Prediction and the aquatic sciences[1]

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Abstract: The need for prediction is now widely recognized and frequently articulated as an objective of research programs in aquatic science. This recognition is partly the legacy of earlier advocacy by the school of empirical limnologists. This school, however, presented prediction narrowly and failed to account for the diversity of predictive approaches as well to set prediction within the proper scientific context. Examples from time series analysis and probabilistic models oriented toward management provide an expanded view of approaches and prospects for prediction. The context and rationale for prediction is enhanced understanding. Thus, prediction is correctly viewed as an aid to building scientific knowledge with better understanding leading to improved predictions. Experience, however, suggests that the most effective predictive models represent condensed models of key features in aquatic systems. Prediction remains important for the future of aquatic sciences. Predictions are required in the assessment of environmental concerns and for testing scientific fundamentals. Technology is driving enormous advances in the ability to study aquatic systems. If these advances are not accompanied by improvements in predictive capability, aquatic research will have failed in delivering on promised objectives. This situation should spark discomfort in aquatic scientists and foster creative approaches toward prediction.

Résumé : La nécessité de la prédiction est maintenant largement reconnue, et souvent formulée comme un objectif des programmes de recherche en sciences aquatiques. Il s'agit là en partie de l'héritage d'une position préconisée par l'école de la limnologie empirique. Cette école présentait toutefois la prédiction de façon étroite, et ne parvenait pas à rendre compte de la diversité des approches prédictives ni à placer la prédiction dans un contexte scientifique adéquat. Des exemples tirés de l'analyse des séries chronologiques et de modèles probabilistes orientés vers la gestion permettent d'élargir les approches et les perspectives de la prédiction. Le contexte et la justification de la prédiction est une amélioration de la compréhension. Il est donc nécessaire de voir la prédiction comme une aide à la construction du savoir scientifique, une meilleure compréhension amenant à une meilleure prédiction. L'expérience montre toutefois que les modèles prédictifs les plus efficaces consistent en une représentation condensée des caractéristiques clés des systèmes aquatiques. La prédiction reste importante pour l'avenir des sciences aquatiques. Les prédictions sont nécessaires pour évaluer les problèmes environnementaux et pour tester les bases scientifiques. La technologie permet des progrès remarquables dans les moyens d'étude des systèmes aquatiques. Si ces progrès ne s'accompagnent pas d'une amélioration de la capacité de prédiction, la recherche en sciences aquatiques n'aura pas réussi à atteindre les objectifs promis. Cette situation, qui semble dérangeante pour les chercheurs en sciences aquatiques, doit susciter la recherche d'approches créatives de la prédiction.

[Traduit par la Rédaction]

Introduction

In the final year of his life, the Canadian limnologist F.H. Rigler published two papers promoting an "empirical approach" to the development of general theories in the aquatic sciences. One paper argued that many phenomena studied by ecologists were unpredictable, at least based on current theory (Rigler 1982*a*). As an alternative to focusing on phenomena that were conceptually obscure or inherently unpredictable, Rigler advocated seeking general relationships such as regression models to identify ecological properties and processes that were predictable. By starting from empirical relationships, more "explanatory theories" would likely emerge, providing a better basis for scientific advancement. A second paper called for a closer integration of fisheries science and limnology (Rigler 1982*b*). Rigler complained that traditional limnology and fisheries science were far too separate given many common problems. He again promoted predictive approaches within and among the two disciplines as means toward achieving integration. These two papers presented an outline of an approach that become widely known as "empirical limnology" and was a strongly advocated by both Rigler and R.H. Peters in numerous papers and books (e.g., Rigler 1975; Peters 1991; Rigler and Peters 1995).

While the philosophy of the empirical limnologists was highly controversial (Lehman 1986; Carpenter and Kitchell 1988; Shrader-Frechette and McCoy 1993), the work of Rigler, Peters, and associates focused attention on the issue of prediction. The significance of prediction either as a component of the scientific process or as a means toward improved application of the aquatic sciences was either not widely appreciated or at least not widely discussed prior to their work. This has changed. In this essay, I contend that there is now an increased recognition of and emphasis on prediction in the aquatic sciences. The need for predictions

Received January 11, 2000. Accepted July 20, 2000. Published on the NRC Research Press web site on November 10, 2000.
J15518

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[1]Invited perspective for this 100th Anniversary Issue.

 DOI: 10.1139-cjfas-58-1-63

is clear. The public that funds most aquatic research does so partly in the hope that science will facilitate better management and protection of precious resources. Better management would follow from a more predictive science that could forecast the consequences, costs, and benefits of management actions. For purely disciplinary reasons, there is also a need for predictions to hone, test, and organize theoretical ideas. Thus, it is appropriate to reflect on the concept of prediction in this volume that attempts to foreshadow future concerns and directions for the discipline.

It is important to note at the outset that the ensuing discussion of prediction in this paper is not meant to be placed in opposition to the goal of understanding in science. While some empirical limnologists in the past minimized understanding as a scientific objective (e.g., Peters 1991), the discussion here is oriented toward integrating prediction and understanding.

One reason for discussing the interaction of prediction and understanding is that past examples of predictive approaches, especially those deriving from the empirical limnologists, largely represent only one of many possible approaches to prediction. As a consequence, there is a danger that prediction has been viewed too narrowly or, worse, as inapplicable to many scientific endeavors. I argue that there are a variety of approaches to making predictions and a need for an expanded view. Predictive approaches can and should interact productively with mechanistic studies and experiments. By reconciling these different facets of scientific activity, prediction takes a significant but not dominant place within research programs designed to enhance scientific understanding and contribute to the improved management of aquatic systems.

Prediction defined

Prediction in common usage is foretelling or stating in advance an outcome based on some belief or experience. In science, predictions derive from theory. In keeping with the common definition, theory represents scientific experience from which predictions are derived, but this analogy has limits. Theories are organized bodies of knowledge that consist of a set of conceptual constructs that offer causal explanations of some domain of observable phenomena (Pickett et al. 1994). Thus, predictions drawn from scientific theory are to be taken differently from those provided by clairvoyants. Theories represent a very special form of experience. They are the organization of scientific knowledge.

The logical structure of a theory allows mathematical, graphical, and verbal descriptions of natural phenomena. These descriptions lead to predictions that, given a set of circumstances or precedents, a particular result or response should be observed. Some distinguish between predictions and forecasts (Pickett et al. 1994). The latter do not necessarily derive from theory and may be largely correlative, reflecting little understanding but nonetheless still useful in science. The most common use of forecasting is to project current knowledge into the future using a model. Thus, forecasting is based on or includes time. Predictions can be time independent. For example, a theory might suggest an evolutionary pattern or process that could then be tested by gathering data from fossils or by an experiment.

Despite these distinctions between prediction and forecasting, I will lump the two in this paper. Many scientific predictions seem hybrids of those extracted specifically from theory with those derived more loosely from various types of models that may not have the status of theory. Recognizing the difference in practice is difficult, and there are surely differences among scientists about what body of knowledge constitutes theory (and hence provides predictions) and what body of knowledge is less well established theoretically and hence does not yield formal predictions. Much of the knowledge in aquatic science is organized loosely, if at all, into theory. The goal for most practicing scientists is to predict usually with some form of a model, and so I focus on predictions in this sense.

An important recognition is that predictions in the aquatic sciences are usually probabilistic. We seek models that define the most likely state or states of nature and their uncertainties. This is particularly the case when making predictions for management (Walters 1986). Various means for making such predictions are available including Bayesian and maximum likelihood approaches (Hilborn and Mangel 1997). The key point is that predictions derive from models of the natural world that express or amalgamate scientific understanding of a problem. Probabilities in predictions represent an important feature in expressing the quality of scientific knowledge, as a means of communicating to nonscientists, and as a source of inspiration for scientific research that seeks to reduce uncertainty.

Prediction as a goal

Large-scale global environmental problems have spawned many national and international research initiatives and targeted programs in all areas of environmental science. These efforts usually have mission statements that reveal prediction as a core objective.

Mission statements from two marine programs are representative. The U.S. Global Ocean Ecosystem Study (GLOBEC) seeks to “develop basic information about the mechanisms that determine the variability of marine animal populations” (www.nsf.gov/geo/egch/gc_globec.html). Studies that couple physical and biological processes are proposed to achieve this objective. The goal for prediction in this case comes second: “Once projects directed toward understanding the impact of physical phenomena in marine ecosystems are well advanced, U.S. GLOBEC investigators must address the question of predicting the future responses to the climatic scenarios that researchers deem probable in the sea.” The international version of this program has a similar goal with a component specifically focused on Atlantic cod (*Gadus morhua*) (www.pml.ac.uk/globec/):

> The International Council for the Exploration of the Sea (ICES) and GLOBEC have joined together to develop an innovative programme to advance the **understanding and prediction of variability in fish** stock recruitment, both in the short term (annual forecasts) and in the long term (“climate effects”). Cod has been chosen to serve as the candidate species for this exercise because its biology is well-known and supported by ample data bases, it has a

> pan-Atlantic distribution, and its abundance and distribution have been shown to be sensitive to specific past examples of environmental variability. These considerations provide Cod and Climate Change (CCC) with the possibility of developing new capabilities in predicting fish recruitment from a better understanding of the interaction of physical processes and population dynamics.

This quote illustrates that large programs like GLOBEC not only have general scientific goals, but also specific ones that are of immense practical importance.

Similar to GLOBEC, the U.S. portion of the international Joint Global Ocean Flux Study (JGOFS) has two core objectives (www1.whoi.edu/mzweb/overview.htm). The first is "to determine and understand on a global scale the processes controlling the time-varying fluxes of carbon and associated biogenic elements in the ocean, and to evaluate the related exchanges with the atmosphere, sea floor, and continental boundaries." The second is "to develop a capability to predict on a global scale the response of oceanic biogeochemical processes to anthropogenic perturbations, in particular those related to climate change." The JGOFS and GLOBEC examples are justified partly in the context of anticipated global climate change and partly in the context of the need to view the ocean system at very large scales including the global scale. The consequences of climate change are the major goals for prediction in these studies.

Limnologists are also interested in prediction. One example is the Freshwater Imperative, a general research agenda designed to "identify research frontiers and opportunities in limnology" (Naiman et al. 1994). The goal of the Freshwater Imperative is "to acquire a *predictive* understanding of freshwater ecosystems and resources that can be used to improve detection, assessment, and forecasting of environmental effects and to develop management and mitigation alternatives for scenarios of potential environmental change." Much like the marine programs, prediction is viewed here as first being fostered by basic scientific understanding and second serving as a means to develop better management of freshwaters in the context of a changing environment. Prediction is in this case and for the GLOBEC cod study cited above a way of connecting research programs to pragmatic endpoints.

A cynic might argue that these mission statements of large programs are designed primarily to persuade the funders of science to support basic research with prediction and application as props to make the research efforts appealing. While I agree that their purpose is to promote research, I believe that these statements also reflect the growing aspirations of many scientists to use their work in addressing demanding environmental problems. My view is supported by calls from both scientific societies and distinguished researchers for work directed at the problems of human-driven environmental change (e.g., Lubchenco et al. 1991; Vitousek 1994; Tilman 1998).

The mission statements of large research programs are also evidence that the need for prediction identified by the early empirical limnologists has in fact diffused widely through the aquatic sciences. The challenge, of course, is to deliver on these statements and actually provide predictions. One way the cynical and the aspiring should judge large research programs retrospectively is to determine not only how the programs contributed to scientific advances, but also the quality of predictions that were actually produced.

Types of prediction

The empirical limnology school presented prediction in the form of regression models (Peters 1986, 1991). The approach was largely based on comparisons among aquatic systems. This gave the resulting models generality and established patterns against which to evaluate other systems.

While these models are useful and their predictions easily understood, the approach has shortcomings. First, regressions as used in this context predict only the annual or seasonal means for a given system based on data from multiple systems, and the resulting predictions are usually imprecise. An example is a study that I conducted of zooplankton biomass (Pace 1986). A regression model summarized the relationship between mean summer zooplankton biomass and lake total phosphorus (TP) explaining 86% of the variation. Confidence limits, however, were wide, and the model provides a poor basis for predicting the biomass of zooplankton in an individual lake. For example, assuming a typical lake in the data set with a TP of 12 $mg \cdot m^{-3}$, predicted mean zooplankton biomass within the 95% confidence interval varies roughly threefold. Such models are not very useful, either for drawing inference in specific cases, for modeling, or for managing individual systems. These shortcomings and criticisms of regression predictions from comparative studies have been previously noted (Shapiro 1979; Carpenter and Kitchell 1988; Carpenter et al. 1991) as have statistical problems associated with regression methodology (McArdle 1987; Prairie et al. 1995).

Nevertheless, the shortcomings of regressions are not a reason to dismiss the empirical approach. Comparative analyses provide a means of evaluating patterns. For example, in my study noted above, one question concerned whether residual variation in relationships between phosphorus and chlorophyll concentrations in lakes could be partly explained by zooplankton biomass or community size structure. Comparative analysis revealed that zooplankton biomass did not explain residual variation in phosphorus–chlorophyll relationships, but the relative dominance of larger zooplankton was associated with lower chlorophyll per unit TP (Pace 1984). The results of this study illustrate how comparative studies can be used to evaluate and test aspects of general patterns. The effects of grazers on primary production in aquatic systems have become a central research topic as evidenced by further comparative work (Carpenter et al. 1991; Quirós 1998) as well as experimental and theoretical studies (Carpenter and Kitchell 1993; Scheffer 1998).

Comparison of systems remains a valuable and now accepted means of evaluating and debating generalizations. Comparative papers are often well cited. For example, in the highly experimental field of aquatic microbial ecology, papers on methods, concepts, and comparisons were among the 10 most cited (Duarte et al. 1997). The contributions of comparative studies can also stimulate debate and raise new questions. Current discussions regarding the relative rates of primary production and respiration in the ocean are largely based on comparisons of data from many studies, the resulting statistical models, and interpretations of both the data and models (Del Giorgio et al. 1997; Duarte and Agusti 1998; Williams 1998).

A limitation of comparative studies is that they usually focus on prediction of means at the scale of a system with little consideration of temporal dynamics or spatial variation. Yet these latter features are critical in structuring ecological systems and determining variation. Other types of predictions for other scales of resolution are often needed, and a variety of models suitable for making these predictions are available. This paper cannot consider all the possibilities or review the various statistical and simulation approaches to prediction. Some of the situations requiring different types of predictions can be noted, and these naturally suggest possible models and approaches. When considering aquatic systems, we can imagine that predictions are needed for the future state or dynamics of a system (temporal predictions), for a new place (spatial predictions), for a new circumstance (altered systems), as well as for general cases. These problems are typically approached both formally and informally with verbal and graphical models. These models do not provide estimates of uncertainty, and so, analytical, statistical, and simulation modeling methods are needed. Regression models are most suitable for some predictions in the last category (general case). Other statistical approaches such as time series analysis, geostatistics, and Bayesian methods are useful for predictions about time, place, and altered state (e.g., consequences of a management action), respectively. Analytical and simulation models can also serve as predictive tools and can be applied to many problems (e.g., space, time, altered state). Large-scale simulations are the tools envisioned by the global marine programs noted above (GLOBEC, JGOFS) for making predictions about the ocean under scenarios of changing climate. Sensitivity analysis and simulations of varying scenarios can be used to assess uncertainty with these models.

Examples of prediction

Some examples are useful to portray the application of predictive models to problems not suitable for standard linear regression. Dynamic interactions are a central feature of ecological systems. Dynamic models are useful to project present and future changes of ecological systems. There are several approaches to dynamic models, including mechanistically oriented simulations and statistically oriented methods of time series analysis. A time series model of rotifer dynamics illustrates the approach and the forecasts (predictions) that such models can make. Figure 1*a* presents rotifer abundance before and after the invasion of the zebra mussel (*Dreissena polymorpha*) in the Hudson River estuary, New York, U.S.A. (Pace et al. 1998). Zebra mussels invaded the Hudson in the early 1990s and became abundant in 1992. At that time, there was a precipitous drop in both phytoplankton and microzooplankton biomass that has subsequently been sustained (Strayer et al. 1999). A time series model based on data for 1986–1995 captures this shift by including a term for the presence or absence of zebra mussels (Fig. 1*a*).

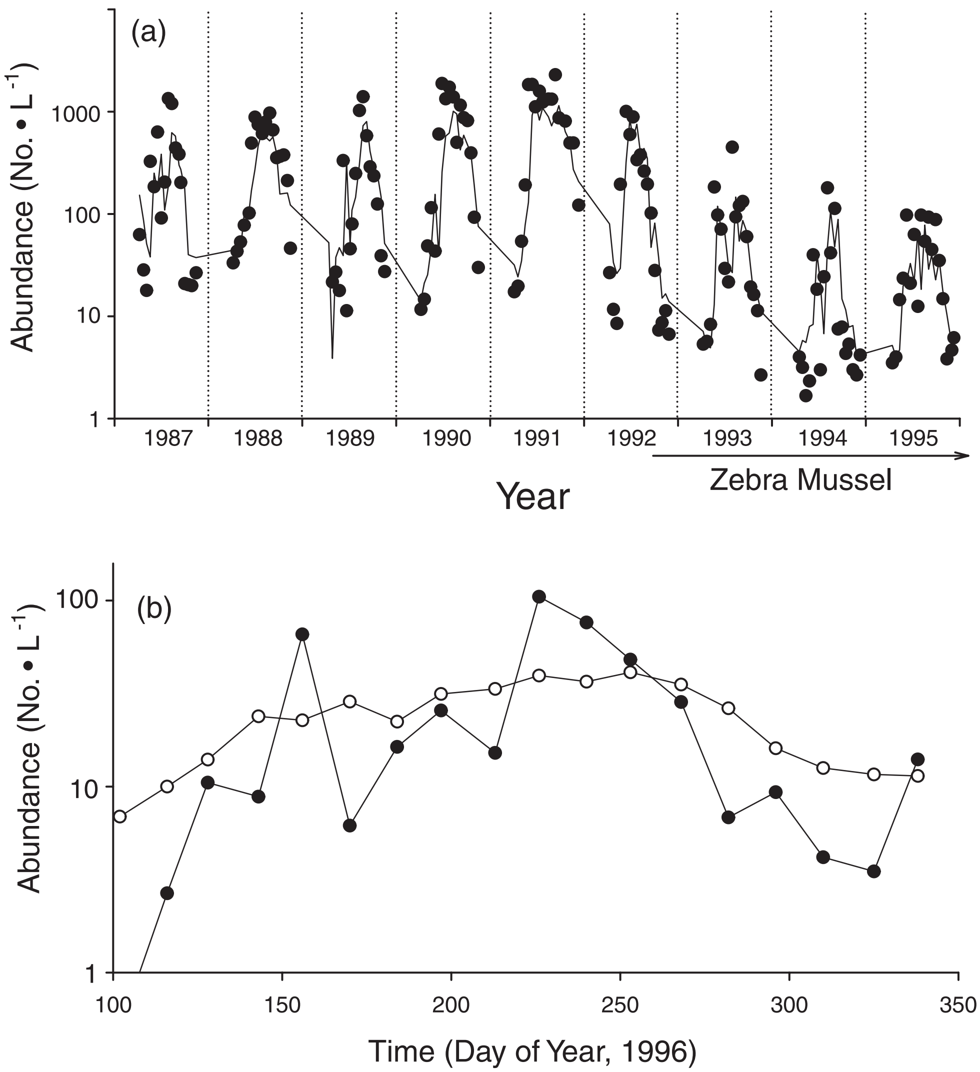
The model can be tested by comparing forecasts with data from 1996 (Fig. 1*b*). Predictions from the model are well correlated with observations (r = 0.81, p = 0.004). The model, however, underrepresents the dynamics of the rotifer community, missing both maxima and minima in the time series (Fig. 1*b*), suggesting that additional parameters are needed and that measurement error along with natural population variability increases the overall variation in the data relative to that predicted by the model. Nevertheless, the model does represent the principal features of rotifer dynamics and further predicts a rapid recovery (not shown) were zebra mussels to decline.

The time series model is limited in that it contains no specific mechanism for the relationship between rotifer abundance and zebra mussels. Two possible mechanisms causing the decline were reduction in rotifer food and (or) direct consumption of rotifers by zebra mussels (Pace et al. 1998), but the model is purely empirical and does not distinguish among these likely causes or other less plausible mechanisms (e.g., an effect of zebra mussels on other species that in turn affect rotifer abundance or a disease introduced by zebra mussels that impacts rotifers). Experiments could distinguish among some of these mechanisms, and an alternative model could incorporate mechanisms but would require increased knowledge of the system and the estimation of additional parameters.

While not presented in Fig. 1*b*, the rotifer forecasts have associated confidence intervals. Predictions as probabilities are particularly useful in the context of management problems. In many aquatic systems, harmful algal blooms are a serious concern, and reductions in nutrient loading are often a proposed management action. How can the benefits of reductions or dangers of excess loading best be stated given the inherent uncertainties? Stow et al. (1997) illustrated an approach using a 19-year record of cyanobacterial blooms in Lake Mendota, Wisconsin, U.S.A. A logistic regression that includes observation error in the independent (spring TP) and dependent variables (mean summer biomass of cyanobacteria) provides a model for the data (Fig. 2*a*). This model can then be used to state specific probabilities of a high-biomass or bloom year for a given spring TP (Fig. 2*b*). For example, if loading is relatively low such that spring TP is 0.08 $mg \cdot L^{-1}$, the probability of mean summer cyanobacterial biomass exceeding a bloom threshold (5 $\mu L \cdot L^{-1}$) is only about 5%. If spring TP is 0.12 $mg \cdot L^{-1}$, the probability increases dramatically to greater than 60%. Hence, management efforts to lower spring TP to a threshold below 0.08 $mg \cdot L^{-1}$ would dramatically lower the risk of blooms.

A second example of probabilistic predictions is a decision table for a fishery modified from Hilborn et al. (1993). The average yield over a 5-year period is projected based on a stock–recruitment model. Three states of the population are considered along with the probability associated with each stock biomass for two harvesting scenarios (Table 1). The example makes it clear that the variable outcomes of management depend on both harvesting policy and the uncertain state of the population. Harvesting at a 200-kt quota in the first year and at 26% of the stock in subsequent years could result in either the highest or the lowest yield depending on the true biomass of the population (Table 1). While this example is somewhat simplified relative to an actual fish population management problem (Hilborn et al. 1993), the key point is that the various yields represent predictions of a series of alternative states. These predictions form a basis

Fig. 1. (*a*) Time series model (line) and measurements (circles) of rotifer abundance in the Hudson River. Zebra mussels invaded the Hudson, resulting in a significant decline of rotifers beginning in 1992. (*b*) Forecasts from the model (open circles) are compared with data (solid circles) for the year 1996. The model and data for 1987–1995 are from Pace et al. (1998), with forecasts compared with previously unpublished data. Note the log scale on the ordinate.



for summarizing and presenting information to decision-makers, and they make explicit the uncertainties and risk.

The examples that I have presented are necessarily simple because of limited space to convey details. Thus, I have not specifically described either a simple general model (e.g., stock–recruitment, chemical mass balance) or a more complex simulation model (e.g., nutrient cycling, energy flow, population dynamics) because these are more difficult to explain. A variety of models of modest to more substantial complexity are useful for making predictions. Such models are used in forecasting to evaluate scenarios like climate change. This type of forecasting has been (e.g., De Stasio et al. 1996; Stefan et al. 1996) and will likely continue to be an important research topic. One goal should be to challenge predictions from these forecasts as much as possible with data in order to assess the quality of projections and to give credibility to the modeling. This comparison can be accomplished by evaluating models with data from paleo- and contemporary studies not used in the formulation of the original model. This form of prediction and comparison with data needs to become a standard by which models are presented and their contribution evaluated.

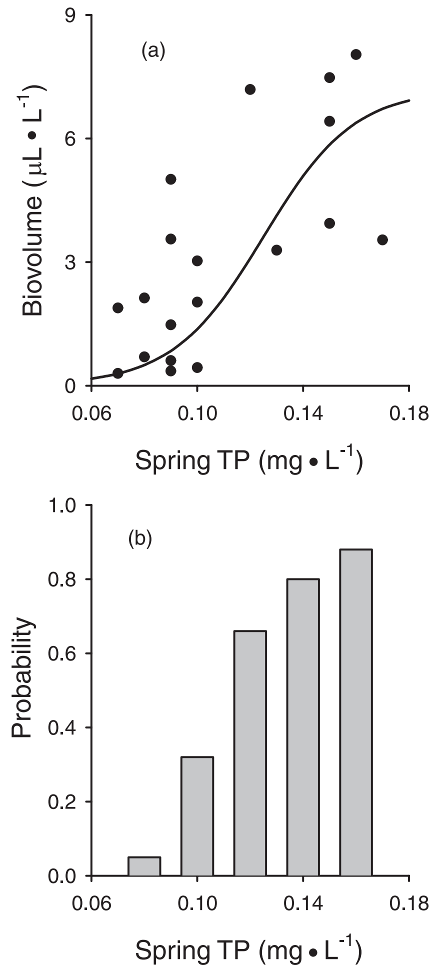
Table 1. Sample decision table showing the expected yield of a fishery over 5 years for three states of the stock and two harvest rates.

	Stock biomass (probability)		
Policy	0.9 Mt (0.57)	1.5 Mt (0.40)	2.1 Mt (0.03)
Constant 150-kt quota	136	150	150
200-kt quota (year 1)	122	154	166

Note: Probabilities for the stock biomass are indicated in parentheses. Quotas are constant for the first policy (150-kt quota) or at a percent harvest rate (26%) of the stock after a set quota in year 1. The example is modified from table 2 of Hilborn et al. (1993).

In the context of model–data interaction, biological oceanographers are adopting data assimilation methods from meteorology and physical oceanography (e.g., Lawson et al.

Fig. 2. (*a*) Relationship between spring TP and cyanobacterial biovolume in Lake Mendota, Wisconsin, based on annual means from 19 years of observations. (*b*) Probabilities for cyanobacteria exceeding a bloom threshold ($5\,\mu L \cdot L^{-1}$) as a function of spring TP based on the model presented in Fig. 2*a*. The model and data are from Stow et al. (1997).



1996; McGillicuddy et al. 1998; Spitz et al. 1998). Essentially, this approach involves updating forecasts derived from models. Data are iteratively "assimilated" into the model and used to improve the time-evolving simulation. This approach is especially germane to complex, dynamic situations where long-range forecasts are unlikely to be accurate. Weather forecasting that tracks the development and progression of storms provides a familiar example. Advances in data acquisition and processing make the use of assimilation methods feasible in some cases for coupled physical–biological models.

Data assimilation methods might be particularly useful for event-related forecasts of critical phenomena such as harmful algal blooms (Franks 1997). In this case, combinations of remote sensing of plant pigments in conjunction with hydrodynamic models and possibly in situ measurements (e.g., temperature, currents) would provide the basis for models to forecast the formation, evolution, and fate of blooms. This vision of forecasting might be applicable to many applied situations where variable ecological processes affect endpoints of human interest and management concern.

Interaction of prediction with mechanism and understanding

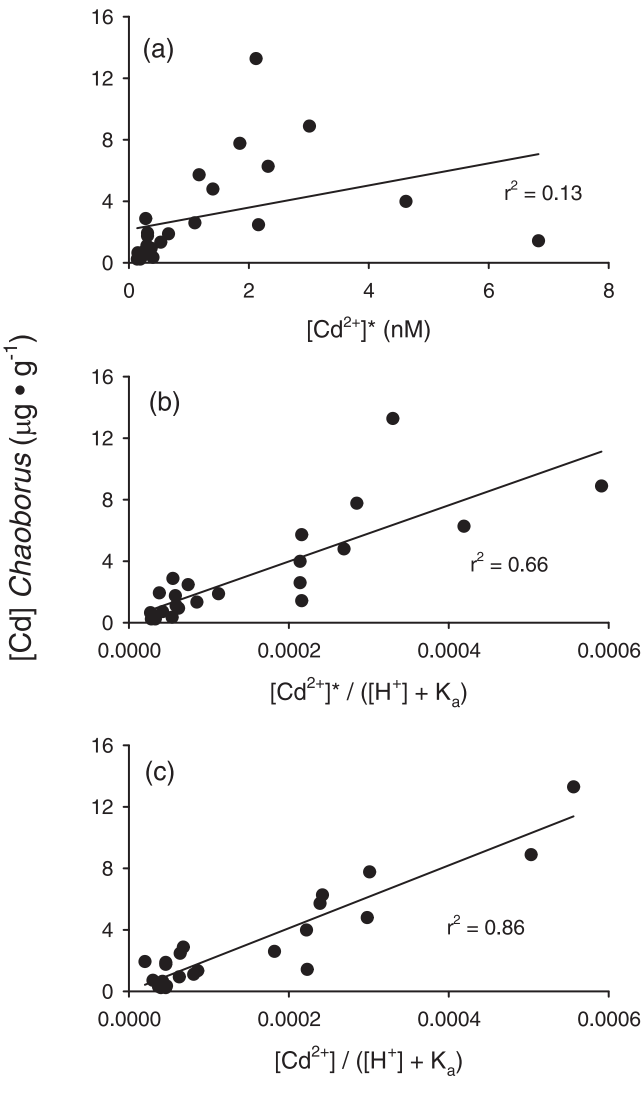
One criticism of predictive approaches is that predictions can be based on poor understanding and still yield statistically significant correlations. For example, a good prediction of the number of priests in North American cities could probably be obtained by counting the number of painters in phonebooks. Analyses of ecological systems suffer from this problem, as many of the independent variables are correlated (Downing 1991). Further, in highly interactive aquatic systems, so-called dependent variables may not be truly dependent but feed back on and affect the state of independent variables. These problems with prediction are, however, correctable when there is an appropriate interaction between scientific understanding and prediction.

All predictions are subject to refutation — this is a real strength. Hence, predictions based on poor principles such as my priest–painter example can be rooted out by appropriate testing and refinement. More importantly, prediction can and should interact profitably with mechanistic understanding. This interaction should improve prediction while keeping the mechanistic science aimed squarely at the problem. Coupling predictive goals with mechanistic studies helps to avoid narrow inquiry with little or no improvement in global understanding. Thus, prediction and understanding are interactive.

Better understanding can lead to better models facilitating better predictions, but this relationship is not absolute. We cannot define all the mechanisms of aquatic systems and hope to build models based on a complete understanding of all parts. Mechanistic research may not contribute to prediction, even though science is often pursued as if the only way to build valid predictions was through detailed studies (Walters 1998). Experience suggests instead that key mechanisms need to be collected into relatively condensed models. This is where prediction and understanding come together. Condensed models work because they capture critical processes that drive aquatic systems. The challenge remains to integrate understanding of specific mechanisms at various spatial and temporal scales in order to derive effective and reasonable models for relevant problems. This line of thinking raises questions concerning limits to prediction. Will successful predictions inevitably be mostly limited to short time and system-specific scales or can we achieve longer term and among-system predictions? At present, I do not think that this question can be answered. In the future, organizing and assessing predictive ability over various scales will likely be an important task.

An example of condensed models enhanced by understanding is illustrated by a study of metal concentrations in the common aquatic dipteran larvae *Chaoborus punctipennis* (Hare and Tessier 1996). In this study, concentrations of Cd were measured in water and in larvae for 23 lakes. Predictions of the concentration of Cd in larvae are poor when the free ion concentration of Cd (i.e., Cd^{2+}) is used (Fig. 3*a*). Predictions are improved when the competition between H^+ and Cd for biological uptake sites is taken into account (Fig. 3*b*). The prediction is further improved when the availability of Cd is calculated using models that estimate Cd complexation by dissolved organic matter (Fig. 3*c*). Thus,

Fig. 3. Relationship of Cd concentrations in *Chaoborus punctipennis* to (*a*) free metal ion concentration, (*b*) free metal ion concentration normalized for competition between Cd and H^+ for biological uptake sites where K_a is the equilibrium constant of acid relative to uptake sites, (*c*) and as in Fig. 3*b* but where Cd concentration is also corrected for complexation with dissolved organic matter. Data and relationships are from Hare and Tessier (1996).



understanding the chemical interactions affecting the availability and uptake of Cd substantially improves predictions and leads to a relatively condensed model for that purpose (Hare and Tessier 1996). Predictions from this model have been extended and applied to other species of *Chaoborus* over a wide range of environmental conditions (Hare and Tessier 1998). The model works well because *Chaoborus* do not appear to regulate Cd, and hence body burdens reflect environmental conditions, and because the model derives from first principles of chemical activity and availability (Hare and Tessier 1998). This example illustrates the interaction of prediction and understanding. The goal of science is understanding, which is defined by Pickett et al. (1994) as "an objectively determined, empirical match between some set of confirmable, observable phenomena in the natural world and a conceptual construct." Prediction, therefore, is not an end but a means to better understanding.

While purely statistical models such as those promulgated by the empirical limnologists have a place in building scientific understanding, they are at best precursors for models derived from more fundamental principles. Livingstone and Imboden (1996) described this distinction well for models of lake hypolimnetic oxygen depletion. In their terms, "inductive models" are purely empirical, statistical fits between independent and dependent variables, while "deductive models" utilize general principles to make predictions for specific cases. The latter models fit the formal job ascribed for predictions derived from theory. In the case of lake oxygen models, inductive or empirical models employ sets of predictor variables to describe oxygen depletion. Deductive models utilize general functions of volumetric oxygen consumption (associated with the water) and areal oxygen consumption (associated with sediments) to describe oxygen depletion. These deductive models have the advantage of being easily understood and may provide better predictions where conditions are novel (e.g., climate change) (Livingstone and Imboden 1996).

Interestingly, it is typically the case that so-called "deductive models" are often based partly on purely empirical information, while "inductive models" are closely connected to general principles. For example, in the case of oxygen models, the volumetric rate of oxygen consumption in the deductive model of Livingstone and Imboden (1996) is a fixed value derived from widespread observations. This handy empiricism works well but begs the question why or if all lakes share a rather similar value of microbial oxygen consumption in the hypolimnion. The inductive models of the empirical limnologists are not derived simply from convenient correlations without conceptual content. The most enduring of these models such as those that describe lake eutrophication (Dillon and Rigler 1974; Vollenweider 1976) are based on two general concepts. The first is elemental mass balance and description of that balance by a continuously stirred reactor model. The second general concept is that nutrients may limit primary and secondary production in ecosystems. Both concepts are critical foundations for the success of the subsequent empirical descriptors known as nutrient loading models (Smith 1998).

Livingstone and Imboden (1996) were correct to call for the formulation of models in more fundamental terms wherever possible. This facilitates better application and more widespread possibilities for prediction. I view their distinction of inductive and deductive models as useful, but there is a need to recognize the two types of models as endpoints of a continuum. The implications for prediction, however, are important. Predictions can be derived from purely statistical models but may be more robust and general when formulated in an analytical framework, as Livingstone and Imboden (1996) argued. These latter, more analytical models need not be purely deterministic. Analytical models often tend to present single answers as graphs and appear attractive relative to purely empirical models with their large, conspicuous errors. Uncertainty, however, resides in the underlying empiricisms used to parameterize analytical models, and these uncertainties can be profitably projected as in the case of the fishery decision table described above (Table 1).

Perspective

Given the goal of science as understanding, why accept prediction as an important standard and objective for aquatic science? The traditional reason is that testing of predictions is one means to judge the adequacy of understanding. Given the complexity of aquatic systems, it is easy to overestimate understanding, and predictions allow us to confront our general models and assess their adequacy against reality (i.e., data). There are several additional reasons to value prediction. First, there is little doubt that human-driven changes in aquatic systems will require increased efforts in scientific analysis and predictive management in the future. Second, predictive approaches can be guides for research programs helping to keep attention focused on ultimate objectives and not small problems. Third, if aquatic scientists take the mandate for prediction seriously, there should be sufficient dissatisfaction with our current abilities to foster new and creative approaches.

Predictions are clearly needed for practical reasons. This can easily be understood by considering the problems of water quality and fisheries that dominate the applied concerns of aquatic scientists. Globally, water expropriation for human use is estimated at 54% of accessible runoff (Postel et al. 1996). Such heavy usage implies shortfalls of high-quality water, at least in some areas of the globe. Curiously, even water-rich regions of the world such as the boreal portion of Canada have water quality problems driven by climate change, acid deposition, and ultraviolet exposure, leading to pessimism about the future condition of freshwater ecosystems (Schindler 1998). Hence, predictions of the consequences for water resources of various anthropogenic uses and impacts will remain an important task for aquatic sciences in the foreseeable future (Likens 1992; Postel and Carpenter 1997; Gleick 1998).

A similar list of concerns applies to fisheries where global stocks are heavily exploited and capture fisheries appear to be at a maximum near 100 Mt·year^{-1} (Botsford et al. 1997; Food and Agriculture Organization (FAO) 1998). Fishing interacts with numerous other features of the environment and economy to create enormous variation in fish stocks. While some of the most creative approaches to science and management have evolved from the challenge of managing variable fish stocks, the problems remain difficult. Failures in fishery management have been spectacular, as well documented in the case of Atlantic cod (Walters and Maguire 1996; Myers et al. 1997). While the underlying sources of these failures may reflect political and management problems as much as scientific limitations (e.g., Hutchings et al. 1997), there can be no doubt about the need for better and more predictive science.

Better predictions should have positive consequences for our ability to manage the environment. By forecasting the consequences of current human activity, it may be possible to forestall some of the worst environmental degradation that the future appears to hold. This is the hope of such scientific efforts as the Intergovernmental Panel on Climate Change where current scientific information is used to evaluate the consequences of global warming (Watson et al. 1996). At more local and regional scales, aquatic ecologists will also need to make explicit the consequences of human activity. If connections among society, economy, and ecological systems can be made plain, strong public sentiments for environmental protection should promote better ecosystem management (Folke 1998).

Prediction should also play an important role in research programs. Predictive models reveal important variables, and these can illuminate underlying causal interactions and contribute to theory. Conceptual constructs often arise from attempts to explain empirical regularities. Theories are also confirmed, refined, or discarded based on tests of their predictions. Thus, prediction has a fundamental role in both the establishment and the evaluation of theory.

Predictive objectives for research may also help to discriminate among possible topics for investigation, thereby aiding efficient progress. A predictive orientation keeps research efforts focused on central questions.

Some would argue against the emphasis that I have placed on prediction and argue for an increased emphasis on the identification and study of mechanisms. Without detailed understanding of controlling mechanisms, prediction, in this view, is a false goal. One reviewer of an earlier version of this paper commented that causal understanding is needed “before application of predictive modeling.” I agree that mechanistic understanding is important but think that placing a high value on prediction will help the field move more efficiently toward identifying key mechanisms from a larger universe of possible mechanisms for a given problem. I do not mean to discount, however, the value of mechanistic research, and I am not advocating strictly statistical modeling approaches to prediction. An important point here for the reader is that when it comes to scientific approaches and ways of promoting progress, there are many strongly held and apparently opposing views. One goal of this paper is to encourage constructive discussion and to argue that prediction is an aspect of aquatic sciences worthy of deeper inquiry by all, regardless of favored approaches.

Progress is often born from dissatisfaction. I have articulated here the need for prediction, yet currently, the ability to make either general or specific predictions about aquatic systems is very limited and imprecise. If prediction is held as a standard, this limitation should cause dissatisfaction and discomfort among aquatic scientists. This state is often a source of creativity. Advances likely will come from those who cannot abide the current situation and seek alternative, novel pathways. Hence, prediction should foster advances.

I foresee great progress ahead in the ability to measure and study aquatic systems. There is no doubt that new technology is rapidly improving the acquisition of data and the transmission of information. New means for probing oceans, estuaries, lakes, rivers, and streams are becoming widely available. Methodological improvements alone will probably drive significant new discoveries about the nature of aquatic systems. But what if the ability to make predictions does not improve concomitantly over the next couple of decades? This goal seems more tenuous at present and, if not realized, will represent a significant failure.

Predictive improvement will not happen as an accidental consequence of scientific advances. Instead, prediction must become a significant standard for the aquatic science of the future. This change would help orient aquatic research toward developing both a sounder foundation and a more usable science.

Acknowledgements

I thank the many colleagues who have helped to shape my thoughts on this topic. They will recognize their input. C. Stow and J. Hare kindly provided data from their original papers for Figs. 2 and 3, respectively. Initial versions of the manuscript were improved by the suggestions of J. Cole, D. Strayer, K. Banse, Y. Prairie, and two anonymous reviewers.

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