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I am submitting herewith a dissertation written by Dennis Michael McDermot entitled: "An Individual-Based Modeling Study of Lake Fish Communities in Lake Mendota Wisconsin: The Importance of Considering Food Web Interactions." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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# An Individual-Based Modeling Study of Lake Fish Communities in Lake Mendota Wisconsin: The Importance of Considering Food Web Interactions.

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Dennis Michael McDermot

August 1998

For John

*Requiem Aeternam*

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## Abstract

A general individual-based fish community simulator is presented. The model tracks the daily feeding, growth, movement, reproduction, and mortality of individuals of up to six species for multiple generations in up to three spatial boxes. The version presented in this dissertation is based on Lake Mendota, Wisconsin. Six species are followed: yellow perch, bluegill, white bass, cisco, walleye, and northern pike. The environment consists of daily temperature, dissolved oxygen, and prey densities in each of the epilimnion, hypolimnion, and littoral zone spatial boxes. Feeding parameters and larval mortality rates were calibrated until all species persisted at reasonable biomasses, with realistic mean lengths at age and diets by life stage. A general introduction and overview is given in Part 1. In Part 2 alternative baseline calibrations are presented which differ in their degree of interannual variability. Correlation analysis of survival and growth rates showed that larvae were influenced by competition, yearlings by predation, and young of the year (YOY) juveniles by both. Adult growth was density-dependent for planktivores and positively related to forage biomass for piscivores. Cisco dynamics were effectively independent of the other species. The calibrated model was used to compare the effects of a biomanipulation experiment (piscivore enhancement) versus a coincident cisco die-off event, and to evaluate alternative stocking regimes for their ability to sustain improved water quality. Predicted total zooplankton consumption was used to indicate effects on algae and water quality. The effects on community composition of piscivore enhancement and cisco die-off differed between the low and high variability baseline conditions. Under both baseline conditions, cisco die-off produced similar short-term but much larger long-term reductions in zooplankton consumption than piscivore enhancement. Delayed changes in YOY juvenile and larval survival illustrated complex indirect food web responses to piscivore enhancement. None of the three alternative stocking regimes analyzed yielded ideal management results. Stocking either had little effect on zooplankton consumption or resulted in significant changes in piscivore mean lengths or in the composition of the fish community. In Part 3 the importance of food web structure in determining population responses to global climate change is examined. Six alternative food

webs were configured as subsets of the 6-species Lake Mendota food web: two versions of the 6-species food web, which differed in yellow perch biomass, a 3-species (yellow perch, bluegill, white bass) competition food web, two versions of a 2-species (yellow perch, walleye) predator-prey food web differing in yellow perch biomass, and a 1-species (yellow perch) population model. All food webs included yellow perch. To simulate climate change, published predictions of changes in temperature and dissolved oxygen in Wisconsin lakes under 2x atmospheric $CO_2$ were superimposed onto temperature and dissolved oxygen profiles for Lake Mendota. Population responses of yellow perch to climate change depended upon food web arrangement. Yellow perch abundance decreased in response to climate change in the 3-species and high-biomass 6-species food webs, and increased in the remaining food webs. Population responses in the 1-species model were consistent with predictions based only on yellow perch bioenergetics (increases in size, abundance, and biomass), but were modified in other food web by competition and predation in the model. White bass and northern pike were relatively minor components of the food web under baseline conditions but emerged as dominant species under climate change. A summary of results and concluding remarks are given in Part 4. Adapting to environmental changes will require understanding of changing ecological processes at many levels. Individual-based models provide a method for integrating processes from individuals to communities.

Key words: individual based, multi-species, fish, simulation model, biomanipulation, Lake Mendota, predation, density dependence, depensatory mortality, population dynamics, food web global warming, climate change.

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# Part 1

# General Introduction

## 1.0 Background

Lake Mendota, Wisconsin has been called the most studied lake in the world. The largest (3985 ha) and deepest (25.3 m) of the lakes in the Yahara River drainage basin, Lake Mendota is an important water resource for the city of Madison. Lake Mendota supports an extensive recreational fishery, particularly for yellow perch, as well as for game fish such as walleye and northern pike (Johnson and Skaggs 1992). Changes in habitat, variable recruitment of fish stocks, unpredictable climate effects, and complex interactions among species are among the many variables with which managers of the Lake Mendota fishery must contend (Johnson et al. 1992; Johnson 1993; Johnson and Kitchell 1996).

Lake Mendota faces recurring water quality challenges in the form of summertime blooms of noxious blue-green algae. Drainage into Lake Mendota comes mostly from agricultural areas, resulting in a diffuse source for a high nutrient load which is difficult to control (Kitchell 1992). Blue-green algae blooms are related to a complex interaction of nutrient loading, particularly phosphorous, herbivory by zooplankton, and planktivory by fish (Lathrop 1992). The lake stratifies in summer, and the hypolimnion becomes anoxic for much of the season. In some years, production of hydrogen sulfide in the anoxic hypolimnion can result in a distinctly unpleasant odor on the lake (Brett M Johnson, personal communication).

During 1987 to 1989, an ambitious attempt was made to address water quality and fisheries issues in Lake Mendota simultaneously through biomanipulation. Walleye and northern pike were extensively stocked, and strict size and bag limits were imposed on fishing in an effort to enhance the stocks of these species. It was hoped that enhancement of piscivorous fish would produce a cascade effect down the food chain, whereby enhanced piscivores led to reduced planktivorous fish, increased herbivorous zooplankton, and ultimately reduced summertime algae biomass (Kitchell 1992). Results of this effort were generally positive, but confounded by the unexpected loss of cisco (a dominant planktivore in Lake Mendota) in the summer of 1987 due to causes unrelated to the biomanipulation (Rudstam et al. 1993; Johnson and Kitchell 1996).

Lake Mendota in the future will face further changes due to the effects of global climate change. Estimates based on general circulation models (GCM) of global climate predict a 4.5 °C increase in mean air temperature for Wisconsin with a doubling of atmospheric $CO_2$. When these predictions are applied to water quality models for Wisconsin lakes (Stefan and Fang 1994; Hondzo and Stefan 1993; DeStasio et al. 1996; Robertson et al. 1992), they predict warmer surface temteratures, lower dissolved oxygen in the hypolimnion, more extreme stratification, and less ice cover. These changes in climate will directly affect nearly every component of the lake ecosystem, and changes in one component may cascade through the food web to produce unexpected indirect effects. For example, metabolism and growth in fish is directly temperature dependent. Changes in fish growth will alter fish community dynamics through affects on size-based competitive and predative interactions and size-based maturation and fecundity. Changes in the fish community can affect water quality by impacts on herbivorous zooplankton (Lathrop 1992). Efforts to predict population responses to climate change so far have focused mainly on predicting changes in favorable habitat which largely ignore biotic interactions (Stefan et al. 1996; Magnuson and DeStasio 1995; Magnuson et al. 1990).

In this work, we explore the role of food web interactions in determining population responses to evnvironmental changes (biomanipulation, cisco die-off, and climate change) using an individual-based simulation model. Individual based modelling is an approach which explicitly tracks the feeding, growth, reproduction, mortality, and other processes of individual organisms. Population and community level effects are determined by the collection of individuals (DeAngelis and Gross 1992; VanWinkle et al. 1996). Individual based models are appropriate when the the outcomes of interactions among organisms depend strongly on attributes of the individual, such as the many size-based interactions among fish (DeAngelis and Gross 1992; Stein et al. 1992; Crowder et al. 1992). Climate change will also impact fish most directly on an individual level by affecting their bioenergetics. The individual-based approach has the potential to integrate processes across many scales, from individual physiology to community dynamics. This approach has been applied to multispecies interactions in fish (Rose et al. 1996; Clark and Rose

1997, Van Winkle et al. 1993). So far, these models have been limited to only a few species. Clark and Rose (1997) and Van Winkle et al. (1996) examines competitive interactions between brook char and rainbow trout. Predator-prey interactions between yellow perch and walleye were modeled by Rose et al. (in review). We are not aware of any previous individual-based models that simulate the long term dynamics of a many-species fish food web.

**2.0 Overview of Parts**

We present an individual-based fish food web simulation model for up to six species in a lake environment of up to three spatial compartments. The model is calibrated to simulate the Lake Mendota fish food web consisting of yellow perch (*Perca flavescens*), bluegill (*Lepomis macrochirus*), white bass (*Morone chrysops*), cisco (*Coregonis artedii*), walleye (*Stizostedion vitrium*), and northern pike (*Esox lucius*). We then utilized the model to compare the effects of the biomaipulation versus the cisco die-off, and to explore the importance of food web structure in mediating the effects of global climate change.

Each part is complete with its own abstract, introduction, discussion, tables, and figures. Tables, figures, and references are provided in appendices at the end of each part in which they are cited. A final appendix is provided containing parameter estimates used in model development. Part 1 contains a general introduction and overview. Model development and simulation results are divided between Part 2 and Part 3.

Part 2 contains a detailed description of the model configured for the 6-species Lake Mendota food web, baseline results, and an exploration of biomanipulation. For model corroboration, baseline predictions of species biomass, diets, and size at age of model fish are compared to published estimates for Lake Mendota. A correlation analysis of baseline simulations is presented which examines the roles of competition and predation within the model. A simulation experiment is presented to compare the effects on zooplankton of the biomanipulation versus the confounding cisco die-off. Three alternative stocking regimes are examined to determine whether

the positive efects of biomanipulation can be maintained in the long term. Part 2 concludes with a general discussion of model results and consideration of issues related to model complexity.

Part 3 tests whether the effects of global climate change on population dynamics will depend on the food web structure in which the population is imbedded. The section begins with general introduction to global climate issues, followed by a brief description of the model for Lake Mendota. Six alternative food webs are presented, all subsets of the 6-species Lake Mendota food web presented in Part 2. These six food webs are: two versions of the 6-species food web, a 3-species competitive food web (yellow perch, bluegill, white bass), two versions of a 2-species predator-prey food web (yellow perch, walleye), and a 1-species population (yellow perch). A global change scenario for Lake Mendota is presented based on published predictions for climate change effects in Minnesota and Wisconsin lakes are superimposed on temperature and DO data for Lake Mendota. Comparison of the effects of the global change scenario applied to each of the alternate food webs focuses on the population responses of yellow perch, the only species represented in all six food webs. Part 3 concludes with a discussion of issues related to climate change and food web interactions.

Part 4 contains a general summary of model results, and some concluding discussion of the theoretical and practical issues explored in this work. Results are related to the overall objectives of the study. Objectives included exploring questions of ecological interest as well as methodological issues. Limitations of predictive models in ecology are discussed.

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# Part 2

# An Individual-Based Model of Lake Fish Communities:

# Application to Biomanipulation in Lake Mendota Wisconsin

**Abstract.**-- A general individual-based fish community simulator is presented. The model tracks the daily feeding, growth, movement, reproduction, and mortality of individuals of up to six species for multiple generations in up to three spatial boxes. The version presented in this paper has been configured and calibrated for Lake Mendota, Wisconsin. Six species are followed: yellow perch, bluegill, white bass, cisco, walleye, and northern pike The environment consists of daily temperature, dissolved oxygen, and prey densities in each of the epilimnion, hypolimnion, and littoral zone spatial boxes. Feeding parameters and larval mortality rates were calibrated until all species persisted at reasonable biomasses, with realistic mean lengths at age and diets by life stage. Two alternate baseline calibrations are presented which differ in their degree of interannual variability. Correlation analysis of survival and growth rates showed that larvae were influenced by competition, yearlings by predation, and young of the year (YOY) juveniles by both. Adult growth was density-dependent for planktivores and positively related to forage biomass for piscivores. Cisco dynamics were effectively independent of the other species. The calibrated model was used to compare the effects of a biomanipulation experiment (piscivore enhancement) versus a coincident fish die-off event, and to evaluate alternative stocking regimes for their ability to sustain improved water quality. Predicted total zooplankton consumption was used to indicate effects on algae and water quality. The effects on community composition of piscivore enhancement and cisco die-off differed between the low and high variability baseline conditions. Under both baseline conditions, cisco die-off produced similar short-term but much larger long-term reductions in zooplankton consumption than piscivore enhancement. Delayed changes in YOY juvenile and larval survival illustrated complex indirect food web responses to piscivore enhancement. None of the three alternative stocking regimes analyzed yielded ideal management results. Stocking either had little effect on zooplankton consumption or resulted in significant changes in piscivore mean lengths or in the composition of the fish community.

Key words: individual based, multi-species, fish, simulation model, biomanipulation, Lake Mendota, predation, density dependence, depensatory mortality, population dynamics, food web.

## 1.0 Introduction

The importance of multispecies interactions affecting fish population dynamics has been recognized since the earliest days of ecology (Forbes 1887; Volterra 1926). Multispecies interactions that have been studied include top-down trophic cascade effects (Kitchell 1992; Carpenter et al. 1987; Carpenter and Kitchell 1993; Xi et al. 1994; Rudstam et al. 1993), bottom-up energy flow (Neill 1988), and competition within the same trophic level (Forney 1977; Werner 1977; Clark and Rose 1997). In addition to competition and predation, species interactions can often involve behavioral changes for which the larger population consequences are unclear (Werner and Hall 1988; He et al. 1993). Rarely, if ever, do populations exist in isolation. From a fisheries management perspective, the importance of multispecies interactions is well recognized, but these interactions are generally too poorly understood to guide policy (Gulland 1989; Kerr and Ryder 1989; Murawski 1991).

Species interactions can be particularly complex in fish communities (Carpenter 1988). During its lifetime, a fish will typically grow several orders of magnitude in size. Fish also exhibit high fecundity and mortality rates. Population abundances often decline by many orders of magnitude between eggs and adults. A single species can occupy many different trophic niches, from planktonic larvae to top predator. Asymmetric interactions, in which two species may interact as predator and prey at one stage in their life cycles and as competitors at other life stages, are common (Stein et al. 1988; Persson 1988). Cannibalism, which can be an important factor affecting population dynamics (Dong and DeAngelis, in press), often depends on the population dynamics of forage species (Chevalier 1973).

A variety of models have been used to simulate fish community dynamics (Rose et al. 1996). These approaches have included budget models of energy flows among ecosystem compartments, coupled single-species models that simulate populations through time, and holistic models that incorporate features of both. These models can all be considered aggregated approaches, in that they represent population abundances or biomass as state variables and treat interspecific interactions with relatively few, lumped parameters.

There are a number of limitations inherent to these aggregated modeling approaches. Budget models tend to focus on equilibrium conditions, rather than on the temporal dynamics of populations. Coupled single-species models use lumped parameters to represent species interaction effects which often have little biological meaning. Holistic models often represent the mean attributes of fish populations. However, it is the atypical individual, not the average, that survives (Crowder et al. 1992). For all of the aggregated approaches, population parameters which may have a clear biological interpretation, such as mortality rates, can still be difficult to estimate reliably. Finally, individual-level behaviors, such as movement, choice of feeding patch, and vulnerability to gape-limited predators, which can be important to fish population dynamics, are difficult to represent realistically in aggregated models.

Individual-based models have the potential to directly overcome many of the limitations of traditional aggregate models (Van Winkle et al. 1993; DeAngelis and Gross 1992; Tyler and Rose 1994; DeAngelis et al. 1994). Individual-based models track the growth, survival, reproduction, and behavior of individuals. The sum over individuals at any given time yields the population, and if multiple species are represented, the community. Though population-level data may be difficult to obtain, most species are well studied as individuals. Basic biological information pertaining to life history, metabolism, growth, and reproduction is generally available for most fish species (Carlander 1977; Hewitt and Johnson 1992). Many predatory and competitive interactions in fishes are size-based encounters between individuals, and representing these interactions in individual-based models is relatively straightforward. Behavioral responses can be also simulated directly, provided the actual mechanisms of those behaviors are known. In theory, if the individual level processes can be adequately represented, then realistic population and community level dynamics should result (Rose et al. 1996).

Despite their intuitive appeal, individual-based models present problems of their own. Large amounts of data are required for model formulation and corroboration. While individual-based models can handle individual-level variability in processes, most data for estimating model parameters are reported as means. Gaps in available data on individual-level processes are often filled in with information from other species, other systems, or by educated guess.

Estimates of mortality rates that span the entire life cycle are notoriously difficult to obtain. Though in theory individual behaviors may be directly simulated, such behaviors are often difficult to quantify.

The individual based approach has been recently applied to multispecies situations involving fish (Rose et al. 1996; Clark and Rose 1997). These models have so far been limited to only a few species. We are not aware of any individual-based models that simulate the long term population dynamics of a many-species fish food web.

In this paper, we present an individual-based simulation model of a fish food web typical of north temperate U.S. lakes. The model tracks individuals of up to six species for multiple generations in up to 3 spatial boxes. The model is constructed as a generic fish food web simulator, which can be easily adapted to a variety of lakes. The version presented in this paper has been configured for Lake Mendota, Wisconsin. We selected Lake Mendota because its fish community has been extensively studied, and because it was the site of a lake-wide food web manipulation experiment (Kitchell 1992). The accumulated database provides the basis for ground truthing the individual-based model. Once calibrated, we then use the model to compare the effects on zooplankton of the biomanipulation versus a coincident fish die-off event.

**2.0 Model Overview**

Six fish species are represented: yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), bluegill (*Lepomis macrochirus*), white bass (*Morone chrysops*), and cisco (*Coregonis artedii*). These species comprise the major species in Lake Mendota (Kitchell 1992; B. Johnson, personal communication).

The model is multi-generational, with the young-of-the-year (YOY) population determined by spawning of adults. Individuals develop through the following life stages: egg, yolk-sac larva, larva (exogenous feeding to 20 mm), YOY juvenile (20 mm to age-1), yearling, and adult. An adult that has reached maturity is also a spawner. Eggs and yolk-sac larvae are followed as cohorts from each spawner. Feeding fish are followed as individuals throughout their lives. Feeding, growth, reproduction, mortality, and movement are evaluated daily. For each individual,

the model keeps track of total length (L, mm), wet weight (W, grams), life stage, age (years), and spatial compartment.

The lake environment is separated into three homogeneous compartments representing the littoral, epilimnetic, and hypolimnetic zones (Figure 1)*. Environmental variables in each compartment include daily temperature and dissolved oxygen (DO). Water temperature varies with lake depth. By governing the maximum water column depth inhabitable by fish, DO affects the available habitat and water temperatures fish experience. Prey densities in each compartment include zooplankton, benthos, forage fish, and the YOY and yearling individuals of the six modeled species. Below, we describe the model for Lake Mendota. Values for species and environmental parameters are listed in Appendix 3.

## 3.0 Lake Environment

### *3.1 Spatial Compartments*

Three spatial compartments (littoral zone, epilimnion, hypolimnion) are represented (Figure 1). The dimensions of the three compartments are based on Lake Mendota. Surface area is 996 ha for the littoral zone, 2987 ha for the epilimnion, and 2525 ha for the hypolimnion. Littoral zone depth (thickness) is set to 5 m, and the thermocline depth, which separates the epilimnion and hypolimnion, is set to 10 m. The amount of the hypolimnion and epilimnion that fish can inhabit depends on specified DO concentrations. Fish avoid water with DO concentration less than 4 mg/L.

### *3.2 Daily temperature*

In each spatial compartment, fish may experience a range of available temperatures. Maximum and minimum daily temperatures are specified for surface waters (littoral zone and epilimnion) and for the hypolimnion. In the littoral zone temperature is uniform with depth. Maximum and minimum littoral zone temperatures are both assumed equal to the maximum epilimnion temperature (i.e. surface temperature in the lake). Epilimnion and hypolimnion temperatures are assumed to decrease with water depth, with maximum temperatures occurring

at the top and minimum temperatures occurring at the bottom of each compartment. The minimum temperature of the epilimnion is assumed to be the same as the maximum temperature of the hypolimnion. Thus, three unique daily temperatures are generated: (1) littoral zone and maximum values for the epilimnion, (2) minimum values for the epilimnion which are also maximum temperatures for the hypolimnion, and (3) minimum temperatures for the hypolimnion. Maximum and minimum daily temperatures are generated from a trigonometric function:

$$T = T_a + T_b * \cos(0.0172t) + T_c * \sin(0.0172t) \qquad (1)$$

where t is calendar day, $T_a$, $T_b$, and $T_c$ are regression coefficients with three sets of values each, and the argument of the sine and cosine functions is in radians. The value of 0.0172 ensures one cycle in a 365-day year. Temperature is not allowed to go below 1°C , which is assumed to represent ice cover. Generated daily maximum and minimum water temperatures based on Lake Mendota data and used in model simulations are shown in Figure 2.

*3.3 Dissolved Oxygen*

We assume that fish cannot inhabit water whose DO concentration is less than 4 mg/L. We use the minimum temperature at which DO concentration exceeds 4 mg/L to determine the amount of the hypolimnion and epilimnion that can be utilized by fish each day. The minimum temperature at which DO concentration exceeds 4 mg/L ($T_{DO}$) was estimated from temperature and DO concentrations with depth data from Lake Mendota (Figure 2). The maximum accessible depth of the lake for fish ($D_{max}$) is a decreasing linear function of $T_{DO}$:

$$D_{max} = -1.097 \cdot T_{DO} + 31.61 \qquad (2)$$

$D_{max}$ does not exceed 20 m, the maximum depth of the hypolimnion. If $D_{max}$ is greater than 10 m (i.e., depth at which DO <4 mg/L is in the hypolimnion), then the thickness of the hypolimnion is set to $D_{max}$ -10. If $D_{max}$ is less than 10 m (i.e., depth at which DO <4 mg/L is in the epilimnion), then all fish in the hypolimnion must move up to the epilimnion and the thickness of the epilimnion is

set to $D_{max}$. With average daily maximum and minimum temperatures, the hypolimnion is uninhabitable from day 180 to day 260 when thickness becomes less than 3 m (Figure 3). While the formulation relating DO to temperature is specific to how data were reported for Lake Mendota, the general approach is applicable to other lakes.

*3.4 Prey Densities*

Prey are represented by two zooplankton groups, benthos, forage fish, and the YOY and yearling individuals of the six modeled fish species. The two zooplankton groups are specified based on *Daphnia galeata* and *Daphnia pulicaria,* and the benthos group is based on chironomids. These were selected because they are among the dominant zooplankton and benthos in Lake Mendota and are important as forage for fish (Luecke et al. 1992; Lathrop 1992). Zooplankton, benthos, and forage fish are represented by densities in each compartment, and average weights and turnover rates. Density is updated daily using a discrete logistic function with losses due to consumption by model fish and migration among compartments:

$$N_{j,k}(t) = N_{j,k}(t-1) \cdot r_k \cdot [1 - \frac{N_{j,k}(t-1)}{N^*_{j,k}(t)}] - CON_{j,k} + MIG_{j,k} \quad (3)$$

where k is the prey type, j denotes the spatial compartment, N*(t) is the maximum, or equilibrium density on day t, $r_k$ is turnover rate at N*/2, CON is the total consumption per unit volume by all modeled fish, and MIG is the net immigration rate from other compartments. Simulated prey densities are artificially truncated to prevent them from exceeding their equilibrium densities. This ensures a well behaved return to equilibrium, with no possibility of cyclic or chaotic dynamics. Values of turnover rates (r) determine the rate at which losses due to consumption are replenished, and are set to 0.5/d for *D. galeata* and *D. pulicaria*, 0.3/d for benthos, and 0.15/d for forage fish. Individual prey weights are set to 0.033 mg for *D. galeata*, 0.14 mg for *D. pulicaria*, 3.8 mg for benthos, and 2.0 g for forage fish. Turnover rates and weights per individual were

determined from Lake Mendota data and reported values in the literature (Edgar and Shaw 1995; Shuter and Ing 1997; Lindegaard 1989).

Equilibrium densities are specified to be time-dependent for zooplankton, and constants for benthos and forage fish. Long-term monitoring data from Lake Mendota were used to specify prey equilibrium densities. Equilibrium density of each of the two zooplankton groups in each compartment is assumed to be a unimodal function (single peak) of calendar day (Figure 4). Equilibrium chironomid densities are 2122/$m^2$ in the littoral zone and 224/$m^2$ in the hypolimnion. Forage fish equilibrium density is 0.00833/$m^3$ in the littoral zone. Benthos are absent from the epilimnion, and forage fish are only found in the littoral zone.

Total consumption of prey by modeled fish (CON in equation 3) is computed daily based on the summation of individual consumption rates of modeled fish ($C_j$ in equation 13 multiplied by model fish weight) in each compartment. The summed consumption rate by prey type in a compartment is then divided by the volume of the compartment (liters for zooplankton; $m^2$ for benthos; $m^3$ for forage fish) and mean weight per individual of the prey type to obtain the density of prey consumed.

We assume that net immigration of zooplankton is based on the difference in their densities between compartments. Benthos and forage fish are assumed to not mix among spatial compartments. Net immigration of zooplankton occurs between the littoral zone and the epilimnion, and between the epilimnion and hypolimnion. There is no direct exchange between the littoral zone and the hypolimnion. Net immigration of zooplankton species k into compartment j is computed as:

$$MIG_{j,k} = \sum_{h=1}^{3} m_{h,j}[N_{h,k}(t-1) - N_{j,k}(t-1)] \qquad (4)$$

where $m_{h,j}$ is the daily net immigration rate from compartment h into compartment j. Net immigration rate is 0.2/day between epilimnion and hypolimnion and 0.1/day between the epilimnion and littoral zone. These rates allow for near eventual equilibration among compartments after about 7 days and 15 days, respectively.

## 4.0 Fish processes

### *4.1 Spawning*

Spawners are adults that have reached maturity on the first day of each species' spawning season. Spawning seasons begin on March 1 for yellow perch, walleye, and northern pike, April 1 for white bass, May 1 for bluegill, and November 1 for cisco. All species except bluegill are single-batch, broadcast spawners. Bluegill build nests that are guarded by males and may spawn up to three times per year. For broadcast spawners, only females are considered in spawning. For bluegill, females are paired with males in length order. The longest female available to spawn each day is paired with the longest male, etc. In the general model, survival and fecundity on a nest may be modified by competition among males for a limited number of high quality nest sites. We assume nest sites are not limiting nor vary greatly in their quality in the Lake Mendota version because of its extensive littoral zone.

Fish are assigned a sex (1:1 female to male) at random upon reaching age-2. Probability of an individual being mature increases linearly with its length:

$$p_{mat} = M_m \cdot L + M_b \qquad (5)$$

where $M_m$ and $M_b$ are species-specific coefficients. If a generated uniform random number between 0 and 1 is lass than $p_{mat}$, the individual is mature. All mature fish spawn, although individuals can die during the spawning season prior to releasing eggs or building nests.

Timing of spawning within the spawning season depends on temperature. Each female is randomly assigned a spawning temperature, $T_{SP}$, from a triangular distribution. The coefficients in equation (5), and the minimum ($SP_{min}$), mode ($SP_{mode}$), and maximum ($SP_{max}$) values of the triangular distribution, are set to species-specific values (Appendix 3) based on reported maturity at length data and preferred temperatures of spawning (Becker 1983; Carlander 1977). Eggs are released on the first day when the epilimnion temperature exceeds $T_{SP}$, except for the fall-spawning cisco, for whom eggs are released the first day when the epilimnion temperatures drops below $T_{SP}$. Under average temperature conditions, northern pike spawns in late March (≈day 80),

followed by walleye (≈day 100), yellow perch (≈day 120), and white bass (≈day 160). Cisco spawns in mid to late December just before ice cover. Bluegill spawn up to three times through midsummer (day 180 to day 225). Provided temperature allows for spawning, each individual female and male bluegill is permitted to spawn again after waiting 10 days from when their previous batch initiates exogenous feeding (i.e., reached the larval stage and left their nest).

The number of eggs produced by a female (per spawning batch for bluegill) is a linear function of female weight:

$$F = F_m \cdot W + F_b \qquad (6)$$

where $F_m$ and $F_b$ are species-specific coefficients. The total biomass of eggs (egg weight * F) spawned by a female is deducted from her body weight on the day of spawning. To compensate for this loss, we increased maximum consumption for adult females ($C_{max}$ in equation 10) by a factor of 1.7 for yellow perch, 1.6 for northern pike, 1.5 for bluegill, and 1.2 for walleye, white bass, and cisco. These values were determined by trial and error adjustment until long term mean lengths for males and females matched. Values of $F_m$ and $F_b$, and the average weight of an egg (g/egg), were determined based on reported fecundity of each of the six species (Appendix 3).

*4.2 Eggs and Yolk-sac larvae*

Eggs from each female are followed as a cohort through the egg and yolk-sac larval stages. Rate of development is temperature-dependent. Fractional daily development is computed as:

$$DV = \frac{1}{D_a + \exp(D_c * T)} \qquad (7)$$

where $D_a$ and $D_c$ are species-specific coefficients with separate values for eggs and for yolk-sac larvae. Daily fractional development is summed over time for each female spawner or nest cohort. When the cumulative exceeds 1, development occurs (eggs hatch into yolk-sac larvae or

yolk-sac larvae become larvae). The coefficients of equation (7) are specified for eggs and for yolk-sac larvae for each of the six species (Appendix 3) based on laboratory data on development rates. Upon reaching the larval stage, individuals are followed in simulations. Initial weights of all larvae (mg) are 1.15 for yellow perch, 3.8 for walleye, 11.0 for pike, 1.5 for bluegill, 0.8 for white bass, and 5.9 for cisco. These weights correspond to reported lengths at first feeding.

Daily instantaneous mortality rates of eggs and yolk-sac larvae (Z) are assumed constant. Mortality rates are specified for eggs and yolk-sac larvae for each of the six species (Appendix 3). Each day, the number in each female spawner cohort or nest cohort are updated by multiplying by the fraction surviving ($S=e^{-Z}$). The adult mortality rate is used to determine if individual bluegill nests are lost due to the death of the guarding male.

*4.3 Feeding Individuals: Development*

Larval fish metamorphose to juveniles upon reaching 20 mm in length. The first day of the spawning season is considered the beginning of the simulation year for each species. On the first day of spawning, fish are promoted to next age-class: YOY juveniles become yearlings, yearlings become age-2, age-2 become age-3, etc.

*4.4 Feeding Individuals: Growth*

On each day, the new weight of an individual is used to update its length. A length-weight relationship is specified for each species:

$$L = L_a * W^{L_b} \qquad (8)$$

where $L_a$ and $L_b$ are regression coefficients from length-weight data for each species (Appendix 3). Length and weight are partially uncoupled. Fish can lose weight but not length. To increase in length, a fish must weigh at least the weight predicted from its length.

The daily change in weight of an individual is determined by using a difference equation form of a bioenergetics equation:

$$W_{t+1} = W_t + (E*C - R_{tot})*W_t*\Delta t \quad (9)$$

where E is net assimilation efficiency, C is daily consumption rate (g/g/day), $R_{tot}$ is total metabolic rate (g/g/day), and Δt is one day. E is the combined effect of egestion, excretion, and specific dynamic action (SDA). Egestion, excretion, and SDA are treated separately in most fish bioenergetics models, but can be collapsed into a single term because they are all expressed as fractions of consumption (Hewett and Johnson 1992). Non-linear functions relating consumption and metabolic rates to fish weight and water temperature are from the commonly used "Wisconsin" fish bioenergetics modeling software (Hewett and Johnson 1992). Parameter values for each species were borrowed from existing models developed by others.

#### *4.4.1 THERMOREGULATION*

Consumption and metabolic rates depend on water temperature. We assume that fish seek out their preferred water temperature ($T_{pref}$). The temperature used to adjust consumption and metabolism (T) is the water temperature available in the compartment (ie. $T_{max} > T > T_{min}$ and $T > T_{DO}$) as close as possible to $T_{pref}$. Values of $T_{pref}$ are specified to reflect the warm-water preferences of bluegill (31°C) and white bass (29°C), the cold-water preferences of cisco (10° C), and the intermediate temperature preferences of yellow perch (21°C), walleye (21°C), and northern pike (24°C).

#### *4.4.2 METABOLISM*

Total metabolic rate, $R_{TOT}$, depends on body weight, water temperature, and activity:

$$R_{TOT} = R_a * W^{R_b} * f(T) * A \quad (10)$$

where $R_a$ and $R_b$ determine the weight effect on metabolism, f(T) is the effect of temperature, and A is the activity multiplier on metabolism. Three alternative formulations for f(T) are used to be consistent with the original developers of the species-specific bioenergetics models (Table 1). The specific formulations for f(T) are empirical and their parameters correspond to temperature endpoints commonly reported in laboratory metabolism experiments. Optimal and maximum temperatures associated with metabolism are set to high values so that metabolism increases with temperature (i.e., ascending limb) over the range of temperatures experienced by the fish.

*4.4.3 CONSUMPTION*

Realized consumption is computed based on a maximum consumption rate and a functional response equation. Maximum consumption rate depends on body weight and water temperature, and the functional response equation accounts for how prey availability affects consumption. Maximum daily consumption rate ($C_{MAX}$, g/g/day) is determined by temperature and weight:

$$C_{MAX} = C_a * W^{C_b} * f(T) \qquad (11)$$

where $C_a$ and $C_b$ determine the weight effect on maximum consumption, and f(T) is the same as equation set 2 in Table 1, with parameters values specified for maximum consumption rather than metabolism.

Realized consumption of prey is determined by a Type II functional response equation (Holling 1965) that incorporates $C_{max}$. The total daily consumption of an individual (C, g/g/day) is computed as:

$$C = \sum_{i=1}^{n} C_j \qquad (13)$$

$$C_j = \frac{W * C_{MAX} * V_j \frac{PD_j}{K_j}}{1 + \sum_{k=1}^{n} \frac{V_k \cdot PD_k}{K_k}} \qquad (12)$$

where $C_j$ is the realized consumption rate of prey type j, $V_j$ is the vulnerability (value of 0 or 1) of prey type j to this individual, $PD_j$ is the realized prey density of prey type j experienced by this individual, $K_j$ is the half saturation constant for this individual feeding on prey type j, and k,,j=1..n denotes prey types. YOY and yearling of each modeled fish species are treated as separate prey types.

Realized prey densities available to each individual ($PD_j$ in equation 13) are determined from simulated prey densities. For zooplankton, benthos and forage fish, $PD_j$ is generated from a Poisson distribution with mean equal to the simulated density on that day ($N_j$). For model fish as prey, not all prey on a given day are available to a predator because some individuals can be too large to be eaten. Piscivorous fish, such as walleye and pike in the Lake Mendota version, are typically gape limited (Juanes 1994). Converting the density of modeled fish ($N_j$) to realized density for an individual predator ($PD_j$) depends on the length of the prey relative to the length of the predator. The maximum length of prey that can be eaten for walleye increases with walleye length (Rose et al. in review):

$$GL = \begin{cases} 0.6 \cdot L & \text{if } L<200 \\ 0.6 - [\frac{0.15}{400}(L-200)] & \text{if } 200<L<600 \\ 0.45 \cdot L & \text{if } L>600 \end{cases} \qquad (14)$$

Northern pike are allowed to consume fish prey up to 32% of their own length (Beyerle and Williams 1968). For each individual walleye and northern pike predator, we determine the biomass density ($g/m^3$) of YOY and of yearling individuals of each fish species vulnerable to predation by this predator (i.e., in same spatial compartment and prey length less than GL).

#### *4.4.4 PARAMETER VALUES*

Parameter values that determine net assimilation efficiency, metabolic rate, and maximum consumption rate (Appendix 3) were obtained from previous bioenergetics models (Hewett and Johnson 1992). We obtained parameter values specific to larvae versus juvenile through adult life stages for yellow perch, walleye, and white bass. To summarize the bioenergetics, we show maximum consumption, total metabolism, and growth potential as functions of temperature for a typical sized age-5 adult yellow perch (Figure 5a), and growth potentials of age-5 adults of all species (Figure 5b). Growth potential assumes an individual obtains its maximum consumption every day, and is computed as $E^*C_{max} - R_{TOT}$. Realized growth can be lower than maximum due to prey limitation. Optimal growth occurs at about 16° C for the cold-water species cisco, at 22-24° C for yellow perch, northern pike, and walleye, and at 27-28°C for the warm-water species bluegill and white bass.

Vulnerabilities and K values are assigned to each species in five length categories roughly corresponding to larvae, YOY juvenile during the growing season, YOY juvenile overwinter, yearling, and age-2 and older (Appendix 3). Actual length categories vary among species because of differences in their lengths at these life stages. Vulnerability values (0 or 1) are shown in Table 2 and were determined from reported predator-prey interactions in Lake Mendota. The only growth-related parameters that were calibrated were the K parameters (Appendix 3).

### *4.5 Feeding Individuals: Movement*

Movement of individuals among the three spatial compartments depends on fish length. All larvae reside in the epilimnion. Upon reaching 20 mm in length, bluegill, walleye, and northern pike move to the littoral zone where they remain throughout the remainder of their life Yellow

perch and white bass move to the littoral zone upon reaching 20 mm, but then return to the epilimnion as yearlings (150 mm for yellow perch; 135 mm for white bass). Upon reaching 20 mm, cisco inhabit the hypolimnion as long as DO conditions permit. When DO concentrations in the hypolimnion are below 4 mg/L, cisco move up into the epilimnion.

These movement rules result in YOY and yearling bluegills inhabiting the same compartment (littoral zone) as their predators (walleye and northern pike) throughout their lives. Yellow perch and white bass escape predation when they return to the epilimnion as yearlings. Cisco do not overlap spatially with walleye or northern pike adults, and so are unaffected by model predation. Cisco only overlap with yellow perch and white bass when forced out of the hypolimnion into the epilimnion due to low DO concentrations. Cisco can also compete indirectly with species in the epilimnion by cisco consumption altering the immigration fluxes of zooplankton.

*4.6 Feeding Individuals: Mortality*

Mortality of YOY and yearlings comes from three sources: background mortality, starvation, and predation by other model fish. Starvation occurs if an individual's weight falls below 65% of its predicted weight based on its length (equation 8) for YOY, or below 50% of its predicted weight for yearling and adult. Constant background annual survival ($S_B$) is specified for each life stage of each species (Appendix 3). This rate is assumed to be the same for all spatial compartments. Annual survival is converted to the daily probability of dying as $P_d = 1-\exp(\ln(S_B)/365)$. On each day, if a uniform random number between 0 and 1 is less than $P_d$, then the individual dies.

Predation by model fish is determined from model fish consumption rates. YOY and yearling individuals of each species are treated separately. The daily probability of dying for an individual is computed as the total biomass consumed divided by the total biomass. Total biomass is computed by life stage (YOY or yearling) and by species for the spatial compartment inhabited by the prey individual. Consumed biomass is the total biomass consumed (by life stage, species, and compartment of prey) by all predators to which this individual prey was vulnerable

(i.e. prey size was within predator gape limitation). If a generated uniform random number between 0 and 1 is less than the probability of dying, then the individual is assumed to be eaten.

Age-2 and older individuals die from natural and fishing mortalities. Constant annual natural ($S_N$) and fishing ($S_F$) survival rates are specified for each species (Appendix 3). The combined daily probability of survival [exp(-ln($S_N$)/365)*exp(-ln($S_F$)/365)] is used to adjust population numbers. For biomanipulation simulations, we also include minimum size limits for walleye and northern pike. Individuals smaller than the size limit escape fishing mortality.

*4.7 Numerical Considerations*

Eggs and yolk sac larvae are followed from each female spawner-cohort or from each nest-cohort. Feeding fish are followed as individuals. Each model individual represents a number of population individuals. Each day for which spawner or nest cohorts result in yolk-sac larvae becoming feeding larvae, the number of model individuals introduced that day ($N_{new}$) to represent the new larvae is computed as:

$$N_{new} = \frac{FF_t}{FF_S} \cdot N_{rem} \qquad (15)$$

where $FF_t$ is the number of population first feeders introduced on day t, $FF_S$ is the number of model first feeders projected for the remainder of the spawning season, and $N_{rem}$ is the number of model individuals not yet used. $FF_S$ is computed based on the fecundity of remaining spawners and average egg and yolk sac larval survival rates. Equation (15) ensures that the fixed number of model individuals will be spread over all days when first feeding larvae can potentially be introduced. Each of the introduced model individuals is assumed to represent some number ($N_{sam}$) of identical population individuals. The initial value of $N_{sam}$ on the day of introduction is $FF_t/N_{new}$. $N_{sam}$ is then adjusted for mortality in subsequent days.

Fixed numbers of YOY, yearling, and each age-class of adults are followed for each species. For YOY juveniles and yearlings, a resampling algorithm (Rose et al. 1993) is used to maintain a constant number of model individuals. When a model YOY juvenile or yearling dies, a

replacement is selected at random from those still living. This replacement is then divided into two identical model fish, with each worth one half of the $N_{sam}$ value of the replacement individual. Age-2 and older fish are not subject to predation by other model fish and starvation is rare, so we use a simpler superindividual algorithm (Scheffer et al. 1995), rather than the resampling algorithm. Mortality of age-2 and older individuals is implemented by multiplying each individual's value of $N_{sam}$ by the overall probability of survival of that individual. Consumption rates and population-level variables, such as abundances and mean lengths, are computed based on the number of population individuals associated with each model individual.

Simulations presented in this paper are based on following 100 YOY model individuals, 100 model yearlings, and 50 model fish for each age-2 and older age class up to the maximum age for each species. This results in a total of 3800 model individuals being followed. Simulations that follow more model individuals generate similar results. Typical 100 year simulations using 3800 model individuals require approximately 10 hours of CPU time on a DEC Alpha 3000 workstation.

Upon reaching age-2, the 100 yearling model individuals are collapsed into 50 age-2 individuals by randomly selecting 50 yearlings with probability of selection proportional to their $N_{sam}$ values. The attributes of the selected yearlings (population worth, length, weight, etc.) are used as initial values for the newly created age-2 model individuals. The initial values of $N_{sam}$ for the 50 new age-2 model individuals are uniformly adjusted to result in the correct initial population number of age-2 individuals.

We reduce computational costs by using length categories to approximate the biomass of YOY and yearling vulnerable to a predator. Determining the exact biomass vulnerable to each predator would require evaluating each YOY and yearling model individual for each predator (i.e., nested loops). Instead, using the model individuals present on each day, we compute the biomass of YOY and yearling for each species that are vulnerable to an array of predator lengths of walleye and of northern pike. For each predator, we approximate the biomass vulnerable by using the values in the length category that includes the predator's length. To determine predation mortality on modeled individuals, we use the value of consumed biomass from the prey

length category that includes the prey's length. These biomass arrays by prey and predator length categories only have to be computed once daily, thereby requiring much less computation than nested loops. Results from simulations based on evaluating each predator and prey (nested loops) are indistinguishable from those obtained using 35 prey length categories (0 to 350 by 10 mm) and 30 predator length categories (40 to 640 by 20 mm).

## 5.0 Design of simulations

### *5.1 Overview*

Two sets of simulations were performed: calibration and biomanipulation. Calibration simulations involved the trial and error adjustment of selected parameter values until predicted population biomasses and mean lengths at age were similar to observed values for Lake Mendota. We determined two sets of calibrated parameter values that differed in the degree of interannual variation of population biomasses exhibited by the six species. We refer to these two alternative baseline simulations as the high and the low variability simulations.

Biomanipulation simulations involved comparing the effects on zooplankton of piscivore enhancement (via stocking and changes in fishing size limits) versus a cisco die-off, and evaluating the effectiveness of alternative stocking regimes. Piscivore enhancement versus cisco die-off simulations were performed with both of the two calibrated baseline versions. Stocking regime simulations were performed with the low variability simulation only. Piscivore enhancement mimicked the biomanipulation experiment performed in Lake Mendota (Kitchell 1992). A coincident cisco die-off also occurred greatly confounding interpretation of observed lake responses. We also used the model to assess whether low-level stocking or periodic higher stocking is more effective in achieving the long-term biomanipulation goal of increased zooplankton (and therefore reduced algae and improved water quality). Due to practical considerations, most field biomanipulations are imposed and responses monitored for only a few years (Carpenter et al. 1987; Carpenter and Kitchell 1993; Baca and Drenner 1995; Theiss et al. 1990).

All model simulations were for 100 years. Each simulation started with a specified number of age-2 individuals that roughly corresponded to long-term average abundances from previous simulations. Numbers at subsequent ages were computed from adult mortality rates. Lengths were assigned based on published lengths at age (Carlander 1977; Becker 1988). Weights were obtained from the length-weight relationships. Maturity was determined based on assigned lengths. The first 25 years of each simulation were ignored to eliminate any effects of arbitrary initial conditions. Calibration simulations involved no stocking or fishing size limit restrictions. Biomanipulation simulations used stocking levels and fishing size restrictions based on those imposed on Lake Mendota.

Reported adult biomasses are the total biomass of age-2 and older individuals on August 1. We use predicted growth of age-5 individuals of each species to represent adult growth in general. We use the term forage planktivores as shorthand for yellow perch, bluegill, and white bass. The more general term, planktivores, also includes cisco. Forage plankitivore species exhibited similar dynamics to each other and all were important forage for the piscivores. Cisco dynamics differed from the forage planktivores species. Stocked individuals are not included in YOY survival estimates, but are included in all subsequent survival estimates.

*5.2 Calibration: Baseline*

Values of larval mortality rates and K parameters were adjusted until model predictions satisfied several criteria. All other model parameters were maintained at their *a priori* specified values. Calibration criteria were: persistence of all six species for 100 years, average biomasses and mean lengths at age close to observed values (see data in Figure 7), and realistic diets by life stage. Persistence and diets were qualitative criteria. While we know roughly what each life stage of each species should be eating, rigorous comparison of predicted diets to reported diet data is not possible. We show August diets (based on biomass of prey eaten) for YOY juveniles, yearlings, and adults (represented by age-5), averaged over the simulation. August was generally the month of highest fish consumption rates. Biomasses and mean lengths were graphically compared to Lake Mendota data.

During model calibration we noticed two different general types of community dynamics. Some simulations exhibited high interannual variation in population biomasses while other simulations produced much less variable predictions of population biomasses. We therefore calibrated two versions of baseline conditions. We specified two values of zooplankton turnover rate for *D. pulicaria* in the epilimnion: 0.5/day for the low variability version and 0.9/day for the high variability version. For each of the zooplankton turnover rates, we determined values of larval mortality rates and K parameters that satisfied the calibration criteria. While a zooplankton turnover rate of 0.9/day is unrealistically high for Lake Mendota, the high variability simulation is of theoretical interest by permitting comparison of the effects of low versus high population variability on model responses.

*5.3 Calibration: Predation and Competition*

Correlation analysis was used to determine the strength of predatory and competitive interactions in the high variability baseline simulation. The high variability simulation was analyzed because it generated greater ranges of response variables, making detection of relationships easier. One set of variables consisted of larval, YOY juvenile, and yearling life stage survival (percent surviving the life stage), and adult (age-5) growth (mm/day). A second set of variables included the number entering the life stage (total, summed for piscivores, and for the species), and adult biomass (total, summed for piscivores, and for the species). Each variable in the first set was correlated with each variable in the second set. Values based on totals are reflective of planktivores who dominated population numbers and biomass. We used variables based on piscivores to isolate responses to this trophic level. We used variables based on same species to isolate intraspecific effects. All of the correlation analyses performed are listed in Table 3. For each species, we show six scatter plots corresponding to the relationship with the highest magnitude of correlation coefficient (r) for larval survival, adult growth, YOY juveniles survival with numbers entering and with adult biomass, and yearling survival with the numbers entering and with adult biomass.

Adult growth was analyzed because fecundity and maturation were size dependent. Growth effects of maturation and fecundity can influence population dynamics by affecting lifetime egg production of individuals. Egg, yolk-sac larval, and adult survival were not analyzed. Adult mortality was fixed, and egg and yolk-sac larval mortality depended only on temperature. We used egg production in correlation analysis of larval survival. Egg and yolk-sac mortality rates exhibited little interannual variation making egg production highly correlated to the number of first feeders. We did not examine any relationships between larval survival and adult biomass because larvae are not consumed by model fish.

*5.4 Biomanipulation: Piscivore Enhancement versus Cisco Die-off*

The results of the Kitchell (1992) biomanipulation of Lake Mendota were generally positive, although confounded by a cisco die-off. During 1987 to 1989, Lake Mendota was intensively stocked with walleye and northern pike, and fishing minimum length restrictions and harvest bag limits were imposed to further enhance piscivore populations. The idea was to initiate a trophic cascade in which enhanced piscivore populations would result in reduced planktivores, increased herbivorous zooplankton, and reduced summertime algal blooms. During and just after piscivore enhancement, zooplankton densities in the lake increased and there was a shift in the zooplankton community towards the larger *Daphnia pulicaria*, which is more effective at removing phytoplankton. As hypothesized, algal densities in Lake Mendota declined. However, during the biomanipulation period, almost 99% of the cisco in Lake Mendota unexpectedly died during the summer of 1987. How much of the zooplankton response was due to the intentional manipulation of the piscivores versus the unintended loss of a dominant planktivore is not known.

We performed six model simulations to separate the effects of piscivore enhancement from the cisco die-off. Piscivore enhancement and cisco die-off were imposed separately and together, for each of the two baseline versions of the model. Model predictions were compared to predictions from the corresponding baseline simulation. Cisco die-off was simulated by reducing cisco annual survival for YOY, yearlings, and adults to 1% for year 30 only. Piscivores were enhanced in simulations by stocking walleye and northern pike fingerlings and imposing fishing

size limits. We added 7.2 million 50-mm walleye and 3.1 million 50-mm northern pike on day 180 of years 30, 31, and 32. These values were based on average numbers of fish stocked during 1987-1989 in Lake Mendota. Both fry and fingerlings were actually stocked in Lake Mendota. We converted average numbers of fry stocked to equivalent numbers of fingerlings assuming a near-maximum estimated walleye survival rate (fry to 50 mm) of 30% (Mitzner, 1992) We assumed the same rate for northern pike, and introduced all northern pike fingerlings at 50 mm. Northern pike fingerlings stocked in Lake Mendota were 200-250 mm in length, but we had no estimates for survival from fry to 200mm. As was done in Lake Mendota, we imposed minimum size limits for fishing mortality of 813 mm for northern pike and 381 mm for walleye during years of stocking (years 30-32).

We report predicted annual species biomasses, planktivore biomass, and total zooplankton consumption over time. Total zooplankton consumption was used as an indicator of effects on water quality. Lowered zooplankton consumption would imply the biomanipulation was successful (i.e., more zooplankton and thus less algae).

To illustrate direct and indirect food web effects, we present percent changes in larval and YOY juvenile survival rates, by time period, for piscivore enhancement under the high variability simulation. Percent change was computed as $100*[(Y_E-Y_B)/Y_B]$, where $Y_E$ is the mean value for the piscivore enhancement and $Y_B$ is the mean value for the baseline simulation. Four time periods were used: years 30-33 (during the biomanipulation), years 33-39 (just after the biomanipulation), years 40-49 (somewhat after the biomanipulation), and years 75-100 (long after the biomanipulation). Enhancement should directly affect YOY survival of planktivores due to increased predation pressure, and directly affect YOY survival of piscivores due to stocking affecting competition and cannibalism. Two types of indirect responses are illustrated: changes in YOY juvenile survival in years after the enhancement and changes in larval survival. Larvae are not consumed by model fish and thus any larval survival response had to occur indirectly.

*5.5 Biomanipulation: Stocking Regime*

Three stocking regimes were evaluated for their long-term effects on total zooplankton consumption. Periodic stocking involved imposing the above stocking conditions for the first 3 years of every 10 year period beginning in year 30. Continuous stocking involved adding 1% (low level) or 10% (high level) of the above numbers of 50-mm walleye and northern pike every year between years 30 and 60. Periodic and continuous stocking were simulated using the low variability baseline version because this version was more similar to the conditions in Lake Mendota and exhibited more realistic responses to stocking. We report species biomasses over time, and compare total zooplankton consumption rates and mean adult (age-5) lengths of walleye and northern pike to baseline values.

## 6.0 Simulation results

*6.1 Calibration: Baseline*

All species persisted for the 100 years of both the low and high variability simulations (Figure 6). The major differences between the calibrated values of the two versions were that the low variability version had lower K values (more efficient feeding) of piscivores on model fish, lower bluegill larval mortality (0.12 vs 0.20/d), and higher white bass larval mortality (0.32 vs 0.28/d). The remaining values of calibrated parameters were identical or very similar between the two versions (Appendix 3).

Interannual variation in species biomasses differed between the two versions. Coefficients of variation of annual biomass in the low variability version were less than one-half those for high variability version for yellow perch, walleye, bluegill, and white bass (Table 4). There is indication of predator-prey cycles between the two piscivore species and the three forage planktivores species in the high variability version (Figure 6b). However, the complexity of multispecies food web interactions (multiple prey and multiple predators) results in more complex dynamics than simple single prey-single predator cycles. Cisco dynamics are largely uncoupled

from the other species in both versions. Cisco hatch earliest in the spring thereby experiencing little competition for zooplankton and do not come in direct contact with northern pike or walleye.

Predicted average biomasses and mean lengths at age were generally similar to observed values from Lake Mendota (Figure 7). The greatest discrepancies between predicted and observed values were: higher predicted white bass biomass than observed (Figure 7a), and shorter than observed predicted mean lengths of YOY walleye (Figure 7b) and yearling walleye (Figure 7c) and all life stages of northern pike (Figures 7b,c,d). Adult piscivore mean lengths were highly variable in model simulations, particularly in the high variability simulation. We calibrated parameter values to minimize unrealistically long fish during periods of fast growth, but this resulted in a lowering of the average length below observed means.

Predicted diets by life stage were realistic (Figure 8). Larvae of all species eat the smaller *D. galeata* (results not shown). YOY juveniles of planktivorous species consume zooplankton, starting on the smaller *D. galeata* as larvae and switching to the larger *D. pulicaria* by 45 mm (Figure 8a). Yellow perch also consume benthos by August of their first year. Yearlings and adults of these species continue to consume zooplankton or benthos. Piscivorous species also start on zooplankton, but eat benthos and forage fish by their first August and as yearlings. Adult piscivorous diets are dominated by YOY and yearling yellow perch and bluegill. While model fish should also play more of a role in yearling piscivore diets (Johnson et al, 1992), we were unable to find a combination of calibration parameter values that permitted consumption of mostly fish without eliminating model prey species. We therefore accepted a yearling walleye diet consisting mainly of benthos, and yearling northern pike diet consisting mainly of the forage fish.

*6.2 Calibration: Predation and Competition*

Larval survival depended on competition, yearling survival mostly on predation, and YOY juvenile survival was heavily influenced by both. This pattern was consistent for all species except cisco, whose survival and growth exhibited little dependence on the numbers entering or adult biomass.

Larval survival decreased with increasing numbers entering the life stage (Figure 9). As larvae are not consumed by model fish and all species eat zooplankton, the negative relationship indicates density-dependent growth leading to longer larval stage duration and higher larval mortality.

YOY juvenile survival decreased with increasing numbers entering the life stage (Figure 10) and with increasing adult piscivore biomass (Figure 11). Juvenile survival of white bass was either high or low, with no intermediate values of survival (Figures 10c and 11c). When juveniles and adult piscivore numbers were low, white bass survival was high, while when numbers were high white bass survival was low.

Yearling survival in all species except cisco was governed by predation. Yearling survival was only weakly related to numbers entering the life stage (Figure 12) implying competition was unimportant, except for bluegill (Figure 12b) who showed increasing survival with increasing numbers entering (depensatory mortality). Bluegill were a major prey species for the piscivores. Years of high entering yearlings swamped the predators, who require several years to exhibit a numerical response (increase their abundance), resulting in a positive relationship between yearling bluegill survival and the numbers entering. Yearling survival decreased with increasing adult piscivore biomass (Figure 13) indicating the importance of predatory interactions. Walleye, and to lesser extent northern pike, showed decreasing yearling survival with increasing adult piscivore biomass, implying significant cannibalism.

Adult (age-5) growth rates were density-dependent for the forage planktivores and positively related to the total number of entering yearlings for walleye and northern pike (Figure 14). As with survival, adult growth rate of cisco showed little dependence on numbers entering and white bass adult growth exhibited either high or low values. Adult growth rates of forage planktivores decreased with increasing total number of entering yearlings for yellow perch (Figure 14a) and with increasing adult biomass for bluegill (Figure 14b) and white bass (Figure 14c). Walleye and northern pike adult growth increased with the total number of yearling entering (Figures 14e and f). Yearling are a major prey item for the piscivores. YOY prey fish may be more abundant, but the larger size of yearlings makes them more important to piscivore growth.

*6.3 Biomanipulation: Piscivore Enhancement versus Cisco Die-off*

The long-term effects on species biomass of piscivore enhancement and the cisco die-off differed between the low and high variability simulations (Figure 15). Piscivore enhancement imposed on the low variability baseline simulation resulted in a temporary loss (but eventual complete recovery) of northern pike (Figure 15a), whereas piscivore enhancement imposed on the high variability simulation resulted in the permanent loss of walleye and its replacement by northern pike (Figure 15b). Average northern pike adult biomass for years 60 to 100 under the high variability simulation was more than twice that of the average walleye and northern pike combined biomass under baseline conditions. The switch from walleye to northern pike dominance under the high variability conditions resulted in bluegill becoming more abundant than yellow perch. Cisco die-off alone did not cause loss or dominance shifts in other species (Figures 15c and d) . When piscivore enhancement and the cisco die-off were both imposed, both walleye and northern pike recovered after temporary losses with the high variability simulation, whereas northern pike never recovered with the low variability simulation (Figures 15e and f).

Cisco die-off caused greater and more prolonged decreases in total zooplankton consumption than piscivore enhancement. Averaged planktivore biomass was lower under the cisco die-off than under piscivore enhancement for all but one time period after they were imposed for both the high and low variability versions (Figure 16). Piscivore enhancement alone caused a brief period (about 10 years) of reduced total zooplankton consumption, followed by a period of higher than baseline consumption ("overshoot"), eventually returning to baseline levels (Figures 17a and b). The long term average consumption (years 25-100) under enhancement alone was within 1% of baseline values for both the low and high variability versions. Cisco die-off alone produced an immediate reduction in total zooplankton consumption of about the same magnitude as that caused by piscivore enhancement, but with total zooplankton consumption returning very slowly to baseline levels (Figures 17c and d). The long term average consumption (years 25 -100) under cisco die-off was 175kg/ha compared to 250 kg/ha under baseline for the low variability version, and 200 kg/ha versus 275 kg/ha under the high variability version.

Yellow perch and cisco together were the dominant sources of zooplankton consumption. Cisco consumption accounted for 36% (and yellow perch 39%) of total zooplankton consumption under the low variability baseline simulation and 40% (and yellow perch 44%) under the high variability simulation. The remainder of zooplankton consumption was divided between bluegill (15% in the low variability; 7% in the high variability) and white bass (10% in the low variability, 9% in the high variability).

The combined effect of piscivore enhancement and cisco die-off appeared as the simple sum of their separate effects. Average planktivores biomass by time period (Figure 16) and total zooplankton consumption (Figures 17e and f) with both imposed was roughly the simple net effect of enhancement and cisco die-off separately. Compared to enhancement alone, including the cisco die-off resulted in much delayed northern pike recovery in the low variability version (Figures 15a versus 15e), and eventual walleye recovery in the high variability version (Figures 15b versus 15f).

Piscivore enhancement caused the expected direct effects (Figure 18a). The addition of walleye and northern pike YOY via stocking resulted in decreased survival of their YOY juveniles for years 30-32 (during the enhancement). YOY juvenile survival of piscivores was density-dependent under baseline conditions (Figures 10e and f). More piscivores from stocking and reduced fishing mortality also resulted in lowered YOY juvenile survival of forage planktivores for the periods during or just after the enhancement.

YOY juvenile and larval survival illustrate how predative and competitive interactions caused complex indirect responses. YOY survival of yellow perch, bluegill, and northern pike (walleye went extinct) exhibited an "overshoot" response. After initially decreasing just after enhancement, YOY juvenile survival of these three species increased above baseline levels during years 40-50, before eventually returning to near baseline levels (Figure 18a). Larval survival of yellow perch, bluegill, and white bass increased in the period just after piscivore enhancement (years 33-39), while larval survival of walleye and northern pike decreased during the years of enhancement (Figure 18b). Changes in larval survival are necessarily indirect responses, as piscivore enhancement did not directly affect larvae.

*6.4 Biomanipulation: Stocking Regime*

None of the three stocking regimes analyzed yielded ideal management results. Stocking either had little affect on zooplankton consumption or resulted in significant changes in piscivore mean lengths or in the fish community. Periodic stocking caused repeated periods of higher than baseline total zooplankton consumption (Figure 19a) because of altered predator-prey cycles (Figure 19b). Continuous low level stocking had little affect on total zooplankton consumption (Figure 19c), despite enhanced northern pike (Figure 19d). Continuous high level stocking resulted in the desired lowered zooplankton consumption for the 30 years of stocking (Figure 19e), but also resulted in the loss of northern pike once stocking was terminated (Figure 19f). Model predicted mean lengths of adult walleye and northern pike under the stocking regimes (Table 5) varied more than in Lake Mendota, so some caution is appropriate in their interpretation and results are only suggestive of potential problems. Northern pike mean lengths under periodic stocking exhibited much greater variation year to year than under baseline conditions. Both walleye and northern pike adult mean lengths were much shorter than baseline under continuous high level stocking. As continuous low level stocking had small effects, adult mean lengths were similar between continuous low level stocking and baseline.

**7.0 Discussion**

Our results demonstrate the importance of considering multispecies interactions in fish population dynamics models. Competitive and predative interactions in the model led to density-dependent growth (Figures 9, 10, 14), to both compensatory and depensatory mortality (Figure 11), and to complex direct and indirect food web-mediated responses to piscivore enhancement (Figure 18). Many ecological assessments involving fish focus on the population-level for pragmatic reasons. Empirical information is often collected on a specific population, and there is great uncertainty in quantifying the many possible interspecific interactions that could be important in fish communities. Greater consideration of multispecies interactions will improve predictions of fish population dynamics, and perhaps can help explain some of unanticipated responses in nature that periodically surprise us.

Density-dependent growth was shown to influence population dynamics. Even though larval mortality rate was fixed, density-dependent growth still led to density-dependent survival (Figure 9) by prolonging the larval stage under low food conditions. Growth also affected predation mortality of YOY juveniles by determining their vulnerability to their gape-limited predators. Density-dependent adult growth (Figure 14) affected age at maturation and fecundity, which determined lifetime egg production. The implications of variation in adult mean lengths on maturity and fecundity varied by species. For example, in the high variability baseline simulation, percent mature and fecundity of age-5 walleye increased from 0% maturity and 15413 eggs/female for the 10 years of shortest adult mean lengths to 100% maturity and 19750 eggs/female for the 10 years of longest mean lengths. At the other extreme, bluegill and white bass were always mature by age-2 based on their length, and their fecundity increased by <4% between the 10 years of shortest and longest adult mean lengths.

Cisco dynamics were essentially independent of the other species (Figure 6), and were sensitive to abiotic conditions. Cisco was spatially isolated entirely from piscivore predation, and partially from planktivore competition. Cisco are squeezed into a small compartment and forced into warmer epilimnion waters as the hypolimnion becomes anoxic each year. In baseline simulations where the duration of hypolimnion anoxia was 30 days shorter or longer, cisco declined over 100 years to near or complete extinction. Stein et al. (1995) found that the presence of gizzard shad, which is controlled neither by predators nor by zooplankton, effectively nullified any top-down cascade effect in food webs. As an independently controlled, dominant planktivore, cisco may play a similar role in Lake Mendota.

Our results suggest that the cisco die-off that occurred concurrently with the piscivore enhancement played a major role in the increased zooplankton abundances observed in Lake Mendota. In model simulations, the short term effect of the cisco die-off was at least equal to that of the piscivore enhancement, and the long-term effect of the cisco die-off was greater than that of the enhancement (Figure 17). Because cisco was unaffected by piscivores, it remained as a major source of zooplankton mortality, even when other planktivores were suppressed.

Our results suggest that the long-term effects of biomanipulations should be considered. Piscivore enhancement was able to decrease zooplankton consumption during, or immediately following, the enhancement, but was followed by a period of increased consumption (Figure 19). Neither periodic nor continuous stocking generated the desired responses in the long-term without also affecting some other aspect of the system. Stocking either had little effect on zooplankton consumption or resulted in significant changes in piscivore mean lengths or in the composition of the fish community (Figure 19; Table 5).

White bass dynamics differed from the other species in exhibiting only high or low values of growth and survival (Figure 10). White bass dynamics was characterized by episodic year class failures in the yearling life stage. These year class failures correspond to years of low YOY and yearling bluegill abundance, and high walleye adult biomass leading to extremely high predation pressure on white bass yearlings. In the high variability baseline simulation, mean YOY and yearling bluegill abundances were 1667 YOY/ha and 750 yearling/ha in the 8 years of year class failure compared to 2140 YOY/ha and 1123 yearling/ha in the remaining years. Adult walleye biomass was 44% higher (4.70 kg/ha versus 3.27 kg/ha) in years of white bass year class failure compared to the remaining years. Adult white bass growth was higher than average during the 3 years following each of the year class failures (mean age-5 growth rate of .11 mm/day versus .03 mm/day in remaining years).

The two alternative baseline calibrations resulted in qualitatively different long term responses to the imposed perturbations. Under piscivore enhancement and the cisco die-off, the low variability simulation returned to its original dynamics more quickly than the high variability simulation, which exhibited extreme fluctuations from baseline (Figure 15). These fluctuations in the high variability simulation were sufficient to result in walleye extinction and its replacement by northern pike under piscivore enhancement. The higher *Daphnia* turnover rates and lower predator effectiveness characteristic of the high variability calibration resulted in faster planktivore numerical response rates and slower piscivore numerical response rates. The greater difference between prey and predator response rates increased the time lags of predator responses and

resulted in increased variability. Time lags in predator responses increases variability in predator-prey interactions (Murdoch and Bence 1987).

The growth and consumption processes could be considered the strongest aspects of the model, while movement and reproduction are likely the weakest. Feeding is represented with the functional response approach based on vulnerabilities and predator-prey size ratios. Size-based interactions are relatively straightforward to implement in an individual-based approach. Cannibalism was easily included by treating YOY and yearling of all species as potential prey. The main weakness in the feeding model is that active selective behavior by predators and avoidance by prey were not considered. Predators are assumed to forage essentially at random. The constant parameter disc equation does not allow for adaptive variation in foraging time or prey selection, and often yields poor predictions to altered situations (Abrams 1990). Future model development should consider how to include adaptive foraging behavior. Perhaps the weakest processes in the model are reproduction and movement. Both are represented as relatively invariant processes. Movement is independent of prey availability and predation risks, and the only population feedbacks on reproduction are via predicted lengths of adults. We do not simulate density-dependent effects on movement, maturity, or fecundity. In reality, fish make decisions about whether to move and how much energy to allocate to reproduction dependent on the state of the system (Tyler and Rose 1997; Van Winkle et al . 1996).

We have demonstrated many relationships which argue against looking at populations in isolation, but how much complexity is required? Our decision to represent the six species was based on their importance in Lake Mendota or their potential importance to realistically simulating the biomanipulation experiment and cisco die-off. At minimum, we needed to include yellow perch, walleye, and cisco. Northern pike, though less numerous, was an important target species in the piscivore enhancement effort, and proved in simulations to be capable of replacing walleye as the dominant piscivore. Bluegill was only a minor consumer of zooplankton, yet it was a major food source for the two piscivores. White bass was included because, following the biomanipulation experiment in Lake Mendota, white bass emerged as an important planktivore (Johnson and Kitchell, 1996). Thus, all six species had good reasons to be included, and some

argument could probably be made for including more species. In our judgement, the inclusion of the six species enabled realistic simulation of the major features of the Lake Mendota fish community and biomanipulation experiment, while still being tractable and computationally feasible.

A second aspect of model complexity is the number of calibrated parameters. Even though we only calibrated K values and larval mortality rates, model calibration of the 6 species version involved trial and error adjustment of a total of 91 parameters. With so many degrees of freedom, how do we know when our results are robust or merely an artifact of a particular calibration set? Use of objective calibration methods, such as Monte Carlo filtering (Rose et al. 1991), are possible for complex, nonlinear models but require hundreds of simulations to be effective. In this paper, we addressed the uniqueness issue with ad hoc calibration by presenting the results from two alternative calibrations that differed in their dynamics. Model predictions which agree between calibration versions are less likely to be artifacts. This is only a partial solution to the calibration problem which has always plagued complex models.

We have described a general fish community simulator applied to a six species model for Lake Mendota. We constructed the model to be readily adaptable to other systems. Rose et al. (in review) used an earlier version of the model to simulate yellow perch-walleye dynamics in Oneida Lake. A version of the six species model presented here is being modified to simulate the effects of ruffe introduction on yellow perch and walleye. We have recently configured several alternative food webs from the simulator as subsets of the six species model. We next plan on employing these alternative food webs to compare population responses to global change scenarios.

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# Appendix 1:

# Tables and Figures for Part 2

Table 1. Alternative formulations (equation sets) of the temperature effect on metabolism and maximum consumption used for the six species in the model.

| Equation Set | f(T) | A |
|---|---|---|
| 1 | $e^{RQ*T}$<br><br>RQ is the Q10 value | $RK1*W^{RK4}*e^{(RTO-RTM*T)}$<br><br>RTO is the optimal temperature<br>RTM is the maximum temperature<br>ACT is the activity multiplier<br>RK1 is the multiplier of weight<br>RK4 is the exponent of weight |
| 2 | $V^x * e^{x(1-V)}$<br>*where*:<br>$V = \frac{RTM - T}{RTM - RTO}$<br>$X = \frac{Z^2(1+\sqrt{1+40/Y})^2}{400}$<br>$Z = \ln(RTQ)*(RTM - RTO)$<br>$Y = \ln(RTQ)*(RTM - RTO + 2)$<br><br>RTM is the maximum temperature<br>RTO is the optimal temperature<br>RTQ is the Q10 value | $A = ACT$<br><br>ACT is the activity multiplier |
| 3 | $e^{RQ*T}$<br><br>RQ is the Q10 value | $A = ACT$<br><br>ACT is the activity multiplier |

Table 2. Predator-prey interactions according to the vulnerability values used in the model. A vulnerability value of zero indicates prey were not eaten by that predator. A value of one indicates the prey could be eaten by that predator and is shown with the + symbol.

| species | size class | Prey type | | | | |
|---|---|---|---|---|---|---|
| | | *D. galeata* | *D. pulicaria* | benthos | forage fish | model fish* |
| Yellow perch | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | | |
| | yearling | | + | | | |
| | Age 2+ | | + | | | |
| Walleye | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | + | |
| | yearling | | | + | + | + |
| | Age 2+ | | | | + | + |
| Northern pike | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | + | |
| | yearling | | | | + | + |
| | Age 2+ | | | | + | + |
| Bluegill | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | | |
| | yearling | | + | + | | |
| | Age 2+ | | + | + | | |
| White bass | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | | |
| | yearling | | + | | | |
| | Age 2+ | | + | | | |
| Cisco | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | | | |
| | yearling | | + | | | |
| | Age 2+ | | + | | | |

* Model fish includes age 0,1 yellow perch 20 < L < 150, age 0, 1 walleye L>20, age 0,1 northern pike L>20, age 0,1 bluegill L>20, and age 0,1 white bass 20 < L < 135. Cisco, Larvae < 20mm, age 1 yellow perch L>150, and age 1 white bass L>135 do not overlap spatially with piscivores. Age 1 northern pike are generally beyond the gape size of all but the largest predators.

Table 3. Variables used in correlation analyses performed to compare the importance of predatory and competitive interactions in the high variability baseline simulation. T=total over all species, P=total for piscivores, S=total for species. Total (T) is reflective of planktivores who dominate over piscivores in abundance and biomass.

| Survival and Growth | Correlated With: | |
|---|---|---|
| | Variable | Metric |
| Larval survival | Egg production | T, S |
| Juvenile survival | Number of juveniles entering | T, P, S |
| | Adult biomass | T, P, S |
| Yearling survival | Number of yearlings entering | T, P, S |
| | Adult biomass | T, P, S |
| Adult growth | Number of juveniles entering | T, P, S |
| | Number of yearlings entering | T, P, S |
| | Adult biomass | T, P, S |

Table 4. Coefficients of variation (CV, %) of adult (age-2 and older) biomass of each species for the low and high variability baseline simulations. CVs were computed using annual values for years 25 to 100.

| Species | Baseline Simulation | |
|---|---|---|
| | Low variability | High variability |
| Yellow perch | 9.9 | 24 |
| Walleye | 18 | 42 |
| Northern pike | 31 | 38 |
| Bluegill | 12 | 52 |
| White bass | 30 | 9.0 |
| Cisco | 11 | 13 |
| Total | 6.7 | 14 |

Table 5. Mean (mm) and CVs (%) of mean length of age-5 adults of each species for the high variability baseline, periodic, and continuous stocking simulations. Means and CVs were computed for annual values for years 30 to 60.

| Species | Baseline | | Stocking | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Periodic | | Continuous high | | Continuous low | |
| | mean | CV | mean | CV | mean | CV | mean | CV |
| walleye | 452 | 8.9 | 435 | 21 | 329 | 17 | 410 | 9.0 |
| northern pike | 790 | 9.0 | 578 | 65 | 258 | 91 | 572 | 19 |

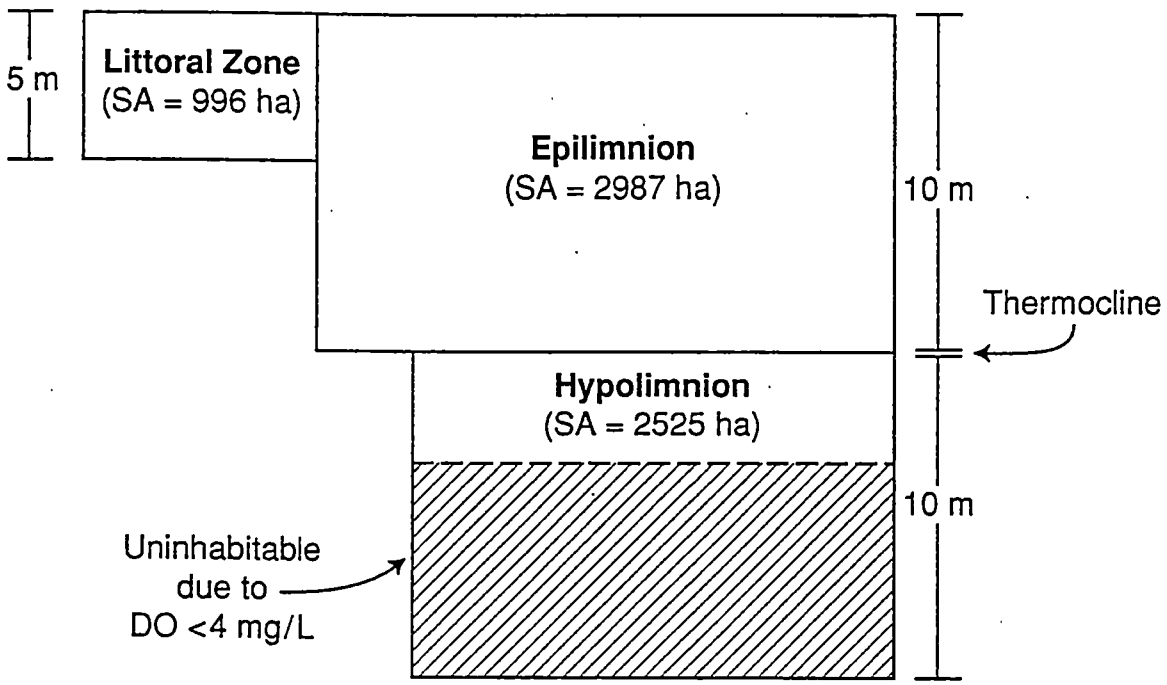


Figure 1. Model compartmentalization of Lake Mendota into epilimnion, hypolimnion, and littoral zones. The region of hypolimnion that becomes uninhabitable due to DO< 4 mg/L varies with day in the simulation.

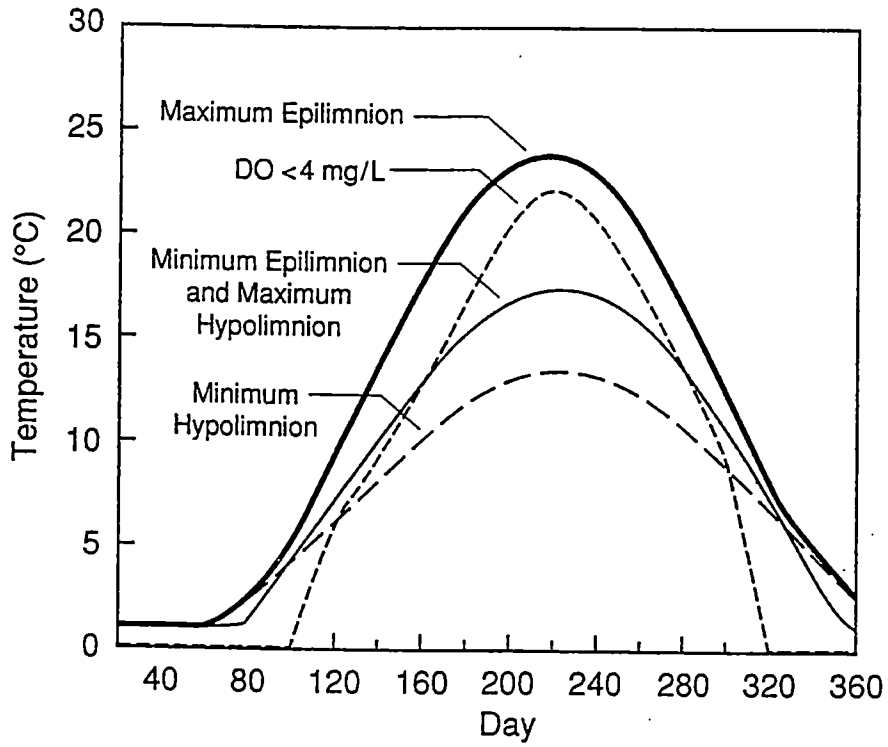


Figure 2. Maximum and minimum daily water temperatures and the temperature at which DO is <4 mg/L. Maximum and minimum water temperatures curves were generated from equation (1) using regression coefficients estimated from Lake Mendota data; the temperature at which DO<4 mg/L was generated by a function fit to Lake Mendota data.

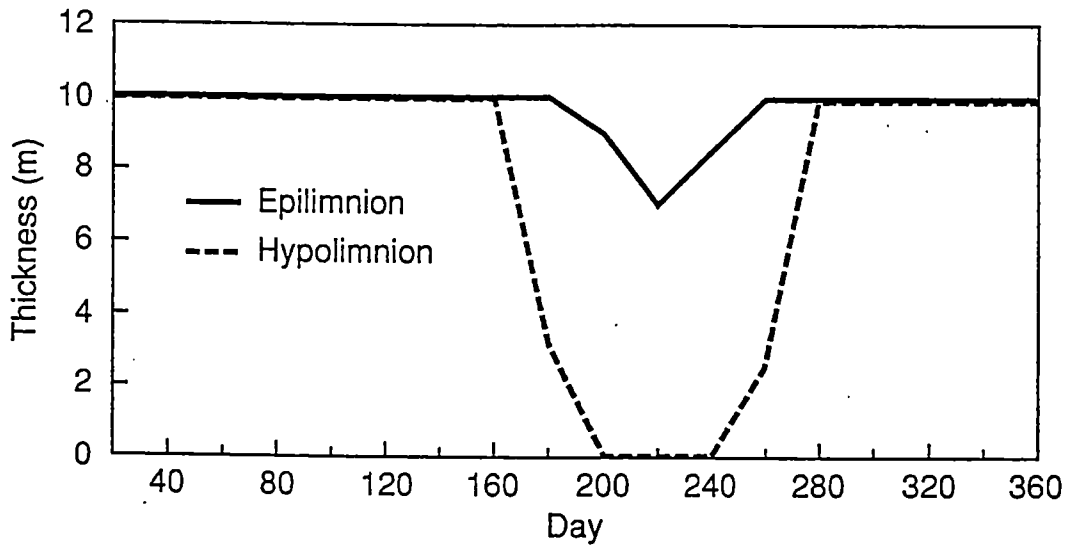


Figure 3. Thicknesses of the hypolimnion and epilimnion due to dissolved oxygen falling below 4 mg/L.

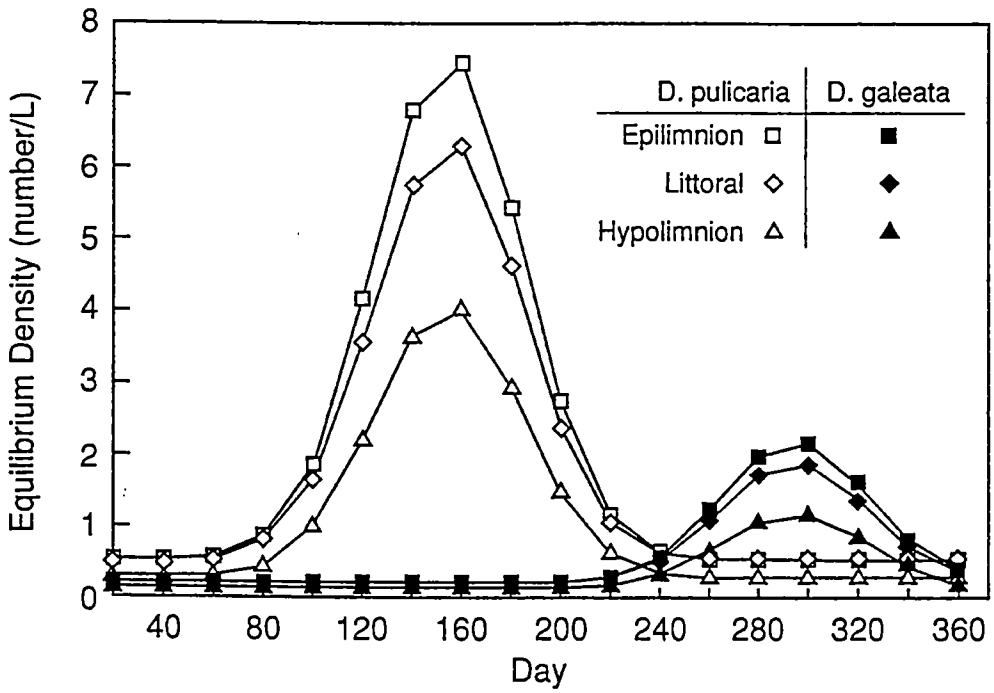


Figure 4. Equilibrium densities of *Daphnia pulicaria* and *Daphnia galeata* with day of year for each model compartment. Curves shown are generated from functions fit to Lake Mendota data.

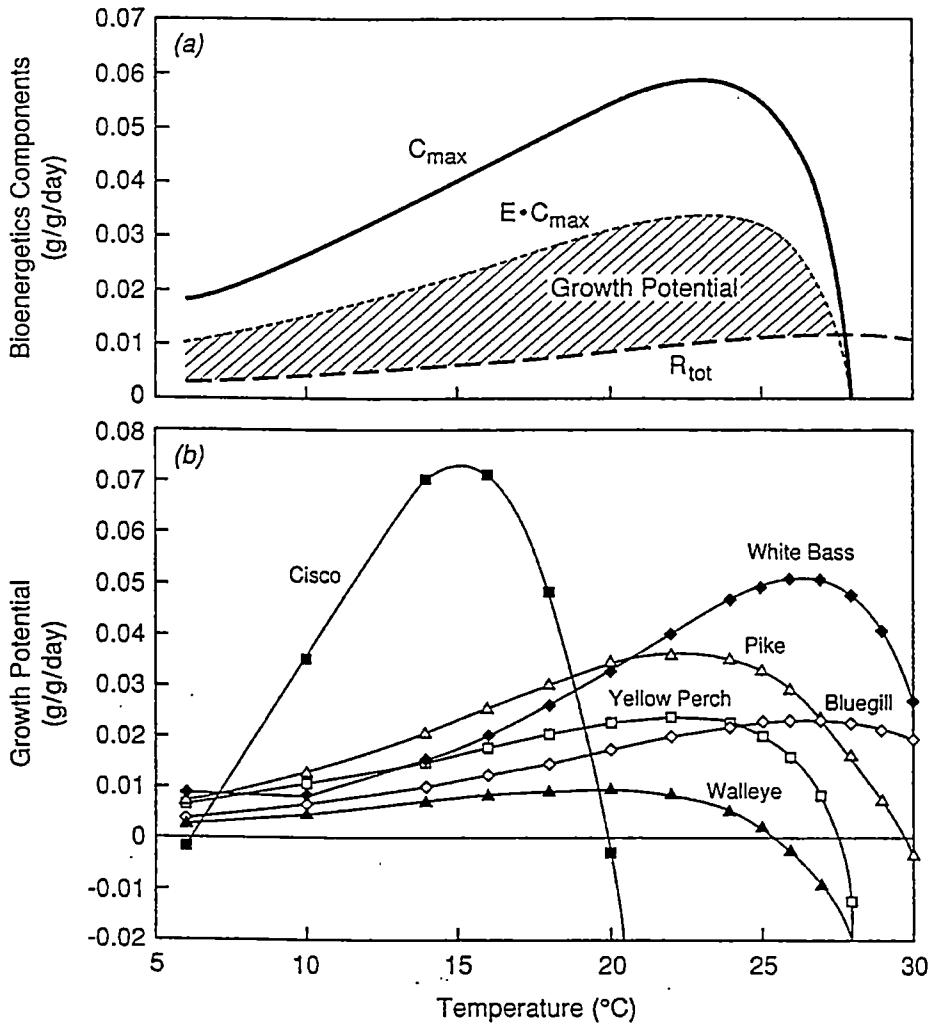


Figure 5. Bioenergetics components and growth potentials for typical sized age-5 adults. (a) yellow perch maximum consumption, metabolism, and growth potential, (b) growth potentials of all six species.

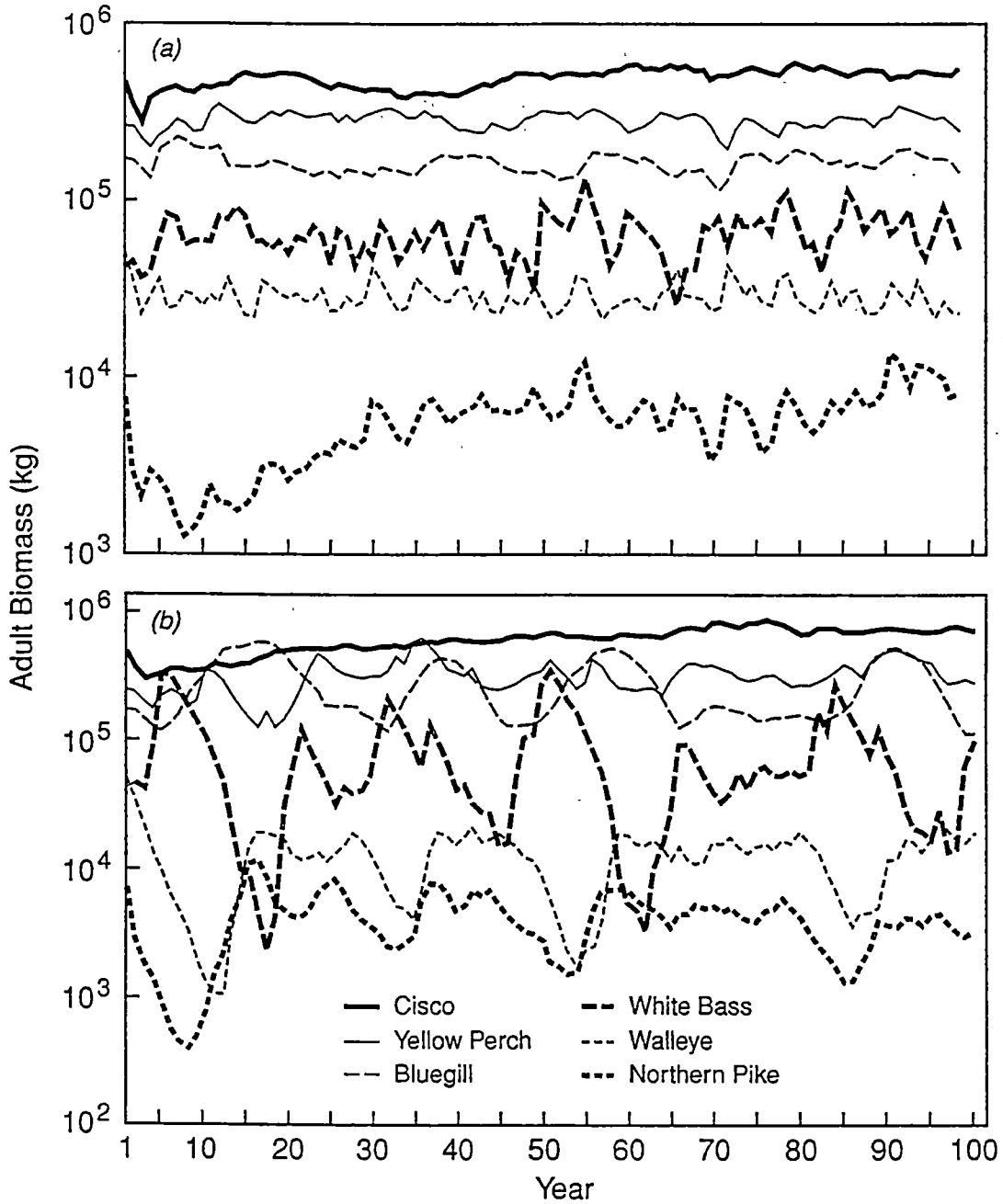


Figure 6. Annual adult biomass of each of the six modeled fish species under baseline conditions. (a) low variability calibration, (b) high variability calibration.

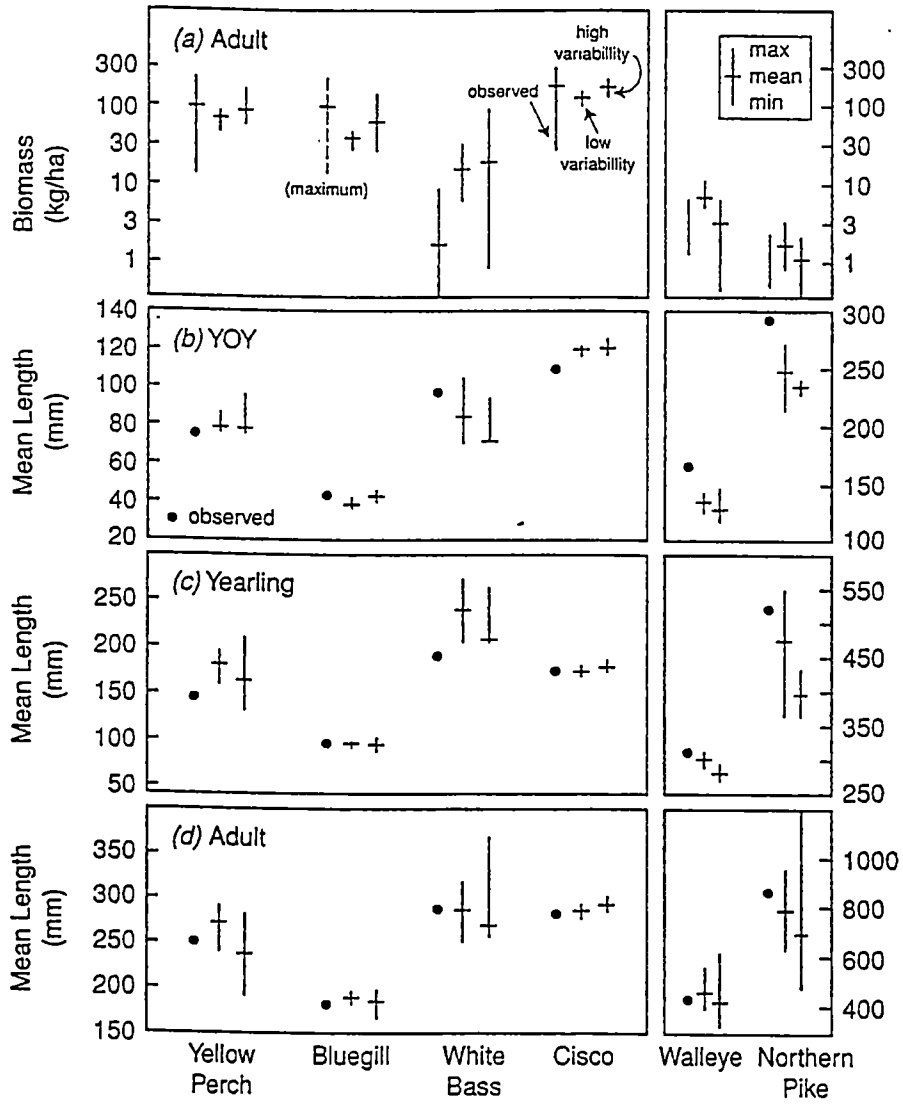


Figure 7. Predicted and observed minimum, mean, and maximum biomass and mean lengths. (a) adult biomass, (b) YOY mean lengths, (c) yearling mean lengths, (d) adult (age-5) mean lengths. Predicted values are shown for the low and high variability baseline simulations. Observed values of bluegill biomass are assumed the same as yellow perch based on their similar relative densities in field samples.

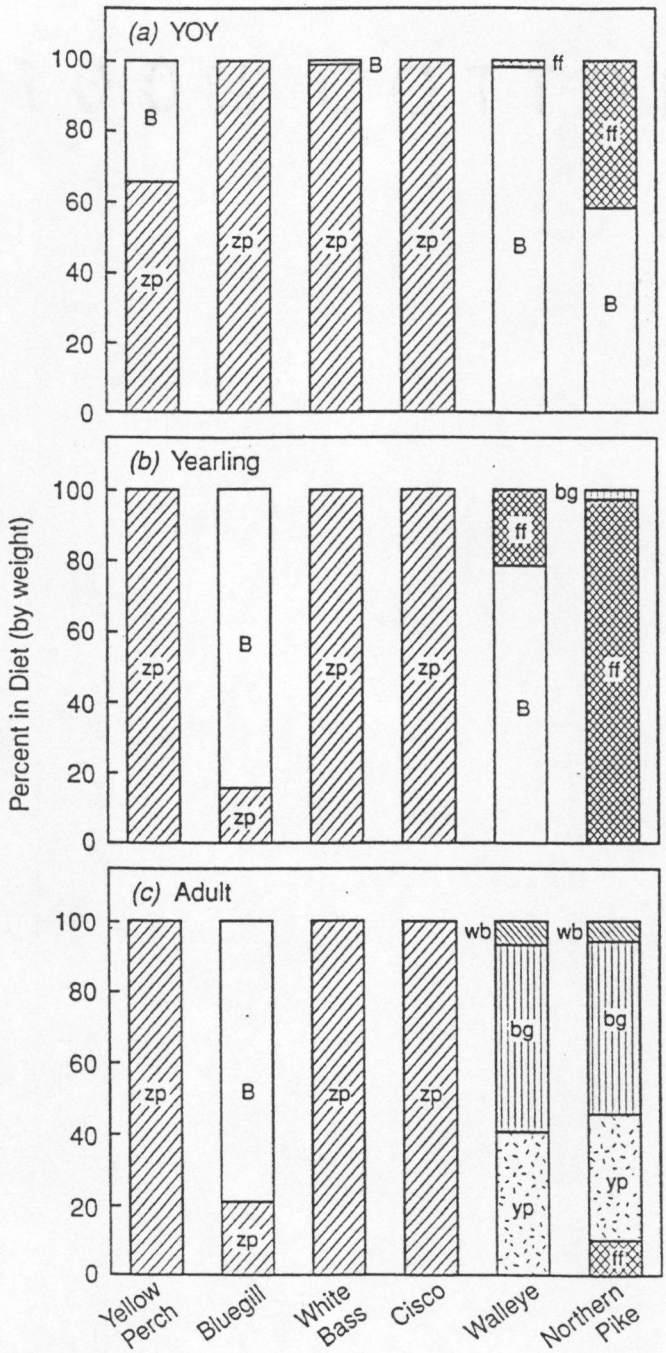


Figure 8. Predicted averaged August diets by life stage for each of the six modeled fish species from the high variability baseline simulation. (a) YOY juveniles, (b) yearlings, (c) adults (age-5).

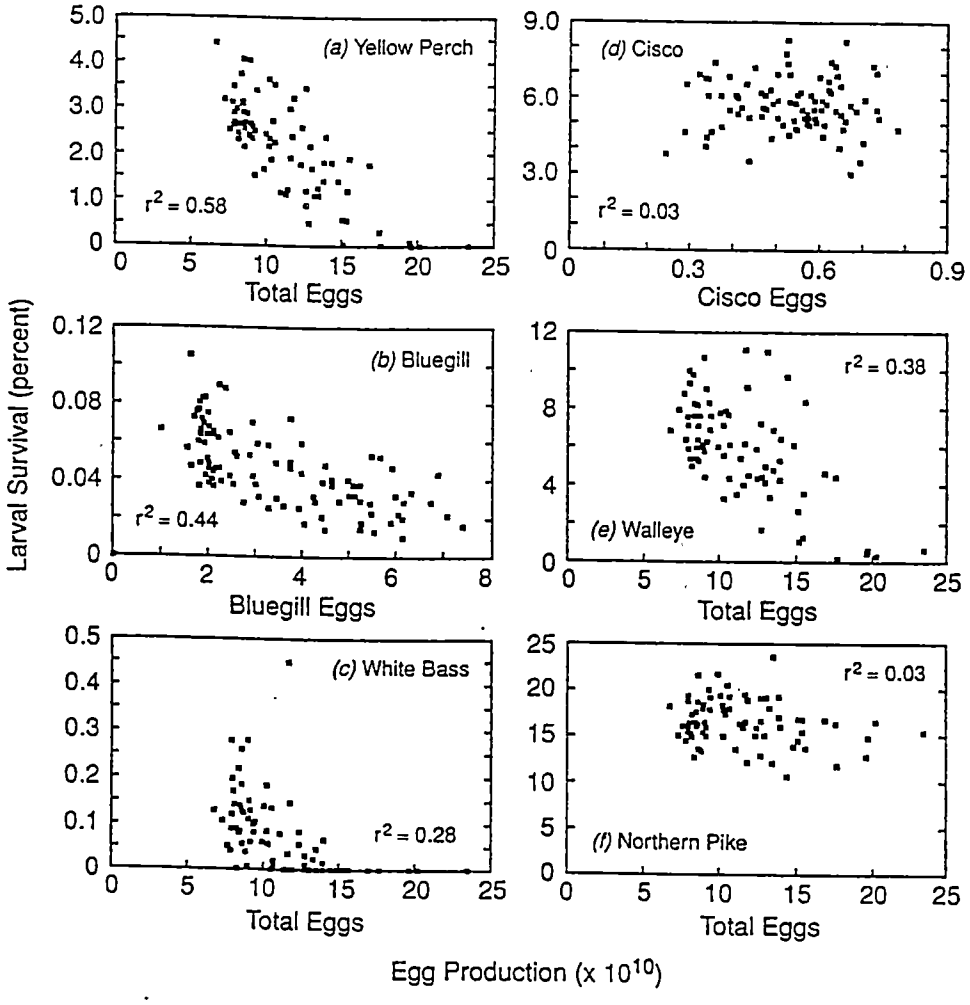


Figure 9. Scatter plots of annual average values of larval survival versus egg production from the high variability baseline simulation. The measure of egg production is noted on the x-axis of each plot. (a) yellow perch, (b) bluegill, (c) white bass, (d) cisco, (e) walleye, (f) northern pike.

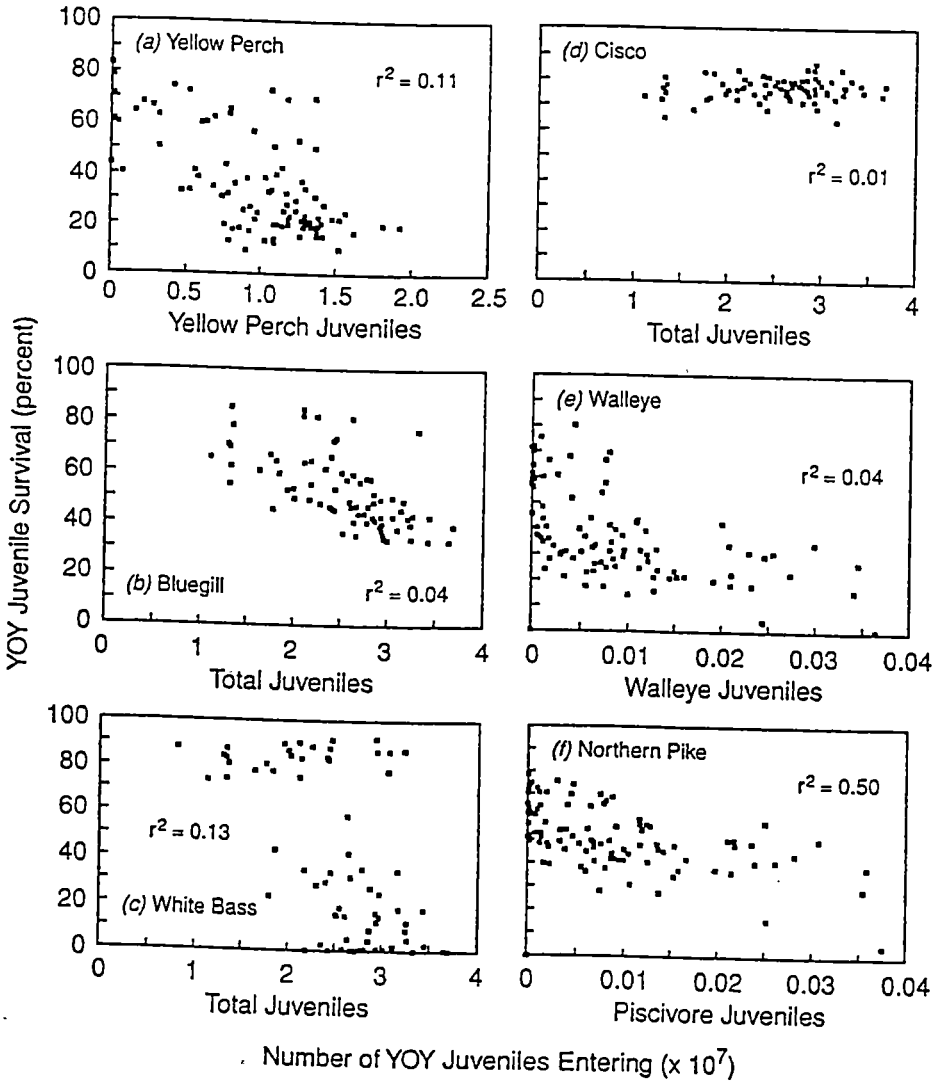


Figure 10. Scatter plots of annual average values of YOY juvenile survival versus the number of YOY juveniles entering from the high variability baseline simulation. The measure of the number YOY juveniles entering is noted on the x-axis of each plot. (a) yellow perch, (b) bluegill, (c) white bass, (d) cisco, (e) walleye, (f) northern pike.

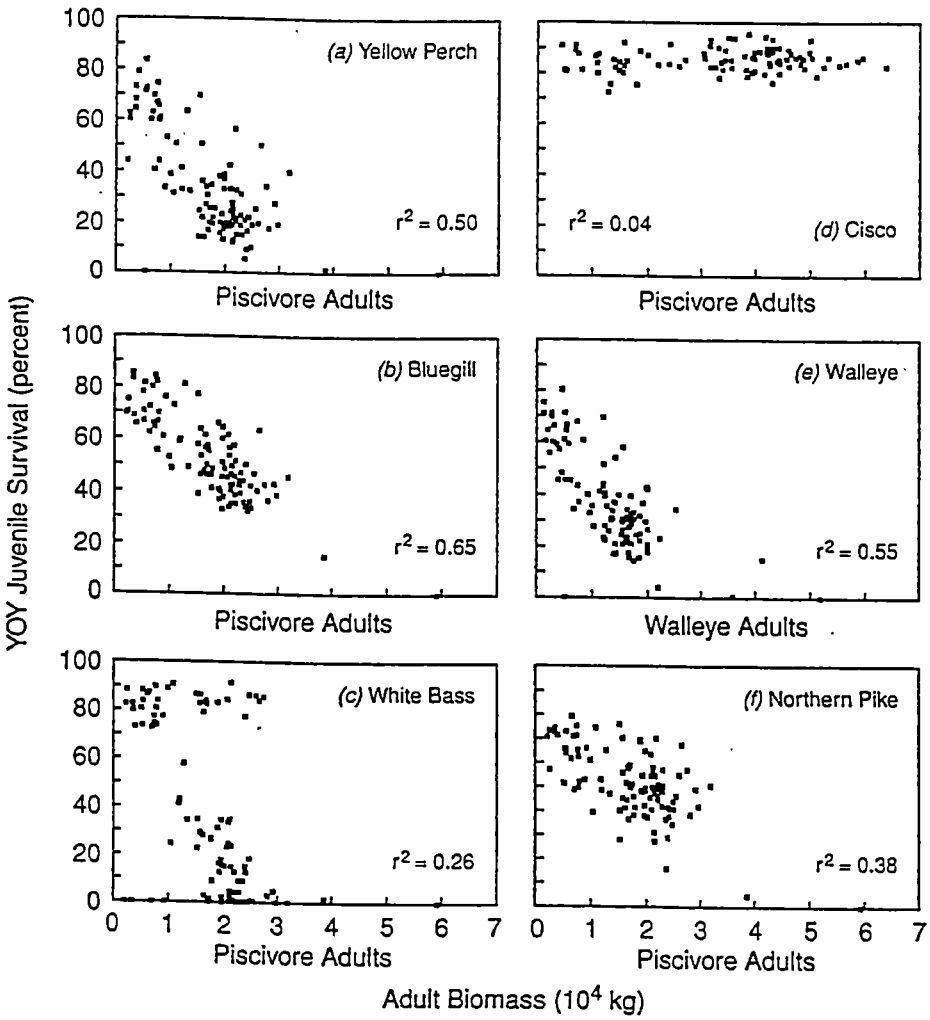


Figure 11. Scatter plots of annual average values of YOY juvenile survival versus adult biomass from the high variability baseline simulation. The measure of adult biomass is noted on the x-axis of each plot. (a) yellow perch, (b) bluegill, (c) white bass, (d) cisco, (e) walleye, (f) northern pike.

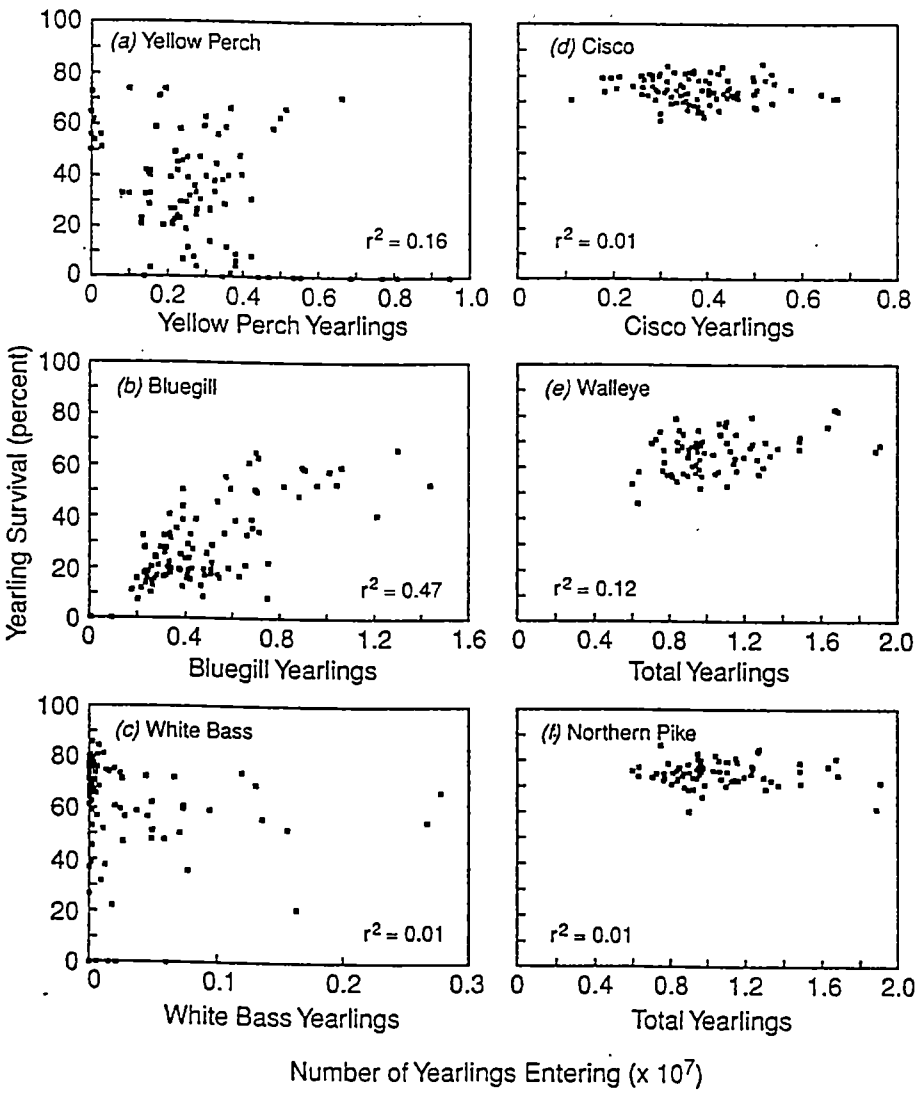


Figure 12. Scatter plots of annual average values of yearling survival versus number of yearlings entering from the high variability baseline simulation. The measure of the number of yearlings entering is noted on the x-axis of each plot. (a) yellow perch, (b) bluegill, (c) white bass, (d) cisco, (e) walleye, (f) northern pike.

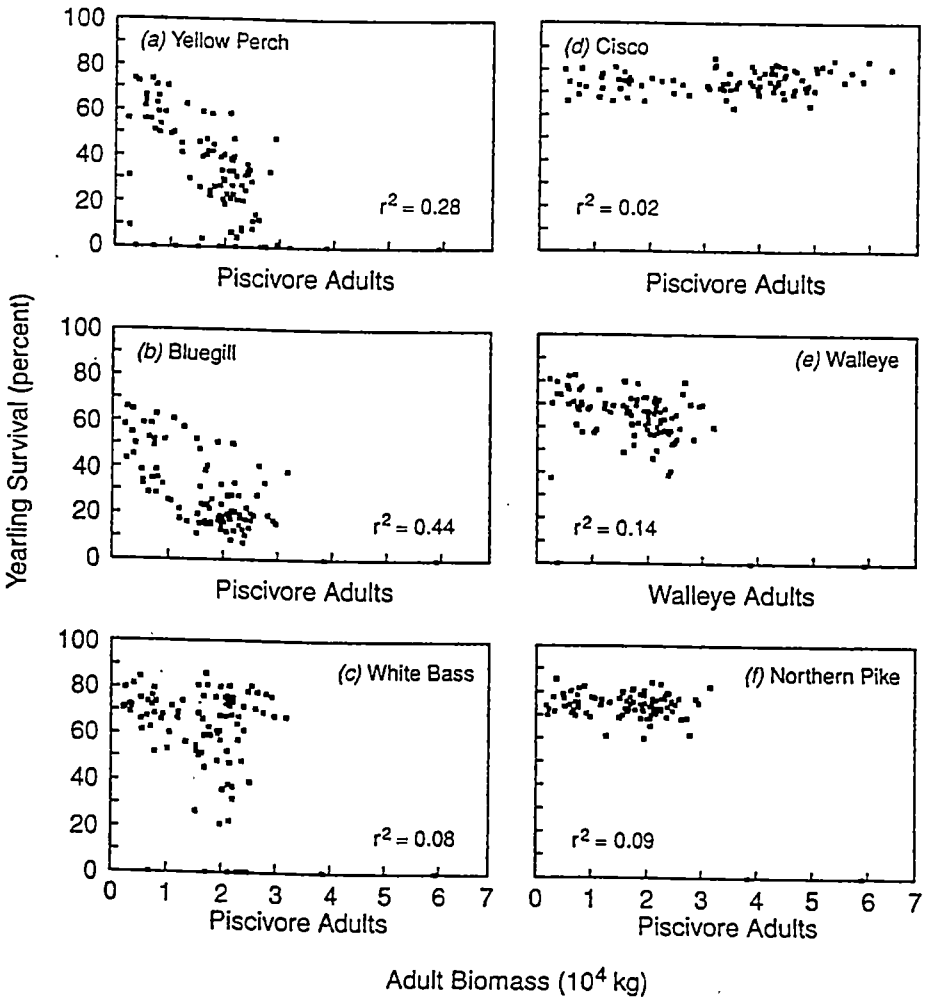


Figure 13. Scatter plots of annual average values of yearling survival versus adult biomass from the high variability baseline simulation. The measure of adult biomass is noted on the x-axis of each plot. (a) yellow perch, (b) bluegill, (c) white bass, (d) cisco, (e) walleye, (f) northern pike.

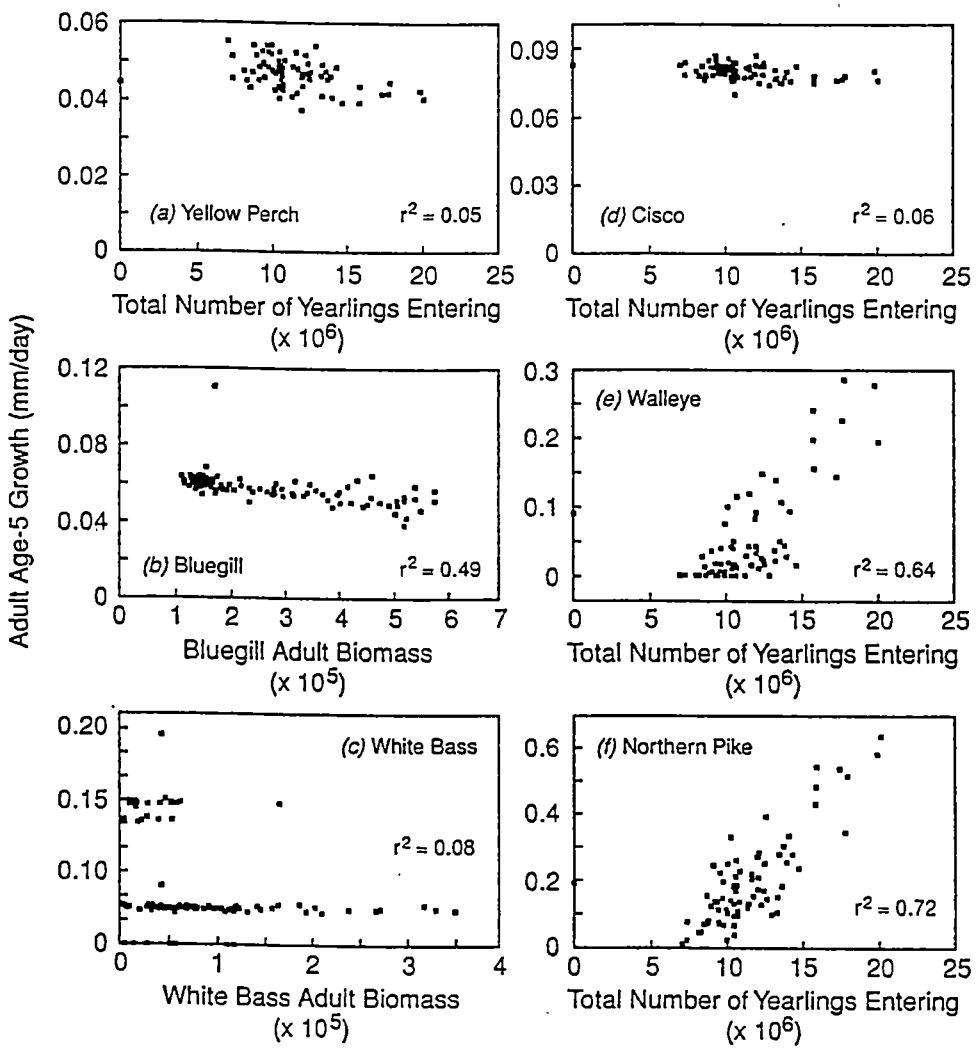


Figure 14. Scatter plots of annual average values of adult growth rate versus either the total number of yearlings entering or adult biomass from the high variability baseline simulation. Adult biomass is based on individual species for bluegill and white bass. (a) yellow perch, (b) bluegill, (c) white bass, (d) cisco, (e) walleye, (f) northern pike.

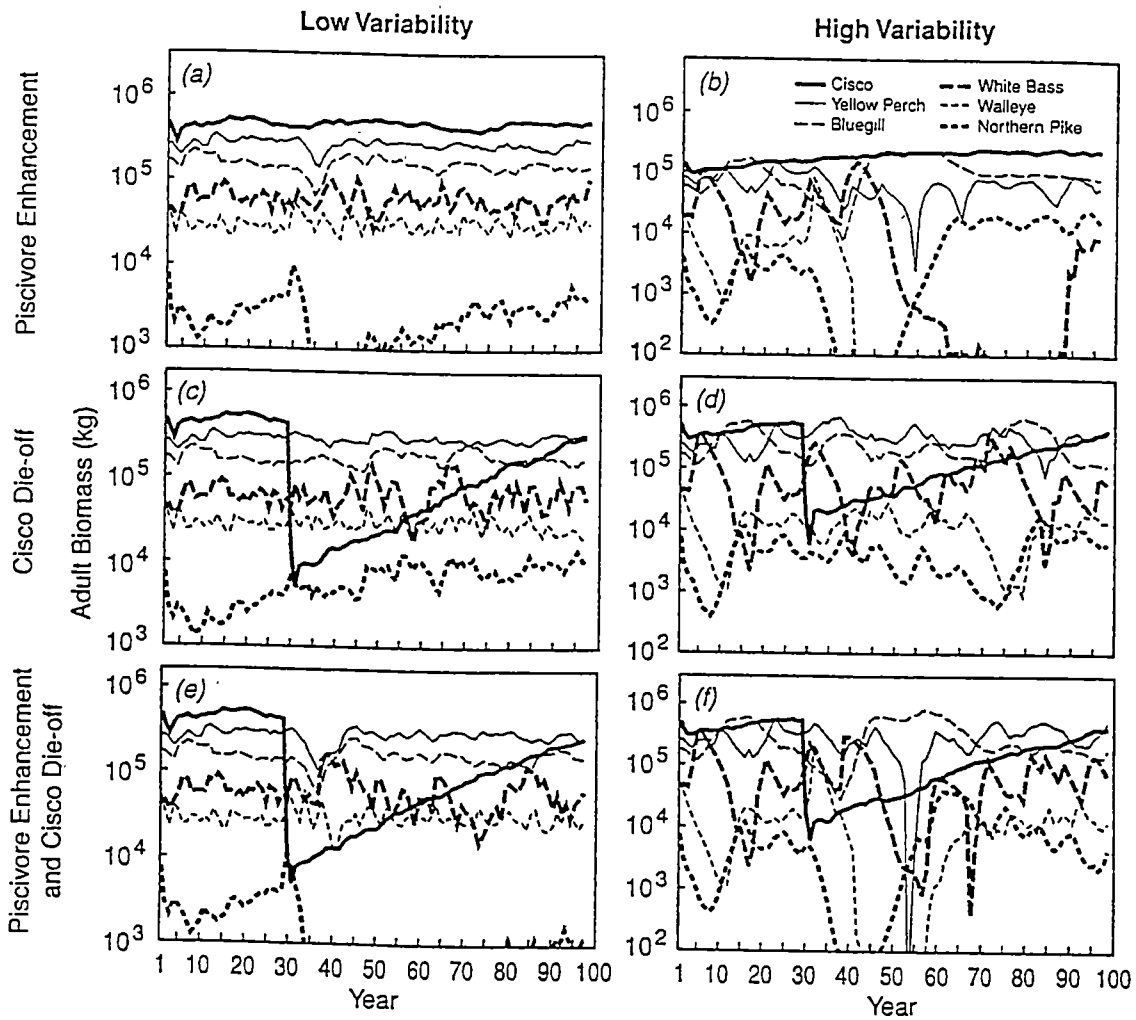


Figure 15. Annual biomass of each of the six modeled fish species for the six combinations of piscivore enhancement alone, cisco die-off alone, and enhancement and cisco die-off imposed on the low variability and high variability baseline conditions.

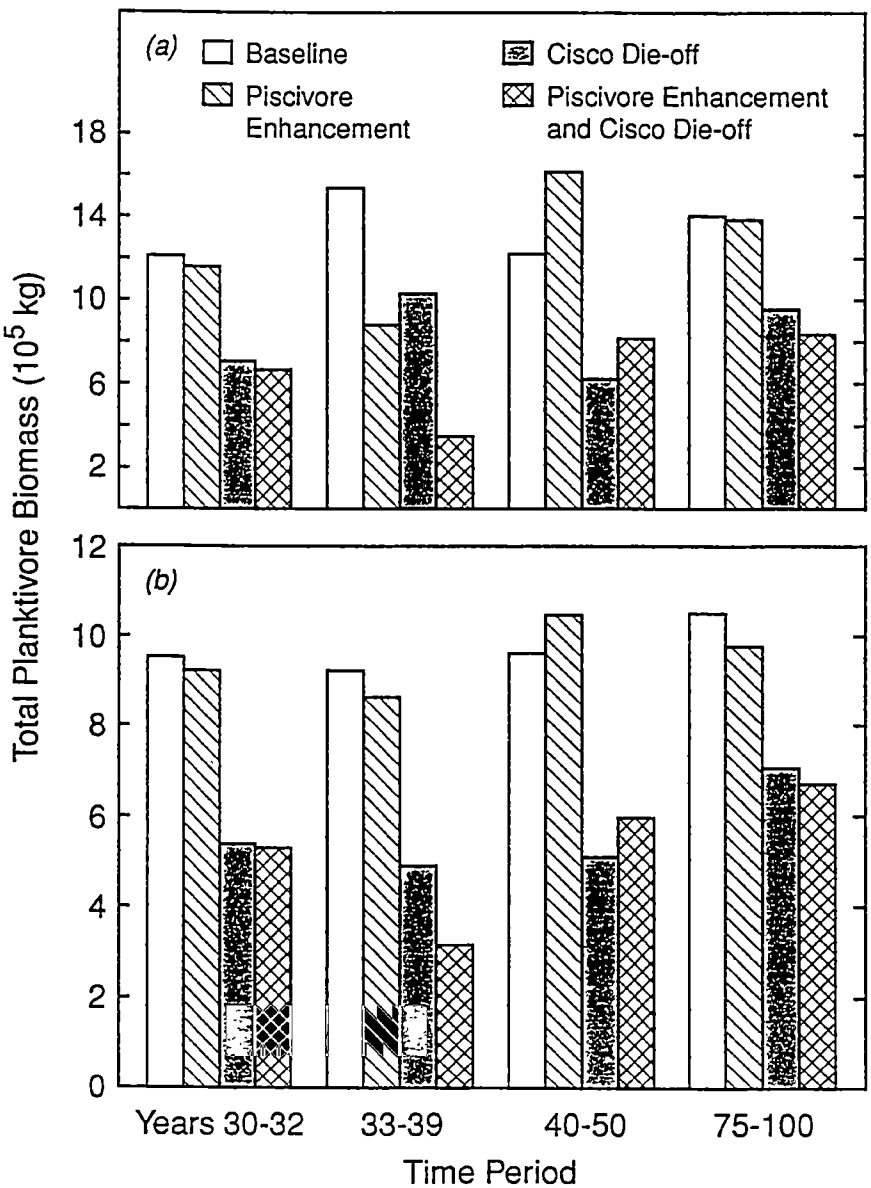


Figure 16. Average planktivore biomass by time period under baseline, piscivore enhancement alone, cisco die-off alone, and enhancement and cisco die-off together. Years 30-32 correspond to the period of enhancement; cisco die-off was imposed in year 30. (a) low variability, (b) high variability

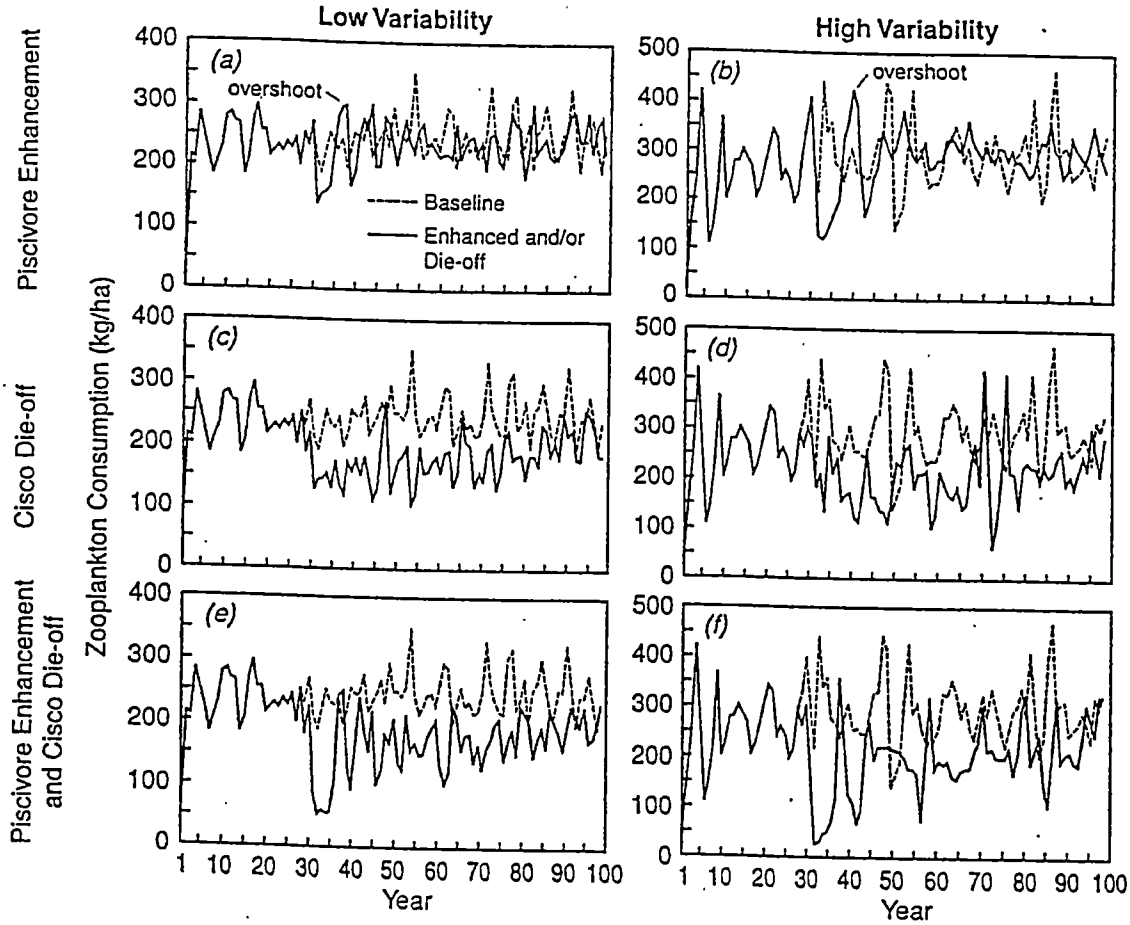


Figure 17. Annual zooplankton (*Daphnia galeata* and *Daphnia pulicaria)* consumed for the six combinations of piscivore enhancement alone, cisco die-off alone, and enhancement and cisco die-off together imposed on the low and high variability baseline conditions. Values under baseline conditions are also shown.

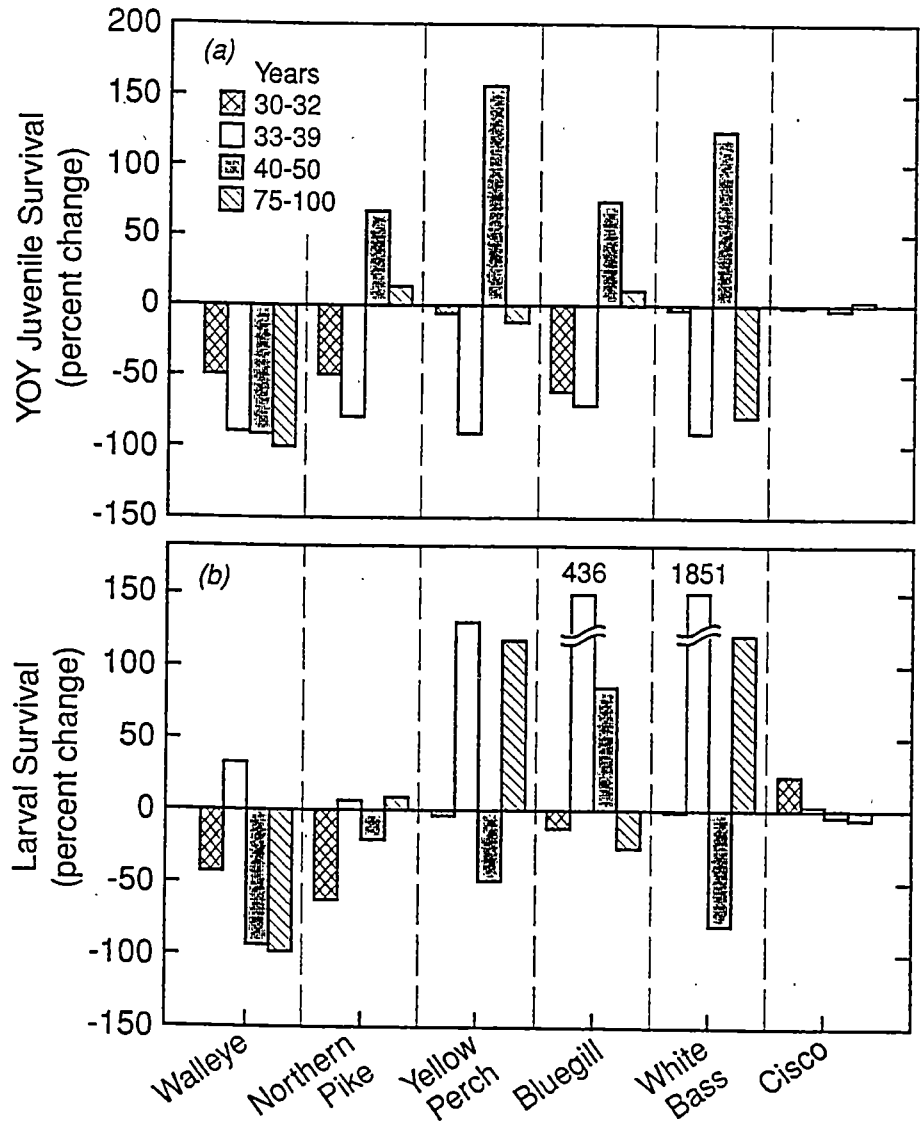


Figure 18. Percent change of average YOY juvenile and larval survival between the piscivore enhancement and baseline simulations for each of four time periods. Results are based on the high variability baseline simulation. (a) YOY juvenile survival, (b) larval survival.

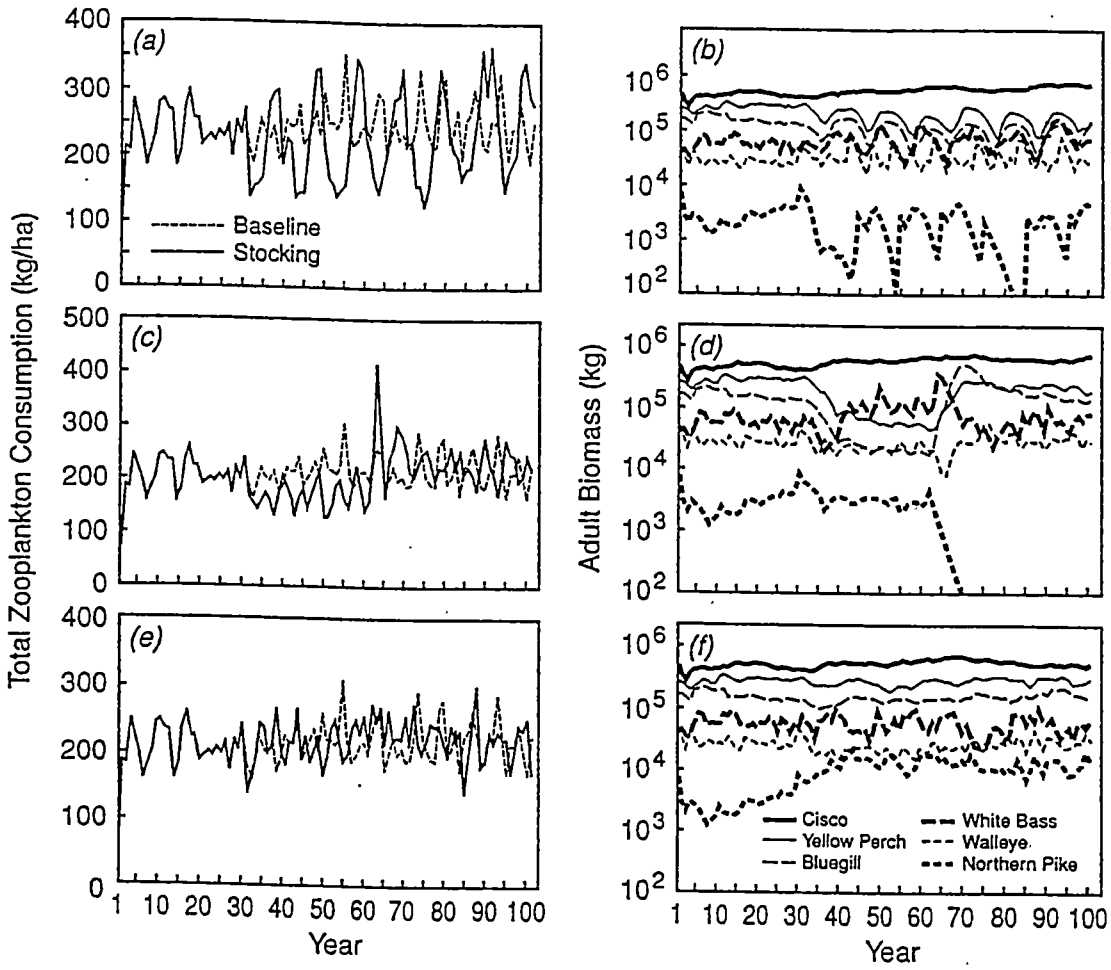


Figure 19. Annual total zooplankton (*Daphnia galeata* and *Daphnia pulicaria*) consumed and annual biomass of each of the six modeled fish species for the three stocking regimes imposed on the low variability baseline simulation. Values of total zooplankton consumption under baseline conditions are also shown. (a-b) periodic stocking, (c-d) high level continuous stocking, (e-f) low level continuous stocking.

# Part 3

# Population Responses of Yellow Perch to Global Climate Change: the Importance of Considering Food Web Structure

**Abstract** - The importance of food web structure in determining population responses to global climate change is examined using a general individual-based fish food web simulator. The model had previously been configured to simulate the six species food web in Lake Mendota, Wisconsin, consisting of yellow perch, bluegill, white bass, cisco, walleye, and northern pike (Part 2). Six alternative food webs were configured as subsets of the 6-species Lake Mendota food web: two versions of the 6-species food web, which differed in yellow perch biomass, a 3-species (yellow perch, bluegill, white bass) competition food web, two versions of a 2-species (yellow perch, walleye) predator-prey food web differing in yellow perch biomass, and a 1-species (yellow perch) population model. All food webs included yellow perch. To simulate climate, change published predictions of changes in temperature and dissolved oxygen in Wisconsin lakes under 2x atmospheric $CO_2$ were superimposed onto monthly temperature and dissolved oxygen profiles for Lake Mendota. Population responses of yellow perch to climate change depended upon food web arrangement. Yellow perch abundance decreased in response to climate change in the 3-species and high-biomass 6-species food webs, and increased in the remaining food webs. Population responses in the 1-species model were consistent with predictions based only on yellow perch bioenergetics (increases in size, abundance, and biomass) but were modified in other food webs by competition and predation in the model. White bass and northern pike were relatively minor components of the food web under baseline conditions but emerged as dominant species under climate change. Implications of model results on policies for climate change and issues related to prediction in ecology with complex models are discussed. Adapting to environmental changes will require understanding of changing ecological processes at many levels. Individual-based models provide a method for integrating processes from individuals to communities.

Key words: global warming, climate change, population, food web, dynamics, individual based, multi-species, fish, simulation model, Lake Mendota, predation, competition, density dependence.

## 1.0 Introduction

Increase in heat-trapping gases in the atmosphere will produce significant world-wide changes in climate. These changes will inevitably have impacts on biological systems at a broad range of scales. Climatic changes will affect organisms at the individual level by affecting a variety of temperature-driven processes (Roberts 1988). Ectothermic organisms such as fish are likely to be strongly affected by changes in climate. Populations will be affected as the range of suitable habitat is expanded for some species and reduced for others (Stefan et al. 1995). Local extinctions and invasions due to shifting population ranges will produce changes at the community level (Shuter and Post 1990; Lodge 1992). Interactions among changing populations can greatly influence and distort expected population level responses to changes in the abiotic environment (Ives and Gilchrist 1992). In this paper, we examine the role of food web structure in determining the population response of yellow perch (*Perca flavescens*) to simulated climate change in Lake Mendota, Wisconsin.

Human activities such as combustion of fossil fuels and changes in land and water use are significantly altering major components of the systems controlling global climate (Vitousek 1992). Since the industrial revolution, atmospheric concentrations of carbon dioxide, one of the principle "greenhouse" gasses, has increased from a previous level of ~280 μL/L to 335 μL/L (Vitousek 1994). Though uncertainty remains in our understanding of the global carbon budget (Sundquist 1993), further increases in atmospheric $CO_2$ concentrations over the next century are likely. An increase in average global surface temperature of 1.5-4.5 °C (best guess of 2.5 °C) with 2x current atmospheric $CO_2$ is now a well accepted estimate (Schneider 1993; Hansen et al. 1981). A variety of general circulation models (GCMs), such as the GISS (Goddard Institute for Space Studies) model, which simulate the large scale interactions of solar radiation, atmosphere, oceans, ice, land, and biota, are being used to project the patterns of climate change. While the predictions of these models vary at regional spatial scales, they generally agree on the continental scale. In general, we can expect warming at higher latitudes to be

above the global average, while warming in the tropics will be less (Schneider 1993; Ramanthan 1988; Hengeveld 1994). Annual mean air temperatures for Wisconsin are expected to rise ~4.5 °C. Warmer air temperatures with 2x atmospheric $CO_2$ (generated by the GISS model), applied to water quality models for Minnesota and Wisconsin lakes, predict warmer surface water, lower dissolved oxygen, more extreme stratification in summer, and shorter periods of ice cover in winter (Stefan and Fang 1994; Hondzo and Stefan 1993; DeStasio et al. 1996; Robertson et al. 1992).

Studies of fish population responses to global climate change have focused mainly on changes in favorable habitat for individual species. Magnuson et al. (1979) introduced the term "thermal niche", arguing that organisms will compete for space and partition space based on favorable temperatures in a manner analogous to competition for consumable resources such as food. Three thermal guilds are typically distinguished for fish in north temperate lakes: cold-water fish with optimal temperatures between 11 and 19 °C, cool-water fish with optimal temperatures between 24 and 26 °C, and warm-water fish with optimal temperatures between 27 and 32 °C (Stefan et al. 1995). Changes in thermal niches resulting from global warming have been estimated for fish in these three guilds in Minnesota and Wisconsin lakes (Stefan et al. 1995; Stefan et al. 1996; Magnuson and DeStasio 1996). Warm- water fish are predicted to benefit by expansion thermal niche in all lakes. Thermal niche should also expand for cool-water fish in oligotrophic and mesotrophic lakes, but could decrease in some eutrophic lakes where cool-water fish are squeezed between warmer surface waters and anoxic deep water (Coutant 1985). Thermal niche for cold-water fish will be severely restricted or eliminated in all but the deepest oligotrophic or most northern lakes (Stefan et al. 1995).

Predictions based only on habitat change that ignore biotic interactions are only first approximations. A species' realized niche may be partitioned by competition with other species (MacArthur 1958; Werner 1977), or portions of its optimal habitat may be unavailable due to the presence of predators (Werner and Hall 1988). Abundances in predator-limited populations may be determined mainly by the dynamic interactions of predator and prey, rather than by habitat

availability. Predictions of population abundances under climate change may depend upon the food web arrangement in which the population is imbedded.

In this part, we test the hypothesis that predicted population response will depend on food web structure using an individual-based fish food web simulator. We examine how six different food web arrangements affect predicted responses of yellow perch to a 2x atmospheric $CO_2$ global warming scenario. Individual-based models of this type explicitly simulate processes, such as feeding, growth, and reproduction of individual organisms (DeAngelis and Gross 1992; VanWinkle et al. 1993). Population level effects are determined by the collection of individuals. If the individual level processes are represented well, then realistic population and community dynamics should result (Rose et al. 1996). Changes in water temperature and dissolved oxygen due to global warming will affect fish primarily through effects on individual bioenergetics and habitat availability. Because many competitive and predative interactions are sized based, changes in bioenergetics and habitat can have complex cascading effects through the population and community. The individual-based approach can help to bridge the gap between these individual level effects and resulting population and community level responses (Dunham 1992; Murdoch 1992; Shugart et al. 1992).

**2.0 Synopsis of Methods**

The individual based-model is multi-generational, multi-species, and spatially explicit. It was constructed as a generalized fish food web simulator for lake environments, and then calibrated to Lake Mendota Wisconsin (Part 2). Six fish species are represented in the full food web version: yellow perch (*Perca flavescens*), bluegill (*Lepomis macrochirus*), white bass (*Morone chrysops*), cisco (*Coregonis artedii*), walleye (*Stizostedion vitreum*), and northern pike (*Esox lucius*),. Young-of-the-year (YOY) populations are determined by spawning of adults. Growth and development is determined by individual consumption rates. Planktivore species (yellow perch, bluegill, white bass and cisco) consume zooplankton and benthos, whose densities are simulated for each compartment. Piscivore species (walleye and northern pike) consume individual model

fish (Table 1). The lake environment is divided into three spatial compartments representing the epilimnion, hypolimnion, and littoral zones (Figure 1).

We configured six food webs as subsets of the 6-species Lake Mendota food web (Figure 2). Two versions of the 6-species food web were calibrated in Part 2 which differed in the foraging efficiency of the piscivores. The version with more efficient predators was characterized by lower planktivore biomass and lower interannual variability. We refer to these two versions as the low-biomass and high-biomass 6-species food webs. We also constructed 3- species, 2-species, and 1-species versions of the model. The 3-species competition model (yellow perch, bluegill, white bass) did not include piscivore predators. The low-biomass and high-biomass versions of the 2-species predator-prey food webs included yellow perch and walleye. A 1-species population model included only yellow perch. The 3-, 2-, and 1- species food webs were constructed by deleting species from the low-biomass 6-species version, and recalibrating selected parameter values until certain standard criteria on biomass and adult sizes were satisfied.

To simulate the environmental effects of global warming in Lake Mendota, we superimposed predicted changes in water temperature and dissolved oxygen in Minnesota and Wisconsin lakes (Stefan and Fang 1994; Hondzo and Stefan 1993; DeStasio et al. 1996; Robertson et al. 1992) onto temperature and dissolved oxygen profiles for Lake Mendota. From the temperature and dissolved oxygen profiles, we derived the daily temperature and dissolved oxygen experienced by fish in model simulations for baseline and 2x $CO_2$ conditions. Baseline and climate change conditions were simulated for each of the six food webs. We compared predicted population abundances, biomasses and adult sizes between baseline and climate change simulations.

### 3.0 Model Description: Overview

The model is multi-generational, with the young-of-the-year (YOY) population determined by spawning of adults. Individuals develop through the following life stages: egg, yolk-sac larva,

larva (exogenous feeding to 20 mm), YOY juvenile (20 mm to age-1), yearling, and adult. An adult that has reached maturity is also a spawner. Eggs and yolk-sac larvae are followed as cohorts from each spawner. Feeding fish are followed as individuals throughout their lives. Feeding, growth, reproduction, mortality, and movement are evaluated daily. For each individual, the model keeps track of total length (L, mm), wet weight (W, grams), life stage, age (years), and spatial compartment.

The lake environment is separated into three homogeneous compartments representing the littoral, epilimnetic, and hypolimnetic zones. The dimensions of the three compartments are based on Lake Mendota (Figure 1). Environmental variables in each compartment include daily temperature and dissolved oxygen (DO). Water temperature varies with lake depth. By governing the maximum water column depth inhabitable by fish, DO affects the available habitat and water temperatures fish experience. Prey densities in each compartment include zooplankton, benthos, forage fish, and the YOY and yearling individuals of the six modeled species. Below we briefly describe the model for Lake Mendota. A full model description may be found in Part 2.

## 4.0 Model Description: Lake Environment

### *4.1 Daily temperature*

Three daily temperature values are generated representing surface temperature, temperature at 10 m depth, and temperature at 20 m depth. These temperatures limit the range of temperatures fish may experience in each compartment. Temperatures within the epilimnion and hypolimnion are assumed to decrease with depth. Maximum epilimnion temperature occurs at the surface. Minimum epilimnion temperature and maximum hypolimnion temperature are the temperature at 10 m depth, and minimum hypolimnion temperature is the temperature at 20 m depth. Maximum and minimum littoral zone temperatures are both assumed equal to the surface temperature. Baseline daily water temperatures used in model simulations are shown in Figure 3a.

*4.2 Dissolved Oxygen*

We assume that fish cannot inhabit water whose DO concentration is less than 4 mg/L. As DO concentrations decline in the summer, the maximum depth accessible to fish decreases. The maximum depth ($D_{max}$) at which DO concentration exceeds 4 mg/L (Figure 3a) and the temperature at this depth ($T_{DO}$) (Figure 4a) are regression equations fit to Lake Mendota data. Fish do not inhabit water deeper than $D_{max}$, nor do they experience water temperature colder than $T_{DO}$.

*4.3 Prey Densities*

Prey are represented by two zooplankton groups representing *Daphnia pulicaria* and *Daphnia galeata*, a benthos group representing Chironomid larvae, a forage fish group representing an assembly of small bodied fish, and the YOY and yearling individuals of the modeled fish species. Equilibrium prey densities are time dependent for zooplankton, and constant for benthos and forage fish. Equilibrium density (N*) of each of the two zooplankton groups in each compartment is assumed to be a unimodal function (single peak) of calendar day (Figure 5). Equilibrium Chironomid densities are set to 2122/$m^2$ in the littoral zone and 224/$m^2$ in the hypolimnion. Forage fish equilibrium density is set to 0.00833/$m^3$ in the littoral zone. Benthos are absent from the epilimnion, and forage fish are only found in the littoral zone. Realized prey densities are updated daily in each compartment based on a logistic function with constant turnover rate for return to equilibrium, and losses due to consumption by model fish and due to migration of zooplankton among compartments. Prey were assumed to be unaffected by temperature and dissolved oxygen levels. Turnover rates in each compartment set to are 0.5/day for *D. galeata and D. pulicaria,* 0.3/day for benthos, and 0.15/day for forage fish.

## 5.0 Model Description: Fish Processes

### *5.1 Spawning and Early Development*

Spawners are adults (age 2 and older) which have reached maturity on the first day of each species' spawning season. With average lengths at age, adult bluegill and white bass are mature by age 2, yellow perch and cisco by age 3, walleye by age 4, and northern pike by age 5. Timing of spawning within the spawning season depends on temperature. Individual spawners are assigned spawning temperatures from a triangular probability distribution with species specific minimum, mode and maximum values (Appendix 3). Individuals spawn on the first day that surface temperatures reach their assigned spawning temperature. Under average baseline temperature conditions, northern pike spawns in late March (≈day 80), followed by walleye (≈day 100), yellow perch (≈day 120), and white bass (≈day 160). Cisco spawns in mid to late December just before ice cover. Bluegill spawn up to three times through midsummer (day 180 to day 225). The number of eggs produced by a female (per spawning batch for bluegill) is a linear function of female weight:

$$F = F_m \cdot W + F_b \qquad (1)$$

where $F_m$ and $F_b$ are species-specific coefficients (Appendix 3).

Eggs from each female are followed as a cohort through the egg and yolk-sac larval stages. Rate of development is temperature-dependent. Fractional daily development is computed as:

$$DV = \frac{1}{D_a + \exp(D_c * T)} \qquad (2)$$

where T is daily surface temperature, and $D_a$ and $D_c$ are species-specific coefficients with separate values for eggs and for yolk-sac larvae (Appendix 3). Daily fractional development is

summed over time for each female spawner or nest cohort. When the cumulative exceeds 1, development occurs (eggs hatch into yolk-sac larvae or yolk-sac larvae become larvae). Upon reaching the larval stage, individuals are followed in simulations. Daily instantaneous mortality rates of eggs and yolk-sac larvae (Z) are assumed constant. Mortality rates are specified for eggs and yolk-sac larvae for each of the six species (Appendix 3).

*5.2 Feeding Individuals: Growth and Consumption*

On each day, the new weight of an individual is used to update its length. A length-weight relationship is specified for each species:

$$L = L_a * W^{L_b} \quad (3)$$

where $L_a$ and $L_b$ are regression coefficients from length-weight data for each species (Appendix 3). Length and weight are partially uncoupled. Fish can lose weight but not length. To increase in length, a fish must weigh at least the weight predicted from its length.

The daily change in weight of an individual is determined by using a difference equation form of a bioenergetics equation:

$$W_{t+1} = W_t + (E*C - R_{tot}) * W_t * \Delta t \quad (4)$$

where E is net assimilation efficiency, C is daily consumption rate (g/g/day), $R_{tot}$ is total metabolic rate (g/g/day), and $\Delta t$ is one day. E is the combined effect of egestion, excretion, and specific dynamic action (SDA). Nonlinear functions relating consumption and metabolic rates to fish weight and water temperature are from the commonly used "Wisconsin" fish bioenergetics modeling software (Hewett and Johnson 1992). Parameter values for each species were adapted

from existing models developed by others (Rose et al. in review; Post 1990; Hewett and Johnson 1992; Breck 1988; Johnson 1993).

To summarize the bioenergetics, we show maximum consumption ($C_{max}$), total metabolism ($R_{tot}$), and growth potential as functions of temperature for a typical sized age-5 adult yellow perch (Figure 6a), and growth potentials of age-5 adults of all species (Figure 6b). Growth potential assumes an individual obtains its maximum consumption every day, and is computed as $E^*C_{max} - R_{TOT}$. Realized growth can be lower than maximum due to prey limitation. Optimal growth occurs at about 16° C for the cold-water species cisco, at 22-24° C for cool-water yellow perch, northern pike, and walleye, and at 27-28°C for the warm-water species bluegill and white bass.

*5.2.1 Consumption*

Realized consumption of prey is determined by a Type II functional response equation (Holling, 1965) that incorporates $C_{max}$. The total daily consumption of an individual (C, g/g/day) is computed as:

$$C = \sum_{j=1}^{n} C_j \qquad (5)$$

$$C_j = \frac{W * C_{MAX} * V_j \frac{PD_j}{K_j}}{1 + \sum_{k=1}^{n} \frac{V_k \cdot PD_k}{K_k}} \qquad (6)$$

where $C_j$ is the realized consumption rate of prey type j, $V_j$ is the vulnerability (value of 0 or 1) of prey type j to this individual, $PD_j$ is the realized prey density of prey type j experienced by this individual, $K_j$ is the half saturation constant for this individual feeding on prey type j, and k,,j=1..n denotes prey types. For zooplankton, benthos, and forage fish, $PD_j$ is generated from a Poisson distribution with mean equal to the simulated density on that day ($N_j$). For model fish as prey, $PD_j$ is the biomass density of prey fish in the compartment whose length is less than the gape size of the individual predator. Vulnerabilities and K-values were specified by length class. Vulnerabilities were based on published diet information. K-values were calibrated to produce reasonable mean lengths at age for all species.

*5.3 Feeding Individuals: Movement*

Movement of individuals among the three spatial compartments depends on fish length. All larvae reside in the epilimnion. Upon reaching 20 mm in length, bluegill, walleye, and northern pike move to the littoral zone where they remain throughout the remainder of their life. Yellow perch and white bass move to the littoral zone upon reaching 20 mm, but then return to the epilimnion as yearlings (150 mm for yellow perch; 135 mm for white bass). Upon reaching 20 mm, cisco inhabit the hypolimnion as long as DO conditions permit. When DO concentrations in the hypolimnion drop below 4 mg/L, cisco move up into the epilimnion. Energetic costs for movement were not considered.

*5.4 Feeding Individuals: Mortality*

Mortality of YOY and yearlings comes from three sources: background mortality, starvation, and predation by other model fish. Starvation occurs if an individual's weight falls below 65% of its predicted weight based on its length (equation 3) for YOY, or below 50% of its predicted weight for yearling and adult. Constant background annual survival ($S_B$) is specified for each life stage of each species (Table 2; Appendix 3).

Predation by model fish is determined from model fish consumption rates. YOY and yearling individuals of each species are treated separately. The daily probability of dying of an individual is computed as the total biomass consumed by all predators to which this individual prey is vulnerable divided by the total biomass. If a generated uniform random number between 0 and 1 is less than the probability of dying, then the individual is assumed to be eaten.

Age-2 and older individuals die from natural and fishing mortalities. Constant annual natural ($S_N$) and fishing ($S_F$) survival rates are specified for each species (Appendix 3). The combined daily probability of survival [$\exp(-\ln(S_N)/365)*\exp(-\ln(S_F)/365)$] is used to adjust population numbers of age 2 and older individuals.

## 6.0 Design of Simulations

### *6.1 Overview*

Two sets of 100 year simulations were performed: food web calibration and climate change. Food web calibration involved removing species from the low-biomass 6-species food web followed by trial and error adjustment of a limited set of parameters (Table 2) until several criteria were satisfied. Six distinct food webs were calibrated (Figure 2): two versions of the 6-species food web, a 3-species competition food web, two versions of a 2-species predator-prey food web, and a 1-species population model. The low- and high- biomass versions of the 6-species and 2-species food webs differ in their predicted yellow perch biomass. Competition is more important in the high-biomass 6-species version and piscivore predation is more important in the low-biomass version.

Climate change simulations involved comparing responses of yellow perch populations under simulated global warming with baseline simulations for all six food webs. Global warming conditions were determined from published predictions of temperature and dissolved oxygen in Minnesota and Wisconsin lakes (Table 3) based on the GISS model simulation of a doubling of atmospheric $CO_2$ (2x $CO_2$) (Stefan and Fang 1994; Hondzo and Stefan 1993; DeStasio et al. 1996; Robertson et al. 1992).

All simulations began with a specified number of age-2 individuals. Numbers of individuals at subsequent ages were determined by adult mortality rates. The number of age-2 individuals was chosen to result in initial adult densities close to observed values in Lake Mendota. Initial lengths of individuals were determined by published length at age data for each species. All simulations began with baseline conditions. In climate change simulations, 2x $CO_2$ conditions were imposed years 30-100.

*6.2 Alternative Food Webs*

We constructed six distinct food webs from the six species pool. All of the food webs included yellow perch (Figure 2). The food web models differed only in their constituent species, and in the values of a limited set of calibration parameters. Calibration parameters were limited to functional response half-saturation feeding constants (K in equation 6), larval mortality rates and YOY juvenile and yearling background mortality.

Two of the six food webs were alternative versions of the 6-species food web. In Part 2, we calibrated two versions of the 6-species food web for Lake Mendota, which differed in their degree of interannual variability. In addition to lower interannual variability in adult biomasses, the low-variability version also generated lower average yellow perch adult biomass compared to the high-variability version (100 kg/ha vs. 51 kg/ha). In this part, we refer to these alternate calibrations as the low-biomass and high-biomass 6-species food webs. Piscivores and planktivores were more tightly coupled in the low-biomass version. With less predation pressure in the high-biomass version, competition among planktivores was more important. The low-biomass version differed from the high-biomass version in having lower piscivore K values (more efficient predators) and lower zooplankton turnover rates (0.5/day versus 0.9/day for D. pulicaria in the epilimnion). More effective predators reduced the time lag between planktivore (prey) fish dynamics and the numerical response of piscivore predators. Shorter time lags generally result in increased stability in predator-prey models (Murdoch and Bence 1987). We included both

versions of the 6-species food web in order to compare the effects of calibration differences on model predictions.

The low-biomass version of the 6-species food web was used as the basis for the construction of the remaining four food webs. We first performed simulations with species in the six species food web simply deleted to obtain the 3, 2, and 1 species food webs. For all but one of these derived food webs, selected parameters were then recalibrated until: (1) all species in the food web persisted for 100 years, (2) mean lengths of adults (age-5) for all species were biologically reasonable, and (3) average yellow perch adult biomass was similar to the value from the low-biomass 6-species food web. This last criterion allows better comparison of yellow perch responses to climate change among the six food webs. Calibration parameters were restricted to YOY and yearling background mortality rates (to adjust for removal of piscivore predators), walleye K-values feeding on fish (to adjust for removal of planktivore prey), and larval mortality rates (to balance yellow perch biomass with changes in walleye K-values). We derived two versions of the 2-species food web (high and low biomass). When we simply deleted the other species, predicted dynamics were realistic and average yellow perch adult biomass was similar to the high-biomass 6-species food web with no changes in calibration parameters. We included this version as the high- biomass 2-species food web. We also derived a recalibrated low-biomass 2-species food web that produced yellow perch biomass similar to the low-biomass 6-species food web.

*6.3 Climate Change*

Daily temperature and DO concentrations used in baseline conditions were changed under the 2x $CO_2$ scenario. We first explain how daily temperatures and DO were estimated under baseline conditions. We then describe how we adjusted temperature and DO to simulate climate change.

Lake Mendota data were used to estimate maximum and minimum daily temperatures for each compartment, maximum inhabitable depth, and minimum temperature at which DO is 4mg/L

or higher. Maximum and minimum water temperatures for each compartment (Figure 3) were determined by fitting regression equations relating temperature to day of the year using monthly temperatures from the temperature at depth profile for Lake Mendota (Figure 7a). Maximum and minimum values for the littoral zone were based on the regression equation fitted to surface (0 m depth) temperatures. Epilimnion maximum and minimum temperatures used values measured at 0 m and 10 m depth, and hypolimnion maximum and minimum temperatures used values measured at 10 m and 20 m, respectively. Maximum inhabitable depth as a function of day of the year ($D_{max}$, Figure 4) was determined by fitting an empirical function to monthly values of the depth at which DO equaled 4 mg/L from DO with depth isopleths for Lake Mendota (Figure 7b). The minimum temperature at which DO is 4 mg/L or higher as a function of day of year (Figure 3) was based on fitting a function to a data set of monthly temperatures derived by superimposing the 4mg/L DO with depth isopleth onto temperature with depth isopleths.

Climate change was simulated by adjusting temperature with depth and DO with depth isopleths based on predicted monthly changes in temperature and DO (Table 3). These adjustments were based on studies that used GCM predictions under baseline and 2x $CO_2$ conditions to infer likely temperature and DO changes in Wisconsin and Minnesota lakes (Stefan and Fang 1994; Hondzo and Stefan 1993; DeStasio et al. 1996; Robertson et al. 1992). The monthly adjustments to temperature and DO concentrations were applied to the temperature with depth and DO with depth isopleths (Figure 8). We then repeated the same estimation procedures used for baseline conditions for fitting maximum and minimum temperatures, maximum inhabitable depth, and temperature at 4 mg/L DO using the adjusted temperature and DO with depth isopleths. Robertson et al. (1992) predicts changes in ice cover on Lake Mendota. To incorporate these effects we set the day on which temperatures equal 1 °C to be 14 days earlier in the spring, and 8 days later in the fall. The resulting functions that relate temperatures, maximum depth, and temperature at 4 mg/L DO to day of year are shown in Figures 3b and 4b.

All six food webs were simulated for 100 years under baseline and climate change conditions. For the climate change simulations, changes in temperatures and DO were imposed

beginning in year 30. The first 40 years of all simulations were eliminated to minimize the effects of initial conditions on model predictions.

*6.4 Prediction Variables*

The basic prediction variables were annual adult (age-2 and older) abundances and biomasses and mean length at age-5 of each species. We use mean length at age-5 as representative of adult size in general. Abundances, biomasses, and mean lengths were values on August 1 of each year of the simulation. We also present additional predictions for yellow perch under climate change. We focus on yellow perch because it is the only species found in all six food webs. These additional variables are average annual larval, YOY juvenile, and yearling survival rates, and average annual eggs per spawner.

For the calibration of the alternate food webs, we present annual adult abundances to show species persistence. Predicted mean lengths of age-5 individuals are compared to reported values to satisfy the second calibration criterion of realistic sizes. We also show minimum, average, and maximum yellow perch biomass across all six food webs to show that recalibration was successful in producing the desired similar biomasses.

For climate change, we present annual adult abundances over time for all species in the six food webs to compare to baseline conditions. We also compare minimum, average, and maximum mean lengths at age-5 for all species between baseline and climate change simulations to detect any growth effects. Predicted responses are summarized by showing the percent changes relative to baseline in yellow perch average abundance, mean length at age-5, and biomass for each food web. Predicted changes are computed as $100*[Y-Y_b]/Y_b$ where Y is the average value (years 40-100) under climate change and $Y_b$ is the average value under baseline. Percent changes in yellow perch larval survival, YOY juvenile survival, yearling survival, and eggs/spawner, and in biomass of the other species are also shown to help explain differences in yellow perch responses across food webs. Finally, we also note some of the responses to climate change exhibited by species other than yellow perch.

## 7.0 Simulation Results

### *7.1 Alternative Food Webs*

Time series of adult abundances (Figure 9) showed that all species persisted for 100 years, and adult sizes of all species were realistic (Figure 10). The dynamics of 6-species interactions are complex, but some indication of predator-prey interactions can be seen (Figure 9 a,b). Predator-prey cycles are evident in abundance time series for both versions of the 2-species model (Figure 9 d,e).The 1-species population model shows cycles (Figure 9 f) which, in the absence of predators, must be driven by density dependent reproduction, growth and survival of yellow perch.

The 3-species, 2-species and 1-species food webs either generated similar average adult yellow perch biomass or used identical parameter values as the low biomass 6-species version. For the 3-species and 1-species versions, we were able to match average yellow perch biomass to the low-biomass 6-species version (Figure 11) by adjusting only background YOY and yearling mortality rates; no calibration of larval mortality or feeding parameters was required (Table 2). For the 2-species model, when we removed northern pike, bluegill, white bass and cisco, average yellow perch biomass matched well with the high-biomass six-species model without adjusting any parameters (Figure 11). To get yellow perch biomass in the 2-species food web to match average biomass in the low-biomass 6-species food web, it was necessary to recalibrate the K-values and larval mortality rates. The recalibrated version has lower predator feeding constants (K) (Table 2), lower planktivore biomass, and lower range in values for yellow perch biomass (Figure 11). The differences in parameters and yellow perch biomass between the high- and low-biomass 2-species food webs were similar to the differences between the high- and low-biomass 6-species food webs.

### *7.2 Climate Change.*

Predicted population dynamics and adult sizes were realistic under climate change. Adult abundances persisted for all species (except cisco) in all six food webs (Figure 12). Cisco

became extinct in both 6-species food webs. Mean lengths of age-5 adults under climate change were similar to baseline values for all species except white bass (Figure 10). Adult white bass mean lengths consistently increased under climate change (Figure 10 b).

Population responses of yellow perch to climate change depended upon the food web arrangement and on the calibration choices within a given food web (Figure 13). Yellow perch adult abundance under $2xCO_2$ conditions decreased relative to baseline for the high-biomass 6-species and 3-species food webs, whereas yellow perch abundance increased in the 1-species, both versions of the 2-species, and the low-biomass 6-species food webs. The two 6-species food webs differed only in their calibration, and yet generated opposite predictions of yellow perch response to climate change. Average yellow perch biomass increased in all food webs, except for the 3-species food web where little change was predicted. However, the magnitude of predicted changes in biomass varied greatly among food webs, ranging from little change to a 110% increase for the 1-species food web. Mean lengths of adult yellow perch also increased relative to baseline for all food webs.

Changes in yellow perch biomass reflected the combined effects of changes in abundance and in mean length. In the 3-species food web, abundance decreased by 50% whereas mean length increased by 20%, leading to little change in biomass. The greatest change in biomass occurred in the 1-species food web where abundance and mean length both increased by 20%, resulting in a 110% increase in biomass. Changes in mean length generally acted to offset decreases in abundances. Density dependent growth compensated for lower abundances. Except for the 1-species food web, changes in mean lengths were higher (12% and 20%) when abundances declined than when abundances increased (<7%).

Responses of yellow perch abundance to climate change depended on a complex mix of competitive and predative interactions, which varied in importance among food webs. The greater importance of competition in the high-biomass 6-species version resulted in a decrease in yellow perch abundance, whereas the greater importance of predation in the low-biomass 6-species version permitted yellow perch to increase. Yellow perch also declined in the 3-species version, in

which planktivore competition was intense because of lack of piscivores. In the 2-species and 1-species food webs, yellow perch increased because their predator (walleye) declined, or no piscivore was present.

Changes in yellow perch larval, YOY juvenile, and yearling survival rates also reflected differences in competition and predation among the alternate food webs. Larval survival decreased in all food webs, except for little change in larval survival in the low-biomass 2-species food web (Figure 14). Changes in larval survival result from differences in larval growth. Larval mortality is based on a fixed daily rate and they are not consumed by model fish. Lower survival can only result from increased starvation or reduced growth leading to longer larval stage duration. YOY juvenile survival decreased and yearling survival increased in all food webs but in the low-biomass 6-species food web. Competition was important in these food webs, as the high-biomass 6-species food web was designed to emphasize competition, the 3-species and 1-species food webs lacked piscivores, and the high-biomass 2-species food web lost its only piscivore (walleye). In the low-biomass 2-species food web, in which walleye persisted, predicted changes were small. Both YOY juvenile and yearling survival were able to increase in the low-biomass 6-species food web which was calibrated with tightly coupled piscivore and planktivore dynamics, thereby relaxing competition.

Changes in yellow perch eggs per spawner reflect the changes in adult growth. Eggs per spawner of yellow perch increased in all food webs, as did adult mean length. Increased adult length led to higher fecundity and earlier age of maturation of individual adults.

The responses of species other than yellow perch were generally consistent with expectations based on bioenergetics. The minimum inhabitable water temperature ($T_{DO}$) for fish in the epilimnion under 2x $CO_2$ conditions exceeded 25 $^0$C from day 210 (July 29) to day 225 (Aug 13). (Figure 3). In the littoral zone temperature exceeded 25 °C from day 180 (June 29) to day 230 (Aug 18). Species tolerant of higher temperatures tended to increase while others tended to decline. The cold water cisco went extinct in all food webs (Figure 12 a,b). Warm-water bluegill and white bass have the same temperature preferences, but bluegill has less scope for growth

(Figure 6b). Bluegill abundance increased in the low competition low-biomass 6-species food web, but decreased in the highly competitive 3-species food web (Figure 15a). White bass were the most tolerant of the planktivores. White bass biomass increased in all food webs, and increased most in the highly competitive 3-species food web (Figure 15b). Growth potential for northern pike remains high, though no longer optimal at the maximum littoral zone temperatures under 2x $CO_2$ conditions. The less tolerant walleye experience reduced and even negative growth potential at temperatures beyond 25 °C (Figure 6b). Northern pike abundance and biomass increased and walleye abundance and biomass decreased in both 6-species food webs, with northern pike becoming the dominant piscivore (Figure 12 a,b). Northern pike abundance and biomass both greatly exceeded walleye in the high-biomass 6-species food web. In the low-biomass 6-species food web, northern pike and walleye abundances were approximately equal, but northern pike biomass was much larger. Walleye abundance and biomass also decreased in the high-biomass 2-species food web. Recalibration of K-values permitted walleye to persist in the low-biomass 2-species food web.

**8.0 Discussion**

Our results demonstrate that population responses to global climate change can depend upon the particular food web arrangement in which the population is imbedded. Yellow perch abundance decreased relative to baseline under 2x $CO_2$ conditions in two of the six food webs (three-species and high-biomass six-species), but increased in the other four (Figure 13). Bluegill abundance also decreased relative to baseline in the three-species and in the high-biomass six-species models, but increased in the low-biomass six-species model (Figure 15). White bass abundance increased in the three-species model, but decreased in both six-species models. Food web arrangement also determined the magnitude, though not the direction of changes in yellow perch adult size and biomass (Figure 13). Direct temperature affects on growth were straightforward, but density dependent growth and survival coupled with interspecific competition and predator-prey interactions acted to modify population responses.

Simple analysis of thermal niche would suggest yellow perch, bluegill, white bass and northern pike would increase, walleye would decrease, and cisco would go extinct in Lake Mendota. Bluegill and white bass are warm-water species for whom thermal niche should expand. Cisco, a cold-water species, will likely face extinction in the lake. For the remaining cool-water species, Magnuson and DeStasio (1996) predict expansion of thermal niche for yellow perch in Lake Mendota. The temperature preference of northern pike is slightly warmer than that of yellow perch (Figure 6), so we can expect expanded thermal niche for northern pike as well. Walleye prefer temperatures slightly cooler than yellow perch and northern pike. We found no published predictions for walleye in Lake Mendota, but an analysis of Lake Michigan predicted decreased thermal niche for walleye (Magnuson et al. 1990). For the temperature changes projected for Lake Mendota, peak summer temperatures are beyond the favorable growth range for walleye.

Predicted responses to global warming in yellow perch size and abundance from the 1-species food web support preliminary predictions based on thermal niche and individual bioenergetics, but were modified in other models by food web interactions. Warmer temperatures resulted in enhanced growth, abundance, and biomass in the one-species model. The individual level response (increased size) was consistent across all food webs in direction, though not in magnitude. Population level responses (changes in abundance and biomass) were modified by food web interactions in both direction and magnitude.

Differences in the response of yellow perch to climate change among the different food webs reflect the interplay of competition and predation in the model. For example, In the 1-species food web (no interspecific competition or predation) yellow perch abundance and biomass increased as predicted by its bioenergetics. In the 3-species competitive food web yellow perch abundance and biomass decreased, while white bass biomass increased 1000% (Figure 13, 15c). In the 6-species food webs, competition among planktivores was combined with predation by piscivores. The presence of a strong predator has been seen to reduce the effects of competition (Paine 1966). In both 6-species food webs, increase in white bass biomass was less pronounced

than in the 3-species food web. In the low-biomass food web, where predation was stronger, yellow perch increased in biomass and abundance. In the high-biomass 6-species food web, where predation was weaker, changes in yellow perch and bluegill biomass and abundance were intermediate between those in the low-biomass 6-species food web and the 3-species food web where piscivores were absent.

Simulated climate change resulted in qualitative changes in food web composition. Cisco, a dominant planktivore under baseline conditions, became extinct under 2x $CO_2$ conditions. Northern pike and white bass were both of relatively minor importance under baseline conditions, but emerged as major components of some food webs in 2x $CO_2$ simulations. In the 3-species competition food web, white bass biomass increased over 1000% relative to baseline with global warming. Northern pike increased 1200% to 1800% from baseline in both biomass and abundance, replacing walleye as the dominant predator in both 6-species food webs. Under 2x $CO_2$ northern pike abundance was equal or greater than walleye abundance and northern pike biomass exceeded the biomass of northern pike and walleye combined in baseline simulations in both 6-species food webs. These changes were generally consistent with the tolerance of species to high temperature. The planktivore and piscivore with the highest temperature tolerances (white bass and northern pike) increased, while those with lowest tolerance (cisco and walleye) decreased. Yellow perch and bluegill had intermediate tolerances, and their responses were strongly affected by food web interactions.

It is difficult to determine the cause of changes in growth and survival. Climate change involved altered temperatures and less habitat due to low DO concentrations. Temperature affects the timing of spawning, and egg and yolk-sac larva development rates. Increased temperature can directly cause changes in growth rates. Growth rates of adults affect age of maturation and fecundity. Growth rates of larvae affect survival through the larval stage. Temperature changes influence the match between prey and predator sizes during the year. Piscivores are represented in the model as gape limited predators, and the movement of planktivores, which affects their vulnerability to predation, is length based. The direct effects of temperature are mediated by size-

based competitive and predative interactions. In Part 2 we analyzed the high-biomass 6-species food web and showed that larval survival was density-dependent (related to number of eggs), yearling survival was controlled by predation (related to piscivore biomass), and YOY juvenile survival was influenced by both. Climate change effects cascade from individual responses to the population and community levels via complex temperature and size-based interactions, making it difficult to tease apart effects.

Given all the arguments for considering food web complexity, it must also be recognized that increasing model complexity has its price. Initial calibration of the full six-species model required the trial and error adjustment of 91 separate parameters. Many other parameter estimates were based on data which contained their own level of uncertainty. With this many degrees of freedom, it is impossible to be certain whether our results are robust or merely an artifact of a particular choice of calibration. This concern is well illustrated by the difference between the low-biomass and high-biomass versions of the 6-species and 2-species food webs. The different versions were identical, except for different calibrated values of a few parameters (Table 2). Yet, in the high-biomass 2-species food web, walleye biomass was greatly reduced by climate change, while in the low-biomass version, walleye was unchanged. Yellow perch abundance increased in the low-biomass 6-species food web but decreased in the high-biomass version. The problem of calibration in complex models is a perennial one for which no single, universally applicable solution has been found. Computation time for this model made objective calibration methods, such as Monte Carlo filtering (Rose et al. 1991), impractical. We chose therefore to address the issue of uniqueness in ad hoc calibration by presenting alternative calibrations for the 2- and 6- species models. The alternative versions allow us to examine explicitly how choice of certain parameters (such as predator feeding efficiency) can affect model predictions. Predictions which are consistent across alternative calibrations are more likely to be robust.

To reduce model complexity, we made two simplifications in the implementation of climate change: no interannual variability in temperature and dissolved oxygen, and climate

change imposed as a simple step function in year 30. Simulations using the low-biomass 6-species model in which annual mean surface temperature varied randomly by up to 2 $^{o}$C above or below baseline values were essentially identical to baseline simulations. We also ran simulations using the low-biomass 6-species model where 2x $CO_2$ conditions were imposed gradually from years 30-80. Population biomass mean and range for all species over years 80-100 under gradual implementation of climate change were nearly identical to the corresponding averages for years 40-100 with climate change implemented as a step function in year 30.

Certain recent changes in the Lake Mendota fish community were similar to model predictions. Our model predicts the extinction of cisco and the resurgence of white bass as a response to climate change (this result was robust across calibrations). In the summer of 1987, cisco unexpectedly died out from Lake Mendota (Kitchell 1992; Rudstam et al. 1993). In following years, white bass density in Lake Mendota increased substantially (Johnson and Kitchell 1996).The probable cause for the cisco die-off was a warm summer combined with low dissolved oxygen (Rudstam et al. 1992; Johnson and Kitchell 1996; Magnuson personal communication). In simulations where we artificially removed cisco without changing climate (Part 2), there was no corresponding increase in white bass, supporting the view that the enhancement of white bass in Lake Mendota was also due to temperature, rather than simply the removal of a dominant competitor for zooplankton (Johnson and Kitchell 1996). Similar changes in species composition in Lake Mendota have been observed many times over the past century (Johnson and Kitchell 1996), so we are not suggesting that recent events are due to global change. Rather we suggest that the loss of cisco and increase in white bass in response to temperature illustrate how environmental changes can be reflected by population changes of certain indicator species (Carpenter et al. 1992; Holmes 1990). As white bass and cisco in Lake Mendota are both at the extremes of their respective ranges, both are likely to be sensitive to environmental changes, and may serve as early indicators of climate change.

Genuine prediction of population responses to global climate change is not likely to be possible in most cases. We have demonstrated that the usual approach of projecting habitat

changes for single populations is not sufficient. Changing populations must be considered within the larger food web context. We have also seen how previously minor components of a food web may emerge as major players in the new environment (e.g. white bass, northern pike). It will not be possible to construct complex predictive models to examine every population of interest, and even if it were, there are still limits to the predictive power of such models. We can only make best guess predictions based on habitat change and simulation models, guided by the experience and intuition of those in the field. In the end we still must "expect the unexpected." Management policies based on trying to predict and forestall change, or reactive policies aimed at maintaining status quo are not likely to succeed (Healy 1990). Change is inevitable in ecology, and anthropogenic effects greatly accelerate the process. Adjusting to changing ecological systems will require an understanding of systemic changes occurring at all levels, from climate changes at a continental scale to the physiology and behavior of the individual. Individual-based models like the one presented here provide a straightforward method for integrating processes across many biological levels, from the individual to the community.

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# Appendix 2:

# Tables and Figures for Part 3

Table 1. Predator-prey interactions according to the vulnerability values used in the model. A vulnerability value of zero indicates prey were not eaten by that predator. A value of one indicates the prey could be eaten by that predator and is shown with the + symbol.

| species | size class | Prey type | | | | |
|---|---|---|---|---|---|---|
| | | D. galeata | D. pulicaria | benthos | forage fish | model fish* |
| Yellow perch | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | | |
| | yearling | | + | | | |
| | Age 2+ | | + | | | |
| Walleye | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | + | |
| | yearling | | | + | + | + |
| | Age 2+ | | | | + | + |
| Northern pike | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | + | |
| | yearling | | | | + | + |
| | Age 2+ | | | | + | + |
| Bluegill | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | | |
| | yearling | | + | + | | |
| | Age 2+ | | + | + | | |
| White bass | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | + | | |
| | yearling | | + | | | |
| | Age 2+ | | + | | | |
| Cisco | yoy < 45 mm | + | + | | | |
| | yoy > 45 mm | | + | | | |
| | yearling | | + | | | |
| | Age 2+ | | + | | | |

* Model fish includes age 0,1 yellow perch 20 < L < 150, age 0, 1 walleye L>20, age 0,1 northern pike L>20, age 0,1 bluegill L>20, and age 0,1 white bass 20 < L < 135. Cisco, Larvae < 20mm, age 1 yellow perch L>150, and age 1 white bass L>135 do not overlap spatially with piscivores. Age 1 northern pike are generally beyond the gape size of all but the largest predators.

Table 2. Parameter recalibration from the low-biomass 6-species food web to the 3-, 2-, and 1-species food webs. Abbreviations: YP = yellow perch, BG = bluegill, WB = white bass, WE = walleye.

| Parameter | Food Web | | | | |
|---|---|---|---|---|---|
| | low-biomass 6 -species | 3 - species | low-biomass 2- species | high-biomass 2-species | 1 - species |
| YOY, yearling daily survival fraction | All species: 0.75 | YP, WB : 0.20<br>BG: 0.09 | No change | No change | YP: 0.30 |
| Daily larval mortality rate | YP: 0.065<br>WE: 0.10 | No change | YP: 0.11<br>WE: 0.05 | No change | No change |
| Adult WE K-values feeding on fish | model fish: 1.2<br>forage fish: 0.5 | No change | model fish: 0.3<br>forage fish: 0.1 | No change | No change |

Table 3. Changes in epilimnion and hypolimnion monthly temperature (°C) and dissolved oxygen (mg/L) under 2x atmospheric $CO_2$ based on reported values from GCM models. Values given are change from baseline conditions. (Sources: Stefan and Fang 1994. Env. Management. 18:73-92; Hondzo and Stefan 1993. Climate Change. 24:187-211; DeStasio et al. 1996. Limnol. Oceanogr. 41:1136-1149; Robertson et al. 1992. Climate Change. 21:407-427).

| | Month | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
| Temperature (°C) | | | | | | | | | | |
| Epilimnion | 0 | +4 | +4 | +3 | +2 | +3 | +4 | 0 | 0 | 0 |
| Hypolimnion | 0 | 0 | -2 | -2 | -2 | -2 | -2 | +1 | +1 | 0 |
| Dissolved Oxygen (mg/L) | | | | | | | | | | |
| Epilimnion | 0 | -1 | -1 | -0.8 | -0.5 | -0.5 | -0.8 | -1 | -0.5 | 0 |
| Hypolimnion | -1 | -2 | -6 | -4 | 0 | 0 | -4 | -5 | -1 | 0 |

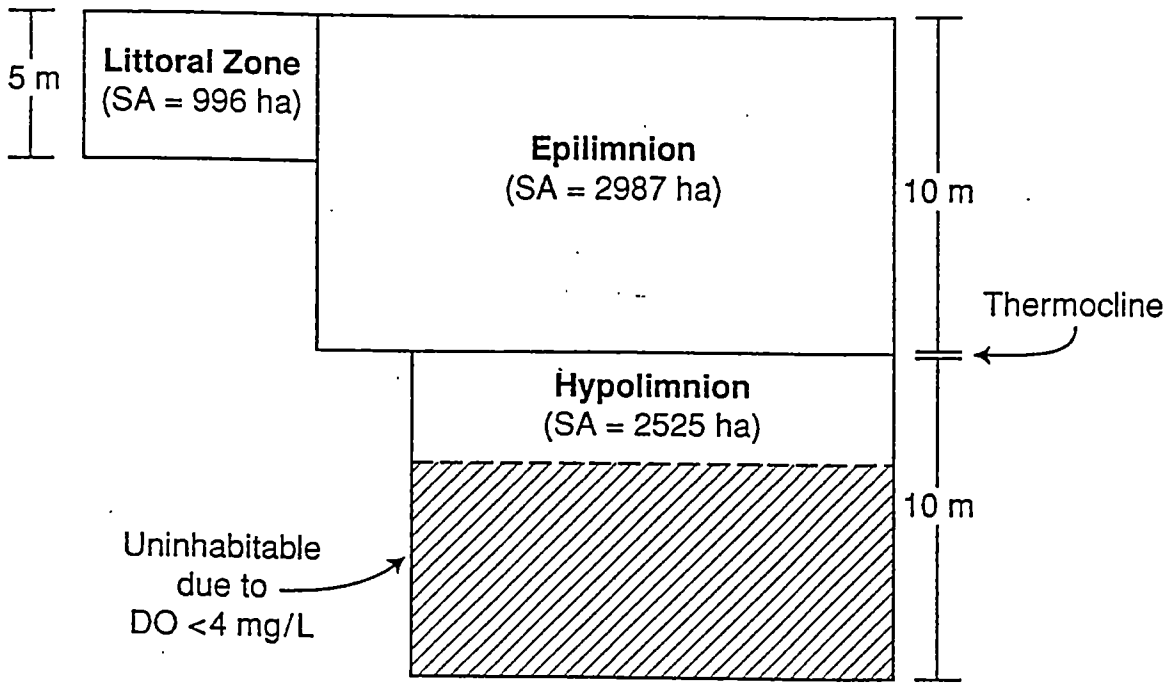


Figure 1. Model compartmentalization of Lake Mendota into epilimnion, hypolimnion, and littoral zones. The region of hypolimnion that becomes uninhabitable due to DO< 4 mg/L varies with day in the simulation.

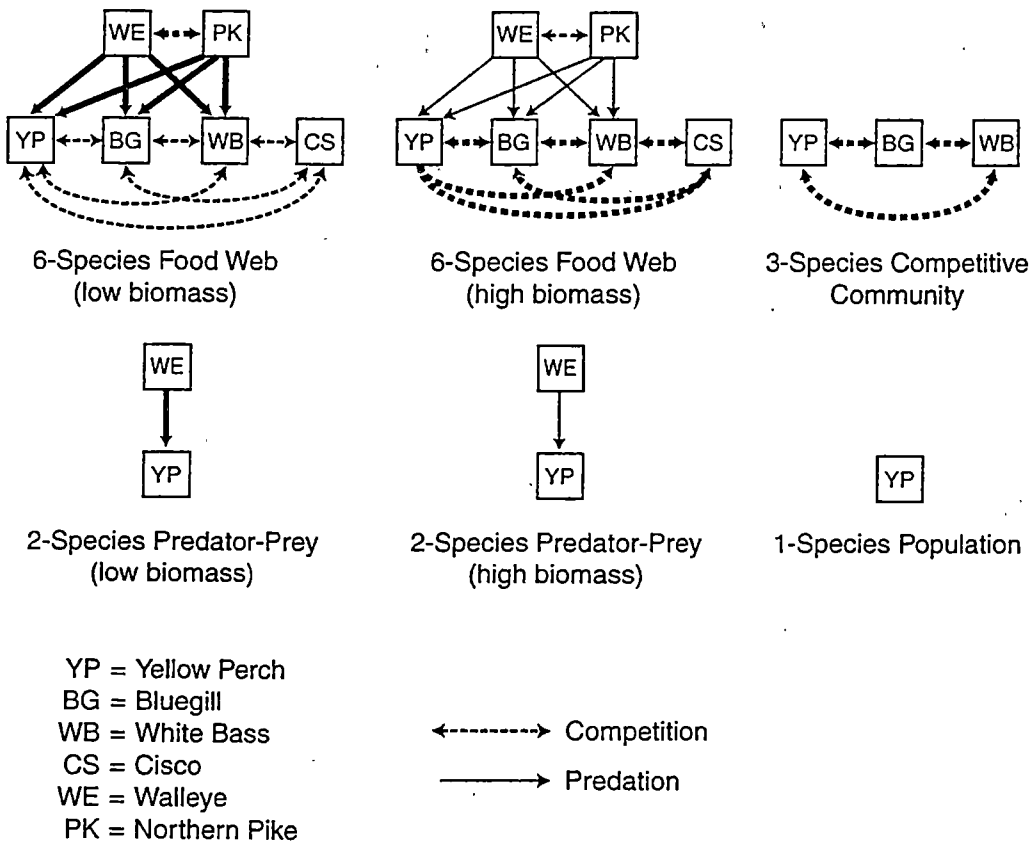


Figure 2. Schematic representation of the six alternate food web structures showing predative and competitive interactions among modeled fish species. Bold lines indicate stronger interactions.

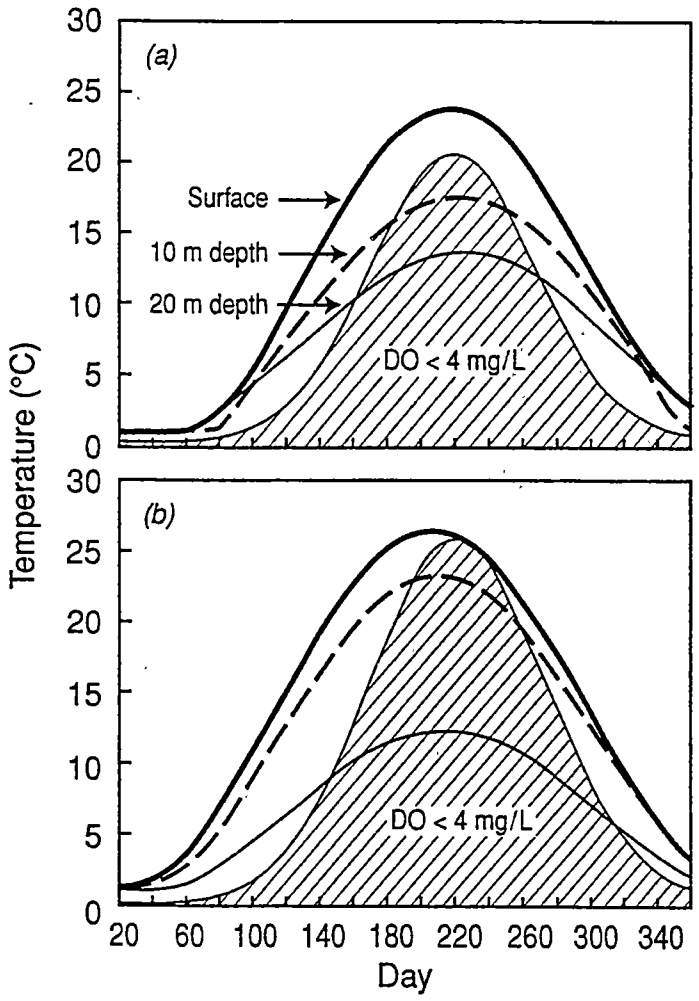


Figure 3. Daily water temperatures at the surface, 10m, and 20m depths, and the temperature at which DO is <4 mg/L, under (a) baseline and (b) 2x $CO_2$ conditions.

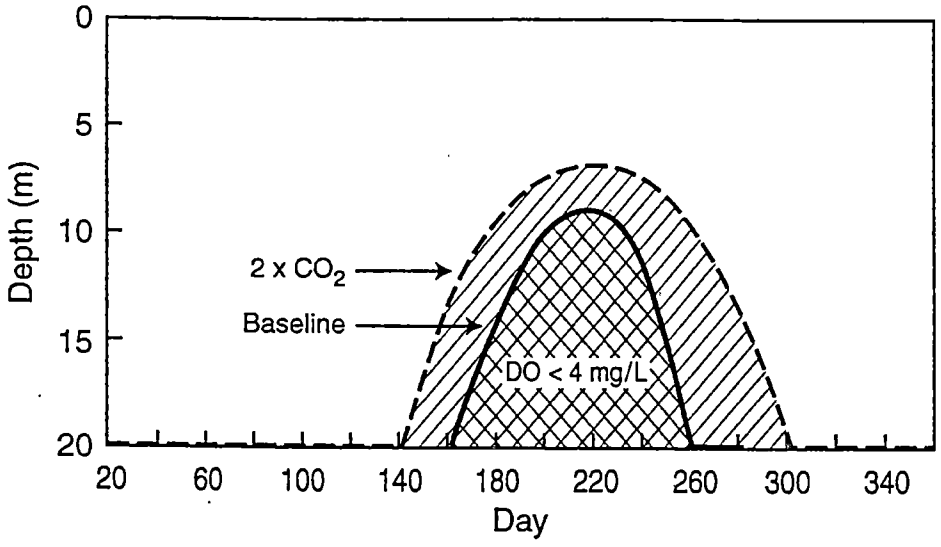


Figure 4. Maximum inhabitable depth ($D_{max}$) due to DO falling below 4 mg/L as a function of day of year for (a) baseline and (b) 2x $CO_2$ conditions.

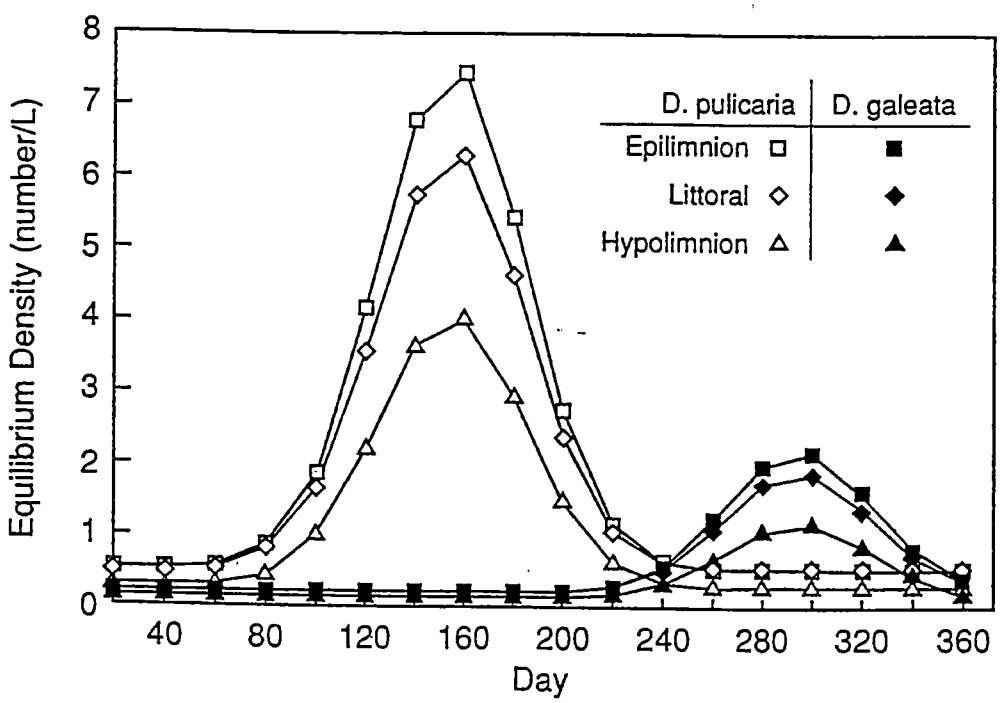


Figure 5. Equilibrium densities of *Daphnia pulicaria* and *Daphnia galeata* as a function of day of year for each model compartment. Curves shown are generated from functions fit to Lake Mendota data.

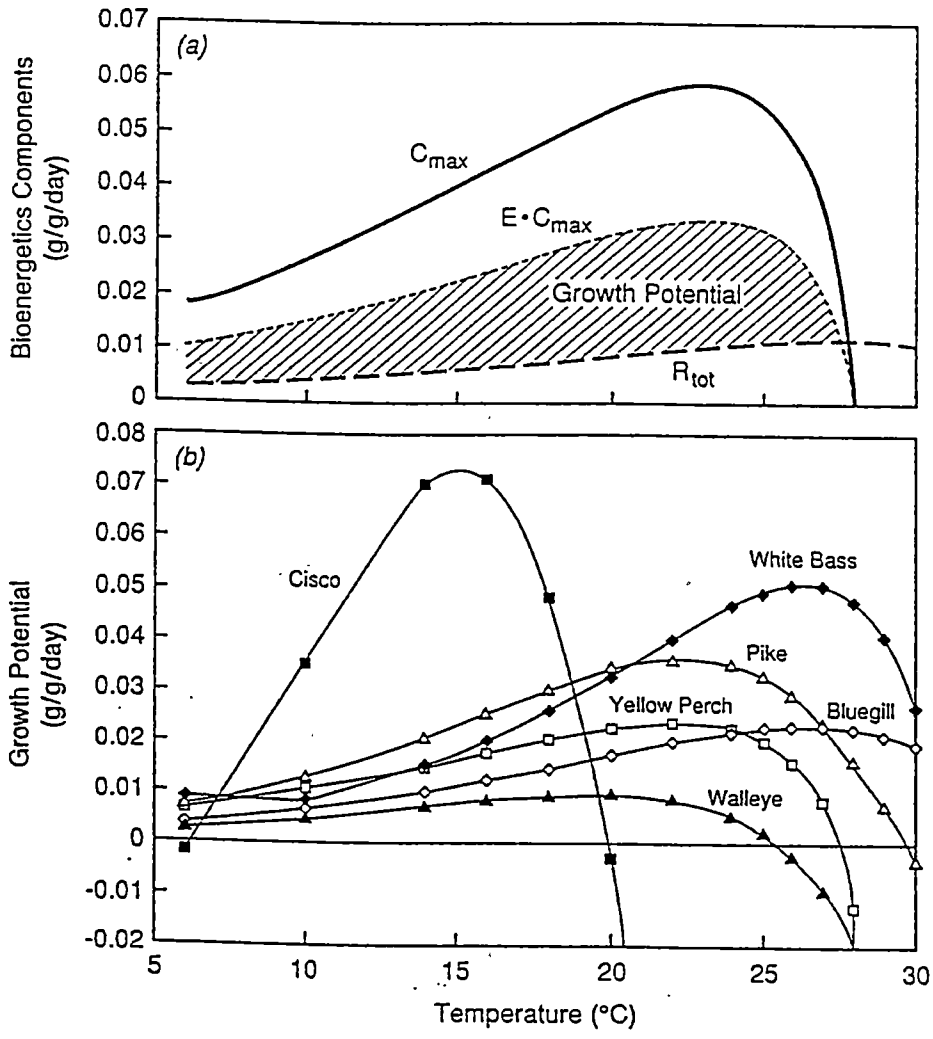


Figure 6. Bioenergetics components and growth potentials for typical sized age-5 adults. (a) yellow perch maximum consumption, metabolism, and growth potential, (b) growth potentials of all six species.

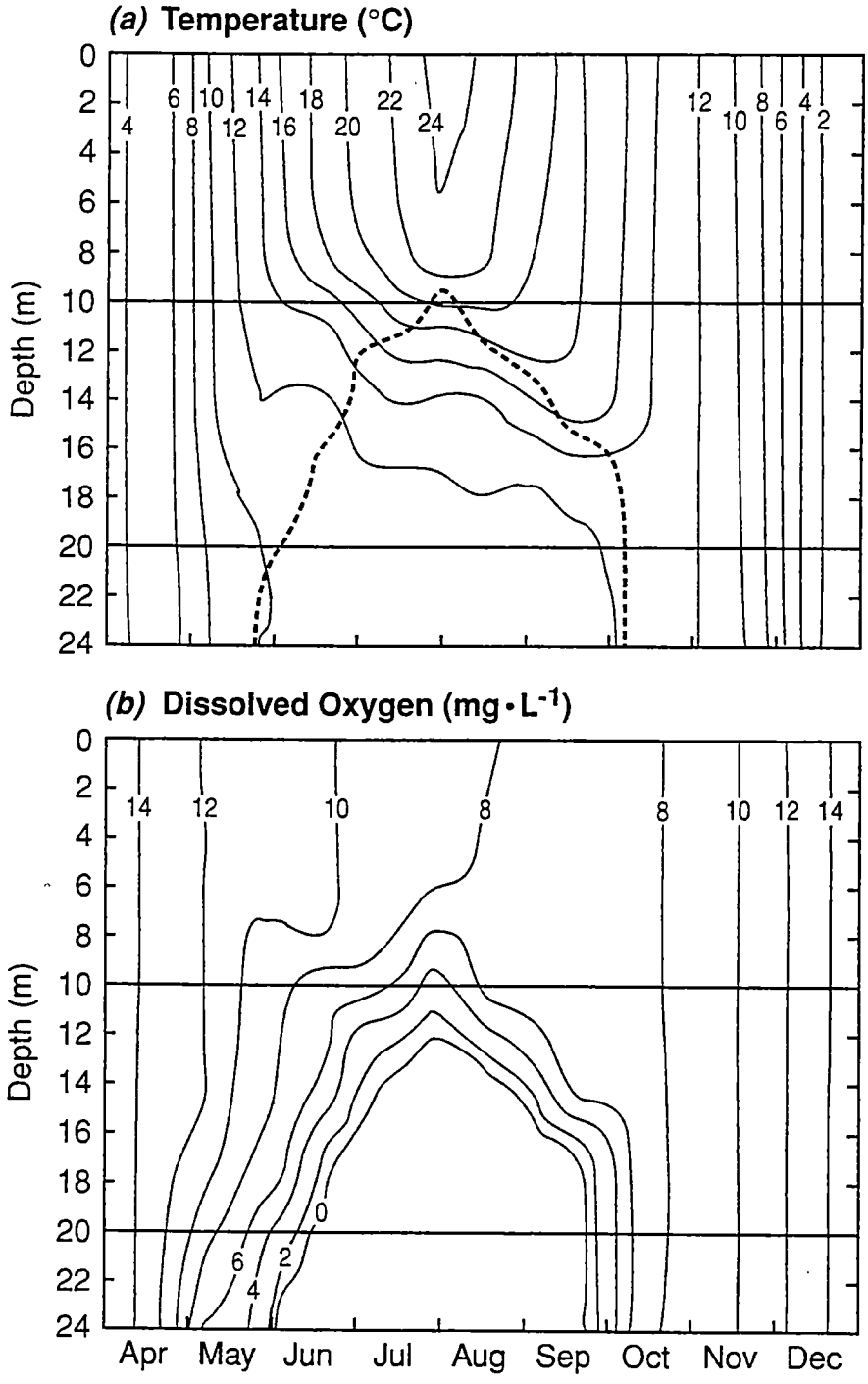


Figure 7. Baseline temperature (a) and dissolved oxygen (b) with depth during 1986 in Lake Mendota, Wisconsin. The 4 mg/L DO isopleth is shown as a dashed line on the temperature profile. (reprinted from Lathrop, R.C., 1992. Lake Mendota and the Yahara River chain. in J.J. Kitchell (Editor) Food Web Management. A Case Study of Lake Mendota. Springer-Verlag, New York. pp. 17-29.)

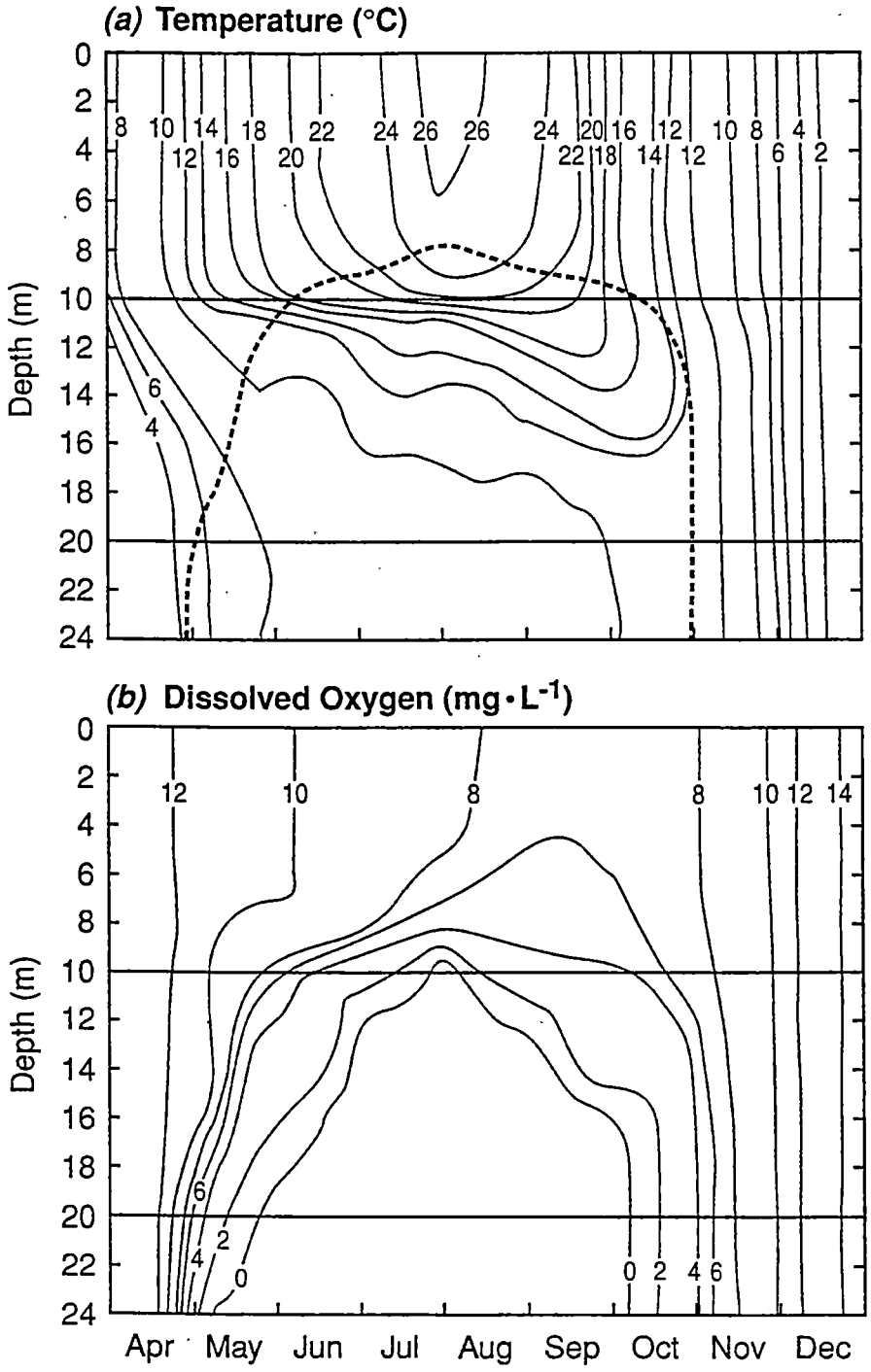


Figure 8. Projected temperature (a) and dissolved oxygen (b) with depth in Lake Mendota under 2x $CO_2$ conditions. The 4mg/L DO isopleth is shown as a dashed line on the temperature profile.

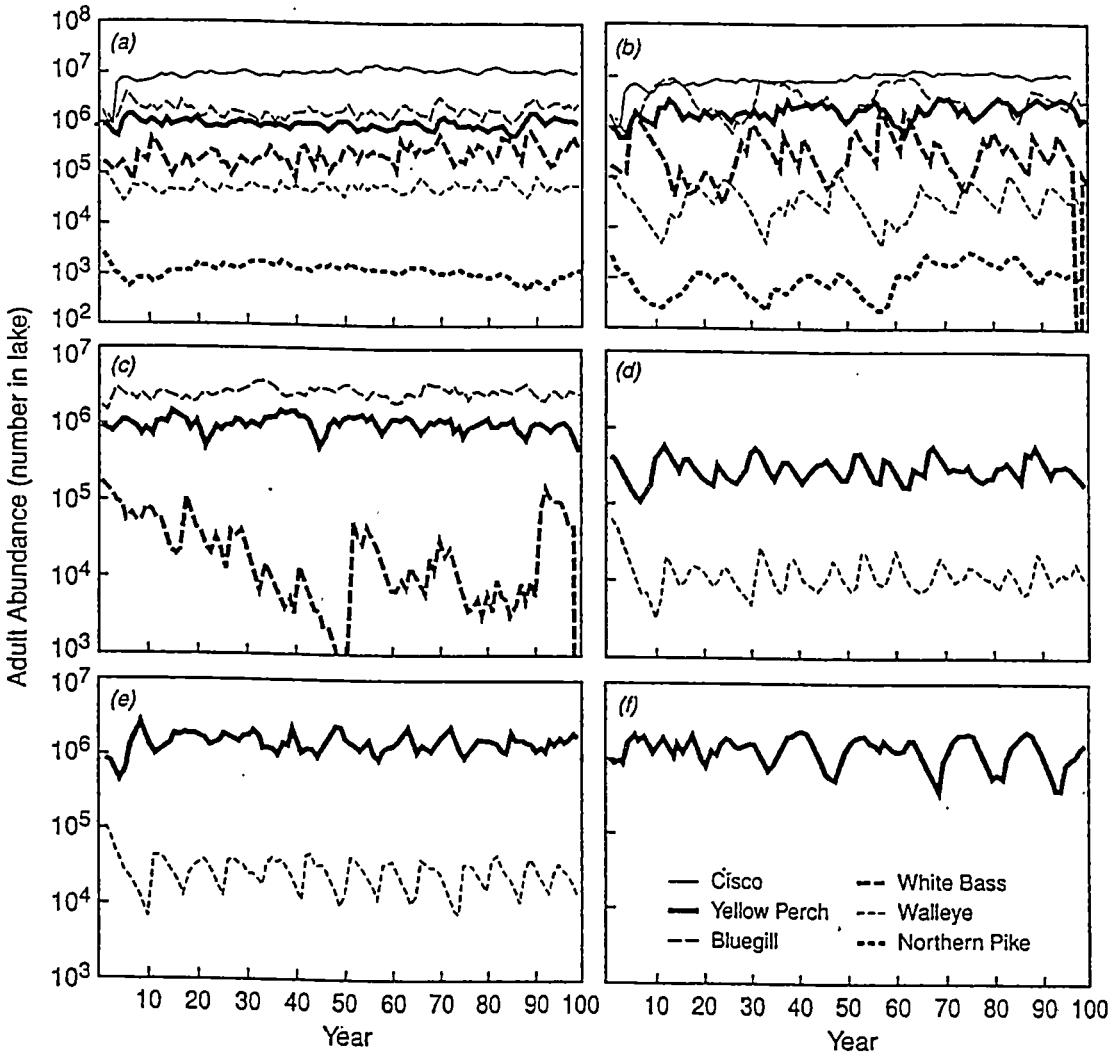


Figure 9. Annual abundances of all species under baseline conditions in the six alternative food webs. (a) low-biomass 6-species (b) high-biomass 6-species (c) 3-species (d) low-biomass 2-species (e) high-biomass 2-species (f) 1-species.

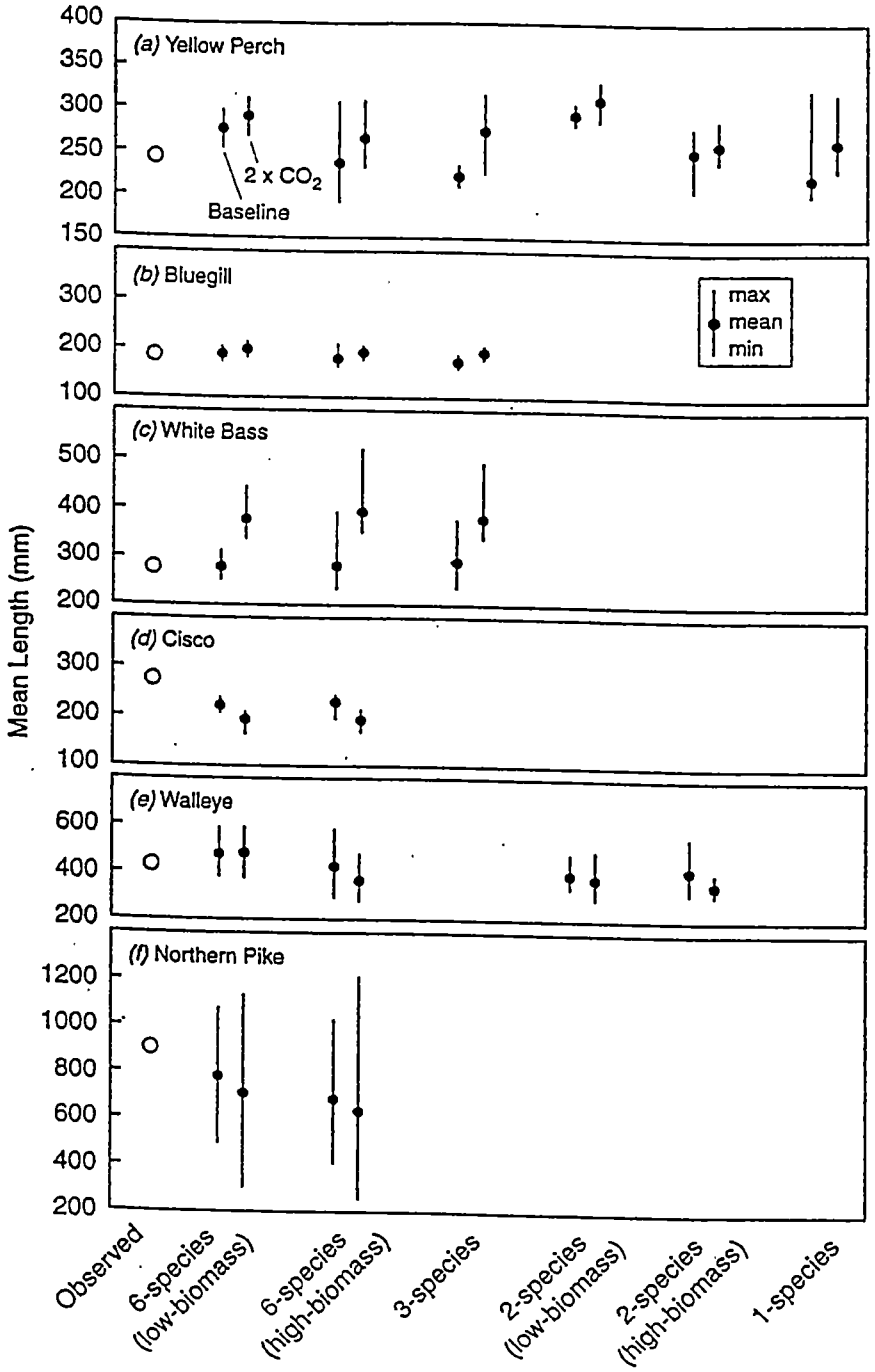


Figure 10. Minimum, mean, and maximum age 5 mean lengths for baseline and 2x $CO_2$ simulations for all six alternative food webs. (a)yellow perch, (b) bluegill, (c) white bass, (d) cisco, (e) walleye, (f) northern pike. Observed mean values, shown as horizontal lines, are from Becker, G.C., 1988. The Fishes of Wisconsin. Univ. of Wisc. Press, Madison.

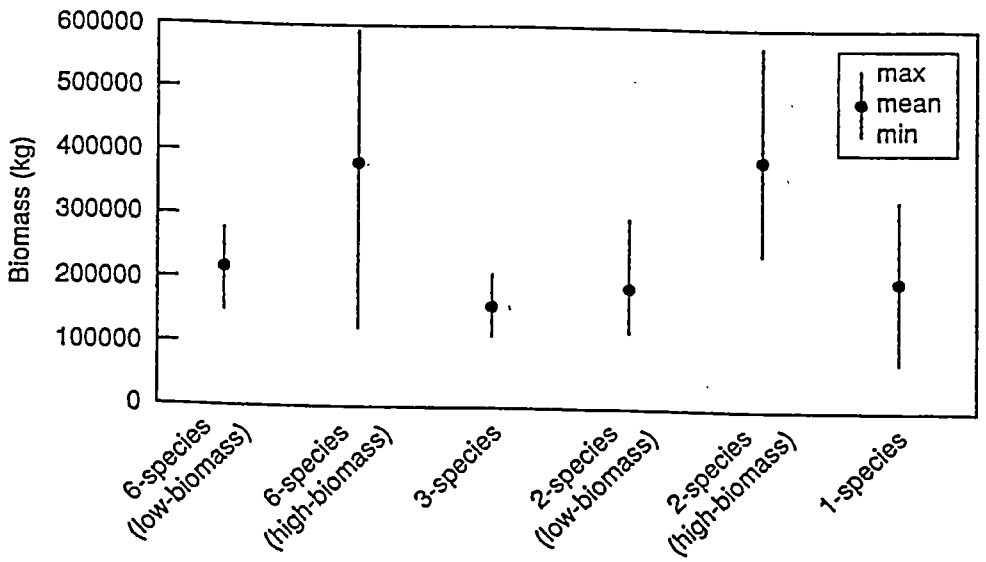


Figure 11. Minimum, mean, and maximum yellow perch adult biomass for baseline conditions in each of the the six alternative food webs.

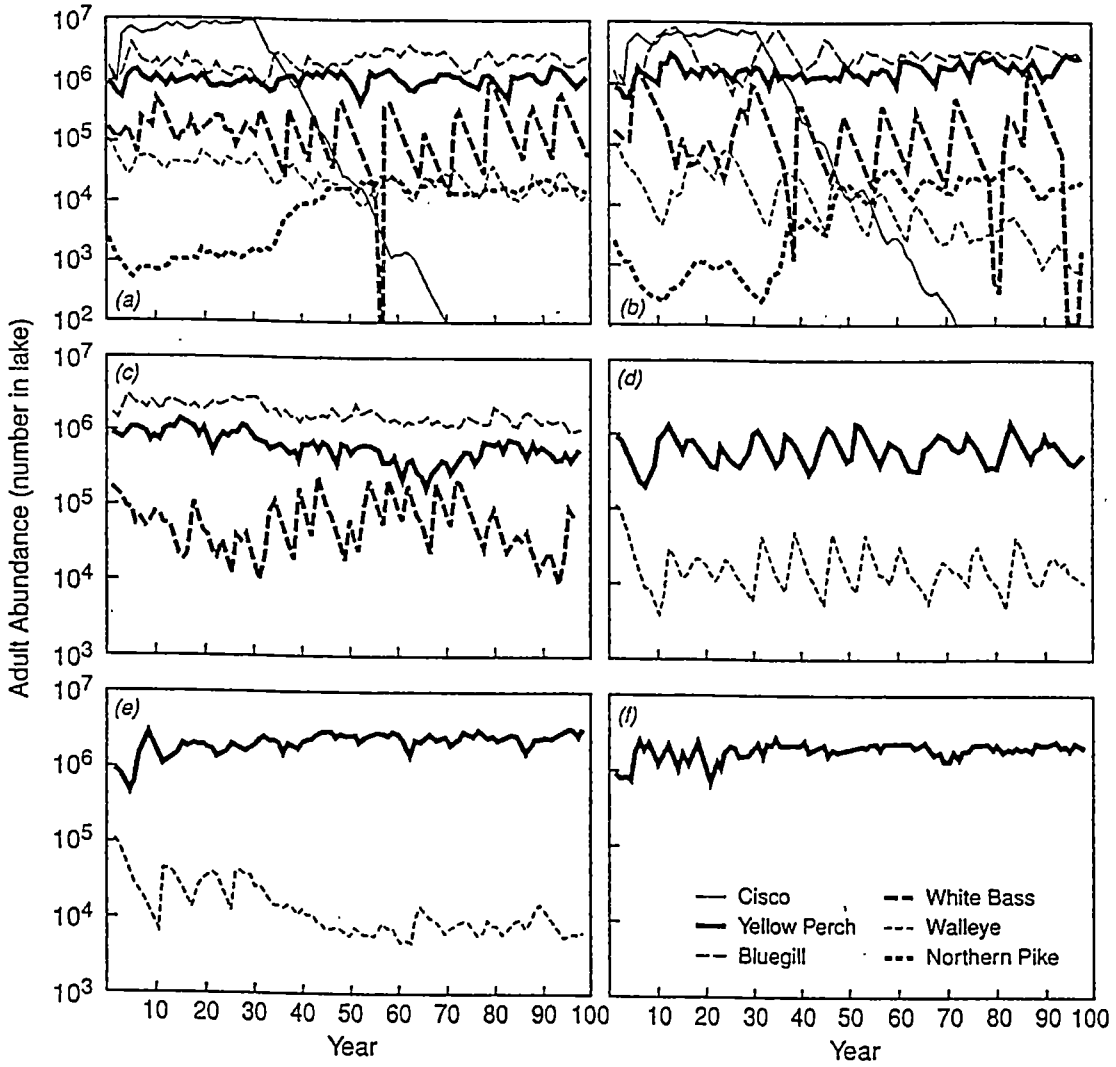


Figure 12. Annual abundances of all species under 2x $CO_2$ conditions in the six alternative food webs. (a) low-biomass 6-species (b)high-biomass 6-species (c) 3-species (d) low-biomass 2-species (e) high-biomass 2-species (f) 1-species.

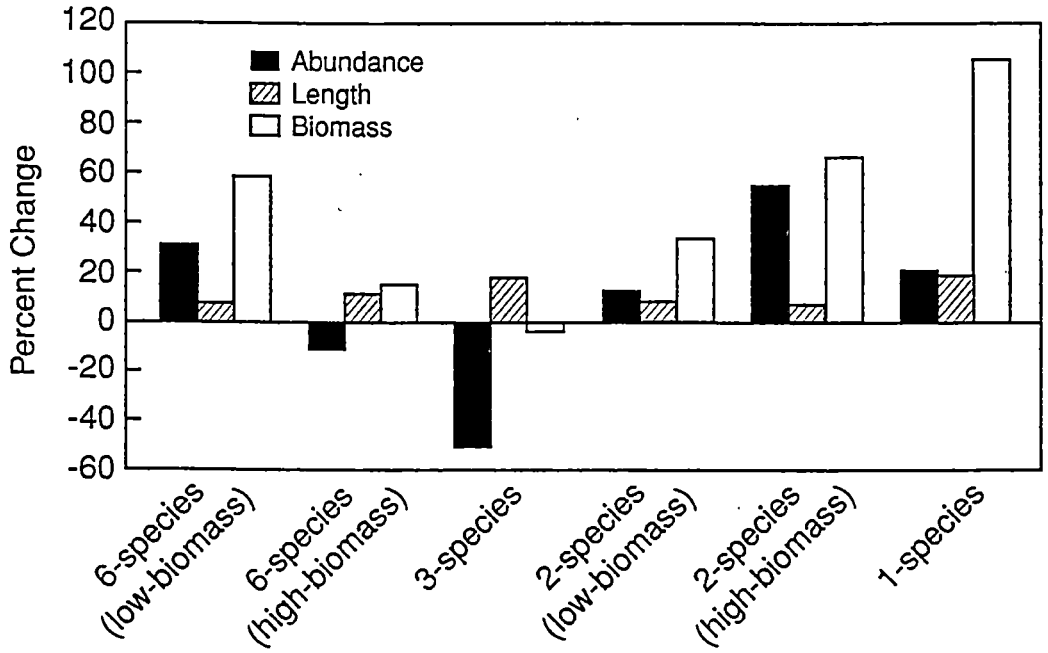


Figure 13. Percent change in average adult yellow perch abundance, mean length, and biomass between the 2x $CO_2$ and baseline simulations for the six alternative food webs.

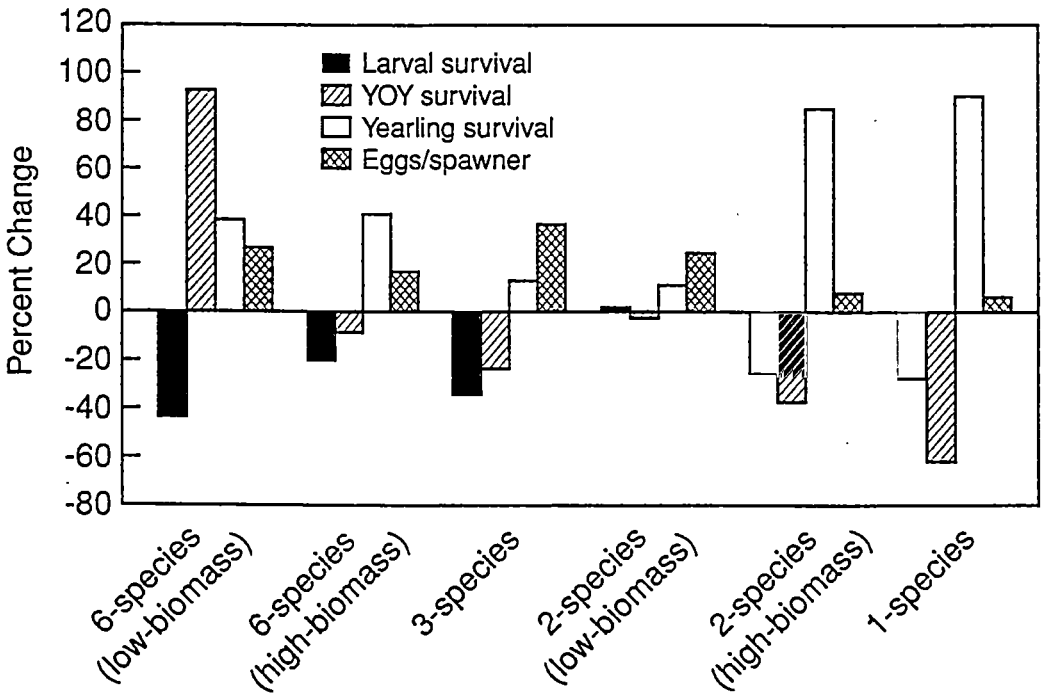


Figure 14. Percent change in average yellow perch larval, YOY, and yearling survival, and fecundity (eggs/spawner), between the 2x $CO_2$ and baseline simulations for all six alternative food webs.

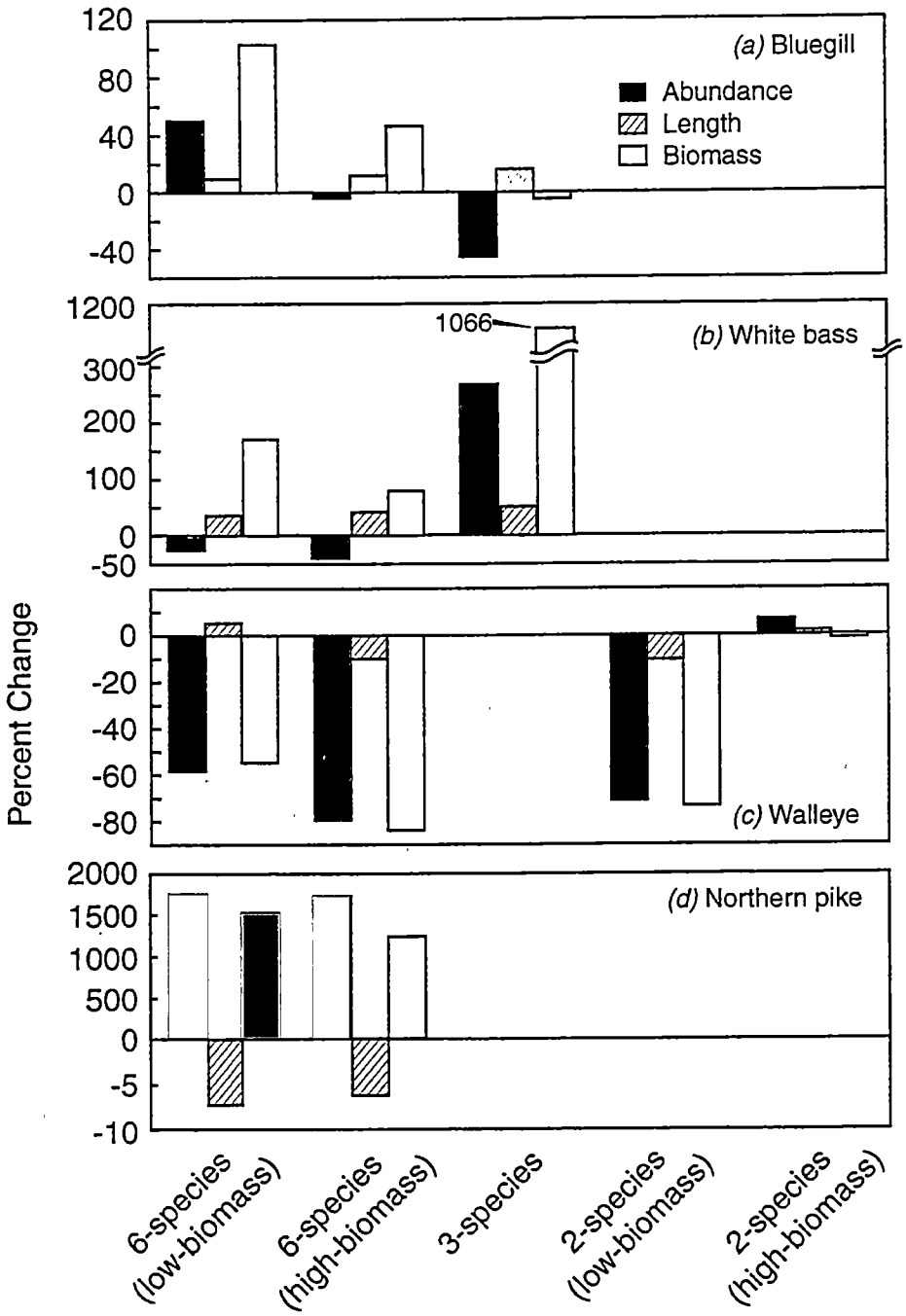


Figure 15. Percent change in average adult abundance, mean length, and biomass between 2x $CO_2$ and baseline simulations for all six alternative food webs for (a) bluegill, (b) white bass, (c) walleye, (d) northern pike.

# Part 4

# Summary and Conclusions

## 1.0 Objectives

The primary goal of this research was to explore the role of food web interactions in mediating population responses to environmental and biotic change. We selected to address this goal by using an individual based food web model calibrated to Lake Mendota, Wisconsin. The specific ecological perturbations we examined were biomanipulation vs cisco die-off, and global climate change. Biomanipulation and cisco die-off were historical events for which our predictions could be judged against observations. Climate change predictions were more speculative, but at the same time allowed for greater theoretical exploration through the use of alternative food webs.

A secondary goal for this project was to explore the practicality of the individual-based approach in modeling many-species food webs. We constructed a spatially explicit, multi-generational, many-species, individual-based, fish food web simulator, and calibrated our model to realistically simulate the six-species food web in Lake Mendota, Wisconsin. We compared the responses of alternate calibrations of the model under identical perturbations. Several strengths and limitations to our approach were identified. Some of the limitations may be addressed in the future by changes to the model or by increases in computing power, other limitations are inherent costs of a highly complex model.

## 2.0 Summary of Results

### *2.1 Model Overview*

Six fish species are represented: yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), bluegill (*Lepomis macrochirus*), white bass (*Morone chrysops*), and cisco (*Coregonis artedii*). These species comprise the major species in Lake Mendota (Kitchell 1992; B. Johnson, personal communication).

The model is multi-generational, with the young-of-the-year (YOY) population determined by spawning of adults. Individuals develop through the following life stages: egg, yolk-sac larva, larva (exogenous feeding to 20 mm), YOY juvenile (20 mm to age-1), yearling, and adult. An adult that has reached maturity is also a spawner. Eggs and yolk-sac larvae are followed as

cohorts from each spawner. Feeding fish are followed as individuals throughout their lives. Feeding, growth, reproduction, mortality, and movement are evaluated daily. For each individual, the model keeps track of total length (L, mm), wet weight (W, grams), life stage, age (years), and spatial compartment.

The lake environment is separated into three homogeneous compartments representing the littoral, epilimnetic, and hypolimnetic zones. Environmental variables in each compartment include daily temperature and dissolved oxygen (DO). Water temperature varies with lake depth. By governing the maximum water column depth inhabitable by fish, DO affects the available habitat and water temperatures fish experience. Prey densities in each compartment include zooplankton, benthos, forage fish, and the YOY and yearling individuals of the six modeled species.

*2.2 Model Corroboration with Lake Mendota*

Model calibration resulted in two versions of the 6-species Lake Mendota food web, differing in their degree of interannual variability. For both of these versions, predicted adult biomass, lengths at age, and diets were generally within the range of observed values for Lake Mendota. The low variability version was calibrated with lower piscivore half-saturation feeding parameters (K), indicating more efficient feeding by piscivores, and lower zooplankton turnover rates. Lower zooplankton turnover combined with more effective predators reduced the time lag between predator and prey numerical responses. Reduced time lags enhances stability in predator-prey models (Murdoch and Bence 1987).

*2.3 Baseline Correlation Analysis*

Correlation analysis of high-variability 6-species baseline simulations indicate that larval survival is heavily influenced by competition, yearling survival by predation, and YOY juvenile survival by both. Adult growth depended on competition for planktivore species, and on prey density for piscivores. Depensatory mortality was observed in yearling bluegills due to swamping

of predators. White bass dynamics were characterized by recurrent year class failures in years of high predation pressure. Cisco dynamics were essentially independent of other species.

*2.4 Biomanipulation*

Cisco die off caused greater and more prolonged decreases in total zooplankton consumption than piscivore enhancement. Piscivore enhancement alone resulted in an initial decrease in zooplankton consumption of nearly the same magnitude as cisco die-off, followed by an overshoot period of higher than baseline consumption. The long term average zooplankton consumption under piscivore enhancement alone was within 1% of baseline. Cisco die off alone resulted in a large initial decrease in total zooplankton consumption which returned slowly to baseline as cisco biomass recovered. The combined effect of cisco die-off and piscivore enhancement appeared as the simple sum of their separate effects.

The long term effects on species biomass of piscivore enhancement differed between the low- and high-variability baseline simulations. In the low-variability version, piscivore enhancement resulted in a temporary loss of northern pike, while in the high-variability version piscivore enhancement resulted in the extinction of walleye and its replacement by northern pike. These effects were modified when combined with a cisco die-off. When piscivore enhancement and cisco die off were combined northern pike did not recover in the low-variability version, and walleye did not become extinct in the high-variability version.

YOY juvenile and larval survival illustrate how predative and competitive interactions caused complex indirect responses to piscivore enhancement. YOY survival of yellow perch, bluegill, and northern pike exhibited a delayed overshoot response. A period of increased YOY survival followed the initial period of decreased survival (a direct effect of piscivore enhancement). Larval survival increased for planktivores (except cisco) and decreased for piscivores following piscivore enhancement. Because larvae are not subject to predation in the model, changes in larval survival are necessarily indirect effects.

None of the three long-term stocking regimes analyzed yielded ideal management results. Periodic stocking caused repeated periods of high zooplankton consumption due to altered predator-prey cycles. Continuous low-level stocking had little effect on zooplankton, and continuous high level stocking had deleterious effects on piscivore growth rates and sizes by causing prolonged reduction in their food base.

*2.5 Alternate Food Webs*

Six alternate food webs were calibrated from the six species Lake Mendota species pool. The low-variability and high-variability versions used in the biomanipulation study are referred to in the climate change study as the low-biomass and high-biomass 6-species food webs respectively. A 3-species competition food web including yellow perch, bluegill, and white bass, a low-biomass and a high-biomass version of a 2-species predator-prey food web including yellow perch and walleye, and a 1-species food web including only yellow perch, were produced by removing species from the low-biomass 6-species food web, then readjusting calibration parameters. The 3-specie, low-biomass 2-species, and 1-species food webs were calibrated so that yellow perch biomass matched the low-biomass 6-species food web. Yellow perch biomass in the high-biomass 2-species food web matched the high-biomass 6-species food web with no change in calibration parameters. Low-biomass calibrations of the 6- and 2-species food webs had lower K-values for piscivores (indicating more effective predators) than in the high-biomass calibrations. Thus the low-biomass versions were calibrated to emphasize the effects of predation, while the high-biomass versions were calibrated to emphasize competition.

*2.6 Climate Change*

Population responses of yellow perch to climate change depended upon the food web arrangement, and on calibration choices within a given food web. Yellow perch abundance under climate change decreased relative to baseline for the high-biomass 6-species and 3-species food webs, whereas abundance increased in the 1-species, both versions of the 2-species, and the

low-biomass 6-species food webs. Yellow perch adult mean length increased in all food webs, though the magnitude of this increase depended on food web. Increases in length were generally greater in food webs where abundance decreased. Changes in biomass reflected the combined effects of changes in abundance and length.

Changes in species abundance were suggestive of the differential roles of competition and predation among the food webs. The greater importance of competition in the 3-species and high-biomass 6-species food webs resulted in a decrease in yellow perch and bluegill abundance, whereas the greater importance of predation in the low-biomass 6-species food web permitted yellow perch and bluegill to increase. Changes in yellow perch growth and survival were difficult to interpret, and reflect the complex interactions of competitive and predative effects.

Responses of species other than yellow perch were generally consistent with expectations based on bioenergetics, and also reflected competitive and predative interactions in the model. Species tolerant of higher temperature tended to increase. Northern pike replaced walleye as the dominant piscivore in both 6-species food webs. Warm water white bass was the most temperature tolerant and increased substantially in the 3-species competition food web. Warm water bluegill had less scope for growth than white bass. Bluegill decreased in abundance in the 3-species food web where white bass increased most, but increased in the low-biomass 6-species food web where competition was less intense. Cold water cisco became extinct.

**3.0 Concluding Remarks**

We have demonstrated the importance of considering food web interactions for predicting population responses to biotic and environmental changes. In Part 2, we showed how competitive and predative interactions within the model affect important vital rates at each life stage. Model responses to piscivore enhancement reflected the expected direct effects of predation, as well as indirect effects due to density dependence. Indirect food web effects compensated for increased predation, resulting in an "overshoot" response in years following piscivore enhancement. Shifts in species dominance within the food web were also observed, with northern pike replacing

walleye, and bluegill replacing yellow perch in some simulations. Manipulation of piscivore species are shown to have far reaching effects, even beyond the anticipated "trophic cascade".

In Part 3, yellow perch population responses to climate change were shown to depend upon food web structure. Cool water yellow perch abundance decreased in food webs where competition with warm water white bass and bluegill was most intense. However in food webs where interspecific competition was absent, or reduced by predation, yellow perch abundance increased as predicted by its bioenergetics. We also observed extinction of cisco, and the replacement of walleye by northern pike. The loss of cisco was seen to have impacts on zooplankton dynamics in our model as well as in Lake Mendota (Rudstam et al. 1993; Johnson and Kitchell 1996) and predation by northern pike is possibly a more effective control on prey populations in Lake Mendota than predation by walleye (Kitchell and Carpenter 1992). To understand the effects of climate change in Lake Mendota fully, we must consider all of these changes together. This can only be accomplished by considering the full food web, rather than isolated populations.

This paper expands the scope of the individual-based modeling approach to a many-species food web. We presented a many-species, full life cycle, individual-based fish food web simulation model in a spatially explicit lake environment. The model was calibrated to realistically simulate a specific lake food web, then applied to answer questions of both practical and theoretical importance.

The model was computationally intensive. Each model day, each model fish is evaluated for consumption, growth, mortality, reproduction, and movement. Over the course of a 100 year simulation with 6-species, this process is repeated 139 million times, requiring 10 hours CPU time on a DEC Alpha 3000 workstation. In fact, if all the model fish evaluated in the course of this study (final runs only - not counting trial and error calibration) were placed nose to tail, assuming an average size of 250 mm, they would reach approximately 600,000 kilometers - two full light-seconds, or 15 times around the equator of the earth.

Even so, there were still many important features of the lake ecosystem which were not included in the model. Some, such as the effects on egg survival of competition for favorable spawning sites, were reluctantly abandoned due to the lack of sufficient data for a quantitative model. Other features, such as a detailed model for water quality, zooplankton dynamics, or angler numbers and effort, were simply beyond the practical scope of this study, despite their obvious importance. Given the computational time required for simulations and the difficulties we already had in interpreting results, it is doubtful whether any further model complexity could have greatly improved our analysis.

Our results also highlight the problem of calibration and uniqueness of parameter values in complex models. Initial calibration of the model for Lake Mendota represented a significant portion of model development time. The addition of each new species represented a geometric increase in the number of potential interactions in the model. More and more calibration trials were required for a model which ran slower and slower. We also showed that model results can depend strongly on calibration decisions. As computer power continues to increase, the computational limitations will continue to decrease. However, as computational barriers to model complexity are removed, model calibration will become more and more of a problem. Careful model development and implementation will be needed to minimize the number of required parameters. In hindsight, many inefficiencies in our approach are now seen, whose removal could increase speed and reduce the number of parameters substantially. Still, there seems to be no way of avoiding the fact that a model of this size will require extensive calibration, and as models become more complex, sensitivity to parameterization is also likely to increase. Computationally efficient methods for objective model calibration are desperately needed.

We have demonstrated that consideration of food web complexity cannot be ignored. We have also argued for the necessity of considering the individual as the fundamental unit in population and community models. Yet, we have also demonstrated that the very complexity of food web models can raise questions about their predictive power and robustness due to sensitivity to calibration. We must therefore ask, is genuine prediction in ecology even possible?

Even simple ecological models can generate unpredictable "chaotic" dynamics (May 1974). Inherent unpredictability may only be masked, not removed, in complex "realistic" simulations such as this work. Climatic variability, human disturbance, species invasions, epidemics, all add further dimensions of unpredictability. The present state of a system can depend on the historical sequence of random events (Drake 1990). It is said there is no such thing as a typical year for Lake Mendota (Kitchell 1992). Then why attempt to predict a typical response in a system where surprises are the norm?

In some respects, a predictive theory of ecology is like a predictive theory of history. Both fields contain vast areas of uncertainty, and are sensitive to small events occurring at critical moments, and to the local character of a particular region. Historians and ecologists are both better at explaining the past than at predicting the future. At least ecologists don't have to deal with the personality of a single individual with control over the whole population. To our knowledge, there is no President of the United States of Walleye to issue ultimatums to His Majesty, the Emperor of Pike.

Not long ago, weather prediction was no more reliable than predictions in community ecology are today. Meteorologists also must contend with complex dynamical systems, random events, and anomalous local effects. In time, as we continue to learn about the basic mechanisms driving ecological systems, and as our ability to synthesize interdependent processes into realistic models becomes more refined, our ability to predict future events will also improve. In the mean time, the very attempt to make predictions in the face of uncertainty refines our understanding of complex ecological systems. Modeling efforts such as this one are a step along the way, building on the contributions of others, and providing a basis for further development in the future.

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# Appendix 3:

# Parameter Estimates for Lake Mendota

# Appendix 3

Species and environmental parameter estimates for the Lake Mendota version of the individual-based model. Parameters are presented in separate tables corresponding to respiration, growth and consumption, reproduction, mortality, environmental variables, and the K parameters of the functional response relationship. Tables 6 and 7 refer to Part 3. All other tables refer to the model description given in Part 2.

Sources are indicated in the tables by superscripts: a) Becker, 1988. b) Breck, 1993. c) Carlander 1977. d) Coutant, 1977. e) Franklin and Smith, 1963 f) Kitchell, 1992 g) Rose, et.al. in review. h) Hewitt and Johnson, 1992. i) Johnson 1993, j) Post, 1990. k) callibration. l) Johnson, B. W., unpublished data m) educated guess.

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Table 1. Parameter values for respiration. Numbers in parentheses indicate values used for larvae of that species.

| parameter | defined | y. perch [G,J] | walleye [G,J] | pike [H] | bluegill [H,(B)] | w. bass [I] | cisco [H] |
|---|---|---|---|---|---|---|---|
| $T_{pref}$ [D] | page 21 | 20.6 | 20.6 | 24 | 31 | 29 | 10 |
| $R_a$ | eq. 10 | 0.035 | .0271 (.056) | 0.0025 | 0.0154 | .0024(.013) | 0.0031 |
| $R_b$ | eq. 10 | -0.2 | -0.15 (-0.22) | -0.18 | -0.2 | -0.252 | -0.112 |
| eq. set | table 1 | 2 | 2 | 1 | 2 | 3 | 1 |
| RQ | table 1 | 2.1 | 2.1 | 0.55 | 2.1 | .093 (2.16) | 0.047 |
| RTO | table 1 | 28 (32) | 32 (27) | 0.1222 | 36 (37) | 31.3 | 0.025 |
| RTM | table 1 | 32 (34) | 32 (30) | 0 | 40 (41) | 34.3 (31.3) | 0 |
| RK1 | table 1 | ** | ** | 1 | ** | ** | 7.23 |
| RK4 | table 1 | ** | ** | 0 | ** | ** | 0.25 |
| ACT | table 1 | 1.0 (4.4) | 2.0 (3.0) | 1 | 1.1 (1.0) | 1.0 (1.5) | 0 |

Table 2. Parameter values for growth and consumption. Numbers in parentheses indicate values for larvae of that species.

| parameter | defined | perch [G,J] | walleye [G,J] | pike [H] | bluegill [H,(B)] | w. bass [I] | cisco [H] |
|---|---|---|---|---|---|---|---|
| $L_a$ | eq. 8 | 39.1(45.9) | 49 | 60[C](55.1)[E] | 43.4 (42.0) | 50.3 | 53.2[A] |
| $L_b$ | eq. 8 | .34 (.33) | .33 (.31) | .32[C] (.34)[E] | .297 (.299) | 0.303 | .325[A] |
| E | eq. 9 | 0.57 | .64 (.57) | 0.634 | 0.576 | 0.62 | 0.57 |
| $C_a$ | eq. 11 | .25 (.51) | .25 (.45) | 0.303 | .182 (.273) | .604 (.480) | 1.61 |
| $C_b$ | eq. 11 | -.27 (-.42) | -0.27 | -0.18 | -0.274 | -0.252 | -0.32 |
| CTM | Table 1 | 28 (32) | 28 | 34 | 36 (37) | 32 (31.3) | 26 |
| CTO | Table 1 | 23 (29) | 22 (25) | 24 | 27 (31) | 27.8 (28.3) | 16 |
| CQ | Table 1 | 2.3 | 2.3 | 2.59 | 2.3 | 2.86 | 3.53 |

Table 3. Parameter values for reproduction.

| parameter | defined | perch[G] | walleye[G] | pike | bluegill | w. bass | cisco |
|---|---|---|---|---|---|---|---|
| $M_m^{A,C}$ | eq. 5 | 0.0109 | 0.008 | 0.0028 | 0.0192 | 2.0* | 0.0107 |
| $M_b^{A,C}$ | eq. 5 | -1.489 | -3 | -1.4 | -0.827 | 0 | -2.322 |
| $SP_{max}^{A,C}$ | page 18 | 11 | 13 | 4.4 | 26.7 | 26.1 | 6 |
| $SP_{min}^{A,C}$ | page 18 | 7 | 4 | 1.1 | 19.4 | 12.5 | 3 |
| $SP_{mode}^{A,C}$ | page 18 | 9 | 7 | 2.5 | 23 | 19.1 | 4 |
| $F_m^A$ | eq. 6 | 183 | 70.6 | 22.6 | 203.56 | 845 | 30.1 |
| $F_b^A$ | eq. 6 | -3658 | -7900 | 0 | 0 | 0 | 0 |
| $D_a$ (eggs)$^{A,C}$ | eq. 7 | 140 | 45 | 109.7 | 66.35 | 2 | 168.4 |
| $D_c$ (eggs)$^{A,C}$ | eq. 7 | -0.17 | -0.1 | -0.216 | -0.1414 | 0 | -0.126 |
| $D_a$ (ys larv)$^A$ | eq. 7 | 3 | 8 | 10 | 4 | 8 | 3 |
| $D_c$ (ys larv)$^A$ | eq. 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| egg weight[A] | page 19 | 0.00115 | 0.0019 | 0.0068 | 0.00045 | 0.00009 | 0.0049 |

Table 4. Parameter values related to mortality. Daily mortality rates (1/d) are shown for egg, yolk sac larva, and larva; annual survival fractions are shown for YOY, yearling, and adults.

| | y. perch | walleye | n. pike | bluegill | w. bass | cisco |
|---|---|---|---|---|---|---|
| egg[K] | 0.18 | 0.18 | 0.18 | 0.18 | 0.18 | 0.03 |
| yolk sac[K] | 0.18 | 0.18 | 0.18 | 0.18 | 0.18 | 0.18 |
| larvae (low var.)[K] | .065 | .100 | .080 | .120 | .320 | .125 |
| larvae (high var.)[K] | .065 | .095 | .085 | .200 | .280 | .128 |
| yoy[M] | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 |
| yearling[M] | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 |
| age 2+, natural[L] | 0.90 | 0.90 | 0.90 | 0.90 | 0.90 | 0.90 |
| age 2+, fishing[L] | 0.70 | 0.60 | 0.60 | 0.70 | 0.70 | 0.80 |

Table 5. Parameters values related to environmental variables in Part 2. Parameters for temperature are defined in equation 1. Parameters for zooplankton are for the following function: $Y=a + b*\exp[-0.5*((x-c)/d)^2]$. Daily temperatures are shown in Figure 2, and equilibrium zooplankton densities are shown in Figure 4.

| | epilimnion | hypolimnion | littoral |
|---|---|---|---|
| Max. temp [F] | | | |
| $T_a$ | 10.53 | 8.895 | 10.53 |
| $T_b$ | -11.19 | -6.652 | -11.19 |
| $T_c$ | -7.35 | -5.411 | -7.35 |
| Min. temp [F] | | | |
| $T_a$ | 8.895 | 7.324 | 10.53 |
| $T_b$ | -6.652 | -4.689 | -11.19 |
| $T_c$ | -5.411 | -4.008 | -7.35 |
| *D. galeata* [L] | | | |
| a | 0.18463 | 0.09942 | 0.18463 |
| b | 2.0277 | 1.0918 | 1.72 |
| c | 293.33 | 293.33 | 293.33 |
| d | 30 | 30 | 30 |
| *D. pulicaria* [L] | | | |
| a | 0.50498 | 0.27191 | 0.50498 |
| b | 7.0785 | 3.8115 | 5.9 |
| c | 153.5 | 153.5 | 153.5 |
| d | 30 | 30 | 30 |

Table 6. Parameters values related to temperature (T) in Part 3. The form of the regression equations is: $T = T_a + T_b \cos(.0172\ t) + T_c \sin(.0172\ t)$, where t is calendar day.

| | Surface | 10 m depth | 20 m depth |
|---|---|---|---|
| Baseline temperature | | | |
| $T_a$ | 10.53 | 8.895 | 7.324 |
| $T_b$ | -11.19 | -6.652 | -4.689 |
| $T_c$ | -7.35 | -5.411 | -4.008 |
| 2x $CO_2$ temperature | | | |
| $T_a$ | 13.75 | 12.06 | 6.328 |
| $T_b$ | -11.39 | -9.803 | -5.001 |
| $T_c$ | -5.271 | -5.134 | -2.951 |

Table 7. Parameter values related to dissolved oxygen in Part 3. The form of the regression equations is: $D_{max}$ , $T_{DO}$ = a + b * exp[-0.5 * ((t-c)/d)$^2$ ] , where t is calendar day.

| Dissolved Oxygen Conditions | | | | |
|---|---|---|---|---|
| | $D_{max}$ - baseline | $T_{DO}$ -baseline | $D_{max}$ - 2x $CO_2$ | $T_{DO}$ - 2x $CO_2$ |
| a | 24.28 | 0.33 | 25.56 | 0.054 |
| b | -15.53 | 20.44 | -19.01 | 25.73 |
| c | 217.3 | 219.5 | 220.6 | 222.87 |
| d | 41.62 | 47.38 | 67.33 | 51.04 |

Table 8. Values of the K parameters of the functional response relationship (equation 13) for yellow perch. Values for zooplankton (zp) are number/L, for benthos are number/m2, and for fish as prey are number/m3. These values were calibrated.

| Yellow Perch | | | |
|---|---|---|---|
| size class | prey type | Low variability | High variability |
| 0-20 mm | small zp | 0.1 | 0.1 |
| 20-45 mm | small zp | 1.0 | 1.0 |
| | large zp | 0.5 | 0.5 |
| 45-75 mm | large zp | 0.3 | 0.3 |
| | benthos | 1000 | 1000 |
| 75+ mm | large zp | 0.7 | 0.7 |
| age 2 + | large zp | 10.0 | 12.0 |

Table 9. Values of the K parameters of the functional response relationship (equation 13) for walleye. Values for zooplankton (zp) are number/L, for benthos are number/m2, and for fish as prey are number/m3. These values were calibrated.

| Walleye | | | |
|---|---|---|---|
| size class | prey type | Low variability | High variability |
| 0-20 mm | small zp | 0.3 | 0.3 |
| 20-45 mm | large zp | 1.0 | 1.0 |
| | benthos | 400 | 450 |
| | model fish | 4.1 | 4.1 |
| 45-100 mm | benthos | 400 | 450 |
| | model fish | 0.8 | 0.8 |
| | forage fish | 0.5 | 0.5 |
| 100 + mm | benthos | 850 | 800 |
| | model fish | 0.5 | 0.7 |
| | forage fish | 0.01 | 0.05 |
| age 2+ | model fish | 1.2 | 1.5 |
| | forage fish | 0.5 | 0.5 |

Table 10. Values of the K parameters of the functional response relationship (equation 13) for northern pike. Values for zooplankton (zp) are number/L, for benthos are number/m2, and for fish as prey are number/m3. These values were calibrated.

| Northern Pike | | | |
|---|---|---|---|
| size class | prey type | Low variability | High variability |
| 0-20 mm | small zp | 0.2 | 0.2 |
| 20-45 mm | large zp | 1.0 | 1.0 |
| | benthos | 400 | 500 |
| | model fish | 12.1 | 12.1 |
| 45-100 mm | benthos | 1000 | 1500 |
| | model fish | 0.4 | 0.4 |
| | forage fish | 0.2 | 0.2 |
| 200 + mm | model fish | 1.9 | 2.2 |
| | forage fish | 0.17 | 0.03 |
| age 2+ | model fish | 19.0 | 22.0 |
| | forage fish | 0.5 | 0.5 |

Table 11. Values of the K parameters of the functional response relationship (equation 13) for bluegill. Values for zooplankton (zp) are number/L, for benthos are number/m2, and for fish as prey are number/m3. These values were calibrated.

| Bluegill | | | |
|---|---|---|---|
| size class | prey type | Low variability | High variability |
| 0-20 mm | small zp | 0.1 | 0.1 |
| 20-45 mm | small zp | 1.0 | 1.0 |
| | large zp | 1.0 | 1.0 |
| | benthos | 400 | 400 |
| 45-75 mm | large zp | 6.0 | 6.0 |
| | benthos | 2000 | 2000 |
| 75 + mm | large zp | 8.0 | 8.0 |
| | benthos | 8500 | 8500 |
| age 2+ | large zp | 35 | 35 |
| | benthos | 9000 | 9000 |

Table 12. Values of the K parameters of the functional response relationship (equation 13) for white bass. Values for zooplankton (zp) are number/L, for benthos are number/m2, and for fish as prey are number/m3. These values were calibrated.

| White Bass | | | |
|---|---|---|---|
| size class | prey type | Low variability | High variability |
| 0-20 mm | small zp | 0.1 | 0.1 |
| 20-45 mm | small zp | 1.0 | 1.0 |
| | large zp | 0.5 | 0.5 |
| | benthos | 1000 | 1000 |
| 45-75 mm | large zp | 0.5 | 0.5 |
| | benthos | 1000 | 1000 |
| 75+ mm | large zp | 2.5 | 2.5 |
| age 2 + | large zp | 40.0 | 40.0 |
| | model fish | 20.0 | 20.0 |

Table 13. Values of the K parameters of the functional response relationship (equation 13) for cisco. Values for zooplankton (zp) are number/L, for benthos are number/m2, and for fish as prey are number/m3. These values were calibrated.

| Cisco | | | |
|---|---|---|---|
| size class | prey type | Low variability | High variability |
| 0-20 mm | small zp | 1.0 | 1.0 |
| 20-45 mm | small zp | 18.0 | 18.0 |
| | large zp | 6.0 | 6.0 |
| 45-75 mm | large zp | 26.0 | 26.0 |
| 75+ mm | large zp | 36.0 | 36.0 |
| age 2 + | large zp | 75.0 | 75.0 |

# Vita

Dennis McDermot was born in Meadville, Pennsylvania on June 16, 1964. He entered Allegheny College, Meadville Pa, in September 1982, and received a Bachelor of Science degree in Biology and Mathematics in June 1986. After working for a year in an environmental testing laboratory, he entered the graduate program in Applied Mathematics at the University of Colorado, Denver in August 1987. In August 1989, he transferred to the University of Tennessee, Knoxville, Mathematics Department, where he completed a Master of Science degree in August 1992. After traveling for four months in India, he returned to the University of Tennessee in January 1993 to begin work on his Doctorate in Ecology. The Doctorate degree was completed in August 1998.