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Review

Antarctic pelagic ecosystems on a warming planet

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High-latitude pelagic marine ecosystems are vulnerable to climate change because of the intertwining of sea/continental ice dynamics, physics, biogeochemistry, and food-web structure. Data from the West Antarctic Peninsula allow us to assess how ice influences marine food webs by modulating solar inputs to the ocean, inhibiting wind mixing, altering the freshwater balance and ocean stability, and providing a physical substrate for organisms. State changes are linked to an increase in storm forcing and changing distribution of ocean heat. Changes ripple through the plankton, shifting the magnitude of primary production and its community composition, altering the abundance of krill and other prey essential for marine mammals and seabirds. These climate-driven changes in the food web are being exacerbated by human activity.

Highlights

Polar pelagic ecosystems have an important role in Earth's biogeochemistry.

Distinct from other pelagic food webs, polar systems are structured by sea ice, which drives overall productivity and ecosystem structure.

Polar pelagic food webs are short and changes in the base of the food web rapidly cascade across trophic levels.

Rapid declines in Antarctic sea ice and an increase in extreme weather suggest state changes that are altering marine ecosystems.

Global implications of changing high-latitude marine systems

Polar marine ecosystems are regions of high seasonal productivity and, despite their remoteness, provide society with food, fuel, and fiber [1,2]. These regions have a disproportionately large role, relative to their size, in Earth's biogeochemical cycles [3,4]. On a planetary scale, polar systems regulate climate by influencing planetary albedo, atmospheric heat uptake, freshwater storage as ice, global ocean circulation, and sea levels. The large and rapid changes observed in the polar oceans and cryosphere [5,6] have profound implications for Earth, marine and terrestrial ecosystems, and human society [7,8]. For example, the Southern Ocean accounts for up to half of ocean CO_2 uptake [9], leading to ocean acidification, and fertilizes three-quarters of the biological production in the global ocean north of 30°S [10]. The Southern Ocean also accounted for over one-third of the total global ocean heat increase since the 1970s, accelerating to over half during 2005–2017 [5]. Over geological scales, changes in the Southern Ocean have been implicated in shifts in global climate through an increased ocean **solubility carbon pump** (see Glossary) and **biological carbon pump**, which drive carbon storage in the deep sea and, thus, reduce atmospheric CO_2 [11].

Polar marine ecosystems are productive and are experiencing trended change reflecting changes in multiple physical drivers (Figure 1). Increased discharge from the Antarctic Ice Sheet is impacting ocean salinity and stratification in some sectors, especially west Antarctica, and has the potential to disrupt ocean circulation over large spatial scales. Ocean warming is strongly implicated in these ice sheet changes, and is also inherently linked to changes in sea-ice concentration, thickness, and extent. Other climatic changes are manifest, including a strengthening and poleward contraction of the mid-latitude winds that overlie the Southern Ocean, which initially led to an expansion of Antarctic sea-ice extent through wind-driven advection, but was then followed by its recent dramatic decreases in step with the buildup and release of subsurface ocean heat [12,13]. This has profound implications for ocean food webs, the productivity and structure of which are regulated by the seasonal expansion/retreat of sea ice, resulting in extreme

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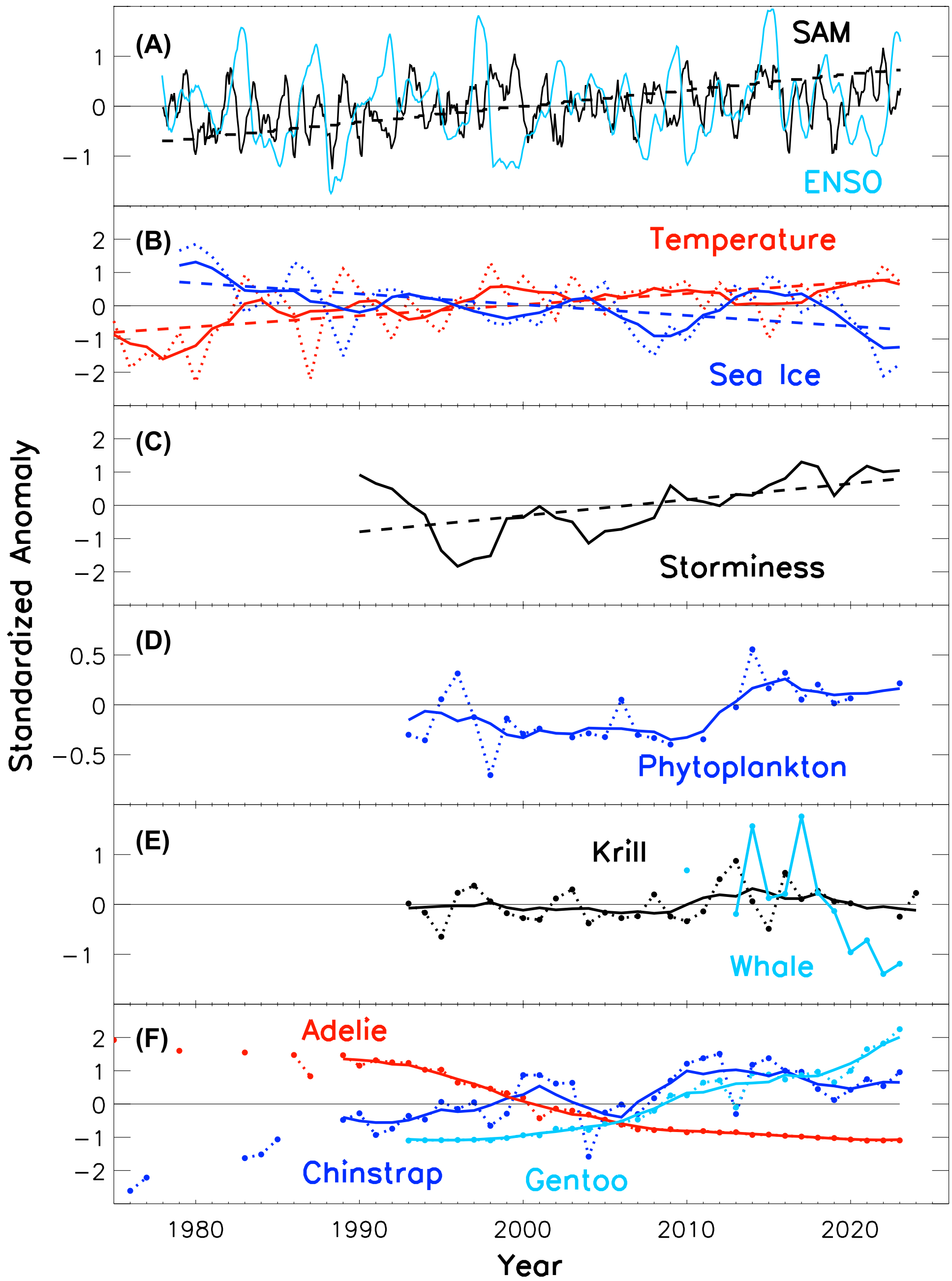

Figure 1. Decadal variability along the West Antarctic Peninsula. Long-term trends observed in (A) climate cycles, (B) physical drivers (winter air temperature and sea ice duration), (C) summer storminess derived from ERA5 reanalysis from the European Centre for Medium-Range Weather Forecast weather reanalysis, (D) January depth-integrated phytoplankton, (E) January Antarctic krill (*Euphausia superba*) abundance and whale pregnancies, and (F) penguin (Adélie, *Pygoscelis adeliae*; gentoo, *Pygoscelis papua*; and chinstrap, *Pygoscelis antarcticus*) breeding pairs at Palmer Station. Data collected by Palmer LTER program. Shown are standardized anomalies (dotted), smoothed multi-yearly variability (unbroken), and long-term trends (broken) for those series with trends at P <0.05 significance. Abbreviations: ENSO, El Nino Southern Oscillation; SAM, **southern annual mode**.

Glossary

Antarctic Circumpolar Current (ACC): ocean current flowing clockwise from the west to east around Antarctica. This current is a fundamental feature of the Southern Ocean and has an estimated transport of ~100–150 Sverdrups (1 Sverdrup is 1 million m^3s^{-1} of transport), making it the largest ocean current.

Antarctic krill: krill refers to ~86 species of crustaceans (called euphausiids) in the ocean. Antarctic krill is one of five species of krill that lives in the Southern Ocean in great abundance. It is a critical food source for the entire food web and, thus, is considered to be 'keystone' species for the Southern Ocean.

Biological carbon pump: biologically driven sequestration of carbon from the atmosphere and land runoff to the ocean interior and seafloor sediments.

El Nino-Southern Oscillation (ENSO): recurring climate pattern associated with changes in ocean temperatures in the Central and Eastern tropical Pacific Ocean; these changes alter wind and rainfall globally.

Marginal ice zone: transitional zone between open sea and dense drift ice spanning between 15% and 80% ice concentration.

Microbial loop: in aquatic systems, the process by which particulate and dissolved organic carbon is recycled back into the food web via bacteria.

Mixed layer depth: region in an upper water column where turbulent mixing has homogenized hydrographic properties (temperature and salinity). Often, this is present in the surface layers of the ocean, where turbulence driven by wind forcing induces mixing.

Solubility carbon pump: CO_2 is more soluble in cold water and cold water is denser and more likely to sink into the deep ocean, sequestering carbon to the deep sea.

Southern annular mode (SAM): climate driver that refers to the north–south movement of the strong global westerly winds blowing continuously in the mid to high latitudes of the southern hemisphere.

Stratification: vertical layering of waters in the ocean, typically with layers of higher density at greater depths. Increased stratification denotes sharper interfaces between layers.

seasonality and interannual variability in ecosystem functioning. Given the growing likelihood of rapid regime changes, understanding the ecological response is critical. Unfortunately, these regions are remote with limited access and sustained sampling is rare. The West Antarctic Peninsula (WAP) is unique as it is home to multiple international time series that provide insights to understanding polar marine ecosystem resilience on a warming planet; in this review, we use insights from these sustained studies to comment on the potential future ecological trajectory of polar seas.

Ice and polar ocean food webs

Sea ice structures the seasonality and ocean ecology of high-latitude systems in multiple ways (Figure 2). The growth of sea ice during autumn and winter provides a physical barrier between the ocean and intense winter winds and extreme low temperatures of the atmosphere [14,15]. In the spring, sea ice attenuates the light available for photosynthesis, provides protection from storm mixing, and, once melted, is a source of low-salinity surface water, which helps stratify the surface ocean during the early summer. Ocean stabilization and stratification are tied to the onset of spring/summer phytoplankton blooms, elevated new and net community production, and carbon export [16]. Winter–spring preconditioning, expressed in the timing of sea-ice retreat, is a dominant physical force governing biological processes across trophic levels [17,18]. The sea ice provides a physical substrate that harbors a diverse microbial community [19] and has been hypothesized to provide seed populations for spring phytoplankton blooms in the **marginal ice zone**. The high algal concentration within or released from winter sea ice provides food for larval *Euphausia superba* (hereafter referred to as **Antarctic krill**, although several species of krill exist in the Southern Ocean), which also use the under-ice habitat as a refuge from predators [20].

Compared with temperate and tropical ecosystems, these polar systems experience high levels of natural climate variability intrinsic to polar seasonality and the impact of both regional and remote climate modes that can make distinguishing long-term trends in the system a challenge. Ecosystem responses are filtered through relevant biological timescales for organisms that vary from days–weeks for bacteria, phytoplankton and some microzooplankton, to years for krill, to nearly decades for seabirds, seals, and whales. Thus, the impact of a given disturbance is taxon- and life-history dependent; nevertheless, these food webs are among the marine systems that are most vulnerable to climate change [6]. Given growing evidence that the dramatic and persistent Antarctic sea-ice decreases are due to a state change (or regime shift) in atmosphere-ocean-ice interactions [12,13], these related impacts will imprint differently on the distinct components of the ecosystem, given the intrinsic timescales on which they function.

Antarctic pelagic food webs comprise a short, tightly coupled, productive ecosystem. The short food web centers around the keystone Antarctic krill, which provides abundant food for higher trophic levels supporting large populations, many seasonally migratory, of seabirds, seals, whales, and fish [21] (Figure 3). There is strong fidelity between trophic responses and environmental factors driven by the presence of sea ice [22]. Other sea-ice ecosystems also exhibit tightly coupled food webs [23,24]. High summer phytoplankton concentrations are associated with winters of extensive sea-ice cover and result in high krill recruitment [18,25]. Successful krill recruitment has been linked to shorter Adélie penguin (*Pygoscelis adeliae*) foraging trips and higher Adélie penguin chick fledging mass, which is indicative of chick survival after fledging [26,27]. Additionally, annual pregnancy rates in humpback whales are strongly correlated with winter sea-ice extent from the previous year due to its impact on krill availability [28]. Changes in sea-ice extent and concentration, such as those observed and those predicted to occur further as climate change progresses, will alter the food web significantly, with individual drivers being distinct for each trophic level, reflecting the interactions between species, ocean, atmosphere, and land

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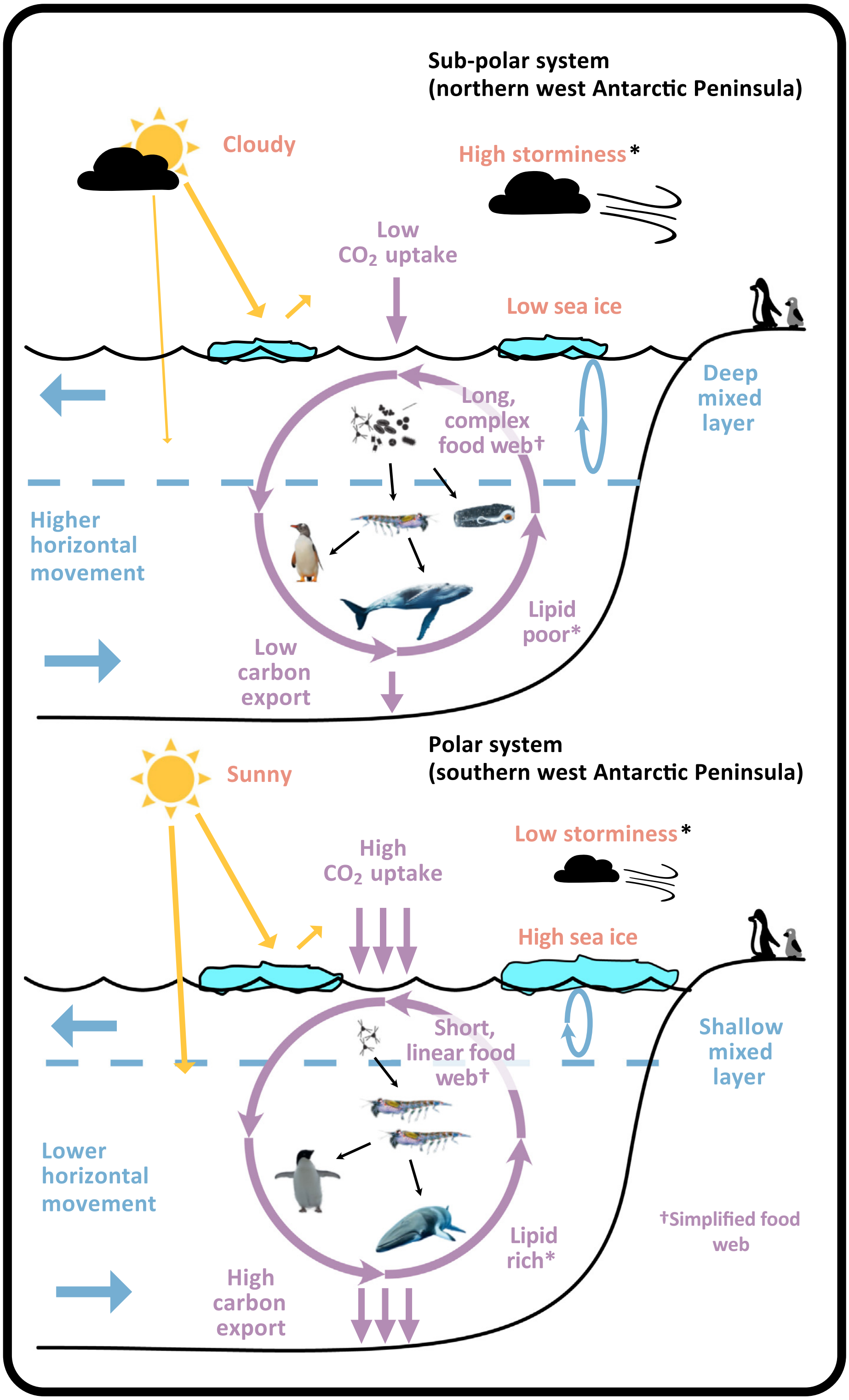
Figure 2. Components of the Southern Ocean ecosystem. Clockwise, starting from top left (with photo credit): Prospect Point on the coast of the western Antarctic Peninsula (D. Steinberg); diatom bloom viewed under the microscope (C. Shea); ice algae on underside of an overturned ice flow (left) and the pteropod, *Limacina helicina antarctica* (right) (D. Steinberg); Antarctic krill, *Euphausia superba* (D. Steinberg); crabeater seal, *Lobodon carcinophaga* (A. Corso); Antarctic silverfish, *Pleuragramma antarcticum* (D. Steinberg); humpback whales, *Megaptera novaeangliae,* bubble net feeding on Antarctic krill (D. Johnston); and Adélie penguin, *Pygoscelis adeliae*, colony (D. Steinberg).

(Box 1). Declines in the sea ice will favor species that have life-history strategies not dependent on ice as opposed to ice-dependent species, which rely on ice as breeding habitats, feeding areas, and resting surfaces. For example, long-term declines in ice-obligate Antarctic Silverfish



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Box 1. Tracking foraging dynamics of higher trophic levels

Krill predators around Palmer Station located on the West Antarctic Peninsula, including pygoscelid penguins and baleen whales, compete for a shared resource, the distribution and abundance of which in the water column affect the foraging behavior of each species (Figure I). Using advanced biologging telemetry, quantitative surveys of prey availability, and physiological measures of animal health and reproductive success, provides a better understanding how inter and intra-annual changes in the environment (e.g., storms and sea-ice cover) affect local prey fields and differentially affect krill predators with varying life histories, foraging behaviors, and energetic demands. While penguins are directly tied to prey immediately surrounding their breeding colonies, baleen whales are more mobile and can access prey across a wide spatial range. Different phenologies and changes in the timing and frequency of environmental disturbance have different impacts on how krill predator populations are affected in this ecosystem.

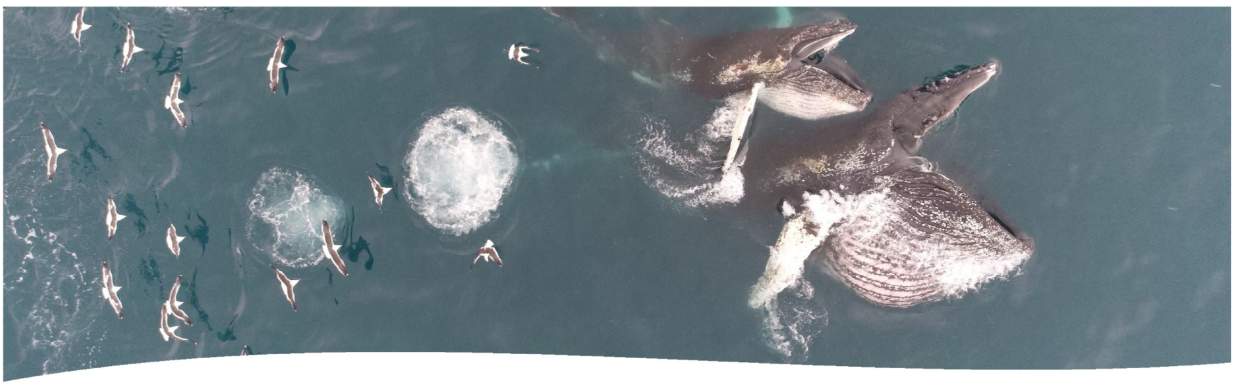

Figure I. Mother and calf humpback whales (*Megaptera novaeangliae*) foraging for Antarctic krill (*Euphausia surperba*).

(*Pleuragramma antarctica*) larval abundance are associated with warmer sea surface temperatures and decreased sea ice [29].

The seasonal upper-ocean primary productivity translates to high particulate organic carbon export to deep waters in summer [16,30]. On the continental shelf, this high export fuels a rich and diverse benthic community that is sustained even through the low-flux winter months by a benthic 'food bank' of organic matter accumulated during the summer bloom period [31]. Krill fecal matter contributes a disproportionately large fraction of the carbon export, as measured by sediment traps on Antarctic continental shelves [32,33]; however, deep ocean sediment traps show higher contributions from marine snow and phytodetritus [34,35]. Pulses of organic carbon export are also spatially variable and linked to animal behavior, with modeled fecal pellet production by krill swarms or aggregations increasing carbon export in the marginal ice zone by up to 61% [36]. While short food webs leading to efficient export of organic carbon are characteristic of polar regions, the effects of complexity in the polar food web on biogeochemistry have been underappreciated. Although the short food web is believed to reflect efficient krill grazing of large diatom cells [37], krill are omnivorous and can significantly supplement their phytoplankton diet with metazoans, such as copepods, and with heterotrophic protists [38,39]. The extent to which heterotrophic protists remove primary production also varies widely in the Southern Ocean (see Table 4 in [40]), modulating the proportion of primary production funneled through the **microbial loop** versus that available for export.

While sea ice structures the timing and overall productivity of the food web, both local- and large-scale geography and circulation influence many of the ecological interactions resulting in

Figure 3. Climate change is expected to alter food webs as the system transitions from a polar system to a subpolar system. The top schematic is characteristic of a subpolar system, while a polar system is illustrated in the bottom panel. Asterisks indicate unappreciated processes in the past.

biological hotspots [41,42]. A defining feature of the Southern Ocean is the world's largest ocean current, the **Antarctic Circumpolar Current (ACC)**. This flows clockwise around the continent, and contains in its mid-depths the warm source water from which all other Southern Ocean water masses are derived. In some sectors, the ACC borders the continental shelves, such as in the west Antarctic Peninsula, where it delivers heat to the coasts via glacially carved cross-shelf canyons [43]. Thus, ocean-driven melting of marine-terminating continental ice is enhanced in these regions, modulating the upper ocean properties, including stratification. These regions are characterized by enhanced diatom blooms, abundant krill, and penguin breeding colonies [44,45]. The delivery of warm circumpolar water is predicted to increase for portions of the East Antarctic Ice Sheet in coming years [46]. In other sectors (Ross and Weddell Seas), the circumpolar current is separated from the continental shelves by expansive subpolar gyres, leading to relatively cool ocean conditions on the adjacent continental shelves.

Projecting the future for Antarctic marine ecosystems

Global climate change will manifest as a change in the trends, annual amplitudes, and frequency of extreme events for a range of physical drivers (warming and more frequent marine heatwaves, melting glacial ice, reduced sea ice, ocean acidification, and increasing storminess). These changes will restructure ecological systems [7], and a core challenge is to understand this resilience to change and potential trajectories of these ecological systems [47]. Understanding the resilience requires insight into both the capacity of the system to remain unaltered in the face of change and the potential for the system to recover to its predisturbed state [48]. Predicting ecological trajectories requires understanding ecological responses to, and variability resulting from, the interactions of multiple disturbances often operating over a range of temporal and spatial scales [49,50]. Such studies are rare in marine ecosystems, reflecting the limited number of sustained time-series efforts in the ocean and the difficulty in resolving the ecologically relevant temporal and spatial scales using ships [51].

The ability to project future trajectories for Antarctic marine ecosystems depends strongly on the skill of physical climate projections and, in particular, changes with time of seasonal sea-ice extent and phenology and the loss of continental ice. In contrast to the Arctic, where there is strong evidence for a basin-scale decadal decline in sea-ice extent and thickness [52], changes in Antarctic sea ice over the first 29 years of satellite observations (1979–2007) were characterized by regionally opposed changes, or other regions with little to no change, followed by a remarkable shift to circumpolar-wide extremes, first involving record highs (up to 2015), then an abrupt transition to record lows thereafter [12,13,52,53]. The use of coupled Earth System models to project the future evolution of sea ice and other components of the climate system throughout this century have struggled to capture the temporal evolution of Antarctic sea ice; thus, there is low confidence in the current state of predictions [54]. However, on multi-decade timescales, agreement between models suggest that continued climatic warming will exert pressure on sea ice toward further retreat and potentially trigger further changes in its persistence.

Under standard low and high greenhouse gas emission scenarios for the 21st century, coupled climate models project sea surface temperature rises, increased water column **stratification**, and reduced **mixed layer depth** over much of the Southern Ocean [55]. It is accepted that such models do not robustly capture shelf-sea processes and most omit key features, such as interactive ice sheets and glacial discharge; nonetheless, significant further changes in ocean circulation, stratification, and ice–ocean interactions are expected. Projected Southern Ocean biogeochemistry includes regions with increased net primary production due to enhanced light from lower sea-ice cover and shallower mixed layers, lower surface pH from uptake of excess anthropogenic CO_2, and low subsurface oxygen from altered solubility and ventilation.

Trajectories in phytoplankton productivity and community composition?

The WAP spans a wide latitudinal gradient and, therefore, also a wide climate gradient, with a maritime climate in the north and polar climate regimes in the south. The climate gradient is predicted to migrate southward with continued warming. The WAP ecosystem will shift from that typical of a dry, cold, polar climate to a warmer, wetter, maritime one over time (Figure 4). In a polar state, characterized by extensive landfast shelf and sea ice, there are shorter periods of the open water in the spring/summer, resulting in lower seasonal sunlight available to fuel photosynthesis; therefore, initial ice decline is predicted to increase primary productivity dominated by large-sized diatoms [56]. Eventually, declines in sea ice cover will result in extensive open water exposed to intense winter/spring winds and storms that drive some of Earth's deepest winter mixed layer depths [57]. In turn, this is predicted to lead to light limitation of photosynthesis as phytoplankton are more continually mixed below the critical depth for growth, resulting in declines in primary productivity [17]. Alternatively, increased wind mixing may upwell nutrients, specifically iron, supporting phytoplankton growth that is iron limited in large regions of the Southern Ocean [58], mostly in deep or continental slope waters and less so over the shelf

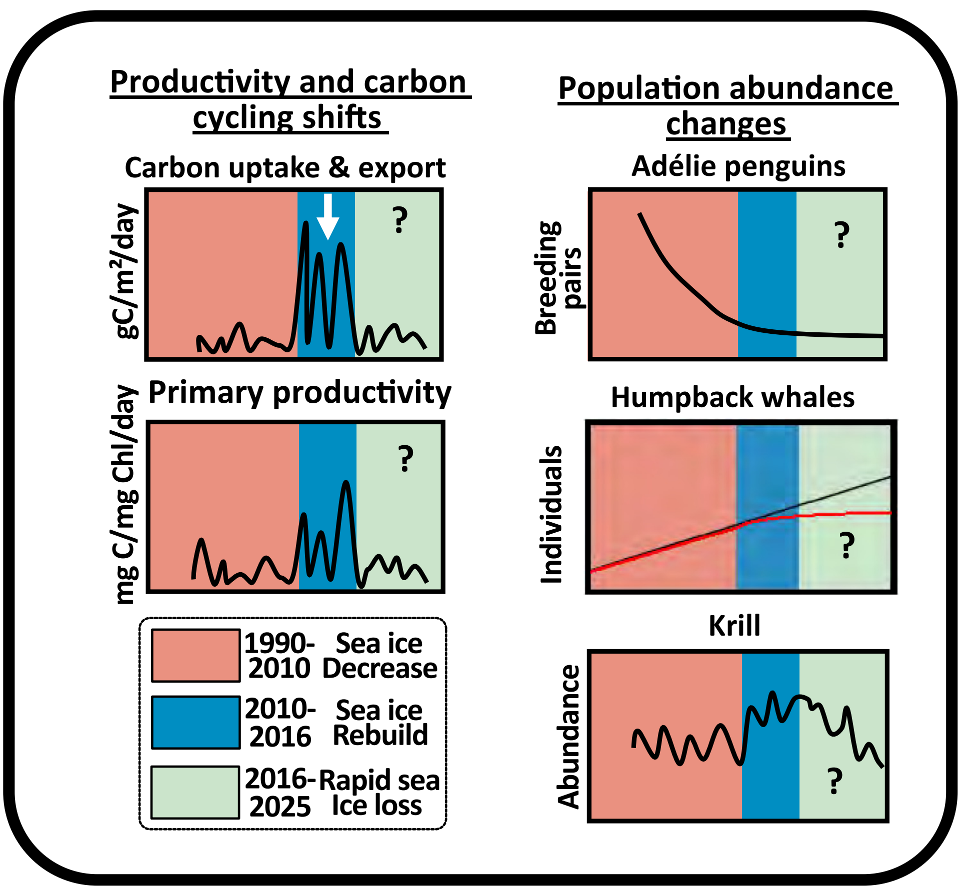

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Figure 4. Predicted trajectories of different trophic levels with pelagic polar systems on a warming planet. The white arrow indicates years of strong storm activity. Panels for carbon uptake and export, Adélie penguins (*Pygoscelis adeliae*), humpback whales (*Megaptera novaeangliae*), and Antarctic krill (*Euphausia superba*) are presented. The two lines shown for the whale panel indicate two different scenarios with (red) and without (black) krill food limitation.

[59]. Understanding the relative balance between nutrient and light limitation of phytoplankton remains a critical research question because the Southern wind intensity has been increasing [60,61]. In the WAP, annual changes in phytoplankton biomass are currently small, reflecting the offsetting combination of later start dates in phytoplankton spring blooms compensated by larger phytoplankton blooms in the austral fall [62]. Increasing spring wind speed is likely a mechanism for later spring start dates due to deeper wind mixing. Increased phytoplankton blooms during the late season have been associated with the increased stratification associated with the glacial and sea-ice melt [63]. However, the shift in overall phytoplankton biomass will impact the ecosystem through bottom-up effects.

Shifts in phytoplankton community composition will also affect food-web dynamics. Warming will be associated with declines in overall diversity [64] and changes in the phytoplankton size distribution [65]. These changes are predicted to have a significant impact on zooplankton, which have variable grazing efficiencies for different-sized particles [66]. Additionally, phytoplankton taxa have unique biochemical profiles reflecting distinct cellular compositions (e.g., pigments, proteins, lipids, or carbohydrates) and their light-chemical environment [67]. This variability can provide a range of food qualities for grazers [68]. Antarctic phytoplankton produce energy storage lipids associated with higher light levels, which can then influence the energy density of krill that consume them [69]. The maximum photoperiod is in summer, which can facilitate high food-quality krill during the penguin chick rearing period [70].

Trajectory in secondary production?

Changes in seasonal sea-ice extent, primary production, and phytoplankton community composition in turn exert bottom-up control on the marine food web, in particular through Antarctic krill populations, which are sensitive to both phytoplankton prey concentration and seasonal sea-ice extent [18]. In the coastal WAP, Antarctic krill recruitment is high following years with relatively high winter sea-ice extent and duration, leading to higher summer chlorophyll concentrations [18]. Higher krill recruitment in those years could reflect increased food availability fueling growth and/or sea ice providing critical habitat for overwintering larval krill [20]. Sea ice itself is also a reservoir for calorie-rich ice-associated phytoplankton [71]. The lifespan of Antarctic krill is ~6 years; thus, multiple consecutive years with low sea ice would be predicted to reduce Antarctic krill recruitment and, therefore, the population size of this keystone species. Indeed, Antarctic krill populations have significantly decreased in the northern part of the Southwest Atlantic sector of the Southern Ocean, once the center of highest krill densities, leading to contraction of their range poleward as the region has warmed [72]. The commercial krill fishery is also focused in the region; therefore both warming and fishing must be considered for ecosystem-based management of krill [73].

Changes in zooplankton other than Antarctic krill with continued warming are also predicted [74]. For example, the ice or crystal krill (*Euphausia crystallorophias*) is a high-latitude coastal species associated with cold water and sea ice with a thermal tolerance and habitat range even more restricted than that of *E. superba*. Although crystal krill is expected to decline as warming eventually reduces suitable habitat, interestingly, its abundance in the southern west Antarctic Peninsula has increased, attributed to an increase in primary production, or to earlier spring sea ice retreat being favorable for larvae [25]. Other key taxa, such as salps (pelagic tunicates) and pteropods (pelagic snails), show increases in warmer sea surface temperature, lower sea-ice years, which are correlated with coupled modes of climatic variability, including the **El Nino Southern Oscillation (ENSO)** cycle [25,75]. Salp biomass in the Southern Ocean has increased and their distribution has expanded southward, intruding into areas historically dominated by Antarctic krill [76,77]. A marine ecosystem model predicts continued replacement of krill by salps based on simulating effects on the food web driven by changes in primary production [78]. Salps form high-density 'blooms' and produce large, fast-sinking fecal pellets [79], which can be important in carbon export in the Southern Ocean [80,81]; thus, changes in salp distribution and abundance have consequences for the biological carbon pump. While warming and sea ice loss is initially predicted to increase the abundance of pteropods, they are likely to be increasingly impacted by the negative effects of ocean acidification leading to undersaturation of aragonite [82] (a mineral form of calcium carbonate), inhibiting shell calcification in thecosome (shelled) pteropods or causing shell dissolution [83].

Trajectory in high trophic levels?

Climate and trophic changes have the potential to degrade Antarctic biodiversity, including negative impacts on seabird and marine mammal populations, as well as ecosystem services [84,85]. In Antarctica, two predominant whale species are commonly observed. Humpback whales (*Megaptera novaeangliae*), considered to be a subpolar species, migrate to Antarctic waters during the austral summer to feed on krill and are increasing along the Antarctic Peninsula, recovering from their near extirpation due to commercial whaling [86,87]. Their pregnancy rates are tied to krill availability [28]. Minke whales (*Balaenoptera acutorostrata*) are also krill predators exhibiting ice-associated behavior; however, estimating their population size and trends is challenging due to their elusive behavior. Therefore, continued shifts in the presence of sea ice and the associated impact on the krill will ripple up to this higher trophic level.

Different seal species in Antarctica exhibit ice-obligate and avoiding behavior and, therefore, contrasting responses to climate change reflect different life-history strategies [88]. Six species of seals breed in Antarctica: those that are ice obligate include the crabeater (*Lobodon carcinophaga*), Weddell (*Leptonychotes weddellii*), Ross (*Ommataphoca rossii*), and leopard (*Hydrurga leptonyx*) seals, while the Antarctic fur seal (*Arctocephalus gazella*) and southern elephant seal (*Mirounga leonina*) are ice tolerant. Crabeater and Weddell seals may be most impacted by sea-ice change and Ross and leopard seals by altered food-web dynamics, while fur and elephant seals may exhibit range expansions with sea-ice declines, but may eventually be impacted by shifts in food resources or predation [89,90].

There are two true polar penguin species, the Emperor (*Aptenodytes forsteri*) and Adélie penguin, both of which have life histories associated with sea ice; climate projections indicate population declines related to reduced ice environments and cascading effects on their prey and habitat [42,91–93]. Rates of population decline may be regionally specific, and refugia may exist where climate change is less pronounced. Along the Antarctic Peninsula where Adélie and Emperor breeding populations are largely in decline, ice-intolerant penguin species, such as the gentoo penguin (*Pygoscelis papua*), are expanding their breeding range and have growing breeding populations (Figure 1) [93–95]. With continued climate change, a growing krill fishery [96] and shifts in storm frequency, it is unclear how long gentoos can sustain their rapid colony growth. Penguin populations are affected by not only the presence of sea ice and food resources, but also storms, which can shift precipitation on land, impacting breeding habitat quality, breeding success, and chick fledging mass through wetting and increased thermoregulatory costs [97,98]. As climate and human activities persist, top predators serve as indicators of ecosystem health and enable us to identify the factors that pose the greatest threats and to prioritize our conservation and monitoring efforts.

Concluding remarks

Accelerating climate change in the Southern Ocean is driving changes in polar marine food webs, with warming predicted to transition the system away from tightly coupled, short polar marine food webs, which provide significant carbon export and support a diverse array of migratory organisms taking advantage of the highly productive summer months. A warmer future will see the

Outstanding questions

How will long-term ‘press’ (climate warming), subdecadal (interannual changes in sea ice cover), and shorter-term ‘pulse’ (storms, extreme events) disturbances interact to drive changes in the food web for the Southern Ocean? Long-term climate-driven shifts in seasonal sea ice, continental ice melt, and storminess are changing the physics and chemistry of the Southern Ocean in ways that are not well understood. Changes in sea ice, storm forcing and extreme events, such as marine heatwaves, are predicted to accelerate, with poorly understood consequences for Antarctic ecosystems.

How do ocean transport and mixing dynamics interact to modulate marine primary productivity, krill, and krill predators? Krill are a keystone marine polar species connecting phytoplankton and higher trophic-level seabirds and marine mammals, and krill aggregations are critical to the effectiveness of predator foraging behavior and carbon cycling. Changes in ocean mixing and circulation may affect krill through altered phytoplankton density, passive advection and dispersion, or cue active vertical movements. These changes can reduce prey availability and, therefore, the foraging success of higher trophic-level predators that have evolved life histories to thrive on dense krill aggregations during the short spring and summer seasons.

How will changes in the structure of the Antarctic food web affect cycling and export of carbon to the deep sea? The structure of the Antarctic pelagic food web has a fundamental role in regulating net community production, air-sea exchange of CO_2, and the export of organic carbon to the deep ocean (the biological pump). Food-web interactions affect the assimilation and trophic transfer efficiency of energy and carbon throughout the food web.

How will changes in primary and secondary producers, and their energy storage, affect higher trophic levels? Differences in prey quality (lipid, carbohydrate, and caloric content) affect the ability of predators to meet their energetic demands, and has implications for penguin demography, such as penguin chick mass and breeding success. Lipid-rich planktonic rise of a lower productivity system with relative increases in cycling carbon within the microbial loop. Understanding the pace of change and whether the state transition is reversible remains an open question (see Outstanding questions). Given the significant seasonal and interannual variability in polar systems, sustained sampling will be critical to detecting and attributing the long-term trends driven by a warming planet and will require new tools to resolve the relevant spatial and temporal scales for the ecology in remote and harsh polar environments. The prominent role of these polar marine systems in Earth's elemental cycling makes this a critical focus for oceanography, ecology, and climate science.

species may provide a buffer to environmental variability or unfavorable conditions and without these high-quality prey penguin demographics may suffer. Changes in climate may alter prey quality by changing the nutrient and light environment.

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Declaration of interests

None declared by authors.

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