Anthropogenic impacts on marine ecosystems in Antarctica

Richard B. Aronson,1 Sven Thatje,2 James B. McClintock,3 and Kevin A. Hughes4
1Department of Biological Sciences, Florida Institute of Technology, Melbourne, Florida. 2School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton, United Kingdom. 3Department of Biology, University of Alabama at Birmingham, Birmingham, Alabama. 4British Antarctic Survey, Natural Environment Research Council, Cambridge, United Kingdom

Address for correspondence: Richard B. Aronson, Department of Biological Sciences, Florida Institute of Technology, 150 West University Boulevard, Melbourne, Florida 32901. raronson@fit.edu

Antarctica is the most isolated continent on Earth, but it has not escaped the negative impacts of human activity. The unique marine ecosystems of Antarctica and their endemic faunas are affected on local and regional scales by overharvesting, pollution, and the introduction of alien species. Global climate change is also having deleterious impacts: rising sea temperatures and ocean acidification already threaten benthic and pelagic food webs. The Antarctic Treaty System can address local- to regional-scale impacts, but it does not have purview over the global problems that impinge on Antarctica, such as emissions of greenhouse gases. Failure to address human impacts simultaneously at all scales will lead to the degradation of Antarctic marine ecosystems and the homogenization of their composition, structure, and processes with marine ecosystems elsewhere.

Keywords: Antarctic Treaty; Antarctica; biodiversity; biological invasion; biotic homogenization; conservation; global warming

Introduction

Although terrestrial impacts in Antarctica have been recognized for decades,1–3 the marine systems were assumed to be protected from human influences by two attributes: the physical barrier to water exchange created by the Antarctic Circumpolar Current (ACC; Fig. 1) and the related physiological barrier created by cold sea temperatures at high southern latitudes. The ACC, one of the most powerful ocean currents on Earth, has physically isolated the Southern Ocean (SO) from adjacent seas for millions of years. The oceanographic frontal system of the ACC, especially the Polar Front (known as the Antarctic Convergence in the more traditional literature), also protects the SO physiologically from life thriving in warmer, Subantarctic waters. The steep drop in temperature across the Polar Front is a major physiological barrier to colonization by any organism insufficiently adapted to polar temperatures. For example, the absence from Antarctic waters of reptant decapod crustaceans (benthic, walking decapods, including brachyuran crabs, astacid lobsters, and anomuran king crabs) is a direct result of their physiological intolerance of cold sea temperatures.4,5

A recent review of the geography of human impacts on marine ecosystems described the waters surrounding Antarctica as being among the least affected in the World Ocean.6 This ranking is no cause for celebration considering the multifarious crises facing marine ecosystems worldwide; not doing as poorly as others that are in terrible shape is hardly tantamount to having a clean bill of health. Furthermore, the assessments of the polar regions were limited by gaps in scientific information and did not include projections of future impacts.6

The marine ecosystems of Antarctica face immediate impacts on local to regional scales that include overfishing, pollution, and the introduction of alien species. They are also vulnerable to longer-term impacts from global climate change, specifically
rising sea temperatures and ocean acidification. Polar ecosystems are especially sensitive to these two aspects of global change, and the deleterious effects of warming and acidification will occur sooner in the marine environment than one might assume from the modifier “longer-term.” Climate change is already causing perceptible changes on a decadal scale, reversing at an accelerated pace processes and resultant biotic patterns that are known to have occurred during past climatic shifts.

We begin with a brief overview of Antarctic marine systems and the effects of the polar environment on marine life. We then review and synthesize what is known about the impacts of local, regional, and global perturbations of marine environments surrounding the Antarctic continent. Environmental disturbances and stresses generated at all three scales are occurring simultaneously at present, and the interactions of small- and large-scale disruptions are reorganizing marine food webs in Antarctica. Whether or not similar reorganizations occurred in the past, the salient issues are the rates at which they are now occurring and their desirability in terms of economics, aesthetics, ethics, and human survival.

**Marine environments of Antarctica**

It is a truism that the Arctic is an ocean surrounded by continents, whereas the Antarctic is a continent surrounded by ocean. The SO, the body of water that surrounds Antarctica, is bounded to the south by the continent itself and to the north by the ACC (Fig. 1). The SO covers approximately 34.8 million km², or about 9.6% of the surface area of the World
The Arctic Ocean receives considerable input of fresh water from continental runoff, compared to virtually no fresh water running off from Antarctica into the SO.2,7 The ACC, also known as the West Wind Drift, is a complex, wind-driven oceanographic structure. Traditionally viewed as a physical barrier isolating the SO from the rest of the World Ocean, the ACC is, in reality, porous like other ocean currents.8 Eddy formation is particularly active off southern South America, the closest continental-shelf environment to Antarctica.9,10 It is here that the Andes mountain range submerges to form the Scotia Arc. The Scotia Arc is a chain of ridges, seamounts, and islands east of the Drake Passage, which is the body of ocean between the southern edge of Tierra del Fuego and the South Shetland Islands. The Scotia Arc re-emerges as the mountain range that comprises the Antarctic Peninsula. Despite the oceanic and benthic bridges across and under the ACC, the Antarctic fauna is isolated, with at least 50–60% species-level endemism.11

Pelagic food webs in Antarctica are far more complex than the diatoms, krill, penguins, and whales that have monopolized the traditionally simplistic view of the system.2,12 Antarctic food webs, like pelagic food webs elsewhere, include a diversity of primary producers and consumers, as well as important microbial components. The break-up of sea ice in the austral spring and summer increases primary productivity dramatically, providing the shelf benthos with a brief injection of carbon that in most locations accounts for the majority of energy input for the year.13,14

A number of authors have highlighted the unique physical oceanography of Antarctica and its biotic consequences.7,15 The continental shelves surrounding Antarctica are short in horizontal extent, steeply sloping, and very deep compared to shelves elsewhere in the world. Antarctic shelves average 450 m in depth and extend to >1000 m at their deepest. Shelf breaks in Antarctica are correspondingly less distinct than elsewhere in the world. The weak temperature gradient from shelf depths to deep water and the unusual bottom topography have allowed elements of the deep-sea fauna to move down and back up the shelf and slope as glaciers have advanced and retreated. Such macroecological migrations account in part for the deep-sea affinities of the shelf fauna.15

The constancy of sea temperatures, which generally hover within a few degrees of the freezing point of seawater, and the short, predictable growing season have combined to drive the evolution of a cold-adapted, slow-growing, long-lived, stenothermal invertebrate fauna in benthic habitats.16 The primary source of physical disturbance is the scouring of shallow bottoms by grounded icebergs.17 In addition to its ecological impacts, ice scour over geological time has complicated historical reconstructions of the fauna and its origins by erasing much of the Pleistocene and Holocene fossil record on the Antarctic shelves.18

Benthic food webs in coastal marine habitats from the Arctic to the Subantarctic are dominated by durophagous (skeleton-breaking) predators, principally teleostean (modern bony) fishes, neoselachian (modern) sharks and rays, and reptant decapods. The near absence of these modern, durophagous taxa in Antarctica stems from the idiosyncrasies of historical biogeography, physiological tolerance, and phylogenetic constraint.19 With essentially no fast-moving shell-crushers structuring benthic communities in Antarctica, the top predators of the shallow-bottom fauna are asteroids (sea-stars), nemerteans (ribbon worms), pycnogonids (sea spiders), and other slow-moving invertebrates of a Paleozoic functional grade (Fig. 2).20 The deep-sea influence and the absence of post-Paleozoic predators permit dense populations of epifaunal suspension feeders to thrive in shallow-benthic habitats, conferring on Antarctic nearshore communities a distinctly anachronistic, Paleozoic character.19 Paleontological data from Seymour Island, off the Antarctic Peninsula, suggest that the trend toward a retrograde benthic ecology began in the Eocene around 41 million years ago when a sharp drop in coastal sea temperature drastically reduced durophagous predation.21

Low carbonate saturation states in the SO (and in the Arctic Ocean) combined with low temperatures make calcification in Antarctica (as well as the Arctic) an energetically costly process.22–24 The limited capacity of organisms to calcify either their feeding apparatus or their architectural defenses against predation, and suppression of the power output of muscle tissue at cold temperatures, are, in addition to the absence of modern predators, reasons for low levels of durophagy in Antarctica.19,25–27 Calcifying planktonic organisms, including
Figure 2. Elements of the benthic fauna in Antarctic shelf habitats that are of a Paleozoic functional grade. (A) Aggregation of predatory seastars, *Odontaster validus*, at McMurdo Sound, 32 m depth. Also visible are giant nemerteans, *Parborlasia corrugatus*. (Photo by R.B. Aronson.) (B) Aggregation of *P. corrugatus* at McMurdo Sound, 32 m depth. (Photo by R.B. Aronson.) (C) Cluster of Antarctic brachiopods, *Liothyrella uva*, at Signy Island, South Orkney Islands, 20 m depth. Two sea urchins (*Sterechinus neumayeri*) and a sea cucumber (*Cucumaria* sp.) are visible at the top of the photograph. (Photo by Simon Brockington, courtesy of the British Antarctic Survey.) (D) Dense population of ophiuroids, *Ophionotus victoriae*, on the Weddell Sea shelf at a depth of 289 m. The two larger individuals are encrusted by sponges. The fish is *Pagetopsis macropterus*, a nototheniid. Notothenioids are the only teleosts that persist in benthic shelf environments in Antarctica, surviving by virtue of the antifreeze glycoproteins (AFGPs) they produce to prevent ice crystals from forming internally. They are not durophagous, which explains the lack of a flight response in the ophiuroids. (Photo by Julian Gutt, © Alfred Wegener Institute/Marum, University of Bremen; used with permission.) (E) Serolid isopod, *Frontoserolis bouvieri*, near Palmer Station, Anvers Island, Antarctic Peninsula. Serolids are similar to trilobites in gross morphology and ecological function, although they are phylogenetically distinct. (Photo by Dan Martin; used with permission.) (F) Sessile and semi-mobile suspension-feeders in a soft-sediment habitat on the Weddell Sea shelf, 304 m depth. The suspension-feeders include crinoids, sponges, cnidarians, and bryozoans. (Photo by Julian Gutt, © Alfred Wegener Institute/Marum, University of Bremen; used with permission.)

Thecosomatous (shelled) pteropods, currently live close to the limit of their ability to secrete shells. Ocean acidification will soon pose serious risks to these calcifying organisms in Antarctica and, therefore, to the higher trophic levels that depend on them (see section “Ocean acidification”).

**Impacts of local- to regional-scale human activities**

**Historical whaling and sealing**

Whaling and sealing over the past few centuries have dramatically reduced populations of apex predators.
in the SO. Sealing dates back to 1788, when British and American sealers moved into the SO following Captain Cook’s reports on the abundance of large, mammalian predators in those waters. Both whaling and sealing ceased abruptly in the first half of the twentieth century as stocks declined precipitously. At South Georgia, which remained one of the more profitable hunting areas, British legislation attempted to counteract the declines in stocks through protection of breeding grounds and more restrictive hunting licenses. These actions allowed stocks of southern elephant seals (Mirounga leonina) and fur seals (Arctocephalus gazella) to recover.29

Industrial-scale whaling in the SO began at Grytviken, South Georgia in 1904 and ended with the 1965 season. Baleen oil was an essential product during the Industrial Revolution; it was a superior lubricant to mineral oil, and it was used in pharmaceuticals and other chemical products. Whale meat and bones were ground and used as fertilizer and feed for livestock. From 1905 to 1965, ∼175,000 whales were processed at South Georgia alone, and overall 1.5 million whales were removed from the SO ecosystem (http://www.sght.org/). It should be noted that illegal and unreported whaling, primarily by Soviet factory ships, continued into the mid-1980s.30

A prominent example of the shared history of pelagic top predators in the SO over the past two centuries is that of the southern elephant seal. Historically, southern elephant seals existed far beyond the species’ current range, which today is predominantly Subantarctic.31 They were close to extinction following uncontrolled hunting in the nineteenth century; however, hunting ceased at South Georgia in 1964. Southern elephant seals have since experienced a population rebound following protection of the species, but they failed to regain their former geographic range. It remains unclear why overall numbers have decreased significantly by about 50% over the last 40 years, with the exception of colonies outside the SO, at Peninsula Valdés, Patagonia, Argentina.29,32–34 One hypothesis is that, following protection from hunting, the species’ rapid recovery caused it to overshoot carrying capacity, and the population has since equilibrated in competition with other marine predators.29 Overfishing of cephalopods and deep-water fishes (primarily notothenioids), which form the majority of their prey in cold waters, could be the primary determinant of population sizes of elephant seals.

Today, all whales and seals in Antarctica are protected from hunting through international agreement overseen by the International Whaling Commission (IWC). Japan is the only country that still exploits whales in the SO, doing so under the guise of scientific research. Japan has thus far prevented the IWC from establishing the SO as a sanctuary for whales.35 At present, Japanese whales predominantly target minke whales (Balaenoptera bonaerensis),36 and the country has not demonstrated any willingness to end its whaling activities in Antarctica.

Recent changes in the abundance of top predators may also be the result of climate-mediated shifts in the pelagic system.37 In addition, fishing pressure has caused most stocks to decline, potentially affecting the food sources of whales and seals (see above and section “Fishing pressure” below). The impacts of climate change are, therefore, difficult to disentangle from the effects of long-term human exploitation.38

Fishing pressure

Significant levels of fishing, primarily on notothenioids, commenced in the Scotia Sea area in 1962. Fisheries in the SO subsequently concentrated on the Scotia Sea, including South Georgia; the western Antarctic Peninsula (WAP); and the islands of the southern Indian Ocean, including Crozet, Kerguelen, Heard, and the Prince Edward Islands. Catches varied widely during the first decades of exploitation, a pattern that was likely driven by the effects of environmental variability on recruitment. Long-term patterns in almost all finfish species and their predators, however, reveal the impact of fisheries in causing the collapse of stocks.38 Today, several fish stocks have plummeted to less than 20% of the original stock sizes.39,40 Fisheries are now controlled by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR; see section “The Antarctic Treaty and other controls”), and many fisheries in the Atlantic sector of Antarctica have been temporarily closed to exploitation of key target-species such as the Patagonian toothfish, Dissostichus eleginoides. However, fishery regulations are generally not enforced, and illegal fishing activity exceeds legal catches in some sectors of the SO.41 The reduction of fish stocks, with little sign of
recovery,\textsuperscript{38} appears to be having a drastic impact on the middle trophic levels, which have effectively been reduced to dominance by Antarctic krill (\textit{Euphausia superba}) and myctophid fish.\textsuperscript{42,43}

The Soviet Union began a fishery for Antarctic krill in the early 1960s, and several other nations joined the fishery in the 1970s and 1980s.\textsuperscript{44} Krill are directly consumed by humans, used as fish bait, and employed as fish feed in aquaculture and the aquarium trade. The catch peaked in the early 1980s and then declined through the 1990s and early 2000s. CCAMLR sets catch quotas that are considerably higher than current landings. The ecological impact of the krill fishery in Antarctica is poorly understood, but declining stocks in the SO, possibly caused by a reduction in sea ice (see section “Global warming”), as well as a recent increase in fishing effort, are cause for concern.\textsuperscript{45,46}

\textbf{Shipping traffic}

Ships have a long and romanticized history in Antarctica, dating back to what has come to be known as the Heroic Era of polar exploration. Vessels with hulls built of wooden planks first plied the seas of Antarctica as early as 1820, when members of either a British, Russian, or American expedition first laid eyes on the continent.\textsuperscript{47} Wooden vessels continued to be active in Antarctica through the middle and late nineteenth and early twentieth centuries. Such efforts were concentrated primarily on whaling and sealing, although expeditions to establish sovereignty and to lay claim to the South Pole, such as those of Robert Scott, Roald Amundsen, and Ernest Shackleton, also had their place.\textsuperscript{48} Importantly, ventures in marine-biological research, such as the British Discovery Expeditions conducted aboard the \textit{H.M.S. Challenger} during the period 1872–1876, established that marine life was surprisingly bountiful on the sea floor and in the water column.

Modern shipping in Antarctica began in earnest during the International Geophysical Year of 1957–1958.\textsuperscript{49} It was at about this time that many of the currently established Antarctic research stations were either built or permanently occupied. These stations generally were—and still are—resupplied by ships with ice-strengthened, steel hulls that can navigate the sea ice to varying degrees. Supply ships also rely to a large extent on simply avoiding sea-ice conditions by concentrating their activities in the austral summer months. In some cases, helicopters are used for the last leg of the journey to ferry supplies from the edge of the sea ice to a nearby research station. A number of countries routinely operate large research vessels equipped with built-in laboratories, and most of these also serve as resupply vessels.

The U.S. McMurdo Station, located on the southern tip of Ross Island in the Ross Sea, is the largest research station on the Antarctic continent, with up to 1,200 inhabitants each austral summer.\textsuperscript{49,50} It requires by far the greatest shipping infrastructure to support its annual operations. Each year, a polar-class ice breaker deploys to the Ross Sea to break out a shipping passage to McMurdo Station. Resupply vessels are then able to provide the station with fuel and other needs.

The impacts of shipping on marine ecosystems in Antarctica are similar to those discussed in the next section on tourism. They include contributions to air and water pollution, the transport of invasive species on hulls and in ballast tanks, and environmental and human risks associated with fires, groundings, and sinkings. These latter risks are especially great in such a remote location, under weather conditions that are often severe.

\textbf{Tourism}

Tourism in Antarctica had its modest inception in the late 1950s and early 1960s when Argentine and Chilean naval freighters took groups of tourists to the South Shetland Islands and WAP. Tourism became firmly established in the mid-1960s. Since then, the vast majority of tourists visiting Antarctica have done so aboard smaller vessels offering “expedition cruises.” These cruises frequent a variety of sites along the northern and central reaches of the WAP and use launches to land tourists at locations offering scenery, geology, field stations, historic bases and huts, and wildlife.

Statistics compiled by the International Association of Antarctic Tour Operators (IAATO) indicate that the numbers of annual visits were relatively low (<1,000 tourists per year) over an initial 25-year period spanning 1965–1966 to 1990–1991. Tourism increased to more than 33,000 visits per year in 2007–2008 and then declined to about 21,000 per year in 2009–2010 as the global economy contracted (Fig. 3). The numbers of visits are likely to rebound in coming years as tourists increasingly seek unique and remote destinations.
Coincident with the sharp increase in expedition-style cruises over recent decades has been the advent of the “cruise only” style of travel to Antarctica. In this option, tourists travel to the Antarctic Peninsula aboard relatively large cruise ships, which carry up to several thousand passengers each. These larger ships do not offer passenger landings due to logistical constraints and voluntary guidelines in the Antarctic Treaty and IAATO protocols that recommend the numbers of tourists be no more than 100 per landing. Large-ship cruises began in 1999–2000 with about 1,000 passenger visits to Antarctica, then rapidly increased to about 15,000 tourist visits by 2009–2010 (Fig. 3). With the addition of approximately 500 tourist visits each year via commercial air, the annual number of tourists visiting Antarctica has been as high as 46,069 (in the 2007–2008 season; Fig. 3). Adding nature guides and other support staff increases this peak number to 74,178 visitors.

With large numbers of tourists visiting the exceptionally fragile polar system over a tourist season that has now increased to about 173 days per year, and with the majority of tourists making repeated landings, there is great potential for negative environmental impacts on both terrestrial and marine habitats. Key concerns about the burgeoning tourism industry in Antarctica include interactions with wildlife, pollution, introduction of invasive species, and disruption of scientific research activities. There has been little monitoring of human impacts to date, although there have been recent calls to initiate comprehensive and systematic monitoring programs.

Published studies of tourist impacts on wildlife along the Antarctic Peninsula have focused on the pygoscelid penguins. Results have been mixed, with some studies finding no impact of human disturbance on penguin physiology, behavior, breeding success, or population trends, whereas other studies do report impacts. Responses to human visitation may be species-specific. For example, studies of gentoo penguins, Pygoscelis papua, found decreased breeding productivity in areas with frequent tourist visits as compared to control sites lacking tourists. In contrast, either no measurable effect or enhanced productivity was found in Adélie penguins, P. adeliae, at sites frequently visited by tourists. Regardless of these mixed outcomes, it is prudent to rigorously enforce legislation established in the Antarctic Treaty designed to protect wildlife from tourists by, for example, keeping tourists a set distance from nesting penguins.

*Figure 3. Estimated numbers of passengers traveling annually to Antarctica aboard expedition and cruise-only tour ships between 1992 and 2010. Data from unpublished IAATO report.*
There are almost no studies of the potential impacts of tourism on other species of Antarctic birds. A short note was published on the lack of impact of tourists on the predatory behavior of skuas (*Catharacta* sp.) foraging within a gentoo penguin rookery. Although we are unaware of scientific studies of the prospective impacts of tourism on Antarctic seals, the recent establishment of breeding colonies of elephant and fur seals along the WAP coincident with rapid climate warming has accentuated the need to evaluate potential population and behavioral impacts of visits by tourists to seal colonies. Williams and Crosbie reviewed the possible impacts of tourism on whales in Antarctica. Despite the potential for noise from ship engines to harm marine mammals, these authors concluded that the positive benefits of tourist ships providing platforms for whale research could outweigh any negatives.

Tourism also pollutes the environment. Carbon dioxide (CO₂), sulfur dioxide (SO₂), nitrogen dioxide (NO₂), and particulates are released to the atmosphere from the exhaust of ship engines, and hydrocarbons are released into the sea from the outboard engines of launches and fuel leaks from cruise ships. Most Antarctic tour operators have recently upgraded their launch fleets with cleaner, four-cycle engines. This change not only has reduced oil contamination in seawater, but also has abated noise pollution near sensitive wildlife areas.

Tourism has been implicated in oil spills in Antarctica. The best-known example is the sinking of the Argentine naval vessel *Bahia Paraiso* off the U.S. Palmer Station on January 28, 1989. The ship, which resupplied research stations and also carried 130 tourists, was departing Palmer Station following a tour visit when it ran aground. It floated free three days later, drifted a short distance, and then rolled over and sank in shallow water. The *Bahia Paraiso* spilled 600,000 L of diesel fuel into the sea (see section “Pollution”). Fortunately, no tourists or crew members were injured as they abandoned ship.

The generation of litter, such as plastics, is another potential source of pollution related to tourism in Antarctica. Cruise staff, guided by IAATO protocols, generally do an excellent job of educating tourists about the negative ecological impacts of littering in Antarctica (JBM, personal observation).

The International Maritime Organization (IMO) has established guidelines to minimize the input of nonnative species to Antarctic waters; neverthe-
Bahía Paraíso discussed earlier, as well as the more recent sinking of the tour ship *MV Explorer* which carried 154 tourists and crew members on November 24, 2007, are good examples of these risks. Fortunately, in both instances, the weather was good and the tourists could be safely and rapidly transported by small boats to a shore-based station or to another cruise ship, respectively; however, had the weather been inclement, the outcome in either case could have been disastrous.

The advent of larger, cruise-only ships visiting Antarctica has raised concerns about the risks of having to evacuate and rescue several thousands of passengers in such extremely cold and remote seas. The IMO recently banned the use of heavy fuels in Antarctica.65 The ban, which will come into effect on August 1, 2011, will effectively exclude large cruise ships from Antarctica, significantly reducing risks to the environment and human life.

**Pollution**

Pollution from local human sources occurs at a small scale in the context of the 34.8 million km² area of the SO and the 18,000-km Antarctic coastline. Environmental practices have improved with the implementation of the Protocol on Environmental Protection to the Antarctic Treaty in 1998. Also known as the Environmental Protocol or Madrid Protocol, it applies to the area south of 60°S latitude.66 With the notable exception of sewage, all waste must be removed from Antarctica, open burning of waste is prohibited, and nations are obliged to clean up past waste-disposal sites. Contaminants continue to be released into the marine environment, however, as a result of current or past waste-management practices, accidents and fuel spills, and scientific activities.3,67 In this section, we discuss chemical and sewage pollution from research stations and ships, and the minor but ongoing impact of science itself.

**Chemical pollution from research stations.**

Sources of long-term, local pollution are concentrated around the ∼75 research stations, roughly half of which are situated along the WAP, and most of which are situated on coastal, ice-free ground. Some of these stations are located adjacent to sensitive shallow-water, soft-sediment, marine habitats. Most present-day marine pollution comes from sewage outfalls, abandoned dump sites, accidental oil spills, and exhaust emissions.58,69 The environmental impacts of establishing a research station or other facility on coastal, ice-free ground are twofold: the displacement of local wildlife during construction, and the emission of pollutants into the marine and terrestrial environments during its functional lifespan and possibly beyond. Pollution levels depend upon the duration of the station’s presence, its source of electrical power and waste-management practices, and the capacity of the local environment to degrade or remove contaminants.

Until the 1980s, waste from research stations was generally dumped locally and typically included batteries, food waste, building materials, laboratory chemicals, sewage, shipping containers, fuel drums, and waste oil and lubricants.70 Rubbish was dumped on land, tipped into the sea, or left on transient sea ice to be carried away and deposited in deeper water when the sea ice broke up. Between the mid-1950s and late 1980s, whole abandoned research stations built on floating ice shelves were left to calve off and fall into the sea (e.g., the British Halley I, II, III, and IV stations on the Brunt Ice Shelf (Fig. 4) and the South African SANAE I, II, and III stations on the Fimbul Ice Shelf). The legacy of earlier waste-dumping activity is still evident near some research stations, with heavy metals, hydrocarbons (including polyaromatic hydrocarbons, or PAHs), and persistent organic pollutants (POPs) still detectable many years after release.71–74 In some cases, contaminants continue to leach into the marine environment from abandoned waste dumps and fuel-contaminated ground, particularly during the summer when the pollutants can be mobilized by meltwater.75,76

Described as having “one of the highest toxic concentrations of any body of water on Earth,” the most polluted marine site in Antarctica is probably Winter Quarters Bay, Ross Island. Beginning in the mid-1950s, the bay served as a dump for McMurdo Station.49,50,77 Although dumping ceased in the mid-1980s and wastewater treatment commenced in 2003, pollution levels remain high. The local environment has shown some signs of detoxification, and limited recovery of marine communities has been observed;74,78 however, some pollutants are likely to persist for many years to come. At this site as elsewhere, however, contamination and its associated impacts on benthic communities are localized to within a few hundred meters of the pollution sources.74,78–80
Effects of contaminants on Antarctic marine ecosystems are poorly understood, but some species may be more sensitive to chemicals than their temperate equivalents. Exposure of Antarctic marine invertebrates to increasingly contaminated sediments caused decreased survival and increased avoidance behavior, and chemical pollutants caused genotoxic effects and pathological anomalies in Antarctic fish exposed to sewage. Where multiple pollutants are present, determining the causative agent of observed biological effects may be difficult; for example, it is unclear what the relative contributions are of organic pollutants (PAHs and polychlorinated biphenyls, or PCBs), pathogens, and heavy metals to the pathological conditions found in fish around the McMurdo Station outfall.

Some organic pollutants, including dichlorodiphenyltrichloroethane (DDT) and PCBs, are toxic, persist in the environment for long periods, and can bioaccumulate at high levels in the food chain. These POPs can be transported over great distances in the atmosphere and ocean currents, and their sources are generally considered to be outside Antarctica. Geisz et al. suggested that Antarctic glaciers have accumulated DDT that came to Antarctica via long-range atmospheric transport over several decades, and they highlighted glacial meltwater as a likely source of this pollutant in coastal marine habitats. Although PCBs are prohibited within Antarctica, inadvertent release still occurs locally. High levels of polybrominated diphenyl ether (PBDE) flame retardants were found indoors at McMurdo Station and in effluent sludge, sediments, fish, and invertebrates near the sewage outfall. The minimum standards of wastewater treatment dictated by the Environmental Protocol, therefore, seem unable to prevent release of PBDEs and other chemicals into the Antarctic environment.

Cleanup of abandoned dumpsites and contaminated ground is an obligation under the Environmental Protocol, but not if it will result in greater environmental damage due to disturbance and remobilization of the pollutants. Removal of surface rubbish has been undertaken at some sites; in recent years, however, the potential use of alternative...


**Chemical pollution from ships.** Antarctic waters have been designated as a Special Area under MARPOL (the International Convention for the Prevention of Pollution from Ships), and as such they are provided with a higher level of protection than other oceanic areas. Annex IV of the Environmental Protocol sets forth legislation to prevent marine pollution and prohibits the discharge by ships of oil, garbage, or chemicals into the Antarctic Treaty area except in emergencies. Other forms of pollution are ongoing. Butyltins, including tributyltin (TBT), which have been detected in Antarctic marine sediments, possibly originated from the antifoulant coatings on the hulls of ships. Increases in shipborne tourism in the past decade have increased exhaust emissions. More dramatically, there have been a number of incidents in which ships have run aground, resulting in oil spills. In response, the States Parties to the Antarctic Treaty (see section “The Antarctic Treaty and other controls”) have liaised with the IMO to prohibit the carriage or use of heavy-grade oils in Antarctic waters (see section “Tourism”), because when spilled they cause more serious and longer-lived environmental impacts than lighter fractions.

To date, the scale and impacts of oil spills at sea have been relatively small (Table 1), with the sinking of the Bahía Paraiso near the U.S. Palmer Station constituting Antarctica’s largest oil-spill incident to date. Impacts following the spill included local mortality of intertidal marine invertebrates and complete failure of that season’s reproduction of the local population of skuas, Catharacta maccormicki; however, within two years, little contamination of sediments or invertebrates was evident. These impacts were modest compared to oil spills elsewhere; should a larger-scale spill occur, however, the infrastructure generally does not exist in Antarctica to undertake a large-scale coastal cleanup or to clean oil-soaked birds and marine mammals.

**Sewage pollution.** At Antarctic stations and on fishing, tourist, research, and resupply vessels, sewage and gray water can originate from bathrooms, kitchens, and laundry facilities. It can contain human waste with associated microorganisms, including pathogenic bacteria, viruses, and fungi; organic material, such as food waste and toilet paper; and chemicals, including brine from desalination plants, detergents, hydrocarbons, heavy metals, and other contaminants. Different components of sewage can have different marine impacts: nutrients can cause microbial blooms that reduce oxygen levels in seawater; suspended solids can bury sessile invertebrates and interfere with feeding activities; and the impacts of toxic chemicals have already been discussed.

Until the early 1960s, raw sewage from stations was either released into the nearshore marine environment or buried in pits, whereas ships simply dumped sewage overboard. As the populations of stations increased, so did sewage production. Most coastal stations developed sewage systems that emptied into the sea, onto the intertidal zone, or onto the sea ice. Current legislation concerning sewage release in Antarctica is found in Annexes III and IV of the Environmental Protocol. For pragmatic reasons, sewage is the only type of waste that is permitted to be released into the Antarctic environment on a large scale. Sewage discharge also represents the only example in which the intentional release of nonnative species into the environment—human-derived fecal microorganisms—is widely permitted within the Antarctic Treaty area.

Ships are permitted to discharge sewage in Antarctic waters >12 nautical miles (>21 km) off the coast, but the options for sewage disposal at Antarctic stations are more constrained. Where complete removal of the waste is not feasible, as is widely the case, sewage should be discharged into the marine environment, but only where conditions exist for initial dilution and rapid dispersal. Large quantities of waste, generated by an average summer station population of 30 people or more, should at a minimum be treated by maceration.

Gröndahl et al. surveyed 71 Antarctic stations and found that 37% of permanent stations and 69% of summer stations lacked any form of sewage.
Table 1. Recent fuel spills from national operator and tourist vessels in the Antarctic region

<table>
<thead>
<tr>
<th>Vessel</th>
<th>Date</th>
<th>Location</th>
<th>Volume of fuel spilled</th>
<th>Reported impacts</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nella Dan</td>
<td>December 3, 1987</td>
<td>Macquarie Island, Subantarctic</td>
<td>270,000 L light marine diesel</td>
<td>Mortality of marine invertebrates within 2 km, some oiling of penguins</td>
<td>89</td>
</tr>
<tr>
<td>Bahía Paraiso</td>
<td>January 28, 1989</td>
<td>Near U.S. Palmer Station, Antarctic Peninsula</td>
<td>600,000 L diesel</td>
<td>Immediate mortality of intertidal invertebrates, oiling of intertidal algae, longer-term impacts on local bird populations</td>
<td>90, 91</td>
</tr>
<tr>
<td>Explorer</td>
<td>November 23, 2007</td>
<td>King George Island, Antarctic Peninsula</td>
<td>185,000 L diesel, 24,000 L lubricants, 500 L gasoline</td>
<td>None reported, oil slick measured ~4.6 × 0.2 km</td>
<td>92</td>
</tr>
<tr>
<td>Nordkapp</td>
<td>January 30, 2007</td>
<td>Deception Island, Antarctic Peninsula</td>
<td>~1,000 L diesel</td>
<td>None reported</td>
<td><a href="http://www.iaato.org">www.iaato.org</a></td>
</tr>
<tr>
<td>Ushuaia</td>
<td>December 4, 2008</td>
<td>Wilhelmina Bay, Cape Anna, Antarctic Peninsula</td>
<td>Unknown</td>
<td>None reported, oil slick observed around vessel ~50 × 500 m</td>
<td><a href="http://www.iaato.org">www.iaato.org</a></td>
</tr>
</tbody>
</table>

On the other hand, some larger stations have implemented sewage-treatment procedures that clean their effluent in excess of their national standards for water quality.95–98 Processing generally includes maceration, screening, and settling of raw sewage, followed by aerobic biological treatment and in some cases disinfection by ultraviolet (UV) irradiation.98 The use of such complex systems at smaller stations is widely regarded as expensive and impractical, and it will be a challenge to scale down existing technologies. Given the relatively pristine nature of the Antarctic environment, however, Riddle67 recommended that secondary treatment followed by effective disinfection should become standard practice across the continent.

The Environmental Protocol also obliges nations to monitor the impacts of ongoing activities, such as sewage disposal; however, information on the extent and impacts of sewage pollution on wildlife, including marine invertebrates, fish, birds, and marine mammals, is publicly available only for a minority of stations, and it probably does not exist at all for ships. Indicators of sewage pollution used in Antarctica include microorganisms, such as fecal coliforms,99–101 *Escherichia coli*,102 enterococci,102,103 bacteriophages,104 and *Clostridium perfringens*,105,106 as well as chemicals such as fecal sterols.106,107 Before the installation of a wastewater-treatment facility, microbial and chemical indicators of sewage pollution around McMurdo Station were detectable ~1 km from the outfall.104,105,108 Reports from more typical-sized stations of 50- to 100-person capacity show sewage pollution to be more localized, with background levels of indicators found within a few hundred meters of the
outfall. The extent of sewage pollution is influenced by the number of people on station generating the waste, the efficiency of any treatment facility, and physiographic features affecting dispersal and dilution rates. To complicate matters, however, natural variations in environmental factors such as algal blooms, salinity, water depth, sea-ice formation, and solar radiation can significantly alter the number of viable microbial sewage indicators detected. As an example, the ability of solar radiation to deactivate fecal coliform bacteria in Antarctica is enhanced with increasing exposure time and decreasing radiation wavelength, ozone-column depth, cloud cover, and solar-zenith angle.

Although they are essential for the purpose of risk assessment, studies of the impacts of sewage pollution on marine biotas have been performed near only a few Antarctic outfalls. Fecal bacteria released into Antarctic seawater at ~0 °C can persist for many weeks in a viable but nonculturable state, and their capacity to infect and cause disease in indigenous wildlife is unknown. Antarctic wildlife can harbor pathogenic microorganisms common in sewage, which in some cases have been associated with disease. To complicate matters even further, many bird and some seal species that are found in Antarctica during the summer months have foraging or migratory ranges that take them outside Antarctica and potentially expose them to other sources of sewage. Marine invertebrates can accumulate microbial pathogens; for example, Clostridium perfringens was found in the guts of common invertebrate and fish species around the McMurdo Station outfall. The bivalve Laternula elliptica was found to accumulate coliform bacteria, which could conceivably be transferred up the food chain.

Marine invertebrates can be affected by both acute and long-term release of sewage. During an accidental spill of sewage into an Antarctic aquarium, only the giant Antarctic isopod Glyptonotus antarcticus survived unharmed. The release of untreated sewage over several decades resulted in reduced abundance of benthic invertebrates around the outfalls at the Australian Casey Station (population 20–50 people) and McMurdo Station. In areas receiving the highest levels of organic input from the McMurdo outfall, the formation of an anaerobic microbial biofilm caused avoidance behavior in the seastar Odontaster validus and other macrofaunal scavengers. Following the initiation of sewage treatment at the site, there was a drop in abundance of polychaete species that are tolerant of organic enrichment (Capitella perarmata and Ophryotrocha notialis) and some recolonization of sewage-intolerant polychaetes (Spiophanes cherrniae and Galathowenia scotiae). The negative impacts of sewage are generally localized around outfalls, and improving standards of sewage treatment throughout Antarctica should reduce impacts further.

Pollution from scientific experiments. Scientific experiments and practices, as opposed to the infrastructure required to support scientific activities, can also litter the marine environment, albeit on a small scale. Unrecovered equipment includes radiosondes attached to weather balloons, data loggers and batteries left on sea ice, experimental apparatus lost from seafloor stations through iceberg impacts, unrecovered nets and marine sampling equipment, and larger pieces of equipment, including the United Kingdom’s self-propelled research submersible Autosub, which was lost beneath the Fimbul Ice Shelf. All scientific activities should be subject to prior environmental impact assessments, which set out mitigation methods to minimize impacts and ensure that any pollution is justified by the scientific benefits.

Prospectus. Implementation of the Environmental Protocol in 1998 raised environmental standards across the Antarctic Treaty area, with improved waste-management and pollution-control practices reducing ongoing contamination of the marine environment. The interpretation of the Protocol’s legislation and the rigor with which it is applied, however, vary greatly among nations operating in the region, and, therefore, the legacy of earlier pollution remains. Antarctic marine environments are at increasing risk of oil spills from burgeoning marine traffic in the region, and further contingency planning and investment in infrastructure will be necessary to deal with accidents.

Mineral extraction

The Antarctic Treaty currently prohibits the extraction of oil and other mineral resources from Antarctica. If the escalating interest in mineral extraction from the Arctic seafloor is any indication,
Antarctica could be at risk too.\textsuperscript{125–128} Considering the geographic isolation and harsh conditions of Antarctica, however, the high costs and logistical difficulties of exploiting mineral resources render industrial-scale attempts unlikely in the foreseeable future.

The Antarctic Treaty and other controls

The vulnerability of Antarctic ecosystems to human impacts was recognized at an early stage of the modern era of Antarctic exploration. International regulation began in 1946 with the establishment of the IWC and the entry into force in 1948 of the International Convention for the Regulation of Whaling.\textsuperscript{3}

Twelve nations signed the Antarctic Treaty (hereafter referred to as the Treaty) in Washington, DC, on December 1, 1959. The Treaty entered into force on June 23, 1961 and is an open-ended commitment (http://www.scar.org/treaty/). The purpose of the Treaty is to hold territorial claims in abeyance and ensure that the region is subject to peaceful international cooperation. Its stated goal is, “In the interest of all mankind that Antarctica shall continue forever to be used exclusively for peaceful purposes and shall not become the scene or object of international discord.”

The Treaty includes all areas south of 60°S latitude, including islands and ice shelves. It is important to recognize, however, that this leaves major parts of the SO, situated south of the ACC system but north of 60°S, unprotected and outside the agreement zone.\textsuperscript{129} Article VI of the Treaty states, furthermore, “Nothing in the present Treaty shall prejudice or in any way affect the rights, or the exercise of the rights, of any State under international law with regard to the high seas” within the Treaty area (south of 60°S).

At this point, 43 states have signed the Antarctic Treaty. Of these, 28 are Consultative Parties with a scientific interest and presence in Antarctica. By joining the Treaty, Accessing States, which are those countries with no active engagement in Antarctica, demonstrate their interest in becoming involved. Many Accessing States have subsequently become Consultative Parties. The interests and motivations of the signatories vary widely.\textsuperscript{130}

Throughout its existence, the Treaty has been augmented by supplementary agreements from the Antarctic Treaty Consultative Meetings (ATCMs), which in recent years have been held annually (Table 2). For example, the Convention for the Conservation of Antarctic Seas (CCAS) and CCAMLR acknowledge that there are particularly vulnerable, as well as commercially attractive, species that require special protection. These secondary agreements, with the Antarctic Treaty at their core, comprise the Antarctic Treaty System. Supplements to the Treaty do not all have the same status. CCAS and CCAMLR are independent agreements, but they commit their parties to essential parts of the Treaty such as Article IV, which deals with the legal status of territorial claims.

The Scientific Committee on Antarctic Research (SCAR) was created in 1958 as a committee of the International Council of Science (ICSU). SCAR is charged with the international development and coordination of Antarctic research. It provides international organizations and the Antarctic Treaty System with independent advice. SCAR draws from experts from all its member states to reach the best consensus on science priorities. SCAR develops and recommends research priorities that are implemented into national research programs by Treaty members. In 1988, the Council of Managers of National Antarctic Programs (COMNAP) was initiated, with the aim of coordinating logistics and infrastructure associated with international research activities in Antarctica.

The Treaty relies on the willingness of each member state to comply. There is no independent control or any kind of active enforcement throughout most of the Treaty System. Controls on logistical support and scientific activities at research stations and elsewhere in Antarctica rely on the commitment of the governments promoting those activities.

The CCAMLR agreement recognized the lack of management of the resources of the open seas of the SO. The agreement covers the high seas from the Antarctic continent to about 50°S and, consequently, reaches beyond the oceanic parts of the Treaty area. CCAMLR seeks to protect the fishery resources of the SO in particular, and the entire marine ecosystem in general. Members of the CCAMLR Commission provide advice for sustainable management and implementation for fish stocks in the SO.\textsuperscript{131} Despite the success of the approach in some of the CCAMLR management areas,\textsuperscript{132,133} fish stocks have plummeted over the last few decades, with little sign of recovery (see section “Fishing pressure”).
Table 2. Summary of political milestones in the development of the Antarctic Treaty System

<table>
<thead>
<tr>
<th>Year</th>
<th>Location</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1958</td>
<td>The Hague</td>
<td>Establishment of the Scientific Committee on Antarctic Research (SCAR)</td>
</tr>
<tr>
<td>1959</td>
<td>Washington</td>
<td>Antarctic Treaty signed by 12 Consultative Parties (presently ratified by 43 states)</td>
</tr>
<tr>
<td>1961</td>
<td>(Global)</td>
<td>Antarctic Treaty entered into force</td>
</tr>
<tr>
<td>1961</td>
<td>Canberra</td>
<td>First Antarctic Treaty Consultative Meeting</td>
</tr>
<tr>
<td>1972</td>
<td>London</td>
<td>The Convention for the Conservation of Antarctic Seals (CCAS)</td>
</tr>
<tr>
<td>1980</td>
<td>Canberra</td>
<td>The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR)</td>
</tr>
<tr>
<td>1988</td>
<td>Hobart</td>
<td>Establishment of the Council of Managers of National Antarctic Programs (COMNAP)</td>
</tr>
</tbody>
</table>

Since the drafting of the Antarctic Treaty, the impacts of human activities in Antarctica have changed dramatically (see sections “Shipping traffic” and “tourism”). To mitigate the threat of introductions of alien species in ships’ ballast water, the States Parties agreed in 2006 to voluntary guidelines for ballast-water exchange. Such exchange should take place in deep water at the Polar Front to prevent coastal waters from outside the Treaty area from being carried to Antarctica. 134

The greatest flaw in the Treaty System is its tolerance of the territorial claims in abeyance that are maintained by several States Parties, some of which have taken the precaution of including in their claims areas adjacent to the Treaty area, north of 60°S.128,135 This strategic positioning for claims on Antarctic territory may not have been cause for concern when the Treaty entered into force in 1961; however, the United Nations Convention on the Law of the Sea (UNCLOS) has recently set the stage for asserting rights over areas of seafloor that are natural extensions of a states’ territory. The recent rush for undersea real estate in the Arctic (see section “Mineral extraction”) raises concerns about the prospects for continued cooperation in Antarctica.128

Impacts of global-scale human perturbations

Ozone depletion

In 1985, investigators at the British Antarctic Survey documented a thinning in the stratospheric ozone (O₃) layer over Antarctica.136,137 The “ozone hole,” which appeared (and still appears) each austral spring, was causally connected to atmospheric concentrations of chlorofluorocarbons, or CFCs. CFCs were used widely as refrigerants and spray propellants.

Stratospheric ozone filters solar UV-B radiation, and the removal of that filter over Antarctica poses ecological threats. Risks of increased UV-B reaching the Earth’s surface in Antarctica include DNA damage to terrestrial and marine life, as well as photoinhibition of marine phytoplankton and consequent alterations to ecosystem dynamics.138 There are also complex linkages between ozone depletion and global warming.139,140 Ozone depletion appears to be slowing the warming-induced loss of sea ice,141 a loss that is already having serious consequences for pelagic food chains (see section “Global warming”).

The Montreal Protocol of 1987 phased out CFCs and other ozone-depleting compounds. Emissions have declined drastically, concentrations of ozone in the stratosphere have been stabilized, and the ozone hole is shrinking—erratically—in what is arguably humanity’s greatest victory to date on behalf of the global environment. CFCs, however, are likely to persist in the atmosphere for at least the next 50 years,139 and closure of the ozone hole will be complicated by climate change142 and anthropogenic emissions of brominated compounds.143

Introduced species

Natural routes of biotic interchange. The effectiveness of the ACC as a barrier to invasion by Subantarctic marine fauna has come into question in recent years.144,145 Much of Antarctica’s marine biodiversity has evolved in isolation since the end of the process of Antarctic cooling ~14 million years ago.146–149 There is, however, evidence for several avenues of long-term faunal exchange with the Subantarctic.
There are strong affinities between the extant marine benthic faunas of the Antarctic Peninsula and the Magellanic Region of South America.145 The traditional view is that these affinities are the result of a common geological history prior to the opening of the Drake Passage and establishment of the ACC, which began ∼41 million years ago; however, with the application of molecular tools it has become increasingly plausible that genetic exchange continued even after the development of the ACC and its frontal system.151 Furthermore, the traditional perception that many or most benthic species living at high latitudes cannot disperse over long distances because they lack drifting stages needs to be reevaluated.152 Leese et al.,153 for example, recently demonstrated the ability of an Antarctic benthic isopod, Septemserolis septemcarinata, to disperse across major zoogeographic barriers within the SO. Benthic organisms can use pumice, driftwood, and kelp rafts to travel long distances.154–156 Anthropogenic flotsam, such as plastic debris, contributes to the mobility of invertebrates in the SO.157

The first record of Subantarctic decapod larvae in Antarctica, in shallow water off King George Island at the northernmost tip of the Antarctic Peninsula (62°15’S), raised the question of how these organisms arrived at this region.144 The record also included copepods, Acartia spp., which were previously unknown from Antarctic waters. Thatje and Fuentes144 suggested that pelagic organisms could cross the current system entrained in warm-core eddies or in substantial intrusions of Subantarctic waters breaching the ACC. The ACC has an exceedingly complex mesoscale structure, and satellite imagery reveals eddy structures over a wide range of scales (see section “Marine environments of Antarctica”). Although the degree of porosity of the ACC remains unknown, the biogeographic affinities and molecular evidence reviewed above suggest that its importance in the evolution of the Antarctic fauna has been underestimated.

Eddies in the SO are short lived, because the Coriolis effect is attenuated at high latitudes. Organisms trapped in warm-core rings moving south of the ACC die from exposure to cold sea temperatures once the eddies dissipate; however, survival and establishment of Subantarctic marine invertebrates in Antarctica is now becoming increasingly likely as a consequence of rapid climatic warming.19

Biogeographic affinities between Subantarctic Magellanic and Antarctic faunas suggest a second route of interchange over evolutionary time. Faunal elements could have migrated along the topographic highs of the Scotia Arc. This “stepping-stone hypothesis” suggests that benthic organisms could have overcome the shorter distances between islands more easily than the oceanographic barrier of the ACC.145,158 Without further molecular analyses, however, faunal relationships along the Scotia Arc could equally represent a biogeographic relict from an evolutionary history extending back before the fragmentation of Gondwana and the development of the ACC.147 Migration along the Scotia Arc is one plausible explanation for the populations of king crabs (Lithodidae) that have recently been discovered along the continental slope of the WAP (Fig. 5).19

Human-mediated invasions. Expanding ship traffic and tourism in Antarctica have elevated concerns about introductions of exotic species. As discussed in “Tourism,” the release of ballast water could potentially introduce organisms from anywhere in the world into Antarctic seas. Most species released from ballast water should not survive in Antarctica, but the potential introduction of cold-adapted species from the Arctic is a serious threat.16 The use of double-hulled ships since the 1980s has increased the thermal insulation of ballast water and the likelihood that globally operating ship traffic could facilitate the transport of Arctic organisms into Antarctica.

Global warming

Benthic food webs. The thermal tolerance of a marine ectotherm is largely a product of selective pressures exerted by the temperature range of the habitat(s) in which it lives. Because Antarctic marine organisms live in water that is extremely cold year-round, they are predominantly cold-stenothermal (Fig. 6); most species do not tolerate sustained temperatures exceeding the narrow temperature window of Antarctic waters (see section “Marine environments of Antarctica”).16 This physiological constraint makes them particularly vulnerable to the effects of global warming.164,165

Marine ectotherms in Antarctica exhibit slow metabolic rates, low rates of physiological performance, slow growth, depressed rates of calcification, reduced fecundity, and slow larval development.
Impacts on Antarctic marine ecosystems

Figure 5. Species of king crab (Anomura: Lithodidae) from the Southern Ocean and adjacent seas. (A) Paralomis birsteini from 1100 m depth on the continental slope of the WAP in the Bellingshausen Sea.159 (Photo of preserved specimen by S. Thatje.) (B) P. elongata from the Spiess Seamount near Bouvet Island (~300 m). (Photo of living animal by S. Thatje.) (C) P. spinosissima from South Georgia (~1200 m). (Photo of preserved specimen by Sally Hall.) (D) Lithodes confundens from the shallow Patagonian Shelf, southwestern Atlantic Ocean (<100 m). (Photo of living animal by S. Thatje.) King crabs are globally distributed and found predominantly in polar and deep seas. They are important benthic predators and support regional fisheries. To date, more than 120 species have been described, but many more undescribed species are expected to thrive in the deep sea and on remote seamounts. Lithodid lineages that radiated through the deep sea over geologic time are preadapted to cold-water conditions in Antarctica. Lecithotrophy enables them to decouple larval development from the strong seasonality of primary production in the Southern Ocean. The adults are also able to subsist at cold temperatures in a torpid, hypometabolic state. These features are prerequisites for thriving in Antarctic waters and may allow Southern Ocean species to invade shelf habitats over the next 50–100 years as waters warm.159

compared to related temperate and tropical taxa.27,164,166–171 Global climate change is now raising sea temperatures in Antarctica, with the waters off the WAP warming more rapidly than in most other locations in the World Ocean.172,173 The ability of Antarctic species to respond to climate change by raising the rates of key physiological processes is limited by their stenothermal physiology, and although certain Peninsular species might be able to move southward into cooler waters, the continental landmass sets a limit to such range shifts. Extinctions of some elements of the Antarctic biota are, therefore, a real possibility.165,174

Decapod crustaceans constitute the least successful invertebrate taxon in Antarctica, being represented primarily by benthic and pelagic shrimp.175 The absence of reptant decapods is a direct result of their limited capacity to downregulate the concentration of magnesium ions in their hemolymph. Relatively high [Mg²⁺] in their hemolymph, in combination with low temperatures, anesthetizes the animals, and the reduced aerobic scope that results is the factor primarily responsible for their failure to survive at low temperatures.1,164 Rising sea temperatures are on the verge of permitting lithodid king crabs and other reptant decapods to overcome the magnesium constraint and reinvade. Larvae of reptant decapods are already entering Antarctic waters in warm-core rings from the ACC, populations of lithodids have been discovered on the continental slope off the WAP, and increasing ship traffic is raising the risk that exotic decapods will be introduced (see section “Introduced species”).19,159,176 Because lithodids are generalized, durophagous invertivores, their successful reinvasion of shallow-shelf habitats off the WAP could have dire consequences for the unique benthic communities.19,20
temperature.

...c render polar warm-stenothermal compared to temperate species but eury-

...nvironmental conditions are narrower than at temperate latitudes, but there

...l marine ectotherms are largely driven by the temperature ranges of the habitats in which they live. At temperate to tropical latitudes, seasonality affects that range. Ectothermal species in temperate environments are eurythermal: they tolerate a wide range of temperatures over the seasons. Ectotherms enduring polar conditions face a narrow temperature range and are clusthenothermal. The range of temperatures in tropical environments is narrower than at temperate latitudes, but there is still some seasonal variation; tropical marine ectotherms are warm-stenothermal compared to temperate species but eurythermal compared to polar species. Stenothermy renders polar and tropical marine ectotherms vulnerable to small increases in temperature.

Like the crustaceans, the fish fauna of Antarctica is depauperate of durophagous predators. The endemic notothenioids are the only teleosts in shallow-water habitats, and they are not durophagous. They radiated in Antarctica after the Eocene, and they survive to this day because of a key adaptation: antifreeze glycoproteins (AFGPs), which prevent ice crystals from forming in their tissues. The absence of durophagy in the notothenioid clade is an accident of phylogenetic history unrelated to the acquisition of AFGPs; we know this because durophagous teleosts in the Arctic have convergently evolved AFGPs. Warming seas in Antarctica will likely remove the physiological constraint that currently prevents invasion by teleosts lacking AFGPs. The notothenioids themselves are sensitive to elevated temperatures and lack a heat-shock response, so they are at risk from global warming.

Durophagous, bottom-feeding sharks and rays are absent from Antarctica, as are pelagic, piscivorous sharks. Skates are rare, and the only species known to prey on a variety of calcified benthic organisms is Raja georgiana. The constraints on benthic sharks and rays, and their prospects for invading shallow-benthic communities in Antarctica, are less certain than for the teleosts and reptant decapods.

**Pelagic food webs.** Pelagic food webs off the WAP are already changing as sea temperatures warm. There is evidence that the relative abundances of salps and krill are temperature-, ice-, and productivity-mediated, with salps (Salpa thompsoni) preferring warmer, less icy, and less productive conditions than Antarctic krill (Euphausia superba) and outcompeting the krill for food. This could mean dramatic shifts in pelagic food webs in Antarctica, because most species of whales, penguins, and seals depend, either directly or indirectly, on krill. Another hypothesis, which is not entirely incompatible with this scenario, is that historical whaling released krill from predation pressure, and that increased krill populations partially account for the increase in chinstrap penguins. Fraser et al. concluded that neither hypothesis fully explains the observed pattern; rather, the three species’ differing preferences for sea ice accounts for their different responses to climatic warming.

**Ocean acidification**

Marine organisms living in polar seas are uniquely vulnerable to the impacts of ocean acidification because low temperatures and oceanic mixing patterns depress the saturation state of calcium carbonate. As a result, the mineral forms of calcium carbonate—aragonite and calcite—have lower saturation states in polar regions than at temperate and tropical latitudes. Models project that, under business-as-usual rates of atmospheric emissions of CO₂, surface waters of the SO will become undersaturated with respect to aragonite by the end of this century or earlier, whereas calcite will become undersaturated ~50 years thereafter. Declining seawater pH in the SO will suppress the...
secretion by marine organisms of calcified shells and other skeletal elements, partially dissolve their exposed skeletal elements, and have additional impacts on their physiology. These incipient impacts make Antarctic seas the bellwether of future effects of ocean acidification on marine organisms at lower latitudes.

In the water column, ocean acidification can alter rates of photosynthesis and the diversity of phytoplankton through the pH-dependent speciation of nutrients. Among zooplankton, the thecosomatous pteropods are especially vulnerable. These tiny gastropods with aragonitic shells can attain densities of thousands of individuals per cubic meter and influence carbon flow, seasonal patterns of phytoplankton abundance, and concentrations of dimethyl sulfide. Dimethyl sulfide has the potential to alter linkages between the ocean and atmosphere, and thereby influence global climate. Ongoing work by V. Fabry et al. suggests that reductions in aragonite saturation in the Ross Sea could result in the outright dissolution of the shells of the Antarctic pteropod Limacina helicina, barring any physiological compensation. When Arctic pteropods, Chlo pyramidata, were experimentally exposed to hypercapnia (high CO₂) that reduced seawater pH to a level at which aragonite concentrations were similar to those predicted for the end of this century, their thin shells completely dissolved within 2 days. Ramifications of the loss of the cosomatous pteropods include the loss of a major pathway of carbon flux to deeper water via their planktotrophic larvae, particularly those bearing calcified shells or skeletal elements.

The adult stages of benthic invertebrates appear to be vulnerable as well. The shells of several species of Antarctic bivalves and a brachiopod suffered significant loss of mass after only one month when held in seawater at 4°C and pH 7.4. This is the pH expected if burning of fossil fuels continues at present levels for the next few centuries and the atmospheric concentration of CO₂ increases to 1,900 ppmv from its present value of 388 ppmv. By two months, severe erosion of the surface layers of the shells had occurred, exposing structural prisms within the shell architecture (Fig. 7).

Antarctic benthic marine invertebrates generally exhibit low metabolic rates and very slow development and growth compared to similar taxa at lower latitudes. Because of their prolonged life histories, opportunities will be limited for acclimation or adaptation to seawater that by the end of the century will likely become corrosive to calcium carbonate. The loss or altered population dynamics of seastars, sea urchins, and other strong interactors could fundamentally change the trophic dynamics of the benthos.

Other ecologically important elements of the benthic biota that are at risk include coralline algae and cold-water corals. Coralline algae, which secrete high-magnesium calcite, are especially vulnerable. Dead thalli of a common Antarctic coralline alga exhibited rapid dissolution in seawater at pH 7.4, with cracking of the conceptacle pores and a significant reduction in mass after 56 days at 4°C. There are as yet no studies published on the
impacts of ocean acidification on living adult stages of Antarctic benthos.

Our understanding of the prospective impacts of ocean acidification on Antarctic marine life is in its infancy, and several important questions remain. How will concurrently warming seawater temperatures associated with climate change interact with ocean acidification? Will fisheries in the SO be affected? Will ocean acidification further reduce the limited resistance of shelled invertebrates to the skeleton-crushing activities of invasive predators, and/or further limit the abilities of those predators to secrete calcified feeding structures? Will increased growth rates in response to warming and less costly calcification compensate for ocean acidification in some ectotherms? Baseline monitoring of ocean chemistry needs to be continued and expanded in Antarctica to provide context for field and laboratory studies of the impacts of acidification on physiology, growth, and calcification.28

The future of marine biodiversity in Antarctica

Marine biotas worldwide are being degraded and globalized by biological invasions, climate change, pollution, and a host of other anthropogenic perturbations. Even the putatively isolated continent of Antarctica is no longer exempt from biotic homogenization. Ecological diversity has long been described and modeled using the metaphor of information content. To carry that metaphor forward, in terms of global biodiversity, we are in the process of “dumbing down” the endemic fauna of Antarctica and its unique ecology.

Multiple causative factors are responsible for any observed environmental pattern in time or space. The task of the ecologist is to determine the relative contributions of those various causes, rather than to attempt to falsify all but one cause.206 The number of cross-references in this review should make it clear that interacting combinations of human-generated disturbances and stresses on local, regional, and global scales drive the trajectories of degradation of marine ecosystems in Antarctica. Halting and reversing that degradation will, therefore, require policy and action at all of those scales.

Acknowledgments

We are grateful to Kevin Arrigo, Angelika Brandt, Hugh Ducklow, William Fraser, John Lawrence, Polly Penhale, Stephanie Vos, and two anonymous reviewers for advice and discussion. Margaret Amssler assisted with editing, and Lauren Toth and Peter Fretwell assisted with graphics. RBA and JBM thank the U.S. National Science Foundation for continuing support of their research in Antarctica. During the writing of this paper, RBA was supported by NSF grant ANT-0838846, and JBM was supported by grants ANT-0838844 and ANT-1041022. JBM also acknowledges support provided by an Endowed Professorship at the University of Alabama at Birmingham. ST’s research was supported by grants from the Total Foundation (Abyss2100) and the Royal Society. This paper contributes to the British Antarctic Survey’s Environment Office Long-Term Monitoring and Survey project as part of the Polar Science for Planet Earth Programme. It is
Contribution number 41 from the Institute for Research on Global Climate Change at the Florida Institute of Technology.

Conflicts of interest
The authors declare no conflicts of interest.

References


75. Snape, I., D.B. Gore, C.M. Cole & M.J. Riddle. 2002. Contaminant dispersal and mitigation at Casey Station:


Impacts on Antarctic marine ecosystems

Aronson et al.


