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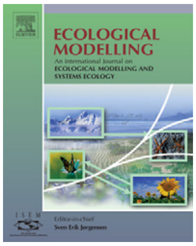

# A comparison of individual-based and matrix projection models for simulating yellow perch population dynamics in Oneida Lake, New York, USA

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## ABSTRACT

Both individual-based models (IBMs) and matrix projection models are commonly used to simulate fish population dynamics. We questioned whether matrix models could be used to predict population responses of the prey in a highly coupled predator–prey system. The matrix approach was evaluated for predicting yellow perch population responses to changes in survival, and comparing the responses to those from a detailed IBM. The IBM explicitly modeled effects of walleye predation and competition with yellow perch, whereas the matrix models used averaged values, and in some cases density-dependent relationships, for survival, growth, and reproduction of yellow perch that implicitly included walleye effects. We used the output from a 200-year simulation of the IBM as data for estimating the elements of three alternative versions of a matrix projection model. We constructed an age-structured matrix model and two stage-within-age matrix models for yellow perch. The stage-within-age versions both represented the young-of-the-year (YOY) stages, but differed in the timestep used for updating their density-dependent relationships (annual or daily). The predictions of the matrix models were first compared with the IBM under baseline conditions to confirm that parameter estimation of the matrix models was reasonable. We then simulated reduced and increased egg or adult survival in each model, and compared the relative responses among the four models. Predicted yellow perch spawner abundance under baseline conditions was similar among the IBM and two matrix models that used annual density-dependence, but underestimated by the stage-within-age matrix model that used daily density-dependence. Averaged annual abundances, YOY and yearling survival rates, and sizes at age were generally similar between the IBM and matrix models under baseline conditions. Density-dependent YOY survival was critical for accurately predicting yellow perch responses to changed egg and adult survival rates. Predicted responses to changed survival rates from the stage-within-age matrix model with daily density-dependence differed most from the IBM, and consistently predicted changes in juvenile stage survival opposite to those predicted by the other models. The matrix models that used annual density-dependence predicted similar abundance responses as the IBM to changed egg and adult survival rates. If sufficient data are available, we recommend a population and multispecies modeling approach. If data are available only for the species of interest, then we favor the stage-within-age matrix model with annual density-dependence

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because the stage structure for YOY allows for flexibility and because it performed better than other matrix models when compared to the IBM.

## 1. Introduction

Both individual-based models (IBMs) and matrix projection models are commonly used to simulate fish population dynamics. Matrix models have been widely used for decades for fish and other taxa (Caswell, 2001), and form the basis for much of fisheries stock assessment and management (Heifetz and Quinn, 1998; Quinn and Deriso, 1999). IBMs have been gaining popularity in ecology due to increasing computing power and their potential for better understanding the complex dynamics exhibited by populations and communities (DeAngelis and Mooij, 2005). A large portion of the 900 IBMs recently reviewed by DeAngelis and Mooij (2005) were developed to study fish population and community dynamics.

The individual-based approach offers advantages and disadvantages for modeling fish population dynamics (DeAngelis and Rose, 1992). IBMs literally simulate thousands of individuals, keeping track of their traits such as size, age, sex, and location. Equations and rules are defined that govern how the traits of each individual vary over time. The equations and rules potentially depend on the state of the individual, the states of other nearby or related individuals, and environmental conditions. IBMs allow for individual variation in these traits, local interactions among individuals, and, in spatially explicit applications, relatively easy representation of movement (Tyler and Rose, 1994). Density-dependent growth, mortality, and reproduction emerge from the collective outcome of individual processes, rather than having to be explicitly defined *a priori* by the model developer. There are also disadvantages to IBMs, including that they require large amounts of data, customized computer coding, can exceed even today's fastest desktop computers, and produce large amounts of multivariate output that is often hard to validate and interpret. Grimm (1999) further criticized IBMs for their lack of generality and unclear relationship to classical theories of population ecology.

Relative to IBMs, matrix projection models offer a somewhat contrasting set of advantages and disadvantages. Matrix models track the numbers of individuals in a series of age or stage classes that comprise the life cycle of the population of interest (Caswell, 2001). Matrix models are relatively easy to construct, and they 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 and, when necessary, can be easily solved numerically (Dixon et al., 1997). Equilibrium (eigenvalue) analysis of matrix models generates many useful metrics about population dynamics, such as the population growth rate, stable age or stage distribution, elasticities, 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, focus on population dynamics, thereby forcing the developer to greatly simplify community and food web effects, and density-dependent relationships must be defined as part of the model development. Furthermore, incorporation of density-dependence and stochasticity results in matrix models that can no longer be easily analyzed using the eigenvalue technique (Cushing, 1997; Tuljapurkar, 1997).

In this paper, we evaluate the capability of the matrix projection approach for predicting yellow perch population responses to changes in survival by comparing matrix model predictions to those from a detailed IBM. We used the output from a previously developed IBM of yellow perch and walleye dynamics for Oneida Lake as the basis for constructing three versions of matrix projection models for yellow perch. We then changed egg and adult survival rates in all four models and compared predicted responses of yellow perch among the models. Our overarching question was whether matrix models can be used to predict population responses of the prey in a highly coupled predator–prey system that had a high degree of individual variation and size-specific interactions. We chose the Oneida Lake IBM as the basis of the comparison because the yellow perch–walleye predator–prey system in Oneida Lake should present a challenge for the population matrix models because many of the predator–prey and competitive interactions in the IBM are dependent upon the sizes of the individual fish. We conclude with a discussion of the importance of specifying density-dependent relationships, how our final version of the matrix models relate to the classical matrix approach, and our recommendation for which version of the matrix model to use.

## 2. Methods

### 2.1. Description of the modeled system

Oneida Lake provides an excellent system for evaluating matrix projection models because the dynamics and interactions between walleye and yellow perch have been studied for over 50 years (Forney, 1974, 1980; Mills et al., 1987; Mills and Forney, 1988; Hall and Rudstam, 1999; Rudstam et al., 2004). Field studies have documented the size-dependent predator–prey and competitive interactions between walleye and yellow perch. In most years, young-of-the-year (YOY) yellow perch were the dominant prey of walleye; white perch, gizzard shad, and young walleye were of secondary importance in walleye diets (Prout et al., 1990). Yellow perch recruitment was shown to be dependent upon the size-selective predation of YOY and yearling yellow perch by adult walleye, while walleye recruitment was shown to be partly determined by the abundance and size of YOY and yearling yellow perch prey (Forney, 1971, 1974, 1980).

An IBM was developed and corroborated for Oneida Lake using the long-term data (Rose et al., 1996, 1999). The IBM was used to examine predator–prey interactions, and the effects of alternative prey and density-dependent growth and mortality,