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Ecological Responses to Climate Change on the Antarctic Peninsula

The peninsula is an icy world that's warming faster than anywhere else on Earth, threatening a rich but delicate biological community

James McClintock, Hugh Ducklow and William Fraser

The crack of an iceberg splitting away from the Marr glacier reverberates through the halls of the Bio Lab at Palmer Station, on the western shore of the Antarctic Peninsula. That sound has grown increasingly familiar to the three of us. (We've spent a collective total of 36 seasons at Palmer.) The retreat of the Marr glacier—and even more dramatic losses of ice elsewhere on the peninsula—signals ongoing environmental change. The average midwinter temperature here has increased by 6 degrees Celsius since 1950; this is the highest rate of warming anywhere on the planet, five times the global average.

The isolated biological community of the peninsula and its coastal waters evolved in a polar climate that remained relatively stable for many millennia. Now, as the climate shifts, we are trying to document and understand how the ecosystem responds. Our studies focus on three segments of the community. Ducklow works with marine plankton, the small organisms that swim or drift near the sea surface. McClintock's realm is the benthos, the community of bottom-dwelling plants and invertebrate animals. And Fraser studies the penguins and other seabirds that dwell at the triple interface of land, air and sea.

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Climatic Regime Change

The Antarctic Peninsula is the long, curving arm that reaches north from the Antarctic mainland and extends its fingers toward the tip of South America. Forty million years ago, the peninsula was an isthmus connecting the two continents. Then tectonic activity carried Antarctica farther toward the South Pole, opening up the Drake Passage, which is now a thousand kilometers of open water between Cape Horn and the northern extremity of the peninsula.

The creation of the Drake Passage removed the last land barrier to ocean circulation at latitude 60 degrees south. The result was the formation of the Antarctic Circumpolar Current (ACC), which flows from west to east, or clockwise as seen from the South Pole. The ACC is the strongest and fastest of all ocean currents, transporting a volume of water equivalent to 30,000 times the flow at Niagara Falls.

The development of this circumferential current had a profound effect on the Antarctic climate and biota. The ACC isolated the continent from warmer waters and more temperate atmospheric conditions to the north, cooling both the air and the sea. It was probably at about the time the current became established that the permanent ice cap grew to cover almost the entire continent. (Antarctic ice now sequesters almost two-thirds of the planet's freshwater.)

Within the context of this frigid world, the Antarctic Peninsula is unusual in several respects. In part the difference is just a matter of latitude: From its base at 75 degrees south, the peninsula extends 1,500 kilometers north to beyond the Antarctic Circle, reaching 63 degrees at the tip.

Naturally, the climate moderates somewhat with distance from the pole, but there are other factors working as well. Around most of the continent, the ACC is separated from direct contact with the continental shelves and coastal waters by circulatory gyres and by embayments such as the Ross Sea. On the western shore of the peninsula, however, the ACC impinges directly on the continental shelf break, a narrow zone where the sea floor plunges steeply from a depth of about 700 meters to 3,000 meters. The ACC wells upward here and floods onto the continental shelf, which has a mean depth of approximately 400 meters. (The Antarctic shelf is about twice as deep as shelves elsewhere, being depressed like the rest of the continent by the weight of the ice it bears.)

The upwelling of the ACC brings both warmth and nutrients to the coastal waters of the western peninsula. Surface waters there range in temperature from a winter low of just above –2 degrees Celsius (the freezing point of seawater) to a summer high of about +1 degree. The temperature of the ACC water is +2 degrees, with little seasonal variation. Although +2 is far from balmy by the standards of summer beachgoers, the slight warming has a tremendous biological impact.

Figure 1. Penguins, the iconic species of Antarctica, would seem to be right at home in a raging snow storm. But the storm seen here was a late-spring blizzard that had a devastating effect on this nesting colony of Adélie penguins on an island off the western shore of the Antarctic Peninsula. The storm struck on November 19, 2001, when many of the breeding pairs were incubating eggs. The snow itself caused only a minor disruption, but over the next few days warmer weather led to rapid melting. The melt water flooded nests, killing eggs and newly hatched chicks. Warming trends on the peninsula have brought more-frequent spring storms, a factor that has probably contributed to a decline in the Adélie population. (Photograph courtesy of Heidi Geisz.)

The peninsula also differs from the rest of Antarctica in its response to recent global climatic trends. Whereas the continent proper has not warmed appreciably in the past century, there has been a 3.4-degree increase in the mean annual temperature along the peninsula. And, as already noted, the average midwinter temperature has climbed 6 degrees since 1950. If the trend continues, the average midwinter temperature will rise above the freezing point of seawater by the middle of this century. After that, sea ice will not form in most years, leading to a regime change in the ecosystem. Already, in the past quarter-century, the mean extent of sea ice coverage along the western peninsula has declined by 40 percent, and the average annual duration of sea ice cover has shortened by 80 days.

The glaciers and ice shelves along the peninsula are also in retreat. Glacial ice is formed not from seawater but from accumulated precipitation on land, which then flows into the sea to form a shelf. Over the past 50 years, rapid warming has triggered the loss of eight peninsular ice shelves. For example, in 2002 a section of ice the size of Rhode Island broke away from the Larsen B ice shelf on the eastern side of the peninsula. On the western shore, a 400-square-kilometer chunk of the Wilkins ice shelf collapsed just this past March.

A Paleozoic Community

The geological history of Antarctica has presented some obvious adaptational challenges to the inhabitants of the land and the surrounding seas. Some 200 million years ago, when Antarctica was part of the southern supercontinent Gondwana, the climate was temperate and the biota included land plants, insects, reptiles and many kinds of fish. As the continent migrated toward the pole, most of these organisms perished, but a few adapted to the harsh conditions and flourished.

Studies of invertebrate fossils from Seymour Island, along the eastern peninsula, have given us a glimpse of the region's marine fauna 45 million years ago, in the mid-Eocene. Of particular note are thick-shelled gastropods and bivalve mollusks, whose heavy armor indicates an abundance of durophagous predators: organisms that get at their prey by crushing. Such predators include fish with well-developed jaws and large-clawed crabs.

Later in the Eocene, water temperature in the Southern Ocean abruptly fell by 14 degrees Celsius. Among the victims of this rapid cooling were essentially all the durophagous marine predators. These animals must exert strong forces to crack open shells and often

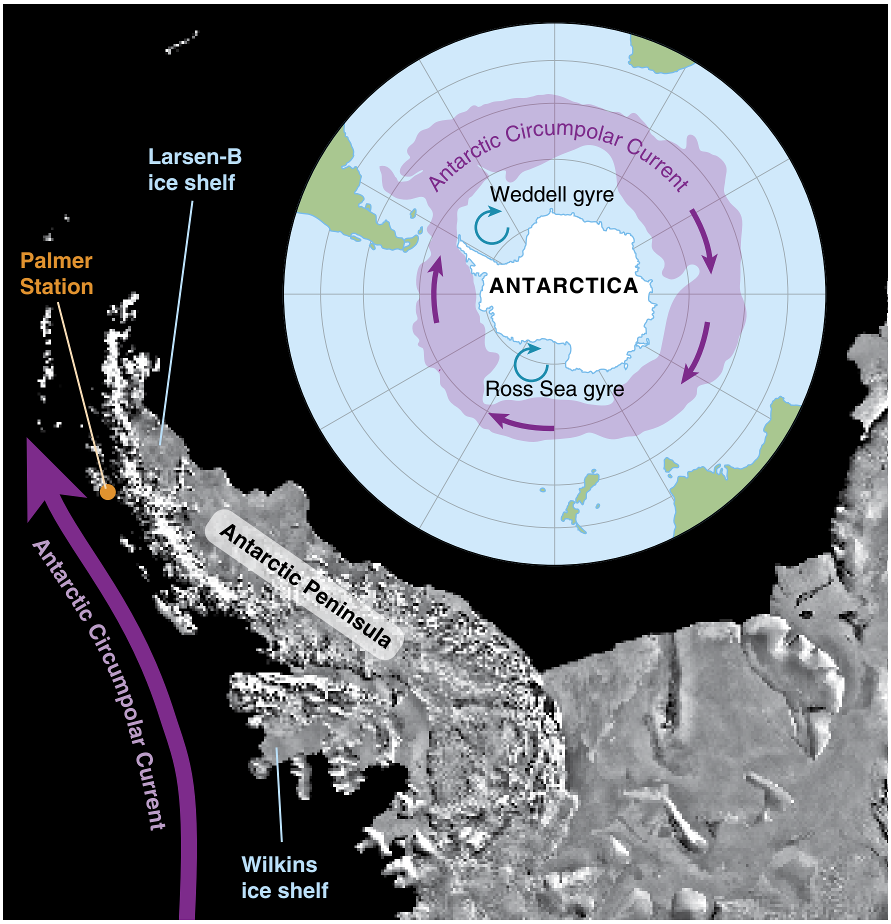

Figure 2. The Antarctic Peninsula, a curving arm of land reaching toward the tip of South America, has the richest biological community on the Antarctic continent. The peninsula is generally warmer than the interior of the continent, in part simply for reasons of latitude. Another important influence on the peninsula is the Antarctic Circumpolar Current, which brings nutrient-rich and slightly warmer waters to the western shores of the peninsula. Elsewhere, the current is separated from the landmass by gyres and embayments. Palmer Station, where the authors conduct their research, is on Anvers Island, off the western coast of the peninsula and just north of the Antarctic Circle.

move rapidly as well; both of these activities are inhibited by low temperature. In the absence of durophagous predators, the invertebrate community on the peninsular continental shelf has lost the defensive shell architectures commonly found in warmer waters. Except for chemical defenses, the invertebrates are poorly equipped to withstand predator attacks.

The benthic community today looks rather like an assemblage of organisms from the Paleozoic Era, before durophagous predators were widespread. Snails, clams and brachiopods have unusually thin, delicate, shells. A preponderance of animals are filter feeders; among them are soft corals, crinoids, bryozoans, tunicates, brachiopods and sponges. Many of the species are endemic—found here and nowhere else. There is a tendency to gigantism among sponges, sea spiders, isopods and ribbon worms (Nemertea). The only common fishes are notothenioids—members of a family whose secret to survival in a sub-freezing environment is a natural antifreeze molecule, a glycoprotein, or sugar-coated protein. The antifreeze probably evolved in a single Antarctic notothenioid species, but a subsequent adaptive radiation has given rise to some 250 species today.

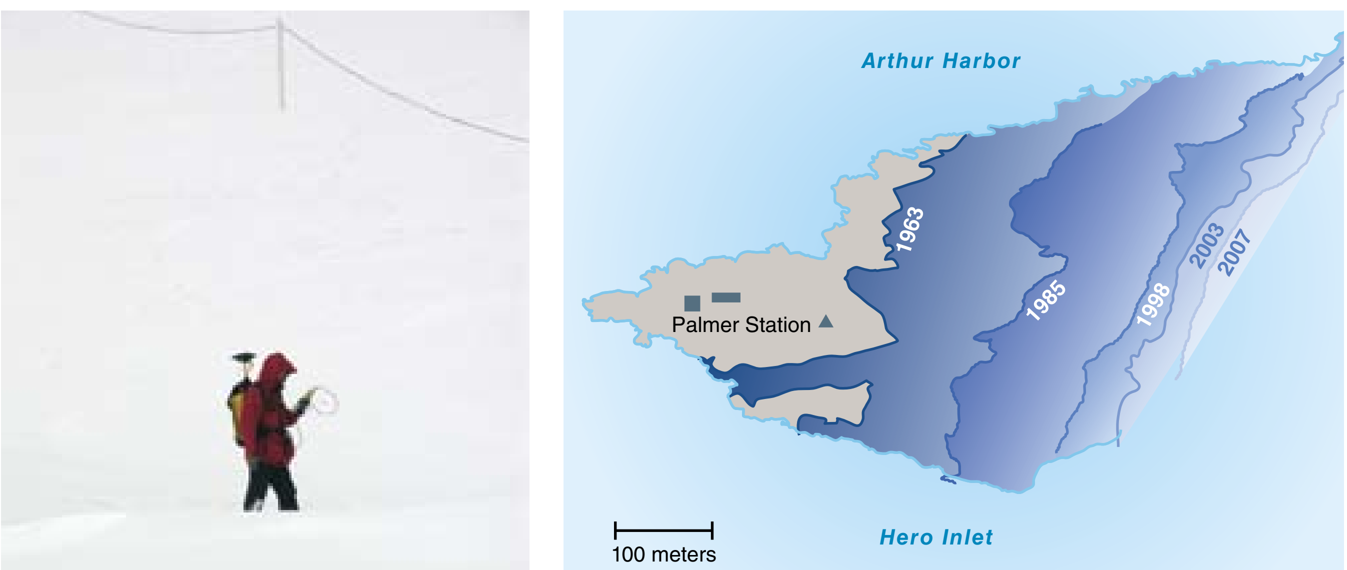

Figure 3. Marr glacier, which once covered most of the island on which Palmer Station is situated, has been retreating since the station was founded in the 1960s. The scientific crew at the station has documented the retreat of the glacial boundary through a series of surveys; in recent years, the survey has been completed by walking along the glacier margin while wearing a GPS-equipped backpack *(photograph at left)*. Whereas the glacier once loomed over the three main buildings of the station, it is now half a kilometer away.

The Base of the Food Chain

The western coast of the Antarctic Peninsula is a highly productive ecosystem, but it is also closely attuned to the rhythms of the physical environment and thus is vulnerable to disruption. Of particular importance are fluctuations in sea ice, both seasonally and from year to year.

A bloom of phytoplankton in spring and summer depends on the annual cycle of the ice. Many single-celled plants overwinter in pockets of liquid within the ice. In the spring melt, the phytoplankton are released and exposed to increased sunlight, stimulating their growth and causing the bloom. Diatoms—single-celled phytoplankton with siliceous shells—are best adapted to the sea ice margin and dominate the blooms over the continental shelf of the western peninsula. The diatoms are the preferred food for Antarctic krill, a key link in the food chain; krill pass energy and nutrients captured by phytoplankton up to penguins, seals and whales.

As regional warming reduces both the extent and the duration of sea ice cover, changes are already evident at most levels of the food web. In some areas, for example, there are indications that diatoms are being replaced by cryptophytes—smaller phytoplankton lacking mineral shells. If such a shift becomes widespread, it will surely have observable effects at higher trophic levels.

Krill, which are crustaceans that resemble shrimp, are the principal Antarctic zooplankton. They are highly dependent on sea ice; without it they cannot complete their life cycle and breed successfully. Juvenile krill congregate under the ice, browsing on the algae growing in fissures and using the ice habitat as a refuge from predators. As sea ice declines, the krill habitat is shrinking in space and time.

In addition to krill, two other groups are major components of the zooplankton: salps and pteropods. Salps are gelatinous, transparent organisms that look a little like jellyfish although they are actually chordates, primitive relatives of the vertebrates. They pump water through mucus feeding webs and skim off the adhering food particles. Individual salps can be as large as 10 centimeters, and colonies are meters long. They can be voracious predators, clearing large volumes of water of all particles larger than a few micrometers. Salps are pelagic organisms, usually inhabiting offshore waters with lower plankton concentrations (their feeding nets become clogged in blooms); they are carried onto the continental shelf by intrusions of the circumpolar current. Salps have few predators, which makes them a dead end in the food chain.

Pteropods are gastropod mollusks, sometimes called sea butterflies; they are swimming pelagic snails with calcium carbonate shells. Like salps, pteropods commonly feed with mucus nets, but they are herbivores, grazing on phytoplankton. Moreover, unlike salps, they have predators and thus participate in the food chain.

As sea ice declines and intrusions of offshore warm water increase in frequency and volume, the various kinds of zooplankton respond differently. A large-scale decline in krill populations has been under way for decades, although changes in sea ice may not be the only cause. Increasing predation could also be a factor, since the regulation of whaling has allowed a slow recovery of krill-eating whale species. But the ongoing reductions in sea ice are expected to have further adverse effects on krill. In contrast, salps may be increasing over the western peninsular continental shelf, in response to changes in ice and water properties. This replacement of krill by salps has potentially grave consequences for an Antarctic food web that is highly dependent on krill as food for larger predators, including penguins.

Shelled pteropods are threatened by another factor related to climate change: ocean acidification. As the level of carbon dioxide in the atmosphere increases, the ocean absorbs some of the excess. The CO_2 lowers the *p*H, and the acidified water dissolves the carbonate shells of mollusks, corals and other organisms. The consequences of acidification could be particularly intense for the shelled pteropods of the Southern Ocean, with detectable effects by late in the present century.

In summary, it appears that current climatic trends are likely to be detrimental to crustacean and molluscan members of the zooplankton, while favoring the "gelatinous" organisms, including the salps as well as tunicates and a few other groups. Similar changes have already happened or are currently in progress for other reasons throughout the world's oceans.

The shifting balance between krill and salps will affect still another planktonic community: bacteria and other prokaryotic microorganisms. But it remains unclear how the bacteria will respond to population changes at higher levels in the food chain. Elsewhere in the world, rising populations of gelatinous zooplankton appear to reroute organic matter into the bacterial biomass. Whether this "microbialization" will

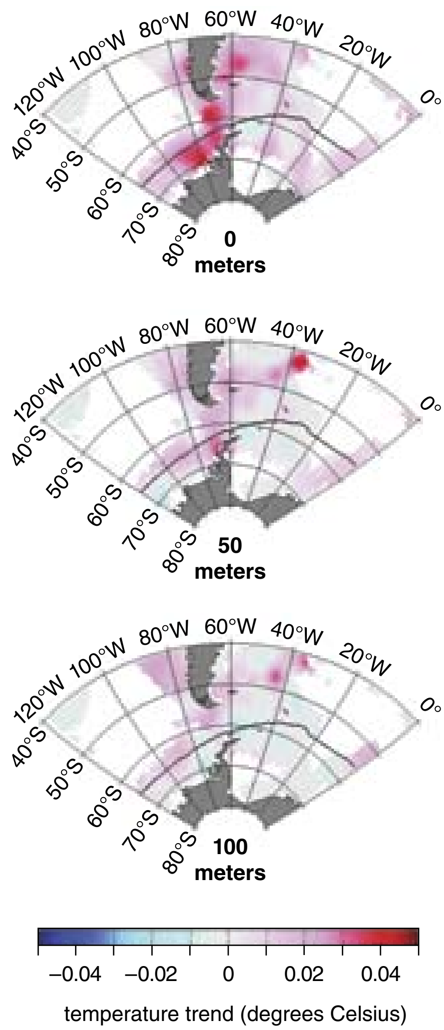

Figure 4. A survey of seawater temperatures indicates a strong warming trend in the region west of the Antarctic Peninsula. The temperature data were analyzed by Michael P. Meredith and John C. King of the British Antarctic Survey, who collated a variety of measurements made between 1955 and 1998, projecting them onto a uniform grid of 1-degree squares. The maps give trends in summer water temperature at three depths—the sea surface, 50 meters and 100 meters. The warming is strongest by far at the surface, suggesting it is brought about largely by atmospheric warming. Another factor is a decline in winter sea ice, which can be both a cause and an effect of warmer seas in summer. (Illustration courtesy of Michael P. Meredith.)

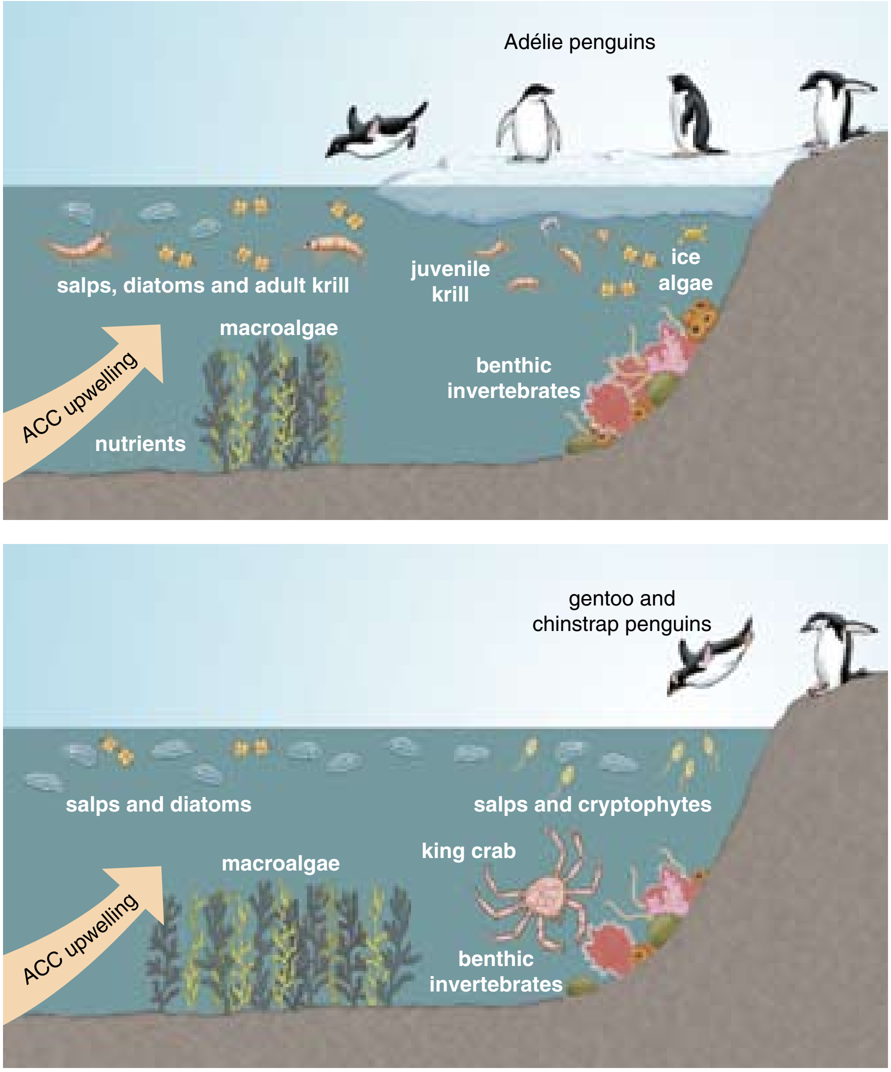

Figure 5. The biological community on the western shelf of the Antarctic Peninsula is highly sensitive to environmental change. A major influence on the existing community *(upper panel)* is the presence of extensive sea ice in winter and its persistence in summer. The ice shelters diatoms and other "ice algae" as well as the juvenile krill that feed on these primary producers. Ice cover is also essential to Adélie penguins, which use it as a thoroughfare to reach isolated feeding "hot spots" nourished by upwellings of the Antarctic Circumpolar Current. Shade from the ice probably limits the territory of the kelp-like macroalgae growing on the sea floor. There is also a thriving community of benthic invertebrates such as sponges and corals. The effects that warmer air and water will have on these organisms cannot be predicted with certainty, but a few likely consequences are shown in the lower panel. Loss of sea ice will be detrimental to diatoms and krill but may favor the gelatinous, filter-feeding organisms called salps as well as small cryptophytes. Scarce winter ice will also disrupt the foraging habits of Adélie penguins, whereas chinstrap and gentoo penguins prefer ice-free regions. Macroalgae might be able to expand their territory. The most dramatic (but also most speculative) consequence of warming could be an influx of crabs or other predators that feed by crushing their prey.

also happen in cold Antarctic waters is not yet known.

Ironically, atmospheric carbon dioxide—the main culprit in global warming—may in turn be susceptible to influence by ecosystem changes in the Southern Ocean. Planktonic organisms take up CO_2, converting it into carbon-rich organic compounds, some of which ultimately fall to the sea floor and are withdrawn from active circulation. The effect of various marine population shifts on this biological carbon pump is not known. An abundance of salps could increase carbon sequestration, because salps excrete large, rapidly sinking fecal aggregates. Bacteria, on the other hand, break down complex carbon compounds and release CO_2. If this microbial respiration increases, oceanic CO_2 storage may be reduced, creating a positive feedback loop: CO_2 induces warming, which decreases the CO_2 capacity of the oceans, bringing further warming.

Forests of the Antarctic

Dive beneath the water's surface near Palmer Station and you enter a surprisingly lush and diverse benthic community. The steep rock slopes are densely populated with sessile invertebrates such as sponges and corals, along with a variety of grazing mollusks and other bottom-dwelling animals. The plant community is equally impressive. Some 90 percent of the sea floor is covered by large algae, whose waving fronds form dense stands much like the kelp beds of temperate seas. These are the forests of Antarctica.

All of these organisms are obviously well adapted to life in frigid water. How will they respond to the climatic changes expected in the coming decades and centuries?

The giant algae could in some respects be beneficiaries of warming. Their growth is limited mainly by access to sunlight, since they are shaded by sea ice for part of each year. As warming continues to erode the extent of the ice, the undersea forests are likely to expand into territory previously unavailable for colonization. But the further effects of changes in the plants' environment are hard to predict. With more energy available for photosynthesis, the algae may invest more of their resources in chemical defenses to prevent herbivores from consuming their tissues. The result could be a fundamental change in the dynamics of the community of organisms supported by the algae.

Among the benthic invertebrates, one potential trouble spot is in the timing of embryonic and larval development. Data gathered for species from various latitudes show a striking correlation between water temperature and time to maturity. The developmental processes are much slower in the Arctic and Antarctic, where reaching adulthood can take four or five times as long as it does in the tropics. Moreover, at the cold end of the temperature scale the slope of the graph is very steep, so that even slight temperature shifts correspond to a substantial change in development time. This finding suggests that environmental warming could shorten the embryonic and larval stages of life. The consequences of any change in the duration of development could be disastrous for those species that synchronize their breeding cycle with seasonal planktonic blooms. The eggs would hatch and the larvae would emerge into a sea that had insufficient resources to support them.

Early studies of polar ecology suggested that synchronization should not be a critical issue, because most immature offspring were expected to be "brooded"—supported by yolk or other parental resources rather than feeding on their own. This idea is so widely accepted that it has a name: Thorson's Rule, after the Danish zoologist Gunnar Thorson. However, more recent studies have revealed that some of the most ecologically dominant Antarctic benthic invertebrates have larvae that do indeed feed on plankton. As seawater temperatures along the Antarctic Peninsula continue to rise rapidly, these species may have their life cycle disrupted. Of course some of them may also be adversely affected in more direct ways by the temperature change. From a human perspective it may seem incongruous to speak of "thermal stress" in water a few degrees above freezing, but that is indeed a hazard for cold-adapted life forms, and some of them may not survive.

Another prospective community-altering impact was vividly brought to our attention recently when adult specimens of the spider crab *Hyas araneus* were dredged up from waters off King George Island, near the northern tip of the Antarctic Peninsula. This crab species is native to sub-Arctic northern waters and probably reached the Antarctic by traveling as larvae or juveniles in ship ballast water. What's most surprising is that the crabs were able to survive and grow in the colder waters of the Antarctic.

Crabs run into serious difficulty at very low temperature. As in many other animals, their activity level is reduced in the cold, but in addition they face a peculiar physiological challenge. Crabs cannot cleanse their bloodstream of magnesium, which has a narcotic effect. The magnesium concentration is no greater in cold water, but the narcosis is more severe there because the animals are already slower-moving. Below a threshold temperature, the crabs are immobilized and die.

Warming trends along the peninsula are removing this physiological barrier. The specimens discovered at King George Island are not the only evidence. In 2007 a population of large, deep-water king crabs (*Paralomis birsteini*) was discovered at a depth of 1,100 meters on the Antarctic continental slope. At these depths, the temperature is slightly higher than it is in shallow water, allowing the crabs to overcome the magnesium narcosis.

An invasion of crabs would present a significant threat to benthic invertebrates that lack defenses against crushing predators. And, as with the planktonic shelled pteropods, ocean acidification magnifies the risk. As absorbed CO_2 continues to lower the *p*H of seawater, benthic invertebrates whose larvae or adults rely on calcified skeletal elements may either be killed outright or, with weakened shells, become increasingly vulnerable to durophagous predators. Evidence from temperate latitudes indicates that larvae of such key invertebrates as oysters and sea urchins can suffer significant decalcification-related mortality when exposed to seawater with even modestly lowered *p*H. Chemical and physical properties of southern seawater are

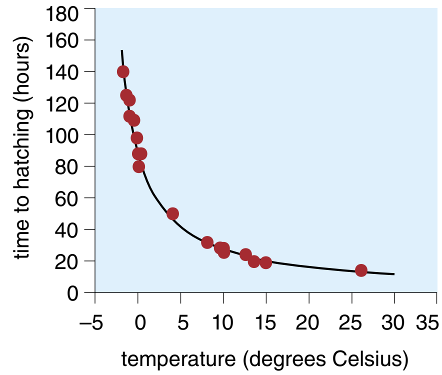

Figure 6. A correlation between water temperature and development time in marine organisms suggests that the Antarctic fauna would be extremely sensitive to environmental warming. The data record the duration of embryonic development for echinoderm species (sea urchins and starfish) living in climates that range from polar through temperate to tropical. At the cold end of the spectrum, where temperatures are barely above the freezing point of seawater (–2 degrees Celsius), the curve is steep. A change of a degree or two can slow development significantly. For organisms that synchronize their development with events such as plankton blooms, such a shift would be disastrous.

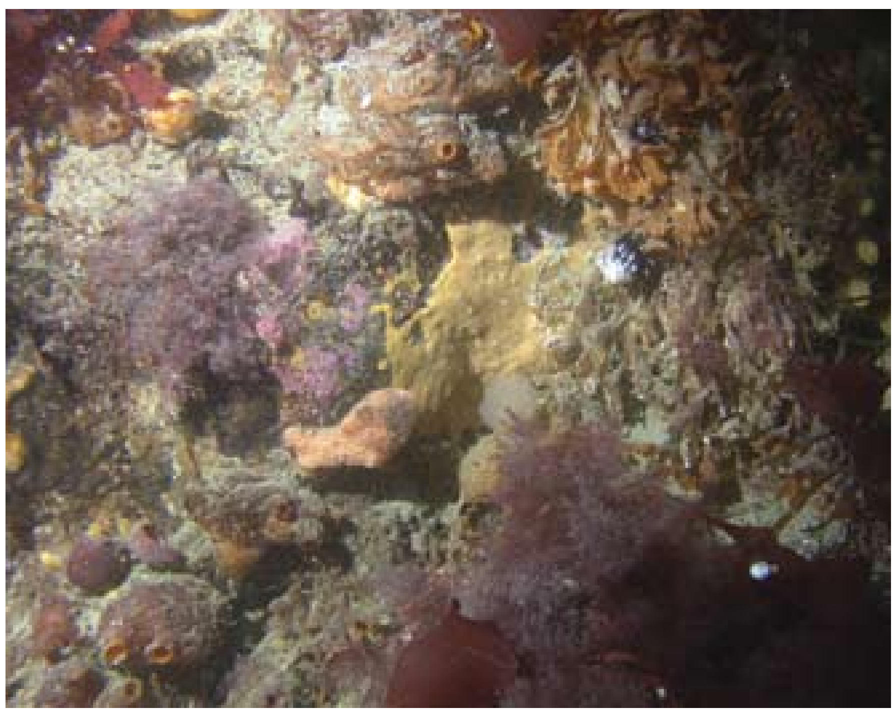

Figure 7. A diverse and unusual community of benthic invertebrates thrives in the waters off the western Antarctic Peninsula. The bright yellow patch near the center of the image is an encrusting sponge; several orange tunicates with conspicuous siphon openings are also visible, along with a variety of soft corals. At the lower left, just above a tunicate with a pair of siphons, are two brachiopods with reddish shells. In addition to these sessile organisms there are also grazing animals, including a small, pale-shelled snail at the lower right and two gray-and-black nudibranchs to the right of the yellow sponge. A distinctive feature of the Antarctic invertebrate community is a lack of defenses against predators that attack their prey by crushing. Such predators have been absent since the Eocene, leading to delicate, thin-shelled body plans. (Photograph courtesy of Bill Baker.)

Figure 8. Colonies of algae, anchored to the sea floor and extending fronds toward the surface, form dense forests in areas off the western Antarctic Peninsula, much like the kelp beds of temperate oceans. The species visible here is *Cystosphaera jacquinotii*. (Photograph courtesy of Bill Baker.)

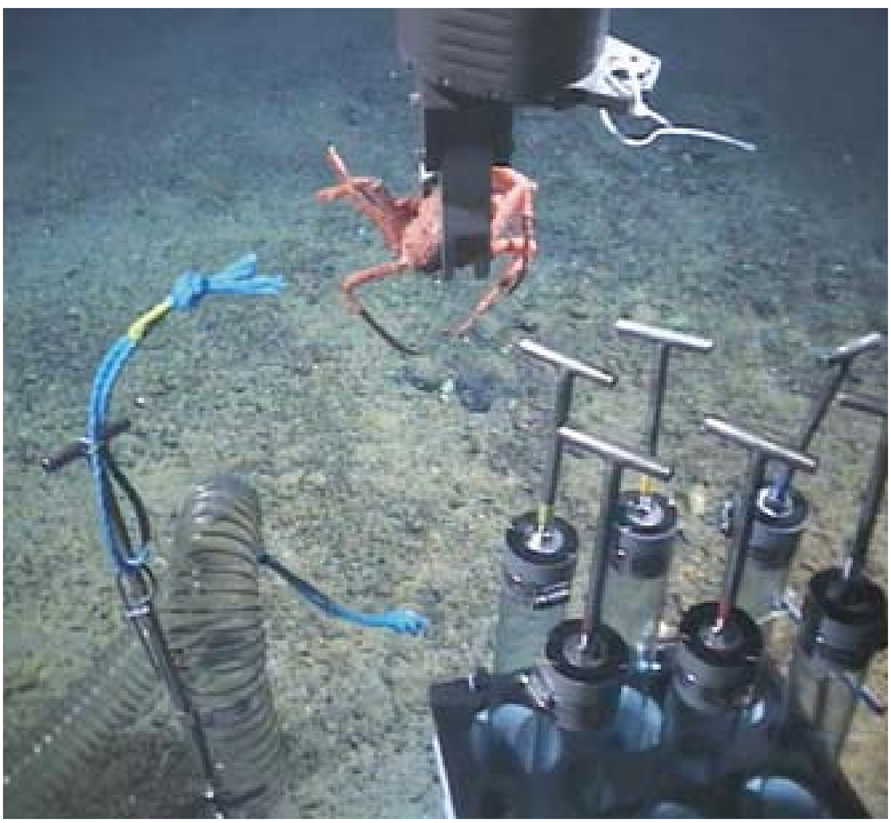

Figure 9. Crabs native to the deeper waters of the Southern Ocean have lately been discovered on the Antarctic continental slope, within a few hundred meters of depths where they would threaten the benthic invertebrates of the continental shelf. Crabs cannot tolerate extreme cold; in the Antarctic they have been confined to deep basins, which are slightly warmer than surface waters. Further climate change could allow them to expand their range. The specimen seen here, a king crab of the species *Paralomis birsteini*, was captured in 2007 on the inaugural voyage of the remotely-operated vehicle *Isis* at a depth of 1,100 meters. The image, extracted from a video sequence, has been enhanced to remove artifacts and increase resolution. (Photograph courtesy of Sven Thatje.)

known to inhibit calcification, and so it seems likely that the biota of this region will be among the first to show the effects of global ocean acidification.

Displaced Penguins

The top predators of the Antarctic Peninsula—the seabirds and seals—are highly sensitive indicators of ecosystem change. Because they are long-lived and wide-ranging, their life histories integrate the effects of marine environmental variability over long periods and large areas. From a more practical point of view, these species are also good candidates for the role of canary in the coal mine because they are abundant and readily accessible. They breed on land (but feed at sea), and so it is comparatively easy to gather data on their reproductive success, their population, their diet and other aspects of their biology. In some sectors of Antarctica, databases on these predators now span seven decades, making them among the best-studied wild vertebrates on Earth. Importantly, the long time series allow investigators to distinguish genuine trends from mere ecosystem noise.

On the western Antarctic Peninsula, and specifically in the vicinity of Palmer Station, one such study has been going on for more than 30 years. The subjects of the study are three closely related species of penguins, the Adélie, the gentoo and the chinstrap, collectively known as the brush-tailed penguins because of their long, stiff tail feathers.

Although the three penguins are members of the same genus, they have quite different life histories and favor different habitats. Adélie penguins are a true Antarctic species, distributed all around the coast of the continent, though only in areas where sea ice can be relied on to last throughout the winter. Chinstrap and gentoo penguins, in contrast, tend to avoid areas with persistent sea ice; they evolved in sub-Antarctic habitats where conditions favor open water with only minimal sea ice. At Palmer Station, Adélies are in decline, whereas gentoos and chinstraps are growing more abundant.

Adélie penguins have always occupied territory near Palmer Station, but gentoos and chinstraps were unknown there until recent years. The first chinstrap colony was established in 1976, and gentoos arrived in 1994. Thus biologists from the station have been able to observe the entire history of these local populations. Carbon-14 dating of material excavated from local colonies (both active and abandoned) reveals evidence of Adélie occupation going back 700 years, but no hint of the other two brush-tailed species. Thus it appears the environmental conditions promoting the local presence of gentoos and chinstraps are unprecedented in the period covered by this record.

Adélie penguin populations are decreasing throughout the mid- to northern Antarctic Peninsula, and there is wide concurrence that this regional trend is correlated with a gradual decrease in the availability of winter sea ice. However, the exact role played by sea ice in the ecology of the species has remained uncertain, primarily because few winter studies have been conducted. In a recent effort to address this gap in our understanding, the penguins' movements, distribution and foraging were monitored continuously for 24 months using satellite telemetry, at-sea censuses and extensive field collections of diet information.

A key finding of the study is that Adélie penguins find their prey in winter primarily at isolated "hot spots" where the topography of the sea floor creates upwellings of warmer water from the circumpolar current; the upwellings in turn promote congregations of krill and fish. The birds' access to these hotspots requires winter sea ice. Adélie penguins do not forage at night, and hence they cannot travel far to find food during the short days of the polar winter. Only by migrating over the sea ice can they stay close enough to their feeding grounds. As sea ice continues its long-term retreat in the waters of the western Antarctic Peninsula, Adélie penguins will lose access to the most productive winter foraging regions.

A second process implicated in the shrinking of Adélie populations is increasing snowfall over the Antarctic Peninsula. Although it may seem counterintuitive that a polar species would be adversely affected by snow, Antarctica is a polar desert with low average precipitation, and it is in this environment that Adélie penguins evolved. Snow has been increasing over the peninsula since at least the beginning of the 20th century. The loss of sea ice is one factor causing this change in weather patterns. Exposing open ocean to the atmosphere brings higher levels of evaporation and increasing cloud cover. Spring blizzards during the Adélie penguins' breeding season (November) have increased in frequency and severity. The storms kill large numbers of eggs and chicks when the snow eventually melts and floods the nests.

Some of the same factors that are negatively affecting Adélie penguins are helping chinstrap and gentoo penguins to prosper. Both of the latter species have maintained their sub-Antarctic breeding chronologies; by breeding approximately three weeks later than Adélie penguins, they reduce the risk of nest flooding in the aftermath of spring blizzards. In winter, both species forage successfully in ice-free areas. Chinstrap penguins accomplish this by migrating north beyond the sea-ice zone. Gentoo penguins winter at their summer breeding colonies, but they choose sites for these colonies close to areas where fast currents or an upwelling of warmer water ensure that sea ice does not persist.

Ice, Krill and Penguins

Much remains to be understood about the food web that culminates with penguins and other avian and mammalian predators. Some two decades ago, the prevailing model for the dynamics of these populations was the "krill surplus hypothesis." According to this view, krill populations had long been held in check by baleen whales, but when those whales were nearly exterminated in the 20th century, krill were released from predation; the ensuing surplus led to significant population growth in other krill-dependent predators. This explanation no longer seems fully adequate. Although krill are indeed a key component of the food web and critical to the diets of many top predators, the surplus hypothesis cannot explain the population trends in brush-tailed penguins, for example. Because all three species have diets dominated by krill, a surplus would

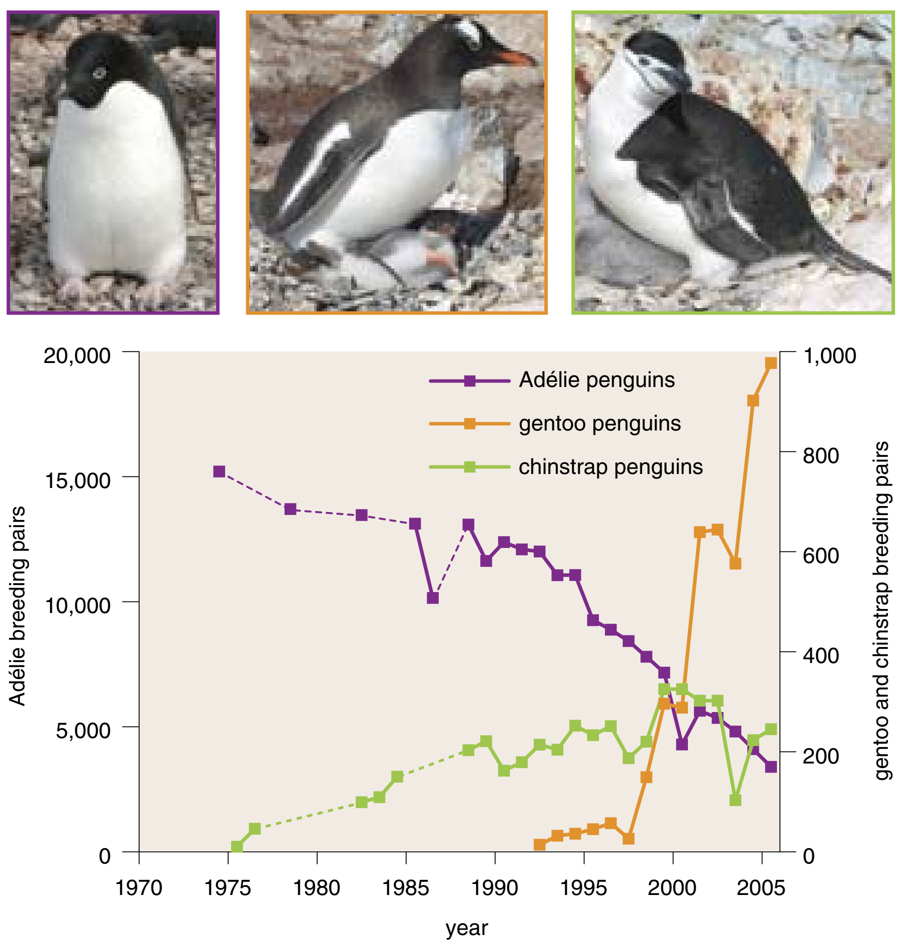

Figure 10. Shifts in the penguin population on the western Antarctic Peninsula are attributed to changes in precipitation patterns and sea ice. Adélie penguins *(scale at left)* are native to the region and are still the most abundant species, but their population has dropped to a third of its level 30 years ago. The birds are adversely affected by spring blizzards and a loss of sea ice. Gentoo and chinstrap penguins *(scale at right)*, whose traditional territory is far to the north, have become established in the area near Palmer Station for the first time in at least 700 years.

Figure 11. Flooding of nests following a spring blizzard ends the once-a-year breeding season for a pair of Adélie penguins. The parents are the two birds facing the nest. The female, at left, was unable to hold off laying the egg until after the storm passed, and the embryo has failed to survive. The storm is the same one shown in Figure 1, but a day later and on a different nearby island. (Photograph courtesy of Heidi Geisz.)

be expected to produce similar trends in all of them.

An analogous situation has been observed among seals. Like Adélie penguins, Weddell seals are ice-dependent, and their populations have plummeted, while the populations of ice-avoiding fur and elephant seals have increased significantly. Of the three species, only fur seals are krill-dependent. An obvious inference is that sea ice, rather than diet, is the dominant factor governing the animals' response to climate change.

In the years since the krill-surplus hypothesis was first put forward and then challenged by the ice-reduction hypothesis, we have learned that krill themselves are an ice-dependent species. Without sea ice, krill do not reproduce successfully because the larvae need to graze on phytoplankton on the underside of the ice to survive winter. Along the northern half of the western Antarctic Peninsula, and in much of the Atlantic sector of the Southern Ocean, there is no krill surplus; on the contrary, this area has experienced an 80 percent decrease in krill abundance over the past 30 years, attributed to loss of winter sea ice.

Theories of top-predator population dynamics are necessarily shifting to take into account changes in both krill abundance and winter ice cover. Sea ice is increasingly regarded as the variable that mediates food-web interactions. The extent of the ice has a direct impact on krill reproductive success and abundance. Then the presence or absence of ice determines which predators are best able to reach the prey populations. This double effect of sea ice may explain why some krill-dependent but ice-avoiding predators, such as gentoo penguins, have continued to increase even as krill abundance has decreased.

Our collective observations, spanning microbiota to megafauna and encompassing the many complex relationships between taxa, paint a picture of the Antarctic Peninsula as an environment undergoing unprecedented ecological shifts in response to climate change. We would not claim to fully understand all the mechanisms driving the patterns we have observed; we are acutely aware that much more research is needed. But we have learned enough to conclude that this unique ecosystem is in peril. We sound an urgent call to mitigate all the factors under human control that are contributing to global climate change.

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