

RESEARCH REVIEW

Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota

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Abstract

Antarctic and Southern Ocean (ASO) marine ecosystems have been changing for at least the last 30 years, including in response to increasing ocean temperatures and changes in the extent and seasonality of sea ice; the magnitude and direction of these changes differ between regions around Antarctica that could see populations of the same species changing differently in different regions. This article reviews current and expected changes in ASO physical habitats in response to climate change. It then reviews how these changes may impact the autecology of marine biota of this polar region: microbes, zooplankton, salps, Antarctic krill, fish, cephalopods, marine mammals, seabirds, and benthos. The general prognosis for ASO marine habitats is for an overall warming and freshening, strengthening of westerly winds, with a potential pole-ward movement of those winds and the frontal systems, and an increase in ocean eddy activity. Many habitat parameters will have regionally specific changes, particularly relating to sea ice characteristics and seasonal dynamics. Lower trophic levels are expected to move south as the ocean conditions in which they are currently found move pole-ward. For Antarctic krill and finfish, the latitudinal breadth of their range will depend on their tolerance of warming oceans and changes to productivity. Ocean acidification is a concern not only for calcifying organisms but also for crustaceans such as Antarctic krill; it is also likely to be the most important change in benthic habitats over the coming century. For marine mammals and birds, the expected changes primarily relate to

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their flexibility in moving to alternative locations for food and the energetic cost of longer or more complex foraging trips for those that are bound to breeding colonies. Few species are sufficiently well studied to make comprehensive species-specific vulnerability assessments possible. Priorities for future work are discussed.

Keywords: Antarctica, benthos, climate change, krill, marine ecosystems, marine mammals, ocean acidification, penguins, plankton, sea ice

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Introduction

Antarctic and Southern Ocean marine ecosystems have been changing for at least the last 30 years (Turner *et al.*, 2009a, 2013). The most obvious physical changes to date include increasing ocean temperatures, poleward shift of ocean fronts and regionally contrasting changes in the extent and seasonality of sea ice (Böning *et al.*, 2008; Bracegirdle *et al.*, 2008; Sokolov & Rintoul, 2009; Turner *et al.*, 2009a, 2013; Stammerjohn *et al.*, 2012). These changes have had, and will continue to have profound implications for marine ecosystems around Antarctica and in the Southern Ocean, although the effects may be regionally specific (Smetacek & Nicol, 2005; Boyd *et al.*, 2008; Nicol *et al.*, 2008; Massom & Stammerjohn, 2010). We, hereafter, refer to these marine ecosystems collectively using the acronym ASO to connote the combined marine areas of the circumpolar Antarctic continental shelf and the Southern Ocean.

The Southern Ocean, defined here as waters south of the Subtropical Front, is of major importance in the Earth System (Turner *et al.*, 2009a). The ecosystem dynamics of the region are dominated by the Antarctic Circumpolar Current (ACC) and its frontal systems, polar seasonality, and the annual advance and retreat of sea ice (Constable *et al.*, 2003; Grant *et al.*, 2006; Constable & Doust, 2009; Massom & Stammerjohn, 2010). The Southern Ocean is characterized as a High Nutrient, Low Chlorophyll (HNLC) system because of the limitation of phytoplankton growth by micronutrients across much of the open ocean (Strzepek *et al.*, 2011; Boyd *et al.*, 2012). The highest primary production occurs in conjunction with shallow waters, linked to the supply of iron (Smetacek & Nicol, 2005).

Reviews have previously been undertaken on the structure, function and change of the Southern Ocean ecosystem at sector and regional scales (Ducklow *et al.*, 2012a; Murphy *et al.*, 2012a,b, 2013; Nicol & Raymond, 2012; Smith *et al.*, 2012); we endeavour to uniformly apply terminology on different spatial scales where 'sector' is defined in the text and corresponds approximately to an ocean basin (Atlantic, Indian, West Pacific, East Pacific), 'region' applies to a scale akin to, for example, the Weddell and Ross Seas, west Antarctic Peninsula, East Antarctica, Kerguelen Plateau; and 'area' is more of a local scale such as an ice shelf or

island. Some circumpolar syntheses of the ecology of particular habitat types and the consequences of change are also available (e.g. sea-ice habitats – Massom & Stammerjohn, 2010; general – Turner *et al.*, 2009a). In addition, a comprehensive assessment of the biogeography of ASO biota is currently underway (De Broyer & Koubbi, 2014) but will not include assessments of climate change impacts. A clear gap in these reviews is a close examination of how specific changes in physical habitats may impact directly on the ecology of species at different trophic levels (Fig. 1), thereby giving rise to indirect impacts on one or both of bottom-up (production) and/or top-down (predation) forcings in the ecosystem (Fig. 2). Here, we update this body of literature to (i) summarize the changes in marine habitats due to climate change; (ii) consider the general mechanisms of how taxa may be directly impacted by these changes; and (iii) compare and contrast the ecosystem changes in the different sectors of the ASO as a result of those impacts on biota i.e. the ecosystem impacts of climate variability and change. Importantly, this synthesis will provide a comparative framework for assessing the likelihood of future climate change impacts.

This synthesis is comprised of two papers. This article undertakes the first two parts of the assessment – habitats and direct effects on biota. The latter is based on the known regional changes the biota have experienced and knowledge of the drivers of those changes. In the second (companion) article, we examine more closely the observed and expected responses of ecosystems to climate change in the different ASO sectors and consider how these systems may respond in future, particularly with respect to their resilience and the potential for alternative stable regimes to arise.

Insufficient data are currently available to make comprehensive species-specific vulnerability assessments (including the concepts of *exposure*, *sensitivity*, *potential for impact*, and *adaptive capacity*) similar to that of Daw *et al.* (2009) for commercially harvested species and of Hollowed *et al.* (2013) for Arctic species. Nevertheless, there is sufficient knowledge to identify key interactions for many of the groups. Firstly, we describe the general attributes of the pelagic and benthic habitats of the Southern Ocean and how they have changed in recent decades – the *exposure* component of a vulnerability assessment. We then synthesize knowledge of, and

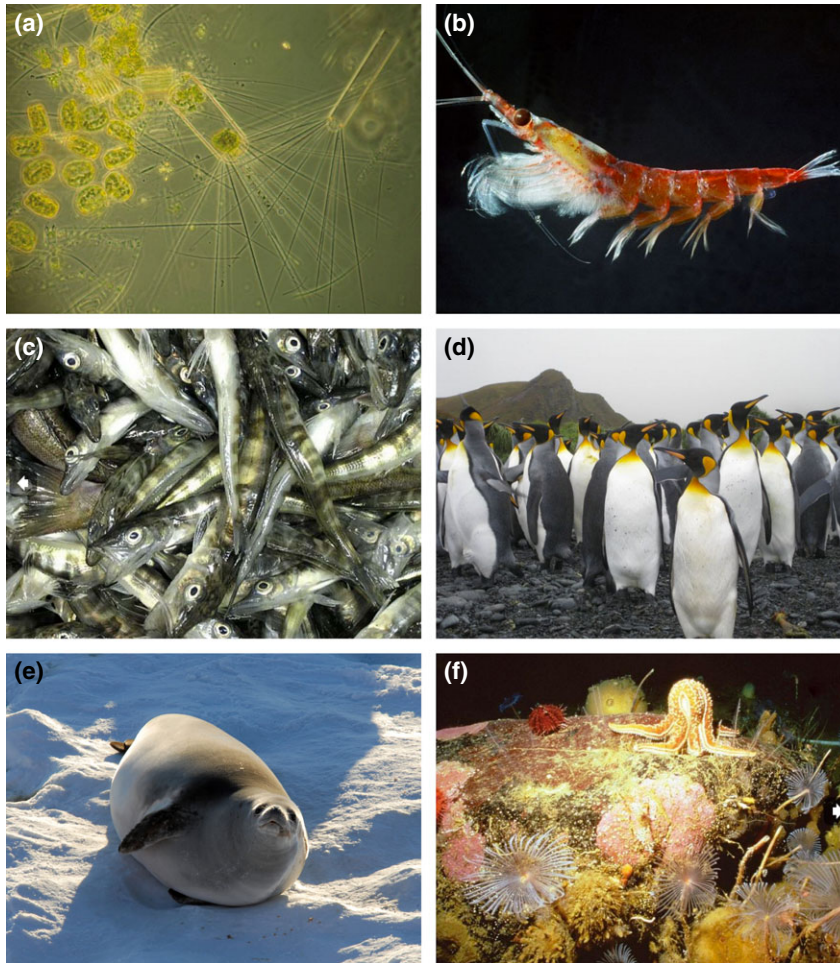


Fig. 1 A broad range of Antarctic marine taxa are responding to climate change impacts in Southern Ocean habitats, for example: (a) phytoplankton communities (photo: ACE CRC), (b) Antarctic krill (photo: S. Brookes), (c) mackerel icefish (photo: AFMA), (d) king penguins (photo: Clint D), (e) crabeater seals (photo: D. Costa), and (f) benthic species (photo: A. Tabor).

provide some current views on, the role of changing habitats in driving changes in the following groups – microbes, zooplankton and salps, Antarctic krill (*Euphausia superba*), fish and cephalopods, marine mammals and seabirds, and benthos. This article concludes by summarizing the primary changes expected for different biota and the gaps needing to be filled to describe more fully the autecological response of ASO biota to climate change impacts.

Exposure: observed and predicted change in physical habitats

Habitats in the Southern Ocean are structured by oceanic and topographic features. From south to north, the Antarctic continental shelf, the seasonally variable sea-ice zone (comprising both stationary fast ice and moving pack ice) and oceanic fronts approximately delimit

zonal biogeographic regions with distinct physical, chemical, and biological characteristics (Fig. 3). The major circulation features of the Southern Ocean are strongly steered by bathymetry, and the large Ross and Weddell gyres tend to isolate much of the Antarctic coastal region from the relatively warm waters of the ACC. Zonal homogeneity is broken by features such as these gyres, the Antarctic Peninsula, the Scotia Arc in the southwest Atlantic, the Kerguelen Plateau in the Indian sector, and the Macquarie Ridge and seamounts to the northwest of the Ross Sea in the western Pacific sector (Grant *et al.*, 2006; Kaiser *et al.*, 2009). These topographic features create four natural sectors of the Southern Ocean – the Atlantic, Indian, West Pacific and East Pacific sectors (Fig. 3).

The highly seasonal and variable physical properties are major drivers of the dynamics of Southern Ocean ecosystems: winter reductions in irradiance

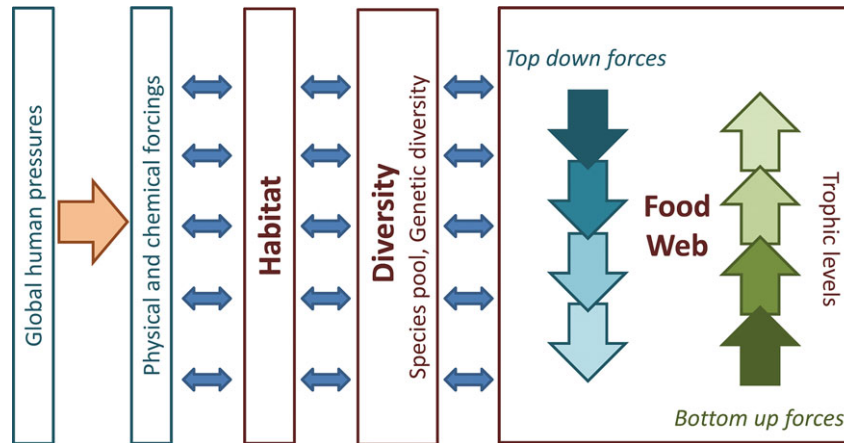


Fig. 2 Schematic illustrating how changes in the physical environment affect habitats, species diversity, and then food webs. The large horizontal arrow shows the effects of global human pressures in the system. The food web can be considered as a number of trophic levels, which may be impacted by bottom-up and/or top-down forces in the food web. Small double-headed horizontal arrows indicate the connections between components, including potential feedbacks. The number of those horizontal arrows indicates that changes in habitats, diversity, and food webs may occur at any trophic level, potentially giving rise to both bottom-up and top-down effects.

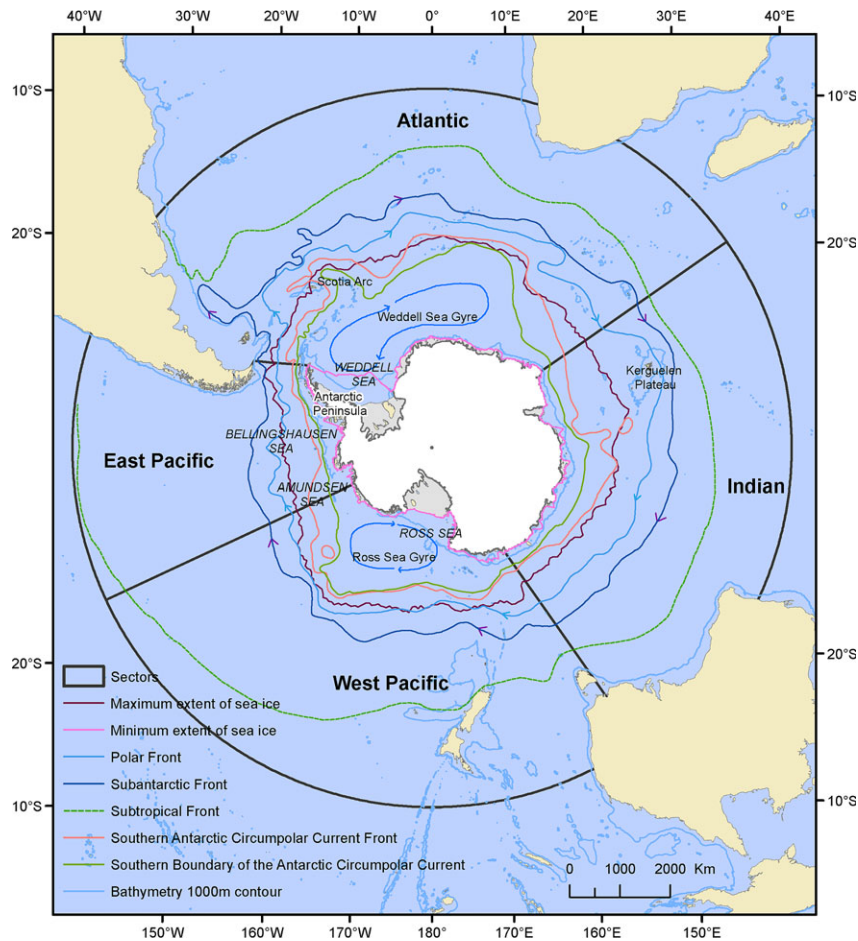


Fig. 3 Major physical features of the Southern Ocean, including key locations referred to in the text, major sectors differentiating the ecosystems, minimum and maximum extent of sea ice, the Subtropical, Subantarctic and Polar Fronts, Southern Boundary of the Antarctic Circumpolar Current, and the 1000 m countour. (Color in the online version)

and water temperature, and winter increases in mixed layer depth, nutrients, and sea-ice extent (Figs 4 and 5). These habitat variables combine, for example, to control the availability of light and nutrients for primary producers and to influence access to food and breeding habitat for species dependent on sea ice. The magnitude and interaction of these seasonal factors varies between different regions of the Southern Ocean, giving rise to substantial regional variation in the distribution of habitats (Grant *et al.*, 2006) (Fig. 6).

The El Niño/Southern Oscillation (ENSO) is one of the dominant modes of climate variability that influ-

ences the ASO on subdecadal time scales and is triggered from the tropics (Kwok & Comiso, 2002). The Southern Annular Mode (SAM) is the dominant mode of extratropical variability in the Southern Hemisphere (sen Gupta *et al.*, 2012). It operates on timescales from weeks to decades, including interannual periods, and is particularly pronounced in the magnitude and position of the zonal winds. On decadal to multidecadal timescales, significant modes of variability include the Pacific Decadal Oscillation and the Atlantic Multi-decadal Oscillation (sen Gupta *et al.*, 2012) which may, in turn, cause variability in physical habitats in the ASO.

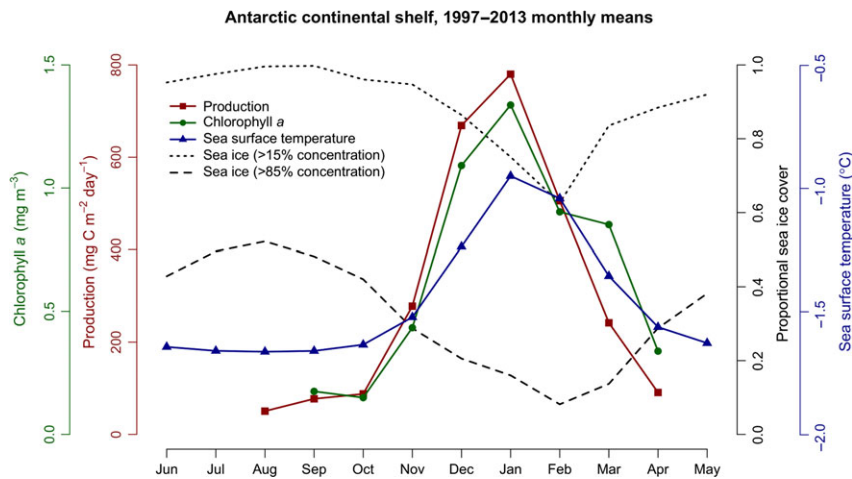


Fig. 4 Mean annual cycles for production, chlorophyll *a*, sea surface temperature (SST) and sea ice over the Antarctic continental shelf (modified from O’Brien *et al.*, 2009). Production and chlorophyll *a* are from Arrigo *et al.* (2008) and Feldman & McClain (2013), respectively. SST is derived from the NOAA Optimum Interpolation 1/4 Degree Daily Sea Surface Temperature Analysis (Reynolds *et al.*, 2007). The seasonal cycle for sea ice is represented as the proportion of this region covered by ice of at least 15% (small dashed line) and at least 85% (large dashed line) concentration. Sea-ice concentration data are the NASA Bootstrap SMMR-SSM/I combined dataset from the US National Snow and Ice Data Centre {<http://nsidc.org>; Comiso, 1999}. Monthly means are for time series from 1997 to 2013, apart from chlorophyll *a* which is 2003–2013. (Color in the online version)

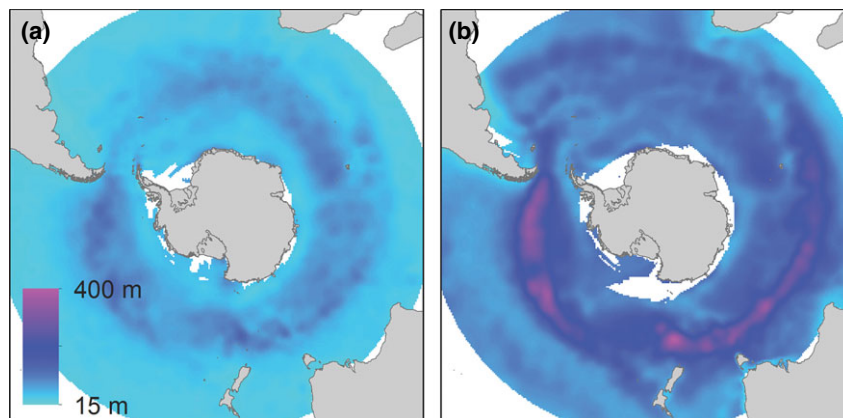


Fig. 5 Mean summer (a) and winter (b) mixed layer depth for the Southern Ocean (from Sallée *et al.*, 2010). Summer months are November–April, winter months are May–October. (Color in the online version)

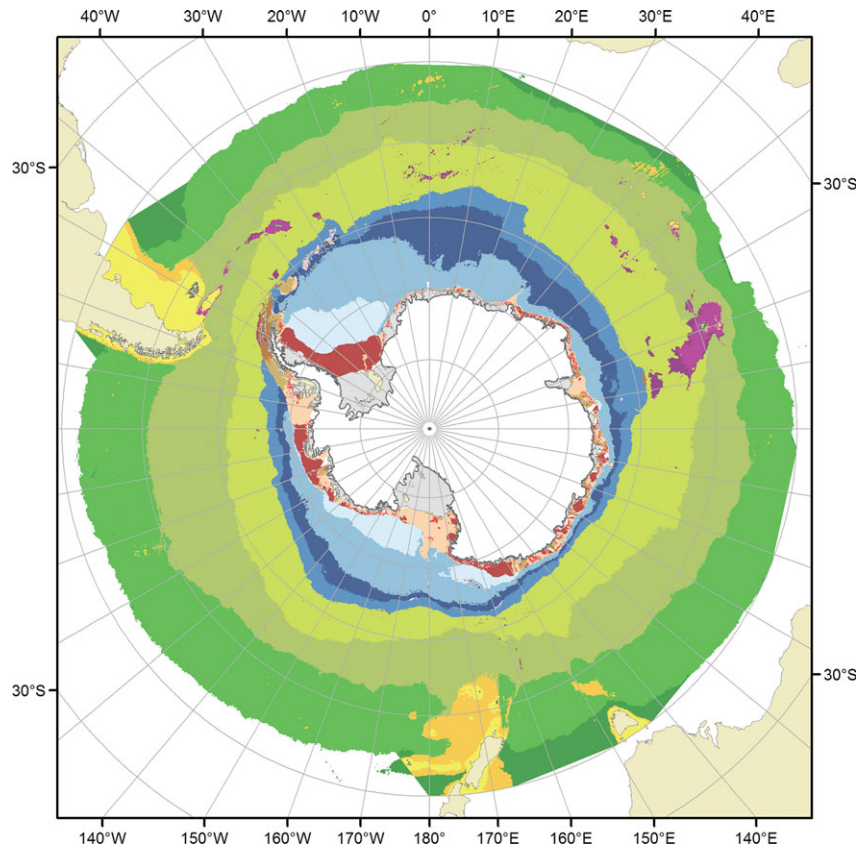


Fig. 6 Pelagic regionalization for the Southern Ocean (B. Raymond, Australian Antarctic Division, 2011, updated from Grant *et al.*, 2006). Twenty cluster types are derived from sea surface temperature, depth and sea ice cover data layers. Methods for regionalization follow those of Grant *et al.* (2006). (Color in the online version)

Observed changes in ocean habitats include deep-reaching warming (Böning *et al.*, 2008; Gille, 2008) and freshening due to increased precipitation and glacial discharge (Böning *et al.*, 2008; Durack & Wijffels, 2010; Hellmer *et al.*, 2010; Helm *et al.*, 2010; Jacobs & Giulivi, 2010). A southward shift of the fronts of the ACC, estimated using sea surface height, has been suggested as a mechanism to explain at least some of the observed Southern Ocean warming (Gille, 2008; Sokolov & Rintoul, 2009; Sura & Gille, 2010). Changes in surface fluxes of heat and freshwater may also have played a role in the warming (Meijers *et al.*, 2011b).

Many observed changes in physical habitats have likely been driven by the pole-ward shift and strengthening of the westerly winds (SAM becoming positive in recent decades; for relative roles of greenhouse gas forcing and ozone hole in these changes see Cai *et al.*, 2005; and Thompson *et al.*, 2011). For example, stronger wind forcing in the Southern Ocean has been linked to an increase in eddy kinetic energy (Meredith & Hogg, 2006) and pole-ward eddy heat flux (Hogg *et al.*, 2008), the latter of which could also contribute to warming.

Bathymetry, fronts, and eddies are important for bringing nutrient-rich deep water to the surface. Most regions of elevated chlorophyll in the ASO are related to regions of upwelling of nutrients due to the interaction of the ACC with topography (Sokolov & Rintoul, 2007). Eddies are increasingly thought to be a major driver of Southern Ocean systems (Meredith & Hogg, 2006), not only for their control on primary and secondary production but also because they may be features used by marine mammals and seabirds to assist with foraging (Sokolov *et al.*, 2006).

The oceanic mixed layer depth (MLD) is a major controller of primary production: deeper mixed layers bring more nutrients to the surface but result in phytoplankton spending less time in shallower water where photosynthetically active radiation (PAR) is highest. Wind and air-sea heat exchange cause these depths to vary throughout the Southern Ocean; different regions may have a consistently deep or shallow mixed layer, even though they are at the same latitude (Dong *et al.*, 2008; Sallée *et al.*, 2010; Meijers *et al.*, 2011a) (Fig. 5). Further, responses of the surface MLD to monthly

variations in the SAM has been shown unexpectedly to vary asymmetrically between regions (Sallée *et al.*, 2010).

The coastal systems around Antarctica comprise deep shelf areas (~500 m depth) broken by canyons and cross-shelf depressions (Grant *et al.*, 2006) (Fig. 7). Banks of ~500 m depth or less are scoured by icebergs (Dowdeswell & Bamber, 2007). Recurrent coastal polynyas, areas of open water within pack ice, are prevalent in the lee of coastal promontories and grounded icebergs and where katabatic winds cascade seawards from the continental ice sheet (Barber & Massom, 2007). These areas are highly productive (Arrigo & Van Dijken, 2003) and some are important for the formation of Antarctic Bottom Water (Rintoul, 1998): dense water that spills down the continental slope and spreads northward (Meredith *et al.*, 2011), in turn influencing the benthos with its water chemistry and organic particulates.

Sea ice is critically important to the ASO ecosystem. It structures the habitat, serves as a resting and breeding platform, provides food resources and refugia, serves as a seasonal nutrient storage before releasing those nutrients during melt, and affects reproductive cycles, recruitment, and foraging behaviour for a wide range of species (Massom & Stammerjohn, 2010; Thomas & Dieckmann, 2010). The interannual variability in sea-ice extent and changes in the timing and duration of the sea-ice season can be important drivers of the

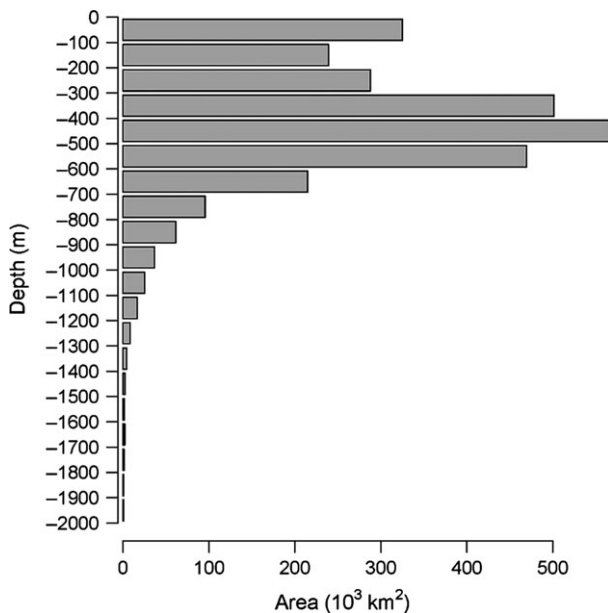


Fig. 7 Total area between 100 m depth contours in the regions around Antarctica less than 2000 m deep (modified from O'Brien *et al.*, 2009).

interannual variability in the ecosystem as a whole (Massom & Stammerjohn, 2010; Murphy *et al.*, 2012a). In contrast to the Arctic, the overall extent of Antarctic sea ice has increased slightly since satellite observations first became available in 1979. Indirect evidence from methanesulphonic acid measurements in ice-sheet cores (Curran *et al.*, 2003; Abram *et al.*, 2013) and from historical whaling records (de la Mare, 1997, 2009) indicate a decline in sea ice between the 1950s and 1970s (but see Ackley *et al.*, 2003).

Compared to the recent overall trend, much stronger and sometimes contrasting regional changes have occurred; sea-ice extent has increased by 4.5–5% per decade in the Ross Sea and decreased by 5–6% per decade to the west of the Antarctic Peninsula during the satellite era (Comiso *et al.*, 2011; Stammerjohn *et al.*, 2012). Over the same period, the seasonal duration of sea ice has shortened on the west side of the Antarctic Peninsula by 3.1 ± 1.0 days yr^{-1} , which is comparable to the greatest rate of sea-ice loss observed in the Arctic (Stammerjohn *et al.*, 2012). In contrast, the duration in the western part of the Ross Sea has increased by 2.4 ± 0.4 days yr^{-1} . These changes in the regional distribution of sea ice have been linked to changes in wind patterns, including a pole-ward shift and strengthening of the westerlies and an increase in strength of the Amundsen Sea low pressure system (Turner *et al.*, 2009b,c, 2013). Other factors may include changes in sea-ice advection from source areas and thermodynamic processes (Holland & Kwok, 2012), and increased glacial melt causing stabilized upper layers conducive to sea-ice formation and persistence (Bintanja *et al.*, 2013). By comparison, change in patterns of sea-ice seasonality in East Antarctica is more complex (Massom *et al.*, 2013).

Changes in sea ice will affect benthic habitats, particularly in shallow coastal areas, through changes in light conditions (Clark *et al.*, 2013). Further, increases in surface production due to thinning ice could lead to increases in allochthonous nutrient inputs to the benthos. These habitats may also be affected by abrupt loss of ice shelves such as has happened on the Antarctic Peninsula (Cook *et al.*, 2005; Cook & Vaughan, 2010). As well, freshening and changes in chemistry of Antarctic Bottom Water (Rintoul, 2007) may be important to these habitats in future.

The breakup of ice shelves can expose benthic and pelagic areas to more light, with ensuing increases in primary production (Peck *et al.*, 2010). Icebergs resulting from this breakup will increase bottom scour in shallow areas (Barnes & Souster, 2011; Gutt *et al.*, 2011). Meltwater from icebergs may release reservoirs of iron and other nutrients stored in the continental ice from dust deposited over millennia, which in turn will

increase primary productivity (Boyd *et al.*, 2012). Moreover, further ice shelf disintegration may happen if rates of warming experienced in the Antarctic Peninsula area occur in other regions (Scambos *et al.*, 2003).

In addition to climate change processes, CO₂ enrichment and absorption by the Southern Ocean is causing a shift towards more acidic conditions (Midorikawa *et al.*, 2012). As CO₂ is more soluble in cold polar waters than in temperate waters, the cold polar waters will become corrosive to calcium carbonate earlier than warmer waters at lower latitudes (McNeil & Matear, 2008; Moy *et al.*, 2009). Decreased concentration of carbonate ions in the Southern Ocean will potentially impact the physiology of organisms, as well as carbonate deposition by calcifying organisms (Moy *et al.*, 2009; Byrne, 2011; Kawaguchi *et al.*, 2011, 2013; Roberts *et al.*, 2011a; Ingels *et al.*, 2012; Bednaršek *et al.*, 2012a).

Projections of future conditions using coupled ocean-atmosphere models are confirming past findings for the Southern Ocean (e.g. Russell *et al.*, 2006) of continuing southward movement of fronts, warming and freshening of surface waters, and increased stratification (see Gupta *et al.*, 2009; Meijers *et al.*, 2012; Bracegirdle *et al.*, 2013; Sallée *et al.*, 2013a,b). These changes are expected to arise from an intensification of winds (positive SAM) and a southward expansion of the subtropical gyres (Meijers *et al.*, 2012). They are also likely to increase upwelling of warm, salty, nutrient-rich water, and potentially lead to more incursions of warm Circumpolar Deep Water on to the Antarctic continental shelf (e.g. see Gupta *et al.*, 2009). However, there is a need for increased investigation into the mechanisms by which this is achieved and the impacts of such incursions on the ice shelves (e.g. Dinniman *et al.*, 2012).

Projections from climate change modelling experiments point to an altered upper ocean, with both increased density stratification (surface warming and increased precipitation) and shallower surface mixed layers. Enhanced stratification will reduce the supply of nutrients from the deep ocean (Boyd *et al.*, 2008), whereas a shallower mixed layer will increase mean irradiance levels. Model projections of the joint outcome of these changes to the upper ocean (by 2100) reveal that the rate of net primary production will increase in subantarctic waters, and south of the ACC, and mainly decrease in the polar waters between these regions (Arrigo *et al.*, 2008; Bopp *et al.*, 2013). Although nutrient fluxes are also affected by large-scale upwelling of Circumpolar Deep Water at the Antarctic Divergence (driven by wind-induced Ekman transport), predictions for changes in upwelling are equivocal. Wind strengths are expected to increase, but much of the expected increase in Ekman transport may be

mitigated by an increase in pole-ward eddy transport (Lovenduski & Gruber, 2005; Hogg *et al.*, 2008). Models and scaling arguments suggest that stronger winds will likely cause stronger upwelling, but that the magnitude of the response is less than expected due to the wind alone because of partial compensation by eddy fluxes (Farneti & Delworth, 2010; Meredith *et al.*, 2012; Morrison & Hogg, 2012).

Sea ice is expected to decrease in extent (Bracegirdle *et al.*, 2008), volume (Arzel *et al.*, 2006) and annual duration (i.e. lengthen the open water season) (Stammerjohn *et al.*, 2012). However, the prognosis for sea ice remains one of the greatest uncertainties surrounding ASO habitats in the model projections as there is still some discrepancy between observations and model simulations of Antarctic sea-ice extent; observations show a small increase in sea-ice extent in recent decades while climate models show a decline over the same period (Maksym *et al.*, 2012; Turner *et al.*, 2012).

Vulnerability: effects on biota

Marine microbes

In the ASO, primary productivity is strongly mediated by micronutrient availability (especially iron), temperature, carbonate chemistry and light, due to deep vertical mixing and extreme seasonal fluctuations in irradiance and sea-ice cover (Boyd *et al.*, 2008, 2012; Smith & Comiso, 2008; Melbourne-Thomas *et al.*, 2013). Iron limitation in much of the open Southern Ocean has resulted in low standing stocks of phytoplankton (Strzepek *et al.*, 2011; Boyd *et al.*, 2012). Large phytoplankton (large diatoms >20 µm and, in some areas, colonial *Phaeocystis antarctica* up to 6 mm long) are the dominant primary producers (Arrigo *et al.*, 1999), particularly in the coastal waters that contribute most to annual carbon export fluxes. Although infrequently dominant, small phytoplankton (flagellates and unicellular *Phaeocystis antarctica* 5–10 µm and small diatoms <20 µm) represent another energy pathway.

Marine microbes mediate global climate through photosynthetic carbon fixation from atmospheric CO₂. Some phytoplankton also influence cloudiness and atmospheric albedo over the Southern Ocean, thereby altering the global heat balance. Increased cloudiness and albedo occurs through the release of volatile plankton metabolites, such as dimethyl sulphide (Charlson *et al.*, 1987; Kasamatsu *et al.*, 2004a,b; Krüger & Graßl, 2011) and isoprenes (Meskhidze & Nenes, 2006), or nonvolatile organics in bubbles (Quinn & Bates, 2011).

Functional assemblages of phytoplankton are predictably associated with physical and ecological features and processes (temperature, ice retreat, mixed

layer depth, iron availability, bloom development, grazing, and senescence), but little is known about whether the geographical distributions of these functional groups have changed in the Southern Ocean. Small flagellates dominate the low-nutrient regions of the pelagic Southern Ocean, while diatoms are most abundant in the more nutrient-rich Polar Front region and on the continental shelves, along with the haptophyte *Phaeocystis antarctica*. However, warming of the ocean may favour southwards range extensions by certain groups, as has been observed for the coccolithophorid, *Emiliania huxleyi* (Cubillos *et al.*, 2007), and the heterotrophic dinoflagellate *Noctiluca scintillans* (McLeod *et al.*, 2012). *N. scintillans* was observed 240 km south of Tasmania in the subantarctic zone in December 2010 (McLeod *et al.*, 2012), and can be linked to the intensification of the East Australian Current, which is likely to continue to strengthen and transport warm water and resident phytoplankton further south (Cai *et al.*, 2005).

Rates of growth, metabolism and activity of auto- (phytoplankton) and heterotrophs (bacteria and microzooplankton) and viruses may be enhanced by warming (Rose & Caron, 2007; Danovaro *et al.*, 2011). However, the overall response of a taxon will be a combination of its physiological response to increased temperature coupled with any nutrient and light limitation, and the tolerances of that taxon to environmental change (Rose & Caron, 2007; Boyd *et al.*, 2008; Feng *et al.*, 2009). For example, there is no consistent effect of increased temperature on bacterial growth rates in polar seas (Kirchman *et al.*, 2009). Heterotrophic bacterial assemblages in the western Antarctic Peninsula shelf region responded positively in density to warmer temperatures in some years and negatively in others (Ducklow *et al.*, 2012b). It is therefore difficult to predict changes in the relative abundance and activity of microbial taxa with warming (Marchant *et al.*, 2001).

Ice-associated primary production in the ASO, comprising ice algal production and pelagic production at retreating sea-ice edges, is expected to decline with predicted decreases in sea-ice extent (Arrigo & Thomas, 2004; Arrigo *et al.*, 2008; Vancoppenolle *et al.*, 2013). Algae are found living on the bottom, and in the interior and surface layers of sea ice. Their annual growth cycle is influenced by availability of suitable habitat and seasonal variations in PAR. At the population (local) scale growth is modulated by the *in situ* light regime, which in turn is negatively impacted by increasing ice and snow thickness, and nutrient availability, which is dependent on sea-ice permeability (Golden *et al.*, 1998; Tison *et al.*, 2008; Raymond *et al.*, 2009; Arrigo *et al.*, 2010, 2012; Taylor *et al.*, 2013). Large-scale assessments of the effects of changing

sea-ice conditions on ice algal production remain difficult because observations are sparse and accurate models are not well developed in capturing the complexity of physical and biogeochemical processes or algal productivity in sea ice (Vancoppenolle *et al.*, 2013). A recent analysis of a large circum-Antarctic observational dataset showed that the vertical distribution of ice algae is dependent on ice thickness, and suggests that predicted changes in sea-ice thickness (e.g. Arzel *et al.*, 2006) may impact on the availability of ice algae as food for pelagic herbivores (Meiners *et al.*, 2012).

Increased pelagic primary production at sea-ice edges (marginal ice zone) occurs during the spring and summer sea-ice retreat. Production of melt water and reduced wind-mixing (due to partial sea-ice cover) act to increase ocean surface layer stratification, which may result in extensive phytoplankton blooms (Smith & Nelson, 1985). Sea ice may also release nutrients, in particular the micronutrient iron (Lannuzel *et al.*, 2007), and may seed the water column with ice algae (Lizotte, 2001). Other than the physical properties of the sea ice, the rate of sea-ice retreat and wind speed are considered important drivers of ice-edge blooms (Constable *et al.*, 2003; Fitch & Moore, 2007).

Changes in marginal ice zone dynamics due to changes in atmosphere–ocean–sea ice interactions may affect primary production. The predicted decrease in sea-ice extent will reduce the total marginal ice zone area, which is then expected to decrease productivity in the marginal ice zone. However, this will depend on the interplay between changes in *in situ* irradiance, stratification, and surface mixing (Arrigo & Thomas, 2004; Arrigo *et al.*, 2008). Also, wave–sea ice interactions contribute to increasing the marginal ice zone (Massom & Stammerjohn, 2010), which may give rise to greater marginal ice zone habitat in future because of increasing winds. The prognosis is currently unknown and will depend on the time scales of interest. The removal of ice in the past few decades in the west Antarctic Peninsula has resulted in deeper mixed layers and a consequent reduction in available irradiance, decreased phytoplankton biomass and size, and reduced productivity (Montes-Hugo *et al.*, 2009; Venables *et al.*, 2013). However, the timing of the bloom was not related to winter sea-ice extent but more to the seasonal cycle of irradiance (Venables *et al.*, 2013).

Reduced productivity might be transient. Increased atmospheric temperatures are expected not only to increase heat input to the surface waters but also to increase meltwater from coastal sources, both of which could enhance production from increased metabolism, the increased stratification and input of iron reservoirs from the ice sheet (Dierssen *et al.*, 2002; Boyd & Ellwood, 2010; Gerringa *et al.*, 2012).

Ocean acidification notably affects shell thickness in calcifying protists such as foraminifera (Moy *et al.*, 2009). More generally, it is expected to increase the energetic costs of calcification (Shi *et al.*, 2010; Hoffmann *et al.*, 2012), change the availability of nutrients and affect cell physiology (Orr *et al.*, 2005; Shi *et al.*, 2010; Byrne, 2011; Bednaršek *et al.*, 2012b). However, the responses of marine microbes to ocean acidification are difficult to predict because of multiple interacting environmental stressors combined with indirect feedbacks within the complex microbial food web (Boyd, 2011). Viruses are relatively unaffected by CO₂ concentrations (Larsen *et al.*, 2008), but are likely to be affected indirectly by host organisms becoming more vulnerable to infection (Danovaro *et al.*, 2011). Activities of some bacterial hydrolytic enzymes decreased with acidification (Yamada & Suzumura, 2010), suggesting that bacterial respiration of some substrates may decline due to ocean acidification. Enhanced CO₂ may promote growth in large diatoms (Engel *et al.*, 2008; Tortell *et al.*, 2008; Feng *et al.*, 2009), however nanoplankton have been found to be more successful than diatoms under enhanced CO₂ conditions in natural communities in the Bering Sea (Hare *et al.*, 2007). The potential for differential responses to enhanced CO₂ between phytoplankton functional groups in the Southern Ocean has not yet been determined.

Zooplankton and salps

Atkinson *et al.* (2012b) reviewed the different zooplankton functional groups in the Southern Ocean (copepods, euphausiids, salps, *Themisto gaudichaudii*, pteropods, appendicularians, carnivorous macroplankton), noting that few studies have investigated their thermal tolerances and metabolic behaviours. Zooplankton assemblages are closely related to the different frontal zones in the Southern Ocean (Hunt & Hosie, 2005, 2006a,b; Pinkerton *et al.*, 2010; Ward *et al.*, 2012; Hosie *et al.*, 2014). Shifts in the fronts are expected to result in concomitant changes in zooplankton distributions.

Reanalysis of historical data and comparisons of results from the Discovery Investigations with present-day studies showed equivocal results in terms of changes in the relative importance or distribution of zooplankton taxa in the Drake Passage, Antarctic Peninsula and southwest Atlantic (Ward *et al.*, 2008; Takahashi *et al.*, 2010). Mackey *et al.* (2012) combined historical data (1928–1935) from the Discovery Investigations to investigate the relationship between macrozooplankton abundance in the Atlantic sector and water temperature. They then used this relationship to model the effect of the observed >1 °C rise in water temperature in this region (Meredith & King, 2005;

Whitehouse *et al.*, 2008), on the distributional ranges of various taxa. A modelled uniform 1 °C temperature rise produced a pole-ward shift for all taxa analysed, which ranged across all groups reviewed by Atkinson *et al.* (2012b). These authors predicted that widespread polar/subpolar species, which have a wider thermal tolerance, would appear 4–12° in latitude further south. In contrast, sub-Antarctic taxa with a narrower tolerance were less likely to extend their range southward because of the steep temperature gradient across the Antarctic Polar Front.

Salps are omnivorous filter feeders, feeding mostly on smaller phytoplankton. Traditionally they were understood to avoid sea ice and only occur in areas where Antarctic krill typically dominates when krill abundance is low (Loeb *et al.*, 1997). More recently though, salps and krill have been found to co-occur in areas where sea ice has declined in the west Antarctic Peninsula, and salps have been calculated to be the major grazers on phytoplankton where the salps bloom in those areas (Bernard *et al.*, 2012). The degree to which salps become prominent in future remains uncertain because the drivers of their abundance have not been elucidated. However, salps and krill are adapted to be successful in different environments, namely open ocean and coastal regions respectively. In regions with complex oceanography (e.g. off the Antarctic Peninsula, within the Marginal Ice Zone and polynyas), salps and krill may coexist for short periods but their respective habitat requirements may be important in keeping salps and krill spatially separated in the long term. Low temperature and high particulate concentrations associated with sea-ice retreat may keep salps from invading the high Antarctic regions (Pakhomov *et al.*, 2002).

Calcifying zooplankton, such as the pelagic molluscan pteropods, are vulnerable to ocean acidification, although the degree to which they will be affected is yet to be determined (Roberts *et al.*, 2011a; Bednaršek *et al.*, 2012b).

Krill

Antarctic krill is the dominant herbivore in many parts of the Southern Ocean and the major route for transfer of carbon between primary producers and upper-trophic levels (Murphy *et al.*, 2012a). The life cycle of krill is tightly linked to the seasonality of the Antarctic environment (e.g. timing, duration and characteristics of sea ice, photoperiod, and temperature; Nicol, 2006; Kawaguchi *et al.*, 2007). The distribution of Antarctic krill and the 'krill-based' food web is influenced by the winter extent of sea ice, as krill is positively dependent upon sea ice for reproduction, survival and recruitment

(Kawaguchi & Satake, 1994; Siegel & Loeb, 1995; Nicol, 2006; Murphy *et al.*, 2007a; Wiedenmann *et al.*, 2009; Flores *et al.*, 2012). The Southern Boundary of the ACC also appears to be an important factor as it aligns with much of the northern extent of the range of Antarctic krill except in the Atlantic sector, where this boundary extends further to the north (e.g. Nicol, 2006; Atkinson *et al.*, 2009; Jarvis *et al.*, 2010). Antarctic krill tend to co-occur with their main food source, large diatoms (e.g. Bernard *et al.*, 2012); other dominant herbivores, such as salps and copepods, exploit smaller size classes of phytoplankton (Moline *et al.*, 2004).

Importantly, different life stages of Antarctic krill will experience different changes in the physical environment because each life stage predominantly occurs in a different habitat. Eggs and early larvae experience diverse physical conditions as they descend to deep water then rise in the water column, while mid-late larvae and juveniles are thought to depend on the sea-ice environment for growth and survivorship, and subadults and adults generally live in areas where juveniles are less frequently found (Nicol, 2006; Meyer, 2012). Postlarval krill may also experience different environmental conditions as a result of advection either by transport in currents (Murphy *et al.*, 2004; Fach *et al.*, 2006; Quetin *et al.*, 2007; Piñones *et al.*, 2011), or in association with sea-ice movement (Murphy *et al.*, 2007b; Thorpe *et al.*, 2007).

Antarctic krill densities are reported to have declined in the Scotia Sea by approximately 30% since the 1980s (Atkinson *et al.*, 2004), in parallel with decreases in extent and duration of winter sea ice. However, the degree to which the overall abundance of krill has declined is still a matter of considerable debate (e.g. Nicol & Brierley, 2010; Atkinson *et al.*, 2012a). The combined effects of changes in sea-ice extent, ocean chemistry, temperature and food abundance and/or distribution on Antarctic krill have not yet been investigated, and the overall prognosis for krill populations is ambiguous. In addition, the prognosis will be affected by changes in the food web, such as from the recovery of whale populations (Murphy *et al.*, 2012a).

Krill may respond to warming with an increased metabolic rate although the overall growth rate of individuals will depend on food supply. Increased temperatures in the Antarctic Peninsula region may enhance krill productivity provided that metabolic requirements do not exceed ingestion rates (and that food is available). However, the response is likely to be negative around South Georgia where water temperatures in this area have already increased (Mackey *et al.*, 2012), as further temperature increases could cause metabolic costs to rise to a level where they are not sustainable (Murphy *et al.*, 2007a; Wiedenmann *et al.*, 2008; Hill

et al., 2013). Such spatial variability in factors influencing krill populations is likely to result in region-specific responses. These responses may be further affected by the (as yet unknown) potential of krill to adapt physiologically and behaviourally. For example, it has been shown that krill can exploit the full depth of the ocean, and thus their potential habitat is far greater than once thought (Schmidt *et al.*, 2011).

Krill may be susceptible to increasing UV-B compared to other Antarctic organisms, based on DNA base composition (Jarman *et al.*, 1999), but at the same time their ability to acquire compounds that provide protection against UV exposure (Newman *et al.*, 2000), and their behavioural response to UV-A, would reduce their exposure to UV-B and therefore the risk of UV-B damage to DNA (Newman *et al.*, 2003). A significant correlation between krill density and Antarctic ozone depletion in the Antarctic Peninsula region has been reported suggesting direct and/or indirect UV impacts on krill density (Naganobu *et al.*, 1999).

Recent research combining experimental results and ocean circulation modelling indicates that the survival of krill embryos may be negatively affected by increasing ocean acidity (Kawaguchi *et al.*, 2011). These effects were manifested within the range of acidification that is projected to occur over the depth range that krill embryos are exposed to during their development (Kawaguchi *et al.*, 2013). Further study is needed for all other life stages along with the combined effects of acidification with other environmental stressors to improve understanding of the overall impacts of climate change on the life history of krill.

Finally, the Antarctic krill fishery may play an increasingly important role in influencing krill populations in coming years. This fishery has significant opportunity for expansion, and could become the largest fishery in the world (Nicol & Endo, 1997; Nicol *et al.*, 2012). Krill fishing activity has been affected by changes in sea-ice extent around the Antarctic Peninsula (Everson & Goss, 1991; Kawaguchi *et al.*, 2006). Fishing was initially restricted to summer and autumn, but since the mid-1990s operations have occurred year-round due to the extended ice-free season (Kawaguchi *et al.*, 2006, 2009).

Fish & cephalopods

The Southern Ocean is characterized by high macro-scale endemism of fish species – especially the neritic Notothenioids (86% of which are endemic). This endemism is due to the major oceanic fronts barring meridional dispersal combined with the geographic isolation of sub-Antarctic islands (Eastman & McCune, 2000). Notothenioids are the most abundant fish fauna over

continental and island shelves, and seamounts (Kock, 1992). On the Antarctic continental shelf, the Antarctic silverfish, *Pleuragramma antarcticum*, dominates the neritic fish fauna. Its eggs and larvae are strongly associated with sea ice. Antarctic toothfish, *Dissostichus mawsoni*, and Patagonian toothfish, *D. eleginoides* occur over the continental shelf, and on the margins and slopes of sub-Antarctic shelves, respectively. Mackerel icefish, *Champsocephalus gunnari*, occur in shelf areas less than 500 m in depth and many localized subpopulations have been identified throughout the range of this species (Kock & Everson, 1997).

In the oceanic zone, myctophids and bathylagids dominate (Gjøsaeter & Kawaguchi, 1980; Hulley, 1981; Collins *et al.*, 2012). Distributions of species in these families show a high degree of correlation with depth and many are closely associated with oceanographic features, particularly frontal zones. *Krefflichthys anderssoni* and *Gymnoscopelus braueri* are the most abundant species in the Polar Frontal Zone, while *Electrona antarctica*, *G. braueri*, and *Bathylagus* spp. dominate south of this area to the continental shelf/ice edge (see Collins *et al.*, 2012). These fishes, along with Antarctic silverfish and mackerel icefish, constitute the midtrophic level between mesozooplankton and many top predators (seabirds, marine mammals, large fish, and cephalopods) and may provide alternative energy pathways (Murphy *et al.*, 2013).

Projected changes for Southern Ocean fish under the impacts of climate change are unclear and any shifts in the future will need to be interpreted with respect to the potential confounding effects of fisheries. A southward movement of Southern Ocean frontal systems is expected to cause southward shifts in the distributions of myctophid species, given their strong association with fronts (Hulley, 1981; Collins *et al.*, 2012). It could also result in isolated populations restricted to island shelves becoming locally extinct, if they are unable to adapt to warmer ocean temperatures. Similarly, icefish could be vulnerable to ocean warming around currently productive sub-Antarctic islands because of their limited distribution and reliance on highly oxygenated cold water as they lack haemoglobin (Kock & Everson, 1997; Near *et al.*, 2012).

Postlarval toothfish are generalist predators (Roberts *et al.*, 2011b) that can migrate over large distances and occupy a very broad range of depths (from the near-shore to at least 2500 m; Hanchet *et al.*, 2008; Collins *et al.*, 2010; Duhamel *et al.*, 2011; Welsford *et al.*, 2011). Hence, toothfish might be relatively resilient to environmental change by being able to descend or move to more favourable areas. However Antarctic toothfish has antifreeze glycoproteins in its blood that are not present in Patagonian toothfish, and the ecology of

early life stages of both species is poorly understood; there are known environmental relationships affecting toothfish recruitment (Belchier & Collins, 2008), so toothfish may also be vulnerable to a changing environment. These factors are likely to be important in governing the responses of these species to change. The extent of thermal habitat preferred by *D. mawsoni* may contract over the next 30 years (Cheung *et al.*, 2008), but the data used to generate these scenarios excluded the Ross Sea, which is an area of high abundance of this species and currently increasing annual sea-ice extent.

Finfish fisheries may have greater access to stocks from reductions in sea-ice extent and a shortening of the sea-ice season. At present, fisheries for Antarctic toothfish around the Antarctic continent are limited to a summer season because of the difficulty of accessing the primary fishing grounds on the continental slope, which are covered by sea ice for much of the year.

Squid are important in Southern Ocean food webs (Murphy *et al.*, 2012a). This is mostly known from the prevalence of squid in the diet of many top predators, often identified from squid beaks (Xavier & Cherel, 2009). Nevertheless, there are major gaps in our current knowledge of their ecology (Collins & Rodhouse, 2006). Predicted temperature increases for the coming 100 years are unlikely to have major effects on squid in the Southern Ocean other than changes in distribution near the limits of their range (Rodhouse, 2012).

Marine mammals and seabirds

Seabirds and marine mammals are some of the best studied taxa in the Southern Ocean. Many possible taxa-specific responses to climate change, including those resulting from habitat dependencies, tolerances and adaptability, and changes in food availability, have been described (Trathan *et al.*, 2007). For example, foraging and reproductive success may be impacted by changes to sea ice, which is an important feeding and breeding habitat for crabeater seals *Lobodon carcinophagus* (Ducklow *et al.*, 2007, 2012a; Costa *et al.*, 2010), but could impede foraging for some penguin populations (Emmerson & Southwell, 2008; Massom *et al.*, 2009). Other factors not related to foraging may also be important. For example, increased snow precipitation which accumulates in breeding colonies can decrease survival of chicks of Adélie penguins when accompanied by reduced food supply (Chapman *et al.*, 2011).

Responses of marine mammals and birds to variability in the physical environment in the ASO have been considered at both regional and circumpolar scales (Ainley *et al.*, 2005, 2010). However, populations of the same species may not be responding in a uniform way around Antarctica because of regional differences in

changes to the physical environment. While many species have been responding negatively to warmer conditions (e.g. Barbraud & Weimerskirch, 2001, 2003; Fraser & Hofmann, 2003; Jenouvrier *et al.*, 2003, 2005b; Xavier *et al.*, 2003; Forcada *et al.*, 2005, 2006; Lea *et al.*, 2006; Trathan *et al.*, 2007; Costa *et al.*, 2010; McIntyre *et al.*, 2011; Barbraud *et al.*, 2012), some species are responding positively in some regions. For example, in the rapidly warming west Antarctic Peninsula region populations of Adélie penguins (*Pygoscelis adeliae*) have been declining, apparently due to decreases in sea-ice extent (e.g. Trivelpiece *et al.*, 2011; Ducklow *et al.*, 2012a; Lynch *et al.*, 2012). These reductions in Adélie penguin populations are in contrast with population increases in the Ross Sea and some parts of eastern Antarctica (Ainley *et al.*, 2005; Jenouvrier *et al.*, 2006; Kato & Ropert-Coudert, 2006; Smith *et al.*, 2012) where patterns of sea-ice change and variability are quite different (Massom *et al.*, 2013).

Trends in marine mammal populations are known only for a few species. At South Georgia in the Atlantic sector, Antarctic fur seal (*Arctocephalus gazella*) populations have been increasing rapidly since their commercial exploitation during the 19th century, but now show a strong negative response to an increasingly warm environment (Forcada *et al.*, 2005, 2008). In the western Antarctic Peninsula sightings of Weddell seals have declined while sightings of Antarctic fur seals and elephant seals have increased (Siniff *et al.*, 2008). Few reliable estimates of trends in depleted whale populations are available but humpback whales are known to be increasing rapidly (Zerbini *et al.*, 2010).

Long-term downward trends in the populations of some seals and seabirds in the subantarctic of the Indian and Pacific sectors of the Southern Ocean have been interpreted as a region-wide shift to a system with lower productivity (Weimerskirch *et al.*, 2003; Jenouvrier *et al.*, 2005b; ; Lea *et al.*, 2006; McMahan *et al.*, 2009), although comparative data on prey abundances are not yet available. Similarly, changes in the abundance of seabird populations on the coast of Adélie Land in eastern Antarctica and shifts in their breeding phenology may be related to climate events and climate change impacts (Barbraud & Weimerskirch, 2006; Hindell *et al.*, 2003, 2012; Jenouvrier *et al.*, 2005b, 2009). At other locations with similar monitoring programmes in East Antarctica, there are currently no obvious phenological changes for some species (Emmerson *et al.*, 2011).

Flying seabirds, such as albatrosses and petrels, may be less constrained than penguins in their foraging range during the breeding season. While these birds respond to climate variability (Inchausti *et al.*, 2003; Jenouvrier *et al.*, 2005a; Barbraud & Weimerskirch, 2006; Nevoux *et al.*, 2010; Péron *et al.*, 2010; Rivalan *et al.*, 2010; Rolland

et al., 2010; Barbraud *et al.*, 2011; Weimerskirch *et al.*, 2012), the underlying ecological mechanisms of these effects are not clear.

The interpretation of changes in marine mammal and seabird populations in the Southern Ocean needs to incorporate the potential population- and system-level effects of past exploitation (Murphy, 1995; Murphy & Hofmann, 2012). The near extirpation of Antarctic fur seals and baleen whales through commercial sealing and whaling in the nineteenth and twentieth centuries was a major perturbation to the Southern Ocean ecosystem as these species represented the dominant krill-feeding predator biomass. Decreases in albatross and petrel populations are due to incidental mortality in long-line fisheries in southern and temperate waters where these birds forage (Weimerskirch *et al.*, 1997; Tuck *et al.*, 2001; Arnold *et al.*, 2006). Recovery of these populations and/or continued fishery mortality will make interpretations of change more difficult because of the potential confounding effects between recovery/fishery mortality and other causes of ecosystem change (Croxall *et al.*, 2002; Trathan & Reid, 2009; Rolland *et al.*, 2010; Barbraud *et al.*, 2012; Trathan *et al.*, 2012). Further, competitive interactions and predation may constrain the recovery of some populations (Trivelpiece *et al.*, 2011; Schwarz *et al.*, 2013).

Changes in habitat location and/or quality may affect the foraging success of marine mammals and seabirds, depending on how much their foraging ranges need to change and the time when preferred prey are available. Capital breeding enables animals to forage widely and accumulate and store energy prior to giving birth, and then provision young using stored body reserves (Drent & Daan, 1980; Costa, 1993). Mysticete cetaceans and most phocid seals are extreme capital breeders (Costa, 1993; Lockyer, 2007), and often use foraging grounds that are spatially and temporally separate from breeding areas, thereby disassociating reproductive success from local food availability. The other strategy is income breeding where food needs to be accessed and delivered to the young immediately. The remaining marine mammals and all seabirds have this strategy as they forage more or less continuously during pup or chick rearing and must return to breeding colonies to nourish their offspring (Costa & Shaffer, 2012), thus linking reproductive success with local prey abundance (Costa, 1993; Forcada *et al.*, 2005; Lea *et al.*, 2006; Trathan *et al.*, 2006; Costa & Shaffer, 2012). Most albatrosses and petrels are a potential exception due to their wide foraging range (Forcada & Trathan, 2009; Costa & Shaffer, 2012; Weimerskirch *et al.*, 2012).

Income breeders are particularly susceptible to effects of climate change when they are tied to land-based colonies during breeding. If prey availability decreases

within the breeding foraging range then breeding success will decline (Costa, 2008; Forcada & Trathan, 2009). For example, for king penguins (*Aptenodytes patagonicus*) on Îles Crozet in the Indian Sector of the Southern Ocean, foraging habitat models and climate models project a doubling of the distance to reach optimal foraging zones, far beyond the usual foraging range for this species (Péron *et al.*, 2012). Not all ASO islands are suitable for sub-Antarctic land-based predators, which limits opportunities to move to alternative breeding sites that would also need to be within reach of predictable prey resources (Xavier *et al.*, 2003).

Benthos

Antarctic benthos exists in a physical environment that in some respects (e.g. temperature, salinity) is very stable, but in other aspects (e.g. irradiance, physical disturbance, seasonal flux of primary productivity) can be highly variable (Kaiser *et al.*, 2013). Impacts of climate change on ASO benthos will differ between habitats on the continental shelf, slope and in the deep sea (Brandt & Gutt, 2011). Ice scour down to depths of 500 m (the extreme limit) is the major form of disturbance on benthic shelf communities (Gutt & Piepenburg, 2003; Smale & Barnes, 2008; Smale *et al.*, 2008). Increased scour will increase patchiness of shallower shelf areas and, thus, increase the prevalence of early successional species, with associated changes in ecosystem composition and function (Clarke *et al.*, 2007). For example, the survivorship of some longer-lived species will be reduced, such as for the bryozoan *Fenestrulina rugula* (Barnes & Souster, 2011). In the last 12 years the chances of *F. rugula* colonies reaching 2 years of age and reproducing have halved as a result of iceberg scouring. The most likely response to increased ice disturbance of typical Antarctic species would be a slight shift in distribution, resulting in a contraction of species' bathymetric ranges to deeper areas (Smale & Barnes, 2008).

Change in the ice environment may have the most significant effects on benthic assemblages through change in seasonal production of phytoplankton, which may in turn alter the magnitude, timing, quality, and duration of the seasonal pulse of phytodetrital rain from the spring bloom (Ingels *et al.*, 2012; Lohrer *et al.*, 2013). Some invertebrates time their reproduction to the spring bloom, such as some filter feeding holothurians (Gutt *et al.*, 1992) and peracarid crustaceans (Pearse *et al.*, 1991; Baird & Stark, 2013). Change in surface production may arise through collapse of ice shelves (Peck *et al.*, 2010), enabling benthic taxa to colonize these areas (Gutt *et al.*, 2011, 2013). Changes to benthic-pelagic coupling will arise but the outcomes are unpredictable at this stage. While surface production may

increase with the loss of ice shelves and sea ice, changes of the microbial assemblages to smaller phytoplankton and, thus, smaller zooplankton could give rise to greater recycling of nutrients in the surface layers and less export of organic matter to the benthos.

Benthic macroalgae contribute significantly to Antarctic coastal food webs, both directly and as detritus (Heywood & Whitaker, 1984; Wiencke, 1996; Gillies *et al.*, 2012). Ice disturbance in shallow waters seems likely to select for fast growing macroalgal species with low competitive capability; increased ice disturbance may therefore change both the species richness and biomass of Antarctic macroalgal assemblages (Quartino *et al.*, 2001). These algae are likely to benefit from the greater light, warming and increased nutrient loads from meltwater (Wiencke, 2010). As a result, shallow water benthic communities may become dominated by macroalgae, with concomitant reductions in biodiversity (Clark *et al.*, 2013). Several cold temperate macroalgal species have already been reported in Antarctic waters (Müller *et al.*, 2011). These introductions may be a result of transport on ships rather than migrations as the ACC still forms a barrier to dispersal from more temperate-subantarctic locations to higher latitudes.

Benthic animals may be vulnerable to change in temperature (Barnes & Peck, 2008). Most experiments have shown that polar benthic species have less capacity for tolerance than species elsewhere; many species are unable to perform essential functions when temperatures are raised only 2–3 °C (e.g. swimming in scallops or burying in infaunal bivalve molluscs) and mortality is induced in some species by temperature increases of 5–10 °C above normal conditions (Peck, 2005). Antarctic species are so sensitive to temperature change that an increase in temperature of 2 °C has been theorized to cause population or species removal from the Southern Ocean (Peck *et al.*, 2004).

Calcified marine macroinvertebrates and coralline algae are a significant component of benthic communities in Antarctica (Amsler *et al.*, 1995; Clarke & Johnston, 2003). The potential effects of ocean acidification in benthic ecosystems at high latitudes are poorly understood; there is very little experimental evidence of impacts on benthic invertebrates, although a number of studies have considered possible dissolution of skeletons (Orr *et al.*, 2005; McClintock *et al.*, 2009), and reduced success of fertilization and early life-history stages in invertebrates (Hofmann *et al.*, 2010; Byrnes, 2011; Ericson *et al.*, 2012).

Conclusions

The general prognosis for Antarctic and Southern Ocean marine habitats under increased climate change

is for an overall warming and freshening of the present-day system, strengthening of westerly winds, with a potential pole-ward movement of those winds and the frontal systems, and an increase in eddy activity. There will be regional variability in many habitat parameters, including in sea ice. Notably, the future seasonal variation in habitat conditions will not be consistent with the current seasonal cycle, which may impact the timing and magnitude of primary production and, thus, have consequences for other species depending on the spring bloom.

The known responses of individual taxa to these changes in the physical environment are summarized in this article (Table 1). These responses will be

governed by how easily the taxa can tolerate change within existing physiological flexibility, adapt to new environmental regimes or migrate to alternative sites that enable survival. Further, vulnerability of marine biota in the Southern Ocean to disease may be important but is currently not well understood (Kerry & Riddle, 2009). The ultimate consequences of such changes are not well understood; they are expected however to go beyond shifts in species ranges and possibly may result in novel functional organization and dynamics of ASO food webs and reduced biodiversity.

Our review indicates that microbes and zooplankton are expected to generally move south as the ocean conditions in which they are normally found move south,

Table 1 Summary of known direct responses of biota to changes in physical parameters in Antarctica and the Southern Ocean. PAR = photosynthetically active radiation, UV = ultraviolet radiation. Acidification includes altered carbonate chemistry and pH. Sea ice includes consideration of thickness, concentration, and extent without differentiating the factor/s causing change in each group of organisms. The symbols used in the table denote a positive (+) or negative (–) direct effect of an increase in the physical variable on particular taxa (see text for details as to the reasons). ‘?’ indicates where there is likely to be a response but the direction is uncertain, i.e. the result may be variable in space, time or for specific taxa or the evidence is equivocal

| Taxon | PAR | UV | Temperature | Ocean acidification | Mixed layer depth | Sea ice | Move with fronts | Eddies |
|----------------------------------|------------------------|----|-------------------------------|---------------------|-------------------|--|------------------|--------|
| Diatoms | + (<3 °C) – (>3 °C) | – | + | | + | – | + | |
| Flagellates, <i>Phaeocystis</i> | – | + | – | | – | – | + | |
| Microzooplankton | | ? | + | ? | | – | + | |
| Bacteria & viruses | | – | + | | | – | + | |
| Zooplankton | | | + | | | | + | |
| Salps | | | | | | – | + | |
| Antarctic krill | | – | + antarctic – subantarctic | – | | + | | |
| Nototheniid fish | | | – | | | | | |
| Myctophid fish | | | + | | | | + | |
| Oegopsid squid | | | ?– | ?– | | | | |
| Southern Elephant seal | | | | | | ? | | + |
| Antarctic Fur seal | | | | | – | ?+ | + | + |
| Crabeater/Weddell seals | | | | | | + | | |
| King penguin | | | | | | | + | + |
| Emperor penguin | | | | | | ? | | ? |
| Adélie penguin | | | | | ? | + no ice to lower ice conditions – heavy ice conditions | | |
| Chinstrap penguin | | | | | ? | + | | |
| Macaroni penguin | | | | | | – | | + |
| Baleen Whales | | | | | | ? | | ? |
| Wandering Albatross | | | | | | | + | + |
| Black-browed Albatross | | | | | | + | + | |
| Antarctic fulmar | | | | | | + | ? | ? |
| Benthos | | | – | | | | | |
| Macroalgae | + | | | | | | | |
| Calcifying benthic invertebrates | | | | – | | | | |

although their timing of maximum seasonal production may alter depending on changes in nutrient supply, mixed layer depth and the timing of the sea-ice advance and retreat relative to day length. For Antarctic krill and finfish, which have the means to move large geographic distances, the latitudinal breadth of their range will depend on the degree to which they can tolerate warming oceans and changes to productivity in the areas in which they currently live. These tolerances are largely unknown.

An overarching issue for invertebrates and fish is how the acidity of seawater may affect calcification and reproductive physiology of these organisms. Evidence to date suggests that calcifiers are being affected, and Antarctic krill may be affected by the predicted range of change in pH over the next 100 years. For Antarctic shelf and deep-sea benthos, ocean acidification is likely to be the most important change in their habitat over the coming century.

For marine mammals and birds, the expected changes primarily relate to their flexibility in moving to alternative locations for food and the energetic cost of longer or more complex foraging trips, if they are bound to breeding colonies in summer. At present, the effects on these species appear variable because of regional differences in changes in the physical environment that might impact on foraging trip duration; for example, how the sea-ice pack might impact breeders constrained to the Antarctic coast or the distance of frontal systems and eddies (that are used for foraging) from sub-Antarctic islands. An additional factor requiring consideration is whether suitability and/or availability of land-based breeding sites is changing.

For Antarctica and the Southern Ocean, comprehensive species-specific vulnerability assessments are difficult. Many of the changes reviewed here will be compounded by the indirect food-web effects that will ensue. Nevertheless, climate change will not just impact primary producers, but can impact directly the habitats and ecologies of species at different trophic levels causing changes to both bottom-up and top-down forcings in the ecosystem.

To better assess the autoecological responses of these species to habitat change, and how these responses need to be factored into ecological models for the region, the following variables need to be estimated for key species:

1. Physiological responses of primary producers to the expected physical conditions in the Southern Ocean, particularly near to the Antarctic continent;
2. Constraints to growth and reproduction of invertebrates, given local conditions such as production and temperature;

3. The relative importance of winter vs. summer food acquisition on the reproductive performance of marine mammals and birds; and
4. The cost to land-based predators of shifts in optimal locations of prey.

Here, we review the autecological responses of organisms to climate change impacts in Antarctica and the Southern Ocean. While this relates to tolerances and ecological adaptability of taxa, a gap in knowledge is how well species may respond evolutionarily to the rapid changes occurring in these ecosystems (Turner *et al.*, 2009a, 2013). If evolutionary adaptation is not possible and refugia are not available then those species that are cold-adapted or restricted to particular habitats that are declining may be lost.

A great challenge for Antarctic and Southern Ocean science is to develop methods for assessing current and future impacts of climate change on ecosystem structure and function. Particular challenges lie in evaluating regional differences in the rate and direction of responses, and in integrating knowledge on the species-level responses but also the indirect effects that may be promulgated through the food web. This review provides a first step towards addressing these challenges by synthesizing current knowledge and identifying key uncertainties and vulnerabilities for Antarctic marine species and functional groups.

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