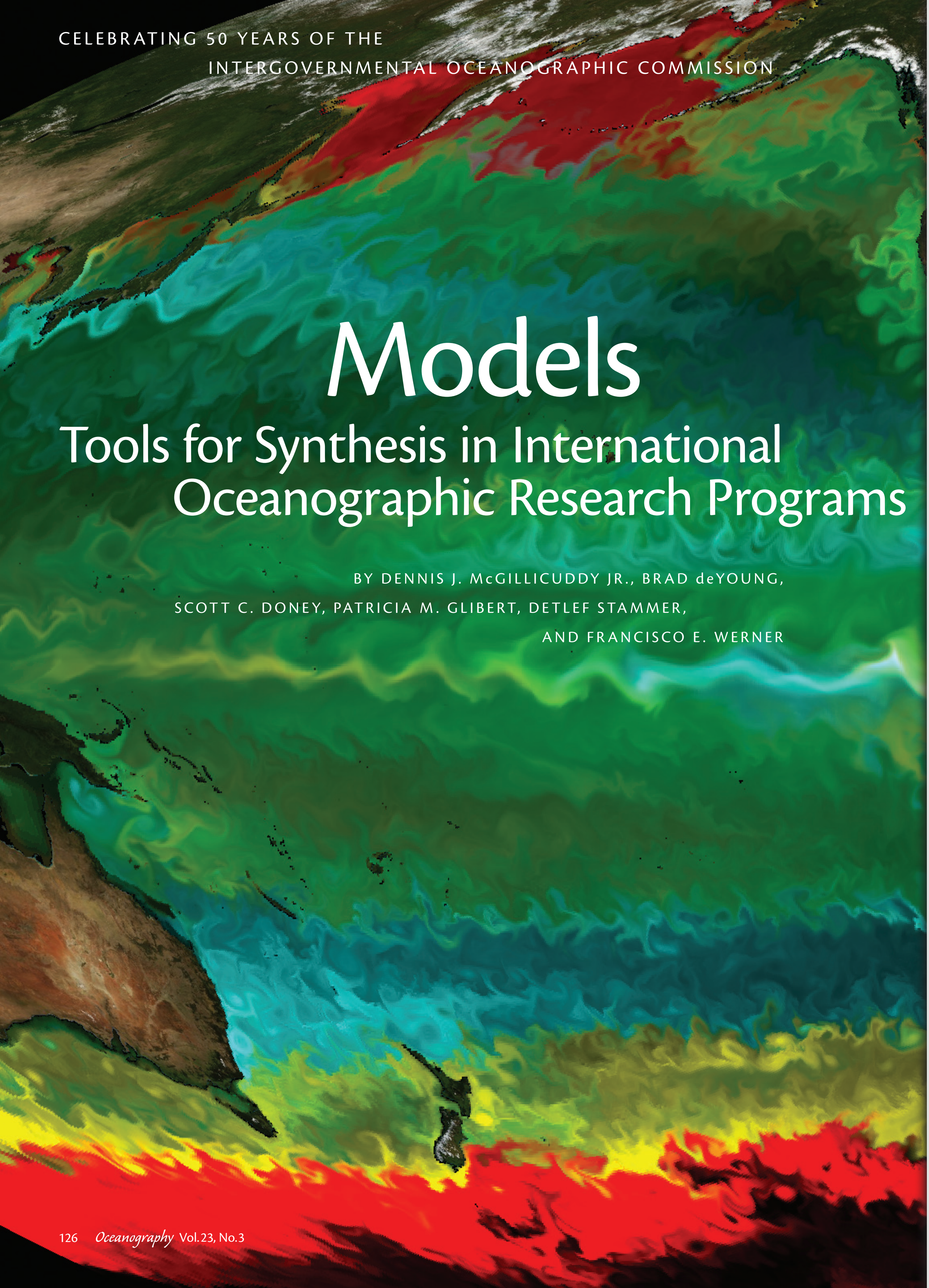



# Models

## Tools for Synthesis in International Oceanographic Research Programs

BY DENNIS J. McGILLICUDDY JR., BRAD deYOUNG, SCOTT C. DONEY, PATRICIA M. GLIBERT, DETLEF STAMMER, AND FRANCISCO E. WERNER

## INTRODUCTION

Through its promotion of coordinated international research programs, the Intergovernmental Oceanographic Commission (IOC) has facilitated major progress on some of the most challenging problems in oceanography. Issues of global significance—such as general ocean circulation, the carbon cycle, the structure and dynamics of ecosystems, and harmful algal blooms—are so large in scope that they require international collaboration to be addressed systematically. International collaborations are even more important when these issues are affected by anthropogenic processes—such as climate change, $CO_2$ enhancement, ocean acidification, pollution, and eutrophication—whose impacts may differ greatly throughout the global ocean. These problems require an entire portfolio of research activities, including global surveys, regional process studies, time-series observations, laboratory-based investigations, and satellite remote sensing. Synthesis of this vast array of results presents its own set of challenges (Hofmann et al., 2010), and models offer an explicit framework for integration of the knowledge gained as well as detailed investigation of the underlying dynamics. Models help us to understand what happened in the past, and to make predictions of future changes—both of which support the development of sound policy and decision making. We review examples of how models have been used for this suite of purposes, focusing on areas where IOC played a key role in organizing and coordinating the research activities.

## OCEAN CIRCULATION

Ocean circulation fundamentally impacts physical, biological, and chemical constituents not only of the ocean itself but also of the coupled climate system. Obtaining accurate descriptions of ocean circulation and its variability, as well as circulation changes on climate time scales, are therefore of paramount importance. However, observing ocean circulation in its entirety is impossible based on observations alone. In the last few decades, substantial progress has been made in developing an ocean observing system, which is now evolving into an integrated global observing and information system (Hall et al., 2010). Nevertheless, it is generally accepted that the best description of time-varying ocean circulation and its transport properties will require merging all available ocean observations with the dynamics embedded in ocean circulation models. This combination of observations with models is usually referred to as "state estimation" or "data assimilation."

The vision of ocean state estimation as a means of merging all ocean observations into a dynamically consistent description of time-varying ocean circulation goes back to the beginnings of the World Ocean Circulation Experiment (WOCE; Munk and Wunsch, 1982). However, achieving this vision required significant development of in situ and satellite observing technology, together with improvements of ocean models and enhanced computational capabilities. Important milestones in the latter respect included the development of inverse methods that can be applied to ocean general circulation models using supercomputers. This undertaking required coordinated international activities, to which IOC organizational efforts contributed a great deal (through the World Climate Research Programme [WCRP] and the Global Ocean Data Assimilation Experiment [GODAE]). Success of this activity has hinged on long-term national financial commitments, and the existence of expertise in ocean observations, modeling, and assimilation, as well as infrastructure for information technology.

The many methods available for performing data assimilation all solve constrained least-squares problems, either exactly, by iteration, or sequentially (Wunsch, 2006). Various approaches differ in the extent to which they are dynamically self-consistent and whether or not they provide an estimate of the error of the result. One example of a climate-oriented ocean synthesis effort that built upon earlier WOCE results is Estimation of the Circulation and Climate of the Ocean (ECCO; Stammer et al., 2002; Wunsch et al., 2009), which began in 1999 with funding provided through the US National Oceanographic Partnership Program. Close to a decade of sustained consortium effort was necessary to develop the ECCO ocean modeling and assimilation environment, which encompasses a modern primitive equation (PE) model (e.g., the MITgcm; Marshall et al., 1997), its adjoint (Giering and Kaminski, 1998), and first pilot applications to ocean problems (Marotzke et al., 1999). ECCO results are especially useful for describing the ocean's transports of heat and freshwater, and for estimating unobserved quantities

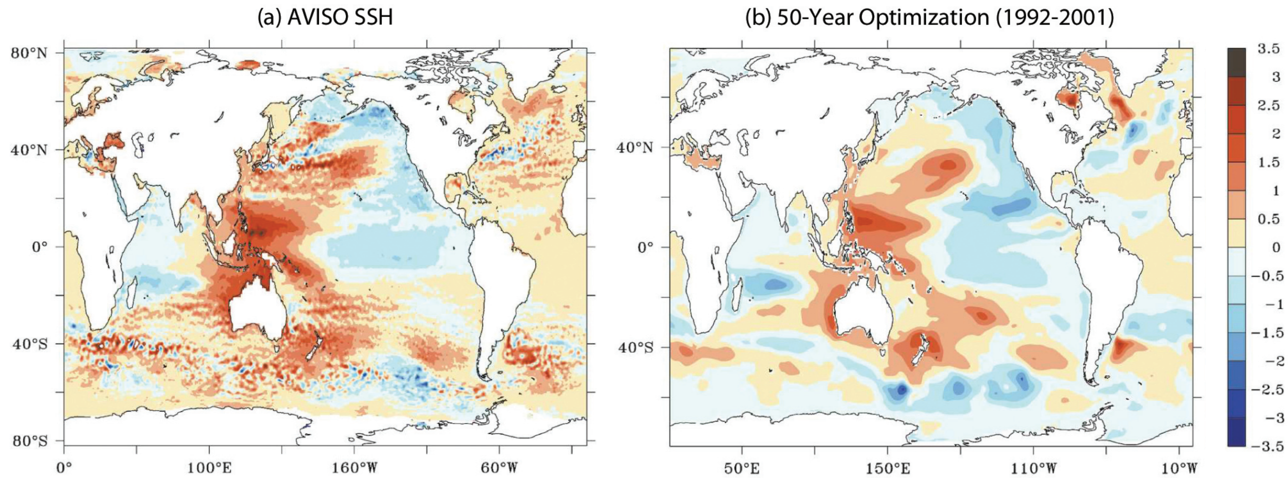


Figure 1. (a) Observed trends in sea surface height (SSH) compared with (b) simulated Estimation of the Circulation and Climate of the Ocean (ECCO) trends over the period 1992–2001. Units are cm $yr^{-1}$. Altimeter products were produced and distributed by AVISO (http://www.aviso.oceanobs.com), as part of the Ssalto ground processing segment

such as the meridional overturning circulation. ECCO hydrodynamic fields also provide a framework for investigations of ocean biology and biogeochemistry, including transport estimates for $CO_2$, nutrients, and oxygen in "offline" tracer simulations.

Sea level and its variability are of specific societal concern, representing an integral comprised of different individual aspects of ocean circulation and its transport properties. Changes in sea level potentially can have substantial impact on society, and understanding ongoing and past changes and their regional characters is therefore of considerable interest. Over large parts of the world ocean, ECCO results correspond closely with observed trends during the recent era of sustained altimetric observations (Figure 1), confirming that observed sea surface height changes are primarily induced by steric (heat and salt-driven) changes in sea level. Moreover, this demonstration of skill provides confidence in the model's validity for hindcasting and forecasting beyond the data-rich time period, roughly from 1992 to present (Wunsch et al., 2007; Köhl and Stammer, 2008).

Through the international efforts of IOC/GODAE and WCRP/CLIVAR (Climate Variability and Predictability), several global ocean data assimilation products are now available for use in climate and ocean services applications. Lee at al. (2010) provide a detailed summary of such products and underlying approaches, which vary widely in their computational requirements and also in the degree to which model dynamics are imposed on the resulting circulation estimates. Some assimilation products span the past several decades; others focus on the data-rich period. Ongoing applications of those systems include many aspects of operational oceanography and climate research, such as sea level variability and changes, water-mass analysis, and mixed-layer heat balance. A summary of the products has also been distilled by CLIVAR's Global Synthesis and Observations Panel (see http://www.clivar.org/data/synthesis/directory.php).

An intercomparison of some of the existing state estimates, performed under the auspices of CLIVAR, revealed a large spread in some ocean synthesis results (Stammer et al., 2010). To some extent, differences appear to be due to underlying data sets and their errors; however, current insight suggests that the choice of approach dominates (i.e., results

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cluster around methods of data assimilation). The study underscores the need to further improve ocean state estimates and especially highlights the need to characterize uncertainties of existing estimates of ocean circulation and derived products.

Understanding these apparent discrepancies in state estimates in terms of differences of underlying models, model resolution, imposed data sets and approaches, among others, is not simple. One way forward could be to facilitate a concerted comparison effort using the same model domain, resolution, data constraints, control parameters, period, etc., in order to clearly distinguish differences in the "free run" models and the impact of data assimilation. However, previous experience with process-oriented models shows that even under such well-defined circumstances it remains a challenge to identify detailed causes for differences. Another potential way forward would be to obtain realistic error information for the suite of individual products and use this information to produce an ensemble estimate, which then should be more accurate than individual estimates. In either case, such initiatives will need to involve many groups performing data assimilation, and will provide an improved scientific basis for ocean state estimation and all of its relevant applications.

## CARBON CYCLE

The ocean plays a pivotal role in the global biogeochemical cycles of carbon, nitrogen, phosphorus, silicon, and a host of other biologically active elements such as iron and other trace metals. Ocean carbon dynamics are particularly relevant to current discussions of rising atmospheric carbon dioxide ($CO_2$) and climate change. Well-tested numerical models are needed to quantify the historical uptake of anthropogenic $CO_2$ by the ocean and to assess future changes in marine biogeochemistry and carbon storage under a warmer, high-$CO_2$ world. The development of ocean biogeochemical models is synergistic with laboratory studies and ocean field observations at many levels: experiments and process studies provide the conceptual framework for identifying the key processes that need to be considered in model formulation and in estimating parameter values; process-studies, time-series, and survey data provide essential constraints on model dynamics and for evaluating overall performance; models offer a test bed for exploring hypotheses, quantifying processes that are difficult to observe directly, extrapolating to larger space scales and longer time scales, and designing new observation systems.

"...MODELS OFFER AN EXPLICIT FRAMEWORK FOR INTEGRATION OF THE KNOWLEDGE GAINED AS WELL AS DETAILED INVESTIGATION OF THE UNDERLYING DYNAMICS."

The field of ocean biogeochemical modeling benefitted greatly from the initiation, in the late 1980s, of the field components of the international Joint Global Ocean Flux Study (JGOFS) (Fasham et al., 2001). Modeling has also been integral in the rationale for and implementation of subsequent international research programs such as Surface Ocean Lower Atmosphere Study (SOLAS), Integrated Marine Biogeochemistry and Ecosystem Research (IMBER), and the CLIVAR/CO2 Repeat Hydrography Program. IOC contributes greatly to ocean biogeochemical research through the International Ocean Carbon Coordination Project (IOCCP), which fosters better integration of sampling programs, data compilation, and data synthesis for topics such as temporal changes in ocean carbon inventories and the spatial patterns and variability of surface ocean $pCO_2$ and air-sea $CO_2$ flux (Doney et al., 2009), and for the coordination of biogeochemical time-series stations. International coordination more specifically focused on biogeochemical modeling has been led through JGOFS; the Global Analysis, Intercomparison, and Modeling (GAIM) task force; and the Global Carbon Project (GCP). Similar efforts have occurred at the national and multinational level through programs such as the US JGOFS Synthesis and Modeling Project (Doney and Ducklow, 2006) and the European Union CARBOOCEAN Project (http://www.carboocean.org).

The Ocean Carbon-cycle Model Intercomparison Project (OCMIP, 1995–1998) was pivotal in advancing global-scale ocean biogeochemical modeling. Phase 2 of OCMIP (1998–2002) brought together about a dozen international modeling groups to conduct a standard suite of ocean simulations for chlorofluorocarbons, radiocarbon, inorganic carbon system variables, and biogeochemical fields. Model results were compared systematically with field data from the WOCE/JGOFS Global $CO_2$ Survey. OCMIP depended especially on synthesis products created by the GLobal Ocean Data Analysis Project (GLODAP; Key et al., 2004). OCMIP-2 established a baseline for assessing ocean carbon model skill and in particular identified observation-based tracer metrics (e.g., chlorofluorocarbons and radiocarbon) for evaluating and choosing among different model estimates of ocean uptake of anthropogenic $CO_2$ (Matsumoto et al., 2004). Major products from the project included future projections of oceanic anthropogenic $CO_2$ uptake and the resulting ocean acidification for the twenty-first century (Orr et al., 2005). Follow-on studies used OCMIP results and new model variants to track horizontal transport and air-sea exchange of natural and anthropogenic $CO_2$ (Gruber et al., 2009). Analysis of interannual variability and secular trends in net ocean carbon storage suggest the efficiency of ocean removal of anthropogenic $CO_2$ may be declining with time (Le Quéré et al., 2009).

The OCMIP Phase-2 models used relatively crude representations of ocean biology (Najjar et al., 2007), and parallel research was underway to improve model treatment of nutrient supply, primary production, phytoplankton-zooplankton dynamics, export flux, and particle sinking and remineralization. The JGOFS process studies and time-series observations were essential in this regard, as was the advent of routine global satellite ocean color observations, beginning with Sea-viewing Wide Field-of-view Sensor (SeaWiFS) in 1997. A key technical advance involved the application of inverse models and data assimilation techniques to marine food-web data. For example, Friedrichs et al. (2007) conducted a systematic comparison of optimized model results from multiple ecosystem model structures for several sites. They determined that models with single phytoplankton groups could exhibit considerable model skill but only when optimized individually for each different biogeographic regime. Models with multiple phytoplankton groups, on the other hand, could be optimized for one environment and then applied successfully to other biogeographic regimes. Simulated plankton species are often aggregated into functional groups distinguished by size class, production of calcified or siliceous shells, or ability to carry out specific biogeochemical processes such as nitrogen fixation or dimethylsulfide production (Hood et al., 2006a).

The newest generation, three-dimensional ocean biogeochemical models typically incorporate phytoplankton functional groups, multiple limiting nutrients, flexible elemental composition, and iron limitation (e.g., Moore et al., 2004; Le Quéré et al., 2005). Other significant developments involve the application of high-resolution, mesoscale eddy resolving simulations for regional coastal domains (Gruber et al., 2006) and ocean basins (Oschlies, 2002; McGillicuddy et al., 2003). In some cases, phytoplankton community composition has been modeled in an eddy-resolving context, yielding strikingly rich phenomenology that reflects many aspects of observed large-scale biogeography (Figure 2).

For an individual investigator, the task of developing and evaluating these ever more complex simulations is daunting, and international collaborations have been forged to facilitate model evaluation and speed the model design cycle, an approach encapsulated in the Dynamic Green Ocean Project (http://lgmacweb.env.uea.ac.uk/green_ocean/model/model.shtml) and the follow-on MARine Ecosystem Model Intercomparison Project (MAREMIP; http://lgmacweb.env.uea.ac.uk/maremip/index.shtml). Such models have great utility for analyzing the seasonal dynamics and interannual variability of ocean biology and chemistry as quantified with the growing capability of ocean observing systems. More sophisticated coupled marine-ecosystem-biogeochemistry models also are increasingly used in future climate and carbon cycle projections to characterize the ocean impacts due to anthropogenic climate change (Sarmiento et al., 2004; Steinacher et al., 2009) and possible feedbacks via changes in the air-sea flux of $CO_2$ and other radiatively active trace gases (Friedlingstein et al., 2006).

## ECOSYSTEM DYNAMICS

Our ability to model marine ecosystems has advanced substantially in recent years. Some of this progress is the result of technical developments in modeling and computer capabilities, but the most significant impact has been through the numerous interdisciplinary programs that have stimulated

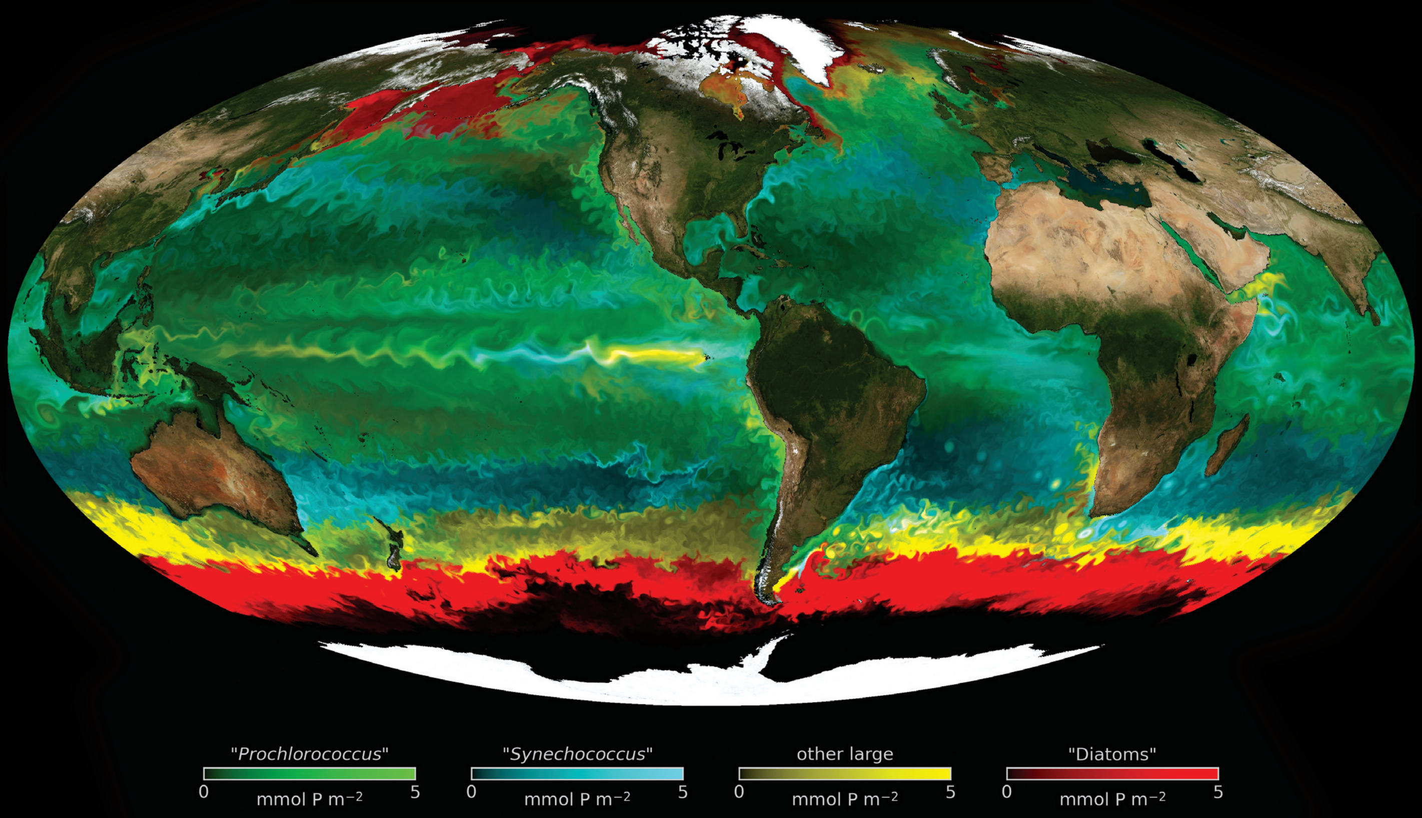


Figure 2. Snapshot distribution of four major functional types of phytoplankton in an 18-km resolution version of the MIT ocean model. The simulation explicitly represents the transport and biological transformations of organic and inorganic forms of nitrogen, phosphorus, iron, and silicon. In addition, 78 "phenotypes" of phytoplankton are resolved as well as two simple grazers. Explicit interactions of the phytoplankton community, resource environment, and grazers lead to the selection for the fittest virtual phytoplankton physiologies, and shapes the community structure of the model. Simulations with lower physical resolution, but otherwise identical, are described in Follows et al. (2007), Dutkiewicz et al. (2009), and Barton et al. (2010). After several years of integration, about 20 types account for almost all of the biomass in the model. Here, the biomass is aggregated into four broader functional groups based on the physiological characteristics of the initialized set of organisms. Diatom analogs (red) were defined as large-size-class cells that require silicon. *Prochlorococcus* analogs or a subset thereof (green) were defined as small-size-class cells that could not use nitrate as a nitrogen source. Two remaining functional groups are small, nitrate-using cells (blue) and nondiatom large cells (yellow). Color shading reflects the group while the opacity of the color reflects the abundance. *Figure courtesy of Mick Follows, Oliver Jahn, Chris Hill, and Stephanie Dutkiewicz (MIT)*

ecosystem studies (Barange et al., 2010). In that context, the Global Ecosystem Dynamics Program (GLOBEC) played a central role. The Scientific Committee on Oceanic Research (SCOR) and IOC initiated GLOBEC in 1991 "to understand how global change will affect the abundance, diversity and productivity of marine populations comprising a major component of oceanic ecosystems" (http://www.globec.org).

Three key characteristics have supported the expansion of ecosystem modeling: (1) development of advanced, realistic, and computationally achievable hydrodynamic models that describe circulation fields at the scales needed, (2) coupling of hydrodynamic and biological models, and (3) enhanced complexity and realism of the biological models, building upon laboratory and field studies. It is not simply the quality and realism of the physical modeling that has influenced ecosystem models; it is also the availability of these models through various user-group and public domain initiatives such as that for ROMS (Regional Ocean Modeling System; http://www.myroms.org), POM (Princeton Ocean Model; http://www.aos.princeton.edu/WWWPUBLIC/htdocs.pom), GOTM (General Ocean Turbulence Model; http://www.gotm.net), ADCIRC (Advanced Circulation Model; http://www.unc.edu/ims/adcirc), and FVCOM (Unstructured Grid Finite Volume Coastal Ocean Model; http://fvcom.smast.umassd.edu/FVCOM), among others.

The challenge of understanding how organisms disperse in the ocean was first identified by Hjort (1914) almost a century ago in his studies of North Sea fish populations. Most marine organisms undergo a planktonic stage in their life cycles (i.e., they are at the mercy of the circulation field for weeks to months), making quantitative understanding of transport and dispersal an essential component in the study of marine ecosystems. Modeling studies began with the exploration of the dispersal of passive particles (i.e., representing planktonic organisms with no behavioral component) by the physical (circulation) flow field. With the advent of individual-based models (IBMs), simple "particle tracking" was enhanced to include biologically relevant traits. Early successes establishing the capability of IBMs were demonstrated by modeling the transport of herring (*Clupea harengus*) larvae in the North Sea (Bartsch et al., 1989), cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larval retention on Georges Bank (Werner et al., 1993), and the movement of anchovy larvae from their spawning sites to nursery areas in the Benguela Current System (Mullon et al., 2003).

While accurate simulations remain a challenge for hydrodynamic models at certain spatial and temporal scales (Werner et al., 2007), perhaps a greater challenge is the proper representation of behavior. For example, coupled modeling of copepod life history and upwelling dynamics on the Oregon shelf (Batchelder et al., 2002) reveals how diel vertical migration influences the distribution of copepods across the shelf (Figure 3). This model explicitly includes vital rates (behavior, growth, reproduction, and mortality) so that the life history of the drifting copepod could be tracked through space and time. In the absence of vertical migration, copepods concentrate in surface waters, but are relatively scarce on the inner shelf. In contrast, when the individuals undergo vertical migrations, most are located in the nearshore region. Coupled biophysical models are crucial to disentangling the complex dynamics of upwelling systems such as those found off the west coast of southern Africa (Parada et al., 2008). In particular, the transport of eggs and larvae to the Agulhas Bank from the spawning grounds is influenced by the strength of the coastal current, upwelling dynamics, and the spatial structure and timing of the spawning. Mullon et al. (2002) used coupled modeling to explore the evolutionary implications of spawning in the Benguela upwelling system.

Integrating across multiple trophic levels and large spatial scales remains one of the challenges for ecosystem dynamics modeling (deYoung et al., 2004). Advances in this area were achieved by researchers working together on the North Pacific (Kishi et al., 2007). They developed a biomass-based model built on a multicompartment lower-trophic-level marine ecosystem model coupled to a bioenergetic model for two different fish—Pacific saury (*Cololabis saira*) and herring (*Clupea pallasii*) (Rose et al., 2008). Another group (Lehodey et al., 2003), working on Pacific skipjack tuna (*Katsuwonus pelmais*), successfully coupled upper- and lower-level trophic models. They combined a prey model for tuna with a biogeochemical model (Chai et al., 2003) embedded within a three-dimensional ocean circulation model.

Population connectivity is the exchange of individuals among geographically separated subpopulations that comprise a metapopulation (Cowen et al., 2007). This topic has become one of the central paradigms for population studies and one of the goals of ecosystem

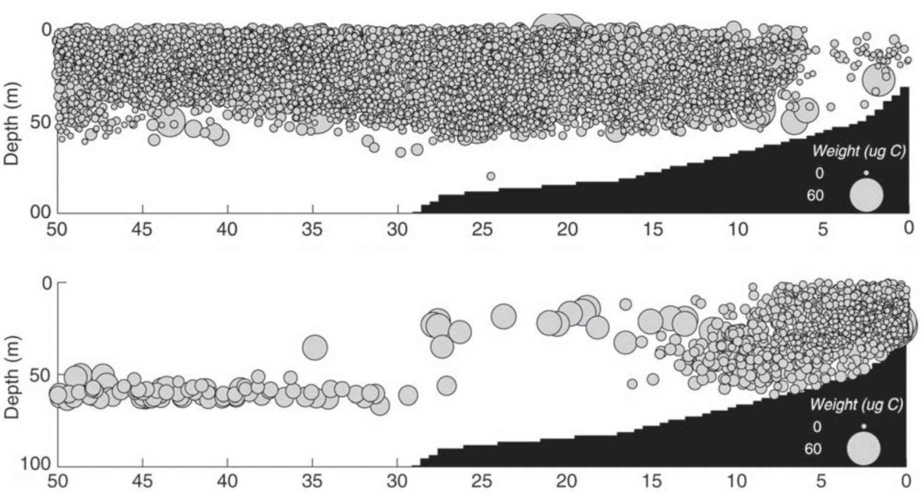


Figure 3. Two different results for a coastal upwelling simulation. The upper panel shows the copepod distributions after 40 days for a simulation in which there is no copepod diel vertical migration. In the lower panel, there is copepod vertical migration with the speed dependent on light, food concentration, the individual's weight, and hunger. Bubble size is related to individual copepod weight. The horizontal axis shows the distance from shore in kilometers. *From Batchelder et al., 2002*

modeling. Physical circulation modeling on ecologically relevant spatial and temporal scales has now moved beyond the continental shelf to the open ocean, enabling and stimulating ecosystem studies at the basin scale (deYoung et al., 2004). The previously mentioned work on tuna in the tropical North Pacific is one example. Another is the work of Speirs et al. (2006) on the copepod *Calanus finmarchicus* in the North Atlantic. Using a model that integrated observational data and biological and physical model structures, Speirs et al. were able to explore the basin-scale connectivity of *Calanus*. They demonstrated the high level of connectivity over the North Atlantic, showed the dependence of mortality on temperature, and explored different hypotheses underlying the organism's resting state (diapause). Such modeling work has influenced our understanding of the coupling between the shelf and the deep ocean and has changed our perspective on shelf and open ocean ecosystem dynamics.

Integration of observations and models has advanced our understanding of marine ecosystems and population dynamics, and the connectivity, dispersal, and mixing of populations. Models have contributed to the explanation of variability in fisheries, and have led to changes in approaches to fisheries management (Fogarty and Botsford, 2007). The results of the ecological modeling and genetic studies (Palumbi, 2004; Cowen et al., 2007) have shifted our perspective on marine population connectivity, suggesting that larval retention near local populations may be more important for maintaining population structure and persistence than was previously believed. The earlier paradigm was that marine populations were quite "open" and that larvae were plentiful and widely dispersed (Caley et al., 1996). Models linking dispersal and connectivity in systems such as coral reefs have shown the importance of closed population structures at smaller spatial scales (Cowen et al., 2000). These population and dispersal models will prove important for the consideration and design of marine protected areas, which have been suggested as an approach to improve fisheries by enhancing the rebuilding of overharvested stocks, protecting essential fish habitat, and reducing the risk of stock collapses (Gell and Roberts, 2003). The growing interest in connectivity and application of population models may provide significant benefit to fisheries management.

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## HARMFUL ALGAL BLOOMS

Harmful algal blooms (HABs) are those proliferations of algae that can cause fish and shellfish kills, produce toxins harmful to human health, and develop biomass accumulations that can alter ecosystems in other deleterious ways. It is now well recognized that HAB events are growing in frequency, extent, and duration throughout the world (e.g., Anderson et al., 2002; Glibert et al., 2005; Heisler et al., 2008). Responding to the urgent need for scientific information on this topic, IOC and SCOR facilitated the development of the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) program in 1998. The goal of GEOHAB is to "foster international co-operative research on HABs in ecosystem types sharing common features, comparing the key species involved and the oceanographic processes that influence their population dynamics" (http://www.geohab.info).

HABs produce a wide range of toxins that may accumulate in predators and organisms higher in the food web, ultimately affecting humans when seafood is consumed, when toxin-laden aerosols are inhaled, or, in the case of freshwater HABs, when contaminated water is consumed. Toxic syndromes include paralytic, amnesic, diarrheic, and neurotoxic shellfish poisoning, as well as cyanotoxin-related illnesses, among others (Landsberg, 2002; Backer and McGillicuddy, 2006). Evidence is also mounting that more subtle effects are also expressed in response to HABs by fish and wildlife. For example, a neurotoxin produced by one of the toxic forms of algae has been shown to induce seizure and memory loss in laboratory animals (Tiedeken and Ramsdell, 2007), and embryonic deformities in oysters have been attributed to toxic algae as well (Glibert et al., 2007). The direct and indirect effects of these events on human health and ecosystem function are all of concern, and forecasts and predictions are needed to understand when and how they may occur and how such patterns may change in the future. To address these needs and to fully advance HAB models that describe, as well as forecast, such events, the HAB modeling community is engaging, and must continue to engage, internationally with climate scientists, marine ecologists, invasive species experts, watershed modelers and hydrologists, social scientists, economists, managers, and policymakers (Glibert et al., 2010). The goal herein is to provide a few examples of the types and models and the challenges that they present. In particular, we focus on HABs associated with eutrophication, as Anderson et al. (2010, in this issue) provide an overview of other types of HABs.

Although many factors contribute to the global spread of HAB events, there is growing appreciation that eutrophication is one of the major reasons that such blooms are now reported with increasing frequency in coastal waters (Anderson et al., 2002; Glibert et al., 2005; Glibert and Burkholder, 2006). In order to relate HABs to nutrient loading—and thus help to establish the extent to which eutrophication may be a contributing factor—good models of nutrient export from land-based sources—both regionally and globally—are required. Nutrient loads, which reflect a rate of delivery of nutrients from watersheds and airsheds, cannot be estimated from nutrient-concentration data alone, which are static measures at a given point in time. Researchers use many types of models to estimate the rate of nutrient loading from land to coastal waters. However, at the global scale there are very real challenges: these models rely on available data, but for many regions of the world, data on nutrient export and loading are either not available or not easy to obtain. Dispersal of nutrients and their interaction with the physical dynamics of the receiving waters are also difficult to quantify. Although some aspects of river plume dynamics are understood, nutrient plumes from nonpoint sources are still difficult to characterize fully. Estimating loads that directly affect algae must also correctly estimate timing. Many loads also follow very specifically the time period when fertilization of fields occurs seasonally (Glibert et al., 2001, 2006). Furthermore, many loading models are based on annual averages, yet blooms occur seasonally or episodically.

Spatially explicit models are helping to advance our understanding of nutrient loads. One such effort is the Global Nutrient Export from Watersheds (NEWS) program, an activity fostered directly by IOC. The NEWS system of models is unique in that it can be used to estimate magnitude, sources, and form (particulate, dissolved inorganic, and organic) of different elements (C, N, and P) (Seitzinger et al., 2005). This suite of models, based on data from more than 5,000 exoreic basins, includes natural sources, such as $N_2$ fixation and P weathering, and anthropogenic sources (nonpoint inputs from fertilizer by crop type, $N_2$ fixation by crops, atmospheric N deposition, and manure by animal species, as well as point sources from sewage, as estimated by human population and treatment level [see Figure 4; Dumont et al., 2005; Seitzinger et al., 2005]). The models also account for hydrological and physical factors including water runoff, precipitation intensity, land use, and slope, as well as in-water removal processes such as dams and reservoirs and consumptive water use. Comparison of these models' results with the distribution of several HAB species shows, for example, that the dinoflagellate *Prorocentrum minimum* is associated with regions of high dissolved

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inorganic nitrogen (DIN) and phosphorus (DIP) exports that are strongly influenced by anthropogenic sources (such as fertilizers and manure for DIN; Figure 5; Glibert et al., 2008).

Algae may respond differently to nutrient loads or variations in the relative proportion of nutrients. To capture these differences, models require physiological or process-oriented details. For example, many process-oriented models contain explicit descriptions of biochemical processes, such as the rate of uptake of a particular nutrient, but many such processes are poorly characterized or variable under different growth conditions (Glibert and Burkholder, 2006). For most HABs, quantitative data on the full range of nutritional pathways are lacking. A few models are beginning to incorporate the breadth of nutritional flexibility observed for many HABs—that is, the ability to use organic nutrients or to eat other cells (e.g., Hood et al., 2006b)—but understanding and modeling these processes are a real challenge in phytoplankton physiology (Burkholder et al., 2008; Flynn and Mitra, 2009; Raven et al., in press). Some process models are based on a single nutrient, such as nitrogen (N), although multi-element models provide a more complete approach, as many HABs occur in nutrient regimes where the relative proportions of N to P are not in preferred balance for algal growth.

Blooms associated with eutrophication result not only from the availability of sufficient nutrients, but also from a combination of physical, chemical, and biological mechanisms and their interactions with other components of the food web. Many of these processes and interactions are not well understood, making it challenging to capture these interactions accurately in a model. Organism behavior also needs to be captured in models that attempt to explain why one species—a HAB—may bloom when another does not. Some of these types of behaviors, such as diel vertical migration, or formation of temporary or long-term cyst stages, may be associated with nutritional triggers but have not been well characterized in eutrophic systems. In this context, it is also important to understand why microzooplankton or macrozooplankton fail to control the phytoplankton population, which must be the case if blooms develop (Irigoien et al., 2005). Understanding top-down control is as important as understanding factors relieving bottom-up control for HAB development (Stoecker et al., 2008).

The time scales of forecasts range from short term (days to seasons) to long term (years to decades). Both types of forecasts provide bridges between research and management, linking research on HAB causes and impacts to applications that can lead to management outcomes. For example, short-term predictions provide advance warnings that can alert local, state, and federal agencies and individuals to prepare for and respond to HABs in a timely fashion and alleviate the deleterious effects of HAB presence on human and ecosystem

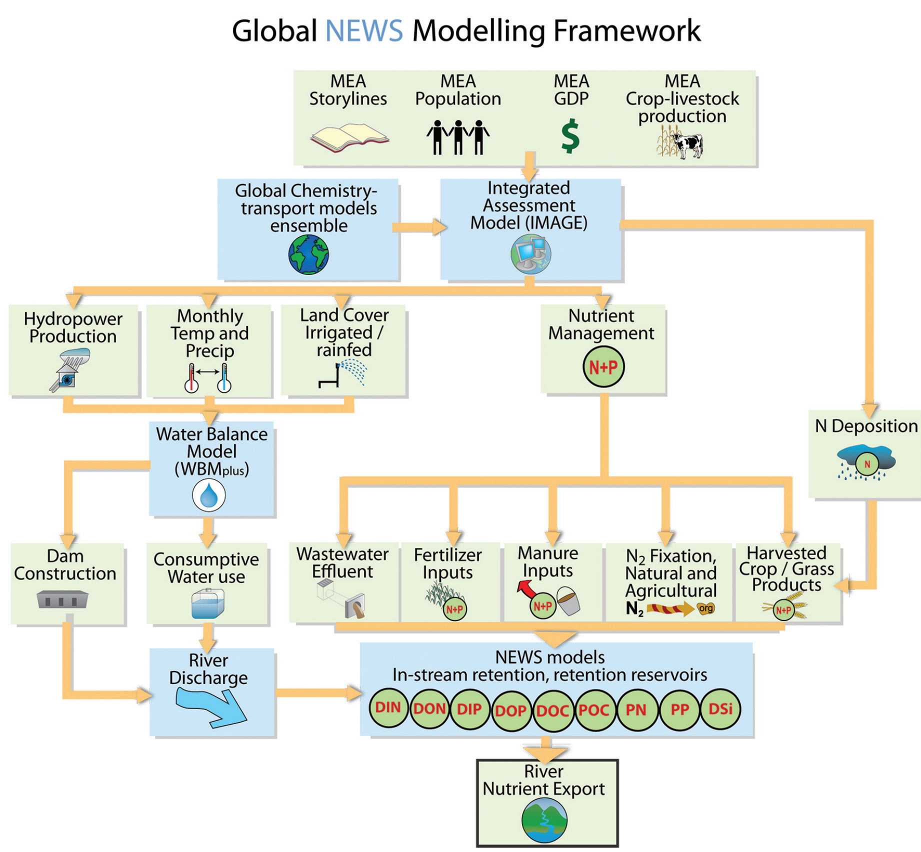


Figure 4. Conceptual diagram of the construction of the Global Nutrient Export from Watersheds (NEWS) model, illustrating the factors taken into account that affect nutrient loads and the submodels that are used to estimate nutrient processing leading to nutrient export. *Redrawn from Seitzinger et al. (2005)*

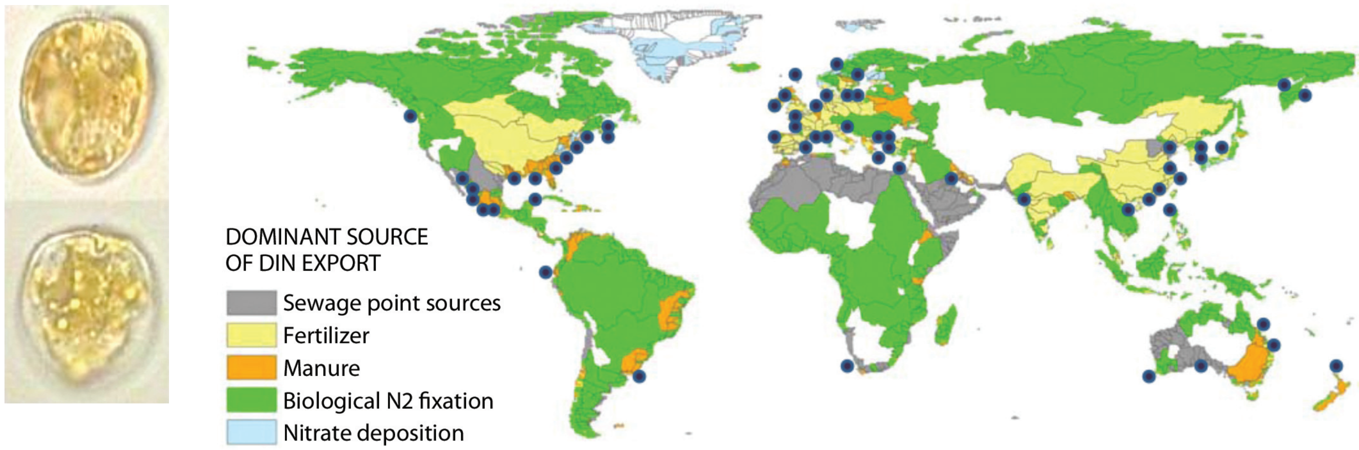


Figure 5. Global distribution of the documented blooms of the HAB dinoflagellate *Prorocentrum minimum* (dots) in relation to export of inorganic nitrogen by dominant form. The inset photo is a picture of *P. minimum*. Bloom occurrence data were compiled from multiple sources in the literature. The base map is a Global NEWS model (from Dumont et al. 2005), reproduced with permission of the American Geophysical Union, and the overall figure is reproduced from Glibert et al. (2008) with permission of Elsevier.

health, as well as provide a means to assess the effectiveness of management strategies on HAB prevention. HAB forecast systems in the United States are in various phases of development (Stumpf, 2008). One for *Karenia brevis* in the eastern Gulf of Mexico is operational (http://www.csc.noaa.gov/crs/habf). The HAB prediction system in Chesapeake Bay (http://155.206.18.162/cbay_hab/index.php) uses real-time and forecast data acquired and derived from a variety of sources to drive multivariate, habitat suitability models of HAB species, such as *Karlodinium veneficum* and *Prorocentrum minimum*, in order to generate daily nowcasts and three-day forecasts of their relative abundance and bloom probability.

Predictions may also supply information on bloom sources (e.g., cyst beds, eddies), triggers (e.g., nutrients, water-column stratification), trajectory (e.g., landfall), duration, decline, toxicity, and impact risk analysis. Longer-term projections offer a tool to evaluate HAB responses—intensity, frequency, distribution, and impacts—to proposed management and land-use/land-change policies and climate change. Projecting the long-term effects of nutrient loading on HABs will enable management actions to reduce loads and minimize HABs, leading to multiple benefits, such as planning for restoration and aquaculture facilities and reducing an excessive monitoring burden on state and local agencies. There is an ongoing quest for better models of nutrient loading, transport, and mixing. The current models are adequate for many applications, but we need higher-resolution nutrient loading models and hydrodynamic models as well as better coupling between the two. On multiyear scales, there is much to be learned from the interactions of nutrient loading and other environmental factors, such as changes in temperature and precipitation that may occur due to regime shifts and/or climate change (Najjar et al., 2000; Howarth, 2008). Ultimately, forecast models must be not only robust but also simple enough to be operational and affordable to managers. Ensembles of models and integrated ecosystem models that couple the atmosphere, the land, and the coastal ocean are required to enable quantitative estimation from airshed to ocean, to investigate ecosystem response to climate changes, and to further explore changes in HABs that are to be expected in the future as eutrophication increases.

## CONCLUSIONS

With our growing dependence on the ocean for natural resources, transportation, and recreation, society's need to know about the ocean continues to increase. Expanding international cooperation will be required to integrate the data from both basic and sophisticated observing networks emerging throughout the global ocean. The need to address longer temporal scales, local to global spatial scales, and more interdisciplinary questions will require more diverse multinational teams of investigators both to develop and to implement future models. Such models will continue to serve as focal points for integration and synthesis of observations into useful estimates of the physical, biological, and chemical state of the ocean, as well as predictions about the future. Societal need for the latter is becoming ever more pressing as we face the challenges inherent in a changing climate. With IOC leadership, past and ongoing large-scale projects, like those discussed here and elsewhere in this issue, have addressed challenging ocean problems from a multidisciplinary and multiscale approach, and have produced significant new understanding of processes underlying changes in coastal, regional, and global oceans over the past 50 years. It is critically important that IOC continue as a leader in international coordination, as the demand for knowledge of the ocean accelerates.

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