

An oblique slant on deep-sea biodiversity

Michael A. Rex

Organisms at the bottom of the deep seas might seem to be immune from large-scale shifts in climate. Not so, according to a study which reveals links between benthic biodiversity, glaciation and the Earth's obliquity.

Early theories on deep-sea biodiversity assumed that the sea floor is spatially and temporally uniform, and is buffered from climatic change at the surface by the overlying water column. That changed with Hessler and Sanders¹ discovery of surprisingly high species diversity in the deep sea, just 30 years ago, which inspired a period of intense ecological research in this largest and least known of Earth's ecosystems².

In consequence, the perspective of ecological stability and independence has gradually given way to recognition of a much more dynamic and heterogeneous environment, one which functions as an integral part of the global biosphere. For example, we now know that the structure of biological communities shows pronounced variation on local, regional and global scales^{3,4}, and that surface–benthic coupling is mediated through the rapidly sinking remains of phytoplankton (phytodetritus)^{5,6}, and through organismic life cycles that include migration between benthic and pelagic habitats⁷. But this new picture of a complex and variable deep sea has been restricted to brief ecological timescales — we have had only three decades of quantitative sampling, and *in situ* experiments have lasted only a year or two.

On page 624 of this issue⁸, Cronin and Raymo add an entirely new dimension to our understanding by showing that deep-sea biodiversity can also vary on geological timescales of 10^3 – 10^4 years. These long-term fluctuations in diversity correspond in a remarkably consistent way to climatic shifts at the surface associated with glaciation and ultimately linked to changes in solar insolation that attend the planet's 41,000-year obliquity cycle. During this cycle, the tilt of the Earth's axis of rotation varies with respect to the plane of its orbit, altering seasonality.

Cronin and Raymo's study focuses on benthic ostracod species, minute crustaceans from a core of the ocean floor taken in the North Atlantic by the Deep Sea Drilling Project. Ostracods were sampled

along the core at intervals representing 3,500–4,000 years; altogether, they span a 450,000-year segment of the Late Pliocene, 2.85 to 2.40 million years ago, during which well-documented glacial–interglacial cycles occurred. Ostracods are preserved in deep-sea sediments because of their heavily calcified bivalved shells, and they are the only deep-sea multicelled organisms to have left an abundant fossil record. Variation in their species make-up along the core provides a natural experiment of how deep-sea diversity changes with time in response to glaciation.

Cronin and Raymo were able to analyse this relationship in a precise way. Their approach was to compare ostracod species diversity to oxygen-isotope ratios in the remains of foraminiferans (shelled protozoans, which were collected from the same position in the core, and so have the same geological age), and to Mg:Ca ratios in the ostracod valves. These ratios reflect the history of surface-ice volume and bottom-

water temperatures, respectively. The relationships between ostracod species diversity and these climatic indicators were followed through 11 cycles of glaciation. The results show that diversity is depressed during glacial advances and recovers during interglacial phases throughout the time sampled. Not only do climatic and diversity cycles match with a high degree of statistical significance, but the amplitudes of the changes also correspond. Diversity declines most during severe glacial episodes.

Cronin and his colleagues show elsewhere^{9,10} that these glacial oscillations in diversity are not accompanied by extinction and origination of species. Rather, they represent a periodic attenuation of an assemblage of organisms that persists through the time sampled. Data from other deep-sea cores reveal that some species lost to the assemblage during glacial advances have shallower (but still deep-sea) refugia from which they can later recolonize affected areas. So, at least on geological timescales of 10^5 years in this phase of the Pliocene, local ostracod diversity fluctuates, and evolutionary diversification is not apparent in this region of the North Atlantic. Along with related evidence on foraminiferans from earlier in the Cenozoic^{11,12}, some 30–60 million years ago, Cronin and Raymo's findings require a re-evaluation of the basic notions that physical and biotic stability in the deep sea on geological timescales have promoted diversity, and that deep-sea communities are immune from major climatic events.

What is the causal connection between glaciation and deep-sea ostracod diversity? Cronin and Raymo doubt that direct effects of variation in bottom-water temperatures

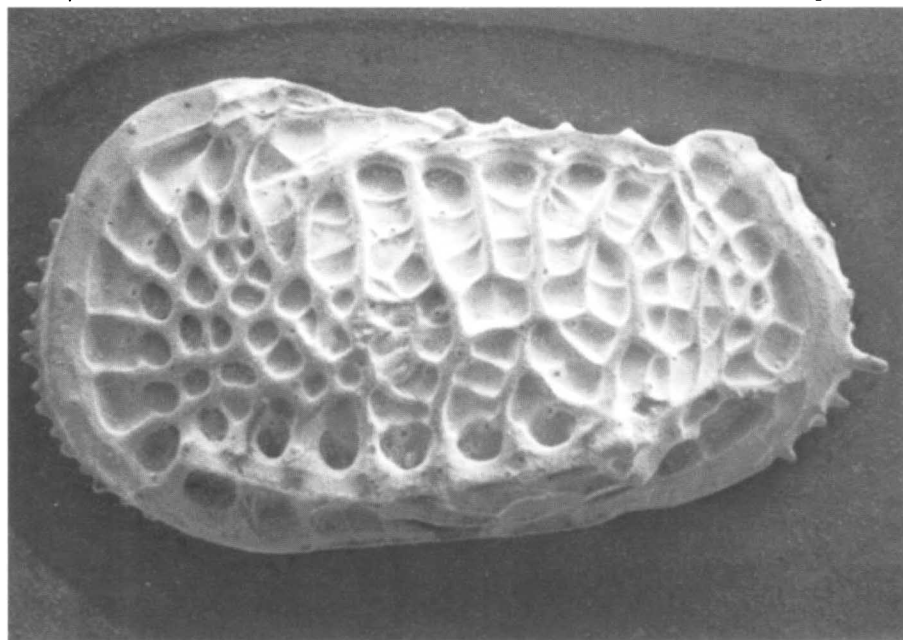


Figure 1 Scanning electron micrograph of *Poseidon amicus*, a member of deep-sea ostracod assemblages that are characteristic of interglacial periods. In reality, the length of this left valve is about 1 mm. (Micrograph courtesy of Deena Grinbaum.)

and dissolved nutrients are involved. Instead, they propose that the answer lies in climatically driven shifts in surface production and consequently nutrient input to the benthos from sinking phytodetritus. As a generality, this seems quite reasonable, because community structure in living deep-sea assemblages has been associated with nutrient input, and there is evidence of variation in overhead production from pelagic elements found in deep-sea cores.

Beyond this, it is hard to be more specific. The relationship between nutrient input (or productivity in surface environments) and species diversity has become a hot issue in macroecology. But there is still little agreement on the exact biological interactions involved, the scales on which they might operate, whether the mechanisms are equilibrium or nonequilibrium, and, indeed, even the correct statistical shape of the relationship¹³⁻¹⁶. Cronin and Raymo understandably steer clear of this empirical and theoretical quagmire, which can be approached critically only through controlled experimental tests on living deep-sea communities, and then with great difficulty. From their results, however, it seems increasingly likely that one or more features of nutrient input (rate, spatio-temporal variation, quality) are involved in shaping patterns of deep-sea biodiversity, past and present.

The sheer scale of events invoked in this study is certainly unprecedented in deep-sea ecology. Cronin and Raymo draw plausible links between diversity in the deep-sea benthos through geological time, surface production, patterns of glaciation and planetary behaviour. Their analysis shows the tremendous promise of a multidisciplinary approach, including palaeontology, palaeoclimatology and contemporary ecology, to develop a historical, global-scale understanding of deep-sea biodiversity. □

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1. Hessler, R. R. & Sanders, H. L. *Deep-Sea Res.* **14**, 65-78 (1967).
2. Gage, J. D. & Tyler, P. A. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor* (Cambridge Univ. Press, 1991).
3. Etter, R. J. & Grassle, J. F. *Nature* **360**, 576-578 (1992).
4. Rex, M. A. *et al.* *Nature* **365**, 636-639 (1993).
5. Billett, D. S. M., Lampitt, R. S., Rice, A. L. & Mantoura, R. F. C. *Nature* **302**, 520-522 (1983).
6. Graf, G. *Nature* **341**, 437-439 (1989).
7. Young, C. M. & Eckelbarger, K. J. (eds) *Reproduction, Larval Biology, and Recruitment of the Deep-Sea Benthos* (Columbia Univ. Press, New York, 1994).
8. Cronin, T. M. & Raymo, M. E. *Nature* **385**, 624-627 (1997).
9. Cronin, T. M., Raymo, M. E. & Kyle, K. P. *Geology* **24**, 695-698 (1996).
10. Cronin, T. M. *et al.* *Paleoceanography* **10**, 259-281 (1995).
11. Kennett, J. P. & Stott, L. D. *Nature* **353**, 225-229 (1991).
12. Thomas, E. & Gooday, A. J. *Geology* **24**, 355-358 (1996).
13. Ricklefs, R. E. & Schluter, D. (eds) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Univ. Chicago Press, 1993).
14. Huston, M. A. *Biological Diversity: The Coexistence of Species on Changing Landscapes* (Cambridge Univ. Press, 1994).
15. Brown, J. H. *Macroecology* (Univ. Chicago Press, 1995).
16. Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, 1995).

Schizophrenia

An emerging pathophysiology

Eric J. Nestler

The aetiology and pathophysiology of schizophrenia have been the focus of intensive research for decades, during which time the so-called 'dopamine hypothesis' has predominated. Because all clinically effective antipsychotic drugs are antagonists of D2-like dopamine receptors (which include the D2-, D3- and D4-receptor subtypes), excessive dopamine-mediated neurotransmission or high levels of D2-like receptors in the brain were thought to underlie schizophrenia.

In recent years, the dopamine hypothesis has given way to more complicated — and realistic — views of the disorder. The new picture invokes pathophysiological mechanisms in specific brain pathways that involve more than a simple increase or decrease in the activity of a single neurotransmitter or receptor type. It is in this context of an emerging, and more sophisticated, view of schizophrenia, that Okubo *et al.*¹ report their findings on page 634 of this issue. They have used positron emission tomography to show that there are reduced levels of D1-like dopamine receptors (which include the D1- and D5-receptor subtypes) in the prefrontal cortex of patients with schizophrenia. This reduction is also seen in patients who have never been exposed to antipsychotic drugs — an important control, as chronic treatment with antipsychotic drugs can also decrease levels of the D1 receptor in the prefrontal cortex of non-human primates².

This is an exciting time for research into schizophrenia. The development of brain imaging has allowed the brains of schizophrenics to be studied directly, and it is becoming increasingly feasible to understand these images within a cellular and molecular context. Considerable attention has been paid to the prefrontal cortex which, along with related limbic cortical structures (for example, the cingulate cortex), has been implicated as an important neural substrate of schizophrenia. These regions are thought to contribute particularly to the cognitive impairment and 'negative symptoms' (decreased motivation and expressed emotion) of schizophrenia; but they may also contribute to the 'positive symptoms', such as hallucinations and delusions.

Much is known about the expression and cellular/subcellular localization of dopamine receptors within the primate prefrontal cortex. The expression of D1-like receptors is around ten times higher than that of D2-like receptors. The D1 receptors are expressed predominantly by pyramidal neurons, on their dendritic spines³ (Fig. 1). This is an ideal location for modulation of the glutamate-mediated inputs to these neurons — inputs that mainly come from other pyramidal neurons and thalamic neurons. The D5 receptors are also expressed (at lower levels) by pyramidal neurons, but they are localized to the shafts of dendrites⁴. The distribution of D2-like receptors is not as

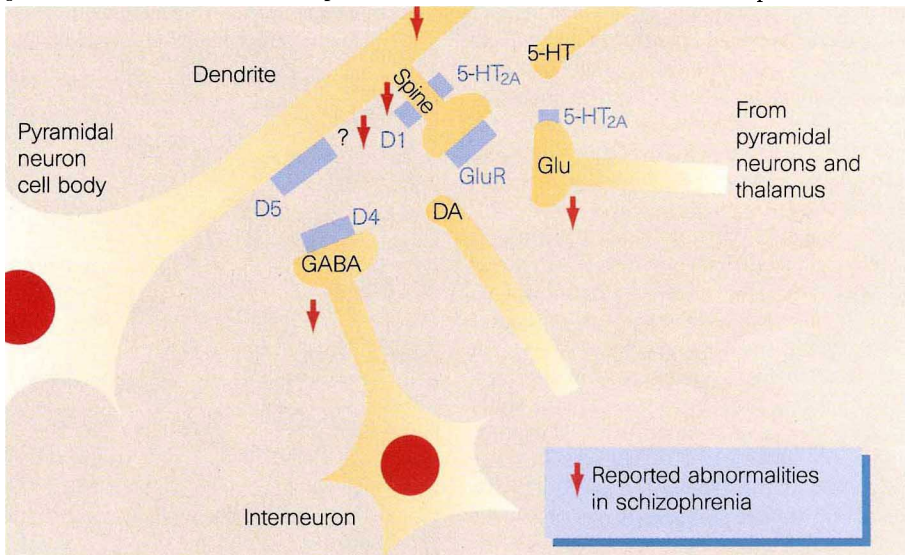


Figure 1 Localization of dopamine receptors within the synaptic organization of the prefrontal cortex (highly simplified). Okubo *et al.*¹ have found that one of the neural abnormalities associated with schizophrenia is a reduction in the levels of D1-like (D1 and D5) receptors. D1 receptors are restricted to dendritic spines, close to glutamate receptors; D5 receptors are localized to dendritic shafts; D4 receptors are enriched in GABA-containing interneurons; D2 and D3 receptors are present at lower levels in the prefrontal cortex, and they may be expressed in several neuronal elements. Glu, glutamate; GluR, glutamate receptors; GABA, γ -aminobutyric acid; DA, dopamine; 5-HT, serotonin.