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Modeling Marine Harmful Algal Blooms: Current Status and Future Prospects

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3.1   Introduction

A model is a simplification of reality, and the purpose of this chapter is to explore the limitations and potentials for such simplifications to serve useful roles in the management and mitigation of harmful algal blooms (HAB). Others, such as Glibert *et al.* (2010), have provided overarching reviews on factors that may actually be associated with predicting events; here, the emphasis is upon assessing the state of the art, and how to advance it. Some of the challenges identified stem from issues specific to HAB science, while others apply to plankton research in general; challenges in both have arguably hindered progress in the development of HAB forecasting capability and management tools. These challenges can best be addressed by closer collaboration among researchers conducting laboratory, field, and modeling work. Improved interactions among these communities can be facilitated by clarification of terminology used in the various subfields (for discussion and an attempt to provide some clarity, see Flynn *et al.*, 2015b). Indeed, models can provide useful dynamic test beds for exploring and testing hypotheses, guiding future iterations of field and laboratory investigations, and providing an improved overall level of understanding.

Simplification in modeling can be extreme, as represented by a statistical fit of a regression line through data; and, in some cases, such models can be entirely adequate. At the other end of the spectrum, models may purport to describe temporal dynamics of dozens of organism types within 3D spatial scenarios. While it may be argued that all models are imperfect and that models are designed specifically to tackle individual questions, such views malign the real value and potential of adequately constructed models in informing us about the real world, how we think it works, and how our understanding may be in error. Errors may reside at conceptual levels as well as in the conversion of understanding into equations and parameter values. Nevertheless, both statistical/empirical and mechanistic models can provide tools for scientific investigation as well as prediction. Choice of approach depends on the specifics of the application and purpose of the model in that context.

The more complex models typically are built upon (and thence should enhance) mechanistic understanding. Complexity does not refer here to factors such as spatial resolution or pure computation load, but rather to the degree of conceptual complexity that underpins the description. For biological components, complexity refers more to the level of physiological detail applied to each organism grouping (ecological functional type; Flynn *et al.*, 2015b); complexity does not relate simply to the number of groups, each of which could contain the same very simple conceptual structure differing only in the value ascribed to traits such as organism size or maximum growth rate.

Typically, model components describing physiological features of organisms are empirical; that is, they describe behavior that accords with empirical data (i.e., that which is observed). At the extreme, empirical descriptions may relate factors that in reality are only distantly related to each other. Care

must be taken when using such relationships, especially in a predictive mode. On the other hand, empirical approaches can help identify the relative importance of multiple factors relevant to HAB phenomena, therefore contributing to knowledge of the underlying dynamics. At the other extreme are systems biology approaches that are akin to dynamic biochemistry pathway descriptions. One may argue that feedback processes akin to those controlling the biochemistry (ecophysiology) of the individual organism types should be a feature of mechanistic models (Flynn *et al.*, 2015b); the behavior of the modeled organism is then an emergent property of the interactions between various processes, mimicking reality. In practice, however, even the most mechanistic of models includes empirical components that do not contain such feedbacks. A parallel between such "empirical" and "mechanistic" descriptors as applied to ecosystem models can be seen. At one extreme, empirical models could relate bloom events to climatic features by statistical fits to data, and at the other extreme mechanistic models could describe temporal dynamics of detailed interactions between named organisms in a 3D description of watery space. A rigorously constructed and tested mechanistic description (at both the autecology and ecology levels), built upon a high level of understanding, has potential to provide a firmer basis for prediction into an uncertain future, such as that presented by climate change. From such models, robust empirical simplifications may be built to ease computational burdens, but such a route differs greatly from an *a priori* empirical simplification based upon approaches such as statistical fits between data from past events. Critically, however, sufficient scientific understanding is needed to be able to build such mechanistic models, and we need to appreciate that even mechanistic models may have limited predictive power in regimes where the dynamics are intrinsically chaotic (Benincà *et al.*, 2009).

Here, emphasis is placed upon descriptions of simulators of HAB that describe systems dynamics, and thus contain time as a dimension. Deployment of models in management ranges from short-term forecasting, often driven in part by external data from remote sensors, while other approaches use fully computational simulators in a what-if predictive mode, for example in consideration of proposed coastal engineering or of sewage outfall design. The construction and testing of dynamic models are severe tests of our understanding of the real system. Even after decades of research, our understanding of the underpinnings of HAB events remains incomplete. Indeed, our understanding of growth dynamics, loss processes, excystment and encystment, and factors promoting toxicity for individual species is wanting. Understanding is promoted by attempts to build models from a conceptual basis (akin to flow diagrams or food web schematics), and comparing the output of such models to empirical evidence. Confidence in the behavior of models under all plausible conditions promotes increasing confidence in the value of using such models in a predictive setting, whether that be for toxic HAB (T-HAB) or for algal blooms that cause aesthetic and/or ecosystem damage (ecosystem-disruptive HAB, or ED-HAB).

From here onward in this chapter, the term T-HAB refers to bloom events linked to biotoxins. The bloom of the T-HAB species itself may be of minor consequence (cryptic) from a total plankton biomass perspective, and the toxins often have their impact far from the sphere of algal trophic dynamics (i.e., on mammals and birds, rather than on their zooplanktonic grazers). Furthermore, the causative organisms need not necessarily be toxic all the time, and toxicity can develop significantly with limited concurrent biomass growth. The term ED-HAB is used to describe ecosystem-disruptive mass growths of organisms that developed at least in part because growth was not constrained by grazers. ED-HAB events may develop because the algae are *de facto* unpalatable to the usual grazers of microalgae (hence, the typical trophic interactions are blocked). Alternatively, ED-HAB may develop where the grazers cannot contain the algal production, perhaps because those grazers are themselves contained by the activities of higher trophic organisms, such as planktivorous fish or ctenophores. When mass growths die, their decay frequently causes ecosystem disruption due to deoxygenation of the water column and/or of the benthos. (The term *ecosystem disruptive algal bloom*, or EDAB, as proposed by Sunda *et al.*, 2006, for specific reference to blooms of algae unpalatable to grazers, falls within our term ED-HAB.)

While various aspects of T-HAB and ED-HAB overlap, the causative organisms and the events themselves typically differ greatly in detail and scale, and thence also in the ways in which one may elect to model their development and progression. That said, the proliferation of any species (be it cryptic or dominant in biomass) is a function of the rates of growth and losses of that particular species set against those of competitors and

predators. It may thus be expected that studies (and models) of HAB species alone cannot provide mechanistic understanding of the events; a more holistic understanding and simulation capability is required of planktonic (if not also benthic) systems.

If there were confidence that HAB events ran along a set pattern, that future events could be mapped against past events, then statistical models could be safely deployed (noting that one should not use regression statistics to predict results outside of the data range used to configure the model fit). However, set against the uncertainties of climate change and the vagaries of human activities that affect nutrient release into aquatic systems, removal of fish, modification of coastal topography, and so on, conditions enabling or supporting future HAB events, and especially T-HAB events, may well not conform to past events. The need to develop mechanistic understanding and deploy that within the framework of computational modeling thus becomes strengthened. This is not, however, to minimize the importance of short-term forecast-mode HAB modeling, which operates over time scales of days to weeks, coupled with weather forecasting and data collection in real or near-real time (e.g., Raine *et al.*, 2010). Such programs provide early warnings to resource managers and users to enable them to take what mitigating action they can (e.g., Applied Simulations and Integrated Modeling for the Understanding of Toxic and Harmful Algal Blooms [ASIMUTH]; see www.asimuth.eu; Anderson *et al.*, 2015, sect. 17.5.3).

3.2 Building Models to Describe Ecological Events

In broad terms, studies of plankton can be divided at the extreme between those conducted in the laboratory (in which variations in the abiotic environment and the biological composition are both controlled) and those conducted in the field (where the abiotic system is not controlled and the biotic composition is often highly complex). By the same token, modeling studies may be divided along similar lines, into those that are relatively highly detailed physiologically and those that allocate computational resources more toward descriptions of the physical environment and thence use simple descriptions of biology. Depending on their complexity, studies in mesocosms align more or less with laboratory or field studies.

A schematic of idealized interactions between laboratory and field research efforts is shown in Figure 3.1 and described in the associated legend. The reason for conducting physiological experiments is to provide a better understanding of how individual biological and trophic interactions function, with studies run under guidance from those working in the field to identify the organisms of interest and the types of events (e.g., transients in temperature, nutrient availability, etc.) for which detailed information is lacking. From the understanding developed through such biological studies, models can be constructed and run to test hypotheses under different environmental conditions.

One line of hypotheses particularly worthy of consideration is to explore which parameters, and which model components, exert most leverage on model performance. This is of use in two ways. Firstly, components or features are identified that warrant the most attention for both future model and experimental (laboratory/field) work. Secondly, those components that may be safely simplified or even deleted from computationally expensive models can be dealt with accordingly. This complex-to-simple approach (akin to an engineering approach of overbuilding and then testing for weakness and redundancy) is, however, not typically undertaken in biological modeling work. While flasks contain complex organisms growing in simple physics, the seas never contain simple organisms growing in complex physics. Acknowledging this situation presents an important reality check when considering the status of different generations of ecosystem models (Figure 3.1).

Two other points are worth making at this juncture. Plankton ecosystem models have many of their roots in biogeochemical studies. As such, they tend to place comparatively little emphasis upon the physiologically and ecologically complex food webs that encompass HAB events. Indeed, the modeling of zooplankton (noting that many HAB are mixotrophs, and also that algal blooms can only develop in the absence of effective grazing pressure) is well known to be weak (Mitra *et al.*, 2014a). For many applications to HAB, the current basis of plankton ecosystem models may thus appear less than optimal. The other point is that, although specific subcomponents used in these ecosystem models are often informed by laboratory measurements (e.g., phytoplankton growth rate as a function of temperature and light), the models have rarely if ever been actually tested against robust data series as generated in laboratory conditions. Some attempts have been made to
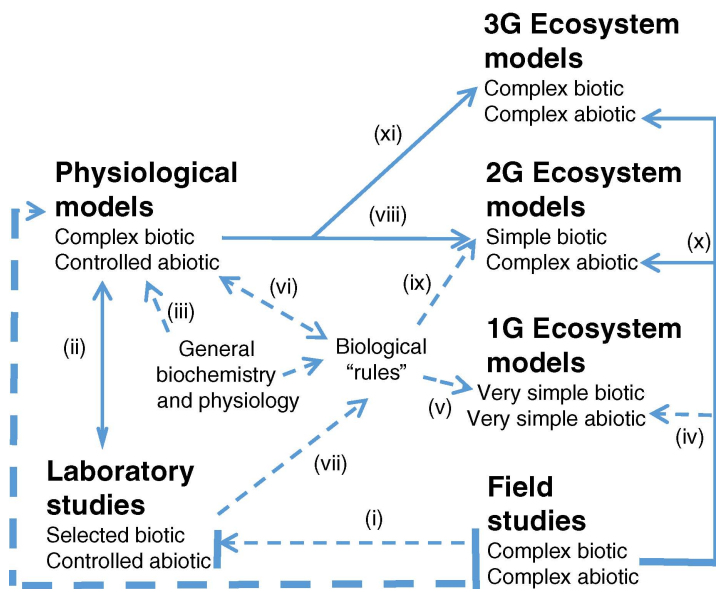
3G Ecosystem models
Complex biotic
Complex abiotic

2G Ecosystem models
Simple biotic
Complex abiotic

1G Ecosystem models
Very simple biotic
Very simple abiotic

Physiological models
Complex biotic
Controlled abiotic

General biochemistry and physiology

Biological "rules"

Laboratory studies
Selected biotic
Controlled abiotic

Field studies
Complex biotic
Complex abiotic

(i) (ii) (iii) (iv) (v) (vi) (vii) (viii) (ix) (x) (xi)

Figure 3.1 Schematic for the development of ecosystem models. Conditions and biological composition at field sites inform the laboratory study of selected organisms grown under controlled conditions (i) Information, and data, from laboratory studies (ii), together with generic biochemical and physiological understanding (iii), enable the construction and testing of complex systems biology–style models describing the physiology (autecology) of organisms, and thence coupled models of simple trophic systems. Typically, the flow of information (ii) is from experimental to modeling research, although models can be used to design *in silico* experiments to aid hypothesis setting for further rounds of laboratory studies. First-generation (1G) ecosystem models, as typified by Fasham *et al.*'s (1990) type NPZ models, contained much-simplified representations of the abiotic system (iv), together with very simple models of the biota configured from biological rules (v) built from general and theoretical principles (vi) such as Monod and Holling kinetics, perhaps including concepts developed from physiological models, and data such as maximum growth rate estimates from laboratory studies (vii). The current, developing, second-generation (2G) ecosystem models contain greatly enhanced abiotic descriptions; however, the biotic descriptions typically do not make use of advances from physiological models (viii) but deploy enhanced developments from biological rules (ix). Future (third-generation, or 3G) ecosystem models may be expected to describe abiotic systems with ever greater fidelity, with the aspiration that these will also serve as platforms for placement of systems biology–style physiological models (xi) within high-resolution abiotic simulators.

use mesocosm experiments for this purpose (e.g., Aksnes *et al.*, 1994). Whether models are fit for purpose is gauged by comparison of model output, typically in terms of areal biomass, against spot sample points (oceanographic stations) or against satellite images of events at the sea surface. The use of field data carries with it the burden of transformations between pigment abundance and biomass, between cell and organism counts in different volumes of water, and so on. Those interested in T-HAB and ED-HAB need to ask whether they consider models originally constructed for biogeochemistry (rather than ecology) as representing a suitable basis for best progress.

Taking all the above into account, the schematic of Figure 3.1 describes a research effort that is in reality all too often dispersed and isolated, rather than coupled. For the most part, conceptual detail on the physiology of plankton, let alone on HAB species, gained from laboratory experiments does

not make it to ecosystem models. While many scientists may (with justification) worry that experiments with laboratory cultures cannot replicate events in reality, not least because of the potential adaptation of cultured organisms to artificial conditions during long-term laboratory growth, it is difficult to see how the underpinning biochemical and physiological framework would be so overturned that laboratory results are not of value. The utilization of "biological rules" in ecosystem models, which include concepts of allometric scaling and "trait trade-offs," may be viewed as of particular concern for the task at hand, because these do not appear to be applicable to many of the planktonic organisms associated with HAB or indeed of planktonic predator–prey interactions in general (Hansen *et al.*, 1994; Flynn *et al.*, 2015b). There are also some obvious important aspects of plankton ecology that are underemphasized, if not absent, in most models. An example concerns

descriptions of encystment and excystment, although for the most part comprehensive data on the death rates of cysts and the triggers for excystment are also lacking (Hense, 2010). Another important avenue that is underexplored and hence poorly considered in models is the role of micronutrients and of allelopathic interactions (Pohnert *et al.*, 2007).

3.3 Limitations to What Models Can Do, and Why

3.3.1 Building Models

How useful HAB models may be depends on how well the model describes reality. Models can be used for various purposes. Conceptual models help the formulation of ideas, to identify at a phenomenological level the strengths and weaknesses in knowledge; however, it is only at conversion of the conceptual model into a mathematical model that a quantification develops of what is known, and what is not known. For each of the interactions, one may commence by configuring a response curve between the driver and consequence. For example, one may generate relationships between satiation in a consumer and its feeding rate; as satiation develops (gut becomes full), feeding is slowed. Response curves may have a negative or positive slope; they may be linear, curvilinear, sigmoidal, or of more complex form. In all instances, organisms can upregulate or downregulate aspects of their physiology depending on the environment, thereby introducing plasticity into the parameters of such response curves (Flynn *et al.*, 2015; Kana and Glibert, 2016). Establishing the form of the curve is the first step in converting, for example, the conceptual model of a food web diagram into a dynamic model.

Relatively little is known about the nonlinearities in these response curves. Two examples of importance to the topic of modeling HAB relate to the key role of grazers in permitting or controlling bloom development. This is of particular concern for ED-HAB (Mitra and Flynn, 2006; Sunda *et al.*, 2006). The decline in food quality when phytoplankton exhaust nutrients does not necessarily have the simple linear consequence one may expect from stoichiometric ecology (Sterner and Elser, 2002); rather, it may have a distinctly nonlinear response resulting in prey rejection at low levels of nutrient stress leading to formation of an ungrazed bloom (Mitra and

Flynn, 2005, 2006). Understanding just how important subtle changes in biochemical stoichiometry may be, for example how changes linked to ocean acidification may have far-reaching consequences on plankton ecology, has just begun (Flynn *et al.*, 2015a; Cripps *et al.*, 2016). Another feature of grazers commonly modeled as linear relates to assimilation efficiency (AE); this is typically held constant in zooplankton models, although it is well known to vary with quality and quantity of phytoplankton prey (Mitra *et al.*, 2014a). Modeling to account for changes in AE generates very different predator–prey dynamics that can see a much more rapid removal of a bloom than would otherwise be expected from simple models (Flynn, 2009). For the formation of ED-HAB, on account of insufficient grazer control due to the success of planktivorous higher trophic levels, such challenges in modeling the activity of consumers extends beyond microzooplankton and copepods. While closure terms may often be deployed in such instances, this approach is not a substitute for adequate understanding of the role of trophic cascades in ED-HAB ecology.

3.3.2 Model Complexity

A fundamental challenge in modeling centers on the issue of a "simplification of reality." In a more ideal world, where resources and thence data and computational power were less limiting, complex models would be built and their behavior explored to identify how best to achieve simplifications by progressively deleting or otherwise simplifying components. Indeed, some modelers now use a complex-to-simple approach; this provides a route to generate empirical models from mechanistic models (see "Introduction," this chapter). There are many modelers who quake at the number of parameters in complex biological descriptions, concerned as to how these will all be estimated; however, an appropriately formulated mechanistic model actually does not have that many real free parameters for adjustment. Most parameters are used to describe the shape of response curves, and model behavior is largely insensitive to their exact value. Fasham *et al.* (2006) give an example of a complex phytoplankton model placed in an ecological setting; they discuss the (non)issue of the parameter count.

More often, however, the starting point for model construction is a discussion regarding which minimum set of parameters and equations is needed to confront a specific issue; only if this

simple model fails are additional complexities added. The challenge in the simple-to-complex approach is deciding what constitutes a failure (Franks, 2009) that perhaps then warrants increasing complexity to include additional factors. Statistical approaches such as *maximum likelihood* offer methods to frame model–data comparisons in terms of a hypothesis test, thereby allowing quantification of the confidence with which one model fits the observations better than another (Stock *et al.*, 2005, 2007). Examples of errors that develop during initial simplification include using single rather than multiple variable stoichiometries, and incorporating inappropriate functional type descriptions and associated food web linkages. The last mentioned is particularly problematic given growing appreciation for the role of mixotrophy in aquatic protist ecology (Flynn *et al.*, 2013; Mitra *et al.*, 2014b), and linked to the fact that many (protist) HAB species are mixotrophic (Burkholder *et al.*, 2008). The extent of this particular failing runs across all parts of the HAB research spectrum, from issues of field monitoring (are chlorophyll and inorganic nutrient levels really the best indices for the presence and activities of mixotrophic protists?) to defining conceptual and thence mathematical models.

A consequence of the drive for simplification is the need to group organisms together; it would be impractical to describe the dozens up to perhaps hundreds of individual species present in a real ecosystem. In ecology, organisms are typically grouped (irrespective of phylogenetic origin) according to the way that they interact with environmental factors (Gitay and Noble, 1997), thus forming "functional type" grouping. Plankton functional types (PFTs) appropriate for modeling HAB may be expected to be quite different from such groupings intended for biogeochemical modeling (with their emphasis on "diatoms," "coccolithophorids," etc.). In biogeochemistry applications, little emphasis is placed on competition and predator selection processes, or on features such as consideration of mixotrophs that acquire their photosystems from prey (the nonconstitutive mixotrophs; Flynn and Hansen, 2013; Hansen *et al.*, 2013; Mitra *et al.*, 2016). These factors may be of critical importance to describe the types of events that lead to (or block) development of T-HAB or ED-HAB events. Understanding the causal basis for coexistence or mutual exclusion of species on the run up to, during, and then after plankton blooms appears fundamental to the task at hand.

It is at this point worth considering the interface between molecular biology and modeling. The application of molecular biology to HAB and general plankton research has brought to our attention the great variety of life forms, and the presence of different species and subspecies. There is thus a stark contrast between molecular and mathematical biology, because while modeling inevitably merges the activity of organisms together and is a topic driven by trophic dynamics, molecular biological research represents almost a diametric contrast. Linkage of omic signatures to physiological status and toxicity could, however, be of great value to modelers, generating data for validation. The use of automated molecular tools may also help in building PFT groupings as well as for the detection and monitoring of HAB (Scholin *et al.*, 2009).

From the foregoing, it may be tempting to conclude that empirical approaches, based on statistical methods or expert systems, may be no less robust than attempting to deploy dynamic mechanistic-based models. There is, however, one fundamental problem; as mentioned in this chapter, it assumes that future patterns of behavior have already been seen in previously collected data series. With the permutations of potential change (natural fluctuations as well as anthropogenic forcing), it seems likely that future conditions will be outside the envelope of variations in the recent past. This is perhaps not so much an issue for short-term management of existing coastal systems (although extreme weather conditions may become more common with climate change), but it is an issue in considerations of the design of coastal engineering projects and watershed management, with a need for risk analyses played out over decades. In consequence, there is a need to try to encapsulate understanding of all the factors that impinge upon HAB events within models. Like weather forecasts, there is a need to appreciate that, at best, capabilities for predicting HAB are limited, deal with probabilities, and most likely will depend on inputs from different model types and approaches. Indeed, the corollary drawn with weather forecasting is particularly apposite given that the weather plays such an important role in the initiation and termination phases of HAB events, and indeed of plankton growth in general.

3.3.3 The Need for Data

Data availability is important, and of equal importance is the form of the data. Conceptual food web diagrams, and simple models such as Lotka–Volterra predator–prey descriptions, have no need for data with specific units. However,

systems dynamics models have an absolute need to correctly account for units; most are based upon a single or multiple currencies. Classic marine biogeochemical models use nitrogen (N) as the sole currency (Fasham *et al.*, 1990); nutrients and biomass are defined as mol N m^{-3}, with rates as mol N m^{-3} d^{-1}. Allied to this usage of a single currency is the assumption of fixed Redfield ratios for C:N:P:(Si). More complex models employ variable stoichiometries and multiple functional types within trophic levels (C:N:P; Baretta *et al.*, 1995). Given what is known about HAB, the bases for development of toxicity and poor palatability for grazers, and the ability of microalgae to use and hence compete for different nutrients including prey (Flynn *et al.*, 2013), multiple variable stoichiometric models can be seen to present various advantages over single-currency models (Flynn, 2010a). That is all the more so when one considers that, in the future, the nutrients limiting growth may differ from those that do so at present due to the damming of rivers and changes in land use, fertilizer applications, and rainfall patterns (Rabalais *et al.*, 2009). Correctly modeling the usage of different nutrients is important as it affects the potential to predict the nutrient limitation of phytoplankton successions (Flynn, 2005, 2010b).

The need for data of a certain type presents a modeler with various challenges, as transforms (with associated assumptions) are then required to interconvert data types. As an example, algal biomass is typically estimated in terms of chlorophyll (and that often as *in vivo* fluorescence of the bulk population), while zooplankton are often estimated as numbers per unit volume with some level of taxonomic detail. In contrast, the representation of these groups in models may be as N-biomass, with the phytoplankton and zooplankton each described as one or just a few functional types. Decisions upon such matters, nutrient currency and how best to collate or group data, affect the modeling activity and thus scope for use of the final product.

3.3.4 Validating Models

Models should be constructed and tuned through reference to one set of data, and then validated against another separate data set. That is to say, the model is typically run against real data and selected (constant) parameters adjusted to enable the best fit of the model output to data. The model is then run again under a new set of conditions, in line with the drivers for a different documented scenario, and its output compared to the new real data series. Too often, data series are not available to support both tuning and validation. It is thus important to appreciate the limitations of modeling; sufficient knowledge of the biotic and abiotic system is often lacking to achieve more than a phenomenological fit of model to data. A good outcome is if model output satisfactorily aligns with the validation data series, ideally with respect both to timings of events and to magnitude. Getting the model to replicate the timing of an event is often considered more important than simulating the magnitude correctly, but for HAB management both are important.

3.4 Modeling T-HAB and ED-HAB Events

There are fundamental differences between describing T-HAB versus ED-HAB dominated blooms, and versus blooms dominated by benign organisms (accepting that any bloom could become so large that it could cause damage to the ecosystem upon its death through deoxygenation – at which point it would conform to what is termed here a form of ED-HAB). Cyanobacterial T-HAB and *Phaeocystis* ED-HAB may be dominated by these organisms growing in near-monospecific blooms, while blooms of T-HAB dinoflagellates may contain the organism of interest (e.g., *Alexandrium*) growing as only a small proportion of total primary producers. Understanding what enables the growth of a particular HAB organism in competition with that of other organisms, and against losses due to abiotic (typically out-mixing or washout events) or biotic (grazing) processes, lies at the heart of any mechanistic attempt to explain bloom growth. There is also the important issue of bottom-up and top-down influences. The top-down influences may be considered as just grazers upon the HAB species themselves (Irigoien *et al.*, 2005; Stoecker *et al.*, 2008), but actually they also include their activity upon their competitors (Flynn *et al.*, 2008), and for mixotrophs also their prey (Adolf *et al.*, 2008; Glibert *et al.*, 2009; Hansen *et al.*, 2013). Thus, proliferation of one species may occur not because of its competitive advantage in growth rate or nutrient acquisition, but because it is not the subject of such great grazing pressure (Mitra and Flynn, 2006; Flynn, 2008). The course of such developments will likely change if the activity of the next grazer up the food web is altered, with potential for ED-HAB formation. (Grazers include benthic

organisms such as bivalves, and not just zooplankton.) Models are ideal for exploring such cascade events, although clearly the predictions can only be as robust as the data and knowledge used to build the model.

Much of the conceptual bases for describing ED-HAB events driven by eutrophication is present in extant modeling platforms; these provide linkage between physics, nutrient load, and light (including self-shading as the bloom develops) to primary production in an environment where the simulated grazers of those primary producers are themselves typically subjected to a density-dependent closure term (Mitra, 2009). It should be possible to use suitably constructed multi-nutrient models (see Flynn, 2005) to conduct hypothesis testing of what types of nutrient loads and ratios (noting that the former are more important than the latter – Flynn, 2010a) are likely to raise risks of ED-HAB events; however, allelopathic interactions are also recognized as important features of HAB plankton interactions (Pohnert *et al.*, 2007; Granéli *et al.*, 2008). And, like feedbacks from grazing, allelopathic interactions have potential to generate positive feedbacks where the increasingly dominant organism rapidly overpowers its competitors due to the escalation of cell-density-dependent interactions. Physical processes, and behavioral traits such as vertical migration, have clear potential to affect allelopathic interactions by bringing organisms together or conversely by dispersing them. While allelopathic interactions may well be important features of ED-HAB events, they are typically absent from ecosystem simulators.

Modeling the growth of cryptic T-HAB species presents a different, if not greater, challenge to that for ED-HAB. How necessary is it to model the growth of the biomass-dominant species in addition to that of the T-HAB species, and at what level of detail? If there is a close coupling to other species (as for the mixotrophic T-HAB *Dinophysis* for the supply of acquired photosystems from a specific sequence of other plankton; Hansen *et al.*, 2013), then a line of exploration for model complexity can be developed. Ultimately, work can only progress using the information at hand. Theoretical/conceptual models may help here, in exploring the likely sensitivity of different trophic interactions and processes, and hence guide field and laboratory studies. Models of these, as much as for any system, can usefully act as platforms for generating and testing hypotheses as well as guiding empirical research (Figure 3.1).

3.5 How Good Are Current HAB Models?

Predictive HAB models take a variety of forms, including conceptual, empirical, and numerical approaches (McGillicuddy, 2010). As the sophistication of such models has increased and the data sets used to evaluate them have expanded, the metrics by which their skill can be assessed have begun to receive more attention (Lynch *et al.*, 2009). Examples of the various approaches to HAB prediction are provided (Table 3.1) and the means by which they have been evaluated. See Anderson *et al.* (2015) for a more complete review of recent and ongoing predictive modeling efforts.

Empirically based models have shown predictive skill in a variety of contexts. For example, Blauw *et al.* (2010) related nuisance foam events in Dutch coastal waters to *Phaeocystis globosa* ED-HAB blooms, predicting their occurrence on the basis of relationships with environmental parameters such as mixed layer irradiance and nutrient availability using a "fuzzy logic" approach. In a hindcast of the period 2003–2007, the model predicted 93% of the observed foam events – an impressive record of "true positive" outcomes; however, there were also many "false positives" in which the model predicted a foam event but none occurred. Of course, it is also of interest to quantify "true negatives" and "false negatives" for a more complete assessment of model skill. From a management perspective, the relative importance of different types of error may differ. For instance, in protecting public health from exposure to toxins, a false positive may be more tolerable than a false negative. From the viewpoint of the tourist trade, however, false positives for HAB can prove highly costly.

In some regimes, remote sensing is a valuable input into HAB predictive systems. In the eastern Gulf of Mexico, T-HAB of the toxic dinoflagellate *Karenia brevis* are dense enough to be detected in satellite imagery (Figure 3.2, top). Not only does such imagery provide a means for bloom identification following ground truthing, but also it can feed forecasts of bloom transport, extent, intensification, and impact (Stumpf *et al.*, 2009). Each of these aspects has been evaluated in the context of an operational forecasting system, with accuracies in the range of 73–99% (Figure 3.2b, bottom). It is important to note that the resolution of the forecast and validation data are not sufficient in this example to yield skill at scales finer than 30 km, and considerable patchiness of the *K. brevis* population and

Table 3.1 Summary of predictive modeling approaches discussed in the text.

Example	Inputs	HAB models	Model outputs	Duration, spatial dimension
Phaeocystis foam events in Dutch coastal waters; Blauw *et al.* (2010)	T, S, DIN, DIP, solar irradiance, K_d, wind	Empirical (fuzzy logic)	Foam event identification, magnitude	0D; hindcast
Karenia brevis in the eastern Gulf of Mexico; Stumpf *et al.* (2009)	RS Chl	Empirical (rule-based decision tree)	Bloom identification, magnitude, extent, impact	2D; 3-day forecast twice weekly
	RS Chl, wind	Transport	Bloom magnitude, extent, impact	
Pseudo-nitzschia along U.S. west coast; Anderson *et al.* (2011)	RS Chl, R_{rs} (3 wavelengths), *T, S from hydrodynamic model*	Empirical (generalized linear model)	Cell abundance, pDA, cDA	2D; nowcast
Various H/ED-ABs in Chesapeake Bay (Figure 3.4); Brown *et al.* (2013)	Month, *T, S, DO, Chl, DIN NH_4, TON, TSS, K_d from physical-biological-biogeochemical model**	Empirical (logistic regression, neural network, hierarchical decision tree)	Probability of occurrence; relative abundance (*Karlodinium veneficum* only)	2D; 3-day forecast
Cyanobacterial blooms in the Baltic; Roiha *et al.* (2010)	ICs and BCs for hydrodynamic and biogeochemical models (notably, wintertime DIN and DIP), climatology, *atmospheric forcing*	Physical-biological-biogeochemical*	Bloom probability	2D; seasonal ensemble
Alexandrium fundyense in the Gulf of Maine; McGillicuddy *et al.* (2011)	Cyst distribution, *hydrodynamic ICs and BCs from global model*, nutrient climatology, river fluxes, *atmospheric forcing*	Physical-biological, population dynamics	Cell concentration	3D; seasonal ensemble, weekly 7-day forecast

BCs, boundary conditions; cDA, cellular domoic acid; Chl, chlorophyll; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; DO, dissolved oxygen; HAB, harmful algal bloom; ICs, initial conditions; K_d, diffuse attenuation coefficient; pDA, particulate domoic acid; R_{rs} remote sensing reflectance; RS Chl, remotely sensed chlorophyll; TON, total organic nitrogen; TSS, total suspended solids. In the inputs column, observations are in regular font, and model-based quantities are in italics.
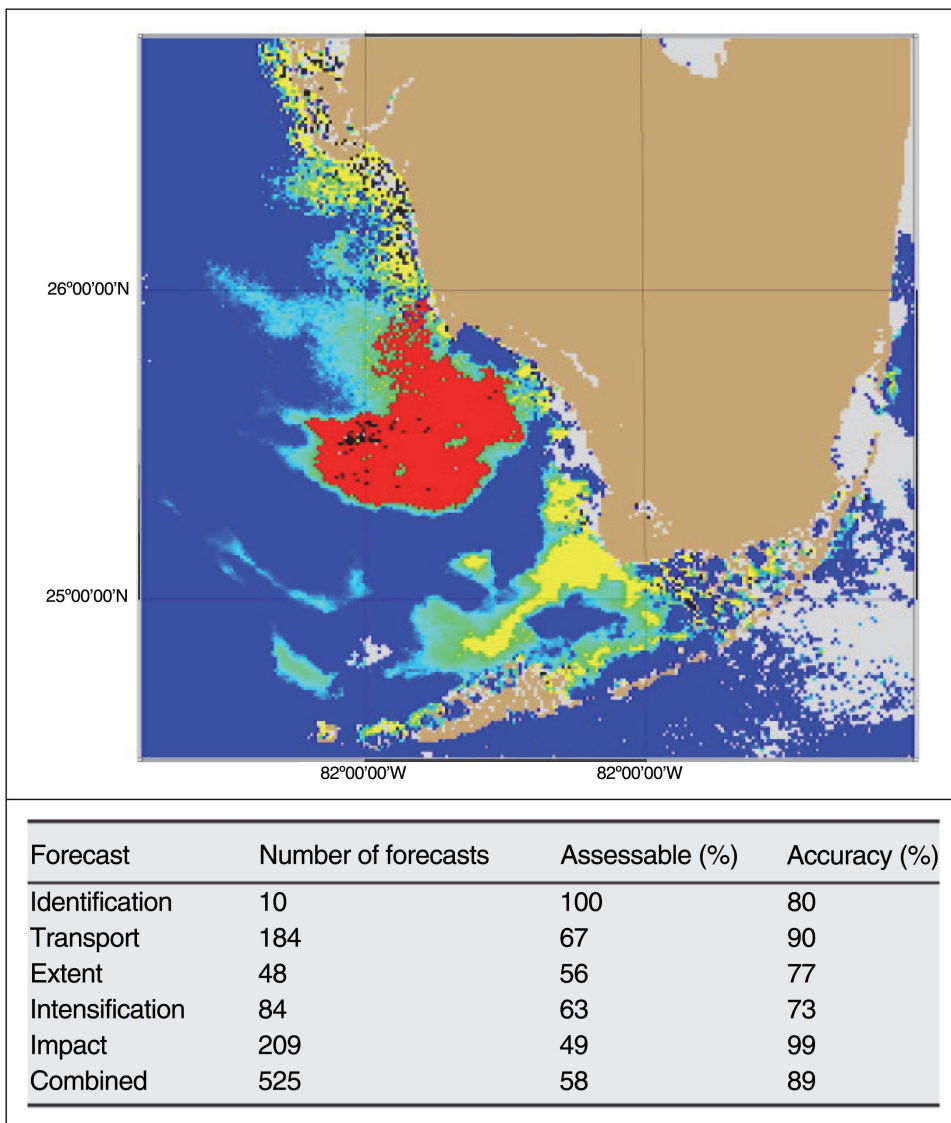*Models that explicitly include non-HAB phytoplankton and zooplankton.

Forecast	Number of forecasts	Assessable (%)	Accuracy (%)
Identification	10	100	80
Transport	184	67	90
Extent	48	56	77
Intensification	84	63	73
Impact	209	49	99
Combined	525	58	89

Figure 3.2 (Top) SeaWiFS satellite image from November 21, 2004. Yellow areas indicate where the chlorophyll anomaly based on Stumpf *et al.* (2003) exceeded 1 μg L^{-1}; cyan and green show anomalies between 0 and 1; blue indicates no positive anomaly. Red represents locations of *K. brevis* blooms based on the criteria listed in Stumpf *et al.* (2009, table 1). The yellow areas did not match the criteria and are thus not considered to be due to *K. brevis*. (Bottom) Forecasted bloom components and percentage of assessable forecasts for the period October 2004–April 2006. In this context, accuracy is defined to be the sum of true positives and true negatives divided by the total number of forecasts. *Source*: From Stumpf *et al.* (2009), with permission of Elsevier.

associated impacts exist at spatial scales finer than that. An analogous forecast system is emerging for cyanobacterial blooms in the Great Lakes of North America, in which short-term forecasts of bloom transport are based on satellite imagery and a hydro-dynamic model together with a particle-tracking algorithm (Wynne *et al.*, 2013).

Yet another approach to combining remote sensing with models is being used to predict T-HAB of diatoms of the genus *Pseudo-nitzschia* along the west coast of the United States. Logistic generalized linear models (GLMs) utilize time of year (month), remote-sensing reflectance at three wavelengths, and model-based temperature and salinity (Figure 3.3, top) to predict concentrations of *Pseudo-nitzschia* cells, as well as the particulate and cellular forms of the toxic domoic acid (par-ticulate domoic acid [pDA] and cellular domoic
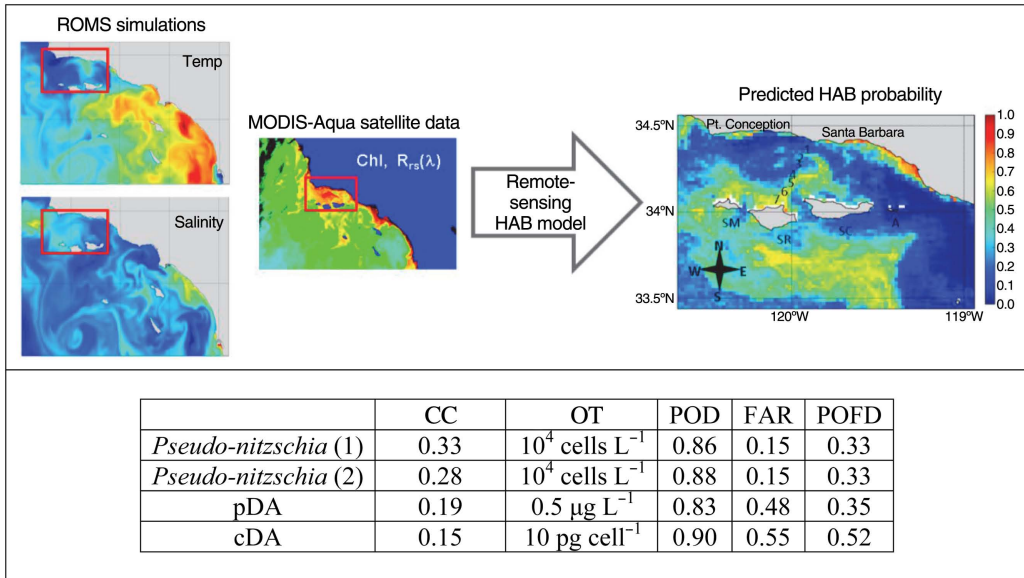
	CC	OT	POD	FAR	POFD
Pseudo-nitzschia (1)	0.33	10^4 cells L^{-1}	0.86	0.15	0.33
Pseudo-nitzschia (2)	0.28	10^4 cells L^{-1}	0.88	0.15	0.33
pDA	0.19	0.5 µg L^{-1}	0.83	0.48	0.35
cDA	0.15	10 pg cell^{-1}	0.90	0.55	0.52

Figure 3.3 (Top) Schematic of ROMS model and MODIS satellite products used to compute the "remote-sensing" T-HAB models for predicting the probability of elevated *Pseudo-nitzschia* abundance and toxin concentrations in the Santa Barbara Channel off the coast of central California. Numbers in the far-right map denote monthly "Plumes and Blooms" sampling stations 1–7, with station 1 nearest the mainland and station 7 off the shelf of Santa Rosa Island. The Santa Barbara Channel Islands from west to east are: San Miguel Island (SM), Santa Rosa Island (SR), Santa Cruz Island (SC), and Anacapa Island (A). (Bottom) Model skill assessment for two generalized linear models of *Pseudo-nitzschia* cell concentration, particulate domoic acid (pDA), and cellular domoic acid (cDA). The correlation coefficient (CC) is Nagelkerke's r^2. Probability of detection (POD), false alarm ratio (FAR), and probability of false detection (POFD) are calculated from optimized threshold values (OT). *Source*: From Anderson *et al.* (2011), with permission of the American Geophysical Union.

acid [cDA]) produced by these algae (Anderson *et al.*, 2011). These predictions have been evaluated using the 2004–2010 time series of data used to build the models (Figure 3.3, bottom). Although the correlation coefficients between the predicted and observed quantities are modest (Nagelkerke's r^2 ranging from 0.20 to 0.46), the probability of detection (POD; the ratio of true positives to the sum of true positives and false negatives) ranges between 83 and 90%. The false alarm ratio (FAR; false positives divided by the sum of true positives and false positives) is only 15% for *Pseudo-nitzschia* cell concentration, yet 48–55% for domoic acid constituents. An alternative metric for false positives normalizes them by the sum of true negatives and false positives, yielding the probability of false detection (POFD). POFD is about double the FAR for *Pseudo-nitzschia* cell concentration, and lower than the FAR for pDA and cDA. It is important to note that the skill assessment was performed using the same data used to calibrate the model (albeit with cross-validation). As longer time series become available, it will be possible to evaluate (validate) the model with independent observations.

Whereas the Anderson *et al.* (2011) approach uses remote sensing together with model-predicted temperature and salinity, Brown *et al.* (2013) utilize the output of a coupled physical-biogeochemical model to forecast the probabilities of HAB events and the presence of waterborne pathogens in Chesapeake Bay. These probabilities are derived from multivariate empirical habitat models (trained using *in situ* observations) that feed on model-based predictions of a suite of environmental variables. A summary of the target species, their habitat models, and model accuracy is provided in Figure 3.4, along with example forecasts to illustrate the high resolution of the predictions. Forecast accuracy, defined as the sum of true positives and true negatives divided by the total number of forecasts, ranges from 77 to 93%.

Coupled physical-biogeochemical models have shown prognostic utility themselves in circumstances where and when the algal biomass predicted by such models constitutes the bulk of the HAB of interest. Such is the case for cyanobacterial blooms in the Baltic Sea, for which the areal fraction of cyanobacterial accumulation is correlated with the concentration of chlorophyll-*a* during the bloom
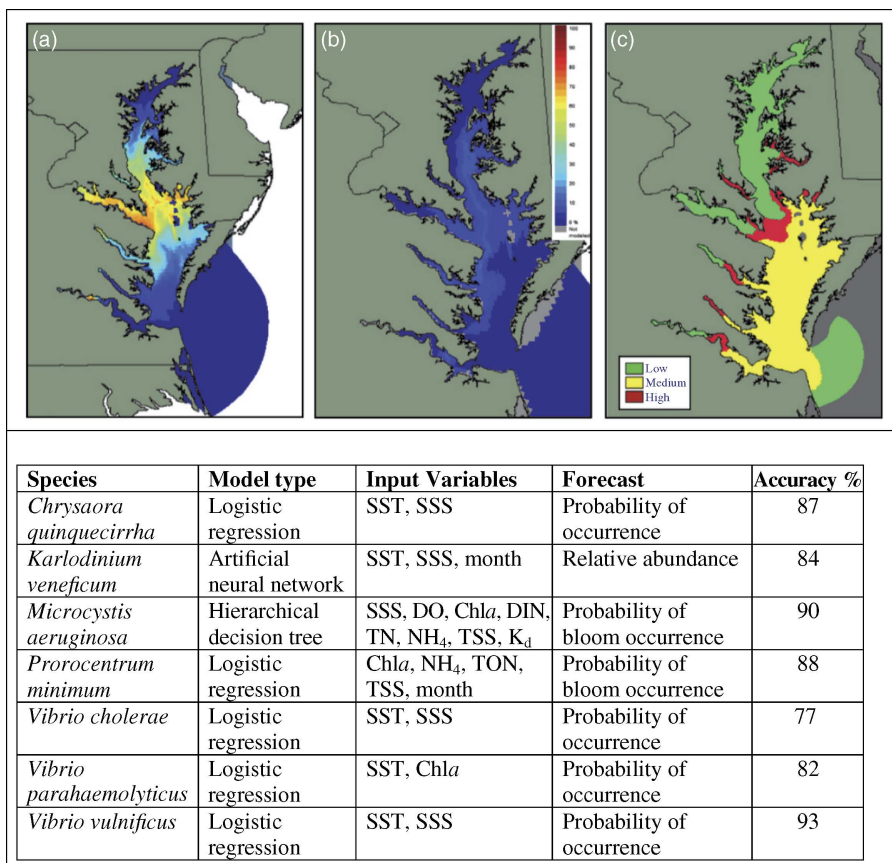
Figure 3.4 (Top) Examples of species forecasts generated by the Chesapeake Bay Ecological Prediction System (CBEPS). (a) Likelihood of encountering sea nettles *Chrysaora quinquecirrha* on 17 August 2007. (b) Likelihood of *Vibrio vulnificus* on 20 April 2011. (c) Relative abundance of *Karlodinium veneficum* on 20 April 2005. Legend: low: 0–10 cells/ml; med: 11–2000 cells/ml; high: >2000 cells/ml. Color bar for likelihood is the same for both A and B. (Bottom) Synopsis of organism habitat models used in the CBEPS. Chl*a*, chlorophyll-*a* concentration; n, sample size; SST, sea-surface temperature; SSS, sea-surface salinity; TON, total organic nitrogen; TSS, inorganic suspended solids. Accuracy is expressed as the number of correct forecasts/n. *Source*: From Brown *et al.* (2013), with permission of Elsevier.

Species	Model type	Input Variables	Forecast	Accuracy %
Chrysaora quinquecirrha	Logistic regression	SST, SSS	Probability of occurrence	87
Karlodinium veneficum	Artificial neural network	SST, SSS, month	Relative abundance	84
Microcystis aeruginosa	Hierarchical decision tree	SSS, DO, Chl$a$, DIN, TN, NH$_4$, TSS, K$_d$	Probability of bloom occurrence	90
Prorocentrum minimum	Logistic regression	Chl$a$, NH$_4$, TON, TSS, month	Probability of bloom occurrence	88
Vibrio cholerae	Logistic regression	SST, SSS	Probability of occurrence	77
Vibrio parahaemolyticus	Logistic regression	SST, Chl$a$	Probability of occurrence	82
Vibrio vulnificus	Logistic regression	SST, SSS	Probability of occurrence	93

season (Kahru and Elmgren, 2014). Roiha *et al.* (2010) describe an ensemble forecasting system that provides quantitative predictions of cyanobacteria distributions in the Baltic, for which springtime phosphorus concentrations are a predictor of basin-scale spatial variations in the blooms. Likewise, Stumpf *et al.* (2012) linked springtime river discharge and total phosphorus load to interannual variability in cyanobacterial blooms in Lake Erie (North America), thereby providing the basis for seasonal forecasts.

In contrast to coupled physical-biogeochemical models that represent the bulk properties of an ecosystem, single-species population dynamics models offer an attempt to capture the life cycles of particular organisms. In some cases, ecological forecasts have been facilitated by specific characteristics of the population dynamics of HAB species.

For example, interannual variations in the extent of T-HAB of the toxic dinoflagellate *Alexandrium fundyense* in the Gulf of Maine are influenced by the abundance of resting cysts (McGillicuddy *et al.*, 2011; Anderson *et al.*, 2014). Specifically, years with more abundant cysts are prone to more widespread blooms, as inferred from the along-coast extent of shellfish toxicity (Figures 3.5 and 3.6). In fact, the correlation coefficient for the time series of cyst abundance and the most southerly latitude of shellfish harvesting closures is -0.93 ($p = 0.02$) for the period 2005–2009. This relationship provides the basis for seasonal ensemble forecasts of T-HAB extent via a coupled physical–biological model that includes germination, growth, and mortality of *A. fundyense* cells, which are followed up with weekly nowcast and forecast simulations (McGillicuddy *et al.*, 2011). In years when conditions were
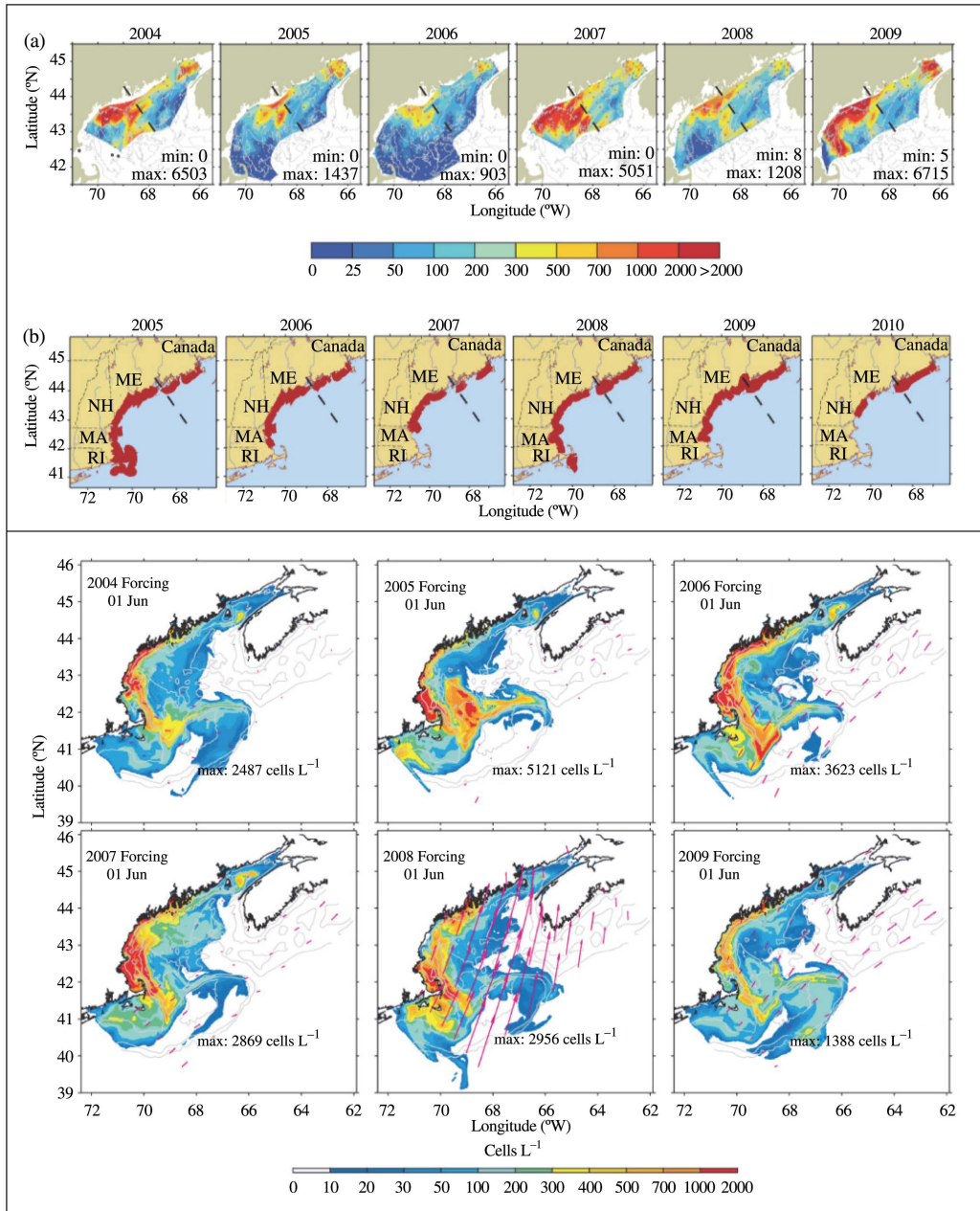
Figure 3.5 Top: (a) *Alexandrium fundyense* cyst abundance in the Gulf of Maine, 2004–2009. Minimum and maximum values are indicated in each panel. Open circles denote the locations of sediment samples used to construct the maps. (b) Spatial extent of PSP closures, 2005–2010. The calculations for the western Gulf of Maine and southern New England presented in Figure 3.6 pertain to the area south and west of the dashed line. Bottom: Ensemble *A. fundyense* forecast for 01 June, based on the autumn 2009 cyst map together with hydrodynamic and atmospheric forcing from 2004 to 2009. Pink arrows depict the instantaneous wind-forcing. Maximum (max) cell concentrations in each panel are indicated at the lower right. *Source*: From McGillicuddy *et al.* (2011), with permission of Association for the Sciences of Limnology and Oceanography, Inc.

"normal," this approach provided skillful hindcasts (He *et al.*, 2008) and forecasts (Li *et al.*, 2009); however, in 2010, the forecast system failed. Despite an unusually high abundance of resting cysts, a large-scale T-HAB event did not materialize (Figure 3.5, middle panel, Figure 3.6), thus putting the forecast in the category of a false positive. Observations from shipboard surveys and the coastal observing system
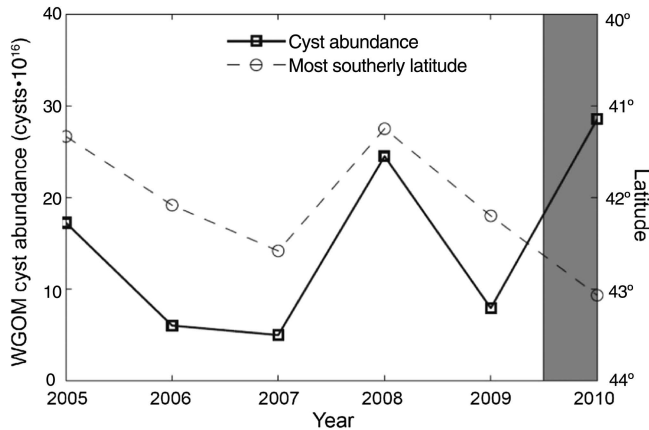
Figure 3.6 Time series of cyst abundance in the western Gulf of Maine (WGOM) and the most southerly latitude of coastal shellfish toxicity closures (note axis reversal). For visual compatibility and correlation analysis, the cyst abundance time series has been shifted by 1 year, such that the autumn of 2004 is reported as 2005, and so on. These calculations pertain to the area south and west of the line running southeast from Penobscot Bay (Figure 3.5, upper panel). *Source*: From McGillicuddy *et al.* (2011) with permission of Association for the Sciences of Limnology and Oceanography, Inc.

revealed water mass variations that had a direct impact on *A. fundyense*'s niche: near-surface waters were warmer, fresher, and lower in nutrients than prior years, leading to unfavorable growing conditions. Moreover, a weaker than normal coastal current lessened the along-coast transport of the *A. fundyense* that were present. Thus, the potential for a large bloom set by the high abundance of resting cysts was not realized because of anomalous environmental conditions.

This last example highlights the challenge of making ecological forecasts in a changing ocean environment. In essence, the forecast system for *A. fundyense* in the Gulf of Maine is predicated on the hypothesis that, all else being equal, a higher abundance of resting cysts will lead to a more widespread bloom. However, in 2010, all else was not equal: failure of the forecast was a direct consequence of the fact that conditions were outside the envelope of prior observations used to construct the model. In particular, nutrient concentrations were quite different from the climatological values used in the ensemble forecast and weekly real-time predictions. In the future, augmentation of the coastal observing system with nutrient sensors should help avoid this mode of false positive in the forecast model.

Looking toward the future, it is likely that a changing climate will lead to variations in oceanic conditions that are outside the ranges experienced in the recent past; certainly, that is so with respect to ocean acidification with potential changes in phytoplankton succession (Flynn *et al.*, 2015a). Such changes would influence the severity and extent of different types of HAB events (e.g., Meier *et al.*, 2011). Moreover, anthropogenic perturbations to coastal ecosystems continue to increase, yielding demonstrable impacts on T-HAB and associated toxin production (Glibert and Burkholder, 2011). Given the highly nonlinear nature of ecological systems, these changing conditions may have unexpected consequences for HAB species. As such, predictive modeling efforts will need to be designed in a manner that makes them adaptable to regime shifts that are almost certain to occur as earth's climate varies (Dippner and Kröncke, 2015).

3.6 Future Modeling of T-HAB and ED-HAB: Managing Expectations

Although a generalized framework for predicting HAB may be a long way off, good progress is being made with site-specific models in various regional applications. Enhancements may be expected to come from generalized conceptual studies of plankton dynamics relating the potential for development of sustained high-biomass ED-HAB under certain conditions of nutrient loading (concentrations of nutrient N, P, and Si), light (and hence interacting with mixing layer depth and absorbance), temperature, and pH. Studies of physical systems may then enable some level of proactive identification of water bodies becoming more or less susceptible to ED-HAB under developing climate change scenarios, with reinforcement of such identifications

from placement of suitable configured biological models within the physics framework. Identifying low-risk environments should be possible; certain conditions are clearly more or less conducive to high-biomass events.

Managing expectations from models for cryptic T-HAB is important; however, if toxicity can be aligned with specific physiological states such as P-stress in the presence of adequate ammonium or nitrate (Flynn, 2002; John and Flynn, 2002), then modeling should again be able to perform a useful role in supporting a traffic-light approach to risk management. It should be noted that simply considering nutrient concentrations and ratios (i.e., N:P) need not support an understanding of the likelihood of a toxic event. This is because of the importance of nutrient and light fluxes into the system (Flynn, 2010a), and the consequences of different levels of biological and physiological interactions (competition, mixotrophy, self-shading, predator–prey interactions, etc.).

3.7 Improving Our Capabilities

3.7.1 Changes in the Biological–Modeling Interface

The fundamental challenge to future progress rests in improving our basic understanding of physiology and ecology, and of how these interrelate when set within a given physical system. In essence, the linkages shown in Figure 3.1 need to become more active. More of the same types of studies that have been conducted over the past decades are now needed. At least four things need to change from a biological model perspective.

1) The types of data collected in especially laboratory experiments need to be broadened. Thus, there is a need for data in terms of C, N,P biomass and so on, and not just with respect to organism numbers, or chlorophyll; the problem is that organism size and pigment content (as applicable) vary with growth status, and for trophic dynamics both biomass and stoichiometric quality are important.

2) More attention needs to be paid to the types of abiotic drivers applied in experiments, and the combination in which they are applied. The most obvious drivers in question are light, temperature, and pH. With respect to the latter, linked to the subject of ocean acidification, it is notable that changes in pH during bloom growth rather than growth at any particular (fixed) pH have been indicated by modeling to be important (Flynn *et al.*, 2015a).

3) An enhanced understanding is required for realistic organism–organism interactions horizontally (competitors), upward (predators), and downward (prey) from the HAB species of interest. The absence of data for encystment and excystment is another shortcoming in some regimes. A better holistic understanding of what is going on between organisms is needed when they grow under the types of conditions (including biomass densities and hence nutrient loading) likely in nature under climate change and land use change scenarios.

4) There is a need to understand the implications of mixotrophy for plankton ecology. Emphasis has been hitherto placed on abiotic photo-autotrophic drivers for growth of HAB (inorganic nutrients, light), ignoring the potential role of DOM and of prey fields. The impact of this paradigm change for the understanding of protist ecophysiology (Mitra *et al.*, 2014b, 2016) will take some time to work through.

In essence, while modeling could be criticized for being for the most part not mechanistic enough to enable predictive simulations, in part this simply reflects inadequacies within the wider science to understand the underlying ecological interactions and measure the appropriate parameters. This is not a new observation, and it applies to plankton research in general, but it is one that needs acting upon through coordinated field and laboratory experimental work together with modeling. It also requires that modeling (as systems modeling, with time as a variable) becomes more fully embedded in the ecology and physiological science.

None of this is going to occur quickly or cheaply. Phenomenological understanding (born of what many may dismiss as observational "natural history") always develops before sufficient data are gathered to support empirical, let alone mechanistic, modeling; however, this phenomenological understanding, viewed as non-numeric data, is actually of great potential value and often overlooked in modeling. During recent workshops on enhancing models of mixotrophic protists (leading to Mitra *et al.*, 2014b, 2016), there was a specific attempt made to engage in "expert witness validation." Expert witness validation requires that modelers work with experts in physiology and ecology to build conceptual understanding and then models that conform to the essence of what is seen in nature

Table 3.2 Suggested realized and potential scope for modeling in T-HAB and ED-HAB natural and management science.

	Uses for models in HAB science	Now	Future
i	Provide a focus for investigations and discussions by providing a rigorous framework for testing knowledge	✓	✓
ii	Drive closer links between scientists at all levels, for fully integrated programs	✓	✓
iii	Provide a platform for testing generic "What-if?" questions	✓	✓
iv	Provide a platform for testing organism-specific "What-if?" questions	✗	✓
v	Provide a generalized predictive geographic capacity for algal blooms	✓	✓
vi	Provide a detailed predictive geographic capacity	✓	✓
vii	Provide a detailed predictive temporal geographic capacity	✗	?

and understood from experimental manipulations. This approach also recognizes the importance of generalities in ecology rather than specifics to a strain or particular experimental setup.

Careful consideration is required on what modeling may provide us with respect to T-HAB and ED-HAB; a general summary is attempted in Table 3.2. The history of applied plankton modeling is rooted in the support of biogeochemical science and in algal blooms in drinking water lakes, where the description of biotic details took (and still largely takes) a backseat to describing the abiotic features. T-HAB and ED-HAB are functions equally of abiotic and biotic features. Some combination of using mechanistic, physiology-based models and complex abiotic descriptions (third-generation, "3G ecosystem" models in Figure 3.1) played out in different physicochemical scenarios should be able to provide an enhanced management tool for mitigating against the occurrence of T-HAB and especially ED-HAB. When linked with weather and coastal physics projections, there should be reasonable scope for site-specific capabilities as well. Moving to the detail of what species and what toxins in particular, when, and where represents a far greater challenge. While waiting for that advance, there is good reason to draw some comfort from the developing coupled remote-sensing and abiotic modeling platforms for near-future forecasting.

Acknowledgments

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