

remembering the output from the previous processing step and using it as input for the next, the authors used a network involving feedback loops. They trained the network using simulations of pathways taken by foraging rodents. The system received information about the simulated rodent's linear and angular velocity, and about the simulated activity of place and head-direction cells — the latter two acting as an 'oracle' for the current location and head direction of the rodent.

The authors found that patterns of activity resembling grid cells spontaneously emerged in computational units in an intermediate layer of the network during training, even though nothing in the network or the training protocol explicitly imposed this type of pattern. The emergence of grid-like units is an impressive example of deep learning doing what it does best: inventing an original, often unpredicted internal representation to help solve a task.

Grid-like units allow the network to keep track of position on the basis of path integration. Can they also help the system to learn to navigate efficiently from its current position to a goal location? To address this question, Banino *et al.* added a reinforcement-learning component, in which the network learned to assign values to specific actions taken at specific locations. Higher values were assigned to actions that brought the simulated rodent closer to the goal, acting as a reward. The grid-like representation markedly improved the ability of the network to solve goal-directed tasks, compared to control simulations in which the start and goal locations were encoded instead by place and head-direction cells. The trained network found smarter shortcuts when obstacles such as closed doors were removed (Fig. 1), and even extrapolated paths towards goals in a previously unexplored annex of a familiar environment. These results support the idea that grid cells enable the brain to perform vector calculations (calculations about the length and direction of a path) to assist path planning through compartmentalized⁶ or previously unexplored⁷ environments.

In the future, the authors' network could be used to explore the consequences of interactions between grid and place cells. In the current network, the simulated place layer does not change during training. However, in the brain, grid and place cells influence each other in ways that are not well understood. Although real-life place cells can remain spatially selective in the absence of grid-cell inputs⁸, these inputs seem important when an animal is far from external landmarks that can be used to define locations^{9–11}. Under these conditions, place cells presumably rely on path integration and grid cells to maintain an accurate estimate of position. By developing the network such that the place-cell layer can be modulated by grid-like inputs, we could begin to unpack this relationship.

From a broader perspective, it is interesting that the network, starting from very general

computational assumptions that do not take into account specific biological mechanisms, found a solution to path integration that seems similar to the brain's. That the network converged on such a solution is compelling evidence that there is something special about grid cells' activity patterns that supports path integration. The black-box character of deep-learning systems, however, means that it might be hard to determine what that something is.

Likewise, the fact that the grid representation enhanced goal-directed performance is a compelling proof-of-concept of the role of grid cells in the brain. But the authors had to use correlational analyses, guided by qualitative intuitions, to indirectly infer that the network was making vector calculations. The inability to directly manipulate these calculations in the model makes it difficult to examine the computational principles, algorithms and encoding strategies that make grid-cell representations of space such an efficient solution for navigation. As such, the theoretician ends up in the same quandary as the experimentalist: trying to tease apart a poorly understood complex system to understand it. Making deep-learning systems more intelligible to human reasoning is an exciting challenge for the future. ■

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OCEANOGRAPHY

Climate change and oxygen in the ocean

Computer simulations show that areas of the ocean that have low levels of dissolved oxygen will expand, but then shrink, in response to global warming — adding to an emerging picture of the finely balanced processes involved.

LAURE RESPLANDY

Global warming has reduced the amount of dissolved oxygen in the ocean by 2% since 1960 (ref. 1). A major concern is that the rate of loss of dissolved oxygen has already increased by up to 20% in tropical waters, expanding the volume of regions called oxygen minimum zones (OMZs), where levels of dissolved oxygen are already very low^{2,3}. The expansion of tropical OMZs threatens the survival of marine organisms that rely on dissolved oxygen for respiration, and affects the biogeochemical cycling of carbon and nitrogen, potentially amplifying global warming⁴. Writing in *Global Biogeochemical Cycles*, Fu *et al.*⁵ suggest that, in the long term, tropical OMZs might shrink after their initial expansion, reversing their impact on warming.

Although, overall, tropical oceans have lost dissolved oxygen in the past 50 years, observations indicate strong regional and temporal variations. For example, OMZs have clearly

expanded since the 1970s in the equatorial Pacific and Atlantic oceans^{3,6}, but a long-term reconstruction⁷ of the OMZ close to the Californian and Mexican coasts suggests that it had been shrinking for a century before it started to expand in the 1990s. In the Indian Ocean, the northern part of the OMZ is shrinking, whereas the southern part is expanding⁸.

Three competing processes control the levels of dissolved oxygen in the ocean. The first is the transfer of atmospheric oxygen to the surface ocean (which, in turn, is tied to oxygen solubility, the capacity of the water to hold on to dissolved oxygen). The second is ocean circulation (ventilation), which carries the oxygen-rich surface waters to the ocean interior. And, finally, there is the biological respiration of dissolved oxygen, the process by which microorganisms consume organic matter produced at the surface as it sinks to the deep ocean. OMZs develop in tropical intermediate waters (those at depths of 200–1,000 metres) because the physical supply

of oxygen is low, but the biological demand for it is high.

As the ocean warms, the solubility of oxygen within it declines, and vertical stratification — the formation of distinct layers of water — increases, limiting the exchange of oxygen between surface and intermediate waters. Together, these changes reduce the supply of oxygen to the ocean interior and expand OMZs. Increased stratification also reduces the supply of nutrients to surface waters, limits biomass production⁹ and reduces the export of organic matter to the deep ocean. This biological effect lowers the demand for oxygen in underlying waters and reduces the volume of OMZs. In addition, local changes in ventilation in OMZs can act to shrink these zones^{5,10}.

Globally, the direct effect of declining solubility explains half of the observed loss of oxygen in the upper 1,000 m of the ocean, and a combination of biological and ventilation effects accounts for the other half¹. In tropical OMZs, however, the balance between these processes is more subtle and the relative contributions harder to tease out¹¹. Numerical models of Earth systems can provide a mechanistic understanding of these past changes in oxygen and why they vary in space, and can inform us about changes to expect in the future.

Fu and colleagues used long-term simulations of the Earth system to reproduce the observed historical decline in dissolved-oxygen levels in the tropical ocean, and to project the evolution of OMZs between the twenty-first and twenty-third centuries (Fig. 1). In their model, the volume of OMZs initially expands, then levels off around the year 2150, and finally shrinks until 2300. The authors also introduce a modelling framework that can disentangle the contributions to this pattern that are made by solubility, ventilation and the reduction in biological export and respiration. In their model, the shift from OMZ expansion to contraction occurs when the biological effects become more prominent than the solubility effect, in 2150. Ventilation further tips this balance, as it switches from an initial slowdown that reinforces the expansion effect of solubility before 2150, to a reinvigoration that reinforces the OMZ contraction controlled by biological effects after 2150.

The findings suggest that about half of the OMZ expansion that occurred between 1900 and 2150 could be reversed by the year 2300. Moreover, the core of the OMZ (the region that has the lowest levels of dissolved oxygen) might contract to become smaller than it was in pre-industrial times, and could possibly act as a negative climate feedback that dampens

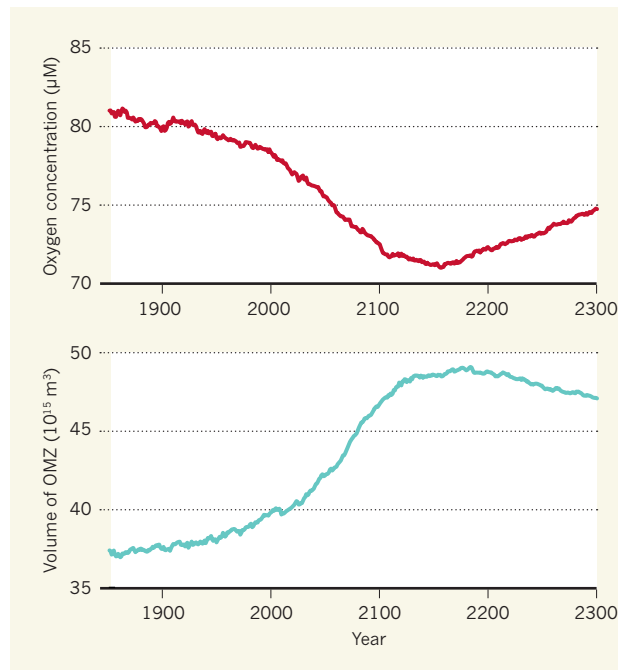


Figure 1 | Projections of oxygen concentrations and volumes of oxygen minimum zones (OMZs) in tropical seas. a, Fu *et al.*⁵ have used computer simulations of the Earth system to reproduce the observed historical decline in dissolved-oxygen concentrations (measured in micromoles per litre) in tropical-ocean intermediate waters (which occur at latitudes between 30°N and 30°S at depths of 200–1,000 metres), and to project how such oxygen levels might vary between the twenty-first and twenty-third centuries. The simulations suggest that oxygen levels will decline until about 2150, level off and then increase until 2300. b, The authors also simulate changes in the volume of oxygen minimum zones — ocean regions where dissolved-oxygen levels are less than 20 µM. The volume mirrors the pattern shown in a. However, the factors that contribute to the simulated changes are finely balanced.

global warming. The formation of a smaller OMZ core would certainly limit the production of nitrous oxide¹², a powerful greenhouse gas, and limit the consumption of nitrate nutrients for respiration, which in turn could boost the efficiency of the ocean's biological carbon sink¹³.

Fu and co-workers' study highlights the extreme sensitivity of OMZs to biological and physical changes, and the difficulty of quantifying and anticipating these changes. Different Earth-system models currently project dramatically different changes in OMZ volume (ranging from –2% to +16% by 2100)¹⁴. So how much confidence can we have in OMZ projections?

In fact, Earth-system models agree on many aspects of future OMZs. Modelled changes in oxygen solubility are relatively well constrained and are tied to surface warming^{14,15}. The reduction in biological export identified by Fu *et al.* is robustly produced by other models^{11,14}, and most models also project a strengthening of the ventilation in tropical OMZs¹⁶. Uncertainties arise from the differences in the magnitude and timing of these changes. Simulated reductions in biological export by 2100 vary between 1% and 40%¹⁵, and changes in ventilation can

vary by a factor of two between models¹⁶. These differences, even when small, can tip the balance of oxygen levels in OMZs, shifting them from expansion to contraction.

The challenge now is to constrain this subtle balance and the possible shifts in OMZ volume not only in time, as Fu *et al.* have done, but also between regions. For example, reduced biological export and consumption of oxygen is likely to have driven the OMZ contraction reported along the Californian and Mexican coasts⁷, whereas weakening ventilation probably underlies the OMZ expansion in the equatorial Pacific. Other factors, such as the supply of nutrients from anthropogenic aerosols, winds or ocean acidification, could also locally offset the effects of changes in solubility and stratification¹⁷. OMZ climate feedbacks — the reinforcing or dampening of climate change by OMZs — are tied to global OMZ volume, but establishing local OMZ responses will be crucial if we are to assess the impacts on ecosystems and ecosystem services, such as fisheries. ■

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