Hale-Bopp

combination rate at low temperature.

The detection by ISO of water vapor in the stratospheres of the four giant planets was unexpected on thermochemical grounds (*12*). Water, which is abundant in the troposphere, freezes out at the cold tropopause. What mechanism could be delivering water to these upper atmospheres? External fluxes implied by the observations are similar on all planets, on the order of 10^5 to 10^7 oxygen atoms per square centimeter. This similarity suggests that interplanetary dust is an important source. These observations may thus provide a means of estimating the production of dust, possibly from comets, at large heliocentric distances. Another possible source is micrometeorite erosion from either the rings or the icy satellites surrounding the planets.

Hyakutake

In addition, a signature from CO_2 was seen on Jupiter, Saturn, and Neptune (*12*). On Neptune, this species could be supplied by the same external source as H_2O, if the CO_2/H_2O ratio in the infalling material is a few percent, as observed in cometary nuclei. But this source alone is not sufficient for Saturn. Another possibility is the formation of CO_2 by reaction of CO with OH radicals produced by the photolysis of H_2O. Within this framework, the nondetection of CO_2 on Uranus would result from a much lower abundance of CO in its atmosphere than on the other giant planets. On Jupiter, the limited spatial resolution of the ISO measurements allows us to infer that CO_2 is concentrated in the southern hemisphere and not detectable at high northern latitudes. This peculiar distribution suggests that the presence of CO_2 is a remnant of the collision of Comet Shoemaker-Levy 9 that struck Jupiter in July 1994 near 45° south latitude. The cometary impacts deposited large amounts of CO and H_2O in the upper atmosphere. As predicted by postcollision evolution models (*13*), CO_2 is subsequently produced by the reaction of CO with OH radicals.

Observations of the solar system with ISO have gratified planetary scientists with a wealth of new findings. Although some measurements still need to be fully analyzed and understood, infrared astronomers are looking ahead to new opportunities, including NASA's Space Infrared Telescope Facility (SIRTF), scheduled for 2001, and the Far Infra-Red and Submillimetre Telescope (FIRST), an ESA cornerstone mission, planned for 2007.

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PERSPECTIVES: ECOLOGY

The Plankton and the Planet

Conrad W. Mullineaux

What determines how fast photosynthetic organisms in the oceans grow? The question is of crucial importance for understanding the global ecosystem. The phytoplankton are the base of the oceanic food chain, and thus their growth rate ultimately controls the biomass that the oceans can support. Furthermore, the phytoplankton make a major contribution to global oxygen production and carbon dioxide absorption. A world in which the phytoplankton grew a little faster, or a little slower, would be a very different place. On page 840 of this issue, Behrenfeld and Kolber (*1*) report some new information on the factors that limit the growth of the phytoplankton.

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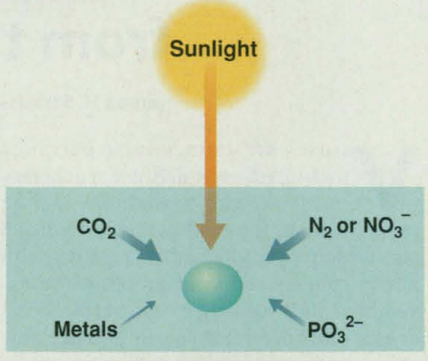
The phytoplankton are tiny, mostly single-celled, organisms. In the open oceans, the dominant species are prokaryotes, principally *Prochlorococcus* and *Synechococcus*. *Prochlorococcus* is usually present in far greater numbers [Behrenfeld and Kolber report 70,000 to 200,000 cells per milliliter (*1*)]. *Synechococcus* is a cyanobacterium (a blue-green alga). Molecular phylogenetic studies (*2*) show that *Prochlorococcus* is also a cyanobacterium, although it has an unorthodox pigment composition. In terms of sheer numbers, *Prochlorococcus* may well be the dominant organism on this planet, yet it was only recently discovered (*3*).



Essential ingredients. Raw materials required for growth of a marine photosynthetic organism. Materials that are essential but always abundant in seawater are not indicated.

The basic materials that phytoplankton need to build copies of themselves are relatively simple (see figure). They need sunlight as an energy source, water, and inorganic nutrients. Carbon is obtained by "fixing" carbon dioxide. Nitrogen may be obtained from nitrate; if this is unavailable, some cells will fix molecular nitrogen. Phosphorus and sulfur come from phosphates and sulfates dissolved in the seawater. In addition to these bulk constituents, the phytoplankton require trace nutrients. A number of metals, including iron, are required as essential cofactors of photosynthetic complexes and other proteins (*4*).

The growth rate of the phytoplankton depends on the supply of these raw materials. Their relative availability is vastly different in different environments. In the simplest case, one particular nutrient is limiting in any given environment. If the supply of the limiting nutrient were gradually increased, the phytoplankton would grow faster until something else became limiting. The factors that could limit growth in different marine environments include the amounts of iron (*5*), nitrate (*6*), phosphate (*7*), carbon dioxide, and light. Close to the surface, light is present in excess, and the ultraviolet component of sunlight can actu-

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ally inhibit photosynthes (*8*). However, in deeper water, light becomes limiting.

It is a fairly simple matter to measure the availability of the various raw materials in the ocean. Can we then predict which nutrient is limiting? In practice we cannot do this with any confidence because the interactions between the phytoplankton and their environment are so delicate and so complex. The ultimate test is simply to try adding more of a particular material and see what happens. The most spectacular example of this experimental approach has been a pair of open-ocean iron-enrichment experiments (IronExI and IronExII) (*5*). In these experiments, enough iron was added to the equatorial Pacific to raise the dissolved iron concentration to 4 nM over an area of about 70 km^2 (*5*). Remarkably, the iron enrichment caused a huge, though temporary, bloom of phytoplankton. This provided convincing evidence that iron availability is the factor that limits phytoplankton growth in this region of the Pacific. However, this conclusion cannot necessarily be extrapolated to other regions of the ocean, where nitrate or phosphate could be limiting.

Do we need an IronEx enrichment experiment (and the equivalent for all the other possible limiting nutrients) for every area of the ocean? This might be the only way to definitively determine the rate-limiting factors in a particular region. In the meantime, some provisional answers can be obtained by devising physiological tests for nutrient limitation. Behrenfeld and Kolber now report a simple physiological indicator of iron limitation in phytoplankton (*1*). Their test is based on the measurement of fluorescence—light that is absorbed by the photosynthetic pigments of the cells but subsequently escapes. Fluorescence measurements are a vital tool in photosynthesis research (*9*). They can give information on everything from the fast early steps in the chemistry of photosynthesis (by using subnanosecond laser pulses) to the global distribution of photosynthetic organisms (by using remote sensing from satellites). Fluorescence measurements can also indicate the mechanisms that photosynthetic organisms use to adjust the function of their photosynthetic apparatus. One such mechanism is the state transition, a rapid rearrangement of the photosynthetic complexes in response to a change in illumination conditions (*10*). State transitions are responsible for a characteristic diurnal variation in phytoplankton fluorescence. Behrenfeld and Kolber report that this pattern is altered specifically under conditions of iron limitation. Iron enrichment changed the state transition fluorescence signature of phytoplankton in the wild, and comparable effects could be seen in laboratory-grown pure cultures of *Synechococcus*. This provides a nice link between laboratory and field studies of the physiology of photosynthetic prokaryotes. Many photosynthetic acclimation mechanisms have been characterized almost entirely on the basis of laboratory studies. It is exciting to see these mechanisms at work on such a huge scale in the real world.

The underlying reasons for the effect on state transitions are not yet certain. Behrenfeld and Kolber give a very plausible interpretation based on the effects of iron limitation on the ratios of different photosynthetic complexes in the cell. However, the situation is remarkably complex in a lab culture of *Synechococcus*, let alone in a mixture of diverse species in the open ocean.

Whatever the physiological explanation, it appears that fluorescence measurements can provide a simple and reliable indicator of iron limitation. The results suggest that iron limitation is much more widespread than previously thought. Primary production appears to be iron-limited, not only in the equatorial Pacific but also in a huge area of the south Pacific (though not in the Atlantic). Widespread iron limitation has interesting implications, because iron is a trace nutrient—a little iron could make a great difference to primary production in vast areas of the oceans. Past episodes of climatic and environmental change may be linked to changes in iron availability in the oceans (*11*). The development of an efficient way to make iron available might even lead to large-scale iron fertilization, which in turn could make the oceans more productive. Furthermore, an iron-fertilized ocean could act as a better sink for atmospheric carbon dioxide (*12*), possibly buffering some of the effects of global warming.

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PERSPECTIVES: VIRAL RNA REPLICATION

With a Little Help from the Host

James H. Strauss and Ellen G. Strauss

Viruses are intracellular parasites that infect cells and use machinery inside the cell to multiply. During multiplication, the viral genomes replicate and these progeny genomes, together with newly synthesized viral proteins, are assembled into new virus particles. What does a virus need from a cell to make new copies of its genome other than metabolic machinery that produces such basic materials as energy, DNA and RNA precursors, and ribosomes to produce viral proteins? Viral genomes usually encode polymerases to synthesize new RNA or DNA, helicases to unwind double-strand RNA or DNA during replication, DNA-binding proteins, proteases, and capping enzymes that add a structure called a cap to the 5′ ends of messenger RNAs. Viral genomes are small, however, with limited coding capacity, so viruses must borrow host proteins to complete their replication machinery. The interactions between a virus and its host have been shaped by long stretches of coevolution, and the borrowed proteins do not necessarily serve the same function in viral replication as they serve in the host. Identification of these borrowed host proteins, which perform essential functions during viral replication, is important for understanding virus-host interactions, which influence the host range and virulence of the virus. The search for such proteins has heated up in the last few years.

DNA viruses use facets of the host cell machinery that replicate and transcribe DNA—hardly a surprising fact, because any DNA virus that replicates in the nucleus has access to such machinery. The intimacy of these interactions is illustrated by differences between the closely related tumor viruses SV40 (a monkey virus) and

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