

Linking Life History Theory, Environmental Setting, and Individual-Based Modeling to Compare Responses of Different Fish Species to Environmental Change

WEBSTER VAN WINKLE, KENNETH A. ROSE, KIRK O. WINEMILLER,
DONALD L. DEANGELIS, AND SIGURD W. CHRISTENSEN

*Environmental Sciences Division, Oak Ridge National Laboratory
Post Office Box 2008, MS-6038, Oak Ridge, Tennessee 37831-6038, USA*

ROBERT G. OTTO

R. G. Otto & Associates, Post Office Box 306, Vienna, Maryland 21869, USA

BRIAN J. SHUTER

*Fisheries Research Section, Ontario Ministry of Natural Resources
Box 5000, Maple, Ontario L6A 1S9, Canada*

Abstract.—We link life history theory, environmental setting, and individual-based modeling to compare the responses of two fish species to environmental change. Life history theory provides the framework for selecting representative species, and in combination with information on important environmental characteristics, it provides the framework for predicting the results of model simulations. Individual-based modeling offers a promising tool for integrating and extrapolating our mechanistic understanding of reproduction, growth, and mortality at the individual level to population-level responses such as size-frequency distributions and indices of year-class strength. Based on the trade-offs between life history characteristics of striped bass *Morone saxatilis* and smallmouth bass *Micropterus dolomieu* and differences in their respective environments, we predicted that young-of-year smallmouth bass are likely to demonstrate a greater compensatory change in growth and mortality than young-of-year striped bass in response to changes in density of early life stages and turnover rates of zooplankton prey. We tested this prediction with a simulation experiment. The pattern of model results was consistent with our expectations: by the end of the first growing season, compensatory changes in length and abundance of juveniles were more pronounced for smallmouth bass than for striped bass. The results also highlighted the dependence of model predictions on the interplay between density of larvae and juveniles and characteristics of their zooplankton prey.

Predicting the responses of fish populations to environmental change continues to be a major challenge in fisheries science. Populations are routinely challenged by natural and anthropogenic changes in the environment, such as variations in temperature and runoff and changes in stocking and fishing practices. In trying to interpret population responses to such changes, scientists are faced with a diversity of life history strategies, life stages, and environmental settings (Winemiller and Rose 1992); limited understanding of mechanisms involved in regulation of populations and communities (Rothschid 1986); and evidence indicating that differences among individuals are likely to be important (Lomnicki 1992). Given this situation, we believe that integrating existing knowledge about the processes underlying reproduction, growth, and mortality of individuals belonging to fish species with different life histories will help scientists meet the challenge of prediction.

In this paper we link life history theory, environmental setting (i.e., the spatial and temporal characteristics of the abiotic and biotic components of the local environment), and individual-based modeling to compare the responses of two fish species to environmental change. Life history theory provides the framework for selecting representative species, and in combination with information on important environmental characteristics, it provides the framework for predicting the results of model simulations. Individual-based modeling offers a promising tool for integrating and extrapolating mechanistic understanding of reproduction, growth, and mortality at the individual level to population-level responses such as size-frequency distributions and indices of year-class strength. Based on the trade-offs between life history characteristics of striped bass *Morone saxatilis* and smallmouth bass *Micropterus dolomieu* and differences in the environments of these two

species, we predicted that young-of-year smallmouth bass undergo greater compensatory adjustments in growth and mortality than young-of-year striped bass in response to changes in density of early life stages and turnover rate of their prey. We tested this prediction with a simulation experiment.

Life History Theory and Species Selection

Analyses of the variation in life history characteristics among fishes have taken the approach of associating differences in environmental setting with selection for alternative suites of life history characteristics (Kawasaki 1980; Roff 1984; Winemiller 1989, 1991; Winemiller and Rose 1992). Basic demographic relationships predict trade-offs between size at maturation, fecundity, and survival of early life stages or parental investment per progeny (Roff 1984; Winemiller 1991).

Nine species of North American freshwater and marine fish have been selected for an ongoing research program in which compensatory responses are being compared across species with contrasting life history strategies (Otto 1987); the species are bay anchovy *Anchoa mitchilli*, yellow perch

Perca flavescens, walleye *Stizostedion vitreum*, winter flounder *Pleuronectes americanus*, California halibut *Paralichthys californicus*, brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, striped bass, and smallmouth bass. One way the differences among these life history strategies can be illustrated is by their relative position within a three-dimensional life history space defined by axes for length of females at maturation, fecundity, and parental investment per progeny (Winemiller and Rose 1992) (Figure 1). Parental investment per progeny is calculated as the sum of mean diameter (mm) of unfertilized eggs and an index of parental care that ranges from 0 (bay anchovy, California halibut, and winter flounder) to 4 (smallmouth bass) (Winemiller and Rose 1992).

To demonstrate the linking of life history theory, environmental setting, and individual-based modeling, we compared the response of young-of-year striped bass and smallmouth bass to similar perturbations. The striped bass life history (Figure 1) is characterized by sexual maturity at 3–6 years of age, large adult size (to over 1,200 mm in total length), a short spawning season (6–8 weeks), high

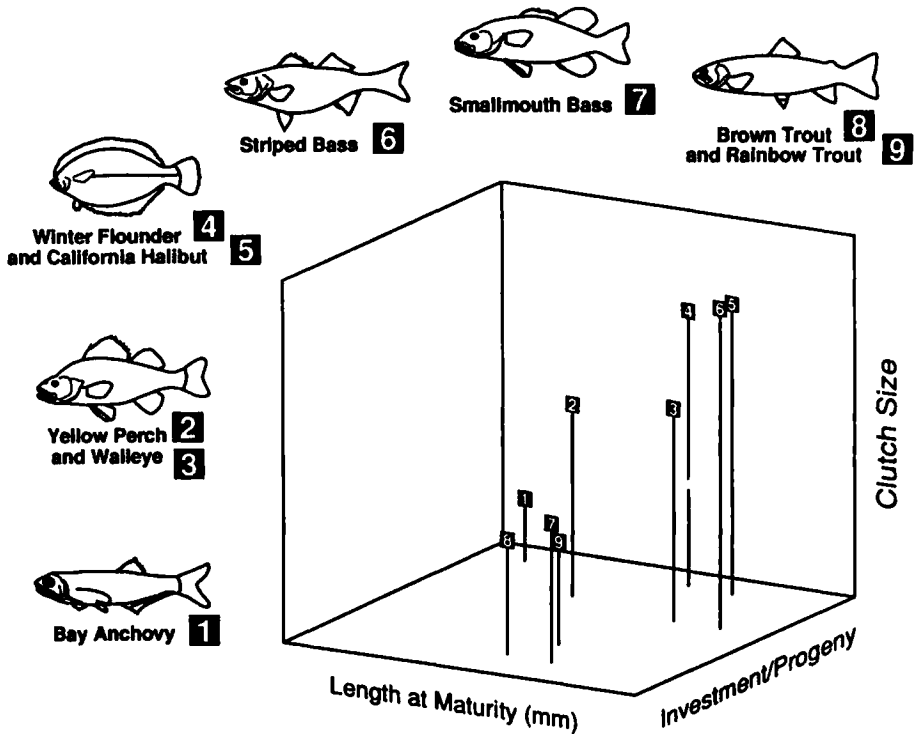


FIGURE 1.—Relative positions of nine North American fishes within three-dimensional life history space as defined by length at maturity, fecundity, and parental investment per progeny.

fecundity (15,000–4,000,000 eggs per female), intermediate-size eggs (1.8 mm in diameter), anadromous spawning migrations, group spawning, no parental care, and long life spans (30 years or more in some populations) (Setzler et al. 1980). Most long-lived species with this suite of life history characteristics exhibit an occasional very large year-class, and striped bass is no exception (Setzler et al. 1980). In an evolutionary sense, the strategy of producing large numbers of eggs is well suited for exploiting the occasional occurrence of favorable conditions for growth and development. Even under the best of conditions, mortality for eggs and larvae is high. Yet, the high fecundity typical of this strategy provides a buffer for high losses during the early life stages, provided that favorable conditions are experienced in some years at the appropriate time and place.

Species with life histories like that of striped bass may experience a density-dependent response in growth and mortality of early life stages by way of changes in food availability, habitat limitations, or predation. However, these conditions probably occur only intermittently over a time scale of several years. Stochastic abiotic factors such as spring temperature and precipitation regimes may be the ultimate driving variables that produce conditions for strong recruitment years (Winemiller and Rose 1992).

Smallmouth bass occupy a position similar to that of trout and quite distinct from that of striped bass within the life history continuum for North American teleost fishes (Figure 1). Basic features of the smallmouth bass life history include sexual maturation at 2–4 years of age, intermediate adult size (to 680 mm in total length), a brief spawning season (2–6 weeks during the spring), intermediate fecundities (5,000–20,000 eggs), intermediate-size eggs (2.0–mm in diameter), monogamous or polygamous mating, male guarding of nest and brood, intermediate to long life spans (6–14 years), and somewhat limited dispersal during both young-of-year and adult life stages (Carlander 1977).

Species with life histories like that of smallmouth bass are expected to respond to environmental changes in a density-dependent manner to a greater extent and with greater frequency than species with life history characteristics similar to those of striped bass. Male parental care is a requirement for persistent smallmouth bass populations over much of the species' native range. Survival of smallmouth bass during early life stages depends on availability and stability of suitable nesting habitat, success of males in guarding the

brood until the juveniles disperse, and availability of food for the young of year, especially near the nest before the young disperse (Winemiller and Rose 1992). These traits set the stage for competition for limited nesting habitat among adult males and for limited food among spatially restricted young, potentially resulting in density-dependent growth and mortality during early life. There is also evidence for negative density dependence between nesting males and the total male population resulting from exploitative competition for food or interference competition for space during the nonbreeding seasons (Ridgway et al. 1991). Comparable data for striped bass are lacking, but the operation of such mechanisms seems unlikely.

Individual-Based Modeling and Description of Species Models

Our individual-based modeling of species with contrasting life history strategies is designed to provide a comparative basis for predicting species differences in mechanisms of population regulation. The individual-based models for striped bass and smallmouth bass are similar in their representation of young-of-year dynamics, and each produces realistic results for spawning and for growth and mortality of eggs, larvae, and juveniles (DeAngelis et al. 1991; Cowan et al. 1993, this issue; Rose and Cowan 1993, this issue; Jager et al., in press). Both models begin with spawning by individual adults in a single spatial compartment; then they follow the daily growth and mortality of individual progeny through the early life stages. Differences between the models arise from differences in the life history characteristics of the two species and the environments they inhabit, but the models were developed with a common framework to permit cross-species comparison. To further ensure comparability of these two models for the present analysis, the formulation and parameter values for maximum turnover rate of zooplankton prey in the smallmouth bass model (B. J. Shuter and others, unpublished) were used in the striped bass model in place of the original formulation (Rose and Cowan 1993: equation 38); test simulations indicated that the differences between these two formulations had a trivial effect on results from the striped bass model.

Three important differences between the two models are the representations of spawning, prey encounters, and success of fish larvae in capturing prey (DeAngelis et al. 1991; Rose and Cowan 1993). The smallmouth bass model represents spawning in greater detail than the striped bass

model because of the important role of adult smallmouth bass males in nest site selection and parental care; in contrast, striped bass reproduce by broadcast spawning.

Encounters of larvae with zooplankton prey are simulated somewhat differently in the striped bass and smallmouth bass models to reflect differences in prey densities and sizes in the eutrophic Potomac River estuary, the study site for striped bass, and oligotrophic Ontario lakes, sources of smallmouth bass data (Rose and Cowan 1993; Shuter, personal communication). As used in the models, the average numerical density of zooplankton is higher for the Potomac by a factor of 4.3, and the average biomass density is higher by a factor of 1.7, relative to Ontario values. In the smallmouth bass model, a realistic distribution of growth rates for larvae was obtained by modeling prey encounters as a Poisson process, defined by observed averages for zooplankton density and patchiness. In the striped bass model, however, allowing each larva to encounter zooplankton at the average densities observed in the Potomac River resulted in unrealistically high growth rates. Consequently, we represented striped bass encounters with zooplankton according to the observed probability distribution of measured prey densities. The resulting simulated larval growth rates were reasonable; most modeled striped bass larvae experienced low densities of zooplankton (near the median density), and occasional larvae encountered average or higher zooplankton densities.

Representation of prey capture success differed between the two models to reflect differences in the ontogenetic development of striped bass and smallmouth bass. Striped bass begin exogenous feeding at the relatively small size of 5 mm; smallmouth bass begin feeding at 9 mm. In general, probability of capture for small, first-feeding larvae is low (Blaxter 1986). Thus, feeding success during the first few days of foraging was represented in greater detail in the striped bass model, and probability-of-capture functions were specified for each zooplankton prey type. Probability of capture for smallmouth bass was assumed to be 1.0 for all larvae for all prey encountered.

Design of Simulation Experiment and Results

We designed a two-factor simulation experiment to compare responses of young-of-year striped bass and smallmouth bass to similar changes in two environmental factors that influence the interplay between larvae and their food.

The factors we varied were (1) area of the model compartment and (2) turnover rate of larval prey. Then we followed the consequences of these effects on larvae into the juvenile life stage until the end of the first growing season. Individual-based processes that could lead to compensatory responses at the population level did not operate in either model before the larval life stage, but they were operative for both larvae and juveniles. Specifically, prey densities could be reduced to a level such that growth of individual fish was reduced, which could lead to higher mortality from predation and other size-dependent causes. We defined the larval life stage of striped bass as starting with first feeding at a length of 5 mm and ending with metamorphosis to the juvenile life stage at 20 mm. We defined the larval stage of smallmouth bass as starting with first feeding and swim-up at a length of 9 mm and ending when the guarding male abandons the brood and the young disperse at 25 mm.

Relative to the baseline area for each species, we decreased the area of the model compartment by a factor, A , of 0.3 or 0.1 and increased the area by a factor of $A = 3.0$. The reciprocal of this factor, $1/A$, is the relative density of model individuals in the absence of compensation. Changing the area of the model compartment had no effect on model results until individuals become feeding larvae, and changing the area did not change the number of individuals in the model compartment.

Striped bass and smallmouth bass are both found in a wide range of environments that have differing levels of productivity. By varying prey turnover, we could simulate low- and high-productivity systems. A second reason for varying prey turnover is that this is one of the most critical, yet poorly known, input parameters affecting density-dependent feedback in our models. Specifically, we decreased the maximum turnover rate for the baseline by a factor of 0.25 for all zooplankton groups.

Based on the trade-offs between life history characteristics for striped bass and smallmouth bass and differences in prey densities discussed above, we had the following two expectations for how our changes would influence subsequent growth and mortality to the end of the first growing season:

- smallmouth bass would exhibit a stronger density-dependent (i.e., compensatory) growth response than striped bass, as indicated by a greater relative change in length; and
- as a consequence of a stronger density-de-

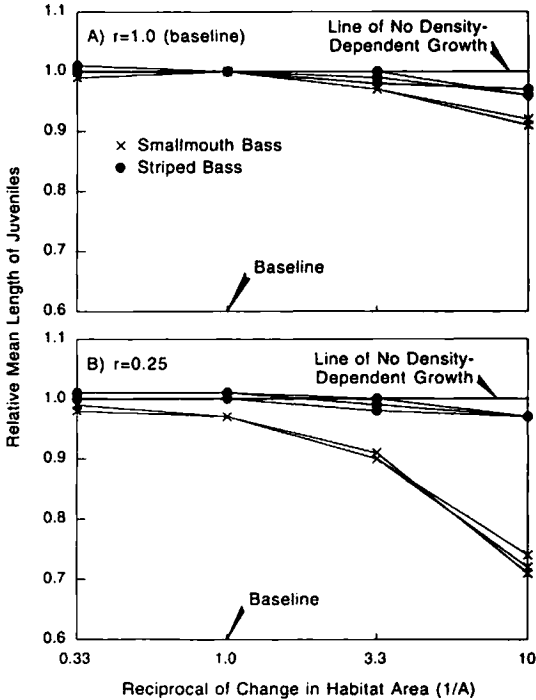


FIGURE 2.—Results from three simulations of the individual-based models for striped bass and smallmouth bass comparing the relative (i.e., normalized to the baseline result for each of the three random number seeds) mean length of juveniles at the end of their first growing season (October 1) as a function of the reciprocal ($1/A$) of the factor used to change the area of the model compartment. This reciprocal is the relative density of model individuals in the absence of density-dependent compensation. Results are presented for two values of the multiplier of the maximum turnover rate (r) for zooplankton prey groups. The reference line of “no density-dependent growth” indicates the situation in which the growth of young of year is independent of habitat area and zooplankton turnover rate.

pendent growth response, smallmouth bass would exhibit a stronger density-dependent (i.e., compensatory) mortality response than striped bass, as indicated by a greater relative change in abundance.

Simulations with each factor combination were repeated three times for each model; a different random number seed was used for each run. The mean length and number of juveniles on October 1 were recorded for each simulation and then divided by the mean length and number of juveniles for the baseline simulation that used the same random number seed. Expressing the effects as relative mean length and relative number of juveniles

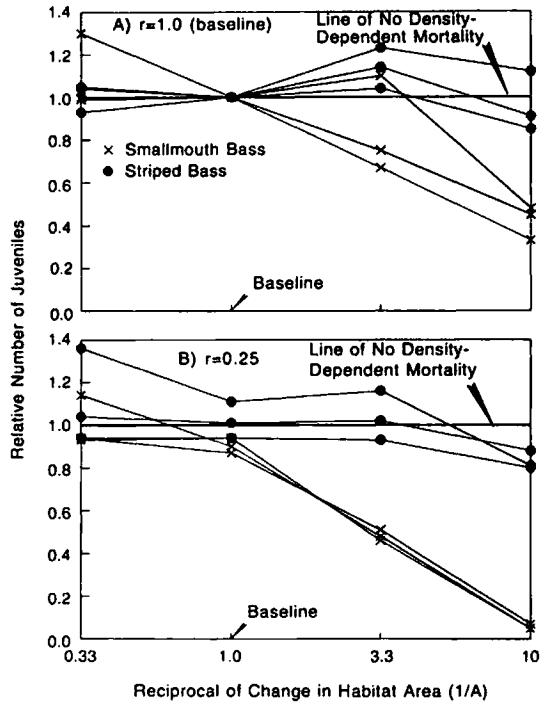


FIGURE 3.—Results from three simulations of the individual-based models for striped bass and smallmouth bass comparing relative (to baseline) number of juveniles at the end of their first growing season (October 1) as a function of the reciprocal ($1/A$) of the factor used to change the area of the model compartment. This reciprocal is the relative density of model individuals in the absence of density-dependent compensation. Results are presented for two values of the multiplier of the maximum turnover rate (r) for zooplankton prey groups. The reference line of “no density-dependent mortality” indicates the situation in which year-class strength at the end of the first growing season is independent of habitat area and zooplankton turnover rate.

standardized model predictions and permitted direct comparisons between species.

The pattern of model results was generally consistent with our a priori expectations: by the end of the first growing season, compensatory changes in length and abundance of juveniles were more pronounced for smallmouth bass than for striped bass (Figures 2, 3). The length of juvenile striped bass was essentially independent of our changes in area and prey turnover rate. The decrease in relative length was less than 10% at even the smallest area value (i.e., largest $1/A$, meaning highest density and greatest chance for food to be limiting). This independence is indicated by the striped bass curves that lie almost parallel to the horizontal line of “no density-dependent growth”

in Figure 2. The mean length of juvenile smallmouth bass, however, decreased as area decreased from baseline, especially when prey turnover was reduced, indicating that food was limiting (Figure 2). Mean length did not consistently increase for either species when the area of the model compartment was increased above the baseline area (i.e., when 1/4 and density of young of year was decreased).

Model results for relative number of juveniles (Figure 3) varied more than those for length of juveniles. Nevertheless, juvenile abundance decreased more for smallmouth bass than for striped bass at areas smaller than baseline (i.e., at densities higher and survival lower than for baseline), as predicted. This difference was particularly evident at the lower value for zooplankton turnover rate (Figure 3B). When area was increased above baseline (i.e., density was decreased below baseline), at least one of the six simulations with each model resulted in a notable increase in number of juveniles.

Discussion

We have demonstrated an approach for comparing responses of different fish species to environmental change by linking life history theory, environmental setting, and individual-based modeling. We used individual-based models developed from a common conceptual framework. Each model was configured with species-specific and site-specific data. The two species we selected for a model experiment, striped bass and smallmouth bass, differ in easily measurable life history characteristics, especially in investment per progeny (Figure 1). Smallmouth bass have slightly larger eggs than striped bass (2.0 mm versus 1.8 mm in mean diameter), they are nearly twice as large at first feeding (9 mm versus 5 mm in mean length), and they have the benefit of a guarding male until young of year are 20 mm or more in length. One consequence of these differences between the two species is that the probability of survival through the larval life stage is approximately an order of magnitude greater for smallmouth bass than for striped bass (0.04 versus 0.003 for the two model baselines). In addition, the environmental settings for the two specific populations we modeled—oligotrophic Lake Opeongo for smallmouth bass and the eutrophic Potomac River for striped bass—differ in the density of prey for young-of-year fish; based on field data at the two sites, as used in the model, the average numerical density of zooplankton is higher in the

Potomac by a factor of 4.3, and the average biomass density is higher by a factor of 1.7. This difference in prey densities was accentuated in the models by opposite differences in the numerical density of fish larvae. The average density of larvae in the baseline simulations during the 30 d around the peak larval abundance was $0.015/\text{m}^3$ for striped bass and $0.057/\text{m}^3$ for smallmouth bass; if this difference commonly occurs in the field, it further increases the likelihood that smallmouth bass are more food-limited than striped bass.

The potential for density-dependent growth and mortality responses by young of year is embedded in the individual-based process formulations for both of these models. That these density-dependent responses were manifested to a greater extent for smallmouth bass than for striped bass suggests that the potential for such responses in the field may be greater for smallmouth bass than striped bass. Each model was developed and tested for striped bass or smallmouth bass populations in specific aquatic systems. The tests demonstrated the capabilities of these models to simulate observed growth rates, length-frequency distributions, and relative survival (DeAngelis et al. 1991; Rose and Cowan 1993; Jager et al., in press). Having established these correspondences for the species separately, we are reasonably confident that the differences in simulation results between the two species reflect real differences (at least in degree) in the processes underlying young-of-year growth and mortality and the linkage of these processes with prey dynamics, and that they are not artifacts of the modeling process. Although the two models we used are configured for specific sites, we predict that compensatory changes in young-of-year growth and survival in response to environmental change are more common for smallmouth bass than striped bass regardless of the site. This prediction, however, remains to be tested. Such results have not been observed to date for young-of-year smallmouth bass in Lake Opeongo.

These two individual-based models currently simulate only the first year of life. Mechanisms influencing the growth, mortality, and reproduction of individual adults might also elicit a compensatory response at the population level. An example is the negative association between the density of nesting males and the density of all adult males, possibly the result of competition for food or space during the nonbreeding season, that was inferred for smallmouth bass by Ridgway et al. (1991).

Life history theory has been used by other investigators to tackle the challenge of predicting the response of different fish species to environmental change. Adams (1980) investigated theoretical life history patterns in terms of r and K selection and compared these patterns with actual trends in life history characteristics of marine fishes. Armstrong and Shelton (1990) used a Monte Carlo model to explore the influence of spawning style and adult survival on the spawning success of individual clupeoid fish during their life span when the survival of the early life stages was determined according to different spectra of environmental variability. Barnthouse et al. (1990) and Schaaf et al. (1987) each used life history theory and Leslie matrix simulation models to investigate the influence of life history characteristics on the vulnerability of fish to contaminant-induced stress. Leaman (1991) examined the reproductive styles and life history characteristics of lightly and heavily exploited Pacific ocean perch *Sebastes alutus* relative to the predictions of life history theory.

In all of the studies just cited, the premise was that relationships among key life history and environmental characteristics reflect essential features of a species' environment on an evolutionary scale, and that the adaptive nature of life history strategies provides insights into how contemporary populations might respond to anthropogenic environmental changes. Life history theory deals with individual- and population-level traits as adaptations for coping with alternative environmental settings. By extension, life history theory provides a framework for predicting how environmental changes might affect different fish species. The potential of a process-oriented, individual-based approach for testing these predictions is just beginning to be realized (DeAngelis et al. 1990; DeAngelis and Gross 1992; Van Winkle et al. 1993, this issue). At the same time, the importance of considering biological mechanisms that influence reproduction, growth, and mortality is once again being emphasized as a complement to the holistic ecosystem approach (Sale 1990; Shepherd and Cushing 1990; Pepin and Myers 1991).

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