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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
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The Antarctic-Magellan connection: macrobenthos ecology on the shelf and upper slope, a progress report*

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SUMMARY: Ecological work carried out on the Antarctic and Magellan shelves since the first IBMANT conference held at the UMAG, Punta Arenas in 1997 is summarized to identify areas where progress has been made and others, where important gaps have remained in understanding past and present interaction between the Antarctic and the southern tip of South America. This information is complementary to a review on shallow-water work along the Scotia Arc (Barnes, 2005) and recent work done in the deep sea (Brandt and Hilbig, 2004). While principally referring to shipboard work in deeper water, above all during the recent international EASIZ and LAMPOS campaigns, relevant work from shore stations is also included. Six years after the first IBMANT symposium, significant progress has been made along the latitudinal gradient from the Magellan region to the high Antarctic in the fields of biodiversity, biogeography and community structure, life strategies and adaptations, the role of disturbance and its significance for biodiversity, and trophic coupling of the benthic realm with the water column and sea ice. A better understanding has developed of the role of evolutionary and ecological factors in shaping past and present-day environmental conditions, species composition and distribution, and ecosystem functioning. Furthermore, the science community engaged in unravelling Antarctic-Magellan interactions has advanced in methodological aspects such as new analytical approaches for comparing biodiversity derived from visual methods, growth and age determination, trophic modelling using stable isotope ratios, and molecular approaches for taxonomic and phylogenetic purposes. At the same time, much effort has been invested to complement the species inventory of the two adjacent regions. However, much work remains to be done to fill the numerous gaps. Some perspectives are outlined in this review, and suggestions are made where particular emphasis should be placed in future work, much of which will be developed in the frame of SCAR's EBA (Evolution and Biodiversity in the Antarctic) programme.

Keywords: macrobenthos, Antarctic, Magellan region, biodiversity, biogeography, ecology, evolution, disturbance.

RESUMEN: LA CONEXIÓN ANTÁRTICO-MAGALLÁNICA: ECOLOGÍA DEL MACROBENTOS EN LA PLATAFORMA Y TALUD SUPERIOR, UN INFORME SOBRE LA LABOR REALIZADA. – Las investigaciones ecológicas llevadas a cabo en la plataforma antártica y de Magallanes, desde la primera reunión del IBMANT en Punta Arenas en el año 1997, se resumen en este trabajo, con el fin de identificar las áreas en que se han realizado progresos considerables, así como aquellas en las que aún quedan muchos aspectos por cubrir para poder comprender tanto el pasado como el presente de las interacciones entre las áreas antárticas y el "Cono Sur" de Sudamérica. La información que aquí se ofrece complementa la revisión de los trabajos realizados en aguas someras a lo largo del Arco de Scotia (Barnes, 2005) así como los trabajos más recientes ejecutados en el mar profundo (Brandt and Hilbig, 2004). Si bien esta revisión que aquí presentamos se centra principalmente en trabajos realizados a bordo de buques oceanográficos y en aguas profundas, se presentan también las investigaciones más relevantes hechas en las bases de tierra. Seis años después del primer congreso IBMANT son numerosos los progresos realizados a lo largo del gradiente

latitudinal desde la región de Magallanes hasta las zonas de la Alta Antártida en los campos de biodiversidad, biogeografía, estructura de comunidades, estrategias de vida y adaptaciones, papel de las perturbaciones y su significado para la biodiversidad así como en los aspectos referentes al acoplamiento trófico entre el sistema bentónico, la columna de agua y el hielo marino. Se ha perfeccionado nuestro conocimiento del papel de los factores evolutivos y ecológicos para las condiciones ambientales pasadas y presentes, así como para la composición y distribución de especies y funcionamiento del ecosistema. Además de los avances por parte de la comunidad científica en el conocimiento de las interacciones entre estas dos regiones geográficas, son numerosos los progresos que se han producido a nivel metodológico, como por ejemplo nuevas aproximaciones analíticas para comparar la diversidad entre zonas a partir de análisis de imágenes, determinación de crecimiento y edad, modelaje trófico empleando los valores de las proporciones de determinados isótopos estables, así como el trabajo con métodos moleculares con aplicaciones taxonómicas y filogenéticas. Paralelamente se ha realizado un gran esfuerzo en completar el inventario de especies de las dos regiones adyacentes. Sin embargo, queda todavía mucho trabajo por hacer para cubrir los vacíos aún existentes en el conocimiento de ambas regiones. En esta revisión se presentan algunas perspectivas, así como sugerencias, para el trabajo a realizar en el futuro, gran parte del cual se desarrollará en el marco del programa EBA (Evolution and Biodiversity in the Antarctic) del SCAR.

Palabras clave: macrobentos, Antártida, región magallánica, biodiversidad, biogeografía, ecología, evolución, perturbación.

INTRODUCTION

Macrobenthic research is just one major topic in the frame of the IBMANT (Biological Interactions between the Magellan Region and the Antarctic) approach, which encompasses the outcome of 40 Ma of evolution in these last fractions of the Gondwana continent (Crame, 1999). IBMANT deals with the consequences of tectonics and climate change, continental drift and glaciation, as well as with those environmental and biotic factors, which are presently structuring the biota on either side of the Drake Passage (Fig. 1). Macrobenthos is an important issue in this context, because it is a particularly rich compartment, which due to its relative site fidelity preserves many characters over longer time scales than the rapidly changing plankton. In our specific case, we are looking for the
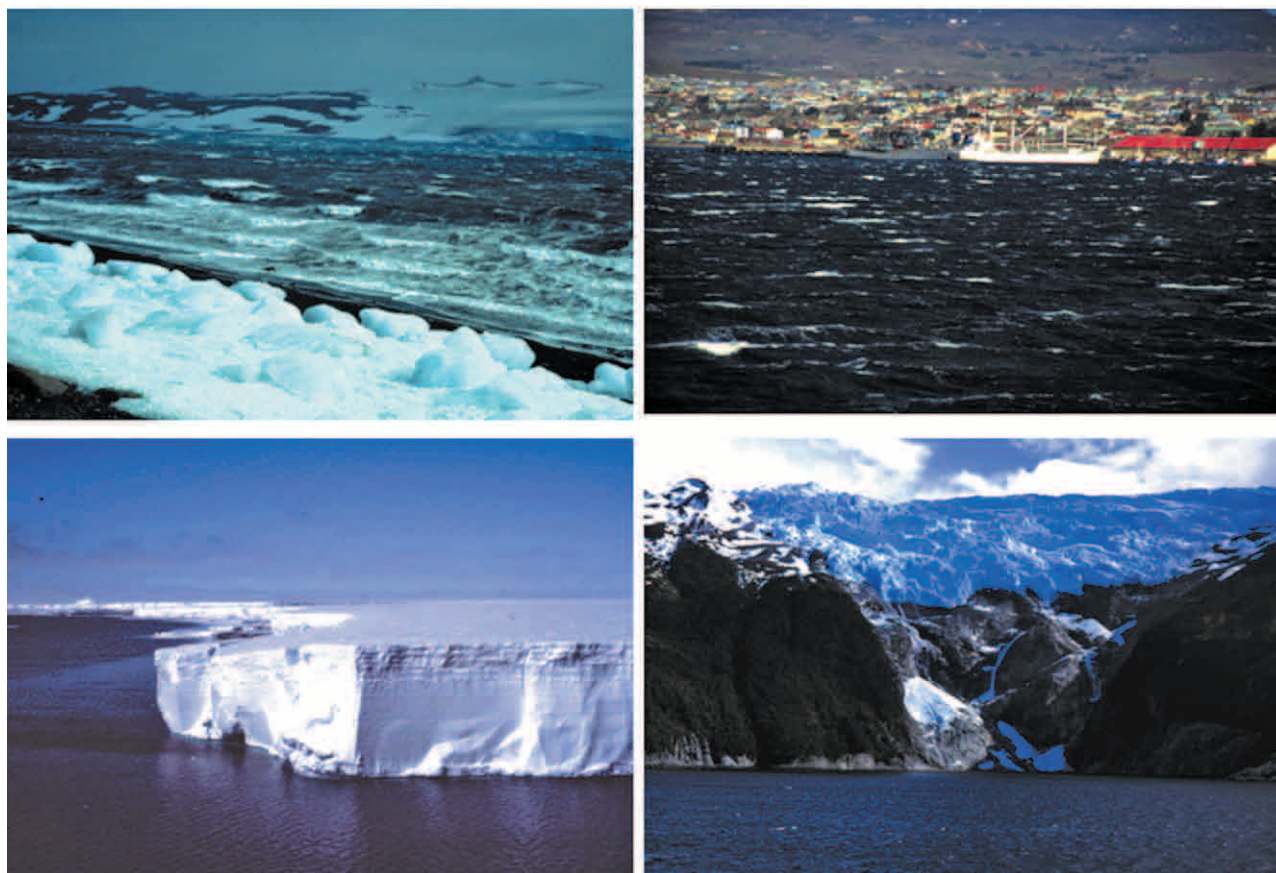

FIG. 1. – Shallow waters exposed to the effects of storm and ice are a typical aspect at King George Island (above left) whereas in the polynya facing the ice shelf margin in the Weddell Sea (below left) "shallow" bottoms begin at about 150-200 m depth. While surface waters are usually fairly calm, the seafloor is disturbed by large icebergs (see Fig. 9). In the Straits of Magellan, open shores may be exposed to heavy storms but without ice effects (above right, off Punta Arenas) whereas glaciers produce cold, low salinity waters and heavy siltation in the fjords (below right). Photos AWI; W. Arntz.
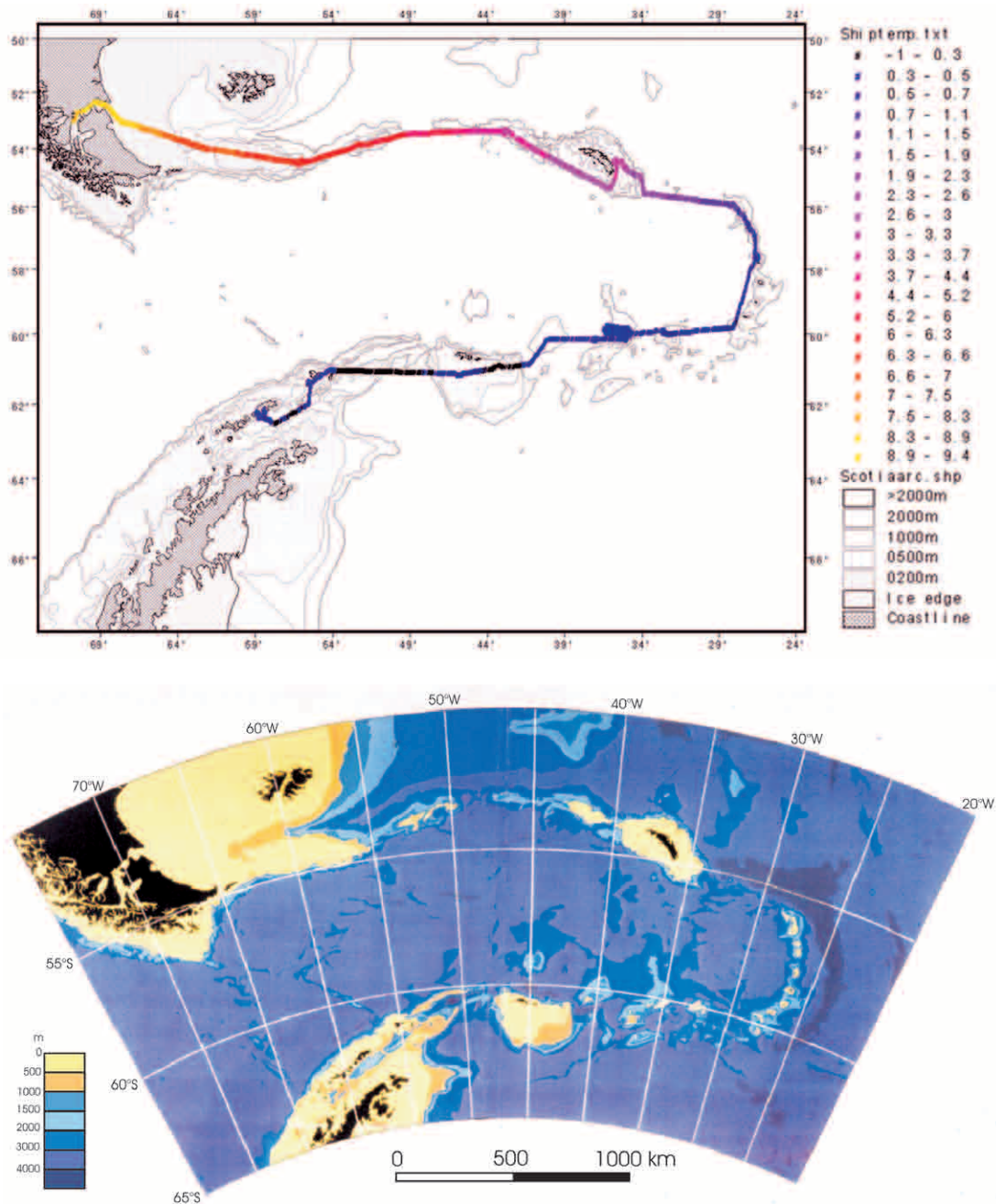
Fig. 2. – Sea surface temperatures (°C) along the Scotia Arc during the LAMPOS cruise (ANT XIX/5) of RV "Polarstern" (April 03 to May 05, 2002). Temperatures are shown from the start of the cruise in Punta Arenas to the South Shetland Islands, revealing that the Polar Front was south of South Georgia in April 2002. (From R. Knust, unpubl.; map courtesy M. Thomson).

common heritage of those parts of the great south continent, which drifted apart while major ocean gateways opened around Antarctica, giving rise to a vigorous circumpolar current system and the Antarctic Convergence (Polar Front). Unfortunately, the exact temporal sequence of those large-scale events in the past, particularly where the Drake Passage is concerned, is not yet as clearly understood as would be desirable for the purpose of linking environmental and evolutionary processes (see Thomson, 2005). It is very likely that major events, rather than gradual cooling over large periods, had marked effects, but we are still unable to establish a close connection between past physical events and biological processes.

A particularly interesting area for studying biogeographic and evolutionary links between the Magellan region and the Antarctic is the Scotia Arc, the only recent island and shallow-water bridge to the Antarctic, which was studied during the LAMPOS

"Polarstern" cruise (Arntz and Brey, 2003; for nearshore research see Barnes, 2005). Cross-transport of meroplanktonic larvae (Thatje and Fuentes, 2003) through frontal zones, e.g. by eddies (Glorioso et al., 2005), might provide a connection between the northern and southern branches of the Scotia Arc, but this is more likely for deep than for surface waters (Fahrbach, pers. comm.). Clearly, W-E transport with the Westwind Drift/Antarctic Circumpolar Current (ACC), as can be seen from large amounts of drifting macroalgae (pers. obs.) and fauna rafted on algae or debris (Helmuth et al., 1994; Barnes, 2002; Thiel and Gutow, 2004; Barnes, 2005) is more likely than the reverse, or than cross-transport in this area. The situation is complicated by temperature differences between the northern and southern branch (Fig. 2). For some molluscan taxa, extremely far travel with the ACC has been registered between Patagonia and New Zealand (16,000 km; Beu et al., 1997), but even this may be easier than „island hopping" between the two branches of the Scotia Arc or movement against the main current direction.

This review compiles data from various cruises and some shore stations. Of course not all the information included here was created within the IBMANT frame, but the programme certainly stimulated interest in the Magellan-Antarctic connection, with a focus on work on the continental shelves. Deep-sea macrobenthos studies within the ANDEEP context, which were presented at the same Conference in Ushuaia, are published in another volume (Brandt and Hilbig, 2004). Taxonomic work is only marginally included in this review, because a full presentation would have gone far beyond its scope.

RECENT PROGRESS

Links to the past

Evolutionary and ecological factors shaping present-day environmental conditions and species composition

Much new information has been created in recent years on climate fluctuation and glaciation in Antarctica and the Southern Ocean in the past. Some of it is based on carbon and oxygen isotope records from fossil foraminifers in deep-sea sediments (Zachos et al., 2001a,b). These and other data have led to conclusions about the origin of the present Antarctic ice sheet, formation of the Antarctic Cir-

cumpolar Current (ACC) and the gradual cooling of the ecosystem. There seems to be a consensus now that ice growth on East Antarctica began at least 40 Ma ago, and that the Tasman ocean gateway was essentially open by 34 Ma (Mackensen, 2004). However, while an improved scenario is developing on larger time scales, certain details of greatest interest to the biologists, such as the definite opening of the Drake Passage — a subduction zone — and the date of formation of a vigorous ACC, that seemed to be solved almost 30 years ago (Barker and Burrell, 1977) remain obscure, as has been reviewed in a recent paper (Barker and Thomas, 2004). Ocean gateways do not open overnight; the change from shallow seas connecting the former parts of Gondwana to the present deep-sea floor in the passage separating them must have been a gradual one. The Antarctic Circumpolar Current (ACC) is the mightiest current system on Earth, and to function the way it does it requires deep water without major obstacles (Barker and Thomas, 2004). Even nowadays, the relatively narrow opening of the Drake Passage creates numerous eddies as the West Wind Drift is forced through it (Glorioso et al., 2005). A simultaneous definite opening of the two large gateways on either side of the Antarctic continent about 34 Ma ago, as is postulated by some geologists, seems unlikely from a biological point of view because of the much greater difference between the Australian and Antarctic marine fauna as compared to the relatively narrow faunistic relations between the Antarctic and South America (Arntz and Ríos, 1999). In fact, some molecular datings of major faunal changes (see below) might rather support a final separation of the Antarctic and South American continents by cold deep water at the time of mid-Miocene cooling (16-14 Ma) when the "tectonic reorganisation of the gateway regions may have altered poleward heat and moisture transport, resulting in Antarctic ice growth and global cooling" (Shevenell et al., 2004). At any rate, notwithstanding the existence of intermittent continental ice sheets since the E/O transition, there is a marked $d^{18}O$ increase in middle Miocene cores that may have resulted from an increasing ice volume and deep-water cooling (Wright et al., 1992), and which reflects one of the major steps in the process of Antarctic isolation.

In general, not one single event such as a meteorite impact seems to have shaped evolution in the Antarctic, but rather various tectonic, climatic, and oceanographic changes that influenced different

taxa in different ways (Clarke and Johnston, 2003). Several Southern Ocean gastropod and bivalve genera can be traced back to at least the late Eocene (Crame, 1997). The origins of part of the present fauna are even with the coastal fauna of Gondwana prior to break-up, potentially going back to the Mesozoic or Palaeozoic (Aronson and Blake, 2001; Gili *et al.*, in prep.). Are the high Antarctic three-dimensional communities of sessile suspension feeders (sponges, bryozoans, anthozoans, ascidians) on high Antarctic soft bottoms a result of environmental conditions, which resemble those in Cretacean shallow epicontinental seas? For example, the lack of continental and riverine runoff from a frozen continent and the ensuing transparency of the water might favour sessile suspension feeders in a similar way. There are other similarities to palaeo-conditions such as the lack of "skeleton-breaking" predators (Aronson and Blake, 2001). The fragmentation of Gondwana influenced the fauna particularly by the introduction of a Tethyan element through the Weddell Province (Clarke and Crame, 1989).

During evolution *in situ*, climate change and glaciation resulted in the extinction of some groups, and provided evolutionary opportunities for others. More recently, development of the fauna may have been triggered by exchange along the Scotia Arc, possibly assisted by eddies, and with the deep sea (for processes, ecological barriers and pathways involved in such exchange in the Arctic see Vermeij, 1991).

Present global warming may well provide once more a situation where exchange is enhanced. Conditions in the Potter Cove (South Shetland Is.), under heavy siltation from a melting glacier, show what the Weddell Sea shelf might look like under continued warming. However, conditions may have been less stable than supposed hitherto even during major glaciations, when the advancing ice cap pushed shelf sediments down the continental slope (Thatje *et al.*, 2005b). Presently there is a gradient of decreasing turbidity and increasing importance of sessile soft-bottom suspension feeders from Patagonia to the high Antarctic. Exceptions, such as the highly structured gorgonian assemblages on Burdwood Bank and in some Patagonian fjords, live on hard bottoms, as do most recent sessile suspension feeders worldwide.

For the Magellan region, recent work has concentrated mainly on the development after the last ice age. Glaciation in this region never quite reached the extremes occurring on the Antarctic continent, but there still was an extensive ice cap around the Late Glacial Maximum (LGM) about 21 ky BP (Clapperton, 1993b) and later (Clapperton *et al.*, 1995), the remainders of which are still recognizable in the South Patagonian Icefield. The fjords and channels of Patagonia and Tierra del Fuego were covered by a thick ice cap from 35 to 55°S during the LGM (Clapperton *et al.*, 1995; Benn and Clapperton, 2000). During this period the Southern Ocean suffered distinct cooling, accompanied by an expansion of Antarctic winter and summer sea ice (Gersonde *et al.*, 2003). Northward expansions and withdrawals of the ACC seemingly were also the main reasons for millennial-scale climate variations after the LGM and during Patagonian glacial retreat until about 12 ky BP (Lamy *et al.*, 2004). The LGM and the processes during gradual warming, which was interrupted by various glacier readvances (Clapperton, 1993a), probably shaped much of the biogeographic pattern that we find nowadays. The sea level was lower during glaciation than today, and the earliest seawater incursion into the Straits of Magellan after the retreat of the glaciers occurred only around 8 ky BP (McCulloch and Davies, 2001). Since then, the ice sheet has been retreating substantially (Lamy *et al.*, 2002), leaving as ultimate remains under global warming conditions the South Patagonian Icefield and a number of glaciers descending from the mountain chains of the Andes and the Cordillera Darwin.

During the Holocene, shifts of the latitudinal position of the Southern Westerlies became the principal climate factor in the "Cono Sur" (Lamy *et al.*, 1999, 2001, 2002). Temperature and salinity reached maximum values shortly after the "Holocene optimum" at about 6 ky BP and then started their decline to modern values (Lamy *et al.*, 2002). Reduced advection of cold, nutrient-rich Subantarctic water through the ACC, reduced precipitations, diminished advection of Chilean fjord water of low salinity and/or reduced supply of freshwater and micronutrients characterised the Chilean/Argentinean fjord region during the mid-Holocene. Continental rainfall increased again during the late Holocene, from about 4 ky BP, and decreasing temperatures point to another equatorward shift of both the ACC and the Westerlies in the period until present. Recently, Rignot *et al.* (2003) estimated the volume change of the largest 63 glaciers in Patagonia and found an acceleration of ice loss since 1995 as compared to the preceding period. Thinning of these glaciers is faster than can be explained from warmer air temperatures and

decreased precipitation, and their contribution to sea level rise is relatively higher than that of Alaska glaciers (Rignot et al., loc.cit.).

Recolonisation of the Beagle Channel and the Straits of Magellan, in comparison to the open oceans off Patagonia and Antarctic deep waters, occurred quite recently, as these areas became gradually ice-free only during glacial retreat after the LGM.

Recent ("ecological") factors shaping the benthos have been studied for quite some time, with emphasis on the Weddell and Ross seas in the high Antarctic, the Antarctic Peninsula, the Scotia Arc and the Straits of Magellan. Trends do not always go into the same direction: While the Peninsula is experiencing a period of rapid warming by about 0.5°C per decade, the Ross and Weddell seas appear to be undergoing a period of cooling (Vaughan et al., 2003). Glacier retreat is reported from the western side of the Antarctic Peninsula and the Magellan region, and ice shelf retreat from the eastern side of the Antarctic Peninsula (Vaughan and Spouge, 2002). Inorganic silt of glacier origin increasingly impoverishes and alters benthic communities in such areas (Klöser et al., 1996; Mutschke et al., 1996; Thatje and Mutschke, 1999) and adds to the effect of storms, waves, ice scour by bergs and growlers, anchor ice and biotic interaction (Sahade et al., 1998; Barnes, 2005).

The combination of evolutionary and ecological factors shapes the aspect of present-day assemblages in the Southern Ocean, presumably with a certain increase in importance of evolutionary, and a decrease in importance of ecological processes towards the pole. Presently, ecological factors may be gaining importance (Poulin et al., 2002), making the Antarctic Peninsula less Antarctic and more similar to the Magellan region, but in the large-scale context of geological and climate history this represents just another oscillation.

We may have a long way to go until we can associate major extinctions, radiations etc. in the sea with specific tectonic, climatic, glaciological or oceanographic events. Hopefully, however, we may be able—in close cooperation with other disciplines—to identify some major events when several important groups were affected at the same time (see Thomson, 2005).

New molecular results on radiation and extinction in the Antarctic benthos

Some progress has been made in molecular and biochemical work on extinction and radiation of species. Antarctic decapods suffered major extinctions whereas pycnogonids, amphipods, and isopods underwent major radiations. Fish, not dealt with explicitly in this review, suffered broad extinction, and the teleost taxon Notothenioidei showed rapid active radiation within a few million years (Bargelloni et al., 2000; Eastman, 2000; Pisano and Ozouf-Costaz, 2000). Chen et al. (1997) put the basal notothenioid radiation at about 15 Ma, which would coincide fairly well with the mid-Miocene cooling event and presumed significant growth of the East Antarctic ice sheet (Eastman and Clarke, 1998, Clarke, 2003a).

The isopod families Antarcturidae and Serolidae (Fig. 3) are among these latter taxa (Brandt, 1991, 2000; Brandt and Poore, 2003). Held (2000) did a molecular study on 16 species of serolid isopods from Antarctic waters, the deep sea, South America and Australia. This investigation has important consequences for understanding the biogeography of the Serolidae, indicating that all Antarctic species studied form a monophyletic group, which stems from species with closest extant relatives in South America. The 3 deep-sea species included in the study are closely related to species living on the Antarctic shelf, indicating parallel colonisation of the deep sea by way of polar submergence. The radiation of the shelf serolids probably occurred after the opening of the Drake Passage and increasing isolation of the Antarctic (Held, 2000).

Speciation rate of polar taxa does not seem to be slower than in warm water taxa (Held, 2001), a suggestion made also by Clarke and Crame (1997). "This suggests that the continuous evolutionary change (....) will not be mutation-limited" (Clarke, 2003a). This seems paradox in view of the long embryonic development, slow growth, late first maturity, reduced fecundity and retarded generation time of most Antarctic invertebrates (Arntz et al., 1994).

Speciation seems to continue at a high pace nowadays. E.g., sequences from the mitochondrial 16S ribosomal RNA gene show that the serolid isopod *Ceratoserolis trilobitoides* consists of several species (Held, 2003), as had been suspected before by Wägele (1986) because of the polymorphism in this "species". At least four species seem to form the *Glyptonotus antarcticus* group (Held and Wägele, 2005). There may be many more cryptic species in the Antarctic benthos, raising considerable doubts as to the generally assumed "circumantarctic" distribution of the benthos.
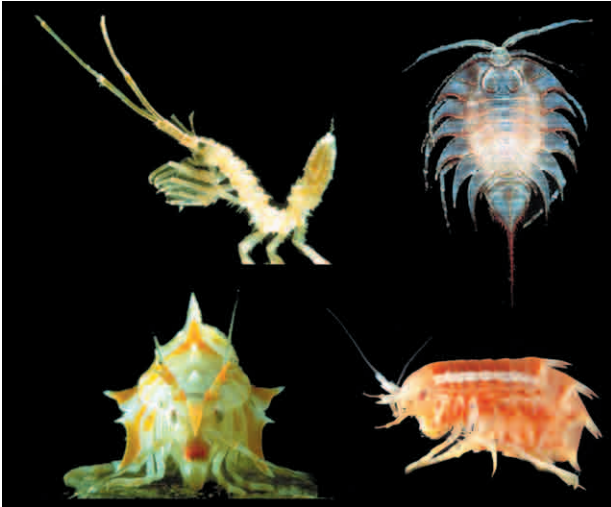
F<small>IG</small>. 3. – Among those peracarid crustaceans that radiated in the Miocene, Antarcturidae and Serolidae (above) are the most spectacular cases among the isopods while Epimeriidae and Iphimediidae (below) represent the amphipods. Due to their abundance and ubiquity, some species of these families are excellent candidates for checking circumantarctic distribution and cryptic speciation. (Photos: M. Klages, M. Rauschert).

Phylogenetic origins of Antarctic amphipod crustaceans are difficult to elucidate, because no fossil remains of this group have been found in the Antarctic. Lörz and Brandt (2004) studied phylogenetic relations of 14 species in the amphipod families Iphimediidae and Epimeriidae (cf. Fig. 3), both dominant taxa in the Antarctic benthos, which may result in a rearrangement, as e.g. the Eusiridae turned out to be closer to the Iphimediidae than thought hitherto. Ontogenetic characters were not helpful in revealing phylogenetic changes in two *Epimeria* species by Coleman (1990). So far no deep-sea material of the two amphipod families has been retrieved from the Antarctic, which might be helpful for the reconstruction of phylogenetic trees and the descendence of shallow-water forms in the high Antarctic Weddell Sea. Recent calculations arrive at a radiation date for Antarctic *Epimeria* species of 15.7 Ma (Lörz and Held, 2004, based on the cirripede rate of substitution). This would correspond better than previous datings with the proposed formation of the Antarctic Circumpolar Current isolating Antarctica (see above). High intraspecific variability suggests continuing speciation in the genus *Epimeria*.

Another molecular study dealing with the phylogeny of the common Antarctic sea urchin *Sterechinus neumayeri* (Lee *et al*., 2004) revealed close relations to the South American urchin *Loxechinus albus*, concluding that the two species may have

diverged from the lineage of a southernmost South American sea urchin by vicariance as Antarctica and South America separated. However, the temporal range given for this process, with 24-35 Ma ago, appears rather wide to relate it to specific environmental situations.

The phylogenetic relationship between the limid bivalves *Limatula ovalis,* living in the high Antarctic, and *L. pygmaea,* from the Subantarctic and the Magellan region were studied by Page and Linse (2002). Proposed divergence of these and a third species, *L. hodgsoni,* was between about 1.4-8.0, 6.8-19.1 and 0.2-2.9 Ma, depending on the molecular clock used, i.e. probably after the final opening of the Drake Passage and the formation of the Polar Front. This might be taken as a hint that the Polar Front is not as effective a barrier as usually thought.

Species distribution, zonation, biogeography and biodiversity

Completing the record

Enhanced research on the Magellan-Antarctic gradient has considerably increased data on biogeographic distribution and taxonomy of many taxa. Notable recent examples are Antarctic macroalgae (Wiencke and Clayton, 2002) and echinoids (David *et al*., 2005), Magellanic shelled molluscs (Linse, 2002), opisthobranchs (Schrödl, 2003), and particularly, polychaetes (Parapar and San Martín, 1997; San Martín and Parapar, 1997; Cantone *et al*., 2000; Gambi *et al*., 2000; Montiel *et al*., 2004, 2005). For a taxonomic update of all benthic groups see Clarke and Johnston (2003). Further information is being compiled on, e.g. Magellanic asteroids and Antarctic cnidarians. As this recent work adds to a large extant literature, the Southern Ocean shelves are now rather among the better studied parts of the world ocean. This does not hold, however, for the deep-sea areas surrounding Antarctica (Linse, 2004).

In some cases biogeographic patterns begin to emerge for recently studied taxa, which add to the data presented at IBMANT I (Arntz and Ríos, 1999). Macroalgae show a marked reduction from the Magellan region (Santelices, 1989, Cornejo, 1996) along the Antarctic Peninsula towards the high Antarctic, whose continental shelf exhibits a very sparse macroflora (Wiencke *et al*., 1998; Wiencke and Clayton, 2002). There are, however,

differences between the Ross Sea and the Weddell/Lazarev seas, where hitherto a single small piece of red alga has been found (Gambi, pers. comm.), which might be allochthonous. Polychaete similarity with the Magellan region is greater at the Antarctic Peninsula than in the Weddell Sea (Montiel *et al.*, 2005). The same is true for isopods and cumaceans (Brandt *et al.*, 1997, 1999). Like in other taxa, Antarctic endemism is currently reduced by new finds in adjacent areas. Tanaidaceans were subject of two recent studies in Admiralty Bay (Blazewicz and Jazdzewski, 1996) and the Beagle Channel (Schmidt and Brandt, 2001). Surprisingly, the Peninsula material showed a lower overlap (abt. 10%) with the Weddell Sea (Sieg, 1992) than the Magellan region (25%).

The IBMANT I compilations of decapod crustaceans in the Magellan region (Arntz *et al.*, 1999) and their Southern Ocean distribution (Gorny, 1999) have been complemented by recent finds of lithodids in the Amundsen and Ross seas (Arana and Retamal, 1999; Thatje and Lörz, 2005) and near Bouvet Island (Arntz and Brey, 2005; Spiridonov *et al.*, in press), of caridean shrimp along the Scotia Arc (Arntz and Brey, 2003; Romero *et al.*, 2003a), and of thalassinids in the Beagle Channel (Thatje, 2000; Thatje and Gerdes, 2000). The general picture is still valid; only caridean shrimps have been collected on the high Antarctic shelves, and except for king crabs (Anomura: Lithodidae), no anomurans and no brachyurans live in Antarctic waters as for these latter groups, the deep water of the Drake Passage and the Polar Front are a true faunal barrier (Thatje *et al.*, 2003, 2005a, but see Thatje and Fuentes, 2003). The Lithodidae have so far not been found on the high Antarctic shelves (Thatje and Arntz, 2004).

The "bell-shaped latitudinal curve", species richness and diversity

Latitude by itself is not an environmental factor, but it reflects to a certain degree some basic ecosystem properties such as day length, light, temperature and production. On the other hand, a comparison of the conditions along the Atlantic and Pacific coasts of America (Boschi, 2000; Gutt *et al.*, 2003) reveals that there are other factors, which make a differentiation necessary (see also Gallardo and Penchaszadeh, 2001; Valdovinos *et al.*, 2003). Therefore it is not surprising that the controversial issue of a bell-shaped curve (see Arntz and Gili, 2001), with
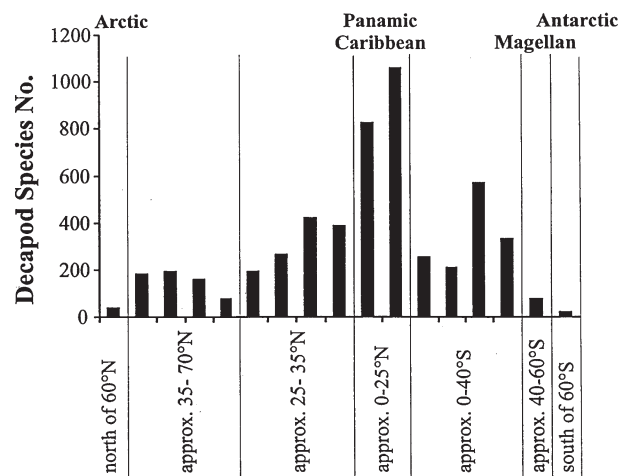

FIG. 4. – Numbers of decapod species from the Arctic to the Antarctic (data from Boschi, 2000). Note that the bars in the different latitudinal ranges do not represent consecutive latitudinal values but are from separate counts of species. This is one of the few cases where a "bell-shaped latitudinal curve" seems to exist, and in the case of decapods species numbers are indeed very low in the Antarctic.

decreasing species richness toward the pole, suggested by some authors for the terrestrial realm worldwide (see Gaston and Chown, 1999) and marine areas of the northern hemisphere (Roy *et al.*, 2000), seems to occur only in a few taxa in the southern hemisphere, whereas in many others even an increase from the Magellan region to the Antarctic can be observed.

A clear latitudinal cline is shown by macroalgae, whose distribution is highly dependent on water depth, light and temperature. In contrast to the (partly shallow) Ross Sea, in the southern Weddell Sea the non-existence of shallow bottoms excludes macroalgae (see above). Species richness in decapod crustaceans also seems to follow a bell-shaped curve (Boschi, 2000; Dworschak, 2000; Fig. 4); however, with marked differences in the subgroups (cf. above). A bell-shaped curve may apply to some extent also to fish, which are not dealt with here.

For gastropods and bivalve molluscs there is a clear decrease in species richness from the tropics to the Antarctic, but "local hotspots" deviate from a continuous decrease (Crame, 2000 a,b), and in the SE Pacific there is even a steep increase between 42°S and Cape Horn (55°S) (Valdovinos *et al.*, 2003). The number of polychaete species does not reveal a decreasing pattern along the Chilean Pacific coast (Hernández *et al.*, 2005) nor a Magellan-Peninsula-Weddell Sea gradient (Montiel, pers. comm.). Overall, latitudinal clines in species richness do not seem to be a general dominant pattern within the Antarctic due to a mostly non-meridional

orientation of most of the shelves (except for the Peninsula) and the circumpolar currents (Clarke and Johnston, 2003). Obviously, the paradigm of a bell-shaped curve in general has to be abandoned for the southern hemisphere in favour of an asymmetric distribution of most taxa (Gray, 2001; Crame, 2000a).

Considerable progress has been made in the past decade in collecting and publishing quantitative data on zoogeographical patterns. To relate these data to ecosystem functioning along a latitudinal gradient, sampling has to be standardized in time and space, analytical methods have to be comparable, and many if not all species have to be determined. Even if these conditions are fulfilled, the innate complexity of biological systems and their dynamics may complicate comparisons. The ultimate step of relating Antarctic data to those of the Magellan region has not yet been taken, although the methodological prerequisites for such a comparison are now available.

From many scattered data we know that species richness in the Antarctic can range from very high to very low; overall the species richness was found to be higher than formerly expected (Arntz et al., 1997; Clarke and Johnston, 2003), also in the deep sea (Brandt and Hilbig, 2004). In some taxa species richness has been increasing steeply in past years due to increased sampling, as has best been documented in amphipods (De Broyer et al., 2003). The most speciose groups in the Antarctic are polychaetes, gastropods, amphipods and isopods. Macroalgae, decapods, bivalves (and teleost fish and selachians) are poorly represented if compared with these taxa at lower latitudes, even in the Magellan region, whereas pycnogonids and many suspension feeding taxa are particularly species rich. Echinoderms are well established on both sides of the Drake Passage. Decapods and fish were previously well represented in Antarctic waters, but impoverished in the course of Antarctic cooling (Thatje et al., 2005a and lit. therein); other groups incl. pycnogonids, amphipods, isopods (and teleost fish) have undergone marked radiations (Lörz and Held, 2004). However, in all cases it is only some lines that have diversified (Clarke and Johnston, 2003). Poor groups can have a high share in the worldwide species (e.g., priapulids).

Species numbers per haul in bottom trawls (Table 1) or Agassiz trawls (not shown) are much higher than in temperate regions (own unpubl. data). Raw data of all species determined on EASIZ I with the help of many specialists arrived at a number of about 800 defined species. Gutt et al. (2004) made an extrapolation using species accumulation approaches (Ugland et al., 2003) and calculation of the unknown number of species, which were not represented in the samples, as a function of the rare species (Colwell, 1997), arriving at an estimate for total macrozoobenthic species between 2100 and 10,000 for the Weddell Sea shelf and between 11,000 and 17,000 for the entire Antarctic shelf. Both estimates are likely too low, because the method is conservative; trawls were used, which are known to be selective; and the assumption is that there really is a circumantarctic fauna (cf. Held, 2003; Held and Wägele, 2005), i.e. all assemblages to be found in the future would resemble those that have been described to date.

This kind of species richness extrapolation cannot be used to compare diversity, which is a function of species numbers and their numerical share. However, assuming that the reduced species numbers in the samples are representative, the calculated „pseudodiversities" should also be representative of true diversities. Seabed photography and UW video fulfil this important criterium by focussing only on the mega-epifauna, as has been shown in a bipolar comparison (Gutt and Starmans, 2001).

The importance of considering scales in diversity studies was shown by Starmans and Gutt (2002), who used UW video to compare mega-epibenthic assemblages in the Weddell and Bellingshausen seas with Arctic assemblages (NE Greenland) in a depth range between 35 and 585 m. At regional scale (gamma diversity) taxa richness was greater in the Antarctic than in the Arctic, although shallow sites in the Arctic were slightly richer in species and species turnover (beta diversity), indicating also higher habitat diversity. At the local scale (alpha diversity) species numbers were higher in the Antarctic. As a next step, macrobenthic diversities derived from Antarctic photographs (Gutt and Starmans, 1998) might be compared with the material taken by Gutt et al. (1999) from the Magellan region.

Community structure

Numerous soft-bottom investigations on macrobenthic communities have recently been carried out in the southern hemisphere using both visual and invasive methods at different sites in Antarctica and covering in total a wide latitudinal range (for the period before IBMANT I, see Gerdes et al., 1992 and citations therein): Saiz-Salinas et al., 1997;

TABLE 1. – Number of invertebrate species per bottom trawl haul. A, in the Kapp Norvegia to Halley Bay area on cruise EASIZ I (ANT XIII/3). B, in the Kapp Norvegia - Austasen area on cruise EASIZ III (ANT XVII/3). Source: Sirenko *et al.* (1997, 2001); further details there. For exact positions, net characteristics, trawling duration, iceberg disturbance etc. see also Balguerias *et al.* in Arntz and Gutt (1997) and Knust *et al.* in Arntz and Brey (2001).

A: EASIZ I, No. station	5	9	11	12	13	14	15	16	17
Mean depth	230	589	336	485	630	855	437	244	467
Porifera	27	6	17	22	20	28	15	20	34
Bryozoa	16	4	23	39	22	6	32	32	22
Polychaeta	14	12	22	18	15	8	26	18	1
Prosobranchia	15	4	16	5	8	3	9	6	8
Opisthobranchia	1	2	3	1	1	2	2	2	3
Bivalvia	11	9	7	4	2	1	8	2	5
Amphipoda	4	3	6	20	10	2	21	10	14
Holothuroidea	6	6	9	9	5	10	8	10	12
Asteroidea	8	5	10	7	12	7	12	12	16
Ophiuroidea	10	12	11	12	13	9	12	9	16
Ascidiacea	7	3	10	12	9	4	11	9	12
30 other taxa	48	33	43	47	45	27	46	33	54
Total	167	99	177	196	162	107	202	163	197
B: EASIZ III, No. station		65	85	102	109	119	124	135	136
Mean depth		648	318	312	311	237	269	251	260
Porifera		19	32	26	20	23	17	12	16
Bryozoa		26	30	35	31	27	28	16	19
Polychaeta		16	24	21	18	17	17	11	12
Prosobranchia		8	14	12	11	15	7	8	27
Opisthobranchia		1	3	3	5	3	2	1	4
Bivalvia		10	11	10	6	9	11	11	13
Amphipoda		5	15	33	23	36	12	13	30
Holothuroidea		16	14	17	10	15	12	9	10
Asteroidea		18	20	26	16	23	14	10	10
Ophiuroidea		15	20	16	16	14	10	8	10
Ascidiacea		11	22	25	11	13	9	11	9
30 other taxa		63	83	82	66	64	55	57	63
Total		208	288	306	233	259	194	167	223

Arnaud *et al.*, 1998; Starmans *et al.*, 1999; Gambi and Bussotti, 1999; Ramos, 1999; Cattaneo-Vietti *et al.*, 2000a; Gambi *et al.*, 2000; Piepenburg *et al.*, 2002; Cranmer *et al.*, 2003; Lovell and Trego, 2003). However, direct comparisons across latitudes remain rare.

Using a multibox corer Gerdes *et al.* (1992) had presented first abundance and biomass figures from the Weddell Sea shelf and slope and reviewed the data available at that time. Piepenburg *et al.* (2002) compared abundances and biomasses along two shelf/slope transects in the Drake Passage and Bransfield Strait. Table 2A summarizes the results of grab and corer based studies on the high Antarctic Weddell Sea shelf and in the Peninsula area. These studies showed the macrobenthos to occur often extremely patchy at the different sites, with minimum and maximum values of abundance and biomass (sieved over 500 μm) varying between 100 to more than 47,000 ind. m^{-2} , and 0.1 and 1673 g wet wt. m^{-2}, respectively. The Lovell and Trego (2003) epi- and infauna studies with grabs at Port Foster revealed even higher abundances but compa-

rable biomass, because of sieving over 300 μm mesh size with groups such as foraminiferans, poly- chaetes, and nematodes being numerically domi- nant. Whereas a pronounced shelf-slope gradient in benthic abundances and biomasses was found everywhere in the Antarctic and the Magellan region, there did not seem to be any clear latitudinal trend in these parameters (Gerdes and Montiel, 1999; Piepenburg *et al.*, 2002). Macro- and megabenthic assemblages are most likely deter- mined by food supply (which is depth-dependent), but apparently respond differently to secondary dri- ving forces such as, e.g. seabed topography.

Locally biomasses can be extremely high, not only in the high Antarctic sponge dominated sus- pension feeder communities (Gili *et al.*, 2001; Gerdes *et al.*, 2003), but everywhere. The bivalve *Laternula elliptica* reaches biomasses of up to 5 kg wet wt. m^{-2} in the Potter Cove (Mercuri *et al.*, 1998), which is comparable to very productive upwelling beaches off Peru and Chile (Arntz *et al.*, 1987). Dif- ferent species of scallops contribute to high benthic biomasses both in the Straits of Magellan and the

TABLE 2. – Macrobenthos community studies in the Atlantic sector of the Antarctic region (Drake Passage to Weddell Sea shelf) and in the Magellan region using invasive methods. For older data compare Gerdes et al., 1992 and further citations therein.

| Region	Method (No. of samples)	Water depth (m)	Bottom	Abundance Ind. m^{-2} Min.- Max.; (Mean)	Biomass g wet weight m^{-2} Min.-Max.; (Mean)	Annual production (g C m^{-2})	Dominant groups	Authors
A. Antarctic region								
Weddell Sea	multibox corer (233)	170-2037	soft bottom with mud, sand, gravel, boulders	131-12,846 (3806)	0.12-1673.0 (222.6)		sponges, holothurians, asteroids, polychaetes	Gerdes et al., 1992
Weddell Sea shelf	multibox corer	132-548			12.0 (3.6 g C m^{-2} y^{-1})		sponges, echinoderms, polychaetes	Brey and Gerdes, 1999
Bransfield Strait	multibox corer (27)	200-800		7198-10,956	184.6-529.4			Piepenburg et al, 2002
Drake Passage	multibox corer (32)	100-2000		731-14,483	49.3-951.6			Piepenburg et al, 2002
South Shetland Islands	van Veen grab, box corer (130)	42-671		160-4380	23.3-5205.0 (1169.0)		ascidians, sponges, polychaetes,	Saiz-Salinas et al., 1997
South Shetland Islands, Peninsula	Agassiz trawl	40 - 850	mud, sand, gravel	semiquantitative	semiquantitative		polychaetes, echinoderms, ascidians, crustaceans	Arnaud et al, 1998
Deception Island	grab samples (8)	155	poorly sorted mud, sand, rocks, cobbles, boulders	34,754-141,669	13-436 [1]		forams, nematodes, polychaetes	Lovell and Trego, 2003
B: Magellan region								
Straits of Magellan	multibox corer (76)	8-459	high proportion of sand and gravel, partly with clay and mud	409-4727 (1591)	16.8-392.8 (96.8)		bivalves, polychaetes, crustaceans	Gerdes and Montiel, 1999
Beagle Channel	multibox corer (64)	38-348	high proportion of sand and gravel, partly with clay and mud	673-8782 (3643)	10.1-1466.3 (301.6)		bivalves, crustaceans, polychaetes, echinoids	Gerdes and Montiel, 1999
Continent. shelf off the eastern entrance of the Beagle Channel	multibox corer (67)	14-1162	high proportion of sand and gravel, partly with clay and mud	1049-7730 (3983)	1.3-662.8 (119.0)		holothurians, crustaceans, polychaetes, gastropods	Gerdes and Montiel, 1999
Straits of Magellan	multibox corer, Reineck box corer (94)	8 - 571		174-4972 (1857)	0.16-22.88 (2.7) [2]	0.738		Thatje and Mutschke, 1999
Beagle Channel	multibox corer, Reineck box corer (119)	14-348		668-13,521 (4467)	0.54-16.99 (5.2) [2]	1.108		Thatje and Mutschke, 1999
Continent. shelf off the eastern entrance of the Beagle Channel	multibox corer (31)	102-1139		1136-4379 (2319)	0.05-14.51 (2.9) [2]	0.684		Thatje and Mutschke, 1999
South Patagonian Icefield	Reineck box corer (42)	20-711		30-1245 (627)	0.01-17.35 (2.1) [2]	0.393		Thatje and Mutschke, 1999
Magellan region	multibox corer	14-349			7.3 [2]	5.1	molluscs, crustaceans, polychaetes, echinoderms	Brey and Gerdes, 1999

[1] 0,3 mm mesh size; [2] g C m^{-2}
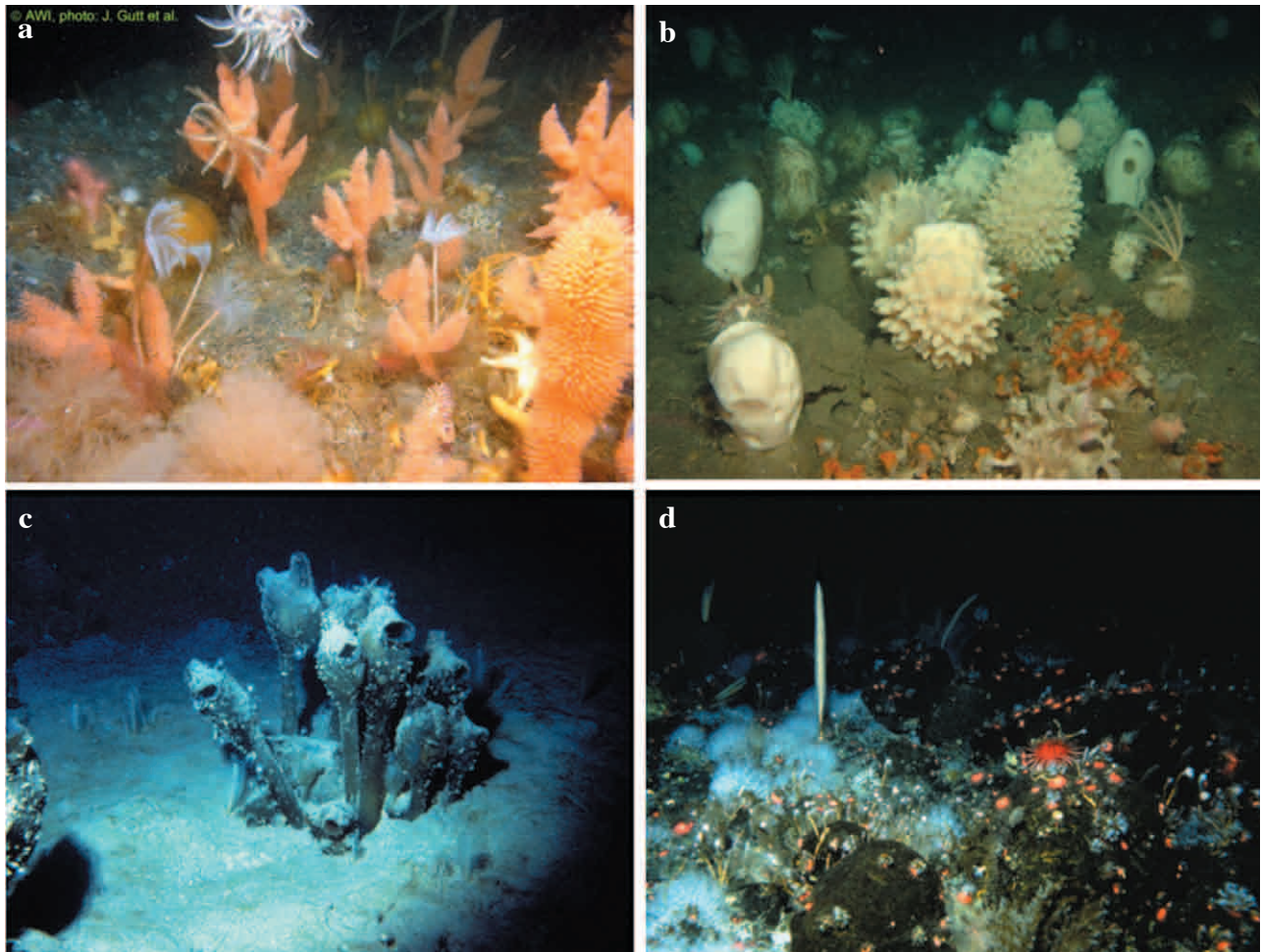
FIG. 5. – Typical aspects from Antarctic sessile suspension feeder communities. a) and b) gorgonian resp. sponge dominated (Weddell Sea shelf, 220 to 240 m; photos WG J. Gutt); c) ascidian and pennatularian dominated (Potter Cove, King George I., 30 m, under heavy siltation from glacier; photo S. Kühne); d) hydrozoan and stoloniferan dominated (hard bottom with boulders and cobbles on the isolated Four Seasons Bank, eastern Weddell Sea, 70 m; photo: WG J. Gutt).

Antarctic (Arntz and Gorny, 1996; Chiantore *et al.*, 2000; Heilmayer *et al.*, 2003).

In their comparison of mega-epibenthic communities by UW video between Antarctic areas and NE Greenland (cf. above), Starmans *et al.* (1999) detected distinct differences in community structure between all areas. Sessile suspension feeders dominated the assemblages in the Weddell Sea, probably due to favourable bottom currents, but were scarce in the other Antarctic areas (Fig. 5). Another community analysis of mega-epibenthos with a UW camera on the Weddell and Lazarev Sea (99 to 1243 m depth), where faunistic patterns were best explained by a combination of water depth and geographic gradient, was done by Gutt and Starmans (1998). There was a positive correlation between the abundance of large sponges and the number of all other taxa, and a gradient from rich, diverse suspension feeder assemblages to poorer assemblages with a higher share of deposit feeders.

Cranmer *et al.* (2003) recently sampled a megafaunal epifauna community at 150-160 m in Port Foster (Deception I.) using UW camera and bottom trawl. Compared to the high Antarctic this community was rather poor, maybe due to volcanic eruptions and their effects described already earlier by Gallardo and Castillo (1969), Gallardo (1987) and Arnaud *et al.* (1998). Principal dominants were the echinoderms *Ophionotus victoriae* and *Sterechinus neumayeri*, but even these with low abundances. Lower importance of epi- vs. infauna at the Peninsula was found as published before (cf. Arntz *et al.*, 1997). Faunal distribution turned out to be patchy similar to the high Antarctic (Starmans *et al.*, 1999). In Arnaud *et al.*'s (1998) semiquantitative trawl study at the tip of the Peninsula, shallow (40-130 m) stations differed from deeper stations, besides the Deception I. stations mentioned above.

Due to recent Italian studies, Terra Nova Bay is now a second well-known area in the Ross Sea

beside McMurdo Sound. These benthic communities differ substantially from the McMurdo assemblages 650 km to the south, which does, however, not necessarily reflect a latitudinal cline. Benthos community structure in Terra Nova Bay was studied from the intertidal to 150 m depth by Cattaneo-Vietti *et al*. (2000a) and at three sites between 450 and 810 m depth by Gambi and Bussotti (1999). Abundances were low (between 430 and 1040 ind. m^{-2}, 0.5 mm mesh). Two sites showed more constant conditions and a high organic input from the water column, site 3 was highly disturbed. The benthos was predominantly small and the community likely to be immature.

Shallow hard bottoms to abt. 35 m in Terra Nova Bay were investigated by divers (Gambi *et al*., 2000). Polychaetes were the most abundant and diverse taxon followed by molluscs and amphipods. The area was widely covered by the macroalgae *Iridaea cordata* and *Phyllophora antarctica*. This zone receives frequent disturbance by sea ice.

Benthic communities in the Magellan region were studied by several authors (Table 2B). Information on community structure was published by Gutt *et al*. (1999), and on the impoverished fauna in the glacier region (South Patagonian Icefield) by Mutschke *et al*. (1996) and Thatje and Mutschke (1999). The specific fauna of the intertidal cobble and boulder fields in the Magellan Straits was described by Mutschke *et al*. (1998) and Ríos and Mutschke (1999). The fauna in this highly heterogeneous environment was richer than previously mentioned, but was dominated by few polychaete and mollusc species. Some species in this community have a wide Subantarctic distribution. Comparisons can be made with the stony beaches at Arctowsky (Jazdzewski *et al*., 2001) and King Sejong (Kim, 2001), both at King George Island. At Arctowsky, high abundance (50,000 ind m^{-2}) and biomass (600 g wet wt. m^{-2}) characterised the fauna. Biomasses in the Magellan community were similar (330 – 3300 g wet wt. m^{-2}), but abundances were two orders of magnitude lower.

Barnes and de Grave (2001) investigated the "encrusting fauna" along 25 degrees of latitude from Tierra del Fuego to the Ross Sea. The authors found distinct Patagonian, Falkland (!) and Antarctic groupings. The Antarctic grouping revealed a cline from more northerly and shallow to more southerly and deeper sites (details in Barnes, 2005).

As within the Antarctic, densities and biomasses in the Magellan assemblages appeared rather variable. No distinct latitudinal gradients between both regions were detected (cf. Piepenburg *et al*., 2002), although the Magellanic fauna in general reveals higher production and productivity as pointed out by Brey and Gerdes (1999). Conversely, comparisons based on faunal composition allowed to distinguish different regions. Using trawl catches (Arntz *et al*., unpubl. data) and multibox corer samples (Gerdes and Montiel, 1999), the various subregions are clearly discernible even on the level of higher taxa. The Scotia Arc with its intermediate position reveals closer association to the Magellan fauna on the northern branch, whereas the southern branch was faunally more closely associated to the Peninsula fauna. South Georgia occupied an intermediate position. Adding the Weddell Sea shelf and Bouvet Island to the picture, average similarity was greatest between the high Antarctic and Peninsula and lowest between the Magellan region and Bouvet Island. Winkler (1994) found clear differences between the Scotia Arc incl. South Georgia and the high Antarctic Weddell Sea. The Scotia Arc and the Magellan region were mostly separated on species and genus level.

Depth gradients

Improved data are now available also on zonation. A report on the zonation of macroalgae by Quartino *et al*. (1998) complements former work by Klöser *et al*. (1996) in the Potter Cove, South Shetland Is. In this Cove, shallow macrofaunal zonation was studied by Sahade *et al*. (1998), confirming former findings of Dayton (1990) that communities are poor in very shallow water due to the influence of ice, storms etc., and increase in richness toward deeper water below the major impact of growlers, anchor ice and other disturbants.

Due to the ice shelves, almost no free shallow sites exist on the Weddell/Lazarev shelves. An exception is the Four Seasons Bank close to Kapp Norvegia, with distinct zonation belts (Arntz and Brey, 2005). Part of the species normally occurring at these depths may live under the ice shelves; e.g. *Adamussium colbecki* (cf. above), which is common in the Ross Sea (Chiantore *et al*., 2001).

A distinct allopatric depth distribution in the Weddell Sea was found in the serolids *Ceratoserolis trilobitoides* (shallow) and *C. meridionalis* (deep), and the aegids *Natatolana oculata* and *N. obtusata* (shallow) vs. *N. intermedia* (deep) (Summary Review in Arntz and Gutt, 1999).

Cattaneo-Vietti *et al.* (2000a) found a clear depth zonation from the intertidal to 150 m depth in Terra Nova Bay: a rocky shore with a poor upper zone at 2-3 m, algal belts to 70 m with a diverse vagile fauna, *Sterechinus* and *Odontaster;* below a complex community dominated by sponges and cnidarians with high biomass and species richness. Soft bottoms start at 20-30 m depth. These communities are characterized by the bivalves *Laternula elliptica, Adamussium colbecki, Yoldia eightsi* and polychaetes *(Tharyx cincinnatus* and others). On muddy sands at 150 m depth other polychaetes and brachiopods dominate. Similar diversity of epibenthic habitats in the Weddell Sea was described by De Broyer *et al.* (2001a,b).

Significant differences among polychaete taxa distributed in shallow and deep waters of the Paso Ancho (Straits of Magellan) were found by Montiel *et al.* (2001). A distinct zonation in this area has also been reported for other benthic groups (Ríos and Mutschke, 1999; Ríos *et al.*, 2003).

Latitudinal and longitudinal exchange

Environmental conditions change markedly on the latitudinal gradient but less on a longitudinal gradient, where exchange in the Southern Ocean is enhanced by the circular current systems and may occur over large distances (Beu *et al.*, 1997). There is a latitudinal cline in the severity of environmental conditions (mainly ice and wind disturbance, with gradients in opposite directions; Barnes and Arnold, 1991). Traffic, e.g. of algae in a N-S direction across the Polar Front is presumably difficult unless there is ship transport (see below). The role of eddies (Glorioso *et al.*, 2005) for latitudinal transport in the Scotia Arc has yet to be determined. Besides environmental factors, the dispersal abilities of larvae or drift stages also determine the success of exchange (Jablonski *et al.*, 2003).

In shallow water, sharp differences were recorded north and south of the Polar Frontal zone in rock fauna, both in the number of species and in individual species distributions (Barnes and Arnold, 1991). The shelf fauna in the Scotia Arc revealed a predominantly Magellanic faunal composition on the northern branch of the Arc and a predominantly Antarctic one on the southern branch, as one would expect (Arntz and Brey, 2003), but there were exceptions, which may be due to shifts in the position of the frontal zone (cf. Fig. 2). In the Drake Passage, the southern slope is clearly Antarctic, howev-er with a better developed endofauna than in the high Antarctic whereas the typical high Antarctic epifauna is largely missing. Conversely, the northern slope is colonized by typical Magellan elements, which is best documented in the distinct southern limit of many decapod crustacean taxa (Arntz and Ríos, 1999; Arntz *et al.*, 1999; Gorny, 1999; Lovrich *et al.*, 2005).

Longitudinally, floating algae patches between the Argentinean coast and Burdwood Bank, >100 km offshore, and macroalgal communities at South Georgia demonstrate there is much eastward transport with the Circumpolar Current. However, the role of the South Sandwich Islands as a potential connecting agent for soft-bottom fauna seems to be low, similar to the shallows (Herdman and Discovery banks) due to their swept bottoms and strong currents (Arntz and Brey, 2003). Convey *et al.* (2002) have described the "extremely depauperate" conditions of the South Sandwich Islands with their remote position and lava or pumice bottoms, which were documented also in the LAMPOS cruise. Bouvet Island, lying even further east, was sampled during the BENDEX cruise; the first faunal analyses indicate Antarctic conditions and relations principally with the Antarctic Peninsula (Arntz and Brey, 2005; Arntz, in press). Theoretically, larvae or other dispersal stages arriving at Bouvet might travel with the Weddell gyre to the Lazarev or eastern Weddell Sea coasts, but so far there has been little faunal support for this hypothesis.

Circumantarctic transport is a prerequisite for the often cited "circumantarctic distribution" of many faunal elements, which is favoured by similar conditions around the entire continent and the (counter) clockwise current systems. A comparison of three Antarctic shallow-water sites (Atka Bay, Four Seasons Bank, Marguerite Bay) based on UW video transects distinguished the individuality of these sites; there was no greater similarity between the two former and the latter, despite very different distances for larval dispersal. The data also indicated that there is little exchange with adjacent deeper areas; otherwise the two former sites should also show greater similarity (Raguá-Gil *et al.*, 2004). This poses the question how the few shallow sites in the Weddell Sea maintain their typical aspect of Antarctic shallow water fauna. Circumantarctic shallow-water exchange should be seriously hampered by the existence of the large ice shelves in the Weddell Sea and extended areas of permanent sea ice on the eastern side of the Penin-

sula. However, the shallow-water bivalve *Laternula elliptica* was found at the isolated Hilltop site (Brandt *et al*. in Arntz and Gutt, 1999), together with many shallow-water hydroids (Gili, unpubl. data). Only 7 scallop (*Adamussium colbecki*) specimens have been found up to now in the entire Weddell Sea (Linse, pers. comm.). In summary, dispersal mechanisms of the shallow-water fauna are still far from clear.

Invasions

Due to its distinct environmental gradients, the Antarctic is an ideal natural laboratory under present global warming conditions. Recent arrivals of "alien" macroalgae at the Antarctic Peninsula were registered by Wiencke *et al*. (1998) in the Potter Cove, King George Island, comprising rare records such as *Durvillea antarctica* but also cosmopolitans (Wiencke and Clayton, 2002).

Recent literature mentions an increase of plastic debris as potential vehicles in the Circumantarctic Current (Convey *et al*., 2002; Barnes, 2002, 2005). These debris are sometimes preferred to macroalgae, which are known to transport invaders, and may represent a greater danger because of their "longevity" (Barnes, 2005). On the other hand, Convey *et al*. (loc. cit.) did not detect any evidence of colonisation by biota.

Another interesting aspect is the present attempt of the Decapoda, one of the taxa poor in species in the Antarctic, to return to the cold (Aronson and Blake, 2001; Anger *et al*., 2003; Thatje and Arntz, 2004; Thatje *et al*., 2005a). There seems to be an increasing mismatch towards the pole between environmental variables (decreasing temperatures, seasonally limited food availability) and typical decapod properties (see below). This mismatch seems to have been the reason for the expulsion or extinction of Antarctic decapods in the Tertiary as well as for the failure of recolonisation in recent times, despite obvious pressure from the Magellan region (Arntz *et al*., 1999; Thatje *et al*., 2003). In the case of continued global warming, this pressure from other decapod taxa including the brachyurans is likely to increase. This suggestion is supported by recent detections at the Antarctic Peninsula of 9 "alien" specimens of meroplanktonic larvae belonging to Magellanic decapods (Thatje and Fuentes, 2003) and the find of the North Atlantic brachyuran *Hyas araneus* reported for 1986 by Tavares and Melo (2004; however, see also Thatje *et al*., 2005a for discussion).

Specific Antarctic traits, strategies and adaptations

Reproductive strategies and population dynamics

Reproductive strategies change along latitudinal gradients, which is mainly due to differences in temperature, primary production cycles and food availability. Already before IBMANT II, there was a substantial literature describing special Antarctic characteristics, see e.g. Pearse *et al*., 1991; Clarke, 1992; Arntz *et al*., 1992, 1994 and refs. therein. Specific polar characteristics had been identified, but it was also clear that there were numerous exceptions, and that very different adaptations to polar conditions had been developed.

One of the traditionally controversial issues is "Thorson's rule" (for the background see Clarke, 1992; Pearse, 1994; Arntz and Gili, 2001). Stanwell-Smith *et al*. (1999) contributed a very important paper on the occurrence of pelagic marine invertebrate larvae in shallow water at Signy Island, where they registered a total of 181 pelagic larval types, many more than ever found in Antarctic waters. However, even this number is low in view of the high benthic species number in these waters (see above), and densities were extremely low in comparison with those in temperate regions. For most described morphotypes species identification remains unclear and the number of species with certain larval types may be biased by considering subsequent ontogenetic stages of the same species (Arntz and Gili, 2001). Another recent approach in Admiralty Bay (Freire *et al*., 2005) yielded somewhat higher meroplanktonic larval numbers in shallow water, but still much less than at lower latitudes. In a first attempt to evaluate conditions in deeper, high Antarctic waters, a Dutch-German team found extremely low numbers of meroplanktonic larvae off Kapp Norvegia (Arntz and Brey, 2005; Lavaleye *et al*., 2005), which principally supports Thorson's rule. Furthermore, many of the pelagic larvae found hitherto are lecithotrophic and occur year round, and some (such as the Caridea) have a high starvation resistance (cf. Thatje *et al*., 2004, 2005c).

Why do some of the most abundant Antarctic shallow-water species deviate from the more frequently found patterns of non-planktotrophic development, and have become broadcasters (Poulin *et al*., 2002)? These broadcasters include *A. colbecki, L. elliptica, O. validus, O. meridionalis, S. neumayeri, Porania antarctica,* and *Ophionotus victoriae*

whereas the vast majority of other species are brooders or lecithotrophic. The authors explain the apparent ecological success of the first group by advantages in recolonisation e.g., after iceberg disturbance whereas the other species rather reflect an evolutionary success, permitting them to survive under conditions of glaciation. The question is, of course, whether demersal drift stages or lecithotrophic larvae would not serve the same purpose.

Contrary to the Antarctic, meroplanktonic larvae of benthic invertebrates are very common in the Straits of Magellan and the Beagle Channel, and many of them are planktotrophic with either extended or abbreviated development (Thatje et al., 2003). The meroplankton community studied in November 1994 was dominated by decapod crustacean larvae, followed by polychaetes, echinoderms, cirripedes and molluscs.

Many individual studies have recently shed more light on reproductive strategies and population dynamics along the cold temperate Magellan to high Antarctic gradient. Growth of some endemic Antarctic macroalgae is restricted to very low temperature values (0-5°C, in some cases 10°C), much lower than for cold-temperate species (Wiencke and tom Dieck, 1989, 1990; Bischoff-Bäsmann and Wiencke, 1996; Gómez et al., 1998). Light requirements for the completion of the life cycle of several Antarctic algal species are very low. Reproduction and growth of early stages takes place under dim light in winter (Wiencke, 1990a,b; 1996). The photosynthesis apparatus remains intact in some species (e.g., *Iridaea chordata)* during prolonged darkness but not in others such as *Palmaria decipiens* (Weykam et al., 1997). Day length strongly governs the seasonal growth of many algal species (Wiencke, 1990a,b), and a minimal window of 10 days with 5 hours of light is required for formation of gametangia and gametes in large brown algae such as *Desmarestia anceps* (Wiencke et al. 1996), which explains the drop-out of many species on the latitudinal Ross Sea gradient towards McMurdo (Wiencke and Clayton, 2002). Similar studies in the Magellan region are necessary to extend the latitudinal aspect to the north.

Decapod reproductive biology has now been studied in the Antarctic and Magellan regions along a wide latitudinal range of 23 degrees of latitude (Arntz and Thatje, 2002; Thatje et al., 2003, 2004). Growth was found to be slower, and mortality lower in Antarctic caridean shrimps than in related species living at lower latitudes. First maturity occurs at an advanced age and size, and longevity is very high (up to 10 yr or more) in the Weddell Sea (Gorny et al., 1992). The caridean shrimps have adapted to the latitudinal gradient by reducing fecundity, better equipping their fewer eggs, and hatching as large, morphologically advanced larvae with a distinct starvation resistance (Gorny et al., 1992, 1993; Romero et al., 2003 a; Thatje and Lovrich, 2003, Thatje et al., 2004). However, the step to complete lecithotrophy has not yet been undertaken by any caridean species except *Sclerocrangon boreas* in the Arctic, see Thatje et al. (2003), and seems to be a phylogenetic constraint in marine representatives of the taxon. Adaptation to increasing seasonality in this group has been achieved mainly by reducing the pelagic larval phase, e.g. in *Campylonotus vagans* (Magellan, Thatje and Lovrich, 2003) and *Chorismus antarcticus* (Antarctic, Bruns, 1992; Gorny et al., 1992; Thatje et al., 2003). Further characteristics are a decrease of moults and larval instars towards the pole, reduced energetic losses in very thin cast exuviae (Thatje et al., 2003) and low Mg^{2+} concentrations in the haemolymph (Frederich et al., 2000, 2001). The latter has, however, so far been confirmed only for adult stages. Adaptation of reptant decapod taxa to all these characteristics has been less efficient, and particularly the extended larval development and low starvation resistance may have caused evolution to select against Antarctic reptants (Thatje et al., 2003, 2005a). An exception is the anomuran family of lithodid crabs, which besides the deep sea has conquered also high latitudes in both polar regions. Southern Ocean lithodids combine fully lecithotrophic larvae equipped with sufficient lipid reserves with strongly reduced demersal instars and a high tolerance against the cold (Lovrich and Vinuesa, 1996; Anger et al., 2003, 2004). However, this tolerance may not yet be perfect, as lithodids have not been found on the very cold high Antarctic shelf with temperatures of less than -1.8°C (Fig.6) while the temperature threshold for successful larval development seems to be around 0 to 1°C (for temperature thresholds and discussion see Anger et al., 2003, 2004; Thatje et al., 2005a).

A number of interesting studies has been undertaken further north along the Chilean Pacific coast, which are related to the subject of decapod coldwater adaptation. These studies (Brante et al., 2003; Fernández et al., 2003) tried to integrate the cost of brooding in the reproductive effort to obtain a more
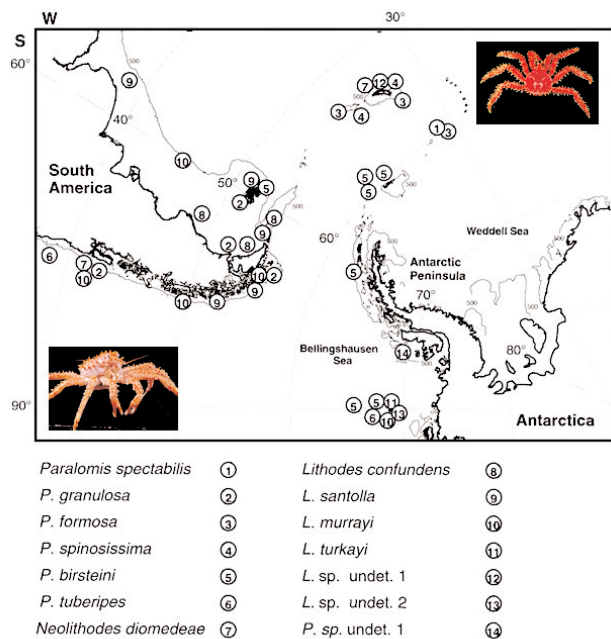
FIG. 6. – Distribution of lithodid crab species (Anomura) caught hitherto off southern South America, the Falkland Is. (Malvinas), along the Scotia Arc and the Antarctic Peninsula, and in the Bellingshausen Sea. Despite hundreds of hauls taken, not a single crab has ever been caught in the icy waters of the Antarctic continental shelf. (From Thatje and Arntz, 2004).

Paralomis spectabilis	①	*Lithodes confundens*	⑧
P. granulosa	②	*L. santolla*	⑨
P. formosa	③	*L. murrayi*	⑩
P. spinosissima	④	*L. turkayi*	⑪
P. birsteini	⑤	*L.* sp. undet. 1	⑫
P. tuberipes	⑥	*L.* sp. undet. 2	⑬
Neolithodes diomedeae	⑦	*P.* sp. undet. 1	⑭

reliable estimate of reproductive investment, also along the latitudinal gradient. Temperature affects the period of embryo ventilation events, maternal abdominal flapping frequency, embryo losses during the brooding period, and the cost of embryo ventilation per unit of time. Crab females are able to adjust oxygen supplies to embryos according to their needs (Baeza and Fernández, 2002), but this may affect investment in reproduction, and might have important implications on larval survival and development.

While the quality of reproductive output changes with latitude towards a better outfit of less eggs and more lipid investment per embryo, the cost of embryo ventilation decreases with temperature, suggesting a trade-off between investment in eggs and the cost of providing oxygen to the embryos at different temperatures (latitudes). Should this not favour also the reptants, which are missing in cold water? Apparently the combination of very slow embryonic development with a mismatch between reduced metabolism and low food availability in the larval phase (Thatje *et al.*, 2003), combined with physiological constraints, counteract this advantage, as is the case also in the circumantarctic genus *Munida*, which has not conquered Antarctic waters despite an enormous dominance of up to 80% on the Magellan side (Tapella *et al.*, 2002; Arntz *et al.*, 1999).

At least some Antarctic suspension feeders have similar growth and reproduction rates to those of their temperate relatives (Orejas *et al.*, 2000) due to efficient food assimilation. Substantial progress has been made in elucidating reproductive strategies in this traditionally neglected group, which dominates the high Antarctic benthos over wide areas.

Antarctic ascidians are hermaphrodites and have lecitotrophic larvae. The genera *Cnemidocarpa*, *Molgula* and *Pyura* in Potter Cove exhibit strong seasonality in their reproduction. *M. pedunculata* and *C. verrucosa* reproduce in winter, *P. setosa* in summer. Paradoxically, the two winter-spawning species are the two most successful species in this ecosystem. Perhaps they are avoiding salp predation on the larvae, which is more intense in summer (Sahade *et al.*, 1998). Combining results from colonisation panels and respiration measurements, Kowalke *et al.* (2001) showed ascidians from Potter Cove to have high growth rates, favoured by a low basal metabolism and extended longevity. These properties, together with their ability to survive under intense sedimentation, make them effective competitors among benthic suspension feeders.

In gorgonians the number of eggs per mature polyp is in the same order of magnitude as in non-polar areas. During autumn in some female polyps larvae ready to be released were found together with oocytes in early stages of development, suggesting an extended development period from early spring to late austral summer. Thus these organisms might be in a continuous reproductive state, which would enable them to recruit successfully at any time, e.g. in areas disturbed by icebergs. This would explain, too, why *Primnoisis* sp. is among the first dwellers in iceberg scours. Their larvae are not pelagic but might function as drift stages (Orejas, own obs. EASIZ II).

Two size classes of oocytes in different developmental stages were found in *Ainigmaptilon* (Orejas *et al.*, 2002) in summer and autumn. The apical and medial parts of the colonies showed highest fecundity. The relative frequency of the largest size class decreased in the autumn samples. *Ainigmaptilon* is characterized by an extended oogenesis period (>1yr). Spawning seems to be delayed until the autumn-winter season, as was also observed in some *Thouarella* during EASIZ III. No larvae of this species were detected in summer and autumn. The absence of larval stages during autumn was surprising, considering that many octocoral species had larvae ready to be released, leaving the reproduction of *Ainigmaptilon* still as a mystery. The type of fertil-

ization (external or internal) could not be determined. Our data do not allow us to state any special Antarctic features in the reproductive biology of *Ainigmaptilon,* although we think they exist.

Bryozoans have lecithotrophic larvae, which spend a very short time in the water column before settlement. The number of larvae produced daily is very small. The larvae of some species are incubated for up to 10 months before being released (Barnes and Clarke, 1998). Reproduction time in the Antarctic is summer and autumn (Zabala *et al*., 1997; Barnes and Clarke, 1998; Bader, 2002).

Cellaria incula growth and age was analysed by stable carbon and oxygen isotope analysis (Brey *et al*., 1999). The growth of one complete branch of this species takes one year; maximum age of a colony is likely to be more than 14 yr. P/B was 0.67, the highest value measured for any benthic invertebrate south of 62°S. Similar to another bryozoan, *Melicerita,* this fast-growing species is a pioneer in the recolonisation of iceberg scours (see below).

In a latitudinal comparison of pectinids, Heilmayer *et al*. (2003) studied the Antarctic scallop *Adamussium colbecki* in relation to (a.o.) the Magellan species *Zygochlamys patagonica*. Despite the fact that growth efficiency in pectinids was found to decrease at higher temperatures, the absolute growth of *A. colbecki* was found to be much slower than that of the Magellan species. *A. colbecki* attains a high age (Chiantore *et al*., 2003, Heilmayer *et al*., 2003 and references therein). Growth of the Antarctic shallow-water bivalve *Laternula elliptica* was studied by Voigt (2004) using material from King George Island. He reconstructed growth over 40 years (1961-2001), revealing interannual growth fluctuations correlated with changes in sea surface temperatures and ENSO indices. Very slow embryonic development of Antarctic molluscs had already been shown by Hain and Arnaud (1992) before IBMANT I.

The polychaete families Polynoidae and Sabellidae have a greater variability in reproductive features than assumed hitherto: *Harmothoe* spp. brood their eggs under the elytra, *Myxicola* cf. *sulcata* incubates its embryo within the tentacle crown (Gambi *et al*., 2001).

Very slow embryonic development rates were found in the three echinoderms *O. validus, O. meridionalis* and *S. neumayeri*, 2-20 times slower than their temperate or tropical relatives (Stanwell-Smith and Peck, 1998). The authors proposed a window of optimal temperatures between +0.2°C and +1.7°C for *S. neumayeri* embryo development and

viability. Embryos of further two species are released in winter, when water temperature is constantly below –1.6°C. Temperature, not larval food supply and predation during planktonic phases is the dominant ecological factor for these species.

Similar to most invertebrates, growth was found to be very slow and maximum age high in high Antarctic notothenioids (Morales-Nin *et al*., 2000) and zoarcids from the Peninsula (Brodte, 2001).

Susceptibility of living resources (decapods, molluscs) to exploitation

The vulnerability of exploited or exploitable invertebrate stocks to fisheries is intimately related to the population dynamics of the respective target species. Three of the Antarctic caridean shrimp species *(C. antarcticus, N. antarcticus* and *N. lanceopes)* occur in appreciable quantities (see, e.g. Arntz and Gorny, 1991). However, their late maturity, low fecundity and slow growth (Gorny *et al*., 1992) do not encourage a fishery, and the damage to be expected from a trawl fishery would be much greater than the potential benefit (Arntz *et al*., 1994).

After heavy decimation of the spawning stock by the fishery, the population dynamics of lithodid crabs *(L. murrayi, P. granulosa)* have been studied in the Beagle Channel by various authors, mainly from Argentina (Lovrich and Vinuesa, 1996; Lovrich, 1997). Chilean landings of these two species in the XI and XII region have been oscillating between about 3000 and 9000 t annually between 1999 and 2004 (SERNAP, 2005). Notwithstanding their ability to adapt to (sub)polar conditions, this group is quite vulnerable to overfishing. It would be interesting to study the lithodids detected recently in the high Antarctic (Arana and Retamal, 1999) to check whether this taxon also reveals the kind of latitudinal reproductive gradients found in caridean decapods (Gorny *et al*., 1992). An exploratory fishery on lithodids, mainly *P. spinosissima,* off South Georgia in 1994-96, with a precautionary TAC of 1600 t, yielded only about 500 t (CCAMLR, 1994, 1996; Collins *et al*., 2002), but seems to have decimated the stock to a very low level. Exploitation has since been restricted to occasional bycatches in the roundfish fishery (Fanta, pers. comm.).

Another anomuran taxon, the squat lobster *Munida* spp., is distributed in the Magellan region incl. the northern branch of the Scotia Arc until South Georgia (Romero *et al*., 2003a) but is missing in Antarctic waters, probably due to its reproductive

characteristics which have recently been studied by Tapella *et al.* (2002) and Thatje *et al.* (2003). This very common genus is of potential use as a fisheries resource in Chile and Argentina.

The Antarctic scallop *(A. colbecki)* is one of the key species in the Ross Sea (Heilmayer *et al.*, 2003), whereas only few scattered individuals have so far been found in the Weddell Sea. Due to its consumption and production this active suspension feeder seems to play a significant role in the trophic web of the Ross Sea shelf. However, it would be very vulnerable to exploitation compared to other pectinids because of its very low overall growth performance and productivity.

Magellan bivalve resources include the scallops *Chlamys vitrea* and *Zygochlamys patagonica* and the mussel *Aulacomya ater,* all of them being exploited in Chile with 1999-2004 catches in the XI + XII region oscillating between about 100 and 2000 t (SERNAP, 2005), and several "almejas" (mostly Veneridae: *Venus antigua, Retrotapes exalbidus, Tawera gayi*) as potential resources. The gastropod *Adelomelon* sp. is gradually becoming exploited on the Atlantic side (Cledón, 2004); Volutidae *(Harpovoluta)* also occur in the Antarctic but are too rare to serve as a potential resource. Other gastropods, above all Muricidae and Buccinidae (*Trophon geversianus, Argobuccinum* spp.), do not play a great role commercially at this time but exploratory culture has been started for some species that might replace the reduced *Concholepas* stocks in Chile (C. Gallardo, pers. comm.).

Clearly the Magellan benthic ecosystem (Fig. 7) hosts many more potentially exploitable resources, at least for human consumption, than the Antarctic. Altogether there is increasing evidence, however, that all benthic crustacean and most mollusc species of potential commercial value in the Antarctic and along the southern border of the Magellan region deserve special care, with increasing tendency toward the high Antarctic, if exploitation is envisaged. The virtual destruction of most Antarctic fish stocks, which is presently culminating with the severe reduction of the last commercially important species *Dissostichus eleginoides* and *D. mawsoni* (Collins *et al.*, 2003; CCAMLR, 2005) should be taken as a warning indicating the vulnerability of cold water stocks to exploitation.

Tolerance limits and other adaptations

Much progress has been made in understanding physiological mechanisms of temperature adapta-

FIG. 7. – Trawl catches in the Magellan region are similar to high Antarctic catches in the dominance of echinoderms, but are quite different in the often striking appearance of large brachyuran and anomuran decapods and bivalves. Brachiopods are occasionally dominant in both areas. Canal Brecknock, 480 m (above) and I. Pícton, 63 m (below); photos W. Arntz.

tion; how did climate variability in the past influence biogeography and evolution of marine ectotherms? These questions are dealt with in the review by Pörtner *et al.* (2005) and recent work by Peck (2001) and Clarke (2003b).

Oxygen supply in the tissues may determine thermal tolerance and limit maximum size. A latitudinal cline in maximum size of amphipods due to better oxygenation and the architecture of the vascular system in cold water was detected by Chapelle and Peck (1999). Maximum sizes showed an inverse relationship to water temperature, which may explain the large size of many Antarctic amphipods. It should be noted, however, that the greater number of Antarctic amphipod species is rather small.

The benthic diatoms *Gyrosigma subsalinum* and *Odontella litigiosa* exhibited extremely low upper survival temperatures of 5-7°C in Potter Cove, and growth occurred only in the narrow range of 0-7°C. Optimal temperature for growth was 0°C, for photosynthesis 5°C. The northern limit of *G. subsalinum* is the 4°C summer isotherm, corresponding to the

northern limit of the Antarctic, whereas *O. litigiosa* could also live in the Subantarctic up to the 7°C summer isotherm (Longhi *et al.*, 2003).

Surprisingly high values of lethal temperatures in Antarctic Peninsula molluscs (L_{t50} of *Laternula elliptica,* 14.9°C and *Nacella concinna,* 15.5°C), which are not likely to be reached by global warming in the near future, were found by Urban (1998). Reburial temperatures, however, were much lower (B_{t50} of *L. elliptica:* 3.6°C). Similar temperature threshold patterns have been suggested to be valid in lithodid crabs (Anger *et al.*, 2003, 2004); so L_{t50} may not be an adequate measure to indicate limits of survival (cf. Abele, below).

Distribution limits of macroalgae are not only set by ice abrasion and substrate, or biological factors such as competition (Klöser *et al.*, 1996) and herbivory (Iken, 1996; Iken *et al.*, 1998) but also by depth due to metabolic prerequisites. The upper distribution limit is determined by the capability for dynamic photoinhibition, a process by which excessively absorbed photosynthetically active radiation is dissipated as heat (Hanelt, 1996, Bischof *et al.*, 1998). For the lower distribution limit the low light requirements for photosynthesis and growth are of primary importance. Some algae are unable to inhabit depths greater than 30m. A critical daylight length during which algae are exposed to light saturated irradiances may be the key factor setting the lower distribution limits of these species (Gómez *et al.*, 1998).

The acclimatisation of Antarctic macroalgae to seasonal changes in light was investigated by Lüder (2001), using the photosynthetic apparatus of the alga *Palmaria decipiens* in culture experiments.

Light conditions also seem to play a major role for sponges in the Terra Nova ecosystem, between 70 and 120 m depth (Cattaneo-Vietti *et al.*, 2000b). They seem to survive oligotrophic conditions in winter by direct uptake of diatoms, which live for a long time in the sponge tissue. Spicules in the hexactinellid *Rossella racovitzae* conduct light as natural optical fibres and thus provide the diatoms with light.

Apart from specific Antarctic problems such as extremely low temperatures, seasonality of primary production and food shortage, stress caused by global warming and increased UV-B radiation has become an important issue in recent years. While the major part of the continent does not yet show signs of warming, the Antarctic Peninsula has experienced a distinct temperature increase by >1.5°C since the middle of the 20th century (Vaughan *et al.*, 2003), and the "ozone hole" continues to stress ben-

thic life in shallow water. Both the effects of warming and of increased radiation are particularly interesting to study on the Magellan-Antarctic gradient.

Oxidative stress may be caused by hypoxia, hyperoxia, intoxication, high temperatures, but also by UV irradiation, liberating reactive oxygen species or leading to a dysfunction of the cellular antioxidant defense system (Abele *et al.*, 1998). Oxidative stress is critical for membrane integrity, may cause a disturbance of subcellular structures and eventually limit survival. In the Potter Cove (King George Is.) the effects of temperature increments causing oxidative damage in inter- and subtidal molluscs *(Yoldia eightsi, N. concinna)* were studied. "Critical temperatures" for survival, Tc of *L. elliptica* were 9°C, of *Y. eightsi* 4-5°C. No Tc was given for *N. concinna,* however oxidative stress occurred at 4°C, and mortality at 9°C, which seems very low for an intertidal animal. Paradoxically, intertidal animals seem to be more sensitive to warming than subtidal ones.

Under increased UV-B radiation, amphipods seek protection under algae. Unprotected in the laboratory they react with stress and higher mortality (Obermüller *et al.*, 2003). Hernando *et al.* (2001) identified repair and protective mechanisms that allow Antarctic algae to survive and reproduce under increased UVB radiation. Despite the existence of such mechanisms, the combination of rising temperatures and persistence of the ozone hole is a severe threat to Antarctic and Magellanic benthos, which may induce major changes in the near future.

Trophic strategies and coupling between subsystems

Trophic strategies on the Magellan-Antarctic gradient are mainly determined by a change from dominant endo- to dominant epifauna and shorter primary production cycles towards the pole. The energy flow through the Weddell Sea benthos was shown to be more diverse than in the Magellan region (Brey and Gerdes, 1999). While information on feeding strategies and food webs in the Antarctic has increased considerably in recent years, little new information has been created from the Magellan region (Schnack-Schiel and Isla, 2005).

The traditional view of Antarctic sessile suspension feeder communities feasting during the short period when fresh primary production is available from the algal blooms and "hibernating" without food uptake during the rest of the year became doubtful, when Barnes and Clarke (1995) demon-

strated that certain Antarctic shallow-water suspension feeders are able to feed throughout the year with only short periods of starvation. They feed on pico- and nanoplankton (between 0.2 and 20 mm), which in these areas dominate the water column and the sediment most of the year (Clarke and Leakey, 1996; Cripps and Clarke, 1998) whereas phytoplankton (microplancton) is dominant only during short periods.

Similar finds by Orejas *et al.* (2001) on the deeper shelf of the high Antarctic Weddell Sea made it likely that the algal blooms rather play an indirect role through sedimentation, resuspension and advection (Gili *et al.*, 2001), and that trophic strategies under the pack ice are similar to those found in shallow water. In late summer (Feb/Mar), food input from the pelagial to the benthic system is rich as indicated by ROV pictures (Arntz and Gutt, 1997, Summary Review). However, food analyses of benthic suspension feeders in EASIZ I and II revealed that apart from some specific zooplankton feeders such as certain hydrozoans (Gili *et al.*, 1998) most benthic organisms made little use of these larger particles, despite their abundance. Instead, they ingested the food web based on bacteria, nano- and picoplankton, unicellular organisms and organic detritus contained in the seston (Orejas *et al.*, 2000; Gili *et al.*, 2001).

In the context of glaciation, pack ice cover must be considered an important evolutionary factor, as it may have prevented new production in the water column, and may have stimulated suspension feeders to rely more on resuspended and advected material (Arntz and Gili, 2001). This would indicate that benthic suspension feeders in these areas still maintain a feeding strategy, which served during glaciation, despite the fact that under present conditions fresh algal food is available during certain periods of the year. Towards the Magellan region, this fresh food window is open for most of the summer half.

The "new view" of less dependence on the short seasonal microalgal blooms in the Antarctic has now been supported by various studies. A wide range of diets was found in four cnidarian genera in the Antarctic, the hydrozoans *Oswaldella* and *Tubularia;* the stoloniferan *Clavularia*, and the anthozoan *Anthomastus,* indicating opportunistic behaviour by feeding on all available food sources and sizes (Orejas *et al.*, 2001). Main food of *Tubularia* and *Anthomastus* was zooplankton, *Oswaldella* fed on the fine fraction of seston, and *Clavularia* on resuspended material. In the two Antarctic octocorals

Primnoisis antarctica and *Primnoella* sp., feeding experiments showed that components of seston, including the fine fraction of suspended organic matter, are an important part of the diet (Orejas *et al.*, 2003). In terms of the number of cells captured, the diatom *Fragillariopsis* was the most important food for *Primnoisis* whereas dinoflagellates dominated in *Primnoella.* Mesozooplankton was very scarce in the diet of these gorgonians but may have some importance because of its high carbon content. Despite their relatively small contribution to biomass, hydrozoans capture large amounts of zooplankton and seston, and play an important role in transferring energy from the pelagic to the benthic ecosystem (Gili *et al.*, 1998). Not all of them are carnivores although *Tubularia ralphii,* an exception in that it feeds on large particles, clearly is one: its predation rate was estimated at 1790 prey items $m^{-2}d^{-1}$, with a diet consisting entirely of planktonic copepods (Arntz and Gutt, 1999, Summary). Conversely, the Subantarctic hydrozoan *Silicularia rosea*—the other large particle feeder—feeds on benthic diatoms (Gili *et al.*, 1996). Another unusual trophic strategy was reported of the hydrozoan *Hydractinia angusta* living on *Adamussium* shells in Terra Nova Bay (Cerrano *et al.*, 2000): It ingests tube feet and pedicellariae of sea urchins *(Sterechinus)* grazing on the scallop shell, as well as masses of diatoms living in a kind of symbiosis in the hydrorhiza of the colony. There may be more examples for the trophic versatility of Antarctic suspension feeders.

The varied diet composition typical of opportunists, together with their feeding on the fine fraction of seston as indicated by experiments, reveals that passive suspension feeders in deeper waters, too, are likely to continue feeding under winter conditions in the high Antarctic.

In Terra Nova Bay carbon flux to the benthos is enhanced by katabathic winds, favouring the development of benthic detritus, and of large active suspension feeders such as *Laternula elliptica* (Povero *et al.*, 2001). This species is of great importance for benthopelagic coupling through biodeposition, as it enhances particle fluxes to and from the seabed, and has an important output of nutrients through excretion (Mercuri *et al.*, 1998).

Stable isotope ratios have turned out to be increasingly useful for trophic modelling attempts in the Antarctic. N isotopes serve as indicators of a consumer's trophic position relative to that of species occupying lower trophic positions. Wide ranges in $\delta^{15}N$ ratios in most benthic taxa of Antarc-

tic food webs indicate feeding across a range of trophic levels. This is due to the high amount of omnivory, the ability of vertical niche expansion, the presence of multiple carbon sources, and the 3-dimensionality of the Antarctic benthos. The hypothesis that 3-dimensional habitats support longer food chains than 2-dimensional habitats has not been fully explored (Briand and Cohen, 1987; Pimm *et al*., 1991), but it is consistent with recent findings that in Antarctic food webs the distance from phytoplankton to pelagic top predators is 2.5 trophic levels, whereas the distance to benthic top predators is about 3.5 trophic levels. At the Antarctic Peninsula seaweeds provide an important food source in the web, whereas krill *Euphausia superba* is important as food in the pelagic Weddell Sea food web (U. Jacob, unpubl. data).

A stable isotope approach to the eastern Weddell Sea food web, with a focus on 90 amphipod species, was made by Nyssen *et al*. (2002). In 8 amphipod species isotopic composition was compared with their previously described gut contents. Feeding strategies seem to remain stable over time. Amphipods do not belong to one trophic category but display a continuum of feeding modes from suspension feeders to scavengers.

Recent studies on the role of amphipods in the Antarctic food web, including aspects such as trophic guilds, were summarized by De Broyer *et al*. (2003). Other recent publications of the Belgian group include Dauby *et al*., 2001a (trophic diversity of amphipods); Dauby *et al*., 2001b (importance of amphipods as predators); and Dauby *et al*., 2003 (amphipods as food for higher trophic levels). Many of the > 820 known species are of paramount importance as food to many invertebrate and vertebrate taxa. Annual consumption of amphipods was estimated at 60 million t (which would make them the second most important taxon after the krill (Dauby *et al*., 2003)). Feeding of amphipods in the Potter Cove, King George Island was investigated by Momo *et al*. (1998). Most amphipods were detritivores and scavengers, herbivores were few despite large macroalgal stocks in the area.

Trophic relations between macroalgae and herbivores in the Potter Cove were studied by Iken *et al*. (1998). The herbivorous gastropod *Laevilacunaria antarctica* is not deterred by polyphenolic extracts of brown algae. Towards higher latitudes, where macroalgae are missing, herbivory gives way to specialized feeding strategies and increased necrophagy (Arnaud, 1970).

High Antarctic caridean shrimps, despite very different mandible shapes and stomachs, and despite living in different habitats, seem to make an exception (Storch *et al*., 2001). They had ingested very similar food, and there did not seem to be a relation, either, to life style or habitat preferences; these shrimps were truly omnivorous. Shrimps in the Magellan region seem to be omnivorous, too, but detrital food there is derived from terrestrial sources (Romero *et al*., 2003b). Comoglio and Amin (1999) studied the stomach contents of lithodid crabs in the Beagle Channel.

Schrödl's (2003) book on South American sea slugs contains notes on their biology. Similar monographs on other Magellanic and Antarctic taxa are urgently required.

Fish in the food web off the Antarctic Peninsula are important inshore benthos and zooplankton feeders, linking the upper and lower levels of the food web (Barrera-Oro and Casaux, 1998; Barrera-Oro, 2002). Olaso *et al*. (2000) studied the trophic ecology of the family Artedidraconidae in the eastern Weddell Sea, and Vacchi *et al*. (2000) investigated coastal fish predation (incl. its impact on the benthos) in the Ross Sea.

Few studies seem to exist on mutualisms. Sirenko (2002) makes an exception, describing the symbiosis between the gastropod *Dickdellia labioflecta* and pycnogonids.

The role of disturbance and its significance for biodiversity

Ice as a disturbant still plays a certain role in Magellan waters (cf. Fig. 1), but is decreasing in importance due to global warming and becomes increasingly more important towards the pole. In the Magellan region, local scouring effects of small icebergs or growlers may occur in the shallow water of some fjords, but such effects have not been reported. There are, however, distinct ice effects off the Patagonian ice fields caused by low salinity due to freshwater input (Dávila *et al*., 2002) and increased siltation, resulting in an impoverishment in benthic species richness, abundance and biomass as mentioned above.

In a similar way, fine inorganic particles from glacier abrasion in Potter Cove (South Shetland Is., Antarctic Peninsula) favour ascidians, pennatulids, large *Laternula elliptica* and cumaceans and suppress sponges, small bivalves and polychaetes, whose filtering apparatus may be clogged (Kowalke

et al., 2001; Kowalke and Abele, 1998; Tatián *et al.*, 1998; Sahade *et al.*, 1998). On hard bottoms the foliage of macroalgae, particularly of large kelp *Himanthothallus*, may act as a disturbant in addition to ice effects; ascidians dominate here, too, due to their high competitive abilities (Sahade *et al.*, 1998).

The effects of large-scale disruption as occurred with the Larsen ice shelf (east coast of Antarctic Peninsula; Domack *et al.*, 2005) has not yet been studied in macrobenthic communities. However, a project has been developed (Gutt, unpubl.) and from all we know, remarkable changes have to be expected (Arntz, 1998).

Whereas information on ice disturbance is somewhat stagnant at lower latitudes, it has improved substantially in the high Antarctic. Gutt and Starmans (2001) analysed abt. 25 km^2 of video transects and UW photos on the Weddell Sea shelf and found signs of iceberg disturbance on 42-70 % of the bottoms. Fairly recent iceberg scours of different age cover about 7% of the Weddell Sea shelf, but in iceberg resting sites like Austasen the coverage is much higher, and only 20% are unaffected (Arntz and Gutt, 1999, Summary). Near Kapp Norvegia, icebergs cover a considerable part of the shelf between 200 and 400 m depth; iceberg resting sites can extend over areas between 40 and 170 km^2 (Knust *et al.*, 2003). Based on survey data

and growth studies of the pioneer species *Cellaria incula* (Brey *et al.*, 1999), Gutt (2001) concluded that each square metre at depths <500 m on the Antarctic shelf is disturbed by icebergs every 340 yr on average.

Despite its immediate destructive effects, it is evident now that iceberg scouring enhances diversity whereas glaciers cause faunal impoverishment (Gutt, 2001). Iceberg disturbance destroys the fauna at small scale, but the large variety of successional patterns increases diversity at medium (regional) scales (Gutt *et al.*, 1998; Gutt, 2001; Gutt and Piepenburg, 2003; Fig. 8).

Cluster analysis of macrofauna clearly separated fresh scours, old scours and undisturbed areas (Knust *et al.*, 2003). Fresh scour marks were characterized by lowest total abundance and low biomass. Dominant taxa in fresh scours were polychaetes and crustaceans followed by juvenile brittle stars; tunicates and sponges were absent. In old scour marks a dominance of echinoderms, polychaetes, and brittle stars was found as well as of bryozoans and smaller sponges (both increasing), and in undisturbed areas a high dominace of sponges and echinoderms with bryozoans (however, the latter less dominant than in old scours).

A detailed taxonomic approach using polychaetes (Gerdes *et al.*, 2003) showed highest densi-
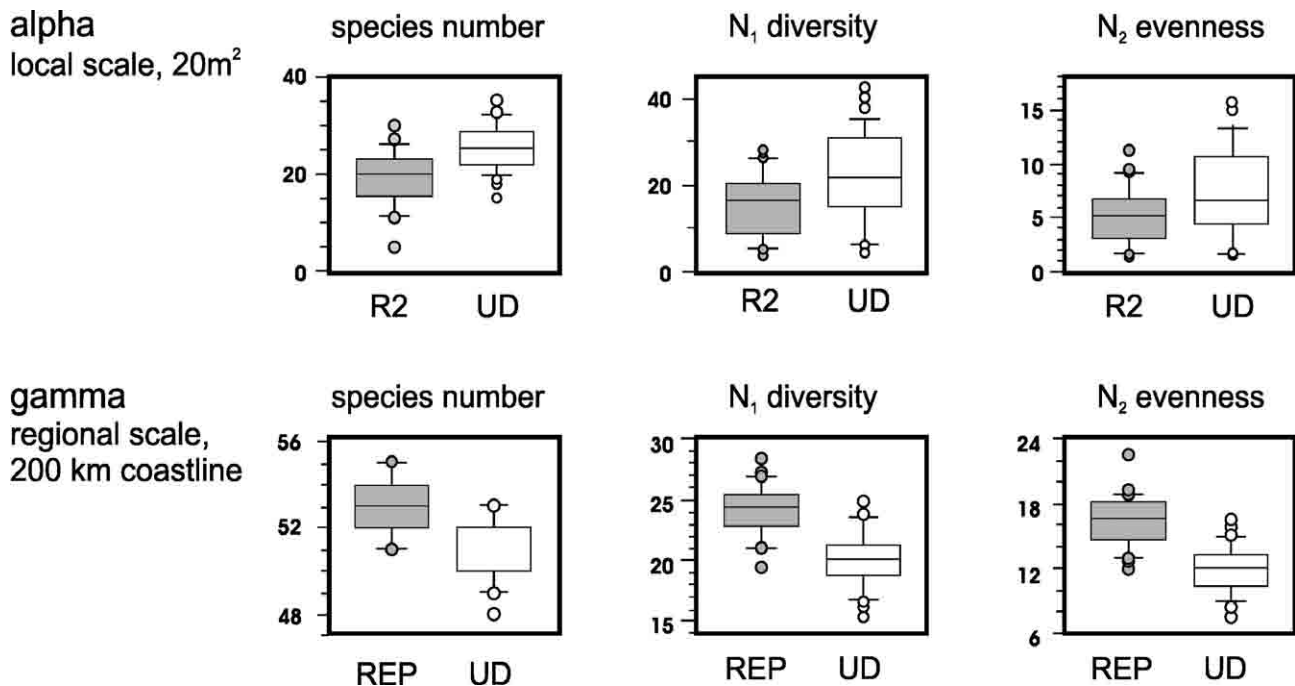

FIG. 8. – Dependence of Antarctic diversity and evenness on spatial scales. On larger scales values increase in areas subject to iceberg scour due to the simultaneous presence of different successional stages. REP, R2 are recolonisation stages, UD undisturbed areas. From Gutt and Piepenburg (2003), redrawn.
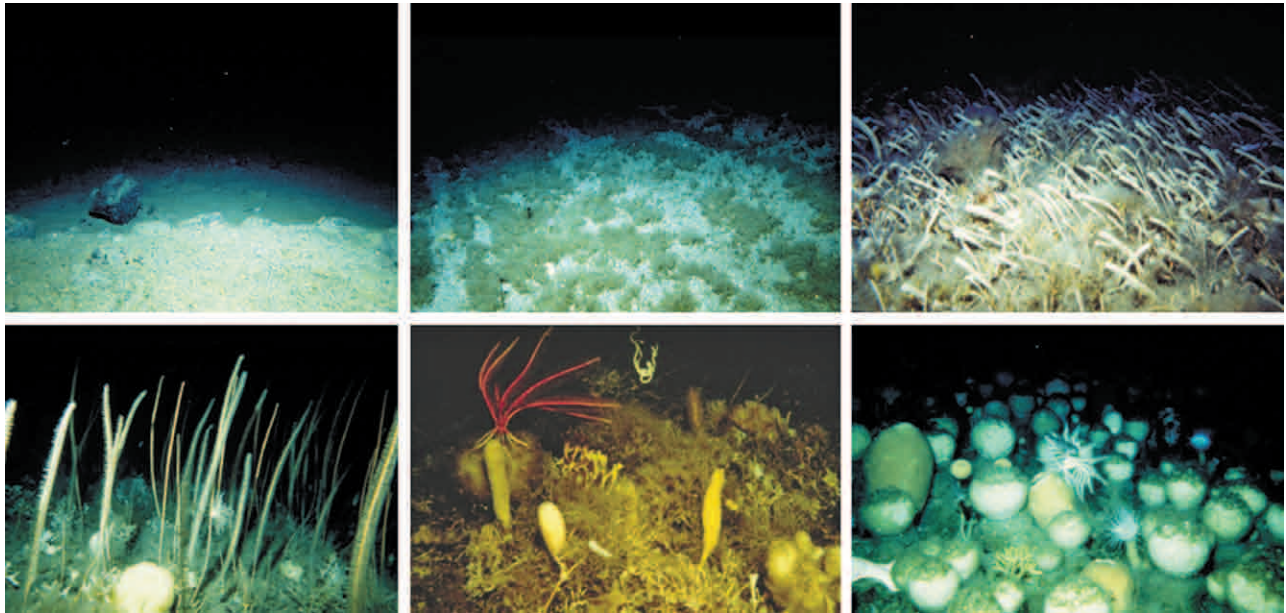
FIG. 9. – Hypothetical succession after iceberg impact, from the devastated stage via pioneer stages to a fully developed epibenthic assemblage (southeastern Weddell Sea). There are alternative successional stages, but the exact time scale for the process of recolonisation is still unknown. (Photos: WG J. Gutt)

ties and habitat species richness in undisturbed areas, followed by old and young scours. The polychaete fauna was found to be impoverished in iceberg scours also in terms of the variety of feeding types and life styles.

Various early colonisers were identified: colonial ascidians *(Synoicium),* bryozoans *(Cellaria, Cellarinella),* the stalked sponge *Stylocordyla,* the solitary ascidian *Molgula,* the gorgonians *Primnoisis, Ainigmaptilon* and the polychaete *Pista* (Gutt *et al.*, 1996; Arntz and Gutt, 1999, Summary Review; Bader, 2002). *Stylocordyla borealis* might be able to regenerate lost bodies if only the stem is left after a disturbance (Gatti, 2001). The stem contains only 20% of the total organic carbon of an individual. Other sponges produce buds under certain circumstances (Teixidó *et al.*, in press). Both may be mechanisms to speed up recolonisation.

Megafauna from UW camera and video transects produced data with a higher resolution and, consequently, better distinction between different successional stages (Fig. 9) in the Antarctic (e.g. Gutt and Starmans, 1998, 2001; Starmans *et al.*, 1999; Gutt and Piepenburg, 2003) and Magellan benthos (Gutt *et al.*, 1999). Teixidó *et al.* (2002, 2004) applied methods of landscape ecology to analyse quantitatively spatial patterns in Antarctic megabenthic communities. Using standardized UW camera photos and landscape indices, spatial patterns were studied in an undisturbed benthic assemblage and through successional stages after

iceberg disturbance. The results describe a gradient from early stages of recovery with low coverage, low complexity of patch shape, small patch size, low diversity, and patches poorly interspersed to later stages with higher values of these indices. There was no fixed sequence of pioneer species during this process, but the pioneers occurred in high (sometimes almost monospecific) densities and were patchily distributed. Dominant taxa in this successional phase were demosponges, gorgonians, bryozoans, polychaetes and ascidians. Some species of these major taxa exhibit much faster growth than is normally found in Antarctic waters (e.g. Brey *et al.*, 1999; Kowalke *et al.*, 2001). In an advanced stage of succession it was mainly bryozoans that dominated. In this stage the highest values were encountered of cover area and density. The climax stage was characterized by large and presumably very old demosponges and siliceous sponges as well as (other) bryozoans, ascidians and gorgonians, whose cover area and density was, however, reduced as compared with the previous stage. Different growth forms dominated the various successional stages, and life strategies (presence of pelagic larvae or drift stages, brooding, budding) seemingly determined to a certain extent the course of succession. The most successful pioneers were characterized by tree-shaped growth form, relatively fast growth, and low to intermediate dispersal capacity of their larvae (Teixidó *et al.*, 2004).

In view of the inherent difficulties to collect material and data regularly in the Antarctic (less so in the Magellan region), consistent long-term data series are rare. In this case spatially explicit modelling of processes shaping diversity patterns may be a useful approach to answer questions on ecosystem functioning. A first attempt is presently being made to simulate benthic succession after iceberg scouring, emphasizing the role of biological characteristics such as dispersal, growth and recruitment, interactions between species inhabiting different successional stages and basic environmental parameters (Johst *et al.*, unpubl.; Potthoff, pers. comm.). The first results from this modelling suggest that former assumptions as to the extremely low pace of Antarctic community development may have to be reconsidered, and that the dispersal mode plays a very important role.

Hill's diversity concept (Hill, 1973) of a gradient with increasing weight of equitability and decreasing species numbers was used as a gradient of measures with increasing sensitivity to any kind of impact or environmental change, and applied to Antarctic benthos data to check the "intermediate disturbance hypothesis" (Gutt and Piepenburg, 2003). The authors did not find a decrease of diversity due to increasing competitive displacement at a late stage of succession following devastation of the community by grounding icebergs. However, adding to this concept landscape measures describing spatial patterns by computing areas covered by organisms and their circumference, an effect of competition seemed to occur (Teixidó *et al.*, 2002).

Other compartments in the high Antarctic benthal such as meiofauna and demersal fish are also affected by iceberg scouring (Lee *et al.*, 2001 a,b; Brenner *et al.*, 2001; Mintenbeck, 2001; Knust *et al.*, 2003). Through area fragmentation and continuous creation of free spaces, natural disturbance thus might be a process favouring speciation, and this process might be more active under present conditions in the Antarctic than in the Magellan region.

Anthropogenic disturbance affecting assemblages at the seafloor is another field, where comparisons on a latitudinal gradient would provide interesting results on benthic resilience.

Lenihan and Oliver (1995) investigated the structure of benthic communities around McMurdo station and the changes due to anthropogenic contamination as compared to two large-scale natural disturbances, anchor ice uplift and iceberg scour. The effects were similar; however contamination had a much more long lasting effect, and recovery from it was expected to be much slower. Human impact and the development of benthic communities responding to sewage, also at Mc Murdo, are studied by Conlan *et al.* (2003). A former sewage outlet, which ended at the shoreline, was replaced in 1991 by another outlet at 18 m depth, 56 m distant from shore; from 2003 the sewage has been treated. Presently a lot of contamination continues, also due to dumping of chemical waste in a nearby bay. Recovery velocity is followed under polar conditions after sewage abatement.

Human impact is also investigated in benthic communities at Casey (Stark and Riddle, 2003). Differences between impacted and reference stations around Casey Station are probably due to heavy metals and hydrocarbons. Field experiments have been conducted to demonstrate a causal relationship, showing that different assemblages developed at polluted and non-polluted sites.

Deficiencies and perspectives

Even though considerable progress has been made since the first IBMANT Conference in Punta Arenas, numerous gaps still remain in our knowledge, some of which were already identified during IBMANT I:

- Major tectonic, oceanographic and climatological events that supposedly shaped Antarctic biotic evolution should be identified and related to the molecular genetic results. Presently neither the former nor the latter approach provide a firm base to arrive at comprehensive conclusions across disciplines.

- Relations and interactions of the Antarctic with surrounding areas other than the Magellan region remain obscure; differences in similarity level with Antarctic biota between South America and Australia should be studied as an indirect measure of continental drift related evolutionary changes.

- Concerning almost all subjects dealt with in this review, research in the Magellan region must be strengthened. Presently the state of knowledge is much better for the Antarctic than for the "Cono Sur".

- More "circumantarctic" species should be studied using molecular techniques to detect cryptic species. For biodiversity purposes, traditional taxonomy remains important as most larger taxa (e.g., polychaetes) require identification to species level.

- Accessible fossil evidence is restricted to few sites in the Antarctic (Taviani *et al.*, 1998; Crame, 1999; Malumian and Olivero, 2005), and the record is only slowly improving.

- There is evidence for a convergent evolution of high Antarctic sessile suspension feeders to similar morphotypes as in the Cretaceous or earlier, however it requires further study of the responsible ecofactors.

- The Scotia Arc and Bouvet Island (see Arntz, in press) are clearly undersampled, considering their potential significance as transitory areas between the Magellan region, the tip of the Antarctic Peninsula and the high Antarctic.

- Further shallow areas should be studied in those high Antarctic regions where they are very scarce, to enable comparisons with shallow-water biota inside and outside the Antarctic and to elucidate the origin of their fauna.

- Areas under permanent pack ice cover and areas recently disclosed by ice shelf calving should be studied and compared with polynya areas to identify the consequences of extreme oligotrophy, and to follow recolonisation.

- Perturbation effects such as those from iceberg scour should be inflicted experimentally, and should include modelling approaches, to enable verification of successional processes and their duration, which will allow an improved judgement on ecosystem vulnerability and recoverability.

- Recolonisation experiments on soft and hard substrates, both short- and long term, should provide further data on the pace of succession and resilience under polar conditions.

- Influences from climate oscillations such as ENSO or the Antarctic Circumpolar Wave (White and Peterson, 1996) have been suspected by various authors but need more attention.

- More data on life cycles, reproductive strategies and physiological adaptations of benthic key species are badly needed.

- Meroplanktonic larvae, in particular, deserve an increased research input in deeper shelf areas.

- Close cooperation with physiologists should be enhanced, because it may lead to causal explanation of empirical ecological finds.

Similar to the EASIZ programme (Arntz and Clarke, 2002), which finished in 2004, the recently designed SCAR programme EBA (Evolution and Biodiversity in the Antarctic) provides an excellent thematic background for the continuation of IBMANT research on the interaction between the Antarctic and other remnants of Gondwana. Furthermore, cooperation with ANDEEP may enable us to check those potential links via the deep sea, which have emerged from research on the Antarctic and Magellan shelves.

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