

are not completely unexpected. Some previous studies have suggested high ratios based on TIMS U-Th dating of carbonate samples (13, 18, 19) and the apparent correlation between ^{14}C -dated marine sediments and the Greenland ice record (20). However, these studies lacked precision and often yielded noisy data. The unprecedented resolution and accuracy of U-Th ages in the new record strengthen the case for elevated $^{14}\text{C}/^{12}\text{C}$ between 30,000 and 40,000 years ago, although one previous study based on the annually laminated sediments of Lake Suigetsu in Japan (21) contradicts the results. It suggests atmospheric $^{14}\text{C}/^{12}\text{C}$ ratios close to the modern value between 30,000 and 40,000 years ago (22).

To illustrate the implications of Beck *et al.*'s extended calibration, consider the age of the prehistoric paintings recently discovered in the Chauvet Cave in southern France. Among the wild animals painted by Cro-Magnon people in this cave, we find numerous woolly rhinoceroses (see the figure). Charcoals used for these prehistoric paintings have been dated by ^{14}C

accelerator mass spectrometry (23). The four available ^{14}C ages are indistinguishable within error and give a weighted average of $\sim 31,000$ ^{14}C yr B.P. The calibrated age of the Chauvet paintings would thus be $\sim 38,000$ calendar yr B.P. according to the new record, but only $\sim 33,000$ calendar yr B.P. using the Suigetsu record.

The broad agreement of the new Bahamian record with previous results suggests that the "old chronology" is probably correct, but some problems must be resolved before we can update and extend the INTCAL98 curve. Future work on varved sediments beyond 30,000 yr B.P. should indicate whether the Suigetsu varves are accurately dated or whether these annual counts provide only lower bounds on absolute ages (22).

References and Notes

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PERSPECTIVES: ECOLOGY

Marine Bugs and Carbon Flow

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Oceans are thought to act as carbon sinks: Atmospheric CO_2 is assimilated during photosynthesis by plankton in the ocean and is converted to organic carbon, which then enters the food chain. Twenty-five years ago the flow of carbon through organisms in the open ocean appeared simple: Algae "fix" CO_2 during photosynthesis and are eaten by zooplankton, which in turn serve as food for fish (1). Since then, however, the simple diagrams of plankton food chains in ecology textbooks have had to be redrawn many times as new findings have added extra layers of complexity. For example, ubiquitous unicellular cyanobacteria are important producers of organic carbon (2, 3). Carbon and other organic compounds dissolved in the ocean are metabolized by heterotrophic bacteria, and these bacteria are eaten by protozoa (4, 5). To complicate matters further, viruses regulate bacterial populations (6), and photosynthetic protozoa can also be predators (see the figure) (7). With the report by Kolber *et al.* (8) on page 2492 of this issue, the diagrams in ecology textbooks will have to be redrawn

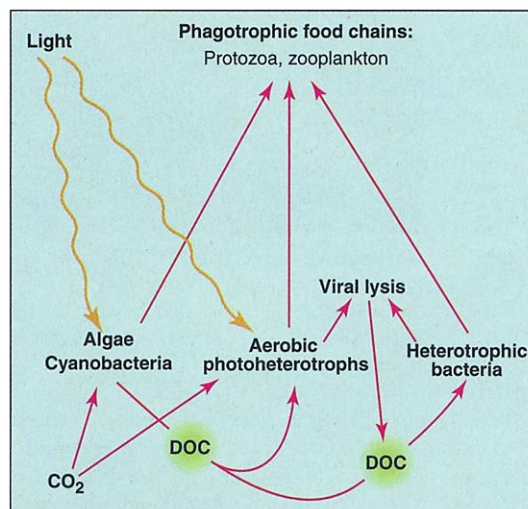
again. These investigators provide evidence that a long-ignored group of bacteria could be a key determinant of carbon flow in oceans. This group is composed of aerobic anoxygenic photoheterotrophs that

metabolize carbon when it is abundant or trap light and CO_2 for energy by photosynthesis when it is not.

Photosynthetic bacteria belong to one of five unrelated eubacterial lineages. Of these, only the cyanobacteria (like their green eukaryotic cousins that contain chloroplasts) carry out oxygenic photosynthesis: They use H_2O as a hydrogen donor to reduce CO_2 to organic matter with the production of O_2 as a metabolite.

All other photosynthetic bacteria engage in anoxygenic photosynthesis that depends on reductants other than water (usually reduced sulfur compounds, H_2 , and ferrous iron), without the production of O_2 . These anoxygenic phototrophs—purple sulfur bacteria, purple nonsulfur bacteria, green sulfur bacteria, green nonsulfur bacteria, and *Heliobacter*—are usually anaerobes (they have oxygen-independent respiration) but some are oxygen-tolerant and may even use O_2 respiration in the dark, although photosynthesis is confined to anoxic conditions.

Photosynthetic bacteria have special chlorophylls—bacteriochlorophylls—characterized by absorption peaks in the near-infrared part of the spectrum; they also possess accessory photosynthetic pigments (carotenoids) that enable them to absorb blue light. These bacteria are



Tangled webs and carbon flow. The flow of carbon through microorganisms in the water column of the open ocean. Components include protozoa, zooplankton, algae, cyanobacteria, viruses, heterotrophic bacteria, and aerobic (anoxygenic) photoheterotrophic bacteria. Dissolved organic carbon (DOC) is derived from the photosynthetic activities of cyanobacteria, algae, and other sources.

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common in light-exposed anaerobic habitats such as shallow-water sediments and stratified lakes (9, 10).

About 20 years ago, a new group of photosynthetic bacteria—the aerobic anoxygenic photoheterotrophs (belonging to the α -group of proteobacteria)—was discovered. In contrast to other known anoxygenic phototrophs, these microbes are obligatory aerobes: They metabolize carbon and other organic substrates and use O_2 -dependent respiration, but they also contain bacteriochlorophyll a, carotenoids, as well as photosynthetic reaction centers and light-harvesting complexes. Although the amount of bacteriochlorophyll in these photoheterotrophs is lower than in other photosynthetic bacteria, they are capable of fixing CO_2 during photosynthesis, and light enhances their growth. Their ancestors appear to be purple nonsulfur bacteria, and they have arisen independently several times during evolution. So far, they have not attracted much attention, although they are abundant in organic-rich sediments (on the surface of seaweeds) (11) and in seawater (12, 13).

Kolber *et al.* (8) are the first to calculate the abundance of these microbes in the upper open ocean. They extracted and quantified bacteriochlorophyll a from seawater, and directly counted infrared fluorescent microorganisms. They identified strains of these aerobic anoxygenic photoheterotrophs from the Atlantic and Pacific

oceans and found that they all belonged to the genus *Erythrobacter*. In the northeastern Pacific Ocean, these anoxygenic photoheterotrophs constitute about 11% of the total bacterial population in the upper 150 m of the water column (although this figure may be an underestimate, as nonliving bacterial “ghosts” may have been included in the total count of bacteria) (14). In this region of the Pacific, the ratio of bacteriochlorophyll a to chlorophyll a (the principal photosynthetic pigment of cyanobacteria and algae) is about 1%, but in more oligotrophic (nutrient-poor) areas this ratio increases to as much as 10% (the authors suggest a global mean ratio of 5 to 10%). The amount of CO_2 assimilated by these anoxygenic photoheterotrophs is likely to be far less than that assimilated by oxygenic photosynthetic bacteria, but their ability to produce energy from light provides them with a significant survival advantage. As long as they have light, these microbes do not have to depend on the metabolism of carbon or other organic substrates to generate energy.

The Kolber *et al.* work adds a new dimension to our current picture of the flow of carbon in the ocean. Our ability to predict the production of organic matter and to quantify the extent to which oceans act as sinks for atmospheric CO_2 depends crucially on our understanding of the marine microorganisms through which carbon flows. The new findings provide additional

challenges for those attempting to model the flow of organic matter and energy through ocean water columns. Although Kolber *et al.* suggest that aerobic anoxygenic photoheterotrophs are especially important in oligotrophic regions of oceans, I would not be surprised if they prove to be key players in coastal waters as well.

Conventional wisdom dictates that the organisms in the ocean's water column consist principally of bacterial species that have not been described or cultured. With their new work, Kolber *et al.* flout convention by culturing and identifying a major constituent of the ocean's bacterial biota.

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PERSPECTIVES: PLATE TECTONICS

A Graveyard for Buoyant Slabs?

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For 20 years, there has been a lively debate over whether large-scale convection deep within Earth involves the whole mantle or is divided into two layers separated at the prominent seismic discontinuity at 660-km depth. Protagonists of layered convection—generally geochemists—base their arguments on differences in trace element, isotopic, and rare gas abundances between ocean-island and mid-ocean ridge volcanic rocks (1, 2). Those favoring whole-mantle convection—generally geophysicists—cite success in modeling geophysical observables and seismic tomographic imaging (3).

Attempts to reconcile the two views have led to compromise models in which chemical inhomogeneities are maintained through

incomplete stirring, either on a local scale (4, 5) or because of temporary ponding of subducted material at the base of the upper mantle followed by avalanches of material into the lower mantle (6). Delayed penetration of the discontinuity in the latter class of models has been attributed primarily to differences in viscosity and to kinetic hindrance induced by the phase change believed to be responsible for the 660-km discontinuity. On page 2475 of this issue, Chen and Brudzinski (7) propose a different model in which large volumes of subducted material may be retained in the mantle transition zone, at depths of 400 to 700 km, because of buoyancy.

Previous workers have interpreted seismic evidence for cool, slablike bodies in the lower mantle as evidence that subducted lithosphere had penetrated the discontinuity. Chen and Brudzinski turn the argument around and ask why there is no seismic sign of a large and very strong tem-

perature anomaly in the lower mantle beneath Tonga, the fastest and coldest subduction zone in the world. Subduction in the northern part of Tonga occurs at a rate of ~250 mm/year, sufficient to produce a slab extending to the base of the seismogenic zone (700 km) in just 3 million years—much too fast for thermal assimilation. Why, then, is there no evidence for a cool slab extending deep into the mantle?

The authors reason that the visibility of a slab can be reduced substantially if its mineralogy counteracts the tendency for colder slabs to have faster seismic velocities, thereby diminishing its contrast in seismic tomography. They then show that a very large slab remnant appears to be “floating” beneath Fiji (see the figure). They also provide an explanation of the “outboard” earthquakes that occur west of and above the lithospheric slab currently subducting beneath the Tonga arc.

The authors begin with the simple premise that the presence of earthquakes indicates cold temperatures (8) and hence would be expected to yield fast seismic velocities. They then show that in the region of “outboard” earthquakes, the seismic ve-

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