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Great Lakes Modeling Summit: Focus on Lake Erie

Council of Great Lakes Research Managers. Modeling Summit Planning Committee

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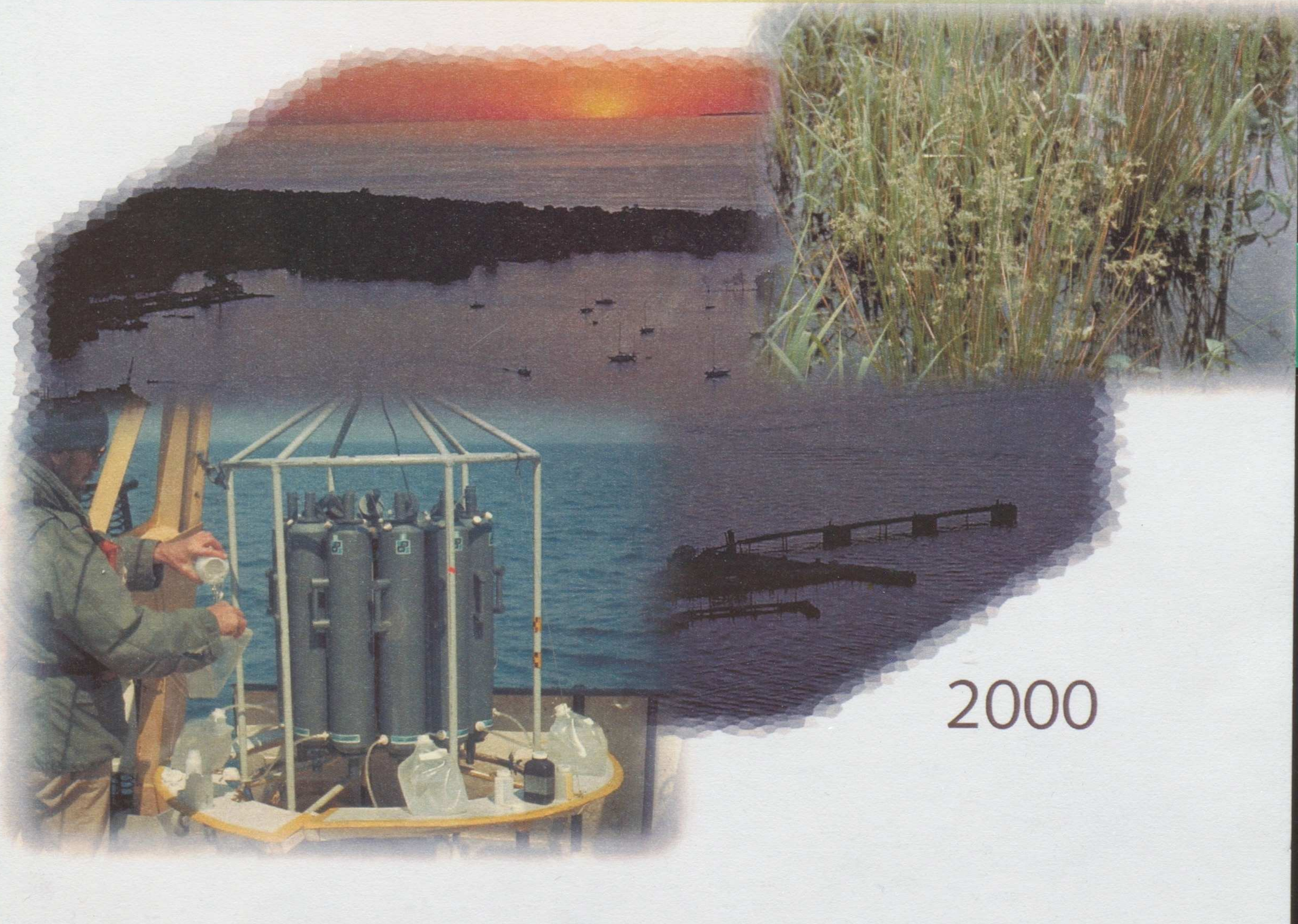
Great Lakes Modeling Summit

Focus on Lake Erie



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Council of
Great Lakes
Research Managers

Report to
the International
Joint Commission

Great Lakes Modeling Summit: Focus on Lake Erie

Modeling Summit Planning Committee

Council of Great Lakes Research Managers

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Modeling Summit Planning Committee

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and W. Gary Sprules

On behalf of the Council of Great Lakes Research Managers we would like to thank the authors for contributing white papers for the summit and the following Panel members: Bob Lange, New York State Department of Environmental Conservation; Tim Johnson and Tom Stewart, Ontario Ministry of Natural Resources; Glenn Warren, Environmental Protection Agency, Great Lakes National Program Office; and Todd Howell, Ontario Ministry of Environment.

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TABLE OF CONTENTS

continued

FIGURES AND TABLES

Appendix B

Appendix C

Appendix D

Appendix E

continued

continued

Appendix F

Appendix G

Appendix H

Appendix I

I. BACKGROUND

The Lake Erie Task Force completed its report in February of 1997 providing a conceptual model of the Lake Erie Ecosystem that is now being used by the Parties. As part of the development of the model, a workshop of modelers and resource managers was held in September of 1996 and it was recommended by the Task force that these groups be brought together on a regular basis. Further, the Task Force recommended that the Council of Great Lakes Research Managers be the vehicle or catalyst for such a summit.

II. INTRODUCTION

The Council of Great Lakes Research Managers (Council) was established in 1984 to enhance the ability of the International Joint Commission (IJC) to provide effective leadership, guidance, support and evaluation of Great Lakes research programs with particular reference to programs required or funded pursuant to the provisions of the Great Lakes Water Quality Agreement.

On May 27-28, 1999 the Council hosted the Great Lakes Modeling Summit: Focus on Lake Erie, at the International Association for Great Lakes Research 1999 Conference at Case Western Reserve University in Cleveland, Ohio. The Summit was a continuing effort to bring modelers together with resource managers to discuss the application of models to management issues. This year, the focus was on Lake Erie. The Lake Erie at the Millennium Issues Workshop, held at the University of Windsor in November 1998, had identified 71 Lake Erie management issues that were grouped into the following six broad categories:

1. Eutrophication/Primary production
2. Exotic Species/Nuisance Aquatic Species
3. Upper Food Web Exploitation
4. Ecosystem Stability
5. Habitat Structure and Function
6. Contaminants

The Great Lakes Modeling Summit was organized to address these identified management categories. Summit invitees were each asked to prepare a 7-8 page white paper describing a model that would address as many of these issue categories as possible. The goal was to achieve a quantitative/predictive capability for the Lake Erie ecosystem. In other words, the Council was trying to assess the potential for models to help implement the “Ecosystem Approach to Management” for Lake Erie. In order to meet this challenge, each model, at a minimum, was to include the following state variables:

- nutrient concentrations;
- total algal biomass;
- blue-green algal biomass;
- walleye biomass;
- fish body burdens of bioaccumulative chemicals (e.g., PCBs);
- zebra mussel biomass; and
- richness and evenness of the fish community trophic levels between algae and top predator fish.

Further, the model was to indicate which stressors control these variables and whether or not they were susceptible to management actions. The invitees were asked to state explicitly their perception of the management problem being addressed. Also, the white papers were to include modeling assumptions, data, monitoring and research needs, relevant space and time scales, and other constraints needed for describing the model. Submitted white papers can be found in Appendix A-I. Two groups of Lake Erie Managers were invited as panelists to provide comments and answer questions at the Summit. Panelists were asked to consider the following three questions in their discussion:

1) What did you find useful/not useful in the paper?
2) Where are the gaps in data or research that affect the utility of the models?
3) What are the most important barriers to the application of the models?

Summit organizers met with panelists following the Summit to prepare summaries for the morning session on May 28. A copy of the program can be found in Appendix I.

III. DISCUSSION AND RESULTS

The Summit was attended by approximately 100 people including researchers, managers, and students and generated considerable discussion.

Several areas of agreement were reached among the participating modelers:

1. Primary productivity must be better understood (the bacterial component has been neglected);
2. Spatial gradients in Lake Erie are too important to ignore (west to east and nearshore/offshore);
3. Better calibrations of models are needed (confirmation should be conducted under radically different conditions;
4. Modeling approaches are complimentary (duplication of effort is healthy for complex topics);
5. Current monitoring programs are not sufficient to support even the most modest of modeling projects (there is no long-term commitment to monitoring);
6. Carbon budgets need to be refined to better account for zebra mussel impacts and the role of bacterial activity; and
7. Models themselves are principally pedagogic, and it is the experience and insight gained from building them, not precise model predictions, that outfit the scientist for helping managers.

Several unanswered questions remained after the Summit for which the modelers could not reach concensus:

1. What is the appropriate level of aggregation? (Can we lump state variables across space and time?);
2. Uncertainty of the appropriate degree of emphasis on the lower foodchain vs. the upper foodchain (range of time and space scales apply as one moves up the food chain);

3. Uncertainty in the linkages across the foodchain (zooplankton); and
4. Are zebra mussels limited by vertical transport of particulate matter or by food production?

The panelists also had points of agreement:

1. Diversity of approaches is good, but there is confusion on which way to proceed.
2. The benefits of modeling vs. the price tag needs to be articulated and resolved.
3. There is utility in having both predictive and diagnostic models.

Both the modelers and the panelists agreed that future plans should be made to hold a session in which modelers and managers collaborate to implement a solution to a pressing management problem.

IV. CONCLUSIONS AND RECOMMENDATIONS

The Modeling Summit continues to be an effective way to bring together modelers and resource managers to discuss how ecosystem modeling can aid in accomplishing the goals of RAPs, LaMPs and indicator selection and development. The Council is pleased to convene the summit at various venues including SOLEC and IAGLR and notes that its objective of identifying research needs, gaps and priorities is furthered by the regular scheduling of these events. Future summits may continue to be held on a lake specific basis or be organized around other themes such as a session in which modelers and managers collaborate to implement a solution to some pressing management problem.

The Council recommends:

Sufficient monitoring programs and coordinated research programs are essential to the development of modeling projects which can provide assistance to managers in addressing pressing management issues.

Through its continuing promotion of modeling research and model development in the Great Lakes, the Council hopes to support the Ecosystem Approach and to promote the IJC's Ecosystem Modeling recommendation in the Ninth Biennial Report on Great Lakes Water Quality, which states:

> *Governments support the development and application of models to assist in the testing, evaluation and implementation of ecosystem indicators, monitoring strategies and management strategies for water quality, contaminants, fisheries and other ecosystem issues.*

This concept that models can be used to synthesize what we know about how a system behaves in response to external stimuli makes models a valuable tool for making Great Lakes ecosystem assessments and for supporting management decisions. Models can provide great insight and make projections, but only with the support of <u>monitoring</u>, which provides model inputs and credibility, and <u>research</u>, which provides understanding and model parameterization. The white papers in the appendix of this report all make suggestions regarding the monitoring and research needs to accomplish this goal for the Lake Erie ecosystem.

Appendix A

Program

Great Lakes Modeling Summit: Focus on Lake Erie

Chairs: David M. Dolan, Joseph V. DePinto, and Joseph F. Koonce

THURSDAY, MAY 27, 1999

8:20 AM	PLENARY (STROSACKER AUDITORIUM)
9:40 AM	R. G. KREIS. **Integrated ecosystem response models for Lake Erie.**
10:00 AM	J. FITZPATRICK and D. DiToro. **A retrospective of eutrophication modeling in Lake Erie.**
10:20 AM	Panel Response
10:40 AM	BREAK
11:00 AM	W. G. SPRULES, O. E. Johannsson, E. S. Millard, M. Munawar, D. S. Stewart, J. Tyler, R. Dermott, S. J. Whipple, M. Legner, T. J. Morris, D. Ghan, and J. M. Jech. **Trophic transfer in Lake Erie: A whole food web perspective.**
11:20 AM	R. T. Heath, R. Sturtevant, D. Shoup, and P. Enflo. **Modeling the effects of nutrient concentrations on community production and ecosystem stability: Framework for a Great Lakes model.**
11:40 AM	Panel Response
12:00 PM	LUNCH
1:00 PM	J. V. DEPINTO, V. J. Bierman, T. J. Feist, and J. Kaur. **Development of a process-oriented aquatic ecosystem model for Lake Erie.**
1:20 PM	M. Colavecchia, S. George, R. Knight, S. Ludsin, and P.A. Ryan. **The Lake Erie System Model: a fuzzy cognitive map to support development of ecosystem objectives.**
1:40 PM	Panel Response
2:00 PM	D. A. Culver, M. R. Loewen, P. Hamblin, M. Charlton, and J. Coakley. **Ecological modeling of Lake Erie trophic dynamics - 1999.**
2:20 PM	J. F. KOONCE and A. B. Locci. **Resolution of issues of scope and detail in the development of the Lake Erie ecological model.**
2:40 PM	Panel Response
3:00 PM	BREAK

3:20 PM S. J. WHIPPLE. **Monte Carlo analysis in model parameterization: a multi-trophic level ecosystem simulation model of Lake Ontario.**

3:40 PM J. V. DEPINTO, S. Liu, T. C. Young, and W. G. Booty. **Demonstration of an approach for reducing modeling uncertainty for PCB's in Lake Ontario.**

4:00 PM S. LIU and J. V. DePinto. **Object oriented modeling of the Great Lakes Ecosystem.**

4:20 PM D. N. ATKINSON and J. F. Koonce. **Effects of aggregating cohort dynamics on the reliability of age-structured population models.**

4:40 PM T. HUSAIN and M. Munawar. **Ecological risk assessment modeling for Lake Erie - Multi-media mass balance approach.**

FRIDAY, MAY 28, 1999

8:20 AM J. J. FITZPATRICK, D. M. DiToro, and M. B. Meyers. **Eutrophication modeling in the 90's.**

8:40 AM L. BOEGMAN, P. Hamblin, and M. Loewen. **Two-dimensional modeling of zebra mussel effects in Lake Erie, Stage One: Validation of temperature, currents, and water levels.**

9:00 AM D. C. LAM and W. M. Schertzer. **A water quality model for phosphorus cycles in pre- and post-zebra mussel years in Lake Erie.**

9:40 AM H. T. MORRISON, G. D. Haffner, and D. M. Whittle. **Application of a benthic/pelagic food web bioaccumulation model to answer contaminant-related questions in Lake Erie.**

10:00 AM M. A. HALTUCH and P. A. Berkman. **Modeling expansion of exotic mussels on Lake Erie sediments using geographic information systems.**

10:20 AM BREAK

10:40 AM DISCUSSION - INTEGRATION SESSION

Appendix B

Integrated Ecosystem Response Models for Lake Erie

Russell G. Kreis, Jr.

U.S. Environmental Protection Agency
Office of Research and Development

National Health and Environmental Effects Research Laboratory

Mid-Continent Ecology Division, 9311 Groh Road
Grosse Ile, MI 48138

ABSTRACT

Intensive binational efforts have been directed toward improving water quality and reducing anoxia in Lake Erie since the 1960s. A large cast of agencies, scientists, and engineers were involved through monitoring, interdisciplinary studies, and modeling. United States Environmental Protection Agency (USEPA) eutrophication models have been post-audited and forecasts were sufficiently accurate to establish target phosphorus loads and mitigate anoxia.

Because Lake Erie has multiple uses, issues, and stressors with various effects, predictive modeling is required for setting priorities and evaluating risk-based management options. An integrated modeling approach such as that being applied in the Lake Michigan Enhanced Monitoring/Mass Balance Project should be adopted which includes: surface wave, hydrodynamic, atmospheric transport and deposition, sediment transport, eutrophication, sorbent dynamics, contaminant/water quality, and food chain bioaccumulation models. It is proposed that this construct be enhanced by including: ecosystem productivity (both lower and upper food web components), explicit microbial models, and effects models for fish, avian, and wildlife species. It is evident that an integrated construct requires multiple models in a unified computational framework and the collaboration of a number of specialists and groups. Similarly, the construct provides a means for identifying monitoring and research needs.

INTRODUCTION

It is evident that Lake Erie has experienced numerous ecosystem changes over the past century and changes continue to occur during the 1990s. A great deal of progress has been made in restoring the ecosystem and beneficial uses (Makarewicz and Bertram 1993). However, continued changes to the system are projected to occur with respect to water levels, potential global warming impacts, exotic species introductions, recreational fish species, forage fish species, lower food chain elements, shoreline and wetlands alteration, nutrients, contaminants, sediments, and the various processes and relationships governing the ecosystem (University of Windsor 1999; USEPA/Environment Canada 1999).

The Great Lakes community has been a national leader in ecosystem modeling for the past 30 years (O'Connor and Mueller 1970; O'Connor *et al.* 1975; Kitchell *et al.* 1977; Chapra and Sonzogni 1979; Schwab *et al.* 1984; Sonzogni *et al.* 1987; Lesht *et al.* 1991; Mackay 1991; Gobas 1992; Schneider 1992; Rand *et al.* 1993; Madenjian and Carpenter 1993; Madenjian *et al.* 1993; Mackay *et al.* 1994; Gobas *et al.* 1995; Madenjian 1995; Madenjian *et al.*1995; Jain and DePinto 1996; Morrison *et al.* 1997). The USEPA has been directly involved and sponsored collaborators in the development, calibration, application, and verification of Great Lakes models (Paul and Lick 1974; O'Connor *et al.* 1975; Thomann and DiToro 1975; Bierman and Richardson 1976; Rodgers and Salisbury 1981; Canale and Auer 1982; Bierman and Swain 1982; Richardson *et al.* 1983; Thomann and Connolly 1984; Libicki and Bedford 1985; Auer and Canale 1986; DiToro *et al.* 1987; Martin *et al.* 1991; Connolly *et al.* 1992; DePinto *et al.* 1993; Endicott and Cook 1994; Velleux *et al.*

1995; Skoglund *et al.* 1996; Endicott *et al.* 1998; Rygwelski *et al.* 1999, among others). The intent of modeling is to simulate the system and its processes to provide a better understanding of the ecosystem, however, with the ultimate goal of predictive capabilities for forecasting alternative scenarios to guide ecosystem management priorities and options.

Modeling goals are reflective of the holistic ecosystem approach which recognizes the inter-related physical, chemical, and biological components of the system. The model suite being proposed addresses the International Association of Great Lakes Researchers 1999 (IAGLR'99) Modeling Summit objectives of nutrient concentrations, total algal biomass, blue-green algal biomass, walleye biomass, fish body burdens of bioaccumulative contaminants, and zebra mussel biomass. These models do not explicitly address richness and evenness of various trophic levels but could potentially be calculated. The objectives of this briefing document are to: 1) provide an overview of Lake Erie eutrophication modeling efforts; 2) propose an integrated suite of models for development and application to Lake Erie; and 3) project future enhancements to the modeling framework which have implications for Lake Erie and the Great Lakes.

ECOSYSTEM RESPONSE MODEL FOR LAKE ERIE

An integrated modeling framework should be established and adopted for Lake Erie which utilizes the advances made through the history of Great Lakes modeling. In the 1960s and 1970s, a primary concern regarding Lake Erie water quality was over-enrichment by nutrients which stimulated algal production and accelerated the eutrophication process. The consequences of eutrophication are adverse taste and odor and filter-clogging problems at municipal water intake facilities; reduced water column transparency; overgrowth of algal assemblages, nuisance blooms and undesirable species composition at the primary producer level; oxygen depletion; degradation and impairment of habitat quality; loss of submerged aquatic vegetation, and degradation of biological communities. The causes of eutrophication revolve around the interactions of nutrients such as phosphorus, nitrogen (N) and silica, nutrient loadings, and the growth of primary producer communities. The subsequent undesirable effect of eutrophication was anoxic conditions in large expanses of Lake Erie. Binational mathematical modeling approaches to eutrophication were undertaken to forecast phosphorus reductions required to reduce anoxic conditions (O'Connor *et al.* 1975; DiToro and Connolly 1980). Model forecasts of phosphorus loads, phosphorus concentrations, chlorophyll, dissolved oxygen, and the areal extent of anoxia where sufficiently credible to promote phosphorus loading reductions from point sources, a phosphate detergent ban, and alternative agricultural practices. Post audits of the eutrophication model during the 1980s and 1990s suggest that model predictions were reasonably accurate toward attaining the goal of reducing anoxic conditions (DiToro *et al.* 1987; Zahakos *et al.* 1993).

During the late 1970s much of the modeling emphasis was redirected from eutrophication to contaminant models. A great number of efforts have and continue to be exerted in various contaminant models. These efforts build upon the construct and concepts developed over the years and have culminated in recent modeling efforts in the lower Fox River/Green Bay Mass Balance Project (Martin *et al.* 1991; Connolly *et al.* 1992; DePinto *et al.* 1993; DePinto 1994; Hydroqual 1995a; Martin *et al.* 1995; Velleux *et al.* 1995; among others). Feasibility of the mass balance approach for contaminants was demonstrated on a large Great Lakes embayment and has now been extended to the examination of an entire lake through the Lake Michigan Mass Balance Project (Endicott *et al.* 1992; USEPA 1993; Belestsky *et al.* 1997; Rygwelski *et al.* 1999).

It is proposed that a suite of models similar to those being applied and developed for the Lake Michigan Mass Balance Project (Figure 1) be established and developed for Lake Erie. The integrated suite of models being proposed target anthropogenic contaminants and include atmospheric transport, surface wave, hydrodynamics, sediment transport, eutrophication, sorbent dynamics, contaminant transport and fate, and food web bioaccumulation models which are reflective of the inter-related nature of the system. Several levels of models are being employed including screening-level, level II, and level III models which reflect increasingly greater time resolution, space scale resolution, and complexity of parameterization (USEPA 1993). Models are within the mass balance concept and are based upon the principle of conservation of energy, momentum, and mass. The proposed suite of models will address many of the multiple questions confronting Lake Erie managers concerning impaired beneficial uses including, for example, nutrients, sediments, water quality, habitat quality, exotic species, lower food chain productivity, fisheries, and contaminants (University of Windsor 1999; USEPA/Environment Canada 1999).

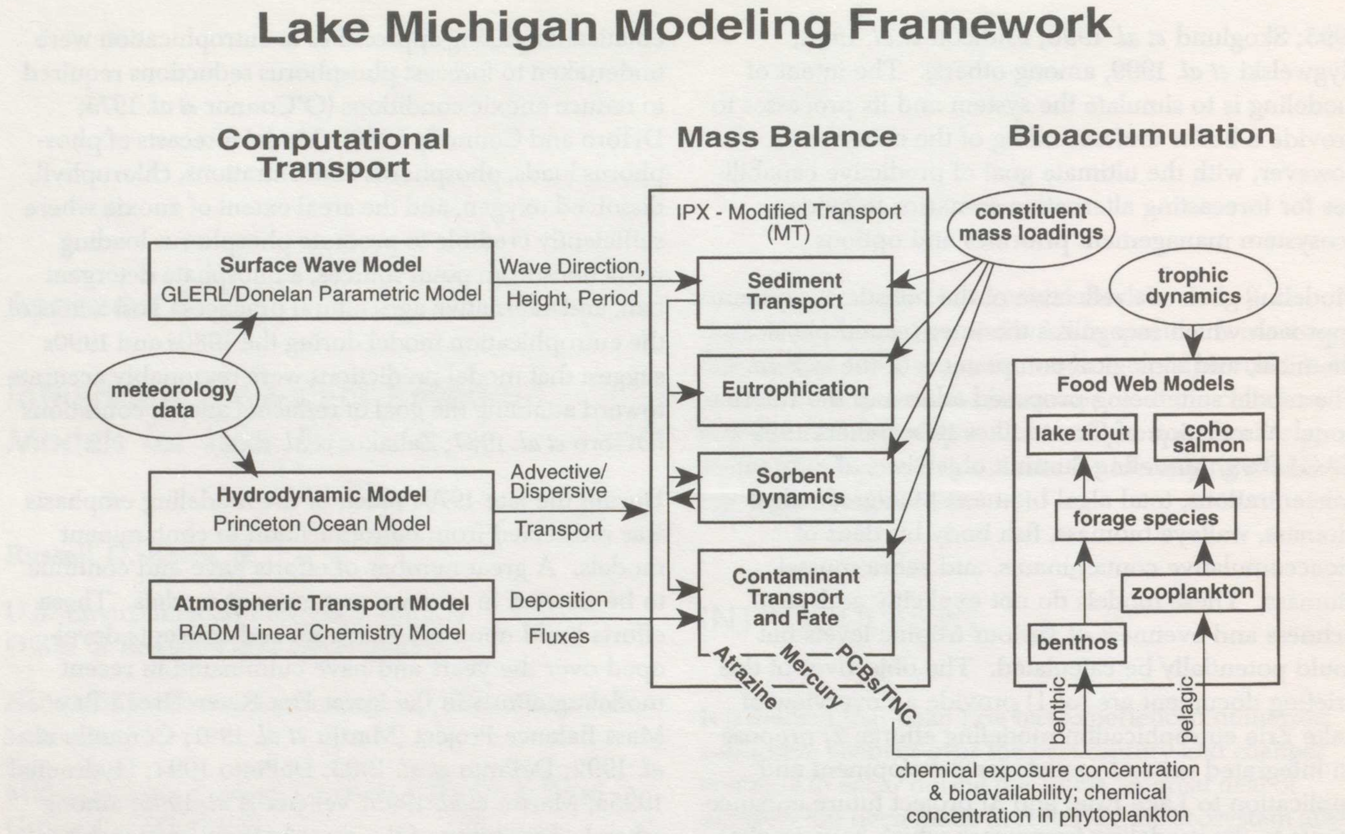

Figure 1 Lake Michigan Modeling Framework

The modeling framework provides a construct for integrating load estimates, ambient monitoring data, process research efforts, and modeling and leads to the development of scientifically credible, predictive cause-effects tools for decision-making. These models require extensive data where numerous physical, chemical, and biological data are required for various media including air, water, sediments, and biota. This framework therefore underscores the importance of monitoring and trends. Over the past years, monitoring frequency and intensity have decreased. For the mass balance construct, synoptic sampling and monitoring is required for all parameters at least at a seasonal frequency and, many times, at an intensity which is typically not applied during routine monitoring. This becomes particularly apparent because of the changing conditions and relationships in Lake Erie during the past decade and that these changes are anticipated to continue (University of Windsor 1999; USEPA/Environment Canada 1999). Similarly, it guides particularly important directions of research needs with emphasis on ecosystem relationships, processes, and rates. Over 40 research priorities have been identified for Lake Michigan modeling, for example: soil load measurements from shoreline and bluff erosion, in-lake particle settling and resuspension velocities for biotic and abiotic solids, improvements of hydrodynamic flow estimates and model parameterization for the Straits of Mackinaw, measurement of air-water exchange fluxes for contaminants, couple atmospheric and lake mass balance models, and diet and range of movement determinations for upper and lower food chain elements. Even though data requirements and modeling development require considerable financial resources, the costs associated with remedial and regulatory actions addressed within the modeling framework are, at a minimum, an order of magnitude greater. For example, the estimated $28 billion expended on the lower Great Lakes for nutrient control far exceeds the expenditures for monitoring, data, research, and modeling for the decision-making process.

This modeling construct is comprised of linked sub-models with a general movement toward a unified computation framework for certain sub-models. These require collaboration of modelers with different expertises and the need for the linked models to be based upon the same concepts and to be computationally compatible. No one model or modeler can answer the multiple questions which must be

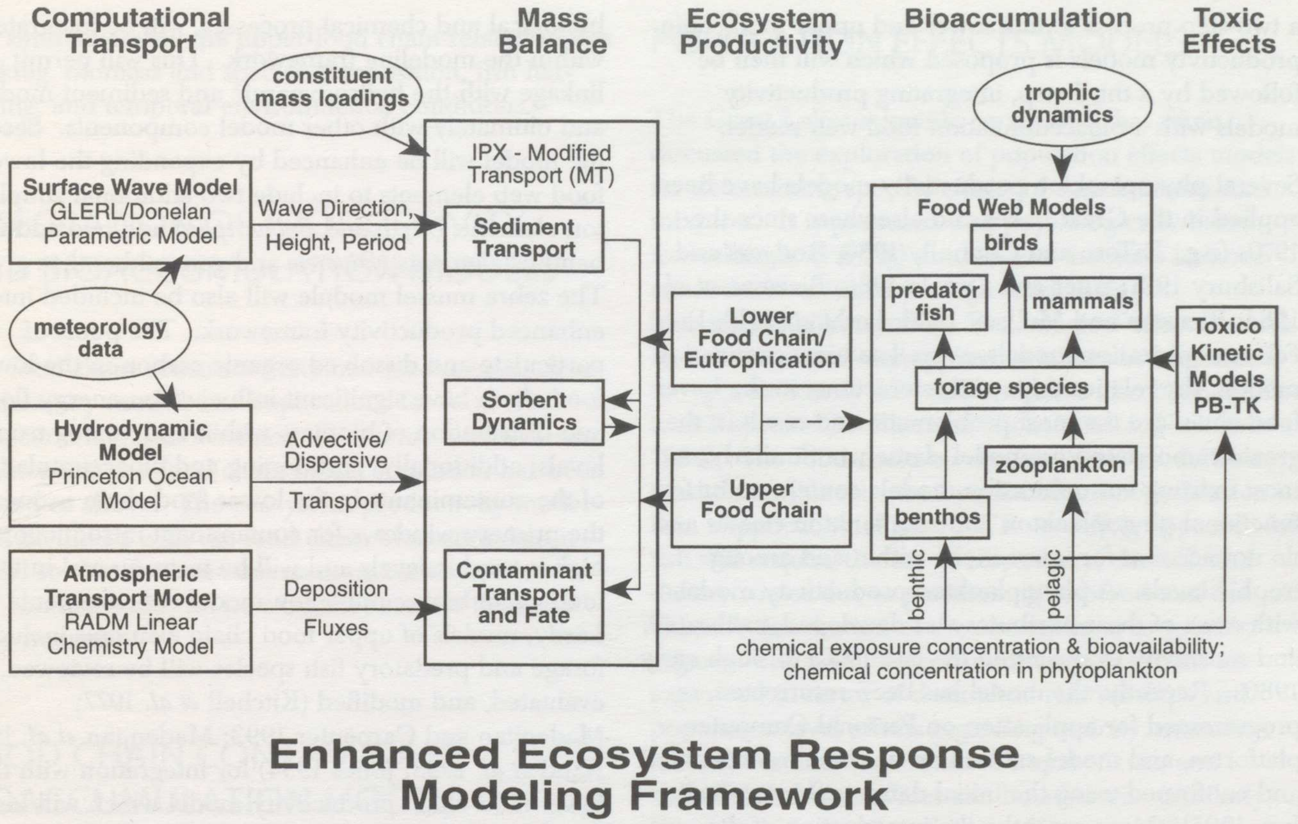

Figure 2 Enhanced Ecosystem Response Modeling Framework

addressed in an holistic ecosystem approach. Certainly collaboration and coordination is required on many levels, e.g. management, field design, sample collections, sample analyses, database development, and modeling application.

ENHANCEMENTS FOR INTEGRATED ECOSYSTEM RESPONSE MODELS FOR LAKE ERIE

Visioning for the future in response to the needs of the scientific community and to answer the integrated management questions for effective ecosystem decision-making is a necessity. Response to the structure, function, and processes of large lakes due to the fact that the ecosystem and its' components are integrated with one another suggests that additional modeling components are needed. The above-described Mass Balance Construct has had certain portions already applied (Endicott *et al.* 1992; Belestsky *et al.* 1997; Rygwelski *et al.* 1999) and certain portions are moving toward completion in development. However, additional developmental activities are underway and are planned using Lake Michigan as the developmental platform, and these enhancements should be kept as goals for developing integrated response models for Lake Erie (Figure 2).

ECOSYSTEM PRODUCTIVITY MODEL

It has been recognized that nutrient dynamics and lower food chain productivity must be integrated with fish production models into a single model framework to account for ecosystem production, feedback mechanisms among trophic levels, and effects of multiple stressors. In the past, most production models were specifically directed toward nutrients and the lower food chain (related to eutrophication) or toward the upper food chain as related to fish stocking and fish harvesting issues. When previously attempted, these models have been extremely cursory in nature and have only been partially successful in application. To account for multiple stressors, the ecosystem productivity model must also be ultimately linked to a food chain contaminant bioaccumulation model. Therefore a two-step process to link lower and upper food chain productivty models is proposed which will then be followed by a third step, integrating productivity models with a bioaccumulation food web model.

Several phytoplankton productivity models have been applied in the Great Lakes and elsewhere since the 1970s (e.g., DiToro and Connolly 1980; Rodgers and Salisbury 1981; Auer and Canale 1986; Bierman *et al.* 1984; Bierman and McIlroy 1986; Lesht *et al.* 1991). For eutrophication models, as well as bioaccumulation models, the relationships and interactions in the lower food chain are the most problematic and result in the greatest uncertainty in model elements. Similarly, most existing eutrophication models contain no or few functional phytoplankton and zooplankton classes and do not account for interactions within and among trophic levels. A phytoplankton productivity model with most of these attributes was developed, calibrated, and sensitivity evaluated in the late 1970s through early 1980s. Recently, the model has been resurrected, reprogrammed for application on Personal Computer platforms, and model calibration has been re-examined and confirmed using the initial datasets (Limno-Tech, Inc. 1995). More recently, the introduction of the zebra mussel in the Great Lakes has greatly disrupted the ecosystem and has presented an array of new environmental issues and problems which have not been addressed in the past. A zebra mussel module has been developed and coupled with the multi-class phytoplankton model for use in Saginaw Bay (Limno-Tech, Inc. 1997). The inclusion of zebra mussels in the modeling framework has been necessitated by their introduction into the Great Lakes system and subsequent impacts on habitat, nutrients, food webs, and relationships; it has been demonstrated that these relationships have been extensively altered by zebra mussels. Additionally, this model has been recently recalibrated and simulation results indicate that measured data and model output are in good agreement, demonstrating predictive capabilities.

Present development in the Lake Michigan Project includes enhancements and refinements to this model framework and will include several steps. The multi-class phytoplankton model to be applied includes green algae, diatoms, non-N-fixing blue-green algae, N-fixing blue-green algae, and other algae and is the most resolute model applied in the Great Lakes. The cycling, movement, and production of carbon by and within phytoplankton will be of particular concern due to that fact that the majority of organic carbon production in the lake is autochthonous. First, the multi-class phytoplankton/zooplankton model, with associated biological and chemical processes, will be integrated within the modeling framework. This will permit linkage with the hydrodynamic and sediment models and ultimately with other model components. Second, the model will be enhanced by expanding the lower food web elements to include two additional zooplankton elements (*Mysis* and *Bythotrephes*) and two additional benthos elements (*Diporeia* and general benthos group). The zebra mussel module will also be included into the enhanced productivity framework. The pools of particulate and dissolved organic carbon in the lower food chain have significant influence on energy flow and distribution of biomass within and among trophic levels; additionally, partitioning and bioaccumulation of the contaminants in the lower food chain is one of the primary windows for contaminant introduction to higher trophic levels and will be instrumental in the food chain bioaccumulation model enhancements. Lastly, models of upper food chain elements including forage and predatory fish species will be reviewed, evaluated, and modified (Kitchell *et al.* 1977; Madenjian and Carpenter 1993; Madenjian *et al.* 1993; Rand *et al.* 1993; Jones 1994) for integration with the lower food chain productivity model which will form an ecosystem productivity model. These efforts will result in a productivity model with a greatly resolved eutrophication/lower food chain component, including zooplankton, benthos, zebra mussels, and linkages to upper food chain (fish) productivity with predictive capabilities for stocking and catch dynamics.

Great effort has been given to the understanding of microbial processes and production. These have revealed the overwhelming complexity of bacterial dynamics in both benthic and pelagic environments. Generally, modeling of microbial dynamics has not been extremely successful and has been implicitly included productivity models. It is suggested that attempts should be made to explicitly include microbial dynamics in both benthic and pelagic productivity models. Similarly, because of their role ecosystem productivity, particularly regarding carbon cycling, microbial processes will also have implications to food chain contaminant bioaccumulation models.

The resultant ecosystem productivity and biomass model will be able to be applied to the examination of eutrophication issues as a stand-alone model. However, it can also be applied for the entire food chain for the determination of trophic level interactions and biomass sustainability at an given trophic level or trophic element. This integrated model can be used to quantify top-down and bottom-up management strategies as it relates to nutrients and the lower food chain and simultaneously the upper food chain related to fish stocking, biomass and species composition, fish harvesting, and temporal environmental conditions.

INTEGRATION OF PRODUCTIVITY AND BIOACCUMULATION MODELS

The food chain construct described for the ecosystem productivity models has implications for food chain bioaccumulation models and the interactions between productivity and food chain bioaccumulation has been alluded to above. The ecosystem productivity model must be linked with the food chain bioaccumulation model so that dynamic interactions between biomass and contaminants can be examined, rather than in a static manner.

FOOD CHAIN CONTAMINANT BIOACCUMULATION MODEL

During the past five years, there has been considerable fusion of engineering and bioenergetics modeling approaches in the food chain bioaccumulation realm. This fusion will continue and greater strides will be made in the understanding of carbon/energy dynamics. In fact, the first step in this process has been attempted by including caloric principles within a food chain bioaccumulation construct. The interface of the lower food chain elements, their processes, and carbon pools will be critical to the understanding of contaminant accumulation. Refinements of lower food chain elements and carbon/sorbent dynamics in the existing model will be required.

It is proposed that a food chain contaminant bioaccumlation construct similar to that applied to fish, be extended to piscivorous mammalian and avian species. Little or no effort has been devoted to the modeling of contaminant dynamics in wild populations of these biotic groups. Typically, a partitioning or calculation approach has been applied. Some target populations for the avian group include eagles, cormorants, and terns and for the mammalian wildlife, mink. Problematic will be the determination of diet and range of movement of wild populations, as well as the sacrifice of individuals to determine body burden concentrations.

POPULATION EFFECTS MODELS

The Great Lakes scientific community has often discussed the exploration of population effects models for determining specific effects of contaminants and mixtures. It is proposed that physiologically-based, toxicokinetic (PB-TK) models and the mass balance construct be merged through food chain bioaccumulation models. Toxicological effects models have been effectively applied to laboratory mammals for approximately 25 years and have also been applied to fish species (McKim and Nichols 1994; Nichols *et al.* 1994). The food chain bioaccumulation model being used determines the total contaminant body burden of fish. Application of the PB-TK modeling approach for fish will require the use of respiratory, dermal, and dietary routes due to partitioning to blood and the ultimate distribution of the contaminant to specific organs. The resultant concentrations in organs are examined in terms of dosimetric relationships and population-level effects regarding toxicity, mortality, deformities and reproductive impairments, and behavioral abnormalities can be assessed. Similarly, these could be projected in the future considering mass balance projections for water and dietary exposures to provide management alternatives.

CONCLUSIONS AND RECOMMENDATIONS

It is recommended that an integrated ecosystem response modeling framework be established and adopted for Lake Erie. The proposed framework consists of a suite of models which reflect the inter-related nature of the ecosystem. Collaboration of multi-disciplinary scientists and engineers will be required. Ecosystem productivity should be incorporated into the existing mass balance framework used for contaminants to predict production-contaminant interactions. Enhancements to bacterial, phytoplankton, zooplankton, benthos, and zebra mussel components together with upper food chain production must be realized. Piscivorous mammalian and avian species should be addressed within food chain contaminant bioaccumulation models. The merging of physiologically-based, toxicokinetic models and the mass balance modeling construct should be initiated for the ability of predicting population-level effects of contaminants. The mathematical modeling construct provides an opportunity for a consistent method for identifying research priorities and underscores the importance for monitoring and trends data.

Appendix C

A History of Eutrophication Modeling in Lake Erie

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INTRODUCTION

The pollution of the Great Lakes from municipal and industrial sources was perceived to be a serious problem as early as the 1950s. This perception was even greater for Lake Erie, which during the 1960s and 1970s was known as the "Dead Sea of North America." Historically, a large part of Lake Erie's water quality problems appeared to be related to eutrophication. During the summer months, windrows of *Cladophora glomerata* covered large portions of the lake's shoreline. The surface waters of the western basin and parts of the central basin of Lake Erie were populated with *Aphanizomenon flosaquae*, giving the impression that someone had poured green paint on the water surface. The subsequent settling and decay of this and other algal biomass resulted in widespread hypoxia and anoxia in the bottom waters of the lake, further stressing commercial and sport fisheries, which were already suffering from the stresses of over-fishing. While part of the eutrophication problems of the Great Lakes was due to increased phosphorus loadings associated with population growth, the post-World War II development of phosphorus-based detergents was also identified as a significant contributor to increased phosphorus loadings to the lakes. In its 1969 report to the United States and Canada, the International Joint Commission (IJC) concluded that phosphorus enrichment had accelerated the eutrophication of Lake Ontario and had resulted in a condition of advanced eutrophication in the western basin of Lake Erie. The IJC offered a number of recommendations to deal with the problem of eutrophication, including:

- immediate reductions in the phosphorus content in detergents;
- implementation of programs aimed to reduce point source inputs (municipal and industrial) of phosphorus;
- development of programs for the control of phosphorus from agricultural sources; and
- regulation of any new uses of phosphorus which could result in appreciable additions to the lakes.

Subsequent to the 1969 IJC report, the United States and Canada signed the Great Lakes Water Quality Agreement (1972), which charted a course of action for the two governments in dealing with Great Lakes water quality problems. That Agreement, together with the 1972 Amendments of the Federal Water Pollution Control Act, which called for research and technical development with respect to Great Lakes water quality, including an analysis of present and projected future water quality under varying conditions of wastewater treatment and waste disposal, provided the impetus for water quality modeling of the Great Lakes.

The purpose of this paper is to provide a history of the development and application of mathematical models of the eutrophication processes in Lake Erie and to comment on the potential use of eutrophication models in an ecosystem approach to address Lake Erie water quality problems. However, we would be remiss if we did not include in this history the research and development efforts conducted in the other lakes of the Great Lakes system.

MODEL EVOLUTION

Initial Efforts Leading to LAKE 1

One of the first eutrophication modeling studies of Lake Erie was reported by DiToro *et al.* (1973). This work, which focused on western Lake Erie, grew out of work performed by Hydroscience (1973) for the Great Lake Basin Commission. The original Hydroscience study provided an assessment of the feasibility of applying a limnological systems analysis to the water resources problems of the Great Lakes. During the study, Hydroscience developed and calibrated a demonstration water quality model for the western basin of Lake Erie. The demonstration model included chlorides, coliform bacteria, eutrophication, and a food chain model of cadmium.

The demonstration eutrophication model used seven vertically integrated segments and a steady-state circulation pattern (Figure 1a) to represent the physical and transport features of the western basin of Lake Erie. The estimates of the circulation pattern in western Lake Erie were based on hydrodynamic model computations developed by Gedney (1971) and on observed current information reported by Herdendorf (1967). The kinetic framework (Figure 1b) employed for the eutrophication model incorporated eight

Figure 1a
Steady State Transport for Seven Compartment Western Lake Erie Model

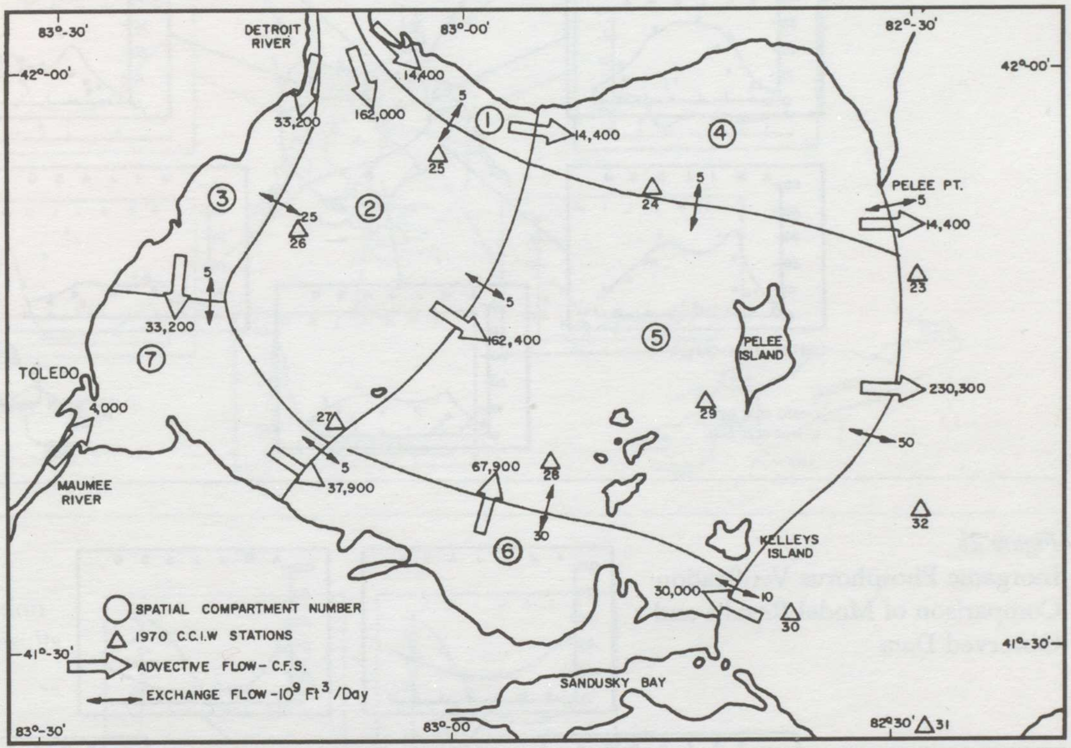
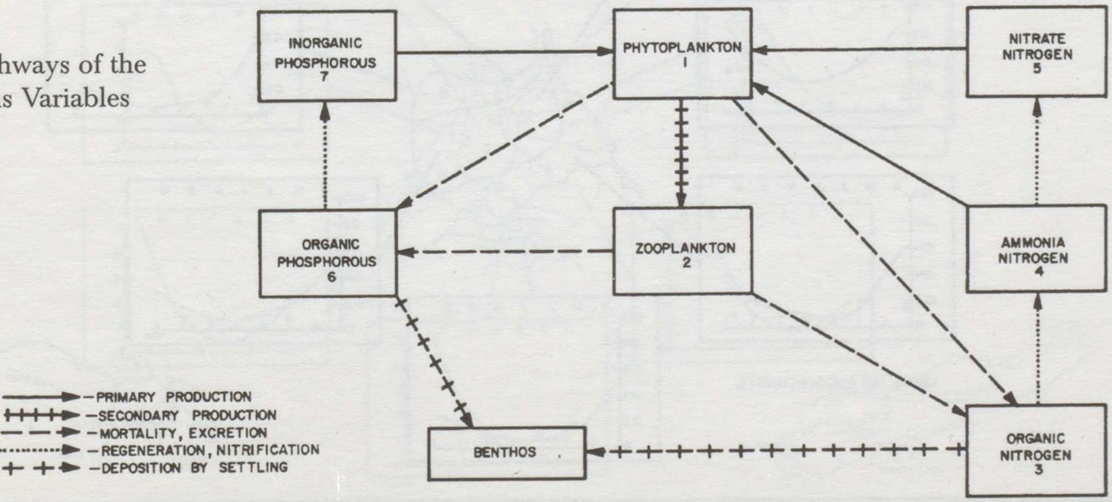


Figure 1b
Kinetic Pathways of the Endogenous Variables



state-variables (phytoplankton chlorophyll, herbivorous zooplankton carbon, carnivorous zooplankton carbon, organic and inorganic phosphorus, organic nitrogen, ammonia nitrogen and nitrate nitrogen) and followed the phytoplankton-zooplankton-nutrient model first structured by DiToro *et al.* (1971) for the Sacramento-San Joaquin Delta. Using water quality data collected by the Canadian Centre for Inland Waters (CCIW) and the USEPA, the eutrophication model was calibrated for the year 1970. Initial calibration results were encouraging. The magnitudes and shapes of the calculated curves for phytoplankton biomass, as indicated by chlorophyll-a (Figure 2a), inorganic phosphorus (Figure 2b), ammonia nitrogen (Figure 3a)

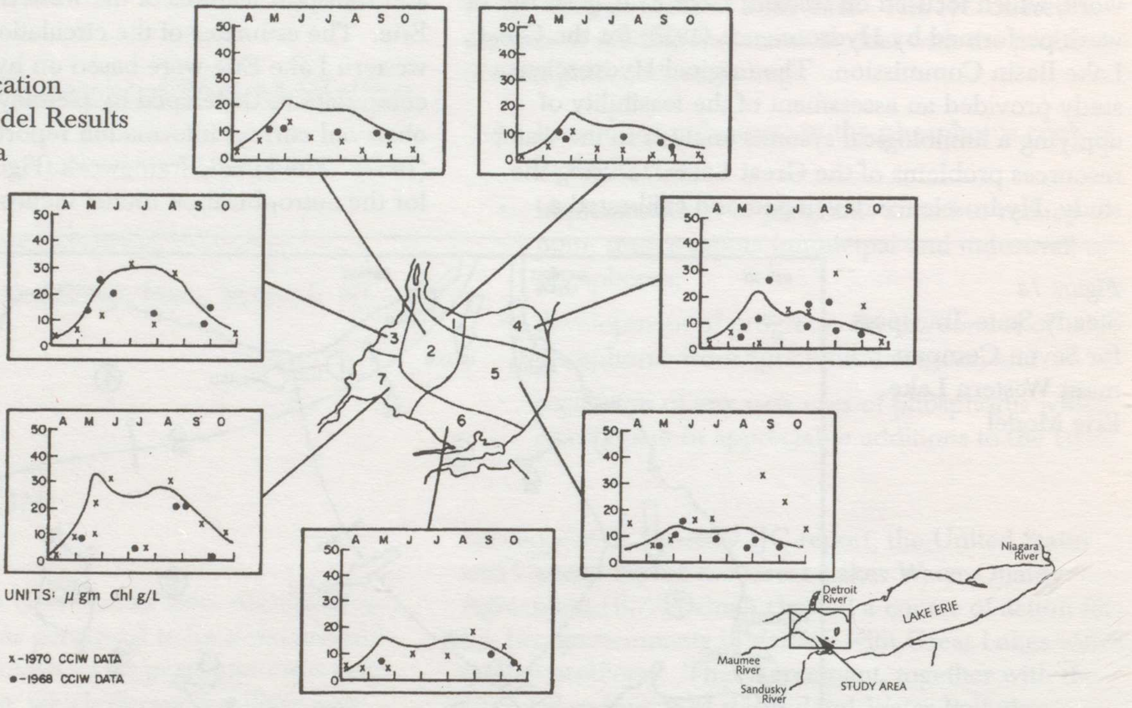


Figure 2a
Chlorophyll Verification
Comparison of Model Results
and Observed Data

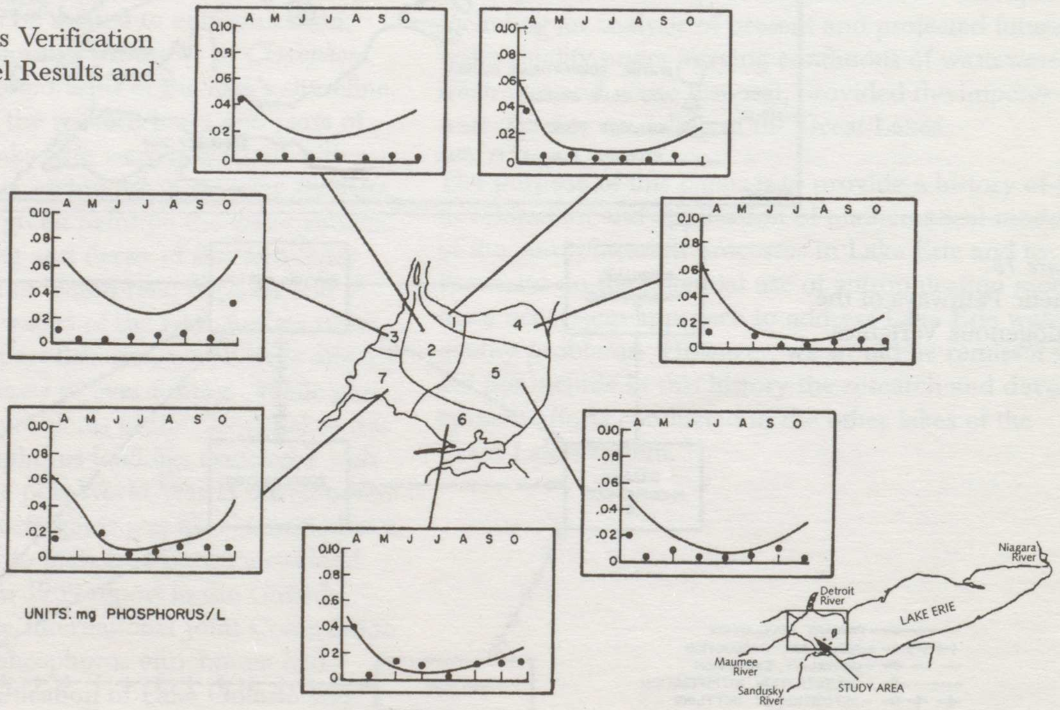


Figure 2b
Inorganic Phosphorus Verification
Comparison of Model Results and
Observed Data

and nitrate nitrogen (Figure 3b) were in reasonable agreement with the observed data, although some systematic deviations were observed. The calibrated model was also used to hindcast lake water quality for the year 1930. Estimates of chlorophyll-a, used to validate the 1930 hindcast calculations, were based on observations of algal cell counts collected by the U.S. Department of Interior, Fish and Wildlife Service for the period 1928-30 (Wright *et al.* 1955) and a relationship between chlorophyll-a and total algal cell counts (Figure 4a) based on USEPA western Lake Erie surveillance data for the period 1967-1968. Model computations of chlorophyll-a for the 1930 hindcast compared reasonably to the observed data (Figure 4b) and provided an encouraging test of the Lake Erie western basin eutrophication model.

Figure 3a
Ammonia Nitrogen Verification Comparison of Model Results and Observed Data

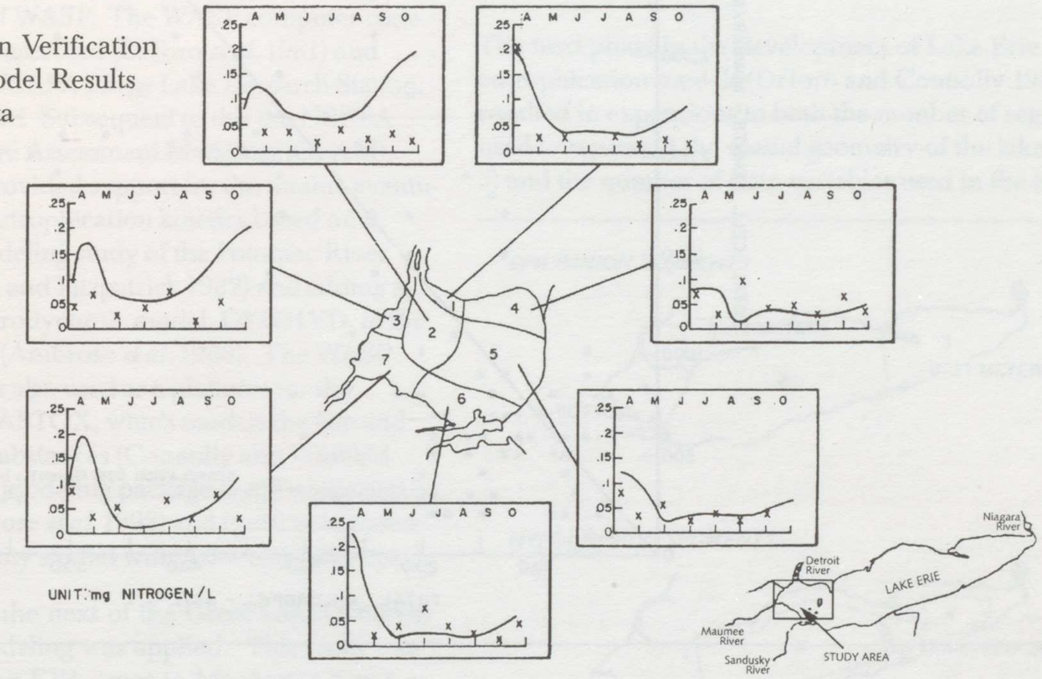


Figure 3b
Nitrate Nitrogen Verification Comparison of Model Results and Observed Data

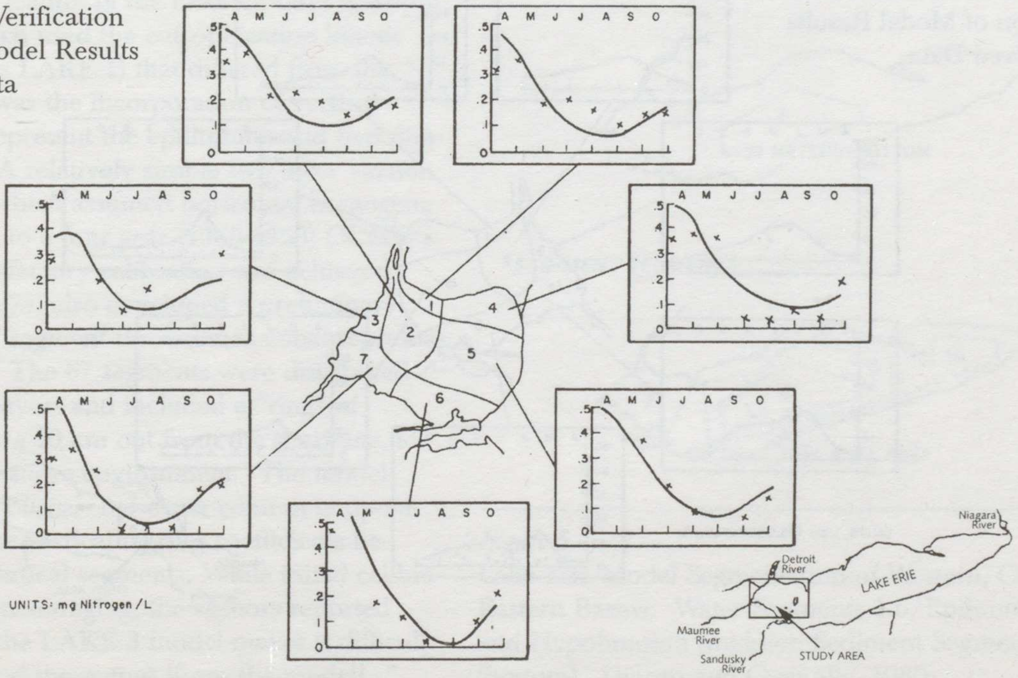


Figure 4a
Relationship Between Total Algal Cell Counts and Total Chlorophyll Measurements in Western Lake Erie

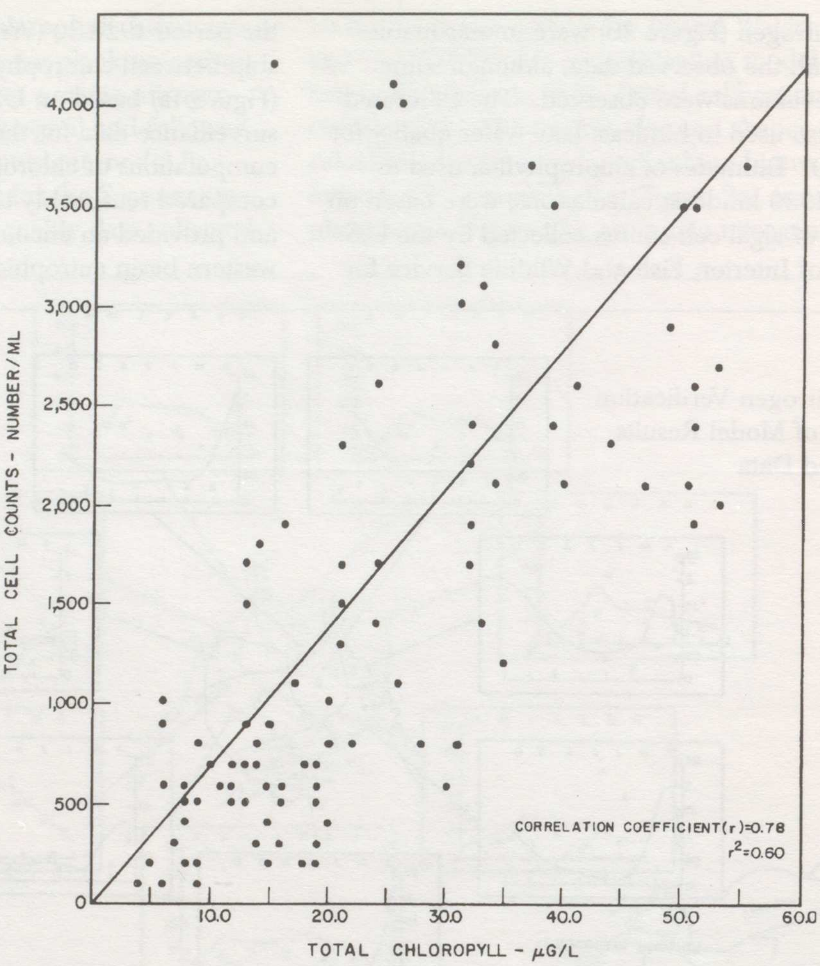
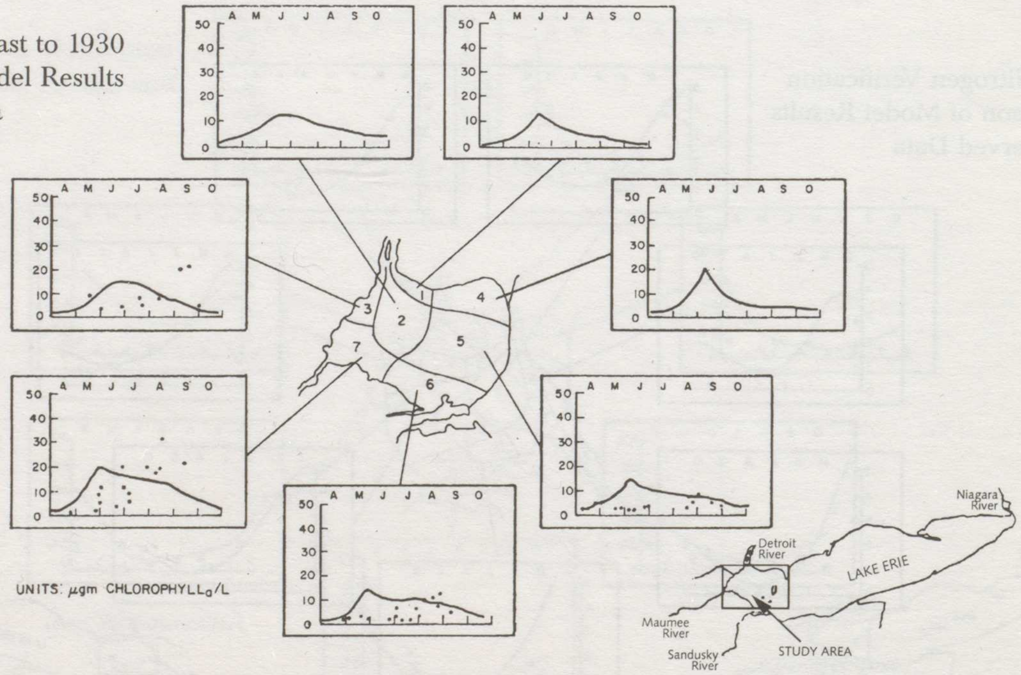


Figure 4b
Chlorophyll Hindcast to 1930 Comparison of Model Results and Observed Data



It was also during this time that the generalized water quality modeling code known as WASP (Water Analysis Simulation Program) came into being. The earlier Sacramento-San Joaquin Delta model developed by DiToro *et al.* (1971) used an IBM 1130 version of the Continuous System Modeling Program (CSMP), a continuous system simulation language (cf. Speckhart 1976). While CSMP was very effective for "bread-boarding" models, it was not a practical tool for running multi-segment water quality models; hence, leading to the development of WASP. The WASP computer code was eventually documented (DiToro *et al.* 1981) and transferred to the USEPA Large Lake Research Station, Grosse Ile, Michigan. Subsequent to this the USEPA Center for Exposure Assessment Modeling (CEAM), Athens, Georgia provided support for the model, eventually updating the eutrophication kinetics based on a eutrophication modeling study of the Potomac River Estuary (Thomann and Fitzpatrick 1982) and adding a riverine-based hydrodynamic model, DYNHYD, to the modeling package (Ambrose *et al.* 1988). The WASP computer code was also used as a platform for the development of WASTOX, which models the fate and transport of toxic substances (Connolly and Winfield 1984). The WASP modeling package is still supported by the USEPA (Ambrose *et al.* 1993) and is still being used in many water quality studies within the United States.

Lake Ontario was the next of the Great Lakes wherein eutrophication modeling was applied. This work was performed under an EPA grant to Manhattan College and resulted in a two-volume EPA Ecological Research Series Report (Thomann *et al.* 1975; Thomann *et al.* 1976). The major feature of the Lake Ontario eutrophication model (which used the eutrophication kinetic structure known as LAKE 1) that differed from the Lake Erie model was the incorporation of vertical segmentation to represent the epilimnion and hypolimnion of the lake. A relatively simple two layer version of Lake Ontario, which assumed horizontal homogeneity, was calibrated to a four year (1966-1969) CCIW data set and a satisfactory calibration was achieved. Thomann *et al.* (1975) also developed a preliminary calibration of a 67 segment three-dimensional representation of the lake. The 67 segments were distributed over five vertical layers and included a "ring" of segments, extending 10 km out from the shoreline, to represent the near-shore environment. The model used vertical casts of seasonal water column temperature to calibrate the vertical mixing coefficients between adjoining vertical segments. While initial calibration results were encouraging, the authors reported that, "The size of the LAKE 3 model makes it difficult to fully comprehend the output [from the model]..." and subsequent application of the LAKE 3 model was limited. Thomann *et al.* (1976) also performed some long-term simulations and noted that it would require a number of years for lake phytoplankton biomass and primary productivity to respond to reductions in phosphorus inputs to the lake.

LAKE 1A

The next phase in the development of Lake Erie eutrophication models (DiToro and Connolly 1980) resulted in expansions in both the number of segments used to represent the spatial geometry of the lake (Figure 5) and the number of state-variables used in the kinetic

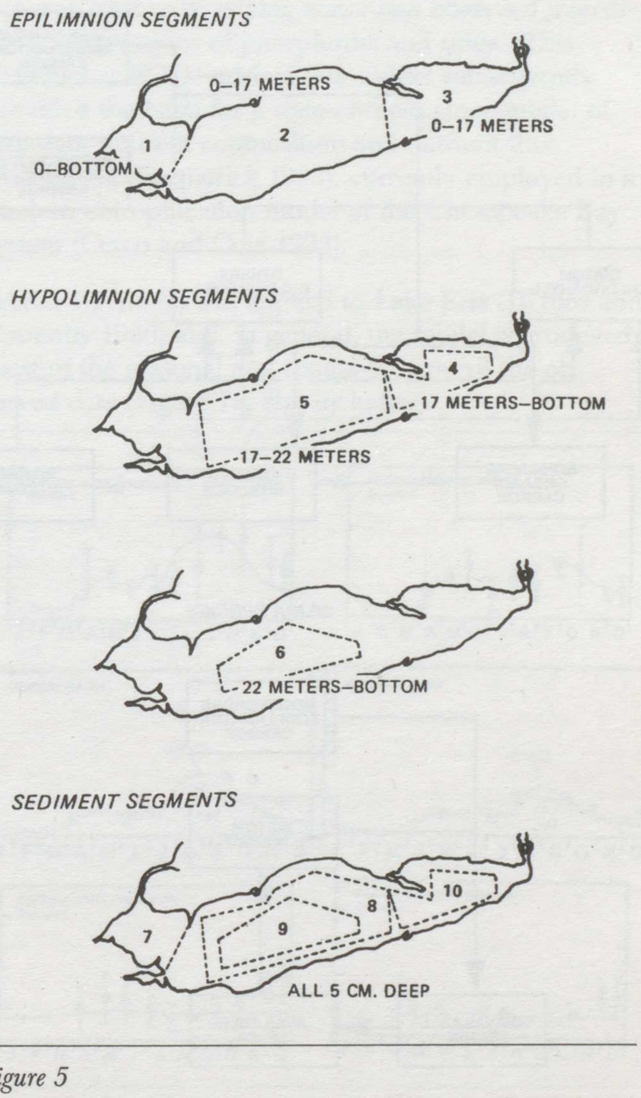


Figure 5
Lake Erie Model Segmentation of Western, Central and Eastern Basins: Water Segments 1-6, Epilimnion (top) and Hypolimnion (middle); Sediment Segments 7-10 (bottom). DiToro and Connolly, 1980.

framework (Figure 6). The revised model segmentation divided the lake into five segments, three to represent the epilimnion of the western, central, and eastern basins of the lake and two segments to represent the hypolimnion of the central and eastern basins of the lake.

The number of state-variables was expanded from 8 to 15 and included: diatom and non-diatom chlorophyll-a, herbivorous and carnivorous zooplankton, detrital organic nitrogen, ammonia nitrogen, nitrate nitrogen, unavailable phosphorus and soluble reactive phosphorus, unavailable silica, soluble reactive silica, detrital organic carbon, dissolved inorganic carbon, alkalinity, and dissolved oxygen. The kinetic framework of the model was expanded in part to better represent the observed seasonal patterns in phytoplankton growth (diatoms and non-diatoms) and the observation that silica appeared to be the nutrient limiting spring phytoplankton growth. The other reason for expanding the kinetic framework of the model by adding total inorganic carbon and alkalinity state-variables was to reduce the degrees of freedom in model calibration. Since a major concern of the authors was to ensure that the reactions involving oxygen were correctly incorporated and since carbon dioxide (inorganic carbon), as well as oxygen, is produced or consumed as a consequence of primary production, algal respiration and oxidation of organic carbon, by including dissolved

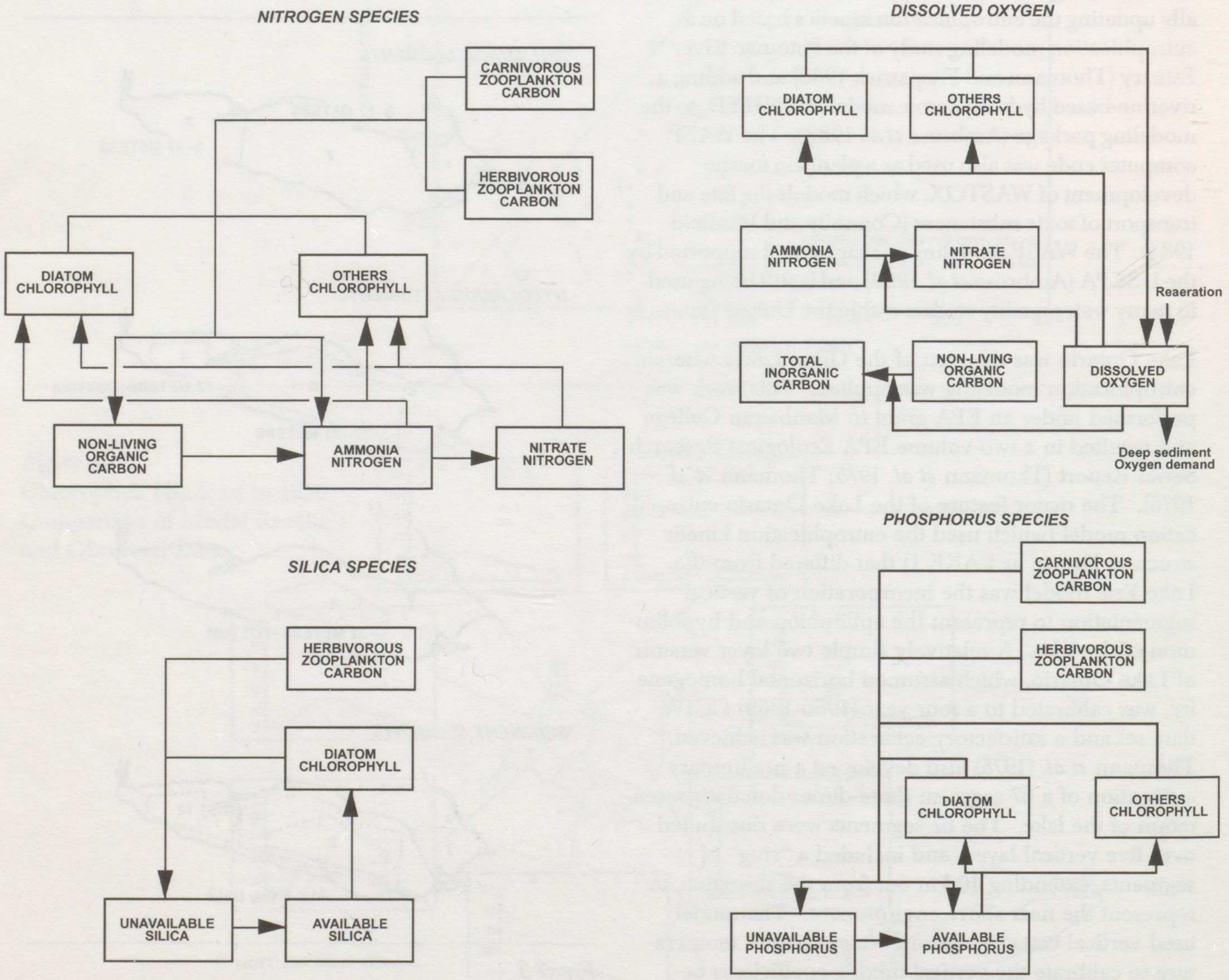


Figure 6
Lake Erie State Variable Interactions. Representations of nitrogen (top left) and silica (bottom left) and dissolved oxygen (top right) and phosphorus (bottom right) nutrient cycles. DiToro and Connolly, 1980.

inorganic carbon and alkalinity, it was possible to check model computations against observations of pH. Furthermore, since alkalinity production and destruction could be calculated for each of the relevant processes in the kinetic framework, using appropriate stoichiometric ratios, adding dissolved inorganic carbon and alkalinity to the calculation actually decreased the degrees of freedom, since there was no increase in the number of constants used during model calibration and since more data were available for model-data comparisons.

An additional feature of the LAKE 1A kinetic framework was the inclusion of a preliminary model of sediment oxygen demand (SOD) and sediment nutrient flux. The SOD/nutrient flux model was incorporated because it was realized that interactions between lake waters and sediments could have a profound effect on the concentrations of oxygen and nutrients in a comparatively shallow lake such as Lake Erie. Analysis of observed nutrient fluxes and measurements of SOD indicated that areal fluxes from the sediments of Lake Erie were substantial sources to the water column based on a volumetric basis. Additionally, it was observed that the occurrence of hypoxia and anoxia dramatically increased certain nutrient flux rates to the water column. The preliminary SOD/nutrient flux model utilized a single sediment layer and included a one-dimensional mass transport equation for the concentrations of dissolved substances (ammonia, CO2, and the oxygen-demanding end-products of organic carbon decomposition, i.e., sediment oxygen demand) and first-order decay for detrital organic nitrogen and organic carbon. At the time of their study, the authors believed that the complete analysis of phosphorus and silica fluxes would require a rather elaborate computation of solution-precipitate chemistry, which was beyond the scope of the study. Instead they used an empirical approach which relied on observed interstitial water concentrations of phosphate and silica. During periods of bottom water aerobic conditions, it was assumed that phosphorus and silica fluxes did not occur. During periods of bottom water anaerobic conditions, the diffusive exchange was set to the same value used for ammonia, CO2, and oxygen. Phosphorus and silica fluxes were then computed using this diffusion coefficient and gradients in concentration between bottom overlying water and observed interstitial concentrations of phosphorus and silica. This preliminary SOD/nutrient flux model subsequently provided the basis for a state-of-the-science model of sediment nutrient composition and nutrient flux (DiToro and Fitzpatrick 1993), currently employed in a modern eutrophication model of the Chesapeake Bay system (Cerco and Cole 1993).

LAKE 1A model was applied to Lake Erie (DiToro and Connolly 1980) and, in general, the model reproduced most of the seasonal and spatial features of the observed data (Figure 7a, 7b), including:

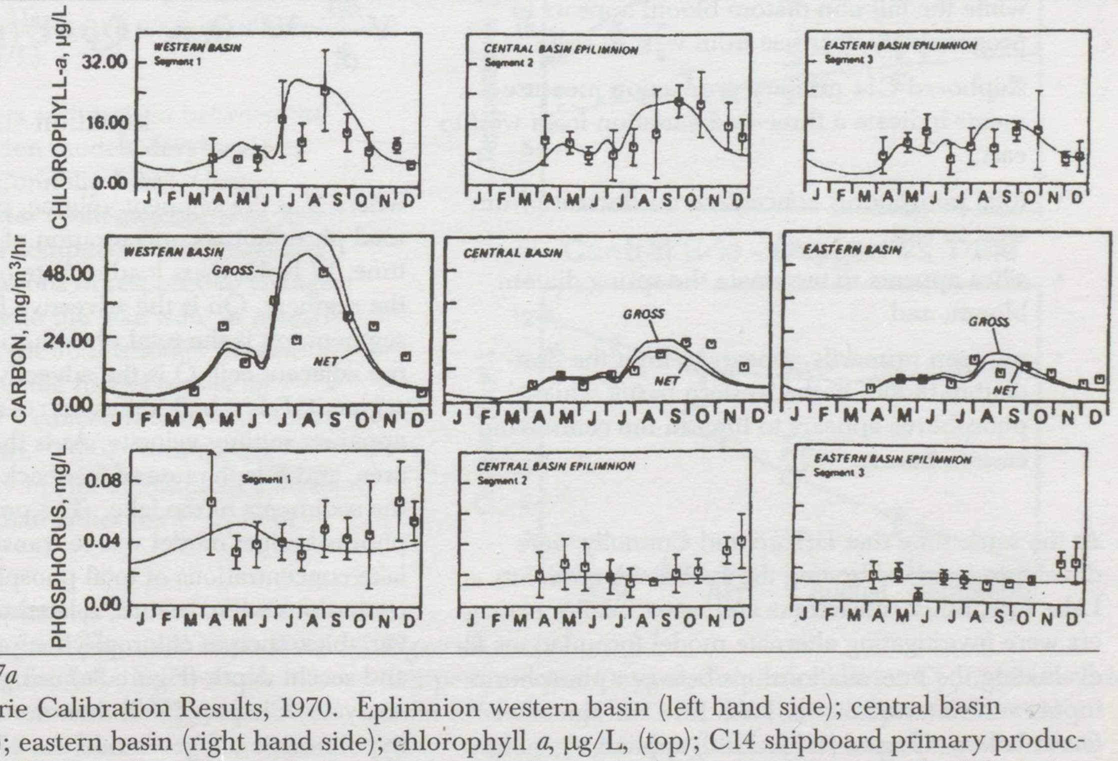


Figure 7a

Lake Erie Calibration Results, 1970. Eplimnion western basin (left hand side); central basin (center); eastern basin (right hand side); chlorophyll *a*, μg/L, (top); C14 shipboard primary production mg C/m3/hr (middle); total phosphorus mg/L (bottom). Symbols: mean + standard deviation.

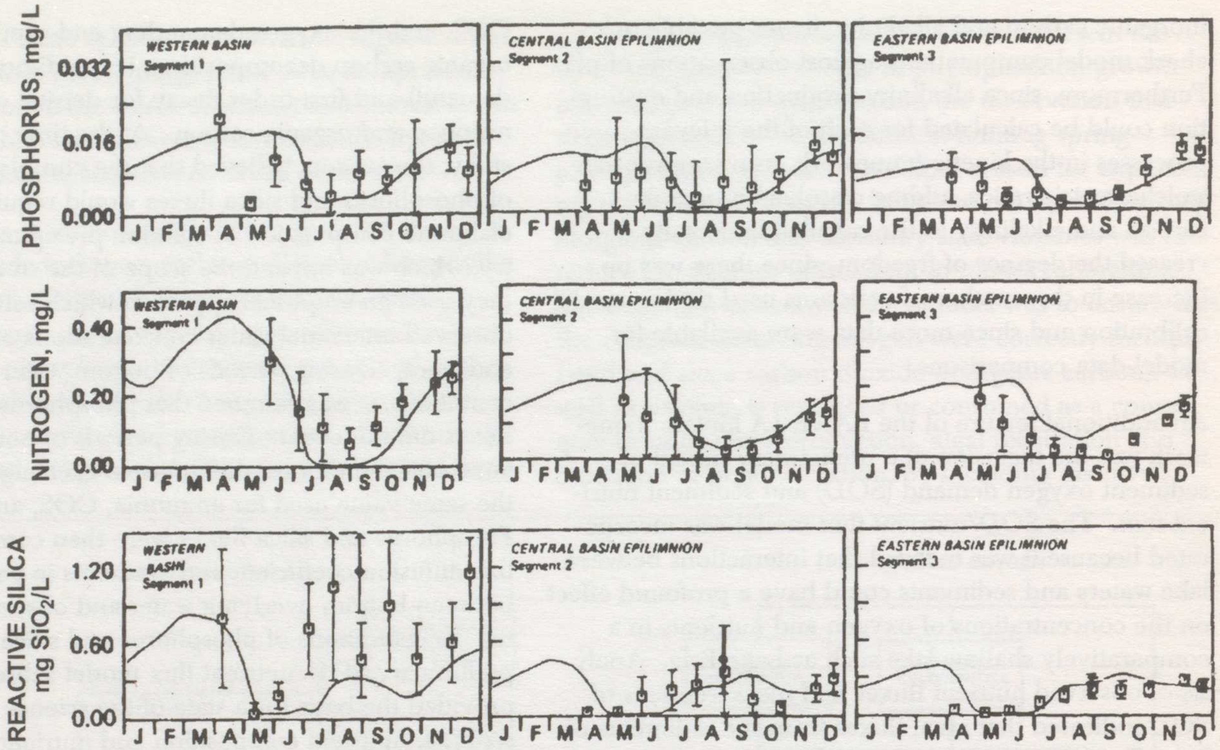


Figure 7b

Lake Erie Calibration Results, 1970. Eplimnion western basin (lefthand side); central basin (center); eastern basin (right hand side); orthophosphorus (top); nitrate nitrogen (middle); reactive silica (bottom).

- the observation that the spring diatom bloom was similar in magnitude across the three basins, while the fall non-diatom bloom appears to progressively decrease from west to east;
- shipboard C14 primary production measurements indicate a three-fold variation from west to east;
- total phosphorus concentrations decrease from west to east;
- silica appears to terminate the spring diatom bloom; and
- nitrogen primarily appears to limit the non-diatom bloom in the western basin, while phosphorus appears to limit in the central and eastern basins.

At the same time that DiToro and Connolly were developing and calibrating the LAKE 1A model to Lake Erie, other researchers and water quality managers were investigating alternate model formulations for evaluating the interrelationships between phosphorus inputs and water quality in Lake Erie and the other Great Lakes. Chapra (1977; 1980) applied a general total phosphorus budget mass balance equation (shown in Equation 1) to each of the Great Lakes:

$$V\frac{dp}{dt} = W + Q_b p_b - Qp + E'\left(p_b - p\right) - vA_s p + F$$

Equation 1.

where V is the segment volume, p is the mean annual total phosphorus concentration of the segment, t is time, W is the mass loading rate of total phosphorus to the segment, Qb is the advective flow from an adjacent segment, pb is the total phosphorus concentration of the adjacent cell, Q is the advective flow leaving the segment, E is a bulk diffusion coefficient, v is the apparent settling velocity, As is the segment surface area, and F is the rate of feedback of phosphorus from the sediments of the lake. The purpose of the phosphorus budget model was to transform loadings into in-lake concentrations of total phosphorus. These concentrations were, in turn, related to other trophic variables, such as chlorophyll *a*, primary production, and secchi depth (Figure 8a) using statistical correlation analysis. Chapra (1980) then developed a hypolimnetic oxygen model for Lake Erie and using observed epilimnetic and hypolimnetic temperature and oxygen data (Figure 8b) found the following relationship for the lake:

$$DO_{min} = 10.22 - 0.054\, P_r$$

where DOMIN is the minimum concentration of hypolimnetic oxygen just before turnover and Pr is the mean annual surface production, which could be estimated from the relationships shown in Figure 8a. Chapra (1980) then utilized this model to develop system response matrices for each Great Lakes model segment.

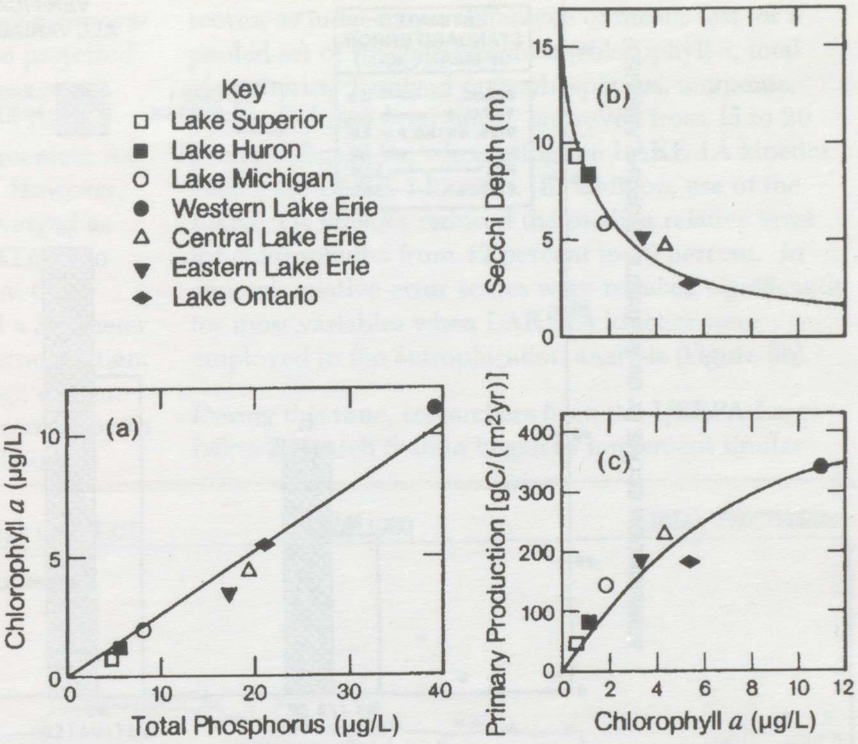


Figure 8a

Correlations Between Surface Water Quality Variables

Vollenweider *et al.* (1980) reported on the formulation of a phosphorus loading plot model (Vollenweider 1966) and its application by Rast and Lee (1978) to the Great Lakes system. The phosphorus loading model was then used to predict changes in the average chlorophyll-a concentrations and secchi depths that would result in each of the Great Lakes from the implementation of proposed phosphorus loading objectives contained in the 1978 Great Lakes Water Quality Agreement. For Lake Erie, the Vollenweider model projected a 33 percent reduction in average chlorophyll concentrations (from 5 ug/L to 3.3 ug/L).

Bierman (1980) made a comparison between the Lake Erie eutrophication models developed by DiToro (DiToro and Connolly 1980), Chapra (1980) and Vollenweider (Vollenweider *et al.* 1980) and found that model computations of projected phosphorus concentrations in response to changes in phosphorus loading to the lake were in reasonably good agreement with one another. In general, agreement among the model results for projected chlorophyll *a* concentrations was not as good as for phosphorus. The DiToro model computed significantly higher chlorophyll *a* levels in the western basin than either the Chapra or Vollenweider models.

However, there was better agreement in the central and eastern basins. The most important water quality indicator for Lake Erie was dissolved oxygen concentration in the hypolimnion of the central basin. It was here that the greatest divergence between the models was observed.

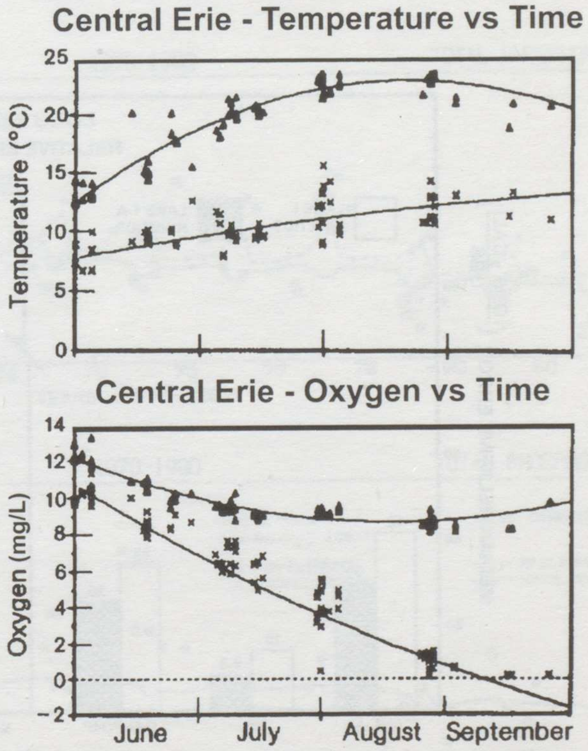


Figure 8b

Temperature and Oxygen Concentration for Central Lake Erie from 1967 through 1972 for the Summer Stratified Period (June through September). Triangles designate surface data (1m depth) and x's designate bottom data (>=22m depth).

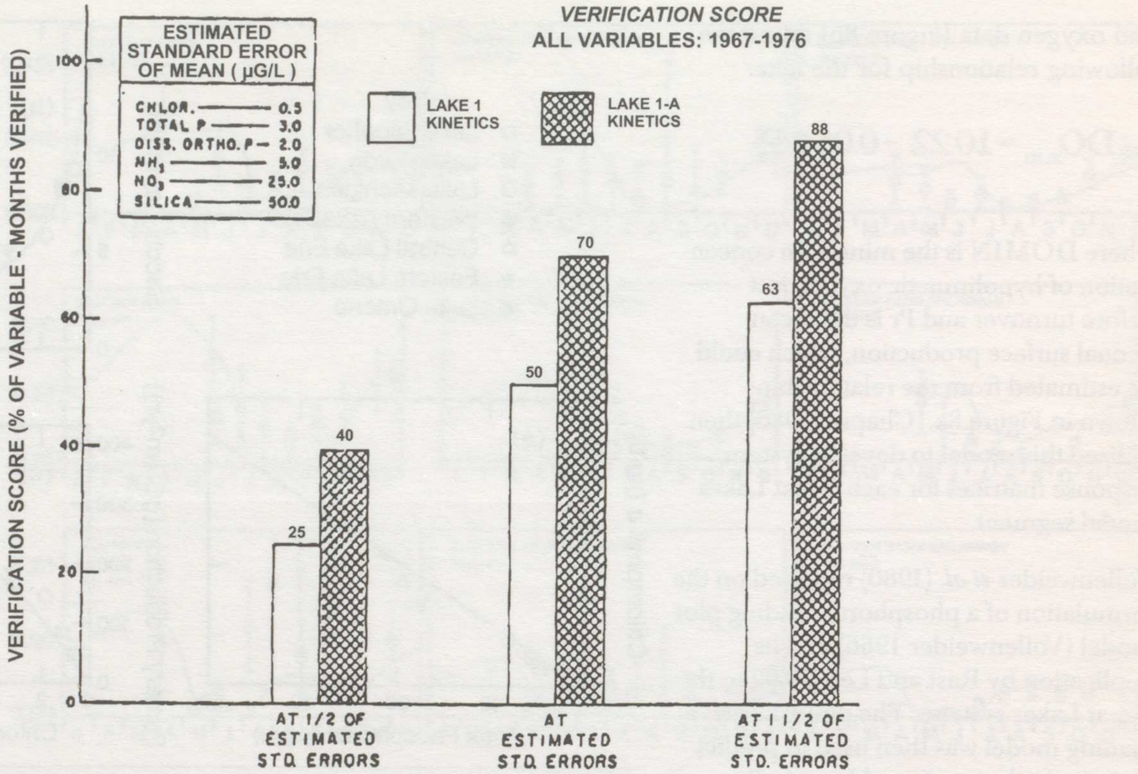


Figure 9a
Verification Scores, Difference of Means Test, Pooled Six-state Variables, 1967-1976

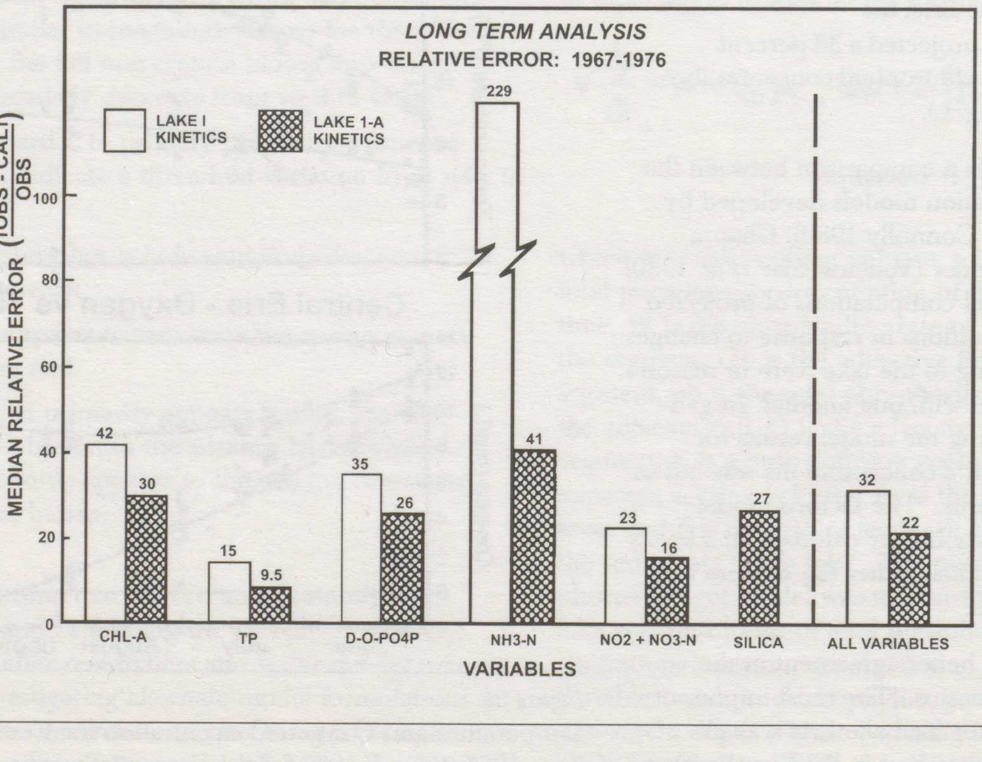


Figure 9b
Relative Error Scores, Six-state Variables and Across All Variables

The DiToro model projected dissolved oxygen concentrations that were 2 mg/L higher than those projected by the Vollenweider model in the loading range of 8,000 to 10,000 metric tonnes (MT)/yr. The DiToro and Chapra models were in reasonable agreement for phosphorus loads less than 12,000 MT/yr. However, results for the two models progressively diverged as phosphorus loads increase above 12,000 MT/yr. In part, this may have been due to the fact that the Vollenweider and Chapra models assumed a 3.3 meter hypolimnion depth at the end of summer stratification, while the DiToro model represented average concentrations below a depth of 17 meters in the central basin at the end of summer stratification. In addition, Bierman concluded that computations from the DiToro model were more representative of volumetric conditions, while the Vollenweider and Chapra models were more representative of areal conditions.

The LAKE 1A modeling framework was also applied to Lake Ontario and a modeling analysis of ten years of Lake Ontario data was reported by Thomann and Segna (1980). Thomann and Segna (1980) also used statistical analysis to help quantify the calibration of the model to the observed data and further compared on a statistical basis the improvement in model calibration provided by the LAKE 1A kinetic formulation versus the LAKE 1 kinetics. In summary, Thomann and Segna (1980) found model verification scores, as judged by a difference of means test for a pooled set of six state-variables (chlorophyll-a, total phosphorus, dissolved orthophosphorus, ammonia, nitrate and dissolved silica), improved from 15 to 20 percent (Figure 9a) when using the LAKE 1A kinetics versus the LAKE 1 kinetics. In addition, use of the LAKE 1A kinetics reduced the median relative error for chlorophyll-a from 42 percent to 30 percent. In general, relative error scores were reduced significantly for most variables when LAKE1A kinetics were employed in the eutrophication analysis (Figure 9b).

During this time, researchers from the USEPA Large Lakes Research Station began to implement similar

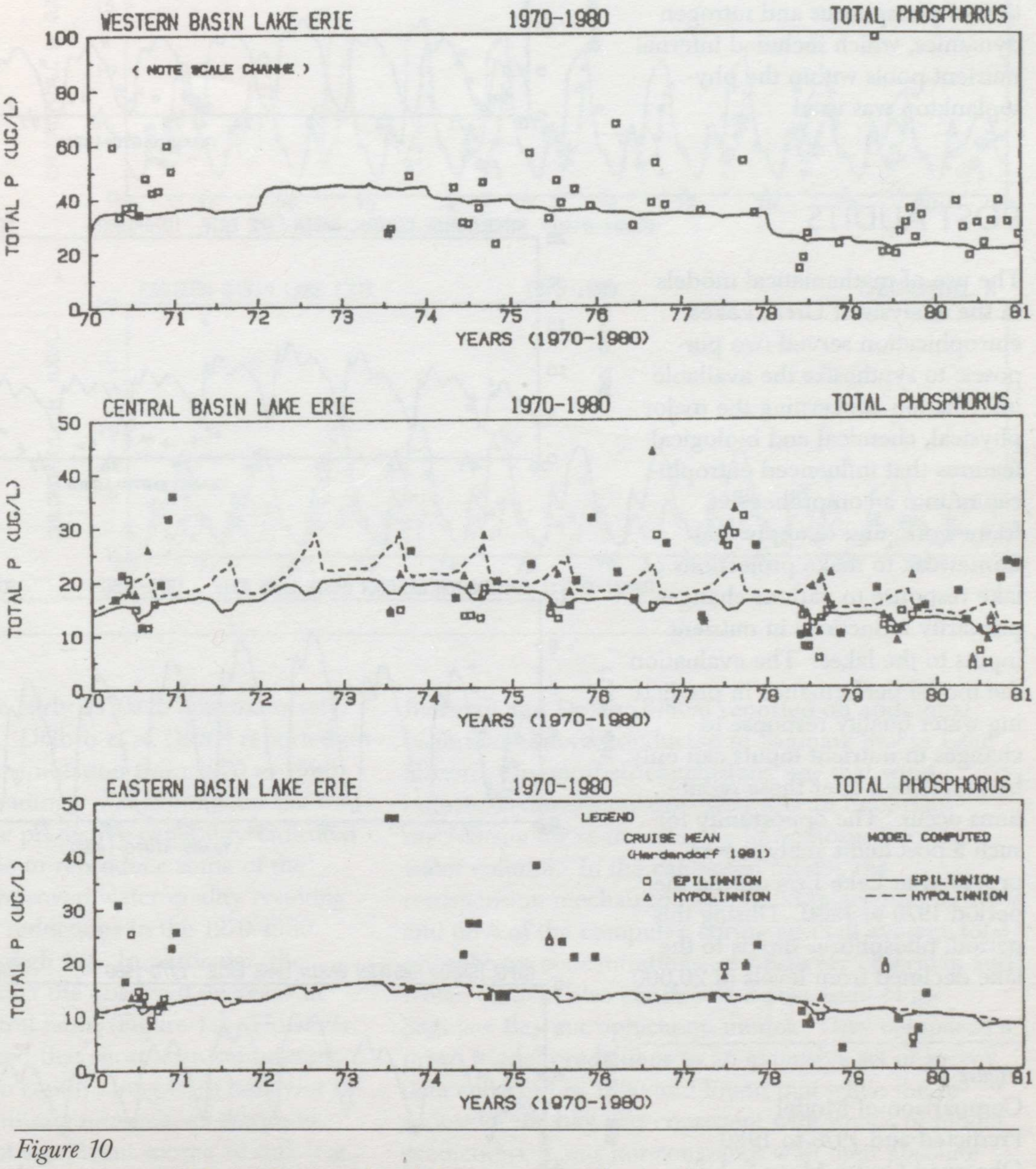


Figure 10
Comparison of Model Predicted and 1970 to 1980 Observed Cruise Mean Total Phosphorus Data

versions of the DiToro and Thomann eutrophication models. In particular, Bierman *et al.* (1980) developed and calibrated a multi-class internal nutrient pool phytoplankton model for Saginaw Bay in Lake Huron. The Bierman model differed from the DiToro and Thomann models in that phytoplankton biomass was partitioned into five functional groups: diatoms, greens, N2-fixing blue-greens, non-N2-fixing blue-greens and "others." In addition, a more detailed kinetic representation of phosphorus and nitrogen dynamics, which included internal nutrient pools within the phytoplankton was used.

POST AUDITS

The use of mathematical models in the analysis of Great Lakes eutrophication served two purposes: to synthesize the available information concerning the major physical, chemical and biological features that influenced eutrophication into a comprehensive framework; and to apply that framework to make projections of lake response to various changes, primarily reductions in nutrient inputs to the lakes. The evaluation the model performance in predicting water quality response to changes in nutrient inputs can only be performed after these reductions occur. The opportunity for such a post audit analysis was provided in Lake Erie during the period 1970 to 1980. During this period, phosphorus inputs to the lake declined from levels of 20,000

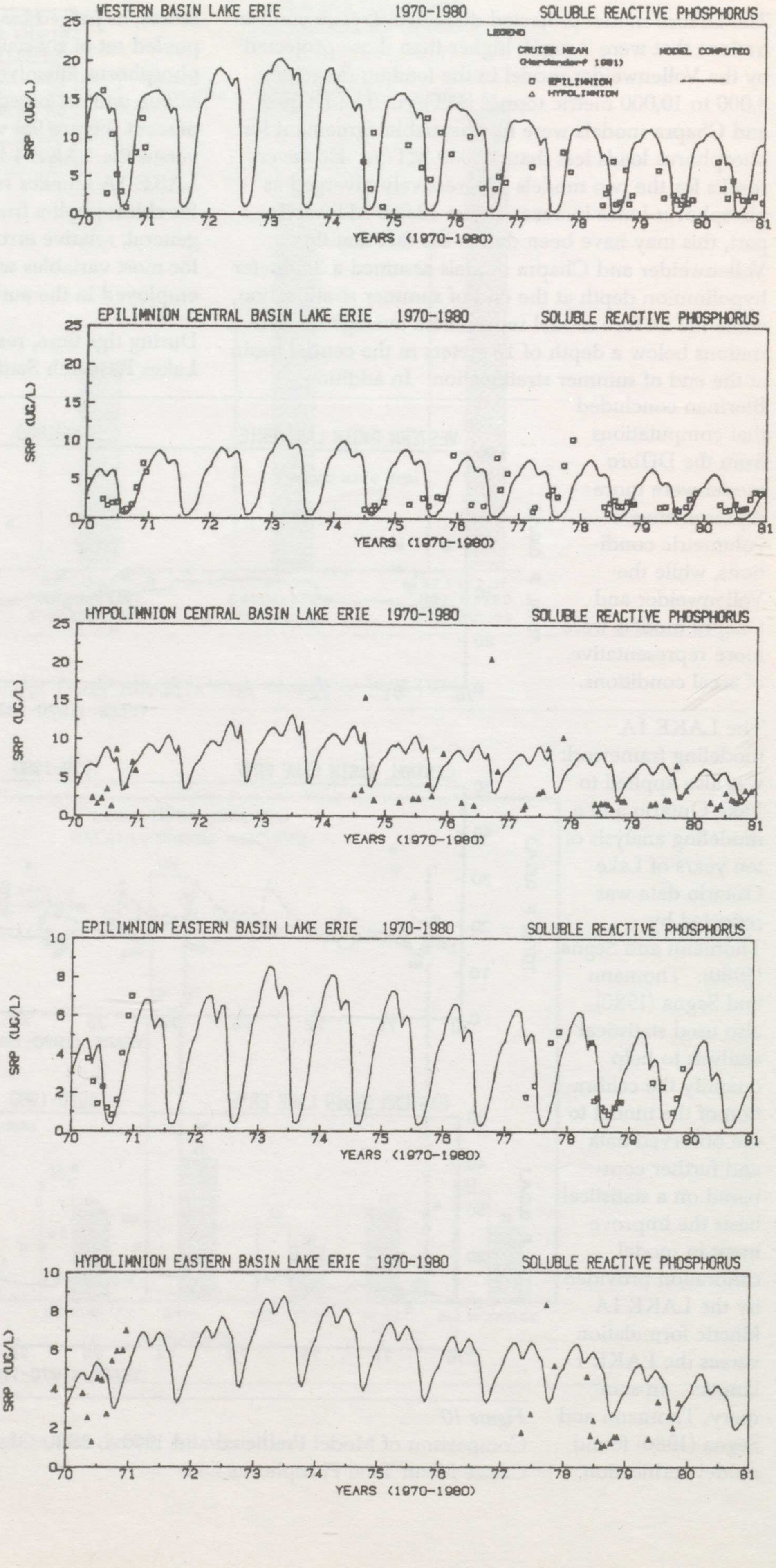


Figure 11
Comparison of Model Predicted and 1970 to 1980 Observed Cruise Mean Soluble Reactive Phosphorus

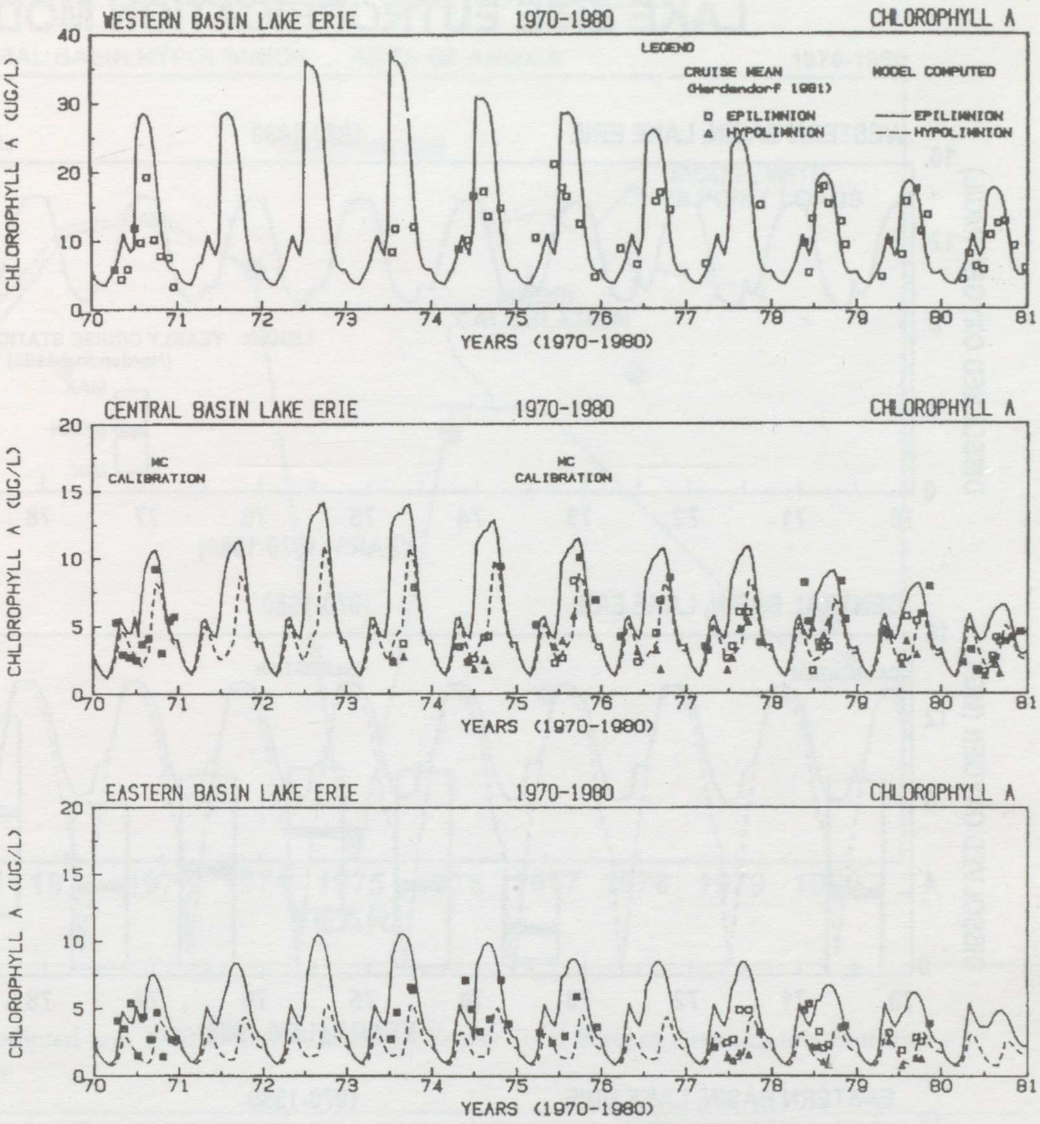


Figure 12
Comparison of Model Predicted and 1970 to 1980 Observed Cruise Mean Chlorophyll *a* –Western, Central, and Eastern Basins of Lake Erie

to 25,500 MT/yr in the early 1970s to approximately 13,500 MT/yr in 1980. DiToro *et al.* (1987) reported on the results of a 10-year simulation from 1970 to 1980 using measured lake loadings. An examination of the model's long time scale predictive capability indicated that the model was able to reproduce some of the observed features of improved water quality resulting from total phosphorus reductions in the 1970-1980 decade (Figures 10 through 13). In particular, the model was able to predict the observed decrease in anoxia area of the central basin (Figure 14). However, the results also illustrated that short-term calibrations (e.g., one year) failed to capture long-term behavior of certain variables (e.g., nitrate nitrogen, as shown in Figure 15) if a small but significant source or sink (e.g., sediment denitrification) was not well calibrated in short-term computations.

Bierman and Dolan (1986a) reported on additional calibration efforts conducted in Saginaw Bay in Lake Huron. One of their conclusions was that wind-induced sediment resuspension was an important mechanism for re-introducing phosphorus into the water column. In the calibrated model, the resuspension mechanism was found to account for 36% and 68% of the computed spring and fall average total phosphorus concentrations, respectively. Bierman and Dolan (1986b) also conducted a post audit of the Saginaw Bay eutrophication model. They compared a priori model predictions to an extensive set of survey data collected in 1980 and found that while the response of the bay was consistent with trends of model predictions, it was not consistent with their absolute values in all cases. In particular, observations were consistent with model predictions that threshold odor

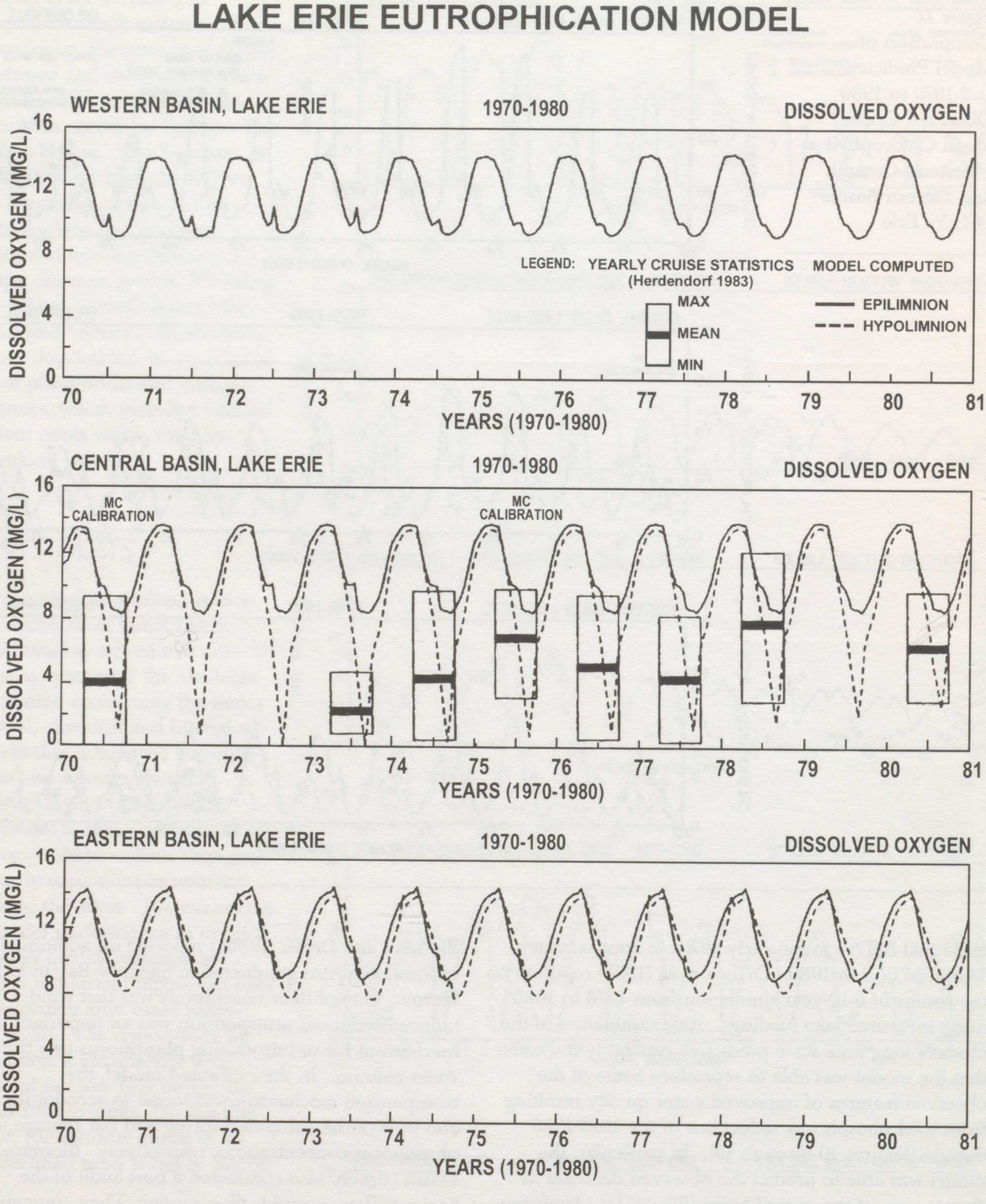


Figure 13

Comparison of Model Predicted and 1970 to 1980 Observed Yearly Dissolved Oxygen Statistics – Western, Central, and Eastern Basins of Lake Erie

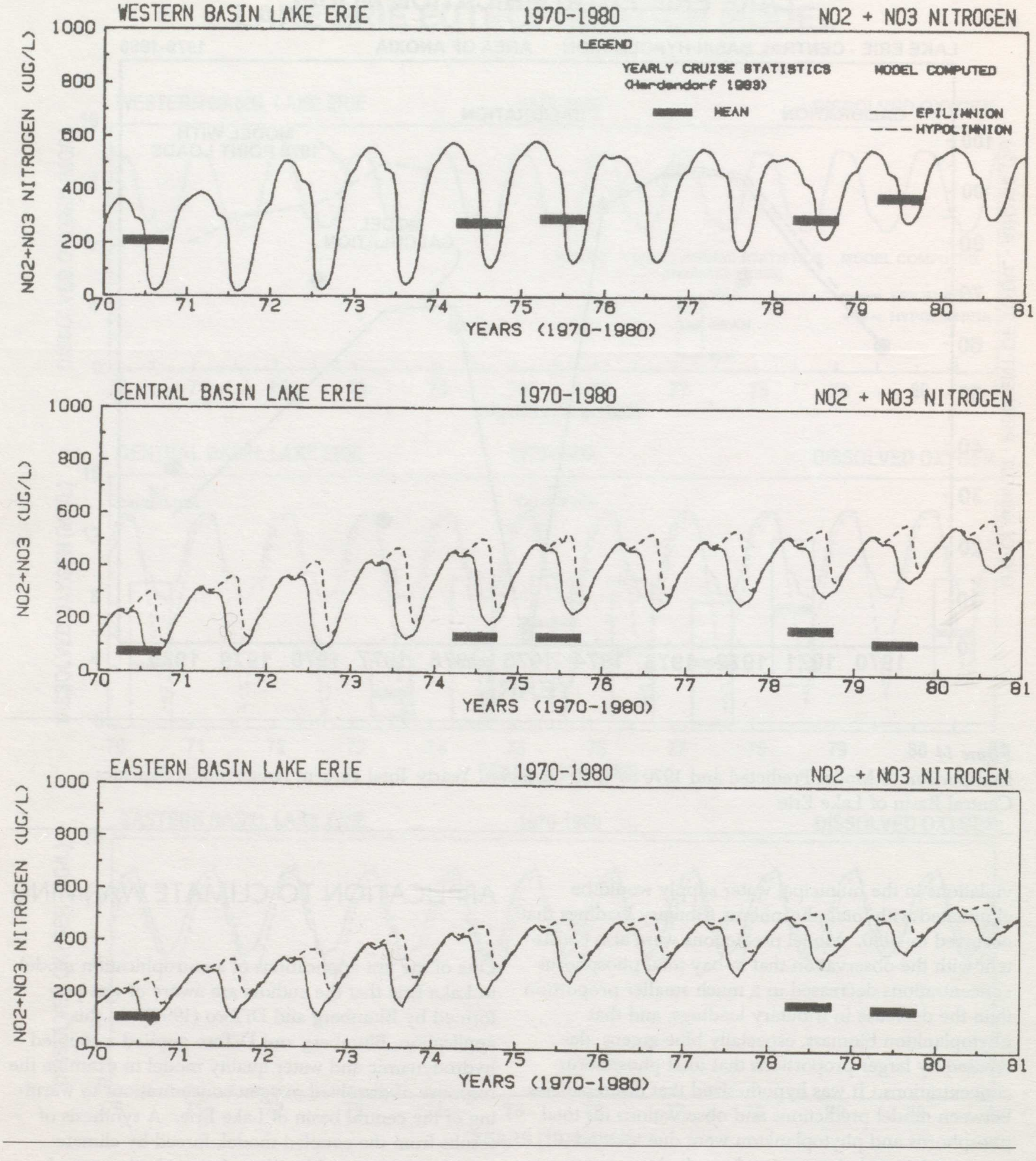


Figure 15

Comparison of Model Predicted and 1970 to 1980 Observed Yearly Mean Nitrite Plus Nitrate Nitrogen Statistics – Western, Central, and Eastern Basins of Lake Erie modeled decline was predicted to be due to warmer lake temperatures, which would increase the rates of bacterial activity in the hypolimnion waters and sediment, rather than due to thermocline location and volume of water below the thermocline. While the 1 mg/L decline in the epilimnion would not greatly affect fish life, the projected declines to 3 mg/L or less in the hypolimnion could pose a threat to adult "coldwater" fish life.

CURRENT STATE-OF-THE-SCIENCE

In many ways, the current state-of-the-science in eutrophication modeling has not changed appreciably from the models of DiToro, Thomann, and Bierman. The basic linkages between nutrients, phytoplankton biomass, primary production, nutrient recycle, and dissolved oxygen in today's eutrophication models are quite similar to the Great Lakes' models. Most modern eutrophication models still use the Monod theory for which algal growth rates depend upon external nutrient concentration rather than the formulations in which growth rate depends on the internal cellular nutrient concentration (e.g., Bierman 1980). However, one recent modification to the structure of algal growth dynamics is the inclusion of variable nutrient stoichiometry for phytoplankton biomass. In their model application to Chesapeake Bay, Cerco and Cole (1993) included a function which permitted variation in the carbon to phosphorus (C:P) ratio for phytoplankton biomass. This empirical function was developed from observed C:P ratios and soluble reactive phosphorus data in the upper bay. HydroQual (1995b) recently implemented a more process-based function for variable carbon to nutrient stoichiometry, which also included variable carbon to chlorophyll stoichiometry, in a modeling study of the Massachusetts Bays system. This model formulation was based on a model developed by Laws and Chalup (1990). A unique feature of this model is that it accounts for variable carbon to chlorophyll ratios in phytoplankton due to both light and nutrient status.

Perhaps the two most significant changes that have been incorporated into modern eutrophication models are: (1) the addition of a coupled water column/sediment nutrient flux submodel; and (2) the direct coupling of time-variable three-dimensional hydrodynamic and water quality models. The sediment nutrient flux model framework accounts for the deposition of organic matter from the water column to the sediment bed of the water body, its subsequent diagenesis or decomposition, and the flux of resulting end-products back to the overlying water column. The model includes sediment processes for temperature and oxygen-dependent nitrification-denitrification, sorption of dissolved inorganic phosphorus and dissolved inorganic silica to sediment solids and the sorption of dissolved inorganic phosphorus to iron hydroxides in the aerobic layer of the sediment. The model also considers the generation of sediment oxygen demand, hydrogen sulfide and methane from the reduction of organic matter. The model was developed and calibrated in Chesapeake Bay to an extensive multi-year data set (DiToro and Fitzpatrick 1993). The model has been further verified against a wide-range of nutrient conditions using an extensive nutrient flux data set obtained from the University of Rhode Island MERL mesocosms. The model successfully reproduced the observed sediment nutrient composition and nutrient flux data using essentially the same parameter set as was used for Chesapeake Bay. The only parameters to be changed between the two calibrations were the temperature-correction coefficients associated with diagenesis and the aerobic/anaerobic partition coefficients for phosphorus sorption. The MERL data were collected more frequently than the Chesapeake Bay data and, therefore, included more "cold weather" measurements than did the Chesapeake Bay data set. These additional data required minor adjustments to these temperature coefficients in order to reproduce the "cold weather" data. It also appeared reasonable that the phosphorus partition coefficients might be different between the two systems given differences in the iron content of the sediments in Chesapeake Bay and the MERL mesocosms (Narragansett Bay).

Examples of the coupling of water quality models to high resolution time-variable three-dimensional hydrodynamic models include the Chesapeake Bay system (Cerco and Cole 1993), the Massachusetts Bays system (HydroQual 1995b; Blumberg and Fitzpatrick 1999). The use of well calibrated hydrodynamic models to drive water quality model computations is that it removes a degree of freedom in model calibration, i.e., the external specification of advective and dispersive transport. In addition, the use of high resolution hydrodynamic/water quality models removes, to a large degree, the "numerical errors" or numerical dispersion associated with coarse-grid or box water quality models.

RELEVANCE OF EUTROPHICATION MODELS TO LAKE ERIE WATER QUALITY PROBLEMS

While to a large degree the issue of eutrophication has been addressed in Lake Erie and signs of improvement in water quality and ecosystem health have been observed (Bertram 1993; Makarewicz 1993; Schloesser *et al.* 1995; Krieger *et al.* 1996), there still remain a number of environmental concerns within the lake. These include:

- primary production and total algal biomass;
- blue-green algal biomass;
- walleye production;
- invasion by non-native species (e.g., zebra mussels);
- fish body burdens of bioaccumulative chemicals (e.g., polychlorinated biphenyls (PCBs)); and
- richness and evenness of fish community trophic levels between algae and top predator fish.

At present it would seem that modern state-of-the-science eutrophication models could play an important role in helping to address some of these water quality issues through an "ecosystem approach." Certainly eutrophication models address the first two issues directly. Consideration should be given to updating the existing Lake Erie eutrophication water quality models to include the sediment nutrient flux model and coupling to time-variable three-dimensional hydrodynamic models of the lake. Primary production of organic carbon is also essential to understanding and modeling of the fate and transport of toxic materials in the lake, since many of these materials sorb to dissolved and particulate matter. The coupling of the eutrophication and sediment nutrient flux model may also help to understand the trapping and bio-availability of toxic metals in sediments, since sulfide is a state-variable in the sediment nutrient flux submodel. Some zebra mussel modeling has been conducted by Limno-Tech, Inc. and may provide a useful starting point for integration into a eutrophication/zebra mussel ecosystem modeling package. HydroQual, Inc. has recently completed work on the development of a suspension and deposit feeder model for the Chesapeake Bay system. This submodel, which is linked to the water column/nutrient flux model of the Bay, has also successfully been applied to Jamaica Bay, New York with minimum changes in model parameters.

We believe that coupling eutrophication models to fisheries models becomes more speculative, although some efforts have been initiated in Chesapeake Bay and the Great Lakes community. While coupled hydrodynamic/water quality models of eutrophication can provide information (e.g., water temperature, available food, dissolved oxygen, etc.) to fisheries models, the projections of walleye production and fish community structure and diversity are made more complicated by the interactions between various predator/prey fish species, the impacts of overfishing, and perhaps the relatively long life-spans of the fish themselves. Perhaps the area requiring the greatest research and monitoring effort is the area of the fishery.

Appendix D

Trophic Transfer in Lake Erie: A Whole Food Web Modeling Perspective

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INTRODUCTION

The Lake Erie ecosystem has experienced major perturbations such as reductions in phosphorus loading, variations in commercial fish harvests, and the invasion of exotic species such as dreissenid mussels and white perch (*Morone americana*). These perturbations have precipitated food web changes that include reductions in the abundance of many fish species, shifts in composition and productivity of the algal community, emergence of a more diverse littoral invertebrate community, and the virtual loss of the deepwater amphipod, *Diporeia hoyi*, from the east basin. Formulating management plans for an ecosystem undergoing such fluctuations is almost impossible without models that provide a detailed quantification of the complex of ecological processes. In this paper we present one such model that quantifies the transfer of material from prey to predator at each of the major trophic links in the Lake Erie pelagic food web.

OBJECTIVES

Our goal is to:

a) provide a quantitative summary, over a specified spatial and temporal scale, of the biomass and consumption for all major trophic groups in the pelagic waters of Lake Erie; and
b) relate the energy demands of the predator to the biomass, energy consumption, and production of prey at each major trophic link in the food web.

Our model is not a dynamic simulation, nor does it explicitly represent the many detailed processes involved in the transfer of energy through a food web. Compartments in the model represent the mean biomass of component trophic groups over moderate spatial and temporal scales. The input to each trophic group is consumption of prey, and output from the group is consumption by its predators. Production of each trophic group is also retained in the model. Since the model is not dynamic the biomass of each trophic group does not change in response to gains and losses during a time period. The model simply provides a summary of these seasonal gains and losses, and the biomass, for each trophic group.

The model is designed to identify linkages in the food web that may be approaching an unstable state. In reality the biomass of any trophic group would fluctuate through time according to variations in consumption and losses. Only a persistent imbalance between consumption and losses would lead to a change in biomass. Trophic groups with high biomass would clearly have a higher capacity to sustain persistent net losses than groups with low biomass. Since our model represents only the mean state of the Lake Erie food web, we consider a trophic group to be unstable if there is an excess of losses to predators over gains from prey, and if this excess is large relative to the biomass of the group. Such instability would be evidenced by excessive energy demands by predators on zooplankton (planktivorous fish and carnivorous invertebrates) compared to total algal energy consumption and resultant production by zooplankton, particularly if

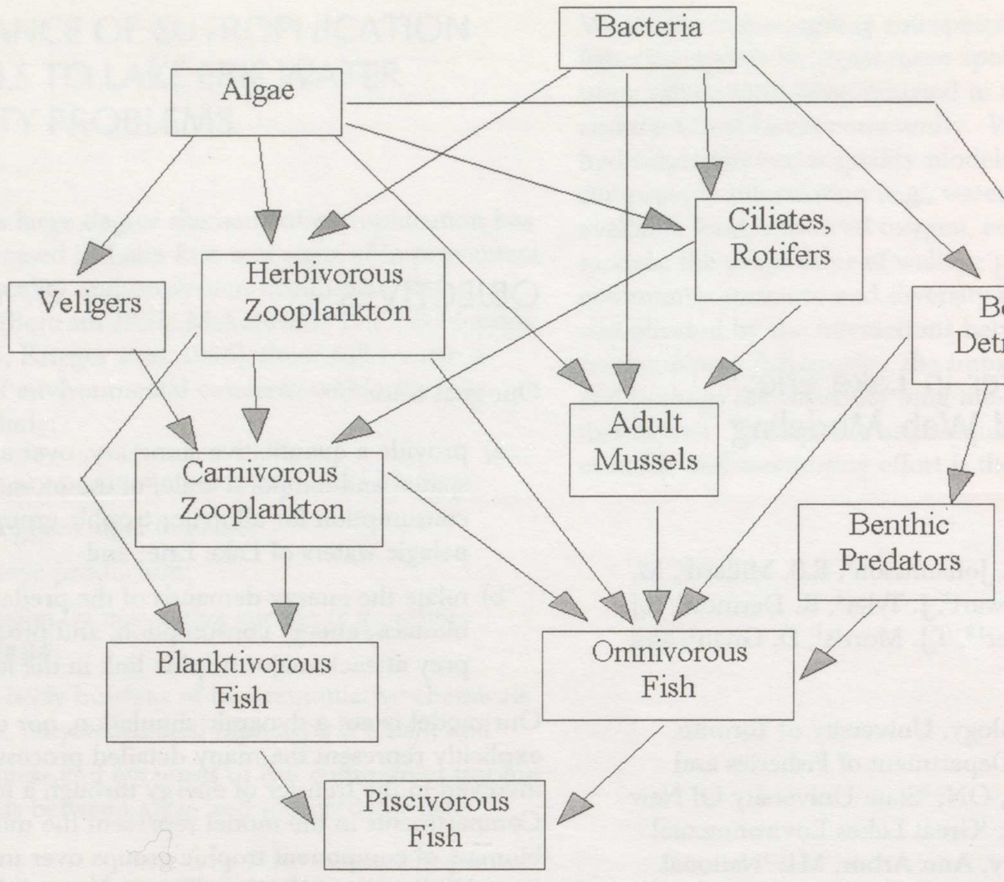

Figure 1
The Food Web of the West Basin of Lake Erie as Represented in the Trophic Transfer Model

zooplankton biomass were low. In this instance an appropriate management response could be to increase stocking rates of piscivorous fish or to increase harvesting rates of planktivorous fish.

The strength of our model lies in an extensive and highly coordinated database of field measurements. This is made possible by ensuring uniformity of personnel and techniques on all research cruises and by employing, where possible, automated sensors such as hydroacoustics, an Optical Plankton Counter (Sprules *et al.* 1992), and flow cytometry (Legner *et al.* 1999).

The model comprises 12 compartments or state variables (Figure 1). The example shown is for the west basin of Lake Erie - a similar model is constructed for the central and east basins. The compartments or state variables represent mean seasonal biomass (May – October) of the trophic groups in fresh grams/m^2 and the arrows indicate consumption of prey by predators in fresh grams/m^2/season. Trophic groups comprise varying numbers of species that are considered to have a common trophic position.

Consumption by each trophic group is determined by applying a measure of growth efficiency to estimates of production. Depending on the trophic group, seasonal production is based either on direct measurements in the field or laboratory, or on various algorithms that convert biomass to production. Phytoplankton photosynthesis (>net production) is measured by exposing integrated epilimnetic water samples labeled with C14 to a light gradient in a shipboard incubator. Photosynthetic parameters are derived from the photosynthesis vs. light relationship determined in the incubator experiments. These parameters, along with data on transparency, chlorophyll, and mixing depth, are used to calculate daily rates of integrated water column photosynthesis using computer programs (Fee 1990). Production of bacteria, ciliates + rotifers, Dreissena, and benthic invertebrates is computed by multiplying mean seasonal biomass by a turnover or growth rate taken from the literature. Zooplankton production is estimated either from direct egg-ratio calculations or from biomass measurements multiplied by temperature- or mass-dependent production: biomass ratios taken from the literature. Fish production and consumption is based on bioenergetic models (Hewett and Johnson 1992) which use species-specific physiological rates in a mass balance of feeding gains against activity, respiration, digestion, excretion, growth, and reproduction for a cohort of known numbers and size at the beginning and end of the season.

Production is scaled to consumption through division by growth efficiencies taken from the literature for the various trophic groups. The only exception is fish, for which consumption is estimated by the bioenergetics model.

The biomass estimates underlying these production and consumption values are based on extensive field programs run on Lake Erie since 1992. Within the constraints of ship availability we endeavoured to sample the whole lake three times each year. In practice this was rarely achieved, but between the years 1992-1996 we managed to obtain good data on all trophic groups during spring before thermal stratification, during the summer period of full stratification, and during the fall when stratification was weakening. A network of about 50 sampling stations covering all basins as well as offshore and nearshore areas was established. Many of these stations were oriented along a series of six transects running across the breadth of the lake or between islands in the west basin. During a typical research trip of roughly two weeks, data taken during the day at each station would include thermal and light profiles, nutrients, chlorophyll, phytoplankton, ciliates, rotifers, and zooplankton. At night, hydroacoustics and the Optical Plankton Counter would be towed along the transects to estimate fish and zooplankton biomass, abundance, and size distributions. Collections of benthic organisms were made with a Ponar grab or box core at most of the sampling stations in the summers of 1992 and 1993. In addition, we sampled a smaller series of reference stations once every two weeks to obtain density, biomass, and production data on the smaller organisms with higher growth rates.

To estimate production and consumption for the model, data from all stations/transects for a particular basin were averaged in a seasonally-weighted manner over years to give a mean growing season value (May - October). Hence the final model is a representation of the mean state of the ecosystem for the period 1992 to 1996.

TARGETED STATE VARIABLES

Nutrient concentrations

Nutrients are not explicitly incorporated in our model. Primary production is a seasonally and spatially averaged carbon uptake rated based on water column light intensities, chlorophyll levels and physiological properties of the phytoplankton. However seasonal phytoplankton photosynthesis rates have been related to seasonal mean total phosphorus concentrations for relatively unimpacted lakes or basins (Millard *et al.* 1996). Hence it would be possible to use this relationship to predict changes in photosynthesis caused by changes in phosphorus, or to determine whether seasonal photosynthesis falls above or below the expectation for unimpacted lakes. Increased or decreased seasonal photosynthesis would then be available as additional input to the grazers in our model.

Total Algal Biomass
Zebra Mussel Biomass

Both appear as state variables in our model. Algal biomass was estimated from microscopic examination of samples, but production was determined from independent experiments.

Blue-green Algal Biomass
Walleye Biomass

Blue-green algal biomass can be estimated from the microscope data. However, the current representation of our model includes only total algal biomass. Furthermore we do not have adequate data to compute zooplankton consumption of blue-green algae specifically. PISCIVOROUS FISH seasonal production is a summation of production for walleye, lake trout, rainbow trout, and coho and chinook salmon, each of which is derived from species-specific bioenergetic models. Thus it would be possible to specify production for each species separately, and to recover biomass data from inputs to the bioenergetics models.

Fish Body Burdens
of Bioaccumulative Chemicals

Our model incorporates no measures of chemical contaminants at all. The original goals were to estimate only seasonal production and consumption of trophic groups, and there was no attempt to model the effects of contaminants.

Richness And Evenness of Intermediate Fish Trophic Levels

Our state variables at this level of the food web include only PLANKTIVOROUS FISH (smelt) and OMNIVOROUS FISH (yellow and white perch). Since our goal was to relate prey production to predator consumption at major trophic linkages only, we felt it was adequate to model two intermediate fish groups. The abundance and biomass data for bioenergetic models of these groups came principally from bioacoustic monitoring. It is difficult to identify acoustic targets to species. In the east basin we considered all acoustic targets to be smelt; in the central basin we considered those in less than 20 m of water to be yellow and white perch, and those offshore to be white perch or smelt depending on target size and thermal stratum; in the west basin we considered all targets to be yellow and white perch, the proportions taken from trawl catches.

State Variables in Relation to Stressors

No stressors are explicitly modeled. The model is a static representation of seasonal supply/demand at various trophic linkages for each basin of the lake. Including stressors was not one our original objectives, nor would this make much sense because there are no dynamic processes and feedbacks in the model.

ADDRESSING LAKE ERIE MILLENNIUM MANAGEMENT ISSUES

1. Eutrophication/Primary Production

Primary productivity is included in our field measurements and is retained in our model. The empirical relationship between seasonal algal production and mean phosphorus concentration could be used to simulate changes resulting from eutrophication. However because of the nature of our model, this would simply generate higher primary productivity without any dynamic effect on any other state variable. It would simply increase algal supply in relation to the demands for it in the model.

2. Exotic Species/Nuisance Aquatic Species

The only exotic species explicitly included in our model are the dreissenid mussels. Other exotics such as white perch appear in the OMNIVOROUS FISH compartment, and *Bythotrephes* in the CARNIVOROUS ZOOPLANKTON. Any new exotics predicted to enter the food-web could be added to our model if knowledge of potential biomass, annual production, predators, and prey were available. The model would specify whether there is adequate prey production to support such an invader, or whether consumption of the invader, when added to that by existing species, would lead to overexploitation of the particular prey groups.

3. Upper Food Web Exploitation

Additional harvesting of predatory fish in our model could be simulated by reducing the biomass, and hence production and consumption, of PISCIVOROUS FISH. No changes to the state variables in the model would result because our model is not dynamic. Such a simulation would simply indicate what additional harvesting of piscivores would be required to relieve energy demands on the planktivorous fish.

4. Ecosystem Stability

One of the major goals of our trophic transfer model is to identify potentially unstable links in the food web. Such instabilities would exist if there is evidence of a sustained excess of predator demand over prey supply, particularly if prey biomass is low. In this sense, then, our model addresses issues related to ecosystem stability.

5. Habitat Structure and Function

There are no features of the habitat that explicitly appear in the model. Some habitat information is included indirectly through, for instance, allowing zooplankton production to be partially determined by vertical temperature stratification. Similarly the nearshore habitat (less than 20 m deep) was used to segregate “yellow and white perch acoustic targets” from “smelt acoustic targets” in the central basin. However none of this habitat information is used explicitly in the model to determine trophic interactions.

6. Contaminants

No contaminant information is included in the trophic transfer model, nor was our intention ever to simulate such effects.

MANAGEMENT PROBLEM BEING ADDRESSED

The principal objective of our modeling approach is to identify linkages in the food web of Lake Erie at which there is an imbalance in energy supplied by prey and that demanded by the predator. For example preliminary analyses indicate that the energy requirements of dreissenid mussels far outstrip what is available from algae, rotifers and ciliates, and pelagic bacteria - their principal prey in our model. This suggests a) severe resource competition between mussels and other algal grazers (zooplankton, benthic detritivores); b) that mussels are accessing alternate energy sources, such as benthic detritus, not explicitly included in our model; or c) that mussel biomass will decrease through time, although the current biomass is very large. In any instance the simulation confirms that mussels are having a large impact on the Lake Erie ecosystem.

The management problem is that exotic invaders such as the mussel can seriously modify the pattern of energy flow through the Lake Erie food web. Algal production that would normally flow to zooplankton and then to fish is now concentrated in mussels which are largely unutilized by any predators in the lake (the flow from mussels to omnivorous fish diagramed in our model is minor). Mussels thus represent an energy sink, at least on a short to moderate time scale. It does not appear that mussels can easily be removed from the lake, so our analysis confirms that a new state of the ecosystem exists, and that a return to past configurations that produced high yields of smelt and yellow perch is unlikely.

MODELING ASSUMPTIONS

Our primary assumptions are embedded in the patterns of energy flow indicated by the arrows in Figure 1. Secondary assumptions relate to the proportion of the total energy consumed by a predator that comes from its various prey groups. Feeding pathways and allocation of consumption are based either on our collective "expert knowledge" of these matters for Lake Erie, or on direct analyses of diets such as those required to determine fish consumption and production from bioenergetic models. We also assume that reasonable estimates of production can be derived by multiplying mean seasonal biomass of a trophic group by a seasonal growth rate, and that consumption can be determined by dividing production by growth efficiency. Finally, we assume that averages taken over the whole lake or across seasons or years constitute a reasonable "snapshot" of the state of the Lake Erie food web – effectively an assumption that the system does not change much from one year to the next.

RELEVANT SPACE AND TIME SCALES

The time and space scales over which averages are taken to generate the "snapshot" of the Lake Erie food web referenced above depend on the state variable being measured. In theory it should be possible to standardize the scales, but our experience has been that this is not always easy. Thus algal production data might be based on one particular year in which rather complete sampling of the lake wide stations was achieved for two or three seasons. On the other hand, estimates of zooplankton production from the towed Optical Plankton Counter might be based on several years of data which in total cover most parts of the lake in most seasons. Furthermore, expensive lake wide cruises that last up to two weeks cannot be performed very often, so it is important to collect companion data more frequently at fewer reference stations. This is particularly necessary for smaller organisms with more rapid turnover rates. Data from these reference stations can be combined with lake wide station data to benefit from the high temporal resolution of the former and the good spatial resolution of the latter.

DATA/MONITORING/ RESEARCH NEEDS

The data requirements for our Trophic Transfer Model are considerable. It requires good field sampling estimates of the biomass of all component trophic groups at an extensive series of lake wide stations or transects, and during each of the major stratification periods within a year. Since these data can rarely be obtained at high enough frequency to capture the principal dynamics of the smaller organisms (algae, microbes, zooplankton), an additional series of reference stations that can be visited more frequently (say every two weeks) is necessary. Since the model is not dynamic, it cannot generate the complete response of the food web to some new condition such as higher nutrient loadings or increased piscivore stocking. It can only compare supply and demand at the various trophic linkages of the existing static model under a scenario of increased algal production or increased piscivore production/consumption. To modify the model to reflect a new state of the ecosystem would necessitate extensive new field data on all trophic groups.

OVERALL MODEL UTILITY

We feel our trophic transfer model can help to address management issues by pinpointing major pathways of energy flow and their susceptibility to perturbations. It indicates linkages which need further investigation, and whether there is enough energy flowing through a linkage to warrant the time and expense of investigation. Finally, it provides a holistic snapshot of conditions and production in the lake against which process-oriented models can be calibrated.

Appendix E

Modeling the Effects of Nutrient Concentrations on Ecosystem Stability: Framework for a Great Lakes Model

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[1] Kent State University and [2] Northeast-Midwest Institute

ABSTRACT

The effects of nutrients on algal productivity are not transferred directly to production at higher trophic levels and can not be modeled as if they were. Rates of processes and time scales at different trophic levels require a modular approach to a comprehensive model of the Great Lakes. Predator growth is based ultimately on prey availability and life histories of predators. Factors that control availability of preferred prey (e.g. top-down vs. bottom-up) are unresolved. Prey availability is ultimately controlled by carbon (C)-flow from the base of the food web, but many factors besides nutrient loading influence C-flow to forage fish. Here we focus on factors at the base of the food web that influence C- and phosphorus (P)-flow and the efficiency of energy transfer from phytoplankton to forage fish. Specifically, we consider a detailed model of the base of the food web that includes phytoplankton production, grazing interactions and processes in the microbial food web (MFW): bacterial production and bacterivory. The model is constructed from authentic field data and fit into an exact steady state model in a unique way. Phosphorus concentration is the major forcing in this model. The model is examined for ecosystem stability to loading perturbations. Examination of factors to which C- and P-flow is most sensitive indicates much more attention needs to be given to the significance of MFW, especially in offshore communities.

INTRODUCTION

Models are maps. As with any map, their value can be measured by the accuracy they deliver us at desired goals. But the best maps are those that do more than merely guide: they aid in their own refinement. Useful ecosystem models provide more than an accurate representation of our current views of ecosystem structure and function. The most useful ecosystem models allow us to explore the validity of the views on which they are based and to identify research most necessary for their improvement. For this reason ecosystem models need to be viewed as transitory products of a continuing iterative modeling process, useful not only for prediction of outcomes of ecosystem function and management scenarios but also for refinement of our views of the salient ecosystem features which provide those functions.

Ecosystems are those units of nature that control and regulate the efficiency of energy flow from the base of the food web to the highest trophic levels; they also regulate the efficiency of nutrient cycling, thereby regulating the availability of critical, "growth-limiting" nutrients (Margalef 1968). Energy flow into productive ecosystems is controlled by energy and nutrient availability and the efficiency of photosynthetic taxa to convert those resources into biomass. Not every Joule of energy fixed by primary production at the base of the food web is transferred with equal efficiency to the highest trophic levels (Slobodkin 1959). Both the energy fixed by primary producers and the efficiency of trophic transfer from the base to the highest trophic levels is currently viewed as a function of the efficiency of the taxa and the food web nexus involved (Kerfoot *et al.* 1988, deRuiter *et al.* 1995). Ecosystem-level questions are those related to the overall function of energy transduction into biomass, efficiency of trophic transfers, efficiency of nutrient recycling, and continued availability of critical or limiting nutrients.

Ecosystem management must necessarily be concerned with identification and regulation of those factors most important in controlling the efficiency of energy flow and nutrient cycling. Because ecosystems exist in a varying environment, their management must be particularly concerned with investigating their stability to perturbation and identifying those structures most important to their homeostatic regulation. Lake Erie communities are generally studied and modeled as a set of interacting populations rather than as an ecosystem, where matters of trophic efficiency or stability to nutrient perturbations are considered. Because Lake Erie is an incompletely understood ecosystem, management scenarios based on current knowledge likely will need revision. Models for management of the Lake Erie ecosystem need to provide more than a quantitative representation of ecosystem behavior giving reasonably accurate predictions of outcomes of potential management scenarios. They need to be constructed in such a way as to direct future research efforts directed at better descriptions of Lake Erie ecosystem function and those factors that control it.

Here we present a complex model of the base of the food web that explictly addresses ecosystem stability to nutrient perturbation. We briefly discuss extension of this model to include exotic species (e.g., zebra mussels) and eutrophication issues. We especially address the necessity of considering nearshore and offshore communities separately. This model is an extension of an earlier modeling effort by Sturtevant and Heath (1995) to add portions of the base of the food web to the Lake Erie Ecosystem Model (LEEM) constructed by Prof. J. Koonce. Accordingly, we compare models at the base of the food web and higher trophic levels and consider C- and P-flow from the base of the food web to prey fish communities.

MODEL CONSIDERATIONS

Phosphorus loading does not translate directly to fish biomass. Models that implicitly take such a view are simplistic and likely to mislead if used in driving management decisions. Phosphorus availability has frequently been shown to constrain phytoplankton production (Schelske 1979; Hartig and Wallen 1984). Accordingly, management strategies to limit growth of noxious phytoplankton have sought to decrease P-loading to Lake Erie (GLWQA, IJC 1987). The success of this management strategy is evidenced both by decreased concentrations of detectable nutrient concentrations in Lake Erie and the expected response of phytoplankton communities. In the late 1980s, the soluble reactive phosphorus (SRP = phosphate and possibly other readily available P-compounds) concentrations were very low in mid-to-late summer in Lake Erie, which is characteristic but not diagnostic of

Table 1

Lake Erie Management Issues, Ecosystem State Variables of Interest, and Modeling Needs

	INPUT STRATEGIES	OUTPUT STRATEGIES
LAKE ERIE MANAGEMENT ISSUES	Eutrophication and Primary Production Ecosystem Stability Exotic Species (affecting base of food web) Contaminants (entering based of the food web)	Upper Food Web Exploitation Exotic Fish Species Contaminants (entering fish directly)
ECOSYSTEM STATE VARIABLES OF INTEREST	Nutrient Concentrations Total Algal Biomass Blue-Green Algal Biomass Zebra Mussels Biomass	Walleye Biomass Fish Community Richness and Evenness Fish Body Burdens of Bioaccumulative Chemicals
MODELING NEEDS	Base of Food Web (nutrients to zooplankton) Time Scale: hours–days	Age Structured Population (prey and predator fish) Time Scale: months–years

P-limited lake communities (Charlton *et al.* 1993). There was a consistent decrease in phytoplankton biomass from 1958 through 1987 with dramatic decreases in the abundance of nuisance cyanophytes (Makarewicz 1993) that paralleled the decline in P-loading (Nichols and Hopkins 1993).

Effects of increased phytoplankton production on production at the highest trophic levels is unclear. Recent studies indicate there is little reason to presume that such effects would be direct and linear. Piscivore biomass in Lake Erie is affected not only by availability of prey fish, but also by their quality (Knight *et al.* 1984; Hartman and Margraf 1992; Hartman 1998), and by factors which influence spawning success and recruitment, such as suitability of nursery habitat (Knight 1977), seasonal temperature (Kitchell and Stewart 1977; Madenjian 1991; Madenjian *et al.* 1996), predation pressure (Hartman and Margraf 1993), and age at first reproduction which is controlled by food availability (Henderson and Nepszy 1994; Madenjian *et al.* 1996). Factors controlling prey fish biomass and species composition are not as well studied. Whether prey fish are controlled primarily by food limitation (e.g. Hartman *et al.* 1992; Gopalan *et al.* 1998), or by predation pressure (e.g. Knight and Vondracek 1993), or by each of these at different seasons or places is unclear.

We see two different levels of concerns in Lake Erie management issues, necessitating two different levels of modeling efforts. One set of concerns are closely related to P-loading strategies (Input Strategies); the other set of concerns are related to game fish biomass, health, and upper food web exploitation (Output Strategies). Shown in Table 1 are the various concerns and variables best addressed by different models with different time scales; of course, the eventual modeling effort is to pull these together. Because much of the management strategy of Lake Erie has focused on Input Strategies and especially on control of P-loading, we believe a major modeling effort must be made to model the base of the food web, especially to explore the ecosystem consequences of nutrient perturbations to it.

MICROBIAL FOOD WEB AND LAKE ERIE COMMUNITIES

The traditional view that transfer of phytoplankton fixed carbon can be determined (and modeled) simply by estimation of algivorous grazing rates of microcrustaceans is no longer tenable in Lake Erie. Advent of novel techniques (Sherr *et al.* 1987b) to observe the structure and function of the microbial food web (MFW) indicate its significance to C-flow in Lake Erie plankton communities, and especially, they point to the likelihood that C-flow in nearshore (NS) communities differs from that offshore (OS) in fundamental ways. This is important because theoretical considerations imply that as the MFW becomes a stronger "C-link", the energetic efficiency of C-flow from algae to higher trophic levels decreases (Pomeroy and Wiebe 1988).

Nutrient-rich nearshore areas are more productive of algae, bacteria, protozoans, and macro-zooplankton than nutrient-poor offshore regions. Both coastal and offshore sites in the central basin of Lake Erie are dominated by heterotrophic nanoflagellates, but the portion of plankton community C in protists was significantly greater in offshore communities (Hwang and Heath 1997a). Nearshore and offshore protist guilds differed taxonomically: Chrysochromulina dominated OS communities and Dinobryon occurred only at OS sites in association with colonial diatoms; ciliates were more diverse NS than OS (Hwang and Heath 1997a; 1997b). The fraction of bacterial production grazed by protists was significantly greater OS, where protists grazed virtually the entire daily bacterial production, compared against generally grazing less than 25% of bacterial production at coastal sites (Hwang and Heath 1997b). These recent findings suggest that the MFW is more tightly coupled to phytoplankton production OS than NS and is more important in transfer of C to higher trophic levels than investigation of NS sites alone would indicate. Whether this is due to appearance of different bacterial taxa NS vs. OS or a relationship that depends on metabolic alterations within taxonomically similar microbial communities remains to be shown.

Whether bacterial abundance alone controls seasonal and spatial increases of bacterivore populations in the Great Lakes which are most important in the MFW is unresolved (Carrick and Fahnenstiel 1989; 1990). Recent studies indicate a considerably greater fraction of C is passed through the microbial loop OS than in coastal regions. Not only does this indicate the contribution of the MFW to overall C-flow to higher trophic levels may differ between NS and offshore OS communities, it also indicates that when OS communities are viewed as "dilute NS communities" the C-flow to higher trophic levels is likely to be underestimated. Bacterivorous rotifers dominated at both NS and OS sites, and all cladocerans (except *Leptodora kindtii*) grazed bacteria. Rotifers grazed between 40% (NS) to 75% (OS) of bacterial production, while cladocerans and calanoid copepods generally grazed less than 25% of daily bacterial production (Hwang and Heath 1999, in press).

A MODEL OF THE BASE OF THE FOOD WEB

A catenated P- and C- model of the base of the food web including elements of the microbial food web was constructed using field data from a study of P- and C-dynamics along a nearshore-to-offshore transect in Lake Erie. The transect ran from Sandusky Bay to the international boundary in the central basin. Study sites included a station in the Sandusky sub-basin as well as a station east of the Pelee-Lorain Ridge, encompassing a steep trophic gradient ranging from hyper-eutrophic conditions in Sandusky Bay to mesotrophic conditions bordering on oligotrophic at those stations furthest offshore. Data were collected at monthly intervals from May through September in 1993 and 1994. Details of C- and P-dynamics have been reported elsewhere (Hwang 1995; Hwang and Heath 1997a; 1997b; Hwang and Heath 1999; Sturtevant 1998).

Field observations included phytoplankton enumerated to species, bacterioplankton (counted as a single taxon), protists (enumerated to species where possible, and to genus otherwise), rotifers (enumerated to species), and microcrustaceans (enumerated to species). Field observations also included estimation of free CO_2, phosphate (detected as SRP and confirmed via Rigler bioassay; Rigler 1966), dissolved organic carbon (DOC) (detected via the hot-dry combustion method with a Shimadzu TOC-200 Carbon Analyzer), and dissolved organic phosphorus (DOP) (detected as the difference between total soluble P and SRP). Rates of processes were also measured at each station on each sampling date. Rate of photosynthesis was estimated from chlorophyll-corrected P-I curves and measured light intensity in situ (Fahnenstiel and Scavia 1987). Bacterial production was measured by rates of incorporation of 3H-leucine and 3H-thymidine (Reimann and Bell 1990). Bacterivorous grazers and grazing rates by protists, rotifers, and microcrustaceans were estimated by the fluorescent-label technique (Sherr *et al.* 1987b). Impact and rate of grazing by microcrustaceans (cladocerans and copepods) was estimated in microcosms from which microcrustaceans had been removed vs. those amended with 1X, 2X and 4X quantities of microcrustaceans (Sorrick 1995).

Models were constructed from field observations for each site investigated and each sampling date. We considered phytoplankton, bacterioplankton, protists, rotifers, and microcrustaceans as single taxonomic units. Storages are shown in units of mol/L, and rates are shown in units of mol/L/hr. Models were constructed so that flows were expressed as pseudo-first order processes operating near steady state. Although each site-date model was constructed from data collected at that station on that date, Table 2 shows means and standard deviations of all measurements taken at nearshore stations and all measurements taken at offshore stations. C- and P- models were catenated by considering that when grazers ingested prey, the ingestate contained the C:P ratio of their prey, even though they excreted different C:P ratios. Details of model construction and catenation of C- and P- models can be found in Sturtevant (1998).

Table 2
Average Storage Size and Process Rates in Nearshore and Offshore Stations

		Nearshore		Offshore	
		Mean	SD	Mean	SD
Carbon Pools (µmolC/L)	DIC	36	8	38	8
	DOC	497	327	291	284
	Algal C	124	89	5	4
	Bacterial C	14	4	6	1
	Profozoan C	4	2	1	1
	Microzooplankton C	4	3	2	2
	Macrozooplankton C	13	10	1	1
Carbon Pools (µmolC/L/hr)	Photosynthesis	0.44	0.49	0.03	0.03
	EOC Release	0.19	0.29	0.03	0.03
	Bacterial Production	0.46	0.58	0.02	0.04
	Algal Respiration	0.27	0.22	0.01	0.01
	Bacterial Respiration	0.19	0.05	0.05	0.02
	Protozoan Respiration	0.01	0	0	0
Carbon Pools (µmolC/L/hr)	Microz. Respiration	0	0	0	0
	Macroz. Respiration	0.023	0.02	0	0
	Bacteria - > Algae	0	0	0	0
	Bacteria - > Protozoa	0.05	0.03	0.02	0.03
	Bacteria - > Microz.	0.15	0.21	0.02	0.03
	Bacteria - > Macroz.	0.03	0.02	0.02	0.05
	Algae - > Microz.	0.119	0.123	0.03	0.03
	Algae - > Macroz.	0.03	0.06	0	0
	Protozoa - >Microz.	0.03	0.03	0.01	0.01
	Protozoa - > Macroz.	0.15	0.19	0.03	0.06
	Microz. - > Macroz.	0.07	0.11	0	0
	Macroz. - > Out	0.26	0.29	0.06	0.08
	Microz. - > DOC	0	0	0	0
	CO2 Input	0.121	0.268	0	0.01
	CO2 - > Out	0.158	0.14	0.08	0.152
	DOC Input	0.378	0.568	0.01	0.03
	DOC - > Out	0.118	0.271	0.02	0.03

(continued)

Table 2 (continued)

Average Storage Size and Process Rates in Nearshore and Offshore Stations

		Nearshore		Offshore	
		Mean	SD	Mean	SD
Phosphorus Pools (nmolP/L)	PO4	300	300	300	300
	DOP	700	500	700	500
	Algal P	1700	1100	300	200
	Bacterial P	400	200	200	100
	Protozoan P	41	22	12	10
	Microzooplankton P	33	16	7	5
	Macrozooplanton P	92	88	8	7
Phosphorus Flows (nmolP/L/hr)	Phosphate - > Algae	99	213	5	8
	Phosphate - > Bacteria	33	51	10	23
	DOP - > Algae	83	129	18	35
	DOP - > Bacteria	3	6	18	44
	DOP - > Phosphate	6	10	2	4
Phosphorus Flows (nmolP/L/hr)	Bacteria - >Algae	0.03	0.07	0.09	0.1
	Bacteria - > Protozoa	1.4	1.1	0.7	1.1
	Bacteria - > Microz.	3.1	3.7	0.9	1.2
	Bacteria - > Macroz.	0.9	1.2	0.9	2.1
	Algae - > Microz.	2.4	3.6	4.2	7.4
	Algae - > Macroz.	0.8	1.7	0.6	0.9
	Protozoa - > Microz.	0.2	0.3	0.1	0.1
	Protozoa - > Macroz.	1.4	1.8	0.3	0.6
	Microz. - > Macroz.	0.461	0.689	0	0
	Macroz. - > Out	1.9	2.4	0.4	0.6
	Bacteria - > Phosphate	3	6	4	8
	Bacteria - > DOP	2	3	3	5
	Algae - > Phosphate	4	0.5	4	9
	Algae - > DOP	3	2	2	5
	Protozoa - > Phosphate	0.5	0.4	0.3	0.6
	Protozoa - > DOP	0.5	0.7	0.2	0.4
	Microz. - > Phosphate	1.9	2.6	4.2	7.4
	Microz. - > DOP	1.3	1.7	0.7	1.2
	Macroz. - > Phosphate	0.9	1.3	0.8	0.9
	Macroz. - > DOP	0.6	0.8	0.5	1.2
	Phosphate Input	117	223	12	29
	Phosphate Output	8	21	12	16
	DOP Input	83	125	16	26
	DOP Output	3	4	5	9

Our aim was to analyze these models for total system throughput, average path length, cycling efficiency and stability using techniques requiring the model to be at steady state, sensu strictu. Although our observations provided "snapshots" of the pelagic plankton communities, which were likely to approximate a steady state closely, it was unlikely that any of these "snapshots" would be exactly at steady state. A steady state model for each site-date was derived from the corresponding "snapshot" model using a novel approach, based on the earlier work of Strong (1986a; 1986b). Each "snapshot" model was expressed as a point in 54-dimensional space, in which each dimension corresponded to a particular flow. Steady state and linkage constraints were used to define a region in the 54-dimensional state space containing the set of all possible steady states. A series of MATLAB routines on a Maple V platform were used to calculate the nearest steady state point on the surface of the steady state region to the "snapshot" data point (outside the steady state region) as a least squares scalar fit (Sturtevant 1998). The "snapshot" models were then adjusted to this 54-dimensional least squares best fit steady state model for analysis.

In all cases examined, the "best fit steady state" model was closer to the "snapshot" model from which it was derived than to any other snapshot model, indicating that the "snapshot" models constructed from field data were internally consistent and close to steady state. Figure 1 a and b show July 1994 steady state models for Upper Sandusky Bay and central basin of Lake Erie, respectively.

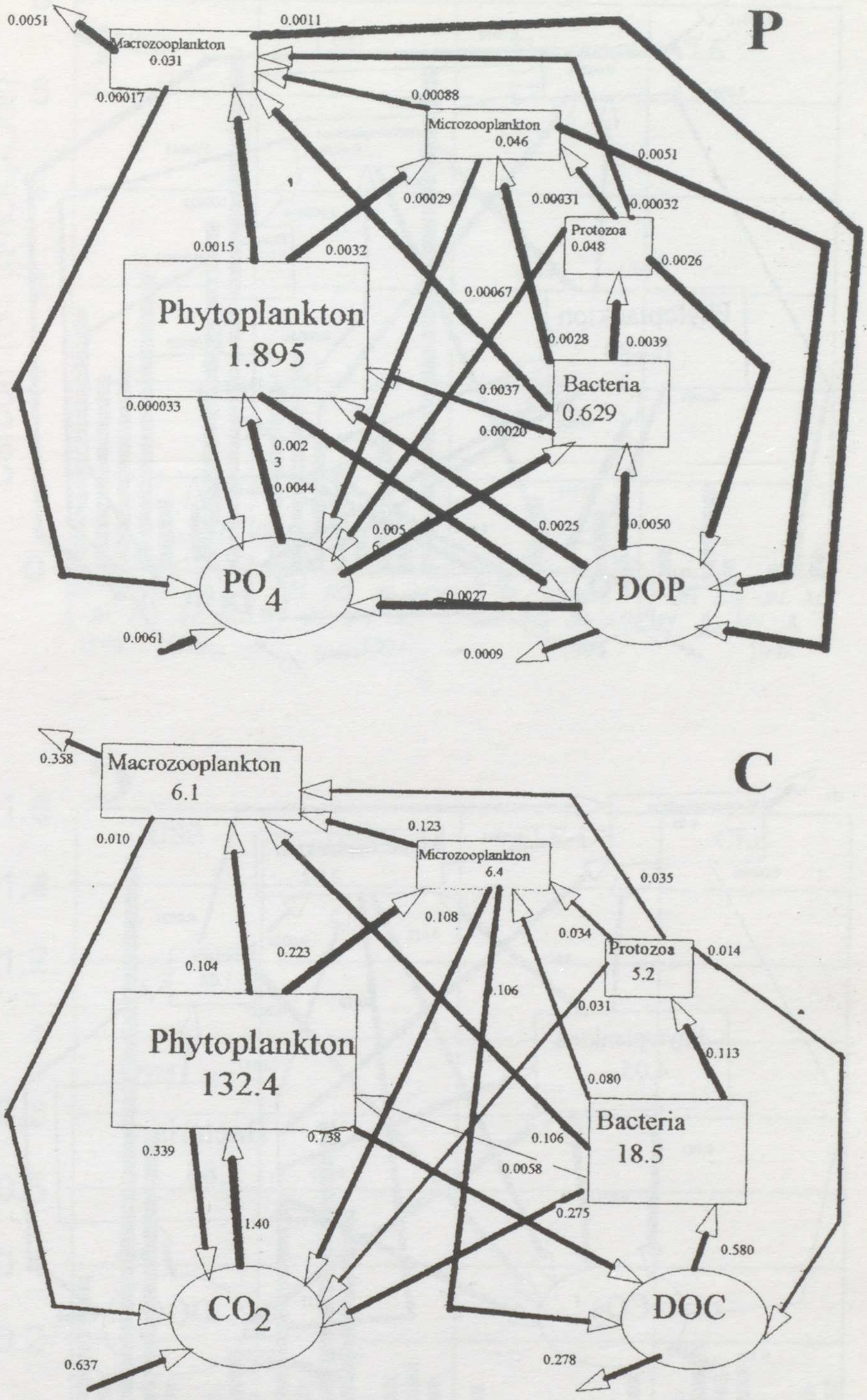

Figure 1a
Steady State Model Derived from Data in July 1994

All storages are in μM, and all processes are in units of μM per hour.
Upper Sandusky Bay, an example of a "nearshore" station.
Scalar distance from "snapshot" model=0.29.

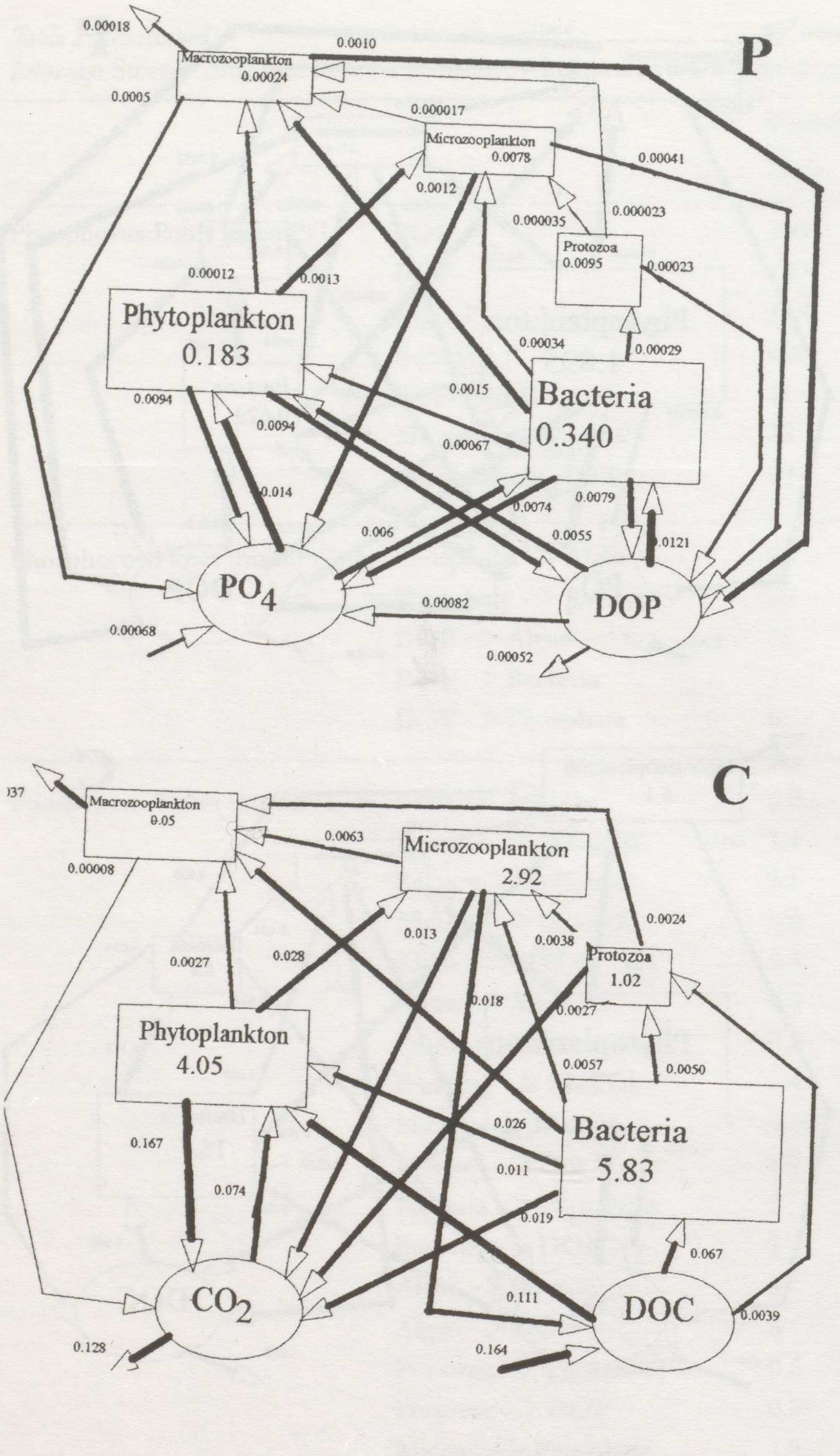

Figure 1b
Steady State Model Derived from Data in July 1994

All storages are in μM, and all processes are in units of μM per hour. Central basin of Lake Erie, an example of an "offshore" station. Scalar distance from "snapshot" model=0.22.

MODEL ANALYSIS

Flow analysis was conducted on the C- and P- steady state models separately using the methods of Finn (1976). The C-model was treated as a 6-compartment model (DOC, algal C, bacterial C, protist C, rotifer C, and microcrustacean C), whereas the P-model was treated as a 7-compartment model (phosphate P, DOP, algal P, bacterial P, protist P, rotifer P, and microcrustacean P) on the grounds that a release of phosphate followed by re-uptake constituted a recycling loop likely to occur, while respiration of CO_2 and re-uptake was unlikely due to relatively large concentrations of CO_2 in the water. Flow through each component was calculated from flow matrices for each compartment and Total System Throughflow (TST). TST was used as a scaling factor, to permit comparison of nearshore and offshore models with widely different absolute TST. Average path length (APL) was the average number of compartments through which a C or P atom passes between the time it entered and left the ecosystem. APL= (TST)/Z , where Z was the sum of all inflows. APL made no distinction between straight flows and flows lengthened through recycling. Separation of straight and recycled flows allowed calculation of a cycling index (CI), indicating increased residence pathlength an atom had because of recycling.

The roles of algae and bacteria in C- and P-models differed between coastal models and offshore models, indicating that although the NS and OS communities are structured similarly, they functioned differently. TST was significantly higher for coastal than offshore models (Figure 2). C- and P-models differed considerably in the significance of recycling processes. Only about 10 percent of C-TST was recycled, while greater than 40 percent of P-TST was recycled (Sturtevant 1998). The proportion of algal C flux lost through respira tion declined slightly along the NS-OS gradient, while the fraction of nascent photosynthate released as DOC increased along the transect; these trends resulted in a greater portion of C transferred to higher trophic levels via grazing at intermediate stations along the transect (Figure 3). Bacterial C-flux was unchanged along the transect and equally apportioned between respiratory losses and transfer to bacterivores in both NS and OS steady state models. Steady state P-models indicated both algae and bacteria transferred more P to higher trophic levels in NS systems than OS. Cycling Indices (CI) for P-models were consistently higher than CI for C-models for the same station and date. Overall, C-models averaged CI = 0.11 and P-models averaged CI = 3.56 (Sturtevant 1998). This indicated P-recycling was more important than C-recycling, consistent with the view that nutrient cycles for the limiting nutrient should be more retentive. Cycling indices for C increased significantly as the season progressed and tended to increase more in OS systems than NS (Figure 4); no similar seasonal trend was noted for CI in P-models.

We examined the stability of these NS and OS models to nutrient pulses (i.e. DOC, DIP, and DOP). Despite the importance of stability in ecological systems, there have been relatively few tests of its various facets using data from real ecosystems (Ives 1995). Deterministic stability analysis is difficult to apply to data (DeAngelis and Waterhouse 1987; Cottingham and Carpenter 1994). Analysis of the coefficients for equations used to generate steady state models

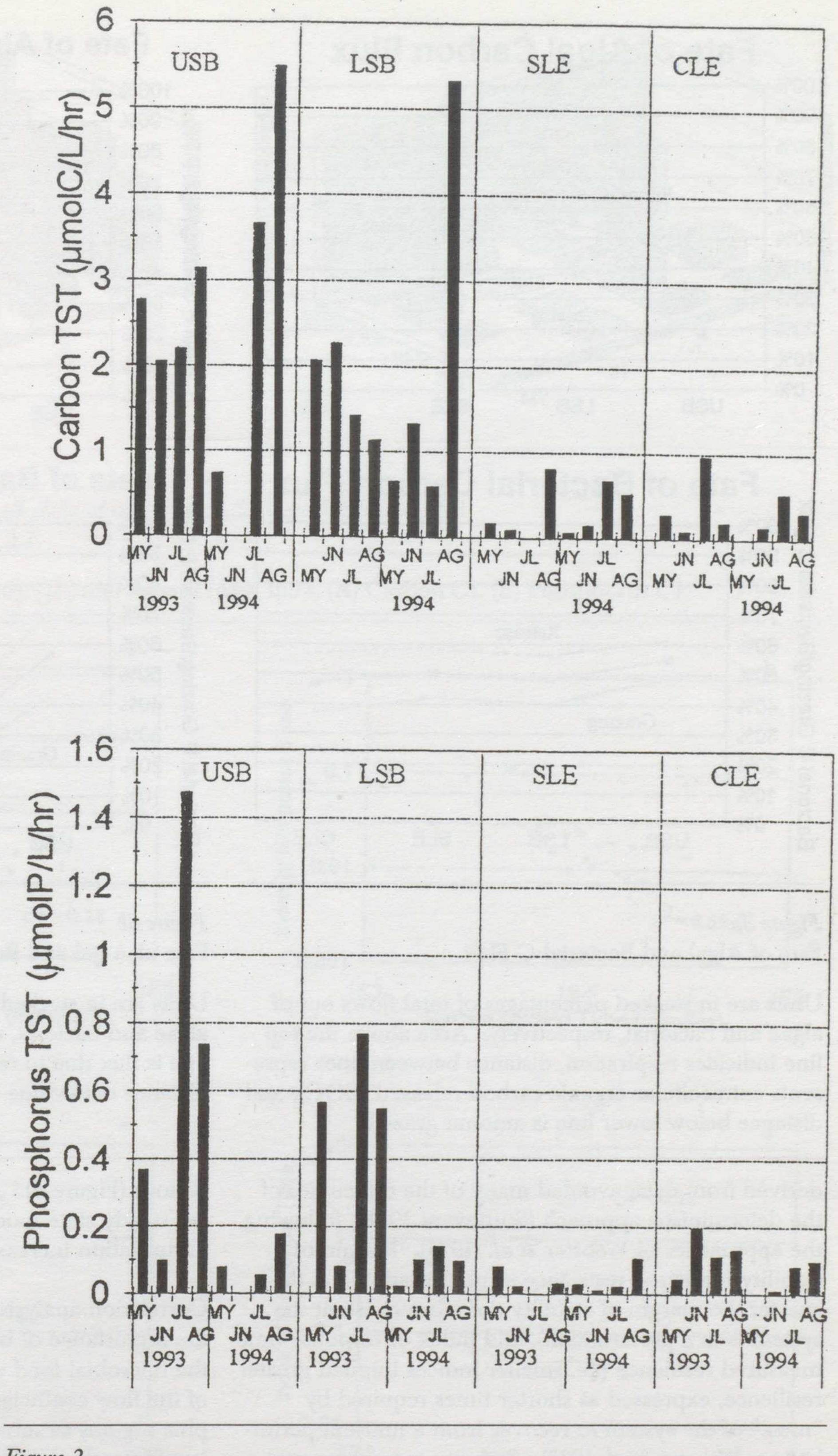

Figure 2

Total System Throughflow (TST) of Steady State Models of the Coastal Stations USB and LSB and the Offshore Stations SLE and CLE

Dates are in May (MY), June (JN), July (JL) and August (AG) 1993 and 1994. All units are mol per L per hour. (A) Carbon TST. (B) Phosphorus TST.

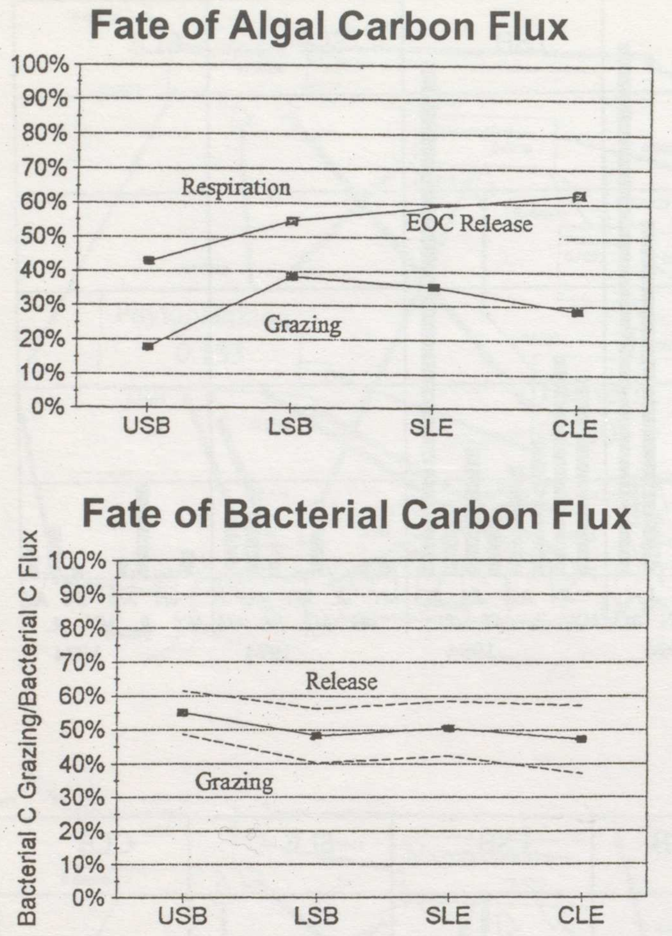

Figure 3a
Fate of Algal and Bacterial C Flux

Units are in stacked percentages of total flows out of algae and bacterial, respectively. Area above the top line indicates respiration, distance between lines represents extracellular organic carbon released (EOC), and distance below lower line is amount grazed.

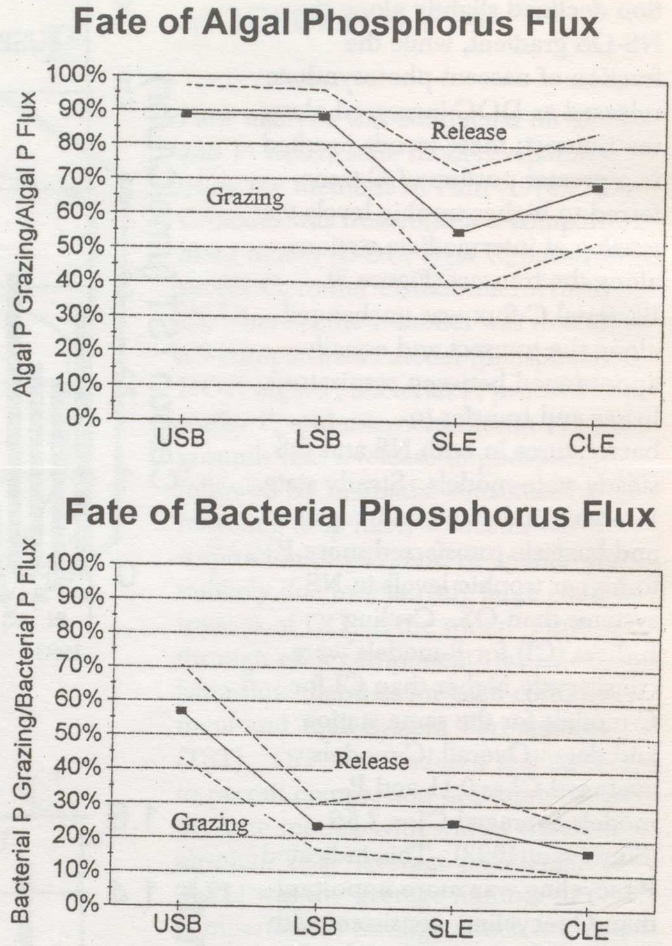

Figure 3b
Fate of Algal and Bacterial P Flux

Units are in stacked percentages of total flows out of algae and bacteria, respectively. Distance above solid line is flux due to release as phosphate or DOP; distance below line is percent total flux due to grazing.

derived from data, avoided many of the difficulties of the deterministic approach (Sturtevant 1998), following the approaches of Webster *et al.* (1975). Margin of stability measured resistance to perturbation (i.e. the greater the margin of stability the more resistant the system is to a perturbation), and index of response time measured resilience (i.e. smaller indices implied greater resilience, expressed as shorter times required by "most" of the system to recover from a nutrient perturbation, Webster *et al.* 1975). Stability measures were calculated separately for each of the 29 site-date steady state models and correlated to measures of nutrient retention and recycling. In general, steady state models of systems with a high degree of P-recycling were less resistant but more resilient to P-pulse perturbations (Figure 5). As C- and P- retention increased in the steady state models, resistance of those systems to perturbation increased.

Correlation analysis and sensitivity analysis indicated the importance of bacterial activities and their role in the microbial food web (MFW). Correlation analysis of the flow coefficients was used to identify homomorphic regions as sub-structures within the context of the larger steady state models. Although the size of the compartments varied by greater than an order of magnitude from NS to OS ecosystems, the MFW behaved as a homomorphic subregion in both the C- and P-steady state models (Figure 6), having similar pseudo-first order transfer coefficients among the

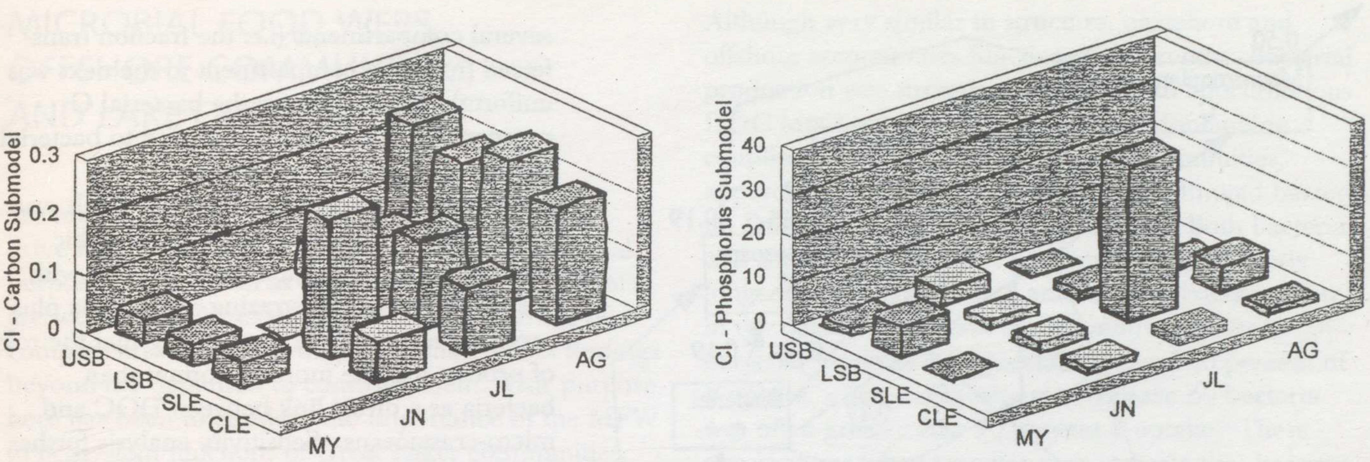

Figure 4
Cycling Indices (CI) of Steady State Models of the Coastal Stations USB and LSB and the Offshore Stations SLE and CLE

Dates are in May (MY), June (JN), July (JL) and August (AG) 1994. (A) Carbon CI. (B) Phosphorus CI.

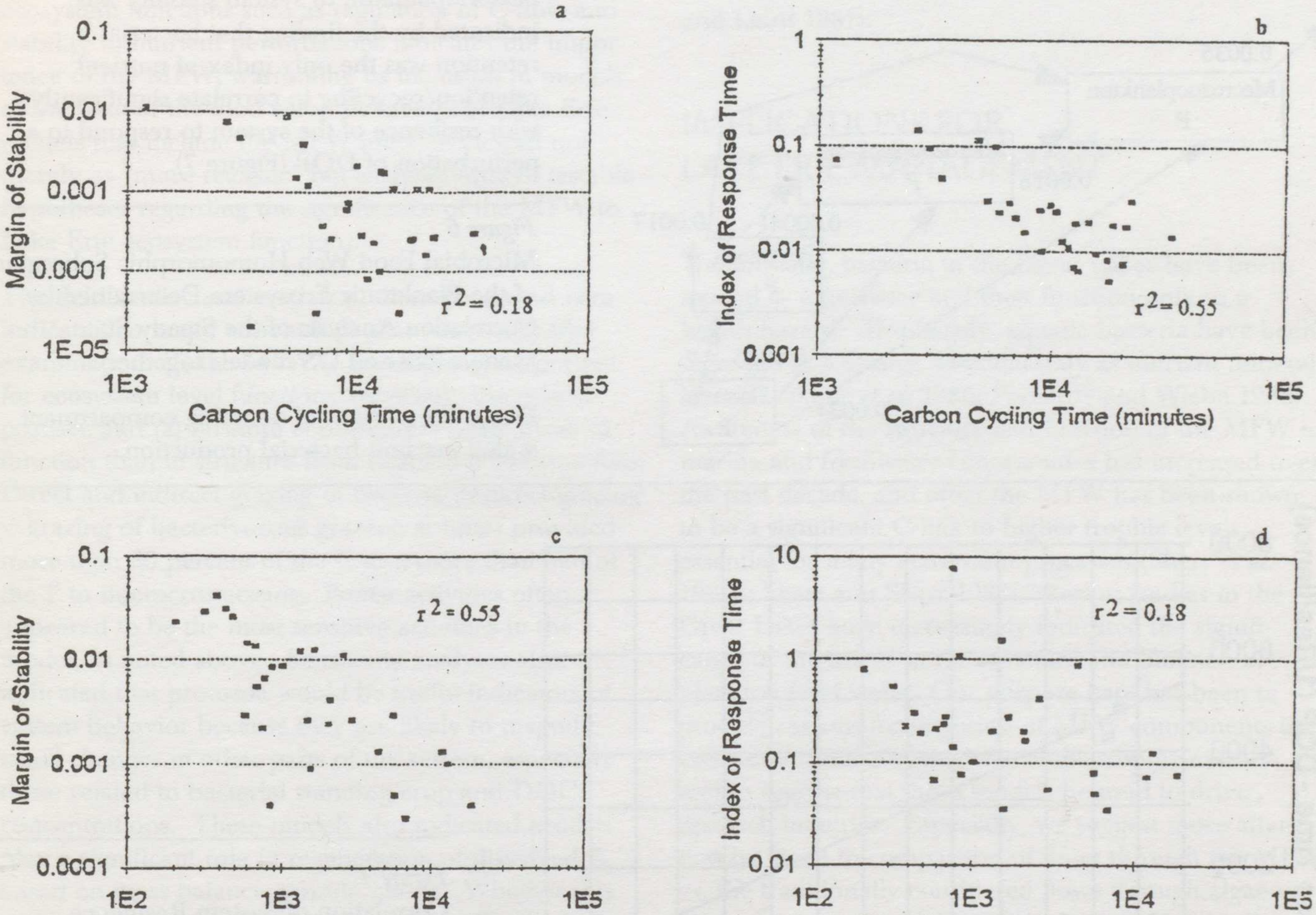

Figure 5
Comparison of Steady State Stability Indices, Margin of Stability (resistance, left column) and Index of Response Time (resilience, right column) for Carbon Models (top row) and Phosphorus Models (bottom row)

several compartments (i.e. the fraction transferred from one compartment to the next was uniform). Flows through the bacterial C compartment were linearly related to bacterial uptake of DOC; the transfer of C from microcrustaceans to higher trophic levels was predictable as a part of this homomorphic subregion and correlated most strongly with the rate of protozoan grazing on bacteria plus protist uptake of DOC, suggesting that the role of protists may be more important than bacteria as a direct link between DOC and micro-crustaceans. Sensitivity analysis further emphasized the possible importance of protistan bacterivory: as the protistan bacterivorous grazing coefficient was altered ± 10 percent, bacterial P varied by 88 percent, protist P by 233 percent, microcrustacean P by 78 percent, and bacterial P release by 87 percent (Sturtevant 1998). The significance of bacterioplankton to system stability was indicated by the finding that bacterial P retention was the only index of nutrient retention/recycling to correlate significantly with resilience of the system to respond to a perturbation of DOP (Figure 7).

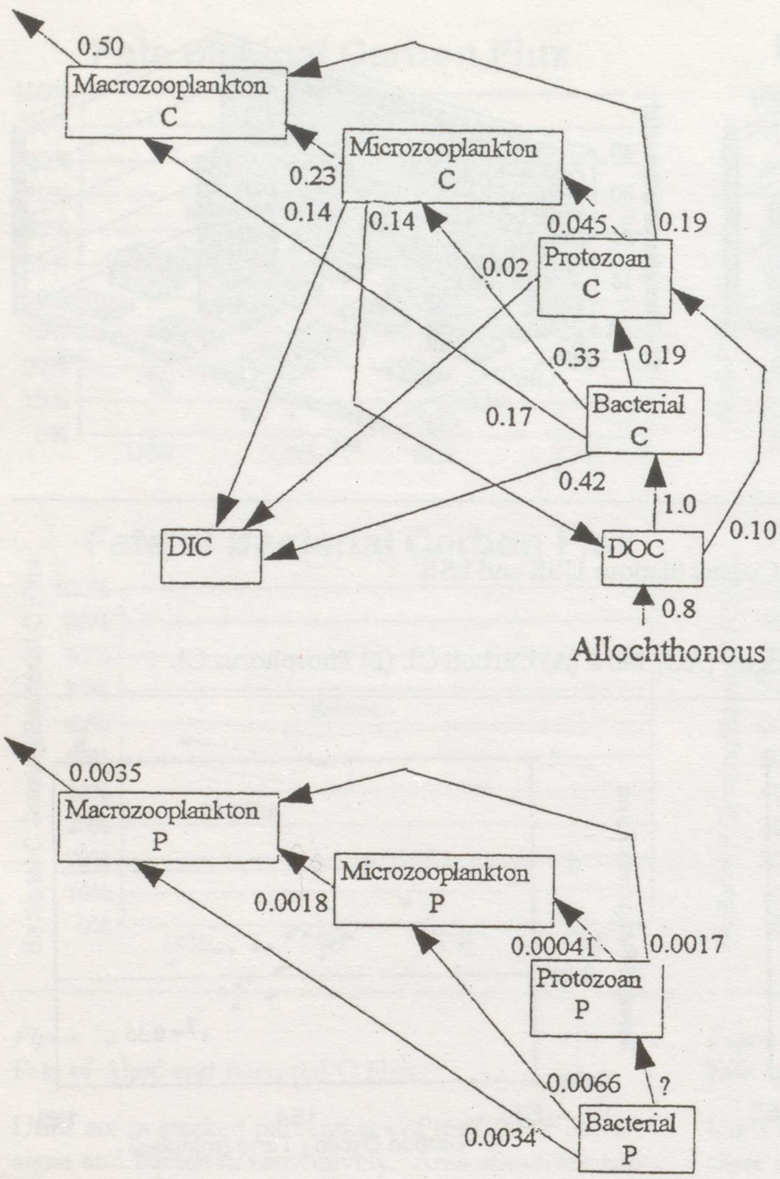

Figure 6
Microbial Food Web Homomorphic Subregion of the Planktonic Ecosystem Determined by Correlation Analysis of the Steady State Models (NS and OS models together).

Fluxes are portion of donating compartment scaled per unit bacterial production.

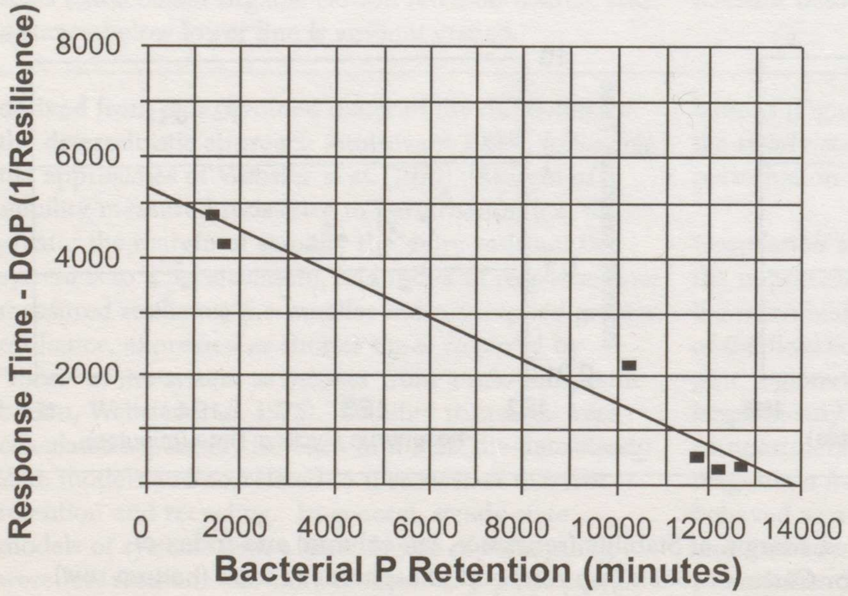

Figure 7
Correlation of System Resilience (Inverse Response Time) to Systems Perturbed by DOP Pulses vs. Bacterial P Retention

Units are minutes.

MICROBIAL FOOD WEBS, OFFSHORE COMMUNITIES, AND LAKE ERIE MODELS

We maintain that models are best used when they drive further investigation for scientific and practical purposes, rather than as ends in themselves. Models are tools useful for examining the consequences of complex arrays of data; they can't show novel findings beyond the data used to construct them. Our purpose here has been to consider the importance of the MFW to ecosystem functions of Great Lakes communities. Our approach has been to construct steady state models of nearshore and offshore communities in Lake Erie from field data collected using contemporary techniques designed to gather accurate information on the MFW, as well as those variables traditionally studied such as phytoplankton production and microcrustacean grazing. Analysis of these models for ecosystem functions such as regulation of C-flow and stability to nutrient perturbations indicates the importance of the MFW, warranting its inclusion in models of the base of the food web. Behaviors of Lake Erie models that include the MFW must be viewed not merely as "more realistic" but as generators of testable hypotheses regarding the significance of the MFW to Lake Erie ecosystem functions.

The field studies and models of them presented here indicate two major conclusions that warrant further examination: (1) the MFW is considerably important for ecosystem level functions, especially the role of protists; and (2) offshore communities differ more in function than in structure from nearshore communities. Direct and indirect grazing of bacteria (indirect grazing = grazing of bacterivorous grazers) at times provided more than 80 percent of the C and more than half of the P to microcrustaceans. Protist activities often appeared to be the most sensitive activities in the model, as noted above. Sensitivity analyses also indicated that protozoa would be useful indicators of system behavior because they are likely to magnify small changes in other parts of the system, especially those related to bacterial standing crop and DOC concentrations. These models also indicated protists play a significant role in regeneration of dissolved P, based on mass-balance considerations. Whether this will be supported by further studies specifically designed to examine this issue remains to be seen, but similar findings have been made in other systems (Jurgens and Gude 1990; Taylor and Lean 1991).

Although very similar in structure, nearshore and offshore communities functioned differently. Bacterial production was strongly correlated with allochthonous DOC input, so phytoplankton - bacterioplankton coupling was much stronger in OS communities, apparently due to the dependence of C-limited bacteria on DOC released from phytoplankton. Both bacteria and zooplankton appeared to retain C significantly longer in OS systems. NS and OS ecosystems differed in the degree of nutrient regeneration: nearshore bacterial P-release was generally around 10 percent of P-uptake, while in OS systems P-release by bacteria was often greater than 90 percent P-uptake. These observations taken together may indicate that bacteria were P-limited NS but C-limited in OS communities. Transfer of algal-C and bacterial-C was much more efficient in NS systems than OS. Likewise, a higher proportion of bacterial-P was transferred to bacterivores in NS systems. Such differences have been suggested previously in Great Lakes communities but without resolution (Moll and Brahce 1986; Scavia and Laird 1987).

IMPLICATIONS FOR LAKE ERIE MANAGEMENT

Traditionally, bacteria in the Great Lakes have been treated as a nuisance and their function only as a health hazard. Trophically, aquatic bacteria have been regarded as a C-sink, essential only as nutrient mineralizers (Ducklow *et al.* 1986; Pomeroy and Wiebe 1988). Awareness of the structure and function of the MFW in marine and freshwater communities has increased over the past decade, and often the MFW has been shown to be a significant C-link to higher trophic levels, essential for many ecosystem processes (Sherr *et al.* 1987a; Sherr and Sherr 1988). Recent studies in the Great Lakes have increasingly indicated the significance of the MFW in the structure and function of plankton food webs. Our purpose here has been to provide reasons for inclusion of MFW components in Lake Erie models of the base of the trophic cascade and to suggest that those models be used to drive research inquiries. Especially, we suggest more attention be given to comparison of flows through the MFW vs. the traditionally considered flows through algae via microcrustacean grazing and those factors that influence the relative contribution and efficiencies through each of those pathways. Exclusion of MFW from Lake Erie models could conceivably lead to management decisions that would lead to damage of the MFW and may mislead estimates of C-flux to higher trophic levels.

As an example of the need to include the MFW into research plans and models we mention briefly the effects of zebra mussels on the base of the food web. With the advent of the zebra mussel, *Dreissena polymorpha*, much attention has focused on loss of phytoplankton from the water column: zebra mussel damage to plankton communities has frequently been viewed exclusively as loss of phytoplankton and concomitant loss of C-flow to higher trophic levels. We see it otherwise. Zebra mussels graze bacterioplankton as well as phytoplankton (Cotner *et al.* 1995); they also graze heavily on protists (Lavrentyev *et al.* 1995), suggesting that zebra mussels could have a profound effect on processes that depend upon an intact MFW. Zebra mussels in Saginaw Bay, Lake Huron, excreted large amounts of ammonium to the water (Gardner *et al.* 1995) and greatly increased ammonium regeneration and decreased community ammonium uptake rates. In some systems it has been shown that protistan bacterivory can control populations of nitrifying bacteria (Lavrentyev *et al.* 1997), suggesting alteration of MFW by dreissenids could have profound effects on processing of ammonium released by zebra mussels. Zebra mussels also have a profound effect on P-dynamics at the base of the food web. Not only do these mussels release large amounts of phosphate, they also cause a great decrease of phosphate uptake by phytoplankton and bacterioplankton (Heath *et al.* 1995). Phytoplankton uptake appears to slow due to alteration from P-limited to P-replete physiological conditions, but bacterial P-uptake may slow due to extreme C-limitation caused by loss of phytoplankton DOC release (Heath *et al.* 1996).

ACKNOWLEDGMENTS

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Appendix F

Conceptualization of an Aquatic Ecosystem Model for Integrated Management of Lake Erie

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Historically, mathematical modeling of aquatic resources within the Great Lakes has focused on assessment and evaluation of management strategies for individual management issues (e.g., eutrophication, fisheries, toxic chemical exposure). With the advent of the "Ecosystem Approach" for governing and managing the Great Lakes, we have begun to observe and recognize that actions directed toward one management area can impact other problem areas. This realization has led us to a vision for the next generation of aquatic resource models, which incorporates these ecosystem linkages by coupling models of heretofore separate problem domains. In this paper we will present the conceptual framework for a Lake Erie Aquatic Ecosystem Management Model that can address important Lake Erie management issues. The conceptual model contains the aquatic biotic and abiotic components that are necessary to investigate some of the important ecosystem linkages between nutrient dynamics, phytoplankton functional groups, zooplankton, benthic populations (including zebra mussels), forage fish, top predator fish, and bioaccumulative chemicals of concern (such as PCBs). Progress toward this vision is exemplified by results of three ongoing projects: investigation of the effect of nutrient loadings and zebra mussel functioning on phytoplankton dynamics in Saginaw Bay; application of a screening-level model of the potential impact of zebra mussels on cycling and potential for bioaccumulation of PCBs in Lake Erie; and conceptualization of a Lake Michigan coupled pelagic-benthic food web model as part of the Lake Michigan Mass Balance Study. Additional model development, process research and field data acquisition is needed in many areas before this framework can be applied for supporting management decisions in Lake Erie. Some broad areas for research include: upper food web predator-prey interactions, population dynamics and coupling with lower food web; determination of organic carbon flow pathways through the microbial food chain, benthic primary and secondary production and coupling with pelagic food web; dynamic effects of trophic structure and function on contaminant bioaccumulation; dreissenid population dynamics and processing of nutrients and contaminants; and the impact of fine-scale physical processes on ecosystem-level biological interactions in the system. Also, a coherent field program that includes measurement of all relevant stressors (e.g., nutrient and contaminant loads, zebra mussel density distribution), all important all system response variable, and process rates where possible would be very valuable in the site-specific calibration of this ecosystem model to Lake Erie.

INTRODUCTION AND PROBLEM STATEMENT

Lake Erie has undergone tremendous changes over the past 15-20 years. Most of those changes can be attributed to significant phosphorus loading control measures implemented in the basin. However, some of the recent changes may be the result of the invasion of Dreissenids (zebra and quagga mussels) to the lake. In any event there is considerable interest in developing an understanding of these ecosystem changes and how they are related to management actions on Lake Erie (e.g., nutrient control, toxics load reduction, fish consumption advisories, fish management programs). This interest is evidenced by publications such as the Journal of Great Lakes Research special issue on "Evidence for the

Restoration of the Lake Erie Ecosystem," 19(2), 1993 and by workshops such as "The Changing Face of the Lower Great Lakes Ecosystems," co-hosted by the New York Sea Grant Institute and the Great Lakes Program at the University at Buffalo (February 5, 1994). Also, the stakeholders within the Lake Erie basin are currently in the process of developing and implementing a Lake Erie Lakewide Management Plan (LaMP), which has the task of identifying beneficial use impairments in Lake Erie as a whole and developing and implementing a management plan for eliminating those impairments. The LaMP process requires the use of an Ecosystem Approach for managing the lake and, therefore, requires a quantitative understanding of the Lake Erie ecosystem structure, function, and response to multiple stressors acting in concert. In particular, the response of Lake Erie ecosystem to changes in loads of nutrients and bioaccumulative contaminant of concern–both manageable stressors–needs to be understood and quantified.

The need for an Ecosystem Approach to managing Lake Erie has led to a vision for the next generation of aquatic resource models, which incorporates important ecosystem linkages by coupling models of heretofore separate issues. The conceptual ecosystem model presented in this paper contains the aquatic biotic and abiotic components that are necessary to investigate some of the important ecosystem linkages between nutrient dynamics, phytoplankton functional groups, zooplankton, benthic populations (including zebra mussels), prey fish, sport fish, and bioaccumulative chemicals of concern (such as PCBs). Progress toward realization of the vision is exemplified by results of three ongoing aquatic ecosystem modeling projects: investigation of the effect of nutrient loadings and zebra mussel functioning on phytoplankton dynamics in Saginaw Bay; application of a screening-level model of the potential impact of zebra mussels in Lake Erie on cycling and potential bioaccumulation of PCBs; and conceptualization of a Lake Michigan Ecosystem Model as part of the Lake Michigan Mass Balance Study.

HISTORIC PERSPECTIVE - NEED FOR A LAKE ERIE AQUATIC ECOSYSTEM MANAGEMENT MODEL

In order to develop a quantitative understanding of how management actions affect the structure and function of the Lake Erie ecosystem, it is important to review the history of the lake's responses to changes in both manageable and unmanageable stressors. Because of its morphology and hydrology, Lake Erie is the most susceptible of the Laurentian Great Lakes to cultural eutrophication. The history and description of past and current problems of Lake Erie is quite nicely related in a monograph published by the Ohio Sea Grant College Program (1987). Changes through the 1970s have been well documented in a special issue of the Journal Great Lakes Research (Boyce *et al.* 1987), and additional changes through the 1980s are reported in another Journal Great Lakes Research special issue (Makarewicz and Bertram 1993). Briefly, beginning with human settlement in the early 1800s, draining of vast coastal wetlands and clear-cutting of forests in rich uplands greatly increased the loading of nutrient-rich sediments to the lake and, in the process, accelerated eutrophication and destroyed fish habitat. The tremendous population and industrial boom during the first half of the twentieth century (population within the basin increased from about 4 million in 1900 to about 14 million in 1980) caused additional stress from municipal and industrial inputs of nutrients and toxic substances. Finally, extensive development of agricultural lands within the basin (approximately 67% of the current land use in the basin) resulted in large pesticide loadings and additional nutrient inputs to the lake. By the 1960s large mats of blue-green algae covered much of the western basin and southern shore of the lake and the central basin hypolimnion exhibited a large area of anoxia as summer progressed.

By the mid- to late 1960s the total phosphorus loading to Lake Erie was over 20,000 MT (metric tonnes)/yr. The scientific community had come to a consensus that phosphorus load reduction was the only valid solution to the cultural eutrophication problem in the Great Lakes. With the signing of the Great Lakes Water Quality Agreement in 1972 and its revision in 1978, the governments in the U.S. and Canada implemented a program of phosphorus load reduction that was unprecedented in any region of the world (DePinto *et al.* 1986a). Through the insights gained by development and application of nutrient-eutrophication models, a program of total phosphorus load reduction was established for each Great Lake. Target total phosphorus loads were established for each lake (11,000 MT/y was the target load for Lake Erie) on the basis of modeling results to achieve certain water quality goals (7 g/L and 5 g/L chlorophyll-a for the western and central/eastern basins of Lake Erie, respectively)(Task Group III 1978). The major load reductions were achieved through phosphate detergent bans and municipal point source controls, which were largely achieved in the Lake Erie basin by the early

1980s. However, it had been determined that the target load for Lake Erie could not be achieved without an additional 30% reduction in nonpoint sources. Best management practices (BMPs) were implemented on agricultural lands within the basin (DePinto *et al.* 1986a). By 1992, 34% of the Ohio Lake Erie basin land used for corn and soybeans was being farmed using conservation tillage practices (Ohio Lake Erie Office 1993). Dolan (1993) reported the IJC estimates of total phosphorus to Lake Erie from 1986-90. He found that point source inputs remained fairly constant between ~2200-2500 MT/year (corresponding to very close to an average of 1 mg/L effluent concentration), but he noted that the nonpoint tributary loading varied from a low of 3837 MT/year in 1988 to a high of 9063 MT/year in 1990. The tributary loads were closely related to the hydrologic runoff for a given year and were almost solely responsible for the ± 3000 MT/y variation around the Lake Erie target load.

In response to the phosphorus load reduction program in the Great Lakes, Lake Erie phosphorus levels and phytoplankton biomass had dropped considerably by the mid-1980s. Bertram (1993) noted that spring isothermal total phosphorus levels in the central basin had dropped from close to 20 g/L in the 1970s to the target of 10 g/L by 1987. Makarewicz (1993) concluded that a significant reduction in phytoplankton biomass had occurred in all three basins of Lake Erie between 1970 and the mid-1980s. During his five year study from 1983-87, he found average phytoplankton biomass values of 1.88±0.12 g/m^3 (dry wt.), 1.04±0.075 g/m^3, and 0.63±0.071 g/m^3 for the western, central, and eastern basins, respectively. These values represented a 52-89% reduction in mean basin-weighted algal biomass from 1970 values measured by Munawar and Munawar (1976). Also, slight but delayed improvements in the degree of summer anoxia in the central basin have been observed (Bertram 1993; Charlton *et al.* 1993). El-Shaarawi (1987) confirmed that a statistically significant reduction in chlorophyll-a had taken place between 1968 and 1980. He also developed a statistical model that demonstrated a significant relationship between total phosphorus and dissolved oxygen depletion rate, so long as lake level is also included in the regression.

The Lake Erie responses to phosphorus load reductions are very close to those predicted by DiToro and Connolly (1980) in their modeling work used to establish the target load in 1978. Their post-audit examination of the model's long-term predictability indicated that it had reasonably well predicted the lake's response to the phosphorus load reductions through the 1980s (DiToro *et al.* 1987). They were remarkably accurate in their prediction of changes in phosphorus and chlorophyll a levels in all three basins and in hypolimnetic oxygen depletion rates in the central basin. This success should give us confidence that we understand the causal chain between phosphorus loading to Lake Erie and it phytoplankton biomass, so that we can potentially identify perturbations to this relationship that might be imposed by the insertion of zebra mussels into the trophic structure.

Through the accelerated eutrophication process in Lake Erie, its fish community of the lake suffered considerably. Since the late 1800s, the combined effect of stream obstruction, wetland draining, extreme pollution, heavy siltation, increased flooding, over fishing and introduction of exotic species has led to the extinction or virtual elimination of several important sport and commercial fish species, including sturgeon, cisco, whitefish, and blue pike (Arnold 1969; Beeton 1969). By the 1960s, the walleye population had plummeted and yellow perch produced the major commercial catch in the lake (White 1987). Also, the rainbow smelt, introduced accidentally in the 1930s, was becoming a major planktivorous species in the lake. However, the major water pollution control efforts in the Great Lakes through the 1970s and early 1980s, along with commercial catch restrictions, seems to have led to a rebound in the walleye population in the lake. According to White (1987), only slightly more than 100,000 walleye were caught by Ohio anglers in 1975, but almost 4.5 million were taken in 1986. Today walleye and yellow perch are the dominant game fish in the system, but there is a lake trout restoration program being undertaken in the eastern basin (Coldwater Task Group 1994). This recovery of walleye and the relative success of the lake trout program is attributed in large part to the major improvement in Lake Erie water quality over the past twenty years. Yellow perch are not doing as well in Lake Erie, with the predominant reason being given as competition from white perch.

Just when the Lake Erie ecosystem seemed to have recovered to its healthiest state in many years, it was hit with the invasion of zebra mussels. Zebra mussels were first discovered in the Great Lakes in Lake St. Clair in June, 1988 (Hebert *et al.* 1989); judging from the shell size it was theorized that the introduction had taken place some time in 1986. The first confirmed sighting in Lake Erie was in July 1988 (O'Neill and MacNeill 1991; Leach 1993). By the summer of 1989, extensive colonies of up to 30,000 to 40,000 individuals per square meter were reported in the western basin

(Ontario Ministry of Natural Resources 1990; Wu and Culver 1991). It is now known that virtually the entire lake has been infested; even the deeper waters of the eastern basin have not been spared. In 1991, a second species of *Dreissena* was discovered in Lake Ontario waters (May and Marsden 1992); originally identified as the "quagga" mussel, it has recently been given the taxonomic identification *Dreissena bugensis* (Spidle *et al.* 1994; Rosenberg and Ludyanskiy 1994). The quagga has become the dominant dreissenid in the deeper waters of Lake Erie, especially in the eastern basin where it outnumbers the zebra mussel by 14 to 1 at water column depths greater than 20 meters (Mills *et al.* 1993).

The literature is replete with impacts associated with zebra mussels clogging water intake pipes in the Great Lakes (LePage 1993; Kovalak *et al.* 1993). Much of the early research on the problem of zebra mussels in the Great Lakes was devoted to controlling their propensity to clog water intake pipes and foul the hulls of vessels. However, more recent emphasis has been placed on the ecological impacts of this invasive genus. Two very good overviews of the zebra mussel problem in North America are presented in a Sea Grant coastal resources fact sheet (O'Neill and MacNeill 1991) and a National Oceanic and Atmospheric Adminstration/ Great Lakes Environmental Research Laboratory (NOAA/GLERL) report (GLERL and CILER 1994). A very good collection of the early research findings on the biology, impacts and control of zebra mussels in North America is presented in a book edited by Nalepa and Schloesser (1993).

Many of the impacts of zebra mussels in the Great Lakes result not only from its ability to colonize on hard surfaces but from the mussel's role as a suspension feeder capable of filtering all particles down to a size of 1 um from the water column (Sprung and Rose 1988). Given a typical filtration capacity of 1 liter/day-individual and typical (for suitable substrate) densities of 103-104/m^2, mussels can filter 1-10 meters of water column per day free of phytoplankton and similar sized particles. This filtered material is either assimilated (converted to zebra mussel biomass) or deposited to the bottom substrate as feces or pseudofeces.

The water quality impacts of zebra mussels in the Great Lakes have been well documented. Holland (1993) demonstrated a 100% increase in transparency accompanying an 82-92% decrease in planktonic diatoms after establishment of zebra mussels in western Lake Erie. This greatly increased light penetration could have a significant impact on growth of submerged aquatic vegetation in bays and nearshore waters of the lakes. Nicholls and Hopkins (1993) reported a >90% decrease in phytoplankton densities along the North Shore of Lake Erie over the same period. But the recent changes in phytoplankton density cannot be directly attributed to phosphorus loading reductions. As Figure 1 shows, Nichols and Hopkins (1993) demonstrated that the relationship

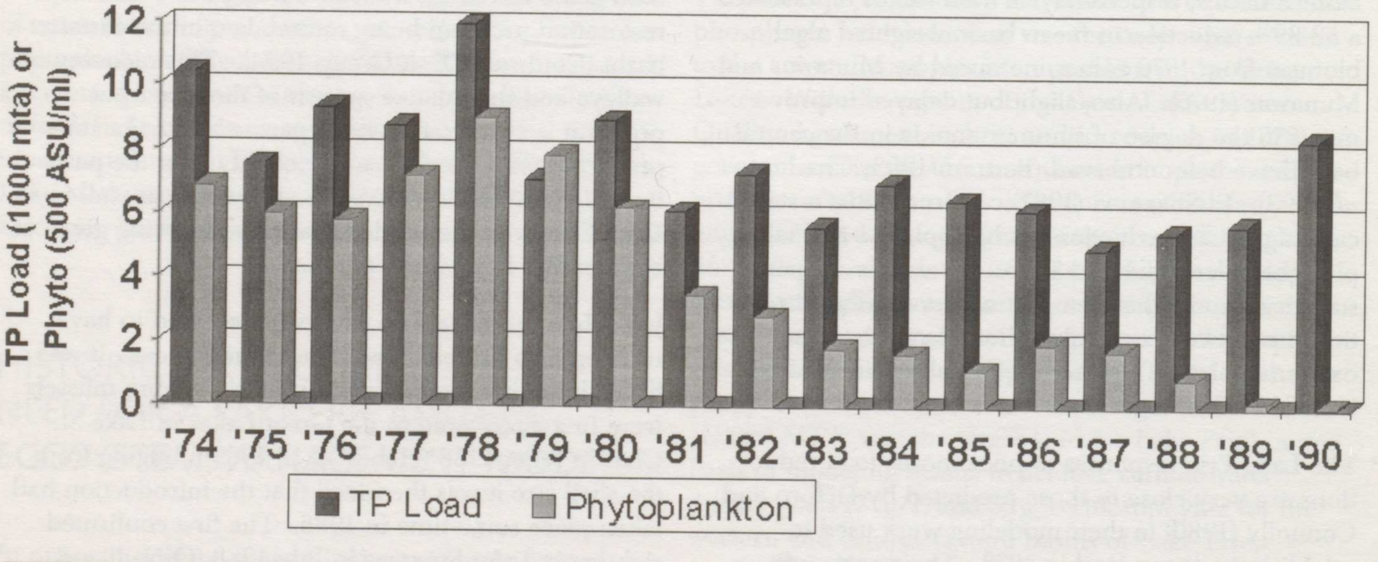

Figure 1
Historical Trends of Total Phosphorus Load and Phytoplankton Density in the Western Basin of Lake Erie (from Nichols and Hopkins 1993)

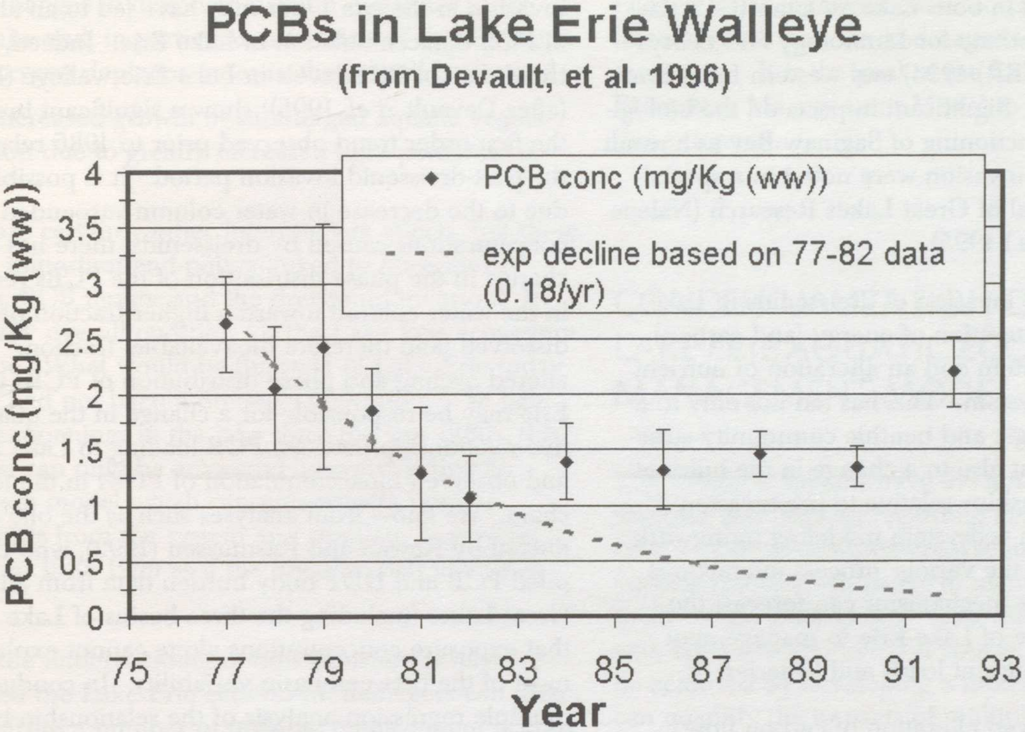

Figure 2
PCB Concentration in Lake Erie Walleye

Dashed line represents exponential fit to data for period from 1977-1982 (shows decline at first-order rate of 18%).

between phosphorus load reductions and phytoplankton response (as predicted by eutrophication models (DiToro *et al.* 1987)) that existed in western Lake Erie for the period 1974-1987 no longer applied to data collected subsequent to the zebra mussel invasion. Beginning in 1988 and especially in 1989-90 there was an additional decrease in phytoplankton biomass, with no decrease in phosphorus load. The only logical hypothesis is that the additional loss of algal biomass is due to feeding of zebra mussels on algae. This is another hypothesis that can be tested by an appropriately designed Lake Erie Aquatic Ecosystem Management Model.

In addition to affecting phytoplankton density by filter feeding, zebra mussels may pose an indirect effect on algal density and seasonal patterns. Bierman *et al.* (1998) have demonstrated that renewed blue-green algal blooms in Saginaw Bay subsequent to the zebra mussel invasion are not only the result of selective rejection of blue-greens by zebra mussels but are enhanced by increased sediment-water phosphorus fluxes in late summer. They postulate that an indirect effect of the large zebra mussel induced flux of algae and associated nutrients in spring and early summer is appropriate conditions for a late summer pulse of nutrients at a time when temperatures are favorable for blue-green algal growth. Effler and Siegfried (1998) confirmed that zebra mussels contribute to an alteration in phosphorus dynamics in a system by noting that the zebra mussel invasion of the Oswego River had led to a significant enhancement of soluble reactive phosphorus in the water column without a significant change in the total phosphorus concentration. DePinto *et al.* (1986b) demonstrated that phytoplankton growth in Lake Erie in the late summer was largely controlled by recycle of phosphorus in the water column and from the sediments. If dreissenids are altering the spatial and temporal nature of this important process in Lake Erie, then it is crucial to understand the mechanisms involved and to incorporate them into our modeling framework.

In addition to their impact on primary production, zebra mussels can affect secondary production. Griffiths (1993) attributed increases in benthic fauna (amphipods, flatworms, snails, worms) in Lake St. Clair following the zebra mussel infestation to a combination of alteration of benthic habitat structure and deposition of feces and pseudofeces. On the other hand, Nalepa and co-workers found significant reductions in the abundance of native North American freshwater mussels (Unionidae) in both Lake St. Clair (GLERL and Cooperative Institute for Limnology and Ecosystems Research (CILER) 1994) and western Lake Erie (Nalepa *et al.* 1993). Significant impacts on the biological structure and functioning of Saginaw Bay as a result of the zebra mussel invasion were noted in a special section of the Journal of Great Lakes Research (Nalepa and Fahnenstiel (eds.) 1995).

It is evident that the invasion of dreissenids in Lake Erie has led to an alteration of energy (and carbon) flow through the system and an alteration of nutrient cycling within the system. This has led not only to a change in both pelagic and benthic community structure and function but also to a change in the nutrient-productivity relationships relative to pre-invasion conditions. Only an ecosystem modeling framework that integrates all of the various process interactions and system feedback mechanisms can forecast the quantitative response of Lake Erie to management actions relative to nutrient loads and fisheries.

The dreissenid-induced alteration of carbon flow through the Lake Erie system may also be having an impact on bioaccumulation of contaminants like PCBs in top predator fish such as walleye. Again, this impact must be viewed in the context of how the lake behaved prior to the Dreissenid invasion. Like the other Great Lakes, the loadings of persistent, bioaccumulative chemicals (like PCBs) to Lake Erie peaked in the early 1970s and dropped off in response to use bans and source controls implemented through the 1970s and early 1980s. Lake Erie, however, did not appear to suffer nearly as much as Lake Ontario in terms of bioaccumulation of persistent chemicals like PCBs in top predator fish. Fish consumption advisories were not nearly as restrictive in Lake Erie. Although the loadings of PCBs to Lake Erie were comparable to Lake Ontario on a volumetric basis, the top predator fish did not appear to accumulate PCB nearly as much. Rathke and McRae (1989) used 1985 data from Lake Erie to demonstrate a typical PCB biomagnification from approximately 0.015 ppm in net plankton to 0.2 ppm in smelt to 1.5 ppm wet weight in walleye. At the same time, PCBs in lake trout in Lake Ontario–PCB loading to the two lakes in the mid-1980s was about the same–was in the range of 4-6 ppm wet weight (DeVault *et al.* 1996; Heustis *et al.* 1996).

It has been hypothesized that the higher levels of suspended solids in Lake Erie served, through adsorption and settling, as a mechanism for reducing bioaccumulation through the grazing food chain. If this is true, then it is possible that the Dreissenid invasion in the late 1980s may have led to an alteration of PCB bioaccumulation in Lake Erie. Indeed, the trend data of PCB levels in Lake Erie walleye (Figure 2 (after Devault *et al.* 1996)) show a significant break in the first-order trend observed prior to 1986 relative to the post-dreissenid invasion period. It is possible that, due to the decrease in water column suspended solids concentrations caused by dreissenids, there has been a change in the phase distribution of the PCBs remaining in the water column toward a higher fraction of the dissolved (and therefore bioavailable) fraction. This altered cycling and phase distribution of PCBs in Lake Erie may be responsible for a change in the quantitative relationship between PCB loading to Lake Erie and observed bioaccumulation of PCBs in the food chain. We know from analyses such as the one conducted by Rowan and Rasmussen (1992), who compiled PCB and DDT body burden data from all of the Great Lakes (including the three basins of Lake Erie), that exposure concentrations alone cannot explain most of the between-basin variability. In conducting a multiple regression analysis of the relationship between these data and basin-specific properties, they concluded that ecological attributes such as fish lipid content, organism trophic level, and structure of the food chain had to be considered. Findings such as these also point to the potential importance of zebra mussels in PCB cycling and bioaccumulation in Lake Erie. Testing this hypothesis is another important goal of the proposed Lake Erie Aquatic Ecosystem Management Model and process research necessary for its development.

MANAGEMENT QUESTIONS FOR LAKE ERIE

Presented above is some evidence that recent ecological changes in Lake Erie are the result of a combination of phosphorus load reductions, the dreissenid invasion, and loss of fish habitat. Among the most significant potential impacts are:

1. Reduced carrying capacity of the lake for sport fish such as walleye and yellow perch;
2. Shifts in phytoplankton species succession that includes to renewed late summer blue-green algal blooms;
3. Increased bioaccumulation of contaminants like PCBs through the food chain;

4. Changes in dissolved oxygen dynamics in the lake and, in particular, alteration of hypolimnetic oxygen depletion rates in the central basin; and
5. Increased growth of submerged aquatic vegetation due to greatly increased light penetration.

There are certainly other intermediate effects, but these are the important end-points linked to phosphorus loading, PCB inputs, and the dreissenid invasion. In fact, a key overall question for the Lake Erie ecosystem might be "What would be the state of Lake Erie today if there had not been a dreissenid invasion?" In light of the happenings in the lake since the late 1980s, this question can only be answered by constructing an ecosystem model which can numerically remove dreissenids from the system and simulate its progression from 1985-1999 as if the invasion had not taken place.

Given the understanding of how dreissenids have impacted the Lake Erie ecosystem, managers can then choose from a number of possible management actions that are available for addressing the ecological impacts of concern. Among the actions that can be implemented either alone or in combination are:

1. Do nothing new and allow the natural homeostasis of the system operate to alleviate the problem (i.e., No Action Scenario);
2. Implement efforts to reduce loading of phosphorus and sediments to the lake, probably through additional agricultural BMPs;
3. Allow an increase in the phosphorus loading to the lake by permitting wastewater treatment plants to discharge treated waste with more than the currently required 1 mg/L of total phosphorus;
4. Continue efforts to reduced the loading of bioaccumulative chemicals of concern (industrial chemicals and pesticides);
5. Institute a program of walleye habitat restoration that will provide more natural spawning habitat;
6. Institute a program to reduce human exploitation of forage fish in Lake Erie, so as to increase the food supply for walleye; and
7. Institute a program to control dreissenid numbers and biomass (this program could include harvest, reproduction controls, and/or planting of mussels predator populations).

Each of these management actions has potential impacts (both positive and negative) throughout the ecosystem. It is the goal of the Lake Erie Aquatic Ecosystem Management Model to identify and quantify those impacts.

CONCEPTUALIZATION OF LAKE ERIE AQUATIC ECOSYSTEM MANAGEMENT MODEL

Mathematical models have the ability to synthesize and integrate information regarding the interaction among components of complex ecosystems. This capability enables resource managers to identify how decisions made in one management area will affect the system with regard to another. Of course, this goal can only be achieved by developing a modeling framework that can quantify the impacts of multiple stressors, both natural and anthropogenic, acting in concert on key ecosystem components to generate multiple response endpoints. The principal stressors and system responses to be quantitatively linked by the Lake Erie Aquatic Ecosystem Management Model are depicted in Figure 3. The system responses in represent quantitative measures of ecological impacts mentioned above that will result from a specified set of ecosystem stressors, some of which can be affected by the management actions listed in the previous section.

The general strategy for constructing the Lake Erie Aquatic Ecosystem Management Model will be to formulate coupled modules (or submodels) that can be activated as required to develop a system-specific application. Each of these modules will have "generic" components that are potentially important but may take on different attributes in different ecosystems. For example, there will be a benthic suspension feeder that may be represented by the attributes of dreissenids in Lake Erie. At the upper end of the food web, the system will contain a number of components and age classes for prey fish and predator fish; these constituents can also be parameterized to represent particular species on a site-specific application basis.

The modular structure for a Lake Erie Aquatic Ecosystem Management Model that integrates the management issues mentioned above is depicted in Figure 4. Also shown in this diagram are the various system stressors and the linkages between modules (arrows) that are needed to represent the most important ecosystem

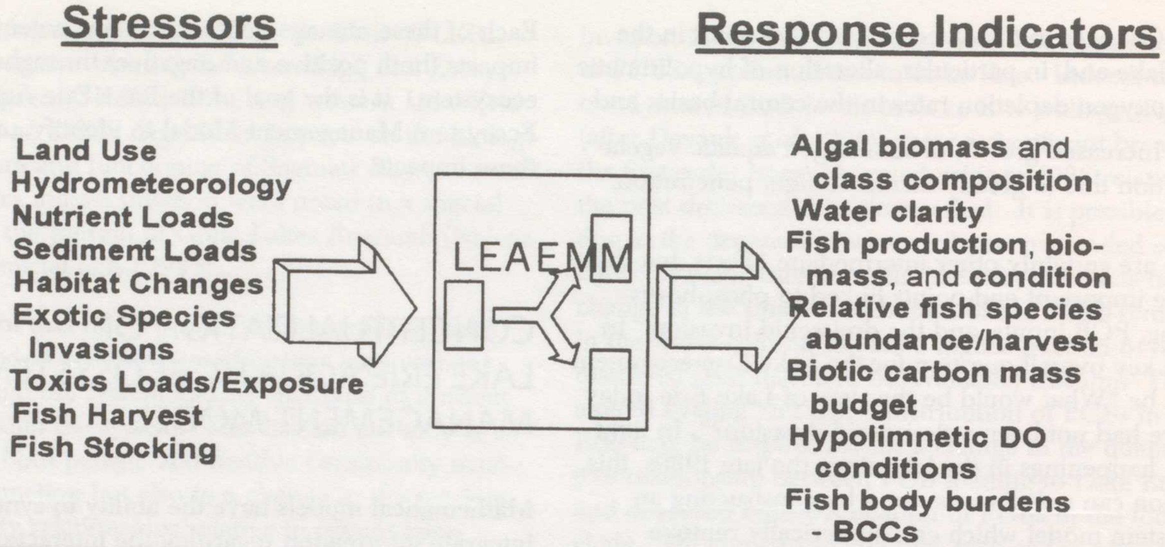

Figure 3

Lake Erie Aquatic Ecosystem Management Model Relates Multiple Response Endpoints to Multiple Stressors Acting in Concert

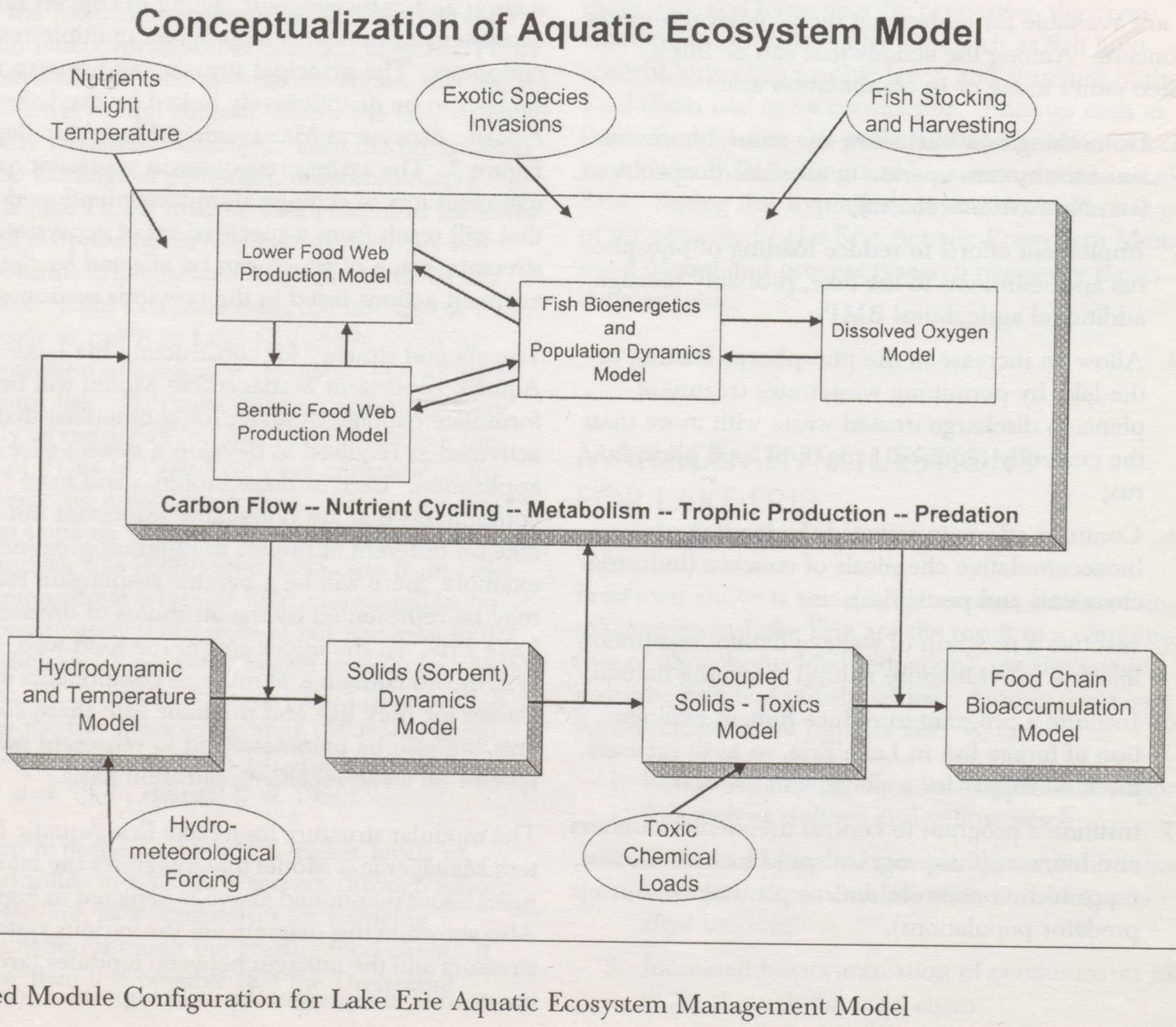

Figure 4

Integrated Module Configuration for Lake Erie Aquatic Ecosystem Management Model feedbacks or homeostatic processes. For example, unusually successful walleye recruitment can have a top-down effect on the lower food web; an increase in predator fish can cause a decrease in prey fish, which in turn will reduce the predation pressure on zooplankton.

It should be noted, however, that integration of single-issue models as depicted in Figure 4 is not trivial. While the Great Lakes has a wealth of experience and success in developing and applying the single-issue models, relatively little work has been conducted on coupling these models into an ecosystem analysis framework. The experience gained through our initial ecosystem modeling efforts (briefly discussed below) has made us aware of the many scale dependency and kinetic process linkage issues that are involved in formulating coupling aquatic ecosystem models by coupling what we have learned and developed through our single-issue modeling. It has also made us confident that the proposed conceptual approach to developing models of complex ecosystem interactions can be accomplished.

The first step in converting the overall framework depicted in Figure 4 into a conceptual model that can address the management issues of concern is to determine the ecosystem components (state variables) that need to be included. In establishing the key state variables in the model, one must also consider the "currency" of the model. For example, in most eutrophication models the "currency" involves a measure of the biomass in various biota compartments (i.e., chlorophyll-a or dry weight for phytoplankton) as well as the nutrient concentration in various biotic and abiotic compartments that are relevant to the problem definition. In an aquatic ecosystem model such as the one conceived for Lake Erie, one needs a common currency for biomass throughout the food web in addition to tracking both the nutrient content (phosphorus, nitrogen, and silica) and the PCB content in all important biotic and abiotic compartments of the system. We believe that the best biomass measure for this model is organic carbon. It has several advantages for a single currency to be used across the entire food web. First, it relates reasonably well with bioenergetics analysis of organisms. It also can be used as an aggregate biomass measure for the lower food web (plankton), while it can be used to represent average size for individual organisms higher up the food chain; then biomass of a given species becomes the product of individual carbon level and species density. This is important because some processes impact individual size while others (like reproduction and recruitment) operate on numbers of a given species or age class within a species. Two other important reasons for using organic carbon as the common biomass currency for this model are that it greatly facilitates the mass balance modeling of hydrophobic organic compounds like PCBs and that it also facilitates cycling of nutrients through organisms based on carbon to nutrient stoichiometries.

Combining the integrated module configuration shown in Figure 4 with the carbon biomass concept, one can develop a conceptual model for carbon flow through the Lake Erie aquatic ecosystem. This carbon flow diagram is depicted in Figure 5. Each box in Figure 5 represents a functional reservoir of organic carbon within the sediment-water system. Each of these reservoirs has basic characteristics with respect to how they process carbon and how they are coupled with other carbon reservoirs within the system. As indicated in the diagram it is possible for a given functional reservoir to contain more than one species or more than one age class of a given species. In this way an ecosystem hierarchy is developed where there are certain higher-level functions that are characteristic of all compartments within a reservoir (e.g., all phytoplankton contain chlorophyll-a, obtain energy and synthesize new biomass by primary production, settle through the water column, and are potentially grazed on by zooplankton) but different classes of species within the phytoplankton reservoir may have specific properties or behaviors that make differentiation necessary within a specific problem context. For example, if one wants to investigate the implications of blue-green algae not being grazed by zooplankton or zebra mussels, then the phytoplankton reservoir must comprise of at least two classes (or objects in programming terminology), one for blue-greens and one for all other phytoplankton. If concerns such as the effects of silica, nitrogen, phosphorus, light, and temperature on seasonal succession are important then a finer differentiation such as indicated in the phytoplankton reservoir in Figure 5 may be warranted. Similar arguments can be made for having multiple classes within each of the other reservoirs in Figure 5.

It should be noted that Figure 5 presents only the carbon flow diagram, however it does contain all of the functional reservoirs in the prototype Lake Erie Aquatic Ecosystem Management Model. The fate and transport of nutrients and PCBs through this system is not shown because of space limitations. However, this carbon flow conceptualization can serve as a framework for building nutrient and PCB mass balance equations into the overall framework. In fact some of this model coupling has already been accomplished in the projects discussed below.

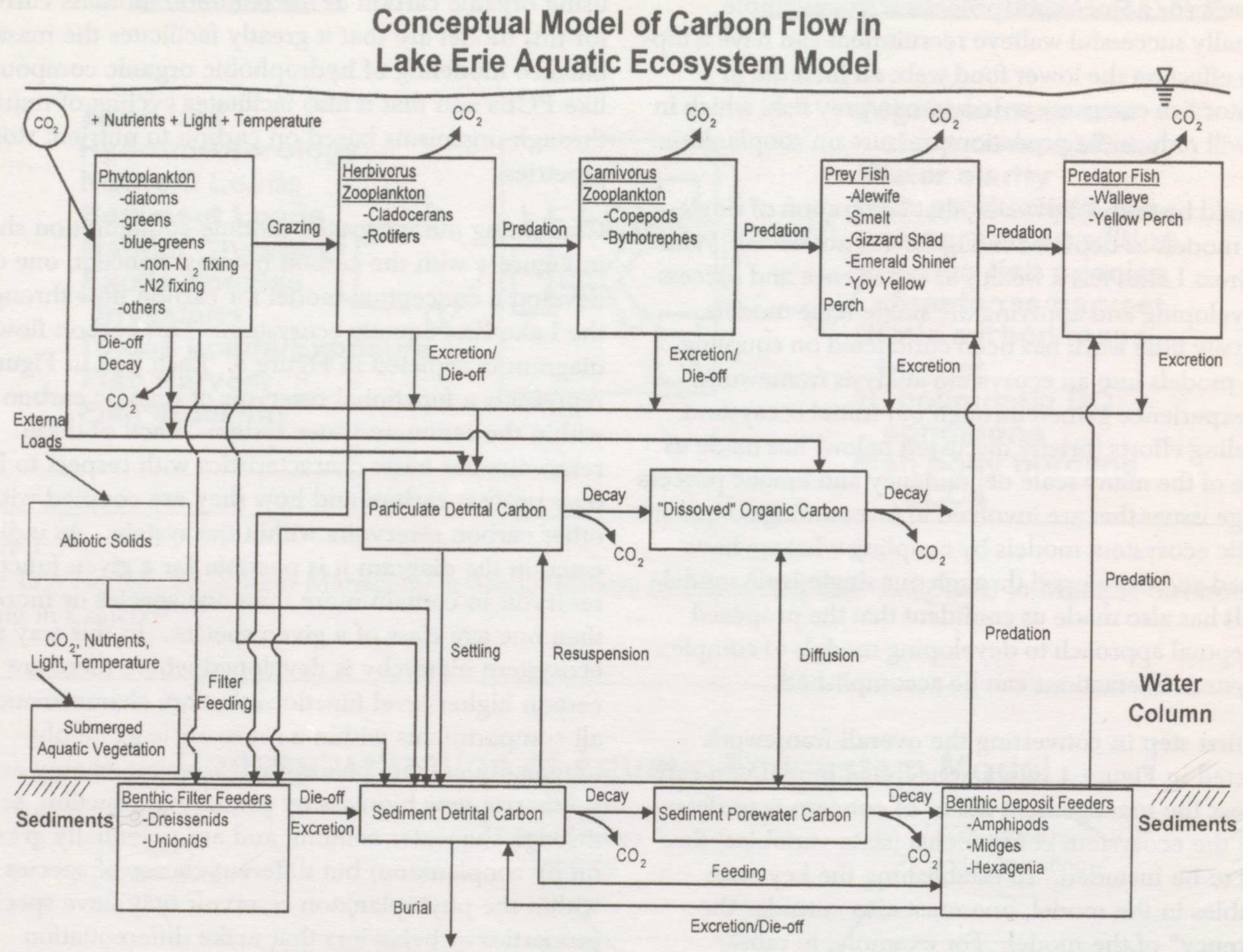

Figure 5

Conceptual Model of Carbon Flow in the Proposed Lake Erie Aquatic Ecosystem Management Model

PROGRESS TOWARD AN OPERATIONAL AQUATIC ECOSYSTEM MODEL FOR THE GREAT LAKES

The Principal Investigators are not only recognized leaders in the Great Lakes modeling community but are at the forefront of research in the development and application of aquatic ecosystem models. Bierman, DePinto, and Feist are working on a project, funded by EPA-GLNPO, to develop a nutrient-phytoplankton-zebra mussel-PCB mass balance model for Saginaw Bay. This ecosystem model is being formulated by coupling previously developed (through EPA funding) individual-issue models: a nutrient cycling, multi-class phytoplankton model (Bierman and Dolan 1981; Bierman *et al.* 1984; Bierman and Dolan 1986a; 1986b); coupling a zebra mussel bioenergetics model to the phytoplankton model (Limno-Tech, Inc. 1995; Limno-Tech, Inc. 1997); and finally, with the ongoing project, coupling of a PCB mass balance model with the coupled phytoplankton-zebra mussel model. DePinto previously conducted a screening-level modeling analysis of the impact of zebra mussels in Lake Erie on the cycling and bioaccumulation potential PCBs (DePinto and Narayanan 1997; DePinto *et al.* 1997). Bierman, Feist, and DePinto are also working on the Lake Michigan Mass Balance Study to develop an enhanced carbon mass balance model that can provide an accurate simulation of organic carbon dynamics in Lake Michigan for use as input to the hydrophobic organic carbon mass balance model being developed for that system. DePinto has also developed a whole-lake annual average nutrient-trophic transfer model (Jain and DePinto 1996) to investigate the trade-offs between phosphorus control and fish stocking levels on salmonid fish production in Lake Ontario.

RESEARCH AND DATA NEEDS

Development of a modeling framework such as the one presented above to the point where it can be used confidently for supporting management decisions in Lake Erie would benefit from further research and monitoring in three broad areas: model development, process research, and field measurements. There is a symbiotic relationship among these three components that must be considered in any aquatic ecosystem assessment. Models can provide great insight and make projections, but only with the support of monitoring, which provides model inputs and credibility, and research, which provides understanding and parameterization for model development.

Modeling research takes the form of developing new modules for the proposed Lake Erie integrated framework and coupling them with existing modules at the appropriate time and space scales (see Figure 4). There are several modules and linkages that require significant development work in the construction of a Lake Erie Aquatic Ecosystem Management Model depicted in Figure 4:

- development of a microbial loop carbon flow submodel that can account for the substantial flow of organic carbon through the lower pelagic (phytoplankton, heterotrophic microbes, and zooplankton) and benthic food webs of the system;
- upper food web (zooplankton - fish) bioenergetics, predator-prey interactions, and population dynamics and coupling of this module to lower food web;
- benthic production and coupling to pelagic modules (including zebra mussel population dynamics, other benthic fauna (deposit feeders), predator-prey interactions, and benthic flora (SAV, benthic algae) production and growth and nutrient cycling processes);
- development of a sediment carbon diagenesis sub-model that can provide data input to the solids dynamics module along with carbon production and transformation rates in the water column;
- development of a contaminant bioaccumulation module that responds appropriately to dynamic output from the food web carbon flow module (including the dynamic effects of trophic structure and function on bioaccumulation, and the dynamic effects of organism metabolism and growth rates on bioaccumulation); and
- development of an appropriate linkage between a fine-scale, three-dimensional hydrodynamic / heat budget model and the remainder of the ecosystem model in a way that provides the necessary resolution in physical environment (water transport and temperature regimes) within which all biochemical processes take place.

Development and parameterization of the modeling framework described above would benefit from process experimental research in several areas. Among the highest priority areas are:

a) identification of the factors controlling zooplankton production, biomass, and species succession, and quantification of the role of zooplankton in carbon transfer to the upper food web;
b) identification and quantification of the factors controlling predator-prey interactions among organisms in the pelagic and benthic food webs; and
c) fundamental studies of processes responsible for governing particle dynamics in the water column and sediments of the system (including particle deposition processes, particle resuspension processes (both physical and biological in origin), and carbon decay processes.

Last but certainly not least in importance is the collection of field data to provide inputs for models and data for comparison with model output. In general, this effort should be as coordinated and coherent as possible. It should be conducted at appropriate spatial and temporal scales relative to modeling needs; and it should be designed so that a less intensive subset of the field data can be collected on a long-term basis to provide valuable trend information. Field monitoring falls into three categories: monitoring of external stressors; monitoring of models output variable (i.e., system response variables), and field monitoring of the rate and extent of processes included in the conceptual model of the system. With regard to external stressors, such measurements as sediment, nutrients, and bioaccumulative chemicals of concern loadings is essential. Other stressor related measurements include dreissenid densities, hydrometeorological conditions, and fish stocking and harvesting. Also, routine in situ monitoring of all response variables (model output) upon which management decisions are made should be conducted at space and time scales appropriate to the variable of interest. Typical response variables include: algal biomass and class composition; fish biomass, species composition, age distribution and condition;

nutrient levels (including organic carbon) in water, sediments, and biota; bioaccumulative chemical concentrations in water, sediments, and biota; dissolved oxygen and particulate matter spatial and temporal profiles. Finally, field measurement of the rate and extent of process incorporated into the model can provide a very valuable set of additional constraints on calibration and field confirmation of the model. This component of the field program might include measurement of processes such as primary production, zooplankton production, fish growth rates, bottom sediment resuspension rates, areal hypolimnetic oxygen depletion rate, and air-water mass transfer rates.

Mathematical mass balance models provide an excellent means of synthesizing what we know about the behavior of an aquatic system. The next generation of such models should focus on integrating the components of the system that are important to the range of management areas being addressed for that system. With very important management questions regarding nutrient controls, toxic chemical exposure, exotic species invasions, and fisheries management, Lake Erie provides an excellent ecosystem within which to demonstrate the feasibility and utility of this next generation of models.

Appendix G

The Lake Erie System Model

(A fuzzy cognitive map to support development of ecosystem objectives)

Hans Biberhofer[1], Maria Colavecchia[1], Sandra George[1], Roger Knight[2], Stuart Ludsin,[3] and Philip Ryan[4]

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Agencies and concerned citizens are developing ecosystem objectives for the Lake Erie Management Plan (LaMP) as directed by the Great Lakes Water Quality Agreement (1987). The level of change in the Lake Erie ecosystem precludes adoption of objectives based on return towards pristine conditions, and conflicts exist between and among stakeholder interests and agency policies. A model of ecosystem components, values, impacts and remediation measures was developed in order to explore possible system configurations. The model structure is fuzzy cognitive map in which physical processes are typically represented as linear (phosphorus loading), while biotic responses are represented logistically as niche (Hutchinsonian-Fry) response surfaces (Figure 1). The model essentially provides a flexible book-keeping function for a range of knowledge from general knowledge to peer reviewed science. All relationships are documented and can be audited. The model can be exercised by varying initial conditions and controllers which represent human effects (e.g. land use, exploitation), in order to produce scenarios of the future. Organization of these scenarios by cluster analysis identifies potential ecosystem states. Ecosystem Objectives will be written as a characterization of a single state, selected with public consultation. This is a progress report on behalf of the Ecosystem Objectives Subcommittees of the LaMP Workgroup and Public Forum.

INTRODUCTION

Agencies and special interest groups need to understand that meeting their need in the Lake Erie system can have a great number of implications elsewhere in the ecosystem. The model is intended, in order to show the full implications of potential changes in management, but at a low level of resolution. Its primary application will be to represent the complexity of the Lake Erie system while making forecasts of the future and thereby showing all of the implications of particular management actions or policies. The model is not quantitative and all forecasts are relative to current conditions.

ASSUMPTIONS

Man can control some features of the Lake Erie ecosystem including: land use and consequent effects including silt/sediment loss from land and deliver to lake, contaminant loading, phosphorus loading, and restoration of natural environments; harvesting of fish and wildlife; and disturbance of natural systems.

Ecosystem configuration and characteristics are expected to change if these factors are manipulated. It should be possible to map the ripple of change that should follow manipulation or restoration of these features, and record it as a forecast. Such a forecast would show all the implications of change such as increased phosphorus loading, such as fish community composition and changed water transparency with implications for aesthetic values, and area of littoral zone. If we examine a large number of scenarios of intervention, we should be able to describe some patterns in these forecasts, which may permit them to be grouped for consideration as descriptions of possible future states of Lake Erie. Evaluation of feasibility, and consultation with agencies and the public about the desirability of these states, would lead to selection of a single state description as a desired future state. Ecosystem objectives would be written in a way to achieve the desired state. Strategic and tactical plans to achieve objectives would be developed using other models or analyses.

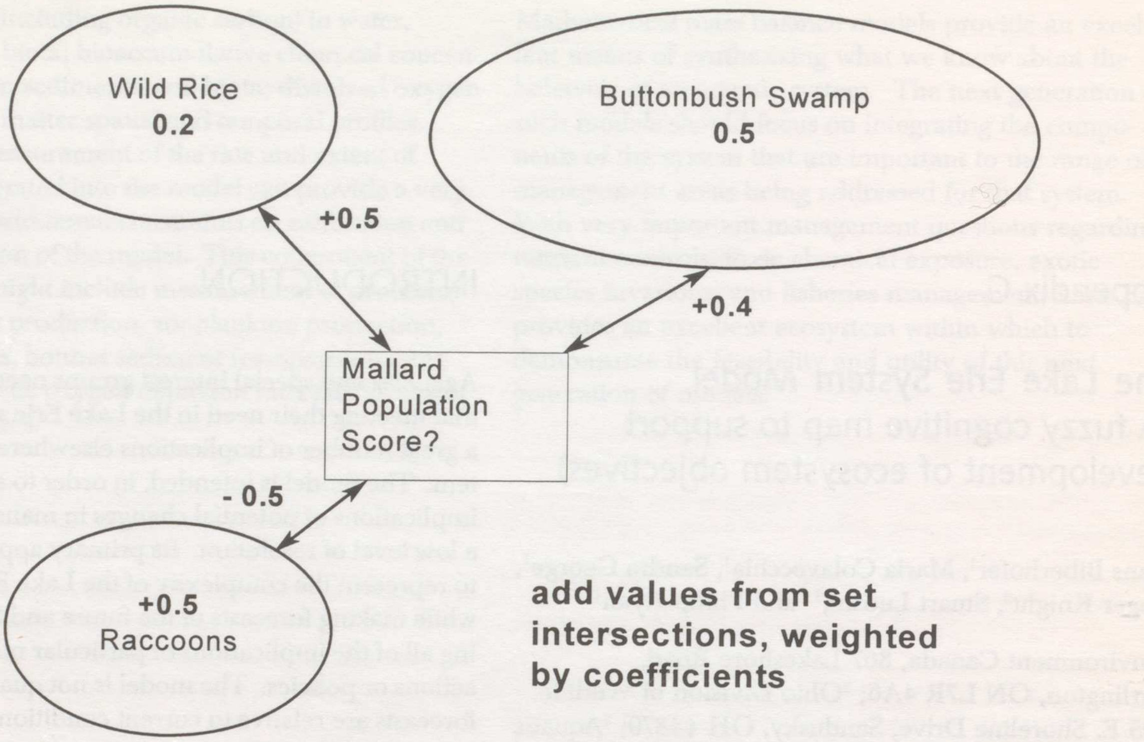

Figure 1
A Practical Application of the Hutchinson-Fry Niche Concept

FUZZY COGNITIVE MAP

The model is a neural net representation of 180 components, processes or other factors that were deemed necessary to represent the Lake Erie system and some associated values at steady state. The best way to think about the interactions is that they are the rules about how we expect the ecosystem to function. The level of representation of interactions is simple and explicit.

The likelihood of a healthy duck population existing is indicated by the score in the mallard population box. This example is a practical application of the Hutchinson-Fry niche concept.

For other components, the model provides a simple index function. The model is trained to produce outcomes by coefficients.

RELEVANCE TO GREAT LAKES

The model incorporates the major linkages between land uses and ecological consequences at a practical level of resolution. It incorporates the implications of eutrophication, exotic species, exploitation, habitat supply and contaminants. It includes state variables such as nutrients, algae, walleye, and zebra mussels. Although contaminants are represented in the model, we do not offer any forecasts which will include contaminants at levels above those anticipated from implementation of zero discharge policy.

The model has fostered dialogue between agencies and the public forum. It is being recognized as a valuable public education tool.

Appendix H

Ecological Modeling of Lake Erie Trophic Dynamics - 1999

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Since 1970, decreased phosphorus and increased nitrogen input have affected the functioning of the Lake Erie pelagic ecosystem (including algal, zooplankton, and fish abundances), even before the introduction of dreissenids further altered biological balances in the lake. The temporal and spatial heterogeneity of the lake requires mathematical modeling techniques to separate the effects of these changes, and to provide opportunities to allow prediction of long term variation in water quality and fish production. We include vertical turbulent transport of algae and nutrients in our model, because zebra mussels affect the ecology of the lake from their position within the benthic concentration boundary layer, both by consuming suspended and benthic algae and by mineralizing these materials and releasing nutrients at very high rates. The previous plankton-dominated system worked much differently. Accordingly, we are particularly interested in changes in the role of zebra mussels in the internal loading of nutrients and transfer of toxic compounds, both of which are reflected in the changes in the abundance and ecology of toxic cyanobacteria (e.g., *Microcystis*) in the lake. We are using intensive sampling of plankton and water quality from 1995 through 1998 to calibrate the models.

INTRODUCTION

The ecosystem approach is especially germane to the management of a lake the size of Lake Erie, where biological processes are influenced extensively by external forcing functions and internal recycling of carbon and nutrients, all in a framework of the physical processes (predominately water movement) that influence the temporal and spatial variability of the dominant biological phenomena. Our modeling approach thus includes temporal and spatial variation in state variables (abundance of nutrients, organisms, and pollutants), rates of biological processes (photosynthesis, grazing, respiration, excretion, etc.), rates of external loading relative to internal loading of important nutrients, and vertical turbulent transport of dissolved and particulate components of the system. Vertical transport is particularly important with respect to the relative roles of zooplankton and zebra mussels on the lower trophic level dynamics of the lake.

Assumptions Function of biological components in the lake can be characterized by a series of observations based on extensive observation and experimentation on lakes and ponds throughout the world. Hence, these will be inherent assumptions included in the model structure.

1. Algal abundance and species composition is influenced by the absolute and relative abundance of nutrients:
    a. Under low phosphate concentrations, small algae species (edible) are competitively favored relative to large green and blue-green filamentous species. Many large algae also store phosphorus in times of abundance in polyphosphate granules and then can supply daughter colonies for weeks.
    b. The small algae most easily eaten by crustacean zooplankton grow best when the inorganic nitrogen to reactive phosphate (N:P) ratio in the pond is above 7:1 by weight.
    c. Algae favor ammonia over nitrate as an N source.

   d. N:P ratios <7:1 often favor nitrogen-fixing bluegreen algae, many of which are filamentous (inedible by many zooplankton) and/or may produce toxins harmful to fish and zooplankton.
   e. Even in the absence of low N:P ratios, high absolute phosphate-P concentrations can favor growth of toxic bluegreen algae such as *Microcystis.*
   f. Unique nutrient needs, such as silica by diatoms, can strongly influence the relative abundance of algal taxa.
2. Cladoceran and copepod production is enhanced by a high abundance of edible algae:
   a. Filamentous algae are less desirable, and may cause interference with grazing activities. Hence lower nutrients, resulting in less overall algae may not result in a proportionate decline in zooplankton, since filamentous algal "weed species" may be those that decline the most.
   b. Edible algae are overgrazed when cladocerans persist in high densities causing "clearwater periods," reflected particularly in a decline of diatoms.
3. In the absence of fish predation, *Daphnia* suppresses copepods and smaller cladocerans such as Bosmina through competition for food.
4. Under lower edible algal availability during clearwater periods, crustacean zooplankton reproduction rates decline, making them numerically more susceptible to fish predation. A "mid-season decline" of crustacean zooplankton is often seen as a result of the combination of increasing fish predation and declining algae for egg production.
5. Planktivorous stages of Lake Erie fish preferentially select large crustaceans, with copepods being preferred over cladocerans.
6. Juvenile fish hatch out at different times of the year, with walleye and whitefish being early, with white bass, white perch, and yellow perch being as much as two months later. Hence, the seasonal dynamics of zooplankton differentially affects the recruitment of Lake Erie fish species.
7. Juvenile fish undergo dietary ontogenetic changes, with preferred prey typically changing from zooplankton to benthos to fish or from zooplankton to fish.
8. The "mid-season decline" of zooplankton may force juvenile fish to switch from eating zooplankton to benthos early, resulting in slower growth, survival, and recruitment. Fish that do not switch to benthos readily (e.g. white bass), may experience poor recruitment in the presence of abundant taxa that do (e.g. white perch, yellow perch), when zooplankton are scarce. Walleye, on the other hand, have already switched to fish before cladocerans replace copepods in dominance (by biomass) in the plankton.
9. Variation in abundance of adult fish appears to be determined more by recruitment of young of year fish than by the rate of exploitation of the adults, at least under current management techniques.
10. Zebra mussels have caused major biological changes in the lake:
    a. In many areas of the lake, zebra mussels are now the dominant benthic grazer of algae, replacing (at least in impact) the chironomids, amphipods, and oligochaetes important in the 1970s and 1980s.
    b. Zebra mussels probably influence algal abundance in the euphotic zone more by their mineralization (release of N and P) of algae they eat that would have sedimented and decomposed slowly in the sediments, than they do by their consumption of algae growing up in the water column. (MANY will argue this point.)
    c. Zebra mussels have changed the dynamics of movements of toxic compounds (PCBs, metals, and algal toxins (e.g. microcystin)) by making small particles more available to benthic grazers such as amphipods through the production of feces and pseudofeces.
11. Physical processes profoundly affect the biological processes occurring in the lake.
    a. Thermal stratification in the central and eastern basins (beginning approximately June 15 at a temperature of 15°C each year) effectively cuts the hypolimnion off from the euphotic zone.
    b. Even at times or places with thermal gradients below 1°C/5 m, benthic boundary layer phenomena effectively limit zebra mussel grazing to the bottom meter of the water column, with impacts on upper levels limited by the flux to the boundary layer caused by turbulent diffusion.
    c. Turbulent diffusion is affected by diel penetrative convection (overnight cooling), development of a seasonal thermocline, development of the diel thermocline (which may be limited to the top few meters of the lake, and by shear stress at the thermocline and lake bottom during seiche events.

d. Seasonal heating of the lake affects the rate of biological processes at all trophic levels, by a factor of 2-3 for every 10°C change in temperature.

THE MODEL

Components of the model (Figure 1) include nutrients: silica, ammonia, nitrate, phosphate, total phosphorus, phosphorus in sediments; plankton: five taxa of phytoplankton (Table 1), six taxa of herbivorous zooplankton (including zebra mussel veligers), and three taxa of predatory crustacean zooplankton; benthos: zebra mussels, four taxa of other macrobenthos; and fish: 11 taxa of planktivorous fish, and six taxa of piscivorous fish. State variables for these taxa are simplified in Figure 1 for convenience. Forcing functions include seasonal and spatial variation in solar radiation, nitrogen and phosphorus loading, turbidity, and temperature. Phytoplankton photosynthesis and growth are influenced by concentrations of nitrogen, phosphorus, silica, turbidity, and solar radiation. The release of nitrogen and phosphorus by all animals is an important component of internal loading of these nutrients, and the release by adult zebra mussels in the benthos is particularly relevant to present and future changes in Lake Erie function. The microbial loop is not explicitly included in the model due to the paucity of information on its activity in the lake. This should be examined in the future.

Within the biotic component of the model, phytoplankton abundance and taxonomic composition is influenced by nutrient concentrations and selective grazing by zooplankton. Adult zebra mussels influence algae that settle or are mixed turbulently into the concentration boundary layer. They also eat rotifers and small crustacean zooplankton, which swim near the benthos. They also release planktonic algae rejected as pseudofeces, which may be consumed by other benthos, such as amphipods. Filamentous phytoplankton and other large colonial forms (e.g. Microcystis) negatively affect zooplankton grazing. The first five planktivorous fish taxa in Table 1 eat plankton primarily in their first year of life, but many switch to benthos as well. This is symbolized by the connection of the benthos compartment with the arrow from planktivorous to piscivorous fish (Figure 1). This arrow further refers to the facts that piscivores consume planktivores, and that many planktivores become piscivores as they mature.

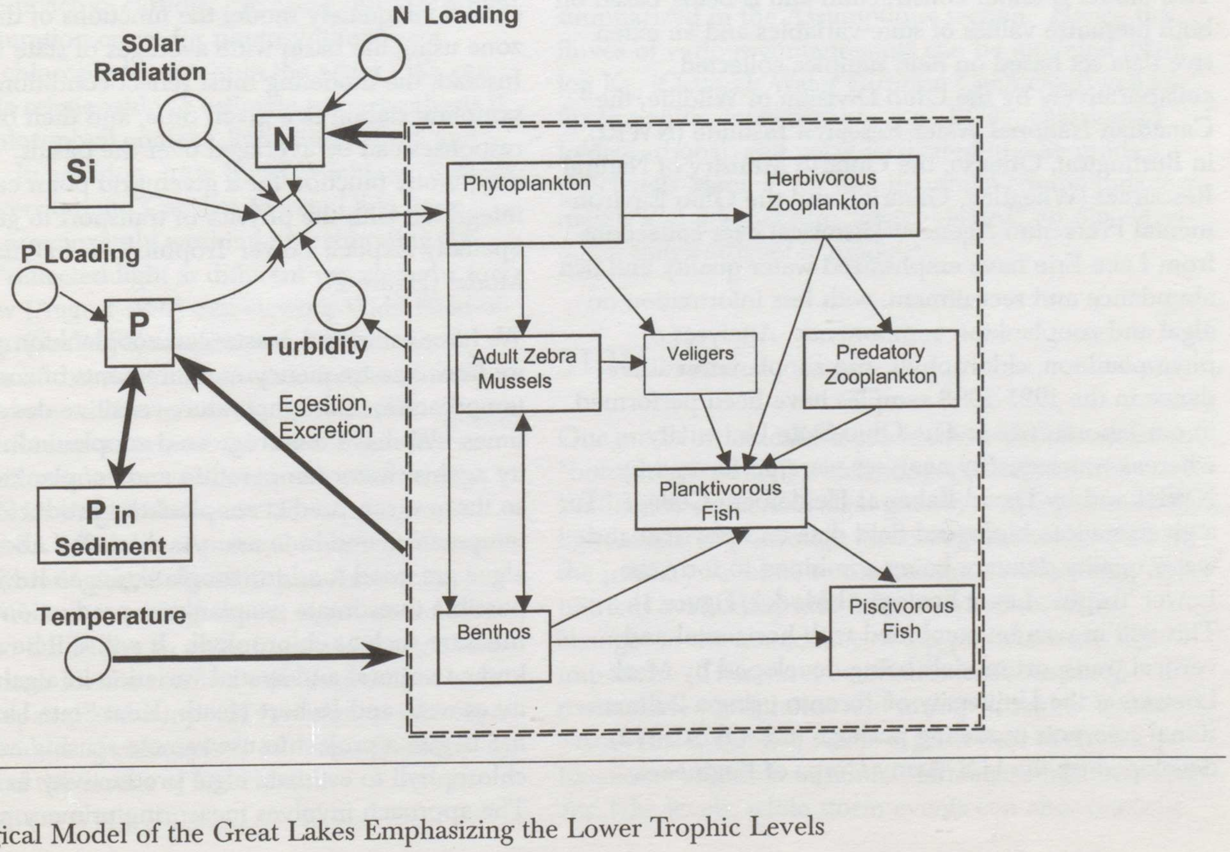

Figure 1
An Ecological Model of the Great Lakes Emphasizing the Lower Trophic Levels

Table 1

Taxonomic Composition of Biota Included in the Model as State Variables. Planktivorous fish taxa marked with * have a significant benthic component to their diet, at least during their first year of life.

Phytoplankton	Herbivorous Zooplankton	Predatory Zooplankton	Benthos	Planktivorous Fish	Piscivorous Fish
• Cryptophyta	• *Daphnia*	• *Leptodora*	• *Dreissena*	• Walleye	• Walleye
• Chrysophyta	• Other Cladocera	• *Bythotrephes*	• *Hexagenia*	• Yellow Perch*	• Yellow Perch
• Chlorophyta	• Calanoida	• *Epschura*	• Amphipoda	• White Perch*	• White Perch
• Cyanophyta	• Cyclopoida		• Oligochaeta	• White Bass*	• White Bass
• Pyrrhophyta	• Rotifera		• Diptera	• F. W. Drum*	• F. W. Bass
	• Dreissinid Veligers			• Smelt	• Smelt
				• Trout Perch*	
				• Gizzard Shad*	
				• Alewife*	
				• Emerald Shiner*	
				• Spottail Shiner*	

MODEL CONSTRUCTION

This model is under construction and is being based on both literature values of state variables and an extensive data set based on field samples collected collaboratively by the Ohio Division of Wildlife, the Canadian National Water Research Institute (NWRI), in Burlington, Ontario, the Ontario Ministry of Natural Resources (Wheatley, Ontario), and the Ohio Environmental Protection Agency. Historical data collections from Lake Erie have emphasized water quality and fish abundance and recruitment, with less information on algal and zooplankton components. Analyses of phytoplankton, chlorophyll, and zooplankton abundance in the 1995-1998 samples have been performed in our laboratories at The Ohio State University, whereas water quality analyses were performed by NWRI and by David Baker at Heidelberg College. For a given station, biological field data and physical and water quality data are being combined to form the Lower Trophic Level Ecological Model (Figure 1). This will in turn be combined with horizontal and vertical transport models being developed by Mark Loewen at the University of Toronto using a 2-dimensional reservoir modeling package (CE-QUAL-W2) developed by the U.S. Army Corps of Engineers.

Phytoplankton, zooplankton, and planktivorous fish are sensitive to light, temperature, and nutrient concentrations they experience in non-linear ways. Hence one cannot adequately model the functions of the pelagic zone using the basin-wide averages of state variables. Instead, the modeling must reflect conditions at a given sampling station at a given time, and then biotic responses can be averaged over the basins. In this way, biotic function for a given grid point can be integrated with the physics of transport to generate a Spatially Explicit Lower Trophic Level Dynamics Model (Figure 2).

We have estimated crustacean zooplankton productivity from size-frequency measurements of zooplankton, temperature, and temperature-sensitive development times. We have then regressed zooplankton productivity against water temperature and zooplankton biomass so that we can predict zooplankton productivity from temperature and biomass. As discussed above, not all algae are good food for zooplankton, so it will not be possible to estimate zooplankton production from a measure such as chlorophyll. It will still be useful to know temporal and spatial variation in algal productivity as well, and Robert Heath (Kent State University) has begun a project to use remote sensing estimates of chlorophyll to estimate algal productivity in the lake. The approach involves measuring primary productivity

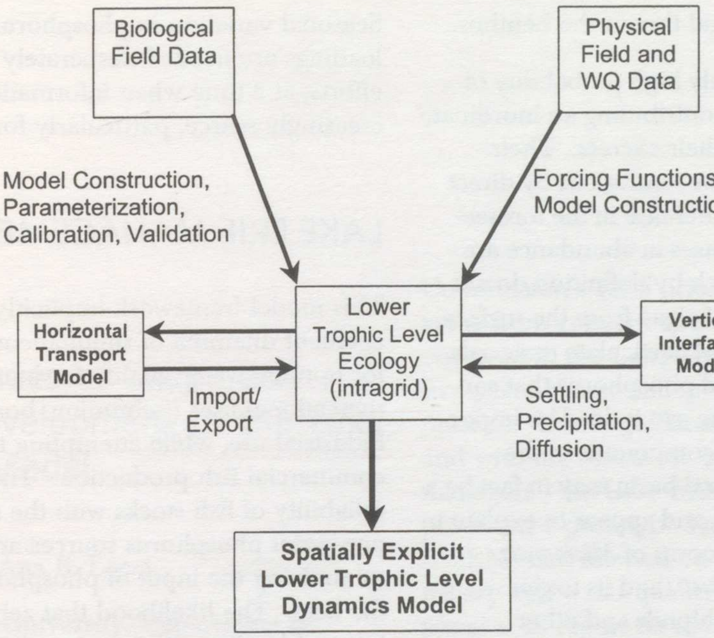

Figure 2
Process for Constructing a Spatially Explicit Lower Trophic Level Dynamics Model

as a function of light level and chlorophyll content at a number of sites on a number of occasions. Using a "photosynthetron," Heath incubates Lake Erie water containing algae and measures photosynthesis by the uptake of radioactive carbon. He also calibrates a light intensity saturation curve for photosynthesis as a function of chlorophyll content in the water. We can then use this relationship to estimate photosynthesis if we know chlorophyll content, light attenuation, and day length. In addition, Judy Budd (Michigan Technological University) and Carolyn Merry (Ohio State University) are currently working on calibrating the intensity of reflected light at different wavelengths for NASA's new (August 1997) Sea-viewing Wide Field-of-View Sensor (SeaWiFS) satellite to Lake Erie conditions. Some of this satellite's sensors are particularly designed to be sensitive to wavelengths associated with chlorophyll fluorescence and the satellite can detect them at 4 km resolution. Although the satellite contributes to NASA's global ocean color monitoring mission, NASA officials are particularly pleased that they are calibrating their algorithms to fresh water locations. We are providing seston, algae, and chlorophyll data to Dr. Merry to assist in providing "ground truth" functions for the satellite. We then will be able to estimate spatial and temporal variation in photosynthesis by combining chlorophyll estimates from SeaWiFS and the results of Dr. Heath's photosynthetron work.

CONTAMINANTS

Our assumption is that contaminant levels are currently too low to modify the robust biological functions summarized in the Assumptions section. Hence the fluxes of various contaminants can be modeled using log K_{ow} (Octanol: Water Partition Coefficient) values for lipophilic contaminants (e.g., PCBs, chlorinated hydrocarbons), and using facilitated uptake models (Michaelis-Menten) for non-lipophilic compounds (e.g., metals and microcystin) "piggy-backed" on our developing nutrient/trophic model.

STRESSORS

Our model is basically a productivity-driven model (a "bottom-up" model) which suggests that nutrient availability influences algal growth with a feedback on light availability through associated turbidity. Hence, the primary stressors to the system are those that affect nutrient availability and light penetration, while changes in the abundance of top predators are less important. Therefore, external nutrient loading, particularly phosphorus and nitrogen, and to a lesser extent silica, will determine a great deal of the lake function. Variation in rainfall influences nutrient input and lake levels, while storm events can alter nutrient flux from the sediment and algal flux to the benthos.

Zebra mussels have an extremely high probability of modifying these dynamics by contributing an inordinate amount to internal loading by their excreta. Their impact on surface water algal concentrations by direct grazing cannot be expected to increase in the foreseeable future, because their increases in abundance are now in soft-sediment areas which by definition do not have high turbulent transport of algae from the surface. However, their mineralization of particulate materials, releasing dissolved nitrogen and phosphorus that can diffuse up into the euphotic zone can indeed be important. Recent increases in these compounds in the western basin and western central basin may in fact be a result of zebra mussel activities, and appear to explain in part the recent recurrence of blooms of *Microcystis.* Zebra mussels also make *Microcystis* and its toxins (microcystins) available to amphipods and other macrobenthos through their production of copious feces and pseudofeces. These pathways were not previously part of Lake Erie function, and microcystins can be passed on to fish, either by direct consumption of zebra mussels (freshwater drum, round gobies) or by consumption of macrobenthos (smallmouth bass).

NEEDS

A major deficiency at this point is information on the physics of the interaction of zebra mussels in the benthos with the algae in the pelagic zone. Totally mixed reactor models applied by many investigators are simply wrong, even for the western basin. Application of marine mixing models is a step in the right direction, but the energy subsidy provided by tidal fluxes makes turbulent mixing there much greater than that observed in Lake Erie. We also need much more information on spatial distribution and size distribution of zebra mussels, particularly as they expand to low turbulent energy, soft substrates. Side-scan sonar may be important here. More information on ecological distinctions on the roles of zebra and quagga mussels is needed as quaggas increase their importance in the western basin.

Most of our data on phytoplankton distribution are from surface samples, whereas it is clear that highest concentrations may be far below the surface. Even so, remote sensing of chlorophyll distribution discussed above will enable us to better model the profound variation in surface algal abundance under the influences of rivers, cities, and upwelling events.

Seasonal variation in phosphorus, nitrogen, and silica loadings are needed desperately for the modeling efforts, at a time when information is becoming increasingly scarce, particularly for the Detroit River.

LAKE ERIE MANAGEMENT

This model framework implicitly addresses the management dilemma of simultaneously managing the lake for optimal water quality for human consumption and recreational uses (swimming, boating, etc.) and for industrial use, while attempting to maximize sport and commercial fish production. The improvement of the reliability of fish stocks with the reduction of point and non-point phosphorus sources argues in favor of minimizing the input of phosphorus and nitrogen to the lake. The likelihood that zebra mussel-mediated internal loading will increase the availability of these nutrients into the foreseeable future suggests that we will have to try ever harder to minimize external loading of these nutrients to the lake and that modeling the changes associated with zebra mussel influences are a high priority for achieving the two goals of water quality and fish production.

Appendix I

Resolution of Issues of Scope and Detail in the Development of the Lake Erie Ecological Model

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The Lake Erie Ecological Model (LEEM) arose as a modeling framework to address both scientific and management uncertainties about causes of recent instabilities of the Lake Erie ecosystem. Model design and implementation decisions were guided and reviewed by a group of managers and scientists under the aegis of the International Joint Commissions' Lake Erie Task Force. Design criteria required that the model provide a framework for joint consideration of lake-wide effects of invasion of zebra mussels, declining phosphorus loading, continuing toxic contamination, and fish harvesting on the structure of the fish community of Lake Erie. Meeting these criteria required explicit representation of trophic structure and nutrient limitations on primary production. Solutions to the problems of deciding on scope and resolution of the model are discussed. These trade-off decisions about model design have important implications for the scientific and practical usefulness of the modeling framework.

INTRODUCTION

With the adoption of the 1995 Priorities and earlier initiatives of the Council of Great Lakes Managers, the International Joint Commission has explored the potential of mathematical models to help with the implementation and assessment of an ecosystem approach to management. In the 1995 Priorities (IJC 1995), the Lake Erie Task Force created the Lake Erie Ecosystem Modeling Project as part of the Commission's 1995 priority for Lake Erie. The priority arose from concern about the rapid changes that had occurred in the Lake Erie ecosystem over the previous five years in association with the invasion of zebra mussels. Under guidance of the Lake Erie Task Force and with the assistance of a core group of Lake Erie managers[1], the Lake Erie Ecosystem Modeling Project produced a prototype Lake Erie Ecological Model (LEEM) that focused on overlapping interests of fishery and water quality managers. The goal of this paper is to report on the full implementation of LEEM[2] in the context of a regional ecological risk assessment project funded by the U.S. Environmental Protection Agency[3] and to review its contribution to ecosystem based management of the Lake Erie ecosystem.

LEEM DESCRIPTION

Modeling Framework

LEEM is a simplified representation of the food web of the Lake Erie ecosystem. The model simulates energy flow and contaminant movement by implementing a set of rules, which describe the feeding behavior of individual animals (Figure 1). By assuming that phosphorus loading limits the overall productivity of the Lake Erie ecosystem, LEEM constrains food web energetics to obtain consistency with observed productivity and biomass levels. Phosphorus loading thus acts

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1. The Core Advisory Group included representatives from each State with Lake Erie jurisdiction (Michigan Department of Natural Resources, Ohio Department of Natural Resources, Pennsylvania Boat and Fish Commission, and the New York Department of Environmental Conservation), the Province of Ontario, U.S. Fish and Wildlife service, and Environment Canada.
2. http://environment.cwru.edu/framindx.htm
3. EPA project number R825150-01-0, Modeling and Multiobjective Risk Decision Tools for Assessment and Management of Great Lakes Ecosystems.

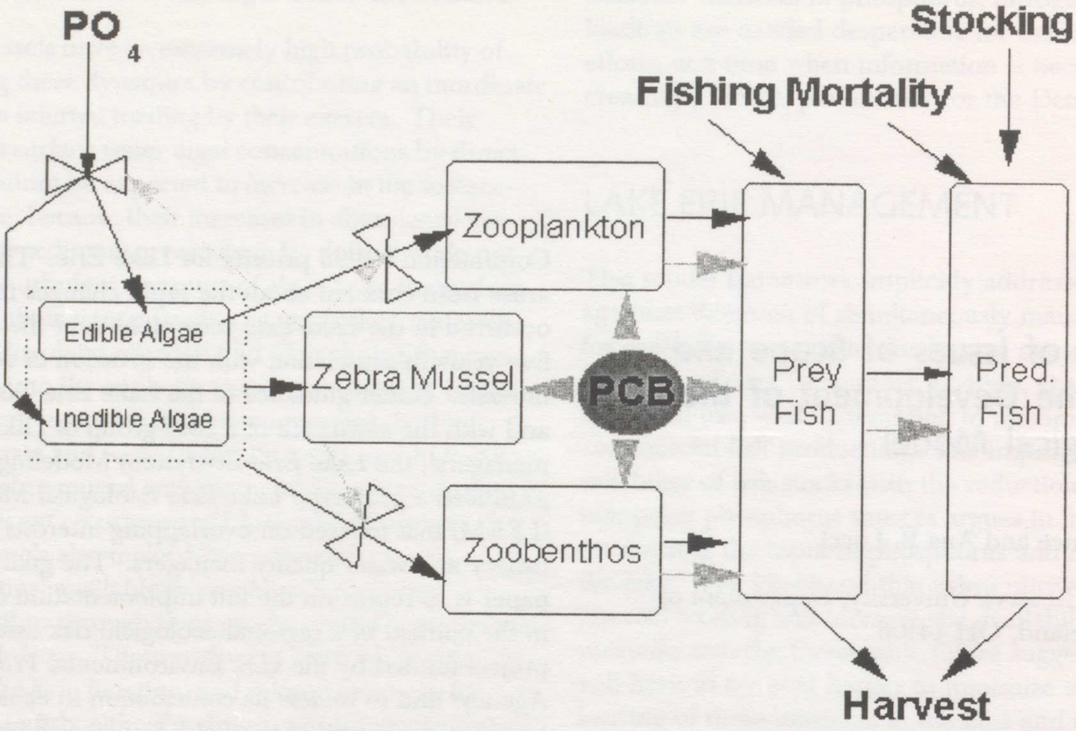

Figure 1

Schematic Diagram of the Lake Erie Ecological Model, showing an explicit primary production component and emphasizing feedback of zebra mussels on the magnitude (through effects on phosphorus cycling) and allocation of primary production to edible and inedible components due to effects of grazing. Contaminant movement through the food chain is also shown.

as the main forcing function through regulation of primary production, which depends jointly upon phosphorus loading and internal recycling by zebra mussels. LEEM also implicitly[4] incorporates physical habitat constraints by relating fish reproduction to availability of suitable habitat and by incorporating habitat structure into predator-prey interactions. With the explicit representation of two types of fisheries and the possibility of augmenting natural reproduction by stocking of hatchery-reared fish, LEEM further provides the option of exploring effects of exploitation policies on harvest and fish community structure. The modular structure of LEEM allows exploration of future appearance of non-indigenous fish species.

ASSUMPTIONS

Spatial and Temporal Scaling

A major simplification in LEEM is the choice of spatial and temporal scales for representing interactions in the Lake Erie ecosystem. The model assumes a whole-lake spatial[5] aggregation and simulates changes in the ecosystem at a minimum of one-year intervals. This assumption means that the model is most realistic for fish populations and progressively less realistic for zebra mussels, zoobenthos, and zooplankton, whose populations exhibit substantial seasonal variability.

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[4] Implicit incorporation refers to the representation of ecosystem structure through parameter values. Explicit incorporation of ecosystem structure occurs through state variable specification.

[5] Alternative versions of the model provide varying spatial resolution. A western basin model simulates seven fish species within the western basin of Lake Erie. An eastern basin version provides the option of exploring reduced nutrient inputs to the eastern basin with explicit focus on the 10 most important fish species in eastern Lake Erie.

Zooplankton and zoobenthos dynamics, therefore, are simplified to steady-state approximations of mean annual abundance and productivity. Zebra mussels and Quagga mussel are treated as a single mussel type with only annual total biomass dynamics. Fish migration is assumed to average lake-wide gradients in productivity, but spatial heterogeneity of fish populations is preserved through the explicit consideration of habitat overlap among fish species and lower trophic level components of the ecosystem. Nearshore and tributary habitat also act to limit recruitment of year-class cohorts to fish populations.

Linkage of Primary Productivity and Phosphorus Loading

Phytoplankton and other primary producers are represented implicitly in the model. The model assumes that phosphorus loading determines lake-wide primary productivity. Productivity of zooplankton and zoobenthos thus depend upon phosphorus loading through primary productivity. The model separates primary production into two phytoplankton components: edible (available for zooplankton grazing) and inedible (mainly blue-green algae), which enter the food web through the benthos. Zebra mussel density partitions primary into these two fractions. Biomass of each fraction is a function of the production to biomass ratio, which is assumed to be size dependent.

Contaminants Move through the Food Chain

The model simulates four contaminants (PCB, DDT, atrazine, and mercury). Contaminant loadings and mass balances are not explicitly represented. The model assumes an input data set consisting of annual mean concentrations of each contaminant in lake water. Contaminant body burdens of organisms at lower trophic level are predicted from estimated bioaccumulation factors, and contaminant body burdens of all other individuals depends upon the annual balance of contaminant uptake (ingestion and absorption) and excretion.

Bioenergetics of Growth and Reproduction

Growth of individual fish depends upon feeding according to annualized, theoretical expectations from bioenergetics models. Except for rainbow trout and lake trout, all fish species rely on natural reproduction for recruitment. Predicted reproduction depends upon fecundity and fertility coefficients, which vary by species and age. Habitat limitations are imposed through coefficients affecting egg mortality and through a density dependent limitation of spawning and nursery habitat supply limitation. Reproduction also depends upon an annually varying stochastic factor that represents effects on climate factors on spawning success and early life-history survival of each fish species.

Functional Predator and Prey Interactions

Feeding by all age groups of fish depends upon a common set of rules rather than upon a predefined set of feeding relations. Predators are assumed to search a defined habitat volume and randomly encounter prey items. Probability of capture of a prey item depends upon the ratio of prey to predator size and on a habitat overlap coefficient.

Table 1
Summary of LEEM State Variables for the Whole-lake Version

Category	Description	Number of State Variables
Lower Trophic Level	Abundance of zooplankton and zoobenthos and biomass of zebra mussels	3
Fish Species	Abundance and size of 14 fish species with age structure	218
Contaminants	4 contaminants as body burden in each trophic state variable	448

MODEL STRUCTURE

State Variables

LEEM explicitly incorporates three categories of state variables (Table 1). The model recognizes 7 to 14 age-structured fish species, three lower trophic levels groups, and contaminant body burdens for each of the trophic variables. The whole lake version includes 669 state variables. Implicitly, the model also includes two more phytoplankton state variables, but growth of zooplankton, zoobenthos, and zebra mussels depend upon primary production rather than biomass.

Driving Variables

Phosphorus loading is the fundamental driving variable for the model. State variable dynamics also depend upon ambient contaminant concentrations, climate influence on fish reproduction, suitability of nearshore and tributary habitat, and annual fishing effort for commercial and recreational fishing. For stocked fish species, the model requires annual amounts of stocking as yearling-equivalents.

Management Options

Including control of annual nutrient loading, LEEM provides for fish management control through fishing and stocking. The model provides two types of fisheries (commercial and recreational) with age-specific catchability schedules varying by species. Options are also available for stocking to supplement natural reproduction for any species. Since LEEM does not have fixed feeding relations, the model allows exploration of the consequences of possible intentional or unintentional introduction of exotic fish species.

LEEM APPLICATION

Because LEEM is a simplification of a complex ecosystem, the applications are primarily heuristic. As Oreskes *et al.* (1994) have noted, models of large-scale, complex systems all share the problem of fundamental incompleteness in system description. Peters (1991, p. 110-128) has argued that the reductionism required to formulate any ecosystem model severely restricts its rejection on the basis on incorrect predictions[6]. The dilemma created with modeling a complex system is that any simplification or attempt represent the structure of a real system is false at some level and will thus yield incorrect predictions of system behavior. Solutions to this dilemma depend on the context of applications.

Judgment about the validity of model or its predictions depends on a specific problem setting. From a scientific point of view, a model is no different from any other hypothesis. Solving a problem or advancing understanding requires hypothesis testing through error detection. In this sense, heuristic application of a model is like other hypothesis testing, which requires making potentially refutable predictions. The context for application of a model depends upon criteria for determining whether a prediction is true or not. As in general hypothesis testing, heuristic applications of models must iteratively cycle between hypothesis generation and hypothesis testing. True predictions of a model or derivative hypothesis must be challenged more rigorously. Alternatively, incorrect predictions require exploration of possible sources of the error in model assumptions, structure, and test implications. The credibility and usefulness of a model, therefore, emerges from its contribution to the understanding of a particular management question or scientific problem.

TESTING, CALIBRATION, AND VALIDATION

For LEEM, model calibration and testing has focused on understanding recent changes in the Lake Erie fish community. After an impressive recovery from a depressed state in the 1960s Hatch *et al.* (1987), walleye populations had begun to decrease along with yellow perch and smelt (Koonce *et al.* 1999). Initial prototype development and model testing began with a western basin version of the model (Koonce and Locci 1995), which had only seven fish species. IJC convened two modeling summits (1995 and 1996) to evaluate the adequacy of the model and recommend changes. The current version of the model (14 fish species with a whole lake spatial resolution) emerged from this

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[6] Peters developed this theme more extensively in Rigler and Peters (1995, p. 95-114).

[7] The analysis of parameter uncertainty of LEEM is being undertaken by Benjamin Hobbs and Richard Anderson (Dept of Geography and Environmental Engineering, Johns Hopkins University) in the context of the EPA funded project on Ecological Risk Assessment.

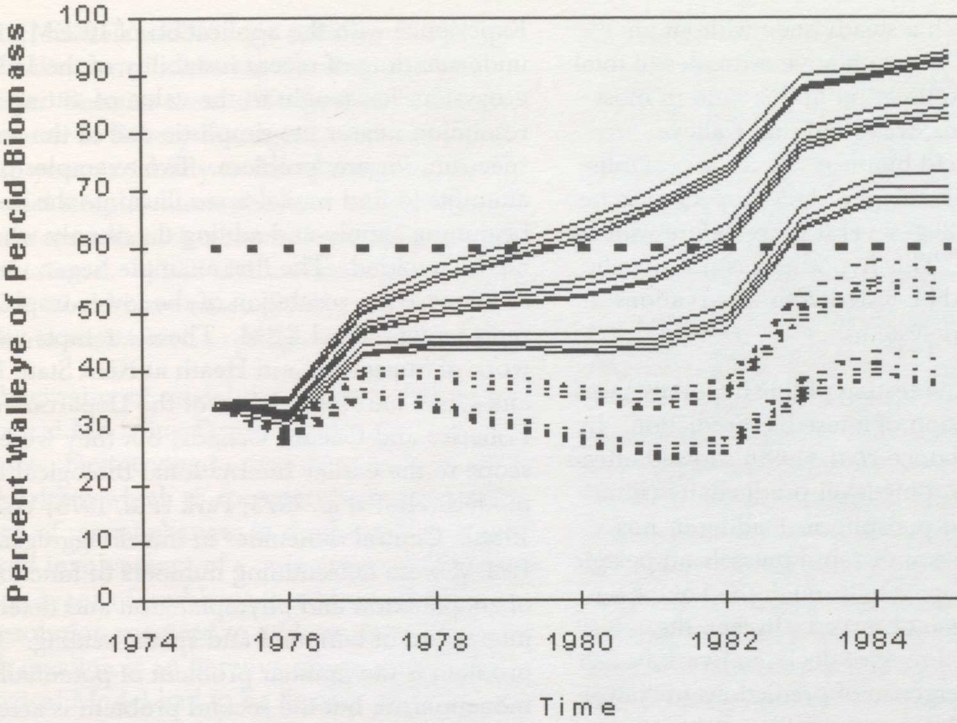

Figure 2
LEEM Simulations of Walleye Recovery for Varying Levels of Exploitation

Dotted lines are scenarios that did not result in a predator-prey oscillation. The horizontal dashed line is the apparent threshold of percent walleye biomass of total percid biomass at which a predator-prey oscillation is induced in simulations.

evaluation process (Koonce and Locci 1996). In response to specific concerns with declining productivity of the eastern basin, Lake Erie fisheries biologists assisted with the development of an eastern basin version that includes ten fish species. Model code and documentation is available on the Internet at http://environment.cwru.edu/framindx.htm.

Estimation of model parameters depended upon literature values and on Lake Erie data. The model requires estimation of 1,942 parameters. Many of these parameters are linked through biological processes and have fixed rules for their relationships. Even with optimistic assessment of the ability to estimate these biological relationships from "first principles," however, the model is over-determined with respect to calibration data sets. Although detailed studies of parameter uncertainty are ongoing[7], model calibration primarily has focused on recruitment and habitat overlap parameters. Virtual population reconstructions of walleye and yellow perch along with diet studies provided by fishery agencies were the basis of initial model calibration. Koonce *et al.* (1999) and Locci and Koonce (1999) contain additional details of model calibration and testing.

PREDICTIVE CAPABILITY

Heuristic applications do involve predictions. However, falsifiable predictions tend to be about general characteristics of system rather than specific future states. Figure 2, for example, shows a testable prediction derived from repeated scenarios of LEEM. Simpler models such as the Lotka-Volterra predator-prey models, predict limit cycles of predator and prey with amplitude of the cycle dependent upon initial displacement from the equilibrium abundance of prey and predator as determined by model parameters. Introducing satiation feeding into such models (i.e. increasing their realism), leads to damped oscillations instead of stable limit cycles. To assist in the evaluation of the hypothesis that the decline in walleye abundance in the 1990s was the result of a predator-prey oscillation, a number of LEEM scenarios were run to explore the effects of various rates of increase of walleye. These simulations indicated that there appeared to be a threshold of the ratio of predator to total fish biomass at which increasing predator biomass would induce an oscillation. Below this threshold, predator and prey biomass would approach a steady-state without an oscillation. Since lack of quantitative estimates of total fish biomass preclude estimation of this ratio in most large aquatic ecosystems, we found that walleye proportion of total percid biomass was an acceptable surrogate. In Lake Erie, this threshold appeared to be crossed in the early 1980s–several years before walleye reached peak biomass. This hypothesis is not specific to Lake Erie, and could be tested with observations in other percid dominated systems.

The role of LEEM in the testing of this hypothesis was to assist in the formulation of a testable prediction. In similar applications, Koonce *et al.* (1999) showed effects of alteration of lower trophic level productivity (simulating effects of reduced phosphorus loading or possible effects of the invasion of zebra mussels on pelagic productivity) would propagate through the Lake Erie food web differently than observed. In fact, the difference in expected timing of decline of various fish species is a critical divergence of predictions of "lower trophic level" and predator-prey oscillation hypotheses for explaining the decline of walleye, yellow perch, and smelt during the 1990s.

DISCUSSION

Understanding how models will be tested is essential to model design. Without a context for judging extent of model error, it is nearly impossible to resist the lure of completeness offered by reductionism. All models are simplifications of real systems and are thus incorrect at some level of detail. In the development of LEEM, there were many criticisms raised about the adequacy of the model's representation of lower trophic level complexity or of the lack of explicit spatial resolution that were attempted in the earlier water quality models of DiToro and Connolly (1980) and Lam *et al.* (1987). Balancing these calls for increasing resolution were the preferences of members of the Core Advisory Group to address primarily issues of common concern. Their needs were for a framework within which they could evaluate management options to deal with causes of declining fish populations. They did not perceive a need for detailed lower trophic level models or detailed nutrient mass-balance estimations, but they also did not know whether these details would be required for correct predictions of fish population dynamics. A fundamental challenge in the development of LEEM, therefore, was to find the proper balance between complexity of model design and simplicity of interpretation.

Experience with the application of LEEM to aid understanding of recent instability of the Lake Erie ecosystem has taught us the value of setting model resolution nearer the simplistic end of the complexity spectrum for any problem. Two examples of our own attempts to find model error illustrate the merit of beginning simply and adding detail only when it can not be avoided. The first example began with an effort to increase the resolution of the lower trophic level representation in LEEM. These attempts were the work of Sturtevant and Heath at Kent State University and Ghan and Johannsson of the Department of Fisheries and Oceans Canada, but they were similar in scope to the earlier International Biological Programme models (Huff *et al.* 1973; Park *et al.* 1975; Walters *et al.* 1980). Central difficulties in this disaggregation of LEEM were determining numbers of functional groups of zooplankton and phytoplankton and determining the interaction of temporal and spatial scaling. The first problem is the familiar problem of potentially endless reductionism, but the second problem is actually more formidable. Simulating rapidly changing abundance of phytoplankton and zooplankton requires short time steps (of days or less), but at these time scales, spatial pattern dynamics also become significant to local population dynamics. Increasing time resolution without increasing spatial resolution requires ignoring the contribution of spatial pattern dynamics (i.e. diurnal migration or aggregation in fronts). However, including spatial pattern dynamics greatly increases model complexity–perhaps even beyond reasonable computational demands. The whole-lake spatial resolution of LEEM avoids this difficulty by assuming that annual fish movement patterns compensate for spatial pattern dynamics. On an annual basis, it is sufficient to describe the probability distribution for occurrence in habitat regions to predict the interactions of species. LEEM relies on a habitat overlap coefficient to define these interactions. This assumption is not valid for basin specific versions of LEEM. In the basin specific versions, effects of fish migration among basins must be included in mortality parameters.

The second example deals with decisions on aggregation of state variables more directly. May *et al.* (1979) proposed a multi-species fishery model based on a much simpler representation of a fish community than LEEM's. The main simplifying assumption in their model was elimination of age structure. With the help of Atkinson and Zaremba (Department of Biology, Case Western Reserve University), we explored the effect of age-group aggregation on model predictions. In this case, we found substantial differences in model behavior were induced by inclusion of age-structure.

In particular, models without age structure tend to damp variability much more rapidly than age-structured models. Because these differences in predicted behavior matter to fishery managers, who must deal with year-to-year variability in fish abundance, the computational simplification obtained by eliminating age structure renders such a model less relevant to the problem of interest. Without this reference problem, however, we would have much greater difficulty in finding criteria with which to judge model adequacy.

From the beginning of model development, the Lake Erie Ecological Modeling Project has sought to fulfill two purposes. First, trying to provide managers a framework within which to consider the management implications of recent changes in the Lake Erie ecosystem required involvement of a core group of managers to decide on types of problems to address and the levels of resolution required to address them. Because framework creation is an iterative process, the Lake Erie Ecological Model had to be flexible and easy to modify. The second purpose of model development was to obtain additional experience with the ways models of various types can be linked to enhance understanding of the ecological factors that are contributing to the rapid changes in the Lake Erie ecosystem. LEEM has been used to explore the interactions of factors contributing to the recent decline of important fisheries in Lake Erie (Koonce *et al.* 1999; Locci and Koonce 1999). These applications indicate that the model has the potential to make these two contributions. LEEM, however, will not address all ecological issues confronting management of Lake Erie. From the outset, we have emphasized that LEEM will have a primarily heuristic value, and we find that using a model heuristically requires linkage of the process of evaluation of management issues and model development. Model development without linkage to use ultimately loses criteria for judging model adequacy.

Without application of a model to a specific problem context, many of the issues raised in evaluation and testing can not be resolved. LEEM and other similar models seem to sit on a cusp of complexity and simplicity. Attempts by Sturtevant and Heath to include more resolution of structure of primary producers in LEEM encounters formidable obstacles of defining appropriate spatial and temporal resolution as well as parameter estimates. Similarly, with the development of an ecosystem model for Lake Ontario, DePinto and Jain (1995) reported that lack of data precluded the application of a detailed model of energy and nutrient flows and compelled use of a simpler model. These experiences echo the findings from efforts during the International Biological Programme to develop comprehensive ecosystem models (Huff *et al.* 1973; Park *et al.* 1975). While it was possible to construct models linking hydrology of watersheds with detailed biology of lake ecosystems, the behavior of these systems was not all that different from predictions based on much simpler models (Walters *et al.* 1980).

Application of LEEM to the problem of understanding recent changes in the Lake Erie fish community has also confirmed the existence of fundamental gaps in research and monitoring. In attempting to find errors in model predictions, we have encountered a lack of some very basic data from the Lake Erie ecosystem. Since the early recognition of possible eutrophication problems in Lake Erie, phosphorus loading has been considered an important factor to regulate. Unfortunately, we no longer have reliable estimates of annual loading, and, more significantly, we know even less about the biological availability of phosphorus loading now entering the Lake Erie ecosystem. The lack of understanding of phosphorus and productivity linkage is further eroded by the lack of lake-wide estimates of primary production. The recent publication of results of lake-wide sampling of phytoplankton and zooplankton (Graham *et al.* 1996) provides some information, but we still do not have estimates of whole lake biomass productivity. Without such estimates, we have found it very difficult to set reasonable constraints on fish productivity. This is a particular problem in reconciling the estimates of walleye abundance through virtual population reconstruction with the levels of productivity indicated in Graham *et al.* (1996). It is also clear from our model studies that the fish species have far more reproductive capacity than observed. A critical missing element is adequate understanding of the role of habitat limitation in the regulation of recruitment of dominant fish species.

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Conceptualization of Aquatic Ecosystem Model