

BY JAMES A. YODER,
SCOTT C. DONEY,
DAVID A. SIEGEL,
AND CARA WILSON

Study of Marine Ecosystems and Biogeochemistry Now and in the Future

Examples of the Unique Contributions from Space

ABSTRACT. Ocean color remote sensing has profoundly influenced how oceanographers think about marine ecosystems and their variability in space and time. Satellite ocean color radiometry (OCR) provides a unique perspective for studying the processes regulating marine ecosystems and biogeochemistry at scales difficult to study with ships and moorings. Satellite OCR is especially useful when supported by other in situ and space observations. In this review, we highlight three areas related to marine ecosystems and biogeochemical processes to which satellite observations have made important and unique contributions: understanding the responses of ocean ecosystems to physical processes operating at meso- to global scales, coupled physical-ecosystem-biogeochemical modeling, and marine living resource management.

INTRODUCTION

As part of the celebration of the United Nations International Year of the Ocean and of the fiftieth anniversary of the National Science Foundation, the Ocean Studies Board of the National Research Council sponsored a major symposium in 1998 entitled “50 Years of Ocean Discovery.” The symposium included a plenary talk by Richard Barber and Anna Hilting on achievements in biological oceanography, and they chose ocean color remote sensing as one of the landmark achievements. The written version of the talk concluded their section on ocean color with the following: “Space-based analysis changed not only our perception of the ocean, but also our ideas of what constitutes good biological oceanography. ... Having seen the totality of the oceans, mankind can no longer maintain the concept of discrete or isolated components of the ocean” (Barber and Hilting, 2000). This comment is appropriate for satellite ocean color radiometry (OCR), and also for other satellite observations of the ocean relevant to understanding marine ecosystems and biogeochemistry. Simply put, one cannot underestimate the significance to biological oceanography of the availability, for the first time, of temporal sequences of an important ecological/ biogeochemical parameter such as phytoplankton chlorophyll *a* (Chl *a*) at regional to global ocean scales. Satellite OCR provides data products most closely related to marine ecosystem and biogeochemical processes, although the value of OCR measurements is increased when supported by other in situ and space observations. For example, vector winds, altimetry for sea surface height (SSH), sea surface temperature (SST),

and microwave radiometry for sea ice cover have proven their value for understanding how the physical environment, including ocean circulation and mixing, affects marine ecosystems.

This manuscript briefly reviews examples of unique and important contributions from global satellite OCR missions such as the Coastal Zone Color Scanner (CZCS), Sea-viewing Wide Field-of-view Sensor (SeaWiFS), Moderate Resolution Imaging Spectroradiometer (MODIS)-Aqua, MEdium Resolution Imaging Spectrometer (MERIS), and others in three topical areas related to marine ecosystems and biogeochemical processes: (1) understanding the responses of ocean ecosystems to physical processes operating at meso- to global ocean spatial scales and at daily to interannual time scales, (2) coupled physical-ecosystem-biogeochemical modeling, and (3) marine living resource management. The spatial and temporal scales mentioned above traditionally

the only observations for much of this time-space regime. We do not try to cover all of the important current and potential applications for satellite observations related to marine ecosystems and biogeochemistry—some of these topics are covered elsewhere in this issue. (See Bourassa et al., 2010, for CO₂ and other gas fluxes; Eakin et al., 2010, for coral reef monitoring; and Fu et al., 2010, for eddy dynamics.)

BACKGROUND ON OCEAN COLOR RADIOMETRY

OCR refers to measurements of the small fraction of sunlight radiance that initially enters the ocean and is then backscattered across the air-sea interface. The absorption and scattering properties of the ocean change the spectrum of backscattered radiance (commonly referred to as water-leaving radiance or $L_w(\lambda)$, where λ is wavelength) from that of the incoming solar radiance. Thus, $L_w(\lambda)$ provides information on the dominant

“OCEAN COLOR REMOTE SENSING HAS PROFOUNDLY INFLUENCED HOW OCEANOGRAPHERS THINK ABOUT MARINE ECOSYSTEMS AND THEIR VARIABILITY IN SPACE AND TIME.”

present great challenges for measuring biological and biogeochemical properties and processes using ships and moorings, and thus were the initial research focus for many of the studies that employed new satellite data sets. Satellite OCR measurements and derived products are not as accurate or precise compared to in situ measurements, but they are

dissolved and suspended in-water constituents, including photosynthetic pigments such as Chl *a* contained by microscopic phytoplankton.

For open ocean waters, Chl *a* and other pigments are among the dominant absorbers of sunlight entering ocean waters (other than water molecules), particularly in a broad wavelength band

centered in the blue region of the spectrum near 440 nm. The $L_w(\lambda)$ spectrum shifts from blue toward green wavelengths as Chl *a* increases (more blue absorption). Chl *a* is the key pigment involved in photosynthesis (primary production), and phytoplankton are the principal photosynthetic organisms in the ocean. Thus, satellite measurements of $L_w(\lambda)$ that began with the 1978 launch of CZCS on NASA's Nimbus-7 spacecraft provided a new and revolutionary tool for biological oceanographers to study the mean distribution of phytoplankton biomass (as indexed by Chl *a*) in the surface waters of the global ocean and also its variability on temporal and spatial scales not previously possible (e.g., Barber and Hilting, 2000). CZCS was a proof-of-concept mission, having only three spectral bands useful for in-water algorithms that were centered at 443, 520, and 555 nm, plus a band centered at 670 nm that was used for atmospheric correction algorithms. Because there was no sustained program for calibration and validation, the quality of the data was difficult to assess during the eight-year CZCS mission, particularly in the final years. Subsequent missions such as SeaWiFS, MODIS-Aqua, and MERIS featured sensors with more spectral bands to support better algorithms and more data products, and with ongoing programs to calibrate and validate measurements of $L_w(\lambda)$

(e.g., Antoine et al., 2008).

The optical properties of ocean waters are not biphasic with water and Chl *a* as the only important constituents. Furthermore, $L_w(\lambda)$ has to be extracted after passing through the atmosphere, which also has complex optical properties. Measurements of the optical properties of ocean waters from space are not possible except under substantially cloud-free conditions, and even under ideal viewing conditions, $L_w(\lambda)$ is at most 10% of the radiance reaching the satellite sensor. Thus, atmospheric contributions to top-of-atmosphere (TOA) radiance spectra have to be accurately measured or calculated (atmospheric correction) to retrieve meaningful information about the ocean from TOA measurements. Other dissolved and suspended substances affecting ocean optical properties include colored dissolved organic matter (CDOM) and suspended sediments. These constituents often overwhelm the contribution of Chl *a* to $L_w(\lambda)$, particularly in coastal waters. Another factor complicating ecological interpretation is that satellite and other measurements of OCR above the water's surface integrate water-leaving radiance over about one optical depth (defined as $1/K$, where K is the radiance attenuation coefficient with units of m^{-1}). That depth depends upon water clarity and ranges from as deep as 30–50 m in the open ocean to less than

1 m in turbid coastal waters. A common assumption is that satellite OCR measurements represent conditions in the mixed layer.

BASIN TO GLOBAL SCALES AND LONG-TERM TRENDS

Figure 1 is a global Chl *a* map (composite image) made by merging all the SeaWiFS cloud-free imagery from the first 10 years of data collection. The image illustrates important features of the global ocean, including the comparatively high Chl *a* concentrations near the coast, effects of upwelling along the equator, and plumes of major rivers such as the Amazon and Orinoco, which extend well offshore into the Atlantic and Caribbean, respectively. Away from the coasts, mean Chl *a* concentrations are higher at latitudes poleward of ca. 40° compared to lower latitudes as a result of seasonal phytoplankton “blooms.”

One of the important and unique applications of basin- to global-scale Chl *a* maps is for calculating global ocean primary production. Using algorithms that incorporate OCR-based Chl *a* to calculate regional- to global-scale estimates of annual net primary production (NPP) provides important insights into the function of ocean ecosystems and biogeochemical processes. Before satellite data were available, estimates of annual global ocean NPP based only on in situ data differed by as much as five to 10 times. To a good first approximation, NPP can be calculated from maps of Chl *a* concentration, incident solar irradiance, plus some additional physiological parameters derived from in situ measurements (e.g., Platt and Sathyandranath, 1988) or from satellite

James A. Yoder (jyoder@whoi.edu) is Vice President for Academic Programs and Dean, Woods Hole Oceanographic Institution, Woods Hole, MA, USA. **Scott C. Doney** is Senior Scientist, Woods Hole Oceanographic Institution, Woods Hole, MA, USA. **David A. Siegel** is Professor, Department of Geography, and Director, Earth Research Institute, University of California, Santa Barbara, Santa Barbara, CA, USA. **Cara Wilson** is Research Oceanographer, National Oceanic and Atmospheric Administration-National Marine Fisheries Service, Southwest Fisheries Science Center, Pacific Grove, CA, USA.

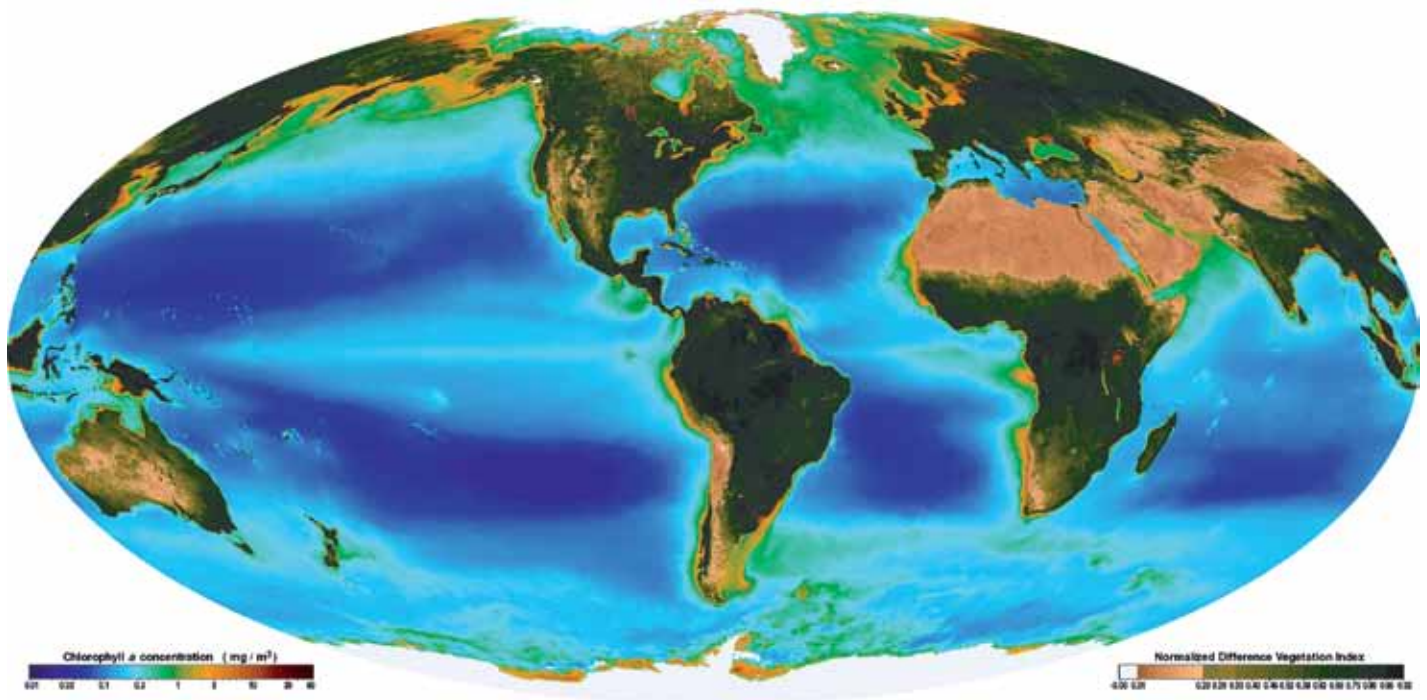


Figure 1. Composite Chl *a* and land vegetation index (NDVI) image calculated using all SeaWiFS data collected from 1997–2007. A composite image is similar to a mean image, although the number of observations for any given pixel differs across the image owing to differences in orbital coverage and in cloud-free conditions. Image courtesy of G.C. Feldman, NASA-GSFC Ocean Color Group (<http://oceancolor.gsfc.nasa.gov>)

measurements (Behrenfeld et al., 2005). Calculations of annual global ocean NPP based on Chl *a* derived from OCR measurements, but using different methods and assumptions, tend to agree within 10–20% owing to the importance and dominance of Chl *a* in the calculation. A key finding from calculations based on satellite data is that ocean and terrestrial NPP contribute more or less equally to global productivity (Field et al., 1998).

Figure 1 does not capture variability in space and time, and quantifying and explaining that variability at regional to global scales is one of the primary scientific accomplishments of satellite OCR to date, with hundreds of manuscripts published on this topic (e.g., Abbott and Zion, 1987; Campbell and Aarup, 1992; Antoine et al., 2005; Thomas et al., 2003, 2004; Yoder and Kennelly, 2006). Satellite

OCR records, supported by SST, SSH, and data from other ocean sensors, are now sufficiently long to begin to resolve the effects on marine ecosystems and biogeochemical cycles of interannual phenomena such as El Niño–Southern Oscillation (ENSO). The 1997–1998 ENSO event caused dramatic changes in the global ocean, and for the first time, satellite observations were able to quantify the impact of a large ENSO event on the productivity of the global biosphere. Figure 2 shows for the first time the change in ocean and land vegetation and the calculated impact on NPP of the biosphere during the transition from the El Niño phase to the La Niña phase during a big ENSO event. The results show that global NPP changed by about 6 Pg yr^{-1} during the transition (equivalent to about 6% of total global NPP) with most of the response from the

ocean (Behrenfeld et al., 2001). Further insight into the dynamics affecting Chl *a* variability in the equatorial Pacific during this ENSO cycle was provided by empirical orthogonal function (EOF) analyses of a two-year time series of SeaWiFS Chl *a* imagery and SSH (Wilson and Adamec, 2001). The analyses showed a symmetric off-equatorial Chl *a* increase during the La Niña phase between 2° and 18° (N and S) across most of the Pacific caused by an increase in surface nutrients related to a shoaling thermocline. This latter study is a good example as to how multiple satellite observations are used to understand basin-scale dynamics and their impacts on ocean Chl *a* time/space variability.

The most important applications for future ocean satellites include helping to understand how the ocean may be changing and separating the effects of

interannual forcing (e.g., by ENSO) from trends caused by changing climate or other human impacts. Recent studies (Gregg et al., 2005; Antoine et al., 2005; Behrenfeld et al., 2006; Polovina et al., 2008; Vantrepotte and Mélin, 2009) indicate that Chl *a* is either increasing or decreasing in different regions of the global ocean, with the most significant trend being a general decrease of Chl *a* in the mid-ocean gyres. SST-based stratification indices show a relation between decreasing Chl *a* and increasing

stratification, suggesting a link to a gradual warming of ocean surface waters (Behrenfeld et al., 2006). Most of the trend analyses began with the launch of SeaWiFS in 1997, which coincided with one of the largest ENSO events of the century. An alternative interpretation of the trend toward lower Chl *a* during the years following the launch of SeaWiFS can be found in the record of interannual variability caused by the ENSO cycle that began in fall 1997. In fact, other analyses (e.g., Yoder and Kennelly, 2003, 2006)

of coincident Chl *a* and SST records showed significant global anomalies from 1997–2001, including high Chl *a* anomalies in the La Niña phase, which began in 1998. Thus, the decline in Chl *a* during the SeaWiFS era may in part be a relative decline only in relation to the comparatively high mean global Chl *a* concentrations during the 1998 La Niña phase of ENSO.

Distinguishing between long-term trends and cycles was also the topic of a study that analyzed CZCS observations from 1979–1983, SeaWiFS observations from 1998–2002, and SST observations from both periods (Martinez et al., 2009). The results showed that basin-scale phytoplankton responses were related to the Pacific Decadal Oscillation (PDO) and the Atlantic Multidecadal Oscillation (MDO), and there is little evidence (yet) to suggest long-term trends. Comparing satellite records with the results of climate models incorporating ocean ecosystems and biogeochemical cycles indicates that the magnitude of the Chl *a* changes observed during the SeaWiFS era are not unusual (Henson et al., 2010; Yoder et al., 2010). Henson et al. (2010) concluded that 40 years of observations will be required to sort out the effects of natural modes of climate variability, such as ENSO, from trends related to a changing climate and changing ocean. Partitioning the effects of ocean cycles from long-term trends and the impacts on marine ecosystems will be a major future challenge that ocean satellites can help to resolve.

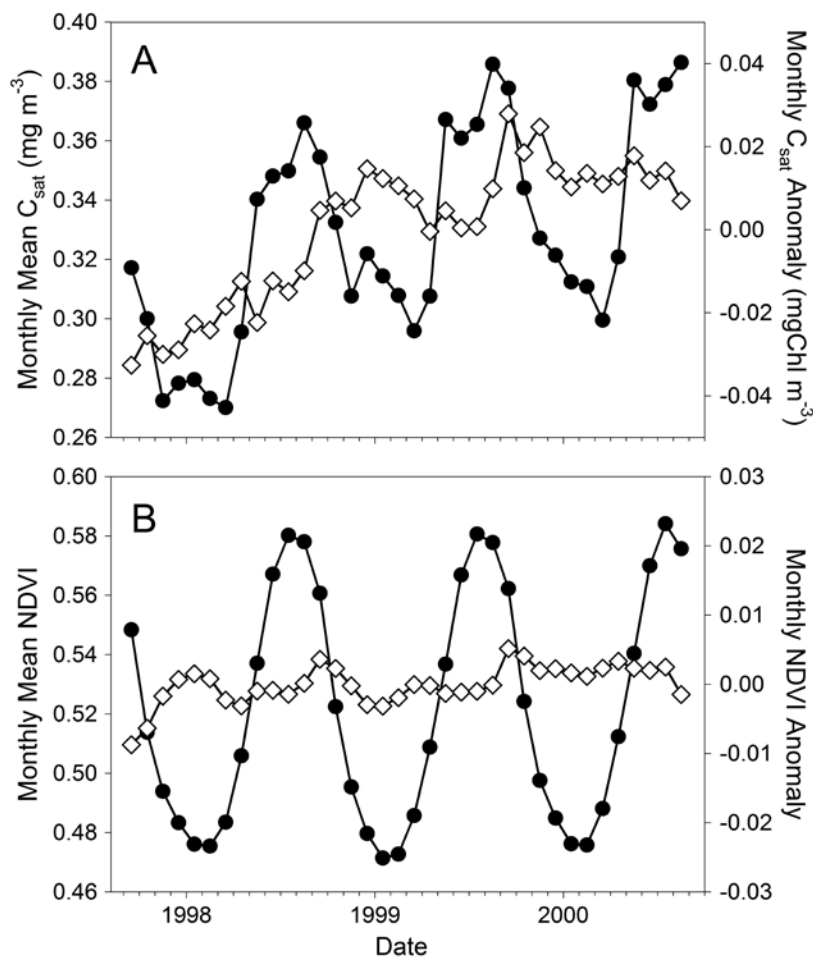


Figure 2. Phytoplankton Chl *a* biomass change during ENSO transition. (A) Ocean – SeaWiFS Chl *a*. (B) Land – SeaWiFS land vegetation index (NDVI). In both (A) and (B), global monthly means are indicated by black circles and monthly deviations from the overall mean (anomalies) by open squares. Changes in ocean and land vegetation during the transition led to a global productivity increase of 6 Pg yr⁻¹, with most of the response in the ocean. From Behrenfeld et al. (2001)

MESOSCALE PROCESSES

The ocean mesoscale (i.e., physical processes occurring on spatial scales of tens to hundreds of kilometers and

temporal scales from a few days to many weeks) dominates ocean energetics throughout most of the ocean (e.g., Robinson, 1983; Fu et al., 2010). Mesoscale eddies are thought to have a large influence on pelagic ocean ecosystems and biogeochemical cycles through their lateral stirring and mixing of the water column and their ability to vertically displace isopycnal surfaces that in turn influence light and new nutrient availability in the euphotic zone (e.g., McGillicuddy et al., 1998; Garçon et al., 2001). Perturbations caused by ocean mesoscale processes often mask the natural seasonal to interannual cycles of the sea, making the unaliased sampling of the ocean from fixed locations difficult to interpret (e.g., Dickey et al., 1991; Wiggert et al., 1994).

Field investigations aimed at understanding the coupled physical-biological effects of ocean eddies were revolutionized by the advent of satellite observations. First, infrared and visible imagery were used to estimate SST and upper-ocean Chl *a* patterns; then in more recent years, satellite altimetry was used to study SSH anomalies. The 1980s Warm Core Rings program was among the first studies to integrate satellite observations into a field sampling program focused on the ocean mesoscale (e.g., Joyce et al., 1984). This highly interdisciplinary study used SST and Chl *a* satellite imagery as tools to guide the ship sampling and to study changes in warm core ring features at higher resolution than was possible from ships alone (Smith and Baker, 1985; Evans et al., 1985). In recent years, satellite altimetry observations have often been used to coordinate field sampling of ocean eddies because of their

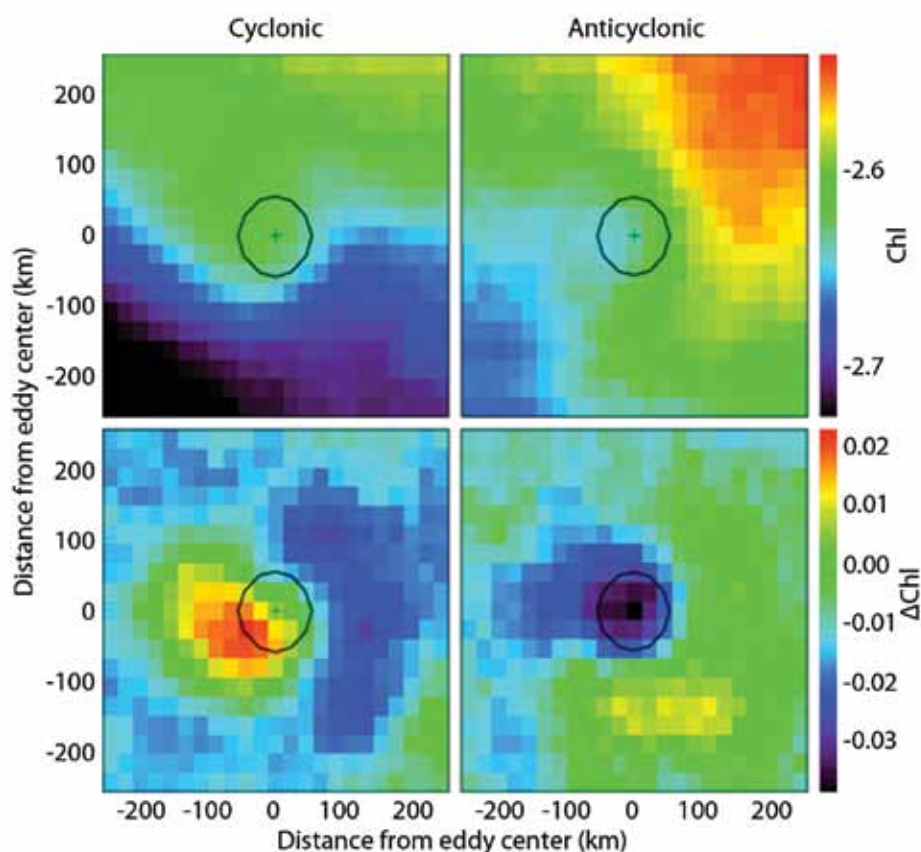


Figure 3. Plan-view depictions of log₁₀-transformed mean Chl *a* (top panels) and the mean spatial anomaly of log₁₀-transformed Chl *a* (Δ Chl *a*, bottom panels) for cyclonic (left panels) and anticyclonic (right panels) eddies in the Sargasso Sea. Panels are 500 km on a side centered on the eddy center following each eddy. Only eddies with trajectories greater than three weeks are used. Spatial anomalies, Δ Chl *a*, are calculated after removing a large-scale spatial mean (~ 325 km) from the log₁₀-transformed Chl *a* field. The black circle is the trace of an average eddy size. In recent work of author Siegel and colleagues, a total of 8093 cyclonic and 6105 anticyclonic eddy-centric images were used to construct these plan view depictions.

all-weather capabilities to measure SSH (e.g., McGillicuddy et al., 2007).

Satellite imagery can be used to study the impact of a single eddy along its trajectory (Siegel et al., 2008), and this approach has also been expanded to include thousands of eddies, enabling mean spatial patterns in Chl *a* to be assessed in eddy-centric coordinates. In Figure 3, mean spatial patterns in log-transformed Chl *a* (upper panels) and Chl *a* anomaly (Δ Chl *a*; lower panels) are shown for a total of 8093 cyclonic (left panels) and 6105 anticyclonic (right panels) eddies from the Sargasso Sea (recent work of author Siegel and

colleagues). Studies of multiple eddies are critical because the scale of the mean eddy-centric spatial Chl *a* signals is very small (~ 0.001 mg m⁻³), below detectable in a normal laboratory setting. Second, the Chl *a* patterns give a sense of rotation consistent with the sign of the features (counterclockwise for cyclones and clockwise for anticyclones). This results in higher Δ Chl *a* values to the west of the eddy center for the cyclone and to the east of center for the anticyclone (Figure 3). Finally, the Δ Chl *a* signal is strongly reduced within an anticyclonic eddy, whereas a general increase is found inside cyclonic eddies

owing to upwelling.

The advent of high-quality satellite ocean color imagery and altimetry observations has enabled researchers to investigate the biological responses of westward-propagating features in satellite sea level distributions (e.g., Uz et al., 2001; Cipollini et al., 2001). The perturbations in Chl *a* signals showed remarkable coincidence with westward-propagating SSH anomalies, with characteristics similar to baroclinic Rossby waves, prompting these researchers to interpret an important role for Rossby waves in pelagic ecosystem dynamics (e.g., Dandonneau et al., 2003; Killworth et al., 2004). Recently, these features have been interpreted as nonlinear eddies and not linear Rossby waves (Chelton et al., 2006; see also Siegel et al., 1999), which has important implications for the potential impact on biological and biogeochemical processes. The distinction is that eddies, unlike Rossby waves, can strongly upwell nutrient-rich waters, thus stimulating phytoplankton productivity.

Future advances in understanding the interactions of ocean mesoscale features and the ocean biosphere will come from improvements in how we see the ocean from space and the clever use of these improved observations. Technological advances are important, but they need to be sustained for significant periods of time. For example, Figure 3 was constructed using thousands of identified eddies spanning over five years of merged ocean color data products (Maritorena et al., 2010). Many of the coupled ocean processes have subtle effects, especially in the open ocean, and thus require long-time-series observations to resolve.

SATELLITE REMOTE SENSING AND BIOGEOCHEMICAL/ ECOLOGICAL MODELING

The availability of satellite observations has contributed substantially to the rapid growth in ocean ecological and biogeochemical numerical modeling over the last two decades. Ocean biological modeling is data limited, almost inherently, and observations feed into several facets of modeling, including model development (e.g., choosing parameterizations and parameter values), forcing, and data-based evaluation (Doney, 1999). Early and ongoing modeling work often involves local one-dimensional, vertical models (simulations on depth versus time) linked closely to in situ time-series measurements (Fasham et al., 2001; Friedrichs et al., 2007). Moving to three-dimensional spatial domains greatly expands the data requirements, quickly surpassing the availability of most in situ data sets. The near-global spatial coverage and good temporal resolution of satellite OCR and ancillary physical data become an invaluable resource, complementing and enhancing in situ data and model simulations.

A primary application of satellite data is in assessment of how well model calculations match observations (model skill), particularly for basic metrics such as surface Chl *a* or NPP (Stow et al., 2009; Doney et al., 2009). A number of new global marine ecosystem models were introduced post SeaWiFS that depended to a large degree on satellite OCR data to judge basin-scale spatial patterns and seasonality for prognostic simulations (Aumont et al., 2003; Gregg et al., 2003; Moore et al., 2004; Lima and Doney, 2004; Le Quere et al., 2005) and inverse model and data assimilation

solutions (Schlitzer, 2002; Gregg et al., 2009). Products derived from satellite OCR measurements also can be used more directly to constrain marine ecosystem dynamics through data assimilation techniques for one-dimensional (Friedrichs, 2002) and three-dimensional simulations (Gregg, 2008).

Overall, the current generation of global simulations captures well the gradients across major biomes (e.g., equatorial upwelling bands, oligotrophic gyres, subpolar gyres) and the timing of seasonal blooms, though there is often considerably weaker skill in absolute magnitude, seasonal phasing, and specific features in bulk chlorophyll and primary production (Figure 4). As the length of the satellite record increases, more modeling studies also are examining the mechanisms and skill for capturing interannual variability in ocean biology in the global models (Dutkiewicz et al., 2001; Schneider et al., 2008; Doney et al., 2009). Some of the errors in global simulations reflect too-low model spatial resolution, and substantial improvements are possible in some cases with higher-resolution, regional coastal (Gruber et al., 2006) and open-ocean domains (Oschlies et al., 2000). The results of eddy-resolving simulations that generate their own internal physical and biological variability can be compared statistically to measures of eddy variability in satellite ocean color observations (Doney et al., 2003).

Many upper-ocean ecosystem models parameterize the complexity of the plankton community by aggregating organisms into concentrations of biomass for distinct trophic levels, so-called phytoplankton-zooplankton-nutrient (PZN) models. A recent

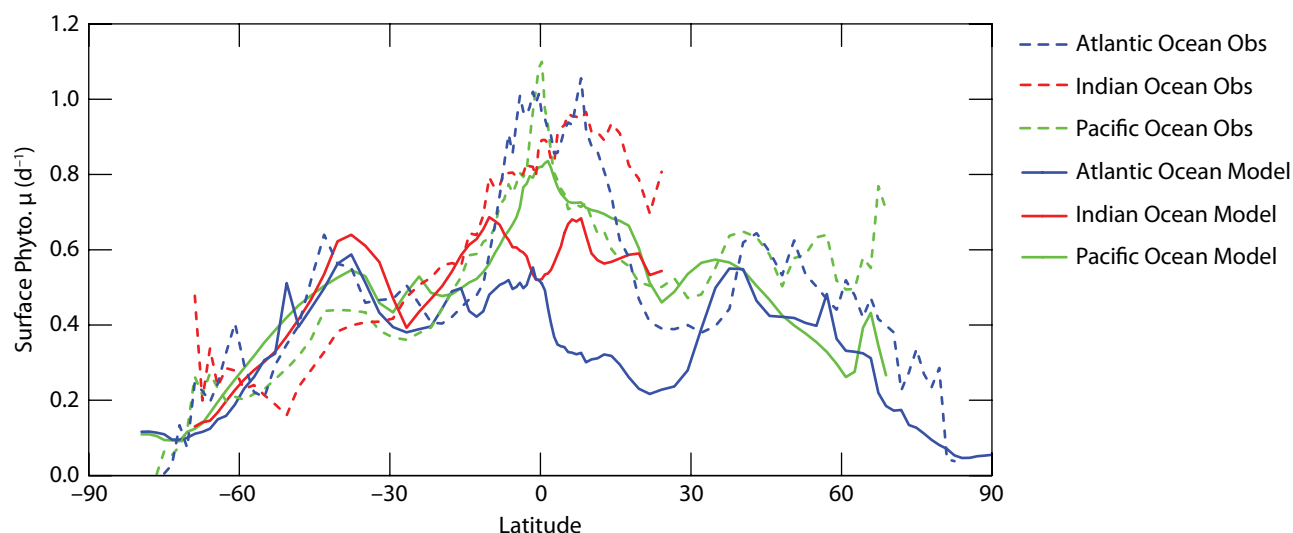


Figure 4. With new algorithms and remote sensing data products, it is now possible to test model-predicted physiological responses to changing environmental conditions. The plot compares phytoplankton specific growth rates (1 d^{-1}) from a global model (solid line; Doney et al., 2009) with those calculated from satellite observations (dashed line; Westberry et al., 2008). The results are displayed as zonal averages for three basins: Atlantic (blue), Indian (red), and Pacific (green). The simulation underestimates specific growth rates in the tropical Atlantic and Indian basins, likely due to excessive model phosphorus and iron limitation, respectively. Adapted from Doney et al. (2009)

modeling trend is the incorporation of so-called functional groups that have a common ecological or biogeochemical role, for example, calcifiers and nitrogen-fixing diazotrophs (Hood et al., 2006). In some cases, these functional groups match up well with satellite-derived estimates of plankton community structure or size class, perhaps the most straightforward example being distributions of coccolithophores (Iglesias-Rodriguez et al., 2002; Gregg and Casey, 2007) and calcification rates (Balch et al., 2007).

In PZN models and their variants, phytoplankton Chl *a* is computed typically using either fixed chlorophyll/biomass ratios or variable chlorophyll/biomass schemes that depend upon phytoplankton nutrient and light status. NPP is parameterized in terms of temperature, light, and nutrients—including nitrogen, phosphorus, and iron. Estimates of primary production from prognostic ecosystem simulations are now being incorporated into

intercomparisons of primary production estimates made from satellite measurements (Carr et al., 2006; Friedrichs et al., 2009). The export flux of sinking organic matter is a key biogeochemical process that is essential to accurately include in model simulations, but this process cannot be measured directly from space. However, empirical relationships with satellite observables (e.g., SST, Chl *a*) can be used to generate spatial export fields (Laws et al., 2000; Dunne et al., 2005), which can in turn be used for evaluating biogeochemical model simulations (Gnanadesikan et al., 2002; Najjar et al., 2007).

Numerical models are essential for understanding the possible range of future climate change impacts on marine ecosystems and NPP (Steinacher et al., 2010), and satellite observations help evaluate and validate models. For example, satellite data are useful for assessing the sensitivity of ocean biology to interannual and decadal climate

variability in coupled ocean-atmosphere models (Schneider et al., 2008). More diagnostic approaches apply empirical relationships between ecological and physical variables to climate model trends to characterize climate impacts. Sarmiento et al. (2004), for example, estimated changes in ocean NPP using satellite-derived surface chlorophyll regressions and satellite primary production algorithms; Iglesias-Rodriguez et al. (2002) estimated changes in coccolithophore distributions using a satellite-based, statistical ecological niche model.

APPLICATIONS FOR ECOSYSTEM-BASED APPROACHES TO FISHERIES (RESOURCE) MANAGEMENT

The continuity, global coverage, and high temporal and spatial resolution of satellite data make them an important tool for monitoring and characterizing marine ecosystems in relation to management applications of living

marine resources, including fisheries. Although satellites do not observe fish stocks directly, Chl *a*, SST, SSH, ocean winds, and sea ice characterize critical habitat that influences marine resources. Most of the spatial features that are important to ecosystems (i.e., ocean fronts, eddies, convergence zones, river plumes, and coastal regions) cannot be adequately resolved without satellite data. Similarly, satellite data are crucial for resolving the timing of processes such as upwelling, harmful algal blooms (HABs), seasonal transitions, and ENSO events that have important impacts on living marine resources.

Recruitment

Of the many types of data available from satellites, OCR is particularly relevant to fisheries management because it is the only remotely sensed parameter that directly measures a biological component of the ecosystem (see Figure 5;

Wilson, et al., 2008). However, the relationship between Chl *a* and a specific fish stock depends upon the number of linkages between phytoplankton and the higher trophic level. For some species, such as anchovies and sardines, that eat phytoplankton at some points in their life cycle, the linkage can be direct (Ware and Thomson, 2005), whereas for other species, there are many trophic levels in between and the relationship can be nonlinear. For species with a relatively direct link to phytoplankton, satellite OCR data can be used to examine how environmental variability affects annual recruitment—the number of new individuals entering a stock. Availability of a good food source is important for successful recruitment; hence, many fish reproduce near the seasonal peak in phytoplankton abundance. The long-standing Cushing-Hjort, or match-mismatch, hypothesis states that recruitment success is tied to timing

between spawning and the seasonal phytoplankton bloom (Cushing, 1969, 1990). However, this hypothesis has been difficult to prove or disprove with traditional shipboard measurements that have limited spatial and temporal resolution. Using satellite ocean color data, interannual fluctuations in the timing and extent of the seasonal bloom can be determined and compared to larval abundance data. This approach has confirmed the match-mismatch hypothesis for both haddock and shrimp in the North Atlantic (Platt et al., 2003; Fuentes-Yaco et al., 2007).

Global estimates of NPP calculated from Chl *a*, in conjunction with fish catch statistics and food web models, can be used to estimate the sustainability of the world's fisheries (Pauly and Christensen, 1995). For example, discrepancies between the values of satellite-derived NPP and reported fish catches have been used to demonstrate spurious trends in global fish catches as reported by the Food and Agriculture Organization (FAO) of the United Nations (Watson and Pauly, 2001).

Tagging

Electronic tagging of living marine resources is a key methodology to gather information needed for accurate and responsible fisheries management. Satellite data are crucial to place track data in an environmental context in order to fully understand foraging and migration patterns, fish behavior and feeding ecology, habitat selection, and individual and population-level responses to environmental and climate variability. This approach has been used to characterize the environment of a wide variety of tagged species—for

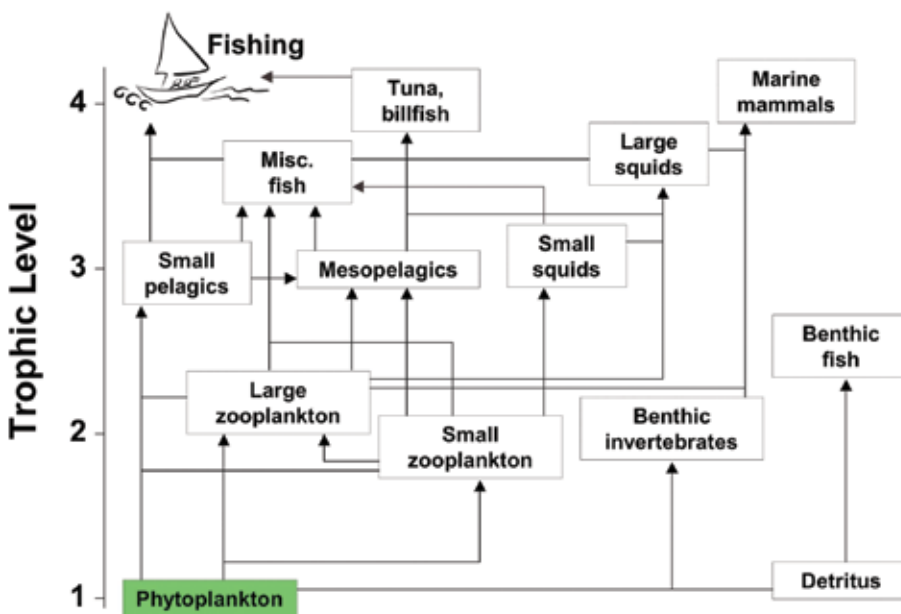


Figure 5. Simplified oceanic food web, showing the varying complexities in the linkages between phytoplankton, which is measured by satellite ocean color data, and higher trophic levels. Modified from Pauly and Christensen (1993)

example, turtles, penguins, seals, sharks, tuna, and salmon—to better understand both their behavior and their habitat (Block et al., 2003; Hinke et al., 2005; Ream et al., 2005; Polovina et al., 2006; Weng et al., 2007). The habitat information provided by these types of studies establishes a foundation upon which to build management tools for the protection of species at risk. For example, the biggest mortality factor for loggerhead sea turtles is fisheries bycatch. Thus, there is considerable interest in being able to spatially separate the fishery from the loggerheads, but this separation requires having a reasonable estimate of the loggerhead habitat. By analyzing satellite SST, Chl *a*, altimetry, and wind data, together with telemetry data from tagged loggerheads, seasonal habitat maps of loggerhead distribution can be determined (Polovina et al., 2000, 2004, 2006; Kobayashi et al., 2008). This information is currently provided, in near-real time, to fishers so that they can stay out of loggerhead habitat. It supports improved management of living marine resources and benefits the fishers, who operate under strict limits on the number of turtle interactions allowed.

FUTURE CAPABILITIES AND DIRECTIONS

Satellite OCR sensors have improved significantly since CZCS, and those interested in scientific and operational applications look to further improvements for the future. NASA is planning new and advanced missions as part of the United States' decadal survey plan (National Research Council, 2007) that will provide new opportunities for studying marine ecosystems and biogeochemistry from space. The plan includes

several satellite OCR missions that will greatly improve the quality of moderate resolution polar orbiting observations (Aerosol-Clouds-Ecosystems [ACE]) and provide hourly resolved viewing from geostationary orbit (Geostationary Coastal and Air Pollution Events [GEO-CAPE]) as well as observations of hyperspectral imagery on unprecedented spatial scales (60-m; Hyperspectral Infrared Imager [HyspIRI]). NASA recently announced a Pre-ACE mission (PACE) to include the OCR requirements with a launch tentatively scheduled for 2019.

In general, the desired capabilities for advanced OCR sensors of the future depend upon the application. For example, those interested in applications requiring multiple observations of one region of the ocean during a single day are interested in OCR sensors in geostationary orbit that can provide coverage of a ca. 500 km x 500 km region at ca. 300-m spatial resolution every 30 minutes during daylight hours. South Korea successfully launched the first OCR instrument, Geostationary Ocean Color Imager (GOCI), in geostationary orbit over the East China Sea in 2010 with the first image acquisition in July 2010. Data distribution will begin in early 2011 following completion of GOCI in-orbit tests. A follow-on mission is planned for launch in January 2018.

Coastal oceanographers are taking advantage of the European Space Agency (ESA) MERIS imagery with its 300-m x 300-m spatial resolution and high spectral resolution. Coastal scientists need more spectral bands (than on SeaWiFS and MODIS) in the 350 to 700 nm range to support comparatively complex algorithms that can distinguish

the contribution of multiple constituents (e.g., Chl *a*, CDOM, sediments, bottom reflection) within optically complex coastal waters. ESA has approved the Sentinel-3 mission that will include the Ocean and Land Color Instrument (OLCI) with capabilities similar to MERIS. MERIS should operate until the launch of Sentinel-3 in 2012, providing a continuous time series of observations of high interest to coastal scientists.

Those interested in basin- to global-scale processes need 1- to 4-km spatial resolution and one- to two-day coverage of the global ocean. In 2010, the National Polar-orbiting Operational Environmental Satellite System (NPOESS) was restructured. NOAA and NASA now have responsibility for a satellite in the afternoon orbit, which will include the Visible/Infrared Imager Radiometer Suite (VIIRS). VIIRS has OCR bands and is capable of producing imagery comparable to SeaWiFS and MODIS-Aqua (minus the Chl *a* fluorescence capability). The first VIIRS is scheduled for launch in September 2011, as part of the NPOESS Preparatory Project (NPP). Recent developments suggest that NPP-VIIRS has the potential to also produce science quality data as well as serve the operational community.

Until recently, most applications of OCR imagery were based on products produced by simple band-ratio algorithms for calculating Chl *a* concentration (O'Reilly et al., 1998). More sophisticated algorithms are now in use and will yield more and improved data products in the future, particularly when applied to data from advanced sensors. New algorithms are based on inversion techniques that incorporate multiple spectral bands to calculate

Chl *a*, sediment content of coastal waters, and important biogeochemical constituents such as particulate carbon (C) and colored organic material (COM; Siegel et al., 2002; Doerffer and Schiller, 2007). COM includes CDOM, as well as the detritus particles from dead plankton. The additional products expand the capabilities for studying ecosystems and biogeochemical cycles. For example, the C-to-Chl *a* ratio, as well as satellite measurements of Chl *a* fluorescence, provide insight into phytoplankton physiology—an important new development for using satellites to study marine ecosystems and their responses (Behrenfeld et al., 2005, 2009). An intriguing new algorithm development is the potential to calculate indices of ecosystem structure, including phytoplankton cell size (Kostadinov et al., 2009; Mouw, in press) and one or more phytoplankton taxa for at least some regions of the global ocean (Sathyendranath et al., 2004; Alvain et al., 2008). Thus, future sensors and new algorithms will significantly expand the scientific applications of OCR data and, in particular, will add new capabilities for studying marine ecosystems from space.

With respect to fisheries applications, satellite data are still underutilized by scientists and managers. For example, stock assessment, the periodic estimate of the total population of a given stock, whether it be commercial or protected, is a key aspect of fisheries science. Yet, incorporation of environmental data of any kind into stock assessment models has rarely been successfully achieved. Because the environmental factors impacting populations from year to year are complex, poorly understood, and

difficult to measure, they have largely been excluded from traditional assessment models, greatly limiting their accuracy and effectiveness (Koeller et al., 2009). Major changes to fish stock assessment methodology, such as incorporating environmental data, would compromise the interannual time series of a stock population derived from stock assessments. Nevertheless, there has been a recent move toward ecosystem-based management of fisheries (Browman and Stergiou, 2005; Sherman et al., 2005; Frid et al., 2006). This trend has given new impetus to better understand the environmental factors influencing fish stock dynamics, and to try to include environmental variability as an integral part of the assessment process. The availability of satellite data such as OCR, SST, and altimetry will make the incorporation of environmental data into stock assessment an easier task.


CONCLUSIONS

The launch of CZCS on Nimbus-7 in 1978 initiated a new era for biological oceanography, and some have identified it as a landmark achievement for ocean science. OCR imagery provided the first data time series at regional to ocean-basin scales of a parameter (initially just Chl *a*) directly related to ocean ecological and biogeochemical processes. In addition, satellite measurements of SSH, SST, and other parameters have provided critical observations for ocean biologists to understand and quantify the important links between ocean physics and ecosystem/biogeochemical processes on scales previously not well understood from limited in situ data. Fisheries scientists are increasingly using ocean satellite data to help

manage marine living resources, and it is likely that such use will increase in the future as ecosystem-based management replaces more traditional management practices. OCR measurements also led to improved estimates of mean ocean primary production, at regional to global scales, and its variability, including impacts of major ENSO events. We now know, for example, that the ocean and land contribute about equally to global productivity. The ocean modeling community has also benefitted from image time series to validate, initialize, and parameterize models, in particular, the three-dimensional regional- to global-scale models that incorporate ecosystems and biogeochemistry. Looking to the future, we see increasing use of satellite OCR, SST, SSH, and other measurements to improve regional to global models by including better eddy dynamics and their effects on biogeochemical processes, to enhance understanding of mesoscale processes and the links between biological and physical processes, to gain new insights into submesoscale processes using time series of high-spatial-resolution imagery, better imaging of coastal processes, and to support ecosystem-based management of ocean resources, including fisheries. Furthermore, a longer time series of calibrated OCR measurements from future missions will help resolve whether the changes observed in OCR imagery during the past 10+ years are related to ocean cycles or reflect long-term trends driven by changes in Earth's climate.

ACKNOWLEDGEMENTS

The authors are grateful for financial assistance from NASA, NOAA, and their respective home institutions.

We thank those who helped with the figures for the manuscript including M. Behrenfeld, G. Feldman, N. Kuring, and I. Lima. Comments from two reviewers led to significant improvements to the manuscript. 

REFERENCES

- Abbott, M.R., and P.M. Zion. 1987. Spatial and temporal variability of phytoplankton pigment off northern California during coastal ocean dynamics experiment 1. *Journal of Geophysical Research* 92:1,745–1,755.
- Alvain, S., C. Moulin, Y. Dandonneau, and H. Loisel. 2008. Seasonal distribution and succession of dominant phytoplankton groups in the global ocean. *Global Biogeochemical Cycles* 22(3), GB3001, doi:10.1029/2007GB003154.
- Antoine, D., A. Morel, and J.-M. Andre. 1995. Algal pigment distribution and primary production in the eastern Mediterranean as derived from coastal zone color scanner observations. *Journal of Geophysical Research* 100:16,193–16,209.
- Antoine, D., A. Morel, H.R. Gordon, V.F. Banzon, and R.H. Evans. 2005. Bridging ocean color observations of the 1980s and 2000s in search of long-term trends. *Journal of Geophysical Research* 110, C06009, doi:10.1029/2004JC002620.
- Antoine, D., F. d'Ortenzio, S.B. Hooker, G. Bécu, B. Gentili, D. Tailliez, and A.J. Scott. 2008. Assessment of uncertainty in the ocean reflectance determined by three satellite ocean color sensors (MERIS, SeaWiFS and MODIS-A) at an offshore site in the Mediterranean Sea (BOUSSOLE project). *Journal of Geophysical Research* 113, C07013, doi:10.1029/2007JC004472.
- Aumont, O., E. Maier-Reimer, S. Blain, and P. Monfray. 2003. An ecosystem model of the global ocean including Fe, Si, P co-limitations. *Global Biogeochemical Cycles* 17(2), 1060, doi:10.1029/2001GB001745.
- Balch, W.M., D.T. Drapeau, B.C. Bowler, and E. Booth. 2007. Prediction of pelagic calcification rates using satellite-measurements. *Deep-Sea Research Part II* 54:478–495.
- Barber, R.T., and A.K. Hilting. 2000. Achievements in biological oceanography. Pp. 11–21 in *50 Years of Ocean Discovery: National Science Foundation 1950–2000*. National Academies Press, Washington, DC.
- Behrenfeld, M.J., E. Boss, D.A. Siegel, and D.M. Shea. 2005. Carbon-based productivity and phytoplankton physiology from space. *Global Biogeochemical Cycles* 19, GB1006, doi:10.1029/2004GB002299.
- Behrenfeld, M.J., R.T. O'Malley, D.A. Siegel, C.R. McClain, J.L. Sarmiento, G.C. Feldman, A.J. Milligan, P.G. Falkowski, R.M. Letelier, and E.S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–755, doi:10.1038/nature05317.
- Behrenfeld, M.J., J.T. Randerson, C.R. McClain, G.C. Feldman, S.O. Los, C.J. Tucker, P.G. Falkowski, C.B. Field, R. Frouin, W.E. Esaias, and others. 2001. Biospheric primary production during an ENSO transition. *Science* 291:2,594–2,597.
- Behrenfeld, M.J., T.K. Westberry, E.S. Boss, R.T. O'Malley, D.A. Siegel, J.D. Wiggert, B.A. Franz, C.R. McClain, G.C. Feldman, S.C. Doney, and others. 2009. Satellite-detected fluorescence reveals global physiology of ocean phytoplankton. *Biogeosciences* 6:779–794.
- Block, B.A., D.P. Costa, G.W. Boehlert, and R.E. Kochevar. 2003. Revealing pelagic habitat use: The Tagging of Pacific Pelagics Program. *Oceanologica Acta* 25:255–266.
- Bourassa, M.A., S.T. Gille, D.L. Jackson, J.B. Roberts, and G.A. Wick. 2010. Ocean winds and turbulent air-sea fluxes inferred from remote sensing. *Oceanography* 23(4):36–51.
- Browman, H.I., and K.I. Stergiou. 2005. Politics and socio-economics of ecosystem-based management of marine resources. *Marine Ecology Progress Series* 300:241–242.
- Campbell, J.W., and T. Aarup. 1992. New production in the North Atlantic derived from seasonal patterns of surface chlorophyll. *Deep-Sea Research* 39:1,669–1,694.
- Carr, M.E., M.A.M. Friedrichs, M. Schmeltz, M.N. Aita, D. Antoine, K.R. Arrigo, I. Asanuma, O. Aumont, R. Barber, M.J. Behrenfeld, and others. 2006. A comparison of global estimates of marine primary production from ocean color. *Deep-Sea Research Part II* 53:741–770.
- Chelton, D.B., M.G. Schlax, R.M. Samelson, and R.A. de Szoek. 2007. Global observations of large oceanic eddies. *Geophysical Research Letters* 34, L15606, doi:10.1029/2007GL030812.
- Cipollini, P., D. Cromwell, P.G. Challenor, and S. Raffaglio. 2001. Rossby waves detected in global ocean color data. *Geophysical Research Letters* 28:323–326.
- Cushing, D.H. 1969. The regularity of the spawning season of some fishes. *Journal of Physical Oceanography* 33:81–92.
- Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: An update of the match mismatch hypothesis. *Advances in Marine Biology* 26:249–294.
- Dandonneau, Y., A. Vega, H. Loisel, Y. du Penhoat, and C. Menkes. 2003. Oceanic Rossby waves acting as a “hay rake” for ecosystem floating by-products. *Science* 302:1,548–1,551.
- Dickey, T., J. Marra, T. Granata, C. Langdon, M. Hamilton, J. Wiggert, D. Siegel, and A. Bratkovich. 1991. Concurrent high resolution bio-optical and physical time series observations in the Sargasso Sea during the spring of 1987. *Journal of Geophysical Research* 96:8,643–8,663.
- Doerffer, R., and H. Schiller. 2007. The MERIS Case 2 water algorithm. *International Journal of Remote Sensing* 28:517–535.
- Doney, S.C. 1999. Major challenges confronting marine biogeochemical modeling. *Global Biogeochemical Cycles* 13:705–714.
- Doney, S.C., D.M. Glover, M. Fuentes, and S. McCue. 2003. Mesoscale variability of Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite ocean color: Global patterns and spatial scales. *Journal of Geophysical Research* 108, 3024, doi:10.1029/2001JC000843.
- Doney, S.C., I. Lima, J.K. Moore, K. Lindsay, M.J. Behrenfeld, T.K. Westberry, N. Mahowald, D.M. Glover, and T. Takahashi. 2009. Skill metrics for confronting global upper ocean ecosystem-biogeochemistry models against field and remote sensing data. *Journal of Marine Systems* 76:95–112.
- Dunne, J.P., R.A. Armstrong, A. Gnanadesikan, and J.L. Sarmiento. 2005. Empirical and mechanistic models for the particle export ratio. *Global Biogeochemical Cycles* 19, GB4026, doi:10.1029/2004GB002390.
- Dutkiewicz, S., M. Follows, J. Marshall, and W.W. Gregg. 2001. Interannual variability of phytoplankton abundances in the North Atlantic. *Deep-Sea Research Part II* 48:2,323–2,344.
- Eakin, C.M., C.J. Nim, R.E. Brainard, C. Aubrecht, C. Elvidge, D.K. Gledhill, F. Muller-Karger, P.J. Mumby, W.J. Skirving, A.E. Strong, and others. 2010. Monitoring coral reefs from space. *Oceanography* 23(4):118–133.
- Evans R.H., K.S. Baker, O.B. Brown, and R.C. Smith. 1985. Chronology of warm-core ring 82B. *Journal of Geophysical Research* 90:8,803–8,811.
- Fasham, M.J.R., B.M. Balino, M.C. Bowles, R. Anderson, D. Archer, U. Bathmann, P. Boyd, K. Buesseler, P. Burkill, A. Bychkov, and others. 2001. A new vision of ocean biogeochemistry after a decade of the Joint Global Ocean Flux Study (JGOFS). *AMBIO Special Issue* 10:4–31.
- Field, C.B., M.J. Behrenfeld, J.T. Randerson and P. Falkowski. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* 281:237–240.
- Frid, C.L.J., O.A.L. Paramor, and C.L. Scott. 2006. Ecosystem-based management of fisheries: Is science limiting? *ICES Journal of Marine Science* 63:1,567–1,572.
- Friedrichs, M.A.M. 2002. Assimilation of JGOFS EqPac and SeaWiFS data into a marine ecosystem model of the central equatorial Pacific Ocean. *Deep-Sea Research Part II* 49:289–319.
- Friedrichs, M.A.M., M.-E. Carr, R.T. Barber, M. Scardi, D. Antoine, R.A. Armstrong, I. Asanuma, M.J. Behrenfeld, E.T. Buitenhuis, F. Chai, and others. 2009. Assessing the uncertainties of model estimates of primary productivity in the tropical Pacific Ocean. *Journal of Marine Systems* 76:113–133.

- Friedrichs, M.A.M., J.A. Dusenberry, L.A. Anderson, R. Armstrong, F. Chai, J.R. Christian, S.C. Doney, J. Dunne, M. Fujii, R. Hood, and others. 2007. Assessment of skill and portability in regional marine biogeochemical models: The role of multiple planktonic groups. *Journal of Geophysical Research* 112, C08001, doi:10.1029/2006JC003852.
- Fu, L.-L., D.B. Chelton, P.-Y. Le Traon, and R. Morrow. 2010. Eddy dynamics from satellite altimetry. *Oceanography* 23(4):14–25.
- Fuentes-Yaco, C., P.A. Koeller, S. Sathyendranath, and T. Platt. 2007. Shrimp (*Pandalus borealis*) growth and timing of the spring phytoplankton bloom on the Newfoundland-Labrador Shelf. *Fisheries Oceanography* 16:116–129.
- Garçon, V.C., A. Oschlies, S.C. Doney, D.J. McGillicuddy, and J. Waniek. 2001. The role of mesoscale variability on plankton dynamics in the North Atlantic. *Deep-Sea Research Part II* 48:2,199–2,226.
- Gnanadesikan, A., R.D. Slater, N. Gruber, and J.L. Sarmiento. 2002. Oceanic vertical exchange and new production: A comparison between models and observations. *Deep-Sea Research Part II* 49:363–401.
- Gregg, W.W. 2008. Assimilation of SeaWiFS ocean chlorophyll data into a three-dimensional global ocean model. *Journal of Marine Systems* 69:205–225.
- Gregg, W.W., and N.W. Casey. 2007. Modeling coccolithophores in the global oceans. *Deep-Sea Research II* 54:447–477.
- Gregg, W.W., N.W. Casey, and C.R. McClain. 2005. Recent trends in global ocean chlorophyll. *Geophysical Research Letters* 32, L03606, doi:10.1029/2004GL021808.
- Gregg, W.W., M.A.M. Friedrichs, A.R. Robinson, K.A. Rose, R. Schlitzer, K.R. Thompson, and S.C. Doney. 2009. Skill assessment in ocean biological data assimilation. *Journal of Marine Systems* 76:16–33.
- Gregg, W.W., P. Ginoux, P.S. Schopf, and N.W. Casey. 2003. Phytoplankton and iron: Validation of a global three-dimensional ocean biogeochemical model. *Deep-Sea Research Part II* 50:3,143–3,169.
- Gruber, N., H. Frenzel, S.C. Doney, P. Marchesiello, J.C. McWilliams, J.R. Moisan, J.J. Oram, G.-K. Plattner, and K.D. Stolzenbach. 2006. Eddy-resolving simulation of plankton ecosystem dynamics in the California Current System. *Deep-Sea Research Part I* 53:1,483–1,516.
- Hinke, J.T., D.G. Foley, C. Wilson, and G.M. Watters. 2005. Persistent habitat use by Chinook salmon (*Oncorhynchus tshawytscha*) in the coastal ocean. *Marine Ecology Progress Series* 304:207–220.
- Henson, S.A., J.L. Sarmiento, J.P. Dunne, L. Bopp, I. Lima, S.C. Doney, J. John, and C. Beaulieu. 2010. Detection of anthropogenic climate change in satellite records of ocean chlorophyll and productivity. *Biogeosciences* 7:621–640.
- Hood, R.R., E.A. Laws, R.A. Armstrong, N.R. Bates, C.W. Brown, C.A. Carlson, F. Chai, S.C. Doney, P.G. Falkowski, R.A. Feely, and others. 2006. Pelagic functional group modeling: Progress, challenges and prospects. *Deep-Sea Research Part II* 53:459–512.
- Iglesias-Rodriguez, M.D., 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, 1100, doi:10.1029/2001GB001454.
- Joyce, T., R. Backus, K. Baker, P. Blackwelder, O. Brown, T. Cowles, R. Evans G. Fryxell, D. Mountain, D. Olson, and others. 1984. Rapid evolution of a Gulf-Stream warm-core ring. *Nature* 308:837–840.
- Killworth, P.D., P. Cipollini, B.M. Uz, and J.R. Blundell. 2004. Physical and biological mechanisms for planetary waves observed in satellite-derived chlorophyll. *Journal of Geophysical Research* 109, C07002, doi:10.1029/2003JC001768.
- Kobayashi, D.R., J.J. Polovina, D.M. Parker, N. Kamezaki, I. Cheng, I. Uchida, P. Dutton, and G. Balazs. 2008. Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997–2006): Insights from satellite tag tracking and remotely sensed data. *Journal of Experimental Marine Biology and Ecology* 356:96–114.
- Koeller, P., K. Friedland, C. Fuentes-Yaco, G. Han, D. Kulka, J. O'Reilly, T. Platt, A. Richards, and M. Taylor. 2009. Remote sensing applications in stock assessments. Pp. 29–42 in *Remote Sensing in Fisheries and Aquaculture*. M.-H. Forget, V. Stuart, and T. Platt, eds, IOCCG Report No. 8, Dartmouth, Canada. Available online at: <http://www.ioccg.org/reports/report8.pdf> (accessed September 21, 2010).
- Kostadinov, T.S., D.A. Siegel, and S. Maritorena. 2009. Retrieval of the particle size distribution from satellite ocean color observations. *Journal of Geophysical Research* 114, C09015, doi:10.1029/2009JC005303.
- Laws, E.A., P.G. Falkowski, W.O. Smith, H. Ducklow, and J.J. McCarthy. 2000. Temperature effects on export production in the open ocean. *Global Biogeochemical Cycles* 14:1,231–1,246.
- Le Quéré, C., S.P. Harrison, I.C. Prentice, E.T. Buitenhuis, O. Aumont, L. Bopp, H. Claustre, L.C. da Cunha, R. Geider, X. Giraud, and others. 2005. Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology* 11:2,016–2,040.
- Lima, I., and S.C. Doney. 2004. A three-dimensional, multi-nutrient, size structured ecosystem model for the North Atlantic. *Global Biogeochemical Cycles* 18, GB3019, doi:10.1029/2003GB002146.
- Maritorena, S., O.H. Fanton d'Andon, A. Mangin, and D.A. Siegel. 2010. Merged satellite ocean color data products using a bio-optical model: Characteristics, benefits and issues. *Remote Sensing of the Environment* 114:1,791–1,804.
- Martinez, E., D. Antoine, F. D'Ortenzio, and B. Gentili. 2009. Climate-driven basin-scale decadal oscillations of oceanic phytoplankton. *Science* 326:1,253, doi:10.1126/science.1177012.
- McGillicuddy, D.J. Jr., L.A. Anderson, N.R. Bates, T. Bibby, K.O. Buesseler, C.A. Carlson, C.S. Davis, C. Ewart, P.G. Falkowski, S.A. Goldthwait, and others. 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. *Science* 316:1,021–1,026.
- McGillicuddy, D.J. Jr., A.R. Robinson, D.A. Siegel, H.W. Jannasch, R. Johnson, T.D. Dickey, J. McNeil, A.F. Michaels, and A.H. Knap. 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394:263–265.
- Moore, J.K., S.C. Doney, and K. Lindsay. 2004. Upper ocean ecosystem dynamics and iron cycling in a global 3-D model. *Global Biogeochemical Cycles* 18, GB4028, doi:10.1029/2004GB002220.
- Mouw, C.B., and J.A. Yoder. In press. Optical determination of phytoplankton size composition from global SeaWiFS imagery. *Journal of Geophysical Research*.
- Najjar, R.G., X. Jin, F. Louanchi, O. Aumont, K. Caldeira, S.C. Doney, J.-C. Dutay, M. Follows, N. Gruber, F. Joos, and others. 2007. Impact of circulation on export production, dissolved organic matter and dissolved oxygen in the ocean: Results from Phase II of the Ocean Carbon-cycle Model Intercomparison Project (OCMIP-2). *Global Biogeochemical Cycles* 21, GB3007, doi:10.1029/2006GB002857.
- National Research Council. 2007. *Earth Science and Applications from Space: National Imperatives for the Next Decade and Beyond*. Committee on Earth Science and Applications from Space: A Community Assessment and Strategy for the Future, 456 pp.
- Oschlies, A., W. Koeve, and V.C. Garçon. 2000. An eddy-permitting coupled physical-biological model of the North Atlantic 2. Ecosystem dynamics and comparison with satellite and JGOFS local studies data. *Global Biogeochemical Cycles* 14:499–523.
- Pauly, D., and V. Christensen. 1993. Stratified models of large marine ecosystems: A general approach and an application to the South China Sea. Pp. 148–174 in *Large Marine Ecosystems: Stress, Mitigation and Sustainability*. K. Sherman, L.M. Alexander, and B.D. Gold, eds, AAAS Press, Washington, DC.
- Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature* 374:255–257.
- Platt, T., and S. Sathyendranath. 1988. Oceanic primary production: Estimation by remote sensing at local and regional scales. *Science* 241:1613–1620.

- Platt, T., C. Fuentes-Yaco, and K.T. Frank. 2003. Spring algal bloom and larval fish survival. *Nature* 423:398–399.
- Polovina, J.J., G.H. Balazs, E.A. Howell, D.M. Parker, M.P. Seki, and P.H. Dutton. 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography* 13:36–51.
- Polovina, J.J., E.A. Howell, and M. Abecassis. 2008. Ocean's least productive waters are expanding. *Geophysical Research Letters* 35, L03618, doi:10.1029/2007GL031745.
- Polovina, J.J., D.R. Kobayashi, D.R. Parker, M.P. Seki, and G.H. Balazs. 2000. Turtles on the edge: Movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fisheries Oceanography* 9:71–82.
- Polovina, J.J., G.T. Mitchum, N.E. Graham, M.P. Craig, E.E. DeMartini, and E.N. Flint. 1994. Physical and biological consequences of a climate event in the central North Pacific. *Fisheries Oceanography* 3:15–21.
- Polovina, J.J., I. Uchida, G. Balazs, E.A. Howell, D. Parker, and P. Dutton. 2006. The Kuroshio Extension Bifurcation Region: A pelagic hotspot for juvenile loggerhead sea turtles. *Deep-Sea Research Part II* 53:326–339.
- Ream, R.R., J.T. Sterling, and T.R. Loughlin. 2005. Oceanographic features related to northern fur seal migratory movements. *Deep-Sea Research Part II* 52:823–843.
- Robinson, A.R., ed. 1983. *Eddies in Marine Science*. Springer-Verlag, Berlin, 609 pp.
- Sarmiento, J.L., R. Slater, R. Barber, L. Bopp, S.C. Doney, A.C. Hirst, J. Kleypas, R. Matear, U. Mikolajewicz, P. Monfray, and others. 2004. Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles* 18, GB3003, doi:10.1029/2003GB002134.
- 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 Ecology Progress Series* 272:59–68.
- Schlitzer, R. 2002. Carbon export fluxes in the Southern Ocean: Results from inverse modeling and comparison with satellite-based estimates. *Deep-Sea Research Part II* 49:1,623–1,644.
- Schneider, B., L. Bopp, M. Gehlen, J. Segsneider, T.L. Frölicher, P. Cadule, P. Friedlingstein, S.C. Doney, M.J. Behrenfeld, and F. Joos. 2008. Climate-induced interannual variability of marine primary and export production in three global coupled climate carbon cycle models. *Biogeosciences* 5:597–614.
- Sherman, K., M. Sissenwine, V. Christensen, A. Duda, G. Hempel, C. Ibe, S. Levin, D. Lluch-Belda, G. Matishov, J. McGlade, and others. 2005. A global movement toward an ecosystem approach to management of marine resources. *Marine Ecology Progress Series* 300:275–279.
- Siegel, D.A., D.B. Court, D.W. Menzies, P. Peterson, S. Maritorena, and N.B. Nelson. 2008. Satellite and in situ observations of the bio-optical signatures of two mesoscale eddies in the Sargasso Sea. *Deep-Sea Research Part II* 55:1,218–1,230.
- Siegel, D.A., E. Fields, and D.J. McGillicuddy Jr. 1999. Mesoscale motions, satellite altimetry and new production in the Sargasso Sea. *Journal of Geophysical Research* 104:13,359–13,379.
- Siegel, D.A., S. Maritorena, N.B. Nelson, D.A. Hansell, M. Lorenzi-Kayser. 2002. Global distribution and dynamics of colored dissolved and detrital organic materials. *Journal of Geophysical Research* 107(C12), 3228, doi:10.1029/2001JC000965.
- Smith, R.C., and K.S. Baker. 1985. Spatial and temporal patterns in pigment biomass in Gulf-Stream Warm-Core Ring 82B and its environs. *Journal of Geophysical Research* 90:8,859–8,870.
- Steinacher, M., F. Joos, T.L. Frölicher, L. Bopp, P. Cadule, V. Cocco, S.C. Doney, M. Gehlen, K. Lindsay, J.K. Moore, and others. 2010. Projected 21st century decrease in marine productivity: A multi-model analysis. *Biogeosciences* 7:979–1,005.
- Stow, C.A., J. Jolliff, D.J. McGillicuddy Jr., S.C. Doney, J.I. Allen, M.A.M. Friedrichs, K.A. Rose, and P. Wallhead. 2009. Skill assessment for coupled biological/physical models of marine systems. *Journal of Marine Systems* 76:4–15.
- Thomas, A.C., D.W. Townsend, and R. Weatherbee. 2003. Satellite-measured phytoplankton variability in the Gulf of Maine. *Continental Shelf Research* 23:971–989.
- Thomas A.C., P.T. Strub, M.E. Carr, and R. Weatherbee. 2004. Comparisons of chlorophyll variability between the four major global eastern boundary currents. *International Journal of Remote Sensing* 25:1,443–1,447.
- Uz, B.M., J.A. Yoder, and V. Osychyn. 2001. Pumping of nutrients to ocean surface waters by the action of propagating planetary waves. *Nature* 409:597–600.
- Vantrepotte, V., and F. Mélin. 2009. Temporal variability of 10-year global SeaWiFS time-series of phytoplankton chlorophyll *a* concentration. *ICES Journal of Marine Science* 66:1,547–1,556.
- Ware, D.M., and R.E. Thomson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* 308:1,280–1,285.
- Watson, R., and D. Pauly. 2001. Systematic distortions in world fisheries catch trends. *Nature* 414:534–536.
- Weng, K.C., A.M. Boustany, P. Pyle, S.D. Anderson, A. Brown, and B.A. Block. 2007. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology* 152:877–894.
- Westberry, T.K., M.J. Behrenfeld, D.A. Siegel, and E. Boss. 2008. Carbon-based primary productivity modeling with vertically resolved photo acclimation. *Global Biogeochemical Cycles* 22, GB2024, doi:10.1029/2007GB003078.
- Wiggert, J., T. Dickey, and T. Granta. 1994. The effect of temporal undersampling on primary production estimates. *Journal of Geophysical Research* 99:3,361–3,371.
- Wilson, C., and D. Adamec. 2001. Correlations between surface chlorophyll and sea surface height in the tropical Pacific during the 1997–1999 El Niño-Southern Oscillation event. *Journal of Geophysical Research* 106:31,175–31,188.
- Wilson, C., J. Morales, S. Nayak, I. Asanuma, and G. Feldman. 2008. Ocean colour radiometry and fisheries. Pp. 47–58 in *Why Ocean Colour? The Societal Benefits of Ocean-Colour Technology*. T. Platt, N. Hoepffner, V. Stuart, and C. Brown, eds, IOCCG Report No. 7, Dartmouth, Canada. Available online at: <http://www.ioccg.org/reports/report7.pdf> (accessed September 21, 2010).
- Yoder, J.A., and M.A. Kennelly. 2003. Seasonal and ENSO variability in global ocean phytoplankton chlorophyll derived from 4 years of SeaWiFS measurements. *Global Biogeochemical Cycles* 17, 1112, doi:10.1029/2002GB001942.
- Yoder, J.A., and M.A. Kennelly. 2006. What have we learned about ocean variability from satellite ocean color imagers? *Oceanography* 19(1):152–171. Available online at: http://www.tos.org/oceanography/issues/issue_archive/19_1.html (accessed October 1, 2010).
- Yoder, J.A., M.A. Kennelly, S.C. Doney, and I.D. Lima. 2010. Are trends in SeaWiFS chlorophyll time-series unusual relative to historic variability? *Acta Oceanologica Sinica* 29:1–4, doi:10.1007/s13131-010-0016-0.