Seeing Microbes from Space

Remote sensing is now a critical resource for tracking marine microbial ecosystem dynamics and their impact on global biogeochemical cycles

Douglas G. Capone and Ajit Subramaniam

Microbiologists studying aquatic environments are benefiting from their use of remote sensing technologies. With access to data gathered by remote sensors on aircraft and satellites, microbiologists now can analyze microbial population dynamics with greater breadth and a novel perspective.

Remote sensing instruments exploit electromagnetic radiation to study surface processes on earth. Passive sensors use reflected sunlight or heat being emitted by objects along the earth's surface, while active sensors transmit laser or microwaves that are then reflected back to and recorded by the sensor. Many orbiting satellites currently map ocean properties such as color, surface temperature, height, wind velocities, roughness of the ocean surface, and wave height. Plans call for additional sensors for mapping salinity, as well as the vegetation canopy using active light detection and ranging (LIDAR). Although most remote sensing instruments are limited to near-surface properties, subsurface processes often can be inferred.

There are several advantages to using remote sensing techniques, such as accessing otherwise difficult locations and rapidly mapping large swaths of the earth's surface. For example, sensors that are aboard polar-orbiting satellites can map the entire surface of the earth each day. Each two-minute scene recorded by such a satellite sensor, which has a 1-km spatial resolution, would take 11 years to sample for a ship traveling at about 20 km per hour.

Mapping the Oceans Using Ocean Color

One form of remote sensing uses the color of water to infer what it contains. For example, many of us consider the deep blue color of oceans or other large bodies of water to mean that they are clean, whereas the brown color of rivers and streams mean they are carrying suspended mud or other materials.

This instinctive knowledge forms the basis of ocean color science. Sunlight that enters the ocean can either be absorbed or scattered back (Fig. 1). Pure water absorbs most red light but strongly scatters most blue light. Thus, open ocean waters with very little material in them appear deep blue, while waters carrying dissolved organic materials that absorb blue light strongly appear brown. Chlorophyll-containing microalgal assemblages—phytoplankton—absorb both blue and red light, making phytoplankton-containing waters look green. In addition, chlorophyll emits a small fraction of the absorbed light at a longer wavelength as red fluorescence, providing another signal for remote sensing. Scientists use these variations in the color of water to estimate the amount of phytoplankton, suspended sediment, and dissolved organic material.

Several satellite-borne sensors, including the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS), Moderate-Resolution Imaging Spectroradiometer (MODIS-Terra, MODIS Aqua), Medium Resolution Imaging Spectrometer (MERIS), and the Ocean Colour Monitor (OCM), measure specific wavelengths of light emanating from ocean surfaces (see the online article for a full list of satellite sensors). Perhaps the best and most obvious example of the microbiological exploitation of satellite technology is the broad-scale mapping of phytoplankton in the oceans (Fig. 2) (http://oceancolor.gsfc.nasa.gov). This technology enables us to describe spatial, seasonal, and interannual patterns and dynamics of oceanic plants and is used to infer rates of photosynthetic carbon uptake, often referred to as pri-

Douglas G. Capone is the Wrigley Professor of Biological Sciences in the Wrigley Institute for Environmental Studies and Department of Biological Sciences, University of Southern California, Los Angeles, and Ajit Subramaniam is a Doherty Associate Research Scientist at the Lamont Doherty Earth Observatory of Columbia University, New York.

FIGURE 1
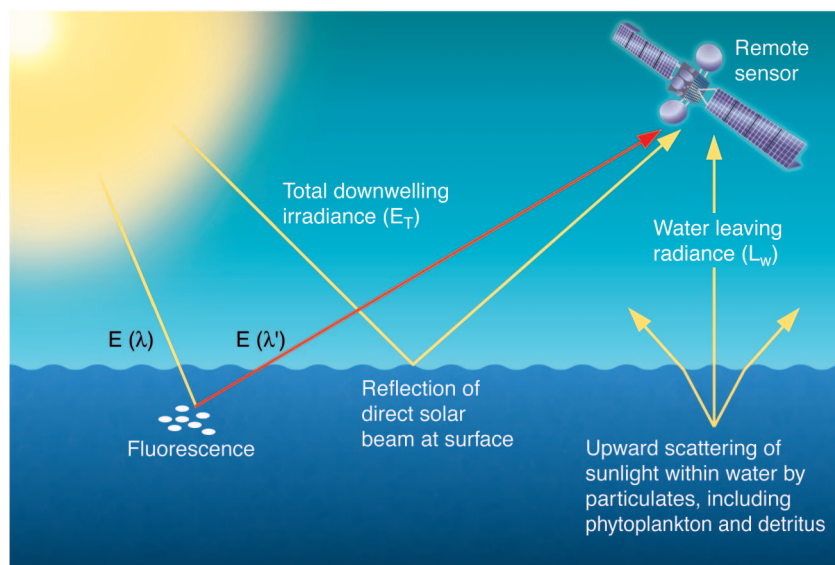
The color of the ocean is recorded by a satellite sensor by measuring the "remote sensing reflectance (R_{rs})" at specific wavelengths. R_{rs} is the ratio of light leaving the water (L_w) to the light incident on it (E_T) and is determined by the absorption (a) and backscattering (b_b) of light in the water column ($R_{rs} = L_w/E_T \propto b_b/(a + b_b)$).

mary production. Through such analyses, we more fully understand the role of ocean microbiota in the global carbon cycle.

Satellite Observations Provide a Means for Detecting Specific Organisms

Interest in learning how to more fully characterize phytoplankton populations in the great expanses of the world's oceans continues to grow. We now recognize a range of "functional groups" of marine autotrophs that are characterized by their biogeochemical role in different elemental cycles. Scientists now can identify and quantify monospecific blooms of certain microalgae and cyanobacteria. And, by coupling these measurements with ecosystem modeling, we can estimate the broad-scale biogeochemical impacts of these populations.

In many areas, including the oceans around Antarctica, along the eastern boundaries of the Atlantic and Pacific Oceans, and along the equator (Fig. 2), a phenomenon referred to as upwelling brings nutrient-rich waters from deep in the ocean to the surface. This phenomenon is being studied by a suite of sensors, including those that map sea surface temperatures (SST), surface wind velocities, and sea surface height (SSH). These nutrient enrichments result in high densities of diatoms and other eukaryotic microalgae in surface waters. Diatoms serve as major primary producers in important food webs, contributing substantially to the cycling of silicon in the sea and to the sinking of carbon from surface waters. Diatoms also dominate segments of open ocean that were experimentally fertilized (Fig. 3A). Researchers are developing algorithms to discriminate diatoms from other phytoplankton.

Indeed, satellites are being used to detect a range of specific phytoplankters. For instance, they are used to map the planktonic marine cyanobacterium *Trichodesmium* that occurs throughout the marine tropics (Fig. 4). In addition to its role in fixing carbon through photosynthesis, this organism also fixes nitrogen gas to produce organic nitrogen, making this otherwise scarce nutrient available in waters where it resides. Although *Trichodesmium* lacks specialized heterocyst cells that some nitrogen-fixing cyanobacteria depend on, it contains proteinaceous vacuoles, or gas vesicles, providing cells with buoyancy and keeping such populations near the surface where light is plentiful. *Trichodesmium* occurs as individual trichomes as well as multifilament aggregates, often referred to as colonies (Fig. 4a and b).

Several optical properties make *Trichodesmium* an excellent microbe for study by remote sensing. For instance, its gas vesicles are very highly reflective. Furthermore, unlike most eukaryotic algae, it contains phycoerythrin as a major accessory pigment. The absorption and fluorescence spectra of this pigment are readily distinguished from chlorophyll a. Finally, its near-surface habitat (staying in a zone within about 50 m from the ocean surface) makes it relatively easy to observe. Indeed, astronauts aboard the space shuttle frequently see and photograph its more extensive blooms (Fig. 4D). Algorithms that are based on the six color bands detected by the SeaWiFS satellite can be used to identify *Trichodesmium*-associated chlorophyll (Fig.

A Childhood at the Seashore, a Career Studying Marine Microbiology

When Douglas Capone visited California in 1997 to interview for his current job, the dean quizzed him about a two-year gap during his undergraduate days. "I was involved in some radical activities on campus, and I was asked to leave," Capone told the dean, who asked in reply, "You're not going to do that here, are you?"

Hardly. Those indiscretions during the heady Vietnam War years of the late 1960s and early 1970s marked a time of widespread protests and plentiful personal uncertainties. Capone faced them as an unenthusiastic premed student at Seton Hall University in South Orange, N.J. Like many of his contemporaries, he vehemently opposed the war and thus participated along with other student activists who took over an administration building. In 1970, Capone dropped out of school, worked at several jobs, and then hitchhiked around the country. "I was drifting, trying to figure out where I wanted to go in my life," he recalls.

Soon enough, Capone was drawn to studying the ocean, and that is how he continues to spend his adult life. Today he directs the marine environmental biology program at the University of Southern California (USC) Wrigley Institute for Environmental Studies. His research focuses on the role and importance of marine microbes in major biogeochemical cycles. "We study the natural populations of bacteria and archaea in different environments and try to tease out what they are doing," he says. "Most of my current work is focused on the nitrogen cycle."

He and his colleagues are focusing on oceanic nitrogen fixation—the biological conversion of nitrogen gas into biologically useful forms of nitrogen. Capone believes that nitrogen fixation may be a key in determining how much carbon dioxide tropical oceans can absorb.

After his two-year excursion from college, Capone enrolled at the University of Miami, where he received a B.S. degree in biology in 1973. He stayed there for his doctoral studies and, in 1978, received a Ph.D. in marine sciences from the University of Miami Rosenstiel School of Marine and Atmospheric Science. "Having matured a bit, and while finishing my basic undergraduate degree in biology, I got into a work-study program at the marine laboratory on Virginia Key, near Key Biscayne," he recalls. "I was just a grunt in the laboratory, doing Winkler O_2 titrations, grinding corals and analyzing them—but the exposure to the researchers there and their focus on the ocean's microbial world really got my attention."

Before moving to California, Capone was on the faculty at the University of Maryland and served in its center for environmental science in the Chesapeake Biological Laboratory in Solomons, Md. Earlier, he worked in the Marine Sciences Research Center at the State University of New York at Stony Brook and was a visiting scientist in the department of chemistry at the Brookhaven National Laboratory, Upton, N.Y.

Capone met his wife, Linda Duguay, a marine physiological ecologist who is now a science administrator, during graduate school at the University of Miami. They have two daughters, 25 and 20. Their older daughter works as an account manager with the Advisory Board Co. in Washington, D.C., while the younger is a sophomore at USC. Both focus on business, he says, adding that "the younger one now has a minor in environmental sciences—possibly a concession to us."

In a typical year, he spends about 30–50 days at sea. Capone first came to love the ocean while growing up near the Jersey shore. His parents, both office workers in Newark, N.J., took Capone and his younger sister to the shore on weekends. By the time Capone started high school, they had moved there permanently.

"When I was young, I loved to surf and fish, so a career that kept me close to the water seemed logical," he says. "The sea has always lured me. It's been a defining focus of my activities, both professionally and recreationally. Of course, marine microbiology is more than a career—it's a passion." When on land, he runs most days (often on the beach!), and enjoys skiing. But, not surprisingly, his favorite vacations are at the shoreline. "A busman's holiday," he says.

Marlene Cimons
Marlene Cimons is a freelance writer in Bethesda, Md.
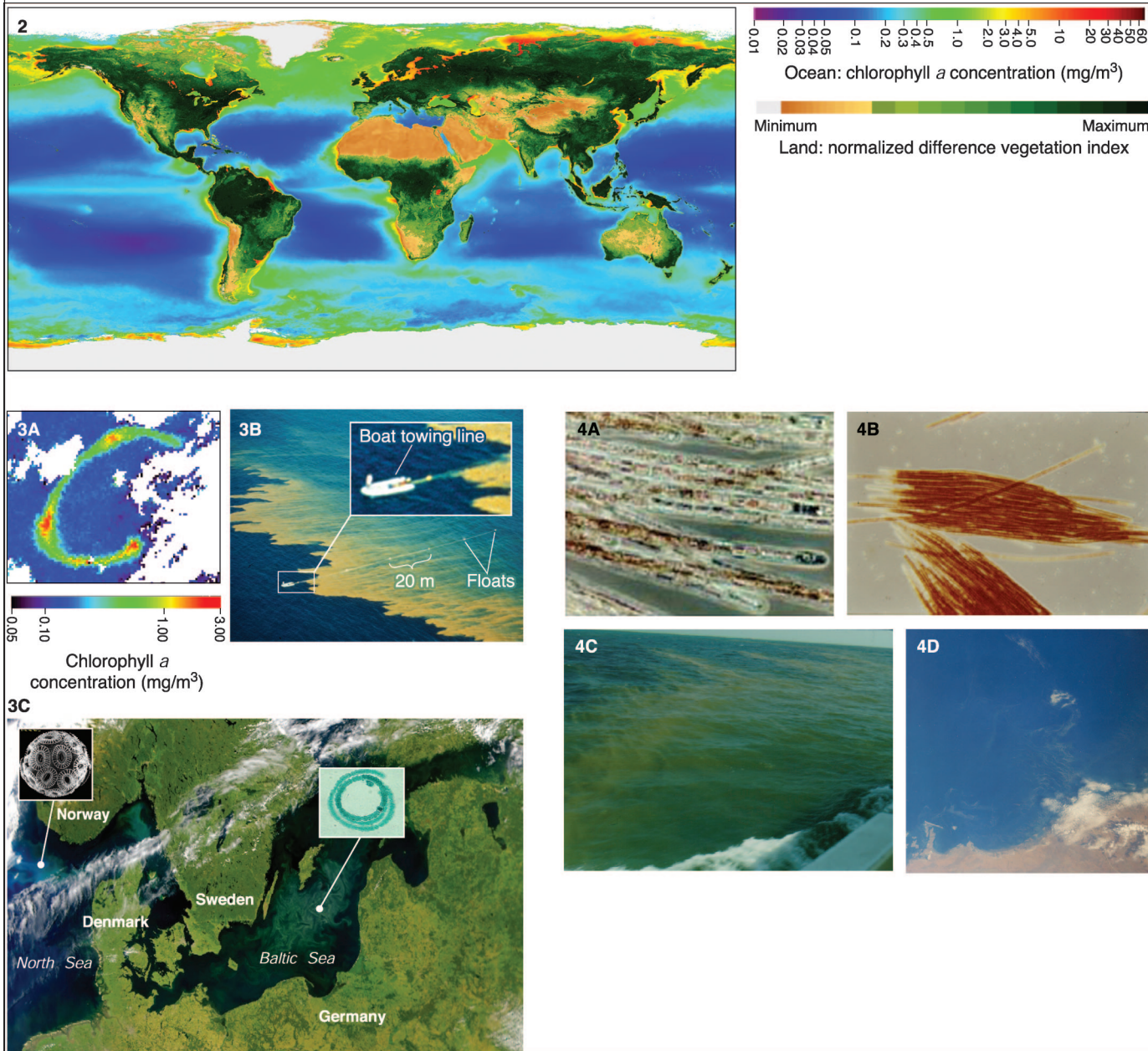
F I G U R E 2 - 4

Fig. 2. Global annual average plant biomass map derived from the SeaWiFS satellite. The oceanic biomass is mapped as chlorophyll concentration while the terrestrial biomass is indicated as the normalized difference vegetation index.

Fig. 3. A bloom of diatoms induced by open ocean iron fertilization experiment (SOIREE) in the Southern Ocean in February 1999 as detected by the SeaWiFS satellite on 23 March 1999; (B) a SeaWiFS "true color" image showing blooms of Coccolithophores in the North Sea and a diazotrophic cyanobacterium, *Nodularia*, in the Baltic Sea from July 1999; (C) a photograph of an intense "red tide" *Noctiluca* bloom off Southern California.

Fig. 4. *Trichodesmium* trichomes (A), colonies (B) a surface bloom in the Capricorn Channel and (D) a photo from the space shuttle of NW Australia. The highly reflective features in (A) are gas vesicles. Each filament in (A) is about 10 um in diameter. The colony in B is about 5 mm by 10 mm. The bloom seen in the space shuttle photo extends over 100 km.

FIGURE 5
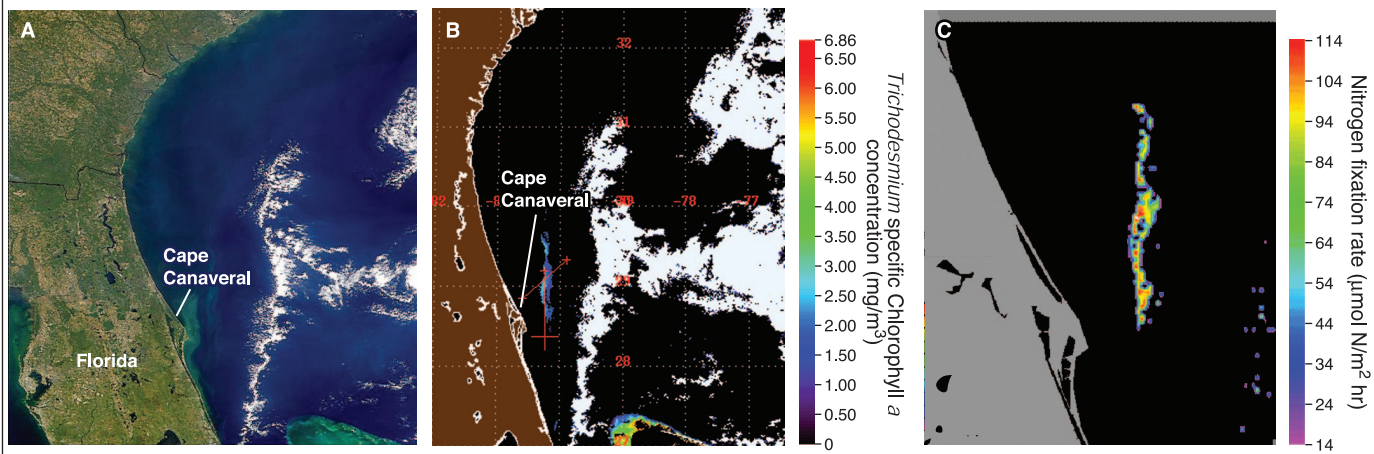
True-color image of a *Trichodesmium* bloom (A), the *Trichodesmium* derived chlorophyll (B), and modeled N_2 fixation (C). From Subramaniam et al., 2002, and Hood et al., 2002, reprinted with permission of Elsevier.

5B). However, the detection threshold is relatively high, about 0.8 mg per cubic meter, which represents a substantial bloom.

Trichodesmium is not the only microorganism that is specifically detectable from space. Coccolithophores, a group of the *Prymnesiophyte* algae, form calcium carbonate plates, or coccoliths, on their outer surfaces. They participate in carbon cycling by producing both organic carbon and particulate inorganic carbon from dissolved inorganic carbon. Coccolith plates are highly reflective at short wavelengths and turn the water milky blue when found in high concentrations (Fig. 3B).

Growth of the nitrogen-fixing cyanobacterium *Nodularia* is responsible for the massive bloom visible seasonally at the center of the Baltic Sea (Fig. 3B). These cyanobacteria have optical properties similar to *Trichodesmium*, proliferate in the late summer, and have been mapped using ocean color satellite sensors. Such cyanobacterial blooms accumulate at the surface, changing the reflectance of microwaves transmitted by synthetic aperture radar (SAR) satellite sensors. These SAR sensors allow us to map these blooms even in cloudy conditions and at spatial resolutions as fine as 10 m.

Other monospecific blooms can also be observed from space. *Phaeocystis* spp., another Prymnesiophyte, often form mucilaginous mats when cells bloom at high latitudes such as in waters surrounding Antarctica. The mucilagi-

nous coating gives such mats a high reflectance in the green part of the spectrum, allowing scientists to develop algorithms that can distinguish *Phaeocystis* blooms from other phytoplankton blooms such as those of diatoms that also have high reflectances. *Phaeocystis* and diatoms play different roles in the carbon cycle at high latitudes, with the latter helping to draw down carbon when the bloom sinks. *Phaeocystis* is also biogeochemically important because it produces dimethylsulfoniopropionate, which is degraded to dimethyl sulfide that escapes into the atmosphere to join the atmospheric sulfur cycle and contributes to cloud formation.

In coastal areas, noxious or toxic blooms are recurrent and can interfere with recreational and commercial uses of these waters. Often referred to as harmful algal blooms (HABs) (http://www.whoi.edu/redtide/), they are an emergent problem. Although there are no current optically based, organism-specific algorithms for mapping these blooms, they often are monospecific and can be spectacular in intensity (Fig. 3C), making them easy to detect by satellite. Coastal management agencies typically use satellite images to identify locations with substantial biomass to direct sampling to determine whether they are due to HABs. Scientists at the National Oceanic and Atmospheric Administrations Coastal Services Center are using remote sensing, in-situ field measurements, and buoy data to provide a HAB bulletin for the Gulf of

Mexico coastal management community (http://www.csc.noaa.gov/crs/habf/).

Beyond Chlorophyll to Other Products and Indirect Approaches

Ocean color analysis is used to measure parameters other than phytoplankton biomass. For instance, satellite imagery of global cloud cover is used to estimate the photosynthetically available radiation (PAR) available at the sea surface every day. Apart from being key to photosynthesis, a measure of the penetration of light in the water column is also an important water quality measure and K490, the diffuse attenuation coefficient at 490 nm, is a standard global ocean color product.

Other algorithms are used or are being developed to estimate particulate inorganic carbon in the form of liths from coccolithophores, total suspended solids, particulate organic carbon, and the absorption due to colored dissolved organic matter (CDOM) from highly refractory, riverborne organic material. Maps of CDOM help us to understand the influence of terrestrially derived organic material on the marine ecosystem as well as the dynamics of dissolved organic matter in the open ocean. Dissolved organic carbon is the primary substrate for heterotrophic marine bacterioplankton, and photobleaching CDOM conditions it for consumption by bacteria. Thus, tracking CDOM may be useful for understanding bacterial activity in surface ocean waters.

Apart from ocean color, there are other satellite resources which may be exploited for studying the distribution and activity of oceanic microbes. For example, although *Vibrio cholerae* cannot be detected directly by satellite sensors, marine plankton are a significant marine reservoir of these bacteria. In the Bay of Bengal, the annual cycle of SST is similar to that of cholera cases, and SSH is a good indicator of incursions of plankton-laden waters. Combined, the two provide a statistically significant correspondence with the incidence of cholera in Bangladesh.

SAR measures the roughness of the sea surface that can be altered by surfactants or phytoplankton blooms at the surface. SAR, which is an active remote sensing technique, can be used even when clouds are present and with resolutions of 10 m. SAR imagery is being used, for example, to study toxic cyanobacterial blooms in the Baltic Sea and to map oil spills. Potentially, it could also be used to follow the dispersion and microbiological degradation of such spills.

Modeling and Scaling

One objective in remotely detecting populations of microalgae, specific phytoplankters, or functional groups is to analyze their dynamics as a context for estimating their ecological and biogeochemical importance.

For instance, we can use remote sensing to measure phytoplankton concentrations, then model primary production by the phytoplankton globally. The growth rate of phytoplankton depends mainly on phytoplankton concentration, the amount of light the phytoplankton receives for photosynthesis, and factors such as temperature and the supply of nutrients to sustain growth. Since most nutrients in the open ocean come from the deep where it is very cold, maps of sea surface temperatures can be used as a proxy for surface nutrient maps. By combining satellite-based maps of incident light, phytoplankton concentrations, and SST, we can create global maps of primary production and carbon fixation rates. Similarly, for a diazotroph such as *Trichodesmium*, we have developed models to predict in situ nitrogen fixation based on remotely sensed biomass and solar flux (Fig. 5C).

However, although *Trichodesmium* can be directly detected only at high surface densities, these organisms are found throughout most oligotrophic oceanic warm waters in appreciable abundance. Indeed, warm surface waters (Fig. 6A) that tend to be depleted of combined inorganic nitrogen such as nitrate (Fig. 6B) are habitats where one typically finds *Trichodesmium* and other diazotrophs. Thus, we use SST measurements from the satellite sensors to estimate the area of warm waters (e.g., 25°C) as a proxy for estimating nutrient-depleted zones, then scale these estimates based on rates of nitrogen fixation determined on oceanographic cruises.

SSH is another useful parameter with ecological relevance. SSH indicates the depth of the thermocline, the thermal discontinuity between warm surface waters and cold, nutrient-rich deep waters. Through much of the oceans, SSH inversely correlates with chlorophyll concentrations. That is, normally, a low SSH and shallow

thermocline indicates a proximal source of deep nutrients resulting in high chlorophyll. However, in certain areas of the oligotrophic ocean, such as the southwest North Atlantic Ocean, high SSH is coincident with high chlorophyll. This unusual finding appears to indicate an area of the ocean where higher levels of nitrogen fixation may support higher algal biomass despite a paucity of nutrients.

Remote sensing can also provide insights on large-scale controls of microbiological processes in the ocean. Throughout much of the surface ocean, dissolved iron is available only in trace concentrations (less than nanomolar). A primary source of iron is through deposits of atmospheric dust. Nitrogen-fixing microorganisms, particularly those that also carry out photosynthesis, need relatively high quantities of iron to satisfy the demands of specialized enzymes. Satellite sensors have been used to estimate the atmospheric aerosol optical thickness, a measure of the particulate burden in the atmosphere, globally (Fig. 6C). The most intense deposits of dust, and hence iron, into the oceans occur in the tropical North Atlantic from the Sahel desert of Africa (Fig. 6D).

Bright Prospects amid Looming Uncertainties

Paralleling development of remote sensors is the deployment of passive and active sensors on buoys to monitor microbial populations and other characteristics, including nutrient concentrations, pigment spectra, and photosynthetic rates (e.g., by fast-repetition-rate fluorometry). Perhaps the most exciting prospect from a microbiological standpoint would be to link remote sensing with other key technology developments affecting marine molecular ecology. For example, soon instruments will be deployed on buoys capable of detecting specific organisms, genes, their expression, and metabolic pathways. Then, linking "sea truth" data from such sites with information being gathered by satellites will greatly enhance the value of the infor-

FIGURE 6
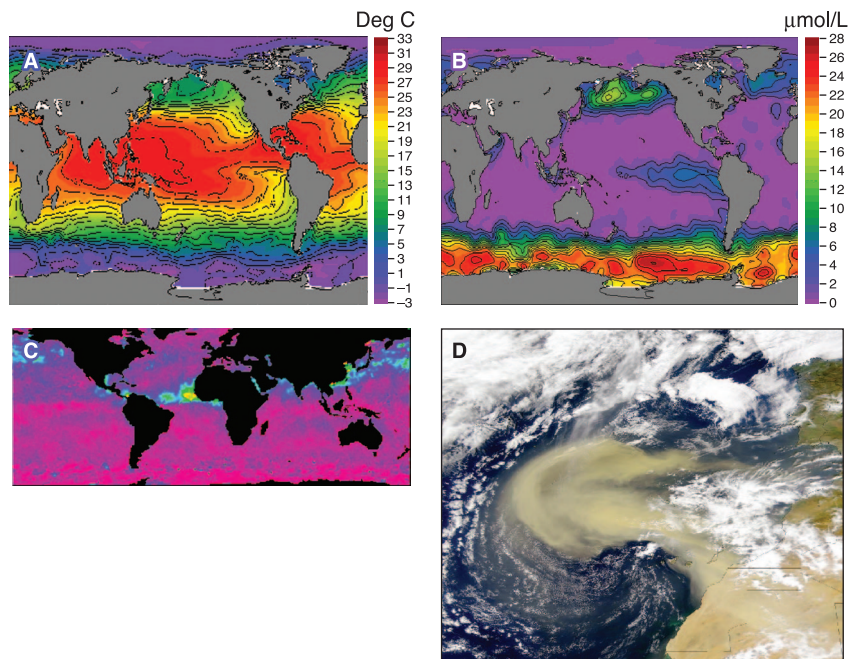
Distributions of SST (A) concentrations of nitrate (B) and aerosol optical thickness (AOT) (C) in the global ocean. (D) A true color SeaWiFS image of a major dust storm off northwest Africa. SST and AOD are derived from the NOAA AVHRR satellite, nitrate from the World Ocean Atlas/ WOCE data set.

mation being gleaned from each separate approach.

The ocean optics field is moving toward deploying more sophisticated sensors that will likely improve our ability to resolve and quantify ocean microbes and processes associated with their activity. For instance, the goals of the Earth System Science Pathfinder program, which is sponsored by the National Aeronautics and Space Agency (NASA), include an explicit effort to better understand phytoplankton physiology and study functional microbial groups from space.

The proposed NASA Physiology LIDAR-Multispectral (PhyLM) mission would characterize key upper-ocean carbon cycle components, including phytoplankton carbon biomass and physiology. This mission would use a multispectral sensor capable of measuring up to 40 wavebands in the ultraviolet, visible, and near infrared. This instrument thus could measure phytoplankton fluorescence for a biomass index in regions that are too optically complex for inversion algorithms. This mission would also

be expected to determine particle scattering from which phytoplankton carbon, particle abundance, and particle size spectra can be estimated. Elsewhere, there is an increasing focus on remote sensing of the coastal ocean, with plans to use geostationary satellites and hyperspectral sensors. A geostationary satellite can scan the coast of the United States several times a day, allowing us to understand tidal effects and transport and diurnal changes, and would enable us to reduce interference from coastal convective clouds.

The upper troposphere and lower stratosphere are regions of study for instruments on NASA's Aura satellite, one of a triptych of Earth-observing missions. Those instruments measure materials affecting air quality, including carbon monoxide, nitrogen dioxide, sulfur dioxide, ozone, and aerosol particulates, providing global maps that can help to distinguish between their industrial and natural sources. Aura also measures vertical distributions of greenhouse gases such as methane, water vapor, and ozone that will provide insights about their production by microbial and physical processes in tropical upwelling regions. The Orbiting Carbon Observatory, a satellite mission planned for launch in 2007, will measure carbon dioxide, another greenhouse gas that is affected by microbial and human activity.

Although NASA has future plans for ocean color sensors aboard satellites, there are no budgeted science follow-on ocean color missions to the Earth Observing System. This lapse may be due, in part, to scientists not effectively explaining their needs for future missions. Because remote sensing is now a critical resource for tracking ecosystem dynamics, any lapses in key satellite assets will greatly constrain our ability to detect and document these changes.

SUGGESTED READING

Behrenfeld, M. J., E. Boss, D. A. Siegel, and D. M. Shea. 2005. Carbon-based ocean productivity and phytoplankton physiology from space. Global Biogeochem. Cycles **19**:GB100610.1029/2004GB002299.

Boyd, P., et al. 2000. A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. Nature **407**:695–702.

Capone, D. G. 2001. Marine nitrogen fixation: what's the fuss? Curr. Opin. Microbiol. **4**:341–348.

Coles, V. J., C. Wilson, and R. R. Hood. 2004. Remote sensing of new production fuelled by nitrogen fixation. Geophys. Res. Lett. **31**:10.1029/2003GL019018.

Hood, R., S. Subramaniam, L. May, E. Carpenter, and D. Capone. 2002. Remote estimation of nitrogen fixation by *Trichodesmium*. Deep-Sea Res. Part II **49(1–3)**:123–147.

Iglesias-Rodriguez, D. M., C. W. Brown, S. C. Doney, J. Kleypas, D. Kolber, Z. Kolber, P. K. Hayes, and P. G. Falkowski. 2002. Representing key phytoplankton functional groups in ocean carbon cycle models: Coccolithophorids. Global Biogeochemical Cycles **16**(4):1100.

Lobitz, B., L. Beck, A. Huq, B. Wood, G. Fuchs, A. S. G. Faruque, and R. Colwell. 2000. Climate and infectious disease: Use of remote sensing for detection of *Vibrio cholerae* by indirect measurement. Proc. Natl. Acad. Sci. USA **97**:1438–1443.

Moran, M. A., W. M. Sheldon, Jr., and R. G. Zepp. 2000. Carbon loss and optical property changes during long-term photochemical and biological degradation of estuarine dissolved organic matter. Limnol. Oceanogr. **45**:1254–1264.

Sathyendranath, S., L. Watts, E. Devred, T. Platt, C. Caverhill, and H. Maass. 2004. Discrimination of diatoms from other phytoplankton using ocean-colour data. Marine Ecol. Progress Ser. **272**:59–68.

Subramaniam, A., C. W. Brown, R. R. Hood, E. J. Carpenter, and D. G. Capone. 2002. Detecting *Trichodesmium* blooms in SeaWiFS imagery. Deep Sea Res. Part II **49** (1-3):107–121.

Subramaniam, A., S. Kratzer, E. J. Carpenter and E. Söderbäck. 2000. Remote sensing and optical in-water measurements of a cyanobacteria bloom in the Baltic Sea. Sixth International Conference on Remote Sensing for Marine and Coastal Environments, Charleston, SC, Veridian ERIM International.