

Challenges of deep-sea biodiversity assessments in the Southern Ocean

Angelika Brandt^{1*}, Huw Griffiths², Julian Gutt³, Katrin Linse², Stefano Schiaparelli⁴, Tosca Ballerini^{5,6}, Bruno Danis⁷ & Olaf Pfannkuche⁸

¹ Zoological Institute and Zoological Museum, Biocenter Grindel University of Hamburg, Martin-Luther-King-Platz 3, Hamburg D-20146, Germany;

² British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK;

³ Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Alten Hafen 26, Bremerhaven D-27568, Germany;

⁴ Di.S.T.A.V., Università di Genova, C.so Europa 26, I-16132, Genova, Italy & Italian National Antarctic Museum (MNA), Viale Benedetto XV N° 5, Genova I-16132, Italy;

⁵ Mediterranean Institute of Oceanography (MIO), Aix-Marseille Université, Université de Toulon, CNRS/INSU, IRD, MIO, UM 110, 13288, Marseille, Cedex 09, France;

⁶ Université de Toulon, Aix-Marseille Université, CNRS/INSU, IRD, MIO, UM 110, La Garde Cedex 83957, France;

⁷ Marine Biology Laboratory, Université Libre de Bruxelles, 50, Avenue FD Roosevelt, Brussels B-1050, Belgium;

⁸ GEOMAR, Helmholtz-Zentrum für Ozeanforschung Kiel, Wischhofstr. 1-3, Geb. 14, Kiel 24148, Germany

Received 1 April 2014; accepted 28 July 2014

Abstract Despite recent progress in deep-sea biodiversity assessments in the Southern Ocean (SO), there remain gaps in our knowledge that hamper efficient deep-sea monitoring in times of rapid climate change. These include geographical sampling bias, depth and size-dependent faunal gaps in biology, ecology, distribution, and phylogeography, and the evolution of SO species. The phenomena of species patchiness and rarity are still not well understood, possibly because of our limited understanding of physiological adaptations and thresholds. Even though some shallow water species have been investigated physiologically, community-scale studies on the effects of multiple stressors related to ongoing environmental change, including temperature rise, ocean acidification, and shifts in deposition of phytoplankton, are completely unknown for deep-sea organisms. Thus, the establishment of long-term and coordinated monitoring programs, such as those rapidly growing under the umbrella of the Southern Ocean Observing System (SOOS) or the Deep Ocean Observing Strategy (DOOS), may represent unique tools for measuring the status and trends of deep-sea and SO ecosystems.

Keywords biodiversity assessment, Southern Ocean, deep sea, gaps, limits, monitoring

Citation: Brandt A, Griffiths H, Gutt J, et al. Challenges of deep-sea biodiversity assessments in the Southern Ocean. *Adv Polar Sci*, 2014, 25: 204-212, doi: 10.13679/j.advps.2014.3.00204

1 Introduction

More than 50% of the Earth's surface lies below 3 000 m water depth^[1]. In the past decade, the question of how

many species there are on Earth and in the Ocean^[2] has been raised repeatedly. Fueled by the knowledge of the unprecedented loss of species on Earth^[3], some authors think that the Earth might approach a state shift in its biosphere, potentially due to anthropogenic influences^[4]. Some authors have highlighted the importance of taxonomy in uncovering changes in faunal composition, such as those linked to global

* Corresponding author (email: Abrandt@uni-hamburg.de)

change^[5]. The biodiversity of the SO is high, especially in the deep sea, and reflects changes in climate, oceanographic, and tectonics, both in the past and more recently^[6-8]. Authors have tried to understand the origin and evolution of SO taxa, in the context of shifts in the SO between warm and cold periods in the Pleistocene and Holocene^[7,9-11]. There is strong molecular evidence that some shelf (or shelf-inhabiting) taxa survived glacial cycles and further evolved in the deep SO^[8,12-13], and that modern deep-sea fauna is ancient^[14-15]. Conversely, some SO species have exhibited polar emergence^[9,16]. A number of sound biogeographic analyses have been published in the last decade under the umbrella of the Census of the Antarctic Marine Life (CAML, <http://www.coml.org/projects/census-antarctic-marine-life-caml>), in an attempt to understand the biological diversity of this unique and poorly understood environment. These studies contribute to a better understanding of how varying taxa survive in the cold SO surrounding Antarctica^[17-21]. Despite recent successful expeditions, information on macrobenthic community diversity and habitat heterogeneity in the deep sea is still too scarce or heterogeneous for a preliminary comparison with corresponding data from shelf habitats^[22-23]. Even if efforts have been made recently towards the online publication of raw biodiversity data, by means of dedicated information networks^[24], it is extremely important that the scientific community continues to mobilize knowledge in an open fashion. Some authors^[25] have stressed the rapid decline of research data with time, gauged from the relationship between the age of scientific publications and the odds of a data set being extant. A recent discussion^[26] showed that, in the long term, research data cannot be reliably preserved by individual researchers, and further demonstrates the urgent need for policies mandating data sharing via public archives.

The increased knowledge of SO biodiversity, differences between SO shelf and deep-sea communities, and vulnerability due to climate change has been reviewed^[27], reflecting the enormous international effort of CAML. However, there are still limitations in the SO deep-sea biodiversity assessments, and some challenges are discussed here. It will be necessary to overcome some of these challenges and design more appropriate sampling strategies to monitor changes in the deep SO, in times of rapid climate change.

The present study does not aim to present a review; its purpose is to outline the gaps in SO deep-sea biodiversity research that currently complicate SO deep-sea monitoring.

2 Discussion of challenges

The Census of the Marine Life (CoML, <http://www.coml.org/>) represents a decade of discovery, whereby a collective effort was made to assess the diversity, distribution and abundance of marine life. One of the flagship projects of the CoML was the 5-year CAML, which investigated the distribution and abundance of SO marine biodiversity^[6,27-29]. This project also analyzed how SO biota evolved, how single

species were affected by climate change, and how potential environmental changes in the future could alter ecosystem services^[30].

This project, together with CeDAMar (Census of the Diversity of Abyssal Marine Life, <http://www.cedamar.org/de/>), explored the biodiversity of several previously unknown bathyal and abyssal deep-sea ecosystems. Some of these results, compiled as part of a multinational and multidisciplinary project working under the CoML umbrella, are already published^[6,31-33].

Raw data on the occurrence and distribution of marine species are available in global-scale information systems, such as OBIS (Ocean Biogeographic Information Facility, <http://www.iobis.org/>), or GBIF (Global Biodiversity Information System, <http://www.gbif.org/>). Within CAML, over 18 000 SO taxa were identified and included in a taxonomic register. This register is part of the biodiversity information system, Antarctic Marine Life: the SCAR-Marine Biodiversity Information Network (SCAR-MarBIN; www.scarmarbin.be), now searchable throughout the new Antarctic Biodiversity Information Facility (ANTABIF) project (www.biodiversity.aq), which plays the role of an Antarctic data node for both OBIS and GBIF. More than 700 species new to science were discovered^[6-7,34], more than 3 000 species barcoded^[35], and a SO Plankton Atlas was produced^[36]. Moreover, a new Biogeographic Atlas of the Southern Ocean is released in August^[34] (<http://atlas.biodiversity.aq>). Unknown habitats were explored for the first time, including mounts^[37], the SO deep sea^[32], the Amundsen Sea^[15], life underneath the collapsed Larsen A and B ice shelves^[38-39], hydrothermal vents on the East Scotia Ridge^[40], and seep ecosystems west of the Antarctic Peninsula^[41-42]. The lasting legacy of CAML is as a unique benchmark for monitoring change in the SO and many scientists will work for years on the biodiversity, biogeography and conservation aspects for multiple marine taxa and habitats. The development of molecular techniques is an advance that promises to revolutionize knowledge on the diversity and biogeography of the Antarctic marine biota^[43-45]. CAML supported these projects through a large DNA barcoding effort^[35]. Molecular techniques are rapidly evolving, becoming ever more sophisticated and with higher resolution^[46], allowing the recognition of a wealth of cryptic species within what were once regarded as single widely distributed species, such as the isopod *Glyptonotus antarcticus* Eights, 1852, the nudibranch *Doris kerguelensis* (Bergh, 1884) and the pycnogonid *Colossendeis megalonyx* Hoek, 1881^[47-49]. Not only does this work increase the number of known species (i.e. the richness) in the SO, it may also dramatically change biogeographic patterns, typically reducing the known range size or depth range due to the split of one into several species^[50], hence affecting our interpretation of the evolutionary history of the fauna.

Despite CAML's recent progress, there remain some problems, gaps in knowledge and unanswered questions^[27,51]. This is partly due to the high costs and long wire times for the deep-sea deployment of trawled gear or corers. These



Figure 1 Typical deep-sea gear used for data acquisition: (1) profiling drifter, (2) manned bathyscaph “Jago”, (3) towed tracer injector, (4) glider swarm, (5) ROV “Kiel 6000”, (6) oceanographic anchorage with acoustic linkage to landers and satellites, (7) AUV “Abyss”, (8) Geomar modular lander, and (9) mini-lander with OBS (ocean bottom seismometer).

time constraints could be overcome by the development of efficient and time-saving autonomous deep-sea sediment and organism samplers. Despite great advancements in deep-ocean technology in the past three decades (especially with regard to obtaining physical environmental data, Figure 1), autonomous deep-sea samplers and ocean observatories are still missing in the deep SO. These would allow sampling of sufficient seafloor for the investigation of benthic deep-sea organisms, and save ship-time.

Rapid climate change drives the scientific community to identify requirements for long-term monitoring, such as: (i) the selection of essential Ecosystem Ocean Variables (eEOVs) to be measured and monitored; (ii) the geographic areas on which to focus; and (iii) the technologies and standard research techniques for the development of an international strategy for the SO and global deep-ocean observatories. Discussions on the selection of eEOVs have just started and will likely produce guidelines for new and standardized sampling strategies in the near future^[52].

2.1 Operations at different temporal scales (from sea-ice to the benthic realm)

Ecological studies in the SO are often difficult to compare, as studies typically operate at different spatial and temporal scales (at different geographic areas and in different seasons). Ecological processes, like pelagic productivity at the surface of the ocean, operate at short time scales from hours and days to months, whereas those in the deep sea usually operate at timescales from months to thousands of years. For example, approximately 1 cm of sediment is deposited in 1 000 years at abyssal depths^[53]. Evolutionary developments, e.g. those determined by long-term climate changes, are most effective at periods of thousands of years to many millions of years^[54], e.g. the processes that occurred in the Tertiary and led to the establishment of the psychrosphere and polar oceans^[55].

Conversely, investigations of benthopelagic coupling processes have revealed that a pulse of freshly produced natural organic matter can reach the seafloor within days^[56], leading to a response of the benthic community in terms of an increase of ATP (adenosine-triphosphate, a proxy for biological activity) in less than 8 d^[57].

2.2 Sampling bias with geography

In the recent decade, international initiatives and collaborations have increased our knowledge of SO biodiversity patterns and our understanding of which processes are most important in driving these patterns^[27,56,58-59]. These projects include ANDEEP (ANtartic benthic DEEP-sea biodiversity, colonization history and recent community patterns; <http://www.cedamar.org/en/section1/repository/andeeep.html>), SYSTCO (SYSTEM COupling, <http://www.polarjahr.de/ANDEEP-SYSTCO.241+M52087573ab0.0.html>), BIOPEARL (Biodiversity Dynamics: Phylogeography, Evolution

and Radiation of Life; http://www.antarctica.ac.uk/bas_research/our_research/previous_research/gsac/bioflame.php), BIANZO (Biodiversity of three representative groups of Antarctic Zoobenthos; <http://www.belspo.be/belspo/fedra/proj.asp?!=de&COD=SD/BA/02A>), and CEAMARC (Collaborative East Antarctic Marine Census; http://www.ga.gov.au/image_cache/GA15520.8pdf)^[6,15,58-62].

Poorly investigated areas, such as the Amundsen Sea, Bouvetøya, or bathyal and abyssal areas of the Weddell, Scotia and Ross seas, were recently investigated by international expeditions^[6,15,38,62-64]. Records of macro- and megafaunal richness for several Antarctic locations revealed greater marine richness than anticipated^[65]. However, faunistic comparisons of different ocean realms are increasingly biased with depth. At larger spatial scales, first estimates of SO species richness on the continental shelf^[66-67] and in the deep sea^[6] have been published. Other areas that are understudied include deep-water hard rock habitats, e.g. canyon and trough walls, volcanic lava fields and rocky seamounts, as they are difficult or impossible to sample with trawling and coring gear and require remotely operating vehicles with sampling appliances. Recent expeditions of the ChEsSo (Chemosynthetically driven ecosystems south of the Polar Front: biogeography and ecology, <http://www.noc.soton.ac.uk/chess/science/chesso.html>) project explored hard rock habitats along the East Scotia Ridge and in the Bransfield Strait by a remotely operating vehicle (ROV) and underwater camera system. These expeditions highlighted not only areas of hydrothermal fluid flows^[40,68], including some associated with vent-endemic fauna^[40,69-70], but also recorded species on these hard rock habitats, such as the carnivorous sponge *Abyssocladia*, a giant actinostolid anthozoan^[40], the newly described shrimp *Eualus amandae*^[71] and stalked carnivorous ascidians (Linse, personal observation), that had not been previously reported in the SO.

Additional knowledge gaps are due to bias in the sampling gear. Different gears are regarded to be either quantitative or qualitative (i.e. corers vs. trawled gear). Because of a lack of standardized procedures, different working groups and expeditions have used a variety of different mesh sizes (not all scientists use fine mesh-sized gear and sieves), protocols or fixation methods^[72] and could not always identify, count or weigh all or comparable sets of taxonomic groups. Singular or replicate deployments at stations, as well as general sampling standards, often differ between research groups and might weaken statistics associated with faunistic or zoogeographic comparisons. The use of fine-mesh may dramatically increase the number of new records in purportedly well-known shelf areas^[73], which is likely the case for the deep sea. Sampling effort with geography is illustrated in Figure 2.

2.3 Sampling bias with depth

Most SO samples are obtained from the continental shelves; this area and its biology is the best known in the

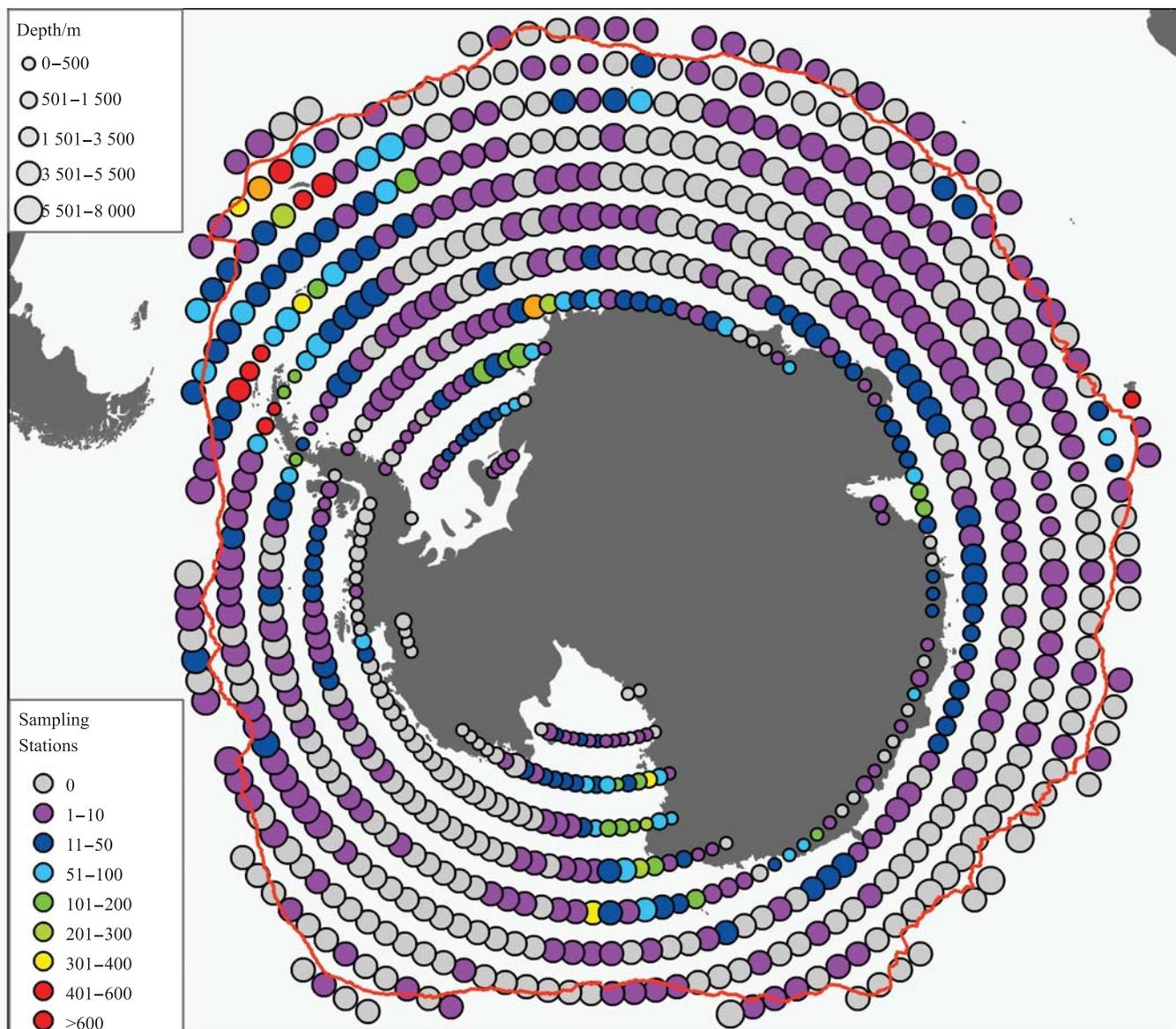


Figure 2 Numbers of benthic invertebrate sampling stations in the Southern Ocean. The circles represent the midpoint of each grid cell, which comprises 3 degrees latitude by 3 degrees longitude. Colors indicate the number of distinct latitude and longitude combinations (sites) of benthic records. The size of each circle represents the mean depth of the seafloor within that grid cell. The red line indicates the mean position of the Polar Front. Data available from ANTABIF^[85].

SO. However, with increasing depth, our knowledge of the SO fauna decreases because of the small amount of samples available at bathyal and abyssal depths, linked to logistic constraints and cost-intensive long wire times^[6,66]. In some areas, like the deep shelf and upper slope areas, sample deployments have been recently complemented by ROVs and towed camera systems, which provided valuable additional information on benthic species and communities, especially at larger scales. These studies highlighted new types of benthic communities^[37-38]. The standardized usage of gear and standardized deployments in benthic studies have led to new SO discoveries regarding deep-sea endemism and biogeography. High biodiversity was reported in all size classes, even down to abyssal depths^[6-7], especially when

surveys used trawled gear equipped with small mesh sizes, like epibenthic sledges and trawls with small mesh-sized inner nets^[7,74-75]. Sampling gear for deployment at varying depths is illustrated in Figure 1.

2.4 Body size

Our knowledge of the biology, distribution, zoogeography, and evolution of species of all animal phyla is size dependent. The smaller the species (nano-, meiobenthos, <1 mm), the less we know about them. For example, nematodes are usually known only to genus level because of the lack of taxonomists and the problems of species' discrimination^[7]. This knowledge gap also includes a lack of information

on species' life histories and their diets; our knowledge of the SO food web is mainly based on diets of large pelagic predators, and thus it is largely unknown what benthic bottom dwellers feed on. This might be due to scientific effort and the concentration of benthos sampling on continental shelves. Exceptions to this trend are some well-known tiny species of Foraminifera, as detailed knowledge on these contributes to climate reconstructions^[76-77]. In contrast, large sponges are still very difficult to identify and discriminate, despite their role in benthic habitat architecture.

Another immense gap in our knowledge of SO biodiversity is related to prokaryotes. Even if huge quantities of data are generated by new next-generation sequencing technologies (such as 454, Illumina, Ion Torrent), our understanding of potential patterns in bacterial diversity in the Oceans is very much in its infancy. Specific efforts need to address this gap, by adapting information systems to this domain of life. The Microbial Antarctic Resource System is such an initiative, which is intended to progressively fill this knowledge gap^[78].

2.5 Patchiness and rarity

In many marine areas (especially in the deep sea), more than 50% of all species occur in samples as singletons (species found with only one individual)^[15,29,79-80]. These low numbers of individuals make it difficult to judge whether the distribution of such species can be explained by patchiness due to ecological drivers such as food availability or, alternatively, by a rather homogeneous distribution in combination with general rarity. Underwater images can help answer this question, because they provide a good documentation of the presence, density and distribution of mega-epifaunal animals. However, small macrofaunal and meiofaunal epi- and almost all endobenthic species are not evaluable on these images.

For example, investigations based on sampling multiple spatial scales across the Weddell and Scotia Sea slope and abyss documented that Isopoda can be rich and abundant on local and regional scales, with their distributions being patchy rather than rare^[6,80].

2.6 New and cryptic species, taxonomy and databases

Sampling in the unknown deep sea of the SO and adjacent deep-sea basins greatly increased the number of known species, especially of isopod crustaceans, most of which were new to science^[6]. First insights into the biotic and abiotic processes shaping and driving SO deep-sea communities^[6,27,80] were provided. However, describing new species is usually time consuming. Furthermore, a lack of scientists trained in taxonomy means that the gap in taxonomic descriptions and the tremendous mismatch between taxonomically described species and recorded morphospecies in many deep-sea areas can complicate the understanding of the biotic response of deep SO organisms to abiotic processes, such as climate

change. For some biological questions, molecular tools have revolutionized morphological approaches in the past few decades. The genetic identification and delineation of cryptic species, which cannot be differentiated morphologically, have challenged taxonomy and biodiversity estimates^[81]. In the past decade, CAML tried to overcome this impediment with the establishment of an SO barcoding project^[35] as well as the establishment of biogeographic databases (such as SCAR-MarBIN and the Register of Antarctic Marine Species [RAMS]), which have become powerful tools for cataloguing species as a solid benchmark against which changes in species composition can be measured.

2.7 Perspectives

The new SCAR (Scientific Committee of Antarctic Research; <http://www.scar.org/>) scientific research projects AntEco (the State of the Antarctic Ecosystem; <http://www.scar.org/researchgroups/progplanning/#AntEco>) and AnT-ERA (Antarctic Thresholds—Ecosystem Resilience and Adaptation, <http://www.scar.org/srp/ant-era>)^[82] will help build on the foundations that CAML provided. These projects also face the urgent and crucial need to improve current sampling devices and international sampling standards, strategies and designs, to overcome scientific gaps and challenges before new biodiversity crises occur^[4].

One priority of the Southern Ocean Observing System (SOOS, <http://www.soos.aq/>) is to assess the design for an efficient, long-term structure for measuring the status and trends of the SO ecosystems; DOOS (Deep Ocean Observing Strategy Overview and Progress; <http://www.indeep-project.org/news/deep-ocean-observing-strategy-overview-and-progress>) aims to cover the global deep-sea area. Filling all the gaps mentioned above through various international initiatives and national programs will result in more and better generalization in deep-sea biology, which is still in its infancy.

This is a challenging goal, especially in the deep SO. The network of monitoring stations should cover areas where climate-induced environmental changes already occur (e.g. at the polar front or west of the Antarctic Peninsula, or where sea-ice extent increases), as well as areas where changes are expected in the next decades and areas that are expected to remain relatively stable (for compilation of information, see reference [83]). Stations should cover different habitats, for example those defined by sediment differences and bottom topography, such as trenches, over-deepened basins, plains, mounts and slopes. Regular sampling could be guaranteed as part of international long-term programmes, and/or monitoring stations should be situated close to regularly sailed routes of research vessels, for example close to Antarctic stations. The latter, however, could again cause sampling bias with geography, as many research stations are situated close together, such as on King George Island. International agreements on joint monitoring strategies might help to overcome this problem and provide new platforms from which changes can be measured.

Organism composition should be analyzed following standardized protocols, including abundances (densities), diversity^[84] and biomass (for megabenthos) as obligatory parameters^[23]. Replicate sampling should be applied covering different spatial scales to obtain maximal representativeness, consider spatial autocorrelation effects and provide a sound basis for spatial and temporal comparisons. Molecular or genetic monitoring should be included to measure the changes that cannot be detected using morphological techniques. The biological sampling should be combined with routine in situ and remote measurements of ecologically relevant physical and chemical variables, such as temperature, salinity, oxygen, sea-ice, pH, sediment characteristics, POC, DOC, nutrients and biological bulk parameters such as primary and secondary production. Mid-term changes in biodiversity need to be identified as well as the drivers of these changes, two questions that had been identified to be of high priority by the 1st SCAR Horizon Scan^[86]. An appropriate timescale and frequency of monitoring has to be negotiated for the detection of changes. Within such a framework, general background knowledge on SO deep-sea biodiversity must continue to increase through consistent area-wide surveys. The results should be permanently made available through existing web platforms that enhance and allow data accessibility and exchange.

Moreover, many scientific questions cannot be solved on the basis of a handful of organisms obtained by means of ROVs or on the basis of seafloor photographs (AUVs) (autonomous underwater vehicles), despite the valuable information they provide on distribution patterns at any spatial scale and in so far inaccessible habitats, e.g. under the sea-ice and ice shelves. Such technology can be seen in Germany, for example, where the research institutes GEOMAR in Kiel and MARUM in Bremen administer and operate a fleet of modern underwater vehicles and landers (Figure 1). However, deep-sea biologists will also have to collaborate with engineers developing robotics (artificial intelligence) to address the urgent need to design innovative, modern autonomous underwater sampling devices for sampling larger amounts of sediment and organisms than ROV technology currently allows.

Acknowledgments These data were presented during the Southern Ocean Observing System Scientific Steering Committee (SOOS–SSC) meeting held in Shanghai in May 2013. SOOS is supported by the Institute for Marine and Antarctic Studies (IMAS, University of Tasmania), which hosts the SOOS International Project Office. The Office is sponsored by numerous international organizations (www.soos.aq/index.php/about-us/sponsors). This is ANDEEP publication # 194.

References

- 1 Witte U, Wenzhöfer F, Sommer S, et al. In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. *Nature*, 2003, 424(6560): 763-766.
- 2 Mora C, Tittensor D P, Adl S, et al. How many species are there on Earth and in the ocean? *Plos Biology*, 2011, 9(8): 1-8.
- 3 May R M. How many species are there on earth? *Science*, 1988, 247(4872): 1441-1449.
- 4 Barnosky A D, Hadly E A, Bascompte J, et al. Approaching a state shift in Earth's biosphere. *Nature*, 2012, 486(7401): 52-58.
- 5 Costello M J, May R M, Stork N E. Can we name Earth's species before they go extinct? *Science*, 2013, 339(6118): 413-416.
- 6 Brandt A, Gooday A J, Brix S B, et al. The Southern Ocean deep-sea: first insights into biodiversity and biogeography. *Nature*, 2007, 447(7142): 307-311.
- 7 Brandt A, De Broyer C, Ebbe B, et al. Southern Ocean deep benthic biodiversity//Rogers A D, Johnston N M, Murphy E J, et al. *Antarctic Ecosystems: An Extreme Environment in a Changing World*. Chichester: Blackwell Publishing Ltd., 2012: 291-334.
- 8 Allcock A L, Strugnell J M. Southern Ocean diversity: new paradigms from molecular ecology. *Trends in Ecology and Evolution*, 2012, 27(9): 520-528.
- 9 Brandt A. Zur Besiedlungsgeschichte des antarktischen Schelfes am Beispiel der Isopoda (Crustacea, Malacostraca). *Ber Polarforsch*, 1991, 98: 1-240.
- 10 Thatje S, Hillenbrand C D, Larter R. On the origin of Antarctic marine benthic community structure. *Trends in Ecology and Evolution*, 2005, 20(10): 534-540.
- 11 Leese F, Agrawal S, Held C. Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. *Naturwissenschaften*, 2010, 97(6): 583-594.
- 12 Raupach M J, Mayer C, Malyutina M, et al. Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. *Proc Roy Soc Lond B*, 2009, 276(1658): 799-808.
- 13 Barco A, Schiaparelli S, Houart R, et al. Cenozoic evolution of Muricidae (Mollusca, Neogastropoda) in the Southern Ocean, with the description of a new subfamily. *Zoologica Scripta*, 2012, 41(6): 596-616.
- 14 Thuy B, Gale A S, Kroh A, et al. Ancient origin of the modern deep-sea fauna. *PLoS One*, 2012, 7(10): 1-11.
- 15 Linse K, Griffiths H J, Barnes D K A, et al. The macro- and megabenthic fauna on the continental shelf of the eastern Amundsen Sea, Antarctica. *Continental Shelf Research*, 2013, 68: 80-90.
- 16 Riehl T, Kaiser S. Conquered from the deep sea? A new deep-sea isopod species from the Antarctic shelf shows pattern of recent colonization. *PLoS One*, 2012, 7(11): 1-24.
- 17 Linse K, Griffiths H J, Barnes D K A, et al. Biodiversity and biogeography of Antarctic and Sub-Antarctic Mollusca. *Deep-Sea Research II*, 2006, 53: 985-1008.
- 18 Griffiths H J. Antarctic marine biodiversity—what do we know about the distribution of life in the Southern Ocean? *PLoS One*, 2010, 5(8): e11683.
- 19 Griffiths H J, Whittle R J, Roberts S J, et al. Antarctic crabs: Invasion or endurance? *PLoS One*, 2013, 8(7): e66981.
- 20 Downey R V, Griffiths H J, Linse K, et al. Diversity and distribution patterns in high Southern Latitude sponges. *PLoS One*, 2012, 7(7): 1-16.
- 21 Pierrat B, Saucède T, Brayard A, et al. Comparative biogeography of echinoids, bivalves and gastropods from the Southern Ocean. *Journal of Biogeography*, 2013, 40(7): 1374-1385.
- 22 Gutt J, Barnes D K A, Lockhard S L, et al. Antarctic macrobenthic communities: a compilation of circumpolar information. *Nature Conservation*, 2013, 4: 1-13.
- 23 Gutt J, Griffiths H J, Jones C D. Circumpolar overview and spatial heterogeneity of Antarctic macrobenthos communities. *Marine Biodiversity*, 2013, 43(4): 481-487.
- 24 Danis B, Griffiths H. Polar science: bid for freely accessible

- biodiversity archive. *Nature*, 2009, 458(7240): 830.
- 25 Vines T H, Albert A Y K, Andrew R L, et al. The availability of research data declines rapidly with article age. *Current Biology*, 2013, 20(1): 94-97.
 - 26 Gibney E, Van Noorden R. Scientists losing data at a rapid rate. *Nature*, 2013, doi: 10.1038/nature.2013.14416.
 - 27 Kaiser S, Brandão S N, Brix S, et al. Pattern, process and vulnerability of Southern Ocean benthos—a decadal leap in knowledge and understanding. *Marine Biology*, 2013, 160(9): 2295-2317, doi: 10.1007/s00227013-22326.
 - 28 Gutt J, Hosie G, Stoddart M. *Marine Life in the Antarctic/Mcintyre A D. Life in the world's oceans: Diversity, distribution, and abundance.* Oxford: Blackwell Publishing Ltd, 2010: 203-220.
 - 29 Schiaparelli S, Danis B, Wadley V, et al. The census of Antarctic marine life: The first available baseline for antarctic marine biodiversity//Verde C, Di Prisco G. *Adaptation and evolution in marine environments: The impacts of global change on biodiversity.* Berlin: Springer, 2012: 3-20.
 - 30 Worm B, Lotze H K, Jonsen I, et al. Part IV Oceans future. The future of marine animal populations//McIntyre A D. *Life in the World's Oceans.* Oxford: Blackwell Publishing Ltd., 2010: 315-330.
 - 31 Baker M C, Ramirez-Llodra E Z, Tyler P A, et al. Biogeography, ecology, and vulnerability of chemosynthetic ecosystems in the deep sea. Chapter 9. diversity of abyssal marine life//McIntyre A D. *Life in the world's oceans.* Oxford: Blackwell Publishing Ltd., 2010: 161-182.
 - 32 Ebbe B, Billett D S M, Brandt A, et al. Chapter 8. Diversity of abyssal marine life//McIntyre A D. *Life in the World's Oceans.* Oxford: Blackwell Publishing Ltd., 2010: 139-160.
 - 33 Menot L, Sibuet M, Carney R S, et al. New perceptions of continental margin biodiversity. Chapter 6. Diversity of abyssal marine life//McIntyre A D. *Life in the World's Oceans.* Oxford: Blackwell Publishing Ltd, 2010: 79-101.
 - 34 De Broyer C, Koubbi P, Griffiths H J, et al. *The CAML/SCAR-MarBIN Biogeographic Atlas of the Southern Ocean.* Cambridge: Scientific Committee on Antarctic Research, 2014, in press.
 - 35 Grant R A, Griffiths H J, Steinke D, et al. Antarctic DNA barcoding; a drop in the ocean? *Polar Biology*, 2011, 34(5): 775-780.
 - 36 McLeod D J, Hosie G W, Kitchener J A, et al. Zooplankton atlas of the Southern Ocean: the SCAR SO-CPR survey (1991–2008). *Polar Science*, 2010, 4(2): 353-385.
 - 37 Bowden D A, Schiaparelli S, Clark M R. A lost world? Archaic crinoid-dominated assemblages on an Antarctic seamount. *Deep-Sea Res Part II*, 2011, 58(1-2): 119-127.
 - 38 Gutt J, Barratt I, Domack E, et al. Biodiversity change after climate-induced ice-shelf collapse in the Antarctic. *Deep-Sea Res Part II*, 2011, 58(1-2): 74–83.
 - 39 Gutt J, Cape M, Dimmler W, et al. Shifts in Antarctic megabenthic structure after ice-shelf disintegration in the Larsen area east of the Antarctic Peninsula. *Polar Biology*, 2013, 36(6): 895-906.
 - 40 Rogers A D, Tyler P A, Connelly D P, et al. The discovery of new deep-sea hydrothermal vent communities in the Southern Ocean and implications for biogeography. *PLoS Biol*, 2012, 10(11), doi: 10.1371/journal.pbio.1001234.
 - 41 Domack E, Ishman S, Leventer A, et al. A chemosynthetic ecosystem found beneath Antarctic ice shelf. *Eos*, 2015, 86: 269-276.
 - 42 Niemann H, Fischer D, Graffe D, et al. Biogeochemistry of a low-activity cold seep in the Larsen B area, western Weddell Sea, Antarctica. *Biogeosciences*, 2009, 6(11): 2383-2395.
 - 43 Grant R A, Linse K. Barcoding Antarctic Biodiversity: current status and the CAML initiative, a case study of marine invertebrates. *Polar Biology*, 2009, 32(11): 1629-1637.
 - 44 Strugnelli J M, Rogers A D, Prodöhl P A, et al. The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics*, 2008, 24(6): 853-860.
 - 45 Allcock A L, Barratt I, Eléaume M, et al. Cryptic speciation and the circumpolarity debate: a case study on endemic Southern Ocean octopuses using the coxI barcode of life. *Deep-Sea Res Part II*, 2011, 58(1-2): 242-249.
 - 46 Peterson B K, Weber J N, Kay E H, et al. Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS One*, 2012, 7(5): e37135.
 - 47 Held C, Wägele J W. Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae). *Scientia Marina*, 2005, 69(S2): 175-181.
 - 48 Wilson N G, Schrödl M, Halanych K M. Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelensis* (Mollusca, Nudibranchia). *Molecular Ecology*, 2009, 18(5): 965-984.
 - 49 Krabbe K, Leese F, Mayer C, et al. Cryptic mitochondrial lineages in the wide spread pycnogonid *Colossendeis megalonyx* Hoek, 1881 from Antarctic and Subantarctic waters. *Polar Biology*, 2010, 33(3): 281-292.
 - 50 Griffiths H J, Barnes D K A, Linse K. Towards a generalized biogeography of the Southern Ocean benthos. *J Biogeogr*, 2009, 36(1): 162-177.
 - 51 Griffiths H J, Danis B, Clarke A. Quantifying Antarctic marine biodiversity: The SCAR-MarBIN data portal. *Deep Sea Research Part II: Topical Studies in Oceanography*, 2011, 58(1): 18-29.
 - 52 Constable A J, Melbourne-Thomas J, Corney S P, et al. Change in Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global Change Biology*, 2014, doi: 10.1111/gcb.12623.
 - 53 Ericson D B, Ewing M, Wollin G. Sediment cores from the Arctic and Subarctic Seas. *Science*, 1964, 144(3623): 1183-1192.
 - 54 Peck L S. Organisms and responses to environmental change. *Marine Genomics*, 2011, 4(4): 237-243.
 - 55 Gerlach S A. *Spezielle Ökologie-Marine Systeme.* Heidelberg: Springer Verlag, 1994: 1-226.
 - 56 Sachs O, Sauter E J, Schlüter M, et al. Benthic organic carbon flux and oxygen penetration reflect different plankton provinces in the Southern Ocean. *Deep-Sea Research I*, 2009, 56(8): 1319-1335.
 - 57 Graf G. Benthic-pelagic coupling in a deep-sea benthic community. *Nature*, 1989, 341(6241): 437-439.
 - 58 Brandt A, Bathmann U, Brix S, et al. Maud rise—a snapshot through the water column. *Deep-Sea Research Part II*, 2011, 58(19-20): 1962-1982, doi: 10.1016/j.dsr2.2011.01.008.
 - 59 Brandt A, Ebbe B, Urich B. Southern Ocean biodiversity—from pelagic processes to deep-sea response. *Deep-Sea Research II*, 2011, 58(19-20): 1945-1947.
 - 60 Hosie G, Koubbi P, Riddle M, et al. CEAMARC, the Collaborative East Antarctic Marine Census for the Census of Antarctic Marine Life (IPY # 53): an overview. *Pol Sci*, 2011, 5(2): 75-87.
 - 61 Ingels J, Vanreusel A, Brandt A, et al. Possible effects of global environmental changes on Antarctic benthos: a synthesis across five major taxa. *Ecology and Evolution*, 2012, 2(2): 453-485, doi: 10.1002/ece3.96.
 - 62 Lörz A N, Kaiser S, Bowden D A. Macrofaunal crustaceans in the benthic boundary layer from the shelf break to abyssal depths in the Ross Sea (Antarctica). *Polar Biol*, 2013, 36(3): 445-451, doi: 10.1007/s00300-012-1269-1.
 - 63 Arntz W E, Thatje S, Linse K. Missing link in the Southern Ocean:

- sampling the marine benthic fauna of remote Bouvet Island. *Polar Biol*, 2006, 29(2): 83-96.
- 64 Kaiser S, Barnes D K A, Sands C J, et al. Biodiversity of an unknown Antarctic Sea: assessing isopod richness and abundance in the first benthic survey of the Amundsen continental shelf. *Marine Biodiversity*, 2009, 39(1): 27-43.
- 65 Barnes D K A, Kaiser S, Griffiths H J, et al. Marine, intertidal, fresh-water and terrestrial biodiversity of an isolated polar archipelago. *J Biogeogr*, 2009, 36(4): 756-769, doi: 10.1111/j.1365-2699.2008.02030x.
- 66 Clarke A, Johnston N M. Antarctic marine benthic diversity. *Oceanography Marine Biology Annual Review*, 2003, 41: 47-114.
- 67 Gutt J, Sirenko B I, Smirnov I S, et al. How many macrozoobenthic species might inhabit the Antarctic shelf? *Antarct Sci*, 2004, 16(1): 11-16.
- 68 Aquilina A, Connelly D P, Copley J T, et al. Geochemical and visual indicators of hydrothermal fluid flow through a sediment-hosted volcanic ridge in the central Bransfield Basin (Antarctica). *PLoS One*, 2013, 8(1): e54686.
- 69 Marsh L, Copley J T, Huvenne V A I, et al. Microdistribution of faunal assemblages at deep-sea hydrothermal vents in the Southern Ocean. *PLoS One*, 2013 7(10): e48348.
- 70 Buckeridge J S, Linse K L, Jackson J A. *Vulcanolepas scotiaensis* sp. nov, a new deep-sea scalpelliform barnacle (Eolepadidae: Neolepadinae) from hydrothermal vents in the Scotia Sea, Antarctica. *Zootaxa*, 2013, 3745(5): 551-568.
- 71 Nye V, Copley J, Linse K. A new species of *Eualus* Thallwitz, 1891 and new record of *Lebbeus antarcticus* (Hale, 1941) (Crustacea: Decapoda: Caridea: Hippolytidae) from the Scotia Sea. *Deep-Sea Research II*, 2013, 92: 145-156.
- 72 Eleftheriou A. *Methods for the study of marine benthos*, 4th edn. New York: Wiley, 2013: 1-465.
- 73 Schiaparelli S, Ghiglione C, Alvaro M C, et al. Diversity, abundance and composition in macrofaunal molluscs from the Ross Sea (Antarctica): results of fine-mesh sampling along a Latitudinal Gradient. *Polar Biology*, 2014, 37(6): 859-877.
- 74 Brandt A, Barthel D. An improved supra- and epibenthic sledge for catching Peracarida (Crustacea, Malacostraca). *Ophelia*, 1995, 43(1): 15-23.
- 75 Brenke N. An epibenthic sledge for operations on marine soft bottom and bedrock. *Mar Technol Soc J*, 2005, 39(2): 10-21.
- 76 Krüger S, Leuschner D C, Ehrmann W, et al. North Atlantic Deep Water and Antarctic Bottom Water variability during the last 200 ka recorded in an abyssal sediment core off South Africa. *Global and Planetary Change*, 2012, 80-81: 180-189, doi: 10.1016/j.gloplacha.2011.10.001.
- 77 Mackensen A. High epibenthic foraminiferal $\delta^{13}C$ in the recent deep Arctic Ocean: implications for ventilation and brine release during stadials. *Paleoceanography*, 2013, 28(3): 574-584, doi: 10.1002/palo.20058.
- 78 Murray A, Van de Putte A, Youdjou N, et al. mARS: creating the Microbial Antarctic Resource System. 2014. <http://share.biodiversity.aq/MARS/Vision/mARSVision.pdf>
- 79 Ellingsen K, Brandt A, Ebbe B, et al. Diversity and spatial distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean. *Polar Biology*, 2007, 30(10): 1265-1273.
- 80 Kaiser S, Barnes D K A, Brandt A. Slope and deep-sea abundance across scales: Southern Ocean isopods show how complex the deep sea can be. *Deep-Sea Research Part II*, 2007, 54(16-17): 1776-1789.
- 81 Bickford D, Lohman D J, Sodhi N S, et al. Cryptic species as a window on diversity and conservation. *Trend Ecol Evol*, 2007, 22(3): 148-155.
- 82 Gutt J, Adams B, Bracegirdle T, et al. Antarctic Thresholds-Ecosystem Resilience and Adaptation a new SCAR-Biology Programme. *Polarforschung*, 2012, 82(2): 147-150.
- 83 Turner J, Barrant N E, Bracegirdle T J, et al. Antarctic climate change and the environment: an update. *Polar Record*, 2014, 50(3): 237-259, doi: 10.1017/S0032247413000296.
- 84 Brandt A, Gutt J. Biodiversity of a unique environment: the Southern Ocean benthos shaped and threatened by climate change//Zachos F, Habel J C. *Biodiversity hotspots*. Heidelberg: Springer Publishers, 2011: 503-526, doi: 10.1007/978-3-642-20992-5.
- 85 Danis B, Van de Putte A, Youdjou N, et al. The Antarctic Biodiversity Information Facility. World Wide Web publication, 2014. <http://www.biodiversity.aq>.
- 86 Kennicutt II M C, Cassano J J, Liggett D, et al. Six priorities for Antarctic Science. *Nature*, 2014, 512: 23-25.