TROPHIC DYNAMICS AND ECOSYSTEM INTEGRITY IN THE GREAT LAKES: PAST, PRESENT, AND POSSIBILITIES

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ABSTRACT. The Great Lakes are perhaps unique among large lakes of the world in the degree to which fish population dynamics and water quality resources can be influenced by management at the bottom of the food web or from the top of the food web. Nonmanagement factors known to affect fish quality and quantity and water quality include toxic contaminants, short-term weather events and long-term climatic changes, exotic species invasions, and evolutionary changes of existing species. Because fisheries-based revenues to the Great Lakes region are presently estimated at $2-4 billion per year, it would seem prudent to determine the extent to which management and nonmanagement factors influence fish quality and quantity, as well as water quality. Here we present a comprehensive, yet preliminary, conceptual and mathematical modeling approach that describes causal relationships among fish food web, nutrient cycling, and contaminant processes in the southern basin of Lake Michigan. Our approach identifies weaknesses in the data base that are important to the predictive usefulness of such a model. We suggest that our comprehensive modeling approach will be useful in transforming some surprises into expected events. For instance, the model predicts that contaminant concentrations in salmonines will decrease by nearly 20% if _Bythotrephes_, an exotic carnivorous zooplankton, successfully establishes itself in Lake Michigan.

PREDICTION OF GREAT LAKES ECOSYSTEM DYNAMICS

Our ability to predict Great Lakes ecosystem dynamics with simulation models is proportional to our combined understanding in four subject areas.

1) We must know what is there: biomass of biotic compartments, numbers of individuals and age-class distribution of important fish species, and physical and chemical characteristics of water masses.

2) We must understand basic cause-and-effect linkages among biotic, chemical, and physical factors.

3) We must quantify water movement and rates of material transfer (e.g., carbon, nutrients, contaminants) among biotic and abiotic compartments.

4) We must know system inputs (e.g., solar, nutrient, contaminant, fish-stocking inputs) and outputs (chemical, biological, and hydrological) that affect system behavior.

Yet even with perfect knowledge in these four areas, simulation models cannot be expected to be 100% accurate, since they are abstractions of the system under study. In addition, models are more retrospective than truly predictive (Holling 1987); the predictive power of models is constrained by the domain of existing knowledge. For example, it is unlikely that anyone could have predicted, before the fact, the invasion of the Great Lakes by alewives (Alosa pseudoharengus) or sea lamprey (Petromyzon marinus) and their subsequent impacts on Great Lakes ecosystems. Therefore, not only is the efficacy of predictive models limited by data availability, but in a larger sense, by our inability to predict many system-modifying events that lie ahead. Thus, surprise, as defined by Holling (1987), "...when perceived reality departs qualitatively from expectation [e.g., a model prediction]" should really be of no surprise to anyone who uses or builds models.

Fortunately, significant and truly unpredictable system-modifying events can be spaced widely over time. It is during these time windows that the worth of predictive simulation models can be greatest, especially with regard to understanding and predicting the impacts of management actions on existing ecosystem characteristics. Here, we present work under way on a simulation model that may be useful for understanding Lake Michigan ecosystem dynamics now and in the future. We use the model to test the hypothesis that the effects of ecosystem management actions are not independent. That is, one management action might affect the anticipated outcome of another management action (a potential surprise?). We also use the model to test the hypothesis that successful establishment of the exotic zooplankton species, Bythotrephes, in the Great Lakes will short-circuit contaminant transfer to salmonines. Through these simulation experiments, we suggest that models may help transform some potential Great Lakes surprises into expected events.

Prediction Uncertainty and Its Relationship to Surprise

The usefulness of a model relies on proper matching of models with well-defined questions and proper model parameterization. The first aspect of model reliability is a conceptual issue; the second is a data issue. Without appropriate conceptual grounds, a model will be of little use regardless of how well it is parameterized. On the other hand, the usefulness of a model that is conceptually superior can be limited by parameterization with uncertain information.

Uncertain information can be categorized in four ways:

1) There are data that are variable, but well-defined statistically (e.g., some model coefficients).

2) There are needed data that are presently unknown (e.g., many contaminant loading functions), but can be defined given proper resources.

3) There are events that we know can happen but we are limited in our ability to quantify their magnitude, importance, and probability of occurrence (e.g., toxic chemical spills).

4) There are events that are totally unexpected, but amenable to being understood after the fact (e.g., the successful invasion of the Great Lakes by alewives, sea lamprey, and *Bythotrephes*).

When an exotic species successfully invades a system and alters it, models must be redesigned so that future predictions incorporate new information. It is impossible for modelers to predict something that is not initially accounted for in a model unless the model has the ability to self-evolve (Fontaine 1981).

The first two categories of uncertainty are easily accommodated in modeling projects. Performing sensitivity and uncertainty analyses can help identify the possibility and probability, respectively, of events occurring in an ecological system. These analyses also can help identify research and monitoring that is needed to minimize uncertainty (Bartell et al. 1983). Uncertainty analysis provides a method for predicting the probability that a particular environmental event will occur. By conducting an uncertainty analysis, future events that might be perceived as surprises can now be identified as having some probability of occurrence. Probabilities are calculated by incorporating statistical information about input and parameter variability into simulations. For example, Fontaine and Lesht (1987) used statistical distributions of basin-specific Great Lakes phosphorus inputs and settling rates in a simulation model to forecast the probability of basin-specific phosphorus concentrations. In Lake Michigan, the predicted distribution of steady-state phosphorus concentrations was between 4 and 7 ug/L, given phosphorus load reduction capabilities specified in the United States and Canada 1978 Water Quality Agreement. While the probability of measuring a concentration near the mean value of 5 ug/L was higher than that of measuring an extreme concentration, the probability of encountering a near-extreme value could be predicted and would no longer be viewed as a surprise when it occurred. Thus, if the proper analytical tools are applied to models, they can be used to transform what would normally be perceived as surprises into expected events.

Uncertainty analysis techniques would not have predicted the recent appearance in the Great Lakes of the carnivorous zooplankter Bythotrephes. Successful invasion of such an exotic species can bring about dominance shifts in existing species, altered functional attributes in existing species, or little change at all. At best, the predictive modeler can incorporate new species into a model, as necessary, to speculate upon their impact. For example, Scavia et al. (1988) evaluated the impact of Bythotrephes and predicted that it could cause Lake Michigan's plankton community to revert to a species composition observed during the 1970s.

Dominance shifts in species composition can also occur if a nonbiological perturbation is of sufficient magnitude. For example, a series of unusually severe winters (Eck and Brown 1985), coupled with predation by stocked salmonines (Stewart et al. 1981; Kitchell and Crowder 1986) greatly reduced alewife recruitment and subsequent population size in Lake Michigan. The decline in alewives led to decreased predation on zooplankton populations. This led to a shift in the species composition of both zooplankton and phytoplankton populations, and a decrease in phosphorus concentrations. The occurrence of this type of surprise might have been predicted if models had incorporated statistical information about the variability of winter severity and the relationship of alewife recruitment to it.

Management Actions and Their Relationship to Surprise

Whenever the objectives of Great Lakes ecosystem management are discussed, the following are most often mentioned:

1) Grow large numbers of trophy-sized sport fish.

2) Reduce basin-specific total phosphorus concentrations to those specified in the United States and Canada 1978 Water Quality Agreement.

3) Reduce contaminant concentrations in fish, water, and sediments to safe levels.

4) Obtain enough money and knowledge to predict how to do 1, 2, and 3.

The Great Lakes are perhaps unique among large lakes of the world in the degree to which the fisheries and water quality resources can be influenced by management at the bottom of the food web (nutrient load reductions) or at the top of the food web (fish stocking and harvesting allowances, and sea lamprey control). For example, the bow tie symbols in Fig. 1 represent control points available to managers for influencing the characteristics of major food web pathways and water quality in southern Lake Michigan.

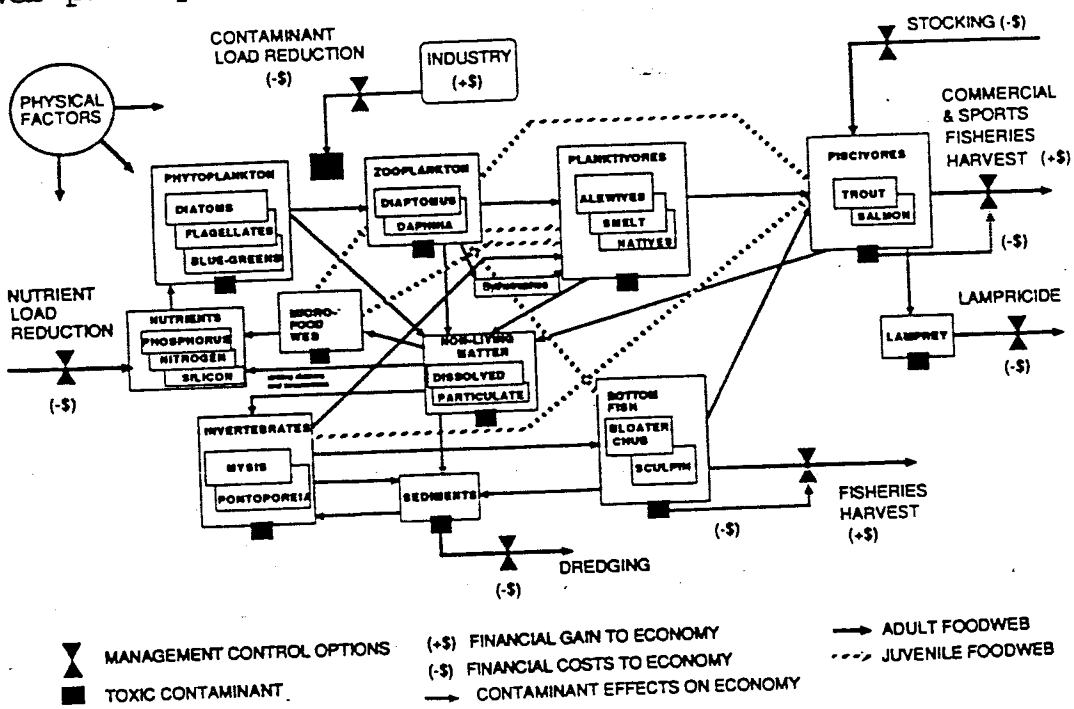

FIG. 1. Conceptual diagram of major food web and contaminant processes in southern Lake Michigan (>100 m depth contour only). Bow tie symbols indicate management options. Note that there is a financial cost associated with each management action. If management actions in the Great Lakes are not independent, then implementing one action will affect the costs of other actions. As cost minimization is a goal of managers, potential management synergisms should be understood and used advantageously.

We suggest that exercising control at these points in attempts to manage the Great Lakes ecosystem may lead to surprises, but only because mental and mathematical models may not be comprehensive enough. A recent example of a Great Lakes surprise is the observation that improved regulation of pollution inputs to the Great Lakes has improved water quality to such an extent that it is now possible for sea lampreys to spawn in areas that they previously could not (Moore and Lychwick 1980, J. Heinrick, U.S. Fish and Wildlife Service). Unfortunately, some of the additional spawning will be difficult to control through conventional means, especially in areas such as the St. Marys River. This raises concerns as to whether lamprey attacks on desirable sport fish will increase. With a more encompassing conceptual approach, perhaps this surprise could have been anticipated.

Management-induced changes in one part of an ecosystem may bring about changes in other parts of the ecosystem. For instance, Scavia et al. (1986, 1988) present a strong case for top-down control of epilimnetic plankton and water-quality dynamics by alewives (whose dynamics are controlled to some extent by stocked salmonines) during the summer in Lake Michigan. Their model strongly indicates that decreased zooplanktivory resulting from the decline in alewives, rather than phosphorus load reductions, was the major cause of the observed water-quality changes. The latter is an example of cascading food-web effects (Carpenter et al. 1985). McQueen et al. (1986), however, suggest that the relative importance of bottom-up versus top-down control will depend on the trophic status of lakes. They found that the impact of top-down effects are quickly attenuated at the top of the food webs of eutrophic lakes. In oligotrophic lakes, however, top-down effects appear to be weakly buffered, and significant impacts are seen at the phytoplankton level. Carpenter and Kitchell (1988), on the other hand, emphasize that the magnitude and duration of top-down pressure on food webs (e.g., from stocked salmonines in the Great Lakes) is of overriding importance compared to nutrient loading effects on food-web structure. Thus, the relative importance of top-down, bottom-up, stochastic events, and management activities on the structure and function of Great Lakes ecosystems deserves clarification.

Surprises may result when the use of one management tool unexpectedly affects the anticipated outcome of another management tool; effects of separate management actions may not be independent. Examples of the nonindependence of management actions abound in many fields. For instance, in the medical field it is well known that certain pharmaceuticals will enhance or negate the intended purpose of other pharmaceuticals. Other examples of the interdependence of management activities are reported by Gall (1986).

A PRELIMINARY MODEL OF SOUTHERN LAKE MICHIGAN ECOSYSTEM DYNAMICS

Goals

The conceptual framework represents a working hypothesis of how ecological and related economic factors are linked in southern Lake Michigan (Fig. 1). Shown are the major ecological, contaminant fate, and management characteristics of the lake. Using this conceptual framework and a simulation model based upon it we initiated a program to accomplish the following:

1) Improve our understanding of the underlying causal mechanisms of observed fish-community dynamics and year-to-year variability in southern Lake Michigan.

2) Understand the relative importance of benthic and pelagic food-web pathways to the numbers and biomass of economically important fisheries and their bioaccumulation of contaminants.

3) Identify data inadequacies and needs for field and laboratory experiments through the process of attaining objectives 1 and 2, above.

4) Determine if (and to what extent) fisheries, phosphorus, and contaminant management strategies affect (enhance or negate) each other's success.

5) Identify cost-effective methods for attaining fisheries, contaminant, and phosphorus management goals.

6) Determine which fisheries management techniques can produce results (e.g., increased yield or recruitment) that are distinguishable from expected variability of the natural population.

Model Description, Assumptions, and Limitations

Our model builds on that developed by Scavia et al. (1988), with the exception that aggregated alewife and aggregated salmonine populations were included. A bioenergetics approach was used to model the dynamics of these fish populations, using parameters derived from Stewart and Binkowski (1986) and Stewart et al. (1983). Because alewife and salmonine populations are treated as aggregates, age-class specific stocking and harvesting strategies cannot be evaluated yet. Bloater chub (*Coregonus hoyi*) and *Mysis* are also included in the model, but at this time are represented as constant biomass storages available for consumption by salmonines and alewives, respectively. Dynamic representation of bloaters and *Mysis* awaits development of bioenergetic models for them and improved definition of their role in the food web. Accomplishment of the latter should improve our understanding of the dynamics of material fluxes between the pelagic and benthic zones and the importance of these materials to benthic food webs.

Pathways describing the behavior of a persistent contaminant were overlaid on the ecological model and include processes such as uptake, depuration, trophic level transfers through consumption, and sorption reactions with particles. Because ecological processes that affect particle formation are usually ignored in toxicant fate models, this coupled ecosystem-contaminant dynamics model can be used to determine the importance of ecological processes to the prediction of contaminant dynamics. Coupled ecosystem-contaminant pathways that remain to be defined include contaminant dynamics of benthicinvertebrates and bottom fish and resuspension and biological-chemical dynamics of settled, particle-associated contaminants.

Simulation Conditions

The model of Scavia et al. (1988), with the modifications noted above, was initialized with mid-1970s nutrient and plankton conditions. Because estimates of Great Lakes fish biomass range widely, a matrix of possible mid-1970s alewife and salmonine biomass values (both lakewide and individual weights) was initially tested in the model to determine a combination that would reproduce plankton and nutrient dynamics that have been observed at the >100 m depth contour. The fish biomass estimates that produced the best match of model and data (according to criteria specified in Scavia et al. (1988) were 15,000 metric tons (MT) and 10,000 MT of lakewide alewife and salmonine biomass, respectively. Average initial wet weights of alewives and salmonine that yielded the most realistic results were 7 g and 454 g, respectively. Therefore, these lakewide and individual fish biomass values were used in all subsequent simulation experiments.

To test for potential management- and nonmanagement-induced surprises, the model was run with a variety of phosphorus loading, lamprey control, and *Bythotrephes* initial conditions. In all simulations a persistent, nondegrading, highly partitioned (k_{oc} = 2 X 10^5 lw kg. org. carbon (C)$^{-1}$) contaminant was loaded to a contaminant-free system at a hypothetical, steady rate of 1 unit per cubic meter per day to determine how differing conditions would affect contaminant concentrations in salmonines. Phosphorus (P) was added at three levels: 0.0055, 0.0035, 0.0015 µg P per liter per day to simulate the effects of relaxed, present, or more-stringent phosphorus load regulations. Lamprey control was set as either present or absent by increasing salmonine mortality by an additional 12.7% per day in the latter case. Bythotrephes was programmed as either initially present (0.005 mg carbon per liter) or absent. If present, it was programmed to either strongly prefer Daphnia over Diaptomous or to show equal preference for both prey. The former case is believed to be the most plausible. Bythotrephes was assumed to be a preferred prey item for alewife. All told, 18 different simulation conditions were evaluated and together represent a very limited sensitivity analysis of the model. An uncertainty analysis of the model has not been performed yet.

RESULTS AND DISCUSSION

Under all simulation conditions, predation pressure on alewives by salmonines caused alewife biomass to decline from an initial 15,000 MT to a steady-state value of about 3,000 MT. These results apply only to fish dynamics at the >100 m depth contour. Before declining, alewife biomass increased 6% and 7% from their initial biomass, with and without existing lamprey control, respectively. The absence of lamprey control led to decreased salmonine biomass and less predation pressure on alewives. Declines in alewife biomass brought about changes in phytoplankton and zooplankton composition, and dissolved phosphorus concentrations, (Figs. 3-7; Scavia et al. 1988). At the time that alewife biomass began to decline, lakewide salmonine biomass had nearly doubled to about 18 MT. After that point, salmonine biomass decreased, leveled, or increased in direct relationship to the preference factor setting for salmonines feeding on bloater chub. Determination of this preference factor is, therefore, central to our ability to extend predictions of salmonine biomass and contaminant concentrations further. If the major percentage of salmonine diets shift from alewife to other species and if salmonine feeding rates remain the same as before the decline in alewives, it is these other species that will primarily dictate future salmonine biomass and contaminant dynamics. Since there is considerable uncertainty about how salmonines would adapt to low alewife availability, the results reported here correspond to the point in time that salmonines are at their peak biomass, just before the decline in alewives.

Effects of Bythotrephes

The model was used to explore the effect of the presence (two feeding preference scenarios) or absence of the exotic species Bythotrephes on salmonine contaminant concentration. The most striking finding was that the presence of Bythotrephes brought about reductions in salmonine contaminant concentrations (Fig. 2). Greatest reductions (17%) were predicted when Bythotrephes preferentially fed on Daphnia over Diaptomous, the scenario thought to be most likely. If Bythotrephes preferred Daphnia and Diaptomous equally, predicted reductions in salmonine contaminant concentrations were about 8%. These predicted changes in salmonine contaminant concentration represent a field-testable hypothesis. In addition, the predictions transform what could have been viewed as a surprise into an expected event.

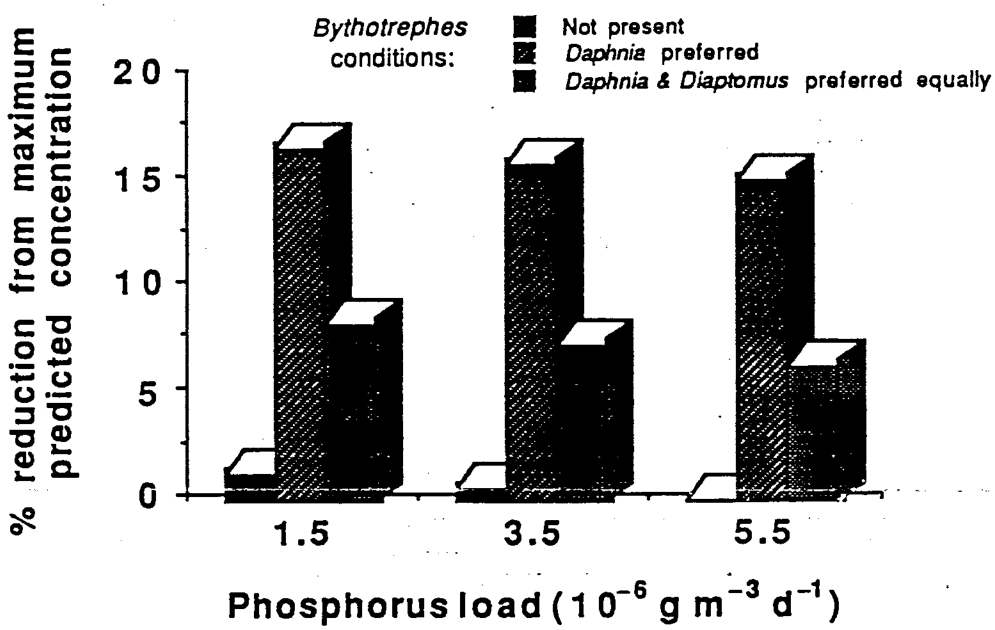

FIG. 2. Predicted differences in salmonine contaminant concentrations under three phosphorus loads and three Bythotrephes conditions. Note that the ordinate expresses the percent of maximum simulated contaminant concentration.

Why did salmonine contaminant concentrations decrease when Bythotrephes were present in the model? The model suggests that Bythotrephes will short-circuit the transfer of contaminants up the food web, primarily by affecting Daphnia dynamics. Changes in Daphnia biomass dynamics, in turn, cascade down the food web and affect algal and particle dynamics. All of these changes in food-web dynamics affect the amount of contaminant predicted to reach the alewife. Bythotrephes directly competes with alewives for Daphnia biomass and thereby reduces alewife consumption of Daphnia-associated contaminants. Although alewife consume Bythotrephes, the alewife do not receive the same contaminant flux from them that they would have from direct consumption of Daphnia. This is because Bythotrephes do not assimilate all of the Daphnia's biomass and associated contaminants; the unassimilated portion is shunted to the particulate organic carbon pool.

A secondary effect of Bythotrephes on ecosystem contaminant dynamics is suggested by the model. In simulations with Bythotrephes, Daphnia biomass is suppressed because total predation pressure on Daphnia increases due to the presence of two predators instead of one. The decrease in Daphnia biomass leads to an increase in the biomass of their preferred food items, green and blue-green algae. As a result, the flux of sinking algal biomass and associated contaminants to hypolimnetic sediments increases. This model prediction represents another hypothesis that could be field-tested. Unfortunately, the model is not at the stage of development where the subsequent fate of the increased contaminant flux to the sediments can be predicted. It is likely that most of this increased contaminant flux would end up in benthic invertebrates and bottom-feeding fish. If so, it should eventually become available to salmonines if they shift their diets from alewife to bloaters as alewives decline.

Effects of Management Actions

We hypothesized that the effects of individual or multiple management actions might lead to surprises. This hypothesis was tested by determining the effects of three phosphorus load scenarios and the presence or absence of lamprey control on salmonine contaminant concentrations. The model predicted that control of phosphorus loads and lamprey would have little effect on salmonine contaminant concentrations. Only a 1% change in salmonine contaminant concentration was predicted for sizable increases or decreases from present phosphorus loads (Fig. 2). Eliminating lamprey control led to a 5% decrease in peak salmonine biomass and a small increase (<1%) in salmonine contaminant concentrations. Therefore, over the period from initial to peak salmonine biomass, simulations indicate that management-induced surprises will be minimal. However, preliminary simulations of all ecosystem state variables to steady state show that management-induced surprises can be quite large. Unfortunately, steady-state solutions to the model are extremely speculative because of insufficient information on coupled benthic-pelagic food web and contaminant dynamics.

LOOKING FORWARD

Refinement and improvement of this comprehensive model for southern Lake Michigan contaminant and ecosystem dynamics will continue. At the present stage in model development, however, simulation experiments suggest that the successful establishment of an exotic zooplankton species might provide more surprises than the effects of one management activity on another. It cannot be emphasized enough, however, that the model is in an early stage of development; present results may change as the model is improved. By using this comprehensive modeling approach, we may transform some potential surprises into anticipated events. The key to facilitating the transformation is to ask well-focused questions and to build models that recognize and incorporate the fact that "surprise emerges from coupling of human time and spatial scales with smaller and larger ones in nature" (Holling 1987).

Data Needs and Model Uncertainty

Future work should address the data inadequacies that limit the predictive capability of the model. Better estimates of fish biomass across age-class distributions are needed, and better understanding of coupled benthic-pelagic carbon flow is required. Improved understanding is also needed regarding the role of lipids in food web bioenergetics and contaminant transfer from prey to predator. In addition to these data needs, future modeling and monitoring work should address the following question: "Given present conditions, what is the expected variability of Great Lakes water quality constituents (e.g., phosphorus, PCBs) and the biomass, quantity, and characteristics of Great Lakes organisms?" Without knowing this, it will be difficult to say whether a surprise has actually happened since the range of expected behavior is unknown. As demonstrated by Fontaine and Lesht (1987) and Bartell et al. (1983), probabilistic models can help define expected behavior ranges of ecological variables and their dynamics. Given the ability to define the range of expected ecological behavior, the question that should then be asked by ecosystem managers is: "What management techniques will produce results that can be distinguished from the expected variability of the system?" In other words, why manage if an effect cannot be demonstrated at some point?

Economic-Environmental Trade-Offs

Politicians, managers, scientists, and end users of Great Lakes resources undoubtedly support the fish and water quality management objectives listed earlier. However, the priority assigned to each objective may vary depending on the user's perspective. This results in a classic multi-objective optimization modeling problem. It is a multi-objective optimization problem because more than one goal is desired, but all goals more or less compete for money from a common, limited environmental funding base. It is also a modeling problem since predictions are desired. Identifying a solution that is acceptable to all interested parties is complicated by the fact that the optimization (whether mathematically or intuitively based) has to be performed with uncertain information regarding the future of short-term weather events, long-term climatic change, exotic species invasions, evolutionary changes of existing species, politics, management activities, and toxic contaminant spills. An approach that combines results from comprehensive environmental models, such as discussed here, with uncertainty analysis and "surrogate worth tradeoff" techniques (Haimes 1977) is needed by decision-makers to holistically understand, manage, and anticipate surprises in the Great Lakes.

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NOTES

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