

OUTSIDE JEB

The little feathered ecosystem engineer



All animals have an effect on the environment, but some key species – called ecosystem engineers – can have a particularly large influence. Their impact can be positive, by creating and maintaining habitats and increasing biodiversity, but they can also be negative, by destroying habitats and reducing biodiversity. Interestingly, the magnitude of the effect that an ecosystem engineer has on the environment is often not a reflection of their size. Some are huge, such as elephants, which provide water for other animals during the dry season by digging up desiccated water holes until water flows. But others are tiny, such as plankton in the oceans, which influence the amount of light reaching the plants down below. In particular, the transportation of marine-derived nutrients by animals is vital in shaping not only oceans but also freshwater and terrestrial ecosystems. Ivan González-Bergonzoni from the Universidad de la República, Uruguay, and his international team of researchers decided to observe this phenomenon from a seabird's perspective.

The seabird in question is the little auk (*Alle alle*), which constitutes the largest population of seabirds in the North Atlantic region, where they consume enormous amounts of zooplankton on a daily basis. The team travelled to the North Water Polynya between Northwest Greenland and Canada, which is home to 60–70 million breeding pairs, to collect samples from terrestrial and freshwater habitats at sites with and without colonies in order to measure the content of

marine-derived nutrients in the form of nitrogen and carbon stable isotopes. These samples came from a wide range of sources, including soil, algae, scats and fur. In addition, the researchers also tracked the flight paths of a number of little auks, as the birds also distribute nutrients via their droppings during their foraging trips. The team found a huge increase in marine-derived nitrogen levels, almost 10-fold, in the terrestrial and freshwater samples from colony sites as well as the associated flight paths; this is greater than the nitrogen transfer provided by fish. However, the levels of marine-derived carbon only increased in the freshwater ecosystems and not in terrestrial areas.

Next, to determine the effect of the additional nutrient load, the team measured the species richness and physical–chemical characteristics of freshwater communities while also measuring the species richness and the productivity of the vegetation in the terrestrial habitats, which allowed them to quantify what the increase in nitrogen levels actually means for the ecosystems. The higher nutrient levels at little auk sites and flight paths contributed to an increased algal biomass in the freshwater ecosystems and increased vegetation in the terrestrial areas, suggesting much better primary productivity as a result of these small birds. In addition, many more animals, such as hares and muskoxen, were seen at terrestrial sites near the colonies, in contrast to the more barren areas that were not colonised by the little auks. Conversely, the team found that the species richness in the freshwater ecosystems near little auk colonies was reduced, probably because of the increase in water acidity and the algae that flourished as a result of nutrient enrichment.

González-Bergonzoni and his group have unequivocally shown that a single tiny bird species, the little auk, has a massive impact on the habitats of the North Water Polynya. By shaping these environments, the little auk is truly an ecosystem engineer and its loss would probably result in a very different landscape. It is

vital that we understand which animals are significant ecosystem engineers in order to conserve habitats and protect biodiversity.

10.1242/jeb.147397

González-Bergonzoni, I., Johansen, K. L., Mosbech, A., Landkildehus, F., Jeppesen, E. and Davidson, T. A. (2017). Small birds, big effects: the little auk (*Alle alle*) transforms high arctic ecosystems. *Proc. R. Soc. B* **284**, 20162572.

Clare Stawski
University of New England
cstawsk2@une.edu.au

Lateralisation helps sailfish snatch sardines



When we pick up a pen to write, we tend to use either our right or our left hand. This lateralisation helps us react rapidly and cuts down on how much nerve tissue we need. But if you are a predator, lateralisation may be costly: if prey can anticipate your angle of attack, it may help them escape. This predictability might select against lateralisation in predatory species. However, Ralf Kurvers from the Center for Adaptive Rationality in Berlin, and an international team of collaborators suspected that group-hunting sailfish, *Istiophorus platypterus*, might have the best of both worlds. As sailfish attack schools of sardines by slashing and tapping their prey with elongated bills, the team wondered whether the communal fish might dodge the costs of lateralisation while exploiting its benefits by hunting in a pack, where, despite individual-level lateralisation, attacks still come from all angles.

Snorkelling off the coast of Cancun in Mexico, the researchers filmed wild sailfish

hunting and analysed the movies back in the lab. The team then identified individual sailfish using each fish's unique dorsal fin morphology and found that sailfish consistently attack from either the right or the left, suggesting that the fish demonstrate lateralisation. Knowing that the fish appear to favour one side over the other, the team suspected that the teeth lining the dominant side of the fish's bills would be more abraded, in much the same way that humans are more likely to injure their dominant hand. To test this idea, they compared the condition of micro-teeth in sailfish bills and found that tooth abrasion was always more pronounced on one side or the other. Together, this behavioural and morphological evidence points to lateralisation in individual sailfish.

So, if sailfish are lateralised, does this reduce their hunting success by helping sardines to pre-empt their angle of attack? The team answered this question by seeing how the strength of lateralisation in each sailfish correlated with its sardine capture success. The result was clear: increased lateralisation promotes hunting success and sailfish are more likely to successfully snatch a sardine if attacking from their preferred side.

Given that lateralisation often incurs costs for predators, how does this trait help sailfish on the hunt? The team suspected that group hunting could reduce the costs of lateralisation if hunting groups contain a mix of right- and left-billed sailfish. To test this idea, the team randomly selected individuals that they observed hunting at least three times, and put them together into random groups that varied in size from 1 to 15 fish. They calculated how lateralised these groups were by averaging the mean laterality of each of the group members. As the hunting groups increased in size, the overall degree of lateralisation across the entire group declined. That is, although individuals may be lateralised, the net lateralisation of the group is reduced as the number of left-lateralised fish cancels out the number of right-lateralised animals. So, hunting in a group provides the unexpected benefit of allowing individual predators to exploit the benefits of lateralisation, while their prey still have no idea which direction the next attack is coming from.

10.1242/jeb.147389

Kurvers, R. H., Krause, S., Viblanc, P. E., Herbert-Read, J. E., Zaslansky, P., Domenici, P., Marras, S., Steffensen, J. F., Svendsen, M. B. S., Wilson, A. D. M. et al. (2017). The

evolution of lateralization in group hunting sailfish. *Curr. Biol.* **27**, 521–526.

C. Ruth Archer
University of Exeter
c.archer@exeter.ac.uk

Oceans of oxygen, gone



'Hypoxia' is a well-used word among JEB authors. These past 10 years have seen it used in over 80 titles, 200 abstracts and 800 articles, which means great effort is being put towards understanding the physiological responses of animals to low oxygen. Good thing, because rising atmospheric temperatures are making the Earth's aquatic habitats more hypoxic. Sunke Schmidtke and his team at GEOMAR's Helmholtz Centre for Ocean Research in Kiel, Germany, were familiar with the biotic and abiotic theories underlying this trend, but decided to quantify just how much oxygen the World Ocean has lost in recent years.

The Kiel team isn't the first to inventory the World Ocean for oxygen, but they certainly went farther and deeper than anyone before. They started by locating five publicly accessible databases from the likes of NOAA and Pangaea and then used these to piece together an elaborate profile of oceanic oxygen at 78 depth levels over the past 50 years. This more than quadrupled the volume of water previously analysed for oxygen and allowed them to paint a detailed picture of how the past 50 years has affected the World Ocean's oxygen content. Perhaps unsurprisingly, they have not been kind.

From the broadest perspective, Schmidtke and his colleagues found that the World Ocean currently contains around 227 petamol (10^{15} mol) of oxygen. That's a lot of oxygen – over seven quadrillion kilograms of the stuff – but it's about 4.8 petamol less than it was in 1960,

meaning 150 trillion kilograms of oxygen have disappeared from the World Ocean over the past 50 years. This begged two questions: how were these changes distributed throughout the ocean?; and where did all the oxygen go?

The team set about answering the first question by directing their analyses towards particular ocean basins. All 10 basins they examined lost oxygen, but some lost more than others. The largest fraction of oxygen (~40%) was lost in the North and Equatorial Pacific, while the smallest fraction (~1%) was lost in the North Atlantic. Interestingly, the team found that the rapidly changing Arctic Ocean swung well above its weight class in terms of its contribution to oxygen depletion: 7.6% of the total lost oxygen despite containing a meagre 1.2% of the world's seawater. Perhaps most unsettling, the World Ocean's anoxic regions have quadrupled in size since 1960.

As for where all the oxygen went, the team's prime suspect was reduced oxygen solubility; as rising atmospheric temperatures drag world oceanic temperatures up with them, less oxygen is able to dissolve into the seawater, owing to water's physicochemical properties. The team combed through their temperature data and found that reduced oxygen solubility did indeed play a role – particularly in the ocean's uppermost 1000 m – but only accounted for 15% of all oxygen lost. To account for the other 85%, the team suspected biological and chemical patterns of oxygen consumption in combination with complex ocean ventilation dynamics. These processes are each influenced by climate variability in ways that could theoretically explain the Kiel team's results, but future studies will be needed to address these hypotheses directly.

So, the world ocean is definitely becoming more hypoxic, impacting the marine ecosystem as a whole in ways that are complex and, in many cases, not good. It also means that there will be plenty of work for those researchers publishing on the hypoxic adaptations of animals, keeping them busy for years to come as we attempt to get to grips with this complex ecological calamity.

10.1242/jeb.147405

Schmidtko, S., Stramma, L. and Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature* **542**, 335–339.

Matthew D. Regan
University of British Columbia
regan@zoology.ubc.ca

Fidgety embryos grow longer limbs



The great evolutionary biologist Leigh van Valen famously quipped: ‘Evolution is the control of development by ecology’. This aphorism neatly portrays how natural selection, over generations, sculpts organism development and results in the wonderful diversity of form exhibited in the animal kingdom. Nowhere is this more obvious than limb morphology – from wings to fins – in vertebrates. But van Valen never imagined the process of development being directly manipulated by an organism’s environment. By and large, development is controlled by genetics, so the most obvious variations in limb anatomy between different species are encoded in the genome. However, limb morphology also exhibits substantial variation within individuals of the same species, especially when development takes place in different conditions. This suggests that, beyond the genome, an

animal’s environment may more directly control development.

To investigate the immediate impact that environment, particularly temperature, has on limb morphology, Andrea Pollard from the Royal Veterinary College, UK, and her colleagues studied the development of dwarf crocodiles. They observed that crocodiles incubated at 32°C had longer limbs than their siblings developing at 28°C (even relative to their larger total body size). More interesting still, the two groups had differently proportioned limbs: the warmer animals had longer tibiae (corresponding to the human shinbone) but short toes, whilst the cooler animals possessed ‘paddle-like’ limbs with elongated toes. The authors hypothesise that the differences may equip animals for better locomotor performance in their respective environments after hatching, as the fossil record intriguingly suggests that highly aquatic crocodylian ancestors – with more paddle-like limbs – inhabited cool temperate climates whereas extinct equatorial species – with longer legs but shorter toes – were terrestrial. But how could temperature have such a specific effect on limb development? The clue came from observing embryo activity; those incubated at higher temperature made more frequent spontaneous movements within the egg.

Pollard and her colleagues had identified a tantalising correlation between embryonic movement and limb development, but to provide an unequivocal link between the two they had to move to a more convenient organism to investigate: developing chicken embryos in eggs. The team was able to suppress the chick’s limb movement with a drug that paralyses muscle contraction. Just like the less active crocodiles at low temperature, the

immobilised chicks grew shorter and disproportioned limbs. The researchers also took snapshots of the birds’ development over time and they saw that different parts of the limb were more sensitive to muscle paralysis at different times.

In the final leg of their experiments, the team used molecular techniques to understand how movement is conveyed to the developing bones. They saw that cell division in specific growth zones – ‘growth plates’ – was slowed in the immobilised chicks. They also looked at gene expression in the nascent limbs, which was particularly rewarding during the critical periods when immobilisation had differing effects on growth in different parts of the limb. During one period, 58 genes were differentially expressed in the femur, in which immobilisation affected development, compared with the tibiotarsus (the avian equivalent of the tibia), which was not affected by muscle inhibition. They additionally saw that several genes associated with cell contraction were downregulated in the chicks that had been immobilised.

This intriguing new study demonstrates that embryonic development is not just a passive result of historical natural selection; development can be directly influenced by environment, and animals may be active architects of their own anatomy.

10.1242/jeb.147413

Pollard, A. S., Charlton, B. G., Hutchinson, J. R., Gustafsson, T., McGonnell, I. M., Timmons, J. A. and Pitsillides, A. A. (2017). Limb proportions show developmental plasticity in response to embryo movement. *Sci. Rep.* **7**, 41926.

William Joyce
Aarhus University
william.joyce@bios.au.dk