



Future Challenges in Southern Ocean Ecology Research

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The Southern Ocean is experiencing relentless change. The Antarctic and Southern Ocean community, represented by 75 scientists and policy-makers from 22 countries, recently met to formulate a collective vision on the priorities for Antarctic research for the next two decades and beyond. Here, we assess high-interest research areas related specifically to Southern Ocean life and ecology that, although not all retained as the 80 top priorities among the addressed scientific domains, are of considerable relevance to the biology and ecology of the Southern Ocean. As certain regions of the Southern Ocean ecosystems have witnessed abiotic and biotic changes in the last decades (e.g., warming, climate variability, changes in sea ice, and abundance of marine organisms), such an exercise was urgently needed. We concluded that basic biological information on the taxonomy of numerous organisms is still lacking in areas, such as the deep-ocean floor or the under-ice environments. Furthermore, there is a need for knowledge about the response and resilience of Antarctic marine ecosystems to change. The continuation of a long-term commitment and the development and use of innovative technology to adequately monitor the Southern Ocean ecosystems is required. Highlighting the most important Southern Ocean research topics allow the identification of the challenges and future requirements in technological development, and both research and funding strategies for the various stakeholders.

Keywords: Southern Ocean, future research, policy making, ecology, conservation

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INTRODUCTION

The Southern Ocean represents 9.6% of the world's oceans and plays a key role in various global cycles and budgets. It is a major contributor to global oceanic primary production and biodiversity, exports nutrients to the world's ocean basins, and contributes to the global currents system transferring heat and CO_2 from the atmosphere to the deep ocean and O_2 in the opposite direction

(Sarmiento et al., 2004; Turner et al., 2009). In the last 30 years, manifold regional change (e.g., in water temperature, in currents, stratification, shifts in oceanic front positions, increase in westerly winds, changes in sea-ice extent with dramatic consequences on wildlife, changes in Antarctic krill Euphausia superba abundance) took place in the Southern Ocean (Constable et al., 2014; Ropert-Coudert et al., 2014; Gutt et al., 2015). The "stability" of the Earth System (including natural background dynamics) is under threat, with the rate of change is accelerating (with core elements of climate change and biosphere integrity, that can drive the Earth System into a new state), suggesting that the current changes are only minor compared to the expected future trends (Rockstrom et al., 2009; Steffen et al., 2015). These trends include, inter alia, increased ocean warming, widespread decrease of sea ice, increase of aragonite undersaturation (acidification), and the interaction of these (and other) environmental factors that affect the Southern Ocean ecosystems (Gutt et al., 2015).

Although, our understanding of Southern Ocean biological processes (e.g., distribution, feeding ecology, reproduction; **Figure 1**) has improved considerably in recent years, the capacity of organisms (at population, community and/or species level) to

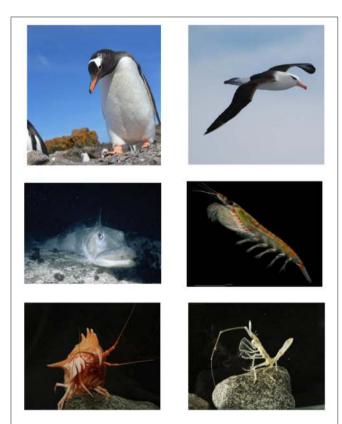


FIGURE 1 | Examples of the marine biodiversity in the Southern Ocean. Gentoo penguins *Pygoscelis papua* (J. C. Xavier, MARE-UC/BAS), black-browed albatross *Thalassarche melanophrys* (J. C. Xavier, MARE-UC/BAS), icefish *Chaenocephalus aceratus* (Doug Allan, BAS), Antarctic krill *Euphausia superba* (Russ Hopcroft, AAD), amphipod *Epimeria rubrieques* (Torben Riehl, ZM-UH), and isopod *Litarcturus* cf. *antarcticus* (Torben Riehl, ZM-UH).

adapt to changes and the dynamics of biological cycles remain poorly understood. This knowledge, however, is essential for predicting biological responses to predicted physical changes (IPCC, 2013).

The First Scientific Committee on Antarctic Research (SCAR) Antarctic and Southern Ocean Horizon Scan, held in April 2014 in New Zealand, brought together 75 scientists and policymakers from 22 countries to suggest priorities for Antarctic Research in the coming two decades and beyond (Kennicutt et al., 2014, 2015). The Horizon Scan process (Sutherland et al., 2011), through which these priority issues were selected, has been described by Kennicutt et al. (2015). The authors identified several questions that fell widely into six research themes that might guide researchers to the full potential of Antarctic and Southern Ocean science (Kennicutt et al., 2014). Here, we focus on three topical clusters (Southern Ocean life and ecology, the marine biosphere and the physical environment, and biotic responses to change) that were identified as priority issues during the Horizon Scan and that relate specifically to Southern Ocean research. Our aim is to: (i) assess high-interest research areas that, although not retained at the end of the Scan [(Kennicutt et al., 2014, 2015) list the full top 80 questions], entered the exercise selection process for Southern Ocean biology and ecology, and (b) identify the challenges and requirements in technological developments, research strategies (e.g., monitoring and coordination), as well as links with stakeholders (e.g., policy makers, NGO's, industry) and the general public, specific to Antarctica and Southern Ocean biological research.

RESEARCH RELEVANT TO SOUTHERN OCEAN LIFE AND ECOLOGY

Besides a detailed compilation of research questions in the Data sheet 1 in Supplementary Material, we outline a number of issues related to the questions that were voted on the Southern Ocean life and ecology sessions herewith.

Identification of Major Marine Ecosystem Processes in the Southern Ocean

The continuous warming of parts of the Southern Ocean calls for an evaluation not only of the increasing temperature, but also of its impact on other physical and biological parameters. This is especially relevant to species endemic to the Southern Ocean (characterized by narrow environmental niches) that may display poor adaptability/acclimation/plasticity to rapid environmental changes. A key issue is identifying which species will be threatened by the changes because of their inherent physiological limitations. Increasing ocean acidification (i.e., decreasing seawater pH) is expected to profoundly alter Southern Ocean ecosystems (Orr et al., 2005) but recent evidence suggests that some Antarctic species can cope with lowered pH (Suckling et al., 2014). Taxonomy remains a key approach for uncovering changes in faunal composition related to global change processes (Costello et al., 2013).

Identifying the linkages between terrestrial and marine systems, particularly in inter-tidal and near-shore areas, where de-glaciation on land may have important effects on local marine ecosystems (Schloss et al., 2012; Gutt et al., 2015; Hernando et al., 2015), needs further research due to the predicted increase levels of ice melting, potential land-originated fresh water runoff, and potential increase in sea level (Golledge et al., 2015). In addition, although there is evidence of glacier impact on benthic communities at a local scale (Pasotti et al., 2015), it is essential to understand the factors that can explain the high spatial patchiness of Antarctic shelf-inhabiting benthos at local and regional scales.

Understanding the synergistic effects of multiple environmental stressors, including ocean acidification, sedimentation, and hypoxia, on benthic habitats will prove particularly challenging; however this is paramount to the understanding of whole ecosystem changes.

Investigate the Food Web Structure and Functioning of the Southern Ocean

Some basic biological information on primary production, zooplankton, nekton, and top predators from various regions of the Southern Ocean is still missing (**Figures 2A,B**; Griffiths et al., 2014). Benchmark knowledge has been gathered through the Census of Marine Life, and its flagship project, the 5 year Census of Antarctic Marine Life (CAML), which investigated, between others, the diversity, distribution, functions, and abundance of Southern Ocean marine organisms (Gutt et al., 2010; Kaiser et al., 2013), culminating into the Biogeographic Atlas of the Southern Ocean (Brandt et al., 2014b; De Broyer et al., 2014). However, knowledge gaps are still present concerning the biology, distribution, and diversity of most marine groups. As

of today, very little information is available from the microbial realm (including viruses), particularly on their distribution in Southern Ocean ecosystems and their role in fueling and recycling organic matter in the different systems' compartments. Similarly, we know very little of the life cycle of many plankton and nekton species (of which large numbers remain unidentified) particularly under the sea ice, at the ice-ocean water interface and in the open ocean regions, or of the recruitment success any population dynamics of ecologically important taxa (e.g., cephalopods or myctophid midwater fish). In this context, from the food-chain perspective, meso- and top predators (e.g., albatrosses, seals, penguins) are currently being considered as early ecological indicator species of changes in the Southern Ocean and are used as ecological indicators of the status of lower trophic levels (Hindell et al., 2003; Xavier and Cherel, 2009).

For benthic marine ecosystems, it is important to document and understand benthic functional diversity and to identify the ecological drivers of the different communities. Which environmental factors are responsible for the development of shelf-inhabiting filter-feeder dominated communities? Why are patches of such assemblages found in a gradient from aggregations restricted to a few meters to eco-regions extending to tens of kilometers? Furthermore, there is a need to investigate the dynamics of benthic systems, including seasonal variability, in order to map biodiversity, and biomass hot spots, as well as to elucidate turn-over rates between trophic levels and community-level nutrient cycles including consumption, carbon sequestration, and re-mineralization. Some of these challenges do relate to deep sea ecosystems (Brandt et al., 2007, 2012), in which our understanding of deep-sea organisms dynamics in a physically changing ocean, and under a varying climate,

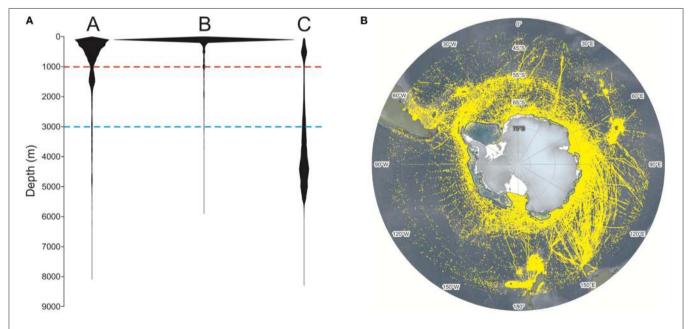


FIGURE 2 | (A) The relative distribution of benthic sampling intensity (A), pelagic sampling intensity (B), and seafloor area with depth (C). The red line indicates the 1000 m depth (shelf break) and the blue line indicates the 3000 m depth abyssal plain; after (Griffiths et al., 2014) (B) The relative distribution of geographical sampling intensity (yellow dots; ~1.07 million distinct records) across the Southern Ocean (after Griffiths et al., 2014).

is key to evaluating the role of these organisms. The deep-sea, where ecological communities are diverse yet mostly unknown, represents one of the frontiers to explore in the coming decades as the basics of ecosystem functioning (Brandt and Ebbe, 2011) and changes in species functioning and food-web structure are almost unknown (Brandt et al., 2014a,b). The relatively stable Southern Ocean deep-sea ecosystems holds an enormous potential for evolutionary research, for example in determining the key factors that lead to speciation events in this vast environment. Moreover, it is important to understand the contribution to carbon and nutrient sequestration/recycling of the various plankton and benthic communities in the deep sea, on the slopes, and on/across the biomass-rich shelves.

Only when these gaps in knowledge are filled, the Antarctic marine systems can be described qualitatively and quantitatively and considered in a wider context that will allow predictions in a changing environment.

FUTURE CHALLENGES AND REQUIREMENTS IN METHODOLOGICAL AND TECHNOLOGICAL DEVELOPMENTS

Future Requirements for Southern Ocean Life and Ecology Research

Antarctic life sciences are constrained by the paucity of autoecological baseline data for key marine organisms (Kennicutt et al., 2014), particularly micro-organisms despite their fundamental importance in ecosystem functioning (Danovaro et al., 2014). There is vastly more data on species distribution compared to how they function and their productivity. Besides traditional - but often methodologically challenging - censuses, future generations of scientists will have to foster international coordination to conduct long-term monitoring programs and obtain biological information about poorly known species and their interactions, either directly, or through the use of ecological indicator species. These long-term, multi-national monitoring programs will also help to improve the quality and selection of data for the next generation of climate and food-web models. The accurate selection of essential Ecosystem Ocean Variables (Constable et al., 2014), for instance, is required to reliably predict regional or global Antarctic marine ecosystems (Murphy and Hofmann, 2013; Xavier et al., 2015).

Antarctic ecosystem services are increasingly important and there is an urgent need to clarify their role and the impacts of change. How does ecosystem functioning inform ecosystem services? How does it contribute to the global budget, and more specifically, to the Southern Ocean? Marine Protected Areas (MPAs), which have been implemented with varying success throughout the world's oceans, may play a crucial role in protecting Southern Ocean environments. Our ability to implement and then determine the efficiency and effectiveness of MPAs in protecting ocean resources is paramount in ensuring their sustainable exploitation and—will again—require long-term monitoring. For this, a better understanding of the structural and functional differences between the regions of the Southern Ocean is also crucial.

International organizations, such as the SCAR and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), gather expert scientific groups for whom monitoring is a key issue necessary to conduct academic research, promote species conservation, area protection, and ecosystem sustainability for Southern Ocean life. The recentlyestablished international initiative Southern Ocean Observing System (SOOS; www.soos.aq/) in alliance with the Global Ocean Observing System (www.ioc-goos.org/) and the Deep Ocean Observing Systems (www.ioc-goos.org/deepocean), aim at coordinating and expanding the efforts to collect scientific data in the Southern Ocean, and to develop a coherent and efficient observing system that will deliver the data required to address key scientific and societal challenges. Improved coordination of ecological process studies can be facilitated by international SCAR initiatives, such as the biology programs AnT-ERA (www.scar.org/srp/ant-era) and AntEco (www.scar.org/srp/anteco).

Under requirement and/or pressure from stakeholders to provide comprehensive knowledge of Southern Ocean ecosystems, it is essential to apply the often-invoked demand for standardization. This refers to sampling methods as well as analyses and strategies, even in simple parameters, such as absence/presence and abundance. The CCAMLR ecosystem monitoring program (CEMP) has put considerable effort into this issue, and has been collecting data on various species around the Southern Ocean since 1987 (Agnew, 1997). These efforts must be continued and expanded while encouraging research groups to use CEMP as a standard procedure for their data collection. Standardization and coordination, however, must not block the development of new technology and ideas, but rather complement these. In addition, efforts have to be made in order to obtain integrative results that are representative for entire communities or trophic components of the ecosystem.

Similarly, the challenges of conducting cutting-edge Antarctic marine science require a network of logistics and technologies to be developed, combining neural networks, data collection coordination, and a wide range of devices (Meredith et al., 2013). Future research vessels may have state-to-the-art instrumentation and laboratory facilities on board, together with next generation of non-invasive technologies (e.g., marine remotely operated vehicles, and autonomous underwater vehicles, gliders and rovers), as well as advanced Lander technology (i.e., any platform that carries one or more instruments to the seabed, remains there until it is recovered). Furthermore, autonomous profiling floats will continue to be extremely useful to collate valuable information and provide long-term trends in the future (Gille, 2002; Sallée et al., 2010; Tagliabue et al., 2014; Heuzé et al., 2015). Using such data, with those possible obtained from satellites (due to improved accuracy and uncertainty) will also aid our information about Ocean processes (Sarmiento et al., 1998; Arrigo et al., 1999; Arrigo, 2005; Hauck et al., 2015), ecology and food webs dynamics (Gillett and Thompson, 2003; Weimerskirch et al., 2012; Siegel et al., 2014; Laufkötter et al., 2015; Xavier et al., 2015). These technologies are efficient and environmentally friendly and will dramatically improve the spatial and temporal coverage of biological and physical sampling of the Southern Ocean. Moreover, they will help underpin how ecological observations should be collected, and assess Essential Ocean Variables (EOV's), that are in the focus of large international Antarctic programs, such as SOOS (Meredith et al., 2013, 2015).

Taxonomic descriptions of new species, providing the baseline knowledge on which all other research is built, has to be ensured, e.g., through support of taxonomists and the advancement of programs, such as Description language for Taxonomy (Dallwitz et al., 1993), combined with molecular methods. In parallel, technological progress and constant miniaturization have allowed animal data-recording or data-transmitting devices (Cooke et al., 2004; Ropert-Coudert and Wilson, 2005) to become increasingly useful in monitoring a wider range of parameters on smaller species without concern for adverse impacts. Forecasted miniaturization, concomitantly to the widening of the market for bio-logging technologies will result in the development of increasingly cheaper devices. This will open avenues for largescale monitoring operations at the circumpolar level in the coming decades. The development of new sensors and on-board data-processing systems augurs for future studies to determine in situ, and store, in enhanced memories, information about the environment at fine scales so as to provide a true dynamic vision of the state of the Southern Ocean. Linking the foraging behavior, trophic interactions and population dynamics of top predators, will also contribute significantly to the development of more efficient food-web models, which are crucial for the assessments of the life in the changing Southern Ocean. Universal food-web models (e.g., bringing together trophic interactions, biodiversity, biotic, and abiotic parameters, under evolutionary contexts), following previous research in this direction (Steinacher et al., 2010; Bopp et al., 2013), may be developed to explain the evolutionary origin of a high biodiversity in the Southern Ocean, their ecological coexistence and future response to ongoing environmental change. Finally, the continuous improvements for realizing cost-effective high-throughput molecular sequencing will also impact various disciplines, including biogeochemistry, following previous work (Bohmann et al., 2014; Zhan and MacIsaac, 2015).

Develop Southern Ocean Marine Food Webs Forecasting Systems

Modeling forecasting tools have been developed and available to allow predictions, although there is a need for improvement (Xavier et al., 2015). From a marine food webs forecasting perspective, in order to improve worldwide biological forecasting (i.e., predicting biological responses of organisms from local to global scales) (Barnosky et al., 2012), we need to be able to evaluate the ecological tipping points of Southern Ocean ecosystems (Gutt et al., 2013). Moreover, assessing how these tipping points may affect Southern Ocean functioning is a relevant issue for the coming 20 years. To this end, in addition to traditional monitoring, we need to conduct experimental manipulations over long timescales (e.g., several decades) on ecological indicator species (defined here as any biological species

that defines a trait or characteristic of the environment) or groups of species.

It remains a challenge to incorporate life-history parameters (e.g., growth, mortality) within static species distribution models (Gutt et al., 2012) that correlate biogeography with recent and future environmental dynamic components. Furthermore, it is difficult to consider all ecologically relevant species, or the entire community, under multiple—instead of single—stressors in ecological risk models (Gutt et al., 2015). Special attention should be paid to invasive marine species or indigenous species that extend their biogeographic range and may cause a diversity shift that will disturb an existing dynamic equilibrium between trophic guilds.

One of the questions of interest to Antarctic marine resource managers and policy makers concerns with our ability to differentiate ecosystem changes and climate-driven change from the effects of fisheries exploitation (Figure 3). With respect to management of Southern Ocean living resources, in the face of near-future environmental change, CCAMLR endorsed the development of a feedback management strategy. This system will use information on the status of the ecosystem to alter the levels of harvesting and spatial management of the Antarctic krill fishery. Such an approach offers the opportunity to make the initial attempts to forecast, and respond accordingly to, the potential impacts of climate change (CCAMLR, 2014) through signals from components of the ecosystem such as meso- and top predators. Similar initiatives must be carried out for other currently commercially exploited species, such as toothfish and icefish, whilst knowledge gaps in the ecology of species that have the potential to be exploited in the future should urgently be identified. The possibility to use Antarctic top predators as oceanographic samplers has already been demonstrated. For example, Southern elephant seals Mirounga leonina habitat cover huge areas of the Southern Ocean and are therefore useful to examine physical and biological changes occurring in the vast, remote, Southern Ocean throughout the year (Roquet et al., 2013). Further developments in the use of top predators as oceanographic samplers, bearing ethical concerns in mind, would not only address key issues on the ecology of the species, but also be an important step toward a more complete sampling and monitoring of the Southern Ocean.

Build Comparative Marine Research Programs between Polar Regions

The Arctic and the Antarctic differ in age, stability and heterogeneity, human presence, and ecosystem services (Meltofte et al., 2013; Walton, 2013), yet various marine species occur at both poles (De Broyer et al., 2014). How polar ecosystems are responding and will respond to change is paramount to our understanding of worldwide processes, and therefore much insight can be gained from comparative studies (Smetacek and Nicol, 2005; Convey et al., 2012; Bennett et al., 2015). Comparing these Polar Regions at species- and ecosystem-functioning levels will be very important in the coming years, under climate change scenarios, through collaboration across the international

scientific community (e.g., Under SCAR and the International Arctic Science Committee expert groups).

Support an Ethical Perspective While Conducting Antarctic Science

Southern Ocean ecosystems are remote, sometimes isolated and may, consequently, be more easily affected by changes. Signals of natural dispersal, colonization, and diversification for Antarctica and the Southern Ocean are now at risk of being overwhelmed by impacts associated with changing climates and rapidly increasing human movement both into the region and between its distinct regions (Chown et al., 2015). These characteristics imply that scientists must exert special care when conducting their experiments and, in this context, the international nature of Antarctic Science calls for a greater coordination among countries in defining ethical guidelines that will address the challenges of the coming decades. Based on the Protocol on Environmental Protection to the Antarctic Treaty (Madrid Protocol) national Antarctic programs should continue

to submit their science proposals to the impartial, national environmental agencies, but procedures may differ for each country. This diversity in the evaluation processes means that the same survey or experiment submitted to two different countries may not experience the same level of restriction. In addition, ethics committees could be aware of specific scientific approaches (e.g., animal experiments with higher vertebrates entailed by working in the Southern Ocean) and make sure that their regulations still allow for data collection to take place. Absence of data could indeed be extremely prejudicial to producing effective conservation measures.

Establish and Further Develop Education and Outreach More Efforts

Due to the huge public interest in Antarctic animals (e.g., penguins, seals, whales) education and outreach efforts like those conducted during the Antarctic Treaty Consultative Meetings, by the Association of Polar Early Career Scientists and the Polar Educators International, as well by national programs,

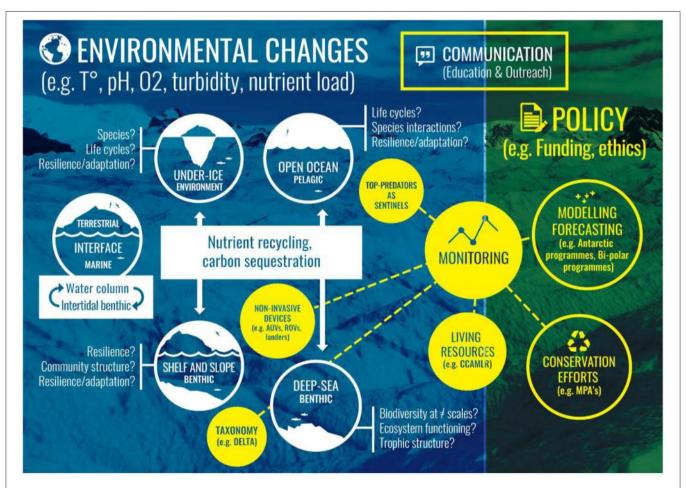


FIGURE 3 | Conceptual diagram illustrating gaps of knowledge in Southern Ocean life and ecology research, examples of the main needs for technological developments, and how these must be linked to monitoring and modeling efforts to forecast future changes in the Southern Ocean. The results of these research fields/gaps may have policy applications, such as on conservation efforts, concomitant with a strong communication (education and outreach) component.

have raised Antarctic science profiles to a broader audience than the scientific and conservation communities currently reached (Baeseman et al., 2011; Walton et al., 2013; May et al., 2014). As such, Antarctic marine ecologists should be encouraged to engage in science communication to the general public, address societal concerns about Antarctic environmental issues (Pace et al., 2010; Xavier et al., 2016), and be actively involved in providing the best scientific information and advice to policy making bodies. If Antarctica-is to be protected, remote ecosystems like the Southern Ocean deep-sea, under-ice shelves and those under permanent sea-ice, will have to be studied and monitored more intensively than in the past and principles of modern conservation science must be applied (Kennicutt et al., 2014), and be promoted within society and in future research initiatives.

CONCLUSIONS

The first SCAR Antarctic and Southern Ocean Science Horizon Scan identified the most urgent science questions to be addressed within the next two decades. Based on the questions originally sent by the scientific community we consider the major gaps in the present ecological knowledge that are essential to shed light on tomorrow's Southern Ocean life and ecology. We concluded that basic biological information on the taxonomy (and the physiology) of organisms, ranging from viruses to top predators (particularly the former), is still lacking, as well as in areas such as the deep-ocean floor or the under-ice environments. At an ecosystem level, the response and resilience to change is largely unknown, rendering accurate forecasting virtually impossible in the near future. However, a future thorough understanding of these responses will be crucial for quantifying the importance of the various components of Antarctic ecosystem services (e.g., biodiversity and carbon sequestration), and the relative impact of future environmental change on these services. Filling in these gaps will require the continuation of a longterm commitment and the development and use of innovative technology to adequately research and monitor the Southern Ocean ecosystems, to detect changes at an early stage, and to evaluate multi-stressor effects in marine ecosystems in order to improve modeling efforts focused on interactive effects. Importantly, disciplines like taxonomy and long-term monitoring should receive strong logistical and financial support if we are to predict likely consequences of climate change and other threats. Finally, informing stakeholders, policy makers and the general public on the results of these studies will draw attention to the importance of this unique ecosystem, emphasize its global pivotal role, and most importantly, its increasing vulnerability to human-induced changes.

AUTHOR CONTRIBUTIONS

JX, AB, and YR coordinated the manuscript and all the authors contributed (writing and reviewing) the manuscript. All authors were highly active at the Horizon Scan, coordinating sessions with the Horizon Scan.

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SUPPLEMENTARY MATERIAL

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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