Antarctic ecosystems in transition – life between stresses and opportunities

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ABSTRACT

Important findings from the second decade of the 21st century on the impact of environmental change on biological processes in the Antarctic were synthesised by 26 international experts. Ten key messages emerged that have stakeholder-relevance and/or a high impact for the scientific community. They address (i) altered biogeochemical cycles, (ii) ocean
acidification, (iii) climate change hotspots, (iv) unexpected dynamism in seabed-dwelling populations, (v) spatial range shifts, (vi) adaptation and thermal resilience, (vii) sea ice related biological fluctuations, (viii) pollution, (ix) endangered terrestrial endemism and (x) the discovery of unknown habitats. Most Antarctic biotas are exposed to multiple stresses and considered vulnerable to environmental change due to narrow tolerance ranges, rapid change, projected circumpolar impacts, low potential for timely genetic adaptation, and migration barriers. Important ecosystem functions, such as primary production and energy transfer between trophic levels, have already changed, and biodiversity patterns have shifted. A confidence assessment of the degree of ‘scientific understanding’ revealed an intermediate level for most of the more detailed sub-messages, indicating that process-oriented research has been successful in the past decade. Additional efforts are necessary, however, to achieve the level of robustness in scientific knowledge that is required to inform protection measures of the unique Antarctic terrestrial and marine ecosystems, and their contributions to global biodiversity and ecosystem services.

Key words: adaptation, benthic dynamism, biogeochemical cycles, climate change, invasion, new habitats, ocean acidification, primary production, range shifts, sea ice

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I. INTRODUCTION

Life in the Antarctic makes a key contribution to our knowledge of the global biosphere due to its uniqueness and connectivity to adjacent ecosystems. The observed impacts and projected risks of rapid climate change for Antarctic biotas (Rogers et al., 2020) are a function of the severity of the hazards, the exposure and vulnerability of the biotas to stresses (Convey & Peck, 2019), and their capacity to adapt or escape. Research strategies are needed to assess further the uniqueness and resilience of Antarctic biotas to inform decision-makers and conservationists on regional and global priorities (Meredith et al., 2019).

The findings in this synthesis focus on studies published since 2010, building upon research carried out since the beginning of the 20th century. This research included basic biological approaches (e.g. taxonomy), targeted studies on key species such as Antarctic krill Euphausia superba (Miller & Hampton, 1989), and ecological studies of biogeochemical cycles, including fluxes of energy to apex predators and physiological adaptations. For a broad coverage of historical results see e.g. Laws (1984), Smith (1990), Hempel (1994), and Knox (2006). Notable research into Antarctic life sciences during the past century includes the demonstration of how life, particularly fishes, evolved and adapted physiologically to the ice-cold environment (di Prisco, Maresca & Tota, 1991). Since then, the rapid development of biomolecular methods has enabled a variety of advances. New research platforms (e.g. research stations, ships) and novel instrumentation (e.g. satellites, landers, autonomous underwater vehicles, robotic floats and automated observatories) have allowed much-improved investigations of biological developments and environmental changes. While numerical and conceptual models often originated in more-accessible ecosystems, specific analytical tools have also been developed to obtain deeper insights into Antarctic-specific ecological processes. Highly focused studies of Antarctic biotas and their environments have been conducted under international initiatives, such as the Ecology of the Antarctic Sea Ice Zone (EASIZ), Evolution and Biodiversity in the Antarctic (EBA) and additional research initiatives of the Scientific Committee on Antarctic Research (SCAR) and the Scientific Committee on Oceanic Research (SCOR).

In 2010, SCAR launched the Scientific Research Programme ‘Antarctic Thresholds – Ecosystem Resilience and Adaptation’ (AnT-ERA) to facilitate biological process-focused research in marine, freshwater and terrestrial ecosystems facing various stressors. Since then, a vast array of results ranging from molecular to ecosystem levels has been generated. Examples, are assembled in the Antarctic Climate Change and the Environment report and its regular updates to Antarctic Treaty Meetings (Turner et al., 2014).

This synthesis aimed to identify the most important climate-dependent findings from the past decade on biological processes in Antarctic ecosystems. These findings are synthetically synthesised into scientific messages, with associated levels of confidence. Where appropriate the findings are assembled independently for the marine, limnetic or terrestrial ecosystem from which they originate, to identify similarities and contrasts across these ecosystems. Results were considered to be ‘most important’ if they (i) were novel and could be clustered into messages with considerable relevance for the scientific community, research and funding strategies, projects and textbooks, or (ii) have relevance for stakeholders, such as: the Intergovernmental Panel on Climate Change (IPCC), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the United Nations Decade of Ocean Science for Sustainable
Development, the Antarctic Treaty System with its nature conservation initiatives, the Commission for Environmental Protection (CEP) and the Commission on the Conservation of Antarctic Living Resources (CCAMLR). Stakeholders also include science managers, politicians, journalists, and the general public. Some of the findings reflect questions raised by the 1st Scientific Antarctic Committee on Antarctic Research Antarctic and Southern Ocean Science Horizon Scan, the implementation of which has recently been assessed (Kemnicutt et al., 2019).

II. MATERIALS AND METHODS

A SCAR AnT-ERA workshop held in Coimbra, Portugal, in 2019 identified 10 high-level scientific key messages (Fig. 1) on biological processes in the Southern Ocean and on the Antarctic continent, which fall into 31 more detailed sub-messages (Fig. 2). These are discussed in detail in Section III. The messages and sub-messages were developed by consensus of the 23 experts from the AnT-ERA steering committee and invited guest experts, who jointly authored this assessment and whose areas of expertise are provided as online supporting information in Appendix S1. We are aware that other groups might identify different key questions, but we attempted to include all scientific themes, groups of organisms, Antarctic regions and ecosystems. We restrict our survey to research published from 2010 onwards, other than in a few exceptional cases. While our 10 key messages are interrelated to some extent, the aggregation of focused results cannot always reflect these thematic overlaps. Only the most recent publications and only those considered to be ‘most important’ (for definition see above) are cited. Numerous additional valuable results have been published that are referenced in the publications mentioned herein.

To verify the relevance of our key messages, the peer-reviewed literature for 2010–2020 was analysed in a standardised way by using in the Web of Science the key words listed in Appendix S2. The results are illustrated in Fig. 2. To document the progress of knowledge in the past decade values are also provided for period 1970–2020 in Appendix S2.

To assess the level of confidence of the sub-messages, IPCC AR5 methodology was applied (Mach et al., 2017; IPBES, 2019; see Appendix S3), which categorises the quantity/quality of evidence in combination with the agreement between them as: ‘limited’, ‘emerging’, ‘divergent’, or ‘robust’). Important results were initially proposed by experts, then discussed during the workshop or by later correspondence until agreement among all authors was reached. Principally this classification depends not only on the quality/quantity of the evidence and agreement between conclusions, but also on the wording of the message. The confidence level is higher for simple and general statements, but lower if an evidence-based message tries to capture the complexity of a system. The high-level key messages themselves were considered too general to be assessed in this way.

III. RESULTS

Of the literature resulting from our search terms predominately referring to Antarctic biotas in transition as a response to environmental change (Morley et al., 2020), 67% were published in the past 10 years. Only 33% of the papers identified were from the 1970 to 2010 period (see Appendix S2). Even for the traditional theme of ‘adaptation’, 56% of papers since 1970 were written between 2010 and 2020. This predominance is due to a steadily increasing knowledge on biochemical processes within single cells, often subsumed under the term ‘adaptation’, and a shift from qualitative to quantitative ecosystem-level analyses. It is still challenging to link these two extremes by up- and downscaling approaches to assess the variability and sensitivity of ecological functions (Gutt et al., 2018; Neumann et al., 2019). Figure 1 shows that our 10 messages affect humans most in their connection with climate regulation, followed by nature conservation and to a lesser extent with human food provision and bioprospecting, including for medicine and lifestyle products and applications (Fig. 1). The literature survey (Fig. 2) identified topics with high societal interest and relevance, such as the responses of biotas to climate change (message 3) and short- to mid-term biogeochemical cycles (message 1), and adaptation of species to polar conditions (message 6), to be numerically best represented in the scientific literature. However, not all globally relevant or emerging themes, such as long-term carbon sequestration by benthic processes (part of message 1), ocean acidification (message 2) and pollution (message 0), have been intensively investigated in the Antarctic.

(1) Changes in the Antarctic cryosphere modify pathways of marine and terrestrial biogeochemical cycling in different ways

Antarctic ecosystems play a central role in regulating global biogeochemical cycles, particularly in the ocean, and affect the global climate system (Henley et al., 2020). Changes in these functions are rapid, hampering our ability to describe and assess their outcomes fully. Cascading effects ultimately can impact processes at all ecosystem levels, determining the stability and resilience of Antarctic biotas and their interactions both on land and in the ocean.

(a) Anthropogenic pressures accelerate nutrient release and buildup of organic matter resulting from the melting of terrestrial and sea ice

Microbially maintained subglacial brines can be reservoirs of nutrients such as iron, and organic matter, connecting the land, including subglacial lakes, with the ocean (Hawkins et al., 2014; Vick-Majors et al., 2020). Similarly, land-based glaciers are a significant source of nutrients and organic matter for stream and cryolake ecosystems (Bagshaw et al., 2016). Warming enhances these transport processes. The sediment fluxes that accompany nutrient transport produce additional
Ten themes on Antarctic ecosystems in transition

Consequences: in lakes, pulsed sediment flux can lead to short-term turbidity, initially resulting in decreased photosynthetically active radiation and net primary production, followed by increases in both variables (Obryk et al., 2016). Marine benthic biomass is expected to increase due to enhanced export of carbon to the sea-bed (Jones et al., 2013) and to contribute to carbon sequestration as a negative feedback of climate change feedback (Barnes, 2017). In the open ocean, the numbers of icebergs increase when calving rates from glaciers and ice shelves rise due to atmospheric and ocean warming. These changes affect the stimulation of primary production, especially through fertilisation (Wu & Hou, 2017), with consequences for food webs, but also create phytoplankton losses due to complex hydrodynamic and biogeochemical processes (Vernet et al., 2011), creating another negative feedback from climate change (Hopwood et al., 2019).

Due to warming of the Antarctic Peninsula, blooms of green snow algae strongly influenced by marine nutrient inputs are expected to shrink in some areas, due to ice melt, and to expand in others, especially close to bird and seal colonies, resulting in a net increase in biomass and, thus, to act as a significant carbon sink (Gray et al., 2020).

(b) Climate-induced breakdown in sea and freshwater ice coverage, and changes in ocean-circulation patterns modify stratification of water columns; primary production is expected to increase, while carbon and nutrient fluxes will be altered.

Climate change effects, including increased freshwater inputs, strengthen shallow marine water-column stratification, stimulating the production of large-cell diatoms and the haptophyte Phaeocystis antarctica (Kaufman et al., 2017; Woch et al., 2011).

Fig 1. Relationships between 10 themes, for which we synthesized our 10 evidence-based scientific key messages (left) and fields of applied research in Antarctica and the Southern Ocean represented by ecosystem goods and services (nature’s contributions to people) or related applications (right). Thicker lines indicate stronger relationships.
Hofer et al., 2019), but also the growth of other small flagellates (Mendes et al., 2018). In contrast to most other oceans, intense nutrient trapping is expected due to warming in the Southern Ocean (Moore et al., 2018). This process will increase total marine net primary production, which will also be enhanced by increased light from shorter sea ice-cover periods (Moreau et al., 2015). As a consequence, increasing CO₂ uptake could occur, especially along the West Antarctic Peninsula (WAP) (Brown et al., 2019). Models project, especially for highly productive areas such as the Ross Sea and WAP, that increased rates of remineralisation (Henley et al., 2018) support pelagic ecosystem function (Petrou et al., 2016). Furthermore they increase the amount of food available to krill and salps and through them, albeit to different extents, support higher trophic levels (Flores et al., 2012; Henschke et al., 2016) and further remineralisation (Plum, Hillebrand & Moorthi, 2020). However, nutrient upwelling could be reduced, with negative impacts on phytoplankton growth. A projected increase in westerly winds (positive Southern Annular Mode in combination with the long-term Amundsen Sea Low) would regionally promote upwelling of nutrient-rich waters, compensating the shallowing of mixed-layer depths and increased stratification (Deppeler & Davidson, 2017). Planktonic production is expected to

**Fig 2.** Scientific key messages/themes, sub-messages (left, abbreviated) with assessment of ‘confidence’ of the sub-messages [centre; after Mach et al. (2017) and IPBES (2019)] and number of scientific publications per key message over the period 2010–2020 resulting from the literature survey (right; for search terms see Appendix S2). WAP, West Antarctic Peninsula.
increase anthropogenic CO₂ uptake with ongoing climate change due to a decreasing buffering capacity of the ocean (Hauck & Völker, 2015). Models have also predicted that Southern Ocean primary production and related ecosystem functions will maintain high oxygen concentrations in adjacent surface waters (Keller et al., 2016). In freshwater inland water bodies, perennial ice covers have profound impacts on primary producers (Sutherland, Howard-Williams & Hawes, 2020), and a shift to seasonal ice cover will gradually break down highly stratified water columns, leading to increased primary production and other, as yet unknown, consequences for ecosystem processes (Obyrk, Doran & Priscu, 2019).

(c) Mass loss of inland and shelf ice leads to increases in habitat availability and suitability

Glacial retreat increases the available ground for slow colonisation in maritime terrestrial systems, which can result in local increases in biomass and productivity (Favero-Longo et al., 2012). Indirect impacts of inland ice melt on habitat are mediated through increased meltwater production. Resulting expansions of stream volume and wetted soil area, and lake level rise in the endorheic lakes common in much of Antarctica, will enhance habitat area and/or quality. For increasing terrestrial connectivity, through increased streamflow, see Section III.9. In marine ecosystems, ice shelf collapses expand suitable habitat for plankton blooms (Bertolin & Schloss, 2009), depositing fresh organic matter onto the sea floor, which represents a new biological (‘blue’) carbon uptake in the Southern Ocean water column (Peck et al., 2010) and suitable territory for benthos (Gutt et al., 2011; Sané et al., 2012). However, evidence is still insufficient regarding whether the sea-bed accumulates enough organic matter to act as a long-term carbon sink (Isla & DeMaster, 2018).

(d) Anthropogenic iron fertilisation of pelagic systems seems inefficient in sequestering carbon dioxide

Studies on iron limitation combined with ocean acidification (e.g. Hoppe et al., 2017), especially for high-nutrient low-chlorophyll pelagic systems, have been used to assess carbon cycling and sequestration. In a more applied approach, an iron-fertilisation experiment, north of the polar front in the Atlantic sector of the Southern Ocean showed significant changes in pelagic community composition and ecological functions. However, it found no enhanced export of organic matter from surface waters to deeper layers (Laglera et al., 2017), even though signals in the deep sea generally mirrored processes in the euphotic layer. Upwelling meant that a calculated 66% of remineralised carbon reaching 1000 m depth was re-exposed to the atmosphere after only 38 years (Robinson et al., 2014). Iron fertilisation can even reduce natural deep-ocean CO₂ storage (Salter et al., 2014).

(2) Ocean acidification potentially stresses vulnerable Antarctic key biotas

Ocean acidification (OA) is another anthropogenic climate-related stressor affecting marine species, with ocean uptake of atmospheric CO₂ reducing carbonate concentrations and pH. Models project a rapid shallowing of the water depths below which carbonate dissolution will occur in almost the entire Southern Ocean that will affect calcifying and non-calcifying life forms. Thus, OA may become one of the most serious pressures on marine organisms and ecosystems.

(a) Species respond specifically to ocean acidification; some can potentially acclimatise

Responses of primary producers (including growth and photosynthesis) to simulated OA vary among species and with duration of exposure, ranging from positive to negative. The dominant phytoplankton species, the haptophyte Phaeocystis antarctica, is more tolerant to OA than the abundant diatoms Chaetoceros debilis and Fragilariopsis kerguelensis (Trimborn et al., 2017). This may have feedbacks to climate, as Phaeocystis is a source of dimethyl sulhide, modifying cloud properties and cooling air temperatures. Responses of key Antarctic invertebrate species parallel those in non-polar regions, with early life-history stages being generally more vulnerable. For example, development and/or carbonate structures of young Antarctic krill, echinoderms and molluscs may be disrupted (e.g. Bylenga, Cummings & Ryan, 2017), and the hatching success and suitable habitat of krill is projected to decrease (Kawaguchi et al., 2013). Across a range of species, adult life stages show effects of exposure to end-century pH levels [e.g. on survival, shell dissolution, reproductive development; Manno et al., 2017; Dell’Acqua et al., 2019]. Other species/stages are not adversely affected, including adult Antarctic krill (Ericson et al., 2018). Negative effects are observed only in association with increased temperatures (e.g. development of Antarctic dragonfish (Gymnodraco acuticeps); Flynn et al., 2015), and warming may have stronger effects than acidification (e.g. in some nototheniid fishes; Enzor, Hunter & Place, 2017). Longer-term studies reveal the potential for compensatory responses to OA: polar brachiopods produce a thicker shell in response to dissolution of the outer layer (Cross, Harper & Peck, 2019). Among the meiofauna, foraminifera are expected generally to suffer from OA, especially where shallowing of the calcite compensation depth is predicted, whilst nematodes seem to be more robust and show species-specific responses (Ingels et al., 2012).

(b) Communities respond differently to ocean acidification, with ecosystem implications depending on the response of ecological key species

Direct investigations of rates of change associated with OA (Negrete-Garcia et al., 2019) and community-level responses are rare. Short-term (~2 week) studies of coastal Antarctic systems have revealed reductions in primary production
and increases in bacterial activity (e.g. Deppeler et al., 2018). Under-sea-ice microalgal communities showed only modest productivity increases and no change in biomass or composition (Cummings et al., 2019). In a three-month in situ experiment, benthic diatoms changed their phototactile vertical migration behaviour, affecting their photo-physiology and net production (Black et al., 2019). However, crustacean grazer assemblages remained unaffected after 1 month at end-century OA conditions (Schram et al., 2016).

Predictions of ecosystem-level changes require knowledge of which species and functional groups will be, and will not be, impacted by acidification (in combination with other stressors), and particularly their long-term ability to adapt to these changes.

(3) Physical processes in the atmosphere force rapid ecosystem changes in climate change hotspots

Biological responses to warming and related physical processes over the last 50 years along the WAP (listed in Table 1) indicate what other Antarctic marine and terrestrial ecosystems may experience with predicted large-scale climate change under similar forcing variables. Important changes in the biology of krill species (Euphausiacea) and their competitors and predators are described in Section III.3b.

(a) Algal blooms are increasing along the West Antarctic Peninsula (WAP)

Phytoplankton dynamics along the WAP respond to sea ice-mediated changes in the water column. Years of higher winter ice extent and duration, reduced winds, and increased water-column stability favour high summer phytoplankton biomass (Venables, Clarke & Meredith, 2013; Saba et al., 2014; Schloss et al., 2014). Moreover, ice type (fast, grease, pack or brash ice), temperature and water column properties contribute to phytoplankton composition and cell size structure of early summer blooms with small cryptophytes in relatively warm water and larger diatoms under prolonged summer stratification combined with wind-induced mixing (Biggs et al., 2019). A 40% increase in primary production in a sampling area off the northern WAP between 1997 and 2010 was associated with longer production seasons due to sea ice retreat and ocean warming (Moreau et al., 2015); however, there are regional disparities that have reversed in the past decade. In the northern offshore WAP region, years of low winter sea ice and a relatively deep mixed layer observed between 1995 and 2006 correlated with lower phytoplankton biomass and a shift towards small size-dominated microbial plankton (Montes-Hugo et al., 2009). Observations since 2010 revealed increases in phytoplankton biomass in the northern WAP that are above the long-term average (Schofield et al., 2017) and a decrease in average biomass with deepening mixed-layer depths in southern inshore WAP sites (Kim et al., 2018). Future projections indicate that primary production (along with nitrate consumption) will increase further in this area. In this case, iron additions from melting in glacial environments may allow complete nitrate depletion in some coastal waters, which is currently rarely observed (Hofer et al., 2019).

Microbes such as eukaryotic phototrophs and prokaryotic photoheterotrophs, chemoheterotrophs and aerobic anoxygenic phototrophs characterise spring and summer microbial communities, whereas winter communities harbour a higher proportion of archaeal and bacterial chemolithoautotrophs (Grzymski et al., 2012; Luria et al., 2016). Kim & Ducklow (2016) suggested an increasingly important role of marine heterotrophic bacteria in future warmer coastal WAP food webs. The role of viruses in microbial processes and ecosystem functions remain understudied in the Southern Ocean, although this information is critical to predicting future changes in microbial dynamics.

(b) Marine biological hotspots in fjords experience ecosystem changes due to warming-induced glacier melt and retreat

Atmospheric warming and increased incursions of warm Circumpolar Deep Water onto the continental shelf have caused rapid retreat of fjord tidewater glaciers at the WAP (Cook et al., 2016). In Potter Cove on King George/25 de Mayo Island (KGI), benthic structure shifted markedly from dominance by ascidians towards a mixed community comprising e.g. sea-pens, sponges, bivalves, sea anemones and ophiuroids, resulting from increased sedimentation rates following glacier retreat (Sahade et al., 2015). By contrast, newly ice-free seabed has sustained explosive growth of obviously sedimentation-tolerant ascidians (Lagger et al., 2018). In the
adjacent Marian Cove, megazoobenthic assemblages changed with distance from the retreating glacier front, suggesting that physical disturbance is a major process shaping benthic communities (Moon et al., 2015), and some benthic diatoms (e.g. *Pavilia* sp.) reported rarely in previous studies showed an intense and persistent bloom from which herbivorous and filter-feeding consumers benefited (Ha et al., 2019). The observed processes in the two KGI fjords allow the conclusion that climate-induced glacial retreat will alter ecosystem structure and functioning in additional fjords along the WAP, including those that have experienced little glacial retreat so far (see e.g. Lundesgaard et al., 2020).

Fjords in the WAP region are also known as local hotspots of biodiversity (Pabis, Sicinski & Krymarrays, 2011), with e.g. two million tons of Antarctic krill and >300 feeding humpback whales *Megaptera novaeangliae* (Nowacek et al., 2011) observed in single fjords, and up to 38-fold higher megafaunal abundances compared to the adjacent continental shelf (Grange & Smith, 2013).

(c) Additional hotspots of climate change impact are to be expected in the future or exist already at a local scale

A significant decrease in late-summer sea ice concentration is projected for the Bellingshausen and Amundsen Seas as a consequence of geographically extending climate change (Meredith et al., 2019). Similar consequences to those already experienced for decades by the WAP region (see Section III.3a), must be expected also for these currently cooler sectors of the Southern Ocean, since they have similar pelagic and benthic systems. A southward shift of the Antarctic Circumpolar Current remains controversial (Cristofari et al., 2018; Meijers et al., 2019). If it reaches >4 km per decade (Yang et al., 2020), it will have a crucial impact on the entire pelagic system (Cheung et al., 2009), with cascading effects on higher tropic levels (see also Section III.5a) due to shifts in the steep gradient in sea-surface temperature. Bokhorst, Convey & Aerts (2019) found that terrestrial biodiversity hotspots are often related to penguin and seal excrement, which creates conditions adequate for local and potentially invasive plants to establish. When seasonal ice cover is reduced in lakes, exposing open water, variations in the precipitation–evaporation balance can increase desiccation and salinisation, and the lakes will become important hotspots of climate change impacts on biodiversity (Verleyen et al., 2012).

(4) Benthic communities exhibit unexpected dynamism – from explosive growth to mass mortality

Until recently, Southern Ocean benthic systems were described as characterised by long-term stability and slow biological processes. Novel evidence demands a paradigm shift towards populations and community dynamics ranging from ‘slow–stable’ in a global context to ‘fast–variable’ compared to the majority of the Antarctic benthos, with profound implications for their resilience or vulnerability.

(a) Some benthic near-shore populations are sensitive to complex environmental forcing

In McMurdo Sound (Ross Sea), the glass sponges *Anoxycalyx joubini* and *Rossella nuda* showed virtually no growth over a 10-year observation interval (Dayton et al., 2013, 2016). They were mostly >2 m tall, some were killed by the predatory starfish *Acodontaster conspicuus* with no subsequent recruitment. While artificial substrates deployed in the 1970s were not significantly colonised by epifauna until 1989, they were found in 2010 to be totally covered by *A. joubini* and other sponges, some of which had grown to 50 cm in diameter. They continued growing until 2015, when most specimens died due to amphipod infestation, predation or sedimentation. These unexpectedly strong population dynamics in an environment that is both very cold (at nearly −2°C) and very stable in temperature were only weakly correlated with shifts in phytoplankton productivity driven by the calving of a massive nearby iceberg. While such dramatic changes were not observed for sponges on natural substrates, similar population shifts of echinodermals and bivalves were clearly attributable to the alteration of the marine production regime affected by regional iceberg and sea ice dynamics (Dayton et al., 2019; Kim, Hammerstrom & Dayton, 2019b). In addition, sea ice cover duration and thickness as well as snow cover, all related to climate change, were important large-scale variables in explaining the diversity and functional traits of coastal benthic communities in this area (Cummings et al., 2018). In laboratory experiments, demosponge species exhibited extreme phenotypic plasticity in metabolic physiology, with differences in metabolism among species being greater than seasonal changes (Morley et al., 2016), a finding that contributes considerably to our understanding of high benthic dynamism. See Section III.3b for climate change impacts on the WAP benthos.

(b) Benthic recolonisation after sea ice and iceberg disturbance fosters mass occurrence of pioneer species

Twelve years after the Larsen A ice shelf disintegrated in the western Weddell Sea, recruits of the glass sponge *Rossella cf. villosa* dominated the newly exposed seafloor (Gutt et al., 2011). Dense aggregations of holothurians indicated unusually successful recruitment. Ophiuroid assemblages shifted from suspension- to deposit-feeder dominance. Abundant ascidian species disappeared, whilst formerly rare species doubled in abundance. Typical macrobenthic deep-sea species, assumed to characterise the sub-ice shelf benthos, may vanish when conditions turn to Southern Ocean shelf ‘normality’ (Gutt et al., 2013; Segelken-voigt et al., 2016). These shifts are most likely caused by changes in food availability driven by ice shelf disintegration, current patterns, unpredictable sea ice dynamics (Cape et al., 2014) and prey–predator interactions. Meiofaunal communities
generally responded more slowly to change, still resembling those of food-limited deep-sea habitats 5 years after the Larsen B ice shelf disintegration (Rose et al., 2014). However, two nematode genera were found to be rapid colonisers (Raes, Rose & Vanreusel, 2010).

After local devastation of the benthos due to anchor ice uplift in McMurdo Sound, the demersal sponge Homaxinella bal-jourensis recruited immediately and grew rapidly (Dayton et al., 2016). Sponges of this genus were also abundant near the terminus of tidewater glaciers in the Ross Sea and in iceberg scours in the Weddell Sea (Gutt et al., 2011). The demersal Stylocordyla chupachups, gorgonians such as Primnoisis sp. and Aningaptilon antarcticus, as well as the hydrozoans Corymorpha spp. and Oswaltdella antarctica, are further examples of pioneer species. The patchwork of dynamic stages of recolonisation increase regional beta-diversity (Turner et al., 2014).

(c) Demersal fish stocks recover only very slowly from commercial fishery

Commercial bottom trawling in the Southern Ocean between the 1960s and 1990 led to a substantial depletion of the target and by-catch nototheniid rockcod and icefish species. The recovery time of these populations has been estimated to last 2–3 decades because of slow growth and low fecundity. A more recent study indicated that even this estimate was too optimistic, because the fish habitats around the South Shetland Islands are also severely impacted by rapid climate change (Marschoff et al., 2012; Barrera-Oro, Marschoff & Ainley, 2017).

(5) Range shifts, expansions, contractions and invasions are driven by environmental changes and human impacts

Distribution shifts have been observed and predicted for a variety of Antarctic species. They are driven by changing climate (in marine and terrestrial habitats) and/or human introductions (mainly in terrestrial habitats). Human movements and declining ocean barriers enhance connectivity of the Antarctic to the rest of the world, facilitating biological invasions. Warmer temperatures boost species’ range expansions, threatening adapted local specialists.

(a) Species geographical distributions are moving rapidly with changing environments

Consistent, long-term distribution shifts are occurring in the Southern Ocean, with warming resulting in poleward shifts in many species. For example, in response to the strengthening and southward shift of westerly winds, the foraging range of wandering albatross (Diomedea exulans) shifted southwards (Weimerskirch et al., 2012). However, the direction and extent of range shifts vary among species. Some albatrosses and petrels shifted southwards from the 1990s to 2000s, but white-chinned petrels (Procellaria aequinoctialis) occurred further north (Peron et al., 2010). Of seven Southern Ocean seabird species, the foraging ranges of four are projected to contract in the north, instead of shifting polewards (Krüger et al., 2018). Historical hotspots of post-larval Antarctic krill abundance have moved southwards from the Southwest Atlantic Sector to the WAP shelf system over the past 90 years. Sharp decreases in juveniles and new recruitment since the 1970s are attributed to increased temperatures and winds, and a reduction in sea ice (Atkinson et al., 2019). Krill habitat quality is projected to continue to shift southwards and impact phenology due to warming and changes in phytoplankton biomass (Veytia et al., 2020), subsequently impacting the foraging habitats of their predators, such as crabeater seals (Hückstädt et al., 2020). On the WAP shelf, a large reduction in the distribution of a key sea ice dependent species, the Antarctic silverfish (Platyrhagmus antarcticus), suggests a local population collapse (Parker et al., 2015). Ninety per cent of lanternfish (Myctophidae) species are also predicted to shift polewards (Freer et al., 2019). Terrestrial nematodes, tardigrades, and rotifers are wind-dispersed across vast geographical space whereas springtails (Collembola) generally disperse long distances via open waterways. Climate-driven changes that lead to increased frequency and magnitude of extreme wind and meltwater events will likely expand the geographic range of cosmopolitan taxa. Similarly, the geographic ranges of more endemic species are predicted to contract concomitant with landscape-scale changes in habitat suitability (Adams et al., 2014).

Increasing temperatures alone are not predicted to result in wholesale extinction or invasion of Antarctic life, but 79% of Antarctic endemic sea-floor invertebrate species (down to 1000 m) are projected to face reductions of habitats characterised by suitable temperature conditions. The 963 species with ranges that cross the Polar Front were projected either to lose (53.5%) or to gain (46.5%) potential habitat (Griffiths, Meijers & Bracegirdle, 2017). King penguin (Aptenodytes patagonicus) colonies are predicted to disappear or decline in most of the sub-Antarctic, but new colonies may appear as the winter sea ice disappears (Cristofari et al., 2018). Models for baleen whale populations generally predict declines, as the abundances of their prey decrease due to warming, but impacts vary among populations. If whales adapt their migratory behaviour, some species (e.g. minke whales, Balaenoptera bonaerensis) may benefit from changing conditions, while others (e.g. southern right whales, Eubalaena australis) will decline (Tulloch et al., 2019). For contraction of species found under disintegrating ice shelves and the expansion of the ‘normal’ shelf fauna into such areas, see Section III.4b.

(b) Species expand their ranges in a warming Antarctic – faster, greener, and more competitive

Range expansion is most obvious in the terrestrial realm where habitat availability is predicted to increase by ~25% by the end of the 21st century (Lee et al., 2017). Deglaciated terrains can be colonised rapidly, supporting an increased...
diversity and abundance of bacteria, lichens and bryophytes (Favero-Longo et al., 2012). In particular, taxa with wider ecological response amplitudes are predicted to thrive, with evidence available for hypoliths (Ier et al., 2016) and soil microbial communities. A general trend emerges that warmer temperatures boost terrestrial ecosystem productivity. Between 1991 and 2002, with increasing temperature, four out of six monitored chironomid species increased their growth rates by 124% (Sancho, Pintado & Green, 2019). Moss growth rates have quadrupled over the past approximately 50 years (Amesbury et al., 2017), and also the two Antarctic native vascular plants Colobanthus quitensis and especially Deschampsia antarctica proliferated.

Such changes can cause drastic shifts in terrestrial populations because locally adapted species may have evolved life-history trade-offs that result in decreased resilience. Endemic lichen species have shown little to no potential to acclimatise (Colesie et al., 2018) and for Antarctic tardigrades, changes in soil hydrology can modify physical constraints and alter their abundance (Andriuzzi et al., 2018).

In the marine realm, range expansions of various zooplankton species are linked to differences in sea ice changes with warming. From 1993 to 2013, the abundance of non-ice-dependent krill Thysanoessa macrura increased in coastal and shelf waters of the northern WAP region, while the abundance of sea ice-dependent crystal krill Euphausia crystallorophias increased in the south (Steinberg et al., 2015). Furthermore, sub-polar penguin species, including chinstrap (Pygoscelis antarctica) and gentoo (P. papua), increased in abundance in the northern WAP region as Adélie penguins (P. adeliae) have declined (Ducklow et al., 2013). Range expansions of king crabs (Necithodes yaldwyni) with reproductively viable populations were recently reported in the Palmer Deep and on the WAP slope (C.R. Smith et al., 2012b; Griffiths et al., 2013).

A warming Antarctica enhances prospects for invaders and colonisation

In the terrestrial realm, humans have introduced non-native organisms, including the grass species Poa annua. While the two native vascular plants have been shown to be capable of withstanding competition for space, this might change with climate warming (Cavieiras et al., 2018). The flightless chironomid midge Eretmoptera murphyi was introduced to Signy Island in the 1960s, accelerating nutrient cycling and potentially outcompeting in the future the indigenous and endemic chironomid Belgica antarctica, highlighting the importance of biosecurity measures (Bartlett et al., 2020).

The occurrence of invasive species has been most evident at sites with high human visitation frequency. Monitoring programs have detected high levels of non-native species (e.g. 233 individuals from 14 orders) around Scott Base (Newman et al., 2018). However, clear evidence of an impact of invasive taxa at highly visited sites is missing (Velasco-Castrillon, Hawes & Stevens, 2018). Antarctica is currently unsuitable for most of the globally invasive terrestrial species; however, areas of the Antarctic Peninsula are predicted to become suitable for up to six of these species within the 21st century (Duffy et al., 2017).

In the marine realm, four non-native invertebrates (crustacean, bryozoan, ascidian, cnidarian) and one cryptogenic kelp have been recorded (McCarthy et al., 2019). Antarctica is not as physically isolated as previously thought. Newly identified mechanisms for colonisation include rafting on kelp or passive transport in surface waters, as eddies and storms move southwards across the Polar Front (Fraser et al., 2018). The risk of human-introduced invasive species is linked to ship activity, with approximately 180 vessels and 500+ voyages into Antarctic waters annually (McCarthy et al., 2019).

Sentinel species and communities warn of environmental changes

Long-term observations of selected species can be valuable indicators of change. The use of lichens as biomonitors for warming is increasing, especially on the sub-Antarctic islands (Sancho et al., 2019), and mosses are used as proxies for coastal climate change in the regionally drying East Antarctica (Robinson et al., 2018).

In the ocean, extreme sea-surface temperature events decrease population growth in black-browed albatrosses (Thalassarche melanocephala; Pardo et al., 2017), making them valuable sentinels. Food stress caused by climate change increased the heterozygosity of breeding Antarctic fur seal (Arctocephalus gazella) females by 8.5% per generation over the last two decades (Forcada & Hoffman, 2014). Southern elephant seals (Mirounga leonina) produce pups of poorer condition in years with lower ocean productivity within their foraging ranges (Oosthuizen et al., 2015). In the WAP, precipitous declines (80% since the mid-1970s) of Adélie penguins in the north and increases in the south (Ducklow et al., 2013) have been attributed to differences in Antarctic krill availability and recruitment (Trivelpiece et al., 2011) and changes in sea ice, precipitation and snowmelt (Cimino et al., 2016). A geographic shift of areas of ecological significance based on aggregations of various top predators has been projected, which has relevance for future conservation and protection measures (Hindell et al., 2020). New ways of using marine top predators as sentinels for trends in environmental conditions are emerging. For example, the adiposity of humpback whale blubber is a proxy of sea ice conditions in the preceding year (Bengtson Nash et al., 2018).

‘Ecosystem Essential Ocean Variables’ represent a complex combination of biological traits and ecologically relevant physico-chemical variables related to biological functional groups (Constable et al., 2016). They can be used as sentinels of changing environmental conditions, including single ecosystem components such as marine benthic communities, since they complement world-wide initiatives such as the Long-Term Ecological Research (LTER) network. Specifically, bivalve shells and fish otoliths can record
environmental signals such as changing sea ice dynamics and temperature over their lifetimes (Trevisiol et al., 2013).

(6) Survival and resilience of species depend on their adaptation and acclimation potential

Abilities to respond to changing Antarctic environments vary among organisms, shaped by distinctive selective pressures they experienced in their respective habitats during their evolutionary history. Marine waters hover chronically around −1.9°C, just above the freezing point of sea water, while terrestrial temperatures fluctuate widely seasonally, even daily, reaching vastly lower extremes. Marine ectotherms have adapted to remain active in pervasive constant cold, while terrestrial organisms have adapted to quiescent tolerance of prolonged aridity and frozen habitats, and to burst into growth during a finite window of more element conditions. Knowledge of the complexity of adaptations of organisms to polar conditions is crucial to infer which species will become winners or losers in response to climate change, and to predict resilience, tipping points and impacts on ecosystem services.

(a) Feeling the cold – low temperatures damage proteins and constrain organismal performance but may also drive protein functional innovation

(i) Marine systems. Cold can prevent proteins from forming properly. With Southern Ocean temperatures at or near freezing point year-round, Antarctic nototheniid fishes are the most cold stenothermal marine vertebrates globally (Verde, Parisi & di Prisco, 2006), and are found to sustain high levels of protein damage. The repair machinery responsible for recycling improperly formed or damaged proteins in their cells runs 2–5 times faster than in lower latitude species (Todgham, Crombie & Hofmann, 2017). At the organism level, growth, embryonic development and post-prandial processes are 3–10 times slower than the expected effects of low temperature in Antarctic species, a consequence of problems in producing proteins at low temperatures (Peck, 2018). Cellular proteins and membrane lipids can be damaged by the high oxygen concentrations in cold water. Neuroglobin and cytoglobin were discovered in Antarctic fishes, including the haemoglobin-less channichthyid species, suggesting the evolution of functional innovations to mitigate such oxidative damage. Under experimental conditions, neuroglobin showed oxygen-related functions but its precise role in protection from damage remains unknown (Cuypers et al., 2017, Giordano et al., 2020).

(ii) Terrestrial systems. For Antarctic terrestrial organisms, shifts in the frequency of soil freeze–thaw cycles represent a physiological challenge. Small, poikilothermic animals with limited mobility – such as Scottia amanda lindsayae, the dominant nematode in Taylor Valley, Dry Valleys, East Antarctica – experienced population shifts with an increased frequency of soil freeze–thaw cycles between 1999 and 2001. Fewer juveniles reached maturity, and reduced reproductive success ultimately had the potential to impact population size (Knox et al., 2016; T.E. Smith et al., 2012). Similarly, for Antarctic mosses (Bramley-Alves et al., 2014) and lichens, ice encapsulation at subfreezing temperatures can have detrimental effects (Bjerke, 2011), even if some of the isolated symbiotic photobionts exhibit high cryoresistance (Hajek et al., 2012).

(b) Feeling the heat – Antarctic species are vulnerable to change; their thermal resilience is poor, complex and variable

(i) Marine systems. Ocean warming is a key climate change stressor. New research has tested the thermal resilience of Antarctic marine species. At the organismal level, species generally require 2–15 times as long as temperate species to acclimate to warming (Peck, 2018). Their long-term limits are about 2–3°C above ambient temperature, similar to species of the thermally stable tropics, compared to 6–9°C for temperate species (Peck et al., 2014). Some experiments show significant plasticity in early-life stages (Suckling et al., 2015), and no single cellular or physiological mechanism sets the thermal limits, because different species fail for different reasons (M.S. Clark et al., 2017b). Recently, the first long-term (two-year) field experiment showed that 1°C warming doubled growth rates in most species, and community structure changed dramatically (Ashton et al., 2017). At 2°C warming, growth was not faster, or even was slower, species had not acclimated, and there were stress responses and indicators of cell death (Clark et al., 2019).

At the cellular level, brain lipid membranes are especially vulnerable to heat, and neuronal impairment is the first impact of acute heat stress. While broadly stenothermal, Antarctic fishes vary in acute thermal tolerance, e.g. brain synaptic membrane fluidity varies among species (Biederman et al., 2019), with the more thermal-tolerant fish being least fluid. In short-term thermal acclimation, homeoviscous (i.e. maintenance of optimal fluidity) responses also vary among species, with membrane lipid remodelling occurring in one but not in a related sympatric species (Malekar et al., 2018).

Recent comparative studies on thermal responses showed that for Antarctic fish, differences exist among latitudes and species within and across regions. This complexity is evident even for only a small number of studied species, in terms of Critical Thermal Maximum as a measure for thermal tolerance (Beers & Sidell, 2011), in terms of cellular transcriptional response to warm acclimation (Huth & Place, 2016), or to acute heat stress (Bilyk, Vargas-Chacoff & Cheng, 2018). Furthermore, analyses of the X-ray structure of haemoglobin of Eleginops maclovinus demonstrate that mechanisms underlying ATP regulation and the Root effect are diverse between sub- and high-latitude Antarctic notothenioids (Coppola et al., 2012). This finding suggests that the distinct evolutionary history of each lineage may have influenced the extant genotype and adaptive potential to future change.
(ii) Terrestrial systems. Many Antarctic terrestrial biotas, in contrast to most marine organisms, have broad environmental tolerances allowing them to survive wide temperature fluctuations, including sub-Antarctic caterpillars, microarthropods and nematodes, all of which can cope with increased and/or variable temperatures (e.g. Everatt et al., 2013). Furthermore, McGaughran et al. (2010) showed that the metabolic rate of the springtail Cryptopygus antarcticus travea on Marion Island was strongly correlated with microclimatic variables affecting microhabitat variation. Metabolic rate, through its influence on energy assimilation, significantly affects life-history trait evolution and on Marion Island the differences in microclimate appear to promote plasticity in springtail metabolic responses. Similarly, Chown, Hau & Sinclair (2016) showed that fluctuating temperatures had a minor influence on caterpillar metabolic rate, again indicating plasticity to microhabitat variation. For Antarctic vegetation, thermal resilience is complex. For instance, a study of Antarctic lichens indicated that symbiosis integrity is highly imbalanced with changes in frequency and magnitude of warming events (Colesie et al., 2018).

(c) Feeling climate change – can genetic adaptations keep pace with environmental shifts?

Climate change and other environmental shifts will likely favour species with short generation times (e.g. bacteria), which can rapidly alter their genetic make-up and adapt (Verde et al., 2016), and, thus, reduce the impact on ecosystem processes. Many terrestrial and marine invertebrates and vertebrates, vascular plants, as well as microbes, both prokaryotes and eukaryotes are also exposed to environmental shifts. In groups with long generation times, the time needed for genetic adaptation might be too long to allow adaption to change (Peck, 2011).

The two main mechanisms effecting genetic change are mutation and gene flow within and among populations. Most Antarctic species may be poor in this respect under rapid environmental change, due to long generation times, slow growth rates, and large (hence fewer) eggs, all of which reduce rates of production and fixation of novel genetic material in populations (Peck, 2018). To assess capacity for adaptive potential, entry points include whole-genome sequencing, tests of functional responses to stress to evaluate adaptive plasticity, and estimation of genetic variability in populations to gauge survival potential. Only a handful of Antarctic marine vertebrate genomes have been sequenced and analysed to date: for two penguins (Li et al., 2014) and five notothenioid fishes (Shin et al., 2014; Bargelloni et al., 2019; Chen et al., 2019; Kim et al., 2019a). One of these studies compared the genomes (and transcriptomes) of the high-latitude cold-adapted Antarctic toothfish Dissostichus mawsoni and a basal non-Antarctic and closest sister species, which never experienced the same selective pressure, to identify Antarctic-specific adaptations (Chen et al., 2019). These include co-opted genes for intracellular freeze resistance, expansion of specific gene families that combat oxidative stress, a rapid amplification of transposable elements potentially related to speciation, and shifts in genetic and developmental programs enabling secondary pelagicism and niche expansion.

(d) Brood care and nesting of Antarctic fish call for modified management and conservation strategies

Since 2010, the use of cameras has revealed important ecological and ethological attributes of Antarctic fishes, especially in terms of reproductive strategies. We now know that nesting and parental care of embryos is typical, as observed in at least two dozen notothenioid species, including icefishes (Ferrando et al., 2014), dragonfishes (La Mesa et al., 2019), plunderfishes (Jones & Near, 2012) and nototheniids (Eastman et al., 2013). As these species cover most Antarctic fish families, nesting and parental care are likely their prevailing strategies. The keystone species, the Antarctic silverfish utilises the sub sea ice platelet layer as a nursery ground (Vacchi, Pisano & Ghigliotti, 2017). In addition, for the Antarctic toothfish Dissostichus mawsoni, areas and timing of reproduction, as well as the pelagic nature of the eggs, have been discovered (Parker et al., 2019). This new knowledge is key for improving conservation and management strategies of Antarctic marine living resources.

(e) Bioprospecting is still in its infancy but enzymes seem to be most promising

The systematic search for bioactive metabolites (bioprospecting) in the Antarctic focusses on marine benthic invertebrates, krill species, fishes, microbiomes, fungi and plants. Such metabolites can be used as scaffolds for biotechnological applications in medicine (e.g. for anticancer, anti-inflammatory, and antibacterial applications, and cardiovascular disease prevention), as well as in the development of lifestyle products, cryopreservation, and environmental technologies (Tripathi et al., 2018). Currently, enzymes seem to be most promising (Bruno et al., 2019). Nevertheless, despite the Southern Ocean being considered “a prolific resource of bioactive chemicals” (Núñez-Pons & Avila, 2015, p. 1127), market-ready products are still rare. An example for genetic engineering is the introduction of the DaCBF7 gene isolated from Antarctic hairgrass Deschampsia antarctica into rice cultivar, resulting in increased low-temperature tolerance (Byun et al., 2015). A breakthrough for the use of antifreeze glycoproteins, e.g. in medicine and food technology, is yet to come.

(7) Marine organisms, their life cycles and trophic interactions, are intrinsically linked to changing sea ice dynamics

Net overall Antarctic sea ice extent abruptly and unexpectedly plummeted to an unprecedented record minimum in 2016 and has remained below its long-term climatological...
average ever since (Reid et al., 2020). Models project a 25% decrease by 2100 (Maksym, 2019). Given the tight relationships between sea ice, and pelagic and benthic food webs, including higher trophic levels, projected changes in sea ice extent, volume, seasonality and properties (e.g. thickness) are expected to have significant ecological ramifications for all Southern Ocean biotas.

(a) Tight relationships between sea ice, primary producers and marine herbivores suggest that changes in sea ice will have major impacts on pelagic food webs

Sea ice provides a substrate for ice-algal communities, which serve as an important food source for pelagic herbivores when food in the water column is scarce, and provides protection from predators (Meyer et al., 2017). Pteropods, copepods and young Antarctic krill overwinter under the sea ice, where ice algae provide a crucial food source to sustain energy reserves (Johnson et al., 2019). For the pack-ice zone in the northern Weddell Sea, a high dependency of herbivores, e.g. overwintering ice-associated copepods and larval Antarctic krill, on ice-algal carbon has been found (Kohlbach et al., 2018). Off East Antarctica, larval Antarctic krill fed primarily on ice algae (O’Brien et al., 2017), but showed dietary plasticity between years with different sea ice conditions (Jia et al., 2016).

Sea ice is also important in priming spring phytoplankton blooms, which are strongly correlated with Antarctic krill recruitment and penguin foraging (Saba et al., 2014), and in regulating zooplankton community composition. Anomalous years of high salp and pteropod summer abundance were correlated with warmer sea-surface temperatures and less sea ice in the spring, and inversely related to abundance anomalies of Antarctic krill that dominate in summers following higher winter ice extent (Steinberg et al., 2015). Habitat suitability models also showed a close association of squid species with sea ice (Xavier et al., 2016b).

(b) Sea ice controls benthic community composition and function

Direct links have been established between sea ice conditions, pelagic primary productivity and, subsequently, coastal benthic communities (e.g. Cummings et al., 2018). Persistent, multi-year sea ice can result in decreased in situ primary production, through its influence on light availability, with consequences for diversity and abundance of primary consumers. Changes in phytoplankton (size class structure) under thicker, multi-year, land-fast sea ice with reduced under-ice light affected benthic invertebrate abundance by altering the quality of food (Kim et al., 2019a). At a site with multi-year sea ice, the quantity and quality of benthic algal detritus was lower relative to that at a site with thinner, annually formed ice (Lohrer, Cummings & Thrush, 2013). A decrease in duration of sea ice cover, and the associated increased light and reduced sedimentation, resulted in a regime shift from an invertebrate- to an algal-dominated community (G.F. Clark et al., 2017a). On the deeper shelf, the dominance of the polychaete Aunostrocheus lanosus covaried with pack ice duration, while other species exhibited nonlinear or only small responses (C.R. Smith et al., 2012a). A simulated benthic community on the deeper shelf and slope did not show major changes under increased primary production resulting from sea ice loss (Jansen et al., 2020).

Although future land-fast ice characteristics are difficult to predict, there will undoubtedly be changes in composition and function of coastal benthic communities in a warming world. Encouragingly, plasticity of feeding modes and generality of functional traits may confer resilience to sea ice-associated productivity changes (Cummings et al., 2018; Wing et al., 2018), with functionally diverse communities likely to store more carbon in a reduced sea ice environment (Barnes & Sands, 2017). Hints for benthic biomass decrease and composition shifts in a high-latitude area, assumed to be caused by sea ice increase, are provided by Pineda-Metz, Gerdes & Richter (2020). It this long-term study the relatively large area of investigation was characterised by high faunistic patchiness as well as high sea ice variability and different methodological approaches were applied.

(c) Not too much, and not too little – penguin and seal populations are sensitive to local variation in sea ice conditions

Sea ice characteristics influence the foraging and breeding success of ice-obligate vertebrates in a non-linear fashion, whereby thresholds in sea ice concentration and extent are evident. For example, Adélie penguin breeding success is affected by icescape conditions. Deviations from optimal sea ice concentrations result in increased foraging effort by adults and reduced breeding success (Le Guen et al., 2018). Persistence of sea ice throughout chick-provisioning periods in the absence of polynyas, in combination with anomalous precipitation and changes in sea ice firmness, explain massive breeding failures (Ropert-Coudert et al., 2018). Population growth rates of emperor penguins (Aptenodytes forsteri) are maximised at intermediate sea ice concentrations (Jenouvrier et al., 2012). Indeed, rapid emperor penguin population changes have already been observed in relation to changing sea ice conditions (Fretwell & Thrathan, 2019), and 80% of all populations are projected to be nearly extinct by 2100 under the business-as-usual IPCC scenario, whilst 91% will survive under the 1.5°C Paris Agreement goal (Jenouvrier et al., 2020). Ice-obligate seals (e.g. Weddell seals, Leptonychotes weddellii) are seemingly less affected by short-term icescape perturbations, but more frequent disruptions, such as iceberg events causing large sea ice extent, may result in long-term negative population effects (Chambert, Rotella & Garrott, 2012).

These results suggest that sea ice requirements by seals and penguins are complex, and that many ice-dependent populations rely on intermediate sea ice concentrations for successful breeding. Therefore, not only do projected long-term sea ice declines threaten ice-obligate breeding seal and penguin
species, but shorter-term local increases and decreases of sea ice stress these populations by increasing travel distances of adults and altering the distribution of suitable foraging patches. For climate-induced range expansion and contraction, see Section III.5b.

(8) Anthropogenic pollution and the responses of biota remain under-surveyed in Antarctic ecosystems

Anthropogenic pollutants in marine and terrestrial environments, especially novel waste products such as macro- and microplastics, persistent organic pollutants (POPs) and heavy metals, increasingly attract scientific interest and the attention of decision makers. Although currently insufficient, knowledge on the impacts of such pollutants on biotas is essential for informing both Antarctic Treaty policy and national legislation to prevent ecosystem damage.

(a) Pollutants accumulate in ecosystems and impact top predators

The Antarctic is an environmental sink for anthropogenic bio-accumulative POPs and heavy metals, reaching atmospheric, marine (from sea surface to the deep sea) and terrestrial environments (Isla, Pérez-Albaladejo & Porte, 2018). Biomagnification of toxic polychlorinated biphenyls (PCBs) has been reported across marine foodwebs. Studies on top predators, such as skua species and wandering albatross, showed that increasing POPs and trace metals contributed to a decrease in long-term reproductive performance, but did not affect survival rate or long-term breeding success in south polar skuas (Catharacta maccormicki; Goutte et al., 2018). Fish and squid show a decreasing trend for at least partly anthropogenic Hg levels that are bioaccumulated in the food chain (Cipri et al., 2018; Seco et al., 2019). The biological impacts, however, are still unknown.

A first Environmental Risk Assessment for soil biotas on King George Island showed different responses, from neutral to negative, for bacteria, cladocerans, microalgae, and macrophytes to contamination of toxic trace elements (Pereira et al., 2017). Pesticides and other legacy chlorinated hydrocarbons are detectable in different vegetation types as well as soils along the Antarctic Peninsula (Cabrero et al., 2012).

(b) Plastics occur in the environment and in organisms but profound impact studies are lacking

Macroplastics have rarely been quantified in the Antarctic (e.g. Waller et al., 2017) and little is known about the response of biotas. Entanglements by plastic packaging bands and other waste have been recorded over a 25-year time series in 1033 Antarctic fur seals, mainly juveniles (44%; Waluda & Staniland, 2013). Quantities of plastic debris items (>5 mm) regurgitated after ingestion by grey-headed (Thalassarche chrysostoma) and black-browed albatrosses in and around their nests at Bird Island (South Georgia) increased significantly from near zero between 1994 and 2019. The number of items per breeding pair varied by an order of magnitude across three albatross species, including the wandering albatross and the southern giant petrel (Macronectes giganteus; Phillips & Waluda, 2020). Long-lines lost during fishing activities between 2008 and 2017 reached an estimated total length of 12553 km in the areas monitored by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR Secretariat, 2018).

Microplastics comprised of fibres and fragments have already been detected in coastal sediments, water, sea ice (Munari et al., 2017; Kelly et al., 2020) and top predators. For example, they were present in 20% of the diet of penguins (Bessa et al., 2019). Microplastics were absent in some offshore water and sediment samples (Kuklinski et al., 2019; Barnes, Walters & Goncalves, 2010) but found at other sites (Isobe et al., 2017). Laboratory studies demonstrated the potential for Antarctic krill to ingest microplastic particles (Dawson et al., 2018), our knowledge on in situ accumulation of microplastics in tissues of Antarctic organisms is extremely poor. The title Plastics everywhere… of the publication of the first evidence for plastic fragments ingested by the collembo- lan Cryptopygus antarcticus emphasised that plastics have even entered the Antarctic terrestrial food web, and, thus, the most remote region on earth (Bergamii et al., 2020).

(9) Continental biotas are highly endemic and at risk from climate change

Isolation of terrestrial and limnetic habitats by glaciers and coastal ice sheets as well as topographic barriers has resulted in local populations with high levels of genetic distinctiveness. Increased connectivity and/or dispersal of individuals among habitats as a consequence of warming and human activity will potentially disrupt co-adapted gene complexes developed over millions of years. These findings need to be considered in biosecurity strategies.

(a) Terrestrial and limnetic populations have genetically diverged and speciated

A high degree of endemism among Antarctic terrestrial and limnetic invertebrates has been hypothesised for decades. Recent genetic advances have confirmed this speculation and identified endemism in a wide range of organisms, including groups once thought to be globally distributed, such as diatoms (Soulireau et al., 2013; Kociolek et al., 2017), cyanobacteria (Jung et al., 2019), lichens (Jones et al., 2015) and rotifers (Felisca-Castrillón et al., 2014; Iakovenko et al., 2015). Further, it has become increasingly clear that terrestrial and limnetic habitats support taxa that have survived multiple glacial cycles over millions of years. Many taxa have undergone evolutionary radiations on the continent, specifically springtails (Collins et al., 2020), including in locations not previously considered refugial, such as the Antarctic Peninsula for Schistidium moss species (Biersma et al., 2018).
Distribution patterns are driven by landscape isolation combined with species-specific dispersal abilities. Geographic scales of isolation are influenced by dispersal abilities. Species that are suited to airborne dispersal, such as nematodes, can show broad-scale patterns of diversity (Adams et al., 2014). Other taxa, including some springtails and copepods, have low dispersal capacity and remain genetically isolated with small distribution ranges (<10 km; Bennett et al., 2016; Karanovic et al., 2014 due to geomorphological barriers such as glaciers and ice sheets (Carapelli, Leo & Frati, 2017).

Antarctica’s warming will increase landscape connectivity and biotic interactions. In contrast to today’s habitat fragmentation by inland ice and topographic dispersal barriers, the Pleocene was a period of relatively high habitat connectivity. Currently, the world is heading for similar conditions to the Pleocene with high CO₂ concentrations and rising temperatures. Increased habitat connectivity, also present during interglacial periods, enhances dispersal (Lee et al., 2017) and reduces local endemism by mixing genetically distinct populations. The distribution and abundance of continental taxa was previously thought to be driven primarily by abiotic drivers (Hogg et al., 2006). However, biotic interactions between different nematode species, fungi, and cyanobacteria are now known also to shape such communities (Caruso et al., 2019; Lee et al., 2019). As a consequence of increased connectivity, interactions such as resource competition among species may develop, more suitable habitats may become available, and novel niches and/or habitats for invasive species may be created (Hughes et al., 2019; Lee et al., 2017).

Recently discovered assemblages are driven by particular environmental conditions. Recently discovered habitats extend our knowledge of evolutionary and ecological processes in the Antarctic and contribute to global assessments of biodiversity and ecosystem functioning.

Subglacial lakes contain active and functionally diverse microbial communities. Nearly 4000 operational taxonomic units of Bacteria and Archaea have been identified on the basis of 16 s subunit DNA sequences from water and sediments recovered from subglacial Lake Whillans (Christner et al., 2014). Various metabolic groups have been detected that comprise relatives of species known to use reduced N, S or Fe and CH₄ as energy sources. Chemosynthetic carbon-fixation pathways appear to underpin their community metabolism (Achberger et al., 2016; Purcell et al., 2014).

New results from other subglacial lakes, believed to have persisted in near isolation for hundreds of thousands of years (Bulat, 2015) and to contain unique organisms, await widespread application of clean-drilling techniques. While changing climate does not pose immediate threats to these ecosystems, they remain vulnerable to risks of contamination if rigorous drilling protocols are not sustained (Mikuški et al., 2016).

Rare new habitats are vulnerable to environmental changes due to their uniqueness. The sea anemone Edwardsiella andrillae and antarcturid isopods use the underside of ice shelves as their habitat (Daly, Rack & Zook, 2013; Bornemann et al., 2016). Scientific questions arising from these discoveries include whether the sea anemone is endemic to the ice subsurface, how the isopods colonised this habitat and whether these populations mix genetically with benthic relatives of the assumed same species.

Hydrothermal and geothermal habitats are hotspots of unique biotas. Chemosynthetic marine assemblages living at hot hydrothermal vents on the East Scotia Ridge are dominated by the yeti crab (Kiwa tyleri), stalked barnacles, limpets, peltspoorid gastropods, anemones, and a sea star (Linse et al., 2019), and constitute a new vent-fauna province. Below the former Larsen B ice shelf, a low-activity seep (Niemann et al., 2009) with a seep-specific nematode fauna (Hauquier et al., 2011) was observed and analysed, while a small patch of bacteria occurred on the sediment at a different location (Gutt et al., 2011). In the Ross Sea at 10 m water depth a bacterial mat, based on a hydrogen sulfide and methane seep was discovered, and may have an impact on greenhouse gas emission from marine methane reservoirs (Thurber, Seabrook & Welsh, 2020). On land, geothermally active regions allow species to survive in isolation on ice-free land or in sub-ice caves, from which recolonisation of the rest of the continent could have taken place (Fraser et al., 2014). The hot fumarolic soils on Mount Erebus are home to cosmopolitan thermophiles, endemic archaea and bacteria (Herbold et al., 2014). On Deception Island, bacterial and archaeal taxa are reported from a wide range of environmental conditions (Bendia et al., 2018).

Unusually dense aggregations of hydrocorals occur regionally on the upper continental slope off East Antarctica (Post et al., 2010). The East Antarctic Admiralty and Scott Seamounts have unique benthic biodiversities that represent different colonisation histories. They comprise stalked crinoids (Hyocrinidae), brachiopods, and suspension-feeding ophiuroids (Ophiocamax), as well as a high abundance of predators, including lithodid crabs, regular sea urchins, and sea stars (Bovenden et al., 2011). The sea floor below floating ice shelves, e.g. Larsen A and B as well as Amery, is colonised by deep-sea life forms and a sparse shelf fauna that mostly depend on an advected food supply (Gutt et al., 2011; Post et al., 2011).

IV. CONCLUSIONS

This literature survey demonstrated the substantial progress in research around our 10 key messages on
Antarctic ecosystems under stress and how important most themes behind these messages are. However, there is a clear need for further study in many of these themes to underpin socially relevant opinion-forming, decisions and actions.

(2) A clear conclusion from the 10 key messages discussed herein is that life in the Southern Ocean and Antarctica is highly sensitive to environmental changes. We conclude that the greatest anthropogenic threat to Antarctic ecosystems is – and will be in the future – climate change. This judgment differs from the conclusions of the IPBES Global Assessment (IPBES, 2019), which considered exploitation to represent the greatest risk for global marine and terrestrial ecosystems. This difference is due to the currently low economic importance of exploitable Antarctic resources, as well as the little land and ocean use.

(3) Although Antarctic terrestrial and marine ecosystems are sometimes regarded as relatively homogeneous, the responses of Antarctic biotas to environmental changes vary considerably across regions, habitats, ecosystems, communities and organisms, even at the infra- and extracellular level. The highly diverse environmental demands and position in the food web will determine whether species become losers or winners in response to predicted circumpolar warming (Morley, Barnes & Dunn, 2019).

(4) Intermediate levels of confidence, defined along axes of quality/quantity of evidence and agreement among publications, were assigned to the majority of our sub-messages (Fig. 2). However, the classification of only seven of our 31 detailed sub-messages as ‘robust’ shows that a sound scientific basis for decisions on the management and protection of Antarctic ecosystems is not yet fully established. Antarctic biological variability, complexity and uniqueness resulting from non-linear processes at all levels of biological organisation from molecules to ecosystems remain poorly understood. In addition, the rarity of year-round and multi-year monitoring and circumpolar-scale observations limits our understanding of past, present and future biological processes.

(5) Analyses of the impact of multiple stressors (e.g. warming, oxygen depletion and CO2 increase; Gutt et al., 2015) are ‘emerging’ challenges for many of the 10 key messages (Portner & Gutt, 2016). The most difficult complex to unravel will be cause-effect relationships on multiple pathways, which cascade via bottom-up or top-down interactions through trophic levels, e.g. from phytoplankton to sediment communities, where carbon is sustainably sequestered, or from primary producers to top predators (Constable et al., 2016).

(6) Changes observed along the Antarctic Peninsula may be harbingers for the future of the entire continent. On land, ecosystem functions such as productivity may increase, while marine organisms adapted to high-latitude conditions may suffer because southward escape is blocked by the continent (Griffiths, Meijers & Bracegirdle, 2017). Elevated CO2 uptake through increased primary production and eventually higher productivity at exploitable trophic levels may superficially be seen as favourable. Conversely, biodiversity loss and possible negative feedbacks resulting in reduced long-term CO2 sequestration, are not yet predictable with any accuracy. Obtaining a more comprehensive inventory of organisms and communities to help answer such questions may now be possible with advances in environmental DNA analyses (Cowart, Murphy & Cheng, 2018), particularly in pelagic systems, and seabed-imaging methods in benthic habitats.

(7) This synthesis showed that comparisons across ecosystems, e.g. among marine, limnetic and terrestrial or among different groups of organisms, are useful with regard to adaptation or range shifts. Detailing similarities and fundamental differences between two systems can provide added value in understanding the origin, structure and functioning of the systems under study.

(8) The uniqueness and rarity of biotas in the small terrestrial, ice-free areas of Antarctica justifies their protection. The Southern Ocean makes a remarkable contribution to global biodiversity and ecosystem services (nature’s contributions to people) under increasing anthropogenic stress (Chown & Brooks, 2019). Protection and conservation strategies should consider that Antarctic biotas and their functioning are more connected to the rest of the world than previously understood.

(9) Pollution in both marine and terrestrial Antarctic habitats has recently attracted particular attention, especially regarding microplastics. Quantification of the impacts of pollutants and the responses of different biotas, especially of key species, is needed to develop efficient management strategies. This emerging field demonstrates the need for flexibility in research strategies to react rapidly to new threats and unexpected findings, further developing links between science and policy (Hughes et al., 2018).

(10) The development of novel concepts in Antarctic science (Xavier et al., 2016a) demands the implementation of question-driven research programs, ideally collaborative and integrative, while avoiding potentially negative effects of competition for research resources or the maintenance of traditions. To address the big challenges, a balance is necessary between applied approaches, e.g. solving climate-, conservation- and ecosystem-management problems, and academic freedom to carry out fundamental research, which in turn informs applied approaches.

V. ACKNOWLEDGEMENTS

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Bartlett, J. C. & Beers, J. M. (2010). Plastics everywhere: first evidence of polyethylene fragments inside the common Antarctic collemboiid Cryptopygus antarcticus. Biology Letters 16, 20200093.

Bentley, M. L. & Schloss, P. R. (2009). Photosynthesis production after the collapse of the Larsen A ice shelf. Antarctic. Polar Biology 32, 1435–1446.

Bessa, F., Ratcliffe, N., Otero, V., Sobral, P., Marques, J. C., Valuá, C. M., Trathan, P. N. & Xavier, J. C. (2019). Microplastics in Gentoo penguins from Antarctic region. Scientific Reports 9, 14191.

Bjerre, J. W. (2011). Winter climate change: ice encapsulation at mild subfreezing temperatures kills freeze-tolerant lichens. Environmental and Experimental Botany 72, 401–408.

Black, J. G., Stark, J. S., Johnstone, G. J., McNinn, A., Boyd, P. W., McKinlay, J., Wootton-Johnson, S. & Runcie, J. W. (2019). In-situ behavioural and physiological responses of Antarctic microphytobenthos to ocean acidification. Scientific Reports 9, 1890.

Borrhorst, S., Convay, P. & Aerts, R. (2019). Nitrogen inputs by marine vertebrates drive abundance and richness in Antarctic terrestrial ecosystems. Current Biology 29, 1721–1727.

Bornemann, H., Held, C., Nachtigall, D., Owsiaknowski, N., Richter, C. & Steinmetz, R. (2016). Seal research at the Drescher inlet (SEAD). In The Expedition PS96 of the Research Vessel POLARSTERN to the Southern Weddell Sea in 2013/14 (Vol. 700, ed. M. Schröder Bermenhaven, Germany: Alfred-Wegener-Institut, Polar- und Meeresforschung), pp. 116–129. Reports on Polar and Marine Research.

Bowden, D., Schlaparelli, D. A., Clark, M. R. & Rickard, G. J. (2011). A lost world? Archaic crinoid - dominated assemblages on an Antarctic seamount. Deep-Sea Research Part I 58, 119–127.

Bradley-Atvye, J., King, D. H., Robinson, S. A. & Miller, R. E. (2014). Dominating the Antarctic environment: byrophytes in a time of change. In Photosynthesis in Bryophytes and Early Land Plants (eds T. D. Hansson and S. K. Rice), pp. 309–324. Springer, Dordrecht.

Brown, M. S., Munro, D. R., Feiyan, C. J., Sweeney, C., Duclo, H. W. & Schwab, O. M. (2019). Enhanced oceanic CO2 uptake along the rapidly changing West Antarctic Peninsula. Nature Climate Change 9, 46–53.

Bruno, S., Coppola, D., Prisco, G., Giordano, D. & Verde, C. (2019). Enzymes from marine polar regions and their biotechnological applications. Marine Drugs 17, 344.

Bulu, S. (2013). Microbiology of the subglacial Lake Vostok: first results of borehole-frozen lake water analysis and prospects for searching for lake inhabitants. Philosophical Transactions of the Royal Society B 374, 20140292.

Bylenga, C. H., Cummings, V. J. & Ryan, K. G. (2017). High resolution microscopy reveals significant impacts of ocean acidification and warming on larval shell development in Lutarnia elliptica. PLoS One 12, e0172506.

Buyn, M. V., Lee, J. L., Cui, L. H., Kang, Y., Oh, T. K., Park, H. Lee, H. & Kim, W. T. (2015). Constitutive expression of DcBP7, an Antarctic vascular plant Deschampsia antarctica CBF homolog, resulted in improved cold tolerance in transgenic rice plants. Plant Sci. 236, 61–74.

Carreeza, A., Dachs, J., Barruel, D. & Jones, K. C. (2012). Influence of oceanic matter content and human activities on the occurrence of organic pollutants in Antarctic soils, lichens, grass, and mosses. Environmental Science & Technology 46, 1396–1405.

Carpe, M. R., Vernet, M., Kabiri, M. & Spreen, G. (2014). Polynya dynamics drive primary production in the Larsen A and B embayments following ice shelf collapse. Journal of Geophysical Research: Oceans 119, 572–594.

Carpe, M., Vernet, M., Kabiri, M. & Spreen, G. (2014). Polynya dynamics drive primary production in the Larsen A and B embayments following ice shelf collapse. Journal of Geophysical Research: Oceans 119, 572–594.
Hauck, J. & Völker, C. (2015). Rising atmospheric CO2 leads to large impact of biology on Southern Ocean CO2 uptake via changes of the Revelle factor. Geophysical Research Letters 42, 1458–1464.

Haquique, F., Ingens, J., Guett, J., Rais, M. & Vanreusel, A. (2011). Characterisation of the nematode community of a low-activity cold seep in the recently ice-sheet free Larsen B area, eastern Antarctic Peninsula. PLoS One 6, e22240.

Hawkins, J. R., Waytham, J. L., Tranter, M., Raiswell, R., Benning, L. G., Statham, P. J., Tedstone, A., Niemow, P., Lee, K. & telling, J. (2014). Ice shelf collapse: a significant source of highly reactive nanoparticulate iron to the oceans. Nature Communications 5, 3929.

Hempel, G. (1994). Antarctic Science Global Conour, p. 287. Springer Verlag, Berlin.

Henley, S. E., Cavan, E. L., Fawcett, S. E., Kerr, R., Monteiro, T., Sherrill, R. M., Bowie, A. R., Boyd, P. W., Barnes, D. K. A., Schloss, I. R., Marshall, T., Flynn, R. & Smith, S. (2020). Changing biogeochemistry of the Southern Ocean and its ecosystem implications. Frontiers in Marine Science 7, 581.

Henley, S. F., Jones, E. M., Venables, H. J., Meredith, M. F., Firing, Y. L., Dittrich, R., Hein, S., Steffels, J. & Dougans, J. (2016). Macronutrient fluxes, and potential carbon export, in the production/export dynamics of two bays in the Western Antarctic Peninsula. Progress in Oceanography 174, 105–116.

Hogg, I. D., Cary, S. C., Convey, P., Newsham, K., O'Donnell, A., Adams, B. J., Aslarije, J., Frati, F., Stevens, M. I. & Wall, D. H. (2006). Biotic interactions in Antarctic terrestrial ecosystems: are they a factor? Soil Biology & Biochemistry 38, 3055–3061.

Hoppé, C. M. J., Klaas, C., Onseaar, S., Soppa, M. A., Cheah, W., Laglera, I. M., Santos-Echeandia, J., Ront, B., Wolf-Gladrow, D. A., Bracher, A., Hoppepa, M., Straas, V. & Tremborn, S. (2017). Controls of primary production in two phytoplankton blooms in the Antarctic circumpolar current. Deep-Sea Research Part II 130, 63–73.

Hopwood, M. J., Carroll, D., Höfer, J., Achterberg, E. P., Meire, L., Le Moigne, F. A. C., Bach, L. T., Eich, C., Sutherland, D. A. & González, H. E. (2019). The role of water column stability and wind mixing in the production/export dynamics of two bays in the Western Antarctic Peninsula. Antarctic Science 31, 135–138.

Horner, S. M. Subramanian, et al., p. 56. IPBES Secretariat, Bonn.

Hussey, N. E., Webster, C., Jardine, M. P., Curran, A. J. M., Swearer, S. E., Hindell, M. A., Hindell, M. A., Mecklenburg, S. R. & Costa, D. P. (2014). Environmental predictors of foraging range in Weddell seals (genus Leptonychotes) in the Southern Ocean and its ecosystem implications. Frontiers in Marine Science 7, 581.
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Isla, E. & DeMaster, D. (2018). Labile organic carbon dynamics in continental shelf sediments after the recent collapse of the Larsen ice shelves off the eastern Antarctic Peninsula: A radiochemical approach. Geochimica et Cosmochimica Acta 242, 34–50.

Isla, E., Pérez-Albaladejo, E. & Power, C. (2010). Toxic aromatic signature in Antarctic continental shelf and deep sea sediments. Scientific Reports 8, 913-4.

Itoh, A., Uchiyama-Matsumoto, K., Uchida, K. & Tokai, T. (2017). Metaproteomics in the Southern Ocean. Marine Pollution Bulletin 114, 623–626.

Janssen, J., Dunstan, P. K., Heil, N. A., Kourbi, P., Melbourne-Thomas, J., Cantele, C. R. & Johanson, C. R. (2020). Integrated assessment of the spatial distribution and structural dynamics of deep benthic marine communities. Ecological Applications 30, e02065.

Jenouvrier, S., Holland, M., Ills, D., Labroussée, S., Landrum, L., Garnier, J., Caswell, H., Weimerskirch, H., LaMare, D. J., R. & Ferrari, C. (2020). The Paris, agreement objectives will likely halt future declines of emperor penguins. Global Change Biology 26, 1170–1184.

Jenouvrier, S., Holland, M., Stroyek, J., Barbraud, C., Weimerskirch, H., Serrezes, M. & Caswell, H. (2012). Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. Global Change Biology 18, 3341–3355.

Jia, Z., Swadling, K. M., Meiners, K. M., Kawaguchi, S. & Virtue, P. (2016). The zooplankton food web under East Antarctic pack ice: a stable isotope study. Deep-Sea Research Part II: Topical Studies in Oceanography 133, 189–202.

Johnson, K. M., Wong, J. M., Hoshiba, J., Sugano, C. S. & Hofman, G. E. (2012). Decreased genotypic diversity of the Antarctic prorocentrum, Limacina helicina Antartic. Marine Environmental Research 64, 49–59.

Jones, C. D. & Near, T. J. (2012). The reproductive behaviour of Pygospio elegans confirms widespread egg-guarding parental care among Antarctic notothenioids. Journal of Fish Biology 80, 2029–2035.

Jones, D. O. B., Yoo, A., Wei, C.-L., Hensen, S. A., Ruhl, H. A., Watson, R. A. & Gehlen, M. (2013). Global reductions in seafloor biomass in response to climate change. Global Change Biology 20, 1691–1672.

Jones, T. C., Hogg, I. D., Wilkins, R. J. & Green, T. A. (2015). Microsatellite analyses of the Antarctic endemic lichen Buellia frigida Darb. (Physciaceae) suggest limited dispersal and the presence of glacial refugia in the Ross Sea region. Polar Biology 38, 941–949.

Jung, P., Brügge-Williams, L., Schermer, M. & Büdel, B. (2019). Strong in combination: Phosphatic approach enhances arguments for cold-adapted assemblages of Antarctic notothenioids. Marine Ecology Progress Series 620, 1–12.

Karanovic, T., Gibson, J., Hawes, I., Andersen, D. & Stevens, M. (2014). Dicyclops (Copepoda: Cyclopoida) in continental Antarctica, including three new species. Antarctic Science 26, 250–260.

Kaufman, D. E., Ducklow, H. W., Joy, K. M. & Livezey, B. E. (2009). Antarctic benthic responses. Ecography 32, 468–479.

Kneip, L., Rams, J. A., Xavier, J. C., Grebmeil, D., González-Solés, J., Gery, M. V., Phillips, R. A., Wansies, R. M. & Pávaita, V. H. (2018). Projected distributions of Southern Ocean albatrosses, petrels and fisheries as a consequence of climatic change. Ecography 41, 195–208.

Koubbi, P., Wickworski, L., Koper, M., Gralla, T., Lenczko-Koper, H., Olfert, M. & Caswell, S. (2018). Antarctic Circumpolar Current, as revealed by a circum-Antarctic study. Marine Pollution Bulletin 149, 110573.

La Mesa, M., Pinedo-Metz, S. E. A., Rignell, E. & Eastman, J. T. (2019). Spatial distribution and habitat preferences of demersal fish assemblages in the southeastern Weddell Sea (Southern Ocean). Polar Biology 42, 1045–1054.

Lagger, C., Nimi, M., Torre, L., Servetto, N., Tatu, M. & S. (2018). Climate change, glacier retreat and a new ice-free Island offer new insights on Antarctic benthic responses. Ecography 41, 579–591.

Laglera, L. M., Tovar-Sánchez, A., Verme, M. H., González, H. E., Nau, H., Mangels, G., Hooke, M., Mazzocco, M. G., Montemor, M., Naqvi, S. W. A., Stenfelt, S. & Wolf-Gladrow, D. A. (2017). Iron partitioning during LOHAFEX: copepod grazing as a major driver for iron recycling in the Southern Ocean. Marine Chemistry 196, 148–161.

Liao, R. M. (1984). Antarctic Ecology, p. 850. Academic Press, Cambridge.

Le, T. P., Makalavanay, T. P., Guerriero, L. D., Vian, S. De Peer, S. & Cowan, D. A. (2016). Comparative metagenomic analysis reveals mechanisms for stress response in phytoplankton from extreme hyperarid deserts. Genome Biology and Evolution 8, 2737–2747.

Lee, C. K., Katko, A., Raymond, B. Barbraud, C., Beaulieu, M., Bost, C.-A. Delord, K., MacIntosh, A. J. J., Meyer, X., Racilot, T., Sumner, M., Takahashi, A., Thibot, J.-B. & Ropert-Coudert, Y. (2018). Reproductive performance and diving behaviour share a common sea-ice concentration optimum in Adélie penguins (Pygoscelis adeliae). Global Change Biology 24, 5304–5317.

Lee, C. K., Laughlin, D. C., Botton, E. M., Caruso, T., Joy, K., Barret, J. E., Braby, L., Nielsen, U. N., Adams, B. J., Wall, D. H., Hopkins, D. W., Pointing, S. B., McDonald, I. R., Cowan, D. A., Banks, J. C., Stichbury, G. A., Lean, J., Zawar-Reza, P., Katuragi, M., Hough, I. D., Sparrow, A. D., Storey, B. C., Allan, Green, T. C. & Cary, S. C. (2019). Biodiversity Antarctica are an unexpected yet critical control on the complexity of an abiotically driven polar ecosystem. Communications Biology 2, 62.

Lee, J. R., Raymond, B., Bracegirdle, T. J., Chades, I., Fuller, R. A., Shaw, J. D. & Terauds, A. (2017). Climate change drives expansion of Antarctic ice-free habitats. Nature 547, 49–54.

Li, C., Zhang, Y., Li, J., Kong, H., He, H., Pan, X., Lu, D., Deng, Y., Li, Q., Jin, L., Wu, H., Chen, Y., Liu, Y., Liu, Y. & Liu, S. (2014). Two Antarctic penguin genomes reveal insights into their evolutionary history and molecular changes related to the Antarctic environment. GigaScience 3, 27.

Linse, K., Copley, J. T., Connolly, D. P., Larter, R. D., Pearce, D., Polunin, N. C. V., Bost, D. A., Chen, G., Clarke, A., Glover, A. G., Graham, A. G., Huyvenne, V. A. L., Marsh, L., Reid, W. D. K., Rottgerman, C. C. V. et al. (2019). Fauna of the Kemp caldera and its upper bathyal hydrothermal vents (South Sandwich arc, Antarctica). Royal Society Open Science 6, 190150.

Lohrer, A. M., Cummings, V. J. & Thrush, S. F. (2013). Altered Sea ice thickness and permanence affects benthic ecosystem functioning in coastal Antarctica. Ecosystems 16, 224–236.

Lundsgaard, O., Winsor, P., Truffer, M., Merrifield, M., Powell, B., Stavehill, H., Aistle, D. & Chilcott, B. (2020). Hydrography and energetics of a cold fjord: Aedvord Bay, western Antarctic Peninsula. Progress in Oceanography 181, 102224.

Lurie, C. M., Amaral-Zettler, L. A., Ducklow, H. W. & Rich, J. J. (2016). Seasonal succession of free-living bacterial communities in coastal waters of the Western Antarctic Peninsula. Aquatic Microbiology 7, 1731.

Mach, J. K., Mayrstr{"o}m, D. M., Friedman, P. T. & Field, C. B. (2017). Unleashing expert judgements in assessment. Global Environmental Change 44, 1–14.

Maksym, T. (2019). Arctic and Antarctic Sea ice change: contrasts, commonalities, and causes. Annual Review of Marine Science 11, 187–213.
Malkar, V. C., Morton, J. D., Hider, R. N., Cruickshank, R. H., Hedge, S. & Metcalfe, V. J. (2018). Effect of elevated temperature on membrane lipid saturation in Antarctic nototopid Notocara gouldii. *Proc. R. Soc. Lond. B* 285: 20172264.

Mann, C., Böhmke, N., Talling, G. A., Peck, V. L., Comeau, S., Ahoki, D., Bakker, D. C. E., Bauerfeind, E., Bergan, A. J., Berning, M. I., Buitenhuys, E., Burridge, A. K., Cherici, M., Fletter, S., Fransson, A., et al. (2017). Shelled pteropods in peril: assessing vulnerability in a high CO2 ocean. *Earth-Science Reviews* 169, 132–145.

Marchetti, B., Buss, O. R., Ackley, N. S. & Ainley, D. G. (2012). Slow recovery of previously depopulated demersal fish at the South Shetland Islands, 1983–2010. *Fisheries Research* 125–126, 206–213.

McCarthy, A. H., Peck, L. S., Hughes, K. A. & Aldridge, D. C. (2019). Antarctica: the final frontier for marine biological invasions. *Global Change Biology* 25, 3916–3929.

McGaughran, A., Convey, P., Stevens, M. I. & Chown, S. L. (2010). Metabolic rate, genetic and microclimate variation among springtail populations from sub-Antarctic Marion Island. *Polar Biology* 33, 909–918.

Meijer, A. J. S., Meredith, M. P., Murphy, E. J., Chambers, D. P., Bednarská, N., Mostajir, B., Adhikari, D., Bednarská, N. P., Cruickshank, R. H., Hughes, K. A., Peck, L. S., Griess, A. G., Goosse, H., Vacchi, M., Giglio, E., Alescio, N. S., Ainey, D. G. (2012). Revising the role of ocean dynamics in a changing climate of regional warming along the Western Antarctic Peninsula. *Marine Systems* 454, 1–23.

Mendes, C. R. B., Tavano, V. M., Segabianni, D. A. M., Belchier, M. & Mankoff, K. D. (2018). Evolutionary trade-offs in metabolic rates, genetic and microclimate variation among springtail populations from sub-Antarctic Marion Island. *Polar Biology* 41, 2555–2568.

Mendes, C. R. B., Tavano, V. M., Segabianni, D. A. M., Belchier, M. & Mankoff, K. D. (2018). Evidence for extreme phenotypic plasticity in metabolic rate, genetic and microclimate variation among springtail populations from sub-Antarctic Marion Island. *Polar Biology* 41, 2555–2568.

Mierzwia, H., Rosati, P., Sciare, J., Mihalopoulos, N., Hoffer, K. A. J., Barnes, D. K. A., Rastelli, E., Corinaldesi, C., Dunn, M. J., Britten, G. L., Goosse, H., Vacchi, M., Giglio, E., Alescio, N. S., Ainey, D. G. (2012). Revising the role of ocean dynamics in a changing climate of regional warming along the Western Antarctic Peninsula. *Marine Systems* 454, 1–23.

Moffet, A. J., Convey, P., Stevens, M. I. & Chown, S. L. (2010). Organisms and responses to environmental change. *Marine Geosciences* 14, 239–253.

Montes-Hugo, M., Donen, S. C., Ducklow, H. W., Fraser, W., Martinson, D., Stammes, M. S. E. & Schofield, O. (2009). Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323, 1470–1472.

Mooij, L. W. M., van den Brink, E. R., Kim, J.-H. & Ahn, I.-Y. (2015). The impacts of climate change on Antarctic nearshore mega-epifungal assemblages in a glacial fjord on King George Island: responses and implications. *Ecological Indicators* 57, 290–292.

Moore, J. K., Frey, S. W., Pineau, E. M., Lindsay, K., Lomo, M., Donohue, S. C., Harwood, N., Hoffmann, F. & Randerdon, J. T. (2011). Sustaining climate warming drives declining marine biological productivity. *Science* 335, 1139–1143.

Moreau, S., Montajet, B., Bélinger, S., Schloss, I. R., Goosee, H., Van capponoille, M., Demers, S. & Ferréry, A. G. (2015). Climate change enhances primary production in the Western Antarctic Peninsula. *Global Change Biology* 21, 2191–2205.

Morley, S. A., Berman, J., Barnes, K. A. D., de Juan Carbonell, C., Downey, R. V. & Peck, L. S. (2016). Extreme phenotypic plasticity in metabolic physiology of Antarctic demersal species. *Frontiers in Ecology and Evolution* 3, 157.

Morley, S. A., Abele, D., Barnes, K. A. D., Grégoire, C. A., Cotté, G., Gutt, J., Henley, S. F., Hoyer, K. A. J., Hughes, K. A., Martin, S. M., Moffat, C., Raphael, M. N., Stammes, S. E., Suckling, C. C., Tuulolli, V. W. D., et al. (2020). 1–4: Global drivers on Southern Ocean ecosystems: changing physical environments and anthropogenic pressures in an earth system. *Frontiers in Marine Science* 7, 1–24.

Morley, S. A., Barnes, K. A. D. & Dunn, M. J. (2019). Predicting which species succeed in climate-forced polar seas. *Frontiers in Marine Science* 5, 507.

Multani, C., Infanti, V., Scoponi, M., Rastelli, E., Cornalda, C. & Morley, S. A. (2017). Megaplancton in the sediments of Terra Nova Bay, Ross Sea, Antarctica. *Marine Pollution Bulletin* 122, 161–165.

Negrete-García, G., Loven suspended, N. S., Haury, C., Krumhaid, K. M. & Lauvset, S. K. (2017). Increased emergence of a shallow aragonite saturation horizon in the Southern Ocean. *Nature Climate Change* 7, 313–317.
Antarctic ecosystems in transition

Pörtner, H. O. & Gutt, J. (2016). Impacts of climate variability and change on (marine) animals: physiological underpinnings and evolutionary consequences. Integrative and Comparative Biology 56, 31–44.

Post, A. L., Beaman, R. J., O’Brien, P. E., Eléaume, M. & Riddle, M. J. (2011). Community structure and benthic habitats across the George V shelf, East Antarctica: trends through space and time. Deep-Sea Research Part II 58, 105–118.

Post, A. L., O’Brien, P. E., Beaman, R. J., Riddle, M. J. & de Santis, L. (2010). Physical controls on deep water coral communities on the George V land slope, East Antarctica. Antarctic Science 22, 371–378.

Purcell, A. M., Mikucki, J. A., Achberger, A. M., Alekhnina, I. A., Barrante, C., Christensen, B. G., Ghos, D., Michaud, A. B., Mitchell, A. C., Prescu, J. C., Scherrer, R., Skidmore, M. L., Vick-Majors, T. J. & the WISSARD Science Team (2014). Microbial sulfur transformations in sediments from subglacial Lake Whillans. Science 344, 594.

Raes, M., Rose, A. & van Rensen, A. (2010). Response of nematode communities after large-scale ice-sheet collapse events in the Antarctic Larsen area. Global Change Biology 16, 1618–1631.

Redf. P., Stammerjohn, S., Massom, R. A., Barreira, S., Scambos, T. & Longinotti, K. (2014). Ice-shelf-covered mesobenthic communities of the Antarctic continental shelf resemble those of the deep sea. Marine Biodiversity 45, 743–762.

Saba, G. K., Fraser, W. R., Saba, V. S., Iannucci, R. A., Coleman, K. E., Doney, S. C., Dickson, A. G., Miles, T. N., Packard, D. L., Ricketts, T. H., Skirrow, D., Swift, S. T., Wiggert, J. D. & Zettler, E. R. (2015). Climate change and glacier retreat drive shifts in Antarctic terrestrial diatoms. Proceedings of the Royal Society B: Biological Sciences 282, 20150534.

Saba, G. K., Fraser, W. R., Saba, V. S., Iannucci, R. A., Coleman, K. E., Doney, S. C., Dickson, A. G., Miles, T. N., Packard, D. L., Ricketts, T. H., Skirrow, D., Swift, S. T., Wiggert, J. D. & Zettler, E. R. (2015). Climate change and glacier retreat drive shifts in Antarctic terrestrial diatoms. Proceedings of the Royal Society B: Biological Sciences 282, 20150534.

Seco, J., Xavier, J. C., Coelho, J. P., Pereira, B., Targuled, G., Pardal, M. A., Bastmante, P., Stowasser, G., Brierley, A. S. & Pereira, M. E. (2019). Spatial variability in total and organic mercury levels in Antarctic krill Euphausia superba across the Scotia Sea. Environmental Pollution 247, 332–339.

Segelken-Voigt, A., Bracher, A., Dorschel, B., Gutt, J., Huneke, W., Link, H. & Pfenninger, D. (2016). Spatial distribution patterns of ascidians (Ascidiaeae: Tunicata) on the continental shelves off the northern Antarctic Peninsula. Polar Biology 39, 2107–2117.

Shin, S. C., Adin, D. H., Kim, S. J., Pyo, C. W., Lee, H., Kim, M. K., Lee, J. L., Lee, J. E., Dietrich, H. W., Ponteithwe, J. H., Edwards, D., Lee, S. G., Lee, J. H. & Park, H. (2014). The genome sequence of the Antarctic bullhead notoften reveals evolutionary adaptations to a cold environment. Genome Biology 15, 50.

Smith, C. R., DeMaster, D. J., Thomas, C., Sibun, P., Grange, L., Evard, V. & Deleo, F. (2012a). Pelagic-benthic coupling, food banks, and climate change on the West Antarctic Peninsula shelf. Oceanography 25, 189–201.

Smith, C. R., Grange, L. J., Honig, D. L., Naude, L., Huber, B., Guidi, L. & Deleo, F. (2012b). Antarctic crustacean grazer community composition in a changing West Antarctic peninsula. Frontiers in Marine Science 2, 394.

Stammerjohn, S. (2011). How deep is deep enough? Ocean iron fertilization and global climate change. Deep-Sea Research Part II 58, 1631–1643.

Torgersen, J. S. (2012). Climate-driven changes in the mesoscale phytoplankton community in a coastal region on the West Antarctic Peninsula shelf and potential invasive impacts. Polar Research 31, 102611.1–102611.14.

Turner, J. A., Mikucki, J. A., Alekhnina, I. A., Barrante, C., Christensen, B. G., Ghos, D., Michaud, A. B., Mitchell, A. C., Prescu, J. C., Scherrer, R., Skidmore, M. L., Vick-Majors, T. J. & the WISSARD Science Team (2014). Microbial sulfur transformations in sediments from subglacial Lake Whillans. Science 344, 594.

Vanreusel, A., Ahnh, D. H., Saba, V. S., Iannucci, R. A., Coleman, K. E., Doney, S. C., Dickson, A. G., Miles, T. N., Packard, D. L., Ricketts, T. H., Skirrow, D., Swift, S. T., Wiggert, J. D. & Zettler, E. R. (2015). Climate change and glacier retreat drive shifts in Antarctic terrestrial diatoms. Proceedings of the Royal Society B: Biological Sciences 282, 20150534.

Vanreusel, A., Ahnh, D. H., Saba, V. S., Iannucci, R. A., Coleman, K. E., Doney, S. C., Dickson, A. G., Miles, T. N., Packard, D. L., Ricketts, T. H., Skirrow, D., Swift, S. T., Wiggert, J. D. & Zettler, E. R. (2015). Climate change and glacier retreat drive shifts in Antarctic terrestrial diatoms. Proceedings of the Royal Society B: Biological Sciences 282, 20150534.
Velasco-Castrillón, A., Hawes, I. & Stevens, M. I. (2018). 100 years on: a re-evaluation of the first discovery of microfauna from Ross Island, Antarctica. *Antarctic Science* 30, 209–219.

Vinables, H. J., Clarke, A. & Meredith, M. P. (2013). Wintertime controls on summer stratification and productivity at the Western Antarctic peninsula. *Limnology and Oceanography* 58, 1035–1047.

Verde, C., Giordano, D., Bellas, C. M., di Prisco, G. & Aneddo, A. M. (2016). Polar marine microorganisms and climate change. *Advances in Microbial Physiology* 69, 187–215.

Verde, C., Parisi, E. & di Prisco, G. (2006). The evolution of thermal adaptation in polar fish. *Gor. 385, 137–145.

Verleyen, E., Hoogdgon, D. A., Gibson, J. & Iwura, S. (2012). Chemical limnology in coastal East Antarctic lakes: monitoring future climate change in centres of endemism and biodiversity. *Antarctic Science* 24, 23–33.

Vernet, M., Sines, K., Chakos, D., Cefarelli, A. O. & Ekern, L. (2011). Impacts on phytoplankton dynamics by free-drifting icebergs in the NW Weddell Sea. *Deep-Sea Research Part II* 58, 1422–1435.

Vettia, D., Cornet, S., Meiners, K. M., Kawaguchi, S., Murphy, E. J. & Bestley, S. (2020). Circumpolar projections of Antarctic krill growth potential. *Nature Climate Change* 10, 568–575. https://doi.org/10.1038/s41558-020-0758-4.

Vick-Majors, T. J., Michaud, A. B., Skidmore, M. L., Turetta, C., Barrante, C., Christner, B. C., Dore, J. E., Christianson, K., Mitchell, A. C., Achberger, A. M., Mirucci, J. A. & Prisco, J. C. (2020). Ecosystems beneath the West Antarctic ice sheet and the sub-ice marine environment. *Global Biogeochemical Cycles* 34, e2019GB006446.

Walker, C., Griffiths, H. J., Waluda, C. M., Thorpe, S. E., Lomas, I., Moreno, B., Pacherres, C. O. & Hughes, K. A. (2017). Microplastics in the Antarctic marine system: an emerging area of research. *Science of the Total Environment* 598, 220–227.

Waluda, C. M. & Staniland, I. J. (2013). Entanglement of Antarctic fur seals at Bird Island, South Georgia. *Marine Pollution Bulletin* 74, 244–252.

Weimerskirch, H., Louzao, M., de Grissac, S. & Delord, K. (2012). Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335, 211–214.

Wing, S. R., Leichter, J. J., Wing, L. C., Stokes, D., Genovese, S. J., McMullin, R. M. & Shatova, O. A. (2018). Contribution of sea ice microbial production to Antarctic benthic communities is driven by sea ice dynamics and composition of functional guilds. *Global Change Biology* 24, 3642–3653.

Wu, S.-Y. & Hou, S. (2017). Impact of icebergs on net primary productivity in the Southern Ocean. *The Cryosphere* 11, 707–722.

Xavier, J. C., Brandt, A., Ropert-Coudert, Y., Badhe, R., Gutt, J., Havermans, C., Jones, C., Costa, E. S., Lohmann, G., Schloss, I. R., Kennicutt, M. C. II & Sutherland, W. J. (2016a). Future challenges in Southern Ocean ecology research. *Frontiers in Marine Science* 3, 94.

Xavier, J. C., Raymond, B., Jones, D. C. & Griffen, H. (2016b). Biogeography of cephalopods in the Southern Ocean using habitat suitability prediction models. *Ecosystems* 19, 220–247.

Yang, H., Lohmann, G., Krebs-Kanzow, U., Ionita, M., Shi, X., Sidorenko, D., Gong, X., Chen, X. & Gowan, E. J. (2020). Poleward shift of the major ocean gyres detected in a warming climate. *Geophysical Research Letters* 47, e2019GL083868.

VII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article. **Appendix S1.** List of authors with their expertise, on which the synthesis was built. **Appendix S2.** Search terms for key messages used in the literature survey in *Web of Science* including numbers of publications 1970–2020 and 2010–2020; results from 4 September 2020. **Appendix S3.** Scheme showing how the confidence of the scientific sub-messages was assessed following the IPCC AR5 and IPBES methodology (Mach et al., 2017; IPBES, 2019).

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