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

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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

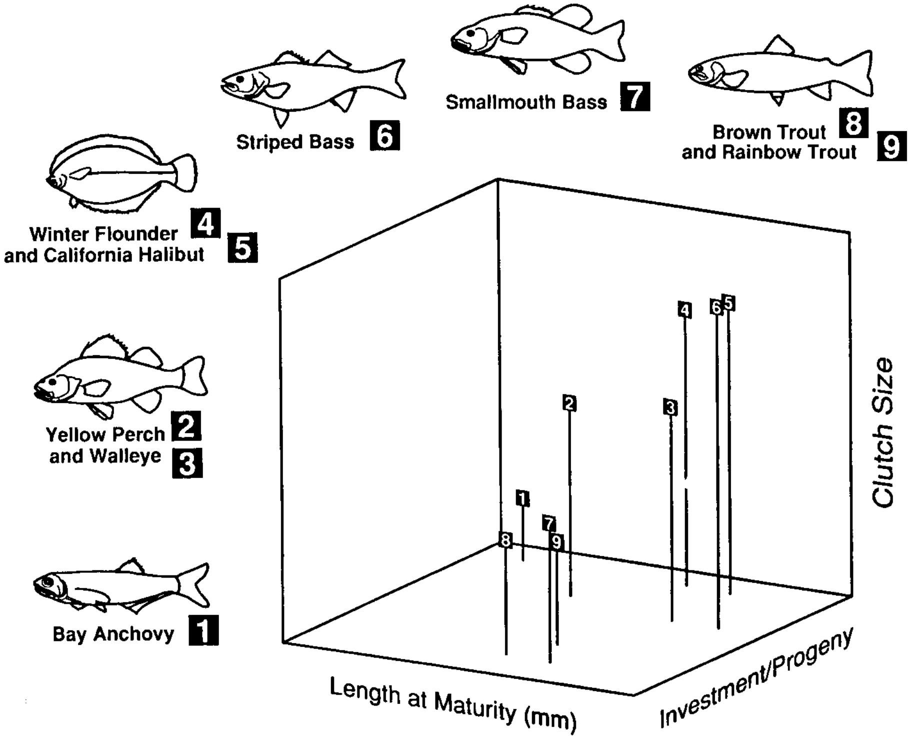

FIGURE 1.—Relative positions of nine North American fishes within three-dimensional life history space as defined by length at maturity, fecundity, and parental investment per progeny.

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-