LEEM: The Base of the Food Web: Final Report

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Summary

The prototype Lake Erie Ecosystem Model (LEEM) was commissioned by the International Joint Commission (IJC) and constructed to aid in anticipating the effects of declining nutrient loading, invasion of zebra mussels and loading of toxic organic contaminants on fish populations in Lake Erie. Its intent was to serve as a framework for addressing additional issues of concern to the Lake Erie Task Force and to serve as a useful "gaming" tool for Lake Erie managers interested in forecasting the results of possible management strategies. LEEM is a hybrid Visual Basic simulation model with EXCEL spreadsheet interfaces to manipulate input parameters and to explore output from model runs. It is a highly detailed model at the upper trophic levels, modeling fish populations taking into consideration spatial and temporal heterogeneities. It accounts for the 16 major game fish and forage fish species in Lake Erie, modeling the fish taxa on an annual basis. Extensive testing and calibration with historical data sets show that the prototype LEEM successfully modeled fish populations and provided scientifically reasonable predictions of the results of potential management efforts.

Despite its biological realism and explicit detail at higher trophic levels, the prototype LEEM is highly aggregated at the lower trophic levels. The goal of this project was to expand the prototype LEEM to include greater detail at the lower trophic levels, allowing increased usefulness of the model as a management tool in assessing events among the components at the base of the food web without losing the performance characteristics and usefulness of the model behavior of higher trophic levels. Our objectives were to disaggregate the "primary production" component into "edible phytoplankton", "inedible phytoplankton", "edible benthic algae", "inedible benthic algae", and "macrophytes". Grazing on primary production was re-modeled to include possible "top-down" effects on primary producers. Also, the "zebra mussel" compartment was modeled to include a recycling loop, modeling the release of available P, to examine the possible effects of zebra mussels on ecosystem function (Heath, et al. 1995). The model included physiological and ecological characteristics within phenomenological differential equations in such a way that the model parameters could easily be altered by scientists and managers interested in exploring and using this model. We calibrated the revised model (using a "back door" procedure) and found that it provided scientifically reasonable estimates of the behavior of components at the base of the food web without altering the successful modeling behavior of the higher trophic levels. Exploration of the model indicated that recycling of P by zebra mussels could have a major impact on zooplankton, zoobenthos and Y-O-Y fish production. Some of the modifications from this project have been incorporated into the revised model, LEEM Version 0.2, accessible on the Internet at <http://129.22.156.18/LEEMP.htm>.

Background

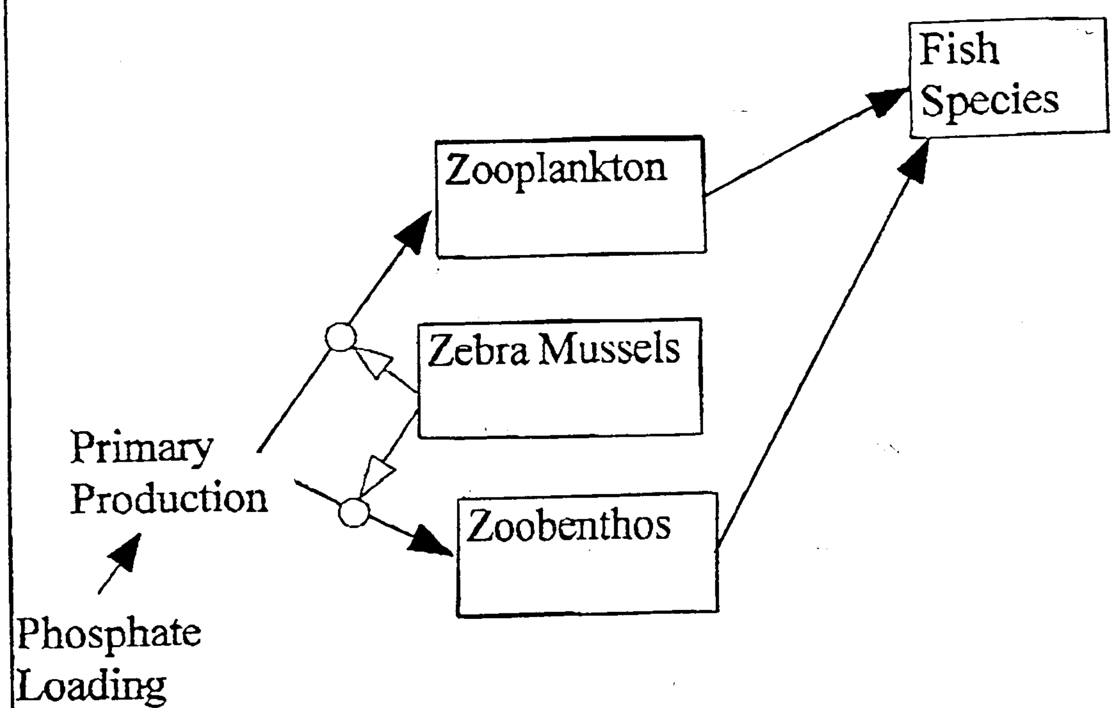
The prototype Lake Erie Ecosystem Model (LEEM) was commissioned by the International Joint Commission (IJC) and constructed by Prof. Joseph Koonce and Dr. Ana Locci at Case Western Reserve University (CWRU) in association with Software Kinetics, the LURA group (Toronto, ONT) and the IJC. It was developed (1) to aid in anticipating the effects of declining nutrient loading, invasion of zebra mussels and loading of toxic organic contaminants on fish populations, (2) to serve as a framework to address additional issues of concern to the Lake Erie Task Force, and (3) to serve as a useful "gaming" tool for Lake Erie managers to aid in anticipating the results of possible management strategies. The prototype LEEM was intended to serve as a summary of scientific understanding of the interactions that destabilize the Lake Erie ecosystem and to focus the overlapping interests of fisheries and water quality managers in the Lake Erie basin.

LEEM is a hybrid Visual Basic simulation model with EXCEL spreadsheet interfaces to manipulate input parameters and to explore output from model runs. This combination provides the robustness of calculation necessary for a highly complex scientific model with an exceptionally accessible interface suitable for multiple simulation runs ('gaming' scenario applications) by the end user (Lake Erie managers).

Conceptually, LEEM is a component model consisting of population submodels run in parallel and linked by informational constraints. It is a highly detailed model at the upper trophic levels, modeling fish populations taking into consideration spatial and temporal heterogeneities. It accounts for the 16 major game fish and forage fish species in Lake Erie, modeling the fish taxa on an annual basis. Each fish species is modeled as an age-structured population, using sophisticated phenomenological equations to account for well known physiological and behavioral characteristics of each taxon. It has been extensively examined and found accurately to describe populations sizes of the various fish taxa over the past 20 - 25 years. The successful behavior of the prototype LEEM argues strongly that it may serve as predictive resource, useful to scientists and lake managers interested in anticipating the feasibility and effects of putative management strategies on the Lake Erie fishery.

Despite its biological realism and explicit detail at higher trophic levels, the prototype LEEM is highly aggregated at the lower trophic levels (Figure 1). Primary production, zooplankton and zoobenthos are each treated as one 'population'. The model is driven by P-loading with primary production as an implicit function of that loading. Therefore the prototype does not have the capability of examining shifts in phytoplankton and zooplankton taxa that have occurred over the same interval, presumably due to the same constraints (Makarewicz 1993a, 1993b; Nichols and Hopkins 1993). Zebra mussels are included, but only as grazers of "primary production", so the different effects of this nuisance mollusc on phytoplankton, benthic algae and macrophytes (Dorgelo 1993; Lowe and Pillsbury 1993; Skubinna, et al. 1993) are not expressed in the prototype. Nutrient flows are all unidirectional, and the model does not account for recycling and remineralization effects by zebra mussels or zooplankton. Inclusion of greater detail of the base of the food web is necessary in order to explore the possible consequences of zebra mussels on the Lake Erie ecosystem. For example, recent studies indicate that zebra mussels may release such large quantities of available P that they may greatly stimulate benthic algal growth and cause the growth of inedible phytoplankton (Heath, et al. 1993).

Figure 1: Schematic Diagram of the Prototype LEEM
Base of the Food Web



Goals and Objectives

The goal of this project was to expand the prototype LEEM to include greater detail at the lower trophic levels and to increase usefulness of the model as a management tool capable of assessing events among the components at the base of the food web. In addition to refining current fisheries and water quality management applications, increased resolution at the base of the food web may allow new applications such as prediction of nuisance algal blooms. A related goal was to make these changes without altering the performance of the LEEM at the higher trophic levels, where it has been very successful in "predicting" events of the past 20 years, useful as a "gaming" resource management tool for lake managers.

Our specific objectives were:

1: Model Design - alterations to make the model a scientifically more complete representation of the base of the food web.

2: Disaggregation of primary production into edible and inedible algae (both planktonic and benthic) and also to include macrophytes.

3: Model calibration - using historical data and verifying that this altered model continued to exhibit the same behaviors at the levels of forage fish and game fish.

4: Model exploration - exploration of the effects of recycling and remineralizing processes on population dynamics and ecosystem function.

5: Incorporation into LEEM Version 0.2.

In the discussion below alterations are described in detail to assist future modelers working with this model. All values remain accessible to investigators who may wish to alter them or question the assumptions behind the values in greater detail.

Accomplishments

Objective 1: Model design.

In order to refine the model structure for the base of the food web in the LEEM, it was necessary first to understand the structure employed in the prototype model to avoid changing what already worked well. Several months were spent running model simulations and exploring the Visual Basic code and EXCEL interfaces in order to gain both programming and scientific insights into the model structure. In addition to the base of the food web, special attention was given to the structures governing the relationships between the base of the food web and higher trophic levels (e.g. zooplankton and zoobenthos to fish) because these form the interface between the altered structures (the base of the food web) and those remaining unaltered from the prototype.

In the prototype LEEM, primary production was treated as a single state variable (i.e. as one compartment). No subdivisions were made as to basin specificity, region specificity (e.g. benthic vs pelagic, nearshore vs offshore), general type (macrophyte, epiphyte, plankton) or edibility, despite a highly detailed structure on most of these same counts at higher trophic levels. The original model treated zooplankton, zoobenthos, zebra mussels and the 16 species of fish of varying age classes as varying widely in their distributions within the lake despite feeding on a single food source that was modeled as being of uniform composition and homogeneously distributed. Even within the context of an annualized scale, we felt this to be an over-simplification and likely to lead to a misrepresentation of system behavior. We felt that a more accurate description of system behavior would be achieved by disaggregating primary production into 5 subgroups (macrophytes, edible phytoplankton, inedible phytoplankton, edible benthic algae and inedible benthic algae) each of which is distributed appropriately throughout the lake. This disaggregation of primary production forms the core of the alterations we made to LEEM within the scope of this project. Changes to the basic submodel structure necessitated by this disaggregation are summarized in Figure 2.

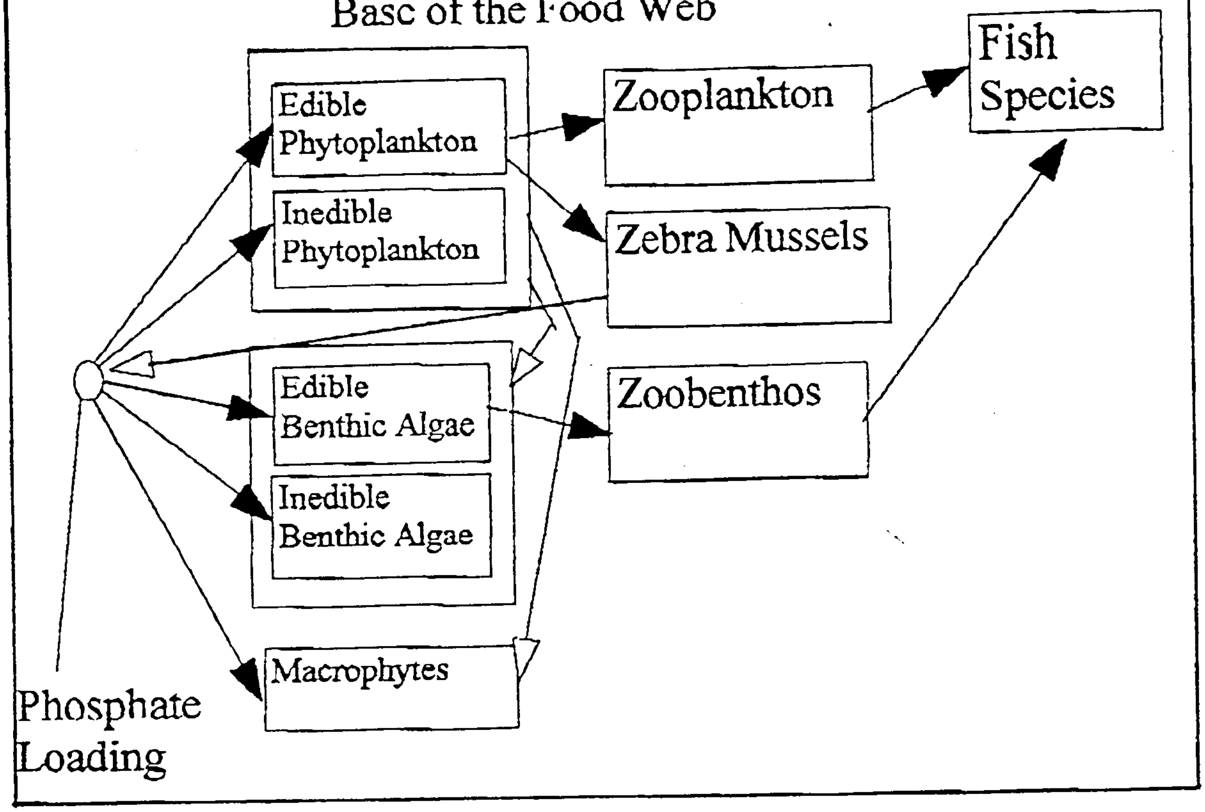
Within the mathematical structure of the prototype model, primary production was treated as a state variable similar to turbidity rather than as a living 'population' component (similar to zooplankton) of the system. This structure posed several difficulties to the process of disaggregating primary production. Rather than deal with those problems on an *ad hoc* basis, we concluded that it would be simplest to treat the primary production subgroups as individual population groups and to move the calculation of primary production subgroups into the same code loops in which zooplankton and zoobenthos populations were calculated. This required renumbering the populations of the entire model (making primary production subgroups species 0-4, zooplankton species 5, etc.) and extensive modifications scattered throughout the Visual Basic code structure and the EXCEL interfaces. By making these modifications we avoided repeating extensive sections of code within a separate 'primary production' section. For example, by structuring edible phytoplankton as a population component calculated in the same loops as zooplankton, the code was already in place for calculation of population size, biomass, contaminant burden, and distribution within the lake.

Primary production was modeled in the prototype LEEM as a simple linear function of phosphorus loading. This system did not allow exploration of possible "top-down" control of primary production. A more realistic behavior is produced by modeling primary producer groups using an equation structure similar to those used to model the behaviors of zooplankton and zoobenthos. In this way, the increase of primary production is a function of both the nutrient concentration and the physiological characteristics of the primary producers. Losses to grazing were modeled as functions of both the grazer and the primary producer compartments. Non-grazing mortality of the primary producers was modeled as a density-dependent function of each of the primary producers:

Gain Non-grazing mortality .... Grazing mortality ....

$$dX/dt = X*(((Vm*S)/(kt+S)) - km_1*X - km_2*N_{ZP} - km_3*N_{ZM} - km_4*N_{ZB})$$

Figure 2: Schematic Diagram of the Modified LEEM Basc of the Food Web



where X = Primary Producer compartment
S = Phosphorus Loading
N_{ZP} = Zooplankton
N_{ZM} = Zebra Mussels
N_{ZB} = Zoobenthos.

Individual primary producer components varied in the factors important for mortality, and this approach provided a means for separating each from the other primary producers. Figure 3 shows the new equation structures.

In addition to the implicit feedbacks through predator controlled predatory losses of primary production, we also included explicit nutrient feedbacks from zebra mussels to phosphate availability, to account for the mineralizing effects of zebra mussels. The prototype LEEM did not include feedback loops that influence the behavior of the lower trophic levels. Although fish species influenced each other's abundance in a complex interactive manner, the lower trophic levels were modeled to behave in a linear, deterministic manner in which phosphorus inputs alone determined primary production, and primary production in turn determined zooplankton and zoobenthos abundance and food availability to fish. Inclusion of feedback, especially at the lower trophic levels provided a more realistic assessment of the effects of zebra mussels on primary production and ecosystem response.

Objective 2: Disaggregation of primary production.

Primary production was first transformed from a state variable to a population variable within the framework of the code. This process involved major changes to nearly all of the model subcomponents in both Visual Basic and EXCEL interfaces. Primary production was assigned as 'Population 0' and all other populations were renumbered (e.g. "zooplankton" was previously numbered as Population 0). Calculation of primary production was integrated into the same loop structures in which zooplankton were calculated. Several model runs were conducted at this point to ensure that this structural change did not alter the behavior of the model. Primary production was then disaggregated into 5 subgroups assigned as species 0 through 4, again renumbering the higher trophic levels.

Initially, primary production was divided evenly among the subgroups and grazers were allowed to graze all subgroups evenly in order to avoid altering model behavior. EXCEL interfaces for habitat distributions of the various subgroups were added although they were not functionally connected to the Visual Basic calculations of predatory mortality. Regardless of the initial zooplankton distribution pattern, zooplankton were assumed to be available to all planktivorous fish (regardless of fish distribution in regions of the lake); all primary production was available to all zooplankton in the model. Although this lacks in "biological reality" it was necessary to develop the model in these steps to maintain the integrity of the existing prototype model.

Equations governing primary production (5 equations) and the equations governing the grazing of primary production (3 main equations plus habitat overlap) were altered to match the

Figure 3: Equations for primary production in the modified LEEM

$dM/dt = M*(((Vm_1*S)/(kt_1+S))-km_1*M-km_2*(EP+IP))$
$dEP/dt = EP*(((Vm_2*S)/kt_2+S))-km_3*(EP+IP)-km_4*ZP-km_5*ZB-km_6*ZM)$
$dIP/dt = IP*(((Vm_3*S)/kt_3+S))-km_7*(EP+IP))$
$dEB = EB*(((Vm_4*S)/kt_4+S))-km_8*(EB+IB)-km_9*(EP+IP)-km_{10}*ZP-km_{11}*ZB-km_{12}*ZM)$
$dIB/dt = IB*(((Vm_5*S)/kt_5+S))-km_{13}*(EB+IB)-km_{14}*(EP+IP))$

M = Macrophyte
EP = Edible phytoplankton
IP = Inedible phytoplankton
EB = Edible benthic algae
IB = Inedible benthic algae
ZP = Zooplankton
ZB = Zoobenthos
ZM = Zebra mussels
S = Phosphorus concentration based on phosphorus loading
Vm = Maximum phosphorus uptake velocity
kt = Half-saturation constant for phosphorus uptake
km_1 = Macrophyte density-dependent mortality
km_2 = Phytoplankton shading of macrophytes
km_3 = Edible phytoplankton density-dependent mortality
km_4 = Zooplankton grazing on edible phytoplankton
km_5 = Zoobenthos grazing on edible phytoplankton
km_6 = Zebra mussel grazing on edible phytoplankton
km_7 = Inedible phytoplankton density-dependent mortality
km_8 = Edible benthic algae density dependent mortality
km_9 = Phytoplankton shading of edible benthic algae
km_{10} = Zooplankton grazing on edible benthic algae
km_{11} = Zoobenthos grazing on edible benthic algae
km_{12} = Zebra mussel grazing on edible benthic algae
km_{13} = Inedible benthic algae density dependent mortality
km_{14} = Phytoplankton shading of inedible benthic algae

structures shown in Figure 3. These alterations were done in a stepwise fashion to assure that the model additions would not drastically alter the modeled behavior of the higher trophic levels in the model. Inedible primary production components were set equal to zero and the two compartments of "edible algae" (edible phytoplankton and edible benthic algae) were given essentially the same structure as the initial primary production compartment. This alteration maintained the same behavior of higher trophic levels in the prototype LEEM.

Next we modeled the remineralization of phosphorus by zebra mussels. An element was added to the basic equation to model feedback to the nutrients from zebra mussels.

X = g0 + g1 * PO4Load(TI) + ZmPO4Recycle * N(7,1)

Where	PO4Load(TI)	=	phosphorus loading at time (TI)
	N(7,1)	=	zebra mussel abundance
	ZmPO4Recycle	=	phosphorus release (additional load) per ZM.

Addition of these equations greatly increased the total primary production. The model was recalibrated iteratively by altering the values for g0, g1, and ZmRecycle.

Equations for "inedible primary producers" (i.e. macrophytes, inedible phytoplankton, and inedible benthic algae) were next incorporated into the model. Alterations in these components do not effect the behavior of components of the higher trophic levels in the model because we included no grazing (i.e. we did not model the possibility of partial grazing on these components), and we did not include competition coefficients between these components and those that were grazed. Although these components did not affect the behavior of higher trophic levels they were affected by the behavior of other groups.

Finally, we modeled "top-down" control of edible primary production by modeling the grazing in a Holling Type II manner (DeAngelis 1992). Addition of these "top-down" controls effectively added feedback loops from grazers onto primary production. These additions greatly changed the modeled behavior of components at trophic levels both higher and lower than the zooplankton grazers. Non-linear structures for governing "growth" of primary production, discussed in the model design above, were not incorporated due to difficulties in model calibration.

Objective 3: Model calibration.

The base of the food web (primary production, zooplankton and zoobenthos) in the prototype LEEM was not extensively calibrated or validated. Primary calibration was done by a 'back door' method (without data) as necessary to make the higher trophic levels (zebra mussels and fish) calibrate within the bounds of the historical data for phosphorus loading (used as input). Validation was to order of magnitude to the unpublished estimates of Borgamun and of Millard (Locci, pers. com.). Primary production calibrations are intended to include primarily phytoplankton, although edible benthic algae may also have been included in the prototype back door calibration procedures. Calibration of the base of the food web on the annualized time scale employed in the prototype

LEEM was necessarily an approximation of annual production, rather than an exact model of integrals of daily or seasonal productivity. Such detail was beyond the intent of this project. Uses requiring hourly or daily models of individual primary producer populations need to develop separate models explicitly for their use, rather than depending on models such as LEEM.

Extensive recalibration of the disaggregated model was difficult and was not carried out to a greater extent than necessary to extend the usefulness of the prototype model. The model was recalibrated to maintain the historical fish abundance within reasonable approximations of the prototype model. Sufficient data of historical trends for the disaggregated components were not available to conduct a more detailed quantitative recalibration of these components. Behaviors of the lower trophic level components were examined under a variety of scenarios including manipulations of external P-loading, and alterations in the rate of zebra mussel invasion into Lake Erie. The model responses to these scenarios were consistent with scientific expectations based on historical trends following reductions in P-loading and introduction of zebra mussels.

Objective 4: Preliminary exploration of implications of our model alterations:

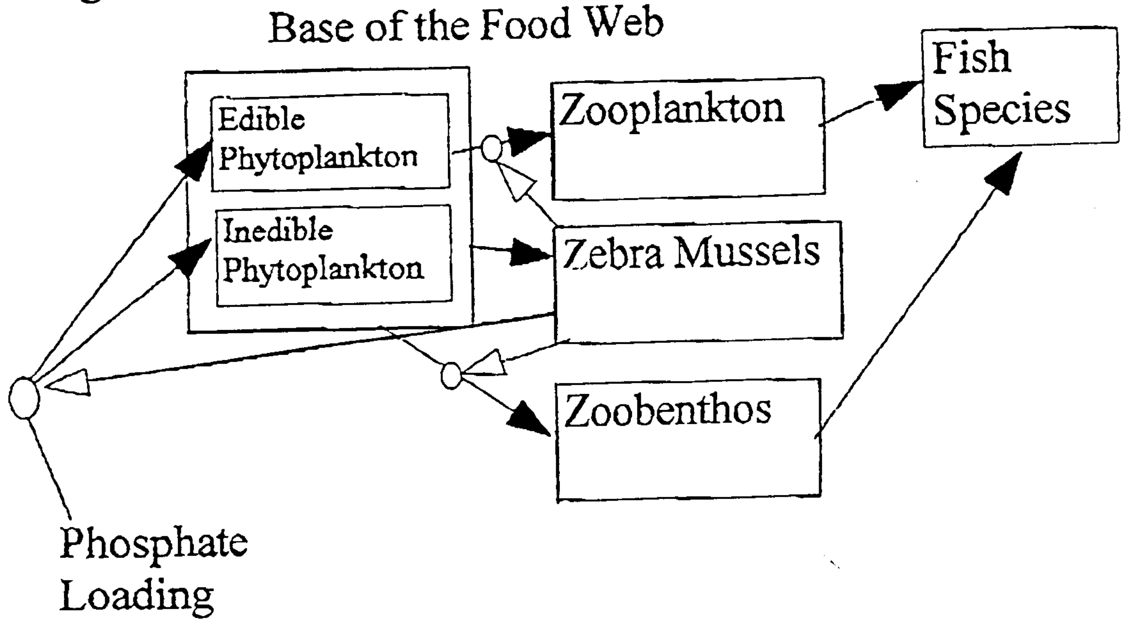
A portion of the work accomplished in this study was examined more deeply as part of a LEEM Model Testing Workshop sponsored by the IJC at Case Western Reserve University in April 1996. During this workshop R. Sturtevant and S. Whipple completed a preliminary assessment of the significance of incorporation of a simple feedback, modeling the releases of phosphate by zebra mussels, based on the data and a hypothesis by Heath (1995). Our results showed that inclusion of this nutrient release could have an important effects on the population dynamics of zooplankton, zoobenthos and young-of-the-year fish.

Objective 5: Incorporation into the LEEM model.

Some of the results of this project have been incorporated into the LEEM Version 0.2 and are available on the Internet <http://129.22.156.18/LEEMP.htm>. LEEM Version 0.2 now incorporates the structure explored in the workshop as well as a simple disaggregation of the primary production based on edibility of phytoplankton to zebra mussels (see Figure 4). The current LEEM version was made without changing primary production from a state variable to a population variable. The primary production was reformulated into biomass (kg wet weight per year) to facilitate possible on-going changes to the model structure and to move to more explicit mass-balance accounting of energy flows. This simple formulation was easier to calibrate than the more extensive disaggregation developed in this project.

As the need arises for a more detailed and realistic model of the base of the food web, we hope that the remainder of our accomplishments may be incorporated into future versions of LEEM, accessible to researchers interested in exploring the implications of the feedback loops incorporated and the top-down controls of primary production. Also, we believe that this model provides the possibility of being useful to resource managers, interested in conducting model scenarios of potential management plans.

Figure 4: Schematic Diagram of LEEM Version 0.2
Base of the Food Web



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