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Ecological Modeling of Lake Erie Trophic Dynamics - 1999

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Abstract 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.

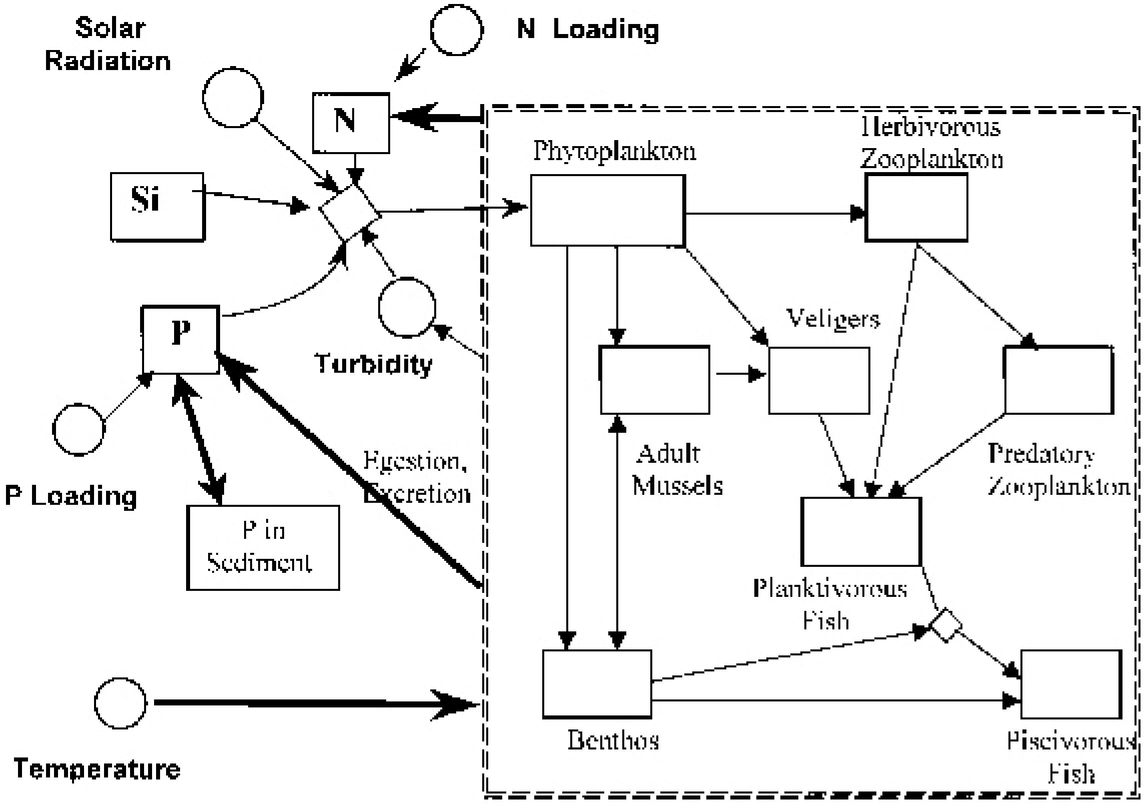
   b. The small algae most easily eaten by crustacean zooplankton grow best when the inorganic nitrogen to reactive phosphate (N:P) ratio in the pond is above 7:1 by weight.
   c. Algae favor ammonia over nitrate as an N source.
   d. N:P ratios <7:1 often favor nitrogen-fixing blue-green algae, many of which are filamentous (inedible by many zooplankton) and/or may produce toxins harmful to fish and zooplankton.
   e. 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^{o}C each year) effectively cuts the hypolimnion off from the euphotic zone.
    b. Even at times or places with thermal gradients below 1^{o}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^{o}C change in temperature.

The Model Components of the model (Figure 1) include **nutrients**: Silica, Ammonia, Nitrate, Phosphate, Total Phosphorus, Phosphorus in sediments; **plankton**: 5 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, N and P loading, turbidity, and temperature. Phytoplankton photosynthesis and growth are influenced by concentrations of N, P, Si, turbidity, and solar radiation. The release of N and P 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 (Fig. 1). This arrow further refers to the facts that piscivores consume planktivores, and that many planktivores become piscivores as they mature.

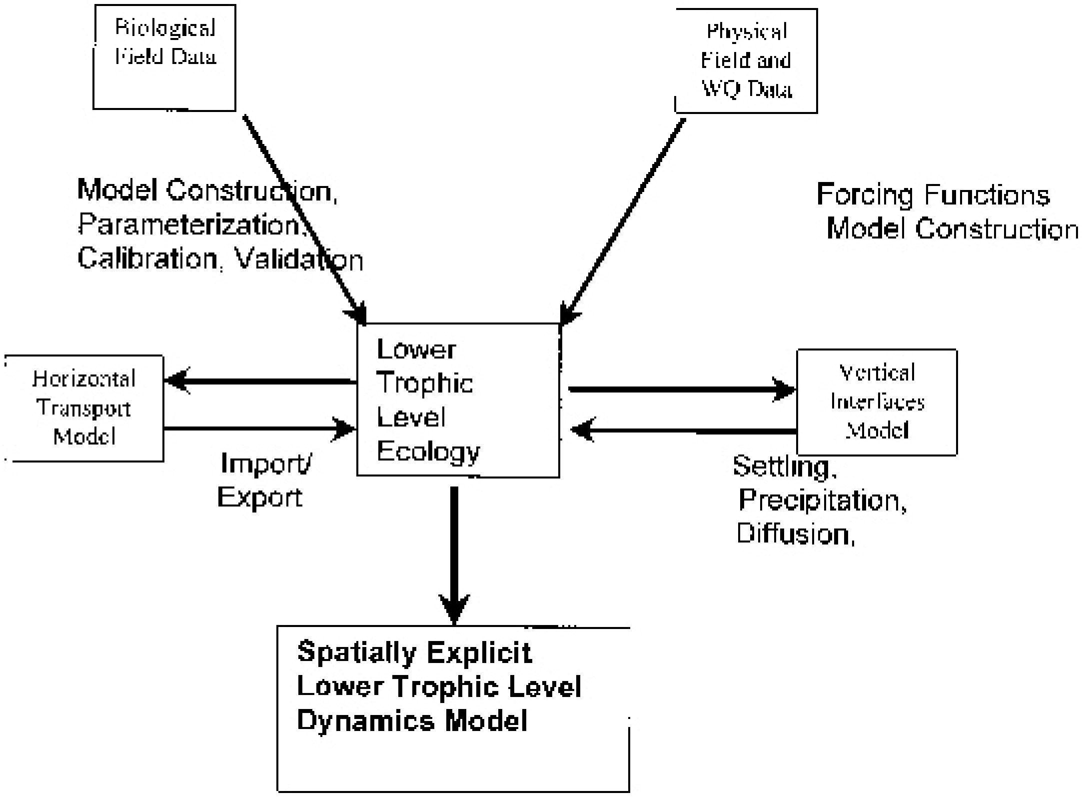
Table 1. Taxonomic composition of biota included in the model as state variables. Planktivorous fish taxa marked with * have a significant benthic component to their diet, at least during their first year of life.

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	• *Epischura*	• Amphipoda	• White Perch*	• White Perch
• Cyanophyta	• Cyclopoida		•	• White Bass*	• White Bass
	• Rotifera			• F.W. Drum*	

• Pyrrhophyta	• Veligers	Oligochaeta • Diptera	• Smelt • Trout Perch* • Gizzard Shad* • Alewife* • Emer. Shiner* • Spot. Shiner*	• F.W. Drum • Smelt

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 US 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 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} 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 N and P 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 P 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.