growth are based on these assumptions. Similarly, relatively high NSC pools in trees have been interpreted as an overabundance of carbon. This has generated a heated debate about the extent to which mature trees are carbon-limited, with important implications for modelling[8].

Transplanted seedlings with more NSC perform better[9]. The study by O'Brien *et al.*[4] is consistent with this, and supports a change in the way we think about NSC storage[10]. NSC storage may not be a passive 'overflow', but a requirement to protect plants from dehydration. If so, carbon assimilation and demand for growth and storage should be tightly coordinated, and slow growth could be, in part, an evolutionary selected strategy to allow storage. Because trees are large and long-lived, those that 'play it safe' and allow greater storage have a greater chance to cope with future stress and survive. In the long term, surviving trees may accumulate NSC, but this may reflect, in part, a consequence of the safest evolutionary strategy.

The osmotic role of NSC storage in seedlings[4] highlights the need for a better understanding of the role and regulation of NSC storage in mature trees, and suggests that current attempts to incorporate NSC storage in ecosystem models[11] are certainly worthwhile. ❐

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BIODIVERSITY

Penguins in peril

Climate-driven demographic changes could cause drastic decline in the global emperor penguin population, driving some colonies to extinction.

Madan K. Oli

Few species depend on sea ice to the extent that emperor penguins do. Recent climate change, especially warming in the Antarctic, has substantially reduced seasonal sea ice concentration and duration, and these patterns are predicted to continue[1,2]. What might this mean for emperor penguins? In a study published in *Nature Climate Change*, Stéphanie Jenouvrier and colleagues[3] show that the global emperor penguin population will decline drastically, and many colonies will face substantial risk of extinction by 2100.

Standing over 1.2 m tall and weighing up to 45 kg, emperor penguins are the largest of all extant penguin species. The stars of film and documentary alike, they are visually appealing and biologically fascinating; they are adapted to the extreme Antarctic environment and are the only species of penguin with the habit of breeding in the middle of winter. Many important aspects of their life cycle depend on sea ice[1,2,4]. Penguins depend on fixed sea ice (fast ice) for successful reproduction and gather at traditional breeding sites (colonies) during March–April when sea ice is thickening. They need just the right amount of sea ice at just the right time. Too little sea ice will constrain the availability of breeding sites, reduce prey availability and can also make penguins vulnerable to predation. Too much sea ice means longer foraging trips for parents, lower feeding rates for chicks, and consequently, lower adult survival and reproductive success. Higher air or sea surface temperatures and early breakup of sea ice will reduce survival, and multiple years of poor sea ice will cause population declines and eventually local extinction[2,5].

Using long-term demographic information from the Terre Adélie penguin population, sea ice concentration data, and sophisticated, multi-pronged modelling techniques, Jenouvrier *et al.*[3] investigate what the future might hold for these obligate sea ice breeders. First, they linked seasonal sea ice concentration anomalies (SICa; deviations from long-term seasonal averages) to survival and reproduction of penguins by modelling these parameters as functions of SICa for four biologically relevant seasons in the penguin life cycle. Based on these estimates, they developed a two-sex, seasonal, climate-driven population model. Next they employed an ensemble of ten IPCC climate models to forecast sea ice concentration, which allowed the determination of SICa. Finally, they fed the projected SICa data to the demographic model, which was subsequently used for population projections and viability analyses. Their results indicate that the Terre Adélie population of emperor penguins will decline from around 6,000 to only 400 breeding pairs by 2100, and that the population will face a high risk of quasi-extinction (a reduction to less than 10% of its current size). These conclusions are not new[4,7]. But the present study is innovative and exciting because of the steps Jenouvrier *et al.*[3] took to expand the Terre Adélie population study to make a species-level threat assessment.

There are 45 currently known colonies of emperor penguins. The authors argue that most of these colonies have never been visited by humans, and it is highly improbable that they will ever be the focus of long-term demographic studies. How does one go about making species-level inferences when detailed data are only available for one out of 45 colonies? Emperor penguins depend on sea ice for breeding, brood rearing and feeding. We also know that climate change will undoubtedly affect the sea ice environment in and around all emperor penguin colonies. If one can determine current sea ice concentration, quantify how climate change will influence the sea ice environment and determine how the altered sea ice environment will influence penguin demography at each colony, it should be possible to make species-level inferences regarding the dynamics and persistence of emperor penguin populations under climate change. Using these precise steps, Jenouvrier *et al.*[3] show that the global population of emperor penguins will probably decline substantially and that 20% of the penguin colonies could go functionally extinct by 2100. The colonies located at northerly latitudes face a greater risk of drastic population declines or demise compared with colonies located poleward.

These projections are alarming but are they alarmist? The evidence suggests not. All available data show evidence for substantial warming in Antarctica[1,2,9], and general circulation models (GCMs) under most scenarios predict further decline and greater variability in sea ice concentration[1,4]. In fact, the recent extinction of an Emperor Island colony of emperor penguins has been directly linked to decline in seasonal sea ice concentration and duration attributable to warming temperatures[2].

Anthropogenic climate change has been shown to have caused local extinction or severe population declines in several species of plants and animals[10]; many more species are predicted to face substantial extinction risk[11]. However, we still know very little about the mechanisms underlying climate change-induced extinctions or population declines[10]. This is, in part, because most studies reporting species-level assessment

Emperor penguins raising their offspring on sea ice.

of threats due to climate change do not explicitly consider demographic processes, despite the fact that population-level effects of environmental change are mediated through climatic influences on demographic parameters. A full understanding of the effects of climate change on biological populations requires an understanding of the causal links: how climate change influences key environmental drivers, how those drivers affect various components of the life cycles of species, and finally, how those climate-driven demographic changes affect population dynamics and persistence. The study by Jenouvrier *et al.*[3] makes these links explicit by showing how climate change affects the key environmental driver (sea ice environment) and how reductions in sea ice concentration and duration driven by climate change adversely affect penguin survival and reproductive success. Finally, they combine detailed knowledge of demography and population dynamics at Terre Adélie with GCM-predicted changes in the sea ice environment to assess the threat faced by the global population of emperor penguins. Despite grim and somewhat depressing results, this study serves as an excellent example of a scientifically rigorous and demographically-based approach to the assessment of climate change risks faced by biological populations. ❒

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CLIMATE CHANGE ECOLOGY

Older and wiser

Historical records of long-lived marine organisms may provide the key to understanding how marine ecosystems will respond to projected climate change.

Heidi Burdett

Over the next century, the oceans are expected to become more acidic than has been experienced for the past 800,000 years as a consequence of the continued rise in atmospheric carbon dioxide (CO_2) levels. Understanding and projecting the effect that this may have on marine ecosystems has become a global concern in marine science. Writing in *Nature Climate Change*, Sophie McCoy and Federica Ragazzola[1] advance our understanding of the effects of long-term climate change on marine ecosystems. Using museum specimens, they effectively conduct a 30-year long 'experiment' in the natural environment, showing that long-term declines in oceanic pH differentially affect red coralline algae — a type of heavily calcified red seaweed — depending on their growth morphology.

The oceans have absorbed around a third of the CO_2 produced by human activity, helping to partially mitigate rising atmospheric CO_2 levels. However, once in the oceans, CO_2 causes seawater pH to reduce; since the Industrial Revolution, oceanic pH has decreased by ~0.1 units,