



Modeling of HABs and eutrophication: Status, advances, challenges

Patricia M. Glibert^{a,*}, J. Icarus Allen^b, A.F. Bouwman^{c,d}, Christopher W. Brown^e, Kevin J. Flynn^f, Alan J. Lewitus^g, Christopher J. Madden^h

^a University of Maryland Center for Environmental Science, Horn Point Laboratory, PO Box 775, Cambridge, MD 21613, USA

^b Plymouth Marine Laboratory, Prospect Place West Hoe, Plymouth PL1 5LT 3DH, UK

^c Netherlands Environmental Assessment Agency, PO Box 303, 3720, AH Bilthoven, The Netherlands

^d Geochemistry, Faculty of Geosciences, Utrecht University, P.O. Box 80.021, 3508 TA Utrecht, The Netherlands

^e National Oceanic and Atmospheric Administration, College Park, MD 20742, USA

^f Institute of Environmental Sustainability, Department of Pure and Applied Ecology, Swansea University, Swansea SA2 8PP, UK

^g National Oceanic and Atmospheric Administration, 1305 East West Highway, Silver Spring, MD 20910, USA

^h South Florida Water Management District, Everglades Division, 8894 Belvedere Rd, West Palm Beach, FL 33411, USA

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ABSTRACT

Harmful algal blooms (HABs) are often associated with eutrophication of coastal waters and estuaries. However, identifying quantitative relationships between nutrient input and proliferation of specific algal species is very challenging and complex. The complexity arises from the diversity of sources, forms and fluxes of nutrients both exported into and cycled within the system, the diversity of algal mechanisms for acquiring nutrients, and the interaction of the target harmful species with other members of the food web. Even more challenging is the development of forecasts and predictions, both on the short term and on the long term. Short term scales (days to weeks) are necessary for managers to prepare for, and respond to events; longer scales are needed to enable strategic planning to prevent HAB events, mitigate their impacts, or estimate the interactive effects of anthropogenic activities and climate change. To address these needs the HAB modeling community will need to engage with climate scientists (assess climate change scenarios), marine ecologists (describe organism ecophysiology), invasive species experts, watershed modelers and hydrologists (estimate future changes in the land derived inputs), and socio economists, managers and policy makers (define future land use scenarios and to interpret results in a policy context).

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1. Introduction

The term “eutrophication” has been defined in various ways (e.g., Nixon 1995; Richardson and Jørgensen, 1996; Andersen et al., 2006). Central to all definitions is the concept that the enrichment of water by nutrients causes an enhanced biomass and/or growth rate of algae, which, in turn, leads to an undesirable disturbance in the balance of organisms present in the water and to the quality of the water body concerned. The result of eutrophication is often seen as an increase in total algal biomass, frequently dominated by a single species or species group. By definition, these deleterious growths often form harmful algal blooms (HAB) (Hallegraeff, 1993; Anderson et al., 2002; Glibert et al., 2005; Glibert and Burkholder, 2006; Heisler et al., 2008). The effects of such HABs include overgrowth and shading of sea grasses, oxygen depletion of the water from algal and bacterial respiration (especially on death of the algal biomass), suffocation of fish from stimulation of gill mucus production, direct toxic effects on

fish and shellfish, and mechanical interference with filter feeding by fish and bivalve mollusks (Anderson et al., 2002; Landsberg, 2002; Backer and McGillicuddy, 2006). Of additional concern with the development of high-biomass algal blooms, and more than likely a factor in their development, is a reduced transfer of energy to higher trophic levels, as many HAB species are not efficiently grazed, resulting in a decreased transfer of carbon and other nutrients to fish stocks when HAB species replace more readily consumed algal species (Irigoien et al., 2005; Mitra and Flynn, 2006a,b). For example, some HAB species secrete allelopathic substances that inhibit co-occurring species (Pratt, 1966; Gentien and Arzul, 1990; Granéli et al., 2008) and suppression of grazing occurs above a certain concentration of the HAB species (Tracey, 1988).

Although eutrophication is occurring globally, nutrient export from coastal watersheds is not evenly distributed (Seitzinger et al., 2002, 2005; Howarth et al., 2005; Glibert et al., 2006). Eutrophication and nutrient pollution are occurring due to the increase in human population, the increasing demands on energy, increases in nitrogen (N) and phosphorus (P) fertilizer use for agriculture, changes in diet, leading to more meat production and animal waste, and expanding aquaculture industries (e.g., Smil, 2001; Galloway and Cowling, 2002;

* Corresponding author. Tel.: +1 410 221 8422.

E-mail address: glibert@hpl.umces.edu (P.M. Glibert).

Galloway et al., 2002; Howarth et al., 2002; Wassmann, 2005; Fig. 1). Global inorganic nitrogen export to coastal waters is estimated to be highest from European and Asian watersheds, although significant discharge also occurs from the United States and other parts of the world (Seitzinger and Kroeze, 1998; Dumont et al., 2005; Harrison et al., 2005a,b; Van Drecht et al., 2003). This rate of nutrient export to coastal waters has increased dramatically in recent years in some parts of the world. For example, China, which used less than 5 million metric tonnes of N fertilizer annually in the 1970s now uses more than 20 million metric tonnes per year, representing 25% of global N fertilizer consumption (Glibert et al., 2006), leading to significant increased N pollution of its coastal waters. Crop uptake commonly amounts to only 50% of the fertilizer N applied (Peoples et al., 1995). The remainder is lost via various pathways, including ammonia volatilization, denitrification, runoff and leaching, or accumulates in the soil. The importance of the different losses depends on various factors, such as the timing of application, weather, soil temperature and pH and other factors (Bouwman et al., 2002; Khakural and Alva, 1995; Wali et al., 2003; Glibert et al., 2006). In some regions excess N loading has skewed the nutrient ratio away from that normally considered suitable for phytoplankton growth towards P limitation (e.g., Matson et al., 1999). Phosphorus loading, however, is often cited as the major cause of HABs in freshwaters (e.g., Oliver and Ganf, 2000; Schindler et al., 2008) where N_2 -fixing algae often dominate, compensating for any deficit in N.

Nutrients can stimulate or enhance the impact of toxic or harmful species in several ways (Anderson et al., 2002). At the simplest level, harmful phytoplankton may increase in abundance due to nutrient enrichment, but remain in the same relative fraction of the total phytoplankton biomass. Even though non-HAB species are stimulated proportionately, a modest increase in the abundance of a HAB species

can promote noticeable differences in the ecosystem because of its harmful or toxic effects. More frequently, a species or group of species dominates in response to nutrient enrichment or a change in the ratios of nutrient enrichment.

Natural resource managers and public health officials need better tools to forecast HAB events and to predict the composition of algal species and assemblages that may occur under conditions of changing nutrient loads. The requirements for models for understanding HABs in eutrophic systems are not only great, but also complex. This complexity ranges from the need for accurate estimates of nutrient loading rates, well parameterized physiological models, and mechanistic and integrated ecosystem models. Conceptually these needs can be viewed as components of a nested suite of models (Fig. 2). Herein we provide a broad review of the types of models and approaches for understanding HABs that are required in eutrophic systems, recent advances that have been developed, and recommendations for how these modeling approaches can and should be advanced to lead to better predictive capacity of HABs in eutrophic systems.

2. Nutrient loading models

2.1. Types of models and recent advances

One of the core needs for modeling HABs in eutrophic systems is an estimate of nutrient loads. Nutrient loads, which reflect a rate of delivery of nutrients from water- and air-sheds, are not estimated from nutrient concentration data, which are static measures at a given point in time. Various hydrological models, such as the Spatially Referenced Regressions on Watersheds (SPARROW), Soil and Water Assessment Tool (SWAT), and Nutrient Export from Watersheds

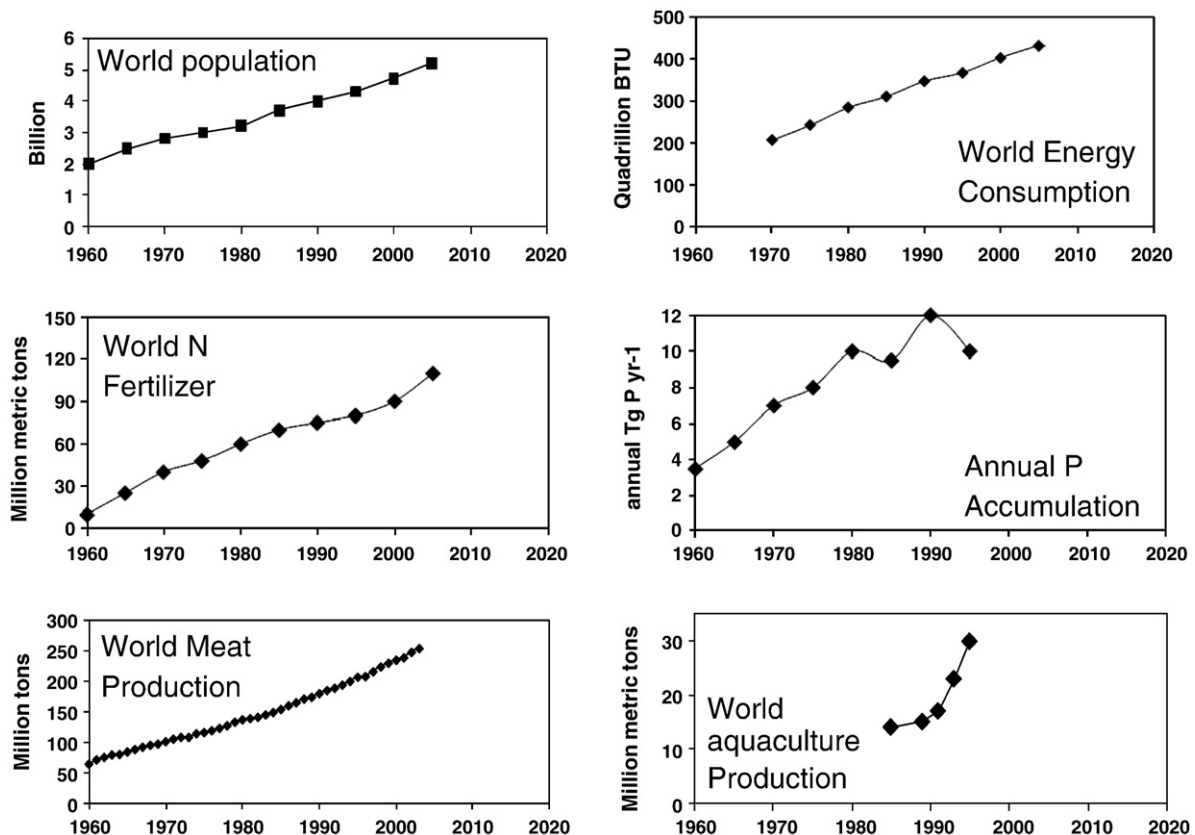


Fig. 1. General trends in population, energy consumption, fertilizer use and accumulation, meat and aquaculture production from 1960 to present.

Data compiled from www.census.gov/ipc/www/img/worldpop.gif, Global Fertilizer Industry, www.fertilizer.org, and the Food and Agriculture Organization of the United Nations (2007).

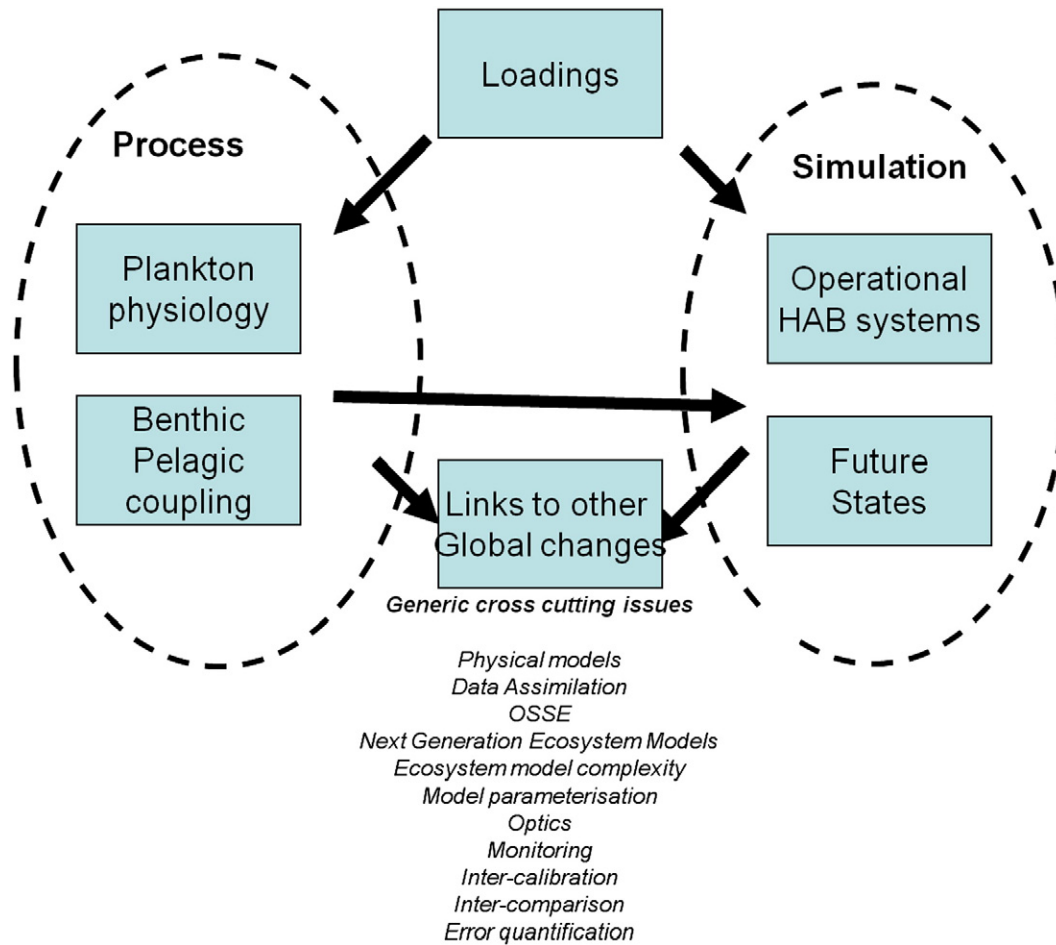


Fig. 2. Modeling HABs in eutrophic systems requires a range of model types, but each type of model is ultimately coupled to the other and all share many cross-cutting issues. Models of loadings are linked to models of processes, and they both are linked to simulation models. All of these must also be coupled to models that estimate other global changes.

(NEWS), estimate nutrient loading, taking into account the broad range of nutrient sources and their alteration across the landscape. The SPARROW model has been used extensively in the USA to estimate nutrient loads to receiving waters, such as the Gulf of Mexico (Robertson et al., 2009; Hoos and McMahon, 2009). SPARROW uses statistical relationships to relate water-quality monitoring data to upstream sources and watershed characteristics that affect the fate and transport of nutrients (e.g., Smith et al., 1997).

Another such empirical model is the Global NEWS model. The NEWS system of models is unique in that it can be used to estimate magnitude and sources of different elements (C, N, and P) and different forms (particulate, dissolved inorganic and organic) (Seitzinger et al., 2005a). This suite of models, based on data from more than 5000 exoreic basins, includes natural sources such as N_2 fixation and P weathering, and anthropogenic sources (non-point inputs from fertilizer by crop type; N_2 fixation by crops, atmospheric N deposition, and manure by animal species; point sources from sewage, as estimated by human population and treatment level) (Seitzinger et al., 2005a). 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 (Fig. 3). The models were validated as described by Dumont et al. (2005) and Harrison et al. (2005b). The input data bases are at a resolution of $0.5^\circ \times 0.5$ and the resulting maps represent nutrient export for mid-1990s conditions, using units of nutrient yield ($kg\ N\ or\ P\ km^{-2}$ of watershed yr^{-1}), dominant watershed source, and percent contribution from anthropogenic sources.

Global comparisons of NEWS-estimated nutrient loadings, by form, and one HAB species, *Prorocentrum minimum* have recently been made (Glibert et al., 2008). This HAB species is associated with regions of high dissolved inorganic nitrogen (DIN) and phosphorus (DIP) exports that are strongly influenced by anthropogenic sources (such as fertilizers and manures for DIN). Blooms of this species were also linked to regions with relatively high anthropogenic contributions to dissolved organic N and P export. Yet, these relationships should be viewed as only an initial step in associating individual species with global nutrient changes as nutrient yields do not necessarily reflect the nutrient that the cells may encounter at any particular point in time. Nutrient yields estimated by NEWS are annual averages whereas HABs frequently are ephemeral events, and little or no effort has been made to incorporate event time scales. Thus, there may be a temporal mismatch. Furthermore, as described below, the likelihood for a species to bloom depends on a complex suite of factors, not just single nutrient forms and supply levels. Much more rigorous quantification of these relationships is required, and global relationships need to be developed for many more HAB species.

Another important application of nutrient loading models is estimating the potential change in loads due to predicted changes in anthropogenic practices on land use. An integrated modeling approach connecting socioeconomic factors and nutrient management to river export of N, P, C and silica (Si) was undertaken using an updated version of the NEWS model. Past (1970–2000), and future trends (2000–2030–2050) in river nutrient export globally based on four Millennium Ecosystem Assessment (MEA) scenarios were

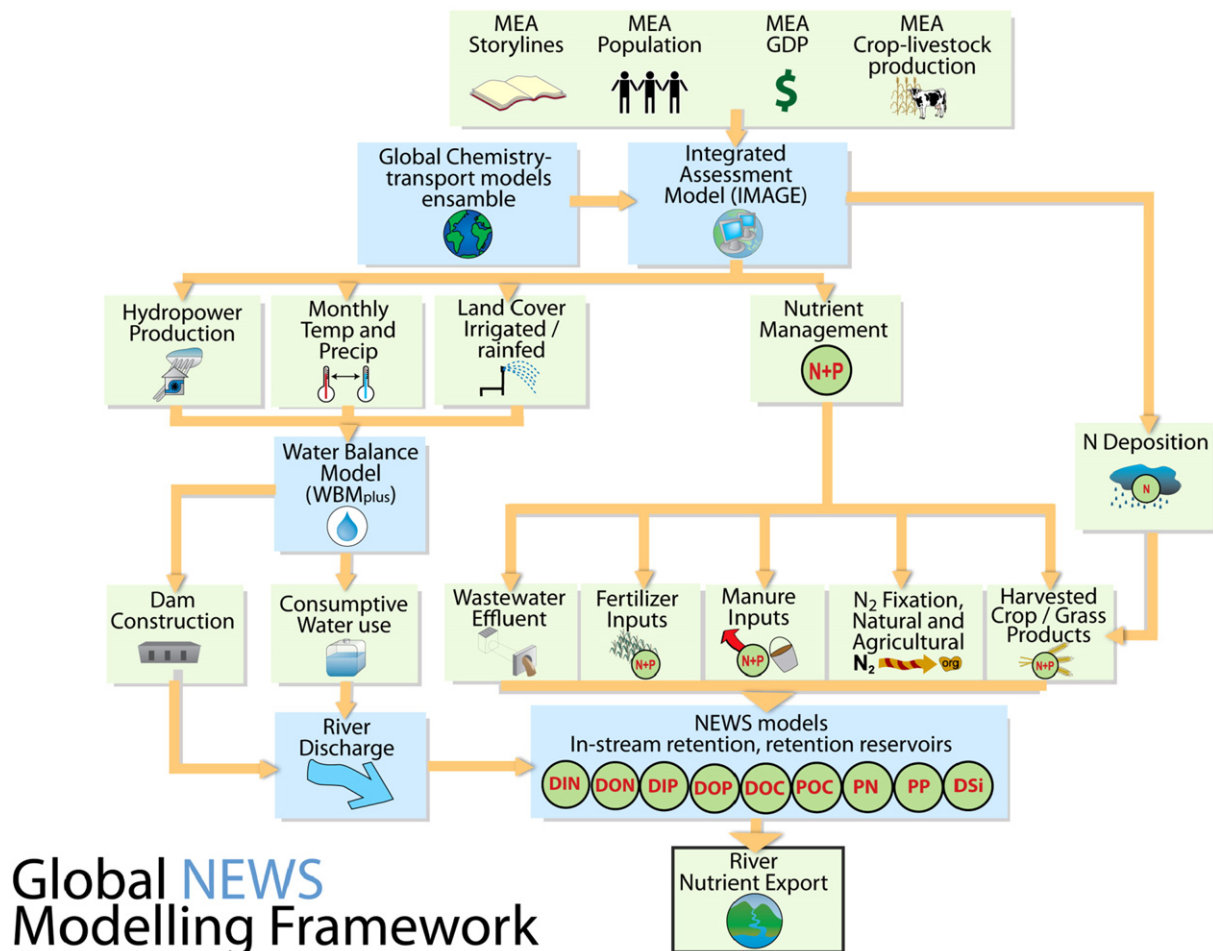


Fig. 3. Conceptual diagram of the Global NEWS model construction, submodels and parameters used in developing the spatially explicit Global NEWS nutrient maps. Reproduced from [Seitzinger et al. \(2010\)](#) with permission.

analyzed ([Bouwman et al., in press](#)). The MEA scenarios were based on storylines developed by the Intergovernmental Panel on Climate Change (IPCC) and translated into changes of the main anthropogenic drivers, i.e. demography, economic development and agricultural production ([Alcamo et al., 2006](#)). The four MEA scenarios differ in terms of environmental management and in degree and scale of connectedness among and within institutions across country borders. The Technogarden and Adapting Mosaic scenarios were developed assuming pro-active environmental management, while Order from Strength and Global Orchestration scenarios assume re-active environmental management. Global Orchestration and Technogarden reflect trends towards globalization, while regionalization is assumed in Order from Strength and Adapting Mosaic. Scenarios with reactive approaches to environment management had higher river nutrient export; however, even in the scenario assuming a pro-active approach, continued increases in river export of nutrients is projected in many regions as a result of population growth, urbanization and economic development ([Fig. 4](#)). Continents with primarily industrialized countries, low-income countries, and countries in rapid economic transition differed in nutrient export trends and relative contribution of watershed nutrient sources. The most dramatic changes in nutrient export for all scenarios were in South Asia. Risks for coastal eutrophication will likely continue to increase in many regions for the foreseeable future.

Fertilizer use is an important driver. Fertilizer use is at the beginning of the N cycle in the complex agricultural system, with N in animal feed being converted to animal manure that is recycled in the system. During this recycling of N various loss pathways lead to

emissions (mainly ammonia) and re-deposition. The N surplus represents the actual N loss to the environment. N surpluses are the difference between the N inputs and the export in harvested crops, grass and grazing. This surplus is determined by agricultural efficiency. For the global system as a whole, this efficiency is ~50%, implying that ~50% of all inputs are lost to the environment ([Smil 2001](#)). This efficiency has actually decreased in the past decades as a result of increasing N fertilizer use in low-input countries. In industrialized countries and several high-input agricultural systems in developing countries, there have been important increases in the N use efficiency due to improving agricultural management. The potential effects of such changes on nutrient export are difficult to quantify, but simple dilution in the ocean is not necessarily harmless and, as shown in more detail below, altering nutrient loading, ratios or forms can have effects on algal populations and succession.

2.2. Challenges and opportunities for advancement

A number of issues must be considered when dealing with spatially explicit nutrient loading models and advancement in many areas of these will lead to improvements in the prediction of nutrient loads and ultimately the relationships between these loads and HAB outbreaks. Not all models are equally robust in estimating all nutrient types or forms. In relating nutrient export or loadings to individual species, the specific nutrient forms and/or nutrient ratios may relate more specifically to individual species than general algal biomass (which relates more generally to total nutrient input). Too often algal biomass is described in units of chlorophyll, or worse as chlorophyll

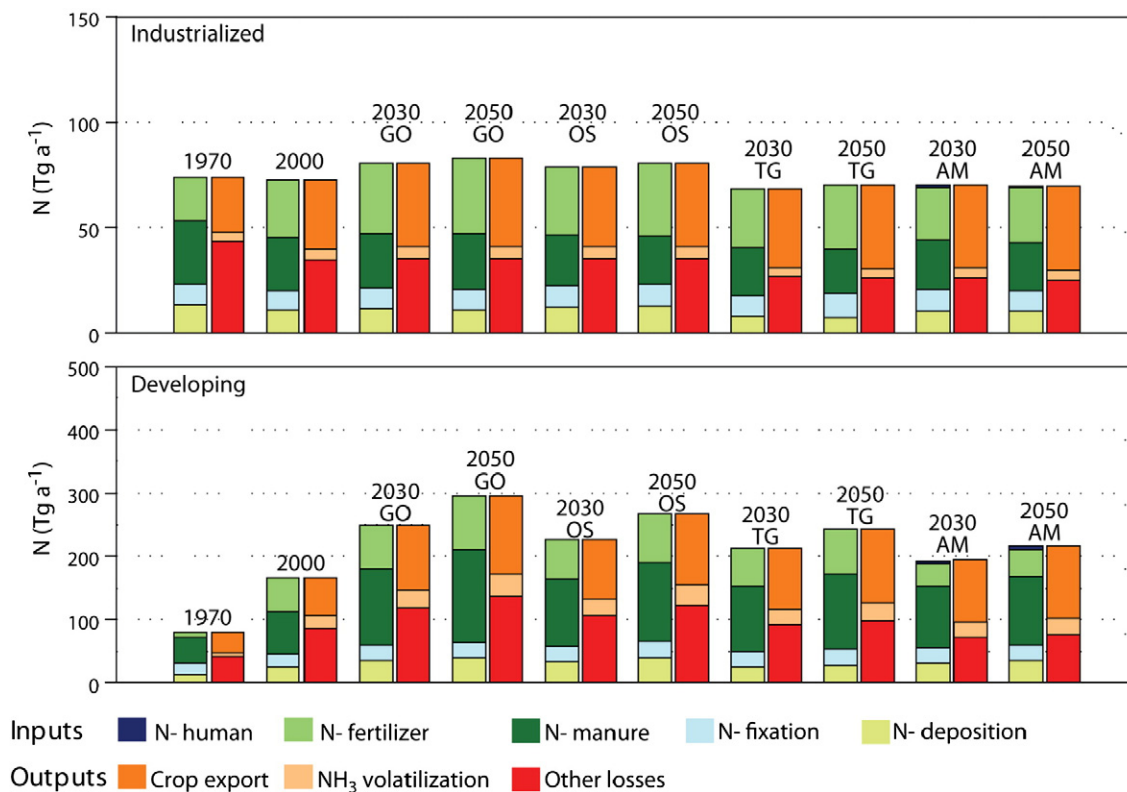


Fig. 4. Global nitrogen surface balance for 1970 and 2000, and for 2030 and 2050 for the four Millennium Ecosystem Assessment scenarios for industrialized and developing countries. Global Orchestration (GO) portrays a globally connected society that focuses on global trade and economic liberalization and takes a reactive approach to ecosystem problems, but also takes strong steps to reduce poverty and inequality and to invest in public goods, such as infrastructure and education. In contrast, Order from Strength (OS) is a regionalized and fragmented world, concerned with security and protection, with the emphasis primarily on regional markets, paying little attention to public goods, and taking a reactive approach to ecosystem problems. TechnoGarden (TG) is a globally connected world, relying strongly on environmentally sound technology, using highly managed, often engineered, ecosystems to deliver ecosystem services, and taking a proactive approach to the management of ecosystems in an effort to avoid problems. In Adapting Mosaic (AM), the fourth scenario, regional watershed-scale ecosystems are the focus of political and economic activity. Local institutions are strengthened and local ecosystem management strategies are common; societies develop a strongly proactive approach to the management of ecosystems based on simple technologies. Scenarios indicate that major changes are expected in the developing countries.

Based on data from Bouwman et al. (in press).

fluorescence, neither of which correlate well with actual C-biomass (Kruskopf and Flynn, 2006). Chlorophyll is also an unfortunate measure when so many HABs are mixotrophic.

Data availability on nutrient export and loading is an important issue in many parts of the world. For many regions there are good loading measurements and models; for other regions the data are poor. As noted above, data on changes in anthropogenic activities that may result in changes in nutrient loadings or rates, such as changes to sewage discharge, agricultural or aquacultural practices (fertilization form, feed used in aquaculture), laws that cap nutrient inputs, and many others, are very difficult to obtain for many regions. Another issue is the scale of the model – from regional to global. Spatial dimension of the loading model is an important consideration. Dispersal of the nutrient and the interaction with the physical dynamics of the receiving water are difficult to quantify. While river plume dynamics may be reasonably well understood, plumes of nutrients from nonpoint sources are still largely difficult to resolve.

Temporal issues are also of key importance. Temporal issues range from the scale of cellular physiology to bloom dynamics, to seasonal and interannual variability, and to the scale on which climate or regime shifts occur. Many loads are highly pulsed and episodic, resulting from storms, landslides or even volcanic eruptions (Heisler et al., 2008). Many loads also follow very specifically the period of time when fertilization of fields has seasonally occurred (Glibert et al., 2001, 2006). Seasonality is of particular importance in monsoonal regions where the load can shift dramatically. For example, the central west-coast of India is a dynamic aquatic ecosystem exhibiting a strong

seasonal gradient, both in environmental variables and plankton assemblages. This area is strongly influenced by the southwest monsoon during June to September and the changes associated with its onset have marked effects on the phytoplankton community, food-web, and production. Occurrence of phytoplankton blooms during southwest monsoon in tropical estuaries is a common phenomenon (e.g., Villanoy et al., 2006).

3. Process models

3.1. Types of models and recent advances

The goal of developing process-oriented models for eutrophic systems is to describe the emergent properties of such systems and hence have an explanatory predictive capacity for individual species responding to various known and predicted nutrient conditions. “Emergence” is a term used to describe the appearance of new properties which arise when a system exceeds a certain level of size or complexity (Davies, 2004). The development of process models often requires the use of functional-type approaches. There are multiple constructs of process oriented models. At the most basic level these are represented by single-nutrient based nutrient–phytoplankton–zooplankton (NPZ) models (Fasham et al., 1990), and perhaps at the extreme, even of single species models. However, such approaches may be inadequate as a basis for models with emergent properties because of the interconnectivity in ecosystems typically subjected to

eutrophication. Some of the salient aspects of process models as related to eutrophic systems are considered here.

3.1.1. Ecophysiology

Physiological models take one of a variety of forms. Traditional biomass-based models (often either single nutrient, N or C) are relatively simple, have few variables as they assume fixed stoichiometry (usually Redfield) and operate using Monod kinetics. These models are unsuitable, and indeed are considered as dysfunctional for descriptions of algal growth under variable nutrient conditions (Goldman and Glibert, 1983; Flynn, 2005a,b, 2009b). Further, such models are incapable of describing trophic interactions correctly because of the implications of variable stoichiometry and, for HAB species, the implications of the accumulation of noxious chemicals during nutrient stress (Mitra and Flynn, 2005, 2006). A common use (and, in some cases, misuse) of such models in the context of eutrophication and HABs is the resource-ratio theory (Tilman, 1977, 1982), which links the ratio of nutrients (such as N:P, P:Si, N:Si) to species succession (Flynn, 2010-this issue). Physiologically-based mechanistic models contain explicit descriptions of biochemical processes. Such descriptions may operate within variable stoichiometric biomass-based models (Flynn, 2001, 2003), or may be allied to individual based model (IBM) descriptions. IBMs offer the opportunity to describe allometric and cell-cycle processes but are thus more complex. It may be expected that IBM strategies will be given wider prominence in models of eutrophic processes, as this facilitates interfacing biological descriptors with the new generations of abiotic descriptors. However, certain groups, most notably bacteria, filamentous cyanobacteria, and colonial species such as *Phaeocystis*, are not readily amenable to such a treatment.

Multiple currency models (C vs N vs P vs Si for example) are particularly useful in physiological descriptions, as stoichiometry is a reflection of the nutrient status of the cell. In typical eutrophic conditions the minimum configuration of multiple currency models is expected to consider C:N:P. Many systems will also require inclusion of Si, and some (especially those associated with deforested areas) may require inclusion of iron (Fe). Variable elemental stoichiometric models should become the norm. Multi-element descriptions in such stoichiometric models, as opposed to Redfield constructs, provide a basis for the development of mechanistic models that contain functional response descriptors with recognized physiological bases. They also support bioenergetic descriptions, which may be important for predicting the survival of organisms under unfavorable conditions.

Adding to the complexity of the formulation of relationships between nutrient availability and uptake, production, growth or biomass (reviewed in Flynn, 2003), is the now widely-recognized understanding that a range of nutrient forms, including organic, and in some cases, particulate nutrients, are involved in the ecology of HABs. At the biomass densities associated with eutrophic conditions, any such interactions may be expected to be strengthened (e.g., Berman, 1997; Carlsson et al., 1999; Glibert et al., 2004; Glibert and Legrand, 2006; Burkholder et al., 2008). In eutrophic habitats phagotrophic mixotrophs, in particular, have been shown to attain higher growth than when in phototrophic mode alone (e.g., Adolf et al., 2008; Glibert et al., 2009a). Yet for many HABs, quantitative data about the role of mixotrophy in nutrition, growth, and blooms are lacking, especially relating laboratory information to natural field assemblages, so that the relative importance of photosynthesis, dissolved organic nutrients, and ingestion of prey remain unknown (Burkholder et al., 2008). Indeed, modeling mixotrophy is an extreme challenge in plankton physiology because of the intrinsic complexity (Flynn and Mitra, 2009; Raven et al., 2009; Fig. 5). It appears also that great care needs to be taken in attempting to simplify the description of mixotrophs, especially in the absence of data for rate processes (Mitra and Flynn, 2010-this issue).

Our ignorance of the identity, concentration and flux of dissolved organics is exceeded only by our weakness in modeling such processes (Flynn et al., 2008). This problem extends also to the best studied organic nutrients, such as urea, amino acids and vitamins. Added to all the above is the problem of determining the nutrient concentration actually perceived by the organisms, as affected by diffusion gradients and other processes. This is a function not only of physical processes, but also of the biological processes that affect motility (sinking and swimming) and the release of mucus and other colloidal materials. As the latter is typically a reflection of nutrient-limited phototrophy, there is potential for a positive feedback process. This feedback may also be associated with a lessening of grazing (which in turn restricts nutrient regeneration) and with toxin accumulation (Mitra and Flynn, 2005).

The ecophysiology of the component organisms present in the ecosystem affects not only their own growth potential but also the activities of others. This linkage to other organisms is either expressed explicitly through direct trophic linkage or through spatially and/or temporally indirect mechanisms. Inasmuch as studies of ecophysiology are logistically demanding even in the laboratory, and the matrix of conditions for experiments extensive, the full range of effects of all

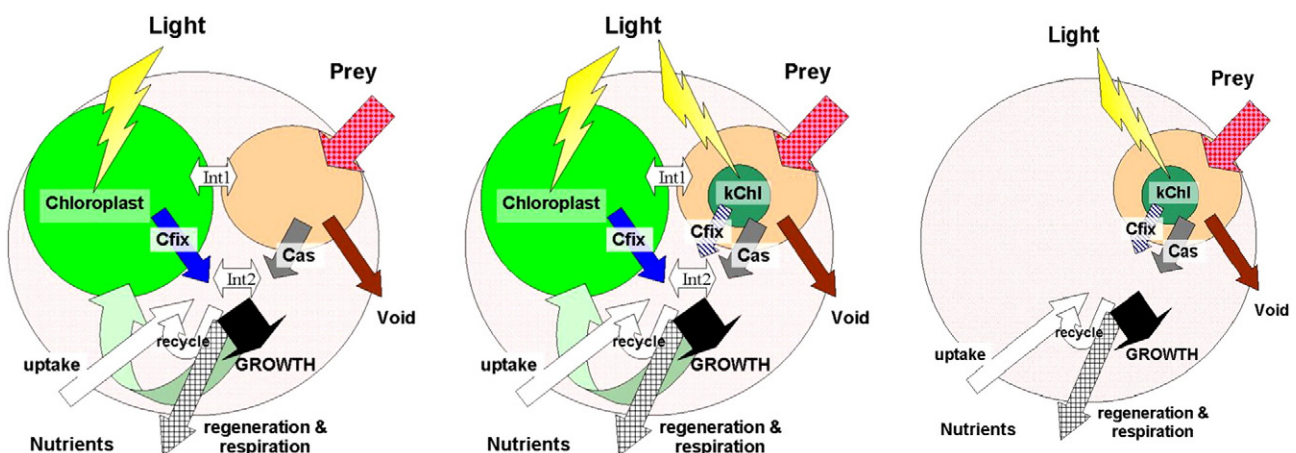


Fig. 5. Different configurations of mixotroph physiology achieved using the model of Flynn and Mitra (2009). Left: phototrophic mixotroph obtaining additional nutrition by prey consumption – Int1 indicates competition for space within the cell between chloroplasts and food vacuole (only for phagotrophic species); Int2 indicates interactions between biosynthesis based upon new C-fixation and from prey digestion. Middle: combination of interactions from mixotroph and kleptochloroplastic C-fixation and prey digestion. Right: mixotroph performing photosynthesis using kleptochloroplasts from captured prey – digestion of the chloroplasts is restricted by products of C-fixation; when the kleptochloroplasts fail they are replaced. Adapted from Raven et al. (2009).

physico-chemical parameters (temperature, salinity, pH, nutrient concentrations, turbulence, light etc.) are not known even for a single species (Flynn, 2005a,b). For example, nutrient uptake processes are a function not only of factors such as temperature, salinity and pH, but also of the nutritional or growth state of the organism at the time of nutrient delivery (Flynn et al., 1999; Glibert and Burkholder, 2006). The range of nutritional capability of many HAB species also adds to the complexity of adequately parameterizing nutrient acquisition.

One approach to modeling HAB physiology within a complex ecosystem is to represent the HAB species with a detailed model, but to describe other groups by aggregate models (e.g., “other flagellates”). This approach has been termed a rhomboid strategy (deYoung et al., 2004; Mitra and Davis, 2010). Allometric approaches may be appropriate for descriptions of general trophic interactions (e.g., Chisholm, 1992), though there are important exceptions to such allometric “rules”. Most notably, large diatoms often have maximum growth rates far in excess of the growth rates of smaller non-diatoms. A detailed description of non-HAB species may be warranted, for example, for descriptions of prey growth dynamics in support of mixotrophic HABs, of specific predators, or of indicator species that may not even have a close trophic association with the HAB.

One such model is that of the heterotrophic dinoflagellate *Pfiesteria* sp. (Zhang et al., 2004; Hood et al., 2006; Fig. 6). This model is composed of *Pfiesteria* zoospores, microzooplankton, the zooplankter *Acartia*, dissolved inorganic nitrogen (DIN), organic nitrogen (DON), diatom, cryptophytes, and detritus. In addition to modeling the total biomass of *Pfiesteria*, this model followed the time dependency of *Pfiesteria* zoospores' cell size and abundance. In this model two forms of *Pfiesteria* were represented in an idealized way, a form in which the toxin is not inducible “NON-IND”, and one in which toxin is present, “TOXIC-A”. In the model, “NON-IND” *Pfiesteria* is kleptoplastidic, does not utilize DON, and has a relatively fast growth rate. In contrast, “TOXIC-A” is not kleptoplastidic, utilizes DON, and has a slower growth rate. This model was subsequently used to simulate effects of physical, chemical, and biological conditions and processes on *Pfiesteria* population dynamics (Zhang et al., 2004; Hood et al., 2006). An important lesson from the operation of this model, and from others such as Flynn (2008) and Flynn and Irigoien (2009), is the sensitivity of the system to the activity of the grazers of the HAB species and their competitors. Modeling HABs requires far more than modeling just the HAB species itself. For mixotrophic species, clearly a thorough understanding, and hence competent model, of prey species

is required. Physiologically-based models are likely to be overly complex for routine usage but may be useful as drivers for Turing tests in which complex models are used to generate a reality. By this means a data series can be generated of detail exceeding that which may be determined from real sampling methods, and free from the errors associated with such methods (notably enabling instantaneous, perturbation-free “sampling”). Critically, of course, it requires that the models used for generating the “reality” in this analysis are widely accepted as representing the state-of-the-art in their construction and operation. This approach may be used to a) develop simpler models, and b) to determine which processes are most important in nature (aided by reference to field data). This has been used by Mitra and Flynn (2010-this issue) in an attempt to identify a simplified description of mixotrophy.

3.1.2. Organismal life cycles

In systems most likely impacted by eutrophication, a close coupling between life cycle stages of organisms is likely. This is important not only for HABs species but also for other components of the system. Eutrophication (either direct from nutrient availability, or indirect via trophic interactions) can stimulate the formation of temporary or long-term resting stage (e.g. encystment, and/or excystment) (e.g., Steidinger and Garcés, 2006). Germination and subsequent migration of organisms provides a route for the transference of particulate nutrients from sediments into the water column. This is a general issue, not just for HABs, but for other species in the system that may, or may not, interact directly with the HAB species. These processes are important because they affect the removal and transformations of elements (nutrients) for HAB development, as well as predator–prey interactions. Linkage between these processes and climatic/meteorological events, affected by inter-annual variability, seasonality and lunar cycles requires attention. Life cycle and other events are often described using an IBM approach because it enables a description of the cell-cycle, allometric and behavior issues related to it, and because of the importance of geographic location and depth in the water column. However, other approaches may also be appropriate (Hense, 2010-this issue).

Some of these changes in behavior have potential for promoting synergistic feedbacks in trophic dynamics. For example, diel vertical migration in response to light-nutrient gradients may drive all cells to the surface at high densities; this would be exacerbated by advective processes, promoting sexual behavior and transmission of viruses and pathogens. Dense accumulations formed by such behavior shades competitive phototrophs. The development of prey rejection through nutrient-stress has been suggested, via promotion of anti-grazing activity, to offer a route for the establishment of an ungrazed HAB (Mitra and Flynn, 2005).

3.1.3. Benthic–pelagic coupling

While most HABs are associated with growth and activity, and advection within the water column, eutrophic events are typically associated with shallow coastal areas, lakes, estuaries and the like. As a consequence, biogeochemical and trophic interactions between the water column and benthos are most likely important. This warrants inclusion of model descriptions of biogeochemical processes. Typically such processes are described empirically but the drivers for these processes need a closer association with those affecting HABs. Beyond the empirical description of generic benthic biogeochemical processes, there are a series of trophic and life-cycle interactions such as bioturbation as well as abiotic events that may promote fluxes of nutrients in and out of the benthic zone, and transformations of nutrients that originally entered during the primary eutrophication event. Historically far less emphasis has been placed on modeling benthic processes compared with pelagic, however there are a few models which attempt to capture the range of processes required (e.g., Ebenhöf et al., 1995; Ruudij and van Raaphorst, 1995).

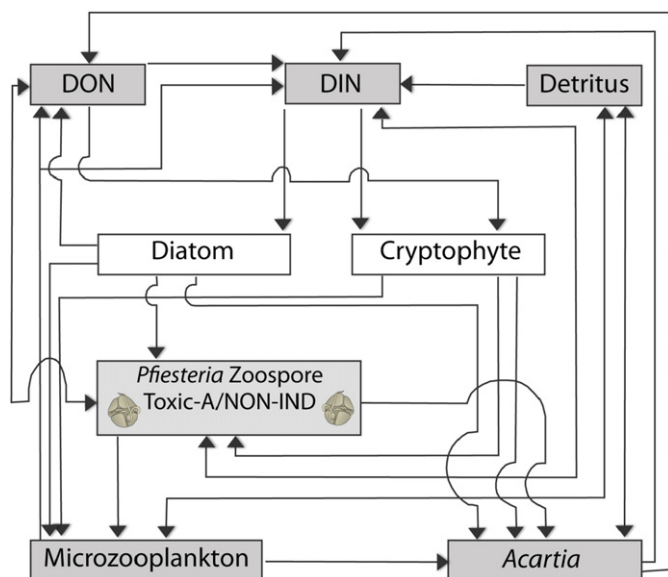


Fig. 6. Generalized schematic of the 8-compartment *Pfiesteria* model. Reproduced from Zhang et al. (2004) and Hood et al. (2006) with permission.

While most benthic processes may be best considered through empirical approaches, detailed descriptions of the growth and trophic dynamics of benthic organisms that graze the plankton, such as bivalves, are warranted. This is because the activity of these organisms can directly affect the plankton community (for example by removing planktonic prey that may also be prey for mixotrophic HABs, or competitors for common nutrients), the meroplanktonic stages may be subject to interactions with HAB species, and of course these organisms often form an important interface between humans and HABs through accumulation of shellfish toxins.

The importance of attached and floating macroalgal and rooted macrophyte growth in some systems also should not be ignored. While these may remove nutrients associated with eutrophication, and shade light from planktonic forms, on their collapse and decay these growths may provide an organic loading that may promote the growth of mixotrophic HABs. One such example comes from Florida Bay, USA, where the Seagrass Ecosystem Assessment and Community Organization Model (SEACOM) was developed. SEACOM is a mechanistic simulation model of seagrass–water column interactions on an ecosystem scale describing the biomass, production, composition and distribution of submersed aquatic vegetation (SAV) – *Thalassia* (turtle grass), *Halodule* (shoal grass), and *Ruppia* (widgeon grass) – as well as phytoplankton in the water column (Madden and McDonald, 2007). A focus of model development is the effects of hydrologic and salinity restoration on the SAV and phytoplankton communities as managed adjustments of the timing and amount of freshwater discharge are implemented. This model (Fig. 7) is being used to refine Minimum Flows and Levels (MFLs) of the freshwater input from the Everglades watershed required to maintain the SAV community and ecosystem health in Florida Bay. The model is also used to test hypotheses about various flushing rate and P recycling rate scenarios, response of the algal community, the impact on the water column light regime, and ultimately the SAV community. Blooms of algae have been a frequent occurrence in Florida Bay in recent years with considerable negative economic and ecological consequences (Fourqurean and Robblee, 1999; Glibert et al., 2009b).

3.2. Challenges and opportunities for advancement

It is now widely recognized that descriptions of variable elemental (if not chemical, e.g., fatty acid) stoichiometry within organisms are essential in models of ecosystem functionality. This is particularly so for primary producers (including mixotrophs), not only because phototrophy lends itself to significant variability in C:N:P(:Si):Fe, but also because changes in nutrient physiology associated with such variations in stoichiometry are linked to accumulation of noxious and toxic compounds (Granéli and Flynn, 2006). Coupled with the above is the difficulty in modeling loss processes associated with viral and pathogenic attack, infauna activity and burial/exposure of resting stages in sediments. The importance of so-called programmed cell death, and programmed sexual cycles (after so-many vegetative cycles) remain poorly understood, but has clear potential for affecting HAB dynamics. The largely qualitative understanding of organism life cycles needs quantification, particularly in eutrophic systems. The role of density-dependent processes, which are most likely to be exacerbated in eutrophic systems, requires parameterization. Changing organism behavior has the power to shape and reshape ecosystem dynamics. The high biomass potential of eutrophic waters offers the capacity to exaggerate behavioral responses through enhanced biomass levels which increase the frequency of organism–organism interactions, decrease between-contact periods (thus minimizing respiratory costs), and increasing chemical concentrations.

Switching between nutritional modes can affect the growth rate of organisms and have a cascading ecosystem response (e.g., Adolf et al., 2008; Glibert et al., 2009a). These behavioral responses typically reflect biochemical (physiological) responses and include nutrient switching, prey switching, and switching between nutritional modes (mixotrophy). Responses more typically termed behavioral, associated with swimming and diel vertical migration, are also associated with nutritional triggers but have not been well characterized in eutrophic systems. Modeling of such switches is often crude, and sometimes flawed (Mitra and Flynn, 2006b), but critically affects the dynamics (e.g., HAB development – Mitra and Flynn, 2006a; mixotrophy nutrient switching – Flynn and Mitra, 2009).

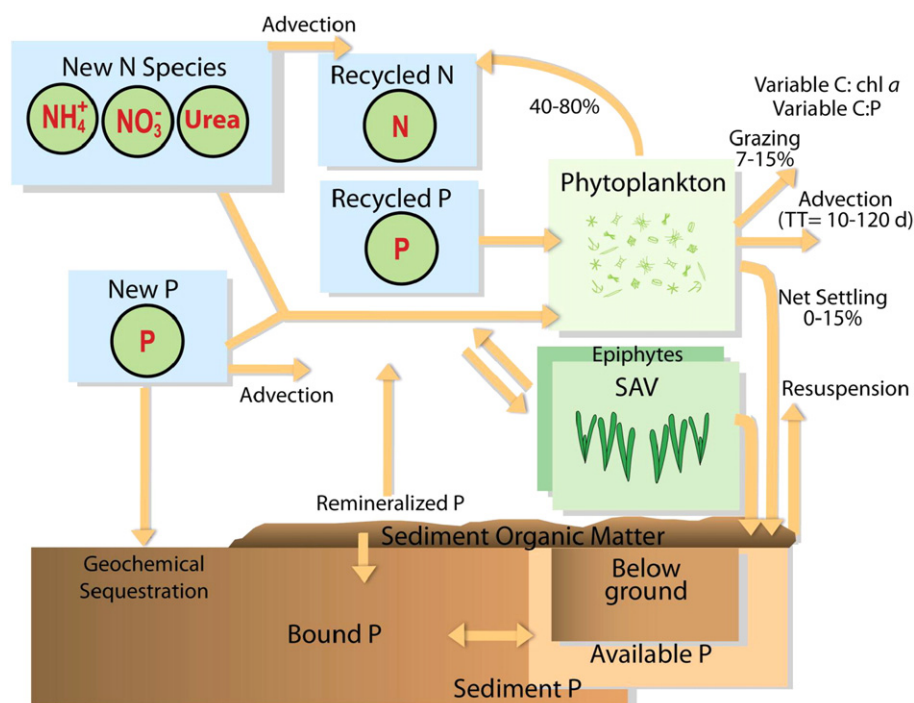


Fig. 7. Conceptual model of the Florida Bay, USA, SAV-phytoplankton ecosystem numerical model.

A primary challenge for describing behavior is that of identifying and parameterizing functional response curves relating the stimulus to the response; typically these take the form of Michaelis–Menton type curves describing nutrient uptake as a function of nutrient concentration, or grazing rates as a function of prey concentration. Description and placement of these response curves within models is relatively easy, using sigmoidal curves which are typical of biochemical allometric interactions. As far as possible, a mechanistic basis should be developed for such responses because the multitude of potential interactions will likely preclude the complete parameterization of the stimulus–response matrix. Modeling the growth of HABs requires that attention is also given to modeling those species that share the common environment. These organisms are important for the conditioning of the environment through removal and/or addition of nutrients and other chemicals, through grazing and other such interactions. For example, modeling *Dinophysis* may be expected to require effort to also be directed towards *Myrionecta* and cryptophytes because these groups are involved in a kleptochloroplastic exchange (Johnson et al., 2006; Kim et al., 2008).

Important challenges include studying the cycling of nutrients, and the positive feedback processes that may exacerbate or minimize interactions. Some of these are relatively simple (stoichiometric) but many may relate to processes that are synergistically related to changes in nutrient status, such as toxin, allelopathic and anti-grazer impacts. Even simple stoichiometric interactions require careful consideration, particularly as eutrophication is usually associated with shifts in nutrient (elemental) ratios and nutrient forms in the incoming nutrient stream which may ultimately affect C:N:P within the primary producers (but see Flynn, 2010-this issue).

The impacts of eutrophication upon toxin production act through two routes; the enhancement of biomass and hence of overall toxin burden in the water, and secondly the enhancement of per capita toxin content through nutrient stress associated with disturbed elemental ratios in the water column and thence in the organisms. Because eutrophic systems are often associated with coastal areas used for shellfish and/or finfish harvesting, the primary concern has been of toxins that affect humans (e.g., shellfish toxins or ichthyotoxins). These are chemicals for which we typically have analytical techniques which may be applied to experimental studies and as aids to model development (e.g. John and Flynn, 2002). However, there is a more insidious class of toxins, and other processes, which are important for the biological warfare waged within the ecosystem, and for which we have relatively little knowledge. This group includes not only anti-grazer compounds and processes such as spines and mucus, and allelopathic chemicals (Mittra and Flynn, 2005; Pohnert et al. 2007). For many of these we have little direct knowledge, and hence few data (even qualitative data) for modeling. Eutrophication, however, may be expected to enhance the role of these processes for the same reason as given for shellfish toxins (Granéli et al., 2008). One of the best studied of these chemical classes is polyunsaturated aldehydes, and while the value of these chemicals as defense toxins produced by diatoms against their copepod grazers has been called into doubt, there is no question as to the potential damage that a eutrophic-enhanced bloom of diatoms could cause on copepods through such a mechanism (Flynn and Irigoien, 2009). Allelopathy is clearly a density-dependent process, linked to the accumulation of chemicals in the water column, and may be expected to be enhanced in eutrophic waters.

Studying and then parameterizing models describing the involvement of anti-grazer and anti-competitor processes is complex, requiring an understanding of the ecophysiology of several members of the ecosystem. In turn this generates an experimental matrix of conditions that is logistically challenging, especially when the interacting organisms cannot be physically separated prior to chemical analysis. While most emphasis is often placed on the synthesis of toxins, modeling the deterioration and loss of toxins is a

topic that warrants further investigation (John and Flynn, 2002). Studies in which naturally occurring groups of organisms are brought together under controlled quasi-natural conditions are required, recognizing that these are very difficult experiments to conduct well. In this context, a critical question is why the microzooplankton fail to control the growth of the phytoplankton (Irigoien et al., 2005). Understanding the failure of top-down control is as important as understanding factors relieving bottom-up control for HAB development (Stoecker et al., 2008). In large measure this may be related to the more complex behavioral and life cycle of higher trophic levels that in turn control the microzooplankton. Certainly the age structure of copepods (Flynn and Irigoien, 2009; Flynn, 2009a) and the operation of intraguild cannibalism (Mittra, 2009) all operate to affect the dynamics significantly. The effects of temperature in these dynamics are also important, especially given the differential effect on heterotrophy (Rose and Caron, 2007), that mixotrophy is important in many HABs, and that bloom development itself raises local water temperature in blooms.

4. Forecast models

4.1. Types of models and recent advances

HAB forecasts provide an estimate of the likelihood of occurrence, abundance, or both, of a HAB species at a given location and time in the future. The time scales of forecasts range from short- (days to seasons) to long-term (years to decades). Short-term forecasts – termed predictions here – carry the expectation of accurately reproducing future events, while longer term forecasts – termed projections here – are considered to possess a high degree of uncertainty. Both have relevance in terms of understanding the relationships between HABs and eutrophication.

Both short- and long-term HAB forecasts provide a bridge between research and management, linking research on HAB causes and impacts to applications that can lead to improved management outcomes (e.g. advanced management knowledge; changes in management strategies; improved environmental conditions; societal benefits). 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 the HAB presence on human and ecosystem health, as well as provide a means to assess the effectiveness of alternative management strategies on HAB prevention. The 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. The longer-term projections offer a tool to evaluate the response of HABs – their intensity, frequency, distribution, and impacts – to proposed management and land-use/land-change policies and climate change. In regards to eutrophication, 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, reduction in drinking water contamination, and a reduction in monitoring burden on state and local agencies.

HAB forecasts will likely be most effective when applied through a regional ecosystem-based management approach where physical, chemical, biological, economic, and socio-economic data about the present condition of the coastal environment and expected future conditions are integrated and considered together. An important use of HAB forecasts is in goal-setting – e.g., determining the amount of nutrient abatement required to decrease HAB magnitude, frequency, extent, and/or impacts. This includes an adaptive management approach (Holling, 1978), where it is critical to validate and reassess goals according to any new and improved understanding of the ecosystem effects and changing conditions (from management

actions, climate change, regime changes, etc). Short-term predictions and long-term projections both rely on the application of our basic knowledge and understanding of HABs and their interaction with the environment. HAB forecasts employ information from empirical and process/mechanistic models to develop a predictive relationship between causative factors and HAB parameters, and their impacts.

Forecast models can be simple (involving a limited number of variables or one or few species) or complex (system-scale). The complexity of models is limited by our understanding of ecosystem dynamics, and so various process-level models are often not fully developed. Therefore, simple models are often the strategy employed, whether they are appropriate or not. The model and supporting data requirements for HAB forecasts vary with region and HAB species. Forecast approaches include use of: a) observations coupled with transport models; b) mechanistic models; c) empirical statistical models; d) hybrid mechanistic and statistical models; e) coupling of b, c, and d with real-time observing systems, and f) food web models. Typically, operational forecast systems will couple circulation models (which may be linked to transport models), population dynamic models (process models), and ecological conditions models (e.g. nutrient loading models). For instance, the system that forecasts “red tide” blooms of the dinoflagellate *Karenia brevis* on the west shelf of Florida detects probable blooms in satellite ocean color imagery and uses a simple transport model to predict the likely movement and location of landfall (Stumpf et al., 2003).

HAB forecast systems in the U.S. are in various phases of development (Stumpf, 2008), and only that for *Karenia brevis* in the Eastern Gulf of Mexico is in operational status (<http://www.csc.noaa.gov/crs/habf/>). Nutrient loading/availability is incorporated in all of these as a triggering factor (e.g. Lake Erie, Chesapeake Bay, California) or a factor in bloom duration/prolongation. For example, the HAB prediction system in the Chesapeake Bay (http://155.206.18.162/cbay_hab/index.php) uses or will use real-time and forecast data acquired and derived from a variety of sources to drive multi-variate, habitat suitability models of HAB species, such as *Karlodinium veneticum* and *Prorocentrum minimum*, in order to generate daily nowcasts and 3-day forecasts of their relative abundance and bloom probability. The empirical habitat models for three HAB species in the Chesapeake Bay, including the two species mentioned above and the diatom *Pseudo-nitzschia* (Anderson et al., submitted for publication), require estimates of dissolved inorganic N, particulate N, and P. Other variables used in the habitat models include chlorophyll concentration and dissolved oxygen, both of which will likely be affected by changes in regional nutrient loading, and the ecophysiology of the organisms and whole system. At the seasonal scale, forecasts of the likelihood of occurrence and intensity of *Microcystis aeruginosa* in the Potomac River and *P. minimum* in the Maryland region of Chesapeake Bay during the summer are generated based on flow and nutrient loading conditions through mid-May (<http://www.eco-check.org/forecast/chesapeake/2009/>).

HAB prediction systems are being developed and implemented around the world. Most of these focus on short-term predictions. Examples include *Cochlodinium polykrikoides* predictions based on temperature in Korea (Kim et al., 2003), predictions of diatoms (various species) red tides based on rain and river discharge in Japan (Ishizaka et al., 2006), and predictions of *Gymnodinium catenatum* blooms based on downwelling conditions in Portugal and Spain (Moita et al., 2003). The Harmful Algal Blooms Expert System (HABES) project uses fuzzy logic models to predict conditions favoring blooms and harmful effects from 7 species from various European waters, including *Phaeocystis globosa* and *Dinophysis* spp. in the Dutch coastal zone (Blauw et al., 2006).

Longer-term projections also are needed and forecast models are being developed to examine how anthropogenic activity, eutrophication and HABs may be accelerated due to climate change, including influences from circulation and temperature structure of the ocean.

Concurrently, increasing population, likely to be centered on the coast (e.g., NOAA, 2004), and changes in land-use will lead to increased nutrient loading to coastal waters. These and other factors, such as invasive species, ocean acidification, overfishing, and pollution, will impact HAB distribution and abundance on a regional and to global basis. In the context of climate change the focus of marine ecosystem model modeling activity has largely been on C cycling at a global scale (Le Quéré et al., 2005; Moore et al., 2002; Aumont et al., 2003).

Data analysis only allows one to look at the current state; modeling will allow exploration of the consequences of these changes on HAB distribution beyond the climate envelope. Models can be used to attribute the various factors, identifying the important factors causing these distributional changes. Numerical models with feedbacks are the only way to explore ecosystem response beyond the current climate envelope. In the Chesapeake Bay, for example, a regional earth system model, which consists of a coupled atmospheric, land, and ocean model, complete with biological and geochemical components, is being implemented with dynamic downscaling of the seasonal to interannual and climate forecasts and IPCC projections for the Chesapeake watershed to routinely generate seasonal predictions and decadal projections of HABs and other organisms, e.g. pathogens, and ecological conditions (<http://www.climateneeds.umd.edu/chesapeake/>).

The role of such models is very different, however, from that of models required for HAB research, and the constructional detail of the biological descriptions are inadequate (see Section 3.1.1). These models also do not resolve the loadings of coastal zone spatially, temporally (see Section 2.1), or in terms of key processes. At the same time, shelf seas modelers have focused primarily on eutrophication and nutrient cycling resulting in numerous medium-to-high resolution regional models, ranging from simple nutrient–phytoplankton–zooplankton–depth (NPZD) models (Fasham et al., 1990) to highly complex, coupled physical–biogeochemical ecosystem models (e.g. Allen et al., 2001; Schrum et al., 2006). Such models are used routinely, and are beginning to be applied in a climate context. For example, the European framework project Marine Ecosystem Evolution in a Changing Environment (MEECE; www.meece.eu) seeks to address the broad range of ecosystem responses to climatic and anthropogenic drivers at a regional scale. Parameterization to study ocean acidification and end-to-end ecosystem models (e.g. those simulating the response of trophic levels from phytoplankton to top predators) are being rapidly developed and implemented. Simulation strategies are required to make reliable hindcasts, including reanalysis simulation and error quantification. A reliable hindcast means making the best available simulation of the current state of the system in question, using the best available external forcing (e.g. meteorology, land derived inputs), whose skill has been assessed against observations.

A challenge is to get emergence from ecosystem models in the sense of allowing model organisms to evolve and adapt to their environment rather than just occupy niches. Bedau (1997) highlights two “vague but useful hallmarks of emergent phenomena”: that emergent phenomena are somehow constituted by and generated from underlying processes and that these phenomena are somehow autonomous from these underlying processes. Follows et al. (2007) used such an approach towards generating biogeography; a marine ecosystem model was seeded with many phytoplankton types, whose physiological traits were randomly assigned from ranges defined by field and laboratory data. Global scale simulations generated an emergent community structure and biogeography consistent with observed global phytoplankton distributions. This is a model of selection not adaptation. Further, emphasis was placed upon bottom-up phytoplankton dynamics, with scant effort directed to the predators, and none directed to mixotrophy. The methodologies used by Follows et al. (2007) provide a conceptual framework within which we can create emergent ecosystems combining generic cells with food web interactions, but requires significant upgrading in

scope to be of utility for predicting HABs. To address issues such as physiological adaption to ocean acidification or the plasticity of response in food web dynamics requires a theoretical framework which allows processes to adapt. The system of infinite diversity (SID) approach (Bruggeman and Kooijman, 2007) simulates biodiversity by describing the ecosystem with one generic population model and species characterising parameters and models phytoplankton succession as evolution of the parameter value distribution and this approach may provide one starting point.

4.2. Challenges and opportunities for advancement

There is an ongoing quest for better models of nutrient loading, transport and mixing. The current models are adequate for many applications, but our needs are for higher resolution nutrient loading models and hydrodynamic models and for better coupling between the two. On multi-year 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, 1999; Najjar et al., 2000; Howarth and Marino, 2006; Howarth, 2008). Spatially explicit modeling will be of importance in advancing this understanding. For example, estimates of the net anthropogenic nitrogen input to 16 major watersheds of the northeast USA show that increases of up to 45% are expected in watersheds where precipitation is expected to increase, but that in drier regions, decreases of only 10–20% are expected (Howarth, 2008). Clearly, linking climate and nutrient loading estimates is a significant challenge, but an even greater challenge will be predictions of how such changes may affect the relationship between nutrients and HABs. Not only will loading rates change, but so too will water temperature and trophodynamics among other factors. In addition to determining trends in environmental conditions such as temperature, there is a need to understand the consequences of climate variability and possibility/probability of increased extreme events, both in frequency and magnitude. Current models provide possible realizations of future states on a regional and global basis, but are insufficient to address the response of HABs to climate change that we face. The development of integrated ecosystem models that couple the atmosphere, land, and coastal ocean to enable the quantitative estimation from air-shed to the ocean is required to investigate ecosystem response to climate. This activity is beginning, but will require considerable computation capabilities to run routinely at the time and space resolution required.

An assessment of the confidence that can be placed on model results must take into account the complex combination of model and observational uncertainties. Model errors derive from inaccuracies in the model structure itself, process descriptions, parameterisation, initialisation and forcing functions. Errors in observations arise from basic measurement error, inadequate sampling of a process (i.e. aliasing of small scale signals to large scales due to under-sampling) or lack of replication in highly heterogeneous systems and issues of methodology. A crucial issue is balancing precision (how well the model fits each data point) with trend (i.e., how well it reproduces the observed fluctuations). For example, even when the trend is well reproduced small differences in the timing of an event can lead to large errors in precision. The choice of error statistic is crucial and a comprehensive validation process must consider several. A variety of univariate and multivariate methods are now being used to assess model skill (e.g. Stow et al., 2009; Allen and Somerfield, 2009; Jolliffe et al., 2008), the choice of which is dependent on the questions being asked and the data available for confronting the model.

High model skill depends on the fidelity of all model components, and also upon the adequacy of the data used for its parameterisation and validation. Models depend on parameters that are not always easily measured or available and knowledge of fluxes, dynamics or physiological variable is often not adequately captured in models. In

many cases, also, data on a relevant process may be obtained using multiple methods, but such techniques may not be inter-comparable, and such subtleties are not well captured in models. One such example is the measurement of productivity, which may be by use of ^{14}C , ^{18}O , or variable fluorescence. Whereas ^{14}C measurements determine the rate of incorporation of C, ^{18}O experiments measure the water splitting reaction and non-cyclic electron transport, and variable fluorescence instruments (e.g. FRRF, PAM) measure photochemical efficiency of the photosystem II pathway; these rates are not equivalent (Suggett et al., 2009). There are many other examples of methodological issues where data from one method are not equivalent to data obtained via another method, yet used interchangeably in models. The estimation of rate processes can be critical; models tuned only against the usual state variables of nutrients and biomass can fit data using erroneous or dysfunctional descriptions of rate processes (two wrongs making a right) (Mitra et al., 2007; Mitra and Flynn, 2010–this issue). As rate process data invariably carries wide ranges of error, and empirical fits to data can be so misleading, it is imperative that model structure is fit for purpose (Flynn, 2009b).

All ocean models have some biases with respect to observations. Data assimilation offers a way to reduce these biases and improve a model's representation of the observed state of the system in question. In particular, these kinds of simulation allow us to make the best possible model quantification of key biological processes over the periods which have suitable data. The application of data assimilation has demonstrated the value of constraining the physical environment; improved descriptions of physical mixing lead to better estimates of the C cycle at a global scale. The next stage is to develop complementary assimilation techniques to constrain biological models. Multiple models ('ensembles') are the preferred approach to develop a range of future predictions and hence an idea of the range of future ecosystem responses (Fig. 8). Ideally such ensembles would be derived from multiple combinations of different biological and physical models which are then assessed to decide which outcomes are more likely (probable) than the others. Ensemble simulations also provide the opportunity to explore the uncertainties introduced by parameter and driver choices. This is important, for example, when assessing the sensitivity of biological models to changes in hydrodynamic environments. Again, robust validation of hindcast simulations is required to underpin this activity and where necessary to help weight the ensembles.

5. Summary

Understanding and quantifying the relationships between eutrophication and HABs, and developing both short and long term

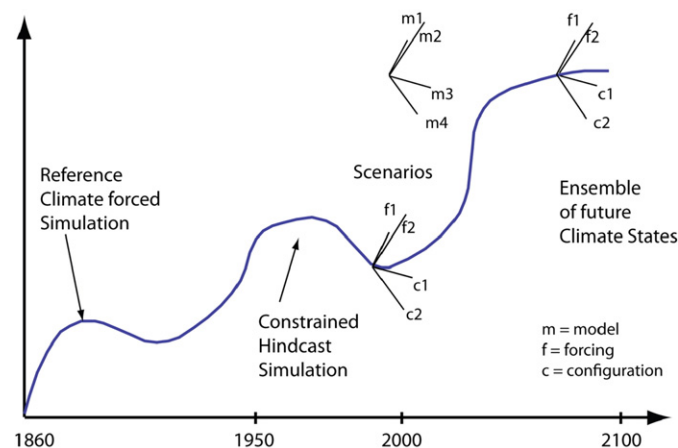


Fig. 8. Schematic diagram of the simulation strategy for future climate scenarios. Modified from Jason Holt, Proudman Oceanographic Laboratory, UK.

predictive capabilities will require a suite of modeling approaches. Loading models draw on the complexity of nutrient sources from individual water- and air-sheds and how they are modified by human population, agricultural and aquacultural practices, precipitation, land use and slope and many other factors. Coupling nutrient discharge to the response of a single species or group of species requires models of hydrologic properties of the receiving water for estimating retentiveness of the nutrient, as well as knowledge of the rates and pathways by which nutrients are consumed and recycled and how such rates and pathways are affected by physico-chemical factors. The plasticity of nutritional pathways, as well as the plasticity of food web interactions, including grazing, allelopathy, symbioses and other interactions, creates immense challenges for model constructs. Capturing dynamic behavior, including adaptation will continue to be a challenge. Ultimately forecast models must be robust, but must be simple enough to be operational and affordable to managers. Ensembles of models and integrated ecosystem models that couple the atmosphere, land, and coastal ocean are required to enable the quantitative estimation from air-shed to the ocean and to investigate ecosystem response to climate changes and to further explore the changes in HABs that are to be expected in the future as eutrophication impacts increase. The HAB modeling community will need to engage with climate scientists, for climate change scenarios and model uncertainty analysis; plankton and marine ecologists to improve the description of physiology and ecology in the models; invasive species experts to characterize and parameterize such changes; watershed modelers and hydrologists to estimate future changes in the land derived inputs; socio economists, managers and policy makers, to help define future land use scenarios and to interpret results in a policy context.

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