



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



Angelika Brandt<sup>a,\*</sup>, Katrin Linse<sup>b</sup>, Kari E. Ellingsen<sup>c</sup>, Paul J. Somerfield<sup>d</sup>

<sup>a</sup> Zoological Museum, Centre of Natural History, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

<sup>b</sup> British Antarctic Survey, Natural Environmental Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

<sup>c</sup> Norwegian Institute for Nature Research, Fram Centre, P.O. Box 6606 Langnes, 9296 Tromsø, Norway

<sup>d</sup> Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK

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### 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  $\Gamma^+$  (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.

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### 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; Gaston et al., 1997; Rex et al., 1997, 2005a,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 and 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., 2007a,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; 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.

\* Corresponding author.

E-mail addresses: [abrandt@zoologie.uni-hamburg.de](mailto:abrandt@zoologie.uni-hamburg.de) (A. Brandt), [kl@bas.ac.uk](mailto:kl@bas.ac.uk) (K. Linse), [kari.ellingsen@nina.no](mailto:kari.ellingsen@nina.no) (K.E. Ellingsen), [pjs@pml.ac.uk](mailto:pjs@pml.ac.uk) (P.J. Somerfield).

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,b,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 lecithotrophic 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 lecithotrophic 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., 2007a). 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 27–60 cm above the seafloor) and a suprabenthic sampler (deployed 100–133 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 min at a velocity of 1 knot (1852 m h<sup>-1</sup>), 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 h 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<sup>-2</sup>) 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*<sup>\*</sup>) was calculated by dividing *S* by local density. Average taxonomic distinctness ( $\Delta^+$ ) was calculated for isopods and bivalves in each sample. Average taxonomic distinctness is defined as:  $\Delta^+ = [\sum \sum i < j \omega_{ij}] / [s(s-1)/2]$ , where *s* is the number of species present, the double summation is over  $\{i = 1, \dots, s; j = 1, \dots, s, \text{ such that } i < j\}$ , and  $\omega_{ij}$  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  $\omega_{ij}$ , 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.

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