

Annual Review of Marine Science

Antarctic Futures: An
Assessment of Climate-Driven
Changes in Ecosystem
Structure, Function, and
Service Provisioning in the
Southern Ocean

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Keywords

climate change, Southern Ocean, biodiversity, impacts

Abstract

In this article, we analyze the impacts of climate change on Antarctic marine ecosystems. Observations demonstrate large-scale changes in the physical variables and circulation of the Southern Ocean driven by warming, stratospheric ozone depletion, and a positive Southern Annular Mode. Alterations in the physical environment are driving change through all levels of Antarctic marine food webs, which differ regionally. The distributions of key species, such as Antarctic krill, are also changing. Differential responses among predators reflect differences in species ecology. The impacts of climate change on Antarctic biodiversity will likely vary for different communities and depend on species range. Coastal communities and those of sub-Antarctic islands, especially range-restricted endemic communities, will likely suffer the greatest negative consequences of climate change. Simultaneously, ecosystem services in the Southern Ocean will likely increase. Such decoupling of ecosystem services and endemic species will require consideration in the management of human activities such as fishing in Antarctic marine ecosystems.

1. INTRODUCTION

The Southern Ocean and Antarctic coastal seas, as defined by the Convention for the Conservation of Antarctic Marine Living Resources (**Figure 1**), make up approximately 10% of the area of the world's ocean (CCAMLR 2018). They are cold; dominated by the world's largest ocean current system, the Antarctic Circumpolar Current; and isolated by a steep thermal gradient at the Antarctic Polar Front. The Southern Ocean ventilates the global ocean; absorbs heat, fresh water, and oxygen; and takes up approximately 10% of anthropogenic carbon dioxide (CO₂) emissions (Turner et al. 2009, Hauck et al. 2015). It is also known for the formation of large volumes of bottom water that transport macronutrients northward (Hauck et al. 2015). The marine biota of the region can be traced back to the Mesozoic era and the breakup of Gondwana (Rogers 2012). The isolation of the Antarctic continent some 33 million years ago (Kuhnt et al. 2004) and subsequent cooling led to a unique, cold-adapted marine biota that supports large populations of marine predators, including seabirds, whales, and seals (e.g., Rogers 2012, Rogers et al. 2015).

Animals have been hunted in the Antarctic since the late eighteenth century, beginning with the hunting of fur seals for hides and continuing with whaling, which was followed in the late twentieth century by fishing. Current fished resources include toothfish (*Dissostichus eleginoides* and *Dissostichus mawsoni*), Antarctic krill (*Euphausia superba*), and mackerel icefish (*Champsocephalus gunnari*). Overexploitation characterized many earlier fisheries; Antarctic fur seals (*Arctocephalus gazella*) were hunted to near extinction by the late nineteenth century, and whale populations were seriously depleted by the mid-1960s before a ban on commercial hunting in 1986 (Rogers et al. 2015). The recoveries of populations of pinnipeds and cetaceans took place at different rates, although for some of the larger species it has been slow (e.g., blue whale, *Balaenoptera musculus*; Branch et al. 2007). Therefore, the Southern Ocean ecosystem was not in a steady state before the effects of ozone depletion and climate change were understood.

In this review, we synthesize current knowledge of the influence of climate change in the Anthropocene on ecosystem structure and function in the Southern Ocean and Antarctic coastal seas. Previous reviews on the effects of climate change on Antarctic marine ecosystems have emphasized potential impacts on individual components of the Southern Ocean biota (e.g., Constable et al. 2014) or the footprint of environmental changes under future climate-change projections (e.g., Gutt et al. 2015). Here, we focus on impacts of climate change in the present and future

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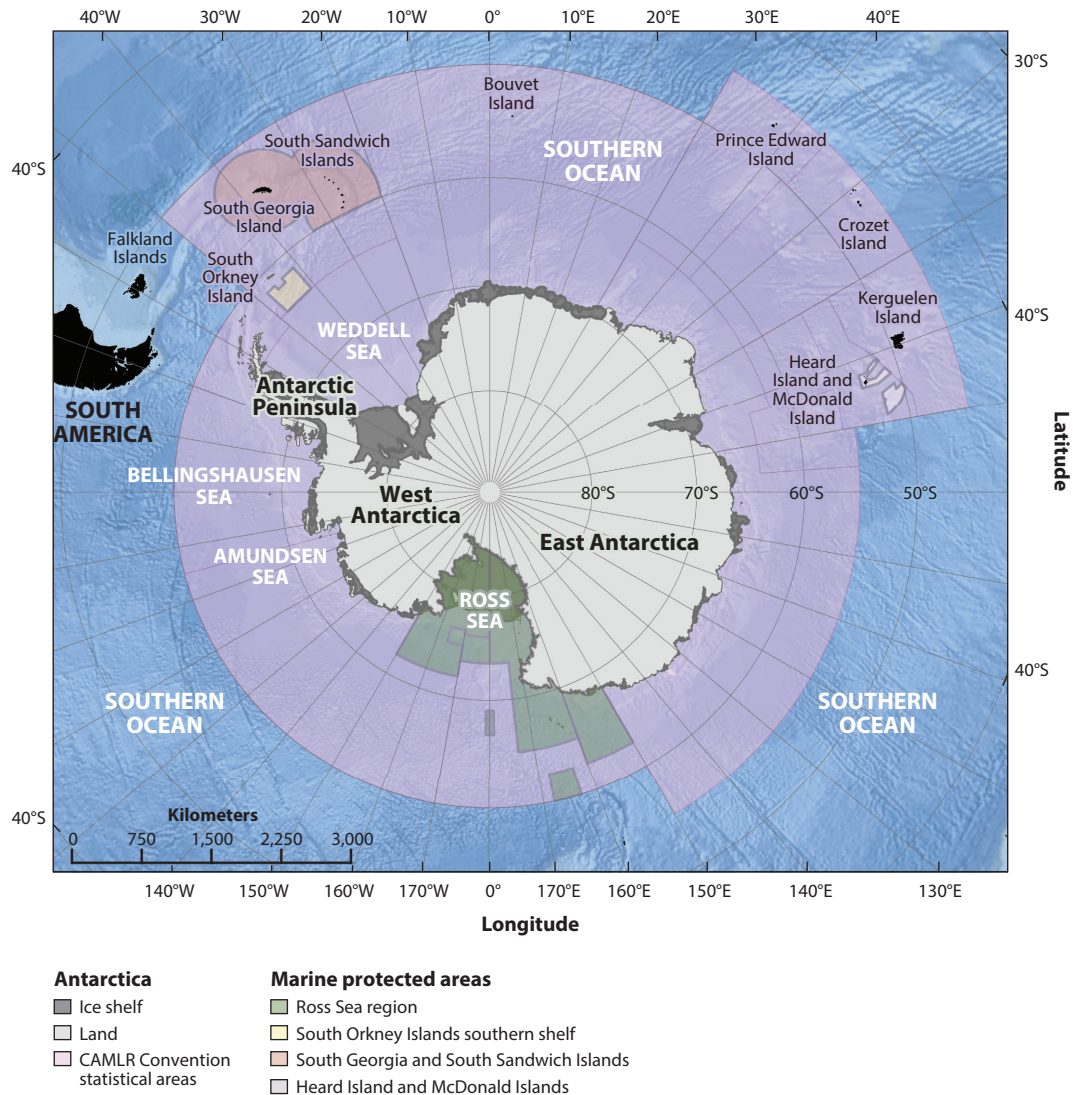


Figure 1

Map of Antarctica and the Southern Ocean, showing key geographic regions and the area covered by the Convention for the Conservation of Antarctic Marine Living Resources (CAMLR Convention).

(2050–2100) on biodiversity and ecosystem service provisioning (*sensu* Grant et al. 2013). Based on the findings reviewed here, we make recommendations for management and conservation of Southern Ocean marine ecosystems and highlight gaps in the science, including observations, experimental studies, and modeling.

We begin by reviewing the physical environmental changes in the Southern Ocean, their links to biogeochemistry, and the dynamics of the Southern Ocean carbon sink within the broader Earth system. We then look at the potential impacts of future climate change on pelagic communities, with an emphasis on Antarctic krill, salps, and top predators. We examine two regions of the Antarctic, the Western Antarctic Peninsula (WAP) and the Ross Sea, where contrasting bottom-up

changes to marine ecosystems have occurred that epitomize differences in climate-change effects on the Southern Ocean. The implications of climate change and other human impacts for Antarctic marine biodiversity and ecosystem service provisioning are then considered. Finally, we discuss the management implications for the Southern Ocean in the context of both ecosystem service provisioning and conservation.

2. CHANGES IN THE PHYSICAL OCEAN, BIOGEOCHEMISTRY, AND CO₂ UPTAKE

2.1. The Physical Ocean

The physical changes in the Southern Ocean comprise deep-reaching warming and freshening of surface waters (e.g., Haumann et al. 2016); changes in stratification and mixed-layer depth (e.g., Pellichero et al. 2017); changes in ocean circulation, especially upwelling, and mixing (e.g., Armour et al. 2016); changes in the duration and extent of sea ice (e.g., Comiso et al. 2017), particularly fast ice (Barnes et al. 2018); the breakup of ice shelves (e.g., Liu et al. 2015); a decrease in oxygen levels in the water column (e.g., Schmidtko et al. 2017); and a decrease in ocean pH (e.g., McNeil & Matear 2008). These changes are driven by atmospheric and oceanic warming resulting from the increase of CO₂ in the atmosphere, the ozone hole (e.g., Thompson et al. 2011, IPCC 2013, Swart et al. 2018), and the positive state of the Southern Annular Mode (SAM), leading to a poleward shift and strengthening of westerly winds that were thought to have shifted the fronts of the Antarctic Circumpolar Current (Roemmich et al. 2007, Xing et al. 2017), although more recent evidence suggests that fronts have not significantly moved (Chapman 2017, Chambers 2018). Stronger winds are also associated with the amplification of eddy kinetic energy and southward eddy heat flux (Swart & Fyfe 2012). Upwelling of relatively warm deep water along the Antarctic continental shelf, particularly on shelves situated in West Antarctica, appears to have driven an observed acceleration in basal ice shelf melt in recent decades (e.g., Cook et al. 2016).

2.2. Biogeochemistry and the Southern Ocean as a Sink of Anthropogenic CO₂

Polar marine ecosystems in a changing world were discussed by Smetacek & Nicol (2005). Constable et al. (2014) gave an update of our knowledge about the current state and recent changes of primary production and cycling of elements in the Southern Ocean.

The amount of dissolved inorganic carbon in the southern part of the surface Southern Ocean is relatively high compared with that of many other oceanic regions for two reasons: (a) the high solubility of CO₂ in cold water and (b) the upwelling of old CO₂-rich water masses (**Figure 2**). Surface-ocean dissolved inorganic carbon decreases by more than 100 μmol kg⁻¹ between 65°S and the position of the Antarctic Polar Front (between 45°S and 55°S). Although large parts of the Southern Ocean are considered to be high-nutrient, low-chlorophyll regions, extended phytoplankton blooms develop in regions with deep mixed layers (>80 m; Hoppe et al. 2017), resulting in large drawdown of CO₂ (Jones et al. 2017) and reduction of dissolved inorganic carbon. Although the upwelling of CO₂-rich water masses leads to oversaturation and thus CO₂ outgassing in the south, the Southern Ocean (south of 40°S) is taking up approximately 10% of anthropogenic CO₂ emissions (e.g., Khatiwala et al. 2009) through a combination of the physical carbon and biological pumps.

The physical carbon pump is driven by ocean circulation, mixing, and heat exchange in combination with the strong temperature dependence of CO₂ solubility (i.e., the solubility carbon pump). The strength of this pump is increasing with rising atmospheric CO₂ levels. However, in the Southern Ocean, because of stronger winds forcing the circulation, including upwelling,

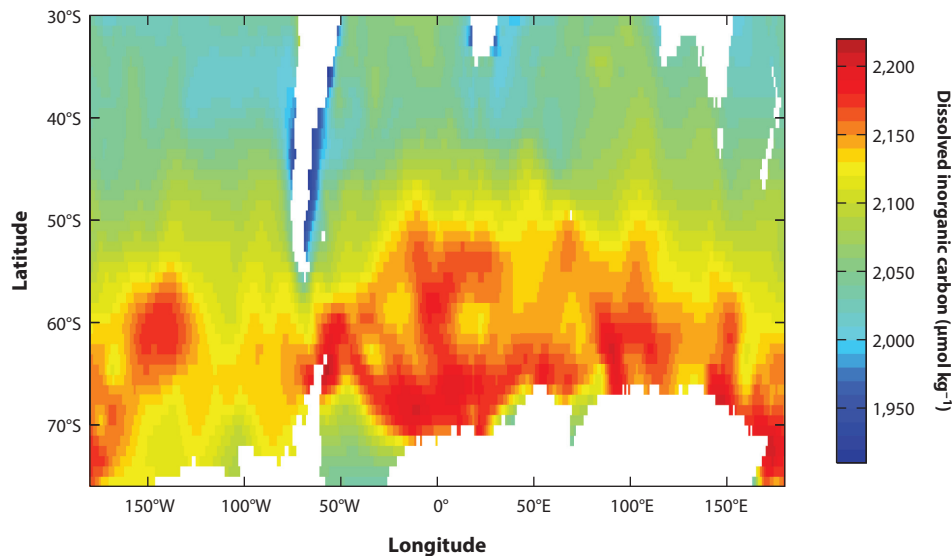


Figure 2

Surface-ocean dissolved inorganic carbon, showing high surface concentrations in the south caused by upwelling of CO_2 -rich water masses. Data are from Global Ocean Data Analysis Project (GLODAP) version 2b.

northward Ekman transport and mesoscale eddy activity are also changing. The largest atmospheric pattern of variability in the Southern Hemisphere is the SAM. Positive values of the SAM index correspond to stronger westerlies. The SAM has increased over the last four decades, driven by seasonally recurring depletion of stratospheric ozone over Antarctica (the ozone hole) and increased levels of greenhouse gases (Thompson et al. 2011). The impact of wind forcing on Southern Ocean CO_2 uptake has been studied by Le Quéré et al. (2007), Landschützer et al. (2015), and others. Le Quéré et al. (2007) saw a weaker-than-expected increase of the Southern Ocean carbon sink, and this work led to an intensification of the already ongoing discussion among physical oceanographers about the response of the Southern Ocean circulation (Böning et al. 2008). However, Landschützer et al. (2015) identified a reversal in the trend of a decreasing CO_2 sink in the Southern Ocean, reflecting an increase in the air–sea differential of CO_2 . This in turn reflected a stalling of the growth of surface-ocean $p\text{CO}_2$. This discussion also brought eddy compensation (Ekman effect opposed by an increase in eddy fluxes) to the recognition of the wider oceanographic community as a mechanism that offsets the effects of greater wind stress on the Antarctic Circumpolar Current (e.g., Hogg et al. 2015).

There are currently three main methods to estimate the changes in the Southern Ocean CO_2 sink: flux products based on surface-ocean $p\text{CO}_2$ observations (Landschützer et al. 2015), inversions based on atmospheric observations (Le Quéré et al. 2007), and ocean biogeochemistry models (Le Quéré et al. 2016b). All three methods suggest that the Southern Ocean CO_2 sink was weaker than expected during the 1990s and stronger than expected during the 2000s (**Figure 3a**). The variability in the Southern Ocean CO_2 sink in the ocean models is much less than is inferred from the observations (atmospheric and oceanic) and is closer to the expected trend in the absence of climate variability (red line in **Figure 3a**); however, there are also large differences among ocean models (Le Quéré et al. 2016a) (**Figure 3b**). The Southern Ocean is the most uncertain region for the representation of CO_2 fluxes across models (**Figure 3b**). A key bias common across ocean

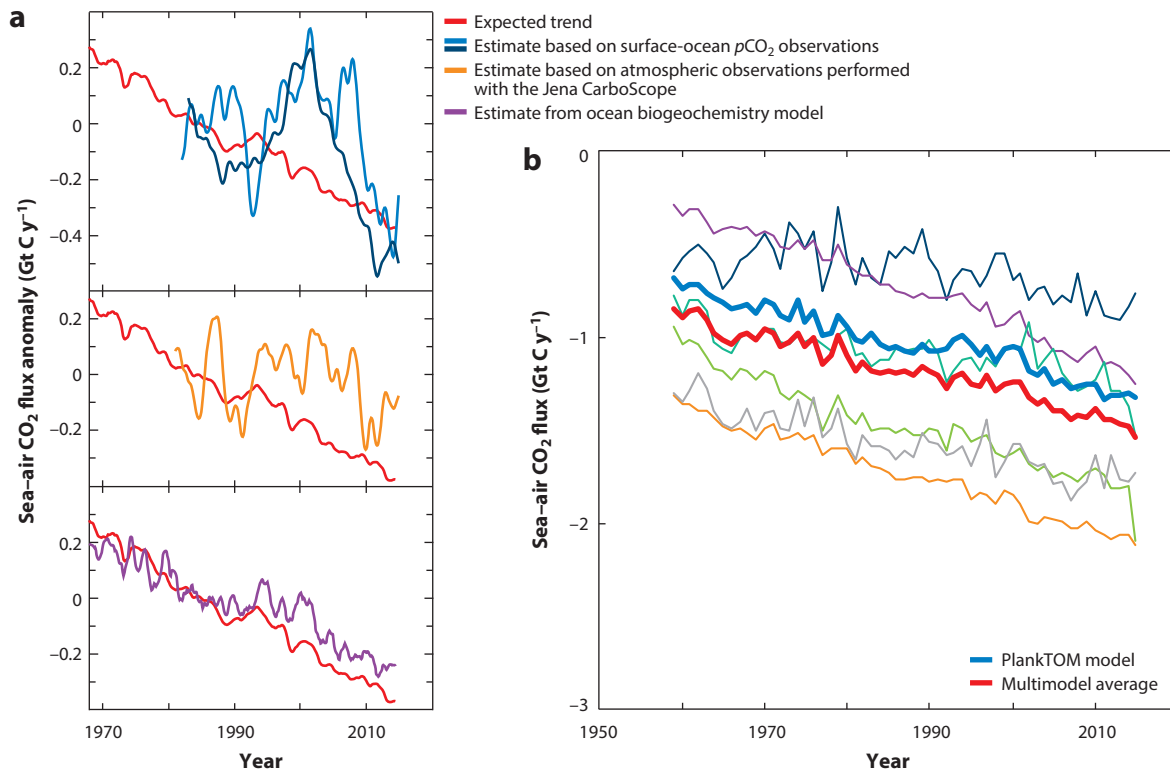


Figure 3

Estimates of the Southern Ocean (south of 30°S) sea-air CO₂ flux. (a) Estimates of the CO₂ flux anomaly in the presence of climate variability calculated using various methods, compared with the expected trend of an increasing sink in the absence of climate variability (red line, repeated in each of the three subpanels; data updated from Le Quéré et al. 2007). The top subpanel shows two estimates from flux products based on surface-ocean pCO₂ observations (data updated from Landschützer et al. 2015), the middle subpanel shows an estimate from an atmospheric inversion based on atmospheric observations performed with the Jena CarboScope (Le Quéré et al. 2016a), and the bottom subpanel shows an estimate from an ocean biogeochemistry model (Le Quéré et al. 2016b). (b) Estimates of total Southern Ocean sea-air CO₂ flux from multiple ocean models. Panel b adapted from Le Quéré et al. (2016a).

models has been the systematic overestimation of the summer chlorophyll biomass in the Southern Ocean. The PlankTOM model has largely removed this bias through the inclusion of crustacean microzooplankton grazing and zooplankton trophic cascades (Le Quéré et al. 2016b).

How will the strengths of the physical and biological carbon pumps develop in the future? From a chemical point of view, one would expect a reduced strengthening of the pump because of the change in the Revelle or buffer factor (R), leading to less and less relative increase of DIC for the same amount of relative CO₂ increase. From a biological point of view, one would expect little change in the strength of the biological carbon pump if biological production and export were not greatly affected by changes of the marine carbonate system. In contrast to these expectations, Hauck & Völker (2015) found a stronger impact of biological production on the oceanic uptake of CO₂ under high values of CO₂ and R . The degree of CO₂ undersaturation (with respect to atmospheric CO₂) in Southern Ocean surface water generated by biological production is greater than it was in preindustrial times. Combined with special circulation features in the Southern Ocean (the formation of mode and intermediate waters), this undersaturation results in a larger-than-expected carbon sink.

Most biogeochemical models show an increase of export production south of 44°S, with large uncertainties in part depending on the supply of bioavailable iron (Hauck et al. 2015). The uptake of CO₂ between 30°S and the Antarctic continent increases during all seasons and is driven largely by rising atmospheric CO₂ levels, with the increased *R* acting as an amplifier.

3. CHANGES IN SPECIES, COMMUNITIES, AND ECOSYSTEMS

3.1. Pelagic Prey Species: Krill and Salps

Antarctic krill (*E. superba*) is a particularly successful cold-water species in terms of biomass and distribution and one for which conceptual models of its life cycle are well developed (e.g., Quetin & Ross 2009). It occurs mainly in large swarms and is a major food source for various marine mammals, birds, seals, and fish (e.g., Trathan & Hill 2016). It plays a potentially important role in biogeochemical cycling (e.g., Belcher et al. 2019) and is the main target of Antarctic fisheries. There is evidence of strong environmental controls on krill recruitment, distribution, and growth (e.g., Murphy et al. 2012). Sea ice has a major influence on survival during the first overwintering period (Loeb et al. 1997). Temperature and the availability of diatoms and large phytoplankton cells affect *E. superba* growth, while ocean currents influence distribution (e.g., Quetin & Ross 2003, Murphy et al. 2012). Regional-scale population variability and change have been linked to winter temperatures, sea ice timing and extent, and the SAM (e.g., Loeb et al. 1997; Quetin & Ross 2003; Atkinson et al. 2004, 2019; Murphy et al. 2012), with the strength of these relationships varying between regions. In the Atlantic sector of the Southern Ocean, which contains more than 50% of the circumpolar krill stock, there has been an apparent poleward contraction of krill distribution over the past 90 years coupled with declines in both recruitment and population density linked to the positive SAM anomalies (e.g., Atkinson et al. 2004, 2019; for an alternative view, see Cox et al. 2018) (Figure 4). Projection models suggest that future scenarios involving increased temperatures, reduced sea ice cover (Cavanagh et al. 2017), and reduced diatom production are likely to cause further habitat contraction and population decline (e.g., Hill et al. 2013, Piñones & Fedorov 2016, Klein et al. 2018). However, one study has suggested that climate change might increase the availability of suitable habitat during the first overwintering period for krill (Melbourne-Thomas et al. 2016). Any negative changes in krill distribution and abundance have the potential to increase competition between krill predators and krill fisheries (e.g., Klein et al. 2018).

Salps are gelatinous tunicates that have a similar average size to Antarctic krill but can reach three times the maximum length of krill and have contrasting habitat requirements (Pakhomov et al. 2002) and a radically different life cycle, with alternating sexual and asexual reproduction (Foxton 1966). *Salpa thompsoni* is the most numerous and widely distributed of three salp species that occur south of the Antarctic Polar Front (Pakhomov et al. 2002). It is recorded from the Subtropical Convergence to the shelf waters of the Antarctic continent, reaching its greatest densities within the Antarctic Polar Frontal Zone (Foxton 1966, Pakhomov et al. 2002). Water temperature and food concentration are likely to be the main factors that trigger asexual reproduction and localized rapid population increases (Pakhomov et al. 2002, Pakhomov & Hunt 2017). Individual growth rates suggest that the life span of *S. thompsoni* could be as long as two years (Loeb & Santora 2012) or as short as three months (Henschke et al. 2018). It is a flexible species that can tolerate a range of habitats associated with relatively warm (>0°C) and lower-salinity water masses. In contrast to krill, *S. thompsoni* biomass declines rapidly as sea ice cover increases (Pakhomov et al. 2002, Atkinson et al. 2004). It seems unable to establish persistent large Antarctic populations, and its occurrence at high latitudes is likely sustained by advection of warmer waters toward the south (Henschke & Pakhomov 2019).



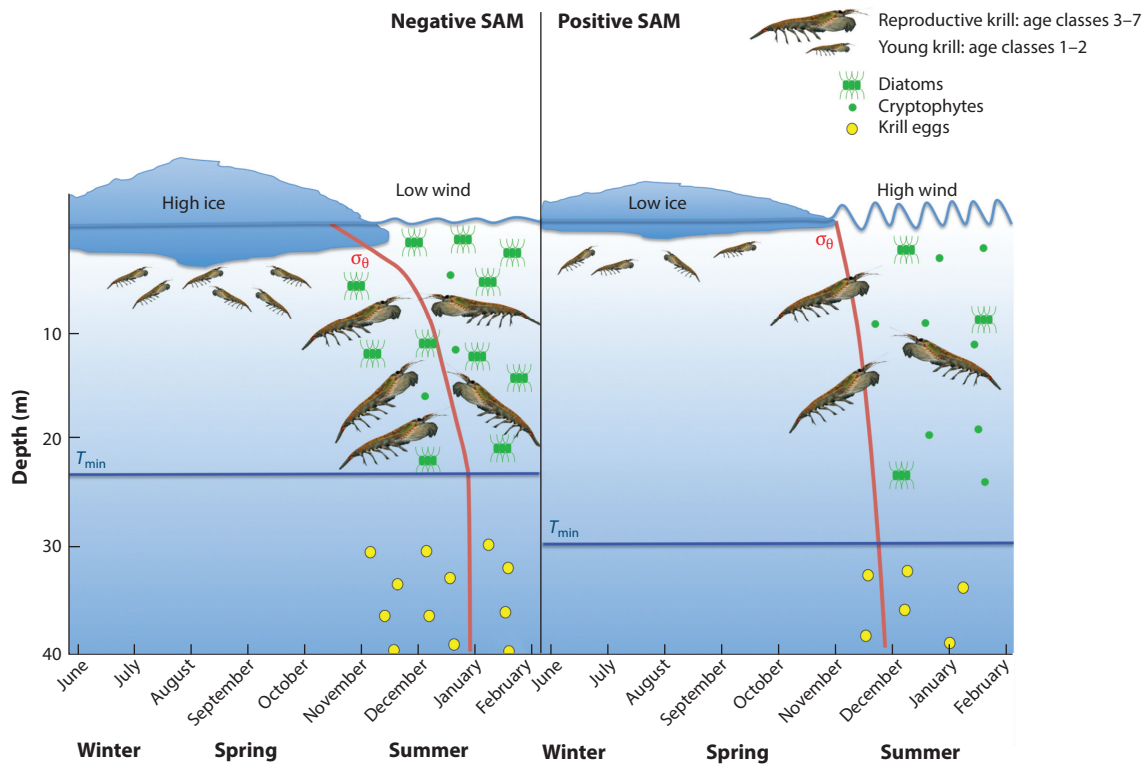


Figure 4

Ecosystem responses to Southern Annular Mode (SAM) forcing on the Western Antarctic Peninsula (Saba et al. 2014). σ_{θ} is the density of the seawater at any given depth; its gradient defines the vertical stability of the water column. T_{\min} is the minimum temperature in the water column, an indicator of cold, remnant deep water from the previous winter.

The earlier perception that salps are not predated and are therefore a carbon sink is changing with increasing evidence of their importance in the diets of various Antarctic animals (reviewed in Pakhomov et al. 2002). They are nonselective and highly effective filter feeders that are able to capture a wide range of prey sizes (1 μm –1 mm) but preferentially digest small flagellates and to some degree diatoms (Atkinson et al. 2012). Krill, by contrast, are active predators of copepods, microzooplankton, and salps, while also feeding on phytoplankton and actively selecting for diatoms (Haberman et al. 2003). The relative importance of zooplankton and phytoplankton in the diet of krill in the Southern Ocean is unclear and may have a significant influence on interactions between krill and salps (Atkinson et al. 2012). Both krill and salps are major grazers of primary producers and important mediators of vertical carbon flux (Pakhomov et al. 2002, Alcaraz et al. 2014, Belcher et al. 2019). Salps produce larger, faster-sinking (up to 2,700 m d^{-1}), and more carbon-rich (up to 37% dry weight) fecal pellets than krill, increasing the speed and efficiency of the transfer of nutrients and carbon from surface waters to depth (Phillips et al. 2009). Even in areas where salps are not the dominant plankton biomass (e.g., the Scotia Sea), their pellets contribute disproportionately to downward carbon flux; furthermore, during diel migration (a behavior that krill also exhibit), salps migrate down to approximately 300–500 m during summer and reside at depths of 500–1,000 m during winter, thus potentially increasing the carbon flux into deeper waters (Manno et al. 2015). However, the rate of attenuation of krill and salp fecal pellets is highly

variable (Iversen et al. 2017, Belcher et al. 2019), which means that estimates and projections of downward carbon flux are highly uncertain.

Observations suggest that a general increase in salp densities and a southward shift in their distribution has already occurred (Pakhomov et al. 2002, Atkinson et al. 2004). Antarctic krill and *S. thompsoni* habitats seem to overlap significantly at mesoscales, although this is not immediately obvious at micro- and macroscales (Pakhomov et al. 2002). Several regional models now include both krill and salps. These models have recreated the historic WAP decline in krill and increase in salps (Hoover et al. 2012) and suggested further declines in krill biomass with increases in salp biomass by 2050 (Suprenand & Ainsworth 2017). These projections indicate the potential for salps to replace Antarctic krill in some regions. The only ecosystem model of the entire Southern Ocean available today has highlighted the importance of salps in iron recycling (Maldonado et al. 2016), a process important because the Southern Ocean is an iron-limited system. With the observed and potential future increase in salp abundance, their inclusion in biogeochemical models is becoming increasingly important to better understand the Southern Ocean carbon cycle (Pakhomov et al. 2002, Henschke et al. 2016).

Work is currently underway to create the first life cycle and population models for *S. thompsoni* (Henschke et al. 2018) and to add a plankton functional type (PFT) representing salps to the PlankTOM model. However, a key limitation to the advancement of PFTs within biogeochemical models is the paucity of data on physiological requirements and limitations, feeding preferences, and biomass (Pakhomov et al. 2002, Le Quéré et al. 2016b).

Because of their importance as the dominant grazers in the Southern Ocean, the response of krill and salps to future climate change has a variety of implications for predators, fisheries, and biogeochemical cycling. Projections suggest southward shifts in the distributions of both species. The potential for competition between these species, should further habitat contraction occur, is unclear because of gaps in the understanding of the ecology and life history of both species. Understanding the impacts of change in these ecosystems will require better assessments of the distribution and abundance of krill and salps in different sectors of the Southern Ocean.

3.2. Mesopredators: Penguins, Whales, and Seals

The Southern Ocean is well known for its spectacular populations of predators, including seabirds (penguins, albatrosses, and petrels), seals, and whales (Rogers et al. 2015). Whales and seals, in particular, were heavily affected by hunting from the eighteenth to the twentieth century and are still recovering from severe depletion (Rogers et al. 2015). This, coupled with regional differences in environmental change, has significantly complicated interpretation of current trends in the populations of these animals.

3.2.1. Penguins. Population trends in penguins vary according to species and the geographic location of colonies. For example, Adélie penguins (*Pygoscelis adeliae*) are stable or increasing in the East Antarctic region but declining on the WAP (Lynch & LaRue 2014, Casanovas et al. 2015, Southwell et al. 2017). Chinstrap penguins (*Pygoscelis antarctica*) are also declining in the WAP but are stable in the South Sandwich Islands (Naveen et al. 2012, Casanovas et al. 2015, Lynch et al. 2016), with the caveat that volcanic activity can impact populations (Roberts et al. 2017). Gentoo penguins (*Pygoscelis papua*) are increasing on the WAP, possibly at the expense of Adélie and chinstrap penguins; Adélie penguin declines are thought to be driven particularly by changes in sea ice resulting from climate change (e.g., Forcada & Trathan 2009, Lynch et al. 2012, Lima & Estay 2013, Casanovas et al. 2015, Cimino et al. 2016). Gentoo penguin populations are expanding most at the south of their range (Casanovas et al. 2015). Emperor penguins (*Aptenodytes forsteri*)



breed largely below the Antarctic Circle, but their populations have not yet been surveyed over a sufficient time period to detect long-term changes (Fretwell & Trathan 2009).

Trends over the last 30,000 years in penguin population sizes show responses to climate consistent with those observed in the present (e.g., Clucas et al. 2014), and gentoo patterns in particular are thought to vary as a result of warmer conditions (e.g., Levy et al. 2016, Roberts et al. 2017). Many of the ice-tolerant or pagophilic species may be experiencing an optimal level of ice cover (e.g., Younger et al. 2015), based on modeling (Jenouvrier et al. 2014, Cimino et al. 2016) and observations of colony decline (e.g., Jenouvrier et al. 2009) or colony loss (e.g., Trathan et al. 2011).

Multiple lines of evidence show that chinstrap and Adélie penguins forage on the shelf, shelf break, or slope and are specialist predators of krill (e.g., Miller & Trivelpiece 2008, Miller et al. 2010, Chapman et al. 2011, Gorman et al. 2014). By contrast, gentoo penguins are more generalist, near-shore foragers (e.g., Miller et al. 2010, Emslie et al. 2013). Gentoo penguins show a high level of population genetic structure at the population level, are locally differentiated (e.g., Levy et al. 2016), and remain in their breeding areas over winter (Hinke et al. 2012), unlike other pygoscelids.

3.2.2. Seals. The Southern Ocean pinniped community is dominated by two species of otariids [sub-Antarctic (*Arctocephalus tropicalis*) and Antarctic (*A. gazella*) fur seals] and five species of phocids [southern elephant (*Mirounga leonina*), crabeater (*Lobodon carcinophagus*), Weddell (*Lep-
tonychotes weddellii*), leopard (*Hydrurga leptonyx*), and Ross (*Ommatophoca rossii*) seals]. For the most part, accurate estimates of numbers are difficult to obtain and are available only for a subset of these species owing to logistic and technological constraints associated with counting. The most studied species is the southern elephant seal, whose populations have increased in the seven decades since the end of elephant seal hunting in this area. Four genetically distinct populations are currently recognized (Slade et al. 1998, Corrigan et al. 2016). Three of these, those at South Georgia, the Valdes Peninsula, and Kerguelen, are either currently stable or increasing slightly (Hindell et al. 2016), while the Macquarie Island population (the only significant breeding population in the southern Pacific) is decreasing, although the mechanism is unclear (McMahon et al. 2005).

The population status and trends for the remaining four phocid species are less clear despite their importance in the Southern Ocean ecosystem. Their numbers are estimated together under the broad definition of pack-ice seals (Southwell et al. 2008). Despite considerable effort by scientists in the Antarctic Pack-Ice Seal Census to survey numbers and distribution, comparison of observations with those collected previously remain difficult. The population trajectories are unclear (Southwell et al. 2012). However, there have been some suggestions of a decrease in numbers in the WAP (Forcada et al. 2012).

These four pack-ice seal species inhabit a highly changeable environment that is particularly sensitive to climate change. Logistical limitations to sampling the region make reliable estimates extremely challenging. However, modern satellite technology is making it feasible to count these animals from space, and this approach has the promise of finally providing a platform for improving current Southern Ocean estimates of these seals, which range from 15 million to 50 million (Southwell et al. 2012).

Sub-Antarctic and Antarctic fur seals were harvested most intensively for their pelts (Rogers et al. 2015). Since the end of this exploitation in the early twentieth century, fur seal numbers have increased dramatically, and populations have now reestablished on islands from where they were previously removed (Wynen et al. 2000, Rogers et al. 2015). Indeed, only the presence of predators (leopard seals, Hooker's sea lions, and possibly killer whales) has limited the growth of populations below the maximum rate (Boveng et al. 1998, Robinson et al. 1999).

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3.2.3. Whales. Baleen whale populations around the Antarctic are recovering, albeit slowly, from intense commercial whaling that removed more than 2 million animals from the Southern Ocean in the twentieth century (Clapham & Baker 2001). Currently, the logistics involved with survey methods and small population sizes precludes generating accurate population trends for some species. For example, blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), and sei (*Balaenoptera borealis*) whales are broadly distributed and do not appear to have focused breeding grounds that allow for access to many individuals to determine population trends. Antarctic minke whales (*Balaenoptera bonaerensis*) were not subject to extreme harvesting and are thought to have maintained relatively high and stable abundances around the Antarctic. However, this species associates very closely with sea ice as a preferred habitat (e.g., Williams et al. 2014), and sea ice cover and duration around the western side of the WAP have rapidly decreased (Stammerjohn et al. 2012). Thus, there is concern that available habitat, and therefore carrying capacity, in this region is diminishing quickly and that the number of Antarctic minke whales able to exist there could decline. Humpback whale (*Megaptera novaeangliae*) populations around the Southern Ocean appear to be increasing considerably, some at their biological maximum growth rate (e.g., Bejder et al. 2016). As a species with high fidelity to tropical breeding grounds and established migratory corridors, humpback whales are ideal for studying population trends through a variety of techniques (e.g., photo-identification mark-recapture, molecular genetics). Because they generally prefer open water to sea ice, available habitat around the Antarctic Peninsula is increasing. This increase in habitat (and decrease in habitat for minke whales) coupled with a lack of increase in sympatric fin and blue whale populations in this region, as well as high abundances of krill, could allow for a significant and continued increase in humpback whale numbers around the WAP.

Baleen whales in Antarctica feed almost exclusively on krill. The vast majority of diets reflect the available biomass of different krill species, with Antarctic krill being the most dominant. While both humpback and minke whales are generalist feeders globally, in the Antarctic their diets are largely euphausiid based.

There is a lack of information on most baleen whales with respect to phenology and behavioral responses to climate change. However, recent work by Weinstein & Friedlaender (2017) indicates that humpback whales around the WAP continue foraging in open water throughout the austral fall and even into winter, with their distribution and behavior around the WAP changing from broad distributions across the continental shelf in summer to more focused use of the Gerlache and Bransfield Strait regions and associated coastal bays in fall and winter. This being the area that remains ice free the longest, the whales appear to concentrate here and feed vigorously until they migrate to tropical breeding grounds or are forced into offshore waters by encroaching sea ice (Friedlaender et al. 2016).

For a summary of the observations and predicted future responses for the species discussed above, see **Supplemental Table 1**.

3.3. Regional Changes

While the Southern Ocean is often addressed as a single ocean in terms of climate change, its effects, and responses of species, strong regional differences in changes to the physical environment are evident. Regional differences in the structure of marine ecosystems and biological communities have meant that responses to climate-change effects at the regional level are complex and contrasting. Here, we examine these differences through analyses of responses in the WAP and Ross Sea regions.

3.3.1. Responses of biological communities to climate change: the Western Antarctic Peninsula region.

Current understanding of climate-change impacts on the physical oceanography and biogeochemistry of polar ecosystems was last summarized by the Intergovernmental Panel on Climate Change (IPCC) Working Group II report on impacts (Larsen et al. 2014). General models of climate-change impacts on ocean ecology and biogeochemistry suggest that the effects of physical forcing on ecosystem components (e.g., krill, seabirds, net community production, and others; see below in this section as well as Sections 3.3.2 and 3.3.3) are modulated through changes in phytoplankton assemblages (Saba et al. 2014, Kim et al. 2016).

For example, Saba et al. (2014) showed that blooms of diatom populations along the WAP were triggered by negative SAM conditions and melting of heavy sea ice that led to high krill egg production. This egg production subsequently led to successful recruitment, and ultimately increases in the survival of newly fledged penguin chicks (**Figure 4**). In this example, changes in wind forcing associated with SAM conditions caused increased sea ice, whose subsequent melting produced favorable conditions for diatom growth. The physical forcing elicited a response by phytoplankton, and subsequent changes in the ecosystem occurred in response to the phytoplankton change.

Phytoplankton populations in Antarctic marginal sea ice zones and continental shelves with high concentrations of macro- and micronutrients (iron) tend to be light limited (but see Annett et al. 2017). Sea ice melt stabilizes the surface layer, alleviates light limitation, and triggers phytoplankton blooms. In parts of the Antarctic Peninsula, glacier retreat and ice shelf disintegration have opened new areas to penetration of solar irradiance, creating areas of new phytoplankton growth (Peck et al. 2010). Seasonal sea ice losses around West Antarctica, particularly in the southern Antarctic Peninsula and South Orkney Island regions, have extended bloom durations, primary consumer growth, and benthic carbon stocks (Barnes 2015). By contrast, in the region to the north of Anvers Island, phytoplankton stocks declined from 1978 to 2006 in response to declining sea ice and a less stable water column, leading to deeper vertical mixing and increasing light limitation (Montes-Hugo et al. 2009). The duration rather than magnitude of phytoplankton bloom may be most important to blue carbon storage and sequestration, though (longer meal times for consumers lead to a larger proportion of the bloom being stored in animals rather than reworked in the microbial loop; see Barnes 2017). The IPCC report on impacts in polar regions cited these responses with high confidence (Larsen et al. 2014).

These trends have now been updated through 2015 using Moderate Resolution Imaging Spectroradiometer (MODIS) data (**Figure 5**). The new observations validate the original findings, showing similar north–south changes with increasing phytoplankton stocks to the south (red areas in the **Figure 5a**) and decreasing stocks to the north (blue areas in the **Figure 5a**). The transition zone of no change between these two areas has migrated roughly 400 km south since the original observations of Montes-Hugo et al. (2009), indicating the extension of the southern edge of the blue region south over the last decade. At that rate, phytoplankton could be declining along the entire WAP in another decade (around 2030). The mean size of phytoplankton cells is also changing (**Figure 5b**). The region of declining large phytoplankton ($>20\ \mu\text{m}$, i.e., diatoms) is principally over the shelf, and the region of increasing diatoms is offshore in slope water and the Antarctic Circumpolar Current. The overall conclusion from these observations is that phytoplankton stocks are declining and that diatoms are decreasing in importance along the WAP. Diatoms are the principal food source for krill, and their decline has important implications for food web dynamics. However, smaller phytoplankton cells, such as ciliates and flagellates, are important for many suspension-feeding benthos, which may increase growth performance as a result (Barnes 2017). What is less certain is how marine ecosystems and their services will function if this region becomes ice free year-round.

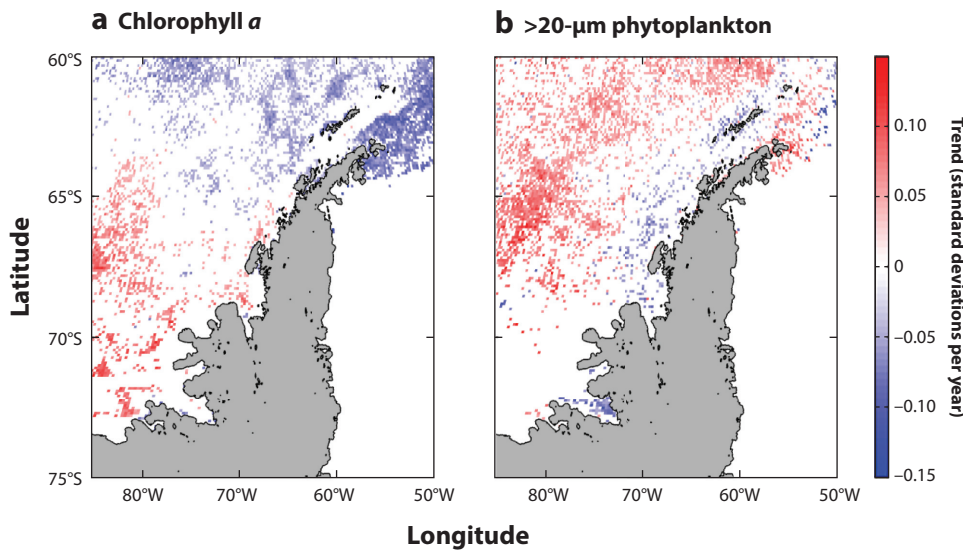


Figure 5

Trends in (a) total phytoplankton concentration and (b) phytoplankton cell size along the Western Antarctic Peninsula. Each colored pixel is a significant ($p < 0.05$) regression against time from 1997 to 2015. Data and plot courtesy of Dr. Maria Kavanaugh, Woods Hole Oceanographic Institution and Oregon State University.

The WAP is predicted to warm if current emissions continue (Marshall et al. 2004). Positive SAM conditions are predicted to occur more frequently over the WAP region (Thompson & Solomon 2002). Accordingly, we predict sustained sea ice losses; decreases in stocks of phytoplankton, diatoms, and krill; and increases in salp densities in the coming decades.

3.3.2. Net community production and export. Export of fixed organic carbon from the upper ocean (i.e., the euphotic zone, or approximately the upper 100 m) is the key biogeochemical process linking marine primary production to the global carbon cycle (Falkowski et al. 2000). A variable fraction of the inorganic carbon fixed by primary production is exported from the surface euphotic zone (Buesseler et al. 2007). The exported fraction (typically 5% to approximately 30% of the total primary production) may be in the form of large, rapidly sinking particles; small, suspended particles; and/or dissolved organic carbon. Gravitational sinking of large particles is the most commonly studied process and is often assumed to be the most important (Henson et al. 2012). This process has been studied using moored sediment traps for 20–30 years in some locations, including the WAP (Ducklow et al. 2008, Buesseler et al. 2010). There is substantial interannual variability in the export flux, but no directional, long-term trend has been observed. However, there are trends at least in phytoplankton (see Section 3.3.1), one of the major sources of sinking particles.

Not all the primary production is exported. The majority is consumed by herbivores, including both microzooplankton and mesozooplankton, or broken down in the microbial loop and respired back to CO_2 . The fraction of the primary production that eludes respiration is termed the net community production and sets an upper bound of fixed organic carbon available for export (Yager et al. 2012). Net community production is difficult to measure, and as yet there are no long-term observations (Eveleth et al. 2017) (**Figure 6**). Short-term, seasonal-scale observations have shown that export and net community production are decoupled and do not appear to be balanced over

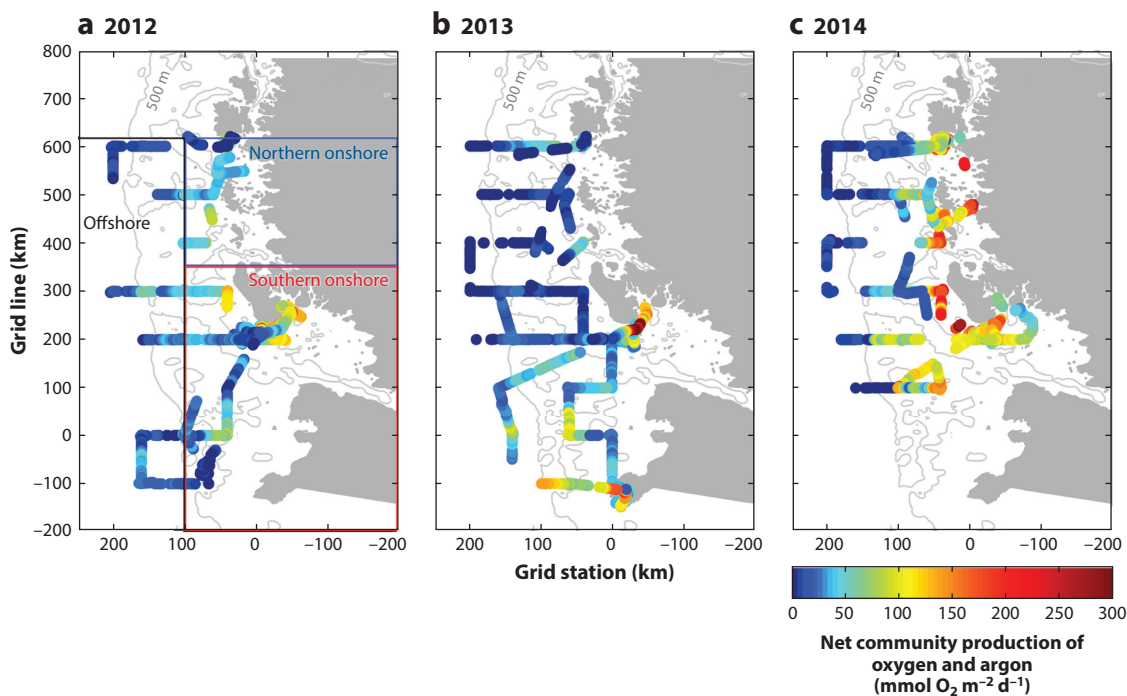


Figure 6

Net community production of oxygen in austral summer of (a) 2012, (b) 2013, and (c) 2014 on the Palmer Long Term Ecological Research (LTER) grid. The thin gray lines show the 500-m isobath. The black, blue, and red boxes mark the designated offshore, northern onshore, and southern onshore subregions, respectively. Figure adapted from Eveleth et al. (2017).

the seasonal scale (Stukel et al. 2015). On the basis of these observations and a suite of box models, advection and mixing of suspended particles could be a major pathway for export in the carbon cycle of the “leaky” marginal ice zone (Stukel et al. 2015). If this is true, we might be missing a major component of the export flux.

3.3.3. The Ross Sea. The Ross Sea continental shelf supports a mean net annual primary production of approximately 83.4 Tg C y^{-1} , equivalent to a mean shelf-wide productivity of $0.82 \text{ g C m}^{-2} \text{ d}^{-1}$ over a growing season of four months (Arrigo et al. 2008)—one-third of the total estimated annual production of the Southern Ocean. Arrigo et al. (2008) further estimated that waters of the Ross Sea continental shelf account for more than 25% of the estimated total CO₂ uptake of the entire Southern Ocean. Despite this high primary production, macronutrients (nitrate, phosphate, and silicate) are rarely depleted from Ross Sea surface waters during the growing season. However, the availability of the micronutrient, iron, can limit phytoplankton growth in the Ross Sea during parts of the growing season (reviewed in Smith et al. 2014a).

McGillicuddy et al. (2015) provided an annual budget for dissolved iron demand and supply in the Ross Sea that accounted for inputs from benthic sources, sea ice melt, Circumpolar Deep Water, and glacial melt (Figure 7). This analysis shows that the two largest sources of dissolved iron are the winter reserve (dependent on benthic sources) and sea ice melt (enriched with iron from several sources, including atmospheric deposition, scavenging from seawater, glacial melt, and algal production), providing approximately equal contributions that make up more than 80% of the total. The remainder of the supply is provided by iron associated with modified Circumpolar

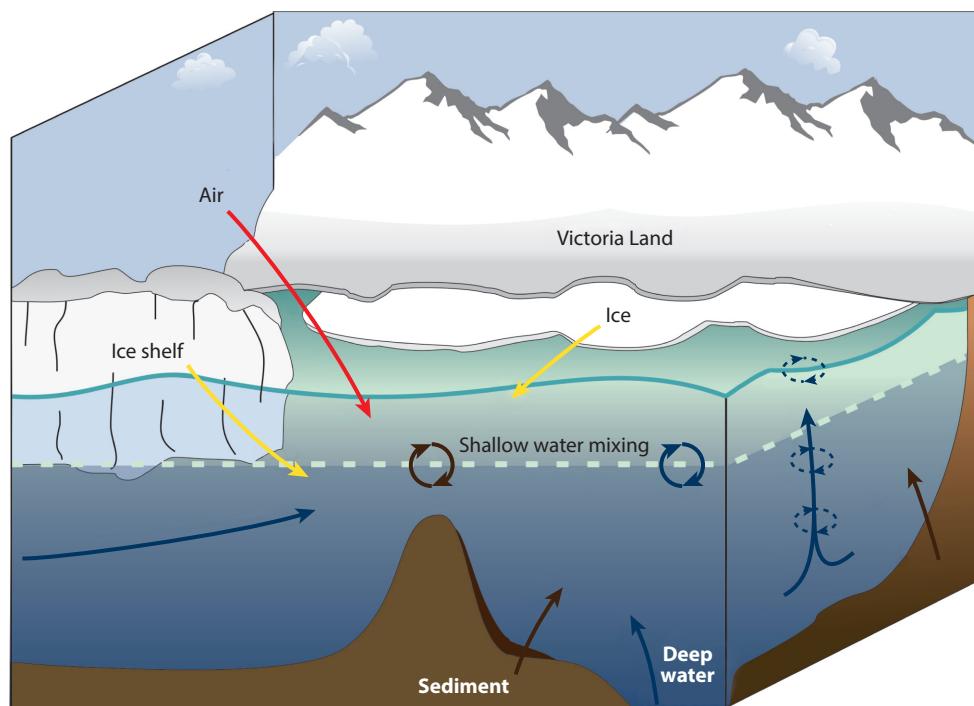


Figure 7

Iron sources in the Ross Sea. Figure reproduced from Smith et al. (2014a).

Deep Water; the contribution from glacial ice is negligible. In a related study that used passive tracers in a high-resolution (5- and 1.5-km horizontal spacing) circulation model implemented for the Ross Sea, Mack et al. (2017) estimated the magnitude and pathways for dissolved iron supply to surface waters. The simulated spatial patterns of tracers showed considerable spatial heterogeneity in the source of dissolved iron supply. The dominant iron source to the surface mixed layer along the outer portion of the shelf and along the western Ross Sea is from sea ice melt. The iron supply to the inner shelf is dominated by the benthic iron source. The overall total dissolved iron supply to the Ross Sea estimated from the simulations from all sources varied from 5.60 to $7.95 \mu\text{mol m}^{-2} \text{y}^{-1}$, with the benthic supply comprising 32–50% of the total. The dependency on sea ice melt as a primary source of dissolved iron makes the iron supply in the Ross Sea vulnerable to changes in sea ice concentration.

Phytoplankton biomass and composition in the Ross Sea are coupled to sea ice distribution, mixed-layer depth, and light availability. Phytoplankton growth in the Ross Sea, which is controlled largely by light availability (Smith et al. 2014a), shows a seasonal cycle (late October to early March) that is characterized by succession in the phytoplankton assemblage (**Figure 8**). The spring bloom, dominated by *Phaeocystis antarctica*, is followed by a secondary bloom dominated by diatoms (see Smith et al. 2014a). Kaufman et al. 2014 characterized the spatial and temporal transition from a *Phaeocystis antarctica*-dominated assemblage to a diatom-dominated assemblage in the Ross Sea using high-resolution autonomous glider data (including temperature, salinity, fluorescence, and optical backscatter) collected during the 2010–2011 austral summer. The changing character of the phytoplankton assemblage has implications for biogeochemical cycling because of the differing elemental ratios and roles in the food web of the two functional types

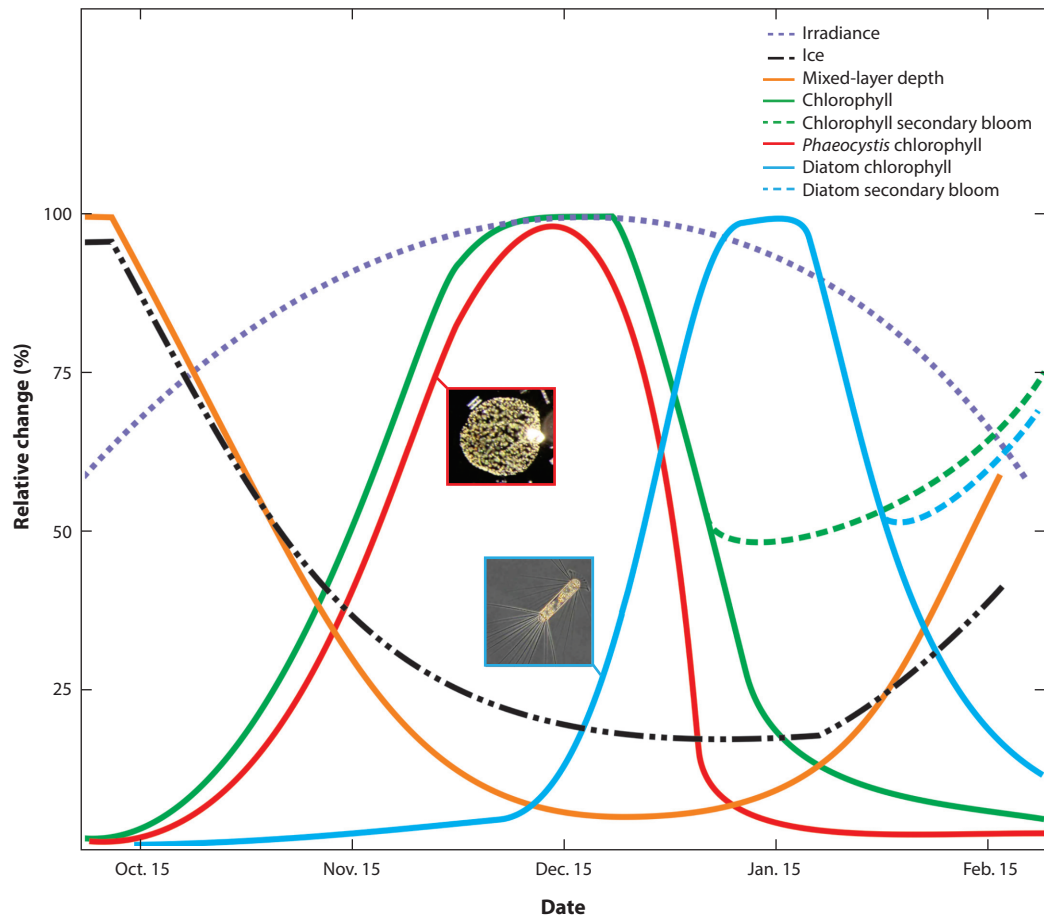


Figure 8

Seasonal progression of phytoplankton in the Ross Sea. Figure reproduced from Smith et al. (2014a).

(Kaufman et al. 2014, Smith et al. 2014a). Much of the primary production in the Ross Sea is exported to depth rather than consumed (Smith et al. 2014a).

Studies of the distribution, physiology, and ecology of meso- and microzooplankton in the Ross Sea are limited but indicate biomasses that are lower than expected relative to the high primary production and limited grazing impact. The three important mid-trophic-level consumers—Antarctic krill, crystal krill (*Euphausia crystallophias*), and Antarctic silverfish (*Pleuragramma antarcticum*) (Pinkerton et al. 2010)—are associated with specific habitats (Davis et al. 2017). The low biomasses of these species have been attributed to a trophic cascade driven by the high abundance of mesopredators and apex predators, many of which feed heavily on krill and/or Antarctic silverfish that in turn feed principally on krill (Ainley et al. 2006). Also, the fidelity of these species for specific habitats (Figure 9) that have limited availability in the Ross Sea has been suggested as a mechanism that limits their distribution (Davis et al. 2017). This habitat specificity makes these species vulnerable to changes in the production and availability of food sources and to changes in sea ice distribution and timing, which are important to their life history. Upper-trophic-level mesopredators are abundant in the Ross Sea (reviewed in Smith et al. 2014a), and the

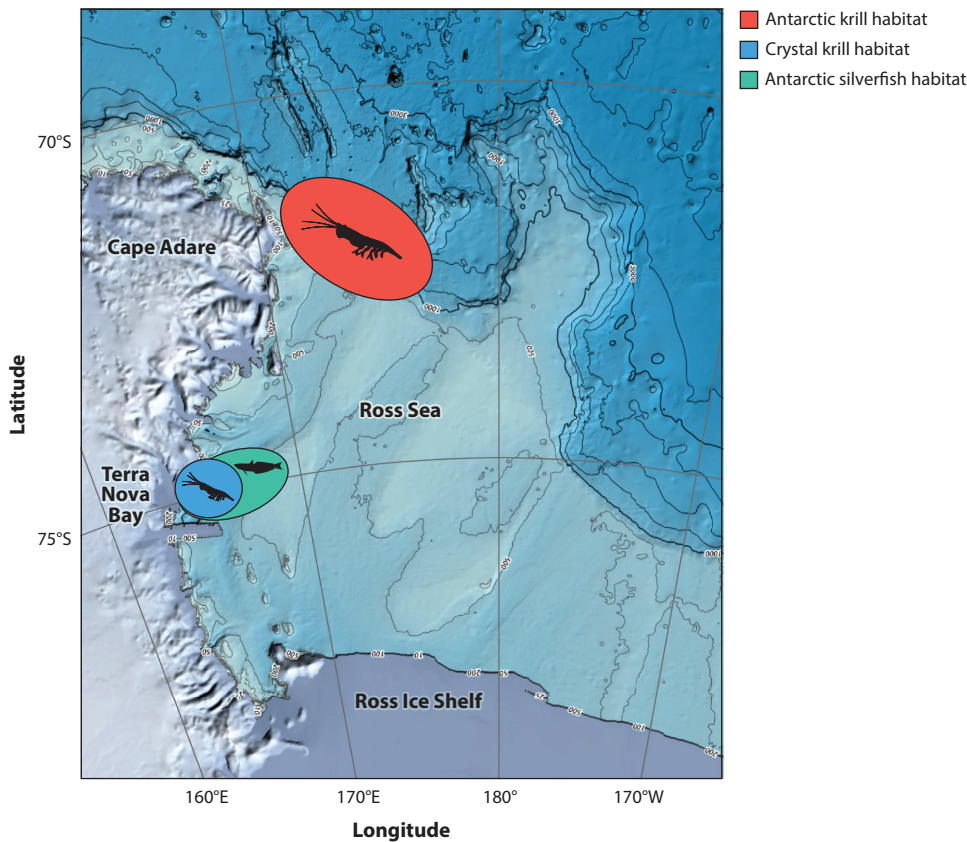


Figure 9

Distribution of primary habitats for Antarctic krill, crystal krill, and Antarctic silverfish in the western Ross Sea. Figure adapted from Davis et al. (2017).

fish fauna are dominated by notothenioids, including the commercially fished Antarctic toothfish (*D. mawsoni*).

The Ross Sea is relatively undisturbed by direct human activity, with the exception of commercial fishing, but warming, freshening, and modified atmospheric forcing are ongoing (reviewed in Smith et al. 2014a). An examination of the effects of projected changes in atmospheric temperatures and winds on the circulation of the Ross Sea using a high-resolution sea ice–ocean–ice shelf model indicated that the summer sea ice concentration will decrease by 56% by 2050 and 78% by 2100 and that the Ross Sea polynya will expand during the summer by 56% by 2050 and 78% by 2100 (Smith et al. 2014b). As a result, the duration of shallow mixed layers over the shelf will increase by 8.5 and 19.2 days by 2050 and 2100, respectively, and the mean summer mixed-layer depths will decrease by 12% and 44%, respectively. An implication of these changes is that annual phytoplankton production will increase by approximately 14% and shift toward assemblages that are dominated by diatoms (Smith et al. 2014b). The growth of some phytoplankton-consuming benthos has already rapidly increased in the region, which is thought to be a direct result of bloom lengthening driven by winds that expands the extent of polynyas (Barnes et al. 2011).

Kaufman et al. (2017) evaluated the effect of climatic changes on phytoplankton assemblage composition, primary production, and export using a one-dimensional biogeochemical model,

which included diatoms and both solitary and colonial forms of *Phaeocystis antarctica*. The model was forced with atmospheric projections for 2050 and 2100 (atmospheric conditions and wind) used in the Smith et al. (2014b) analysis, which was based on the Ross Sea circulation model described by Dinniman et al. (2007, 2011). Simulations using these projections show increases in primary productivity by 5% and 14% by 2050 and 2100, respectively, with a proportional increase in carbon export. In the first half of the twenty-first century, diatom biomass increases while *Phaeocystis antarctica* biomass decreases because of shallower mixed-layer depths, which favor diatom growth. In the second half of the twenty-first century, earlier reduction of sea ice extends the period of low-light conditions that are favorable to *Phaeocystis antarctica* growth. As a result, *Phaeocystis antarctica* biomass increases, and diatom biomass remains relatively constant.

The consequences of these changes include a shift to diatoms, favoring herbivores such as copepods and krill. However, the reduction in sea ice will have negative impacts on ice-associated species, such as crystal krill and Antarctic silverfish, and possibly top predators (e.g., Adélie penguins, crabeater seals, and baleen whales) that depend on these species if no alternative prey are available via prey switching.

4. CLIMATE-CHANGE IMPACTS ON BIODIVERSITY AND ECOSYSTEM SERVICES

4.1. Climate-Change Impacts on Biodiversity

We considered the probability of biologically meaningful change related to 16 environmental variables associated with Southern Ocean marine habitats from the present day to 2100 (for methods for projections of future changes in physical parameters, see the **Supplemental Appendix**). For each parameter, we scored the likelihood of change and magnitude of biological impact (see **Tables 1** and **2**). The implications of change may include, for example, consequences for ecosystem function and service provisioning and could further challenge safeguarding, conservation, and management. Each parameter was debated and scored by a subset of authors with expertise in Southern Ocean composite biodiversity during the 2017 Antarctic Futures workshop (Rogers & Frinault 2017). The indicative probability of change adopted the IPCC's Representative

Table 1 Relationships between the likelihood and agreement scores used in Table 2 and IPCC guidelines (see Mastrandrea et al. 2010)

Probability	IPCC likelihood term	Severity of impact score	Manifestation of impacts at ecosystem/species level	Level of agreement
9	Very likely	7–9	Significant population decrease leading to a threat of extinction under International Union for Conservation of Nature (IUCN) Red List provisions Severe ecosystem modification leading to impacts on ecosystem function and/or ecosystem service provision	High
6–8	Likely	4–6	Significant population decrease, including range contraction Ecosystem modification	Medium
4–5	About as likely as not	1–3	Limited impact, with some effects on species distribution and population dynamics	Low
2–3	Unlikely			
1	Very unlikely			

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Table 2 Assessment of likely impacts of climate change and other human activities on Antarctic marine communities or species

Parameter	Antarctic subregion	Deep benthic		Deep pelagic		Shallow benthic		Shallow pelagic		Coastal (including intertidal)	
		E/RR	NE/NRR	E/RR	NE/NRR	E/RR	NE/NRR	E/RR	NE/NRR	E/RR	NE/NRR
Ocean warming	West	9;3	9;1	9;2	9;1	9;7	9;4	9;5	9;2	9;8	9;7
	East	7;3	7;1	7;2	7;1	7;7	7;4	7;5	7;2	7;8	7;7
Freshening	West	1;1	1;1	1;1	1;1	1;1	1;1	9;7	9;7	9;6	9;6
	East	1;1	1;1	1;1	1;1	1;1	1;1	1;1	1;1	1;1	1;1
Sea ice decline	West	8;4	8;3	8;3	8;2	8;7	8;6	8;8	8;7	8;8	8;7
	East	8;4	8;3	8;3	8;2	8;7	8;6	8;8	8;7	8;8	8;7
Ice shelf disintegration	West	NA	NA	NA	NA	7;3	7;3	7;3	7;3	7;2	7;2
	East	NA	NA	NA	NA	7;7	7;7	7;7	7;7	7;6	7;6
Sedimentation	West	2;2	2;2	2;1	2;1	2;3	2;3	2;3	2;3	8;9	8;9
	East	2;2	2;2	2;1	2;1	2;3	2;3	2;3	2;3	2;3	2;3
Sea level rise	West	9;1	9;1	9;1	9;1	9;1	9;1	9;1	9;1	9;1	9;1
	East	9;1	9;1	9;1	9;1	9;1	9;1	9;1	9;1	9;1	9;1
Ocean acidification	West	6;1	6;1	6;1	6;1	8;2	8;2	8;3	8;3	8;2	8;2
	East	6;1	6;1	6;1	6;1	8;2	8;2	8;3	8;3	8;2	8;2
Wind (driven by ozone losses)	West	5;4	5;3	5;3	5;2	7;7	7;5	7;5	7;4	7;8	7;6
	East	5;4	5;3	5;3	5;2	7;5	7;4	7;5	7;4	7;6	7;4
Ocean circulation	West	1;2	1;1	1;2	1;1	4;7	4;6	4;7	4;6	6;6	6;7
	East	1;2	1;1	1;2	1;1	4;7	4;6	4;7	4;6	6;6	6;7
Ultraviolet radiation decrease	West	NA	NA	NA	NA	NA	NA	6;1	6;1	6;1	6;1
	East	NA	NA	NA	NA	NA	NA	4;1	4;1	4;1	4;1
Oxygen	West	4;5	4;5	4;6	4;6	4;5	4;5	4;6	4;6	4;6	4;6
	East	4;5	4;5	4;6	4;6	4;5	4;5	4;6	4;6	4;6	4;6
Nutrient increase (e.g., iron)	West	3;7	3;7	3;8	3;8	3;7	3;7	3;8	3;8	3;8	3;8
	East	4;7	4;7	4;8	4;8	4;7	4;7	4;8	4;8	4;8	4;8
Primary production	West	3;7	3;7	3;8	3;8	3;7	3;7	3;8	3;8	3;8	3;8
	East	3;7	3;7	3;8	3;8	3;7	3;7	3;8	3;8	3;8	3;8
Fisheries	West	7;8	7;8	3;8	3;6	3;8	3;6	8;7	8;7	3;8	3;6
	East	7;8	7;8	3;8	3;6	3;8	3;6	7;7	7;7	3;8	3;6
Pollution	West	8;4	8;4	8;2	8;2	8;4	8;4	8;3	8;3	8;5	8;5
	East	8;4	8;4	8;2	8;2	8;4	8;4	8;3	8;3	8;5	8;5
Nonnative species introduction	West	1;1	1;1	1;1	1;1	5;8	5;8	7;8	7;8	8;9	8;9
	East	1;1	1;1	1;1	1;1	4;8	4;8	6;8	6;8	6;9	6;9

Changing environmental factors or impacts are listed in the far-left column (rows), and different biological communities are listed along the top (columns). In each cell, the first value indicates the likelihood that the environmental factor or impact will change, the second value indicates the severity of the impact on the community, and the color indicates the level of agreement, as detailed in **Table 1**. Abbreviations: E/RR, endemic/range-restricted species; NE/NRR, nonendemic/non-range-restricted species; NA, not applicable.

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Concentration Pathway 8.5 scenario—the pathway with the highest greenhouse gas emissions rising unabated through the twenty-first century (IPCC 2013).

The variables considered include climate-driven physical changes such as ocean warming, freshening, and acidification (**Supplemental Figures 1–20**) and those more directly related to human activity, including fishing, pollution, and nonnative species introduction. While some variables are interconnected or secondary products of others, and some may interact, for the purposes of the current assessment each was evaluated as a separate entity (see **Table 2**). To account for regional differences, we considered variables for two subregions: West Antarctica, including the Amundsen and Bellingshausen Seas and the Scotia Arc, and East Antarctica, including the Ross and Weddell Seas (**Figure 1**). To account for the differential susceptibility of communities from different habitats to environmental forcing (Sweetman et al. 2017), we considered changes in variables and impact across five habitat types: deep benthic, deep pelagic, shallow benthic, shallow pelagic, and coastal (including intertidal); shallow habitats were defined as depths of less than 1,000 m, and deep habitats were defined as depths of 1,000 m or more (IPCC 2013). Likewise, we also accounted for species range, as this can contribute to vulnerability to impacts as a result of overall population size and connectivity (i.e., endemic/range-restricted populations versus nonendemic/non-range-restricted populations; Young et al. 2018), the caveat being that range is poorly characterized for many Antarctic species.

The indicative probabilities of parameter change and scoring of impact were assigned values by consensus using the range of 0–10 (lowest to highest; no scores 0 or 10 were actually given). Values for probability of change are equated to the IPCC Fifth Framework guidance for assignment of uncertainty (Mastrandrea et al. 2010), and the severity of impact was assigned on a scale from limited impacts to those posing a significant extinction risk or risk of severe and negative ecosystem change (see **Table 1**). Levels of agreement were also assigned according to Fifth Framework guidance (see **Table 1**). The resulting values for each parameter are provided in **Table 2** in an *a*:*b* format, where *a* corresponds to the probability of (anthropogenically driven) change and *b* corresponds to the predicted degree of impact (see **Table 1**). Justification for these values is presented in the **Supplemental Appendix**.

Expert opinion suggested differences in the probability of changes in West and East Antarctica, most notably in ocean warming, freshening, UV radiation exposure, fisheries, and nonnative species introduction. These different probabilities reflect regional differences in physical variables, climate-change effects, ecosystem structure, and exposure to direct human activities. Another feature of the analysis was the much higher vulnerability of endemic/range-restricted species to the impacts of changes in the physical environment arising from climate change or direct human activities such as fishing. While regional endemism is relatively unusual in the Southern Ocean (Hogg et al. 2011), especially in deep-water and pelagic ecosystems, some regions have a high occurrence of endemic species, particularly sub-Antarctic islands such as South Georgia and Kerguelen (Hogg et al. 2011, Rogers et al. 2015, Griffiths et al. 2017). The analysis also highlighted a much higher perceived vulnerability of shallow-water and coastal ecosystems to impacts of climate change.

4.2. Southern Ocean Marine Ecosystem Goods and Services to 2100

The Millennium Ecosystem Assessment describes ecosystem goods and services (together referred to as just “services”) as “the benefits people obtain from ecosystems” (Millenn. Ecosyst. Assess. 2005, p. v); these services both tangibly and intangibly reflect nature’s contributions to humanity (Pascual et al. 2017). This assessment classifies services into four areas: (*a*) provisioning, (*b*) cultural, and (*c*) regulating services (all of which have direct effects on humanity), along with (*d*) supporting

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Table 3 Anticipated variation in Southern Ocean ecosystem functioning of goods and services by 2100

Ecosystem service	Anticipated variation
Provisioning	
Food and subsistence supply	↑
Marine genetic resources and biomedicinals	↑↑
Abiotic (oil/gas/minerals)	↑↑
Energy (renewables)	↑
Cultural	
Science, tourism, and education	↑↑
Regulating	↑
Carbon sink	↑
Air regulation	↑
Climate/weather regulation	↑
Nutrient cycling	?
Supporting	
Habitat provision	↕
Nutrient cycling	?

Key: ↑↑, strong increase; ↑, increase; ↕, increases in some areas but decreases in others; ?, not predicted.

services (which are essential for the production of the first three types of services and indirectly affect humankind) (Millenn. Ecosyst. Assess. 2005). Broadly, provisioning services comprise, for example, fisheries, mineral, and genetic resources; cultural services are associated with aesthetic, spiritual, and inspirational qualities and include objective educational, recreational, and tourism sectors; regulating service contributions can include climate and environment management and control by the carbon cycle, chemical sequestration and release, and atmospheric and oceanic circulation; and supporting ecosystem services may include the production of, for example, oxygen, biomass, nutrient cycling (also a regulating service), and further habitat provisioning in regions beyond the Southern Ocean. These areas can also overlap (see Millenn. Ecosyst. Assess. 2005, Grant et al. 2013).

We scored Southern Ocean marine ecosystem services for comparative 2100 yields versus contemporary offerings. Anticipated service variations are presented in **Table 3** as preliminary guidance only, and evaluation of monetary values of services is not included.

As stressed by Keys (1999), the Antarctic wilderness is being increasingly opened up to human access through infrastructure such as research stations, tourism, and fisheries activity. However, increased human interaction with an ecosystem may adversely impact continued yields of its services. Given that technological advancements can enable human presence in Southern Ocean regions, access could be further facilitated if climate change were to reduce ice coverage, making some areas newly accessible and extending seasonal access in others. Increases in ecosystem service provisioning to 2100 were anticipated for direct services (**Table 3**), while indirect supporting services were more contentious.

Provisioning of food resources exported from the Southern Ocean marine ecosystem is predicted to increase as resources become easier to access and primary production rises (Peck et al. 2010). This will be driven by projected increases in the global human population and resulting demand for animal-derived protein (e.g., Béné et al. 2015). This prediction assumes that resources and stocks are managed sustainably, given that stock depletion is a risk (Cheung 2018). Sea ice retreat and changes in other physical variables may decrease the productivity of Antarctic

species, challenging fishery expansion and management (e.g., Cheung et al. 2008 for Antarctic toothfish). Species sensitivity, tolerance thresholds, and/or adaptation to climate-change-driven environmental shifts are likely to shift food webs (as discussed above for the WAP and Ross Sea; see also Constable et al. 2014). Climate-induced changes may result in the arrival and semiresidency of nonnative, mobile, temperate species through poleward extension of their distribution ranges (Clarke et al. 2005, Barnes et al. 2006, Cheung 2018). However, the likelihood of successful establishment of such species is uncertain (McBride et al. 2014). Taking these factors into consideration, we do not anticipate that the proposed increase in food and sustenance supply will be strong.

We note that there are potentially untapped fisheries resources in the Southern Ocean, including the ridge-scaled grenadier (*Macrourus carinatus*) (Laptikhovsky 2010) and mesopelagic lanternfish (myctophids), the latter of which have not been commercially important since 1989–1991 (CCAMLR 2013). The biomass of mesopelagic fish may be larger than previously recognized (e.g., St. John et al. 2016, Inst. Mar. Res. 2017), and fishing of this resource may increase in the future. Furthermore, as Southern Ocean regions become more accessible and the global human population increases (along with, by extension, its food demand), rogue activity by illegal, unreported, and unregulated fishing may increasingly affect supplies and populations, which could additionally imply changes to ecosystems, communities, and resource security (Teschke et al. 2016).

We envisage comparatively strong growth of genetic and natural product resources to 2100 (Table 3). The predicted growth is based on the Southern Ocean ecosystem being considered a source of unique genetic diversity and host to many endemic species, supporting continued exploration and bioprospecting (e.g., Rogers 2012). As an example, the Southern Ocean marine ecosystem is a known resource of antibacterials (Casillo et al. 2017) and host to marine sponges with bioactives that have promise in oncology applications (Olsen et al. 2016).

Regarding provisioning of abiotic resources, including renewable energy, hydrocarbons, and minerals, the exploitation of geographical areas falling under the Antarctic Treaty System is not permitted. However, with the Antarctic Treaty System up for review in 2048, some of its restrictions may be challenged (Teschke et al. 2016, Liggett et al. 2017). Thereafter, exploitation of hydrocarbon and mineral resources can take place only if a binding legal regime for management of such activities has been adopted by three-quarters of the Antarctic Treaty Consultative Parties. Several countries have expressed an interest in exploiting abiotic resources in the Antarctic waters and continent (e.g., China and Russia; Rogers et al. 2015). Given the extreme conditions of the Southern Ocean and the distances to coastal states with refining capacity, pursuing oil and gas reserves may be economically unattractive (Rogers et al. 2015). Similarly, the availability of new forms of hydrocarbon reserves (such as shale gas) in the short term and moves to decarbonize the global economy in the longer term also make prospecting in the region less likely.

Seabed mineral resources present in areas beyond national jurisdiction (ABNJs) are currently governed by the United Nations International Seabed Authority (ISA 2018). However, multilateral agreement regarding the ABNJ designation within the Southern Ocean remains contentious and is governed under the Antarctic Treaty System (Johnson 2017). Extreme weather in this area, and perhaps distances to land-based refineries or ore processing facilities, may make marine mining for minerals in the region economically unattractive at least in the near to medium term (Rogers et al. 2015).

The use of wind energy by research stations is providing a precedent for further utilization of ecosystem provisioning services in the Southern Ocean ecosystem (Llano & McMahan 2018). However, we point out that wind turbines can be dangerous for birds, and so the use of solar energy

is increasing in coastal locations where bird mortality can be a problem. Future developments in energy capture, storage, and exportation may also emerge (Wong et al. 2012).

Cultural ecosystem services are expected to strongly increase to 2100. This expectation is supported by upward trends in scientific and educational interest, adventure tourism, and ecotourism (O'Connor et al. 2009, Griffiths 2010, Liggett et al. 2017). Tourism, for example, has seen an increase from approximately 10,000 visitors per season in the early 2000s to more than 45,000 in 2016–2017 (IAATO 2017). This tourism takes place mainly on cruise ships and through onboard educational expeditions, but the idea of hosting tourists within a more permanent regional infrastructure has also been broached (Liggett et al. 2011). Aside from the wilderness, the ecosystem's main attraction is its charismatic species such as penguins, seals, and whales, and cruise routes are often determined by the locations of these populations (Bender et al. 2016, Deininger et al. 2016). Adventure-tourism activities are extending further using, for example, submersible technologies (Liggett et al. 2017). The anticipated growth in tourism is also supported by the increased accessibility of the area. For example, in the WAP region, climate change has led to declines in glaciers and reductions in the extent and duration of sea ice (Cook et al. 2005, Montes-Hugo et al. 2009, Stammerjohn et al. 2012, Turner et al. 2014), facilitating tourism and extending the tourism season (Stewart et al. 2017). If this tourism is not effectively managed, however, it may lead to levels of environmental degradation, potentially affecting reproduction and displacing wildlife populations (Bargagli 2008, Dunn et al. 2019).

Regulating services of the Southern Ocean marine ecosystem are anticipated to increase (Table 3). As outlined in Section 2.2, stronger westerlies have driven higher CO₂ uptake by the solubility pump. Modeling has also suggested higher uptake of CO₂, associated with the increasing Revelle factor and surface undersaturation of CO₂ driven by biological production (Section 2.2). Biological carbon storage and sequestration are predicted to further influence atmospheric and climate conditions through algae and nutrients discharged by climate-induced increases in meltwater, prolonged phytoplankton blooms, and strengthening of water column stratification, resulting in enriched photosynthetic proficiency and overall increased regional primary productivity (Arrigo et al. 2008, Peck et al. 2010, Deininger et al. 2016, Barnes 2017, Deppeler & Davidson 2017, Barnes et al. 2018). Such potential increases in biological CO₂ capture support the region's continued contributions to climate and weather regulation (see Sabine et al. 2004, Le Quéré et al. 2007, Peck et al. 2010). However, the dependency of primary production on light and iron concentrations may hinder efficiencies (Boyd et al. 1999, Park et al. 2017).

Phytoplankton is fundamental to the Southern Ocean carbon pump (Deppeler & Davidson 2017; see Section 3.3.1), and Antarctic krill is a key species in the Southern Ocean pelagic food web, providing a pivotal link between phytoplankton and higher trophic levels—factors that may be sensitive to a changing climate (Flores et al. 2012, Murphy et al. 2016, Belcher et al. 2017). While pelagic consumers dominate the conversion of carbon capture to storage, benthic consumers have a key role in the conversion of biologically stored carbon (termed blue carbon) to genuine sequestration through burial (Barnes et al. 2018). Indeed, there is evidence that over the past 25 years benthic blue carbon has doubled around West Antarctic seas, driven by sea ice losses, thereby working as a negative feedback on climate (Barnes 2015).

Influencing the regulation of abyssal ocean cooling and ocean ventilation is a further critical service of the Southern Ocean marine ecosystem; for example, the Weddell Sea is a significant source of the Antarctic Bottom Water that pushes the global ocean circulation (Orsi et al. 1999, Deininger et al. 2016). However, these services are expected to be negatively affected by global warming, with a potential reduction in deep-ocean ventilation (Orsi et al. 1999, Rintoul et al. 2001, Snow et al. 2018) that has unknown consequences for deep-sea ecosystems. Regulating services from the storing of water in ice sheets, ice shelves, and sea ice influence sea level and/or the Earth's



albedo (Turner et al. 2009, Grant et al. 2013). Predicted ice loss in Antarctica resulting from global warming is expected to cause sea level rise (DeConto & Pollard 2016), with the West Antarctic ice sheet, for example, predicted to contribute to 7% or more of the total projected sea level upsurge between now and 2100 (a rise of approximately ≤ 1.4 m) (Turner et al. 2009).

It is challenging to judge how nutrient cycling services may change (Deppeler & Davidson 2017). They may potentially increase because of prolonged phytoplankton blooms (Barnes 2017). However, nutrient circulation to oceanic regions beyond the Southern Ocean may be reduced compared with the magnitude of present exports, potentially leading to habitat deprivation, possibly followed by decreased biomass and fishery yields in additional regions (Moore et al. 2018).

In conclusion, climate-change influence on the Southern Ocean ecosystem may increase the supply of some ecosystem services and enable further human exploitation by 2100. However, climate change may not necessarily be beneficial to contemporary Southern Ocean species, its marine ecosystem, or directly or indirectly dependent regions and their environmental well-being.

5. CONCLUSIONS

The Southern Ocean and coastal Antarctica are undergoing major changes in physical conditions as a result of anthropogenically driven climate change. These changes differ regionally and with latitude. On a regional basis, significant changes in ecosystem structure have been observed and are generated from changes in primary producers and consumer populations that are propagating through the food web. Direct impacts of climate change on predator populations (e.g., cetaceans and some penguins) are being detected and are resulting from changes in the presence of fast ice and sea ice, although the patterns vary among regions and even subregionally. They are also manifesting in changes to benthic coastal communities as a result of ice shelf disintegration and glacial retreat, although these phenomena are less well studied and their implications poorly understood.

Given the expert assessment undertaken here (**Table 2**), it seems likely that range-restricted species are most vulnerable to decline, or even extinction, with potential replacement by non-native species from lower latitudes. These changes are anticipated to continue or accelerate as climate change drives further changes in physical variables, such as sea surface temperature and sea ice duration and extent. Projections for the future generally point toward a southward retreat or expansion of elements of the biota, including important ecosystem components such as Antarctic krill and salps, and/or habitat loss. Such changes in the Southern Ocean may occur at a time when, as a result of an increasing global human population, ecosystem service provisioning becomes more important. In particular, enhanced carbon sequestration and fisheries resources from increasing populations of native species, invasive species, or newly identified resources (such as myctophids) are possible in the short to medium term. Greater access to parts of the Southern Ocean as a result of reduced ice shelf and sea ice area and (in the latter case) duration suggests that direct human impacts on the region are likely to increase (see **Table 2**). The Antarctic therefore represents a challenging management scenario where rising pressure to exploit potentially increased availability of resources is combined with climate impacts that in turn may accelerate loss of the endemic biodiversity of the Southern Ocean.

This challenge is recognized by the Convention for the Conservation of Antarctic Marine Living Resources, which considers both conservation and fisheries management in an ecosystem-based management framework. Including a wider understanding of the links between biodiversity and ecosystem service provision will be crucial for developing conservation and management strategies that include future climate impacts.

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FUTURE ISSUES

1. There is an urgent need to expand the spatial and temporal resolution of oceanographic and biological measurements across the Southern Ocean. The Southern Ocean Observing System (<http://www.soos.aq>) is intended to make sustained observations of essential ocean variables around the Antarctic (Rintoul et al. 2012), but biological measurements are much more difficult to obtain (Constable et al. 2016). The scope of monitoring programs for Antarctic predators and mesopredators must also be expanded spatially and temporally and should include a wider range of species (e.g., smaller petrels) to assess the effects of environmental change together with other human impacts on these species.
2. Patterns of species distribution in Antarctic marine ecosystems, including basic information such as population size, connectivity, and species range, are particularly poorly understood, and baseline data are needed to enable monitoring of biodiversity loss or changes in Antarctic marine communities as a result of climate change and other human activities.
3. End-to-end or linked models that operate across the different levels of ecosystems and are linked to management strategies are a priority for the Southern Ocean.
4. The threat to Southern Ocean biodiversity posed by climate change is serious, especially for sub-Antarctic regions and/or for range-restricted species, and specific management measures are needed to protect vulnerable communities of organisms, especially where direct human impacts from, e.g., fishing or tourism may interact with climate change to damage ecosystems, habitats, and species.
5. The fact that ecosystem service provisioning (e.g., carbon sequestration, fisheries, and tourism) may actually increase in the Southern Ocean as a result of climate change against a background of loss of endemic biodiversity is particularly challenging from a management perspective. Such a scenario may break the link between ecosystem service provisioning and endemic species richness, meaning that biodiversity must be specifically managed in the Antarctic.
6. Given the vulnerability of some communities to environmental change and human impacts identified here, and in the absence of important data on species distribution and resilience, there is an urgent need to accelerate progress toward a circum-Antarctic network of marine protected areas covering all bioregions in the Southern Ocean (e.g., Douglass et al. 2014).
7. Protecting biodiversity is likely to require the development of new and innovative concepts in environmental management, such as assisted migration (e.g., of sub-Antarctic species from isolated islands to locations farther south), or economic or other mechanisms that explicitly recognize and encompass the value of biodiversity in and of itself as well as in relation to ecosystem service provisioning.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.



AUTHOR CONTRIBUTIONS

A.D.R. conceived of the original workshop at Somerville College, University of Oxford (Rogers & Frinault 2017), the results of which formed the basis of this article. All authors contributed to specific aspects of the article: A.D.R., Section 1, biodiversity analysis, and overall planning and writing; B.A.V.F., Section 1, ecosystem service provisioning, and overall planning and writing; D.K.A.B., biodiversity analysis and ecosystem service provisioning; N.L.B., physical oceanography; R.D., marine predators and management implications; H.W.D., Western Antarctic Peninsula and modeling; A.S.F., marine predators; T.H., marine predators; S.L.H., krill and salp dynamics and management implications; E.E.H., Ross Sea and modeling; K.L., biodiversity analysis; C.R.M., marine predators; E.J.M., krill and salp dynamics, management implications, and modeling; E.A.P., krill and salp dynamics; G.R., modeling of changes of physical parameters and biodiversity analysis; I.J.S., marine predators; D.A.W.-G., biogeochemistry; and R.W., biogeochemistry and modeling. All authors reviewed and revised the manuscript through various drafts.

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