HOT TOPICS IN MARINE BIOLOGY 8.2

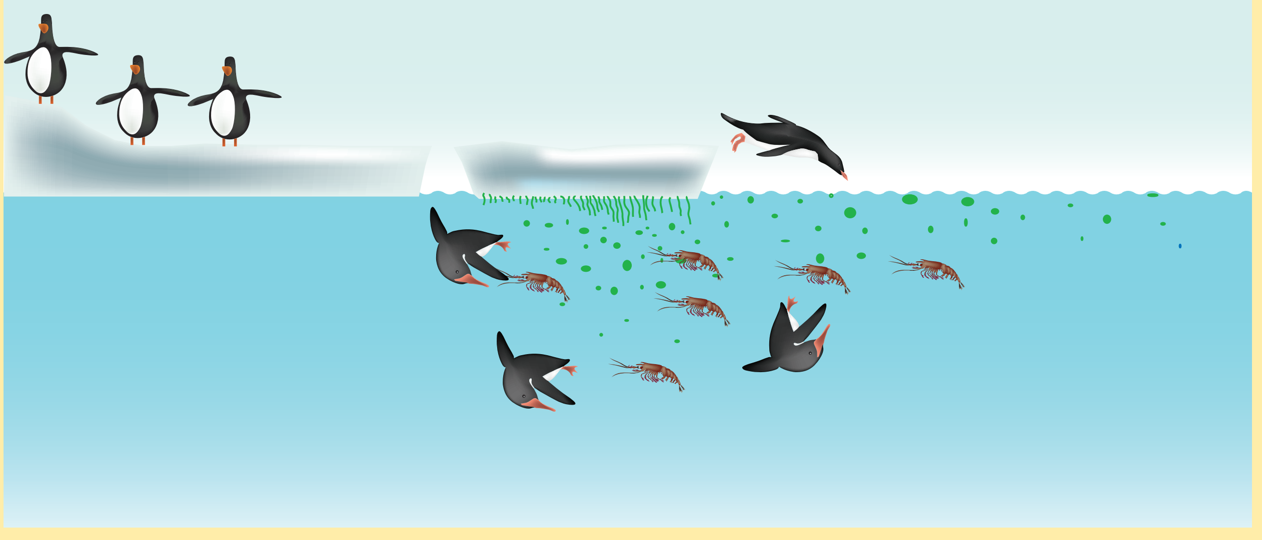
Last March of the Penguins? Climate Change and a Bottom-Up Trophic Cascade

In Chapter 3 we discussed the phenomenon of trophic cascades. In many ecosystems, feeding connections have tremendous impact on the fate of marine populations. The reduction in population size of a top carnivore, such as a sea otter in a kelp forest, will have a dramatic impact on its prey, such as sea urchins. This in turn will have an indirect effect on the next level down, and kelps, the food of sea urchins, may increase in abundance. Reverse reverberations on a predator will also occur when its prey is removed. We can expect similar strong interactions when an important structural element of a community is affected. The great decline in sea grasses around the world has had devastating effects on the many species that depend on the shelter provided by these sea grasses. These crucial connections teach an important lesson: External driving forces that affect species belonging to interacting food chains, or affect crucial organizing elements in communities, will have disproportionate effects on the community.

Climate change in recent decades is just the sort of driving force that can have such a strong impact. As discussed in Chapter 2, sea surface temperature is increasing around the globe, with disproportionate effects in the Northern Hemisphere, especially in the decline of Arctic Ocean ice cover. But Antarctic sea ice near the Antarctic Peninsula is also on the decline, and therein lies a series of cascading effects on an important marine food chain involving ice algae, krill, and a number of species of penguin (**Box Figure 8.3**).

Krill (see Chapter 7) are shrimplike herbivorous animals a few centimeters in length that often dominate the zooplankton of surface waters of high productivity such as upwelling centers of the coastal and open oceans. Krill is the Norwegian word for "whale food," and this tells us much about their distribution and importance in oceanic systems. They are especially abundant in the Antarctic and are crucial food for a wide variety of important populations of baleen whales, other marine mammals, and penguins. If krill decline, we should expect a **bottom-up effect on predators** higher in the food chain. Krill are also a major fishery, and overfishing has been a major worry because of the potential indirect impacts on the species that depend upon krill. Krill are still very abundant, and commercial fishing and seafood production have been hampered because krill decompose rapidly and the shells are difficult to remove. Still, the economics of declining world fisheries have resulted in increased fishing impacts. Concern for overfishing in the Antarctic began when krill fishing greatly increased in the 1970s, and a 1980 international treaty (Conservation of Antarctic Marine Living Resources) allowed the imposition of fishing limits. The fishing take in recent years has actually been less than the limit imposed by a scientific committee. On the other hand, krill fishing has been on the rise since 2000 owing to uses for krill in the aquaculture industry, because extracts are useful in fish food and potentially in medical applications.

Enter climate change. A crucial trophic connection to sea ice may be causing devastating impacts on populations of Antarctic predators, especially penguins. Krill are famous for associating with concentrations of food and are notable for their swarming behavior. In recent decades, a rich community of algae, protistans, and bacteria has been found associated with sea ice, living within cracks and suspended from the bottom of the ice. The species appear to be similar to those found in open waters, and some must just be introduced passively into cracks and water streams within the ice. In recent years, molecular DNA markers have been used to survey the occurrence and relative abundance of ice microorganisms. Some of these organisms also grow actively within the ice and on the bottom of the ice, suspended into the water.



BOX FIG. 8.3 Links among sea ice, ice algae, krill, and penguins.

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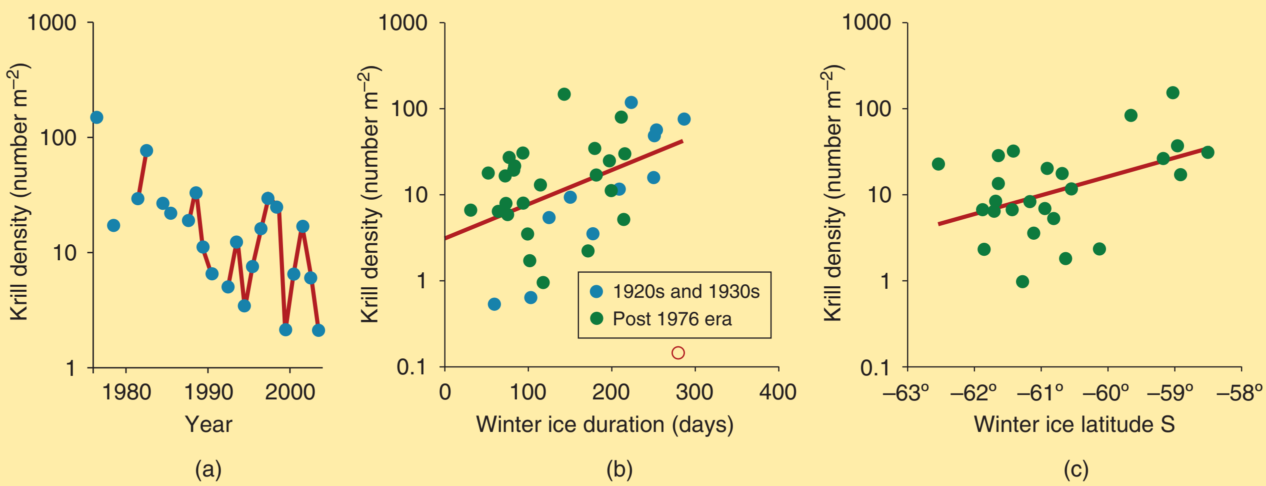
This so-called **ice algae** has high productivity. It is a small fraction of open Southern Ocean primary production on an annual basis but is very concentrated spatially and is often abundant in seasons when open-water phytoplankton are less so. So, sea-ice algae may have a crucial impact on grazers that might seek the food source when food is not abundant elsewhere. There also is evidence that phytoplankton that get trapped in sea ice can provide seed populations for more open-water phytoplankton blooms when the spring–summer phytoplankton bloom occurs. Ice melt water produced in spring and summer tends to stabilize the water column seaward of the ice, and primary production is elevated there. Whalers hunted near the ice edge for krill feeders such as blue whales because they were known to congregate there, presumably for the krill. A 25% reduction in ice at this edge occurred in the Antarctic in the 1950s and 1960s, perhaps owing to carbon dioxide–driven climate change.

A key connection in this trophic cascade is the discovery of a strong association between krill and sea ice. Especially in the winter, the evidence suggests that larval krill depend upon sea-ice algae, although adults are more widespread in abundance beyond the border with the ice (See Quetin and others, 1996). The sea ice may also be a refuge for krill against predation. Whatever the specific mechanism, one tends to find more krill where sea ice is more extensive in winter. A striking association between krill and sea ice was discovered by the use of an autonomous underwater vehicle; echolocation surveys consistently showed strong peaks of krill abundance under the ice, up to a distance of 11 km from the edge. Krill abundance was far less offshore (Brierley et al., 2002). Overall, we can conclude that krill are strongly associated with sea ice and ice algae and that the dependence is focused on the larval stages and especially important in parts of the year (e.g., November) when alternative foods are not common. The larvae appear to starve more readily than adults and, therefore, are very tied to the food available from the ice.

Krill recruitment success has fluctuated greatly in recent decades. A recent study demonstrates that krill in the Southern Ocean have declined dramatically in the period 1926–2003 (Atkinson and others, 2004) and it is likely that this is largely due to the decline in sea ice in this area. Krill abundance shows a strong positive correlation with the duration of winter ice, and krill also increase when ice reaches farther from the Antarctic continent (**Box Figure 8.4**).

At last we come to the penguins (**Box Figure 8.5**). Penguins are abundant in the Antarctic Ocean and nearby latitudes and are very dependent on both high-quality breeding areas on land/ice and oceanic feeding areas. Much of what we know about penguin population change comes from studies of the Antarctic Peninsula (the peninsula on a map of Antarctica that seems to point to the tip of South America). In this region, sea ice has fluctuated considerably. Overall, penguins are on the decline, although the details and dependencies are complex. Abundant species such as Adelie and chinstrap penguins depend upon krill for food, and their fate is tied directly to krill abundance and proximity. They have declined about 50% since the 1970s, and recruitment of Adelie juveniles to the parent population has declined by 80% (Lynch et al., 2012). Analysis of satellite images can now be done at the 0.5 m scale, and such analyses show that breeding areas for chinstraps have declined by at least half on Deception Island from 2003 to 2010 (Naveen et al., 2012). Fledging has not changed very much and tends to increase and decrease to the same extent for all species. In the summer breeding colonies, conditions do not seem to differ much for the species as well. This suggests that the problem is at sea and falls mainly on juvenile Adelies and chinstraps foraging in the winter. Adelies and chinstraps depend more on the ice and march more closely to the beat of the krill, which is becoming fainter. Chinstraps are less affected than Adelies by ice decline; they do better in open water and have had short-term intradecadal increases in past decades when sea ice retreated, relative to Adelie penguins.



BOX FIG. 8.4 (a) Change of krill abundance in a sector of the Antarctic Ocean near the Atlantic. Relationship between krill abundance and (b) duration of winter sea ice cover and (c) latitude to which ice extends. Data come from a series of years spanning several decades. (After Atkinson et al., 2004)

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(a)

(b)

BOX FIG. 8.5 (a) The Adelie penguin *Pygoscelis adeliae*; (b) Adelie penguins swimming. (Photographs by Jerónimo Pan)

On the other hand, Gentoo penguins have not declined in the past decades (Hinke et al., 2007). They are larger and have elongated bills and may feed more on fish than the Adelie and chinstraps penguins. Gentoos are also less ice dependent.

Gentoos have actually increased in places such as the South Orkney Islands. This obviously makes for a complex story, since not all penguins are endangered equally (Forcada and others, 2006). Changes in ice cover will fall heaviest on the Adelie penguins, which are the most ice dependent for breeding and molting sites. Chinstraps benefit to some extent from ice reduction because expanses of ice reduce their access to breeding sites. But, in the longer run, the warming effects on krill may be negative, and they too may continue to decline. Gentoo penguins forage more closely to their nesting sites and are more resistant to krill decline and have an alternative food in fish. They seem less vulnerable to reductions in sea ice than the very vulnerable Adelies and chinstraps. ■

from the egg. To keep warm in winter, thousands of adults and chicks huddle together to retain heat.

Petrels and their allies—the albatrosses, petrels, shearwaters, and diving petrels—have large external nostrils, which may be useful to smell prey, and a hooked bill. Gabrielle Nevitt and colleagues discovered that many species of this group can accurately smell krill-related odors in the Antarctic Ocean and therefore will aggregate over patches of krill (Nevitt et al., 1995; Nevitt, 2000). They can also detect dimethylsulfide (DMS), which is a breakdown product of a compound produced by phytoplankton that is transferred into the atmosphere (see Chapter 10). DMS is often associated with upwelling centers, which are often found in the region of seamounts. Seabirds are attracted to phytoplankton blooms in these local upwelling regions, because zooplankton and small fish accumulate around the phytoplankton. Nevitt has argued that these long-distance-flying birds may store a mental map of the distribution of patches of high DMS concentrations over broad areas of the ocean.

The albatrosses (**Figure 8.33**) can have wingspans of over 3 m and are superb gliders, taking advantage of the steady winds in the southern oceans. They are nearly all colonial, and breed on open and windswept ground. They range from the giant petrel, which preys on other birds, to the small-fish-eating puffins to the zooplankton-straining prions, which have comblike plates on each side of the mouth. They may nest in colonies from several thousand to just a few, and some species participate in long-ranging migrations.

Pelicans and their relatives—the boobies, gannets, and cormorants—include many brightly colored and ornamented species. They are mainly tropical, but some species nest in the Arctic and Antarctic. While some, such as frigate birds, fly far out to sea, most species of this group stay closer to land. They are diverse in hunting methods, from the plunging dives of gannets to the underwater pursuit of cormorants. As opposed to the broad gliding habit of albatrosses, frigate birds are capable of tight maneuvering in the air. Feeding in this group is restricted to fishes.

Gulls, **terns**, and **auks** comprise by far the most diverse group of seabirds. They can be found in the millions, although their breeding colonies are in the thousands and not particularly larger than others, such as those of gannets. The herring gull, a complex of closely related species, extends over vast areas of the Northern Hemisphere and can be found breeding in a wide variety of shoreline and island habitats. Terns are smaller and more marine in prey hunting and habitat than gulls. They are most abundant in diversity in the tropics, although the Arctic and Antarctic