Chapter 21

Simulating Predator-Prey Dynamics of Walleye and Yellow Perch in Oneida Lake: An Assessment of Multispecies Matrix Projection Models

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Introduction

Fisheries management is attempting to shift focus from population-level analyses to ecosystem-based approaches (Alaska Sea Grant 1999; NMFS 1999; Link 2002; Latour et al. 2003). Ecosystem-based fisheries management requires multispecies models, and these models must be tested to ensure they have sufficient accuracy to inform management decisions. The development of multispecies models have increased since the 1970s, as sufficient computing power became available, but most efforts have resulted in demonstration mode applications and the conclusion that sufficient data were lacking to adequately configure the models (Rose and Sable 2009). Recent advances in data collection methods, and demands for ecosystem-based fisheries management, have fueled a resurgence of interest in multispecies modeling. The time is now for quantitative evaluation of multispecies modeling approaches.

Oneida Lake offers an excellent opportunity for the development and testing of multispecies models. Long-term studies spanning decades have chronicled walleye *Sander vitreus* and yellow perch *Perca flavescens* fisheries, competition, and predator–prey interactions, and have documented how perturbations have affected food web dynamics (this book). An individual-based model (IBM) was previously developed that simulated walleye and yellow perch population dynamics, and was used to examine the effects of alternative prey, zebra mussels *Dreissena polymorpha*, and cormorant predation on perch and walleye interactions (Rose et al. 1996, 1999; Rutherford et al. 1999; Rutherford and Rose, Chapter 20). The IBM was calibrated and corroborated using the extensive Oneida Lake database. In this study, we developed two alternative formulations of multispecies matrix projection models that simulated walleye and yellow perch predator–prey dynamics, and used the IBM as the basis for assessing the ability of the matrix models to predict responses to changes in survival rates. The matrix approach is simpler and more accessible than the IBM, and is widely used in fisheries management (Rose and Cowan 2003). Using the IBM results as "truth," our basic question

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was whether we could construct multispecies matrix models that accurately predicted yellow perch and walleye responses to changes in their survival rates.

Extending the matrix projection approach to multispecies situations is attractive because matrix modeling has a long history in fish population dynamics, and underlies much of stock assessment performed in support of management decisions (Quinn and Deriso 1999; Rose and Cowan 2003). Others have attempted to extend the general philosophy of separately modeling age and stage-classes, as in the matrix modeling approach, to multiple species by making stage-or age-specific rates dependent on the other species (e.g., Strange et al. 1992; Zhang et al. 2000; Gourley and Kuang 2004). These models were done for specific systems, used for highly theoretical analyses, or were done to illustrate how food web interactions can affect the population dynamics of the species of interest and therefore management advice (Rose and Sable 2009). To our knowledge, rigorous testing of multispecies matrix modeling using simulated data has not been done.

There are advantages and disadvantages to using matrix models for population and community analysis. Matrix models are relatively easy to construct and make use of readily-available demographic data (age, size, or stage-specific) on survival, growth, and reproductive rates. Matrix models have been widely used in ecology because they are mathematically tractable or can be solved numerically with relative ease (Caswell 2001). Eigenvalue analysis of matrix models generate useful population metrics such as the population growth rate, stable age or stage distribution, sensitivities, and reproductive values by age or stage. The disadvantages to matrix projection models are that they do not easily permit temporal memory in individual variation, are limited to a few spatial boxes, reduce community and food web effects to single species relationships, and density-dependent relationships must be defined *a priori*. Incorporation of density-dependence and variability results in nonlinear, stochastic matrices that prevent easy analysis using eigenvalues (Tuljapurkar et al. 2003; Doak et al. 2005; Ellner and Rees 2006). Recent studies have assessed the performance of population matrix models for handling differing levels of individual variation, autocorrelation within individual traits, and size-dependent interactions (Pfister and Stevens 2003; Sable and Rose 2008). Much less evaluation of multispecies matrix modeling has been performed.

Sable and Rose (2008) compared simulation results from an age-structured and a stage-within-age structured matrix population model of yellow perch with simulation results from the Oneida Lake IBM. Age and stage-specific rates for the two matrix population models were calculated from the baseline outputs of the IBM. The yellow perch population matrix models included density-dependent and stochastic age and stage-specific elements that were dependent upon yellow perch abundances and implicitly accounted for the walleye interactions explicitly modeled in the IBM. New simulations were performed with the two matrix population models and the IBM, and the resulting changes in age and stage-specific abundances and rates were compared among the models. For this study, we expanded the model comparison of Sable and Rose (2008) by explicitly modeling the walleye population dynamics and interactions with the yellow perch population to determine if two-species matrix community models could predict similar population responses and community dynamics to the IBM. By adding the walleye population matrix and coupling it to the yellow perch population matrix, we could directly determine how changing each population affected the other.

The two-species matrix models were constructed by making certain elements within each of the matrices dependent on the abundance or biomass of the other species. We constructed purely age-structured and stage-within-age two-species models. Parameters of the two matrix

model formulations were obtained from an analysis of output generated by a baseline simulation of the previously-developed IBM. We then changed the survival rates of yellow perch and walleye adults in the IBM and the two (i.e., age-structured and stage-within-age) matrix models, and compared the predicted responses of yellow perch and walleye among the IBM and matrix models. We conclude by discussing the importance of correctly specifying density-dependent and interspecies interactions within the stage and age structures of the matrix models, modifications we made to the age-specific growth elements of the classic matrix approach, and potential next steps in the continued evaluation of these multispecies approaches for modeling the Oneida Lake fish populations.

Methods

Overview of Model Comparison

We treated the IBM as the known standard for comparisons with the two multispecies matrix models (Figure 1). The matrix models used the same age structured (annual time step) formulation for age-1 and older classes, but differed in their representation of YOY stages. The purely age-structured version represented yellow perch and walleye YOY as a single age-class (egg to age-1) and used an annual timestep for all age classes (i.e., Leslie formulation), while the stage-within-age version represented yellow perch and walleye YOY as separate egg, yolk sac larva, feeding larva, and juvenile stages and used a daily timestep for the YOY stages.

In the first step of our comparison, we simulated 200 years of baseline conditions with the IBM (Figure 1a), and removed the first 15 years of the simulation to eliminate effects caused by initial conditions. We used baseline conditions for the IBM simulation because alternative prey, zebra mussels, and cormorants were absent or assumed to be at low abundances, thus the walleye and yellow perch should be most coupled to each other as predator and prey (Rose et al. 1999). We generated daily and annual outputs of walleye and yellow perch lengths, weights, stage and age abundances, and egg production. We analyzed the IBM output for density-dependent processes and interspecific interactions, and used them to link the appropriate elements in the matrix models to species abundances and biomasses. We simulated 200 years of baseline conditions in the matrix models and compared their predicted means and variation in abundances and vital rates for years 16–200 to the baseline IBM outputs.

In the second step of our comparison, we independently reduced the adult survival rates of yellow perch and adult fishing mortality rates of walleye over 200 years in all three models, and compared the predicted responses in mean yellow perch and walleye abundances and vital rates from years 16–200 (Figure 1b). Results from the second step were not used to recalibrate the matrix projection models estimated from the IBM output in the first step.

Description of the Individual-Based model

The IBM simulated the daily dynamics of walleye and yellow perch consumption, growth, mortality, and spawning in Oneida Lake (Rose et al. 1996, 1999). It is described in detail in Rose et al. (1999) and Rutherford and Rose (Chapter 20) and will only be briefly described here. The growth and survival of progeny from each female were simulated as they developed through
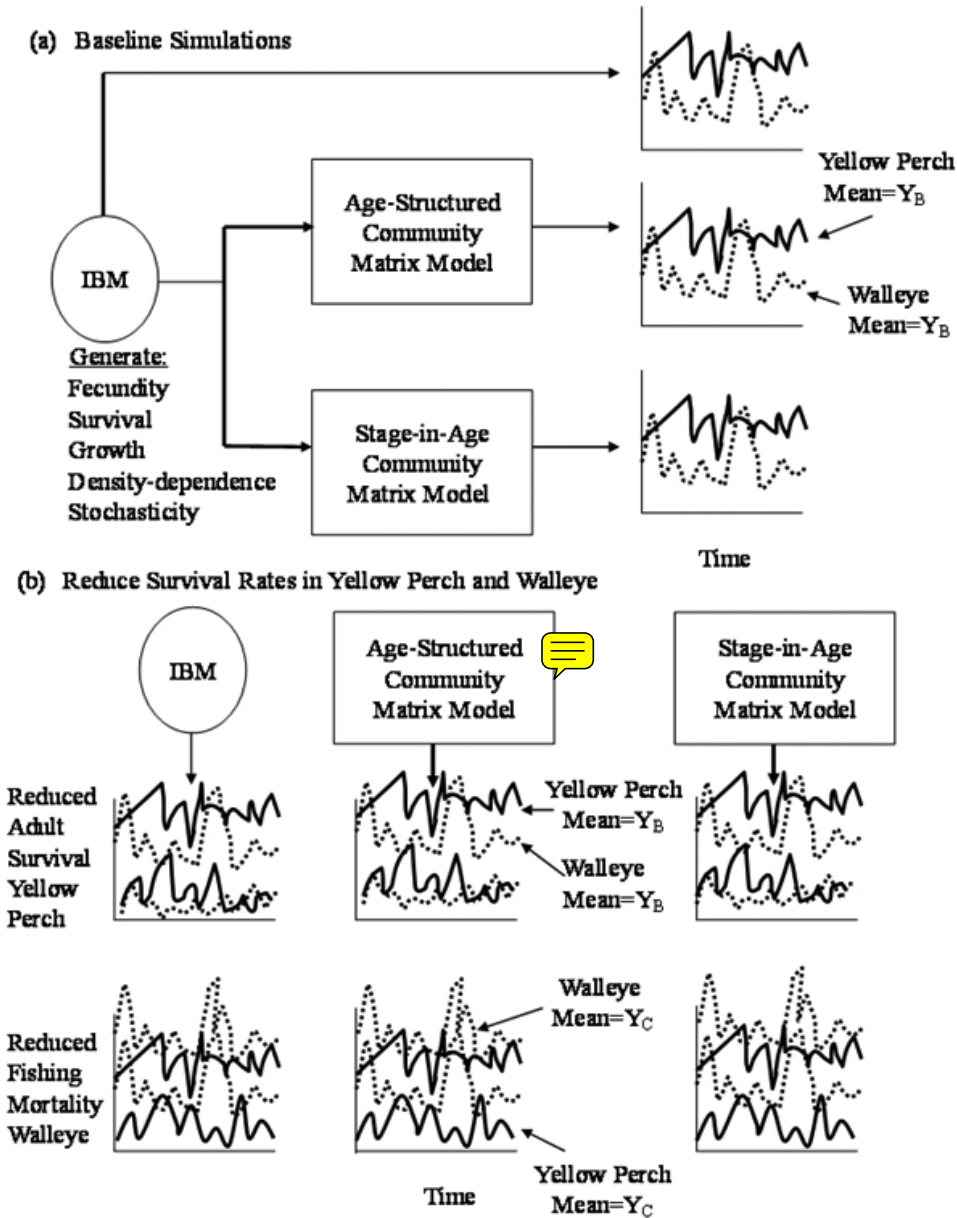
Figure 1. Schematic showing how the two multispecies matrix projection models were (a) constructed from and compared with the baseline IBM output. The output related to fecundity, survival, growth, density-dependence, and stochasticity generated from the IBM was used to estimate the elements of the two baseline community matrix models. Mean values from predicted time series of the matrix models (Y_B) were evaluated for agreement with the baseline IBM. Then (b) reduced yellow perch adult survival and reduced adult walleye fishing mortality were simulated independently in all three models. Mean values from the changed survival simulations (Y_C) were compared among the models using the percent relative change from the mean value under baseline conditions (Y_B) where % Change = $(Y_C - Y_B)/Y_B$ * 100.

successive life stages (egg, yolk sac larva, feeding larva, YOY juvenile, yearling, adult). Eggs and yolk sac larvae were followed as cohorts while feeding larvae, juveniles, yearlings and adults were followed as individuals. Yellow perch had a maximum life span of 10 years; walleye had a maximum life span of 12 years. Adult yellow perch and walleye were individually evaluated for spawning on April 10 (day 100) of each year. Development to hatching and to first feeding was temperature-dependent and the numbers of individuals in each female-cohort were reduced daily by specified egg and yolk sac larval mortality rates. Upon entering the larval stage with the initiation of exogenous feeding, a sample of individuals were generated from each female-cohort and followed as model individuals for the rest of their lifetime.

Daily growth in weight of larvae, juveniles, and adults was represented by the difference form of a bioenergetics equation. Maximum consumption rate and metabolic rate were dependent upon the daily temperature and the individual's weight. Availability of prey determined how much an individual actually consumed each day, and was constrained to be less than their physiologically-allowed maximum consumption rate for that day. Individual length and weight was updated daily based on the growth increment calculated from the bioenergetics equation and length-weight equations.

Seven prey types were simulated in the IBM. Zooplankton was assumed to represent *Daphnia*, benthos was representative of chironomids, and the forage fish prey type was based on YOY white perch. Zooplankton, benthos, and forage fish were modeled as densities that were updated daily based on a discrete version of a logistic population growth function estimated from field data. The remaining four prey types were YOY juvenile and yearling yellow perch and walleye individuals, who each had their own unique length and weight. The IBM included model individuals eating other model individuals.

Realized consumption by each model individual each day was based on a Type II multispecies functional response relationship that depended on the density and vulnerability of the prey, and feeding-efficiency (modeled through the half-saturation constant of the functional response) parameters of the predator. For zooplankton, benthos, and forage fish prey types, vulnerabilities were specified between each prey type and the YOY, yearling, and age-2 and older yellow perch and walleye.

Larvae died at fixed rates for each species because they were not consumed by model individuals. Predation mortality of juvenile and yearling yellow perch and walleye individuals were computed from the daily consumption of yellow perch and walleye model individuals. Predation mortality from adult (age-2 and older) walleye was the major source of mortality on YOY and yearling yellow perch and walleye. Adult (age-2 and older) yellow perch mortality was fixed at $0.30 \cdot yr^{-1}$. Adult walleye natural mortality was fixed at $0.06 \cdot yr^{-1}$, and an additional fishing mortality function were applied to all walleye age-4 and older. The fishing mortality function on walleye decreased with increasing forage fish biomass (forage fish plus YOY and yearling yellow perch and walleye individuals) because adult walleye were less apt to be caught when natural forage was available.

Description of the Multispecies Matrix Models

Model Formulations.—The two multispecies matrix models used the same age structure for age-1 through the maximum age-class (i.e., age-9 for yellow perch and age-11 for walleye), but differed in their structure of the YOY (Table 1). The density-dependent and interspecific relationships were used to update the associated matrix elements each year. Stochasticity

Table 1. Parameters and equations for survival, growth, maturity, and fecundity that determine the elements of the two versions of the multispecies matrix projection models. The two versions of the matrix model used the same values for age-1 and older age classes. YOY were represented by (a) annual age-specific survival for the age-structured version, or (b) daily mortality rates (z) and stage durations (D, in days) for the stage-within-age version. The coefficients for growth in length and weight by age are shown for Age-5 perch and walleye as an example. Coefficients differed among the age classes but the functional forms remained consistent across ages for yellow perch and for walleye.

Age-1 and older age classes	Yellow perch	Walleye
Yearling survival		$Y=1.065 - 4.26E^{-6}*WAB$
Survival of age i	$Y= 0.1456 - 2.56E^{-6}*YE - 7.17E^{-7}*WAB$ 0.7007	0.9345 (age-2 and 3) $Y= 0.90 - 2.59E^{-6}*WAB + 4.75E^{-6}*YY(t-1)$ (ages 4 – 10)
Growth in length by age (ΔLi)	$Y=16.2 - 1.81E^{-5}*YAB - 7.13E^{-5}*YY$	$Y=84.37 + 0.0025*YY(t-1) - 7.07E^{-4}*WAB$
Growth in weight by age (ΔWi)	$Y=34.25 - 4.38E^{-5}*YAB - 1.8E^{-4}*YY$	$Y=561.1 + 0.018*YY(t-1) - 0.005*WAB$
Spawner weight (SWi) conversion from mean weight-at-age (Wi)		Age-3: $Y= 619 - 6.11E^{5}/(W_3)^{1.5}$ Age-4: $Y=480 + 0.46*W_4$ Age-5: $Y=846 + 0.18*W_5$ Age-6: $Y=1229 + 1.2*(W_6)^3$
Fraction mature at age i	$H(L_i) = 0.00146 + 0.98/(1 + \exp(-(L_i-197.5)/9.32))$	$H(Li) = -0.1878 + 1.27/(1 + \exp(-(L_i-352.8)/30.91))$
Fecundity at age i (eggs/female)	$F_i = 183 * W_i - 3658.0$	$F_i = 70.6 * SW_i -7900.0$
a) Annual YOY survival	–	0.000042
b) Daily stage-structured matrix		
Egg z	0.0199	0.2119
Egg D	21.3	20.2
Yolk-sac larva z	0.090	0.1462
Yolk-sac larva D	3	8.5
Feeding larva z	$Y=0.0189 + 8.58E^{-9}*YE$	0.1409
Feeding larva D	35.6	20.1
Juvenile z	$Y=0.009 + 3.61E^{-8}*WAB - 4.41E^{-10}*YE$	$Y=0.0039 + 4.4E^{-10}*WE + 7.5E^{-8}*YY(t-1)$
Juvenile D	295.3	310.1

WE=walleye egg production; YE=yellow perch egg production; YY=yellow perch yearlings and YY(t–1)=yellow perch yearlings from previous year; WAB=walleye adult biomass; YAB=yellow perch adult biomass.

was imposed for each of the relationships. Matrix elements that were not affected by density-dependence or species interactions used constant averaged values from the IBM output.

Age-1 and older classes in the matrix models had off-diagonal elements only, and these were estimated from the averaged age-specific survival rates. Age-specific fraction mature and fecundity were used to estimate the matrix elements of the top row. We used a postspawning matrix formulation (eggs as first class) but did not need to adjust the fecundities by survival rates, as is usually done (Caswell 2001), because we accounted for the survival-related adjustments in how we simulated the matrix models.

Walleye lengths and weights at age varied greatly in the IBM baseline simulation, and we were unable to get the matrix models to agree with the IBM baseline results for walleye when maturity and fecundity were fixed at age. Because we were using the IBM output as "truth" to construct and compare the matrix models, we modified the classic matrix approach to allow length and weight at age to be dependent on yellow perch and walleye abundances and biomasses, and thus to vary over time for each age-class (Table 1). Dynamic length and weight at age allowed for density-dependent and interspecific effects on maturity and fecundity by age. Lengths and weights at age were updated each year based on last year's sizes and this year's annual growth increments. Fraction mature at age was determined from the age-specific mean length (Table 1). Walleye mean weights at age sometimes differed from the mean weight of the mature walleye spawners in the age-class. Relationships were used to convert mean weight at age to mean weight of spawners for walleye (Table 1, R^2 values between 0.07 and 0.38). The mean spawner weight was used to determine fecundity of walleye. This conversion was not necessary for yellow perch whose mean weights at age were very similar to the mean spawner weights at age in the IBM output.

The age-structured YOY version simply used a single annual relationship to determine egg to age-1 survival (Table 1a), while the stage-within-age version potentially had relationships for the duration (D) and daily mortality rate (z) for the feeding larvae and YOY juvenile stages (Table 1b). The stage-based YOY matrix had nonzero values for both the diagonal element (P) and the off-diagonal element (G) corresponding to each of the YOY stages. P was the probability of surviving and remaining in the current stage, and G was the probability of surviving and growing into the next stage class. We calculated the YOY stage matrix elements from the daily survival rate (σ, where $\sigma = e^{-z}$) and stage duration (D) according to Caswell (2001):

$$P_i = \sigma * (1 - \rho) \tag{1}$$

$$G_i = \sigma * \rho \tag{2}$$

$$\rho = \frac{\sigma^D - \sigma^{D-1}}{\sigma^D - 1} \tag{3}$$

Given we estimated duration and daily mortality rates from the IBM output, we could specify the P and G values of the matrices associated with this stage. If duration or mortality rate were dynamic (i.e., determined from density-dependent or interspecific relationships), then new P and G values were determined each year. We used the values of the abundances and biomasses at the beginning of each year to determine the new P and G values for the upcoming year.

Density-Dependent and Interspecific Interactions.—We examined the baseline IBM output (years 16–200) for evidence of density-dependence and interspecific interactions within the survival rates, growth rates, and stage durations that determined the values of the elements of the matrix models. We systematically explored the IBM output by plotting these rates against various measures and combinations of walleye and yellow perch abundances and biomasses. Daily IBM output was averaged to obtain one value per year for the vital rates, abundances, and biomasses. Simple linear or multiple linear regression equations using the stepwise selection procedure (SAS Institute Inc. 2002) were fit for each response variable (rate) and all of its associated candidate explanatory variables (abundances and/or biomasses). We examined the explanatory variables included in the regression equations for collinearity and partial significance by examining the Mallow's C(p) statistic and partial residual plots. The simple linear or multiple regression equation with the highest R^2 value was selected for each response variable, as long as the R^2 value of the best fit model exceeded 0.10. This minimum statistic was selected because Sable and Rose (2008) found that density-dependent relationships with similarly low R^2 values were correctly defined for yellow perch population matrix models and from the baseline IBM output. Eggs and yolk sac mortality rates, and stage durations of all YOY stages, were treated as constant values (Table 1) because they showed no dependence on yellow perch or walleye abundances and biomasses in IBM output. The mortality rates and growth increments for which density-dependent or interspecific relationships were specified for yellow perch are shown in Figure 2 and for walleye in Figure 3, and listed for both species in Table 1. Growth increments (in weight and in length) had separate relationships for each age (e.g., age-5 perch growth in Figure 2e, 2f). The annual IBM output is included with the fitted regression relationships in Figure 2 for the readers to see.

We deviated from fitting linear functions for YOY survival of yellow perch in the age-structured YOY matrix version (Figure 2c). Spawner-recruit relationships are not typically monotonic, so we used a cumulative Lorenzian function (Table 1) provided by Tablecurve (SPSS 1998) which closely resembled a sigmoidal survival response and which better described the survival relationship given by the baseline IBM output.

Stochasticity.—Stochasticity was incorporated into each density-dependent and interspecific relationship included in the matrix models. We used the mean and standard deviation of the residuals from the fitted regression equations to define normal or lognormal distributions of the stochastic deviates for the matrix models (Table 2). The residuals from most of the regression equations were normally-distributed as indicated by the Shapiro-Wilkes statistics ($p > 0.05$), with the exception of walleye annual growth increments for ages-3, 6 and 7 walleye, for which we used the better-fitting lognormal distribution. Stochastic deviates were randomly generated from the distributions once per year for the matrix models and applied as modifiers to the stage or age-specific rate value predicted from the functions (Table 1; Figures 2 and 3).

Model Comparison

We performed two sets of comparisons between the IBM and the two multispecies matrix models: baseline simulations and predicted responses to changed survival rates. For baseline conditions, we compared time series plots of the annual number of yellow perch and walleye spawners. We examined the degree of coupling and cycling dynamics of yellow perch and
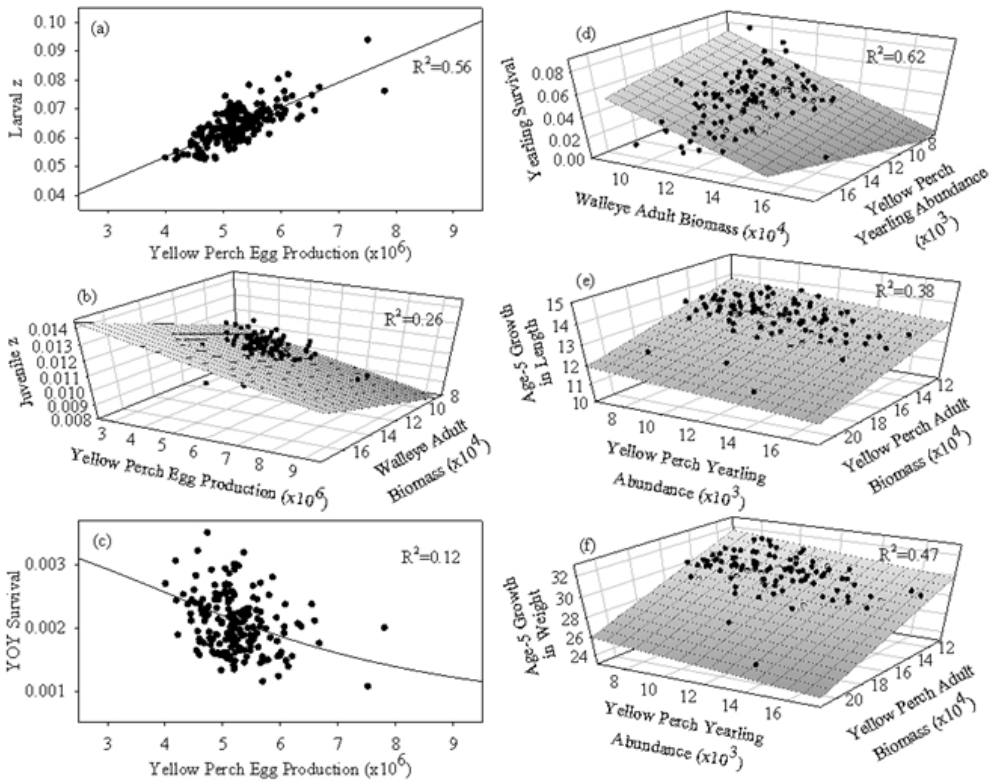
Figure 2. Regression functions fit to IBM output for density-dependent and interspecific relationships included in the two versions (age-structured YOY and stage-within-age YOY) of the yellow perch matrices within the multispecies matrix models. (a) larval daily mortality (z = day^{-1}), (b) juvenile daily mortality (z = day^{-1}), (c) YOY annual survival fraction, (d) yearling survival fraction, (e) age-5 growth length (ΔL_5 = mm·yr^{-1}), and (f) age-5 growth in weight (ΔW_5 = g·yr^{-1}). The black circles are annual mean values of baseline IBM output.

walleye total adults using cross-correlation and partial autocorrelation coefficients (Berryman and Turchin 2001). We also compared a suite of output variables averaged over years for each population under baseline conditions. These averaged output variables (with coefficients of variation, % CV) were annual values of: total egg production, number of entering yearlings (age-1), number of entering age-2 recruits, number of spawners, larval, juvenile, YOY and yearling survival rates, lengths, weights, maturity and fecundity of ages 4, 5, 6. Egg production and spawner abundances represented the overall population response, and entering yearlings and age-2 represented recruitment at two important ages. Yearling and adult walleye consume many YOY and yearling yellow perch; age-2 and older individuals are no longer vulnerable to walleye predation. We recorded the reproductive values for ages 4, 5, and 6 yellow perch and walleye because these age classes represented intermediate-sized adults with dynamic maturity and fecundity. Maturity and fecundity at age were functions of length and weight at age, respectively. Because the matrix models were constructed from the IBM output, we expected general agreement among the three models under baseline conditions.

The second comparison was between the predicted responses of the IBM and multispecies matrix models to changed adult survival rates for both species. In all three models, we
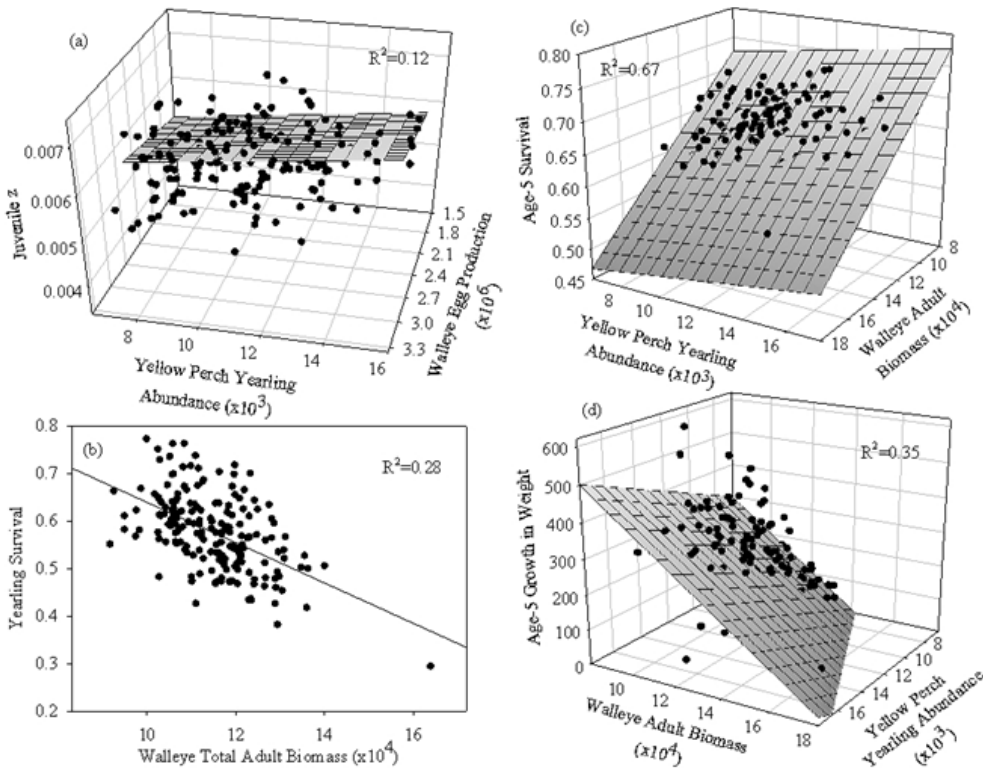
Figure 3. Regression functions fit to IBM output for density-dependent and interspecific relationships included in the two versions (age-structured YOY and stage-within-age YOY) of the walleye matrices within the multispecies matrix models. (a) juvenile daily mortality (z = day^{-1}), (b) yearling survival fraction, (c) age-5 survival fraction, and (d) age-5 growth in weight (ΔW_5 = mm·yr^{-1}). The black circles are annual mean values of baseline IBM output.

simulated a 10% reduction in adult survival of yellow perch (age-2 and older) and a 13% increase in the survival of age-4 and older walleye (fishable ages). Changes to adult survival in the matrix models were imposed by multiplying age-specific survival fractions at the beginning of each year by a constant (e.g., 0.9 for 10% reduction in perch adults), and imposed after density-dependence and species interactions affected adult growth and survival. The reduction in yellow perch adult survival was imposed similarly in the IBM, but imposing the walleye survival changes in the IBM was more complicated because the IBM separated natural and fishing mortality for walleye. Using trial-error simulations, we simulated an average 13% increase in walleye survival by reducing monthly fishing mortalities by 2% after any forage fish and density-dependent effects in the IBM had occurred.

We report the percent change from baseline for each of the three models for averaged abundances of yellow perch and walleye, and for averaged values of survival rates and reproduction that resulted from density-dependent and interspecific relationships. Percent change from baseline was computed by calculating the average value for the output variable over the 200-year simulation (Y_C), and expressing the relative change from the averaged baseline value (Y_B) as $[(Y_C - Y_B)/Y_B * 100]$. We compared the averaged abundances of spawners, eggs, yearlings, and age-2 recruits, survivals for YOY and yearlings, and age-5 maturity, fecundity,

Table 2. Standard deviations of the residuals from the regression models describing density-dependence and interspecific interactions in the matrix models. The standard deviations define the distributions for the randomly-generated stochastic deviates applied to the response variables calculated from the regression models. Normal distributions were used for all relationships except ages-3, 6, and 7 walleye growth, which used lognormal distributions. All means for normally-distributed residuals are equal to 0.0; the means for the lognormal distributions are reported in parentheses.

	Yellow perch		Walleye	
Larval z	0.0041			
Juvenile z	0.0008		0.0006	
YOY survival	0.0004			
Yearling survival	0.0065		0.0670	
Adult survival by age i	0.0201			
Annual growth:	Length	Weight	Length	Weight
Age-1 (Yearling)			4.71	5.91
Age-2	0.393	0.724	8.27	23.7
Age-3	0.377	0.844	0.34 (–0.06)	0.39 (–0.08)
Age-4	0.361	0.934	12.6	69.7
Age-5	0.370	0.891	11.9	88.7
Age-6	0.356	1.058	0.42 (–0.09)	0.47 (–0.11)
Age-7	0.337	1.186	0.51 (–0.13)	0.55 (–0.15)
Age-8	0.328	1.263	7.86	94.8
Age-9			5.5	77.4
Age-10			4.3	60.4

and survival (for walleye only). We categorized the percent change from the mean baseline value as very small threshold response (<10%), small (10–20%), moderate (>20–40%), and large (>40%). The predicted responses from the models were considered to be in agreement when they were within the same category or near values within adjacent categories.

Results

Baseline Simulations

Predicted time series of yellow perch and walleye spawner abundances (Figure 4) were generally similar between the IBM and the two multispecies matrix models. Cross-correlations between annual values of walleye and yellow perch total adults over years showed similar and moderate coupling within the IBM and two multispecies matrix models. All three models showed the highest cross-correlations between this year's yellow perch total adults and walleye total adults from 2 and 3 years later. Lag -2 cross-correlation values for the IBM, age-structured YOY model, and stage-within-age YOY model were –0.38, –0.37, and –0.18, and for lag -3 years were –0.25, –0.35, and –0.13. Partial autocorrelation coefficients for both walleye and for yellow perch total adults were highest at lag 1 (last year's value most correlated to this year's value) and ranged from 0.52 to 0.75 in all three models; partial coefficient values at increased lags quickly decayed after the first year.
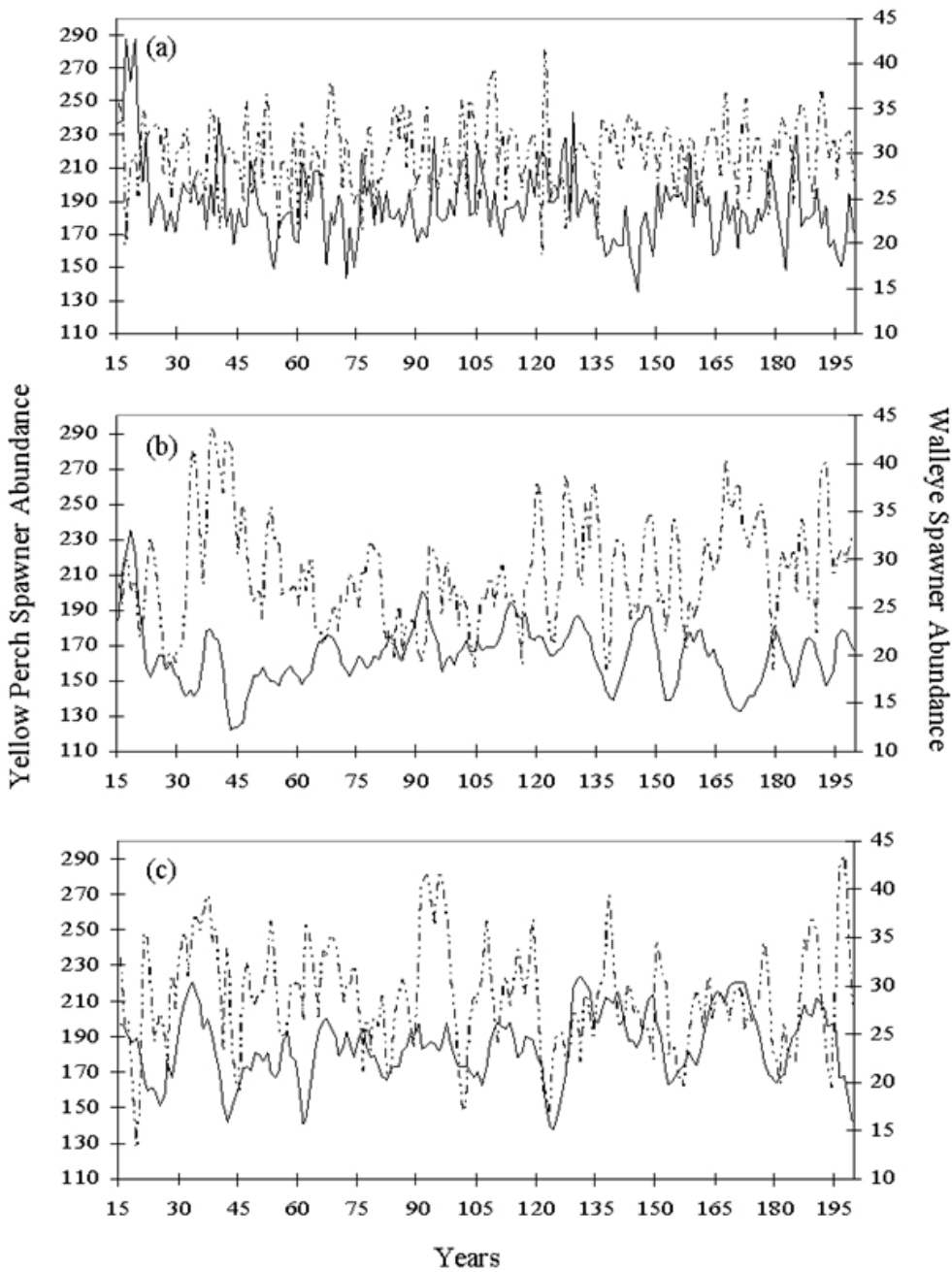
Figure 4. Predicted yellow perch (solid line) and walleye (dashed and dotted line) annual spawner abundances over years 15–200 for the (a) IBM, (b) age-structured YOY multispecies matrix model, and (c) stage-within-age YOY multispecies matrix model.

Predicted mean values and CVs over years were generally similar for stage abundances and survival rates of yellow perch and walleye (Table 3). Predicted mean length, weight, fraction mature, and fecundity at age in yellow perch adults were similar among the IBM and matrix models with little annual variation, whereas differences between the models and greater inter-annual variation were more apparent for walleye (e.g., see age mature and fecundity for species in Table 3). Lengths and weights were variable in the IBM outputs, more so than the field data suggest (Rose et al. 1999). The variation in walleye growth and sizes at age in the IBM was hard to capture with the matrix models, and the models often predicted different mean reproductive values for intermediate age classes of walleye. Fecundity was more similar across models for walleye, but showed less annual variation within the matrix models (Table 3). However, given the rather large interannual variation in lengths and weights at age of walleye from the IBM, and our desire to avoid calibrating the matrix model predictions to IBM output, we opted to not further adjust the matrix models.

Responses to Reduced Adult Survival Rates in Yellow Perch

Predicted yellow perch abundance responses to reduced adult survival of yellow perch were similarly moderate to large for spawners and eggs, and less similarly small to moderate for yearlings in all models, but the IBM predicted a continued moderate decline for age-2 recruits while the matrix models predicted very little response (leftmost bars in Figure 5a–d). Reducing yellow perch adult survival caused only small to very small walleye abundance responses in the IBM and matrix models (leftmost bars in Figure 5e–h). The IBM and matrix models usually predicted opposite responses in abundances, yet responses were generally near or below the very small 10% threshold response so it was difficult to say that walleye responses differed across models.

The increases in perch YOY survival due to reduced adult perch survival were similarly large in all three models (leftmost bars Figure 6a), while the matrix models overestimated the increase in yearling survival (Figure 6b). The matrix models underestimated maturity at age-5 (Figure 6c) while predicting similarly small to very small increases in fecundity (Figure 6d). The overestimated increase in yearling survival of the perch matrix models resulted in the observed difference for age-2 recruits with the IBM (leftmost bars in Figure 5d). Because the yellow perch age-2 recruits rebounded from the perch survival reduction in the matrix models, the matrix models predicted less reduction in adult perch numbers which led to smaller responses in growth-mediated adult maturity and fecundity (Figure 6c, 6d).

All survival and growth responses of walleye to reduced yellow perch adult survival were near or below the very small 10% threshold response (leftmost bars in Figure 6e–i). Other changes to yellow perch were simulated with the models but not presented here because each simulation predicted similarly small and often opposite responses across models for walleye. All simulations which changed yellow perch numbers, including the presented reduced adult survival, indicated that changes in the yellow perch prey (Figure 5c) population had little effect on the walleye predator population. The predicted responses of the IBM and multispecies matrix models were most often in opposite direction, even though the magnitude of the model responses were very small to negligible for the walleye rates.

Table 3. Predicted means and % CVs (SD/mean * 100) given by the IBM, age-structured multispecies matrix model, and stage-within-age multispecies matrix model for population abundances and rates which showed density-dependence and/or species interactions in yellow perch and walleye.

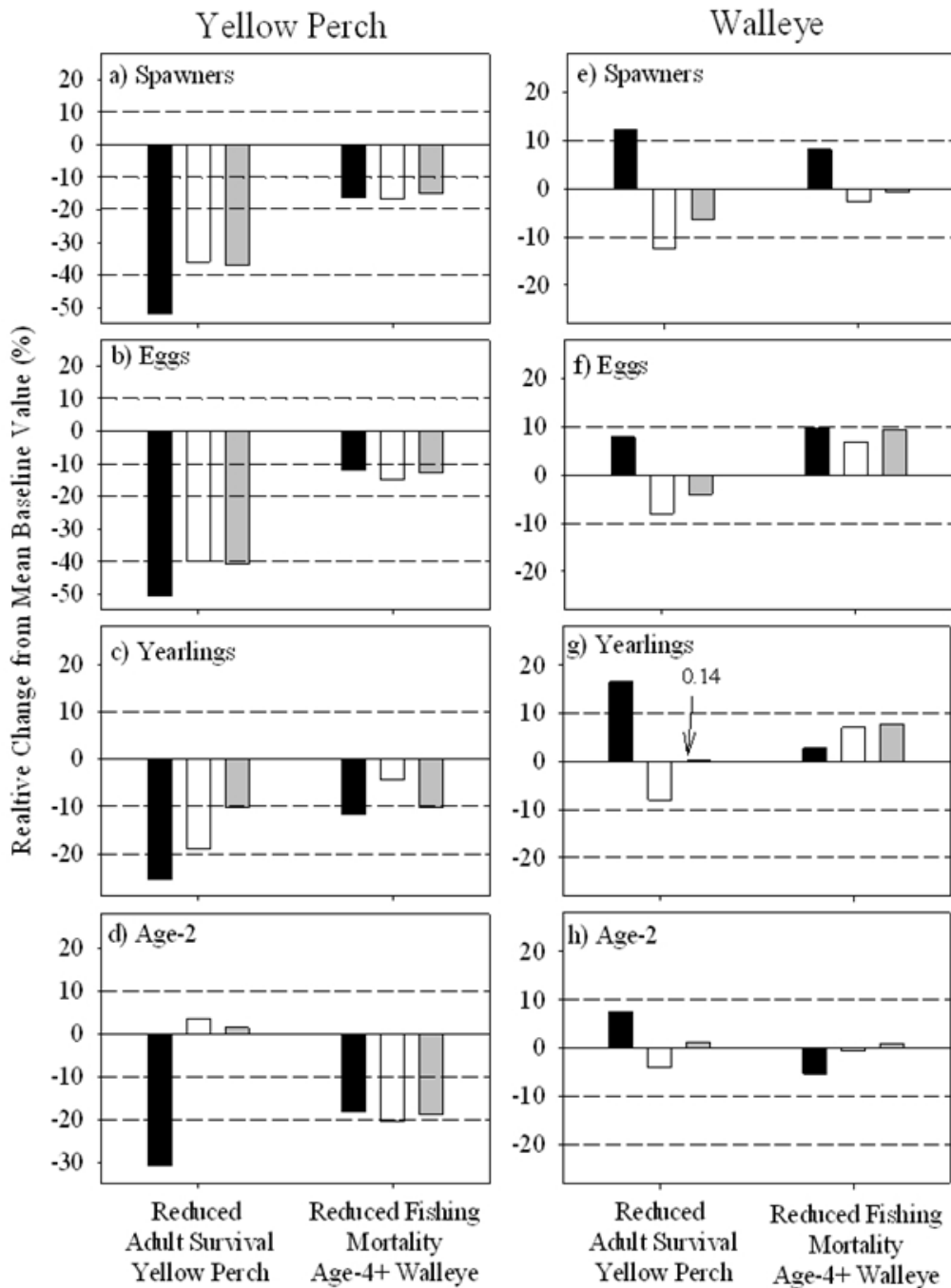|	Yellow perch			Walleye		
	IBM	Age matrix	Stage-in-age matrix	IBM	Age matrix	Stage-in-age matrix
Spawners	188	164.5	185	29.4	28.2	28.4
	(12.0)	(10.7)	(10.6)	(14.3)	(19.7)	(19.7)
Eggs	5,250,000	4,434,624	4,960,430	2,490,000	3,043,441	3,032,312
	(10.0)	(10.8)	(10.1)	(15.0)	(15.0)	(14.0)
Yearlings	10,740	10,498	10,189	103	128	104
	(21.0)	(21.5)	(28.9)	(33.0)	(15.0)	(20.2)
Age-2 recruits	371	307	357	59.5	68.4	60
	(26.0)	(26.9)	(29.3)	(37.0)	(19.0)	(24.2)
YOY survival	0.00202	0.00239	0.00207	0.00042	0.00042	0.00035
	(20.8)	(22.4)	(29.9)	(31.9)	(0.0)	(20.0)
Yearling survival	0.04	0.0302	0.0368	0.575	0.537	0.575
	(30.0)	(30.4)	(27.9)	(14.0)	(14.6)	(13.5)
Age-4 mature	0.298	0.299	0.284	0.256	0.085	0.0984
	(28.5)	(5.4)	(7.0)	(54.6)	(90.6)	(97.6)
Age-4 fecundity	18,380	17,790	17,543	37,405	36,389	36,731
	(4.6)	(1.5)	(1.7)	(14.7)	(4.7)	(5.7)
Age-5 mature	0.615	0.639	0.614	0.428	0.243	0.29
	(15.9)	(3.8)	(4.7)	(40.5)	(80.6)	(72.6)
Age-5 fecundity	22,920	22,728	22,355	58,536	57,784	58,412
	(3.8)	(1.9)	(1.9)	(12.6)	(2.1)	(1.9)
Age-6 mature	0.839	0.869	0.853	0.508	0.458	0.536
	(8.1)	(1.6)	(1.9)	(38.4)	(51.9)	(45.7)
Age-6 fecundity	27,985	28,302	27,663	83,605	81,471	82,224
	(3.5)	(1.9)	(1.9)	(14.6)	(1.8)	(2.3)

Figure 5. Model-predicted relative changes (%) in mean yellow perch (a) spawners, (b) eggs, (c) yearlings, (d) age-2 recruits, and walleye (e) spawners, (f) eggs, (g) yearlings, (h) age-2 recruits for reduced yellow perch adult survival and reduced walleye fishing mortality simulations. ■ = IBM, □ = age-structured YOY multispecies matrix model, and ◪ = stage-within-age YOY multispecies matrix model. Dashed lines indicate ± 10% response threshold, the ± 20% and ± 40% response categories.
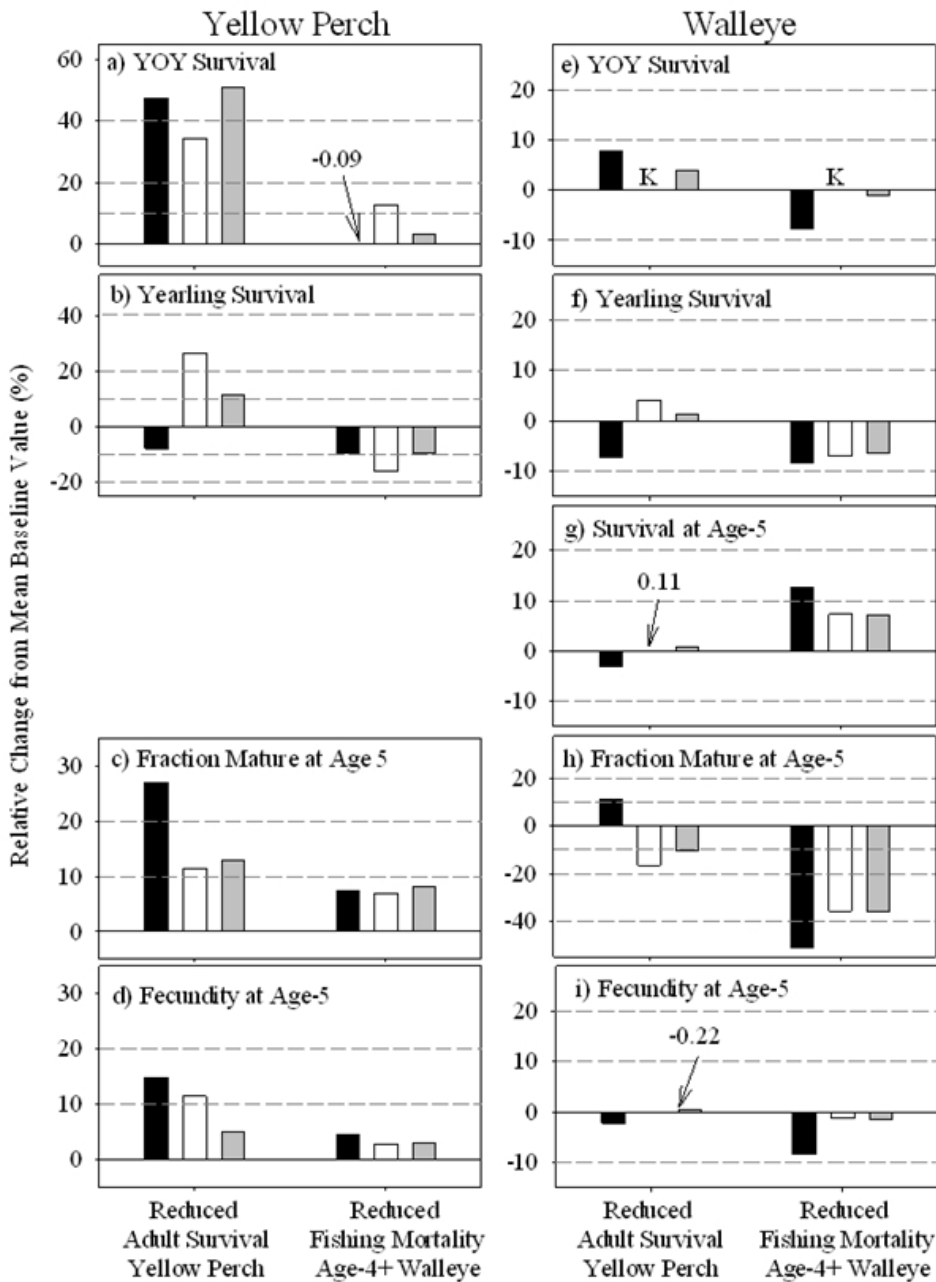
Figure 6. Model-predicted relative changes (%) in mean yellow perch (a) YOY survival, (b) yearling survival, (c) age-5 fraction mature, (d) age-5 fecundity, and walleye (e) YOY survival, (f) yearling survival, (g) age-5 survival, (h) age-5 fraction mature, and (i) age-5 fecundity for reduced yellow perch egg survival and reduced walleye fishing mortality simulations. ■ = IBM, □ = age-structured YOY multispecies matrix model, and ▣ = stage-within-age YOY multispecies matrix model. Dashed lines indicate ± 10% response threshold, the ± 20% and ± 40% response categories.

Responses to Increased Adult Survival Rates in Walleye

Predicted responses in yellow perch abundances to increased adult walleye survival were nearly equal and small across models (rightmost bars in Figure 5a–d). Walleye abundance responses to increased walleye adult survival (and all additional simulations which changed walleye abundances not presented here) were very close to or below the very small 10% threshold for all models (Figure 5e–h). The IBM and matrix models agreed in direction of response for egg and yearling abundances (Figure 5f, 5g), yet again the small magnitude in responses across models prohibits us from stating that the model predictions were the same. Still, the very small differences in walleye predators elicited very similar larger-magnitude reductions to their yellow perch prey (Figure 5c, 5d) across models.

Walleye survival and growth responses to increased adult survival in the fishable walleye age classes were generally at or below the very small 10% threshold response (rightmost bars in Figure 6e–i), with exception of moderate and large reductions in walleye adult length and fraction mature at age (Figure 6 h). Reduced growth and reproductive capacity at age for walleye resulted from combined effects of density-dependence (i.e., walleye total adults increased between 8% and 12% in all models with decreased fishing mortality) and reduced perch prey numbers (Figure 5b and 5c).

The very small and small increases in the adult walleye predators caused similar reductions to yearling yellow perch survival (rightmost bars in Figure 6b). Juvenile mortality and yearling survival provided the only direct predator–prey links for walleye and yellow perch within the yellow perch population matrices (Figure 2b, 2d). The functional relationship for yearling survival sufficiently captured the perch prey response (Figure 6b). Very small increases in yellow perch YOY survival and age-specific reproduction were at or below the 10% threshold (rightmost bars in Figure 6a, 6c, 6d) and were the result of density-dependent effects from small reductions to yellow perch eggs (Figure 5b) and total perch adults (see Figure 5d, reductions in total perch adults were nearly equal to the 20% reduction shown for age-2).

Discussion

Our strategy in this evaluation of multispecies matrix models was to provide a test of the models under conditions resembling how they would be used in real applications. We treated the IBM output as "field data" and estimated the matrix models using simple regression analysis. Granted, 200 years of field data are unrealistic, but we wanted to set-up conditions for evaluating the models rather than blaming their performance on limited data. We then applied the matrix models to typical scenarios of trying to predict the responses of both the prey and predator species to changed survival rates. In our case, we had the true answer available to use in terms of the IBM-predicted responses. We tried to avoid using information about the inner workings of the IBM to influence our configuration of the matrix models, and we did no further adjustments to the matrix models based on their performance under the changed survival simulations. Thus, we left open the distinct possibility that we would conclude that the matrix models performed poorly.

Based on our analysis, we conclude that the multispecies matrix models were generally successful in predicting the prey (yellow perch) responses and less successful with the predator (walleye) responses, although we must caveat this conclusion by reminding the readers

of the small magnitude in walleye responses across models which prohibited us from clearly stating that model predictions agreed or disagreed. The changed survival simulations (two simulations presented here and two additional simulations not presented) resulted in many very small (<10%) responses of walleye, which weakened the power of our evaluation of the walleye responses. Perceived differences between the very small responses could have been caused by the stochasticity added to the functional rates of the matrix models. Alternatively, the added stochasticity could have caused the perceived small differences between the models. Larger changes to survival rates of walleye resulted in unrealistic dynamics in the IBM, which is not at all related to the multispecies matrix model performance. The matrix models successfully captured the long-term baseline dynamics (Table 3) and the moderate degree of coupling between yellow perch and walleye (Figure 4), which was somewhat expected since the matrix models were constructed from the IBM output.

Predicted responses of yellow perch averaged abundances, survival rates, and maturity and fecundity were generally in good agreement with the IBM, with the exception of the yearling survival response to reduced perch survival (Figure 6b). When the walleye predator population was manipulated, if even by a small amount over time, the predicted perch responses were similar across models for the yellow perch (Figure 5a–d).

In contrast, the predicted responses in averaged walleye abundances, survival rates, and maturity and fecundity were usually opposite between the IBM and matrix models but too small in magnitude to conclude that the models agreed or disagreed (leftmost bars in Figures 5e–h and 6e–i). Even though most walleye responses were very small in magnitude across models, the consistent disagreement between the IBM and matrix models for all simulations (presented and not presented) suggest that the walleye predators were not responding in the same way to changes in their perch prey. Below we use the observable success with yellow perch, and contrast yellow perch with walleye, to discuss some potential reasons for the questionable performance of the multispecies matrix models with walleye.

While we easily identified density-dependent and interspecific relationships for larval and juvenile stages, and YOY annual survival in yellow perch from the IBM output, we had much more difficulty identifying these relationships in walleye YOY stages. For example, in our regression analysis of the IBM output, we found no evidence of density-dependence or species interactions when we treated YOY walleye as a single age-class, and we were able to identify only weak correlations between walleye juvenile daily mortality, walleye egg production, and yearling yellow perch abundance (Figure 3a). The IBM, on the other hand, exhibited responses in walleye larval survival (20% increase) and juvenile survival (10% decrease) when perch adult survival was decreased (leftmost bar shows a combined overall YOY survival increase of 8% in Figure 6e). Also, the IBM showed evidence of cannibalism in YOY walleye at low prey abundances (Rose et al. 1999) but we found no evidence of cannibalism in walleye YOY annual survival or juvenile mortality rates to incorporate within the age and stage structures of the matrix models. Although mortality of walleye YOY and yearlings from cannibalism is low within the IBM (Rose et al. 1999), it can greatly change the size structure and dynamics of the population (Dong and DeAngelis 1998).

The fact that we had difficulty predicting larger and more similar walleye predator responses across models suggest that the age-specific survival and growth linkages between the population matrices for walleye were likely weaker and perhaps incorrectly estimated for the walleye predators. Age-specific adult growth and reproductive responses of walleye were generally very small when their perch prey were manipulated (leftmost bars in Figure

6f–i), and underestimated somewhat by the matrix models when their own numbers were manipulated (rightmost bars in Figure 6 g–i). Density-dependent and prey-mediated growth responses have been more difficult to estimate and capture within the age structure of fish populations (Lorenzen and Enberg 2002; Sable and Rose 2008).

We also question how well we captured the large variation in sizes at age of walleye, and therefore maturity and fecundity, predicted by the IBM. Dynamic sizes at age were one of our few major modifications that we made to the classic matrix projection approach. We modeled growth increments by age in length and in weight so that fraction mature and fecundity at age varied annually within the matrix models. Examination of the IBM output convinced us that we needed to model annual growth increments in order to capture the wide variation in reproductive values by age. However, we did observe a suggestion of a mis-fit between the matrix models and the IBM for walleye size and reproductive values at age (Table 3). Furthermore, in the changed survival rate simulations, we sometimes incorrectly predicted changes in walleye sizes at age. For example, a 10% reduction in walleye adult survival (simulation not presented in paper) resulted in a 27% increase in mean weight of age-5 walleye in the IBM versus only 12% and 13% increases in the two matrix models. There were also situations when the matrix models predicted similar responses in walleye growth and sizes at age, but then predicted different responses in maturity and fecundity. Under reduced fishing mortality of walleye (increased adult survival, Figures 5 and 6) the IBM predicted a 15% reduction in walleye age-5 weight while the two matrix models predicted 11% and 12% reductions. However, associated with these changes in mean weight, the IBM predicted a 9% decrease in fecundity while the matrix models predicted a 1% decrease in fecundity (rightmost bars in Figure 6i).

We tried to simplify the dynamic sizes at age algorithm to see if that improved the performance of the matrix models for walleye. We re-ran the analysis using age-specific growth increments in weight only for walleye and for yellow perch, and then updated lengths at age in the matrix models based on species-specific length-weight curves. This simplification resulted in greater differences between the IBM and matrix models for both the baseline simulation and the predicted responses to changed survival rates. Another simplification to the dynamic sizes at age would have been to relate fraction mature and fecundity (rather than via growth) directly to yellow perch yearling abundance and adult walleye biomass (Caswell and Neubert 2005). If we directly modeled maturity and fecundity, we would have assumed fixed mean lengths and weights at age and adult biomass could then only vary according to adult abundance. However, total annual adult abundance and total adult biomass in the baseline simulation were not correlated in the IBM ($R^2 = 0.009$ for yellow perch; $R^2 = 0.06$ for walleye), and when total adult abundances of yellow perch and walleye were substituted into the regression equations for total adult perch and walleye biomasses, the R^2 values decreased dramatically. We conclude that growth needs to be dynamic within the matrix models, and that length and weight need to have the option to be partially independent, although we are still somewhat unclear on how these age-specific rates can be correctly defined within the models.

We thought that maybe our imposition of linear regression models was too restrictive and that the response variables (Table 2) could be better represented with more flexible regression models. We used the TableCurve 2D (SPSS 1998) and 3D (SPSS 2002) curve-fitting programs to fit complicated linear and nonlinear regression models to the same relationships we used with simple linear regression models (Figures 2 and 3). The fit of the best-fitting complicated linear and nonlinear equations differed little from the fit provided by the simple linear regression models. For example, the best-fit complicated model for walleye juvenile daily mortality

yielded an R^2 of 0.122 compared to an R^2 of 0.120 with the simple regression equation, and the complicated model for yellow perch yearling survival yielded an R^2 of 0.63 compared to an R^2 of 0.62 with the simple equation. Even so, we re-ran the analysis using the best-fit complicated linear or nonlinear regression equations because maybe there were important differences near the extremes of the values of the explanatory variables under changed survival rate simulations. Using the complicated or nonlinear regression equations we obtained yellow perch and walleye responses almost identical to those obtained with the original analysis that used the simple linear regression equations.

Our evaluation showed that, at least for the Oneida Lake situation, multispecies matrix modeling was easier for the prey population than the predator population because it was simpler to define dynamic survival processes for the prey than to define the dynamic survival and growth processes for the predator. Both formulations of the multispecies matrix models performed well for yellow perch when compared with the predictions of the IBM, but had more difficulty capturing the subtle YOY and yearling survival processes and subtle growth and reproductive responses of the walleye. If extensive information is available for both the predator and prey, we suggest that both multispecies IBMs and matrix models be investigated. If extensive data are not available for one or more species, which is often the case in many systems, then single species modeling may be appropriate, with the knowledge that species interactions have been much simplified. If the multispecies matrix modeling approach is used, we suggest using caution when defining and interpreting the dependence of predator rates on the prey, as our results suggest that simulating the population dynamics of the predator is more uncertain.

This evaluation of the matrix modeling could not have been done without the long-term data and studies of Oneida Lake that lead to the relatively high confidence we have in the IBM, including knowing the limits of perturbations that could be applied to the IBM. Our next steps in evaluating the multispecies matrix modeling approach would be: (1) further refinement of the matrix modeling approach for walleye, especially the growth related aspects; (2) simulation of other time periods (e.g., high forage fish; zebra mussels) using the Oneida Lake IBM (Rutherford and Rose Chapter 20), with the hope that larger walleye responses could be simulated with the IBM; (3) comparing the IBM and multispecies matrix models to real data collected for Oneida Lake. We first wanted to determine where and how the matrix models differed from the IBM, but it is possible that not all differences between the models in our study were a fault of the matrix approach. For example, the IBM predicted more variation in walleye size than what the Oneida Lake data suggest (Rudstam et al. Chapter XX). It would be interesting to determine if the age-structured growth processes of the multispecies matrix models better define the Oneida Lake data than those processes within the IBM. Continued testing of development of multispecies modeling approaches is critical for implementing ecosystem-based fisheries research and management.

Summary

Ecosystem-based fisheries management requires multispecies models, and these models must be tested to ensure they have sufficient accuracy to inform management decisions. Oneida Lake offers an excellent opportunity for the development and testing of multispecies models. Long-term studies spanning decades have chronicled walleye and yellow perch fisheries, competition, predator–prey interactions, and perturbations within the lake food web. A previously-constructed individual-based model (IBM) of Oneida Lake was calibrated and cor-

roborated with the extensive database on walleye and yellow perch dynamics. From the IBM, we developed two alternative formulations of multispecies matrix projection models (age-structured and stage-within-age YOY) that simulated walleye and yellow perch predator–prey dynamics, and used the IBM as the basis for comparing predictions of the matrix models to changes in the prey and predator survival rates. Selected elements in the yellow perch matrix and walleye matrix depended on their own abundances and biomasses (density-dependence) and the abundances and biomasses of the other species (interspecific interactions). Averaged annual abundances, survival rates, and maturity and fecundity at age under baseline conditions were similar between the IBM and two matrix models. Under changed survival rates, predicted responses in yellow perch were usually similar and larger between the IBM and matrix models; predicted walleye responses were usually very small in magnitude across models, and often opposite between the IBM and matrix models. The multispecies matrix models were more successful in predicting the yellow perch prey responses than the walleye predator responses. We suspect the difficulties in predicting larger and similar walleye responses in the IBM and matrix models was due to the large amount of variation in walleye sizes within the IBM, and our difficulty in describing density-dependent and prey-mediated survival and growth responses in the age structure of the walleye predator population matrix models. Continued evaluation of the multispecies modeling approaches would involve simulating different time periods (e.g., increased forage fish, cormorant predation) for more variation within the IBM, and perhaps directly comparing the modeling approaches to the Oneida Lake data.

Acknowledgments

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