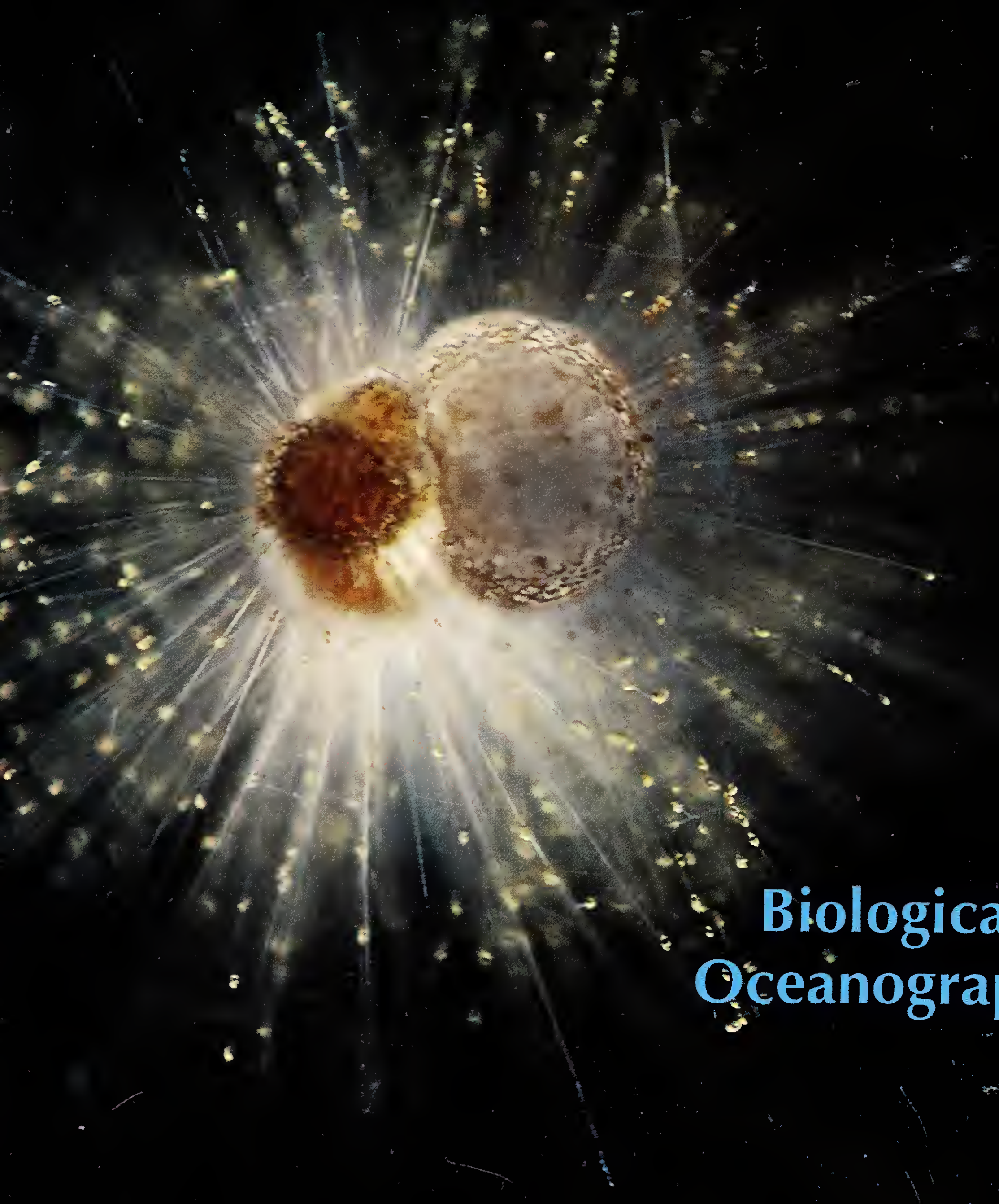
Oceanus

Volume 35, Number 3, Fall 1992



Biological Oceanography

Oceanus Class Research Vessels

Neil McPhee

R/V Oceanus *makes a port call in Madeira in April 1992, R/V* Endeavor *returns to home port with flags flying after a long cruise, and R/V* Wecoma *is loaded for a physical oceanography cruise off the Pacific coast.*

University of Rhode Island

Keith Bradley

Three of the seven "intermediate" sized ships (45 to 61 meters long) in the US University-National Oceanographic Laboratory System are *Oceanus* class vessels. R/V *Oceanus* is operated by the Woods Hole Oceanographic Institution, R/V *Endeavor* by the University of Rhode Island, and R/V *Wecoma* by Oregon State University. The 54-meter ships, delivered in 1975 and 1976, were funded and are owned by the National Science Foundation. They are general-purpose ships, that is, they are designed for flexibility, to accommodate a wide range of research needs at sea. They carry scientific parties of 12 to 16 people. As the ships are reaching the mid-life point, plans are under way for refits that include reconstruction of their deck houses to allow for additional bunks and larger laboratories, machinery overhauls, and combination of their distinctive paired stacks into single stacks behind the deckhouses.

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BIOLOGICAL OCEANOGRAPHY

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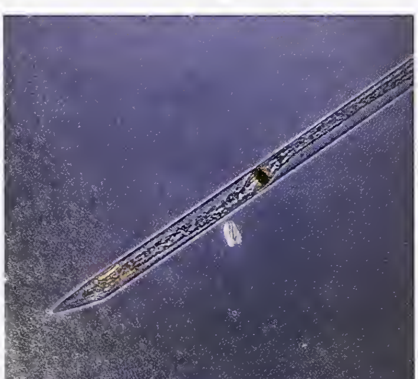
Sallie W. Chisholm



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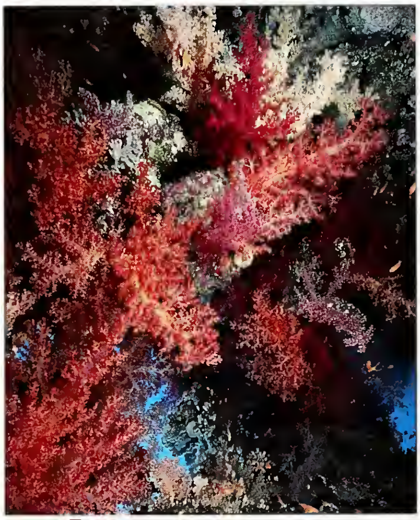
Rick Sammon

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DEPARTMENTS

ON THE COVER: Symbiosis, the mutually beneficial coexistence of two organisms, is common among marine animals. Even single-celled animals such as this planktonic foraminiferan can have symbionts. In this case, the symbionts are the golden-brown algae dispersed throughout the foraminiferan's spines. Photo by Allan W. H. Bé and David A. Caron

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Biodiversity, Riodiversity

James M. Broadus

As the "Earth Summit" (more properly, the United Nations Conference on Environment and Development or UNCED) convened in Rio de Janeiro this past summer, many Americans expected their country to be portrayed politically as an isolated international bad guy on the control of global warming. As it turned out, the US was isolated as a bad guy, but not on global warming. Instead, the fashionable new global issue Americans learned about from Rio concerns the conservation of biological diversity. It may be interesting to review what the fuss was all about and how it relates to the ocean.

Let's begin with the Earth Summit itself. The Rio Conference commemorated the 20th anniversary of the first world conference on the environment, the 1972 Stockholm Conference. The 1972 meeting had elevated environmental protection to the realm of high politics and established the principles that environmental protection can be consistent with economic-development aspirations and that less-developed countries require assistance from richer countries to protect their environments for the common good. It had fostered the creation of environmental ministries in a number of countries and led to the establishment of the United Nations Environment Programme (UNEP). The 1992 Rio Conference was intended to reinforce all these achievements and, especially, to bring about agreement on specific measures, including funding mechanisms, to serve both economic development and environmental protection goals.

The Rio Conference was, in fact, a split event, comprising the official intergovernmental meetings from which proclamations and legal conventions were issued, and also the less-official meetings to accommodate a vast range of nongovernmental organizations with pet causes to promote, interests and methods to compare, and products and services to sell. In all, over 40,000 people from 180 countries took part, including some 9,000 journalists and more than 100 heads of state. UNCED Secretary General Maurice Strong described the event as "the most important conference in the history of humanity." A number of participants at Rio, however, wondered whether the conference had enough coherence or resulted in enough concrete progress to warrant such hyperbole.

This is not to say that there were no results. The official conference issued five major products, and all of them touch on ocean affairs in one way or another.

- *The Rio Declaration.* This is a list of broad principles that the participating governments agree should guide their future economic development and environmental protection activities and investments. There is, of course, plenty of platitude here, but the first principle stated is of major importance: The well-being of human beings is the central concern and fundamental standard. Among its many other findings, The Rio Declaration also endorses the problematic "precautionary principle" discussed previously in this space (*Oceanus*, Spring 1992).
- *Declaration of Principles on Forestry.* General guidelines on the importance of "sustainable" forestry practices were adopted instead of a legal convention on forestry, because some developing countries feared international intrusion into their domestic forestry management policies.
- *Framework Convention on Climate Change.* This was expected to be the main

Rick Sammon

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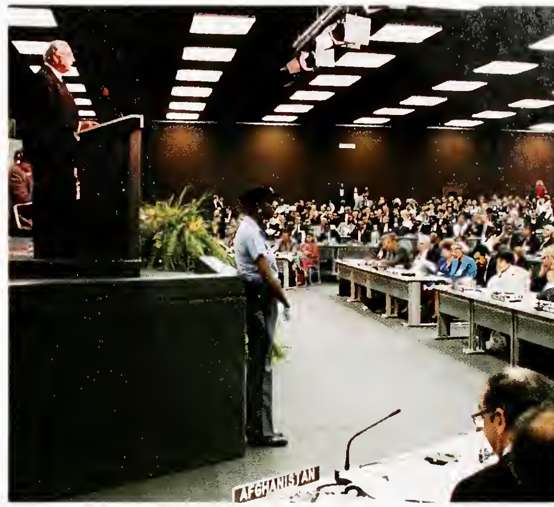


More real diversity is found on a typical coral reef than is found among opinions about biodiversity expressed at the Rio Conference.

point of contention, but widespread agreement was reached once European proponents backed away from their insistence on binding "targets and timetables" for greenhouse gas reductions. This opened the way for US participation, and 154 countries joined in agreeing to reduce harmful levels of greenhouse gas emissions, develop national plans for mitigating global warming, and increase scientific knowledge of the problem. As a framework convention, the agreement is very general and vague. There are ample qualifiers and escape phrases to serve everybody's needs, and any specific, tough measures that might be invoked are left to be worked out in later negotiations.

- *Agenda 21*. This is really the core product of the Rio Conference. It is a comprehensive master plan, in the indicative planning tradition, for actions to achieve sustainable development. As adopted by all 180 participating countries, the plan is described in a 900-page document. Its proposals are divided into 40 chapters and more than 100 program areas. Core chapters on implementation and financing of the plan call on the UN General Assembly to establish a "high-level commission on sustainable development" to take charge of post-Rio follow-up to the Agenda 21 plan, and to recruit funding assistance through existing multilateral mechanisms such as the Global Environment Facility (GEF) jointly administered by the World Bank, the UN Development Programme, and UNEP. In its topical chapters, Agenda 21 calls for: more general use of environmental impact statements, more attention to safe drinking water, routine development of toxic-release inventories, the use of environmentally "sound" technologies, the international transfer of such technology on terms favorable to developing countries, and expanded public participation in the development and environmental policy process.

Agenda 21 speaks of ocean affairs in some detail. Chapter 17, entitled "Protection of the Oceans, All Kinds of Seas, Including Enclosed and Semi-Enclosed Seas, and Coastal Areas and the Protection, Rational Use and Development of their Living Resources," contains some of the document"s most comprehensive and detailed proposals. (The title itself, however quaint, conveys the leaden, legalistic tedium of the document as a whole, but it only hints at the mind-numbing repetitiveness.)

The oceans chapter addresses seven program areas:

1) *Coastal Resources Management* calls for "integrated" management cutting across specific resources, attention to "ecosystem" manage-

ment through regional coordination of national programs, development of extensive data banks, and a global conference before 1994 to exchange national experiences.

2) *Environmental Protection* draws attention to the Law of the Sea Convention as the framework for action, highlights the importance of land-based sources of marine pollution and seeks guidelines from global experts with binding controls only at the regional level, and suggests several measures to strengthen the regulation of vessel-source pollution.

3) *High Seas Living Resources* discusses the controversial fishing of straddling stocks (those that inhabit over their life span more than one nation's economic zone) and highly migratory species and calls for an intergovernmental conference "as soon as possible."

4) *Living Resources Under National Jurisdiction* reiterates nations' rights and duties under the Law of the Sea to protect threatened habitats and species and lists actions to promote sustainable fisheries development;

5) *Critical Uncertainties* recognizes the value of improved information and endorses creation of a Global Ocean Observing System, development of national and international data banks for sharing information, and assessment of the effects of ozone depletion on the marine environment.

6) *International Cooperation* contains the usual rhetoric, but somewhat surprisingly grants that trade sanctions may be needed to enforce national environmental protection laws and only suggests that such sanctions incorporate the "principles" of nondiscrimination, least-restrictive measures, transparency of measures, adequate notification, and (again the usual) special consideration for developing countries.

7) *Small Islands* notes the special sensitivity of small islands to the issues addressed in the oceans chapter and recommends appropriate implementation of research, planning approaches, and coastal management programs. This section also contains the bizarre claim that "Most tropical islands are also now experiencing the more immediate impacts of increasing frequency of cyclones, storms, and hurricanes associated with climate change." (Don't believe it.)


Kilaparti Ramakrishna/Woods Hole Research Center

US Environmental Protection Agency administrator William K. Reilly led the US delegation to the Earth Summit. Here, Reilly follows US president George Bush into the plenary session before Bush's speech.

- *Biological Diversity Convention.* This is where the media jumped on the United States for refusing to join an international consensus. The convention intends to assure that national actions are taken to curb the destruction of biological species, habitats, and ecosystems. Suggested actions include national regulations, imposing legal responsibility on nations whose private companies do ecological harm elsewhere, transferring technology to poor countries on favorable terms, and compensating developing countries for extraction and exploitation of their indigenous genetic material. US Environmental Protection Agency administrator William K. Reilly, who led the US delegation, said, "The US early on supported the need for a biodiversity convention, so it was a perverse twist that we alone rejected it....In public relations terms, we never recovered from it."

It is important to note that biological diversity is not a very precise object of conservation. Like "sustainability," it seems easier to advocate than to define. The Rio Convention takes it to encompass all the earth's plant, animal, and microorganism species, and the ecosystems of which they are a part. That, of course, pretty well covers everything.

It describes a biologically diverse planet, but it hardly defines a "diversity" resource that can be conserved in the face of competing demands on scarce conservation resources. In a resource sense, biodiversity comprises the variety within and differences among genetic codes, species, and higher taxa, and habitats and ecosystems. In this same sense of variety and distinctiveness, oceanic biological diversity may be especially important, even though the marine environment is generally believed to harbor fewer species than land. However, Rutgers marine ecologist Fred Grassle, following in the path of Woods Hole Oceanographic Institution's Howard Sanders, determined that some benthic ecosystems on the continental slope exhibit species richness to rival tropical rain forests. Even more striking, perhaps, is the observation made by Grassle and others that, at higher taxonomic levels where the distinctiveness between groups is greater, marine systems are more diverse than terrestrial and freshwater systems combined. For example, 28 animal phyla are found in the ocean, of which 13 are found only there, compared to 14 freshwater and 11 terrestrial phyla, with only one of those unique to those habitats.

Not only do we need to know more about biological diversity in the oceans, we need to know more about biological diversity, period. We surely need to know more about how to measure it, estimate its uses, and conserve its use, so that we can make smarter protection and preservation decisions. We may not know enough about the sources of demand for this intrinsically valuable resource, and about the nature of threats to its viability, to formulate sensible international laws. This is particularly so if those laws make major new assignments of property rights and severely constrain trade institutions in a "property" that is so vaguely understood. William Reilly, who personally supported the Rio biodiversity convention, still called attention to "financial and legal concerns related to a proposed regime to single out as especially unsafe biotechnology, and language suggesting that intellectual property rights are subordinate to other rights recognized in the treaty."

The Rio biodiversity convention may help conserve marine biological diversity. More likely it is only one element, an initial step, in a larger process of learning by doing. Finding itself standing alone against a monolithic bloc of treaty supporters, the US delegation to Rio might well have felt envy for the rich diversity found in the sea.

James M. Broadus, an economist, is Director of the Marine Policy Center at Woods Hole Oceanographic Institution.

An Introduction to Biological Oceanography

David A. Caron

In many ways, biological oceanography as it is practiced today still encompasses the three ages of discovery, description, and quantification.

Few scientific topics elicit such genuine interest as the biology of marine organisms. Perhaps this is because the ocean is the ancestral home of all creatures on Earth, or because oceans cover nearly three-quarters of our planet's surface. Most likely, however, it is the seemingly endless variety of creatures inhabiting the ocean that so strongly piques our curiosity.

Broadly speaking, biological oceanography is the study of marine organisms and their interactions with their environment. The field is distinguished (narrowly, in some opinions) from marine biology in that biological oceanographers generally consider marine organisms within the context of their natural environment rather than as topics unto themselves. This predilection allows biological oceanography to exist as an amalgam of a variety of scientific fields rather than as a "pure science." Biological oceanographers are educated in chemistry, physics, mathematics, and geology, and have extensive training in biology. This field is more interdisciplinary than most other branches of science, including other oceanographic disciplines.

Most introductory oceanography textbooks trace the modern discipline to the "Age of Discovery" (the late 1400s and early 1500s), although many observations and descriptions of marine life were made before then. During this age, and through the next few centuries, the enormous breadth of the world ocean was realized, and the precursors to our modern maps of its borders and water-circulation patterns were formulated. With the spread of European civilization throughout the world, written accounts of the types and distributions of marine organisms increased rapidly, and their taxonomy, the classification of these plants and animals into coherent groups, was begun. By the mid-18th century, the Linnaean system was firmly established in the scientific community. It is still used today to name all organisms, using two-word latinized names that only biologists seem able to remember or pronounce (try saying *Pulleniatina obliquiloculata* three times fast!).

It was not until the latter part of the 19th century, however, that most scientific historians agree oceanography became a truly legitimate science. During this period, naturalists began to sample and observe

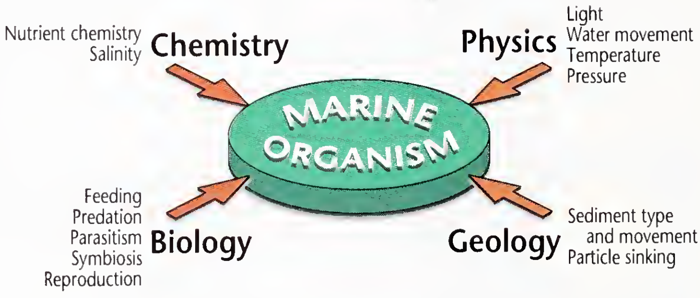
All photos accompanying this article are by author Dave Caron deep-ocean life, and interesting hypotheses emerged as to how these marine organisms evolved and functioned, particularly at great ocean depths. One hypothesis by noted English naturalist Edward Forbes maintained that the deep ocean was devoid of all life; another suggested that the evolution of animals on Earth could be traced back to creatures found as one went deeper into the ocean's depths. This latter hypothesis arose with Norwegian scientist Michael Sars's recovery of deep-sea organisms that were previously known only from the fossil record. These hypotheses, promulgated by prominent scientists of the time, culminated in the first major oceanographic voyage, the *Challenger* Expedition. This voyage, which began just 120 years ago, is generally considered responsible for the birth of oceanography as a bona fide science.

From this recent beginning, biological oceanography moved rapidly through a "descriptive" period, during which much of the known taxonomic diversity of marine species was recorded, many species' behaviors (reproductive adaptations, feeding behaviors, etc.) were characterized, and geographical and depth distributions for numerous species were demarcated.

In our present age of "quantification," biological oceanographers interpret and apply an ever-increasing wealth of knowledge about the biology of marine organisms to the ocean environment. These efforts include (but are not restricted to) the following broad goals:

- to fully describe the species diversity of marine communities, from the smallest microscopic forms to the largest individuals;
- to expand extensive observations of surface-dwelling species to the deep ocean, and to obtain a more accurate picture of the distributions, abundances, and activities of these deep-living forms;
- to determine the chemical, physical, and biological factors that control each species' survival in the ocean, and to understand the roles of individual species in complex marine communities (this goal requires a thorough understanding of each species' basic biology, feeding and reproductive behavior, growth rate, physiology, fecundity, etc.); and
- to quantify the flow of energy and elements through marine food webs, by experimentally investigating and mathematically modeling these communities.

In many ways, biological oceanography as it is practiced today still encompasses the three ages of discovery, description, and quantification. Newly discovered species are continually described in the literature, and major discoveries still await us. This is particularly true for the study of deep-ocean organisms, such as Rich Harbison's bathypelagic jellies, on page 18. Even for many well-known species, new facets of their physiology, behavior, and ecology are regularly revealed, and it will be quite a while before we fully grasp the complexity of their existences.



The interdisciplinary nature of biological oceanography is largely a consequence of the diverse types of information that must be considered in order to understand the ecology of marine organisms.

Jayne Doucette/WHOI Graphics

Land and Sea: Dissimilar Yet Similar

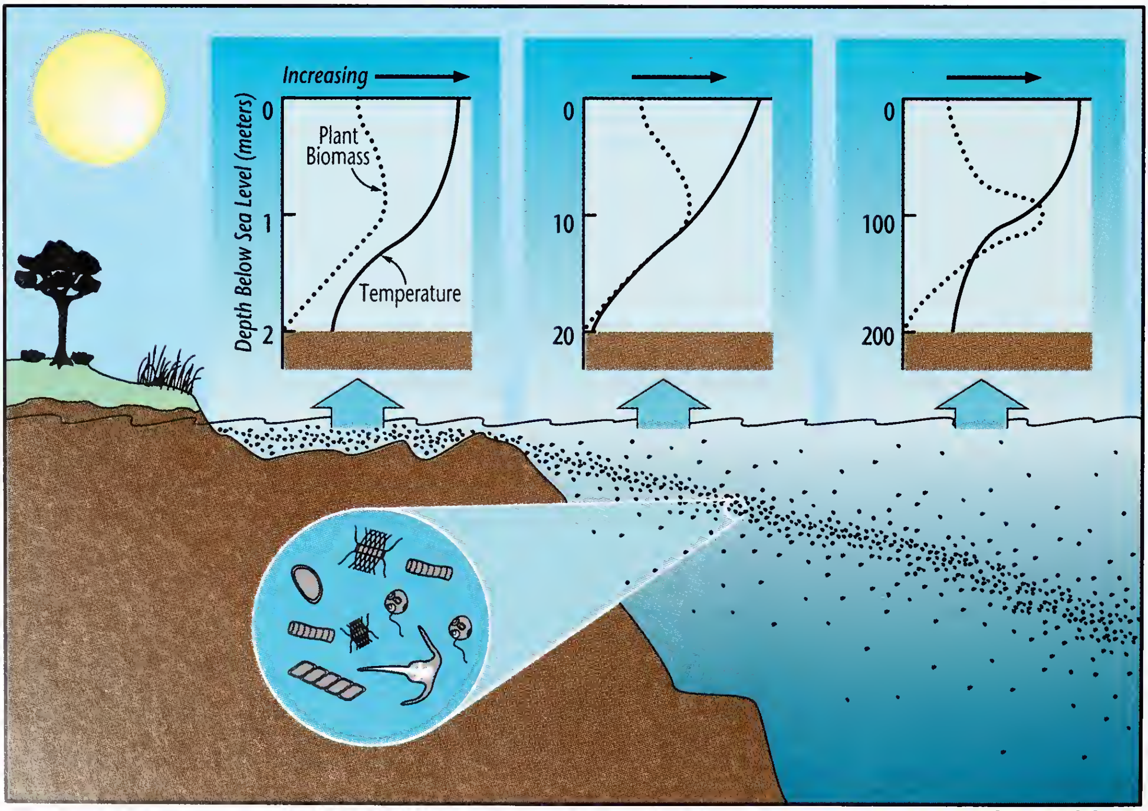
Representative depth profiles of temperature and plant biomass in a shallow coastal lagoon (left), a coastal sea (middle), and a deep subtropical basin (right) during the summer. The vertical extent of these profiles demonstrates the variability in the "productive" layer of the ocean. Such profiles, obtained using instruments attached to a hydrographic cable and displayed on a computer screen onboard ship in real time, are useful to biological oceanographers for identifying interesting biological and physical features of the water column for further study.

At first glance, the ocean appears to be composed of a bewildering array of creatures so peculiar in form and function to land-dwelling species like ourselves that it seems unlikely that we would find any similarities with our terrestrial environment. Actually, the opposite is true. Although the organisms composing marine communities are indeed very different from land organisms, at the same time these assemblages are highly analogous in the ways that they function.

As on land, the vast majority of energy that supports communities of marine animals is supplied via plants by the process of photosynthesis. Just as terrestrial plants absorb carbon dioxide, nutrients, and light energy to produce organic material, marine plants use these same building blocks to construct organic molecules necessary to sustain their own existence and the existence of all marine creatures. Even in the remarkable thermal vent communities of the deep ocean, the chemosynthetic process conducted by bacteria is analogous to the photosynthetic process of plants in the ocean's lighted waters.

Photosynthesis is usually referred to by oceanographers as "primary productivity," because it is the basis for life in the ocean and the primary source (directly or indirectly) of nutrition for all organisms. Plants absorb the sun's energy and transform it into the chemical bonds of organic molecules. Once converted into chemical bonds, the energy is then available to animals when they consume and digest the plants.

Measuring the rate of photosynthesis and identifying the factors that



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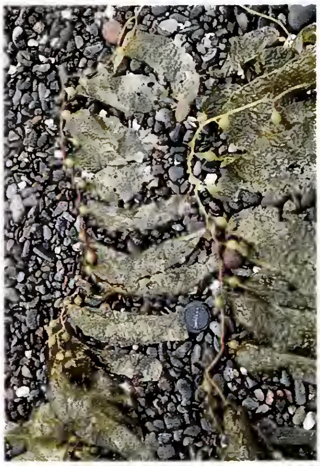
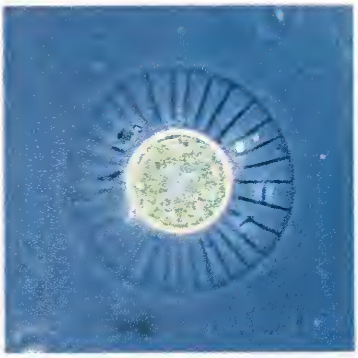




control the rate are major research topics in biological oceanography today, as is determining the fate of the plant material (consumption, digestion, defecation, degradation, and sinking). These may seem like simple tasks, but measuring primary production in the ocean is complicated by the nature of marine plants. Most terrestrial plants are large structures that can be easily examined and measured. Although large, multicellular plants (woody, flowering plants and large seaweeds) grow in salt marshes and coastal waters, the most abundant and ubiquitous ocean plants are microscopic algae, the phytoplankton. Phytoplankton comprise a complex community of several thousand species ranging in size from about 1 micrometer up to a few millimeters, a range of more than 1,000 times. Measuring the growth rates of this diverse assemblage of microscopic, single-celled creatures is not easy, and as Penny Chisolm explains beginning on page 36, there is still considerable debate about which factors limit the growth of these organisms in the ocean.

At each step in the food web, some energy is converted to the consumer's organic material, some is converted to heat and work energy (subsequently lost in the process of respiration), and some is excreted as unused organic waste. Typically, only a small fraction (10 to 20 percent) of the organic material and the energy contained in it is converted into the consumer's body material. The losses to respiration and organic waste excretion are quite significant. For this reason, communities of organisms grouped according to their nutritional mode are sometimes represented as an energy pyramid. According to this scheme, plants occupy the base of the pyramid because they are the energy source for all other organisms in the community.

Marine primary producers vary tremendously in size and form. Phytoplankton ranging in size from 1-micrometer cyanobacteria (top, center) to approximately 200-micrometer diatoms (top,right) are representative of the smallest primary producers. Macroscopic algae such as large kelp (far left; note lens cap for scale) and some vascular plants such as these mangroves (bottom) represent the other end of the size spectrum.

Species that feed directly on plant material, the herbivores, occupy the second level in such conceptualizations as an energy pyramid. Herbivores vary tremendously in size in the ocean as they do on land. Just as a caterpillar and a cow both consume plant material (a leaf, or blades of grass, respectively), in the ocean, single-celled animals a few micrometers in diameter may feed on microscopic algae while a manatee several meters long may consume large aquatic plants. From the point of view of energy transfer through food webs, however, all four interactions constitute herbivory.

The ocean's primary producers are mostly minute, dictating that their consumers, the herbivores, will be quite small themselves (often microscopic) or equipped with extremely fine filters for sieving this plant material from the water. A variety of planktonic herbivores are indeed small, while many sediment-dwelling species such as clams feed by sieving algae from the water.

Identifying the major consumers (of all sizes) of plants in the ocean and the rates at which plants are consumed is a central theme in marine research. As with the phytoplankton, the study of these ocean herbivores (and small carnivores) is complicated by their small size and wide vertical and geographical distributions. Beginning on page 100, Peter Wiebe, Cabell Davis, and Charles Greene review some new acoustical and optical methods for studying these deep-ocean creatures to address these deficiencies.

Identifying the major consumers of plants in the ocean and the rates at which plants are consumed is a central theme in marine biological research.

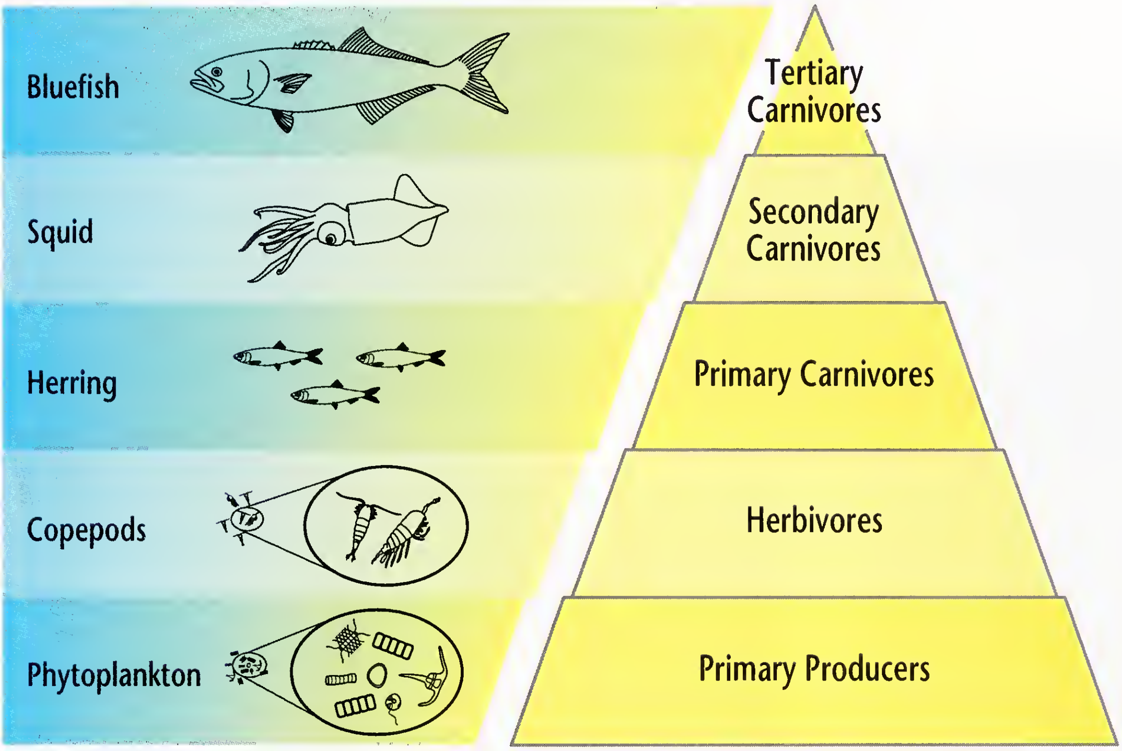
Despite their diversity, oceanic plants and herbivores support the relatively few animal species near the top of the food web. As on land, carnivores occupy the pyramid's uppermost compartments. In the ocean, this niche is composed of the larger fishes and sharks. Human beings typically have more familiarity with these larger, higher-level carnivores, and a fair amount of respect when intruding on their habitats. Although humans are not permanent residents of the marine environment, they also occupy one of these top consumer niches as eaters of fish. Because energy is rapidly dissipated as it moves through food webs, and because many marine primary producers are microscopic, relatively few larger carnivores can be supported (compared to the number of primary producers).

The growth and death of plants and animals in the ocean inevitably produces a large amount of dead organic material, and here again there is a strong analogy between the ways that the land and ocean function. Bacteria (and their consumers) are the primary agents for returning the elements contained in nonliving organic matter back to an inorganic form in both terrestrial and aquatic environments. This mechanism for returning some of the dead organic material back to marine food webs is known as the "microbial loop" among biological oceanographers such as Larry Pomeroy, whose article on this topic begins on page 28.

Divide and Conquer: Specialization in Biological Oceanography

The topics biological oceanographers study and the methods they employ are nearly as diverse as the organisms inhabiting the ocean. Because of the vast breadth of the field, most oceanographers have specialized interests. These may involve a particular group of organisms (such as bacteria, jellyfish, or marine mammals) or an environment (for example, salt marshes, ocean plankton, or the deep-sea benthos). Investi-

Trophic Relationships in a Simple Food Web



Jayne Doucette/WHOI Graphics

gators may also focus on a particular level of inquiry, ranging from in-depth biochemical process studies in a particular microorganism species to the response of an entire marine organism community of organisms to an external stimulus.

Subcellular research on marine organisms has been a popular research topic for many years as scientists endeavor to understand the physiology and biochemistry of marine species. This field is presently witnessing a revolution in traditional methodology. Beginning on page 47, Ed DeLong and Bess Ward describe how molecular biological techniques, pioneered in the biomedical field, hold great promise for providing a new generation of tools for addressing important questions in biological oceanography.

At the other end of the spectrum, research at the community level glosses over the activities of individual organisms and populations in an attempt to determine how communities as a whole function. A common approach is to group organisms with a similar nutritional mode or position in the food web, which reduces the biological community's enormous complexity. Without this reduction, most attempts to investigate community-level processes would be too complicated for even the most sophisticated computers.

Much community-level work is conducted through the use of mathematical models. Modelers grapple with the task of coordinating our accumulated knowledge of how marine plants and animals interact

A simplistic means of reducing the complexity of a community into a managable size is to group species by their nutritional mode. In the energy pyramid depicted here the size of each compartment indicates the amount of energy passing through each group. Organisms in one compartment are prey for the organisms in the compartments above. Note that the amount of energy produced in one compartment can never be greater than the energy produced in the compartments above it.

with their environment and each other. Distilling beautiful marine organisms and complicated biological processes into mathematical equations may seem rather dull and unfulfilling, but the ramifications of this process are quite meaningful. Useful models not only condense existing knowledge, but usually point the way to future research by identifying aspects of community function that are poorly understood. Some models also aid in predicting the effects of ecosystem changes on the community that inhabitats it. With the availability of powerful computers, the field of biological modeling is expanding rapidly. Hal Caswell and Solange Brault describe this new wave of modeling on page 86.

David Caron

Practical Applications of Biological Oceanography

Increasing our understanding of how marine communities function is not solely a scholarly endeavor. Ultimately, society expects the rewards of biological oceanographic research to be applied to critical issues such as the assessment of human impact on marine communities and the sensible commercial exploitation of the ocean's resources. The need to invoke oceanographic knowledge will undoubtedly increase as human encroachment on the marine environment increases. For example, the commercial competitiveness of modern aquaculture ventures benefits from extensive information on the biology of the target species. This information may help the aquaculturist cope with disease, eliminate or retard predation by invading species, and optimize feeding schedules and waste removal. In managing free populations, quotas on the size and numbers of a finfish or shellfish that may be taken from a locale reflect the best scientific prediction of the losses that these populations can withstand and still remain healthy. These predictions take into account the species' reproductive capability, natural predation losses, longevity, and physical and meteorological factors.

Allan W. H. Bé and David A. Caron

Symbiosis, mutually beneficial coexistence, is a common behavior among marine species. All corals feed using tentacles to capture prey (top), but many species also possess microalgae within their tissues that impart a brownish color to the living animal (center). Captured prey provide a source of energy for the animal, while waste products from their digestion provide nutrients for algal growth. Some of the organic material produced by the algae is shared with the host. Even single-celled animals such as planktonic foraminiferan (bottom) can possess symbionts (in this case, golden-brown algae dispersed throughout the spines of the foraminiferan).

Assessing the impact of human activities on the marine environment and its biota has become a major environmental and political issue in recent years. Making intelligent decisions about the disposal of municipal and industrial wastes presupposes a knowledge of the effects these materials will have on the ocean's biota. Studies on the fate of a wide variety of anthropogenic materials including sewage, pesticides, and toxic metals have been conducted in the past, and many more are under way.

Many anthropogenic substances are not harmful in trace amounts, but can become toxic when they are concentrated in living tissue as they move through marine food webs. This process of "biomagnification" or "bioamplification" can threaten the survival of species (like human beings) that are the ultimate consumers in food webs. Accurately predicting the effects and movement of these materials in marine food webs requires a working knowledge of the tendencies of individual species to accumulate these substances. By studying naturally occurring toxic substances and the organisms that produce them, Don Anderson and Alan White have a "natural experiment" for examining the ramifications of bioamplification in marine communities, as they detail beginning on page 55.

We strive to understand how the ocean functions, define the limits of its abilities to absorb our activities, and assure that we do not exceed those limits.

Biological oceanography plays a central role in assessing human impact on our environment. The Joint Global Ocean Flux Study (see JGOFS, *Oceanus* Spring 1992) is an important multinational program designed to examine the ocean's role in the global carbon cycle. Although this study is primarily "pure" research, one of JGOFS's ultimate goals is to be able to predict how the ocean may respond as the carbon-dioxide content of Earth's atmosphere increases. Because carbon is a major component of living tissue, the success of the JGOFS program relies on a thorough understanding of the biological processes controlling carbon's movement through oceanic food webs.

Reviewing these practical applications, it is clear how important biological oceanography is in addressing the future of our planet. Researchers in many different aspects of biological oceanography share a common goal: We strive to understand how the ocean functions, define the limits of its abilities to absorb our activities, and assure that we do not exceed those limits. Ultimately this knowledge is critical to the continued health of the ocean, the planet, and our own future.

Gather a shell from the strewn beach
And listen at its lips: they sigh
The same desire and mystery,
The echo of the whole sea's speech.
And all mankind is thus at heart
Not anything but what thou art:
And Earth, Sea, Man, are all in each.

—*The Sea-Limits*
Dante Gabriel Rossetti

David A. Caron is an Associate Scientist in the Biology Department at Woods Hole Oceanographic Institution. Like most biologists, his career began with a childhood interest in how living things functioned, leading to many impromptu experiments on the survival of small wild animals under the rigorous conditions of backyard captivity. This experimental aptitude was later honed by studies at the University of Rhode Island and the MIT/WHOI Joint Program in Biological Oceanography because there seemed to be far more bizarre creatures to tease in the ocean than on land. His research involves the ecology of aquatic microorganisms, which includes many, many interesting species. He is a native of Massachusetts where most small organisms still give him a wide berth.

The Gelatinous Inhabitants of the Ocean Interior

G. Richard Harbison

Ecology can be thought of as an attempt to understand the wonderfully complex drama of life. The plants and animals are the performers, interacting with one another in a bewildering melange of subplots. The ecologist's job is to study these subplots, and try to figure out how they fit together into an overall coherent (or at least plausible) pattern. Among the most bizarre and beautiful of these actors are the gelatinous zooplankton, which are not familiar to most people, since they are usually found in the open ocean, far from land.

G Richard Harbison

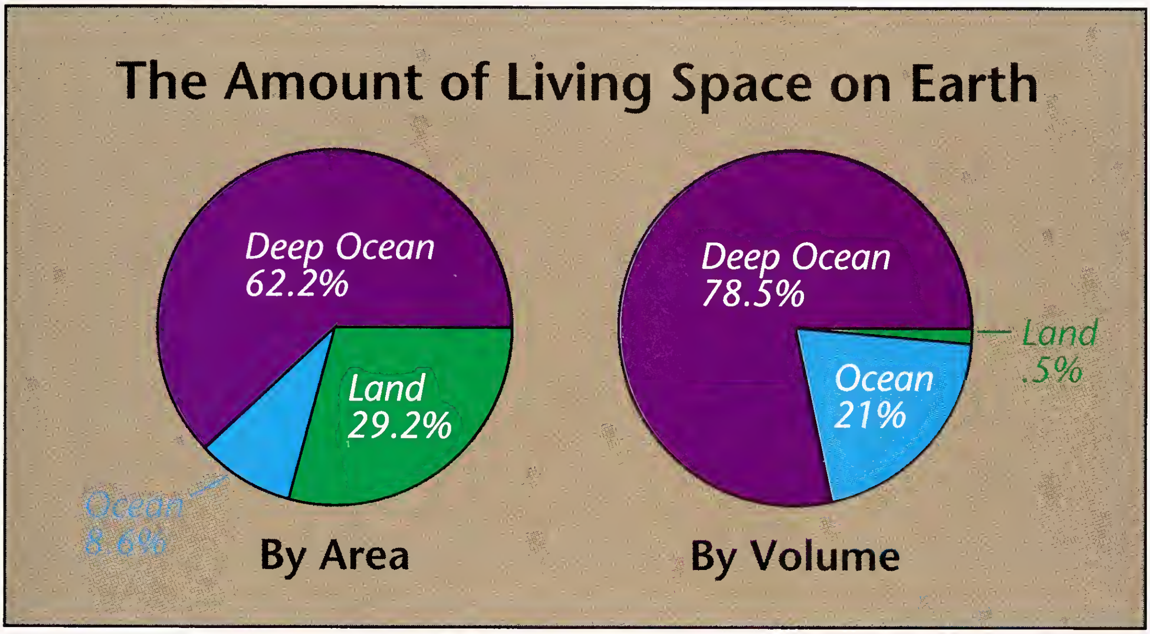
Although squids are usually not gelatinous, this one, Megalocranchia *sp., is. The internal organs, and especially the silvery ink sack, can be seen through its transparent body.*

Most planktonic animals spend their entire lives in the water column, unconnected with either the surface or the bottom of the sea. The bodies of many open-ocean planktonic animals are composed of extremely watery tissues. Although they superficially resemble one another, many are not closely related at all, and, in fact, belong to different phyla. These translucent animals are called "gelatinous zooplankton," and they include members of the phyla Cnidaria (the medusae and siphonophores), Ctenophora (the comb jellies), Mollusca (pteropods, heteropods, and some squids), and the Chordata (salps). This last phylum is highly significant to us, since it is the one to which we also belong.

The gelatinous body plan appears to be a fundamental adaptation to life in the open sea, since it is there that gelatinous organisms attain their greatest diversity and abundance. Very few gelatinous zooplankton are found in lakes and streams, and they are not nearly as diverse close to shore as they are in the deep sea where their adaptations reflect the peculiar nature of their open-ocean environment. When compared to our terrestrial environment, the open ocean seems a strange and alien place.

In fact, it is so strange and alien that it is difficult to picture what it is like to live there.

The open-ocean environment is essentially boundless. Jim Childress, a deep-sea biologist at the University of California at Santa Barbara, uses a pair of simple pie diagrams to illustrate its almost inconceivable vastness. If one divides up the living space on Earth on the basis of area (as Earth appears from a space station), then land comprises about 30 percent, shallow oceans (less than 1 kilometer deep) make up about 9 percent, and the deep ocean (more than 1 kilometer deep) constitutes



Considered on the basis of area alone, land comprises about 30 percent of Earth's living space (left). But unlike land, oceanic life exists throughout the water column. Taking the ocean's volume into account, land's contribution to global living space decreases to 0.5 percent (right).
Jack Cook/WHOI Graphics

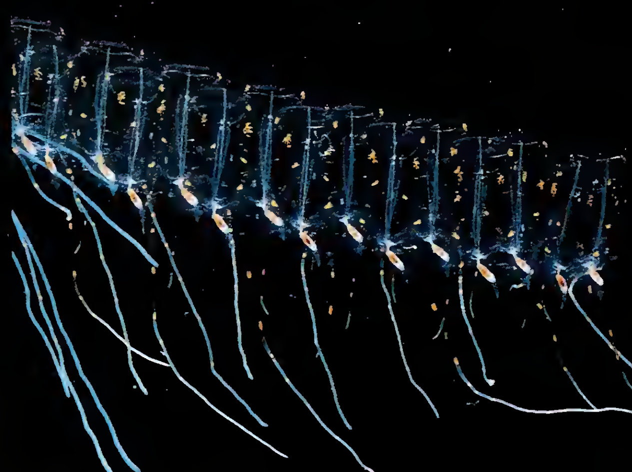
about 62 percent of the living space. However, as Childress points out, the entire volume of water in the ocean is a suitable habitat for life, whereas living organisms are found only as a thin skin on the land. Therefore, when Earth's living space is charted on the basis of volume, the picture is quite different: Land then comprises only 0.5 percent of the planet's living space. Ours is indeed the water planet, far more so than most people imagine. Although the deep ocean makes up over three-quarters of the living space, it is presently being studied by only a handful of biologists.

The vastness of the open ocean may be daunting to biologists, but it is of fundamental importance to the lives of planktonic animals. It is the only truly boundless environment on Earth—since it is four kilometers deep *on average*, planktonic animals can move about freely in three-dimensional space without ever encountering either the surface or the bottom. Imagine living in an environment where the only surfaces that one ever encounters are other organisms or their detrital remains. There are no hard surfaces to run into, so there is no need for an animal to develop a sturdy body to withstand the mechanical stresses of daily life to which we are so accustomed.

The open ocean's vastness also acts as an immense buffer. Below a few hundred meters, seasonal changes in temperature and salinity are, for all practical purposes, nonexistent. Below a kilometer in depth, the

***Left:** The deep-sea medusa* Periphylla periphylla *eats bioluminescent prey, and its dark gut is probably designed to conceal the flashes of its prey as it digests them. Otherwise, their dying flashes could reveal the medusa's location in the permanent darkness of its environment.*

***Below left:** The siphonophore,* Sulculeolaria *sp., spreads its tentacles to catch prey.*



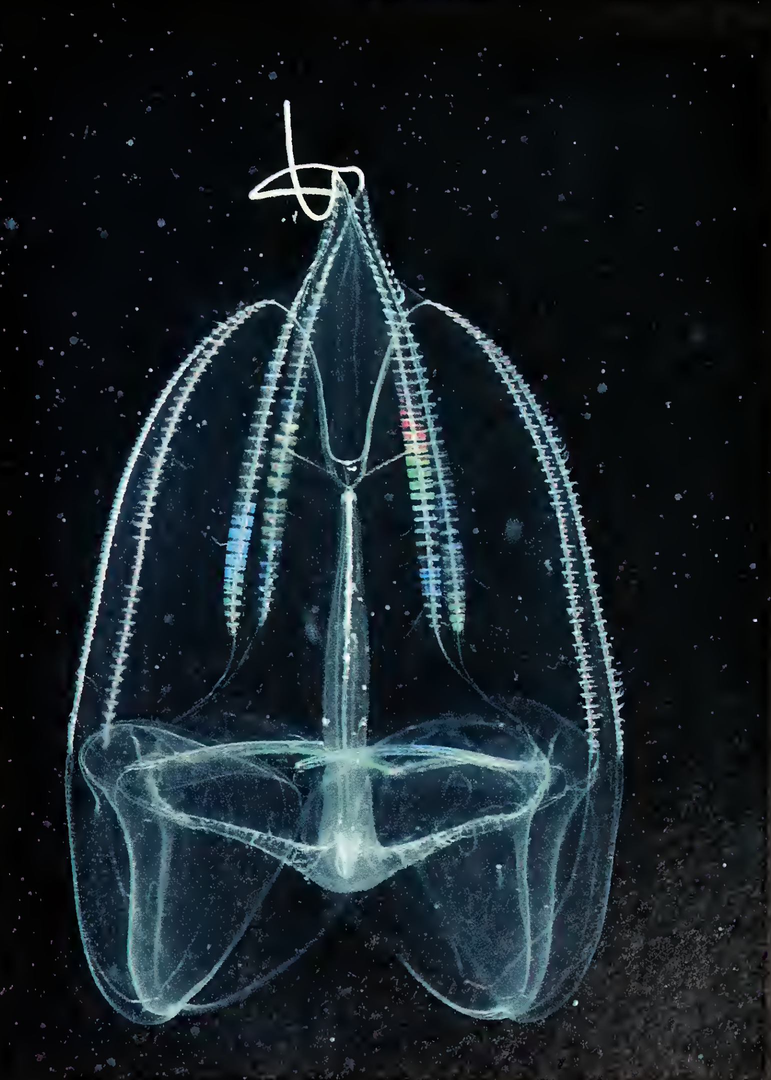
***Above:** Salps are in the same phylum as humans, the Chordata. They are filter-feeders that consume microscopic plants and animals by pumping water through their tubular bodies. This chain of* Traustedtia multitentaculata *includes many salps, each about 3 centimeters long. Their guts can be seen between their "tails" at the lower end of each animal.*

Photos by G. Richard Harbison and Ron Gilmer

Above: *The siphonophore* Forskalia *sp., photographed in the laboratory, has a tiny gas-filled float that can be seen at the upper end of the animal. The transparent structures surrounding it are nectophores or swimming bells. The pigmented region of the animal contains the feeding polyps and their tentacles.*

Above right: *The medusa* Calycopsis *sp. was photographed in the field with its tentacles spread. Medusae capture their prey with stinging cells, or nematocysts.*

Right: *Ctenophores, such as this* Eurhamphaea vexilligera, *are not related to either medusae or siphonophores, and are placed in a separate phylum. Though it has no eyes itself, the rows of red dots that line the sides of the animal release bioluminescent ink when it is disturbed, presumably to help elude visual predators.*



The transparency of many oceanic animals may be simply due to the fact that there is no need to be opaque.

constant temperature is only a few degrees above freezing. Since sunlight only penetrates a few hundred meters into the water, most of this vast environment is in perpetual darkness, punctuated only by scattered lights of bioluminescing animals. One can scarcely imagine what it is like to live there, where the slightest movement can reveal an animal's position, as its swimming turbulence sets off a minefield of bioluminescent organisms. When we enter this environment with submersibles, our bright lights shatter the tranquil darkness. Thus, it is surprising that so many animals seem undisturbed by our presence and our lights. Animals with eyes adapted to the perpetual gloom must surely be blinded, yet many of them have little or no reaction. This certainly shows that vision must be a very minor sense to them, even though it seems of overwhelming importance to us.

Because ultraviolet light penetrates ocean depths even less than visible light, many animals that live there are transparent. It has been suggested that transparency is an adaptation that provides concealment from predators, and in some cases this may be so. However, the transparency of many oceanic animals may be simply due to the fact that there is no need to be opaque. Our own opaque skins prevent ultraviolet-radiation damage. For animals that live below ultraviolet light's penetration depth, there is simply no need for protection against it. Many deep-dwelling gelatinous animals are nevertheless brightly colored, and these colors may be used to conceal them from predators.

Gravity is another force that has a great effect on the construction of our own bodies, but operates in an extremely different way on oceanic plankton. Since most gelatinous animals are nearly neutrally buoyant, they have no need to struggle against an overwhelming pull of gravity, or to develop strong skeletons to withstand its effects. Gelatinous animals are free to develop large, elaborate, and delicate feeding structures, since the force of gravity is neutralized by the density of their watery medium, and the turbulence produced by storms at the surface seldom propagates to great depths.

Indeed, the open-ocean environment compels them to develop these elaborate structures for another reason: food is extremely dilute. Most primary production in the open sea occurs near the surface, where microscopic plants use sunlight to turn carbon dioxide and water into sugars (photosynthesis). The stable temperature structure of the open sea reduces the movement of nutrient-rich deep water up into the surface waters. As a result, the nutrients needed for the photosynthesis and growth of plants are lowest in those areas where sunlight can penetrate. This keeps the concentration of the microscopic plants very low, compared with levels found close to shore. The reason that open-ocean water is such a transparent, vivid blue is because of the low concentration of plant material in the water. Since there are so few primary producers at the base of the food chain, the levels of food available to animals living in the open sea are low. Therefore, there is a premium on maximizing size while using a minimum of protoplasm, since larger animals can exploit the open sea's dilute resources more efficiently than small ones. Thus, the gelatinous zooplankton, with their large, delicate, watery bodies, are admirably adapted for life where food is scarce.

Many gelatinous animals are also able to go for long periods without feeding, and simply "de-grow" or shrink as they starve. Given the low levels of food available, this makes our encounters with siphonophores over 20 meters long even more significant. The extreme delicacy of these immense animals attests to the lack of turbulence and other mechanical stresses in the deep sea, and also shows what a benign environment this is for life. These siphonophores must be extremely old, since it must require many years for them to attain such great sizes.

Since their delicate, watery bodies seem so well adapted for life in this alien environment, it is not surprising that gelatinous animals are so ubiquitous in the open sea. Although biological oceanographers have done a great deal of work on planktonic animals living in the upper kilometer of the open sea, the vast majority of it (the regions below 1 kilometer) still remains essentially unexplored. Investigations with submersibles reveal that as one goes deeper, the gelatinous zooplankton become more diverse, even more delicate, and still larger. Many of these animals can only be collected with extremely gentle techniques—they are shredded into unrecognizable mush by nets. Near the surface of the open sea, nets can collect only a fraction of the animals that are there. As one goes deeper, the fraction that nets can collect becomes smaller and smaller. For this reason, a large percentage of the gelatinous animals that we have collected at great depths are new to science. Given the present state of our knowledge of the organisms that inhabit the ocean depths, it should be obvious that we can have few correct insights into the processes that are occurring in the ocean's interior.

After all, if we don't know who the actors are, how can we possibly know what the play's about?

G. Richard Harbison is a Senior Scientist at the Woods Hole Oceanographic Institution. He grew up in Florida, but traces his interest in scuba diving and marine biology to the movie Creature from the Black Lagoon. *Florida inspired his love for the cold. His recent field work has been annually bipolar—scuba diving for jellies in the arctic in northern summer, and through the Antarctic sea ice during southern summer.*

Ron Gilmer

The deep-sea ctenophore Bathocyroe fosteri *was first collected with the submersible* Alvin *and is named after* Alvin *pilot Dudley Foster.*

"Animals" That Photosynthesize and "Plants" That Eat

Diane K. Stoecker

Mixotrophy appears to be so advantageous that many different mechanisms for combining "animal" and "plant" functions in one cell have evolved.

In ecology, we usually think of organisms in the food web as producers (the plants) or consumers (the animals). The "plants" make their own food through photosynthesis, converting carbon dioxide and water into organic carbon using the energy of sunlight; and the "animals" eat the "plants" and smaller "animals." Except for a few odd creatures (such as the Venus flytrap, a bog plant that catches insects to supplement its diet of water, carbon dioxide, and minerals), these distinctions work fairly well among the larger terrestrial organisms. In the sea, however, mixotrophy, the use of more than one nutritional source, such as feeding *and* photosynthesis, is common, making it difficult for marine ecologists to separate the producers from the consumers. Therefore biologists and ecologists are reevaluating the usefulness of the traditional scheme of classifying organisms as producers (plants) and consumers (animals) in an effort to find new ways of describing ecosystem structure and food-web dynamics.

The sea's best known mixotrophs are large, multicellular, reef-building corals that use their tentacles to prey on zooplankton but also have microscopic photosynthetic algae living in their tissues. The coral uses some of the organic carbon made by the algae. Without these algal endosymbionts, the corals probably could not thrive and build large reefs in nutrient-poor tropical and subtropical waters. Several other marine invertebrates also have algal endosymbionts, including giant clams.

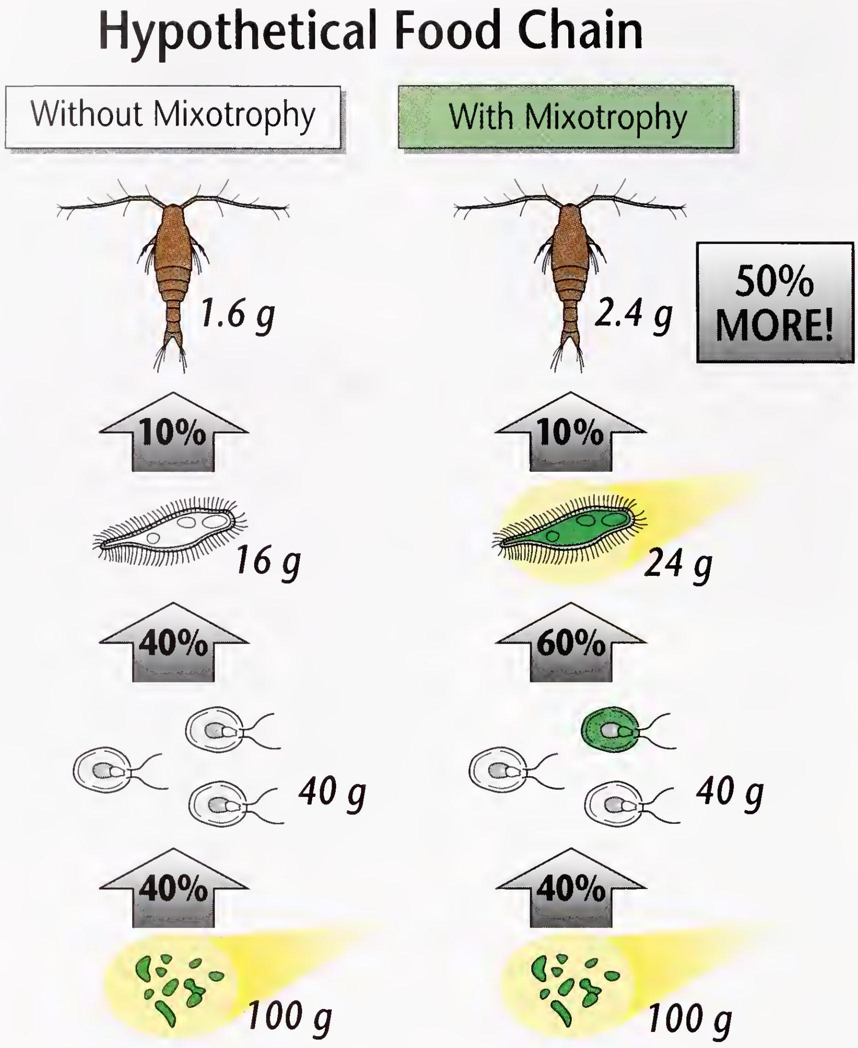
Until about five years ago, it was widely believed that photosynthetic mixotrophy was largely confined to tropical marine organisms that lived in nutrient-poor environments. Recent work by plankton biologists is changing our views on mixotrophy, however. Among the one-celled Algae and Protozoa that make up the bulk of the sea's small plankton, species that both eat and photosynthesize are common. As a matter of fact, mixotrophy appears to be so advantageous that many different mechanisms for combining "animal" and "plant" functions in one cell have evolved.

One of these ciliates is green; the other is not. At left is a species of Strombidium *that has taken an innovative approach to adding "plant" functions to an "animal" cell: They eat phytoplankton, digest most of their algal food, but retain the phytoplankton's chloroplasts. The "enslaved" chloroplasts convey a green color to the ciliate. Below is another species of* Strombidium *that does not use this feeding approach. These ciliates are about 40 micrometers long.*

Some larger protozoans (organisms usually categorized as consumers), have algal endosymbionts, including many of the beautiful radiolarians and foraminiferans found floating in sunlit but nutrient-poor tropical waters. Planktonic foraminiferans range in size from 60 micrometers up to 1 centimeter. Radiolarians have an even larger size range, from 10 micrometers up to 3 meters for some colonial forms. Larger members of these groups often capture and feed on copepods and other zooplankton. But in addition to capturing prey, many of these protozoans also depend on photosynthesis by their algal symbionts. As in the reef-building corals, we believe organic carbon produced by the algae supply most of the basic energy needs of the "animal" cell, and captured prey probably supply materials needed for growth and reproduction. Thus, like the reef-building corals, foraminiferans and radiolarians with algal symbionts can survive and grow in nutrient-poor waters where prey are scarce. Also like the corals, foraminiferans and radiolarians are important components of tropical and subtropical marine ecosystems because they are both producers and predators. Foraminiferans, like corals, have calcium-carbonate skeletons; radiolarians have silica skeletons. Much of the seafloor is covered with the calcerous or siliceous remains of these symbiotic protozoans, and some limestones and cherts are composed of their fossilized remains. Thus these symbiotic mixotrophs are particularly important in biogeochemical cycles in the sea.

Another common group of planktonic protozoans, the ciliates (ranging in size from 10 to 200 micrometers), have taken a stranger approach to adding "plant" functions to an "animal" cell. Some species contain chloroplasts, organelles responsible for photosynthesis in plant cells. "Green" ciliates eat phytoplankton (microscopic algal cells). Most

The efficiency of transferring biomass up a food chain increases if planktonic mixotrophs are one of the links. Food chains are inefficient in that with each link in the chain, energy is lost; thus, the longer the chains, the less food reaches the top to the bigger organisms. In both chains, the production by small algae at the base is the same. Without mixotrophy, each protozoan link is about 40 percent efficient (it takes about 100 grams of food to make 40 grams of protozoan). However, with mixotrophy, this number increases to 60 percent, making the food web on the right more efficient.



Jayne Doucette/WHOI Graphics

of the algal cell components are digested, but some of the chloroplasts are functionally retained in the ciliate. These "enslaved" chloroplasts produce organic carbon that the ciliate uses to cover much of its energy demand, a trick that amazes and puzzles both cell biologists and oceanographers. "Green" ciliates are ubiquitous in upper, sunlit ocean layers, from the tropics to polar, ice-covered seas. They have even been found growing in brine-filled pockets of Antarctic sea ice!

Protozoa are not the only mixotrophic cells in the plankton. Many of the phytoplankton can capture and eat other cells; flagellated algal cells commonly ingest bacteria or other small cells. Some bloom-forming dinoflagellates can capture ciliates and other small "animals." It is interesting that many of the photosynthetic algal species responsible for noxious blooms in coastal waters are reported to either consume other cells or to have the capacity to take up dissolved organic carbon (another method of nutrition). It is possible that pollution, particularly eutrophication leading to high levels of bacteria and organic matter in seawater, may favor some of the less-desirable species of mixotrophic algae.

Mixotrophy may have an important influence on the flow of energy and materials through planktonic ecosystems. Theoretically, photosynthetic mixotrophs should use ingested carbohydrates and proteins more efficiently for growth than organisms that gain energy only from ingested food. This would increase the efficiency of transferring energy and materials to higher trophic levels (generally bigger organisms). If this is true, we can no longer safely separate production from consumption in our food-web dynamics models.

The study of one-celled planktonic organisms shows us that mixotrophy is advantageous not just in nutrient-poor tropical waters, but in environments ranging from rich estuaries to the ice-covered polar oceans. It reveals the amazing capacities of one-celled organisms to combine "plant" and "animal" functions in one cell. Mixotrophy is forcing us to find new ways to describe ecosystem structure and food-web dynamics, providing new challenges for marine biologists, cell biologists, and biological oceanographers who describe and predict the flow of energy and materials through planktonic ecosystems.

In 1991, Diane Stoecker worked at McMurdo Sound, Antarctica, investigating algae and protozoa living in the sea ice.

Jessie Alstatt

Diane K. Stoecker lives on the Warwick River, a tributary of Chesapeake Bay, and has planktonic Protozoa in her backyard. She is an Associate Professor at Horn Point Environmental Laboratories, part of the University of Maryland System. For years she was a scientist at Woods Hole Oceanographic Institution, where she still has many friends and colleagues. She has worked on mixotrophic protozoans, particularly ciliates that enslave chloroplasts, in environments ranging from Woods Hole harbor to Antarctica and the equatorial Pacific.

The Microbial Food Web

Lawrence R. Pomeroy

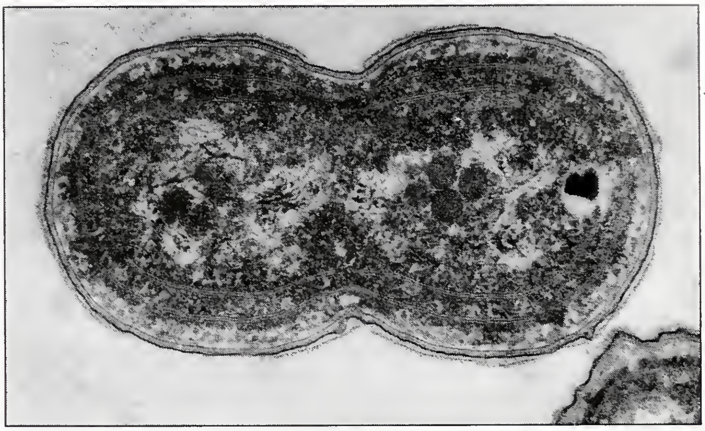
We now recognize a spectrum of marine microorganisms that are potentially—but not actually—a complete food web unto themselves.

Our ideas about the ocean's food web are influenced by our relationship to it and our ability to see the organisms in it. We see the fishes, and we enjoy being terminal consumers of that part of the food web. With help from microscopes, we can also see the plankton on which the fishes feed and phytoplankton that give the water a sheen or color. But there is much more to the ocean's food web than what meets the eye. Important parts are composed of organisms that are virtually invisible, even to ordinary microscopes. Only recently have we been able to identify all the food web's major invisible components and evaluate them as movers of energy and materials in the ocean.

Inklings of this invisible, microbial ocean community surfaced as long ago as 1908, when marine biologist H. Lohmann discovered that the fine filters some planktonic organisms used for feeding were concentrating very tiny green flagellates from seawater. Two decades later, V. I. Vernadskii, the founder of biogeochemistry, suggested that, because of their abundance, the little green flagellates might be the most significant living movers of materials on Earth. He was on the right track, but many more decades passed before the technology became available to measure feeding and growth rates of these and other, even smaller, microorganisms in the sea. Only in the last decade have marine scientists been able to routinely measure the growth rates of marine microorganisms in seawater, and to largely complete an inventory of the major marine microorganism groups. However, we still have only a superficial understanding of marine microbial diversity and natural history: who eats whom, how, and when. We are also just beginning to appreciate the variations in the microbial food web with latitude and depth in the ocean, and how it interacts with the more visible web of invertebrates and fishes.

Photosynthetic Microorganisms

We now recognize a spectrum of marine microorganisms that are potentially—but not actually—a complete food web unto themselves. Photosynthetic microorganisms synthesize organic compounds using the sun's energy, and other microorganisms consume them, creating the food web's tiers. With the exception of coastal seaweeds and floating *Sargassum* (a sprawling brown algae) in the Atlantic Ocean and the Gulf of Mexico, all of the ocean's photosynthetic organisms are microrganisms. All tiny, planktonic plants are called phytoplankton, but many photosynthetic plankton are in fact not plants but blue-green bacteria. In tropical and subtropical latitudes, the genus *Trichodesmium* is a major photosynthetic population. Water abundant with chains of *Trichodesmium* cells, approximately a millimeter long and arranged in bundles, appears to be sprinkled with sawdust. At the other size extreme are solitary spheres just 1 micrometer in diameter, members of the genus *Synechococcus*. Their abundance and role in ocean photosynthesis was first recognized by J.M. Sieburth (University of Rhode Island) and John Waterbury and colleagues (Woods Hole Oceanographic Institution, WHOI) in 1979. In the tropics and subtropics, a liter of water may contain several million of them. *Synechococcus* ranges into cooler water than *Trichodesmium*. It is abundant in surface waters of the world's oceans when the water is warmer than 5°C.



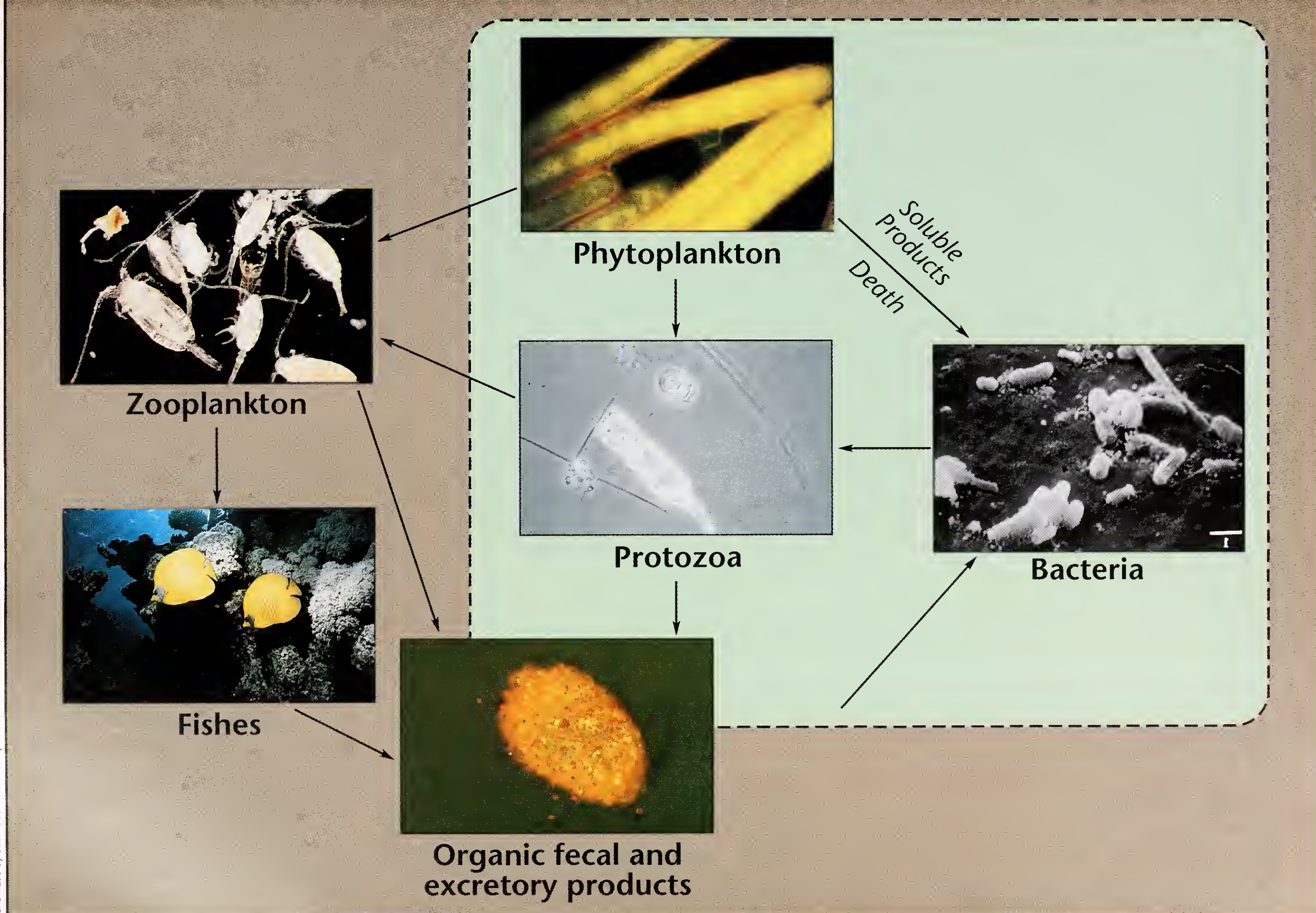
John Waterbury

Members of the genus Synechococcus *exist as solitary spheres approximately 1 micrometer in diameter. These photosynthetic microorganisms are very abundant in the tropics and subtropics, where 1 liter of seawater may contain several million.*

The true plants are photosynthetic cells with defined nuclei, such as diatoms. Most major groups of true phytoplankton were identified long ago. What we have recently come to appreciate is how small many of them are, and how much of the ocean's photosynthesis is accomplished by organisms less than 10 micrometers in size. Even some diatoms are no more than 10 micrometers long, and the "little green flagellates" first seen by Lohmann are ubiquitous and productive. A recent discovery (1988) is the abundance of a primitive group called prochlorophytes. Robert J. Olson (WHOI) and Sallie W. Chisholm (Massachusetts Institute of Technology) detected a faint but distinctive fluorescence that proved to come from prochlorophytes, which are slightly smaller than the 1-micrometer *Synechococcus*. The instrument they used aboard ships was a large, complicated clinical flow cytometer that automatically counts and measures individual phytoplankton cells.

We now perceive that a large part of oceanic photosynthesis involves very small plants and bacteria—so small they cannot be detected or eaten by the typical copepod, which is about 2 millimters long. As a general rule, organisms consume food roughly 10 percent the size of their own bodies. Smaller food requires unusual feeding adaptations. Some marine organisms have fine filters to feed on organisms much smaller than themselves, but most zooplankton do not, so those tiny photosynthetic organisms ranging in size from around 0.5 to 10 micrometers are eaten mostly by 5-to 100-micrometer organisms. This is the size range of Protozoa, and the ocean abounds with all the major protozoan groups.

Not all tiny flagellates are green plants. Many do not have plant pigments, but instead ingest bacteria, either the blue-green *Synechococcus* or nonpigmented ones. Ciliated and amoeboid protozoans are also abundant. Considering all this, we can safely say the ocean does contain an entire food web of microorganisms. Because it is to some degree a self-contained web of microscopic producers and consumers, it is often



Schematic by Jack Cook/WHOI Graphics

In this simplified schematic of the oceanic food web, the green portion represents the "microbial loop." Figures shown are not to scale. A portion of a bundle of Trichodesmium *filaments represents the phytoplankton; the protozoan shown is* Tintinopsis, *a ciliate that lives inside its cone-shaped house constructed of fibers it secretes; the bacteria are assorted marine bacteria (scale bar is 1 micrometer); the organic fecal pellet shown is from a crustacean, and is viewed with ultraviolet light, causing fluorescence, the fish are blue-cheeked butterfly fish (photo by Rick Sammon); and the zooplankton are various crustaceans (photo by Andrew Syred/Science Photo Library).*

called the microbial loop. Much of the food produced photosynthetically by microorganisms is consumed by other microorganisms, and may never enter the food chain of larger invertebrates and fishes. But, as we shall see, there are links as well as competition between microorganisms and fishes, sometimes to the advantage of fishes or their prey, and sometimes to the advantage of microorganisms.

Microbial Consumers

Nonphotosynthetic bacteria are major consumers of energy and materials in the sea. We did not realize this until about 20 years ago, because conventional methods for assessing bacterial populations, counting colonies grown on agar plates, did not work well in the sea, and therefore the numbers of bacteria were greatly underestimated. Now we attach fluorescent compounds to bacterial DNA so we can see and count (using a microscope) individual bacteria in seawater samples. After this method was developed by R. Zimmermann and L.-A. Meyer-Reil, we learned that most oceanic bacteria are smaller than the visible light wavelengths, and can be seen with a microscope only when fluorescently tagged. In fact, there are about 100 million 0.2-micrometer bacteria in every liter of seawater, at all depths and latitudes. Multiplying by the number of liters of water in the ocean, we estimate that there are 10,000,000,000,000,000,000,000,000,000 bacteria in the ocean, making them arguably the most abundant organisms on Earth.

Nonphotosynthetic bacteria are major consumers of energy and materials in the sea.

The presence of large numbers of bacteria everywhere in ocean water and their ability to use many sorts of particulate and dissolved organic materials has a major impact on the way materials and food energy move through the ocean. Bacteria cannot consume solid food, but must absorb organic materials from seawater, their surrounding solution. Dissolved organic materials are released into seawater by phytoplankton, protozoans, and zooplankton. Marine bacteria can remove useful compounds that are present in concentrations as low as a few billionths of a gram per liter. Bacteria also have enzymes on their cell surfaces capable of digesting solid organic materials and breaking down proteins into amino acids and complex carbohydrates into simple ones. So although they cannot ingest whole organic particles, they can externally digest them in this manner, making them available in a soluble form. Any nonliving particle in the ocean, for example, a zooplankton fecal pellet, is quickly colonized by relatively large, fast-growing bacteria that digest much of the particle, releasing dissolved organic compounds into the surrounding water for use. Small organic particles in the ocean probably have an average lifetime of a few days before they are digested by bacteria.

Many kinds of particles fall through the ocean, from dead whales to dust blown from continental deserts. Large objects that fall at a rate faster than approximately 100 meters per day may pass through the water without being digested by bacteria. Not only do whales and large fishes fall to the bottom; so do fecal pellets of the larger zooplankton, and some of the larger phytoplankton at the end of a North Atlantic spring bloom. But most animals that die in the sea, and the majority of fecal materials they produced when they were alive, are so small that they fall slowly through the water and are digested by bacteria before

Although it can fix nitrogen, Trichodesmium *runs out of other essential nutrients and dies, producing these rafts of detritus.*

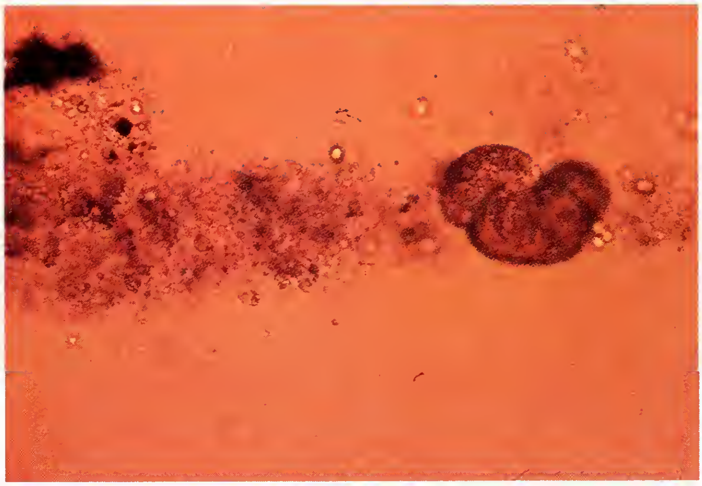
reaching bottom. Most never fall beyond the upper, wind-mixed 100 or so meters of the ocean. This is bad news for our atmosphere, because it means that relatively little organic carbon is carried to the deep ocean sediments to help remove carbon dioxide from the atmosphere. But it is good news for the phytoplankton and blue-green bacteria that depend on continuous nitrogen and phosphorus supplies. Protozoans feeding on bacteria and the smallest phytoplankton are recycling nitrogen and phosphorus that might otherwise be lost with particles falling to the deep ocean, where there is no sunlight and therefore no photosynthesis.

Putting Small Particles into Larger Packages

Bacteria not only digest organic particles in the sea; they also help create more particles. Many bacteria secrete sticky polymers, probably to help them concentrate very dilute substances from seawater. These sticky, mucuslike polymers work in concert with small eddies in ocean water to aggregate bacteria and other water particles. These aggregates are also called marine snow, because to a diver they look like snowflakes. You can see them in most television productions featuring undersea photography. In marine snow we find everything in the sea: pollen, smokestack soot, all sorts of inorganic particles carried from land by winds, as well as zooplankton remnants, living and dead phytoplankton, living bacteria, and protozoans. Like the smaller fecal particles that become aggregated with everything else, the aggregates are largely digested in a matter of days by the bacteria living in them. We see a continual formation and digestion of particles, mostly to the benefit of bacteria and their protozoan predators. Farooq Azam (Scripps Institution of Oceanography) suggests that this aggregation-digestion sequence is an important part of the microbial food web, because it facilitates the conversion of particulate organic matter to dissolved organic matter that bacteria can use, and at the same time produces larger aggregates that zooplankton can consume.

In shallow coastal waters, where large seaweeds and terrestrial plant materials are abundant, we see a variation of this process in which both wave action and invertebrate feeding activities grind large plants into fine detritus that bacteria then colonize. Duplicating this process in the laboratory, Bopaiah Biddanda (now at the University of Texas) found that detritus particles were quickly embedded in aggregates of bacteria and their polymers and were digested in the usual two or three days. In coastal waters, where this detrital soup is thick enough to be an important nutrition source, we find a number of invertebrates and fishes whose feeding methods are specialized to capture detritus with filtering devices. The microorganisms living on and within the detritus particles are probably an important part of that nutrition, because they are far richer in protein than is the detritus itself. This is one of the connections between the food webs of macroorganisms and microorganisms. Nevertheless, because they can grow rapidly when conditions are favorable, bacteria probably digest most of the detritus before detritus-feeding animals find it. Using filters to feed off the microbial food web can be a successful way of life for mullet or marine worms, but it is not efficient for transfering energy out of the microbial loop.

Another link between the micro and macro food webs was discovered recently in major coastal upwellings off the west coasts of North and South America and Africa: Water rising from a depth of several hundred meters is rich in nitrate and supports dense blooms of phytoplankton. Using a combination of observations, experiments, and mathematical modeling, Suzanne Painting (University of Cape Town) found that although the upwellings are highly productive for phytoplankton, individual pulses of upwelled water become nitrate-depleted after several weeks. When the nitrate supply diminishes, phytoplankton growth tapers off, before zooplankton in the upwelling have had time to complete a life cycle. The zooplankton must then change their diets to something similar in size, completing production of their eggs and juveniles by eating ciliates that have also become abundant by feeding on the smaller phytoplankton in the upwelled water. This kind of diet switching, linking the food webs of protozoa and the larger zooplankton, is probably more common than we realize.



Scatology can be colorful. These are the fecal ribbons of salps, zooplankton that use fine filters to remove just about everything from the water. The Mickey Mouse hat in the center is pine pollen that fell into the sea 70 miles east of Jacksonville, Florida, and the black spots are probably smokestack soot.

Linking microbial biomass production to the zooplankton food web may suggest that microorganisms are major contributors to the productivity of fishes, but there is evidence to the contrary. Now that the production rates for nonphotosynthetic bacteria and Protozoa have been measured in many parts of the ocean, it appears that microorganisms, especially bacteria, are in one way or another consuming a large fraction of the sea's total photosynthetic production. Moreover, microbial respiratory rate measurements suggest that most of that production is lost in the microbial loop, destined never to feed fishes. Surprising as it may seem, bacteria appear to be competing successfully with zooplankton for a number of food sources that either could use. This is because bacteria as a group have potentially short generation times and great versatility in utilizing many food sources: They can use a suddenly appearing resource before the zooplankton can increase their numbers enough to compete for it.

Limits to Microbial Growth

If bacteria are so swift and versatile, how do larger, slower-growing organisms manage to compete at all?

Realizing that bacteria are present in their billions everywhere in the ocean and are rapid-response experts leads us to ask another question: If bacteria are so swift and versatile, how do larger, slower-growing organisms manage to compete at all? Microbiologists have long held to a dogma of "microbial infallibility." Bacteria are said to be able to digest any organic compound and acclimate to any temperature. Indeed, what various bacteria can do is impressive. Bacteria growing at temperatures greater than 100°C are the basis of the thermal-vent food web on the seafloor; bacteria also thrive in sea ice. But every dogma has its day, and then is challenged. Questions about microbial infallibility are now beginning to emerge. We know that some new synthetic plastics and organic materials created in the laboratory give bacteria digestive problems, and we have surprising evidence that there are some temperature problems bacteria have not solved. W.J. Wiebe (University of Georgia) finds that bacteria's ability to utilize extremely dilute solutions of organic materials in the ocean is temperature dependent. At the lowest temperature they normally experience, all bacteria tested so far can grow and respire rapidly only when usable dissolved organic materials are in higher concentrations than are ordinarily found in seawater. This means that bacteria's dominance of available food sources in ocean water diminishes in winter. Although we do not yet fully understand why bacteria have this limitation, we find that their activities in the ocean are often regulated by a combination of low temperature and low dissolved-organic-material concentrations. This provides windows of opportunity for both zooplankton and invertebrates on the ocean's bottom. During early spring, when many of them are preparing to reproduce, bottom-dwelling zooplankton, worms, molluscs, and crabs may get a more leisurely and copious meal before bacteria move in to clean up the scraps.

It is also remarkable that in spite of their potential to reproduce rapidly (sometimes doubling in an hour), the number of bacteria in ocean water everywhere varies by less that a factor of 100. Why are their numbers so constant? We have some clues. One is the presence of hundreds of thousands of Protozoa in every liter of seawater, and their ability to reproduce almost as quickly as bacteria. Tom Fenchel (Aarhus University) has shown that protozoans can control a burst in bacterial growth by grazing it down. Another fate of marine bacteria is to be infected by a fatal virus. Ø. Bergh and colleagues (University of Bergen), Lita Proctor (UCLA), and Jed Fuhrman (University of Southern California) found that viruses are abundant in seawater, and some specifically infect bacteria. If the numbers of bacteria rise much above a trillion per liter, viral epidemics may reduce their numbers. These feedback controls within the microbial loop help maintain its stability.

Recognition of the impact of microbial activities on the movement of energy and materials in the ocean is so recent that we have not yet fully appreciated its significance. Because of their rapid growth and versatility, microorganisms could become important components of aquaculture systems and not just the source of infections and other problems, as they are today. At present microorganisms provide our best strategy for cleaning up oil spills without secondary damage to the ecosystem. Will people ever use them directly as a food source? Perhaps, but for now it is easier—and more enjoyable—to be at the top of the food web.

The microbial food web is composed of very small and often delicate organisms that must be studied at sea as soon as they are collected. Oceanographic ships have laboratories that can be equipped to study the microbiology and biochemistry of these microorganisms. The group above is working aboard R/V Cape Hatteras *(Duke University/University of North Carolina).*

Larry Pomeroy began at the top of the ocean's food chain as a commercial fisherman in the Gulf of Mexico and spent the following 50 years working his way down to the bacteria. He is Alumni Foundation Professor of Zoology and Marine Sciences Emeritus at the University of Georgia and is a recipient of the G.E. Hutchinson Medal of the American Society of Limnology and Oceanography and the A.G. Huntsman Medal of the Bedford Institute of Oceanography.

What Limits Phytoplankton Growth?

Sallie W. Chisholm

This entire cycle of biosynthesis and regeneration is collectively referred to as the "biological pump."

Without phytoplankton there would be no life to speak of in the open sea. These microscopic unicellular plants form the base of the marine food web, fueling all of the higher organisms with the products of their photosynthesis. On a global scale, annual phytoplankton photosynthesis is roughly equivalent to that of plants and trees on land, even though their total biomass is only 0.2 percent of that of terrestrial plants. How is this possible? Phytoplankton grow very fast. They can double their biomass on the order of days, whereas it takes land plants months to years.

Phytoplankton: The Living Carbon Pump

Nearly all of the organic carbon produced through phytoplankton photosynthesis, known as "primary production," is consumed, oxidized, and regenerated back to carbon dioxide as it passes through the food web. In the open ocean, roughly 90 percent of this regeneration occurs in the sunlit surface waters. Here the wind-driven "mixed layer" is in equilibrium with the atmosphere, and the regenerated carbon dioxide escapes from the surface waters. Organic matter not consumed by herbivores at the surface settles slowly to the deep ocean in the form of dead particulate material. These amorphous blobs of organic carbon are colonized and slowly degraded to carbon dioxide by bacteria and other microorganisms as they descend to the ocean floor. Oxygen is consumed in the process. This entire cycle of biosynthesis and regeneration is collectively referred to as the "biological pump."

The pump serves to concentrate carbon dioxide in the deep sea, where it is isolated from the atmosphere for decades to centuries. Only through global ocean circulation, in which surface waters sink in some areas, and drive deep water to the surface in others (see *Oceanus*, Summer 1992), does this carbon dioxide eventually come back into contact with the atmosphere and reequilibrate. Meanwhile, the deep ocean serves as a massive reservoir of concentrated carbon dioxide. If the biological pump were to shut off tomorrow—if phytoplankton ceased to exist—the deep-sea reservoir of carbon dioxide would eventually equilibrate with the atmosphere, tripling the atmospheric carbon dioxide content and altering Earth's climate through the greenhouse effect.

Diatom and cyanobacteria images by T. Villareal/Smithsonian CCRE

There are thousands of phytoplankton species. They most often occur as single cells, ranging from 0.6 to 500 micrometers in diameter, but some form chains and colonies. These diatoms, Thalassiosira *(top left) and* Ethnodiscus *(top right), have ornate cell walls of amorphous silicon. The lower photos show cyanobacteria (blue-green algae), the only phytoplankton that can satisfy their nitrogen requirement using nitrogen gas, which is very abundant in the oceans. Other phytoplankton must acquire nitrogen in forms such as nitrate and ammonium, which occur in limiting quantities in surface waters.* Trichodesmium *(bottom left), a colonial form, can be seen with the naked eye and looks like tufts of sawdust floating through crystal-clear waters in places like the Caribbean (see photo on page 32).* Richelia *(bottom right) lives as a symbiont inside the diatom* Rhizosolenia, *and shares some of its nitrogen with its host. It is not clear what* Richelia *gets in return—perhaps other nutrients such as iron or phosphorus, or simply flotation.*

Thus understanding how phytoplankton growth is regulated is essential for building predictive models of the global carbon cycle, and for understanding how life in the oceans would respond to changes in global ocean circulation patterns induced by climate change. It is also of central importance for understanding and predicting world fish production. Almost all fish, be they herbivores or top predators, have their origins in phytoplankton.

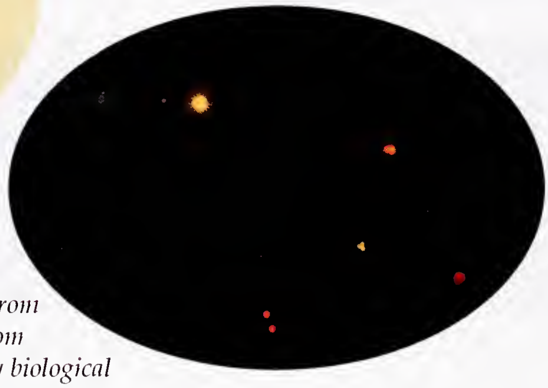
Light and Nutrients: The Driving Forces

Phytoplankton, like land plants, require light and inorganic nutrients, particularly nitrogen and phosphorus, to grow and reproduce. With a few exceptions (noted below), all other nutrients are available in excess supply in ocean-surface waters relative to the availability of these two elements and the cells' requirements. Light attenuates exponentially with depth in natural waters. Thus, since phytoplankton cannot grow at less than 1 percent of full sunlight, they are restricted to the upper 200 meters of the ocean. Essentially all life in the sea is fueled by processes in this thin layer that represents less than 5 percent of the total ocean volume.

Since phytoplankton are free floating ("plankton" is from the Greek *planktos*, meaning "drifting") and generally denser than water, their need to remain in surface waters poses a problem of positioning. Some can regulate their buoyancy or swim, but on average the phytoplankton community tends to sink. Conveniently, solar heating of the top "mixed" layer sets up a temperature gradient, the thermocline, that (along with prevailing salinity gradients) effectively isolates the top few hundred meters from the thousands of meters below. The wind-driven mixing of this top layer serves to keep the phytoplankton suspended in the life-sustaining sunlit zone, where they grow and reproduce by dividing in half. Ultimately they meet their fate as food for zooplankton and other organisms higher up in the food web.

Thermocline depth is dynamic, shoaling when solar irradiation is high, and deepening when wind sheer and surface cooling is sufficient to

In terms of numerical abundance, the tiny cyanobacteria (prokaryotic phytoplankton) dominate the seas. A typical sample from the open ocean contains over 100,000 cells per milliliter. These cells are so small (less than 1 micron in diameter) that they were unrecognizable until epifluorescence microscopy became available. With this type of illumination, the chlorophyll in the cells fluoresces red, and the accessory pigment, phycoerythrin, fluoresces yellow and orange.



Two types of cyanobacteria are shown here, Prochlorococcus *(red) and* Synechococcus *(yellow and orange). Measurements of phytoplankton fluorescence, either collected from pumped samples at sea or sensed remotely from airplanes using lasers, are commonly used by biological oceanographers as a measure of total phytoplankton biomass.*

erode it. When it is shallow, as in temperate-latitude summer, the collective phytoplankton community is never limited by light. Although the cells may be stressed by low light when they are swept to the bottom of the mixed layer, they spend sufficient time near the surface to assimilate energy for growth. In winter, however, strong winds and diminished solar heating drive the thermocline—and phytoplankton—to depths where light is extremely low. On average, there is no net phytoplankton growth or production: Organic carbon the phytoplankton produce through photosynthesis is consumed by their respiration.

Thermocline depth also regulates the nutrient supply to the phytoplankton. The biological pump depletes nutrients in the surface waters and concentrates them at depth throughout the oceans. The barrier to mixing set up by the thermocline greatly impairs the return flux of these nutrients to the surface; thus much, and sometimes most, of the primary production is driven by nutrients regenerated in the surface waters through zooplankton grazing and bacterial action. This fraction of the production maintains the biological pump, rotating through the tightly balanced cycle of production and consumption in the surface waters, but it does not contribute to net community production. That is, it does not deliver carbon to the deep sea or export it from the local ecosystem as fish production. Only the supply of "new" nutrients from deep waters can drive net community production in any given ocean province.

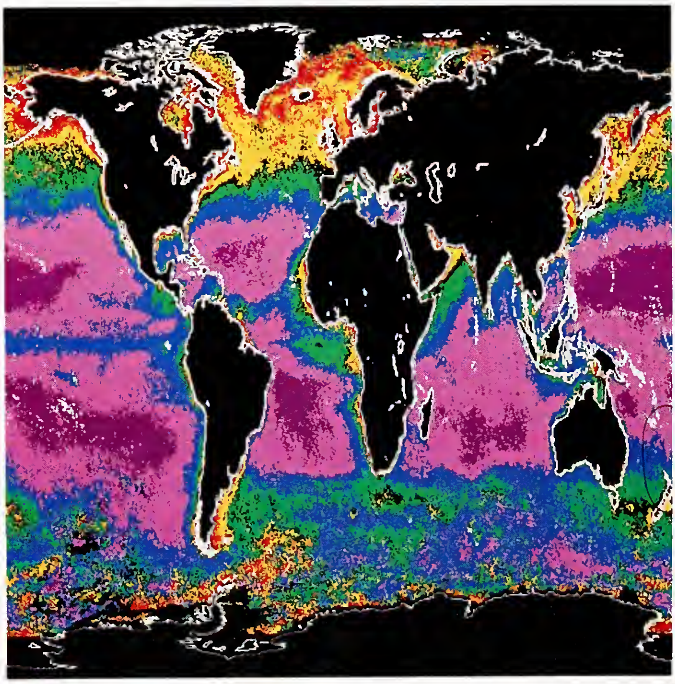
Three major mechanisms supply nutrient-rich deep waters to the surface, and they define the major biogeochemical provinces of the oceans: 1) In the vast central gyres of the Atlantic and Pacific, the only means of nutrient replenishment to the surface is slow diffusion across the thermocline. Net community production is less than 10 percent of total production in these stable ocean deserts.

2) In the more physically dynamic areas, such as temperate and subarctic seas, periodic wind-driven mixing events deepen the thermocline and entrain nutrients from below. This generates seasonal cycles of high production, characterized by dramatic spring blooms, which are an expression of the joint actions of light and nutrients on regulating production.
3) Finally, in some of the most productive areas of the oceans, the homes of some of the world's greatest fisheries, nutrient-laden water ascends to the surface through upwelling. The driving forces of upwelling are prevailing winds along the western edges of continents and in the Indian Ocean, and diverging major surface currents in the equatorial Pacific and the Southern oceans.

Thus phytoplankton can only grow in surface waters where light is abundant, yet the nutrients they require exist in abundance only in the dark, deep sea. This apparent conflict is actually a highly tuned regulatory valve in the machinery of the biological pump. Consider, for example, the rough equivalence of the depth of the mixed layer and the euphotic zone throughout the world's oceans, the latter defined by the phytoplankton's capacity for photosynthesis. Not surprisingly, phytoplankton photosynthesis has evolved to function optimally over the range of light intensities imposed by the physics of their environment: A simple case of adaptation and natural selection. The interaction is not completely one way, however, for in some situations the absorption of light energy by phytoplankton pigments can actually influence the heat distribution in the surface waters, reinforcing the stratification that keeps the phytoplankton in the surface layer.

In the relationship between phytoplankton and the major plant nutrients, we find an even more intimate connection. The phytoplankton and the distributions of dissolved nutrients in the sea have "coevolved" over three billion years to the extent that life processes—the biochemistry of the sea—have molded the chemistry of the oceans and atmosphere. We owe our appreciation of this relationship in large part to Alfred C. Redfield, a Harvard professor and Woods Hole Oceanographic Institution scientist in the early part of this century.

False color imagery from a seven-year average of satellite pictures reveals the major biogeochemical provinces of the oceans. The areas of lowest phytoplankton biomass, the huge central gyres, are shown in pink and purple. The areas of highest biomass, upwelling areas and areas where seasonal winds deliver nutrients to the surface, are indicated by the red, orange, and yellow tones. Blue and green indicate areas of moderate phytoplankton crops, some of which contain unutilized nutrients.



Redfield's Vision

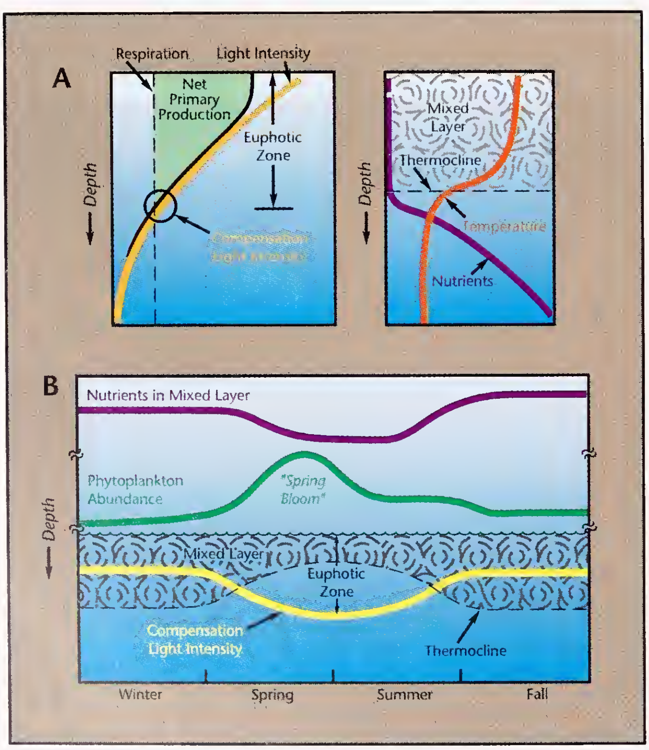
In several visionary papers, the first written in 1934, Redfield laid out (with enviable clarity) a novel view of the ocean ecosystem. He observed that unlike the major ions in seawater, which occur in roughly the same proportions in the different oceans, the essential nutrients involved in the "biochemical cycle," primarily nitrogen and phosphorus, differ greatly in their abundance from place to place. He concluded that there "must be a biochemical circulation which is different from, though dependent upon, the physical circulation of the water. The presumptive agency of fractionation which separates the biochemical from the inactive elements in sea water is the selective absorption of the former in the synthesis of protoplasm near the surface, followed by the sinking of the [organic] matter to greater depths prior to its decomposition." The "agency of fractionation" that so intrigued Redfield is precisely the "biological pump" discussed above.

In formulating his hypothesis, Redfield engaged in the following armchair experiment: Imagine taking a sample of water from the deep sea, containing its characteristic quantities of nutrients, bottling it, and bringing it to the surface where it can be bathed in sunlight and seeded with phytoplankton. Through photosynthesis, phytoplankton will convert available carbon dioxide into organic matter until the nitrogen and phosphorus are used up, and the oxygen in the sample will equilibrate with the atmosphere, its solubility determined by the prevailing temperature and salinity in the surface water. If we then take the sample

Light and Mixing

Now the question is: Why is summer, which on land uniformly represents a production maximum, plankton poor, and why are spring and autumn, which represent transitional times on land, plankton rich?

—*Theodor Buse, 1915*



Jack Cook/WHOI Graphics

Light intensity attenuates exponentially with depth in the ocean, and phytoplankton photosynthesis decreases with decreasing light intensity; respiration is independent of light. Thus at some depth the two become equal, and below this there is no net production. The depth at which photosynthesis is equal to respiration marks the bottom of the *euphotic zone*, and the light intensity at this depth is called the *compensation light intensity*.

The upper productive layers of the oceans are isolated from the deep water by the sharp density gradient set up by the thermocline as shown in A (top). The top of the thermocline marks the bottom of the *mixed layer*—the depth to which phytoplankton can be carried by the wind-driven mixing at the surface.

When the mixed-layer depth is shallower than the bottom of the euphotic zone as in B (left bottom), photosynthesis always exceeds respiration and there is net production. When it is much deeper, as in winter, the low average light intensity experienced by the phytoplankton prohibits net production. This dynamic, combined with the entrainment of nutrients into the surface waters through deep mixing, results in the "spring bloom" of phytoplankton typically observed in temperate seas.

and place it back in the deep sea, and if the biogeochemical cycle is operating in perfect balance, we should find that the oxygen in the sample is precisely enough to completely oxidize all of the organic matter back to carbon dioxide, nitrogen, and phosphorus.

Albert Redfield, left, and H.P. Smith work in the lower lab of R/V Atlantis *in the 1930s.*

Redfield supplied compelling evidence in support of his theory. He first noted that the elemental composition of plankton "protoplasm" is relatively invariable, containing 106 carbon(C) atoms and 16 nitrogen (N) atoms for every phosphorus (P) atom, and calculated that it would take 276 atoms of oxygen to completely oxidize (regenerate) organic matter of this composition back to carbon dioxide, inorganic nitrogen, and phosphorus. These proportions—106C:16N:1P, minus 276 oxygen atoms—have become known as the "Redfield Ratio." Redfield reasoned that the amounts of dissolved carbon, nitrogen, and phosphorus in seawater, known to vary enormously in absolute concentration, should vary *in constant proportion* from place to place. Furthermore, he argued, if indeed the biology is controlling the chemistry, the ratios of change in their concentration in seawater ought to be 106C:16N:1P. Finally, he maintained, the difference in oxygen concentration between the surface waters and the oxygen minimum layer, which represents the oxygen consumed in the regenerative process, should also vary in the calculated proportion.

Compiling data on the chemical composition of seawater from numerous expeditions in the Atlantic, Indian, and Pacific oceans, Redfield was able to demonstrate that indeed, the ratios of the inorganic

Photosynthesis: Life From the Sun

The products of *photosynthesis* are the source of energy for nearly all for life on Earth. Through this process, land plants and phytoplankton convert the sun's energy to chemical energy. The net reaction is:

$$6CO_2 + 12H_2O \xrightarrow{\text{chlorophyll \& sunlight}} 6O_2 + C_6H_{12}O_6 + 6H_2O$$

$6CO_2$ carbon dioxide + $12H_2O$ water → $6O_2$ oxygen + $C_6H_{12}O_6$ glucose (sugar) + $6H_2O$ water

The reverse of this reaction is *respiration*, a process carried out by all organisms, plants, bacteria, and humans alike, that live in environments where molecular oxygen is present. Energy is released in respiration, and this energy drives the biochemical reactions that constitute living systems.

Fueled by solar energy, the balanced cycle of photosynthesis and respiration is the driving force of nearly all life on Earth.

elements C:N:P dissolved in seawater were remarkably similar to the ratios of these elements in the plankton themselves. Also, the oxygen consumed between the surface and the deep ocean varied, with some interesting exceptions, in accordance with the Redfield Ratio over vast oceanic regions. Master of understatement, Redfield concluded: "That compounds of such great importance in the synthesis of living matter are so exactly balanced in the marine environment is a unique fact and one which calls for some explanation, if it is not to be regarded as a mere coincidence." In subsequent papers, he went on to argue quite convincingly that the only way this exact balance could have come about is through the biochemical regulation of the chemistry of the sea.

When people unfamiliar with life in the oceans ask me what I study, I always prepare myself for a familiar response to my answer. As I unveil the wonders of phytoplankton—their diversity and beauty, their profound importance in marine ecosystems, and their pivotal role in the global carbon cycle—I watch people's expressions evolve from bemused interest to masked skepticism. "Surely she is blowing this out of proportion," I hear them thinking, "These little things couldn't possibly be that important or I would have heard about this before." Sensing their skepticism, I grope for ways to find familiar common ground. I tell them that phytoplankton are the same organisms that form the green algal scums on ponds in late summer. This makes matters worse. "How can they be good for the oceans and bad for ponds?" they ask, clearly frustrated and losing interest. I explain that they are "good" when they exist in the context of a balanced food web, but some of them can go "bad" when the web is knocked out of harmony by natural or, most likely, human disturbance. I can see that this resonates a little bit, but by this time I have lost my credible edge. My audience either politely changes the topic, or finds an excuse to move on. I am left with a feeling of opportunity lost—and the rather absurd sensation that I have let my phytoplankton down…This article is an attempt to make it up to all of you.

—SWC

Exceptions to Redfield's Rules

Redfield's "rules" are not, of course, always precisely obeyed. In particular, in many areas of the deep ocean the oxygen consumed in the regenerative process does not conform tightly to the ratio16N:1P, minus 276 oxygen atoms. But this does not negate the theory; it simply means that the biology and chemistry of the oceans, though tightly coupled, are not perfectly balanced on a global scale. The places where the system is out of balance not only provide us with insights into the regulation of phytoplankton production, but they are of profound significance in the context of geoengineering, the (hypothetical) deliberate intervention in Earth's biogeochemical cycles.

Of particular interest are areas where nitrogen and phosphorus concentrations in the deep ocean are high relative to the amount of oxygen consumed in the regeneration process. Recall from our armchair experiment that this could only occur if some fraction of the nutrients in these waters did not originate from remineralization of organic matter produced at the surface. So where do these "preformed nutrients" come from? To answer this question we have to consider the global circulation of the oceans.

Global Ocean Circulation

Earth's ocean basins are connected through a large circulation pattern that functions, metaphorically speaking, like a conveyer belt. The belt is driven by density differences between water masses that originate from uneven distributions of heat and salinity in the oceans. About half of the water in the deep sea originates from the sinking of cold, salty surface water in the North Atlantic. For reasons that are not yet clear, this water has not been completely stripped of nitrogen and phosphorus by the phytoplankton before it sinks—hence the term "preformed nutrients." This North Atlantic Deep Water wanders slowly southward toward the Southern Ocean surrounding Antarctica. Here, some of it mixes with the local deep water, upwells to the surface where it is cooled and oxygenated, and sinks again—still rich in nutrients. A portion of the collective deep Antarctic water travels directly north and east along the ocean bottom to the Indian and Pacific oceans, while the remainder takes an excursion around the Antarctic continent before beginning its northwestward journey. On their way, these water masses collect a rain of organic matter, produced by photosynthesis at the surface, and periodically upwell to join the surface waters that are on a compensating westward journey. This is a long, slow process. It would take thousands of years to make the entire journey.

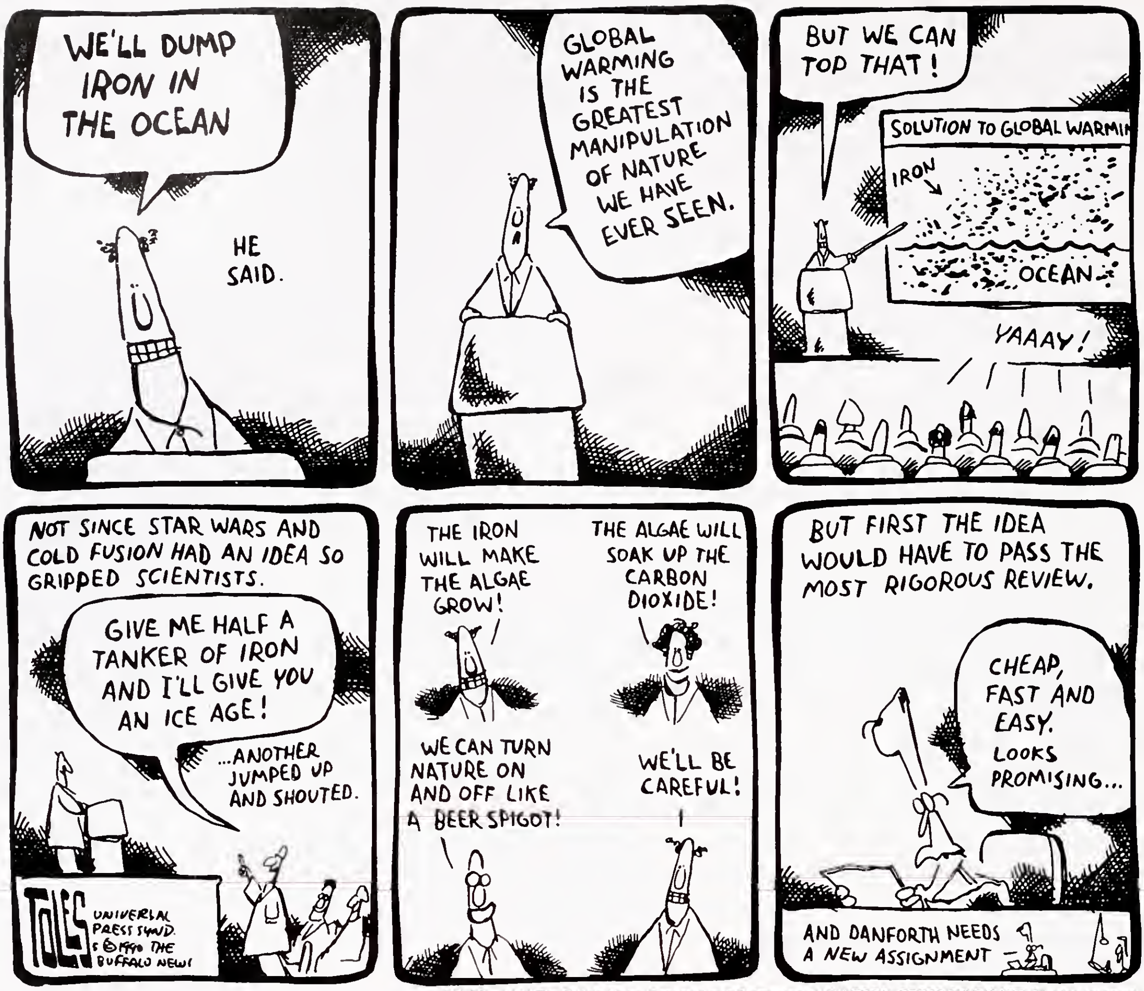
But to get back to our original question—Where do the preformed nutrients that generate "anomalous" Redfield Ratios come from?—they come from surface waters in which the nutrients are not completely assimilated by phytoplankton before the water sinks out of the sun-bathed zone. But what limits the phytoplankton in these waters? Why is the biological pump operating at less than optimal efficiency? Why can't the phytoplankton draw down the nutrients completely, as they can in other regions? This is a noteworthy question in terms of the global carbon cycle, for if the pump could be made to operate more efficiently in these areas, the flux of carbon to the deep sea could, in theory, be enhanced. This has not escaped the attention of those who see geoengineering as a valid option for reversing the anthropogenic disturbances we have imposed on the global carbon cycle. For reasons that will become clear in a moment, the Southern Ocean in particular has become the focus of much attention, and controversy, in this regard.

Why is the biological pump operating at less than optimal efficiency? Why can't the phytoplankton draw down the nutrients completely?

Iron and the Southern Ocean

The Southern Ocean, which surrounds the antarctic continent, comprises 10 percent of the world's ocean surface and contains the largest reservoir of unutilized nutrients in the surface waters of the sea. Although light availability is highly seasonal, in summer the daily supply of sunlight is equal to that in the tropics. And although temperatures are low, the species that thrive there can grow as fast as their tropical counterparts. Thus it is unlikely that temperature and light supply to the surface alone are preventing the phytoplankton from exhausting the nutrient supply.

Several years ago a new hypothesis was put forward by John Martin (Moss Landing Marine Laboratory). Martin, who had been studying iron distribution in the sea for some years, noticed that iron concentrations were extremely low in areas far removed from the continents. He deduced that most of the iron needs of phytoplankton in the open ocean had to be supplied from the surface, through atmospheric dust input. He also noticed that this input was minimal around the Antarctic. He hypothesized that phytoplankton growth in the Southern Ocean, and other nutrient-rich areas of the open sea, such as the equatorial and subarctic Pacific, were limited by iron.



To test this hypothesis, Martin and his colleagues launched an expedition to the Antarctic. There they added small amounts of iron to bottles containing seawater and incubated them at ambient sunlight to see if the iron would stimulate growth. Although this sounds like a relatively easy experiment, ships ooze iron out of every pore and it is extremely difficult to collect a sample, handle it, and place it in a bottle without contaminating it with iron. The only credible result from these types of experiments are positive results, for if one doesn't see growth stimulation in the experimental bottles relative to the controls, critics will always argue (and rightfully so) that the samples were inadvertently contaminated and were not iron-limited to begin with. But Martin's team and several others have now repeatedly demonstrated that when you add iron to bottles of water collected from the Southern Ocean, phytoplankton bloom. In doing so, they draw down the major nutrients, nitrogen and phosphorus, to essentially zero. In terms of the Redfield Ratio, for every 0.005 atoms of iron (Fe) supplied, one atom of phosphorus, 16 of nitrogen, and 106 of carbon are assimilated into organic matter. Thus the "new and improved" Redfield Ratio is 106C:16N:1P:0.005Fe, minus 276 oxygen atoms.

Martin has also shown that iron stimulates phytoplankton production in the equatorial areas and subarctic Pacific, but the Southern Ocean is the largest nutrient-rich area of the sea, and more importantly, it is the only one of the three where surface waters sink and are isolated from the atmosphere for hundreds of years. Thus if nitrogen and phosphorus were completely converted to organic matter in the surface waters before they sank, significantly increased amounts of carbon would be delivered to the deep sea. It didn't take Martin long to realize that if the iron hypothesis were correct, it would take relatively small amounts of iron—roughly 300,000 tons—to relieve the iron limitation in the surface waters of the entire Southern Ocean. "Give me a half-tanker of iron," he said only half-jokingly, "and I'll give you an ice age"—referring to the relationship between atmospheric carbon dioxide concentration and global climate.

Martin's hypothesis has catalyzed four years of intensive controversy and research on the ecology of the Southern Ocean, and other nutrient-rich seas, and most scientists are now convinced that iron at least plays a role in regulating production in these areas. Oceanographers are divided, however, on the issue of exactly what would happen if iron suddenly became available to Southern Ocean phytoplankton through intentional fertilization (geoengineering). It is quite possible, for example, that light limitation imposed by the deep mixed layer in this region would put an upper limit on the amount of nitrogen and phosphorus that could be assimilated by the phytoplankton, and productivity would not change dramatically. It is also likely that zooplankton grazing would keep the phytoplankton populations in check, recycling the carbon dioxide in the surface waters and thwarting the goal of carbon burial in the deep sea. We simply cannot predict with certainty at this point.

Most scientists are now convinced that iron at least plays a role in regulating production in some areas.

But even if iron were the sole limiting factor, most oceanographers do not think that massive fertilization of the Southern Ocean should be considered a viable policy option for reducing atmospheric carbon dioxide concentrations. For even the most optimistic model calculations show that its impact on the rising carbon dioxide concentrations in the atmosphere would be relatively small. These same models predict that, as a result of global ocean circulation patterns, increased productivity in the Southern Ocean would cause significant changes in the distribution of nutrients and oxygen throughout the world's oceans. Of particular concern is the prediction that oxygen would become depleted over significant regions of the deep oceans as a result of the enhanced carbon burial. Our understanding of the ocean's global "metabolism" is not adequate to predict the collective consequences of such changes.

The one thing we can predict with certainty, however, is that effective, large-scale ocean fertilization would dramatically alter the composition of the marine food web. The addition of nutrients to any phytoplankton community inevitably disturbs the delicate balance between existing species and gives a few species an exclusive competitive edge, to grow faster and dominate the others. Such changes at the base of the food web propagate rapidly through the higher trophic levels, selecting for different species of zooplankton, fish, and other marine organisms. Although we know that change would be inevitable, we cannot predict with any certainty exactly how the food web would evolve. It is a highly interdependent system with many links and cross-links; often the integrity of the entire system is maintained by a few relatively inconspicuous keystone species, and the role of these species is only unveiled after the system has been perturbed.

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It should be clear at this point that there is no simple answer to the question posed by the title of this article. Sunlight, nitrogen and phosphorus, iron, and probably other trace elements all play roles in regulating phytoplankton production; no single factor appears to exclusively limit production throughout the world's oceans. As is often the case when a simple answer eludes us, perhaps the problem is in the question itself. Perhaps we have not paid sufficient attention to Redfield's image of the oceans as a system in which the living and nonliving components are highly interdependent, having coevolved since the beginning of life on Earth. The evolution of the living components of the system is shaped by the laws of natural selection. The evolution of the nonliving components, that is, the changes in their chemical speciation and global distributions, is shaped both by life processes and geophysical forces. We need only consider the origins of the oxygen in our atmosphere to appreciate that the relative importance of life processes in this dual dynamic has grown significantly since life began. Remembering that Earth is still young, and life in the seas is constantly evolving, one cannot help but wonder if the biochemical processes in the sea will play an ever increasing role in regulating ocean chemistry as Earth matures. Perhaps at some time in the far distant future, everything, and nothing, will limit productivity in the sea.

One cannot help but wonder if the biochemical processes in the sea will play an ever increasing role in regulating ocean chemistry

Sallie W. Chisholm (who for mysterious reasons is known as "Penny" to all but the published page) is a biological oceanographer who has devoted her career to the study of phytoplankton ecology. She developed her interest in phytoplankton as an undergraduate at Skidmore College, but never saw an ocean until she went to the Scripps Institution of Oceanography for postdoctoral work. There her profound naivete about the oceans was exposed when her colleagues succeeded in convincing her that there was mail delivery at sea through a complex network of "mail buoys." Despite this, she managed to land a job at Massachusetts Institute of Technology where she is a Professor in the Civil and Environmental Engineering Department and currently serves as Director of the MIT/WHOI Joint Program in Oceanography/Applied Ocean Science and Engineering.

Biological Oceanography from a Molecular Perspective

Edward F. DeLong and Bess B. Ward

New tools are beginning to provide answers to long-standing questions about life in the sea.

Biological oceanography focuses on the abundance, variety, and distribution of life in the sea. More specifically, biological oceanographers try to understand how marine organisms and biological processes affect, and are affected by, physical, chemical, and geochemical ocean processes. Many key questions in biological oceanography were recognized very early, during the first large, multidisciplinary oceanographic cruises of the late 1800s. These problems include characterizing life in the deep sea, quantifying energy and carbon flows through marine food chains, understanding the natural history and biogeography of particular species, and determining interdependent biotic and abiotic oceanic processes.

However, some critical questions in biological oceanography remain largely unanswered, simply due to a lack of appropriate methods. For instance, even the seemingly simple task of species identification has sometimes proven difficult, especially with smaller planktonic plants, animals, and microbes. Furthermore, the relative activity and involvement of marine biota in global oceanic processes is also often difficult to assess. The ecological significance, abundance, and natural history of many marine creatures is still poorly understood, largely because these organisms have so successfully eluded the analytical nets cast by biological oceanographers. New tools, developed in molecular biology laboratories over the last several years, are now beginning to provide answers to these long-standing questions about life in the sea.

"Who's Out There ?"

Identifying and differentiating planktonic species can often be difficult, because some organisms that are genetically very different look very similar. Conversely, the juvenile and adult forms of a single species often look completely different, and so their genetic identity cannot be inferred simply from their appearance. Consequently, identifying and tracking both the larval forms of higher organisms and morphologically nondescript microbial species can be challenging. Molecular biological techniques are helping to get around some of these difficulties.

New Nucleic Acid Identification Techniques

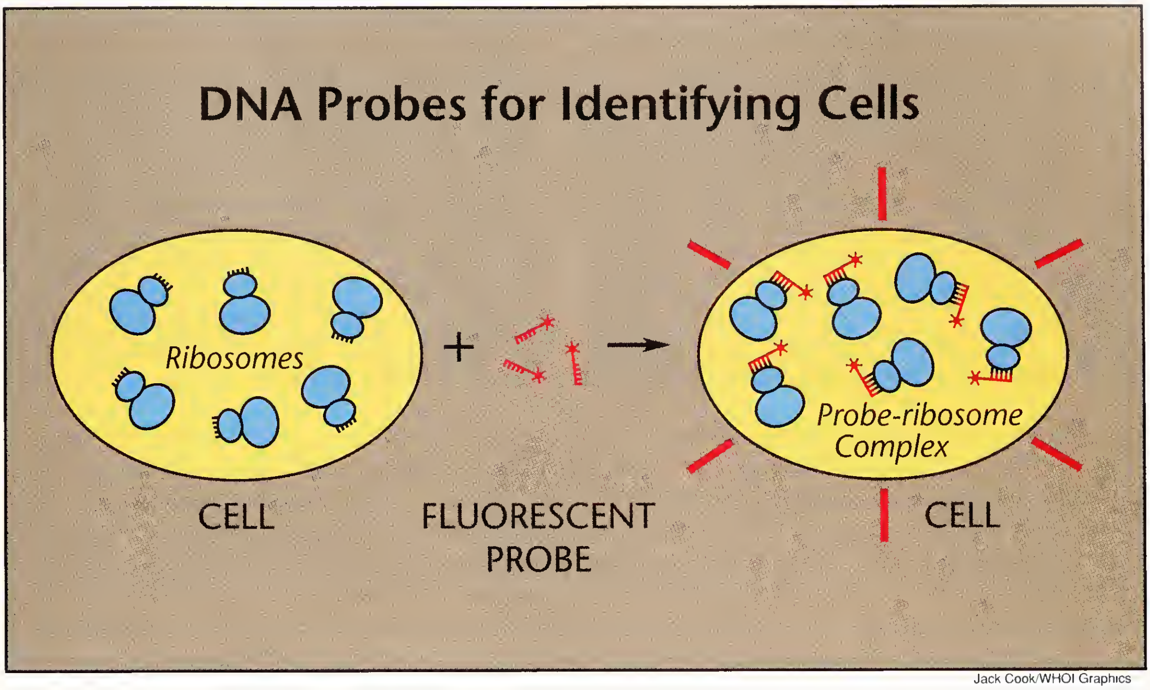
Biological oceanographers only recently (in the last 20 years or so) discovered the remarkable abundance of oceanic microorganisms (about one million per teaspoon of seawater!) and their significant metabolic activity (see The Microbial Loop, page 28). These discoveries prompted a good deal of new research, aimed at understanding the ecological role of small, single-celled plankton. However, some serious stumbling blocks have prohibited a thorough understanding of the nature and distribution of these tiny bacterioplankton (free-floating bacteria).

Traditionally, microbes are identified and described by growing them under controlled laboratory conditions. Unfortunately, most of the naturally occurring marine bacteria that we can directly count under a microscope are not easily cultured in the laboratory—microbiologists' thumbs just haven't been green enough, so only a few of the million or so microbes in each milliliter of seawater are well identified. However, the new techniques borrowed from molecular biological laboratories are changing this.

Numerically speaking, planktonic bacteria are the most abundant creatures in central-ocean surface waters. For this reason they were the first study subjects for the emerging field of "molecular ecology." In these studies, researchers took a new tack to identify the abundant bacterioplankton of the nutrient-poor central-ocean gyres: Instead of trying to isolate individual bacterial species in pure culture, they instead isolated the bacterioplankton's genetic material (deoxyribonucleic acid or DNA), which is also useful for identification purposes. Since DNA can be extracted directly from a mixed microbial population, it isn't necessary to cultivate individual microbial species.

Jack Cook/WHOI Graphics

Bacterioplankton are abundant in the ocean but very hard to isolate for study because populations are so mixed together. Instead of trying to isolate pure bacterial species, biologists can more easily isolate the bacterioplankton's genetic material (DNA). First, individual genes are isolated by cloning them into bacteria, then the DNA sequence of each gene from each organism (named A, B, C, etc. here) is obtained. The letters G,A,T, and C stand for the four nucleic acid building blocks of DNA. Once the DNA sequences are known, the genealogy of each organism can be inferred.

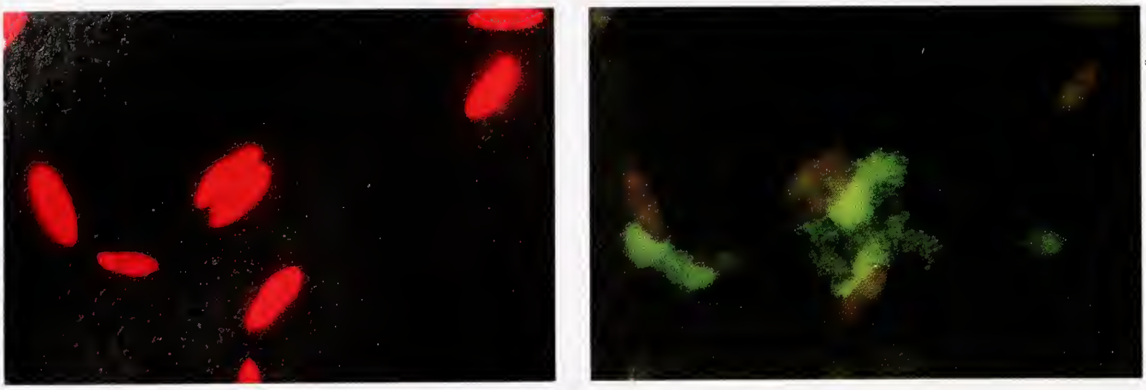


Jack Cook/WHOI Graphics

Because some genes more-or-less randomly accumulate mutational changes, their sequences can provide information about an organism's evolutionary history and genealogy. Such gene sequences were used to study complex mixed assemblages of marine bacteria. Using cloning techniques of molecular biology, a collection of genealogically informative genes was extracted from these complex marine microbial populations. By isolating the individual genes and determining their DNA sequences, it was possible to infer their genealogy, and therefore the genealogy of the specific organisms they came from. Using this method, the identity and biological characteristics of individual oceanic bacterioplankton could be inferred for the first time. Some of the most abundant microbes from open-ocean surface waters turned out to be entirely new, undescribed marine bacteria. Interestingly, comparing DNA sequences of microbes from the central northern Atlantic and Pacific oceans revealed that some of the most abundant species of planktonic bacteria from opposite sides of the globe are virtually identical.

When comparing genes of different organisms, it is possible to find "signature sequences," strings of DNA that are characteristic of certain groups or species. Taking it one step further, these signature sequences can be used as probes to identify individual cells if a fluorescent tag is applied.

New identification techniques are being developed by comparing the DNA sequences of *homologous* genes of different organisms. (Homologous genes in different organisms have identical origins and functions, but their DNA sequences are usually not identical.) It is possible to find "signature sequences" within these genes, strings of DNA sequence that are diagnostic for specific groups or species. DNA "probes" can then be designed that will bind *exclusively* to these signature sequences. The probes, when tagged with a fluorescent molecule, can even be used to identify individual cells. Probes will penetrate most microorganisms' cell walls, but will stick only to those cells that contain the correct signature sequence in their nucleic acids. In this way, individual cells of particular microbial species can be "color coded" with



E. DeLong

Identification of a marine ciliate, and the bacteria upon which it feeds. Actively growing microbial populations were fixed to microscope slides, and tested with DNA probes specific for eukaryotes (red) and bacteria (green). By exciting the samples with light of different wavelengths, the different cell types can be individually detected. Left:A marine protist (ciliate), which has bound a eukaryote-specific, fluorescently labeled (red) DNA probe. Right:The same microscopic field as at left, but showing the fluorescence from a green labeled, bacterial-specific DNA probe.

specific DNA probes, which have been linked to different colored fluorescent dyes. Though these techniques are still being developed, it is becoming possible to follow the distribution and abundance of specific marine microorganisms, even those that can't be cultured.

New Immunological Identification Techniques

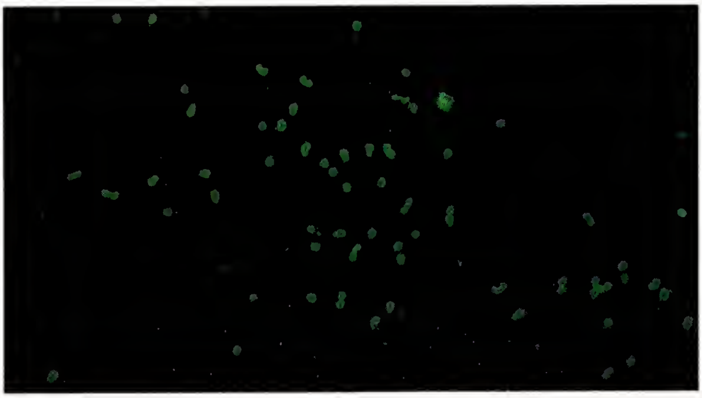
For microorganisms and planktonic larvae that can be cultured or collected in pure form in large enough quantities, immunological methods can be used to identify and count individual organisms in natural communities. The organism itself generates the antibody; it's protein components are *antigens*, substances that, when injected into mammals (usually rats or rabbits), are recognized as foreign and cause the mammalian host to produce antibodies against them. These antibodies, which bind to antigen-bearing cells, can then be used as specific probes for the organism in seawater. When tagged with fluorescent molecules, the antibodies provide another means to "color code" individual cells of particular strains of microorganisms. Immunofluorescence assays have been developed for a number of marine bacteria strains. Abundances estimated from these assays in various parts of the ocean indicate that each individual strain comprises a small part of the total bacteria, implying that natural communities are diverse assemblages of many different strains.

Immunological assays have also been used to identify the larvae of larger organisms, which are very small and look nothing like the adult organisms. Larval distributions and settling patterns can be addressed in this way. Protozoans, small planktonic organisms that often feed on bacteria and themselves play a crucial role in the food chain, have also been studied using immunological methods. They are not only small, but fragile; they disintegrate in samples intended to enumerate them, and they leave behind no hard parts in the guts of predators that consume them. Ecologists often wish to study food chains by identifying who eats whom. In the case of very small predators, or predators that prey on organisms that possess no hard parts, visually identifying gut contents is impossible. However, the prey organism's protein antigens may still be detectable in immunological assays of these gut contents.

Potential applications of molecular technologies for identification, quantitation, and study of marine-species distributions are numerous. Molecular techniques are now being successfully applied to the study of symbioses, which are very common in the marine environment. Intimate, interdependent symbiotic relationships often develop between animal and microbial species; the animal provides a protected home for the microbial symbiont within its body, and the microbe provides its animal host with essential nutrients or functions. Because it is often difficult to identify specific microbial symbionts, unraveling the life history of symbiotic relationships and mapping the distribution of microbial symbionts within and without the host can be challenging. Do microbial symbionts live freely outside their animal hosts? Are there many different types of intracellular symbionts inside one specific animal host, each with a different function? How does an animal host pass on the tiny microbial symbionts to its progeny? These types of questions are now being answered with the use of molecular probes, such as the fluorescently tagged DNA probes described above, which can be used to sensitively and specifically identify elusive microbial symbionts.

Immunofluorescent staining of a bacterium. This organism, Nitrosomonas marina, *was isolated from the Atlantic Ocean. Antibodies were raised against a pure culture of the bacteria, and these cells are visible due to the fluorescence of the antibody tag . The immunofluorescent assay has been used to enumerate* Nitrosomonas *in natural seawater, where it is present at around 10,000 to 100,000 cells per liter. This represents about 0.01 percent of the total bacterial population in seawater.*

Molecular techniques also contribute to studies of the distribution, diversity, and population biology of larger and commercially important marine organisms. One prominent technique employs the polymerase chain reaction (PCR), which allows researchers to generate large amounts of a specific gene from very small amounts of starting DNA. This is a boon to field ecologists and biological oceanographers, because often only a very few precious specimens, or an extremely small amount of material, can be retrieved after long forays at sea. It is possible, using techniques like PCR, to sacrifice only a small portion of a field-collected specimen for DNA analysis, and save the rest of the sample for other studies, such as morphological characterization or pigment analysis. PCR is particularly useful for developing assays that identify differences between closely related species, or different populations of the same species. For example, researchers are now tracking the distribution of several species of very closely related spiny lobster larvae (*Panulirus* sp.), which float freely in the plankton in their early developmental stages. Previously, the larvae of these species could not be distinguished, but PCR techniques now allow for their rapid identification, and require only the tissue from one leg of one tiny planktonic juvenile! Now it is possible to answer questions about how the distributions of different planktonic juvenile species correspond to the distribution and abundance of the respective adults. Such information is



B. Ward

useful in fisheries management, for determining the survival and recruitment of commercially important species.

Molecular techniques are also being used to study some of the ocean's largest inhabitants. For example, DNA sequencing techniques have been used to show differences between and within species of large game fish such as the blue marlin *Makaira nigricans*. These studies have identified two major evolutionary lines of blue marlin, and show that the representation of each lineage differs between the Atlantic and Pacific oceans. This information is important because Atlantic blue marlin stocks are currently considered endangered. These studies are beginning to point the way towards rational approaches for maintaining genetic diversity in commercially important species.

The examples discussed show how questions about "Who's out there?" are being addressed, using DNA and protein signatures of organisms that are otherwise difficult to identify. As these and similar methods develop, more and more information on marine-life abundance, distribution, and diversity will be obtained, increasing the scientific "payload" of oceanographic expeditions.

Molecular methods help scientists address questions about the functions and activities of marine organisms in the environment.

"What Are They Doing?"

Unlike the situation in higher organisms, knowing what the organisms are is not always enough to answer the question of how they live. For example, once you know an organism is a cat, you are safe in making certain assumptions about its lifestyle: nocturnal, carnivorous, etc. Once you know an organism is, for example, a pseudomonad (one of the most commonly isolated genera of bacteria in both terrestrial and aquatic environments), you have hardly narrowed the field at all. Pseudomonads include bacteria that require oxygen and those that can live without it, those that require nitrogenous compounds in their diet and those that can fix atmospheric nitrogen, and those that can live on sugars as a sole carbon source as well as those that subsist on "toxic" aromatic hydrocarbons. Some of the ecological characteristics that enable pseudomonads to thrive are also shared by other diverse genera. Genetic exchange occurs when genes that are carried on mobile genetic elements (such as plasmids) are transferred from one organism to another. This exchange is possible between cells of the same or of different species. Thus, bacterial species whose taxonomic positions are distant might nevertheless possess very similar metabolic characteristics. With their short generation times and vast population sizes, these bacteria have had more chances for genetic exchange over geological time than have other organisms, and thus metabolic capabilities often occur across species lines.

Molecular Probes for Function and Activity

Molecular methods also help scientists address important questions concerning the functions and activities of marine organisms in the environment. In order to understand a process, such as nitrogen fixation, photosynthesis, denitrification, or toxic-metal resistance, we must study not just the distribution of a species, but also the distribution of that species' metabolic abilities (and the genes that encode them). To determine whether a process is occurring at any particular time, one needs to detect the enzyme that performs the process or the enzyme's activity.

Since enzymes are proteins, they can be purified and used as antigens, to produce specific antibodies that can be used as probes for the enzyme. Then, without culturing or identifying individual organisms in a seawater sample, the total proteins can be purified from the sample and probed for the enzyme's presence. In the case of inducible enzymes (enzymes produced by the organism in response to a signal from the environment), the enzyme's presence is a strong indication that the process it performs was indeed occurring in the water at the time of sampling. This gives us an idea of the distribution of processes such as nitrogen fixation and denitrification without identifying organisms or making difficult rate measurements.

Alternatively, for such processes as nitrogen fixation and denitrification that are turned on in response to environmental changes, one might detect the "message" (messenger ribonucleic acid, or messenger RNA) that tells the cell when to make the proteins that catalyze that specific process. Many enzymatic reactions are regulated by the organism's sensing critical cues that result from environmental change. These cues "turn on" specific genes, by initiating the synthesis-specific "messages," messenger RNAs, that ensure production of the correct enzymes for a given process. Since messenger RNA comprises a small proportion of the cell's total nucleic acids and is degraded very rapidly, detecting the message for a particular process is difficult. However, the ability to detect this message could provide a sensitive indicator of how and when genes are turned off and on. This approach is being developed for studying photosynthesis in the surface ocean, by developing probes for the message of the enzyme ribulose bisphosphate carboxylase. This is a key enzyme in the "Calvin cycle" used by most plants, algae, and photosynthetic bacteria to convert carbon dioxide into cellular material.

The main mechanism for transfer of nitrogen from atmosphere to biosphere is nitrogen fixation. In this process organisms reduce atmospheric nitrogen to ammonia and "fix" it into cellular nitrogen. Since nitrogen is often the limiting factor to growth within an ecosystem, organisms' ability to fix nitrogen is ecologically advantageous. The opposite process, loss of fixed nitrogen from biosphere to atmosphere, occurs during anaerobic respiration of certain bacteria. Both processes are performed solely by bacteria and both are sensitive to oxygen, making their detection and measurement in natural environments difficult. The overall balance between nitrogen fixation and denitrification may control long-term, global productivity in the oceans. It is important, therefore, to determine the capability for nitrogen fixation and denitrification among marine bacteria.

Molecular probes are used to identify some of the genes involved in nitrogen fixation and denitrification.

Molecular probes are used to identify some of the genes involved in nitrogen fixation and denitrification. The nucleic acid of some key nitrogen-fixation genes has been sequenced from some more familiar nitrogen fixers, such as cyanobacteria, also known as blue-green algae. Although nitrogen-fixation genes of various organisms are homologous, they are not identical. Consequently, it hasn't been possible to use a gene cloned and sequenced from freshwater cyanobacteria as a probe for nitrogen fixation in marine cyanobacteria. To get around this problem, the PCR, discussed above can be used to generate many copies of the nitrogen-fixation genes from a marine cyanobacterium, *Trichodesmium*, and that DNA sequence then serves as a probe for nitrogen-fixation genes in marine samples. This molecular probe is being used to identify and quantify similar sequences in other organisms present in seawater samples. Thus the nitrogen fixation genes, and the potential for nitrogen fixation, can be detected in organisms that haven't been cultured, and in samples where nitrogen fixation can't be detected using other approaches.

Where To Next ?

Future applications of molecular techniques should allow researchers to cast finer-meshed research nets over broader areas.

Armed with molecular tools, biological oceanographers are now better equipped to answer some long-standing questions. Many of the examples discussed here focus on the microbial world, not only because of the authors' biases, but also because microbial studies represent some of the first successful applications. Molecular applications are not confined to studying just the very small, however, and similar techniques are currently being applied to understanding the genealogical relationships and population biology of some of the oceans largest inhabitants: dolphins, whales, and large game fish. Understanding genetic diversity in the marine environment, the distribution of different populations of the same species, and the dispersal, survival, and recruitment of larval species are goals of these studies. This information is useful for assessing environmental impact, maintaining genetic diversity, and managing fisheries. Molecular probes for function are helping to answer questions about how the activities of marine organisms vary with environmental change, and how these organisms affect major biogeochemical cycles in the sea. Future applications of molecular techniques to biological oceanography should allow researchers to cast finer-meshed research nets over broader areas, and improve our knowledge of the natural history of marine organisms, their functional and genetic diversity, and the complex interplay between biotic and abiotic processes in the world's oceans.

Ed DeLong became interested in marine processes at the age of three, when he was swept off his feet and dragged partially out to sea by a strong undertow off the northern California coast. Oceanic processes continue to engulf him. After receiving his Ph.D. at Scripps Institution of Oceanography, he spent several years as an Assistant Scientist in the Biology Department at Woods Hole Oceanographic Institution. Ed is currently an Assistant Professor of Marine Biology at the University of California, Santa Barbara.

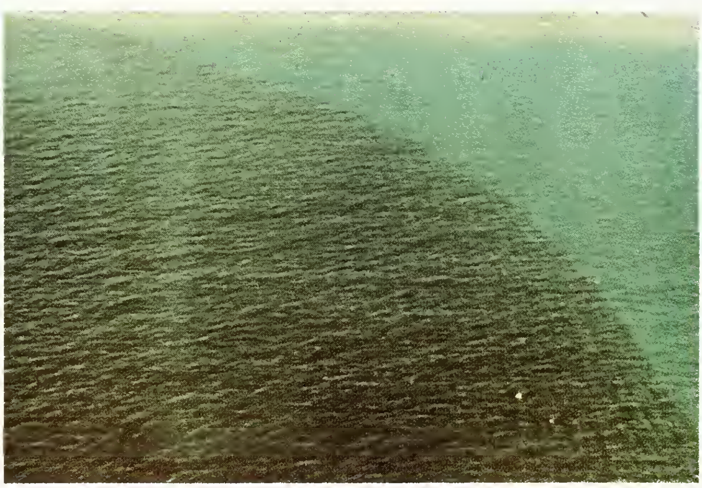
Bess Ward was a latecomer to oceanography, having had her first engulfing experience while wading fully clothed on the beach in Savannah, Georgia, at the ripe old age of 13. She was a member of the Food Chain Research Group at Scripps Institution of Oceanography for several years, and is now an Associate Professor of Marine Sciences at the University of California, Santa Cruz.

Marine Biotoxins at the Top of the Food Chain

Donald M. Anderson and Alan W. White

In November 1987, whale-watch cruise participants off Cape Cod, Massachusetts, delighted in the antics of a large humpback whale known to many as "Torch" by his tail-fluke markings. Those observing Torch's energetic feeding behavior and breaching were horrified to see him floating dead at the water surface just 90 minutes later. This was not a typical stranding, when whales (or other marine animals) swim into shallow water and die. One pilot whale and 13 other massive humpbacks (*Megaptera novaeangliae*) died at sea in a very rapid and unusual manner that mystified marine pathologists. The whales floated ashore in five weeks; other victims undoubtedly washed out to sea and were never noticed. During the previous 10 years, only three humpbacks were found by a stranding recovery network in this same area. The 1987 mortality rate thus appears to be equivalent to nearly 50 years of "typical" mortality.

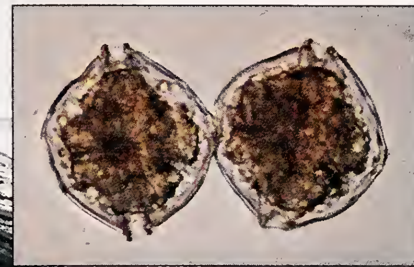
What caused this extraordinary event? No one will ever know for sure, but strong evidence indicates that the whales died from natural biotoxins originating in single-celled algae or phytoplankton. Thousands of microscopic algae species constitute the base of the marine food chain, and among these are a few dozen species that contain potent toxins. Some of these toxins accumulate in shellfish, fish, and other marine animals, and move through the food chain, affecting humans, marine mammals and other top-of-the-chain consumers. Blooms of these algae are commonly called "red tides," since in some cases these tiny plants can increase in abundance until they dominate the planktonic community, changing the water color to red, brown, or even green. Although human illness and death occur from the consumption of



Florida Marine Research Institute/Florida Department of Natural Resources

A toxic "red tide" bloom shows as the darker color in Florida waters.

Greg Early/New England Aquarium



Yasuwo Fukuyo/WESTPAC, IOC

A dead humpback whale on the shore of Massachusetts Bay. Evidence suggests that the massive animal died from an algal toxin, probably produced by the dinoflagellate Alexandrium *(small photo) accumulated by mackerel that it had eaten.*

seafood containing algal toxins, especially in developing countries, humans are usually well protected by federal and state monitoring programs that detect the toxins at an early stage and restrict harvesting or sale of the affected resources. Marine animals at the top of the food chain are not so fortunate. It is now clear that these toxins affect marine animals and seabirds in important ways that have long gone unnoticed.

Whales

The humpback whales that washed ashore in 1987 in Cape Cod Bay died suddenly at sea. Many still had fish in their stomachs, evidence of recent feeding. They had considerable blubber and seemed in good health. The pattern of the deaths prompted a search for an acutely toxic substance, but tissue analyses did not reveal unusual levels of metals, organic chemicals, or other toxic agents.

Because the whales died in waters where the red-tide dinoflagellate *Alexandrium* causes annual outbreaks of paralytic shellfish poisoning (PSP), natural biotoxins were investigated. This seemed an unlikely prospect, however, since it was November, a month when *Alexandrium* is not typically found in the region. Furthermore, throughout all of 1987, there was no PSP toxicity anywhere along the New England coast. It was thus not surprising when visual and chemical examination of plankton net-tow material from the whales' feeding area revealed no signs of *Alexandrium* cells or their toxins. However, an analysis of the mackerel that the whales had been eating revealed the presence of saxitoxin (STX), one of the PSP toxins that *Alexandrium* produces. This was an unexpected finding, in part because of the lack of PSP in the region in 1987, but also because, until then, PSP toxins were known to kill fish but not to accumulate in the tissues of living vertebrates.

Further analyses revealed that the STX was not present in the mackerel flesh, but was concentrated in the liver, kidney, and other organ tissues. Average concentrations were 52 micrograms per 100 grams of tissue, equivalent to a total body burden of 80 micrograms of STX per kilogram of fish. Most of the mackerel samples from the northeastern United States tested positive for STX, whereas Pacific Ocean mackerel tested negative. Extracts of whale kidneys, livers, and stomachs also tested positive for STX or STX-like compounds, whereas similar samples from other whales and dolphins that had died unrelated to this incident showed no such toxicity.

The implication was that the whales died by consuming STX-laden mackerel. But how much STX did the whales consume, and how much is lethal to these animals? The humpbacks had begun their migration to warmer, southern waters, and were feeding heavily, at about 4 percent of their body weight per day. Feeding on mackerel, this corresponds to a daily STX dosage of 3.2 micrograms per kilogram of whale body weight. Unfortunately, no data exist that directly address the effect this amount of toxin has on a whale. The minimum lethal STX dose for humans is estimated at 7 to 16 micrograms per kilogram, which is two to five times higher than what scientists believe the whales received.

Such a low dose might still be lethal to a whale, however. First, 30 percent of a humpback's body mass is metabolically inactive blubber, so water-soluble STX would bypass this tissue and concentrate in more physiologically sensitive areas. Second, the whales would have received continual toxin doses as they fed, whereas human mortality statistics are based on a large dose obtained at a single feeding. Furthermore, during a dive, marine mammal blood is channeled predominantly to the heart and brain (known as the mammalian diving reflex), exposing those sensitive organs to the toxin while limiting contact with the liver and kidney where metabolism and excretion would occur. Most importantly, perhaps, is that the STX need not have killed the whales directly: Even a slightly incapacitated animal might have difficulty orienting to the water surface and breathing correctly. The affected animals may actually have drowned following a sublethal exposure to STX.

These are all speculations, but the evidence is strong that these enormous animals died from a natural marine biotoxin that originates in microscopic algae, but is transmitted through the food chain to the top consumers. Many questions remain to be addressed, including how the mackerel became toxic, how they survived carrying a potentially lethal toxin dose, and why this kind of whale mortality was never observed before 1987 or thereafter. This event and the ensuing research have taught us how important it is to search for STX and other red-tide toxins when investigating marine mammal strandings and mortalities.

Evidence is strong that these enormous animals died from a natural marine biotoxin that originates in microscopic algae.

Dolphins

Another significant event that overlapped with the humpback whale deaths was a massive mortality of bottlenose dolphins (*Tursiops truncatus*). From June 1987 to February 1988, over 740 dolphins were found dead along the Atlantic coast between New Jersey and Florida. Again, undoubtedly many other dead animals drifted out to sea or were scavenged. Unlike the healthy humpbacks in Cape Cod Bay, which died quickly, most of the dead dolphins exhibited pathologies typically associated with chronic physiological stress. These observations and the temporal and spatial patterns of the dolphin deaths were not indicative of a primary infectious disease, and no known chemical pathogen was consistently isolated from dolphin tissues. Organic contaminant levels (PCBs and DDT) in some of the dead dolphins were high, but in many other dead animals the levels were within the same range as those from control (aquarium dolphin) tissues. The evidence suggested that the dolphins were dying from opportunistic infections and other causes that were only fatal because the animals were already physiologically weakened by an unknown agent.

Success in tracing the humpback whale deaths to a red-tide biotoxin suggested that a similar investigation was warranted with the dolphins. However, the geographic range of the STX-producing alga is far north of


Pat Tester/NMFS, Beaufort Laboratory


US Dept. of Agriculture

This bottlenose dolphin, washed up on Virginia Beach, Virginia, is one of approximately 750 that fell victim between 1987 and 1988 to an enormous die-off along the US coast between New Jersey and Florida. Toxin from the alga Gymnodinium breve *(small photo) may have been responsible for weakening the animal's immune system so that it eventually died from infections or other secondary causes.*

where the dolphins were dying, so attention shifted to a different red-tide alga that causes fish mortalities and shellfish toxicity predominantly along Florida's west coast. Called *Gymnodinium breve*, this alga produces a suite of toxins called brevetoxins. In the ensuing investigation, 8 of 17 dolphin livers tested positive in a rigorous set of analyses for brevetoxin-like compounds, compared to negative results for 17 control samples obtained from dolphins killed in other incidents. The only sample of dolphin stomach contents tested proved to be positive, as did viscera samples from menhaden caught where some of the mortalities occurred.

There were insufficient data to support a rigorous conclusion, and the results indicated only that brevetoxin-like compounds were present in some of the animals and their prey; however, the suggestion that brevetoxins were involved in at least some of the dolphin deaths was strong. How could the dolphins have been exposed to the toxin, especially since these mammals tend to migrate along the US Atlantic coast, whereas *G. breve* red tides occur primarily within the Gulf of Mexico? One explanation has been offered that is quite controversial among scientists familiar with the mortality event. In October 1987, a major *G. breve* red tide struck the North and South Carolina coasts, having been transported from Florida in the Gulf Stream. This places the toxic alga in waters where the dolphins were dying, but does not explain the deaths that occurred between June and October. However, from January through April of that year, a *G. breve* red tide occurred in the eastern Gulf of Mexico, and, though evidence is sketchy, traveled south, possibly around the Florida peninsula to the Atlantic coast. Menhaden, which filter plankton such as *G. breve* from the water as food, and Spanish mackerel, which are menhaden predators, were abundant in the coastal region where this bloom was presumably transported. Dolphins feeding on menhaden and Spanish mackerel could have received continuous low doses of brevetoxin as they migrated along the Atlantic coast. If this scenario is valid, the dolphins could have received brevetoxin doses that were not directly lethal, but nonetheless stressed them physiologically; the weakened animals were then eventually infected with bacterial and viral pathogens that ultimately caused the mortalities.

Evidence for this scenario is circumstantial. Other explanations are possible, but no clear alternatives have been proposed. Though unresolved, this investigation led to two important conclusions:

- brevetoxin can accumulate in planktivorous fishes and perhaps in their predators, and
- bottlenose dolphins can encounter red-tide biotoxins through the food chain.

As we write, another unusual dolphin mortality is occurring, this time in the Gulf of Mexico. Perhaps the lessons from five years ago will help unravel the mysteries surrounding yet another marine-mammal die-off.

Fish

For years algal toxins have been associated with mass mortalities of marine fish; for example, in the Gulf of Mexico, nearly annual red tides of the toxic dinoflagellate *Gymnodinium breve* cause spectacular fish kills. In this case, the fish are directly exposed to the algal toxins. When fish swim through *Gymnodinium* blooms, the fragile algae break open as they pass through the gills, releasing toxins that the gills absorb. The toxins burst the fish's red blood cells, and the fish die of asphyxiation. It is not uncommon for Florida's west-coast beaches to become covered with tons of dead fish, causing million-dollar losses to tourism and other recreation-based businesses.

Algal toxins can also cause fish kills as a result of toxin transfer through the food web. On a pleasant day in July 1976, the St. Andrews Biological Station, on the Bay of Fundy, received reports that hundreds of tons of adult herring were dead off Grand Manan Island. The news was particularly alarming because the herring fishery is an economic mainstay of that region. A flurry of research activity followed and determined that the herring had succumbed to toxins of the PSP-producing, red-tide dinoflagellate *Alexandrium*, which reaches the peak of its annual bloom during this period. Examination of the herring stomachs revealed pteropods (small planktonic snails that are herring's favorite food) that had fed on *Alexandrium* and were full of its toxins.

The possibility that Bay of Fundy herring might be contaminated with these potent toxins sent a shudder through the fishing industry. Fortunately, in terms of human health, subse-

Florida Marine Research Institute/Florida Department of Natural Resources

Dead fish on a beach in Florida following the red tide event shown on page 55. Beaches are often littered with dead and rotting fish for miles during these outbreaks. The cost of removal and disposal is significant, as is the loss due to tourist avoidance of these areas.

quent laboratory studies found that herring and other fish are very sensitive to these toxins. Unlike shellfish, herring die before they accumulate the toxins in their flesh to levels that would be dangerous to humans. So the human risk is thus confined to consumption of animals that eat whole fish, including the viscera, such as other fish, marine mammals, and birds. (It remains an enigma how and why Atlantic mackerel, mentioned earlier in connection with the 1987 humpback whale kill, live with substantial levels of the toxins in their guts).

Through similar food web events, *Alexandrium* toxins have been implicated in fish kills along the Atlantic coast, including herring, menhaden, sand lance, bluefish, dogfish, skates, and monkfish.

Algal blooms present a tremendous problem for aquaculturists around the world. Blooms can wipe out entire fish farms within hours. Many different algae have been implicated in such blooms, sometimes with indications that toxins are involved. Often, however, biotoxins are not the problem. Some bloom algae form a thick slime on fish gills that prevents the fish from breathing. Others possess sharp spines that stick into the gills and destroy them. Or some blooms simply strip all the oxygen from the water, either during the night as the concentrated algae respire, or when the bloom crashes and all the algae die at once, leaving no escape for fish in aquaculture cages.

Thierry Work, California Department of Fish and Game

A brown pelican on a beach near Santa Cruz, California, in September 1991 paralyzed by domoic acid from eating anchovies that had eaten toxic algae (diatoms).

Birds

A connection between marine algal toxins and seabird kills has been recognized for years, especially along the North Sea coast of the United Kingdom. In September 1991, an entirely unexpected and novel event occurred along the coast of northern California. A sudden mass mortality of brown pelicans and Brandt's cormorants near Santa Cruz puzzled wildlife experts. They conducted assays for pesticides, heavy metals, and other pollutants, but were unable to determine the cause of death. Thinking biotoxins might possibly be involved, they then conducted mouse bioassays (the standard method for PSP detection) on the birds' stomach contents, as well as on anchovies that the birds had been eating. The injected mice started behaving in strange ways, arching their backs and scratching behind their ears.

The clue was the itchy ears. The veterinarian in charge of the study recalled an article mentioning mice with these scratching symptoms during toxin bioassays. His continued sleuthing led him to suspect a new kind of algal toxin, first reported in 1987 when more than 100 people in eastern Canada were poisoned from eating contaminated mussels; three of the victims died. Investigating that episode, Canadian researchers found that a new toxin, domoic acid, was involved, and that it was produced by a marine diatom. As with other algal toxins, domoic acid was concentrated in tissues of mussels that had fed on the diatoms. This new type of poisoning was named Amnesic Shellfish Poisoning because a number of the victims experienced memory loss; about 10 of them still do.

Back to California and the pelicans. Samples of pelican and anchovy stomach contents were sent to Canadian investigators for analysis. Bingo! They found domoic acid at high levels, both in the birds' and the anchovies' stomach contents. The culprit was the diatom *Pseudonitzschia australis*, a close relative of the diatom that caused the Canadian problem. The anchovies ate the diatoms and passed the domoic acid along to the birds. Unlike the birds, it appears that the anchovies were not affected by the toxins. Tests conducted later not only confirmed the presence of domoic acid in anchovy viscera, but also suggested the presence of the toxin in the flesh, leading to the closure of the anchovy fishery because of public health concerns. Domoic acid has since been detected in shellfish at several locations in the US and has caused closures of razor clam and Dungeness crab fisheries in the Northwest, but so far the pelican and cormorant kill in California is the only reported incident where marine animals have been harmed by this toxin.

Looking Ahead

Toxic "red tides" have long been recognized as problems for human health and the fishing industry, but in recent years, these problems have been expanding throughout the world: There are more toxic species, more resources are affected, larger areas are affected, and blooms are more frequent. Although red tides are natural phenomena, they can be stimulated by human activities such as pollution or habitat alteration. As scientists struggle to understand the many factors underlying this disturbing trend, it is increasingly apparent that humans are not the only ones affected: Many innocent and unsuspecting marine animals are dying or being debilitated by algal toxins. We may be able to explain more mortality events with this knowledge, but our challenge is to ensure that human activities are not making a natural phenomenon worse, for our sake and theirs.

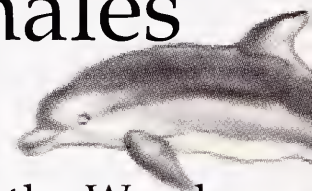
Our challenge is to ensure that human activities are not making a natural phenomenon worse.

Acknowledgment: Much of the work summarized in this article was conducted by scientists other than the authors, particularly Joseph Geraci (University of Guelph), Daniel Baden (University of Miami), Christopher Martin (National Marine Fisheries Service), Yuzuru Shimizu (University of Rhode Island), and Thierry Work (California Department of Fish and Game).

Donald M. Anderson is a Senior Scientist in the Biology Department of the Woods Hole Oceanographic Institution, where he is actively involved in research as well as national and international activities related to harmful algae and their effects. Having received his Ph.D. from the Civil Engineering Department of the Massachusetts Institute of Technology in 1977, he is living testimony to the fact that a career in biological oceanography is possible without any prior appropriate training. His research has focused on the toxic red-tide phenomenon for nearly two decades. He admits that solutions to the problem are no nearer now than they were when he started, though he is confused at a higher level and about more important things.

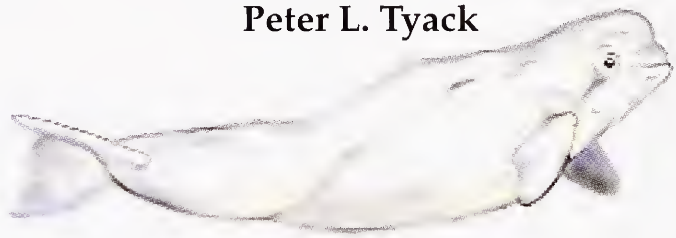
Alan W. White received a Ph.D. in biology from Harvard University in 1972, conducting his thesis research at the Woods Hole Oceanographic Institution. Since then he has lived and worked in Canada, Japan, and Israel, investigating toxic red-tide algae, marine biotoxins, and their effects on fisheries and public health. In 1990 he joined the National Marine Fisheries Service in Woods Hole to guide responses to the new problem of contamination of offshore shellfish in the Gulf of Maine with red-tide toxins.

Dolphins, Belugas, and Pilot Whales



Marine Mammal Studies at the Woods Hole Oceanographic Institution

Peter L. Tyack



Imagine it is 1950. The whaling industry has been rebuilt after World War II. During the 1948/1949 whaling season, 7,400 blue whales and over 17,000 finback whales have been caught in the Antarctic. Next to nothing is known about marine mammals except what can be gleaned from dead animals.

This is the setting in which marine mammal bioacoustics was born, with the publication of a scientific paper and the pressing of a phonograph recording of beluga whale sounds. William Schevill (Woods Hole Oceanographic Institution, WHOI, and Harvard University) and his wife Barbara Lawrence (Museum of Comparative Zoology, Harvard University) had sought a site where they could see and record just one species of cetacean without the confusion of other noisemakers. They found it at Quebec's Saguenay River, where beluga whales were common but other cetaceans were seldom sighted. "Particularly striking is the great variety of *Delphinapterus* sounds and their rapid and apparently continuous succession," they wrote. "This loquaciousness contrasts markedly with most terrestrial herd mammals and compares with such chatterboxes as monkeys and men."

The next two decades were very productive for researchers interested in how marine mammals use sound. They learned that dolphins do not use sound just for social communication, but also for exploring their environment, using echolocation. Many marine mammal species were found to be highly vocal, and the sounds of many different species were identified. One problem in this work was the difficulty humans have in locating sounds under water. A sound recorded in the presence of one species might be made by a different species swimming below but unseen by observers at the surface. William Watkins (WHOI) developed a hydrophone array that could be deployed from a ship at sea and used to locate the origin of each sound. Schevill and Watkins collaborated to

Dolphin and whale sketches by E. Paul Oberlander/WHOI Graphics correctly identify the sounds of blue-water species, such as the clicks of sperm whales or the low-frequency pulses of finback whales.

By the 1960s, research was beginning to reveal some unusual characteristics of marine mammal sounds. Human skill for learning to imitate different sounds is critical to the development of our natural communication, but other terrestrial mammals do not appear able to modify their sounds based upon what they hear; instead, they inherit a species-specific vocal repertoire. There is much more evidence for vocal learning in marine mammals. Richard Backus (WHOI) and Schevill showed that sperm whales can imitate a depth sounder so precisely that they create false targets. Other researchers showed that dolphins can imitate a variety of man-made sounds, and that humpback whales learn, rather than inherit, the acoustic structure of their long, complicated songs.

These data, coupled with hints of interesting social organization, are what brought the cetaceans to my attention as a student in the 1970s. I was trained in animal behavior, and in a reading course with Schevill was struck by the enormous opportunity and lack of ongoing research on acoustic communication and social behavior in cetaceans. A wonderful year studying whales and dolphins in a remote camp in Patagonia sealed my career plans. During the 1970s and 1980s I have been fortunate to be part of an accelerating effort to study the social functions of whale and dolphin sounds. Marine mammals have a reputation for being difficult to study. It can often take years to develop innovative yet practical methods to take to sea for solving a scientific problem. As a member of a large lab with a long history, I have benefited from being able to tap expert opinion about which techniques are likely to work. It is particularly rewarding for me to see how rapidly students in this environment can successfully develop and apply new techniques to address long-standing problems. Three of our students, Amy Samuels, Cheri Recchia, and Liese Siemann, describe their work here. A fourth, Laela Sayigh, has just completed her thesis on signature whistles of wild bottlenose dolphins, and this work is described in *Oceanus*, Spring 1989.

It can take years to develop innovative yet practical methods to take to sea for solving a scientific problem.

The key to understanding communication in a species is to understand the basic problems posed by its social life. As we learn more about the problems marine mammals face at sea, we discover how they use acoustic communication to help solve them. The primary biological division among whales separates those with teeth from those that strain their food with baleen. Some baleen whales disperse over large oceanic areas during their breeding season; males appear to use songs to advertise their location both to females and other males. However, many toothed whales and dolphins belong to more permanent groups. For research on dolphins, Amy Samuels has adapted behavioral-study techniques that were initially developed with primates that live in similar groups. Her detailed studies of dominance in captive-dolphin populations yield quite a different picture than the more casual observations previously reported.

Why the emphasis on *acoustic* communication in marine mammals? Light penetrates seawater so poorly that marine mammals often cannot see social partners. Sound, on the other hand, carries exceptionally well under water, and many marine mammal species specialize in using sound to learn about their environment and to communicate with social partners. Oceanographers have long known the power of sound to explore and communicate in the sea, and as we develop better acoustic techniques ourselves, we are better able to study marine mammals. In order to tease apart the patterns of signal and response that make up a communication system of, it is critical to be able to identify which animal produces which vocalization. I have developed several techniques to solve this problem. Cheri Recchia uses one of these techniques, an acoustic datalogger, to record the patterns of vocalization and behavior of individual beluga whales as they interact in captive groups. This study clearly marks how far this field has come since beluga whales were first recorded some 40 years ago.

In the 1950s and early 1960s, the prime conservation question regarding whales concerned whether the whaling industry catches could be sustained. Modern whalers were remarkably effective; between 1904 and 1978, they killed over 330,000 blue whales and 692,000 fin whales in the Antarctic alone. The stocks of baleen whales appeared to be so reduced that in 1970 the US declared nine of the twelve species endangered. Though strict quotas were set on intentionally killing whales, fishermen still killed some cetaceans incidental to fishing operations—American tuna fishermen in the early 1970s were killing hundreds of thousands of dolphins each year in the eastern Tropical Pacific. The Marine Mammal Protection Act of 1972 was passed in large measure to stop this large but unintentional kill (*Oceanus*, Spring 1989). It requires the government to determine the status of all marine mammal populations, and to ensure that human activities do not harm them. While data on how many whales are killed have been available, they are difficult to interpret without knowing the structure of whale populations. For example, while there still may be tens of millions of spinner dolphins worldwide, one distinct population in the Pacific has been reduced from perhaps 2,000,000 to 400,000 over the last two decades. Two pilot whale species are still caught, both intentionally and unintentionally, and also strand in large numbers in different parts of the North Atlantic.

Liese Siemann's research on the genetic structure of pilot whale populations in the western North Atlantic can help to resolve the impact on the population level of this catch. Her analyses reveal surprising results with obvious implications both for population genetics and for efforts to protect these species.

All three of these students are bringing fresh insights into behavior, communication, and genetic structure to marine mammal studies.

Peter L. Tyack is an Associate Scientist in the Department of Biology at the Woods Hole Oceanographic Institution. He studied biology at Harvard University and animal behavior at Rockefeller University. He cannot remember when he was not interested in the behavioral adaptations of marine mammals to life in the sea.

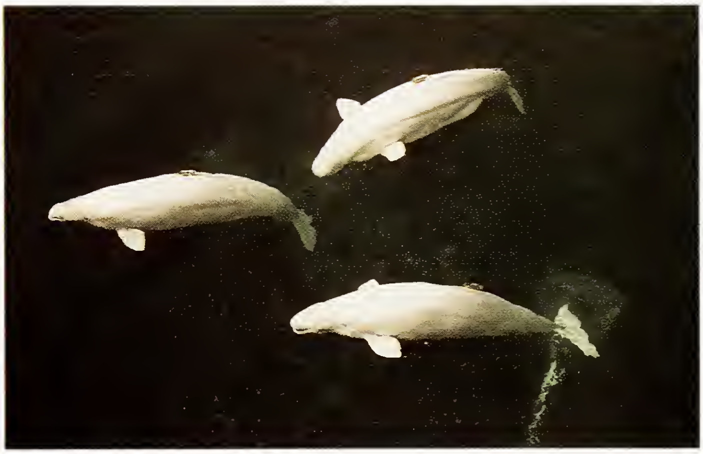
The "Sea Canary"

Its Vocal and Social Behavior

Cheri Recchia

Beluga whales (*Delphinapterus leucas*) are well known for their vociferous nature—early sailors, hearing the myriad calls of these small, toothed whales through wooden-hulled ships, nicknamed them "sea canaries." Captive belugas often imitate sounds in their environments, including the squeals of bus brakes and subway trains, ambulance sirens, their trainers' whistles, and even human speech. A whale at the Vancouver Public Aquarium in British Columbia, Canada, was even reported to produce intelligible imitations of his name, "Logosi."

Why are these animals so vocal? And why do they make so many different kinds of sounds? Answering these questions requires understanding social relationships among belugas. This is best accomplished by observing captive animals, where recognizable individuals can be consistently monitored under conditions of good visibility. In addition, we need to know how the animals respond to one another's sounds and to know which animal makes which sound. At present, this is simplest with captive whales because underwater sounds are extremely difficult to localize.



Cheri Recchia, WHOI/New York's Aquarium for Wildlife Conservation

Although Inuk, Manyak, and Sikku, the three beluga whales at the Point Defiance Zoo and Aquarium, are wearing dataloggers, only Manyak's is visible. Once the animals are fully trained, their behavior appears to be largely unaffected by wearing dataloggers.

Peter Tyack recently solved this problem by developing a small programmable, data-recording device called a "datalogger" that allows precise attribution of recorded vocalizations to individuals. I adapted a datalogger technique, which was originally developed for studying the sounds of bottlenose dolphins (*Tursiops truncatus*), for use with beluga whales for my thesis research. Currently I study beluga sounds at four public aquaria:

- New York's Aquarium for Wildlife Conservation in Brooklyn, New York,
- John G. Shedd Aquarium in Chicago, Illinois,
- Point Defiance Zoo and Aquarium in Tacoma, Washington, and
- Vancouver Zoo and Public Aquarium in Vancouver, British Columbia.

Trainers at each of these facilities have habituated their belugas to wearing dataloggers. I make regular trips to each aquarium and conduct datalogger sessions at times when the belugas are most interactive with each other and least so with people, usually in early morning.

Each datalogger contains an underwater microphone linked to a small computer that stores information about detected sounds, and each is equipped with two soft suction cups that hold the unit gently on an animal's back. At the beginning of an hour-long research session, trainers place a datalogger on each whale in the study group, and the belugas then swim and interact freely while I record their vocalizations. During analysis, I compare the data from all the loggers. The loudest version of a particular vocalization was recorded by the datalogger worn by the vocalizing individual.

I also collect detailed behavioral observations of the belugas' social interactions as part of these sessions. It is important that these observations be as systematic, objective, and unbiased as possible. Amy Samuels (see accompanying article) developed a sampling protocol for studying bottlenose dolphin behavior, and I adapted her technique for my studies with captive belugas. The protocol employs "focal-animal follows," observation periods during which the observer watches one individual (the focal animal) and records its interactions with other group members. This allows the observer to control the amount of time spent watching each individual, and helps counter the natural tendency to focus on particularly conspicuous behaviors; if I am concentrating on only one whale, I am more likely to see subtle interactions that may be as or even more important than flashy displays. Like Amy, I also collect data on how much time individual whales spend close to (within one body length of) other group members, and who their preferred associates are. All of this behavioral information will help me to understand the types of relationships that exist between these whales, and to formulate a social context for interpreting their vocal behavior.

Cheri Recchia, WHOI/New York's Aquarium for Wildlife Conservation

Trainer Martha Haiff-Saif and a volunteer place mock-up dataloggers on Newfy, Kathy, and Natasha, three of the beluga whales at New York's Aquarium for Wildlife Conservation. The mock-ups are used by the trainers to habituate the belugas to wearing dataloggers.

An exciting new dimension was added to my work in August 1991, when two beluga whale calves were born at New York's Aquarium for Wildlife Conservation. Very few belugas have been born in captivity, and, before these two, none had survived beyond four months of age. I was able to videotape the birth and first seven days of each calf's life, and aquarium staff have been making periodic recordings for me since then. The data will enable me to study the development of vocal behavior in these two calves. I will also be looking at social development, particularly mother-calf interactions, changes in the mother-calf relationship as the calves approach weaning age (about 2 years), and how the calves interact with each other and with other group members. The mother-offspring relationship is an important component of social organization in many species, and this is likely true of beluga whales as well.

An understanding of beluga whales' vocal and social behavior will be useful for captive-animal husbandry. Knowing the behavioral con-

Casey nuzzles his mother, Kathy, at New York's Aquarium for Wildlife Conservation. Young calves spend much of their time touching or rubbing against their mothers.

texts of particular vocalizations and the vocal repertoires of individual animals, combined with monitoring vocal behavior, may provide early indications of changing social dynamics, breeding conditions, or general health of captive belugas. Additionally, this work will lay the foundation for studying wild belugas. Once we have detected behavioral patterns in captive whales, we can use these as starting points from which to look for similar patterns in wild animals.

Using acoustics is also one of the simplest and least expensive ways to monitor animals that spend much of their time underwater. Arrays of underwater microphones, placed in strategic locations, could be used to track the movements of wild belugas, and perhaps even to estimate numbers of animals. This in turn would greatly facilitate effective management of beluga populations. First, however, we must learn more about the "sea canary" in its captive environment.

This work would not be possible without the continuing cooperation of the staff (and belugas) of New York's Aquarium for Wildlife Conservation, John G. Shedd Aquarium, Point Defiance Zoo and Aquarium, and Vancouver Public Aquarium, and the author heartily thanks them all. This research is supported by grants from the Ocean Ventures Fund and the Coastal Research Center of the Woods Hole Oceanographic Institution.

Cheri Recchia has wanted to work on whales and dolphins ever since she can remember. To advance this goal, she obtained her undergraduate degree in zoology at the University of Guelph, many miles from the nearest ocean but home, nonetheless, to four marine-mammal scientists. As a student, she got her first look at real live whales while working for David Gaskin in the Bay of Fundy. There, showing a remarkable lack of common sense, she decided to do her graduate work on these elusive animals. She came to Woods Hole Oceanographic Institution to work with Peter Tyack, and has since enjoyed being splashed, bitten, and generally abused by bottlenose dolphins and beluga whales.

Lessons from Baboons for Dolphin Biology

Amy Samuels

Before coming to Woods Hole Oceanographic Institution to study social lives of bottlenose dolphins (*Tursiops truncatus*) with Peter Tyack, I was firmly planted on dry land, with predominantly terrestrial professional interests and research focused on the behavioral ecology of East African baboons (*Papio cynocephalus*). How did a land-loving primatologist like me make the switch to the social intricacies of elusive marine animals who have no thumbs, hair, or facial expressions? The shift from savannah to sea, and from one social, long-lived mammal to another, was surprisingly not as challenging as was the contrast between two scientific cultures. Though studies of terrestrial mammals have progressed to fine-grained analyses of behavior, research on the difficult-to-see, difficult-to-follow dolphins remains in a descriptive, natural-history phase. An historical example from the field of primate behavior illustrates how much this difference may matter.

Jeanne Altmann/Brookfield Zoo

Amy Samuels studies the behavior of wild baboons in Amboseli National Park, Kenya. In the background are elephants and the foothills of Mt. Kilimanjaro.

In early days of primate behavioral research, baboon society was believed to be male-dominated and based upon rigid, stable, dominance hierarchies of adult males. Relationships among females were regarded as fluid, and strongly influenced by a female's reproductive status or her male mating partner. Now, 30 years later, we realize that it is the females, not the males, who form the core of baboon society, and that females have stable, lifelong dominance relationships based upon female kinship, whereas male relationships change as males of different size, condition, and fighting ability join and leave the group.

How is it that our early ideas about baboon society so completely missed the mark? In large part, the answer lies in the ways that behavioral data were then collected: Early naturalists made careful, detailed notes in diary format about behaviors that caught their eye. More often than not, their attention was caught by flashy fights among large, noisy males, and not by subdued interactions among diminutive females. Observations were usually idiosyncratic to the scientist who made them, and findings from one study to another frequently could not be compared. To counter this natural human tendency to note what is flamboyant and to miss what is subtle, systematic observational techniques for behavioral research have been developed and refined over the years. Thus, our present understanding of baboon society is based not on what is eye-catching, but instead on several decades of systematic behavioral sampling techniques, precisely defined units of behavior, and quantitative records of individually known animals.

Not so for studies of dolphins and whales. Long-term popular and scientific interest in the behavior of bottlenose dolphins has resulted in a literature that is sizable and insightful, but reflects the qualitative, descriptive, and subjective nature of the field of dolphin behavior. From this anecdotal literature comes our current view of dominance relationships among dolphins, which bears a striking resemblance to now-discarded ideas about baboon society: Captive dolphin groups are believed to be male-dominated and structured by rigid male relationships, whereas female relations are thought to be subtle, changeable, and perhaps determined by male mating partners. In contrast to this behavioral description, population data from long-term field studies show that close associations among maternal kin are a pervasive feature of wild dolphin society. Is it a paradox or an artifact that behavioral data on dominance relations among female dolphins do not reflect bonds among female relatives indicated by the population data?

To resolve apparent paradoxes like this one, some cetacean biologists have recently begun borrowing techniques from behavioral studies of terrestrial animals. In the spirit of this new movement, I developed a procedure for quantifying dominance relationships among dolphins, adapted from methods for dominance assessment of baboons devised by Jeanne and Stuart Altmann and co-workers (The University of Chicago). Having applied this procedure with colleagues at the Chicago Zoological Society, we can now summarize dominance patterns within the dolphin group at Brookfield Zoo from more than six years of quantitative records of two males and eight females (with two to four females in the group at any one time). Briefly, dominance relations were determined from records of agonistic encounters within pairs of dolphins. A "winner" could be identified when one of the pair, the "loser," displayed only submissive behavior (such as flinch or flee) and no aggressive behavior (threaten, chase, hit, or bite), in response to aggressive or neutral behavior by the other dolphin, the "winner." Winning is thus determined not solely by aggression, but by the ability to make one's opponent back down.

We found male dolphins indisputably dominant to all females at all times. Male dominance persisted, despite older or larger female competitors and despite the protracted illness of one male. Further, although

Mike Greer/Brookfield Zoo

At Brookfield Zoo, Amy Samuels studies the behavior of Nemo, an adult male bottlenose dolphin. In an effort to study dominance patterns in dolphin populations in a systematic manner, she relies heavily on study techniques that were developed for observing baboons.

females rarely "discussed" social status with each other, relationships among females appeared stable over periods of several years and could be predicted by two interrelated factors: body size and age. Between the two males, however, dominance relations were less clear: Over the six years, the two males took turns being the dominant partner and punctuated long periods of calm with brief periods of intense rivalry.

The patterns we observed among dolphins at Brookfield Zoo run counter to prevailing views on dolphin dominance, but our study cannot single-handedly resolve the dilemma. We have, after all, documented patterns within a single group, and that group embodies several potential confounds, including a captive setting, the presence of a maturing "teenage" male, and an absence of female kin. Thus, however careful and quantitative our methods, our results may not be typical of wild dolphin society. Nonetheless, we accomplished something significant: We created a blueprint for systematically studying the behavior of an elusive, evasive creature. By taking advantage of lessons from baboon watchers and opportunities for close, consistent observations of captive dolphins, we were able to develop methods that can be used when visibility and accessibility are less favorable, and that can be compared from one study to another.

Howard Greenblatt/Brookfield Zoo

From studying dolphins in captive settings (such as this one at Brookfield Zoo), the author has learned much about dolphin dominance hierarchies. Her next goal is to apply what she has learned to the study of wild dolphin populations.

My next goal is to apply this new technique to investigate the role of dominance within a wild dolphin society in Shark Bay, Western Australia. Perhaps methods like this one will be employed by others who study dolphin behavior, enabling us to unite results from comparable studies to form a clear picture of the social life of dolphins.

Amy Samuels, Behavioral Biologist for the Chicago Zoological Society, became interested in marine studies at six when she discovered that sea monkeys were actually brine shrimp. After undergraduate studies in biological anthropology and a master's degree in ecology from the University of California at Davis, Samuels collaborated with Jeanne Altmann in Kenya. At the foot of Mt. Kilimanjaro at Amboseli National Park, her studies focused on behavioral ecology of baboon mothers and infants, and social maturation of "teenage" female baboons. She then began a similar investigation of baboons at Brookfield Zoo. In response to the Brookfield Zoo's commitment to further the understanding of dolphins, Samuels works with dolphins there and at field sites in Florida and Australia. At Woods Hole Oceanographic Institution, Samuels's doctoral work concentrates on behavioral endocrinology of dolphins.

Pilot Whale Research Using Small Tissue Samples

Liese Siemann

Because cetaceans spend most of their time underwater, the research necessary for understanding their population structure and dynamics has been extremely difficult to do using traditional observational or mark-and-recapture techniques. However, recent advances in molecular biology now make it possible to study the structure of marine mammal populations with only small tissue samples. For instance, the polymerase chain reaction (PCR, see Biological Oceanography from a Molecular Perspective, page 47) can be used to amplify specific regions of DNA, making tens of thousands of copies from only one piece of DNA. This ability to amplify DNA is especially valuable because tissue samples used in cetacean research are often taken from rare museum specimens or from small bits of skin collected in the wild.

Paul Erickson

Determining the relationships between pilot whale populations in the North Atlantic is the focus of Liese Siemann's work. Her methods require only small tissue samples from individual whales, allowing her to obtain data from many different sources.

Analysis of mitochondrial DNA (mtDNA) is popular for studying the genetic structure of whale, dolphin, and porpoise populations. Mitochondria are the intracellular organelles responsible for cellular respiration, and they contain their own circular, double-stranded DNA, which is distinct from the better known DNA that is found in the nucleus. A number of characteristics make mitochondrial DNA useful for population genetics studies. Because each cell contains roughly 10,000 copies of mtDNA, it is relatively easy to isolate. In mammals, mtDNA evolves more rapidly than nuclear DNA. Yet because there are rapidly and slowly evolving regions interspersed throughout the mitochondrial genome, mtDNA is useful for examining genetic variation within and between populations, or studying the evolutionary relationships between higher taxa. Finally, mtDNA appears to be maternally inherited through the egg cytoplasm, and it can be used specifically to study female lineages.

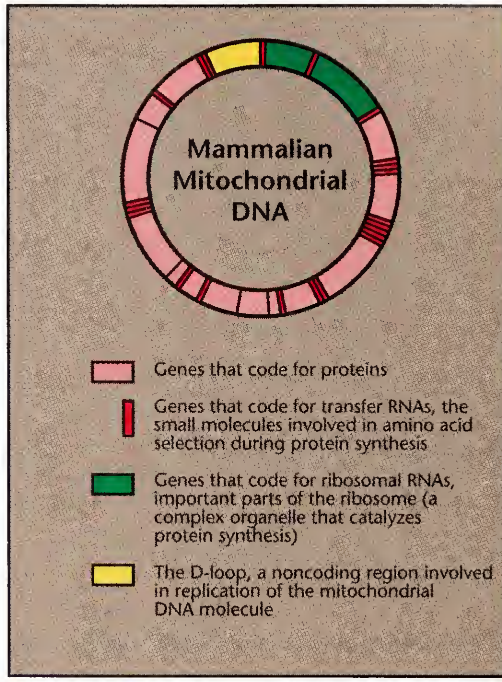
My research involves studying mtDNA variation in the North Atlantic long-finned pilot whale (*Globicephala melas*). A recent increase in mass strandings around Cape Cod has caused a growing interest in coastal pilot whale populations. In addition, North Atlantic pilot whales are incidentally taken by commercial fisheries operating in US waters and are or have been hunted in parts of their range. Although the long-finned pilot whale is not presently considered an endangered species, losses in the western North Atlantic due to strandings (more than 100 whales from December 1990 to December 1991) and incidental catches (about 297 whales from 1977 to 1988) may be significant to the local pilot whale population in waters around Cape Cod and Long Island. To evaluate the potential effects of these losses, we must first understand the relationships between pilot whales in these waters and the rest of the North Atlantic.

Using nothing more than a small skin sample, we can now gain the knowledge necessary to properly manage cetacean stocks.

The New England Aquarium maintains a collection of tissue samples that are routinely taken from pilot whales that strand on New England coastlines. In addition, a National Marine Fisheries Service program places observers aboard commercial fishing vessels that incidentally catch marine mammals, and these observers often collect tissues. Samples from both these programs are used for many studies, including research on reproductive physiology, diet and nutrition, and contaminant concentrations, as well as genetics. With their help, I have obtained a collection of samples from over 90 pilot whales that stranded on Cape Cod or were caught by fisheries operating in North Atlantic waters south of Cape Cod. My preliminary analysis focused on sequence variation in one of the most rapidly evolving regions in the mitochondrial genome, a noncoding region known as the D-loop. I have determined DNA sequences from 25 pilot whales, and, surprisingly, I have found no sequence variation in the D-loop. This contrasts sharply with data from Atlantic white-sided dolphins (*Lagenorhynchus acutus*) and bottlenose dolphins (*Tursiops truncatus*), where I found significant D-loop sequence variation among only three individuals within each species. Consequently, there may be very little mitochondrial genetic variation in western North Atlantic pilot whales. This situation has no simple explanation.

One suggestion is that populations exhibiting extremely low levels of mtDNA variability have experienced severe population bottlenecks in the recent past. Since mtDNA is maternally inherited, a population reduced to just one female and one or more males would contain only one transmissible mtDNA type. Such a population would have no mtDNA variability if no new females immigrate into the population and if there has not been enough time since the bottleneck occurred for mutations to arise and become established in the population as new mtDNA types. Because pilot whales can disperse long distances and were never heavily hunted in waters around Cape Cod and Long Island, a severe population bottleneck seems unlikely. However, the pilot whale population off Newfoundland was overhunted between 1947 and 1972, when a total of 54,348 whales were taken from a population estimated at 60,000 whales before 1947. It is not known if the Newfoundland population and the Cape Cod–Long Island population are the same. If they are, the decimation of this population by the Newfoundland whale fishery could have substantially depleted the amount of mtDNA variation in western North Atlantic pilot whales.

The social behavior of pilot whales might also influence their mtDNA variability. Pilot whale pods are multifemale groups that range from 10 to 1,000 individuals, and the smaller pods appear to remain stable for periods of months to years. They are thought to consist of a core of related females and their offspring accompanied by reproductively active adult males that are unrelated to the females. If mtDNA types from individuals belonging to a single female lineage are identical, then mtDNA variation would be found primarily between pods. Furthermore, if pilot whale pods are closed social units for females, the North Atlantic pilot whale population could be described as a collection of many coexisting subpopulations of female lineages. Studies using computer simulations suggest that a subdivided population could show the effects of an apparent population bottleneck even if the population did not decrease in size; genetic variation can be lost in subdivided populations when subpopulations frequently become extinct and are reestablished by individuals from other subpopulations. Because of an extreme tendency of pilot whales to remain with their pods, they have been hunted for centuries by driving entire pods ashore for easy slaughtering. This "extinction" of pods, followed by growth and subdivision of surviving pods, could have led to the loss of mtDNA variation in North Atlantic pilot whales.



Jack Cook/WHOI Graphics

Every cell contains about 10,000 copies of mitochondrial DNA (mtDNA) making it easy for researchers to isolate. The mtDNA is circular, as shown, and has both rapidly and slowly evolving regions. This makes it a good source for identifying genetic variation between populations. Currently Liese Siemann focuses on determining DNA sequences of the D-loop, a rapidly evolving mtDNA region, in determining if different groups of North Atlantic pilot whales are related.

The Marine Mammal Protection Act of 1972 provides protection for marine species and population stocks (defined as "a group of marine mammals that interbreed when mature"). By protecting population stocks, the US government formally recognized the importance of preserving the genetic structure of populations. If species are to survive and be maximally productive, their conservation must include efforts to maintain sufficient numbers of individuals belonging to each of the genetic stocks found within the species. Using nothing more than a small skin sample, we can now gain the knowledge necessary to properly manage cetacean stocks. My preliminary research has indicated that variability of mtDNA in the western North Atlantic pilot whale may be extremely low. This information about the genetic structure of pilot whales in the North Atlantic may turn out to be critical for their conservation.

Liese Siemann attended Cornell University and Oxford University as an undergraduate, where her studies focused primarily on cell and molecular biology. Realizing she would rather follow her childhood dream of studying whale behavior, she entered the MIT/WHOI Joint Program in Biological Oceanography in 1988 to pursue her Ph.D. with Peter Tyack. When she is not at work, once again ironically doing molecular biology, she can usually be found in her backyard stable caring for her two horses.

Whale Falls

Chemosynthesis on the Deep Seafloor

Craig R. Smith

In 1987 **Alvin** *chanced upon the skeleton of a whale resting at 1,240 meters in the Santa Catalina Basin.*

The deep seafloor is a biological desert—a region where animal biomass and production are typically supported only by the small rain of organic material arriving from productive surface waters thousands of meters above. In the late 1970s, however, deep-sea "oases" were discovered at hydrothermal vents. Here sulfide-rich effluents support dense communities of free-living bacteria, as well as tube worms and mollusks living in symbiosis with chemoautotrophic bacteria (internal bacteria that fix organic carbon using chemical energy from reduced compounds such as sulfide).

Similar communities were soon discovered at petroleum and sediment pore-water seeps, as well as in deep anoxic basins along oceanic margins (see *Oceanus*, Winter 1991/92). All these deep-sea "chemosynthetic" communities depend on geological "focusing" of reduced chemicals (such as sulfide or methane) at the seafloor, where bacteria can oxidize them to produce organic compounds that serve as food for higher organisms. Following these finds it seemed clear that such communities occur only along specific geological features, such as mid-ocean ridges and continental margins; the vast sediment plains of the abyss must indeed be deserts, devoid of even an occasional chemosynthetic oasis.

However, large concentrations of fresh organic matter can also yield substantial amounts of sulfide. In this case, anaerobic bacteria decompose the organic material, using sulfate (rather than oxygen) as an electron acceptor, and convert it to sulfide. This process produces dramatic odors at shallow-water sewer outfalls, and in theory could occur when large organic parcels, such as whale carcasses, sink to the nutrient-poor seafloor. Until recently, however, scientists had never observed organic-rich whale remains on the deep seabed.

This changed in 1987 when the research submersible *Alvin* chanced upon the lipid-rich skeleton of a 21-meter-long whale resting at 1,240 meters in the Santa Catalina Basin off the southern California coast. Subsequent visits to the skeleton in 1988 and 1991 revealed that the bones of this blue or fin whale were covered with thick bacterial mats similar to those observed at hydrothermal vents and seeps. The bone surfaces were also encrusted with a diverse assemblage of invertebrates, including mussels (*Idasola washingtonia*), limpets, snails, and polychaete

The vertebral column of the whale skeleton in Catalina Basin is clear in the flyover view at right, taken from DSV Alvin. *Vesicomyd clam shells pepper the sediment, and white bacterial mats cover the ends of bones. Each vertebra is about 30 centimeters long. Centimeter-long mussels and limpets harboring serpulid polychaetes encrust the surface of the whale rib below. This bone was recovered from the Catalina Basin skeleton.*

C. Smith

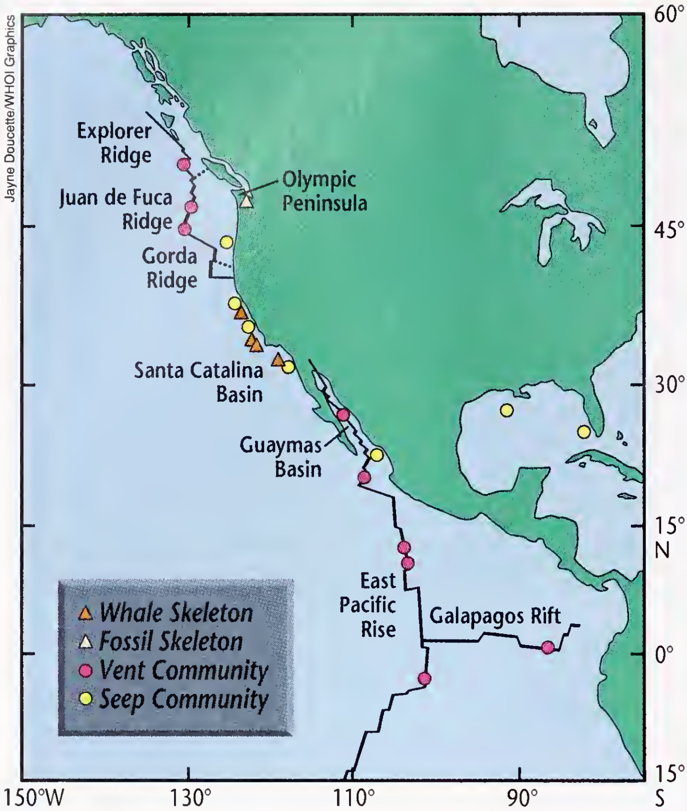
H. Kukert

worms. The sediments adjacent to the bones were sprinkled with dead shells from large vesicomyid clams, and numerous living clams (possibly *Vesicomya gigas*) peeped from sediments beneath bones. These clam, mussel, and limpet species are not normally found in the Santa Catalina Basin; nonetheless, they had achieved substantial population sizes (hundreds to thousands of individuals), and very large biomasses, on a single whale carcass.

Sulfide-Based Chemosynthesis

Several lines of evidence indicate that the whale-skeleton community in Catalina Basin is nourished, at least in part, by sulfide-based bacterial chemosynthesis. Studies conducted in the laboratory of microbiologist

Jayne Doucette/WHOI Graphics



Sites of known chemosynthetic communities on whale bones, hydrothermal vents, and seeps in the Northeast Pacific are shown here. Various species found on the Catalina Basin whale skeleton have also been collected from Guaymas Basin and Juan de Fuca vents, and from whale bones and seeps off the coast of California.

Jody Deming (University of Washington) revealed that the gill tissues of large vesicomyid clams and bone-encrusting mussels contain substantial amounts of enzymes that are characteristic of chemoautotrophic metabolism; transmission electron microscopy indicated that these enzymes were associated with endosymbiotic bacteria. After examining the carbon-13 and nitrogen-15 contents of the clam and mussel tissue, Steve Macko (University of Virginia) suggested that the clam derives all its nutrition from chemoautotrophy, while the mussel utilizes other energy sources as well (perhaps by feeding directly on whale-bone organics). Two other clam species collected at this whale skeleton (the vesicomyid *Calyptogena pacifica* and the lucinid *Lucinoma annulata*) are known to derive nutrition from endosymbiotic, sulfide-oxidizing bacteria. Thus, a substantial proportion of the rich, faunal assemblage at the whale skeleton seems to be supported by chemoautotrophic production.

What is the current sulfide source at the Catalina Basin skeleton, and why does the chemosynthetic assemblage hug the bones? The answers lie within the whale skeleton. To maintain buoyancy, the bones of living whales are rich in oils, as much as 60 percent lipid by weight. The central portions of the Catalina Basin bones still contain large lipid concentrations, which are being decomposed by anaerobic bacteria. The resulting reduced compounds (particularly hydrogen sulfide) diffuse outward through the bone matrix, providing an energy source for chemoautotrophic bacteria living on the bones and in the tissues of host animals such as clams and mussels.

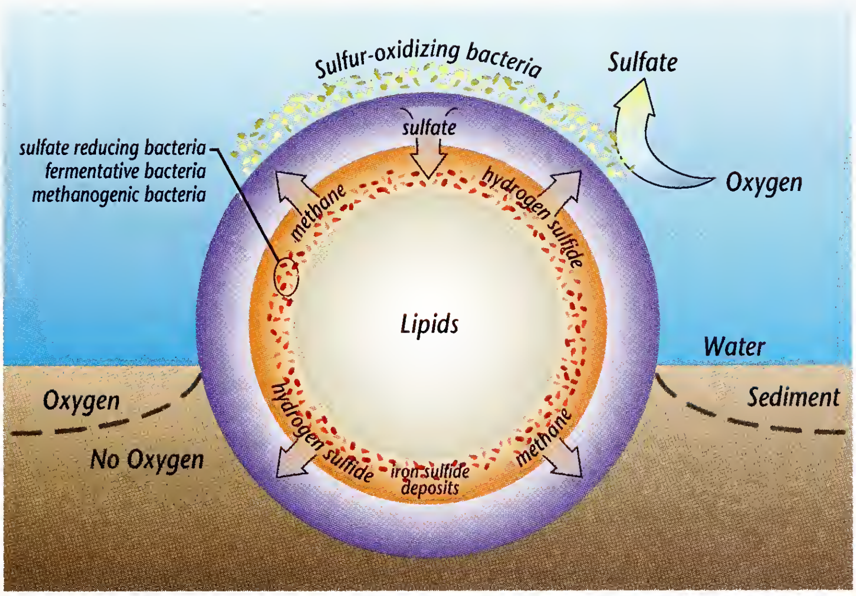
Stepping Stones on the Seafloor?

An especially intriguing aspect of the Catalina whale-fall community is its taxonomic relationship to other chemosynthetic assemblages in the deep-sea. Components of this assemblage have been found on whale bones dredged from the deep sea off central and northern California, and, perhaps, from New Zealand (this, so far, is based are photographic evidence). In addition, two of the whale-fall limpets (*Pyropelta corymba* and *Pyropelta musaica*) and the mussel *I. washingtonia* occur at hydrothermal vents; in fact, these limpets hail from the "fire limpet" family Pyropeltidae, originally thought to occur only at hydrothermal vents as grazers of sulfur bacteria. Some whale-fall species are also reported from wood falls in the North and South Pacific, and from anoxic sediments on the California slope. Thus, the whale-skeleton assemblage appears to be related to faunas from a broad range of chemosynthetic, deep-sea habitats, which are often geographically isolated and short-lived. One of the mysteries surrounding these communities concerns how this specialized fauna disperses between these ephemeral habitat "islands."

Calculations that suggest sulfide-rich whale falls may be surprisingly abundant (with an average spacing of about 25 kilometers in the deep northeast Pacific) lead to the hypothesis that whale falls might provide dispersal stepping stones for deep-sea dwelling species that are dependent on chemosynthesis. The large whale species, in combination, are cosmopolitan, so whale falls can occur virtually anywhere in the abyss. Sunken whale bones may thus provide oases for sulfide-dependent animals (especially hard-substrate species such as limpets) over vast reaches of open-ocean sediments. Discoveries last year of fossil chemosynthetic communities on fossil whale skeletons from the Olympic Peninsula suggest that whale falls may have provided dispersal stepping stones for more than 30 million years.

Important questions about deep-sea whale-fall communities remain unanswered, including: How rapidly do chemosynthetic communities develop when whale carcasses reach the seafloor, and how long do they

H. Kukert



Jayne Doucette/WHOI Graphics

The cross section of a vertebra above was recovered from the Catalina Basin whale skeleton. The dark bone periphery is depleted of lipids, while the cream-colored central region is lipid rich. Many microbial processes are thought to be occurring inside these lipid-rich whale bones. Lipids at the bone core are decomposed by a community of sulfate-reducing, fermentative, and methanogenic bacteria residing at the lipid periphery. Reduced chemical species, especially sulfide, released from these bacteria diffuse outward to support free-living and endosymbiotic chemoautotrophic bacteria at bone margins. The reduced species diffuse in all directions, consuming oxygen and causing anoxia beneath the bones.

persist? What proportion of the diverse species assemblages found at hydrothermal vents can actually colonize whale skeletons? We have initiated a research program to address these and related questions, using whale remains implanted in vent and nonvent deep-sea settings. The dead-whale material is obtained, with permission through the National Marine Fisheries Service, from cetaceans that die and become stranded on the California coast due to natural causes. We hope that these "burial-at-sea" experiments will soon help to shed light on the importance of whale carcasses as habitat islands for chemosynthetic communities at the deep seafloor.

Hilary Maybaum

Author Craig Smith (right) and a student catalogue animals attached to a whale bone recovered from the deep seafloor using DSV Alvin.

Craig R. Smith is an Associate Professor in the Department of Oceanography at the University of Hawaii. He became interested in the oceans as a small boy living on a workboat in the Mediterranean Sea. His love for the sea was reinforced by years of schooling in the middle of Michigan. He now studies the ecology of the seafloor with his children Taina and Melanie on Hawaii's beaches, and with Alvin *and surface ships in the deep ocean.*

Through the Thermocline and Back Again

Heat Regulation in Big Fish

Francis G. Carey

The big oceanic fishes, tunas, billfish, and sharks, are dramatic animals—large, powerful, and beautiful. The size and mobility of some species allow them to travel long distances, from warm tropical waters for spawning to colder, rich, productive areas for feeding. These seasonal migrations may take them across ocean basins.

Because of their spectacular form and their economic importance, there is a considerable body of scientific knowledge about them, especially regarding fisheries management, age and growth studies, and evaluations of stock conditions. Tag-recapture programs have outlined the seasonal migrations of some of these fish and revealed the great distances they may travel. In recent years there has been increased effort to study how these fish function. However, these are dwellers of the open sea; their life in the vast ocean is a challenge to observe, and most are very difficult to maintain in captivity. While there have been some laudable successes in major public aquaria and research facilities, it is a major undertaking to catch them without injury and keep them in good health; and even then, an aquarium situation does not allow detailed study of their lives.

Small acoustic transmitters attached to the fish make it possible to follow them for periods of several days to a week.

Using Sound to Study Big Fish

John Kanwisher (Woods Hole Oceanographic Institution) promoted the use of acoustic telemetry to study these fish some 25 years ago. Small acoustic transmitters attached to the fish make it possible to follow them for periods of several days to a week. (Radio transmitters can be used in fresh water, but even a centimeter of seawater blocks radio signals, so radio telemetry at practical frequencies is not possible in the sea.) The transmitters broadcast information including swimming depth, water temperature, and body temperature, and sometimes swimming speed, heart rate, or tail beat. Information from the acoustic signal is coded as pulses of ultrasound so that the device beeps more rapidly with increasing depth or temperature.

Our acoustic telemetry techniques are severely limited. Measurements on a few parameters in each experiment are combined with whatever environmental measurements we can make aboard a ship, such as temperature-depth profiles, the position of the sound-scattering layers and bottom depth, light intensity, and, when available, current position and strength. From this scattered information we piece together a picture of the fish's activity. Our situation is nothing like the wealth of information available to ethologist Jane Goodall watching a group of habituated chimps in a natural setting. However, the glimpses we obtain often bring new knowledge, so this narrow view beneath the surface can be rewarding and exciting.

The fish, although very powerful and sometimes dangerous, are also delicate, and we must work fast in order to minimize their stress.

These are not well-controlled experiments. The fish, although very powerful and sometimes dangerous, are also delicate, and we must work fast in order to minimize their stress. It has not been possible to refine our techniques in a captive situation, and we can rarely recover the animal at the end of the experiment to see if the position and function of the various sensors were really as we thought. We release the fish with a fervent wish—"Gee, I hope that is OK." Because of this lack of control, it is important to keep the questions and the experiments simple.

The ocean itself is a noisy place, and our boat is always a major source of noise. Fortunately, most ship sounds are at frequencies well below our signal, but there is usually some shaft squeal or cavitation noise from dings on the propeller. Cetaceans are another noise source, and their powerful whistles and clicks cover the frequencies we use. Dolphins can be particularly loud at night; sometimes we can hear nothing else on our hydrophones. Fortunately, they come and go, and there are usually quieter periods when we can locate our fish and take some data. In our first open-ocean experiment in 1970, we attached a transmitter to a large bigeye tuna and released it. I ran into the lab on R/V *Gosnold* to see how it was working, but heard only loud howls, whistles, and buzzes of the type familiar to those who listen to distant AM radio stations at night. I panicked, for I knew my trouble-shooting skills were not up to fixing what I thought was a major electronic problem. Then came the call: "Porpoises on the bow!" A dozen *Tursiops* were whistling and cackling into the hydrophone. When they went away, all was quiet and we had a fine, strong signal from the fish.

Where Do They Go? How Fast Do They Get There?

We have attached transmitters to over 60 large pelagic fish and followed them for periods of one to six days. Travel speed can be estimated from its distance traveled over a period of time. This gives a minimum speed, as the fish's course may have been longer and more circuitous than that of our tracking vessel. Recently, however, we have been placing speedometers on the fish, and we find that the speed telemetered from the fish agrees with that estimated from time and distance, usually a steady 1 to 3 knots.

Doubtless, the fish sometimes move rapidly when feeding or avoiding danger, and many observers have described such bursts. There are a number of anecdotal accounts of tuna schools moving fast, but we have not seen much fast swimming during our experiments. There is probably little routine use for high speeds. Water is a dense, viscous medium and the power required for swimming increases with the square of the speed. Therefore, high speeds require a disproportionate increase in energy expenditure. By swimming at speeds of several knots, and moving constantly on a steady course, the fish can cross oceans in a few months. It is interesting that a 5-meter white shark and a 0.5-meter cod (only one-tenth as long) both swam in this speed range. The larger fish could easily move faster, but if 2 knots will take it where it is going, then 2 knots appears to be fast enough.

Some yellowfin tuna and swordfish exhibit clear, daily movement cycles. Swordfish we followed near Gorda Bank in Baja California, and also on Georges Bank, moved onto the bank during the day, remaining near the bottom at depths of 100 to 200 meters. An hour before sunset they moved offshore, coming to the surface over deep water during the hours of darkness. At first light they descended again and returned to the bank. Some of these fish returned to the same spot on the bank each day, but moved over a wide area of deep water at night. We guessed that they were hunting squids on the surface at night, and feeding on bottom-dwelling fish on the bank during the day. We observed this daily cycle only for swordfish near fishing banks. Swordfish in deep water did not make the inshore-offshore movements seen near fishing banks, but followed a course guided by currents or other factors that we haven't identified. They did have a clear cycle of vertical movements, however, going deep during the day and staying near the surface at night.

Marty Snyderman

Blue sharks are among the large open-ocean fish the author follows for heat regulation studies.

National Oceanic and Atmospheric Administration/National Marine Fisheries Service scientists in Hawaii, who have had much experience following yellowfin tuna, find that the fish there commonly spend the day in coastal waters or near offshore fish-aggregating devices (moored buoys with suspended materials that attract pelagic fish), but range widely over deep water at night. Hawaiian scientists also find that skipjack tuna, ahi, move in a cyclical pattern, ranging over deep water at night, but returning to a bank during the day. In situations where there are landmarks, the fish may orient to them in their daily routine of movements.

Following Prey in Daily Ups and Downs

Many oceanic animals undertake such daily vertical movements. The primary production of food by photosynthetic algae occurs in the euphotic zone, the upper 200 meters or less of the ocean. Animals that graze on phytoplankton must feed in near-surface waters. Where there is light, however, visual predation is an important factor. Many organisms move deeper during daylight hours to avoid the danger of being seen by

Streamlined for Speed?

Among the 60 large pelagic fish tracked in the last 20-odd years are bluefin, bigeye and yellowfin tuna, blue marlin and swordfish, blue sharks, mako sharks, and one impressive 5-meter white shark. All streamlined and powerful, the tunas are especially beautiful, with the eyes, gill covers, and pectoral and pelvic fins perfectly faired in, and the surface glistening smooth. An albacore's body shape resembles a high-speed laminar-flow aircraft wing. These body forms capture our imagination. How fast they must go! Many authors assume that they swim very fast, and many estimates of top speeds are quite unrealistic. The experience of Carey and colleagues in following these fish, however, indicates that they swim slowly and continuously at speeds of 1 to 3 knots.

Sleek blue shark with pilot fish.

predators. A whole community of predators, including crustacea, fish, squids, and jellies, move hundreds of meters up and down daily in concert with the herbivores, who must feed in the near-surface euphotic zone. This community descends an hour before sunrise, is deepest at midday, and rises to near the surface an hour after sunset. Vertical movements keep the predators near the smaller animals that are their prey, but in low light, which helps them, in turn, avoid larger predators. The community is known as the deep sound-scattering layer from its discovery during the early years of echo-sounder use.

Swordfish, which are part of this vertically migrating community, must be the ultimate visual predator. Their eyes are huge. (In one paper I wrote "eyes as large as grapefruit" and was returned the comment "give diameter in millimeters." I changed the sentence to "eyes as large as oranges." Pommological analogies aside, the eyes are very large.) They meet in the middle of the head, the way eyes of a bird often do. Large eyes give great light-gathering power, and typically are found in animals needing dim-light vision. Though we lack swordfish eye light-sensitivity measurements, it is safe to assume that they can see well in light ranging from dim twilight to near dark. Increased visual sensitivity is an evolutionary countermove that allows the swordfish to continue to prey on a community of animals that remains in near darkness to avoid other visual predators. Our telemetry experiments with swordfish over deep water, in regions where there is a well-developed community of vertically migrating animals, show that the swordfish moves in the same manner, and may locate itself in the most dense region of the scattering layer.

Thermal Regulation in Fish

There are large temperature differences between the warm upper layers of the ocean and the cold water below the thermocline a hundred meters or so beneath the surface. Temperature gradients of 15° to 20°C are not uncommon within the depth range of pelagic fish. By moving a few hundred meters vertically, an animal may encounter a greater temperature change than it experiences seasonally or in moving thousands of miles horizontally.

Many organisms can acclimate to slow temperature changes. Their tissues adapt over periods of weeks or months so that they function as well in the cold of winter as in the heat of summer. Rapid temperature changes do not allow such acclimation, however. Most animals malfunction if they are suddenly cooled 10° or 20°C. The nervous system is most sensitive to cooling, and the higher functions are the first to deteriorate. Ladd Prosser (University of Illinois) and his students had a nice demonstration of this. A catfish was taught to respond in a certain way to a flash of light. On cooling 10°C this conditioned response disappeared. The fish could still maintain an upright position, swim, and respire, but the learned response was gone. Divers have similar experiences. If careless, they can become dangerously chilled, with body temperature dropping several degrees. In this state one can still climb back into the boat, walk, eat, or drink, but do mental arithmetic? Forget it!

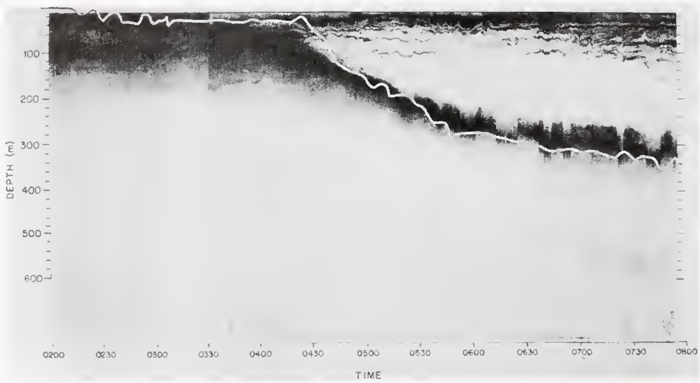
We have found swordfish passing through temperature gradients of 19°C as they swim up and down. The rate of temperature change in any system is strongly dependent on dimensions, as household experience confirms. For example, meat must be brought to around 180°F to be cooked. While this may take only a few minutes for a thin hamburger, it will take all morning for the Thanksgiving turkey. Time constants for temperature change may be milliseconds at the cellular level, seconds for plankton, minutes for 10- to 100-gram animals, and hours for large animals like the pelagic fish we follow. This means that smaller animals are locked to ambient temperature, but larger ones may be able to manipulate body temperature and achieve a certain thermal independence from the environment.

It would be a triumph of the scientific method to relate that on finding how the daily routine of the swordfish took it through large temperature changes, and knowing that its great size might allow it some temperature tricks, we went on to investigate what it was doing with body temperature. Our experience was as disorderly as most science, however. We found the temperature trick first, and only later learned why it might be useful. Many years ago, I found the inner regions behind a swordfish's eyes were warm, the brain even warmer, and a region below the brain warmer still. The swordfish brain is about as big as the last joint of my index finger. Beneath the brain sits the brain heater: a remarkable mass of dark, mustard-brown tissue packed with mitochondria (the chemical engines of the cell) about the size of a hen's egg. The brain heater is insulated by fat and fatty bone, and receives a massive blood supply. It was the discovery of this brain heater that prompted us to begin the swordfish telemetry experiments. We wanted to learn what the fish did that would make such a structure useful.

By careful measurement and dissection, it was possible to use external features on the head to guide the thermistor probe of one of our transmitters down into the cranial cavity so that it was near, but not in, the brain. In the first of two such experiments, the fish was disturbed, and perhaps seriously injured by our

Frank Carey (yellow suspenders) and colleagues outfit a blue shark with transmitters aboard R/V Oceanus *(WHOI). When a seawater hose is placed in its mouth, Carey finds that a shark usually lies quietly on the deck. The dark cloth over the eyes also calms the fish. For this experiment, a depth, water temperature, and body temperature transmitter is being installed at the base of the dorsal fin. A second transmitter on the head will report cranial temperature.*

Doug Mayer



This is a composite figure showing the depth of a large swordfish obtained by acoustic telemetry, superimposed on an echogram made with a 50-kilohertz echosounder. A dense assemblage of organisms produced the heavy band of echo returns near the surface at night. About an hour before sunrise at 0445, these animals started to descend. The swordfish went with them, staying with the sound-scattering layer. The swordfish remained with this community, probably preying on squid and fish both near the surface at night and at depth during the day.

manipulations, and did not swim up and down at dusk and dawn as we expected. However, it did give us a day and a half of temperature records showing temperature elevation in excess of 10°C above water temperature. During a second experiment, a fisherman was slapped in the face by the bill and severely injured. This incident discouraged me from ever trying the procedure again with another swordfish. We stabilized the injury and released the fish. Fortunately, it behaved as we hoped: At daybreak it descended into 10°C cooler water, but the cranial temperature only decreased by 5°C. The temperature elevation in the cranium was greater in cold water than in warm. The brain heater regulated the temperature of the swordfish central nervous system.

We humans are cerebral chauvinists who admire the dolphins for brains that are larger than ours. We are not impressed with grape-sized brains in great fish. In one translation of a beastiary by Oppian of Calicia we read of the swordfish:

Nature her bounty to his nose confined.
Gave him a sword, left unarmed his mind.

Not quite right, for it appears that the brain heater may be an effective armament for this large predator.

Two factors allow large fish to manipulate their body temperatures. The first is size: Thermal diffusion through a large mass is a slow process. The second is a way to reduce convective heat transfer by the circulatory system. Blood circulation between gills and tissues provides a convective cooling system that seems to lock even a large fish to water temperature. Some large fish, however, are much warmer than water temperature: We have measured giant bluefin tuna temperatures more than 20°C above water temperature. Mackerel sharks also maintain elevated temperatures, and, as noted above, the brain and eyes of the billfishes may be warm. These warm fish have an anatomical trick: They have all installed countercurrent heat exchangers in the circulation between the gills and the tissues. The heat exchangers are masses of small, parallel vessels with venules and arterioles intermingled so the arterial and venous blood streams are in excellent thermal contact. The cold incoming arterial blood is warmed as it flows close to venules carrying warm blood away from the tissues. These vascular structures, such as the one serving the swordfish brain heater, can be remarkably efficient, and may exchange more than 98 percent of the excess heat between venous and arterial streams. A fish with such a system can be many degrees warmer than the water.

Elevated body temperatures may offer a number of advantages, such as increasing the power available from muscle and speeding up nervous system functions. From our experience in following the temperature responses of many of the large pelagic fish, we feel that a major advantage of elevating body temperature is the opening of a larger environment to the individual. By actively controlling their body temperatures, the large fish are able to move into the cold water below the thermocline and expand their niche (the space and resources available to them). They can follow the community of vertically migrating animals into deep water and feed on these fish and squids during the day as well as at night.

In looking for cold-blooded fish to use as comparisons with our experiments with warm-bodied tunas, mackerel sharks, and billfish, we settled on the blue shark. This is a large and abundant pelagic shark, easy to catch, tough, and easy to work on. We knew from examination of the circulatory system that it had no heat exchangers in the blood supply to the muscle. A good control species, the beautiful blue color of this shark suggests adaptation to the blue surface waters of the open sea. But in our first experiments we were surprised to find that it regularly left the surface and swam up and down through the thermocline, passing through large temperature changes as it moved between the surface and depths as great as 600 meters. These vertical excursions were repeated at one- to three-hour intervals. The oscillations were marked during the day, but reduced at night when the sharks often remained near the thermocline.

Most of our blue shark experiments were done in several-thousand-meter-deep slope water in the New York Bight, during the late summer, fall, and early winter. At this time and place, the sharks frequently had pelagic octopods, *Alloposis mollis*, in their stomachs. These purple creatures have a membrane between the arms that extends down almost to the tip. (They resemble rumpled umbrellas with large eyes.) The 1-kilogram *Alloposis* are vertical migrators usually found below 200 meters depth. If the sharks were going deep to find *Alloposis*, why were they returning to the surface? By recording temperature deep within the swimming muscles during such excursions, we learned that the muscle temperature rose and fell with water temperature; however, the rate of warming as the fish rose through the thermocline was more than twice as fast as the rate of cooling as it descended into cold water. As a result of this thermal hysteresis, the average muscle temperature was 4°C warmer than the water. This is behavioral thermoregulation, using heat acquired in the warm surface water to stay warmer than the cold water at depth. Because they are large animals, cooling by conductive heat transfer is less important than convective heat transfer through the circulatory system. By changing cardiac output to speed up convective heat transfer and warming when near the surface, and then to slow the cooling while deep, blue sharks can manipulate their body temperatures.

The limited view acoustic telemetry offers of life within the ocean has been unusually productive because of our great ignorance about that environment. Our simple, imperfect, observations have revealed many unexpected phenomena, and we expect there is a great deal more to be learned using current advances in technology that greatly broaden the types of observation possible and improve their quality.

Frank Carey has been at the Woods Hole Oceanographic Institution for about 30 years. He writes: "This career has given me freedom to pursue my interests with very few constraints. I have benefited greatly from the help of a large number of colleagues who gave me access to technical skills and knowledge that would have been slow and painful to obtain on my own. The Woods Hole community also attracts the kind of people who volunteered as cannon fodder on research cruises and who put up with often trying conditions and my own crankiness when things were not going well."

Life Cycles and Population Dynamics

Mathematical Models for Marine Organisms

Hal Caswell and Solange Brault

Since dynamics is inherently a quantitative field, mathematical models are fundamental to population dynamics studies.

Biologists have long recognized levels of organization in the living worlds. From the level of cells through increasingly complex levels of tissues, individual organisms, populations, communities, and ecosystems, each level has its own important processes, interesting questions, and methods and approaches. The levels, of course, are not independent. Finding answers to questions about processes at one level often requires examining those at work in higher or lower levels, but crossing the boundaries between levels is not usually easy.

Many biological oceanographers, like other ecologists, are preoccupied with population dynamics problems, understanding changes over time in the abundance and structure of populations. Also, like other ecologists, they recognize that the mechanisms determining these changes operate at the level of the individual life cycle: The rates at which individuals are born, develop, grow, mature, reproduce, and eventually die (collectively called the *vital rates*) determine whether a population increases or decreases, fluctuates or remains constant, persists or becomes extinct. Since dynamics is inherently a quantitative field, mathematical models are fundamental to population dynamics studies, and it is essential to develop a modeling approach that can incorporate life-cycle information and draw population inferences from it.

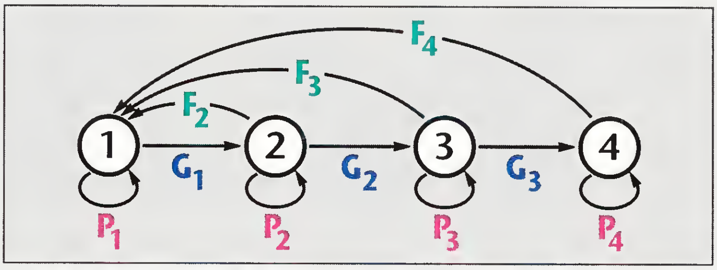
Models describing life cycles in terms of age have been used in ecology for over half a century. Recently, however, models have been developed that can describe life cycles in terms of other variables, such as size or developmental stage. Why is this important? Because age is a poor predictor of an individual's status for the many marine organisms that have complex life cycles, and/or because it is often impossible to know an individual's age, but relatively easy to measure its size or describe its developmental stage.

Developing a Model

This model, the same type used to describe the loggerhead sea turtle's life cycle, illustrates the basic process of model development.

First, we define a set of biologically relevant life cycle stages, such as age or size classes, developmental stages, or other categories. We then create a *life cycle graph* showing the transitions that are possible among these stages over a time interval.The interval selected depends on the organism; for long-lived species it may be a year, for short-lived species a day or even an hour. The coefficients on the arrows represent the *vital rates*, the rates of transition from one stage to another. In this example, four size classes are represented by four circles. Individuals in the two largest size classes reproduce, at rates F_3 and F_4. Individuals in each size class have a probability G of growing into the next size class, and a probability P of remaining in the same size class.

Once we have outlined the life cycle, we describe the population by counting the individuals in each stage of the life cycle. We use a system of equations to convey the change in the abundance of each stage, in terms of the vital rates. This is the matrix notation of the equations corresponding to this life cycle diagram.



$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}(t+1)=\begin{bmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix}\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}(t)$$

Jayne Doucette/WHOI Graphics

The coefficient in row i and column j of the matrix is the vital rate appearing on the life cycle diagram from stage j to stage i. By analyzing this model, we can use the mathematical properties to derive population dynamics conclusions. The simplest approach is to pick an initial population and iterate the equations—this can even be done on a personal computer with a spreadsheet program!

These models can be used to address a number of problems:

- As individual organisms develop, their morphology, behavior, and environmental relationships can change drastically. For example, benthic invertebrates have planktonic larvae that bear little or no resemblance to the adults and experience completely different environments. Some life cycles also include multiple reproductive modes, some sexual and some asexual, as in the case of many corals. We can ask how important these different stages or modes of reproduction are to population growth, and whether this importance varies from habitat to habitat, or from time to time, and make comparisons across groups of taxa with different ecological properties.

• Vital rates are affected by the abiotic environment, the abundance of resources, and competitive, predatory, and mutualistic interactions with other species. Some changes are natural, while others are triggered by pollution and other anthropogenic effects. Whatever their source, environmental changes alter vital rates, which in turn change the population dynamics. Models help to quantify the impact of changes. We can identify the points in the life cycle where an organism is most vulnerable to the effects of environmental change, and, if we are lucky, maybe even predict those effects in advance.

• The approach above can also be used to assess possible management strategies for protecting threatened or endangered species. If we must choose between strategies that protect different stages in the life cycle or those designed to increase survival or reproduction, we must first know how the proposed changes will impact the population.

Although the range of possible applications is nearly endless, the structured population modeling approach is relatively simple.The end result is a mathematical description of how abundance at each stage in the life cycle changes over time.

The equations in the Box (overleaf) are mathematically simple, but they include a great deal of biological information. This model permits us to go a step further and integrate that information into two important indices: The *population growth rate*, l, and the *sensitivity* of that growth rate to changes in the vital rates. The population growth rate answers the question, If these conditions were maintained forever, how fast would this population grow? The answer obviously depends on all of the vital rates, but some of those rates may be more important than others. The growth-rate sensitivity quantifies this importance. If the population growth rate is very sensitive to changes in, say, adult survival, then any environmental factor that affects adult survival will have a great impact on population dynamics. Each of these indices measures a population-level consequence of individual-level vital rates, providing two answers to the question of how individual life cycles determine population dynamics.

*Orange and yellow sponges are overgrowing some soft corals (*Alcyonium *sp.) that are growing on rocky substrate. Two* Alcyonium *colonies have elongated in preparation for fission. Both are in contact with the yellow sponge.*

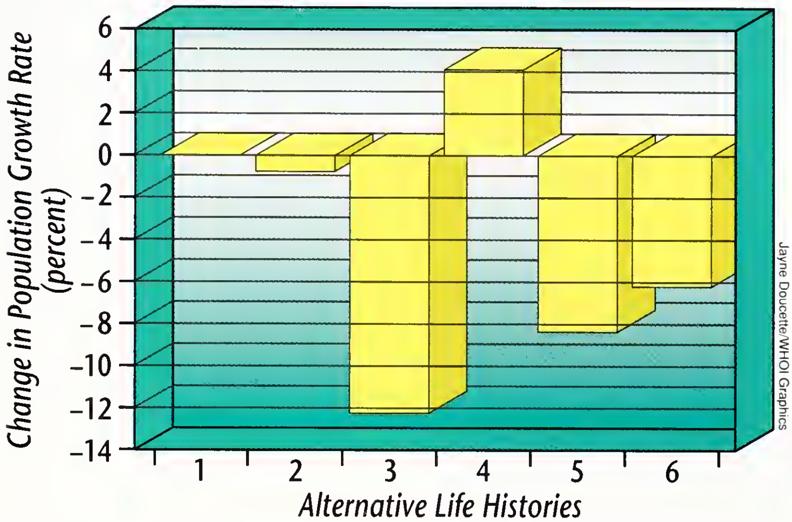
Catherine S. McFadden

Soft Corals: Sexual and Asexual Reproduction

Corals are colonial animals, made up of interconnected clonal polyps. Through asexual processes, coral colonies can grow by *budding* new clonal polyps (where a small part of the colony becomes differentiated and separates), or via *fragmentation* (breaking into many pieces) or *fission* (breaking into two more-or-less equal parts). Colonies also reproduce sexually, by producing free-living larvae that later attach to rock surfaces and start new colonies. The corals' extremely plastic growth process means that we can't detect their ages: A small colony could be young, or it could be old and fragmented.

Both asexual and sexual reproduction contribute to population growth, but which is more important? This question was recently addressed by Catherine McFadden (now at Harvey Mudd

College) in a study of intertidal soft corals. Individual colonies were measured and monitored for 15 to 20 months at four sites. A size-classified model was designed to calculate the growth rate of each of the four populations. The relative importance of the asexual and sexual reproductive modes was determined via a series of experiments on the model that would be impossible to perform in real life. By changing the model's parameters, McFadden eliminated specific life-history elements (for example, colony fission as a reproductive mode), then calculated



This bar graph forecasts how a soft coral's growth rate will change if different life-history modifications are made. The modifications include 1) The observed life history, with both sexual and asexual reproduction; 2) Sexual reproduction eliminated; 3) Asexual reproduction eliminated; 4) Sexual reproduction eliminated and replaced with an equivalent amount of asexual reproduction; 5) Asexual reproduction eliminated and replaced with an equivalent amount of sexual reproduction; and 6) Asexual reproduction eliminated, and sexual reproduction increased.

how that elimination affected the population growth rate. A clear conclusion emerges from this theoretical experiment: vegetative reproduction is most important to the population's growth, whereas sexual reproduction is a minor component of these corals' life histories. Similar conclusions were reached in other studies of corals. (This does not mean, however, that sexual reproduction may not become important under certain conditions. Free-living larvae are corals' only means of long-distance travel, and thus are crucial for colonizing new areas.)

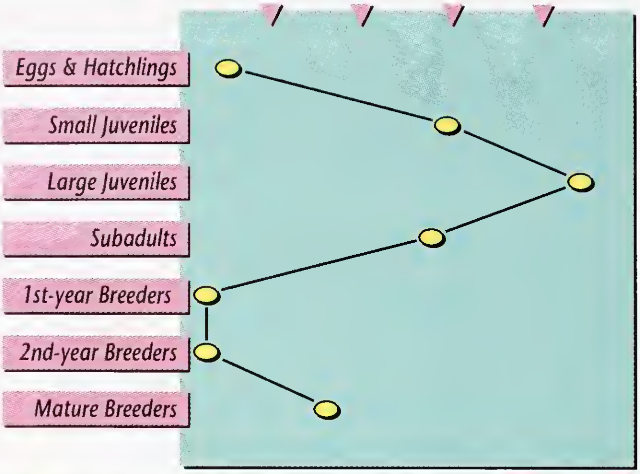
In this study, a structural population model was crucial for understanding the importance of alternative modes of reproduction; in real life, we cannot perform an experiment where one reproductive mode is eliminated. The model thus allows us to "dissect out" a life-history process to see what would happen to the population without it, and even to "transplant"an alternative process into the model.

Conservation Strategies for Sea Turtles

Structured population models are increasingly used to identify problems and evaluate strategies in conservation and population management. In recent efforts toward the conservation of marine turtles, stage-classified models have been important. Many marine turtle populations have declined to the brink of extinction. Until recently, most conservation efforts focused on protecting eggs on nesting beaches, but it was not known whether this was the best strategy, or whether protecting other periods of the turtle life cycle could be more successful.

These issues were addressed by Deborah Crouse (now at the Center

Using mathematical models to analyze conservation strategies for loggerhead turtles, Crouse and her colleagues found that if conservation efforts were focused on just eggs and hatchlings (below), even if all survived, the population would not increase; but if large juveniles were protected instead, the population would stabilize.



Jayne Doucette/WHOI Graphics

Barbara Schroeder/Center for Marine Conservation, Washington DC

for Marine Conservation) using a stage-classified population model of the threatened loggerhead sea turtle. As yet we have no accurate method for determining marine turtles' ages, so an age-based model was not possible. Instead, the model was based on identifiable stages in the turtle's life cycle: egg, juvenile, subadult, novice breeder, and mature breeder. Analyzing the population matrix reveals that the population growth rate was less than one, which supports the conclusion that the current vital rates are not capable of supporting population growth—the population will indeed decline if the situation remains as it is.

The goal of a management strategy is to change one or more of the vital rates in such a way as to increase the population growth rate. This study used sensitivity analysis to determine the impact on the rate of increase brought about by protecting different stages. It showed that juvenile and subadult survival most strongly affected population growth. To illustrate their point, Crouse and her colleagues asked, If protection efforts were to focus on a single stage, how much of an increase in survival would be necessary to obtain a nondeclining population? They found that if all eggs and hatchlings survived, the population would still decrease; in contrast, if the survival of large juveniles and breeders were increased by 14 to 19 percent, the population would stabilize.

Translated into management strategy, this means that the large animals needed to be protected, as well as their eggs. Historically, the shrimp-trawl fishery was the largest direct cause of human-induced mortality in juvenile and adult loggerheads. Turtle excluder devices (TEDs) were developed to fit in shrimp-trawl throats and allow turtles to escape from the net. Crouse's loggerhead population model significantly impacted the debate on using TEDs as a management tool by showing that an increase in large-animal survival would have a great effect on the population. In 1987, the National Marine Fisheries Service instituted a regulation requiring TED use in US Atlantic and Gulf Coast waters where sea turtles are found.

Copepods: The Adaptive Value of Vertical Migration

Population managers are not the only ones interested in evaluating the effects of changes in life-history parameters. Natural selection does it all the time. To claim that a behavior or structure is adaptive, one must show that its effects on the vital rates translate into an increase in fitness, where fitness can be measured by the population growth rate. One such model was recently applied to studies of copepod vertical migration. Copepods are planktonic animals that resemble small shrimp and feed on phytoplankton. Like shrimp, they hatch from eggs and undergo several shell molts during their development. Until they reach adult stage, each new molt signifies a new stage, recognizable by a specific body shape or number of appendages.

Like many other types of zooplankton, copepods often move up and down the water column in a daily cycle, usually down from the surface at daybreak and back up to the surface around dusk. This diel vertical migration (DVM) may carry the copepod from the warm surface water across the thermocline to colder deep water. DVM can vary or not happen at all, depending on the developmental stage, time, or place, even within a single species.

Why do copepods bother to travel up and down the water column every day?

Various hypotheses have been advanced to answer the question, Why do copepods bother to travel up and down the water column every day? One of these, the "demographic advantage" hypothesis, focuses on the consequences of DVM to population growth by weighing the possible costs and benefits of migrating, using the population-increase rate as a common fitness "currency." But what *are* the costs and benefits of vertical migration? First, the cooler water below the thermocline has two main effects on the individual copepod's growth: slowing development rate and allowing it to reach a larger size (and, consequently, produce more eggs). These affect fitness in opposite ways: slower development means a lower population-increase rate, but higher fecundity means a higher rate. Second, DVM allows copepods to avoid visual predators by moving to darker depths during daylight hours, which is a clear benefit. Thus the behavior pattern of DVM affects several vital rates (growth, survival, and reproduction) in different ways. What is the net effect on the population?

To address this question, Mark Ohman (Scripps Institution of Oceanography) used a structured population model to compare fitness of migrating and nonmigrating individuals of the copepod *Pseudocalanus* sp., which exhibits DVM in the late larval stages, when individuals are relatively large.

First, Ohman built an age-structured model of the copepod population that included DVM effects on individual growth and fecundity, but did not consider predation mortality. He found that the costs of DVM (slower development) outweighed its benefits (larger adult size and more eggs). However, when he included even a small reduction in mortality, due to predator avoidance, the outcome was reversed and

DVM became advantageous. This interpretation of DVM as a predator-avoidance mechanism agrees with the observed behavior: When visual predators are abundant, the normal DVM is observed (copepods are found deeper during the day); when nocturnal predators predominate, the normal DVM is reversed; and when there are few predators around, copepods tend not to migrate.

Steve Bollens (Woods Hole Oceanographic Institution, WHOI) reached similar conclusions in his study of another copepod species, *Euchaeta elongata*. These adult females carry conspicuous egg sacs that should make them more vulnerable to visual predators. Bollens found that females without egg sacs migrate, whereas females with eggs stay in deeper water both day and night. As in Ohmans's study, Bollens's population model indicated that staying deep is only advantageous if predator-caused mortality is included in the calculations; otherwise, the costs of migrating outweigh the benefits.

Adding More Complexity

Simplifying—extracting the essential life-cycle elements, biological interactions, and physical factors—is the task that confronts us now.

As interesting as they are, these examples share a common limitation. Each one describes a population in terms of the vital rates measured (or hypothesized) at some point in time and space. They consider the effects of possible changes in vital rates, but include no mechanisms to describe how the vital rates are determined. Vital rates are not static; they vary in response to the physical environment, resource availability, and interactions with predators and competitors. Many questions, especially those involving spatio-temporal patterns in response to physical factors, require that we extend the structured life-cycle modeling approach to include the dynamic factors that affect vital rates.

Conceptually this is straightforward; one simply considers the vital rates as functions of the physical environment (light, temperature, salinity) and the abundance of resources, predators, and competitors. The resulting model can even be embedded in a dynamic description of the current field for some part of the ocean.

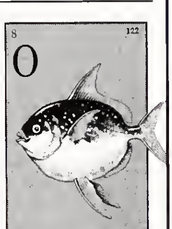
A good example of this modeling approach was produced by Cabell Davis (WHOI) in a study of *Pseudocalanus* sp. on Georges Bank. Observations showed a characteristic spatial pattern of population structure around the bank. In December, the population was dominated by adults along the bank's western edge, and mid-stage individuals on the eastern half. By February, this pattern had shifted in a clockwise pattern around the bank, with adults in the western and northern areas and juveniles in the southeast and southwest regions. Davis hypothesized that this pattern could result from the interaction between the copepods' life cycle (which is temperature dependent) and the clockwise circulation pattern on the bank.

Davis constructed a model that classified individuals by both developmental stage and age, in which individuals grow, die, and reproduce at rates dependent on temperature, and the population moves in space according to current patterns around Georges Bank. Davis's "computer copepods" grew, died, and reproduced while being entrained by a physical processes model simulating the circulation around the bank. He then compared the spatial patterns of copepod abundance at different stages in this simulated population to the pattern he observed from many animal samplings on Georges Bank over time. The agreement between the observed and simulated spatial distributions shows that the hypothesis tying together physical processes and population dynamics is reasonable. In this case, leaving aside the animals' life history would not allow us to adequately explain the large-scale spatial patterns of their abundance.

Davis's model for *Pseudocalanus* is complex, even though it includes only a limited set of biological and physical processes. It is easy to imagine including more, but in practice such models become enormously complicated, straining the resources of even the largest computers and—more importantly—producing results that strain mathematical ecologists' ability to interpret them. Simplifying—extracting the essential life-cycle elements, biological interactions, and physical factors—is the task that confronts us now. Developments in mathematics, ecology, computers, and oceanography guarantee that the results will be exciting.

Hal Caswell was trained in mathematical ecology at Michigan State University. He spends much of his time figuring out ways to model populations. Somehow he became convinced that turning organisms into equations reveals similarities where before there appeared to be only differences. As a result, he continues to confuse his colleagues at Woods Hole Oceanographic Institution (where he is a Senior Scientist in the Department of Biology) by mixing studies of bryozoans, corals, polychaetes, and whales with analyses of grasses, Daphnia, *insects, and birds.*

Solange Brault completed her Ph.D. on the population dynamics of moths and wasps at Imperial College in London. This obviously prepared her well for her present work on population models of killer whales and pilot whales at the Northeast Fisheries Science Center in Woods Hole. Her interest in marine ecology dates from her early graduate studies on subtidal benthic communities in eastern Canada, where she learned that the capacity for being very cold is one of the requirements for becoming a true field oceanographer. Hence the moths and wasps.



GLOBEC

Global Ocean Ecosystems Dynamics

Mark Huntley

GLOBEC scientists are studying how physical processes that affect planktonic organisms are likely to shift with changes in global climate.

The environment of our planet is changing. Many of the changes are thought to be the consequences of human intervention into natural processes, but paleoclimatic records reveal that Earth has experienced at least some similar changes in the past. Studies of shifts in our planet's physical and geochemical environments are critically important, but equally urgent is the challenge of assessing the biological consequences and sustainability of biological life-support systems in the face of such global change.

Under GLOBEC, the GLOBal ocean ECosystems dynamics program, oceanographic and fisheries scientists are addressing how global environmental changes would affect the abundance and production of animals in the sea. Their objective is to understand the mechanisms that determine how the abundances of key marine animal population sizes vary in space and time.

Scientists cannot predict with complete certainty the impact that global change will have on the oceans and atmosphere. Nevertheless, reasonable predictions include global warming from the "greenhouse effect," altered precipitation patterns, and a rise in sea level. The common thread in all these scenarios is that changing global climate affects physical phenomena in the sea. From large scales such as the circulation of the entire Gulf of Alaska, to smaller scales of turbulence, mixing, and transport nearshore and in oceanic fronts, the oceanic environment is likely to change due to atmospheric warming and increased freshwater input.

All animals in the sea are affected to some degree by the dynamics of their watery environment, but the lives of planktonic animals are most tightly coupled to the physics of the fluid medium. GLOBEC scientists are studying how physical processes that affect planktonic organisms are likely to shift with changes in global climate. Most marine animals spend at least the early portion of their life—if not their entire life—in the plankton, feeding on microscopic plants that are also planktonic. Therefore GLOBEC focuses on marine zooplankton.

The GLOBEC strategy is to assess the impact of changing ocean physics at the level of the individual organism, and then at the level of populations of organisms. This is a "first principles" approach to understanding the dynamics of ocean ecosystem change based on interactions between organisms and their biological and physical environments.

GLOBEC

GLOBAL OCEAN ECOSYSTEMS DYNAMICS

A Component of the U.S. Global Change Research Program

Funding for the US GLOBEC program, whose national steering committee was formed in early 1989, has come from the National Science Foundation (NSF), the National Oceanic and Atmospheric Administration (NOAA), and the Office of Naval Research (ONR). GLOBEC is a component of the US Global Change Research Program, and its US efforts are coordinated with similar research initiatives in other countries.

The strategy is to assess the impact of changing ocean physics at the level of the individual organism, and then at the level of populations of organisms.

GLOBEC Research Goals

The central scientific goals of GLOBEC research are:

- To vastly increase our understanding of the fundamental processes determining marine animal abundances, fluctuations in abundances, and the secondary production of ocean ecosystems, in the context of a changing global climate;
- To develop and apply new methods for evaluating key life-history parameters of marine animal populations, including mortality, reproduction, and growth; and
- To acquire the capability to predict how marine animal populations will be affected by global change.

Intensive research and development is planned in three key areas: mathematical modeling, new technology, and interdisciplinary field studies.

Mathematical Modeling

In any investigation, the first step is to determine what we know and what we don't know. The first step in GLOBEC is a modeling effort to reveal how well we are able to apply our present knowledge of physical oceanography to the known population biology of marine organisms with numerous, distinct, planktonic life stages. This will tell us where our knowledge breaks down, suggest where we need to develop new instrumentation, and aid in the design of multi-ship, multi-investigator field research programs.

Six modeling research programs are currently under way in three broad areas of emphasis:

(1) Conceptual studies of simplification and predictability that include

developing methods for scaling, pooling, and averaging, and extending the limits of predictability in the chaotic ocean environment;

(2) Prototype investigations of biological processes in idealized flows, where the effects of various fluid dynamical environments on biological processes such as swimming, feeding, metabolism, and aggregation are examined with numerical simulations; and

(3) Site-specific models, where the effects of changes in climate and physical circulation on marine animal populations are examined using historical data from specific sites in the ocean.

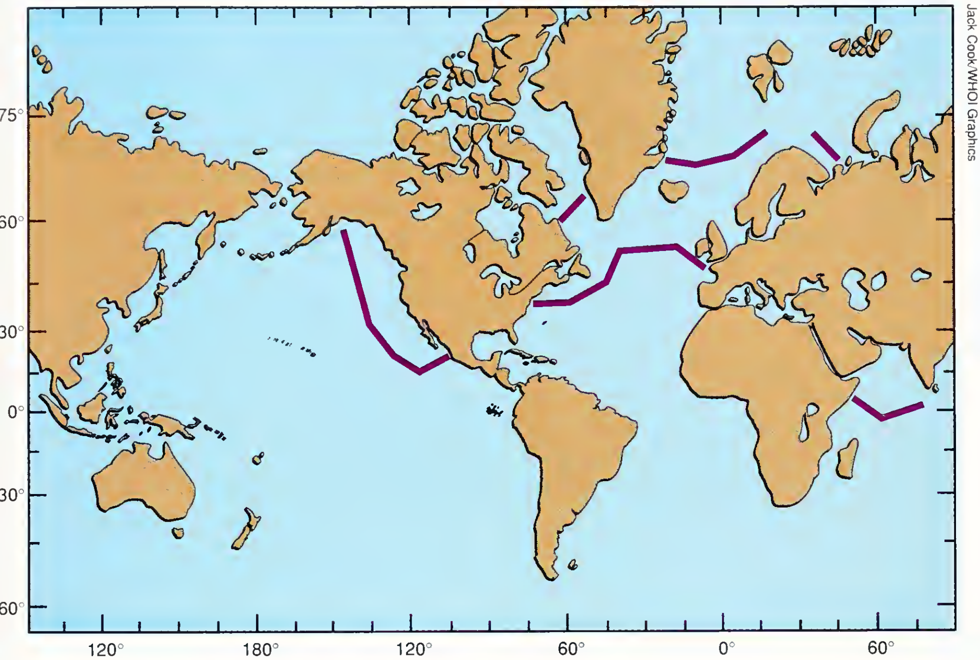
New Technology

To fundamentally change the practice of biological oceanography in the context of GLOBEC, we require new field sampling technologies and biotechnological methods. Field sampling technology is instrumentation for measuring zooplankton distribution and abundance. The principal tool for sampling zooplankton today is the plankton net, just as it was aboard HMS *Challenger*, whose world-encircling investigations marked the advent of oceanographic science more than a century ago. However, a variety of new technologies have recently come upon the scene, although none of them are widely used yet. These include high-frequency acoustics, optical imaging, and electromagnetic detection devices. Unlike the many varieties of plankton nets, which allow observations only at relatively coarse scales (hundreds to thousands of meters), these new technologies offer the possibility to make continuous measurements at very fine scales (centimeters to meters). These instruments may well change the practice and understanding of biological oceanography in the same way that the conductivity/temperature/depth (CTD) probe changed physical oceanography several decades ago.

The tremendous explosion of knowledge in the biological sciences over the past decade provides an array of new methods just waiting to be applied in biological oceanography.

Biotechnological methods promise rapid and accurate taxonomic identification, as well as easier assessment of the physiological rates of zooplankton. Identification is now accomplished as it has been for centuries, by observing the subject organism under a microscope. Measuring physiological functioning rates such as growth, respiration, and feeding has for decades depended on "bottle" experiments: A small number of animals are placed in a container, and rates are inferred from changes in their bodies or, more often, their environment. The physiological rates of the entire population are then extrapolated from relatively few measurements. These approaches are about to change.

The tremendous explosion of knowledge in the biological sciences over the past decade provides an array of new methods just waiting to be applied in biological oceanography. For example, species identification can now be accomplished using genetic probes, immunological methods, or image analysis (see Biological Oceanography from a Molecular Perspective, page 47). Because of our improved understanding of biochemistry, many physiological rates can now be assessed by measuring the activities of certain enzymes that play major roles in respiration, digestion, growth, and protein and lipid biosynthesis. These methods are generally faster than the bottle-incubation approach, and therefore open up the possibility of replacing a single measurement with thousands of measurements, greatly improving the space and time resolution for observing physiological rates of marine populations.



Research sites of key interest to the GLOBEC program (clockwise, in purple) include the Alaska Gyre and coastal northeast Pacific Ocean, the North Atlantic Ocean, the northwestern Indian Ocean, and (not shown here) the Bellingshausen Sea in the Southern Ocean.

Field Research Programs

Certain key GLOBEC sites in a number of oceanic regions have been identified, including the North Atlantic, Southern, Indian, and Pacific oceans. Each site has been suggested for different reasons, but they all share common attributes:

- Coupled ocean-atmosphere models suggest that global climate change will have a significant impact on some aspect of the ecosystem;
- There exists in each area a relatively long historical record that identifies the most important species in the ecosystem, and tells where and when they are likely to be located; and
- Some consideration was given to the prospects for international collaboration, the relation to other global change programs (such as the World Ocean Circulation Experiment and the Joint Global Ocean Flux Study), and the likelihood that results from a given region might have general application to other areas of the global ocean.

North Atlantic Ocean. Global climate models predict that some of the greatest increases in sea surface temperature are likely to occur in the North Atlantic Ocean. This may not only change the location and magnitude of major ocean currents, but may also directly affect the success of marine animal populations. One species of great interest in this region is the ubiquitous Atlantic cod, exploited as a fishery since the 16th century. In the past decade there has been a significant decrease in the cod populations throughout its range, which includes Georges Bank, the Grand Banks of Newfoundland, the Iceland Shelf, the Norwegian Sea, and the North Sea. The reason for this decrease is not known, although changes in local climate are a suspected cause. On recently documented decadal time scales, cod stocks have declined in concert with fluctuations in winds, sea temperature, and salinity. Correlations appear to exist, but the mechanisms are unknown. Proposals to the Joint

National Science Foundation/National Oceanic and Atmospheric Administration GLOBEC Program Office were due in September for an interdisciplinary field research program based in the Atlantic Ocean, from Georges Bank to the Labrador Sea.

Key unanswered questions for this area include how adult cod locate spawning sites and how populations are retained or exported from their preferred areas of aggregation. Similar questions pertain to the copepods *Calanus finmarchicus*, *Pseudocalanus* spp. and *Centropages* spp., which form the bulk food resource for larval and juvenile cod. These species occur on the productive shallow banks of the Northwest Atlantic Ocean in spring and summer and are thought to find refuge in local deep basins during winter, but the specific mechanisms of this behavior are unknown. As for important bottom-dwelling species such as sea scallops, little is known of how populations are maintained on the same shallow bank areas; the mechanism certainly involves an interaction between food availability, reproductive activity, release of planktonic larvae into ocean currents, and the factors that stimulate settlement of larval stages onto surfaces appropriate to growth.

Life cycles of animals throughout the marine antarctic food web are adapted to the annual change in sea-ice cover.

Southern Ocean. Global climate change is predicted to be greatest at high latitudes, with principal effects likely to be increased concentrations of atmospheric carbon dioxide, increased temperature, and changes in ocean circulation. The Antarctic ice sheet contains 90 percent of the world's fresh water, representing a potential sea level rise of 60 meters. Major portions of the ice sheet are known to have disintegrated on time scales of approximately 100 years during past ice ages. Sea ice covers half of the Southern Ocean in winter, and less than 10 percent in the summer. During the last glacial period the winter sea ice covered almost the entire Southern Ocean.

Life cycles of animals throughout the marine antarctic food web are adapted to the annual change in sea-ice cover. The entire biological cycle of the Southern Ocean is linked to the annual production of melt water, which stabilizes the upper ocean and stimulates the production of marine plants that ultimately feed all higher trophic levels. Furthermore, seasonal pack ice creates a unique habitat for a variety of animals, from seals and penguins to the abundant, shrimplike krill upon which most of them feed.

Concern for the effects of global climate change on marine animal populations in the Southern Ocean led to a meeting of scientists from 12 nations, sponsored by GLOBEC, and held at Scripps Institution of Oceanography in mid-1991. Key species recommended for study included the Antarctic krill, *Euphausia superba*, and selected species of fish, penguins, and bottom-dwelling crustaceans. It was generally agreed that the largest gap in our knowledge concerns the behavior and dynamics of animal populations during winter, when few research expeditions have been carried out. Only the first steps in planning have taken place with respect to the Southern Ocean, and if studies are initiated they will not likely begin before the latter half of the decade.

Indian Ocean. The monsoon-driven oceanographic regime of the northwestern Indian Ocean makes this region of key interest as a GLOBEC study site. Steady wind forcing occurs during alternating northeast (December to February) and southwest (May to August) monsoons, with intermediate lulls in the wind during spring and fall.

This region, one of the few places on Earth where a complete switch in wind direction is interspersed with regular lulls, makes it ideal for the study of air-sea interactions and ecosystem response to physical changes. For example, phytoplankton blooms occur during monsoons, but plant biomass crashes between monsoons, rendering it a biological desert. Similar massive variations ripple up the food chain, affecting zooplankton, as well as myctophid fishes and tuna, both of which are important fisheries.

Pacific Ocean. The GLOBEC scientific steering committee is interested in the development of field research programs in the Pacific Ocean, and sponsored a meeting in late 1991 at University of California, Davis, to recommend specific studies. Areas of likely interest include the buoyancy-driven coastal regime of the Alaska Current, which maintains large populations of salmon, pollock, herring, shrimp, and crab; the Alaska Gyre, which supports many of the same species but is truly an open-ocean ecosystem; and the eastern boundary current systems, the California and Humboldt currents, which support a variety of important fisheries and are strongly affected by the unique climatic event, El Niño/Southern Oscillation.

Phytoplankton blooms occur during monsoons, but plant biomass crashes between monsoons, rendering it a biological desert.

The Next Decade

Understanding the effects of global climate change on marine animal populations will require a concerted effort by biological oceanographers, physical oceanographers, meteorologists, mathematical modelers, and engineers around the world. It is a problem we cannot ignore, dependent as we are on the biological resources of the ocean—not just for economic reasons, but because life on this planet depends on biogeochemical cycles. GLOBEC and associated programs will bring to oceanography new concepts from modeling, new instruments from technology development, new insights and predictive capability from field research, and a great increase in understanding the climatic and fluid dynamical mechanisms that affect marine animal populations.

For further details about GLOBEC, contact Sharon Lynch, US GLOBEC Program Office, Division of Environmental Studies, University of California, Davis, Davis, California 95616.

Mark Huntley is a Research Biologist at Scripps Institution of Oceanography, La Jolla, California, whose principal research interest is the physiological ecology and population dynamics of zooplankton. He currently serves as a member of the GLOBEC scientific steering committee.

Visualizing Life in the Ocean Interior

Instruments for Probing the Depths

Peter H. Wiebe, Cabell S. Davis, and Charles H. Greene

For more than 100 years, remotely operated instruments have been fundamental to observing and collecting organisms.

The ocean interior is a dark, inhospitable environment for an ecologist, one difficult to study by virtue of its size and inaccessibility. Except for short periods of viewing the surface from the deck of a research vessel or the ocean interior from a submarine or in a wetsuit, an open-ocean ecologist cannot "see" into this fascinating three-dimensional habitat to visualize the spatial arrangement and daily activities of the organisms living there. This is in stark contrast to terrestrial ecologists who can stroll through forests, meadows, savannas, or deserts, simultaneously viewing the structural complexity and the patterns of the ecosystem.

As a result, from the beginning of modern biological oceanography more than 100 years ago, remotely operated instruments have been fundamental to observing and collecting organisms. While we have some understanding of the creatures that inhabit this largest Earth ecosystem, on the whole its environment and its inhabitants are still poorly known. However, recent technological advances promise a new era of greater ability to remotely sense (and therefore study) the animals of the ocean interior.

For most of this century, biological sampling of the deep ocean has depended upon winches and steel cables to deploy a variety of instruments. For the most part, the samplers fall into three classes:

- water-bottle samplers that take discrete samples of relatively small volumes of water (a few liters),
- pumping systems that sample intermediate volumes of water (tens of liters to tens of cubic meters), and
- nets of many different shapes and sizes that are towed vertically, horizontally, or obliquely and sample much larger volumes of water (tens to thousands of cubic meters).

Depth-specific collecting nets opened or closed mechanically, either with weighted "messengers" traveling down the towing cable by gravity to trigger a trip mechanism, or by a pressure- or flow-meter activated release.

An ingenious system invented by Sir Allister Hardy is known as the continuous plankton recorder. This towed sampler is a streamlined box with a small seawater opening at the front. Two fine sheets of plankton gauze behind the opening filter animals from the seawater as they are slowly wound onto a propeller-driven takeup spool. When the gauze is unrolled, the flattened animals can be counted and their spatial distribution and abundance recorded. This system was developed in the 1920s and still is used for sampling the North Atlantic.

In the 1950s and 1960s, conducting cables and transistorized electronics were adapted for oceanographic use, and more sophisticated net systems began to do more than collect animals at specific depth intervals. Multiple net systems now carry sensors to measure water properties such as temperature, pressure/depth, conductivity/salinity, plant fluorescence/biomass, and beam attenuation/total particulate matter. They also measure net properties such as volume of water filtered, net speed, and altitude from the bottom, as well as net function such as an alarm to tell when a net closes. One widely used British system, the RMT, carries three nets and uses acoustical telemetry to send information about net depth and water temperature to the surface, and to receive commands to change nets. An American system, the MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) carries nine nets along with all of the sensors listed above, and uses conducting cable to transmit data to and from the net system for display and computer processing in real time. A Canadian system known as BIONESS (Bedford Institute of Oceanography multiple Net and Environmental Sensing System) carries 10 nets and many of the same sensors. Hardy's continuous plankton recorder also has electronic variants, beginning with the Longhurst-Hardy plankton recorder developed in the mid 1960s.

In spite of their advanced features, all instruments deployed from cables to collect organisms are limited in their temporal and spatial coverage. This is not only because of the large amount of time it takes to collect a sample (tens of minutes to an hour or more, and many hours to complete an entire multiple net haul), but also because of the time required (hours to a day or more) to identifiy and count individuals by species under a microscope. For many studies, time-series observations are needed for periods of time much longer than an expedition's duration. For example, the duration of a generation of some species is months to a year or more, and sampling should cover the entire period. Conventional sampling, using the tools described, is often limited to periods when the weather is cooperative. When the seas get rough, instruments are lashed to the deck and hatches are battened down. Work can only resume when the seas are calm. In the course of a year, about half of the ocean, surface and subsurface, is unavailable for study because it is too rough and we lack the platforms and instruments to permit work to continue. Unfortunately, it is precisely during these periods that observations are dearly needed, and our ignorance of the impact of such events on animal life is the greatest.

Electromagnetic radiation in the range of visible light and high-frequency sound are being harnessed in a variety of ways to create surrogate "eyes."

New technologies are, however, beginning to overcome these difficulties. Electromagnetic radiation in the range of visible light and high-frequency sound are being harnessed in a variety of ways to create surrogate "eyes." By creating images of the organisms living in the oceans, these eyes are leading to new insights about organisms' spatial patterns and behavior.

Although seawater transmits visible light poorly (it is absorbed, scattered, and reflected far more in seawater than in air), the electronics revolution and the advent of low-priced video cameras has made it possible to develop an instrument dubbed the video plankton recorder (VPR), which promises to revolutionize the way we obtain information about oceanic plankton. The VPR is the newest manifestation of the continuous plankton recorder.

In its current form, the system is mounted on a towed body that has a bank of four cameras on one forward-facing side arm and a strobe light on the other side arm. Each of the cameras, which take video images at 60 fields per second, are aimed at a particular volume of water in front of the towed body. A zoom-telephoto lens and extension tube is fitted to each camera and adjusted so that each camera has a different magnification. The fields of view range from half a centimeter to 10 centimeters and can resolve individuals as small as 10 micrometers (a micrometer is one millionth of a meter) in the field illuminated by the flashing strobe. Remarkably clear images of plankton frozen in space are transmitted to the surface in real time on fiber-optic cable, another recent technological advance that allows use of the VPR in the deep ocean. A sensor package similar to the one the MOCNESS carries provides information about the animals' physical and biological environment.

High-frequency sound in the 100-kilohertz to 1-megahertz range can be used to detect animals tens to hundreds of meters away from the sound source.

The VPR is also being configured for use on moorings using batteries and satellite telemetry and on remotely operated vehicles (ROVs). Use of the VPR on dynamically positioned ROVs will allow tracking of individual plankton to quantify their swimming and feeding activities. Observations like these will provide important information about the interactions between planktonic predators and prey and the effects of small-scale physical processes on planktonic swimming behaviors.

Exploring the Possibilities of Sound

Although the transmission of light in seawater is quite limited, the transmission of sound at low and moderately high frequencies (1 hertz to 100 kilohertz) is much greater. Above 100 kilohertz, sound in seawater is very rapidly attenuated primarily because it is absorbed due to the salt (principally magnesium sulfate). In spite of this limitation, high-frequency sound in the 100-kilohertz to 1-megahertz range is proving exceedingly useful for studies of zooplankton and free-swimming animals because it can be used to detect the presence of animals tens to hundreds of meters away from the transducer (sound source).

Sonar systems were first developed in the 1930s and 1940s for military purposes, but biologists quickly became involved when it was discovered that most of the acoustic backscattering (reflection of sound from particles in the water) was caused by organisms in the water column. Acoustical techniques have been used for many years by fisheries biologists to assess fish stocks, but only recently have high-frequency acoustics has been employed in plankton studies.

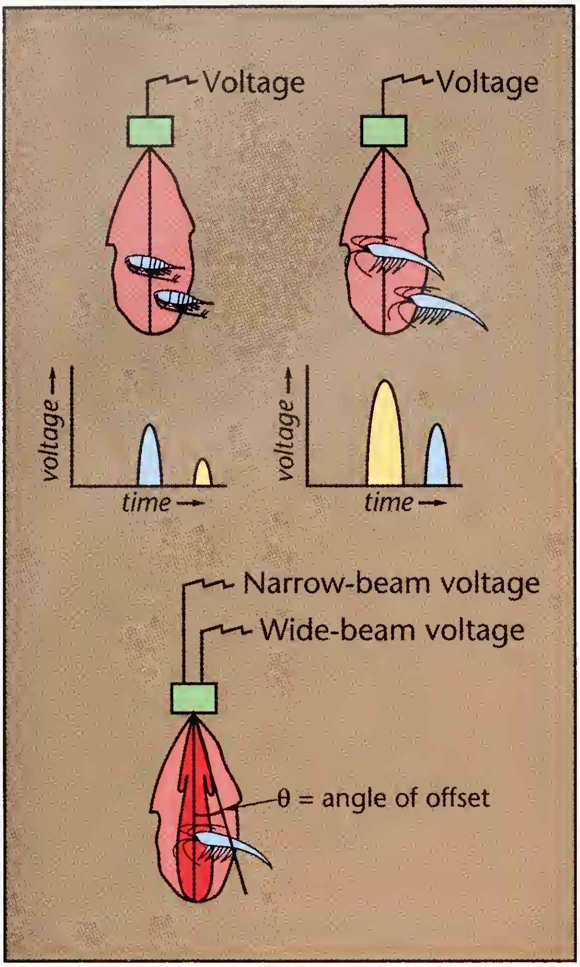
During the last decade, two acoustic methods for estimating zooplankton biomass, numerical abundance, and size distribution have developed rapidly. The instrument employing the first method carries an array of 21 transducers each tuned to a different frequency (100 kilohertz to 10 megahertz). Known as MAPS (Multiple Acoustic Profiling System), this system fires each transducer sequentially, and then selectively records the acoustic backscattering only from animals in a

The video plankton recorder (VPR) is being deployed from the starboard side of R/V Endeavor, *during a May 1992 cruise to Georges Bank. While towing the VPR system in a warm-core ring to the south of Georges Bank, this image of* Trichodesmium *was obtained. (A slower camera image of* Trichodesmium is *on page 37.)*

zone 1 to 2 meters away from the transducers. Echoes coming back to the system are usually from more than one individual, and it is important to understand that the amount of sound backscattered depends on the animal's size and the sound frequency being used. Thus, small animals are only detectable with high frequencies, whereas large animals can be detected with all frequencies. To estimate the numbers of individuals and their sizes, a sophisticated mathematical inversion technique is used to answer the question: Given the amount of backscattering at each frequency and a model of how different sizes of animals scatter sound, what combination of numbers of individuals of various sizes best fits the data received at each frequency?

In contrast to the multifrequency approach, the second method in its simple form uses only a single frequency, but has two beams, one narrow and one wide. This dual-beam method (figure overleaf) solves a serious problem found in all single-beam systems, namely the determination of an individual's position in the acoustic beam. When a transducer produces sound, maximal energy is transmitted on the main axis of the beam. As sound travels away from the transducer, it spreads and the energy per unit area drops inversely with range, but the maximum energy at any range is still on the main axis. The amount of energy reflected back to the transducer from an animal is therefore dependent upon where in the beam the animal is located. If the amount of energy reflected is to be used to estimate the animal's size, then its position in the beam must be known. The dual-beam architecture solves that problem by transmitting with the narrow beam and listening for the return on both beams. As an individual moves off axis, less and energy is received on the narrow beam compared to the wide beam. Thus, the difference in the energy returned between the two beams is a measure of the animal's off axis position.

In a conventional dual-beam system deployment, transducers are



Jack Cook/WHOI Graphics

With a single-beam echosounder (above), we can't tell if an echo is from a large individual at the edge of the beam or a small individual at the center of the beam. With the dual-beam system (below), the ratio of the voltage returned on the narrow and wide beams permits the individual's off-axis angle (θ) to be calculated, and its absolute acoustic size can then be determined.

mounted facing down in a streamlined body, and the system makes acoustic measurements while being towed along a track line. A single section provides two-dimensional information (depth versus distance along the track line), and when repeated provides a time series of changes in the area. Three-dimensional information can be developed if parallel track lines in the form of a grid (or some other configuration such as a star pattern) are quickly run. Of course, to reconstruct the spatial pattern, the assumption that water and animal movements are negligible during the period of observation must be true. This is often not the case, and more complicated sampling designs are needed that take such movements into account. Still, with the new instrumentation becoming available, we are just now in a position to create very high-resolution two- and three-dimensional acoustic images of the spatial distribution of plankton.

During a May 1992 expedition to Georges Bank, we deployed a dual-beam echo sounder for a series of track lines approximately perpendicular to the bathymetry on the Bank's southern flank. One track line extended from the southern flank to the well-mixed area on top of the Bank, a distance of about 17 nautical miles. We also conducted four studies using grids about 1 nautical mile on a side, running six legs spaced 370 meters apart within the grid.

A striking feature was the great differences in backscattering between the site on the Bank's southern flank and the well-mixed region, with the latter having substantially lower backscattering (about five times less). In addition, there were major differences in the vertical distribution of the acoustic scatterers in these two regions, with pronounced stratification of the scatterers at mid-depths or the surface at the southern flank site and little or no stratification of the scatterers at the well-mixed site. On the transect between the southern flank site and the well mixed site, an abrupt transition between the two regions was observed about midway along the track line.

There was also substantial fine- and coarse-scale horizontal and vertical variability along the transect and the grid lines especially at the southern flank site. Periodic horizontal variation in mid-depth layers suggests internal-wave motion. Smaller-scale scallop-shaped structures on the bottom margin of mid-depth layers suggests periodic bottom mixing or turbulence events that appear to dilute backscattering in the main, mid-depth layer and increase scattering near the bottom. None of these structures would have been detected by conventional net systems, but "seeing it" provides an image of processes affecting the animals that were not known about or even envisioned when the study was planned.

Minimizing the Effects of Noise

The view from the top is, however, increasingly biased, at least with regard to individual acoustic size measurements. Like snow on a television screen that increases as the television transmitter is further away from the set, so too the contribution from ambient noise increases with range, and the smallest, then larger, individuals can no longer be distinguished from the noise. A pattern of increasing individual size with depth could be real, or it could be that smaller individuals are hidden by noise. An alternative deployment scheme that eliminates this problem involves mounting the acoustic system on a research submarine so that the transducer points horizontally, and making acoustic profiles as the submarine travels between the surface and the seafloor. Horizontal track lines in layers of animals at intermediate depths are also possible with this configuration, and there are clear advantages to being in the submarine looking at the larger animals that pass by as the submarine moves along. However, the kind of mapping that can be done from a fast-moving ship cannot be done from a research submarine, so new strategies are required if we are to take advantage of the benefits each has to offer.

Submarines are expensive to operate and dive time is precious. ROVs, on the other hand, offer some of the same capabilities but are less expensive to operate and far more accessible. An ROV equipped with a dual-beam system and other environmental sensors has been used to study sound-scattering layers in Puget Sound and below the ice pack in the Eastern Arctic Ocean.

We are just now in a position to create very high-resolution two- and three-dimensional acoustic images of the spatial distribution of plankton.

The marriage of acoustics with other technologically advanced systems can enhance the capabilities of both. For example, the MOCNESS provides depth specific collections of animals and a broad suite of environmental measurements. Yet, the volume sampled at any given depth is small and the patchiness of the animals is so large that many tows are required to adequately characterize the community. It is also well known that larger animals actively avoid capture by net systems and so their true abundance is not known. By the same token, while the acoustic systems provide a much more comprehensive image of the patchiness of the animal populations, the identity of the acoustically measured individuals is unknown. Very recently, using the same fiber-optic cable that made the VPR possible, the dual-beam acoustics system became an integral part of the MOCNESS. Another conceivable "marriage" would be between the VPR and a dual-beam equipped MOCNESS.

A variety of autonomous instrumentation has served the physical oceanographic community for years; biological sensors developed during the last decade hold promise for monitoring phytoplankton with autonomous instruments. When combined with satellite telemetry systems they will enable researchers to deploy systems, return home, and receive the field information in near real-time at their laboratories.

As part of the May 1992 expedition to Georges Bank, BIOSPAR (BIOacoustic Sensing Platform And Relay), a prototype autonomous dual-beam, dual-frequency, downlooking sonar buoy, was moored in approximately 80 meters of water adjacent to a physical oceanographic mooring in a stratified area on the Bank's southern flank. Acoustic backscattering profiles were obtained for one minute every 15 minutes at 1-meter depth intervals throughout the water column. All data were stored on an optical disk unit in the buoy for processing later, and some of it was transmitted in reduced form to shore daily over a four-day period via satellite. The full data complement was telemetered in real time to the ship when it was within 5 to 10 kilometers of the buoy. Data from MOCNESS tows near BIOSPAR will be compared with BIOSPAR data.

The instrumentation discussed here represents a small subset of new, technologically advanced instruments being developed in laboratories around the country and abroad for studying life in the deep sea. The very real need to study the ocean environment in a much more detailed and comprehensive way can only be fulfilled by the continued development of remote-sensing systems like those described above. Significant, immediate challenges must be surmounted, such as the processing and storage of the massive amounts of data produced by these instruments. Visualization tools and techniques must be developed and applied to the data to enable researchers to reconstruct images of organisms' spatial and temporal patterns. These images, essential to the interpretation of complex data sets, require very high-speed computers and parallel processing techniques that have only recently become available to biological oceanographers.

Immediate challenges must be surmounted, such as the processing and storage of data.

We conduct our research in an exciting time because the new instrumentation is truly leading to a new age of ocean exploration, an age in which our understanding of the dynamics of the ocean ecosystem should increase significantly. This will inevitably lead to increased awareness of our dependence on ocean life forms and our need to wisely manage and protect the ocean ecosystem.

Growing up near the seashore in central California, Peter Wiebe developed a love for and a curiosity about the oceans at a very early age. After undergraduate studies in Northern Arizona, a region whose oceans disappeared 40 million years ago or so, making Peter a little late to be able to study them, he gained his formal training in biological oceanography at Scripps Institution of Oceanography. He is a Senior Scientist at the Woods Hole Oceanographic Institution (WHOI), where he has never been known to complain about not having enough to do.

Cabell S. Davis is an Associate Scientist in the Biology Department at WHOI. He entered graduate school in Woods Hole with the intention of studying fish populations, but somehow became permanently sidetracked lower in the food chain and now studies the ecology of marine zooplankton. His interests include field sampling of zooplankton using a towed video microscope, growing the little beasts in the laboratory, coaching his kids' soccer team, and fly fishing. His two young children are the only kids in their school who know that copepods are the most plentiful animals on Earth.

Charles H. Greene is Director of the Ocean Resources and Ecosystems Program at Cornell University's Center for the Environment. He arrived at WHOI as a postdoctoral fellow in 1985, and, once there, made the fateful decision to pursue his research interests in bioacoustical oceanography. As a WHOI Visiting Scientist, he continues this research with studies in the Arctic, Atlantic, Pacific, and Southern oceans. Although globetrotting takes a large toll on his available time, Professor Greene is strongly committed to undergraduate and graduate teaching along the shores of Lake Cayuga. When last seen, he was trying to raise the Lake's salinity to 34 percent in an attempt to convince the powers that be that Cornell was not just another landlocked university in upstate New York.

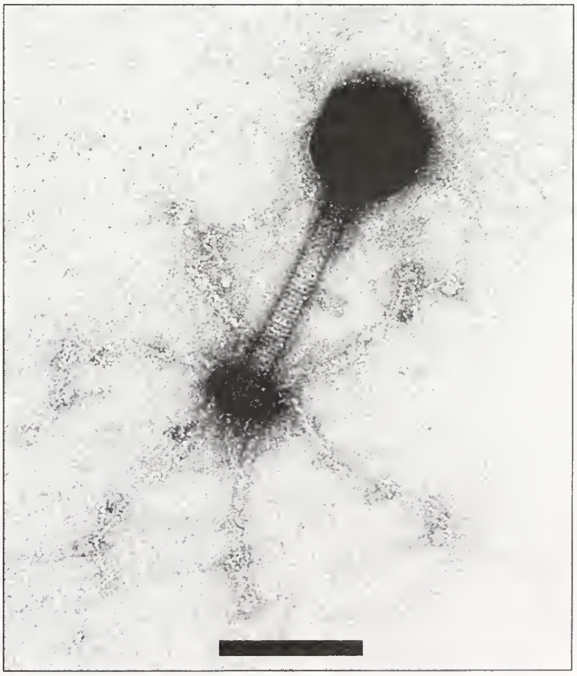
Viruses of Marine Bacteria

John B. Waterbury

Viruses are among the smallest and most numerous creatures in the sea. Strictly speaking, they are neither living nor nonliving, but lie on the borderline between. Viruses are parasites of cellular organisms including plants, animals, and bacteria. Individual virus species are very host specific, usually able to attack only a single host species or even single clones within a species.

Viruses occur in two states: one outside of cells and the other inside. Outside cells they exist as tiny particles that contain one or several molecules of nucleic acid, either DNA or RNA, that are usually but not always surrounded by a protein "coat." Viruses are smaller than cells, varying from 20 to 200 nanometers (a nanometer is one millionth of a millimeter) and their architecture ranges from roughly spherical bodies to complex structures like the ones illustrated. Outside cells, they are incapable of replication or metabolism. To replicate, a virus attaches to a host cell at a specific site and introduces its own nucleic acid into the cell. The virus's genetic material then commandeers the host cell, inducing it to produce the components required to make more viruses.

Viruses have long been known to exist in seawater, but in the last few years their role in marine microbial ecology became controversial as it was discovered how abundant they actually are. Using electron microscopy, it is not uncommon to find between 10,000 and 10,000,000 viruses per milliliter of seawater, many of them recognizable as tailed, bacterial viruses. In light of their abundance, it has been suggested that viral infection might be a significant cause of marine bacteria and phytoplankton mortalities. At least for bacteria, this has not proven to be the case. Bacteria have developed highly effective lines of defense to prevent viral attack, principally resistance. This is usually acquired through a single genetic mutation that alters the virus attachment site on the bacterial cell wall, preventing the virus from attaching.



A bacterial virus, as seen by electron microscopy, is a very small (the bar represents 100 nanometers) but complex structure. The major components are the head, the contractile tail, and six radiating tail fibers.

Thus when a bacterium and its specific viruses are isolated from a single seawater sample, almost all the bacterial isolates are found to be resistant to their co-occuring

The tails of these two bacterial viruses (right) have contracted, revealing the central core that transmits the nucleic acid from the head of the virus into the cell of the bacterial host. The bar in this image represents 100 nanometers. Numerous viral particles are adsorbed to the surface of one end of a ruptured bacterial cell (below). The tail of the viral particle in the upper left corner of this electron micrograph has contracted, and the central core has penetrated the bacterial cell wall.

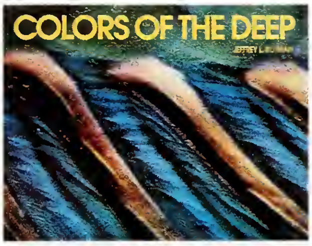
All Creature Feature photos are by author John B. Waterbury

viruses. However, some sensitive host cells persist, and these are responsible for releasing viruses at concentrations that typically result in a viral population about an order of magnitude lower than its host population. The virus-sensitive bacteria persist because they possess a subtle ecological advantage over their resistant counterparts. The viral attachment sites on their cell surfaces have other specific cellular functions. For example, their viral attachment sites may be proteins also involved in nutrient transport. Upon modification to confer resistance, nutrient transport may become less effective. Despite this and other possible ecological costs, the rapid acquisition of resistance is crucial for the stable co-existence of bacteria and their viruses, and prevents substantial bacterial mortality from viral attack.

There is a certain sense of deja vu associated with marine microbial ecologists' recent suggestion that viruses might be responsible for a large fraction of bacterial mortality in the oceans. For several decades following their discovery early in this century, viruses were advanced as agents to treat diseases caused by bacteria. Viruses were isolated that infected the bacteria causing a variety of diseases including cholera, diphtheria, dysentery, gonorrhea, and the plague. However, in each case, virus therapy failed, mainly because of the bacteria's ability to defend themselves against viral attack by rapidly acquiring resistance.

John B. Waterbury is an Associate Scientist in the Department of Biology at the Woods Hole Oceanographic Institution.

Colors of the Deep



By Jeffrey L. Rotman and Joseph S. Levine, 1990. Thomasson-Grant, Inc., Charlottesville, VA; 130 pp. - $45.

I laid this book on the floor and "read" it standing upright on my feet. It is a large (11.25 by 14.75-inches) book and the photographic images appeal best when viewed at a distance slightly greater than arm's length .

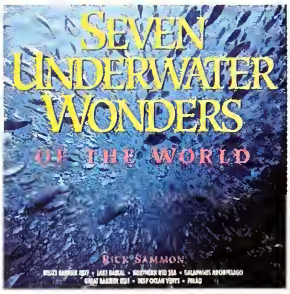
The images show details of fish and invertebrate morphology using macrophotography. The quality of the photographs and printing is excellent. The text, written by Joe Levine, is a series of short essays describing various topics such as whether or not fish can see color, coral biology, camouflage, fish color patterns, etc. The book emphasizes close-up detail of various animal body parts, and the detail allows the reader to really examine the surface texture of a variety of skin, scales, fins, and polyps. The book is like a marine biologist's version of an art book.

The book does not, however, provide a context for the images, that would allow the reader to truly appreciate the detail. It is hard to visualize the overall animal from a macroscopic detail of one fin, a mouth, or an eye. Although the photos are in stunning color and do stand alone in the abstract, I believe part of the fascination is that the photos show parts of actual living animals. As it is, only the expert amateur diver or marine biologist will be able to mentally connect the photographs in the book to images of whole animals. The identifications in the book use only English common names, so it is not easy to cross reference to other books and determine exactly which species was photographed, and where.

This picture book is a feast for the eye, but it may not satisfy the imagination or intellectual thirst of an amateur or professional naturalist.

—Phillip S. Lobel
Associate Scientist, Department of Biology
Woods Hole Oceanographic Institution

The Seven Underwater Wonders of the World



By Rick Sammon, 1992. Thomasson-Grant, Inc., Charlottesville, VA; 180 pp. - $29.95.

There is no shortage of beautiful underwater images today. Between glossy coffee-table books, calendars for environmental causes, and the pages of *National Geographic*, we can be surrounded with coral reefs and exotic fish in our living rooms and offices. *The Seven Underwater Wonders of the World*, by Rick Sammon, stands above much of the rest, offering a fresh look, with exquisite photography and an engaging, informative text, at some of the most magnificent scenery under water.

A diver, photographer, and writer, Sammon is also president of CEDAM, an international marine exploration organization dedicated to Conservation, Education, Diving, Archaeology, and Museums. The idea for this book was born when he and his wife Susan, after a spectacular dive on the Kenyan coast, mused on the ways that wonders of the sea, and the need to protect them, could be conveyed to the public. This led to an informal list of underwater "wonders" and later to the formation of a committee of divers, scientists, and environmentalists to select the "Seven Underwater Wonders of the World."

It must have been a difficult task, but the list boiled down to the chapters of this book: the Belize Barrier Reef, Lake Baikal, the northern Red Sea, the Galapagos Islands, Australia's Great Barrier Reef, the deep-ocean vents, and the atolls of Palau. Although dominated by tropical coral reef habitats, the list is especially interesting for its inclusion of Baikal and the hydrothermal vents. These two very different kinds of underwater wonders rarely show up in underwater photography books, but their images are as intriguing as those of riotous coral reefs, and their geology and biology are perhaps even more marvelous.

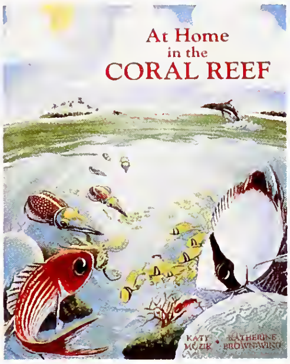
Sammon's book is full of stunning photographs, but it is really a book to read—a book about marine life, about diving, about photography, and about urgent needs for conservation. The narrative is personal and immediate; reading it is a pleasure to match the pictures. His seven stories of encounter with these extraordinary underwater places weave together threads of travelogue, history, science, anthropology, and a well-founded concern for the future of these special sites and others like them. He provides accurate scientific information, local anecdotes, and eco-political perspectives without ever seeming to digress from his explorations.

In the pictures and text, one message is clear: For all their beauty and scientific value, many of these underwater wonders are endangered by human civilization. On the seemingly resplendent Belize Barrier reef, the grouper fishery is on the brink of decline from overexploitation. Pristine Lake Baikal, the largest body of fresh water in the world, is seriously polluted along parts of its shore from pulp mills, clear-cut logging, and urban sewage. The reefs at Ras Muhammad are at risk both from prospective mineral exploitation and trashing by careless divers. In the Galapagos, where the unique terrestrial faunas of the islands long ago suffered the upheaval of introduced species and indiscriminate hunting, the marine environment is now endangered by rising tourism, development, and commercial fishing. Happily, Sammon can report that progress toward protection is being made in many instances, but he also details the kind of persistent effort from conservationists and scientists that is required to prevail against commercial interests or government inattention.

Most books of glossy underwater pictures can be opened at random and leafed through in any direction. In this book, browsers, caught in the interplay of words and images that recreate these special places, will quickly become readers. It's a beautiful work—visual, literate, scientific, and ethical—and recommended to anyone interested in wonders.

—Laurence P. Madin
Associate Scientist, Department of Biology
Woods Hole Oceanographic Institution

At Home In The Coral Reef



By Katy Muzik, illustrated by Katherine Brown-Wing, 1992. Charlesbridge Publishing, Watertown, MA; 28 pp. - $14.95.

Katy Muzik is a colorful marine-science personality who has just left her present position as associate of the Museum of Comparative Zoology at Harvard University to spend more time teaching and lecturing to young people. She's a popular lecturer, who has been known to travel to schools via subway, wearing her costume of diving suit, snorkel, and fins. If Muzik maintains the same light, friendly tone in her lectures that she does in her new book *At Home In The Coral Reef*, her young audiences are in for a treat.

Most of the book, which is appropriate for a five-to-seven-year old with an interest in the ocean, concerns the journey of a planula, a baby coral, to a new reef home. This journey is a good framework to have selected; it provides a story line while also allowing the reader to learn about the varied terrains and populations of many different environments in and around a coral reef. The tiny planula is carried to the surface, to a lagoon, to a mangrove swamp, to a beach, to a polluted area, and finally to a spot that is deep enough, healthy enough, rocky enough, and well-enough lit to provide a good home. By explaining the fragility of the coral reef environment from the perspective of a baby coral, Katy Muzik makes an effective environmental statement, without being didactic.

I like this book. So did Sarah J. (age seven) and Lucy (age five) with whom I shared it. I do have a quibble with the book's design, particularly the integration of text and illustration. Each spread features text in a column down the left-hand side, with spot illustrations of specific coral reef creatures beneath the text. The rest of the spread is taken up with a panoramic drawing that relates to the text. But the small, specific creatures do not. Over and over my eye would move from the text to the unrelated spot illustrations. I kept thinking, "Am I supposed to be looking at these things? Why isn't there anything written about them?" So the first few readings of the book were a little confusing. This problem dissipates on subsequent readings, and Katherine Brown-Wing's rather impressionistic renderings are pretty to look at. We all particularly liked those of her drawings that were done from an underwater perspective.

—Deborah Kovacs
Author, childrens' literature
and Editor, *Ocean Explorer*

To the Editor...

I just finished reading vol. 34, no. 3 (you can see how far behind I am in my reading). I particularly enjoyed the article on elasmobranchs, as I have used films and materials of Dr. Gilbert's for years in my marine biology classes. I have one question....the authors refer to a "gland unique to elasmobranchs...referred to as the nidamental or shell gland" on page 48. I've been dissecting squid (*Loligo pealii*) for years with my classes. Mature females have nidamental glands! I know squid are not elasmobranchs. Could you clarify?

Many thanks and keep up the fine work with your publication. I use *Oceanus* regularly in my classes.

—Michael W. O'Shea
Marine Biology Teacher
Teaneck High School
Teaneck, New Jersey

You are correct in pointing out that female squid do have a nidamental gland, which secretes an elastic egg membrane. Our comments throughout our article on elasmobranch reproductive strategies, however, were meant to extend only to vertebrate animals, and were never intended as comparisons with invertebrate animal groups. More accurately, then, the phrase about the uniqueness of the nidamental gland should have included "among vertebrates." We apologize for any confusion.

—Carl A. Luer, Ph.D.
—Perry W. Gilbert, Ph.D.
Mote Marine Laboratory
Sarasota, Florida

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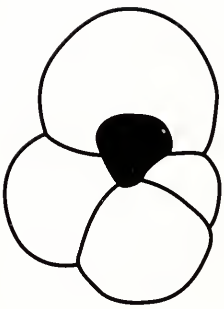
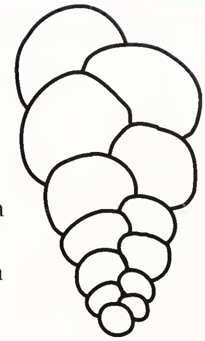
Marine Geology & Geophysics

Volume 35, Number 4, Winter 1992/93

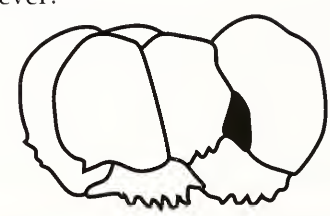


Marine Geology & Geophysics concludes our series on four basic disciplines in oceanography with discussions of state-of-the-art seafloor mapping and uses of sound to chart layers of Earth's crust beneath the ocean. The issue features properties of seafloor rock, the latest on continental margin and arctic research, and the special structures of the Pacific seafloor. There will be new technology, ocean policy, and expert opinion on erosion and sea-level rise. And *Creature Feature* poses the intriguing question: Is extinction forever?



Body shapes like these reappear several times in the plankton fossil record.

Watch for our boxed-set offer for Volume 35 issues on four oceanographic disciplines: *Marine Chemistry* (Spring), *Physical Oceanography* (Summer), *Biological Oceanography* (Fall), and this issue, *Marine Geology & Geophysics* (Winter).



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