Case Study 5: Rapidly Diverging Population Trends of Adélie Penguins Reveal Limits to a Flexible Species' Adaptability to Anthropogenic Climate Change

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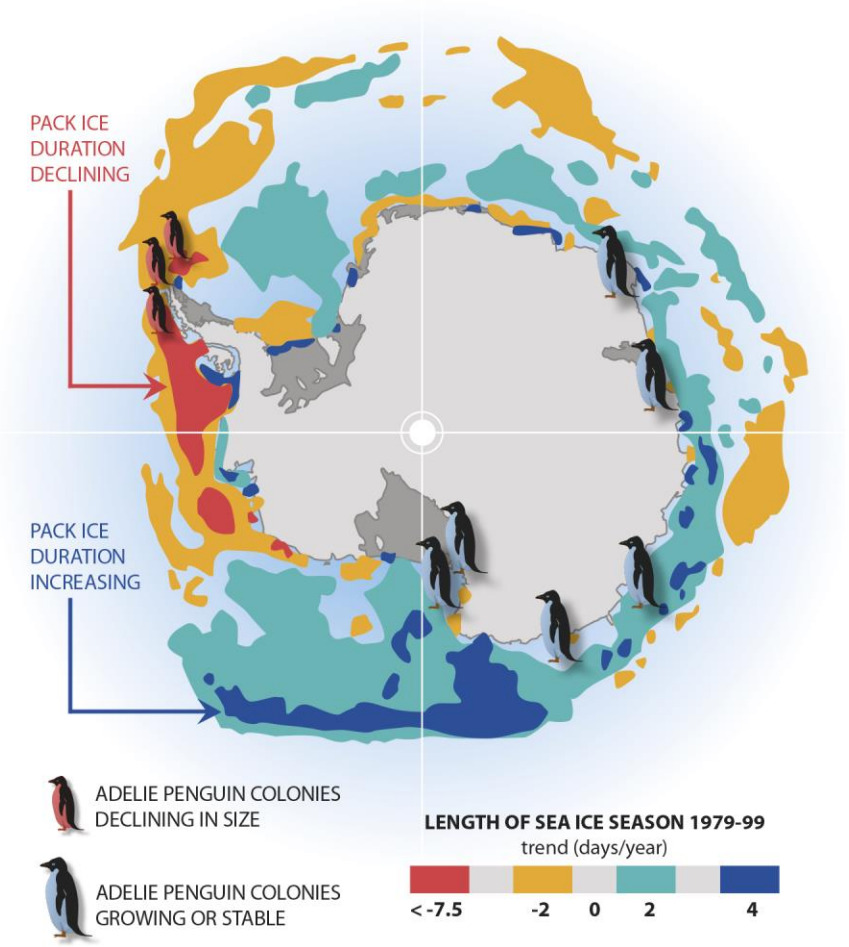
Adélie penguins (*Pygoscelis adeliae*) thrive in some of the most dramatically variable habitats and weather on Earth. They spend much of their life at sea, more than 40m underwater, often under sea ice, where they find their food. They also spend roughly 3-months per year mostly on land, living in dense colonies for breeding. They regularly contend with the transition between open and frozen ocean, and with terrain alternately blanketed in snow and ice then swept clear by high winds. Adélie penguins are one of only a handful of species to be able to survive extended periods in sub-zero air temperatures, out of the relatively warm water that harbors most of the biodiversity to be found at the highest latitudes of the Southern Ocean. They require both ice free terrain to nest and nearby open water to forage. The combination of these two things is rare in Antarctica, but where they are found, so too are Adélies.

Over the past 12-15 million years, Adélie penguins have contended with a wide range of climates and consequent impacts to their habitat. Ice sheets have repeatedly expanded and retreated hundreds of kilometers, destroying or creating nesting habitat, and Adélie populations have grown and shrunk corresponding to interglacial and glacial periods, respectively (Li et al. 2014). The comings and goings of Adélies through geologic time, as determined by dating subfossil bones, have been used to validate the dates of ice sheet advances and retreats. A warm period 2,000 to 4,000 yr BP is even known as the "penguin optimum" due to the widespread extent of ancient penguin colonies found from this time period – including places where they have not yet re-occupied (Baroni and Orombelli 1997).

Due to recent and ongoing changes in climate and sea ice, Adélies are now encountering changes of magnitudes previously inferred from the geologic and genetic record, but at a faster pace. Between 1979 and 2010, the period of time during which the sea ice field in Antarctica expands, or the "sea ice season" (Fig. CS5.1; Stammerjohn et al. 2012), has declined by 3 months in the Arctic and in the Antarctic Peninsula region. This change in persistence coincides with dramatic reductions in the overall extent of sea ice in both those regions. The opposite is true in East Antarctica and in the Ross Sea region, where the sea ice season has extended by two months over the same period. These changes are among the largest phenological shifts so far associated with anthropogenic climate change, and along with warming temperatures and increasing precipitation, have profound implications to sea ice ecosystems (Sailley et al. 2013). In response, Adélie penguin breeding populations are retreating southward from much of the Antarctic Peninsula region – places continuously occupied by Adélies for 500 - 800 years (Emslie 2001) – but are slowly increasing as sea ice loosens farther south in that region (Lynch et al. 2012). Concomitantly, Adélie populations in the southern Ross Sea are expanding rapidly (Lyver et al. 2014; Fig. CS5.1), in some cases exploiting nesting habitat recently exposed by retreating ice sheets (LaRue et al. 2013).



The mechanisms driving these changes also relate to the specific adaptations of Adélie penguins to the sea ice environment. During summer months, the presence of 6-15% sea ice cover is optimal; more or less ice and foraging trips grow longer, with less food delivered to chicks (Ballard et al. 2010a). The sea ice itself is a substrate for diatom growth and subsequent grazing by krill and copepods, which in turn are food for small fish (especially sea ice dwelling silverfish - *Pleuragramma antarcticum*) and penguins. Silverfish are also major prey for Adélie penguins, particularly in the Ross Sea region (Ainley et al. 2003). It is possibly the loss of silverfish that explains the decrease in Adélie penguins in the northern Antarctic Peninsula

region. Without sea ice, the foodweb in the Southern Ocean is far less complex, and less suited to higher trophic level predators like penguins, being dominated by algae (*Phaeocystis antarctica*) with limited grazing by pteropods, which penguins and fish do not appear to consume. Sea ice is also a platform for Adélies to rest upon, molt, and seek shelter from predators, and can provide a source of fresh water when snow accumulates on its surface.

Sea ice variability has also substantially impacted Adélie penguin migratory patterns through time, with today's populations ranging from essentially non-migratory at the more northerly parts of their range, to long-distance migratory at the southern-most portions – with annual journeys of up to ~18,000 km (round trip) – an astounding feat for a flightless animal (Ballard et al. 2010b). Their apparent need for some amount of daylight during all phases of their annual cycle appears to limit the potential range of wintering and migration to north of 72.7°S – the latitude of zero mid-winter twilight. It is likely that, due to climate change, more suitable breeding habitat will become available further south than it currently exists (as glaciers retreat and free up more coastline for nesting), but it may not be possible for Adélies to migrate much further than they already do and still have sufficient time to raise young, given the short breeding season of high latitude ecosystems. In this way, Adélies are caught between astronomically imposed limits and anthropogenic climate change.

The diverging Adélie penguin population trends described above are projected to continue during the next few decades, after which sea ice, as warming reaches 2^{o}C above pre-industrial levels, is predicted to decrease everywhere in the Southern Ocean (Ainley et al. 2010). With the retreat of sea ice, Adélie penguins and the other 3 truly ice-obligate seabird species (Antarctic petrel – *Thalassoica antarctica*, Snow petrel – *Pagodrama nivea*, and Emperor

penguin - *Aptenodytes forsteri*) will eventually disappear (Ainley et al. 2010, Jenouvrier et al. 2014), to be replaced by ice-tolerant and ice-avoiding species.

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