more widespread) in real samples. This is the test implemented in this study.

We refer to species only found at a single station as 'uniques' and species found at only 2 stations 'duplicates' following the terminology of Colwell and Coddington (1994). The term ‘range size’ refers to the number of stations at which a species was found within the study area; i.e. we do not relate ‘range size’ to the entire geographical range of species (Gaston et al., 1997).

*2.3* Multivariate analyses

Measures of resemblance define the degree to which samples are similar (or dissimilar). Inter-sample resemblances were calculated using the Bray-Curtis coefficient (Bray and Curtis, 1957, Clarke et al., 2006), using presence-absence data (i.e. this is equivalent to the Sørensen coefficient, Clarke et al., 2014). As with most resemblance measures suitable for biological data, this uses information on species present in both samples, or species present in one sample and not the other, in order to define the resemblance between those samples. Shared absences are ignored. In situations where two samples share no species a resemblance between those samples cannot be defined with such measures, and where occurrences are sparse (as in this study) multivariate dispersion may be large, masking differences among groups of samples.

An alternative approach is to use a presence/ absence measure based on ‘taxonomic dissimilarity’, using the mean path length through the taxonomic hierarchy from a species in sample 1 to its nearest relation in sample 2. Instead of similarity between two samples coming only from taxa that match at the species level, contributions can now come from related species (e.g. a different species but in the same genus). Such a presence/absence based ‘beta-diversity’ coefficient was defined by Iszak and Price (2001), and considered in detail by Clarke et al. (2006). This is an extension of the ‘alpha-diversity’ index of taxonomic distinctness, Δ+ (Clarke and Warwick, 1998; Warwick and Clarke, 2001). As for Δ+ the path length between species *i* and *j* is denoted by *ωij*, where for a standard Linnean classification the steps from species to genus, genus to family, etc. are regarded as equal, and the largest path length (e.g. between species in different phyla) is fixed at 100. The path length *ωii* between identical species is defined to be zero. In a unified notation, taxonomic dissimilarity between sample 1 (species subscripts *i*) and sample 2 (species subscripts *j*) is then formally defined as:



where *s*1, *s*2 are the number of observed species in samples 1 and 2. In words, Γ+ (gamma+) is the mean of all path lengths between each species in one sample and its closest relation in the other sample. Clarke et al. (2006) show that Γ+ reduces exactly to the presence/absence form of the Bray-Curtis coefficient when the taxonomic hierarchy is completely flattened, so that all species are in (say) the same genus. The advantage of Γ+ is that two samples with no species in common, and thus with Bray-Curtis dissimilarity of 100%, can now take a range of dissimilarities <100. If two samples tend to have species in similar genera or families to each other their taxonomic dissimilarity is low, whilst if they do not share many evolutionary branches the dissimilarity will remain large.

Differences among groups of samples are visualized using non-metric multidimensional scaling (MDS) and tested using ANOSIM. The focus of this study is on differences in community composition and taxonomic dissimilarity among depth bands, inferred from sparse data collected from a wide geographical range and at different times. To avoid confounding apparent differences among depths with differences among geographical regions with different sampling effort, sampled on different occasions, we used 2-way crossed ANOSIM (Warwick et al., 1990) with depth and area as factors. This constrains the analysis to only consider differences among depth bands within areas, which are then averaged to infer global patterns across the dataset. While the analysis also outputs information about differences among areas (averaged over depth bands) the unevenness of sample coverage renders these analyses less useful, and as they do not contribute to the aims of this study they are not considered further here. Taxa contributing to resemblances within and among groups of samples were explored using 2-way SIMPER (Platell et al., 1998).

*2.4 Analytical software*

The majority of analyses were conducted using PRIMER v6 (Clarke and Gorley, 2006). The methods are described in detail in Clarke et al. (2014).

**3. Results**

*3.1. Species richness, distribution and life history traits*

Sampling effort, as determined by haul length, varied among stations (Table 1). Haul length increased with water depth (haul length = 7.70.depth0.74, R² = 0.57, Fig. 2A). At the same time there was a decrease in density (individuals.1000 m-²) of both isopods (density = 5.107.haul length-1.75, R² = 0.25) and bivalves (density = 5.106.haul length-1.55, R² = 0.34) with increasing haul length, with the number of bivalves recovered consistently less than the number of isopods (Fig. 2B). Species density (S\* = number of species.individual-1.1000 m2) was tightly and negatively coupled to densities of individuals for both isopods (S\* = 7.05.density-0.61, R² = 0.83) and bivalves (S\* = 5.54.density-0.85, R² = 0.81), with the number of bivalve species for a given density of individuals declining more rapidly with depth than that of isopods (Fig. 2C). Combining these relationships, with increasing depth (Fig. 2D) there was an increase in the number of species observed for a given density of individuals for both isopods (S\* = 3.10-5.depth1.24, R² = 0.29) and bivalves (S\* = 6.10-6.depth1.40, R² = 0.32). The effects of decreasing densities of individuals and increasing haul length with depth, and increasing numbers of species for a given density of individuals with depth, combined in such a way that there was no significant relationship between the number of species observed (S) and the sampling effort, as measured by haul length (R² < 0.01 for both isopods and bivalves). Thus, importantly, patterns in S (Fig. 2E) and the presence/absence structure of the data are not influenced by differences in sampling effort among stations. There was a weak relationship between the number of isopod species sampled and depth (S = -4.10-06.depth2 + 0.024.depth + 13.27, R² = 0.18) with a tendency for S to be highest at intermediate depths (3000-4000 m), whereas there was no apparent relationship between S and depth (R² <0.01) for bivalves.

A total of 619 isopod species were identified, ranging from 2 to 85 at any one station (Table 1). 316 species were only found at one station (termed “uniques”), and 132 species were found at only two stations (termed “duplicates”), so 72% of the isopod species were only found at one or two stations (Table 2). The number of unique isopod species found at a given station varied from 0 to 29. Some isopod species were relatively widespread. *Betamorpha fusiformis* (family Munnopsidae) was recorded from 29 stations, while *Eurycope* sp. 1 "complanata" (family Munnopsidae) was found at 22 stations. Variability among the stations was high, and species richness at 2 stations from intermediate depths in the South Shetland area (105-7, 152-6) was lower than expected.

81 bivalve species were identified, with 0 to 18 species per station (Table 1). The highest number of species were recorded in samples from >4500 m. At station 132-2, in the Weddell Sea, no bivalves were sampled at all, and at 2 other stations from intermediate depths (121-11 from the Weddell Sea, and 152-6 in the South Shetland area) richness was very low (Fig. 2). Only 17 bivalve species were uniques, and 22 duplicates (Table 2), making up 45% of all bivalve species. The number of unique species found at a given station varied from 0 to 5. The most widespread bivalve species (*Vesicomya* sp. 1; family Vesicomyidae) was recorded from 30 stations, and the second most widespread (*Axinulus* sp. 1; family Thyasiridae) from 29. Thus, bivalves had fewer restricted-range species and more widespread species than isopods.

All isopod species identified were brooders (Fig. 3A), and inbenthic, epibenthic and suprabenthic species occurred (Fig. 3B). Most identified bivalve species reproduce via larvae, though some species are also brooders (Fig. 3C). Most bivalve species live inbenthically (infaunally), however, few also occur epibenthically (Fig. 3D).

At the deepest station (139-6), in the South Sandwich Trench at 6348 m, only epibenthic isopods occurred, and only 1 inbenthic bivalve species was recorded. At the majority of stations, most isopod species were epibenthic, and inbenthic species occurred less frequently, although at some stations from the Weddell Sea and South Sandwich Islands areas (80-9, 42-2, 114-4, 133-3, 141-10, 143-1) more species were suprabenthic. Among bivalves, epibenthic species occurred infrequently, and at several stations (99-4, 105-7,137-4, 142-6, 143-1) only inbenthic species were recorded.

*3.2. Average* taxonomic distinctness

There was a weak positive relationship between Δ+ and S for isopods (Δ+ = 40.S0.03, R2 = 0.17) but not for bivalves, and a weak declining trend in Δ+ with increasing depth for bivalves (Δ+ = -0.001.depth + 71.1, R2 = 0.11) but not for isopods. Average taxonomic distinctness (Δ+) of isopods and bivalves at the majority of stations was consistent with a hypothesis of random assembly from the regional species pool, as most samples lie within the permuted 95% probability limits (Fig. 4). Where samples fall outside expected limits they fall below the funnel, indicating assemblages of species more closely related to each other. The majority of stations with more closely related isopod assemblages were from intermediate depths (ca. 2000-3000m) and those with more closely related bivalve assemblages were from the deepest zone (>4000m).

*3.3.* Multivariate analyses

Differences among depth bands in isopod assemblage composition, defined by the Sørensen coefficient (Fig. 5A), were significant (Table 3). Pairwise ANOSIM tests indicate that the main differences in composition were between shallower stations (<3000m) and those in the deepest band (>4000 m), and that assemblages from stations in intermediate bands (2000-3000 m and 3000-4000 m) do not differ. Differences in isopod composition defined by Γ+ (Fig. 5B) were greater (higher ANOSIM R values), allowing the null hypothesis of no differences among depth bands to be rejected with greater confidence (lower p values), and the overall pattern among pairwise results (Table 3) is one of significant differences among assemblages in different bands, with the exception of those from intermediate depths (2000-4000 m). Note that although the pairwise test for differences between samples from >2000 m and those from 3000-4000 m failed to achieve significance at p<0.05 despite having comparable R values (Table 3), these tests had limited power (only 36 possible permutations).

Differences among depth bands in bivalve assemblage composition, defined by the Sørensen coefficient (Fig. 5C), were significant but less so than for isopods (Table 3) and the only significant pairwise test was between samples in the shallowest band (<2000 m) and the deepest (>4000 m). Again, differences in bivalve composition defined by Γ+ (Fig. 5D) were greater and more significant. The overall pattern is similar to that derived from the isopods, namely one of differences between samples from shallower bands and deeper ones with no differences among samples from 2000 m to 4000 m. One important difference, however, is the lack of a significant difference between samples in the deeper bands (>3000 m) for bivalves.

Given the lack of statistical support for differences in community composition between samples from 2000-3000 m and 3000-4000 m these samples were combined for the SIMPER analysis (Table 4). A high similarity indicates many species in common between samples, and therefore a low turnover of species. For this reason dissimilarity (100-similarity) is sometimes used to indicate beta diversity within groups of samples. Among isopod samples the average Sørensen similarity within depth bands was generally low compared to that of bivalves, indicating higher beta diversity at all depths. The results presented focus on taxa contributing up to 25 % of similarity within, or dissimilarity between, samples from different depth bands. Even with this focus the majority of contributing isopod species are infrequent, occurring in less than 50 % (a frequency of 0.5) of samples in any band. None occurs in all samples (frequency = 1) in any band. Even so, there are clear differences in community composition, with different taxa contributing to similarities within different depth bands. Species of isopod with the highest contributions to similarity among samples from < 2000 m tend to be rare or absent from deeper bands, while those characterising samples from > 2000 m tend to occur with varying frequency over a wide range of depths, with the exception of *Dubinectes nodosus* which characterises samples from > 4000 m. Of species contributing to dissimilarities among depth bands, many are rare (with low frequencies of occurrence). Of those contributing up to 25 % of dissimilarities between samples from < 2000 m and 2000-4000 m the majority (20/30) are more frequent at intermediate depths. Similarly, of those contributing to dissimilarities between samples from 2000-4000 m and from > 4000 m the majority (26/37) are more frequent at intermediate depths. In contrast, frequencies of occurrence of bivalve species contributing up to 25 % of similarities/dissimilarities are generally higher, fewer species contribute, and the overall patterns appears to be one of a more even gradient in species composition.

**4. Discussion**

*4.1. Antarctic shelf and other deep-sea areas*

The SO is characterized by an almost isothermal water column and an isostatically depressed Antarctic continental shelf facilitating species’ submergence and emergence processes (e.g. Brandt, 1991; 2007a-c; Brown et al., 2011 and references therein), possibly leading to high species richness at intermediate depths. The long geological and hydrographical isolation of the SO, the development of its cold climate combined with high but seasonal primary production might have encouraged the development of high species richness and adaptive radiations of some taxa, and a complex biogeography, as well as high endemism of some taxa on the Antarctic continental shelf (Brandt et al., 2012, Kaiser et al., 2014; De Broyer et al., 2014 and references therein).

The vast majority of benthic sampling in the SO has been on the Antarctic shelf and upper slopes (Griffiths et al., 2011), therefore, studies on macrofaunal diversity and assemblage composition are often restricted to the shelf or upper continental slope (e.g. Gutt et al., 2013 a, b; Griffiths et al., 2014; Schiaparelli et al., 2006, 2014). The three ANDEEP expeditions have increased our knowledge on the SO deep-water fauna, and especially the macrofauna, immensely (Brandt et al., 2005a, 2009; Ellingsen et al., 2007; Kaiser et al., 2007). However, during other expeditions, e.g. the Spanish BENTART and UK BIOPEARL (BIOdiversity dynamics: Phylogeography, Evolution And Radiation of Life) (Troncoso and Aldea 2008, Linse 2004), occasional deep-water samples below 1000 m have also been taken. Based on the species-area relationship, sampling intensity in different studies might play an important role for diversity patterns which we cannot exclude.

On the Antarctic shelf (Arntz et al., 1994; Brandt, 1991), the number of isopod species (> 300 species) is lower than in the deep sea, where 674 isopod species are reported (Brandt et al., 2007a-c), other brooding peracarid taxa, like Tanaidacea and Amphipoda, in contrast, decrease in species richness with increasing depth (De Broyer et al. 2014 and references therein). Isopod composition of the SO shows most biogeographic links to the fauna of the South Atlantic, like the Southern Polar Front, where 107 species were identified (Meyer-Löbbecke et al., 2014), and the abyssal Angola Basin (Brandt et al., 2005b) where 100 species were found, followed by the North Atlantic (Brandt et al., 2004). In the North Atlantic, the composition of Isopoda has been studied north of Iceland at the Kolbeinsey Ridge (33 species) as well as off East Greenland (52 species), by means of the same type of EBS (Brandt, 1993, 1995, Brandt et al., 1996; Piepenburg et al., 1997). At shallower stations in the Beagle Channel, Patagonia, 25 species of Isopoda were reported (Brandt et al., 1997a, b)).

The composition of the bivalve fauna in the SO in general shows high similarities with the bivalve faunas reported from deep-sea areas in the Atlantic and Pacific (Hain 1990). Over the last decades, the studies on SO molluscs included faunistic descriptions of molluscan assemblages, from different Antarctic regions (e.g. Cattanneo-Vietti et al., 2000; Arnaud et al., 2001; Schiaparelli et al., 2006, 2014; Troncoso et al., 2007; Troncoso and Aldea, 2008). Fewer studies have focused on bivalve composition in deeper water or from continental slope to deep-sea basins. Linse (2004) described the deep-water bivalves of the Scotia Arc, their composition, distribution and relationships to the Antarctic shelf fauna and summarized earlier work on Antarctic bivalves. Aldea et al. (2008) investigated bathymetric zonation (45 to 3304 m) of bivalves in West Antarctica and reported eighteen species from bathyal depth, which comprise those also collected in this study. Schiaparelli et al. (2006) studied the diversity of molluscs in the Ross Sea off Victoria Land and the Balleny Islands between 25 m and 1389 m depth, and identified 37 bivalve species. Fourteen of the species were collected at stations deeper than 600 m, resembling the shallowest depth zone analysed in this study. Individuals of these 14 species collected in the Ross Sea also occur at the shallowest (< 2000 m) stations of this study. To date, no bivalve records from the deeper continental slope (> 1500m) or abyssal exist from the Ross Sea.

*4.2. Life history traits*

As isopods brood their offspring in a brood pouch (marsupium) they are likely to have a reduced gene flow (e.g. Raupach et al., 2007) compared with bivalves, and this might explain the correlation of species richness with densities within this taxon. Species with differing lifestyles were found at different stations in our study, although no significant pattern of distribution of suprabenthic, epibenthic or inbenthic species could be observed. At any one station numbers of inbenthic species such as Macrostylidae or Leptanthuridae were generally lower than numbers of epibenthic and/or suprabenthic species such as Desmosomatidae and, especially, Munnopsidae (Fig. 3).

Most deep-water bivalves identified live inbenthically, such as protobranchs and most heterodonts and anomalodesmatans. Within the pteriomorphs, some species of *Limopsis*, *Adacnarca* and pectinoids have an epibenthic life style. All of these are present in the SO deep-sea samples and can easily disperse via currents through lecitotrophic or planktotrophic larval stages (Fig. 3) possibly explaining that species richness in bivalves does not depend on densities. Representatives from only four genera, the philobryid *Adacnarca*, the mytilid *Dacrydium*, the limid *Limatula* (*Antarctolima*) and the montacutid *Mysella*, however, are known for brooding their young. Therefore, larval development of the majority of bivalve species might explain their much wider biogeographic distribution than that of isopods and the independence of species richness from densities. The Thyasiridae, the largest lamellibranch family, have planktotrophic larvae (Payne and Allen, 1991). It is therefore assumed that the majority of abyssal bivalve species have dispersing larvae (Brault et al., 2013). Allen (2008) reported that protobranchs have lecithotrophic larvae that disperse demersally. This taxon typically dominates at abyssal depths (Zardus, 2002). Recent modeling results on dispersal in the Atlantic deep-sea protobranchs predicted maximal dispersal ranges from 237 km to 749 km (McClain et al., 2012). Dispersal capabilities in deep-sea bivalves can also be enhanced by hermaphroditism as shown in *Yoldiella* by Reed et al. (2014). Pearse et al. (2009) posed the question whether SO species diversity can be explained through selection for brooders or rather speciation within brooding clades. These authors discuss three different scenarios which might account for the unusually high number of benthic marine invertebrate species in the SO. They found little or no evidence that non-pelagic development would be a direct adaptation to conditions in the Southern Ocean, however, concluded that the powerful Antarctic Circumpolar Current passing through Drake Passage for over 30 million years could have transported species with non-pelagic development to new habitats in the SO where they diversified and displayed adaptive radiations in some families. This could explain the higher species numbers of isopods compared with bivalves.””

Energy investment into individual eggs increase with increasing latitude leads to lowered fecundity (Laptikhovsky, 2006). Larger eggs require more time to complete the non-feeding phase of development than smaller eggs, increasing the risk of embryonic or larval mortality while being in the plankton (Marshall and Bolton, 2007). With lower fecundity and increased risk of mortality, there could be strong selection for non-pelagic development, eliminating mortality in the plankton altogether.

Pearse et al. (2009) also discussed that speciation could be enhanced in brooding taxa when refuges formed on the Antarctic continental shelf during Pliocene-Pleistocene glacial maxima, fragmenting populations into small isolated units which could have undergone speciation. If these formed repeatedly during the glacial-interglacial cycles, a “species diversity pump” could have been created and explain high numbers of local species as well as the presence of many closely related cryptic species around the Antarctic continent (e.g. Held, 2000), mainly at shelf and slope depths.

However, pattern and modes of larval development and dispersal of other major macrofaunal molluscan taxa in deep-sea for example, the Gastropoda are much better known than those of Bivalvia (Rex et al., 2005a, b). However, Gastropoda are only worked up to species level from half of the SO deep-sea stations (from ANDEEP I-II). They account for 84 benthic species and also show no clear relationship between SO deep-sea gastropod density and species richness with depth (Schwabe et al., 2007).

Differences in the life histories of these taxa might also explain that isopods had the highest proportion of rare (restricted-range) species (uniques and duplicates), and the planktotrophic species of bivalves had a wider spatial distribution than those of brooding isopods (Table 2). However, isopods with swimming capabilities (Munnopsidae) have wider distribution ranges and occur in higher densities than epi- and especially inbenthically living isopod species.

*4.3 Southern Ocean deep sea*

Influences of depth, latitude and longitude on SO deep-sea isopod and bivalve species richness are previously described for 21 stations by Brandt et al. (2005a, 2009; Ellingsen et al., 2007). Numbers of isopod species at the ANDEEP I-III stations (i.e., the 40 stations used in this study) confirmed a weak relationship with depth and were characterized by an unimodal peak at 3000-4000 m (Brandt et al., 2012). Brandt et al. (2009) reported SO isopod species richness to be highest around 3000 m with 241 species, and with 146–241 species between 3000 and 4000 m. This high species richness at bathyal and upper abyssal depths lies at depths where the seafloor area is largest (Griffiths et al., 2014) increasing niche availability in terms of space and possibly selecting for dietary specializations (Würzberg et al., 2011 a, b). Geomorphology is most variable at bathyal slope stations (De Broyer et al., 2014 and references therein) possibly providing a wealth of ecological niches as well as a higher potential for deposition of organic matter and thereby enhancing species richness. At bathyal depths Munnopsidae is the most speciose isopod family followed by Desmosomatidae, Haploniscidae, Ischnomesidae, Antarcturidae, and Serolidae. At the deepest stations in the South Shetland and South Sandwich Trenches only epibenthic and suprabenthic isopods occurred being dominated by Munnopsidae, while only one inbenthic bivalve species is reported. This could be explained by the limited amount of organic matter reaching lower abyssal and hadal depths (Jamieson, 2015), where inbenthic filter feeders might suffer from starvation, whereas munnopsid isopods might actively search for their preferred food sources. While our study shows no relationship of bivalves to depth, Brandt et al. (2009) reported highest numbers of species (80) on the shelf and upper slope to about 1200 m with the most frequent families Yoldiidae, Thyasiridae, Cuspidariidae, and Limidae. Despite the paucity of SO deep-sea samples, we may hypothesize that environmental setting (such as topography, geomorphology, water-mass and sediment characteristics, input of particulate organic carbon (POC)) as well as evolutionary factors (e.g. glaciological history) drive slope distinctness and eurybathy (Brey et al., 1996). These factors have shaped the evolution of the SO slope faunas and might have led to the pattern of distribution and assemblages described herein.

At the shallower stations < 2000 m most characteristic isopods explaining similarity occurr inbenthically (*Leptanthura glacialis*), epibenthically (*Austroniscus* sp. 6) or were able to swim (*Disconectes* sp. 2) and the inbenthic bivalve species (*Yoldiella valettei*). At intermediate depths (2000-4000 m) only munnopsid species characterized the similarity of Isopoda (*Eurycope* “*complanata*” Bonnier, 1896, *Eurycope* sp. 3, *Ilyarachna antarctica* Vanhöffen, 1914, *Munneurycope* cf. *nodifrons*, *Storthyngurella triplispinosa* (Menzies, 1962), and *Betamorpha fusiformis* (Barnard, 1920). At this depth band the bivalve species *Axinulus* sp. 1 and *Vesicomya* sp. were most characteristic. At the deepest and most isolated stations > 4000 m (South Sandwich and South Shetland trenches), only Isopoda contributed to Sørensen similarity, the munnopsid isopods *Betamorpha fusiformis* and *Dubinectes nodosus* (Menzies, 1962) besides the epibenthic desmosomatid species *Disparella maiuscula* Kaiser & Brix, 2005. However, the presence of cryptic species within some widely distributed isopod species which cannot be discerned morphologically (e.g. Raupach and Wägele, 2006, Raupach et al., 2007; Brökeland and Raupach, 2008), could tamper our results regarding species richness, distribution and taxonomic distinctness.

The difficulties associated with estimating and comparing species richness from sampling data are well known (Colwell et al. 2012), with species richness tending to increase non-linearly with the number of individuals identified, the number of samples collected or the area sampled. As a result observed richness tends to be a downwardly biased estimate of true richness (however that may be defined). Methods intended to adjust for differences in sampling effort, for example by calculating ratios of species per individual or species per unit of sampling effort, may seriously distort richness values and should never be relied upon (Chazdon et al. 1999). While methods that are based on an explicit statistical sampling model (and we could here include the widely used ES(n) measure of richness) may provide a resolution for many applications (Gotelli and Colwell 2011) the assumptions underlying each model may be questionable. For a number of reasons, such as the requirement to deploy a length of wire 1.5 × water depth and the effects of sea state on the ship, the intended standardised intensity of sampling of a haul of 10 minutes at 1 knot was not achieved at the stations sampled. Instead tow length increased with depth. While potentially this could render information on the numbers of species captured unreliable, there was a consistent decline in densities of individuals captured, and in increase in the number of species captured for a given density of individuals, with increasing haul length (and therefore with depth). Putting these different relationships together there was no apparent relationship between sampling effort (haul length) and the numbers of species captured and we conclude, therefore, that patterns in the numbers of species, and therefore the presence/absence structure of the dataset analysed in this study, are robust.

One of the motivations for this study was to compare patterns in diversity and community composition of isopods, which tend to brood their young, and bivalves, largely do not, with a view to teasing out the influence of such trait differences on observed distributions and the relative importance of different factors in determining those patterns. While there was no apparent relationship between bivalve species richness and depth, S for isopods showed a weak relationship, a unimodal curve with highest numbers at intermediate depths (2000-4000 m) as previously described in a range of papers based on some of the data analysed here (Brandt et al. 2005a, 2009, 2012; Ellingsen et al., 2007). As mentioned in the introduction, such a relationship with depth has widely been reported for many different taxa (e.g. Rex, 1973, 1981; Etter and Grassle, 1992; Brandt et al., 2007 a, b; Ellingsen et al., 2007), and the factors driving such patterns have been the focus of many studies (see Carney, 2005; McClain and Etter, 2005). Similarly, density declines exponentially with depth for both isopods and bivalves, reflecting patterns reported for a variety of taxa elsewhere in the deep sea (Rex et al. 1997; Carney, 2005; McClain 2014). The relationship between local density (or abundance) and the number of species is not commonly reported in deep-sea studies. Here, the number of species for a given density of individuals increases with depth for both isopods and bivalves. This potentially drives much of the observed pattern in species numbers at larger scales, and is worthy of further investigation. Overall, however, it is remarkable that although isopods are always richer in species the underlying relationships of declining density with depth, or species density with density of individuals, and increasing species density with depth, are all so similar (Fig. 2) implying some commonality in cause. Thus we may conclude that although there may be more species of isopods as a possible result of brooding leading to reduction in gene-flow (Raupach et al, 2007) or a greater diversity of life-history traits, or possibly because bivalves tend to be larger or more restricted in their ability to specialize in life-history or diet, the general patterns of occurrence of both isopods and bivalves are probably driven by the same factors associated with depth discussed widely in the deep-sea literature, such as food availability, food quality, and possibly differences in physiology (Carney, 2005).

Although the data analysed here are extremely sparse, with the majority of species only found at one or two stations (Table 2), there is enough information for a meaningful analysis of changes in species composition with depth based on the presence/absence of species. For both isopods and bivalves the overall pattern is one of significant difference among depth bands, especially between the shallowest (< 2000 m) and the deepest (> 4000 m), with no difference between groups of samples from intermediate depth bands (2000 – 4000 m). This supports the view that there is not a unique fauna on the Antarctic slope (Kaiser et al. 2011). The same analysis conducted using Γ+ instead of the Sørensen coefficient shows an increase in R for the majority of tests. The two coefficients are closely related, and if all species were in the same genus they would be the same (Clarke et al., 2006). The differences between the two sets of results, therefore, are attributable to the influence of relationships among taxa on the calculation of Γ+. As ANOSIM R is a scaled measure of the separation of groups, calculated from the rank resemblances within and among groups, higher values indicate that samples within depth bands are more similar, and samples in different groups are less similar. It appears, therefore, that although the majority of both isopod and bivalve species are rare, each tends to have one or more closely-related species within the same depth band, but not in different depth bands. This suggests that a focus purely on numbers of taxa misses important information about how different those taxa are from each other, which may turn out to be highly relevant in terms of understanding the ecological, functional or evolutionary consequences of observed variation in composition.

Similarly, the alpha measure of relatedness (Δ+) provides a useful contrast to species richness. The two measures are not structurally related (Clarke and Warwick, 1998; Clarke et al., 2014), so any observed relationships are interpretable. There is only a weak positive relationship between isopod Δ+ and S, implying that rare species tend to be closely related to less rare species, with no relationship to depth. In contrast, there is no relationship between Δ+ and S for bivalves, but a weak tendency for Δ+ to decline with depth, indicating that in shallower waters the species that are found tend to be more closely related than in deeper waters. The multivariate analyses suggest that there are different communities of both isopods and bivalves in shallow (< 2000 m) and deep (> 4000 m) waters, with a great deal of overlap in between them at intermediate depths. If these two assemblages contain many closely related species, for example different species but in the same genus in the deep assemblage and the shallow, then a decrease in Δ+ at intermediate depths might be expected, and we might conclude that the increase in S observed for isopods at intermediate depths reflects this overlap. In fact there is a tendency for assemblages of isopods from some stations at intermediate depths to have low Δ+, supporting this view, but for bivalves the only stations with lower than expected Δ+ are from > 4000 m, indicating a slight loss in taxonomic variety with increasing depth. In general, however, the assemblages observed at the majority of stations are entirely consistent with a hypothesis of random assembly from the regional species pool (Somerfield et al., 2009), with no evidence of taxonomic (or ecological/functional, Somerfield et al., 2008) specializations associated with life at different depths. It appears, therefore, that while most species are rare, they tend to fall into a limited number of higher taxonomic categories across the whole of the vast sampled SO domain, suggesting a limited range of viable ecological or functional strategies for each body plan.

*5. Conclusions*

The analyses presented here are based on data with a robust presence/absence structure, not confounded by differences in sampling effort. Both isopods and bivalves showed significant differences in species composition, primarily driven by differences between a shallower assemblage and a deep one, with much overlap between 2000 and 4000 m. Richness of isopods varied with depth, in part reflecting the overlap between the shallow and deep assemblages, whereas it did not for bivalves. In contrast, bivalves tended to have reduced taxonomic variety at depth, probably reflecting a reduction in viable life-history strategies with decreased energy availability. Although most species had restricted distributions, with 72% of the isopod species and 45 % of bivalve species restricted to one or two stations, there was a tendency for each species to have other closely-related species elsewhere within the same depth band. Isopods were more speciose, but bivalves generally had a wider distribution than isopods. We suggest that this might in part be a function of the dispersal capability of larvae and adults.

**Contributors**

AB designed and realized the ANDEEP expeditions, AB and KL identified the material, PJS performed the statistical analyses, all contributed to the writing process.

**Acknowledgements**

Financial support for the ANDEEP expeditions was provided by the German Science Foundation. KEE acknowledges the support of the Research Council of Norway and PJS acknowledges support from the UK Natural Environment Research Council. We are grateful to Saskia Brix, Stefanie Kaiser, Wiebke Brökeland, Madhumita Choudhury and Marina Malyutina for help in sorting and identification of isopods. This is ANDEEP publication # 200.

**References**

Aldea, C., Olabarria, C., Troncoso, J.S., 2008. Bathymetric zonation and diversity gradient of gastropods and bivalves in West Antarctica from the South Shetland Islands to the Bellingshausen Sea. Deep-Sea Res. II 55, 350–368.

Allen, J.A., 2008. Bivalvia of the deep Atlantic. Malacologia 50, 57-173.

Arnaud, P.M., Troncoso, J.S., Ramos, A., 2001. Species diversity and assemblage of macrobenthic Mollusca from the South Shetland Islands and Bransfield Strait (Antarctica). Pol. Biol. 24, 105-112. Arntz, W.E., Brey, T., Gallardo, V.A., 1994. Antarctic zoobenthos. Oceanogr. Mar. Biol. Annu. Rev. 32, 241–304.

Arntz, W.E., Brey, T. & V.A. Gallardo 1994. Antarctic zoobenthos. Oceanography and Marine Biology: an Annual Review, 32, 241-304.

Brandt, A., 1991. Zur Besiedlungsgeschichte des antarktischen Schelfes am Beispiel der Isopoda (Crustacea, Malacostraca). Ber. Polarforsch. 98, 1-240.

Brandt, A., 1993. Composition, abundance and diversity of peracarid crustaceans on a transect of the Kolbeinsey-Ridge, north of Iceland. Polar Biol. 13, 565–576.

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

Brandt, A., 1997a. Abundance, diversity, and community patterns of epi- and benthic-boundary layer Crustacea Peracarida at 75°N of East Greenland. Polar Biol. 17, 159–174.

Brandt, A., 1997b. Suprabenthic Peracarida (Crustacea, Malacostraca) sampled at 75°N off East Greenland. Polar Biol. 17, 462–464.

Brandt, A., Barthel, D., 1995. An improved supra- and epibenthic sledge for catching Peracarida (Crustacea, Malacostraca). Ophelia 43, 15–23Brandt, A., Hilbig, B., 2004. ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) - a tribute to Howard L. Sanders. Deep-Sea Res. II, 51, 1457-1919.

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

Brandt, A., Ellingsen, K.E., Brix, S., Brökeland, W., Malyutina, M., 2005a. Southern Ocean deep-sea isopod species richness (Crustacea, Malacostraca): influences of depth, latitude and longitude. Polar Biol. 28,284-289.

Brandt, A., Brenke, N., Andres, H.-G., Brix, S., Guerrero-Kommritz, J., Mühlenhardt-Siegel, U., Wägele, J.-W., 2005b. Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola basin. Org. Divers. Evol. 5, 105–112.

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

Brandt, A., Gooday, A.J., Brix, S.B. et al., 2007a. The Southern Ocean deep sea: first insights into biodiversity and biogeography. Nature 447, 307-311.

Brandt, A., DeBroyer, C., DeMesel, I., Ellingsen, K., Gooday, A., Hilbig, B., Linse, K., Thomson, M.R.A., Tyler, P., 2007b. The biodiversity of the deep Southern Ocean benthos. Philos.Trans.R.Soc. Biol.Sci. 362, 39–66.

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

Brandt, A., Linse, K., Schüller M., 2009. Bathymetric distribution patterns of Southern Ocean macrofaunal taxa: Bivalvia, Gastropoda, Isopoda and Polychaeta. Deep-Sea Res. I 56, 2013-2025.

Brandt, A., De Broyer, C., Ebbe, B., Ellingsen, K.E., Gooday, A.J., Janussen, D., Kaiser, S., Linse, K., Schüller, M., Thomson, M.R.A., Tyler, P.A., Vanreusel, A.,2012. Southern Ocean deep benthic biodiversity. In: Antarctic Ecosystems: An Extreme Environment in a Changing World, First Edition. Edited by Alex D. Rogers, Nadine M. Johnston, Eugene J. Murphy and Andrew Clarke. Blackwell Publishing Ltd., pp. 291-334.

Brandt, A., Vassilenko, S., Piepenburg, D., Thurston, M., 1996. The species composition of the peracarid fauna (Crustacea, Malacostraca) of the Northeast Water Polynya (Greenland). Medd. Groenl. Biosci. 44, 1–30.

Brenke, N., 2005. An epibenthic sledge for operations on marine soft bottom and bedrock. Mar. Technol. Soc. J. 39, 10-20.

Brault, S., Stuart, C.T., Wagstaff, M.C., McClain, C.R., Allen, J.A., Rex, M.A., 2013. Contrasting patterns of α- and β- diversity in deep-sea bivalves of the eastern and western north Atlantic. Deep-Sea Res. II 92, 157-164.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs, 27, 325–349.

Brey, T., Dahm, C., Gorny, M., Klages, M., Stiller, M., Arntz, W.E. 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? Ant. Sci. 8 (1), 3-6.

Brökeland, W., Raupach, M.J. 2008. A species complex within the isopod genus Haploniscus (Crustacea: Malacostraca: Peracarida) from the Southern Ocean deep sea: a morphological and molecular approach. *Zool. J. Linnean Soc.* 152, 655–706.

Brown, J.H., 1995. Macroecology. The University of Chicago Press, London

Brown, B., Gaina, C., Müller, R.D., 2011. Circum-Antarctic palaeobathymetry: Illustrated examples from Cenozoic to recent times. Palaeogeo. Palaeoclimat., Palaeoecol. 231, 158–168.

Carney, R.S. 2005. Zonation of deep biota on continental margins. Oceanography and Marine Biology - An Annual Review 43, 211-278.

Cattaneo-Vietti, R. Chiantore, M., Schiaparelli, S. Albertelli, G., 2000. Shallow- and deep-water mollusc distribution at Terra Nova Bay (Ross Sea, Antarctica). Polar Biol. 23, 173–182.Clarke, A., 1992. Is there a latitudinal diversity cline in the sea? Trends Ecol. Evol. 7, 286-287.

Chazdon, R.L., Colwell, R.K., Denslow, J.S. 1999. Tropical tree richness and resource-based niches. Science 285:1459.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219.

Clarke, K.R., Gorley R.N., 2006 PRIMER v5 (& v6): User manual/tutorial, PRIMER-E, Plymouth UK, 192pp

Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a ‘biological effects’ study. Mar. Ecol. Prog. Ser. 46, 213–226.

Clarke, K.R., Somerfield, P.J., Chapman, M.G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. J. Experim. Mar. Biol. Ecol. 330, 55-80.

Clarke KR, Gorley RN, Somerfield PJ, Warwick, RM (2014) Change in marine communities: an approach to statistical analysis and interpretation, 3rd edn. PRIMER-E, Plymouth. 256 pp.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35, 523–531.

Clarke, K.R., Warwick, R.M., 2001. Change in marine communities, an approach to statistical analysis and interpretation*,* 2nd ed*.* Plymouth: PRIMER-E Ltd, 172 pp.

Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Trans. Royal Soc. London B 345, 101–118.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L., Longino, J.T. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5: 3-21. doi: 10.1093/jpe/rtr044

Connolly, S.R., MacNeil, M.A., Caley, M.J., Knowlton, N., Cripps, E., Hisano, M., Thibaut, L.M., Bhattacharya, B.D.*,* Benedetti-Cecchi, L., Brainard, R.E., Brandt, A., Bulleri, F., Ellingsen, K.E., Kaiser, S., Kröncke, I., Linse, K., Maggi, E., O’Hara, T.D., Plaisance, L., Poore, G.C.B, Sarkar, S.K., Satpathy, K.K.,Schückel, U., Williams, A., Wilson, R.S., 2014. Commonness and rarity in the marine biosphere. Proc. Nat. Ac. Sci. 111, 8524-8529.

De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d’Acoz C. d’, Van de Putte A.P., Danis B., David B., Grant S., Gutt J., Held C., Hosie G., Huettmann F., Post A., Ropert-Coudert Y. (eds.), 2014. Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, XII + 498 pp.

Ellingsen, K., Brandt, A., Hilbig, B., Linse, K., 2007. The diversity and spatial distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean. Polar Biol. 30, 1265-1273.

Ellingsen, K.E., Clarke, K.R., Somerfield, P.J., Warwick, R.M., 2005. Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. J. Anim. Ecol. 74, 1069-1079.

Etter, R.J., Grassle, J.F., 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature 360, 576-578.

Gaston, K.J., Blackburn, T.M., 1996. Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. J. Anim. Ecol. 65, 701-714.

Gaston, K.J., Blackburn, T.M., Lawton, J.H., 1997. Interspecific abundance- range-size relationships: an appraisal of mechanisms. J. Anim. Ecol. 66, 579–601.

Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L., Sheader, M., 2002. Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. Mar. Ecol. Prog. Ser. 240, 157-170.

Gotelli, N.J., Colwell, R.K. 2011. Estimating species richness. In: Magurran AE, McGill BJ, editors. Frontiers in Measuring Biodiversity. New York: Oxford University Press. p. 39-54.

Griffiths, H.J., Danis, B., Clarke, A.C., 2011. Quantifying Antarctic marine biodiversity: The SCAR-MarBIN data portal. Deep-Sea Res. II 58, 18-29.

Griffiths, H.J., Van de Putte, A., Danis, B. 2014. Data distribution: Patterns and implications. In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d’Acoz C. d’, Van de Putte A.P., Danis B., David B., Grant S., Gutt J., Held C., Hosie G., Huettmann F., Post A., Ropert-Coudert Y. (eds.), 2014. *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, XII, 16-26.

Gutt, J., Barnes, D.K.A., Lockhard, S.L., van de Putte, A., 2013a. Antarctic macrobenthic communities: a compilation of circumpolar information. Nature Conserv. 4, 1-13.

Gutt, J., Griffiths, H.J., Jones, C.D., 2013b. Circumpolar overview and spatial heterogeneity of Antarctic macrobenthos communities. Mar. Biodiv. 43, 481-487.

Hain, S., 1990. The benthic seashells (Gastropoda and Bivalvia) of the Weddell Sea, Antarctica. Ber. Polarforsch. 70, 1–181.

Held, C., 2003. Molecular evidence for cryptic speciation within the widespread Antarctic crustacean Ceratoserolis trilobitoides (Crustacea, Isopoda). In: Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M. & W.J. Wolff (eds.): Antarctic Biology in a Global Context, 135-139.

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

Izsak, C., Price, A.R.G., 2001. Measuring β-diversity using a taxonomic similarity index, and its relation to spatial scale. Mar. Ecol. Prog. Ser. 215: 69–77.

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

Kaiser, S. Griffiths, H. J., Barnes, D. K. A., Brandão, S. N., Brandt, A., 2011. Is there a distinct continental slope fauna in the Antarctic? Deep-sea Res. II 58, 91–104.

Kaiser, S., Brandão, S.N., Brix, S., Barnes, D.K.A., Bowden, D., Ingels, J., Leese, F., Schiaparelli, S.,Arango, C., Bax, N., Blazewicz-Paszkowycz, M., Brandt, A., Catarino, A.I., Danis B., David, B., De Ridder, C., Dubois, P., Ellingsen, K.E., Glover, A., Griffiths, H.J., Gutt, J., Halanych, K., Havermans, C., Held, C., Janussen, D., Lörz, A.-N., Pearce, D., Pierrat, B., Riehl, T., Rose, A., Sands, C.J., SoleriMembrives, A., Schüller, M., Strugnell, J., Vanreusel, A., Veit-Köhler, G., Wilson, N., Yasuhara, M., 2013. Pattern, process and vulnerability of Southern Ocean benthos - a decadal leap in knowledge and understanding. Mar. Biol. 160, 2295-2317.

Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. J. Anim. Ecol. 72, 367-382.

Kruskal, J.B., Wish, M., 1978. *Multidimensional Scaling*. Sage Publications, Beverly Hills, CA

Laptikhovsky, V., 2006. Latitudinal and Bathymetric Trends in Egg Size Variation: A New Look at Thorson’s and Rass’s Rules. Mar. Ecol. 27, 7– 14.

Leese, F., Agrawal, S., Held, C., 2010. Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. Naturwissenschaften 97, 583-595.

Levin, L.A., Dayton, P., 2009. Ecological theory and continental margins: where shallow meets deep. Trends Ecol. Evol. 24, 606-617.

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

Magurran A.E., 2004. Measuring biological diversity. Blackwell Publishing, Oxford, 1-256.

Marshall, D. J., Bolton, T. F., 2007. Effects of Egg Size on the Development Time of Non-feeding Larvae. Biol. Bull. 212: 6-11.

Meyer-Löbbecke, A., Brandt, A., S. Brix, S., 2014. Diversity and abundance of deep-sea Isopoda along the Southern Polar Front: Results from the SYSTCO I and II expeditions. Deep Sea Res. II 108, 76-84.

McClain, C.R. 2004. Connecting species richness, abundance and body size in deep-sea gastropods. Global Ecol. Biogeogr. 13:327-334

McClain, C.R. Etter, R.J. 2005. Mid-domain models as predictors of species diversity patterns: bathymetric diversity gradients in the deep sea. Oikos 109. 555-566.

McClain, C.R., Stegen, J.C., Hurlbert, A.H., 2012. Dispersal, environmental niches and oceanic-scale turnover in deep-sea bivalves. Proc. R. Soc. B 279, 1993–2002.

Paterson, G.L.J., Wilson, G.D.F., Cosson, N., Lamont, P.A., 1998. Hessler and Jumars (1974) revisited: abyssal polychaete assemblages from the Atlantic and Pacific. Deep-Sea Res. 45, 225-251.

Payne, C.M., Allen, J.A., 1991. The morphology of the deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. Phil. Trans. R. Soc. B 334, 481-562.

Pearse, J.S., Mooi, R., Lockhart, S.L., Brandt, A., 2009. Brooding and Species Diversity in the Southern Ocean: Selection for Brooders or Speciation within Brooding Clades? In: ”Smithsonian at the Poles: Contributions to International Polar Year Science” ed. Igor Krupnik, Michael A. Lang, and Scott E. Miller, pp. 181-196. Proceedings of Smithsonian at the Poles Symposium, Smithsonian Institution, Washington, D.C., 3-4 May 2007. Washington, D.C.: Smithsonian Institution Scholarly Press.

Piepenburg, D., Ambrose, W.G., Brandt, A., Renaud, P.E., Ahrens, M.J., Jensen, P., 1997. Benthic community patterns reflect water column processes in the Northeast Water Polynya (Greenland). J. Mar. Syst. 10, 467–482.

Platell, M.E., Potter, I.C., Clarke, K.R., 1998. Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. Mar. Biol. 131, 719-734.

Raupach, M.J., Malyutina, M., Brandt, A., Wägele, J.W., 2007. Molecular data reveal a highly diverse species flock within the deep-sea isopod *Betamorpha fusiformis* (Crustacea: Isopoda: Asellota) in the Southern Ocean. Deep-Sea Res. II 54, 1820–1830.

Raupach, M.J., Wägele, J.-W., 2006. Distinguishing cryptic species in Antarctic Asellota (Crustacea: Isopoda) - a preliminary study of mitochondrial DNA in Acanthaspidia drygalskii. Ant. Sci. 18(2), 191-198.

Reed, A.J., Morris, J.P., Linse, K., Thatje, S., 2014. Reproduction in deep-sea protobranch bivalves *Yoldiella ecaudata, Yoldiella sabrina*,and *Yoldiella valettei* (Yoldiidae) from the Southern Ocean. Polar Biol. 37, 1383-1392.

Rex, M.A. 1973. Deep-sea species diversity: Decreased gastropod diversity at abyssal depths. Science 181, 1051-1053.

Rex, M.A. 1981. Community Structure in the Deep-Sea Benthos. Annual Review of Ecology and Systematics 12, 331-353

Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L., Wilson, G.D.F., 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature 365, 636-639.

Rex, M.A., Etter, R.J., Stuart, C.T., 1997. Large-scale patterns of species diversity in the deep-sea benthos.In Ormond, R.F.G., Gage, J.D. & M. v. Angel (eds.), Marine Biodiversity: Patterns and Processes. Cambridge University Press, Cambridge, 94-122.

Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P., Warén, A. 2005a. A source-sink hypothesis for abyssal biodiversity. Am. Natural. 165, 163-178.

Rex, M.A., Crame, A., Stuart, C.T., Clarke, A. 2005b. Large-scale biogeographc patterns in marine molluscs: a confluence of history and productivity? Ecology 86, 2288-2297.

Rex, M.A., Etter., R.J. 2010. Deep-Sea Biodiversity: Pattern and Scale. Harvard University Press.

Sanders, H.L., Hessler, R.R., 1969 Ecology of the deep-sea benthos. Science 163, 1419-1424.

Schiaparelli, S., Lörz, A.N., Cattaneo-Vietti, R., 2006. Diversity and distribution of mollusc assemblages on the Victoria Land coast and the Balleny Islands, Ross Sea, Antarctica. Ant. Sci. 18, 615–631.

Schiaparelli, S., Ghiglione, C., Alvaro, M.C., Griffiths, H.J., Linse, K., 2014. Diversity, abundance and composition in macrofaunal molluscs from the Ross Sea (Antarctica): results of fine-mesh sampling along a Latitudinal Gradient. Polar Biol. 37, 859–877.

Schwabe, E., Bohn, J.M., Engl, W., Linse, K., Schrödl, M.2007. Rich and rare—First insights into species diversity and abundance of Antarctic abyssal Gastropoda *(Mollusca).* Deep-Sea Res. II *54, 1831–1847.*

Somerfield, P.J., Clarke, K.R., Warwick, R.M., Dulvy, N.K., 2008. Average functional distinctness as a measure of the composition of assemblages. ICES J Mar. Sci. 65, 1462-1468.

Somerfield, P.J., Arvanitidis, C., Vanden Berghe, E. (eds), 2009. Theme Section. Large-scale studies of the European benthos: the MacroBen database. Mar. Ecol. Progr. Ser. 382, 221-311.

Somerfield, P.J., Arvanitidis, C., Faulwetter, S., Chatzigeorgiou, G., Vasileiadou, A., Amouroux, J., Anisimova, N., Cochrane, S., Craeymeersch, J., Dahle, S., Denisenko, S., Dounas, K., Duineveld, G., Grémare, A., Heip, C., Herrmann, M., Karakassis, I., Kędra, M., Kendall, M., Kingston, P., Kotwichi, L., Labrune, C., Laudien, J., Nevrova, H., Nicolaidou, A., Occhipinti-Ambrogi, A., Palerud, R., Petrov, A., Rachor, E., Revkov, N., Rumohr, H., Sardá, R., Janas, U., Vanden Berghe, E., Włodarska-Kowalczuk, M., 2009. Assessing evidence for random assembly of marine benthic communities from regional species pools. Mar. Ecol. Progr. Ser. 382, 279-286.

Tittensor, D.P., Rex, M.A., Stuart, C.T., McClain, C.R., Smith, C.R., 2011. Species–energy relationships in deep-sea mollusks. Biol. Lett. 7, 718–722. (doi:10.1098/rsbl.2010.1174)

Troncoso, J.S., Aldea, C., García, F.J., Arnaud, P.M., Ramos, A., 2007. Quantitative analysis of soft bottom Molluscs in Bellingshausen Sea and Peter I Island. Polar Res. 16, 126–134.

Troncoso, J.S., Aldea, C., 2008. Macrobenthic mollusc assemblages and diversity in the West Antarctica from the South Shetland Islands to the Bellingshausen Sea. Polar Biol. (2008) 31, 1253–1265.Warwick, R.M., Clarke, K.R., 1995. New ‘biodiversity’ measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol. Prog. Ser. 129, 301-305.

Warwick RM, Clarke KR, 1991. A comparison of some methods for analyzing changes in benthic community structure. J. Mar. Biol. Ass. U.K. 71, 225-244.

Warwick, R.M., Clarke, K.R., 2001. Practical measures of marine biodiversity based on relatedness of species. Oceanogr. Mar. Biol. Ann. Rev. 39, 207-231.

Warwick, R.M., Clarke, K.R., Gee, J.M., 1990. The effects of disturbance by soldier crabs, Mictyris platycheles H. Milne-Edwards, on meiobenthic community structure. J. exp. Mar. Biol. Ecol. 135, 19-33.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213-251.

Witman, J.D., Etter, R.J., Smith, F., 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. PNAS 101, 15664-15669.

Würzberg, L., Peters, J., Schüller, M., Brandt, A., 2011a. Diet insights of deep-sea polychaetes derived from fatty acid analyses. Deep-Sea Res. II 58, 153-162. doi:10.1016/j.dsr2.2010.10.014.

Würzberg, L., Peters, J., Brandt, A. 2011b. Fatty acid patterns of Southern Ocean shelf and deep sea peracarid crustaceans and a possible food source, foraminiferans. Deep-Sea Res. II 58 (19-20), 2027-2035.

Young, C.M., 2003. Reproduction, development and life-history traits. In: Tyler P.A. (ed) Ecosystems of the deep oceans. Elsevier p. 381-426.

Zardus, J.D., 2002. Protobranch Bivalves. Adv. Mar Biol. 42, 1-65.

FIGURE LEGENDS

Figure 1. Map of epibenthic sledge stations sampled from RV *Polarstern* during the ANDEEP I – II (2002, white circles) and ANDEEP III (2005, black circles) expeditions.

Figure 2. Relationships between: A. depth (m) and haul length (m); B. density (individuals.1000 m-2) and haul length (m); C. species density S\* (species.individual-1.1000m2) and density; D. species density S\* and depth; E. species richness (S) and depth. ×, isopods; ●, bivalves. A.-D. in log/log scale, E. in linear/linear scale. See text for regression equations and R2 (all significant at p<0.05).

Figure 3: Reproduction and life-styles of Isopoda and Bivalvia at each station. The illustration is based on data from Supplementary Table 1.

Figure 4: Average taxonomic distinctness (Δ+) plotted against the number of species (S) for Isopoda (A) and Bivalvia (B). Also shown are the mean and 95 % probability limits derived from 999 random draws of species from the regional species poll (the complete list from all 40 stations) with selection probabilities conditioned on the frequency of occurrence of species. Symbols indicate depth bands: ⬥, >2000 m; ◇, 2000 – 3000 m; ▲, 3000 – 4000 m; 🞎 > 4000 m. Labelled samples indicate assemblages significantly (p < 0.05) more closely related than expected under a null hypothesis f random assembly.

Figure 5. Nonmetric multidimensional scaling ordination plots showing relative similarities among stations based on A. Sørensen and B. Γ+ based on isopod species composition, and C. Sørensen and D. Γ+ based on bivalve species composition. Symbols as in Figure 4.

Figure 1. Map of epibenthic sledge stations sampled from RV *Polarstern* during the ANDEEP I – II (2002, white circles) and ANDEEP III (2005, black circles) expeditions.



Figure 2. Relationships between: A. depth (m) and haul length (m); B. density (individuals.1000 m-2) and haul length (m); C. species density S\* (species.individual-1.1000m2) and density; D. species density S\* and depth; E. species richness (S) and depth. ×, isopods; ●, bivalves. A.-D. in log/log scale, E. in linear/linear scale. See text for regression equations and R2 (all significant at p<0.05).



Figure 3: Reproduction and life-styles of Isopoda and Bivalvia at each station. The illustration is based on data from Supplementary Table 1.



Figure 4: Average taxonomic distinctness (Δ+) plotted against the number of species (S) for Isopoda (A) and Bivalvia (B). Also shown are the mean and 95 % probability limits derived from 999 random draws of species from the regional species poll (the complete list from all 40 stations) with selection probabilities conditioned on the frequency of occurrence of species. Symbols indicate depth bands: ⬥, >2000 m; ◇, 2000 – 3000 m; ▲, 3000 – 4000 m; 🞎 > 4000 m. Labelled samples indicate assemblages significantly (p < 0.05) more closely related than expected under a null hypothesis f random assembly.



Figure 5. Nonmetric multidimensional scaling ordination plots showing relative similarities among stations based on A. Sørensen and B. Γ+ based on isopod species composition, and C. Sørensen and D. Γ+ based on bivalve species composition. Symbols as in Figure 4.



Table 1

Sample details and summary statistics (density as individuals.1000 m􀀀2 and number of species, S) for isopods and bivalves. The area abbreviations are: BS = Bellingshausen Sea; CB = Cape Basin; DP = Drake Passage; PB = Powell Basin; SSa = South Shetland area; SSI = South Sandwich Islands; WS = Weddell Sea.



Table 2

Density and range of the most abundant Isopoda and Bivalvia at the 40 stations. Number of uniques and duplicates are given.



Table 3

Summary of 2-way crossed ANOSIM results. Values of the ANOSIM R statistic with p < 0.05 in bold. Pairwise tests for differences between areas not shown



Table 4

Condensed summary of 2-way SIMPER analysis showing frequencies of occurrence of isopod and bivalve species contributing to Sørensen similarity within (bold), and dissimilarity between (<or>) depth bands (samples from 2000-3000 m and 3000–4000 m combined) averaged over all areas, up to a cut-off of 25%. Right-hand column indicates species contributing to dissimilarities between samples from <2000 m and >4000 m.

