ELSEVIER

Deep-Sea Research II 51 (2004) 1457–1465

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Introduction to ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns)—a tribute to Howard L. Sanders

Angelika Brandt[a,*], Claude De Broyer[b], Andrew J. Gooday[c], Brigitte Hilbig[d], Michael R.A. Thomson[e]

[a]Zoological Institute and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany
[b]Institute Royal des Sciences Naturelles de Belgique, Rue Vautier 29, 1040 Bruxelles, Belgium
[c]Southampton Oceanographic Centre, Empress Dock, Southampton SO14 3HZ, UK
[d]Department of Zoology, Ruhr-Universität Bochum, Universitätsstr. 150, D44780 Bochum, Germany
[e]Centre for Polar Sciences, School of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK

Available online 27 October 2004

We dedicate the present volume to the late Howard Sanders, who passed away after a long illness on 7 February 2001. When as a young scientist at the Woods Hole Oceanographic Institution he, together with his colleague Bob Hessler and his technical assistant George Hampson, collected and analyzed the first "quantitative" samples of deep-sea benthos (today one would call them semi-quantitative), he may not have had any idea how instrumental the resulting time-stability hypothesis would prove to be for at least four decades of biological deep-sea research. The image of the deep-sea floor being a lifeless desert or, at best, a desolate place harboring a depauperate fauna was shattered when investigations along a transect between Bermuda and Gay Head, a cliff on the island of Martha's Vineyard off Massachusetts, revealed that while densities decreased with depth, species richness actually increased. Since then, many more samples have been collected, our knowledge, limited as it may still be, has increased dramatically, and many new theories and hypotheses have been developed. Nevertheless, the work and personality of Howard Sanders are still something one feels obligated to measure up to. With ANDEEP I and II, we may not have entered as much of a terra incognita as Sanders and colleagues did 40 years ago, but our excitement was certainly comparable. We sincerely hope Howard would approve if he could hold this volume in his hands.

1. Background of ANDEEP

Biodiversity—defined as the variety and variability of genomes, species and populations, communities and ecosystems in space and time—is a central aspect of modern biology. The assessment of Antarctic biodiversity, the understanding of its role in ecosystem functioning, and requirements for its conservation are of particular importance in the context of global environmental changes.

Biogeography is closely linked to biodiversity. It is concerned with the geographic distribution of species and taxa in our biosphere, tries to explain patterns of distribution, and can help

*Corresponding author. Tel.: +49 (0) 40-42838-2278; fax: +49 (0) 40-42838-3937.
E-mail address: abrandt@zoologie.uni-hamburg.de (A. Brandt).

0967-0645/$ - see front matter
doi:10.1016/j.dsr2.2004.08.006

to identify the origin of species on the basis of their phylogenetic relationships. Any attempt to conserve species and their habitats must be based on profound knowledge of biodiversity and biogeography. Without reliable information about species assemblages and communities, we will not be able to adequately protect the environment and its living organisms.

Even though roughly three quarters of the earth's surface is covered by ocean, with more than 90% being deep-sea (continental slopes to hadal depths), with an average depth of 3729 m, the abyss (3000–6000 m) covers about 74% of the deep-sea. However, information on biodiversity is still very much concentrated on terrestrial ecosystems, most prominently on tropical rain forests. In contrast, the faunas living in the largest ecosystem on earth, the deep-sea floor, are very poorly known, especially in the Antarctic where there has been a notable lack of intensive biological sampling effort. Without doubt, the Antarctic deep-sea to this day harbors many unknown taxa, despite the fact that many nations have intensified their Antarctic research activities during the last 20 years. Contrary to the knowledge of the benthos of the Southern Ocean shelf areas, the knowledge of the Southern Ocean deep-sea is scarce, and as in other oceans of the world, in Antarctica the deep-sea floor is the largest single benthic habitat, yet remains the least studied (Clarke and Johnston, 2003).

Since the beginning of modern deep-sea research (e.g. Sanders et al., 1965; Sanders and Hessler, 1969), attempts to describe and explain patterns of species diversity have become a major goal in deep-sea biological research. On regional spatial scales, for example, within a single basin, diversity is influenced by environmental factors such as organic matter fluxes, bottom-water oxygen concentrations, current velocity, and sediment type (Levin et al., 2001). There is also evidence for the existence of patterns in biodiversity at larger (global) scales; in particular, an apparent decrease in species richness among a number of taxa from the equator towards the poles (Poore and Wilson, 1993; Rex et al., 1993; Thomas and Gooday, 1996; Rex, 1997; Culver and Buzas, 2000).

Biodiversity research in Antarctica based on evolutionary biology and biogeography has particular significance because the Antarctic ecosystem is of considerable age. Climatic cooling can be dated back at least to the Oligocene, about 35 million years ago (Barron et al., 1991; Clarke and Crame, 1992). Because of the antiquity of this ecosystem, Southern Ocean organisms, especially those living on the continental shelf, have had a long time available in which to evolve.

The last 40 million years saw major changes to the palaeogeography of the Scotia Sea–northern Weddell Sea region as the last remaining connection between Antarctica and the old Gondwana supercontinent (the Antarctic Peninsula–South America link) broke down. Continental fragments were dispersed eastward as both submerged and partially emergent masses to form the Scotia Arc, and new oceanic basins were formed. This resulted in a number of increasingly isolated continental shelf areas and allowed the ingress of the South Pacific into the South Atlantic with the completion of the Antarctic Circumpolar Current.

This historical background may explain the adaptive radiation events observed in many benthic or benthopelagic taxa (e.g. Notothenioidei, Amphipoda, Isopoda, Gastropoda). Watling and Thurston (1989) memorably characterized the Antarctic as an 'evolutionary incubator' for the amphipod family Iphimediidae. These radiation processes, and the long time span available for evolution, probably explain the high degree of endemism, approaching 90% in taxa such as sponges, peracarid crustaceans, and some gastropod families, that characterises Antarctic communities.

However, these generalizations apply specifically to shelf faunas. We do not know whether the biological properties mentioned countless times as characteristics of the Antarctic fauna, such as gigantism, late maturity, decreased number of offspring, long life spans, etc., also apply to Antarctic deep-sea organisms. The ANDEEP expeditions were carried out in order to address these basic gaps in our knowledge of Antarctic biology.

The deeper waters of the Scotia and Weddell seas include some of the least explored parts of the world's oceans, and we know almost nothing about the bottom-dwelling animals that inhabit them. In contrast to the isolated shelf, waters deeper than 1000 m have broad connections with the Pacific, South Atlantic, and Indian oceans. Hence, the faunal assemblages of bathyal and abyssal areas around Antarctica may be similar to those living at comparable depths elsewhere, and the degree of endemism much lower in the deep sea than on the shelf.

In addition, the Weddell Sea is potentially an important source for taxa presently living in the Atlantic and other neighboring parts of the deep oceans. Periodic extensions of the ice sheet possibly enhanced rates of speciation on the continental shelf and slope around Antarctica. Antarctic bottom water is generated at the Southern Ocean ice margins. It is cold, highly saline, and has—on the one hand—probably led to the isolation of the benthic shelf faunas due to the Cretaceous temperature decrease (Clarke and Crame, 1992). On the other hand, deep bottom-water production in the Weddell Sea also may have acted as a larval distribution mechanism, driving Antarctic deep-water fauna northwards into the Atlantic Ocean over evolutionary time-scales. It is unknown whether the development of the deep-water production influenced the migration potential of brood-pouch carrying Isopoda and thus enhanced submergence of some species.

Another important question concerns the potential faunistic links between South America and Antarctica, and whether faunal exchange is still possible today, either by island hopping or migration through the deep-sea basins. In other words, does the Antarctic deep sea constitute a barrier or a route for faunal migration between South America and the Antarctic Peninsula? The formation of the Weddell Sea began during Jurassic time (165 million years ago), but a continental link between South America and Antarctica persisted until just over 20 million years ago. Geographical and climatic changes, including intermittent periods of global warming and global sea-level rise and fall, are likely to have influenced the movement of species in and out of the Antarctic region.

The considerations outlined above led us to pursue the following specific objectives during the ANDEEP surveys:

- To conduct the first comprehensive survey of megafaunal, macrofaunal and meiofaunal deep-water communities in the Scotia and Weddell seas.
- To investigate the similarity of the Scotia and Weddell Sea fauna at taxonomic (morphological) and genetic (molecular) levels to the fauna of Atlantic basins, on the one hand and Antarctic shelf on the other.
- To describe the variety of seafloor habitats in tectonically active and inactive regions and to determine the influence of 'habitat diversity' on species and genetic diversity over a variety of spatial scales.
- To determine the importance of life history strategies and larval biology for species distributional patterns and geographical ranges.
- To investigate the evolutionary processes that have resulted in the present biodiversity and distributional/zoogeographical patterns in the Southern Ocean deep sea.

In a broader sense, ANDEEP may enhance our understanding of some important general issues in deep-sea biology. The project will certainly provide a wealth of new information about the scale and patterns of species diversity in the deep ocean (Etter and Mullineaux, 2000; Levin et al., 2001), add to our knowledge of deep-sea species ranges and the relationship between local and regional diversity (Stuart and Rex, 1994), and may ultimately lead to a better understanding of the origins of faunas inhabiting these remote regions.

ANDEEP has particular relevance to the controversial issue of global (latitudinal) diversity gradients. As mentioned above, there is evidence that diversity decreases from the tropics to the poles in some deep-sea taxa. Gradients are particularly pronounced in the northern hemisphere, a fact that probably reflects the geologically recent origin of the Arctic Ocean. This hypothesis was first published by Poore and Wilson (1993) and also supported by Rex et al. (1993) on the basis of epibenthic sledge samples taken down to 4000 m depth. In a response to the publication of Rex et al. (1993), Brey et al. (1994) examined diversity gradients in the southern hemisphere, using data from the shelf and upper slope of the eastern and southern Weddell Sea. They demonstrated that species richness for bivalves, gastropods, and isopods is comparable to that found in tropical regions around 20°S.

However, Brey et al. (1994) were forced to compare Agassiz trawl and box corer data with epibenthic sledge data from Poore and Wilson (1993) and Rex et al. (1993). ANDEEP samples were taken with a whole range of gear and will provide a rich source material that can be used to test whether or not a latitudinal diversity gradient really exists in the southern hemisphere. A more precise and detailed description of latitudinal diversity trends in the deep ocean may help to promote a better understanding of some fundamental controls on patterns of biodiversity in marine ecosystems over geological and ecological time scales. ANDEEP contributes to the large-scale analysis of deep-sea biodiversity within CeDAMar (http://www.coml.org/descrip/cedamar.htm), one of the core field projects of the Census of Marine Life.

2. Sampling programme

Seven potential target areas were selected for the ANDEEP expeditions (Fig. 1). During ANDEEP I (ANT XIX-3), Target area 1 in the Drake Passage was sampled in addition to stations off Elephant, King-George and Livingston islands. During ANDEEP II (ANT XIX-4) we proceeded to sample target areas 3, 4, and 6. The next expedition, ANDEEP III is planned for the austral summer of 2005, when we hope to be able to sample target areas 5 and possibly 2.

Target area 1 on the Shackleton Fracture Zone was chosen in order to investigate whether or not this tectonic feature might provide a submarine bridge for faunal migration between southern South America and the Antarctic Peninsula.

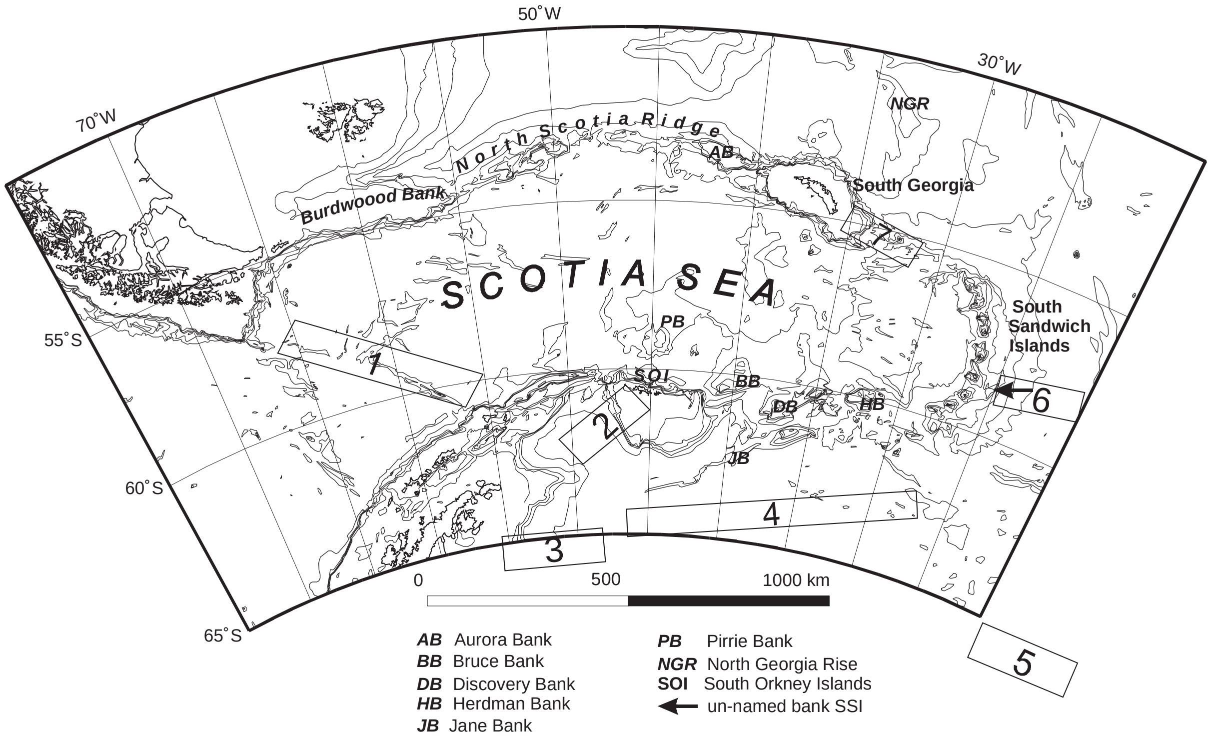

Fig. 1. Target areas of ANDEEP.

Target area 2 off the South Orkney Islands was selected because the shelf fauna in that area is relatively well-known. This provides an opportunity to determine whether shelf species also occur in the deep-sea and exhibit a higher than expected degree of eurybathy.

Target area 3. The arguments for this area were similar to those for area 2 as it provides a link between the eastern shelf of the Antarctic Peninsula and the Weddell Sea abyssal plain. However, the area is rarely accessible because of the concentrations of pack ice that occur in the northwestern Weddell Sea under the influence of the Weddell gyre.

Target area 4 presented an opportunity to sample a long transect across an abyssal plain, with the additional advantage of the slopes leading down to the plain having been sampled before (ANT XV/3 in 1998). We thus had a chance to answer questions concerning species ranges in homogeneous large-scale environments as well as faunal shifts down slope.

Target area 5 is situated off the Kapp Norvegia shelf where the benthic fauna is well-known. Like areas 2 and 3, it provides an opportunity to investigate possible changes between the shelf and the abyssal plain. The shelf off Kapp Norvegia has been sampled during several previous expeditions aboard R.V. 'Polarstern' and represents a 'house garden' with which to compare slope data.

Target area 6 near the South Sandwich Islands was selected because of its remoteness and the resulting lack of data. Only a few expeditions carried out by Russian scientists have provided data on the benthos in this tectonically active region.

The stations actually sampled during ANDEEP I and II are shown in Fig. 2. All publications in this volume will refer to this figure for reference.

The potential cruise track for ANDEEP III is illustrated in Fig. 3.

3. Synthesis and conclusions

3.1. Meiofauna

Prior to ANDEEP, only a limited amount of information was available regarding deep-sea meiofauna in the Southern Ocean. Meiofaunal studies within ANDEEP concerned metazoan taxa, mainly nematodes and harpacticoid copepods, as well as the foraminiferans. The foraminiferans usually accounted for more than half of all meiofaunal organisms and were diverse (Cornelius and Gooday, this issue). They consisted of a mixture of hard-shelled, multi-chambered agglutinated and calcareous species together with soft-shelled, monothalamous taxa, which increased in relative abundance with increasing water depth. Many of the Weddell Sea species are typical bathyal and abyssal forms that are already well known from the North Atlantic and elsewhere. Some are found living within small aggregates of phytodetritus, a very similar association to that observed at bathyal and abyssal sites in the North Atlantic.

There seem to be, therefore, close ecological parallels, as well as faunal links, between the deep-water faunas of the Weddell Sea and those of other oceanic regions. Many of the foraminiferal species, particularly the soft-shelled monothalamous (single-chambered) forms, collected during ANDEEP II were undescribed. One monothalamous species has now been described as *Conqueria laevis* (Gooday and Pawlowski, 2004) and another is described in the present volume (Gooday et al., this issue). Both of these new species are characterized on the basis of molecular and morphological criteria. This is the first time that DNA sequences have been obtained from deep-sea foraminifera.

Data on the metazoan size fraction (32–1000 μm) from the South Sandwich Trench (Vanhove et al., this issue) revealed unexpectedly high standing stocks, situated above world ocean's regression line of meiobenthic abundance against water depth. In particular, the greatest trench depth at 6300 m gave surprising results with regard to food supply and availability. The trend confirms earlier results from Antarctic continental margins (Vanhove et al., 1995). The meiofaunal parameters lacked the general bathymetric trends of deep-sea benthos due to the complexity of sediments, which in turn were the result of physical processes, bioturbation activity of invertebrate taxa and food supply along the South Sandwich Trench.

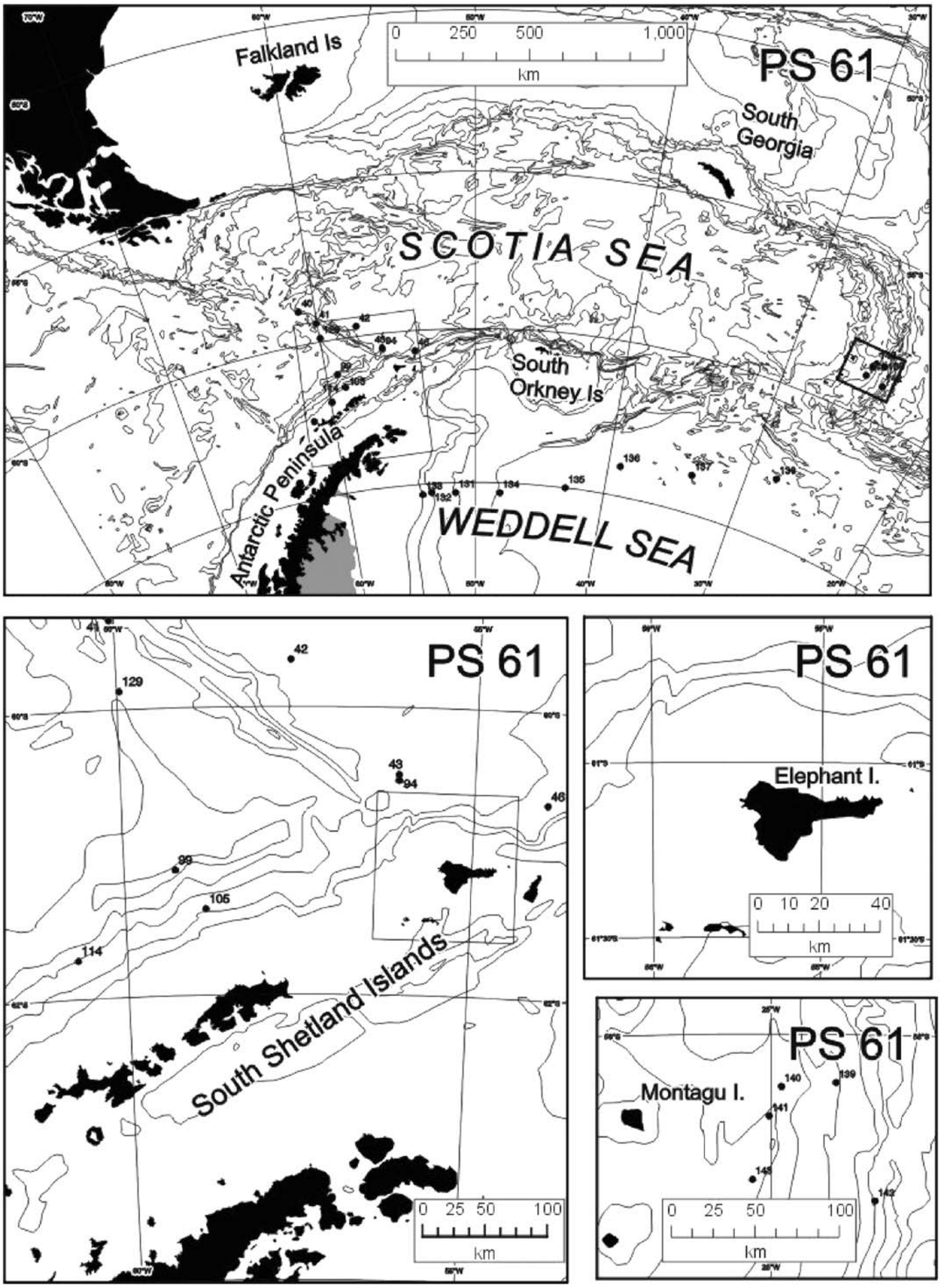

Fig. 2. Stations of ANDEEP I & II (Map: Paul Cooper, BAS).

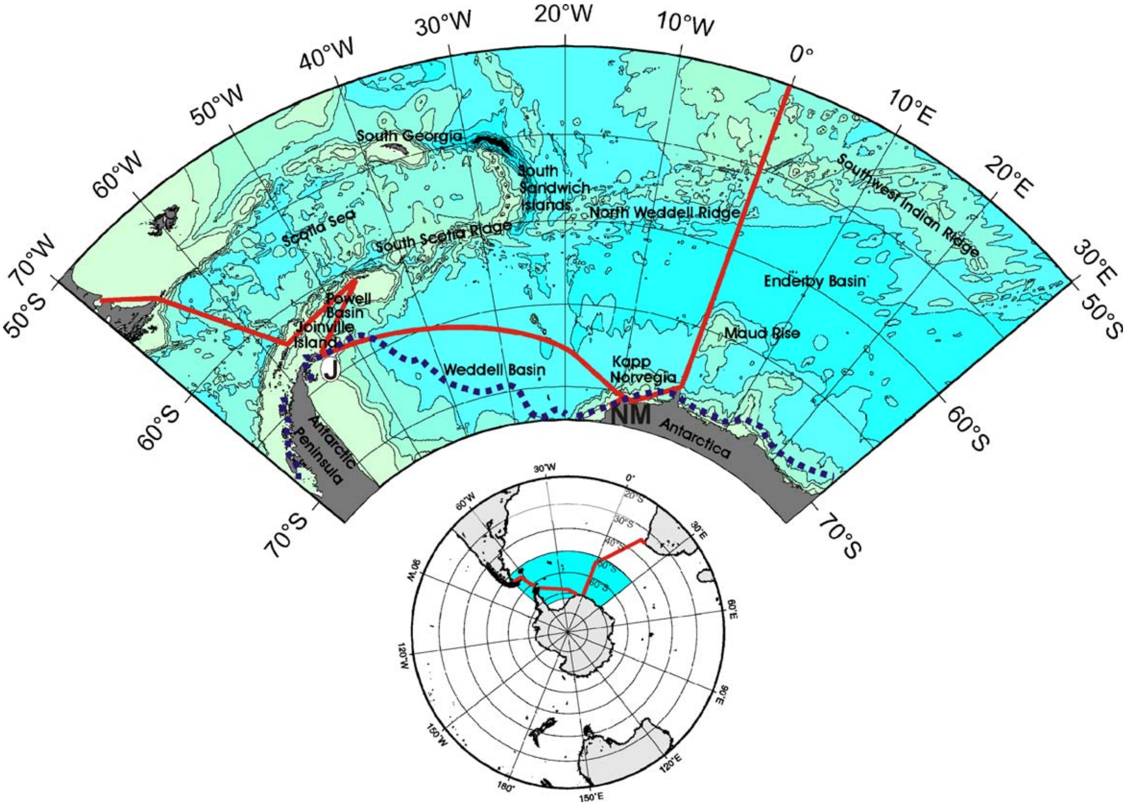

Fig. 3. Map with envisaged cruise track. The dashed line represents the long-term average of the ice edge (15% concentration) in February (Map of Prof. E. Fahrbach, AWI).

Nematodes predominated over the other taxonomic groups as is the rule for all deep-sea communities. They belonged to 94 genera, resulting in a high diversity of the presumable diatom-feeding Chromadoridae and monhysterid bacteria consumers. The 3000-m line forms a transit with changing overlap with shallower and deeper sites. Investigations at species level were restricted to the morphological identification and/or description within selected nematode genera (*Dichromadora*, *Manganonema*, *Desmodorella*, *Desmodora*, and *Molgolaimus*). Many species tend to be widespread and eurybathic in the Atlantic sector of the Southern Ocean, though some of them are not found in the South Sandwich Trench (such as *Dichromadora parva*, *Dichromadora polarsternis*, *Dichromadora polaris*, *Desmodora campbelli*, *Desmodorella aff. Balteata*, etc). Some species are spatially restricted to the South Sandwich Trench (Vermeeren et al., this issue; Ingels et al., 2004; Fonseca et al., 2004).

Downward and subsequent horizontal movement of nematode genera and families, despite strong separation of sites led to the wide distribution of families and genera (Vanhove et al., 1999) and only of some species suggest that radiation of deep-sea nematodes, occurs at the species level.

3.2. Macrofauna

Data from the Southern Ocean deep sea have shown that in very general terms, the macrofauna does not differ too much in composition on higher taxon level from that of other deep-sea regions of the world oceans. Many if not most of the macrofaunal species are new to science. For example, Southern Ocean deep-sea Isopoda show a high degree of endemism probably due to the neglectable sampling effort in the Southern Ocean deep-sea in the past (Brandt et al., this issue). Most important taxa are Polychaeta, Peracarida (Crustacea) and Mollusca (Bivalvia and Gastropoda). Nonetheless, ANDEEP revealed some surprising results. Within the Peracarida it was the Amphipoda, that comprised a major fraction of the material (32% of all individuals), surpassed only by Isopoda (38%). This is in sharp contrast to other deep-sea samples where amphipods are much less important in terms of abundance. Within the scavenging guild some 62 species of Amphipoda were collected. 98% of the individuals belong to Lysianassoidea. 31 species were collected deeper than 1000 m. High species richness was discerned for the eastern Weddell Sea shelf compared with other Antarctic areas. The Antarctic slope also seems to be richer in Amphipoda than other areas investigated, while in the abyss, scavenger species richness appears to be lower in Antarctica. A richness gradient was thus observed from the shelf to the deep. A number of amphipod species extend their distribution from the shelf to the slope and only one to the abyssal zone (De Broyer et al., this issue). Some interesting associations between cidaroid echinoids and Amphipoda are described (Berge et al., this issue).

The brooding Peracarida were characterized by a high diversity including many rare and new species, and only a minor amount of the species were known from other deep-sea basins. In contrast, within the Polychaeta we found many more species that seem to have crossed the barrier between the Southern Ocean and adjacent oceans, and although we do not know the reasons, we might suspect differences in the biology (Hilbig, this issue). For example, brooding is much less common among polychaetes (at least as far as we know), making larval dispersal a possibility for wide distributions, possibly along with a particularly high physiological flexibility in coping with large temperature and pressure changes. Data on reproductive stages of some polychaetes suggest that species limited to abyssal depths are reproducing there. Other species with broader depth ranges may be receiving recruits from slope depths.

Our knowledge of the deep-water bivalve fauna of Antarctica is poor. However, the deep-water bivalve fauna sampled during ANDEEP was species rich. 40 species of bivalves belonging to 17 families were found. At least seven of these species are new to science. In comparison with the shelf fauna of the Scotia Arc the deep-water bivalve community showed similar species richness. This indicates that there is no diversity decline with depth in Antarctic bivalves, but it does provide evidence for underestimated species richness in deep water because of lack of sampling (Linse, this issue).

3.3. Megafauna

Megafauna was found to be distinctively less diverse than the other two size classes. Most important taxa were Porifera, Mollusca, Echinodermata, and Brachiopoda, but not all of the material has been worked up to date.

Within the Porifera, new Hexactinellida from the deep Weddell Sea are moderately diverse and include 14 species belonging to 12 genera, of which five species and one subgenus are new to science (Janussen et al., this issue). To date, 20 hexactinellid species have been reported from the deep Weddell Sea. This apparent high "endemism" of Antarctic hexactinellid sponges is most likely to be the result of undersampling of the Southern Ocean deep-sea fauna. A zoogeographic distinction between oceanic and continental species exists.

From the Paleocene to the Pliocene pectinid bivalve molluscs inhabited coastal areas around the Antarctic continent. Today, all of the *Chlamys*-like genera are extinct around Antarctica and restricted to lower latitude habitats along the surrounding continents. The only remaining scallop in the High Antarctic Zone is the large endemic, thin-shelled *Adamussium colbecki* (Berkman et al., this issue). *Adamussium* has a circumpolar distribution with its highest abundances in Antarctic coastal areas, in contrast to the offshore habitats where its ancestors had predominated since the Oligocene.

The cephalopod fauna of the Southern Ocean deep-sea yielded an unusual and relatively large collection of octopods comprising four species in two genera. One genus is new to science (Allcock et al., this issue).

Acknowledgements

We are grateful to the German Science Foundation and all national funding agencies of the ANDEEP collaborators. Thanks are due for logistical support to the Alfred-Wegener-Institute for Polar and Marine Research, to the expedition leader, Prof. Fütterer, and the crew of R.V. Polarstern. We are also very grateful to all contributors and last but not least to the many reviewers.

References

Barron, J., Larsen, B., Baldauf, J.G., 1991. Evidence for late Eocene to early Oligocene Antarctic glaciation and observations on Neogene glacial history in Antarctica; results from Leg 119. In: Barron, J., Larsen, B., Baldauf, J.G. (Eds.) Proceedings of the ODP, Scientific Results, vol. 119, Ocean Drilling Program, College Station TX, pp. 868–891.

Brey, T., Klages, M.M., Dahm, C., Gorny, M., Gutt, J., Hahn, S., Stiller, M., Arntz, W.E., Wägele, J.-W., Zimmermann, A., 1994. Antarctic benthic diversity. Nature 368, 297.

Clarke, A., Crame, J.A., 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. Philosophical Transactions of the Royal Society of London B 338, 299–309.

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

Culver, S.J., Buzas, M.A., 2000. Global latitudinal species diversity gradient in deep-sea benthic foraminifera. Deep-Sea Research I 47, 259–275.

Etter, R.J., Mullineaux, L.S., 2000. Deep-sea communities. In: Bertness, M.D., Gaines, S., Hay, M. (Eds.), Marine Ecology. Sinauer, Sunderland, MA, pp. 367–393.

Fonseca, G., Vanhove, S., Vanreusel, A., 2004. Free-living nematodes from the South Sandwich Trench, with special attention to the biodiversity of the genera *Molgolaimus* and *Manganonema*. Master's Thesis, Ghent University.

Gooday, A.J., Pawlowski, J., 2004. *Conqueria laevis* gen. & sp. nov., a new soft-walled, monothalamous foraminiferan from the deep Weddell Sea. Journal of the Marine Biological Association of the United Kingdom.

Ingels, J., Vanhove, S., Vanreusel, A., 2004. Free-living nematodes at both sides of the Scotia Arc, with special attention to the biodiversity of the genera *Desmodora* and *Desmodorella* (family Desmodoridae). Master's Thesis, Ghent University.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annual Review of Ecology and Systematics 200 32, 51–93.

Poore, G.C.B., Wilson, G.D.F., 1993. Marine species richness (with reply from R.M. May). Nature 361, 597–598.

Rex, M.A., 1997. An oblique slant on deep-sea biodiversity. Nature 385, 577–578.

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.

Sanders, H.L., Hessler, R.R., 1969. Diversity and composition of abyssal benthos. Science 166, 1033–1034.

Sanders, H.L., Hessler, R.R., Hampson, G.R., 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. Deep-Sea Research 12, 845–867.

Stuart, C.T., Rex, M.A., 1994. The relationship between the development patterns and species diversity in deep-sea prosobranch snails. In: Young, C.M., Eckelbarger, K.J. (Eds.), Reproduction. Larval Biology and Recruitment in the Deep-Sea Benthos. Columbia University Press, New York, pp. 119–136.

Thomas, E., Gooday, A.J., 1996. Cenozoic deep-sea benthic foraminifers: Tracers for changes in oceanic productivity? Geology 24, 355–358.

Vanhove, S., Wittoeck, J., Desmet, G., Van den Berghe, B., Herman, R.L., Bak, R.P.M., Nieuwland, G., Vosjan, J.H., Boldrin, A., Rabitti, S., Vincx, M., 1995. Deep-sea meiofauna communities in Antarctica: structural analysis and relation with the environment. Marine Ecology Progress Series 127, 65–76.

Vanhove, S., Arntz, W., Vincx, M., 1999. Comparative study of the nematode communities on the southeastern Weddell Sea shelf and slope (Antarctica). Marine Ecology Progress Series 181, 237–256.

Watling, L., Thurston, M.H., 1989. Antarctica as an evolutionary incubator: evidence from the cladistic biogeography of the amphipod family Iphimediidae. In: Crame, J.A. (Ed.), Origins and evolution of the Antarctic biota. Geological Society Special Publication 47, pp. 297–313.