

# Polar ocean ecosystems in a changing world

Victor Smetacek<sup>1</sup> and Stephen Nicol<sup>2,3</sup>

**Polar organisms have adapted their seasonal cycles to the dynamic interface between ice and water. This interface ranges from the micrometre-sized brine channels within sea ice to the planetary-scale advance and retreat of sea ice. Polar marine ecosystems are particularly sensitive to climate change because small temperature differences can have large effects on the extent and thickness of sea ice. Little is known about the interactions between large, long-lived organisms and their planktonic food supply. Disentangling the effects of human exploitation of upper trophic levels from basin-wide, decade-scale climate cycles to identify long-term, global trends is a daunting challenge facing polar bio-oceanography.**

Polar marine ecosystems are located at the ends of planetary gradients in daily and annual solar radiation and are ice-covered for varying lengths of the year. They harbour, or have until recently, large stocks of conspicuous animal life — birds, seals and whales — which led to the conclusion that polar ecosystems channel a greater proportion of primary production to warm-blooded predators than those at lower latitudes<sup>1</sup>. This early view was explained by short, low-diversity food chains in polar regions, evoking images of simple systems dominated by a few key organisms.

Research conducted over the past two decades has shown that the concept of short, low-diversity polar food chains is overly simplistic. Although comparatively few species do provide the bulk of food to polar marine predators, the planktonic base of their food supply is equivalent in phylogenetic diversity to the planktonic base in temperate climate zones<sup>2,3</sup>, implying that the structure and functioning of pelagic (open-water) food webs are broadly similar across all latitudes. But the key prey organisms for vertebrates vary between polar ecosystems: benthos and fish are the main prey in the north whereas crustaceans are in the south. This indicates that cold adaptation has not favoured a specific food chain. If air-breathing predators play a greater role in polar-ecosystem functioning than they do in lower latitudes, then a decrease in their stocks should have cascading effects down the food chain and lead to marked shifts in ecosystem structure. The evidence for such cascading effects is controversial, however, because of both the absence of baselines against which to assess change<sup>4</sup> and our poor understanding of the carrying capacity of pelagic food webs for higher trophic levels.

Are seasonally ice-covered pelagic ecosystems fundamentally different from their counterparts in adjacent ice-free waters and how will they be affected by the retreat of sea ice in a warming world? Clearly the organisms that live in the sea ice or are dependent on it to complete their life cycles will be most severely affected, but some organisms may actually benefit from sea-ice retreat and overall productivity might actually increase<sup>5</sup>.

In this review we examine the possible effects of a warming world on polar ecosystems and consider only the seas and oceans directly influenced by sea ice and its melting. Because human-mediated change has influenced polar ecosystems at both ends — thinning and retreat of the ice cover and heavy exploitation of top predator populations — unrav-

elling the effects of bottom-up and top-down forcing on pelagic ecosystems is an immediate task facing polar bio-oceanographers.

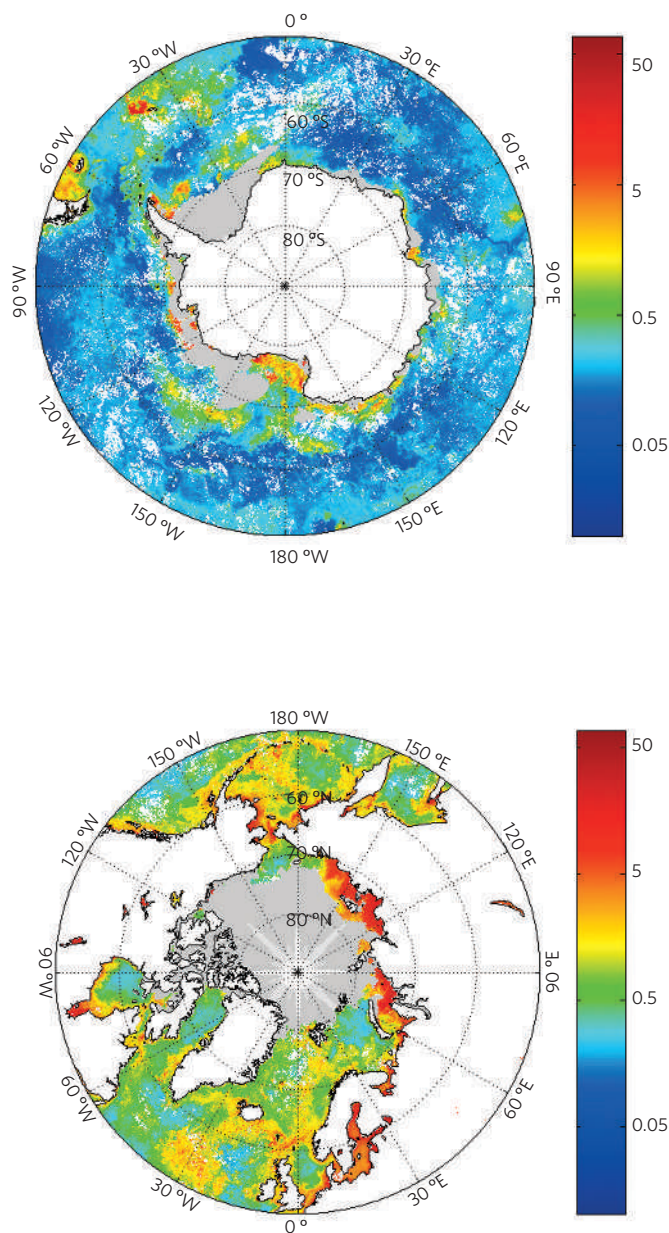
## Polar marine predators

It is widely assumed that marine ecosystems are controlled by bottom-up processes: the supply of nutrients by physical forcing and their conversion to organic matter by phytoplankton photosynthesis. Higher trophic levels simply harvest the levels below them. However, there is no simple relationship between the magnitude of primary production and the biomass and composition of higher trophic levels. That ecosystem interactions are more complex is demonstrated by the marked, decade-scale fluctuations in upper-level predator populations of all high-latitude systems that seem to be linked to corresponding changes in local climate and hydrography. Because the effects of climate change are difficult to disentangle from those of human exploitation, and because the sea-ice environment can directly affect both productivity and the population dynamics of birds and mammals, the mechanisms by which environmental changes are translated up the polar food web have remained elusive. An example from terrestrial ecology is instructive in this context.

The mammalian fauna of northern Eurasia and America, until the end of the last ice age, was morphologically and functionally similar to the extant megafauna of Africa and India. Herds of mammoth, deer, horses and bison, preyed upon by lions and wolves, roamed a landscape covered with a vegetation called mammoth steppe that became extinct together with the megafauna. The megafauna is likely to have conditioned the vegetation at the landscape level by promoting the growth of grasses on which they depended<sup>6,7</sup>. It seems increasingly likely that human exploitation rather than climate change was responsible for the global demise of terrestrial megafauna<sup>8</sup> and consequently its characteristic vegetation<sup>6</sup>. It seems that the wave of extinction proceeded from temperate to Arctic regions. Dwarf mammoths survived on Wrangel Island in the high Arctic and were hunted by humans till only 5,500 years ago<sup>9</sup>.

This insight from terrestrial ecology can assist our understanding of marine ecosystems and the effect of past and ongoing human depredation<sup>10</sup>. First, the wave of megafaunal extinction associated with human expansion in Europe will have also affected the accessible

<sup>1</sup>Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany; <sup>2</sup>Australian Antarctic Division, Department of the Environment and Heritage, Channel Highway, Kingston, Tasmania 7050, Australia; <sup>3</sup>Antarctic Climate and Ecosystems Cooperative Research Centre, University of Tasmania, Hobart, Australia.



**Figure 1 | Composite SeaWiFS images of the Antarctic and Arctic summer of 2002 showing surface chlorophyll a concentration in  $\text{mg m}^{-3}$ . Blue and green indicate low chlorophyll concentrations; reds and oranges are high concentrations. Note the highest levels in coastal areas or in areas in the lee of island groups. The high values along the Siberian shelf are due to turbidity not caused by phytoplankton. White is missing data and grey shows sea ice extent.**

stocks of marine mammals and birds. Temperate populations of marine mammals were probably as large as comparable unexploited polar ecosystems<sup>11</sup>. The European grey whale and the north Pacific sea cow were hunted to extinction in the seventeenth and nineteenth centuries, respectively<sup>11</sup>. Second, marine megafauna, that is, mammals, birds, fish and squid, may be capable of conditioning their aquatic environment, albeit in ways that are very different from their terrestrial counterparts. Thus, terrestrial megafauna are largely herbivorous whereas marine megafauna are predators. How such feedback mechanisms might operate across trophic levels and affect pelagic ecosystem functioning is not clear. Third, it might be too late to unravel the mechanisms of top-down control on marine ecosystems, because the human onslaught on the megafauna continues to proceed unabated

from the land to the sea<sup>4</sup>. The polar regions may be the last refuge for the marine megafauna — the Serengetis of the sea — implying that their teeming animal life is but a reminder of what the temperate oceans were like before human exploitation. These refuges are now threatened by continued exploitation and the effects of global warming on the sea-ice environment.

The effects of the decline in sea ice on polar predators will vary with the respective degree of life-cycle adaptation to seasonality in food supply. Understanding how populations of mobile predators, from fish to whales, are geared to carrying capacities of their environment is a prerequisite if we are to achieve truly sustainable exploitation of large, long-lived organisms as well as their smaller pelagic prey. Carrying capacity will be determined by the food supply of the adult populations, which are more resilient to interannual variation than their juveniles. Relatively stable predator populations will, in turn, exert a stabilizing effect on populations of shorter-lived organisms of lower trophic levels, which tend to be more susceptible to changes in the physical environment. If predators can stabilize their population size around a long-term average food supply, then depletion of their populations through harvesting should result in a decrease in their feeding pressure and changes in food-web structure. Evidence of such a trophic cascade has been reported in a cod-dominated northern ecosystem<sup>12</sup>, and trophic cascades may prove to be the rule rather than the exception. Investigation of top-down effects in marine ecosystems can best be carried out in polar regions because of their shorter history of exploitation and their larger extant megafaunal populations.

**Polar pelagic ecosystems**

The range of marine habitats represented in both polar regions is as broad as that of adjacent temperate climate zones. The north is characterized by extensive, shallow shelf seas surrounding a largely land-locked ocean, whereas the south is dominated by a land-remote, dynamic, open ocean and a very deep continental shelf. Interaction between topography, hydrography and the dynamics of the marine and terrestrial ice covers shapes these habitats. Polar marine habitats are occupied by organisms related to their counterparts in lower latitudes. Indeed, almost all major prokaryote and eukaryote lineages are represented in pelagic food webs of polar waters, indicating that they have successfully adjusted their physiological rates and life cycles to gradual cooling of these habitats while maintaining their functional role within them<sup>3</sup>. Clearly, speciation in the polar realms is driven by much the same combination of environmental conditions and organism interactions as in warmer regions. It follows that ecosystem structures are also similar, with the exception, of course, of the unique polar sea-ice habitat.

Sea ice is permeated by systems of brine channels inhabited by ice biota. This community is generally dominated by pennate diatoms, an algal group that also dominates pore waters of sandy sediments. Adaptation to confinement in narrow spaces is clearly a requirement for the sea-ice habitat, as is the ability to withstand supercooled brine in upper reaches of ice floes. Relatively few species are obligate ice inhabitants, because sea-ice is ephemeral and needs to be annually recolonized from the sea. The distances and time spans spent in water will be short in perennial ice fields and long in regions with short-lived seasonal sea-ice covers. There are accordingly large biogeographical differences in composition of sea-ice biota<sup>13</sup>. Biomass concentrations of microorganisms in sea ice can far exceed those attained in seawater, but their contribution to regional productivity tends to be minor because of the small relative volume of their habitat.

The effect of sea ice on pelagic systems is twofold. First, light penetration into the water column is reduced, negatively affecting underlying pelagic production. Second, in spring, microorganisms and trace elements, particularly iron, which were incorporated in the ice during formation or accumulated as dust in the snow cover, are released into the meltwater-stabilized surface layer. This process accelerates the spring bloom; however, there are great regional differences in the

amount of iron and algae released by sea ice hence the stimulating effect of meltwater on productivity. Under optimal conditions, intense, short-lived phytoplankton blooms grow in shallow surface layers in the wake of the retreating ice, seeded by iron and algal cells from the ice that tend to sink out of the surface layer following nutrient exhaustion<sup>13</sup>. These blooms are similar to the spring blooms of temperate shelves and divert potential food from pelagic to benthic systems<sup>14</sup>.

Despite lower temperatures and stronger seasonality, the productivities of polar ecosystems are similar to those of lower latitudes. The maximum growth rates of polar phytoplankton at *in situ* temperatures are lower than those of their temperate counterparts, but their photosynthetic efficiencies (the proportion of captured photons channelled to photosynthesis) are similar, implying that they are shade adapted<sup>15</sup>. Light intensities decrease with increasing latitude, but this dimming effect is compensated for by the increasing summer day length. Indeed, daily radiation available for photosynthesis during the polar summer is about the same as in the tropics, so primary production rates per day measured in some Arctic blooms rank among the highest values ( $>5 \text{ g C m}^{-2}$ ) recorded anywhere<sup>15</sup>. Broad patterns of annual productivity and phytoplankton species succession are similar across the temperate to polar gradient. Differences can be attributed to seasonality of sea-ice cover and water mass properties rather than to temperature in itself. Apart from areas under perennial ice cover, polar phytoplankton growth is eventually limited during the course of the growth season, as elsewhere, by the supply of iron or macronutrients.

Although growth rates of bacteria and heterotrophic protists (protozoa), which graze on bacteria, decrease with temperature, they do not appear to play a lesser role in polar ecosystems than in lower latitudes<sup>16,17</sup>. Polar macroherbivores have longer life cycles than their temperate counterparts<sup>18</sup> but community composition and biomass vary with regional productivity rather than temperature gradients<sup>19</sup>. Relatively few pelagic herbivores enter winter dormancy, even under ice cover; instead, many maintain a level of activity during the winter commensurate with the dwindling food supply<sup>19,20</sup>. Several species of copepods, amphipods and two species of Antarctic euphausiid (krill) have adapted to life in close association with sea ice, where they feed on ice algae and seek shelter from predators. It is these organisms and their predators that are being affected most by warming.

Summing up, the latitudinal transition from ice-free to ice-covered oceans is not marked by a significant shift in pelagic ecosystem structure and functioning: polar pelagic food webs are not shorter or simpler than elsewhere. However, the ecosystems encircling Antarctica do differ in some respects from those of other oceans, including the Arctic, especially with regard to the role of fish and the structure of benthic communities. Given the fundamental differences in topography, hydrography and history of glaciation it is not surprising that the Arctic and Antarctic oceans will respond differently to a warming world.

### The northern polar regions

At its seasonal maximum, northern sea ice covers  $13.9 \times 10^6 \text{ km}^2$ , extending as far south as  $44^\circ$  latitude in northern Japan and covering most of the extensive continental shelves in the Pacific. Interestingly, the deep southwestern half of the Bering Sea remains ice-free, whereas the northeastern half, located over a shallow, gently sloping shelf some 700 km wide, used to be entirely covered with ice before the 1990s<sup>21</sup>. In the Atlantic, the winter sea-ice margin lies north of  $70^\circ \text{N}$  in the Barents Sea. Perennial sea ice is restricted to the Arctic Ocean where it covers  $6.2 \times 10^6 \text{ km}^2$ , which is equivalent to 42% of the area. Its greatest density lies north of the Canadian archipelago and Greenland. This ice field, comprising multi-year ice floes, is gradually exported south along the Greenland coast and replaced by ice forming along the exposed Siberian shelves. The Arctic multi-year ice field has thinned since the 1970s, as a result of either local melting or increased export due to a change in circulation<sup>22</sup>.

Much of the northern sea ice is formed over shallow shelves that comprise about half the total area of the Arctic Ocean<sup>21</sup>. Sea-ice for-

mation is a dynamic process that, in turbid coastal waters, leads to incorporation of resuspended sediment particles in the ice floes. Some of the iron contained in these sediment particles will be available to phytoplankton upon melting, and the intense Arctic and subarctic blooms that grow until nitrate is depleted in the wake of the retreating ice edge indicate that there is no lack of iron. By contrast, the ice-free, deep southwestern half of the Bering Sea is a typical high-nutrient, low-chlorophyll (HNLC) region and is clearly iron limited (Fig. 1).

Productivity under perennial ice cover in the central Arctic Ocean is constrained by light supply rather than nutrients. The ice-based food chain of the high Arctic, which leads from ice biota to copepods and amphipods, polar cod, seals to polar bears, will suffer from shrinking of the sea-ice cover even though greater areas of open water may enhance overall oceanic productivity<sup>14</sup>. However, any such increase is likely to be modest because of low nutrient concentrations, which are at the lower end of the range reported from high latitude oceans<sup>21</sup>. The Arctic Ocean is impoverished in nutrients because strong, haline stratification prevents admixture of deep, nutrient-rich water either by deep winter convection or upwelling. Buoyancy of the surface layer is maintained by the discharges of many rivers (of low nutrient content) and melting of sea ice advected from the coasts. How changing sea-ice dynamics in a warming world will affect the complex stratification of the Arctic Ocean is uncertain<sup>22</sup>.

The two gateways to the Arctic Ocean, the Barents Sea in the Atlantic and the Chukchi Sea in the Pacific sectors, are much more productive than the Siberian and Canadian shelf seas because of advected nutrients which are retained in the system. Water flowing through the Bering Strait originates from the deep, southwestern Bering Sea, which is rich in nutrients owing to iron limitation. Iron is supplied by admixture with shelf water and from melting ice before and during passage through the shallow (approx. 50 m) strait, rendering this region one of the most productive in the world ocean<sup>21</sup>. Because of its shallow depth, much of the bloom biomass settles out on the sediments where it is used by a rich benthic fauna — the feeding grounds of grey whale and walrus. Nutrient recycling between the water column and sediments is intense. The Barents Sea, in contrast, is deeper and a greater proportion of phytoplankton production is retained in the water column. The exceptionally high copepod biomass of the western Barents Sea, largely attributable to advection from the adjoining Norwegian Sea, supports, or has supported, huge stocks of planktivorous fish — capelin and herring — and their predators, particularly Atlantic cod.

The Bering and Barents Seas differ fundamentally from one another in topography and hydrography, but both maintain, or have maintained, exceptionally large stocks of fish that have been subjected to heavy exploitation<sup>21</sup>. In the Bering Sea, large populations of marine birds and mammals (seals, walrus and whales) feed on fish and benthos but the comparable paucity of these higher predators in the Barents Sea is probably due to heavy human exploitation reaching back to prehistoric times. Because of the warmer climate, European hunters could tide over bad hunting years with subsistence farming. This was not possible in the Bering Sea where human populations were entirely dependent on marine food, in particular walrus, and so maintained a sustainable balance with their food supply for the past millennia. Climate change has severely disrupted their lifestyle in the past decades and is the cause of serious concern today<sup>23</sup>.

Fish stocks in both seas have fluctuated more than tenfold in the past decades partly as a result of fishing pressure but also because of basin-scale climate oscillations accompanied by shifting wind fields, storm frequency, sea-ice cover and circulation patterns<sup>21,24</sup>. Productivity in the Barents Sea is higher in the periods when more warm Atlantic water is advected onto the shelf supplying nutrients and copepods. The situation appears much more complex in the Bering Sea, possibly because its enclosed relatively homogeneous topography and large predator populations leave more scope for top-down-driven oscillations than the advection-dominated regime of the Barents Sea.



Primary productivity can be estimated from satellites but assessing population sizes of fish and their predators is much more difficult, albeit a prerequisite for assessing ecosystem carrying capacity and feedback loops within the biota<sup>23</sup>. A concerted, interdisciplinary effort to carry out comparative studies of the structure and functioning of ecosystems of subarctic seas is currently underway<sup>25</sup>.

Climate models indicate that the trend in poleward retreat of Arctic sea ice is now decoupled from natural, decade-scale cycles and is due to anthropogenic forcing<sup>26</sup>. The same models predict that, by the end of the century, the Arctic Ocean will be predominantly ice-free in summer. The level of productivity in an ice-free water column will depend on the extent of nutrient replenishment by vertical mixing during winter. If the mixing depth remains as shallow as under current stratification, it is feasible that productivity of the deep Arctic will decline with depletion of nitrogen and phosphorus inventories through organic particles sinking to the deep ocean.

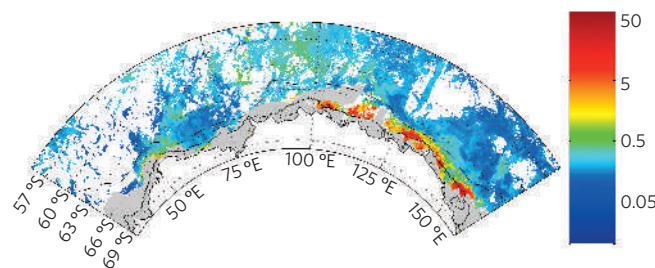
### The ice-covered Southern Ocean

The Antarctic ice cap extends into the ocean along much of the coast. Its weight presses Antarctica 200 m below the level of ice-free continents, and so its continental shelf lies considerably deeper than shelves in other oceans. Extensive shelves, partly covered by floating continental ice, occur only in the Ross and Weddell Seas. Their average depth exceeds 500 m. Land–ocean–atmosphere interaction is severely curtailed by the ice cap, and ‘normal’ mechanisms for supplying iron to the ocean through rivers and dust are absent. Nutrient input from sediments is restricted to shallow inshore environments. Antarctic sea ice, formed over deep water, is sediment-free, so Southern Ocean productivity is iron-limited, and concentrations of macronutrients are rarely exhausted.

Productive regions are restricted to the Antarctic continental margin and only extend offshore where water enriched with iron from land contact or from upwelling along shelves and continental slopes mixes with oceanic water impoverished in iron (Fig. 1). The largest of these regions stretches eastward from the tip of the Antarctic Peninsula towards South Georgia in the Southwest Atlantic sector. The Antarctic krill population is concentrated here, as are the populations of its warm-blooded predators<sup>27</sup>. Where iron is supplied from contact with land-masses, dense ice-edge blooms follow the seasonal melting of the sea ice. These blooms tend to be patchy at the mesoscale (tens to hundreds of km), reflecting underlying hydrography and regional variations in ice algae distribution (Fig. 2). Further, dust settling with snow on ice floes is likely to be another significant source of iron in meltwater<sup>28</sup> that could cause similar patchiness in local phytoplankton density.

Apart from supplying iron, melting sea ice stabilizes a shallow mixed layer (< 40 m), which facilitates accumulation of bloom biomass. However, blooms also occur in deep (> 60 m) wind-mixed layers<sup>3,29</sup>, and artificial blooms induced in iron fertilization experiments indicate that iron availability, rather than shallowness of the mixed layer, is the primary prerequisite for bloom formation<sup>30–33</sup>. Integrated bloom biomass in deep mixed layers can rival or exceed those of shallower layers on an area by area basis although the lower concentrations can reduce grazing rates and favour larger herbivores capable of processing greater volumes. Thus a greater proportion of primary production of deep blooms is likely to be retained within the mixed layer than in shallow blooms.

The dominant algae in shallow blooms tend to be weakly silicified, fast-growing diatom species, whereas larger, grazer-resistant, heavily silicified ones, together with small flagellates, dominate deep blooms<sup>3</sup>. Because frustules of dead diatoms take longer to dissolve than their plasma, biogenic silica reaches greater depths than organic nitrogen and phosphorus. The thicker the frustules, the deeper they are likely to sink before dissolution. Dissolved silicon concentrations in the deep Southern Ocean are exceptionally high because the combination of circumpolar circulation and heavily silicified diatoms retains silicon in deep waters whereas N and P are exported to other oceans in sur-



**Figure 2** SeaWiFS image indicating patchiness in the ice edge bloom in January 2002 off east Antarctica. The sea ice is shown in grey.

face water downwelling north of the Polar Front<sup>34</sup>. A southward retreat of winter sea ice will diminish the areal extent of dense, shallow blooms and increase that of deep blooms with ramifying effects on biogeochemical cycles and grazer populations. Changes in species composition of the phytoplankton community and the seasonality of production<sup>35</sup> can affect food web structure. Geochemical proxies indicate that productivity in the seasonal sea-ice zone (SIZ) was lower during glacial periods when winter sea-ice extended some 5° further North in the Atlantic than today and reached South Georgia<sup>36,37</sup>. This cannot be attributed to unfavourable growth conditions given the higher glacial-iron deposition rates on continental ice and in the sediments<sup>38</sup>. One possibility is that production in the glacial SIZ was higher but was recycled more efficiently by larger populations of grazers and predators.

The fate of bloom biomass depends on the rate of recycling of organic material including iron in the surface layer<sup>3</sup>. Heavily grazed blooms, whether deep or shallow, are likely to retain more biogenic elements in the surface layer than ungrazed blooms because the bulk of faecal material is recycled in the surface layer whereas ungrazed diatoms tend to sink out of it<sup>3,39</sup>. However, mass defecation by dense swarms of krill or salps could swamp the recycling system and contribute to vertical flux<sup>40</sup>. Faecal material of many marine mammals and birds tends to be loose and is dispersed by wave action at the surface (Fig. 3), which also contributes to the recycling pool. Adult predators convert much of their food intake into lipid reserves, retaining energy but releasing essential elements back into the system. Solar energy flowing through the food web in the course of recycled production can thus accumulate as lipids in predators. The larger the animal stock, the greater the proportion of the bloom that is retained and recycled in the surface layer, prolonging the lifetime of essential elements, particularly iron, in the productive layer — is this the marine equivalent of terrestrial ecosystem conditioning?

The major Southern Ocean macroherbivores are copepods, salps and krill, which are often spatially segregated<sup>41</sup>. Antarctic copepods have life cycles of many months to 2 years. Salps reproduce rapidly through both sexual and asexual means but are more abundant in impoverished HNLC waters. Antarctic krill (*Euphausia superba*) have a longer life cycle (5–7 years) and are thus affected by processes on wider temporal and spatial scales<sup>42</sup>. Because of their pivotal role in transfer of primary production to higher trophic levels, krill have received much more attention than other Antarctic herbivores. Nevertheless, there are still some fundamental gaps in our understanding of krill biology and population dynamics.

### Krill links microorganisms to whales

Antarctic krill is a remarkably versatile animal that provides the food base of a range of predators from birds, seals and whales to fish and squid because it exploits both the sea-ice and open-water habitats. In general, krill distribution overlaps with that of winter sea ice, except around South Georgia, but highest densities are found in shelf-break areas with high summer chlorophyll concentrations<sup>27</sup>.



**Figure 3 | A minke whale off the Antarctic Peninsula dispersing nutrients in the surface layer after feeding on krill.** The whale's body is covered in a thick diatom layer. (Photograph provided by J. Brokowski.)



**Figure 4 | A swarm of krill at the surface.** Krill can occupy all layers of the water column which makes them prey to surface, pelagic and benthic feeders. (Photograph by S. Nicol.)

The linkage between the annual abundance and recruitment success of krill and the interannual variation in the extent of sea ice<sup>43</sup> is thought to result from the greater winter feeding habitat offered by extensive sea ice and the effect of sea-ice melt on the subsequent spring bloom. The relationship, however, is not simple and there are both annual and regional exceptions<sup>42,44</sup>. Although the distribution pattern of krill is relatively well established, its overall biomass around Antarctica remains uncertain. Calculations based on potential consumption of primary production by krill suggest an upper limit of 4.4 billion tonnes, and estimates of predator consumption suggest a requirement for 150–300 million tonnes<sup>45</sup>. Extrapolations from acoustic measurements of krill abundance indicate a krill biomass of between 60 and 155 million tonnes, whereas scientific net surveys generally produce values an order of magnitude lower<sup>46</sup>. Analyses of all available scientific net data have indicated a potential 80% decline in krill density in the southwest Atlantic between 1976 and 2004 (ref. 27); however, this trend is difficult to verify. The only acoustic survey time series (from 1981 to present in the Elephant Island region in the SW Atlantic<sup>44</sup>) exhibits rather different trends from net-based surveys from the same region. However, suggestions of negative trends in krill distribution

and abundance should be a cause for concern and warrant further investigation, which will have to overcome problems associated with net avoidance, uncertainty in calibration of acoustic methods, patchy distribution and regional and interannual variability in occurrence in a vast range<sup>46</sup>.

Regional changes in krill abundance have been associated with interannual changes in the extent of sea-ice cover in areas crucial to krill recruitment<sup>27</sup>, but longer-term linkages are more elusive. There is conflicting evidence for change in overall sea-ice extent, although regional changes over the past 30 years are not disputed<sup>47</sup>. Satellite data, available from 1973, reveal considerable interannual and regional variation in sea-ice extent and concentration. There has been no consistent circumpolar trend in the extent of winter sea ice since 1973, although there may have been some changes in ice concentration<sup>47</sup>. Along the Antarctic Peninsula, however, the extent of winter sea ice has decreased markedly in recent years: the climate in this region has been warming faster than any other part of the planet<sup>35</sup>. Sea-ice proxy studies examining the pre-satellite era have suggested that a significant decrease in sea-ice extent occurred during the 1950s to 1970s<sup>48–50</sup>. The likelihood of a major (~20%) decline in sea ice in the middle of the twentieth century cannot be discounted, and such a significant change in the Southern Ocean would have had major effects on the lower trophic levels, with associated ramifications for the upper level predators of the region — but again, long-term data are scarce.

Estimates of population sizes of air-breathing predators are also fraught with uncertainty: few long-term data exist for any species, and there are also severe difficulties in estimating either their local or global abundance. The krill predators expected to show some recent changes are the baleen whales, seals (largely crabeater and fur) and penguins. Decreases in baleen whale numbers have been inferred from the whaling industry in the past century<sup>51</sup>, but the process of recovery is much more difficult to detect and measure accurately. Similarly, crabeater seals were expected to take up the 'krill surplus' made available by the harvesting of baleen whales, but estimates of abundance before whaling are unreliable, as are the data to support an increase in numbers after whaling. A concerted effort to provide an up-to-date, circumpolar abundance estimate is currently underway<sup>52</sup>. Fur seals have been reasonably well monitored and impressive increases in abundance have been recorded at some locations, although this recovery is taking place some 150 years after the end of their exploitation<sup>53</sup>. Penguins, where monitored, show a variety of both long-term and short-term population changes, which seem as much related to the presence of sea ice as to the fluctuations or changes in their food supply<sup>54,55</sup>. It is difficult to distil a coherent trend for the entire suite of krill predators that might be unequivocally associated with a global or regional decline of krill, although localized studies have shown marked trends for individual species<sup>27</sup>. This is not to say that ecosystem shifts have not taken place; rather, that these may be subtle and complex and will involve species-specific responses to their prey, their competitors and the changing environment.

### Concluding remarks

Despite climate change, intense present and past resource exploitation and the unique sea-ice ecosystems, the polar regions still offer the possibility to carry out end-to-end ecological experiments in relatively undisturbed environments. Future changes in polar marine ecosystems will depend as much on global climate change as on our ability to regulate exploitation pressure at sustainable levels, and such regulation will require greater ecological certainty<sup>56,57</sup>. Some physical changes are already upon us and are altering patterns of human behaviour in the northern polar regions. The livelihoods of the indigenous populations subsisting on subarctic and polar marine mammals have been severely jeopardized because their harvesting techniques tend to be tightly linked to seasonality of sea ice<sup>23</sup>. A year-round high Antarctic krill fishing season has become a reality because of declining sea ice in the



**Box 1 | The life of krill**

Euphausiids are a major component of most shelf and open ocean food webs and can occupy a number of trophic levels. They are considerably larger and more active than copepods, and their size and swarming habit makes them an important link between planktonic organisms and higher trophic levels<sup>43</sup>. Antarctic krill are among the larger euphausiids (up to 6 cm) and can live for 11 years (Fig. 4). Their diet is also highly varied and their complex feeding appendages enable them to collect a wide size-range of food from larger plankton (> 6 µm), particularly diatoms, to copepods. They also feed on ice biota by sweeping the underside of floes<sup>44</sup>. Ingested food is crushed internally in a gizzard lined with teeth that shred even strong-shelled diatoms. Large, dense krill swarms can contain some 10<sup>12</sup> individuals, each animal consuming up to 25% of its body carbon per day, making them globally significant consumers, which can leave little in the water column after their passage<sup>43</sup>. In common with shrimp, which they resemble, krill escape from predators by flips of their muscular tail, and krill swarms react to predators in much the same way as fish schools. Adult krill occur in swarms at concentrations of 30,000 animals m<sup>-3</sup> and can contain up to a million tonnes of biomass (~10<sup>12</sup> individuals)<sup>45</sup>. This has made them the target for the Southern Ocean's largest fishery.

Krill eggs are laid off the shelf break and sink to 700–1,000 m before hatching. The larvae undergo metamorphosis during ascent and congregate under the sea ice during winter where they feed on ice biota in this protected environment. Unlike adults, which can survive without food for many months, larval krill rapidly starve to death, so an adequate winter food supply is crucial for successful recruitment<sup>46</sup>. High recruitment rates in the southwestern Atlantic Sector have been observed in years with extensive winter ice cover, indicating the environmental dependence of early larval stages on ice biota and dense blooms<sup>27</sup>. Adult krill (2 or more years old) spend the winter mainly under the sea ice where they can feed on ice biota, feed omnivorously or starve. Because krill are long-lived animals, their population processes are attuned to cycles in the marine environment beyond the purely seasonal<sup>47</sup>. Consequently, iron fertilization experiments aimed at studying the interactions of higher trophic levels with their herbivorous prey, and their food, would have to be at much grander scales than those conducted so far.

southwestern Atlantic<sup>58</sup>. Hunting bans have led to recovery of some mammal stocks in both polar regions, but sadly the population of Antarctic blue whales, the largest megafauna the world has ever seen, has not yet shown significant signs of recovery<sup>31</sup>. Studies in polar waters tend to have a narrow research focus: biogeochemistry and climate, or biodiversity and conservation, but to understand significant changes occurring at the poles, these approaches will have to be coordinated and combined. The polar regions are changing, in some places rapidly, and where these changes are a result of resource exploitation, the rate of change can be modified through management action. Improving our ability to understand ecological processes can, hopefully, ameliorate the combined effects of climate change and the seemingly relentless human tide of marine resource exploitation. ■

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