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Evolution of Antarctic biodiversity in the context of the past: the importance of the Southern Ocean deep sea

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Abstract: Present day Southern Ocean benthic biodiversity is the result of climatic changes based on the break-up of Gondwana in the Cretaceous and the Cenozoic and the physiological potential of the fauna to cope with the climatic deterioration. Though many taxa survived the thermal drop in ocean bottom temperatures, zoogeographic ranges changed and some faunal elements even became extinct, e.g. benthic decapods and teleost fish, opening up new ecological niches and the potential for enormous adaptive radiations within some taxa, like the amphipods and isopods (peracarid crustaceans) and notothenioid fish. Ice-sheet extensions and retreats might have enhanced speciation processes as well as eurybathy. Biodiversity on the Antarctic shelf is high within the polychaetes, molluscs, and echinoderms, and within the amphipods and isopods possibly due to the Cenozoic extinction of the benthic decapods. Moreover, some shelf areas are characterized by accumulations of large suspension feeders like poriferans, bryozoans, ascidians, gorgonians, and hydroids. Palaeoclimatic changes also caused that many taxa of the modern, present day Southern Ocean benthic organisms are characterized by gigantism, slow metabolism, longevity, and a reduced number of offspring combined with late maturation. However, our biological knowledge is mainly confined to Southern Ocean shelf organism; we do not know much about the composition, biodiversity and zoogeography of the Southern Ocean deep sea animals. On this background the deep sea expeditions ANDEEP were born and the background and first results of these are presented herein.

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Key words: ANDEEP, deep sea, geological history, marine biodiversity, Southern Ocean

Introduction

The present day biodiversity of the Southern Ocean marine faunas is the result of the geologic evolution of the continents, the subsequent change of the hydrography and palaeoseaways, the global climate change, faunal extinctions, dispersal capabilities, physiological adaptations, and the zoogeography and evolution of the taxa, which result from this geological framework.

Plate tectonics and palaeoceanography

The Mesozoic opening history of the Southern Ocean between South America, Africa, and Antarctica is still one of the largest gaps in knowledge on the evolution of this region (Jokat *et al.* 2003). What was the shape of the Southern Ocean in early Cretaceous? The initial extent of the Southern Ocean and the palaeopositions of South America and South Africa relative to Antarctica, forming parts of Gondwana are still under debate. Crame (1999) summarized the geologic framework of the rifting and seafloor spreading leading to the break-up of Gondwana, explaining that in Jurassic times Laurasia and Gondwana were still connected. The northward drift of India was followed by the drift and isolation of Africa, and the subsequent separation of India from Antarctica roughly 90 Ma ago. The break-up between Australia and Antarctica started approximately 100 Ma ago (Shackleton & Boersma 1981, Lawver *et al.* 1992), which successively led to a beginning deep water circulation between Australia and East Antarctica, which was not completely developed before Eocene or Oligocene (*c.* 55–35 Ma). At that time, the complete development of the Circumpolar Current was only interrupted by the land bridge between South America and the Antarctic Peninsula (Lawver *et al.* 1992, Storey 1996, Lawver & Gahagan 2003, Baker & Thomas 2004). However, this large water mass already led to a successive climatic deterioration, cooling and glaciation of Antarctica, especially in the east (Huber & Watkins 1992).

Due to the opening of the Drake Passage approximately between 32.5 Ma (Thomson 2004) and 34 Ma (Barker & Thomas 2004) and the development of the Scotia Arc, the Circumpolar Current became effective and caused a further cooling of the Southern Ocean surface water (Clarke & Crame 1989, 1992, Crame 1992, 1994). This assumption is corroborated by Lawver & Gahagan (2003), who regard it likely that the Drake Passage was open to deep water circulation through the Powell Basin by ~31 ± 2 Ma. The development of an extensive deep water circulation between South America and the Antarctic Peninsula, and the successive cooling and glaciation of the continent was probably a key event for the evolution of many Antarctic marine taxa (e.g. Brandt 1999, Crame 1999).

Palaeoceanography and glaciation

During the Eocene, productivity increased during cold periods and during cold to warm transitions, possibly as a result of increased upwelling of nutrient rich waters. In the Oligocene, in contrast, productivity maxima occurred during intervals of low $\delta^{18}O$ values (presumably warm periods) and a proto-polar front successively moved to the south. This profound transition in climate and productivity patterns occurred around 37 Ma ago, coeval with rapid changes towards increasing variability of oxygen and carbon isotope and benthic abundance records and towards larger-amplitude $\delta^{18}O$ fluctuations (Diester-Haass & Zahn 1996). These authors assume that this major change might have resulted from an initial opening of the Drake Passage, at least for surface- and intermediate-water circulation. These dramatic palaeoclimatic changes successively resulted in the generation of the psychrosphere, the cold world's deep sea bottom water, which is linked to the surface water in polar areas (DeConto & Pollard 2003).

Today, the Southern Ocean is isolated by the Polar Front or Antarctic Convergence, which limits the cold surface-water masses to the north and generates the Circumpolar Current, which is characterized by high current velocities (Hellmer & Bersch 1985). The Antarctic Deep Water (ADW) is of special importance for the benthic life. It is generated at the Southern Ocean ice margins, is cold, highly saline, and has led to the isolation of the benthic faunas due to the Cretaceous temperature decrease (Clarke & Crame 1989). The Weddell Sea (besides the Ross Sea and Adélie Land) is one of the main sources of the Southern Ocean Deep Water production. Because of its high density, this water mass sinks down the continental shelf and slope into the Southern Ocean deep sea, where it moves northwards, limited or diverted along ridges, troughs and spreading zones towards other deep sea basins (Patterson & Whitworth 1990). The deep water generation depends on the sea-ice production, which in turn is dependent on atmospheric temperatures, and the sea ice causes the high salinity of the surrounding water masses. Thus, the ADW production might have ceased during interglacial periods or have been stronger than at present during strong glaciation periods. The significant point here is that if ADW production ceased at any time in the past, the barrier to colonization would have been removed and benthic taxa from lower latitudes may have spread into the Antarctic. However, the interactions between sea-ice production and deep water generation are complex, and the gradual changes of the recent glacial cycles are not yet completely understood (Carmack 1990) and a review summary of the scientific discussions of the past 30 years is presented by Barker & Thomas (2004). It is so far impossible to trace the influences of these historic changes on the evolution, development, zoogeography, and range extensions of benthic organisms. Most benthic organisms cannot be found in the fossil records (e.g. Brandt *et al*. 1999), and the deep water palaeontological record remains almost entirely unknown. Therefore, we can only try to reconstruct the importance of these processes on the benthic life using phylogenetic or genomic analyses. Based on fossil ostracod data, Cronin & Raymo (1997) demonstrated a correlation of abundance and diversity of this taxon with the Milankovitch cyclicity.

Biological perspective

Haq *et al.* (1987) and Clarke & Crame (1992, 1997) documented the historic and climatologic consequences of the cooling of the Southern Ocean. Clarke (1990) explained that these temperature changes were only quick at geological time-scales, because even a cooling of eight degrees within three Ma would equal a cooling rate of 0.003 degrees C within 1000 years, a change, which unlikely had a dramatic influence on the evolution and extinction of benthic species. Nevertheless, many species became extinct and some survivors experienced a dramatic radiation (e.g. Watling & Thurston 1989, Brandt 1991, Wägele 1994, Crame & Clarke 1997, Crame 2000a, 2000b). During the gradual physical isolation of the Antarctic Continent in the Late Cretaceous, Early Cenozoic, the "Weddellian Province" was established and characterized by a number of distinctive epifaunal taxa, lacking any tropical/subtropical (i.e. Tethyan) taxa (Zinsmeister 1982). This fauna was affected by the mass extinction event in the Late Cretaceous, but some (e.g. benthic molluscan taxa) crossed the K–T boundary in Antarctica (Stilwell 2003). The successive cooling, glaciation and isolation of the continent had a strong impact on the evolution and radiation of many Antarctic marine taxa and caused the evolution of many key elements of the present-day benthic marine fauna (Vermeij 1978). Krill or notothenioid fish (e.g. Patarnello *et al.* 1996, Bargelloni *et al.* 1999, Eastman 2000, Di Prisco 2003), peracarid crustaceans (e.g. Brandt 1999, 2000) or pycnogonids (Clarke & Johnston 2003) radiated in the Southern Ocean, events comparable to the radiation of the marsupials in Australia (Woodburne & Case 1996). It is well known that a variety of environmental variables directly influence physiologically related functions such as growth, reproduction and behaviour (Feder *et al.* 2000). Molecular evidence dates the radiation of the Notothenioidei to the Middle Miocene (Cheng & Cheng 1999). A key physiological and evolutionary acquisition are the antifreeze glycopeptides in their blood, a development being coincident with the onset of the temperature drop and freezing seawater (Di Prisco 2003). Since species respond differently to climate change, the taxonomic balance in communities and ecosystems changes constantly by means of shifts in resource competition or partitioning and trophic relationships (Chapin *et al.* 1997, Tilman 1999). For example, the Tertiary extinction of the Decapoda Reptantia, is explained by physiological constraints related to haemolymph magnesium regulation capacities in the cold (Frederich *et al.* 2001) and reproductive strategies (i.e. developmental trade-off) (Thatje *et al.* 2003). Their extinction or the extinction of the Teleostei caused the emergence of new adaptive zones previously occupied. These adaptive zones or free ecological niches may have opened opportunities for spectacular adaptive radiations, like for some taxa of the Peracarida (Crustacea Malacostraca) (Brandt 1999, Lörz & Brandt 2004, Lörz & Held 2004) which were also favoured because of their brooding biology, and the Nototheniiformes (Pisces) (Eastman 2000), or the gastropod families Buccinidae, Naticidae, and Turridae (Crame 1997). Interestingly, within the bivalve molluscs especially those clades which have most recently evolved, the heterodonts, have evolved and speciated rapidly in the tropics and are now in the process of spreading to higher latitudes (Crame 2000a), possibly due to climatic changes? There is molecular evidence that many of the previously thought circum-Antarctic species are in reality several cryptic species, presently undergoing speciation processes, *Ceratoserolis trilobitoides* (Isopoda) is an example for this (Held 2003). Radiation processes are the product of the evolution in isolation over long periods of time and are always connected with a high level of endemism (60–90%) which has been reported by many authors for various taxa (e.g. Knox & Lowry 1977, White 1984, Clarke & Crame 1989, Dayton 1990, Brandt 1999). The polar environmental conditions, which successively developed in the Cretaceous, affected especially sensitive early life-history stages (Thorson 1936) and favoured brooding. Peracarid crustaceans bear a marsupium and exhibit brood protection what reduces the migration potential of the descendants, and possibly results in a reduced gene flow. This in turn might have caused local speciations and finally also in adaptive radiations, like that described for the Epimeriidae and Iphimediidae (Amphipoda) (Watling & Thuston 1989) or Antarcturidae and Serolidae (Isopoda) (Brandt 1991, 1999) on the Southern Ocean shelf. Recent records of anomuran lithodid crabs in the Southern Ocean deep sea of the continental slope (for review see Thatje & Arntz 2004) raise the question of the return of the crabs to the Antarctic after their extinction in the Lower Miocene (15 Ma) (Thatje *et al.* 2005) and the possible consequences of the return of these benthic top predators to the Southern Ocean for the benthic communities.

Today, anthropogenic impacts on the environment environmental change, natural selection and evolution and influence the future of the biosphere. For example, Southern Ocean shelf benthic communities have been reported to change due to increased physical disturbance, like iceberg scouring (Gutt & Starmans 1998, Gutt & Piepenburg 2003, Knust *et al.* 2003) or sewage abatement by man (Conlan *et al.* 2003). Present and probable future environmental changes in Antarctica include variations in temperature and ice extension, CO_2, UV-B, and precipitation. Biological responses to these factors, like algal diets in amphipods for UV and antioxidant protection (Obermüller *et al.* 2003), will affect initially the molecular level and determine population fitness and species interactions before it ultimately might affect biogeochemical cycling. Moreover, physical feedback of global climate change will regulate sea ice and primary production, winds and thermohaline ocean circulation, all of which have further biological impacts (Karentz 2003) and might force – as in the Late Cretaceous and Cenozoic – organisms again to survive at greater depths in the Southern Ocean.

We have to assume that many shelf species can physiologically tolerate life at greater depths. Tyler *et al.* (2000) demonstrated larvae of *Sterechinus neumayeri* to be extremely temperature and pressure resistant, and concluded that they could possibly conquer the Southern Ocean deep sea. It is, however, unknown whether the development of the deep water production influenced the migration potential of brood-pouch carrying Peracarida and thus enhanced submergence of some species.

Present day Southern Ocean benthic biodiversity

The present day Southern Ocean biodiversity is the result of different and simultaneously occurring biogeographic and evolutionary processes like the progressive retraction of taxa of a former cosmopolitan distribution established during the Jurassic and Cretaceous periods, of disjunct distributions of genera or species due to continental drift vicariance, active migrations of taxa in and out of the Southern Ocean and to radiation events due to the emergence of new adaptive zones. In general, the Southern Ocean marine ecosystem has a lower percentage of species known to date in most higher taxa than would be expected from its share of the area of the world's oceans (Arntz *et al.* 1997, Gutt *et al.* 2004), a fact probably due to the low sampling effort in huge area of the Southern Ocean deep sea.

While decapod crustaceans like brachyuran and anomuran crabs are important components of Patagonian benthic ecosystems (Gorny *et al.* 1996, Arntz *et al.* 1999), and brachyurans are entirely absent from the Scotia Arc and the Antarctic shelf an slope, 11 species of lithodids have been reported south of the Antarctic Convergence (Thatje *et al.* 2005) and first anomuran and brachyuran larvae have now been reported from the Bransfield Strait of the Antarctic Peninsula (Thatje & Fuentes 2003), possibly indicating a response to global change. The absence or scarcity of these top predators from the Antarctic shelf ecosystem may well have favoured the evolution of the

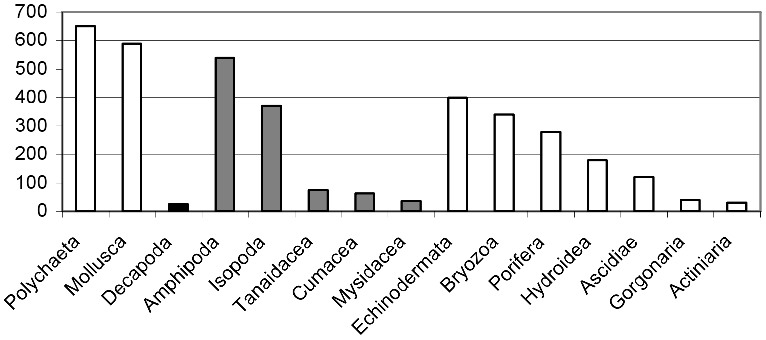

Fig. 1. Biodiversity of some Southern Ocean benthic taxa after Arntz *et al.* 1997, Brandt 1999, De Broyer *et al.* 2003, Clarke & Johnston 2003 (# of species reported from literature / selected taxa); unshaded = peracarid crustaceans, shading = decapod crustaceans.

peracarid crustaceans.

The present knowledge on the biology and the biodiversity of Southern Ocean marine taxa has been referred to in many publications (e.g. Dayton 1990, Arntz *et al.* 1997, Brandt 1999, De Broyer *et al.* 2003, Clarke & Johnston 2003) and species numbers of the Antarctic marine fauna were published by Dell (1972) and White (1984) and recently reviewed by Arntz *et al.* (1997), De Broyer *et al.* (2003) and Clarke & Johnston (2003). The most speciose taxa of the Antarctic benthos are the Polychaeta, Gastropoda, Bryozoa, Amphipoda, Isopoda, and Porifera. The sessile taxa are favoured on the Antarctic shelf due to the poorly sorted glacial-marine sediments (Howe *et al.* 2004) and increasing incidence of dropstones towards the shore (Clarke 1996a). Polychaetes and molluscs are speciose in the Southern Ocean occurring with about 600 species or more (Fig. 1), some taxa of Amphipoda and Isopoda (Peracarida) (unshaded columns in Fig. 1) have radiated due to the extinction of decapod crustaceans (shaded columns) which presently occur with few species, mainly Natantia, in the Southern Ocean (Gorny 1999). Many other epifaunal taxa appear to have adapted well to the coarse grained glacial substrates, as in many areas on the Antarctic shelf sessile filter and particle feeders are especially prominent (e.g. Fig. 1, Bryozoa to Actiniaria) (e.g. Gutt & Starmans 1998, Gutt *et al.* 2000 for community analyses of megafauna). Dense communities of sponges, ascidians, anemones, hydroids, gorgonians, bryozoans, and crinoids are characteristic of the modern Antarctic shelf fauna below the zone of the influence of ice scours and anchor ice formation (Crame 1997, Gutt & Piepenburg 2003) (Fig. 2). This fauna often forms stratified communities of a three-dimensional shape (as seen in tropical rain forests), consisting of sponges, bryozoans, ascidians, gorgonians, hydroids, crinoids, corals and anemones. Associated with these sessile forms are errant and vagile taxa such as echinoderms (ophiuroids, asteroids, echinoids, holothurians), pycnogonids, isopods, amphipods, nemerteans and gastropods.

While estimations of the biodiversity of the Antarctic shelf (Gutt *et al.* 2004) are still weak because many geographic areas are not sampled representatively until today (e.g. East Antarctic, Bellingshausen and Amundsen seas), the influential paper from Grassle & Maciolek (1992) might suggest that there may be a vast number of undescribed species present in the Southern Ocean deep sea as well. However, this area of the Southern Ocean was significantly under sampled in the past, as convincingly demonstrated by Griffiths *et al.* (2003) with the Southern Ocean bivalve distribution using SOMBASE.

Investigations of the biodiversity of the deep sea fauna

In general, the species composition of abyssal deep sea communities is poorly known in comparison with shelf and upper slope environments (Gage & Tyler 1991), their dependence of biotic and abiotic parameters, speciation processes and the regionalization of the fauna even more. However, early deep sea investigations of the 1960s demonstrated an extraordinarily high diversity of benthic faunas of the world oceans (Sanders *et al.* 1965, Sanders 1968, Sanders & Hessler 1969). These early explorers thought that the homogeneity of this ecosystem in space and time caused the diversity ("time-stability-hypothesis"). Other authors believed that contemporaneous disequilibria (including e.g. predation, competition, productivity) would have caused high benthic diversity and published the "intermediate disturbance hypothesis" (Dayton & Hessler 1972; for review summary see Levine *et al.* 2001). Today we know that the deep sea can be at least locally dynamic (Cronin & Raymo 1997, see above) and that the biodiversity of the deep sea can vary regionally and locally (Grassle & Maciolek 1992, Gage & May 1993). The question whether diversity is influenced by stability is still under debate (McCann 2000). Besides benthic deep sea communities, the bottom topography can be quite variable (Rex *et al.* 1997). Vast areas of soft sediment can be interrupted or isolated by complex topographic barriers, tectonically active areas (such as hydrothermal vents), troughs or seamounts (Van Dover 1990).

Species diversity and benthic community patterns may vary tremendously between deep sea habitats. Variability of isopod biodiversity was attributed to depth and latitude (Rex 1981, Etter & Grassle 1992, Rex *et al.* 1993, Poore & Wilson 1993) or to the sediment structure (Gage 1997, Thistle *et al.* 1999). It has been shown that the diversity of

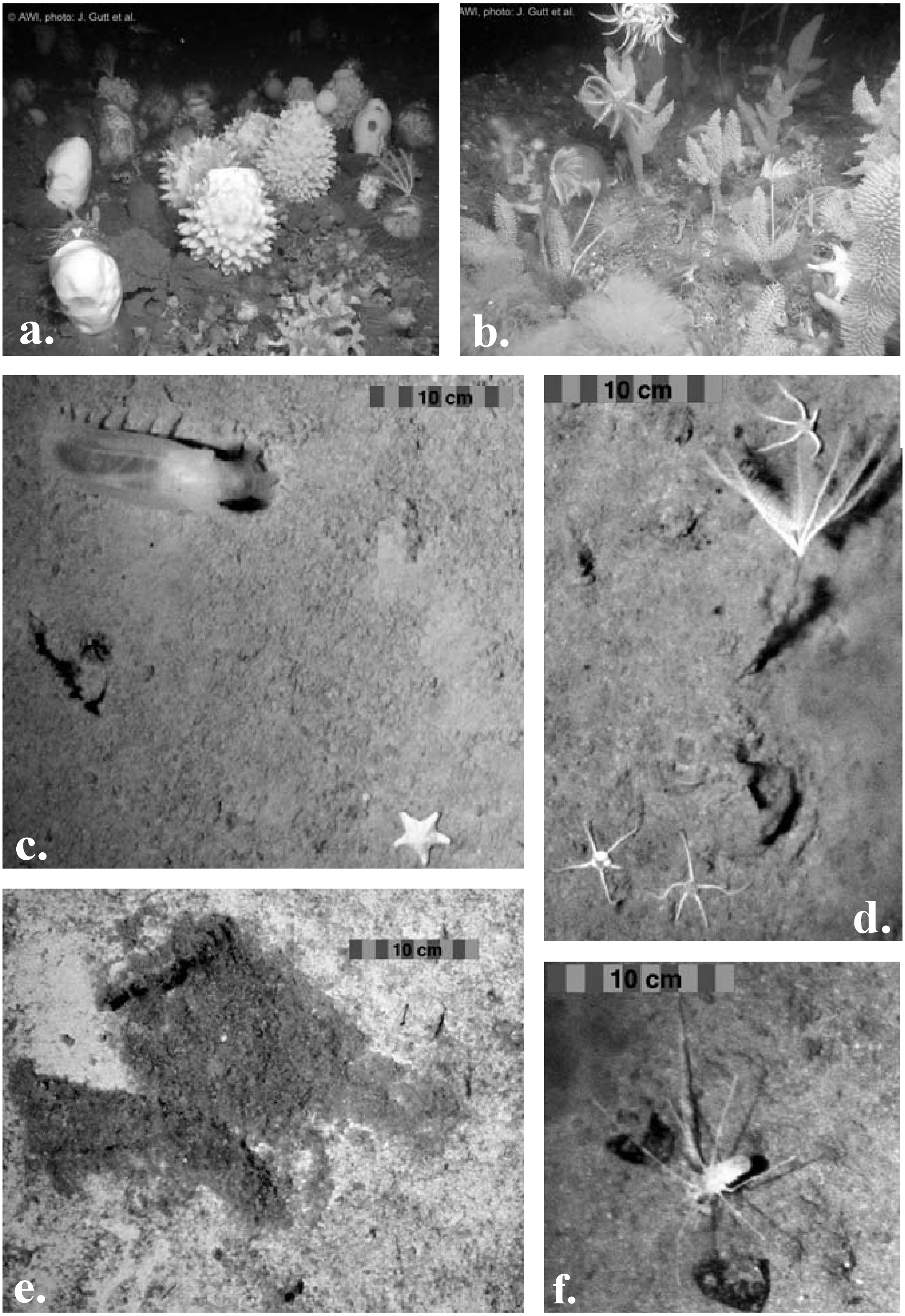

Fig. 2. a–b. Underwater images documenting the megabenthic biodiversity off Kapp Norvegia (Photos: Julian Gutt, AWI). **a.** A sponge association dominated by Hexactinellida. In between bryozoans, starfishes, and ophiuroids can be recognized. **b.** An association of mainly soft corals on which crinoids settle, sabellid polychaetes, bryozoans, starfish, anemones and sponges. **c–f.** Underwater images presenting insight into deep-sea biodiversity of the north-eastern Weddell Sea (Photos: Bob Diaz, VIMS; Diaz 2004), **c.** South Shetland Trench, 2905 m depth, a holothurian and a starfish, **d.** South Sandwich Trench, 6336 m depth, a stalked crinoid and ophiuroids, **e.** north-eastern Weddell Sea, "fluff" in 4992 m, **f.** a munnopsidid isopod in the north-eastern Weddell Sea in 2090 m depth.

the benthic communities on the Norwegian and Australian shelf and continental slope can be as high as in the deep sea (Gray 1994, Gray *et al.* 1997). Borowski & Thiel (1998) demonstrated high densities and species richness as well as diversity of benthic organisms, especially Polychaeta for the Peruvian deep sea (DISCOL experiment).

Despite the fact that latitudinal gradients in species diversity were hotly debated in the literature (e.g. Gray 2001), the basis for these data is still quite weak, as vast areas of the deep sea, especially of the Southern Hemisphere, remain unexplored. We also know only very little about genetic diversity and distances between individuals and populations (Gaston 2000).

Isopoda of the Southern Ocean deep sea

The abyssal isopod fauna of the Southern Ocean deep sea was not investigated in detail until now. Brandt (1991) published a summary of the few data available, published in widespread taxonomic literature. Closely related to some of these Southern Ocean deep sea genera are eyeless species or species with rudimentary eyes, whose phylogenetically related shelf species possess well developed eyes and are endemic for the Southern Ocean. The Antarcturidae, for example, occur in the Atlantic deep sea down to > 7200 m (Kussakin & Vasina 1993). For this family we have to conclude that the deep sea species submerged into the deep sea and had shelf ancestors. For some Janiroidea, like the families Acanthaspidiidae, Munnidae and Paramunnidae, Brandt (1991) hypothesized polar submergence, because the abundant shelf species possess highly developed eyes. The Asellota, which are typical shallow water species known to globally thrive on the continental shelves, can also be found at greater depths in the Southern Ocean deep sea [submergence of the Janiridae, Joeropsidae, Stenetriidae, Munnidae (down to 6110 m), Acanthaspididae (down to 7720 m)] which supports the theory of enhanced eurybathy of the Southen Ocean benthic taxa (Brey *et al.* 1996). Kussakin (1973) was also in favour of the submergence theory of Southern Ocean Isopoda.

Other authors think that the Isopoda have developed in the deep sea *in situ* where they also radiated before they have emerged onto the continental shelves, specially at higher latitudes (e.g. Hessler & Thistle 1975, Hessler & Wilson 1983, Wilson & Hessler 1987). In the Southern Ocean, many species of the deep sea suborder Asellota are also represented on the continental shelf. Emergence has been postulated in Antarctica for example for the Munnopsididae, Haploniscidae, Desmosomatidae, Nannoniscidae and Ischnomesidae (Brandt 1991, 1992, Wilson 1998, 1999). We therefore cannot consider the evolution of the shelf taxa isolated from that of the deep sea fauna. Brandt (1991, 1992) explained that both, submergence and emergence can be observed simultaneously. It is unrealistic to consider emergence to be the most important phenomenon in biogeography (Zenkevitch & Birstein 1960, Broch 1961, Hessler & Thistle 1975) or to stress submergence only (Dahl 1954, Wolff 1960, Kussakin 1973, Menzies *et al.* 1973).

It is very probable that at no time during the Cenozoic the Antarctic shelf ice sheet eradicated the Southern Ocean shelf fauna completely (Brandt 1991, Clarke & Crame 1992), although during the maximal ice extension huge ice masses were reported from north of the Antarctic Peninsula down to 1000 m depth (Canals *et al.* 2000). However, the principally observed wider bathymetric distribution of Antarctic invertebrates when compared to other seas (Brey *et al.* 1996), suggests that many continental slope species found shelter in deeper waters off the shelf during glaciation events. The geological history of the successive breakup of Gondwana, combined with the successive isolation of Antarctica, as well as the climatic deteriorations and/or changes due to the Milankovitch cyclicity, which has determined warm periods, have influenced the distribution and zoogeographic limits of organisms permanently. The subsequent changes in the ice-shelf extension probably led to speciation processes on the Antarctic continental shelf, in some taxa even to adaptive radiations, the reason why Clarke & Crame (1992) refer to Antarctica as a diversity pump. It is unknown to which extent species have migrated up and down the Antarctic continental shelf and slope following ice extensions and retreats during glacial maxima and minima. This possible biological consequence of climate changes might have led to eurybathy which is characteristic for many Southern Ocean species today (Brey *et al.* 1996). Whether the ADW production plays a crucial part for the deep sea Isopoda in colonizing the deep sea of the world oceans and serves as some sort of a diversity pump, remains unclear and to be investigated further. It is possible that the ADW production in the Weddell Sea acts as a distribution mechanism, driving Antarctic deep water fauna northwards into the Atlantic Ocean over evolutionary time-scales. Thus the Weddell Sea may be an important source for taxa presently living in the Atlantic and other neighbouring parts of the deep oceans. Furthermore, the more-or-less isothermal water column of the Weddell Sea and the surroundings of the Antarctic continent provide an obvious conduit for the migration of shallow-water species into the deeper waters.

It is possible that the Southern Ocean deep sea is a centre of evolution for the Isopoda like the shelf and has influenced the composition and species richness of the isopod faunas of the world oceans. Brökeland (2004), for example, already described the *Haploniscus cucullus* complex within the Haploniscidae (Asellota, Janiroidea). Raupach (2004) documented that the deep sea was colonized at least four times independently by the Asellota using molecular methods.

Studying the origin of Southern Ocean biodiversity – International Programmes

The reconstruction of the development of the Scotia Arc and the break-up of Gondwana during the Cenozoic illustrates that the islands of the Scotia Arc and the tip of the Antarctic Peninsula were much closer geographically (e.g. Jokat *et al.* 2003). This is also the reason why many scientists questioned, whether faunal exchange between South America and Antarctica was possible during these times or might even still be. This question was already the topic for a first IBMANT workshop in 1997 in Punta Arenas (IBMANT = Investigación Biológica Marina en Magellanes relacionada con la Antártida), however, during this workshop knowledge about the Southern Ocean deep sea fauna was still negligible. Results of this workshop were published by Arntz & Rios (1999); those of a second IBMANT workshop held in Ushuaia in 2003 will be published soon (Arntz *et al.* in press).

A decade before EPOS (European *Polarstern* Study) (Arntz *et al.* 1990) investigated the areas of Kapp Norvegia, Vestkapp, and Halley Bay on the shelf and slope in the Atlantic sector of the Southern Ocean and provided data on biodiversity, biogeography, and zonation. EPOS was followed by EASIZ (Ecology of the Antarctic Sea-Ice Zone) (e.g. Arntz & Gutt 1997, Arntz & Clarke 2002) which was also a study of ecological processes at organism and community level, especially regarding the role of the sea ice.

LAMPOS (Latin American *Polarstern* Study) and ANDEEP (Antarctic benthic deep sea biodiversity: colonization history and recent community patterns) aimed to understand large-scale gradients in biodiversity patterns. LAMPOS followed the shallows and islands along the Scotia Arc which might act as stepping stones for "island hoppers" (taxa) (Arntz & Brey 2003, Gutt *et al.* 2003), whereas ANDEEP focused on the role and importance of the Southern Ocean deep sea for faunal exchange processes (Fütterer *et al.* 2003, Brandt & Hilbig 2004).

Contrary to the Antarctic shelf which serves as a beautiful evolutionary laboratory due to its isolation and high degree of endemism within many taxa, the deep sea fauna is not isolated. Vast areas surrounding the Antarctic continental shelf are deep sea (Clarke 1996a, 1996b, Clarke & Johnston 2003). However, in the literature we do not find much information about the composition and functioning of the Southern Ocean deep sea benthic communities. Contrary to our knowledge of the benthos of the Southern Ocean shelf areas, the knowledge of the Southern Ocean deep sea is scarce (Brandt 2000, Clarke & Johnston 2003). Faunal elements being pressure tolerant may have migrated up and down the Antarctic continental shelf and slope in the past or in and out of abyssal plains of the world oceans.

Against this background ANDEEP aimed to conduct the first base-line survey of the deep water benthic faunas of the Scotia and Weddell seas, and to investigate the evolutionary and ecological processes and oceanographic changes which have resulted in the present biodiversity and distributional patterns in the Southern Ocean deep sea. Further ANDEEP questions were:

- to investigate the evolutionary processes and oceanographic changes which have resulted in the present biodiversity and distributional patterns in the Antarctic deep sea,
- to investigate the influence of sea-floor habitat diversity on species and genetic diversity in the Antarctic deep sea,
- to investigate the colonization and exchange processes of the deep-sea fauna in relation to changes in seabed geography over geological time,
- to assess the importance of the Antarctic region as a possible source for many of the deep-sea benthic taxa in other oceans.

The first results from the ANDEEP I and II expeditions to the Southern Ocean deep sea are summarized in a special Deep Sea II volume (Brandt & Hilbig 2004).

Some preliminary results for the Southern Ocean deep sea biodiversity based on the ANDEEP expeditions

There is 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 has been recognized (Poore & Wilson 1993, Rex *et al*. 1993, Rex 1997, Culver & Buzas 2000). In contrast to what is known about the benthos of other deep sea areas, and especially shelf areas around the Antarctic continent, our knowledge of the Southern Ocean deep sea faunas is meagre. Although the Antarctic deep sea floor is the largest single benthic habitat, it remains the least studied (Clarke & Johnston 2003). In 2002, the ANDEEP I (ANT XIX-2) and ANDEEP II (ANT XIX-3) expeditions (Brandt & Hilbig 2004) recovered a large number of organisms of all size classes from the Drake Passage, the area of the South Shetland Islands and Trench, the western Weddell Sea and the South Sandwich Trough. ANDEEP made it possible for the first time to compare Southern Ocean deep sea faunas to those collected elsewhere using similar sampling strategies and the same array of gear. ANDEEP III (ANT XXII-3) in 2005 started with a station transect on the Greenwich Meridian in the Cape, Agulhas and northern Weddell Sea Basins. It was also possible to sample some additional sites not envisaged in the original cruise programme; these were located on the NE Peninsula slope, the Bransfield Strait, and in the Bellingshausen Sea off Anvers Island. As in the case of ANDEEP I and II, a variety of sampling gears was used during ANDEEP III to collect animals of all different size classes living in and on the sea floor. After a CTD profile of the water column was obtained at the beginning of each biological station, the sediment profile imaging system (SPI) was deployed in order to obtain still photographs and video footage of the surface of the seafloor and profiles through the sediment-water interface and upper sediment layers. For meiofauna (32–300 µm size range) and macrofauna (size class > 300 µm) investigations, two multicorers and two box corers were used to recover sediment samples of different, but well defined surface areas together with the overlying bottom water. The multicores were also used for the characterization of sediment parameters. Two other biological sampling devices were towed across the bottom and obtained material from a much larger but less well-defined area of seafloor. The epibenthic sledge was also used for the macrofauna and the Agassiz trawl for the larger animals, the megafauna. Additionally, a baited trap was deployed at the beginning of each ANDEEP station to attract and catch scavenging animals, mainly amphipods, not usually collected by other gears. It was recovered approximately 48 hrs later at the end of the station work.

Meiofauna

Prior to ANDEEP, only very limited 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 protist meiofaunal organisms and were diverse. They consisted of a mixture of hard-shelled, multichambered agglutinated and calcareous species together with soft-shelled, monothalamous taxa which increased in relative abundance with increasing water depth. Particular attention was paid to the diverse and usually neglected soft-shelled species (e.g. allogromiids, saccamminids, komokiaceans), the vast majority of which are new to science. Interestingly, many of the much better-known calcareous species in ANDEEP samples also occur in the Northern Hemisphere. For example, *Epistominella arctica*, which is fairly common on the Weddell Abyssal Plain, was first described from the Arctic Ocean. Specimens from these two areas are morphologically identical (Cornelius & Gooday 2004). There seem to be 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 foraminiferans, particularly the soft-shelled monothalamous (single-chambered) forms, collected during ANDEEP II were new to science. One monothalamous species has now been described as *Conqueria laevis* (Gooday & Pawlowski 2004) and another one is in Gooday *et al.* (2004). Both of these new species are characterized on the basis of molecular and morphological criteria.

Prior to the ANDEEP expeditions, far less was known about the metazoan meiofauna in the Antarctic deep sea. A handful of papers dealt with meiofauna at the higher taxon level. Two ANDEEP studies focussed on nematodes at the levels of genera (Vanhove *et al*. 2004) and species (Vermeeren *et al*. 2004). These revealed a high diversity, even at generic level, with as many as 40 genera being present in individual samples. Very little was known about harpacticoid copepods at the species level in the Southern Ocean. One new species was described from ANDEEP II material (Veit-Köhler 2004) and many other new species collected during the second ANDEEP expedition are currently under investigation. Data on the entire metazoan size fraction (32–1000 µm) from the South Sandwich Trench (Vanhove *et al.* 2004) revealed unexpectedly high standing stocks (predominately nematodes), situated above the regression line of meiobenthic abundance against water depth for the World Ocean. In particular, the deepest trench sample (6300 m water depth) yielded unusually high meiofaunal abundances, despite low values for indicators of food availability. 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, some species are spatially restricted to the South Sandwich Trench (Vermeeren *et al.* 2004).

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 (about 85%) (Brandt *et al.* 2004). Most important taxa are Polychaeta, Peracarida (Crustacea) and Mollusca (Bivalvia and Gastropoda). ANDEEP revealed some further surprizing results. Within the Peracarida it was the Amphipoda that comprised a major fraction of the epibenthic sledge material (32% of all individuals), surpassed only by Isopoda (38%). Interestingly, ANDEEP III yielded the same percentage of Isopoda and Amphipoda in the samples as ANDEEP I & II. 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 scavenging amphipod species extend their distribution from the shelf to the slope and only one to the abyssal zone (De Broyer *et al.* 2004).

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 2004). For example, brooding is - as far as we know - much less common among polychaetes, 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 (Hilbig 2004).

Our knowledge of the deep water bivalve fauna of Antarctica is generally 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 cline with depth in Antarctic bivalves but it does provide evidence for underestimated species richness in deep water because of lack of sampling (Linse 2004).

Megafauna

Megafauna was found to be distinctively less diverse than the other two size classes, and much less diverse than on the Antarctic shelf. Both, biological and geological processes structure surface sediments in the Scotia and Weddell Seas. There appeared to be gradients in the degree of bioturbation and type of biogenic structure present with depth: Highest diversity of biogenic structures was seen at shallower depth < 1200 m. Lowest megafaunal richness was seen at depths > 2300 m. Some examples, as documented on Southern Ocean deep sea underwater images are presented in Fig. 2 (Diaz 2004). Most important taxa were Porifera, Mollusca, Echinodermata, and Brachiopoda (Fütterer *et al.* 2003), 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. Five species and one subgenus are new to science (Janussen *et al.* 2004). To date, 20 hexactinellid species have been reported from the deep Weddell Sea. A zoogeographic distinction between oceanic and continental species exists.

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.* 2004).

ANDEEP in CeDAMar

ANDEEP contributes to the abyssal biodiversity data within CeDAMar (Census of the Diversity of the Abyssal Marine Life) (http://www.coml.org/descrip/cedamar.htm), which is one of the core field projects of the CoML (Census of Marine Life) (http://www.coml.org/coml.htm). CeDAMar aims at the documentation of actual species diversity of abyssal plains as a basis for global change and for a better understanding of historical causes and recent ecological factors regulating biodiversity.

In order to answer some of these questions posed for ANDEEP, data from adjacent abyssal ocean basins, especially from the South Atlantic and from neighbouring Southern Ocean abyssal areas are needed. Some of these data were gathered during ANDEEP III, when comparative samples were obtained in the Cape Basin with the same array of gears as used during ANDEEP I & II. Further material was collected during the DIVA-2 expedition with RV *Meteor* in the Guinea Basin at the same time when ANDEEP III took place (March 2005). Further from the north in the South Atlantic, samples are available from the DIVA-1 expedition to the abyssal Angola Basin (Brandt *et al.* 2005). However, this basin is isolated by the Walvis Ridge to the south, which might be the reason why we found only little similarity with the abyssal Southern Ocean Isopoda (comparisons of the material are currently done). Even though it is planned to sample the abyssal South Atlantic more adequately in the framework of CeDAMar within the next decade, the faunistic results of ANDEEP I–III will be a prerequesite to answer the questions above.

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