

Chapter 20

Individual-Based Model Analysis of Walleye and Yellow Perch Population Dynamics in Response to Changing Ecosystem Conditions

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Introduction

Walleye *Sander vitreus* and yellow perch *Perca flavescens* are the dominant predator and prey species in Oneida Lake and support a valuable recreational fishery. Abundances of both species have fluctuated greatly over time due to changes in weather and alterations in food web dynamics resulting from species irruptions and invasions of exotic species. At least one major ecological perturbation has impacted the Oneida Lake ecosystem in each decade since scientific monitoring of the lake began in the late 1950s, and some changes have occurred simultaneously. Although the population dynamics of walleyes and yellow perch in Oneida Lake have been well documented (reviews in Forney 1980; Mills and Forney 1988; Rudstam et al. Chapter 15), recent coincident invasions by zebra mussels *Dreissena polymorpha* that affect lower trophic levels (Idrisi et al. 2001; Mayer et al. 2000), and irruptions of double-crested cormorants *Phalacrocorax auritus* that prey on upper trophic levels (Rudstam et al. 2004) have complicated interpretation of factors influencing percid population dynamics.

A modeling approach often is useful for disentangling effects of multiple factors on fish population dynamics. Whereas statistical analyses of fish population dynamics may be complicated by overlapping effects of multiple factors on individual year classes, a simulation model analysis can cleanly compare differences in factor impacts on fish populations over multiple generations. An individual-based modeling (IBM) approach is particularly appropriate for studying percid population dynamics as many of the trophic interactions and fisheries regulations are size based. Rose et al. (1999) developed an IBM to simulate density-dependent mechanisms of walleyes and yellow perch in Oneida Lake. The model was calibrated to observed abundances, sizes, growth rates, and survival rates of walleye and yellow perch, and reproduced many of the density dependent relationships observed in the empirical database. Rutherford et al. (1999) used the IBM to simulate effects of a zebra mussel-induced energy shunt on walleye and yellow perch dynamics in Oneida Lake. Rose et al. (1996) used the

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model to illustrate multispecies modeling of fish population dynamics, and Sable and Rose (2008, Chapter 21) and Rose and Sable (2009) used the IBM to evaluate whether age and stage structured matrix projection models, which are easier to develop and analyze than IBMs, could simulate the complicated predator–prey dynamics observed between yellow perch and walleyes. The IBM was also adapted by Jaworska et al. (1997) to simulate contaminant effects on yellow perch, and modified by Brenton (1998) to simulate potential effects of ruffe *Gymnocephalus cernuus* invasion on walleyes and yellow perch in Lake Superior.

Despite the complexity of trophic interactions and high recruitment variability reported for walleye and yellow perch, management of the Oneida Lake fishery has remained surprisingly simple (Forney 1980). Before the 1970s, walleye and yellow perch fisheries operated without size or creel limits. By 1970, walleye regulations changed to a 302 mm (12 in) total length (TL) size limit, and a bag limit of five fish per day. After several studies quantified the influence of walleye stocking and yellow perch dynamics on walleye populations and yield, the New York State Department of Environmental Conservation (NYSDEC) adopted a relatively simple management plan (we call Forney’s algorithm) that adjusts walleye size limits depending upon the size of the adult walleye population and the expected incoming walleye recruitment (Forney 1980). Minimum size limits of walleye are set to 302 mm TL if the adult walleye population is relatively large, and incoming recruitment is average or high; minimum size limits are raised to 487 mm TL if numbers of adult walleyes and recruits decline to low levels.

In this chapter, we use the IBM to understand the equilibrium and historical responses of yellow perch and walleye populations to each of the known ecological periods that have occurred in Oneida Lake since the 1950s. Some of these simulations are an update of those previously reported in Rose et al. (1999) and Rutherford et al. (1999), and several of the simulations (e.g., cormorant effects) are new. We compared simulations of the equilibrium responses by walleyes and yellow perch to period conditions with responses predicted when the periods occurred for a decade, each in a historical sequence. The question we wanted to address was whether the yellow perch and walleye population dynamics predicted for each period in the historical sequence were near the equilibrium responses expected for that period, or were the dynamics still in transition. We also compared a constant age of first harvest with a dynamic setting of age of first harvest designed to mimic Forney’s algorithm to assess the ability of simple but dynamic management regulations to maintain percid stock size and harvest in the presence of changing ecosystem conditions. We hypothesized that Forney’s (1980) variable size (age in our version) management algorithm would maintain higher and less variable abundances and yields of both walleyes and yellow perch compared to a constant size (age) limit regulation.

Oneida Lake

Oneida Lake is a large (207 km²), productive lake in central New York with a mean depth of 6.8 m and a maximum depth of 16.8 m and is described in detail in Schneider et al. (Chapter 4) and De Stasio et al. (Chapter 13). Prevailing westerly winds and wind-driven currents generally maintain well-mixed, isothermal conditions throughout the summer. The general lack of vertical stratification and relatively small littoral zone implies that the lake could be approximated in the IBM simulations by a single, well-mixed volume.

We configured the IBM based on studies of the population dynamics and trophic interactions of Oneida Lake walleyes and yellow perch conducted from 1958 to 1991, before the zebra mussel invasion (Forney 1980; Mills and Forney 1988). There were three distinct ecological periods during this time: mayflies, baseline, and forage fish (Figure 1). The mayfly period (1958–1969) was characterized by high densities of mayflies *Hexagenia limbata*, and strong, stable year classes of walleye and yellow perch. The baseline period (1970–1978) was characterized by an absence of mayflies, generally low abundances of white perch *Morone americana* (forage fish), higher rates of walleye cannibalism, and lower and more variable recruitments of yellow perch and walleyes. Yellow perch were the dominant prey of walleyes, and white perch and young walleyes were of secondary importance as walleye forage (Forney 1974; Prout et al. 1990). The forage fish period (1979–1991) was characterized by strong year classes of young-of-year (YOY) white perch or gizzard shad *Dorosoma cepedianum*, higher recruitments of walleyes, and lower recruitments of yellow perch. Adult abundances of both species were highest during the mayflies period, and lower and more variable during the baseline and forage fish periods (Rose et al. 1999).

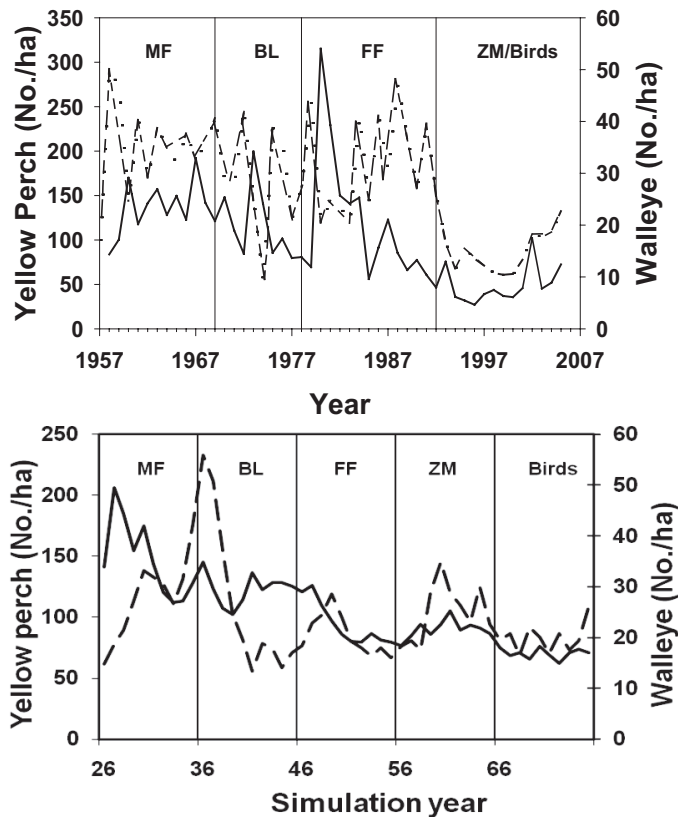


Figure 1. (Top) Observed trends in adult yellow perch abundance (solid line) and adult walleye adult abundance (dashed line) over time in Oneida Lake, New York. The approximate time periods are shown that correspond to the mayfly (MF), baseline (BL), forage fish (FF), and zebra mussel plus cormorant (ZM/Birds) periods. (Bottom) Model simulated adult yellow perch abundance (solid line) and adult walleye abundance (dashed line) for the historical time series simulation. The approximate time periods are shown that correspond to the mayfly (yr 26–35), baseline (yr 36–45), forage fish (yr 46–55), zebra mussel (yr 56–65), and zebra mussel plus cormorant (yr 66–75) periods.

Since the early 1990s, two new periods have been documented in Oneida Lake related to the invasion of zebra mussels and an increase in cormorants (Figure 1). Zebra mussels were found in Oneida Lake in 1990 and were abundant by 1992 (Mayer et al. Chapter 9). The zebra mussel period (starting in 1992) involved major shifts in the water clarity and food web of Oneida Lake that negatively affected yellow perch and walleye abundances and recruitments (Rutherford et al. 1999; Mayer et al. 2000; Irwin et al. 2009). Zebra mussel effects continued in the next period that also saw a dramatic increase in cormorants. Cormorants were first observed nesting in Oneida Lake in 1984, and the population grew slowly and did not appear to have significant effects until the 1990s (Rudstam et al. 2004). Surveys conducted in 1997 documented 300 nesting pairs of cormorants in Oneida Lake, with 1,000–2,000 additional migrants using the lake from August through October (VanDeValk et al. 2002). This zebra mussels plus cormorants period (from 1992 to the present) was characterized by the continuing decline in the abundances and recruitments of walleyes and yellow perch.

Model Description

The IBM simulates the dynamics of yellow perch and walleye populations in Oneida Lake and is described in detail in Rose et al. (1999). The model begins with spawning of individual females of each species and simulates growth and survival of each female's progeny as they develop through successive life stages (egg, yolk sac larva, feeding larva, YOY juvenile, yearling, and adults age-2 and older). Yellow perch year classes are followed in the model until age 10 and walleyes until age 12. Predator–prey relationships represented in the model are depicted in Table 1.

The IBM represents daily dynamics of walleyes and yellow perch in a single, well-mixed compartment 260 m × 260 m × 6.8 m deep, scaled to represent Oneida Lake. The environment in the box consists of daily water temperature and the daily dynamics of a variety of prey types. Each year is 365 d long beginning on January 1.

Spawning and Eggs and Yolk sac Larvae

Adult walleyes and yellow perch are evaluated for spawning on day 100 (April 10) of each year. A female adult is mature if a generated random number is less than the fraction mature for her length. Fraction mature and fecundity increase with female size for both species. Each female is assigned a temperature of spawning from species-specific probability distributions; a female spawns on the first day that simulated temperature exceeds the temperature of spawning.

Each female's spawn of eggs is followed as a cohort. Day of hatching and day of first feeding are temperature-dependent and determined by accumulating daily fractional development rates until the cumulative value exceeds one. Numbers of eggs or yolk sac larvae in each cohort are reduced daily by specified daily mortality rates.

Feeding Life Stages

All first-feeding larvae are assigned identical initial lengths: 6.6 mm for yellow perch and 9 mm for walleyes. Development from larvae to YOY juveniles (metamorphosis) occurs at 20 mm for both species. On April 10 each year, surviving individuals of each year-class are promoted to the next age.

Table 1. Predator prey interactions defined in the percid individual-based model by non-zero vulnerability factors for respective life stages. "YOY" (young-of-year or age-0) are juveniles >20 mm TL. "Yrlg" (yearling) are age-1 individuals. The symbols "X" indicates allowed predator-prey interactions.

Prey/Predator	Yellow perch			Walleye			
	Larvae	YOY, Yrlg	Adult	Larvae	YOY	Yrlg	Adult
Zooplankton	X	X	X	X	X ²		
Benthos		X ¹	X	X	X	X	X
Forage fish					X	X	X
Larval perch				X	X	X	
Larval walleye				X	X	X	
YOY perch			X		X	X	X
YOY walleye					X	X	X
Yrlg perch						X	X
Yrlg walleye						X	X

¹ Yellow perch >30 mm

² Walleye < 100 mm

Daily growth in weight is represented by the standard Wisconsin-style bioenergetics equation (Hanson et al. 1997; Rose et al. 1999). We use parameter values from previously published bioenergetics models (for < age 1 YP YP, Post 1990; for \geq age 1 YP, Kitchell et al. 1977; for walleyes <43 mm TL: Madon and Culver 1993; for walleyes \geq 43 mm, Minton and McLean (1982), Fox (1991)). Maximum consumption and metabolism depend on an individual's weight and water temperature. Egestion, excretion, and specific dynamic action are computed as a fraction of realized consumption. An individual's weight is updated based on growth and then its new length is determined using length-weight relationships.

Realized consumption by individuals is based on a Type II multispecies functional response relationship and is dependent on prey densities, vulnerability of each prey type to the individual predator, and half-saturation constants (K) governing the rate of predator saturation. Vulnerability-adjusted prey densities are obtained by either multiplying densities by a factor less than one (for zooplankton and benthos), or by determining the vulnerability of each individual fish prey item (forage fish, yellow perch, and walleyes) based on its length relative to the predator length. Values of K are specified for size intervals of the predator and each prey type, and were determined by calibration.

A total of seven prey types are represented that encompass the dominant prey eaten by yellow perch and walleyes from first feeding through the adult stage. Zooplankton are represented by the sum of small and medium sized *Daphnia* spp., benthos by *Chironomidae*, and forage fish by YOY white perch and a mix of smaller-sized species. The remaining four prey types, YOY and yearling life stages of yellow perch and walleyes, are simulated as individuals in the model.

Each day, the densities of zooplankton, benthos, and forage fish are updated based on numbers consumed and a specified production rate using a modified logistic population growth function. Production rates of zooplankton, benthos, and forage fish are based upon

unpublished data for Oneida Lake and a review of benthic production and turnover rates (Rose et al. 1999). Equilibrium densities are the maximum densities of each prey type allowed in model simulations (i.e., carrying capacity in the logistic equation). Equilibrium densities of zooplankton are assumed time dependent based on the sum of small and medium *Daphnia* (<1.4 mm) measured weekly in Oneida Lake. Equilibrium density of benthos is assumed to be a constant, and forage fish equilibrium density is assumed to be 10 times higher between July and October than overwinter.

Larval mortality is specified as fixed rates for each species. Mortality rates of juvenile and yearling yellow perch and walleyes are computed from the consumption rates of walleye and yellow perch. Adult (age-2 and older) natural and fishing mortality of yellow perch, and natural mortality of walleyes, are assumed constant rates. Walleye fishing mortality varied by month and for each month was decreased by increasing numbers of YOY yellow perch, walleyes, and forage fish because walleyes are less apt to be caught when their natural forage is available (Lloyd 1996; VanDeValk et al. 2005, Chapter 17). Recent analysis indicates rates of fishing and natural mortality of walleye adults, and fishing mortality for yellow perch are similar to early estimates (Forney 1980; VanDeValk et al. 2002), while natural mortality of yellow perch adults has increased due to cormorant consumption (VanDeValk et al. 2002).

Numerics

The super-individual approach is used for yellow perch and walleye separately in the IBM (Rose et al. 1999). Super-individuals allow for a fixed number of model individuals to be used to simulate variation in population size. Each spawning female's egg is followed as a separate cohort until first feeding is reached. All first feeding larvae are accumulated over females to obtain the total number of first feeders on each day. Each year, 100 model individuals are allocated to days roughly in proportion to the number of first feeders, who are then added to the population on the appropriate day. The initial value of each added model individual is set to the number added on that day divided by the total number of first feeders on that day (e.g., 100 first feeders represented by 10 model individuals each would have an initial worth of 10). Upon reaching age-11 for perch and age-13 for walleyes, these model individuals are removed and replaced by the 100 new model individuals of the new year-class, so that there are always 1000 model individuals representing yellow perch and 1200 model individuals representing walleyes in the simulation. The sum of values over these individuals is the population value. All predator-prey interactions account for the values of individuals, and mortality from all sources reduces the value of individuals over time. To avoid walleyes eating more yellow perch than are available in a day, values of yellow perch and walleyes are updated for predation after each individual is evaluated.

Model Calibration and Corroboration

We previously calibrated the IBM under baseline conditions using yellow perch and walleye abundances, survival rates, growth rates, and diets from the Oneida Lake database. Model corroboration consisted of using the calibrated model to simulate a 30 year time series (after an initial 25 year-period to eliminate effects of initial conditions) consisting of 10 years of mayflies, 10 years of baseline, and 10 years of forage fish conditions. Model predictions of yellow perch and walleye abundances, mean lengths, and survival rates from the 30 years

compared favorably to data synthesized from the mayflies, baseline, and forage fish time periods in Oneida Lake (see Figure 3 in Rose et al. 1999).

Model Simulations

Representation of Periods

We simulated each of the five conditions (mayfly, baseline, forage fish, zebra mussels, cormorants) by altering the parameter values of the baseline model (Table 2). The mayfly and forage fish conditions were simulated the same way as in Rose et al. (1999). The mayfly effect involved increasing densities of benthos prey, reducing predation mortality on yellow perch, and reducing harvest of walleye during the typical mayfly emergence time period of June 5 to July 19. The forage fish effect simply involved increasing the densities of the forage fish prey group, which varied seasonally during each year.

Zebra mussels were simulated as increased benthic production and effects of improved water clarity (Table 2). Increased shunting of energy to benthos was simulated by increasing the baseline benthic densities and the benthic production rate. Improved water clarity was simulated by adjusting the half saturation coefficients (K-values) of the multispecies functional response relationship, and increasing the larval yellow perch mortality rate. Changing the K-values affects how efficient the predator is at eating the prey. Higher K-values imply predators are less efficient, as one-half of the maximum consumption rate is not obtained until prey densities are higher. We reduced the K-values of all life stages of yellow perch and walleyes eating zooplankton, and increased the K-values of all life stages of walleye eating

Table 2. Changes to the baseline model configuration to simulate the mayfly (MF), forage fish (FF), zebra mussel (ZM), and cormorant (Birds) conditions in Oneida Lake.

Factor	Implementation in the IBM
MF	For June 5 to July 19: Triple equilibrium densities of benthos prey group Make YOY and yearling yellow perch invulnerable to walleye predation Eliminate harvest of adult walleye
FF	Triple equilibrium densities of forage fish prey group
ZM	40% increase equilibrium densities of benthos prey group 20% increase in benthos production rate 30% increase in perch larval mortality rate 20% reduction in K-values of yellow perch and walleye eating zooplankton 20% increase in K-values of all walleye eating forage fish and YOY and yearling yellow perch and walleye
Birds	For April 1 to October 27: Additional mortality of YOY, yearling, age-2, and age-3 perch and walleye based on the biomass of each, relative to the estimated total consumption of fish by double-crested cormorants (see text).

YOY and yearling yellow perch, YOY and yearling walleyes, and forage fish. This makes the zooplanktivores more efficient at low zooplankton abundance and the walleye less efficient as piscivores. Finally, we increased the larval mortality of yellow perch from 0.03/d to 0.039/d. Previously in Rutherford et al. (1999), we imposed different magnitudes of changes on the benthos (20% versus 40%), also changed zooplankton densities and production rate, and did not include water clarity effects on feeding parameters and larval mortality.

While the field evidence is lacking for how zebra mussels may have changed survival of YOY yellow perch and walleye, survival rates of yellow perch have declined in the pelagic early juvenile phase (Mayer et al. 2000; Irwin et al. 2009). The results of the single factor simulations that permitted the long-term responses to baseline and zebra mussel conditions to be quantified (described below) showed reasonable reductions in yellow perch and walleye YOY survival. Our changes for zebra mussels, which included increased larval mortality of yellow perch, resulted in a roughly 50% reduction in survival of yellow perch from egg stage to August 15 relative to baseline conditions (survival fraction of 0.010 versus 0.021). Walleye survival from the 9-mm first-feeding stage to October 15 was about 0.12 under the single factor baseline simulation and decreased to about 0.06 under the zebra mussel single factor simulation. Because the changes associated with zebra mussels resulted in a reasonable decrease in YOY walleye survival, we did not need to directly change walleye YOY mortality rates.

The effects of cormorants on walleyes and yellow perch were simulated by imposing a new source of mortality based on field estimates of cormorant densities and their per-capita consumption and diets. We used the average monthly counts of adults for April to October: 330, 320, 374, 462, 843, 1625, and 412. These were averaged from the monthly values for 1994 to 1997 reported in Rudstam et al. (2004). We added 300 chicks to the monthly counts of adult birds for June and July. We assumed each adult bird consumed 456 g wet weight of fish/d, and each chick consumed 327 g wet weight fish/d (Rudstam et al. 2004). Assuming 80% of this consumption of fish was yellow perch and walleyes, we computed the total biomass of yellow perch and walleyes consumed by cormorants each day of the simulation. This percentage consumption of percids is slightly higher than the reported 57–77% of mass consumed by cormorants in Oneida Lake (Rudstam et al. 2004). The probability of being eaten by cormorants was then computed for yearling, age-2, and age-3 perch and for yearling, age-2, and age-3 walleyes as the biomass of that age-group consumed by cormorants, divided by the total biomass of that age-group in the population. If a generated uniform random number was less than the probability of being eaten, then the model individual was removed from the simulation as having been eaten by the cormorants.

Representation of Forney's Management Algorithm

We very crudely mimicked how management of walleye harvest is practiced in Oneida Lake, which we term Forney's algorithm. All other simulations used a constant age-4 as the first age of walleyes that was vulnerable to harvesting. We adapted the essence of Forney's algorithm to the age-structure and idiosyncrasies of the model. On April 10 of each year, the adapted algorithm uses the computed biomass of walleye adults age-5 and older and density of sub-adults age-4 and younger (SA, number/0.1 -ha) from the previous year's October to set the age of first harvest:

$$ER = 1000 (28.71 + 22.9 SA - 24.4 SA^2) \quad (1)$$

The sub-adult density (SA) is used in a quadratic equation to forecast recruitment (ER , numbers in lake) for the upcoming year.

Then, the computed adults from the previous October, and the expected recruitment, are used to set the minimum age of harvest of walleyes for the current year beginning on April 10 (Table 3). We also added the condition that if the density of adult walleyes age-5 and older was very low (<14 individuals/ha) at the beginning of the year (April 10), then the minimum age was set to 6; if adult walleye density was very high (>44 individuals/ha) on April 10, then the minimum age was set to 4.

Design of Single Factor and Time Series Simulations

A total of nine simulations were performed: 6 single factor and 3 time series. The single factor simulations examined the long-term, equilibrium responses to conditions designed to mimic the periods that have occurred in Oneida Lake: baseline (BL), mayflies (MF), forage fish (FF), zebra mussels (ZM), and zebra mussels and cormorants together (ZM-BIRDS). We also simulated long-term responses to cormorants alone (Birds), even though high cormorants did not occur alone in Oneida Lake, to better understand and isolate the effects of increased cormorants. All simulations used 25 years of baseline initial conditions, and then 75 years of the single factor imposed. We analyzed the last 50 years of each simulation because while year-to-year variation still occurred, averaged values of abundances, survival rates, and lengths had stabilized (i.e., 60-years and 40-years yield almost identical mean values). The single factor simulations were designed to document the long-term perch and walleye population dynamics if each of these periods persisted long enough for the populations to reach their quasi-steady state dynamics.

The time series simulations involved imposing the single factors (periods) for 10 years each: 1) in the same order they occurred in Oneida Lake (mayfly, baseline, forage fish, zebra mussels, zebra mussels plus cormorants), 2) in the reverse order, and 3) in the historical order but with Forney's algorithm that dynamically set the age of first harvest. Each simulation used 25 years of baseline conditions, followed by 10 years of each of the five periods for a total of 75 years. We compared the averaged values of abundances, survival rates, and mean lengths of yellow perch and walleyes from each period to the long-term averaged (equilibrium) values obtained from the single factor simulations. The idea was to determine if we were seeing populations reach new equilibrium conditions within each period of the historical time series

Table 3. October adult walleye density (kg/ha), expected recruitment in the lake (Recruits #/ha) predicted from October sub-adult density (equation 1), and the resulting age at first harvest for adult walleyes for the next year beginning April 10. These rules were designed to convert Forney's (1980) fisheries management algorithm, which was size-based, to operate in terms of age (yrs).

Density	Recruits	Age
< 13	<10	6
< 13	10 to 25	5
< 13	>25	5
> 13	<25	5
> 13	>25	4

simulation. The reverse time series simulation was also used to assess whether 10 years was sufficient for the complete responses to changed conditions to be observed in the historical time series simulation. If similar dynamics (i.e., averaged values) were obtained in each period by going forward and in reverse order through the periods, then the results were insensitive to what conditions occurred in the preceding period.

Finally, all single factor and historical and reverse time series simulations used a simple, constant age of first harvest for walleyes. We compared yields and population abundances and inter-annual variability (Coefficient of variation, $CV = 100 \times SD/\text{mean}$) between the historical time series with the constant age versus the historical time series with Forney's algorithm to determine any benefits of dynamically setting the age of first harvest.

We report model output variables that generally match the life stages and months of much of the monitoring data collected from Oneida Lake. Adult densities were the number per hectare of age-3 and older yellow perch and age-4 and older walleyes on April 10. Recruitment was defined as the number of individuals that survive to age-2. Spawners were the number of female individuals that actually spawned that year; they produced the total number of eggs we report. We used mean length at age-4 for yellow perch and at age-5 for walleye as indicators of adult growth. Survival of YOY was separated into stages: egg to 18-mm larvae, 18-mm larvae to juveniles on August 1, juveniles on August 1 to juveniles on October 15 for yellow perch; and egg to 9-mm larvae, 9-mm larvae to juveniles on August 1, and juveniles on August 1 to October 15 for walleyes. We also computed yearling survival rates from change in abundance of age-0 juveniles on October 15 to abundance of age-1 fish on October 15 for both species, and calculated survival rates of age-2 to age-3, and age-3 to age-4 fish based on changes in their abundances from April to April. The egg, 18 mm, and 9 mm abundances used in the survival estimates were the total number produced each year, whereas the August 1 and October 15 abundances were the number of YOY present on that day.

We computed averaged values of the output variables using the last 50 years of each single factor simulation, and for each 10-year period in the historical and reverse time series simulations. We also re-plotted the annual values of adult abundances of yellow perch and walleye from the reverse time series simulation with the historical time series simulation by matching periods. Thus, years 66–75 in the reverse simulation (mayfly) were plotted with years 26–35 of the historical simulation, years 56–65 with years 36–45, etc. To evaluate Forney's algorithm, we compared predicted mean and CV of adult yellow perch and walleye densities, yield in numbers and biomass, and mean weight per individual harvested between the constant age-4 historical time series simulation and the historical time series simulation with Forney's algorithm.

Because the degrees of freedom are arbitrary in our simulations, as we can make our simulations run as long as we like, we do not report the results of statistical analysis of the model outputs. The same difference in mean values can be statistically significant simply by making the simulations longer. Rather we interpret the magnitude of differences in means and CVs, admittedly somewhat subjectively, in the context of what we consider to be biologically important. We also report the results from single simulations of the model. The model is stochastic and results depend on the random number sequence used. Repeated simulations using different random number sequences yielded very similar mean and CV values for the various output variables, and yielded annual time series values that exhibited different year-to-year variation but very similar temporal patterns.

Results

Single Factor Simulations

Simulations of mayflies and baseline conditions resulted in high adult abundances and recruitment of yellow perch, while forage fish and zebra mussels with cormorants (ZM-Birds) resulted in the lowest adult abundances and recruitment (Table 4). Mayflies resulted in long yellow perch adults (205 mm), which caused earlier age of maturation and a large number of spawners (40/ha) and high egg production about twice that of baseline (1.22 versus 0.72×10^6 /ha). YOY survival was about half under mayflies compared to baseline ($S = 0.00266$ versus 0.00595), while yearling survival was almost threefold higher ($S = 0.070$ versus 0.024). The net result was that the mayfly and baseline conditions had similar, relatively high, recruitment to age-2 (36/ha and 35/ha).

Simulations of forage fish and ZM-Birds conditions resulted in low adult abundances and recruitment of yellow perch but for different reasons (Table 4). Forage fish conditions caused relatively larger sizes of walleyes and hence higher predation rates on yearlings, small adult yellow perch (193 mm), which with low adult abundance (71/ha), resulted in relatively few spawners (18/ha) and low egg production (0.54×10^6 /ha). Despite high YOY survival ($S = 0.00753$), yearling survival rates were low, hence recruitment also was low (22/ha). The zebra mussel component of ZM-Birds resulted in large yellow perch adults (ZM = 228 mm and ZM-Birds = 230 mm) and consequently high spawner abundances (44/ha and 36/ha) and egg production (1.82×10^6 /ha and 1.52×10^6 /ha), but also low YOY survival ($S = 0.00249$ and 0.00300). The birds component resulted in low yearling survival that was similar to the low survival predicted for forage fish ($S = 0.014$ for birds versus $S = 0.016$ for forage fish), and lowered age-2 and age-3 survival ($S = 0.65$ and 0.66 for birds versus $S = 0.69$ and 0.70 for forage fish).

The birds-alone simulation showed that the long-term effects of the double-crested cormorants were apparent but moderate in magnitude (Table 4). Adult yellow perch abundance under birds only was somewhat lower than baseline (87/ha for birds versus 109/ha for baseline), and similar to that predicted for zebra mussels (87 versus 88/ha). Survival rates for YOY and yearling life stages were similar or higher for birds only compared to baseline (YOY $S = 0.00726$ for birds versus 0.00595 for baseline; yearling $S = 0.020$ versus 0.024), so that the slightly lower adult abundance was due to lower survival rates from age-2 to age-3 and from age-3 to age-4 (about $S = 0.65$ for birds versus $S = 0.70$ for baseline). While zebra mussels and birds alone yielded similar adult abundances, other aspects of their population responses were quite different. Zebra mussels resulted in longer adult yellow perch than birds alone (228 mm for zebra mussels versus 191 mm for birds) and higher egg production (1.82×10^6 /ha versus 0.60×10^6 /ha) that was offset by much lower YOY survival ($S = 0.00249$ versus 0.00726), resulting in similar recruitment at age 2 (28/ha versus 29/ha).

Like yellow perch, walleye adult densities and recruitments also were highest under mayfly conditions and relatively low under forage fish (39.4 adults/ha for mayflies versus 19.9 adults/ha for forage fish, Table 5). Under mayfly conditions, adult walleyes were short (321 mm) due to density-dependent effects on their growth rates, and thus egg production was not exceptionally high relative to baseline conditions (3.95×10^5 /ha for mayflies versus 3.49×10^5 /ha for baseline). However, mayflies was the only period simulated in which walleye YOY and yearling survival were both high ($S = 0.0000667$ and 0.577), resulting in high recruitment

Table 4. Equilibrium densities (#/ha), total lengths (mm) at age-4, and survival rates (S, fraction) of yellow perch from the single factor simulations: mayflies (MF), baseline (BL), forage fish (FF), zebra mussels (ZM), cormorants (Birds), and zebra mussels with cormorants (ZM-Birds). Mean values were computed using the last 50 years of 100-year simulations in which the conditions were imposed after year 25. YOY life stage survival is computed as change in abundance from egg to 18 mm larvae, from 18 mm larvae to juveniles on August 1, and juveniles from August 1 to October 15; overall YOY survival is eggs to Oct. 15. Yearling survival is abundance change from age-0 October 15 to age-1 October 15; survival from age-2 to age-3 and age-3 to age-4 is abundance change from April 10 to April 10.

Variable	Period						
	MF	BL	FF	ZM	Birds	ZM-Birds	
Age-3 and older adults/ha	114	109	71	88	87	71	
Mean Length of age-4	205	190	193	228	191	230	
Female spawners/ha	40	25	18	44	21	36	
Eggs ($\times 10^6$)/ha	1.22	0.72	0.54	1.82	0.60	1.52	
Egg-18mm survival	0.062	0.133	0.185	0.026	0.164	0.038	
18mm-Aug 1 survival	0.196	0.158	0.176	0.370	0.167	0.307	
Aug 1-Oct 15 survival	0.242	0.293	0.234	0.280	0.272	0.278	
YOY survival	0.00266	0.00595	0.00753	0.00249	0.00726	0.00300	
Yearling survival	0.070	0.024	0.016	0.017	0.020	0.014	
Age-2 recruits/ha	36	35	22	28	29	24	
Age-2 to age-3 survival	0.69	0.69	0.69	0.70	0.64	0.65	
Age-3 to age-4 survival	0.70	0.70	0.70	0.70	0.65	0.66	

Table 5. Equilibrium densities (#/ha), total lengths (mm) at age-5, and survival rates (S, fraction) of walleyes from the single factor simulations: mayflies (MF), baseline (BL), forage fish (FF), zebra mussels (ZM), cormorants (Birds), and zebra mussels with cormorants (ZM-Birds). Mean values were computed using the last 50 years of 100-year simulations in which the conditions were imposed after year 25. YOY life stage survival is computed as change in abundance from egg to 9 mm larvae, from 9 mm larvae to juveniles on August 1, and juveniles from August 1 to October 15; overall YOY survival is eggs to Oct. 15. Yearling survival is change in abundance from age-0 October 15 to age-1 October 15; survival from age-2 to age-3 and from age-3 to age-4 is change in abundance from April to April.

Variable	Period						
	MF	BL	FF	ZM	Birds	ZM-Birds	
Age-4 and older adults/ha	39.4	22.7	19.9	23.1	19.0	23.1	
Mean Length at age-5	321	333	395	382	360	379	
Female spawners/ha	4.9	4.3	6.3	6.8	4.5	6.9	
Eggs ($\times 10^5$)/ha	3.95	3.49	5.09	4.94	3.70	4.88	
Egg-9mm survival ($\times 10^{-3}$)	0.556	0.556	0.568	0.563	0.527	0.529	
9mm-Aug 1 survival	0.407	0.231	0.235	0.130	0.264	0.166	
Aug 1-Oct 15 survival	0.335	0.513	0.444	0.433	0.528	0.450	
YOY survival ($\times 10^{-4}$)	0.667	0.617	0.558	0.296	0.652	0.352	
Yearling survival	0.577	0.459	0.277	0.582	0.385	0.560	
Age-2 recruits/ha	13.3	8.3	6.8	7.9	7.5	8.4	
Age-2 to age-3 survival	0.94	0.94	0.94	0.94	0.89	0.91	
Age-3 to age-4 survival	0.94	0.94	0.94	0.94	0.91	0.92	

to age-2 (13.3/ha). Walleyes grew fast under forage fish (395 mm) because of the increased prey and low adult abundances, but the relatively high egg production (5.09×10^5 /ha) was more than offset by low yearling survival due to cannibalism from larger adult walleyes ($S = 0.277$).

Other than for mayflies, walleye adult abundances and recruitment did not differ as greatly among the conditions as occurred for yellow perch. There were differences among conditions in adult walleye growth and survival rates, so the similar adult walleye abundances and recruitments arose for different reasons. Walleye adults grew fast with added prey under forage fish and zebra mussels conditions (395 mm for forage fish, 383 mm for zebra mussels), which lead to high spawner numbers (6.3/ha and 6.8/ha) and egg productions (5.09 and 4.94×10^5 /ha). However, either YOY survival was low ($S = 0.0000296$ in zebra mussels) or yearling survival was low ($S = 0.277$ in forage fish), negating the high egg production. The isolated response of walleyes to birds alone was relatively low adult abundance (19.0/ha) and low recruitment to age-2 (7.5/ha), similar to forage fish (adults = 19.9/ha, recruits = 6.8/ha). However, adult growth was slow (360 mm), resulting in low spawners (4.5/ha) and egg production (3.7×10^5 /ha), which when combined with moderate YOY and yearling survival ($S = 0.652$ and 0.385) resulted in somewhat low recruitment (7.5/ha). Survival rates from age-2 to age-3, and from age-3 to age-4 were also lower under the bird alone simulation ($S = 0.89$ and 0.91 for birds versus $S = 0.94$ for forage fish). Interestingly, while adding the bird effect to zebra mussels had a negative effect on yellow perch adult abundances (88/ha under ZM to 71/ha under ZM-Birds), adding the bird effect to zebra mussels had no effect on walleye abundances (23.1/ha under ZM to 23.1/ha under ZM-Birds).

Historical and Reverse Times Series Simulations

Time series simulations of adult yellow perch and walleye densities were qualitatively similar to temporal trends of adult densities observed in Oneida Lake from the late 1950s through 2001 (Figure 1). Mean values of adult densities observed in Oneida Lake were positively correlated ($P < 0.01$, $r = 0.92$, $n = 8$) with those predicted by the model. Simulated densities of adult yellow perch peaked early during the mayfly period, progressively decreased from the baseline throughout the period of record ending in the ZM-Birds. Averaged adult abundances during each period was 147/ha for mayflies, 123/ha for baseline, 95/ha for forage fish, 90/ha for zebra mussels, and 70/ha for ZM-Birds. Simulated densities of adult walleyes increased under mayflies before dropping rapidly under baseline, continued to be low under forage fish, and then increased slightly in the zebra mussel period, before declining further under ZM-Birds. Averaged adult abundances (number/ha) were 27.8 under mayflies, 26.9 under baseline, 20.6 under FF, 25.0 under ZM and 19.9 under ZM-Birds.

The mean values and trends predicted for each period of the historical time series simulation were generally robust. Mean adult abundances, recruitment, YOY survival, and mean lengths by period for yellow perch (Figure 2) and for walleyes (Figure 3) were similar among the historical time series, reverse time series, and single factor simulations. Some notable exceptions were the higher yellow perch adult abundances and recruitment and lower walleye adult abundances for the mayfly period for the time series simulations compared to equilibrium values, and large variation in walleye adult mean lengths across the three simulations for the mayfly and baseline periods.

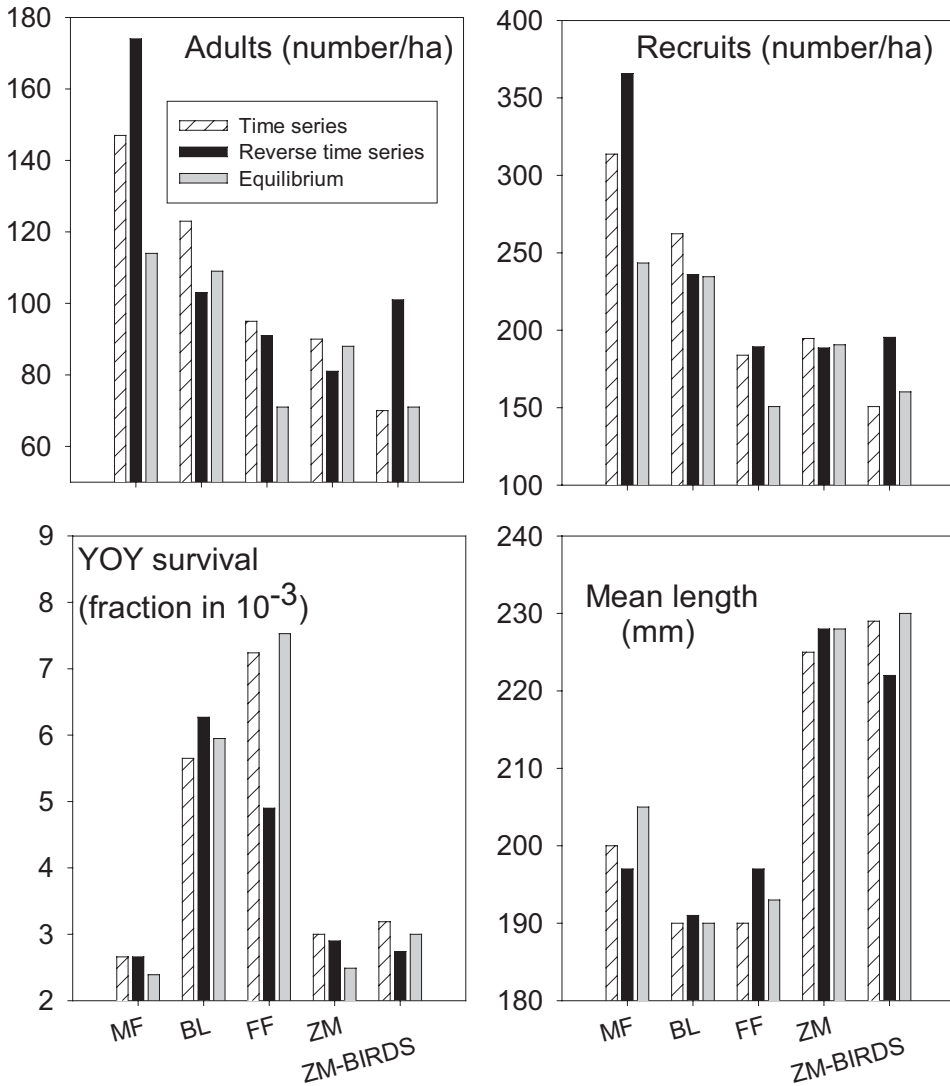


Figure 2. Averaged values of adult abundance, recruitment, YOY survival, and mean total length at age-4 for yellow perch by each 10-year period in the historical time series simulation and the reverse time series simulation. Also shown are the equilibrium values based on averaging the last 50 years of the single factor simulations.

Annual values of adult abundances from the reverse time series simulation, when parsed and re-plotted with their corresponding periods in the historical time simulation, mostly tracked the trends in each period of the historical time series simulation (Figure 4). The two exceptions were yellow perch in the ZM-Birds periods (first in the reverse simulation) and walleyes in the baseline period (third in the reverse simulation). For yellow perch, the ZM-Birds period in the reverse simulation had high abundances entering from the previous period of baseline (initial conditions), whereas the ZM-Birds period in the historical simulation had low adult abundances entering from the ZM period. Walleyes in the baseline condition in the reverse simulation showed a low but increasing adult abundance compared to sharp decline in the historical

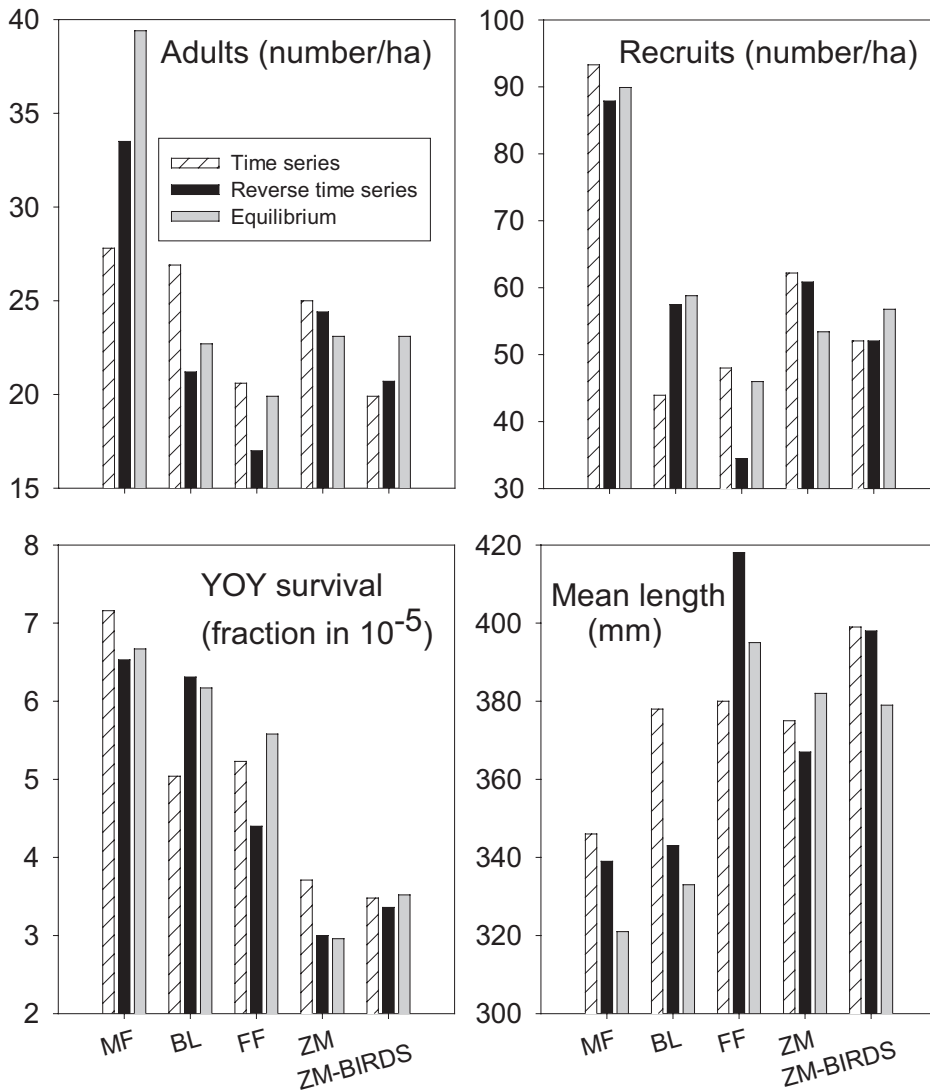


Figure 3. Averaged values of adult abundance, recruitment, YOY survival, and mean total length at age-5 for walleyes by each 10-year period in the historical time series simulation and the reverse time series simulation. Also shown are the equilibrium values based on averaging the last 50 years of the single factor simulations.

simulation. In the reverse time series situation, the preceding period of forage fish resulted in low abundance entering the baseline period, whereas in the historical simulation the preceding period of mayflies resulted in high abundances entering the baseline period. By the end of each of these periods, however, the model had adjusted to the different entering conditions, and similar adult abundances were predicted for the reverse and historical time series simulations.

Fisheries Management Simulation

Our age-based implementation of Forney's algorithm had little effect on yellow perch yield

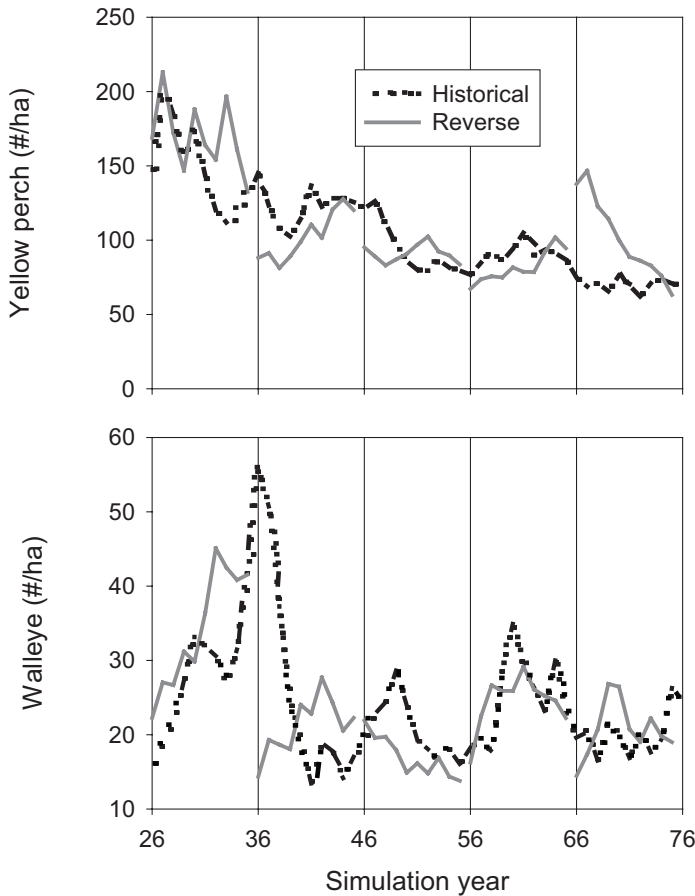


Figure 4. Model simulated adult abundances of yellow perch (upper) and walleyes (lower) for each of the 10-year periods of the reverse time series simulation re-plotted with the same period in the historical time series simulation.

and population dynamics compared to the constant age simulation, and resulted in a less variable walleye population with similar biomass harvested that was comprised of slightly more but smaller fish (Table 6). Mean and CV of adult abundance, yield in biomass and numbers, and average weight of a harvested yellow perch were similar between the constant age-4 and Forney's algorithm simulations. Walleye adult abundance and yield in biomass were also similar between the two simulations. However, the CV of adult walleye abundance was lower for Forney's algorithm compared to the constant age-4 simulation (CV = 26% for Forney's versus 37% for constant age), and the roughly 5,000 g/ha yield had more fish (7.2 versus 6.5) that were smaller in body weight (873 versus 997 g). Frequency distributions of adult walleye abundances and yields suggested that the constant age-4 limit produced fewer years of low catches (number and weight) and population sizes compared to Forney's algorithm (Figure 5).

Discussion

Mayflies were beneficial to yellow perch and walleyes, while forage fish had negative effects. For both species, high adult abundances and recruitment were predicted under the

Table 6. Simulated average and CV of yields (kg and #/ha), adult densities (#/ha), and mean weight of a harvested individual (g) of walleyes (WE) and yellow perch (YP) under a first harvest of age-4 and under Forney's modified management algorithm. Adults are age-3 and older for yellow perch, and age-4 and older for walleyes, recorded on April 10 of each year.

Variable	Constant age-4		Forney's algorithm	
	Mean	CV	Mean	CV
WE yield (g/ha)	5,676 ± 339	21	5,487 ± 384	25
WE yield (#/ha)	6.5 ± 1.0	53	7.2 ± 1.0	51
WE adults (#/ha)	24.1 ± 2.5	37	25.9 ± 1.9	26
Avg. WE wt harvested (g)	997 ± 89	32	873 ± 74	30
YP yield (g/ha)	4,106 ± 250	22	3,902 ± 275	25
YP yield (#/ha)	22.6 ± 2	30	21.1 ± 1.9	32
YP adults (#/ha)	105 ± 9	31	98 ± 9	32
Avg. YP wt harvested (g)	191 ± 15	27	195 ± 14	26

mayfly condition, and low abundances and recruitment were predicted under the forage fish condition. Yellow perch under mayfly conditions grew fast and had high egg production with a net increase in egg to age-2 survival (YOY survival decreased but yearling survival increased even more). Walleyes under mayfly conditions were able to have high YOY and yearling survivals, which did not occur in any of the other conditions. Forney (1980) concluded that the presence of mayflies buffered predation by adult walleyes on YOY yellow perch and YOY walleyes, and created stable abundances of yellow perch and walleye. Essentially, more energy in terms of prey was added to the system so that yellow perch could grow fast and walleyes could eat without increasing the mortality of yellow perch. Earlier IBM simulations by Rose et al. (1999) supported the contention that mayflies stabilized dynamics of yellow perch and walleyes, and these new simulations reported here support that conclusion. Although our model results suggest the primary effect of mayflies on percid recruitment was to buffer predation by adult walleyes on young walleyes and yellow perch, in other areas such as western Lake Erie (Tyson and Knight 2001) and Saginaw Bay, Lake Huron (Schaeffer et al. 2000), mayflies were believed to increase yellow perch recruitment through their positive effects on yellow perch consumption, growth, and size-dependent survival.

Simulations involving forage fish and zebra mussels resulted in low adult abundances and recruitment for yellow perch and walleyes. For yellow perch, increased forage fish densities produced larger walleyes with increased predation rates, and resulted in lower egg production, while zebra mussels and ZM-Birds resulted in low YOY and yearling survival rates. For walleyes, increased forage fish densities caused large walleyes that resulted in higher cannibalism and low yearling survival, while zebra mussels and ZM-Birds caused low YOY survival. The differences in walleye adult abundances among conditions were less than for yellow perch so statements about the relative effects of baseline, forage fish, zebra mussels, birds, and ZM-Birds on walleyes are tentative. However, long-term monitoring of walleye populations in Oneida Lake indicates that adult densities were essentially stable from the late 1950s until the early 1990s (Rudstam et al. Chapter 15).

We included an increased water clarity effect in the zebra mussel simulations that was not included in earlier IBM simulations. In a previous IBM simulation of zebra mussel ef-

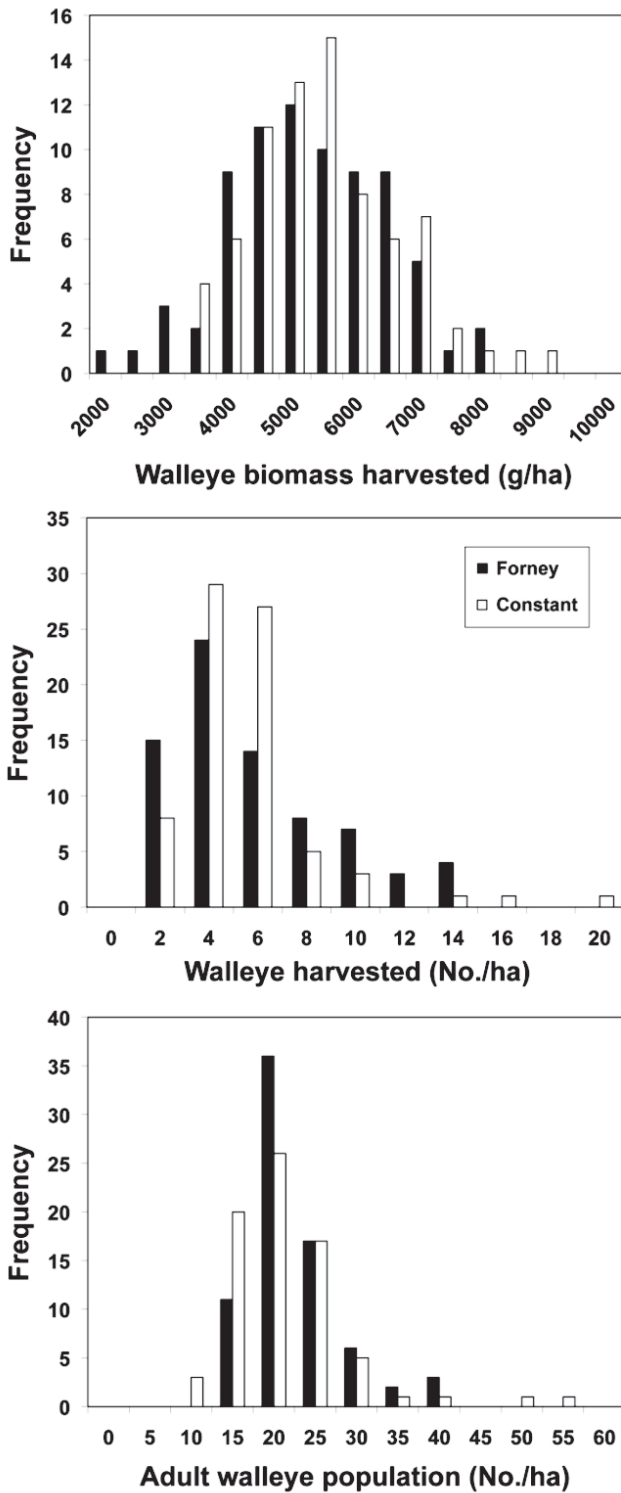


Figure 5. Frequency distributions of walleye biomass harvested (Top), number harvested (Mid), and adult abundances (Bottom) predicted under constant age-4 limit and Forney algorithm.

fects on walleyes and yellow perch, we focused on the consequences of energy being shunted to the benthos, and so imposed reduced zooplankton density and production and increased benthos density and production in model simulations (Rutherford et al. 1999). In these new simulations, we modified the energy shunt effect to only increase benthos, and in addition, we increased mortality of yellow perch larvae, increased the foraging ability of yellow perch and walleyes to eat zooplankton, and lowered the foraging ability of walleyes to eat fish. Mayer et al. (2000) analyzed a 30-year time series of yellow perch lengths and concluded that, after accounting for density dependent effects, growth rate of YOY yellow perch was significantly faster under zebra mussels than in earlier periods. Mayer et al.'s (2001) laboratory experiments indicated that zebra mussels affected the amphipod-yellow perch interaction in two ways. Increased structural complexity decreased amphipod availability to the fish, while increased light associated with higher water clarity increased the ability of yellow perch to feed on amphipods. However, the frequency of amphipods in yellow perch diets increased after the zebra mussel introduction. Similarly, in mesocosm experiments (Thayer et al. 1997) and in field surveys in Lake Erie (Tyson and Knight 2001), yellow perch increased consumption of benthos after zebra mussel invaded, suggesting that increased visibility due to zebra mussel filtration increased yellow perch capture success for both benthic and pelagic prey. When we increased both benthos and zooplankton density and production in the model, we saw faster growth in YOY and yearling yellow perch so we eliminated the zooplankton effect, and only increased benthos densities and production (not zooplankton) and increased the foraging abilities (by lowering the K-values) of yellow perch and walleyes eating zooplankton. Although experiments by DeRobertis et al. (2003) suggested that zooplanktivores would become less efficient at foraging relative to piscivores, studies at Oneida Lake by Wahl et al. (1993) and elsewhere (Bergman 1988; Diehl 1988; Richmond et al. 2004) on yellow perch, and studies by Lester et al. (2004) and Chu et al. (2004) on walleyes suggest that increased light will improve foraging efficiency of yellow perch more than for walleyes. It is also possible that walleye foraging efficiency would decrease owing to increased macrophyte growth and refugia for yellow perch (Zhu et al. 2006). Until further field and laboratory results suggest otherwise and resolve some inconsistencies in the empirical information, our implementation of the zebra mussel effect seems reasonable.

Our simulations suggest that, in the long-term, increased double-crested cormorants negatively affected yellow perch and certainly did not benefit walleyes. Yellow perch adult abundances and recruitment under equilibrium conditions were moderate for birds alone and low for ZM-Birds; however, the effect of cormorants on equilibrium adult abundances and recruitment of walleyes were less dramatic. Averaged walleye adult abundances and recruitment under equilibrium simulations and historical time series simulations were roughly similar to the values predicted for the baseline, forage fish, and zebra mussel conditions. The historical time series simulation indicated that yellow perch seemed to decline during the forage fish period, and then increased during the zebra mussels period before declining again during the cormorants period. For walleyes, the decline in the historical time series simulation occurred earlier during the baseline period and then stayed low during zebra mussels, with the addition of increased cormorants causing stable but low and perhaps less variable adult walleye abundances. Empirical analysis of long-term monitoring data (VanDeValk et al. 2002; Rudstam et al. 2004) indicated that the recent decline in walleye and yellow perch adult abundance was caused mainly by cormorant predation on age-1 through age-3 fish, and not by effects of zebra mussels. Rudstam et al. (2004) suggested that the cormorant effect was larger on yellow

perch than on walleyes. For the year classes of 1993 to 1998, they concluded that cormorants consumed from 21 to 60% of the walleyes expected to recruit to age 4 from the number present as age 1. Similar numbers for yellow perch ranged from 9 to 121%. The model results are in general agreement with these empirical analyses: a relatively large, negative effect for yellow perch and smaller negative effect on walleyes. Double-crested cormorants also have impacted yellow perch populations in other Great Lakes areas. In northern Lake Huron, Diana et al. (2006) estimated cormorant consumption of yellow perch in 1995, and concluded that declining recruitment, and not cormorant predation, was the likely cause for the perceived decline in the yellow perch population. However, a more recent analysis of yellow perch yields, abundances, adult mortality rates, and recruitments from the 1980s through 2004 suggests cormorant predation was the major cause of yellow perch population decline in this area (Fielder 2008, 2010).

The similarity in results among the empirical analyses for Oneida Lake (Rudstam et al. Chapter 16) and our modeling results is not surprising given that we configured the IBM simulations using per-capita consumption rates and abundances of cormorants reported by Rudstam et al. (2004) and VanDeValk et al. (2002). However, the model runs demonstrated the effects over a 75-year time frame (about six walleye generations) with all other factors held constant compared to empirical analyses spanning 14 years (about one generation) with other potentially confounding sources of variation present.

The general agreement between the historical time series, reverse time series, and equilibrium (single factor) simulations implies that 10 years is sufficient to see the major effects of each period and that the order of the periods is unimportant in determining the responses. In a few cases, previous periods affected whether high or low adult abundances would enter a particular period, but the model rather quickly adjusted abundances and recruitment to reflect the conditions in the period of interest. The model set-up was ideal for equilibrium to be reached quickly because we did not include many sources of inter-annual variation that could add noise and thereby slow down the transition to equilibrium conditions. We did additional time series simulations with the periods in different sequence than the historical and reverse sequences, and generally saw similar results (i.e., period-specific averages were similar across different sequences). These results suggest that hysteresis is not a major concern and that if cormorants could be controlled and early life survival increased for yellow perch and walleyes, both populations could rather quickly recover within a decade or so. Our conclusions from the virtual world are highly speculative, given that hysteresis seems to be a reality for Oneida Lake and many other ecosystems (Duarte et al. 2009) because of shifting baselines and ecological regimes (Zhu et al. 2006), real variability and changing environmental conditions (i.e., warmer water temperatures, reduced phosphorus concentrations) (Irwin et al. 2009).

The model simulations suggested that a simple constant age-based limit can maintain stable walleye populations as effectively as an age-based version of Forney's algorithm. The major difference was a lower CV of walleye adult abundances and fewer years of low catch and population abundance under Forney's algorithm compared to the constant age-4 limit, but the reduction in CV was not very large in magnitude. One possible reason for the similar performance of the constant age and Forney's algorithms is that fishing mortality on walleyes is represented as inversely related to forage fish abundance in the model. This acts to stabilize the walleye population because high mortality leads to low walleye abundance, which then reduces predation pressure on forage fish and higher forage fish density. The higher forage fish density then acts to lower the fishing mortality rate on walleyes. VanDeValk et al. (2005,

Chapter 17) documented that in Oneida Lake, walleye catchability was independent of walleye abundance and inversely related to walleye growth, which was a surrogate for forage fish abundance. Density independent catchability has been reported for many, but not all walleye populations (Hansen et al. 2005). Our crude approximation of Forney's (1980) management algorithm did serve to stabilize walleye adult abundance more than a constant age simulation, but the other potential benefits of Forney's algorithm may have been overshadowed by the stabilizing effect of fishing mortality dependent on forage fish density, which was included in both the constant age and Forney's algorithm simulations.

While the argument sounds reasonable, additional model simulations showed that the dependence of walleye fishing mortality rate on forage fish density had only a moderate effect on the relative performance of Forney's algorithm. We repeated the historical time series simulations with a constant fishing mortality for walleye (i.e., 8% per month not dependent on forage fish density) under a constant age-4 and Forney's algorithms, and again obtained similar yields and adult abundances with a reduction in CV of walleye adult abundance of 50% to 34% (compared to 37% to 26% with fishing dependent on forage fish).

Another possible explanation for why a constant age and Forney's algorithm generated similar results is in our implementation of Forney's algorithm. We implemented the algorithm based on age of first harvest rather than size at first harvest. In the model, variance in walleye size increased unrealistically when we imposed Forney's algorithm based on length, so we imposed regulation changes based upon changes in age. This is a deficiency in the model formulation that allows unrealistic growth under certain conditions. Our age-based version of Forney's algorithm could be a major deviation from how the algorithm is intended to operate because using age uncouples the link between density-dependent growth and harvest limits.

Our model simulations were conducted without fry stocking that has occurred in Oneida Lake since the 1890 s (Brown et al. Chapter 5), but Rose et al. (1999) indicated that model results would be robust to stocking of walleye fry. With increased stocking of walleye fry, stabilization is encouraged and would result in reduced coupling of walleye and perch predator-prey population dynamics.

The Oneida Lake database enabled us to develop and test a detailed individual-based model of predator-prey interactions and the dynamics of a simple two-species system. Predator-prey dynamics have been a focus of debate and ecological modeling for decades (e.g., Abrams and Ginzburg 2000), and both simple Lotka-Volterra type models (e.g., Gourley and Kuang 2004; Liu and Chen 2003) and more complex individual-based models (e.g., McCauley et al. 1993; Cuddington and Yodzis 2000) continue to be developed and analyzed. Our analyses enabled full life cycle simulations of yellow and walleyes through a complex pathway of interactions involving competition for prey at some life stages and predator-prey interactions (including cannibalism) at other life stages. Both compensatory and depensatory density-dependent growth and mortality were included. The oversimplification of such complex interactions in mass-action (Lotka-Volterra-like) models has long been a source of criticism (e.g., Hall 1988). Yet, developing more detailed models can be criticized for limited data and high uncertainty. The Oneida Lake situation enabled the development of a complex model with a relatively high degree of confidence. Therefore, our exploratory analyses of the different regime periods and Forney's management algorithm were done in a more realistic situation than typically possible in more data-poor situations. There is a large effort towards developing multispecies fish models, as a step towards ecosystem-based management (Latour et al. 2003). Development and testing of modeling approaches using well-studied systems,

such as was done with the two-species IBM here, can provide a sound foundation for further development of multispecies models. Simple and individual-based predator–prey models will also continue to be developed and used to test key theoretical aspects of population dynamics, such as how to formulate predator–prey interactions, how to incorporate behavioral aspects, population responses arising from density-dependence occurring in multiple life stages, and the effects of different types of stressors and perturbations on population and community dynamics.

Future development and simulations of the IBM should examine effects of reduced primary productivity and increased spatial complexity on walleye and yellow perch dynamics. As light levels in lakes have increased due to zebra mussel filtration and reduced phosphorus levels, aquatic macrophytes have increased (Zhu et al. 2006), creating refugia for young-of-year stages; a spatially-explicit version of the IBM (e.g., four-five spatial strata) would allow for more realistic simulation of walleye and yellow perch encounters. Simulations can be performed to examine recovery approaches for yellow perch and walleye, and to assess how global climate changes might affect yellow perch and walleye population dynamics.

Summary

Walleye and yellow perch are the dominant predator and prey species in the Oneida Lake fish community and support a valuable recreational fishery. Abundances and yields of both species have fluctuated greatly over time in response to fluctuating ecosystem conditions that include disappearance of mayflies, irruptions of forage fish species, invasion by zebra mussels, and establishment of double-crested cormorants. We used an individual-based model (IBM) to disentangle effects of multiple factors on walleye and yellow perch population dynamics by simulating each ecological condition: baseline; high mayfly densities; high forage fish densities; zebra mussel impacts on water clarity, benthos density, and percid foraging efficiency; high cormorant predation; and zebra mussels and cormorants together. We also compared the effect of a constant age-based limit on walleye harvest to an approximation of the existing walleye management plan of Forney (1980) to determine if the existing plan produced higher and more stable walleye yields than the constant age limit.

Model results indicated walleye and yellow perch populations were highest under simulated mayfly conditions, and lowest under high forage fish conditions. Compared to baseline conditions, walleyes were relatively unaffected by zebra mussels but moderately affected by cormorants whereas yellow perch abundances and recruitments declined under both simulated zebra mussel conditions and cormorant conditions, but for different reasons. Survival of yellow perch prerecruits was lower and survival of postrecruits similar under simulated zebra mussels compared to baseline conditions. In contrast, survival of age-1 and postrecruit yellow perch was lower during cormorant conditions compared to baseline conditions. The simulated response of walleye and yellow perch dynamics to changing ecological conditions was robust to length of exposure (10 years versus 75 years), and the order in which the ecological conditions occurred. The general agreement between the historical time series, reverse time series, and equilibrium (single factor) simulations implies that 10 years is sufficient to see the major effects of each period and that the order of the periods is unimportant in determining the responses. Simulated walleye harvests predicted for the constant age limit were similar, but more variable, than those predicted using Forney's management algorithm. The model

results generally support conclusions from empirical studies of walleyes in Oneida Lake, but indicate that zebra mussels may have had a greater impact on yellow perch population trends than was indicated from the historical database. Although speculative, our results suggest that hysteresis is not a major concern and that if double-crested cormorants could be controlled, both yellow perch and walleye populations could recover within a decade or so.

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References

- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15:337–341.
- Bergman, E. 1988. Foraging abilities and niche breadth of two percids under different environmental conditions. *Journal of Animal Ecology* 57:443–453.
- Brenton, B. D. 1998. Simulating the effects of invasive ruffe (*Gymnocephalus cernuus*) on native yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*) population dynamics in Great Lakes waters. Master's thesis. University of Michigan, Ann Arbor.
- Chu, C., C. K. Minns, J. E. Moore, and E. S. Millard. 2004. Impact of oligotrophication, temperature and water levels on walleye habitat in the Bay of Quinte, Lake Ontario. *Transactions of the American Fisheries Society* 133:868–879.
- Cuddington, K. M., and P. Yodzis. 2000. Diffusion-limited predator-prey dynamics in Euclidean environments: an allometric individual-based model. *Theoretical Population Biology* 58: 259–278.
- DeRobertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1517–1526.
- Diana, J. S., S. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. *Journal of Great Lakes Research* 32:306–320.
- Diehl, S. 1988. Foraging efficiency of 3 freshwater fishes: effects of structural complexity and light. *Oikos* 53:207–214.
- Duarte, C. M., D. J. Conley, J. Carstensen, and M. Sanchez-Camacho. 2009. Return to Neverland: shifting baselines affect eutrophication targets. *Estuaries and Coasts* 32:29–36.
- Fielder, D. G. 2008. Examination of factors contributing to the decline of the yellow perch population and fishery in Les Cheneaux Islands, Lake Huron, with emphasis on the role of double-crested cormorants. *Journal of Great Lakes Research* 34:506–523.
- Fielder, D. G. 2010. Response of yellow perch in Les Cheneaux Islands, Lake Huron to declining numbers of double-crested cormorants stemming from control activities. *Journal of Great Lakes Research* 36:207–214.
- Forney, J. L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. *Transactions of the American Fisheries Society* 104:15–24.
- Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. *New York Fish and Game Journal* 27:105–141.
- Fox, M. G. 1991. Food consumption and bioenergetics of young-of-the-year walleye (*Stizostedion*

- vitreum vitreum*): model predictions and population density effects. *Canadian Journal of Fisheries and Aquatic Sciences* 48:434–441.
- Gourley, S. A., and Y. Kuang. 2004. A stage structured predator-prey model and its dependence on maturation delay and death rate. *Journal of Mathematical Biology* 49:188–200.
- Hall, C. A. S. 1988. An assessment of several of the historically most influential theoretical models used in ecology and the data provided in their support. *Ecological Modelling* 43:5–31.
- Hansen, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, WISCU-T-97-001, Madison, Wisconsin.
- Hanson, M. J., T. D. Beard Jr., and S. W. Hewett. 2005. Effect of measurement error on tests of density dependence of catchability for walleyes in northern Wisconsin angling and spearing fisheries. *North American Journal of Fisheries Management* 25:1010–1015.
- Idrisi, N., E. L. Mills, L. G. Rudstam, and D. J. Stewart. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1430–1441.
- Irwin, B. J., L. G. Rudstam, J. R. Jackson, A. J. VanDeValk, J. L. Forney, and D. G. Fitzgerald. 2009. Dependensory mortality, density-dependent growth, and delayed compensation: disentangling the interplay of mortality, growth, and density during early life stages of yellow perch. *Transactions of the American Fisheries Society* 138:99–110.
- Jaworska, J. S., K. A. Rose, and L. W. Barnhouse. 1997. General response patterns of fish populations to stress: an evaluation using an individual-based simulation model. *Journal of Aquatic Ecosystem Stress and Recovery* 6:15–31.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 34(10) 1922–1935.
- Latour, R., M. J. Brush, and C. F. Bonzek. 2003. Toward ecosystem-based fisheries management: strategies for multispecies modeling and associated data requirements. *Fisheries* 28:10–22.
- Lester, N. P., A. J. Dextrose, R. S. Kushnerik, M. R. Rawson, and P. A. Ryan. 2004. Light and temperature: key factors affecting walleye abundance and production. *Transactions of the American Fisheries Society* 133:588–605.
- Liu, X., and L. Chen. 2003. Complex dynamics of Holling type II Lotka–Volterra predator–prey system with impulsive perturbations on the predator. *Chaos, Solitons and Fractals* 16:311–320.
- Lloyd, R. C. 1996. Evolution of management alternatives for the walleye-yellow perch fishery in Oneida Lake, New York. Doctoral dissertation. Cornell University, Ithaca, New York.
- Madon, S. P., and D. A. Culver. 1993. Bioenergetics model for young-of-the-year walleye: and in situ approach using experimental ponds. *Transactions of the American Fisheries Society* 122:797–813.
- Mayer, C. M., A. J. VanDeValk, J. L. Forney, L. G. Rudstam, and E. L. Mills. 2000. Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York to the establishment of zebra mussels (*Dreissena polymorpha*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:742–754.
- Mayer, C. M., L. G. Rudstam, E. L. Mills, S. G. Cardiff, and C. A. Bloom. 2001. Zebra mussels (*Dreissena polymorpha*), habitat alteration, and yellow perch (*Perca flavescens*) foraging: system-wide effects and behavioural mechanisms. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2459–2467.
- McCauley, E., W. G. Wilson, and A. M. de Roos. 1993. Dynamics of age-structured and spatially structured predator-prey interactions: individual-based models and population-level formulations. *The American Naturalist* 142:412–442.
- Mills, E. L., and J. L. Forney. 1988. Trophic dynamics and development of freshwater pelagic food webs. Pages 11–29 in S. R. Carpenter, editor. *Complex Interactions in Lake Communities*. Springer-Verlag, New York.

- Minton, J. W., and R. B. McLean. 1982. Measurements of growth and consumption of sauger (*Stizostedion canadense*): implications for fish energetic studies. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1396–1403.
- Post, J. R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. *Canadian Journal of Fisheries and Aquatic Sciences* 47:554–560.
- Prout, M. W., E. L. Mills, and J. L. Forney. 1990. Diet, growth, and potential competitive interactions between age-0 white perch and yellow perch in Oneida Lake, New York. *Transactions of the American Fisheries Society* 119:966–975.
- Richmond, H. E., T. R. Hrabik, and A. F. Mensinger. 2004. Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. *Journal of Fish Biology* 65:195–205.
- Rose, K. A., E. S. Rutherford, D. S. McDermott, J. L. Forney, and E. L. Mills. 1999. Individual-based model of yellow perch and walleye populations in Oneida Lake, New York. *Ecological Monographs* 69:127–154.
- Rose, K. A., J. A. Tyler, D. Singh-Dermot, and E. S. Rutherford. 1996. Multispecies modeling of fish populations. Pages 194–222 in B. A. Megrey and E. Moksness, editors. *Computers in fisheries research*. Chapman and Hall, London.
- Rose, K. A. and S. E. Sable. 2009. Multispecies modeling of fish populations. Pages 373–397 in B.A. Megrey and E. Moksness, editors. *Computers in fisheries research*, 2nd edition, Springer, New York.
- Rudstam, L. G., A. J. VanDeValk, C. M. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. *Ecological Applications* 14:149–163.
- Rutherford, E. S., K. A. Rose, J. L. Forney, E. L. Mills, C. M. Mayer, and L. G. Rudstam. 1999. Individual-based model simulations of a zebra mussel (*Dreissena polymorpha*) induced energy shunt on walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) populations in Oneida Lake, NY. *Canadian Journal of Fisheries and Aquatic Sciences* 56:2168–2160.
- Sable, S. E., and K. A. Rose. 2008. A comparison of individual-based and matrix projection models for simulating yellow perch population dynamics in Oneida Lake, New York, USA. *Ecological Modelling* 215:105–121.
- Schaeffer, J. S., Diana, J. S., and Haas, R. C. 2000. Effects of long-term changes in the benthic community on yellow perch in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 26:340–351.
- Thayer, S. A., R. C. Haas, R. D. Hunter, and R. H. Kushler. 1997. Zebra mussel (*Dreissena polymorpha*) effects on sediment, other zoobenthos, and the diet and growth of adult yellow perch (*Perca flavescens*) in pond enclosures. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1903–1915.
- Tyson, J. T., and R. L. Knight. 2001. Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. *Transactions of the American Fisheries Society* 130:766–782.
- VanDeValk, A. J., C. M. Adams, L.G. Rudstam, J. L. Forney, T. E. Brooking, M. A. Gerken, B. P. Young, and J. T. Hooper. 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. *Transactions of the American Fisheries Society* 131:27–39.
- VanDeValk, A. J., J. L. Forney, J. R. Jackson, L.G. Rudstam, T. E. Brooking, and S. D. Krueger. 2005. Angler catch rates and catchability of walleyes in Oneida Lake, New York. *North American Journal of Fisheries Management* 25:1441–1447.
- Wahl, C. M., E. L. Mills, W. N. McFarland, and J. S. DeGisi. 1993. Ontogenetic changes in prey selection and visual acuity of the yellow perch (*Perca flavescens*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:743–749.
- Zhu, B., D. G. Fitzgerald, C. M. Mayer, L.G. Rudstam, and E. L. Mills. 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. *Ecosystems* 9:1017–1028.