Impacts of Global Warming on Polar Ecosystems

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3. THE IMPACT OF CLIMATE CHANGE ON ANTARCTIC MEGAFAUNA

by

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THE ANTARCTIC MEGAFAUNA takes in most of the air-breathing predator species: marine birds and mammals. These species are all long-lived and slow to reproduce and are therefore vulnerable to climate changes that increase the variability of their population growth rate. Most of them rank high in the marine food chains and feed on Antarctic krill, their staple food. Except for the cetaceans, which are fully aquatic, all other Antarctic megafaunal species depend on the terrestrial environment to reproduce. The impact of climate change on the megafauna is especially severe in some Antarctic regions and is expressed at several levels. It arises as a consequence of climatic and meteorological changes operating on different temporal scales—from years to decades—and is generally related to global phenomena such as the El Niño Southern Oscillation (ENSO). A number of Southern Ocean marine bird and mammal populations have shown cyclic alterations in their reproductive success, productivity and survival that are consistent with the environmental alterations associated with the ENSO. These take the form of a reduced sea-ice extent and higher air and water temperatures and cause a temporary modification in the structure of marine ecosystems. Their impacts on krill and other prey, together with the transformation they effect on the ice environment of Antarctica, have significant knock-on effects for marine birds and mammals. The reduction in available food and habitat during the crucial breeding and rearing season alters the distribution and abundance of pinniped species, along with that of penguins and other seabirds. Climate change will increase ecosystem fluctuation and only those species capable of adapting to a more variable environment can successfully survive climate change. For the remaining species, these environmental alterations bring changes in their distribution, abundance and certain aspects of their biology.

◀ **Photo 3.1: A group of king penguins (*Aptenodytes patagonicus*).** Penguins, the quintessential Antarctic birds, are severely affected by global warming and its effects on populations of krill, their main food source.

3.1. INTRODUCTION

The Antarctic megafauna consists of aquatic organisms, such as marine mammals and penguins, and other animals, like flying seabirds, that have adapted to life at sea. Most of them depend on terrestrial ecosystems to complete their life cycles. Some complete part of their life cycle on the ice, but others need ice-free surfaces to survive. Antarctica is a frozen desert of which only 4% approximately is free of ice during the summer months, when the coastal ice-free areas essential for their reproduction become available. However, all Antarctic megafauna depend on the ice to at least some extent, in order to rest, rear their young and find food. Ice shelves and sea ice not only provide a critical habitat, but ensure the food supply of most of these species, due to their dynamics and their influence on the oceanographic processes favouring primary production.

The Antarctic continent is covered in ice, extending over the terrestrial medium, including the frozen seabed, and the pelagic system, where it forms shelves. These shelves are dynamic, changing throughout the year in length, breadth, thickness and cohesion. Occasionally chunks break off and drift out to sea as icebergs (photo 3.2). Sea ice forms beyond the ice shelves when the

Photo 3.2: A drifting iceberg, showing the different types of ice formed at successive stages. Ice compression and mineral composition generate the diversity of ice colouration.

surface of the sea freezes due to the low temperatures of the Antarctic winter. Ice shelves and sea ice are both sensitive to small temperature changes, which is why the most important effects of global warming on Antarctic megafauna, mediated by higher atmospheric and ocean temperatures, have to do with the disruption of terrestrial and sea-ice dynamics and their thickness and expanse over time and space. Furthermore, greater freshwater influx into the ocean due to the accelerated melt of glaciers, icebergs and ice shelves is modifying the biodiversity and structure of marine ecosystems, of which megafaunal species are an essential component.

The effects of warming on the megafauna are multiple, but we can single out two main types: those relative to the loss or gain of critical habitat without which the megafauna cannot exist (e.g., the physical environment required for some marine birds and mammals to breed and rear their young); and those that modify food webs with direct repercussions on the food the megafauna consume. The diminishing extent and seasonal duration of the sea ice affects those species that most depend upon it to complete their reproductive cycle. Other, less ice-dependent species probably benefit from this reduction, so it is reasonable to expect alterations in food webs and species communities, as well as in their distribution and abundance. In many instances, the consequences of global warming stem from the interaction of many different factors, giving rise to distinct population responses among different species, which bring about changes in communities and ecosystems. These changes are expressed regionally and on differing time scales as a function of the local impact of warming, the climate cycles related thereto and the repercussions on each megafaunal species.

The impact of global warming on the megafauna coincides with other anthropogenic impacts, such as the expansion of marine fisheries and, to a lesser extent, the increase of tourism in certain areas of the Antarctic continent. While the impact of tourism is probably low for the moment, more intense fisheries in the Southern Ocean may disrupt the equilibrium of some marine ecosystems, with direct and indirect effects on the megafauna. To understand the full repercussions of man's actions, we must study their ecosystems impacts on a combined basis, starting with the regions most affected by global warming, i.e., where its effects are most readily detectable. It is these regions that are suffering the most far-reaching ecosystem changes, and the most severe impacts on their megafauna, above all those species sensitive to ice loss.

The impact of global warming on Antarctic megafauna is not as readily apparent as it is in the Arctic, where the accelerated loss of sea ice, especially during the summer, is jeopardising the reproductive success and survival of species like the polar bear (*Ursus maritimus*) (Derocher 2005). Other species affected, though to a lesser extent, are harp seals (*Pagophilus groenlandicus*) and hooded seals (*Cystophora cristata*) (Johnston et al. 2005), since both species are heavily reliant on ice shelves and sea ice for rearing their young. Nevertheless, one southern region where similar changes are now being detected is the Antarctic Peninsula.

The western Antarctic Peninsula is among the world regions that is warming up the fastest. The average annual temperature rises recorded at scientific bases during the last 50 years are up to 10 times greater than the equivalent figures for the planet as a whole (Vaughan et al. 2003). And in the last few decades, the ocean's surface temperature has risen by approximately 1°C, with increases sharpest in the winter months (Meredith and King 2005). Since the 1960s, the changes in atmospheric circulation known as the Southern Annular Mode (SAM) have contributed to increase the force of the westerly winds over this area (Marshall, Van Lipzig and King 2006). These impacts are irrefutable evidence of the connection between human activity and the destruction of large areas of ice shelf, among the best known being the Larsen Ice Shelf.

3.2. THE ANTARCTIC MARINE ECOSYSTEM AND THE IMPORTANCE OF KRILL FOR THE MEGAFAUNA

Antarctic ecosystems are conditioned by their strongly seasonal climate and the extreme temperatures of the long winter. Large changes in solar irradiation and the extent of the sea ice create very different conditions from winter to summer that are of direct importance to Antarctic organisms. The way species respond may depend on their levels of tolerance and adaptation to extreme temperatures (Peck, Webb and Bailey 2004). However, their distribution and abundance are mainly determined by the availability of food sources, and here the outcome is decided over the brief summer months, when conditions favour their development. This is the case of the marine plankton, the organisms at the base of the food chain, and for the rest of the organisms that depend on them to complete their reproductive cycles and survive the winter months with their scarce resources. For the plankton, the most productive areas of the Antarctic Ocean are the continental margins, where the terrestrial minerals carried and deposited by the seasonal ice melt favour the blooming of phytoplankton near the shoreline. Also, the ice melt helps to stabilise surface sea layers by facilitating the accumulation of seaweed biomass. This highly productive medium is home to an abundance of crustaceans and salps

Photo 3.3: Krill (*Euphasia superba*). The decrease of krill populations caused by global warming is having a negative cascade effect on many of the predator species that make up the large marine bird and mammal community of the Antarctic.

(gelatinous plankton). These are the predominant components of zooplankton and the main food of predators, most of them megafaunal species. The brevity of summer means that food chains are relatively short (Clarke 1985) and hinge upon a few key species, such as Antarctic krill (*Euphasia superba*).

The high density of crustaceans in the Southern Ocean assures them a fundamental role in the structure and function of marine food webs (Smetacek and Nicol 2005; Murphy et al. 2007). This is especially true for euphausiids (krill), an order whose main species have life cycles linked to seasonal changes in the sea ice. Antarctic krill is found in great abundance from the sea ice to the open ocean waters, and is the most important food for fish, squid, seabirds and marine mammals. Sea ice provides seaweed for the krill to feed on and refuge from predators, especially during the larval stage (Smetacek and Nicol 2005). This dependence on ice means that the krill is probably among the groups of species most exposed to the effects of global warming, with indirect consequences for their main predators, which have difficulties finding a similarly copious source of nourishment. These impacts are gravest where krill is abundant and the ice retreat is more advanced.

One of the most productive areas of the Southern Ocean is the southwest Atlantic sector running from the Antarctic Peninsula to the Antarctic Convergence and the Scotia Arch, including South Georgia and the South Sandwich Islands. This is the area with the greatest density of krill in the entire Southern Ocean (Atkinson et al. 2004) and consequently with the greatest diversity and abundance of its main predators, including true seals, fur seals, whales, penguins and other seabirds, especially albatrosses and petrels (Laws 1984). A number of oceanographic phenomena in the Scotia Sea, including the swift flowing Antarctic Circumpolar Current, its bathymetric features and the climate and its interaction with the Pacific Ocean through the Antarctic Circumpolar Current, together with the ice dynamics of the Weddell Sea, alter the pattern of krill transport from the west of the Antarctic Peninsula towards the Scotia Arch and Islands. Because of these interactions, the effects of warming on the climate and oceans in this and other regions remotely connected to it alter the availability and abundance of krill. These connections between the physical environment of planetary regions separated by large distances, such as the Scotia Sea and the tropical Pacific Ocean (Trathan and Murphy 2002), occur as a result of the transfer of climate anomalies in the atmosphere, the ocean's circulation and the physical processes derived from ocean-atmosphere interactions (Turner 2004). Such interactions affect the entire food chain and, ultimately, the population dynamics of marine predators (Forcada et al. 2005; Forcada et al. 2006; Trathan et al. 2006).

In the last 50 years, the expanse of sea ice in this sector of the Southern Ocean has diminished as a consequence of global warming, and glaciers have receded considerably (Cook et al. 2005), increasing freshwater runoff into the ocean. This has directly affected food webs by altering ice dynamics with a negative impact on Antarctic krill (Murphy et al. 2007). The reduction of sea ice in winter modifies the regional variety and composition of phytoplankton, favouring the proliferation of salps to the detriment of krill, whose density and availability to predators drop significantly (Loeb et al. 1997; Atkinson et al. 2004). The increased influx of freshwater from melting glaciers has contributed to the seasonal modification of phytoplankton species diversity, and consequently of the marine zooplankton (Moline et al. 2004). Considering the oceanography and ice dynamics in the Weddell Sea, south of the Scotia Sea, as well as the effect of global climate and the oceanographic conditions of the Pacific Ocean, the impact of warming on the Antarctic Peninsula affects not only the boundaries of the ice and the predators that depend on it, but also the sub-Antarctic islands.

In other Antarctic regions, the ice dynamics differ (Zwally et al. 2002; Parkinson 2004), and the effects of global warming on marine ecosystems are less detectable. For instance, in the Ross Sea, in the Pacific sector of the Southern Ocean, the expanse of sea ice has apparently enlarged in recent years, and the effects of warming are perhaps less perceptible than in the Antarctic Peninsula; however, the temperatures of the troposphere and high atmospheric strata also seem to have risen considerably in these regions (Turner et al. 2006), and their dynamics have decoupled from those of the lower layers that are in contact with the ice. For this reason, we have no accurate picture of the long-term consequences of this rapid warming phenomenon, and it is important to assess its effects on a regional scale. To reach general conclusions about the impacts of warming, we need to make comparative studies of its effects on the marine ecosystems of distinct Antarctic regions.

3.3. ANTARCTIC MEGAFAUNA: LIFE HISTORY, ICE ADAPTATION AND CRITICAL HABITATS

Some groups of megafaunal species, like the pinnipeds (seals and sea lions), and seabirds (mainly penguins, albatrosses and petrels), depend on terrestrial ecosystems to complete their life cycles, while others, like the cetaceans, are exclusive-

Photo 3.4: Emperor penguins (*Aptenodytes forsteri*) diving. Emperor penguins are amongst the vertebrates best adapted to the inhospitable Antarctic conditions. They are the only penguins capable of withstanding the winter season in these latitudes, where temperatures can reach –50 °C.

ly aquatic. Not all the species in these groups evolved and adapted to Antarctic environments in the same manner or during the same geological period, so their development has occurred in different ecological contexts. The variation in the values of life history characteristics (age of sexual maturity, fecundity, growth and survival rate) as a response to extreme environments is specific to each species, and it is this variation that determines their demographics and population dynamics, which in turn determine their distribution and abundance. Furthermore, the ecophysiological adaptations of each species (such as tolerance to extreme temperatures or aquatic or semiaquatic life habits) limit or favour their adaptation to ice and other extreme living conditions. Thus, we need to identify species-specific life history strategies and adaptation mechanisms in order to understand the consequences of global warming on different species.

The marked seasonality of the Antarctic ecosystems forced megafaunal species to adapt their life cycles to the extreme climatological and physical changes that differentiate winter from summer. Almost all megafaunal species reproduce during the southern summer, when the expanse of sea ice recedes, leaving the terrestrial environment more accessible. Nevertheless, this ice-free space is still small, and there is considerable local competition for it. After completing their reproductive activity, most species migrate or disperse because they cannot survive the Antarctic winter. Some species drift at sea looking for food, others disperse towards winter grounds further north, and others remain on the ice, near areas where food is accessible, such as polynyas, the open areas in the ice formed by strong oceanic currents that allow safe access to the sea waters where food may be found.

Given the high seasonality of their life cycles, all species depend on stimuli or environmental signs that tell them the right time to start their migratory movements or to engage in a given life stage. The disruption of these stimuli by global warming (for instance, changes in the onset of the spring melt or ice formation in the autumn, or temperature oscillations) can have serious consequences for populations and communities of living organisms (Barbraud and Weimerskirch 2006). During years when climatic anomalies cause the ice retreat to be particularly extreme, birds and pinnipeds do not return to nest or breed in greater number even though there is more space available, because there is usually an accompanying reduction in the availability of food.

The scarcity of ice-free land and the influence of climate and physical changes in the Antarctic continent make the Antarctic and sub-Antarctic islands an important refuge for the megafauna. Not only do they tend to have more available land and easier access to food, they are also optimum reproductive sites for seabirds and pinnipeds. Many of these islands are a long way from the continent, such as those of the Scotia Arch or the Indian Ocean sector of the Southern Ocean, including the Kerguelen and Crozet archipelagos. The predators inhabiting these archipelagos depend almost exclusively, in most cases, on the food they can find in the pelagic environment, yet the availability of this food, mainly krill or krill predators, may be a lot more variable and unpredictable than in other areas due to interactions between the climate and various oceanographic phenomena.

3.3.1. Life history variability and ice adaptation

During the short breeding season, restricted to the summer months, sea mammals and birds congregate in colonies on land or on ice. However, the two groups have adapted to the seasonal cycles in different ways conditioned mainly by their energy budgets.

3.3.1.1. Seabirds

Seabirds invest the greatest part of their reproductive energy in feeding their young. The chicks must be fed until they become independent of their parents. Penguin chicks fledge a month after hatching. During this time the parents make multiple foraging trips to sea to provide a constant flow of nourishment to ensure their reproductive success, i.e., the survival of their offspring. They accordingly depend on the marine environment to supply them with prey, but are limited by the distance they can travel from the breeding colony and the maximum time they can spend away from the chicks without jeopardising their development. The chicks of other seabirds, particularly the albatross, take longer to become self-sufficient. Those of the wandering albatross (*Diomedea exulans*) may need up to eight months of parental care, making the parents' energy investment in rearing much greater, leading to two-year breeding cycles.

The effects of warming on seabirds have been detected mainly in species, like penguins, that depend on an abundant, constant and nearby source of food, and whose chicks fledge quickly. For these species, ecosystem warming translates as a decline in available food, which directly affects their reproductive success (Fraser and Hofmann 2003; Forcada et al. 2006; Trathan et al. 2006). In years when the expanse of sea ice is small, due to higher temperatures, there is a reduced availability of krill, the main prey for many penguins and some petrels, so they must spend more time at sea looking for food.

Other seabirds that are less dependent on the physical and biological environment near their breeding colonies can forage over distances of hundreds or even thousands of kilometres. For instance, many albatrosses that nest in the sub-Antarctic islands travel for days looking for food, covering hundreds of kilometres before returning to their nests to feed their chicks. This is the case of the black-browed albatross (*Thalassarche melanophrys*) and the grey-headed albatross (*Thalassarche chrysostoma*) (photo 3.5), which nest in South Georgia but travel regularly to the Patagonian continental shelf or the Antarctic Peninsula in search of prey like squid and krill, respectively. Their ability to cover large distances in a short time allows them to look for more distant prey, spreading out the effort of searching for food, thereby maximising the amount transferred to the chicks when they return to the colony. Global warming-driven environmental anomalies have less effect on species like these, which do not depend directly on the sea ice.

For some petrel species, such as the snow petrel (*Pagodroma nivea*) (photo 3.6), ice dependence limits access to food. This species nests exclusively in ice- or snow-covered zones, sometimes hundreds of kilometres away from krill, their main source of food. To feed their young, the parents must regularly cover these

Photo 3.5: A grey-headed albatross (*Thalassarche chrysostoma*) feeding its chick on South Georgia Island after returning from a long foraging journey

long distances, expending a considerable amount of their energy in flight. Given the krill's relationship with the sea ice, the snow petrel faces shortages when the ice recedes, significantly reducing the availability of krill and other ice-dependent resources (Jenouvrier, Barbraud and Weimerskirch 2005). Like most petrels and albatrosses, the snow petrel is a long-lived species that takes a long time to reach sexual maturity and reproduces slowly. This means they must marshal their available energy effectively, allocating more to reproduction than to survival. Reproduction is energetically costly, so the snow petrel survives at the expense of curtailing reproduction in those years when climate conditions and the dynamics of sea ice adversely affect its coverage and the availability of food.

Amongst the Antarctic penguins, the Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) have the greatest affinity for ice. The emperor penguin is one of the best ice-adapted Antarctic vertebrates. It can survive in temperatures of less than -50°C during winter gales in one of the most hostile and extreme environments on the planet. Emperor penguins have one of the longest reproductive cycles, starting in March, during the winter, and ending in December, during the summer. They breed on quick-forming sea ice, the kind that solidifies in winter on the ocean surface and breaks up during the

Photo 3.6: Snow petrel (*Pagodroma nivea*). These seabirds breed in permanently frozen areas far from the sea, so must travel hundreds of kilometres to find the krill with which they feed their chicks.

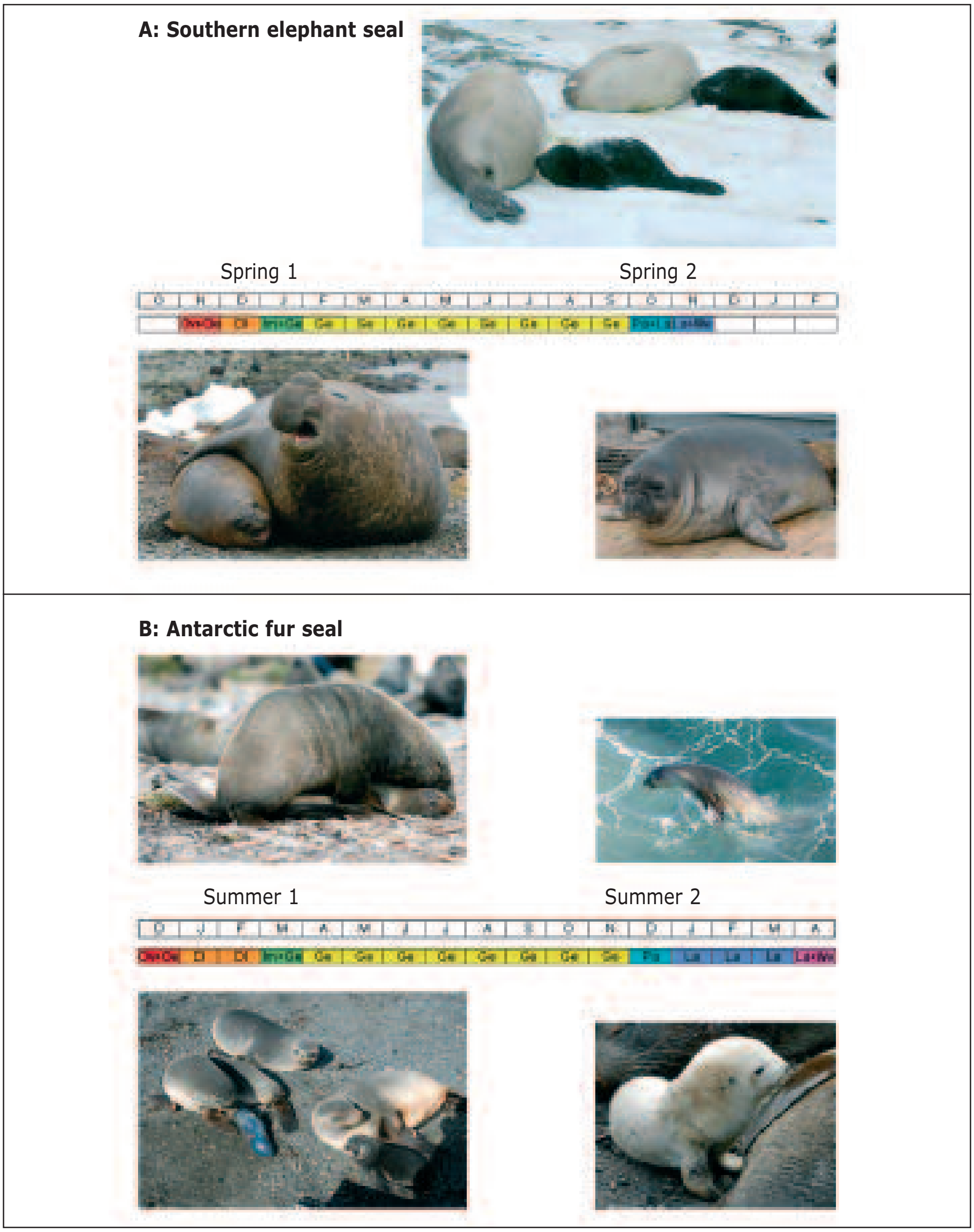
summer. While they incubate and hatch their single egg, and during the first weeks of the chick's life, the male can go for more than three months without food while exposed to extreme temperatures, losing up to 45% of its body weight. Meanwhile, the female feeds at sea, eating mostly fish. Studies of this species in the Indian Ocean sector of the Southern Ocean indicate that males survive less well than females due precisely to this greater investment of energy in reproduction, but that rising temperatures during both summer and winter may decrease the survival rates of both sexes. An extreme reduction of sea-ice cover could push up male mortality in particular (Jenouvrier, Barbraud and Weimerskirch 2005), as a result of lower food availability.

The biological strategies of the emperor penguin and the snow petrel—some of the seabirds most adapted to Antarctic ice—differ in several aspects (Jenouvrier, Barbraud and Weimerskirch 2005). The emperor penguin reproduces almost every year, despite the extreme environmental conditions and what they signify for male adult survival, while the snow petrel may delay reproduction to avoid this cost, as well as having a much shorter reproductive cycle. The emperor also reaches sexual maturity quite young, while the snow petrel may take up to seven years and is possibly longer-lived. However a reduction of sea ice could entail significant long-term population changes for both species.

3.3.1.2. Marine mammals

Unlike seabirds, whose reproductive energy investment is limited to egg laying and incubation, sea mammals have a long gestation period whose final stage requires high energy expenditure from the mothers. The gestation period of Antarctic pinnipeds normally lasts from the end of one summer to the start of the next. Then during lactation, the females must transfer even more energy to their offspring. The lactation period for seals (phocids) lasts a maximum of one month, while for the otarids, specifically the Antarctic fur seal (*Arctocephalus gazella*), it lasts approximately four months. As a rule otarids (sea lions and fur seals) lactate for a period of around one year, but shortening this to four months may be a necessary adaptation to survive Antarctic seasonality. Most pinniped species are able to reproduce during consecutive summers, meaning that the new gestation starts while the previous offspring is still lactating. This makes females more dependent on terrestrial conditions when giving birth, besides environmental conditions and food availability. For the Antarctic fur seal, whose reproductive success is based on shorter lactation periods and earlier offspring emancipation than those of similar species, food scarcity is an even greater challenge than for other pinnipeds.

Figure 3.1: Reproductive strategies of Antarctic pinnipeds

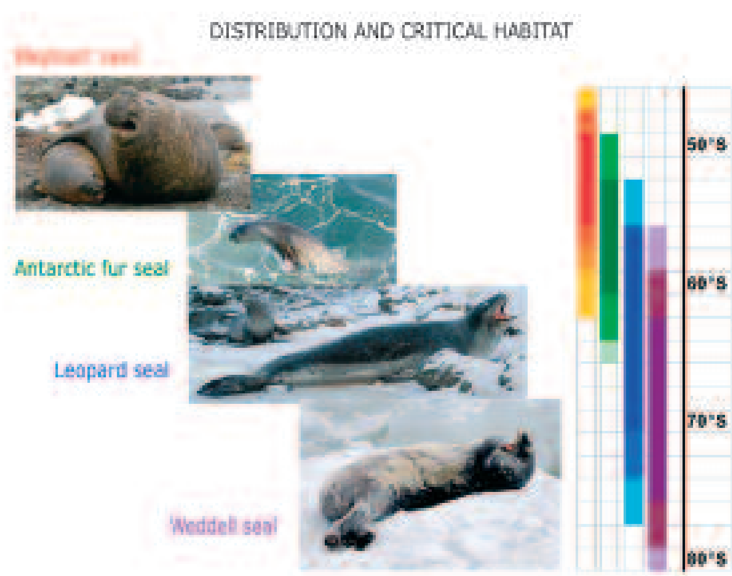


A: For southern elephant seals the length of the lactation period depends on the fat reserves accumulated by nursing mothers far from their breeding grounds. **B:** Antarctic fur seal mothers rear and suckle their pups while simultaneously feeding near the breeding colony. This, and their long lactation period, make the species more vulnerable to resource shortages driven by global warming.

Reproductive cycle: Ov: ovulation; Oe: oestrus; Di: diapause; Im: embryo implantation; Ge: gestation; Pa: partum; La: lactation; We: weaning.

In order to complete their reproductive cycle and transfer the necessary energy to their young during lactation, pinnipeds have developed two different feeding and energy-storing strategies (figure 3.1). One of these, called capital breeding, entails the accumulation of energy reserves as fatty tissue that can be mobilised and put to use during the breeding and rearing period. Adults usually stop feeding at this time, and they require sufficient energy reserves to maintain their bodily functions and metabolism. This is the strategy used by all Antarctic seals, from the southern elephant seal (*Mirounga leonina*) to leopard seals (*Hydrurga leptonyx*), crabeater seals (*Lobodon carcinophagus*), Weddell seals (*Leptonychotes weddelli*) and Ross seals (*Ommatophoca rossi*) (figure 3.2). The other strategy, called income breeding, requires a food source near the breeding colony sufficient to satisfy the energy demands of mother and pup. Like penguins, fur seal mothers make frequent foraging trips to sea before returning to land to suckle their young. This limits the time they can spend feeding at sea—usually no longer than a week—during which female fur seals convert most of the energy ingested into milk. This strategy increases the fur seal's dependence on the environmental conditions determining food availability near breeding colonies.

Figure 3.2: Latitudinal variation of Antarctic seals and fur seals



Each colour in the figure represents a species. The tonal variation in the latitudinal scale on the right shows the variability in their south-north distribution. The most intense colours indicate the mid-point of the distribution and the least intense colours its limits. The Weddell seal is the pinniped most adapted to life on ice and therefore the most resistant to extreme conditions. The Antarctic fur seal is the least adapted to icy conditions and needs ice-free surfaces for breeding.

Photo 3.7: Antarctic fur seal (*Arctocephalus gazella*). The reproductive success of this otarid is conditioned by changes in climate and the abundance of krill.

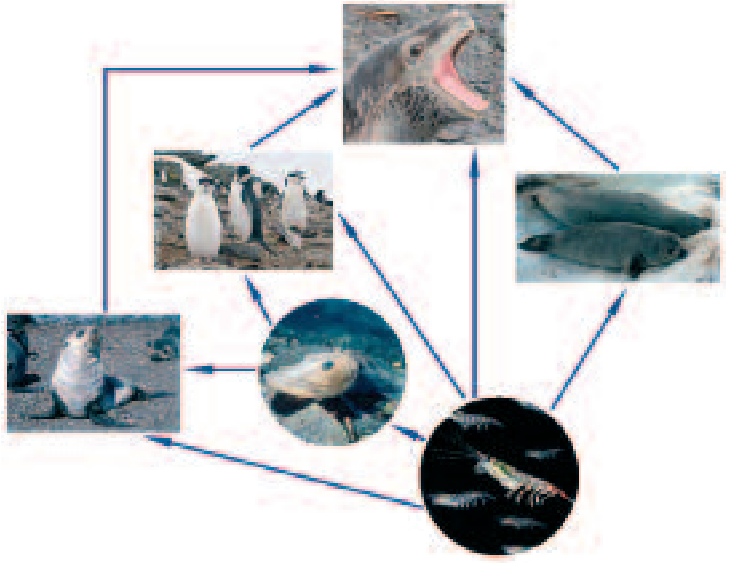
The effects of global warming on the life of pinnipeds are observed mainly during the breeding season or the preceding months, when adults need to accumulate sufficient reserves. The most obvious repercussions are related to climatic disturbances that modify the ecosystems and the main food source of breeding individuals. For instance, the productivity, reproductive success and other vital parameters of Antarctic fur seals breeding on South Georgia have been found to be impaired by the environmental changes arising from the El Niño phenomenon in the tropical Pacific (Forcada et al. 2005). This climate disturbance is transferred to the southwest Atlantic sector of the Southern Ocean, manifesting itself as high sea temperatures and a reduction of sea ice in winter. In this region, the disappearance of the ice cover is associated with decreased food availability for the Antarctic fur seal, affecting both Antarctic krill—their main food—and the fish species that form part of their diet.

El Niño has also been shown to affect the survival of offspring in the case of the southern elephant seal, a species with a completely different strategy from that of the Antarctic fur seal and a broader latitudinal distribution. Elephant seal mothers accumulate lipid reserves by ingesting more food during the final stage of gestation. This generally occurs above the boundary of the Antarctic Convergence, the area that separates the Southern Ocean from the temperate and subtropical ocean waters. After the pups are born, they are suckled for nearly a month, over which time their mothers transfer large amounts of energy. When they are weaned and become self-sufficient, the young have to survive using their own energy reserves and other resources. In some El Niño years, food is more abundant for both mother and offspring, because the oscillation boosts the abundance of squid, one of the seal's main prey species. Greater energy investment during years of climatic anomalies seems to favour the survival of the first-year young on Macquarie Island (McMahon and Burton 2005). For this species and region, El Niño exercises the opposite effects to those observed for the Antarctic fur seal in South Georgia.

The effects of warming on true Antarctic seals are not so evident, due to their capacity to survive on the food reserves they build up outside their breeding season. For these species, in contrast to their Arctic relatives like the ringed seal, receding sea ice does not bar them from access to their primary food source, or leave their offspring more exposed to predators. One of the most ice-adapted Antarctic seals is the Weddell seal (figure 3.2). It feeds mainly on large benthic fish, which do not seem to have become less available with the disappearance of sea ice. Weddell seals are also adapted to extreme temperatures, and their reproductive success depends on environmental conditions. The young may die during extreme temperature conditions and fierce storms, but the mothers are sufficiently well adapted to survive such conditions. The stability of the population is thus ensured, because the mothers survive even though their pups are occasionally lost. The opposite is true for the Antarctic fur seal. Both mother and young are affected by hostile environmental conditions, and consequently their demographic trends and net population growth are affected, potentially causing significant long-term population declines.

Other Antarctic seals have adapted differently to the ice. For example, the leopard seal (figure 3.3), one of the main Antarctic top predators, is associated with ice, particularly quick-forming ice, as well as floating brash ice and drifting icebergs, where it can often be seen resting after hunting forays. Their young are usually born on ice floes and fast ice but, unlike Weddell seals, they do not live permanently on the ice. During the breeding season, leopard seals feed on other ice-associated species like Antarctic krill, some benthic fish species, penguins and, especially, the young of other pinnipeds, mostly crabeater seal pups. In many Antarctic regions, crabeater seal pups are their main source of food. Indeed some speculate that this reproductive cycle, more flexible and adaptable to Antarctic seasonality than those of other seals (like the Weddell and crabeater seals), is precisely to allow the leopard seal to have its pups later than other species, like the crabeater seal, ensuring a ready source of food for pre-breed-

Figure 3.3: The leopard seal and its main prey



The leopard seal is one of the largest Antarctic predators. It is not a specialist and can feed equally on krill or on the pups of other pinnipeds. Yet the cascade effects on food webs produced by climate change may affect the availability of many of its prey species, making it harder to obtain food.

Photo 3.8: Leopard seal (*Hydrurga leptonyx*). This seal is among the largest and most efficient predators in the Antarctic waters, giving it the top place in the food chain. Leopard seals prey on the pups of other seals and on penguin chicks. The photo shows a leopard seal capturing an Adélie penguin underwater.

ing leopard seals. Also, because they are not selective predators, leopard seals can change prey according to availability, which theoretically would make them less vulnerable to climate changes affecting food abundance. Even so, during periods when climate abnormalities reduce the extension of sea ice, the leopard seal too faces a decline in the abundance of Antarctic krill and their many predators, because food webs are substantially altered. In addition, leopard seals go through a period of post-reproductive dispersal associated with climate change-driven sea-ice changes (Jessopp et al. 2004). In years of high sea temperatures and less ice cover, this dispersal phase is altered, and the number of leopard seals travelling to the penguin and fur seal breeding colonies in the Antarctic and sub-Antarctic islands reduces sharply. These conditions are associated with a lower abundance of krill for penguins in the breeding colonies (Fraser and Hofmann 2003), and also seem to suggest that there is less food available for leopard seals.

We have less information about the effects of warming on the remaining Antarctic seal species, especially the Ross seal, whose biology is largely unknown. In the meantime, speculation continues about whether the increase in crabeater seal populations ensues from the demise or decline of the whale in many Antarctic regions. Reduced whale predation pressure on krill may have benefited the effective population size of the crabeater seal by producing the so-called "krill surplus". For many years, this seal species has been thought to represent 70% of the world pinniped biomass, precisely as a result of this surplus, but because it is fundamentally a krill-dependent species, it can also be regarded as one of the worst affected, albeit indirectly, by the impact on krill of global warming. However, it is not known for certain whether this is the case, since abundance estimates are poorly reliable and the species' real population numbers are unknown.

The krill surplus theory, which is now open to question given the evidence of their reduced numbers (Atkinson et al. 2004; see chapter 2), has also been used as a possible explanation for the changes observed in Antarctic penguins (Fraser et al. 1992). However, as discussed in the next section, the combined effects of global warming on the transformation of critical habitats and the increase in marine ecosystem fluctuations with the subsequent alteration of food availability conditions seem a more convincing explanation (Fraser and Hofmann 2003; Forcada et al. 2006).

The impacts of climate change on cetaceans, mainly whales, have yet to be ascertained, because their large dispersal range throughout the Southern Ocean, their extensive migratory movements and their low population density hinder detailed studies of their ecology in relation to the dynamics of ice and climate. Nevertheless, several scenarios and hypotheses have been advanced about the adverse effects of global warming on certain species. The most plausible involve the effects of global climate change on the environment as mediated by cyclical phenomena like El Niño. This is the case for the southern right whale (*Eubalaena australis*), whose productivity and reproductive success seem to have diminished with the increase in global temperature (Leaper et al. 2006). Even so, the exact distribution and abundance of most Antarctic whale species remains unknown, as a result of the overexploitation of many populations for commercial purposes. Some populations are showing signs of recovery, including the most damaged species such as the blue whale (*Balaenoptera musculus*), but their large winter dispersal and low density throughout their range continue to make further studies difficult. At regional scales, it is possible that the diminishing numbers of their main prey caused by an increase in the frequency of climatic disturbances, especially those that have extreme effects on the physical environment and particularly on sea ice, determine the mothers' nutritional status and cause variability in some of their reproductive biological parameters.

3.3.2. Ice adaptation and critical habitats

One of the clearest examples of the effect of global warming on the megafauna is the change in population and distribution observed in congeneric penguin species that live and breed in the same regions. Under these conditions, the transformation or loss of critical breeding habitat is compounded by the fluctuations of the marine ecosystem and the resulting alterations in the availability of food. The most obvious effects have been detected in the Antarctic Peninsula and adjacent islands.

The Adélie, chinstrap (*Pygoscelis antarctica*) and gentoo (*Pygoscelis papua*) penguins, pygoscelids of similar morphology and life history, are the species most affected by the consequences of warming, seen mostly in the Antarctic Peninsula and in the adjacent Antarctic and sub-Antarctic islands (Fraser and Hofmann 2003; Forcada et al. 2006). The gentoo penguin is an essentially sub-Antarctic species with a subspecies in the Antarctic Peninsula. The Adélie penguin has a circum-Antarctic distribution, particularly on the continent, that is closely associated with ice, and is mainly found during winter in its marginal area. The chinstrap penguin is restricted to the maritime area of the north of the continent and during the breeding season inhabits mostly the Antarctic and sub-Antarctic Islands. All three species sometimes co-occur in the same geographical areas and are considered sympatric. However, there is some ecological segregation amongst them due especially to their adaptation to their preferred habitats—largely characterised by the dominance or absence of sea ice—but also to differences in their feeding habits, migratory patterns, reproductive biology and phenology (the timing of different events). The consequences of global warming for these species depend on their affinity for habitats initially dominated by ice, the degree of transformation of these habitats, their ability to exploit alternative ecological niches and the alterations arising in the timing of their reproductive cycle.

The Adélie penguin (photo 3.9) is perhaps the most severely affected by global warming via the loss of critical sea ice habitat, particularly during the breeding season, and the decreased abundance of their main prey, krill, due to the variability of the marine ecosystem and the modification of food webs. This species needs sea ice to survive, and its increased instability reduces their chances of completing their reproductive cycle in years of extreme climatic conditions. This gives rise to significant population fluctuations that make them more vulnerable to warming than their congeneric species. Of these, the chinstrap penguin (photo 3.9) benefits from the enlargement of ice-free territory during the breeding season, but is likewise harmed by the food pressures caused by the recession of sea

Photo 3.9: Adélie (right) and chinstrap (left) penguins. Both species breed on the Antarctic islands, sometimes in colonies where the gentoo penguin, a congeneric species, is also present. The reduction in the expanse and cover of sea ice alters their reproductive habitat and the availability of food during the breeding season.

Photo 3.10: Gentoo penguins, a species potentially benefiting from the effects of warming in certain regions. Although the breeding habitat of the gentoo penguin increases as the sea ice retreats, warming also modifies the marine ecosystem and reduces the availability of its prey.

ice. This species feeds almost exclusively on krill in habitats dominated by this crustacean and does not appear to switch to other prey in years when krill is locally scarce. This causes their populations to fluctuate with extreme climatic conditions, although to a lesser extent than Adélie penguin populations. For the gentoo penguin (photo 3.10), which is adapted to ice-free habitats, receding ice cover caused by warming increases the availability of habitat for breeding, but the consequences of warming on its main prey affect its reproductive success and possibly other population parameters. The gentoos have a lower density than the other species, so their competition with them for food and other resources is less intense. Also the gentoo penguin, unlike its cousins, does not feed predominantly on krill, but also catches fish and other marine species, enabling it to exploit a different ecological niche. Given these congeneric differences, the gentoo penguin might benefit from the effects of warming in some regions.

3.4. THE CONSEQUENCES OF INTERACTING ANTHROPOGENIC EFFECTS FOR ANTARCTIC MEGAFAUNA

For several groups of Antarctic species, the effects of global warming are compounded by adverse anthropogenic effects, such as pollution of their habitats caused by oil spills and the introduction of non-native species (rats and cats, for example), which have proliferated and eliminated whole populations of nesting birds in some sub-Antarctic islands. Most of the invasive species come from temperate climates and benefit from the region's increased summer temperatures, making eradication more difficult—if attempted at all—on the islands where they have become established. Nevertheless, the worst anthropogenic impacts on the megafauna are incidental capture by fisheries and the food loss caused by their intensification.

The groups of species most affected by incidental capture are albatrosses and petrels nesting on sub-Antarctic islands. Many of these species travel long distances from their nesting ground to forage for food at sea, where they also have juvenile dispersal phases that can last for years. Pelagic and demersal longlining are the most damaging types of fishing. Pelagic longlining, which uses nets of more than 130 km fitted with thousands of hooks, is used to catch commercially valuable fish species like tuna and swordfish. Albatrosses have learned to feed on the bait used in these operations, but the fishing lines cause the death by drowning of tens or even hundreds of thousands of seabirds. Demersal longline fishing, usually for Chilean hake, takes place mostly in the waters of the continental shelf and also results in numerous incidental captures.

Photo 3.11: Wandering albatross (*Diomedea exulans*). The seabird with the largest wing span and one of the longest reproductive cycles, breeding only once every two years. During the breeding season, an albatross may travel hundreds of kilometres over several days in search of food before returning to the nest to feed its single chick.

It is estimated that 17 of the 24 extant albatross species are severely threatened by these commercial practices, and the populations of some spending most of the year in Southern Ocean waters are at risk of extinction. Special working groups coordinated by the United Nations have developed surveillance programmes to evaluate the damage caused by these fisheries and are promoting the use of exclusion devices and mechanisms to reduce the rate of incidental capture. Despite these efforts and those of other international groups, the FAO considers that many countries have failed to seriously address this problem. Furthermore, Chilean hake is a species much sought after by illegal fishery operations, many of which are run by vessels under flags of convenience. For them, incidental capture is merely a momentary disruption of business rather than a grave conservation problem that needs to be tackled. The albatrosses nesting in South Georgia are especially sensitive to these commercial fisheries, and their populations are listed as among the most threatened in the world. For some of these species, particularly the grey-headed albatross and the black-browed albatross, decreased availability of food due to global warming is another serious obstacle to their reproductive success.

3.5. IS GLOBAL WARMING A REAL PROBLEM FOR THE ANTARCTIC MEGAFAUNA?

Most of the megafaunal populations studied in regions of the Southern Ocean show changes or fluctuations that are ultimately related to the effect of global warming on the physical environment; in other words, significantly higher temperatures and recession of the sea ice. In some regions, these populations are showing a periodicity in parameters like reproductive success coinciding with the ENSO cycles. Where in-depth studies have been conducted, population processes at the middle and upper trophic levels, such as those affecting krill and their predators respectively, have been shown to be connected to the ENSO-related local environmental variability observed in some regions of the Southern Ocean and tropical Pacific waters. These short-term correlations detected during ENSO oscillations have potential long-term consequences for the structure and function of Antarctic ecosystems that are difficult to explain by any cause other than global change. The cascade effect on food webs and, ultimately, on megafaunal species can now be measured. Although it is yet to be conclusively shown that the ENSO cycles have been altered by global warming, it is accepted that El Niño has appeared with greater frequency in the last 20 years, and there has been a simultaneous progressive retreat of sea-ice cover in the winter, the result of a rise in temperature of anthropogenic origin.

3.6. IS IT POSSIBLE TO PREDICT THE FUTURE?

To predict how increasing greenhouse gas emissions are going to affect Antarctic ecosystems, we can use climate models to study the Antarctic climate and its interactions with the physical environment. Current models predict a several-degree increase in the prevailing temperature over most of the Antarctic continental area during the present century. However, average temperatures over most of the continent are not expected to rise above melting point, so it is possible that warming over the next 100 years will not cause a significant loss of most continental ice. On the other hand, the model also predicts a rise in the temperature of the Southern Ocean that could wipe out 25% of the existing sea ice, although there is great uncertainty surrounding this prediction. Likewise, warmer ocean waters may have a negative effect on ice shelves and accelerate their fragmentation and melting. It seems clear that the retreat of sea ice will continue to affect Antarctic megafaunal species to varying degrees. The consequences will be directly related to each species' dependence on sea ice as its critical habitat and its ability to adapt to the disturbances caused by the seasonal nature of food availability. Alterations in the food chain and variation in prey availability will also modify the environmental carrying capacity of many species, whose populations will increase or decrease in line with changes in this capacity.

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