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REVIEW, CONCEPT, AND SYNTHESIS

Patterns, processes and vulnerability of Southern Ocean benthos: a decadal leap in knowledge and understanding

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Abstract In the Southern Ocean, that is areas south of the Polar Front, long-term oceanographic cooling, geographic separation, development of isolating current and wind systems, tectonic drift and fluctuation of ice sheets amongst others have resulted in a highly endemic benthic fauna, which is generally adapted to the long-lasting, relatively stable environmental conditions. The Southern Ocean benthic ecosystem has been subject to minimal direct anthropogenic impact (compared to elsewhere) and thus presents unique opportunities to study biodiversity and its responses to environmental change. Since the beginning of the century, research under the Census of Marine Life and International Polar Year initiatives, as well as Scientific Committee of Antarctic Research biology programmes, have considerably advanced our understanding of the Southern Ocean benthos. In this paper, we evaluate recent progress in Southern Ocean benthic research and identify priorities for future research. Intense efforts to sample and

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describe the benthic fauna, coupled with coordination of information in global databases, have greatly enhanced understanding of the biodiversity and biogeography of the region. Some habitats, such as chemosynthetic systems, have been sampled for the first time, while application of new technologies and methods are yielding new insights into ecosystem structure and function. These advances have also highlighted important research gaps, notably the likely consequences of climate change. In a time of potentially pivotal environmental change, one of the greatest challenges is to balance conservation with increasing demands on the Southern Ocean's natural resources and services. In this context, the characterization of Southern Ocean biodiversity is an urgent priority requiring timely and accurate species identifications, application of standardized sampling and reporting procedures, as well as cooperation between disciplines and nations.

Introduction

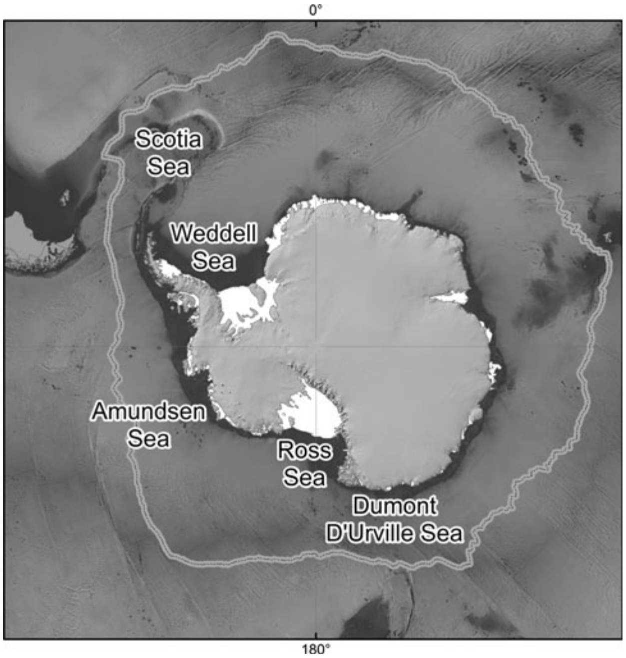

Fig. 1 The Southern Ocean and adjacent seas; the *grey line marks* the Polar Front

In many ways, the seabed around Antarctica seems to be a unique environment (Fig. 1). On the continental shelf, light availability, (iceberg) disturbance and primary production are intensely seasonal. Yet, it also has unparalleled physical constancy of many variables, notably temperature at freezing level. Since the disintegration of the former Gondwana continent, the initiation of the Antarctic Circumpolar Current and accompanied oceanic cooling about 28–41 Ma (Lawver and Gahagan 2003), the Antarctic continental shelf became the most isolated globally and, on the seabed at least, has experienced

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minimal direct anthropogenic impact—despite the decades of heavy whaling and sealing. The Southern Ocean deep sea (i.e., areas below the shelf break), on the contrary, is well connected to adjacent ocean basins by both lack of topographical barriers and northward flow of Antarctic Bottom Water (Clarke 2003). The latter provides potential dispersal routes for deep-sea organisms (Strugnell et al. 2008).

The Southern Ocean influences global weather and oceanic deep-water formation and is a key region for understanding global climatic system and ocean circulation (Sigman et al. 2010). For example, some Southern Ocean areas show amongst the most rapid warming in the world (West-Antarctic Peninsula (WAP), Meredith and King 2005; South Georgia, Whitehouse et al. 2008) and are also projected to be the most influenced by ocean acidification due to raised atmospheric CO_2 (Orr et al. 2005). Amongst the many extremes, perhaps the most striking feature, across geological time, is the changing availability of habitable shelf areas due to the recurrent advance and retreat of ice sheets through glacial–interglacial cycles. The Ross and Weddell Sea shelves are the widest globally (and amongst the deepest) but both were almost entirely covered by grounded ice during the last glacial maximum (Denton and Hughes 2002).

Areas which undergo prolonged isolation, such as the Southern Ocean, usually have unique elements to their biota (i.e., shelf endemism levels between 50 and 80 %; White 1984; Arntz et al. 1997; Griffiths et al. 2009), but the distinctive oceanographic and tectonic history of the Southern Ocean have resulted in more than just endemic species. Many genera and some families are only found south of the PF and certain higher taxa are unusually rich or prevalent (such as pycnogonids, polychaetes, ascidians and peracarid crustaceans, see Fig. 2) compared to non-Antarctic marine ecosystems (Clarke and Johnston 2003). Equally striking is the complete absence of some taxa, such as brachyuran crabs, and rarity of others such as cartilaginous fish, reptant decapods and barnacles (Clarke and Johnston 2003). The shallow shelf is heavily impacted by ice scour, and space on hard substrata is generally dominated by sessile suspension-feeding communities including sponges, bryozoans, anemones, ascidians and crinoids (Dayton 1989). Antarctic benthos typically has prolonged development, age and time to maturation, as well as slow growth and low adult mobility (Arntz et al. 1994). Planktotrophy is overall scarce, but has been reported as contrastingly very common in the shallows (Poulin et al. 2002). Brooding is instead the dominant reproductive mode in some taxa, but other highly successful groups have lecithotrophic or planktotrophic larvae (e.g., asteroids, some echinoids; see Pearse et al. 1991; Poulin et al. 2002; Fig. 2). Further unusual features of Southern Ocean benthos include eurybathy, gigantism in some (i.e., a number of amphipod, isopod and pycnogonid species) and dwarfism in other taxa (e.g., some brachiopod and scaphopod species; see Moran and Woods 2012 for a review) as well as physiological adaptations to low temperatures such as development of antifreeze glycoproteins and lack of blood pigments in Antarctic notothenioid fish (Rahmann et al. 1984).

Any one factor driving the great variety of physiological, ecological and evolutionary characteristics of species inhabiting the Southern Ocean seabed is unlikely. Recent research, particularly over the last decade, has quantified the nature of some biotic and abiotic factors underlying Southern Ocean benthic biodiversity, such as biological interactions, ice-mediated processes, sediment structure, topography and water masses (e.g., Dayton 1989; Brandt et al. 2007; Hétérier et al. 2008; Smale et al. 2008a, b; Schiaparelli et al. 2010; additional references are given in Online Resource 1 [1–6]). Temperature was one of the earliest influences studied on benthic biota. At low temperature, fluids are more viscous and hold more gas, enzyme reactions are slower and muscular crushing is proportionally more energetically expensive (Römisch and Matheson 2003). Recent experimental work has shown that many species have a narrow temperature-survival window and are even more stenothermal in functionality (Peck et al. 2004). Characteristics such as winter cessation of feeding and slow growth, once thought to be linked to temperature, may be more related to food availability and thus to light regime (Barnes and Clarke 1994). On the Antarctic continental shelf, local to regional scale species composition and densities observed seem to be more influenced by ice scour than any other single factor—at small scales this is catastrophic, but at larger temporal and spatial scales ice-mediated disturbance creates a mosaic of communities at different recovery states thus promoting diversity (Gutt and Piepenburg 2003). While ice scour is one of the dominant structuring forces across current ecological time scales, recurrent glaciations are thought to have led to eradication and reinvasion at large shelf scale and have perhaps acted as driver for a ‘biodiversity pump’ initiating species radiations (Clarke and Crame 1992). The varying connectivity of suitable habitats around Antarctica during glacial periods probably promoted allopatric speciation through reproductive isolation in some taxa (Wilson et al. 2007). The considerable depth of the Antarctic continental shelf as well as the isothermal water column may have facilitated

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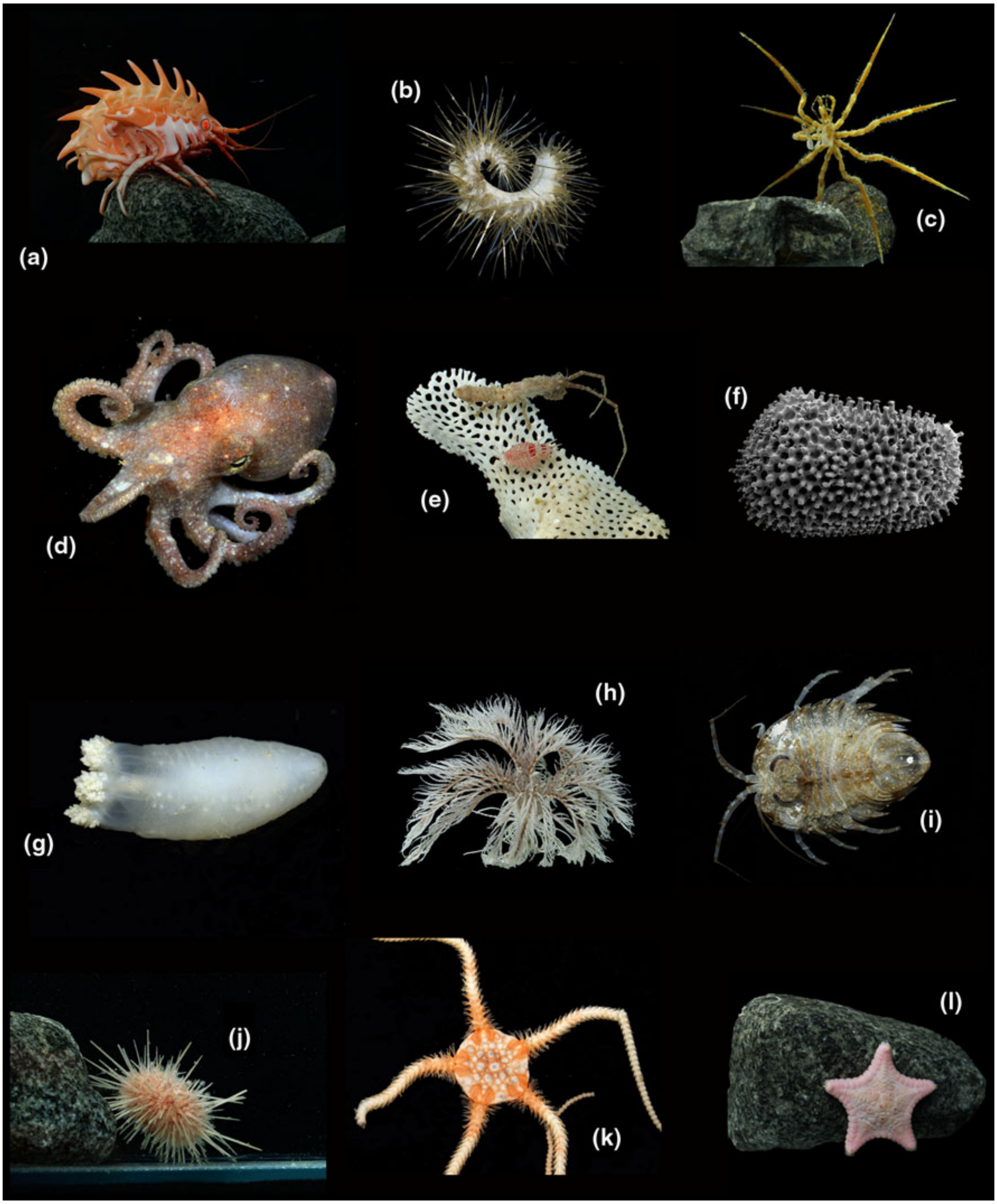

faunal migrations between the shelf and the deep sea (Clarke 2003).

Knowledge, and especially understanding, of the ecological and evolutionary patterns and drivers of Antarctica's benthic biodiversity has tremendously changed since the early voyages in the historic age of Antarctic exploration (e.g., during HMS Challenger [1872–1876], German Antarctic expedition [1901–1903] and SS Terra Nova [1910–1913] expeditions). Early taxonomic monographs contributed greatly to the currently known biodiversity in that the rate of species description has never been greater than between 1880 and 1940 (De Broyer et al. 2011). Post-HMS-Challenger taxonomy builts a baseline for a more ecological, physiological and biogeographic focus of research in the second half of the twentieth century. At that time, researchers had already proposed some theories on macroecological and biogeographic patterns such as latitudinal gradients in species diversity, reproduction modes, body size and range size (Murray 1895; Thorson 1950). Some of these paradigms have only changed little (e.g.,

◀**Fig. 2** Meio-, macro and megafaunal representatives of the Southern Ocean benthos; **a** *Epimeria rubrieques* De Broyer & Klages, 1990 (Peracarida, Amphipoda), is an example of Antarctic gigantism, a species characterized by its enormous dorsal ornamentation, bright colours and giant body size (up to 70 mm); **b** *Antarctinoe spicoides* (Hartmann-Schröder, 1986), a common polychaete species found in the Southern Ocean deep sea; in polychaetes, deep-sea endemism is much lower than on the Antarctic continental shelf partly reflecting differences in isolation between these two realms; **c** *Nymphon australe* Hodgson, 1902, is the most abundant pycnogonid species in the Southern Ocean presenting both eurybathic and circumpolar distributions; **d** *Pareledone turqueti* Joubin, 1905 (Mollusca, Cephalopoda); a specimen collected on the Amundsen Sea shelf. *P. turqueti* is a circum-Antarctic benthic octopus, endemic to the Southern Ocean shelf and slope; **e** *Fissarcturus* sp. (Peracarida, Isopoda) and *Gnathiphimedia* sp. (Amphipoda) on bryozoan; while some taxonomic groups are more prevalent on the Antarctic continental shelf (e.g., bryozoans, amphipods) others are rich and abundant in the Southern Ocean deep sea (e.g., isopods). **f** *Henryhowella* sp., an ostracod collected in the deep Scotia Sea; like in other Antarctic benthic invertebrates, genetic work contradicts previous assumptions of wide bathymetric and geographic distributions in Southern Ocean Ostracoda (Brandão et al. 2010); **g** *Staurocucumis liouvillei* (Vaney, 1914) (Echinodermata, Holothuroidea); holothuroids are very diverse in the Southern Ocean, that is, 10 % of globally described species occur south of the Polar Front, with about one-quarter still being undescribed; **h** *Florometra mawsoni* A.H. Clark, 1937 (Comatulida, Crinoidea); most Antarctic (unstalked) comatulid crinoids, such as *F. mawsoni*, have a restricted dispersal ability, whereas the dispersal potential of *Promachocrinus kerguelensis* Carpenter, 1888 seems to be much higher; **i** *Cuspidoserolis* sp. (Isopoda, Serolidae); serolid isopods are a particularly rich component of the Antarctic shelf benthos and have probably derived from former Gondwanan ancestors; **j** *Sterechinus* sp. (Echinodermata, Echinoidea); all *Sterechinus* species show planktonic development and represent among the most dominant and ubiquitous echinoid genus in Antarctic waters; **k** *Ophiocten dubium* Koehler, 1900 (Echinodermata, Ophiuroidea); ophiuroids are amongst the most dominant group of Antarctic megafaunal assemblages; **l** *Odontaster penicillatus* (Philippi, 1870) (Echinodermata, Asteroidea); despite being amongst the best studied Antarctic groups, recent genetic analyses of the genus *Odontaster* revealed two previously unrecognized lineages within this genus (Janosik and Halanych 2010). **f** is in Public Domain (Encyclopedia of Life, http://eol.org/pages/44719/overview)

rarity of planktotrophic development, tendency to gigantism and slow growth; Barnes and Clarke 2011), some significantly (e.g., hemispheric asymmetry in latitudinal diversity gradients; Culver and Buzas 2000; Linse et al. 2006; Clarke et al. 2007) and others have just started to shift (e.g., with regard to 'large' geographic range size, shelf refuges and 'impoverished' deep-sea benthos; Dayton and Oliver 1977; Brandt et al. 2007; Newman et al. 2009; Brandão et al. 2010; Allcock and Strugnell 2012).

During the last decade, there has been an increasing intensity of reports of Antarctic biodiversity responses to environmental change at high southern latitudes (Orr et al. 2005; Aronson et al. 2007; Kaiser and Barnes 2008; Yasuhara et al. 2009; Trivelpiece et al. 2011; Ingels et al. 2012; see Online Resource 1 [7–10]). Recent initiatives such as the Intergovernmental Panel on Climate Change (IPCC), the SCAR—Evolution and Biodiversity in Antarctica (SCAR-EBA, 2006–2013) programme, the International Polar Year (IPY, 2007–2008) and the Census of Marine Life (CoML 2000–2010) with its Antarctic node, the Census of Antarctic Marine Life (CAML, 2005–2010), as well as its deep-sea component, the Census of the Diversity of Abyssal Marine Life (CeDAMar, 2000–2010) have ramped up the international connectivity of national scientific programmes and scientists aiding accessibility and cross-checking of data (Clarke 2008; De Broyer et al. 2011; Griffiths et al. 2011; Schiaparelli et al. 2013; see Online Resource 1 [11–12]).

The current paper provides a review of achievements of the CoML decade and beyond, and how these have advanced our understanding of Southern Ocean benthic biodiversity—from taxonomy, through biogeography to ecophysiological responses to climate change. It focuses mainly on progress in the assessment of larger macro- and megafaunal invertebrate biodiversity patterns (reflecting taxonomic priorities rather than ecological importance) but also on the often neglected smaller size fractions (i.e., meiofauna and prokaryotes). We assess where we have made most progress and why, but also highlight significant gaps in current knowledge. The first part of the paper is concerned with the tools, which have helped to identify patterns and potential drivers of Southern Ocean biodiversity, while the second part identifies gaps of knowledge and new directions for future research.

Key areas of progress

Sampling the Southern Ocean benthos: major achievements over the last decade

Arguably Antarctic science and scientists have been 'slow' to import and apply new techniques and technology into the Southern Ocean research. A reason for this delay is probably that benthic sampling in the Antarctic is still extremely challenging, as it is cold, remote and parts of it are covered by ice perennially. Yet, despite the adverse conditions, the quality and quantity of benthic sampling has improved considerably. Recent technical advances in the design of sampling equipment, as well as complementary sampling and standardization of methods across institutes and nations, have considerably affected our knowledge and understanding of Southern Ocean biodiversity. Although camera systems have been deployed since the early 1960s (e.g., during U.S. Eltanin, see Menzies and Schultz 1966), the increasing sophistication and availability of digital video and still imaging equipment in recent years, coupled with remarkable advances in the technology of vehicles on which these cameras are deployed (e.g., remotely operated vehicles, ROVs, and autonomous underwater vehicles, AUVs), have made photographic sampling an increasingly important component of benthic research programmes. ROVs and towed camera systems, in fact, complement traditional deployments and sample collections by providing valuable information on benthic communities particularly of less-accessible sites (Bowden et al. 2011; Gutt et al. 2011). Photographic and video imaging operated by SCUBA divers is becoming increasingly important for shallow-marine benthic community survey (Cummings et al. 2006). Furthermore, greater use of small mesh sizes (< 500 μm) across sampling devices (epibenthic sledges and dredges in particular, Brenke 2005) led to new Southern Ocean discoveries (i.e., species, genera and families new to the Southern Ocean and/or science; Brandt et al. 2007; Lörz et al. 2013; see Online Resource 1 [13–15]) even on well-known shelves (Choudhury and Brandt 2009).

In the last decade, there has been a gradual shift from national sampling campaigns towards complementary international collaborations in order to understand the distribution of Southern Ocean biodiversity and its potential drivers [e.g., the ANtarctic benthic DEEP-sea biodiversity, colonization history and recent community patterns (ANDEEP), SYSTCO (SYSTem COupling), the Biodiversity of three representative groups of Antarctic Zoobenthos (BIANZO), the Collaborative East Antarctic Marine Census (CEAMARC) and the IPY-CAML projects; Brandt et al. 2007, 2011; Hosie et al. 2011; Ingels et al. 2012; Lörz et al. 2013]. This has especially been supported by international efforts in the framework of the CAML, IPY and SCAR-EBA programmes by advising standardized sampling protocols and gear types in order to maximize comparability of data obtained. There has been also a move towards consideration of sampling effort as a factor in the interpretation of macroecological and biogeographic patterns (Clarke et al. 2007; Griffiths et al. 2009, 2011).

In some places, sampling intensity (in terms of extent and number of data collections) has increased significantly over the past 10 years, which (arguably) has made parts of the Southern Ocean, such as the eastern Weddell Sea or WAP, some of the better studied marine areas globally (Clarke 2008). Although sample locations are still very unevenly distributed, both geographically and bathymetrically (Griffiths et al. 2011; Fig. 3), recent sampling of the most unknown habitats (such as the intertidal, deep sea, Amundsen Sea; western Weddell Sea; Waller et al. 2006; Brandt et al. 2007, Kaiser et al. 2009; Gutt et al. 2011) has increased the number of taxa known to the Southern Ocean and thus altered the perception of biodiversity and biogeographic patterns (Clarke et al. 2007; Griffiths et al. 2009). Even 'highly accessible' habitats such as the Antarctic intertidal zone which were long thought to be impoverished (Clarke 1996) have been revealed by recent sampling to be surprisingly rich (Waller et al. 2006). Sampling of the Southern Ocean deep seabed greatly increased the number of known species (isopod crustaceans in particular), most of which were new to science (Brandt et al. 2007; Lörz et al. 2013), and also provided new insights into the biotic and abiotic processes shaping Southern Ocean deep-sea communities (Brandt et al. 2007; Kaiser et al. 2007; Hétérier et al. 2008; Schiaparelli et al. 2010); for example, sampling across multiple spatial scales across the Weddell and Scotia Sea slope and abyss has shown that the fauna can be rich and abundant on a local and regional scale, yet with most distributions being patchy (rather than rare; Brandt et al. 2007; Kaiser et al. 2007). Furthermore, these samples highlighted the important role of epibiotic interactions, which may increase local richness and abundance of deep-sea benthic species (Hétérier et al. 2008; see also Schiaparelli et al. 2010).

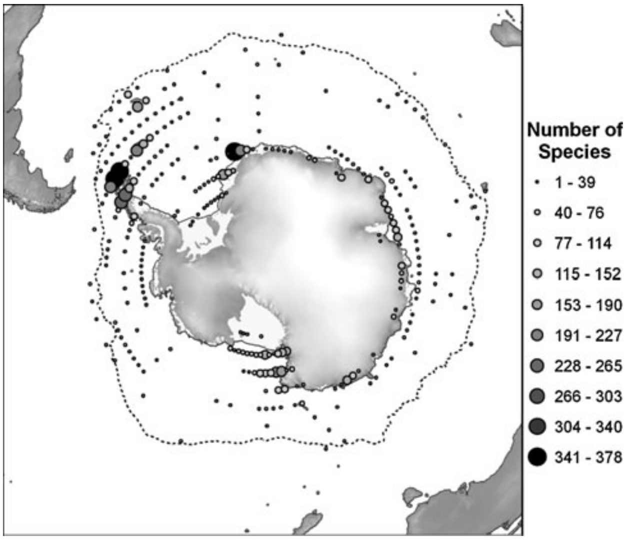

Fig. 3 Number of marine benthic species per 3 by 3 degree grid cell; the size of the *circle* indicates the proportion of species recorded per grid cell; the *dotted line* marks the position of the Polar Front. Data from SCAR MarBIN (De Broyer and Danis 2009)

However, many of the newly recorded Southern Ocean taxa (across cruises, regions and depth) are currently undescribed and not listed in any compilation, which limits the evaluation of biodiversity and broad-scale distribution patterns. So, unless species have been formally described, it is impossible to assess whether species putatively new to science have been collected before.

A giant leap in taxonomy: recent efforts in describing the Antarctic benthos

The fundamental building blocks of biological science, taxonomy and systematics underwent a revolution in the last three decades in that molecular tools have been increasingly used to complement morphological approaches in order to identify and delineate species (Allcock et al. 1997; Hunter and Halanych 2008; Eléaume et al. 2011; see Online Resource 1 [16–17]). As with other disciplines, progress in implementing molecular genetic tools in taxonomy was mostly based on species from tropical and temperate regions and it took longer until they were routinely applied to polar organisms. Until recently, the majority of Southern Ocean material had been preserved in formaldehyde for histological and ecological studies and, thus, was not accessible for molecular genetic studies. However, in the 1990s, standard sampling protocols included ethanol and freezing of samples as a preservative, allowing for DNA-based approaches to taxonomy and systematics (such as analyses of the mitochondrial cytochrome c oxidase sub-unit I [COI] 'barcoding' gene; Hebert et al. 2003). In the Southern Ocean, there has been a concerted international effort, through the Barcode of Marine Life (MarBOL) initiative in collaboration with the Census of Antarctic Marine Life (CAML) to mass sequence the same gene in a wide variety of Antarctic species (Grant et al. 2011).

Most published molecular studies are based on single genetic markers, predominantly the mitochondrial 16S and COI genes and the nuclear ribosomal 18S and 28S genes. Despite the considerable insights, that these may provide, they also have some profound limitations in that a single genetic locus, in particular the mitochondrial, may not represent the full species' or populations' history (Ballard and Whitlock 2004). Therefore, contemporary evolutionary genetic studies should rely on several unlinked markers to disentangle species' and populations' history (see section below).

Much of the delay in the application to the Antarctic or the deep sea has been driven by the lack of suitable samples; since sampling the Southern Ocean is logistically difficult and expensive both in time and finances, many genetic studies have analysed a limited number of specimens from few locations in the Atlantic Sector of the Southern Ocean (e.g., Held and Wägele 2005; Hunter and Halanych 2008). Thus, the validity and representativeness of results on species delineations and speciation processes need further investigation.

Despite being in an early stage in the Southern Ocean compared to other regions, molecular tools have already been used to delineate species in several taxa across different evolutionary lineages and across a range of Southern Ocean locations (e.g., gastropods: Wilson et al. 2009, pycnogonids: Krabbe et al. 2010; Arango et al. 2011; isopods: Held and Wägele 2005; Raupach et al. 2009; amphipods: Lörz et al. 2009; Havermans et al. 2010; ostracods: Brandão et al. 2010; asteroids: Janosik and Halanych 2010; crinoids: Wilson et al. 2007; Hemery et al. 2012; ophiuroids: Hunter and Halanych 2008; nemerteans: Mahon et al. 2010; and polychaetes: Schüller 2011; see Online Resource 1 [18–22]). A particularly interesting result of these efforts is the steep increase in the number of formerly overlooked or cryptic species for the (re-) assessment of their distributional ranges as well as evolutionary history (Held and Wägele 2005; Janosik and Halanych 2010). The realized distribution ranges of the species studied have become either much more restricted (Lörz et al. 2009) or unexpectedly large, even for species with (potentially) limited dispersal abilities (Leese et al. 2010; Arango et al. 2011; Baird et al. 2012).

Across the literature, there has been some confusion about the correct use of the term 'cryptic species' (Bickford et al. 2007); most authors name 'cryptic' lineages as those, which lack morphological differentiation but which show some genetic variability (Bickford et al. 2007). However, some (genetic or morphological) markers are expected to show intra-specific variability, while others do not. Here, we follow the definition followed by most (but not all) authors and refer to 'cryptic' species as those, which lack obvious morphological differentiation, but differ at the genetic level (see Bickford et al. 2007 for a discussion).

While there is no doubt that molecular tools have the potential to increase taxonomic resolution, the increased recognition of cryptic species amongst many Antarctic invertebrates has also posed some new challenges to taxonomy as well as biodiversity estimations (Bickford et al. 2007). Most of these cryptic species remain temporarily named as clades, lineages or even unnamed and are thus essentially invisible to broader uses of biodiversity information (but see Brandão et al. 2010; Janosik and Halanych 2010). In contrast, some morphologically very different (polymorphic) species have been shown to have very little genetic divergence (Díaz et al. 2011; González-Wevar et al. 2010) leading to an overestimation of known biodiversity. The awareness that cryptic and polymorphic species are probably evenly spread across taxonomic groups and habitats (Pfenninger and Schwenk 2007; but see Trontelj and Fiser 2009), would necessitate the investigation of each individual morphologically and genetically (Bucklin et al. 2010) with profound logistical and financial constraints. The remoteness and cost of working in Antarctica means considerable difficulty in getting adequate material from enough locations, which is only part of the problem though. Considerable funding, time and expertise is required to go beyond the initial step of investigating variation at a single genomic locus (such as DNA

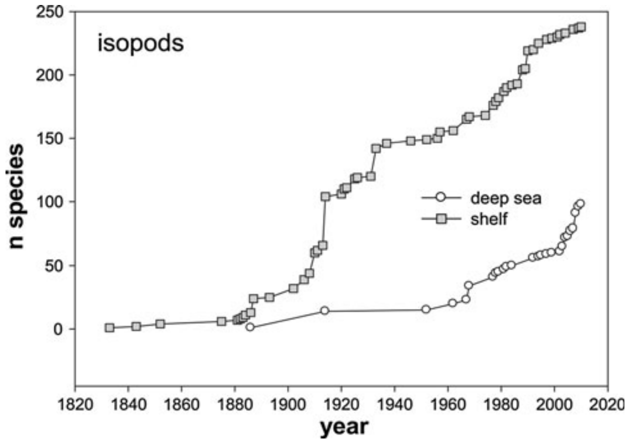

Fig. 4 Rate of species description in shelf versus deep-sea isopod crustaceans; modified from Kaiser and Barnes 2008

barcoding)—however, it is clear that only by combining molecular investigations of nuclear and mitochondrial genes at multiple loci and morphological approaches the phylogenetic results will be more reliable.

With many centres of concern over climate change, the identification of Antarctica's marine biodiversity has become more important than ever before, yet the trend of decreasing taxonomic expertise continues (De Broyer et al. 2011). There have been considerable efforts to improve the situation by developing or improving novel methodologies, such as online identification guides, web-based taxonomy, interactive identification keys, digital drawing tools and microscopic as well as molecular techniques (David et al. 2005; Coleman et al. 2010; see Online Resource 1 [23–24]). These have enhanced the quality and pace of taxonomic descriptions (la Salle et al. 2009), but are no full compensation for the paucity of taxonomic experts. There has also been a drastic improvement in collation and access to records. In the past decade, the number of known benthic species from the Southern Ocean has nearly doubled (from 4,100 to more than 7,100 benthic species, Clarke and Johnston 2003; De Broyer et al. 2011; Fig. 4). However, this is neither due to an increase in sampling nor taxonomic effort (in terms of rate of species descriptions; De Broyer et al. 2011), but, for example, the result of a major international endeavour in compiling and managing biodiversity data (such as the Register of Antarctic Marine Species (RAMS), SCAR-MarBIN and the Antarctic biodiversity information Facility (ANTABIF) as well as taxonomic revisions (Clarke et al. 2007; De Broyer and Danis 2009; De Broyer et al. 2011).

A new (to the Southern Ocean) integrative taxonomy combining, for example, morphological, ecological, phylogenetic and phylogeographic approaches has emerged (Arango and Wheeler 2007; Eléaume et al. 2011; Riehl and Kaiser 2012; see Online Resource 1 [16, 25]) making delineation of species more robust (De Broyer et al. 2011). Today, taxonomy is probably more multidisciplinary than it ever was, combining morphology, ecology, oceanography, biogeography and especially molecular techniques.

Progress in Southern Ocean molecular-phylogenetic and population–genetic studies

Molecular evolutionary studies can be subdivided into those that aim at identifying processes on macro-evolutionary time scales between species or higher-order taxa (phylogeny), those that assess genetic variation between sub-populations within a species (population genetics) and those that connect both disciplines (phylogeography). Despite the pioneer work on pelagic species in the 1980s and 1990s (Kühl and Schneppenheim 1986; Online Resource 1 [26–27]), molecular–genetic studies addressing the spatial partitioning of genetic variation in Antarctic benthic invertebrates were only initiated at the end of the last century (Allcock et al. 1997). Since then the number of studies has increased significantly (Held 2000; Page and Linse 2002; Strugnell et al. 2011; see Rogers (2012) for a review on phylogenetic and population genetic studies on both terrestrial and marine Antarctic taxa). This recent increase in the number of studies was mostly driven by technical advances, in particular the availability of universal primers for Polymerase Chain Reaction (e.g., Folmer et al. 1994) as well as a significant drop in both price and processing time of genetic analyses.

Molecular-phylogenetic studies over the last decade have mainly tested classical biogeographic hypotheses on the origin and evolution of the Southern Ocean benthos (based on work by Dell 1972; Knox and Lowry 1977). These studies have addressed the proposed scenarios (such as vicariance and dispersal, submergence and emergence) and provided independent evidence on the origin and radiation of Southern Ocean benthic species and their relatedness to species from adjacent seas using sequence data (Held 2000; Strugnell et al. 2008; Raupach et al. 2009; González-Wevar et al. 2010). A central finding for several groups is that rather than being a diversity sink, there is growing evidence for in situ origination in the Southern Ocean in several taxonomic groups (Held 2000; Wilson et al. 2007; González-Wevar et al. 2010; Strugnell et al. 2011, Online Resource 1 [16, 28]; but see Goldberg et al. 2005).

Molecular-phylogeographic and population–genetic studies in the Southern Ocean have mostly aimed at investigating the distribution of genetic polymorphism within a species and testing the strength of physical barriers, such as the PF and depth-correlates to gene flow. Key results from these studies can be summarized as follows. First, the PF appears to be a distinct barrier for shelf organisms, with species presumed to occur both in South America and Antarctica showing cryptic species-level divergence/s on either side (Hunter and Halanych 2008; Wilson et al. 2009, Krabbe et al. 2010; Online Resource 1 [29]—but see Leese et al. 2010). Second, several shelf-inhabiting species must have survived past glaciations in independent ice-free shelf habitats (Strugnell et al. 2012). Third, many 'circum-Antarctic' species are now often found to be made up of a series of putative species that may be sympatric (Held and Wägele 2005; Lörz et al. 2009; Wilson et al. 2009; Krabbe et al. 2010, but see Arango et al. 2011). In the case of the prominent crinoid *Promachocrinus kerguelensis* Carpenter, 1888, more rigorous sampling modified findings; initially, its distributional range seemed to be much more restricted; however, with increased sampling effort, all species in the complex appear to have circumpolar distributions (Wilson et al. 2007; Hemery et al. 2012). Fourth, species presumed to be widely distributed may be isolated by depth as a result of, for example, allopatric or parapatric refuges from past glaciation events (Brandão et al. 2010).

Studies based on a single marker such as the popular barcoding gene COI are usually not sufficient to infer the complex evolutionary history of taxa (see section above). Therefore, COI should be regarded as one amongst many (morphological and molecular) character sets. The continuing technical progress in molecular-marker development has brought novel and powerful tools into reach for phylogenetic and population–genetic studies on Antarctic taxa. In particular, the advent of high-throughput sequencing technologies ('next-generation sequencing') now enables the rapid generation of data for the development of molecular markers with comparatively little cost (Leese et al. 2012). Furthermore, conceptual advances in the fields of phylogeny and statistical phylogeography such as model-based inferences using powerful population–genetic models (e.g., coalescent; see Wakeley 2010) and the incorporation of time-calibration points in phylogenies allow for more rigid tests of evolutionary scenarios (Beaumont et al. 2010).

Estimation of Southern Ocean benthic biodiversity

One of the most notable aspects about southern polar biological science in the last decade is the considerable multinational effort to quantify 'biodiversity' (Griffiths et al. 2011). Key advances have been characterized by efforts crossing borders between disciplines and nations as well as information being organized into central open-access databases (De Broyer et al. 2011). This has arguably been the first time that Antarctic biologists across institutes and nationalities worked at the same time, on the same projects towards biodiversity tools that anyone could use, query and cross-check.

There have been renewed efforts to sample remote locations, such as the Amundsen Sea and Bouvetøya shelves, as well as bathyal and abyssal areas of the Weddell, Scotia and Ross seas (Arntz et al. 2006; Brandt et al. 2007; Kaiser et al. 2009; Gutt et al. 2011; Lörz et al. 2013). All records of macro- and megafaunal richness for a discrete Antarctic location (the South Orkney Islands) were collated for the first time to reveal greater marine richness compared to many temperate or tropical archipelagos (Barnes et al. 2009). At a larger spatial scale, the first attempt was made towards the estimation of species richness on the Antarctic continental shelf (Clarke and Johnston 2003; Gutt et al. 2004) and in the deep sea (Brandt et al. 2007).

Data from the last decade have clearly revealed gaps of knowledge—geographically, bathymetrically and taxonomically (Griffiths et al. 2011). Such data have also shown that Antarctic continental shelves are rich compared with most non-polar shelves (except coral reefs) that some taxa are very well represented in the deep sea and that considerations of scale are very important (Brandt et al. 2007; Kaiser et al. 2007; Barnes et al. 2009).

Progress in the understanding of community dynamics in the shallows made similar leaps to those on the shelf (Gutt 2007) and in the deep sea (Brandt et al. 2007). Work on the tempo and mode of colonization and recolonization following catastrophic disturbance events (such as iceberg scouring) stands out as particularly significant because the results were so divergent from a priori expectations (Smale et al. 2008a). Amongst the most important findings were the very high variability (in time and composition) in the way biota recolonized, the quantification of scour intensity and frequency, and the link between these and overlying sea-ice cover (Smale et al. 2008b).

Until the last decade, the vast majority of biological research in the polar regions, and particularly Antarctica, focused on macroscopic life. Yet, probably the richest element of Southern Ocean biodiversity is the most poorly known; our biggest knowledge advances have been in detailing the meiofauna and the microbes. Typically, estimations of meiofaunal biodiversity have been limited to a small fraction of total fauna sampled (e.g., diversity and distribution within the harpacticoid family Paramesochridae; Gheerardyn and Veit-Köhler 2009). Diversity of microfossils (i.e., taxa with calcified skeleton, mostly Foraminifera and Ostracoda) has been investigated for several faunas ranging from the Cretaceous to the Holocene as well as modern core-top faunas from distinct localities (Mikhalevich 2004; see Yasuhara et al. 2007 for an ostracod overview). These records are essential to understand long-term biodiversity dynamics through time, though available Antarctic and Southern Ocean benthic microfossil records are rather fragmentary (Rathburn et al. 1997; Majoran and Dingle 2002).

The advent of molecular techniques, and in particular, high-throughput sequencing (see section above), has made it possible to start estimating the scale of novel microbial biodiversity in the World's oceans. Microbial diversity is massive and as yet incalculable both in terms of population density, species diversity and richness, but patterns are beginning to emerge at different spatial scales. The vast majority of sequences identified may represent new as yet uncultivated diversity, and more importantly many of these closely matched clones from polar or low temperature environments reported elsewhere, hinting at a novel or specialized niche (Jamieson et al. 2012). The drivers of bacterial community composition in marine systems seem to be productivity and substrate availability (Van Hannen et al. 1999; West et al. 2008), while particulate organic matter may be the key determinant of biodiversity (e.g., Ruhl et al. 2008). Thus, microbial progress in some ways has overtaken work on macro-biodiversity work in starting to elucidate drivers of patterns which for the most part remain enigmatic in the Southern Ocean's rich animal benthos.

Projection of polar biological science out into other disciplines and applications could be argued as a key area of progress over the last decade given its considerable increase in frequency. For example, the interdisciplinary initiative Southern Ocean Observing System (SOOS) implements and manages international research on virtually all aspects of the Southern Ocean, from physical oceanographical, through geochemical, to biological sciences to monitor change and evaluate potential impacts of global change on Southern Ocean ecosystems (Rintoul et al. 2009). The increase in knowledge of Southern Ocean benthic biodiversity has enabled its use to study responses to environmental change, of which the most prominent example has probably been the recolonization of the seafloor following ice-shelf collapse in the Larsen A and B regions (Gutt et al. 2011). Although glaciological models at first suggested life were almost entirely eradicated during the last (and perhaps during each) glacial period (Anderson et al. 2002), there is now biological evidence that, as on land, benthic life survived throughout past glaciations in multiple continental shelf refugia (Newman et al. 2009; Allcock and Strugnell 2012). This has considerable ramifications to the interpretation of biodiversity and distribution patterns but also ice-sheet modelling and sea-level projections (Barnes and Hillenbrand 2010).

Advances in investigating large-scale distributions of Southern Ocean benthos

Assessing species' distributions has a long history in Antarctica (Regan 1914; Hedgpeth 1969; Dell 1972; Brandt 1991; Online Resource 1 [30–34]), but more recently, multivariate statistics, geographical information systems (GIS), molecular tools and models to explain large-scale distributions have entered the field (Linse et al. 2006; Göbbeler and Klussmann-Kolb 2010; Gutt et al. 2012). Furthermore, the integration of glaciological and geophysical information into biogeographic analyses (and vice versa) has provided further evidence for glacial refuges and trans-Antarctic seaways and thus casting new light on the origin of Antarctic shelf faunas (Newman et al. 2009; Barnes and Hillenbrand 2010; Vaughan et al. 2011). For example, high faunal similarity of bryozoan assemblages of the Weddell and Ross seas alongside ice-sheet models indicate that a seaway connecting both oceans was present about 100 kya that is much more recent than previously thought (Barnes and Hillenbrand 2010; Vaughan et al. 2011).

Early definitions of subdivisions of the Antarctic biogeographic region were based on the distributions of the fauna (Regan 1914; Online Resource 1 [30–31]), taxon

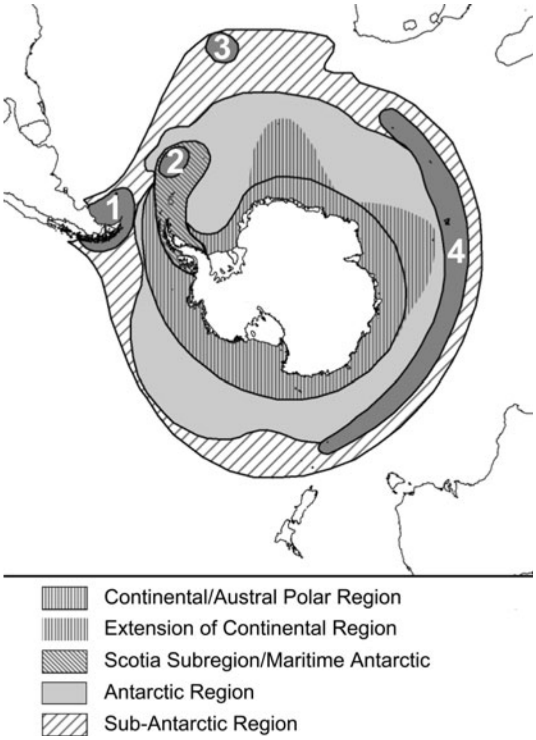

Fig. 5 Previously recognized Antarctic marine biogeographic subregions defined for the benthic realm; *1* Magellan Sub-region; *2* South Georgia District; *3* Tristan da Cunha District; *4* Kerguelen Sub-region (modified after Hedgpeth 1969)

distributions combined with geological (Norman 1937) or oceanographic data (Regan 1914; Online Resource 1 [30–31]) and led to the definitions of a sub-Antarctic/low Antarctic zone and an Antarctic/high Antarctic zone. The scheme proposed by Hedgpeth (1969) was widely accepted by marine benthologists for biogeographic studies in the following three decades (Fig. 5).

The new millenium saw the introduction of relational databases to take the place of the faunal catalogues in biodiversity and biogeographic studies (Budd et al. 2001). For the Southern Ocean, databases like SOMBASE (Southern Ocean Mollusc Data Base, Griffiths et al. 2003) and international initiatives such as SCAR-MarBIN and CAML have greatly advanced knowledge of biogeographic distributions by collating georeferenced species information (Griffiths et al. 2011). They have also become important as a tool to establish baselines for monitoring range shift responses (Barnes et al. 2009).

Recent studies, for example by Linse et al. (2006), Clarke et al. (2007), Griffiths et al. (2009) and Downey et al. (2012), focused on biogeographic patterns of shelled molluscs, pycnogonids and sponges, without including any initial assumptions based on previous studies. Remarkably, the perceived patterns differed little from those proposed by Hedgpeth (1969). However, a greater spatial resolution allowed the investigation of regional patterns within the PF (Clarke et al. 2007). Furthermore, Griffiths et al. (2009) showed that Hedgpeth's division into an East and West

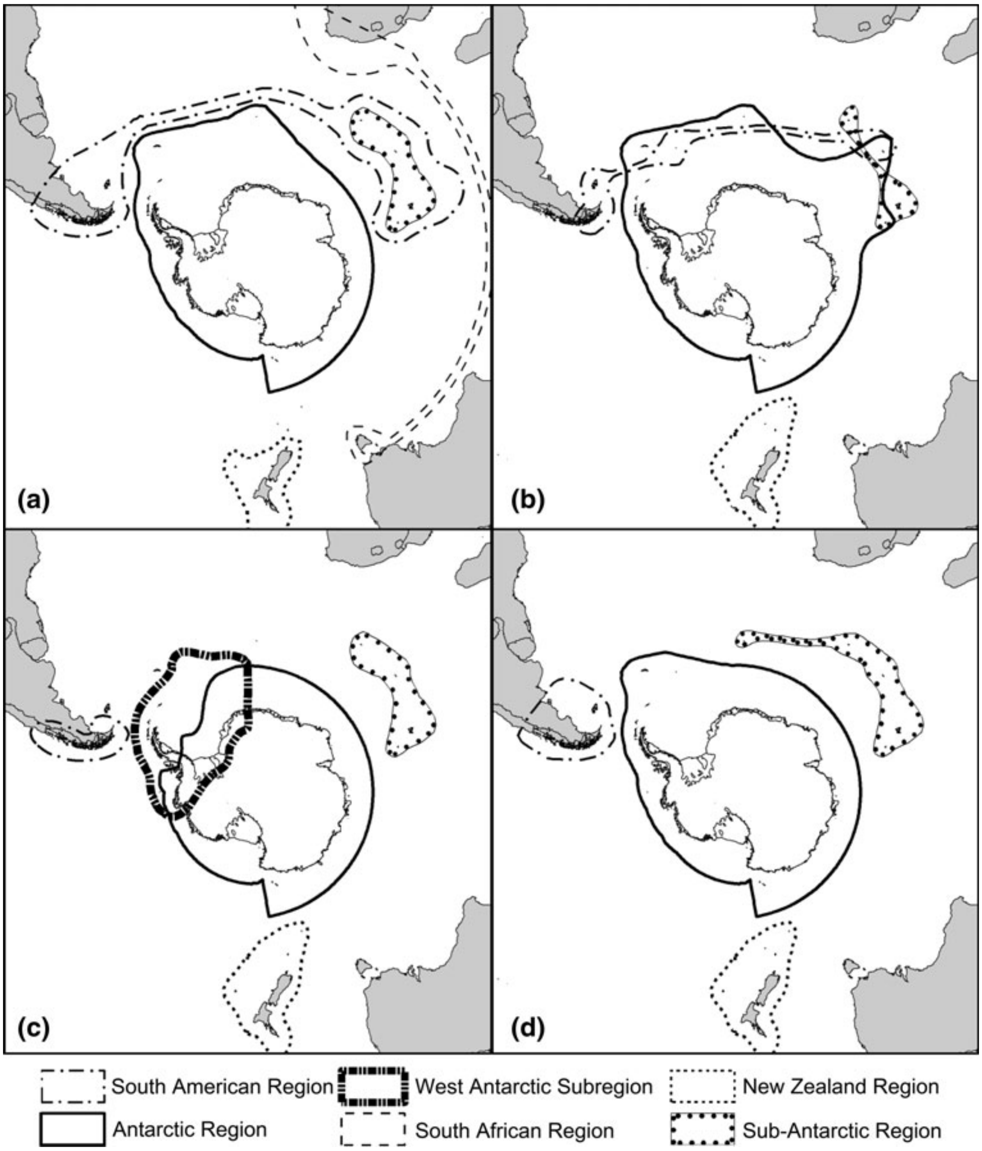

Fig. 6 Recent Antarctic marine biogeographic sub-regions for the benthic fauna: **a** Cheilostomata; **b** Bivalvia; **c** Gastropoda; **d** Pycnogonida; figure reproduced with permission from Griffiths et al. 2009

Antarctic fauna was an artefact due to uneven distribution of samples around Antarctica (Fig. 6) and that levels of endemism were overestimated (compare Arntz et al. 1997).

New algorithms allow a single approach for the identification of areas distinguished by their biological content (biogeography) and the study of organisms in relation to their environment (bionomy). Community models now perform 'ecoregionalization,' which is a truly interdisciplinary approach combining spatial (geography), biological (presence, abundance, probabilities of presence of the species), physical (e.g., depth, temperature) and still more rarely chemical (oxygen, nitrates etc.) data (Beaman and Harris 2005; Gutt et al. 2012; Pierrat et al. 2012; Online Resource 1 [35–36]).

Most Southern Ocean biogeographic studies so far have focused on the assessment of macro- and megafaunal patterns, while analyses conducted on meiofauna have received little attention. Meiobenthos includes soft-bodied taxa (such as nematodes) and microfossil taxa (ostracods and foraminifers), which have been studied by both biologists and micropalaeontologists. Over the past 10 years, greatest advances include the synthesis of modern and Cenozoic distributions of a diverse meiofaunal group, ostracod crustaceans (Yasuhara et al. 2007), as well as the investigation of geographic and bathymetric distribution of selected taxa at low taxonomic (i.e., species and generic) level based on both morphological and/or genetic data sets (Ingels et al. 2006; Fonseca et al. 2007; Pawlowski et al. 2007; Gheerardyn and Veit-Köhler 2009). Two contradictory pictures came from these studies. A review of morphology-based studies revealed high endemism and homogeneity (i.e., circum-Antarctic similarity) of the Antarctic ostracod fauna (Yasuhara et al. 2007), while detailed low-taxonomic level studies based on the re-analyses of the morphology of previously collected specimens and also on genetics of selected taxa suggested contrasting distributional patterns that is spatially very restricted versus widely distributed taxa (Fonseca et al. 2007; Pawlowski et al. 2007; Gheerardyn and Veit-Köhler 2009). A palaeoecological study of deep-sea benthic ostracods revealed systematic faunal change related to Quaternary glacial–interglacial climatic and deep-water circulation changes (Yasuhara et al. 2009). Analyses based on georeferenced databases are still missing for meiofauna though, possibly because of its high diversity and abundance levels, which makes identification to species level prohibitive (e.g., in nematodes: Ingels et al. 2006). Thus, data collation for many meiofaunal taxa is still far from being completed (see SCAR-MarBIN; De Broyer et al. 2011).

A current question for Southern Ocean biogeography is how the results from molecular genetics (cryptic species vs. lumping of species) might translate into biogeographic patterns. Molecular data will probably provide much greater resolution on the nature of the finer-scale biogeographic divisions within the Southern Ocean at regional and sub-regional level, which may or may not change the general patterns. Greater geographic and bathymetric sampling, on the other hand, as well as exploration and finding of new habitats (such as seamounts, under-ice shelves) has led to the discovery of taxa new to the Southern Ocean and/or science with the potential to close some biogeographic gaps (Griffiths et al. 2009; Gutt et al. 2011).

Discovery of new benthic habitats

The discovery of new benthic habitats in the Antarctic during CAML has been closely linked to developments in the use of seabed video and photography as well as optical sensors and multibeam echosound data (German et al. 2000; Gutt et al. 2011; Marsh et al. 2012). These developments have enabled remarkable ecological advances, including the discovery of new species, new behaviours and insights into the spatial structure of assemblages (see Fig. 7). Although early use of cameras showed that sparse invertebrate and fish populations persist under permanent ice shelves (Bruchhausen et al. 1979), recent studies have revealed rich benthic faunal assemblages. On the Amery ice shelf, East Antarctica, 100 km from the nearest ice edge, Riddle et al. (2007) deployed video cameras to 775 m depth through 480 m of ice and recorded a diverse community including abundant sessile and motile fauna. The presence of suspension-feeding taxa and strong seabed currents indicated that the assemblage is likely to be sustained by advection of organic material from open water, rather than preserved in sediments (Riddle et al. 2007). Further evidence of benthic fauna persisting beneath permanent ice shelves came following the disintegration of the Larsen ice shelves in 1995 and 2002. In 2007, scientists were able to observe areas of seabed that were 110 km from the former ice edge (Gutt et al. 2011); they observed several taxa, including holothurians and sponges, normally associated with the deep sea and attributed their presence to the similarity of conditions beneath the ice shelf to those in neighbouring deep-sea environments.

The past decade has also seen the first discovery of chemosynthetic communities in the Antarctic. Observations in the area formerly covered by the Larsen B ice shelf revealed the first evidence of a cold seep fauna; Domack et al. (2005) reported live vesicomyid clams and bacterial mats at a site 100 km from the ice edge. Gutt et al. (2011) revisited this site in 2007, reporting patches of clam shells and bacterial mats, but no live chemosynthetic macrofauna. This seep is apparently of low activity, and it is possible that increased organic sedimentation following disintegration of the ice shelf is already causing assemblage change (Domack et al. 2005; Hauquier et al. 2011; Online

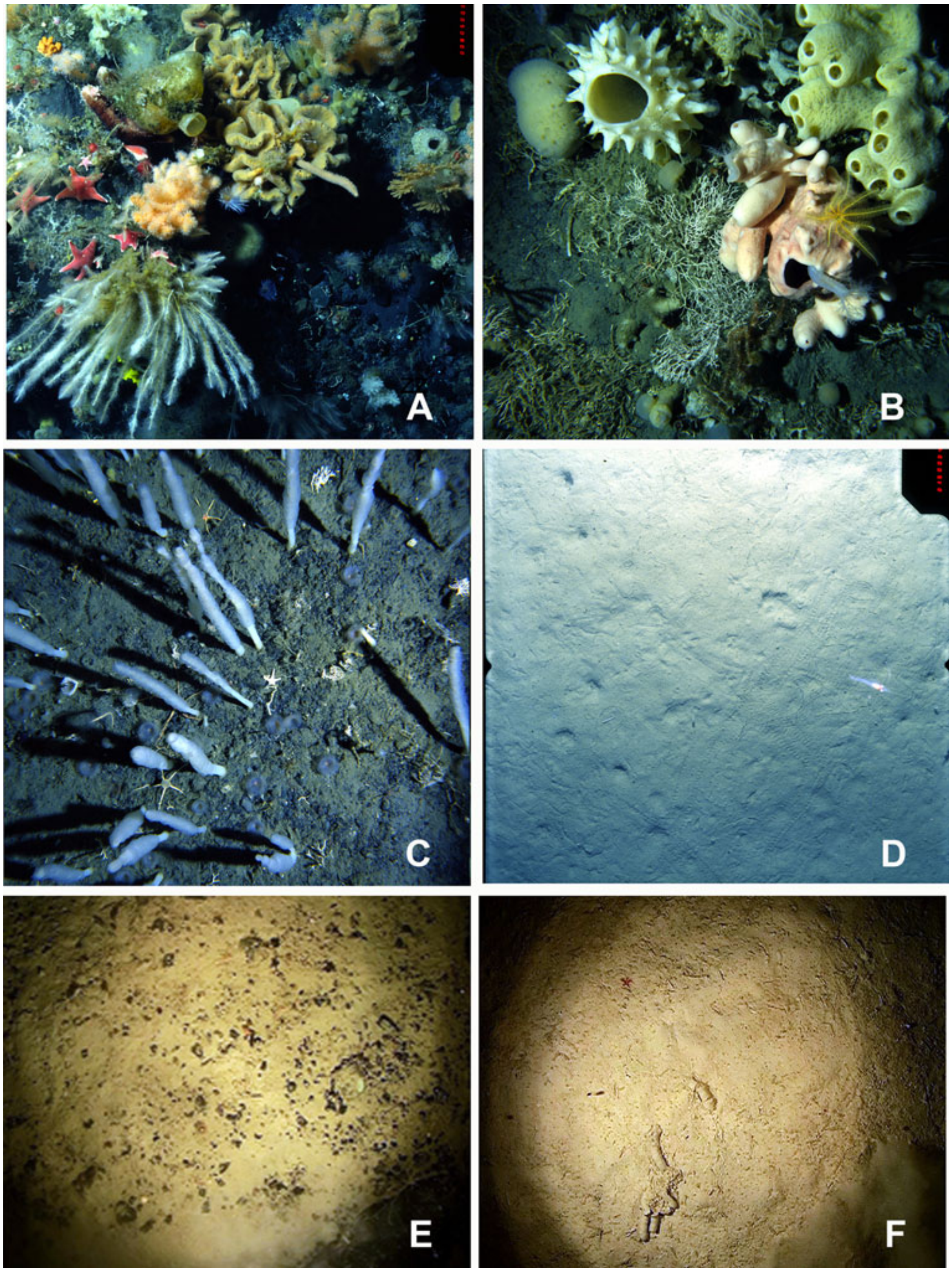

Fig. 7 Seabed imagery of different shelf and deep-sea Antarctic benthic habitats; in addition to corers, grabs and trawls, in situ observations using still and video imaging can provide qualitative information on, for example, the spatial structure of assemblages (such as variability of faunal densities across different spatial scales), biotic interactions as well as geomorphologic features and thus advances the understanding of the benthic ecosystem. **a** continental shelf, south-eastern Weddell Sea (PS 56/111-2, 71.13°S, 11.46°E, 69 m), showing unusually high mega-epibenthic biodiversity at shallow depth (doi:1594/PANGAEA.319917); **b** continental shelf, south-eastern Weddell Sea (PS 39/006-1, 71.52°S, 13.51°W, 223 m), typical Antarctic sponge community including both Hexactinellida and Demospongiae as well as associated fauna—bryozoans, ascidians, holothuroids and crinoids—(doi:10.1594/PANGAEA.319889); **c** continental shelf, south-eastern Weddell Sea (PS 39/007-1, 71.45°S, 13.72°W, 212 m) megabenthic communities dominated by synascidians and polychaetes "most likely" representing a mid-successional stage following iceberg disturbance (doi: 10.1594/PANGAEA.319890); **d** continental shelf, south of South Georgia (PS 61/235-1, 61.19°S, 54.72°E, 324 m), apart from 'Lebensspuren' of mobile fauna no epibenthic or sessile biota were present (doi:10.1594/PANGAEA.220746); **e** continental slope, Lazarev Sea (SYSTCO I, PS 71/17, 70°04′S–003°23‘W, 1,960–2,044 m); the seafloor was characterized by and 5–20 % stone coverage, epifauna was relatively rich and dominated by *Nematocarcinus longirostris* Bate, 1888 (Decapoda), different holothuroids and *Umbellula* sp. (octocoral); **f** Maud Rise, seamount, Weddell Sea (SYSTCO I, PS 71/39, 64°28′S–002°53‘W, 2,117–2,120 m); the surface of the seafloor looked coarse, 1–2 % was covered with stones. The abundance of visible epifauna was low. Only few organisms could be observed more than once—including holothuroids and near-bottom chaetognaths. Images **e**–**f** by N. Brenke, DZMB

Resource 1 [37]). The main significance of these findings, however, is that chemosynthetic ecosystems can persist under ice shelves for thousands of years (Domack et al. 2005). For some years, characteristic water-column signatures have indicated that hydrothermal venting occurs at the East Scotia Ridge. However, it was only in 2009 under the Chemosynthetic Ecosystems of the Southern Ocean (CHESSO) programme that vents were located at the ridge segments E2 and E9 (Rogers et al. 2012). Analyses of the macrofauna from these sites showed that the vent-associated faunal communities are unlike any that have yet been described and form a distinct biogeographic province (Rogers et al. 2012). The communities are being dominated by dense populations of kiwaid crabs and eolepadid barnacles (both crustaceans) and show a clear faunal zonation from the fluid source to the periphery (Marsh et al. 2012; Rogers et al. 2012).

The evidence for life persisting beneath ice shelves has implications for our understanding of how benthic biodiversity has responded to glacial cycles over evolutionary timescales. For non-chemosynthetic fauna, current theories based on the concepts of severely limited survivorship during glacial maxima, dispersal from isolated refugia during interglacial periods, and consequent allopatric speciation (Clarke and Crame 1992; Aronson et al. 2007) may need to be modified to include potentially widespread persistence of life beneath ice shelves during glacial maxima. Furthermore, because seep and vent ecosystems are decoupled from reliance on photosynthetic primary production, conventional assumptions about the ability of life to persist beneath permanent ice shelves may not apply at all for chemosynthetic taxa.

Use of seabed cameras has also yielded insights into the ecology of benthic fauna. These range from novel analyses of faunal distributions in relatively well-studied areas (Barry et al. 2003; Gutt and Piepenburg 2003; Online Resource 1 [38]) to exploration of new regions and observation of new behaviours. On the George V shelf, East Antarctica, cameras on benthic trawls revealed dense populations of stylasterid hydrocorals (*Errina* sp.) at the continental shelf break (Post et al. 2010). Similar populations were also recorded on the north-western shelf break of the Ross Sea using a towed camera system (NIWA unpublished data), while in the Weddell Sea, high abundances of the hydrocoral *Errina laterorifa* Eguchi, 1964 were recorded at an unusually shallow depth close to the edge of the Larsen B ice shelf (Gutt et al. 2011). These discoveries are stimulating research into the environmental drivers of hydrocoral distribution and the genetic relatedness of populations (N. Bax and K. Miller pers comm). On Admiralty Seamount, north of the Ross Sea, assemblages dominated by dense populations of a previously unknown stalked crinoid (Eléaume et al. 2011) were discovered during exploratory towed camera transects (Bowden et al. 2011). These assemblages are extraordinary because of their functional resemblance to those widespread in shallow seas during the Palaeocene, and evidence of predation effects supports the hypothesis that the decline of stalked crinoids resulted from the evolution of mobile predators (Aronson et al. 1997; Bowden et al. 2011). Finally, video has also enabled important insights into the behaviour of Antarctic krill (*Euphausia superba* Dana, 1850). Clarke and Tyler (2008) observed high abundances of krill feeding on the seabed at 3,500 m depth off Marguerite Bay, WAP. This remarkable observation has overturned the existing paradigm that krill were restricted to the upper 150 m of the water column.

Threats, ecophysiology and vulnerability of Antarctic benthos

West Antarctica, in particular the Antarctic Peninsula, is a hotspot of realized and projected climate change, for example, in warming and ice loss (Meredith and King 2005). This rapid physical change in a region which has been one of the most thermally constant for millions of years together with associated shifts in penguins, krill and phytoplankton population size (Trivelpiece et al. 2011) has led to profound concern about impacts on the mainly endemic fauna. Potential vulnerability has been supported by experimental work on lethal and functional limits of acute temperature and pH decline in ectotherms (Peck et al. 2010). Reviews of climate-forced impacts on Southern Ocean biodiversity have concluded that there is little or no evidence of biological response in the majority of trophic levels, guilds and species—it was also clear that we know less than two per cent of the species well enough to be likely to detect any change (Clarke et al. 2007). Knowledge and understanding of Antarctic ectotherm physiology have more than doubled in the last decade, mainly by quantification of oxygen use, protein synthesis, stenothermal range of critical activities (e.g., burrowing in bivalves), production and maintenance of carbonate with decreased pH and gene expression in response to stress.

Attempts to answer questions regarding vulnerability of polar species to changes in the physical environment require an understanding of sensitivity and tolerance to shifts in the abiotic conditions on different levels of biological organization as well as ecophysiological studies conducted on different spatial, temporal and ecological scales (in terms of functional groups) (Ingels et al. 2012). In the last decade, such knowledge has increased markedly with a wide literature of experimental manipulations under controlled conditions established across many taxa (Peck 2005; Young et al. 2006; Clark et al. 2008; Peck et al. 2009, 2010; Janecki et al. 2010; see review for five zoobenthic groups in Ingels et al. 2012). Of particular interest has been the effect of rising temperatures (and associated oxygen limitation) on the physiology and functioning of various marine organisms such as molluscs (Clark et al. 2008; Peck et al. 2010), echinoderms (Peck et al. 2010), crustaceans (Young et al. 2006; Janecki et al. 2010), brachiopods (Peck 2008), ascidians, bryozoans (Barnes and Peck 2005) and certain groups of fish amongst several others (Peck et al. 2009). The rate of temperature rise drastically influences the physiological capability of organisms to cope with it; when temperatures are raised acutely, thermal tolerance is high, while for temperature increases over periods of months the same species can have much lower tolerance levels (Peck et al. 2009).

Ecosystems in the Southern Ocean are projected to be affected more severely by ocean acidification than elsewhere due to the higher solubility of CO_2 at lower temperatures and regular upwelling of CO_2-enriched waters (Fabry et al. 2009); the oceans south of 40°S take up about 40 % of anthropogenic CO_2 (Khatiwala et al. 2009). Recent mineralogical investigations and pH manipulation experiments have revealed considerable variability in organisms' sensitivity to ocean acidification with knock-on effects on ecosystem functioning (Kroeker et al. 2010). Thinly calcified marine organisms such as foraminifers, echinoderms, molluscs and coralline algae, particularly those which use the aragonite form of $CaCO_3$, are considered to be most at risk in the near future (Moy et al. 2009; Bednaršek et al. 2012; Online Resource 1 [39]). Beside the effect on carbonate precipitation in skeletal elements, recent studies have suggested that ocean acidification will affect physiological functioning of marine species, especially in organisms with a low ability to regulate extracellular acid–base balance (Pörtner 2008; Hofmann and Todgham 2010).

A recent development has been the study of the genomic basis of organism responses to climate change-induced effects shedding new light on acclimatization and/or adaptation in marine Antarctic fauna (Pörtner et al. 2007; Somero 2010; Rogers 2012; Online Resource 1 [40]). Genetic lesions (e.g., loss of protein coding genes, disability to regulate gene expressions) that seem to accompany long periods of evolution in thermally stable habitats, such as in the Antarctic marine environment, appear at least partially responsible for the extreme stenothermy found in species like Southern Ocean ectotherms; a characteristic that renders them particularly vulnerable to the predicted rise in temperature (Somero 2010). The ability to adapt to changing conditions depends, for example, on generation time, metabolic rate, temperature and population size (Martin and Palumbi 1993). Antarctic benthic species grow slowly and develop at rates typically 4–18 times slower than similar warm-water species. They can live to greater age and exhibit deferred maturity (Peck et al. 2006), which may slow down molecular change (but see Held 2001). Modern-day observations suffer from the lack of knowledge of genetic and functional as well as adaptation rates between populations exposed to different environmental constraints. A second shortcoming is the fact that site-specific microclimates often differ significantly from the average environment measured for the observed area making our understanding of general processes much more difficult (Clarke et al. 2009).

Gaps of knowledge and future challenges

Present research gaps

The combination of the CoML, IPY and some of the largest ever international Antarctic biological projects (such as ANDEEP, CEAMARC and the Ecology of the Antarctic Sea Ice Zone (EASIZ) projects) has made the past decade one of unprecedented progress in understanding Southern Ocean benthic biodiversity (in terms of development of sampling and analytical techniques and approaches, organization of data and science etc.). In this paper, we have highlighted seven significant areas of progress on Southern Ocean benthic research in the last decade. We are aware though that there are many others that are smaller, more gradual or emerging (such as synecological aspects, conservation biogeography; Terauds et al. 2012)—and that those we discuss are in many ways interlinked. It is the increased intensity, variety and geographic spread of sampling that has partly enabled the improvement in taxonomy, phylogeography, biodiversity and biogeography. Crucially, the level of sampling has reached the point where we can start establishing some approximate population and species ranges and 'hot- or cold-spots' of richness versus sampling effort (Clarke and Johnston 2003; Griffiths et al. 2011).

However, these advances also highlight important gaps of knowledge, such as sufficient information on species' life histories (Blight et al. 2010), interrelationships within the Southern Ocean benthic food web (Würzberg et al. 2011) as well as biogeographic gaps; scientific benthic effort has predominantly concentrated on the continental shelves within 150 km of research stations—with the result that most of the slope and abyss still remain completely unsampled (Griffiths 2010). Even at shelf depth, there are sampling gaps spanning nearly 50° longitude (such as the Amundsen Sea, Fig. 3).

A major theme that has attracted much attention (more so for example than seems to be the case for other continents or oceans) is the assessment of species richness, that is, how taxon-rich is the Antarctic and what are the causes of hemispherical asymmetry in the latitudinal biodiversity cline (Culver and Buzas 2000; De Broyer et al. 2011)? It is clear that species-richness estimates are better for some areas than others, and they also contain more errors for some taxa than others. That is, marine vertebrates are much better known than invertebrates, for instance, polychaetes or nematodes (De Broyer et al. 2011). Despite the level of scientific interest and high Antarctic endemism, alongside 'how rich is Antarctica?' we must also ask how important this question is and how much effort we should put into it? For example, if compliance with the spirit of the International Convention on Biological Diversity is one of the key driving factors behind this question then it could be argued that the best approach is to understand this on an area by area (rather than taxon by taxon) basis. Furthermore, the mere number of species does not tell us anything about, for instance, their function in the ecosystem or their evolutionary origin. So there seem to be much more pending questions about biodiversity such as, will species richness provide ecosystem resilience to non-indigenous species invasion or climate change or both? How and why does it vary so much from place to place within the Southern Ocean? What are the key drivers, at which spatial scale do they act and what does it mean if one area is richer than another?

Despite the wide appreciation of multi-scale studies in ecology, in the Southern Ocean such sampling strategy (i.e., taking quantitative replicate samples multiple distances apart) is still in its infancy. Research on the Antarctic continental shelf has just started to apply rigorous, spatially structured sampling regimes (Cummings et al. 2006; Kröger and Rowden 2008). For example, work that has been done on assessing changes in Southern Ocean deep biodiversity focused on large-scale comparisons (i.e., between ocean basins, regions) partly due to cost and time intensity of deep-sea deployments. Little effort has been made to look at the variability on smaller scales, or whether large-scale comparisons are valid (i.e., is the variability within a region as significant as that between regions, but see Kaiser et al. 2007). Furthermore, studies integrating both ecological and palaeoecological approaches (i.e., spatial vs. temporal and short-term vs. long-term studies) are scarce in the Southern Ocean, although the number of studies linking these data sets is currently increasing elsewhere (e.g., Yasuhara et al. 2012). Advances in this field are, however, crucial in order to gain a more comprehensive understanding of the Southern Ocean ecosystem and biodiversity dynamics through time and space.

Although limited sampling has been done in the Southern Ocean deep sea, even the data from these are often hard to compare because of the high variety of sampling gear used on different expeditions (Kaiser and Barnes 2008). Comparability has been further undermined by different mesh sizes, protocols, taxonomic resolution and data treatment. Even when using the same apparatus (e.g., epibenthic sledge) comparison between samples can be delicate due to, for example, different trawling velocities, towing distances or sediment type (Brenke 2005). So, across institutes advances are required in the application of standardized sampling techniques and protocols in order to increase the power of concerted scientific efforts and data.

Another one of the major themes that has emerged in recent years has been focussing on climate change and life's response to it. We now have an idea how single individuals of selected model species will respond to changes in acidification and temperature rise in a given time frame and under controlled laboratory conditions. However, no generality has yet been reached with respect to how climate change will affect biological diversity in the Southern Ocean as a whole. Most studies deal with just single species, such as the pelagic mollusc *Clio pyramidata* Linnaeus, 1767 (Orr et al. 2005), Antarctic krill (Kawaguchi et al. 2011) or selected taxa (foraminiferans: Moy et al. 2009; echinoids: Sewell and Hofmann 2011). Although these may be regarded as 'key' taxa, they merely represent a snapshot of the whole ecosystem and studies have hardly considered effects on changing interactions between species let alone community-scale effects. Variation in temperature and ocean chemistry (e.g., ocean acidification) as a result of elevated atmospheric CO_2 levels is likely to affect species' distributions. In fact, laboratory experiments have revealed that many of the common ectothermal species in the Antarctic shallows are very sensitive to small acute changes in temperature (see Peck 2005). Although such species seem unable to acclimate to rises of as little as 1 °C above ambient summer maxima, the long-term interpretation of this is unclear and debatable (see Barnes and Peck 2008). For example, scaling short-term (hours to months) experiments to those at longer time scales relevant to climate-induced changes (i.e., years, decades, centuries) may not be valid (but see Barnes et al. 2010), and no experiments to date have factored in seasonal (or other duration) variability in temperature. Furthermore, most studies have only considered single abiotic factors (such as temperature and ocean acidification) for the assessment of potential impacts on species' distributions and rarely included multiple environmental variables. However, physical parameters seem to alter ecosystems in much more complex ways and are often highly inter-correlated. For example, recent warming of surface waters along the WAP already led to a decline in the duration and extent of winter sea-ice cover over the past 25 years and, as a consequence, an increase in iceberg-scour frequency—with obvious negative impacts for benthic biota (Barnes and Souster 2011). Thus, what has become increasingly clear is the need for the integration of data on species' capacities to resist and/or adapt to climate change and the incorporation of ecophysiological information, but also evolutionary processes. To what extent, an ecosystem as a whole responds to physical changes remains almost unknown and is one of the great challenges of the next decade.

New directions and challenges

Biology has never been more important especially on the background of conservation issues, maintenance of ecosystem services (e.g., carbon storage, fisheries) as well as current and future exploitation of the Antarctic environment (Tin et al. 2009; Chown et al. 2012). This paper presented the advances achieved in the last decade in the investigation of Southern Ocean benthos, but also highlighted some important research gaps. So where do we go from here? What are the challenges we are going to face and which research priorities do we need to frame for the next decade?

The Southern Ocean seabed has long been one of the least anthropogenically impacted environments on our planet (Halpern et al. 2008), so it arguably represents one of the most 'natural' laboratories. To date, most of the species described from there are endemic; hence more than anywhere else their potential loss is a global loss. Now, the polar regions are changing at rates unusual in recent time (Mulvaney et al. 2012). So, with anthropogenic impacts on the Southern Ocean benthos accelerating, there is a great demand to further our knowledge and understanding of biodiversity and underlying processes as a sound basis for the protection of the Antarctic ecosystem. However, the lack of taxonomic expertise, combined with the huge proportion of species new to science, do not only hamper the assessment of biodiversity and biogeographic patterns, but also represent a great impediment to conservation planning (Coleman et al. 2010). Furthermore, regional warming coupled with an increase in tourist activities means that the South-polar regions are at high risk for species invasions (Chown et al. 2012). Unlike Antarctic terrestrial habitats though, there have been no established non-indigenous species recorded from the marine realm yet. However, with many species being newly discovered and several representing species complexes, it is impossible to determine the invasive status of a species (Griffiths 2010). Thus, the characterization of Southern Ocean biodiversity is a key priority, requiring both speedy and accurate species identifications as well as standardized sampling procedures. This will mean development and increased application of taxonomic tools (such as DNA barcoding, interactive keys etc.) to accelerate identification processes as well as to provide support for the training of future taxonomists to compensate the decline of taxonomic expertise. As a community, we will also need to improve current sampling devices as well as redesigning the basic structure of scientific cruises in terms of sample design, data management and interpretation, and inevitably establishing international collaboration and agreement beyond anything to date.

Biogeographic databases (such as SCAR-MarBIN, RAMS) have become a powerful tool to collate, catalogue and manage biological data not only for the assessment of large-scale distribution patterns, but also to monitor changes in species spatial distributions and therefore to provide the necessary information to enable informed decision-making (Danis and Griffiths 2009). In the framework of IPY and the CAML, the Antarctic scientific community (through SCAR-MarBIN) has collated an immense amount of data comprising thousands of georeferenced records for more than 7,000 benthic species (De Broyer et al. 2011). However, these data are still not comprehensive enough for some areas and taxa; for example, sufficient fishery data are currently lacking, particularly from actively fished areas such as the Ross Sea, making stock assessment and thus fishery management difficult (Blight et al. 2010). So, it is crucial to enhance information transfer between researchers, commercial industries and policy makers by allowing free accessibility and rapid publication of biodiversity data (Chown et al. 2012).

One of the greatest challenges, not only in the Southern Ocean but globally, is probably to balance the conservation of natural resources and services with an increasing demand for exploitation. Under the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), considerable efforts towards the establishment of a network marine protected areas (MPA) in the Southern Ocean are being made to ensure the protection of its biodiversity (CCAMLR XXVII 2008). In 2009, the first Antarctic high-sea MPA was established south of the South Orkneys (Weddell Sea, CCAMLR-XXVIII 2009). In 2012, South Georgia and the South Sandwich Islands became one of the World's largest designated MPAs spanning more than one-million square kilometres. Proposals were put forward to protect the Ross Sea region and East Antarctica; these were recently withdrawn though, as they failed to reach agreement on matching economic and scientific interests (Cressey 2012). Both proposals are currently still under consideration and will be further discussed during a special CCAMLR meeting in Bremerhaven (Germany) scheduled for July 2013 (Cressey 2012).

To date, less than 1 % of the Southern Ocean seafloor is protected (Ainley and Tin 2012). So, there is a need to push forward MPA planning processes. Additionally, the effectiveness of such MPAs needs to be carefully evaluated (Mora and Sale 2011), in that it does only provide protection of local populations, but does not prevent biodiversity loss due to regional- to global-scale impacts such as ocean acidification, warming and invading species. Hence, it is important to promote cooperation across biological and non-biological disciplines, but also beyond the PF to inform each other and to effectively communicate research activities and outcomes between institutions, governments, stakeholders and the general public.

Over the past 10 years, initiatives such as the IPY and CoML have provided a key platform to coordinate biological science in the Southern Ocean. Yet, how can we carry these efforts forward into the next decade? The SCAR Scientific Research Programmes (SRPs) are transformative scientific initiatives that address compelling issues and emerging frontiers in Antarctic or Southern Ocean science of regional and global importance. After an extremely successful run, the SRP EBA ended in 2013, leading to the start of the next generation of SCAR SRPs from 2013, including the State of the Antarctic Ecosystem (AntEco), and Antarctic Thresholds—Ecosystem Resilience and Adaptation (AnT-ERA). AntEco is divided into three interlinked themes: (a) Evolved patterns, (b) Spatial patterns and (c) Governance, mitigation and adaptation across the Antarctic, sub-Antarctic and Southern Ocean regions. AnT-ERA seeks to define and facilitate the science required to determine the vulnerability and resilience of Antarctic biological systems to change and stress. As a consequence, AnT-ERA will assess the likelihood of crossing biological thresholds—in other words to determine how close we are to the ecological cliff.

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References

Ainley D, Tin T (2012) Antarctica. In: Hilty JA, Chester CC, Cross MS (eds) Climate and conservation. Island Press, Washington, pp 267–277

Allcock AL, Strugnell JM (2012) Southern Ocean diversity: new paradigms from molecular ecology. Trends Ecol Evol 27(9):520–528

Allcock AL, Brierley AS, Thorpe JP et al (1997) Restricted gene flow and evolutionary divergence between geographically separated populations of the Antarctic octopus *Pareledone turqueti*. Mar Biol 129:97–102

Anderson JB, Shipp SS, Lowe AL et al (2002) The Antarctic ice sheet during the last glacial maximum and its subsequent retreat history: a review. Quat Sci Rev 21:49–70

Arango CP, Wheeler WC (2007) Phylogeny of the sea spiders (Arthropoda, Pycnogonida) based on direct optimization of six loci and morphology. Cladistics 23:1–39

Arango CP, Soler-Membrives A, Miller KJ (2011) Genetic differentiation in the circum-Antarctic sea spider *Nymphon australe* (Pycnogonida; Nymphonidae). Deep-Sea Res Part II 58(1):212–219

Arntz WE, Brey T, Gallardo VA (1994) Antarctic zoobenthos. Adv Mar Biol 32:241–304

Arntz WE, Gutt J, Klages M (1997) Antarctic marine biodiversity: an overview. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities. Species, structure and survival. Cambridge University Press, Cambridge, pp 3–14

Arntz WE, Thatje S, Linse K et al (2006) Missing link in the Southern Ocean: sampling the marine benthic fauna of remote Bouvet Island. Polar Biol 29:83–96

Aronson RB, Blake DB, Oji T (1997) Retrograde community structure in the late Eocene of Antarctica. Geology 25:903–906

Aronson RB, Thatje S, Clarke A et al (2007) Climate change and invasibility of the Antarctic benthos. Annu Rev Ecol Evol Syst 38:129–154

Baird HP, Miller KJ, Stark JS (2012) Genetic population structure in the Antarctic benthos: insights from the widespread amphipod. *Orchomenella franklini*. PLoS ONE 7(3):e34363

Ballard JWO, Whitlock MC (2004) The incomplete natural history of mitochondria. Mol Ecol 13:729–744

Barnes DKA, Clarke A (1994) Seasonal variation in the feeding activity of four species of Antarctic Bryozoa in relation to environmental factors. J Exp Mar Biol Ecol 181:117–133

Barnes DKA, Clarke A (2011) Antarctic marine biology. Curr Biol 21:R451–R457

Barnes DKA, Hillenbrand CD (2010) Faunal evidence for a late quaternary trans-Antarctic seaway. Glob Change Biol 16:3297–3303

Barnes DKA, Peck LS (2005) Extremes of metabolic strategy in Antarctic Bryozoa. Mar Biol 147(4):979–988

Barnes DKA, Peck LS (2008) Vulnerability of Antarctic shelf biodiversity to predicted regional warming. Clim Res 37:149–163. doi:10.3354/cr00760

Barnes DKA, Souster T (2011) Reduced survival of Antarctic benthos linked to climate-induced iceberg scouring. Nature Clim Change 1:365–368

Barnes DKA, Kaiser S, Griffiths HJ et al (2009) Marine, intertidal, fresh-water and terrestrial biodiversity of an isolated polar archipelago. J Biogeogr 36(4):756–769. doi:10.1111/j.1365-2699.2008.02030.x

Barnes DKA, Peck LS, Morley SA (2010) Ecological relevance of laboratory determined temperature limits: colonization potential, biogeography and resilience of Antarctic invertebrates to environmental change. Glob Change Biol 16(11):3164–3169

Barry JP, Grebmeier JM, Smith J et al (2003) Oceanographic versus seafloor-habitat control of benthic megafaunal communities in the S.W. Ross Sea, Antarctica. Antarct Res Ser 78:327–354

Beaman RJ, Harris PT (2005) Bioregionalisation of the George V Shelf, East Antarctica. Cont Shelf Res 25:1657–1691

Beaumont MA, Nielsen R, Robert C et al (2010) In defence of model-based inference in phylogeography. Mol Ecol 9:436–446

Bednaršek N, Tarling GA, Bakker DCE et al (2012) Extensive dissolution of live pteropods in the Southern Ocean. Nature Geosci. doi:10.1038/NGEO1635

Bickford D, Lohman DJ, Sodhi NS et al (2007) Cryptic species as a window on diversity and conservation. Trend Ecol Evol 22:148–155

Blight LK, Ainley DG, Ackley SF et al (2010) Fishing for data in the Ross Sea. Science 330(6009):1316

Bowden DA, Schiaparelli S, Clark MR et al (2011) A lost world? Archaic crinoid-dominated assemblages on an Antarctic seamount. Deep-Sea Res Pt II 58:119–127

Brandão SN, Sauer J, Schön I (2010) Circumantarctic distribution in Southern Ocean benthos? A genetic test using the genus *Macroscapha* (Crustacea, Ostracoda) as a model. Mol Phylogenet Evol 55:1055–1069

Brandt A (1991) Zur Besiedlungsgeschichte des antarktischen Schelfes am Beispiel der Isopoda (Crustacea, Malacostraca). Ber Polarforsch 98:1–240

Brandt A, Gooday AJ, Brandão SN et al (2007) First insights into the biodiversity and biogeography of the Southern Ocean deep sea. Nature 447(7142):307–311

Brandt A, Bathmann U, Brix S et al (2011) Maud rise—a snapshot through the water column. Deep-Sea Res Pt II 58:1962–1982. doi:10.1016/j.dsr2.2011.01.008

Brenke N (2005) An epibenthic sledge for operations on marine soft bottom and bedrock. Mar Technol Soc J 39:10–21

Bruchhausen PM, Raymond JA, Jacobs SS et al (1979) Fish, Crustaceans, and the sea floor under the Ross Ice Shelf. Science 203:449–451

Bucklin A, Ortman BD, Jennings RM et al (2010) A ''Rosetta Stone'' for zooplankton: DNA barcode analysis of holozooplankton diversity of the Sargasso Sea (NW Atlantic Ocean). Deep-Sea Res Pt II 57(24–26):2234–2247

Budd AF, Foster CT, Dawson JP et al (2001) The Neogene marine biota of tropical America ("NMITA") database: accounting for biodiversity in paleontology. J Paleont 73:743–751

CCAMLR XXVII (2008) Report of the twenty-seventh meeting of the scientific committee (CCAMLR-XXVII). CCAMLR, Hobart, Australia, http://www.ccamlr.org/en/CCAMLR-XXVII. Accessed 22 Dec 2012

CCAMLR XXVIII (2009) Report of the twenty-eighth meeting of the scientific committee (CCAMLR-XXVIII). CCAMLR, Hobart, Australia, http://www.ccamlr.org/en/CCAMLR-XXVIII. Accessed 22 Dec 2012

Choudhury M, Brandt A (2009) Benthic isopods (Crustacea, Malacostraca) from the Ross Sea, Antarctica: species checklist and their zoogeography in the Southern Ocean. Polar Biol 32:599–610

Chown SL, Lee JE, Hughes KA et al (2012) Challenges to the future conservation of the Antarctic. Science 337(6091):158–159

Clark MS, Fraser KPP, Peck LS (2008) Antarctic marine molluscs do have an HSP70 heat shock response. Cell Stress Chaperon 13(1):39–49

Clarke A (1996) Benthic marine habitats in Antarctica. In: Ross RM, Hofmann EE, Quetin LB (eds) Foundations for ecological research west of the Antarctic Peninsula. Antarct Res Ser 70:123–133

Clarke A (2003) The polar deep seas. In: Tyler PA (ed) Ecosystems of the deep oceans. Elsevier, Amsterdam, pp 239–260

Clarke A (2008) Antarctic marine benthic diversity: patterns and processes. J Exp Mar Biol Ecol 366:48–55

Clarke A, Crame JA (1992) The Southern Ocean benthic fauna and climate change—a historical perspective. Philos Trans R Soc B Biol Sci 338:299–309

Clarke A, Johnston NM (2003) Antarctic marine benthic diversity. Oceanogr Mar Biol 41:47–114

Clarke A, Tyler PA (2008) Adult Antarctic krill feeding at abyssal depths. Curr Biol 18:282–285

Clarke A, Griffiths HJ, Linse K et al (2007) How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. Divers Distrib 13:620–632

Clarke A, Griffiths HJ, Barnes DKA et al (2009) Spatial variation in seabed temperatures in the Southern Ocean: implications for benthic ecology and biogeography. J Geophys Res 114. doi:10.1029/2008JG000886

Coleman CO, Lowry JK, Macfarlane T (2010) DELTA for beginners: an introduction into the taxonomy software package DELTA. ZooKeys 45:1–75

Cressey D (2012) Disappointment as Antarctic protection bid fails. Nature. doi:10.1038/nature.2012.11723

Culver SJ, Buzas MA (2000) Global latitudinal species diversity gradient in deep-sea benthic foraminifera. Deep-Sea Res Pt I 47:259–275

Cummings V, Thrush S, Norkko A, Andrew N, Hewitt J et al (2006) Accounting for local scale variability in benthos: implications for future assessments of latitudinal trends in the coastal Ross Sea. Antarc Sci 18(4):633–644

Danis B, Griffiths HJ (2009) Polar science: bid for freely accessible biodiversity archive. Nature 458. doi:10.1038/458830b

David B, Choné T, Festeau A et al (2005) Biodiversity of Antarctic echinoids: a comprehensive and interactive database. Sci Mar 69:201–203

Dayton PK (1989) Interdecadal recruitment and destruction of an Antarctic sponge population and its effect on local populations of asteroids. Science 245:1484–1486

Dayton PK, Oliver JS (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. Science 197:55–58

De Broyer C, Danis B (eds) (2009) SCAR-MarBIN: the Antarctic marine biodiversity information network. World Wide Web electronic publication. Accessed May 2012

De Broyer C, Danis B with 64 SCAR-MarBIN Taxonomic Editors (2011) How many species in the Southern Ocean? Towards a dynamic inventory of the Antarctic marine species. Deep-Sea Res Pt II 58(1–2):5–17

Dell RK (1972) Antarctic benthos. Adv Mar Biol 10:1–216

Denton GH, Hughes TJ (2002) Reconstructing the Antarctic ice sheet at the last glacial maximum. Quat Sci Rev 21:193–202

Díaz A, Féral JF, David B et al (2011) Evolutionary pathways among shallow and deep-sea echinoids of the genus *Sterechinus* in the Southern Ocean. Deep-Sea Res Pt II 58:205–211

Domack E, Ishman S, Leventer A et al (2005) A chemotrophic ecosystem found beneath Antarctic ice shelf. EOS Trans AGU 86:269–278

Downey RV, Griffiths HJ, Linse K et al (2012) Diversity and distribution patterns in high southern latitude sponges. PLoS ONE 7(7):1–16:e41672. doi:10.1371/journal.pone.0041672

Eléaume M, Hemery LG, Bowden DA et al (2011) A large new species of the genus *Ptilocrinus* (Echinodermata, stalked Crinoidea, Hyocrinidae) from Antarctic seamounts. Polar Biol 34:1385–1397

Fabry VJ, McClintock JB, Mathis JT et al (2009) Ocean acidification at high latitudes: the bellwether. Oceanography 22(4):160–171

Folmer O, Black M, Hoeh W et al (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol Mar Biol Biotech 3:294–299

Fonseca G, Muthumbi AW, Vanreusel A (2007) Species richness of the genus *Molgolaimus* (Nematoda) from local to ocean scale along continental slopes. Mar Ecol 28(4):446–459. doi:10.1111/j.1439-0485.2007.00202.x

German CR, Livermore RA, Baker ET et al (2000) Hydrothermal plumes above the East Scotia Ridge: an isolated high-latitude back-arc spreading centre. Earth Planet Sci Lett 184(1):241–250. doi:10.1016/S0012-821X(00)00319-8

Gheerardyn H, Veit-Köhler G (2009) Diversity and large-scale biogeography of Paramesochridae (Copepoda, Harpacticoida) in South Atlantic abyssal plains and the deep Southern Ocean. Deep-Sea Res Pt I 56:1804–1815

Göbbeler K, Klussmann-Kolb A (2010) Out of Antarctica? New insights into the phylogeny and biogeography of the Pleurobranchomorpha (Mollusca, Gastropoda). Mol Phylogenet Evol 55:996–1007

Goldberg EE, Roy K, Lande R et al (2005) Diversity, endemism and age distributions in macroevolutionary sources and sinks. Am Nat 165(6):623–633

González-Wevar CA, Nakano T, Canete JI et al (2010) Molecular phylogeny and historical biogeography of *Nacella* (Patellogastropoda: Nacellidae) in the Southern Ocean. Mol Phylogenet Evol 56:115–124

Grant RA, Griffiths H, Steinke D et al (2011) Antarctic DNA barcoding; a drop in the ocean? Polar Biol 34:775–780

Griffiths HJ (2010) Antarctic marine biodiversity—what do we know about the distribution of life in the Southern Ocean? PLoS ONE 5:e11683

Griffiths HJ, Linse K, Crame JA (2003) SOMBASE–Southern Ocean mollusc database: a tool for biogeographic analysis in diversity and ecology. Org Div Evol 3:207–213

Griffiths HJ, Barnes DKA, Linse K (2009) Towards a generalized biogeography of the Southern Ocean. J Biogeogr 36:162–177

Griffiths HJ, Danis B, Clarke A (2011) Quantifying Antarctic marine biodiversity: the SCARMarBIN data portal. Deep-Sea Res Pt II 58(1–2):18–29

Gutt J (2007) Antarctic macro-zoobenthic communities: a review and a classification. Antarc Sci 19(2):165–182

Gutt J, Piepenburg D (2003) Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. Mar Ecol Progr Ser 253:77–83

Gutt J, Sirenko BI, Smirnov IS et al (2004) How many macrozoobenthic species might inhabit the Antarctic shelf? Antarc Sci 16:11–16

Gutt J, Barratt I, Domack E et al (2011) Biodiversity change after climate-induced ice-shelf collapse in the Antarctic. Deep-Sea Res Pt II 58:74–83

Gutt J, Zurell D, Bracegridle TJ et al (2012) Correlative and dynamic species distribution modelling for ecological predictions in the Antarctic: a cross-disciplinary concept. Polar Res 31:11091. doi:10.3402/polar.v31i0.11091

Halpern BS, Walbridge S, Selkoe KA et al (2008) A global map of human impact on marine ecosystems. Science 319:948

Hauquier F, Ingels J, Gutt J et al (2011) Characterisation of the nematode community of a low-activity cold seep in the recently ice-shelf free Larsen B area, Eastern Antarctic Peninsula. PLoS ONE 6(7):e22240. doi:10.1371/journal.pone.0022240

Havermans C, Nagy ZT, Sonet G et al (2010) Incongruence between molecular phylogeny and morphological classification in amphipod crustaceans: a case study of Antarctic lysianassoids. Mol Phylogenet Evol 55:202–209

Hebert PDN, Ratnasingham S, de Waard JR (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. Proc Roy Soc Lond B 270:S96–S99

Hedgpeth JW (1969) Introduction to Antarctic Zoogeography. Antarctic Map Folio Series, New York

Held C (2000) Phylogeny and biogeography of serolid isopods (Crustacea, Isopoda, Serolidae) and the use of ribosomal expansion segments in molecular systematics. Mol Phylogenet Evol 15(2):165–178

Held C (2001) No evidence for slow-down of molecular substitution rates at subzero temperatures in Antarctic serolid isopods (Crustacea, Isopoda, Serolidae). Polar Biol 24:497–501

Held C, Wägele JW (2005) Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae). Sci Mar 69(2):175–181

Hemery LG, Eléaume M, Roussel V et al (2012) Comprehensive sampling reveals circumpolarity and sympatry in seven mitochondrial lineages of the Southern Ocean crinoid species *Promachocrinus kerguelensis* (Echinodermata). Mol Ecol 21(10):2502–2518

Hétérier V, David B, De Ridder C et al (2008) Ectosymbiosis is a critical factor in the local benthic biodiversity of the Antarctic deep sea. Mar Ecol Progr Ser 364:67–76

Hofmann GE, Todgham AE (2010) Living in the now: physiological mechanisms to tolerate a rapidly changing environment. Annu Rev Physiol 72:127–145

Hosie G, Koubbi P, Riddle M et al (2011) CEAMARC, the Collaborative East Antarctic Marine Census for the Census of Antarctic Marine Life (IPY # 53): an overview. Pol Sci 5(2):75–87

Hunter RL, Halanych KM (2008) Evaluating connectivity in the brooding brittle star *Astrotoma agassizii* across the Drake Passage in the Southern Ocean. J Hered 99:137–148

Ingels J, Vanhove S, De Mesel I et al (2006) The biodiversity and biogeography of the free-living nematode genera *Desmodora* and *Desmodorella* (family Desmodoridae) at both sides of the Scotia Arc. Polar Biol 29:936–949

Ingels J, Vanreusel A, Brandt A et al (2012) Possible effects of global environmental changes on Antarctic benthos: a synthesis across five major taxa. Ecol Evol 2:453–485

Jamieson RE, Rogers AD, Billett DSM et al (2012) Patterns of marine bacterioplankton biodiversity in the surface waters of the Scotia Arc, Southern Ocean. FEMS Microbiol Ecol 80(2):452–468

Janecki T, Kidawa A, Potocka M (2010) The effects of temperature and salinity on vital biological functions of the Antarctic crustacean *Serolis polita*. Polar Biol 33:1013–1020

Janosik AM, Halanych KM (2010) Unrecognized Antarctic biodiversity: a case study of the genus *Odontaster* (Odontasteridae; Asteroidea). Integr Comp Biol:1–12

Kaiser S, Barnes DKA (2008) Southern Ocean deep-sea biodiversity; sampling strategies and predicting responses to climate change? Climate Res 37(2–3):121–270

Kaiser S, Barnes DKA, Brandt A (2007) Slope and deep-sea abundance across scales: southern Ocean isopods show how complex the deep sea can be. Deep-Sea Res Pt II 54:1776–1789

Kaiser S, Barnes DKA, Sands CJ et al (2009) Biodiversity of an unknown Antarctic Sea: assessing isopod richness and abundance in the first benthic survey of the Amundsen continental shelf. Mar Biodiv 39(1):27–43

Kawaguchi S, Kurihara H, King R et al (2011) Will krill fare well under Southern Ocean acidification? Biol Lett 7(2):288–291

Khatiwala S, Primeau F, Hall T (2009) Reconstruction of the history of anthropogenic CO_2 concentrations in the ocean. Nature 462:346–349

Knox GA, Lowry JK (1977) A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the amphipods and the Polychaeta. In: Dunbar MJ (ed) Polar oceans. Arctic Institute of North America, Calgary, pp 423–462

Krabbe K, Leese F, Mayer C et al (2010) Cryptic mitochondrial lineages in the widespread pycnogonid *Colossendeis megalonyx* Hoek, 1881 from Antarctic and Subantarctic waters. Polar Biol 33:281–292

Kroeker KJ, Kordas RL, Crim RN et al (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol Lett 13:1419–1434

Kröger K, Rowden AA (2008) Polychaete assemblages of the northwestern Ross Sea shelf: worming out the environmental drivers of Antarctic macrobenthic assemblage composition. Polar Biol 31:971–989

Kühl S, Schneppenheim R (1986) Electrophoretic investigation of genetic variation in two krill species *Euphausia superba* and *E. crystallorophias* (Euphausiidae). Polar Biol 6(1):17–23

la Salle J, Wheeler QD, Jackway P et al (2009) Accelerating taxonomic discovery through automated character extraction. Zootaxa 2217:43–55

Lawver LA, Gahagan LM (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeogr Palaeocl 198:11–37

Leese F, Agrawal S, Held C (2010) Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. Naturwissenschaften. doi:10.1007/s00114-010-0674-y

Leese F, Brand P, Rozenberg A et al (2012) Exploring Pandora's box: potential and pitfalls of low coverage genome surveys for evolutionary biology. PLoS ONE 7(11):e49202. doi:10.1371/journal.pone.0049202

Linse K, Griffiths HJ, Barnes DKA et al (2006) Biodiversity and biogeography of Antarctic and sub-Antarctic Mollusca. Deep-Sea Res Pt II 53:985–1008

Lörz AN, Maas EW, Linse K et al (2009) Do circum-Antarctic species exist in peracarid Amphipoda? A case study in the genus *Epimeria* Costa, 1851 (Crustacea, Peracarida, Epimeriidae). ZooKeys 18:91–128

Lörz AN, Kaiser S, Bowden DA (2013) Macrofaunal crustaceans in the benthic boundary layer from the shelf break to abyssal depths in the Ross Sea (Antarctica). Polar Biol 36:445–451. doi:10.1007/s00300-012-1269-1

Mahon AR, Thornhill DJ, Norenburg JL et al (2010) DNA uncovers Antarctic nemertean biodiversity and exposes a decades-old cold case of asymmetric inventory. Polar Biol 33:193–202

Majoran S, Dingle RV (2002) Cenozoic deep-sea ostracods from Maud Rise, Weddell Sea, Antarctica (ODP Site 689): a palaeoceanographical perspective. Geobios 35(1):137–152

Marsh L, Copley J, Huvenne V et al (2012) Microdistribution of faunal assemblages at deep-sea hydrothermal vents in the Southern Ocean. PLoS ONE 7(10):e48348. doi:10.1371/journal.pone.0048348

Martin AP, Palumbi SR (1993) Body size, metabolic rate, generation time, and the molecular clock. Proc Natl Acad Sci USA 90:4087–4091

Menzies RJ, Schultz GA (1966) Antarctic Isopod Crustaceans. I. First photographs of isopod Crustaceans on the Deep-sea Floor. Int Revue ges Hydrobiol 51(2):225–227

Meredith MP, King JC (2005) Climate change in the ocean to the west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604

Mikhalevich VI (2004) The general aspects of the distribution of Antarctic foraminifera. Micropaleontology 50(2):179–194

Mora C, Sale P (2011) Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcoming of protected areas on land and sea. Mar Ecol Progr Ser 434:251–266

Moran AL, Woods HA (2012) Why might they be giants? Towards an understanding of polar gigantism. J Exp Biol 215:1995–2002. doi:10.1242/jeb.067066

Moy AD, Howard WR, Bray SG (2009) Reduced calcification in modern Southern Ocean planktonic foraminifera. Nat Geosci 2:276–280

Mulvaney R, Abram NJ, Hindmarsh RCA et al (2012) Recent Antarctic Peninsula warming relative to holocene climate and ice-shelf history. Nature. doi:10.1038/nature11391

Murray J (1895) A summary of the scientific results of the voyage of H.M.S. Challenger during the years 1872–76. Second part, pp 1432–1462

Newman L, Convey P, Gibson JAE et al (2009) Antarctic paleobiology: glacial refugia and constraints on past icesheet reconstructions. PAGES News 17:22–24

Norman JR (1937) Coast fishes. Part II. The Patagonian region. Discovery Rep 16:1–150

Orr JC, Fabry VJ, Aumont O et al (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Page TJ, Linse K (2002) More evidence of speciation and dispersal across the Antarctic Polar Front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). Polar Biol 25:818–826

Pawlowski J, Fahmi J, Lecroq B et al (2007) Bipolar gene flow in deep-sea benthic foraminifera. Mol Ecol 16:4089–4096

Pearse JS, McClintock JB, Bosch I (1991) Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. Am Zool 421:37–42

Peck LS (2005) Prospects for surviving climate change in Antarctic aquatic species. Front Zool 2:9

Peck LS (2008) Brachiopods and climate change. Earth Env Sci Trans Roy Soc Edinburgh 98:451–456

Peck LS, Webb K, Bailey D (2004) Extreme sensitivity of biological function to temperature in Antarctic marine species. Funct Ecol 18:625–630

Peck LS, Convey P, Barnes DKA (2006) Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. Biol Rev 81(1):75–109

Peck LS, Clark MS, Morley SA et al (2009) Animal temperature limits and ecological relevance: effects of size, activity and rates of change. Funct Ecol 23(2):248–256

Peck L, Morley S, Clark M (2010) Poor acclimation capacities in Antarctic marine ectotherms. Mar Biol 157(9):2051–2059

Pfenninger M, Schwenk K (2007) Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. BMC Evol Biol 7:e121

Pierrat B, Saucède T, Laffont R et al (2012) Large-scale distribution analysis of Antarctic echinoids using ecological niche modelling. Mar Ecol Progr Ser 463:215–230

Pörtner HO (2008) Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. Mar Ecol Prog Ser 373:203–217

Pörtner HO, Peck L, Somero G (2007) Thermal limits and adaptation in marine Antarctic ectotherms: an integrative view. Philos Trans Roy Soc B Biol Sci 362:2233–2258

Post AL, O'Brien PE, Beaman RJ et al (2010) Physical controls on deep-water coral communities on the George V Land slope, East Antarctica. Antarc Sci 22:371–378. doi:310.1017/S0954102010000180

Poulin E, Palma AT, Féral JP (2002) Evolutionary versus ecological success in Antarctic benthic invertebrates. Trends Ecol Evol 17:218–222

Rahmann H, Schneppenheim R, Hilbig R et al (1984) Variability in brain ganglioside composition: a further molecular mechanism beside serum antifreeze-glykoproteins for adaptation to cold in Antarctic and Arctic-boreal fishes. Polar Biol 3(2):119–125

Rathburn AE, Pichon JJ, Ayress MA et al (1997) Microfossil and stable-isotope evidence for changes in Late Holocene palaeo-productivity and palaeoceanographic conditions in the Prydz Bay region of Antarctica. Palaeogeogr Palaeoclimatol Palaeoecol 131:485–510

Raupach MJ, Mayer C, Malyutina M et al (2009) Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. Proc Roy Soc Lond B 276:799–808

Regan CT (1914) Fishes. British Antarctic ('Terra Nova') expedition, 1910. Natural history report. Zool Fish Terra Nova Exped 1:1–54

Riddle MJ, Craven M, Goldsworthy PM et al (2007) A diverse benthic assemblage 100 km from open water under the Amery Ice Shelf, Antarctica. Paleoceanography 22 (P12):P1204. doi:10.1029/2006PA001327

Riehl T, Kaiser S (2012) Conquered from the deep sea? A new deep-sea isopod species from the Antarctic shelf shows pattern of recent colonization. PLoS ONE 7(11):e49354. doi:10.1371/journal.pone.0049354

Rintoul S, Speer K, Hofmann E et al (2009) Southern Ocean Observing System (SOOS): Rationale and strategy for sustained observations of the Southern Ocean. Community White Paper. Ocean Obs-09. Venice, Italy

Rogers AD (2012) Evolution and biodiversity of antarctic organisms—a molecular perspective. In: Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds), Antarctica: an extreme environment in a changing world. Phil Trans Roy Soc Lond 417–467

Rogers AD, Tyler PA, Connelly DP et al (2012) The discovery of new deep-sea hydrothermal vent communities in the Southern Ocean and implications for biogeography. PLoS Biol 10(11). doi:10.1371/journal.pbio.1001234

Römisch K, Matheson T (2003) Cell biology in the Antarctic: studying life in the freezer. Nat Cell Biol 5:3–6. doi:10.1038/ncb0103-3

Ruhl HA, Ellena JA, Smith KL Jr (2008) Connections between climate, food limitation, and carbon cycling in abyssal sediment communities. Proc Natl Acad Sci USA 105:17006–17011

Schiaparelli S, Alvaro MC, Bohn J et al (2010) "Hitchhiker" polynoid polychaetes in cold deep waters and their potential influence on benthic soft bottom food webs. Antarc Sci 22(4):399–407

Schiaparelli S, Danis B, Wadley V et al (2013) The Census of Antarctic Marine Life (CAML): the first available baseline for Antarctic marine biodiversity. In: Verde C, di Prisco G (eds) Adaptation and evolution in marine environments, the impacts of global change on biodiversity. Springer Book Series: From Pole to Pole (Series Eds: Kallenborn R, di Prisco G, Walton D, Barr S) 2, pp 3–19

Schüller M (2011) Evidence for a role of bathymetry and emergence in speciation in the genus *Glycera* (Glyceridae, Polychaeta) from the deep Eastern Weddell Sea. Polar Biol 34:549–564

Sewell MA, Hofmann GE (2011) Antarctic echinoids and climate change: a major impact on brooding forms. Glob Change Biol 17:734–744

Sigman DM, Hain MP, Haug GH (2010) The polar ocean and glacial cycles in atmospheric CO_2 concentration. Nature 466(7302):47–55

Smale DA, Barnes DKA, Fraser KPP et al (2008a) Benthic community response to iceberg scouring at an intensely disturbed shallow water site at Adelaide Island Antarctica. Mar Ecol Prog Ser 355:85–94

Smale DA, Brown KM, Barnes DKA et al (2008b) Ice scour disturbance in Antarctic waters. Science 321:371

Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine the 'winners' and 'losers'. J Exp Biol 213:912–920

Strugnell JM, Rogers AD, Prodöhl PA et al (2008) The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. Cladistics 24:853–860

Strugnell JM, Cherel Y, Cooke IR et al (2011) The Southern Ocean: source and sink? Deep-Sea Res Pt II 58:196–204

Strugnell JM, Watts PC, Smith J et al (2012) Persistent genetic signatures of historic climatic events in an Antarctic octopus. Mol Ecol 21(11):2775–2787

Terauds A, Chown SL, Morgan F et al (2012) Conservation biogeography of the Antarctic. Divers Distrib 18(7):726–741

Thorson G (1950) Reproduction and larval ecology of marine bottom invertebrates. Biol Rev Camb Philos Soc 25:1–45

Tin T, Fleming ZL, Hughes KA et al (2009) Impacts of local human activities on the Antarctic environment. Antarc Sci 21:3–33

Trivelpiece WZ, Hinke JT, Miller AK et al (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci 108:7625–7628

Trontelj P, Fiser C (2009) Cryptic species diversity should not be trivialised. Syst Biodiver 7:1–3

Van Hannen EJ, Veninga M, Bloem J et al (1999) Genetic changes in bacterial community structure associated with protistan grazers. Arch Hydrobiol 145:25–38

Vaughan DG, Barnes DKA, Fretwell PT et al (2011) Potential seaways across West Antarctica. Geochem Geophys Geosyst 12:Q10004

Wakeley J (2010) Natural selection and coalescent theory. In: Bell MA, Futuyma DJ, Eanes WF, Levinton JS (eds) Evolution since Darwin: the first 150 years. Sinauer and Associates, Sunderland, MA, pp 119–149

Waller CL, Worland MR, Convey P et al (2006) Ecophysiological strategies of Antarctic intertidal invertebrates faced with freezing stress. Polar Biol 29:1077–1083

West NJ, Obernosterer I, Zemb O et al (2008) Major differences of bacterial diversity and activity inside and outside of a natural iron-fertilized phytoplankton bloom in the Southern Ocean. Environ Microbiol 10:738–756

White MG (1984) Marine benthos. In: Laws RM (ed) Antarctic ecology, 2nd edn. Academic Press, London, pp 421–461

Whitehouse MJ, Meredith MP, Rothery P et al (2008) Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th Century: forcings, characteristics and implications for lower trophic levels. Deep-Sea Res I 55:1218–1228

Wilson NG, Hunter RL, Lockhart SJ et al (2007) Multiple lineages and absence of panmixia in the 'circumpolar' crinoid *Promachocrinus kerguelensis* from the Atlantic sector of Antarctica. Mar Biol 152:895–904

Wilson NG, Schrödl M, Halanych KM (2009) Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelenensis* (Mollusca, Nudibranchia). Mol Ecol 18:965–984

Würzberg L, Peters J, Schüller M et al (2011) Diet insights of deep-sea polychaetes derived from fatty acid analyses. Deep-Sea Res Pt II 58(1–2):153–162

Yasuhara M, Kato M, Ikeya N et al (2007) Modern Benthic Ostracodes from Lützow-Holm Bay, East Antarctica: paleoceanographic, paleobiogeographic, and evolutionary significance. Micropaleontology 53(6):469–496

Yasuhara M, Cronin TM, Hunt G et al (2009) Deep-Sea ostracods from the South Atlantic sector of the Southern Ocean during the last 370,000 years. J Paleontol 83:914–930

Yasuhara M, Hunt G, Dowsett HJ et al (2012) Latitudinal species diversity gradient of marine zooplankton for the last three million years. Ecol Lett 15:1174–1179

Young JS, Peck LS, Matheson T (2006) The effects of temperature on walking and righting in temperate and Antarctic crustaceans. Polar Biol 29:978–987