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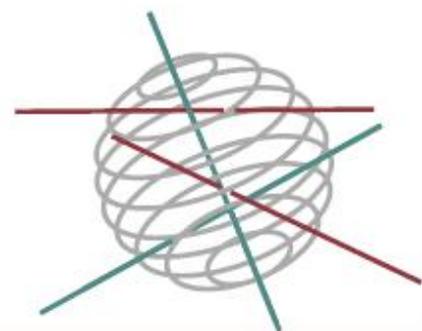## SCIENCE FOR A SUSTAINABLE DEVELOPMENT

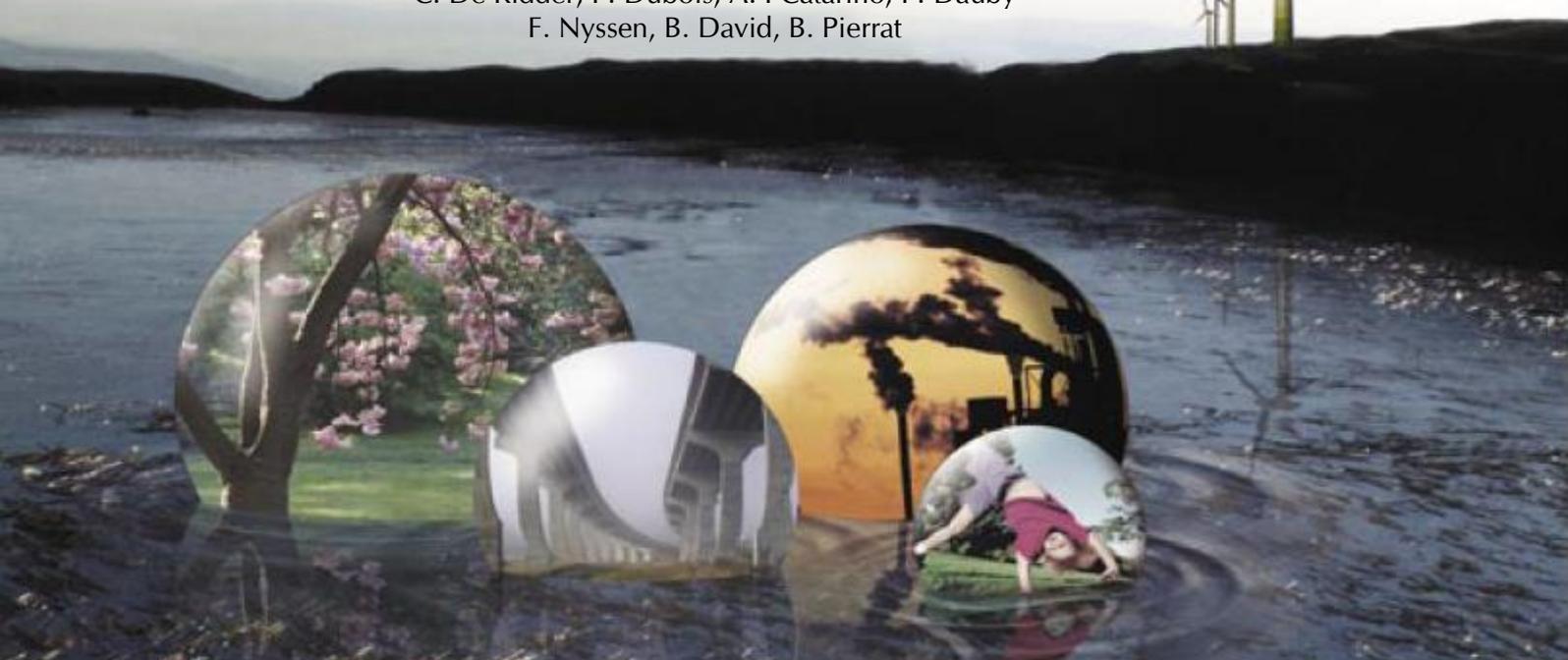**Final Report**

Biodiversity of three representative groups of the Antarctic Zoobenthos - Coping with Change

"BIANZO II"

J. Ingels, A. Vanreusel, M. Raes, F .Pasotti,
K. Guilini, F.Hauquier, P. Martin, C. d'Udekem d'Acoz,
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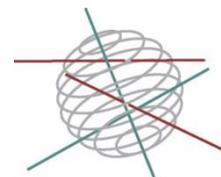F. Nyssen, B. David, B. Pierrat

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Final Report

Biodiversity of three representative groups of the Antarctic Zoobenthos - Coping with Change

"BIANZO II"

SD/BA/02

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TABLE OF CONTENT

1) SUMMARY

a) Context

The improvement of our understanding of ecological processes and the role of biodiversity in the Southern Ocean ecosystems remains a high priority on the research agenda in today's changing world and is inextricably linked to sustainable development policies on a global scale. Global environmental changes influence species distributions and consequently the structure of communities and ecosystems. Only advances in our knowledge of the Southern Ocean biodiversity and processes important for ecosystem functioning can allow us to address complex evolutionary and ecological questions and enable estimations of the expected change of the biota distribution and composition. Polar regions experience greater rates of global change than any other region in the world. Their biota are highly adapted to the extreme environment they are living in and appear vulnerable to shifts in environmental conditions. Antarctic marine species are especially more sensitive to temperature variation as their physiology is set to a narrow range of temperatures. Also changes in food quality and quantity, together with other environmental shifts such as in pH of the seawater, are likely to impact densities, biomass and community composition but also functional aspects of the Antarctic biota.

Because of the key-role of the Southern Ocean for the global ocean system and the growing impact of global environmental change, it is crucial to establish comprehensive baseline information on Antarctic marine biodiversity as a sound benchmark against which future change can be assessed reliably. It is equally important to understand better the ability of taxa to cope with changes in environmental parameters (temperature, pH, ice cover, food quantity and quality) linked to global change, and this from the individual to the community level. Imperative in this approach is to assess how structural and functional characteristics of the biota may be affected by a changing climate. Finally, advanced integrative spatial modelling of the distribution of key species in relation to environmental conditions is needed to predict the future of the marine ecosystems related to climate change.

These aspects are addressed in the Bianzo II project by focusing on benthic organisms and communities, specifically representatives from three different size classes of the zoobenthos: Nematoda (meiobenthos), Amphipoda (macrobenthos) and Echinoidea (megabenthos). These three groups are characterised by a high diversity and many of the well over 4000 Antarctic benthic species described so far (Clarke & Johnston, 2003) belong to these taxa.

These three selected benthic taxa are also ecologically important in terms of biomass, their role in biogeochemical cycles (C and N) and the trophic role they fulfil

in the benthic ecosystem. Furthermore, they are characterised by different biogeographical and diversity patterns, speciation mechanisms, and reproductive and dispersal strategies. Because of these differences and the intrinsic ecological variability between these taxa, it is difficult to assess the extent to which global change will affect the Antarctic benthos in general. Rarely do biodiversity and ecological studies focus on multiple benthic groups. Yet, combining putative size groups in ecological/biodiversity research is imperative to understand the benthic ecosystem as a complex and interactive unity.

b) Objectives

Climate change and its complex and interactive chain of associated effects will affect the physiology, distribution, phenology, and ontogeny of many Antarctic benthic organisms, but the resulting changes from the species to the community level remain poorly quantified and understood. Individual species may appear vulnerable to environmental shifts or regime changes, but community and ecosystem responses may not act accordingly. Therefore we investigated the biodiversity and responses of the three representative groups of benthic organisms to climate change effects from individual species, over populations, up to the community level

During its first phase (2007-2008), BIANZO II aimed at investigating (1) biodiversity patterns of the Antarctic zoobenthos and their causal processes by focussing on the three selected benthic groups (Work package 1: NOWBIO); Furthermore (2) trophodynamic aspects of each of the benthic groups, and their ability to cope with temperature and temperature-related changes (i.e. food composition and availability) but also the effect of pH of the seawater were on the benthos (Work package 2: DYNABIO).

In the second phase (2009-2010) of the project, a joint review paper dealing with the effects of global climate change on the Antarctic zoobenthos is being written, based on the results of experiments, field results and literature data. Information collected in previous studies and in the first two work packages of this project was also used to develop a habitat suitability model in order to identify the drivers of benthic distribution patterns and forecast possible changes of benthic communities related to global change (Work package 3: FOREBIO).

c) Conclusions

i) NOWBIO

(1) Benthic biodiversity in new ice free habitats

Due to large-scale ice-shelf disintegration events, the Antarctic Larsen A and B areas along the Eastern Antarctic Peninsula recently became ice-free. Our study is the first one to investigate benthic communities and their response to the collapse of ice shelves in this area. At the time of sampling, meiofauna community structure at the inner stations, most remote from the original ice margin, was not or only slightly influenced by colonization, and might be structured by local environmental conditions. Communities living close to the former ice-shelf edge are believed to be at an intermediate or late stage of succession. Densities and diversity here were comparable to those at other more northern Antarctic stations in the Weddell Sea, whereas they were considerably lower at the inner stations.

The three echinoid species collected in Larsen A&B areas are good candidates as pioneering species in a changing marine environment. They are known as indirect developers (or at least non-brooders), consistent with high dispersal capabilities. Moreover, this is congruent with the wide Antarctic distribution of these species. These examples stand in contrast to other Antarctic echinoids which are known as direct developers that brood their young and, accordingly, are supposed to present low dispersal capacities. The three Larsen species also display a 'generalist' feeding behaviour which can also be considered a characteristic of pioneering species. Furthermore, the symbiotic communities of echinoids in the Larsen area showed a low diversity and a strong similarity with epibionts present on stones, something which has not been observed in other regions so far. These results suggest that ectosymbioses linked to cidaroids could contribute to benthic colonization of the seafloor in these new ice free areas.

The Larsen ice-shelf disintegration also led to the discovery of a low-activity methane seep. The observation of elevated densities, subsurface maxima and high dominance of one nematode species was similar to other cold-seep ecosystems world-wide and suggested a dependence on a chemosynthetic food source. However, stable 13C isotopic signals were indicative of phytoplankton-based feeding. This implied that the community was in transition from a chemosynthetic community to a classic phytodetritus feeding community, a temporary ecotone as it were. The characteristic parthenogenetic reproduction of the dominant species is rather unusual for marine nematodes and may be responsible for the successful colonisation by this single species.

(2) Cryptic diversity

There is evidence that the species richness of Antarctic amphipods is underestimated, not only for the poorly known deep sea but also for the better-studied shelf fauna. Given the fact that we mainly focused on the Atlantic sector (and the Ross Sea to a lesser extent), we expect that the total Antarctic diversity is even much higher and undocumented. Therefore, additional samples from other areas in Antarctica are needed to assess the real diversity, and evaluate whether some amphipod species have a true circumpolar distribution.

The discovery of cryptic diversity has potentially profound implications for evolutionary theories and biogeography and may be a potentially important factor influencing future conservation decisions. Furthermore, the Census of Antarctic Marine Life (CAML) stated that there is an urgent need for more genetic barcode studies on Antarctic organisms, especially in view of the rate of climate-driven habitat changes which might lead to extinctions. Species identification by DNA barcoding has been shown here to be efficient for amphipod taxa and will facilitate future taxonomic studies, enabling non-specialists to discriminate taxa that are otherwise difficult to identify. It will thus make species identifications faster and more accessible at a lower cost at the same time. In poorly known amphipod groups, high intraspecific genetic divergences suggest overlooked species or species complexes. The barcode application can provide a preliminary signal of species richness.

(3) Biogeographical distribution

Based on extensive datasets with distribution records of the three target taxa, a common biogeographical analysis was undertaken, aiming at comparing geographical and bathymetrical distribution patterns, focusing on the differences between meio-, macro- and megabenthos. The analysis aimed to match these patterns with the biogeographical schemes of other benthic taxa known from literature and to identify potential drivers of the observed patterns. This detailed comparative analysis, which is still ongoing, provides new insights into geographical and bathymetrical distribution patterns, hotspots of species richness and endemism, centre(s) of radiation, circumpolarity and cryptic species, eurybathy, and potential causal factors of the observed patterns.

ii) DYNABIO

(1) Trophodynamics

Investigating food preferences in Antarctic benthos is of crucial importance since the ongoing climate change may alter the natural balances and the functionality of polar ecosystems. Rises in air and water temperature have been claimed to explain shifts in the size range of phytoplankton communities, which may, in turn, affect those

biological components that depend on it. Moreover, warming trends may result in shifts in microbiological activity.

The results of this study indicate that shallow-water meiofauna prefer a phytoplankton food source rather than microbial food. This stands in contradiction with what is found for deep-sea nematodes in the Antarctic, where a microbial food source seems to be preferred over phytodetritus. In shallow waters, however, phytoplankton is of higher quality than in the deep sea where it has been degraded as a result of the sinking process. So these observations may reflect a preference for the most qualitative food, rather than a difference between preferences of deep-sea and shallow-water nematodes.

Also for echinoids it was shown that trophic flexibility can differ according to species, with euechinoid species appearing more "flexible" than cidaroids towards changes in food sources.

Therefore, aptitudes to cope with change in food availability clearly need further studies on the Antarctic and Sub-Antarctic benthic fauna, from species to ecosystem level

(2) Acidification

Although echinoids, having a magnesium calcite skeleton, are assumed to be most vulnerable to ocean acidification, experiments have shown that some species appear robust to changes in pH. Our results suggest acclimatization of natural populations to low pH effects in intertidal and sub-Antarctic areas. However it is not yet possible to precisely answer how the echinoid fauna would face global change and how complex communities will be impacted. This situation partly results to the lack of data on the proximal stress-tolerance processes, and on the nature and weight of interspecific interactions in changing communities. In that context, changes in community components along gradients crossing contrasted environmental conditions should be more precisely examined.

iii) FOREBIO

We also analysed actual species distributions in the Southern Ocean and modelled the mechanisms that structure them. The primary data used for the model were continuously developed within the NOWBIO work package (e.g. for echinoids the database covers more than 4000 georeferenced localities in the Southern Ocean, and more than 6000 when the surrounding cold temperate areas are included). This has increased the power of the modelling approach and makes it now able to compute relevantly species distribution models at the scale of the entire Southern Ocean and enables testing for the impact of environmental variables and future climate scenarios ("single species" approach).

d) Contribution of the project in a context of scientific support to a sustainable development policy

The achievements of the BIANZO II project contribute significantly to the major objectives formulated in the SCAR-EBA-programme and the IPY core activity Census of Antarctic Marine Life. Furthermore, not only were several results of BIANZO included in the Antarctic Climate Change and Environment (ACCE) report, with the BIANZO II achievements we contributed considerably to filling in the earlier listed gaps in knowledge, for which the answers are urgently required for policy makers (Turner et al., 2009).

The BIANZO consortium illustrated the potentially high sensitivity of several marine taxa which are major components of the benthic ecosystem to climate related changes such as changes in food supply, ice shelf collapse, seawater acidification and temperature rise. By means of sensitivity tables based on what we know from own research and a literature review for each of the taxa at different levels of biological organization (from populations to communities or habitats) we illustrated high sensitivity for specific climate related changes in the Antarctic environment, but we also identified major gaps in our knowledge. Furthermore, molecular approaches showed the high cryptic biodiversity present in many of the Antarctic taxa, illustrating that what we know about biodiversity so far is only the tip of the iceberg. Since the climate-induced shift in the food regime leads to a decrease in the rich Antarctic seabed biodiversity, we are currently losing biodiversity of which we will never know the characteristics or its importance. Finally, by developing a spatial model we attempted to forecast the potential impact of climate-related changes on the distribution of selected BIANZO taxa.

e) Keywords

Benthos - Climate change - Ocean acidification - Trophic interactions - Cryptic diversity - Habitat suitability model

2) INTRODUCTION

a) Background and rationale

Evolution and Biodiversity in the Antarctic; The response of life to change. The largest challenge currently facing humankind is the management of the Earth System to ensure a sustainable human future. The Antarctic and the Southern Ocean are fundamental to the Earth System as they influence the pace and nature of change on a global scale. EBA (Evolution and Biodiversity in the Antarctic) an international, multidisciplinary programme (www.eba.aq) that has been approved by the Scientific Committee on Antarctic Research (SCAR) for 2006 – 2013, aims at understanding the evolution and diversity of life in the Antarctic, determining how these have influenced the properties and dynamics of present Antarctic and Southern Ocean ecosystems, and making predictions on how organisms and communities will respond to current and future environmental change. The International Polar Year (2007-2008) offered several unique opportunities for scientific and operational collaboration in the implementation of this ambitious programme.

Polar Regions experience greater rates of climate change than elsewhere on the planet. The biota of these regions is uniquely adapted to its extreme environments, and appears vulnerable to shifts in climate and the environment. In this context, it was and still is widely recognized that there is an urgent need to undertake a structured assessment of the polar oceans biodiversity as a sound benchmark against which future change can be reliably assessed. Comprehensive baseline information on the Antarctic marine biodiversity was therefore established by the IPY core project "Census of Antarctic Marine Life" (2005-2010; www.caml.aq), a regional subset of the global programme 'Census of Marine Life', an unprecedented ten-year initiative, which aimed at assessing and explaining the nature, distribution and abundance of the past, present and likely future biodiversity of the oceans (www.coml.org).

Relying on a profound knowledge of the Antarctic biodiversity and its evolution, the improvement of our understanding of ecological processes involving the role of biodiversity in the Southern Ocean ecosystems remains a high priority on the research agenda in a changing world. Global environmental changes influence species distribution and consequently the structure of communities and ecosystems. Only advances in our knowledge of the Southern Ocean biodiversity and associated ecological processes will allow addressing complex evolutionary and ecological questions and enabling estimations of the expected change in distribution and composition of the biota.

In 2009 the SCAR Antarctic Climate Change and the Environment (ACCE) report was published based on the latest evidence from over 100 world-leading scientists from eight countries. This exhaustive overview of the latest research results (Turner *et al.*, 2009) identified crucial areas for future scientific research, and addressed the urgent questions that policy makers have about Antarctic melting, sea-level rise and biodiversity.

Major conclusions in this report were:

Advanced integrative and spatially explicit ecosystem modelling is needed to predict the future of the marine ecosystem. Such an approach demands widespread samples of ecological key species that are representative for ecological sub-systems, such as plankton, benthos or apex predators and long-term measurements of ecological key processes such as the response to acidification, warming and changes in ice cover and food regime

However, fundamentally important baseline biodiversity and biogeographic survey data are still lacking across most of the continent and parts of the surrounding Southern Ocean – those data and systematic and robust monitoring programmes across a network of representative locations are required to allow anything other than the current ad hoc and serendipitous approach to identifying biological responses to any aspect of environmental change in Antarctica

A better understanding of ecological driving forces within Antarctic ecosystems (terrestrial and marine) must serve as the basis for developing predictive models of the response of the Antarctic biota to climate change.

b) Subject: BIANZO II, coping with change

The achievements of the BIANZO II project contribute significantly to the major objectives formulated in the SCAR-EBA-programme and the IPY core activity CAML. Furthermore, not only were several results of BIANZO included in the ACCE report, with the BIANZO II achievements we contributed considerably to filling in the earlier listed gaps in knowledge, for which the answers are urgently required for policy makers (Turner *et al.,* 2009).

During its first phase (2007-2008), BIANZO II aimed at investigating (1) biodiversity patterns of the Antarctic zoobenthos and their causal processes by focussing on three representative groups of different size categories: the nematodes (meiobenthos), amphipods (macrobenthos) and echinoids (megabenthos) (Work package 1: NOWBIO); (2) trophodynamic aspects of each of the benthic groups, and their ability to cope with temperature and temperature-related changes (i.e. food composition and availability, pH of the seawater) (Work package 2: DYNABIO).

In the second phase of the project (in addition to the continuation of NOW- and DYNABIO), (3) a joint review paper dealing with the effects of global climate change on the Antarctic zoobenthos was written, based on the results of experiments, field results and literature data. (4) Information collected in previous studies (ANTAR3, ANTAR4, BIANZO I) and in the first two work packages of this project was also used to develop a model on the possible changes in the benthic communities due to global environmental change (Work package 3: FOREBIO)

Since Antarctic marine research is mainly performed in an international context, we contributed to several major international projects (ANDEEP-SYSTCO, CAML, ClicOpen, IMCOAS, etc.) and participated in several international oceanographic cruises and land-based expeditions (Polarstern cruises, BENTART cruise, Jubany field campaigns, etc.) in order to perform experiments and collect samples. These international networks offer us great opportunities for interdisciplinary, internationally embedded research (Belgium has no marine research facilities in the Antarctic), but inevitably, they also pose restrictions on the required berths, ship time, and lab space for specific integrated BIANZO objectives. Therefore common overall objectives in this research project were often tackled in taxon specific conditions (through different networks). Differences in study areas, spatial and temporal scales of investigations and approaches hampered the integration of taxon specific results in joint papers or reports. However, whereas many specific objectives in WP 1 and 2 are taxon specific for these reasons, two major (and some additionally minor) actions were undertaken in order to integrate the BIANZO results: (1) the writing of a review paper on the sensitivity of Antarctic benthos to global change and (2) the development of a GIS based model (in collaboration with the university of Dijon) that maps the habitat suitability of major Antarctic taxa within the Echinoidea, Amphipoda and Nematoda in relation to a selection of relevant environmental drivers.

c) WP 1 - NOWBIO: Nature, distribution and evolution of the benthic biodiversity

i) State of the Art before BIANZO II

Nature and distribution of benthic biodiversity. Knowledge of the Antarctic benthic biodiversity was and still is highly patchy in terms of coverage of geographical areas, bathymetric zones, habitats, taxonomic groups, ecofunctional groups, or size spectra. Vast areas of the High Antarctic continental shelf remain untouched and the Antarctic deep sea is hardly explored. During BIANZO I, the ANDEEP sampling campaigns allowed a first study of deep-sea sediments in the Southern Ocean.

A recent survey of the Antarctic macrozoobenthos revealed that 4100 spp. are presently described (Clarke & Johnston 2003) but reliable extrapolations estimated a number of potential species comprised between 11,000 and 17,000 for the entire Antarctic shelf (Gutt *et al.,* 2004).

On the other hand, during the last decade, molecular approaches have provided new insights in many evolutionary and taxonomic issues. Molecular tools have appealing applications such as reliable standardized identification, detection of cryptic species, taxonomic assignment of unknown life-history stages or unrecognizable organic material, reconstruction of phylogenies and phylogeographic studies. Significant advances in the understanding of the evolutionary history of the Antarctic biota are gained from modern molecular techniques. They have for instance allowed divergence times between taxa to be dated, and radiations such as those of notothenioid fishes to be related to climatic or tectonic events. In addition, the detection of cryptic species in some benthic groups (Held & Wägele, 2005; Raupach & Wägele, 2006), may question our current estimation of species richness and our widely accepted view of circum-Antarctic distribution pattern for benthic species (De Broyer *et al.*, 2003).

Meiobenthos - Nematodes. Until the early 90's, hardly anything was known about the ecology and diversity of meiobenthic communities in Antarctica, despite the fact they represent a major component of the marine benthos in terms of densities and diversity. Since then, several researchers from the Marine Biology research group (UGent) have focused their research on distribution patterns within the meiobenthos in general, and nematodes in particular, mostly in the Atlantic sector of the Southern Ocean (e.g. Herman & Dahms, 1992; Vanhove *et al.*, 1995, 1999, 2000, 2004). Temporal and spatial variation in subtidal and shelf communities has been described (Vanhove *et al.*, 2000; Lee *et al.*, 2001a, b) and community shifts along bathymetric gradients were analyzed (Herman & Dahms, 1992; Vanhove *et al.*, 1995, 1999, 2004, Sebastian *et al.*, 2007).

Recently, for a number of selected dominant genera, high local and regional species richness was revealed. Several species found in the Antarctic do show a wide geographical distribution. However the majority of species investigated was new to science. (Vermeeren *et al.*, 2004; Fonseca *et al.*, 2007; Ingels *et al.*, 2006; De Mesel *et al.*, 2006).

Amphipods. In the Southern Ocean, the amphipod crustaceans form the most speciose group, which occur at all depths and in very diverse microhabitats (De Broyer *et al.,* 2001, 2003). They occupy a wide range of trophic niches (Dauby *et al.,* 2001) and constitute a primary food source for the upper trophic levels (Dauby *et al.,* 2003). More than 510 – mostly benthic - amphipod species have been described from the Antarctic region (about 900 species if the sub-Antarctic forms are taken into

account) with 85% endemics (De Broyer *et al.,* 2003). Amphipods, polychaetes and gastropods constitute the most speciose macrobenthic groups in the Southern Ocean (Clarke & Johnston 2003).

Echinoids. About 80 species of echinoids occur in the Antarctic (South of the Polar Front); this corresponds to 10% of the extant species of echinoids and indicates that the Antarctic is a "hot spot" for echinoid biodiversity (David *et al.,* 2005). Antarctic echinoids belong to nine families and seven orders, and display highly diverse morphologies. The echinoid biodiversity in the Antarctic has been clearly structured by the geological and climatic changes. Today, most (65%) of the species belongs to two families that have diversified when Antarctica became isolated and underwent drastic environmental changes. Because of their ecological distribution and their biological features, echinoids are regular members of the Antarctic communities. Interestingly, the Cidaroida, one of the most speciose and widespread order of echinoids, have developed ectosymbioses with a variety of invertebrates (Hétérier *et al.,* 2004, Massin & Hétérier 2004).

ii) NOWBIO objectives

BIANZO II contributed to the establishment of a sound baseline of biodiversity knowledge required for assessing future changes in the Southern Ocean, by:

1   Describing and explaining the nature, distribution and abundance patterns of the biodiversity of the Antarctic nematodes, amphipod crustaceans and echinoids as representative groups of the meio-, macro- and megabenthos. The project focused on the exploration of unknown Antarctic areas and habitats in the CAML framework, the analysis of local and regional patterns of diversity, distribution and endemism with respect to several gradients (depth, basin or latitude), the production of new taxonomic and biogeographic syntheses and the development of new identification tools.

Specific study objectives are:

a.   To assess benthic life under permanent ice shelves (former Larsen A & B) and in deep-sea basins;

b.   To provide basic data to forecast changes in biodiversity (link with FOREBIO);

c.   To pursue the study of selected nematode genera at species level to allow further evaluation of the level of endemism and local and regional species diversity patterns;

    d.   To continue the comprehensive taxonomic revision of the Antarctic amphipod fauna and the synthesis of distribution and ecological data (undertaken during BIANZO I with the support of a strong international group of experts) and to develop electronic interactive identification keys ("Synopses of Antarctic Amphipoda");

    e.   To analyze the biogeographic distributions of echinoids in the light of past and present environmental constraints (link with DYNABIO);

    f.   To emphasize the ecological, evolutionary and functional significance of the ectosymbioses developed by cidaroid echinoids.

2   Assessing evolutionary relationships with the surrounding oceans and world biodiversity on the basis of molecular phylogeny and phylogeography of key taxa (mainly amphipods).

3   Developing and consolidating the existing BIANZO databases and contributing to the development of SCAR-MarBIN, the information network on Antarctic marine biodiversity.

d) WP 2 - DYNABIO: Ecofunctional role of biodiversity in benthic communities and their ability to cope with change

i) State of the art before BIANZO II

Antarctic species were thought to be highly adapted to the extreme environment they live in. They show clear adaptations to the stable cold water temperatures and seasonal food supply, in the form of, for instance, slow metabolic rates, slow seasonal growth and longevity (Knox, 1994; Arntz *et al.*, 1994), and large body-sizes (gigantism, Chapelle and Peck, 1999). Antarctic organisms often have a small thermal tolerance window (Arntz *et al.*, 2005) which is for several megafaunal organisms and fish much smaller than for Arctic animals (Pörtner *et al.*, 2007). This small tolerance, coupled with slow growths and long generation times, drastically reduce the ability of benthic organisms to adapt or to evolve new characters (Peck, 2002, 2005). A change in food composition, quality and quantity, together with other environmental shifts (for instance in temperature or pH of the seawater), are likely not only to impact densities, biomass and community composition but also functional aspects.

Meiobenthos. Functional or physiological aspects of meiofauna in general, and nematodes in specific, remain poorly known. Studies on the trophic position of meiobenthos in temperate and tropical areas have lead to conflicting results (van Oevelen *et al.,* 2006 and references therein) and research in Antarctic and Subantarctic sediments are preliminary and restricted to a limited number of habitats

(Moens *et al.*, 2007). Biomarker analysis of bulk sediment organic matter and of nematodes in different regions and sediment types was carried out to assess the energy source of meiobenthic fauna in Antarctic shelf sediments (Moens *et al.*, 2007). The results of this study suggested substantial selectivity of the metazoan meiobenthos for specific components of the sedimented organic matter, such as ice algae or flagellates, with this selectivity differing between sites and sediments. Laboratory experiments on a number of selected species from temperate regions showed that reproductive success, growth and metabolic activity of nematodes largely depend on temperature, the quality and quantity of food, and to a lesser extent salinity, with different species thriving under different conditions (Moens and Vincx, 2000a,b). A better understanding of the current functionality of the meiobenthic communities in different habitats is needed, and will allow assessing how these processes can be affected by changes in the environment. These changes might also impact structural aspects of the meiobenthic, and more specific the nematode communities, such as community composition and diversity, but also densities and biomass.

Amphipods. During BIANZO I trophic diversity was approached on a number of selected taxa using different techniques, including SEM observations of feeding appendages, stomach content analyses, and other proxy analyses such as stable isotopes or lipid contents (Dauby *et al.*, 2001; Nyssen, 2005). A wide variety of feeding types have been described, with some of them hyper-specialized and thus potentially vulnerable to changes in community structures. At the same time, some species appear to be more opportunist in their diet and able to shift from a diet to another, depending of the food kind and availability. Of particular interest in this project are the scavenging amphipods. Not much is known on their feeding requirements and of the importance of large food falls (from the pelagic) in their diet. Numerous experiments with bait have shown repeatedly that scavengers recognize the appearance of a large food items quite quickly, home in on it in large numbers and are capable of consuming it rapidly and completely (De Broyer *et al.,* 2004). Any change in pelagic systems that alter frequency or size spectrum of food falls can have a direct impact, especially on deep sea communities. Moreover, little is known about metabolism of Antarctic scavengers (or other feeding guilds), but it seems likely it is related to temperature and food quantity.

Echinoids. In the Antarctic, carnivores (Cidaridae) and deposit-feeders (Schizasteridae) are largely predominant and occur "everywhere". In contrast, algivores (mostly Arbaciidae) are almost lacking and restricted to the Peninsula or to the sub-Antarctic islands while omnivores (mostly Echinidae) are moderately present (David *et al.,* 2005). This is quite different from observations in most other marine ecosystems where most regular echinoids are algivores and omnivores (e.g., De Ridder & Lawrence 1982). The scarcity of algivores and their restricted distribution

presumably reflects an unpredictable access to food. Because they are either specialists (carnivores or algivores) or generalists (omnivores), we can expect the echinoids to cope in different ways with global warming. Seasonality of feeding is known to occur for opportunistic echinoids like *Sterechinus neumayeri* which stops feeding during austral winter (Brockington & Peck 2001, Brockington & Clarke, 2001). Particular responses to food availability can be expected as it is observed for other groups such as brachiopods (Peck *et al.,* 2005). Surprisingly, little is known on the trophic plasticity, i.e. on the adaptive response of each of these trophic categories. These data would however be fundamental to understand/predict the potential effects of global warming on the echinofauna. In the context of global change, increasing atmospheric carbon dioxide will result in decreasing ocean pH and carbonate ion concentration. This effect will be particularly important at high latitudes (Orr *et al.,* 2005). Under some scenarios, the entire water column of the Southern Ocean may become undersaturated towards aragonite by 2100. These changes in seawater chemistry will have severe consequences for calcifying organisms and will presumably affect echinoid skeletogenesis. Reduced calcification by both aragonite and calcite-secreting organisms under decreased carbonate ion concentrations has been documented in planktonic and benthic biota (Riebesell *et al.,* 2000, Shirayama & Thornton 2005, Orr *et al.,* 2005). Actually, echinoids secrete high-magnesium calcite and/or amorphous calcium carbonate which are even more soluble than aragonite. Increased carbon dioxide has already been shown to inhibit skeletal growth in a subtropical sea urchin. However, data are lacking for high-latitude calcifiers in general and for larvae in particular (Orr *et al.,* 2005).

ii) DYNABIO objectives

1   To investigate different aspects of the ecofunctional biodiversity of Antarctic benthic organisms,

Specific study objectives are:

a.   To study the trophic position of meiobenthos from shelf to lower slope;

b.   To analyze the dependence of amphipod crustaceans on food availability;

c.   To characterize food preferences of selected amphipod species, as well as trophic habit plasticity in communities along a latitudinal gradient. In parallel, the ecological significance of benthic scavenger assemblages will be evaluated by combining feeding ecology and physiology of representative species of the Antarctic shelf scavenger guild.

2   To assess to what extent benthic organisms and communities can cope with change.

Specific study objectives are:

d.   To assess the impact of change in food quality and quantity and temperature on structural and functional aspects of meiobenthic communities;

e.   To characterise the trophic categories of Antarctic and Subantarctic echinoids and the influence of food resources on their distribution in order to determine their potential response to current and future environmental change in relation to their trophic categories (link with FOREBIO).

f.   To study the impact of seawater acidification due to increased atmospheric carbon dioxide on skeletal growth in both larval and adult sea urchins. The idea is to infer the potential impact of this acidification on sea urchin distributions in the Southern Ocean (link with FOREBIO)

All the results from experimental and field work carried out by the separate institutes (BIANZO II phase 1 + new data) were integrated, in combination with literature data, to produce a review paper that provides an overview about what is known on potentially climate-related effects, such as change in primary productivity (food quality and quantity), glacier melt (increased sedimentation and freshening), increase in frequency of iceberg scouring, collapse of ice shelves, acidification, on the three benthic groups considered in the project

e) WP 3 - FOREBIO: Forecasts for the XXIst century under global change

i)   State of the art before BIANZO II

Global coupled ocean-atmosphere models propose climate evolution scenarios that forecast a global warming that strongly impacts polar seas. In Antarctica, such changes will lead to conditions drastically departing from those of today. The evolution of terrestrial and marine environments has already started, but it will accelerate in the forthcoming decades. For example, mean air temperature increased by 2.5°C in the last 50 years on the Peninsula. This has a severe impact on sea ice and ice shelf dynamics (Vaughan & Doake, 1996) and more than 10000 km2 of ice shelf disappeared in the last 30 years, including 3.200 km2 from Larsen B in 2002. Therefore, even if the exact speed and range of the warming process is still under debate, it is certain that Antarctic ecosystems will be faced to the most important and rapid changes they have ever experienced in the last 40 My.

The easiest adaptive solution for organisms faced to change is to follow their habitat, and to migrate. This is demonstrated by numerous examples of shift in phytosociological associations. Another solution - frequently associated with the former one - is to rely on adaptive flexibility, and to acclimate the new conditions through a phenological response. A third option is to evolve and to develop new heritable characteristics. But this must be compatible with evolutionary rates requiring 103 to 105 years to be effective (Hoffmann & Parsons 1997) and in the scenario of present global warming, this latter solution has to be discarded. In this framework, Antarctic and the Southern Ocean represent an interesting case study associating shift to the South, local acclimatizations, and new competitions. Indeed, regarding the Southern Ocean and their surrounding areas, the future is not a simple matter of shift of ecosystems following their climatic belts as it would be for most other places, but a more complex and dramatic situation. Antarctic endemic fauna will be trapped by the coastline and must acclimate, adapt or disappear, while cold temperate and sub-Antarctic fauna should have the possibility to migrate and/or to change their phenology. This situation may induce new interactions between local species possibly weakened by the warming, and invaders from the North.

The Southern Ocean pristine ecosystem might not be as isolated and protected as expected. There still is some controversy about the role of the Polar Front may play in acting as a barrier that may reduce successful establishments of occasional invaders (Thatje, 2005) and several examples already demonstrate its permeability. Such "travellers" represent potential colonialists whose installation was so far prevented by the drop of temperature across the Polar Front. But the barrier could become considerably weaker, therefore increasing the impact of invading species on the Southern ecosystem (Clarke *et al.*, 2005). Therefore, global change (temperature, precipitations, ice shelf extension…) consequences should be quite dramatic, and it becomes necessary to address the point in order to estimate their potential impact. It has been shown that climate change has already had an influence on bird colonies (Fraser & Hofman, 2003). The rise of ice scour has a great influence on the reduction of shore biota (Barnes, 2005). The reduction of sea surface salinity due to glacial melt-water runoff (Dierssen *et al.*, 2002) has induced a shift in primary production from diatoms towards the smaller cryptophytes (Moline *et al.,* 2004). Several studies have shown that the Antarctic and sub-Antarctic fauna is affected by global warming and that some species display new geographical distributions, such as the emblematic king crab (Thatje *et al.*, 2005) or spider crab (Tavares & De Melo, 2004).

ii) FOREBIO objectives

The major objective of FOREBIO was to develop a model on the possible changes in the benthic communities due to global environmental change. A Geographic Information System (GIS) is constructed, which is being fed with biogeographical (georeference), edaphic, oceanographic, climatic and specific biological data. It relies on distribution data of the meiofauna (mainly nematodes), amphipods and echinoids in order (1) to assess the present day macro-ecological patterns, and (2) to forecast the potential impact of climate-related changes on these selected taxa.

Specific study objectives are:

a.   To construct a Geographic Information System (GIS)

b.   To feed the system with biogeographical (georeference), edaphic, oceanographic, climatic and specific biological data. It will rely on distribution data of the meiofauna (nematodes), amphipods and echinoids

c.   To assess the present day macro-ecological patterns,

d.   To forecast the potential impact of climate-related changes on these selected taxa.

3) METHODOLOGY AND RESULTS

a) Methodology

i) Collection of faunal and environmental material

Samples from previously unknown Antarctic areas and habitats have been collected (1) in the deep Weddell and Scotia Sea (ANDEEP I-III campaigns: 2002, 2005; IPY ANDEEP-SYSTCO campaign: 2008), (2) in the formerly ice-covered Larsen A and B areas (IPY *Polarstern* ANT XXIII-8 expedition: 2006-07) and (3) in the Bellingshausen Sea (BENTART'06 campaign 2005-5006). During the RV Polarstern cruise ANT XXIV-2 to the Southern Ocean and the Weddell Sea in 2007/2008 meiofauna and environmental samples were taken during and after a phytoplankton bloom at 52°S 0°E and along a longitudinal deep-sea transect (1900 – 5300 m) covering 49°S to 70°S. For shallow water systems, all meiofauna sampling was performed in the shallow-water sediments in front of the Fourcade glacier, Potter Cove, King George Island near the Jubany Antarctic station.

Meiobenthic and environmental samples on the shelf and in the deep sea were collected by means of a multicorer; meiobenthic sampling in shallower subtidal waters (ca. 15 m water depth) was conducted by SCUBA divers using plastic push cores, closed off with stoppers. Niskin bottles were used to sample the water column above the bottom in the shallow subtidal. All cores used for analyses were retrieved with min. 5 cm of relatively undisturbed sediment and supernatant ambient water.

Material for meiofaunal community analyses was fixed with 4% buffered formalin. Vertical distribution of the meiofauna was investigated by slicing the sediment core intended for community analysis in sediment slices of 1 cm (0-1; 1-2; 2-3; 3-4; 4-5 cm). Parallel sediment slices were kept frozen for later analysis of environmental variables such as sediment grain size, pigment content, etc., and stable isotope analysis ($\delta 13C$ and $\delta 15N$) and poly-unsaturated fatty acids analysis (PUFAs). Nematodes (100 - 200 per sediment core) were identified up to genus level and sometimes species level (depending on the objectives of the individual studies). The sampling strategy used for the meiobenthos allowed the assessment of spatial variation in terms of community structure and trophic complexity in relation to environmental parameters. In combination with data available at Ghent University (from the Atlantic part of the Southern Ocean and the Ross Sea), distribution patterns of the nematofauna and their possible origin and evolution can be investigated.

Samples for the analysis of macro- and megafauna were collected with diverse sampling gears such as Agassiz trawls and Rauschert dredges. Various collections of amphipods are available for study, including the rich United States Antarctic Project (USARP) material provided by the Smithsonian Institution, Washington.

ii) Data development

One of the most important objectives of the BIANZO II project is the collection of previously ungathered data and the continuous updating and development of the existing data. They are the benchmark against which future scenarios under climate change can be tested and serve as the basis for ecological modelling and any assessment of taxa, communities and ecosystems in terms of biodiversity, biogeography, functioning and sensitivity.

During the whole of the project each partner has endeavoured the completion of databases in order to achieve its objectives. For **nematodes**, genus and species data including geographical and ecological information has been gathered from newly analysed samples and a multitude of historical and recently published literature sources. These data have been integrated in the NeMys database which is connected with the SCAR-MarBIN web portal. These data have contributed to the joint biogeographical paper and have served as input in the FOREBIO model to investigate macro-ecological hypotheses. Starting with the data contained in De Broyer *et al.,* (2007), the Antarctic **amphipod** data has been extended substantially with information available from new samples obtained within the BIANZO programme, through international collaboration and the investigation of different available collections. These data have been added to the Ant'phipoda database which is also accessible through the SCAR-MarBIN portal.

For the **echinoids**, a large number of records have been added to the echinoid database, including the "Synopses of Antarctic Echinoids", an interactive database on CD-ROM. These data have been collected through extensive international collaboration and investigation of available samples and collections worldwide.

In addition to the biological data gathered by the BIANZO partners a large amount of environmental data was collected by the research group from the Université de Bourgogne, mainly through international collaboration, and made available within the BIANZO consortium and on the SCAR-MarBIN website. Further details on these data are mentioned in the FOREBIO sections of this report. In addition, further detailed information on data development has been integrated in the different chapters of this report.

iii) Biogeography (related to joint biogeographical paper)

Biogeographical data on Antarctic nematode species and genera have been gathered from various literature sources and field observations. Amphipod geographic and bathymetric records as well as taxonomical information were taken from De Broyer *et al.,* (2007), and echinoid data were taken from David *et al.,* (2005) and updated through international collaboration and investigating collections and new samples. These datasets are hosted in the BIANZO databases (Nemys.be, Ant'phipoda, Antarctic Echinoids), accessible through the SCAR-MarBIN portal (www.scarmarbin.be/). We also participated in the Antarctic-South-American Interactions (ASAI) in the Marine Environment Workshop and Symposium (nov.2009, Rio De Janeiro) in order to investigate the biogeography of Antarctic fauna.

The Southern Ocean extending from the Antarctic continent up to the Subtropical Convergence, and including sub-Antarctic islands and part of Patagonia (up to 41°S on the Southern Chile side) was considered. The area was partitioned in 30 operational geographic regions, more or less following the limits of the geographical entities used by Linse *et al.,* (2006), Clarke *et al.,* (2007a), Barnes & Griffiths (2008) and Griffiths *et al.,* (2009) to allow a better comparison with previous biogeographical studies. Only the species occurring between 0 m to 1000 m depth were taken into account, except for the bathymetrical analysis, where all depth records were considered.

The bathymetric distribution analysis was performed with species occurring around the continent (incl. Antarctic Peninsula), excluding Scotia Arc and sub-Antarctic records. Bathymetric zones include (1) the shelf zone (0-1000 m), divided in three sub-zones: 0 to 100 m (phytal zone), 100 to 500 m and 500 to 1000 m depth; (2) the bathyal zone (1000-3000 m), divided into two sub-zones: 1000 to 2000 m and 2000 to 3000 m depth; and (3) the abyssal zone: >3000 m.

PRIMER v6 software (Clarke & Gorley, 2006) was used to perform multivariate analyses and determine faunal similarities between the different areas and depth zones. Non-transformed presence/absence data were used to build a similarity matrix based on Bray-Curtis similarities, which was then used to construct a non-metric multidimensional scaling (nMDS) and cluster analyses, in order to display faunal similarities. A preliminary analysis of echinoid distribution was also performed using the Jaccard Index.

Non-metrical Multidimensional Scaling plots are visualisation plots based on similarities or dissimilarities of data in a non-parametric way. MDS is a special case of ordination whereby each item is given a location in a predefined N-dimensional space based on its relative (dis)similarity (cf. Resemblance matrix whereby different types of indices can be used) with other items. This type of ordination plots are

frequently used in ecological investigations to distinguish between faunal components from different areas, habitats, etc. For more information we refer to Clarke & Gorley (2006).

iv) Morphological taxonomy

Nematodes. Identification of the nematodes was done using light microscopy, relying on on-line identification keys (NeMysKey©) and the pictorial key of Warwick *et al.,* (1998). Transmission and scanning electron microscopy were applied for more detailed investigations.

Amphipods. New and poorly known species were described, selected families of the Antarctic fauna revised and all results synthesised as family monographs to contribute to the "Synopses of Antarctic Amphipoda", with the contribution of the Antarctic Amphipodologist Network (16 specialists; 12 countries). Electronic interactive keys for selected families were built using the Delta/Intkey software (delta-intkey.com/). Drawings of *Liljeborgia* species were electronically linked with ADOBE Illustrator and a WACOM drawing board. During this process, the methods described in the literature were improved (e.g. the conception of art brushes for the illustration of spines and thick setae). Our innovations (acknowledged by Coleman, 2009), considerably speeded up the creation of taxonomic illustrations.

Echinoids. The recently published "Synopses of Antarctic Echinoids" and an interactive database (on CD-ROM) are the basic references to identify echinoid species. Any new records were added to the database, which in turn is interfaced with SCAR-Marbin.

v) Molecular taxonomy and phylogeny

Nematodes. Our collaboration with CEMOFE (Centre for molecular phylogeny and evolution, UGent) allowed us to perform molecular analyses when and where needed. A selection of specimens was extracted from Antarctic samples at the Scotia Arc. These specimens were identified to genus level, photographed and a log file was created for them, so that species identification can be vouched in a post-analysis phase. Subsequently the specimens were put in molecular grade ethanol and sent to the Census of Antarctic Marine Life (CAML) barcoding project for analysis; details regarding the analysis protocol can be obtained through the responsible of the CAML barcoding initiative.

Amphipods. During the ANTXXIII-8 (November 2007-January 2008) and ANDEEP-SYSTCO (November 2008-January 2009) campaigns, new samples of *Liljeborgia* were collected for morphological and molecular studies. Extensive *Liljeborgia* material from various museums, collected between 10 and 4000 m depth, was

brought together for morphological studies. Part of the material of the Museum of Verona was also examined. Genetic characterization of selected deep-sea and shelf taxa was conducted by sequencing mitochondrial (COI) and nuclear (28S rRNA) gene fragments. A molecular phylogeny of lysianassoid taxa was constructed, using both markers in order to reveal the evolutionary patterns in these taxa. The molecular analyses also permitted us to evaluate the suitability of the mitochondrial gene COI as a barcoding marker for Antarctic lysianassoids to contribute to "Barcode of Life" (Hebert *et al.*, 2003), and to detect some possible cryptic species complexes in the taxa. The target taxa of our study are Antarctic lysianassoids, more particularly the *orchomenid* genus complex, which comprises the following genera: *Orchomene* (Boeck, 1871), *Orchomenyx* (De Broyer, 1984), *Orchomenella* (Sars 1895) *Abyssorchomene* (De Broyer, 1984) and *Pseudorchomene* (Schellenberg, 1926). The samples were collected during several Polarstern expeditions and originate from different locations in the Weddell Sea, the Antarctic Peninsula and the Scotia Sea, from shelf to abyssal depths. Supplementary samples were obtained from the Ross Sea and King George Island. Amplification of the mitochondrial COI gene was carried out with the polymerase chain reaction using the universal primers LCO1490 and HCO2198 (Folmer *et al.*, 1994). For the 28S, primers 28F and 28R designed by Hou *et al.,* (2007) were used for amplification. PCR products were sequenced bidirectionally with ABI BigDye terminator sequencing protocols. Sequence analysis was performed by using classical and complementary methods for the reconstruction of phylogenetic trees (*e.g.* Maximum Parsimony, Maximum Likelihood, Bayesian Method).

vi) Trophic position and dynamics

Nematodes and other meiobenthic groups. Stable isotopes (δ^{13}C; δ^{15}N: different C-sources) and poly-unsaturated fatty acids (PUFAs: selective take-up of organic matter) analyses were used to investigate trophic position, trophodynamics and selective feeding properties.

In the shallow waters of Potter Cove, King George Island, Western Antarctic Peninsula, cores were collected by SCUBA divers, closed with stoppers and immediately stored at -20°C for analysis. Next to the analysis of natural background samples, the trophic position and selective feeding properties of several meiobenthos groups in Potter Cove marine sediments has been investigated by pulse-chase feeding experiments using ^{13}C labelled food bacteria and diatoms; ^{13}C-labelled diatoms (food source 1) and bacteria (food source 2) were freeze-dried in the laboratory beforehand and added to 12 sediment cores (6 x 30mg of labelled diatoms, 6 x 30mg of labelled bacteria) which were left incubated and aerated at 0°C for 10 days. After 5 and 10 days, the cores were sampled and sliced in sediment layers of 0-1cm, 1-2cm, 2-5cm, 5-10cm and then stored at -20°C prior to analysis.

The sediments were sampled at the beginning and the end of the incubation period. For more detailed protocols of the shallow-water Potter Cove experiments we refer to Pasotti *et al.,* (submitted).

For the Weddell Sea area, near Kapp Norvegia, trophic status, dynamics, and selective feeding properties of Antarctic deep-sea nematodes were – next to natural background samples – also investigated within an experimental setup. Deep-sea multicore sediment samples from Polar Regions were incubated aboard research vessels with ^{13}C-labelled bacteria or diatoms to determine whether the nematode community prefers to utilise freshly settled phytodetritus or a bacterial food source. The cores were collected at ca. 2400 m water depth and incubated onboard for 1, 7, and 14 days in Antarctica (Kapp Norvegia) and the Arctic (Hausgarten site). Natural background deep-sea samples were taken with multicorers and stored at -20°C until analysis; for the deep-sea feeding experiments, core samples were incubated under laboratory-controlled conditions mimicking in-situ habitat and were subsequently stored at -20°c until analysis. For more detailed protocols we refer to Ingels *et al.,* (2010).

To gain insight in the trophic status and the link between the structural and functional nematode (and copepod) diversity on the scale of the Southern Ocean, samples were taken with multicorers from a N-S transect along the Greenwich Meridian, from the Antarctic Convergence towards a the very south of the Weddell Sea. Samples from 6 stations were analysed for ^{13}C and ^{15}N stable isotopes and nematode community structure. A number of samples (sediments and nematodes) have been prepared for fatty acid analysis to investigate the trophic position and feeding behaviour of nematodes within the Antarctic benthic food web and to investigate any latitudinal pattern of nematode trophic characteristics in the Southern Ocean. An additional station at 52° S was revisited after a phytoplankton bloom had settled to enable further comparisons with pre-bloom conditions and study the nematodes (and copepods) and their trophic role in the food web relating to phytoplanktonic bloom conditions in the Southern Ocean. All samples were collected during the ANDEEP - SYSTCO campaign on board of RV *Polarstern* from 12/2008 – 02/2009; for more detailed protocols we refer to Veit-Köhler *et al.* (2011), Guilini *et al.* (in prep.). In addition, samples from the Larsen sub-ice communities in a post-ice shelf collapse phase have been taken and analysed to investigate trophic characteristics of the nematode community. Protocols were identical to those mentioned above for deep-sea samples.

Amphipods. The promising results obtained during BIANZO I on the trophic position of amphipods, were refined by studying new selected species, with emphasis on scavengers. Investigations included gut content analyses, morphological observations and tracing techniques such as stable isotope or fatty acid analyses to

identify the origin of food. The importance of prokaryotes in the digestive tract of amphipods was assessed by epifluorescence or SE microscopy, and by immunological or DNA techniques. Changes in food supply from the water column to the benthos (seasonal or long-term) could force amphipods into a "trophic shift". Feeding experiments were set-up in aquaria, mainly with scavenging species, using different labelled substrates. In parallel, measurements of the energy demand by scavengers (metabolic activity, respiration and body composition) were performed to evaluate the influence of trophic stress (*e.g.* climatic, human-induced…) on the general energy budget of individuals. These results, together with literature information, are being integrated in a balanced model of scavenger assemblage trophic links and energy flows, showing the significance of the scavengers' share in overall benthic energy flow and the potential sensitivity of the system to changes in food supply.

Echinoids. In literature, regular echinoids are considered opportunistic browsers. Although they feed on what is available in their habitat, they usually exhibit some food preferences. Various taxa belong to particular trophic groups: carnivores (Cidaroidea) versus opportunists (many Euechinoidea). Compared to specialized echinoids, the generalists are, at first sight, good candidates to acclimatize to new trophic resources. To identify tolerance ranges of Antarctic echinoids (in order to propose potential responses to environmental changes, i.e. biological filters for FOREBIO) the feeding behaviour of generalist (Echinidae) and specialist (Cidaridae) feeding echinoids were characterized through three series of analyses: (1) a qualitative inventory of gut content through microscopic observations, (2) a stable isotope analysis (gut content, gonads, muscles) and (3) the investigation of genetic features of the digestive micro flora by molecular tools (DGGE and 16S rRNA cloning). Echinoids were dissected on board of the research vessels. For microscopic and genetic observations, gut content samples were isolated and fixed in ethanol 100%. For isotopic analyses, gut contents, gonads and muscles (Aristotle's lantern musculature) were isolated and kept in liquid nitrogen (at -27°C).

vii) Experiments on the ability of the Antarctic zoobenthos to cope with change

Nematodes and other meiobenthic groups. The ability of the Antarctic meiobenthos to cope with warming was tested in shallow-water systems within an experimental setup. Cores collected by scuba divers were incubated under different temperature conditions for a period of 14 days whilst benthic respiration rates were investigated. The aim was to investigate the influence of rising temperatures on the respiration of the Antarctic benthos: microbenthos, meiobenthos and macrobenthos. Temperature treatments were 0°C (ambient temperature), 2°C, 4°C and 6°C. For each treatment, four replicate cores were incubated. Cores were kept at temperature

in water-filled buckets kept at a constant temperature by means of thermostats. Water temperature fluctuations were kept to a minimum by frequent inspection and adjustment. Every day, 10ml of water was sucked out from each core, at 5cm from the sediment surface. The oxygen content of this 10ml water sample was then measured using the Winkler method with a spectrophotometer. The same amount of water was added separately but at the same temperature as the respective core, was added again subsequently. All cores were incubated for 14 days, except for the water samples of the 2°C treatment. This incubation was stopped after three days because of a temporary heat (7°C) shock, which clearly affected the results. The sediment cores were kept for further examination in spite of the temperature failure, however, and a new series of 4 sediment and 4 water cores was added for an incubation period of 10 days. Sediment was collected the day of sampling (Day 0), after 5 days and at the end of the incubation period. From each core, a small amount of sediment was taken for bacterial counts and ATP measurements. The remainder of the core was sliced (0-1cm, 1-2cm, 2-3cm, 3-4cm, 4-5cm, 5cm-rest) The samples were analysed for several structural and functional, community-related parameters, such as densities, vertical distribution, individual and total biomass, nematode community composition, diversity and nutrient fluxes.

Echinoids. The impact of acidification on adults and larvae was assessed firstly on easy-to-obtain temperate and boreal species, and secondly on Sub-Antarctic species, under altered sea-water chemistry. Larvae were grown following standard procedures under normal and altered sea-water composition, covering a pH range from 8.0 to 6.8. Larval development was characterized using embryotoxicity protocols (Warnau *et al.*, 1996), to distinguish between normal and altered general morphologies. Spicule development was quantified using image analysis of micrographs. Morphology of spicules was monitored by SEM. Metabolic parameters and spine regeneration were measured on adult urchins reared in closed-circuit aquaria with normal and altered sea water chemistry. For both larvae and adults, dose-response relationships were established for the different dependent variables under study, related to carbonate and dissolved CO_2 concentrations. Furthermore, cidaroid field specimens from the Weddell Sea were studied in order to assess morphological and chemical changes in spines, according to magnesium-calcite saturation state along depth.

viii)   Communication, integration and valorisation

Workshops and meetings. During the BIANZOII project 7 meetings and workshops were organised to communicate results, pursue integration of the results and concerted research efforts, and align the partners' research strategies, as well as having discussions with the follow-up committee. Meetings and workshops were held on 3/5/2007, 18/6/2008, 20/5/2009, 14/9/2009, 22/2/2010, 17/3/2010, and 21/1/2011.

The meeting minutes of the meetings that where attended by the follow-up committee are available in Annex 2.

Scientific and general outreach. In order to maximise scientific valorisation of the BIANZO II results, multiple oral and poster presentations were given at a multitude of national and international meetings and conferences. These contributions are listed in Section 5 "Dissemination and valorisation." The BIANZO partners have also actively participated in a number of national and international workshops, some with significant immediate results in terms of scientific and general outreach; these are mentioned in the Section 5. In addition, a number of outreach efforts to the general public have been conducted on national and international level. These are also mentioned in Section 5.

Review paper on climate change effects. During two initiating workshops organized in 2009, discussions were held to obtain the structure, objectives and future strategy of a review paper on the expected effects of climate change on the major benthic BIANZO taxa including nematodes, amphipods, echinoids but also foraminiferans and isopods. A strong basis was laid in the discussions of the first workshop, during which an overview was given of the up-to-date information on potential climate change effects on the five benthic groups of interest. This helped the development of a complete integration of all partner results obtained during the BIANZO II project. A flow chart was produced in order to separate the different climate change effects and the different levels of interaction between these effects and the benthic groups of interest. In addition, a sensitivity table template was created, based on own results and literature data in order to have a detailed account of what climate change induced factors will influence the different zoobenthic groups and to what extent the taxa will be influenced (i.e. the sensitivity table will indicate what kind of biotic response a certain effect-range will evoke). Currently, this table is being completed and updated by the partners. During several other meetings, the progress in this integrated manuscript has been discussed and the manuscript is nearing finalisation. A preliminary version of the table will be included in this report as well as an outline of the achieved results within this concerted integrative research effort. Furthermore, Prof. A. Gooday and Prof. A. Brandt, end-users of the BIANZO II phase II project are contributing to the review paper with their expertise on Antarctic Foraminifera and Isopoda, respectively.

ix) FOREBIO

For the purpose of developing, discussing and evaluating FOREBIO and the construction of the GIS models, several workshops were organized. Three main steps were identified in the FOREBIO construction process: 1) building the frame in a GIS environment, 2) adding shared data, and 3) adding specific data (taxon related).

Step 1 was accomplished during 2009 and the GIS-based model is now being constructed further. Step 2, involving the addition of shared data has progressed substantially and involved many contributors beyond the BIANZO network. All BIANZO partners are continuously updating these data with newly available information, and substantial progress has been made, especially during the last year. For echinoids the database covers more than 4000 georeferenced localities in the Southern Ocean, and more than 6000 when the surrounding cold temperate areas are included; this has been achieved through amending existing data and inventorying samples and collections worldwide. The primary data used for FOREBIO actually correspond largely with the data gathered within NOWBIO. For nematodes genera data was gathered from the Nemys database and various literature sources, and ecological information was included. For amphipods, a recapitulatory file was amended, in which all Antarctic and Subantarctic species of amphipod are listed with all available data on taxonomy, species descriptors, geographic occurrences with detailed latitude and longitude data, indication of the locality, mission name and station where the specimens were sampled, water depth, gear and additional information. About 70 percent of these data were collected from the synopsis of the Amphipoda of the Southern Ocean (De Broyer *et al.*, 2009), through the SCAR-MarBIN network. The remaining 30 percent were gathered from the IRScNB's ANT'Phipoda (MISTA) database. The data was compiled and standardised and/or converted to fit the template.

Intensive data collection has increased the power of the modelling approach and has made it possible to compute species distribution models at the scale of the entire Southern Ocean and to test for the impact of environmental variables and future climate scenarios ("single species" approach). It will also be possible to analyse biogeographical relationships between the different regions of the Southern Ocean ("fauna" approach) using ordination or network techniques (this will be accomplished before the end of the BIANZOII project in the case of echinoids).

Species distribution models have been performed by matching abiotic data of the environment to occurrence data using a GIS (software ArcGIS version 9.3) and modelling of fundamental niches has been possible with Maxent (version 3.3.2), a program using a maximum entropy modelling procedure (Phillips *et al.,* 2006). Maxent was developed for assessing species distributions from « presence-only » data. It aims at evaluating the target probability distribution, i.e. the real probability distribution of a species over the whole study area. This can be done under present day conditions to establish suitability distribution maps, but can also contribute to the modelling of future scenarios and predictive distributions. Additionally, Maxent offers the possibility to undertake post-hoc appraisals of the reliability of the results and of secondary data. A complementary exploration has been conducted using GARP (Stockwell and Peters 1999), a program using a genetic algorithm rather different to

that of Maxent, and allows to check the consistency of the results provided by both approaches.

b) Results

The scientific results of all research groups are represented according to the 3 work packages within BIANZOII (NOWBIO, DYNABIO, and FOREBIO). Where possible, integration of the results was pursued. For each topic the appropriate objectives within each WP have been mentioned.

i) NOWBIO – Nature, distribution and evolution of the benthic biodiversity

(1) Structure and function of fauna in the Larsen area – Responses to large-scale ice shelf collapse

NOWBIO objectives 1-a, (b, c, e)

Direct warming effects are observed all over the world, but the Antarctic Peninsula is considered one of the fastest warming areas in the world (King *et al.*, 2003; Chapman & Walsh, 2007). Extreme warming near the peninsula was manifestly expressed in 2002, when 500 billion tons or 3250 km² of ice from the Larsen B ice shelf collapsed at the eastern side of the Antarctic Peninsula, and this in only one month's time (31/01-07/03/2002) (Fig. 7). A few years before, in 1995, the ice shelf of the nearby Larsen A region had already disintegrated completely. The collapse of these ice shelves has indeed been attributed to extreme warming, and the Larsen B collapse happened during the warmest summer on record for the area (Scambos *et al.*, 2000). Ice-shelf collapse initially leads to increased iceberg disturbance and may have detrimental effects on surface primary productivity (Arrigo *et al.*, 2002). Later, the formerly ice-covered area opens up, leading to increased primary production and the opportunity to enter the area for scientific investigations.

Between 11/01/2007 and 22/01/2007, the Larsen area was investigated by a team of researchers with the German research vessel Polarstern (campaign ANT-XXIII/8). A synoptic approach was applied, including different spatial scales, different groups of organisms (from pelagic to benthic, from primary producers to apex predators) and different environmental characteristics at a limited number of sampling stations (Gutt *et al.*, in press). Representatives of the BIANZO II consortium sampled and investigated the continental shelf benthic fauna in the area. The Antarctic shelf is notoriously rich at local as well as regional scales (Arntz *et al.*, 1994), and effects of large-scale ice-shelf collapse events were still visible after 5 years. The investigations of the BIANZO II group were meant to provide information on the following topics: (1) Current status of the Larsen benthic shelf fauna; (2) Biogeography and taxonomy of

certain benthic taxa; (3) Response of the Larsen benthic fauna to large-scale ice-shelf disintegration events/ability of this fauna to cope with a changing environment; (4) Recolonization speed of the Larsen benthic fauna after large-scale ice-shelf disintegration events (5) Identification of the fauna of newly discovered habitats.

(a) Meiofauna

During the ANT-XXIII/8 Polarstern campaign, the Larsen region was sampled for the first time (Fig. 1., indicating stations sampled). Our study was the first that investigated benthic communities in this area by studying the meiobenthic response to the collapse of ice shelves in the Antarctic (Raes et al., 2010).
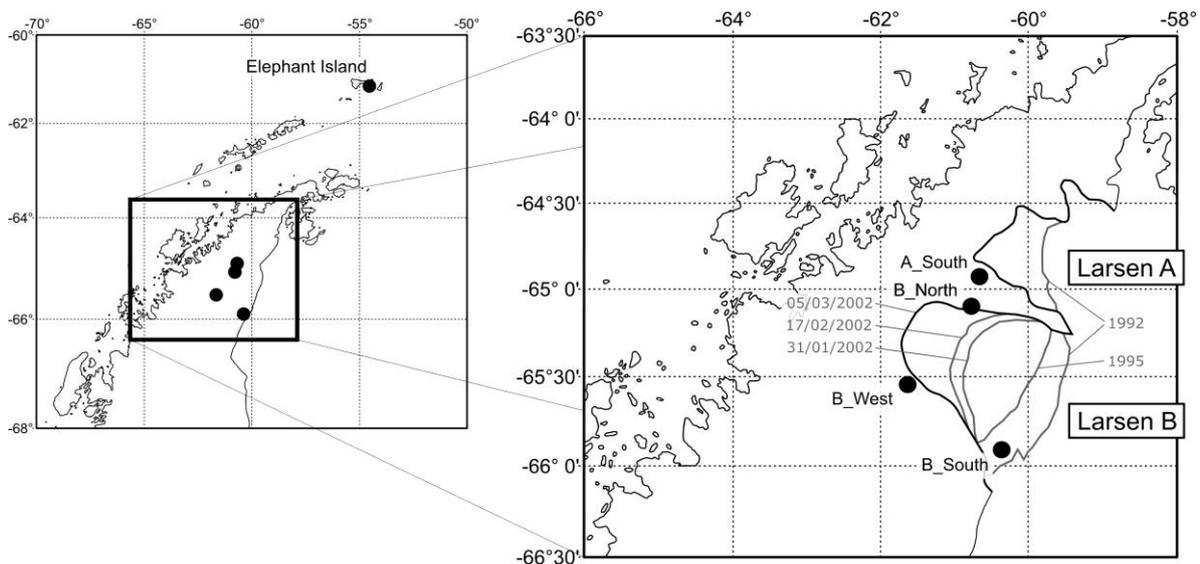
Fig. 1. Map of the study area, with indication of all sampling stations and the maximum ice extent at Larsen A and B between 1992 and March 2002 (*Based on BAS, AMM and ESA ERS imagery)*. The world map is shown in Mollweide projection

Four factors related to ice coverage were considered to have had an influence on the investigated meiobenthic communities (incl. nematodes): (1) length of the period for which each station has been free of shelf ice cover, (2) distance of each station from a rich source of nematodes for colonization, (3) primary production in the water column above the stations, and (4) local environmental factors, such as sediment granulometry and pigment concentration.

Food availability is a major structuring factor for meiobenthic and nematode populations and communities (Vanhove *et al.*, 2000; Gutzmann *et al.*, 2004), and oligotrophic conditions are known to affect meiobenthic and nematode abundance negatively (Vincx *et al.*, 1994; Vanreusel *et al.*, 2000). Extensive and long-term ice cover impedes or, in case of sea ice persisting only for weeks or months, delays phytoplankton production, consequently severely impacting the entire pelagic ecosystem (Arrigo *et al.*, 2002) and the benthic communities. Still, living (and even rich) benthic communities can exist underneath large ice shelves (Oliver *et al.*, 1976;

Riddle *et al.*, 2007; Post *et al.*, 2007). In the area of Larsen B_South, a pre-collapse benthic community was also present at the ocean floor, judging from the low number of iceberg scour marks and the age of sponges collected there (Gutt *et al.*, in press).

The nematode data indicated that pre-collapse, sub-ice communities were impoverished and characterised by low densities, low diversity and high dominance of a few taxa. This may still be visible at a station located deep inside the Larsen B embayment, where the nematode genus *Halomonhystera* was dominant. Post-collapse re-colonization of the "inner" stations, i.e. those located furthermost from the former ice-shelf edge, is believed to be a long-term process. At the time of sampling, community structure at the inner stations was not or only slightly influenced by colonization, and might be structured by local environmental conditions. Our results indicate that a locally increased food supply after ice-cover removal could provoke a faster, local response of the nematode assemblages compared to the response due to recolonisation. Communities living close to the former ice-shelf edge are believed to be at an intermediate or late stage of succession, with a dominance of the *Microlaimus* nematodes, a common Antarctic genus and quick colonizer. Densities here were comparable to those at other Antarctic stations in the range of densities found at other locations in the Weddell, Scotia and Ross Seas (Herman & Dahms, 1992; Vanhove *et al.*, 1995; Fabiano & Danovaro, 1999; Vanhove *et al.*, 2004; Gutzmann *et al.*, 2004; Ingels *et al.*, 2006), whereas they were considerably lower at the inner stations (Raes *et al.*, 2010).

Following ice shelf disintegration, density increase at the inner stations is considered to be a slow process, related to increased food supply, and/or colonization from adjacent ice-free areas. At a colonisation rate of 60.8 m.y^{-1} (Lee *et al.*, 2001), it would take more than 1000 years for the nematode community at station B_West to fully recover its abundance levels. Time needed for the first colonizers to reach the inner Larsen stations seems to be in the order of magnitude of at least a decade or more. This corresponds with recovery speed of macrofauna after iceberg scouring, reported by Barnes & Conlan (2007).

The significantly higher densities, higher diversity and significantly different community structure at B_South in comparison with the inner stations, can be explained by the longer period free of ice cover and, hence, open to potentially increased food supply from sea-surface phytoplankton blooms, in combination with the proximity of the open, western Weddell Sea as a nearby source for advected food and colonization. Quick colonizers might have seized the opportunity to swiftly invade the new space. *Microlaimus,* the dominant genus here, is a rather important and usually (sub)dominant nematode genus in the Antarctic and Subantarctic (Vanhove *et al.*, 1999, Vanhove *et al.*, 2004, Ingels *et al.*, 2006, Sebastian *et al.*, 2007). It is also known as an opportunistic genus that benefits from increased but unpredictable

organic food input (Van Gaever *et al.*, 2004; Van Gaever *et al.*, 2006), and a successful and fast colonizer (Lee *et al.*, 2001a).

Stations A_South and B_North are physically separated by the Drygalski Glacier cliff, so faunal exchange between both stations is very unlikely. Thus, only the recent availability of fresh food could have resulted in the comparable nematode community composition and dominance of *Thalassomonhystera* here. *Thalassomonhystera* is known as an opportunistic genus, which could have taken advantage of the fresh food input, outcompeting several other taxa. The food-rich environment at these stations is most likely the result of a recent phytoplankton bloom in the area. The close proximity of land and increased run-off of meltwater from its glaciers create excellent conditions for the development of large summer blooms (Dierssen *et al.,* 2002; Clarke *et al.,* 2007a).

Our BIO-ENV analysis revealed no perfect match between environmental variables and the observed biological patterns. In our opinion, these patterns can only be explained by a combination of historical (length of ice-free period), geographical (position in the Larsen area) and present-day environmental (food supply, sediment granulometry) effects.

In conclusion, the meiofauna in the Larsen A and B areas has been strongly influenced by the presence and sudden removal of the ice cover in this region, and is only slowly replenished through colonization from the open Weddell Sea. In fact, in a large-scale analysis based on nematode genus relative abundance data, a clear separation between the Larsen stations and other biogeographical areas in the (sub)Antarctic was shown (Fig. 2).
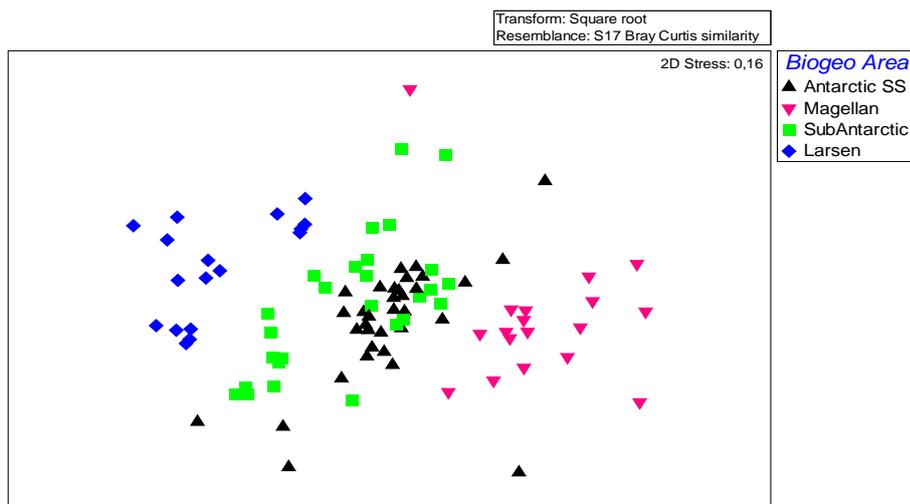
Fig. 2. nMDS based on nematode community data (relative abundance per samples). The nematode communities for the different biogeographical regions are clearly separated in 3-dimensional space (here represented in 2 dimensions with acceptable stress value of 0.16)

The significantly lower average values of taxonomic distinctness (Δ^*) at B_North (and B_West), and the significantly higher value of variation in taxonomic distinctness (Λ^+) for the entire nematode community at station B_North indicate both a low taxonomic spread in the community at this station (i.e. relatively more similar taxa), and a high unevenness in its phylogenetic structure, related to an increase in abundance of an opportunistic genus (*Thalassomonhystera*). The station is also characterized by a high dominance of nematodes. A negative correlation between evenness and a combination of abundant food and fine sediment could be an explanation for the low diversity at B_North (Tietjen 1977; Sebastian *et al.,* 2007).

The ice-shelf disintegration in the Larsen B (2002) area along the Eastern Antarctic Peninsula also led to the discovery of a low-activity methane seepage area. Since both previous ice coverage and reduced cold seep activity are likely to influence benthic meiofauna communities, the nematode assemblage of this low-activity cold seep was characterised and compared to other recently ice-free Larsen A and B stations and other Antarctic shelf areas (Weddell Sea and Drake Passage), as well as cold-seep ecosystems world-wide.

The presence of a low-activity cold-seep area in the Larsen region, posed several new questions regarding the status and trophic position of the meiobenthic community, following ice-shelf collapse. Hauquier *et al.* (accepted) found that densities in the seep samples were relatively high (>2000 individuals per 10cm²) and showed subsurface maxima at a sediment depth of 2-3cm. All samples were dominated by one nematode species of the family Monhysteridae, which was identified as a *Halomonhystera* species and contributed between 79 and 87% to the total community. This combination of high densities, subsurface maxima and high dominance of one species has been observed many times in cold-seep ecosystems world-wide and indicated a dependence on a chemosynthetic food source. A hypothesis rejected by ^{13}C stable isotope results, which indicated a phytodetritus-based food web. This suggested that the community was in transition from a chemosynthetic community to a classic phytodetritus feeding community, a temporary ecotone as it were. Newly-formed intense phytoplankton blooms following the removal of ice, with subsequent sinking of detritus to the sea floor may explain the high densities and low diversity. However, stable ^{13}C isotopic signals (ranging between -21.97 ± 0.86‰ and -24.85 ± 1.89‰) were indicative of phytoplankton-based feeding. It was concluded that the recent ice-shelf collapse and enhanced food input from surface phytoplankton blooms were responsible for the high density and low diversity communities. The characteristic parthenogenetic reproduction of the highly dominant *Halomonhystera* species is rather unusual for marine nematodes and may be responsible for the successful colonisation by this single species. The results also confirmed the colonisation hypotheses posed by Raes *et al.,* (2010), which is explained above.

In addition to the characterization of the nematode community, a new genus of the family Ethmolaimidae was found, based on a new species. Specimens of this species were recovered from reduced, chemosynthetic sediments in Larsen area (low-activity cold seep) at 800 m water depth. Up until now, the family Ethmolaimidae comprised eight genera: *Comesa, Ethmolaimus, Filithonchus, Gomphionchus, Gomphionema, Nannolaimus, Neothonchus* and *Trichethmolaimus.* The new genus is being described by Bezerra et al. (in prep.). The discovery of a new nematode genus from previously unstudied Antarctic habitats, such as the Larsen area, indicates the relatively undocumented nature of Antarctic biodiversity. New species are continuously discovered as sampling effort increases and stresses the importance of the continuation of taxonomic and biodiversity research to unveil the true extent of biodiversity in the Antarctic as has been demonstrated by the Census of Antarctic Marine Life (CAML). The fact that this new genus was also identified in samples of the Gulf of Cadiz at the Darwin mud volcano (1100m) in the NE Atlantic enforces the meiofauna paradigm, even on the species level, and adds to our understanding of global distribution of the Nematodes. Molecular studies in the nearby future should confirm whether the newly discovered species/genera are separated on genomic level, which in turn, will increase our knowledge on molecular nematode diversity on a global scale.

(b) Echinoids

The three species collected in Larsen A&B areas (*Sterechinus antarcticus*, *Sterechinus neumayeri* and *Notocidaris mortenseni ;* unpublished data) are known as indirect developers (or at least non-brooders), consistent with high dispersal capabilities. Moreover, this is congruent with the wide Antarctic distribution of these species (David *et al.*, 2005). On the contrary, it departs from other Antarctic echinoids which are known as direct developers that brood their young and, accordingly, are supposed to present low dispersal capacities. The three species display a 'generalist' feeding behaviour that can be considered as characteristic of pioneering species. Therefore. Considering echinoid life and feeding strategies, the three species are good candidates as pioneering species in a changing marine environment.

(2) Ectosymbioses on echinoids

NOWBIO objectives 1- f

To test the contribution of cidaroid ectosymbioses to local benthic communities, their abundance, distribution, richness, diversity and similarity indexes were compared to those of sessile epibionts occurring on drop stones (Hardy *et al.,* 2011). For this purpose, several cidaroid species and stones were collected at six contrasted areas: Weddell Sea, South Shetlands, Antarctic Peninsula (including Larsen embayments where ice shelves collapsed very recently), Bellingshausen Sea and

Dumont d'Urville Sea. Our results demonstrate the importance of cidaroids for local epibiont diversity. However, contrasting patterns of diversity were found in the different sampling areas, likely due to contrasting environmental conditions (latitude, depth and currents). In contrast with other areas, the symbiotic communities in the Larsen embayments show low diversity values and a strong similarity with epibionts present on stones, the cidaroids sharing more than 80% of epibionts with the surrounding stones. These results suggest that ectosymbioses linked to cidaroids could contribute to benthic colonization of the seafloor in the Larsen embayments. With time, secondary successions are expected to occur, increasing the difference between epibiotic communities on cidaroids and those on stones, and lead to the situations observed in unperturbed sites.

(3) Systematics and phylogeography of Southern Ocean amphipods

NOWBIO objectives 1-d, 2, 3

A thorough descriptive study of *Liljeborgia* species of the Southern Ocean was carried out, in order to establish a foundation for biogeographical and phylogenetic studies of this genus, and a model for phylogeographic studies of Southern Ocean amphipods in general. *Liljeborgia* is an ideal test group because it is present both in shallow and deep water and because the number of species is neither too small nor too large.

The twelve valid species previously recorded in the Southern Ocean were re-described as their previous descriptions were outdated and/or very poor. Based on material from different museums, thirteen new species were described and named, two new species were described but not named (the material was in a bad condition), one species proved to be invalid and the records of two species in the Southern Ocean were considered as resulting from erroneous identifications.

Antarctic and sub-Antarctic species could be divided into two previously unrecognized morphological groups (d'Udekem d'Acoz, 2008), which were subsequently considered as subgenera (d'Udekem d'Acoz, 2010). Actually, the vast majority of *Liljeborgia* species from other parts of the world can also be classified in these two subgenera. Species from the continental shelf were often closely related with abyssal species, suggesting recent faunal exchanges between depth layers. The Antarctic, sub-Antarctic archipelagos and Magellan region were populated by different species of *Liljeborgia*. In the Southern Ocean, some species were only known from the Scotia Arc and islands of the Antarctic Peninsula, while others were only found in the eastern Weddell Sea. However, due to the limited amount of material available for some species, it was not possible to definitively confirm that such species are local endemics within true Antarctic waters. All these data were included in two large monographs (d'Udekem d'Acoz, 2008; d'Udekem d'Acoz,

2009). In addition, the Scandinavian *Liljeborgia* species of the group fissicornis (Crustacea, Amphipoda) have been studied, resulting in the discovery of 3 new species. All those northern species are completely devoid of eyes, while similar species from the Antarctic and sub-Antarctic continental shelf (those of the group georgiana) do have eyes. It is hypothesized that the group fissicornis, which is specific to cold waters, derives from ancestors living on the continental shelf of the Southern Ocean and belonging to the group georgiana. These ancestors would have adapted to deep-sea environments, losing their eyes completely. Then they would have migrated northwards through the cold abyss, and reached the cold but shallow waters of the Arctic/sub-Arctic continental shelf, without redeveloping visual organs (d'Udekem d'Acoz & Vader, 2009). The subsequent discovery of a related abyssal blind species in the equatorial Eastern Atlantic (d'Udekem d'Acoz & Hendrycks, submitted) supports this hypothesis. Furthermore another group of related species from the two poles has been detected: *L. cnephatis* and relatives (Southern Ocean: blind deepwater and eyed shelf species) and *L. macronyx* (Scandinavia: shelf blind species) (d'Udekem d'Acoz, 2010). Since the two groups of *Liljeborgia* are not at all related (they belong to separate subgenera), this suggests a replication of the same scenario.

Recent molecular analyses revealed that a number of so-called "circum-Antarctic" benthic crustacean species are a complex of cryptic species with a restricted geographic distribution. In order to investigate these issues for the genus *Liljeborgia*, fragments of the COI gene were sequenced and used as DNA barcode. Twenty-five specimens were successfully sequenced so far and were clustered in a Neighbour-Joining tree (Fig. 3; Kimura two-parameter model), which focuses on the *georgiana* species group.

In the morphospecies *L. georgiana*, specimens from the same area (e.g. the Ross Sea or Bouvet Island) have the same haplotype. In contrast, distant populations are genetically distinct, as a probable result of the low dispersal capacity of *Liljeborgia* species. This result sharply contrasts with orchomenid lysianassoids, in which some highly mobile species exhibit a remarkable genetic homogeneity throughout the Southern Ocean. Interestingly, the specimens initially identified as *'L. georgiana'* from the continental slope (1,500 m) are genetically very distinct from other shelf samples; a related but clearly distinct morphospecies (*L. semperhiemalis*) is positioned in between. A second examination of the deep *'L. georgiana'* has revealed small but significant differences with *L. georgiana* and was be described as a new species, *L. Bathysciarum* d'Udekem d'Acoz, 2009. The different taxonomic units in the genus *Liljeborgia* (morphospecies and different haplotypes of the same species) seem to have a regional rather than a global distribution.

J9	*L. georgiana* s.l.	West Weddell Sea	200 m
LIL 3-8	*L. georgiana* s.l.	East Weddell Sea	1000 m
LIL 2-6	*L. georgiana* s.l.	Ross Sea	400 m
LIL 6-2	*L. georgiana* s.l.	Bouvetøya	250 m
LIL 6-1	*L. georgiana* s.l.	East Weddell Sea	300 m
H3	*L. georgiana* s.l.	Joinville Island	200 m
B1	*L. georgiana* s.l.	Elephant Island	150 m
E10	*L. georgiana* s.l.	Elephant Island	350 m
C1	*L. georgiana* s.l. *	Elephant Island	300 m
A4	*L. semperhiemalis*	East Weddell Sea	300 m
LIL 1-3	*L. n. sp.* A	Elephant Island	1500 m
LIL 3-3	*L. n.sp.* A	Elephant Island	1500 m
I-15	*L.polydeuces*	Elephant Island	150 m
LIL 2-4	*L. aff. homospora*	East Weddell Sea	5000 m
LIL 3-1	*L. homospora*	East Weddell Sea	3000 m

1 *Liljeborgia georgiana* sensu lato
2 *Liljeborgia* spp. related to *georgiana*
3 *Liljeborgia* group *quadridentata*

* specimen requiring a re-examination

Fig. 3. Neighbour-Joining tree for the Antarctic *Liljeborgia*.

In the framework of the ongoing revision of the Southern Ocean amphipod fauna, undertaken with the collaboration of the "Antarctic Amphipodologists Network", two new families, the Alicellidae fam. nov. and the Valettiopsidae fam. nov., are described based on genera traditionally considered as lysianassoid amphipods. The Alicellidae fam. nov. are deep-sea scavengers often associated with thermal vents. The family contains 6 genera: *Alicella* Chevreux, 1899; *Apotectonia* Barnard & Ingram, 1990; *Diatectonia* Barnard & Ingram, 1990; *Paralicella* Chevreux, 1908; *Tectovalopsis* Barnard & Ingram, 1990; *Transtectonia* Barnard & Ingram, 1990. The Valettiopsidae fam. nov. are deep-sea scavenging amphipods that contain two genera, *Valettiopsis* Holmes, 1908 and *Valettietta* Lincoln & Thurston, 1983 (Lowry & De Broyer, 2008).

An up-to-date catalogue of Antarctic and sub-Antarctic Phoxocephalidae has been established, including 35 species. An extensive list of bibliographical references with synonymy, detailed information on geographic and bathymetric distribution, ecological data, museum locations of type-material, remarks on taxonomic and biogeographical status, are provided for each species. The catalogue is based on taxonomic and ecological literature until 31 December 2006. Additional unpublished records of species from the Antarctic and Subantarctic collections at the Alfred Wegener Institut für Polar- und Meeresforschung, Bremerhaven, and at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, have been included. The taxonomic status of all Southern Ocean species has been checked. Species allocated to the genera *Paraphoxus* and *Parharpinia*, and *Fuegiphoxus uncinatus* require further study to clarify genus allocation. Most of the Southern

Ocean phoxocephalids have a wide bathymetric distribution, equally present in the Antarctic and sub-Antarctic regions. The highest species richness is found above 200 meters depth in the sub-Antarctic region. Of 35 phoxocephalid species reported, 25 are endemic to the Southern Ocean s. lat., 15 are endemic to the Antarctic region and 6 are endemic to the sub-Antarctic region, the latter distributed only in the Magellan province. Endemicity at genus level attains 22% for the whole Southern Ocean, with 3 genera restricted to the Magellan province and one genus to the West Antarctic, Magellan and sub-Antarctic island provinces. Habitat and substrate preferences, dietary and burrowing behaviour are scarcely known for most of the phoxocephalid species from the Southern Ocean (Alonso de Pina *et al.*, 2008).

Another study focuses on the DNA barcoding and the phylogeography of the Antarctic lysianassoid genus complex *Orchomene* (Havermans *et al.*, 2011). A neighbour-joining analysis (Fig. 4) confirmed the monophyly of all species investigated by multiple specimens. The mean of interspecific K2P divergences between species (except species complexes) is 14.5%, ranging from 6.3% (between *Pseudorchomene coatsi* and *Pseudorchomene* sp.) to 20.1% (between *Abyssorchomene chevreuxi* and *Orchomenella (O.) acanthurus*). The frequency distribution of pairwise K2P distances within and between well-defined orchomenid species is shown in Fig. 5. Interspecific divergence exceeds intraspecific divergence to such an extent that a "gap" can be observed. This gap range is the interval between the highest intraspecific and the lowest interspecific distances (Astrin *et al.*, 2006; Meier *et al.*, 2008). In our case, the gap range is about 3.9%. This clear barcoding gap observed in our COI dataset means that the assignment of a specimen to a particular species based on a "threshold" value of sequence divergence would mostly work for this group and would be also efficient to detect new and/or cryptic species (Hebert *et al.*, 2003; 2004). The results of the 28S rDNA confirmed the cryptic species complexes within the orchomenid genus complex.

Furthermore, the neighbour-joining analysis (Fig. 4) revealed clades corresponding to undescribed species (*Abyssorchomene* sp.1, *Abyssorchomene* sp. 2 and *Pseudorchomene* sp.). Moreover, mitochondrial data reveal distinct, monophyletic clades in *Orchomenella (O.) pinguides*, *Orchomenella (O.) franklini*, *Orchomenella (Orchomenopsis) cavimanus* and *Orchomenella (Orchomenopsis) acanthurus*. The genetic divergence between the clades within these four *Orchomenella* species is congruent with species-level divergences in the orchomenid genus complex. In addition, representatives of these four *Orchomenella* species occur in (partial) sympatry. For example, in *Orchomenella (Orchomenella) franklini*, specimens coming from the same sample locations at Joinville Island pop up in clades separated by high genetic distances (Fig. 4). In other species (e.g. *Abyssorchomene plebs*, *Abyssorchomene* sp.1, *Pseudorchomene* coatsi), low genetic divergences could be observed. For example, *A. plebs* showed an average K2P distance of 0.2 % between

specimens of the Antarctic Peninsula, the Scotia Sea, the eastern Weddell Sea and Bouvet Island, as well as between specimens from shelf (270 m) and abyssal depths (2889 m) in the Scotia Sea (Fig. 4).

In addition, a phylogenetic analysis with the combined dataset (COI and 28S rRNA) showed that the taxonomy of the orchomenid genus complex is based on diagnostic characters that are a result of convergent evolution (Havermans *et al.*, 2010). A revision of taxonomy within this lysianassoid group is needed to improve systematic and biodiversity studies. Furthermore, the detection of cryptic species may have some influence of the current views on species richness and distributions in the most abundant group of amphipods in the Southern Ocean. Finally, the DNA barcoding permitted to detect some new species, which contributed to a more accurate estimation of the species diversity within this lysianassoid group.
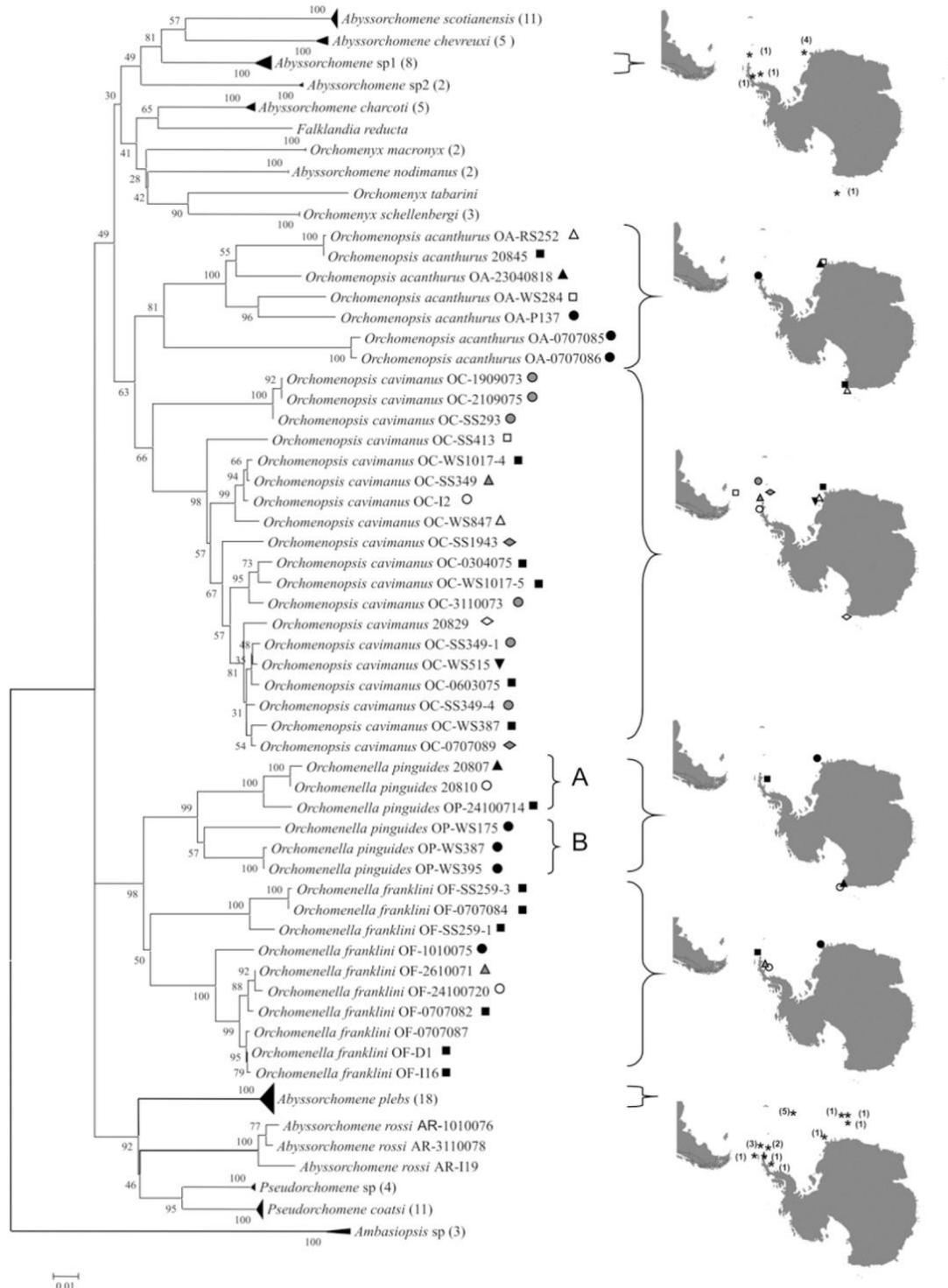
Fig. 4. A neighbour-joining analysis of the COI sequences based on K2P distances of the Antarctic orchomenid species, with the locality indicated for some species. This highlights the presence of species complexes in *O. (O.) acanthurus O.(O.) cavimanus*, *O. (O). pinhuides* and *O. (O.) franklini*.
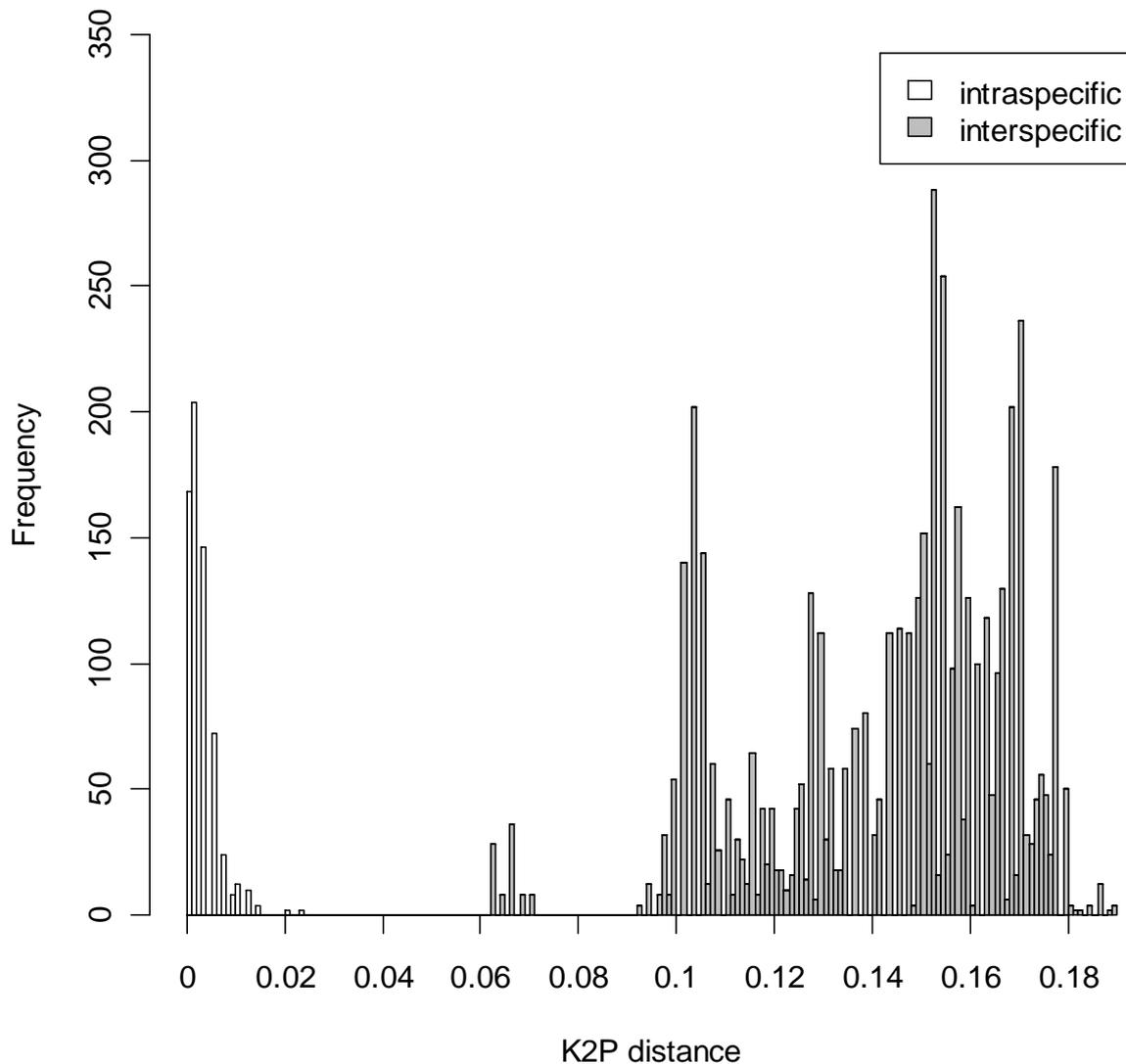
Fig. 5. The frequency distribution of pairwise K2P distances within and between well-defined orchomenid species

> (4) Comparative biogeography of Antarctic meio-, macro- and megabenthos

NOWBIO objectives 1-e; 2; 3

Based on new and complete datasets with distribution records of four target taxa, a common biogeographical analysis was undertaken, aiming to compare geographical and bathymetrical distribution patterns, focusing on the differences between meio-, macro- and megabenthos. The analysis included nematodes, amphipods, asteroids and echinoids. The analysis aimed to match these patterns with the biogeographical schemes of other benthic taxa, in particular with the recent comprehensive biogeographical analyses performed on molluscs (Linse *et al.*, 2006; Clarke *et al.*, 2007b), bryozoans (Barnes & Griffiths, 2008) and general macrobenthos

(Griffiths *et al.,* 2009). Another goal was to identify potential causal factors of the observed patterns.

The classic Southern Ocean biogeographical scheme designed by Hedgpeth (1969, 1970) and Dell (1972), mostly based on benthic distribution patterns, was to a large extent confirmed by biogeographical studies on e.g. Demospongia (352 spp.: Sara *et al.*, 1992), Hexacorallia (122 spp.: Rodriguez *et al.*, 2007), Sipunculida (16 spp.: Saiz-Salinas & Pagola-Carte, 1999), Polychaeta (558 spp.: Knox & Lowry, 1977; Glasby & Alvarez, 1999; Sicinski & Gillet, 2002), Pycnogonida (264 spp.: Munilla & Soler Membrives, 2009), Amphipoda (445 spp.: Knox & Lowry, 1977; 815 spp.: De Broyer & Jazdzewski, 1993; 1996; De Broyer *et al.*, 2007), Echinoidea (79 spp.: David *et al.*, 2005), and Ascidiacea (237 spp.: Primo & Vasquez, 2007). Recent extensive databases on Gastropoda (895 spp.) and Bivalvia (379 spp.) (Linse *et al.*, 2006; Clarke *et al.*, 2007b), Bryozoa (1681 spp.; Barnes & Griffiths, 2008) allowed for new in-depth multivariate biogeographical analyses and provided new insights into the biogeography of the Southern Ocean benthos. Moreover, Griffiths *et al.,* (2009) attempted to generalize Southern Ocean (s.l.) benthos biogeographical traits, partly challenging the Hedgpeth-Dell classic scheme. No biogeographical analysis of the nematode species of the Southern Ocean has been performed so far. The biogeography of Southern Ocean amphipod species was investigated by Knox & Lowry (1977), Watling & Thurston (1989) and De Broyer & Jazdzewski (1993, 1996). The amphipod, echinoid (David *et al.*, 2005) and asteroid (McKnight, 1976) distribution patterns detected mostly fit into the Southern Ocean biogeographical scheme established by Hedgpeth (1970) and Dell (1972).

Distribution data on the Antarctic benthos in general increased enormously during the last two decades. Moreover, extensive biogeographical databases are now being built for some species-rich groups and new insights are progressively provided by molecular analyses. In particular, a number of potential cryptic species has been detected in Antarctic isopods and molluscs (*e.g.* Page & Linse, 2002; Held, 2003; Held & Wägele, 2005; Raupach & Wägele, 2006) and these results may question our current estimation of species richness and our widely accepted view of circum-Antarctic distribution patterns for benthic species (De Broyer *et al.*, 2003).

New complete distribution datasets for Southern Ocean species of the four model taxa were built within the framework of the BIANZO II project (Fig. 6), including Nematoda (meiobenthos: 341 spp.; 1367 records; Raes & Vanreusel, *unpubl.*); Amphipoda (macrobenthos: 859 spp.; 8046 records; De Broyer *et al.*, 2007); Asteroidea (megabenthos: 209 spp.; 3689 records; Danis & Jangoux, *unpubl.*) and Echinoidea (megabenthos: 79 spp.; 1895 records; David *et al.*, 2005).
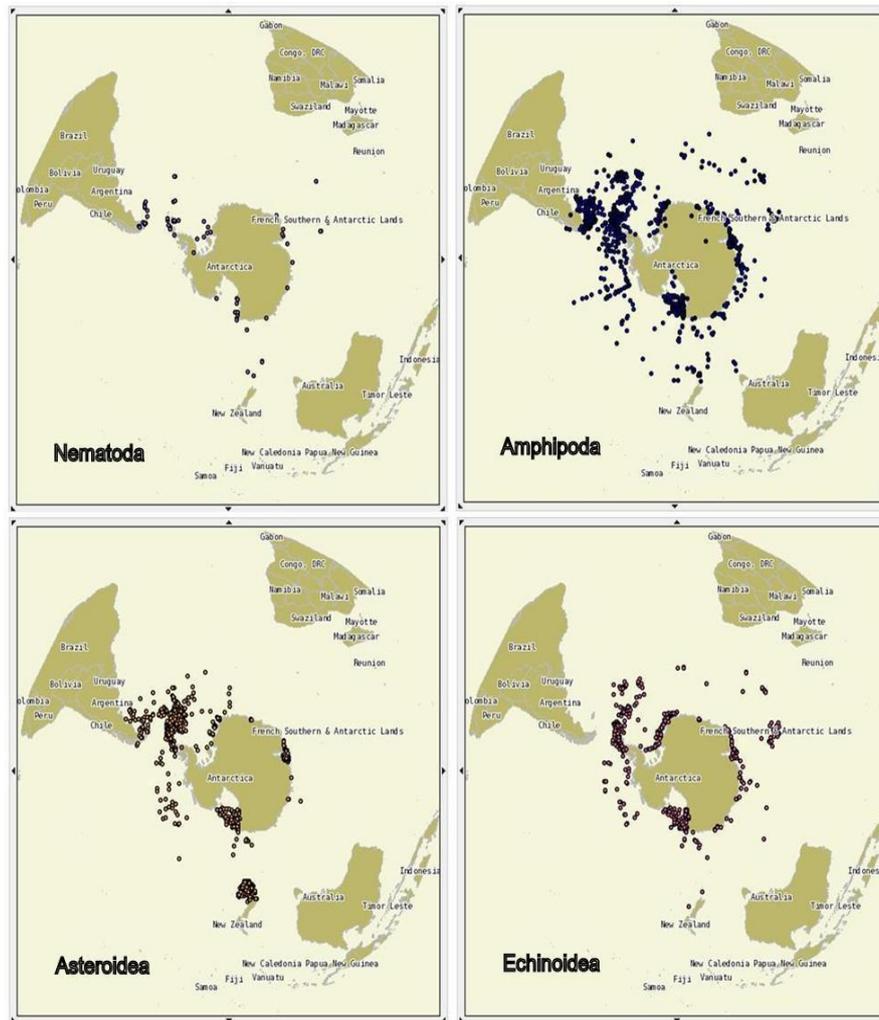
Fig. 6. Distribution records of Nematoda, Amphipoda, Asteroidea and Echinoidea.

For nematode biogeography, species level diversity information at such a broad scale has never been reported in literature before. However, on the genus level, nematode diversity is comparable to that in the Atlantic and Mediterranean, and much higher than in the Arctic Ocean (Vanhove *et al.*, 1999). Amphipod species richness recorded in the geographic regions considered here is shown in Table 1. When comparing respective areas per region, some regions appear as biodiversity hotspots: Weddell Sea, Peninsula + South Shetland Islands, Ross Sea, South Georgia, Kerguelen Islands and Bouvet Island. However, except for Bouvet Island, all of these regions are obviously also the most intensively sampled. There are about 900 species of echinoids in the World Ocean, and 79 of them occur south of the Antarctic Polar Front. These Antarctic species belong to 7 of the 19 Post–Paleozoic echinoid orders and are represented by 9 families (Table 2).

	area (km²)	N. recs.	N. genera	N. spp.	N. endemic spp.	% endemic spp. per region
Weddell sea	639681	658	102	195	12	6.1
Dronning Maud + Enderby Ld	407434	93	19	28	1	3.5
Dronning Maud Ld		58				
Enderby Land		35	19	25	0	0
Prydz Bay region		614	54	75	8	10.6
Davis S. and Wilkes Ld		79	35	47	7	14.9
Adelie Coast + Oates Ld		279	57	93	7	7.5
Ross Sea	679693	749	60	104	11	10.6
Amundsen Sea		31	1	1	0	0
Bellingshausen Sea & Peter Is.	336011	59	16	22	6	27.3
Antarctic Peninsula and South Shetland Is.	457953	495	141	321	70	21.8
South Orkney Is.	91170	10	61	85	5	5.9
South Sandwich Is.	80294	36	19	21	3	14.3
South Georgia	122672	324	97	172	25	14.5
Shag Rocks		26	18	19	1	5.3
Bouvet I.	2626	5	31	31	1	3.2
Heard & McDonald Is.	27332	20	13	14	3	21.4
Magellan area	660552	1104	120	210		
Southern Chile	147186	63	29	31	4	12.9
Southern Argentina	488073	126	47	65	14	21.5
Tierra del Fuego + Estrecho de Magallanes	96920	606	87	134	24	7.9
Falkland Is.	158879	309	71	107	22	20.6
Prince Edward & Marion Is.	3894	194	49	62	13	21.0
Crozet Is.	68455	64	16	18	0	0
Kerguelen Is.	252265	361	71	97	23	23.7
Macquarie I.		96	25	31	4	12.9
Auckland I.		88	37	45	7	15.5
Campbell Is.		93	30	41	4	9.7
Antipodes Is.		7	7	7	0	0
Bounty I.		1	1	1	0	0
Tristan da Cunha and Gough Is.	2293	45	27	32	8	25.0
Antarctic	34800000	5183	205	536	388	72.3
Southern Ocean s.l.		8046	301	859	651	79.8

Table 1. Rate of Amphipod endemism for each sub-region of the SO (*s.l.*).

Several studies recorded the distribution of nematode species within a number of selected, dominant genera over the Atlantic sector of the Southern Ocean (Vermeeren *et al.*, 2004; Fonseca *et al.*, 2006; De Mesel *et al.*, 2006, Ingels *et al.*, 2006). Within the Southern Ocean, many nematode species are rare and only found once or twice. In *Acantholaimus*, 34 of the 55 species were found at only a single station, and 36 species in only one of the four studied regions (*i.e.* Drake Passage, Bransfield Strait, Kapp Norvegica or Vestkapp; De Mesel *et al.*, 2006). In contrast, some species are found in a very broad area: 25 of the 89 species of *Molgolaimus*,

Dichromadora and *Acantholaimus* described above were found in more than 3 Antarctic regions: South Sandwich Trench, Weddell Sea, Drake Passage or Peninsula (Bransfield Strait). Most of the species found in Antarctic sediments were new to science, which may indicate a high degree of Antarctic endemism at species level. *Molgolaimus* communities in the Southern Ocean and the Indian Ocean have only one species, *Molgolaimus sabakii*, in common (Fonseca *et al.*, 2007), and *Dichromadora* communities at similar depths in the Arctic and Atlantic Ocean were completely different in composition compared to the Southern Ocean (Vermeeren *et al.*, 2004). However, faunal exchange with lower latitudes might be possible via the deep sea (Brandt *et al.*, 2007a) and via shallow-water migration routes (Ingels *et al.*, 2006). Whether some nematode species have a true circumpolar distribution is unknown at present. *Desmodorella* aff *balteata*, which was found at many of our study sites in Antarctica, is very similar to *D. balteata* found at hydrothermal vents in the East Pacific Rise at a depth of 2000m. *Desmodora campelli*, originally described from the sub-Antarctic Campbell Islands south of New Zealand, has also been found in Chile and Argentina and recently at both sides of the Scotia Arc. Although this information is very fragmented and these species have often only been reported from a restricted number of sites, it does suggest a very wide distribution over the southern hemisphere. According to Fonseca *et al.,* (2006), morphologically similar species occur in the same geographical region. This does not support the idea of a common origin of deep-sea nematodes, or of Antarctica as a source or sink for benthic biodiversity, but it rather implements that speciation could be driven locally.

orders	families	N. genera	N. spp.	% endemic genera	% endemic spp.
Cidaroida	Cidaridae	5 (3)	21 (17)	60 %	81 %
Echinothurioida	Echinothuriidae	1	1	0	0
Arbacioida	Arbaciidae	1	1	0	0
Temnopleuroida	Temnopleuridae	1	3	0	0
Echinoida	Echinoidae	3	7 (4)	0	57 %
Holasteroida	Plexechinidae	1	2 (1)	0	50 %
	Pourtalesiidae	6 (1)	8 (5)	17 %	62 %
	Urechinidae	4 (1)	6 (3)	25 %	50 %
Spatangoida	Schizasteridae	8 (3)	30 (20)	37 %	67 %
7 orders	9 families	30 (8)	79 (50)	27 %	63 %

Table 2. Echinoid biodiversity in the Southern Ocean (*s.s.*). Number of endemic taxa are in brackets.
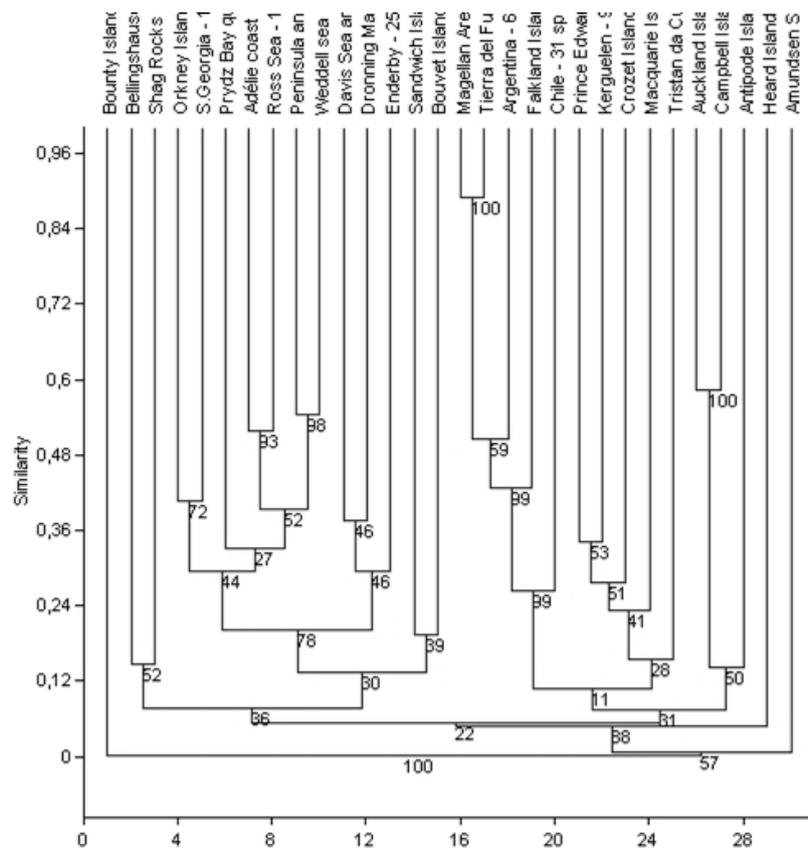
Fig. 7. Amphipod faunal similarity of shelf regions (based on Bray-Curtis similarity index)

	Total species	Atlantic Ocean	Indian Ocean	Australia + New Zealand	Pacific Ocean
Species richness of echinoid species according to longitudinal sectors					
Atlantic Ocean	54		32	14	21
Indian Ocean	50			20	20
Australia, NZ	20				13
Pacific Ocean	27				
Similarity coefficients (Jaccard index = C/N_1+N_2-C) between the echinoid fauna					
Atlantic Ocean	54		0.44	0.23	0.35
Indian Ocean	50			0.40	0.35
Australia, NZ	20				0.38
Pacific Ocean	27				

Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna (depths < 500 m)				
Atlantic Ocean	43	0.39	0.07	0.29
Indian Ocean	28		0.21	0.26
Australia, NZ	6			0.24
Pacific Ocean	20			

Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna (depths: 500 – 1000 m)				
Atlantic Ocean	38	0.18	0.10	0.16
Indian Ocean	22		0.12	0.21
Australia, NZ	7			0.12
Pacific Ocean	12			

Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna (depths: > 1000 m)				
Atlantic Ocean	29	0.21	0.16	0.12
Indian Ocean	17		0.39	0.08
Australia, NZ	8			0.21
Pacific Ocean	9			

Table 3. Species richness and similarity coefficients for Antarctic echinoids, related to longitudinal distribution.

More than 20% of the amphipod species occurring in the regions of Bellingshausen Sea, Peninsula and South Shetland Is, Heard I., Falkland Is., Prince Edward and Marion I. and Kerguelen Is. are endemic (Table 1). The endemic species from the Peninsula and South Shetland Is., South Georgia, Kerguelen Is. and Falkland Is. represent respectively 8.15, 2.91, 2.68, 2.56% of the total Southern Ocean (*s.l.*) endemics. The whole fauna of gammaridean and corophiidean amphipods presents an endemism rate of 72.3% in the Antarctic zone and 79.8% in the Southern Ocean (*s.l.*). Strong faunal similarities of amphipods (more than 50 % of shared species) were found respectively between Peninsula+South Shetlands and the Weddell Sea, the Ross Sea and Adélie+Oates Coasts, Tierra del Fuego and Southern Argentina. There is a less marked similarity between the Falkland Islands and Southern Chile, and between Auckland and Campbell Islands. Around 40% faunal similarity was detected respectively between the South Orkney Islands and South Georgia, between the clusters Adélie+Oates Coasts / Ross Sea and Peninsula+South Shetlands / Weddell Sea, and between Davis Sea+Wilkes Land and Dronning Maud Land. The Antarctic and sub-Antarctic regions *sensu* Hedgpeth (1969) remain clearly distinct (Fig. 7).

Endemism in Antarctic echinoid species is particularly high: 68% of the species are endemic to the Southern Ocean (*s.s.*). The dominant Cidaridae and Schizasteridae are remarkable as most of their species (80% of the Cidaridae species and 83% of the Schizasteridae species) are endemic.

High level of endemism is also observed for Pourtalesiidae and Urechinidae, although these families are less diversified at the species level. Eight Antarctic echinoid species display a circumpolar distribution. Six occur along the coast and 2 off the coastal zone. The coastal species belong to the Cidaridae (*Ctenocidaris rugosa*, *Notocidaris platyacantha*), to the Echinidae (*Sterechinus neumayeri*) and to the Schizasteridae (*Abatus cavernosus*, *Abatus philippi*, *Abatus shackletoni*). These species are either carnivorous or opportunistic carnivorous browsers or deposit/bottom feeders; none of them are strict vegetarian browsers. A brooding behaviour has been reported for 4 of them. Longitudinal distribution of species richness (partly based on Jaccard index and 4 longitudinal sectors) is presented in Table 3.

Distribution patterns of the Antarctic zoobenthos are also influenced by bathymetry. A shift in nematode genus composition is obvious from shelf to lower slope (Vanhove *et al.*, 1995). For instance, the typical deep-sea genus *Acantholaimus* occurred quite abundantly on the Antarctic shelf (De Mesel *et al.*, 2006). Eurybathic distribution patterns in Antarctica are well-described for macrofauna but are less known for meiofauna. Our findings indicate that nematode genera might also have a wider depth range in Antarctica compared to other parts of the world. A wide depth range was found in several *Acantholaimus* species: between 200 m and 2000 m. Muthumbi & Vincx (1997) found some *Acantholaimus* species to occur between 500 m and 2000 m water depth. More information both from Antarctica and from other parts of the world is needed to confirm eurybathic species distribution.

The bathymetric distribution of Antarctic amphipod species (Scotia Arc excluded) reveals three distinct groups: a shelf cluster (0-99 m and 100-499 m), a deep shelf-upper slope cluster (500-999 m and 1000-1999 m) and a deep slope-abyssal cluster (2000-2999 m and >3000 m) (Fig. 7). Half of the 72 Antarctic amphipod species occurring below 1000 m are shelf species that extend their distribution: from a few tens of metres depth up to the upper slope at a maximum depth of 1500–2000 m (in one case even 2894 m). Eighteen species (15 Antarctic endemics) are restricted to the bathyal zone (1000–3000 m) and 13 species (nine endemics) to the abyssal zone (>3000 m depth). A number of scavenger species occur on both shelf and slope, showing in some cases an extended level of bathymetry (De Broyer *et al.*, 2004). *Eurythenes gryllus* is the only scavenger species found on shelf, slope and in the abyssal zone.

It is known as a deep-sea, pan-oceanic stenothermal species, with a benthopelagic life style, that can occur far above the seafloor (Thurston, 1990). Two other species with a widely eurybathic range are *Orchomenopsis cavimanus* (6-3070 m) and *Abyssorchomene scotianensis* (385-3070 m), but small morphological differences have been observed between shelf and deep-sea populations, and a molecular analysis is required to detect potential cryptic species before confirming such very wide eurybathy.

	Total species	0 – 500 m	500 – 1000 m	> 1000 m
Echinoid species richness according to depth ranges				
0 – 500 m	52		43	21
500 – 1000 m	50			24
> 1000 m	41			
Similarity coefficients (Jaccard index = C/N1+N2-C) between the echinoid fauna according to depth ranges				
0 – 500 m	52		0.73	0.29
500 – 1000 m	50			0.36
> 1000 m	41			

Table 4. Species richness and similarity coefficients for Antarctic echinoids, related to bathymetrical distribution.
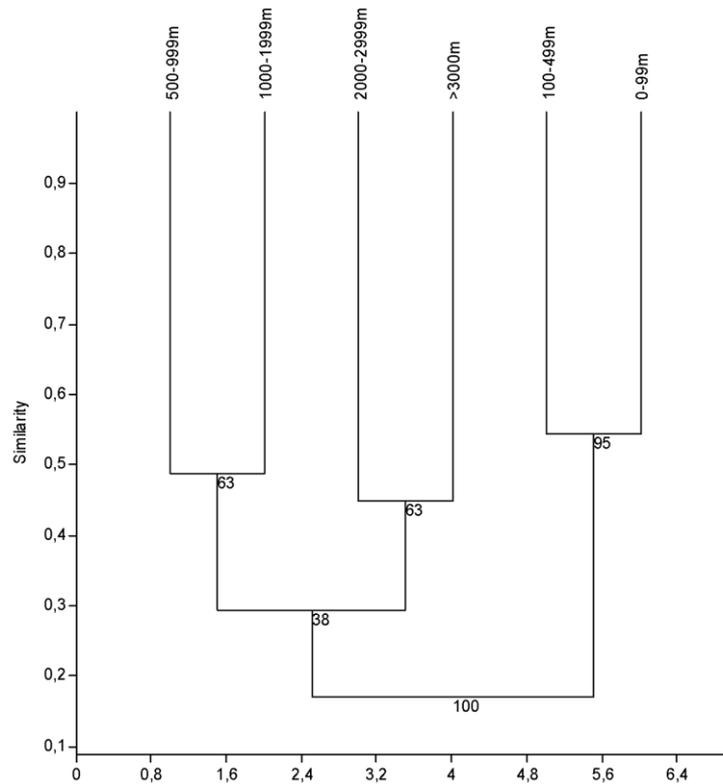
Fig. 7. Cluster analysis of Southern Ocean bathymetric zones (Amphipod data, Bray-Curtis similarity index)

In echinoids, there are stronger similarities between the shelf (from 0 to 500 m depth) and the deeper shelf or upper slope (from 500 to 1000 m) than between the slope and the deep-sea (below 1000 m) (Table 4). The same distribution pattern is observed in the four main retained longitudinal regions.

This detailed comparative analysis, which is still ongoing, provides new insights into geographical and bathymetrical distribution patterns, hotspots of species richness and endemism, centre(s) of radiation, circumpolarity and cryptic species, eurybathy, and potential causal factors of the observed patterns.

ii) DYNABIO – Ecofunctional role of biodiversity in benthic communities and its ability to cope with change

(1) Trophic position, food selectivity, and trophodynamics of Antarctic shallow-water and deep-sea meiofauna (nematodes)

DYNABIO objectives 1-a; 2-d

Investigating meiobenthos food preferences is of crucial importance since the ongoing climate change may alter the natural balances and the functionality of polar ecosystems. Rises in air and water temperature have been claimed to explain shifts in the size range of phytoplanktonic communities (Moline *et al.*, 2004), which may, in turn, affect those biological components that depend on it. Moreover, warming trends at the Western Antarctic Peninsula in the atmosphere and surface waters (Clarke *et al.*, 2007) may result in shifts in microbiological activity. Both these scenarios may influence the importance of phytoplankton (phytodetritus for deep-sea benthos) and bacteria as food sources for meiobenthic detritivorous or bacterivorous metazoans.

In November 2007 the uptake of two labelled food sources (diatom species and bacteria) was investigated in an experiment, in order to identify food selectivity and preferences at Potter Cove on King George Island, close to the Antarctic Peninsula (Pasotti *et al.*, submitted). $\delta^{13}C$ values for Cumacea were greatest with an average of -14.57‰ (Fig. 8), which is close to that of the filter feeder *Nacella concinna* (Corbisier *et al.*,2004) and that of kelp ($\delta^{13}C$ = -14.4‰) as reported by Kaehler *et al.*, (2000) for Prince Edward Islands (Subantarctic). Nematodes exhibited an average stable $\delta^{13}C$ signal of -19.35‰ (Fig. 8), which is lighter (more depleted in ^{13}C) than reported for the nematode community at Martel Inlet ($\delta^{13}C$= -15.6±0.7‰, Skowronski (2002), Corbisier *et al.,* (2004)) but higher than the values ($\delta^{13}C$ = -24.8±1.3‰) found for nematodes in the Bransfield Strait (230m depth, Moens *et al.*, 2007). Corbisier *et al.,* (2004) reported average values of stable $\delta^{13}C$ for microphytobenthos and macro algae of Martel Inlet shallow water sediments, of -16.7‰ and -23.6‰ to -21.1‰, respectively. Nematodes showed an intermediate value in between these two food sources which may mean they can feed on bacteria that degrade macro algae and possibly on microphytobenthos. Copepods show an average $\delta^{13}C$ value of -17.89‰ (Fig. 8), which is close to microphytobenthic values reported by Corbisier *et al.* (2004).
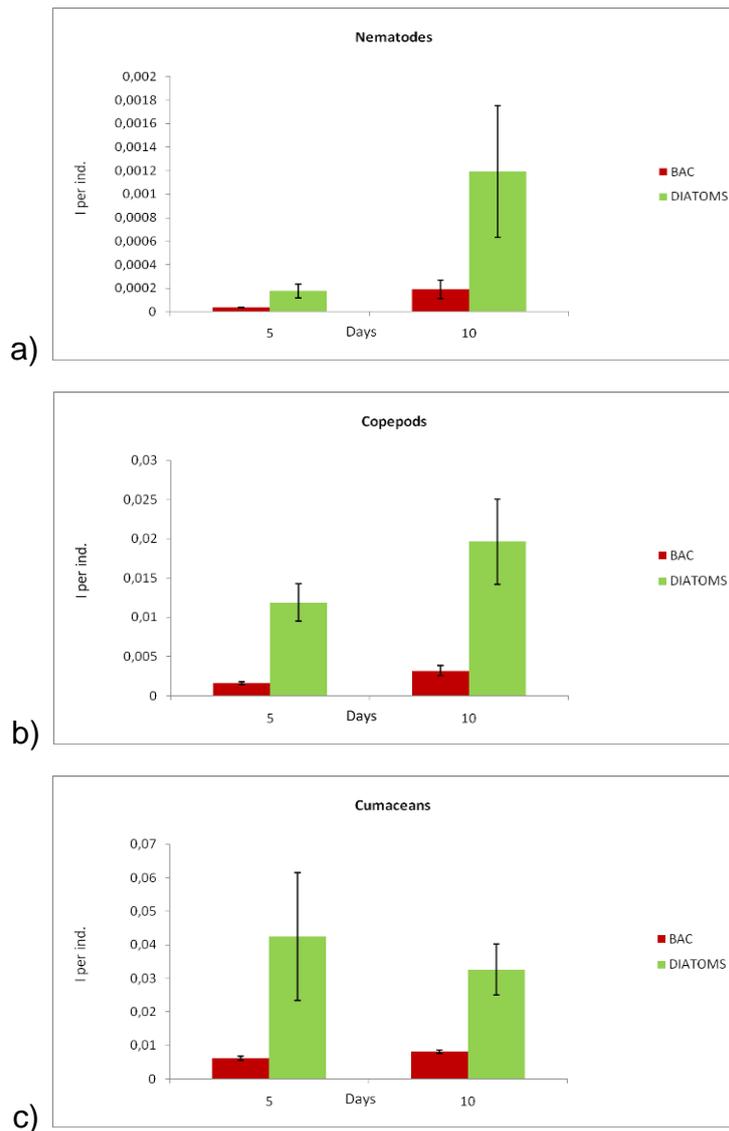
Fg.8. Individual uptake (I per ind.) for Nematodes (a), Copepods (b) and Cumacea (c). Bac=Bacteria; Diatoms=*Thalassiosira weissflogii.*The values are presented as mean value on 3 replicates.with standard error bars.

The results indicate that shallow-water nematodes, copepods and cumaceans at Potter Cove prefer a phytoplankton food source rather than microbial food (Fig. 8). This stands in contradiction with what is found for deep-sea nematodes in the Antarctic, where a microbial food source may be preferred over phytodetritus (Ingels *et al.*, 2010). In shallow waters, however, phytoplankton is of higher quality than in the deep sea where it has been degraded as a result of the sinking process. So these observations may reflect a preference for the most qualitative food, rather than a difference between preferences of deep-sea and shallow-water nematodes. Deeper shelf nematodes may rely on the accumulation of a persistent food bank that buffers the benthic ecosystem from the seasonal variability of the surface productivity (Smith *et al.*, 2006). The shallow-water meiobenthos, on the other hand, may have

adapted to the seasonal nature of food pulses and try to gain more profit from fresh micro-algal food than from bacterial biomass. Antarctic shelf sediments do not seem to be limited in food availability (Vanhove *et al.,* 2000) and it seems that the microbial activity of degrading phytoplankton is so temperature-limited in winter that labile (non-degraded) organic material is permanently available for detritivores (Smith *et al.,* 2006). Nematodes seem to have taken up at a slower rate than copepods and cumaceans (Fig. 9). Cumacea appears to be the fastest (higher uptake at 5 days) group in taking up the micro-algal food source (Fig. 9). After 10 days of incubation time nematode uptake increased substantially, whilst copepod uptake slowed down and cumaceans already started respiring what they had incorporated. The fast uptake and respiration (high activity) of cumaceans can be explained by their behaviour at the sediment-water interface. Cumacea are active swimmers and their position in the water layer immediately above the sediment enables them to "catch" the administered food before it can settle on the sediment surface. Once the food had completely settled, nematodes and copepods would have had the advantage over cumaceans, by being able to move quickly in the upper layers of the sediment and graze the food source. The fact that Cumacea exhibit a decrease of labelling within 10 days may be due to a change in food choice (i.e. between 5 and 10 days they started targeting non-labelled food sources) or a lack of labelled food present in the sediments. Unfortunately we have no sediment data to confirm this.
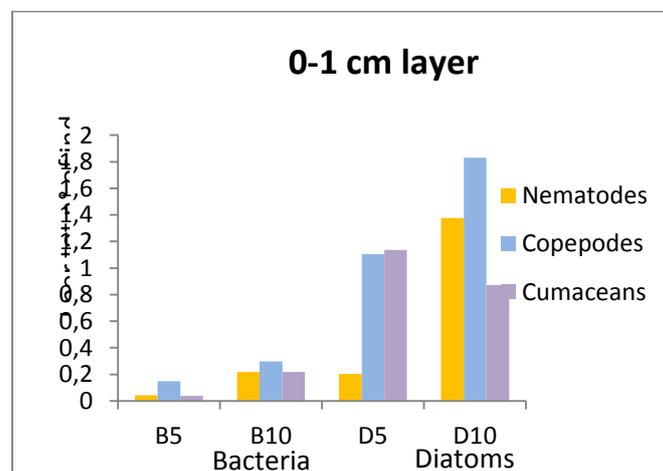
Fig. 9. Total uptake per community (total number of individual). Based on average individual numbers calculated from the 3 environmental replicates.

Nematodes are assumed to play an important role in the carbon flux within the polar bathyal food webs, but knowledge on their natural diets is poor. The selective feeding properties of Antarctic deep-sea nematodes were also investigated within an experimental setup (for protocol details, see Ingels *et al.,* 2010). Natural carbon

isotope signals of nematodes and organic sedimentary carbon showed a clear average offset (+3.2 ‰) indicating selective feeding of the nematode community as a whole. The contribution of bacteria to the diet of nematodes explained this ^{13}C offset and observed natural ^{13}C isotopic signatures. The nematodes showed a clear, relatively rapid (maximum at 6 – 7 days) and significant selective response to the pulse of ^{13}C enriched bacteria in surface sediments of both regions. This indicated that bacteria were preferred over fresh phytoplankton as a carbon source for both Arctic and Antarctic deep-sea nematode communities. These results indicate the importance of bacteria as a contributor to nematode food and presents arguments for the assumed intermediate trophic position of the nematofauna in the Antarctic deep-sea benthic food web (Ingels *et al.*, 2010).

Previous studies showed that nematode standing stock in deep-sea sediments is closely linked to organic matter input, but their response to seasonally varying phytodetritus deposition seems often delayed in time. There is growing evidence that nematodes feed on bacteria rather than using fresh phytodetritus as a food source in the deep sea (e.g. Ingels *et a*l., 2010). In order to further test the uptake rate and potential preference for microbial- related food sources, an *ex situ* enrichment experiment was performed during the ANT XXIV-2 expedition on board of RV *Polarstern* (11/2007-02/2008). Samples from Maud Rise (2120 m depth) were injected with several ^{13}C labelled substrates to label the natural microbiota. When grazing on bacteria took place, the ^{13}C label can be traced in the nematodes. Together with a natural biomarker analysis of selected genera, an integrated view on the degree of selectivity and food preferences of nematodes for particular components of the deep-sea ecosystem will be obtained. A parallel experiment at 1200 m depth in the Hausgarten site (Arctic Ocean) revealed little or no uptake of bacteria by nematodes.

In order to unravel the role of meiofauna in the C-flow through deep-sea sediments of the Antarctic in relation to their biodiversity, and the link between meiobenthic diversity and function, it is essential to reveal interactions in the benthic food web and the trophic position of different meiobenthic taxa and functional groups at locations with contrasting food input. So far, it remains unclear what drives the high local biodiversity of small benthic taxa in the deep-sea, but a relation in productivity is possible. A repeated sampling near the Southern Polar Front and more southward allowed the estimation of the variation in local biodiversity in relation to changing productivity levels. For this purpose a total, 6 deep-sea stations were sampled in the Southern Ocean at a N-S transect along the Greenwich Meridian. Sediment samples were also taken during and after a phytoplankton bloom at 52°S 0°E (December 2007, end of January 2008) to investigate the effect of phytoplankton bloom and subsequently the particulate food flux to the deep sea bed (Guilini *et al.*, in prep.;

Veit-Köhler *et al.*, 2011). These studies contribute to the generalised energy-flux model and food web research, an objective of the ANDEEP-SYSTCO project.

Along the N-S transect, the observed patterns of $\delta^{13}C$ and $\delta^{15}N$ for the two dominant taxa Nematoda and Copepoda did not reflect water depth as might be assumed for deep-sea communities which rely on the input of organic material from the water column. Patterns of $\delta^{13}C$ and $\delta^{15}N$ were more related to the geographical position and the oceanographic situation at the sea surface. Meiofauna organisms showed gradually declining $\delta^{13}C$ (-22 to -28‰) and $\delta^{15}N$ values (12 to 6‰) along the N-S transect. For the nematodes, this suggests a differentiation in nematode functional diversity along the transect as illustrated in Fig. 10. An exception to this relationship was observed for the communities of the southernmost station at 70°S where $\delta^{13}C$ (-25‰) and $\delta^{15}N$ (7.5 to 9.5‰) were more enriched.

The world's oceans show regional differences in surface water dissolved inorganic carbon (DIC) $\delta^{13}C$. South of the Subantarctic Front the values of surface water DIC $\delta^{13}C$ sharply decrease. This already depleted DIC available for micro-algal primary production partly explains our findings of lower $\delta^{13}C$ at the deep-sea floor towards the southern stations. Carbon fixation by ice algae (more enriched $\delta^{13}C$) seemed to play a significant role for the benthic food web at the southernmost station of our study.

Among other factors, a northward transport of surface water is known to be responsible for differences in nitrate concentration and nitrate $\delta^{15}N$ between the high Antarctic and the Subantarctic. This situation was reflected in our findings where we observed clearly enriched $\delta^{15}N$ values in meiofauna organisms from the most northern stations.

At the stations located at 52°S 0°E, fresh phytodetritus originating from the observed phytoplankton bloom in the water column had reached the sea floor by the time of the second visit. Abundances of bacteria and most major meiofauna taxa did not change considerably between the two sampling dates. For copepods, the second most abundant meiofauna taxon after the nematodes, the enhanced input of organic material did not lead to an observable increase of reproductive effort. However, a significant migration of meiofauna towards the sediment surface could be observed following the remains of the phytoplankton bloom that had reached the sea floor. Vertical shifts in meiofauna distribution between December and January could be explained by changing porewater oxygen concentration, total sediment fatty acid content and pigment profiles. Higher oxygen consumption after the phytoplankton bloom has to be attributed to an enhanced respiratory activity of the living benthic component, as neither meiofauna nor bacteria reacted with an increase in individual numbers to the food input. Based on our results we assume that low temperatures and ecological strategies are the underlying factors for the delayed response of

benthic deep-sea copepods to the modified environmental situation in terms of egg and larval production.
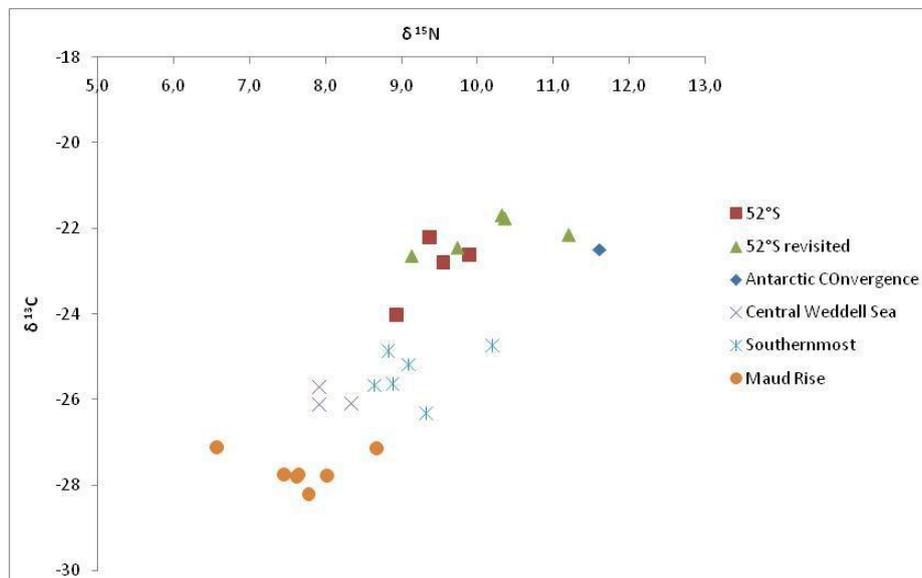
Fig. 10. δ¹³C and δ¹⁵N results from nematode specimens collected along a N-S gradient in the Southern Ocean.

(2) Trophic and metabolic aspects of amphipods

DYNABIO objectives 1-b, c

Eight species of peracarids have been analysed to determine their fatty acid composition. Hierarchical clustering and multi-dimensional scaling (MDS) were performed based on Bray-Curtis similarity, applied to relative abundance data (PRIMER v5; Clarke & Warwick, 1994). Because pelagic species were available, they were included to be compared with their benthic homologues. Statistical analysis separated 8 species into 3 distinct groups at the 80% similarity level (Table 5).

As expected, the first cluster combines the pelagic species *Cyllopus lucasi* and *Hyperiella dilatata*. Both species share the highest proportion of docosahexaenoic acid (DHA) which is consistent with a carnivorous or omnivorous diet on flagellates. The PUFA 18 :4 (n-3), which dominates in the species *Ampelisca richardsoni* (24%), is a major FA in the prymnesiophyte *Isochrisis* sp and the cryptomonad *Chroosomas salina* (Phleger *et al.*, 2002 and references therein). As already demonstrated in Nyssen *et al.,* (2005), scavengers in the third cluster are typically characterised by a very high proportion of MUFAs composed of 18C. Various hypotheses might explain the scavenger's particular fatty acid composition as a very intensive *de novo*

biosynthesis. However, a detailed analysis of the underlying mechanism will be an important task to be developed in the near future.

	CLUSTER 1 (89,4%)	CLUSTER 2 (92,3%)	CLUSTER 3 (80,4 %)
CLUSTER 1	-	33% 18:4n-3 / 22 :6n-3	45,7% 18 :1n-9+7 / 22 :6n-3
CLUSTER 2		-	49,2% 18:1n-9+7 / 18 :4n-3
CLUSTER 3			-

Table 5. Results of SIMPER analysis : within group similarity (% in parenthesis), average dissimilarity (%) and separating fatty acids (FA) (most discriminant).

An experiment on trophic level change in three Antarctic scavengers indicates that the speed of adjustment in body tissue stable isotope ratio as a reaction to a new food source differs between species and depends on lifestyle. This hasn't been revealed before. Fourteen amphipod species, belonging to two families drastically different in trophic habit (Lysiannassidae: mainly opportunistic with a great trend to scavenging; Iphimediidae: specialists consuming particular prey such as hydrozoans and bryozoans), and one isopod species were analysed for stable isotope ratios.

Metabolic rate is a proxy of overall energy expenditure (production + respiration + excretion) of an organism, and hence it is one possible way of estimating energy flow through the individual organism. Oxygen consumption rates of unfed (deprived of food for at least three days), unstressed, and inactive animals were used as a proxy of standard metabolic rate. Oxygen content was assessed using a modified intermitted flow system and oxygen micro-optodes connected to a Microx TX 3–array (® PreSens GmbH, Neuweiler, Germany). During the last cruise, certain expected amphipod species were surprisingly not found. So, owing to the fact that mainly isopod species have been sampled in adequate supply, nearly all experiments have been focused on those. One amphipod (*Eurythenes gryllus*) and two isopods (*Glyptonotus antarcticus* and *Natatolana oculata*) have been used in experiments.

The Specific Dynamic Activity (SDA) experiment was designed to provide a detailed picture of the post-prandial metabolism increase. We encountered many problems with the physiological experiments. First, only experiments implying isopods lead to

valid results. Data for *E. gryllus* have been discarded because of total absence of feeding. So, we changed the protocol and extended starvation as well as feeding periods. Even after all changes made, non-feeding events repeated several times in all species. Secondly, we did encounter technical problems with the water circulating system. During some experimental runs, the diminution of oxygen was more pronounced in the reference chamber than in chambers with animals. This response, probably due to bacteria in the system, was dealt with by cleaning and renewal of the water. Nevertheless, the problem persisted, so all components (tubes, optodes, chambers) had been replaced and the system was rebuilt. The experiments provided the first metabolic data available for those Antarctic amphipods. The first striking feature we registered with scavengers was their ability to cope with long periods of starvation. For the experiments with *N. oculata*, we let the animals starve for six weeks (the maximum observed is in the order of several months), and some specimens did not feed even after such a long period without food. Our specific dynamic action (SDA) results for *G. antarcticus* are in good agreement with the scarce existing literature. In addition, the digestive tract of 7 species was dissected and prepared for SEM observation, results for this study are not yet available.

(3) Temperature effects

DYNABIO objectives 2-d

In November 2007, a laboratory temperature experiment was carried out at the Dallmann laboratory, Jubany station, located near the coast of Potter Cove on King George Island. Clearly, this area is very suitable for performing experiments dealing with the influence of temperature changes on marine benthos, since it is situated in one of the most rapidly warming areas of the Antarctic.

The absorption data are summarized in Fig. 11. There is a strong decline in oxygen concentration (expressed as an absorption coefficient) for all sediment treatments, although the rate of decrease becomes greater with each temperature increase, whereas the 6°C treatment reaches the 'anoxic' phase after 7 days, the 0°C treatment has not reached this phase yet after 14 days. Although the same trend is clear for the water samples, it is less pronounced and subject to small fluctuations. When comparing the sediment and water cores, the oxygen-consuming effect of the benthos is obvious.
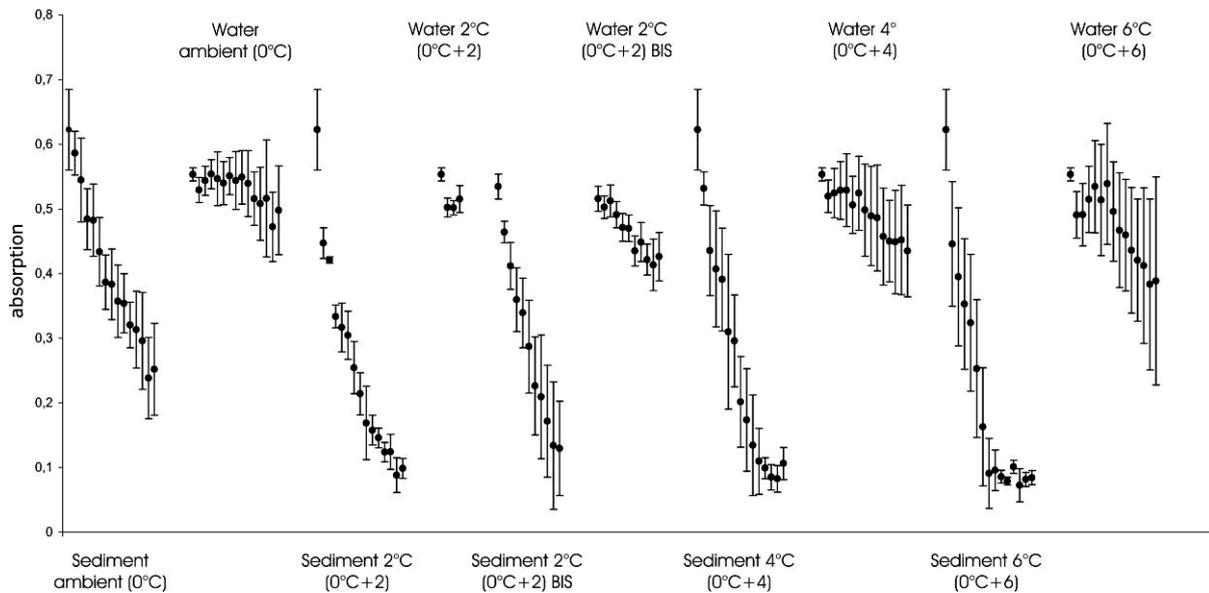
Fig. 11. Absorption data of the benthic communities for different temperature treatments.

More data (densities, biomass, ATP…) will become available when the sediment samples are fully analysed.

The impact of increased food availability on benthic respiration was also investigated: on 19/11/2007, the sediment of some cores was covered by a thick, dark-yellow-green layer of benthic diatoms. Four such cores were incubated at 0°C and compared with the sediment cores taken on 15/11/2007, which did not have any observable diatom layer. Although the initial oxygen concentration (Day 0) was not the same for both treatments, there still was a pronounced trend: benthic respiration was higher in the food-enriched cores, resulting in a faster decline in oxygen concentration in these cores, compared to the 'normal' (not-enriched) sediment cores. In order to test the set-up of the experiments, and to enable a bipolar comparison, analogous experiments were carried out at Koldewey station, Spitsbergen (78°55'N; 11°56'E). Although the ambient temperature was higher here (4°C), and temperature steps of 4°C were used instead of steps of 2°C, the experiments yielded similar results.

(4) Trophic studies on echinoids

DYNABIO objectives 2-e

Preliminary results have been obtained by Marquet (2007) through the comparison of three series of echinoid samples (family Echinidae): (1) *Paracentrotus lividus* from Brittany, (2) *Paracentrotus lividus* from the Mediterranean Sea and (3) *Sterechinus antarcticus* from the Antarctic Peninsula (BENTART-06; Margarita Bay).

Results based on the nature of the gut content and on isotope analyses indicate that *Sterechinus antarcticus* from the Antarctic Peninsula is both a carnivore and a deposit feeder, feeding mainly on sessile animals and sediments. In contrast, the European species *Paracentrotus lividus* feeds mainly on vegetal material. Interestingly, *P. lividus* displays some flexibility in its feeding behaviour along the latitudinal gradient (Brittany versus Mediterranean Sea): the Mediterranean individuals are strictly vegetarian while those from Brittany display a wider spectrum of food sources, feeding both on animals and plants/algae.

Pierre Becker (Post-doctoral fellow supported by the BIANZOII-1 contract) investigated a larger set of samples collected along the Antarctic Peninsula (depth ranges: from 100 to 350 meters) during the campaigns BENTART 06 (R.V. Hesperides) and ANT XXIII/8 (2007; R.V. Polarstern). He focused on one species of Echinidae *Sterechinus antarcticus* (from 8 stations; Table 6) and three species of Cidaridae (*Ctenocidaris gigantea, Ctenocidaris perrieri* and *Notocidaris mortenseni*) (Table 7). The gut content, gut microflora and stable isotopes analyses of S. antarcticus (4-5 individuals/station) were characterized. For the Cidaridae species, the gut content was observed for 3 individuals per station. Molecular techniques were applied on N. mortenseni (3 individuals from PS69/702-9) and C. perrieri (2 individuals from PA39-1), but no bacterial DNA could be amplified from their gut content.

|	Station	Locality	Position (start)	Mean depth (m)	Trawl
Ant XXIII/8	PS69/654-6	Elephant Island	61°22.80'S/ 56°03.84'W	342.5	Small Agassiz trawl
	PS69/685-1	Joinville Island	62°34.61'S/ 55°39.38'W	162.8	Bottom trawl
	PS69/702-9	Larsen B South	65°57.85'S/ 60°28.42'W	218.2	Large Agassiz trawl
	PS69/703-2	Larsen B West	65°30.81'S/ 61°40.06'W	339.0	Bottom trawl
	PS69/725-6	Larsen A	64°54.80'S/ 60°37.46'W	180.6	Large Agassiz trawl
Bentart	PA39-2	Margarita Bay		160	Large Agassiz trawl
	PA43	Adelaide Island		250	Large Agassiz trawl
	LOW47	Bransfield Strait		115	Large Agassiz trawl

Table 6. List of stations analysed for *Sterechinus antarcticus*.

	Species	Station	Locality	Position (start)	Mean depth (m)	Trawl
Ant XXIII/8	*Ctenocidaris gigantea*	PS69/689-3	Joinville Island	62°27.28'S/ 55°20.74'W	216.9	Small Agassiz trawl
	Notocidaris mortenseni	PS69/702-9	Larsen B South	65°57.85'S/ 60°28.42'W	218.2	Large Agassiz trawl
		PS69/721-2	Larsen B North	65°55.41'S/ 60°34.01'W	296.6	Large Agassiz trawl
Bentart	*Ctenocidaris perrieri*	PA39-1	Margarita Bay		160	Large Agassiz trawl

Table 7. List of the stations analysed for Cidaridae.

The results show that all sampled *S. antarcticus* individuals had sediment pellets in their digestive tube but additional fragments of animals (crustaceans, bryozoans, hydrozoans and skeletal parts of other invertebrates) may also occur. In Cidaridae (*C. gigantea*, *C. perrieri* and *N. mortenseni*), the digestive contents always consist of animal remains (hydrozoans and bryozoans). Stable isotope analyses (*S. antarcticus*) show that delta ^{13}C values of the gut contents (-24.12 ± 0.92) are in the range of various marine animals including crustaceans, cnidarians and polychaetes but far from macro algae (-30 to -31). Interestingly, there is a marked enrichment of ^{13}C in the gonads (-19.43 ± 0.67) that could be indicative of a broader source of nutriments (i.e. sediments). Stable-nitrogen isotope ratio (delta ^{15}N) of the muscles (6.47 ± 0.53) corresponds to scavenging marine animals such as ophiuroids and isopods. These results stress the importance of sediments and its associated organic matter in the diet of *S. antarcticus*. Bacterial communities associated with the gut of *S. antarcticus* were characterized by DGGE (Denaturing Gradient Gel Electrophoresis) and 16S rRNA gene cloning analyses. DGGE was used to compare bacterial diversity of the microflora of sea urchins from different stations (bacterial DNA from the gut of three individuals was pooled for each station). Fig. 12 illustrates a DGGE gel obtained from the gut microflora of *S. antarcticus* at seven stations near the Antarctic Peninsula: Elephant Island (654-6), Joinville Island (685-1), Larsen B South (702-9), Larsen B West (703-2), Larsen A (725-6), Margarita Bay (PA39-2) and Bransfield Strait (LOW47). No bacterial DNA was amplified from samples of Adelaide Island (station PA43). A replicate gel was performed, with an identical pattern. Ten phylotypes were revealed on the gels. Only one phylotype (band 1) was present in gut contents from all stations. Other phylotypes were detected in one to

five stations. The bacterial microflora thus varies according to sites and is consequently not specific.
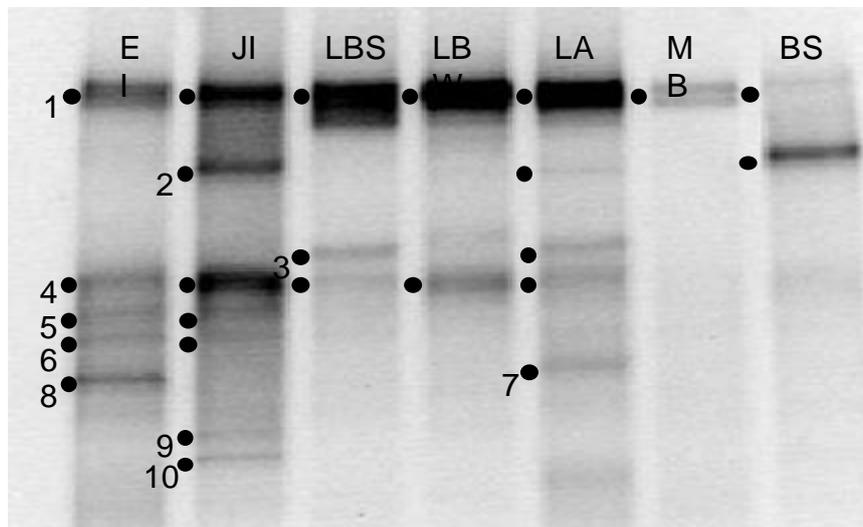
Fig. 12. DGGE gel profile of the 16S rRNA gene fragments from the gut microflora of S. *antarcticus*. BS: Bransfield Strait, EI: Elephant Island, JI: Joinville Island, LA: Larsen A, LBS: Larsen B South, LBW: Larsen B West, MB: Margarita Bay.

Three clone libraries were obtained from the gut microflora of *S. antarcticus* collected at Elephant Island (72 clones, 43% of coverage value), Larsen B West (40 clones, 65% of coverage value) and Margarita Bay (40 clones, 20% of coverage value). Two samples were pooled for construction of each library. Sequences with at least 97% of similarity were gathered, giving 78 operational taxonomic units (OTU). All OTUs were assigned to one or two of the three stations but never to all stations. The most numerous sequences from all libraries belonged to the *Proteobacteria* and particularly *Gamma-* and *Alphaproteobacteria*. *Planctomycetes* was the second most represented group but accounted only for 9% of the total clones and was absent from Larsen B West. Interestingly, about two thirds of the OTUs were related to bacteria from marine sediments. These sediments were of various origins including Wadden Sea, Yellow Sea, Baltic Sea, Bering Sea and Arctic Ocean. OTU 20, accounting for 10 clones from Elephant Island and Larsen B West, was close (96-98% similarity) to *Psychromonas profunda*, a psychropiezophilic bacterium isolated from deep Atlantic sediments (Xu *et al.*, 2003a). Some OTUs belonging to various bacterial groups were related to cold-seep sediments, most from the Japan Trench. In addition to bacteria from sediments, OTU 37, representing 12 clones had 97-99% of sequence identity with *Colwellia psychroerythrus*, a psychrophilic bacterium associated with sea ice from Antarctic coastal areas (Bowman *et al.*, 1997). Most of the remaining OTUs were related to bacteria associated with marine invertebrates such as corals,

sponges and crabs or to *Moritella* sp. Members of this genus such as *M. marina* (Urakawa *et al.*, 1998), *M. profunda* (Xu *et al.*, 2003a), *M. abyssi* (Xu *et al.*, 2003b), *M. dasanensis* (Kim *et al.*, 2008) and *M. japonica* (Nogi *et al.*, 1998) are generally psychrophilic bacteria from deep-sea water or sediments. Our data indicate that the gut microflora of *S. antarcticus* are bacteria occurring in the environment.

In conclusion, the diet of *S. antarcticus* (Echinidae) differs from that of *Ctenocidaris gigantea, C. perrieri* and *Notocidaris mortenseni* (Cidaridae). In both families, all the investigated species are carnivores/scavengers. However, *S. antarcticus* ingests a wider set of animals and is also a deposit–feeder. Its diet is clearly not restricted to food of animal origin. Noteworthy, no macro algae were found in its gut, probably due to low availability or absence of this resource in the investigated stations, especially at their depth range (100-350 meters). Interestingly, the digestive bacterial microflora of *S. antarcticus* is not symbiotic, varies with station (as only one of the ten phylotypes detected by DGGE was found in all stations) and presumably fluctuates with the nature of the ingested food. Moreover, cloning analyses did not reveal clones common to all libraries. Consequently, the digestive microflora is neither specific nor symbiotic but rather consists of transient bacteria. These bacteria seemingly originate from the pellets of sediments ingested by the echinoid as a majority of the clones were related to bacteria from marine sediments. The presence of bacteria related to cold-seep sediments has to be stressed as a recent survey at the Larsen Ice Shelf reports the presence of a chemosynthetic-based ecosystem in this area (Domack *et al.*, 2005). No bacterial amplification was obtained for the gut contents of Cidaridae, which could indicate that their bacterial microflora is poorly developed. These echinoids could rely on intrinsic digestive enzymes; these enzymes could degrade bacteria, preventing their proliferation in the gut. However, further morphological analyses of the digestive tube of these sea urchins are needed to confirm this hypothesis. Regarding its feeding behaviour, *S. antarcticus* might be well-adapted to cope with changes in food resources resulting from global warming. Cidaridae would most presumably be more sensitive to changes although one cannot exclude their acclimatization to a new set of preys.

(5) Ocean acidification effects

DYNABIO objectives 2-f

Anthropogenic CO_2 emissions have been largely absorbed by oceans, resulting in a surface pH which is already 0.1 units lower than during pre-industrial times and is expected to decrease by 0.3-0.4 units by the end of the century. As a consequence, oceans are experiencing a reduction in CO_3^{2-}, which is leading to a drop in calcium carbonate saturation. The Southern Ocean will suffer even lower concentrations of

CO_3^{2-} due to lower surface temperatures and the presence of large amounts of upwelled deep water rich in CO_2.

The main goals of this work were to: (1) determine the impact of seawater acidification on larval and adult sea urchins and (2) establish dose-effect relationships for the most significant effects.

(a) Larval development.

The first experiments were done using *Paracentrotus lividus*, a temperate species, in order to adjust the techniques. Controlled lower pH values were obtained by bubbling CO_2 in seawater. The total alkalinity and pH (total scale) were measured and the pCO_2 and total inorganic carbon calculated, as well as the magnesium-calcite saturation state. The larvae were grown at pH between 8.0-6.8 until the echinopluteus stage (3 days) and fertilization, cleavage and larval development were characterized using embryotoxicity protocols to distinguish normal and altered morphologies. At lower pH, significantly more larvae showed an abnormal morphology and a reduced size. The highest pH at which significant effects on fertilization and cleavage were recorded was 7.6. On the contrary, larval development was only affected below pH 7.4, a value equal or lower than that reported for several subtidal species. This suggests that sea urchins inhabiting stressful intertidal environments produce offspring that may better resist future ocean acidification, indicating a possible acclimatization or adaptation to pH stress

Arbacia dufresnei was studied at control (8.0) and lower pH (7.7 and 7.4) waters. The results show that sub-Antarctic populations of *A. dufresnei* are susceptible to a larval development delay caused by low pH seawaters, with no significant increase of abnormal forms in the tested pH. The obtained Lowest Observed Effect Concentration (LOEC) for post-oral arm length (PL) was pH=7.4. Larvae were isometric between pH treatments. Even at calcium carbonate saturation states lower than 1, skeleton deposition occurred, indicating calcification was most likely affected in an indirect way. The *A. dufresnei* larvae do not seem to be more sensitive than other lower latitude species to ocean acidification, reinforcing the idea of resilience of polar and sub-polar sea urchin larvae towards acidification and underlining its potential to invade further Antarctic ecosystems.

(b) Adults

Adult sea urchins were grown at pH values between 8.0-7.4 during 3-4 weeks. Ocean acidification effects on echinoderms, more specifically on sea urchins, seem to be highly species specific and tolerance to pH can depend on their life history (Clark *et al.,* 2009, Dupont *et al.,* 2010, Moulin *et al.,* 2010). *P. lividus* and *A. dufresnei* seemed to present some degree of coelomic fluid buffer capacity and low seawater pH had no effect on the gonads and body wall metabolic status.

Furthermore, spine regeneration was slightly affected, but at which stage, i.e. wound-healing or calcification rate, low pH affected this process remains unclear. We propose that the capacity to withstand to low pH within the range predicted for 2100-2300 is probably linked to the origin of the studied individuals. The *P. lividus* ones came from a temperate intertidal population submitted to cycling daily and seasonal pH fluctuations (see Moulin *et al.,* 2010 for pH example of intertidal pool daily fluctuation). The *A. dufresnei* individuals belonged to a sub-Antarctic population where cold water pH is expected to be lower thanks to CO_2 higher solubility. The study species appear able to overcome ocean acidification, opening the scope for possible acclimatization of natural populations to low pH effects.

Cidaroid urchins have particular spines covered by a polycrystalline cortex which becomes exposed to seawater when mature as they are no longer covered by an epidermis like the spines of other sea urchins. Despite these characteristics, numerous species live below aragonite saturation horizon, especially at high latitudes. We investigated the morphology and the magnesium content of *Ctenocidaris speciosa* spines collected at different depths from the Weddell Sea. The cortex of *C. speciosa* presents a thicker inner cortex layer and a lower Mg content below the aragonite saturation horizon. Exposed stereome appeared more affected than cortex. It seems that the naked cortex of cidaroid species effectively resists low calcium carbonate saturation state and pH. We suggest that this could be thanks to the important organic matrix that surrounds the crystallites of the cortex.

(6) Sensitivity of Antarctic Zoobenthos to global change-induced drivers

DYNABIO objectives: integrative synthesis on the sensitivity of Antarctic zoobenthos and the first steps towards FOREBIO

Climate change over the past few decades has already caused significant biological and ecological changes in global marine and terrestrial ecosystems (Hughes, 2000, Thomas *et al.*, 2004, Walther *et al.*, 2002), and will continue to impact our planet. Many species are susceptible to climate change, and those of the marine environment are particularly vulnerable because of the physical and biochemical alterations brought to our oceans by increasing emissions and rising temperatures. This is particularly the case for the Antarctic, especially at the Antarctic Peninsula, a region which is experiencing one of the fastest rates of regional climate change on Earth. Continued warming together with increasing CO_2 concentrations in the SO is causing a cascade of environmental effects with far-reaching consequences for the benthic fauna.

Within BIANZOII, we have reviewed the ability of five abundant Antarctic benthic taxa (Foraminifera, Nematoda, Amphipoda, Isopoda, and Echinoidea) to cope with changes in environmental parameters (temperature, pH, ice cover, ice scouring, food

quantity and quality) linked to global change from the individual to the community level (Ingels *et al.*, conditionally accepted). During the BIANZOII workshop of 20th May 2009 at the Marine Biology Department, Ghent University, presentations were given on the up-to-date information gathered through literature reviews on possible climate effects on the benthic groups of interest. Subsequently, a flow chart was constructed, indicating the main effects of climate change on the Antarctic benthic environment.

An elaborate discussion resulted in a sensitivity table visualizing the preliminary basic structure of the review paper on climate change induced effects. Sensitivity tables for all groups are currently being finalised. The manuscript, which is now conditionally accepted (Ingels *et al.*, conditionally accepted) has the following aims: 1) To identify the drivers of faunal changes in the Southern Ocean, 2) To identify the differences in the responses (strength and weakness) in different benthic faunal groups, 3) To identify the impact of global change on the Antarctic benthic fauna.

What follows is an account of the major global change induced drivers that may impact the Antarctic Zoobenthos, an extract from the paper that resulted from it. Following that review, is the preliminary assessment of the sensitivity of each considered group to these drivers. The results and discussion in this section are based on reviewing the literature, integrated with BIANZOII results. The review goes beyond the scope of the three zoobenthic groups contained within the research aims of BIANZO II and includes information for Foraminifera and Isopods (contributions by AJ Gooday and A Brandt, respectively). Any information from this section/extract should be referenced accordingly (Ingels *et al.*, conditionally accepted)

(a) Global change induced drivers for Antarctic benthic faunal change

Since 2000, global anthropogenic CO_2 emissions have been rising at unprecedented rates and exceed worst-case scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) (Raupach *et al.*, 2007). As atmospheric CO_2 concentrations rise, ocean CO_2 uptake increases and the chemical balance of sea water is disturbed, causing the pH to decrease. Consequently, the production of biogenic calcium carbonate (both aragonite and the less soluble calcite) becomes more difficult for certain marine organisms (Gazeau *et al.*, 2007, Orr *et al.*, 2005). Increasing temperatures and CO_2 solubility will cause the calcium carbonate saturation horizon and CCD to shoal, hence exposing organisms to new saturation states which may impact their calcification processes. Southern Ocean waters experience faster acidification rates because of low surface temperatures increasing CO_2 solubility and greater upwelling of deep water containing high levels of CO_2 due to organic matter remineralisation. By 2100, the entire SO water column will become undersaturated with respect to aragonite, whilst the calcite horizon will remain at ~2200 m water depth, although in the Weddell Sea calcite undersaturation is said to

reach the surface waters (Orr *et al.*, 2005). Since preindustrial times, the average surface seawater pH has already been reduced by approximately 0.1 units and projected pH changes in the SO surface waters by 2100 range 0.3 – 0.5 units (Caldeira & Wickett, 2003, McNeil & Matear, 2008, Orr *et al.*, 2005). The predicted decrease of pH and CO_2 solubility changes may impede animals' calcification potential and other physiological processes such as growth and respiration (Pörtner *et al.*, 2004). Furthermore, ocean acidification can cause phytoplankton community shifts which will influence community structure of the higher trophic levels that are reliant on the phytoplankton (Hays *et al.*, 2005). Acidification may also influence activity of bacteria (produce CO_2) and zooplankton (which consume phytoplankton) resulting in changes in the structure and functioning of the marine ecosystem as whole (Pörtner *et al.*, 2004). Marine biota, however, do not respond uniformly to ocean acidification and resulting ecosystem responses to acidification will be different than species responses (Caldeira & Wickett, 2003).

Whilst global oceanic uptake of anthropogenic CO_2 is estimated at about 25-40% (Matear & Hirst, 1999, Takahashi *et al.*, 2009), the SO below 50° S is responsible for only 4-9 % of global anthropogenic CO_2 storage (Sabine *et al.*, 2004, Takahashi *et al.*, 2009). However, air-sea CO_2 fluxes into the SO are relatively high, but its capacity as a sink is limited because most CO_2 is transported northward through deep-water movements (Caldeira & Duffy, 2000). Several climate change studies based on the carbon-climate system predict a decrease in efficiency of the oceans as a sink for anthropogenic CO_2 (Matear & Hirst, 1999, Plattner *et al.*, 2001). Positive feed-back caused by increasing sea-surface temperatures, carbonate chemistry alterations, and changes in ocean circulation will outweigh negative feed-back effects (e.g. increased primary production), hence reducing global oceanic CO_2 uptake by up to nearly 30% during the 21st century (Matear & Hirst, 1999). This is particularly the case for the SO, where the impact of warming, transport processes, and biological effects is larger than in other oceans (Sabine *et al.*, 2004) due to its sensitivity to changes in stratification of the water column and to the fact that this is the region of the world in which deep mixing is normally able to reach into the vast volume of deep water that holds excess biogenic carbon (Sarmiento & Orr, 1991).

Besides reducing CO_2 solubility in seawater, rising temperatures may have direct impacts on the physiology of stenothermal organisms (Peck, 2005) as well as on the extent of sea ice, hence on the life history and biology of many species (Barnes & Peck, 2008). Next to affecting the physiology, phenology and ontogeny of species, temperature increases may also modify geographic distributions of species and alter biological invasion processes (Walther *et al.*, 2009). Within the next 100 years, moderate temperature shifts are expected; models suggest a 0.5 to 1.0 °C rise in SO surface waters in summer, with local temperature increases up to 2.0 °C, but winter temperatures will only increase with a maximum of 0.5 °C. Regardless of seasons,

bottom waters from the surface down to 4000 m depth are expected to warm on average by around 0.25°C, with possible higher temperatures at deeper shelf depths (Barnes *et al.*, 2009a).

The effect of rising atmospheric and sea surface temperatures in the Antarctic have already caused significant changes in sea-ice density over the last 50 years (Zwally *et al.*, 2002), especially at the Antarctic Peninsula (Cook *et al.*, 2005). Recent models predict a reduction in Antarctic sea ice extent of 24 to 33% (Arzel *et al.*, 2006, Bracegirdle *et al.*, 2008), but with considerable regional variation. Numerous Antarctic marine organisms depend on the seasonally dynamic interface between ice and water and small temperature differences can have large effects on this interface and its associated organisms. Variation in sea-ice density and extent does not only influence the sympagic or ice-associated fauna, such as certain copepods, amphipods, algae and micro-organisms, it will also impact animals that depend on algae blooms for food, such as benthic animals relying on phytodetritus from the euphotic zone. A southward retreat of sea ice will modify the extent and density of algae blooms with ramifying effects down the food web (Smetacek & Nicol, 2005). Furthermore, ice melt can lead to substantial release of ice fauna into the water column where it may enhance phytoplankton growth (Gradinger, 1999) or sink to the sea floor, serving as food for the benthos (Gradinger, 2001). The gradual disintegration of ice shelves will also reveal new habitats for both pelagic and benthic organisms as well as euphotic primary production, which in turn may influence the quality and quantity of food available to the benthos (Bertolin & Schloss, 2009, Thrush *et al.*, 2006). In addition, ice shelves attenuate the effect of tidal waves and strong winds on local hydrography, especially in shallow waters. Uncovered waters through a reduction of sea ice extent may therefore lead to increased hydrodynamic disturbance impacting the benthos.

Not only sea ice is under the threat of rising temperatures; deglaciation on land increases glacial discharge in the coastal zones, resulting in higher sedimentation rates which are likely to have a considerable but localised impact on benthic communities (Barnes *et al.*, 2009a). Large scale retreat of maritime glaciers and ice shelves (Cook *et al.*, 2005) will also increase the number of floating icebergs in the short term, leading to increased scouring rates and drop stone densities with detrimental consequences for the benthos (Gutt & Piepenburg, 2003, Lee *et al.*, 2001a, b). Nevertheless, such benthic disturbance will remain limited to the continental shelf, where it is shallow enough for floating icebergs to impact the seabed. In the long term, however, ice scour rates, depth of ice berg scours and drop stone intensity are expected to decrease. As ice sheets and glaciers become thinner and retreat towards land, the number and size of scouring ice bergs that are released into the waters will diminish. On the other hand, reduced iceberg scouring in the long

term may act to lower diversity of benthic communities by reducing disturbance frequencies (Gutt & Starmans, 2001, Johst *et al.*, 2006).

The compounded effects resulting from increased seasonal melting of glaciers, ice sheets and ice shelves, reduced brine rejection and rising water temperatures are in the long term likely to increase freshwater input and reduce salinity along Antarctic coastal waters (Jacobs *et al.*, 2002), especially at the Antarctic Peninsula. However, no large salinity changes are expected during the 21st century, except above 400m water depth, where it may drop with up to 0.3 units (Barnes *et al.*, 2009a). Surface water freshening can have a wide range of effects on both the water column and the seabed, including increased stratification of the water column hence reducing light and oxygen penetration with detrimental biological effects (Barnes *et al.*, 2009a).

Rising temperatures reduce the solubility of oxygen in water, but deoxygenation of Antarctic surface waters solely through increasing temperatures is unlikely to reach levels deleterious for benthic organisms. However, thermal changes co-occur with enhanced stratification, increased CO2 levels and elevated oxygen demand of organisms, which exacerbate the development of hypoxic zones with potentially harmful impacts on marine ecosystems (Hofmann & Schellnhuber, 2009). Furthermore, increased stratification will reduce the flow of dense, oxygen-rich surface waters to the deep sea, hence reducing oxygen availability in this environment (Matear *et al.*, 2000). Because the Antarctic is the principal source of oxygen-rich waters for the global deep-sea environment, reduced flow and deoxygenation effects may have far-reaching repercussions for the global marine biota (Hofmann & Schellnhuber, 2009, Pörtner, 2010).

Rising temperatures and to an extent salinity changes may act to affect hydrographic barriers such as the Polar Front in the SO. The Polar Front represents a distinctive biogeographical discontinuity, setting boundaries for faunal exchange mainly in the upper pelagic. Such exchange may be influenced by regional climate change, enabling invertebrate larvae to establish more southward and threaten Antarctic marine biota (Clarke *et al.*, 2005). However, the considerable temperature changes required to enable invasive migration of larvae from more northward locations and their establishment in the Antarctic, render such threats unlikely (Thatje, 2005).

Climate change and its complex and interactive chain of associated effects will affect the physiology, distribution, phenology, and ontogeny of many Antarctic benthic organisms, but the resulting changes from the species to the community level remain poorly quantified and understood. Individual species may appear vulnerable to environmental shifts or regime changes, but community and ecosystem responses may not act accordingly. In what follows we provide an overview on what is known about the responses of five important groups of benthic organisms to climate change effects from individual species, over populations, and how we think this could affect

the community level. In order to summarize impacts on taxa and understand the potential community impact, we reviewed taxon by taxon and produced a sensitivity table, which shows each taxon's reaction or presumed reaction to the varying environmental threats.

(b) Responses of benthic biota to environmental change: Foraminifera, Nematoda, Isopoda, Amphipoda and Echinoidea.

Foraminifera. Foraminiferal assemblages in the waters around the Antarctic continent are likely to respond to many of the environmental shifts associated with climatic changes. In particular, species with calcareous tests will be disadvantaged by any shoaling of the CCD resulting from ocean acidification. Based on a survey of records from the SO, Saidova (Saidova, 1998) concluded that carbonate dissolution is one of the principle factors influencing the distribution of these assemblages. At present, the depth of the CCD around the Antarctic continent is highly variable, ranging from a few hundred metres on the shelf (Anderson, 1975, Ward *et al.*, 1987) to 4000 m or more in oceanic areas, such as the Weddell Sea (Dittert *et al.*, 1999, Mackensen *et al.*, 1990). The occurrence in some intra-shelf basins, notably the bathyal Crary Trough (384-1079 m) in the SE Weddell Sea, of foraminiferal assemblages consisting almost entirely of agglutinated species reflects the shallow CCD (~550 m) in this part of the Weddell Sea (Anderson, 1975). Similar predominately agglutinated assemblages have been recognised at depths of 620-856 m and 79-796 m in the Ross Sea (Ward *et al.*, 1987). We anticipate that such assemblages will become more widespread in the future.

Climatic changes may modify both the quantity and quality of organic matter fluxes to the seafloor. Such inputs, particularly of labile phytodetritus, exert a strong influence on the density and composition of foraminiferal assemblages (Altenbach *et al.*, 1999, Loubere & Fariduddin, 1999) as well as the bathymetric distribution of particular foraminiferal species (De Rijk *et al.*, 2000). Some deep-sea species bloom in response to seasonally-pulsed phytodetritus inputs (Gooday, 1988). These 'phytodetritus species' occur in the abyssal Weddell Sea where, as in the North Atlantic, they are often found living within phytodetrital aggregates (Cornelius & Gooday, 2004). Indirect impacts arising from changes in the organic matter flux are also possible. A long time-series study (1989-2002) at the Porcupine Abyssal Plain (NE Atlantic) has revealed decadal-scale trends in the abundance of some foraminiferal taxa, in addition to seasonal fluctuations (Gooday *et al.*, 2010). One possibility is that these longer-term changes are associated with sharp increases in the abundance of megafaunal holothurians which in turn reflect changes in the quantity and quality of organic matter reaching the seafloor (Billett *et al.*, 2010). It is possible that similar faunal shifts among benthic foraminifera will occur in the SO in

future decades, as changes in the pH and temperature affect the composition of surface phytoplankton.

The disintegration of ice shelves, leading to a shift from an oligotrophic to a more eutrophic system in areas formerly covered by permanent ice, may affect foraminiferal community composition. Murray and Pudsey (Murray & Pudsey, 2004) described 'live' (rose Bengal stained) and dead (unstained) foraminiferal assemblages from an area of seafloor to the east of the Antarctic Peninsula that previously lay beneath the Larsen Ice Shelf, which disintegrated in 1995. The samples were collected during the 1999-2000 and 2001-2002 seasons. 'Live' foraminiferal densities in these samples were high, reflecting the high levels of primary production in the ice-free surface waters. Presumably, densities were lower prior to the ice shelf disintegration, although in the absence of baseline data from before the breakup of the ice-shelf, this cannot be demonstrated. An important difference between 'live' and dead assemblages is the higher proportion of agglutinated tests in the latter (43-98% compared to 25-66%). Since calcareous foraminifera are generally associated more closely with eutrophic conditions than agglutinated species, this could reflect an increase in surface primary production since 1995. Unfortunately, this attractive interpretation is compromised by the likely post-mortem dissolution of calcareous tests (Murray & Pudsey, 2004).

The breakup of ice shelves and the consequential increased prevalence of dropstones may have either a negative or a neutral impact on many sediment-dwelling organisms, but it would provide sessile foraminifera with additional surfaces on which to live. Dropstones are often densely encrusted with these organisms. A total of 36 species (1 calcareous and 35 agglutinated) have been recognised on drop stones from the abyssal NE Atlantic (Gooday, unpublished). The *Discovery Reports* (Earland, 1933, Earland, 1934, Earland, 1936) include 40 species that were found attached to stones and other hard substrates; all of them agglutinated.

Finally, the effects of oxygen depletion, if any, on benthic foraminiferal assemblages will depend on degree of oxygen depletion and whether or not it is permanent. Evidence from permanent oxygen minimum zones suggests that hypoxia will affect bathyal foraminifera species only when oxygen levels fall below a critical value, possibly 0.5 ml l^{-1} or less (Gooday, 2003, Levin, 2003). Such concentrations possibly could develop in basins with restricted circulation. Species exposed to periodic (e.g. seasonal) hypoxia may be susceptible to less severe levels of oxygen depletion (Levin *et al.*, 2009). However, these fluctuating conditions are usually associated with large rivers that disgorge large amounts of organic matter and nutrients onto continental shelves at lower latitudes. The most likely outcome in Antarctic waters is some diminution of oxygen levels that are not sufficient to affect benthic foraminifera.

Nematoda. Antarctic nematode species and communities are likely to show variable susceptibility to global change effects in the Antarctic, whereby species responses will ultimately depend on their physiological ability to cope with the changing conditions, and community responses depend on species and their interactions. Although no information on specific nematode responses to environmental change are available for the SO, experimental laboratory studies on species from coastal and estuarine areas in temperate regions indicate that rising temperatures, food quality and quantity and salinity changes may have significant effects on the life history, reproduction and feeding characteristics of many species (Forster, 1998, Gerlach & Schrage, 1971, Heip *et al.*, 1978, Heip *et al.*, 1985, Ishida *et al.*, 2005, Kim & Shirayama, 2001, Moens & Vincx, 2000a, b, Pascal *et al.*, 2008a, b, Price & Warwick, 1980, Takeuchi *et al.*, 1997, Tietjen & Lee, 1972, Tietjen & Lee, 1977, Tietjen *et al.*, 1970, Vranken & Heip, 1986, Vranken *et al.*, 1988, Warwick, 1981, Wieser *et al.*, 1974, Wieser & Schiemer, 1977, Woombs & Laybournparry, 1984). The effect ranges tested in these studies, however, go well beyond the expected environmental changes in the Antarctic; hence species responses to the predicted changes are likely to be weaker. Nevertheless, a temperature increase of 2°C may shorten generation times, increase reproductive capacity and respiration, and result in a more opportunistic feeding behaviour of certain nematode species.

Salinity changes of only 0.3 within the next 100 years are unlikely to alter life characteristics of nematode species significantly, especially in coastal areas, where they are adapted to seasonal variability, but it may affect shelf-depth nematodes which are not adapted to such dynamic conditions. Intertidal experimental studies have shown that only extreme salinity changes (salinity of 0 or 40 ‰) induce higher mortality rates, and affect respiration and assimilation rates, whilst fecundity, development times and sex-ratios remained similar under such aberrant salinity conditions(Moens & Vincx, 2000a, b). However, some studies indicate that decreasing salinity can increase generation times of some species whilst reducing the productive potential of others (Tietjen & Lee, 1972).

Climate change induced changes in density and composition of algae blooms may influence the quantity and quality of food that reaches the benthos (Hays *et al.*, 2005, Smetacek & Nicol, 2005). Whilst food density is known to affect respiration, growth, reproduction, and feeding characteristics of certain nematode species, the observed trophic plasticity of many nematodes prevents us from drawing conclusion on clear patterns. However, as a result of different species responses to changes in quality and quantity of food sources, population recruitment, structure, sustenance, and trophic interactions within the food web may be impacted and lead to changes in nematode communities in terms of abundance, biomass, and structural and functional diversity. However, it is important to realise that the investigated rates of (experimental) abiotic change do not fall within the expected ranges of climate

change and severe impacts on species level are therefore not expected. Different species, however, cope differently with abiotic change and community shifts in favour of more resilient species is therefore likely occur.

Temperature changes and associated physicochemical modifications can adversely affect nematode communities. In the 1990s, an anomalous temperature drop of only 0.4°C in the Mediterranean deep sea caused a significant decrease in nematode abundance and functional diversity, concomitant with increased species richness and evenness (Danovaro *et al.*, 2001, Danovaro *et al.*, 2004). The small temperature shift allowed the community to change and resemble more Atlantic nematode assemblages, possibly through migration of species into slightly colder Mediterranean waters. Even when normal temperatures returned, nematode diversity was only partially restored to previous values (Danovaro *et al.*, 2001, Danovaro *et al.*, 2004). This suggests that deep-sea nematode communities are very much affected by relatively small temperature changes. The same may hold true for shallow waters; phenological studies have indicated that nematode abundance and biomass decrease with increasing sediment temperatures (Yodnarasri *et al.*, 2008).

Rising temperatures have already decreased ice extent and density significantly, with far-reaching consequences for nematode communities through increased iceberg disturbance and changes in quality and quality of food. Iceberg scouring significantly affects the nematode community, with removal of over 95% of individuals and a consequent drop in diversity (Lee *et al.*, 2001a, b). Although initial scouring in shallow coastal waters has a deleterious effect, nematode abundance can recover within weeks. Scouring recovery in these areas occur through recolonisation, but without evidence for successional stages, suggesting that the nematofauna in frequently disturbed areas is well adapted to ice disturbance (Lee *et al.*, 2001b). Such successional colonisation and changes in nematode composition, however, are apparent in areas that have become ice free, such as the Larsen area at the Antarctic Peninsula (Raes *et al.*, 2009a, Vaughan *et al.*, 2003). Recent collapse of the Larsen ice shelves has accelerated colonisation of the new ice-free shelf areas because increased primary production at the surface is now able to supply the benthos with food. As a result, nematode communities transformed after ice-shelf collapse from a depauperated, low-diversity status, to a richer and denser community dominated by opportunistic species (Raes *et al.*, 2009a). In coastal areas, reduction of ice extent exposes the shallow waters and benthic environment to wind-driven currents and disturbance events, which may lower nematode abundance and diversity as has been shown in the Magellan area (Chen *et al.*, 1999) and Arctic coastal areas (Urban-Malinga *et al.*, 2004). At the same time increased production of macro-algae and phytoplankton may act to increase nematode densities and change community composition (Fabiano & Danovaro, 1999, Skowronski & Corbisier, 2002, Urban-Malinga & Burska, 2009, Urban-Malinga *et al.*, 2009, Vanhove *et al.*, 2000,

Vanhove *et al.*, 1998). In addition, increased benthic food deposition may lead to deoxygenation of the water through higher decomposition rates and increased respiration (Hofmann & Schellnhuber, 2009). Among the meiofauna, nematodes are the most tolerant to low oxygen concentrations and may attain high densities and dominance (Gutierrez *et al.*, 2008, Levin *et al.*, 2009, Neira *et al.*, 2001a,b). Nevertheless, hypoxia in bottom waters may alter community composition by favouring those nematode species tolerant to low oxygen levels (Hendelberg & Jensen, 1993). However, food availability has a greater impact on nematode communities than oxygen levels in surface sediments(Vanreusel *et al.*, 1995). This is supported by Cook et al. (Cook *et al.*, 2000) who gave evidence that not severe hypoxia, but food quality was the main predictor of nematode abundance in the oxygen minimum zone of the Arabian Sea. Deoxygenation of Antarctic bottom waters may have severe consequences for benthic biota, with nematodes being less affected than other taxa. Community responses to hypoxia may therefore lead to a state in which nematodes are likely to be the dominant metazoan group.

Experimental studies whereby the effect of CO_2 sequestration on meiofauna was investigated indicate that nematodes are relatively sensitive to high CO_2 concentrations in seawater (Barry *et al.*, 2005, Barry *et al.*, 2004, Fleeger *et al.*, 2006, Fleeger *et al.*, 2010, Takeuchi *et al.*, 1997). According to Takeuchi et al. (Takeuchi *et al.*, 1997) drastic impacts only seem to occur under pH conditions of 5.5~6 or less (Takeuchi *et al.*, 1997) and Kurihara et al. (Kurihara *et al.*, 2007a) reported no lethal effects when pH was lowered with 0.80 units below normal (CO_2 concentration of >2000 ppm above ambient). However, the effect that CO_2 and pH have on nematodes (and copepods) can be dependent on the type of source (Barry *et al.*, 2005, Pascal *et al.*). Other studies have reported that severe hypercapnia associated with pH levels of 5~6 severely impairs the survival of nematodes, but also reductions in pH of only 0.2~1.0 units below normal can result in high nematode mortality (Barry *et al.*, 2005, Barry *et al.*, 2004, Carman *et al.*, 2004, Fleeger *et al.*, 2006, Fleeger *et al.*, 2010). This suggests that 'moderate' CO_2 exposure, compared to the range of exposures possible following CO2 release, causes high mortality rates in the most abundant sediment-dwelling metazoans (Fleeger *et al.*, 2006).

Peracarid crustaceans: amphipods and isopods. Both amphipods and isopods are marine ectotherms which are generally considered to be among the most stenothermal organisms on Earth (Aronson *et al.*, 2007, Peck & Conway, 2000), and are characterized by slow physiological rates, growth, and great age (Peck, 2002, Peck & Brey, 1996). They are expected to show particular vulnerability to a change of conditions they are adapted to, and responses to rising temperatures are therefore expected on the species level.

Research performed on the Antarctic amphipod *Themisto gaudichaudi* indicated that individuals living in warmer water exhibit an increased respiration rate, faster growth, earlier sexual maturity and a smaller body size (Auel & Ekau, 2009). At higher temperatures, the increasing oxygen demand reduces the aerobic scope of animals (Peck, 2002) and the demand for food will increase with increasing metabolic needs, leaving less resources for growth and reproduction. In turn, a smaller body size will limit the range of prey they are able to feed on and reduce their mobility. Moreover, smaller adult size and reduced mobility may negatively affect reproduction rates and increase predation risk to a point where predation losses may prevent survival of the population. At the same time, smaller individuals seem more tolerant to acutely elevated temperatures than larger individuals within the same species (Peck *et al.*, 2009). It is likely that where warming is significant over monthly to annual time scales large individuals will be more affected than small ones, especially considering that thermal tolerance levels are lower under chronical temperature rises compared to acute temperature increases (Pörtner *et al.*, 2007). The early loss of larger individuals will impact the population severely since they represent the major reproductive component (Peck *et al.*, 2009). Sea water temperature increases of only a couple of degrees may hence affect peracarids' physiology and are likely to modify drastically the distribution of *T. Gaudichaudi* and many other amphipod species (Auel & Ekau, 2009). Such a selective removal of the larger individuals within a species will probably result in an ecological imbalance, with major consequences for the peracarid community as a whole. Temperature-dependent, selective removal will also be exhibited between peracarid species since temperature effects depend on the feeding behaviour and activity of individual species. Measuring the thermal tolerance limits of 14 Antarctic benthic invertebrates, Peck et al. (Peck *et al.*, 2009) found that the most active animals, three species of preying/scavenging amphipods in this case, exhibited higher tolerance to increasing temperatures than less active species. Such discrepancy between active groups such as predators and juvenile individuals and more passive organisms such as sessile feeders could have far-reaching consequences on the community level by disturbing the ecological balance and complexity.

For isopods, temperature has an effect on rates of transcription of several proteins in the muscles, including actin and myosin heavy chains, with increasing levels of expression as temperature increases in temperate and Antarctic species. In the Antarctic *Glyptonotus antarcticus* rates of protein syntheses were extremely low compared to the temperate isopod *Idotea rescata*. This was probably due to the relatively high energetic cost of protein synthesis for *G. antarcticus* in cold Antarctic waters in association with low rates of oxygen uptake (White, 1975). An experimental study on the effect of temperature and salinity on vital biological functions (response to food odour, righting, swimming and reburying) of the Antarctic isopod *Serolis polita*

suggests that Antarctic isopods are vulnerable to environmental changes and their ability to cope with them is limited. Some biological functions (righting and burying) were more affected than others (swimming). Interaction effects between temperature and salinity showed that *S. polita* was more vulnerable to lower salinities when exposed to higher temperatures (Janecki *et al.*, 2010). The predicted higher temperatures and concomitant decrease in salinity may therefore affect isopod survival to a greater extent than originally thought. Salinity change in itself does not seem to have a strong effect on isopods, but there is some evidence that isopod populations from intermediate salinities were more polymorphic than populations from extreme salinities (Heath, 1975). However, recent investigations of physiological responses to salinity changes of the isopod *Idotea chelipes* from the Baltic brackish waters documented that osmotic adjustment may be more or less costly in terms of energy according to salinity (Lapucki & Nonnant, 2008).

The outcome of global change effects on the survival of individual organisms or populations will not be dictated by its physiological limits, but by ecophysiological constraints on its capacity to perform critical biological functions, such as locomotion and feeding (Pörtner *et al.*, 2007). A temperature effect on the walking and righting of Antarctic crustaceans compared to temperate species (Young *et al.*, 2006) showed that even though Antarctic species have a lower thermal dependence, the thermal scope within which they can perform biological functions is reduced compared to temperate species. This implies that Antarctic peracarids are very much adapted to the narrow, cold temperatures, but also that they are much more vulnerable to aberrant temperature changes than their temperate relatives.

Despite the lack of calcium carbonate in the exoskeleton of amphipods and isopods, implying that lower pH values and shoaling of the CCD would not affect their structural development, ocean acidification presents a real threat to Antarctic peracarids. Several studies (Kurihara *et al.*, 2004a, Kurihara *et al.*, 2004b, Spicer *et al.*, 2007) have shown that acidification will not affect crustaceans in terms of developmental success to the same extent it will affect bivalves (Kurihara *et al.*, 2007b) or sea urchins (Havenhand *et al.*, 2008), but it would certainly retard their embryonic development (Egilsdottir *et al.*, 2009) and in synergy with other factors, such as reduced salinity, it can reduce the number of hatchlings (Egilsdottir *et al.*, 2009, Vlasblom & Bolier, 1971). For the isopod

Glyptonotus antarcticus haemolymph pH values between 7.85 and 8.2 have been measured. Acid –based changes due to respiratory adjustment are poorly buffered in *G. antarcticus* due to the low protein buffering capacity of the haemolymph, implying that it is unable to compensate for temperature changes (Jokumsen *et al.*, 1981). Therefore, species being affected would probably migrate to more favorable

environments or suffer removal from the ecosystem in case such migration is unfeasible.

Climate change has affected crustaceans, including isopod and amphipod species, in the past. For example, Thatje & Fuentes (Thatje & Fuentes, 2003) argued that oceanographic changes in the Polar Front may have caused reinvasion of anomuran and brachyuran crab larvae into the Antarctic from Subantarctic regions. Whilst the cold Antarctic temperatures pose limits to performance that exclude modern predators and circulation patterns form physical barriers preventing invasion from more northern latitudes, global warming is now slowly removing the barriers posed by cold temperatures and circulation patterns, enabling higher trophic level predators such as crabs, durophagous bony fish or sharks (Aronson *et al.*, 2007) to invade the Antarctic and influence the often indigenous character of its marine life. Mouritsen *et al.* (2005) showed that a 3.8°C increase in ambient temperature of the Wadden Sea is likely to result in a parasite-induced population collapse of the widespread amphipod *Corophium volutator* by increasing the transmission rate of their microphallid trematode parasites. Although this study is based on a North Atlantic species, one can easily envisage such a threat to SO amphipod species. Increasing rates of invasion, predation and/or competition, and increased risk of parasitism caused by climate change could not only affect the sustainability of certain species, it may disturb and alter amphipod species distribution and benthic community composition.

In analogy, following the Cretaceous extinction of Decapoda, the isopod families Serolidae and Antarcturidae radiated on the SO continental shelf, indicating successful diversification after re-invasion. In contrast, a genetic population study performed by Leese et al. (Leese *et al.*, 2008) showed that there is currently no effective gene flow for the species *Serolis paradoxa* between Patagonia and the Antarctic Peninsula and that a genetic connection has been absent for time exceeding the last glacial maximum. The authors argue that specimens from the Strait of Magellan and the Falkland Islands very likely represent two distinct species that separated in the mid-Pleistocene (about 1 MY BP) (Leese *et al.*, 2008). Due to their size of few millimetres up to a few centimetres in the deep sea, the brooding and usually less mobile isopods (excluding Munnopsidae) are thought to have a reduced gene flow. However, even though isopods are not very mobile, they may respond with migration to climate change nowadays (Barnes *et al.*, 2009b), especially in the SO deep sea where 50% of all Isopoda sampled during the ANDEEP expeditions are Munnopsidae (Malyutina & Brandt, 2007) which can swim. However, besides their migration potential, Isopoda must also have the ability to adapt to changing environments because they successfully colonized all marine environments from the tropics to the poles and from the shelf to the deep sea; the deepest records of the family Macrostylidae are from > 10.000 m. It is therefore

considered unlikely that extinction will occur in Isopoda due to climate change. However, at local scales, global change effects may affect individual species, generating selection pressures that favour more tolerant species or ecological groups over more vulnerable ones. Benthic isopod assemblages are therefore likely to change and this might also affect species' vulnerability on longer time scales.

Quantity and quality of food is important for all animals, especially early developmental stages, but Isopoda are brooders and at least the offspring or early developmental stages are relatively independent from food input. However, it is known that the SO Isopoda have larger eggs than their boreal and tropical relatives (Wägele, 1989, Wägele, 1987, Wägele, 1988), and variability in food resources may affect the their ontogeny. Trophic diversity of Antarctic amphipods is very high, covering nearly all possible feeding types and displaying high plasticity (Dauby *et al.*, 2001). This suggests that many amphipod species have a wide dietary spectrum and are able to take advantage of different food sources. Shifts in food quality and quantity may therefore not have a severe impact on the survival of these species, although shifts in community composition are likely.

Isopod species composition is correlated with sediment composition. Some prefer coarser substrates, while others occur in muddy sediments (Brandt, 1993, Brandt, 1995, Brandt & Piepenburg, 1994, Brandt *et al.*, 1996). Thus, a change in sediment composition will ultimately affect the species composition of habitats. In the deep sea, which is usually characterized by very fine sediments, Isopoda thrive and are very speciose. One could therefore expect that after glacial melting and an increase in fine sediment fraction on the shelf, that eurybathic deep-sea species could easily colonize the Antarctic shelf and replace those species which cannot cope with the environmental change.

Echinoids. During their life cycle, echinoids are susceptible to a variety of stresses and perturbations, and they display distinct biological and acclimation capacities. Juveniles and adults are epifaunal or endofaunal benthic organisms while, depending on the species, earlier developmental stages are pelagic or benthic (Pearse *et al.*, 1991, Poulin & Feral, 1996).

Departing from the effects reported for stenothermal Antarctic brachiopods, mollusks and fishes (Brockington & Clarke, 2001, Peck, 2005, Peck *et al.*, 2004), the seawater temperature rise in the Antarctic (*ca.* 2°- 4°C in the next 100 years for surface waters, IPCC 2007), could have minor impact on the metabolic activities of post-metamorphic echinoids. This is documented for *Sterechinus neumayeri* in the Antarctic (Belman & Giese, 1974, Brockington & Clarke, 2001, Brockington & Peck, 2001), and is supported by several acclimation experiments using tropical (Klinger *et al.*, 1986, Lares & McClintock, 1991, Ubaldo *et al.*, 2007), and temperate shallow water species (Lawrence *et al.*, 2009, Siikavuopio *et al.*, 2006, Siikavuopio *et al.*, 2008, Ulbricht,

1973b), as well as deep-water species (Ulbricht, 1973a). However, contrary to adults, early life stages could show high sensitivity to seawater temperature rises as indicated by studies carried out on early life stages of *S. neumayeri*. This shallow-water species has planktotrophic pelagic larvae (Bosch *et al.*, 1987). Gamete release coincides with the austral summer (Freire *et al.*, 2006) and embryonic and larval development has an optimal window between 0.2ºC and 1.7ºC outside which development can be impaired (Stanwell-Smith & Peck, 1998). Furthermore, the influx of fresh water from melting ice shelves due to global warming can result in a reduction of larval recruitment. Reductions in salinity from 34 to 30 psu slowed down development rates and decreased the development success of *S. neumayeri* embryos (Cowart *et al.*, 2009). Little is known about the effect of lower salinities on adult Antarctic echinoids. In general, when exposed to salinities within their tolerance range, metabolic rates of echinoderms are not affected (Farmanfarmaian, 1966). In fact, acclimated sea urchin populations have showed an increased tolerance (higher in adults than in juveniles) when exposed to lower salinities (Himmelman *et al.*, 1984).

Antarctic post-metamorphic echinoids are opportunistic feeders, allocate little energy to feeding and are able to react rapidly in the presence of sporadic nutrients (Andrew, 1989, Lawrence & Lane, 1982, Lawrence & McClintock, 1994). Together with the fact that a large range of food items is used by each species (De Ridder & Lawrence, 1982, Jacob *et al.*, 2003, Lawrence, 1975, McClintock, 1994), this suggests that Antarctic echinoids would be able to acclimatize to changes in food resources, i.e., to changes of the benthic components they rely on, such as preys and algae, as a result of seawater temperature rise. Trophic flexibility has been demonstrated for *Sterechinus antarcticus* in the Weddell Sea (Raes *et al.*, 2009b), and for *S. neumayeri* in the Ross Sea where the individuals show a shift from feeding predominantly on detritus (locations with more permanent sea ice in the South) to feeding on more freshly produced algal material (proximity to ice-free water in the North and East) (Norkko *et al.*, 2007). Interestingly, all Antarctic species recurrently ingest detritus. According to Norkko *et al.* (2007), such a detrital pathway may reduce the impacts of large seasonal fluctuations in the availability of primary production. However, long-term consequences of dietary shifts on echinoid populations are complex to predict because of reciprocal effects between different stages of the feeding process which can vary between species. Independently from seawater temperature, the quality and quantity of the ingested food can influence each feeding step, going from ingestion to nutrient allocation to either somatic or gonadic growth, but, in turn, the size of the individual (resulting from somatic nutrient allocation) and its reproductive status (resulting from gonadic nutrient allocation) can also influence the feeding steps (Beddingfield & McClintock, 1998, Lawrence, 1975, Lawrence & Lane, 1982, Otero-Villanueva *et al.*, 2004, Vadas, 1977). This is well documented in

aquaculture studies (Daggett *et al.*, 2005, McBride *et al.*, 1999, Otero-Villanueva *et al.*, 2004, Russell, 1987, Siikavuopio *et al.*, 2006, Siikavuopio *et al.*, 2008), and for the Antarctic species *S. neumayeri* (Brey *et al.*, 1995, Brockington & Clarke, 2001, Chiantore *et al.*, 2002) and *S. antarcticus* (Brockington & Peck, 2001). Data concerning global-change effects on pre-metamorphic stages are scarce, especially for the effects of diet quality on the development of planktotrophic larval stages. According to Marsh et al. (1999), feeding larval stages of *S. neumayeri* are not dependent on phytoplankton availability to complete their early development (up to day 60), and the uptake of dissolved organic matter by embryos and larvae could compensate for a scarcity of particulate food sources. However, food quality and quantity is known to influence greatly the survival, growth and developmental success in larvae as well as metamorphosis and post-larval development in temperate and tropical species (Vaitilingon *et al.*, 2001). Clearly, more research on Antarctic species is needed.

Seawater pH reductions within the range of future predictions impair the larval development of the Antarctic species *S. neumayeri* to a lesser extent than for temperate and tropical species (Clark *et al.*, 2009). One could argue that sea urchins from naturally stressful environments can cope better with a changing environment. An alternative hypothesis is that slower metabolism rates can improve resistance to hypercapnia (Pörtner, 2008). For *S. neumayeri* significant effects were recorded at pH 7.6, a value expected to occur by 2100 according to some predictions, but the short duration of the experiment means that these predictions may not apply to pH effects in the long run (Dupont *et al.*, 2010). However, several studies have demonstrated that even though adult sea urchin mortality does not increase when exposed to lower pH waters, gonad growth can be affected (Kurihara, 2008, Siikavuopio *et al.*, 2007). Unfortunately, impacts of ocean acidification on adult Antarctic echinoids physiology are unknown and require further study. Interestingly, the spines of *Ctenocidaris speciosa*, (Weddell sea) which are lacking an epidermis and are hence directly exposed to physical and chemical conditions of seawater, showed adaptations that provided them with an advantage in acidified deep-sea environments (Catarino *et al.*, unpublished data).

Early echinoid life stages are particularly sensitive to stressors and perturbations (Melzner *et al.*, 2009, Pörtner & Farrell, 2008), making them vulnerable in terms of recruitment success and long-term viability of populations (López *et al.*, 1998, Morgan, 1995). This is in agreement with the global change induced effects on pre-metamorphic stages mentioned above. Under the predicted environmental change, one of the main challenges for the future of Antarctic echinoid populations will be the ability of echinoids to successfully complete their development. Impairment of gonad development or gamete quality in adults could further affect reproduction and recruitment processes. There is very little information available on the effect of

changing availability and quality echinoid food resources, so the long-term effect of diets shifts on the viability of echinoids populations is a great unknown.

iii) FOREBIO – Forecasts for the XXIst century under global change

FOREBIO objectives a-d

As to amphipods, nearly ten thousand rows of data were obtained, giving detailed information on 892 species (including 60 undescribed species) from 312 genera.

Many reports have already shown that Polar seas are impacted by the present-day global warming. To cope with new climate induced changes and survive, Antarctic and Subantarctic marine organisms can migrate, acclimatize or adapt to new prevailing conditions. In addition, new interactions between southernmost species and invaders from Sub-Antarctic regions can be expected. Indeed, new biogeographical distributions have already been documented.

The first step of FOREBIO was to analyse actual species distributions in the Southern Ocean and understand mechanisms that structure them. They are different according to scale of observation. At local scale, species distributions are fully determined by proximal environmental parameters (chemical, physical and biological). At larger scale, they are both inherited from history (Earth history, clade history, etc.), and determined by environmental conditions. The second step was to have access to forecasts regarding the main environmental factors at the temporal scale of several decades (predictions including the end of this century). At this point, PhD-student Benjamin Pierrat and the team in Dijon have built up a comprehensive approach to explore those two steps. The organisation of FOREBIO is illustrated in the flow chart in Fig. 15.
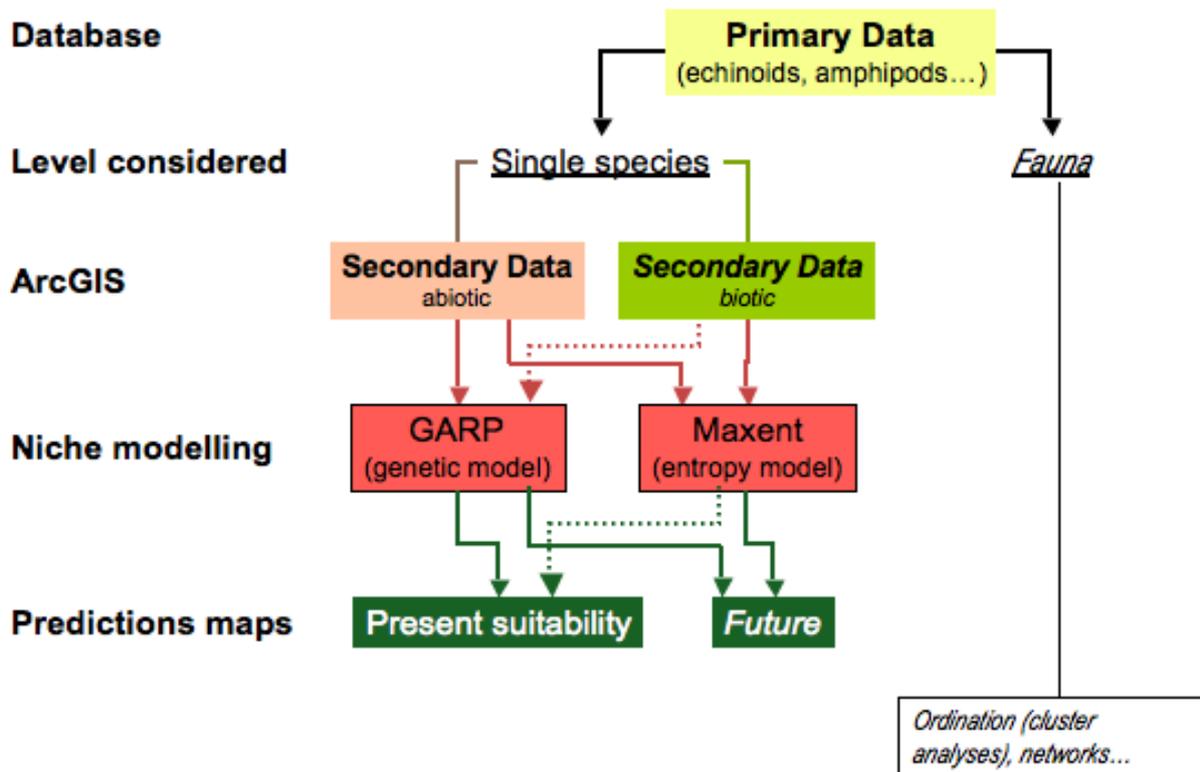
Fig. 15. Flow chart indicating the various steps of the development of the FOREBIO model, based on GIS and Maxent/GARP modelling techniques.

The primary data correspond to the data gathered within the NOWBIO work package, and they have been largely and continuously updated (e.g. for echinoids the database covers more than 4000 georeferenced localities in the Southern Ocean, and more than 6000 when the surrounding cold temperate areas are included). This has increased the power of the modelling approach and makes it now able to compute relevantly species distribution models at the scale of the entire Southern Ocean and to test for the impact of environmental variables and future climate scenarios ("single species" approach). Species distribution models have been performed matching abiotic data of the environment to occurrence data using a GIS (software ArcGIS version 9.3) and modelling fundamental niches with Maxent (version 3.3.2), a program using a maximum entropy modelling procedure (Phillips *et al.,* 2006). It will also be possible to analyse biogeographic relationships between the different regions of the Southern Ocean ("fauna" approach) using ordination or network techniques (this will be accomplished before the end of the BIANZOII project in the case of echinoids). In March 2010 and January 2011, workshops were held to evaluate and discuss the FOREBIO model, test its functions and statistical operations and determine hypotheses with regards to forecasting climate change induced effects on the Antarctic zoobenthos.

The first case study involves echinoids (Pierrat *et al.,* submitted.). Among the set of environmental data available at the scale of the whole Southern Ocean (close to 120 abiotic layers - the secondary data of the chart - have been added to the GIS and are now available for all BIANZO partners), 10 abiotic variables that are ecologically significant to echinoids have been selected: depth, slope, sea ice coverage, sea surface and seafloor temperatures, seafloor salinity, sea surface nitrogen oxide and chlorophyll a concentrations, granulometry and biogenic (either siliceous or calcareous) component of sediments. For species considered so far (*Sterechinus* group), models are mostly determined by three variables: depth, sea-ice coverage and sea surface temperature, which together account for 80 % to 90 % of the distribution patterns. In the near future, biotic secondary data involving taxa that possibly act on echinoid occurrences such as algae (source of food), gastropods (predation), etc., will be added to the model and tested. Regarding the future predictability of the distributions, changes in sea-ice coverage and in sea surface temperature are expected and new distribution models could be computed if predicted future values were introduced in the analysis. However, other variables are also expected to change in the future (chlorophyll a, seafloor temperature, seafloor salinity…), but predicted data for these variables do not exist yet, at least not at the scale of the whole Southern Ocean. This limitation has led us to discuss future distributions only qualitatively so far.

A preliminary attempt, using GIS and Maxent, has also been made for the amphipod genus *Orchomene*, in order to build maps of suitable distribution areas. Three outputs are illustrated below (Fig. 16a-c). The first map (Fig. 16a) corresponds to a probability suitable distribution; each pixel of the map is given a probability of presence of the genus, owing to the secondary data retained in the analysis. The second map (Fig. 16b) is binary (presence/absence) with a threshold fixed in such a way that all pixels with a probability greater than the lowest value obtained for a real presence are switched on (yellow area). The third map (Fig. 16c) is built the same way, but with two thresholds of different strength. Such maps allow comparisons of actual and observed distributions with suitable areas obtained under more or less stringent conditions. They help in identifying areas of patent lack of knowledge, but most importantly they lead to a better understanding of the interaction between abiotic parameters and the distribution of taxa, thereby helping in deciphering the parts played by environmental (edaphic) and historical factors, respectively, in explaining distribution patterns.
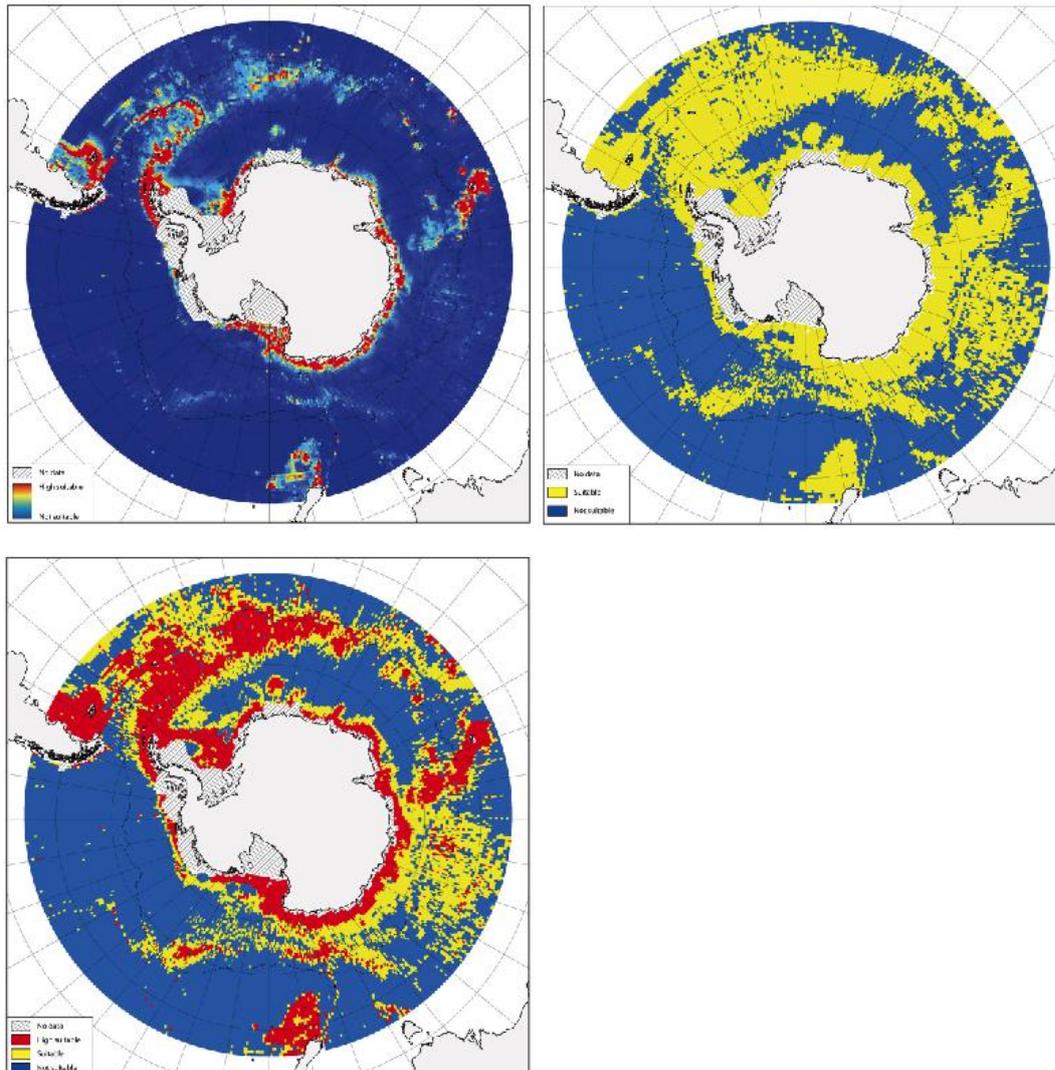
Fig. 16. Suitable distribution areas, predicted with GIS and Maxent for the amphipod genus *Orchomene.*

For nematodes, biogeographical/ecological data was subjected to an exploratory Maxent exercise to explain and predict the occurrence of certain nematode genera and ecological groups. These analyses are still undergoing.

In summary: 1) the primary data are now up to date, but we continue to improve the databases with newly collected materials; 2) a large set of secondary abiotic data, pertaining to the scale of the whole Southern Ocean, is now in ArcGIS (120 layers) and available to all BIANZO partners; 3) biotic secondary data are directly available through the ScarMarBin portal; 4) a user guide detailing the different steps of the approach (GIS, Maxent and GARP) has been presented and distributed to BIANZO partners; 5) two papers are currently submitted for echinoids; 6) by the end of the BIANZOII project, new data sets of nematodes and amphipods will be used to explore precise ecological questions/hypotheses.

4) POLICY SUPPORT

a) Effective support to policy-relevant processes

i) ACCE report

Several BIANZO results were incorporated in the Antarctic Climate Change and the Environment (ACCE – SCAR) Report (Turner *et al.,* 2009). We acted as co-author in chapter 5 but contributed with research results to other chapters too. This comprehensive report focuses on the impact and consequences of rapid warming of the Antarctic Peninsula and the Southern Ocean. It describes what we currently know, and illustrates how human activity is driving rapid climate change. By integrating multidisciplinary evidence into a single source it helps scientists and policy makers to understand the distinction between environmental changes linked to the Earth's natural cycles, and those that are human induced. The work is particularly important because it puts Antarctic climate change into context and reveals the impact on the rest of the planet

(http://www.scar.org/publications/occasionals/acce.html)

ii) EBA and diversitas programmes

The BIANZO II project further contributed to the research priorities defined by the Belgian Science Policy call for proposals, in particular to the priorities set up by DIVERSITAS and the SCAR EBA programme.

Among the five fundamental research themes of DIVERSITAS, BIANZO II contributed to theme 1 (origin, maintenance and change of biodiversity) by the results of work package FOREBIO. The work package DYNABIO focused on theme 2 (role of biodiversity in ecosystem functioning) and work package NOWBIO addressed the theme 3 (systematics: inventory and classification).

On the other hand, BIANZO II contributed to 4 of the 5 SCAR EBA specific objectives:

Evolutionary history of the Antarctic organisms (NOWBIO: phylogeny and phylogeography of selected taxa, cryptic species,…)

Evolutionary adaptation to the Antarctic environment (DYNABIO: trophic adaptations, ability to cope with change)

Patterns and diversity of organisms, ecosystems and habitats in the Antarctic and controlling processes (NOWBIO: spatial variations, unknown areas,…)

Impact of past, current, and predicted future environmental change on biodiversity, and the consequences for Antarctic marine (terrestrial and limnetic) ecosystem function (FOREBIO: modeling the impact of temperature-related changes)

iii) International Polar Year and Census of Marine Life

The International Polar Year (IPY) is a large scientific programme that focused on the Arctic and the Antarctic and took place from 2007 to 2009. IPY, organized through the International Council for Science (ICSU) and the World Meteorological Organization (WMO), is actually the fourth polar year, following those in 1882-3, 1932-3, and 1957-8. IPY involved over 200 projects, with thousands of scientists from over 60 nations examining a wide range of physical, biological and social research topics. It was also an unprecedented opportunity to promote polar research to a wider audience and to bring the effect of climate change in polar regions under political attention.

BIANZO II contributed to the International Polar Year (2007-2008) as IPY activity 391. The project was also integrated in the "Census of Antarctic Marine Life" (CAML, 2005-2010), an IPY core project. The CAML is a five-year project focusing the attention of the public on the ice-bound oceans of Antarctica. Its objective is to study the evolution of life in Antarctic waters, to determine how this has influenced the diversity of the present biota, and to use these observations to predict how it might respond to future change. We were invited and participated in several workshops organized by CAML (Rio De Janeiro, November 2009; Wilhelmshaven May 2010) were we contributed with the BIANZO consortium to a synthesis paper (Kaiser *et al.*, in prep.)

iv) Data management

A special effort is devoted to make the results and data generated by the project widely available by contributing to the Global Biodiversity Information Facility (GBIF), notably *via* the Belgian Biodiversity Platform and its Antarctic component SCAR-MarBIN. In a context of global environmental change and alarming loss of biodiversity, the need to develop the biodiversity knowledge over the world was strongly emphasized by the Convention on Biological Diversity (CBD). However, the CBD provisions are not directly applicable to the Antarctic Treaty region as they concern only sovereign territories. Many of the CBD elements are already implicitly included in the Antarctic Treaty instruments, but the provisions for a systematic inventory of biodiversity, and for managing and disseminating the biodiversity information ("clearing house mechanism") among others remain to be fully implemented

b) Recommendations in the framework of policy support

The ACCE report provides clear evidence for warming of the Southern Ocean which is causing changes in the ecosystem. The BIANZO consortium illustrated the potentially high sensitivity of several marine taxa which are major components of the benthic ecosystem to climate related changes such as changes in food supply (Ingels *et al.*,2010; Pasotti *et al.,* submitted), ice shelf collapse (Raes *et al.,*2010; Hauquier *et a.,* accepted), seawater acidification (Colao (check name of ana *et al*) and temperature rise (Raes *et a.,* in prep). By means of sensitivity tables based on what we know by research and a literature review for each of the taxa at different levels of biological organization (from populations to communities or habitats) we illustrated on one hand the high sensitivity for specific climate related changes in the Antarctic environment, but on the other hand we also identified major gaps in our knowledge (Ingels *et al,* conditionally accepted). Furthermore molecular approaches showed the high cryptic biodiversity present in many of the Antarctic taxa (Havermans et al., in press, 2010), illustrating that what we know on biodiversity so far is only the tip of the iceberg. Since the climate-induced shift in the food regime leads to a decrease in the rich Antarctic seabed biodiversity, we are losing biodiversity already of which we never will know its characteristics or its importance.

Therefore our **major recommendation** for present and future policy is to strengthen at national and international level the need for a global reduction of CO_2 emissions in order to slow down climate change. Since the start of negotiations on the Kyoto Protocol, the Belgian authorities have taken in general a favourable position towards an ambitious climate change regime, both at international and European level. The Belgian position largely results from the clear awareness that a global threat calls for a global solution. However for several aspects (e.g. transport, renewable energy) the actions of Belgian authorities are maybe still too modest, considering the speed and the size of impact of rapid climate change in the Antarctic.

Knowing that loss of ice from the West Antarctic ice sheet will not only impact Antarctic ecosystems, but that it is likely to contribute some tens of centimetres to global sea level by 2100, policy makers need to increase the pressure on the international community to initiate more effective global scale actions.

We further identified three crucial future research initiatives, mainly in the context of climate change and framed in programmed, international priorities of Antarctic research. These initiatives were based on the results of the BIANZOII project and inspired by the recommendation of the ACCE report.

I. Biodiversity research

Fundamentally important baseline biodiversity and biogeographic survey data are still lacking across most of the continent and parts of the surrounding Southern Ocean.Those data and systematic and robust monitoring programmes across a network of representative locations are required to allow anything other than the current *ad hoc* and serendipitous approach to identifying biological responses to any aspect of environmental change in Antarctica. Without a baseline biodiversity survey across much of the continent and Southern Ocean, objective documentation of future biological change and assessment of impacts will be impossible. Also more data on the marine biota are required from especially poorly studied areas like the Amundsen Sea, as the basis for the simulation of the impact of a warming ocean on marine biodiversity. While the study of this diversity has an importance of its own, a sufficient level of knowledge of the diversity (both morphological and molecular) of the present taxa is an inescapable prerequisite for any descriptive, analytical or predictive environmental study.

II. Species and community response to change

More evidence should be sought for the possible effects of change in ocean acidification in Southern Ocean organisms. Also shifts in primary production and their impact on the marine food web should be further investigated. Individual and species level responses (including resilience/resistance) to environmental variability and change require integration across communities, trophic webs and ecosystems. Continued long-term and large-scale observations of functional and structural changes in ecosystems are essential to assess the sensitivity of ecological key species and to ground-truth predictive models

III Modelling climate change effects

Advanced integrative and spatially explicit ecosystem modelling is needed to predict the future of the marine ecosystem. Such an approach demands widespread samples of ecological key species that are representative for ecological sub-systems, such as plankton, benthos or apex predators and long-term measurements of ecological key processes such as the response to acidification, warming and changes in ice cover and food regime.

5) DISSEMINATION AND VALORISATION

a) Follow-up committee

The follow-up committee consists of a heterogeneous group of people from different Belgian and European institutes. The group includes representatives of the scientific community (Prof. Dr. A. Brandt, Prof. Dr. A. Gooday, Prof. Dr. F. Dehairs), but also the coordinator of the Belgian Biodiversity Platform (Dr. H. Segers), the SCAR-MarBIN Scientific Coordinator (Dr. B. Danis), a representative of the department of *Economy*, Science and Innovation of the Flemish government (Dr. R. Herman) and a representative of the media (Dr. G. Chapelle). Each from a different background, they have provided constructive remarks, criticisms and valuable input. In addition, Prof. A. Gooday and Prof. A. Brandt committed to contribute to the review paper on climate change with their expertise on Antarctic Foraminifera and Isopoda, respectively. The follow-up committee was invited on a regular base and feedback was given on our progress and the next steps to be taken in order to achieve the project objectives.

b) Scientific and general outreach activities

Scientific communication. During the project a multitude of oral and poster presentations have been given on national and international conferences and meetings. An exhaustive list of these is presented below. The numerous contributions by different members of the participating institutes have enabled successful scientific outreach and have led to productive discussions with scientists and fruitful collaborations, and invitations to join in workshops and meetings worldwide. BIANZO has been recognised by many Antarctic scientists worldwide as an exciting project with important objectives, producing relevant results for a wide spectrum of biological/ecological scientists.

Communication with general public. During the course of the project many initiatives have been undertaken to engage in informing the general public. Invitations by external institutes and/or organisations to present our science to the general public have been gladly accepted and has resulted in numerous contributions.

The ANT-XXIII/8 expedition with the RV Polarstern to the Larsen A and B regions attracted a lot of media attention. The work on meiofauna (UGent) was featured in articles in De Morgen (27/02/2007) and Het Nieuwsblad (27/02/2007). The Ghent University group also contributed to the section "Op Expeditie" of the Dutch magazine Natuur, Wetenschap & Techniek (July-August 2007). The IRScNB-KBIN group was featured in numerous press articles (*e.g.* Le Soir (26/02/2007), Het Laatste Nieuws (27/02/2007), La Dernière Heure (28/02/2007), Het Nieuwsblad (03/03/2007). A radio

interview was given by H. Robert to RTBF directly from the Polarstern. A sequence on the RTBF TV Journal was also devoted to the results of the Larsen expedition. The work of the ULB group was presented in an article in "Le Soir" (December 20th, 2006).

The publication in Nature (Brandt *et al.*, 2007), with co-authors from the Ghent University group and IRScNB-KBIN, resulted in articles in all Flemish newspapers, a radio interview, an article on the web page of the BBC and a short contribution in the VTM news.

Photographs by Jeroen Ingels (UGent) were shown during the Nacht van de Wetenschap (VUB, 2007). The UGent group is also consulting with the KINA museum in Gent to organise an exhibition on their Antarctic research.

Prof. Vanreusel talked about the life on board of Polarstern at the exhibition on the Belgian Princess Elisabeth Station at Tour & Taxis (Brussels, September 8th 2007; Twee maanden lang op een ijsbreker op zoek naar leven in de Antarctische diepzee).

Two RTBF broadcasts of "Semence de Curieux" were devoted to Antarctic marine biodiversity (interview C. De Broyer, IRScNB-KBIN, March/April 2007). Another interview concerning bioregionalisation of the Southern Ocean appeared on the IPF SciencePoles website (C. De Broyer, October 2007)

The work on Antarctic echinoids was presented to the general public at the Science en fête (CNRS (Centre National de la Recherche Scientifique) and uB; October 13th - October 14th, 2007) by posters (Inventaire des oursins antarctiques, de Bruxelles à Google Earth; Les "autobus" de la mer-études d'oursins antarctiques). A movie of ca. 6' was made by De Marchelier & David (2007) for Mission Culture Scientifique (uB): Les oursins de l' Antarctique. This movie was shown at the Nuit des Chercheurs (uB; September 28th, 2007). Our partner at uB also featured in an article in the French newspaper Le Bien Public (La Recherche en Bourgogne: Les oursins antarctiques sont-ils condamnés à disparaître?; June 24th, 2007) and in the CNRS International magazine (Spotlight on the poles; n°6 April 2007, 18-23).

c) List of outreach activities

Outreach activities are listed per partner and in chronological order

i) UGent

Contribution on Antarctic marine biodiversity research in 3-monthly journal on popular sciences for a general public (MENS ,Nr 77 Oct, Nov, Dec, 2010).

Lecture/presentation by Francesca Pasotti to secondary school classes on science in Antarctica organised by the International Polar Foundation (IPF, Educapoles) in December 2010

Bezerra TN, Pape E, Hauquier F, Ingels J, Vanreusel A (2010) New genus of the family Ethmolaimidae (Nematoda: Chromadorida), found at Gulf of Cadiz and Antarctica. Fourteenth International Meiofauna Conference, Aula Academica, Ghent, 11-16 July 2010. Book of Abstracts, oral presentation 90

Veit-Köhler G, Guilini K, Sachs O, Sauter E, Peeken I (2010) Antarctic deep-sea meiofauna and bacteria react to deposition of particulate organic matter after phytoplankton bloom Fourteenth International Meiofauna Conference, Aula Academica, Ghent, 11-16 July 2010. Book of Abstracts, poster presentation 201

Veit-Köhler G, Guilini K, Würzberg L, Mayr C (2010) Geographical and oceanographical patterns of meiofauna stable isotope signatures in the deep Southern Ocean. Fourteenth International Meiofauna Conference, Aula Academica, Ghent, 11-16 July 2010. Book of Abstracts, oral presentation 79

Guilini K, Vanreusel A (2010) ANDEEP-SYSTCO (ANTarctic benthic DEEP-sea biodiversity: colonisation history and recent community patterns – SYSTem COupling), from census to ecosystem functioning. Belgian International Polar Year Symposium, Royal Academy for Belgian Sciences and Arts, Brussels, Belgium, 26th May 2010. Oral presentation

Hauquier F, Ingels J, Vanreusel A (2010) Characterisation of the nematode community of a low-activity cold seep in the recently ice-free Larsen B area, Eastern Antarctic Peninsula, in: (2010). Seventeenth Benelux Congress of Zoology (BCZ 2010) - 'Classical Biology in Modern Times' October 22-23, 2010, Ghent, Belgium: Abstract book. pp. 68.

Ingels J, Vanreusel A, Martin P, De Ridder C, David B, Guilini K, Pasotti F, Hauquier F, d'Udekem d'Acoz C, Robert H, De Broyer C, Havermans C, Dubois P, Catarino AI, Pierrat B, Saucede S (2010) BIANZO II – Biodiversity of three representative groups of the Antarctic zoobenthos – Coping with change. Belgian International Polar Year Symposium, Royal Academy for Belgian Sciences and Arts, Brussels, Belgium, 26th May 2010. Oral presentation.

Pasotti F, Raes M, Vanreusel A, De Troch M (2010) Investigating the responses of meiofauna in Potter Cove (King George Island, West Antarctic Peninsula) from a climate change perspective: an experimental approach. Fourteenth International Meiofauna Conference, Aula Academica, Ghent, 11-16 July 2010. Book of Abstracts, oral presentation 62

Pasotti F, Vanreusel A (2010) ClicOpen and IMCOAST projects. Belgian International Polar Year Symposium, Royal Academy for Belgian Sciences and Arts, Brussels, Belgium, 26th May 2010. Poster presentation

Pasotti F, Vanreusel A, De Troch M (2010) Investigating the responses of meiofauna in Potter Cove (King George Island, West antarctic Peninsula) from a climate change perspective: an experimental approach. SCAR XXXI - 4th Open Science Conference – Antarctica: Witness to the past and guide to the future, CD-ROM. Abstract number 588

Vanreusel A, Raes M, Hauquier F, Ingels J (2010) Response of nematode communities after large-scale ice-shelf collapse. SCAR XXXI - 4th Open

Science Conference – Antarctica: Witness to the past and guide to the future, CD-ROM. Abstract number 791

Ingels J, A Vanreusel, P Martin, C De Ridder, B David, K Guilini, F Pasotti, F Hauquier, C d'Udekem d'Acoz, H Robert, C Havermans, P Dubois, AI Catarino, B Pierrat, T Saucede (2010) Assessements of BIANZO II– Coping with change. CAML Workshop "Southern Ocean benthic biodiversity and biogeography: What are the key spatial patterns in macro-and megabenthos and what drives them? German Centre of Marine Biodiversity Research (DZMB) in Wilhelmshaven (Germany) 21-25/3/2010, oral presentation

Bezerra T & A. Vanreusel (2009) Biodiversity of Nematoda at the Southern Ocean. Oral presentation hold during a symposium on "Antarctic-South American Interactions in the Marine Environment (ASAI)", organised by the South American Consortium for the Census of Antarctic Marine Life (LA CAML) in Rio de Janeiro, Brazil 5-6/11/2009

Participation by TN Bezerra (UGent) in Workshop "Antarctic-South American Interactions in the Marine Environment (ASAI)". organised by the South American Consortium for the Census of Antarctic Marine Life (LA CAML) in Rio de Janeiro, Brazil on 3-4/11/2009

Active participation in a workshop on the response of marine and terrestrial biota to climate change along the Western Antarctic Peninsula, Mądralin, Poland, 24 – 29/8/2009 - organised in the framework of ClicOpen (Impact of CLImate induced glacial melting on marine and terrestrial COastal communities on a gradient along the Western Antarctic PENinsula)

Organisation and active participation of a CoML (Comarge) workshop on Large-scale patterns in bathyal free-living nematodes at Ghent University (28/01-01/02, 2008).

Vanreusel A (2007) Twee maanden lang op een ijsbreker op zoek naar leven in de Antarctische diepzee. Oral communication at the exhibition on the Belgian Princess Elisabeth Station at Tour & Taxis (Brussels, 8/9/2007)

Raes M, Guilini K, Vanreusel A (2007) Meiofauna at the Poles - Coping with Change. Poster presentation at Thirteenth International Meiofauna Conference, Recife, Brazil (29/7-3/8/2007). Abstract book Poster p. 99

Raes M, Guilini K, Vanreusel A (2007) Meiofauna at the Poles - Coping with Change. Poster presentation at Biodiversity and Climate Change Conference, Brussels, Belgium (21-22/5/2007). Abstract book p. 47-48

ii) IRScNB-KBIN

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin, P (2010) DNA barcoding reveals both cryptic as true circumpolar species in Antarctic Lysianassoidea (Amphipoda). Poster presentation (CH) at the XIVth International Colloquium on Amphipoda, 13-18/09/2010, Seville, Spain

Havermans C (2010). Incongruence between molecular phylogeny and morphological taxonomy: A case study of Antarctic lysianassoids. Poster presentation (CH) at the XIVth International Colloquium on Amphipoda, 13-18/09/2010, Seville, Spain

Hendrycks E, De Broyer C, Havermans C (2010) Preliminary results of baited trap amphipod collections from the DIVA-3 cruise. XIVth International Colloquium on Amphipoda, Seville, Spain, 13-18/09/2010

d'Udekem d'Acoz C (2010) Contribution to the knowledge of European Liljeborgiidae, with systematic remarks on the family. Poster (CUA) presentation at XIV International Colloquium on Amphipoda, University of Sevilla, 13-18/9/2010

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin P (2010). DNA barcoding reveals both cryptic as true circumpolar species in Antarctic Lysianassoidea (Amphipoda). Poster Presentation (CH) at the International Polar Year Oslo Science Conference, 8-12/06/2010, Oslo, Norway

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin P, (2009) DNA barcoding reveals both cryptic as true circumpolar species in Antarctic Lysianassoidea (Amphipoda). Poster presentation (CH) at the Belgian International Polar Year Symposium, 26/05/2010, Brussels, Belgium

Ingels J, A Vanreusel, P Martin, C De Ridder, B David, K Guilini, F Pasotti, F Hauquier, C d'Udekem d'Acoz, H Robert, C Havermans, P Dubois, AI Catarino, B Pierrat, T Saucede (2010) BIANZO II – Biodiversity of three representative groups of the Antarctic zoobenthos – Coping with change. International Polar Year Symposium 26 May 2010, Belgian National Committee on Antarctic Research, Académie des Sciences, Bruxelles

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin P (2010) DNA barcoding reveals both cryptic as true circumpolar species in Antarctic Lysianassoidea (Amphipoda). Participation and Poster Presentation (CH) at the workshop on "Southern Ocean Benthic Biodiversity Patterns" organized by CAML (Census of the Antarctic Marine Life), 21-25/03/2010, Wilhelmshaven, Germany.

Ingels J, A Vanreusel, P Martin, C De Ridder, B David, K Guilini, F Pasotti, F Hauquier, C d'Udekem d'Acoz, H Robert, C Havermans, P Dubois, AI Catarino, B Pierrat, T Saucede (2010) Assessements of BIANZO II– Coping with change. Workshop "Southern Ocean benthic biodiversity and biogeography: What are the key spatial patterns in macro-and megabenthos and what drives them? 21-25/3/2010, German Centre of Marine Biodiversity Research (DZMB) in Wilhelmshaven (Germany)

Udekem d'Acoz, C.d'., Robert, H., Martin P., 2009. Distribution and phylogeographic patterns of the genus *Liljeborgia* (Crustacea, Amphipoda, Liljeborgiidae) in Polar Seas. Poster presentation (CUA) at CAML Final Symposium, Census of Antarctic Marine Life: diversity in Southern Ocean ecosystems. Università degli Studi di Genoa, Italy

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin P (2009) Incongruence between molecular phylogeny and morphological taxonomy: A case study of Antarctic lysianassoids. Oral presentation (CH) at the EDIT Young Taxonomist Symposium, 15-17/12/2009

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin P (2009) DNA barcoding reveals both cryptic as true circumpolar species in Antarctic

Lysianassoidea (Amphipoda). Oral presentation (CH) at the 10th VLIZ Young Scientists' Day, 27/11/2009, Oostende, Belgium

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin P (2009) DNA barcoding reveals cryptic diversity in Antarctic Lysianassoidea (Amphipoda)". Oral presentation (CH) at the Xth SCAR International Biology Symposium, 26-31/07/2009. (Student/Early Career Award for the communication)

De Broyer C, Danis B (2009) How many species in the Southern Ocean? CAML final Symposium, Census of Antarctic Marine Life: diversity and change in Southern Ocean ecosystems, Genoa, Italy, 18-20/5/2009

Havermans C, Zoltán Tamás N, Sonet G, De Broyer C, Martin P (2009) DNA barcoding reveals cryptic diversity in Anatrctic species of Orchomene sensu lato (Crustacea: Amphipoda: Lysianassoidea). CAML final Symposium, Census of Antarctic Marine Life: diversity and change in Southern Ocean ecosystems, Genoa, Italy, 18-20/5/2009

d'Udekem d'Acoz C, Robert H, Martin P (2009) Distribution and phylogeographic patterns of the genus Liljeborgia (Crustacea, Amphipoda, Liljeborgiidae) in Polar Seas. CAML final Symposium, Census of Antarctic Marine Life: diversity and change in Southern Ocean ecosystems, Genoa, Italy, 18-20/5/2009

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9) ANNEX 1: COPY OF THE PUBLICATIONS

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10) ANNEX 2: MINUTES OF THE FOLLOW-UP COMMITTEE MEETINGS

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