

Chapter 19

Recent Advances in Modelling of Harmful Algal Blooms



Peter J.S. Franks

19.1 Introduction

Models have proven to be extremely useful tools in HAB research, from synthesizing knowledge into a conceptual framework to testing hypotheses that would be otherwise intractable. Models have been used to tease apart the dynamics underlying observations, to simulating and predicting bloom events. And, as models improve in predictive ability, they are being increasingly used as management tools.

One of the goals of the Global Ecology and Oceanography of Harmful Algal Blooms Programme (GEOHAB) was to improve prediction of HABs by determining the ecological and oceanographic mechanisms underlying the organism's population dynamics. The approach was to integrate biological, chemical, and physical studies employing enhanced observational and modelling systems (GEOHAB 2001). GEOHAB has supported modelling through its many core projects and activities and in June 2009 supported a workshop on GEOHAB Modelling and Linking Observations to Predictions (GEOHAB 2011). One product of this workshop was a special issue of the *Journal of Marine Systems* containing papers covering a wide variety of modelling approaches—and their challenges.

Since the GEOHAB modelling workshop, I recently reviewed a decade of the modelling of harmful algal blooms (HABs) covering the period 1997–2012 (Franks 2014), building on an earlier review of HAB modelling up to 1997 (Franks 1997). Here I will synthesize advances in the modelling of HABs over the last half decade, 2012–2016, following the same organizational structure I introduced in Franks (2014).

To identify HAB models for this review, I searched *ISI Web of Science* using combinations of the key words “harmful algal bloom HAB model.” Sifting through

P.J.S. Franks (✉)

Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA, USA

e-mail: pfranks@ucsd.edu

the thousands of papers that appeared in this search between 2012 and 2016, I reduced them to just over 100 papers, based on my access to the journals and the paper's subject matter. Selections from these papers form the basis of this synthesis.

Rather than concentrate on the scientific results of the models, I explore the models from a modeller's perspective: how the models were constructed and how they were used to gain insights into the system. Here I organize models into six categories: conceptual, empirical-statistical, process, diagnostic, predictive-simulation, and management.

Conceptual models are syntheses of ideas concerning the dynamics of a system. Conceptual models usually precede mathematical models, though many conceptual models have yet to be formulated as mathematical models.

Empirical-statistical models are often models built up through statistical analyses of observations. They may not include any cause-effect dynamics, but rather describe the system through statistical correlations, lags, and other relationships. Such models can be used in process, diagnostic, predictive, or management modes but are most often used as predictive or management tools. This is due to their relative tractability compared to the more numerically intensive dynamic models. Empirical-statistical models are only interpretable within the limits of the data used to create them; this presents a strong constraint to prediction in the face of changing conditions such as those driven by anthropogenic climate change. Such models are often used to predict one variable (e.g., HAB concentration) given measurements of other variables.

Process models are mathematical models designed to test particular hypotheses concerning the dynamics of an organism or system. They are often used to answer "what if?" questions—what if the organisms had no toxin? What if the organisms had geotaxis rather than phototaxis? What if the nutrient levels were doubled?

Diagnostic models tend to be more intimately tied to data than process models. Typically a diagnostic model is used to identify and quantify the dominant dynamics underlying a set of observations. A set of equations describes the system, and the model is run forward (or sometimes backward) in time, based on initial conditions (often observations) and external forcings (wind, light, nutrients, etc.) to attempt to reproduce the observations. Once an acceptable hindcast is produced, the model can be pulled apart to quantify the processes that were important in leading to the observed patterns. Diagnostic models tend to be interpolative—they help us understand the dynamics that occurred between sets of observations and the dynamics of properties that were not measured.

Predictive-simulation models go a step beyond diagnostic models in attempting to predict the occurrence (timing, location, spatial extent, intensity) of events, rather than hindcasting previous events. Predictive models are extrapolative—they give predictions or forecasts beyond the limits of existing data. Predictive models are a logical increment to diagnostic models—a good diagnostic model should contain the essential ingredients to reproduce future events. Predictive models require a thorough understanding of the essential forcings, conditions, and responses of the system; this knowledge is usually obtained through a progression of process and diagnostic models.

Management models are operational forecast systems. They are typically products of multiple tests of predictive models, to the point that the predictive models have some statistical power. Management models are often run as ensembles of different models or cases, to give some statistical robustness to the predictions or forecasts. State or federal agencies—rather than academic scientists—typically run such operational models, as they attempt to protect the public and inform fishers and those involved in coastal commerce.

In the following sections, I will review recent advances in each of these types of model. I will focus mainly on how they were used, rather than the scientific results they generated. I hope that this review will educate and inspire researchers to develop their own models of HAB dynamics and use them in fruitful ways to answer their questions. In particular, those who make the effort to gather dense sets of laboratory or field data can often benefit from a close collaboration with modellers: the models can reveal surprising facets of the dynamics underlying the observations that might not be obtainable in other ways.

19.2 The Models

19.2.1 *Conceptual Models*

Every model begins as a conceptual model. Before regressions can be run or equations can be written, the researcher has to have some sense of how to reduce an impossibly complex system (reality) down to what they perceive to be its essential elements. This includes the state variables (often the organisms and their constituents), the transfer functions that describe the interactions among the variables, and the forcings such as light, temperature, or nutrients. Conceptual models are the first step in all subsequent models; however, it is often useful to pause at the conceptual model stage to assess what is known and how the pieces might fit together.

Margalef's mandala (Margalef 1978; Margalef et al. 1979) is a useful conceptual model describing the types of organisms that might arise under different environmental conditions. This mandala was recently thoroughly reviewed by Wyatt (2014), who updated the mandala in light of contemporary knowledge of bloom-forming plankton, their life histories, their growth conditions, and their sources of mortality. Glibert (2016) has gone several steps farther in updating the mandala to include 12 dimensions: (1) preference for oxidation state of nitrogen, (2) inorganic nitrogen and phosphorus availability, (3) preference for high light and the ability to be mixotrophic, (4) motility, (5) ambient turbulence, (6) pigmentation, (7) temperature, (8) size, (9) relative growth rate, (10) toxin or reactive oxygen species production, (11) r vs. K strategy, and (12) grazing mortality. Glibert's analysis leverages recent advances in trait-based modelling of plankton (e.g., Litchman et al. 2013; Flynn et al. 2015), which invokes the existence of traits (such as size or nutrient preference) inherent to a species and the tradeoffs an organism must make

in exhibiting a given trait. Glibert's synthesis presents a conceptual framework for subsequent mathematical modelling of HABs.

An interesting conceptual synthesis of the various physiological and ecological mechanisms leading to HABs is presented in Jeong et al. (2015). Using the dinoflagellate, *Cochlodinium (Margalefidinium) polykrikoides* as a model organism, Jeong et al. develop a hierarchy of four generation mechanisms (GM) for HABs. The most basic GM includes nutrients and light; GM2 adds the effects of swimming, while GM3 further includes mixotrophy. GM4 then puts these dynamics into the context of the ecosystem by more explicitly including competition and mortality due to other organisms. These GMs were then synthesized into a "biological interaction map" indicating the types of interaction (grazing, inhibition), the known species, and the direction of the interaction. Simple, general equations were used to describe each GM. These equations could not be solved as presented—the functional forms of the interactions would need to be specified, and the models parameterized with data. This approach, however, laid down the bones for a suite of mathematical models that could serve as testable hypotheses for *C. polykrikoides* HABs.

Conceptual models are particularly useful in synthesizing observations into a coherent description of the system. Accoroni et al. (2015) brought together temperature and nutrient data to understand the occurrence of *Ostreopsis* cf. *ovata* blooms in the Adriatic Sea. By exploring fluctuations and thresholds over several bloom cycles, they were able to construct a conceptual model of bloom dynamics (see Chap. 13, Berdalet and Tester 2018). Tobin et al. (2013) used a similar approach, combining physiological and behavioural observations of different strains of *Heterosigma akashiwo* to develop a strain-specific model explaining how different growth strategies result in different bloom time scales. Gobler and Sunda (2012) summarized knowledge of brown-tide species (*Aureococcus anophagefferens* and *Aureoumbra lagunensis*) to explore conceptual models of bloom formation in response to nutrients, grazing, and the ecological conditions preceding the blooms. A particularly visionary conceptual model was constructed by Visser et al. (2016) to generate predictions concerning the occurrence of cyanobacterial blooms in response to increased atmospheric CO₂ and global warming. Their model was built up through a synthesis of a diverse literature, ultimately helping to focus where future research efforts could be most effectively applied to improve our understanding and predictive ability.

Conceptual models thus serve as a simplified structure for synthesizing information about a complex system. This structure can then be used to motivate further research, as well as the basis for formulating mathematical models of the system.

19.2.2 Empirical-Statistical Models

Empirical-statistical models are used to quantify relationships among observations. Unlike dynamical models that use equations to evolve initial conditions forward in time, empirical-statistical models are often used to predict the value of a variable

given measurements of other variables. In that sense, they are often static (no time dependence), revealing correlations and relationships rather than underlying dynamics. Such models were probably introduced to biological oceanography by Gordon Riley (e.g., Riley 1941) in his seminal studies of plankton fluctuations on Georges Bank and the adjacent continental shelf. Since that time, statistical techniques have improved markedly; much of the growth in HAB modelling studies over the past 5 years has been in empirical-statistical models.

Riley made (for that time) extensive measurements of temperature, nutrients, phytoplankton, and zooplankton and used those measurements to derive correlations among the variables. For a given temperature, phosphate, and nitrate concentration, for example, Riley could predict the phytoplankton concentration with some statistical accuracy.

Modest advances on Riley's multiple linear regressions can be found in the use of various forms of generalized linear models (GLM). The GLM differs from ordinary linear regression in allowing the variables to have non-normal distributions. Singh et al. (2014) used a logistic (or logit) form of GLM in which *Dinophysis* concentrations in the coastal Arabian Sea were categorized as being above or below a threshold concentration. A wide range of predictor variables was considered, with the aim of understanding the effects of climate change on *Dinophysis* bloom dynamics. The model was evaluated based on metrics such as the probability of detection, false detections, and an overall skill metric. The models showed that the N:P ratio was significantly correlated with *Dinophysis* abundance; blooms could be predicted based on linear relationships with sea-surface temperature and salinity, total suspended solids, and N:P. Given predictions of changes in these explanatory variables—and given the assumption that these relationships are unchanging – blooms of *Dinophysis* are predicted to become more frequent.

Feki et al. (2013) used a similar approach but employed a generalized linear mixed-effect model (GLMM) that includes both fixed predictors (the environmental data) and a random component (the sampling sites) for understanding the dinoflagellate *Karenia selliformis* blooms in the southwestern Mediterranean Sea. Particularly notable in this study was the careful approach to processing and reducing the data prior to application of the GLMM, including the use of a generalized additive model (GAM) to reduce redundancy among the different observations. In a GAM, the relationship between the observations and the predicted variable does not have to be linear—the GAM can be used non-parametrically to estimate a smoothed function relating the noisy observations to the predicted variable. Multiple predictors can be incorporated, each with different functional forms. Díaz et al. (2016) used GAMs to explore blooms of the dinoflagellate, *Dinophysis acuta* in an upwelling-influenced ria in Galicia, finding that a combination of a cumulative upwelling index, sea-surface temperature, and tidal range explained 77.3% of the deviance of *D. acuta* blooms. Interestingly, the model showed that the bloom relationship to the upwelling index and tidal range was nonlinear.

Among the many applications of empirical-statistical models to HAB research, I noticed two relatively new approaches that appeared frequently: Bayesian approaches and machine learning approaches. Bayesian statistics differ from

“frequentist” approaches in assigning prior probabilities (with potentially non-normal distributions) to parameters which are then updated to a posterior probability given new data. This approach was used by Obenour et al. (2014) to improve forecasts of cyanobacterial blooms in Lake Erie; by testing different forms of the nutrient-load/nutrient-bloom relationship, each with a different statistical error distribution, they obtained a model that had both high-predictive skill and a statistical characterization of the prediction uncertainty.

One of the problems inherent to statistical modelling of HABs is that most of the time there is no HAB—there are many zero measurements. These often lead to Poisson or negative binomial distributions, though the abundance of zeros can lead to departures from these distributions. To accommodate such zero-heavy data, Cusack et al. (2015) employed a zero-inflated negative binomial (ZINB) model, a specific version of the more general Bayesian hurdle Poisson model used by Cha et al. (2014). In ZINB models the zeros are considered to arise from a mixture of the underlying distribution (negative binomial) and some second process that generates zeros. Hurdle models, on the other hand, separate the zeros (which arise from one process) from the non-zeros that arise from a different process that does not generate zeros. The goal of both models was to predict HABs: cyanobacteria (Cha et al. 2014) or the diatom genus, *Pseudo-nitzschia* (Cusack et al. 2015). Based on these models, Cha et al. were able to define nonlinear functions (and their confidence limits) relating cyanobacterial presence to water temperature and mean weekly freshwater outflow (flushing time) in Lake Paldang (Korea). Cusack et al. were able to use wind and sea-surface temperature to predict *Pseudo-nitzschia* in bays along the southwest coast of Ireland. The key to these statistically successful hindcasts was careful consideration of the non-bloom observations.

Machine-learning approaches to HAB prediction have been employed for several decades, though they appear to be more common in the last 5 years. Bayesian networks (Rigosi et al. 2015; Moe et al. 2016), neural networks (Gokaraju et al. 2012; Millie et al. 2014), and support vector machines (González Vilas et al. 2014; Nieto et al. 2015) have all been employed to understand and predict HABs. Machine-learning techniques take observations and use various algorithms to learn from them to make predictions.

Bayesian network modelling treats observations as “nodes,” which are linked by probabilities, the whole network ultimately generating the probability of an outcome. Because of the two-way probabilistic linking of nodes, the complexity of Bayesian network models increases exponentially with the number of nodes. It is thus desirable to use a conceptual model to limit the complexity of the system. Rigosi et al. (2015) used the model itself to inform the ideal number of nodes by testing models of three, four, and nine nodes—each node being a different data source—with the objective of deriving a model to predict cyanobacterial blooms in lakes. Moe et al. (2016) used a nested approach, using separate modules for (1) the Bayesian network which fed into (2) a process model that was then linked to (3) monitoring data, finally generating (4) a classification system for cyanobacterial blooms in lakes. Both models were used to predict the changes in bloom occurrence under future climate warming scenarios.

Warming was found to increase bloom probability, though this depended on the lake's trophic status and coincident management strategies.

Neural networks (NNs) use layers of nodes to connect observations through different weightings. After being trained with a data set of known inputs and outputs, the NN can be used with new data to predict the outputs. Millie et al. (2014) used 31 hydrological and meteorological predictors (observation data types) to predict presence/absence of freshwater cyanobacterial blooms. To better understand the drivers of the blooms, Millie et al. whittled the predictors down to total phosphorus, temperature, and wind speed as the main drivers controlling bloom occurrence. From this they were able to derive conditions (particularly total phosphorus levels) that would help to mitigate cyanobacterial blooms.

The use of support vector machines (SVMs) to predict HABs is relatively new, even though this technique is particularly applicable to such problems. SVMs are commonly used to classify data; this is often a difficult task, as data may not be easily separable. Data are mapped onto "hyperplanes" on which the data points cluster in obvious ways and are therefore easily separated and classified. The hyperplanes are chosen to maximize the "margin"—the distance between a separating surface and the closest points to that surface on either side. Typically the margin is maximized while the overall error is minimized. As with NNs, the SVM is trained on a known data set; this trained system is then used to classify subsequent data. During the training, optimal parameter values are chosen for the SVM kernel to allow it to optimally classify the data. The end result is a system that can take observations of environmental and biological variables and classify them into, say, bloom and non-bloom conditions. Like other statistical regression techniques, the SVM will additionally give information concerning the relative importance of the data type in determining the output. This approach was used to both predict and understand the drivers of cyanobacterial blooms in a reservoir (Nieto et al. 2015) and *Pseudo-nitzschia* blooms in rias of Spain (González Vilas et al. 2014).

Empirical-statistical models are powerful tools when sufficient data are available. Though they are static in the sense that they do not include dynamic relationships among variables, with sufficient data (which usually means many bloom/non-bloom cycles), they can reveal relationships among environmental and ecological forcings and HAB responses. If conditions remain stationary, they are useful predictive tools and form the basis for most management models.

19.2.3 Process Models

The following three types of model—process, diagnostic, and predictive—tend to be numerical, rather than statistical models. These models contain "state variables" (e.g., nitrate, cell concentration, zooplankton concentration, etc.) connected by "transfer functions" (e.g., grazing rate, nutrient uptake rate, etc.). The dynamics of the model are determined by the choice of state variable, transfer function, and parameters that are used to describe the transfer function.

I have found it useful to distinguish three types of process model: applied mathematics (math), hypothesis testing, and sensitivity analysis. Applied math models tend to be fairly divorced from data, often using seemingly simple nonlinear systems (e.g., phytoplankton-toxic phytoplankton-zooplankton) to explore the model dynamics in relation to the model parameter space: bifurcations, chaotic behaviour, stability, sensitivity, etc. There have always been a substantial number of such models in the literature, and over the last 5 years, such models were the most numerous category. However, I will not be reviewing them here, as they tend not to be incorporated into laboratory or field research in any substantial way, so they remain largely mathematical curiosities for the HAB community.

Using models for hypothesis testing and sensitivity analysis has a long history in HAB research; over the past 5 years, the increase in the amount and availability of data has made such models extremely powerful research tools. Hypothesis-testing models span a wide range of physical and ecological dynamics. Butman et al. (2014) and Waters et al. (2015) both explored the importance of benthic or near-bottom seed populations for HABs, combining models and data in novel ways. Butman et al. used a sequence of physical models to assess sediment resuspension to predict the injection of benthic cysts of *Alexandrium fundyense* into the water column. The models gave spatially and temporally resolved measures of resuspension, including interannual variability from decades-long regional model runs. Exploring the relationship of resuspension to wind stress led to the hypothesis that strong northeast winds in spring could determine subsequent HAB intensity. This hypothesis is an excellent candidate for testing in the field.

Waters et al. (2015) used a novel combination of laboratory and field data, buoyancy-controlled drifters, and a STELLA-based model of organism behaviour to investigate the behaviour of *Karenia brevis* in benthic boundary layers. A particularly novel aspect of the model was that it was incorporated into the software controlling the drifters (in a quarry), so that they behaved similar to the plankton—their vertical movements were determined by their internal N and C stores, calculated from time of day, temperature, and light sensed by the drifters. The combination of data and models supported the hypothesis that near-bottom populations of *K. brevis* could be the inoculum for subsequent dense blooms.

Process models are particularly good tools for exploring how systems work and for testing particular mechanisms controlling system behaviour. Sunda and Shertzer (2014), Yamaguchi and Sai (2015), and Alves-de-Souza et al. (2015) all used models to explore top-down and/or bottom-up controls on HABs, combining laboratory and field data to parameterize, drive, and test their models. The Sunda and Shertzer and Alves-de-Souza et al. models were run without explicit physical forcing, while the Yamaguchi and Sai model was coupled to a one-dimensional (vertical) model to drive nutrient inputs from deep waters. Based on extensive laboratory data (including videos of *Heterosigma akashiwo* swimming), Harvey and Menden-Deuer (2012) developed a model to test the hypothesis that a predator-avoidance behaviour would lead to the formation of dense surface aggregations—HABs. Parameterizing a model with the observed behaviours (persistent upward swimming in the presence of predators but random swimming in their absence),

they showed that dense layers of *H. akashiwo* formed at the surface as the organisms fled their predators, supporting laboratory observations.

These combinations of data and models are powerful tools for understanding the potential for certain dynamics to lead to HAB formation. Models are particularly good for experimenting with such dynamics: their intensity can be changed in a model to explore the outcome given different forcings. Warns et al. (2013) published what may be the first model of the complete life cycle of the dinoflagellate, *Biecheleria baltica*—complete with encystment/excystment dynamics and vegetative and sexual phases. The model was particularly useful in several respects: (1) it served as a platform to synthesize understanding of the *B. baltica* life cycle and physiological responses to environmental forcing, (2) it could be used to understand annual cycles in *B. baltica* abundances, and (3) the environmental forcing could be varied to quantify the sensitivity to changes in temperature. As with Moore et al. (2015) (discussed later), increased temperature was found to cause earlier, more intense blooms and the formation of more cysts.

Coupling HAB models to three-dimensional (3D) circulation models is still a relatively nascent field, but several recent papers demonstrate the utility of 3D models in elucidating transport pathways of HAB organisms. Pinto et al. (2016) used passive numerical drifters in a 3D circulation model of the Iberian coast, showing the possibility of local HAB presence based on transport of toxic cells from distant point sources. Hickey et al. (2013) used a similar approach employing virtual drifters in a well-constrained model of the Oregon-Washington coastal currents to evaluate the influences of source location, wind forcing, and presence and movements of freshwater plumes (Columbia and Fraser Rivers) on the occurrence of *Pseudo-nitzschia* blooms in the region. The model was used to test hypotheses formulated through examination of the field data: the model showed that the Columbia River plume could be both a barrier and a conduit for toxic cells reaching certain shellfish beds. Lai and Yin (2014) performed extensive experiments using their 3D physical model, to test whether physical convergence zones could account for locally dense HABs. They used both neutrally buoyant and vertically migrating numerical drifters in their model of a bay in northeast Hong Kong, testing the effects of stratification and wind on drifter accumulation. They showed that intense HAB patches could form through accumulation, a process not often included in HAB analyses.

Gillibrand et al. (2016) went a step further and included biological dynamics following the numerical drifters—the biology being determined by an individual-based model of *Karenia mikimotoi*. This approach allowed them to assess not only drift pathways but the likelihood of growth and mortality along those pathways. They tested hypotheses of the spatial structure of initial conditions (how the cells were distributed prior to blooms) and the importance of growth and mortality, vertical migration, wind forcing, advection, and temperature—each of these latter processes could be turned on or off in a model run. This is a particularly good example of the use of a relatively complex model for hypothesis testing. The process was made more efficient by using archived flow fields: only the biological models needed to be rerun for each experiment, saving considerable time over fully coupled models.

Ryan et al. (2014) took an interesting approach in modelling *Pseudo-nitzschia* in Monterey Bay: using a physical model that assimilated data such as satellite altimeter, satellite temperature, and in situ CTD data, they used an adjoint model to “predict” where HAB patches may have come from 3.5 days earlier. The adjoint technique runs the model backward and forward to obtain a statistically optimal solution of initial conditions (and sometimes forcings) that would lead to the final (observed) condition. Combining these model solutions with an extensive in situ data set allowed them to assemble a very complete story concerning the physical and biological dynamics governing the appearance of HABs in the bay.

Moore et al. (2015) used global climate model ensemble simulations to force a regional 3D model of Puget Sound. Their goal was to predict the occurrence of the dinoflagellate, *Alexandrium*, under the influence of climate change, and to use the model to understand the contributions of potential effects on HABs. Predicting out to the year 2069, Moore et al. were able to quantify how changes in heat flux, river flow, and coastal upwelling would affect the growth and proliferation of *Alexandrium*. The model experiments were interesting: upwelling, for instance, was assessed through a sensitivity analysis using atmospheric forcing from particular years chosen to represent long-term changes in wind stress. Through a suite of model experiments, heating was found to be particularly important in both increasing growth rates and prolonging the bloom season.

Process models remain one of the most important and useful tools in the HAB modelling repertoire. They are particularly useful for testing hypotheses and exploring the dynamics of HAB systems. Hierarchies of models can be used to investigate the influence of increasingly complex combinations of forcings and dynamics on HABs. Process models are typically the next logical step after a conceptual model and a necessary step to achieving a dynamic, predictive model.

19.2.4 Diagnostic Models

Once a model has been well-calibrated for a system, it can be used to diagnose the dynamics that led to a particular set of observations. In this way, a complex system can be reduced to a simpler one, or the importance of nonlinear events (a particular wind speed and direction at a certain time, a confluence of tides and wind, etc.) can be assessed. “Systems” can be simple laboratory experiments or complex field observations.

Lim et al. (2014) explored the interactions between *Cochlodinium polykrikoides* and the diatoms *Chaetoceros danicus*, *Skeletonema costatum*, and *Thalassiosira decipiens*. Experiments with different combinations of *C. polykrikoides* and the diatoms showed that the diatoms (and their exudates) decreased growth rates and swimming speeds of *C. polykrikoides*. Simple models were used to test hypotheses concerning the nature of the interactions (contact or chemical). Once the models were fit to the data, the parameters revealed threshold concentrations of diatoms that would inhibit *C. polykrikoides* growth. The model fits – obtained using an objective

statistical criterion—also generated information on the unknown model parameters, such as the interaction strengths among the species. The model could thus be used as a diagnostic tool to recover missing or difficult-to-measure information.

Terseleer et al. (2013) took a similar approach, fitting a model to experimental data investigating domoic acid (DA) production in *Pseudo-nitzschia*. With the model parameterized to reproduce time-series experiments with different nutrient limitations, it could then be used to better understand the factors controlling DA synthesis and release. Numerical experiments thus supplemented laboratory experiments to gain understanding about this complex system.

The simplest form of diagnostic model using a 3D circulation model is particle-tracking. Aoki et al. (2012) followed particles representing the raphidophyte, *Chattonella antiqua*, in the Yatsushiro Sea (Japan); the particles were seeded in a bay that was presumed to be a source of blooms in the sea. Curiously, the model showed that the bay was unlikely to have been a source of the blooms. Instead, they likely originated from a coastal location in the sea itself. The model was then used to diagnose the dominant forcings for a sequence of blooms observed in the bay; different combinations of wind and river flow accounted for each of the blooms, showing that a single conceptual model was an inadequate explanation for the various HABs.

Li et al. (2014) went a step further than Aoki et al. in their examination of the advection of *Alexandrium fundyense* in the Gulf of Maine. They released particles every 5 days at 7 sites that had been previously identified as potential source regions and tracked the particles as they were moved about the gulf. The particle locations were used to produce Lagrangian probability density functions for giving the probability of particles released from a given site arriving at another location; these were used to construct a Gulf of Maine coastal connectivity matrix—the probability of a particle released from a given point arriving at another point in a certain amount of time. Through this process Li et al. could quantify the relative strength of source regions, and “attractiveness” of destination regions, as well as assess the interannual variability of transport pathways for *A. fundyense* HABs.

Giddings et al. (2014) took a similar approach to Li et al. (2014) in their study of *Pseudo-nitzschia* sources and advection pathways in the Pacific Northwest of the United States, releasing particles into a model semi-continuously at suspected HAB source regions. They also gave their particles behaviour—in particular a tendency to float. Before the model was used to test HAB pathways, the model currents and hydrography were tested against an extensive data set using skill metrics. The model was then teased apart to diagnose the influence of wind, the Columbia River plume, and source region on the probability of coastal HABs. This is a particularly thorough study embracing numerical modelling, statistical analyses, and thoughtful analysis of the model results to gain understanding of an extremely complex system.

Henrichs et al. (2015) added biological dynamics to their particle-tracking model of *Karenia brevis* in the Gulf of Mexico. In addition to a physiological model for each particle, the organisms (particles) were allowed to migrate vertically—interacting with the surrounding flows—based on their internal nutrient stores.

The interesting twist in this modelling study was that the model was run both forward and backward in time. Forward runs showed where cells from particular source regions might go, while backward runs showed where cells forming observed blooms might have originated. This combination of data, biological model, and physical model proved to be a uniquely powerful tool for gaining understanding of the dynamics underlying observed HABs in the region.

Diagnostic models have been applied to simple laboratory systems and complex natural systems to gain understanding of sources, pathways, and dynamics of HABs. The combination of models and data is synergistic, giving a tool that is more powerful than either approach individually. It is likely that with the advent of new observing systems and enhanced data streams, we will be seeing an impressive increase in the number and utility of diagnostic models of HABs.

19.2.5 Predictive Models

A well-calibrated diagnostic model can be transitioned to a mode in which it is used for out-of-sample forecasts: prediction. Accurate model predictions require that the model remains an accurate depiction of the system in the future, that is, there are no substantial changes in the ecosystem parameters or structure that could not be captured by the model. Predictive models are often used to forecast HABs, both in the near term and increasingly over climatological time scales.

Brown et al. (2013) coupled a detailed and well-calibrated 3D circulation model with empirical-statistical models of a wide range of potentially harmful species, to enable forecasts of—among other things—HABs in the Chesapeake Bay. For example, the model for *Karlodinium veneficum* was an artificial neural network (ANN), while the dinoflagellate, *Prorocentrum minimum*, model was a general linear logistic regression. The circulation model assimilated measurements and was forced with observations (meteorological, river inputs), generating habitat maps that provided the conditions for the HAB predictions. The authors made a significant effort to make the model solutions and predictions available in real time to interested parties. The coupling of the circulation model with empirical models of the various species—rather than a full ecosystem simulation including the target species—was made for a very efficient and statistically robust forecast system.

As useful as the Brown et al. (2013) model is for forecasting, it is not a dynamic model; it does not solve equations giving the rate of change of state variables based upon its sources and sinks. Walsh et al. (2016) developed a dynamic model of the West Florida shelf that includes 29 explicit (and 7 implicit) state variables, including HAB species such as *Karenia brevis* and *Cochlodinium polykrikoides*. The model was run in a 2D (cross-shore section) mode, requiring careful parameterization of the boundary conditions for the biological variables, such as zooplankton and bacteria. This model represents one of the most ecologically complex models formulated to date, presenting significant challenges in parameterization, implementation, and analysis. Such models, however, provide one of the few means to

assess the interaction of HAB species with their ecosystem, rather than treating them as isolated species. This may be the key to gaining a deeper understanding of HAB dynamics.

Kibler et al. (2015) took an intermediate approach between Brown et al.'s use of empirical models for their HAB species and Walsh et al.'s dynamic models: they used empirical data to parameterize temperature-growth rate curves for five different ciguatera-producing species in the Gulf of Mexico and Caribbean Sea. Ensemble averages from a suite of 11 global climate models (GCM) were used to provide temperature data over decadal time scales to hindcast and predict interannual changes in the growth rates of the target species, using those empirical models. Given the GCM predictions of regional temperature changes, three species were predicted to become increasingly dominant, creating higher local risks of ciguatera poisoning, while the other two species were expected to expand their geographic ranges, creating new risks in areas of the western Atlantic.

Note that the Kibler et al. model did not include an ecosystem in which the target species were embedded; there was no mortality or possibility of changes in ecosystem structure in response to the temperature increases. Glibert et al. (2014) addressed this issue by modelling the habitat changes of HAB species, rather than the ecological dynamics of the species. Using a GCM forced with projected climate characteristics, Glibert et al. predicted changes in the HAB genera *Karenia* and *Prorocentrum* driven by nutrient loading and climate change in three regions of the globe: the Baltic Sea and Northeast Atlantic, the Northeast Asian coast, and Southeast Asia. Different patterns of range expansion/contraction were predicted in different regions by the end of this century. Again, this model did not include any HAB dynamics—only changes in the available habitat. Thus, changes in ecosystems or species invasions could not be accommodated in the predictions.

The models discussed here in the context of predicting HABs represent an interesting spectrum of approaches. They all used a well-calibrated physical model—regional or GCM—coupled to biological models varying from empirical to extraordinarily detailed ecosystem representations. The simpler biological models do not allow understanding of the potential for changes in the HAB organism's interactions with its ecosystem, while the detailed ecosystem model has the usual problems associated with poorly constrained parameterizations of physiological and ecological processes. Still, long-term forecasts suggest that some HAB species will become more prevalent or intense and/or will expand their geographic extent as newly favourable habitat opens up due to climate change.

19.2.6 Management Models

Management models are those used to help minimize the economic and health effects of HABs. They typically will take inputs of environmental conditions and HAB cell counts and use them to forecast HAB intensity in a given area. The models differ in how information is processed and used, though a key element is making the information easily accessible to relevant parties.

Hu et al. (2016) developed a system for information delivery, as opposed to forecasting of *Karenia brevis* blooms in the Gulf of Mexico. The system integrated satellite imagery, *K. brevis* cell counts from various stations, and ocean currents from a well-calibrated 3D model. The integrated product is made available to the community in keyhole markup language, which can be plotted with other products in Google Earth. The model will produce maps of *K. brevis* concentrations, and the model can be used to predict bloom trajectories over the next few days. The combination of data and model is particularly useful to extend the effective reach of the field samples, which are comparatively sparse in time and space.

A particularly impressive effort was undertaken in Europe as part of the EU FP7 programme: Applied Simulations and Integrated Modelling for the Understanding of Toxic and Harmful Algal Blooms—"ASIMUTH" (e.g., Davidson et al. 2016). In this effort, data from local and regional shellfish monitoring programmes (acquiring both shellfish toxicity data and HAB species cell counts) were integrated in near-real time with 3D circulation models forced with measured (in situ and remote sensing) meteorological variables. The models were run forward in time to generate 3–5-day forecasts of HAB location, intensity, and toxicity. Silva et al. (2016) deployed the system for the coast of Portugal, predicting *Pseudo-nitzschia* HABs on the coast and in the lagoons and estuaries. For the 2013–2014 period, they achieved a forecast skill of 85% of predictions correct, 12% fail (an unpredicted bloom occurred), and 3% of the predictions were for a bloom that did not occur. Prediction skill depended on the area being considered, as well as biological and physical factors that could not be taken into account in the models. The ASIMUTH system predictions were published in a HAB warning bulletin that could be used by the community to mitigate the economic, health, and societal effects of the HABs.

Ruiz-Villarreal et al. (2016) deployed the ASIMUTH system to forecast *Dinophysis* spp. HABs along the Northwest Iberian coast. In addition to the 3D circulation model and field data on HABs, they included an offline Lagrangian particle-tracking model that took archived model output to predict the transport of HAB patches. The model was tested with data from the 2005 and 2013 diarrhetic shellfish poisoning (DSP) outbreaks and was found capable of forecasting HABs based on predictions of upwelling and downwelling and alongshore advection. A more rigorous statistical test of the model would reinforce its utility as a HAB warning tool.

Maguire et al. (2016) describe the use of the ASIMUTH system to provide forecasts and bulletins concerning HAB species around Ireland and the British Isles. A key element in the development of these warnings was the integration of regional physical models (e.g., Dabrowski et al. 2016; Cusack et al. 2016) with larger-scale models that provided boundary conditions. As in the other ASIMUTH projects, the physical models were integrated with in situ monitoring data to provide the forecasts. In all cases, the models provided not only forecasts, but a synthetic platform for a wide range of data types—from HAB cell counts to wind stresses—that could then be used in a diagnostic sense to better understand the dynamics that led to the blooms and their transport and dissipation. These models thus go well beyond the relatively straightforward statistical forecasts and include a

dynamic component that provides a gateway to improved insights into local and regional HAB dynamics.

Achieving the ASIMUTH goals required the participation of multiple agencies and institutions in multiple countries; this significant effort appears to have paid off in a system that can serve as a global model for regional and large-scale HAB forecasting.

19.3 Conclusions

Our understanding of the dynamics of HABs, in the context of both their ecosystem and their environment, has increased tremendously through the combination of models and data. The engagement of statisticians, physical oceanographers, and modellers with the biologists investigating HABs has been a powerful boon to progress in this field. New statistical techniques have been deployed to understand and predict HABs in response to measured forcings, and new dynamic models of HABs and their ecosystems are enabling a deeper understanding of the processes governing the initiation, growth, transport, and decline of toxic phytoplankton species and their toxins.

Though process models tend to be the most often published, the numbers of empirical-statistical and diagnostic models are increasing every year. It is particularly pleasing to see such impressive progress in the development and deployment of management models; it is likely that their utility will help to justify the decades of public investment in research aimed at understanding HABs.

The great variety of approaches in formulating and analysing HAB models reflects the goals of the researchers and the data and tools/expertise available. Some models are all physics, some are all biology, and most are some fruitful combination of the two. However, it seems clear that the significant advances in the field of HAB modelling over the last half decade have been fueled by a remarkable increase in the frequency, geographic coverage, and range of types of observational data. Future advances in modelling will occur at this junction of models and data, using data to conceptualize models and using models to understand data.

Acknowledgments There are far more published model studies than I am able to review here. I apologize to those whose work I have not included—there just wasn't enough room!

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