on roads, like the networks that already exist for land and climate science. If you think you can produce better maps of road impacts, step forward: Laurance *et al.* have placed their data products online (www.global-roadmap.org).

The second issue concerns policy initiatives to improve global road planning. Multilateral development banks fund roads to promote economic growth; in the same vein, governments build roads to support economic goals, although they also use roads for geopolitical purposes, such as securing national borders. Whether roads are built to expand commerce or improve security, a global plan for road building might be interpreted as an imposition on the priorities of sovereign countries. In particular, the conflict zones identified by Laurance *et al.* are mostly in poor countries — citing the road-planning map and telling those countries not to build roads is hardly going to be popular.

Thus, there is a need for clarity about the purpose of such maps. A global road plan is not intended to 'keep developing countries poor', but rather to highlight the costs as well as the benefits of building roads, in order to motivate a discussion of policy alternatives for sustainable development. This carries implications for the funding priorities underlying bank loans and development assistance. In cases where roads will probably cause ecological damage, governments can cite global road-planning maps to argue for policies that invest in alternative strategies for development. ■

Stephen G. Perz *is in the Department of Sociology and Criminology & Law, University of Florida, Gainesville, Florida 32611, USA.*
e-mail: sperz@ufl.edu

1. Laurance, W. F. *et al. Nature* **513,** 229–232 (2014).
2. Straub, S. Policy Research Working Paper No. 4460 (World Bank, 2008).
3. Forman, R. T. T. *et al. Road Ecology: Science and Solutions* (Island, 2002).
4. Perz, S. G. *et al. Reg. Environ. Change* **12,** 35–53 (2012).

This article was published online on 27 August 2014.

OCEANOGRAPHY

What goes down must come up

A compilation of high-resolution measurements of ocean mixing collected over the past three decades reveals how deep ocean waters return to the surface — a process that helps to regulate Earth's climate.

RAFFAELE FERRARI

Deep ocean circulation is fed by waters that become dense enough to sink into the ocean abyss in the North Atlantic Ocean and the Southern Ocean around Antarctica. These waters carry dissolved carbon away from the atmosphere and into the deep ocean, thereby playing a crucial part in modulating Earth's carbon budget and climate. Despite theoretical and observational efforts dating back to the beginning of the twentieth century, we are still struggling to understand how and where these waters return to the ocean surface — in other words, we know how ocean carbon is 'breathed in', but are still trying to figure out how it is 'exhaled'. Writing in the *Journal of Physical Oceanography*, Waterhouse *et al.*[1] report remarkable progress in resolving this long-running detective story.

The first quantitative hypothesis for the return pathway of high-latitude waters was proposed in a seminal paper[2] by the oceanographer Walter Munk in 1966. He speculated that dense bottom waters are mixed back up to the surface by breaking internal waves. To explain what this means, picture the ocean as a layer cake with colder — and therefore denser — layers at the bottom, and progressively warmer and lighter layers stacked on top. Internal waves are oscillations of these layers, analogous to the more familiar ocean waves that we see at the surface. Occasionally, internal waves overturn and break, much like surface waves on a beach, thereby mixing water from a denser layer into a lighter one and raising the potential energy of the ocean.

Direct *in situ* measurements in the years following Munk's paper, however, failed to detect enough mixing to bring back to the surface all of the high-latitude waters that sink into the abyss (calculated to require rates of approximately 30×10^6 cubic metres per second)[3].

Lacking alternative theories for the return pathway of bottom waters, oceanographers speculated that their measurements sampled areas of weak mixing and missed hotspots of intense mixing. An oceanographic gold rush to find the 'missing mixing' ensued.

Munk and fellow oceanographer Carl Wunsch quantified the amount of missing mixing on a global scale[4] in 1998. They estimated that potential energy had to be supplied at a rate of approximately 0.4 terawatts (1 terawatt is 10^{12} watts) to continuously lift dense bottom waters to the ocean surface. During an internal-wave-breaking event, about 20% of the wave energy is converted into potential energy and lifts fluid, with the rest being dissipated by inconsequential small-scale motions. Internal waves would thus have to be generated at a rate of approximately 2 TW to mix bottom waters back to the surface.

At that time, it was thought that internal waves were mainly generated by variable surface wind at a rate of less than 1 TW. Munk

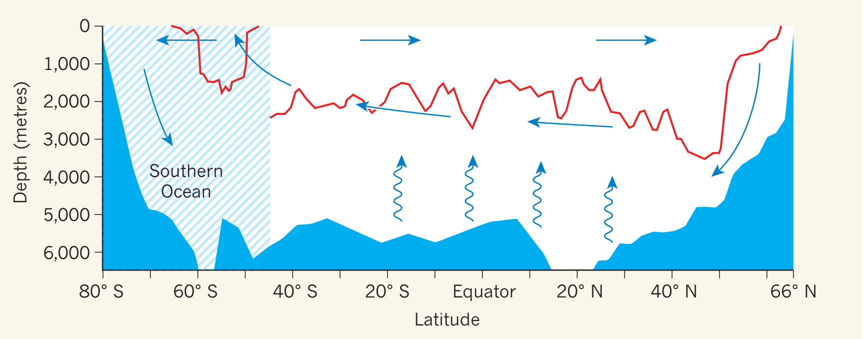

Figure 1 | An emerging model of deep-ocean circulation. Dense waters sink into the abyss at high latitudes north and south (downward arrows). The bottom waters are lifted up to depths of about 2,000 metres by mixing processes (wiggly arrows), and return to high latitudes at these intermediate depths, eventually rising to the surface via the Southern Ocean (southward and upward pointing arrows), closing the circulation loop; shading indicates the extent of the Southern Ocean. Horizontal arrows at the surface indicate the path of waters back to high latitudes. North of the Southern Ocean, the red line indicates the heights of the tallest topographic features below which mixing is strong. In the Southern Ocean, the red line indicates the topography of the Drake Passage, to illustrate topography at latitudes at which deep water is pulled to the surface by winds (the Roaring Forties). Solid blue regions indicate the deepest points at each latitude, based on a 0.25°-resolution bathymetry data set. Waterhouse *et al.*[1] confirm that this scenario is consistent with available observations of ocean mixing. (Adapted from ref. 9.)

and Wunsch[4] suggested, and later work confirmed[5], that internal waves are also generated by tidal forcing at a rate greater than 1 TW. More recently, it was shown that another roughly 0.5 TW is supplied by large-scale currents impinging on the bottom topography[6]. But just as global estimates of internal-wave generation finally seemed to be coming close to the approximately 2 TW required, *in situ* observations showed that internal waves tend to break close to ocean-bottom topography (the equivalent of beaches for surface waves), thus confining mixing to within a few hundred metres of the ocean bottom. So although the energy to support mixing was no longer lacking, the mixing was not delivered uniformly throughout the water column, as was needed to lift waters back to the surface.

The final piece of the puzzle was anticipated in 1998, when another seminal paper[7] pointed out that most of the ocean waters above depths of 2,000 m come to the surface in the Southern Ocean, where winds known as the Roaring Forties, blowing around Antarctica, pull them to the surface along surfaces of constant density. The uplift process therefore requires no mixing. Only in the past few years have oceanographers been able to integrate Munk's hypothesis with the discovery of uplift in the Southern Ocean. The emerging view is that mixing brings bottom waters in all oceans up to about 2,000 m, the characteristic depth of the most prominent oceanic topographic features. The waters then flow at approximately the same depth all the way to the Southern Ocean, where the Roaring Forties lift them to the surface (Fig. 1).

In this new scenario, the potential energy required from mixing is about half that estimated by Munk and Wunsch (the ocean is on average about 4,000 m deep, and mixing lifts the waters up to only half that depth), and it needs to be supplied in the bottom 2,000 m, the characteristic height of the major ocean ridges and sea mountains. Thus, there is no shortage of energy to support mixing, and the mixing is delivered close to the bottom topography, where it is needed. Problem solved? Not quite. *In situ* observations show that the intensity of bottom mixing is highly variable, being strong where topography is rough and bottom flows are fast, and weak elsewhere. Mapping this heterogeneity on a global scale is the next challenge in the quest to track the return journey of abyssal waters to the surface.

Enter Waterhouse *et al.*[1], who have gathered the largest compilation of *in situ* measurements of mixing so far, using them to test whether the new scenario is consistent with all available observations. They confirm that internal waves are indeed generated along the major ridges and sea mountains in the Atlantic, Pacific and Indian oceans. Most importantly, they show that about 70% of the waves break close to the ocean bottom, whereas the remaining 30% propagate away from their generation sites and end up breaking against the continental slopes. They conclude that abyssal waters make their way to the surface along the steep slopes of mid-oceanic ridges and continents, where mixing is strong.

The authors did not address the question of whether mixing is confined to depths below approximately 2,000 m — instead, they lumped together all measurements below 1,000 m. Future work must address this, because the answer is crucial for understanding and modelling the partitioning of carbon between the atmosphere and oceans. It was recently suggested[8] that the drop in atmospheric carbon dioxide concentrations recorded in ice cores from glacial periods is connected to the vertical profiles of ocean mixing. In the present climate, abyssal waters release carbon to the atmosphere when they return to the surface in the Southern Ocean. But in glacial climates, a large fraction of the Southern Ocean was covered by ice, thus trapping carbon in the ocean. This trapping was possible because strong mixing was confined to the ocean bottom, and waters could not be lifted to the surface at ice-free latitudes. Similarly, the present vertical profile of mixing will control the long-term rate (on millennial timescales) at which the ocean takes up the anthropogenic carbon we are releasing into the atmosphere. ■

Raffaele Ferrari *is in the Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Oceanography, Cambridge, Massachusetts 02139, USA.*
e-mail: rferrari@mit.edu

1. Waterhouse, A. F. *et al. J. Phys. Oceanogr.* **44,** 1854–1872 (2014).
2. Munk, W. H. *Deep Sea Res. Oceanogr. Abstr.* **13,** 707–730 (1966).
3. Wunsch, C. & Ferrari, R. *Annu. Rev. Fluid Mech.* **36,** 281–314 (2004).
4. Munk, W. & Wunsch, C. *Deep Sea Res. I* **45,** 1977–2010 (1998).
5. Garrett, C. & Kunze, E. *Annu. Rev. Mar. Sci.* **39,** 57–87 (2007).
6. Nikurashin, M. & Ferrari, R. *Geophys. Res. Lett.* **38,** L08610 (2011).
7. Toggweiler, J. R. & Samuels, B. *J. Phys. Oceanogr.* **28,** 1832–1852 (1998).
8. Ferrari, R. *et al. Proc. Natl Acad. Sci. USA* **111,** 8753–8758 (2014).
9. Lumpkin, R. & Speer, K. *J. Phys. Oceanogr.* **37,** 2550–2562 (2007).

SENSORY SYSTEMS

Sound processing takes motor control

Neurons linking the brain region that controls movement to the region involved in auditory control have been found to suppress auditory responses when mice move, but the reason for this inhibition is unclear. SEE ARTICLE P.189

URI LIVNEH & ANTHONY ZADOR

The key to human cognition lies in the neocortex, a modular brain structure that is unique to mammals. Within each neocortical module, small ensembles of neurons are wired together in stereotyped patterns. Subsets of these neurons send long-range axonal projections to other modules to create systems of circuits that transform the activity of single neurons into complex behaviours such as perception, cognition and motor control. Understanding how different neocortical regions — including the motor, visual and auditory cortices — coordinate their activity is a central challenge in systems neuroscience. In this issue, Schneider *et al.*[1] (page 189) describe a technically sophisticated set of experiments that unravels the mechanisms by which the motor cortex exerts control over the auditory cortex during locomotion.

Locomotion facilitates visual responses in the visual cortex[2] but, conversely, Schneider and colleagues observed that it suppresses sound-evoked responses in the auditory cortex. This observation is intriguing because these responses are also suppressed when an animal vocalizes[3] or engages in an auditory task[4], behavioural states that require careful auditory processing. What is the mechanism by which locomotion suppresses neuronal responses in the auditory cortex?

Neuronal firing rates are determined by the balance between signals that promote and inhibit firing, so, in principle, firing can be suppressed by either a decrease in excitatory signals or increased inhibition. To distinguish between these possibilities, Schneider and co-workers performed the challenging feat of making intracellular-activity recordings from neurons in the auditory cortex of mice running on a treadmill. These experiments revealed that decreased auditory responses during locomotion are the result of an increase in inhibition. Cortical inhibition arises almost entirely from local inhibitory interneurons that make only short-range connections with nearby neurons, so the interneurons are probably driven by long-range excitatory inputs that transmit signals into the auditory